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Mass aggregation of Middle Miocene spine-coated echinoids *Echinocardium* and their integrated eco-taphonomy

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ABSTRACT:

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A unique *"Fossillagerstätte"* of spatangoid echinoids of the genus *Echinocardium* from the Middle Miocene (Badenian) sandy deposits of the Fore-Carpathian Depression, as exposed at Gleboviti (=Chlebowice) in the Ukraine, is characterised by a mass occurrence of tests often preserving their entire spine canopy, apparently unaffected by taphonomic filtering. These echinoids represent a new species, *Echinocardium leopolitanum* sp.nov., and are assumed to have had a similar mode of life as the extant, cosmopolitan species *E. cordatum* (PENNANT, 1777), *i.e.* relatively deep burrowing and confined to the sublittoral. Violent storms and/or storm-generated currents are held responsible for stirring up the sand and for bringing live specimens, of all ontogenetic stages, to the surface upon which followed deposition of a heavy-loaded sediment from which they could not escape. Thus, specimens are interpreted to have been buried alive, with all spines attached. Mass aggregation of tests occurred either in patches laid down in vortical flutes on the current-swept seafloor, or within tabular scrolls of cross-bedded strata where they are locally imbricated. A functional analysis of the spines of *Echinocardium leopolitanum* sp.nov., and primarily of the large, triangular fan of plastron spines, suggests specimens to have been adapted to rapid burrowing throughout a weakly coherent and nutrient-poor sandy bottom.

Ascribed to *Echinocardium leopolitanum* sp.nov. are associated burrows, whose structure is comparable to, if not identical with, those of other *Echinocardium* species. The taxonomic potential of such burrows is discussed and it is suggested that names applied recently in ichnological analyses are in need of a modern revision.

Key words: Echinoids, *Echinocardium*, New species, Eco-taphonomy, Burrows, *Fossillagerstätte*, Miocene, The Ukraine.

INTRODUCTION

Some twenty-five years ago, the senior author attempted (RADWAŃSKI 1977) to demonstrate that traces recognised in various Neogene European sequences were of a present-day type, being indistinguishable from those of present-day producers, and still having no formal status in palaeoichnological nomenclature (*cf.* RINDSBERG 1990). In the present paper this type of traces is recorded, as is the occurrence of fossils in a unique, "present-day" mode of preservation associated with traces of their life activity in the same sediment. Representatives of the spatangoid echinoid genus *Echinocardium*, here assigned to a new species, *Echinocardium leopolitanum* sp.nov., are described from Miocene sublittoral sands in the vicinity of Lviv

(*Lwów* in Polish, *Leopolis* in mediaeval Latin, with the adjective *leopolitanus*), in the Ukraine (*see* Text-fig. 1).

The genus *Echinocardium* GRAY, 1825, of the order Spatangoida CLAUS, 1876, first occurred in the Oligocene (*see* FISCHER 1966), and is well known by its present-day, cosmopolitan species *Echinocardium cordatum* (PENNANT 1777), which is the most widely distributed of all extant heart urchins (*see* HIGGINS 1974 and 1975, for full references). Surprisingly, this genus either has a poor fossil record, particularly in Europe (*see e.g.* VADÁSZ 1915, MORTENSEN 1951, SZÖRÉNYI 1953, MĄCZYŃSKA 1979, 1988, 1991; MIHÁLY 1985, JAGT & DEVOS 1993, PHILIPPE 1998, JAGT & WILLE 2002), or is missing from classic monographs (*e.g.* LAUBE 1871), in stark contrast to the ubiquity of traces attributed to it (*see* ASGAARD & BROMLEY 1974, BROMLEY & ASGAARD 1975, RADWAŃSKI & *al.* 1975, KANAZAWA 1995). This skewed record may result, in part at least, from the fragility of the test, adopted to a burrowing mode of life, as already stressed by KIER (1977, p. 171; *see also* MORTENSEN 1951, NÉRAUDEAU 1991, PHILIPPE 1998). Thus, its preservation potential is very low when test and burrow become dissociated. [On the other hand, any heart urchin may produce a great number of burrows during its life, but upon death, only a single test remains.] In fact, with the exeption of five specimens from the Pleistocene of Rhodes (BROMLEY & ASGAARD 1975), there are no other records of fossil *Echinocardium* preserved in their burrows. Of other spatangoids, some tests of the genus *Schizaster* have been reported to be present at the end of their burrows (KALABIS 1938, D'ALESSANDRO & BROMLEY 1986). In the Miocene sequence studied, all specimens of *Echinocardium*, reported in the present paper, have been found outside burrows.

In order to make sense of the state of preservation of the collected echinoids, a brief account of the biology and habitat of present-day species is given first.

ECOLOGY AND HABITAT OF *Echinocardium*

Various aspects of the biology of extant *Echinocardium*, mostly its cosmopolitan species *E. cordatum* (PENNANT, 1777), have been studied extensively since the classic paper by v.UEXKÜLL (1907). Data obtained either under natural or laboratory conditions may be found in papers by NICHOLS (1959), SCHÄFER (1962, pp. 348-349), BUCHANAN (1966), REINECK (1968), PEQUIGNAT (1970), HOWARD & *al.* (1974), BROMLEY (1990), BROMLEY & *al.* (1995), and KANAZAWA (1992, 1995). Special attention has been paid to its burrowing mode of life, its digging activities, as well as the structure of burrows, which has led to the recognition of identical burrows in the Cenozoic strata (ASGAARD & BROMLEY 1974, HOWARD & *al.* 1974, BROMLEY & ASGAARD 1975, RADWAŃSKI & *al.* 1975, RADWAŃSKI 1977, NODA 1985).

Extant *Echinocardium cordatum* (PENNANT, 1777) occurs along the German coast of the North Sea at depths of 3–40 metres, the burrows extending horizontally at depths of 15–18 cm below the sediment/water interface (SCHÄFER 1962). Along the French coast it occurs from the lowest tide zone to depths never exceeding 16 fathoms (some 30 m), and its lifespan is estimated to be between 3.5 and 4 years (PEQUIGNAT 1970; *cf. also* LAURIN & *al.* 1979). Along the British coast, the species finds the best life conditions and reaches larger sizes in littoral settings, whereas in offshore habitats (down to 30-40 m) it cannot reproduce, and individuals become dwarfish; its lifespan is 7 to 10, even 15 years (BUCHANAN 1966; *see also* ZIEGLER 1998, fig. 614). Intertidal occurrences of *E. cordatum* along the British coast were subsequently studied by HIGGINS (1974). In the Mediterranean, along the Tyrrhenian coast, *E. cordatum* occurs at depths of 6-15 metres; burrows noted from deeper water (down to 50 m) were invariably related to storm-deposited layers (HOWARD & *al.* 1974, p. 191). It may be inferred that the latter record refers to the temporal activity of specimens storm-transported to depths otherwise not populated by the species. In the Adriatic Sea, the species is typical of the zone extending beneath and off the littoral rubble of rocky shores, and ranging in depth between 12 and 20 metres (ERNST & *al.* 1973). It may be assumed that greater depths (down to 150 m), reported previously (STRENGER 1963), actually refer to similar cases of storm-deposited specimens. In Japan, the species was noted at depths of 1-3 metres along the coast of the Japan Sea, and at 10-30 metres along the Pacific coast (KANAZAWA 1992). Along the New Zealand coasts, the species was reported from the intertidal to depths of 33-48, and even 63 metres (HIGGINS 1974).

Functional analyses of the test of *Echinocardium cordatum* (PENNANT, 1777), with special emphasis on spine canopy structure and spine morphology on particular regions of the test, were initiated by NICHOLS (1959), whose findings have been confirmed and/or complemented by a number of subsequent authors (FISCHER 1966, PEQUIGNAT 1970, ELDERS 1975, BROMLEY & ASGAARD 1975, SMITH & CRIMES 1983, SMITH 1984, BROMLEY 1990, KANAZAWA 1992, 1995; ASGAARD & BROMLEY 1996). NICHOLS (1959) and a few subsequent workers have also contributed to our knowledge of other *Echinocardium* species from European waters (BROMLEY 1990, ASGAARD & BROMLEY 1996, DAVID & LAURIN 1996, BROMLEY & *al.* 1997; *cf. also* FÉRAL & *al.* 1995).

Some of the authors above have also followed NICHOLS (1959) in his comparisons of *Echinocardium* burrows with those of other spatangoids (*see* KANAZAWA 1992, 1995; BROMLEY & *al.* 1995; *cf. also* HERTWECK 1972). These studies have allowed numerous fossil burrows, even of Early Cretaceous age, to be attributed to the activity of spatangoids, other than *Echinocardium*, as recorded from various parts of the world, including the United States, Australia, New Zealand, and Japan (*see* REINECK 1968, GOLDRING & STEPHENSON 1970, HOWARD & *al.* 1974, WARD & LEWIS 1975, NODA 1985, D'ALESSANDRO & BROMLEY 1986; *cf. also* GALE & SMITH 1982, fig. 11 for holasteroids). As far as the present authors are aware, such burrows have been noted previously from the Miocene of the Vienna Basin as well (KALABIS 1938).

TEST MORPHOLOGY AND SIZE OF *Echinocardium*

In extant *Echinocardium cordatum* (PENNANT, 1777), test morphology and size are considerably influenced by sediment grain size that supposedly controls the depth to which the animal can burrow (1-20 cm beneath the seafloor; *see* data and/or discussion *in* NICHOLS 1959, BUCHANAN 1966, HIGGINS 1974, KANAZAWA 1992). However, test shape affects the functional ability of spines for burrowing, related to depth and grain size (KANAZAWA 1992). Generally, the more globular a test is, the greater the depth of burrowing and the grain size of sediment in which the burrowing may take place. When grain size is smaller, burrowing is shallower, and the test flatter, and smaller. Comparative studies by HIGGINS (1974) have documented these relationships in the range of diverse habitats and geographic locations (New Zealand *vs* Great Britain).

With regard to size of adults of *Echinocardium cordatum* (PENNANT, 1777), larger dimensions are noted for those living in favourable habitats, *e.g.* up to 45-60 or 79 mm test length in British waters, *vs* 35-50 in New Zealand (HIGGINS 1974). The maximum recorded length (92 mm) is that noted by MORTENSEN (1951, p. 156 *and* pl. 18, figs 1-3, 8) for a specimen from South Africa.

Similarly, widely variable in *Echinocardium cordatum* (PENNANT, 1777) are shape and depth of the frontal groove (= sunken anterior ambulacrum, amb *III*), width of the plastron, and development of the anal fasciole. The taxonomic weight of all these details has long been treated differently by various authors (*see* MORTENSEN 1951, pp. 156-157, pl. 18; NICHOLS 1959, p. 355; FISCHER 1966, p. *U*613; HIGGINS 1974), also in terms of the relationship between *Echinocardium cordatum* (PENNANT, 1777) and congeners distinguished in the literature, such as *E. flavescens* (O.F. MÜLLER, 1776), *E. australe* GRAY, 1851, *E. zealandicum* GRAY, 1851, and *E. pennatifidum* NORMAN, 1868. As is evident from studies by HIGGINS (1974, and references therein), the variation in test morphology also concerns the location of the apical system, the widening of petals at the apical fasciole, the plastron length/width ratio, and the periproct shape. These reference data (*see also* HIGGINS 1975, DAVID & LAURIN 1991) show that *Echinocardium cordatum* (PENNANT, 1777) comprises specimens not so uniformly structured as recognised earlier in a morphometric analysis by KONGIEL (1937/1962) upon a rather limited number (62) of rather small specimens (average length 25 mm). Of other morphological diversities, significant is the structure of the apical system, as recognised by LAURIN & *al.* (1979) at diverse intertidal localities along the Atlantic coast of France.

Surprisingly, many of these morphological variants, including size, are seen in the assemblage of *Echinocardium leopolitanum* sp.nov. studied herein, which inhabited a single type of sandy habitat.

If size variation in the studied assemblage is accepted to reflect ontogeny (growth classes), the various test profiles in *Echinocardium leopolitanum* sp.nov. are thought to represent mainly a spectrum of ecophenotypes, dependent of presumably rather inconspicuous biotic and/or abiotic differences in local sand bodies. The nature of these differences cannot be determined since none of the specimens studied is preserved *in situ* (*i.e.* within its burrow) and all have undergone reworking and/or redeposition, as outlined below.

THE *Echinocardium* BEDS

The sequence that yielded the studied echinoids is within the framework of the Fore-Carpathian Depression, which developed during the Miocene around the Carpathians, and extended from the Vienna Basin (Austria), through the Czech Republic, Poland and the Ukraine, into Romania (*see* RADWAŃSKI 1970, 1977; WYSOCKA 1999, 2002). The Miocene sequence of the Polish and Ukrainian parts of that depression, overlapped from the south by the Carpathian overthrusts (*see* Text-fig. 1), is well recognised to the north by its littoral zone encroaching upon the Central Polish Uplands (Holy Cross Mountains, Lublin Upland; *see* RADWAŃSKI 1969, 1970, 1973) and continuing as far south as the city of Lviv and the village of Gleboviti situated at the south-eastern tip of the littoral/sublittoral

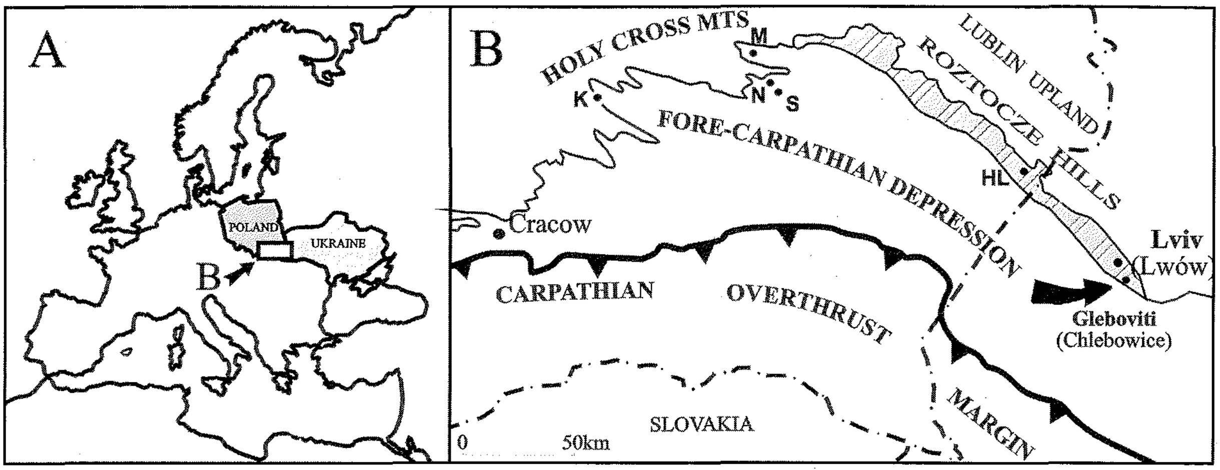


Fig. 1. Map showing location of Middle Miocene (Badenian) *Echinocardium*-bearing sequence at Gleboviti (*arrowed*) at the southernmost tip of the Roztocze Hills (Ukraine)

Indicated are localities: **K** – Korytnica, **M** – Męczennice, **N** – Nawodzice, **S** – Świniary, **HL** – Huta Lubycka

zone, which is well exposed along the Roztocze Hills (*see* Text-fig. 1).

