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A new species of inarticulate brachiopods, *Discinisca steiningeri* sp. nov., from the Late Oligocene (Egerian) of Plesching near Linz, Austria

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(With 2 textfigures and 4 plates)

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Abstract

A new species of inarticulate brachiopods, *Discinisca steiningeri* sp. n., is established for the specimens occurring in the Linz Sands (Egerian stage) exposed at Plesching near Linz, Austria. A relatively rich material of isolated dorsal valves allows the morphological variability of the new species to be recognized and to be compared with that known in other species of the genus, both modern and ancient. The specific characters of the new species are similar to some modern species of *Discinisca* which are typical of the western hemisphere but as yet unknown in the Tertiary deposits of Europe. A comparison with the few other species reported from the Miocene deposits of the Vienna Basin and the Fore-Carpathian Depression shows the distinctness of the new species from the remaining phyletic stocks, which are represented by occasional occurrences of the genus in the ancient sea systems of Central Europe.

Zusammenfassung

Aus den Linzer Sanden (Egerien) von Plesching bei Linz, Österreich, wird *Discinisca steiningeri* sp. n., eine neue Art inartikulater Brachiopoden, beschrieben. Ein relativ reiches Material an Dorsalklappen erlaubt es, die morphologische Variabilität dieser neuen Art festzustellen und mit der anderer – rezenter und fossiler – Arten dieser Gattung zu vergleichen. Die Artmerkmale der neuen Art sind einigen modernen Arten von *Discinisca* ähnlich, die für die westliche Hemisphäre typisch sind. Ein Vergleich mit den wenigen anderen Arten aus dem Miozän des Wiener Beckens und der Karpatenvor-tiefe zeigt deutlich die Isoliertheit der neuen Art vom übergebliebenen phyletischen Bestand.

Introduction

The systematic study of abundant organic communities of diverse marine deposits of the Central Paratethys basins, as exemplified by those of the Korytnica Basin on the southern slopes of the Holy Cross Mountains, Central Poland (BALUK & RADWANSKI 1977, RADWANSKA & RADWANSKI 1984), allowed attention to be focused on certain invertebrate groups which have a special bearing upon recogni-

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tion of ancient environmental conditions. Such are primarily the extant forms, of various taxonomic rank, whose ancestors were occasionally abundant in the Paratethys basins both in Poland and Austria. A more critical insight into the nature of such taxa shows that they either require a major revision, as in the case of the Middle Miocene (Badenian) free-living bryozoans (BALUK & RADWANSKI 1984), or they require an original investigation to advance the knowledge of the ancient biota. The latter case is true for the inarticulate brachiopods of the genus *Discinisca* DALL, 1871, a relatively rich material of which was kept in collection by Prof. Dr. F. STEININGER at the Institute of Paleontology of the University of Vienna.

The purpose of the present paper is to describe this material, which was recovered in the Upper Oligocene (Egerian) deposits at Plesching near Linz in Austria and generously donated by Prof. Dr. F. STEININGER to the authors for investigation.

The investigated material is deposited in the Naturhistorisches Museum in Vienna, in its Geologisch-Paläontologische Abteilung, and kept under the Catalogue Numbers 1988/58–59.

The Lithotope and its Age

The investigated material of the genus *Discinisca* comes from the section of the Linz Sands (Linzer Sande) exposed at Plesching near Linz. The section at the locality called the „Plesching oyster bank“ (Pleschinger Austernbank) was studied in the 1960s in order to examine its ubiquitous paleontological content dominated by diverse invertebrates (STEININGER 1969; PODZEIT & STEININGER 1969; RÖGL & STEININGER 1969; STEININGER, RÖGL & MARTINI 1976, p. 180). The brachiopod material was at that time collected by the late Dr. J. SCHADLER in a part of the sands situated (F. STEININGER, pers. comm.) just above the oyster bank, which is approximately 0.5 m thick and developed more or less directly above the crystalline bedrock of the Bohemian Massif (see PODZEIT & STEININGER 1969, Figs 41 a and 41 b; the latter modified here as Fig. 1).

The ferruginous sand bed overlying the oyster bank is irregularly cemented and, in places, very coarse-grained. All the *Discinisca* material is represented solely by isolated dorsal valves; they are relatively well preserved (see Pls 1–4) and usually firmly adhered to coarser sand grains (see Pl. 4, Fig. 4). In some parts of the sand body, the *Discinisca* valves and their hash are so common that they form a kind of the coquina.

The corneous (chitinophosphatic) valves of the collected *Discinisca* are uniformly yellowish brown; this no doubt represents a diagenetic coloration. An original color or color pattern, reported in some ancient species of the genus (MUIR-WOOD 1929, 1939), is not recognizable in the investigated specimens. The good state of preservation of the corneous valves contrasts distinctly with that of the mollusks. The aragonitic shells of the latter are more or less completely dissolved, with only calcitic ones having been retained (RÖGL & STEININGER 1969).

The age of the Linz Sands is referred to the Egerian stage in the Central

Paratethys, which is correlated with the Chattian and Aquitanian stages in other regions of Europe (RÖGL, HOCHULI & STEININGER 1979; RÖGL & STEININGER, 1984). However, the section of Plesching is dated by the occurrence of the foraminifer species *Miogypsina (Miogypsinoides) formosensis* YABE & HANZAWA as Upper Oligocene (RÖGL & STEININGER 1969).

