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WUCHIAPINGIAN (LOPINGIAN, LATE PERMIAN) BRACHIOPODS FROM THE EPISKOPI FORMATION OF HYDRA ISLAND, GREECE

by SHU-ZHONG SHEN* *and* MATTHEW E. CLAPHAM†

*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, 39 East Beijing Road, 210008 Nanjing, China; e-mail: szshen@nigpas.ac.cn

†Department of Earth and Planetary Sciences, University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA; e-mail: mclapham@ucsc.edu

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Abstract: Twenty-three species of silicified brachiopods are described from four samples in the middle and upper parts of the Episkopi Formation from Hydra Island, Greece. These brachiopods are newly recorded from the region and together with previously described brachiopods from the same localities constitute the most diverse Lopingian (Late Permian) brachiopod fauna reported in southern Europe. The brachiopod fauna is Wuchiapingian as indicated by the associated conodonts. The fauna from Hydra exhibits strong palaeobiogeographical links with the faunas from South China. In addition, palaeobiogeographical affinities with the faunas of Thailand and the northern peri-Gondwanan region are also present, which implies a peri-Gondwanan origin for Hydra. Palaeoecologically, the brachiopod assemblage from sample EP in the middle part of the Episkopi Formation is dominated by pedically-attached and cementing genera and reflects moderate energy conditions above storm wave base and an abundance of hard substrates provided by sponges in the biohermal habitat. By contrast, the brachiopod assemblage in the other three samples from the upper part of the Episkopi Formation is dominated by spinose genera with a free-resting life habit, suggesting soft substrates in a quiet water environment below storm wave base on the outer part of the shelf. New taxa are *Petinospiriferina* gen. nov., *Hustedia episkopiensis* sp. nov., *Waterhouseiella hydraensis* sp. nov. and *Xenosaria tenuis* sp. nov.

Key words: Brachiopoda, Hydra Island, Greece, Episkopi Formation, Wuchiapingian, palaeobiogeography, palaeoecology.

THE Island of Hydra in Greece has attracted a great deal of attention from geologists because of its excellent exposure of Late Palaeozoic and Mesozoic strata (Angiolini *et al.* 1992; Grant 1993*a*, 1995; Grant *et al.* 1991; Nestell and Wardlaw 1987; Renz 1955). Permian strata ranging from Asselian to Changhsingian containing abundant foraminifers, algae and brachiopods have been extensively studied. According to Grant *et al.* (1991), a highly diverse fauna of silicified brachiopods was collected in the 1970s from near the top of the Permian System on Hydra. Originally, Richard E. Grant planned to describe these silicified brachiopods, but only some genera of Productidina, Rhynchonellida and Orthotetida were published (Grant 1972, 1988, 1993*a*, 1995) before he passed away in December 1994. Other Greek Permian brachiopod faunas were described from the island of Khios by Grant (1993*b*) and Angiolini *et al.* (2005). The descriptions in this paper are based on new materials collected from two localities on Hydra Island in 2005 (Text-fig. 1); most of the species are recorded here for the first time in the Lopingian of southern Europe. These new brachiopod records from Hydra play a crucial role in helping to unravel the complex palaeobiogeographical and palaeogeographical evolution of the eastern Mediterranean region during the Permian.

GEOLOGICAL SETTING AND MATERIALS

Four samples with abundant brachiopods were dissolved with hydrochloric acid, yielding 852 silicified brachiopod specimens. Sample EP (Text-fig. 1) was collected southwest of the village of Episkopi (37°18′30.7″N, 23°25′21.9″E), approximately at the same location as USNM9334 (Nestell and Wardlaw 1987) below the cliff-forming upper part of the Episkopi Formation. The block containing silicified fossils was collected from the margins of a small (0.5 m tall) sponge mound.

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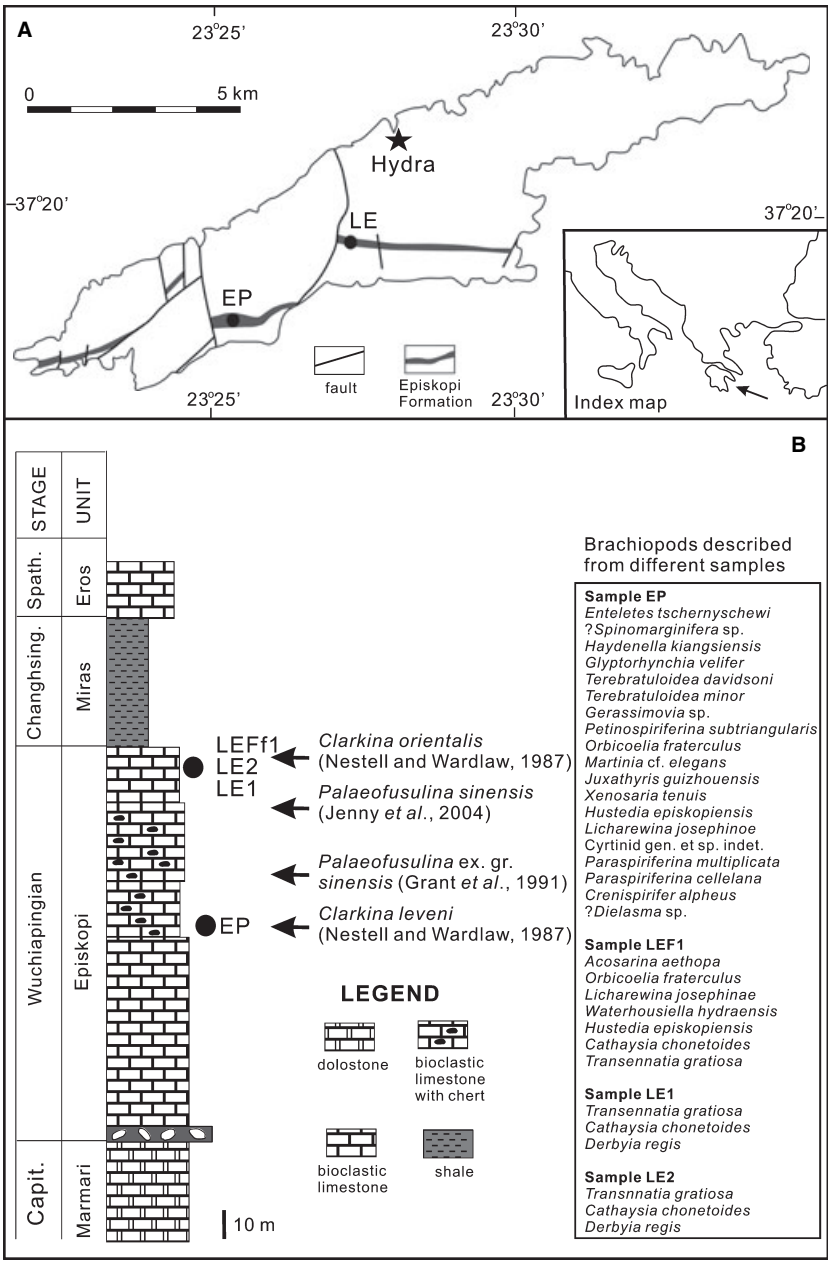


TEXT-FIG. 1. A, Locality map showing the fossil localities and distribution of the Episkopi Formation. B, Stratigraphical column showing the horizons of samples with brachiopods and key fusulinid and conodont fossils previously reported (Revised from Grant *et al.* 1991).

Samples LE1 and LE2 were obtained from silicified beds in the uppermost Episkopi Formation on the slopes of Mount Eros, above Lehusis (37°19′32.4″N, 23°27′24.1″E), approximately at the same location as USNM 9599 of Grant *et al.* (1991) (Text-fig. 1). The sampled beds, each approximately 0.1 m-thick, are composed of poorly bioclastic lime mudstone, and Sample LE2 was collected 0.1 m above Sample LE1 in the stratigraphic section. Sample LEFl is a single float block obtained from the same locality. Although its precise stratigraphic level could not be recognized, it was originally derived from the *c.* 5 m-thick interval containing silicified beds at the top of the Episkopi Formation.

AGE OF THE FAUNA AND PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The Episkopi Formation is Wuchiapingian (Early Lopingian) in age, based on the occurrences of conodonts belonging to *Clarkina* (e.g. Nestell and Wardlaw 1987) and the foraminifers *Codonofusiella, Colaniella*, and *Palaeofusulina* (see Grant *et al.* 1991; Jenny *et al.* 2004). Nestell and Wardlaw (1987) recognized the Wuchiapingian conodont *Clarkina leveni* from USNM9334 in the middle part of the Episkopi Formation, the approximate horizon from which Sample EP was collected. They also

described *Clarkina orientalis*, a late Wuchiapingian species, from the uppermost beds of the Episkopi Formation, suggesting that the entire formation is of Wuchiapingian age. However, both Grant *et al.* (1991) and Jenny *et al.* (2004) noted the presence of *Palaeofusulina sinensis* approximately 40 m below the top of the formation, indicating that the uppermost Episkopi Formation is probably late Changhsingian in terms of fusulinids. Nevertheless, we herein consider the brachiopod fauna from the Episkopi Formation is Wuchiapingian because species of *Palaeofusulina* have been recorded from the middle Wuchiapingian in South China (Wang and Jin 2006).

Nineteen species and four unidentifiable species of brachiopods are described and discussed in this paper. In addition, previously described brachiopods from Hydra include *Ceocypea dischides* Grant, 1972, *Cyndalia rudistiformis* Grant, 1993*a*, *Derbyia regis* Grant, 1995, *Diplanus dilatus* Grant, 1995, *Disphenia myoides* Grant, 1988, *Epicelia episcopiensis* Grant, 1972, *Falafer epidulus* Grant, 1972, *F. triminulus* Grant, 1972, *Goniarina subulata* Grant, 1995, *Lambdarina iota* Grant, 1988, *Schuchertella bassa* Grant, 1995, *Sicelia explicata* Grant, 1995 and *Tropidelasma ptomatis* Grant, 1995. Some of them are also found in our samples, but all these species have been well described and are not repeated in this paper.

The brachiopod fauna described herein generally characterizes a Wuchiapingian (Early Lopingian) age. Among the brachiopod list, *Enteletes tschernyschewi* Gemmellaro, 1899, *Cathaysia chonetoides* (Chao, 1927), *Haydenella kiangsiensis* (Kayser, 1883), *Transennatia gratiosa* (Waagen, 1884), *Terebratuloidea davidsoni* Waagen, 1883, *T. minor* Waagen, 1883, *Juxathyris guizhouensis* (Liao, 1980), *Paraspiriferina multiplicata* (Sowerby, 1829), *Crenispirifer alpheus* (Huang, 1933) are all very common in the Wuchiapingian in South China (Wang *et al.* 1964). *Transennatia gratiosa, Terebratuloidea davidsoni, T. minor* and *Paraspiriferina multiplicata* have been recorded from either the upper part of the Wargal Formation or the Chhidru Formation in the Salt Range, Pakistan. The upper part of the Wargal Formation and the lower part of the Chhidru Formation are Wuchiapingian in terms of the latest conodont data (Wardlaw and Mei 1999). *Martinia elegans* has been recorded from the Chitichun Limestone (Diener 1897) and a Wuchiapingian exotic block in Tibet (Shen *et al.* 2003). In addition, *Derbyia regis* described by Grant (1995) is very close to *Derbyia schellwieni* Frech, 1911, which is common in the Lopingian in South China. *Tropidelasma ptomatis* is also very similar to *T. daijiagouensis* (He and Zhu, 1985) from the Changhsingian in Chongqing City, South China. *Schuchertella bassa* Grant, 1995 is very similar to *Schuchertella semiplana* described by Waagen (1883, p. 608, pl. 55, figs 1–2) from the Chhidru Formation in the Salt Range, Pakistan. *Licharewina josephinae* (Gemmellaro, 1899) has been recently recorded from the Lopingian *Crurithyris-Anidanthus* beds in the lower Urushten Formation at Raskol Cliff, Bzykha River in northwestern Caucasus (Kotlyar *et al.* 2004).

In addition to the above-mentioned Lopingian species, the Hydra fauna also contains some species that have been recorded in the Guadalupian (Middle Permian). *Orbicoelia fraterculus* Waterhouse and Piyasin, 1970, from Hydra is very similar to those described from the Guadalupian Ratburi Limestone in southern Thailand (Grant 1976; Waterhouse and Piyasin 1970). *Waterhouseiella* was erected on the species *Waagenites speciosus* Waterhouse and Piyasin (1970) from the Ratburi Limestone in Thailand. *Licharewina josephinae* was also reported from the Sosio Limestone in Sicily, Italy by Gemmellaro (1899). The Sosio fauna is mostly Wordian in age according to Angiolini *et al.* (2005). *Acosarina aethopa* (Grant, 1993*b*) has been recorded from the *Neoschwagerina* Zone on Khios Island, Greece. *Paraspiriferina cellulana* Cooper, 1976*a* has been recorded from the Roadian Road Canyon Formation and Cibolo Formation and *Xenosaria* is a characteristic genus of the Capitanian Bell Canyon Formation in West Texas, USA. The occurrences of the Late Guadalupian brachiopods from Thailand and West Texas in the Hydra fauna are interesting because of the apparently severe effects of the end-Guadalupian mass extinction. The end-Guadalupian extinction is partly related to the Late Guadalupian global regression, which subsequently led to the withdrawal of marine water from a large part of the Pangean shelves and epicontinental seas (Shen and Shi 2002). Thus, brachiopods were no longer present in many regions that previously had highly diverse Guadalupian brachiopod faunas, such as West Texas and Thailand, due to the absence of marine deposition in those regions. According to Shen and Shi (2002), brachiopods actually experienced a less pronounced end-Guadalupian extinction compared to fusulinids and rugose corals in South China, where marine successions of both Guadalupian and Lopingian age are well developed. The discovery of a highly diverse Wuchiapingian brachiopod fauna on Hydra indicates that more Guadalupian brachiopod genera and species may have ranged into the Lopingian in regions where suitable habitats are preserved, as has been documented in South China (Shen *et al.* 2006). Thus, the end-Guadalupian mass extinction had a much smaller impact than the end-Changhsingian (end-Permian) mass extinction (Shen and Shi 2002).

