

# Badenian (Middle Miocene) echinoids and starfish from western Ukraine, and their biogeographic and stratigraphic significance

#### ANDRZEJ RADWAŃSKI, MARCIN GÓRKA AND ANNA WYSOCKA

Faculty of Geology, University of Warsaw, Al. Żwirki i Wigury 93, PL-02-089 Warszawa, Poland. E-mail: magurka@uw.edu.pl

#### ABSTRACT:

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Echinoderms from the Badenian (Middle Miocene) of the Fore-Carpathian Basin of western Ukraine are facies restricted. The Mykolaiv Beds, stratigraphically older, yielded the starfish *Astropecten forbesi* (complete skeletons), two genera of sand dollars (*Parascutella*, *Parmulechinus*), and numerous other echinoids of the genera *Psammechinus*, *Echinocyamus*, *Spatangus*, *Hemipatagus*, *Echinocardium*, *Clypeaster*, *Echinolampas*, and *Conolampas*. The stratigraphically younger, calcareous Ternopil Beds yielded *Eucidaris* (complete coronae, isolated spines), *Arbacina*, *Brissus*, and *Rhabdobrissus*. Sixteen species of echinoids are distinguished and/or commented. A new brissid, *Rhabdobrissus tarnopolensis* sp. nov., is established. A mass occurrence of some species (*Psammechinus dubius* and *Hemipatagus ocellatus*) contrasts with that of mass aggregations (sand dollars and *Echinocardium leopolitanum*) by dynamic events in selected layers of proximal tempestites. Of special note is the occurrence of very small specimens, interpreted as juveniles ('babies') having been swept out of their restricted biotopes ('nurseries'). Some species hitherto regarded as of Early Miocene age, and the problem of their persistence beyond the Fore-Carpathian Basin and/or migration into that basin during the Middle Miocene transgression are discussed.

Key words: Asteroids; Echinoids; Taxonomy; New species; Fossil behaviour; Ecotaphonomy; Middle Miocene (Badenian); Ukraine.

#### INTRODUCTION

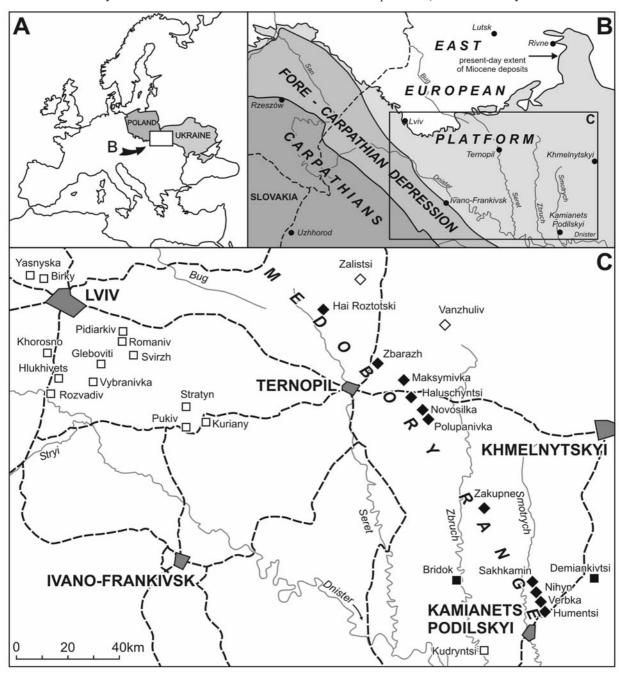
In the studies on the sedimentology and ecotaphonomy of the Badenian (Middle Miocene) of the Fore-Carpathian Basin of western Ukraine, echinoderms represent an important tool in facies and palaeoenvironmental analyses. Thanks to their calcitic skeletons starfish, echinoids, locally dominate over other biota that have been filtered out taphonomically due to their original aragonitic shells. Some echinoderms are important for gauging taxonomic diversity and morphological variability, even beyond the Central Paratethys in Europe.

Until the end of the first half of the twentieth century, small outcrops of the Middle Miocene (Badenian) in western Ukraine yielded just a few isolated echinoderm tests (see Hilber 1882; Łomnicki 1897, 1898). The echnoids collected then, housed now at the Ivan Franko University in Lviv, were taxonomically studied by Szörényi (1953) and the starfish by Kudrin (1957). Since the late 1950s, extensive commercial quarrying for building materials has enabled access to larger exposures of echinoid-bearing strata. An initial report by Radwański and Wysocka (2001) focused on the discovery of an *Echinocardium* species new to science, its burrowing behaviour and its mass occurrence. Further

researches are continuing and some of the results are given in the present report. The aim of the present report is not to revise Szörényi's monograph (1953), which was undetaken by Kroh (2005), but rather to complement her account with new taxa, and to point out their relationship to those comprehensively reviewed and taxonomically revised by Kroh (2005, 2007a, b) from the whole Paratethyan Realm.

#### THE FACIES SETTING AND THEIR AGE

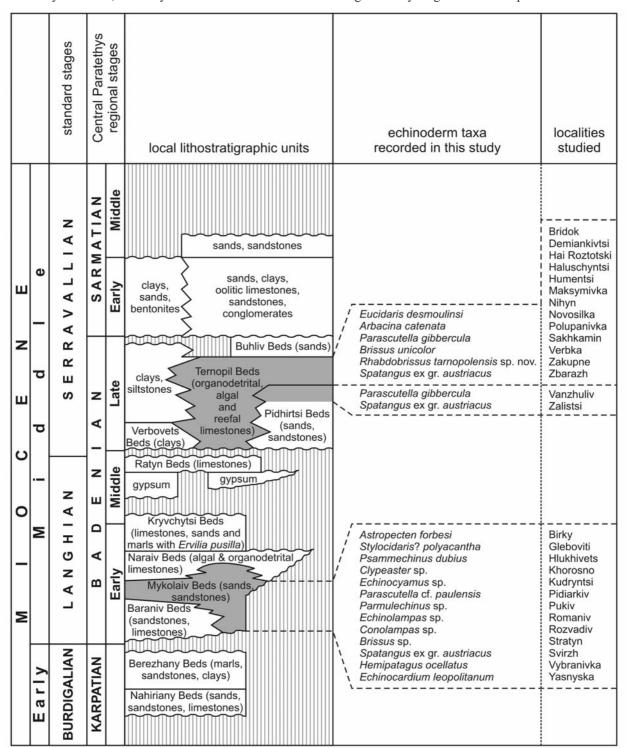
In the Middle Miocene (Badenian) of the Fore-Carpathian Basin of the Ukraine, two basic widely distributed echinoderm-bearing facies are recognised, referred formally (see Text-fig. 2) to the Mykolaiv Beds (= Mykolaiv Sands in Radwański *et al.* 2012a, b) and the Ternopil Beds (= The Medobory Biohermal Com-



Text-fig. 1. Location of the studied Middle Miocene (Badenian) echinoderm-bearing deposits in Ukraine:  $\mathbf{A}$  – Within Europe, at the Poland/Ukraine border;  $\mathbf{B}$  – Close-up, to show the extent of the Miocene basin upon the East-European Platform, and its relationship to the Fore-Carpathian Depression;  $\mathbf{C}$  – Topographic sketch of the Lviv-Ternopil region, to show exposures of the Mykolaiv Beds (*white quadrangles*), Ternopil Beds (biohermal - *black rhombs*, organodetrital – *black quadrangles*), and Pidhirtsi Beds (*white rhombs*)

plex of Radwański *et al.* 2011) respectively. The faunal content of the former, indicative of tropical/subtropical climatic conditions, allows them to be placed within the Middle Miocene Climatic Optimum and, thus, within the Early Badenian, evidently older than the Badenian

Salinity Crisis and the Middle Miocene Cooling (see Harzhauser *et al.* 2003; Böhme 2003; Peryt 2006; Kroh 2007b; de Leeuw *et al.* 2010; Zágoršek *et al.* 2012; Wysocka *et al.* 2012; Wiedl *et al.* 2013). The latter unit is regarded as younger than the evaporitic horizon and



Text-fig. 2. Position of the studied Middle Miocene (Badenian) echinoderm-bearing deposits in Ukraine within the regional (as used traditionally) and standard zonations schemes (compiled from: Andreyeva-Grigorovich et al. 1997, Kroh 2005, Górka et al. 2012)

is dated as Late Badenian (e.g. Andreyeva-Grigorovich et al. 1997; Śliwiński et al. 2012).

#### Mykolaiv Beds

This facies type, which consists mainly of quartz material, is confined to the most westerly regions of the Ukraine, even crossing the border with Poland (Wysocka 1999, 2002; Radwański and Wysocka 2001; Wysocka et al. 2012). It continues towards the south to Khorosno and Stratyn (Radwański et al. 2012a,b), as far as the Dnister River valley, via localities such as Potelich (see Łomnicki 1897; Szörényi 1953) and Yasnyska (the present paper), the city of Lviv and beyond (e.g. at Gleboviti; Radwański and Wysocka 2001). This is the region that has previously been referred to in the literature as the Opole Minor (see Pazdro 1953). Within this area, the Mykolaiv Beds reach a thickness of up to 100 m, but they may also pinch out completely (Teisseyre 1938; Pazdro 1953; Wysocka et al. 2012).

### **Ternopil Beds**

This Ternopil Beds represent a complex of interfingering and/or superposed, coral-poor biohermal facies of blue/green- or red-algal origin (Radwański et al. 2006, 2011; Górka et al. 2012). It has formerly been considered a coral reef or a coral-reef barrier (Dembińska-Różkowska 1932; Pisera 1996). This facies extends in the form of massive limestones of the elevated Medobory Range situated east of the Mykolaiv Beds, running from northwest to southeast, as far as Moldova (see Janakevich 1977; Pisera 1996; Jasionowski et al. 2005, 2006; Radwański et al. 2011). Its thickness is estimated at 40 to 60 m. The facies was formerly well exposed in huge quarries at Zbarazh (Szörényi 1953), Maksymivka (Radwański et al. 2006; Wiedl et al. 2013, locality 30 in fig. 8), Nihyn (Radwański et al. 2011) and elsewhere (Górka et al. 2012).

Besides the biohermal bodies, the Ternopil Beds also contain organodetrital facies, composed mainly of redalgal detritus with an admixture of detrital quartz. These organodetrital deposits form two wide belts parallel to the Medobory Range.

#### Pidhirtsi Beds

Northeast of the Medobory Range the organodetrital facies of the Ternopil Beds is underlain by quartz sands of the Pidhirtsi Beds. Rare echinoids were found within the uppermost part of this unit.

#### SEDIMENTARY AND TAPHONOMIC CONDITIONS

The material studied represents a wide range of preservational states, reflecting skeletal susceptibility and dynamic conditions prevailing in places where echinoderms were buried, or swept out by waves and currents. All the echinoderm skeletons are more or less heavily armoured with sand grains or bioclasts as a result of diagenetic pressure-solution (see Radwański and Wysocka 2004).

The quiet water conditions are reflected by complete or nearly complete skeletons, while more turbulent waters led to skeleton fragmentation to a variable extent. In several sections, or at particular stratigraphic levels, only the most resistant skeletal elements are preserved (e.g., cidaroid spines, spatangid and loveniid plastronal plates). In some cases, thanks to specific features of their test architecture, the echinoid taxa can be recognised based even on small fragments (e.g., *Clypeaster*, *Hemipatagus*). All such elements constitute useful tools for the documentation of both echinoderm habitats and entombment. This approach to extinct material is based on thorough neontological (actuopalaeontological) studies by Nebelsick (1992).

The analyses performed allow successions of both habitats and dynamic events during deposition of Miocene sedimentary sequence to be interpreted, and distinction to be made between autochthonous and allochthonous assemblages (or parautochthonous, see Schneider *et al.* 2009). An alternation of autochthonous (buried *in situ*, often in life position) and allochthonous (redeposited) assemblages throughout the Miocene sequence has been envisaged by Radwański (1970, p. 378 and fig. 3) for the famous starfish-bearing sands at Nawodzice (southern slopes of the Holy Cross Mountains, Central Poland). These were interpreted as storm-generated tempestites which blanketed coeval quiet, sub- to intertidal habitats (see Radwański 1970, fig. 2).

In the Mykolaiv Beds there are localities with both autochthonous and allochthonous assemblages interfingering (e.g., Gleboviti; see Radwański and Wysocka 2001), and those which are all evidently allochthonous (e.g., Khorosno), thus indicative of depths greater than the shallow sub- to intertidal zone.

A more complex picture is furnished by the Ternopil Beds, in which buildups were heavily bioturbated by peri- to intertidal alpheid shrimps, the burrows of which served either as taphonomic traps for biotic hash and/or as refugia and cryptic habitats for live animals (see Radwański *et al.* 2006). During passive infill of such burrows (and of other crevices), autochthonous and allochthonous assemblages have been eventually mixed.

Deposition of the Ternopil Beds was most probably discontinuous. In contrast, deposition within the Mykolaiv Beds was generally continuous and progressed rapidly, leaving no evidence of longer submarine breaks (disconformities, bioerosion, epibiontic overgrowths). A few brief episodes of local emersion (see Radwański *et al.* 2012a) are, however, documented.

Under such facies conditions, echinoderm preservation varies from (near-)exquisite (e.g. complete starfish, coronae of *Eucidaris*, tests of *Spatangus* and *Echinocardium* with spine canopies) to very poor (small test fragments of *Clypeaster*, *Echinolampas*, and *Conolampas*; isolated plastronal plates of *Spatangus* and *Echinocardium*), with intermediate states illustrated by crushed *Parascutella* and transport-selected *Hemipatagus*.

#### SYSTEMATIC ACCOUNT

The echinoid order- and family-level taxonomy, as applied herein, follows the *Treatise on Invertebrate Paleontology* (see Fell and Pawson 1966, Durham 1966b, Fischer 1966). At this level it is well compatible with the new, cladistic classification of Kroh and Smith (2010).

# Repositories

The echinoderm material treated herein is housed in the Museum of the Faculty of Geology of the University of Warsaw (MWGUW). Two specimens are from the collections of the Polish Academy of Sciences Museum of the Earth in Warsaw (MZ8). A few specimens kept in the collections in Lviv and Vienna, are indicated in the respective figure caption.

Class Asteroidea de Blainville, 1830 Order Paxillosida Perrier, 1884 Family Astropectinidae Gray, 1840 Genus Astropecten Gray, 1840 Astropecten forbesi Heller, 1858 (Text-figs 3–4)

1858. Astropecten Forbesi n.sp.; C. Heller, p. 158, pl. 1, figs 1–3. 1892. A. Forbesi (Hell.); F. Sacco, p. 745. ?1927. Astropecten sp.; J. Rakusz, p. 194, pl. 1, fig. 3.

1957. Astropecten forbesi Heller; L.N. Kudrin, pl. 3, figs 1–2. 2001. Astropecten navodicensis Nosowska, 1997; A. Radwański and A. Wysocka, p. 301, figs 4 and 5a.

2004. *Astropecten forbesi* Heller, 1858; A. Radwański and A. Wysocka, p. 387, pl. 7, figs 2–3.

MATERIAL: Khorosno: 1 fragment (MWGUW ZI/55/084); Gleboviti: 3 incomplete specimens and 6 fragments (MWGUW ZI/55/139–143); Yasnyska: one complete specimen (housed in the Town Museum of Natural History, Lviv); all specimens from the Mykolaiv Beds

REMARKS: The discussed specimens correspond well to the holotype of Heller\* (1858, pl. 1, fig. 1; actual photo of the holotype: Text-fig. 3.3).

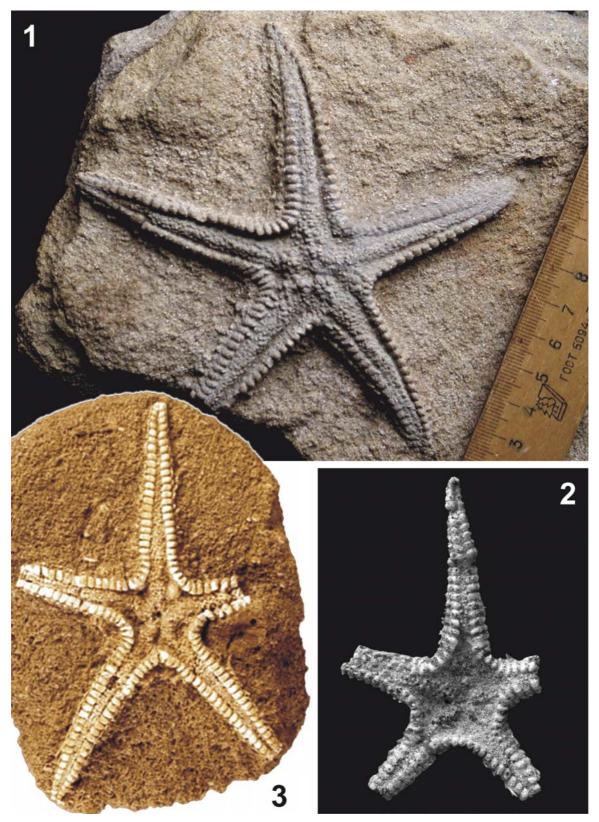
In the Lower Badenian of Ukraine the species was first noted by Łomnicki (1898, pp. 16 and 152); subsequent records are those of Kudrin (1957, p. 285, pl. 3, figs 1–2) and Radwański and Wysocka (2001, p. 312; and 2004, p. 387).

The former species assignation of the material (Radwański and Wysocka 2001, p. 301 and figs 4 and 5a) as *Astropecten navodicensis* Nosowska, 1997, is herein corrected, because the studied specimens are indistinguishable from, or identical with, those of *Astropecten forbesi* Heller, 1858. A further discussion on the status of *Astropecten navodicensis* Nosowska, 1997, as a separate species, or merely an ecophenotype of *A. forbesi* [dwarfish due to environmental (intertidal) influences (? higher/lower salinity,? overwarming,? early mortality], is deferred to another occasion.

