REVISION OF THE ATHYRISININAE, SILURO-DEVONIAN BRACHIOPODS FROM CHINA AND RUSSIA

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ABSTRACT. Athyrisinine brachiopods from the Upper Silurian of Russia and the Lower–Middle Devonian of China and north Vietnam include over 70 species belonging to *Athyrisina* and *Parathyrisina*; generic and subfamilial diagnoses are emended. Five genera are considered synonyms of *Athyrisina* and three of *Parathyrisina*. A neotype is selected and illustrated for *Athyrisina squamosa*, the type species of *Athyrisina*. Four *nomina nova*, *Athyrisina xui*, *Parathyrisina wani*, *P. minima*, and *P. cheni*, are suggested as new substitute names for *Athyrisina tumida* Wang, *in* Xu *et al.* 1978 (primary homonymy), *Athyrisinoides ganxiensis* Wan, *in* Xu *et al.* 1978, *Parathyrisina minor* Zhang, *in* Zhang and Fu 1983, and *Athyrisinoides tudilingensis* Chen, 1979 (secondary homonyms) respectively. A new genus, *Bruntosina*, is described from the Emsian to Eifelian of the Qinling region. A new subfamily, Homeathyridinae, is erected within the Athyrididae with *Homeathyris*, *Pseudohomeospira*, and *Squamathyris* included, revised and their diagnoses emended. *Homeathyris incisus* sp. nov. is described from the Ludfordian of Novaya Zemlya. *Ikella* is revised and excluded from the athyrisinins. The origin and dispersal of the homeathyridins and the athyrisinins are discussed.

KEY WORDS: brachiopods, athyrisinins, Homeathyridinae, *Bruntosina*, Siluro-Devonian, China, Russia, Vietnam.

DURING the process of reviewing brachiopod genera and their contained species for the athyridide section of the revised edition of the Treatise on Invertebrate Paleontology (part H, Brachiopoda) we encountered (Alvarez and Rong 2002) the problem of classifying the athyridide brachiopods commonly included within the athyrisinins (Alvarez and Carlson 1998; Alvarez *et al*. 1998). This was mainly due to their variable external morphology, with abundant intermediate forms (in shape and radial ornamentation) between what one would suppose to be different species or even genera. A more serious problem was the lack of knowledge of the internal structures, such as cardinalia and brachio-jugal system, of many of the athyrisinine species. Consequently, specific discrimination has always been difficult, and authors have shown wide differences of opinion as to where the limits of species should be drawn.

The athyridide brachiopod subfamily Athyrisininae, as here reviewed, is made up of *Athyrisina* Hayasaka, *in* Yabe and Hayasaka 1920, and allied genera, but follows Rong *et al*. (1994; see also Alvarez *et al*. 1998; Alvarez and Rong 2002) in excluding *Retziella* Nikiforova, 1937, and related genera, which some authors (e.g. Boucot *et al.* 1965) included. *Athyrisina* Hayasaka, *in* Yabe and Hayasaka 1920, is among the earliest known brachiopod genera based on Chinese specimens. It ranges from late Pragian–Givetian, being abundant in Emsian–Eifelian rocks in southern and north-western China and north Vietnam (Duong 1980). Since the subfamily Athyrisininae was instituted by Grabau (1931), several new genera were erected and assigned to it. Among them, *Athyrisinopsis* Zhang, *in* Zhang and Fu 1983; *Kwangsia* Grabau, 1931; *Kwangsiella* Grabau, 1932; *Plectospirifer* Grabau, 1931; and *Pseudoathyrisina* Chen, 1979 have been considered, but without discussion, by Alvarez *et al*. (1998) as subjective junior synonyms of the genus *Athyrisina* Hayasaka, *in* Yabe and Hayasaka 1920. *Parathyrisina* Wang, *in* Wang, Yu and Wu 1974 is closely related to *Athyrisina*. The main differences between these two genera, together with the synonymous relationships of *Parathyrisina* with *Athyrisinoides* Chen and Wan, *in* Xu *et al*. 1978 (*non Athyrisinoides* Jiang, *in* Xian and Jiang 1978), *Athyrisinoidea* Chen and Wan, *in* Wan 1980, and *Neoathyrisina* Chen, 1988, are discussed below. A new genus, *Bruntosina*, is erected and illustrated with

Athyrisinopsis gansuensis Zhang, *in* Zhang and Fu 1983, from the upper Lower Devonian (upper Emsian) to lower Middle Devonian (lower Eifelian) of the Qinling region (north-west China) as the type species. This genus is characterized by two or three strong, non-bifurcating plicae on the flanks of the shell and a single, narrower median costa in the ventral sulcus.

Three genera, *Homeathyris* Modzalevskaya, 1997, *Pseudohomeospira* Nikiforova, 1970, and *Squamathyris* Modzalevskaya, 1981, from the Upper Silurian of northern Russia, were commonly considered athyrisinins (e.g. Nikiforova 1970; Modzalevskaya 1981, 1994, 1997*a*, *b*; Grunt 1984, 1986; Alvarez *et al*. 1998; Alvarez and Rong 2002). The revision undertaken here shows that these Silurian genera commonly have a hypothyridid pedicle opening partially closed by deltidial plates, and a large delthyrial chamber with a pedicle support consisting of pedicle collar (*Pseudohomeospira*) or two apical plates (the 'pedicle fulcrum' of Rubel and Modzalevskaya 1967; Modzalevskaya 1985) situated between the dental plates and joined with them at their posterodorsal end (*Homeathyris* and *Squamathyris*). These two characters together with a jugum with very short accessory lamellae has encouraged us to separate them into a new subfamily, the Homeathyridinae.

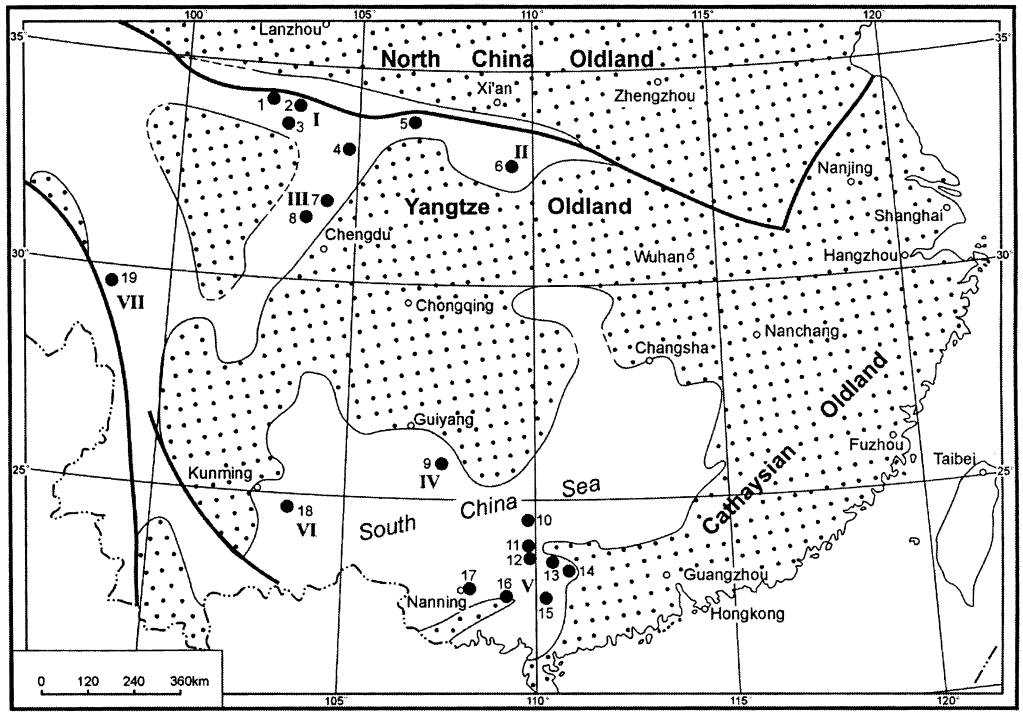
Ikella Tyazheva, 1972, from the upper Emsian–lower Eifelian (*patulus–partitus* conodont biozones) of the western slope of the southern Urals, was commonly considered an athyrisinin. *Ikella* has a weakly costate shell surface, without a sulcus and fold. The revision by one of us (TLM) of topotypical material shows that internally it has a wide, flat cardinal plate, not perforated apically and supported posteriorly by a very short ridge. These characters separate *Ikella* from the athyrisinins and homeathyridins. *Ikella* has external and internal similarities with the retziellids, ornamentation and cardinalia in particular, but the highly crystalline nature of the matrix has made examination of internal structures very difficult; the spiralium is not well known and jugal structures are still unknown, therefore the superfamilial and familial assignments of this genus should be regarded as provisional as Modzalevskaya and Alvarez interpret here while Rong, because of the cardinal shape of *Ikella* differing from that of *Retziella*, prefers to give no assignment to *Ikella*. This ambiguity should be resolved when non-recrystallized topotype specimens that will allow the study of these structures in *Ikella* and also in *Argorhynx*, *Ufonicoelia* and *Gissarina*, genera commonly included within the retzielloids, are found.

The taxonomic revision here shows that the Athyrisininae could be considered a significant biogeographical indicator for the recognition of the South China Province in the Early and Mid Devonian (Hou and Xian 1975; Wang and Zhu 1979; Wang *et al*. 1984; Wang and Rong 1986; Wang *et al*. 1987; Talent *et al*. 2001). Geological significance of the stratigraphical and biogeographical distributions of the Athyrisininae and Homeathyridinae is evaluated in terms of new investigations on these endemic groups (Text-figs 1–4).

The specimens studied in this paper are from different sources. Besides the collections housed in our own institutions, Russian colleagues from the Institute of Geology of the Ufa Scientific Centre of the Russian Academy of Sciences have kindly provided *Ikella* topotypes and other brachiopods from the Southern Urals. The possible topotype specimens (see discussion in Chen and Li 1994) of *Athyrisina squamosa* Hayasaka, holotypes of *Parathyrisina typica* and other species of *Parathyrisina* from the Longmenshan region, northern Sichuan (Text-fig. 1) were kindly provided by the late Chen Yuan-ren who collected them in the 1970s and 1990s. All specimens of *Bruntosina gansuensis*, and related species, from the Tewo-Luqu and Xunyang area (west and east Qinling respectively; Text-fig. 1) were collected by the Research Working Group of the Xi'an Institute of Geology and Mineral Resources and the First Geological Team of Gansu Province in the 1970s. One of us (ZY) took part in these trips and collected most of these brachiopods.

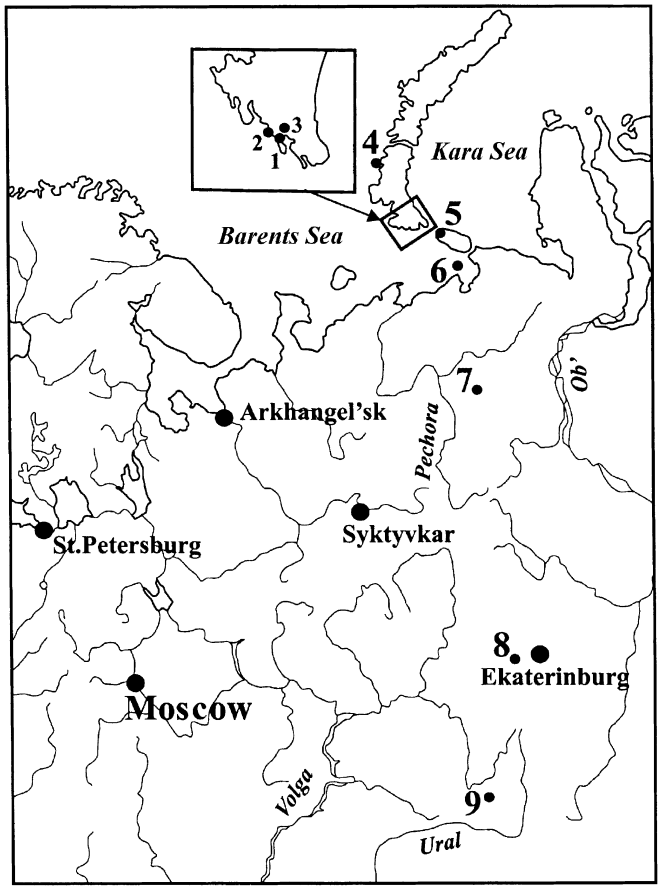
HISTORICAL REVIEW

Hayasaka (*in* Yabe and Hayasaka 1920, p. 176) erected the genus *Athyrisina* based on the type species, *Athyrisina squamosa* Hayasaka, *in* Yabe and Hayasaka 1920, from the Middle Devonian rocks of Sichuan Province. This author included within the genus *Athyrisina*, two more species: *Athyrisina minor* Hayasaka, *in* Yabe and Hayasaka 1920, and *Athyrisina squamosa* var. *rhomboidalis* Hayasaka, 1922. *A. minor* was believed to be from the Middle Devonian rocks in Kwanghsi (now spelled Guangxi) Province (Hayasaka



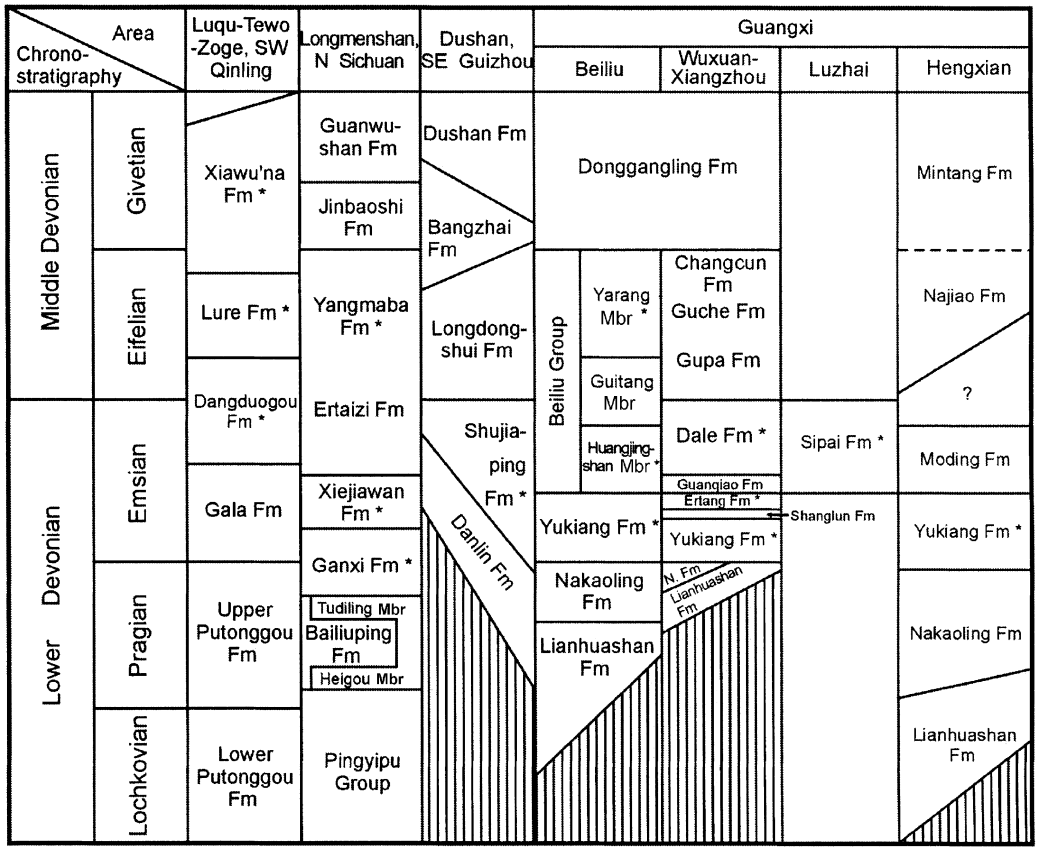
TEXT-FIG. 1. Occurrence of athyrisinids in South China. 1, Dangduo Formation (Emsian–Eifelian), Chakuohe, Luqu, south-eastern Gansu; 2, Dangduo Formation (late Emsian–early Eifelian, Xigeershan, Zorge, north-western Sichuan; 3, Dangduo Formation (late Emsian–early Eifelian), Dangduogou, Tewo, south-eastern Gansu; 4, Xigou Formation (Pragian–Emsian) and Minbaogou Formation (Emsian–Eifelian), Minbaogou, Wenxian, south-eastern Gansu; 5, 'Gudaoling Formation' (Eifelian), Changping, Wafangba, Fengxian, western Shaanxi; 6, Shijiagou Formation (Emsian–Eifelian), Gongguan, Dacigou, Fenzigou, Dangjiagou, Xunyang, eastern Shaanxi; 7, Yangmaba Formation in the Shuimogou Group (Emsian–Eifelian), Heitupo, Shuimo, Wenchuan, northern Sichuan; the type specimens of the type species of *Athyrisina* probably came from this locality, rather than from Pen-chao-tzu (Pianchiaozi), Chao-hua-hsien (Zhaohua County) as recorded by Hayasaka (*in* Yabe and Hayasaka 1920); 8, Bailiuping and Ganxi formations (Pragian–Emsian), Ganxi, and Xiejiawan Formation (Emsian), Yiyangdong, Beichuan, northern Sichuan; 9, Houershan Formation (Middle Devonian), Shujiaping, Houershan, Dushan, south-eastern Guizhou; 10, Sipai Formation (late Emsian), Luma, Sipai, Luzhai, Guangxi; 11, Yuchiang Formation (early Emsian) and Sipai Formation (late Emsian), Qijian, Dale and Miaohuang, Xiangzhou, Guangxi; 12, Sipai Formation (late Emsian) and Yintang Formation (Eifelian), Ertang, Wuxuan, Guangxi; 13, Beiliu Formation (late Emsian–Eifelian), Baima, Pingnan, Guangxi; 14, Middle Devonian rocks, Tengxian, Guangxi; 15, Beiliu Formation (late Emsian–Eifelian), Dafengmen, north of Beiliu, Gunagxi; 16, Yuchiang Formation (early Emsian), Liujing, Hengxian, Guangxi; 17, Yuchiang Formation (early Emsian), Daliancun, Nanning, Guangxi; 18, Miaokao Formation (late Ludlow–early Přídolí), Hongmiao, Qujing, eastern Yunnan; 19, Middle Devonian, Mangkang, western Sichuan. Palaeogeography based on Wang (1985). (Oldland: land with no marine sediments of Early and Middle Devonian age).

1922, p. 55). However, at present, it seems clear that in Hayasaka's papers the type localities and horizons for both species were erroneously quoted (see Grabau 1931; Rong and Yang 1980; Chen and Li 1994). Grabau (1931, p. 509) erected the Athyrisininae and followed Hayasaka's description of *Athyrisina*. In addition to Hayasaka's species, Grabau also assigned *A. uniplicata* Grabau, 1931 and *Athyrisina plicata* (Mansuy, 1912) to *Athyrisina*. It should be pointed out that Grabau (1931, pp. 516, 519) considered the age and locality of the topotypes of *A. minor*, and related species, as doubtful. In fact, in the explanations for



TEXT-FIG. 2. Location map for the Russian specimens studied in this paper. 1, Khatanzeya Peninsula; 2, Fedotov Cape; 3, Kal'vits Bay; 4, Britvin Cape (these four localities are on the South Island of Novaya Zemlya); 5, Vaigach Island (Kara Gate); 6, Dolgii Island; 7, western slope of the Polar Urals (Kozhym River); 8, western slope of the Central Urals (Mikhailov Pond); 9, western slope of the South Urals (Malyi Ik River).

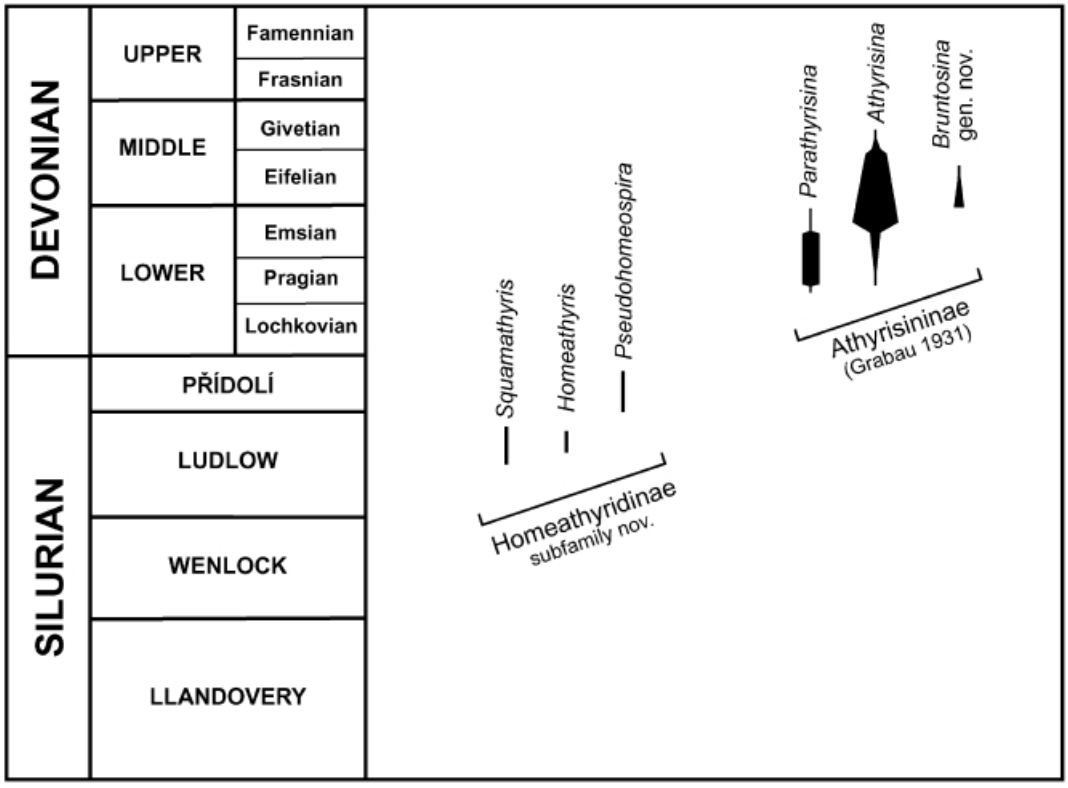
his plate 52, figure 1, Grabau wrote that 'more recent field work in Yunnan Province suggests a possibility that they may be Silurian'. Grabau (1931) also erected *Kwangsia*, with *K. yohi* Grabau, 1931 as type species, and *Plectospirifer*, with *P. heimi* Grabau, 1931 as type species. Surprisingly, and although both genera are very similar to *Athyrisina*, Grabau did not include them in his new subfamily Athyrisininae. One year later, Grabau erected *Kwangsiella* with *K. yohi* Grabau, 1931 as type species. As *Kwangsia* Grabau, 1931 and *Kwangsiella* Grabau, 1932 have the same type species, their names are objective synonyms (see Art. 61.3.4 of the 1999 Code) and *Kwangsia* Grabau, 1931 must be considered the valid name (Art. 23.1). Later, Hou (1963) considered *Kwangsia* Grabau, 1931 as a subjective synonym of *Athyrisina* Hayasaka, *in* Yabe and Hayasaka 1920. Wang *et al.* (1964) followed Hou's concept of *Athyrisina*, but concurred with Grabau's assignment of *A. minor* to *Athyrisina*. Boucot *et al.* (1964, p. 815, pl. 125, figs 16–30; 1965, p. H654, fig. 532, 5a–e) discussed the genus *Athyrisina* and used *A. minor* to illustrate the genus. This was probably due to a combination of the previous generic assignment, possession of a beautiful specimen of *A. minor*, and the similarity of the rhynchonelliform shell in both *A. squamosa* and *A. minor*, although they noted the differences between them. The specimen illustrated (Boucot *et al*. 1964, 1965) was collected by Arthur Bowsher in China, but no exact locality and horizon were recorded. Later, Chu (=Zhu) (1974) proposed *Protathyrisina* based on the type species, *Protathyrisina kutsingensis* Chu (=Zhu), 1974, from the Miaokao Formation (late Ludlow–early Přídolí), Hongmiao, Qujing, eastern Yunnan, south-west China. But Chu (=Zhu) did not discuss the relationships of *P. kutsingensis* with *A. minor* and the other Late Silurian species of *Athyrisina* described by Grabau



TEXT-FIG. 3. Lower and Middle Devonian stratigraphical sequences and correlations in South China (modified after Hou *et al.* 1988).

