Symmetry disorders of the test of the Miocene echinoid *Echinocyamus* from Poland

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This paper presents cases of disorders in the test symmetry in three species of *Echinocyamus* (*E. pusillus*, *E. calariensis*, and *E. apicatus*) from the Miocene deposits of Poland. It is the first study of this topic based on fossil material. The large collection (ca. 60 000 specimens) allowed distinction of several types of these rare disorders (14 specimens), which are illustrated by SEM and explanatory drawings. An example of a deformity formed on the pentamerous system is also presented. The deformations develop in the rudiment; consequently the apical system and the test of the mature individual which is formed at its margin display disorders. The anomalies most commonly appear as an additional growth zone (6-ray symmetry), lack of one growth zone (4-ray symmetry), or both deformations simultaneously (changed 5-ray symmetry). The changes appear in the apical system (number of ocular pores), test (number of petals), and peristome outline. The anomaly linked with the incorrect position of the periproct on the test surface, resulting from the delay of its displacement during early ontogenic stages, is characteristic and unique for such deformations.

Key words: Echinodermata, *Echinocyamus*, symmetry disorders, malformation, Miocene.

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Introduction

The organisation of an echinoid test develops within the body of its larvae (Hinegardner 1975; Smith 1997; Arenas-Mena et al. 1998; Minsuk and Raff 2002). Recently, investigations of the early stages of echinoid development have been carried out along several lines of inquiry (e.g., Arenas-Mena et al. 1998—expression of the *Hox* gene complex; Davison et al. 1998—specification of cell fate in the embryo; Peterson et al. 2000a—the A/P axis in echinoderm ontogeny and evolution; Peterson et al. 2000b—expression in set-aside cells; Popodi and Raff 2001—summary of recent investigations; Aragón et al. 2002—mathematical model for formation of fivefold symmetric patterns; Hart 2002—life history evolution and comparative developmental biology of echinoderms; Minsuk and Raff 2002—pattern formation in a pentameral animal; Morris et al. 2004—expression of an *Otx* gene and the developing central nervous system). However, recent papers rarely extend beyond the metamorphosis stage of an echinoid, after which the test grows into a structure that can potentially be fossilised. Only a few papers describe and illustrate echinoid tests with disordered symmetry—all cases refer to living individuals, either from natural environments or reared (e.g., Koehler 1924; Jackson 1927 and literature cited therein; Hinegardner 1975). Cases of test disorders in fossil material have been very rarely noted (Capeder 1907 and examples in Jackson 1927).

There are several papers referring to the rudiment and early post-larval development stages of echinoderms (e.g., Hotchkiss 1998, 2000a; Wray and Bely 1994; David and Mooi 1998; Saucède et al. 2003). Recent papers (e.g., Saucède et al. 2004) study living and fossil organisms to trace the ontogeny and evolution of this group of animals. The significance of fossils in such analyses increases, when the skeleton structure (EAT: extraxial-axial theory) and rules governing its formation (OPR: ocular plate rule) have been described (David and Mooi 1996, 1999; Mooi and David 1997; David et al. 2000). Both EAT and OPR refer to skeletal parts of animals. So, they are exellent tools in analyses of symmetry disorders in the tests of fossil echinoids.

A rich collection of specimens (ca. 60 000) of the genus *Echinocyamus* van Phelsum, 1774 (order Clypeasteroida, family Fibulariidae) from the Miocene of Poland offers an opportunity to examine for the first time symmetry disorders of the test of fossil irregular echinoids. The *Heterostegina* sands, the sedimentation of which terminated the marine sequence in the Korytnica Bay (Radwański 1969; Bałuk and Radwański 1977; Szymanko and Wójcik 1982; Gutowski 1984), yield particularly well preserved remains of *Echinocyamus* i.e., *Echinocyamus pusillus* Müller, 1776; *E. calariensis* (Lambert, 1907) and *E. apicatus* Mortensen, 1948 (see Mączyńska 1977, 1987, 1991; Ali and Mączyńska 1986; Kroh 2005; Ceranka 2007), which recently have been studied with regard to predator interactions (Ceranka and Złotnik 2003; Złotnik and Ceranka 2005).

This paper is focused on tracing the abnormal ontogeny, based on deformed tests of mature individuals (fossil material does not contain pre-metamorphic stages of sea urchins).

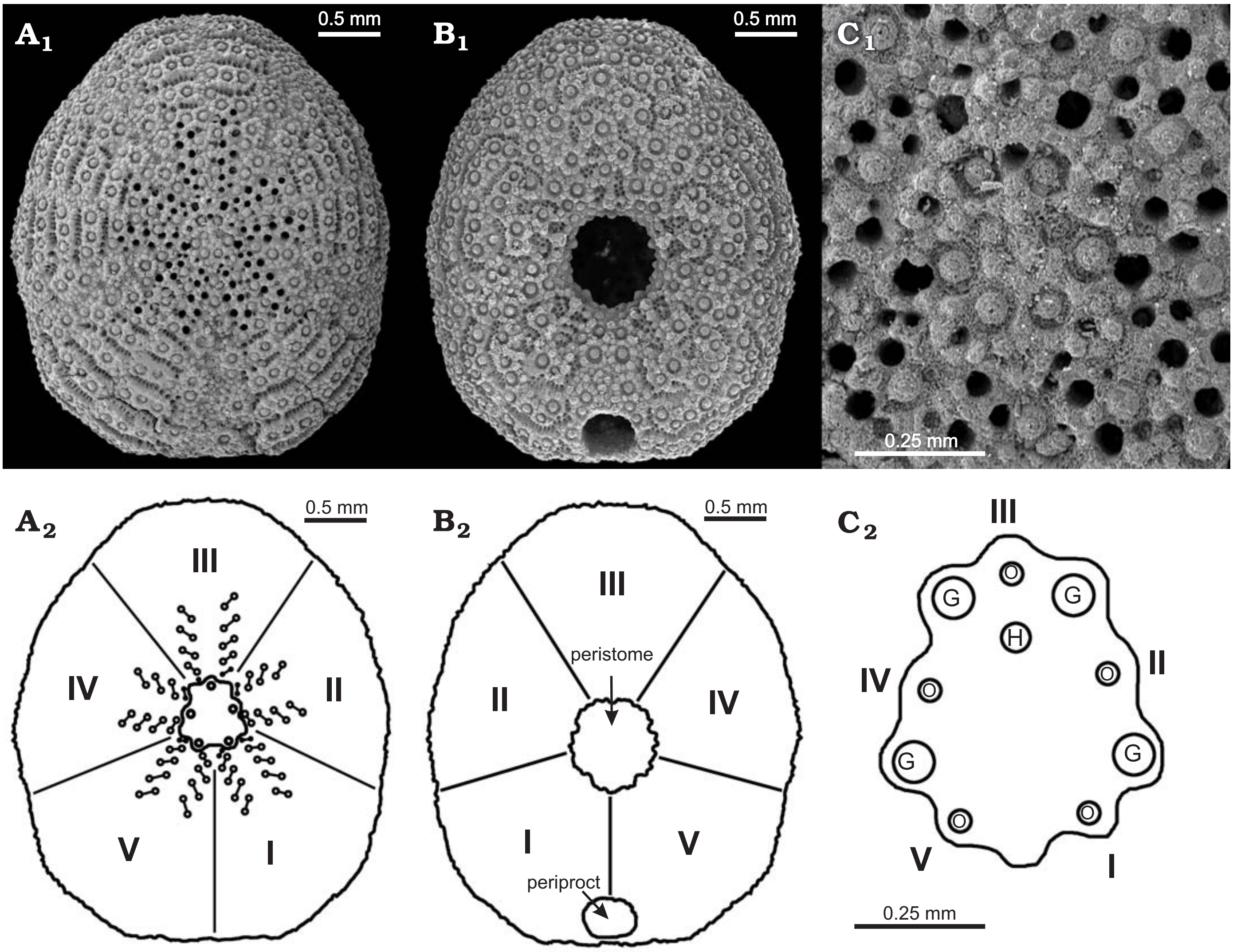

Fig. 1. Correctly developed test of fibulariid echinoid *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/0) from Korytnica, Badenian. **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V, growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

The working hypothesis regarding these deformations goes back to the development stage before echinoid metamorphosis and searches there for the pre-metamorphic causes of symmetry disorders. An alternative hypothesis—that these deformations are secondary to an injury that damaged a formed pentamerous system—is also discussed.