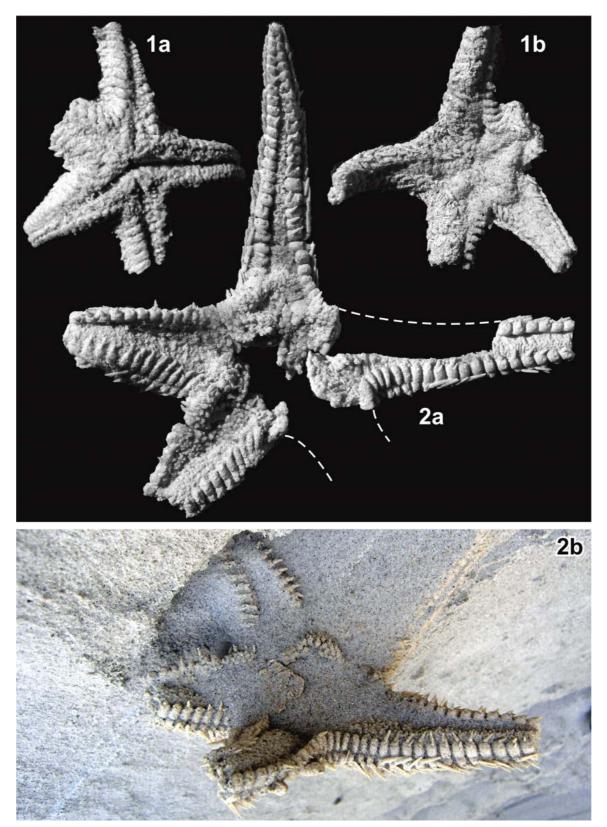
The newly collected material comprises four specimens, all from the Mykolaiv Beds. One individual, from Yasnyska (see Text-fig. 3.1), was collected by Professor D. Drygant (Lviv) from a sequence of loose sand with lenticular calcareous cementations; the asteroid is stretched out on one such cementation. In certain portions of this generally barren sand, the sole co-occurring biota are rare specimens of *Echinocardium leopolitanum* Radwański and Wysocka, 2001; their burrows, however, are ubiquitous.

The three other, incomplete specimens originate from the more diversified sandy sequence at Gleboviti, which is characterised by a mass occurrence, both of tests and burrows, of *E. leopolitanum*. They were collected from a current-aligned set (see Radwański and Wysocka 2001, fig. 4), whereas well-preserved, intact specimens (see Text-figs 3.2, 4.1a, b and 4.2a) are confined to a storm-generated sand bar (Member C of Radwański and Wysocka 2001, fig. 3). Such cases (compare Text-fig. 4.2b) document burial by storm agitation and

<sup>\*</sup> To note, Camill Heller (1823–1917), Doctor of Medicine and Surgery, published his sole palaeontological paper, Über neue fossile Stelleriden, in 1858, when he was the Professor of Zoology at the Jagiellonian University in Cracow (1858–1863) [changed afterwards to same position in Innsbruck (1863–1894); for his curriculum vitae, see Zapfe (1971, p. 47)].



Text-fig. 3. Astropecten forbesi Heller, 1858; all in dorsal view, natural size: 1 – Specimen from Yasnyska, in life position on a cemented sand lense (Town Museum of Natural History, Lviv; courtesy of Professor D. Drygant); 2 – Specimen (No. MWGUW ZI/55/139) from loose sands at Gleboviti; 3 – Holotype, originally illustrated by Heller (1858, pl. 1, fig. 1); photo courtesy of Dr. Andreas Kroh



Text-fig. 4. Other specimens of *Astropecten forbesi* Heller, 1858, from the Mykolaiv Beds at Gleboviti: **1a-1b** – Smaller specimen (No. MWGUW ZI/55/140), in ventral (1a) and dorsal (1b) views, × 0.9; **2a** – Larger specimen (No. MWGUW ZI/55/141), in dorsal view, to show well-preserved paxillae and marginal spines, × 0.9; **2b** – Field photograph of this specimen, when appearing in sands at Gleboviti in September 2009

deposition. In current-bedded strata at Khorosno, fragmentary skeletons attain considerable sizes, with estimated arm lengths of c. 17 cm.

The four specimens presented here are almost fully articulated, a state which is rather exceptional for asteroids in the Central Paratethys (see Vadász 1915; Rakusz 1927; Kroh 2007b, table 2). They are assumed to have been buried rapidly, either still alive, or shortly after death (compare Radwański 1970, p. 378, fig. 3.j; see also Blake and Zinsmeister 1988; Jagt and Codrea 2010).

In the Polish part of the Fore-Carpathian Basin, this species is restricted to mass aggregations of Psammechinus dubius at Świniary (see Radwański and Wysocka 2004, p. 387, pl. 7, figs 2, 3). The question is whether this starfish was a synecological associate, a food competitor or predator, or merely strayed into such echinoid aggregations. Predation on echinoids cannot be excluded. As recorded by Christensen (1970), in extant Astropecten irregularis (Pennant, 1777), a subordinate percentage of stomach contents consists of, in addition to ophiuroids, Echinocardium cordatum (Pennant, 1777). Even specimens of 1 to 2 cm in test length are easily swallowed and digested (see Christensen 1970, fig. 2 and pp. 25, 26 and 30, 31). Tests ejected are completely bare (see Christensen 1970, p. 96). It may thus be assumed that the genus Astropecten has retained its autecological and synecological fixation as prime predator of echinoids and their young since at least the Middle Miocene.

OCCURRENCE: Astropecten forbesi is widely distributed throughout the Middle Miocene (Badenian) sandy facies of the Ukraine, having been recorded from Potelich (Łomnicki 1898), Sukhodoly (Kudrin 1957), Yasnyska, Gleboviti, and Khorosno (the present paper), i.e., from localities that are far apart. Such a pattern of distribution differs from that of echinoids which are confined to merely a few levels within the sandy facies, or to restricted, sand-free calcareous settings (see below). Nevertheless, of note is the occurrence of A. forbesi in Echinocardium-bearing strata in the Ukraine. In the Polish part of the Fore-Carpathian Basin, this species is known from Świniary.

Class Echinoidea Leske, 1778 Order Cidaroida Claus, 1880 Family Cidaridae Gray, 1825 Genus *Eucidaris* Pomel, 1883 REMARKS: The genus, typical of the biohermal Ternopil Beds, is widely represented both by coronae and isolated spines. The specific affiliation of the material, however, is less obvious; it may represent either of the two extinct species, *E. zeamays* (Sismonda, 1842) and *E. desmoulinsi* (Sismonda, 1842), or a closely related extant species, *E. tribuloides* (Lamarck, 1816). Both extinct species are established upon isolated spines, without any primary reference to the coronal fragments. A union of spines and coronae for *E. zeamays* was first proposed by Philippe (1998), soon followed by Kroh (2005), and the present authors (Radwański *et al.* 2006). A union for *E. desmoulinsi* has been proposed by Borghi (1999) who regarded that species as of exclusively Pliocene age.

# Eucidaris desmoulinsi (Sismonda, 1842) (Text-figs 5–6)

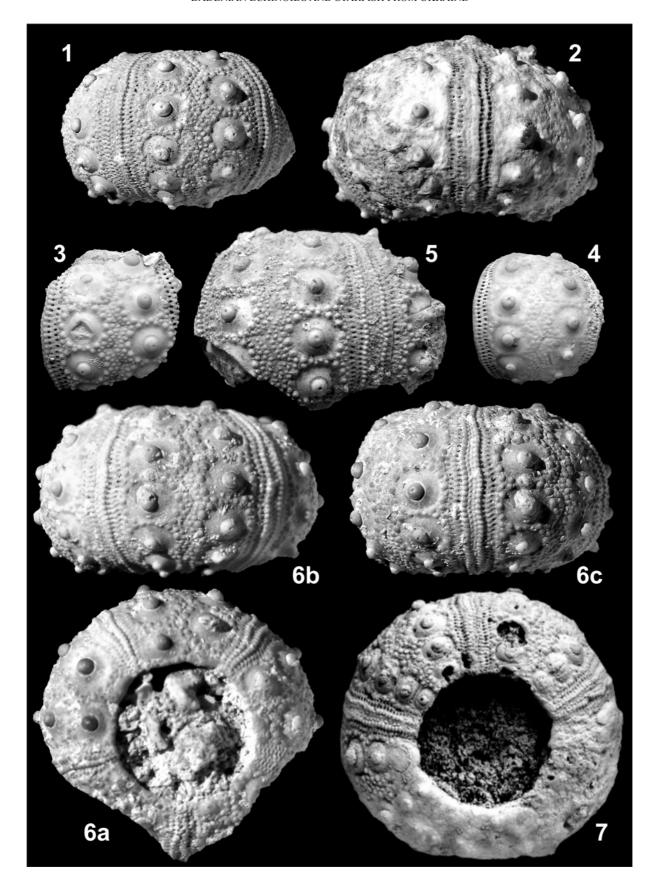
1999. *Eucidaris desmoulinsi* (Sismonda); E. Borghi, pp. 109–111, pl. 3, figs 1–9.

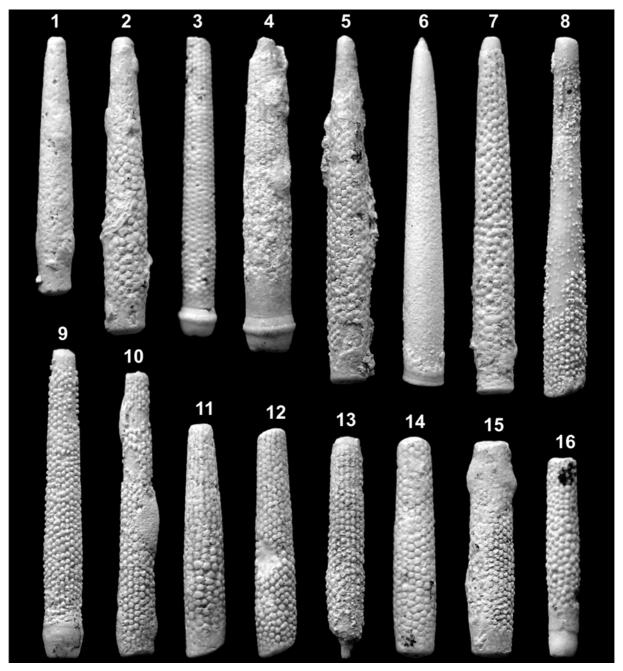
2006. *Eucidaris zeamays* (Sismonda, 1842); A. Radwański *et al.*, pp. 97, 98, pl. 4, figs 1, 2 and text-fig. 9.

MATERIAL: Hai Roztotski: 2 test fragments (MWGUW ZI/55/018-019), 18 spines and/or their fragments; Humentsi: 18 test fragments (MWGUW ZI/55/006-010, -013), over 110 spines and/or their fragments; Maksymivka: 13 test fragments (MWGUW ZI/55/011-012, -014-016), 23 spines and/or their fragments; Nihyn: 1 test fragment (MWGUW ZI/55/017); Novosilka: 1 corona (MWGUW ZI/55/020); Sakhkamin: 5 test fragments, 16 spines (MWGUW ZI/55/001-005, -114); Zbarazh: 1 almost complete corona, over 100 spines and/or their fragments (MWGUW ZI/55/021-022). All specimens are from the Ternopil Beds.

DESCRIPTION: Diameter of coronae usually exceeding 30 mm, 6–7 interambulacral plates per column, areoles largely taking interambulacral plate height with narrow ridge of scrobicular tubercles subambitally, separating the plates in the column. Interradial area relatively wide with dense cover of minute, wart-like tubercles. Spines elongated, of stick-like shaft, ornamented densely by fine granules in up to 16–18 longitudinal ridges.

Text-fig. 5. Fragmentary coronae of *Eucidaris desmoulinsi* (Sismonda, 1842) from various localities of the biohermal Ternopil Beds, all × 2.5. **1-4** – From Maksymivka: 1 – Specimen No. MWGUW ZI/55/014a, to show A and IA columns, 2 – Specimen No. MWGUW ZI/55/014b, to show A column, 3-4 – IA columns of smaller specimens (Nos MWGUW ZI/55/012a and 012b; Fig. 4 taken in proper position [the specimen was upside down in Radwański *et al.* (2006, pl. 4, fig. 1)]; **5** – Larger specimen (No. MWGUW ZI/55/004) from Sakhkamin, to show both IA and A columns; **6** – Larger specimen (No. MWGUW ZI/55/006) from Humentsi, in apical (6a), lateral of IA column (6b), and lateral of A column (6c) views; **7** – Larger, near-complete, but slightly corroded specimen (No. MWGUW ZI/55/021) from Zbarazh; oral view





Text-fig. 6. Primary spines of *Eucidaris desmoulinsi* (Sismonda, 1842) from the biohermal Ternopil Beds at Zbarazh (Specimen Box No. MWGUW Zl/55/022): longer forms interpreted as adapical (items 1–10) and shorter forms interpreted as subambital (items 11–16); all × 5

DISCUSSION: Poorly preserved specimens (two test segments and fragmentary spines) from Maksymivka were referred previously by Radwański *et al.* (2006) to *Eucidaris zeamays* (Sismonda, 1842). The newly collected material, which comprises almost complete coronae and numerous larger fragments (Text-fig. 5), allows its taxonomic revision.

The newly collected coronae differ from those classified as *E. zeamays* by Kroh (2005) in: (i) their larger

size (>30 mm instead of <20 mm) and more numerous interambulacral plates (6–7 rather than 4–6 per column); (ii) areoles largely occcupying the height of the interambulacral plate, leaving a narrow ridge of scrobicular tubercles subambitally to separate the plates in the column; and (iii) the relatively wide interradial area which has a dense cover of minute, wart-like miliary tubercles. These features are apparently displayed by the near-complete corona from Zbarazh (Text-fig. 5.7) and

by larger fragments from Sakhkamin (Text-fig. 5.5) and Humentsi (Text-fig. 5.6a–c), as well as smaller ones from Hai Roztotski, Novosilka, and Nihyn; they all are compatible with those of *E. desmoulinsi*, as presented by Borghi (1999, pl. 3, figs 1, 2). The latter specimens, illustrated by Borghi (1999) from the Italian Pliocene, have recently been commented on by Madeira *et al.* (2011, p. 247) as closely resembling *E. tribuloides*.

The occurrence of complete, or near-complete, coronae of *Eucidaris* in the Ternopil Beds is exceptional from a taphonomic point of view (see Greenstein 1991, p. 531; Hendler *et al.* 1995, p. 207; Madeira *et al.* 2011, p. 246). In the extant *Eucidaris tribuloides* (Lamarck, 1816), from the Caribbean and Atlantic, disarticulation of dead tests (i.e., spine-coated coronae) progresses rapidly (Greenstein 1991; Hendler *et al.* 1995). It may therefore be assumed that the coronae recorded in the Ternopil Beds represent specimens that were entombed rapidly in particular protected spots (taphonomic traps), primarily in alpheid burrows in which most of the specimens were found. None of them preserve spines, or are associated with such. All collected spines occur separately, usually in smaller burrows or bioherm crevices.

The isolated spines, most abundant at Zbarazh (see Text-fig. 6), clearly differ from those of E. zeamays (compare Sismonda 1842, p. 391; Kroh 2003, pl. 1, figs 1-9; and 2005, pl. 6, figs 1-21; Madeira et al. 2011, p. 247) in having an elongated, stick-like shaft, densely ornamented by generally finer granules in up to 16-18 longitudinal ridges, and in lacking any thorn-like burs, either isolated or arranged in the rings. Due to these features, they are compatible with those of E. desmoulinsi, first distinguished by Sismonda (1842, p. 391) and illustrated by Desor (1855, pl. 7, fig. 1). Such spines have usually been noted as being of Pliocene age (see also Agassiz and Desor 1847, p. 32; Airaghi 1901, pl. 1(19), figs 41-43; Borghi 1999, pl. 3, figs 3-9; Dermitzakis et al. 2009, fig. 6); only Vadász (1915, pl. 2(8), fig. 6) regarded them as being of Miocene age.

The collected spines of *E. desmoulinsi* can be subdivided into two groups, with intermediates present: longer and more slender ones (items 1–10 in Text-fig. 6) and shorter and stout ones (items 11–16 in Text-fig. 6). This difference could reflect their original test position, as in *E. tribuloides* (compare Schultz 2005, fig. 67); apical spines are longer and subambital ones shorter and stouter. Moreover, as apparent from other data (Hendler *et al.* 1995, p. 207), depending on biotope conditions, shorter and thicker spines could also reflect higher energy waters, while longer and slender spines (see e.g. Mortensen 1928, pl. 48, fig. 1) could indicate lower energy settings.

On the other hand, the studied subambital (adoral) spines (Text-fig. 6: items 11–16) do not differ from those classified recently as *Eucidaris tribuloides* (Lamarck, 1816), by Madeira *et al.* (2011, fig. 3A–C) from the Mio-Pliocene of the Azores.

Until new material is obtained, the three taxa (*E. zea-mays*, *E. desmoulinsi* and *E. tribuloides*) under discussion are regarded as separate, it not having been possible to determine whether the small-sized *zeamays* sensu Kroh (2005) may become the coeval *desmoulinsi*, sensu this report, when increasing in size.

In the present state of knowledge, the species *Eucidaris desmoulinsi* (Sismonda, 1842) is thought to be a Middle Miocene (Early Badenian) ancestor of the extant *E. tribuloides* (Lamarck, 1816) known since the Late Miocene (see Kroh 2005, p. 7; Madeira *et al.* 2011, p. 247).

The phylogeny and systematics of the species *Eucidaris zeamays* (Sismonda, 1842) are unclear. Its isolated plates are identical with those of *E. desmoulinsi* (see L. Agassiz and Desor 1847, Airaghi 1901, Borghi 1999). Although the coronal fragments ascribed to this species by Kroh (2005) are morphologically very close to those of *E. desmoulinsi*, their spines differ drastically (compare Text-fig. 6 and Kroh's pl. 6). Those shaped by thorn-like burs or their rings (see Kroh 2005, pl. 6, figs 1, 2) do not occur in the present-day *Eucidaris* species (see Mortensen 1928, Schultz 2005); otherwise, they tend to be identical with the adoral spines of the genus *Prionocidaris* A. Agassiz, 1863, and the species *P. verticillata* (Lamarck, 1816) in particular (see Ragaini 1997, pl. 1, fig. 2; Schultz 2005, fig. 88).

OCCURRENCE: *Eucidaris desmoulinsi* is common in the Ternopil Beds.

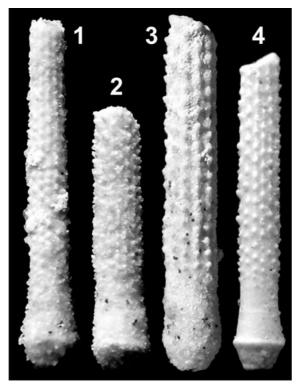
Genus Stylocidaris Mortensen, 1909 Stylocidaris? polyacantha (Reuss, 1860) (Text-fig. 7)

MATERIAL: Khorosno: 10 spines and/or their fragments (MWGUW ZI/55/053); Mykolaiv Beds.