Palaeobiogeographically, the Lopingian fauna of Hydra Island shows strong affinities with the faunas in South China in terms of the presence of *Enteletes tschernyschewi, Cathaysia chonetoides, Transennatia gratiosa, Haydenella kiangsiensis*, *Terebratuloidea davidsoni, T. minor, Juxathyris guizhouensis, Crenispirifer alpheus* and ?*Spinomarginifera*

sp. In addition to these species, the genus *Falafer* has also been recorded from the Changhsingian in South China (Liao and Meng 1986). However, differences between the Hydra fauna and South Chinese faunas are also notable because many endemic genera described by Grant (1972, 1988, 1993*a*, 1995) such as *Disphenia, Lambdarina, Cyndalia* and *Epicelia* have never been reported from South China or elsewhere. There are also links between the Hydra fauna and the faunas in the southern transitional zone (in the sense of Shi *et al.* 1995) and northern peri-Gondwanan region, although typical Gondwanan brachiopod elements are absent in the Hydra fauna. *Transennatia gratiosa, Terebratuloidea davidsoni, T. minor*, and *Paraspiriferina multiplicata* and the genus *Ceocypea* are common taxa in the faunas in the peri-Gondwanan region, such as from the Chitichun Limestone (Diener 1897), the upper Wargal and Chhidru fauna in the Salt Range, Pakistan (Waagen 1882, 1883, 1884, 1885), the faunas from the exotic limestone in the Indus-Zangbo Suture Zone (Shen *et al.* 2003; Shi *et al.* 2003) and the Ratburi Limestone in southern Thailand (Grant 1976; Waterhouse and Piyasin 1970). It is most likely that Hydra was originally situated at the periphery of Gondwana during the earliest Permian (e.g. Angiolini *et al.* 2005). A rifting event began in Early Permian in response to the opening of Neotethys (Gaetani and Garzanti 1991). During the rifting and subsequent drifting process, climatic conditions gradually ameliorated, allowing mixed faunas of the Guadalupian Cimmerian biogeographical province (Grunt and Shi 1997; Shi *et al.* 1995), and finally Lopingian faunas with warm Cathaysian affinities to settle on Hydra Island when it moved into the palaeoequatorial zone (Shen and Shi 2000, 2004). The presence of some North American Guadalupian brachiopod species in the Hydra fauna can be interpreted to migrate into the Palaeotethys after the drain up of the northwestern American basins at the end-Guadalupian or those species are widely distributed in the palaeoequatorial zone.

In summary, the Hydra fauna is Wuchiapingian (Early Lopingian) in age and has a strong palaeogeographical affinity with the Lopingian faunas of South China. However, some links to the southern transitional faunas are also indicated, which may imply the Gondwanan origin of the Hydra fauna (cf. Angiolini *et al.* 2005, fig. 8).

PALAEOECOLOGY

The samples from Hydra contain a rich fauna of brachiopods, bivalves, and gastropods, and a diverse accessory biota of sponges, crinoids, rugose corals, and bryozoans. Brachiopods are the dominant component of Sample EP, comprising approximately 84% of the assemblage (Clapham and Bottjer 2007). Pedically-attached individuals (mainly spiriferids, spiriferinids, and rhynchonellids) dominate the brachiopod assemblage, accounting for 81.5% of all brachiopods. Cementing genera are somewhat common (17% of the brachiopod assemblage), including some specimens of *Epicelia episkopiensis*, *Tropidelasma ptomatis* and a lyttoniid preserved in life position attached to the sponge mound framework. Reclining productids are very rare in sample EP; only two individuals of *Haydenella kiangsiensis* occur in a total of 496 brachiopods. Gastropods are very diverse, but not as abundant, with more than 15 genera comprising about 13% of the sample. Bivalves are rare (less than 3% of the assemblage) and primarily include epibyssate and cemented forms; no infaunal suspension-feeders and only a single deposit-feeding individual are present. Associated fauna in Sample EP includes two individuals of the orthocone nautiloid *Lopingoceras*, two tiny *Acanthocladia*-like bryozoans, a single rugose coral, and one pelmatozoan ossicle. According to our sedimentological analysis and the interpretation of Jenny *et al.* (2004), the sample was deposited in moderate energy conditions above storm wave base in middle shelf environments.

In contrast to Sample EP, the three samples from Lehusis (Samples LE1, LE2, and LEFl) are numerically dominated by small gastropods, with Sample LEFl also containing more than 130 individuals of the microconchid '*Spirorbis*' (Taylor and Vinn 2006). Rhynchonelliform brachiopods only comprise 30–40% of each assemblage (Clapham and Bottjer 2007). Reclining brachiopods are much more abundant than in sample EP, comprising 51% of the LE1 brachiopod population, 26% of LE2, and 78% of LEfl. Bivalves account for 10%–18% of the overall assemblage, with infaunal suspension-feeding forms such as *Astartella* accounting for 70% of LE1, 73% of LE2, and 9% of LEfl. Sample LE1 also contains a single rugose coral and crinoid ossicle, an echinoid spine, and three small fragments of '*Acanthocladia.*' Crinoid debris is more common in Sample LE2 (88 ossicles), which also contains three *Sollasia*-like sponges, two encrusting sponges, and a single tiny fenestrate bryozoan fragment. In addition to the abundant microconchids, Sample LEfl contains 10 unidentified sponge specimens, five rugose coral specimens, three small fragments of a branching bryozoan and two fenestrate fragments, a single chiton plate, and one small prolecanitid ammonoid. Sedimentological analysis indicates that the muddy limestone samples from Lehusis were deposited in quiet water, below storm wave base on the outer part of the shelf.

The guild structure of the benthic communities was strongly influenced by paleoenvironmental conditions in the Episkopi and Lehusis sections. Pedically-attached and cementing brachiopod genera were very abundant, while reclining productids were nearly absent, in the biohermal

environment at Episkopi (Sample EP), where the sponge framework provided numerous hard substrates for attachment. Cemented brachiopods and bivalves, often preserved in life position attached to the sponge framework, are particularly abundant and comprise 17% of the brachiopod assemblage and 12.5% of the bivalve assemblage. Moderate energy conditions, influenced by intermittent storm waves and the presence of firm or shelly substrates near the sponge mound may also have favoured attached genera relative to free-living productids. Abundant pedically-attached species in Sample EP include *Orbicoelia fraterculus*, *Paraspiriferina cellulana*, *Terebratuloidea minor*, and *Glyptorhynchia velifer*, whereas *Schuchertella bassa* was the dominant cemented taxon in the sponge mound environment. In contrast, reclining productids such as *Transennatia gratiosa* and *Waterhouseiella hydraensis* dominated in the Lehusis samples (LE1, LE2, and LEFl) where they were better adapted to the soft, muddy substrates in the outer shelf environment. Most of the abundant pedically-attached rhynchonellids and spiriferinids from Sample EP are extremely rare or not present in the muddy offshore assemblage; only *Orbicoelia fraterculus* is common in samples from Lehusis. Similar patterns are observed among the bivalves, where epibyssate and cementing genera are abundant in the biohermal environment of Sample EP, whereas infaunal suspension and deposit feeders dominate in the quiet water muddy limestones at Lehusis.

SYSTEMATIC PALAEONTOLOGY

All the specimens described in this paper are housed in the Nanjing Institute of Geology and Palaeontology; registration numbers are prefixed NIGP. Classification above genus level largely follows (Williams *et al.* 2000; Williams 2002, 2006). To keep the paper within a reasonable length, descriptions and remarks are provided only for species and genera where necessary and descriptions of poorly-preserved specimens are not provided.

Order PRODUCTIDA Sarytcheva and Sokolskaja, 1959
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETOIDEA Bronn, 1862
Family RUGOSOCHONETIDAE Muir-Wood, 1962
Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Genus WATERHOUSEIELLA Archbold, 1983

Type species. Waagenites speciosus Waterhouse and Piyasin, 1970, from the Ratburi Limestone (of Guadalupian age) in Thailand.

Remarks. Tethyochonetes Chen *et al.*, 2000 is closely similar to *Waterhouseiella* in terms of its costation, size and outline, but differs by its fewer cardinal spines, less convexity, relatively distinct sulcus and strong short lateral septa as Chen *et al.* (2000) noted. *Waagenites* Paeckelmann, 1930, differs from *Waterhouseiella* by its stronger, more simple costation and short median septum in the ventral valve.

Waterhouseiella hydraensis sp. nov.
Plate 1, figures 1–10

Derivation of name. From Hydra Island, the locality of the type material.

Holotype. NIGP143465, a conjoined shell (Pl. 1, figs 6–7).

Paratypes. NIGP143466, a ventral valve (Pl. 1, figs 1–2) and NIGP143467, a dorsal valve (Pl. 1, fig. 3).

Material. Six conjoined shells, 70 ventral valves and 16 dorsal valves. Registered specimens: two conjoined shells (NIGP143468, NIGP143469), three ventral valves (NIGP143470-143472) and two dorsal valves (NIGP143473-143474).

Type locality and horizon. This species is from the Episkopi Formation near Locality USNM9599 of Grant *et al.* (1991) (Sample LEFl).

Diagnosis. Shell very small and strongly concavo-convex, with distinct coarse costellae, moderately developed sulcus and acute cardinal extremities.

Description. Shell very small, trapezoidal in outline, widest at hinge, cardinal extremities acute, with cardinal angle about 60 degrees; hinge with 4 pairs of cardinal spines, pointing distally; interarea low; delthyrium occupied by cardinal process; ventral visceral disc highly convex, well demarcated from ears; sulcus originating from beak, shallow and becoming moderately deep near front margin; dorsal valve deeply concave; ears flat; costellae strong, numbering 15–20 in total, occasionally bifurcating once near front margin, very weak on ears; interspaces as wide as costellae.

Ventral interior with thin median septum, fairly high, but extending only short distance forward, muscle marks weakly impressed in umbonal cavity; dorsal interior with low bilobed cardinal process; alveolus small but deep, socket ridges prominent, extending laterally only one-third of hinge; median septum beginning well in front of alveolus, higher anteriorly, abruptly ending slightly anterior to muscle marks at about midvalve; lateral septa weakly developed; taleolae abundant in radial rows.

Size. 6.3 mm long, 9.6 mm wide and 3 mm thick on the average.

Remarks. The present species differs from the type species by its coarser costae, acute cardinal extremities and more transverse outline.

Suborder PRODUCTIDINA Waagen, 1883
Superfamily PRODUCTOIDEA Gray, 1840
Family PRODUCTELLIDAE Schuchert and Levene, 1929
Subfamily MARGINIFERINIAE Stehli, 1954
Tribe MARGINIFERINI Stehli, 1954

Genus SPINOMARGINIFERA Huang, 1932

Type species. Spinomarginifera kueichowensis Huang, 1932, from the Permian coal-bearing beds at Chenyaoyen, Guizhou, South China.

?*Spinomarginifera* sp.
Plate 1, figures 11–12

Remarks. A conjoined shell (NIGP143475) from the Episkopi Formation at approximately the same location as USNM9334 (Sample EP) is 10.6 mm long, 16.6 mm wide and 7.2 mm thick, strongly geniculated with a moderately convex corpus. Ventral valve has some vague irregular wrinkles and scattered spines on the visceral disc and ears. A few coarse spines are present on ears and between ears and visceral disc. Ventral trail has some costate appearance. Dorsal right ear has at least one coarse spine. The above characters of the specimen, including size, outline, geniculation and spinosity immediately recall the South Chinese species *S. chenyaoyanensis* Huang, 1932, which is very common in the Lopingian (mainly Changhsingian). However, further comparison is hampered because the surface of the Greek specimen is not clearly preserved and the marginal ridge is not well revealed.

This species differs from another common species in the Lopingian of South China, *S. kueichowensis*, by its small size and more strongly geniculated profile. *Spinomarginifera spinocostata* (Abich, 1878) and *S. helica* (Abich, 1878) from the Lopingian in Iran (Fantini Sestini 1965; Fantini Sestini and Glaus 1966) and Transcaucasia are also very close to the present species in terms of their size, strong geniculation and weak irregular concentric wrinkles, but have a narrower visceral disc. *Entacanthadus chioticus* Grant (1993*b*, p. 14, fig. 12) is closely similar to the present species, but has distinct coarse spines on ventral trail and lacks any spines on dorsal valve. *Marginifera ganota* Grant (1993*b*, p. 12, fig. 11) also resembles the present species in profile, outline and spinosity, but has distinct coarse costae on ventral valve.

Tribe PAUCISPINIFERINI Muir-Wood and Cooper, 1960

Genus TRANSENNATIA Waterhouse, 1975

Type species. Productus gratiosus Waagen, 1884, from the Chhidru Formation (Lopingian) in the Salt Range, Pakistan.

Transennatia gratiosa (Waagen, 1884)
Plate 1, figures 13–22

1884 *Productus gratiosus* Waagen, p. 691, pl. 72, figs 3–7.
1927 *Productus gratiosus* Waagen; Chao, p. 44, pl. 4, figs 6–10.
1932 *Productus* (*Dictyoclostus*) aff. *gratiosus* Waagen; Huang, p. 32, pl. 2, fig. 3.
1934 *Productus gratiosus* Waagen; Grabau, p. 34, pl. 10, figs 4–6.
1961 *Dictyoclostus gratiosus* Waagen; Zhang and Jin, p. 411, pl. 4, figs 12–18.
1964 *Dictyoclostus gratiosus* Waagen; Wang *et al.*, p. 291, pl. 45, figs 14–19.
1975 *Transennatia gratiosa* (Waagen); Waterhouse, p. 10.

