

New observations on rhynchonelloid brachiopod *Dzieduszyckia* from the Famennian of Morocco

ANDRZEJ BALIŃSKI and GERTRUDA BIERNAT



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The genus *Dzieduszyckia* is especially well represented and diverse in the Famennian strata of the Middle Atlas, Morocco. In this paper we re-study and re-illustrate the rich collection of *Dzieduszyckia* from Morocco, described by Henri and Geneviève Termier, and originally referred to *Halorella* or *Eoperegrinella*. New data on the internal shell structure of *D. crassicostata*, *D. intermedia*, and *D. tenuicostata* indicate great intraspecific variability in morphology. The structure of crura of three studied species demonstrates that subfamily Dzieduszyckiinae is better placed within the family Halorellidae, instead of Peregrinellidae. Type specimens (lectotypes) of the three species were also selected. An analysis of the stable isotopes of carbon and oxygen of the shell material of *Dzieduszyckia* and carbonate sediment was used to investigate the presumed chemosynthetic nature of its paleoenvironments. The analyses of the Moroccan and Polish material do not show any signature of unusual environmental conditions: they fall in the range of the mean values of $\delta^{13}\text{C}$ for the Late Devonian.

Key words: Brachiopoda, Halorellidae, *Dzieduszyckia*, carbon isotopes, Famennian, Morocco.

Andrzej Baliński [balinski@twarda.pan.pl], and Gertruda Biernat [gbiernat@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Dzieduszyckia is a relatively rare fossil with a broad but disjunct distribution: the genus is known from Laurussia, Kazakhstan, South China, and northern Gondwana (Fig. 1). *Dzieduszyckia* is one of the largest Paleozoic rhynchonelloids and is distinctive because of its bisulcate, strongly costate shell. Although the genus was first described almost a century ago (Siemiradzki 1909), it is still inadequately known. The main aim of the present study is to investigate the internal shell structure of the Moroccan representatives of the genus consisting of at least three species: *D. crassicostata* (Termier and Termier, 1948), *D. intermedia* (Termier, 1936), and *D. tenuicostata* (Termier, 1936). Additionally, new serial sections of one shell, representing the type species *D. kielcensis* (Roemer, 1866) and illustrating the structure of crura, are also presented.

The study is based on material from the collection of Henri and Geneviève Termier, which was described by them in a series of publications during the first half of the twentieth century (see bibliography). This collection was deposited by Dr. Solange Willefert (Division de la Géologie, Rabat) in 1970 in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, where it is presently housed (abbreviated ZPAL). It contains 614 specimens, the majority of which consist of complete to almost complete shells in a rather good state of preservation. The interior of these shells appears to be wholly or partially filled with sparry calcite. It is noteworthy that several of the specimens (unfortunately not all) illustrated by the Termiers have been found in the collection during this

study. Some of these are re-illustrated here, and two additional specimens are illustrated for the first time.

Remarks on the distribution of *Dzieduszyckia*

The distribution of *Dzieduszyckia* has attracted the attention of many authors (e.g., Ager et al. 1972; Biernat 1967, 1988; Cloud and Boucot 1971; Ager et al. 1976; Noll et al. 1984; Campbell and Bottjer 1995a, b). The main features of the distributional pattern of this rhynchonelloid brachiopod is its wide, yet disjunct geographic range and its low diversity but locally high abundance (Fig. 1). Biernat (1967) reported, for example, that *D. kielcensis* (the type species of the genus) from the Kadzielnia quarry near Kielce (the Holy Cross Mts, Poland) collected by G. Push, can occur in exceedingly high abundances with hundreds of specimens found in a single limestone lens. Similar accumulations of this species have been found in the borehole in Ruda Strawczyńska situated about 20 km W from Kielce (Biernat 1967).

Similar rock-forming abundances in limestone lenses were reported for *Leiorhynchus bashkiricus* (Tschernyschew, 1887) (= *Dzieduszyckia bashkirica*) from the western slopes of the South Urals (Nalivkin 1947; Rozman 1962). According to Rozman (1962), *D. bashkirica* also occurs in Kazakhstan in the Zajsan-Irtysh region, but no details have been given of this occurrence. More recently, the species was found in south China (Hou and Wei 1985) and Tadjikistan (Menakova 1991). Biernat (1988) mentioned the occurrence of *Dziedu-*

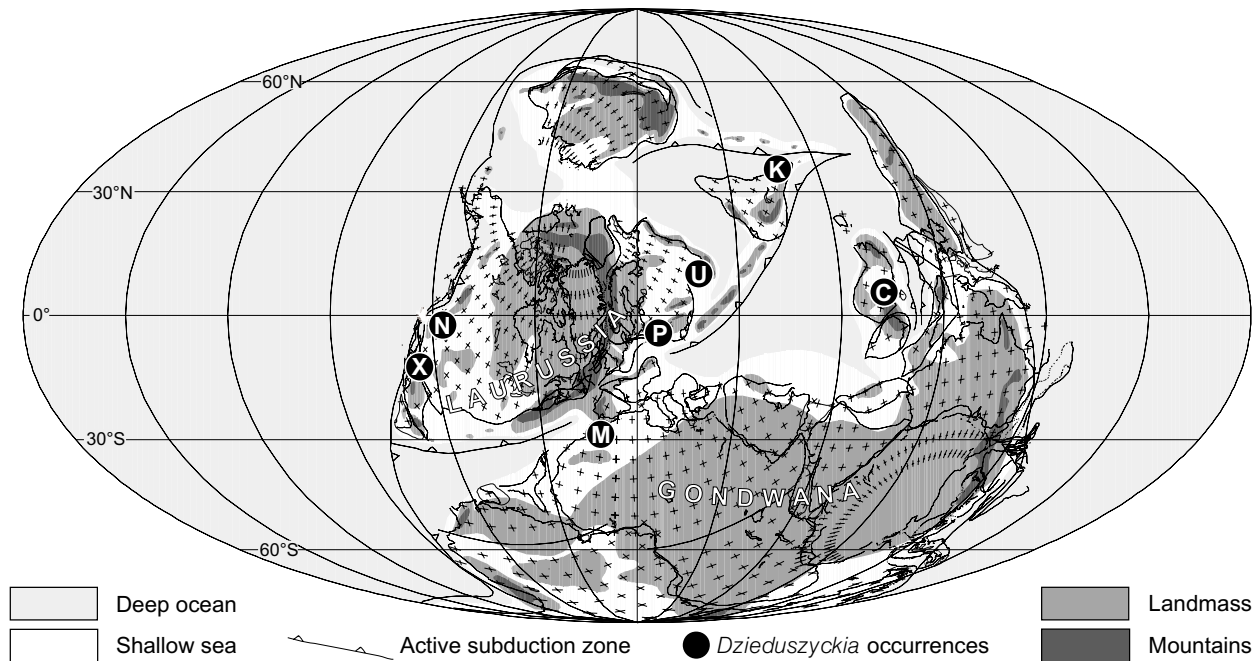


Fig. 1. Distribution of *Dzeduszyckia* in the Famennian (363 Ma) reconstructed paleogeography (adapted from Golonka et al. 1994). Explanation: C, China; K, Kazakhstan; M, Morocco; N, Nevada; P, Poland; U, Urals, X, Mexico.

zyckia in Australia referring to the personal communication from Prof. A. Thomas, but no details were published and, in consequence, this occurrence is not included on our Fig. 1.

In Morocco, *Dzeduszyckia* is represented by a few species found at several outcrops of the Middle Atlas (e.g., Termier 1936, 1938; Termier and Termier 1948, 1959; Choubert 1956; Roulleau 1956; Hollard and Morin 1973; Ager et al. 1976). The detailed description of some occurrences of *Dzeduszyckia crasicostata* from the vicinity of Khenifra was provided by Ager et al. (1976). They found the species to occur in very rich abundances, associated with algal lamellae, especially in the lower part of the concentrations. The associated fossils included dielasmid terebratulids, goniatites, gastropods, nautiloids and worm-tubes.

