A new giant discinoid brachiopod from the Lower Devonian of Algeria

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A new discinoid brachiopod *Gigadiscina* gen. nov., with the type species *G. lessardi* sp. nov., is described from the Lower Devonian (Siegenian) of the Tamesna Basin (South Ahaggar Massif, South Algeria). It is characterised by large size and convexo-planar profile of the shell, with a subcentral pedicle foramen. Micro-ornament is typically discinoid, with small circular pits in radial rows on the post-larval shell surface. Related species of Malvinokaffric Realm origin from South Africa, Falkland Islands, Antarctica, South America, and Libya are reviewed, including the poorly known *Discina anomala* from the Lower Devonian of Germany. The giant size and convexo-planar shells of these discinoids, remarkably similar to recent limpets, are interpreted as adaptation to a habitat in proximity of sandy and gravel beaches in a high-energy environment. Most likely, the conical dorsal valve suppressed drag in turbulent waters, whereas fixation of shell by large, sucker-like pedicle eliminated peeling from the substrate.

Key words: Brachiopoda, Discinoidea, Devonian, Algeria, Germany.

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Introduction

The evolution of Silurian and Devonian discinoids is poorly understood despite over 150 years of study. The modern classification of this group (Holmer and Popov 2000) differs little from the first edition of The *Treatise on Invertebrate Paleontology, part H, Brachiopoda* (Rowell 1965a). This is, at least partly, due to the restricted and often poor material available for study. Since Hall and Clarke (1892) described numerous genera and species from North America, only a few new taxa have been diagnosed, generally from sequences in Europe (Dahmer 1946; Bassett 1986; Havlíček and Mergl 1988; Havlíček 1999; Mergl 2001) and particular sites in the Early Devonian Malvinokaffric Realm (Reed 1925; Rowell 1965; Boucot et al. 2001). It is the purpose of this paper to partially fill the gap in documentation of discinoid brachiopods by description of new Early Devonian species from Algeria and other similar but generally poorly known species from Devonian of Europe and South America.

Institutional abbreviations.—BMNH, Natural History Museum, London; MGB, Marburg University, Germany; ZCM S, Museum of West Bohemia, Plzeň, Czechia (coll. Massa-Mergl).

Systematic palaeontology

Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840

Genus *Gigadiscina* nov.

Type species: *Gigadiscina lessardi* sp. nov.: Lower Devonian, Pragian (Siegenian); Tamesna Basin, Algeria.

Diagnosis.—Discinoid genus characterised by large, convexo-planar, subcircular shell, covered by fine regular concentric rugellae; micro-ornament of uniform, very small deep circular pits over entire surface; dorsal valve highly and obtusely conical, with subcentral apex; ventral valve planar, with subcentral apex; pedicle foramen subcircular, resting at the bottom of shallow circular depression; the foramen leads into very short pedicle tube toward the posterior margin; listrium rudimentary, broad and very short.

Differential diagnosis.—Differs from *Orbiculoidea*, *Acrosaccus*, and *Lochkothele* in having convexo-planar (rather than biconvex) shell, circular pedicle foramen, with very short pedicle tube and rudimentary, very short and broad listrium (rather than narrow pedicle track with long pedicle tube and long listrium); differs from *Schizotreta*, *Oehlertella*, and *Lingulodiscina* by subcentral (rather than submarginal) dorsal apex; differs from *Lindstroemella* and *Discinisca* by circular posteriorly closed pedicle foramen that is open in the latter two genera; differs from *Roemerella* by large size, planar (rather than concave) ventral valve and circular pedicle foramen in depressed area (rather than elongate on elevated area); differs by very large shell from other genera of Discinidae apart of *Discinisca*.