EXPLANATION OF PLATE 1

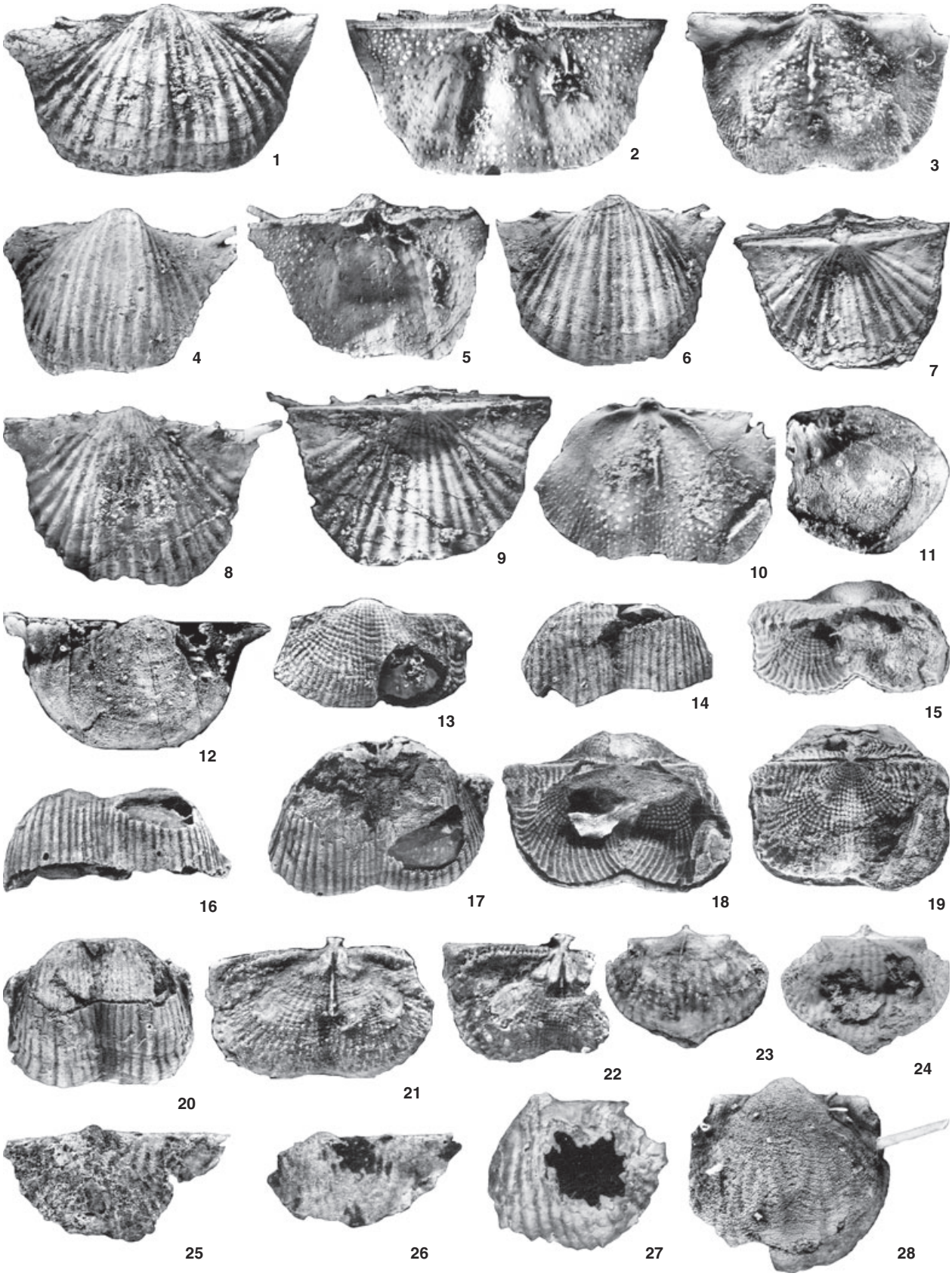
Figs 1–10. *Waterhouseiella hydraensis* sp. nov., sample LEF1. 1–2, NIGP143466, paratype, ventral view and ventral interior; ×5. 3, NIGP143467, paratype, dorsal interior; ×5. 4–5, NIGP143470, ventral view and ventral interior; ×5. 6–7, NIGP143465, holotype, ventral and dorsal views; ×5. 8–9, NIGP143469, ventral and dorsal views; ×5. 10, NIGP143474, dorsal interior; ×5.

Figs 11–12. ?*Spinomarginifera* sp., NIGP143475, sample EP, lateral and ventral views; ×3.

Figs 13–22. *Transennatia gratiosa* (Waagen, 1884), sample LE1. 13–15, NIGP143480, ventral, anterior and dorsal views; ×2. 16–18, NIGP143477, anterior, ventral and dorsal views; ×2. 19–21, NIGP143486, dorsal and anterior views; ×2; 22, NIGP143494, dorsal interior showing the cardinal process, median ridge and bisected elevated muscle platform; ×2.

Figs 23–27. *Cathaysia chonetoides* (Chao, 1927), sample LEF1. 23–24, NIGP143496, dorsal interior and dorsal views; ×3. 25, NIGP143497, ventral view; ×3. 26, NIGP143499, ventral view; ×3. 27, NIGP143500, ventral view; ×3.

Fig. 28. *Haydenella kiangsiensis* (Kayser, 1883), NIGP143501, sample EP, ventral view; ×3.



SHU-ZHONG SHEN and MATTHEW E. CLAPHAM, Wuchiapingian brachiopods

1976 *Gratiosina gratiosa* (Waagen); Grant, p. 131, pl. 33, figs 19–26.
1977 *Asioproductus gratiosus* (Waagen); Yang *et al.*, p. 350, pl. 140, fig. 5.
1978 *Asioproductus gratiosus* (Waagen); Feng and Jiang, p. 254, pl. 90, figs 1–2.
1978 *Asioproductus gratiosus* (Waagen); Tong, p. 228, pl. 80, fig. 7.
1979 *Asioproductus bellus* Zhan (*in* Hou *et al.*), p. 85, pl. 6, figs 7–13; pl. 9, figs 8–10.
1982 *Transennatia gratiosa* (Waagen); Wang *et al.*, p. 214, pl. 92, figs 6–8; pl. 103, figs 4–9.
1987 *Asioproductus septia* Xu in Yang *et al.*, p. 226, pl. 11, figs 19–22.
1989 *Asioproductus bellus* Zhan; Zhan *in* (Li *et al.*), pl. 25, figs 31–36.
2003 *Transennatia gratiosa* Shi *et al.*, p. 1059, figs 3.15–3.19.

Material. Ninety-one specimens. Seventeen conjoined shells (NIGP143476–143492), three dorsal valves (NIGP143493–143495) and more than 30 fragments.

Description. Shell medium in size, transverse in outline, widest at hinge; strongly concavo-convex in lateral profile; trail long, strongly geniculated; ventral visceral region moderately convex, beak small and acute; sulcus beginning anterior to umbo; deepening anteriorly, remaining distinct on trail; ears small, nearly flat; flanks sharply inclined; visceral disc sharply reticulated by crossing of strong costae and rugae; costae continuing forward, becoming much coarser on trail, convergent into sulcus and onto dorsal fold; a row of spines developed between ear and visceral disc; numbering 4–5 on each side; a few coarse spines on ears; lateral spines fine, slanting forward.

Ventral interior with raised adductor platform, ovate in outline; dorsal interior with bilobated cardinal process; median adductor pads highly elevated; bisected by a median ridge beginning between muscle pads, extending anteriorly until midvalve; lateral ridges along posterior margin weakly developed; endospines largely outlining brachial ridges.

Size. 13.7 mm long, 16.8 mm wide and 9.7 mm thick on the average.

Occurrence. This species has been widely reported from the Lopingian (mostly Wuchiapingian) in South China, the Chhidru Formation in the Salt Range, Pakistan and the Episkopi Formation near locality USNM9599 of Grant *et al.* (1991) (Samples LE1, LE2, LEfl).

Remarks. The present specimens are nearly identical with those from the Salt Range, Pakistan, therefore can be safely assigned to the type species. The generic name *Asioproductus* was first used by Zhan (*in* Yang *et al.* 1977) as a new genus, but he did not designate its type species. Subsequently, Zhan (*in* Hou *et al.* 1979) noted that the productid previously referred to *Productus gratiosus* Waagen by Chinese authors represents a new species and was named as *Asioproductus bellus* by Zhan (*in* Hou *et al.* 1979), who designated it as the type species of *Asioproductus*. He emphasized that the type specimens of *P. gratiosus* from the Salt Range, Pakistan show a deep concave dorsal valve but no geniculation and its internal character is still unknown. However, all the external and internal structures of *Asioproductus bellus* Zhan (*in* Hou *et al.* 1979) are identical with those of *Productus gratiosus* Waagen as discussed by Shi *et al.* (2003). Therefore, *Asioproductus* was designated with the same type species of *Transennatia* Waterhouse, 1975 and is apparently a junior synonym of *Transennatia*. *Asioproductus septia* Xu (*in* Yang *et al.* 1987, p. 226, pl. 11, figs 19–22) is considered as a synonym of *T. gratiosa* (Waagen) in terms of its similar size, reticulation and geniculation.

Genus CATHAYSIA Jin *in* (Wang *et al.*, 1966)

Type species. Productus chonetoides Chao, 1927, from the Lopingian in Jiangsi, South China.

Cathaysia chonetoides (Chao, 1927)
Plate 1, figures 23–27

1927 *Productus chonetoides* Chao, p. 62, pl. 16, figs 1–5.
1978 *Cathaysia chonetoides* (Chao); Feng and Jiang, p. 247, pl. 89, fig. 2.
1980 *Cathaysia chonetoides* (Chao); Liao, pl. 6, fig. 26.
1987 *Cathaysia chonetoides* (Chao); Xu (*in* Yang *et al.*), p. 222, pl. 10, figs 11–18, 21.
1994 *Cathaysia chonetoides* (Chao); Xu and Grant, figs 18.16–18.35.

Remarks. A dorsal valve (NIGP143496) and four ventral valves (NIGP143497–143500) from the Episkopi Formation near locality USNM9599 (Samples LE2, LEf1) with transverse outline, distinct costae on visceral disc and rugae on large ears, a distinct anterior nasuta, median ridge and endospines in the dorsal valve are generally comparable with *Cathaysia chonetoides* (Chao, 1927), but further comparison is hampered because all the specimens are incomplete and poorly-preserved. This species is very common in the Lopingian in South China and similar species is also reported from the northwest Caucasus Mountains (Kotlyar *et al.* 2004).

Genus HAYDENELLA Reed, 1944

Type species. Productus kiangsiensis Kayser, 1883, from the Lopingian in South China.

Haydenella kiangsiensis (Kayser, 1883)
Plate 1, figure 28; Plate 2, figure 1

1883 *Productus kiangsiensis* Kayser, p. 185, pl. 26, figs 6–11.
1884 *Productus tumida* Waagen, p. 708, pl. 80, figs 1–3.
1911 *Productus kiangsiensis* Kayser; Frech, p. 129, pl. 21, figs 3a–c.
1927 *Avonia ?kiangsiensis* (Kayser); Chao, p. 125, pl. 14, figs 14–16.
1928 *Thomasia kiangsiensis* (Kayser); Chao, p. 59, pl. 6, fig. 18.
1932 *Linoproductus kiangsiensis* (Kayser); Huang, p. 46, pl. 3, figs 13–15.
1961 *Argentiproductus kiangsiensis* (Kayser); Zhang and Jin, p. 411, pl. 3, figs 13–14.
1965 *Haydenella tumida* (Waagen); Ruzhentsev and Sarytcheva, pl. 38, fig. 9.
1965 *Haydenella kiangsiensis* (Kayser); Ruzhentsev and Sarytcheva, p. 228, pl. 38, figs 6–8.
1977 *Haydenella kiangsiensis* (Kayser); Yang *et al.*, p. 337, pl. 137, fig. 8.
1980 *Haydenella kiangsiensis* (Kayser); Liao, pl. 6, figs 27–28.
1982 *Haydenella kiangsiensis* (Kayser); Wang *et al.*, p. 206, pl. 91, fig. 15.
1989 *Haydenella kiangsiensis* (Kayser); Zhan (*in* Li *et al.*), pl. 25, figs 21, 26; pl. 28, fig. 26.

Remarks. A conjoined shell (NIGP143501) from Sample EP is 12.2 mm long, 14 mm wide and 5.4 mm thick, nearly rounded in outline and has a strongly convex corpus. Vague costae are poorly developed on the visceral disc and ears have 2–3 distinct rugae. Hinge is shorter than greatest width at shell midlength. A row of spines consisting of 3 spines are present between ears and visceral disc. Dorsal valve is deeply concave, and has same weak costellae as ventral valve, but no spines. All the above-mentioned characters suggest that the present species is assignable to *Haydenella kiangsiensis*, but the specimen is slightly smaller than those from South China. This species is very common in the Lopingian in South China.

Haydenella wenganensis Huang (1932, p. 49, pl. 3, figs 16–18) is largely defined based on some immature specimens also from the Lopingian in South China. This species is commonly associated with *H. kiangsiensis* in South China, therefore highly likely a synonym of the present species. *H. minuta* Sarytcheva in Ruzhentsev and Sarytcheva (1965, p. 228, pl. 38, figs 10–11) from the Dzhulfian in Transcaucasia differs from *H. kiangsiensis* by its smaller size and distinct costation.

Order ORTHIDA Schuchert and Cooper, 1932
Superfamily ENTELETOIDEA Waagen, 1884
Family ENTELETIDAE Waagen, 1884

Genus ENTELETES Fischer De Waldheim, 1825

Type species. Enteletes glabra Fischer De Waldheim, 1829, from the Namurian, Russia.

Enteletes tschernyschewi Gemmellaro, 1899
Plate 2, figures 2–6

1899 *Enteletes tschernyschewi* Gemmellaro, p. 134, pl. 27, figs 48–57; pl. 28, figs 1–9.

Material. A conjoined shell (NIGP143461), two ventral valves (NIGP143462, NIGP143463) and a dorsal valve (NIGP143464).

Occurrence. This species is from the Episkopi Formation at approximately the same location as USNM9334 in Hydra Island, Greece (Sample EP).

Remarks. This species is well described and figured by Gemmellaro (1899). It is characterized by medium size, subequally biconvex profile and characteristic weak plication which are developed only near the anterior half of the shell. The ventral sulcus is fairly weak. The nearly parallel dental plates and median septum in ventral valve and strong brachiophore plates in dorsal valve are typical for *Enteletes*. The present specimens match those described by Gemmellaro (1899) very well.

Diener (1897, p. 67, pl. 5, figs 7–10) named a new species *E. tschernyscheffi* from the Chitichun Limestone also after T. N. Tschernyschew, although they have a different spelling. *E. tschernyscheffi* can be readily distinguished from *E. tschernyschewi* by its stronger and more plications and more biconvex profile.

Family SCHIZOPHORIIDAE Schuchert and Levene, 1929

Genus ACOSARINA Cooper and Grant, 1969

Type species. Acosarina dorsisulcata Cooper and Grant, 1969, from the Middle Permian, West Texas, USA (=*Streptorhynchus peregrinus* var. *minutus* Abich, 1878, p. 78, pl. 9, fig. 1a from the Lopingian, Transcaucasia).

Remarks. Cooper and Grant (1969, p. 2) proposed *Acosarina* with *A. dorsisulcata* Cooper and Grant, 1969 as the

type species, which has been widely used in South China and Vietnam (e.g. Liao 1980, 1987; Xu and Grant 1994; Shen *et al.* 1992, Shen and Shi 2007; Shi and Shen 1998). As discussed in detail (Shen and Shi 2007), *Acosarina dorsisulcata* has been considered to be a junior synonym of *Acosarina minuta* (Abich, 1878). Thus, *Acosarina dorsisulcata* is not valid as the type species of the genus *Acosarina* Cooper and Grant, 1969. According to ICZN (International Commission on Zoological Nomenclature) (1999), Article 70.3.2), the type species of the genus *Acosarina* should be refer to *Acosarina minuta* (Abich, 1878) and the two names are cited herein.

