

## The latest Ordovician *Hirnantia* brachiopod Fauna of Myanmar: Significance of new data from the Mandalay Region

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### Abstract

A new, latest Ordovician brachiopod fauna is systematically described from the Hwe Mawng Purple Shale Member (Hirnantian) of the Naungkangyi Group of Pa-thin area, Mandalay Region, Myanmar, revealing one of the most diverse representatives of the typical *Hirnantia* Fauna. Rhynchonelliformean, craniiformean and linguliformean brachiopods studied belong to 23 genera and a few indeterminate taxa, among which the most abundant genus *Kinnella*, along with the four common genera or subgenera (*Paromalomena*, *Pseudopholidops*, *Coolinia*, and *Dalmanella*), and other genera (such as *Cliftonia*, *Draborthis*, *Hindella*, *Hirnantia*, *Leptaena*, *Mirorthis*, *Plectothyrella*, *Pseudopholidops*, *Skenidioides*, and *Xenocrania*) are recorded for the first time. This high diversity *Hirnantia* Fauna represents an ecological differentiation within the benthos of the Sibumasu Terrane during the end

Ordovician global crisis. The palaeoeco-unit named herein as the *Kinnella-Paromalomena* community is assigned to lower BA3. This paper includes a taxonomic revision with the following conclusions: 1) *Sinomena* Zeng et al. and *Yichangomena* Zeng et al. are treated as junior synonyms of *Eostropheodonta* Bancroft; 2) *Hubeinomena* Zeng et al. is regarded as a juvenile form of *Coolinia* Bancroft; 3) *Paramirorthis* Zeng et al. is considered an immature growth stage of *Mirorthis* Zeng; 4) *Shanomena* Cocks and Fortey is treated as a junior synonym of *Paromalomena* Rong; 5) *Scenidium? medlicotti* Reed is redesignated as the type species of *Kinnella* Bergström to replace *Hirnantia? kielanae* Temple. The distribution of the *Hirnantia* Fauna in Myanmar, Thailand and western Yunnan of the Sibumasu Terrane highlights the distinctive nature of the Mandalay fauna, and the analysis of the *Hirnantia* Fauna of Sibumasu shows that Sibumasu was not located far from the South China and Lhasa palaeoplates during late Middle and Late Ordovician.

**Keywords:** Latest Ordovician; *Hirnantia* brachiopod Fauna; Myanmar; faunal cluster analysis

## 1. Introduction

It has been more than 100 years since Reed (1915) first described shelly fossils originally collected by officers of the Indian Geological Survey, at the end of the nineteenth century, from the basal Panghsa-pye Formation (partly Hirnantian) in Northern Shan State, Myanmar. These fossils, collected from a poorly accessible locality, were considered a typical representative of the *Hirnantia* Fauna (Temple, 1965), and were later revised by Cocks and Fortey (2002), although *Hirnantia* itself was not present.

In January 2017, the present authors (Rong, J.Y. and Zhan, R.B.) visited the Mandalay Region at the invitation of the Geological Survey of Myanmar; and a large number of shelly fossils from the Hwe Mawng Purple Shale Member (Hirnantian) of the Naungkangyi Group were collected in the Pa-thin area (Fig. 1). The brachiopods are the most abundant and predominant elements, comprising about 97% of the whole fauna and containing 23 named

genera along with a few indeterminate species which are described and/or illustrated herein. The nature and relationship of the *Hirnantia* Fauna of Myanmar are analyzed. The *Hirnantia* fauna in various regions of the Sibumasu Terrane is briefly reviewed.

The *Hirnantia* Fauna has been documented from many plates or terranes throughout the world, including Africa, Avalonia, Baltica, European Peri-Gondwana (e.g., Carnic Alps, Armorica, Sardinia, Spain, and Portugal), the Kazakhstani terranes, marginal Laurentia, Perunica, San Juan in the Argentinian Precordillera, Sibumasu, South China, Lhasa (central Xizang), and a few others. It is known to be, geographically, the widest distributed brachiopod fauna in Phanerozoic (Rong et al., 2017).

## 2. Geological setting

The Lower Paleozoic rocks of Myanmar mainly outcrop on the Shan Plateau (Aye Ko Aung and Cocks, 2017), where the Ordovician–Silurian boundary strata are widely distributed and usually well exposed. The locality yielding the *Hirnantia* Fauna is exposed along a poorly paved country road, about 40 km east of Mandalay City in the Pa-thin area of Pyin Oo Lwin, Mandalay Region (GPS reading N21°56'24.5" and E96°30'11.2") (Fig. 1).

The Hwe Mawng Purple Shale Member (Hirnantian), originally reported as the basal Panghsa-pye Formation (Reed, 1915; Cocks and Fortey, 2002), yielding the diverse *Hirnantia* fauna, is underlain and overlain conformably by graptolitic shales, i.e., the top Naungkangyi Group and the basal Panghsa-pye Formation respectively (Fig. 2). This 45 cm-thick member is composed mostly of light brown, medium- to thin-bedded silty mudstone intercalated with quartzose wacke (Fig. 3). The *Hirnantia* Fauna is encountered only in the silty mudstone, which generally lacks any macroscopic evidence of major disturbance of the substrate except for a few borings (2–3 mm in diameter), and thus may represent deposition in quiet shelf environments. The quartzose wacke consists of angular to subangular detrital grains, which are matrix supported and poorly sorted. Mineralogical and textural maturities of the wacke are both poor due to the presence of rare feldspar (approximately less than 2% of the whole contents) and a high content of groundmass, respectively. The rare occurrence of

quartzose wacke in the silty mudstone may suggest either a sudden shift from shelf environments into shallower-water settings (e.g., nearshore) due to regression or alternatively, disturbances of seabed (e.g., gravity flows). In the view of sedimentary and fossil evidence, the latter may be more likely.

### 3. Material and methods

The Pa-thin area of the Mandalay Region, where the brachiopods were collected for this study, is located approximately 110 km southwest of the old site of the Northern Shan State reported by Reed (1915). Both sites belong to the Sibumasu Terrane.

Among the associated fossils, surprisingly, trilobites, usually common or abundant associated with the *Hirnantia* Fauna elsewhere, are small in size and rare in both abundance and diversity. There are many co-occurring animal groups, including bivalves, bryozoans, crinoids (debris), gastropods, hyolithids, machaeridians, ostracods, trilobites, and a few others, but they are much fewer than the brachiopods.

All the fossils studied are preserved as moulds. The preservation is good, but the matrix is rather coarse, fragile and easily broken because of the deep weathering and unconsolidated matrix. To display external and internal morphologies in detail, latex casts are needed, although it is challenging to strengthen fossils prior to casting. PVB ethanol solution (a mixture of PVB powder and ethanol) and latex solutions I and II were employed for this purpose. The latex solution was prepared by mixing the commercially available product MOLD BUILDER and water at a volumetric ration of 1:5 (I) and 1:2 (II).

A total of 1221 specimens were examined in this study. To test the sampling sufficiency, we have counted the number of specimens of each species and proceeded with individual rarefaction analysis using the software PAST (Hammer et al., 2001) with steps of 10. The result clearly shows that the curve reaches a nearly horizontal threshold, which indicates that our sample size is sufficient (Fig. 4).

All specimens illustrated herein are housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (catalogue with NIGP as a prefix of registered numbers).

#### 4. Age determination

The bed yielding the brachiopods in the Pa-thin area can probably be correlated with that near the base of the Pangsa-pye Formation in the Northern Shan State (Reed, 1915; Cocks and Fortey, 2002). It is further confirmed by graptolites from the underlying and overlying shales based on Xu Chen's identification.

The graptolites underneath the *Hirnantia* Fauna in the Mandalay Region include *Metabolograptus extraordinarius*, *Normalograptus pseudovenustus*, *Koreanograptus acanthus* and others, indicating a level of the *M. extraordinarius* Biozone, and those from the overlying rocks include *Koreanograptus selectus*, *Normalograptus angustus* and others, suggestive of *Metabolograptus? perscuptus-Akidograptus ascensus* Biozone (Chen et al., [in press](#)). Moreover, most of the brachiopod taxa correlate well with those of the Kuanyinchaio Bed (middle Hirnantian) in Yichang, western Hubei, Central China. Thus, it is more likely that the *Hirnantia* Fauna studied here is of middle Hirnantian age.

#### 5. Faunal analyses

The *Hirnantia* Fauna of Myanmar includes two parts, the Northern Shan State (Reed, 1915; Cocks and Fortey, 2002) and the Mandalay Region (this paper) with a total of 25 genera and species. A faunal list at ordinal and generic levels for faunal records from Sibumasu together with Xainza, central Xizang (Tibet, Southwest China) and Yichang, western Hubei (Central China) is provided for comparison (Fig. 5). The composition indicates that the Myanmar *Hirnantia* fauna is a typical, relatively deeper-water fauna belonging to the Kosov Province during the Hirnantian.

At the ordinal level, nine taxa were present, amongst which the orthides were the most common in both diversity and abundance (39.2% and 43.2% of the entire brachiopod fauna);

the strophomenides were the second (21.7% and 14.5%), but the number of individuals is very low for each genus (fewer than 1% respectively) except *Paromalomena* (13.3%). The orthotetides occupy the third place in terms of diversity (8.7%) and abundance (13.3%); the craniopsides the fourth (13.0%) in abundance and the fifth (4.35%) in diversity; and the craniides (8.7% and 8.9%) virtually equal. The other four (Lingulida, Protorthida, Athyridida and Rhynchonellida) are all 4.35% of the total diversity (Fig. 6). This picture clearly indicates a characteristic aspect of the Ordovician brachiopod fauna, i.e., the continued predominance of the orthides and strophomenides following the first phase of the end Ordovician mass extinction. A key result from the extinction was the major replacement of brachiopod faunas in early Silurian during the subsequent recovery and radiation of the pentamerides/atrypides, taking the niches formerly occupied by the orthides/strophomenides (Rong and Harper, 1999; Harper and Rong, 2001; Huang et al., 2012; Rong et al., 2013).

At the generic level, the most abundant is *Kinnella* (22.2% of the whole fauna), a core element of the *Hirnantia* Fauna. The second place includes four genera, *Paromalomena* (13.4%), *Pseudopholidops* (12.9%), *Fardenia* (*Coolinia*) (12.5%), and *Dalmanella* (10.3%), all common in the fauna. Subsequently, the next seven are *Xenocrania* (7.1%), *Hirnantia* (4.4%), *Hindella* (3.7%), *Draborthis* (3.2%), *Plectothyrella* (2.2%), *Petrocrania* (2.2%), and *Mirorthis* (2.0%). The following 11 genera comprise fewer than 1% of the fauna; *Cliftonia* (0.9%), *Skenidioides* (0.7%), *Minutomena* (0.5%), *Eostropheodonta* (0.4%), *Trucizetina* (0.33%), *Toxorthis?* (0.33%), *Leptaena*, *Aegiromena*, and *Giraldibella* (the latter three, 0.25%), *Levenea* (0.2%) and *Pseudolingula?* (0.1%) (Fig. 6). It should be noted that with the exception of *Paromalomena*, the three strophomenide genera, *Eostropheodonta*, *Leptaena* and *Aegiromena* are so rare in contrast to their occurrences in the *Hirnantia* Fauna of some other regions.

Consequently, the *Hirnantia* Fauna in Myanmar is characterized by its high biodiversity, by the predominant genus *Kinnella*, four common genera (*Paromalomena*, *Pseudopholidops*, *Coolinia* and *Dalmanella*), a number of typical genera of the *Hirnantia* Fauna (e.g., *Eostropheodonta*, *Leptaena*, *Hirnantia*, *Cliftonia*, *Plectothyrella* and *Hindella*), and the

unique substantially low abundance of *Eostropheodonta*, *Leptaena* and *Aegiromena*. A new palaeoeco-unit for this fauna in Mandalay Region is herein established as the *Kinnella-Paromalomena* Community (Fig. 7). Palaeoecologically, *Aegiromena* and *Skenidioides*, rare in our collection, are known mainly in deeper-water facies in the Ordovician and Silurian (Boucot, 1975). Nonetheless, in view of the dominant presence of a number of commonly shallow water, key constituents of the *Hirnantia* Fauna, this community is assigned to lowermost Benthic Assemblage 3 (BA3).

Our compiled data on fauna distribution are analysed using a hierarchical clustering method with Dice, Jaccard, and Ochiai coefficients as similarity measurements. The resulting dendrograms show faunal relationship of the Mandalay *Hirnantia* Fauna with those of western Yunnan, Northern Shan State and Thailand (Sibumasu terrane), Yichang, western Hubei (South China palaeoplate), Xainza, central Xizang (Lhasa), Chu-Ili (Kazakhstanian terranes), and Bohemia (Perunica) (Fig. 8). The dendrograms from all three indices are identical. First, they demonstrate that the fauna of Mandalay is most similar to that from western Yunnan, which is in consistent with the results of Huang et al. (in press). The Mandalay fauna is very similar to those from western Hubei, Central China (Rong, 1984; Zeng et al., 2016) and Perunica (Marek and Havlíček, 1967) as well because of the common presence of many characteristic constituents of the typical *Hirnantia* Fauna (Fig. 5). Such similarity suggests that Mandalay, western Yunnan, and western Hubei were located close to each other, both at low latitudes with rather similar environmental conditions (e.g., water depth, substrate and temperature) in the end Ordovician. Meanwhile, Perunica, with a more distinctive and local taxa of lingulides, craniides, and orthides, should have had faunal communication with Sibumasu and South China largely by currents. Second, based on the available data, the fauna of Mandalay is less close to the Northern Shan State, Xainza, and Chu-Ili than to western Yunnan, South China and Perunica, but further comparison or interpretation are not advisable due to insufficient data from the Northern Shan State, Xainza, and Chu-Ili. Last, the fauna of Thailand where the genus *Aegiromena* occupies 77.9% of the entire brachiopod fauna (Cocks and Fortey, 1997) is clearly differentiated from many other

regions, but similar to those of outer shelf and slope regimes (Rong et al., 2018) because of a commonality of deep-water biofacies (BA4-5). The difference between the fauna from Thailand, therefore, is due more to palaeo-ecological factors than palaeo-geographic factors, as other regions on the dendrograms belong to shallow-water biofacies (BA2-3).

## 6. The *Hirnantia* fauna of the Sibumasu Terrane

The Sibumasu (sometimes Shan-Thai) stretched from western Yunnan, through much of Malay Peninsula, Myanmar, Thailand and west Malaysia, to Sumatra, western Indonesia (Hutchison, 1982; Metcalfe, 2011; Torsvik and Cocks, 2017). Within the Sibumasu, the *Hirnantia* Fauna is known in Northern Shan State (Reed, 1915; Cocks and Fortey, 2002) and Mandalay Region (this paper), Myanmar, southern Thailand (Cocks and Fortey, 1997), and western Yunnan (Rong and Sun, 1983; Huang et al., *in press*) (Fig. 9). A synthesis of the data available is presented below.

1) Myanmar. The *Hirnantia* Fauna is a typical and diverse assemblage. Comparatively, the fauna from Northern Shan State (Cocks and Fortey, 2002) is less diverse than that of Mandalay. Interestingly, *Hirnantia* itself, absent in the Northern Shan State, is identified in the Mandalay collection. In addition, the appearance of *Leptaena*, *Mirorthis*, *Draborthis*, *Plectothyrella*, and *Hindella*, associated with many others (such as *Skenidioides*) has greatly increased the diversity of the *Hirnantia* fauna in Myanmar.

2) Western Yunnan. There are 22 genera from the Wanyaoshu Beds (Hirnantian), Mangshi (Huang et al., *in press*), demonstrating a high diversity, typical *Hirnantia* Fauna in this region. The presence of a distinctive taxon, *Templeella*, is particularly remarkable as it is the first record from the typical *Hirnantia* Fauna. This genus was established by Rozman and Rong (1993) based on *Kaysarella?* sp. from probably the upper Hirnantian of England (Temple, 1968) and also recorded from the lower Rhuddanian of East China (Rong et al., 2013), and Aeronian of Wales and West Mongolia (Temple, 1970; Rozman and Rong, 1993).

3) Thailand. A medium diversity *Hirnantia* Fauna is known in Santun Province, including *Aegiromena*, *Cliftonia*, *Hirnantia*, *Mirorthis*, *Onniella*, and *Paromalomena* (Cocks

and Fortey, 1997). Among them, *Aegiromena* occupies nearly 80% of the whole fauna, suggesting a deeper-water environment setting (likely BA4). It is consistent with the absence of *Dalmanella*, *Eostropheodonta*, *Hindella*, *Kinnella*, *Leptaena*, and *Plectothyrella* and the rarity of *Hirnantia*, *Paromalomena* and *Cliftonia*, distinctive taxa of the typical *Hirnantia* Fauna.

The Middle and Late Ordovician faunas of Sibumasu reveal close affinities with South China (Fortey and Cocks, 1998, 2003). For example, the lithology and trilobites of the Sandbian-lower Katian Pa Kae Formation, southern Thailand are closely similar to those from South China. In particular, the trilobites are identical even at species level to faunas from the contemporaneous Pagoda Formation (Zhou and Dean, 1996; Fortey, 1997; Fortey and Cocks, 1998). Moreover, it is clear that from the Darriwilian onward, brachiopod faunas in South China had many similarities with those of Sibumasu as exemplified by the following cases: 1) the shallow-water *Saucrorthis* Fauna (Darriwilian) is only recorded from South China, Sibumasu and Iran (Cocks and Zhan, 1998; Zhan and Jin, 2005, 2007; Rong et al., 2005; Zhan et al., 2006); 2) the deep-water *Foliomena* Fauna (Katian) occurs in South China and Sibumasu (western Yunnan and Mandalay Region) (Cocks and Rong, 1989; Rong et al., 1999; Zhan and Jin, 2007); 3) the actual presence of shallow and deep-water assemblages of the typical *Hirnantia* Fauna including a rare, distinctive genus *Minutomena*, are recorded only from South China and Sibumasu (Rong et al., 2018; Cocks and Fortey, 1997, 2002). In addition, Hirnantian stratigraphical succession in both South China and Sibumasu are similar: i.e., the *Hirnantia* Fauna-bearing bed occurs between Hirnantian graptolite shales (Fig. 10). Thus, both terranes were not located far from each other, palaeogeographically, during late Middle and Late Ordovician.

## 7. Systematic palaeontology

Among all species recognized, the seven taxa (*Pseudolingula?* sp. (Fig. 11A), *Leptaena* sp. (Fig. 16D–F), *Aegiromena* sp. (Fig. 16A, B), *Toxorthis?* sp. (Fig. 18G–I), *Giraldibella* sp. (Fig. 18J–M), *Trucizetina* sp. (Fig. 19H–J), and *Levenea* sp. (Fig. 19G)) are not described

because of the paucity of material, but illustrated herein. Detailed synonymy lists of the eight species of the common, key, cosmopolitan genera (*Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Paromalomena*, and *Plectothyrella*) of the *Hirnantia* Fauna are provided in Appendix A.