The age of the open-marine sequence, famous for its wealth of diverse biota, inclusive of the littoral/sublittoral zone, and developed at the base of a transgressive cycle, is Middle Miocene (Badenian) in Central Paratethys stratigraphy, corresponding to the Upper Langhian/Lower Serravallian interval of the Mediterranean stage division (*see* Radwański 1970, 1977; Bałuk & Radwański 1977, 1991; Wysocka 1999, 2002).

The section studied is exposed (*see* Text-fig. 2) in a disused (since the 1970s) sand-pit at the village of Gleboviti near Bibrka (=Bóbrka), some 30 km SE off Lviv. Here, the major bulk of the sandy sequence has been excavated, leaving only a minor portion that forms a kind of "erosional" outlier. The exploitation of sand almost reached the Upper Cretaceous basement upon which conifer trees (taxodiaceans of the Baldcypress type), grew profusely prior to the Middle Miocene (Badenian) transgression. Their large, silicified stumps, over 1 metre in diameter, locally stretch from and above a thin cover of the studied sands and/or the fossil soil horizon beneath (Pl. 1, Fig. 1). The section studied (*see* Text-fig. 3) comprises five, more or less uniform members of fine-grained, slightly calcite-cemented quartz sands, the total thickness of which attains some 15 metres. This sandy sequence is capped by a cover of Pleistocene loess, about 3 metres thick. The lithology of the successive members (A – E, in stratigraphic order) may be briefly characterised as follows:

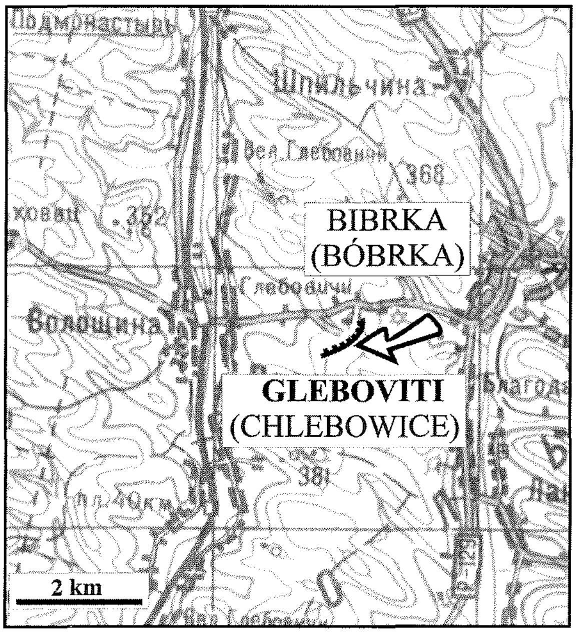


Fig. 2. Location of sand-pit (*arrowed*) at Gleboviti near Bibrka

Member **A** – Sands with sets of tabular cross-bedding and single burrows (escape traces) of sea anemones (*see* Wysocka 2002); locally, silicified conifer stumps stretch out from the fossil soil developed on the Upper Cretaceous basement (*see* Pl. 1, Fig. 1);

Member **B** – Sands with sets of tabular and trough cross-bedding, intersected by abundant burrows of sea anemones, callianassid shrimp (ichnotaxon *Ophiomorpha nodosa* Lundgren, 1891); abundant tests and burrows of *Echinocardium leopolitanum* sp.nov., locally associated with asteroids (*Astropecten*) and lithothamnian rhodoliths (*see* Text-fig. 5). The greatest density of burrows and tests of *Echinocardium leopolitanum* sp.nov. is typical of the upper part of this member, about 1 metre thick (*see* Pl. 1, Fig. 2; and a close-up *in* Text-fig. 4);

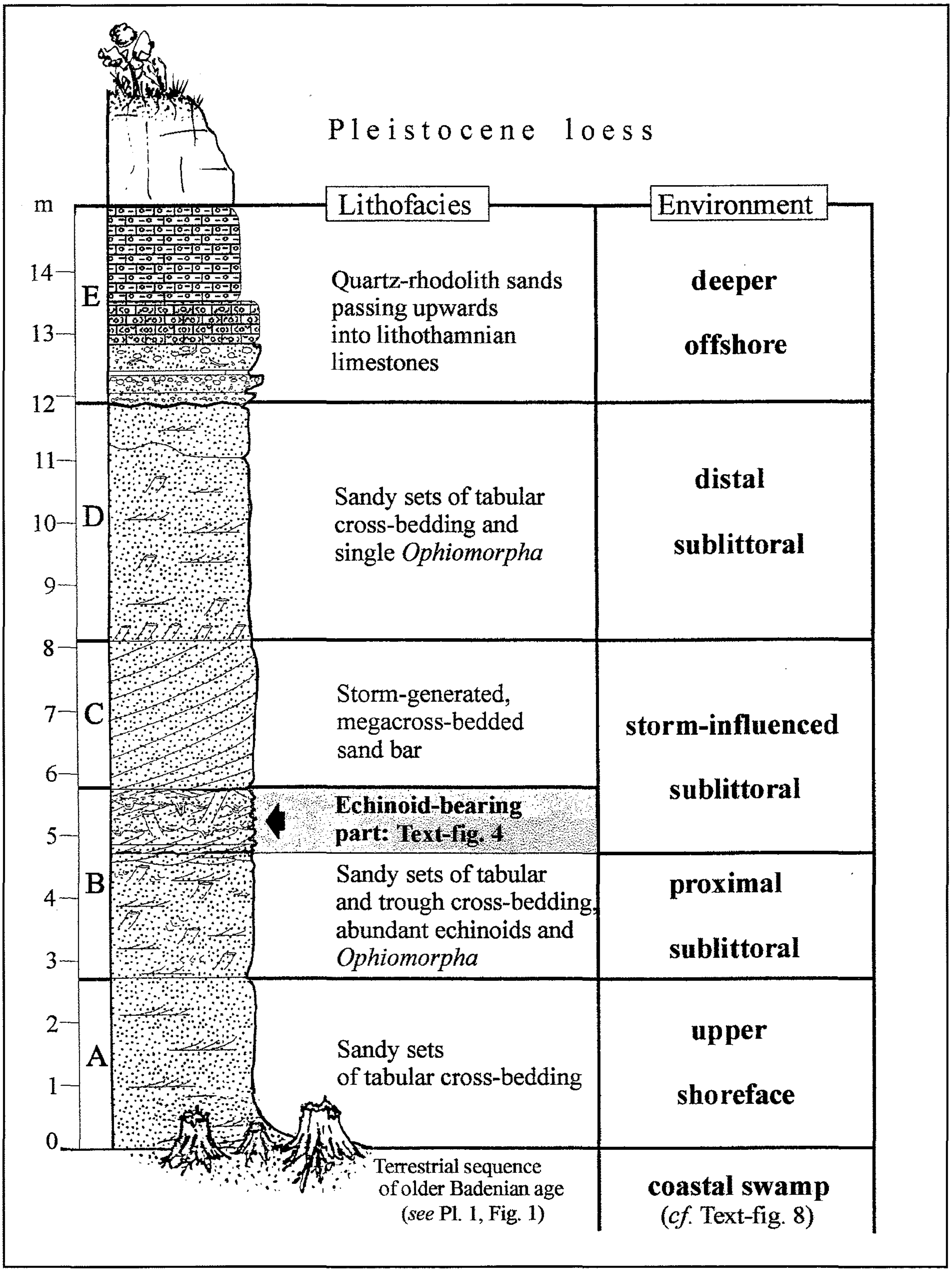


Fig. 3. The studied Middle Miocene (Badenian) sandy sequence exposed at Gleboviti; the mass-aggregated echinoid-bearing part of Member **B** is shown in Text-fig. 4

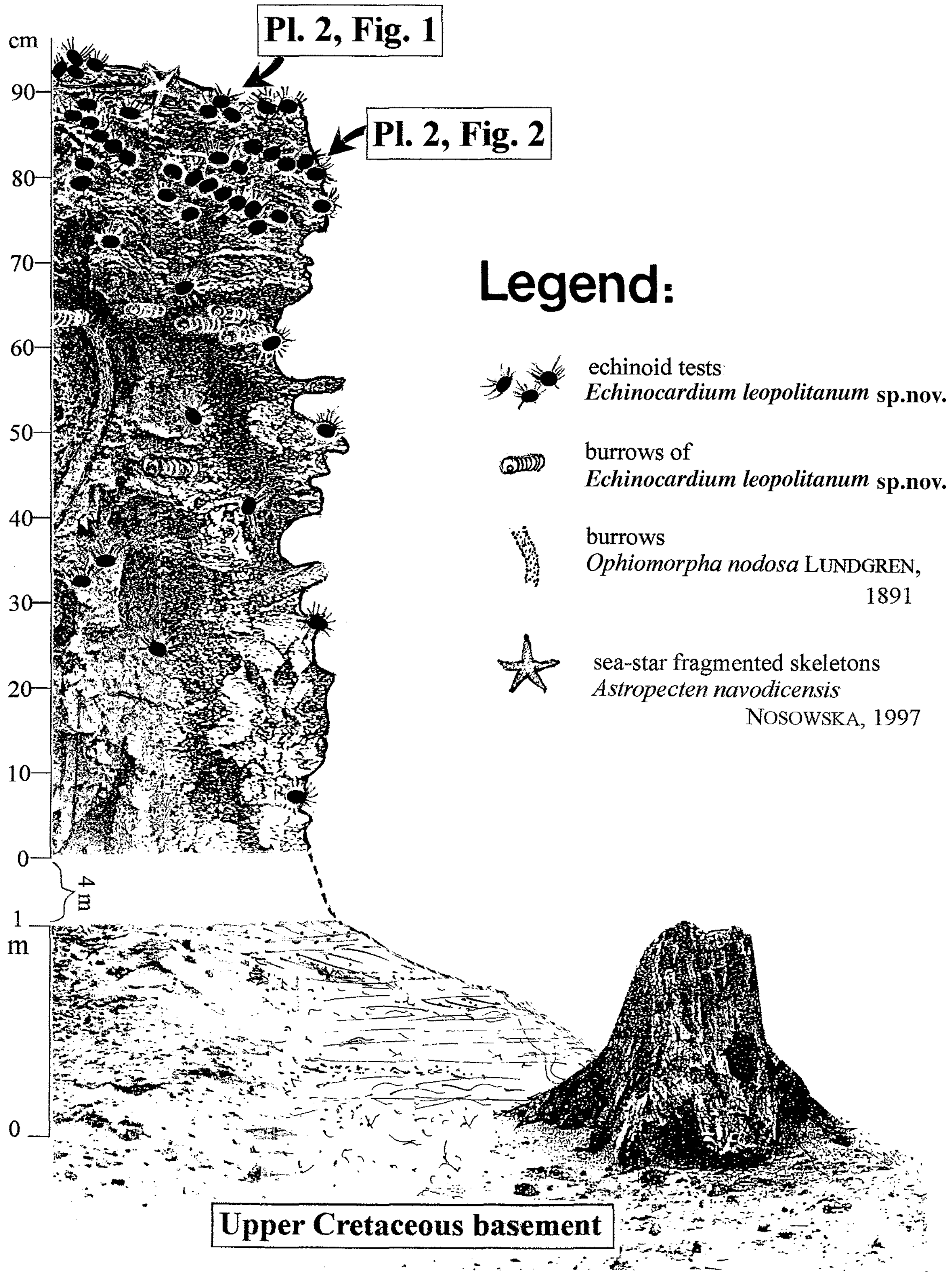
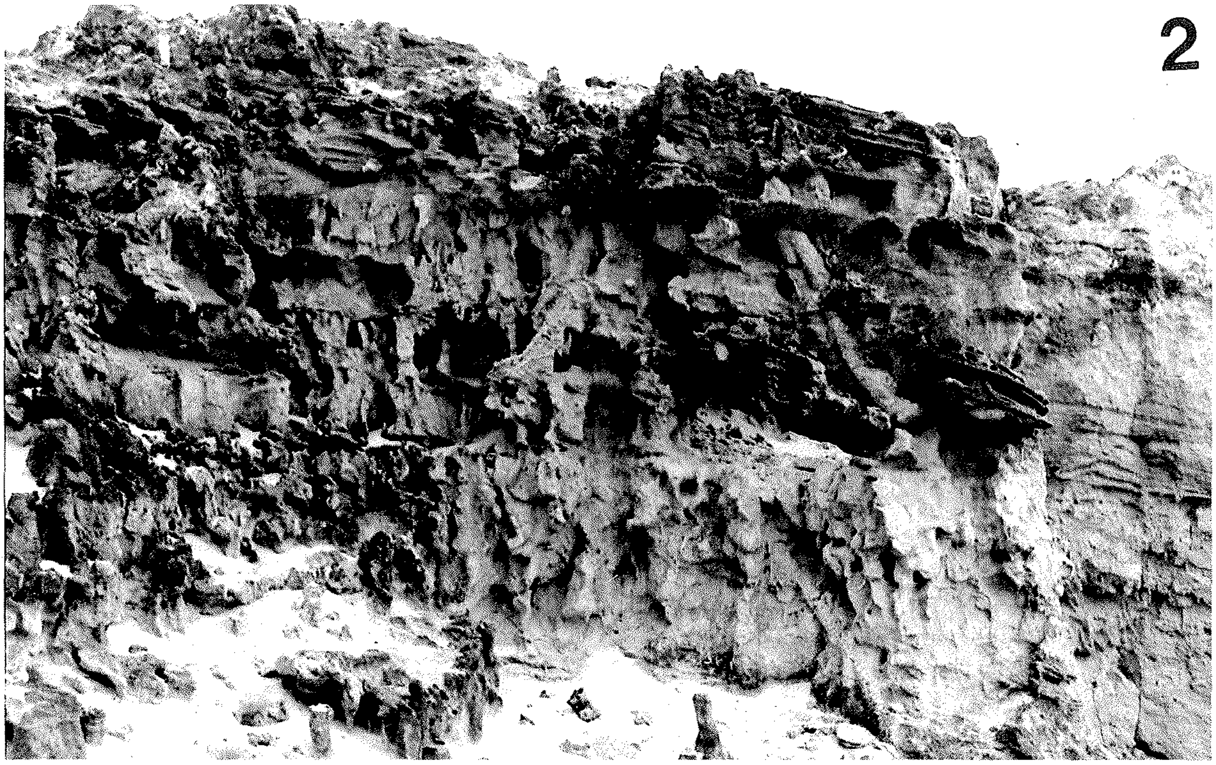


Fig. 4. Close-up of the upper part of Member **B** in the Middle Miocene (Badenian) sequence exposed at Gleboviti sand-pit (*see* Text-fig. 3 and Pl. 1, Figs 1-2); Well visible in the section, due to selective weathering, are burrows *Ophiomorpha nodosa* LUNDGREN, 1891, oriented at various angles, calcitic cementations, as well as bioturbations and tests (*diagrammed*) of the heart-urchins *Echinocardium leopolitanum* sp.nov. occurring in dense aggregations in the topmost part of the Member (*see* Pl. 2, Figs 1-2)