This genus differs from *Schizophoria* and *Orthotichia* Hall and Clarke, 1892 by its long and low ventral median septum and rectimarginate to sulcate commissure. The former feature immediately separates *Acosarina* from *Orthis* Dalman, 1828 and *Dalmanella* Hall and Clarke, 1892. *Kotlaia* Grant, 1993*b* was proposed based on specimens from Pakistan that have numerous tubular costellae on both valves and a very long median septum reaching the anterior margin of shell, unlike *Acosarina* in which the tubular costellae are mostly confined to the ventral valve and the median septum normally extends only over the anterior margin of the muscle area. However, the length of the median septum in *Acosarina* is highly variable, based on numerous specimens from South China (Shen and Shi 2007), ranging from about half of the shell length to nearly reaching the anterior margin. In addition, tubular costellae are very common in South Chinese specimens of *Acosarina* and are probably absent due to the preservation of the silicified specimens. In view of the above comparisons, specimens of *Kotlaia* in Greece and Pakistan seem congeneric with those of South China assigned to *Acosarina*. However, a detailed comparison between the West Texas type specimens of *Acosarina dorsisulcata* Cooper and Grant and those of South China and Greece is necessary to ascertain whether *Kotlaia* is a junior synonym of *Acosarina* or not. We herein use the generic name *Acosarina* in terms of their similar external and internal characters.

Acosarina aethopa (Grant, 1993*b*)
Plate 2, figures 7–13

1993*b* *Kotlaia aethopa* Grant, p. 6, figs 5.1–5.6.
2005 *Kotlaia aethopa* Grant; Angiolini *et al.*, p. 180, figs 10A–K, 11F–G.

Material. An adult conjoined shell (NIGP143451), an immature conjoined shell (NIGP143452), a dorsal valve (NIGP143453) and seven juveniles (NIGP143454-NIGP143460).

Description. Adult shell average size, moderately equally biconvex in lateral profile, nearly circular or slightly transversely elliptical in outline, widest at shell midlength, cardinal extremities nearly rounded; both beaks slightly incurved; interarea broadly triangular; delthyrium and notothyrium open; costellae fine, rounded; interspaces as wide as costellae; dorsal valve with shallow sulcus; umbonal region swollen; anterior commissure slightly sulcate; ventral interior with two short dental plates, broadly divergent around posterior part of muscle area; median septum very long, extending nearly to anterior margin; dorsal interior with short, divergent brachiophore plates.

Size. An adult specimen (NIGP143451) is 11.4 mm long, 14 mm wide and 8.4 mm thick; all the other juveniles are only 3–5 mm long and wide.

Occurrence. This species is from the Episkopi Formation near Locality USNM9599 of Grant *et al.* (1991) (Sample LEfl).

Remarks. Although Grant (1993*b*) considered '*Orthotichia*' *indica* (Waagen, 1884, p. 568, pl. 56, figs 7, 8, 14–16) from the Amb and Wargal Formation in the Salt Range, Pakistan to be a different species from *Kotlaia capillosa* Grant, 1993*b* and *K. aethopa* Grant, 1993*b*, the size, outline and profile of the '*Orthotichia*' *indica* are apparently

EXPLANATION OF PLATE 2

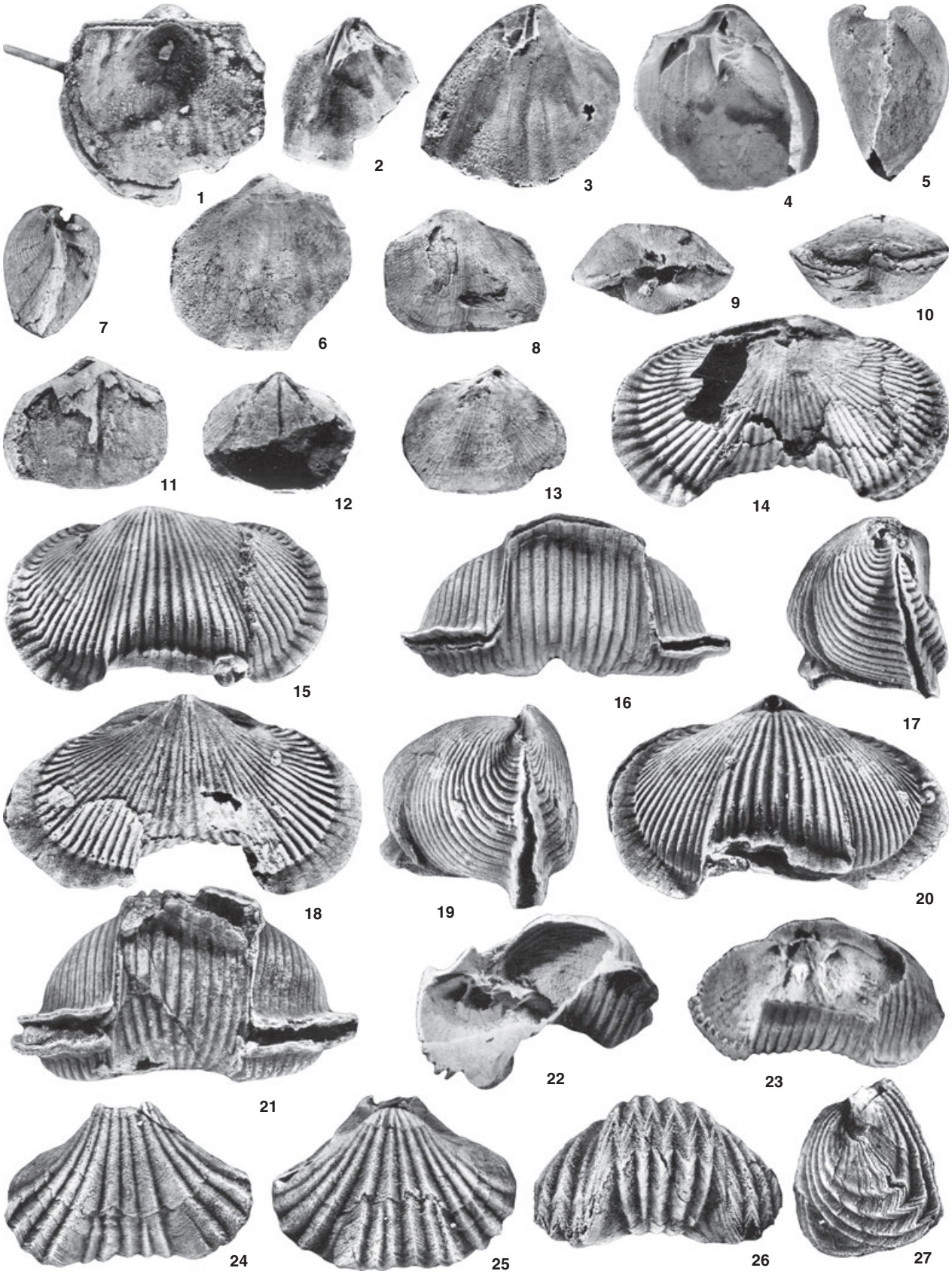
Fig. 1. *Haydenella kiangsiensis* (Kayser, 1883), NIGP143501, sample EP, dorsal view; ×3.

Figs 2–6. *Enteletes tschernyschewi* Gemmellaro, 1899, NIGP143462, sample EP. 2, ventral interior; ×1. 3, 6, NIGP143463, ventral interior showing two dental plates and median septum and ventral view; ×1. 4–5, NIGP143461, interior in ventral view showing dorsal brachial supporting plates and lateral view; ×1.

Figs 7–13. *Acosarina aethopa* (Grant, 1993*b*), sample LE1. 7–11, NIGP143451, lateral, dorsal, posterior, anterior and ventral views, ×2. 12–13, NIGP143452, ventral and dorsal views; ×2.

Figs 14–23. *Glyptorhynchia velifer* (Gemmellaro, 1899), sample EP. 14–17, NIGP143507, ventral, dorsal, anterior and lateral views; ×2. 18–21, NIGP143502, ventral, lateral, dorsal and anterior views; ×2. 22, NIGP143510, shell interior showing the two short dental plates and divided hinge plates; ×2. 23, NIGP143511, shell interior showing the two short dental plates and divided hinge plates; ×2.

Figs 24–27. *Terebratuloidea davidsoni* Waagen, 1883, NIGP143512, sample EP, ventral, dorsal, anterior and lateral views; ×3.



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very close to the above species and it has a long range, probably throughout the Permian. The characteristic tubular costellation has been confirmed from the specimens of the Salt Range, Pakistan (Grant 1993*b*) and South China (Shen and Shi 2007). Therefore, the present species and *K. capillosa* are highly likely junior synonyms of '*Orthotichia*' *indica*. However, the internal details of '*O*'. *indica* from the Salt Range, Pakistan have never been studied; its generic assignment is still pending.

Order RHYNCHONELLIDA Moore, 1952
Superfamily WELLERELLOIDEA Licharew, 1956
Family WELLERELLIDAE Licharew, 1956
Subfamily UNCINUNELLININAE Savage, 1996

Genus GLYPTORHYNCHIA Shen and He, 1994

Type species. Glyptorhynchia lens Shen and He, 1994, from the Changhsing Formation, Guiding, Guizhou, South China.

Remarks. Glyptorhynchia Shen and He, 1994, was suspected to be a nonrhynchonellid and treated as a *nomen dubium* by Savage *in* Williams *et al.* (2000). Actually it is readily recognized as a wellerellid in terms of its coarse costation, short and vertical dental plates and divided hinge plates. It is closely related to *Uncinunellina* Grabau, 1932 and *Anchorhynchia* Jin and Ye (*in* Jin *et al.*, 1979) in terms of its internal structure and costation on surface, but differs by possessing stolidium along the lateral and anterior margins, whereas *Uncinunellina* and *Anchorhynchia* usually have spines with 5–7 lateral spurs across (see Shen and He 1994, pl. 2, fig. 30) that insert into holes near anterior and anterolateral margins to form an interlocking spine system.

Glyptorhynchia velifer (Gemmellaro, 1899)
Plate 2, figures 14–23

1899 *Uncinulus velifer* Gemmellaro, p. 205, pl. 26, figs 51–57.

Material. Seventeen conjoined shells and 6 fragments. Registered specimens: 10 conjoined shells (NIGP143502-143511).

Description. Shell large for genus, transversely elliptical in outline, unequally biconvex in lateral profile, dorsal valve much more convex than ventral valve, widest at shell midlength; ventral valve gently convex; beak acute, straight; foramen small; beak ridges slightly attenuated; sulcus beginning anterior to beak, then flattening and becoming depressed below flanks near midvalve, widening and deepening anteriorly, strongly geniculated at front margin, forming distinct trapezoid anterior tongue and strong uniplicate anterior commissure; sulcus bottom nearly flat; flanks gently declined laterally; dorsal valve strongly convex with a highly elevated fold beginning at midvalve; flanks strongly inclined; anterior and lateral margin with stolidium, stolidium 2–3 mm wide; costae beginning just anterior to beak, low and rounded, bifurcating once anteriorly, with narrow intertroughs; crests flattened near anterior margin, each crest bearing a slight groove anterior to stolidium.

Ventral interior with small hinge teeth; dental plates short and nearly fused to valve walls, nearly vertical to valve floor; dorsal interior with divided hinge plates consisting of two separate plates with deep median division.

Size. 16.8 mm long, 28.3 mm wide and 15.1 mm thick on the average.

Occurrence. This species is from the Episkopi Formation at approximately the same location as USNM9334 in Hydra Island, Greece (Sample EP).

Remarks. The present species can be readily distinguished from the type species *Glyptorhynchia lens* Shen and He (1994, p. 449, pl. 2, figs 31–35) by its large size, earlier costation and larger convexity. It is close to some species of *Anchorhynchia* Jin and Ye (*in* Jin *et al.*, 1979) in view of its costation and size, but can be distinguished by its wide stolidium along the anterior and lateral margins. The present specimens are comparable with the adult specimens figured by Gemmellaro (1899, pl. 26, figs 51–52), but the immature specimens figured by Gemmellaro (1899) appear to have a less biconvex profile.

Family ALLORHYNCHIDAE Cooper and Grant, 1976*a*

Genus TEREBRATULOIDEA Waagen, 1883

Type species. Terebratuloidea davidsoni Waagen, 1883, from the upper part of the Wargal Formation (Guadalupian to Wuchiapingian) in the Salt Range, Pakistan.

Terebratuloidea davidsoni Waagen, 1883
Plate 2, figures 24–27

1883 *Terebratuloidea davidsoni* Waagen, p. 416, pl. 33, figs 1–5.
1933 *Terebratuloidea davidsoni* Waagen; Huang, p. 66, pl. 10, figs 9–10.
1934 *Terebratuloidea davidsoni* Waagen; Grabau, p. 69, pl. 3, figs 12a–c.
1964 *Terebratuloidea davidsoni* Waagen; Wang *et al.*, p. 403, pl. 67, figs 1–5.

Remarks. A conjoined shell (NIGP143512) from the upper part of the Episkopi Formation at approximately the same location as USNM9334 (Sample EP) probably

indicates the presence of this species. The shell measures 17.3 mm long, 22.8 mm wide and 13.8 mm thick and generally comparable with those from the Salt Range, Pakistan in outline and size; but slightly differs by possessing three main and two intercalated short costae in sulcus and six costae on dorsal fold, whereas the Salt Range specimens usually have three costae in sulcus and four on fold. The beak of the present specimen is broken, therefore, the dental plates are not observed.

This species differs from *T. minor* described below by its larger size and more numerous costae in the sulcus and on the fold. The South Chinese specimens described by Huang (1933) and Grabau (1934) are smaller and have a more rounded outline than the types from the Salt Range, Pakistan.

Terebratuloidea minor Waagen, 1883
Plate 3, figures 1–13

1883 *Terebratuloidea minor* Waagen, p. 420, pl. 33, figs 11–12.
1899 *Terebratuloidea elegans* Gemmellaro, p. 127, pl. 26, figs 47–50.

Material. Thirty-four conjoined shells, a ventral valve and a dorsal valve. Registered specimens: Eight conjoined shells (NIGP143513–143520), a ventral valve (NIGP143521) and a dorsal valve (NIGP143522).

Description. Shell medium in size, subtriangular or slightly pentagonal in outline, unequally biconvex in profile, dorsal valve much more convex than ventral valve, greatest width anterior to shell midlength; ventral valve gently convex; beak acute and suberect, truncated by mesothyrid foramen; umbo nearly smooth; sulcus deep, beginning just anterior to umbo; rapidly deepening anteriorly, forming dorsally extended anterior tongue; anterior commissure strongly uniplicate; costae strong, simple, numbering 2 in sulcus and 4–5 on each flank; dorsal valve strongly convex with a very high fold; costae beginning from umbo; numbering 3 on fold and 4–5 on each flank.

Ventral interior with strong teeth and short, vertical dental plates; dental plates very close to valve wall; dorsal hinge plates connecting each other, but divided anteriorly; no median septum.

Size. 8.8 mm long, 10.5 mm wide and 6.6 mm thick on average.

Occurrence. This species is from the upper part of the Episkopi Formation at approximately the same location as USNM9334 (Sample EP).