Class Craniata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Craniopsida Gorjansky and Popov, 1985

Superfamily Craniopsoidea Williams, 1963

Family Craniopsidae Williams, 1963

Genus *Pseudopholidops* Bekker, 1921

*Pseudopholidops partibilis* (Rong, 1979)

(Fig. 11B–H)

- ? 1968 *Paracraniops* sp. – Bergström, p. 7, pl. 1, figs. 4, 5.
- ? 1968 *Paracraniops* sp. – Temple, p. 11, pl. 1, figs. 1–6.
- 1979 *Paracraniops partibilis* – Rong, p. 2, pl. 1, figs. 1, 2.
- ? 1981 *Paracraniops* sp. – Williams and Wright, p. 15, fig. 5G, J.
- 1981 *Sanxiaella partibilis* – Chang, p. 558, pl. 1, figs. 1–6.
- 1983 *Sanxiaella partibilis* – Zeng, p. 113, pl. 13, figs. 23–25.
- 1986 *Sanxiaella* sp. – Mergl, p. 186, pl. 1, figs. 1–4.
- 1994 *Sanxiaella* sp. – Havlíček, p. 64.
- 2002 *Pseudopholidops* sp. – Cocks and Fortey, p. 64.
- 2016 *Craniops partibilis* – Zeng et al., p. 19, pl. 1, figs. 4–7.

**Material:** One hundred and fifty-seven individuals (external and internal moulds of both valves).

**Remarks:** *Sanxiaella* sp. from the Kosov Formation (Hirnantian), Bohemia (Mergl, 1986;

Havlíček, 1994) and *Peudopholidops partibilis* from South China and Myanmar are considered to be conspecific since there are no essential differences between them. *Pseudopholidops anteglacialis* from the upper Katian rocks of Bohemia (Mergl, 2012) is quite similar to *P. partibilis* in many aspects, and they are possibly conspecific, although the former has a more elongate shell, posteriorly wider limbus that disappears at the anterior margin, and a larger, more posterior located, and less distinctive visceral platform.

Order Craniida Waagen, 1885

Superfamily Cranioidea Menke, 1828

Family Craniida Menke, 1828

Genus *Xenocrania* Chen and Rong, 2019

*Xenocrania haimei* (Reed, 1915)

(Figs. 12, 13A–G)

1915 *Palaeocyclus? haimei* – Reed, p. 71, pl. 10, figs. 7–10, non fig. 11.

cf. 1965 *Philhedra stawyensis* – Temple, p. 382, pl. 2, figs. 3–7.

cf. 1968 *Acanthocrania* sp. nov. morph A. – Temple, p. 18, pl. 1, figs. 11, 12, 15–18.

cf. 1978 *Philhedra grayii* – Cocks, p. 31.

cf. 1987 *Philhedra* cf. *grayii* – Temple, p. 28, pl. 1, fig. 10.

cf. 2008 *Philhedra grayii* – Cocks, p. 39.

2019 *Xenocrania haimei* (Reed) – Chen and Rong, figs. 4–10.

**Material:** About 20 external and internal moulds of the dorsal valves. Only dorsal valves preserved.

**Description:** Small (1.3–9.9 mm wide), encrusting, asymmetrical; outline variable; low, moderate sub-conical, sub-central beak located about 15–35% of valve length from posterior margin. Ornament of radial ribs and spines with various morphologies, three types

discernable: 1) Type A: basically continuous radial ribs with undulations on ribs, appearing like many spines linked (Fig. 12A, B); 2) Type B: radially aligned short hollow spines continuously linked one by one, protruding from margins of concentric lamellae, extending anteriorly to be almost aligned parallel to or obliquely to shell surface; and 3) Type C: isolated hollow spines, radially arranged (Fig. 12C). Concentric laminae mainly seen in the type B; interspaces smooth, wider than ribs or spines, without any striations.

Dorsal muscle fields generally not well impressed; anterior adductor scars in front of umbo, teardrop-shaped, larger than posterior ones (Fig. 12D); posterior scars small, elliptical. Limbus is entirely absent. Shell calcareous, punctae very fine, radially aligned. Host ribbing rarely impressed. No ventral valves seen, possibly not calcified.

**Remarks:** The Burmese species was originally referred to a coral genus *Palaeocyclus* (Reed, 1915). However, it is characterized by a craniid shell form and ornament, and is clearly a craniid brachiopod. Cocks and Fortey (2002) treated it as a representative of *Orthisocrania*. *Philhedra? stawyensis* of the Ashgill Shales (Hirnantian) at Hol Beck, England and the *Dalmanitina* Beds (Hirnantian), Holy Cross Mountain, Poland (Temple, 1965), *Acanthocrania* sp. morph A from the upper Hirnantian of Keisley, England (Temple, 1968), and *Philhedra* sp. from the Kosov Formation (Hirnantian) in the Prague Basin, Czech Republic (Havlíček, 1994) are all very similar to *X. haimei*, if not conspecific (Chen and Rong, 2019).

Genus *Petrocrania* Raymond, 1911

*Petrocrania* sp.

(Fig. 13H–J)

1915 *Palaeocyclus? haimei* – Reed, p. 71, pl. 10, fig. 11, non figs. 7–10.

**Material:** Five internal moulds of ventral valves.

**Comparison:** Pending detailed systematic revision (Popov and Holmer, 2000), *Philhedra* can be distinguished from *Petrocrania* mainly by contrasting ornamental patterns: *Philhedra* has an ornament of thick, radially aligned, distinctive hollow spines associated with concentric growth laminae, whereas *Petrocrania* possesses only concentric lamellae lacking spines on its shell surface. The Burmese specimens can be compared with *Philhedra cribrum* (Temple, 1968, p. 15, pl. 2, figs. 1–3, 5–7, 10) from upper Hirnantian of Keisley, England. However, our study is hindered by a poor preservation and the small size of the valves; the musculature and other features are seldom well enough impressed; the matrix is often too coarse to replicate key features; and the paucity of Myanmar valves prevents a statistical comparison. Thus, our taxonomic treatment is provisional.

Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Glyptomenidae Cooper, 1956

Genus *Minutomena* Zeng et al., 2016

**Type species:** *Minutomena yichangensis* Zeng et al., 2016, p. 21, pl. 2, figs. 1–5;  
Kuanyinchaio Beds (Hirnantian), Yichang, western Hubei, Central China.

*Minutomena yichangensis* Zeng et al., 2016

(Fig. 15L–P)

2016 *Minutomena yichangensis* – Zeng et al., p. 22, pl. 2, figs. 1–5.

**Material:** One ventral external mould and two dorsal internal moulds.

**Remarks:** *Minutomena* is characterized by a low biconvex profile, multicostellae with fine concentric fila, well developed dental plates extending anteriorly, curving inward as lateral

ridges to muscle field, bilobed cardinal process with widely divergent socket ridges, and a pair of prominent lateral ridges developed anterior to socket ridges (Fig. 15O, P). The scarcity of Burmese material precludes any possibilities to investigate further the relationship of the genus to other taxa.

Genus *Paromalomena* Rong, 1984

1979 *Paromalomena* (*nomen nudum*) – Rong, p. 2.

1984 *Paromalomena* – Rong, p. 150.

2002 *Paromalomena* (*Shanomena*) – Cocks and Fortey, p. 68.

**Type species:** *Stropheodonta mcmahoni* Reed (1915, p. 76, pl. 11, figs. 1–9); Basal Pangsa-pye Formation (Hirnantian), Northern Shan State, Myanmar.

**Diagnosis:** Small to large, hemicircular; ventral valve slightly convex, dorsal valve weakly concave to nearly flat. Ornament of fine costellae, increase by intercalation; concentric wrinkles or rugae weak, irregular and wavy. Substance of shell coarsely pseudopunctate. Pedicle callus well developed, dental plates thin, short, widely displayed; anterior margin of muscle field faintly visible. Cardinal process small, bilobed; socket ridges short, widely divergent; paired low ridges usually discernable in front of socket plates; muscle field unobservable.

**Discussion:** Temple (1965) firstly pointed out that *Platymena? polonica* Temple, 1965, the type species of *Paromalomena*, was very similar in most features to *S. mcmahoni* Reed, 1915, if not conspecific. Based on the latter, as the type species, *Shanomena* as a new subgenus was established for *Paromalomena* by Cocks and Fortey (2002). They proposed that *P. polonica* differs from *S. mcmahoni* with respect to the shell shape (more plastic and less regular in *P. polonica* than in *P. mcmahoni*) and size (18 mm long and 30 mm wide for *P. mcmahoni* in contrast to the Chinese material of *P. polonica* which is less than 10 mm wide); the style of rugae (much less regular in *P. polonica* than in *P. mcmahoni*), the form of ventral muscle field

(flabellate in *P. polonica* and bilobed in *P. mcMahoni*), and the dorsal trans-muscle septa (absent in *P. mcMahoni* but present in *P. polonica*).

New investigations on a large sample of specimens recorded as *P. polonica* from various regions indicate that its size is highly variable, the smallest one known is 1.6 mm long and 2.2 mm wide in the collections from Poland (Temple, 1965) and the largest at 40 mm wide in Argentinian material (Astini and Benedetto, 1992). Many specimens of *P. polonica* are less than 15 mm wide, smaller than some of the Burmese ones of *P. macMahoni*. However, measurements made by Cocks and Fortey (2002, pl. 3) indicate that *P. mcMahoni* has a shell size ranging from 12 to 15 mm wide in addition to the larger lectotype (32 mm wide). Our examination shows a wide range in shell size: from the smallest at 3.1 mm long, 4.2 mm wide to the largest at 19.4 mm long, 30.5 mm wide (Fig. 14).

Although the convexity, ornamentation, dorsal muscle field and cardinalia are relatively stable, the shell morphology of *P. polonica* is plastic as evident in the specimens from South China and Sibumasu (western Yunnan and Myanmar). Rugae style, the form of ventral muscle field and dorsal trans-muscle ridges in allopatric and sympatric populations of *P. polonica* and *P. mcMahoni* are also highly variable. It is noticeable that there are a pair of low, longitudinal ridges between ventral adductor and diductor scars, obvious in *P. mcMahoni* (Cocks and Fortey, 2002, pl. 3, fig. 7), which are also observed in *P. polonica* recorded from Xainza, central Xizang (Rong and Xu, 1987, pl. 2, fig. 10) and San Juan, Argentina (Astini and Benedetto, 1992, p. 260, pl. 2, fig. 4). This character usually occurs in adult-gerontic individuals and does not occur in smaller shells from Poland, South China and other places. Differences in shell size by itself is an unsound criterion for distinguishing between allopatric fossil populations. In addition, many other features of *P. macMahoni* (e.g., ornamentation, muscle fields, dental plates and cardinalia) are identical to those of *P. polonica*. Consequently, we suggest that *P. macMahoni* and *P. polonica* are conspecific, and *Paromalomena* (*Paromalomena*) and *Paromalomena* (*Shanomena*) consubgeneric. Thus, *P. macMahoni* should be designated as the type species of the genus *Paromalomena*.

**Range and distribution:** Hirnantian, latest Ordovician; cosmopolitan.

*Paromalomena mcmahoni* (Reed, 1915)

(Figs. 14, 15A–K)

Synonymy list see Appendix A

**Type specimens:** The internal and external moulds of a dorsal valve named as *Stropheodonta mcmahoni* from Northern Shan State, Myanmar (Reed, 1915, pl. 11, figs. 1, 2) (= BC 56789) were selected as the lectotype of *Paromalomena mcmahoni* by Temple (1965, p. 410). A dorsal internal mould (BB 30009) from the *Dalmanitina* Beds (Hirnantian), southern Poland was designated as the holotype of *Platymena? polonica* by Temple (1965, p. 407, pl. 15, fig. 2; Cocks and Fortey, 2002, pl. 2, fig. 16). These two species are considered to be conspecific.

**Material:** One hundred and sixty-three external and internal moulds of ventral and dorsal valves.

**Description:** Shells 3 to 18 mm long, 4.5 to 30.5 mm wide, transversely semi-circular; shells compressed, dorsal valve plano to weakly concave, ventral valve gently convex.

Multicostellate, fine, unequally, indistinct on umbones; rare concentric rugae irregular, disjointed. Dental plates thin, short; muscle scars small, broad, faintly visible, extending anteriorly beyond ends of dental plates, anteriorly, ill-defined. Cardinal process lobes small, adjacent posteriorly; socket ridges very short, widely divergent at an angle of about 125°; notothyrial platform depressed, especially at its posterior end; trans-muscle ridges short and thin.

**Remarks:** Morphologically, *P. mcmahoni* has highly variable characters, such as shell size, outline, ornamentation, dental plates, and socket ridges. All these characters may have a wide range of intraspecific variation.

Family Leptostrophiidae Caster, 1939

1967 *Eostropheodontidae* – Havlíček, p. 80.

2016 *Sinomenidae* – Zeng et al., p. 30.

Genus *Eostropheodonta* Bancroft, 1949

1949 *Eostropheodonta* – Bancroft, p. 9.

1968 *Aphanomena* – Bergström, p. 13.

1972 *Eoleptostrophia* (*nomen nudum*) – Harper and Boucot in Amos, p. 11.

1974 *Neokjaerina* – Levy and Nullo, p. 191.

1993 *Pirgumena* – Rõõmusoks, p. 163.

2016 *Sinomena* – Zeng, Chen and Zhang in Zeng et al., p. 36.

2016 *Yichangomena* – Zeng, Zhang and Han in Zeng et al., p. 34.

**Type species:** *Orthis hirnantensis* M’Coy, 1851; Hirnant Formation (Hirnantian), Upper Ordovician, Aber Hirnant, near Bala, Wales, UK. The type species of *Aphanomena* is *A. schmalenseei* Bergström, 1968, p. 13, pl. 5, figs. 3–6; *Dalmanitina* beds (Hirnantian) of Västergötland, Sweden. The type species of *Sinomena* is *S. typica* Zeng, Chen and Zhang in Zeng et al., 2016, p. 37, pl. 12, figs. 1–9; pl. 53, figs. 1, 2; Kuanyinchiao beds (Hirnantian) of Yichang, western Hubei, Central China. The type species of *Yichangomena* is *Y. dingjiapoensis* Zeng, Zhang and Han in Zeng et al., 2016, p. 35, pl. 11, figs. 1–11; pl. 52, figs. 1, 2; locality and horizon *ibid*. For the type species of *Eoleptostrophia*, *Neokjaerina* and *Pirgumena* Rõõmusoks refer to Rong and Cocks (1994) and Cocks and Rong (2000).

**Discussion:** *Eostropheodonta* is chiefly characterized by the presence of a nearly biplanate lateral profile, rare denticles on denticular plates and socket ridges, short dental plates, denticulate socket ridges, a bilobed cardinal process and very weak muscle fields. The striated teeth, are an important feature generally assumed to be absent from rafinesquinids. It is distinguished from the other members of leptostrophiids by the absence of a denticulate

hinge and non-flabellate muscle scar. *Eostropheodonta* is a precursor of the leptostrophiids.

The type species of *Yichangomena* and *Sinomena* are associated with *Eostropheodonta* in the Kuanyinchiao beds of Yichang, western Hubei. Zeng et al. (2016, p. 105) considered that *Sinomena* is similar to *Aphanomena* but can be distinguished by having a trilobed cardinal process, a very short and high median ridge located at the anterior end of the median process and a row of denticles subvertically oriented to the inner walls of the dental plates. However, the so-called trilobed type of the cardinal process may be a misleading term for essentially a modified bilobed cardinal process; the very short, posterior median ridge between two lobes of the cardinal process is interpreted here as the attachment of the diductor muscles in the dorsal valve; it is also present in some topotype specimens of *E. parvicostellata* from the same bed at the same locality of Yichang, western Hubei (Rong, 1984) and in *E. discumbata* from South Africa (Cocks et al., 1970). *Yichangomena* is distinguished from related genera primarily by having a row of denticles located on each side of delthyrium and a pit situated at the front of the trilobed cardinal process. The so-called contrasting style of denticles in the ventral valve is strongly dependent on taphonomy. Thus, these features do exist but are assumed to occur within the range of intra-specific variations among sympatric populations.

*Eostropheodonta* was regarded as the oldest known representative of the leptostrophiids. Many species of the *Hirnantia* Fauna worldwide are ascribed to *Eostropheodonta*, *Aphanomena* and *Rafinesquina*, including a number of species in Avalonia, Baltica, Laurentia, Perunica, Sibumasu, South China, Lhasa, South America and the Africa palaeoplates and Kazakhstani terranes (see Appendix A). The type species of *Eostropheodonta*, *E. hirnantensis* is a well-known, widely-distributed and characteristic constituent of the *Hirnantia* fauna. *E. siluriana* is very similar to *E. hirnantensis* and differs only in having fascicostellate, rather than unequally parvicostellate ornamentation. Wright (1968) questioned the presence of the two distinct species. Cocks (1982) treated *E. hirnantensis*, *E. siluriana* and *E. whittingtoni* as synonyms on the basis of a close examination of their topotypes and other relevant samples from Hirnantian populations.

*Aphanomena* was considered a junior synonym of *Eostropheodonta* (Rong and Cocks, 1994). Its type species, *A. schmalenseei* Bergström, 1968 from the *Hirnantia* Fauna of Sweden was later considered a junior synonym of *E. hirnantensis* by Cocks (2005) who further emphasized its rather variable ornamentation. The two Hirnantian species *A. planoconvexa* from Anticosti, Canada (Dewing, 1999) and *A. luna* from Sweden (Bergström, 1968; Cocks, 2005) are regarded as representatives of *Eostropheodonta*. Some species which were assigned to *Rafinesquina*, i.e., *R. ultrix* from the Hirnantian of Bohemia (Marek and Havlíček, 1967) are also very similar to *Eostropheodonta* and may be assigned to *Eostropheodonta*.

*Eostropheodonta hirnantensis* (M'Coy, 1851)

(Fig. 16C, G, H)

Synonymy list see Appendix A

**Material:** Five internal moulds of ventral and dorsal valves.

**Discussion:** The Burmese species *E. feddeni* was previously represented by rare ventral and dorsal external moulds (Reed, 1915) lacking specimens displaying internal morphology. Based on our new material, we follow Cocks and Fortey (2002) and treat *E. feddeni* as a junior synonym of *E. hirnantensis* in view of its shell outline, size, convexity and ornamentation.

Although the ornamentation has been considered to be of taxonomic significance, it may be highly variable even among specimens from the same population at a single locality (Cocks, 1982; Rong and Cocks, 1994; Benedetto et al., 2013). For example, three types of ornament occur in toptype samples: unequally parvicostellate, evenly multicostellate and fascicostellate (Temple, 1965) and variation between these end members were later found in the collections of Natural History Museum in London (Rong and Cocks, 1994). *E. hirnantensis* from Sweden has a distinctive pattern of ornamentation, being intermediate

between multicostellate and unequally parvicostellate (Bergström, 1968). Several species of *Eostropheodonta* occur in the same beds at the same localities in Bohemia (Marek and Havlíček, 1967), Chu-Ili, Kazakhstan (Nikitin et al., 1980), in Estonia and Latvia (Hints and Harper, 2015), western Hubei (Zeng et al., 2016) and Morocco (Havlíček, 1970). Thus, it is probable that there is an intergradation of ribbing style between parvicostellation and fascicostellation, with *A. parvicostellata* characterized by almost equal parvicostellae in South China (Rong, 1984) at one end of the spectrum and *E. siluriana* with fascicostellae in England and Quebec (Lespérance and Sheehan, 1976; Cocks, 1982) at the other. The discussion above indicates high variabilities and several morphotypes in *E. hirnantensis* may probably exist in large populations. Thus, an alternative hypothesis is that the ornament of *E. hirnantensis* is much more variable in sympatric and allopatric populations than previously thought.