(1931). Furthermore, in the same Palaeontological Atlas of Yunnan in which *P. kutsingensis* was erected, the species *A. minor* and *A. uniplicata* were described, making matters more complicated and confusing. In fact, the status of *A. minor* and *P. kutsingensis* were unclear until the revision of Rong and Yang (1980; see also Rong *et al.* 1994). These authors considered *P. kutsingensis* as a synonym of *A. minor* and documented the latter species to be essentially different, at least at familial level, from *A. squamosa*, the type species of *Athyrisina*. Rong and Yang (1980) stated that *A. minor* was from the Upper Silurian, rather than the Middle Devonian, of the Qujing area, eastern Yunnan. They showed *A. minor* to possess a supported septalium in the dorsal valve, whereas *Athyrisina* has a cardinal plate. Late Silurian species previously assigned to *Athyrisina*, such as *A. minor*, *A. uniplicata*, and *A. plicata*, were rejected from *Athyrisina* and attributed to *Protathyrisina* by Rong and Yang (1980). Wang (*in* Wang and Zhu 1979) recognized two families within the ribbed athyridids, Athyrisinidae (including *Athyrisina*) from the Devonian, and Metathyrisinidae (including *Protathyrisina*) from the Silurian. *Protathyrisina* has been treated as a subjective synonym first of *Molongia* Mitchell, 1921 by Rong *et al.* (1985, 1987) and later of *Retziella* Nikiforova, 1937 by Rong *et al.* (1994). *Retziella* and other related genera (*Molongia* Mitchell, 1921, *Qinlingia* Rong *et al.*, 1987, *Metathyrisina* Rong and Yang, 1981) were assigned by Rong *et al.* (1994) to Retziellidae Rzhonsnitskaya, 1974.

During the period 1974–83, six additional genera of athyrisinins were established: *Parathyrisina* Wang, *in* Wang, Yu and Wu 1974; *Athyrisinoides* Chen and Wan, *in* Xu *et al.* 1978 (*non Athyrisinoides* Jiang, *in* Xian and Jiang 1978); *Pseudoathyrisina* Chen, 1979; *Athyrisinoidea* Chen and Wan, *in* Wan 1980 (*pro*



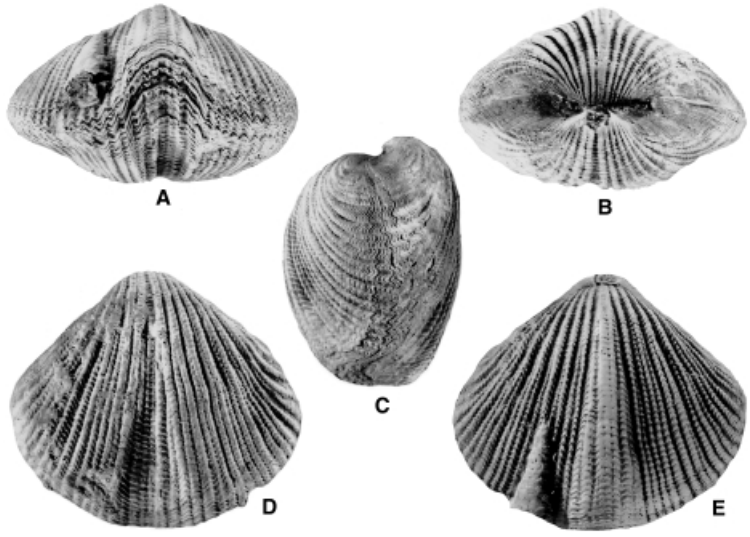
TEXT-FIG. 4. Chronostratigraphical range of athyrisinine and homeathyridine genera.

Athyrisinoides Chen and Wan, *in* Xu *et al*. 1978); *Athyrisinopsis* Zhang, *in* Zhang and Fu 1983 and *Neoathyrisina* Chen, 1988. The type species of *Parathyrisina*, *P. bella* (=*Athyrisina tangnae* Hou, 1963) from the lower Emsian, has a well-developed, rounded ventral sulcus that lacks radial elements, a characteristic feature that differentiates this genus from *Athyrisina*. The other five genera occur in Lower–Middle Devonian strata in the Longmenshan region of northern Sichuan and the Qinling region. Alvarez *et al*. (1998) considered that *Athyrisinoides* Chen and Wan, *in* Xu *et al*. 1978, *Athyrisinoidea* Chen and Wan, *in* Wan 1980 and *Neoathyrisina* Chen, 1988, were subjective synonyms of *Parathyrisina* Wang, *in* Wang, Yu and Wu 1974; and *Athyrisinopsis* Zhang, *in* Zhang and Fu 1983, and *Pseudoathyrisina* Chen, 1979, subjective synonyms of *Athyrisina* Hayasaka, *in* Yabe and Hayasaka 1920.

The genera *Homeathyris* Modzalevskaya, 1997, and *Squamathyris* Modzalevskaya, 1981, from Ludfordian rocks of the western slope of the Polar and Central Urals, Arctic Russia, and *Pseudohomeospira* Nikiforova, 1970 from Přídolí rocks in the same Russian areas (Text-figs 2, 4), were included, since their erection, within the athyrisinins.

STRATIGRAPHICAL DISTRIBUTION

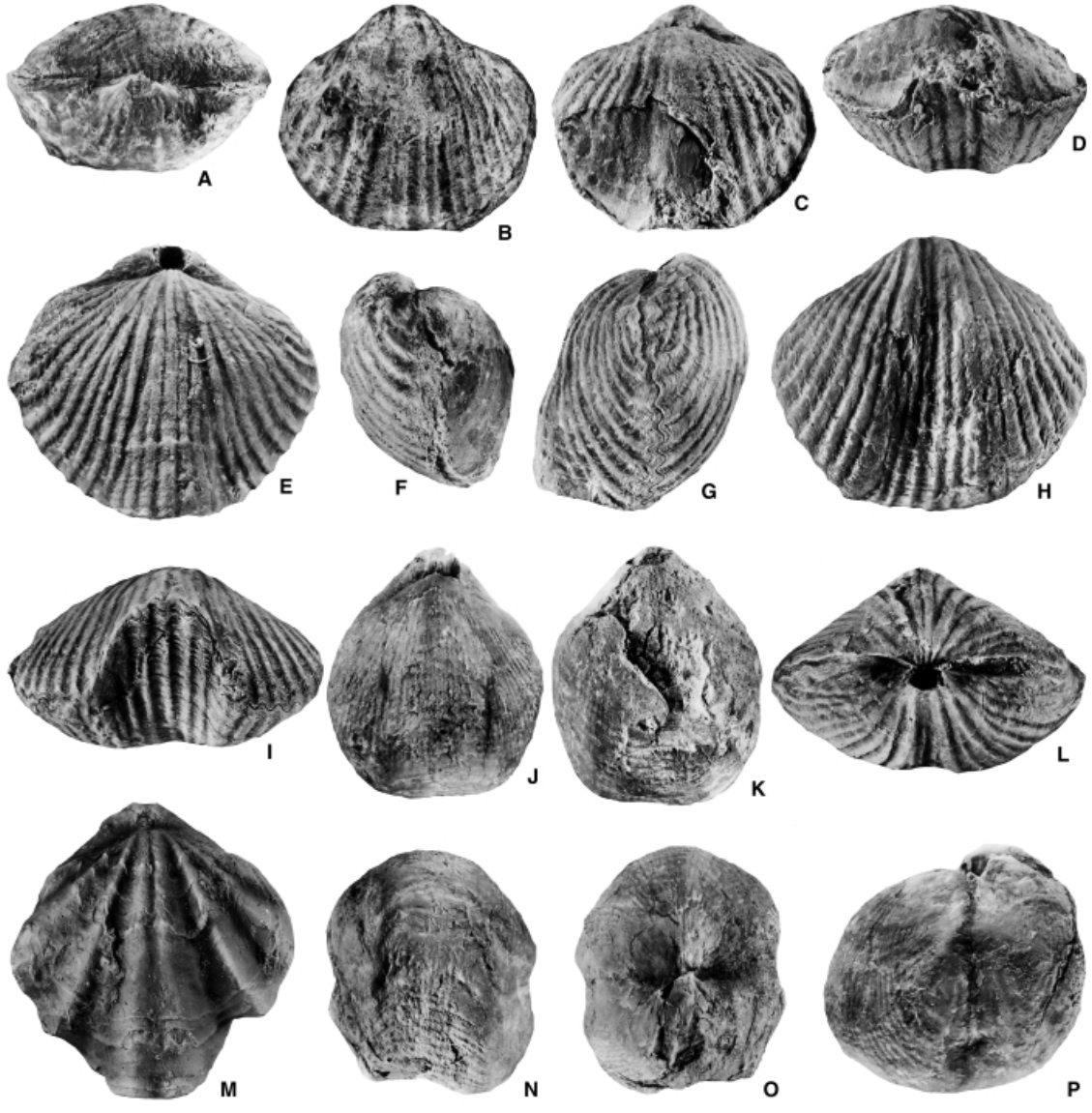
Athyrisinins are known to occur from the upper Pragian to the Givetian in south and north-west China (Text-figs 1, 4). Early and Middle Devonian stratigraphical sequences and correlation of this region are shown in Text-figure 3. Abundant athyrisinins occur mainly in three areas, namely (1) Longmenshan, northern Sichuan; (2) Guangxi-Guizhou; and (3) west and east Qinling. The earliest athyrisinins are documented from the Longmenshan area (Chen 1979). They include two species of *Parathyrisina*, *P. typica* (Chen and Wan, *in* Xu *et al*. 1978) (see Pl. 1, figs 13–17) and *P. tudilingensis* Chen, 1979 [here



TEXT-FIG. 5. A–E, *Athyrisina fasciata* (Chen, 1979), anterior, posterior, lateral, ventral, and dorsal views (CCGB75136), Tudiling Member, Bailiuping Formation (late Pragian), Bailiuping, Beichuan County, northern Sichuan; specimen courtesy of the late Prof. Chen Yuan-ren. All ×1·5.

considered a subjective synonym of *P. tangnae* (Hou, 1963)] from the basal part of the Tudiling Member (upper Pragian) of the Bailiuping Formation. This member is composed mainly of argillaceous limestones intercalated with calcareous shales (Chen 1979) and the athyrisinins are mostly from the argillaceous limestone. Faunal composition, diversity, and lithology of this member suggest near-shore, shallow-water, oxygen-rich, environmental conditions of Benthic Assemblages (BA) 2 and 3 of Boucot (1975). The earliest known species of *Athyrisina*, *A. fasciata* (Chen 1979) (see Text-fig. 5A–E), occurs about 23 m above the beds yielding *P. typica* (Chen and Wan, *in* Xu *et al*. 1978) and *P. tudilingensis* Chen 1979 (now *P. tangnae*) in the same member. The presence of these species and some additional species of both *Parathyrisina* and *Athyrisina* in the Longmenshan area in the upper Pragian (Text-figs 1, 4) indicates a possible source area for the athyrisinins, although their origin is still unknown. More species of these two genera have been recorded from the overlying Ganxi (mainly lower Emsian), Xiejiawan (upper lower Emsian–lower upper Emsian), and lower Yangmaba (upper Emsian–Eifelian) formations. All these formations are of shallow-water origin. No athyrisinins have been reported from the Givetian rocks in this area.

Central and southern Guangxi province are the areas where the athyrisinins are more abundant in Emsian and Eifelian strata. The earliest known species of this group in this area is *Parathyrisina tangnae* (Hou, 1963) (Pl. 1, figs 1–4, 6, 8) from the upper Yukiang Formation (upper lower Emsian, mainly argillaceous limestone interbedded with marls and mudstone) at Liujing, Hengxian, southern Guangxi (Hou 1963; Wang, Liu, Wu and Zhong 1974; Wang, Yu and Wu 1974; Wang and Rong 1986). In terms of community palaeoecology the brachiopod assemblage in which *P. tangnae* occur abundantly has been assigned (Wang and Rong 1986, p. 63) to outer BA 3 (Boucot 1975). No species are present in the overlying Moding Formation owing to the development of siliceous shale facies with a deeper-water brachiopod association, BA 4 of Boucot (1975) (see Wang and Rong 1986, p. 65). The earliest known species of *Athyrisina* in this area is *A. simplex* Chen, 1983 (here considered a subjective synonym of *A. squamosaeformis* Wang, *in* Wang, Yu and Wu 1974) from the Ertang Formation (uppermost lower Emsian, mainly limestone) and the latest *Parathyrisina* is *P. transitoria* Chen and Yao, 1999, from the Dale Formation (upper Emsian) (Chen and Yao 1999). Species of *Parathyrisina* (rare) and *Athyrisina* (abundant) occur from the Dale Formation (upper Emsian, mainly limestone) (Hou and Xian 1975; Wang



TEXT-FIG. 6. A–I, L, *Athyrisina squamosa* Hayasaka, *in* Yabe and Hayasaka 1920. A–D, F, posterior, ventral, dorsal, anterior, and lateral views (NIGP 134223); E, G–I, L, dorsal, lateral, ventral, anterior, and posterior views of neotype (NIGP 134224), Yangmaba Formation (late Emsian) at Heitupo (Black soil slope), Shuimo village (not Shuimo village near Zhaohua), formerly in Guanxian, now in Wenchuan County, northern Sichuan Province; specimens courtesy of the late Prof. Chen Yuan-ren; all ×1·5. J–K, N–P, *Athyrisina*? *dangduoensis* (Zhang, 1987); dorsal, ventral, anterior, posterior, and lateral views of holotype (XB247), Dangduo Formation (late Emsian–Eifelian), east Dangduogou, Tewo County, south-eastern Gansu; ×1·5. M, *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983); dorsal view (BX230), Dangduo Formation (late Emsian–early Eifelian), Dangduobeigou, Tewo County, south-eastern Gansu; ×2.

et al. 1987; Chen *et al*. 1989; Chen and Yao 1999) and the Sipai Formation (upper Emsian, mainly mudstone and shale) in central Guangxi. In all these places, athyrisinins appear to have inhabited more or less shallow water, corresponding to BA 2 and 3 of Boucot (1975) (see Wang *et al*. 1987; Chen *et al*. 1989). Some species of *Athyrisina* occur in the Yarang Member of the Beiliu Formation (Eifelian, mostly

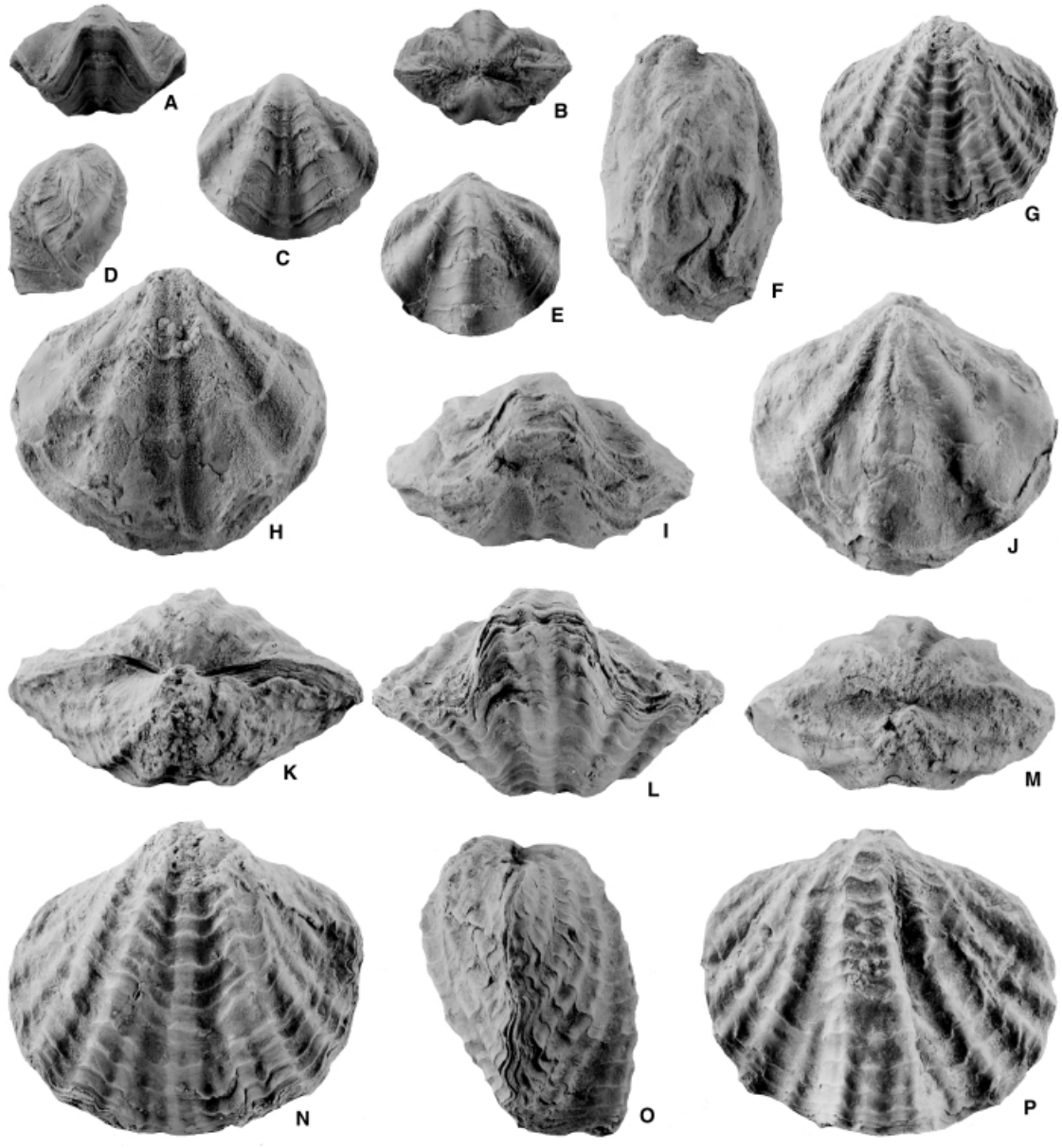
thin to thick bedded limestone) (Text-fig. 3; see also Hou and Xian 1975; Wang and Zhu 1979). This genus does not extend into overlying strata because of unfavourable environmental conditions in the Givetian. Migration of *Athyrisina* to south-eastern Guizhou took place later in the Eifelian. It is represented by *Athyrisina perfecta* Wang, *in* Wang, Liu, Wu and Zhong 1974 (= *Athyrisina tumida* Hou and Xian, 1975) that occurs from the Longdongshui Member of the Houershan Formation, which is composed of thick-bedded sandy limestone intercalated with grey-black limestone of shallow-water origin. Below this member the Shujiaping Member, of grey-white, thin- to thick-bedded, quartz sandstone, yielded no athyrisinins (Hou and Xian 1975; Wang and Zhu 1979).

Development of the athyrisinins in the Qinling area occurred later (later Emsian) but they are more abundant than in the other areas studied. The earliest known athyrisinin in this area is *Athyrisina squamosaeformis* Wang, *in* Wang, Yu and Wu 1974 from the lower Dangduo Formation (upper Emsian–lower Eifelian). Below this formation is the Gala Formation, formed exclusively by dolomites, of a lagoonal facies, that inhibited the possibility of growth of the athyrisinins. Later, various species of athyrisinins, ranging from taxa with very fine costellae [e.g. *A.*? *striata* (Zhang, *in* Zhang and Fu 1983)], to taxa with a few plicae [e.g. *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983) comb. nov.] (Text-figs 6M, 7A–F, H–J, M, 8; Pl. 2, figs 1–25), occur in different shallow-water limestone facies associated with corals and stromatoporoids. This indicates warm, shallow-water, inner shelf BA Zones 2 and 3 of Boucot (1975). Three species, *A. paradoxa* Zhang, 1987, *A. striata* Zhang, *in* Zhang and Fu 1983, and *A. ovata* Zhang, *in* Zhang and Fu 1983, that occur on the Xiawu'na Formation (Givetian), are the youngest athyrisinins (Zhang, *in* Zhang and Fu 1983; Zhang 1987). The number of individuals declined dramatically compared to the Eifelian diversity of this group. These three species are characterized by having small, moderately biconvex shells, with less developed sulcus and fold, and generally with costae, in both sulcus and flanks, not bifurcated and in small numbers. The number of specimens and their diversity decreased as the athyrisinins approached extinction.

In addition to the three areas mentioned above, Longmenshan, Guangxi-Guizhou, and west and east Qinling, the athyrisinins also reached western Sichuan (the Ganzi Block) in the late Emsian or early Eifelian (Hou *et al.* 1988). There they are represented by *Athyrisina* cf. *squamosa* in the Haitong Formation, which is composed mostly of dark grey, carbonate slates intercalated with sandstones and bioclastic marls of shallow-water origin. *A.* cf. *squamosa* was collected from the bioclastic marls.

Most of the homeathyridine collections are from Arctic Russia and the western slope of the Polar and Central Urals (Text-fig. 2). The Silurian geology and stratigraphy of these regions were described by Cherkesova (1970), Patrunov *et al.* (1980), Nekhorosheva (1981), Shurygina *et al.* (1981) and Antoshkina *et al.* (1983). Despite the different stratigraphical successions present in these regions, their deposits are characterized by similar carbonate-terrigenous sedimentation in mainly shallow-water basins. However, there is a detailed correlation between contemporaneous strata of the Dolgii and Vaigach islands, the South Island of Novaya Zemlya, and Polar (Kozhym River) and Central Urals (Mikhailov Pond). The distribution of the homeathyridins in the Upper Silurian sections in these areas is shown in Text-figure 2.

Among the homeathyridins, *Homeathyris plicatella* is the oldest species. Its shells formed coquina lenses in the thin, lumpy, dolomitic limestones of the lower part of the Zelenets Formation (Ludfordian) on Dolgii Island. Together with *H. plicatella*, smooth athyridids, gastropods, bivalves and very rare accumulations of ostracods, also appear in these coquinas. The monotonous faunal composition and lithology of the *Didymothyris didyma* brachiopod Zone in this formation suggest open, near-shore, sublittoral conditions of BA 2–3 of Boucot (1975). Similar accumulations of *H. plicatella* also appear in the lower part of the Zapadno-Khatanzeya Formation (Ludfordian) at the Cape Fedotov section. *H. plicatella* shells were found in the granular and lumpy muddy limestones together with ostracods and rare tabulate and rugose corals. In this section, sedimentation seems to have occurred in the transition between the carbonate shelf and a deeper part of the basin. Stratigraphically, *H. insularis* occurs about 35 m above the beds yielding *H. plicatella*, in the upper part of the Zelenets Formation in one locality on Dolgii Island. The larger size of *H. insularis* shells as compared with *H. plicatella*, suggests that the former lived in a more favourable environment. Their appearance was connected with shoal-water sedimentation during which limestones of different nodule and lump sizes were deposited. Coquinas of smooth athyridids, bivalves, gastropods and rare ostracods and trilobites appear together with the shells of *H. insularis*.



TEXT-FIG. 7. A–F, H–J, M. *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983). A–E, anterior, posterior, ventral, lateral, and dorsal views (XB231), Dangduo Formation (late Emsian), Xiawunagou, Tewo County, south-eastern Gansu; F, H–J, M, lateral, ventral, anterior, dorsal, and posterior views of holotype (XB239), Dangduo Formation (late Emsian–early Eifelian), Pulaigou, Tewo County, south-eastern Gansu; all × 1·5. G, K–L, N–P, *Athyrisina uniplicata* (Zhang, *in* Zhang and Fu 1983) (XB243, holotype). G, ventral valve; × 1. K–L, N–P, posterior, anterior, ventral, lateral, and dorsal views; Shijiagou Formation (early Eifelian), Gunziling, Longjiahe, Xunyang County, eastern Shaanxi; × 1·5.