Remarks.—A few previously described species can be referred to the new genus, mostly from siliciclastic sequences

of Lower Devonian age. Kayser (1892) described two large discinid species from Siegen in Germany, associated with common Siegenian brachiopod fauna but only one, "*Discina*" *anomala*, is referred to the new genus. Valves of *G. anomala* (Kayser, 1892) are remarkably large, with length over 70 mm; ventral valve is planar, with the subcentral pedicle foramen. The second species described by Kayser, i.e., *Discina siegenensis* Kayser, 1892 is biconvex, almost 40 mm wide shell with broad listrium and probably belongs to genus *Orbiculoidea* d'Orbigny, 1847.

Some discinoids from the siliciclastic sequences of the Lower Devonian of the Malvinokaffric Realm have similar morphology. Boucot et al. (2001) described a brachiopod fauna with Malvinokaffric affinity from the Parecis Basin of Brazil. As with other sites within the Malvinokaffric Realm (Rowell 1965b), the large discinids are significant element of this fauna, and represent a low diversity *Orbiculoid* Community within a very shallow intertidal to subtidal environment of benthic assemblage 1 (Boucot 1975). Clarke (1913) described another giant discinoid *Orbiculoidea collis* Clarke, 1913 from the Parana Basin. Rowell (in Boucot et al. 2001) referred several large valves to this species from the Parecis Basin. Figured material (Boucot et al. 2001: fig. 5) is remarkably similar to *Gigadiscina lessardi* but because the morphology of the ventral valve of *O. collis* is unknown, the affinity of the latter is somewhat obscure. Reed (1925) noted a find of a giant discinoid referred by him to *Orbiculoidea collis* Clarke, 1913, from the Bokkeweld Beds of South Africa.

Another giant discinoid is known from the Lower Devonian of the Falkland Islands. The ventral valve was collected by R. Baker in 1931 from ferruginous sandstone between Port Howard and Manybranch Harbour. The specimen (BMNH B 60298) was determined as *Orbiculoidea* aff. *collis* Clarke, 1913, and is referred by us to the new genus. Although the basic morphology is similar, this specimen differs from the species *Orbiculoidea falklandica* Rowell, 1965 from the Falkland Islands and also from the Parecis Basin of Brasilia (Boucot et al. 2001). The latter species is smaller than *Orbiculoidea collis*, about half the size, it has low conical ventral valve, and low dorsal valve. The species *Orbiculoidea* sp. cf. *O. bainii* Sharpe, 1856 from the Horlick Formation (Lower Devonian) of the Ohio Range, Antarctica (Rowell 1965b) may also be referred to the new genus. It is unusually large, having a convexo-planar shell, and a large depressed area encircling the pedicle foramen.

Further species, which may be referred to the new genus, is a ventral valve (Fig. 2B) from borehole core in Tripoli area of Libya. This specimen (BMNH BD 3385) is described herein as *Gigadiscina* sp.

The species *Orbiculoidea magnifica* Mergl, 2001 from the Lower Devonian (Lochkov Formation, Lochkovian) of the Prague Basin (Mergl 2001) is also referred to the new genus. Is has convexo-planar shell, elongate, weakly tapering posterior part of the shell, but its pedicle foramen is more elongate with longer listrium, and the pedicle tube was probably significantly longer than in *Gigadiscina lessardi*. The species *O. magnifica* represents the earliest (Early Devonian) member of this discinoid stock, with a preserved pedicle tube and reduced but distinct listrium.

The origin of the new genus can be traced among the small- to medium-sized, strongly inequivalved and almost convexo-planar discinoids of the late Silurian. These are well represented by *Orbiculoidea rugata* (J. de C. Sowerby in Murchison, 1839) and related species. This group of late Silurian discinoids differs from *Orbiculoidea* d'Orbigny, 1847 (typified by *O. forbesii*) by their convexo-planar shell and by having a shorter, broadly triangular listrium instead of the narrowly spindle-shaped listrium present in *Orbiculoidea*.