*Rafinesquina stropheodontoides* is a common species in the Noix Limestone (probably upper Hirnantian), Missouri (Amsden, 1974). Its dental plates are vestigial or absent; the species is better assigned to *Palaeoleptostrophia*, rather than *Eostropheodonta*.

*Palaeoleptostrophia* was thought to originate in the Rhuddanian (Rong and Cocks, 1994). Interestingly, there is a species of *Palaeoleptostrophia* in the typical *Hirnantia* fauna in South China (Huang's investigation). It lacks dental plates and has numerous coarse pseudopunctae in the posterolateral parts of its triangular ventral muscle field. There occur some specimens of leptostrophiids recorded in the Hirnantian rocks of Latvia and Estonia (Hints and Harper, 2015). Thus, *Palaeoleptostrophia* could be regarded as a progenitor taxon evolved during the crisis interval (early-mid Hirnantian).

Order Orthotetida Waagen, 1884

Suborder Orthotetidina Waagen, 1884

Superfamily Chilidiopsoidea Boucot, 1959

Family Chilidiopsidae Boucot, 1959

Genus *Fardenia* Lamont, 1935

2016 *Hubeinomena* – Zeng et al., p. 37.

**Type species:** *Fardenia scotica* Lamont, 1935; the Quarrel Hill Formation (upper Katian, Upper Ordovician); Drummuck Group (Cautleyan, upper Katian), Quarrel Hill, Girvan, Scotland. The type species of *Hubeinomena* is *H. wangjiawanensis* Zeng et al. (2016, p. 38, pl. 13, figs. 1–8; pl. 14, figs. 1–4; pl. 54, figs. 1–3) from Kuanyinchiao Beds (Hirnantian) of Yichang, western Hubei, Central China.

**Remarks:** Separation of Late Ordovician and early Silurian orthotetoid genera (like *Fardenia*, *Coolinia*, *Chilidiopsis*, and *Saughina*) remains unsatisfactory, particularly regarding the former two taxa. More recently, Cocks (2016) noted that they were all valid genera in terms of the distinctive characters of each; much weight was placed on the development of the notothyrial covers. The proposal that *Coolinia* is a subgenus of *Fardenia* is a short-term solution pending a better understanding of their relationships (Rong et al., 2013).

*Hubeinomena* shares many characters with *Fardenia/Coolinia*, particularly its shell form, size, lateral profile, ornamentation and cardinalia. Zeng et al. (2016, p. 37, pl. 13, figs. 1b, 1c) highlighted a distinctive structure related to dental plates in the ventral valve which they described as ‘wide denticulates on dental plates’ based on internal moulds. However, this is what Dewing (1999, p. 41, text-fig. 35) termed as ‘anteromedian dental notch’ in *Coolinia gamachiana* from the Ellis Bay Formation of Anticosti, Canada. Thus, we consider *Hubeinomena* and *Fardenia/Coolinia* may be co-generic.

Subgenus *Fardenia* (*Coolinia*) Bancroft, 1949

**Type species:** *Coolinia*, provisionally considered a subgenus of *Fardenia* with its type species: *Orthis? applanata* Salter in M’Coy, 1846; Telychian, Upper Llandovery, Cong, County Galway, Ireland.

*Fardenia (Coolinia) cf. dalmani* Bergström, 1968

(Fig. 17A–I, L, O)

? 1915 *Schuchertella pecten* (Linné) – Reed, p. 79, pl. 11, fig. 20.

? 1915 *Schuchertella planissima* – Reed, pl. 11, fig. 17, non others.

cf. 1968 *Coolinia dalmani* – Bergström, p. 17, pl. 6, fig. 10; pl. 7, figs. 1–4.

? 1982 *Coolinia dalmani* – Cocks, p. 774, pl. 82, figs. 7–13.

? 2002 *Coolinia* sp. – Cocks and Fortey, p. 71, pl. 2, fig. 13.

**Material:** More than 100 internal and external moulds of ventral and dorsal valves.

**Description:** Median to relatively large size, ranging from 2–3 mm up to 40 mm in width; weakly biconvex, semi-elliptical outline. Ornament of fine, stout costae and costellae with prominent fine concentric fila; posterior ribs curving toward posterior valve margin. Dental plates short, divergent at about 70°. Cardinal process strong and short, bilobed, fused with short and stout, widely divergent socket plates. Muscle fields of both valves not visible.

**Discussion:** There are many named species or forms under open nomenclature attributed to *Fardenia* or *Coolinia* in the Hirnantian of Avalonia (Temple, 1968), Baltica (Bergström, 1968; Hints and Harper, 2015), Bohemia (Marek and Havlíček, 1967), Kazakhstan (Nikitin et al., 1980), Laurentia (Amsden, 1974; Harper, 1979, 2006; Dewing, 1999), Sibumasu (Reed, 1915; Huang et al, *in press*; this paper), and South China (Rong, 1984; Rong and Li, 1999; Zeng et al., 2016). All possess subparallel posterior ribs, rather than ribs curving toward the posterior valve margin except *F. (C.) dalmani* (Bergström, 1968, pl. 6, fig. 10), *F. (C.) propinqua* (Amsden, 1974, pl. 3, figs. 1a, 2a), and *F. (C.) iliensis* (Nikitin et al., 1980, pl. 19, fig. 6). The latter character is prominent in *F. (C.) dalmani*, but weakly developed in the other two. The Burmese specimens most closely resemble *F. (C.) dalmani* from the Swedish *Hirnantia* Fauna (Bergström, 1968) in many aspects, particularly in possessing posterior ribs curving towards the hinge, a distinctive character of that species. But not all of the Burmese

specimens show this feature. *F. (C.) dalmani* was also recorded from the top of Husbergøya Shale Formation of the Oslo-Asker district, southern Norway (Cocks, 1982), but it does not possess ribbing like that in Swedish *F. (C.) dalmani*. It is not known whether this character is of significant taxonomic value, although it clearly developed in *Valdaria* (Bassett and Cocks, 1974; Yang and Rong, 1982). A complete chilidium is well developed in *F. (C.) dalmani*, but is much smaller in our material.

Genus *Cliftonia* Foerste, 1909

*Cliftonia* cf. *psittacina* (Wahlenberg, 1821)

(Fig. 17J, K, M, N)

Synonymy list see Appendix A

**Material:** Twelve external and internal moulds of ventral (mostly) and dorsal valves.

**Remarks:** Globally, there are more than 11 species from the Hirnantian allocated to *Cliftonia*. They are very similar to each other and differences between species are minor. Variations in many of the morphological characters are remarkable, such as shell form (transverse, circular to elongate), ornamentation (moderate to strong plications), sulcus and fold (moderately to strongly sulcate), dental plates (short to absent), and number of ribs in the sulcus (a single, through three to up to seven). Based on the last character, Bergström (1968) thought that *C. psittacina* closely resembled *C. lamellosa* (Williams, 1951) and both were possibly conspecific. Amsden (1974) stated that the principal distinction between *C. psittacina* (typically transverse shell) and *C. tubulistriata* (nearly subcircular or elongate) from the Edgewood Fauna is only outline. In addition, there are four taxa (*C. elongata*, *C. obovata*, *C. robusta*, and *C. sanxiaensis*) co-occurring in the Kuanyinchiao Beds of Yichang, Hubei, Central China; their differences are herein considered to represent intra-specific variations. The Burmese material is most similar to *C. psittacina* in shell form, size, and

ornamentation, with less well-developed dental plates and less numerous radial ribs than the Swedish type specimens. Since the material under study cannot be revised further, we cannot definitively treat them as synonyms. Additional study is required.

Class Rhynchonellata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Protorthida Schuchert and Cooper, 1931

Superfamily Skenidioidea Kozłowski, 1929

Family Skenidiidae Kozłowski, 1929

Genus *Skenidioides* Schuchert and Cooper, 1931

*Skenidioides* cf. *scoliodus* Temple, 1968

(Fig. 18A–F)

cf. 1968 *Skenidioides scoliodus* – Temple, p. 28, pl. 5, figs. 1–27.

**Material:** Eight external and internal moulds of ventral (mostly) and dorsal valves.

**Description:** Small, 3–5 mm in width, transversely elongated, ventri-biconvex, with low and broad ventral fold and shallow dorsal sulcus. Ornament of rare, low, rounded, coarse, usually simple costae. Spondylium small and short, supported by a very short median ridge. Cardinal process very thin, ridge-like; brachiophore supporting plates converging onto thin median septum extending forward about 90–95% of valve length.

**Remarks:** *Skenidioides* is a well-known, cosmopolitan, relatively deeper-water and long-ranging genus in the Ordovician and Silurian. There are a great number of valid and undetermined species attributed to this genus. However, it is extremely rare during the Hirnantian, recorded only from Wales, UK (Williams and Wright, 1981), and Mandalay, Myanmar (this study). Thus, it is assumed to be a Lazarus taxon through the end Ordovician mass extinction. Herein we compare the Burmese specimens with *S. scoliodus*, since they have a less convex ventral valve, a somewhat different shape of spondylial base, and an

evidently thinner dorsal median septum.

Order Orthida Schuchert and Cooper, 1932

Superfamily Dalmanelloidea Schuchert, 1913

Family Dalmanellidae Schuchert, 1913

Genus *Dalmanella* Hall and Clarke, 1892

**Type species:** *Orthis testudinaria* Dalman, 1828; *Dalmanitina* Beds, Loka Formation (Hirnantian, Upper Ordovician), Borenhult, Östergötland, Sweden. It has been revised in detail by Jin and Bergström (2010).

*Dalmanella testudinaria* (Dalman, 1828)

(Fig. 19A–F)

Synonymy list see Appendix A

**Material:** One hundred and twenty-six ventral (mostly) and dorsal internal moulds.

**Discussion:** There are a number of species assigned to *Dalmanella* which are recorded from the *Hirnantia* Fauna. *D. mansuyi* (Reed, 1915) is characterized externally by a subcircular outline, very slightly convex or even flattened dorsal valve, and ornament of subangular costellae with irregular size and unequal interspaces. It is closest to *D. testudinaria* (Dalman, 1828) from Stawy, southern Poland (Temple, 1965) and may prove to be identical at least in ornamentation (Cocks and Fortey, 2002). We agree that in terms of the cardinalia type and ornament of the dorsal umbo (with a medial interspace) the two species are possibly conspecific.

*D. testudinaria* (Dalman, 1828) occurs in the *Hirnantia* Fauna of many palaeoplates or terranes (e.g., Baltica, Avalonia, Laurentia, Sibumasu, South America, South China, Kazakhstan, Perunica, Lhasa and others), being one of the most widely reported species of

the genus. Its type specimens from Loka Formation (Hirnantian), Borenshult, Östergötland, Sweden (Bergström, 1968) were first revised by Williams and Wright (1963) and recently by Jin and Bergström (2010) in detail. The narrow, bilobate type of cardinal process, the dorsal medial interspace, the absence of aditicles, and punctae of two sizes were considered four of the most important characters defining *D. testudinaria*, with the former two of particular significance when species were compared (Jin and Bergström, 2010). Meanwhile, the pattern of brachiophore supporting plates which converge on to a median ridge should be also considered for recognition of this genus and its species. The great majority of the above records were not listed as *D. testudinaria* by Jin and Bergström (2010) because some key characters noted above were not illustrated. The specimens identified as *D. testudinaria* from the Zhailair Formation (Hirnantian) of Chu-Ili (Nikitin et al., 1980) lacked any significant differences from the type material of the species (Popov and Cocks, 2014, p. 743). *D. testudinaria* from Kuanyinchiao Beds in South China possesses a dorsal medial interspace, a delicate, bilobed cardinal process, divergent brachiophores, convergent supporting plates and other features indicating a close relation with *D. testudinaria*, although it is difficult to determine the nature of the punctae and absence of aditicles. An alternative, therefore, is that many of the above taxa in the *Hirnantia* Fauna may be real representatives of *D. testudinaria* or at least its close relatives. A detailed reappraisal of the type series of the Hirnantian *Dalmanella* along with additional studies of their shell microstructures (such as aditicles and punctae) is needed. However, the dorsal valve of *D. testudinaria* from the upper Kuanyinchiao bed (possibly upper Hirnantian) of Bijie, northwestern Guizhou (Rong and Li, 1999) is substantially more convex than that of the type specimens, and thus is closer to *D. edgwoodensis* (Savage) of the Mid-Continent of USA (Amsden, 1974) which is probably of late Hirnantian age and occupying a warm-water setting.

Genus *Mirorthis* Zeng, 1983

1983 *Mirorthis* – Zeng, p. 116.

- 1984 *Mirorthis* – Rong, p. 130.  
2000 *Mirorthis* – Harper, p. 785.  
2016 *Paramirorthis* – Zeng, Wang and Peng in Zeng et al., p. 62.

**Type species:** *Mirorthis mira* Zeng, 1983, p. 117, pl. 14, figs. 14–17; Kuanyinchiao Beds (Hirnantian), Yichang, western Hubei, Central China. The type species of *Paramirorthis* is *P. minuta* Zeng, Wang and Peng in Zeng et al., 2016, p. 63, pl. 29, figs. 6–11; pl. 30, figs. 1–11; pl. 31, figs. 1–4; pl. 57, fig. 1; locality and horizon *ibid*.

**Remarks:** *Mirorthis* is a distinctive dalmanelloid genus because of the presence of a pair of slender, nearly parallel ancillary struts (Temple, 1965) and widely splayed brachiophore supporting plates (Zeng, 1983; Rong, 1984). Recently, a new genus *Paramirorthis* was established based on the type species *P. minuta* from the *Hirnantia* Fauna of Yichang, western Hubei by Zeng et al. (2016). Our examination, however, suggests that *P. minuta* represents a juvenile stage of *M. mira* in view of its small size, rare costellae, a minute cardinal process and very short, oblique to parallel ancillary struts (Temple, 1965, pl. 7, fig. 4; Rong, 1984, pl. 3, figs. 2, 5, 7, 9). The cardinalia in *P. minuta* displays those of the immature growth stages; the other morphological features of *P. minuta* are the same as those of *M. mira*. Thus, *P. minuta* is considered to be a junior subjective synonym of *M. mira*. The identical horizons and localities of both type species of the two genera further confirm this conclusion.

*Mirorthis mira* Zeng, 1983

(Fig. 20A–F)

- ? 1915 *Dalmanella mansuyi* – Reed, pl. 10, figs. 14, 15.  
1965 *Bancroftina?* cf. *bouceki* (Havlíček, 1950) – Temple, p. 392, pl. 7, figs. 1–4, 6, 7.  
1971 *Hordeleyella* cf. *bouceki* – Havlíček, p. 51, pl. 19, figs. 8, 9.  
1977 *Hordeleyella* sp. nov. – Havlíček, p. 204.  
1983 *Mirorthis mira* – Zeng, p. 117, pl. 14, figs. 14–17.

- 1983 *Mirorthis yichangensis* – Zeng, p. 117, pl. 14, fig. 13.
- 1984 *Mirorthis mira* – Rong, p. 131, pl. 4, figs. 1, 3, 4, 6, 7, 9.
- 1991 *Mirorthis* cf. *mira* – Leone et al., pl. 6, figs. 1–3.
- 1997 *Mirorthis mira* – Cocks and Fortey, p. 124, pl. 2, fig. 8.
- 2000 *Mirorthis mira* – Harper, p. 785, fig. 567.2.
- ? 2002 *Mirorthis* aff. *mira* – Harper and Williams, fig. 5f, g.
- 2008 *Bancroftina?* cf. *bouceki* – Cocks, p. 158.
- 2016 *Mirorthis mira* – Zeng et al., p. 62, pl. 31, figs. 5–11; pl. 57, fig. 2.
- 2016 *Paramirorthis minuta* – Zeng et al., p. 63, pl. 29, figs. 6–11; pl. 30, figs. 1–11; pl. 31, figs. 1–4; pl. 57, fig. 1.
- 2019 *Mirorthis mira* – Colmenar et al., p. 468, figs. 5.3, 5.4, 5.7–5.9.

**Material:** Twenty-five ventral and dorsal (mostly) internal moulds.

**Remarks:** *Mirorthis mira* is generally a rare, but distinctive constituent of the *Hirnantia* Fauna in Avalonia, Baltica, Bohemia, European peri-Gondwana, Sibumasu, and South China, and possibly Morocco. The species is more abundant in Aber Hirnant, northern Wales and Changning, southern Sichuan where *M. mira* occupies 34% and 93.4% of the entire brachiopod faunas, respectively (Temple, 1965; Li et al., 2009). The occurrence of *M. mira* in the Mandalay Region is herein recorded for the first time, although the specimens of the Northern Shan State (Reed, 1915, pl. 10, figs. 14, 15) may belong to *B.? bouceki* (= *M. mira*) (Temple, 1965). Both endopunctae and exopunctae are well displayed in the Yichang material (Rong, 1984), but have not been observed in the Mandalay specimens likely due to poor preservation. Nonetheless, the bilobed cardinal process and well developed fulcral plates warrant assignment to *Mirorthis*.

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Draborthis* Marek and Havlíček, 1967

**Type species:** *Draborthis caelebs* Marek and Havlíček, 1967, p. 280, pl. 2, figs. 9, 10, 16, 17; Kosov Formation (Hirnantian) of Bohemia, Czech Republic.

**Remarks:** *Draborthis*, a distinctive genus of the typical *Hirnantia* Fauna, is represented by only the type species which is confined to the Hirnantian Stage on six palaeoplates (Avalonia, Baltic, Perunica, European peri-Gondwana, South China, and Sibumasu). It was tentatively assigned to the Draboviinae by Marek and Havlíček (1967) in view of its simple cardinal process and thin converging ridges extending from the anterior ends of its brachiophore plates. Subsequently, Temple (1968) suggested that *Draborthis* may belong to Harknessellidae, whereas Havlíček (1977) preferred his original opinion which was followed by Harper (2000).

*Draborthis* is a peculiar genus within the Draboviinae and is easy to recognize due to possession of a rather flat, even slightly concave dorsal valve with a steeply anacline even to catacline interarea, a slender, prominent median ridge extending posteriorly to the cardinal process, and a pair of very short, widely divergent brachiophore plates. *Kinnella* possesses a bilobed cardinal process being continuous with a median ridge, a character close to that of *Draborthis*. But, *Kinnella* has a different ventral exterior and interior, particularly a very high, catacline ventral interarea.

*Draborthis caelebs* Marek and Havlíček, 1967

(Fig. 20G–O)

1967 *Draborthis caelebs* – Marek and Havlíček, p. 280, pl. 2, figs. 9, 10, 16, 17.

1968 *Draborthis caelebs* – Bergström, p. 10, pl. 3, figs. 5–7.

1968 *Draborthis* cf. *caelebs* – Temple, p. 44, pl. 8, figs. 1–8.

1975 *Draborthis caelebs* – Fu, p. 112, pl. 23, figs. 8, 9.

1977 *Draborthis caelebs* – Havlíček, p. 272, pl. 31, figs. 11–18.