Modern versus of ancient taxa in the genus *Discinisca*

The genus *Discinisca*, quite common in certain present-day marine environments, is extremely rare in ancient deposits. Pre-Tertiary species are still poorly

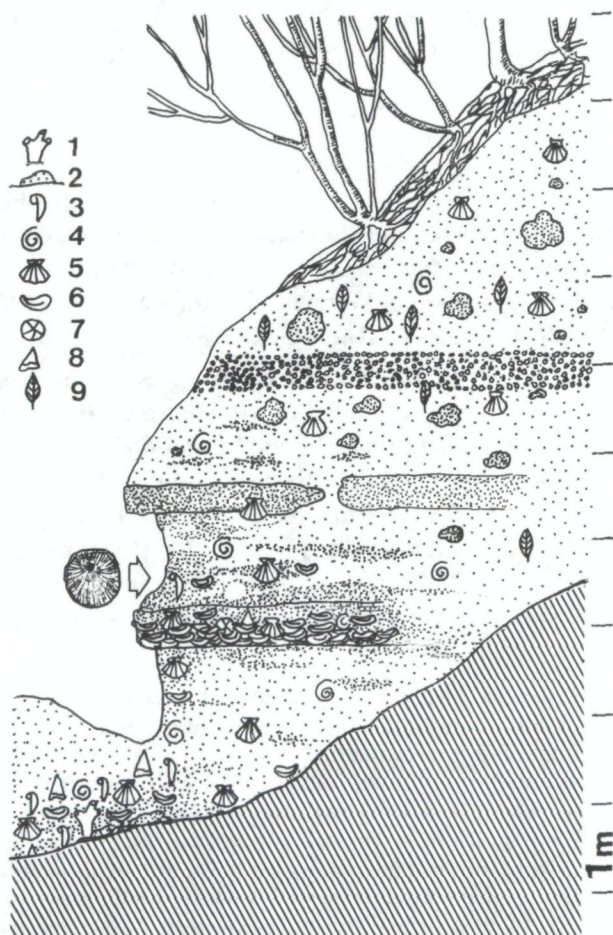


Fig. 1: Schematic section of the Linz Sands (Egerian stage) exposed at Plesching (locality Austernbank), to show the occurrence site (arrowed) of the newly established inarticulate brachiopod species, *Discinisca steingeri* sp. n.; scale in meters is given at right of the section.

Within the sequence developed on the crystalline bedrock (crossed) are indicated: the oyster bank, coarse-grained intercalations, layered and irregular cementations, and the fossil content.

Fossils: 1 - corals, 2 - bryozoans, 3 - articulate brachiopods, 4 - gastropods, 5 - bivalves other than oysters, 6 - oysters, 7 - echinoids, 8 - elasmobranch teeth, 9 - terrestrial plants.

Based on the drawing by H. PERTLWIESER in PODZEIT & STEININGER (1969, Fig. 41 b).

known and their generic attribution often remains unclear (THOMSON 1927, MUIR-WOOD 1929, HERTLEIN & GRANT 1944, ROWELL 1965, STENZEL 1965).

The genus became more common in the Tertiary, where it achieved a worldwide distribution. It developed well in the western hemisphere, where it appeared in the Paleocene of Texas (STENZEL 1965). From the Eocene through the present-day it became well established from the western United States southwards to Chile (HERTLEIN & GRANT 1944, STENZEL 1965, COOPER 1982). A new report on its occurrence comes from the Eocene of New Zealand (LEE 1987).

In the Tertiary deposits of Europe, the genus *Discinisca* was first recognized in England, where it occurred both in the Pliocene Coralline Crag (DAVIDSON 1852, S. WOOD 1874, MUIR-WOOD 1929) and diverse Eocene formations (MUIR-WOOD 1929, 1939).

All other European occurrences of the genus *Discinisca* involve Miocene deposits, from which the genus was first reported by DREGER (1889) from the Vienna Basin in Austria. Subsequent reports were from the Fore-Carpathian Depression in the western Ukraine (LOMNICKI 1897, FRIEDBERG 1921), the Loire Basin in France (DOLLFUS & DAUTZENBERG 1901, DEMORGAN 1915), and again from the Fore-Carpathian Depression in Moravia (CTYROKY & FEJFAR 1963) and Poland (RADWANSKA 1982, RADWANSKA & RADWANSKI 1984).

It should be noted that all Miocene occurrences of the genus *Discinisca*, usually represented by a very low number of specimens, distinctly contrast with the frequency of other, predominantly small-sized brachiopods (paedomorphic genera sensu ASGAARD 1986) in many fossiliferous formations or localities in the Vienna Basin (DREGER 1889) as well as in Rumania (BOETTGER 1901), Italy (SACCO 1902, DREGER 1911), France (DEMORGAN 1915), Hungary (MEZNERICS 1944), Greece (GÉORGIADIS-DIKÉOULIA 1974), Malta (PEDLEY 1976), Spain (LLOMPART & CALZADA 1982), and the Korytnica Basin in Poland (BARCZYK & POPIEL-BARCZYK 1977, RADWANSKA & RADWANSKI 1984).

In Oligocene deposits, the genus *Discinisca* has formerly been reported in the western United States (HERTLEIN & GRANT 1944). The only European report was given from the Netherlands by BOSQUET (1862), who described a species he called „*Discina suessi*“, and which was attributed to *Discinisca* (as „*D. nysti*“ [sic!]) by THOMSON (1927, p. 132); this species, however, displays typical cranioid features (MUIR-WOOD 1929, p. 466; RADWANSKA & RADWANSKI 1984, p. 260) and thus cannot be included into *Discinisca*. At the same time, the specific name *suessi* cannot be used in the genus *Crania* RETZIUS, 1781, since it becomes a secondary homonym both to *C. suessi* BOSQUET, 1859 – a species recently placed by LEE & BRUNTON (1986, pp. 144–145) within the genus *Ancistrocrania* DALL, 1877 – and to *C. suessi* REEVE, 1862, recently renamed by LEE & BRUNTON (1986, p. 152) as *Neocrania reevei* LEE & BRUNTON, 1986. The age of deposits yielding the species described by BOSQUET (1862) is now regarded as Lower Miocene (Dr. A. V. DHONDT, pers. comm.).

The specific differentiation in the genus *Discinisca* is rather great: the gross morphology of the shells ranges from densely or heavily ribbed forms to those which are almost or perfectly smooth. Only few of the present-day forms are characterized well, whilst all the Tertiary and older species have been established upon isolated dorsal valves whose interiors usually remained unknown.

Within the present-day forms of the genus *Discinisca*, three groups of species are distinguishable (DALL 1920, THOMSON 1927, MUIR-WOOD 1929, CTYROKY & FEJFAR 1963, RADWANSKA & RADWANSKI 1984):

(i) Large, lamellose, flexible, without radial sculpture; examples: *D. lamellosa* (BRODERIP, 1834), *D. laevis* (G. de B. SOWERBY, 1822); these two species typically form clusters living on rocky or sandy bottoms (see also DAVIDSON 1888, pp. 195–198; RICHARDS 1974);

(ii) Large, less lamellose, with feeble irregular radiations, more solid; examples: *D. strigata* (BRODERIP, 1834), *D. cumingi* (BRODERIP, 1834);

(iii) Small, with regular radial sculpture, not lamellose, solid; examples: *D. antillarum* (d'ORBIGNY, 1853), *D. stella* (GOULD, 1860), *D. sparselineata* DALL, 1920, *D. indica* DALL, 1920, *D. keiensis* JACKSON & STIASNY, 1937.