Remarks. Terebratuloidea elegans described by Gemmellaro (1899, p. 127, pl. 26, figs 47–50) is considered to be a synonym of the present species in terms of their very close outline, size, profile and costation pattern. The present specimens have a more highly elevated dorsal fold, but otherwise are nearly comparable with the Salt Range specimens. This species differs from *T. davidsoni* by its smaller size and in always having two costae in sulcus and three on fold. *T. depressa* Waagen (1883, p. 419, pl. 33, figs 6–8) differs from the present species by its three costae in sulcus and more transverse outline.

Genus GERASSIMOVIA Licharew, 1956

Type species. Gerassimovia gefoensis Licharew, 1956, from the Permian of the Northern Caucasus.

Gerassimovia sp.
Plate 3, figures 14–25

Remarks. Four conjoined shells (NIGP143523–143526) and a ventral valve (NIGP143527) from Sample EP probably indicate a new species, but three of them are juveniles and the dorsal interior is not observed. The present specimens are characterized by slightly triangular outline, gently biconvex profile and broad and shallow sulcus on ventral valve and weak fold on dorsal valve. Costae with subangular crests begin from the beak, which is truncated by a mesothyrid foramen. Dental plates are totally absent in the ventral valve. This species differs from the type species by its less biconvex profile and from *G. pamirica* Grunt *in* Grunt and Dmitriev (1973, p. 115, pl. 9, fig. 6) and *G. abalakovi* Grunt *in* Grunt and Dmitriev (1973, p. 116, pl. 9, fig. 2) by its costae beginning from the beak and low dorsal fold.

Order ATHYRIDIDA Boucot *et al.*, 1964
Suborder ATHYRIDIDINA Boucot *et al.*, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family COMELICANIIDAE Merla, 1930
Subfamily SPIRIGERELLINAE Grunt *in* Ruzhentsev and Sarytcheva, 1965

Genus JUXATHYRIS Liang, 1990

Type species. Juxathyris apionucula Liang, 1990, from the Cunhouling Member of the Lengwu Formation (Capitanian), Tonglu, Zhejiang Province, South China.

Juxathyris guizhouensis (Liao, 1980)
Plate 4, figures 1–7

1933 *Athyris timorensis* (Rothpletz); Huang, p. 69, pl. 10, fig. 14 (*non* 13, 15–19).

1980 *Araxathyris guizhouensis* Liao, p. 268, pl. 9, figs 1–4.
1980 *Janiceps janiceps* (Stache); Liao, pl. 9, figs 10–13.
1987 *Spirigerella simplex* Liao, p. 113, pl. 6, figs 15–19 (*non* pl. 8, figs 26–30).
2004 *Juxathyris guizhouensis* (Liao); Shen *et al.*, p. 896, figs 8.11–8.23, 13.

Material. Nine conjoined shells, four ventral valves and a dorsal valve. Registered specimens: eight conjoined shells (NIGP143578–143585).

Size. 13.7 mm long, 12.8 mm wide and 9.6 mm thick on the average.

Occurrence. This species is from the Episkopi Formation at approximately the same location as USNM9334 (Sample EP).

Remarks. This species has been described in detail by Shen *et al.* (2004) based on specimens from the Lopingian of South China. The Greek specimens are consistent with those from South China in terms of their elongate outline, uniplicate anterior commissure in adults; two dental plates nearly fused to valve wall and undivided hinge plates, but slightly differ by their less strongly developed uniplicate anterior commissure. *Spirigerella* species with similar outline can be readily distinguished from *Juxathyris* species by their massive strong cardinal process and thickened shell (see Grant 1976, pl. 65, figs 35–49). The juvenile specimens with rectimarginate anterior commissure are somewhat similar to *Juxathyris bisulcata* (Liao, 1980, p. 268, pl. 9, figs 14–17), but can be distinguished by their elongate outline and uniplicate commissure in adults. *Comelicothyris* species from the Changhsingian in Italy (Posenato 2001) bear some similarities to the present species, but can be distinguished by their more widely transverse outline, distinct ventral sulcus and nearly vertical dental plates not fused to valve wall.

Subfamily XENOSARIINAE Cooper, 1976*b*

Genus XENOSARIA Cooper, 1976*b*

Type species. Xenosaria exotica Cooper, 1976*b*, from the Bell Canyon Formation (Capitanian) in West Texas, USA.

Xenosaria tenuis sp. nov.
Plate 4, figures 8–16

Derivation of name. From the Latin 'tenuis' (small), referring to its gentle profile and small size.

Holotype. NIGP143586, a conjoined shell (Pl. 4, figs 8–11).

Paratype. NIGP143587, a dorsal valve (Pl. 4, fig. 16).

Material. Seven conjoined shells (NIGP143588–143594).

Type locality and horizon. This species is from the Episkopi Formation near Locality USNM9334 (Sample EP).

Diagnosis. Small shell, with roundly triangular outline, gently biconvex profile and distinct flat interarea, very weak sulcus on ventral valve, no sulcus on dorsal valve.

Description. Shell small, roundly triangular in outline, gently biconvex in profile; widest at shell midlength; ventral beak slightly incurved, truncated by a circular permesothyrid foramen; interarea distinct, flat, well differentiated from umbonal region by distinct beak ridges; delthyrium wedge-shaped, open; sulcus very weak, beginning from anterior part of ventral valve; anterior commissure gently uniplicate or nearly rectimarginate; dorsal valve evenly and flatly convex; surface smooth except for a few growth lines.

Ventral interior without dental plates; dorsal interior with deep, marginal sockets; hinge plates elevated; inner hinge plates narrow, concave; outer hinge plates supported by outer socket plates; apical foramen not observed.

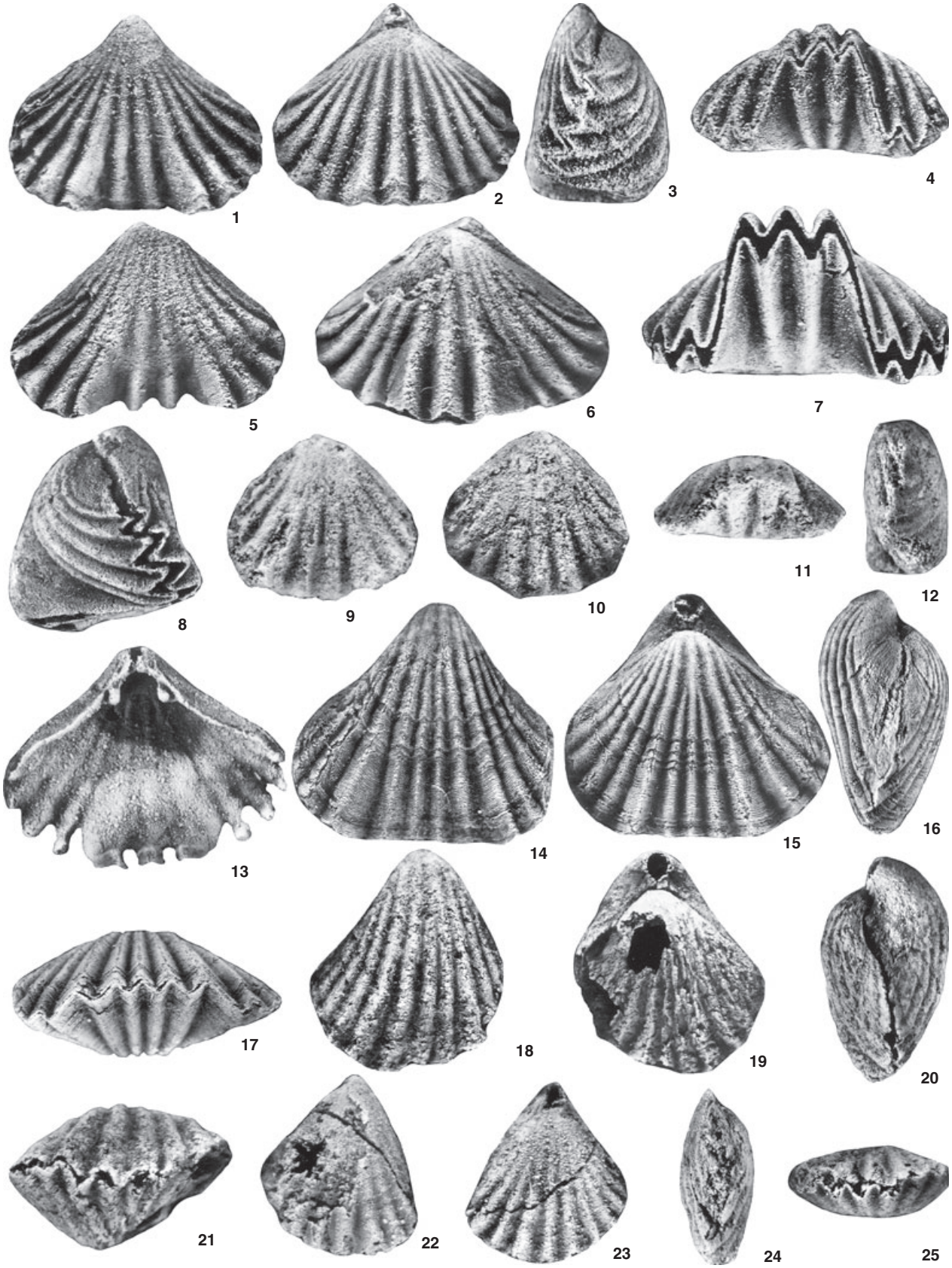
Size. 6.2 mm long, 6.2 mm wide and 3.6 mm thick on the average.

Remarks. According to Cooper (1976*b*), the subfamily is characterized by smooth athyridids without dental plates but with foraminate inner hinge plates. The apical foramen in the inner hinge plate is not observed, therefore, the generic assignment of this species is still pending. However, the ventral interarea with open delthyrium, gentle external profile and other internal structures are comparable with *Xenosaria*. This species can be readily distinguished from the only other species of the genus, *Xenosaria exotica* Cooper, 1976*b*, by its small size, gentle profile, broadly rounded anterior margin and no sulcus on dorsal valve, whereas *X.*

EXPLANATION OF PLATE 3

Figs 1–13. *Terebratuloidea minor* Waagen, 1883, sample EP. 1–4, NIGP143513 ventral, dorsal, lateral and anterior views; ×4.5. 5–8, NIGP143515, ventral, dorsal, anterior and lateral views; ×4.5. 9–12, NIGP143520, ventral, dorsal, anterior and lateral views of juvenile; ×4.5. 13, NIGP143521, ventral interior; ×4.5.

Figs 14–25. *Gerassimovia* sp., sample EP. 14–17, NIGP143523, anterior, ventral, dorsal and lateral views; ×3.5. 18–21, NIGP143524, ventral, dorsal, lateral and anterior views; ×4. 22–25, NIGP143525, ventral, dorsal, lateral and anterior views; ×4.5.



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exotica is characterized by a moderately convex profile and is slightly anteriorly notched.

Suborder RETZIIDINA Boucot *et al.*, 1964
Superfamily RETZIOIDEA Waagen, 1883
Family NEORETZIIDAE Dagys, 1972
Subfamily HUSTEDIINAE Grunt, 1986

Genus HUSTEDIA Hall and Clarke, 1892

Type species. Terebratula mormoni Marcou, 1858, from Upper Carboniferous, Nebraska, USA.

Hustedia episkopiensis sp. nov.
Plate 4, figures 17–24

Derivation of name. From the town of Episkopi, near the type locality of the species.

Holotype. NIGP143595, a conjoined shell (Pl. 4, figs 17–20).

Material. Seven conjoined shells (NIGP143596–143602).

Type locality and horizon. This species is from the Episkopi Formation at approximately the same location as USNM9334 (Sample EP).

Diagnosis. Small, elongate, with fine costae interrupted by concentric growth lines, no sulcus and fold.

Description. Shell small, elongate in outline, moderately to strongly biconvex in profile, greatest width slightly anterior to shell midlength; anterior margin evenly rounded; anterior commissure rectimarginate; costae fine, beginning from beak, numbering 10–16 on ventral valve, with rounded crests, interrupted by concentric growth lines; interspaces as wide as costae; no sulcus and fold; ventral valve moderately to strongly convex; foramen rounded, mesothyrid; internal structures not observed.

Size. 6.3 mm long, 5.3 mm wide and 4.3 mm thick on the average.

Remarks. Cooper (1976*b*) described many different species from West Texas, but none is comparable with the present species in terms of its size, fine costae interrupted by concentric lines and no sulcus and fold. This species can be distinguished from *Hustedia grandicosta* Waagen (1883, p. 491, pl. 34, figs 6–12) from the Chhidru Formation in the Salt Range, Pakistan by its small size, finer and more costae.

Order SPIRIFERIDA Waagen, 1883
Suborder SPIRIFERIDINA Waagen, 1883
Superfamily AMBOCOELIOIDEA George, 1931
Family AMBOCOELIIDAE George, 1931
Subfamily AMBOCOELIINAE George, 1931

Genus ORBICOELIA Waterhouse and Piyasin, 1970

Type species. Orbicoelia fraterculus Waterhouse and Piyasin, 1970, from the Ratburi Limestone in Thailand.

Remarks. Orbicoelia can be distinguished from *Crurithyris* George, 1931 by its total absence of sulcus on both valves, short hinge line and gently convex dorsal valve.

Orbicoelia fraterculus Waterhouse and Piyasin, 1970
Plate 5, figures 7–17

1970 *Orbicoelia fraterculus* Waterhouse and Piyasin, p. 145, pl. 25, figs 16–26; pl. 26, figs 1–4.
1976 *Orbicoelia fraterculus* Waterhouse and Piyasin; Grant, p. 193, pl. 52, figs 1–24.