- 1979 *Draborthis caelebs* – Rong, pl. 1, fig. 12.
- 1981 *Draborthis* sp. – Chang, p. 560, pl. 1, fig. 14.
- 1983 *Draborthis caelebs* – Zeng, p. 116, pl. 15, figs. 1–5.
- 1984 *Draborthis caelebs* – Rong, p. 145, pl. 9, figs. 1–5, 7–10, 12–14.
- 2006 *Draborthis caelebs* – Rong in Chen et al., fig. 10.11.
- 2007 *Draborthis caelebs* – Zhan and Jin, fig. 44B.
- 2015 *Draborthis* cf. *caelebs* – Hints and Harper, p. 413, fig. 11C, E, F.
- 2016 *Draborthis caelebs* – Zeng et al., p. 78, pl. 42, figs. 1–12; pl. 43, figs. 1–11.

**Material:** Thirty-nine internal moulds of ventral and dorsal (mostly) valves.

**Remarks:** *Draborthis caelebs* is a highly variable species in many morphological characters. For example, 1) the disposition of the brachiophore supporting plates ranges from broadly divergent to almost parallel, although the brachiophores are widely divergent, and 2) the development of a pair of thin, converging ridges extending from anterior ends of brachiophore supporting plates is also variable, ranging from prominent to absent.

Genus *Hirnantia* Lamont, 1935

*Hirnantia sagittifera* (M'Coy, 1851)

(Fig. 21A–K)

Synonymy list see Appendix A

**Material:** Fifty-four ventral (mostly) and dorsal internal moulds

**Discussion:** *Hirnantia sagittifera* is basically characterized by very large shells (exceeding 40 mm in length), dorsibiconvex in lateral view, fine multicostellate ornamentation, and relatively stable cardinalia. Our investigation shows that there is a huge range of morphological variation, including shell size, outline, ventral and dorsal muscle fields, dental

plates, cardinalia and others. The cardinal process is remarkably variable, its attachment area commonly crenulated, forming a thin ridge in smaller specimens, but highly elevated with well-developed crenulations on both top and sides in larger ones. When Temple (1965) studied smaller individuals (less than 15 mm wide) of *H. sagittifera* (M'Coy), he described the cardinal process as a short, narrow ridge, so that the bilobed, crenulated attachment surface often almost filled the apex of the cavity. However, the cardinal process was recorded as small with a moderately long shaft, terminated by a small lobate myophore by Cooper (1956, p. 1005), and furthermore it is often described as simple or non-lobate (e.g., Bergström, 1968, p. 11, Lespérance and Sheehan, 1976; p. 723; Havlíček, 1977, p. 267; Cocks, 1982, p. 763). Based on investigation of both young and adult specimens of *H. sagittifera* in Yichang, western Hubei, Rong (1984) showed that its cardinal process has three types: simple with crenulations; bilobate bearing crenulations in larger shells (usually over 20 mm wide); and a mixture of the two types. In some large specimens, there are a pair of minute ridges which lie on either side of the cardinal process, i.e., accessory cardinal processes (see Schuchert and Cooper, 1932) which are also adhered to the diductor muscle scar. The examination of the Burmese material demonstrates that like the cardinal process, there is a large amount of variation in many other characters of the species *H. sagittifera*.

Genus *Kinnella* Bergström, 1968

**Type species:** *Scenidium? medlicotti* Reed, 1915, p. 75, pl. 10, figs. 24, 25, ?26; basal part of the Pangsa-pye Formation (Hirnantian), Upper Ordovician, Northern Shan State, Myanmar. *Kinnella* was proposed by Bergström (1968) based on *Hirnantia? kielanae* Temple, 1965 from the *Dalmanitina* Beds (Hirnantian), Stawy, Poland. While comparing it with *S. medlicotti*, Temple (1965) pointed out that they are very similar to each other. New data in this paper shows that the two species are conspecific because they share many features in common in terms of both ventral and dorsal morphologies.

*Kinnella medlicotti* (Reed, 1915)

(Figs. 21L–V, 22)

Synonymy list see Appendix A

**Material:** More than 200 internal and external moulds of ventral and dorsal valves.

**Discussion:** *Kinnella medlicotti* is characterized by the following features: 1) shell small, usually less than 8 mm wide, the largest known shell width about 12 mm (Bergström, 1968); 2) ventral interarea high and its inclination variable; 3) ornament of multicostellae with rare aditricles; 4) dental plates very short, divergent, continuous as low ridges surrounding muscle field; 5) cardinal process bilobed, with crenulations on its top and sides and continuous anteriorly with a strong median ridge. Examination of the ornament of *K. medlicotti* shows that the dorsal medial interspace is delimited by a pair of primary costae in apical area and a pair of basically symmetrical medially branched, first order costellae anteriorly, suggesting the presence of a primary median costa in the ventral valve *versus* a median interspace in the dorsal valve.

Like many other common taxa in the *Hirnantia* Fauna, there is a large amount of intraspecific variation in populations of *K. medlicotti*, such as different ratios of length/width of ventral muscle fields; different disposition of brachiophore supporting plates from subparallel (35°) to widely divergent (75°) (Fig. 22); different shapes of dorsal adductor scars; differentiation of dorsal median ridge (from well-developed to almost absent); and contrasting development of a pair of convergent ridges extending from distal ends of brachiophore supporting plates (Zeng et al. (2016) considered it a key character of his new species *K. robusta*). When a large population is available, these characters change gradational. Cocks and Fortey (2002, p. 65) first noted that *K. medlicotti* may possibly be conspecific with, and thus a senior synonym of, *K. kielanae*, but because the former is slightly more transverse and appears to have a larger ventral interarea than *kielanae*, they retained them as separate species in that study. In this paper, the differences mentioned above are regarded as intraspecific variation in allopatric and sympatric populations.

*Kinnella kielanae proclinis* from the *Hirnantia* fauna of the Kosov Formation in Bohemia (Havlíček, 1977) was established as a new subspecies based on a catacline to procline ventral interarea, bases of brachiophore supporting plates always divergent, and antero-lateral sides of the dorsal muscle field being straight and converging anteriorly. Likewise, these differences are thought again to be intraspecific variations within populations of *K. medlicotti*. Thus *K. kielanae proclinis* is suppressed as a junior synonym of *K. medlicotti*.

*Kinnella laurentiana* from upper Katian of Manitoulin Island, Ontario, Canada (Stott and Jin, 2007) is similar to *K. medlicotti* in some aspects, e.g., size, delthyrium, cardinal process, and dorsal muscle fields. However, the former differs from *K. medlicotti* in lacking hollow costellae and a bilobate cardinal process, associated with the development of a median costa, rather than a pair of median costae on dorsal valve (Temple, 1965, pl. 9, fig. 3; Rong, 1984, pl. 8, fig. 2; Mergl, 2011, fig. 3F). Thus, *K. laurentiana* may represent a different stock, distinct from *K. medlicotti* (cool-water settings in Hirnantian) in view of its distinctive characters and its occurrence in the low-latitude, warm interval on Laurentia in the late Katian (Fortey and Cocks, 2005).

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonirhynchiidae McLaren, 1965

Subfamily Plectothyrellinae Bergström, 1968

Genus *Plectothyrella* Temple, 1965

*Plectothyrella crassicostis* (Dalman, 1828)

(Fig. 23A–F)

Synonymy list see Appendix A

**Material:** Twenty-seven internal moulds of ventral and dorsal valves.

**Remarks:** There are two subspecies, *crassicos* and *chauveli* within *Plectothyrella* *crassicos* based on Swedish and Moroccan specimens, respectively. Havlíček (1971) thought that the outline and sulcus/fold shape were diagnostic characters for the separation, but it is not easy to discriminate between them using these characters. Villas et al. (1999) proposed a method, that is to count the number of ribs per mm, anteriorly, at a given distance from the umbo, and found that typical *P. crassicos crassicos* (on specimens from England, Sweden and Canada) possesses 4 ribs, whereas *P. crassicos chauveli* (on Moroccan and Spanish specimens) has 1–3 ribs per 5 mm, 10 mm from ventral umbo, thus having significantly coarser ribs than those of the former. In fact the ornamentation of *P. crassicos* is highly variable, including the numbers of ribs in the ventral sulcus (from a single to seven) and the lateral ribs (from seven to eleven). There is a single rib in the sulcus in the Quebec form (Lespérance and Sheehan, 1976) and that from central Xizang (Rong and Xu, 1987), 1–3 ribs in South China (Rong, 1984; Zeng et al., 2016) and East Baltica forms (Hints and Harper, 2015), and 3–7 ribs in the Bohemia form (Marek and Havlíček, 1967; Havlíček, 1990). Thus, the number of ribs in the sulcus varies considerably in the various sympatric and allopatric populations of this taxon. The material from Bohemia suggests an intermediate form with an overlap of the rib numbers across the two subspecies (Villas et al., 1999). In addition, a specimen of *P. crassicos* from San Juan in the Argentinian Precordillera has six ribs on dorsal fold at the anterior valve margin, the first bifurcation producing four ribs at about 5 mm from the dorsal anterior margin and the second with six ribs at 9 to 10 mm at the same distance (Astini and Benedetto, 1992, pl. 2, fig. 10). Generally, the relatively smaller specimens have only a single rib, and larger ones have three or more ribs in the sulcus (Temple, 1965; Bergström, 1968; Marek and Havlíček, 1967; Cocks, 1982). Thus, further investigation of sympatric and allopatric populations of the same species is necessary.

*Dorytreta longicrura* Rong and Li co-occurs with *P. crassicos* from the upper Kuanyinchiao beds (Hirnantian) of Bijie and Renhuai, northern Guizhou. They are similar to

each other in many respects, such as shell form, convexity, ornamentation, and cardinalia including long, curved crura, but different mainly in shell size (*D. longicrura*: shell width commonly 3–4 mm) (Rong and Li, 1999). Thus, we propose that *D. longicrura* may represent the juvenile of *P. crassicositis* and the former species is herein treated as a subjective synonym of the latter.

*Plectothyrella? itacurubiensis* (Benedetto et al., 2013) from possible Hirnantian strata in Paraguay, South America resembles *P. lybica* (Havlíček and Massa, 1973) in its shell shape, ornamentation and the internal morphology of both valves, but different from *P. crassicositis* in having rarer and prominently rounded ribs, a weakly elevated ventral platform, and more massive cardinalia. In view of the above, both species are possibly not *Plectothyrella*, but representatives of *Clarkeia*.

Supperfamily Meristelloidea Waagen, 1883

Family Meristellidae Waagen, 1883

Genus *Hindella* Davidson, 1882

*Hindella crassa* (Sowerby, 1839)

(Fig. 23G, H)

Synonymy list see Appendix A

**Material:** Forty-five ventral (mostly) and dorsal internal moulds.

**Remarks:** Temple (1987) first revised the type material of *Hindella crassa* and concluded that the Hirnantian *H. crassa incipiens* (Williams, 1951) was a subjective junior synonym of the Rhuddanian *H. crassa typica* (Williams, 1951) due to the difficulty in distinguishing the *crassa* samples taxonomically from the topotypes of the two subspecies. This conclusion was accepted by Rong et al. (2013) because *H. crassa* in the latest Ordovician and earliest Silurian shows considerable morphological variation within the topotype material of *H.*

*crassa* from England (Temple, 1987) and many other Hirnantian and Rhuddanian localities.

*Hindella terebratulina* (Wahlenberg, 1821), an early representative of *Hindella* is known to occur in upper Katian of the Siljan Lake Region, Sweden (Sheehan, 1977). *H. cassidea* (Dalman, 1828) and *H. kiaeri* Sheehan, 1977 (pars) from Hirnantian of Oslo-Asker Region, Norway (Sheehan, 1977; Cocks, 1982), and *H. ovoides* (Savage, 1913) from upper Hirnantian, Illinois, USA (Amsden, 1974) are very close, morphologically, to *H. crassa*, if not conspecific. The possibility that *H. terebratulina* and *H. cassidea* are junior synonyms of *H. crassa* cannot be excluded. The local species *H. ? elegans* from *Hirnantia* fauna of Yichang, western Hubei (Zeng et al., 2016) cannot be differentiated from *H. crassa* from the same bed at the same locality and thus is treated as conspecific.

The earliest species of *Hindella* is probably *H. prima* from the mid Katian of the Anarak region in central Iran. Thus *Hindella* may have been originally evolved in temperate latitude peri-Gondwana (Popov et al., 2015).

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## Figure captions

Fig. 1. Location map showing the occurrence of the uppermost Ordovician *Hirnantia* fauna in the Mandalay Region, Myanmar where the brachiopods described in this paper were collected, along with the locality of Reed (1915) in the Northern Shan State (Cocks and Fortey, 2002).

Fig. 2. Stratigraphical correlation of the Ordovician and Silurian boundary strata in the Mandalay Region and the Northern and Southern Shan States, Myanmar. Fossils of the *Hirnantia* brachiopod Fauna studied herein were collected from the Pa-Thin area, eastern Mandalay. Data of Mandalay Region is from Hla Myint (1984), Aye Ko Aung (2012), Maung Thein (2014) and this paper, data of both Northern Shan State and Southern Shan State is from Aye Ko Aung (2012) and Maung Thein (2014).

Fig. 3. Outcrops of the Hwe Mawng Purple Shale Member (Hirnantian, Upper Ordovician) which yields the *Hirnantia* fauna described in this paper.

Fig. 4. Rarefaction curve for the brachiopod collection under study showing sufficiency of sampling. Dotted lines represent 95% confidence intervals.

Fig. 5. Ordinal and generic occurrences of the *Hirnantia* Fauna in various regions including Sibumasu (western Yunnan, Myanmar and Thailand), Lhasa (central Xizang), South China, and Bohemia. Number in circle represents references: 1, Reed, 1915; Cocks and Fortey, 2002. 2, This paper. 3, Cocks and Fortey, 1997. 4, Rong and Sun, 1983; Huang et al., in press. 5, Rong and Xu, 1987. 6, Rong, 1979, 1984; Chang, 1981; Zeng et al., 2016; and others. 7, Nikitin et al., 1980. 8, Marek and Havlicek, 1967; Havlicek, 1977; Mergl, 2012; and others.

Fig. 6. Genus (diversity) and specimen (abundance) percentages of various ordinal groups of the *Hirnantia* brachiopod fauna.

Fig. 7. Diagram showing the number of specimens of each taxon represented by black bars in the lower echelon.

Fig. 8. Cluster analysis of the *Hirnantia* Fauna from western Yunnan, Mandalay Region, Northern Shan State and Thailand (Sibumasu), Yichang, western Hubei (Central China), Xainza, central Xizang (Lhasa), Chu-Ili (Kazakhstanian Terranes), and Bohemia (Perunica) based on the Dice, Jaccard, and Ochiai similarity coefficients.

Fig. 9. Occurrences of the *Hirnantia* Fauna in Sibumasu Terrane (1, Northern Shan State, Reed, 1915, Cocks and Fortey, 2002; 2, Mandalay, this paper; 3, western Yunnan, Huang et al., in press; 4, Southern Thailand, Cocks and Fortey, 1997).

Fig. 10. Correlation of the Middle and Late Ordovician brachiopod faunas of Thailand, Myanmar and western Yunnan, Guizhou and Hubei of Central China.

Fig. 11. (A) *Pseudolingula?* sp., NIGP 169264, external mould of dorsal (?) valve. (B–H) *Pseudopholidops partibilis* (Rong, 1979); (B, C) NIGP 169265, 169266, ventral (?) external moulds; (D) NIGP 169267, dorsal internal mould; (E, F) NIGP 169268, dorsal internal mould (E) and its enlargement (F) showing muscle scars; (G, H) NIGP, 169269, ventral internal mould (G) and its enlargement (H) showing muscle scars. Scale bars represent 0.5 mm unless otherwise noted.

Fig. 12. *Xenocrania haimei* (Reed, 1915). (A, B) Dorsal external mold (B) and its latex cast (A) showing type A of ornamentation; (C) latex cast of a dorsal external mould showing type C of ornamentation; (D) dorsal internal mould showing muscle scars. Scale bars represent 1 mm.

Fig. 13. (A–G) *Xenocrania haimei* (Reed, 1915); (A, B) NIGP 168274, dorsal external mould

(A) and its latex cast (B) showing type A of ornamentation; (C) NIGP 168275, dorsal external mould; (D–F) NIGP 168276, dorsal external mould (E), its latex cast (F) and local enlargement showing type C of ornamentation (D); (G) NIGP 168277, dorsal internal mould showing muscle scars. (H–J) *Petrocrania* sp., NIGP 169270–169272, a dorsal external mould (H), a dorsal internal mould (I), and a dorsal internal mould with impressions of host ribbing (J). Scale bars represent 1 mm unless otherwise noted.

Fig. 14. Shell size range of *Paromalomena mcmahoni* (Reed, 1915) in various regions during the Hirnantian. Data from: 1. Astini and Benedetto, 1992; 2. Rong and Xu, 1987; 3. Cocks and Fortey, 2002; 4. this paper; 5. Temple, 1965; 6. Nikitin et al., 1980; 7. Hints and Harper, 2015; 8. Rong, 1979; 9. Marek and Havlíček, 1967; 10. Rong, 1984; Zeng et al., 2016.

Fig. 15. (A–K) *Paromalomena mcmahoni* (Reed, 1915); (A–E) NIGP 169273–169277, a ventral internal mould of juvenile shell (A) and four ventral internal moulds of adult shells (B–E); (F, I) NIGP 169278, dorsal internal mould (F) and its latex cast (I); (G, H, K) NIGP 169279, dorsal internal mould (G) and its local enlargements showing detail of cardinalia (H) and ornamentation (K); (J) NIGP 169280, latex cast of dorsal internal mould showing cardinalia. (L–P) *Minutomena yichangensis* Zeng et al., 2016; (L, N) NIGP 169281, dorsal external mould (N) and its enlargement (L) showing details of ornamentation; (M, P) NIGP 169282, local enlargement of dorsal internal mould (M) with its latex cast (P) showing details of cardinalia; (O) NIGP 169283, dorsal internal mould. Scale bars represent 1 mm unless otherwise noted.

Fig. 16. (A, B) *Aegiromena* sp., NIGP 169284, 169285, two ventral internal moulds (juvenile (A) and adult shells (B)). (D–F) *Leptaena* sp.; (D, E) NIGP 169286, ventral external mould (D) and its latex cast (E); (F) NIGP 169287, dorsal internal mould showing cardinalia. (C, G, H) *Eostropheodonta hirnantensis* (M'Coy, 1851); (C, H) NIGP 169288, dorsal internal mould (C) and its latex cast (H) showing cardinalia; (G) NIGP 169289, ventral internal mould. Scale

bars represent 1 mm unless otherwise noted.

Fig. 17. (A–I, L, O) *Fardenia (Coolinia) cf. dalmani* Bergström, 1968; (A) NIGP 169290, ventral internal mould; (B, C) NIGP 169291, ventral internal mould and its external mould; (D, G, H) NIGP 169292, dorsal internal mould (D) and its latex cast (G, H); (L, I) NIGP 169293, dorsal internal mould (L) and its latex cast (I); (E) NIGP 169294, dorsal internal mould; (F, O) NIGP 169295, ventral external mould (O), and its local enlargement showing ornamentation (F). (J, K, M, N) *Cliftonia cf. psittacina* (Wahlenberg, 1821); (J, K, M) NIGP 169296, posterior (J), dorsal (K) and anterior (M) views of ventral internal mould; (N) NIGP 169297, dorsal internal mould. Scale bars represent 2 mm unless otherwise noted.