The groups (i) and (ii) are confined to the western coasts of the Americas, the group (iii) primarily to the east coast of Asia (the Indian Ocean, Malay Archipelago, Philippines, China and Japan), with one species (*D. antillarum*) restricted to the shores of the Caribbean and Brazil (d'ORBIGNY 1853; DALL 1871, 1920; THOMSON 1927; COOPER 1977).

All the ancient species may be referred to these three groups (RADWANSKA & RADWANSKI 1984), although some have no modern counterparts. On the other hand, certain authors (MUIR-WOOD 1939, HERTLEIN & GRANT 1944, STENZEL 1965) distinguish only two major groups (having or not having radial sculpture), which are postulated as having either subgeneric (STENZEL 1965) or generic rank (COOPER 1977).

The investigated Oligocene material from Plesching suggests the validity of the tripartite subdivision of the genus. This material represents a population of one species which is considered to be new here. The rather large number of specimens allows the recognition of its specific variability, even of internal characters which are poorly known in almost all ancient species. The specific characters are typical of group (ii) of modern species, although the gregarious occurrence of the specimens is more typical of group (i) indicated.

Systematic Description

The systematic position of the new species is given according to the scheme presented by ROWELL (1965); the above-discussed intrageneric groups of the genus *Discinisca* are not regarded as definite and thus of any taxonomic value.

Phylum Brachiopoda DUMÉRIL, 1806

Class Inarticulata HUXLEY, 1869

Order Acrotretida KUHN, 1949

Suborder Acrotretidina KUHN, 1949

Superfamily Discinacea GRAY, 1840

Family Discinidae GRAY, 1840

Subfamily Disciniscinae SCHUCHERT & LEVENE, 1929

Genus *Discinisca* DALL, 1871

Type species: *Discinisca lamellosa* (BRODERIP, 1834)

Discinisca steingeri sp. n.

(Plates 1–4)

Holotype: The specimen illustrated in Pl. 1, Fig. 1 a–c (Catalogue Number 1988/58).

Paratypes: The remaining specimens presented in Pls 1–4 (Catalogue Numbers 1988/59/1–9).

Derivation of the name: In honour of Prof. Dr. F. STEINGER who first recognized the brachiopod nature of the valves collected at Plesching.

Type locality: Plesching near Linz, Austria.

Type horizon: Upper Oligocene (Egerian).

Diagnosis: Dorsal valves of variable outline, irregularly circular to almost rectangular, with a tendency to have the posterior margin straightened, but slightly indented at mid-line; low-conical to moderately high-conical, with the posterior slope straight to slightly concave, and the anterior slope more or less irregularly convex; apex subposterior to almost posterior; limbus well developed in adult forms; densely spaced fine ribs, pronounced distinctly in the posterior and postero-lateral parts of the valve, become obsolete or disappear in the valve anterior; muscle-scar pattern featured by elongated, narrow, very slightly reniform anterior adductors arching horseshoe-like anteriorly, by narrow, laterally elongated posterior adductors, and by posterior protractors asymmetric, fused along the mid-line and placed anteriorly between or near the posterior adductors.

Material: Some twenty complete specimens, of which the holotype and paratypes are chosen, and about fifty partly damaged specimens.

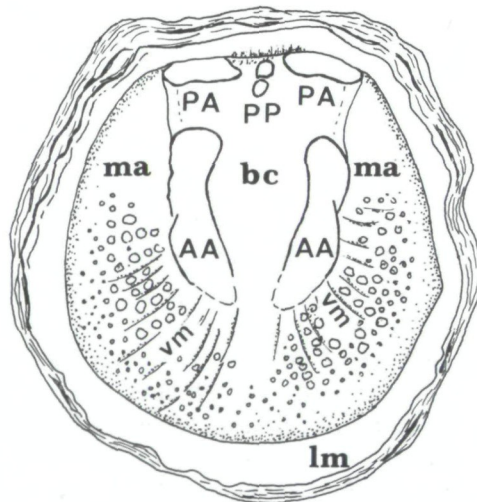


Fig. 2: Morphology of the dorsal valve of *Discinisca steingeri* sp. n., presented as for the holotype (see Pl. 1, Fig. 1 a–1 c); inner view, magn. $\times 5$.

Abbreviations: bc – body cavity, ma – mantle area, vm – vascula media, lm – limbus; muscle scars (terminology after THOMSON 1927, HERTLEIN & GRANT 1944): AA – anterior adductors, PA – posterior adductors, PP – posterior protractors.

Measurements: The holotype (Pl. 1, Fig. 1) is about 15 mm long (at the mid-line) and 14 mm wide; average specimens vary between 9–12 mm in length; the largest specimen (Pl. 2, Fig. 1) is 16 mm long and 13.5 mm wide.

Description: The dorsal valves vary in outline from irregularly circular (as the holotype, Pl. 1, Fig. 1 a–c, and a paratype, Pl. 2, Fig. 1 a–c) to more or less elongated, either anteriorly (Pl. 1, Fig. 2 a–c and Pl. 2, Fig. 2 a–c), laterally (Pl. 3, Fig. 1 a–c), or obliquely (Pl. 3, Fig. 2 a–c and Pl. 4, Fig. 1 a–c). The posterior margin is usually rather long and well individualized by its straight-line course (Pls 1–2), and it is distinctly smaller in laterally and obliquely elongated specimens (Pl. 3 and Pl. 4, Fig. 1). When the posterior margin is longer, it becomes slightly indented at mid-line, and the indentation continues into a concavity of the posterior slope (see Pl. 1, Figs 1–2 and Pl. 2, Figs 1–2). The anterior part is more or less irregularly convex (see Pls 1–2), with maximum convexity variously placed in relation to the apex (compare Pl. 3, Figs 1 b and 2 b with Pl. 4, Fig. 1 b). Laterally, there may appear corrugations of a variable extent (see Pl. 1, Fig. 2; Pl. 2, Fig. 1; Pl. 3, Fig. 1; Pl. 4, Fig. 1), due to which the valves become higher as seen in their side view, and thus they vary from low-conical (Pl. 1, Fig. 2 b), through intermediate (as the holotype, Pl. 1, Fig. 1 b) to moderately high-conical (Pl. 2, Fig. 2; Pl. 3, Fig. 2; Pl. 4, Fig. 1). The apex is situated subposteriorly (Pl. 1, Figs 1–2) to almost posteriorly (Pl. 3, Fig. 1 and Pl. 4, Fig. 1).