The material was collected during field work between 2000–2004 in the vicinity of Korytnica village (Holy Cross Mountains, Poland). The photographs were made in the Scanning Microscope and Microanalysis Laboratory (Faculty of Geology, University of Warsaw) using a JSM-6380LA JEOL scanning electron microscope.

Institutional abbreviation.—MWG, Faculty of Geology, University of Warsaw, Poland.

Other abbreviations.—EAT, extraxial-axial theory; OPR, ocular plate rule.

Typically developed *Echinocyamus* test

The typically developed test of the three examined Miocene *Echinocyamus* species is small (length from 1 to 10 mm, typically 3 mm), oval or pentagonal in outline (Fig. $1A_1$, B_1). The anterior part is often higher and narrower. Test shape is loaf-like to conical, with the culmination always at the apical system, on which the hydropore (equivalent of the madreporite), five ocular pores, and four gonopores occur (Fig. 1C). The petaloid area comprises five ambulacral petals (Fig. $1A_2$). Each petal consists of two columns, of which each is represented as two rows of pores. The pore pair of one respiratory tube foot is composed of pores diagonal to the structure's length. Each petaloid column may comprise up to 7–8 pore pairs, on average 3–4. Pores are round, and their diameter increases with the growth of the corresponding ambulac-

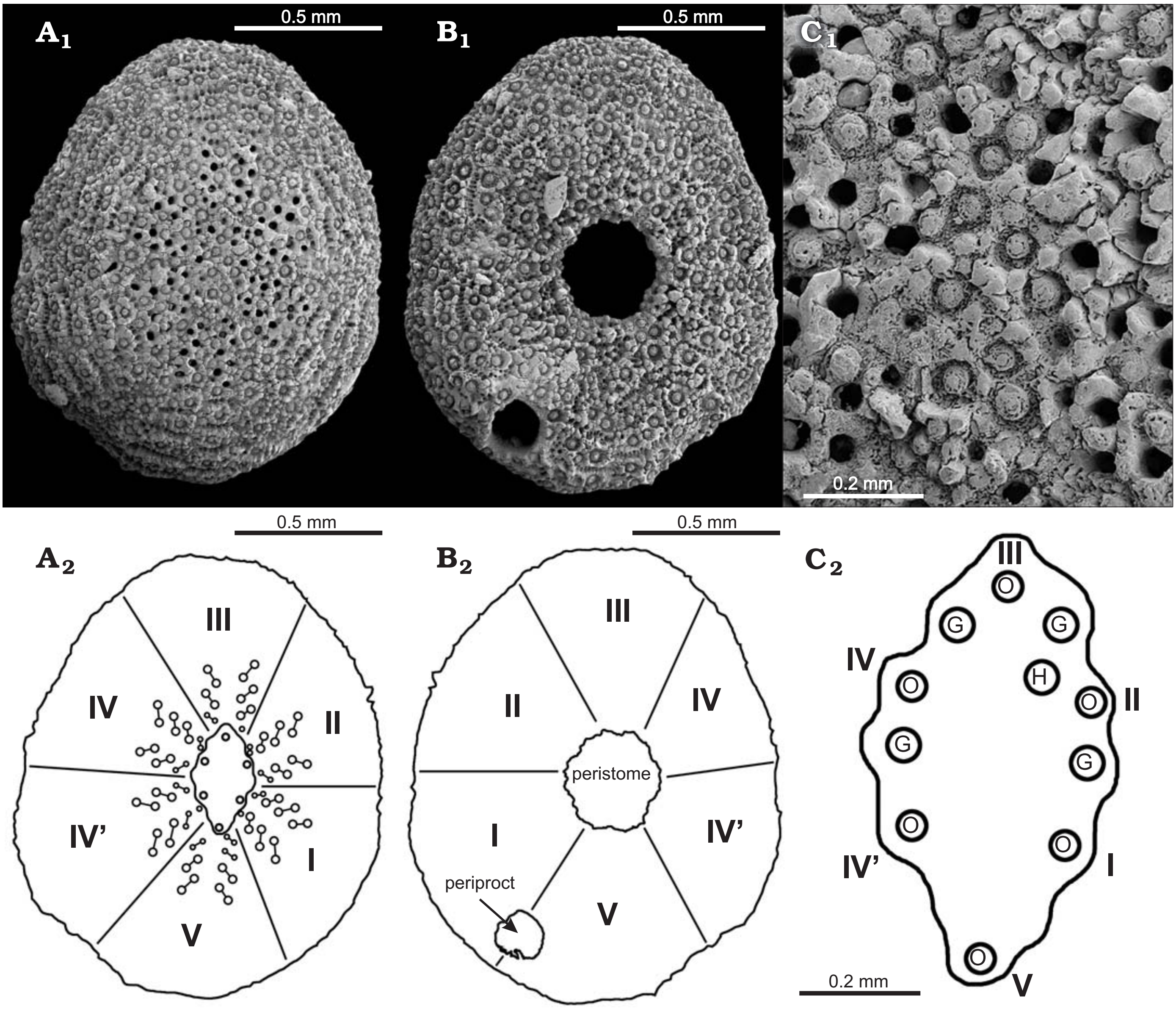

Fig. 2. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/1) from Korytnica, Badenian. L+ anomaly (6-ray symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

ral tube foot. In side view profile, the test margin (ambitus) forms an arc, which is more acute in less arched forms. The oral side is flat or slightly concave with a centrally placed, round or pentagonal peristome (Fig. 1B). The round or transversely oval (*E. pusillus*), transversely oval or lenticular (*E. calariensis*) periproct is located halfway between the mouth opening and the test margin (*E. pusillus*, *E. calariensis*) or marginally (*E. apicatus*)—in the latter case its margin lies in the plane oblique or almost perpendicular to the oral side (Fig. 1B). The periproct is situated always between the first and second pair of interambulacral plates (counting outward from the mouth, not counting the unpaired basicoronal).

The described symmetry deformations cause crucial changes of test and peristome shape. Therefore, the location and shape of the periproct are in practice the only features distinguishing the three species.

Symmetry disorders of the *Echinocyamus* test

Examples of various types of symmetry disorders in *Echinocyamus* individuals have been observed in the Miocene material. A code describing symmetry disorders is applied in this paper. The letter L (R) indicates that the test anomaly occurs to the left (right) of Lovén's axis, in aboral view. The sign "+" ("-") indicates an additional (lacking) growth zone on the side