Species referred.—*Discina anomala* Kayser, 1892: Siegenian, Germany (Kayser 1892). *Gigadiscina lessardi* sp. nov.: Siegenian, Tamesna Basin, Algeria; *Orbiculoidea* sp. cf. *O. bainii* Sharpe, 1856: Lower Devonian, Antarctica (Rowell 1965b); *Orbiculoidea collis* Clarke, 1913: Lower Devonian, Parana Basin, Brazil (Clarke 1913; Boucot et al. 2001); *Orbiculoidea* (*Roemerella*) cf. *collis* Clarke, 1913: Lower Devonian, South Africa (Reed 1925); *Orbiculoidea magnifica* Mergl, 2001: Lochkovian, Prague Basin, Bohemia (Mergl 2001).

Gigadiscina lessardi sp. nov.

Fig. 1A–E.

Holotype: External mould of ventral valve (Fig. 1A), coll. Massa-Mergl (ZCM S 03734/MAME 001a).

Type horizon: Devonian, Pragian (Siegenian), equivalent of the Upper Tadrart Formation.

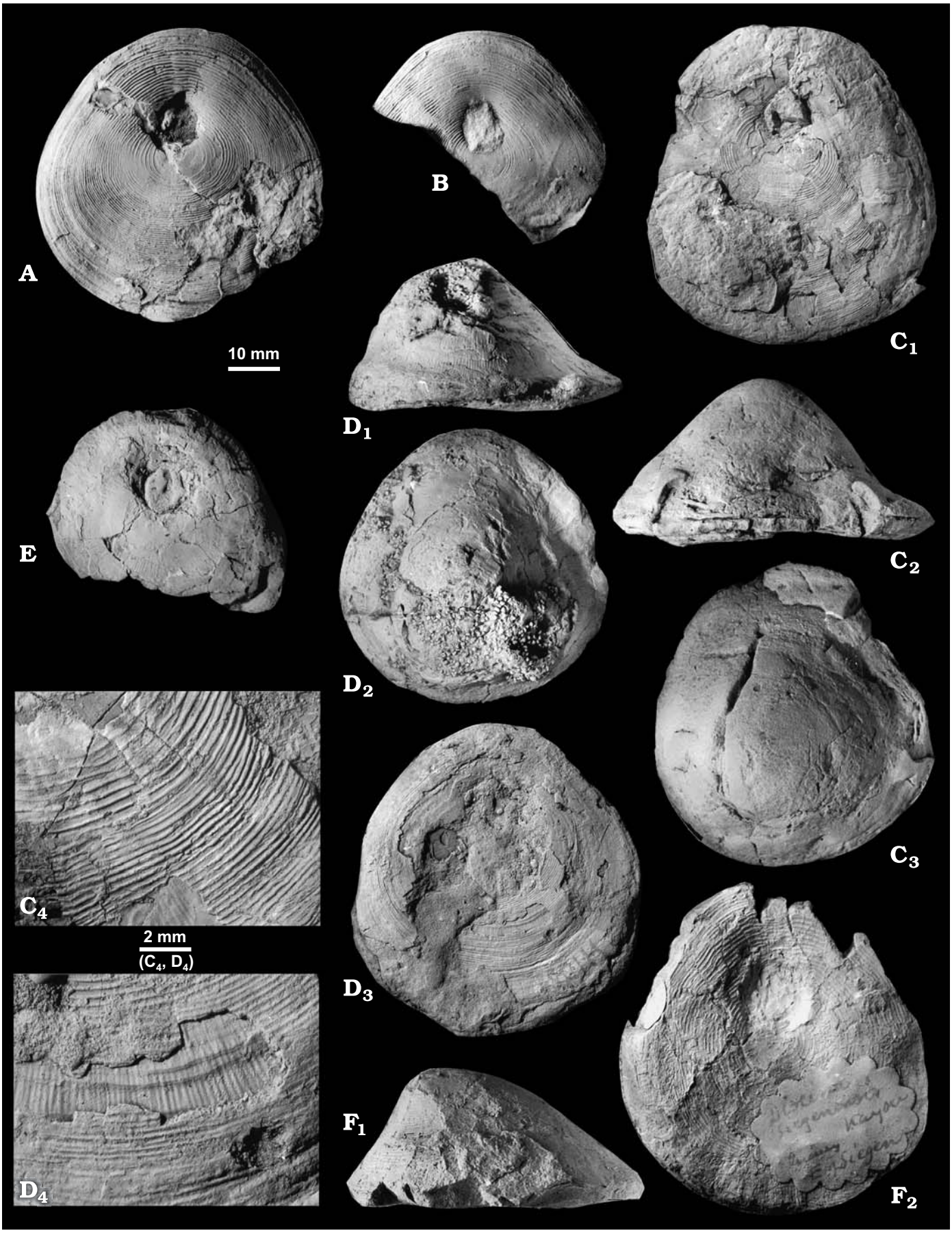
Type locality: Southern Algeria, Tamesna Basin, In Rahir-Tim Amzi section.