Around the margin of the dorsal valve a well-defined limbus of more or less stable width is developed (see Fig. 2), which corresponds to the part overlapping the ventral valve. The limbus is herein regarded as a feature typical of the adult forms, which usually had their valves thicker, but not necessarily larger (see Pls 1–2; Pl. 3, Fig. 1; Pl. 4, Fig. 1). The limbus is poorly developed in specimens of average size but having their valves thinner (Pl. 3, Fig. 2), and in smaller, always thin-valved specimens which are regarded as juveniles (Pl. 4, Fig. 3).

The ribbing begins at the proximal margin of the neanic shell, whilst the brephic (i. e., postlarval, see CHUANG 1977, Fig. 11) shell is perfectly smooth, sculptured only by growth lines. The brephic shell is often ended distally with one more pronounced growth line (clearly visible in Pl. 1, Fig. 2 a). The larval shell (protegulum) is hardly recognizable, since usually the topmost apical part of the valve is damaged.

The finely shaped radial ribs are continuous, densely spaced (interspace of equal size or smaller), and slightly corrugated when intersecting some more pronounced growth lines. The ribs never bifurcate, and their number increases by the appearance of intercalatories. The total number of ribs varies depending on specimen size, ranging from 110 to 140 in average forms and attaining a figure of 166 in the holotype (Pl. 1, Fig. 1), which is one of the largest specimens.

The ribs are strongest in the posterior and postero-lateral parts of the valve, and they become more or less obsolete or even disappear towards the valve anterior, whose surface is thus almost smooth (as in the holotype: Pl. 1, Fig. 1). The disappearance of ribs is advanced to a variable extent throughout the valve in

particular individuals. The almost smooth areas are often distributed patchily (Pl. 2, Fig. 2 and Pl. 3, Fig. 2), and they embrace either a part of one side of the valve (Pl. 1, Fig. 2 and Pl. 2, Fig. 1) or nearly the whole side (Pl. 3, Fig. 1 b). In other individuals, the whole anterior slope becomes destitute of ribs (Pl. 4, Figs 1–2).

The valve interior (see Fig. 2) is sculptured by a pattern of muscle scars, those of the anterior adductors being best pronounced, elongated, narrow, very slightly reniform (bipartite at their external edge), and arching anteriorly in a horseshoe-like shape, but not reaching each other. The posterior adductors are also narrow and laterally elongated; they are situated near the limbus, which sometimes is so overhanging that the scars become invisible in the bottom view of such valves (see Pl. 3, Fig. 1 c). In many valves, including that of the holotype, the posterior protractors are well pronounced; they are small, irregularly shaped, and asymmetrically fused along the mid-line, being placed anteriorly between or near the posterior adductors (Pl. 1, Figs 1 c–2 c). The anterior protractors practically escape detection. In not fully grown valves, all the muscle scars except the anterior adductors are hardly detectable (Pl. 3, Fig. 2 c and Pl. 4, Fig. 3 c).

The whole area amidst the muscle scars, which corresponds to the body cavity, is slightly elevated in relation to the mantle area; it is bordered by faintly marked ridges connecting the external faces of the adductors (anterior and posterior) on both sides of the valve (see Fig. 2).

The mantle area, between the muscle scars and the limbus, is in some specimens sculptured by impressions of the vascula media (sensu WILLIAMS & ROWELL 1965), best visible in the holotype (Pl. 1, Fig. 1 c); it is often covered by minute, wart-like tubercles which are rather irregularly dispersed (as in the holotype and specimens presented in Pl. 3, Fig. 1 c and Pl. 4, Fig. 1 c).

Remarks: The newly established species, *Discinisca steiningeri* sp. n., is represented by a relatively great number of specimens of variable shape and sculpture, but yielded by one sedimentary unit. Their morphological characters vary gradually in the studied specimens, and thus all are herein regarded as belonging to a population of one species. Their variable features may consequently be considered in terms of specific variability. However, almost all species of *Discinisca*, both modern and ancient, are poorly known in this respect. This is obviously the result of a low morphological potential of the genus as well as its inadequate recognition (ROWELL 1965; STENZEL 1965; COOPER 1973, 1977, 1982). Evidence for this is the fact that the gross morphology of the shell exteriors, as studied primarily in dorsal valves, is practically expressed by the apex position and the development and structure of ribs. The size of specimens is often also taken into account in characterizing some species. The internal structure, more precisely the pattern of muscle scars, has hitherto been recorded in a few species.

Concerning the specific variability, one may note that in the two ancient species known in greater numbers – viz. *Discinisca polonica* RADWANSKA & RADWANSKI, 1984, and the newly established *Discinisca steiningeri* sp. n. – the specimens with extreme features differ significantly from average forms. In *Dis-*

cinisca steiningeri sp. n. this is true for the characters of the outline of the posterior margin (straight to indented), the sculpture of dorsal valves (well ribbed to almost smooth), and the development of muscle scars (heavily impressed to merely discernible). It is thought that a specimen combining extreme features could be classified as a separate species.

Size, which is dependent on individual age, may be taken for comparisons if the maturity of the specimen is evidenced. In the species *Discinisca polonica* RADWANSKA & RADWANSKI and *D. steiningeri* sp. n. this is indicated by the well-developed limbus.

Rib number would certainly be diagnostic if comparable growth stages were checked. In fully grown specimens, the greatest number of ribs (about 120) may be recognized in illustrations of the present-day species *Discinisca indica* DALL (see COOPER 1973) and the Miocene species *D. multiradiata* DEMORGAN (see DEMORGAN 1915, Fig. 15); this figure is smaller than in the newly established *D. steiningeri* sp. n.