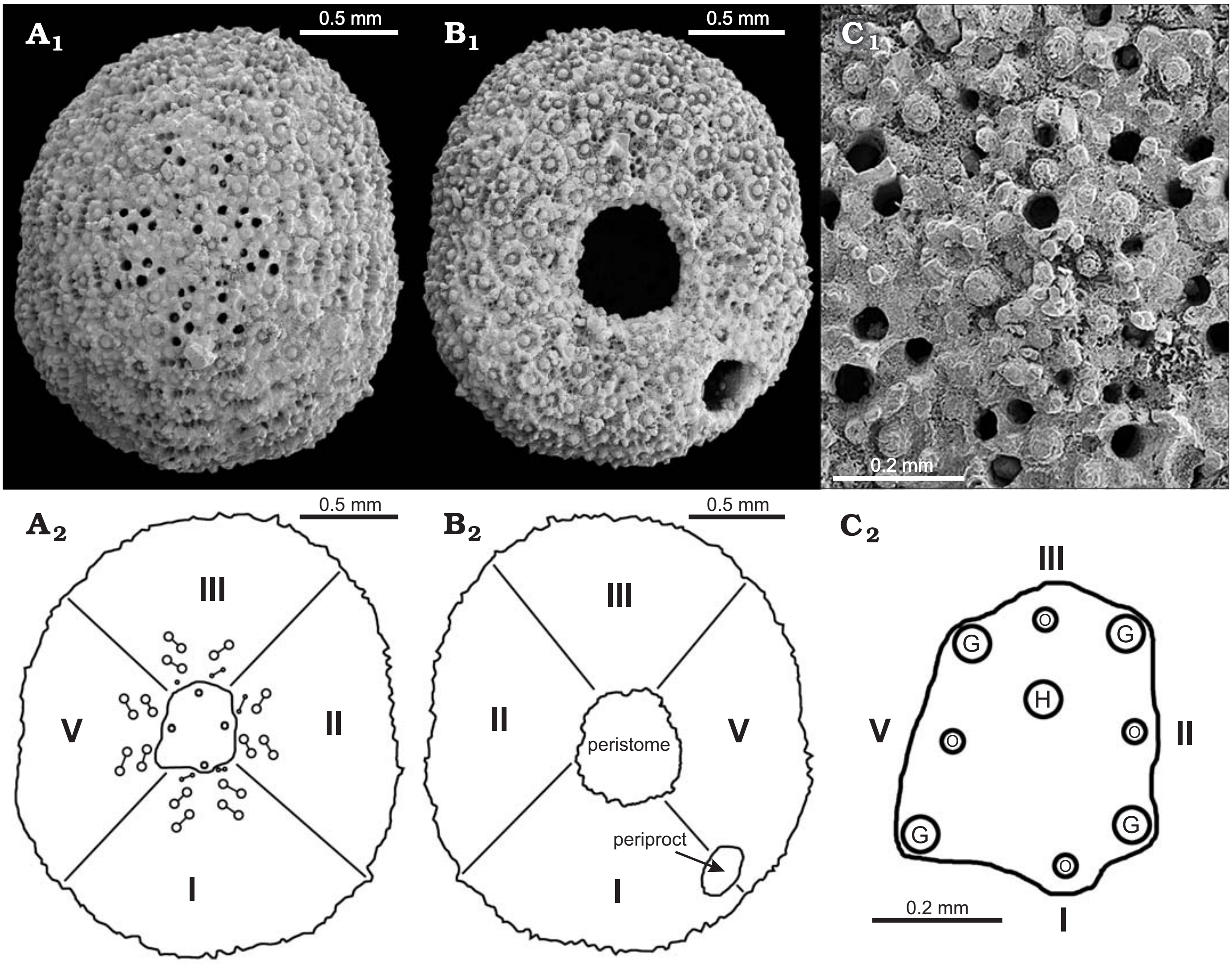

Fig. 3. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/3) from Korytnica, Badenian. L- anomaly (4-ray symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen, A_2, B_2, C_2, explanatory drawings of the same. I–V growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

marked by the letter. A growth zone is defined as an ambulacrum and two half-interambulacra, one on each side of the ambulacrum, plus the ocular plate. Each growth zone is a "developmental unit" or "module" (Saucède et al. 2003). Titles for the descriptions below contain detailed information about the zone or zones to which the anomaly can be referred.

The location of the anomaly on the test surface begins with analysis of the apical system. The presence of a typical pattern (as seen in normal specimens) of gonopores, hydropore and ocular pores indicates the anterior part of the animal (growth zone III) in the symmetry disorder specimen. The second step is linked with counting the growth zones between the anterior of the animal and the periproct. Two zones on each side occur in a correctly developed test. If their number is higher, then we have an additional zone. If it is lower, then one zone is lacking. It is assumed herein that if the periproct is located correctly with regard to the test margin, then the anomalies occur within the growth zone/s not neighbouring the periproct (zones II and/or IV and additional zones II' or IV'). If the position of the periproct on the test is not correct, this is the effect of an anomaly occurring within the zone/s adjacent to the periproct (zones I and/or V and additional zones I' or V').

L+ anomaly (additional zone IV').—This anomaly, resulting in 6-ray symmetry, was observed in two specimens of *Echinocyamus apicatus* (MWG/E/1, see Fig. 2, and MWG/E/2). The anomaly is linked with the appearance of an additional ambulacral area and surrounding half-interambulacral areas (Fig. 2). The test contains three anterior growth zones and three posterior growth zones— which suggests that the additional growth zone appeared in the posterior part of the test. The posterior left ambulacral area (aboral view) is slightly elevated above the others and extends the test margin, disturbing the oval outline of the whole specimen—this is the addi-

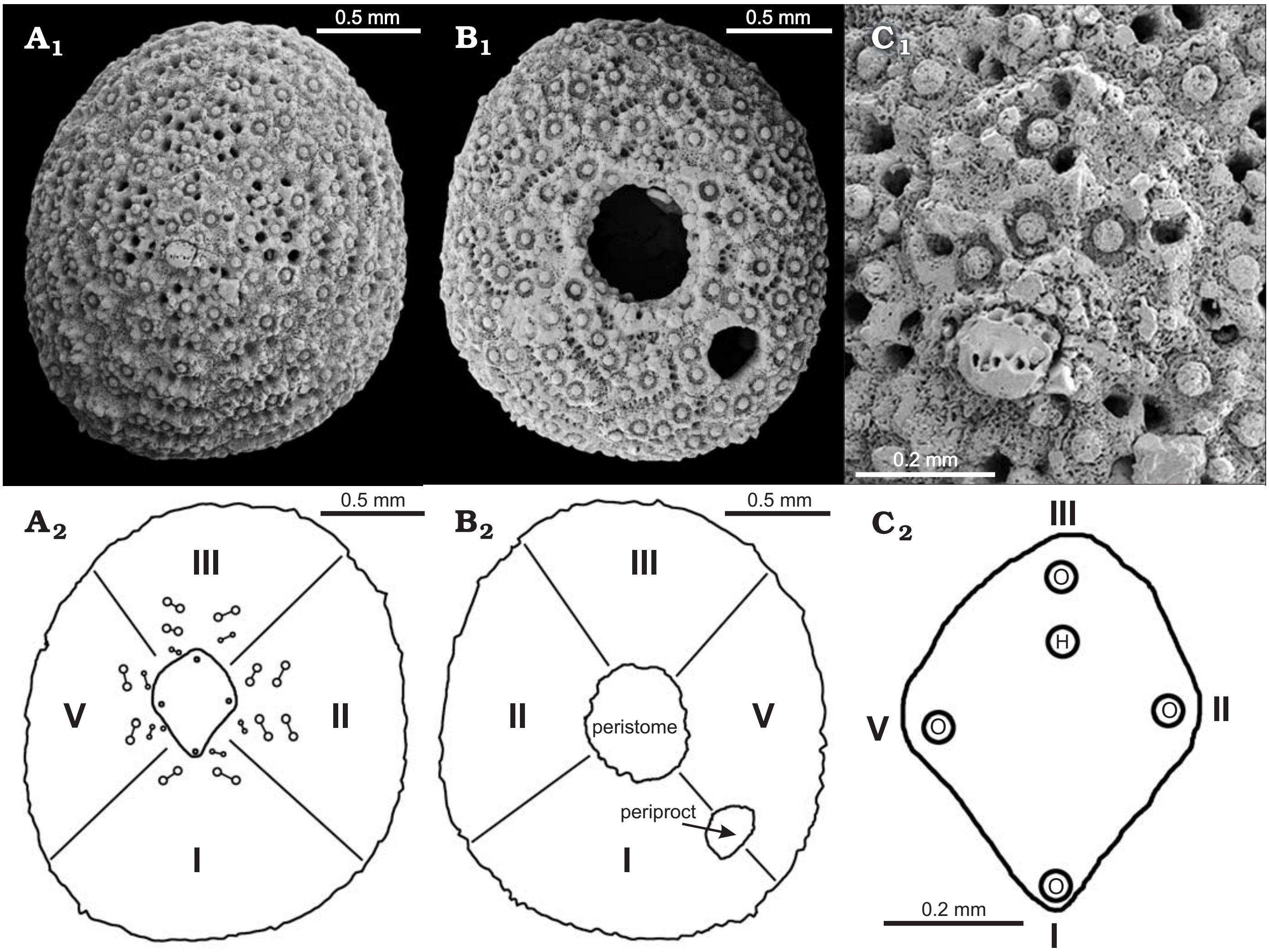

Fig. 4. Deformed test of *Echinocyamus calariensis* (Lambert, 1907) (MWG/E/1P) from Korytnica, Badenian. L- anomaly (4-ray symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V growth zone; O, ocular pore; H, hydropore.

tional growth zone (IV' on Fig. $2A_2$, B_2). All areas have a correctly developed surface microarchitecture. The apical system comprises: a hydropore, 6 ocular pores and 4 genital pores (Fig. 2C). From the aboral view the bilateral symmetry seems to be correct, however, from the oral side it is evident that the symmetry is disordered (Fig. $2B_1$). The anomalies are linked with the rear part of the test, where the additional growth zone is inserted between a "bivium module" comprised of growth zones I and V and containing the periproct, and growth zone IV (Fig. $2B_2$). It is easy to observe that by removing the additional zone and then putting the test together, a regular *E. apicatus* test would appear. It is worth noting that the peristome shape also changes, attaining a regular hexagonal form.