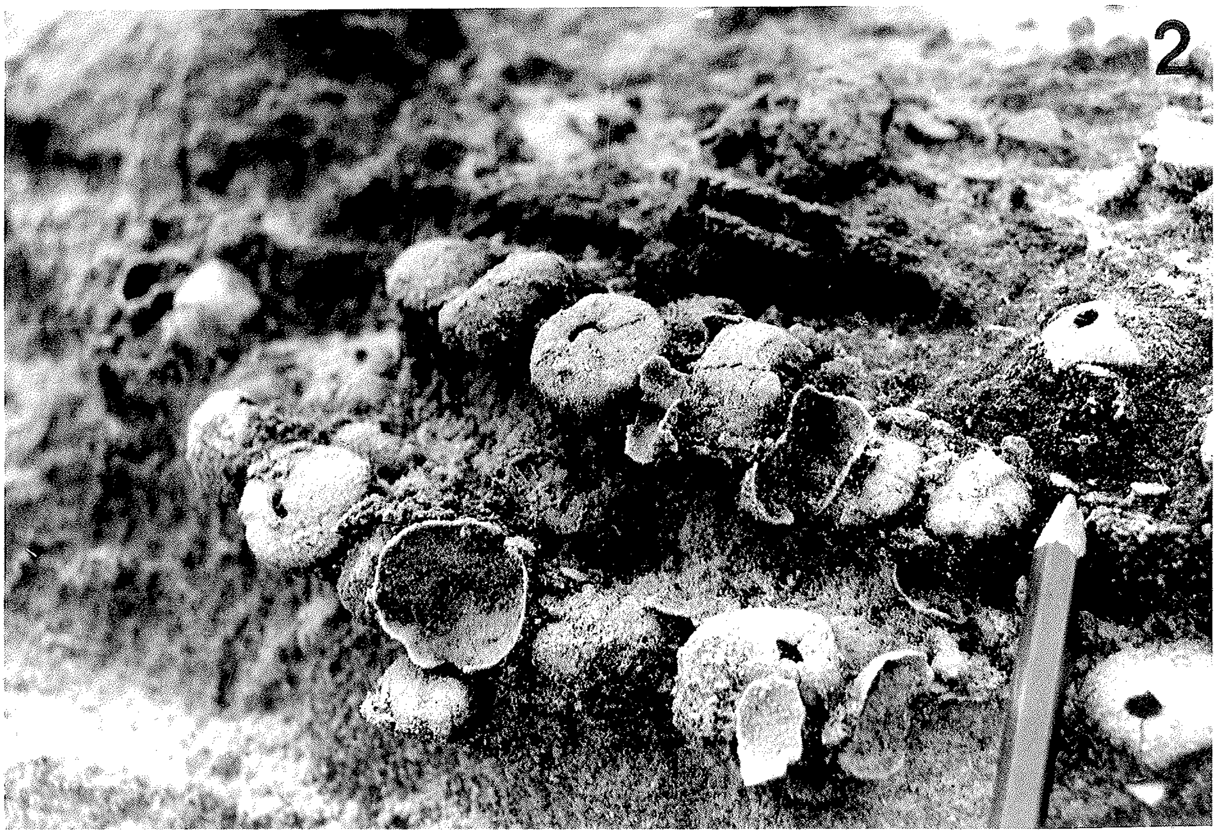


General view of the sandy sequence exposed at the Gleboviti sand-pit

1 – Silicified stumps of taxodiaceans in the lowest part of Member **A**, embedded in Middle Miocene (Badenian) sands and growing from an older soil developed on the Upper Cretaceous basement

2 – Upper part of Member **B**, yielding the most abundant burrows and spine-coated tests of *Echinocardium leopolitanum* sp.nov., as well as burrows *Ophiomorpha nodosa* LUNDGREN (for details *see* Text-fig. 4)


1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Member **C** – Large-scale cross-bedded set of sands with broken tests and burrows of *Echinocardium leopolitanum* sp.nov.;

Member **D** – Sands with sets of tabular cross-bedding and single burrows *Ophiomorpha nodosa* LUNDGREN;

Member **E** – Poorly sorted quartz-rhodolith sands and/or weakly cemented sandstones, passing upwards into lithothamnian limestones.

It should be noted that within the entire section exposed all aragonitic fossils have been removed/dissolved during diagenesis (*cf.* "taphonomic filter" of NEBELSICK 1995), and only calcitic ones survive (*see* Text-fig. 5). Of such associated fossils, spectacular are fragmentary skeletons of starfish (*see* Text-fig. 5a) conspecific with *Astropecten navodicensis* NOSOWSKA, 1997, recently based on a unique material (*see* BAŁUK & RADWAŃSKI 1968, Fig. 3/10-10a; RADWAŃSKI 1970, p. 383, Fig. 3/*j*) from the Nawodzice Sands on the southern slopes of the Holy Cross Mountains in Central Poland (*see* Text-fig. 1). Less impressive associates are rhodoliths (*see* Text-fig. 5b), composed of colonies of the red alga, *Lithothamnion* sp., showing concentric growth lamellae.

PRESERVATION OF *Echinocardium*

The most spectacular feature of specimens of *Echinocardium leopolitanum* sp.nov. studied is their spine canopy preserved more or less completely in many specimens (*see* Pls 3-5), as if unaffected by depositional and diagenetic agents. Such a state of preservation requires special conditions. In any Meso- and Cenozoic deposits the preservation of echinoids with their spines attached is still exceptional (*see* ASLIN 1968; BLOOS 1973, 1983; SMITH 1984, pp. 15-21; NÉRAUDEAU 1991; RADWAŃSKA 1996, 1999, pp. 299, 352-355; JAGT 2000; SCHMID & *al.* 2001). So far, a number of reports have focused on the disintegration rate of echinoid tests, both under natural conditions (SCHÄFER 1962, BLOOS 1983; reference review by NEBELSICK & KAMPFER 1994) and in laboratory tests (NICHOLS *in* ASLIN 1968, KIDWELL & BAUMILLER 1990). The results of these studies, and other data (*see* RADWAŃSKA 1999, p. 299), clearly show the disintegration of echinoid tests to be a matter of days or weeks rather than seasons or months. With regard to the spine canopies, David NICHOLS (*in* ASLIN 1968) noted that specimens reared in tanks lost all their spines within several (5 to 9) days after death. Similarly, the disintegration of skeletons or the removal of soft tis-

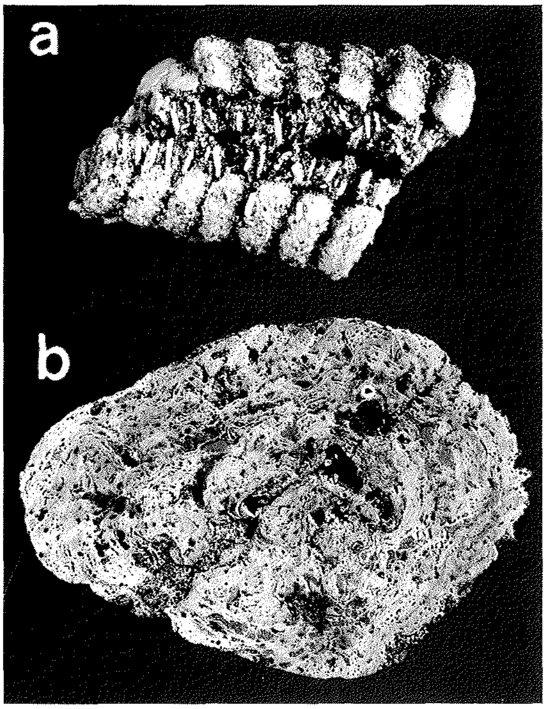


Fig. 5. Fossils associated with *Echinocardium leopolitanum* sp.nov. in Member **B** of the Gleboviti section (*see* Text-figs 3-4)

a – Sea-star *Astropecten navodicensis* NOSOWSKA, 1997 – fragmentary arm (oral view showing inferomarginal ossicles, and spines covering the adambulacral ossicles); × 3

b – Rhodolith, sectioned to show concentric growth lamellae of red algae *Lithothamnion* sp.; × 2

←

Aggregations of tests of *Echinocardium leopolitanum* sp.nov. in the upper part of Member **B** at Gleboviti; both about natural size

1 – Top view of the bed: a patchy streak of tests of variable size (ontogenetic series). The tests are randomly oriented and tightly packed within the streak
Interpretation: Aggregation formed by a violent current, most likely storm-generated, that smoothed the bottom and deposited locally, in a vortical flute, the echinoid tests not being segregated according to their size (weight)

2 – Side view (section) of the bed: streaks of tests, locally imbricated along scrolls of the tabular (diagonal) cross-bedded set (for location *see* Text-fig. 4)
The tests are size-selected and current-oriented, *i.e.* imbricated like as tiles on a roof (or fish scales)
Interpretation: Accumulation formed by a current, most likely storm-generated, that segregated the tests according to their size (weight) and imbricated with their larger faces oriented up-current (current direction was thus from the left). Note, when imbrication progressed, the tests were oriented with their ventral sides upwardly (thus, well visible are the peristomes), to face the current streamlines with the less convex side of the test

In both photos the damage of tests is due to wind action in the exposure sues from the shell in many other invertebrates takes place within a few hours or days (see review by KENNEDY & COBBAN 1976, p. 9; BISHOP 1986; BRIGGS & KEAR 1993, 1994; *cf. also* HOF & BRIGGS 1997).

As far as the material studied is concerned, it is assumed that burial of the spine-bearing echinoids must have been rapid, to form either slurry-bearing mudflows or storm-generated tempestites (*cf.* interpretations discussed by ASLIN 1968, BLOOS 1973, 1983; SMITH 1984, RADWAŃSKA 1999). When taking into account the sandy texture and limited mud fraction of the sequence studied, storms may be seen as the most likely agents.

Some of the specimens studied are not entirely filled, which certainly testifies to their tests having been buried rapidly, with intestines not yet decomposed or, alternatively, specimens still alive, a fact also stressed by ASLIN (1968) for Middle Jurassic acrosaleniids from England.

Consequently, echinoid material studied is inferred to represent primarily specimens buried alive (catastrophic death). This conclusion is supported by size groups represented, ranging from specimens being almost babies (smaller than 1 cm in length), to adults (averaging c. 35-40 mm in length), and to supposedly gerontic individuals (up to 51 mm). The storms or storm-generated currents were thus responsible not only for the final burial of the echinoids but also for dislodging them from their burrows, and controlled further transportation, segregation, and accumulation (locally imbrication) of tests, the live owners of which were enable to escape/withdraw from the bulk of stormy sediment settled upon them.

This assemblage of *Echinocardium leopolitanum* sp.nov. is thus thought to represent a thanatocoenose, in which all live specimens of a community were killed, regardless of ontogenetic stage. A minority, primarily the larger tests (*see* Pl. 6), which lacking spines, may be assumed to have remained on the seafloor for a longer period of time, or to have been dead already and without spines when becoming dislodged from their burrows.

Nevertheless, it is to state that all specimens collected are considered to be conspecific, regardless of their preservation either in the form of naked tests (denuded of spines, thus significant for taxonomic treats) or spine-coated "mummies" without an access to taxonomic features of their tests.

IMBRICATION OF TESTS

The storm-generated deposition took various shapes (*see* Pl. 2, Figs 1-2), one of which are tabular scrolls of cross-bedded strata with imbricated specimens of *Echinocardium leopolitanum* sp.nov. This peculiar structure is worthy of note since imbrication, as it may appear in flat-sided or disc-shaped particles, is a very rare phenomenon in fossils. To the authors' knowledge, the three cases of ammonite shells demonstrated by SEILACHER (1982, fig. 3) from Hettangian-Sinemurian shales of Lyme Regis (Dorset, England), Toarcian *Posidonia* Shales of Holzmaden (Germany), and Ladinian limestones of Epidauros (Greece), respectively, are the best examples.

DIAGENETIC INFLUX: PRESSURE-SOLUTION ARMOUR

Spines in *Echinocardium leopolitanum* sp.nov. adhere firmly to the tests as they are glued by a calcitic precipitate which mummifies the primary pattern of spine distribution. This precipitate is thought to be most likely of concretional nature and bacterially induced, and it developed around the decaying soft tissue, mucus, and/or epithelium of the echinoid corpses.

On the other way, the whole mummified spine-coated tests are armoured by sand grains squeezed into the calcite crystals by pressure-solution processes that occurred within the sediment column (*see* RADWAŃSKI 1965, pp. 187 and 205).

As a result of this, the spine canopies in the majority of specimens studied cannot be removed mechanically, to denude the tests for examination. Moreover, the mummified echinoids remain extremely fragile, being easily broken even by gusts of wind at the outcrop (*see* Pl. 2, Figs 1-2).

SPINE COAT OF *Echinocardium leopolitanum*

Since in all fossil *Echinocardium* species the spine coat was noted as fragmented on one specimen only (PHILIPPE 1998, pl. 26, fig. 6*b*), it is compared to that of the present-day *Echinocardium cordatum* (PENNANT, 1777) in which the variably shaped spines are arranged into distinct groups distributed over particular parts of the test. A functional analysis of these spines (NICHOLS 1959, SMITH & CRIMES 1983, SMITH 1984) has allowed a distinction of six main groups (*see* Text-fig. 6), as follows:

Anterior scraping spines (**s** *in* Text-fig. 6 and Pls 3-5) situated at the anterior ambitus, used to excavate the front wall of the burrow;

Digging spines (**d** *in* Text-fig. 6 and Pls 3-5) situated on the ventral surface of the test in its interambulacral columns, used to excavate the lower parts of the burrow;

Locomotory spines (**p** *in* Text-fig. 6 and Pls 3-5), more or less spatulate, situated on the plastron, and used for forward locomotion;

Anal spines, arranged into a tuft (**at** *in* Text-fig. 6 and Pls 3-5) situated above the periproct;

Subanal spines, arranged into a tuft (**st** *in* Text-fig. 6 and Pls 3-5) situated below the periproct;

Apical spines, arranged into a tuft (**ft** *in* Text-fig. 6 and Pls 3-5) situated on amb *III* near the apical disc, used to protect the funnel-shaped respiratory canal of the burrow.

In tests of *Echinocardium leopolitanum* sp.nov. studied all these groups of spines are easily recognised, preserved almost intact in many specimens (*see* Pls 3-5). Some of their features are considered important from an ecologic or a taphonomic point of view, as follows:

– Anterior scraping spines are developed distinctly in some of the largest specimens only (Pl. 5, Figs 1-3).