The nature of the ribbing in the genus *Discinisca* is not well understood. STENZEL (1965, p. 627) claimed a structural significance in that the ribs stiffen the upper valve, indicating a separate phyletic branch (of the generic rank, as interpreted by COOPER 1977). In *D. strigata* (BRODERIP), however, DALL (1920, p. 277) noted that the fine ribbing (striation) is obsolete or absent on the peripheral part of the upper valve in old specimens, whose valve surface is apt to be quite irregular. In *D. steiningeri* sp. n. the ribs vanish to a variable extent and often patchily throughout the major part of the valve, except of its posterior parts; this is independent of age. Similar features are displayed by such ancient species as *D. lugubris* (CONRAD 1834) from the Miocene of the United States (see THOMSON 1927, HERTLEIN & GRANT 1944) and by two Pliocene species from Japan, *D. sendaiensis* and *D. miyagiensis*, both established by HATAI & HAYASAKA (1965). These three ancient species, however, differ considerably either in size or in the mode of feeble ribbing (see review by RADWANSKA & RADWANSKI 1984).

The newly established species, *Discinisca steiningeri* sp. n., apparently belongs to group (ii) of the present-day *Discinisca* species; it shares features with some modern species, but has no comparable forms recognized in any ancient deposits of Europe. Nevertheless, any analogies between *D. steiningeri* sp. n. and the species of group (ii) may be accidental and, at least in part, caused by better recognition of this group as opposed to the other two.

The significance of certain features displayed by *D. steiningeri* sp. n. has not been satisfactorily explained in modern species. For instance, a tendency of the posterior margin of dorsal valves to be indented was noted in some specimens of *D. strigata* (BRODERIP), although its diagnostic value was questioned (DAVIDSON 1888, p. 203; HERTLEIN & GRANT 1944, pp. 37–38).

Some similarities in shape and sculpture are also displayed by *Discinisca steiningeri* sp. n. to the modern specimens illustrated by COOPER (1977, Pl. 2, Figs 14–24), which were taken off Jamaica and called by him „*Discradisca antillarum* (d'ORBIGNY)“; they differ considerably in all features from the specimens

from Cuba, originally described by d'ORBIGNY (1853, Pl. 28, Figs 34–36). The latter specimens are featured by sparsely distributed ribs (cf. also REEVE 1862; DALL 1871, 1920) and are usually referenced to group (iii) of the *Discinisca* species (see RADWANSKA & RADWANSKI 1984, pp. 262–263).

Of the peculiar features displayed by *Discinisca steiningeri* sp. n., the development of the limbus is to be noted. This has so far been reported only for *D. polonica* RADWANSKA & RADWANSKI, and was caused by a firm adherence of the specimens to small bottom objects in turbulent waters, supposedly in the surfzone. A similar interpretation has been advanced in the illustration in REEVE (1862, Pl. 1, Fig. 1 b) for the species of an allied genus, *Discina striata* (SCHUMACHER). This character, along with all the shape irregularities in the three discussed species, are thus obviously of phenotypic and not of taxonomic significance.

Taxonomic significance is herein ascribed to the pattern of muscle scars: it is stable in all specimens of the investigated population of *Discinisca steiningeri* sp. n. and is also permanent in a population of *D. polonica* RADWANSKA & RADWANSKI composed of specimens variable in their external morphology (RADWANSKA & RADWANSKI 1984). In both these species the muscle-scar patterns are significantly different. On the other hand, a slight similarity in that pattern is apparent between *D. steiningeri* sp. n. and *D. carpathia* CTYROKY & FEJFAR, which will be discussed below.

Ecology and Taphonomy of the Species

The mass occurrence of *Discinisca steiningeri* sp. n. in the section exposed at Plesching allows several conclusions pertaining to its behavior and taphonomic conditions.

Coarse-grained sands, replete with fossils and containing a thick oyster bank, generally indicate a shallow subtidal environment. Here the investigated species lived gregariously; its mode of life may thus be compared with that of some present-day species which form dense populations and whose individuals either live dispersed or tend to form clusters.

Two Recent species of *Discinisca* are known to form clusters, viz. *D. laevis* (SOWERBY) and *D. lamellosa* (BRODERIP). Both live not only attached to rocks, stones and shells, but also to conspecifics at depths down to 45 m (DAVIDSON 1888, pp. 195–198 and Pl. 26, Figs 6 and 10; RICHARDS 1974). The latter species is also known to live near low water along the shores of the Bay of Ancon in Peru, where it forms large masses which are often exposed at extreme ebb tides (DALL 1920, p. 276). *D. strigata* (BRODERIP) on the other hand, shows no tendency to form clusters in intertidal populations; the individuals show a preference for protected habitats (PAINE 1962).

The morphological variability of shell size and outline in adult specimens of *Discinisca steiningeri* sp. n. may be interpreted as resulting from attachment to small protected habitats such as shells, shell hash, or coarser clasts. Except in a few cases the spat and juveniles are missing from the collected assemblage. This

clearly indicates that the assemblage has the character of a necrocoenosis whose members have been deposited in a place over years.

There is little information on the lifespan of present-day *Discinisca* species. When studying an intertidal population of *D. strigata* (BRODERIP), PAINE (1962, p. 598) assumed a single prolonged annual recruitment period, with few or no individuals living as long as two years.

The investigated necrocoenosis of *Discinisca steiningeri* sp. n. is consequently thought to have originated by periodical supplies of adult shells derived from nearshore areas which were densely populated by individuals living discretely rather than in clusters. A short transportation, by wave action and/or littoral currents, was responsible for total damage of the thin and very fragile pedicle valves. Any stronger agitation seems to have been excluded, as indicated by a very good preservation state of the dorsal valves; they often became buried in the sediment almost fresh and were neither worn, cracked, or scaled-off.

A nearshore environment for *Discinisca steiningeri* sp. n. agrees well with the life requirements of present-day *Discinisca* species; a similar environment was also recognized by the present authors for *Discinisca polonica* RADWANSKA & RADWANSKI from the Middle Miocene (Badenian) sequence of the Korytnica Basin in Poland.

The climatic conditions prevailing in the basin in which the Egerian sequence of Plesching was formed may be postulated as being tropical or subtropical. This corresponds to the thermic requirements of most present-day *Discinisca* species (DAVIDSON 1851, 1888; DALL 1871, 1920; THOMSON 1927; HERTLEIN & GRANT 1944; COOPER 1973, 1977, 1982) and of the discussed ancient species from the Korytnica Basin (BALUK & RADWANSKI 1977, RADWANSKA & RADWANSKI 1984).