Etymology: After French geologist Dr. L. Lessard, who made the pioneering field study in the Tamesna area.

Material.—Fourteen complete shells mostly preserved as corroded internal moulds, partially with remains of original phosphatic shell.

Diagnosis.—Species of *Gigadiscina* characterised by posteriorly weakly tapering shell, large pedicle foramen with small and short pedicle tube and rudimentary listrium; differs from *G. anomala* by finer and denser concentric rugellae (8–12 per mm *versus* 3–5 per mm in *G. anomala*).

Fig. 1. **A**–**E**. *Gigadiscina lessardi* sp. nov. from Pragian (Lower Devonian) of Tamesna Basin, In Rahir-Tim Amzi section. **A**. Holotype, ventral valve, latex cast of external mould, ZCM S 03734a/MAME 001a. **B**. Incomplete ventral valve, latex cast of external mould, ZCM S 03734b/MAME 001b. **C**. Complete shell, ventral valve (C_1), side view (C_2), dorsal valve (C_3), and detail of ventral valve exterior (C_4), ZCM S 03735/MAME 002. **D**. Complete shell, side view (D_1), dorsal valve (D_2), ventral valve (D_3), and detail of intervascular ridges in ventral mould (D_4), ZCM S 03736/MAME 003. **E**. Ventral valve, internal mould, ZCM S 03737/MAME 0004. **F**. *Gigadiscina anomala* (Kayser, 1892) from Pragian (Lower Devonian) of Siegen, Germany. Complete shell, side view (F_1), ventral valve (F_2), BMNH B 42906. →


A
B
C1
10 mm
D1
E
C2
D2
C3
C4
2 mm
(C4, D4)
D3
F1
D4
F2

Description.—The shell is 55–60 mm wide and thin-walled in a relation to the shell size. The outline is almost circular with less curved posterolateral margins. Commissure is rectimarginate. The shell width equals shell length.

The dorsal valve is asymmetrical and highly conical, with a rounded apex. The dorsal apex is subcentral (slightly anterior). The anterior slope is steep and gently convex in lateral profile, the posterior slope is similarly steep, straight near the apex but it tends to be concave near the posterior margin. Lateral slopes are straight.

The ventral valve is flat, with dorsally curved posterior and posterolateral margins. The ventral apex is subcentral, situated between the posterior third and the midlength, embedded into flat surface of the valve. The pedicle foramen is large, located at the bottom of weakly depressed circular area. The pedicle foramen continues internally into a very short, narrow, and posteriorly extend pedicle tube. The interiors of both valves are devoid of well-defined visceral areas. Fine radially arranged vascular canals are impressed on the internal surface of the shell.

The ornament consists of fine concentric rugellae with rounded crests. The size of rugellae is almost uniform over the whole surface, with more distant rugellae only in the apical region. There are 12–16 rugellae per 5 mm in the anteromedian part of the shell. The beak region of the ventral valve is covered by inconspicuous rugellae; the earliest coarser rugellae appear 5–6 mm from the apex. The rugellae are evenly spaced over the whole surface with the anteromedian sector of the shell exhibiting weak irregularities. New rugellae originate exclusively by an intercalation.