– Locomotory spines are generally bluntly pin- or stick-shaped, and of a size similar to that of the digging spines, but much thicker than the latter (best seen in Pl. 5, Fig. 2b). Their spatulation is very indistinct and discernible in some specimens only (Pl. 3, Figs 2c and 4c;

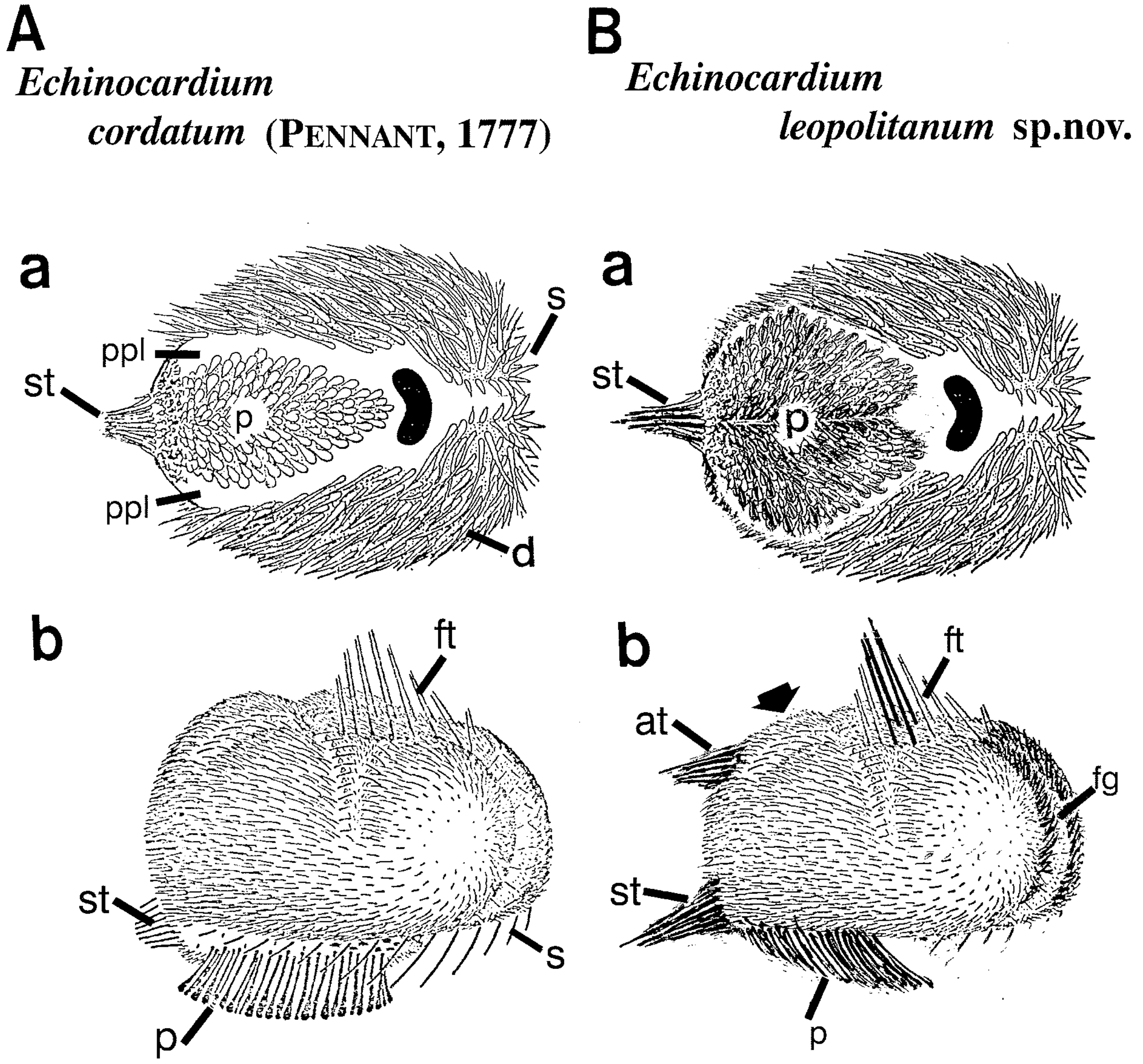


Fig. 6. Arrangement of spines into specialised groups in two species of *Echinocardium*

A – Extant *Echinocardium cordatum* (PENNANT, 1777); **B** – Miocene *Echinocardium leopolitanum* sp.nov. (modified sketch to illustrate differences in test morphology and structure of the spine canopy; arrowed is test posterior not elevated)

a–a – Ventral views; *adopted from* SMITH & CRIMES (1983, fig. 2); **b–b** – Oblique lateral views; *adopted from* NICHOLS (1959, fig. 26*a*)

s – Anterior scraping spines, **d** – digging spines, **p** – locomotory spines, **at** – anal tuft spines, **st** – subanal tuft spines, **ft** – apical tuft spines

Pl. 4, Fig. 5). In all specimens they form a distinct, triangle-shaped fan directed anteriorly that covers the periplastronal plates, and almost reaches in some specimens as far anterior as the peristome (Pl. 3, Fig. 4b). Their set tends to stretch out conspicuously from the test (Pl. 3, Figs 1c, 2c, 4c; Pl. 4, Fig. 1c). On the other hand, the plastron fan at its base (posteriorly) just reaches, or even projects outside, the test circumference in some specimens (*see* Pl. 4, Figs 3-5).

– Apical tuft spines form a circlet of smaller spines conjoined with several much longer ones posteriorly (Pl. 3, Figs 1a, 4a; Pl. 4, Fig. 1a). The whole tuft, however, is usually arranged in a bunch (Pl. 3, Figs 2a, 3a).

Of other spine groups, the small but stout spines bordering amb *III* along the frontal groove (*fg* in Pl. 3), are well preserved in some specimens, with the groove either open (best visible in Pl. 3, Fig. 3a; *also* Pl. 3, Fig. 1a) or closed (Pl. 3, Fig. 2a).

When spine canopies of *E. leopolitanum* sp.nov. are compared to those of extant *E. cordatum* (PENNANT 1777), slight differences are noted, as follows:

– Locomotory spines form a wider, triangle-shaped fan that covers a major part of the ventral testside, which supposedly corresponded to better burrowing capabilities in a nutrient-poor sediment, both internally and externally (loose, pure quartz sand);

– Apical tuft spines are distinctly longer, which may also be interpreted as reflecting deeper burrowing, and/or in a less coherent sediment, to efficiently protect the relatively long respiratory funnel (*see* Text-fig. 7b) and respiratory tube feet;

– Anal spines form a distinct tuft, quite long and sharply pointed, which certainly resulted from the necessity to protect the periproct from becoming smothered in a less coherent sediment. [It should be noted that the anal tuft in extant *E. cordatum* (PENNANT, 1777) may either be weakly developed, and omitted from illustrations of many specimens (those reproduced in Text-fig. 7 including), or be well established in some others – *see e.g.* v.UEXKÜLL 1907, fig. 7];

– Subanal spines also form a distinct, quite long and sharply pointed tuft, most likely to protect the entrance to the sanitary canal (*see* Text-fig. 7a-7b).

The features indicated above are below included in the description of *Echinocardium leopolitanum* sp.nov. Beyond the scope of the present paper is, however, to ascertain whether these features are of any taxonomic significance, or only of ecophenotypic nature.

An intriguing taphonomic feature in *Echinocardium leopolitanum* sp.nov. is the apical tuft which has all its spines invariably folded, *i.e.* tightly put, onto the test. This position of the apical tuft spines characterises the echinoid moving forward through the sediment (*see* Text-fig. 7a), and this suggests that the echinoids were dislodged by a storm when actively digging the sediment, and not when resting temporarily and constructing the respiratory funnel (*see* Text-fig. 7b). Possibly, this could have also resulted in the plastron fan of spines being stretched out distinctly, with all spine tips pointing anteriorly (*see* Pl. 3, Figs 2b, 3b, 4b; Pl. 4, Figs 1b and 5), rather than posteriorly as illustrated in the literature and observable in a collection of specimens of extant *Echinocardium cordatum* (PENNANT, 1777).

SYSTEMATIC DESCRIPTION

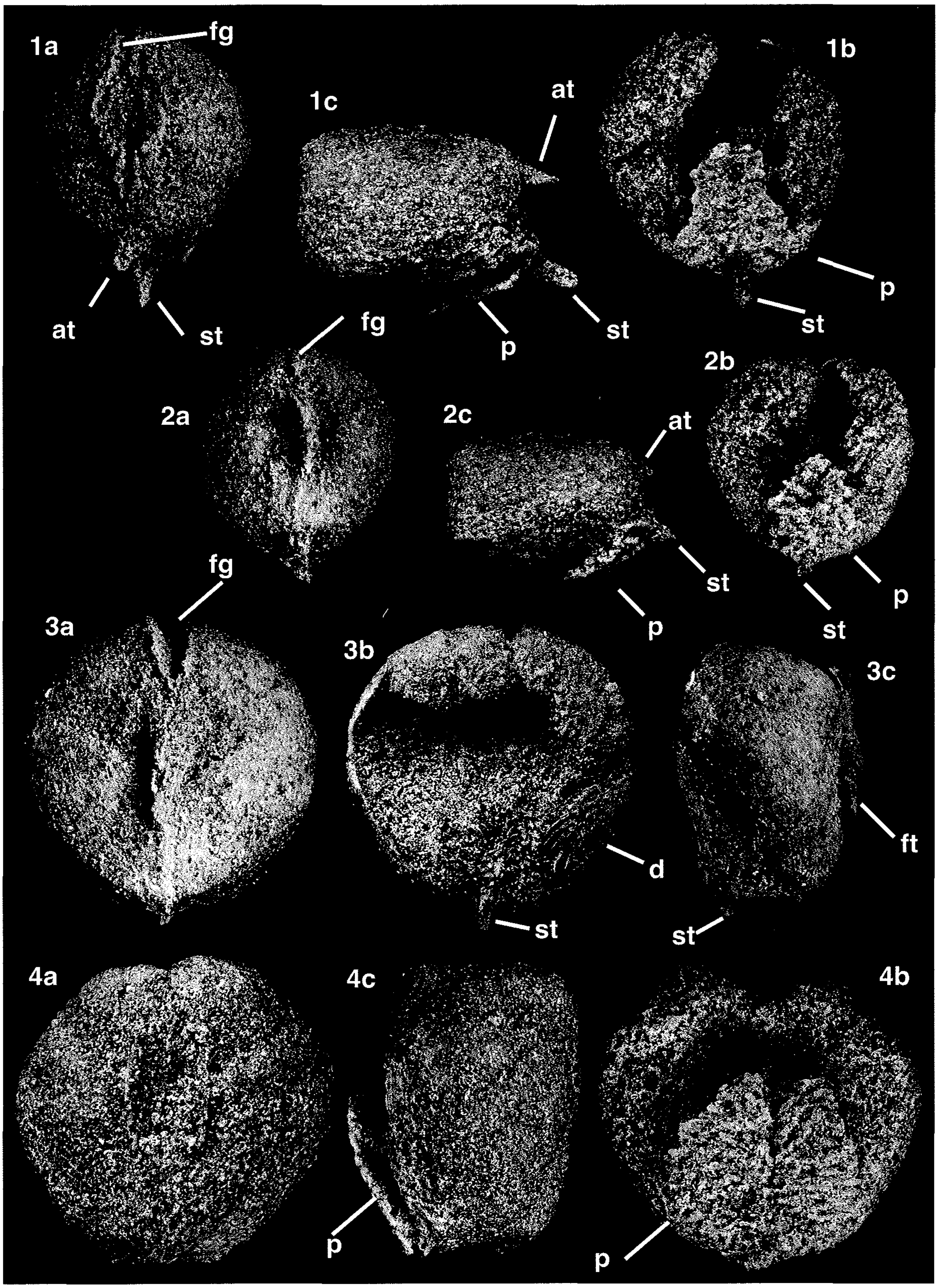
The diagnosis below is based on specimens lacking spines, that is naked (spineless), which in the collected material are solely those of the larger sizes. Such specimens (*see* Pl. 6) are considered fully-grown, or even gerontic. All smaller specimens, regarded as subadult and juvenile, preserve spines and offer only very limited insight into test morphology. Nevertheless, both the latter (*see* Pls 3-4) and the larger, either partly spine-coated or naked specimens (*see* Pls 5-6) are thought to be conspecific, and their features are taken into account in the description.

Echinocardium leopolitanum sp.nov.
(Plates 3-6)

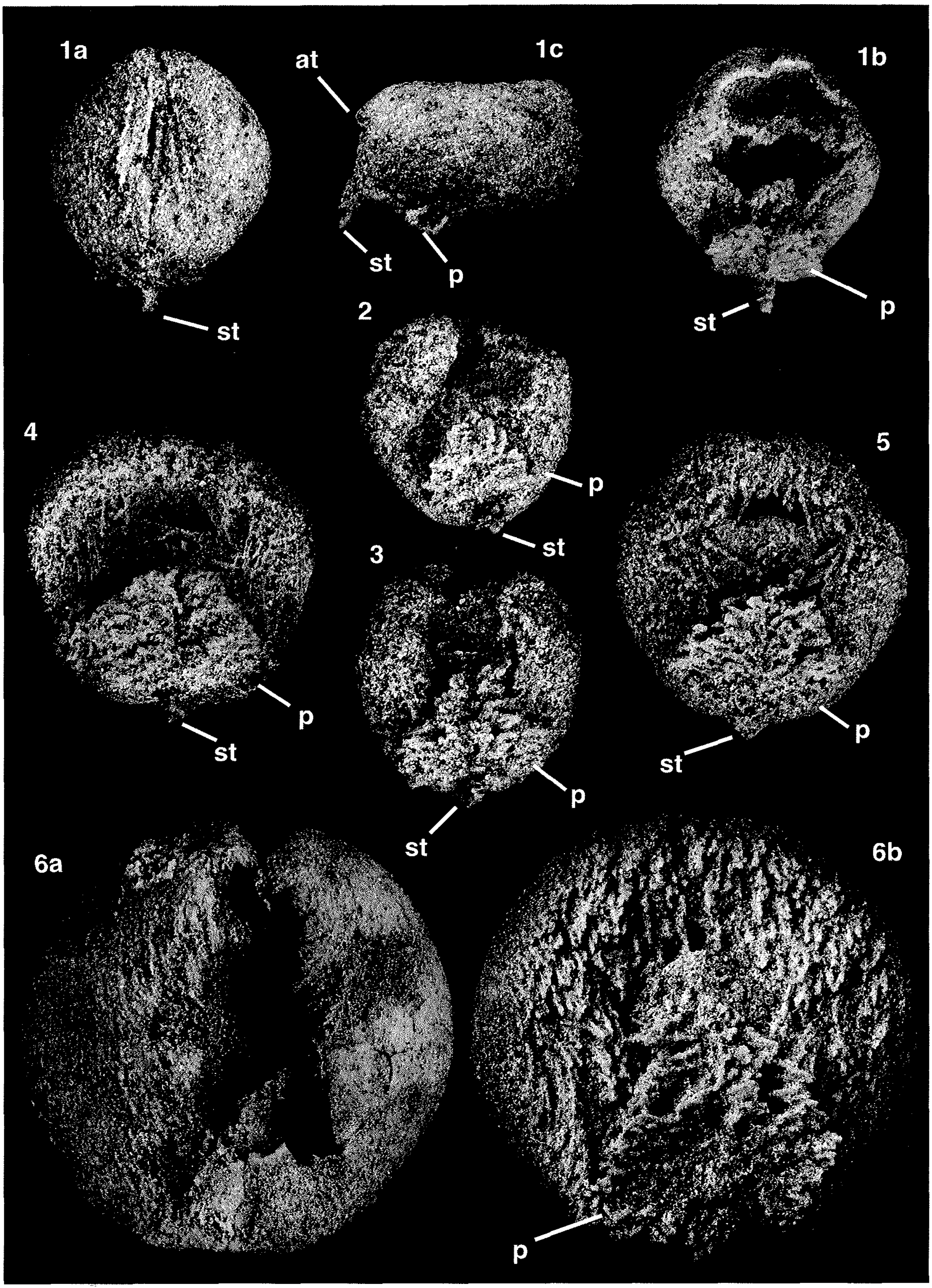
HOLOTYPE: The specimen presented in Pl. 6, Fig. 1a-1d, totally spineless but the best-preserved of all collected tests; kept in the present authors' collection.