L- anomaly (lack of zone IV).—The effect of this anomaly is 4-ray symmetry and was noticed in five specimens (four *Echinocyamus apicatus* MWG/E/3, see Fig. 3, MWG/E/4-6 and one *E. calariensis* MWG/E/1P, see Fig. 4). The ambulacral zones on the aboral side form the shape of a Maltese cross (Figs. 3A, 4A). The tests are oval in outline and are shorter than typical representatives of the species. The apical system contains: a hydropore, 4 ocular pores and 4 gonopores (Fig. 3C). The *E. calariensis* specimen does not possess gonopores. However, this is typical of juveniles of these dimensions (Fig. 4C). Two bilateral axes can be distinguished in the apical system and the test outline—an anterior-posterior axis and an additional perpendicular axis. The oral side contains the periproct (of correct diameter and shape) deflected to the right from the anterior-posterior axis, however, correctly oriented with reference to the test margin (Figs. 3B, 4B). The peristome has a deformed outline comprising four margins corresponding to the particular growth zones (Figs. 3B, 4B).

R- anomaly (lack of zone II).—This anomaly, resulting in 4-ray symmetry, was observed in four specimens of one species: *Echinocyamus apicatus* (MWG/E/7, see Fig. 5; MWG/E/8, see Fig. 6A; MWG/E/9, see Fig. 6B; MWG/E/10, see Fig. 6C). The deformations of the specimen presented in Fig. 5 are in ef-

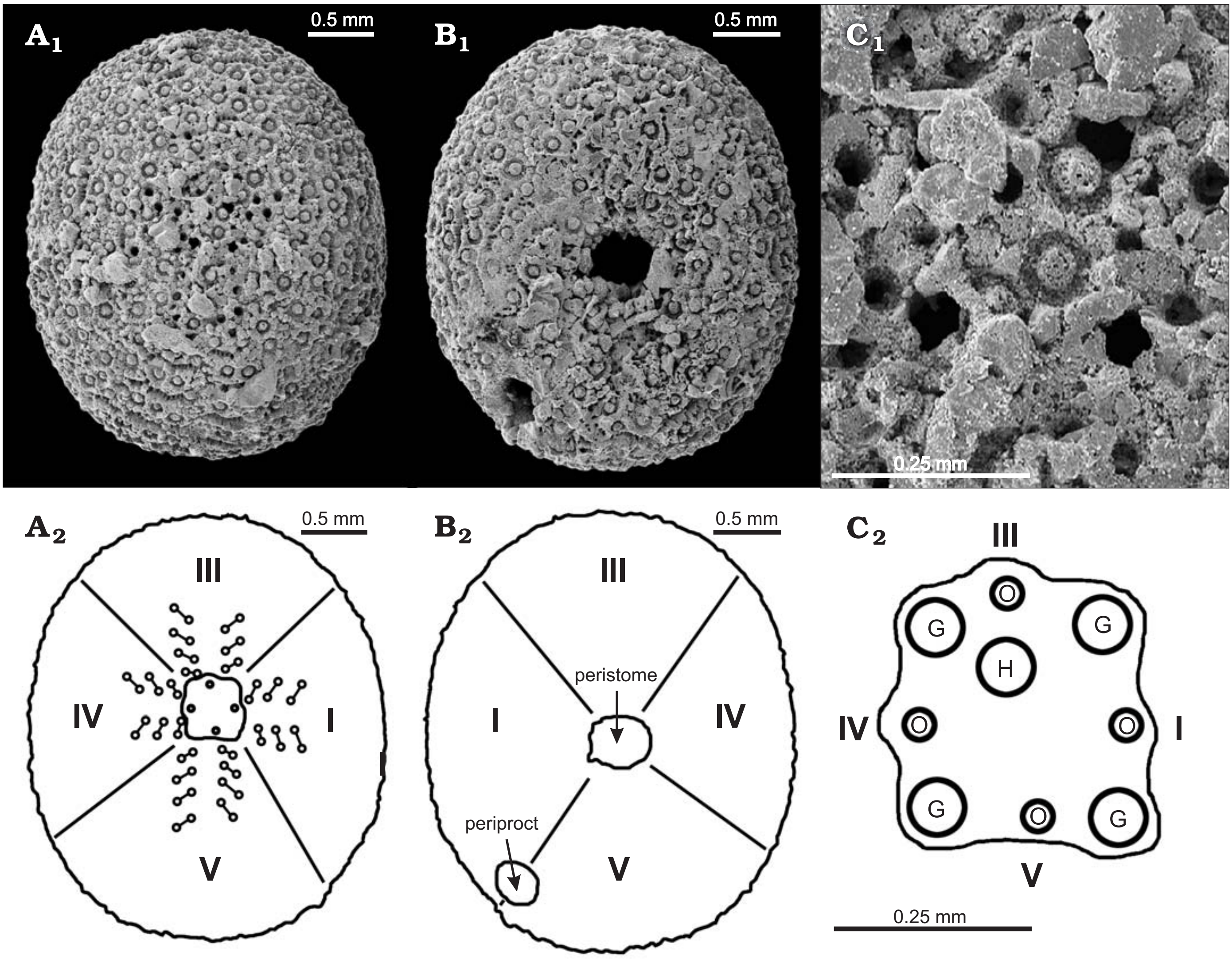

Fig. 5. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/7) from Korytnica, Badenian. R- anomaly (4-ray symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V, growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

fect the mirror image of deformations observed in the previous example. The state of preservation impedes the analysis, but without doubt the aboral side shows four petals forming the Maltese cross pattern (Fig. 5A). The apical system has four large gonopores (sexual dimorphism similar to *E. bisexus*, see Kier 1968), four ocular pores and a hydropore (Fig. 5C). The peristome and periproct have correct dimensions; the periproct is displaced to the left of the axis of bilateral symmetry (Fig. 5B). The studied specimen, along with the specimens illustrated in Fig. 6 display a series of individuals representing a malformation linked with different displacements of the periproct. This series suggests several rules: the closer the periproct is to the peristome (distance measured on test surface), the smaller the deformation of the petal pattern (in ascending order: Figs. 5A_1, B_1, 6A–C). The displaced periproct pushes out the nearest petals, and the test outline gradually changes. The largest deformations take place when the periproct is located at the test margin (Fig. 6B). When it is closer to the apical system (aboral side Fig. 6C_1) or peristome (oral side, Fig. 6A_2), the deformations in the test outline are much smaller. The specimen presented in Fig. 6C has more than one pair of interambulacral plates between peristome and periproct.

Tests of specimens presented in Fig. 6 display an apical system similar to that in the specimen in Fig. 5. Petals in all specimens have a similar number of pore pairs (Fig. 6A_1–C_1).