Individuals or local accumulation of corals were common. *H. incisus* has a wider distribution than *H. insularis.* Both occurred in the capes of Britvin and Fedotov and the Khatanzeya Peninsula on the South Island of Novaya Zemlya, but *H. incisus* also appears in the Kuba Formation in the Central Urals. The shells of *H. incisus* are uncommon in carbonate sandstones of the upper part of the Zapadno-Khatanzeya

TEXT-FIG. 8. *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983), XB230, showing the characteristic single costa in the middle of the sulcus (see also Pl. 2, fig. 1), and variably spaced growth lamellae on any of which there are up to 80 growth lines; ×10.

Formation of the Cape Fedotov section. In this area, *H. incisus* commonly occurs with solenopores, smooth athyridids, *Squamathyris glacialis* and local accumulations of ostracods. In similar carbonate sandstones in the Khatanzeya Peninsula sections, the homeathyridins appear together with stromatoporoids, tabulate and rugose corals, other brachiopods (smooth athyridids, *S. glacialis* and davidsoniids), scarcer ostracods, gastropods, trilobites and bivalves, and single thelodonts. Both sections, at Cape Fedotov and in the Khatanzeya Peninsula, seem to represent shallow-water carbonate-shelf conditions. *H. incisus* and *H. insularis* may have originated from *H. plicatella* and lived in slightly different ecological niches.

The youngest homeothyridin, *Pseudohomeospira polaris*, was first described from Vaigach Island (Nikiforova 1970). Later its distribution widened. The shells were found in coeval deposits in the Khatanzeya Peninsula section (Novaya Zemlya) and in the western slope of the Polar and Central Urals. *P. polaris* is more common on Vaigach Island, where it is dominant in the upper part of the Guba Belush'ya Beds of the Greben' Formation. These beds are composed of 50 per cent argillites, interbedded with nodular and flaggy limestones (Cherkesova 1970). Because of the introduction of large quantities of argillaceous material a poor and monotaxonic brachiopod community (BA 2–3) developed in shallow-water conditions. The silty–clayey rocks of the Kal'vits Formation in the Khatanzeya Peninsula section are characterized by accumulations of fragments of bivalve shells, among which a single *Pseudohomeospira* was present. In the Polar and Central Ural sections (Tselebey and Demid formations) *P. polaris* was found in lumpy limestones supposedly deposited in normal marine shallow-water conditions.

Squamathyris glacialis occurs in the Novaya Zemlya, Dolgii and Vaigach regions in the middle of the Ludfordian. *Squamathyris* is quite abundant in the Cape Britvin and Kal'vits Bay sections. Most of the *Squamathyris* shells occur to the west of the Kal'vits Bay section from the uppermost part of the Krest-toskaya Member (Ludfordian), which is represented by calcareous, argillaceous rocks interbedded

with granular limestones. They show patchy distributions forming lens-like accumulations. In these limestones, besides brachiopods (smooth athyridids and homeathyridins) there are interlayers with bryozoans, rare colonies of rugose corals, crinoids and thelodonts. *S. glacialis* is common in the bioclastic (coral-brachiopod) limestones of the upper part of the Khatanzeya Formation on Vaigach Island. Brachiopods appear with numerous fauna: other brachiopods, tabulate corals, trilobites, bivalves, gastropods and ostracods. On Dolgii Island *S. glacialis* appears in the Zelenets Formation (lower and middle Ludfordian). They occur in the bivalve-ostracod-brachiopod coquinas in the lower part of the Zelenets Formation among laminated dolomitic limestones. In the upper part of the Zelenets Formation shells of *Squamathyris* are found in lumpy limestones, commonly in coquina layers with gastropods and rare ostracods. *S. glacialis* also occurs in the uppermost Zelenets Formation in lenticular, laminated, detrital limestones with flaggy beds of bioclastic limestone (coral limestones). Homeathyridins are uncommon in the latter, formed by compact communities of tabulate corals. *Squamathyris* has sometimes been found together with all three species of *Homeathyris*. All records of the occurrences of *Squamathyris* show adaptations to different ecological niches during this time interval, characterized by the presence of silty and clastic mixtures in carbonate deposits. Squamose growth lamellae, which is the characteristic external feature of *Squamathyris* shells, perhaps allowed them to survive in such environments.

The maximum peak for homeathyridine history took place in the mid Ludfordian. This time interval in all areas mentioned is characterized by profound changes in the brachiopod communities. The main feature in early homeathyridin evolution was their rapid but short radiation and extinction. The ribbed shells of *Homeathyris* and *Squamathyris* have a special structure in the pedicle opening common to other smooth athyridids. This morphological innovation was very specialized and complex. Further evolution of homeathyridins was connected with the simplification of this pedicle structure. As a result, the shells of *Pseudohomeospira*, externally similar to *Homeathyris*, have a pedicle collar which was also developed in other brachiopod taxa. The homeathyridins became extinct in the early Přídolí.

Finally, *Ikella* is known from the upper Emsian–lower Eifelian on the western slope of the South Urals. This genus includes two species: *I. numerosa* and *I. angusta.* Both species are found in the Biisk Regional Stage, which is characterized mainly by bioclastic limestones, with accumulations of brachiopods (pentameroids), numerous ostracods, crinoids, tabulate and rugose corals, and algae (Tyazheva 1961). They inhabited shallow and turbulent waters corresponding to BA 2 and 3.

BIOGEOGRAPHICAL SIGNIFICANCE

During the Silurian, athyridids evolved rapidly (Alvarez and Modzalevskaya 2001) but Silurian athyridid biogeography is not well known with the exception of that of the athyridid superfamily Retzielloidea (Rong *et al.* 1995). Recent investigations of Late Silurian (Ludlow and Přídolí) shallow-water benthic brachiopod faunas, mostly from Asia and Australia (Rong *et al*. 1994, 1995), have shown that a *Retziella* fauna (BA2 and 3) occurred in some parts of Asia and eastern Australia. This fauna is characterized by the common presence of retzielloids (ribbed, impunctate athyrididines with a supported septalium in the dorsal valve) in association with various provincial taxa and many common North Silurian Realm genera. The *Retziella* fauna is known synecologically from BA 2 and 3 in the Sino-Australian Province (Asia and Australia: south-west Tienshan, North and South China, north and central Vietnam, eastern Australia, ?North Korea, ?central Pamir, ?Afghanistan, and ?New Zealand) within the Cordilleran-Uralian Region (Boucot 1975). However, the homeathyridins are known only from BA 2 and 3 in north-west Russia and are unknown from the Sino-Australian Province. Moreover, there are many additional genera, such as *Didymothyris* and *Collarothyris*, among the smooth athyridids in BA 2 and 3 of the European Province (Modzalevskaya 1997*a*, *b*) that are not recorded in the Sino-Australian Province.

Two major units of brachiopod biogeography existed in the Late Silurian: the Malvinokaffric Realm with cold/cool water *Clarkeia* Fauna, and the North Silurian Realm including the Uralian-Cordilleran and North Atlantic regions (Boucot 1975). Within the latter, in addition to the Sino-Australian Province (e.g. Talent *et al*. 2001) with the *Retziella* Fauna and Mongolo-Okhotsk Province with the *Tuvaella* Fauna, the remainder of the Uralian-Cordilleran Region occurs (see Boucot and Blodgett 2001; Zhang 2001). In the North Atlantic region there are two subunits, the European Province with *Dayia*, and the North American

Province with *Eccentricosta* (Boucot 1975, Rong *et al.* 1995). Those areas containing *Homeathyris-Pseudohomeospira* also yielded subrianids, which are common elements in the Uralian-Cordilleran Region. Although Late Silurian brachiopod biogeography in the North Silurian Realm shows a more complicated picture than previously thought, the homeathyridins can be useful in the study of the European Province. Both smooth and costate athyridid genera have their own restricted geographical distribution and can be used as important discriminators for Late Silurian brachiopod biogeography.

Thanks to the major contributions of Boucot *et al*. (1967, 1969), Boucot and Johnson (1973), Boucot (1975) and Talent *et al*. (2001), Devonian brachiopod biogeography is relatively clear. This study further shows that *Athyrisina*, and related genera, may have inhabited shallow waters (BA 2 and 3). The taxonomic revision of the athyrisinins, undertaken here, and the re-study of their temporal and geographical distribution, clearly supports Boucot's suggestions for Devonian biogeography, upheld by Wang *et al.* (1984). The athyrisinins have a restricted geographical distribution: they are known from South China (Guangxi, Guizhou, northern Sichuan, east Yunnan), west and east Qinling, the Songpan-Ganzi Block (western Sichuan) (Text-fig. 1) and north Vietnam. No athyrisinins have been recorded from other regions. Thus, this group is a useful biogeographical tool for analyzing Devonian provincialism (see also Talent *et al*. 2001). The restricted distribution of homeathyridins and athyrisinins (Text-figs 1–2, 4) shows that athyridids have more biogeographical significance in the Silurian and Devonian than previously reported.

PHYLOGENY AND EVOLUTION

The three genera assigned here to the new athyridid subfamily Homeathyridinae, have commonly been included within the athyrisinins (Nikiforova 1970; Modzalevskaya 1981, 1994, 1997*a*, *b*; Grunt 1984, 1986; Alvarez *et al*. 1998; Alvarez and Rong 2002). New investigations have revealed, however, that they are more closely related to the Didymothyridinae than to the Athyrisininae because of the possession of deltidial plates, pedicle supports, and simpler spiralia and jugal apparatus. There is also a temporal gap between the Ludlow–Přídolí, when homeathyrisins existed, and the late Pragian, when the earliest athyrisinins appeared (Text-fig. 4). This gap and their geographical distribution (Text-figs 1–2) support the conclusions mentioned above. In addition, and as pointed out by Modzalevskaya (1996), genera possessing two variably developed plates, situated medially and apically, within a large delthyrial chamber, arose by the mid Ludfordian in both the Didymothyridinae and the Homeathyridinae (e.g. *Didymothyris*, *Homeathyris* and *Squamathyris*) (e.g. Text-fig. 9), whereas genera having a pedicle collar appeared later, in the Přídolí, in both subfamilies (e.g. *Collarothyris* and *Pseudohomeospira*). It seems clear that parallel evolution took place in the Late Silurian within the didymothyridins and the homeathyridins, possibly owing to varied ecological conditions which resulted in a great diversification of forms with much parallelism (see Alvarez and Carlson 1998; Alvarez *et al*. 1998; Alvarez and Modzalevskaya 2001). Pedicle supports formed by variably developed apical plates, situated between the dental plates, were lost in both lineages by the end of the Ludfordian, although other kinds of pedicle supports occurred several times during athyridid evolution (Alvarez *et al.* 1998, p. 849). Whereas homeathyridins and didymothyridins have a similar distribution, homeathyridins are not known from any of the areas where athyrisinins have been found. This fact also supports the idea that the homeathyridins derived from, or shared a common ancestor with, the didymothyridins.

The athyrisinins that are known only from upper Pragian–Givetian rocks of South China and north Vietnam, may have originated not from the homeathyridins (known only from north-west Russia in Upper Silurian rocks) but from the Athyridinae (see Alvarez and Carlson 1998; Alvarez *et al.* 1998). The Athyridinae are common in the Pragian (e.g. *Protathyris*) and Emsian beds (e.g. *Athyris*) in South China, where athyrisinins were very abundant in the late Early Devonian–early Middle Devonian. This distribution, together with the strong similarity in their internal structures (cardinalia, spiralia and jugum) in both the Athyridinae and the Athyrisininae (e.g. Wang and Rong 1986), seems to support the idea that athyrisinins may have been derived from athyridins, in the mid Early Devonian, by the development of a rhynchonelliform, costate shell.

Grunt (1984) pointed out that the athyrisinins (including what we consider now as athyrisinins,

TEXT-FIG. 9. *Squamathyris glacialis* Modzalevskaya, 1981, ventral view of internal mould showing pedicle support, dental plates, and weak muscle scars (CNIGR N10/12011), collected by L. V. Nekhorosheva in 1978 from the Zapadno-Khatanzeya Formation (Ludfordian), Khatanzyeya Peninsula, South Island of Novaya Zemlya (Loc. 7708–8a); ×3.

homeathyridins and retzielloids) are clearly the direct descendants of the rhynchonellids in which calcification of the spiralial supports for the lophophore took place at the end of the Ordovician. However, it is more likely that forms with radial ornament derived from smooth ones several times in different athyridid lineages through the Palaeozoic (Alvarez and Carlson 1998; Alvarez *et al.* 1998; Alvarez and Rong 2002; see also atrypide examples in Copper 2001). In addition to the athyrisinins and the homeathyridins, the Retzielloidea is another good example of the origin of ribbed taxa from smooth ones. Although the origin of the Retzielloidea is still uncertain, they may have branched off from whitfieldellins or shared a common ancestor with them (Alvarez and Carlson 1998; Alvarez *et al.* 1998). The transition from nearly smooth to densely ribbed shells may be found in populations of the same brachiopod species (e.g. Alvarez 1990). Thus, the assumption that homeothyridins and athyrisinins branched off from didymothyridins and athryridins in the Late Silurian and Early Devonian respectively (or shared a common ancestor) seems reasonable.

SYSTEMATIC PALAEONTOLOGY

Repositories and abbreviations. The specimens studied and mentioned are housed in the Palaeontological Collections of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Xi'an, Shaanxi Province, specimen numbers prefixed XB; Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, specimen numbers prefixed NIGP; Chengdu College of Geology, Chengdu, Sichuan Province, specimen numbers prefixed CCGB; and the Tschernyshev Central Geological Research and Exploration Museum, St. Petersburg, specimen numbers prefixed CNIGR.

Phylum BRACHIOPODA Duméril, 1806
Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order ATHYRIDIDA Boucot, Johnson and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson and Staton, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family ATHYRIDIDAE Davidson, 1881
Subfamily ATHYRISININAE Grabau, 1931

Emended diagnosis. Shells small to large, moderately rostrate, commonly with very strong ventral umbo curvature; growth lamellae generally well developed, may be squamose; fold and sulcus well developed; dental plates commonly short (long in *Bruntosina*), converging dorsally, may become subparallel anteriorly; dorsal myophragm absent; cardinal plate and jugum essentially as in *Athyris*, but without cardinal flanges.

Remarks on athyrisinine taxonomic rank. The taxonomic rank of the athyrisinins, and their relationship with other athyridide taxa has experienced several changes since its erection by Grabau (1931, p. 509) as a mono-generic subfamily, the Athyrisininae. Grabau (1931, p. 509) compared *Athyrisina* with *Retzia,*

Rhynchospira (= *Rhynchospirina*), *Athyris*, and *Camarotoechia*. The athyrisinins were promoted by Boucot *et al*. (1964, p. 814; 1965, p. H654) to superfamily rank, within the retziidines, embracing the impunctate, plicate or costate shells with spiralia directed laterally. Not much attention was given, at that time, to characters such as the cardinalia. This classification was followed by many palaeontologists (e.g. Rudwick 1970; Wan and Chen, *in* Xu *et al*. 1978; Wang and Zhu 1979; Chen 1979; Zhang and Fu 1983; Chen 1983; Grunt 1984, 1986; Wang *et al*. 1987; Chen *et al*. 1989). It was Dagys (1974, p. 153, see also p. 165) who first excluded the athyrisinins from the Retziidina, reassigning them, as a family, within the meristelloids, limiting the Retziidina to the punctate forms only. It should be noted that Dagys, lacking specimens of the genus *Athyrisina*, based his assignment on the study of the internal structures of *Retziella weberi* Nikiforova, 1937, the type species of the genus *Retziella.* This genus was excluded by Wang and Rong (1986) from the athyrisinids and promoted, by Rong *et al*. (1994), to family rank, Retziellidae, within the Meristelloidea. The retziellids (*sensu* Rong *et al*. 1994) are characterized by having a simple jugum, without bifurcations, and generally a distinct dorsal median septum that usually supports a septalium. Wang and Rong (1986, pp. 155–156), after restudy of the type material of *Athyrisina* species, found that both the athyrisinins (retziellids excluded) and athyridins had similar internal morphologies. Consequently they included the athyrisinins (with family rank) within the Athyridoidea. The simple development of radial ornamentation was not considered by Alvarez *et al.* (1998, p. 842) as a distinctive character for recognizing families or superfamilies within the athyrididines. Therefore, based on the presence of very similar internal structures (e.g. well-developed apically perforate cardinal plate, and complex jugum with distinct jugal arms) in athyridins and athyrisinins, Alvarez *et al.* (1998, p. 842) followed Wang and Rong (1986) and included the athyrisinins, but with subfamily rank, within the Athyrididae (just as Grabau 1931 did when he erected the subfamily).

Type genus. Athyrisina Hayasaka (*in* Yabe and Hayasaka 1920, p. 176) (= *Kwangsia* Grabau, 1931; *Plectospirifer* Grabau, 1931; *Kwangsiella* Grabau, 1932; *Pseudoathyrisina* Chen, 1979; *Athyrisinopsis* Zhang, *in* Zhang and Fu 1983).

Remarks on the synonymous generic names

Athyrisinopsis. When Zhang (*in* Zhang and Fu 1983, p. 354) established *Athyrisinopsis* she designated *Athyrisinopsis uniplicata* Zhang (*in* Zhang and Fu 1983, p. 354, p. 626, pl. 119, figs 1–3), from the Shijiagou Formation (Eifelian), Gunziling, Longjiahe, Xunyang County, eastern Shaanxi Province, as type species. As defined by Zhang, *Athyrisinopsis* differs from *Athyrisina* in having strongly plicated ornamentation with well-developed growth lamellae and commonly a single median plication, which may bifurcate anteriorly, in the sulcus. *Athyrisina* has costate ornamentation with fine concentric lamellae and commonly several costae in the sulcus. We consider that these differences are specific rather than generic and thus there is no basis for the erection of *Athyrisinopsis*, i.e. it is a junior synonym of *Athyrisina* (see also Alvarez *et al.* 1998; Talent *et al*. 2001; Alvarez and Rong 2002). Accordingly, of the five species erected by Zhang (*in* Zhang and Fu 1983; and Zhang 1987) for *Athyrisinopsis*, we suggest assigning *A. uniplicata*, *A. concentrica*, and *A. trapeziformis* to *Athyrisina*, and *A. gansuensis* and *A. ovata* to *Bruntosina* gen. nov.

Kwangsia. This genus was proposed by Grabau (1931, p. 204) with *K. yohi* Grabau (1931, p. 205, pl. 25, figs 4–5) as type species. According to Grabau (1931, p. 207), *K. yohi* occurs, associated with *Xenospirifer fongi* (Grabau), in Eifelian rocks in the Peima Shale at Pei-Ma-Shih (Baimasi), Teng-Hsien (Tengxian County), Kwangsi (now Guangxi Province). When erected, *Kwangsia* was considered 'a peculiar Atrypoid' (*sic*) and consequently it was not included by Grabau within his new subfamily Athyrisininae (Grabau 1931, pp. 509–523). Boucot *et al.* (1964, p. 810, text-fig. 2; 1965, p. 637, fig. 520,2), following the views of Grabau (1931), assigned *Kwangsia* to Carinatininae, an atrypoid subfamily. Hou (1963, p. 42) noted, for the first time, that in *Kwangsia* the spiral cones were not medially or dorso-medially directed, but postero-laterally. As a result, *Kwangsia* was excluded from the Atrypida, and included within the athyrisinins. Furthermore, Hou, given all the morphological similarities, both internal and external,

considered *Kwangsia* as a junior synonym of *Athyrisina*. Study of original specimens of *Kwangsia* has shown that these larger specimens are closely similar to gerontic *Athyrisina* (see Wang *et al.* 1966). Moreover, the internal morphology, known from serial sections, is very similar in both genera (see, for example, Chen *et al.* 1989, p. 221, text-fig. 4). In the present revision we follow the common Chinese usage (see, for example, Hou 1963; Wang *et al.* 1966; Hou and Xian 1975; Yang *et al*. 1977; Xian and Jiang 1978; Zhang Yan 1984; Wang and Rong 1986; Chen *et al.* 1989) of considering *Kwangsia* as a subjective synonym of *Athyrisina* (see also Alvarez *et al.* 1998; Talent *et al*. 2001; Alvarez and Rong 2002). All *Kwangsia* species are assigned to *Athyrisina* (see list below).

Kwangsiella. Both genera, *Kwangsia* Grabau, 1931 (p. 204) and *Kwangsiella* Grabau, 1932 (p. 82) have the same name-bearing type, *K. yohi* Grabau (1931, p. 205, pl. 25, figs 4–5; 1932, p. 82), so, according to the fourth edition (1999) of the International Code of Zoological Nomenclature (Art. 61.3.4) their names are objective synonyms.

Plectospirifer. This genus was erected, as a subgenus of *Spirifer*, by Grabau (1931, p. 379) who designated *P. heimi* (Grabau, 1931, p. 385, pl. 39, figs 3–5) as type species. *P. heimi* is from lower Hsuimogou Beds (Middle Devonian), Hsuimogou, Sichuan Province. Its holotype is now housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, with specimen number NIGP 1574. Topotypes of *P. heimi* were studied by Wang *et al.* (1964), who noted that it is not a '*Spirifer*-like' brachiopod. *Plectospirifer* is characterized by its rhynchonelliform shell, with a large, circular ventral foramen but without interarea. Wang *et al.* (1964, p. 632) considered, but without further discussion, that *Plectospirifer* is a junior synonym of *Athyrisina*. The view of Wang *et al.* (1964) is followed here (see also Alvarez *et al.* 1998, p. 842). We also support the designation of Hou and Xian (1975) of *P. fongi* Grabau 1931 (p. 380, pl. 40, fig. 12a–f) as type species of *Xerospirifer* Hou and Xian, 1975, and the inclusion (see Wang and Rong 1986, p. 186) of *P. papaoensis* Grabau 1931 (pl. 41, fig. 1a–f) in *Rostrospirifer* Grabau, 1931.

Pseudoathyrisina. The genus *Pseudoathyrisina* was established by Chen (1979, p. 17) from the Tudiling Member (upper Pragian) of the Bailiuping Formation in the Longmenshan area, northern Sichuan. Only the type species, *P. fasciata* Chen, 1979, was included in *Pseudoathyrisina* (Chen 1979, p. 18, pl. 9, figs 1–7). According to Chen, *P. fasciata* is characterized by 'having fasci-costate ornamentation in both flanks, sulcus or fold, and spiralia directed latero-posteriorly'. All these characters are shared with *Athyrisina* and, hence, there is no basis for the separation of these two genera (see also Alvarez *et al.* 1998, p. 842), i.e. *Pseudoathyrisina* is a junior synonym of *Athyrisina*.

Genera assigned. In addition to the type genus we include *Parathyrisina* Wang, *in* Wang, Yu and Wu 1974 [= *Athyrisinoides* Chen and Wan, *in* Xu *et al*. 1978 (*non Athyrisinoides* Jiang, *in* Xian and Jiang 1978); *Athyrisinoidea* Chen and Wan, *in* Wan 1980, and *Neoathyrisina* Chen, 1988 (*pro Athyrisinoides* Chen and Wan, *in* Xu *et al*. 1978)], and *Bruntosina* gen. nov.

Genera excluded. Pseudohomeospira Nikiforova, 1970, *Ikella* Tyazheva, 1972, *Squamathyris* Modzalevskaya, 1981, and *Homeathyris* Modzalevskaya, 1997 differ from *Athyrisina* and related genera in having a hypothyridid pedicle opening partially closed by deltidial plates, a pedicle collar (*Pseudohomeospira*) or two apical plates situated between the dental plates (*Homeathyris* and *Squamathyris*), and a jugum with very short accessory lamellae. Hence, they are removed from the Athyrisininae, as here understood, and placed in a new athyridid subfamily, Homeathyridinae (see below).