Occurrence.—All specimens of the new species were collected in In Rahir-Tim Amzi section (L. Lessard's sample H 1035) in the Tenere Desert of the Tamesna Basin, south of the Ahaggar Massif in South Algeria. In this area, the Lower Palaeozoic comprises a sequence of Cambrian to Devonian strata in a narrow SW-NE trending belt. The basal transgressive Devonian unit bearing the new species is probably of Pragian (Siegenian) age and it rests unconformably on Silurian shale.

Gigadiscina anomala (Kayser, 1892)

Fig 1F.

Discina anomala n. sp.; Kayser 1892: 96: pl. 10: 1–3.

Holotype: Dorsal valve, internal moulds with remains of original ventral valve, deposited in the palaeontological collection of the Marburg University, Marburg, Germany (MGB 2107).

Type horizon: Devonian, Pragian (Siegenian), Siegenian Greywackes.

Type locality: Germany, Siegen, quarry eastward of Siegen, near "Siegena" ironworks.

Material.—The holotype, and two complete shells, preserved in sandstone from the quarry east of Siegen, Germany, housed in the Natural History Museum, London (BMNH B 42906, BMNH B 42915).

Description.—See Kayser (1892).

Remarks.—The holotype is large, strongly asymmetrical, shell 43 mm long, by 45 mm wide, and 20 mm high. Its ornamentation is preserved only in posterolateral slope, with ten dense rugellae per 5 mm. Two other available complete specimens can be referred to *Discina anomala* (Kayser, 1892). The larger specimen is 60 mm long, with the slightly eccentric dorsal apex, a flat ventral valve with a depression around the pedicle foramen, and distinct concentric rugellae covering shell surface. The second specimen is smaller, with an irregular outline and a flat ventral valve covered by concentric rugellae.

Although closely related, the species *Gigadiscina anomala* (Kayser, 1892) differs from *G. lessardi* sp. nov. by having coarser and more distant concentric rugellae on the shell surface. The larger British specimen (BMNH B 42906) has the dorsal apex situated posteriorly while the apex of *G. lessardi* lies anteriorly to midlength. The limited material of *G. anomala* does not allow us to satisfactorily compare the shell outline but, judging from the drawings of Kayser (1892), the holotype, and two additional specimens, the species *G. anomala* has slightly more elongate shell.

Gigadiscina cf. *collis* (Clarke, 1913)

Fig. 2A.

Material.—Single ventral valve, preserved in ferruginous sandstone of Lower Devonian age, collected between Port Howard and Manybranch Harbour in the Falkland Islands, kept in the Natural History Museum, London (BMNH B 60298).

Description.—The ventral valve is some 60 mm long, flat with a shallow depression around the pedicle foramen. The shell is widest slightly anterior to the midlength. The posterior part of the valve is not preserved, but the courses of the rugellae indicate, that the posterior margin is slightly extended. The surface is ornamented by regular, rather fine and uniform concentric rugellae, numbering 14–15 per 5 mm.

Remarks.—The illustrated herein ventral valve may belong to *Orbiculoidea collis* Clarke, 1913 or another closely related species, although the holotype of *Orbiculoidea collis* Clarke, 1913 is known only from a single, dorsal valve (Reed 1925; Boucot et al. 2001). We found out that our ventral valve shares the same style of sculpture hence can be conspecific. Because the size and morphology of the illustrated herein ventral valve is similar to that of *Gigadiscina lessardi* sp. nov. we propose to include *O. collis* to the new genus.

Gigadiscina sp.

Fig. 2B.

Material.—One ventral valve, preserved with original shell in dark-grey siltstone with common sandy grains and fragments of the phosphatic shells, collected from the core of BP borehole in Libya, Tripoli area (borehole BP, well C1–8, core 11, depth 54.15 ft.). The siltstone is referred to Middle to Upper Devonian. The specimen is kept in the Natural History Museum, London (BMNH BD 3385).