L-R+ anomaly (appearance of zone I', lack of zone V).— This kind of anomaly causes changed 5-ray symmetry and was observed in only one specimen of *Echinocyamus apicatus* (MWG/E/11, see Fig. 7). The deformations occur in the posterior part of the test and include the occurrence of atypical growth zones and the presence of a displaced periproct on the aboral side. The zones lying in the posterior part of the individual (I and I' in Fig. 7A_2) do not posses an interambulacral zone in between. The remaining elements are correctly developed, i.e., they begin with ocular pores (Fig. 7C), two correctly de-

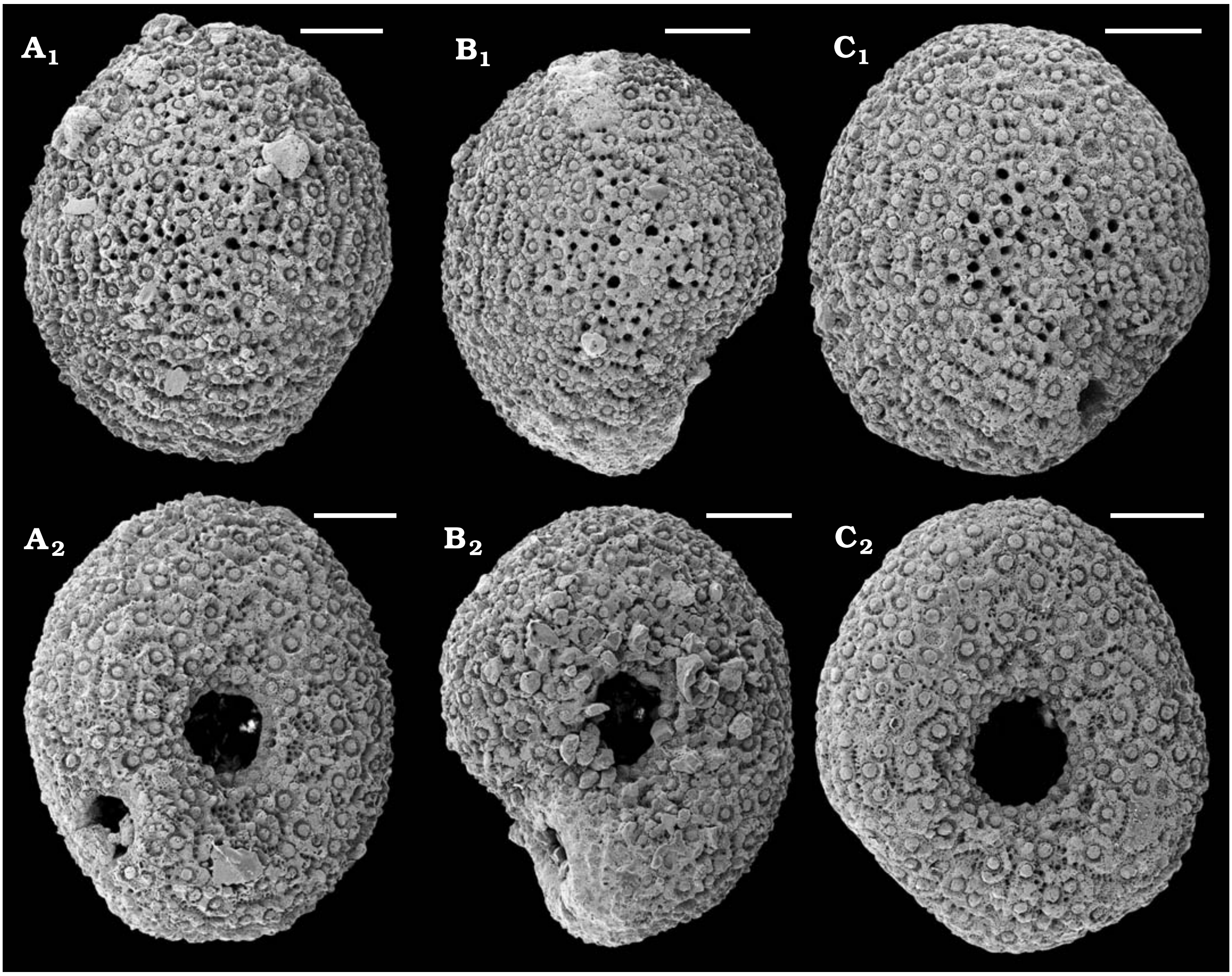

Fig. 6. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 from Korytnica, Badenian, illustrating the changing position of the periproct in R- anomaly (4-ray symmetry). **A**. MWG/E/8; aboral side (A_1), oral side (A_2). **B**. MWG/E/9; aboral side (B_1), oral side (B_2). **C**. MWG/E/10; aboral side (C_1), oral side (C_2). Scale bars 0.5 mm.

veloped petals occur, below which are located zones with unipores of accessory tube feet, reaching right to the peristome. The second deformation is linked with the occurrence of the periproct on the left side of the test and in mid-height of the aboral side (Fig. 7A). However, it lies asymmetrically on the interradial suture of the interambulacral zone, displaced toward the axis of bilateral symmetry of the test. The oral side is developed correctly, apart from the consequences resulting from changes on the aboral side— lack of periproct (Fig. 7B). The test has more than one pair of interambulacral plates between peristome and periproct. The diameter and shape of the peristome and periproct are normal.

L+R- anomaly (appearance of zone IV', lack of zone II).— This anomaly, resulting in changed 5-ray symmetry, was observed in one specimen of each species (*Echinocyamus apicatus* MWG/E/12, see Fig. 8; and *E. pusillus* MWG/E/2P, see Fig. 9). On the aboral side the disorder can be observed as a slight swelling of the right side of the test outline and development of the apical zone typical of regular echinoids, i.e., with five gonopores (Figs. 8, 9). The remaining elements of the apical system, the pattern and development of the petals are normal. On the oral side the anomalies are visible in the incorrect position of the periproct, which it lies on the left side of the individual (this results in swelling of the test outline). The shape and diameter of the periproct and peristome as well as their position in relation to the test margin are correct.

Development of test symmetry in Recent echinoids

Pentameral symmetry is diagnostic of all Recent echinoderms (Peterson et al. 2000a: fig. 6). Because the story of echinoderm evolution is generally one of increasing dominance of ele-

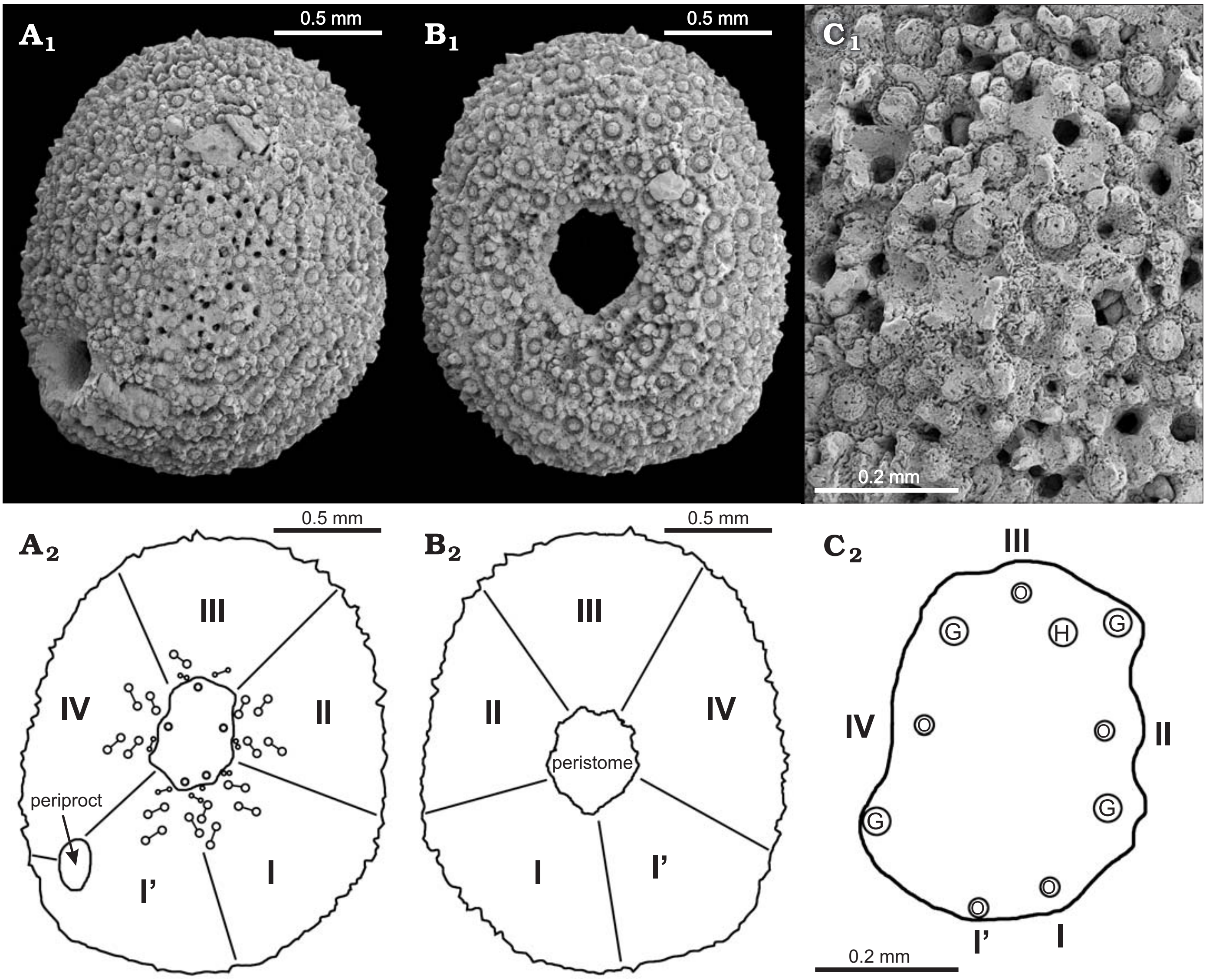

Fig. 7. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/11) from Korytnica, Badenian. L-R+ anomaly (5-ray changed symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen, A_2, B_2, C_2, explanatory drawings of the same. I–IV, growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