Occurrence. Lower Devonian (Pragian) to Middle Devonian (Givetian), in South China (plus western Sichuan and Qinling regions) and north Vietnam.

Genus ATHYRISINA Hayasaka, *in* Yabe and Hayasaka 1920

Text-figures 4, 5A–E, 6A–L, N–P, 7G, K–L, N–P, 10

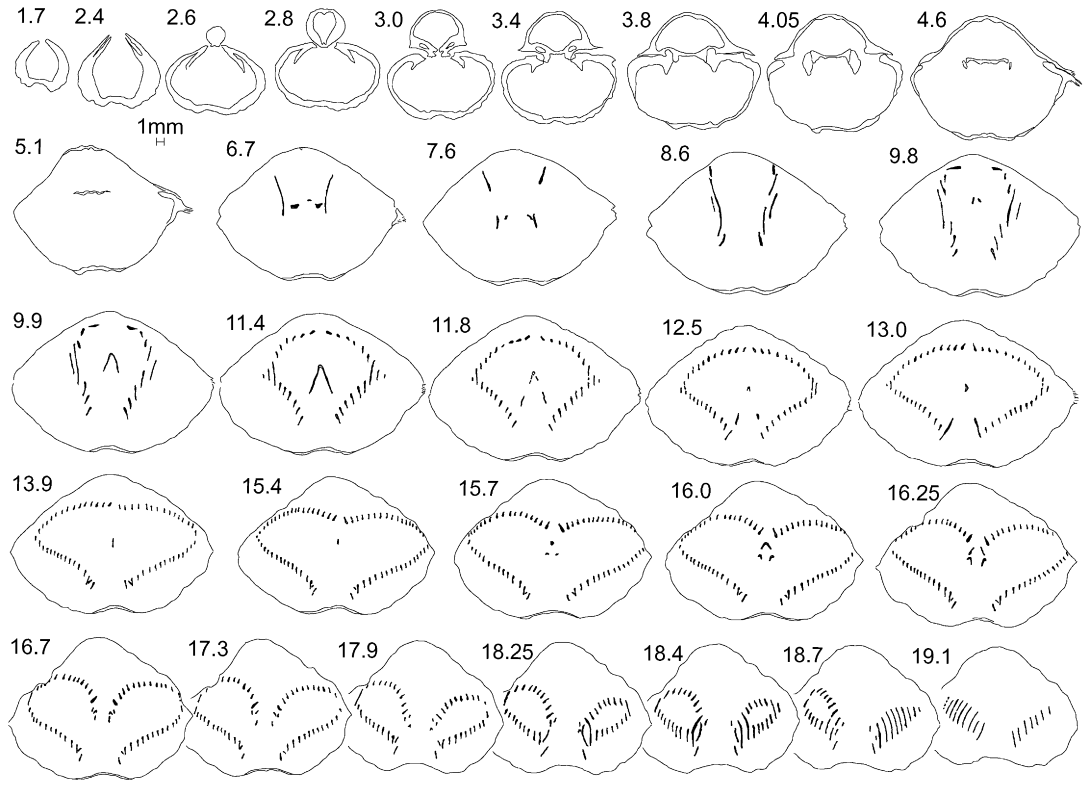
1920 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka, p. 176.
1922 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Hayasaka, p. 50.

1931 *Kwangsia* Grabau, p. 204.
1931 *Plectospirifer* Grabau, p. 379.
1931 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Grabau, p. 509 (*pars*).
1932 *Kwangsiella* Grabau, p. 82.
1963 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Hou, p. 41 (*pars*).
1964 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Wang *et al.*, p. 632 (*pars*).
1964 *Kwangsia* Grabau; Wang *et al.*, p. 447.
non 1964 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Boucot *et al.*, p. 815.
non 1965 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Boucot *et al.*, p. H654.
1966 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Wang *et al.*, p. 603 (*pars*).
1966 *Kwangsia* Grabau; Wang *et al.*, p. 602.
1974 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Wang, *in* Wang, Yu and Wu, p. 40.
1974 *Kwangsia* Grabau; Chu (= Zhu), p. 462
1975 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Hou and Xian, p. 42.
1977 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Yang *et al.*, p. 403.
1978 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Xian and Jiang, p. 303.
1978 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Xu *et al.*, p. 349.
1979 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Chen, p. 14.
1979 *Pseudoathyrisina* Chen, p. 17.
1979 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Wang and Zhu, p. 50.
1979 *Kwangsia* Grabau; Wang and Zhu, p. 56.
1980 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Rong and Yang, p. 265.
1982 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Bai *et al.*, p. 103.
1983 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Zhang, *in* Zhang and Fu, p. 348.
1983 *Athyrisinopsis* Zhang, *in* Zhang and Fu, p. 354.
1983 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Chen, p. 691.
1987 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Zhang, p. 126.
1987 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Wang *et al.*, p. 128.
1989 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Chen *et al.*, p. 220.
1998 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Alvarez *et al.*, p. 842.
1999 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Chen and Yao, p. 229.
2002 *Athyrisina* Hayasaka, *in* Yabe and Hayasaka; Alvarez and Rong, p. 1507.

Type species. Athyrisina squamosa Hayasaka, *in* Yabe and Hayasaka 1920, pp. 180–181, pl. 23, figs 5–6, 16–17, from the Yangmaba Formation, Shuimo Village (not Shuimo, Zhaohua County), Wenchuan County, Sichuan Province, upper Emsian (see Chen and Li 1994, and below).

Emended diagnosis. Small to large shells with rounded subpentagonal to transversely elliptical dorsal outline, with short to relatively long hinge-line, ventribiconvex lateral profile; ventral sulcus and dorsal fold usually well developed; pauciplicate to costellate, radial elements may bifurcate; growth lamellae numerous, commonly well developed; dental plates thin, short, lateral apical cavities very narrow; cardinal plate perforated apically by minute foramen, spiralia with 10–18 whorls.

Remarks on the type locality and topotypes of Athyrisina squamosa. In the original description by Hayasaka (*in* Yabe and Hayasaka 1920) the type material was said to be from the Middle Devonian rocks of Pen-chao-tse (now Pianqiaozi), Chao-hua-hsien (now Zhaohua County), Pao-hing (now Baoxing-fu), northern Sichuan Province. Unfortunately Hayasaka did not state who collected the fossils or the exact provenance. Since then, Chinese geologists with a good knowledge of the geology of the area have commonly doubted the locality and occurrence data for *Athyrisina squamosa*. For example, Hou *et al.* (1988; see also Xian *et al.* 1988) suggested that these specimens were collected from the highest Emsian beds of the Yangmaba Formation in Zhaohua, about 30 km south-west of Guangyuan, rather than from Middle Devonian strata in Pen-chao-tse (Pianqiaozi), both in northern Sichuan Province. In September 1993, Li Xiang-hui visited Pianqiaozi, a small place in the village of Shuimo, 28 km north-west of Zhaohua old town, along the Bailongjiang (White Dragon River, a branch of the Jialingjiang River). He verified that in the Pianqiaozi area most of the rocks exposed are yellowish-green metamorphosed shales



TEXT-FIG. 10. Selected transverse serial sections illustrating the internal structures in *Athyrisina squamosa* Hayasaka, *in* Yabe and Hayasaka 1920; in this specimen the brachidium was broken naturally from the crura and then tilted posterodorsally inside the shell; f134227, upper Emsian, Yangmaba Formation, Shuimo Village, Wenchuan County, Sichuan Province, China; distances measured in mm from the posterior end.

of Silurian age. Few Devonian rocks seem to be present. They consist of quartzites and strongly crystallized limestones with very rare fossils. Li and Chen Yuan-ren did not find any brachiopods, and concluded (Chen and Li 1994) that the well-preserved specimens of *A. squamosa*, illustrated by Hayasaka (*in* Yabe and Hayasaka 1920) were not from the lithologies observed by them in the Pianqiaozi area, Shuimo, Zhaohua County. We follow Chen and Li's (1994) suggestions and consider that the topotypes of *A. squamosa* may have been collected from the Yangmaba Formation (upper Emsian), at Heitupo (Black Soil slope), Shuimo village (not Shuimo, Zhaohua), formerly in Guanxian, now in Wenchuan County, northern Sichuan Province. This is further supported in that (1) the types of *Plectospirifer heimi* Grabau, 1931 and *P. heimi* mut. *alpha* Grabau, 1931 (*sic*), considered in this paper as subjective synonyms of *A. squamosa*, all came from Heitupo, Shuimo; (2) the immense number of *Athyrisina* specimens found at that locality which are considered to be conspecific with *A. squamosa*. During the early 1970s, the local people collected more than 10,000 kg of completely preserved brachiopods, mainly *Athyrisina*, from this locality in a few weeks. All were loose specimens, very well preserved, and easily collected. The morphology of these specimens falls within the intrapopulational variation of *A. squamosa* Hayasaka (*in* Yabe and Hayasaka 1920, p. 180, pl. 23, figs 5–6, 16–17); (3) a large number of brachiopod specimens belonging to *Atrypa*, *Athyrisina*, *Cyrtospirifer*, *Yangzteella* and other genera were collected by locals and sold to drug stores, to prepare Chinese medicine, in many places in Sichuan, Hunan, Hubei and other provinces. For centuries, and to this day, they are ground up and put into suspension in hot water as a drink for cooling down the body. Hence, it was not uncommon to purchase from a drug store good specimens for study as,

for example, did Grabau (1931, p. 515). Thus, it seems reasonable to think that the specimens of *A. squamosa* studied by Hayasaka might have been obtained from a drug store, rather than been collected in the field, and that this could be the origin of incorrect, geographical and stratigraphical data on type his specimens.

Neotype. Hayasaka (in Yabe and Hayasaka 1920, pl. 2, figs 5–7, 16–18) figured four specimens of *A. squamosa* and two of *A. squamosa* var. *rhomboidalis* (*sic*), and provided the measurements for three specimens of *A. squamosa* (p. 53) and four of *A. squamosa* var. *rhomboidalis* (p. 54), none of which was designated as holotype. Grabau (1931, p. 510) repeated Hayasaka's descriptions and measurements, but did not provide illustrations and neither he, nor Hayasaka (1922), designated a type. More recently, Wang *et al*. (1964), in their study of the fossil brachiopods of China, followed Hayasaka's description and provided illustrations similar to those of Hayasaka's paper, but still did not designate a type. Apparently neither a holotype nor a lectotype has been designated, and, although the syntypes collectively constitute the name-bearing types, we do not know, in spite of all our efforts, where Hayasaka's specimens are housed, nor if all topotypes are irretrievably lost. We consider that there is a need to define *A. squamosa* objectively, and as no name-bearing type for reference is believed to exist, and there is no evidence that Hayasaka's specimens still exist, a neotype is selected here (see Art. 75 of the Code 1999). This (Text-fig. 6E, G–I, L) is from as near as is practicable to the original locality and geological horizon (see remarks above). It is housed in the palaeontological collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing (NIGP 134224).

Species assigned. The genus has more external variation than originally described by Hayasaka (*in* Yabe and Hayasaka 1920). To our knowledge, up to 53 species have been assigned to *Athyrisina*, or its subjective synonyms, since its erection. Many of these species are in need of revision, partly because only a few specimens were assigned, frequently only the type, and often with a lack of knowledge of internal characters. The lack of adequate specimens showing the intraspecific and ontogenetic variations make it very difficult to differentiate between species of *Athyrisina*. In spite of this, and because of strong external and internal similarities, together with occurrence at the same locality and horizon, in this paper we consider 13 species marked with an asterisk as subjective synonyms of previously erected athyrisinine species. We assigned 42 species to *Athyrisina*, four are questionably assigned, and eight are rejected.

1. *Athyrisina squamosa* Hayasaka, *in* Yabe and Hayasaka 1920, p. 180, pl. 23, figs 5–6, 16–17; probably from Yangmaba Formation (latest Emsian), Shuimo Village (not Shuimo, Zhaohua County), Wenchuan County, Sichuan Province. Discussion on the locality and horizon is provided above. This species is very abundant in the Longmenshan area where the type material, in all probability, was collected. It is also known from latest Emsian strata of Guangxi and Guizhou (see Hou and Xian 1975, p. 42, pl. 27, fig. 1), west and east Qinling regions (see Zhang *in* Zhang and Fu 1983, p. 349, pl. 117, figs 9–12), western Sichuan, and north Vietnam (see Duong 1980).

2. *Athyrisina alumna* Wang *et al.*, 1987, p. 128, pl. 1, figs 1–18; pl. 2, figs 6–7, 10–12; pl. 8, figs 1–8; text-figs 3–4 [= *Athyrisina plicata* (Mansuy) (*non* Mansuy 1915), Hou and Xian, 1975, p. 42, pl. 21, fig. 10; Yang *et al.*, 1977, p. 403, pl. 160, fig. 3a–d]; from the Shipeng Member of the Dale Formation (late Emsian), Dale, Xiangzhou County, Guangxi. The specimens illustrated as *A. alumna* by Chen and Yao (1999, p. 231, pl. 2, figs 1–3) are similar to *A. wangi* in their characteristic ornamentation.

*3. *Athyrisina beiliuensis* Wang and Zhu, 1979, p. 53, pl. 9, figs 14–18; Beiliu Formation (late Emsian), from Dafengmen, Beiliu County, Guangxi. This species could be a subjective synonym of *A. squamosaeformis* Wang, *in* Wang, Yu and Wu 1974.

4. *Athyrisina bifurcata* Wang and Zhu, 1979, pp. 53–53, pl. 10, figs 1–4; pl. 27, figs 11–16, 23; from the Longdongshui Member of the Houershan Formation (Eifelian), Shujiaping, Houershan, Dushan County, south-eastern Guizhou. Additional data on this species based on the topotype material can be seen in a paper by Chen *et al.* (1989, pp. 221–223, pl. 1, figs 12, 14–15, 17, 20; pl. 2, figs 27, 29–30; pl. 3, figs 1–16; pl. 4, figs 1, 4, 9; pl. 5, figs 2–4, 8, 10–11, 14, 17; pl. 8, figs 1–2, 10; pl. 9, figs 5, 7; with transverse serial sections of *A. bifurcata* in text-fig. 5).

5. *Athyrisinopsis centroplicata* Zhang, *in* Zhang and Fu 1983, p. 128, fig. 6a–e; from the Dangduo Formation (late Emsian–Eifelian), east Dangduogou, Tewo County, south-eastern Gansu. The transverse serial sections of Zhang *in* Zhang and Fu, 1983 (text-fig. 87) do not show a complete cardinal plate.

6. *Athyrisina circularis* Zhang, *in* Zhang and Fu 1983, p. 351, pl. 117, figs 6–7; from the Shijiagou Formation (Eifelian), Gunziling, Longjiahe, Xunyang County, south-eastern Shaanxi. This species, from the East Qinling, has only a single rib, occasionally two, in the ventral sulcus and strong growth lamellae.

7. *Pseudoathyrisina fasciata* Chen, 1979, p. 18, pl. 9, figs 1–7; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Beichuan County, northern Sichuan. This is one of the oldest species of the genus.

8. *Athyrisina globosa* Chen, 1983, p. 692, pl. 3, figs 9–11; from the Ertang Formation (late early Emsian), Ertang, Wuxuan County, Guangxi.

9. *Athyrisina grandicostata* Yang, *in* Yang *et al.* 1977, p. 404, pl. 159, fig. 6; from the Yintang Formation (Eifelian), Qiansi, Xiangzhou County, Guangxi. This species is externally similar to *A. wangi* Chen *et al.*, 1989. Further investigation of the type material is required.

*10. *Plectospirifer heimi* Grabau, 1931 (the type species of *Plectospirifer*), p. 385, pl. 39, figs 5–3; from the Shuimogou Beds (probably Yangmaba Formation) (latest Emsian), Guanxian County, northern Sichuan. We consider this species as a junior subjective synonym of *A. squamosa* Hayasaka (*in* Yabe and Hayasaka 1920) since there are no essential differences between them. Probably, they also came from the same locality and horizon.

*11. *Plectospirifer heimi* mut. *alpha* Grabau, 1931, p. 388, pl. 39, figs 6–8; from the same locality and horizon as *P. heimi* Grabau, 1931. It could be regarded as a subjective synonym of *A. squamosa* Hayasaka (*in* Yabe and Hayasaka 1920)

*12. *Athyrisina heimi ganxiensis* Wan, *in* Xu *et al.* 1978, p. 351, pl. 123, fig. 3 (= *Athyrisina heimi ganxiensis* Wan, 1980, p. 104, pl. 37, fig. 1); from the Yangmaba Formation (latest Emsian–earliest Eifelian), Ganxi, Beichuan County, northern Sichuan. It could be a subjective synonym of *Athyrisina squamosa* Hayasaka (*in* Yabe and Hayasaka 1920).

13. *Kwangsia inflata* Chu (= Zhu), 1974, p. 463, pl. 123, fig 1; from the Pochiao Formation (Emsian), Dazhaizi, Yiliang County, eastern Yunnan. This species is very similar to *Kwangsia perfecta* Wang, *in* Wang, Liu, Wu and Zhong 1974. Further investigation of the type material of these two species is required.

*14. *Kwangsia intermedia* Wang and Zhu, 1979, p. 58, pl. 11, figs 13–14; pl. 12, figs 1–2; from the Baima Shale (Eifelian), Huanglingtou, Baimawei, Pingnan County, Guangxi. There are no substantial differences between this species and *A. yohi* (Grabau, 1931); both probably came from the same locality and horizon.

*15. *Athyrisina longa* Zhang, *in* Zhang and Fu 1983, p. 353, pl. 117, fig. 3; from the Rure Formation (Eifelian), Yiwagou, Tewo, south-eastern Gansu. This species could be a subjective synonym of *Athyrisina striata* Zhang, *in* Zhang and Fu 1983 (see 32 below).

16. *Athyrisina multicostata* Zhang, *in* Zhang and Fu 1983, p. 350, pl. 117, fig. 5; from the Dangduo Formation (late Emsian), Beichagou, Cakuohe, Luqu County, south-eastern Gansu. Similar to *A. subtransversa* Zhang, *in* Zhang and Fu 1983, but evidently smaller than the latter, about half its size. Also close to *Athyrisina ovata* Zhang, *in* Zhang and Fu 1983. Needs further study.

17. *Athyrisina multiplicata* Bai and Lu (MS), *in* Yang *et al.* 1977, p. 403, pl. 160, fig. 4; from the Dale Formation (late Emsian), Dale, Xiangzhou County, Guangxi.

*18. *Athyrisina obesa* Wang and Zhu, 1979, p. 55, pl. 10, figs 5–7; pl. 27, fig. 24; pl. 32, figs 40–43; from the Sipai Member of the Sipai Formation (late Emsian), Qijianwei, Xiangzhou County, Guangxi. Very similar to *A. squamosa* Hayasaka (*in* Yabe and Hayasaka 1920). It could be considered a junior synonym of the latter.

19. *Athyrisina ovata* Zhang, *in* Zhang and Fu 1983, p. 350, pl. 118, fig. 6; from the Gudaoling Formation (Eifelian), Changping, Wafangba, Fengxian County, Shaanxi. Close to *Athyrisina multicostata* Zhang, *in* Zhang and Fu 1983. Needs further study.

20. *Athyrisina paradoxa* Zhang, 1987, p. 127, pl. 110, fig. 13a–d; pl. 111, fig. 1a–d; from the Xiawuna Formation (Givetian), Dangduogou, Tewo County, south-eastern Gansu.

21. *Athyrisina parasquamosa* Zhang, 1987, p. 128, pl. 111, figs 2a–d, 3; from the Rure Formation (Eifelian), Dangduogou, Tewo County, south-eastern Gansu.

22. *Kwangsia perfecta* Wang, *in* Wang, Liu, Wu and Zhong 1974, p. 241, pl. 122, figs 1–7; from the Longdongshui Member of the Houershan Formation (Eifelian), Houershan, Dushan County, south-eastern Guizhou.

23. *Athyrisina primaeva* Chen, 1979, p. 14, pl. 1, figs 11–12; from the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan. This, together with *A. fasciata* (Chen, 1979), is one of the oldest species of the genus.

24. *Athyrisina rara* Wang and Zhu, 1979, p. 54, pl. 9, figs 19–22; from the Dale Formation (late Emsian), Liufengshan, Ertang, Wuxuan County, Guangxi. With the exception of the holotype, which is a long oval shell, all other syntypes (see Wang and Zhu 1979, pl. 27, figs 1–10) are very similar to *A. squamosaeformis* Wang, *in* Wang, Yu and Wu 1974, and may belong to the latter.

25. *Athyrisina raricostata* Zhang, 1987, p. 128, pl. 111, fig. 5a–d; from the Dangduo Formation (late Emsian), Danduogou, Tewo County, south-eastern Gansu.

26. *Athyrisina rostrata* Zhang, *in* Zhang and Fu 1983, p. 351, pl. 117, fig. 4; from the Shijiagou Formation (Eifelian), Gunziling, Longjiahe, Xunyang County, eastern Shaanxi.

*27. *Athyrisina simplex* Chen, 1983, p. 691, pl. 3, figs 1–8; from the Ertang Formation (late early Emsian), Ertang, Wuxuan County, Guangxi. This species could be considered a subjective synonym of *Athyrisina squamosaeformis* Wang, *in* Wang, Yu and Wu 1974 from which it differs only in its smaller size and earlier appearance in the stratigraphical record.