Another representative of the genus, *Dzeduszyckia sonora* Noll, Dutro, and Beus, 1984 lived on the eastern border of Laurussia, in present day Nevada (Cloud and Boucot 1971) and Mexico (Noll et al. 1984). In both these localities *Dzeduszyckia* occurs in the association with bedded barite. Poole et al. (1983) suggested that this association may represent records of sites near deep-sea hydrothermal vents, although barite accumulations are also reported from high productivity areas of the oceans (e.g., Bishop 1988; Dehairs et al. 1992; Dymond et al. 1992; Falkner et al. 1993; Stechter et al. 1996; Thomas et al. 2000). Indeed, reduced vent-seep fluids may produce anomalous sedimentary precipitates, such as barite (Koski et al. 1985; Campbell and Bottjer 1995a, b). These habitats prove inhospitable to a majority of marine invertebrates, and such vent-seep locations are generally colonized by forms characterized by various detoxification strategies (Zierenberg et al. 2000). In addition to its association with bedded barite, another feature relevant to the vent-seep habitat interpretation of *Dzeduszyckia* is its wide, yet patchy distribu-

tion which points to its long-distance dispersal capabilities and prodigious reproductive capacities, traits which are characteristic of vent-seep taxa (see Van Dover et al. 2002).

One line of paleontological evidence used for identifying Paleozoic vent-seep associations is the presence of microbial fabrics, worm-tubes, and high, monospecific concentrations of brachiopods (Campbell and Bottjer 1995a, b; Little et al. 1999; Peckmann et al. 2001). Campbell and Bottjer (1995b), who reviewed 21 Phanerozoic brachiopod occurrences interpreted to represent ancient hydrothermal vent and cold seep habitats, found that the Late Devonian vent-seep settings were dominated by *Dzeduszyckia* (= ?*Eoperegrinella*). The morphologically similar Triassic *Halorella* and Cretaceous *Peregrinella* also share a common habitat (Campbell and Bottjer 1995a; Posenato and Morsilli 1999). Recently, Peckmann et al. (2001) described an Early Carboniferous seep community from the Harz Mountains (Germany), which was dominated by a low-diversity but high-abundance fauna of rhynchonellid brachiopods and rare solemyid bivalves associated with microbial limestones. Interestingly, the rhynchonellid of that community was represented by "*Leiorhynchus*" *contrarius* Roemer 1850 (= *Ibergirhynchia contraria* Gischler, Peckmann, and Sandy, 2003), a form which seems morphologically very close to *Dzeduszyckia*. At present, data are insufficient to resolve the question whether the morphological similarity between those two forms represents phylogenetic closeness, or convergence. However, if the internal structure of *I. contraria* is found to support a close taxonomic affinity with the Late Devonian *Dzeduszyckia*, then *I. contraria* may represent the long searched for missing link between *Dzeduszyckia* and the Triassic *Halorella* (e.g. Ager et al. 1972, 1976; Gischler 2003).

Recent brachiopods are very rarely found in vent-seep associations (Campbell and Bottjer 1995b; Zezina 2000;

Zezenia and Pakhnevitsch 2000). Moreover, Zezenia (2000) and Zezenia and Pakhnevitsch (2000) have noted that those brachiopods found at hydrothermal vents are small, suggesting that vent-seep habitats do not offer favourable living conditions for the present-day brachiopods. The small size is in contrast with the Paleozoic and Mesozoic brachiopods from such vents, which are characterized by strikingly large shell dimensions (e.g., *Dzieduszyckia*, *Halorella*, *Peregrinella*). This phenomenon may be explained by some special adaptations of fossil brachiopods, which are not found among the recent representatives. It seems that chemosymbiosis, which is not known among present-day brachiopods, could be an adaptation that enabled taxa such as *Dzieduszyckia* to flourish in the Famennian vent-seep environments.

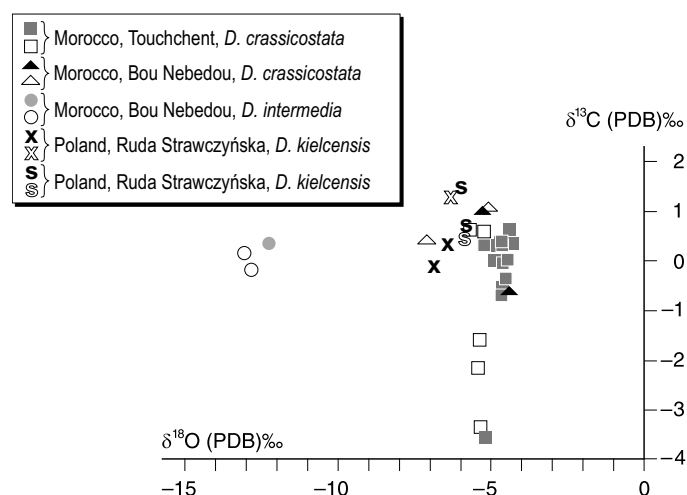


Fig. 2. Stable carbon and oxygen isotopic values from *Dzieduszyckia* samples from Morocco and Poland; solid symbols, shell fabric with admixture of sediment; open symbols, sediment.

Stable isotope analysis

In order to investigate the geologic evidence for the presumed chemosynthetic paleoenvironments of the Moroccan and Polish *Dzieduszyckia* localities, the analyses of the stable isotopes of carbon and oxygen were performed on brachiopod shell fabric and on carbonate sediment attached to these shells. The sampling materials were obtained by microdrilling. Multiple samples were taken from the individual uncleaned shells (anterior and midlength regions) and the sediment. The analyses were done using a Finnigan MAT Delta plus mass-spectrometer, operated by Dr Krzysztof Małkowski (Warsaw). The results are presented relative to the PDB standard, using a NBS-19 reference sample. The accuracy of measurements approximates $\pm 0.02\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.04\text{‰}$ for $\delta^{18}\text{O}$. The results show (Fig. 2) that the majority (87.5% of samples) of the $\delta^{13}\text{C}$ values average from +1.496 to -0.610‰ PDB. Only four (12.5%) samples show more negative values ranging from -1.607 to -3.564‰ PDB, but this merely reflects variability in a single specimen (Fig. 2; multiple datapoints for single specimen of *C. crassicosata* from Touchchent). Thus, almost all obtained values are not isotopically unusual, but rather fall in the range of the mean values of $\delta^{13}\text{C}$ for the Late Devonian global ocean (see Veizer et al. 1999: fig. 10).

The above results contrast with those of Campbell and Bottjer (1995a), who demonstrated that carbonate material from Wilbur Springs (Early Cretaceous, northern California), where the rynchonelloid *Peregrinella* occurs in great abundance, had distinctly ^{13}C -depleted values ranging from -19.25 to -23.94‰ PDB. According to these authors, the values indicate restriction of *Peregrinella* to cold-seep settings. Peckmann et al. (2001) analyzed $\delta^{13}\text{C}$ from carbonates of an Early Carboniferous seep community from the Harz Mountains and obtained values as low as -32‰ PDB.

It is noteworthy that the $\delta^{18}\text{O}$ values obtained in this study are scattered in the low range, from -7.085 to -4.311‰ PDB. However, three values of a specimen of *D. intermedia* from Bou Nebedou, Morocco, are more negative (-12.240 to -13.044‰ PDB). This may be an artifact caused by local diagenetic conditions because another specimen from the

same locality reveals values which are consistent with the remaining datapoints.

In summary, stable carbon and oxygen isotopic analyses on carbonate material (shell fabric and sediment) collected from *Dzieduszyckia* sites in Morocco and Poland do not show any signature of unusual environmental conditions. On the contrary, they reveal values which characterize normal sea-water conditions for the Devonian period. These results most certainly do not support, and in fact may challenge, the hypothesis that *Dzieduszyckia* occurrences are restricted to vent-seep paleoenvironments. It is obvious that any definite statement is premature at present and further study is warranted to verify this intriguing hypothesis.