ments "building" that symmetry, pentamery is less prominently expressed in the very oldest taxa than in more derived forms (Mooi et al. 2005). In regular (non-directional) echinoids this feature is reflected in the arrangement of the test plates, as well as in the position of the peristome and the endocyclic periproct. There is also a second, constantly changing, group of irregular (directional) echinoids, which display a secondary, bilateral symmetry (Saucède et al. 2003), e.g., lamp urchins, heart urchins, and sand dollars.

The body wall of all echinoderms, fossil and extant, is constructed of two major components: axial and extraxial elements that "display radically different embryological origins" (Mooi et al. 2005: 548; see also David and Mooi 1996, 1999). A consequence of this theory (EAT) is that pentamery is intimately associated with the development of axial skeleton—the test's corona (i.e., gene expression in the larval hydrocoel). The axial skeleton is organized into five growth zones (their numeration is identical to the ambulacral areas according to the Lovén system) formed in accordance with the ocular plate rule (Melville and Durham 1966; Saucède et al. 2003) (Fig. 1A, B). Following this mechanism, each growth zone is comprised of an ocular plate and its associated ambulacrum surrounded by two half-interambulacra, one on each side (Mooi et al. 2005). New ambulacral and interambulacral plates are formed next to the ocular plate and move downwards to the oral side while they grow and further plates are added behind. The extraxial skeletal system is limited to the scales present on the periproctal membrane and to the genital plates. In *Echinocyamus* ontogeny the extraxial periproct takes an exocyclic position between adjacent growth zone modules I and V in the corona after the first pair of interambulacral plates have formed.

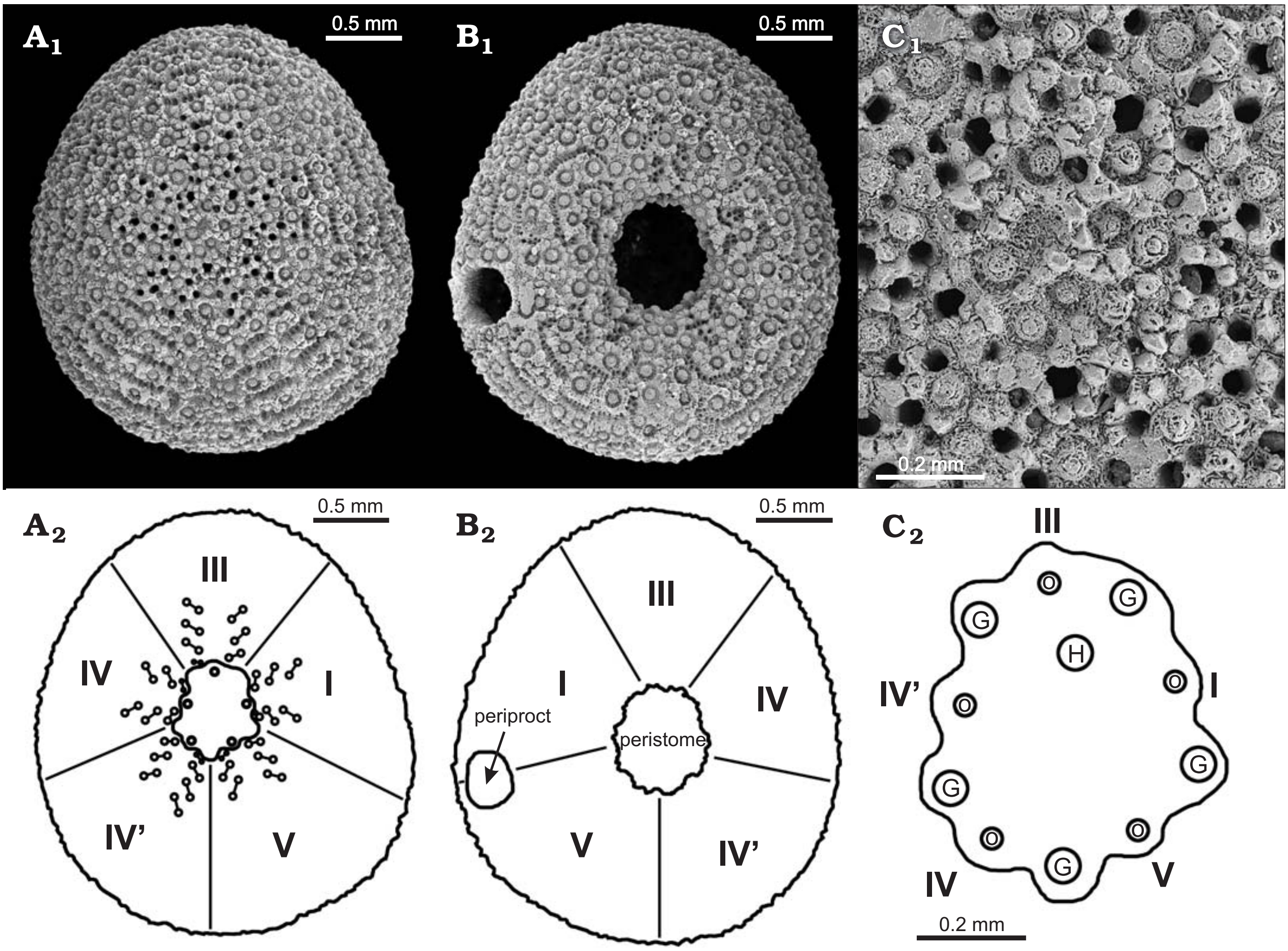

Fig. 8. Deformed test of *Echinocyamus apicatus* Mortensen, 1948 (MWG/E/12) from Korytnica, Badenian. L+R- anomaly (5-ray changed symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

A better understanding of the anomalies requires a closer look at the origins of symmetry. Therefore, the ontogeny of the regular echinoid *Paracentrotus lividus* is presented below (see Gosselin and Jangoux 1998). All processes described below take place also during the embryogeny of irregular form although more rapidly.

Three days after fertilisation, *P. lividus* has already passed the cleavage, blastula, and gastrula stages. Morphological and physiological differentiation of the cells has begun. The archenteron with the accompanying, still symmetrical coeloms, secondary mouth opening and the first skeletal elements reinforcing the first four arms of the larva, have developed (Jura et al. 1985). For the next 15 days, the larva prepares for metamorphosis, floating close to the surface. It develops the first asymmetric structures. This is linked with the faster development of coeloms on the left side of the larva. There also the larval ectoderm undergoes invagination forming the vestibule, which attains its position opposite the hydrocoel and then connects with the latter to form the rudiment—the first indications of a form with radial symmetry (Hinegardner 1975; Emlet 1995). Soon afterwards the primary tube feet and epineural folds develop—this is the beginning of the nervous system. These are the first structures reflecting the symmetry of the growing echinoid (Smith 1997; David et al. 2000; Sly et al. 2002). It is assumed herein that the number of primary tube feet or epineural folds corresponds to the number of the later growth zones. Between days 14 and 18 after fertilisation, a large number of mesenchymal cells start to produce the test (apical system and test plates), conserving the developed symmetry. This is the last moment when substantial disorders in the organism’s plan can take place. Later metamorphosis, when the rudiment is exposed and most larval tissues are resorbed, as well as the later ontogeny, are governed by the earlier established symmetry (Spirov 1996).