DESCRIPTION: Spines with 12-16 well spaced ridges of distinct, saw-like appearance. Despite the poor state of preservation it may be stated that the rims of acetabula show also no traces of crenulation.

DISCUSSION: Several spines from Khorosno (Text-fig. 7) represent the only cidarid record from the Mykolaiv Beds. These are compatible with those recorded by Kroh (2005) as *Stylocidaris? polyacantha* (Reuss, 1860). As noted by Kroh (2005, pp. 2–4), who suggested

this cidarid be placed in the genus *Stylocidaris* Mortensen, 1909, this was so far confined to pelitic settings in Austria (Vienna Basin, Molasse Zone) and Moravia (Czech Republic). The spines (see Kroh 2005, pl. 1, figs 11–18; pl. 3, figs 3–16) are characterised by sparse longitudinal ridges bearing thorn-like granules flexed distally. Those collected at Khorosno (Text-fig. 7), armoured with sand grains and slightly corroded, display well-spaced ridges (12–16 in number; see Text-fig. 7.3), and a less distinct, saw-like appearance (best visible on the left-hand side in Text-fig. 7.2). However, they are here retained in this species for now, following Kroh (2005).



Text-fig. 7. Primary spines of Stylocidaris? polyacantha (Reuss, 1860) from the Mykolaiv Beds at Khorosno (Specimen Box No. MWGUW ZI/55/053); all  $\times$  5

OCCURRENCE: Stylocidaris polyacantha is present in the Early Badenian of the Central Paratethys (Vienna Basin, Transylvanian Basin, and Molasse Zone; see Kroh 2005). This is the first record of this species in the Early Badenian of the Fore-Carpathian Basin.

Order Temnopleuroida Mortensen, 1942 Family Temnopleuridae A. Agassiz, 1872 Genus *Arbacina* Pomel, 1869 *Arbacina catenata* (Desor *in* L. Agassiz and Desor, 1846) (Text-fig. 8) MATERIAL: Maksymivka: five, poorly preserved, denuded tests, all lacking apical system (MWGUW ZI/55/024) and four fragments (MWGUW ZI/55/023); Ternopil Beds.

DESCRIPTION: Test small, hemispherical, apical disc relatively small. Each ambulacral and interambulacral plate with a distinct primary tubercle; primary tubercles arranged in columns, smaller tubercles of variable size occur commonly.

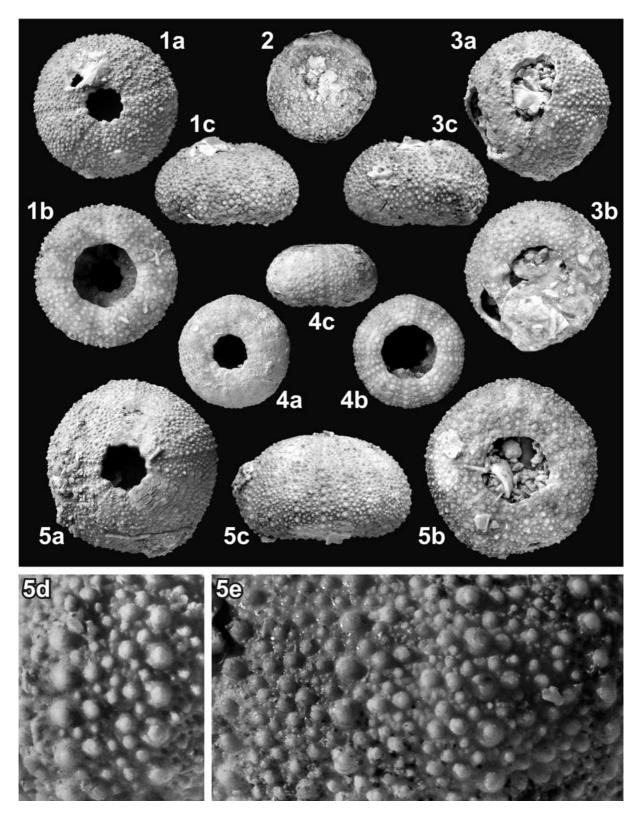
REMARKS: Although placement of these small hemispherical tests in Arbacina is beyond doubt, specific attribution is not clear. Amongst various species in the Rhône Basin (France) and elsewhere in the Mediterranean (see Philippe 1998, pp. 55-60), the form traditionally distinguished in Paratethys basins is A. catenata. However, Kroh (2005, pp. 21, 22) recently cast doubts on those records in view of the inadequate preservation. We here retain this name for convenience, and wish to emphasise its occurrence formerly unknown from the Miocene of the Ukraine. In comparison with A. catenata from the Rhône Basin, well illustrated by Philippe (1998, pl. 7, figs 1-8; pl. 8, figs 1-2), the present specimens (see Text-fig. 8.1-5) differ in having less pronounced primary tubercles; these are almost indistinguishable amidst the other tubercles.

Within the biohermal Ternopil Beds this is the third echinoid species, supplementing the cidaroids and the brissid spatangoids recorded previously (Radwański *et al.* 2006, p. 97; Górka *et al.* 2012, p. 171).

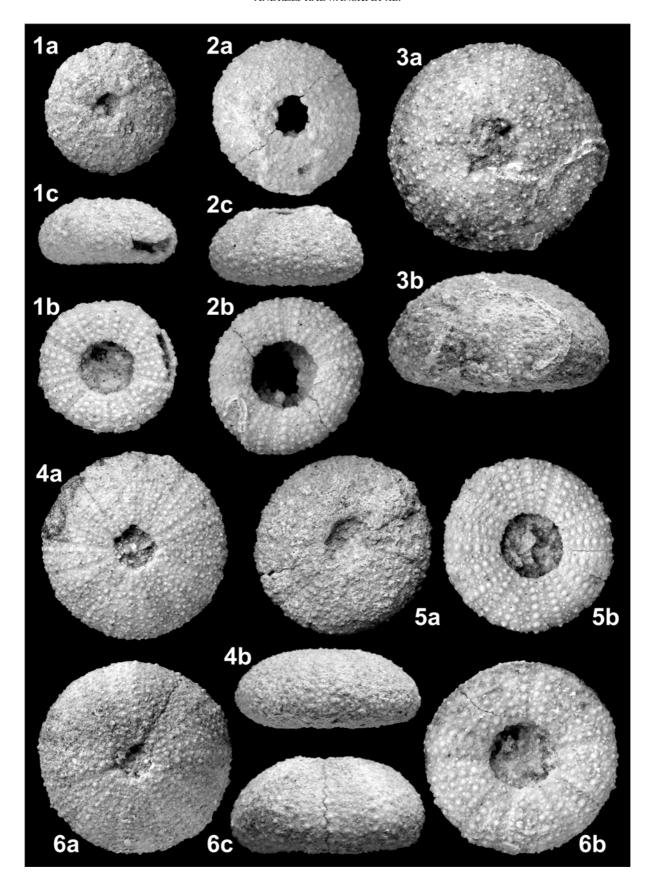
OCCURRENCE: *Arbacina catenata* in the Central Paratethys is known from the Eggenburgian throughout the ?Badenian (see Kroh 2005). Its occurrence in the Ukrainian part of the Fore-Carpathian Basin is restricted to the biohermal facies of the Ternopil Beds.

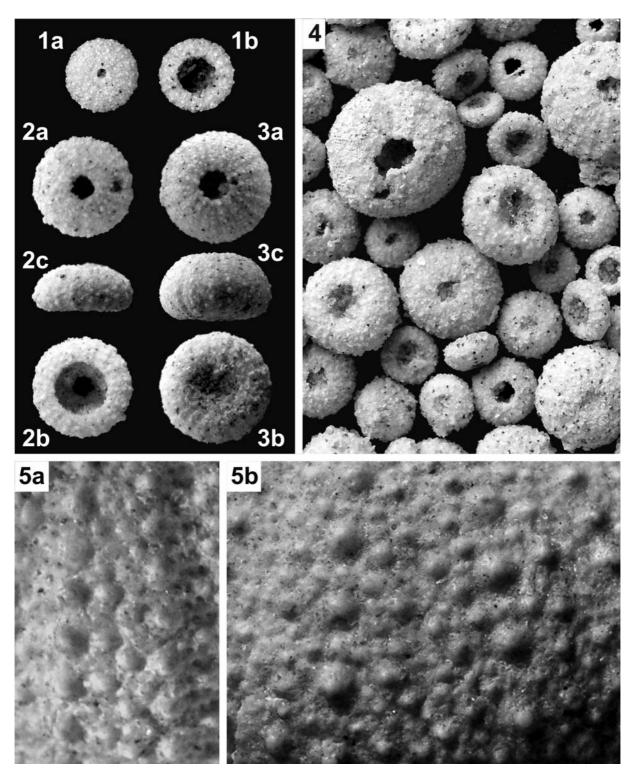
Order Echinoida Claus, 1876 Family Echinidae Gray, 1825 Genus *Psammechinus* L. Agassiz and Desor, 1846 *Psammechinus dubius* (L. Agassiz, 1840) (Text-figs 9–10)

MATERIAL: Hlukhivets: 6 tests and 2 fragments of juvenile specimens (MWGUW ZI/55/144); Khorosno: over 100 tests of medium sized and juvenile specimens and/or their fragments (MWGUW ZI/55/059, -061-065); Kudryntsi: one juvenile (MWGUW ZI/55/113); Pidiarkiv: one juvenile (MWGUW ZI/55/091); Romaniv: 14 tests and 2 fragments of juvenile specimens (MWGUW ZI/55/086); Stratyn: 6 tests and 2 frag-



Text-fig. 8. **1-5c** – Display of *Arbacina catenata* (Desor in L. Agassiz & Desor, 1846) from an inlier of shell grit in the biohermal Ternopil Beds at Maksymivka (Specimen Box No. MWGUW ZI/55/024), × 2; **5d-5e** – close-up view of the specimen figured in **5a-c** to show details of ambulacral (**a**) and interambulacral (**b**) zones, × 8





Text-fig. 10. 1-4—?Psammechinus dubius (L. Agassiz, 1840) from the Mykolaiv Beds at Khorosno: 1-3—Best-preserved specimens (Nos No. MWGUW ZI/55/065a-065c) in various views (a – Aboral, b – Oral, c – Lateral), × 3; 1a-1b – Smallest specimen (No. MWGUW ZI/55/065), the single one preserving the apical disc; 4 – Display of specimens (Specimen Box No. MWGUW ZI/55/063) collected from a single level (all armoured with sand grains by pressure-solution), × 3; 5 – Psammechinus dubius (L. Agassiz, 1840) from the Mykolaiv Beds at Swirzh, close-up view of the specimen No. MWGUW ZI/55/094d (4 in Text-fig. 9) to show details of ambulacral (a) and interambulacral (b) zones, × 10

Text-fig. 9. Psammechinus dubius (L. Agassiz, 1840) from the Mykolaiv Beds at Swirzh: 1-6 – Display of the best-preserved specimens (Specimen Box No. MWGUW ZI/55/094) in various views (a – Aboral, b – Oral or lateral, c – Lateral), all × 2

ments of juvenile specimens (MWGUW ZI/55/099); Svirzh: 53 tests, 3 test fragments (MWGUW ZI/55/092-098); all specimens are from the Mykolaiv Beds.

DESCRIPTION: Test circular in outline, small- to medium sized. One large tubercle to every ambulacral and interambulacral plate, smaller tubercles of variable size commonly present. Pore-pairs forming distinct vertical bands.

REMARKS: The true taxonomic status of *P. dubius* and its allies, which are treated either as subspecies or as distinct species and are widely distributed throughout Europe, albeit beyond the Paratethys basins (see Lambert 1910; Philippe 1998; Kroh 2005), remains unclear. The same concerns its assignment to *Psammechinus*, whose present-day representatives prefer deeper-water habitats (see Fell and Pawson 1966, p. *U*433). Consequently, Kroh (2005, p. 28) regarded placement in *P. dubius* to be tentative on account of the inadequate preservation of nearly all material from the Central Paratethys. We concur, although the name is retained here for now.

In the Polish part of the Fore-Carpathian Basin, this form is well known from the mass aggregations, with spines and lanterns preserved, in several tempestite levels of the Świniary Sands (Radwański and Wysocka 2004), with densities estimated at up to 3,000 specimens at some levels. In contrast to Polish occurrences, only a single specimen from the Early Badenian of Ukraine (from Mykolaiv; see Szörényi 1953, pp. 11 and 58; Kroh 2005, p. 28) was known to date. The newly collected material comprises several tens of specimens from the basal part of marly sands exposed at Swirzh. The denuded tests, which also lack the apical disc and lantern, are clearly allochthonous elements, having probably been current selected, because the majority are of larger size (17-25 mm test diameter; Text-figs 9, 10/5a, b), with smaller ones absent. The species is also ubiquitous (> 100 specimens) in the sandy sequence at Khorosno (see Text-fig. 10), where the smallest tests ('babies' of 3-4 mm across) dominate over those with diameters 10-12 mm (see Text-fig. 10.4); larger individuals have not been found. The state of preservation of these specimens does not allow for final determination, and consequently, they are left herein with a question mark. At both localities, many tests are either half filled with sediment, or remain empty (e.g., Text-fig. 10.2b).

OCCURRENCE: *Psammechinus dubius* is widely distributed throughout the Miocene of the Paratethys (see Kroh 2005). In the Ukrainian Fore-Carpathian

Basin it is commonly found in the Mykolaiv Beds. Its presence in the biohermal facies of Ternopil Beds is uncertain, due to the poor state of preservation of the specimens.

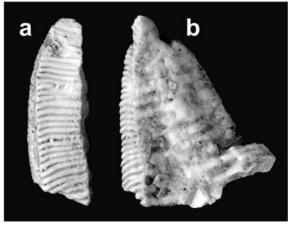
Order Clypeasteroida A. Agassiz, 1872 Suborder Clypeasterina A. Agassiz, 1872 Family Clypeasteridae L. Agassiz, 1835 Genus *Clypeaster* Lamarck, 1801 *Clypeaster* sp. (Text-fig. 11)

MATERIAL: Khorosno: single test fragment (MWGUW ZI/55/080), from the Mykolaiv Beds.

DESCRIPTION: Distinctive in the studied fragment (see Text-fig. 11) are test size and thickness (6 mm), as well as intraplate fracturing to expose the series of ambulacral pores; the curvature suggests this test portion to have come from the adaptical part of a petal.

REMARKS: Fragmentary tests of *Clypeaster* and their associates are useful in eco-taphonomic analysis, as recently demonstrated for present-day (Nebelsick 1992, 1995) and fossil assemblages (Gordon and Donovan 1992, Kroh and Nebelsick 2003).

The present report is the second record of the genus from the Middle Miocene of the Ukraine. The previous one is a single, complete test from Krekhiv [Polish: Krechów] near Lviv, referred to *Clypeaster partschi* Michelin, 1861 by Szörényi (1953, pp. 20, 68; pl. 2, fig. 3) and then to *C. campanulatus* (von Schlotheim, 1820) by Kroh (2005, p. 55). Subsequently, the record itself has been doubted (Kroh 2007b, p. 185).



Text-fig. 11. Distinctive fragment of large-sized *Clypeaster* sp. from the Mykolaiv Beds at Khorosno: **1a-1b** adaptical part of the petal (Specimen No. MWGUW ZI/55/080), to show the series of ambulacral pores in two views; × 2

Suborder Laganina Mortensen, 1948 Family Fibulariidae Gray, 1855 Genus *Echinocyamus* van Phelsum, 1774 *Echinocyamus* sp. (Text-fig. 12)

Compare:

? 2005. *Echinocyamus pusillus* (Müller, 1776); A. Kroh, p. 82 and fig. 34/3.

MATERIAL: Khorosno: 13 tests (MWGUW ZI/55/148); Romaniv: 34 tests, 1 fragment (MWGUW ZI/55/087-088); Rozvadiv: 1 test (MWGUW ZI/55/146); Stratyn: 1 test (MWGUW ZI/55/100); All specimens from the Mykolaiv Beds.

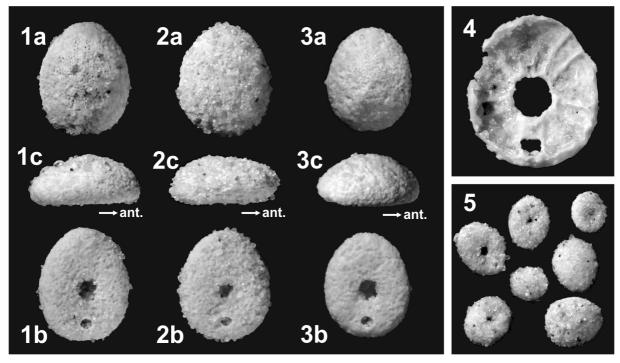
DESCRIPTION: Test small (up to 6 mm in legth), oval in outline. Surface details precluded from further studies due to heavy armour of sand grains. Internal radiating partition present, indicating attribution to the genus *Echinocyamus*.

REMARKS: These extremely small echinoids are left in open nomenclature, because their poor preservation (sand grain pitting) precludes recognition of morphological details. Such forms occur sporadically in the Mykolaiv Beds. This contrasts markedly with the Polish part of the Fore-Carpathian Basin, where hundreds of tests occur at some localities (e.g., Korytnica sands, *Leithakalk* at Pińczów). Formerly, in the Ukrainian part of the Basin very few specimens were noted under different species names (Szörényi 1953, p. 60 and pl. 5, fig. 6).

A comprehensive revision of the genus from the Paratethys was published by Kroh (2005, pp. 77–85), however, no definite taxonomic solution was offered. One specimen from Korytnica, studied by Kroh (2005, fig. 34.5), was referred to as 'Echinocyamus sp. B', characterised by the submarginal position of the periproct, thus differing from other taxa previously recorded from Poland and the Ukraine. The true nature of this form, recorded solely from Poland, remains unclear (Kroh 2005, p. 84). In this context, not discussed herein are several specimens from the Ukraine and Poland which have been left by Kroh (2005, pp. 79–80 and 84) in synonymyof either Echinocyamus pseudopusillus Cotteau, 1895, or Echinocyamus calariensis (Lambert, 1907).

The number of *Echinocyamus* species that have been noted for the Central Paratethys (see Kroh 2005, pp. 77–85) and beyond, is quite high. Of note is a report by Capeder (1906), who erected eleven new species from the Middle Miocene of Sardinia, with some of them regarded valid recently.