*28. *Athyrisina sipaiensis* Wang and Zhu, 1979, p. 55, pl. 10, figs 8–15; from the Dale Formation (late Emsian), Sipaiwei, Luzhai County, Guangxi. Similar to *Athyrisina bifurcata* Wang and Zhu, 1979.
*29. *Athyrisina spinocostellata* Wang and Zhu, 1979, p. 52, pl. 9, figs 9–13; from the Longdongshui Formation (Eifelian), Houershan, Dushan County, south-eastern Guizhou. This species may be regarded as a small *Athyrisina squamosaeformis* Wang, *in* Wang, Yu and Wu 1974.
*30. *Athyrisina squamosa* var. *rhomboidalis* Hayasaka, *in* Yabe and Hayasaka 1920, p. 182, pl. 23, figs 7, 18 (*non Athyrisina rhomboidalis* Zhang, *in* Zhang and Fu 1983, p. 353, pl. 118, fig. 5); probably from the Yangmaba Formation (late Emsian–early Eifelian), Shuimo, Wenchuan County, northern Sichuan (Hou *et al*. 1988; Chen and Li 1994). This species could be a synonym of *Athyrisina squamosa* Hayasaka (*in* Yabe and Hayasaka 1920) as both are similar (*A. squamosa* var. *rhomboidalis* has a slightly more transverse outline) and came from the same horizon and locality.
31. *Athyrisina squamosaeformis* Wang, *in* Wang, Yu and Wu 1974, p. 40, pl. 12, figs 7–12 (lectotype selected by Wang, *in* Wang, Liu, Wu and Zhong 1974, p. 242, pl. 122, figs 12–14, NIGP 22396); from the Longdongshui Member of the Houershan Formation (Eifelian), Houershan, Dushan County, south-eastern Guizhou.
32. *Athyrisina striata* Zhang, *in* Zhang and Fu 1983, p. 352, pl. 117, fig. 1a–e; from the Longjiahe Formation (late Emsian), Gunziling, Longjiahe, Xunyang County, eastern Shaanxi. It could be a small *Athyrisina squamosaeformis* Wang, *in* Wang, Yu and Wu 1974.
33. *Athyrisina subtransversa* Zhang, *in* Zhang and Fu 1983, p. 305, pl. 117, fig. 2a–d; from the Mingbaogou Formation (late Emsian–early Eifelian), Mingbaogou, Wenxian County, south-eastern Gansu. This species has fine costae distributed over the whole shell surface.
34. *Athyrisina sulcata* Zhang, *in* Zhang and Fu 1983, p. 352, pl. 117, fig. 8a–d; from the Dangduo Formation (late Emsian), east Dangduogou, Tewo County, south-eastern Gansu.
35. *Athyrisina tenus* Zhang, 1987, p. 127, pl. 110, figs 11a–d, 12; from the Dangduo Formation (late Emsian), Dangduogou, Tewo County, south-eastern Gansu.
36. *Schizospirifer transversalis* Wang, 1956, p. 388, pl. 6, fig. 3; from the Shizimiao Limestone (Middle Devonian), north of Lianxian County Town, north-western Guangdong. It is doubtful that this species was collected from this locality since no Devonian rocks are exposed to the north of the County Town of Lianxian.
*37. *Athyrisina tumida* Hou and Xian, 1975, p. 43, pl. 27, figs 2–3, 6–8; from the Longdongshui Member of the Houershan Formation (Eifelian), Houershan, Dushan County, south-eastern Guizhou. This species has very similar external morphology, and came from the same locality and horizon as *A. perfecta* (Wang, *in* Wang, Liu, Wu and Zhong 1974), so they must be considered synonyms. An identical species group name (primary homonymy), *Athyrisina tumida*, was established by Wan (*in* Xu *et al.* 1978, p. 351, pl. 123, fig. 2a–c) for athyrisinins from the Yangmaba Formation (latest Emsian), Ganxi, Beichuan, northen Sichuan. Although we consider *Athyrisina tumida* Wan (*in* Xu *et al.* 1978) a subjective synonym of *Athyrisina squamosa* Hayasaka (*in* Yabe and Hayasaka 1920), we suggest *xui* (*Athyrisina xui* Wan, *in* Xu *et al.* 1978) as a new substitute name (*nomen novum*).
38. *Athyrisinopsis uniplicata* Zhang, *in* Zhang and Fu, 1983, p. 354, pl. 119, figs 1–3; from the Shijiagou Formation (early Eifelian), Gunziling, Longjiahe, Xunyang County, eastern Shaanxi. This species is also recorded from the Dangduo Formation (late Emsian–early Eifelian) of Pulaigou, Dangduodonggou, Xiawu'nagou, Wabagou and Pare, Tewo County, south-eastern Gansu and Zhanwagou, Zorge, north-western Sichuan; and the Shijiagou Formation (early Eifelian), Dacigou and Fengzigou, Xunyang County, eastern Shaanxi. See illustration of holotype in Text-figure 7G, K–L, N–P.
39. *Athyrisina wangi* Chen *et al.*, 1989, p. 223, pl. 2, figs 1–26, 28; pl. 3, fig. 3; from the Luhui Member of the Dale Formation (late Emsian), Dale, Xiangzhou County, Guangxi. This species is very similar to *A. grandicostata* Yang (*in* Yang *et al.* 1977, p. 404); further examination of the two taxa is needed.
40. *Kwangsia yohi* Grabau, 1931, pp. 205–207, pl. 25, fig. 4; from Peima Shale (= Baima Shale) (late Emsian), at Peimashih (Baimasi), formerly Teng-Hsien, now Pingnan County, Guangxi. Chen *et al.* (1989), after revision of topotypical material, provided additional data on the umbonal structures (cardinalia and articulation) of this species.
41. *Athyrisina yohi kumaliuensis* Wan, *in* Xu *et al.* 1978, p. 350, pl. 122, fig. 6 (= *Athyrisina yohi kumaliuensis* Wan, 1980, p. 104, pl. 33, fig. 6); from the Xiejiawan Formation (early Emsian), Baiyangdong, Beichuan County, northern Sichuan.

Species questionably assigned

1. *Athyrisinoidea beichuanensis* Wan, *in* Xu *et al.*,1978, p. 353, pl. 123, fig. 4 (= *Athyrisinoidea beichuanensis* Wan, 1980, p. 106, pl. 30, fig. 1); from the Ganxi Formation (early Emsian), Ganxi, Beichuan County, northern Sichuan (poorly known; requires revision).
2. *Athyrisina kochi* Grabau, 1931, p. 521, pl. 53, fig. 1; from Middle Devonian Beds, Lu'nan County (see Wang *et al*. 1964). Interior unknown.

3. *Athyrisina quadriplicata* Grabau, 1931, p. 523, pl. 52, fig. 11; from Wang-Chia Beds (Middle Devonian), southern Gansu. No interiors known. It is unclear whether this species is an athyridoid or a rhynchonelloid. Exact locality and age are also doubtful.
4. *Atrythyris dangduoensis* Zhang, 1987, p. 128, pl. 1, fig. 6a–e; from the Dangduo Formation (late Emsian–Eifelian), east Dangduogou, Tewo County, south-eastern Gansu (see Text-fig. 6J, K, N–P). Internally this species resembles *Athyrisina* more than *Atrythyris* (see Struve 1965, p. 220, figs 4–8).

Species excluded

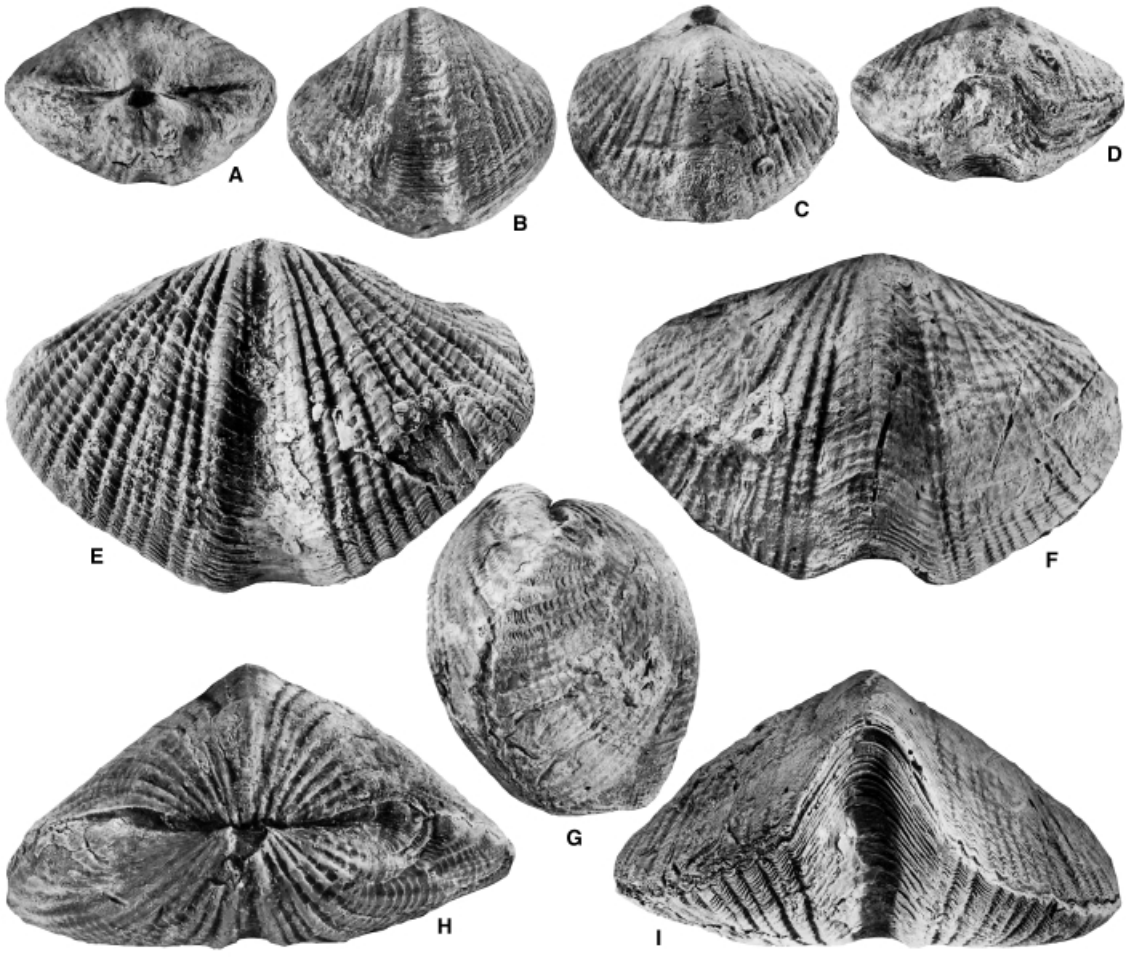
1. *Athyrisinopsis concentricata* Zhang, *in* Zhang and Fu 1983, p. 356, pl. 119, figs 13–14; from the Dangduogou Formation (late Emsian–Eifelian), east Dangduogou, Tewo County, south-eastern Gansu. Although *Athyrisinopsis* is here considered synonymous with *Athyrisina*, this species might not be assigned to *Athyrisina* because of lack of a sulcus or fold and presence of a fine median plica.
*2. *Athyrisinopsis gansuensis* Zhang, *in* Zhang and Fu 1983, p. 355, pl. 118, figs 7–11; from the Dangduo Formation (late Emsian–Eifelian), Pulaigou, Tewo County, south-eastern Gansu Province. Selected as type species of *Bruntosina* gen. nov. (see below).
3. *Athyrisina minor* Hayasaka, *in* Yabe and Hayasaka 1920 (see also Hayasaka 1922, p. 54, pl. 2, figs 8–12). This species was assigned to *Retziella* Nikiforova, 1937, by Rong *et al*. (1994; see also discussion in Rong and Yang 1980).
4. *Athyrisinopsis ovata* Zhang, *in* Zhang and Fu 1983, p. 355, pl. 119, figs 4–5; from the Shijiagou Formation (Eifelian), Dangjiagou, Huilong, Xunyang County, south-eastern Shaanxi; assigned to *Bruntosina* gen. nov. (see below).
5. *Athyrisina plicata* (Mansuy), Grabau, 1931, p. 519, pl. 52, figs 8–10 (*non* Mansuy, 1912); from the Miaokao Formation (late Ludlow–early Přídolí), Hongmiao, Qujing, eastern Yunnan. The concept of *A. plicata* of Grabau (1931) was considered to be a junior synonym of *Retziella minor* (Hayasaka, *in* Yabe and Hayasaka 1920) by Rong *et al.* (1994, p. 565). *Retzia plicata* Mansuy, 1912 was recorded from the Middle Devonian, Lu'na, eastern Yunnan, but internal morphology, age, the exact locality from which the type specimens were collected, and their repository are unknown.
6. *Athyrisinia tangnae* Hou, 1963, p. 416, pl. 2, fig. 3 (the type species of *Parathyrisina* Wang, *in* Wang, Yu and Wu 1974) (see discussion below).
7. *Athyrisinopsis trapeziformis* Zhang, 1987, p. 126, pl. 110, fig. 5a–d; from the Dangduo Formation (late Emsian–Eifelian), Pulaigou, Tewo County, south-eastern Gansu Province. This species is considered a subjective synonym of *Athyrisinopsis gansuensis* Zhang (*in* Zhang and Fu 1983, p. 355), the type species of the new genus *Bruntosina* (see discussion below).
8. *Athyrisina uniplicata* Grabau, 1931, p. 516, pl. 52, figs 1–4; Grabau (1931, p. 519) reported this from Middle Devonian rocks of Yunnan. Rong and Yang (1980) demonstrated that *A. uniplicata* Grabau, 1931 differs from *Athyrisina squamosa* Hayasaka (*in* Yabe and Hayasaka 1920) and assigned it to *Protathyrisina* Chu (=Zhu), 1974. Rong and Yang also selected a neotype (NIGP 46666) for this species, from the Miaokao Formation (late Ludlow–early Přídolí), southern slope of Miaogao Hill, Qujing, eastern Yunnan (see Rong and Yang 1980, pl. 4, figs 1–4). Later, *A. uniplicata* was assigned to *Molongia* by Rong *et al*. (1987) and finally to *Retziella* by Rong *et al.* (1994).

Occurrence. Lower Devonian (upper Pragian) to Middle Devonian (Givetian) in South China Palaeoplate (including northern Sichuan, south-eastern Guizhou, eastern Yunnan, and Guangxi), Qinling region (including western and eastern Shaanxi, south-eastern Gansu and northernmost Sichuan), western Sichuan (Ganzi Block), and north Vietnam.

Genus PARATHYRISINA Wang, *in* Wang, Yu and Wu 1974

Plate 1, figures 1–17; Text-figures 4, 11A–I, 12A–B

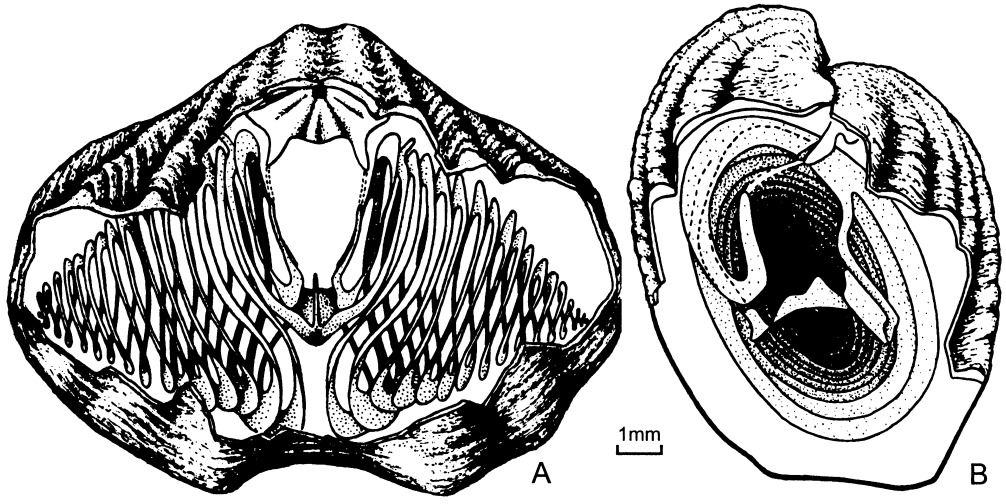
1974 *Parathyrisina* Wang, *in* Wang, Yu and Wu, p. 41.
1975 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Hou and Xian, p. 41.
1977 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Yang *et al.*, p. 404.
1978 *Athyrisinoides* Chen and Wan, *in* Xu *et al.*, p. 351.
non 1978 *Athyrisinoides* Jiang, *in* Xian and Jiang, p. 303.
1978 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Chen and Wan, *in* Xu *et al.*, p. 348.
1979 *Athyrisinoides* Chen and Wan, *in* Xu *et al.*; Chen, p. 18.
1980 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Wan, p. 103.



TEXT-FIG. 11. A–D, *Parathyrisina longmenshanensis* (Chen, 1979), posterior, ventral, dorsal, and anterior views of holotype (CCGB75166). E–I, *Parathyrisina sinensis* (Chen, 1979); ventral, dorsal, lateral, posterior, and anterior views of holotype (CCGB75121A); all specimens from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan; all ×1·5.

1980 *Athyrisinoidea* Chen and Wan, *in* Wan, p. 105 (*nom. nov. pro Athyrisinoides* Chen and Wan, *in* Xu *et al.* 1978, p. 351).
1986 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Wang and Rong, p. 164.
1988 *Neoathyrisina* Chen, p. 36.
1998 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Alvarez *et al.*, p. 842
1999 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Chen and Yao, p. 232.
2001 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Talent *et al*., p. 178.
2002 *Parathyrisina* Wang, *in* Wang, Yu and Wu; Alvarez and Rong, p. 1507.

Type species. Parathyrisina bella Wang, *in* Wang, Yu and Wu 1974, p. 41, pl. 5, figs 21–22; from the Liujing Member of the Yukiang Formation (upper lower Emsian), Liujing, Hengxian County, Guangxi. Hou and Xian (1975, p. 42) considered this species as a junior synonym of *Athyrisin*a *tangnae* Hou, 1963 (p. 416, pl. 2, fig. 3) from the same locality and horizon.



TEXT-FIG. 12. Ventral (A) and lateral (B) views of a reconstructed brachio-jugal system in *Parathyrisina tangnae* (Hou, 1963), upper Pragian–lower Emsian, Guangxi (southern China).

Emended diagnosis. Commonly small to medium, rarely large, transverse subelliptical to subcircular outline, equally to subequally biconvex; pedicle opening large, palintrope reduced; ventral sulcus and dorsal fold rounded, commonly well developed, without radial elements; lateral slopes bearing three or more costae, growth lamellae well developed; interior and jugum essentially as in *Athyrisina.*

Remarks. When he erected *Parathyrisina*, Wang designated *P. bella* Wang, *in* Wang, Yu and Wu 1974 as its type species, and included *Athyrisina tangnae* Hou (1963, p. 416, pl. 2, fig. 3) in his new genus. Later, Hou and Xian (1975, p. 42) pointed out that *P. bella* and *A. tangnae* were conspecific. Recently, Wang and Rong (1986, text-figs 78–81, 83) showed that the spiralium and jugum in *P. tangnae* are very similar to those of *Athyrisina*.

Athyrisinoidea was proposed by Chen and Wan (*in* Wan, 1980, p. 105) as a replacement name for the Devonian brachiopod *Athyrisinoides* Chen and Wan (*in* Xu *et al.* October 1978, p. 351) from northern Sichuan, since the latter was preoccupied by a homonym brachiopod genus erected by Jiang (*in* Xian and Jiang, March 1978, p. 303) with Silurian (Llandovery) brachiopods from northern Guizhou. According to Chen and Wan (*in* Xu *et al*. 1978, and *in* Wan 1980; see also Chen 1979) *Athyrisinoidea* differs from *Parathyrisina* in having a larger shell, different outline, bifurcated plicae, and a large number of whorls in

EXPLANATION OF PLATE 1

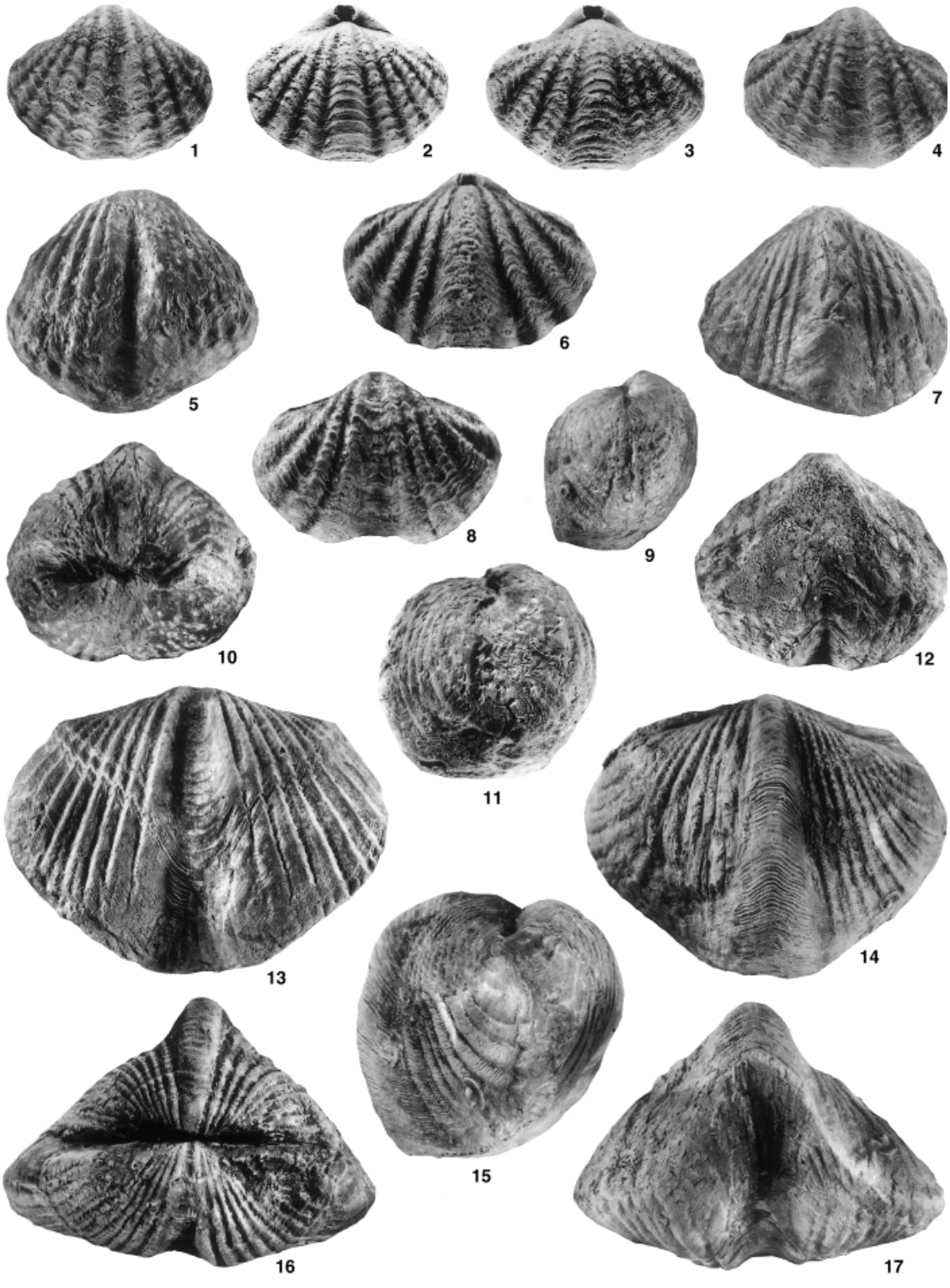
Figs 1–4, 6, 8. *Parathyrisina tangnae* (Hou, 1963), from the Liujing Member of the Yukiang Formation (early Emsian), Hengxian County, Guangxi. 1–2, ventral and dorsal views (NIGP88076). 3–4, dorsal and ventral views (NIGP88069). 6, 8, dorsal and ventral views (NIGP88075). All ×2.

Figs 5, 7, 10–12. *Parathyrisina cheni* (Chen, 1979); ventral, dorsal, posterior, lateral and anterior views of holotype (CCGB75154).

Fig. 9. *Parathyrisina longmenshanensis* (Chen, 1979); lateral view of holotype (CCGB75166) (for more views of this species see Text-fig. 11).

Figs 13–17. *Parathyrisina typica* (Chen and Wan, *in* Xu *et al*. 1978); ventral, dorsal, lateral, posterior, and anterior views of holotype (CCGB75151).

With the exception of *Parathyrisina tangnae* (Hou, 1963), all specimens illustrated came from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan and are ×1·5.



RONG *et al.*, *Parathyrisina*

the spiralium. Most of these differences seem to be related to ontogenetic changes, so we consider *Athyrisinoidea* to be a subjective synonym of *Parathyrisina* (see also Alvarez *et al.* 1998; Talent *et al.* 2001; Alvarez and Rong 2002). *Parathyirisina typica* (Chen and Wan, *in* Wan 1980), the type species of *Athyrisinoidea* Chen and Wan, *in* Wan 1980, can be distinguished from *Parathyrisina tangnae* in having, in the adult stage, more numerous bifurcated plicae on the flanks (compare Pl. 1, figs 1–4, 6, 8 with Pl. 1, figs 13–17).

Species assigned. Of the 14 species assigned to this genus, eight are here regarded as subjective junior synonyms (those marked with an asterisk):

1. *Athyrisina tangnae* Hou, 1963, p. 416, pl. 2, fig. 3; from the Liujing Member of the Yukiang Formation (early Emsian), Liujing, Hengxian County, Guangxi. The width of the shell is commonly between 10 and 22 mm; it has about 3–6 (commonly 4–5) lateral, unbifurcated, costae on each flank.

*2. *Parathyrisina bella* Wang, *in* Wang, Yu and Wu 1974, p. 41, pl. 5, figs 21–22; pl. 6, fig. 1; from the Liujing Member of the Yukiang Formation (early Emsian), Liujing, Hengxian County, Guangxi. This species, the type species of the genus (see Wang *in* Wang, Yu and Wu 1974), was considered by Hou and Xian (1975, p. 42; see also Yang *et al.* 1977, p. 405; Wang and Rong 1986, p. 165; Alvarez and Rong 2002, p. 1507) as a junior synonym of *A. tangnae* Hou, 1963.