PARATYPES: The first is specimen presented in Pl. 6, Fig. 2a-2c, the largest of the spineless specimens, slightly damaged in its periproctal part; the second is the specimen with the well preserved periproctal part which is presented complementarily in Pl. 6, Fig. 3; both specimens in the present authors' collection.

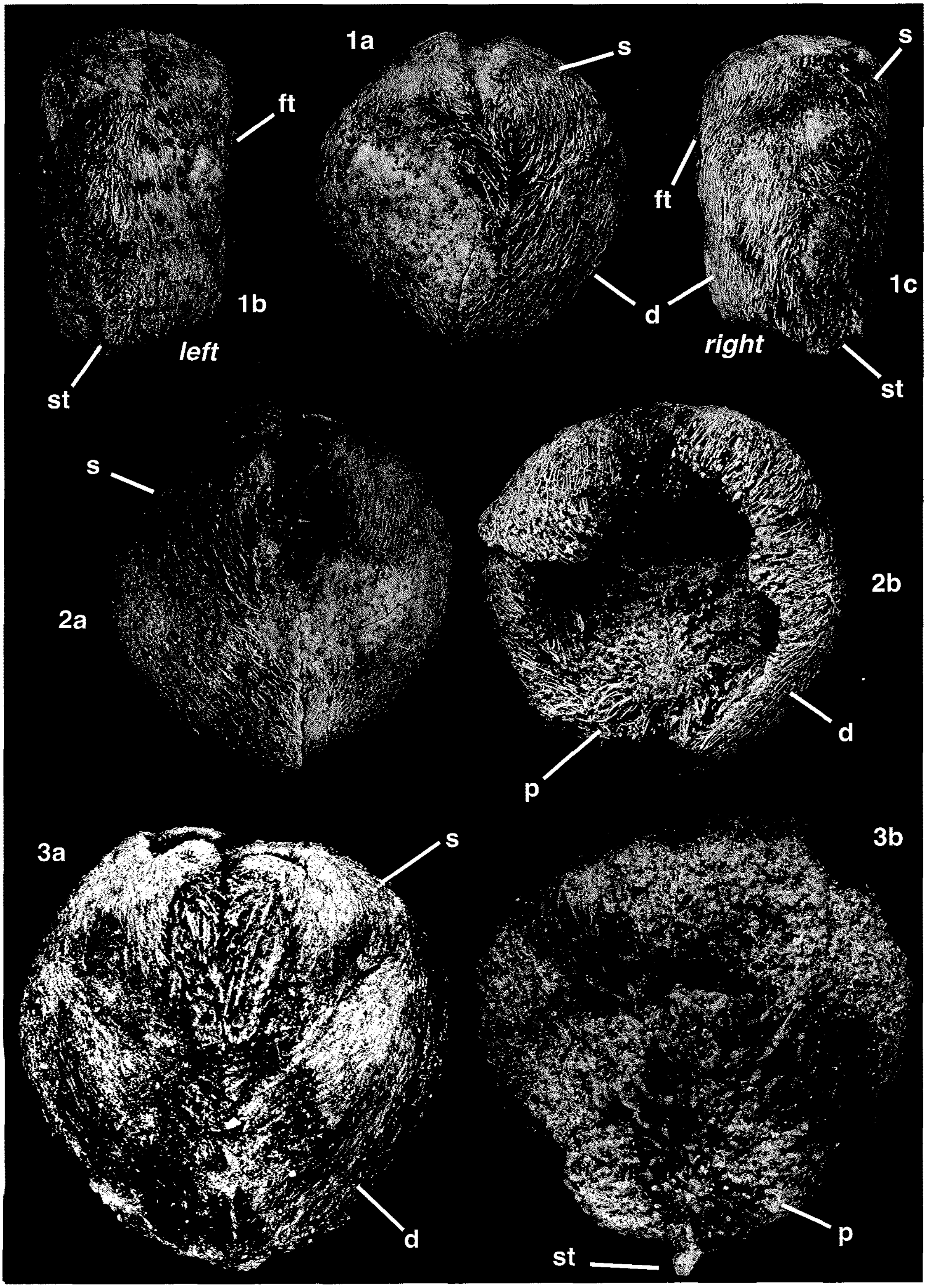
DIAGNOSIS: Test medium- to large-sized, near-circular in juveniles, to slightly heart-shaped in adults, almost box-shaped in lateral profile, with the aboral side tending to become elevated in juveniles but slightly depressed in the largest specimens, and with anterior part tending to be higher than posterior one; frontal groove distinct; petals relatively short, moderately *V*-shaped, abutting against apical fasciole; plastron relatively wide; apical fasciole conspicuous, particularly in larger specimens; subanal fasciole well developed, anal fasciole indistinct; peristome shifted anteriorly in relation to apical system placed centrally; periproct circular to horizontally oval;



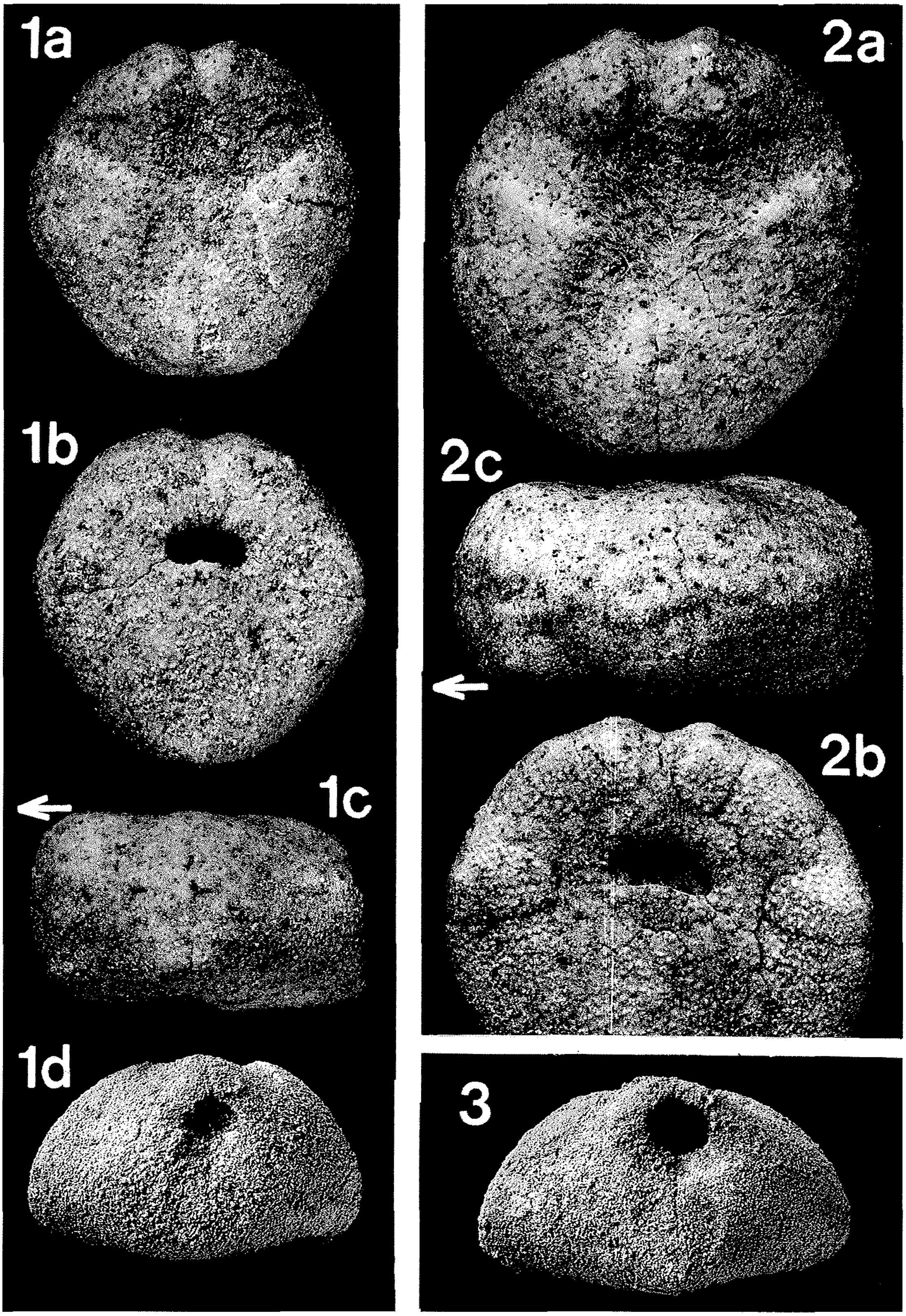
Smaller and medium-sized specimens of *Echinocardium leopolitanum* sp.nov., preserving their coat of spines; all × 1.5
(for spine designation *see* text)



Variably-sized specimens of *Echinocardium leopolitanum* sp.nov., preserving their coat of spines; all × 1.5
(for spine designation *see* text)



Larger (and largest) specimens of *Echinocardium leopolitanum* sp.nov., preserving their coat of spines; all × 1.5
(for spine designation *see* text)



Naked specimens of *Echinocardium leopolitanum* sp.nov.; **1a-1d – Holotype, 2a-2c** and **3 – paratypes**; all × 1.5
Figs 1c and 2c left lateral view: arrows point anteriorly

spine canopy very pronounced, containing strong and relatively long spines forming prominent tufts (apical, anal, and subanal) and a large plastron fan.

TYPE LOCALITY: Gleboviti near Bibrka, some 30 km SE off Lviv, the Ukraine.

TYPE HORIZON: Middle Miocene (Badenian).

DERIVATION OF NAME: Neo-Latin adjective of the name of Lviv, the principal city in the region.

MATERIAL: Some 60 specimens.

DIMENSIONS: The smallest specimen is about 9 mm, the largest 51 mm long.

DESCRIPTION: The **test** is medium- to large-sized (up to 51 mm in length), near-circular in juveniles (Pl. 3, Figs 1-4), to slightly heart-shaped in adults (Pl. 5, Fig. 3 and Pl. 6, Figs 1-2), almost box-shaped in lateral profile (Pl. 4, Fig. 1c; Pl. 5, Fig. 1b-c; Pl. 6, Fig. 1c) with the aboral (dorsal) side tending to become elevated in juveniles (Pl. 3, Fig. 1c and 2c), but slightly depressed in the largest specimens (Pl. 6, Fig. 2c). The anterior tends to be higher than the posterior in juveniles (Pl. 3, Figs 1c and 4c), but this tendency vanishes in adults (Pl. 6, Figs 1c and 2c). The **frontal groove,** distinct though shallow in bare tests (Pl. 6, Figs 1-2), is more pronounced in spine-coated specimens where the bordering spines accentuate its course with comb-like crests (Pl. 3, Fig. 3a), but these spines do cover small, bead-like tubercles in irregular files outside the pore-pairs. The **apical system** is almost central, posterior to the peristome vertical. The **petals** are relatively short, shallowly sunken, low-angled triangularly, moderately *V*-shaped, abutting against the apical fasciole (Pl. 5, Fig. 3a). The broad **plastron** (length/width ratio 1.5-1.7 in bare tests) is vaulted with an indistinct median keel from which the spines diverge fan-like laterally. The **labrum** is wide and gently arched towards the **peristome** (Pl. 6, Figs 1b and 2b). The **periproct** is circular to indistinctly oval horizontally (Pl. 6, Figs 1d and 3). The **apical fasciole** is very pronounced, shaped as a coat-of-arms, and discernible even through the spine canopy (Pl. 5, Fig. 3a). [It apears that the test is much thinner/weaker along this fasciole, having been easily broken and collapsed along and around its course (Pl. 4, Fig. 6a and Pl. 5, Fig. 2a)]. The **subanal fasciole** is well developed, easily seen in bare tests in which a very indistinct trace of the **anal fasciole** may also be detected (Pl. 6, Figs 1d and 3). The peristomial and periproctal plating not preserved in any of the bare tests.

The **spine canopy**, described in detail above, is very distinctive and contains strong and relatively long spines forming prominent tufts and a large plastron fan that distinctly projects from the test.

TAXONOMIC REMARKS: The newly established *Echinocardium leopolitanum* sp.nov. differs from extant *E. cordatum* (PENNANT, 1777), when its typical forms are taken into account (*see* MORTENSEN 1951, pl. 18, figs 6-7; FISCHER 1966, fig. 499/1; HIGGINS 1974, pls 1-6), by:

- being less heart-shaped, and never oval;
- a tendency of the test to become elevated anteriorly, and almost never posteriorly;
- having the apical system situated more anteriorly;
- a frontal groove not markedly sunken;
- petals weakly sunken, not widened distinctly against the apical fasciole;
- having a generally much wider plastron;
- showing the posterior end not truncated vertically or overhanging (*cf.* MORTENSEN 1951, pl. 18, fig. 8), but gently descending or oval-outlined ventrally in bare tests (*see* pl. 6, figs 1c and 2c) [in spine-coated specimens the feature is highlighted by a pronounced subanal tuft (*see* Pl. 3, Figs 1c and 2c];
- having a very strong spine canopy;
- having distinct spine tufts.

These differences recall the features that differentiate *E. cordatum* (PENNANT, 1777) from *E. flavescens* (O.F. MÜLLER, 1776) and *E. pennatifidum* NORMAN, 1868, amongst present-day forms (*cf.* MORTENSEN 1951, NICHOLS 1959, p. 355; *see also* KONGIEL 1937/1962, DAVID & LAURIN 1996, NÉRAUDEAU & *al.* 1998, DAVID & *al.* 1999). Consequently, *Echinocardium leopolitanum* sp.nov. appears more or less closely related to extant *E. cordatum* (PENNANT, 1777), differing only in some details of test morphology, and in canopy structure. Fossil representatives of *E. cordatum* (PENNANT, 1777) have recently been reported, more or less ambiguously, from outside Europe, *i.e.* New Zealand (HENDERSON 1975) and Japan (NODA 1985). According to MORTENSEN (1951, p. 157), the species is known not earlier than the Pliocene (*cf. also* JAGT & DEVOS 1993).

ECOLOGICAL REMARKS: The material studied represents an assemblage of specimens of various ages, the test morphology of which might change during ontogeny and was, in part at least, influenced by habitat conditions. The latter controlled digging ability, and triggered the most successful morphological adaptations, particularly of spines. As spine-canopy characteristics are the same in all specimens studied, it is inferred that they either formed a single population, or represented a few successive generations living under similar/identical biotope conditions. A spectrum of variables of their tests corresponds well with that recognised in extant *E. cordatum* (PENNANT, 1777).