The best preserved specimens from Romaniv (Text-fig. 12.1–3) seem to be very close to the extant



Text-fig. 12. **1-4** – *Echinocyamus* sp. from the Mykolaiv Beds at Romaniv (Specimen Box No. MWGUW ZI/55/087); close to extant *E. pusillus* (O.F. Müller, 1776); 1a, 2a, 3a – Aboral, 1b, 2b, 3b – Oral, 1c, 2c, 3c – Right lateral views; all × 5; 4 – Oral inner view, to show the radial partitions (best visible at interambulacra 2 and at 5 where bordering the peristome), × 10; 5 – Specimens from the Mykolaiv Beds at Khorosno (Specimen Box No. MWGUW ZI/55/148), to show their dense armouring with sand grains by pressure-solution, all × 3

species *E. pusillus* (O.F. Müller, 1776), as reviewed by Kroh (2005, fig. 34.3). The presence of internal radiating partitions (Text-fig. 12.4) clearly indicates their attribution to the genus *Echinocyamus* rather than to *Fibularia* Lamarck, 1816, to which the Ukrainian material was referred by Szörényi (1953) (compare Kroh 2005, pp. 84–85). Tests from Khorosno (Text-fig. 12.5) have a heavy sand armouring and cannot be identified specifically.

OCCURRENCE: In the Ukrainian part of the Fore-Carpathian Basin, the genus *Echinocyamus* is present in the Mykolaiv Beds.

Suborder Scutellina Haeckel, 1896 Family Scutellidae Gray, 1825

REMARKS: Sand dollars, primarily representing this suborder (see Durham 1966b; Kroh 2005), are regarded as having had their acme during the Miocene, with wide distributions and mass occurrences in the Mediterranean and Paratethys basins (Nebelsick and Kroh 2002). The Fore-Carpathian Basin is characterised primarily by the genus *Parascutella* Durham, 1953, whereas the Mediterranean Basin is dominated by the genus *Scutella* Lamarck, 1816 (see Wright 1855; Durham 1966, p. *U*477). The latter genus, as well as all lunulate genera of other families (e.g., *Amphiope, Encope*) and some other thermophilic forms (see Kroh 2007b, pp. 185–195), did not reach the northern Paratethys.

Genus *Parascutella* Durham, 1953 *Parascutella* cf. *paulensis* (L. Agassiz, 1841) (Text-fig. 13)

MATERIAL: Khorosno: 15 test fragments (MWGUW ZI/55/083); Pukiv: 2 tests (MWGUW ZI/55/111); all specimens from the Mykolaiv Beds.

DESCRIPTION: Although the state of preservation of the material is poor, it shows well the typical features of the species: almost circular shape and a flat, cupolalike profile with an almost centrical high (Text-fig. 13). Other diagnostic features are generally less obvious due to the state of preservation. Thus, the investigated specimens are referred to as *Parascutella* cf. *paulensis* (for further details see section on *P. gibbercula*).

OCCURRENCE: Although Kroh (2005) states that the Central Paratethys occurrences (Molasse Zone and Vi-

enna Basin) of *Parascutella paulensis* are restricted to the Late Eggenburgian and Karpatian only, the records of Szörényi (1953) place the specimens from the Ukrainian part of the Fore-Carpathian Basin in the Early Badenian. This may correspond to the possible occurrence of this species in the ?Langhian of France (Philippe 1998, see also Kroh 2005). In Ukraine, this species is quite common in the Mykolaiv Beds.

Parascutella gibbercula (De Serres, 1829) (Text-fig. 14)

MATERIAL: Vanzhuliv: single test (MWGUW ZI/55/115); Zalistsi: single test (MWGUW ZI/55/116); both specimens from the Late Badenian of the Pidhirtsi Beds. Demiankivtsi: single test (MWGUW ZI/55/105) from the Ternopil Beds.

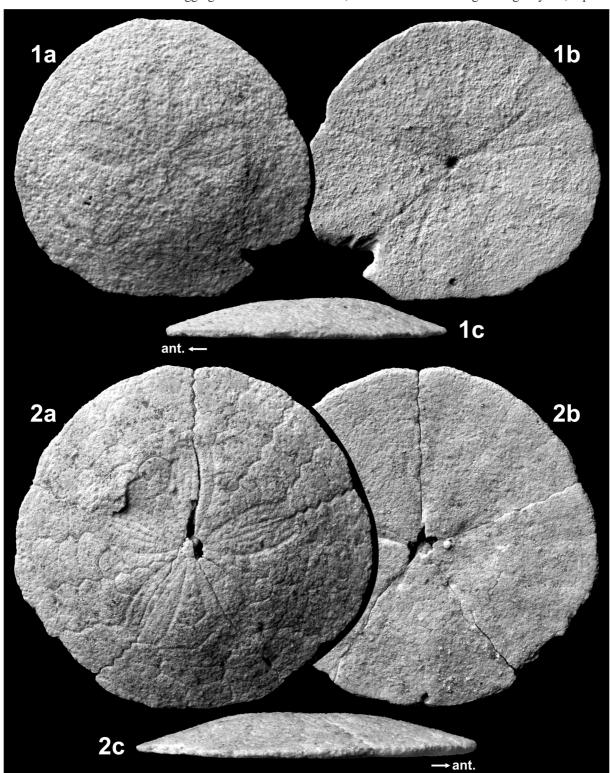
DESCRIPTION: The relatively poor state of preservation of the investigated specimens makes comparison with the type specimens difficult. However, Ukrainian specimens show at least two typical features for *P. gibbercula*: eccentric maximum height and the wedgeshaped profile with strong inflation in adaptical interambulacrum 5 (see Text-fig. 14; and discussion by Kroh 2005, p. 93) (further details and comparison with *P. paulensis* see 'Discussion' below).

DISCUSSION: Kroh (2005) noted that vindobonensis of Laube (1871) was a junior synonym of gibbercula, and that paulensis was not represented in the Middle Miocene of the Paratethys. In contrast to the Polish part of the Fore-Carpathian Basin, where the genus Parascutella is extremely rare (single report from Świniary – Radwański and Wysocka 2004, p. 387: Scutella sp.), it appears to be quite common in Ukraine. Szörényi (1953) distinguished four taxa (including vindobonensis and paulensis) from Kuriany and erected two new taxa from other localities. With one exception, all of these have recently been revised by Kroh (2005, pp. 86, 91), who placed them, definitively or tentatively, into the synonymy of Parascutella gibbercula (De Serres, 1829). Consequently, the latter species has revealed to be the dominant scutellid which lived in the Middle Miocene (Badenian) of Ukraine.

The scutellid material, studied herein, has revealed that the features regarded by Kroh (2005) as critical in distinguishing between *P. gibbercula* and *P. paulensis*, are more equivocal. Marginal indentations, the straight posterior margin with distinct anal notch, the posteriorly eccentric maximum height and the wedge-shaped profile with strong inflation in adaptical interambulacrum 5,

i.e. features that typify *gibbercula* (see Kroh 2005, p. 93), are rarely seen in numerous specimens, especially in smaller-sized tests from a mass aggregation at Pukiv.

The majority of specimens, especially those of larger size (up to 90 mm in length), are nearly circular in outline, with a near-smooth margin and gently flat, cupola-

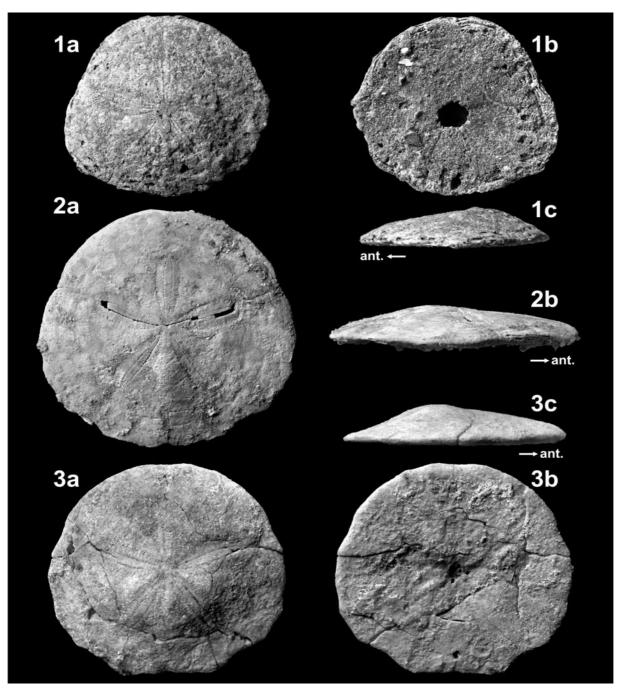


Text-fig. 13. Parascutella cf. paulensis (L. Agassiz, 1841), mass-occurring in the Mykolaiv Beds at Pukiv: 1 – Average-sized specimen (No. MWGUW ZI/55/111b: 1a – Aboral, 1b – Oral, 1c – Left lateral views); 2 – Largest specimen (No. MWGUW ZI/55/111a: 2a – Aboral, 2b – Oral, 2c – Right lateral views); both natural size

like profile (see Text-fig. 13), typical of *paulensis*, to which these mass-occurring specimens from Pukiv are herein ascribed.

The specimens of *P.* cf. *paulensis* from Pukiv are poorly preserved fragments of denuded tests from the 20 m thick calcareous sands succession. The scutellid fragments occur in thicker, up to 1 m, beds, forming resid-

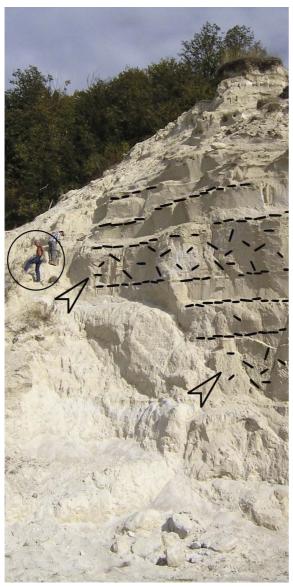
ual lags in their basal parts, or are scattared at random throughout the thickness, quite often oriented vertically in homogeneous layers, clearly of a storm origin. In such proximal tempestites (arrowed in Text-fig. 15), complete tests are missing. In both settings, scutellid tests and their fragments are evidently allochthonous, having been delivered either by bottom currents, or by storms,



Text-fig. 14. Parascutella gibbercula (De Serres, 1829), singly occurring in various localities: 1 – Poorly preserved specimen (No. MWGUW ZI/55/116) from Pidhirtsi Beds at Vanzhuliv (1a – Aboral, 1b – Oral, 1c – Left lateral views); 2 – Larger specimen (No. MWGUW ZI/55/115) from Pidhirtsi Beds at Zalistsi (2a – Aboral, 2b – Right lateral views); 3 – 'Humpbacked' specimen (No. MWGUW ZI/55/105) from organodetrital Ternopil Beds at Demiankivtsi (3a – Aboral, 3b – Oral, 3c – Right lateral views); all natural size

from more nearshore habitats where they could have lived in masses (compare Seilacher 1979, figs 24–26; Nebelsick and Kroh 2002, table 1; Kroh and Nebelsick 2003, fig. 8).

Sand dollar communities are accompanied by *Echinolampas*, whose sturdy fragments (see Text-fig. 17) appear in lags, and large spherical colonies of celleporid bryozoans. The latter, 5–8 cm in diameter, appear very close to forms recorded by Roemer (1870, p. 380 and pl. 41, fig. 7) as *Cellepora globularis* Bronn, 1837, from Upper Silesia in the Polish part of the Fore-Carpathian Basin.



Text-fig. 15. Field sketch, to illustrate mass accumulation of Sand Dollars in the Mykolaiv Beds at Pukiv (September 2009): *Parascutella* cf. *paulensis* (L. Agassiz, 1841), associated with single *Parmulechinus* sp., occurring either within the thicker, storm-generated proximal tempestites (*arrowed*), or as residual lags at bottom of the thinner, current-borne layers.

Mass occurrences of sand dollars, such as that at Pukiv, are unknown from other parts of the Paratethys, but were reported from Lower Miocene strata in Turkey and Egypt, and interpreted as proximal storm deposits (Nebelsick and Kroh 2002, figs 2–9; see also Kroh and Nebelsick 2003). Especially impressive is the Gebel Gharra section near Suez (northern Egypt), where *Echinolampas* and large celleporid bryozoans associated with the 'Cidaroid-Echinacea Assemblage' were interpreted to have occupied habitats just adjacent to those of the 'Parascutella Assemblage' (see Kroh and Nebelsick 2003, fig. 8). This is very helpful in understending the allochthonous assemblage at Pukiv.

Some of the specimens from localities with more coarse-grained deposits (e.g. at Vanzhuliv, Zalistsi and Demiankivtsi), exhibit features typical of *P. gibbercula*. Generally, these specimens are of smaller size (50–67 mm in length; see Text-fig. 14.1–3). It is unclear if such slightly different facies conditions could have caused the observed morphological, and consequently, taxonomic changes. Anyway, our data seem to cast some doubt on the stratigraphic distinction between *P. paulensis* (supposedly Early Miocene) and *P. gibbercula* (supposedly Middle Miocene) as suggested by Kroh (2005, 2007b, table 3; see also Mikuž 2009).

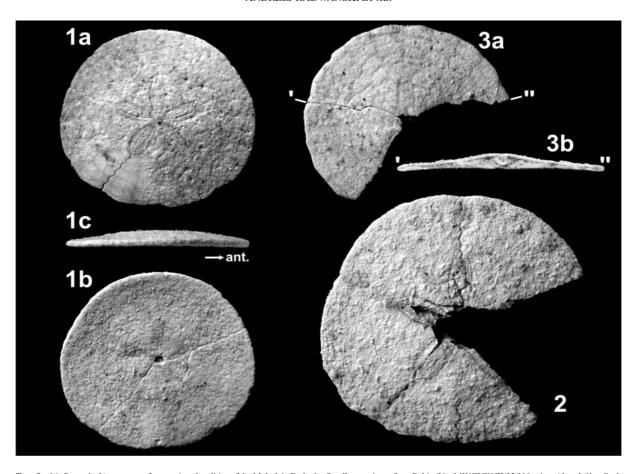
Finally, it seems that some species assignments by Szörényi (1953) are correct. This concerns the four specimens from Kuriany, which she (Szörényi 1953, pl. 1, figs 1–3 and pl. 2, fig. 2) referred to "Scutella paulensis Agassiz" and which correspond to the concept of that species as here understood. Similarly, her "Scutella vindobonensis Laube" from Zhukivtsi (Szörényi 1953, pl. 1, fig. 4, 4a, b), which in fact is an example of gibbercula, was the sole item unquestioned by Kroh (2005, p. 86).

OCCURRENCE: *Parascutella gibbercula* is widely distributed throughout the Early to Late Badenian deposits of the Central Paratethys. It has been recorded e.g. in the Vienna, Styrian, Pannonian and Transylvanian Basins (see Kroh 2005), also in the Ukrainian part of the Fore-Carpathian Basin (Szörényi 1953).

Genus *Parmulechinus* Lambert, 1905 *Parmulechinus* sp.

(Text-fig. 16)

MATERIAL: Khorosno: 1 incomplete test (MWGUW ZI/55/081); Pukiv: one complete (MWGUW ZI/55/110) and one incomplete (MWGUW ZI/55/112) test; all specimens are from the Mykolaiv Beds.



Text-fig. 16. Parmulechinus sp.nov. from various localities of the Mykolaiv Beds: 1 – Smaller specimen from Pukiv (No. MWGUW ZI/55/110a: 1a – Aboral, 1b – Oral, 1c – Right lateral views); 2 – Larger fragmentary specimen (No. MWGUW ZI/55/110b, in aboral view) from Pukiv; 3 – Fragmentary specimen (No. MWGUW ZI/55/081) from Khorosno (3a – Aboral view, 3b – Transverse section along the fissure indicated in Fig. 3a); all natural size

REMARKS: Amongst *Parascutella* from Pukiv, a single complete, medium-sized specimen (48 mm long, 52 mm wide) and another fragmentary one does not represent *P. paulensis* and represent supposedly a new species (see Text-fig. 16.1–2). The complete specimen (see Text-fig. 16.1a–c) is almost circular anteriorly, with very weak marginal indentations, but with a weakly advanced anal notch posteriorly; the profile is gently arched, without median elevations.

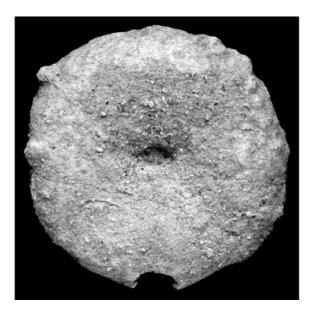
The genus *Parmulechinus*, known from the Oligocene to the Lower Miocene (see Durham 1966b; Phillippe 1998; Kroh 2005, 2007b, table 3), is still poorly known. Its single species, *P. hoebarthi*, known from the Paratethys, is recorded from the Early Eggenburgian (Early Burdigalian) Molasse Zone in Austria (see Kroh 2005, pp. 94–97). Our specimens differ from it, however, in a number of features. The ambital outline of the complete specimen from Pukiv is nearly regular, without the flexuose indentations anteriorly that characterise the Austrian specimens (see Kroh 2005, fig. 38). Also, its near-flat profile (see Text-fig. 16.1c; see also 15.3b) differs from the wedge shape of the Austrian specimens

(compare Kroh 2005, pl. 45, figs 1c, 2c). Additionally, our specimens differ in development of their anal notch, size of petalodium and shape of frontal petal (widely open in *P. hoebarthi* and almost closed in the Ukrainian material). Summarising, our specimens most probably represent a new species. Better material is needed, however, to enable its formal description.

OCCURRENCE: *Parmulechinus* sp. is known solely from the Mykolaiv Beds.

Order Cassiduloida Claus, 1880 Family Echinolampadidae Gray, 1851 Genus *Echinolampas* Gray, 1825 *Echinolampas* sp. (Text-fig. 17)

MATERIAL: Khorosno: 4 test fragments (MWGUW ZI/55/079); Pukiv: 2 test fragments (MWGUW ZI/55/109); all specimens from the Early Badenian of the Mykolaiv Beds.



Text-fig. 17. Largest fragment (oral side, × 0.9) of *Echinolampas* sp. (Specimen No. MWGUW ZI/55/109a) from a scutellid-bearing, current-borne layer of the Mykolaiv Beds at Pukiv (see Text-fig. 16)

REMARKS: The generic assignment of a few thick-walled fragments from a residual lag of scutellid remains (associated with large spherical colonies of the bry-ozoan *Cellepora*) is based on features displayed by the largest fragment, i.e., the oral test surface shown here in Text-fig. 17. However, neither its near-circular outline, size (75 mm across), nor its transversely widened peristome situated almost marginally suffice to identify it to the species level (compare Kroh 2005, pp. 103–125, pls 49–56).