3. *Parathyrisina ganxiensis* Wan and Chen, *in* Xu *et al.* 1978, p. 349, pl. 119, fig. 7a–e (= *Parathyrisina ganxiensis* Wan, 1980, p. 103, pl. 28, fig. 7a–e); from the Ganxi Formation (early Emsian), Ganxi, Beichuan County, northern Sichuan. This species differs from *Athyrisina tangnae* Hou in having a larger number of costae (*c.* 8–10) on each flank.

4. *Athyrisinoides ganxiensis* Wan, *in* Xu *et al.* 1978, p. 352, pl. 122, fig. 1a–d (= *Athyrisinoides ganxiensis* Wan 1980, p. 105, pl. 29, fig. 1a–d); from the Ganxi Formation (early Emsian), Ganxi, Beichuan, northern Sichuan. As *Athyrisinoides* has been regarded (e.g. Alvarez and Rong 2002, p. 1507) as a junior synonym of *Parathyrisina*, *Athyrisinoides ganxiensis* Wan, *in* Xu *et al.* 1978 (p. 352), becomes a homonym of *P. ganxiensis* Wan and Chen, *in* Xu *et al.* 1978 (p. 349) (secondary homonymy, Art. 53.3 of the 1999 Code). The homonym, *Athyrisinoides ganxiensis* Wan, *in* Xu *et al.* 1978, is here rejected and, as it has no known available and potentially valid synonym (Art. 60 of the Code, 1999) we suggest *wani* (*Parathyrisina wani* Wan, *in* Xu *et al.* 1978) as a new substitute name (*nomen novum*).

5. *Athyrisinoidea longmenshanensis* Chen, 1979, p. 21, pl. 10, figs 1a–e–7; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan. This species is 17·4–27 mm wide, has a broad fold and shallow sulcus, and fine, bifurcating costae.

*6. *Parathyrisina minor* Wan, *in* Xu *et al.* 1978, p. 349, pl. 122, fig. 4a–e (= *Parathyrisina minor* Wan, 1980, p. 103, pl. 29, fig. 4a–e) (*non Parathyrisina minor* Zhang, *in* Zhang and Fu 1983, p. 375); from the Ganxi Formation (early Emsian), Ganxi, Beichuan County, northern Sichuan. This species is very similar to *Parathyrisina ganxiensis* Wan and Chen, *in* Xu *et al.* 1978 in both external and internal morphology; it has 7–8 plications on each flank but is a relatively smaller shell (less than 15 mm wide).

*7. *Parathyrisina minor* Zhang, *in* Zhang and Fu 1983, p. 357, pl. 118, figs 3a–e–4a–e (*non Parathyrisina minor* Wan, *in* Xu *et al.* 1978, p. 349); from the Xigou Formation (early Emsian), Minbaogou, Wenxian County, southeastern Gansu. *Parathyrisina minor* Zhang (*in* Zhang and Fu 1983) is a secondary homonym of *Parathyrisina minor* Wan (*in* Xu *et al.* 1978) (see Art. 53.3 of the 1999 Code). Furthermore, although *Parathyrisina minor* Zhang (*in* Zhang and Fu 1983) could be considered a subjective synonym of *P. tangnae* (Hou, 1963), from which it differs in its smaller size (5·5–7·2 mm wide) and in having only three costae on each flank, we reject the homonym *Parathyrisina minor* Zhang (*in* Zhang and Fu 1983) and suggest *minima* (*Parathyrisina minima* Zhang, *in* Zhang and Fu 1983) as a *nomen novum.*

8. *Athyrisinoidea sinensis* Chen 1979, p. 20, pl. 7, figs 1a–e–6a–e; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan. This distinctive species is characterized by having a large shell (23–47 mm wide), with 14–15 (in larger shells) bifurcated costae on each flank, occasionally with 2–4 fine costellae in the ventral sulcus, and with well developed growth lamellae on the whole shell.

9. *Parathyrisina tangnae sichuanensis* Chen, 1979, p. 16, pl. 8, figs 1a–e–3; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan. We consider *P. sichuanensis* as an independent species rather than a subspecies of *P. tangnae*. *P. sichuanensis* Chen, 1979 has medium-sized shells (11·5–18·0 mm wide), fine costae that do not bifurcate (8–10 on each flank), and delicate growth lamellae.

10. *Parathyrisina transitoria* Chen and Yao, 1999, p. 232, pl. 2, figs 4–26; from the Dale Formation (late Emsian), Zhongping, Xiangzhou County, Guangxi. According to Chen and Yao, most specimens of this species have a smooth sulcus and fold, but a few specimens show a few, very weak plications anteriorly on the fold and sulcus and 7–10 slender plications (some of them bifurcating anteriorly) on each flank.

*11. *Parathyrisina tudilingensis* Chen, 1979, p. 15, pl. 5, figs 1a–e–8a–e; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan County, northern Sichuan. This species could be considered as a subjective synonym of *Parathyrisina tangnae* (Hou, 1963).
*12. *Athyrisinoides tudilingensis* Chen, 1979, p. 21, pl. 6, figs 4a–e–5a–e; from the Tudiling Member of the Bailiuping Formation (late Pragian), Bailiuping, Ganxi, Beichuan, northern Sichuan. As *Athyrisinoides* has been regarded (e.g. Alvarez and Rong 2002, p. 1507) as a junior synonym of *Parathyrisina*, *Athyrisinoides tudilingensis* Chen, 1979 (p. 21), becomes a homonym of *Parathyrisina tudilingensis* Chen, 1979 (p. 15) (secondary homonymy, Art. 53.3 of the 1999 Code). Furthermore, although *Parathyrisina tudilingensis* Chen, 1979 (p. 15) could be considered a subjective synonym of *Parathyrisina ganxiensis* Wan and Chen (*in* Xu *et al*. 1978) (they are very similar and came from the same locality and horizon), the homonym, *Athyrisinoides tudilingensis* Chen, 1979 (p. 21), is here rejected and, as it has no known available and potentially valid synonym (Art. 60 of the 1999 Code), we suggest *cheni* (*Parathyrisina cheni* Chen, 1979) as a new substitute name (*nomen novum*). See Plate 1, figs 5, 7, 10–12.
13. *Athyrisinoidea typica* Chen and Wan, *in* Xu *et al.* 1978, p. 352, pl. 122, figs 2a–e–3a–d (= *Athyrisinoides typica* Chen, 1979, p. 19, pl. 6, figs 1a–e–3a–e; pl. 10, fig. 9c; *Athyrisinoides typica*, Wan, 1980, p. 105, pl. 29, figs 2a–e–3a–d); from the Ganxi Formation (early Emsian), Ganxi, Beichuan County, northern Sichuan. This species is characterized by having a large shell (26·5–41 mm wide), high anterior tongue, fine, usually unbranched plications, and uneven growth lamellae.
*14. *Athyrisinoidea zhangjiapoensis* Wan, *in* Xu *et al.* 1978, p. 352, pl. 123, fig. 5a–e (= *Athyrisinoidea zhangjiapoensis* Wan, 1980, p. 106, pl. 30, fig. 2a–e); from the Ganxi Formation (early Emsian), Ganxi, Beichuan County, northern Sichuan. This species is very similar to *Athyrisinoidea typica* in both external morphology and internal structures. They came from the same locality and horizon. We consider them to be conspecific.

Occurrence. Lower Devonian (upper Pragian–upper Emsian) in Guangxi and Sichuan, South China; south-eastern Gansu and north-western Sichuan, western Qinling.

Genus BRUNTOSINA gen. nov.

Plate 2, figures 1–25; Text-figures 4, 6M, 7A–F, H–J, M, 8, 13–14

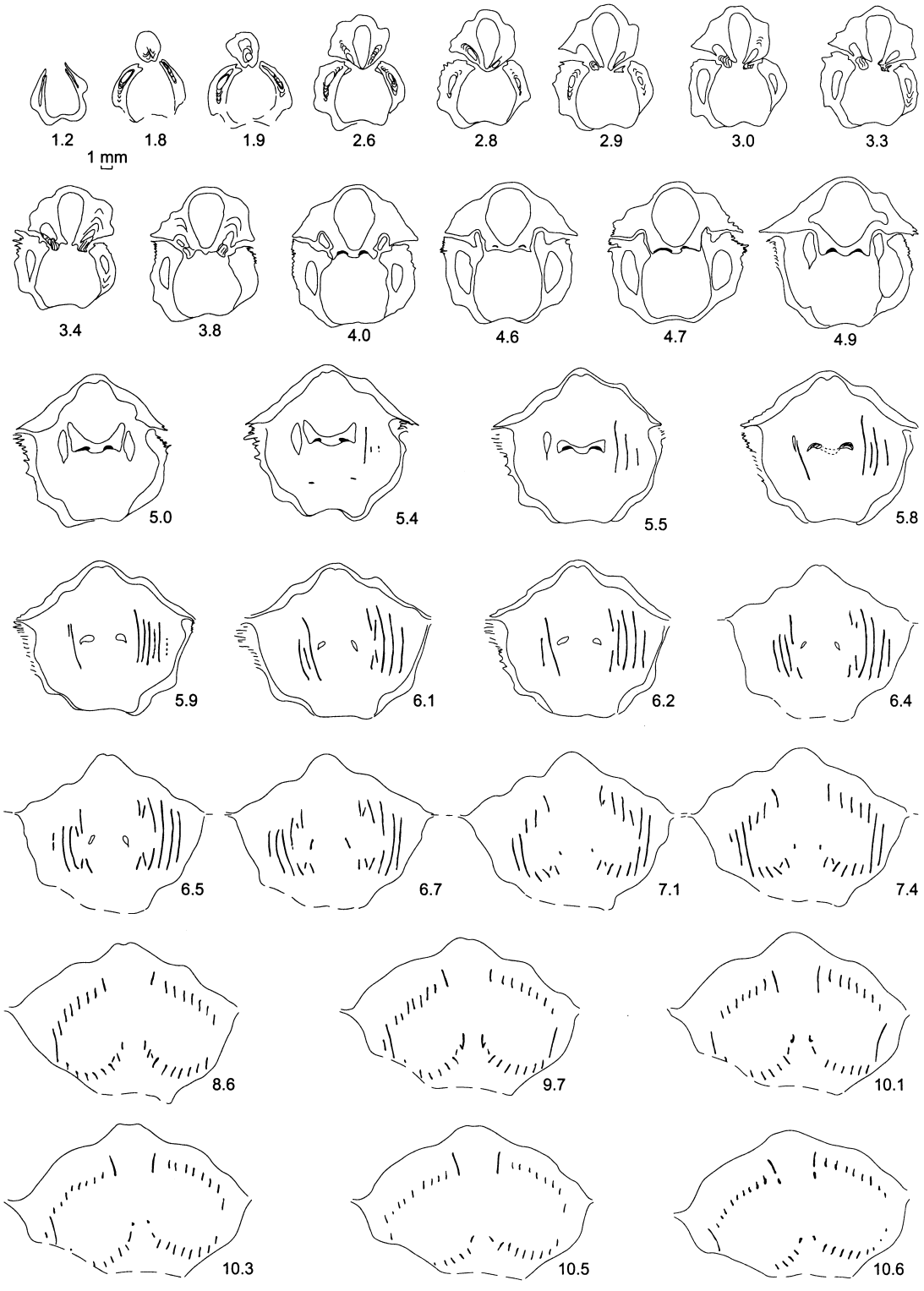
Derivation of name. After C. Howard C. Brunton, and sino, pertaining to China and the Chinese.

Type species. *Athyrisinopsis gansuensis* Zhang, *in* Zhang and Fu 1983, p. 355, pl. 118, figs 7–11, from the Dangduo Formation, Pulaigou, Tewo County, south-eastern Gansu Province, China, Early–Middle Devonian (late Emsian–early Eifelian) [= *Athyrisinopsis trapeziformis* Zhang, 1987, p. 126, pl. 110, fig. 5a–d (XB233, holotpe) from the same locality and formation]. The age determination of the Dangduo Formation is based on mega-benthic fossils (rugose corals and brachiopods) and regional stratigraphical correlation in South China, without support from conodonts and dacryoconarids. Further investigation of the age is required.

Species assigned. In addition to the type species, *Athyrisinopsis ovata* Zhang (*in* Zhang and Fu, 1983, p. 355, pl. 119, figs 4–5, XB247, holotype) from the Shijiagou Formation (Eifelian), Dangjiagou, Huilong Village, Xunyang County, south-eastern Shaanxi Province (East Qinling), is placed in this genus.

Diagnosis. Medium to large, elongate oval, subcircular to transversely oval and nearly equally biconvex shells; ventral sulcus and dorsal fold well developed; pauciplicate on flanks, without bifurcation or intercalation, a single costa is characteristically present in the middle of the sulcus, and a shallow furrow on the middle of the fold; variably spaced growth lamellae on any of which there are up to 80 growth lines; dental plates thin, long, and parallel, lateral apical cavities wider than for the subfamily; cardinalia, spiralium and jugum essentially as in *Athyrisina*.

Remarks. *Bruntosina* has a more restricted distribution than the other athyrisinins; it is only known from the West Qinling Mountains. It resembles *Athyrisina*, the type genus of the Athyrisininae, but has fewer plications (generally 2) on its flanks, the ribs bounding the sulcus being stronger. The radial elements are more numerous in *Athyrisina*, being costae (e.g. *A. squamosa*, the type species of the genus) or costae and costellae (e.g. *A. tenus*). *Bruntosina* characteristically has a single, narrow costa in the middle of the sulcus, whereas *Athyrisina* has three or more ribs (of the same width as those on the flanks) in the sulcus,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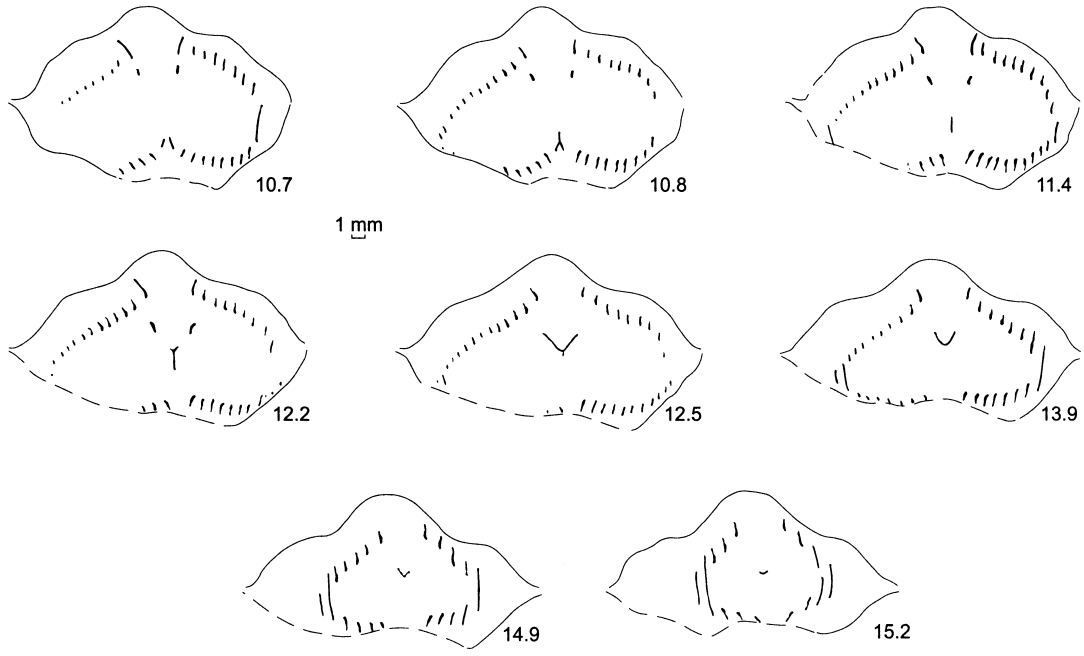


TEXT-FIG. 13. Selected transverse serial sections illustrating the internal structures in *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983), f134228, from the Dangduo Formation, Early–Middle Devonian (late Emsian–early Eifelian), Pulaigou, Tewo County, south-eastern Gansu Province, China; distances measured in mm from the posterior end; distance to the first section is approximate.

and *Parathyrisina* has no radial elements on the sulcus or fold. Growth lamellae are numerous and regularly spaced in *Athyrisina*, but in *Bruntosina* they are variably spaced (up to five on adult valves), with up to 80 fine growth lines on each lamellae. Internally, the dental plates are long and parallel in *Bruntosina*, but very short, with very narrow lateral apical cavities, in *Athyrisina* and *Parathyrisina*.

Occurrence. Upper Emsian and Eifelian of west and east Qinling, China.

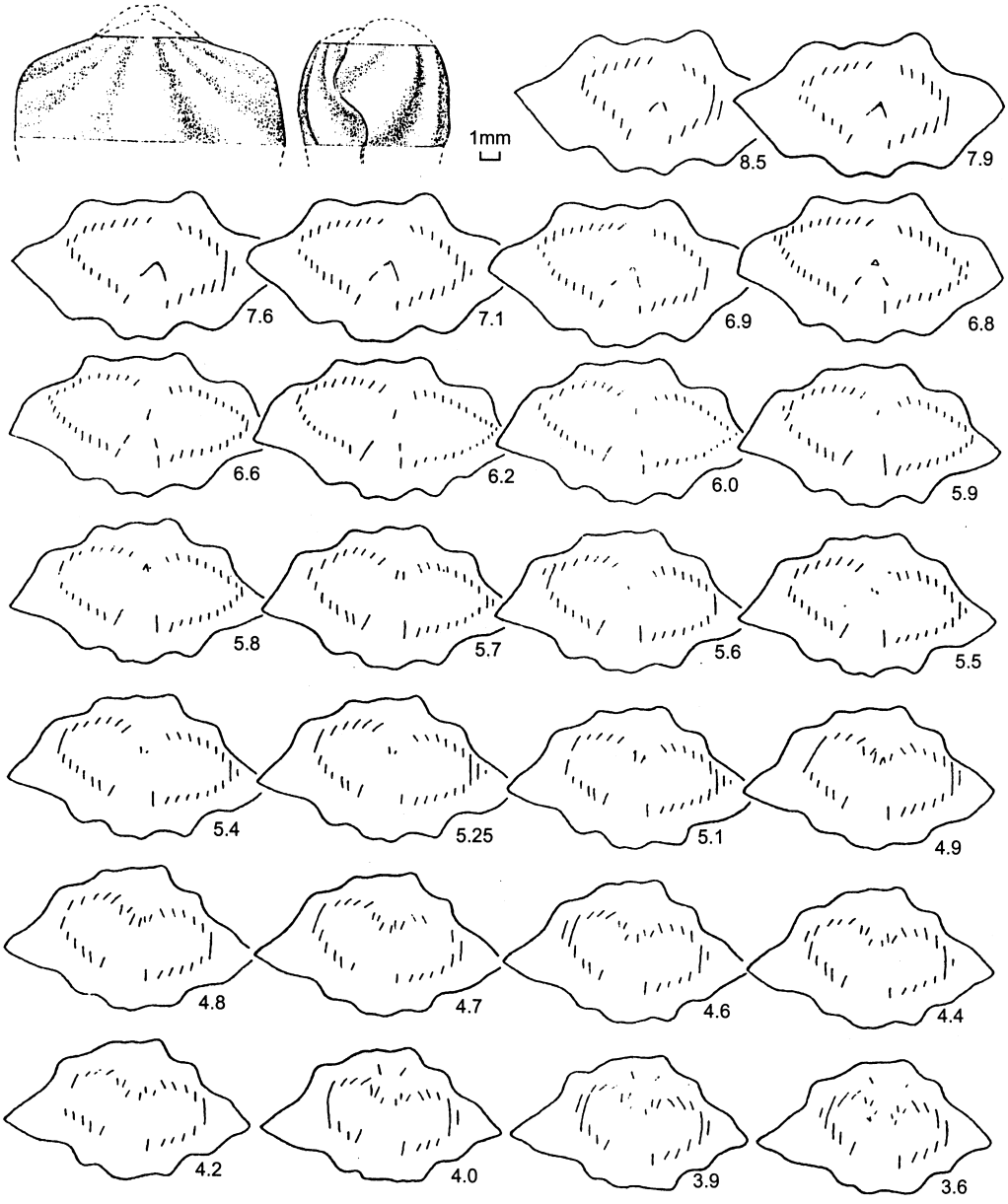
Bruntosina gansuensis (Zhang, *in* Zhang and Fu 1983) comb. nov.

Plate 2, figures 1–25; Text-figures 6M, 7A–F, H–J, 8, 13–14

1983 *Athyrisinopsis gansuensis* Zhang, *in* Zhang and Fu, p. 355, pl. 118, figs 7–11.
1987 *Athyrisinopsis gansuensis* Zhang, *in* Zhang and Fu; Zhang, p. 126, pl. 110, figs 2a–d, 3.
1987 *Athyrisinopsis trapeziformis* Zhang, p. 126, pl. 110, fig. 5a–d.

Holotype. Specimen XB239, from Dangduo Formation, upper Emsian–lower Eifelian, Pulaigou, about 23 km north of Tewo County Town, south-eastern Gansu Province (Text-fig. 7F, H–J, M; see also Zhang, *in* Zhang and Fu 1983, p. 355, pl. 118, fig. 10a–d).

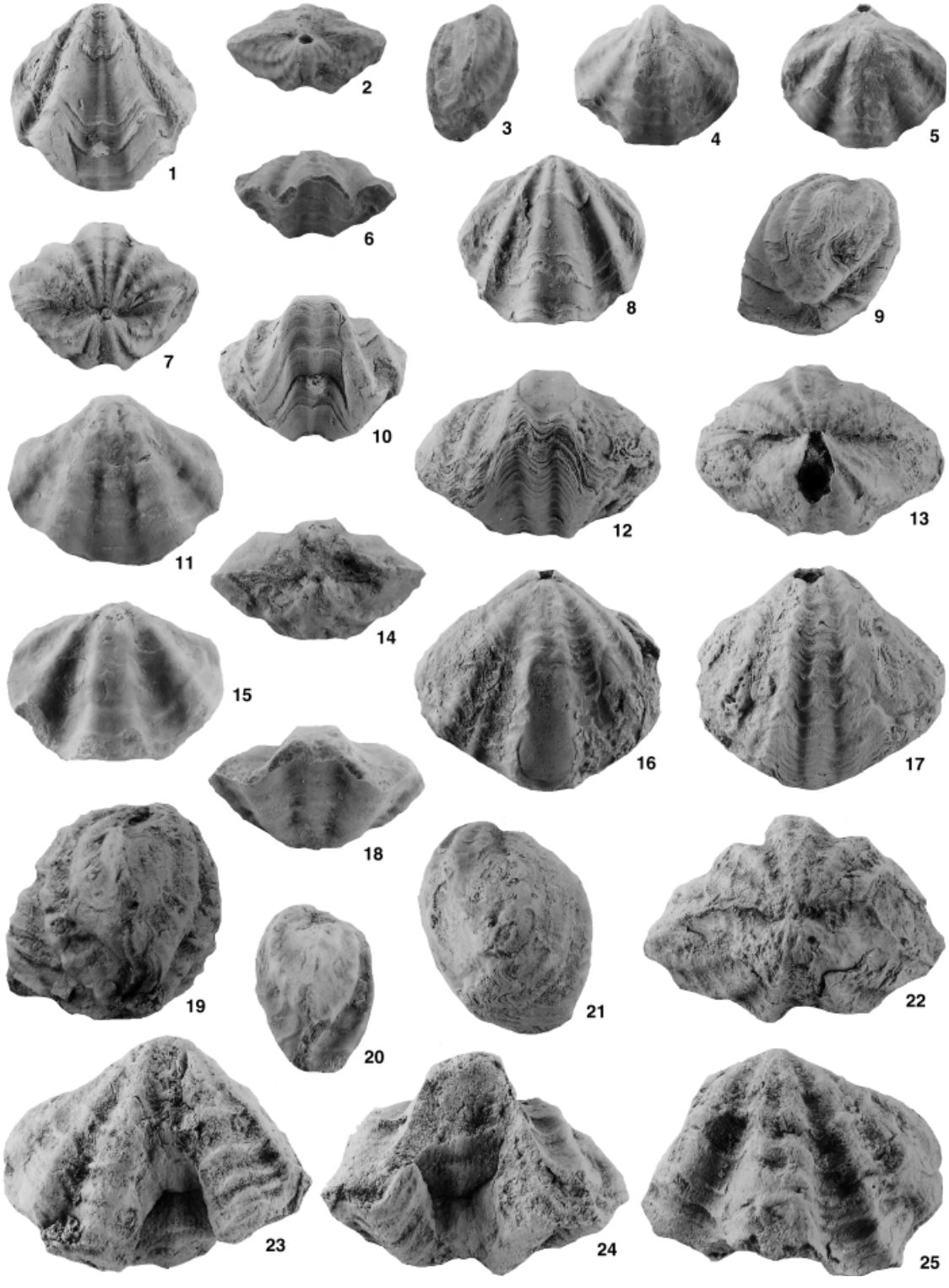
Material and precedence. Besides the holotype and the paratypes, the other specimens described by Zhang (*in* Zhang and Fu 1983), and here revised, are from many localities in the neighbouring areas of the Qinling Region. Some were collected in Pare, Wabagou, Xia Wu'nagou, and Anzigou, about 20 km north-east of Tewo County Town, south-eastern Gansu; others, in Beichagou, Larencakuo, about 30 km south of Luqu County Town, south-eastern Gansu Province; and finally, others are from Zhanwagou, Zorge County, northernmost Sichuan (Text-fig. 1). *Bruntosina gansuensis* is also known from the banks of the upper Bailong Jiang (White Dragon River), and associated streams, in



TEXT-FIG. 14. Selected transverse serial sections illustrating the internal structures in *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983), ventral valve up, f134229, from the Dangduo Formation, Early–Middle Devonian (late Emsian–early Eifelian), Pulaigou, Tewo County, south-eastern Gansu Province, China; distances measured in mm from the posterior end.