Systematic paleontology

Family Halorellidae Ager, 1965

Subfamily Dzieduszyckiinae Savage, 1996

Genus *Dzieduszyckia* Siemiradzki, 1909

Dzieduszyckia nov. genus; Siemiradzki 1909: 85.

Dzieduszyckia Siemiradzki, 1909; G. Biernat 1967: 145–146.

Eoperegrinella gen. nov.; Ager 1968: 61–63.

Type species: Terebratula? Kielcensis, by subsequent designation of F. Roemer (1866); Famennian (Upper Devonian), Kadzielnia quarry, Holy Cross Mountain, Central Poland.

Species assigned: Terebratula? Kielcensis F. Roemer, 1866; *Trematospira (?) baschkirica* Tschernyshev, 1887; *Halorella tenuicostata* H. Termier, 1936; *Halorella intermedia* H. Termier, 1936; *Halorella crassicosata* Termier and Termier, 1948; *Dzieduszyckia sonora* Noll, Dutro, and Beus, 1984.

Remarks.—The genus, as well as the type species, *D. kielcensis* was re-described and re-illustrated by Biernat (1967). She gave emended diagnosis of the genus and designated a type specimen (neotype) of *D. kielcensis* out of six original specimens of the Pusch's collection derived from limestone of

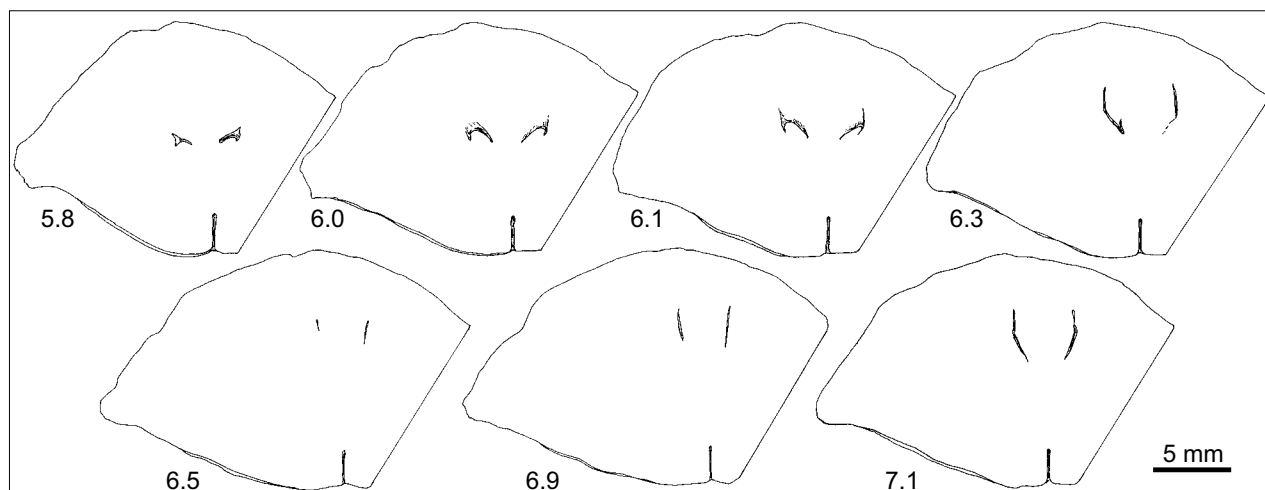


Fig. 3. Transverse serial sections of *Dzieduszyckia kielcensis* (Roemer, 1866) from the Famennian of Ruda Strawczyńska borehole (ZPAL Bp X/895.4 m), Central Poland. Numbers refer to distances in mm from the posterior of the ventral umbo.

the Kadzielnia quarry. Several sections of four shells of the *D. kielcensis* (Biernat 1967: figs. 2, 3; Fig. 3) showed a typical rhynchonelloid interior and thus the taxonomic position of the genus was rectified. This, in turn, allowed the conclusion that the Polish species, as well as several Moroccan ones described as belonging to *Halorella* (Termier 1936, 1938; Termier and Termier 1948, 1950) or *Eoperegrinella* (Ager 1968, 1972; Ager et al. 1976), are in fact congeneric (Biernat 1967).

It was suggested by G.A. Cooper (in: Termier and Termier 1949) that the Moroccan Late Devonian *Halorella* species might be referable to *Dzieduszyckia* Siemiradzki, 1909. This suggestion was at first rejected by Termier and Termier (1949), mainly on the grounds that despite the great morphologic resemblance the Polish genus possessed a spiral brachidium.

Later, Biernat (1967) revised the type material of *Dzieduszyckia kielcensis* from Kadzielnia near Kielce, as well as new material from the Ruda Strawczyńska borehole (about 20 km W of Kielce). She proved that the specimen with a spiral brachidium was an accidental admixture from the Carboniferous of Belgium (see also Roemer 1866), and that the original shells from Kadzielnia represent a true rhynchonelloid.

The present study of the shell interior of the Moroccan species reveals more details concerning the structure of the dental plates, dorsal septum and crura, as well as their variability (Figs. 4, 5, 8, 9). In all sectioned specimens dental plates are distinct but short to very short, confined to the most umbonal region of the valve. They are subparallel to slightly convergent in *D. crassicostata* and *D. tenuicostata*, or slightly divergent in sectioned specimens of *D. intermedia*. The dorsal median septum is high and thicker posteriorly, thin and slightly lowering anteriorly, terminating at about the shell midlength. Crura in all studied species are generally of the ciliform type revealing some similarity with crura of the Late Triassic Halorellidae Ager, 1965. On the other hand, there are evident differences in the structure of crura relative to that of the Cretaceous Peregrinellidae Dagys, 1968. The latter possess a mergiform type of crura, which are developed as long, closely set, parallel and relatively straight, not

curved ventrally structures. It is therefore suggested here that the subfamily Dzieduszyckinae Savage, 1996 is better placed within the family Halorellidae, instead of Peregrinellidae. Our suggestion is in concordance with the earlier opinion of the Termiers who, based on its striking exterior appearance, included Devonian Moroccan forms to the genus *Halorella*.

When introducing his new genus *Eoperegrinella* Ager was aware that it was very close to *Dzieduszyckia* (Ager et al. 1972, 1976) and that Biernat (1967) had suggested, before a formal description was published by Ager, that both genera should be regarded as congeneric. Ager et al. (1972: 173) pointed out that the serial section of the type species of *Dzieduszyckia* published by Biernat (1967) did not show the highly distinctive long, crura characteristic of the Moroccan species. They supposed, however, that this might be merely the result of sectioning that was not continued far enough to show them, or that the crura had been broken off. The present observations prove that, indeed, in almost all specimens sectioned by Biernat, the distal parts of the crura had not been preserved. However, one of the specimens of *D. kielcensis*, which we have now re-sectioned, reveals long crura, essentially identical to those in Moroccan species (Fig. 3). According to Ager et al. (1972) the other characters distinguishing *Eoperegrinella* from *Dzieduszyckia* are the complete absence of dental plates in *Eoperegrinella* and the asymmetry of the latter in *Dzieduszyckia*. However, a few years later, Ager et al. (1976: figs. 5, 6) showed that dental plates were present in *Eoperegrinella* from Morocco. Their presence and the intraspecific variability is also illustrated in the present paper (Figs. 4, 5, 8, 9).