Description.—The single available valve is flat, broadly oval, 35 mm long and 32 mm (estimated) wide, with the max-

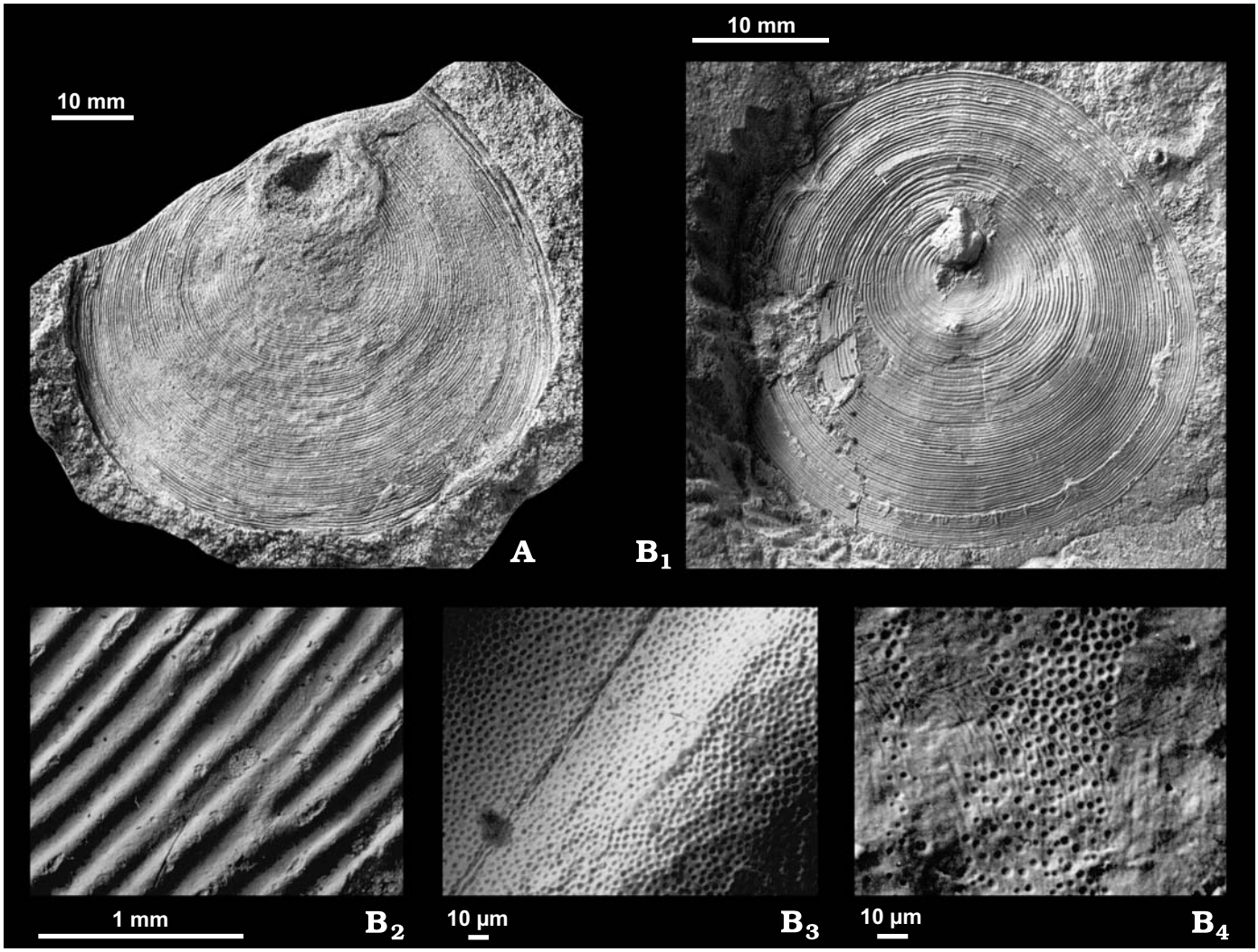


Fig. 2. **A**. *Gigadiscina* cf. *collis* (Clarke, 1913) from Upper Devonian of Falkland Islands, near Port Howard. External mould of ventral valve, BNMH B 60298. **B**. *Gigadiscina* sp. from Middle–Upper Devonian of Libya, Tripoli area (borehole BP, well C1-8). Ventral valve BMHN BD 3385b, external mould (B_1), ventral valve BMNH BD 3385a, detail of ornament (B_2), detail of microornament (B_3), and detail of pitted radial bands alternating with smooth bands (B_4).