From an ecological point of view, the new species is assumed to have adopted a similar mode of life as present-day *E. cordatum* (PENNANT, 1777). A major exception is the prominence of the spine canopy of the former. This is interpreted as a result of an adaptation to more rapid burrowing in less coherent sands, or less effective mucus secretion to reinforce the burrow.

The development of conspicuous tufts is thought to have resulted from burrowing rather deeply, in a pure, weakly coherent sand. This would also explain the presence of relatively weak anterior scraping spines. On the other hand, the development of very distinct apical fasciole was certainly a significant prerequisite for burrowing deeply, as suggested by BROMLEY & ASGAARD (1975, p. 275). The depth of burrowing by *Echinocardium leopolitanum* sp.nov. may be estimated to have been in the order of 15-20 centimetres beneath the sediment/water interface.

With the whole assemblage studied being regarded to represent either a single population or a few successive generations, whose members were killed catastrophically, it may be noted that the number of specimens collected and/or observed in the field (several hundreds), does not differ from population densities recorded for *E. cordatum* (PENNANT, 1777). The only peculiar record comes from New Zealand where an intertidal population was observed to emerge on a hot day (HIGGINS 1974, pl. 7b): an estimate of 200 specimens per m^2.

FOSSIL SPECIES OF *Echinocardium*

A comparison of the newly established *Echinocardium leopolitanum* sp.nov. with fossil species of the genus *Echinocardium* is an embarrassing task. To the truth, all the checked-up reference data on ancient species from Europe allow to recognise their more than arbitrary status. One may agree that they all differ from *E. cordatum* (PENNANT, 1777), but can hardly imagine how they differ one from the other. Moreover, most if not all of them are represented by infrequent, more or less damaged specimens, and some by only internal moulds (=steinkerns) of the test which cannot be critically examined. [Not discussed is a species established verbally (*nomen nudum* according to ICZN rules) upon a coquina-like aggregation of very small (5 to 8 mm long), probably juvenile specimens from the Miocene of Portugal (KOTCHETOFF & *al.* 1975).]

In Europe, Miocene species of *Echinocardium* have been recorded from two separate regions, the first being the Mediterranean (Rhone Basin and northern Africa including), the second, the realm of Paratethys basins to which that of the Fore-Carpathian Depression belongs. In the Mediterranean, commoner *Echinocardium* is known from the Rhone Basin, recently analysed and taxonomically revised by PHILIPPE (1998), who considered them to represent primarily *E. depressum* (L. AGASSIZ, 1847), to which are also referred *E. tuberculatum* GAUTHIER, 1885, and *E. granifer* (LAMBERT, 1915); associated is *E. peroni* COTTEAU, 1877, comparable to extant *E. mediterraneum* (FORBES, 1844) which recognised authors (MORTENSEN 1951, pp. 162-163; BROMLEY 1990, BROMLEY & *al.* 1997) assume to differ from *E. cordatum* (PENNANT, 1777). According to PHILIPPE (1998, p. 229), very close to, and/or conspecific with, *E. depressum* (L. AGASSIZ, 1847) are also specimens and/or species recorded from Egypt, Portugal, and Switzerland. In the latter case, this involves *E. deikei* DESOR, 1857, erroneously identified at the locality Huta Lubycka and others in the Roztocze Hills in Poland, by MĄCZYŃSKA (1979, 1991), whose specimens are discussed hereafter.

Within the Paratethys basins, representatives of the genus *Echinocardium* have long been regarded a rarity. LAUBE (1871) did not list it in his concise monograph, neither does it appear in tabular overviews of Miocene echinoids from the present-day territories of Austria, Slovakia, Hungary, and Romania. It was poorly documented, but first recorded by LÓCZY (1877), and supplemented by VADÁSZ (1915) in his classic monograph of Miocene echinoids of the former Hungarian Monarchy (*i.e.*, Hungary, Slovakia, and Romania). The genus, reported by LÓCZY (1877) and VADÁSZ (1915) only from the territory of present-day Hungary, has recently been revised by MIHÁLY (1985) whose findings are commented upon below.

The Hungarian material presents a taxonomic jungle. The three small (13-15 mm long) specimens referred to by VADÁSZ (1915) as "*Echinocardium intermedium* LÓCZY, 1877" and one of the fragmentary tests identified as "*Echinocardium* nov.sp.ind." (VADÁSZ 1915, text-fig. 120), all have closed petals, a pronounced nodosity anteriorly and laterally, and are elongate-cordiform; these do not belong to the genus at all. The generic assignment of the second of the fragmentary specimens (VADÁSZ 1915, text-fig. 119) is also called into question; MIHÁLY (1985) synonymised it with his new species, *E. biaense* MIHÁLY, 1985, based on a specimen labelled "*Echinocardium biaiensis* n.sp., LÖRENTHEY, 1914" in the collections of the Hungarian Geological Survey. The type specimen, as well as a deformed test designated as the paratype, plus VADÁSZ's specimen (*see* MIHÁLY 1985, pp. 245 and 262; and pl. 5, figs 3-5) fall well into the range of variation of *E. peroni* COTTEAU, 1877, to the synonymy of which the species *E. biaense* MIHÁLY, 1985, should thus be included. The other specimens illustrated by MIHÁLY (1985, pl. 5, figs 6 and 7-8), as "*Echinocardium* cf. *deikei* DES." and "*Echinocardium intermedium* LÓCZY" cannot be identified to species level.

With regard to Ukrainian and Polish occurrences, the genus *Echinocardium* was first recorded by SZÖRÉNYI (1953) in her monograph on Miocene echinoids from the western Ukraine, an area primarily comprising the study area of the Roztocze Hills. Described were a few *Echinocardium* tests kept in collections of Lviv University, and once collected by Polish researchers such as DZIEDUSZYCKI, FRIEDBERG, PAZDRO, and KUCIŃSKI.

Under the name *Amphidetus*, a synonym (*see* MORTENSEN 1951, FISCHER 1966) of *Echinocardium*, SZÖRÉNYI (1953) referred to "*intermedium* LÓCZY, 1877", a limited material (*cf. also* KUDRIN 1957, p. 285) of six small specimens compared by her with *E. peroni* COTTEAU, and a few unnumbered internal moulds of tests classified as "sp.nov.indet." and compared to *E. granifer* (LAMBERT). Unfortunately, detailed comments on the forms described by SZÖRÉNYI are impossible since the illustrations (SZÖRÉNYI 1953, pl. 2, figs 8-8a and pl. 8, fig. 6) are too poor [and, moreover, do not seem compatible with the descriptions (SZÖRÉNYI 1953, pp. 91-92)]. It cannot be ruled out that in fact the moulds, all from Suchodoly, belong to *E. leopolitanum* sp.nov.

In Poland, representatives of the genus *Echinocardium* have been recognised by the senior author and his students (PRZYBYSZEWSKI 1975, JÓZEFKOWICZ 1976) at Świniary and Huta Lubycka, respectively; the material collected was included by MĄCZYŃSKA (1979, 1988, 1991) into her own studies.

In our view, the test from Świniary, illustrated as *Echinocardium biaense* MIHÁLY by MĄCZYŃSKA (1988, pl. 5, figs 1*a*-1*e*; *and* 1991, pl. 1, figs 9*a*-9*d*), should be assigned to *E. peroni* COTTEAU, 1877.

PHILIPPE (1998, p. 231) reassigned to *E. peroni* specimens illustrated as *E. deikei* DESOR, 1857, from Huta Lubycka and neighbouring locality Monastyrz (MĄCZYŃSKA 1979, pl. 9, figs 2 and 4, respectively); the third illustrated specimen (MĄCZYŃSKA 1979, pl. 9, fig. 3) supposedly being a deformed schizasterid. It should be noted that in the present authors' collections there are also several specimens of *E. depressum* (L. AGASSIZ, 1847) from Huta Lubycka.

THE ASSOCIATED BURROWS

The burrows associated with *Echinocardium leopolitanum* sp.nov., and here ascribed to that species, correspond well to those produced by extant *E. cordatum* (PENNANT, 1777), that have been illustrated since almost a century (v. UEXKÜLL 1907, fig. 7; ZAPFE 1935, fig. 1; SCHÄFER 1962, fig. 182; *see also* NICHOLS 1959, figs 16-18, *corrected by* BROMLEY & ASGAARD 1975, figs 28-29).

The *Echinocardium* burrows consist of a more or less horizontal tunnel with a meniscal backfill transected by the sanitary canal situated close to the burrow's sole, and furnished with the vertical respiratory funnel to reach the sediment/water interface (*see* Text-fig. 7). The meniscal backfill is formed when the animal moves through the sediment, pushing it backwards, and producing thereby a blind sanitary canal (Text-fig. 7a) which continues as long as the subanal tube-feet can extend to maintain it not collapsed (*see* NICHOLS 1959, fig. 19). The respiratory funnel is formed when the animal stops burrowing temporarily (Text-fig. 7b); then, a kind of chamber is formed, which may be regarded as a resting, feeding, or living chamber, respectively. In extant *Echinocardium cordatum*, it has been observed (DE RIDDER 1982, BROMLEY 1990) that the animal feeds only when resting in this chamber, and exclusively on particles ingested through the respiratory funnel. With regard to mobility, specimens reared in aquaria have been observed to move forward, and produce a backfill, at a speed of about 5 cm per hour (KANAZAWA 1992).

The lithification grade of the burrows studied varies. Some are hardly detectable in the section at the exposure; others may easily be picked out "three-dimensionally" from the sandstone layer (*see* Pl. 7). Generally, the lower part of the burrow, formed by the ventral side of the echinoid (*see* Pl. 8, Fig. 1), is lithified more firmly than the dorsal one (Pl. 8, Fig. 2), similar to what BROMLEY & ASGAARD (1975, pp. 262-263 and figs 7-8) recorded from Pleistocene burrows of Rhodes. Equally variable is the cementation of particular menisci within the backfill (*see* Pl. 7, Fig. 1a; *cf.* BROMLEY & ASGAARD 1975, p. 262 and figs 5-6). From studies of extant forms it has become apparent that the stronger cementation of the burrows' basal portion is a result of more intensive secretion adorally of mucus by the echinoid (*see* NICHOLS 1959, PEQUIGNAT 1970). If correct, it suggests that the presence of mucus itself has triggered the stronger cementation of some sandy horizons or layers with which the burrows studied are associated (*cf.* BROMLEY & ASGAARD 1975, p. 262).

In the original burrow termination, two types are distinguished. The first involves the blunt termination which corresponds to that part of the burrow referred to herein as "distal", with the echinoid moving forward (*see* Text-fig. 7a). These terminations were formed at the beginning of the burrow ended by a resting chamber at the opposite end, referred to herein as "proximal" (*see* Text-fig. 7a). The second type starts off with

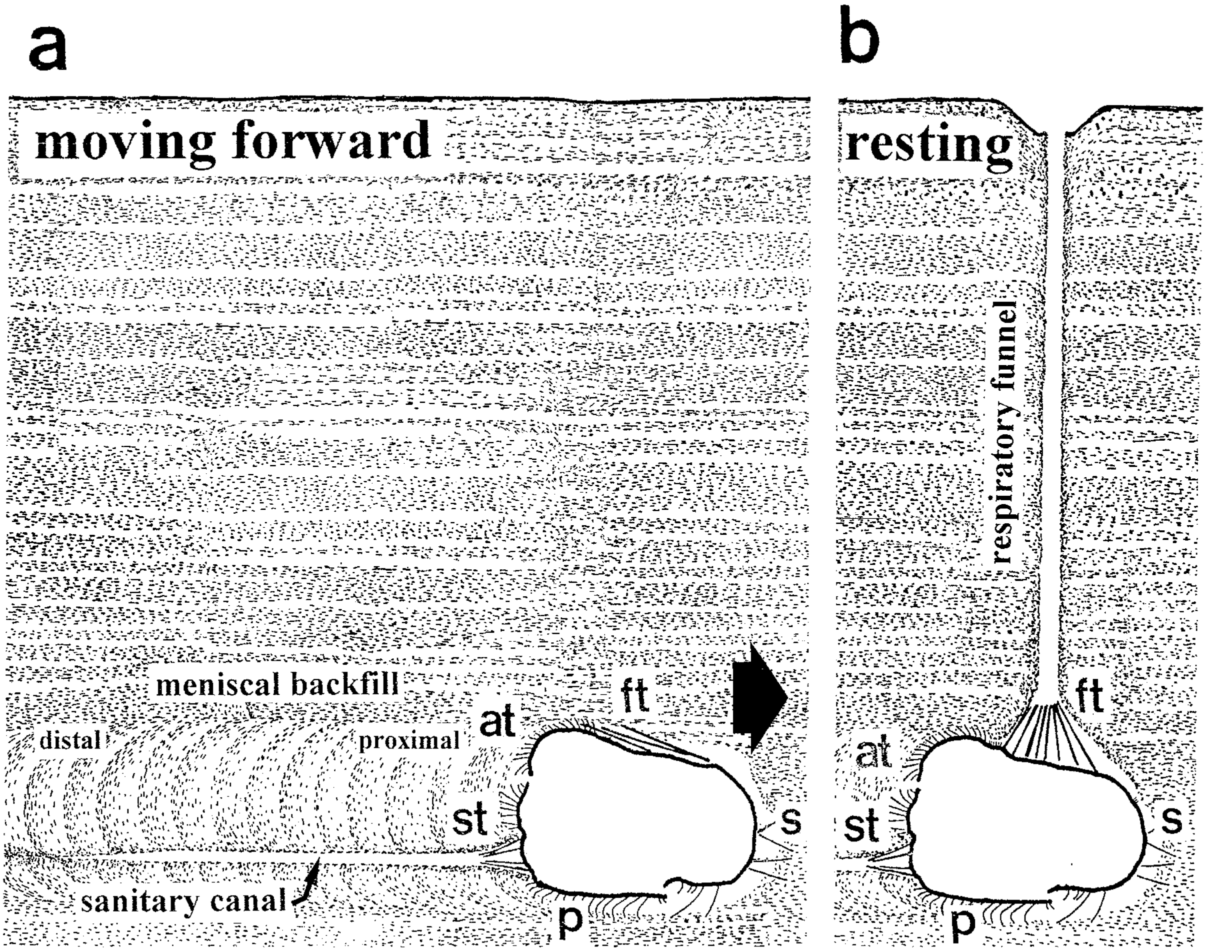


Fig. 7. Schematic presentation of burrows constructed by extant *Echinocardium cordatum* (PENNANT, 1777); *adopted from* BROMLEY & ASGAARD (1975, figs 28-29)
a – Burrow constructed by animal moving forward; **b** – burrow constructed by the resting animal
Abbreviations for the coat of spines as in Text-fig. 6

a chamber, more (Pl. 7, Fig. 3) or less pronounced (Pl. 7, Fig. 2), and to which the meniscal backfill is oriented with its convexity (best visible in the elder specimen in Pl. 7, Fig. 3a). Thus, these chambers are placed just at the "distal" end of the burrows, not at the "proximal" one, as would be expected from literature data (*cf.* Text-fig. 7 a-b). The chamber in such burrows usually is distinctly swollen and more or less rotated to the burrow's course. Moreover, it usually is weathered away, at least in part (see the two burrows in Pl. 7, Fig. 3a), which indicates that its lining with mucus is much weaker than that of the meniscal part of the burrow.