Fig. 18. (A–F) *Skenidioides cf. scoliodus* Temple, 1968; (A) NIGP 169298, ventral internal mould; (B, C, E, F) NIGP 169299, 169300, two dorsal internal moulds (B, E) and their enlargements (C, F); (D) NIGP 169301, dorsal internal mould. (G–I) *Toxorthis?* sp., NIGP 169302–169304, three ventral internal moulds. (J–M) *Giraldibella* sp.; (J) NIGP 169305, ventral internal mould; (K, L) NIGP 169307, dorsal internal mould (K) with its enlargement (L); (M) NIGP 169306, dorsal internal mould. Scale bars represent 1 mm unless otherwise noted.

Fig. 19. (A–F) *Dalmanella testudinaria* (Dalman, 1828); (A) NIGP 169308, ventral internal mould; (B, D–F) NIGP 169309–169312, four dorsal internal moulds; (C) NIGP 169313, ventral external mould. (G) *Leveneia* sp., NIGP 169314, dorsal internal mould showing cardinalia and adductor scars. (H–J) *Trucizetina* sp., NIGP 169315–169317, three dorsal internal moulds. Scale bars represent 1 mm unless otherwise noted.

Fig. 20. (A–F) *Mirorthis mira* Zeng, 1983; (A) NIGP 169318, dorsal internal mould of a juvenile shell showing distinctive cardinalia; (B, E) NIGP 169319, dorsal internal mould (B) and its local enlargement (E) showing cardinalia; (C) NIGP 169322, ventral external mould;

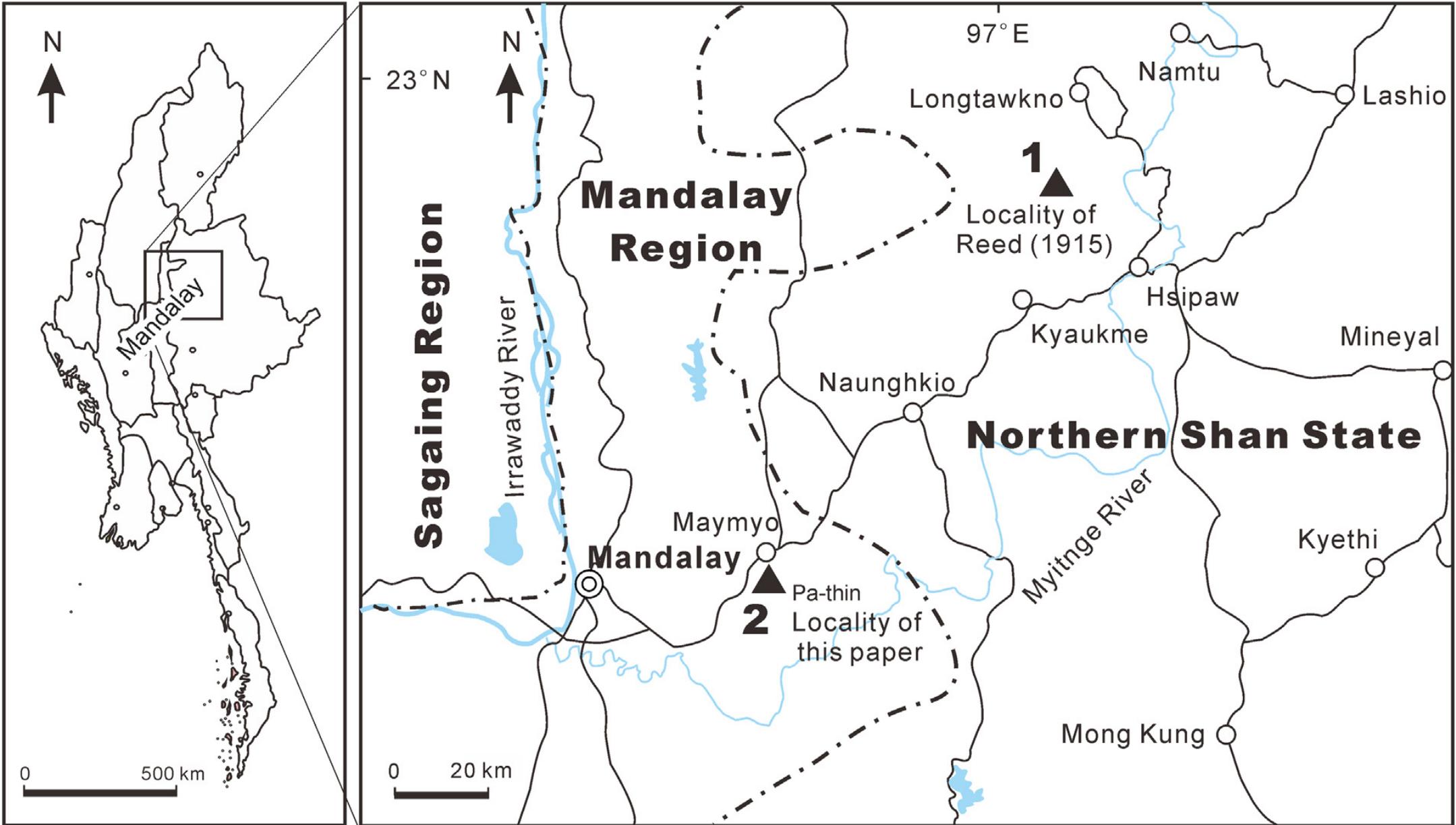
(D, F) NIGP 169320, 169321, two dorsal internal moulds. (G–O) *Draborthis caelebs* Marek and Havlíček, 1967; (G, M) NIGP 169323, 169331, two ventral internal moulds; (H) NIGP 169324, dorsal internal mould of a juvenile shell; (I, N) NIGP 169325, 169326, two dorsal internal moulds; (J) NIGP 169327, latex cast of dorsal external mould; (K, L, O) NIGP 169328–169330, three dorsal external moulds. Scale bars represent 2 mm unless otherwise noted.

Fig. 21. (A–K) *Hirnantia sagittifera* (M’Coy, 1851); (A) NIGP 169332, ventral internal mould of a juvenile shell; (E, H, J, K) NIGP 169333–169336, four ventral internal moulds showing ventral muscle fields; (B–D, F, G) NIGP 169338–169342, five dorsal external moulds showing cardinalia of juvenile (B–D), adult (F) and gerontic (G) shells; (I) NIGP 169337, ventral external mould. (L–V) *Kinnella medlicotti* (Reed, 1915); (L, M, Q) NIGP 169343, ventral internal mould (L) with its lateral (M) and posterior (Q) views; (N, O) NIGP 169344, 169345, two ventral internal moulds; (P) NIGP 169346, lateral view of a ventral internal mould; (R, S) NIGP 169347, dorsal internal mould (R) with its latex cast (S) showing cardinalia and median ridge; (T–V) NIGP 169348–169350, three dorsal internal moulds. Scale bars represent 2 mm unless otherwise noted.

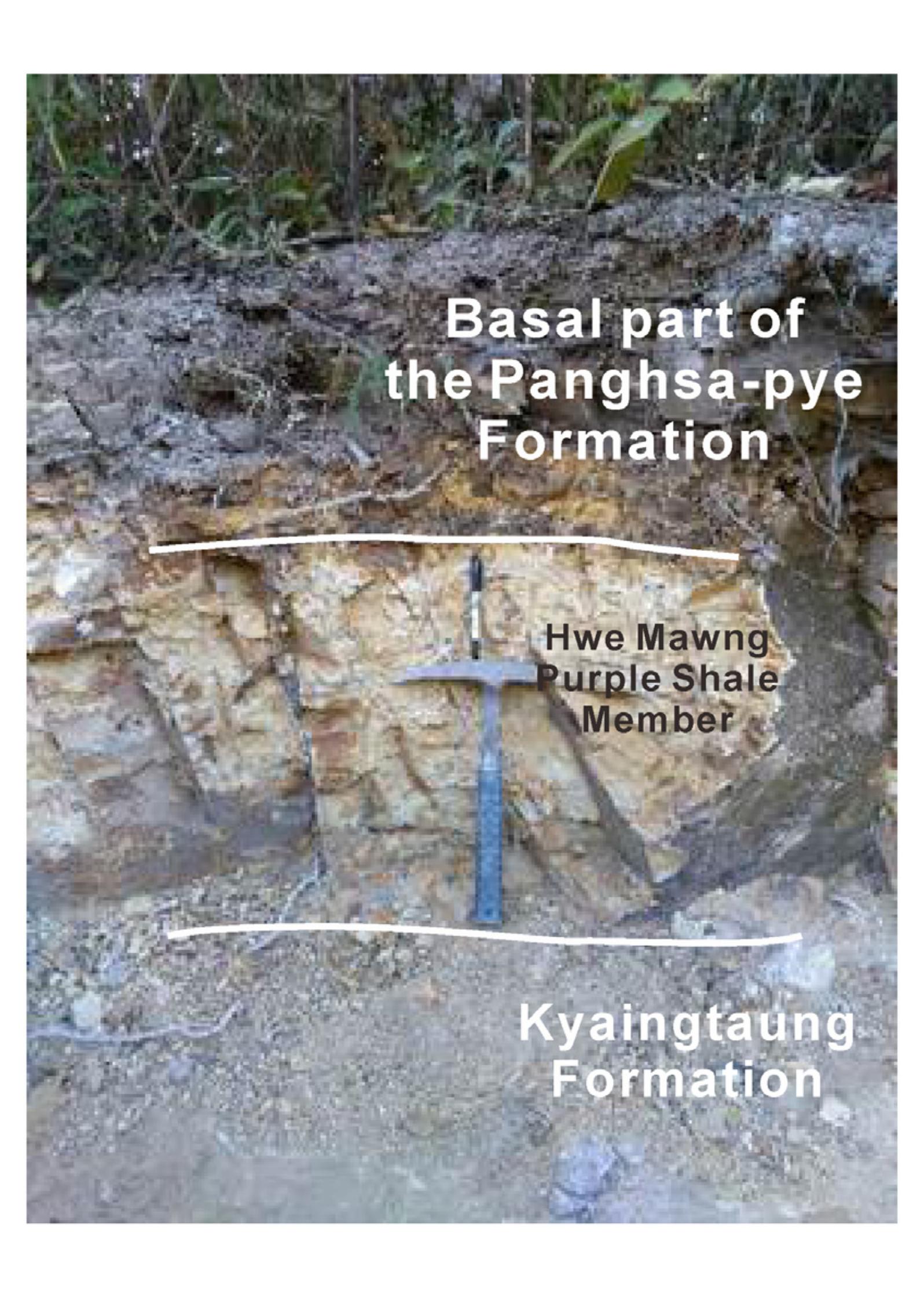
Fig. 22. Various angles of the pair of brachiophore supporting plates (abscissa axis) and number of individuals (ordinate axis) in 50 shells of *Kinnella medlicotti* measured from the specimens of Poland (Temple, 1965), Hubei, South China (Rong, 1984; Zeng et al., 2016), central Xizang (Rong and Xu, 1987), and Myanmar (Cocks and Fortey, 2002; this paper).

Fig. 23. (A–F) *Plectothyrella crassicostis* (Dalman, 1828); (A) NIGP 169351, internal mould of a juvenile adult shell (broken anteriorly); (B, D) NIGP 169352, ventral (B) and dorsal (D) views of internal mould of an adult shell (broken anteriorly); (C, E) NIGP 169353, 169354, dorsal (C) and ventral (E) internal moulds of juvenile shells; (F) NIGP 169355, dorsal internal mould. (G, H) *Hindella crassa* (Sowerby, 1839), NIGP 169356, 169357, two ventral

internal moulds. Scale bars represent 2 mm unless otherwise noted.



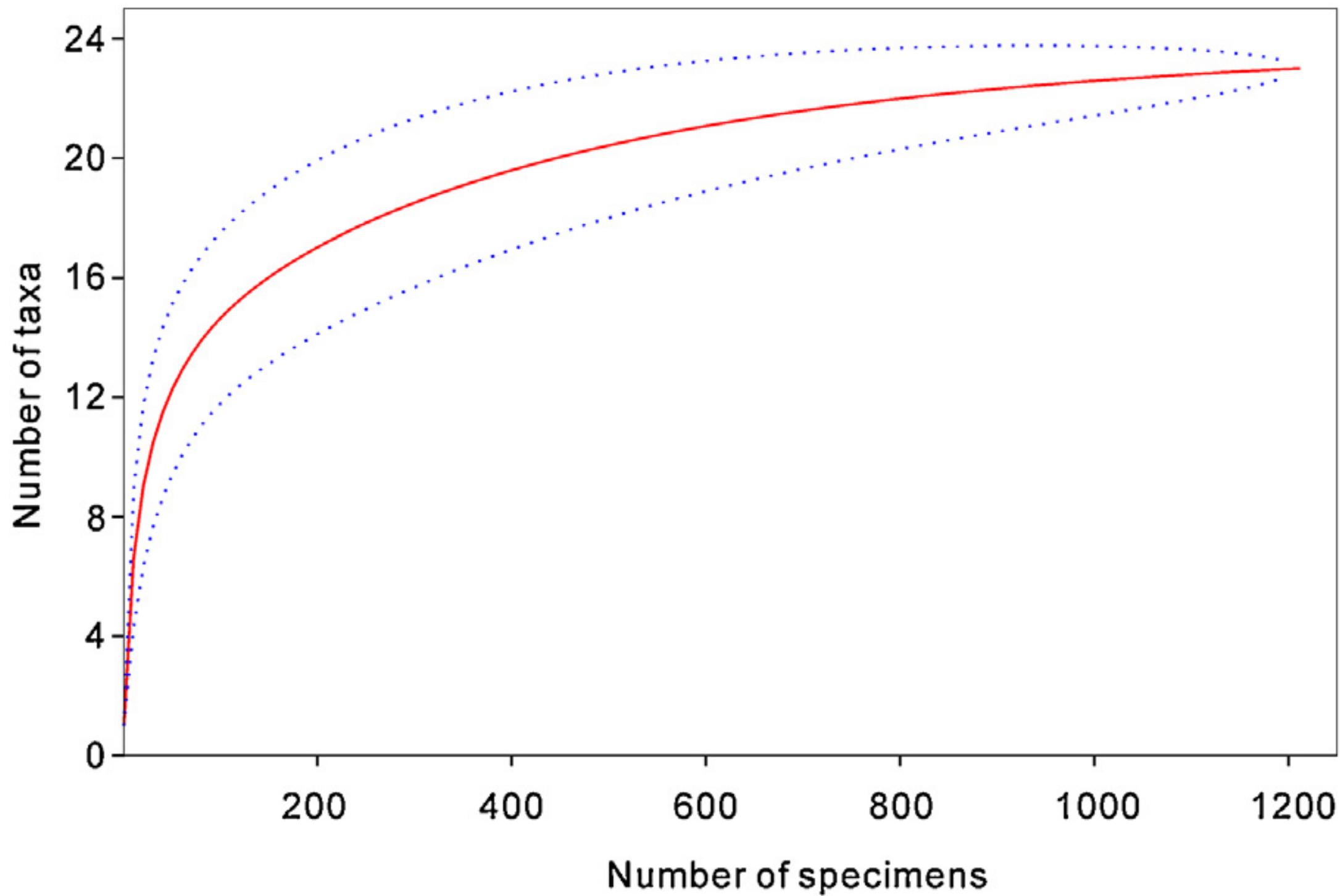
Chronostratigraphy			Pa-Thin, Pyin Oo Lwin Mandalay Region	Northern Shan State	Southern Shan State	
Silurian	Llandovery	Aeronian	Panghsa-pye Formation	Nyaungbaw Formation including Panghsa-pye graptolitic shale	Mibayataung Group	Linwe Formation including Wabya graptolitic shale
		Rhuddanian				
Ordovician	Upper	Hirnantian	Naungkangyi Group	Hwe Mawng Purple Shale Member	Pindaya Group	Tanshauk Member
		Katian		Kyaingtaung Formation		Kunlein Formation

A photograph of a geological outcrop showing a distinct layer of purple shale. A blue geological hammer is placed vertically against the rock face for scale. The rock above the hammer is a reddish-brown color, and the rock below is a greyish-brown color. The purple shale layer is in the middle, showing some fracturing. The background shows some green foliage.