EXPLANATION OF PLATE 2

Figs 1–25. *Bruntosina gansuensis* (Zhang, in Zhang and Fu 1983). 1, 7–10, ventral, posterior, dorsal, lateral, and anterior views (XB230). 2–6, posterior, lateral, ventral, dorsal, and anterior views (XB236, paratype). 11, 14–15, 18, 20, ventral, posterior, dorsal, anterior, and lateral views (XB237, paratype). 12–13, 16–17, 21, anterior, posterior, dorsal, ventral, and lateral views (NIGP f134225). 19, 22–25, lateral, posterior, ventral, anterior, and dorsal views (NIGP f134226). All specimens are from the Dangduo Formation (late Emsian–early Eifelian); 1, 7–10, 19, 22–25 from Dangduobeigou; the others from Pulaigou, Tewo County, south-eastern Gansu. All × 1·5.



RONG *et al.*, *Bruntosina*

Wenxian County, south-eastern Gansu, where the Minbaogou Formation (upper Emsian–lower Eifelian) crops out prominently. This is a remote area, of very difficult access, in the middle of the West Qinling Mountains, at the border between Gansu and Sichuan provinces.

Horizon and locality. Upper Emsian–Eifelian; west and east Qinling Mountains (south-eastern Gansu, northernmost Sichuan, and south-eastern Shaanxi). The horizons containing the specimens are in the Dangduo Formation (upper Emsian–lower Eifelian). *S. gansuensis* (Zhang, *in* Zhang and Fu 1983) occurs mainly in greenish grey limestone of the Dangduo Formation at Pulaigou (the type locality) and other related localities. All available specimens assigned to this species are conjoined valves in excellent preservation (see Pl. 2, figs 1–25 and Text-fig. 8). Community and facies analyses of these horizons suggest quiet, oxygen-rich, warm environmental conditions on the shelf, with well-developed reef-bank facies (Zhang 1987). In addition to the abundant brachiopods, there are also rugose and tabulate corals and stromatoporoids, which sometimes formed reefs. Richness and diversity of brachiopods reached its maximum in the late Emsian and Eifelian when *Bruntosina* gen. nov. occurred. One of the most remarkable features of this formation is the presence of pavements of brachiopods, such as *Athyrisina* and *Uncinulus*, at several horizons.

Diagnosis. Bi- to dorsibiconvex, usually transversely oval to subcircular shells, more rarely of elongate oval outline; commonly about five, variably spaced, growth lamellae on each adult valve.

Comparison. The species *A. ovata* (Zhang, *in* Zhang and Fu 1983, p. 355), from the Shijiagou Formation (Eifelian) of Xunyang County, south-eastern Shaanxi, here assigned to *Bruntosina* gen. nov., differs from the type species by having an elongate oval shell outline, more lateral ribs (3–4), and closely distributed growth lamellae (compare, for example, Zhang, *in* Zhang and Fu 1983, pl. 118, figs 7–10, with pl. 119, figs 4–5). *S. ovata* was previously assigned to *Athyrisinopsis* by Zhang (*in* Zhang and Fu 1983, 1987). The holotype of the type species of *Athyrisinopsis*, *A. uniplicata* Zhang, *in* Zhang and Fu 1983 (illustrated here in Text-fig. 7G, K–L, N–P; see also Zhang, *in* Zhang and Fu 1983, pl. 119, fig. 1a–d, XB243) is from the Shijiagou Formation (Eifelian), Gunziling, Longjiagou, Xunyang County, western Shaanxi. Almost simultaneously, she illustrated another specimen (XB244) of *A. uniplicata* (Zhang, *in* Zhang and Fu 1983, pl. 119, fig. 2), collected from the Dangduo Formation (upper Emsian) in east Dangduogou, Tewo County, south-eastern Gansu Province. Both specimens of *A. uniplicata* differ from *Bruntosina gansuensis* (Zhang, *in* Zhang and Fu 1983), in having a higher number of plications on the flanks and sulcus which increase in number by bifurcation or intercalation, a character never seen in *Bruntosina*.

Remarks. The holotype, the two paratypes (see Zhang, *in* Zhang and Fu 1983, pl. 118, figs 7–8, 10a–d), and seven other topotype specimens (including XB429) differ from the specimens collected by Zhang, in upper Emsian levels of the Dangduo Formation outcropping in Dangduogou and Xiawunagou, Tewo County, south-eastern Gansu Province (e.g. specimens XB230–231; see Zhang, 1987, p. 126, pl. 110, figs 2a–d–3), in having a more transverse shell outline, less convex lateral profile, and much shallower ventral sulcus. But with the number of specimens and range of sizes available it is difficult to test if the differences between these two groups are significant, at least at the univariate and bivariate levels. The difficulty of access to these outcrops of the Dangduo Formation (upper Emsian) in the Qinling Mountains, prevented, in spite of all our efforts, the collection of sufficient specimens to enable us to study the morphological variability of this polymorphic species, or the possible discrimination of a new species for the oldest specimens from Dangduogou and Xiawunagou.

Subfamily HOMEATHYRIDINAE subfam. nov.

Diagnosis. Shells small to medium, biconvex, moderately to strongly rostrate, costate or costellate; growth lamellae commonly poorly developed, but may be squamose (*Squamathyris*); fold and sulcus variably developed, variably developed furrow, commonly shallow, may medially divide the dorsal fold (*Homeathyris*); hypothyridid pedicle opening commonly partially closed by deltidial plates; dental plates commonly short, converging dorsally, may become subparallel anteriorly; large delthyrial chamber with pedicle support consisting of pedicle collar (*Pseudohomeospira*) or two variably developed curved plates, formed of secondary layer, medially and apically situated between dental plates and joined with

them at their posterodorsal end (*Homeathyris* and *Squamathyris*); cardinal plate apically perforated posteriorly; hinge plate ventrally concave in early forms, flat in latest species; spiralium and jugum resembling that of typical athyridines but with very short accessory lamellae.

Type genus. Homeathyris Modzalevskaya, 1997*a*, p. 7.

Genera assigned. In addition to the type genus, *Pseudohomeospira* Nikiforova, 1970, and *Squamathyris* Modzalevskaya, 1981 are placed in this subfamily.

Remarks. These three genera are here removed from the Athyrisininae, where they were commonly placed (Nikiforova 1970; Modzalevskaya 1981, 1994, 1997*a*, *b*; Grunt 1984, 1986; Alvarez *et al*. 1998; Alvarez and Rong 2002). They differ from typical athyrisinins (*Athyrisina* and its allies) in having a hypothyridid pedicle opening partially closed by deltidial plates, in having a pedicle collar (the younger genus, *Pseudohomeospira*) or medially and apically situated plates between the dental plates and joined with them at their posterodorsal end (*Homeathyris* and *Squamathyris*), and in having a jugum with very short accessory lamellae. Homeathyridine internal characters resemble those of some Didymothyridinae (see Rubel and Modzalevskaya 1967; Modzalevskaya, 1985) from which they mainly differ in having costate or costellate external ornamentation (see Modzalevskaya 1980, 1981, 1985, 1997*a*). This was the main reason why *Homeathyris plicatella*, for example, was initially included within the didymothyridins (Modzalevskaya 1980), being later assigned to *Homeathyris* (Modzalevskaya 1997*a*). The homeathyridins differ from the plicathyridins in lacking mixed folding, cardinal flanges, a dorsal myophragm, and a well-developed jugal saddle and accessory jugal lamellae. They also differ in the morphology and disposition of the lateral branches of the jugum. In the plicathyridins, the lateral branches arise almost perpendicular to the primary lamellae and project ventrally for a short distance, up to a point at which they curve abruptly laterally or anterolaterally; then they project anteroventrally at a low angle until they join as a jugal arch (Alvarez 1976, 1990). In the homeathyridins, however, the lateral branches do not curve abruptly laterally or anterolaterally before projecting anteroventrally. As here defined, the homeathyridins are known from the Upper Silurian (Ludlow–Přídolí) of Arctic Russia and the western slope of the Polar and Central Urals, while the athyrisinins range from the Lower Devonian (Pragian) to Middle Devonian (Givetian) of South China (plus western Sichuan and Qinling regions) and north Vietnam.

Occurrence. Upper Silurian, Ludlow-Přídolí, in Arctic Russia, including Dolgii, Vaigach and Novaya Zemlya islands, and the western slope of the Polar and Central Urals.

Genus HOMEATHYRIS Modzalevskaya, 1997

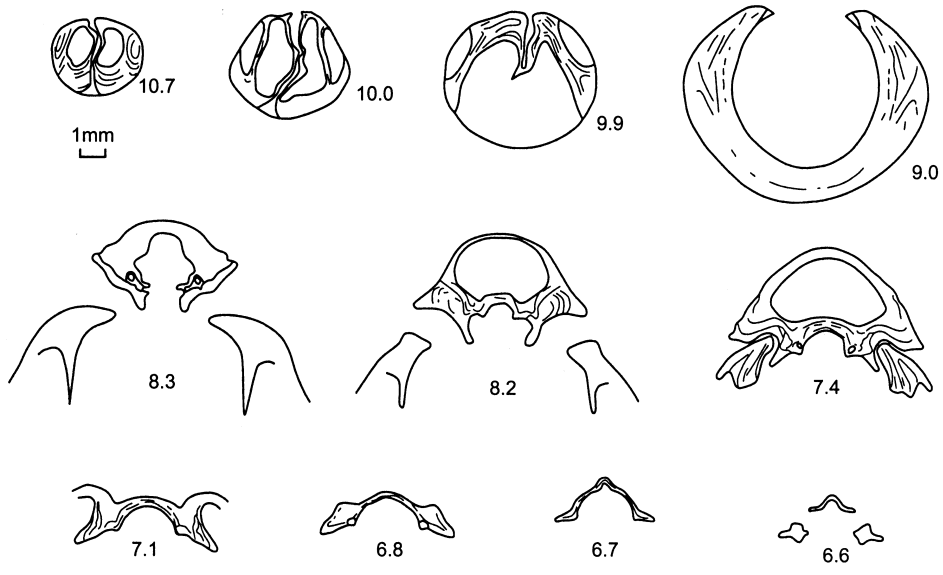
Plate 3, figures 4–5, 16–23; Text-figures 4, 15–16, 19

1994 *Homeathyris* Modzalevskaya *et al.*, p. 66 (*nomen nudum*).
1994 *Homeathyris* Modzalevskaya, p. 147 (*nomen nudum*).
1997*a* *Homeathyris* Modzalevskaya, p. 7.
1997*b* *Homeathyris* Modzalevskaya, p. 209.
2002 *Homeathyris* Modzalevskaya; Alvarez and Rong, p. 1507.

Type species. Homeathyris insularis Modzalevskaya, 1997*a*, p. 7, pl. unnumbered, fig. 3a–b, from Zelenets Formation (Ludfordian), Dolgii Island, Arctic Russia.

Species assigned. In addition to the type species, *Homeathyris plicatella* (Modzalevskaya, 1980, p. 93, pl. 1, figs 18–19, text-fig. 4), from Zelenets Formation, Dolgii Island, Arctic Russia, Upper Silurian, Ludfordian; and *Homeathyris incisus* Modzalevskaya sp. nov. are placed in this genus.

Emended diagnosis. Small to medium, subequally to ventribiconvex shells of subpentagonal to longitudinally oval outline; hypothyridid pedicle opening partially covered by deltidial plates; variably developed furrow divides the dorsal fold medially; ornament of costae or low plications, bifurcated



TEXT-FIG. 15. Selected transverse serial sections illustrating the internal structures in *Homeathyris plicatella* (Modzalevskaya, 1980), CNIGR N2/13099, Zelenets Formation, Ludfordian, Dolgii Island; distances measured in mm from the anterior margin of the shell.

costellae developed in the sulcus and in the median furrow, growth lamellae poorly developed, commonly absent; dental plates short, lateral cavities narrow, delthyrial chamber with two variably developed curved plates medially and apically situated between dental plates and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with 7–10 whorls.

Remarks. *Homeathyris* Modzalevskaya, 1997*a* differs externally from *Pseudohomeospira* Nikiforova, 1970, and *Squamathyris* Modzalevskaya, 1981, in having a variably developed furrow dividing the dorsal fold medially. Growth lamellae are poorly developed in *Homeathyris* and *Pseudohomeospira*, but well developed (being *squamosus*) in *Squamathyris*. Internally, *Homeathyris* and *Squamathyris* have a subtriangular and ventrally concave hinge plate, while this is almost flat in *Pseudohomeospira* (Text-figs 15–18). *Homeathyris* and *Squamathyris* also differ from *Pseudohomeospira* in having medially and apically situated plates between the dental plates and joined with them at their posterodorsal ends, while *Pseudohomeospira* has a pedicle collar (Modzalevskaya 1981, 1997*a*). These pedicle supports are commonly longer, in relation to the total length of the ventral valve, in *Homeathyris* than in the other two genera (Text-figs 9, 15–18).

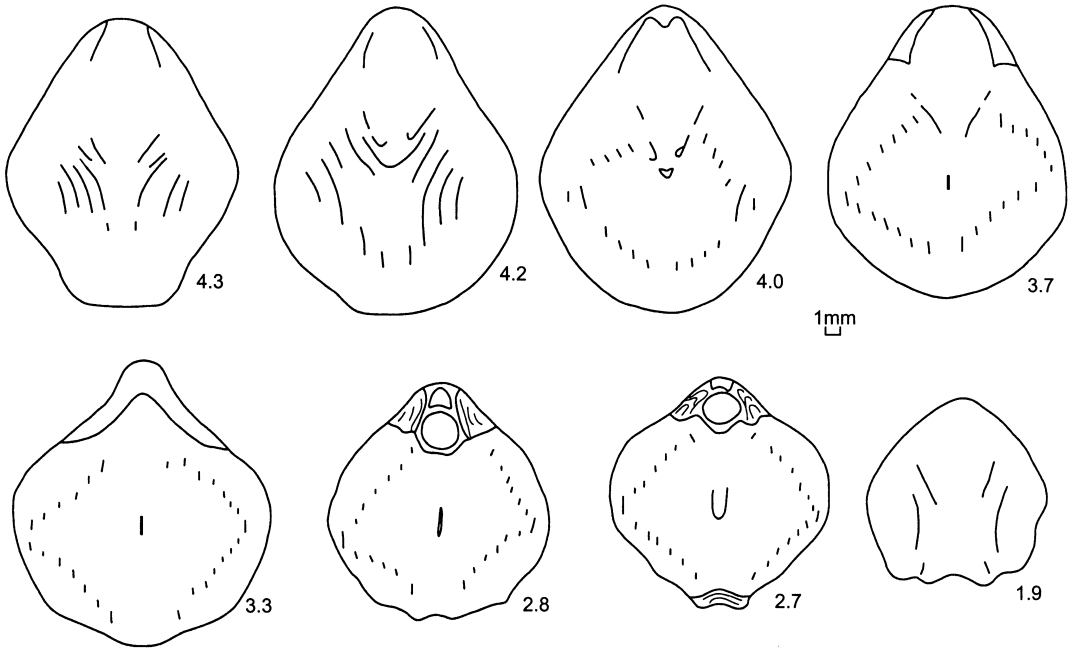
Occurrence. Upper Silurian, Ludfordian, Zapadno-Khatanzea, Zelenets and Kuba formations, *Didymothyris didyma* Zone (Modzalevskaya 1997) in Arctic Russia including the South Island of Novaya Zemlya, Dolgii Island and western slope of the Central Urals.

Homeathyris incisus Modzalevskaya, sp. nov.

Plate 3, figures 18–19, 22–23

1981 *Pseudohomeospira*? sp. Modzalevskaya, pl. 29, fig. 10.
1997*a* *Homeathyris* sp. Modzalevskaya, pl. unnumbered, fig. 1a–b.

Derivation of name. After the characteristically incised anterior margin.



TEXT-FIG. 16. Selected tangential serial sections, parallel to the commissural plane, illustrating the internal structures in *Homeathyris plicatella* (Modzalevskaya, 1980); CNIGR N3/13099, Zelenets Formation, Ludfordian, Dolgii Island; distances measured in mm from dorsal valve.

Holotype. Specimen CNIGR 4/13099, from Zapadno-Khatanseya Formation, loc. 7813–9/1 (Lutfordian), at Cape Fedotov, South Island of Novaya Zemlya, Russian Arctic, collected by L. V. Nekhorosheva in 1978 (Pl. 3, figs 18–19, 22–23).

Other material examined. Specimens attributed to this species came from the Khatanzeya Peninsula on the South Island of Novaya Zemlya (capes Britvin and Fedotov), and Mikhailov Pond on the western slope of the Central Urals.

Diagnosis. *Homeathyris* species resembling *H. insularis* but differing in being subpentagonal, less strongly biconvex, and with a more incurved ventral beak and sharply defined costae; a narrow and deep furrow divides the dorsal fold medially, opposite the ventral sulcus, producing a characteristic emarginate (*incisus*) anterior margin.

Description. Shell of medium size, reaching about 14·5 mm long, 15 mm wide and up to 10 mm thick. Subpentagonal in outline; greatest width normally at midlength. Ventral beak moderately incurved with hypothyridid pedicle opening. Growth lamellae commonly absent. Both valves have 10–12 costae; they are high, sharply crested, bifurcating in sulcus. A narrow and deep furrow divides the dorsal fold medially, opposite the ventral sulcus, producing a characteristic emarginate anterior. Internal morphology, known from serial sections, is similar to that of *Didymothyris didyma*. Spiralia with 9–10 whorls, apices laterally directed, jugum unknown.

Remarks. *H. incisus* can be separated easily from the other two species of the genus by its wider, transverse to equidimensional, subpentagonal dorsal outline (Pl. 3, figs 4–5, 16–23) and thinner, sharply defined costae. In lateral view it has an almost biconvex profile and more incurved ventral beak; the profile of the other two species is ventribiconvex. *H. incisus* differs also in its much deeper furrow opposite to the ventral sulcus, dividing the dorsal fold medially and producing a slightly emarginate anterior margin.

The species *H. plicatella* and *H. insularis* are more like each other, but the latter attains larger dimensions, *H. plicatella* being the smallest species of the genus. *H. plicatella* also differs in its stronger

valve convexity and in having almost smooth umbones; only the anterior two-thirds of the valves have prominent costate, with those bounding the ventral sulcus being stronger than all others. In *H. insularis* costae are lower, more rounded and of similar size; the costae and their interspaces are almost of the same width at the anterior margin. In the new species the interspaces between costae are wider than the costae, and costae in the middle of the dorsal furrow and ventral sulcus are commonly narrower than the others. *H. insularis* is longer than *H. incisus* and, although both are rounded–subpentagonal in outline, the maximum width is much more posteriorly situated in the former. *H. plicatella* and *H. insularis* occur in carbonate rocks in the same section in Dolgii Island, where they form coquinas. *H. insularis* replaced *H. plicatella* during the Ludfordian. The typical shells of *H. incisus* sp. nov. are from a carbonate-terrigenous facies of the Khatanzeya regional stage of the South Island of Novaya Zemlya.

Genus PSEUDOHOMEOSPIRA Nikiforova, 1970

Plate 3, figures 6–15; Text-figures 4, 17, 19

1970 *Pseudohomeospira* Nikiforova, p. 139.
1986 *Pseudohomeospira* Nikiforova; Grunt, p. 166.
1991 *Pseudohomeospira* Nikiforova; Sapel'nikov and Mizens, p. 198.
2002 *Pseudohomeospira* Nikiforova; Alvarez and Rong, p. 1507.

Type species. *Pseudohomeospira polaris* Nikiforova, 1970, p. 139, pl. 7, figs 28–32, text-figs 24–25; from Guba Belush'ya Beds, Greben' Formation in Vaigach Island, Arctic Russia, Upper Silurian (Přídolí).

Species assigned. The type species only.

Emended diagnosis. Small, biconvex, elongate oval, costate shells; ventral sulcus and dorsal fold weakly developed anteriorly; costae subangular or rounded, each valve with 12–16 costae, bifurcating in fold and sulcus; hypothyridid pedicle opening may be partially closed by deltidial plates; pedicle collar present; short ventral ridge may be present apically; dental plates thin, of moderate length, dorsally convergent

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EXPLANATION OF PLATE 3

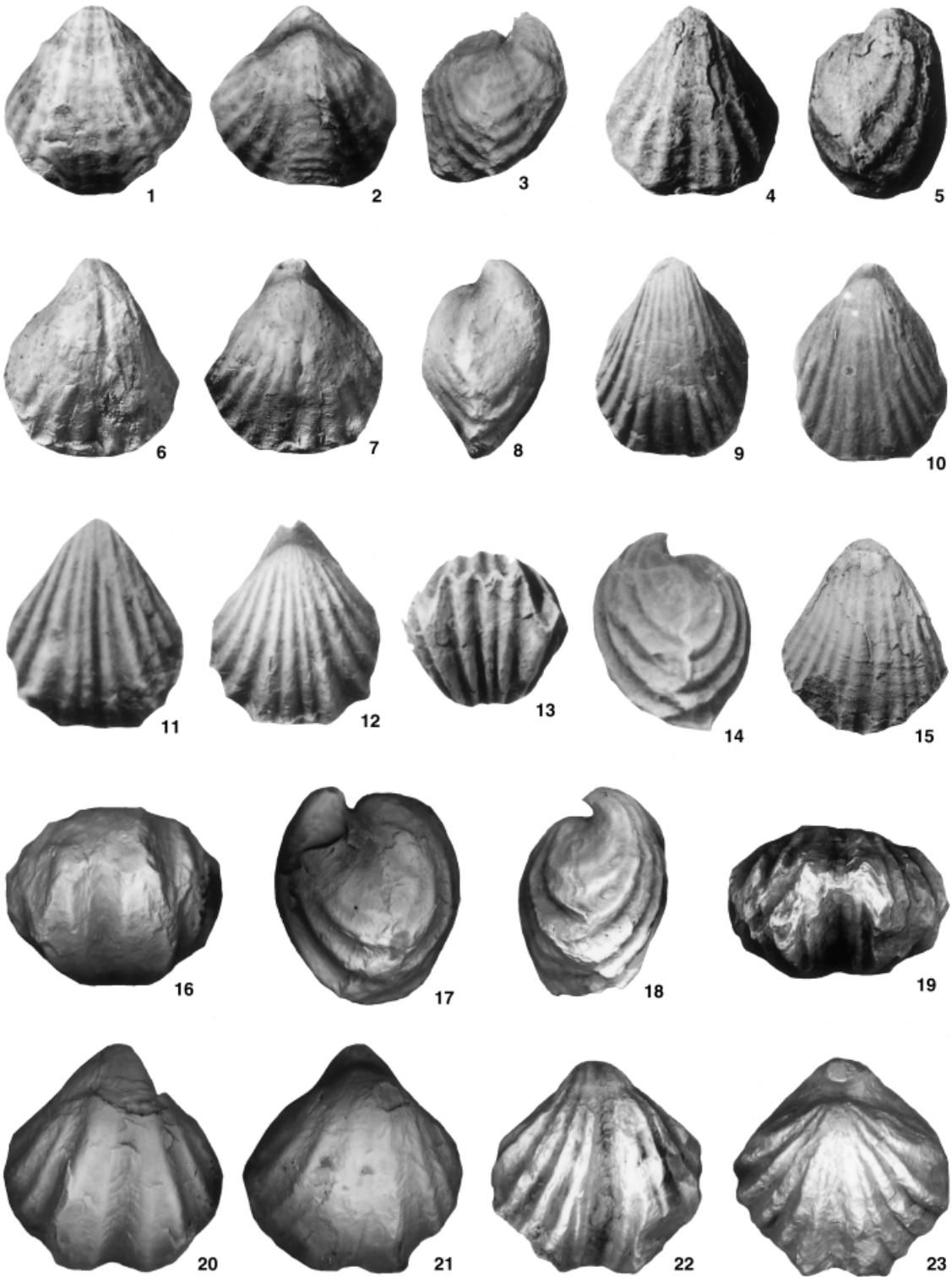
Figs 1–3. *Squamathyris glacialis* Modzalevskaya, 1981, ventral, dorsal, and lateral views of holotype (CNIGR N9/12011), collected by L. V. Nekhorosheva in 1978 from the Zapadno-Khatanzeya Formation (Ludfordian), Khatanzeya Peninsula, South Island of Novaya Zemlya, Arctic Russia (Loc. 7708–8a); ×2.