Genus *Discinisca* in the Paratethys Realm

As seen from the above review of the Tertiary occurrences of the genus *Discinisca* in Europe, the marine regime of the Paratethys basins has offered favorable conditions for these inarticulate brachiopods since the Late Oligocene. The stratigraphically oldest species, *Discinisca steiningeri* sp. n. from the Linz Sands, did not, however, become an ancestor of the younger (Miocene) species, as the morphology of the latter differs considerably.

The oldest of the Miocene species is *Discinisca carpathia* CTYROKY & FEJFAR, 1963, from the Lower Miocene (Carpathian) deposits of Moravia, Czechoslovakia. It is characterised by a much larger size (up to 30 mm) and the presence of fine, but stable ribs (numbering 70 to 75) on the dorsal valves, which are low-conical (CTYROKY & FEJFAR 1963, pp. 162–166, Figs 1–2 and Pl. 7, Figs 1–5). Ventral valves are unknown, and the inner sides of the dorsal ones exhibit anterior adductor scars which are relatively wider and less elongated (CTYROKY & FEJFAR 1963, Fig. 2).

The Middle Miocene stocks of the genus comprise both smooth and ribbed forms. The first are represented by the species *Discinisca leopolitana* (FRIEDBERG,

1921), whose specimens were first reported by LOMNICKI (1897, p. 17) as „*Discina* sp. (*leopolitana* m.)“, although without any diagnosis, description, or illustration. This name, according to the ICZN rules, has obviously been a nomen nudum until adequately described by FRIEDBERG (1921, pp. 6–7 and Pl. 1, Fig. 2) as „*Discina leopolitana* M. Lom. in litt.“. According to the same rules, it is evident that FRIEDBERG is the creator of the species, which has subsequently been cited in the literature under various names (THOMSON 1927, p. 132; MUIR-WOOD 1939, p. 156; HERTLEIN & GRANT 1944, p. 35; CTYROKI & FEJFAR 1963, p. 146). The specimens of this species, featured by small-sized (9 mm by 7 mm), smooth valves, occur rarely in the Middle Miocene (Badenian) deposits exposed just within the city of Lwow (in medieval Latin: *Leopolis*, adjective *leopolitanus*), at present the western Ukraine, Soviet Union. LOMNICKI (1897) mentioned that some specimens were attached to scallops, but FRIEDBERG (1921) had only dorsal valves at his disposal. He recognized them as being almost identical with present-day *Discinisca lamellosa* (BRODERIP), differing only in their smaller size and less eccentric position of the apex. The species thus may easily be compared to group (*i*) of the present-day *Discinisca* species.

The two other species of Middle Miocene (Badenian) age are distinctly ribbed and thus attributable to group (*iii*) of the present-day *Discinisca* species.

The species *Discinisca scutellum* (DREGER, 1889) was established by DREGER (1889, pp. 182–183 and Pl. 1, Fig. 16 a–c) for one, partly damaged, low-conical dorsal valve from the Middle Miocene (Badenian) sandy deposits exposed at Immendorf near Grund in the Vienna Basin, Austria. This small specimen (5 mm by 4 mm), being obviously the holotype, is kept in the collection of the Naturhistorisches Museum in Vienna (NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1861. XXXV. 102); it is actually more damaged than at the time of its illustration. Its inner side is scaled-off and/or worn, the muscle scars thus not being detectable. The outer surface is well preserved and sculptured by sparse ribs (total number 32; interspaces about 3 times wider than the ribs) of a distinctly beaded appearance (clearly illustrated by DREGER 1889, Pl. 1, Fig. 16 b; referred to as fine pustules on ribs by MUIR-WOOD 1929, p. 466).

The species *Discinisca polonica* RADWANSKA & RADWANSKI, 1984, was established by the present authors for small specimens whose dorsal valves (holotype, 4 mm by 3.5 mm, the largest 5 mm by 4 mm) are characterized by low-conical to strongly and irregularly depressed shape as well as by distinct ribs (numbering 40 to 55) which are more or less pustulated. This species occurs rarely in some parts of an oyster shell bed developed only along the rocky shore of the Korytnica Basin; the bed contains ubiquitous remains of such typically littoral invertebrates as diverse corals, bryozoans, cirripedes (*Scalpellum*, *Verruca*, *Balanus*, *Acasta*), chitons (*Cryptoplax*), bivalved gastropods (*Berthelinia*), and other mollusks (BALUK & RADWANSKI 1977, RADWANSKA 1982, VÁVRA 1984, RADWANSKA & RADWANSKI 1984). The whole sedimentary sequence of the Korytnica Basin is of Middle Miocene (Badenian) age, as indicated by the nannoplankton zonation (MARTINI 1977).

The two discussed species from the contemporaneous deposits of the Vienna Basin and the Korytnica Basin – *Discinisca scutellum* (DREGER, 1889) and *D. polonica* RADWANSKA & RADWANSKI, 1984 – due to their extremely small size and distinct, peculiar ribbing (strong but sparse, pustulated ribs) deviate from all other forms of group (iii) of *Discinisca* species and from any ancient species (RADWANSKA & RADWANSKI 1984). These two species are much smaller than any other comparable species and may thus be regarded as pedomorphic (sensu ASGAARD 1986).

The reviewed four Miocene species of the genus *Discinisca* from the Paratethys basins evidently have no relation to the newly established species, *Discinisca steiningeri* sp. n., which is thus considered to represent a separate phyletic lineage connected with the American rather than European species.

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Explanation of plates

Plate 1

Discinisca steingeri sp. n.

Fig. 1. Holotype: 1 a – outer view, 1 b – side view, 1 c – inner view, all $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/58.

Fig. 2. Paratype: 1 a – outer view, 1 b – side view, 1 c – inner view, all $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/59/1.

Plate 2

Discinisca steiningeri sp. n.

Figs 1–2. Paratypes: 1 a, 2 a – outer views, 1 b, 2 b – side views, 1 c, 2 c – inner views, all $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Numbers 1988/59/2–3.

Plate 3

Discinisca steiningeri sp. n.