**Basal part of  
the Panghsa-pye  
Formation**

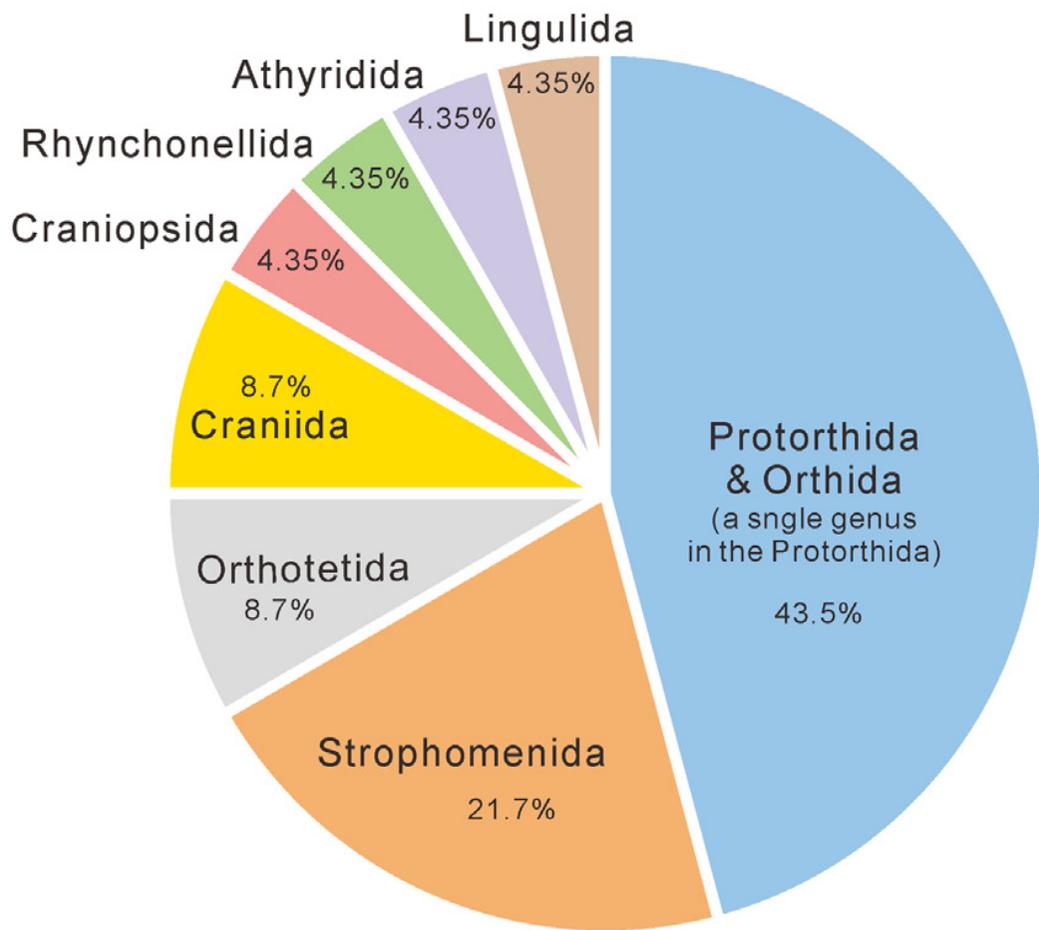
**Hwe Mawng  
Purple Shale  
Member**

**Kyaingtaung  
Formation**

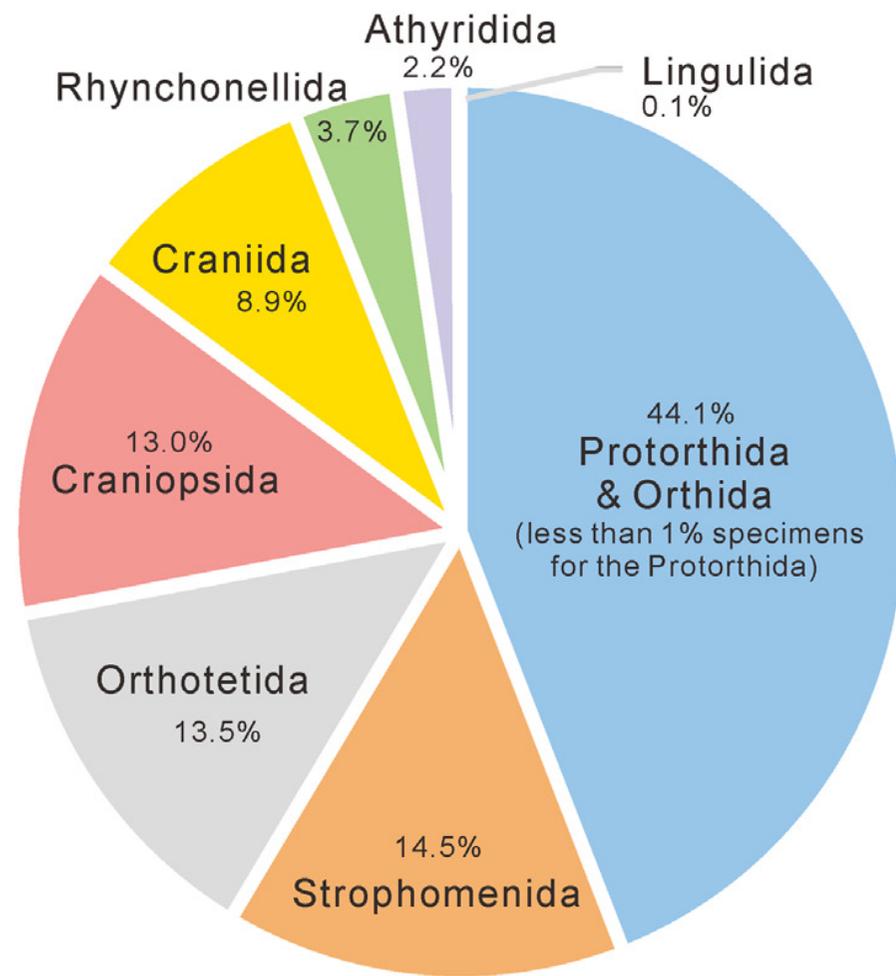


Palaeoplates or terranes Taxon		Sibumasu				Lhasa	S China	Kazakh.	Perunica	Occurrence	
		Myanmar		Thailand	W Yunnan	Xainza	Yichang	Chu-Ili	Prague		
		Northern Shan State	Mandalay, Region	③	④	⑤	⑥	⑦	⑧		
Order	Genus	①	②								
Lingulida	5	<i>Pseudolingula?</i>		●						1	
		<i>Rafanoglossa</i>							●	1	
		<i>Schizotretina</i>						●		●	2
		<i>Tethyrete</i>								●	1
		<i>Orbiculoidea</i>						●	●	●	3
Craniopsida	2	<i>Paracraniops</i>	○					●		2	
		<i>Pseudopholidops</i>		◆		●		◆		●	4
Craniida	2	<i>Xenocrania</i>	○	●		●		●		●	5
		<i>Petrocrania</i>		●		●				●	3
Strophomenida	9	<i>Minutomena</i>		●				●			2
		<i>Leptaena</i>		●		●	●	●	●	◆	6
		<i>Paromalomena</i>	○	◆	●	●	◆	◆	●	●	8
		<i>Eostropheodonta</i>	○	●		●	●	◆	◆	◆	7
		<i>Palaeoleptostrophia</i>				●					1
		<i>Anisopleurella</i>				◆			●		2
		<i>Aegiromena</i>	○	●	◆	◆	●	●	●	●	8
		<i>Eoplectodonta</i>							●		1
		<i>Rugosowerbyella</i>							●		1
Orthotetida	5	<i>Fardenia (Coolinia)</i>	○	◆		◆		●	●	●	6
		<i>Cliftonia</i>		●	●	●	◆	●	●	◆	7
		<i>Triplexia</i>	○		●			●	●		4
		<i>Onychoplecia</i>						●			1
		<i>Streptis</i>							●		1
Protorthida	1	<i>Skenidioides</i>		●		●				2	
Orthida	16	<i>Dolerorthis</i>				●					1
		<i>Giraldibella</i>		●		●			●	●	4
		<i>Comatopoma</i>								●	1
		<i>Toxorthis</i>		●		●		●			3
		<i>Templeella</i>				●			●		2
		<i>Dalmanella</i>	○	◆		◆	●	◆	◆	◆	7
		<i>Onniella</i>			●			●		●	3
		<i>Levenea</i>		●				●			2
		<i>Mirorthis</i>		●	●			●		●	4
		<i>Trucizetina</i>		●				●		●	3
		<i>Drabovinella</i>						●		●	2
		<i>Kinnella</i>	○	◆		●	◆	◆		◆	6
		<i>Himantia</i>		●	●	●	◆	◆	●	◆	7
		<i>Draborthis</i>		●		●		●		◆	4
		<i>Dysprosorthis</i>					●	●			2
		<i>Ravozetina</i>								●	1
Rhynchonellida	3	<i>Plectothyrella</i>		●		●	●	●	◆	5	
		<i>Sphenotreta</i>						●	●	2	
		<i>Dorytreta</i>						●		1	
Atrypida	1	<i>Eospirigerina</i>				●			1		
Athyridida	1	<i>Hindella</i>	○	●		●		●	5		
Total	45		10	23	7	22	11	29	17	26	

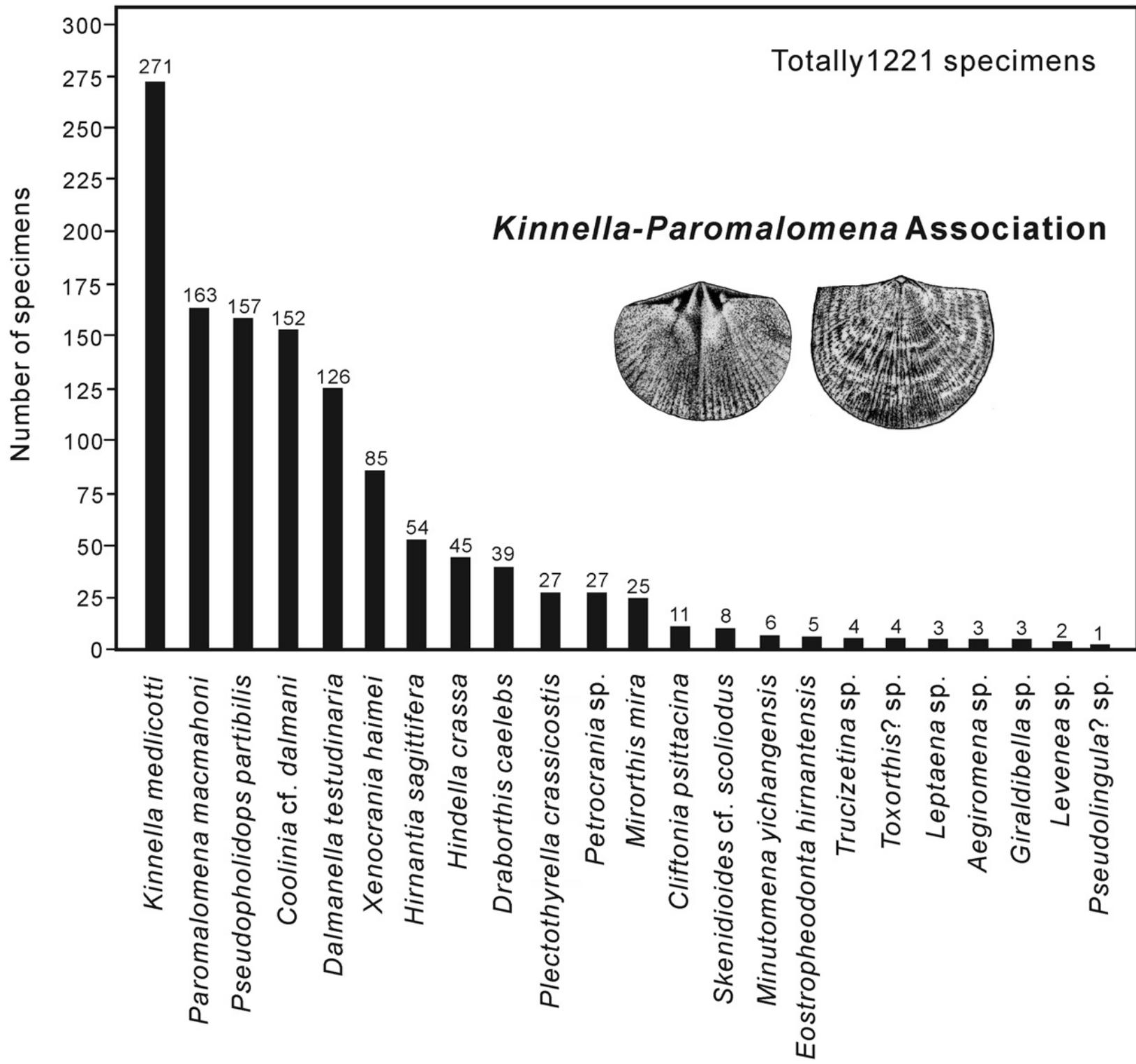
◆ most abundant    ◆ common    ● rare    ○ present

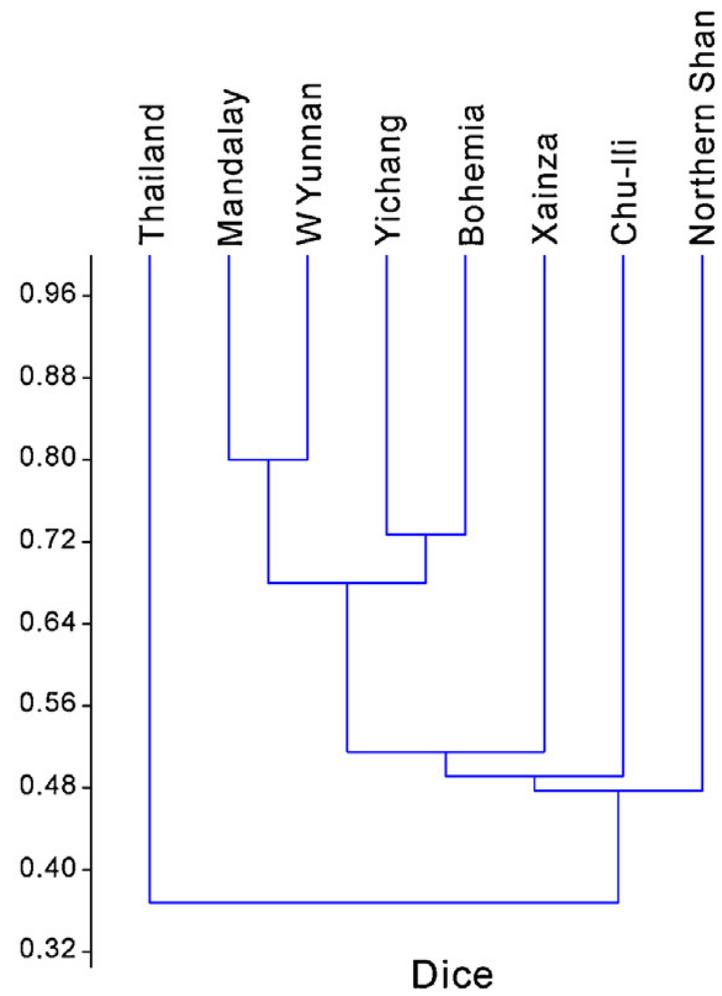
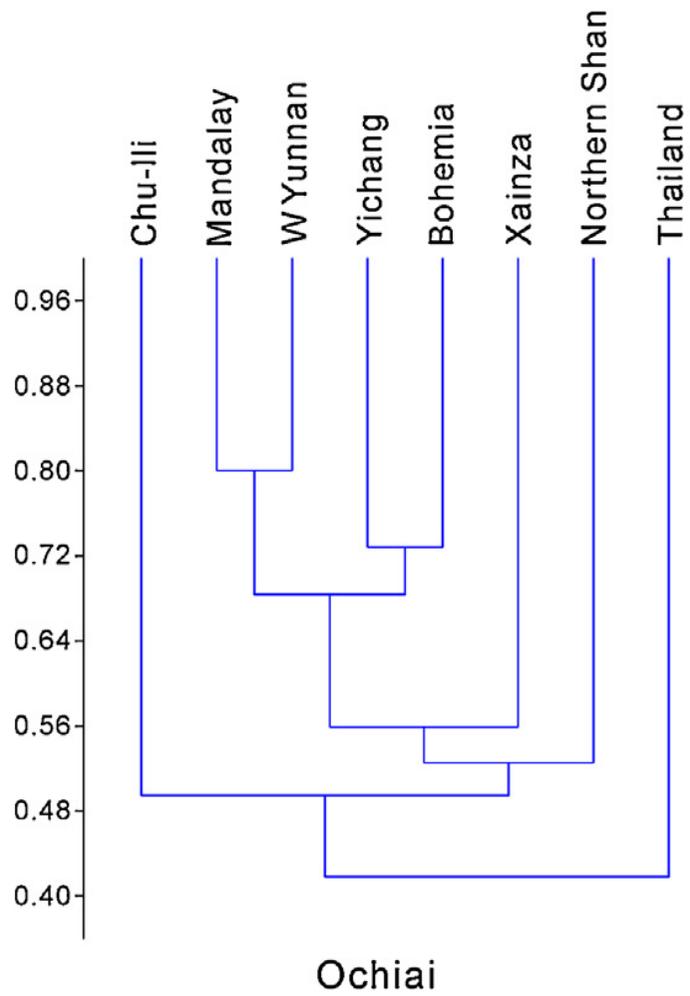
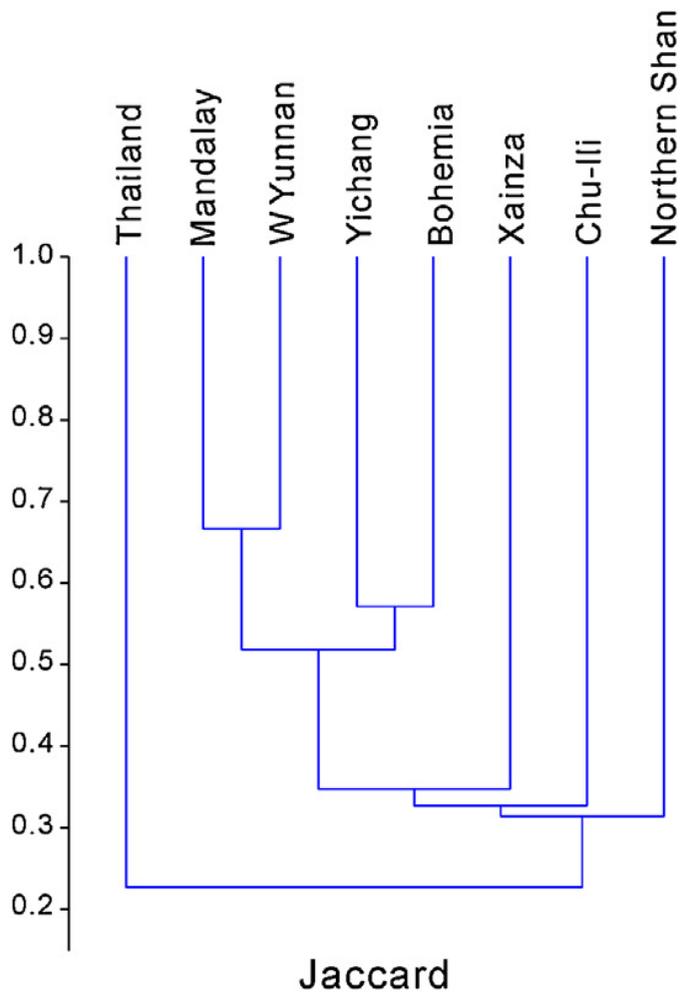


Diversity



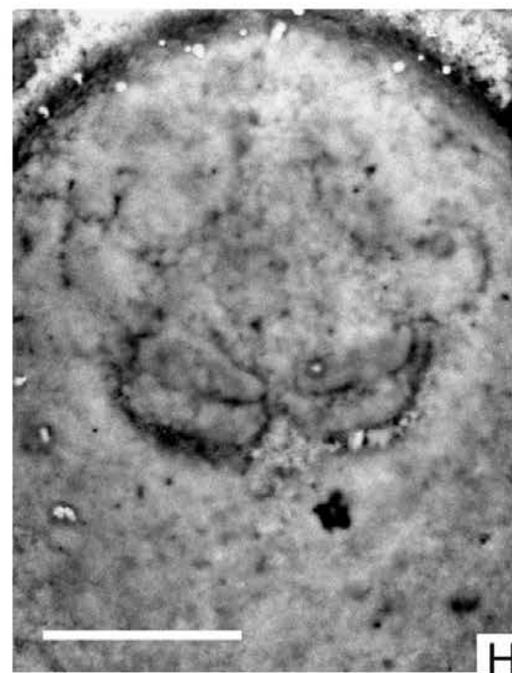
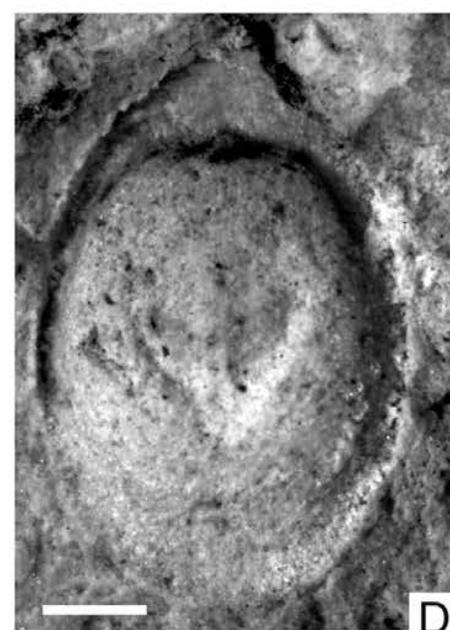
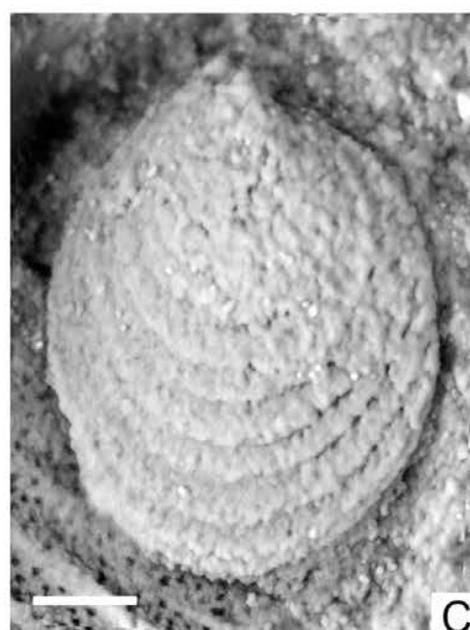
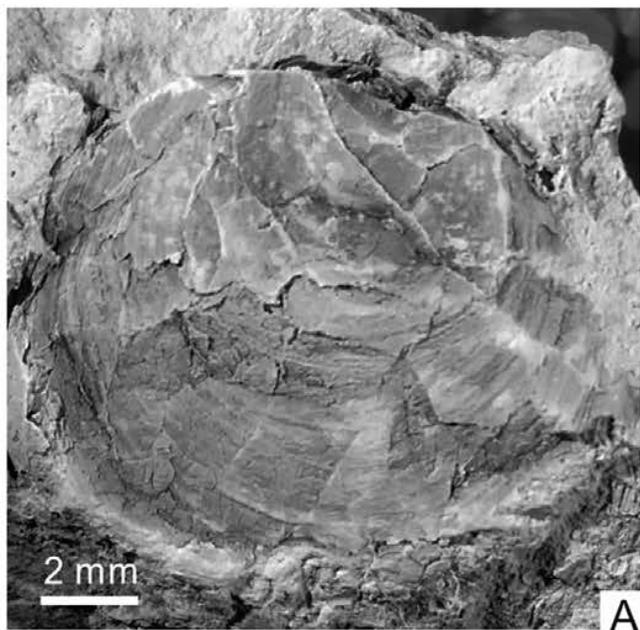
Abundance