According to Biernat (1967), one of the characteristic features of the shell of *Dzieduszyckia kielcensis* is its asymmetry. Ager et al. (1972) however, did not find asymmetry in the Moroccan specimens. The present study of the Termiers' collection reveals that the asymmetric condition of the anterior commissure and lateral shell lobes in *E. crassicostata*, and especially in *D. intermedia*, does occur (see also Termier 1936: pl. 11: 13, 14, 17, pl. 12: 14, 15). In conclusion, there is no rea-

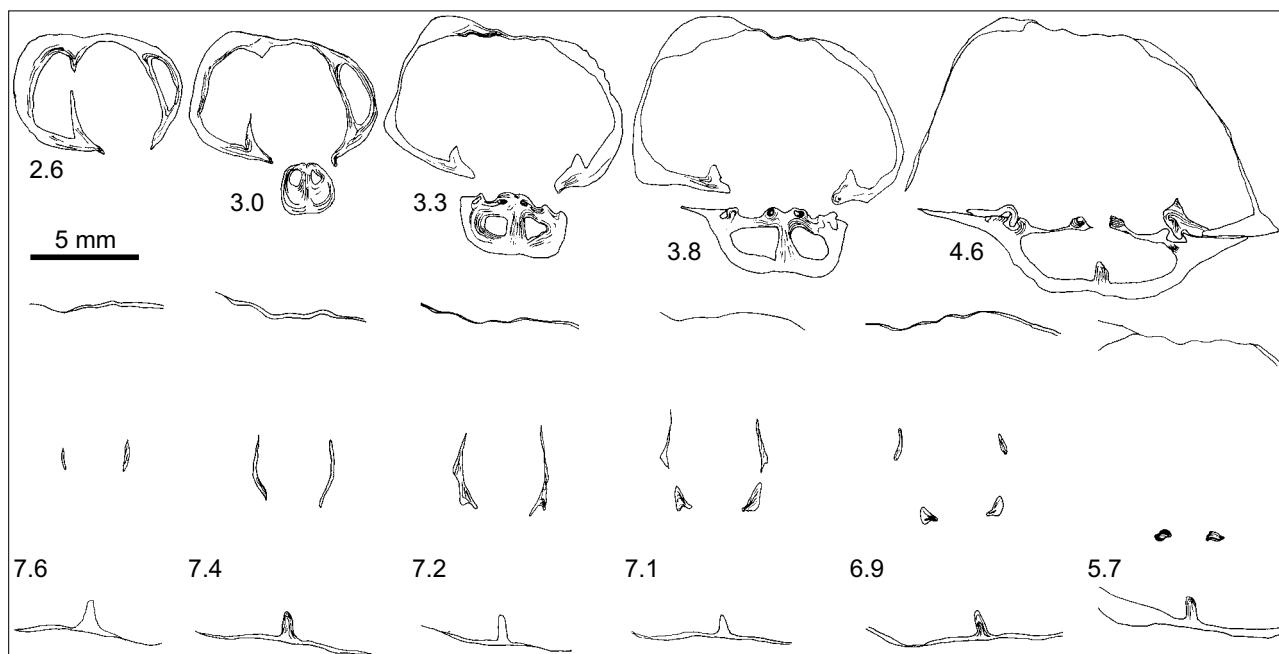


Fig. 4. Transverse serial sections of *Dzieduszyckia crassicostata* (Termier and Termier, 1948) from the Famennian of Bou Nebedou, Morocco (ZPAL Bp XVII/59-1). Numbers refer to distances in mm from the posterior of the ventral umbo.

son to distinguish *Eoperegrinella* from *Dzieduszyckia* and thus both genera should be regarded as congeneric, with the priority of the latter. This view is also supported in the recent revision of the *Dzieduszyckiinae* systematics by Savage (2002).

Dzieduszyckia crassicostata (Termier and Termier, 1948)

Figs. 4–6.

Halorella aff. *amphitoma* Bronn; Termier 1936: 1196–1199, pl.11: 8–18, pl. 12: 1, 2.

Halorella crassicostata nov. sp.; Termier and Termier 1948: 47, figs. 4, 5.

Halorella crassicostata Termier; Termier and Termier 1950: 73, pl. 98: 39, 40, pl. 100: 1, 2, 17.

Eoperegrinella crassicostata (Termier); Ager 1968: fig. 5; pl. 1: 6.

Eoperegrinella crassicostata (Termier and Termier); Ager et al. 1976: fig. 5.

Lectotype: here designated; ZPAL Bp XVII/17-16, Bou-Nebedou, Morocco; Late Devonian, Famennian; illustrated by Termier (1936, pl. 12: 1) and re-illustrated here in Fig. 6D.

Remarks.—When Termier and Termier (1948) introduced a new species name for the *Halorella* aff. *amphitoma* from the Famennian of Morocco they did not designate a type specimen. This is now rectified by choosing a specimen (lectotype) which not only comes from the original Termiers' collection, but was originally illustrated by Termier (1936: pl. 11: 1). This specimen has a large, although slightly incomplete shell; however, together with some other original specimens illustrated here it typifies the species sufficiently.

The external morphology of *D. crassicostata* was described quite sufficiently by Termier (1936) and Termier and Termier (1948). Besides some re-illustrations, additional specimens were illustrated to characterize intraspecific vari-

ability (see also plot-diagrams in Termier and Termier 1948: figs. 1–3). It is noteworthy that the species, like other members of the genus *Dzieduszyckia*, is characterized by a great variability in the general appearance of the shell. Characteristic morphotypes include: more common wide (Figs. 6D, E), elongated heart-shaped (Fig. 6B, C), and wide and very thick, globose shells (Fig. 6A). Ager et al. (1976: 179, fig. 6) also noted an occurrence of a smoother variant of *Eoperegrinella* (new species?) at Sidi Amar near Khenifra.

Previously, the internal shell structure of all Moroccan species was not fully known. The first important data on the interior of *D. crassicostata* were presented by Ager (1968: fig. 5) and Ager et al. (1976: fig. 5). They showed for the first time, in one sectioned specimen, the presence of dental plates, horizontal hinge plates, and ciliform crura. New, additional data on the internal shell structure of the species are presented below from serial sections of three specimens (Figs. 4, 5).

Dental plates are short, subparallel to slightly convergent ventrally. Median septum is high posteriorly, gradually lowering anteriorly, reaches about the shell midlength. Muscle field is deeply impressed but in very large specimens only. Hinge plates are short, horizontal. Crural bases are quite closely set, near the ventral surface of the hinge plates and fused with the top of the median septum, embedded in thickened shell material. Crura are proximally rodlike to slightly flattened horizontally, more or less triangular in cross section. Crural blades are slightly divergent, curve uniformly ventrally, becoming thin and wide, vertical, subparallel to slightly divergent ventrally in cross section at distal ends.

Occurrence.—The species is known from the Famennian limestones of several localities near Khenifra and Khouribga (Middle Atlas, Morocco).