OCCURRENCE: In the Ukrainian part of the Fore-Carpathian Basin *Echinolampas* is present in sandy deposits of the Mykolaiv Beds.

Genus *Conolampas* A. Agassiz, 1883 *Conolampas* sp. (Text-fig. 18)

MATERIAL: Khorosno: one fragmentary specimen (MWGUW ZI/55/082); Vybranivka: one almost complete test (MWGUW ZI/55/106); both specimens are from the Mykolaiv Beds.

DESCRIPTION: Test large, circular in outline, aboral side high, conical; oral side flat, gently depressed adorally. Top of the best preserved specimen situated excentrically. Peristome pentagonal, located centrally, periproct missing. Small tubercles dispersed regularly all over interabulacral zones.

REMARKS: MWGUW ZI/55/106, the better preserved specimen from Vybranivka, shows features typical of the genus *Conolampas* (see Text-fig. 18.1a–c). Unfortunately, the specimen is partly damaged (periproct missing) and deformed. Probably due to this deformation, the top of the test is situated very excentrically. These preclude determination of this specimen to the species level.

MWGUW ZI/55/082, the fragmentary specimen (see Text-fig. 18.2), has a test curvature at the ambitus of 50-55°, and a near-smooth external surface, which are distinctive generic features. It can be estimated that the entire test was relatively tall, conical, and comparable to *C. elegans* (Airaghi, 1900) known from the Vienna Basin (see Kroh 2005, pl. 58, figs 2, 4). According to Kroh (2005, pp. 126, 130, 133), this species is most probably represented in the Middle Miocene of the Ukraine, and namely by eight specimens from Pidiarkiv [Polish: Podjarków], interpreted by Szörényi (1953) as eight separate species, some of them new, and referred mostly to her newly erected genus, *Hypsoheteroclypus* Szörényi, 1953. Durham (1966, p. *U*508) synonymised *Hypsoheteroclypus* with *Echinolampas* Gray, 1825.

OCCURRENCE: In the Ukrainian part of the Fore-Carpathian Basin *Conolampas* is known from the Mykolaiv Beds.

Order Spatangoida Claus, 1876 Family Brissidae Gray, 1855 Genus *Brissus* Gray, 1825 *Brissus unicolor* (Leske, 1778) (Text-fig. 19.2–19.7)

1941. *Plagiobrissus abeli* nov. spec.; G. Reidl, p. 24, figs 1–2. 1953. *Brissus jacquementi* Lambert, 1915; E. Szörényi, pp. 41 and 92, pl. 4, figs 5, 5a, 5b.

1961. *Brissus (Allobrissus) miocaenicus* n.sp.; H. Schaffer, p. 149, pl. 1, figs 1–4 and 6; pl. 2, figs 1–9.

1970. *Brissus unicolor* (Leske), forme typique; J. Roman, p. 125, pl. B/5a–5b.

2005. *Brissus abeli* (Reidl, 1941); A. Kroh, p. 167, figs 76–77, pl. 73, figs 1–4.

2006. Brissus unicolor (Leske, 1778); A. Radwański et al., p. 98, pl. 4, figs 3–5.

MATERIAL: Hai Roztotski: two incomplete tests (MWGUW ZI/55/052 and MZ8Ee 1562); Haluschyntsi: one almost complete specimen (MWGUW ZI/55/029); Humentsi: one test fragment (MWGUW ZI/55/050); Maksymivka: 27 tests and/or their fragments (MWGUW ZI/55/033-040); Nihyn: two incomplete tests (MWGUW ZI/55/047-048); Novosilka: 3 test fragments (MWGUW

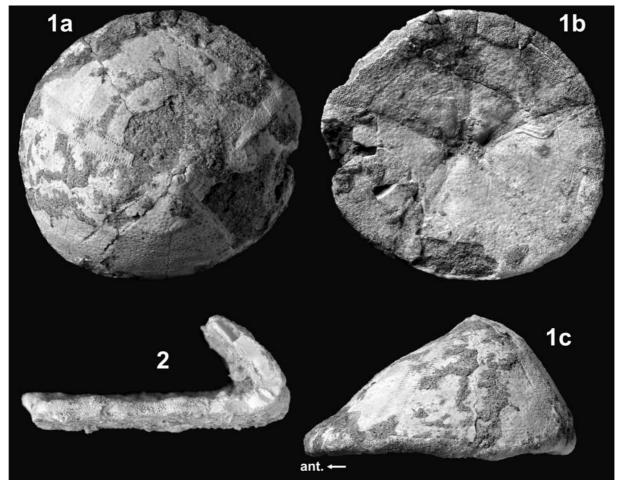
ZI/55/042, -044); Polupanivka: one almost complete test (MWGUW ZI/55/043); Sakhkamin: one mould, two test fragments (MWGUW ZI/55/030-032); Verbka: one test fragment (MWGUW ZI/55/049); Zakupne: 2 test fragments (MWGUW ZI/55/041); Zbarazh: one mould, one almost complete test (MWGUW ZI/55/045-046); Nihyn-Verbka II: one incomplete specimen (MZ8Ee 1562); all specimens are from the Ternopil Beds. The specimens housed in the Museum of the Earth (Warsaw) were collected by Dr B. Studencka.

DESCRIPTION: Test medium-sized to large (over 70 mm), ovate, without anterior groove. Apical disc ethmolytic, with 4 gonopores. Anterior ambulacrum narrow and flush with small pore-pairs. Other ambulacra petaloid and depressed, the angle between anterior pair varies from 175 to almost 190°. Periproct large, on vertical truncate face; peristome kidney-shaped. Plastron very broad and with distinct tubercles, arranged regularly. Labral plate short and wide, in broad contact with following sternal plates. Tubercles on aboral side small

and not differentiated. Peripetalous fasciole well-developed and star-shaped (indented in all interambulacra), subanal fasciole bilobed.

REMARKS: The concept of this form, here considered conspecific with the extant species *Brissus unicolor* (Leske, 1778), was presented by Radwański *et al.* (2006, p. 98). Its present-day distribution within the warm-temperate to subtropical/tropical zone, as well as its biotope variables ranging from sand or shellgrit to reef crevices, correspond well with its occurrence in biohermal pockets and crevices of the Ternopil Beds. Supplemented herein are other occurrences in this facies, and the first record from the Mykolaiv Beds.

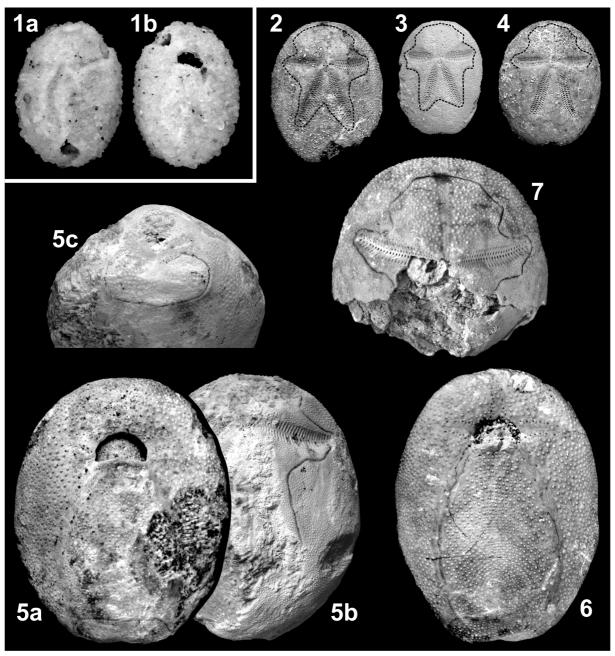
The species was recorded previously from Zbarazh (single specimen; Szörényi 1953), as well as from Haluschyntsi (single specimen) and Maksymivka (five poorly preserved adults; Radwański *et al.* 2006). The specimen from Zbarazh, illustrated by Szörényi (1953) and interpreted (with a query) subsequently as a juvenile or subadult *Brissus abeli* by Kroh (2005, p.



Text-fig. 18. Conolampas sp. from the Mykolaiv Beds: 1a-1c – Complete test (Specimen No. MWGUW ZI/55/106) from Vybranivka, natural size; 2 – Ambital portion of the test (Specimen No. MWGUW ZI/55/082) from Khorosno, to show its profile, × 2

169), is regarded herein as a juvenile *B. unicolor*, as herein understood. Szörényi (1953) referred it to *Brissus jacquementi* Lambert, 1915. Lambert's species has, however, a pyriform, elongated test widened anteriorly (see Lambert 1915, p. 179, pl. 14, figs 14–16). Incidentally, Lambert's species is a junior synonym of *B. bastiae* Oppenheim, 1902, as demonstrated by Philippe (1998, pp. 184 and 240).

Two size classes are present in the studied material throughout the Ternopil Beds; one 30–35 mm in length (see Text-fig. 19.2–4), and the other 70 mm and more (see Text-fig. 19.5–7). Even the largest specimens, however, are smaller than the largest modern representatives of the species, with some attaining 127 mm or more (Hendler *et al.* 1995, p. 242).



Text-fig. 19. 1. *Brissus* sp., from the Mykolaiv Beds; 2–7 *Brissus unicolor* (Leske, 1778), from the biohermal Temopil Beds: 1a-b – Juvenile specimen from Khorosno (No. MWGUW ZI/55/060a: 1a – Aboral, 1b – Oral view, both × 3); 2-4 – Average-sized specimens in aboral views, all natural size (2 from Zbarazh – No. MWGUW ZI/55/046; 3, 4 from Maksymivka – Nos MWGUW ZI/55/039a and 039b); 5-6 – Larger-sized specimens (Nos MWGUW ZI/55/035a and 035b) from Maksymivka, both natural size: 5 – Near-complete test (5a – Oral, 5b – Aboral, 5c – Posterior view; inked, to highlight the subanal fasciole); 6 – Best-preserved oral side of the test, to highlight the structure of plastron; 7 – Anterior part of the larger-sized test (Specimen No. MWGUW ZI/55/049) from Verbka; inked, to highlight the peripetalous fasciole, natural size

B. unicolor (Leske, 1778) is the commonest and the most widely distributed echinoid in the Ternopil Beds. In Europe, the species is similarly abundant only in the Miocene of southern Spain (see Roman 1970), where it co-occurs with the exotic (Persian Gulf provenance) B. latidunensis Clegg, 1933, which has variably been interpreted as a distinct species, a subspecies (Roman 1970, p. 127) or an intermediate (Kier 1972a, p. 102) with B. unicolor. Roman (1970, p. 126) treated as a morphotype of B. unicolor also B. oblongus Wright, 1855, which differs from Leske's species in its slight elongation (see Wright 1855, pl. 5, fig. 2a, b; Roman 1970, pl. B.4a–c).

OCCURRENCE: *Brissus unicolor* is commonly found within the biohermal facies of the Ternopil Beds.

Brissus sp. (Text-fig. 19.1)

MATERIAL: Khorosno: one complete and one incomplete juvenile specimen (MWGUW ZI/55/060); Pukiv: 2 fragments (MWGUW ZI/55/108); all from the Mykolaiv Beds.

REMARKS: The complete specimen from Khorosno (MWGUW ZI/55/060) is an exceptionally small, juvenile specimen ('a baby', 13 mm long) which exhibits all features typical of adults (see Text-fig. 19.1a–b). Due to poor preservation it is left in open nomenclature. Similarly, poorly preserved fragmentary specimens (large fragment of anterior part of test and damaged sternum) are known from Pukiv.

## Genus Rhabdobrissus Cotteau, 1889

REMARKS: The large-sized brissid spatangoids comprise, among others, such taxa as *Plagiobrissus*, *Rhabdobrissus*, *Radiobrissus*, *Eobrissus*, *Metalia* (at least in part) and *Mortensenaster* (see Mortensen 1951; Fischer 1966; Smith *et al.* 2010). The two specimens studied herein are assigned to the genus *Rhabdobrissus*. They possess such distinctive features of the genus as the lack of a frontal groove; the presence of a flush anterior petal and coarser tubercles within the peripetalous fasciole; and anterior and posterior petals that are not deeply indented behind.

The genus *Rhabdobrissus*, treated formerly as a subgenus of the genus *Plagiobrissus* Pomel, 1883 (Fischer 1966, p. *U*603), is now considered an independent

taxon (Smith *et al.* 2010). According to Smith *et al.* (2010), *Rhabdobrissus* comprises solely Recent species, with doubtful taxonomic status. The four species distinguished by Smith *et al.* (2010) are briefly discussed below.

Rhabdobrissus jullieni Cotteau, 1889 (see Fischer 1966, fig. 484.2; illustrated photographically by e.g., Koehler 1915, pl. 11, fig. 6), the type species of the genus (by original designation) is characterised by coarse primary tubercles in the interambulacral zones, except for the posterior (5) one, and some of them are recessed in camellae (see Cotteau 1889; Koehler 1915; Fischer 1966; Smith *et al.* 2010).

Rhabdobrissus pacificus of H.L. Clark (1940, 1948) (see also Caso 1983), bears large primary tubercles concentrated along the peripetalous fasciole and almost flush along the anterior petal (see Caso 1983, fig. 78; Smith et al. 2010). When originally described by Clark (1940, p. 351), based on the material from the west coast of Panama, it was regarded as a juvenile of the West Indies species Plagiobrissus grandis (Gmelin, 1791) (for references see Kier 1975, Hendler et al. 1995). The latter species, the type species of Plagiobrissus (Pomel 1883; see Fischer 1966, Smith et al. 2010), has, however, a frontal groove, one of the generic features of Plagiobrissus and absent in Rhabdobrissus.

Rhabdobrissus costai Gasco, 1876, studied in detail by Mortensen (1913), was selected as type species of a distinct genus, *Mortensenaster*, by Lambert (1923). Its *Rhabdobrissus* affinity was retained, however, by Smith *et al.* (2010). It is known since the Pliocene (recorded from northern Italy by Borghi 1993).

"Plagiobrissus (Rhabdobrissus) sp.", a fragmentary specimen from the Upper Miocene of Morocco (see Lachkhem and Roman 1995, pl. 4, fig. 2), hardly belongs to the genus *Rhabdobrissus*. It has a very high test profile which makes it much closer to the genus *Rhynobrissus* A. Agassiz, 1872 (illustrated by Fischer 1966, fig. 485.2a–c).

Summing up, the studied specimens are closest to the species *Rh. pacificus* (H.L. Clark, 1940). The minor differences still warrant, however, the erection of a new species, which would represent the oldest, Miocene, record of the genus *Rhabdobrissus* Cotteau, 1889.

Rhabdobrissus tarnopolensis sp. nov. (Text-figs 20–22)

MATERIAL: Hai Roztotski: one small fragment of aboral side (MWGUW ZI/55/051); Maksymivka: holotype, one incomplete test (MWGUW ZI/55/027);

Novosilka: paratype – one fragmentary oral side of the test (MWGUW ZI/55/028); all specimens are from the Ternopil Beds.

DIAGNOSIS: A rhabdobrissid spatangoid of ovate test, widened posteriorly, with peripetalous fasciole broadly extended, bowed anteriorly but slightly convex behind anterior petals, and convexly sinuous between posterior petals; frontal pore-pairs of anterior petals adapically atrophied.

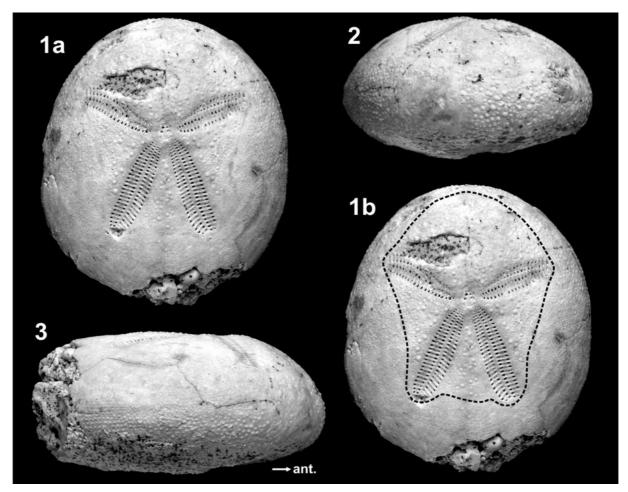
DERIVATION OF NAME: After the Latin version of the city name of Ternopil, western Ukraine.

MEASUREMENTS: Length of the holotype (posterior tip broken off) is 53 mm, total length estimated at 55–56 mm; width at the anterior petals 40 mm, maximum at the end of posterior petals 46 mm. Length of the paratype (posterior part missing) is 51 mm, total length estimated at 56–57 mm; maximum width – 44 mm.

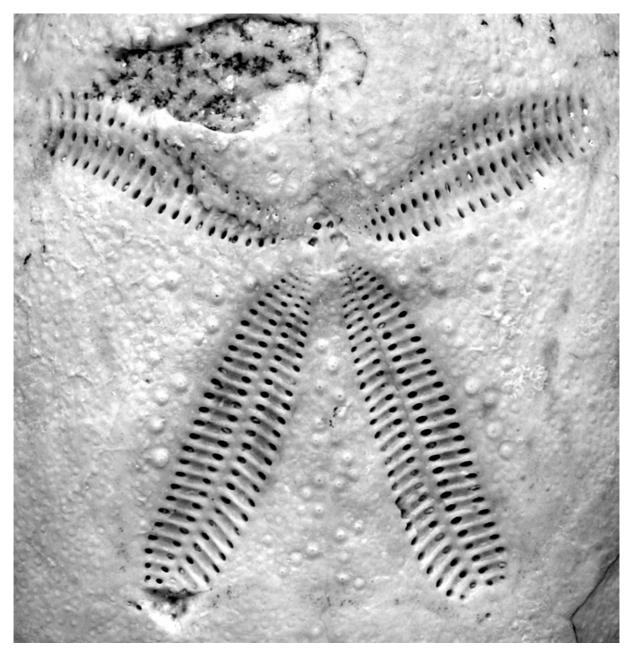
TYPE LOCALITY: Maksymivka near Ternopil, Medobory Hills (Fore-Carpathian Basin), Ukraine.

TYPE HORIZON: Middle Miocene (Late Badenian).