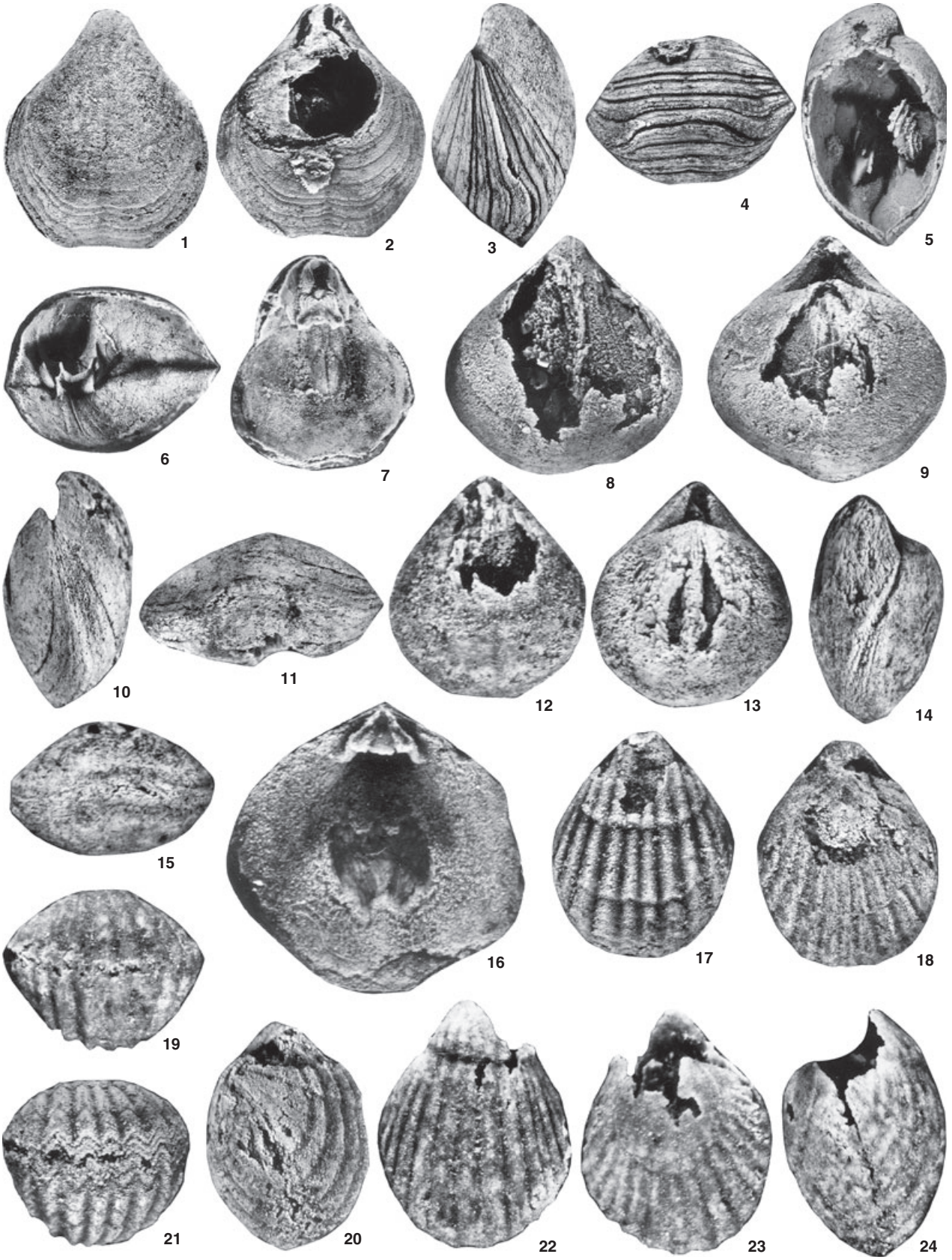
Material. Fifty conjoined shells, 34 ventral valves and 17 dorsal valves from Locality USNM9334, among them 20 conjoined shells (NIGP143533–143552), five ventral valves (NIGP143553–143557) and five dorsal valves (NIGP143558–143562) are registered. Eighteeen conjoined shells, three ventral valves from Locality USNM9559, of which 10 conjoined shells are registered (NIGP143563–143572).

EXPLANATION OF PLATE 4

Figs 1–7. *Juxathyris guizhouensis* (Liao, 1980); sample EP. 1–4, NIGP143585, ventral, dorsal, lateral and anterior views; ×2.5. 5, NIGP143584, lateral view showing the spiralia inside; ×2. 6, NIGP143588, anterior view of shell interior showing the two short dental plates and undivided hinge plates; ×2. 7, NIGP143582, dorsal interior showing undivided hinge plates; ×3.5.

Figs 8–16. *Xenosaria tenuis* sp. nov., sample EP. 8–11, NIGP143586, holotype, ventral, dorsal, lateral and anterior views; ×4. 12–15, NIGP143591, ventral, dorsal, lateral and anterior views; ×7. 16, NIGP143587, paratype, dorsal interior showing the hinge plates; ×7.5.

Figs 17–24. *Hustedia episkopiensis* sp. nov., sample EP. 17–20, NIGP143595, holotype, ventral, dorsal, anterior and lateral views; ×6.3. 21–24, NIGP143599, anterior, ventral, dorsal and lateral views; ×6.3.



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Description. Shell large in size for genus, slightly transverse in outline, hinge line much shorter than greatest width at about shell midlength; cardinal extremities and lateral margin rounded; anterior margin broadly rounded; ventral valve highly inflated; beak obtuse, incurved; interarea high, slightly concave; delthyrium wedge-shaped, open; maximum convexity at umbo; evenly inclined outwards; sulcus totally absent; dorsal valve nearly flat or slightly convex; beak obtuse and very low; interarea low and widely triangular; notothyrium open; no fold; micro-ornament not preserved.

Ventral interior with knob-like teeth, no dental plates and median septum present; a pair of low ridges present along edge of delthyrium; dorsal interior with parallel crural plates.

Size. 12.6 mm long, 14.3 mm wide and 7.9 mm thick on the average.

Occurrence. This species has been recorded from the Ratburi Limestone and the Episkopi Formation at approximately the same locations as USNM9334 (Sample EP) and USNM9599 (Sample LE1).

Remarks. The present species has been described in detail by Waterhouse and Piyasin (1970) and Grant (1976), but the specimens shown by Waterhouse and Piyasin (1970) and Grant (1976) are slightly different in terms of the shell convexity. The specimens shown by Grant (1976) are slightly more convex than those described by Waterhouse and Piyasin (1970), and therefore may represent two different species. The Greek specimens from two localities also belong to two groups. The specimens from the Episkopi Formation near Locality USNM9599 are slightly larger and more convex than those from Locality USNM9334. The former group is close to those described by Waterhouse and Piyasin (1970) and the latter group is close to those described by Grant (1976), but both groups are very close each other in general, so we tentatively treat them as a single species.

This species is closely similar to *Crurithyris extima* Grant (1970, p. 142, pl. 3, figs 1–3d, Text-fig. 1) from the dolomite unit of the Kathwai Member, Mianwali Formation in the Salt Range, Pakistan, which was subsequently considered to be an *Orbicoelia* by Grant (1976), but differs by its larger size and more transverse outline. *Crurithyris speciosa* Wang (1955, p. 146, pl. 83, figs 1–4) may be also referable to *Orbicoelia* Grant (1976) in terms of absence of sulcus on both valves, but differs from the present species by its less transverse outline.

Superfamily MARTINIOIDEA Waagen, 1883
Family MARTINIIDAE Waagen, 1883
Subfamily MARTINIINAE Waagen, 1883

Genus MARTINIA M^c^Coy, 1844

Type species. Spirifer glaber Sowerby, 1820, from the Visean, England.

Martinia cf. *elegans* Diener, 1897
Plate 5, figures 18–27

1897 *Martinia elegans* Diener, p. 54, pl. 8, figs 1, 2; pl. 9, figs 1–2.
1897 *Martinia nucula* Rothpletz; Diener, p. 50, pl. 8, figs 5–6.
2003 *Martinia elegans* Diener; Shen *et al.*, p. 246, pl. 4, figs 11–14; pl. 5, figs 1–5.

Material. Three conjoined shells (NIGP143573–143575), a ventral valve (NIGP143576), a dorsal valve (NIGP143577) and more than 10 fragments.

Description. Shell medium in size for genus, somewhat rhomboid or slightly triangular in outline, moderately biconvex in profile, widest at or slightly anterior to shell midlength; ventral beak incurved; maximum convexity at umbo; sulcus weak, beginning from midvalve, forming distinct anterior tongue near anterior margin; anterior commissure moderately uniplicate; flanks moderately inclined; dorsal valve transversely elliptical in outline, with a distinct wide fold; both valves smooth except for some weak concentric growth lines.

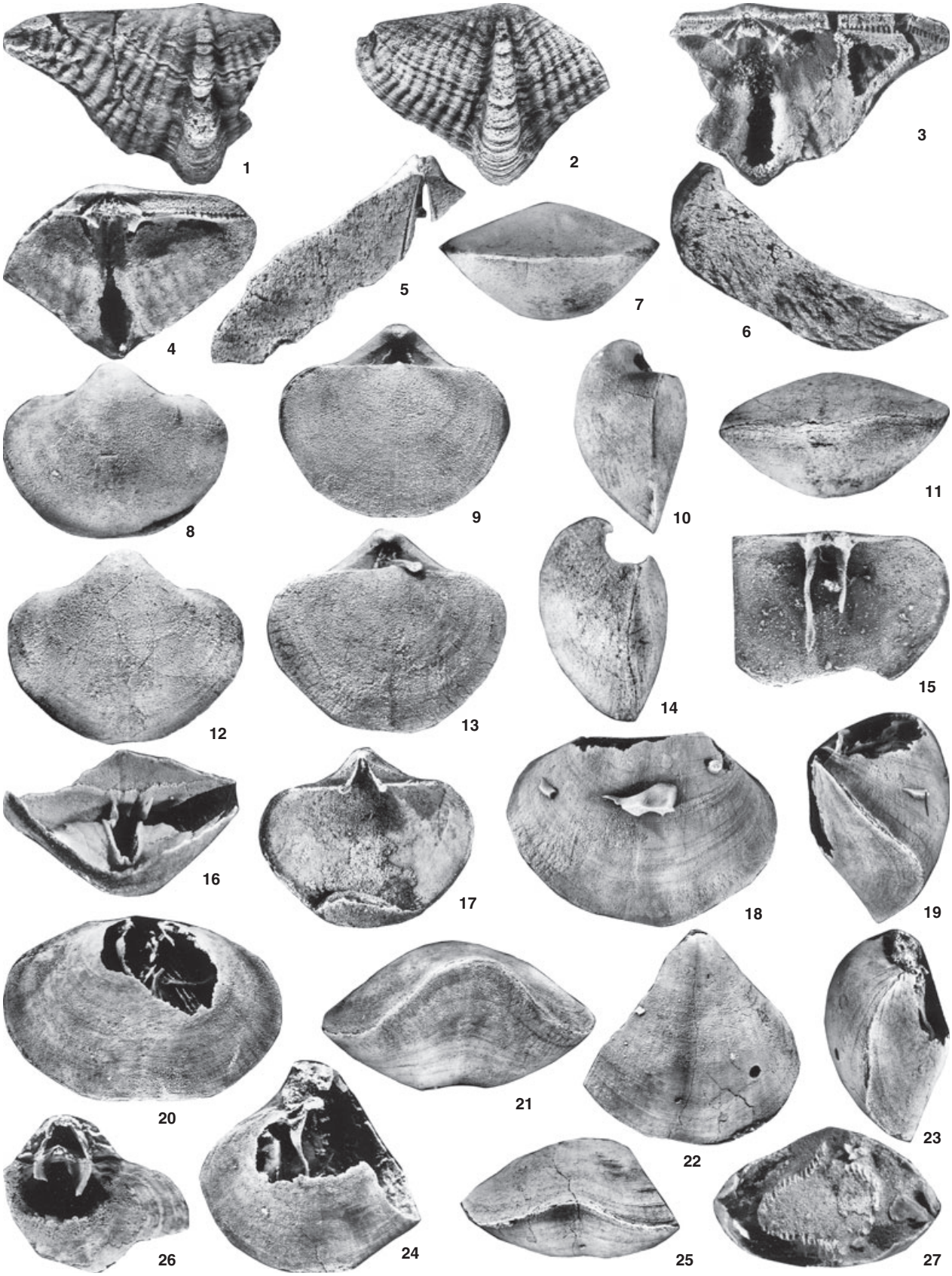
Ventral interior with no plates; dental ridges deep; dorsal interior with divided triangular hinge plates; slightly conver-

EXPLANATION OF PLATE 5

Figs 1–6. *Petinospiriferina subtriangularis* (Schellwien, 1900), sample EP. 1, 3, NIGP143529, dorsal view and dorsal interior; ×3. 2, 4, NIGP143530, dorsal view and dorsal interior; ×3. 5–6, NIGP143532, dorsal and ventral views of an incomplete ventral valve; ×3.

Figs 7–17. *Orbicoelia fraterculus* Waterhouse and Piyasin, 1970, Sample EP. 7–10, NIGP143538, anterior, ventral, dorsal and lateral views; ×2.7. 11–14, NIGP143533, anterior, ventral, dorsal and lateral views; ×3. 15, 17, NIGP143542, dorsal interior and ventral interior views; ×3. 16, NIGP143557, shell interior showing the two crural plates in the dorsal valve and a pair of low ridges along the edge of delthyrium; ×3.

Figs 18–27. *Martinia* cf. *elegans* Diener, 1897, sample EP. 18–21, IGP143573, ventral, lateral, dorsal and anterior views; ×2. 22–25, NIGP143574, ventral, lateral, dorsal and anterior views, ×2. 26, NIGP143577, ventral interior; ×2.5. 27, NIGP143575, a shell showing spiralia inside; ×2.



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gent toward valve floor; spiralia more than 16 coils, pointing laterally.

Occurrence. This species is from the Episkopi Formation at approximately the same location as USNM9334 (Sample EP).

Remarks. This species can be generally assigned to *Martinia* in terms of the absence of any plates and septa in both valves and smooth surface. The present specimens are largely comparable with the immature ones from the Chitichun Limestone in Tibet (e.g. Diener 1897, pl. 9, figs 1–2) in view of the general outline and distinct anterior tongue, but differ by their smaller size if compared with adult specimens. The specimens referred to *Martinia nucula* Rothpletz by Diener (1897, pl. 8, figs 5–6) are considered to be conspecific with the present species. *M. nucula* can be distinguished from the present species by its elongate outline. *M. ceres* Gemmellaro (1899, pl. 33, figs 8–15) and *M. pusilla* Gemmellaro (1899, pl. 33, figs 33–37) from the Wordian in Sicily are also similar to the present species, but differs by their much smaller size.

Order SPIRIFERINIDA Ivanova, 1972
Suborder CYRTINIDINA Carter *et al.*, 1994
Superfamily CYRTINOIDEA Fredericks, 1911
Family CYRTINIDAE Fredericks, 1911

Genus LICHAREWINA Kotlyar, Zakharov and Polubotko, 2004

Type species. Licharewina praetriassica Kotlyar *et al.* 2004, from the late Changhsingian of the northwestern Caucasus Mountains.

Remarks. Elements of the superfamily Cyrtinoidea should be placed in Spiriferinida Ivanova, 1972 (Carter and Johnson *in* Williams 2006) rather than in the Spiriferida Waagen (Kotlyar *et al.* 2004) in terms of its punctuate shell, simple plications, high ventral interarea and smooth fold and sulcus. The superfamily was thought to range only from the Lower Devonian to Early Carboniferous (Carter and Johnson *in* Williams 2006). Kotlyar *et al.* (2004) first documented the occurrence of the superfamily in the Permian. *Cyrtina* Davidson, 1859, with *Calceola heteroclite* Defrance, 1828 as the type species, bears some resemblance to the present genus in view of its deeply conical profile and simple distinct plications on both valves. However, the present genus can be readily distinguished from *Cyrtina* by its long median septum and two parallel dental plates instead of a spondylium in *Cyrtina*, delthyrium covered by imbricated stegidial plates rather than a convex deltidium or apically perforated. The superfamily position of *Licharewina* is not satisfactory in terms of the internal structures and imbricated stegidial plates, but the pyramidal profile, the cardinal process and the plication suggest that it belongs to the Cyrtinoidea.