It has been proved (Saucède et al. 2003) that the genital plate 2 (G2) appears first, and genital plate 4 (G4) last—just before metamorphosis—while G4 remains beyond the circlet

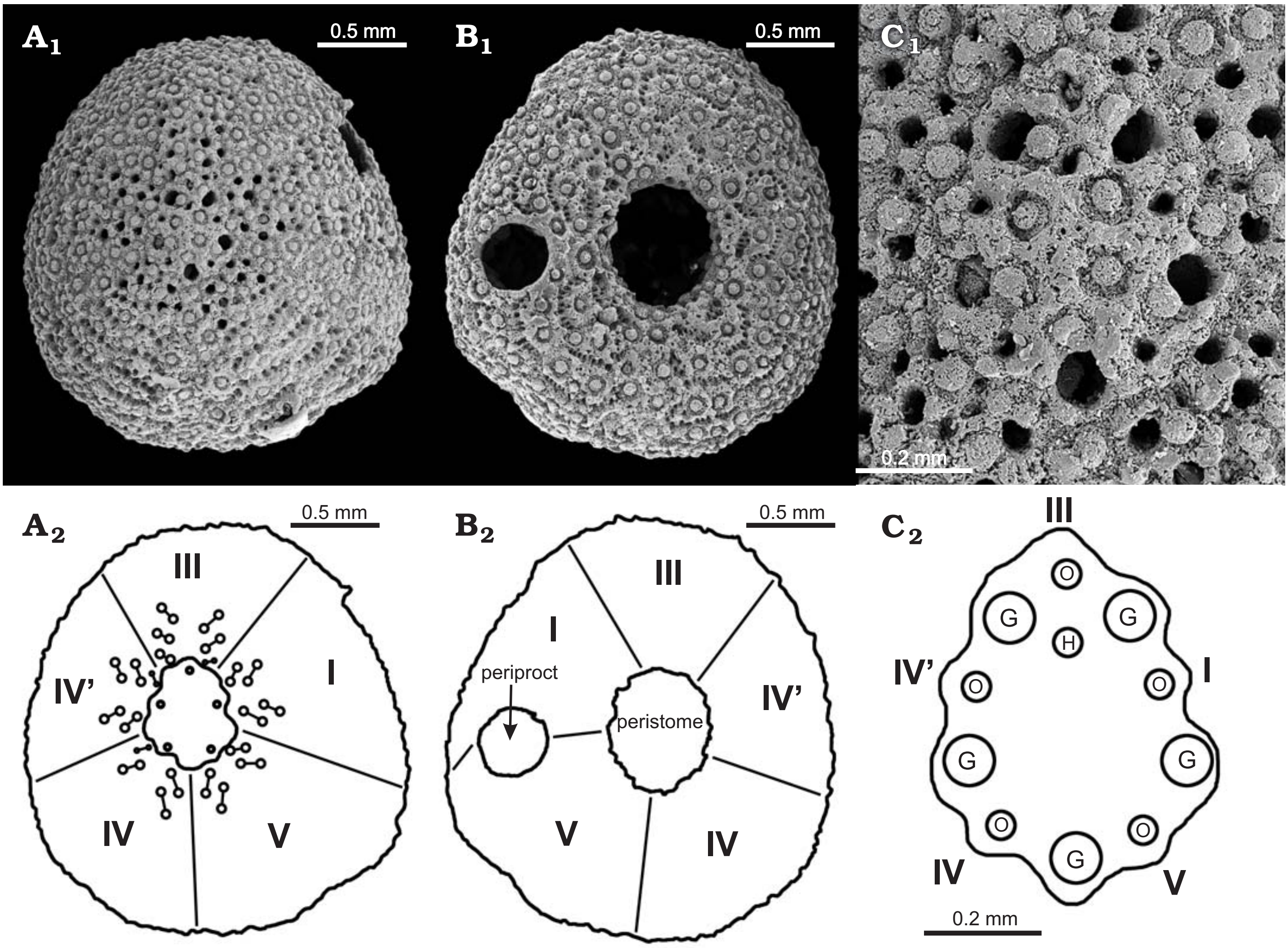

Fig. 9. Deformed test of *Echinocyamus pusillus* Müller, 1776 (MWG/E/2P) from Korytnica, Badenian. L+R- anomaly (5-ray changed symmetry). **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V, growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

of the remaining genital plates during transformation (Fig. 10A). During metamorphosis, the rudiment is exposed and the larval tissues are pushed towards the apical system. In consequence, the genital plates migrate in the same direction, where later they grow until fusion. The developed system has primordial bilateral symmetry about the axis passing through ambulacral area II and genital plate G4—the von Ubisch axis. When genital plate G4 is included in the circlet of the remaining pores, its appearance between G3 and G5 and growth result in the enlargement of the apical system and change of symmetry into that typical of mature individuals—pentameral symmetry with Lovén's axis running through ambulacrum III and genital plate G5 (Fig. 10B). Additionally, in irregular echinoids the test shape is remodelled as a consequence of exocyclic periproct migration, which causes disappearance of the posterior gonopore (Melville and Durham 1966; Jesionek-Szymańska 1968; Saucède et al. 2003).

In clypeasteroid echinoids, including *Echinocyamus*, "the genital plates are no longer discrete and have seemingly fused together to form a single large central plate with hydropores" (monobasal apical system) (Melville and Durham 1966). Another possibility is that the monobasal plate is composed only of G2 (see Emlet 1985). Five ocular plates are present.

Causes of symmetry disorders

Jackson (1927: 491) wrote that symmetry anomalies "may roughly be considered as belonging to one of two types. First, those which are aberrant from the beginning of formation of the skeletal parts and therefore evidently date back to some irregularity in the development of the pluteus. Second, those which had begun to be formed on the pentamerous system, and then through some accident or disease a partial suppression or addition of some parts occured."

The next section contains examples of the first type (except last one). Its causes are therefore discussed in detail.

It has been documented in sea urchins (Hinegardner 1975) that the progeny of inbred lines often includes numerous individuals with 2-, 3-, 4-, 6-ray symmetry. However, only individuals with 4-, 5- and 6-ray symmetry are able to develop, and the 4-ray anomaly is the most common (as in the studied material). According to the cited paper, "there seems to be a loss of symmetry control" (Hinegardner 1975: 686). New investigations have confirmed this opinion. Cross-species hybrids have all parts characteristic of juvenile forms, but most possess an abnormal 5-ray symmetry (Raff et al. 1999). A similar development can be observed in cross-genera hybrids, in which the symmetry is also variable (Raff et al. 2003). In the Miocene basin several species of *Echinocyamus* lived in the same environment. If the intervals at which gametes of different species were liberated were similar, then this might be the cause of the presented disorders.

Another possible cause could be spontaneous mutations, the chances of which are low (on average, a mutation of a particular gene takes place once in ca. 100 000 genital cells), however, expected (Jura et al. 1985). This view has been followed by Dawkins (after Hotchkiss 1998) and Spirov (1996). Spirov (1996) stated that the "ideal" 5-ray model is permanently disordered and "in fixed moment of developmental time the achieved 3-, 4-, 5-fold symmetry of the gene-control pattern will be used as the prepattern for following morphogenetic movements. Gene expression dynamics became frozen by switching off the expression control mechanism. As a result, since this stage, the following morphogenesis proceeds in accordance with 3- or 4- or 5-ray symmetry" (Spirov 1996). This has been supported by the new investigations of Minsuk and Raff (2002), who documented the first stages of structural growth in an echinoid—the rudiment and vestibule are formed autonomously, i.e., the processes taking place in the larval body cannot disturb the foundation of symmetry in the rudiment. Such mutations must have been masked in a large population living on the bottom of Miocene sea.

It has to be pointed out that there is also a different view about the nature of symmetry and its disorders in echinoderms, which is represented by Breder (1955) and Hotchkiss (1998, 2000a). This first author stated that the "echinoids are 'trapped' in their pentagonal organisation" (Breder 1955: 206). The presence of deviations from the ideal 5-ray form should then be attributed to the "teratological incomplete development" (Hotchkiss 2000a: 349), originating during the ontogenic processes.

Causes may be found in the incorrect expression of genes responsible for the foundation and development of symmetry (the *Hox*, *Dlx*, *Otx*, and *Runt* genes) (Arenas-Mena et al. 1998; Martinez et al. 1999; Peterson et al. 2000b; Popodi and Raff 2001; Lowe et al. 2002). *Runt* gene is responsible for the formation of the nervous system and for the foundation of the 5-ray symmetry in the rudiment. Incorrect expression of this gene regulator causes the interruption of primordial tube foot formation—an early structure reflecting symmetry (Nielsen et al. 2003; Morris et al. 2004). It seems that disorders in *Dlx* expression can have a crucial meaning for forming primary lobes in the rudiment, which is the key moment in the origin of symmetry in adult echinoderms (Lowe et al. 2002).