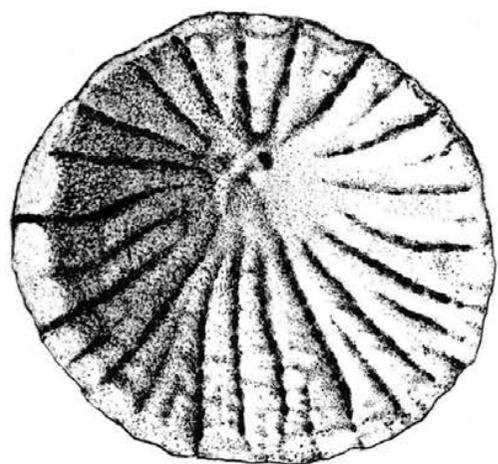




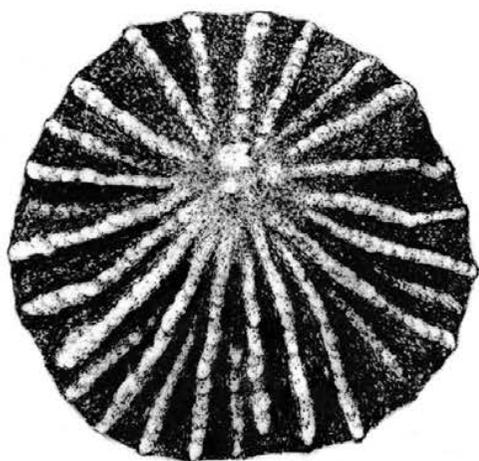


Chrono-stratigraphy			South China		Sibumasu		
					W Yunnan	Myanmar	Thailand
Silurian	Llandov.	Rhuddanian	<i>Cathaysiorthis</i> Fauna BA2-3	Graptolitic facies	Graptolitic facies		Graptolitic facies
		Hirnantian			<i>Aegiomenella</i> BA4-5 <i>Rhynchotrema</i> BA2-3	<i>Hirnantia</i> Fauna BA2-3	
Ordovician	Upper	Katian	<i>Altaethyrella</i> Fauna BA2-3	Graptolitic facies	<i>Foliomena</i> Fauna BA5	<i>Foliomena</i> Fauna BA5	<i>Foliomena</i> Fauna BA5  Graptolitic facies
		Sandbian	<i>Foliomena</i> Fauna BA5				
		Darriwilian	<i>Saucrorthis</i> Fauna mostly BA3		<i>Saucrorthis</i> Fauna mostly BA3	<i>Saucrorthis</i> Fauna mostly BA3	
	Dapingian	<i>Martellia-Yangtzeella</i> Fauna BA2-3					
	Low.	Floian	<i>Sinorthis</i> Fauna BA3				

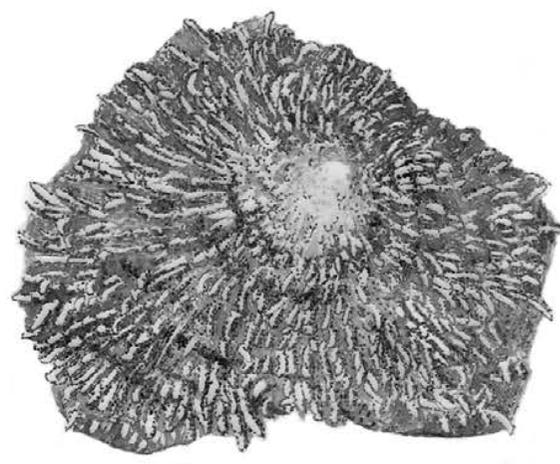




A



B

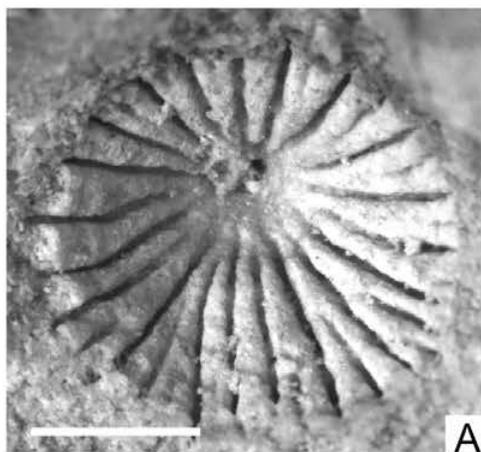


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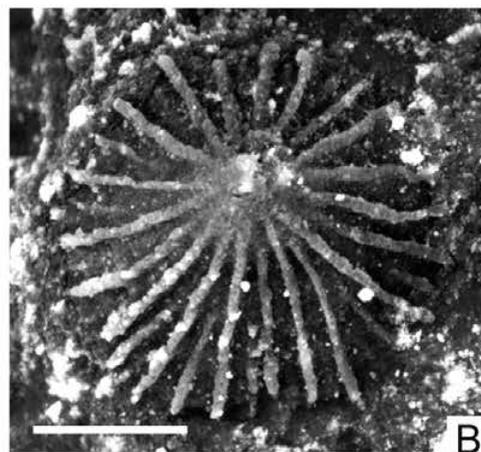


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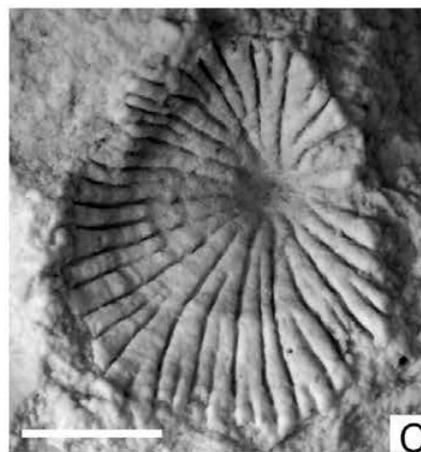




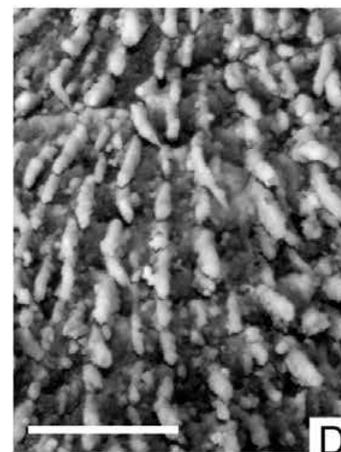
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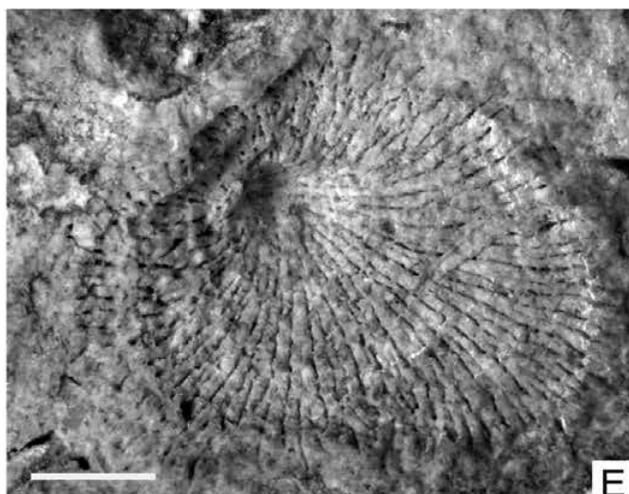
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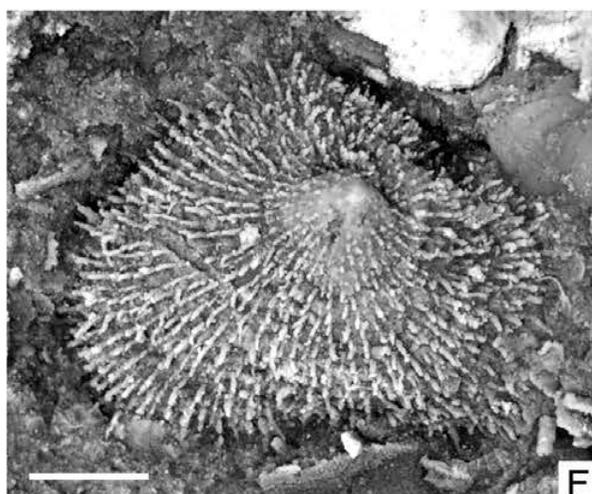
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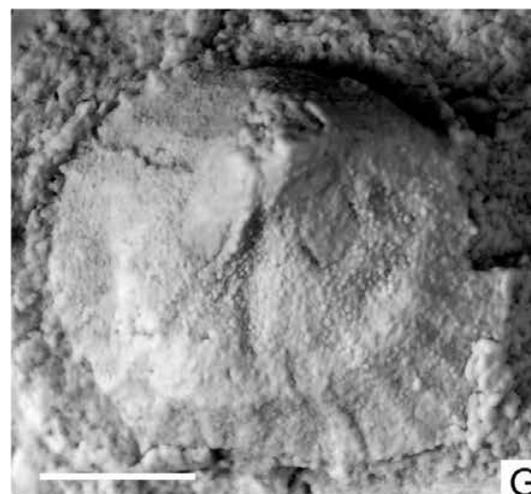
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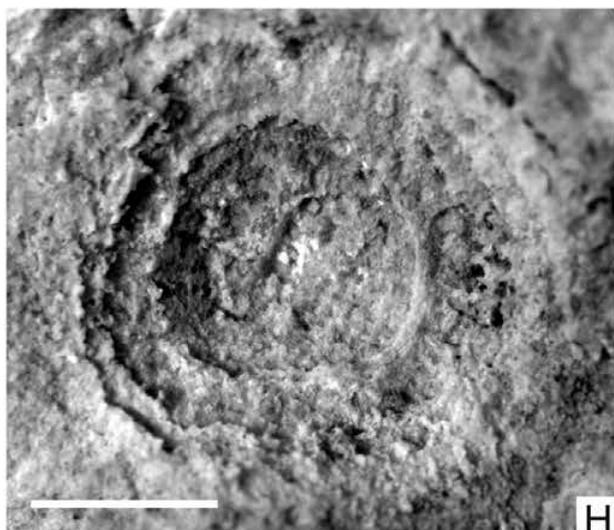
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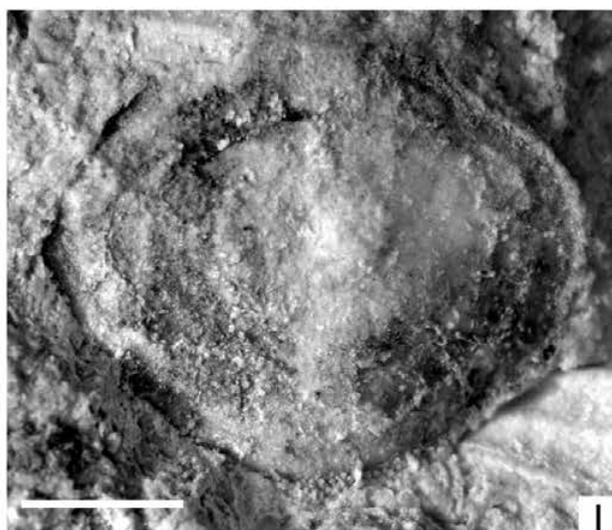
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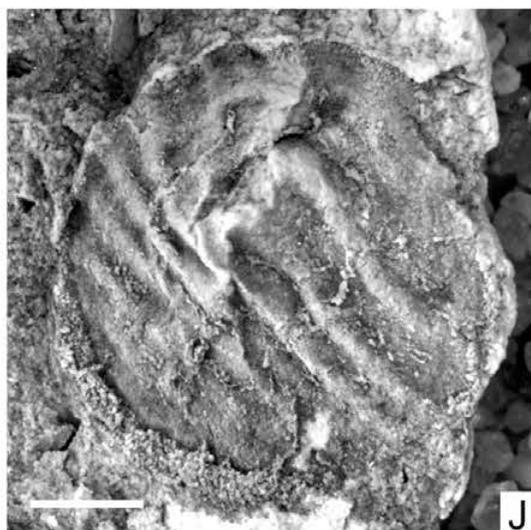
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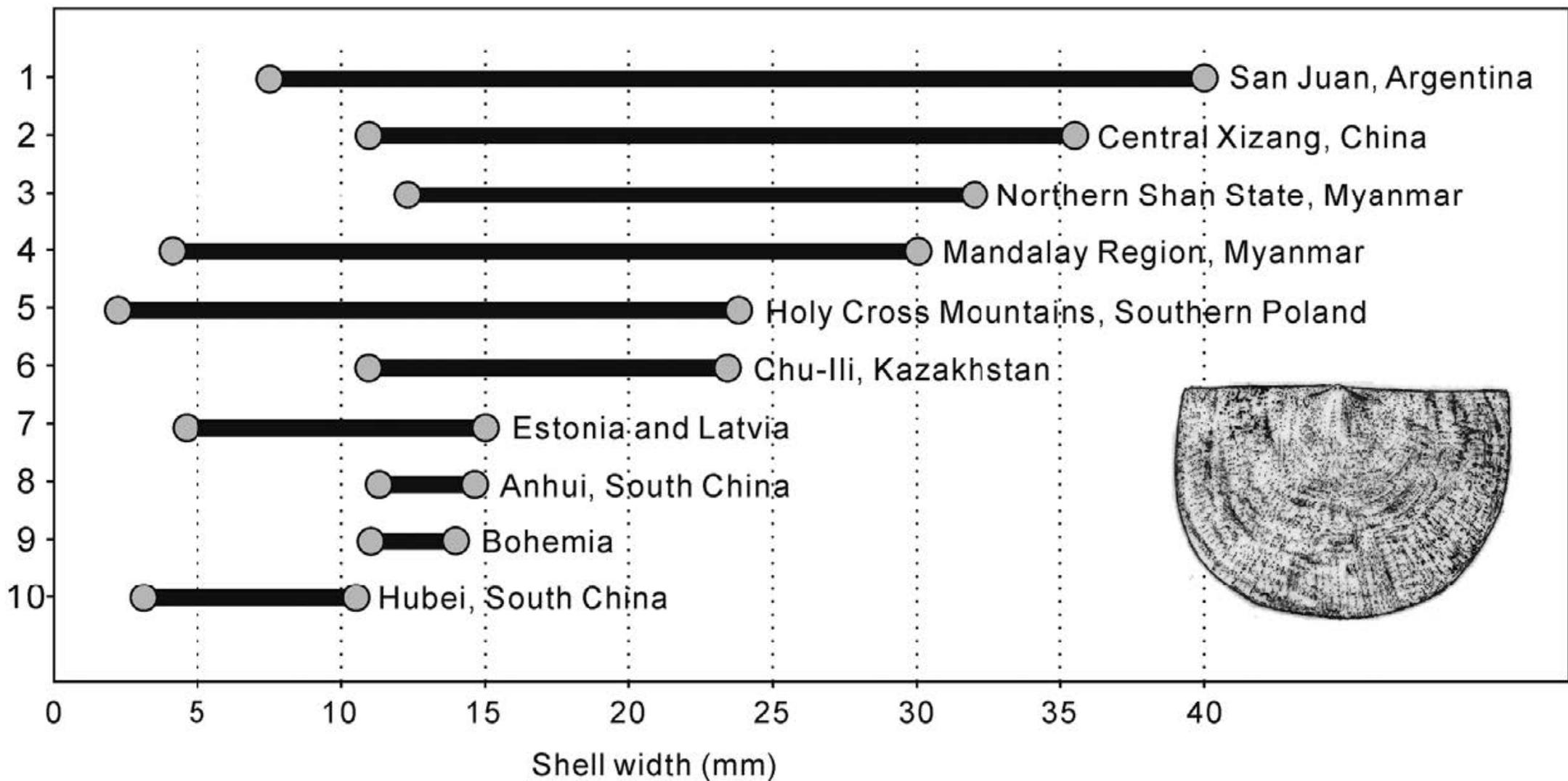
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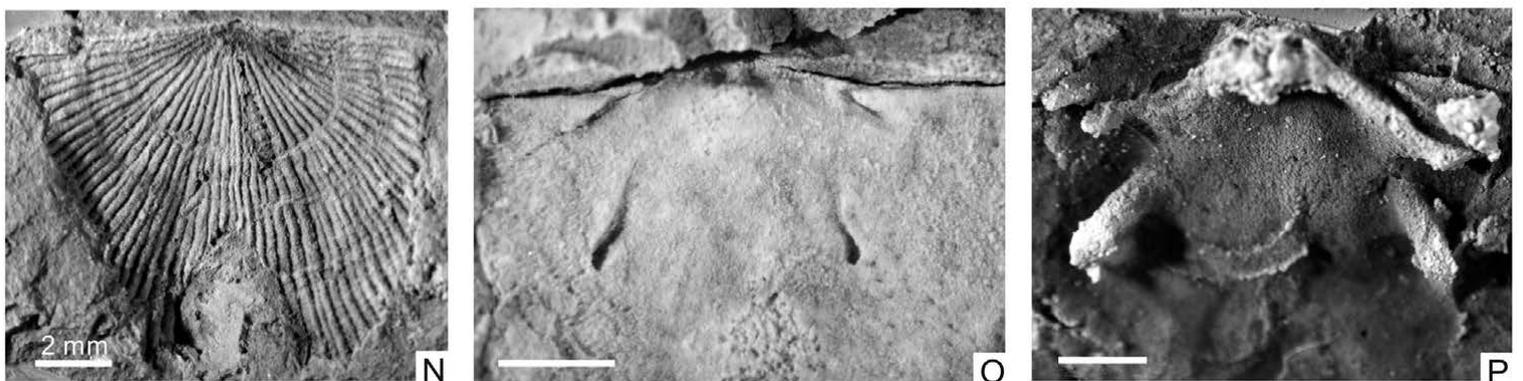
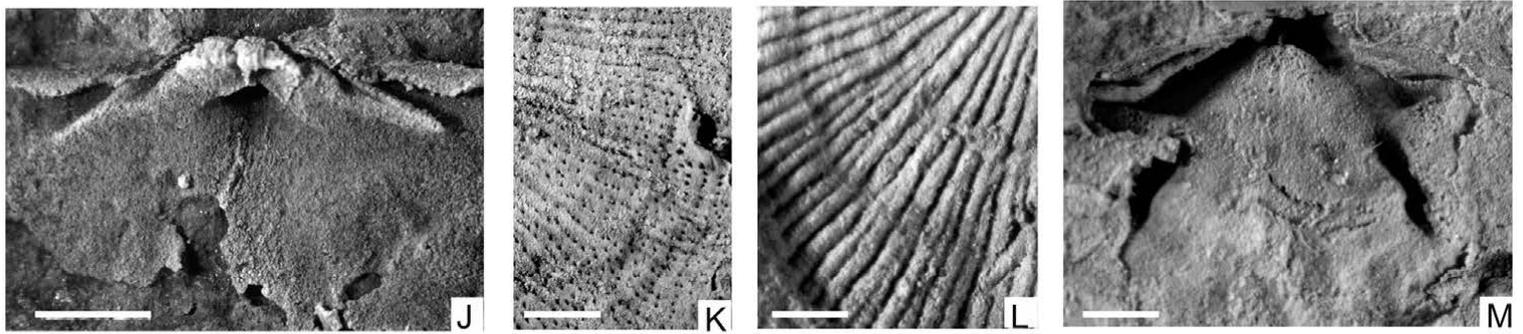
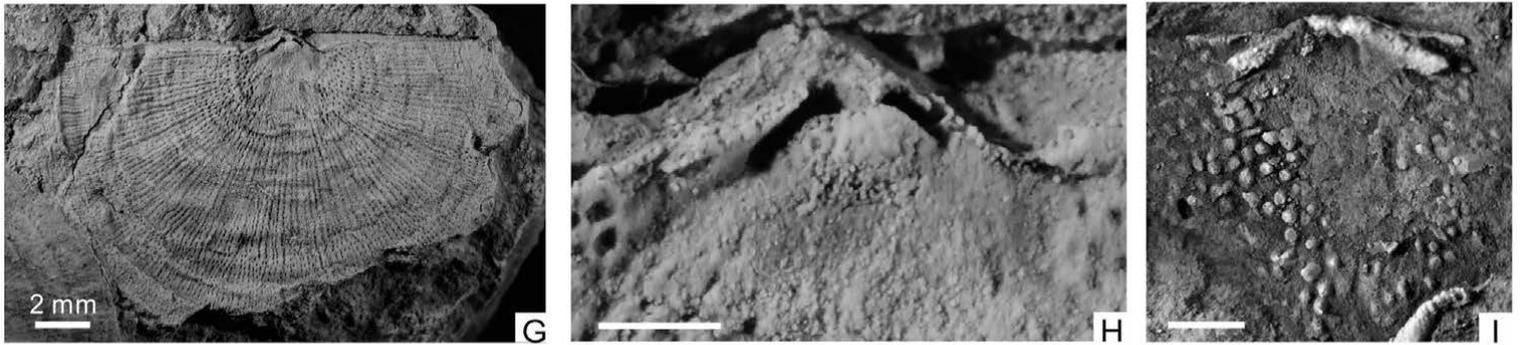
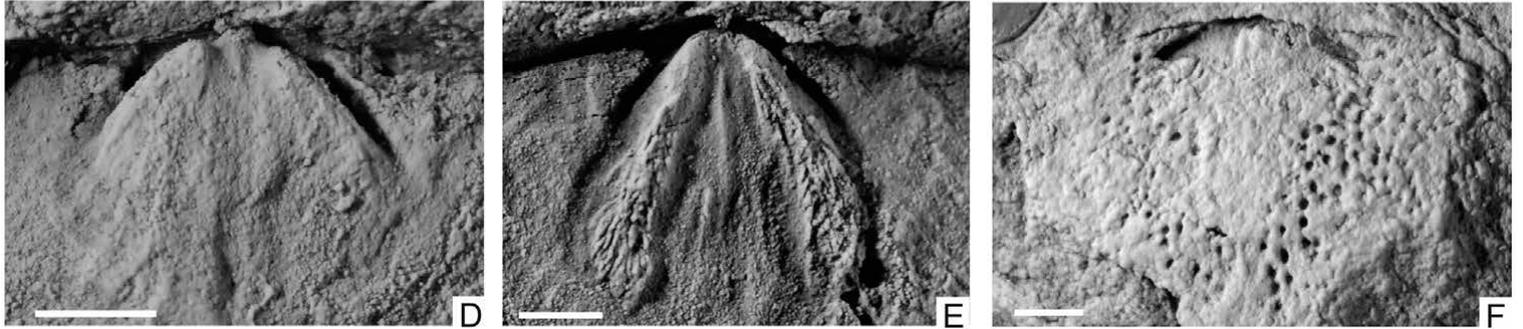
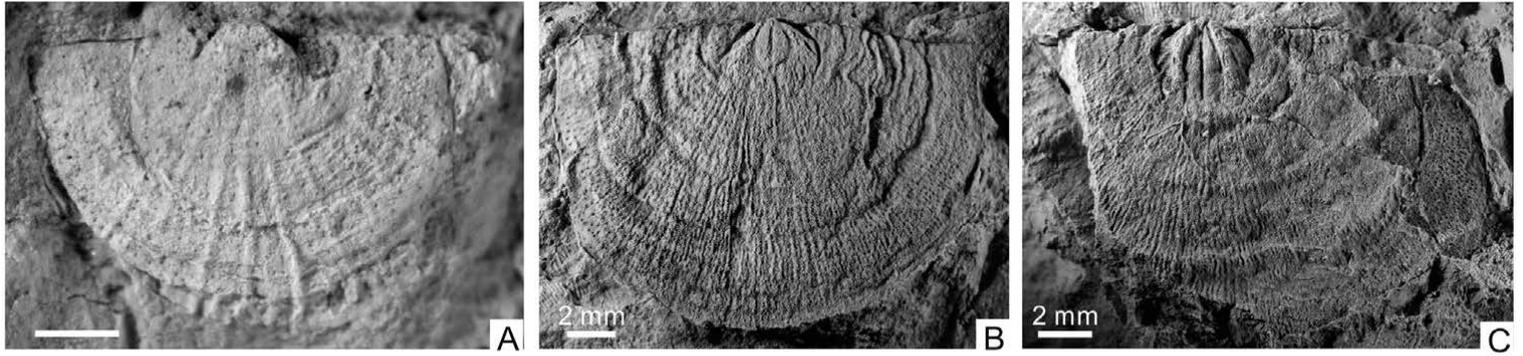