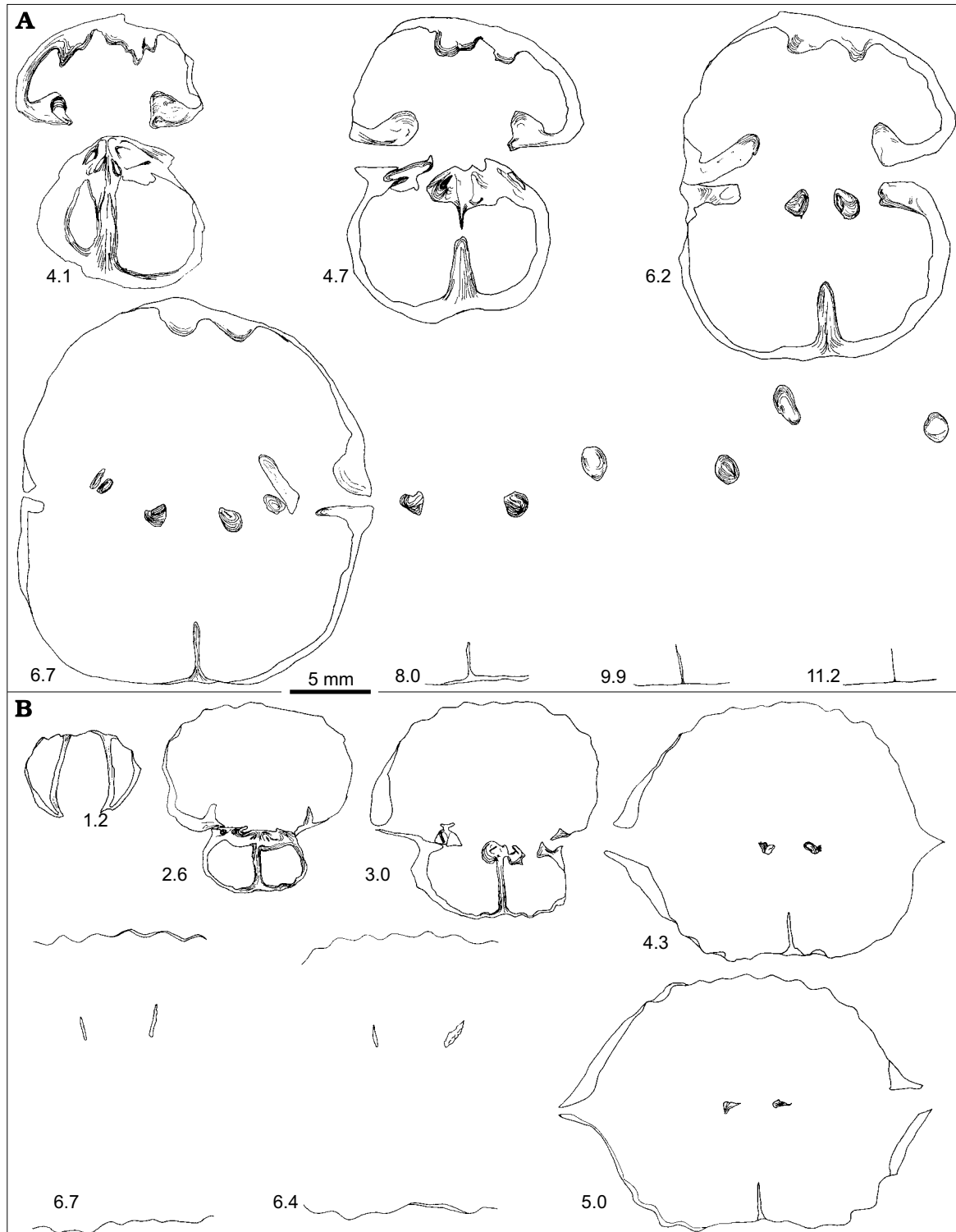


Fig. 5. Transverse serial sections of two specimens of *Dzieduszyckia crassicostata* (Termier and Termier, 1948) from the Famennian of Touchent (A, ZPAL Bp XVII/54-1) and Bou Nebedou (B, ZPAL Bp XVII/59-2), Morocco. Numbers refer to distances in mm from the posterior of the ventral umbo.

Dzieduszyckia intermedia (Termier, 1936)

Figs. 7, 8.

Halorella intermedia nov. sp.; Termier 1936: 1201, pl. 12: 14–16.

?*Halorella* aff. *amphitoma* var. *semialata*; Termier 1936: 1201, pl.13:1–3.

Halorella intermedia var. α Termier; Termier and Termier 1948: 47, figs. 6, 7; 1950: 73, pl. 100: 6–8.

Halorella intermedia var. β Termier; Termier and Termier 1948: 48, figs. 8, 9; 1950: 73, pl. 98: 41, pl. 100: 9, 10.

Halorella intermedia var. *alta* Termier; Termier and Termier 1950: 73, pl. 100: 6–8.

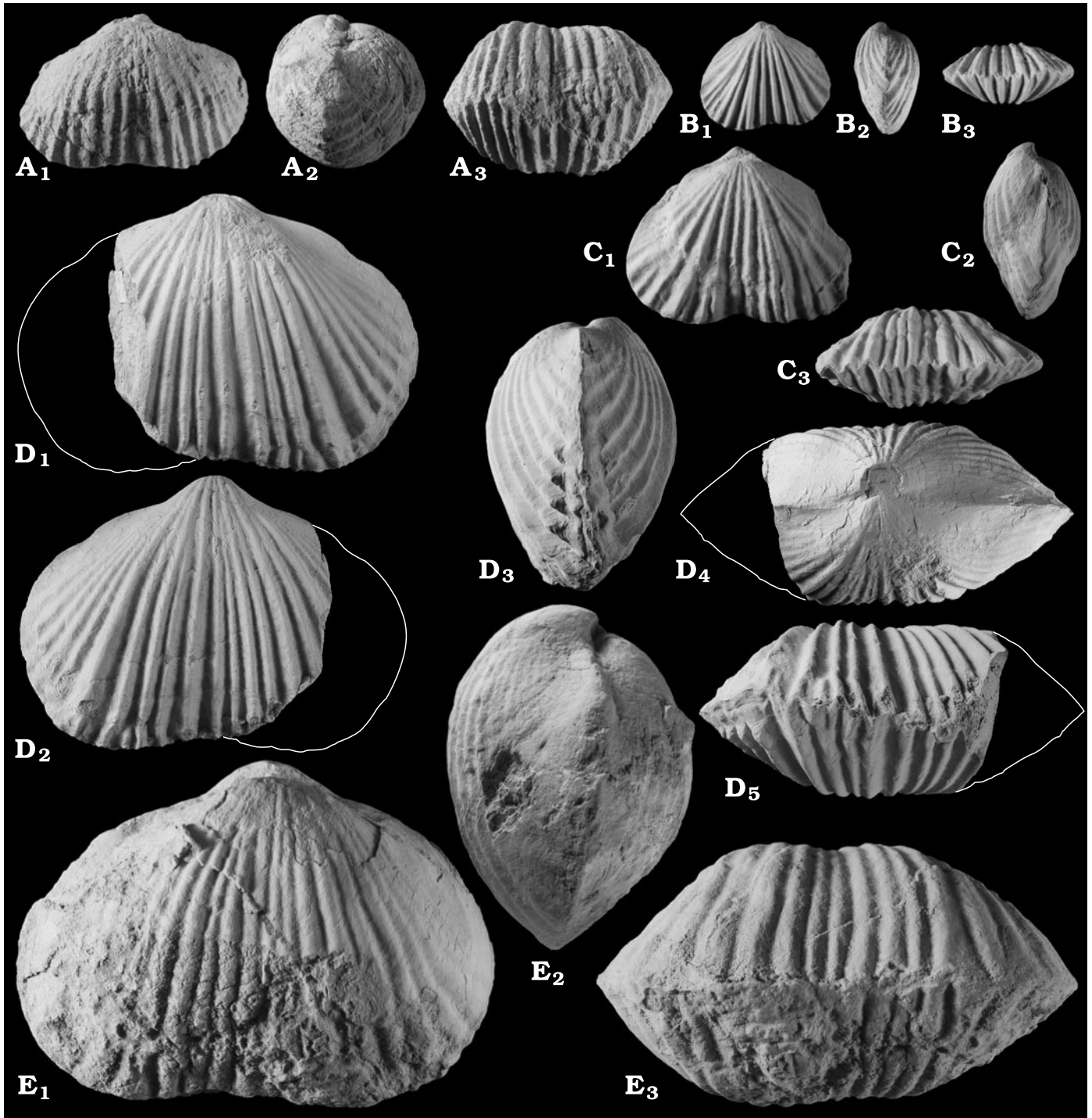


Fig. 6. *Dzieduszyckia crassicostata* (Termier and Termier, 1948) from the Famennian of Morocco. **A.** Globose shell ZPAL Bp XVII/27-1 from Itzer in dorsal (A₁), lateral (A₂), and anterior (A₃) views. **B.** Young shell ZPAL Bp XVII/3-2 from Touchent in dorsal (B₁), lateral (B₂), and anterior (B₃) views. **C.** Young shell ZPAL Bp XVII/3-5 from Bou Nebedou in dorsal (C₁), lateral (C₂), and anterior (C₃) views; figured also in Termier (1936: pl. 11: 15) and Termier and Termier (1950: pl. 98: 45). **D.** Lectotype ZPAL Bp XVII/17-16 from Bou Nebedou in dorsal (D₁), ventral (D₂), lateral (D₃), posterior (D₄), and anterior (D₅) views; figured also in Termier (1936: pl. 12: 1). **E.** Large shell ZPAL Bp XVII/4-3 from Touchent in dorsal (E₁), lateral (E₂), and anterior (E₃) views. All in natural size.