DESCRIPTION OF HOLOTYPE: Test ovate, slightly wider posteriorly, lacking frontal groove; profile also ovate, not inflated; frontal ambulacrum non-petaloid, flush; petals with adapical part of anterior pore pair column atrophied; all petals moderately sunken, closed, not flexed outerly, anterior ones shorter, with interporiferous zone wide (half of pore pair column width) and anterior pore pair column atrophied adapically; posterior ones, slightly longer, diverging at a wide angle (50°), with interporiferous zone relatively narrow (less than half of pore pair column width); apical system ethmolytic, with four gonopores well exposed; peripetalous fasciole distinct, convex frontally, and weakly re-entrant behind anterior and between posterior petals concavely; coarser tubercles scattered almost uniformly throughout peripetalous fasciole, but tending



Text-fig. 20. The holotype of *Rhabdobrissus tamopolensis* sp. nov. from the biohermal Temopil Beds at Maksymivka (Specimen No. MWGUW ZI/55/027): 1a – Overall aboral view; 1b – Same, inked to highlight the peripetalous fasciole; 2 – Anterior view; 3 – Right lateral view; all × 1.5



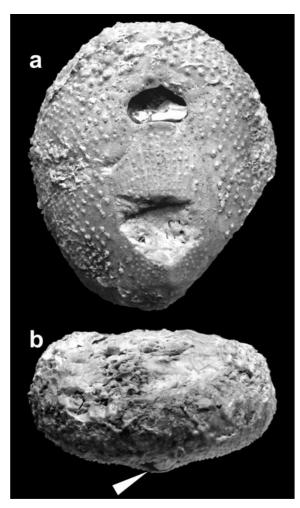
Text-fig. 21. Close-up of the holotype of Rhabdobrissus tarnopolensis sp. nov., to show the extent of the peripetalous fasciole, and the structure of the ethmolytic apical disc and petals (atrophied in frontal pore pairs II and IV);  $\times$  5

to group along the outer sides of posterior petals and along interradial suture of interambulacrum 5. Occluded plates at the distal end of the posterior paired ambulacra, not enclosed by the peripetalous fasciole (see Text-figs 20, 21).

DESCRIPTION OF PARATYPE (from Novosilka): Only part of the oral side, with a large, D-shaped peristome is preserved (see Text-fig. 22). Overall shape of the test is more ideally ovate than that of the holotype.

A narrow amphisternous plastron is bordered by almost parallel ambulacra converging towards the peristome, and covered by small tubercles arranged in transverse rows diverging from the midline and arching anteriorly.

REMARKS. When compared with *Rhabdobrissus pacificus* (H.L. Clark, 1940) presented by Caso (1983, fig. 78), the new species is more hemispherical ambitally, slightly wider posteriorly, and with posterior petals di-



Text-fig. 22. The paratype *Rhabdobrissus tarnopolensis* sp. nov. from the biohermal Ternopil Beds at Novosilka (Specimen No. MWGUW ZI/55/028):  $\bf a$  — Oral view;  $\bf b$  — Anterior view, to show the labrum (arrowed) and damaged dorsum; both  $\times$  1.5

verging at an angle of  $50^\circ$  (instead of  $40^\circ$ ). Also it has coarser tubercles in the peripetalous fasciole more pronounced alongside the external margin of the posterior (I and V) petals and around the interradial suture of interambulacrum 5; interporiferous zone of anterior petals are slightly wider.

The atrophy by the apical part of frontal pore-pairs in the anterior (II and IV) petals, reported as in the Brissidae by Fourtau (1914, pl. 7, fig. 4c; see below for taxonomy), is also noted in the *Atelospatangus*-group of species, referred currently to the family Loveniidae (see Smith *et al.* 2010).

Plagiobrissus hungaricus Vadász (1915, pp. 153, 154 = 231, 232), the only echinoid species from the Paratethys Realm comparable to our species, occupies an uncertain systematic position. The single, poorly preserved original specimen of Vadász (1915, pl. 4

(10), figs 11–13), from the Miocene of Felsö-Orbó (nowadays Garbova de Sus in Romania; see Kroh 2005, p. 195) is best assigned to Radiobrissus geneffensis Fourtau, 1914, known from the Miocene of northern Egypt, and currently considered a member of the genus Metalia Gray, 1855 (Smith et al. 2010). Philippe (1998, p. 201) suggested the affinity of the Hungarian species with Plagiobrissus (Rhabdobrissus) imbricatus (Wright, 1855). The latter species, described from the Maltese Upper Miocene (Messinian) and referred originally to Brissus imbricatus (see Wright 1855, pp. 183, 184), is based, however, on a fragmentary specimen, with its dorsum damaged. Consequently, recent understanding of P. hungaricus is far from clear, but it appears taxonomically different from Rh. tarnopolensis sp.nov.

OCCURRENCE: The species is known from the Ternopil Beds. It lived in shellgrit in crevices of nearshore (shallow sub- to intertidal) coralgal buildups, associated with diverse echinoids and crabs (see Radwański *et al.* 2006).

Family Spatangidae Gray, 1825 Genus *Spatangus* Gray, 1825

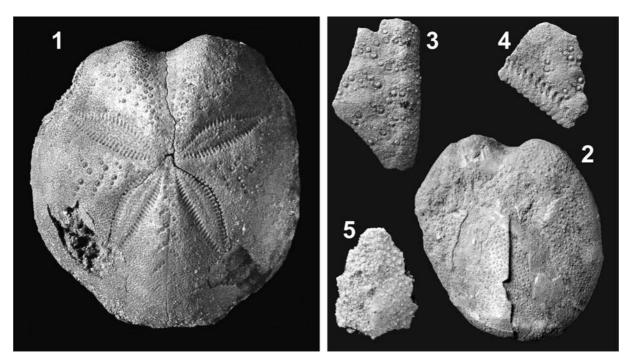
REMARKS. The correct assignment of spatangid tests poses a problem. This has recently been noted by Kroh (2005), who restudied Laube's (1871) types and revised all Paratethys material referred usually to *S. austriacus* Laube, 1871. As a result, apart from the nominal species and specifically indeterminate forms, Kroh (2005) selected two groups, which he treated informally as separate taxa, *Spatangus* sp. 1 and *Spatangus* sp. 2. In the latter Kroh (2005, pp. 182–185) included all former records of *S. austriacus* from Ukraine and Poland.

The material studied herein adds nothing to this discussion. Therefore, we propose to lump all specimens in Laube's species *sensu lato*, and refer them to *Spatangus* ex gr. *austriacus* Laube, 1871.

Spatangus ex gr. austriacus Laube, 1871 (Text-figs 23–24)

2005. *Spatangus* sp. 2; A. Kroh, pp. 182, 183 (cum syn.). 2005. *Spatangus* sp. 2; A. Kroh, fig. 90.1a–c.

MATERIAL: Rozvadiv: one complete test (MWGUW ZI/55/107); Stratyn: one fragmentary test, three test fragments (MWGUW ZI/55/101-102); both from the



Text-fig. 23. Spatangus ex gr. austriacus Laube, 1871: 1 – Denuded test (Specimen No. MWGUW ZI/55/104) from organodetrital Ternopil Beds at Bridok (aboral view), natural size. Various fragments from the Mykolaiv Beds at Stratyn: 2 – Fragmentary test (oral view), to show the well-pronounced plastron (Specimen No. MWGUW ZI/55/101), natural size; 3-4 – Common detritus of the aboral part of test (Specimen Nos MWGUW ZI/55/102a-102b), × 1.5; 5 – Isolated plastron (Specimen No. MWGUW ZI/55/102d), × 1.5

Mykolaiv Beds. Vanzhuliv: one fragment (MWGUW ZI/55/147); Zalistsi: 7 fragments (MWGUW ZI/55/149); all from the Pidhirtsi Beds. Bridok: one test (MWGUW ZI/55/104) from the Ternopil Beds.

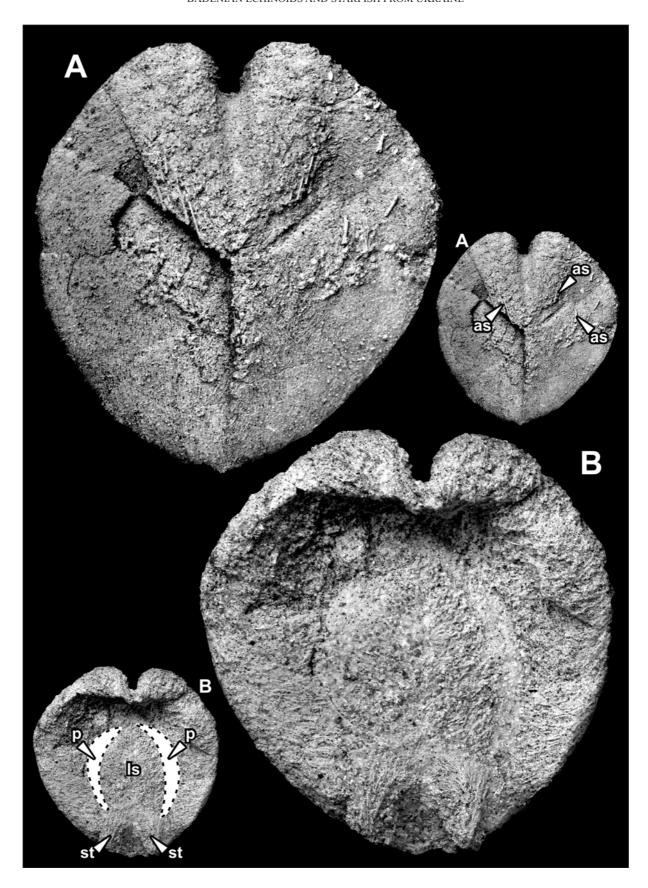
DESCRIPTION: Test heart-shaped of medium- to large size (up to 110 mm in length). Anterior ambulacrum narrow, other ambulacra petaloid and flush. Aboral tuberculation heterogeneous, with coarse primary tubercles arranged in oblique rows or chevrons in all interambulacra. Plastron relatively wide, triangular in outline, with strongly marked indentation.

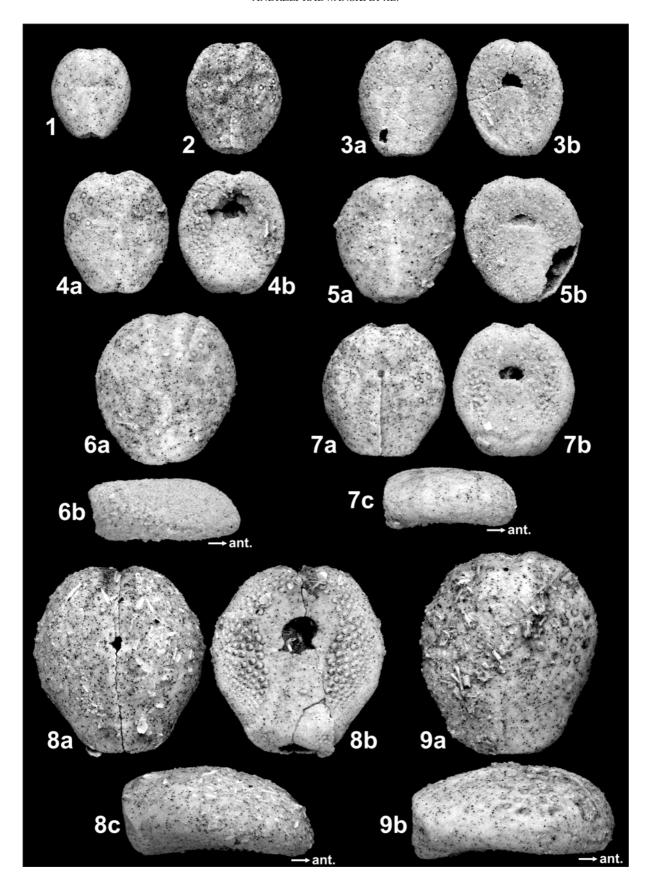
REMARKS. The material studied herein probably represents Kroh's (2005, pp. 182–185) *Spatangus* sp. 2, although this cannot be separated distinctly from the types of *S. austriacus* (see Laube 1871, pl. 19, fig. 2, 2a; Kroh 2005, pl. 75, figs 1a, 2a). Of particular interest is the larger-sized, spine-coated specimen from Rozvadiv (Text-fig. 24). Its preserved spine canopy, unknown as yet from ancient spatangids, exhibits larger primary spines and two subanal tufts (see Text-fig. 24). The chevron-like arrangement of its primary spines is nearly identical

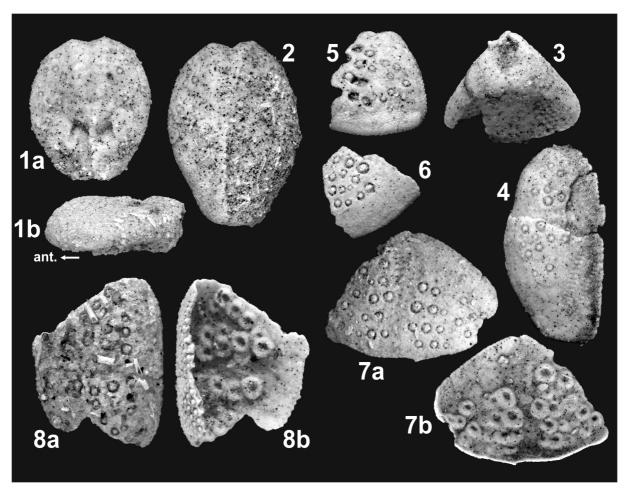
to that (see Kroh 2005, fig. 85) of typical S. austriacus. The specimen has a cordiform shape, a test outline not seen in small- or medium-sized specimens. Moreover, its frontal ambulacrum (AIII) is sunken towards a very deep frontal notch. Its length, approaching 110 mm, is close to that of the largest (126.2 or 124.1 mm) Austrian specimen, and distinctly exceeds the average size range (48.7 to 89.6; see Kroh 2005, p. 178) for typical S. austriacus from the Eggenburgian of the Vienna Basin. The abovementioned largest specimen (see Kroh and Harzhauser 1999, pl. 1, figs 1, 2), exhibits a rare arrangement of primary spines, very close to that (see Kroh 2005, fig. 85) typical of Spatangus sp. 2, but it lacks a cordiform outline and frontal notch. It seems, thus, that neither the extreme size and cordiform shape, nor the arrangement of the primary spines set this apart from S. ex gr. austriacus.

**Eco-taphonomy of the spine-coated specimen.** Ever since the classic studies of Nichols (1959), Durham (1966a, pp. *U*257–*U*265) and Kier (1972b), a wide spectrum of ecological (behavioural and environmental) requirements of extant spatangids has become

Text-fig. 24. Spine-coated specimen of *Spatangus* e gr. *austriacus* Laube, 1871, from the Mykolaiv Beds at Rozvadiv (Specimen No. MWGUW ZI/55/107): **A** – Aboral view, **B** – Oral view; both natural size. Reduced images (of A and B), to indicate: **as** – apical spines, **ls** – locomotory spines, **p** – ambulaera *I* and *V* bordering the plastron, **st** – subanal tufts







Text-fig. 26. Hemipatagus ocellatus (Defrance, 1827) from the Mykolaiv Beds at Khorosno: 1 – Specimen No. MWGUW ZI/55/074: 1a – Aboral, 1b – Left lateral view, both × 1.5; 2 – Pyriform specimen (No. MWGUW ZI/55/071f), × 1.5; 3 – Posterior fragment of test (Specimen No. MWGUW ZI/55/073), to show the subanal fasciole, × 2; 4-6 – Test fragments of larger specimens (Nos MWGUW ZI/55/066a-066b and 069), to show the camellate primary tubercles vanishing towards the test margin, × 1.5; 7-8 – Test fragments of larger specimens (Specimens Nos MWGUW ZI/55/068a-068b), in outer (a) and inner (b) views, to show the development of camellae reaching the test margin, × 1.5

known. Dealing primarily with *S. purpureus* (O.F. Müller, 1776), those authors also noted the analogues with its Neogene ancestors. Modern representatives live shallow-infaunally in coarse material, and are in contact with the sediment/water interface via a funnel-like respiratory tract formed by long apical spines. Both shape and depth of this tract correlate with the sediment type and burrowing depth (see Durham 1966a, pp. *U*260, *U*261). Consequently, it may be stated that depth of burrowing must have been limited in coarse-grained sea floors at Rozvadiv, and that the apical spines (see Text-fig. 24A) were not distinct. In contrast, the relatively long and close-set posterior spines formed conspicuous subanal tufts (marked *st* in Text-fig. 24B) to enable the construction of two sepa-

rate sanitary canals. The spine canopy, almost complete ventrally, but less so dorsally (either underdeveloped, or abraded; compare A and B in Text-fig. 24) indicates that the specimen studied lived semi-infaunally, with its dorsum more or less exposed over the sediment/water interface (compare Nichols 1959, fig. 14 = Durham 1966a, fig. 205).

OCCURRENCE: Spatangus austriacus (sensu lato) is widely distributed throughout the Early Eggenburgian to Late Badenian of the Central Paratethys (see Kroh 2005). In the Miocene of Ukraine it has been recorded in the Mykolaiv Beds, and sandy and organodetrital deposits of the Pidhirtsi Beds and Ternopil Beds.

Text-fig. 25. Display of *Hemipatagus ocellatus* (Defrance, 1827) from the Mykolaiv Beds at Khorosno (Specimens Nos MWGUW ZI/55/071a-071e and 075-078, respectively): **1-9** – Better-preserved specimens of various sizes, to show their number of camellate primary tubercles gradually increasing during test growth (a – Aboral, b – Oral or lateral, c – Lateral), all × 1.5

#### Family Loveniidae Lambert, 1905

REMARKS. Assemblages of small-sized spatangoids represent another group with unclear spatangid/loveniid affinities. This is best exemplified by Defrance's (1827) *ocellatus*, which has previously been assigned either to the spatangid genus *Maretia* Gray, 1855 or to the loveniid *Hemipatagus* Desor, 1858. These two genera have long been treated as separate (Lambert 1908; Philippe 1998) or were synonymised (Mortensen 1951, p. 25; Fischer 1966, p. *U*609). Following recent discussions on the systematic status of these genera (Kroh 2005, 2007a; Smith *et al.* 2010), we refer the studied specimens to the genus *Hemipatagus*, in compliance with Kroh (2007a).

Genus *Hemipatagus* Desor, 1858 *Hemipatagus ocellatus* (Defrance, 1827) (Text-figs 25–26)

1998. *Maretia ocellata* (Defrance, 1827); M. Philippe, pp. 220–223, pl. 22, figs 6–10.

2005. *Hemipatagus ocellatus* (Defrance, 1827); A. Kroh, pp. 191–194, pl. 81, figs 1–4 and pl. 82, figs 1, 2.

2007a. *Hemipatagus ocellatus* (Defrance, 1827); A. Kroh, p. 173, pl. 1, figs 11–14.