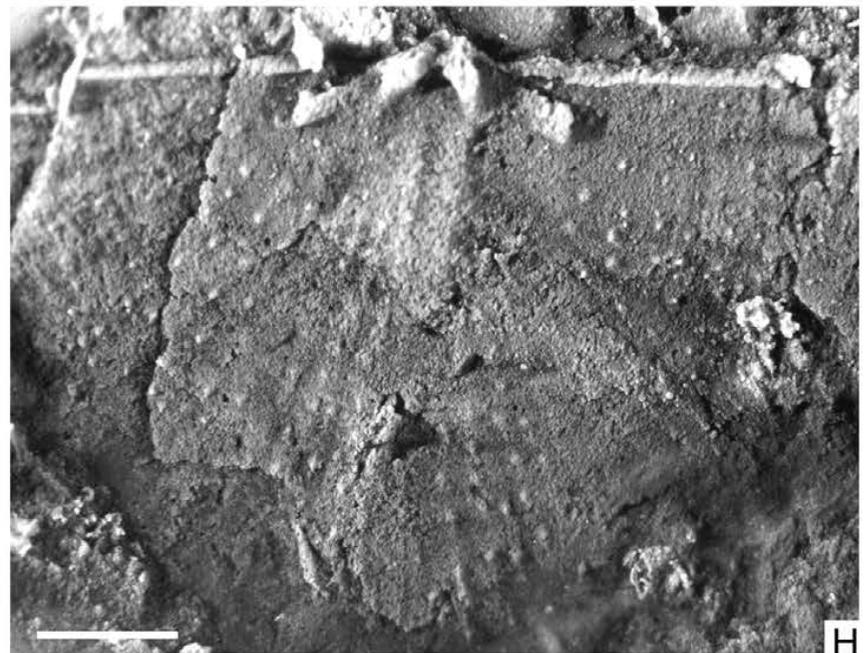
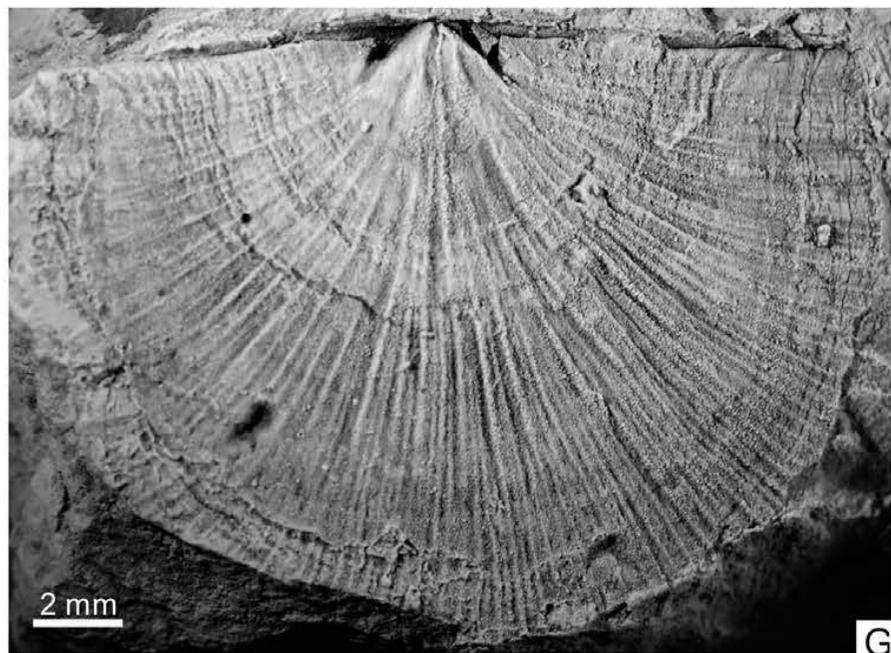
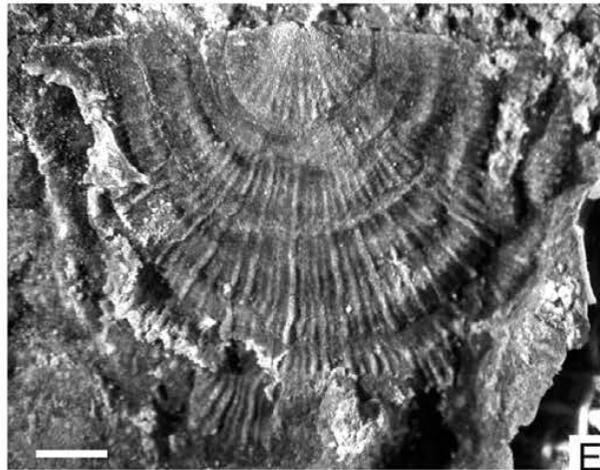
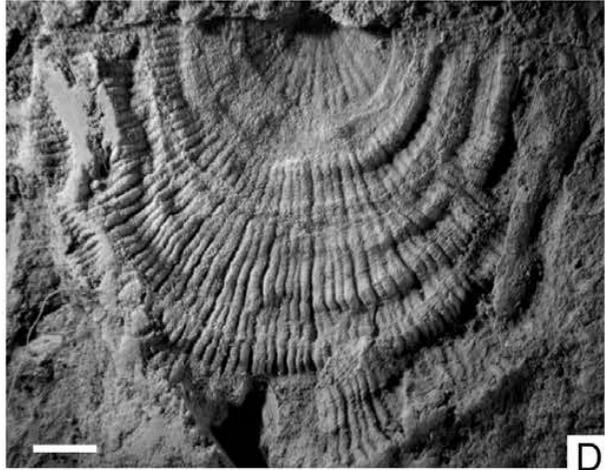
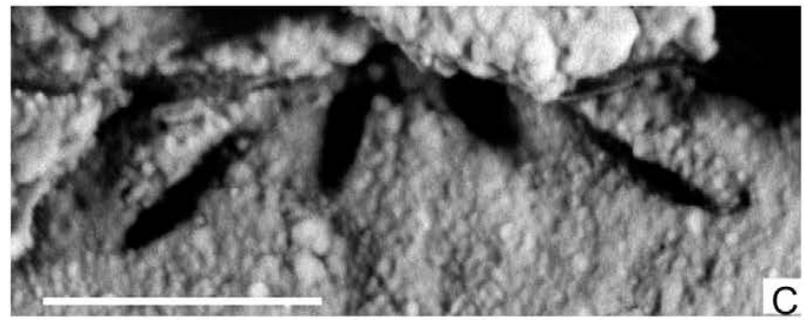
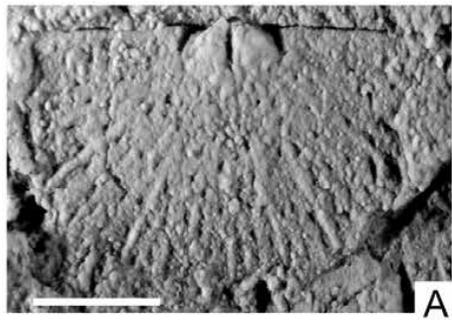
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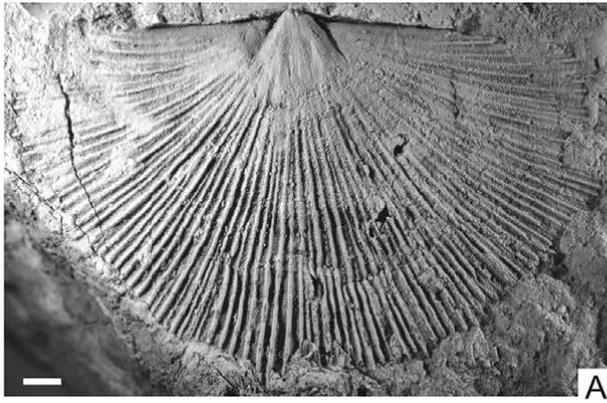


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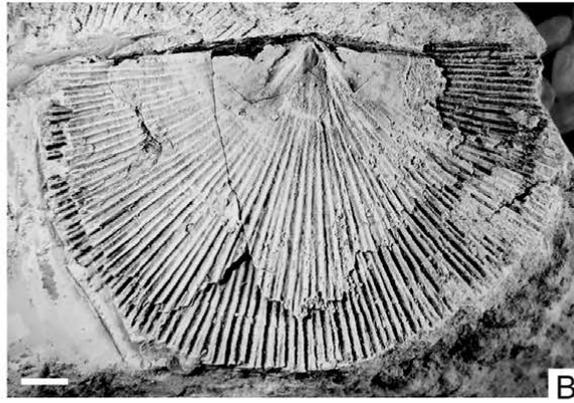




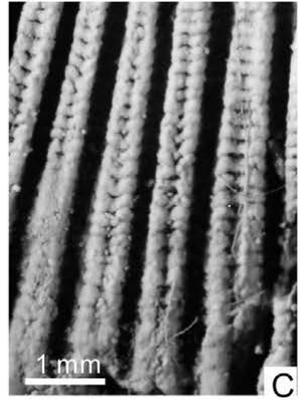




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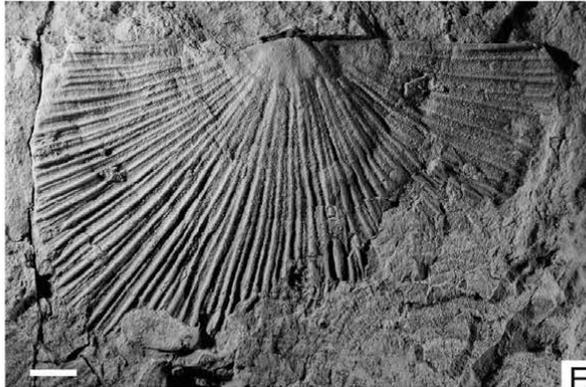
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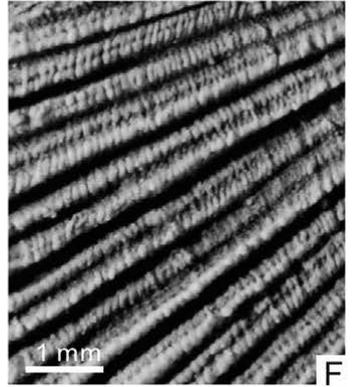
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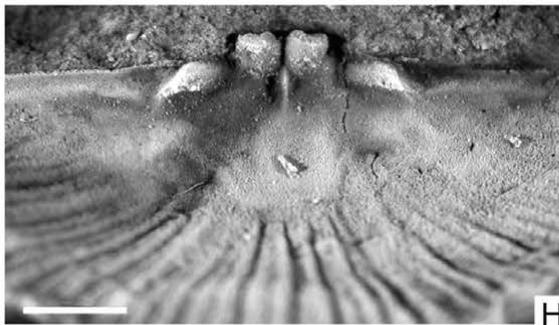
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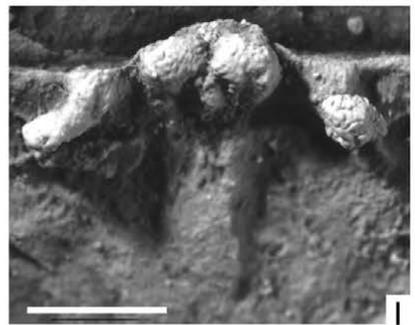
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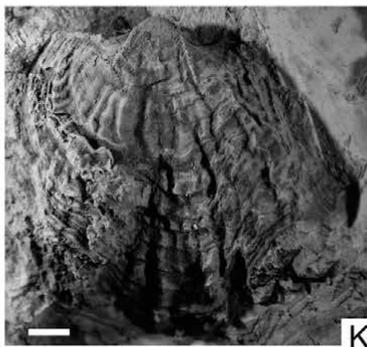
H



I



J



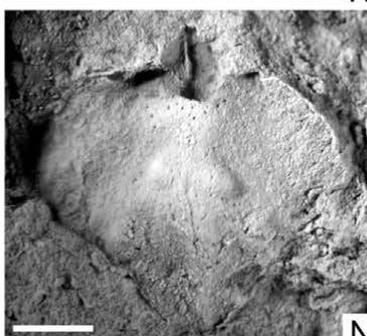
K



L



M



N



O