Halorella intermedia var. *globosa* Termier; Termier and Termier 1948: 48, fig. 14; 1950: 74, pl. 100: 3.

?*Halorella semialata* Termier; Termier and Termier 1948: 48, figs. 15, 16; 1950: 74, pl. 98: 45, 46, pl. 100: 13, 14.

Leiorhynchus (?) *intermedius* (Termier, 1936); Drot 1964: fig. 88.

Lectotype: here designated; ZPAL Bp XVII/37-6, Bou-Nebedou, Morocco; Late Devonian, Famennian; illustrated by Termier (1936, pl. 12: 14) and re-illustrated here in Fig. 7A.

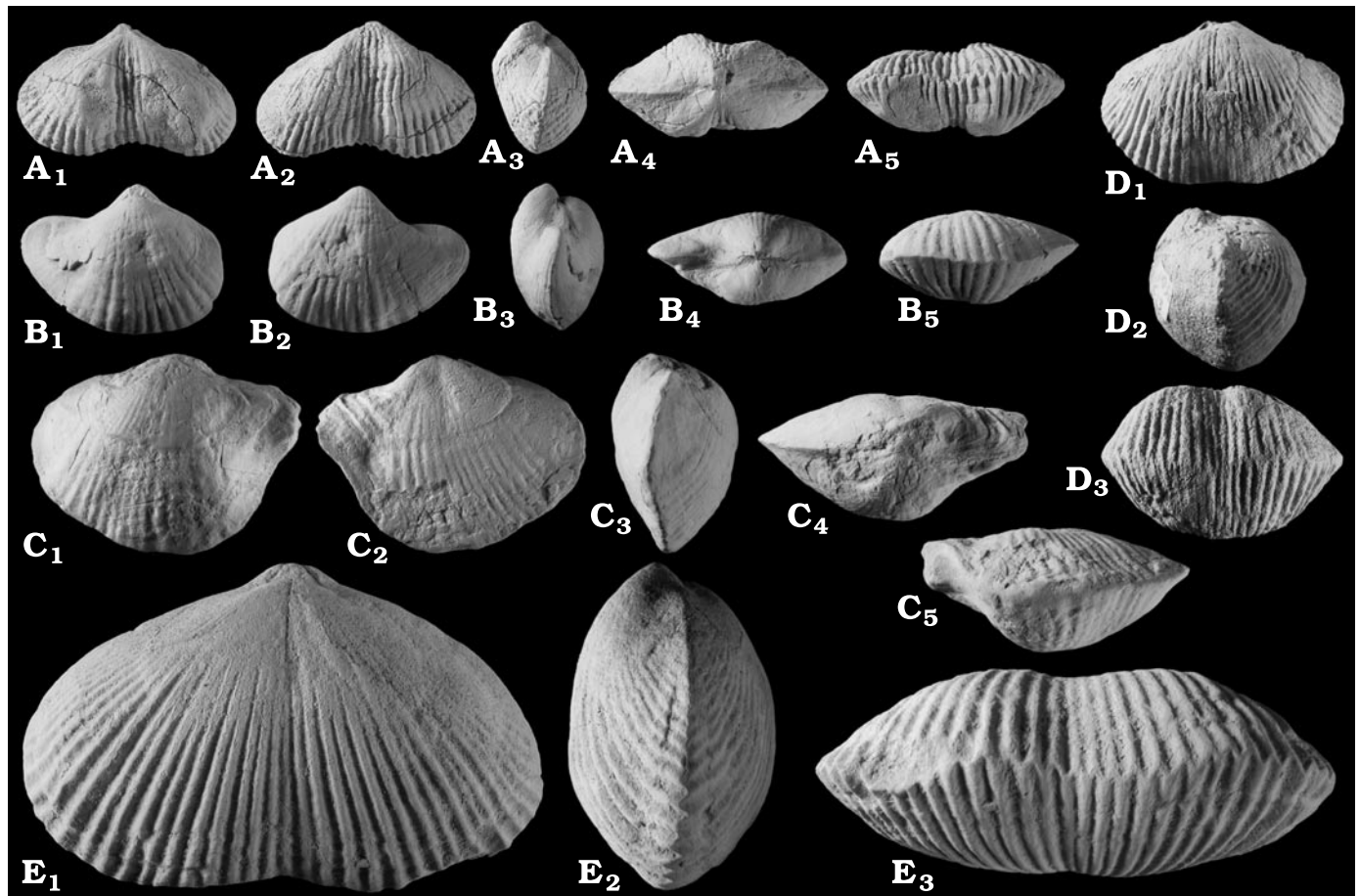


Fig. 7. *Dzeduszyckia intermedia* (Termier, 1936) from the Famennian of Morocco. A. Lectotype ZPAL Bp XVII/37-6 from Bou Nebedou in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views; figured also in Termier (1936: pl. 12: 14) and Termier and Termier (1950: pl. 100: 9). B. Morphotype *alata* ZPAL Bp XVII/8-8 from Ahellal in dorsal (B₁), ventral (B₂), lateral (B₃), posterior (B₄), and anterior (B₅) views. C. Morphotype *alata* ZPAL Bp XVII/41-1 from Bou Nebedou in dorsal (C₁), ventral (C₂), lateral (C₃), posterior (C₄), and anterior (C₅) views; figured also in Termier (1936: pl. 13: 3). D. Morphotype *globosa* ZPAL Bp XVII/28-1 from Bou Nebedou in dorsal (D₁), lateral (D₂), and anterior (D₃) views figured also in Termier and Termier (1950: pl. 100: 3). E. Large shell ZPAL Bp XVII/2-7 from Touchchent in dorsal (E₁), lateral (E₂), and anterior (E₃) views. All in natural size.

Remarks.—According to Biernat (1967: 144, 145) the distinction among some of the species of “*Halorella*” from Morocco is weak and not very decisive. She noted that differences between *H. crassicosata* Termier and Termier, 1948 and *H. intermedia* Termier, 1936 and its varieties were not taxonomically very important. From a purely morphological point of view, there is no possibility to clearly separate the two species in the studied collection (see also biometric diagrams in Termier and Termier 1948: figs. 1–3). However, it may be easier to regard the two forms as valid species when they constitute isolated temporally or spatially populations. This problem, however, cannot be solved at present on a basis of the studied collection, because its stratigraphic and litho-facies context is poorly known.

Termier and Termier (1948) paid attention to the great morphologic variability of *D. intermedia* and described its new varieties (i.e. α , β , *globosa*, *alta*, and *semialta*; see Fig. 7A–E). It is noteworthy that analogous phenotypes can be also recognized among *D. crassicosata* (see Fig. 6B, C). Strange form of the shell of Termiers’ *H. semialata* was con-

sidered by them as a result of teratology (Termier 1936; Termier and Termier 1948). Astonishingly, this form develops a surprisingly consistent morphology of the shell, which is expressed mainly in developing a weaker radial ornamentation confined usually to the median sector of the shell and in asymmetric lobate elongation of one postero-lateral extremity (Fig. 7B, C). It seems unlikely that this kind of invariable deformation was caused simply by living conditions in a crowded associations. It is more probable that the abnormal shell morphology of *H. semialata* was a result of a more specific cause, such as, for example, of infestation by an unknown parasitic or commensal organism.

The internal structure of two sectioned specimens of *D. intermedia* (Fig. 8) seems to be very similar, if not identical, with that in *D. crassicosata*. Minor differences can be noted in the structure of the dental plates, which in the sectioned specimens are subparallel to slightly divergent ventrally. Distal parts of the crura seem to be more massive, less laterally compressed but, most likely, it is merely a result of recrystallization.