Burrows with such a chamber may have been produced by echinoids that had not entered the sandy layer vertically, as recognised by SCHÄFER (1962, fig. 183: *Schachtbau*; ZIEGLER 1998, fig. 624 *E*), but had been introduced into it by rapid burial. This may explain the swelling and twisting of the chamber formed by upside-

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Burrows produced by *Echinocardium leopolitanum* sp.nov.

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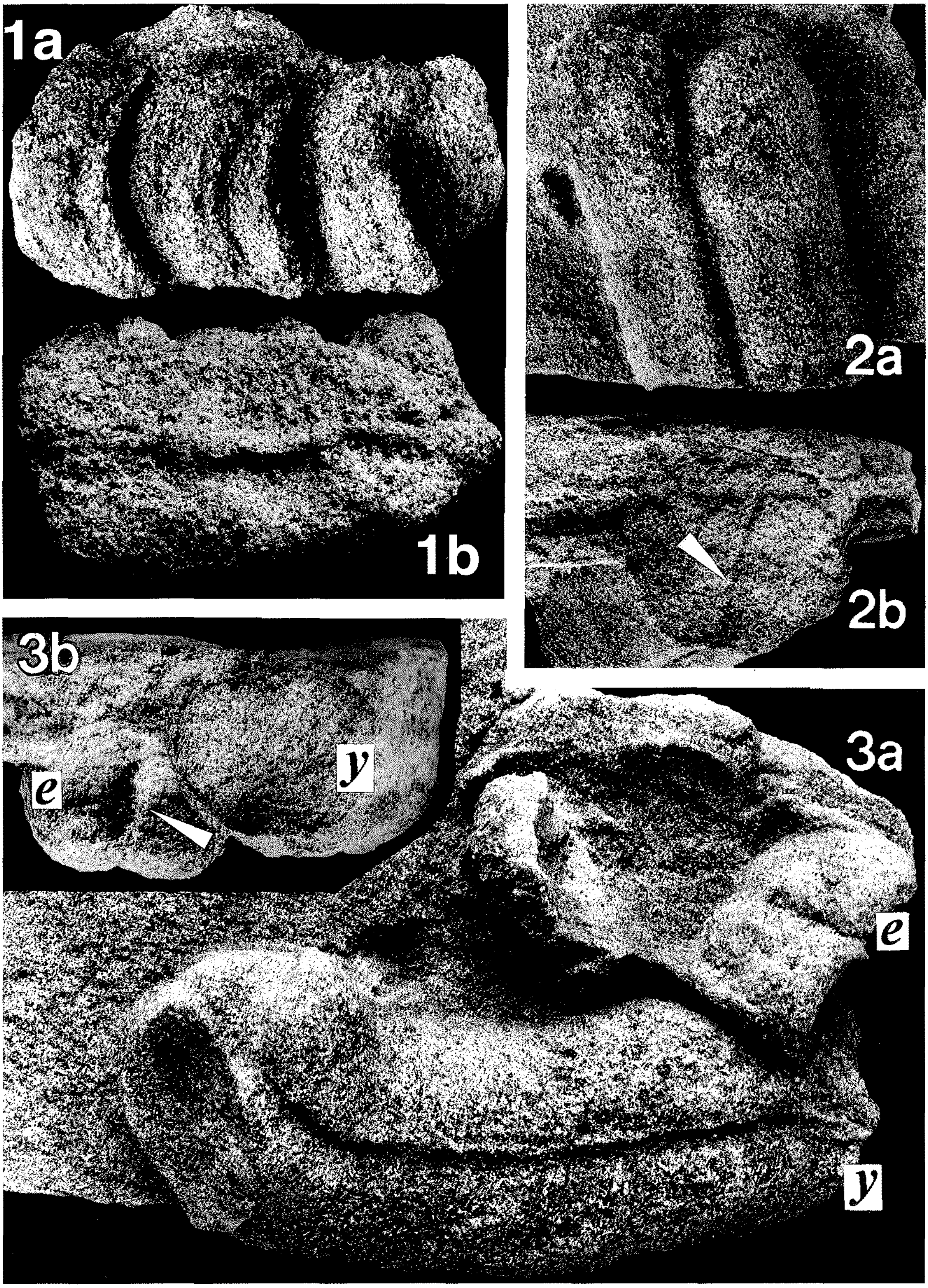
1a - 1b – Meniscal backfill (internal mould) of a median part of the burrow [Likely product of an hour's work of the echinoid; *cf.* KANAZAWA 1992, p. 739]: **1a** – lateral, to show variable cementation of particular menisci; **1b** – bottom view, to show the mould of the sanitary canal; × 1.5

2a - 2b – Distal end of the burrow stuck to lower surface of overlying layer: **2a** – bottom view, **2b** – section, to show the accessory canal (*arrowed*); natural size

3a - 3b – Two burrows with their distal ends, stuck to the overlying layer's sole; the burrows were formed successively – the younger one (*y*) transects the older one (*e*) showing the accessory canal (*arrowed*): **3a** – bottom view, **3b** – section (*cf.* RADWAŃSKI & *al.* 1975, figs 16-17*a*; RADWAŃSKI 1977, pl. 2*b*); natural size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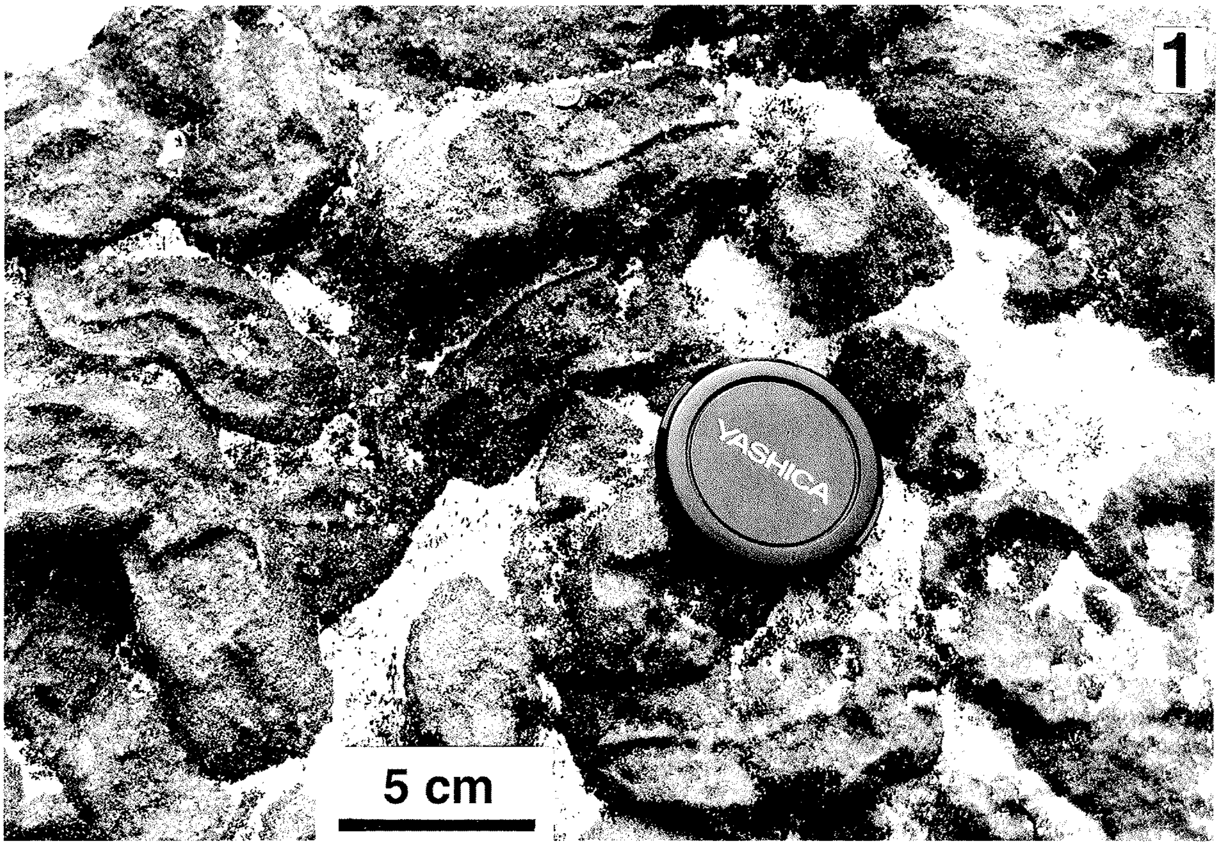
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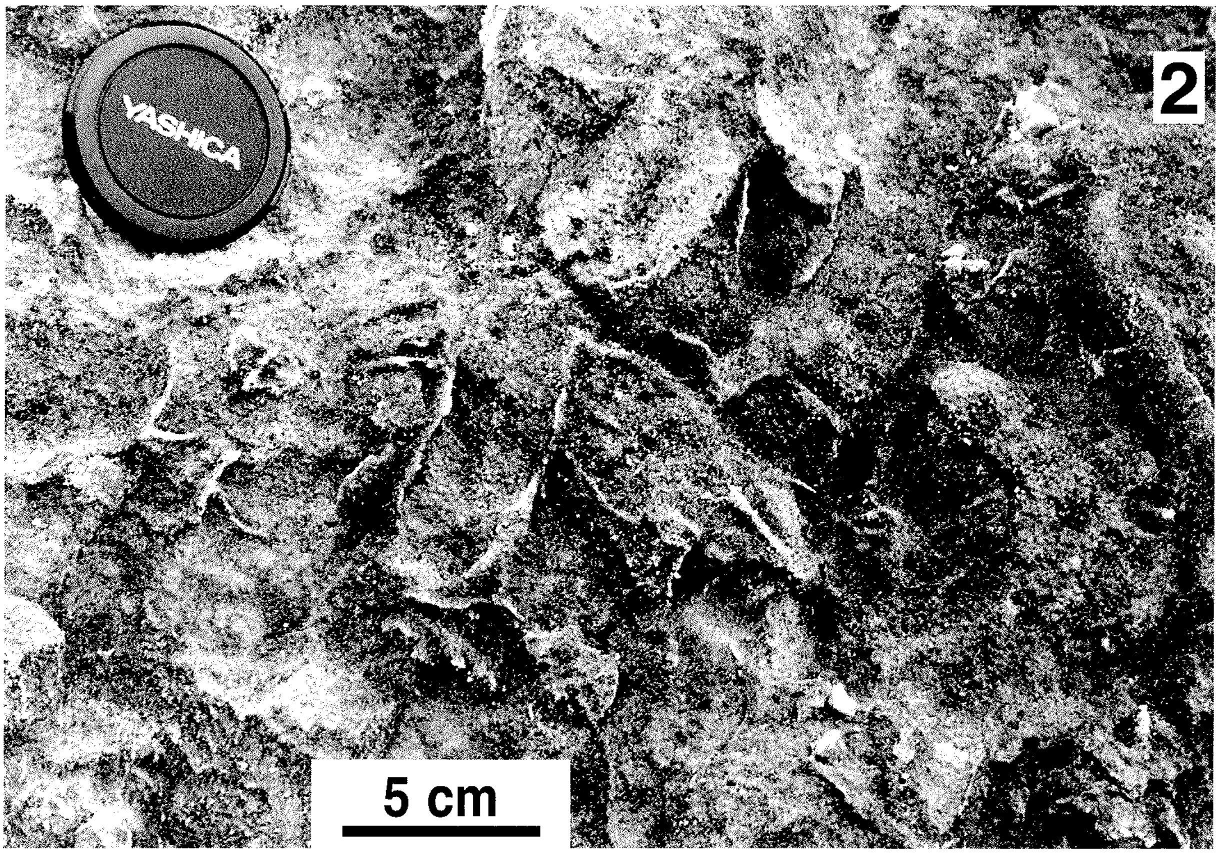
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downed specimens which attempted to escape from this hostile sandy deposit. A rapid escape may explain the limited secretion of mucus by frustrated animal. Consequently, these chambers might be regarded as escape rather than resting, feeding, or living chambers.

A peculiar feature of the burrows studied, particularly of those showing a swollen chamber, is an indistinct, narrow vertical canal continuing from the floor of the burrow to its top (best visible in Pl. 7, Fig. 2b and in the elder specimen in Pl. 7, Fig. 3b). Such a feature has not been reported previously, although it is clearly recognisable in some burrows from the Miocene of Denmark (*see* Radwański & *al.* 1975, fig. 16 – upper figure; less pronounced in figs 16 – lower figure and 17b). This peculiar, accessory canal is assumed to have been formed by an excess of water pumped away by the animal while the sanitary canal had not yet been constructed.

The frequency of burrows within the section studied ranges from solitary ones to mass aggregations in some sandy layers, or horizons (*see* Pl. 8). In some layers the burrows are confined to certain horizons, and oriented more or less horizontally (Pl. 8, Fig. 1); this is interpreted to result from burrowing below a nutrient-rich sand. In other layers the superposed burrows, oriented at various angles, form a dense maze (= total bioturbation of the layer; Pl. 8, Fig. 2); this may be interpreted as a result of either the occurrence of numerous specimens, and/or populations, in sediment enormously rich in food particles at the surface, or long-term burrowing at times of a slow sedimentation rate when the echinoids penetrated at the depth stabily distant to the sediment/water interface.

In massively burrowed horizons, instances of transecting of burrows are locally present (*see* Pl. 7, Fig. 3a-3b). However, they are not as magnificent as examples from the Miocene of Denmark where stacks of four to six burrows may be found (*see* Radwański & *al.* 1975, figs 16 – lower figure and 17a; Radwański 1977, pl. 2b).

PROBLEMS OF TAXONOMY OF *Echinocardium* BURROWS

It was Helmuth Zapfe who in one of his early papers (Zapfe 1935) attributed some burrows from Eocene deposits near Cluj (Klausenburg) in Romania, to the activity of *Echinocardium*. His reference to the resting chamber of *E. cordatum*, illustrated by v.Uexküll (1907), was indeed impressive at a time when little was known of extant producers of burrows. Although Mortensen (1951, p. 152) accepted this attribution, despite the fact that this sequence is older than known range (*see* Mortensen 1951, p. 157; Fischer 1966) of the genus *Echinocardium*, a schematic figure and photographs given by Zapfe (1935, figs 2-4) clearly represent decapod (callianassid) burrows, best comparable to those of *Callianassa biformis* Biffar in the Georgia offshore (U.S.A.), as illustrated by Hertweck (1972, fig. 7; *cf. also* a comment by Reineck 1968, p. 313).

The true *Echinocardium* burrows have long remained unnamed, and been treated as a modern type of trace (Radwański 1977; *see also* Rindsberg 1990). However, since the early 1970s, when due attention was paid to Osgood (1970, p. 295) observation that "*a form must be named if it is not to be 'lost' in literature*", a few authors attempted to use/adopt older formal/informal names for echinoid burrows.