Licharewina josephinae (Gemmellaro, 1899)
Plate 6, figures 1–15

1899 *Cyrtina josephinae* Gemmellaro, p. 150, pl. 30, figs 4–8.
2004 *Licharewina praetriassica* Kotlyar *et al.*, p. 522, figs 6.13–6.20.

Material. A conjoined shell from Locality USNM9334 (NIGP143603), and a conjoined shell (NIGP143604), four ventral valves (NIGP143605–143608) and three dorsal valves from USNM9559 (NIGP143609–143611).

Description. Shell small, semi-circular in outline; greatest width slightly anterior to hinge; cardinal extremities slightly obtuse; anterior and lateral margins rounded; ventral valve deeply conical; beak acute, commonly slightly distorted; ventral interarea very high and flat; delthyrium covered by imbricated stegidial plates, probably open near hinge; beak ridges distinct; plications simple; with subangular crests; each flank with 2–3 plications; sulcus slightly wider than intertroughs on flank; beginning from beak; gradually widening anteriorly; dorsal valve moderately convex, semi-circular in outline; with no interarea; central fold

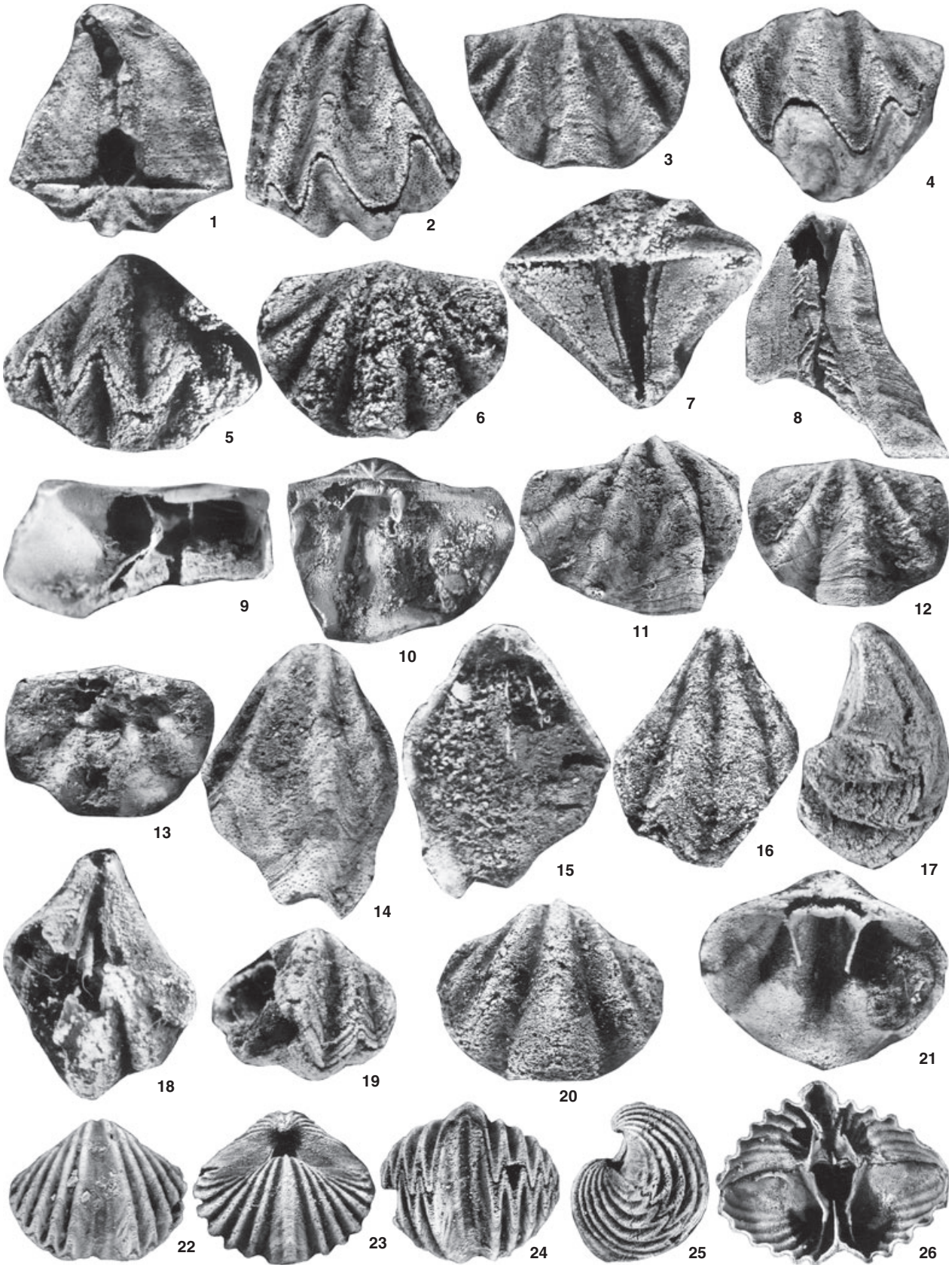
EXPLANATION OF PLATE 6

Figs 1–15. *Licharewina josphinae* (Gemmellaro, 1899). 1–4, NIGP143604, sample LEF1, posterior, ventral, dorsal and anterior views; ×6.7. 5–7, NIGP143603, sample EP, anterior, dorsal and posterior views; ×8.8. 8–9, NIGP143605, sample LEF1, posterior view showing the stegidial plates, and ventral interior showing the two dental plates, median septum is hardly seen; ×4. 10–11, NIGP143609, sample LEF1l; dorsal and dorsal interior views; ×3.5. 12–13, NIGP143610; sample LEF1, dorsal and dorsal interior views; ×3.6. 14–15, NIGP143607, sample LEF1, ventral and ventral interior views; ×7.

Figs 16–21. Cyrtinid gen. and sp. indet., NIGP143613, sample EP. 16–19, ventral, lateral, dorsal and anterior views; ×4. 20–21, NIGP143612, dorsal and dorsal interior views; ×3.6.

Figs 22–25. *Paraspiriferina multiplicata* (Sowerby, 1829), NIGP143614, sample EP, ventral, dorsal, anterior and lateral views; ×2.

Fig. 26. *Paraspiriferina cellulana* Cooper 1976*a*, NIGP143624, sample EP, shell interior showing two dental plates and median septum in the ventral valve and two brachial plates in the dorsal valve; ×2.



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distinct, much higher than lateral plications; anterior commissure uniplicate.

Ventral interior with a long median septum and two nearly parallel dental plates; dental plates first convergent and then divergent toward valve floor; dorsal interior with deep sockets and ctenophoridium; hinge plates separated, but not completely preserved; a median ridge maybe present; shell punctuate.

Occurrence. This species is from the Episkopi Formation near locality USNM9599 (Sample LEf1) and approximately at the same locality as USNM9334 (Sample EP) of Grant *et al.* (1991). This species has also been recorded from late Changhsingian in the northwestern Caucasus Mountains.

Remarks. The present specimens are nearly identical with those described by Gemmellaro (1899) from the Sosio Limestone of Sosio, Sicily. *Licharewina praetriassica* Kotlyar *et al.*, 2004, was considered to be different from *Cyrtina josephinae* Gemmellaro, 1899, by the absence of a spondylium. However, our Greek specimens indicate that *Cyrtina josephinae* Gemmellaro possesses the same internal structure characterized by a long median septum and two dental plates in the deeply conical ventral valve. Therefore, *Licharewina praetriassica* Kotlyar *et al.* is treated as a synonym of *L. josephinae* (Gemmellaro).

Cyrtinid gen. et sp. indet.
Plate 6, figures 16–21

Material. A ventral valve (NIGP143612) and a dorsal valve (NIGP143613).

Description. Shell medium, elongate in outline; greatest width slightly anterior to hinge; cardinal extremities rounded; ventral valve deeply conical; beak high and acute; interarea high, slightly concave; delthyrium open or cover not preserved; beak ridges rounded; sulcus distinct, beginning from beak; forming distinct uniplicate anterior commissure with dorsal fold; dorsal valve strongly convex; plications strong, with rounded crests; intertroughs shallow and narrower than plications; growth lines distinct.

Ventral interior with well preserved median septum; about half of shell length; dorsal interior with deep sockets; hinge plates undivided; crura projecting straight.

Occurrence. This species is from the Episkopi Formation at approximately the same locality as USNM9334 (Sample EP) of Grant *et al.* (1991).

Remarks. The present specimens possibly indicate another new genus of Cyrtinidae. This species can be readily distinguished from *Licharewina* described above by its median septum in the ventral valve and undivided hinge plates in the dorsal valve, rounded plication and rounded beak ridges, although it shares a similar conical profile with *Licharewina*.

Suborder SPIRIFERINIDINA Ivanova, 1972
Superfamily SYRINGOTHYRIDOIDEA Fredericks, 1926
Family SYRINGOTHYRIDIDAE Fredericks, 1926
Subfamily PERMASYRINXINAE Waterhouse, 1986

Genus PETINOSPIRIFERINA gen. nov.

Derivation of name. From the Greek 'petin' winged, and *Spiriferina*.

Type and only known species. Spirifer subtriangularis Schellwien, 1900, from the Trogkofel Limestone (?Early or Mid Permian) of the Carnic Alps.

Diagnosis. Small widely alate spiriferinids, both valves with highly elevated noncostate folds and dorsal valve with an internal hollow groove covered by secondary shell; ribbings fine on surface; growth lamellae strong; syrinx not present.

Remarks. The strongly transverse outline, simple ribbing and dorsal fold and absence of syrinx suggest that this genus may belong to the subfamily Permasyrinxinae Waterhouse, 1986. However, the family position of this genus is questionable because dental adminicula appear not present and the delthyrial plate is unknown. This genus can be readily distinguished from any other genera of the family by its small size, fine ribbings, two folds on both ventral and dorsal valves, and the hollow groove covered by the secondary shell in the dorsal valve. *Tipispirifer* Grant 1976 looks similar to the present species in terms of widely alate outline, but is totally different in view of its distinct costellate ventral sulcus and very low costate dorsal fold which characterizes the subfamily Neospiriferinae.

Petinospiriferina subtriangularis (Schellwien, 1900)
Plate 5, figures 1–6

1900 *Spirifer subtriangularis* Schellwien, p. 79, pl. 11, figs 14–15.

Material. An incomplete conjoined shell (NIGP143528), two dorsal valves (NIGP143529, NIGP143531), an incomplete ventral valve (NIGP143530) and a ventral fragment (NIGP143532).

Occurrence. This species is from the upper part of the Episkopi Formation at approximately USNM9334 (Sample EP) and the Trogkofel Limestone in Carnic Alps.

Description. Shell relatively small in size for spiriferinids, moderately biconvex in lateral profile, widely triangular in outline; lateral margin nearly straight; widest at hinge; cardinal extremities acute, strongly alate, with a cardinal angle about 30 degrees; ventral beak low and acute, slightly incurved; interarea high, widely triangular, concave, moderately apsacline; delthyrium triangular, open; delthyrial plates not observed; beak ridges sharply angular; umbo inflated; sulcus beginning from beak, probably slightly widening and deepening anteriorly, but with a distinct fold in sulcus; fold elevated near anterior margin; flanks gently inclined; dorsal valve also with highly elevated fold; flanks gently inclined; both valves with simple ribbings; ribbings fine, not bifurcating; interrupted by irregular lamellae; microornament and punctae not preserved.

No dental adminicula observed; dorsal interior with socket ridges; hinge plates divided, extending dorsally to form crural plates; cardinal process fimbricate; both valves with deep median groove corresponding to folds, covered by secondary shell.

Remarks. Although the dental plates of the Trogkofel specimens figured by Schellwien (1900) are not known yet, the specimens found from Hydra are so similar to those of Schellwien (1900) in size, high interarea, alate outline, acute cardinal extremities, and distinct two folds on both valves that we believe that they are most likely the same species. *Tipispirifer oppilatus* Grant (1976, p. 217, pl. 58, figs 1–40) from the Ratburi Limestone is somewhat similar to the present species in terms of its transversely triangular outline, but differs by its distinct costellate ventral sulcus and lower fold which suggest the subfamily Neospiriferinae. In addition, the imbricated stegidial plates in *Tipispirifer* are not observed in the present species.

Superfamily PENNOSPIRIFERINOIDEA Dagys, 1972
Family PARASPIRIFERINIDAE Cooper 1976*b*

Genus PARASPIRIFERINA Reed, 1944

Type species. Spiriferina (*Paraspiriferina*) *ghundiensis* Reed, 1944, from the Kalabagh Member of the Wargal Formation, Ghundi, Salt Range, Pakistan.

Remarks. Paraspiriferina can be distinguished from *Crenispirifer* Stehli, 1954 by its lower, more and less angular plications, regularly-spaced growth laminae with hairlike spines. It differs from *Punctospirifer* North, 1920 by its smaller size, rounded cardinal extremities and smaller triangular interarea. *Spiriferellina* Fredericks, 1924 differs from *Paraspiriferina* by its fewer and more angular plications, higher fastigium with flattened crest, deeper sulcus with flattened or raised floor. *Callispirina* Cooper and Muir-Wood, 1951 can be distinguished from *Paraspiriferina* by its sharp plications and fine regularly-spaced growth lines and high crural plates.

Paraspiriferina multiplicata (Sowerby, 1829)
Plate 6, figures 22–25; Plate 7, figures 1–4

1829 *Spirifer nultiplicatus* Sowerby, p. 119.
1862 *Spiriferina octoplicata* (Sowerby); Davidson, pl. 1, fig. 11 (*non* figs 12–14).
1883 *Spiriferina multiplicata* Sowerby; Waagen, p. 502, pl. 39, figs 8, 9.
1897 *Spiriferina margaritae* (Gemmellaro); Diener, p. 15, pl. 1, fig. 7.
1899 *Spiriferina margaritae* Gemmellaro, p. 154, pl. 30, figs 9–23.
1925 *Spiriferina multiplicata* Sowerby; Reed p. 94, pl. 6, fig. 12.
1933 *Spiriferina multiplicata* Sowerby; Huang, p. 57, pl. 9, figs 4, 5.
1964 *Punctospirifer multiplicatus* (Sowerby); Wang *et al.*, p. 584, pl. 113, figs 12, 13.
1976 *Paraspiriferina* cf. *P. ghundiensis* Reed; Grant, p. 235.
1979 *Spiriferellina multiplicata* (Sowerby); Zhan *in* Hou *et al.*, p. 97, pl. 12, fig. 15.
1986 *Punctospirifer multiplicatus* (Sowerby); Liao and Meng, pl. 3, fig. 11.
1987 *Punctospirifer multiplicatus* (Sowerby); Liao, pl. 6, figs 1, 2.