Occurrence.—The species is known from the Famennian

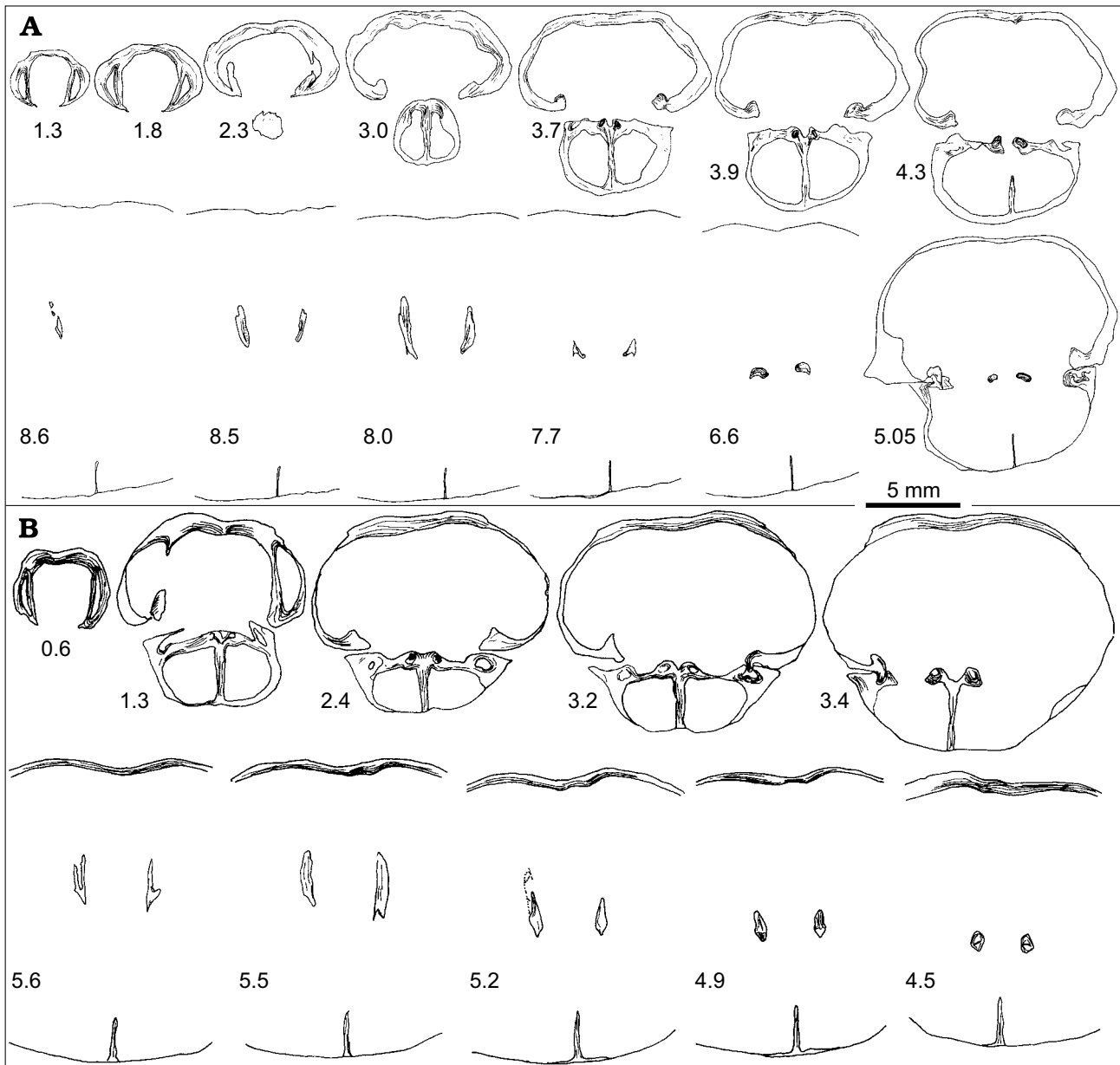


Fig. 8. Transverse serial sections of two specimens of *Dzieduszyckia intermedia* (Termier, 1936) from the Famennian of Brouha Ahellal (A, ZPAL Bp XVII/61-1) and Touchent (B, ZPAL Bp XVII/60-1), Morocco. Numbers refer to distances in mm from the posterior of the ventral umbo.

limestones of several localities near Khenifra (Middle Atlas, Morocco).

D. tenuicostata (Termier, 1936)

Figs. 9, 10.

Halorella tenuicostata nov. sp.; Termier 1936: 1199–1120, pl. 12: 3–13.
Halorella tenuicostata Termier; Termier and Termier 1948: 47, figs. 10, 11; 1950: 73, pl. 98: 42–44, pl. 100: 11, 12, 16.

Lectotype: here designated; ZPAL Bp XVII/38-11, near Bou-Nebedou, Morocco; Late Devonian, Famennian; illustrated by Termier (1936, pl. 12: 6) and re-illustrated here in Fig. 10F.

Remarks.—This species is easily distinguished from all other species of the genus. Externally, it is characterized by me-

dium-sized, rarely larger, very wide, triangular to almost fusiform or sub-cylindrical, finely costate shell. In large individuals, an arrest of growth (at least one) of the shell forming concentric rugae can be observed (Fig. 10D). Sometimes a distinct geniculation of the anterior commissure may be developed (Fig. 10G, D₂). Faint and wide, slightly irregular radial plicae, independent of radial costation, are developed on some large shells (Fig. 10D, F). Posterior sectors of the commissure sharpened, vary from gently convex to distinctly concave in profile, resulting in characteristically curved posteriorly or up-turned lateral shell extremities (Fig. 10E).

D. tenuicostata differs from other species of the genus also in details of the internal shell structure. Serial sections of two shells reveal that dental plates are short but distinct, con-