Figs 1–2. Paratypes: 1 a, 2 a – outer views, 1 b, 2 b – side views, 1 c, 2 c – inner views, all $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Numbers 1988/59/4–5.

Plate 4

Discinisca steiningeri sp. n.

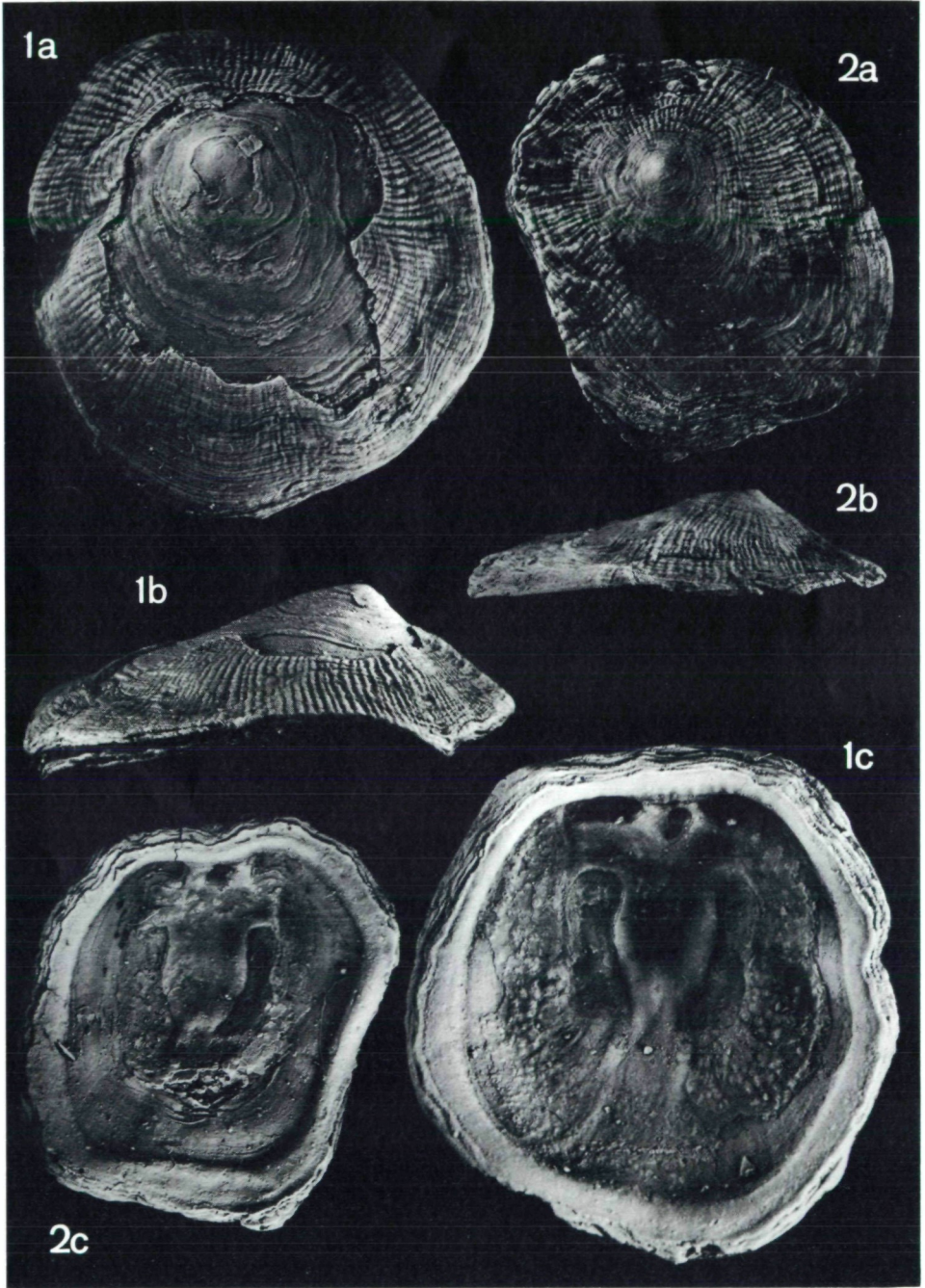
Fig. 1. Paratype, irregularly shaped, with the anterior slope almost smooth: 1 a – outer view, 1 b – side view, 1 c – inner view, all $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/59/6.

Fig. 2. Paratype, with the anterior slope almost smooth; outer view, $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/59/7.