One of such names was *Scolicia*, introduced by de Quatrefages (1849) to name long traces (most probably, on the top surface of layers) from the Upper Cretaceous and/or Lower Palaeocene of the Pyrenees, and considered to be a fossil annelid. However, de Quatrefages did not give any illustration in his brief report, and thus his taxon should be regarded a *nomen nudum* [Even, if we accord its acceptation, upon a study of the topotype material, by Smith & Crimes (1983)]. A comprehensive review of papers discussing *Scolicia* was presented by Häntzschel (1975, pp. *W*106–*W*107), who pointed out considerable differences in its particular groups, none of which has features in common with echinoid burrows. Although the name *Scolicia* was still used by Ward & Lewis (1975), Smith & Crimes (1983; *see also* Ziegler 1998, fig. 625) and Plaziat & Mahmoudi (1988) to classify some forms of echinoid (spatangoid) burrow, it should be borne in mind that in all older literature *Scolicia* was invariably illustrated and/or regarded (*see* Seilacher 1955, pp. 373-376; Häntzschel 1975, pp. *W*106-*W*107) as crawling traces on the upper surface of layers, and reported mostly from deeper-sea, even

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Burrows produced by *Echinocardium leopolitanum* sp.nov.

1 – Bottom view of a sandstone layer, to show the ventral parts of burrows (slightly weathered to expose well the sanitary canals) lithified more firmly than the adjacent sandstone; the burrows are situated in a single plane, suggesting the burrowing activity of echinoids along one horizon just beneath the layer to which the burrows stick

2 – Top view of a sandstone layer, to show the burrows whose lower parts were lithified more firmly than the upper (dorsal) ones, due to which the latter disintegrated and the sanitary canals are exposed; the ubiquitous burrows oriented at various angles to the sediment surface, and their maze produces a total bioturbation of the sandstone layer

bathyal, deposits (flysch in particular) in various countries and in strata of varying age, even Cambrian. In addition, such forms of *Scolicia*, as accepted by HÄNTZSCHEL (1975), who opted for their gastropod origin (as did FÜRSICH 1974), may easily have been produced by a suite of extant animals (*cf.* RADWAŃSKI 1977, p. 233). Apart from crawling traces (trails, furrows) left by the gastropod *Oliva*, best illustrated by FREY (1970, pl. 90, fig. 6), there are also echinoid traces, specifically the sand dollar *Mellita quinquiesperforata* (LESKE), as illustrated by BELL & FREY (1969, figs 3-9), both from U.S. shores, as well as those left by holothurians on sandy beaches in Mozambique, as illustrated by NESTLER (1985, figs 1-2).

Another one of such names is "*Muensteria* VON STERNBERG, 1833" which has long been regarded to be of doubtful validity when reported particularly from flysch deposits (*see* review by FÜRSICH 1974, HÄNTZSCHEL 1975), and at least once ascribed to the burrowing activity of echinoids by HEINBERG (1974), whose schematic drawings to illustrate specimens from the Upper Jurassic of Greenland (HEINBERG 1974, figs 1*B* and 9*C*) however are not convincing at all.

A wide array of various burrow constructions, and a plethora of names, discussed and illustrated by SMITH & CRIMES (1983; *see also* ZIEGLER 1998, fig. 625), followed by PLAZIAT & MAHMOUDI (1988), comprise numerous forms known primarily from flysch deposits, and ranging from the Palaeozoic (even Cambrian: apart from *Scolicia*, also *Monocraterion*). None of these can be ascribed directly and exclusively to the activity of echinoids, referred to as spatangoids, or the *Echinocardium* group by PLAZIAT & MAHMOUDI (1988).

In this context, not discussed is the report of COLELLA & D'ALESSANDRO (1988) on *Scolicia*, ascribed by them to the activity just of the species *Echinocardium cordatum* [sic!], while only fragmented tests of *Spatangus* were found. Moreover, neither lithology of the *Scolicia*-bearing deposits (Facies 'C' of COLELLA & D'ALESSANDRO) nor a poorly photographed trace allow to testify a bathyal depositional setting of that facies referred to by COLELLA & D'ALESSANDRO (1988).

Furthermore, none of the names adopted or introduced by SMITH & CRIMES (1983) and PLAZIAT & MAHMOUDI (1988) have ever been used for intrastratal burrows such as the ones produced by *Echinocardium*. Similarly, almost none of them (except for WARD & LEWIS 1975) have ever been applied to burrow infills (casts) such as the specimens (*see* Plate 8) collected from the section studied.

Apparently, neither ichnogenus nor ichnospecies is available for this type of burrow. In order to escape from a nomenclatorical chaos, a new ichnogenus should be erected to cover all fossil burrows of *Echinocardium*, typical of very shallow environments (intertidal to shallow offshores). Such a name should both reflect the producer, and the depth conditions under which it lived, to substitute lengthy descriptions and ichnotaxonomic debates. A good example of such a widely used name is the ichnogenus *Ophiomorpha* LUNDGREN, 1891, and its ichnospecies *O. nodosa* LUNDGREN, 1891, which covers both to producers (callianassid shrimps, as reviewed by WEIMER & HOYT 1964), and depth at which the burrow may have been constructed.

PALAEOENVIRONMENT AND PALAEOGEOGRAPHIC BACKGROUND

Environmental conditions under which *Echinocardium leopolitanum* sp.nov. lived, burrowed, and died, should first be studied in terms of bathymetry and hydrodynamics.

The section exposed at Gleboviti represents an upward-deepening sequence developed during the Middle Miocene (Badenian) transgression which encroached upon a coastal swamp (*see* Text-fig. 3; *and* WYSOCKA 2002).

In an actualistic (uniformitarian) approach, *E. leopolitanum* sp.nov. may be considered to have lived at depths similar to these of extant *E. cordatum* (PENNANT, 1777), *i.e.* a range of nil or merely a few, to about 20, possibly not more than 30 metres (*cf.* SCHÄFER 1962, BUCHANAN 1966, PEQUIGNAT 1970, ERNST & *al.* 1973, HOWARD & *al.* 1974, HIGGINS 1974, KANAZAWA 1992). Such depths were realised during the first stages of transgression which flooded the continental margins carpeted by the variably structured floral communities. At Gleboviti it was a swampland, in which the taxodiaceans of the Baldcypress type survived in their original growth position (*cf.* Pl. 1, Fig. 1). The coastal swamps inferred are well comparable to those of modern Georgia shores in the United States (*see* Text-fig. 8), to create a similar scenery once advocated for the neighbouring region of Krzemieniec by LILPOP (1929, p. 157; 1957, p. 170). The state of preservation of the taxodiacean stumps is unique along the northern shores of the Fore-Carpathian Depression; in Poland (*cf.* Text-fig. 1), only various abundant small-sized allochthonous plant detritus occurs quite commonly at the base of the marine Middle Miocene (Badenian) sequence on the slopes of the Holy Cross Mountains, both in the rocky shore-bordered Korytnica Basin (*see* RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977, HOFFMAN 1987) and along ancient sandy shores. In the latter regions, extended along the south-easterly and easterly slopes of the Holy Cross Mountains (localities Męczennice, Nawodzice,

A recent counterpart of the setting at Gleboviti prior to the Middle Miocene (Badenian) transgression (*cf.* Text-figs 3-4 and Pl. 1, Fig. 1): Present-day swampland along the Georgia coast (U.S.A.), showing gorgeous, venerably aged Baldcypress (*Taxodium distichum*) with huge, swollen trunks, and draped with an epiphytic bromeliacean, the Spanish Moss (*Tillandsia usneoides*)

Photo by Professor VICTOR A. ZULLO

Świniary – *see* Text-fig. 1), huge sandy bodies yield ubiquitous fossils (*see* RADWAŃSKI 1967, 1970, 1973; BAŁUK & RADWAŃSKI 1968; RADWAŃSKA 1992; NOSOWSKA 1997), whose communities and/or environmental conditions are compared, or commented upon below. In the Ukraine, however, the plant material commonly is very abundant so as to form lignite deposits, locally used commercially (*see* LILPOP 1924; and references *in* WYSOCKA 1999, 2002).

During a subsequent transgressive stage, deeper waters were established in the Geboviti area. The increased depths ranged above wind wave base, in the photic zone, to allow growth of the red algae *Lithothamnion*, and to produce rhodoliths with concentric growth lamellae indicative of permanent transport by waves and/or currents. At such depths, *E. leopolitanum* sp.nov. colonised the seafloor in dense herd-like populations (*cf.* NÉRAUDEAU 1991), not recorded previously for the genus *Echinocardium* GRAY, 1825, in the Neogene of Europe.

An estimation of basin depth at which *Echinocardium leopolitanum* sp.nov. have lived is concordant with that deduced from the presence of *Ophiomorpha* burrows, today produced by callianassid shrimps in intertidal and/or extremely shallow sublittoral settings (*see* data in WEIMER & HOYT 1964). Along the Holy Cross shores, the mass-occurrence of *Ophiomorpha nodosa* LUNDGREN is typical of a protected bay environment (locality Męczennice). Within this intertidal to shallow sublittoral sandy sequence (locality Nawodzice), the frequency of *Ophiomorpha* decreases rapidly towards the open sea (locality Świniary) with depths of 12 or more (but less than 20) metres (RADWAŃSKI 1967, 1970, 1973). The extremely rich fossil assemblage in the sandy sestion at Świniary compares well (*see* RADWAŃSKI 1970, 1973) with assemblages occurring at depths of 5 to 10 fathoms (less than 10 to some 20 metres) in the Gulf of Manaar, Ceylon (*see* HERDMAN 1906). At Świniary, to such depths a few storm-originated supplies of diverse eulittoral biota have been recognised (*see* RADWAŃSKI & WYSOCKA 2002).

Outside Europe, similar depths for a community yielding *Echinocardium* were estimated (15-20 metres), by KIER (1972) for the Upper Miocene Yorktown Formation of Virginia, U.S.A.

The same holds true for sedimentary sequences that have yielded no tests, but in which traces of *Echinocardium* are common.

The Lower Miocene Hagenør-Børup sequence (Vejle Fjord Formation) in Denmark, where *Echinocardium* burrows are common, has previously been interpreted as shallow subtidal with migrating sandbars, amidst which protected depressions were temporarily established, and all alternating with periods of high-energy conditions (RADWAŃSKI & *al.* 1975). A recent, comprehensive analysis of the entire Vejle Fjord Formation (FRIIS & *al.* 1998) offers a scenery of barriers migrating over back-barrier clayey deposits, and influenced by storm wash-over deposition in a coastal area of the Neogene North Sea basin.

In the present-day North Sea basin, comparable facies, locally rich in *Echinocardium* burrows, are known in coastal regions down to depths of about 12 but invariably less than 20 metres (*see* REINECK & *al.* 1968; REINECK & SINGH 1975, fig. 485; CHOWDHURI & REINECK 1978). The same figures are found in studies along the Tyrrhenian coast (*see* REINECK & SINGH 1971; *and* 1975, fig. 462).

To sum up, both coeval organic communities and sedimentary data allow the Gleboviti sequence to be interpreted as having developed at depths of about 10 metres, or a maximum of twenty metres. To such depths storms could easily penetrate, to become fatal for the majority of burrowing biota. Deposition of storm wash-over material, *i.e.* sand, and live or dead echinoids and associated sea-stars, progressed at these or slightly greater depths, in the form of either tempestites with non-selected tests, or tabular (diagonal) cross-bedded strata in which echinoid tests are size-selected and locally imbricated.

Environmental parameters, other than bathymetry and hydrodynamics, are assumed to have been identical with those of the Polish part of the Middle Miocene (Badenian) basin, *i.e.* normal salinity and climatic conditions typical of the tropical and/or subtropical zone with faunal communities predominantly influenced by the Indo-Pacific bioprovince (*see* BAŁUK & RADWAŃSKI 1977, 1991).

FINAL REMARKS

The Gleboviti section falls well within the category of **echinoid biofacies** defined by BOGGILD & ROSE (1985), as *"characterised by a distinctive echinoid assemblage, associated biota, and lithology"*. The echinoid assemblage studied, composed of a single species only, is extremely well preserved as far as particular specimens frozen in their death/burial state are concerned, associated with some calcite-shelled biota. Aragonite-shelled biota are considered to have been removed (dissolved) during diagenesis. The echinoid community is thus interpreted to have undergone **taphonomic loss** (*sensu* LAWRENCE 1968), or to have passed a **taphonomic filter** (*sensu* NEBELSICK 1995). Member *B* in the Gleboviti section which contains almost all specimens of *Echinocardium* *leopolitanum* sp.nov. studied, does represent a unique **"Fossillagerstätte"** (*sensu* SEILACHER & *al.* 1985), both of the echinoids themselves, and of any invertebrates as well.

Among echinoid biofacies in Miocene sequences in the Polish part of the Fore-Carpathian Depression, the one studied may best be compared to that exposed at Świniary (*see* Text-fig. 1). There abundant, spine-coated specimens of *Psammechinus dubius* (AGASSIZ, 1840) are born either scattered throughout the whole sequence, or in mass-aggregations at a few horizons. These layers, replete with complete specimens preserving spines and lanterns in place (*see* RADWAŃSKI 1973, pl. 7), and randomly oriented through 0.5 m thick layers, are herein interpreted as tempestites resulting from violent deposition by storms leading to rapid death of echinoids. Associated are uncommon other echinoids, mostly *Spatangus*, and a few naked tests of *Echinocardium*, the sea-star *Astropecten*, undescribed ophiuroids, rare *Ophiomorpha*, and lithothamnian rhodoliths (*see* RADWAŃSKI 1973, PRZYBYSZEWSKI 1975, MĄCZYŃSKA 1988).

Analogues of the echinoid biofacies studied occur also in the sublittoral sandy-lithothamnian sequence at Huta Lubycka (Roztocze Hills), quite close the Poland-Ukrainian border (*see* Text-fig. 1). This sequence is typified by common *Spatangus* associated with rare *Echinocardium*, as reported by JÓZEFKOWICZ (1976; *see also* MĄCZYŃSKA 1979, PHILIPPE 1998).

In the Ukrainian part of the Miocene sequence, both within the framework of the Fore-Carpathian Depression and of Podolya situated further east, outside the Depression, various sublittoral sands contain rare but diverse, more or less poorly preserved echinoids, as reviewed by SZÖRÉNYI (1953). Locally, associated to echinoids, and recorded by KUDRIN (1957), are complete skeletons of sea-stars *Astropecten forbesi* HELLER, 1858, the species evidently separate from *A. navodicensis* reported herein (*cf.* Text-fig. 5a; and HELLER 1858, KUDRIN 1957, NOSOWSKA 1997).

From the above it appears that the sublittoral sandy sequences of both the Fore-Carpathian Depression and of Podolya, developed at similar depths, favoured life of echinoderms (echinoids, sea-stars, ophiuroids), of which the echinoids were able to form dense populations (? herd mode of life; *cf.* NÉRAUDEAU 1991) and create an echinoid biofacies by mass aggregation due to hydrodynamic agents, and thus produce echinoid *Fossillagerstätten*. In the case of such thin-tested echinoids as *Echinocardium leopolitanum* sp.nov., decisive conditions under which such a *Fossillagerstätte* could form, included burial of live specimens by a catastrophic event and prevention from rapid decay and disintegration on the seafloor.

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