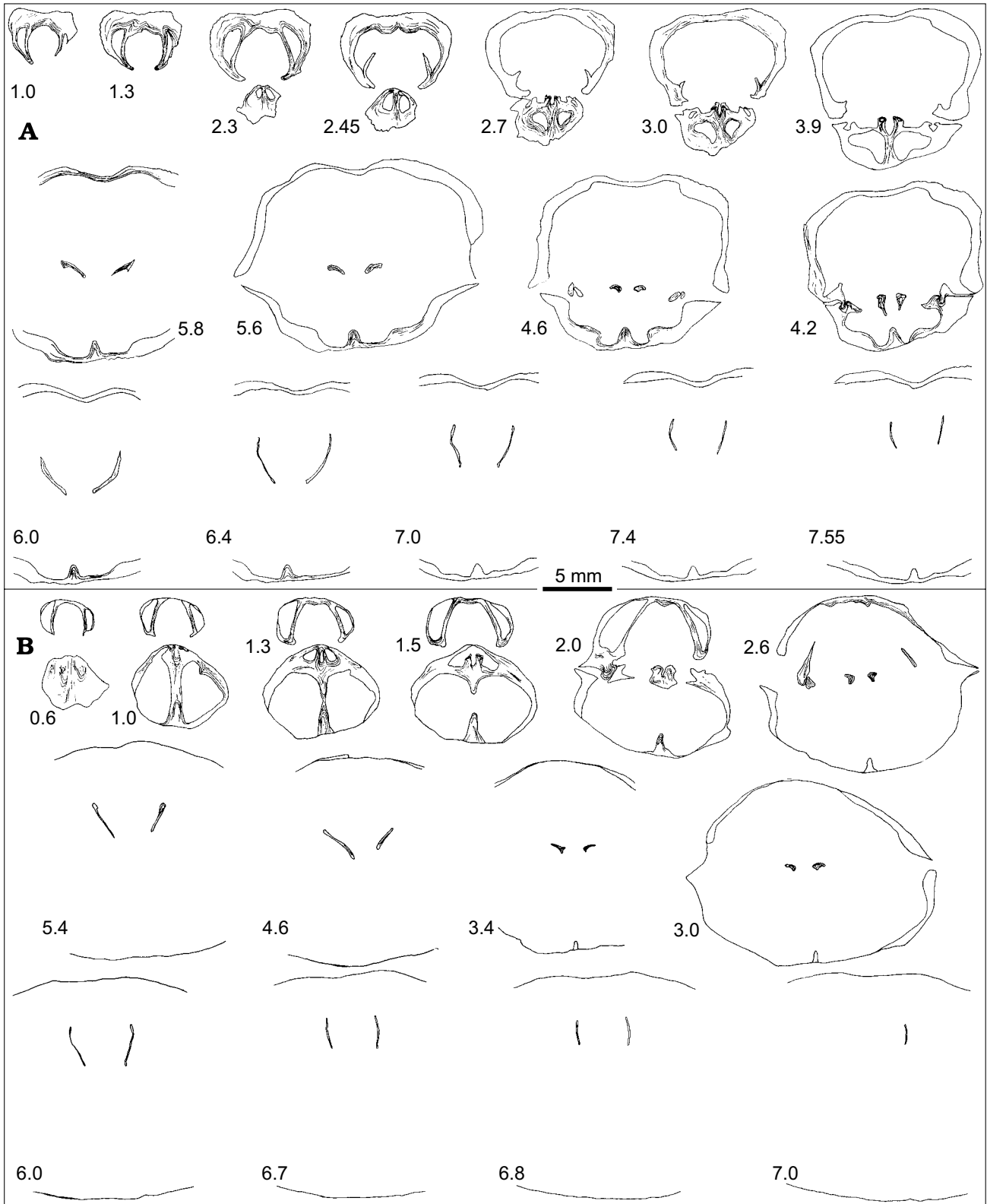


Fig. 9. Transverse serial sections of two specimens of *Dzieduszyckia tenuicostata* (Termier, 1936) from the Famennian of Bou Nebedou, Morocco (A, ZPAL Bp XVII/62-1; B, ZPAL Bp XVII/62-2). Numbers refer to distances in mm from the posterior of the ventral umbo.

vergent ventrally. Crural bases are closely set on the ventral surface of the hinge plates, slightly elevated, forming longitudinal ridges. Proximal parts of the crura are compressed

dorso-ventrally and slightly concave dorsally. Crural blades markedly widen anteriorly (see also Termier 1936: pl. 12: 12–13; Termier and Termier 1959: pl. 98: 44) and twist from

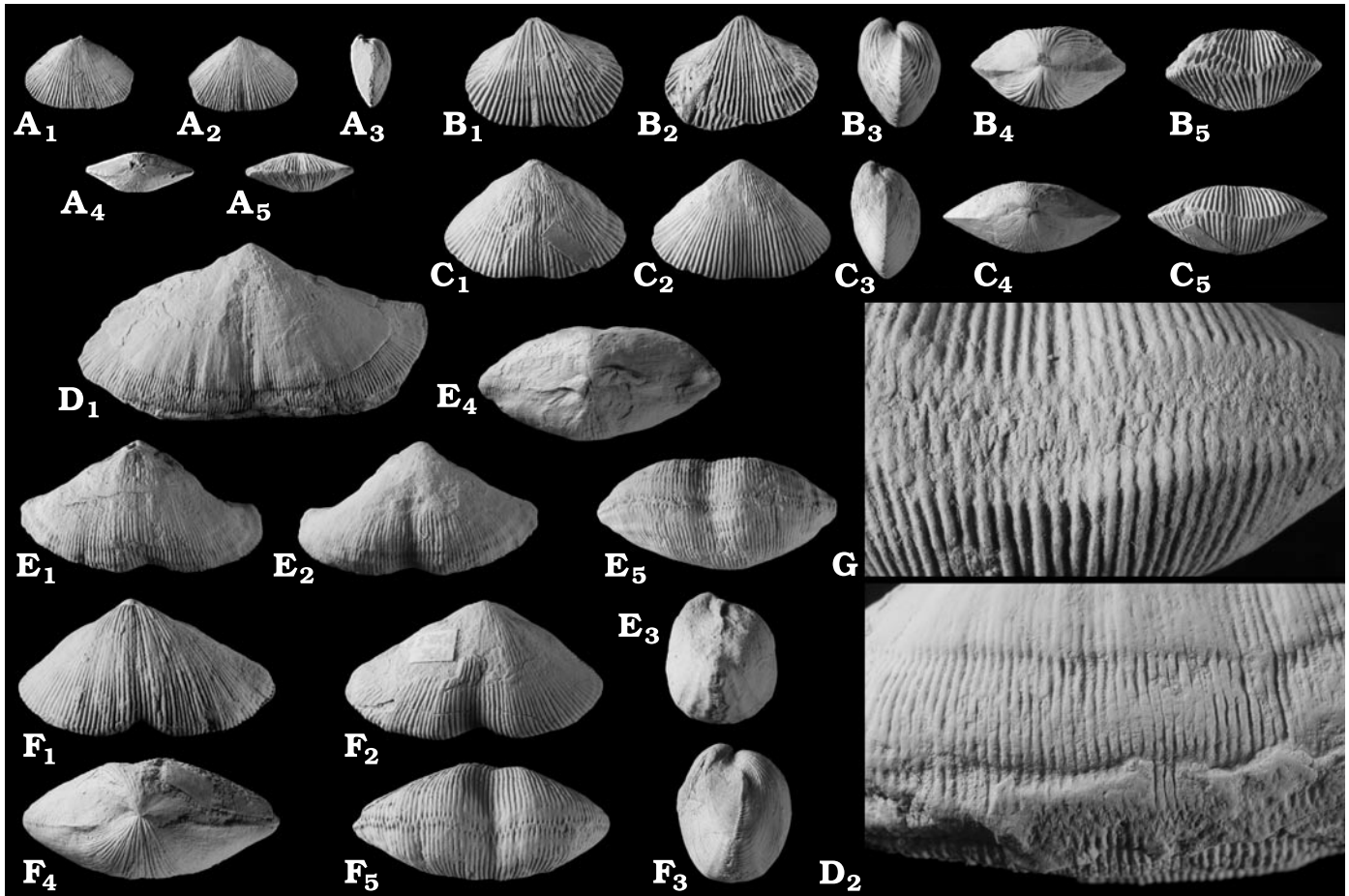


Fig. 10. *Dzieduszyckia tenuicostata* (Termier, 1936) from the Famennian of Bou Nebedou, Morocco. **A.** Juvenile shell ZPAL Bp XVII/38-9 in dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views; figured also in Termier (1936: pl. 12: 3). **B.** Juvenile shell ZPAL Bp XVII/38-7 in dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views; figured also in Termier and Termier (1950: pl. 98: 41). **C.** Juvenile shell ZPAL Bp XVII/38-8 in dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views; figured also in Termier (1936: pl. 12: 5). **D.** Large shell ZPAL Bp XVII/38-1 in ventral view showing fine radial costae and faint radial plication (D_1), and enlargement in anterior view showing concentric rugae and geniculation of anterior commissure (D_2); figured also in Termier (1936: pl. 12: 11). **E.** Complete shell ZPAL Bp XVII/38-10 in dorsal (E_1), ventral (E_2), lateral (E_3), posterior (E_4), and anterior (E_5) views. **F.** Lectotype ZPAL Bp XVII/38-11 in dorsal (F_1), ventral (F_2), lateral (F_3), posterior (F_4), and anterior (F_5) views; figured also in Termier (1936: pl. 12: 6) and Termier and Termier (1950: pl. 98: 42, 43). **G.** Anterior view of the commissure of a large shell ZPAL Bp XVII/38-15 showing geniculation. All in natural size except D_2 and $G \times 3$.

horizontal to vertically subparallel in cross section, becoming slightly convex laterally. Median septum is rather low, attaining about half of the shell length. Dorsal adductor scars are deeply impressed and divided by the median septum.

External and internal differences of *D. tenuicostata* from other known species of the genus make the species quite easily recognizable and well defined, whereas the remaining species of *Dzieduszyckia* are all externally similar to each other and difficult to separate. We decidedly prefer, however, despite the differences mentioned above, to keep the species within the genus *Dzieduszyckia*. Thus, the genus forms distinct and highly characteristic lineage of rhynchonelloid brachiopods which is exceptionally well represented in Morocco.

Occurrence.—The species is known from the Famennian limestones of several localities in vicinity of Bou Nebedou, near Khenifra (Middle Atlas, Morocco).

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