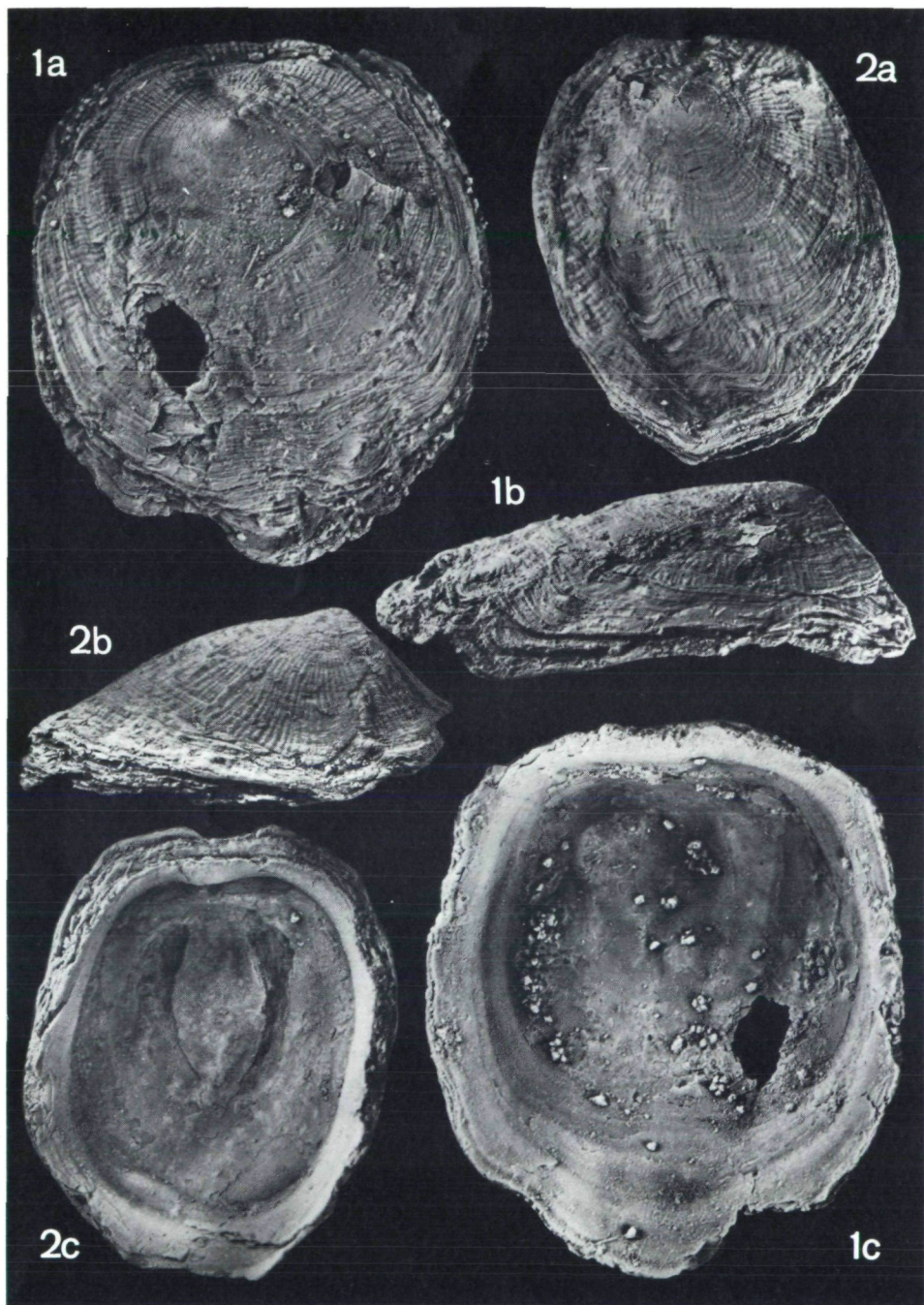
Fig. 3. Paratype, a juvenile specimen with indistinctly marked muscle scars, $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/59/8.

Fig. 4. Another paratype, to show the adhered matrix, $\times 5$. – NHM Wien, Geol.-Paläontolog. Abt.; Catalogue Number 1988/59/9.

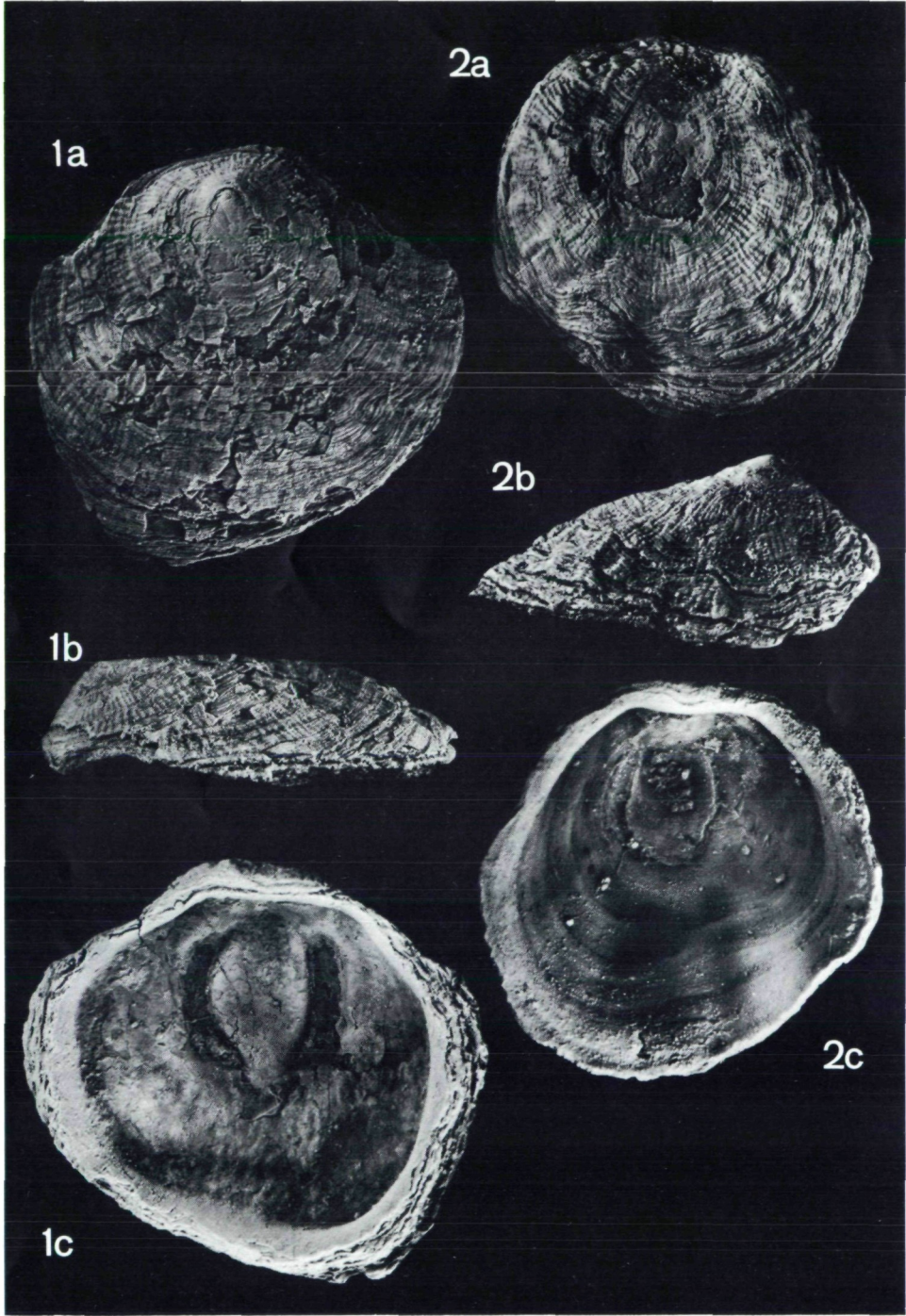
A new species of inarticulate brachiopods, *Discinisca steingeri* sp. nov., from the Late Oligocene (Egerian) of Plesching near Linz, Austria



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