imum width at the anterior third. The posterior half of the valve is slightly extended, but less than in *G. lessardi* sp. nov. and *G. anomala* (Kayser, 1892). The pedicle foramen is small (it is poorly preserved), located immediately posterior to the ventral apex, which lies at about two-fifths of the valve length. The external surface is covered by regular concentric rugellae, anteromedianly numbering 17–18 per 5 mm. Rugellae are low, massive, having thickened bases, separated from one another by equally wide or slightly wider flat interspaces. Unlike the interspaces, the variation of rugellae size is limited. Micro-ornament consists of fine, deep circular pits of uniform size, 2–3 µm in diameter. Narrow radial bands without pitting are observable in posterolateral part of the valve. They are 20 to 50 µm broad, with smooth surface or covered by irregular drapes and scattered circular pits.

Remarks.—The species differs from other species of the genus by finer concentric ornamentation and less extended posterior half of the ventral valve.

Habitat of Early Devonian giant discinoids

The moderately sized (*Orbiculoidea falklandensis*, *O. baini*, *O. siegenensis*) and very large discinoids (*Gigadiscina lessardi*, *G. collis*, *G. anomala*, *G.* sp.) have a broad geographical distribution but were only locally abundant in the coarse siliciclastic rocks of the Lower Devonian. They were generally absent in carbonate facies. Some species have been considered characteristic elements of the Malvinokaffric Realm (Reed 1925; Rowell 1965b; Boucot et al. 2001). However, their presence in the Rheinish Province in Germany and Algeria indicates that their distribution was more likely controlled by environment and lithofacies rather than climate. Their presence indicates the existence, similar to some terebratuloids and *Tropidoleptus*, of low-diversity, high-energy communities, as it is apparent in the Tamesna, Parana, and Parecis basins occurrences.

In the same way as the extant species, the middle Palaeozoic giant discinoids flourished on coarse clastic shoreface facies. Such sediments were widespread and uniform over huge areas not only in the climatically controlled high-latitude Malvinokaffric Realm, but also in the marginal parts of the temperate Rheinish province. The morphology of their shells, with the planar ventral valve and highly arched dorsal valve, allows a strong fixation by large discoidal pedicle to hard substrates (boulders, rocks, other shells). Specimens lived tightly attached, with the ventral valves only slightly elevated above the solid surface. The highly conical dorsal valve created a sufficiently spaced filtration chamber inside the shell.

Some extant invertebrates adapted to a rough marine environment have similarly shaped shells; however, they are of univalved design. Although of a quite different trophic group, patellid and acmaeid gastropods (e.g., limpets *Patella* Linnaeus, 1758, *Acmaea* Eschscholtz, 1830) and even some pulmonate gastropods (*Siphonaria* Sowerby, 1823) have similarly conical shells, which suppress the drag of water turbulence and currents in the surf zone. Their sucker-like foot enables a firm fixation to hard substrates. However, at high tide they are motile and feed on algal sporelings, returning to the same resting place before the water retreats.

The high dorsal valve of *Gigadiscina* probably had the same function as the conical limpet shell. Its shape efficiently suppressed the drag of turbulence and multidirectional water movement in a shallow sublittoral zone. The planar ventral valve with extensive, discoidal, sucker-like pedicle enabled tight fixation close to the substrate and reduced the risk of the shell peeling from the substrate. The giant size of *Gigadiscina* improved its stability on the bottom by development of a large and correspondingly more efficient pedicle. In summary, their convexo-planar profile and big shell size can be considered as appropriate adaptations for an extremely high-energy, shallow sublittoral environment. However, unlike the extant patellids, their upper limit was low water, because similar to their extant relatives (Paine 1962) these discinoids were unable to withstand desiccation.

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