Material. Five conjoined shells (NIGP143614–143618).

Description. Shell medium in size, rotund in outline, strongly biconvex in lateral profile, greatest width slightly anterior to hinge; cardinal extremities rounded; ventral valve strongly convex; beak acute, strongly incurved; interarea concave, broadly triangular; beak ridges poorly defined; delthyrium narrowly wedge-shaped, open; sulcus originating from beak, rapidly deepening and widening anteriorly, with broadly V-shaped floor; flanks moderately inclined; dorsal valve also strongly convex; beak and interarea low; notothyrium broadly triangular; plications simple, with rounded crests; each flank with six plications; sulcus with 1–2 weak plications; dorsal fastigium highly elevated; commonly with 2–3 weak plications on crest; hairlike spines not preserved probably due to the acidic treatment.

Ventral interior with small teeth and short dental adminicula in apex, median septum thin, high extending to half of shell length, abruptly downsloping anteriorly; dorsal interior with lateral elongate sockets; adminicula large, nearly vertical to valve floor, forming notothyrial cavity; spiralia directed toward cardinal extremities.

Size. 11.7 mm long, 14.8 mm wide and 13.2 mm thick on the average.

Occurrence. This species has been reported from the topmost part of the Wargal Formation (Wuchiapingian) and the Chhidru Formation at the Salt Range, Pakistan, the Changhsing Formation at Dapaichong, Hunan Province, the lower part of the Heshan Formation at Heshan, Guangxi Province, from the

Upper Permian in Hechuan, Sichuan Province in South China, the Guadalupian Ratburi Limestone in Thailand, an unknown horizon in India and the Episkopi Formation at Episkopi, Hydra Island, Greece (Sample EP).

Remarks. The present specimens are generally consistent in size, outline and profile with those from the Himalayan region and South China, but differ slightly by the presence of variable costae in the ventral sulcus. The variability of costae in the sulcus, from nearly absent to moderately developed, imply that this character could be an intraspecific variation. The specimens figured as *Spiriferina octoplicata* (Sowerby) by Davidson (1862) apparently indicate a few different genera or species. The specimen in figure 13 of Davidson (1862) can be readily distinguished from all others by its alate outline and the greatest width at cardinal extremities. The specimens in figures 12, 14 also differ from the present species by their wider outline and stronger plications. Specimens described as *Spiriferina margaritae* by Gemmellaro (1899, p. 154) from the Sosio Limestone in Sicily are highly likely conspecific with the present species in terms of their similar outline and costation. The type species described by Reed (1944) is closely similar to the specimens in size, outline and profile by Davidson (1862) and Waagen (1883), therefore could be a junior synonym of the present species. The specimens described as *Trigonotreta multiplicata* (Sowerby) by King (1850, p. 129, pl. 8, figs 15–18) probably represent another genus in terms of their fewer and coarser plications and more transverse outline. The present species differs from *Paraspiriferina gentilis* Grant (1976, p. 236, pl. 64, figs 1–36) from the Ratburi Limestone in Thailand by its much stronger convexity and finer and more plications.

Paraspiriferina cellulana Cooper and Grant, 1976*b*
Plate 6, figure 26; Plate 7, figures 5–14

1976*b* *Paraspiriferina cellulana* Cooper and Grant, p. 2733, pl. 720, figs 49–59.

Material. Twenty-four conjoined shells (NIGP143619–143642), six ventral valves (NIGP143643–143648), six dorsal valves (NIGP143649–143654) and more than 40 fragments.

Description. Shell average size for genus, transversely elliptical in outline, strongly subequally biconvex in lateral profile, greatest width anterior to hinge, at about shell midlength; cardinal extremities rounded; ventral beak acute, strongly incurved dorsally; interarea broadly triangular, concave; delthyrium triangular, open; beak ridges poorly defined; sulcus originating from beak, rapidly deepening and widening anteriorly; sulcus bottom broadly V-shaped; dorsal beak low; notothyrium very low, nearly linear; fastigium moderately elevated, with bluntly angular crest, occasionally with 1–2 weak plications near front margin; anterior commissure strongly uniplicate; each flank of ventral valve with six plications; sulcus smooth or occasionally with 1–2 very weak plications near bottom.

Ventral interior with small teeth; dental ridges deep, anteriorly tapered, slightly convergent toward valve floor; connected by two small triangular plates at apex; dental adminicula thin, short, nearly vertical to valve floor; concave anteriorly; median septum thin, high, steeply sloping at anterior, extending forward about half length of valve; dorsal interior with widely separated adminicula, convergent mesially; crura extending forward from cural bases, about one-third of valve length.

Size. 13.7 mm long, 19.1 mm wide and 12.1 mm thick on the average.

Occurrence. This species has been reported from the Roadian Road Canyon Formation and Cibolo Formation at Road Canyon and Cibolo, West Texas, USA and the Episkopi Formation (Sample EP) at Episkopi, Hydra Island, Greece.

Remarks. The specimens described herein are nearly identical with those of West Texas in view of their size, outline and plications. The specimens figured as *Spiriferina octoplicata* Sowerby by Davidson (1862, pl. 1, figs 12, 14, *non* fig. 11) are closely similar to the present species, but differ by coarser plications and nearly rectangular cardinal extremities. This species differs from *P. multiplicata* described above by its more transverse outline and more plications.

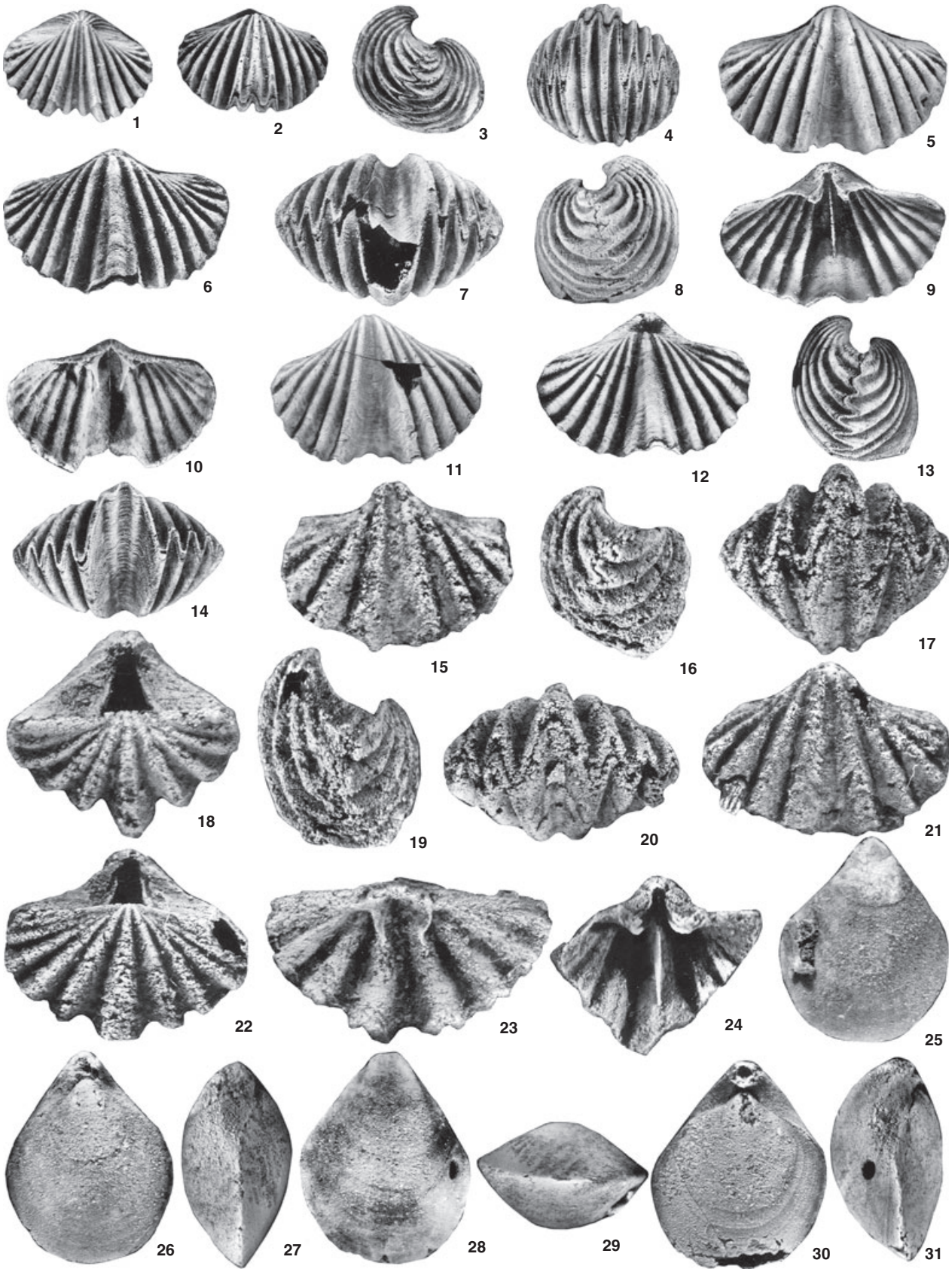
EXPLANATION OF PLATE 7

Figs 1–4. *Paraspiriferina multiplicata* (Sowerby, 1829), NIGP143615, sample EP, ventral, dorsal, lateral and anterior views; ×2.

Figs 5–14. *Paraspiriferina cellulana* Cooper 1976*b*, sample EP. 5–8, NIGP143620, ventral, dorsal, anterior and lateral views; ×2.5. 9, NIGP143647, ventral interior showing the long median septum in the ventral valve; ×2. 10, NIGP143650, dorsal interior showing the crura; ×2. 11–14, NIGP143621, ventral, dorsal, lateral and anterior views; ×2.

Figs 15–24. *Crenispirifer alpheus* (Huang, 1933), sample EP. 15–18, NIGP143655, ventral, lateral, anterior and dorsal views; ×4.7. 19–22, NIGP143657, lateral, anterior, ventral and dorsal views; ×4.3. 23, NIGP143662, dorsal interior showing the crura; ×4.5. 24, NIGP143660, ventral interior; ×4.

Figs 25–31. ?*Dielasma* sp., sample EP. 25–27, NIGP143664, ventral, dorsal and lateral views; ×5. 28–31, NIGP143665, ventral, anterior, dorsal and lateral views; ×5.



SHU-ZHONG SHEN and MATTHEW E. CLAPHAM, Wuchiapingian brachiopods

Family SPIRIFERELLINIDAE Ivanova, 1972

Genus CRENISPIRIFER Stehli, 1954

Type species. Spiriferina angulata King, 1931, from the Hess Formation in Texas, USA.

Crenispirifer alpheus (Huang, 1933)
Plate 7, figures 15–24

1933 *Spiriferina multiplicata* mut. α Huang, p. 59, pl. 11, figs 2–3.
1955 *Punctospirifer alpheus* (Huang); Wang, p. 164, pl. 97, figs 5–8.
1964 *Punctospirifer alpheus* (Huang); Wang *et al.*, p. 584, pl. 113, figs 8–11.
1978 *Spiriferellina multiplicata* (Sowerby); Feng and Jiang, p. 295, pl. 104, fig. 2.
1978 *Punctospirifer alpheus* (Huang); Tong, p. 259, pl. 90, fig. 4.
1980 *Punctospirifer alpheus* (Huang); Liao, pl. 8, fig. 49.
1982 *Punctospirifer alpheus* (Huang); Liu *et al.* 1982, p. 213, pl. 155, fig. 2.
1982 *Punctospirifer alpheus* (Huang); Wang *et al.*, p. 250, pl. 94, fig. 11.
1987 *Punctospirifer alpheus* (Huang); Liao, pl. 6, figs 3–4.
1987 *Crenispirifer alpheus* (Huang); Xu *in* Yang *et al.*, p. 233, pl. 15, figs 26–28.
1994 *Paraspiriferina alpha* (Huang); Xu and Grant, p. 45, figs 35, 36 (1–23).

Material. Four conjoined shells (NIGP143655–143658), a ventral valve (NIGP143659) and three dorsal valves (NIGP143660–143662).

Description. Shell small for genus, transversely elliptical in outline, moderately biconvex in profile, cardinal extremities rounded; hinge line slightly shorter than greatest width at shell midlength; ventral beak obtuse, suberect; interarea broadly triangular, slightly concave; delthyrium wedge-shaped, open; beak ridge distinct; sulcus originating from beak, slightly deeper than interspaces on flank; dorsal valve with fold slightly coarser than costae on flank; costae subangular, with deep interspaces.

Ventral interior with high blade-like median septum extending to more than half of shell length; dental ridges distinct; dorsal interior with deep and rounded sockets; adminicula deeply divided; cardinal process knob-like; crura extending forward from hinge plates; narrowing anteriorly and slightly bowed dorsally; micro-ornament not observed.

Size. 7.8 mm long, 8.9 mm wide and 6.5 mm thick on the average.

Occurrence. This species is from the Episkopi Formation at approximately the same locality as USNM9334 (Sample EP) of Grant *et al.* (1991).

Remarks. This species was assigned to a few different genera, but the subangular costae, relatively deep interspaces, less prominent sulcus and fold, and deeply divided hinge plates all suggest *Crenispirifer*. The Greek specimens are nearly identical with those from the Lopingian in South China in size, outline and costation. The type species differs from *C. alpheus* by its more angular costae and deeper interspaces.

Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDA Waagen, 1883
Superfamily DIELASMATOIDEA Schuchert, 1913
Family DIELASMATIDAE Schuchert, 1913
Subfamily DIELASMATINAE Schuchert, 1913

Genus DIELASMA King, 1859

Type species. Terebratulites elongates Schlotheim, 1816, from the Upper Permian, Thuringia, Germany.

?*Dielasma* sp.
Plate 7, figures 25–31

Remarks. Five conjoined shells (NIGP143663–143667) from the Episkopi Formation at approximately the same locality as USNM9334 (Sample EP) probably indicate the presence of *Dielasma*. These five specimens are very small in size (7.4 mm long, 5.8 mm wide and 4.2 mm thick on the average) and may be immature individuals. They have an elongate outline and rectimarginate anterior commissure. No sulcus and fold is present on ventral and dorsal valves. Ventral interior is unknown, but a highly elevated loop is present in the dorsal valve.

This species is somewhat similar to *Dielasma truncatum* Waagen (1882, p. 345, pl. 25, fig. 13) from the Amb Formation in the Salt Range, Pakistan in view of its outline and size, but differs by that the Salt Range species has a weakly uniplicate anterior commissure. However, the internal details of both species are unclear, therefore it is very hard to identify if they are congeneric or not.

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