MATERIAL: Khorosno: 55 tests and/or their fragments (MWGUW ZI/55/066–078) from the Mykolaiv Beds.

DESCRIPTION: Test ovate with distinct frontal groove. Anterior ambulacrum depressed, other ambulacra petaloid aborally and flush. Peristome kidneyshaped, periproct on posterior truncate face. Subanal fasciole present, peripetalous fasciole absent. Camellate primary tubercles with sunken areoles present on aboral side in anterior and lateral interambulacra. Large tubercles on lateral interambulacra on oral surface.

REMARKS. The assemblage studied comprises > 20 intact specimens and numerous fragments of various sizes from allochthonous bioclast material in cross-bedded sands at Khorosno; these are regarded to have come from a single community which inhabited a nearshore sandy biotope, and which were swept by littoral currents. As a result, the smaller (i.e., supposedly younger) specimens easily survived transport (? in sand suspension, possibly still alive), while the larger, thinwalled tests (probably empty) were subjected to neartotal destruction. In effect, the material collected displays a wider range of variability than previously recorded.

The studied specimens vary in a number of aspects from those documented in the literature. The main morphological variables, which may be listed are as follows: (i) Some smaller specimens (Text-fig. 25.3) are slightly more elongate than larger ones, although some larger-sized specimens with a pyriform shape are also noted (Text-fig. 26.2); (ii) Test profile is much taller; (iii) The posterior face varies, being either truncated anteriorly (Text-fig. 25.6b, 8c; Text-fig. 26/1b) or near vertical (Text-fig. 25.7c, 9b); and finally (iv) The camellate tubercles are more sparsely developed, except in larger-sized specimens (of which only fragments are preserved), where they either become effaced or diminish in size towards the test margin (Text-fig. 26.5–8).

The meaning of the observed variation is uncertain. This may reflect facies dependence or reaction to other environmental conditions, but easily may also result from phylogeny (the material reported in the literature is older). The other obstacle is the fact, that test architecture in the present material can be observed to a limited extent only, because all specimens are more or less heavily encrusted with sand grains due to diagenetic pressure-solution.

Concluding, the assemblage studied herein is thought to represent a single community, and stratigraphically the youngest community of *H. ocellatus*. Neither this species, nor any other echinoid species of comparable overall morphology, has ever been recorded from the Polish part of the Fore-Carpathian Basin.

OCCURRENCE: In the Central Paratethys, *Hemipatagus ocellatus* is known from the Eggenburgian of the Swiss and Austrian Molasse Zone, and from the ?Badenian of the Pannonian and Transylvanian basins (see Kroh 2005). In the Ukrainian Fore-Carpathian Basin it is locally abundant in the Mykolaiv Beds.

Genus *Echinocardium* Gray, 1825 *Echinocardium leopolitanum* Radwański and Wysocka, 2001 (Text-fig. 27)

2001. *Echinocardium leopolitanum* sp. nov.; A. Radwański and A. Wysocka, pp. 304–306, fig. 6B.a-b, pls 3–6. 2005. *Echinocardium leopolitanum* Radwański & Wysocka, 2001; A. Kroh, p. 196.

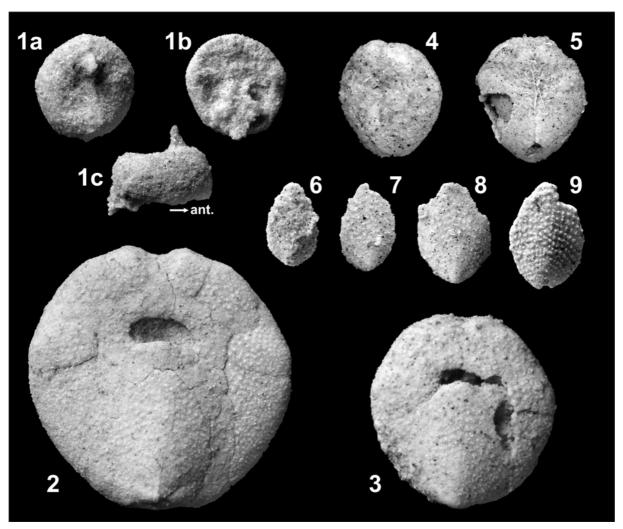
MATERIAL: Gleboviti: over 230 tests and fragments (MWGUW ZI/55/117-137); Khorosno: 4 tests, over 25 test fragments (MWGUW ZI/55/054-057); Pidiarkiv: one test fragment (MWGUW ZI/55/090); all from the Mykolaiv Beds.

DESCRIPTION: Test up to 51 mm in length, near-circular in juveniles and slightly heart-shaped and depressed aborally in adults. Frontal groove shallow, more pronounced in spine-coated specimens. Apical system almost central, posterior to peristome vertical. Petals relatively short, shallowly sunken, low-angled triangularly, moderately V-shaped, abutting against apical fasciole. Plastron broad and vaulted with indistinct median keel. Labrum wide and gently arched towards peristome. Periproct circular to indistinctly oval horizontally. Apical fasciole very pronounced, shield-shaped. Subanal fasciole well developed.

REMARKS. This species, formerly assumed to be endemic, was erected on the basis of rich masses of spec-

imens, most of them preserving spine canopies, from tempestites at Gleboviti [Polish: Chlebowice]. Here we add material from the same locality, but also note the presence of this form elsewhere in Ukraine. All these localities are Middle Miocene (Early Badenian) in age, and not Burdigalian, as suggested by Kroh (2007b, p. 179).

At the Gleboviti sand pit, quarrying in 2006 resulted in the discovery of two pocket-like aggregations of exclusively small specimens (15–20 mm in length) at the bottom of a storm-generated sand bar, which also yielded a complete starfish (see above; Member C in text-fig. 3 of Radwański and Wysocka 2001). These should be interpreted either as transport-selected juveniles ('babies') having been swept out of communities in which the deeper-burrowing adults survived superficial scouring or stir of the sand they lived in, or they



Text-fig. 27. Echinocardium leopolitanum Radwański and Wysocka, 2001, from the Mykolaiv Beds: 1 – Juvenile specimen (a 'baby') from Gleboviti (No. MWGUW ZI/55/124a), with fully preserved spine canopy (1a – Aboral; 1b – Oral view, to show the fan of locomotory spines; 1c – Right lateral view, to expose apical tuft spines); 2-3 – Adult specimens from Gleboviti (Nos MWGUW ZI/55/127a and 119), in oral view, to show the denuded, well-exposed plastrons; 4-5 – Two denuded tests preserved from Khorosno (Specimens Nos MWGUW ZI/55/057a-057b), in aboral views; 6-9 – Isolated plastrons from Khorosno (Specimens Nos MWGUW ZI/55/055a-055d); all × 1.5

have been supplied from restricted biotopes ('nurseries'\*) populated exclusively by youthful individuals (compare Kier 1975, p. 3, for brissids; Néraudeau 1991). Another example of young *Echinocardium* aggregations has previously been noted from the Miocene of Portugal by Kotchetoff *et al.* (1975, p. 75).

The fan of locomotory spines, as well as the apical tuft in juveniles ('babies') in *E. leopolitanum* have a development identical (see Text-fig. 27.1a–c) to that of adults, which documents the deep burrowing of this species, already in early growth stages.

At Khorosno, within various allochthonous assemblages, there are several denuded tests of small specimens (Text-fig. 27.4, 5), as well as quite common isolated plastronal plates which, on account of the posterior keel (see Text-fig. 27.2, 3, 6–9), are referred to this species. These are recognised as the most robust parts of the tests that were crushed during rough water motion and transport. As discussed previously (Radwański and Wysocka 2001, pp. 305, 306), tests of E. leopolitanum have distinctly stronger and longer locomotory spines than the modern pandemic *E. cordatum* (Pennant, 1777). The highly conspicuous tufts of locomotory spines were certainly an adaptation to deeper and/or more rapid burrowing in less coherent sand, or to less effective mucus secretion to reinforce the burrow. Because deep and intense burrowing requires strong locomotory spines, the plastron must become their sturdy base.

Amongst the new localities are Yasnyska, where single specimens and ubiquitous burrows occur in more compact sand mass, and Birky [Polish: Borki] where only burrows, which may be attributed to this species, are preserved in the layered sands.

OCCURRENCE: *Echinocardium leopolitanum* is common in the Mykolaiv Beds.

#### ECO-TAPHONOMIC CONCLUSIONS

In the Middle Miocene of the Ukrainian Fore-Carpathian Basin, the echinoderms are confined to particular facies.

The Mykolaiv Beds, the most widespread one, yields the starfish *Astropecten forbesi* Heller, 1858, and ubiquitous echinoids, such as *Psammechinus dubius* (L. Agassiz, 1840), *Echinocyamus* sp., *Parascutella* cf. *paulensis* (L. Agassiz, 1841), and *Parmulechinus* sp. nov., *Spatangus* ex gr. *austriacus* Laube, 1871, *Hemipatagus ocellatus* (Defrance, 1827), *Echinocardium leopolitanum* Radwański and Wysocka, 2001, *Clypeaster* sp., *Conolampas* sp., and *Echinolampas* sp., and *Stylocidaris? polyacantha* (Reuss, 1860). In this unit

all material is allochthonous (= parautochthonous sensu Schneider *et al.* 2009); echinoids were redeposited from their original biotopes by various dynamic events (currents, storms). The reconstruction of their primary habitats is more difficult. Any autochthonous occurrences in this facies are irregular, burrowing echinoids (*Spatangus, Echinocardium*) which could have been entombed when inside the burrow (compare Radwański and Wysocka 2001); possibly such ones are also the studied starfish having been preserved very close to their life positions (cf. Text-fig. 4.2b).

The biohermal Ternopil Beds yielded less frequent echinoids, such as *Eucidaris desmoulinsi, Arbacina catenata, Brissus unicolor*, and *Rhabdobrissus tarnopolensis* sp.nov. In this unit the echinoderms studied generally form autochthonous assemblages, preserved amidst bioherms, either in interbiohermal gaps or intrabiohermal crevices. Those entombed occasionally inside the bioherms are firmly cemented to algal matrix and remain intact in the rock. Such specimens are usually barely infilled, which suggests that they were either buried alive or soon after death, as discussed previously (Radwański *et al.* 2006, p. 98; pl. 4, figs 6, 7).

In ecological terms, particular attention is paid to the small-sized specimens of some species (*Psammechinus dubius*, *Echinocardium leopolitanum*) of which local mass accumulations are known, which enables conclusions to be drawn on the life behaviour of young individuals, general environmental conditions of communities and taphonomic filtering through transport.

The large-sized echinoids, Clypeaster and Conolampas, come from Khorosno, the locality characterized by the most diverse faunal assemblages. Their allochthonous fragments have been derived from eulittoral habitats and/or nearshore sandy seagrass beds (compare Schneider et al. 2009), their tests having been broken either by surf action, or by predatory attacks. The latter possibility was suggested for the Korytnica Basin (southern Poland) assemblage, where the damage of the largest eulittoral shells is remarkable (see Bałuk and Radwański 1977, pp. 108–110 and pls 7-8). Huge crabs and large vertebrates (some fish or mammals; the latter exemplified by the case of recent Californian Enhydra lutris - see e.g., Hall and Schaller 1964) were assumed as possible predators (Bałuk and Radwański 1977, p. 109).

# BIOGEOGRAPHIC VERSUS STRATIGRAPHIC IMPLICATIONS

As inferred from species diversity and size of echinoids studied, their life conditions (particularly in terms

of the temperature) did not differ significantly from those prevailing in other parts of Paratethys, in spite of the northerly position of the Fore-Carpathian Basin (see Radwański *et al.* 2006; Kroh 2007b, pp. 185, 186). Consequently, it may safely be assumed that the Middle Miocene sequences studied, represented an area which belonged to the warm, Paratethyan biogeographic realm.

The only species in which a size decrease when compared with areas further to the south is noted are two sand dollars, Parascutella gibbercula and P. paulensis. In the Vienna Basin, P. gibbercula attains lengths up to 150 mm (Laube 1871) or even 158.6 mm (Kroh 2005, p. 88) and a similar length (152 mm) was reported recently from Slovenia (Mikuž 2009). For P. paulensis, the difference is less distinct. In the Vienna Basin it attains a length of 118.8 mm (Kroh 2005, p. 93) and in Slovenia 98 mm (Mikuž 2009). In the Rhône Basin (France), P. gibbercula grows up to a length of 124 mm (holotype; see Lambert 1912; Philippe 1998, p. 150), and P. paulensis up to 74 mm (the holotype) or even 92 mm (Lambert 1912; Philippe 1998, p. 131). Summing up, it may be stated that the Ukrainian specimens of P. paulensis may be regarded as matching the size range of the species as noted further to the south, however, in the case of P. gibbercula a size decrease is evident. Taking into account that this tendency concerns just a single species, it is interpreted herein as reflecting rather less favourable facies conditions (coarse sand) than a biogeographically induced pattern.

The basic stratigraphical problem concerns the range of three species, Parascutella paulensis, Spatangus austriacus and Hemipatagus ocellatus, which occur in the Middle Miocene of the study area, and which, according to Kroh (2005, 2007b, table 3), are Lower Miocene forms in the Vienna Basin. Their presence in the Middle Miocene of Ukraine may easily be explained as the gradual extension of their biogeographic ranges to the north into a newly formed marine basin of the Fore-Carpathin Depression during the Early and early Middle Miocene. Of importance is the fact that the Fore-Carpathian Basin started already in the Early Miocene, although this early part of the succession is nowhere exposed, being entirely beneath the Outer Carpathians. The argument that these species were not found in the Middle Miocene in the Vienna Basin is also not contradictory; it may even be suggested that some of the facies in the Vienna Basin (and in adjacent basins), now regarded to be of Early Miocene (Burdigalian, Eggenburgian) age are, at least in part, isochronous with some facies considered to be Middle Miocene (Langhian to Serravallian) in the Ukraine. The paucity of detailed chronostratigraphic data (bio-, chemomagnetostratigraphic) in the facies studied precludes any firm conclusion on this matter. Finally, seaways for echinoderm larval dispersion to the Fore-Carpathian Basin (which came into existence) through the disappearing Outer Carpathian basins is well established. Sedimentation in the outermost parts of the Outer Carpathian basins obviously continued throughout the Burdigalian (Ottnangian and Karpathian) to terminate later, perhaps even straddling the Early/Middle Miocene boundary, as recently discussed by Kotlarczyk (*et al.* 2006, p. 14; see also Harzhauser *et al.* 2003, fig. 2 and Jankowski *et al.* 2012, p. 210).

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# REFERENCES

Agassiz, L. and Desor, E. 1846–1847. Catalogue raisonné des familles, des genres et des espèces de la classe des Échinodermes, p. 32. Paris.

Airaghi, C. 1901. Echinidi terziari del Piemonte e della Liguria. *Palaeontographia Italica*, 7, pp. 149–218.

Andreyeva-Grigorovich, A.S., Kulchytsky, Y.O., Gruzman, A.D., Lozynyak, P.Y., Petrashkevich, M.I., Portnyagina, L.O., Ivanina, A.V., Smirnov, S.E., Trofimovich, N.A., Savitskaya, N.A. and Shvareva, N.J. 1997. Regional strati-

- graphic scheme of Neogene formations of the Central Paratethys in the Ukraine. *Geologica Carpathica*, **48**, 123–136.
- Bałuk, W. and Radwański, A. 1977. Organic communities and facies development of the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **27**, 85–123.
- Blake, D.B. and Zinsmeister, W.J. 1988. Eocene asteroids (Echinodermata) from Seymour Island, Antarctic Peninsula. *Memoirs of the Geological Society of America*, 169, 489–498.
- Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeo-geography Palaeoclimatology Palaeoecology*, **195**, 389–401.
- Borghi, E. 1993. Un echinide attuale rinvenuto allo stato fossile: *Plagiobrissus* (*Rhabdobrissus*) costai (Gasco, 1876). *Bolletino della Società Reggiana di Scienze Naturali*, 13, 1–6
- Borghi, E. 1999. Echinodermi fossili dell'Emilia: i Cidaridi del Plio-Pleistocene. *Parva Naturalia 1999*, pp. 105–126.
- Boucot, A.J. and Poinar, G.O., Jr. 2010. Fossil Behavior Compendium, pp. 1–391. *CRC Press, Taylor & Francis Group*; Boca Raton London New York.
- Capeder, G. 1906. Fibularidi del Miocene Medio di S.Gavino a Mare (Portotorres) Sardegna. *Bolletino della Società Geologica Italiana*, **25**, 495–534.
- Caso, M.E. 1983. Los equinoideos del Pacifico de México. Parte cuarta: Ordenes Cassiduloida y Spatangoida. Publicaciones especiales, Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autónoma de México, 6, 1–200.
- Christensen, A.M. 1970. Feeding biology of the sea-star *Astropecten irregularis* Pennant. *Ophelia*, **8**, 1–134.
- Clark, H.L. 1940. Eastern Pacific expeditions of the New York Zoological Society. XXI: Notes on echinoderms from the West Coast of Central America. *Zoologica (Scientific Contributions of the New York Zoological Society)*, 25 (3, Number 22), 331–352.
- Clark, H.L. 1948. A report on the echini of the warmer Eastern Pacific, based on the collections of the Velero III. Allan Hancock Pacific Expeditions, **8** (5), 225–360. The University of Southern California Press; Los Angeles.
- Clegg, E.L.G. 1933. Echinoidea from the Persian Gulf. *Memoirs of the Geological Survey of India: Palaeontologia Indica, New Series*, **22**, 1–35.
- Dembińska-Różkowska, M. 1932. Polnische Miozänkorallen. *Annales de la Société Géologique de Pologne*, **8**, 97–171.
- Dermitzakis, M.D., Radwańska, U., Radwański, A. and Drina, H. 2009. Lower Pliocene (Zanclean) regressive sequence of Rafina near Pikermi in Attica, Greece: A spectacular locality of mass-aggregated giant balanid