Figs 4–5. *Homeathyris insularis* Modzalevskaya, 1997, ventral, and lateral views of holotype (CNIGR N2/12918), collected by D. K. Patrunov and M. V. Shurygina in 1961 from the Zelenets Formation (Ludfordian), Dolgii Island, Arctic Russia (Loc. 12–77a); ×2.

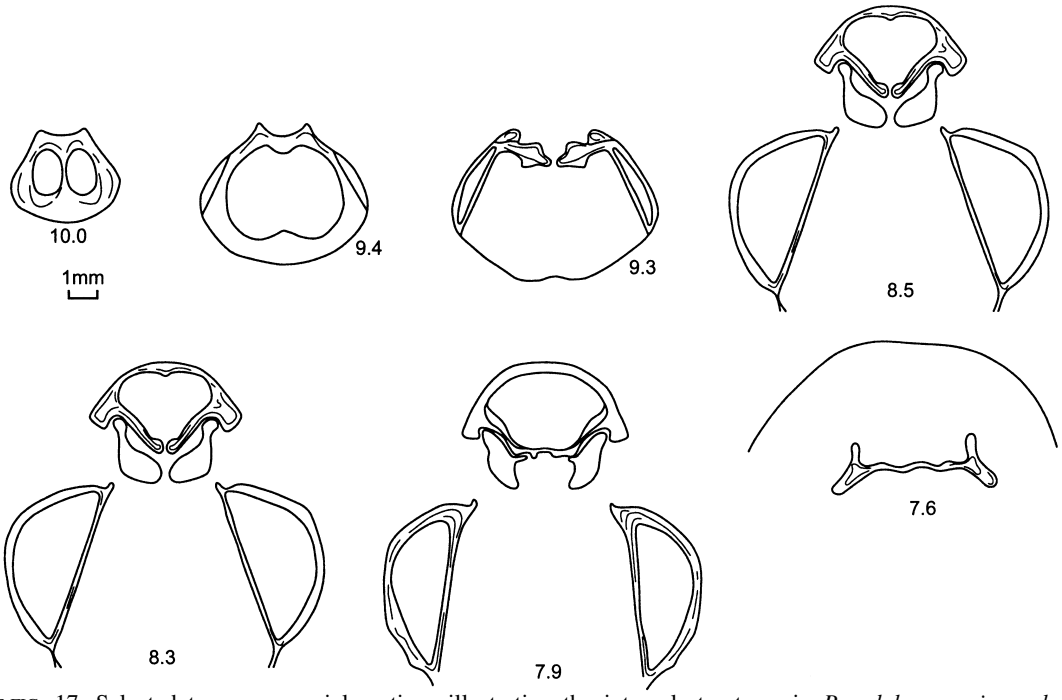
Figs 6–15. *Pseudohomeospira polaris* Nikiforova, 1970. 6–8, ventral, dorsal, and lateral views (CNIGR N27/12774), collected by T. L. Modzalevskaya in 1987 from the Demid Formation (Přídolí), Mikhailov Pond, western slope of the Central Urals (Loc. 911–748/749); ×3. 9–10, ventral and dorsal views of holotype (CNIGR 159/10331), collected by S. V. Cherkesova in 1957 from the Guba Belushya Formation (Přídolí), Vaigach Island (Loc. 42–8), Arctic Russia; ×3. 11–14, ventral, dorsal, anterior, and lateral views (CNIGR N26/12774), collected by A. I. Pershina in 1970 from the Tselebei Formation (Přídolí), Kozhim River, near the mouth of the Syv'yu River, western slope of the Polar Urals (Loc. 236–1464); ×2. 15, ventral view (CNIGR N18/12011), collected by L. V. Nekhrosheva in 1979 from the Kal'vits Formation (Přídolí), Kuznetsov River, South Island of Novaya Zemlya (Loc. 7950–4/5), Arctic Russia (see also Modzalevskaya, 1997*a*, pl. unnumbered, fig. 10); ×3.

Figs 16–17, 20–21. *Homeathyris plicatella* (Modzalevskaya, 1980); anterior, lateral, ventral and dorsal views of specimen CNIGR N1/13099 collected by D. K. Patrunov and M. V. Shurygina in 1961 from the Zelenets Formation (Ludfordian), Dolgii Island (Loc. 11–71), Arctic Russia; ×1·5.

Figs 18–19, 22–23. *Homeathyris incisus* Modzalevskaya sp. nov., lateral, anterior, ventral, and dorsal views of holotype, CNIGR N4/13099 collected by L. V. Nekhorosheva in 1978 from the Zapadno-Khatanseya Formation (Ludfordian), Fedotov Cape, South Island of Novaya Zemlya (Loc. 7813–9/1), Arctic Russia; ×1·5.



RONG *et al.*, athyrisinine brachiopods



TEXT-FIG. 17. Selected transverse serial sections illustrating the internal structures in *Pseudohomeospira polaris* Nikiforova, 1970; CNIGR N86/10629, Tselebej Formation (Přídolí), Kozhim River, western slope of the Polar Urals; distances measured in mm from the anterior margin of the shell.

apically, with very narrow lateral apical cavities, subparallel posteriorly; minute dorsal foramen, very low dorsal myophragm may be present apically; spiralia directed laterally, jugum unknown.

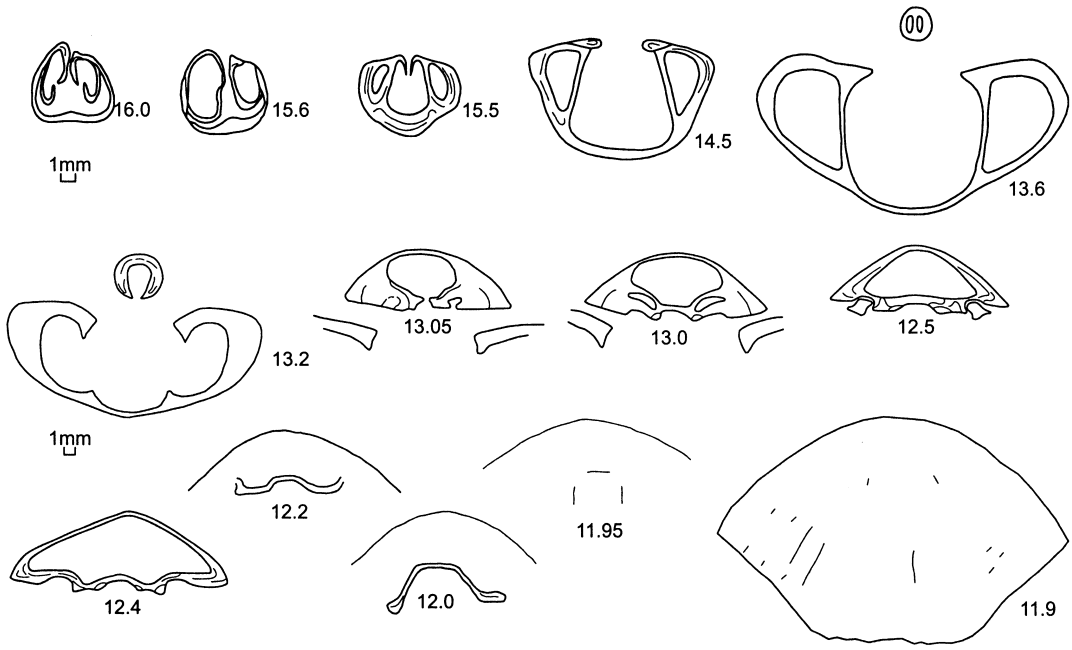
Remarks. *Pseudohomeospira polaris* reaches about 15 mm long, 10 mm wide and 8 mm in corpus thickness, and so is more elongate than species of *Homeathyris* and *Squamathyris*, which are commonly almost equidimensional (Text-fig. 19). *Pseudohomeospira* characteristically has a weakly developed dorsal fold and ventral sulcus displayed only anteriorly. The ventral beak is relatively high, slightly curved, with a hypothyridid pedicle opening partially closed by deltidial plates and the pedicle support resembling the internal characteristics of the didymothyridin genus *Collarothyris* Modzalevskaya, 1970 from beds of Ludlow age in western Russia and adjacent areas. Poor preservation and the type of matrix have made examination of the jugal structures impossible.

Occurrence. Upper Silurian, Přídolí, Kal'vits Formation, Guba Belush'ya Beds, Greben', Tselebey and Demid formations, *Collarothyris canaliculata* Zone (Modzalevskaya 1997*a*) in Arctic Russia, including the South Island of Novaya Zemlya, Vaigach Island and the western slope of the Polar and Central Urals.

Genus SQUAMATHYRIS Modzalevskaya, 1981

Plate 3, figures 1–3; Text-figures 4, 18–19

1981 *Squamathyris* Modzalevskaya, p. 153.
1986 *Squamathyris* Modzalevskaya; Grunt, p. 169.
1991 *Squamathyris* Modzalevskaya; Sapel'nikov and Mizens, p. 199.
2002 *Squamathyris* Modzalevskaya; Alvarez and Rong, p. 1507.



TEXT-FIG. 18. Selected transverse serial sections illustrating the internal structures in *Squamathyris glacialis* Modzalevskaya, 1981; CNIGR N5/13099, Zapadno-Khatanzeya Formation, Ludfordian, Khatanzeya Peninsula, South Island of Novaya Zemlya; distances measured in mm from the anterior margin of the shell.

Type species. Squamathyris glacialis Modzalevskaya, 1981 (p. 154, pl. 29, figs 6–7), from the Zapadno-Khantanzeya Formation, Upper Silurian (Ludfordian), of Khatanzeya Peninsula, Novaya Zemlya, Arctic Russia.

Species assigned. The type species only.

Emended diagnosis. Shell of medium size, biconvex, moderately to strongly rostrate, subpentagonal outline, with strong costae and numerous and squamose growth lamellae; ventral sulcus and dorsal fold moderately developed; hypothyridid pedicle opening restricted laterally by deltidial plates; dental plates short, delthyrial chamber with two variably developed curved plates medially and apically situated between the dental plates and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with up to ten whorls, jugum unknown.

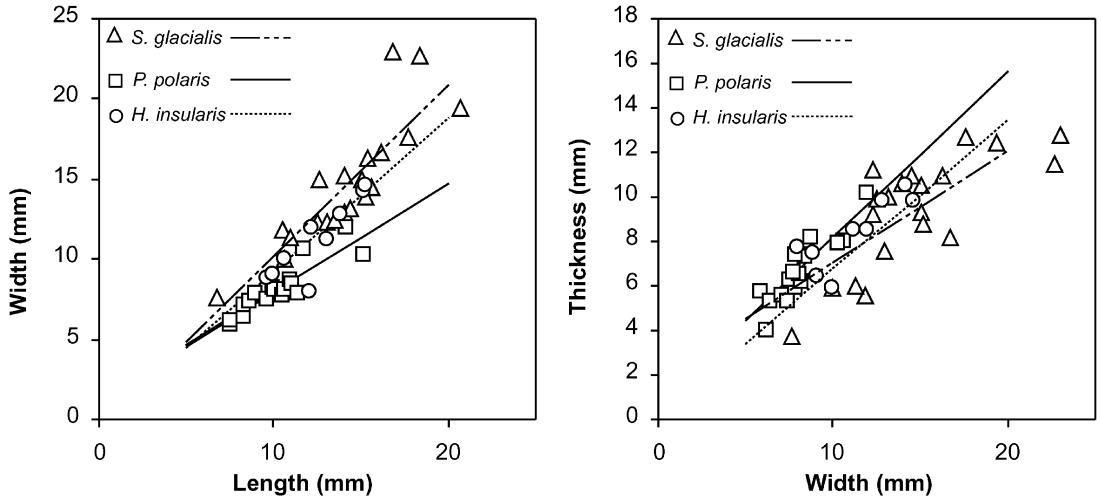
Remarks. See remarks under *Homeathyris*.

Occurrence. Upper Silurian, Ludfordian, Zapadno-Khatanzeya Formation, Krest-toskaya Member, Khatanzeya and Zelenets formations, *Didymothyris didyma* Zone (Modzalevskaya 1997*a*) in Arctic Russia, including the South Island of Novaya Zemlya (Khatanzeya Peninsula, Kal'vits Bay, capes Britvin and Fedotov), Vaigach (Kare Gate) and Dolgii islands.

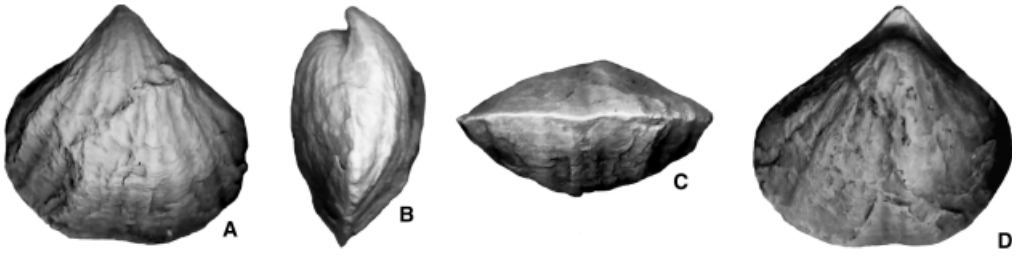
Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974
Family RETZIELLIDAE Rzhonsnitskaya, 1974

Genus IKELLA Tyazheva, 1972
Text-figures 20–21

1972 *Ikella* Tyazheva, p. 205.
1986 *Ikella* Tyazheva; Grunt, p. 167.
2002 *Ikella* Tyazheva; Alvarez and Rong, p. 1507.



TEXT-FIG. 19. Distribution of shell dimensions for specimens of *Squamathyris glacialis* Modzalevskaya, 1981, from the Zapadno-Khatanzeya Formation (Ludfordian) Khatanzeya Peninsula, South Island of Novaya Zemlya, type species of *Squamathyris*; *Pseudohomeospira polaris* Nikiforova, 1970, from the Demid Formation (Přídolí), Mikhailov Pond, western slope of the Central Urals, type species of *Pseudohomeospira*; *Homeathyris insularis* Modzalevskaya, 1997, from the Zelenets Formation (Ludfordian), Dolgii Island, Arctic Russia, type species of *Homeathyris.*

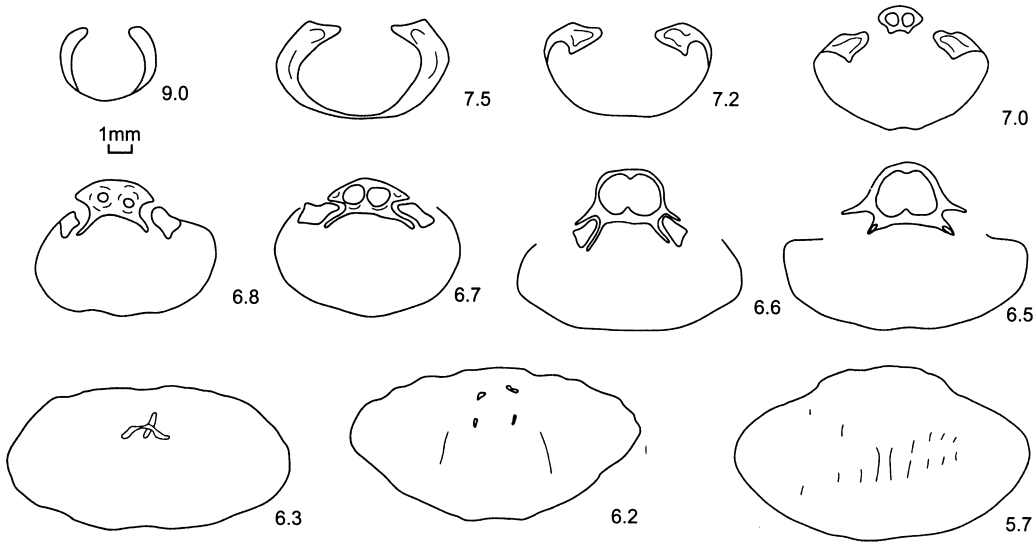


TEXT-FIG. 20. *Ikella numerosa* Tyazheva, 1972, ventral, lateral, anterior, and dorsal views, CNIGR N6/13099, collected by R. A. Zhavoronkova in 1961 from limestone with *Zdimir pseudobashkiricus* (Tchernychev, 1885) (*patulus–partitus* conodont biozones, late Emsian–early Eifelian), below the mouth of the Karagailka River, Malyi Ik River, western slope of the South Urals (Loc. 32a); ×1·5.

Type species. Ikella numerosa Tyazheva, 1972 (p. 205, pl. 52, figs 1–2), from the limestones with *Zdimir pseudobashkiricus* (upper Emsian–lower Eifelian, *patulus–partitus* conodont biozones), on the western slope of the South Urals, Russia.

Species assigned. In addition to the type species, *Ikella angusta* Tyazheva, 1972 (p. 207, pl. 52, fig. 3), from limestones of late Emsian–early Eifelian age, on the western slope of the South Urals (Bashkorkostan), Russia, is placed in this genus. *I. angusta* is said to differ (Tyazheva 1972) from the type species by its more transverse shell, longer beak and wider costae; no interiors are known. The 15 topotypes studied (TLM) of *I. angusta* show great variability in shell outline, and in the width of the radial elements. In addition, both species have similar stratigraphical and geographical distributions. With the data available the species seem to be conspecific, although the study of new, non-recrystallized material, may show internal differences.

Emended diagnosis. Small, subequally to ventribiconvex shells of rounded subpentagonal to elongate subelliptical outline; costae rounded, faint, bifurcating or not, in corresponding position on each valve,



TEXT-FIG. 21. Selected transverse serial sections illustrating the internal structures in *Ikella numerosa* Tyazheva, 1972, CNIGR N 8/13099, from the limestones with *Zdimir pseudobashkiricus* (Tchernyshev), late Emsian–early Eifelian (*patulus–partitus* conodont biozones), Malyi Ik River, eastern slope of South Urals; distances measured in mm from the anterior margin of the shell.

growth lines faint, not lamellose; dorsal fold and ventral sulcus poorly developed anteriorly, commonly absent; delthyrium may be restricted laterally by narrow deltidial plates; dental plates and pedicle support absent; cardinal plate wide, flat, not perforated apically and supported posteriorly by very short ridge; dental sockets deep, bordered by prominent inner socket ridges ventrolaterally directed, overhanging the socket; spiralia with 7–12 whorls, apices laterally directed, jugum unknown.

Remarks. In the original description by Tyazheva (1972), *Ikella* was assigned to '*Incertae Familiae*' mainly because of the poor knowledge of its internal structures. She compared the external ornamentation of *Ikella* with that of *Retzia* King, 1850, from which she said it differed in the absence of dental plates and the shape and disposition of the costae, but Tyazheva did not mention the presence or absence of punctae in the shell of *Ikella*, and did not discuss its inclusion within the superfamily Athyridacea (*sic*). Later, Grunt (1984, 1986) considered that the external ornamentation and the internal structures of *Ikella* clearly resemble those of *Athyrisina* and consequently she assigned *Ikella* to the family Athyrisinidae (*sic*), that, together with the Metathyrisinidae (*sic*), were included by Grunt (1984, 1986) in the superfamily Athyrisinacea (*sic*). Alvarez *et al*. (1998; see also Alvarez and Rong 2002) considered *Ikella* insufficiently described and figured, and that the interiors were still poorly known, so queried the generic attribution of *Ikella* to the athyrisinins, considered by them as a subfamily within the Athyrididae. On Tyazheva's serial sections no dental plates were shown, only rudimentary dental flanges seeming to support the teeth. The cardinal plate appears flat, subquadrate, but not perforated posteriorly. No dorsal septum or myophragm is present in her sections. The revision by TLM of *I. numerosa* topotypes (Malyi Ik River, loc. 32a), kindly sent by colleagues at the Institute of Geology of the Ufa Scientific Centre of the Russian Academy of Sciences, Bashkorkostan, showed that the shell is impunctate, so preventing the inclusion of *Ikella* with *Retzia* and its allies, all of which have a finely endopunctate shell fabric. New serial sections, prepared by TLM, confirm that dental plates and pedicle supports are absent (Text-fig. 21). The cardinal plate is wide, flat, not perforated apically, and supported posteriorly by a very short ridge. Deep dental sockets are bordered by prominent inner socket ridges, which are ventrolaterally directed, overhanging the sockets (Text-fig. 21). Spiralia have 7–12 whorls, with apices directed laterally. The jugum is unknown. The

cardinalia of *Ikella*, as described here, clearly differ from the hinge plates present in the athyrisinids and homeathyridins. It resembles the cardinalia of some retzielloids (e.g. Rong *et al.* 1994; Alvarez and Rong 2002), although typically retzielloids have variably developed outer hinge plates, and the inner hinge plates are absent or form a short, shallow septalium partially covered by long, platelike, crural bases, supported by a moderately high median septum (e.g. *Retziella* Nikiforova, 1937; *Metathyrisina* Rong and Yang, 1981). The highly crystalline nature of the matrix has made examination of internal structure very difficult, so the spiralium remains poorly known and the jugal structures are unknown; therefore, the superfamilial and familial assignments of this genus should be regarded as provisional, as Modzalevskaya and Alvarez interpret here. On the other hand, because the cardinal shape of *Ikella* differs from that of *Retziella*, Rong prefers to avoid assignment to *Ikella*. This ambiguity should be resolved when non-recrystallized topotype specimens that will allow the study of these structures in *Ikella*, and also in *Argorhynx*, *Ufonicoelia* and *Gissarina*, genera commonly included within the retzielloids, are found.

Occurrence. Devonian, upper Emsian–lower Eifelian, limestones with *Zdimir pseudobashkiricus* (*patulus–partitus* conodont biozones), western slope of the South Urals, Malyi Ik River (1·4, 1·7 and 2·5 km below the mouth of the Karagailka River), Bashkorkostan, Russia.

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