- cirripedes. *Hellenic Journal of Geosciences*, **44**, 9–19. Desor, E. 1855. Synopsis des Echinides fossiles, p. 38 and pl.
- Desor, E. 1855. Synopsis des Echinides fossiles, p. 38 and pl 7. [Paris – Wiesbade, 1855–1858].
- Durham, J.W. 1966a. Echinoids: Ecology and Paleontology. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part U (Echinodermata 3, Vol. 1), pp. U211 and U257–U265.
- Durham, J.W. 1966b. Clypeasteroids. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part U (Echinodermata 3, Vol. 2), pp. U450–U491.
- Fell, H.B. and Pawson, D.L. 1966. Echinacea. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part U (Echinodermata 3, Vol. 2), pp. U367–U440.
- Fischer, A.G. 1966. Spatangoids. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part U (Echinodermata 3, Vol. 2), pp. U543–U628.
- Fourtau, R. 1914. Notes sur les Echinides fossiles de l'Egypte. Bulletin de l'Institut Égyptien. 5 Série, 7 (for 1913), pp. 62–71 and 86–94.
- Gordon, C.M. and Donovan, S.K. 1992. Disarticulated echinoid ossicles in paleoecology and taphonomy: The last interglacial Falmouth Formation of Jamaica. *Palaios*, 7, 157–166.
- Górka, M., Studencka, B., Jasionowski, M., Hara, U., Wysocka, A. and Poberezhskyy, A. 2012. The Medobory Hills (Ukraine): Middle Miocene reef systems in the Paratethys, their biological diversity and lithofacies. *Biuletyn Państwowego Instytutu Geologicznego*, 449, 147–174
- Greenstein, B.J. 1991. An integrated study of echinoid taphonomy: Predictions for the fossil record of four echinoid families. *Palaios*, **6**, 519–540.
- Hall, K.R.L. and Schaller, G.B. 1964. Tool-using behavior of the California sea otter. *Journal of Mammology*, **45**, 287– 298
- Harzhauser, M., Mandic, O. and Zuschin, M. 2003. Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition: diversity, palaeogeography and palaeoclimate. *Acta Geologica Polonica*, 53, 323–339.
- Heller, C. 1858. Über neue fossile Stelleriden. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, 28, 155–170.
- Hendler, G., Miller, J.E., Pawson, D.L. and Kier, P.M. 1995.
  Sea Stars, Sea Urchins, and Allies: Echinoderms of Florida and the Caribbean. Smithsonian Institution Press, pp. 1– 390. Washington – London.
- Hilber, V. 1882. Geologische Studien in den ostgalizischen Miocän-Gebieten. *Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt*, **32**, 193–330.
- Jagt, J.W.M. and Codrea, V. 2010. A goniasterid starfish (Echinodermata, Asteroidea) preserved in a mid-Miocene

- rhyolitic ignimbrite, northwest Romania. *Acta Geologica Polonica*, **60**, 275–282.
- Jagt, J.W.M. and Ham, R.W.J.M. van der 1994. Early Palaeocene marsupiate regular echinoids from NE Belgium. Proceedings of the Eighth International Echinoderm Conference Dijon/France/6-10 September 1993, pp. 725– 729. Balkema: Rotterdam.
- Janakevich, A.N. 1977. Middle Miocene reefs of Moldavia, pp. 1-116. Stiinca; Kishinev. [In Russian].
- Jankowski, L., Kopciowski, R. and Ryłko, W. 2012. The state of knowledge of geological structures of the Outer Carpathians between Biała and Risca rivers – discussion. *Biuletyn Państwowego Instytutu Geologicznego*, 449, 203–216. [In Polish].
- Jasionowski, M., Górka, M., Studencka, B. and Poberezhskyy,
  A. 2005. Upper Badenian (Middle Miocene) coralline algal reefs of the Medobory Hills (Paratethys, West Ukraine): preliminary results of palaeontological and sedimentological investigations. *12th Congress R.C.M.N.S.* 6–11 September 2005, Vienna. Patterns and Processes in the Neogene of the Mediterranean Region. Abstracts, pp. 113–115. Wien.
- Jasionowski, M., Górka, M., Studencka, B. and Poberezhskyy, A. 2006. Miocene of Medobory Hills [Podilya, West Ukraine]. In: Wysocka, A. and Jasionowski, M. (Eds), Przebieg i zmienność sedymentacji w basenach przedgórskich. II Polska Konferencja Sedymentologiczna PO-KOS2, 20-23.06.2006, Zwierzyniec. Przewodnik sesji terenowych, streszczenia referatów i posterów, pp. 53–65. Grodzisk Mazowiecki.
- Kier, P.M. 1967. Sexual dimorphism in an Eocene echinoid. *Journal of Paleontology*, **41** (4), 988–993.
- Kier, P.M. 1969. Sexual dimorphism in fossil echinoids. In: Westermann, G.E.G. (Ed.), Sexual dimorphism in fossil Metazoa and taxonomic implications, pp. 215–222. E. Schweizerbartsche Verlagsbuchhandlung; Stuttgart.
- Kier, P.M. 1972a. Tertiary and Mesozoic echinoids of Saudi Arabia. Smithsonian Contributions to Paleobiology, 10, 1–242.
- Kier, P.M. 1972b. Upper Miocene echinoids from the Yorktown Formation of Virginia and their environmental significance. *Smithsonian Contributions to Paleobiology*, 13, 1–41.
- Kier, P.M. 1975. The echinoids of Carrie Bow Cay, Belize. *Smithsonian Contributions to Zoology*, **206**, 1–45.
- Koehler, R. 1915. Echinoderma I: Asteroidea, Ophiuroidea et Echinoidea. In: Michaelsen, W. (Ed.), Beiträge zur Kenntnis der Meeresfauna Westafrikas, Band 1. L. Friederichsen & Co; Hamburg.
- Kotchetoff, B., Kotchetoff, Y. and Da Veiga Ferreira, O. 1975. Contribution a la connaissance des gisements fossilifères miocènes au Nord du Cap d'Espichel. *Comunicaçoes dos Serviços Geológicos de Portugal*, **59**, 59–106.

- Kotlarczyk, J., Jerzmańska, A., Świdnicka, E. and Wiszniowska, T. 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene Early Miocene strata of the Polish Outer Carpathian Basin. *Annales Societatis Geologorum Poloniae*, **76**, 1–111.
- Kroh, A. 2003. The Echinodermata of the Langhian (Lower Badenian) of the Molasse Zone and the northern Vienna Basin (Austria). *Annalen des Naturhistorischen Museums in Wien*, **104 A**, 155–183.
- Kroh, A. 2005. Echinoidea neogenica. Catalogus Fossilium Austriae, Vol. 2, pp. 1–210. Österreichische Akademie der Wissenschaften; Wien.
- Kroh, A. 2007a. Hemipatagus, a misinterpreted Loveniid (Echinodermata: Echinoidea). Journal of Systematic Palaeontology, 5, 163–192.
- Kroh, A. 2007b. Climate changes in the Early to Middle Miocene of the Central Paratethys and the origin of its echinoderm fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253, 169–207.
- Kroh, A. and Harzhauser, M. 1999. An echinoderm fauna from the Lower Miocene of Austria: Paleoecology and implications for Central Paratethys paleobiogeography. Annalen des Naturhistorischen Museums in Wien, 101 A, 145–191.
- Kroh, A. and Nebelsick, J.H. 2003. Echinoid assemblages as a tool for palaeoenvironmental reconstruction an example from the Early Miocene of Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **201**, 157–177.
- Kroh, A. and Smith, A.B. 2010. The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, **8**, 147–212.
- Kudrin, L.N. 1957. Palaeoecological investigations of the lowermost Tortonian deposits from the south-western part of the Russian Platform. Geologicheskij Sbornik Lvovskovo Gologicheskogo Obshestva, 4, 277–294. [In Russian].
- Lachkhem, H. and Roman, J. 1995. Les Échinoides irréguliers (Néognathostomes et Spatangoides) du Messinien de Melilla (Maroc Septentrional). Annales de Paléontologie (Vert.-Invert.), 81, 247–278.
- Lambert, J. 1910-1915. Description des Echinides des terrains Néogènes du Bassin du Rhone. *Mémoires de la Société Paléontologique Suisse*, **37** (1910–1911), **38** (1911–1912), **39** (1913), **41** (1915), pp. 1–240.
- Lambert, J. 1923. Echinides vivants et fossiles recueillis à Madagascar par M. Raymond Decary. Mémoires de la Société de l'Académie d'Agriculture et des Sciences du Département de l'Aube, 85, 13–55. Troyes
- Lambert, J. 1933. Echinides de Madagascar communiqués par M.H. Besairie. Annales Géologiques du Service des Mines de Madagascar, 3, 1–49.
- Laube, G.C. 1871. Die Echinoiden der oesterreichisch-ungarischen oberen Tertiaerablagerungen. Abhandlungen der

- kaiserlich-königlichen geologischen Reichsanstalt, **5**, 55–74.
- Leeuw, A. de, Bukowski, K., Krijgsman, W. and Kuiper, K.F. 2010. Age of the Badenian salinity crisis; impact of Miocene climate variability on the circum-Mediterranean region. *Geology*, **38**, 715–718.
- Łomnicki, A.M. 1897. Atlas Geologiczny Galicyi; Tekst do zeszytu dziesiątego, Część 1: Geologia Lwowa i okolicy, pp. 1–208. Komisja Fizyograficzna Akademii Umiejętności; Kraków. [In Polish].
- Łomnicki, A.M. 1898. Atlas Geologiczny Galicyi; Tekst do zeszytu dziesiątego, Część **2**, pp. 1–167. Komisya Fizyograficzna Akademii Umiejętności; Kraków. [In Polish].
- Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. and Ávila, S.P. 2011. The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, 61, 243–264.
- McNamara, K.J. 1994. Diversity of Cenozoic marsupiate echinoids as an environmental indicator. *Lethaia*, **27**, 257–268.
- Mikuž, V. 2009. Scutellids from Miocene beds in Slovenia. *Geologija*, **52**, 205–212.
- Mortensen, T. 1913. Die Echiniden des Mittelmeeres, eine revidierte Übersicht der im Mittelmeere lebenden Echiniden, mit Bemerkungen über neue oder weniger bekannte Formen. *Mitteilungen aus der Zoologischen Station zu Neapel*, **21**, 1–40.
- Mortensen, T. 1928. A monograph of the Echinoidea; 1. Cidaroidea, pp. 1–551. C.A. Reitzel, Copenhagen H. Milford, London.
- Mortensen, T. 1951. A monograph of the Echinoidea; **5** (2). Spatangoida 2, pp. 1–593. C.A. Reitzel; Copenhagen.
- Nebelsick, J.H. 1992. The Northern Bay of Safaga (Red Sea, Egypt): an actuopalaeontological approach; III, Distribution of echinoids. *Beiträge zur Paläontologie von Österreich*, **17**, 5–79.
- Nebelsick, J.H. 1995. Actuopalaeontological investigations on echinoids: The potential for taphonomic interpretation. In: Emson, R., Smith, A.B. and Campbell, A. (Eds), Echinoderm Research 1995. Proceedings of the fourth European echinoderms colloquium, pp. 209–214. Balkema; Rotterdam/Brookfield.
- Nebelsick, J.H. and Kroh, A. 2002. The stormy path from life to death assemblages: The formation and preservation of mass accumulations of fossil sand dollars. *Palaios*, **17**, 378–393.
- Néraudeau, D. 1991. Lateral variations of size-frequency distribution in a fossil echinoid community and their palaeoecological significance. *Lethaia*, **24**, 299–309.
- Nichols, D. 1959. Changes in the Chalk heart-urchin *Micraster* interpreted in relation to living forms. *Philosophical Transactions of the Royal Society of London*, **B242** (693), 347–437.

- Pazdro, Z. 1953. Tectonic units of the Opole Minor, and phases of their development. Bulletin of the Geological Survey of Poland (top secret, for Survey Staff only; unnumbered), pp. 1–114. Wydawnictwa Geologiczne; Warszawa. [In Polish and Russian].
- Peryt, T.M. 2006. The beginning, development and termination of the Middle Miocene Badenian salinity crisis in Central Paratethys. *Sedimentary Geology*, **188-189**, 379–396.
- Philip, G.M. and Foster, R.J. 1971. Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance. *Palaeontology*, 14, 666–695.
- Philippe, M. 1998. Les échinides miocènes du Bassin du Rhône: révision systématique. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon, 36, 1–441.
- Pisera, A. 1996. Miocene reefs of the Paratethys: a review. In: Franseen, E.K., Esteban, M., Ward, W.C. and Rouchy, J.-M. (Eds), Models for carbonate stratigraphy from Miocene reef complexes of Mediterranean regions. SEPM Concepts in Sedimentology and Paleontology, 5, 97–104. Tulsa, Oklahoma
- Radwański, A. 1970. Dependence of rock-borers and burrowers on the environmental conditions within the Tortonian littoral zone of Southern Poland. In: Crimes, T.P. and Harper, J.C. (Eds), Trace Fossils. *Geological Journal Special Issue* 3, 371–390. Liverpool.
- Radwański, A. and Wysocka, A. 2001. Mass aggregation of Middle Miocene spine-coated echinoids *Echinocardium* and their integrated eco-taphonomy. *Acta Geologica Polonica*, 51, 295–316.
- Radwański, A. and Wysocka, A. 2004. A farewell to Świniary sequence of mass-aggregated, spine-coated echinoids *Psammechinus* and their associates (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, **54**, 381–399.
- Radwański, A., Górka, M. and Wysocka, A. 2006. Middle Miocene coralgal facies at Maksymivka near Ternopil (Ukraine): A preliminary account. *Acta Geologica Polonica*, 56, 89–103.
- Radwański, A., Wysocka, A. and Górka, M. 2011. 'Entobia balls' in the Medobory Biohermal Complex (Middle Miocene, Badenian; western Ukraine). Acta Geologica Polonica, 61, 265–276.
- Radwański, A., Wysocka, A. and Górka, M. 2012a. Miocene burrows of the Ghost Crab *Ocypode* and their environmental significance (Mykolaiv Sands, Fore-Carpathian Basin, Ukraine). *Acta Geologica Polonica*, 62, 217–229.
- Radwański, A., Wysocka, A. and Górka, M. 2012b. Mykolaiv Sands in Opole Minor and beyond: sedimentary features and biotic content of Middle Miocene (Badenian) sand shoals of Western Ukraine. *Geological Quarterly*, 56, 475–492.
- Ragaini, L. 1997. Echinoid fauna from the Quaternary fring-

- ing reef of Aqaba (Jordan). *Palaeontographia Italica*, **84**, 1–19.
- Rakusz, J. 1927. Asteroiden der älteren Mediterran-Stufe aus der Umgebung von Salgótarján. Földtani Közlöny, 56, 191–195.
- Roemer, F. 1870. Geologie von Oberschlesien, pp. 1–587. Nischkowsky; Breslau [Wrocław].
- Roman, J. 1970. Description des Échinides. *In*: C. Montenat and J. Roman, Échinides Néogènes d'Espagne (Provinces d'Alicante et de Murcie). *Annales de Paléontologie, Invertébrés*, **56**, 89–138.
- Roman, J. 1983. Échinides "marsupiaux" (fam. Temnopleuridae) dans le Néogène de l'Ouest européen. *Annales de Paléontologie (Vert.-Invert.)*, **69**, 13–42.
- Sacco, F. 1892. Sopra alcuni Asteroidei fossili. *Atti della Reale Accademia delle Scienze di Torino*, **25**, 739–745.
- Schneider, S., Berning, B., Bitner, M.A., Carriol, R-P., Jäger, M., Kriwet, J., Kroh, A. and Werner, J. 2009. A parautochthonous shallow marine fauna from the Late Burdigalian (early Ottnangian) of Gurlarn (Lower Bavaria, SE Germany): Macrofaunal inventory and paleoecology. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 254, 63–103.
- Schultz, H. 2005. Sea urchins; a guide to worldwide shallow water species, pp. 1–484. Partner Scientific Publications; Hemdingen.
- Seilacher, A. 1979. Constructional morphology of sand dollars. *Paleobiology*, **5**, 191–221.
- Sismonda, E. 1842. Appendice alla monografia degli Echinidi fossili del Piemonte. *Memoria della Reale Accademia della Scienze di Torino, Serie* 2, 4, 385–394.
- Smith, A.B. 1984. Echinoid palaeobiology, pp. 1–190. Allen & Unwin; London.
- Smith, A.B., Stockley, B. and Godfrey, D. 2010. Spatangoida.
  In: Smith, A.B. (Ed.), The Echinoid Directory. World
  Wide Web electronic publication http://www.nhm.ac.uk/palaeontology/echinoids.
- Szörényi, E. 1953. Miozäne Echinoiden aus den westlichen Teilen der Ukraine. *Geologica Hungarica, Series Palaeontologica*, **23**, 1–122.

- Śliwiński, M., Bąbel, M., Nejbert, K., Olszewska-Nejbert, D., Gąsiewicz, A., Schreiber, B.C., Benowitz, J.A. and Layer, P. 2012. Badenian–Sarmatian chronostratigraphy in the Polish Carpathian Foredeep. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 326–328, 12–29.
- Teisseyre, H. 1938. Quelques observations sur la paléogéographie de Roztocze aux environs de Lwów. *Annales de la Société Géologique de Pologne*, **14**, 113–154.
- Vadász, M.E. 1915. Die mediterranen Echinodermen Ungarns. *Geologica Hungarica*, **1** (2), 1–178 (= 79–254).
- Wiedl, T., Harzhauser, M., Kroh, A., Ćorić, S. and Piller, W.E. 2013. Ecospace variability along a carbonate platform at the northern boundary of the Miocene reef belt (Upper Langhian, Austria). *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, http://dx.doi.org/10.1016/ j.palaeo.2012.12.015
- Wright, T. 1855. On fossil echinoderms from the Island of Malta; with notes on the stratigraphical distribution of the fossil organisms in the Maltese beds. *Annals and Magazine of Natural History, Series 2*, **15** (No. 86), pp. 101–127, 175–196 and 262–277.
- Wysocka, A. 1999. Sedymentacja klastycznych utworów badeńskich wschodniej części Roztocza, pomiędzy Zwierzyńcem a Lwowem. Unpublished Ph.D. thesis; Institute of Geology, University of Warsaw. [In Polish].
- Wysocka, A. 2002. Clastic Badenian deposits and sedimentary environments of the Roztocze Hills across the Polish-Ukrainian border. *Acta Geologica Polonica*, **52**, 535–561.
- Wysocka, A., Radwański, A. and Górka, M. 2012. Mykolaiv Sands in Opole Minor and beyond: Sedimentary features and biotic content of Middle Miocene (Badenian) sand shoals of Western Ukraine. *Geological Quarterly*, 56, 475–492.
- Zágoršek, K., Radwańska, U. and Radwański, A. 2012. Bryozoa from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). Bulletin of Geosciences, 87, 201–218.
- Zapfe, H. 1971. Index Palaeontologicorum Austriae. *Catalogus Fossilium Austriae*, **15**, pp. 1–140. Springer-Verlag; Wien New York.

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