Interpretation of symmetry disorders in the Miocene *Echinocyamus*

In the simplest case, test symmetry disorders (Jackson's "first type", 1927) are linked with the development of an additional growth zone or with the lack of one growth zone. The origins of this anomaly most probably lies within the soft tissues of the rudiment; fossil material, however, does not allow such investigations. Palaeontologists thus may speculate based only on fossilised parts and therefore the analysis will start from the development of the apical system. Disorders in the ocular plates of this system must in consequence cause anomalies of the test formed at the margins of the apical system, e.g., growth zone II or growth zone IV. To illustrate this relationship, models of apical systems proposed by Saucède et al. (2003) have been applied. They refer to regular echinoids, but in the author's opinion they can be easily adapted for irregular echinoids (the black area on the schemes reflects the central part of the apical system and not the periproct) (Fig. 10).

L+ anomaly (additional zone IV')—6-ray symmetry.—The anomaly (L+) probably originated in the rudiment, where an additional primordial tube foot grew, from which the later additional growth zone developed (IV' on Fig. $2A_2$–C_2). Adopting the scheme of Saucède et al. (2003), this would be the doubled ocular plate IV (Fig. 10C). Development of this individual took place normally, i.e., without influence on the outline of the test until the time when there was no more place for the newly formed plates within the additional zone. It seems that until this moment the test was quite rigid, therefore the deformations are not evenly distributed, but concentrated at the boundary between growth zones I and II (Fig. 2B). The growth of zone IV resulted in the formation of bilateral symmetry, but expansion of an additional growth zone IV' caused further spreading out of the test and in effect, its destruction, as the "bivium module" with the periproct moved beyond its position on Lovén's axis.

The shape of the peristome also undergoes changes, which suggests that the arrangement of the Aristotle's lantern could be changed into 6-ray (or 4-ray see below) (see examples of *Arbacia punctulata* in Jackson 1927). This hypothesis should be checked against living specimens (e.g., *E. pusillus* or *E. apicatus*).

An anomaly which is a mirror reflection of the anomaly discussed above was illustrated by Koehler (1924: pl. 9: 1 and 5) in living *Clypeaster rosaceus*, a specimen which also has 6-ray symmetry. The only differences between the discussed specimens are on the oral side: the additional zone is inserted between the "bivium module" and growth zone II and lies in the left (oral view) posterior part of the test (R+ anomaly). The doubled growth zone (II) and its "twin" (II') possess one food groove near the peristome, which at a cer-

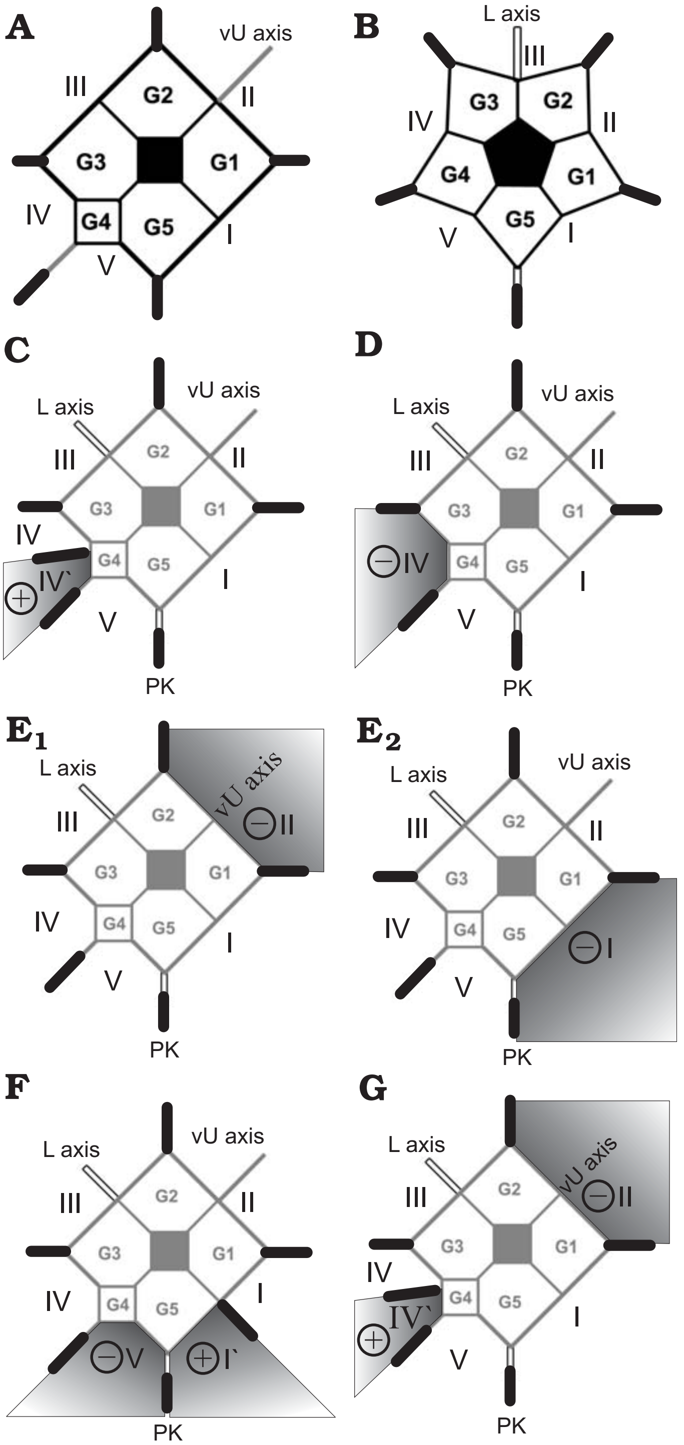

Fig. 10. Models of apical systems. **A**. Primordial (normal) symmetry. **B**. Lovén symmetry. **C**–**G**. Primordial (changed) symmetry. A, B adopted from Saucéde et al. (2003). Abbreviations: L, axis-Lovén's axis; vU, axis-von Ubisch axis; PK, periproct; I–V, growth zone; G1–G5, genital areas.

tain distance bifurcates (see Koehler 1924: pl. 9: 5). From this point right to the apical plate the test is developed as two normal growth zones. According to the OPR each of these growth zones must have its own ocular plate (there should be six ocular plates).

L- anomaly (lack of zone IV)—4-ray symmetry.—This anomaly has its origin in the rudiment, where only four primary lobes have developed, resulting in the lack of a fifth growth zone changing symmetry (Fig. 10D). The growth zone on the left side of the axis of bilateral symmetry (L-) is missing, because the periproct has been relocated to this position. Most probably the primary lobes associated with ocular IV (Fig. 10A) have not developed. The primary pattern of zones has been preserved, which allows the von Ubisch axis to be marked out in the mature individual. It can be traced by superimposing the primordial symmetry pattern (Fig. 10D) onto the photograph of the aboral side of these specimens (Figs. $3A_1$ or $4A_1$). At the same time, the G2-G5 axis, along which the periproct migrated during ontogeny, can be observed. Only the outline of the test corresponds to Lovén's symmetry plan—zone III indicates the anterior part of the organism, II—the anterior right side, etc. This means that the process of shaping the test of irregular echinoids is not linked with symmetry disorders taking place earlier during ontogeny. Each growth zone is predisposed to play a particular role (i.e., ambulacrum III marks the anterior part of organism), which is accomplished despite disorders in other zones. This conclusion supports the idea of "individual ray identities" and validates the search for ray homologies between classes of echinoderms (Hotchkiss 1998). The lack of a certain zone influences the shape of the peristome, which loses its pentagonal outline and the number of ocular pores in the apical system.

The lack of growth zone IV (or II see below) results in the reduction of the test surface, and thus its smaller dimensions in relation to normal individuals of a given species. The additional growth zone results in the opposite effect (see above).

Development of the gonopore close to the axis, along which the periproct was displaced, in the specimen of *E. apicatus* (Fig. 3) is notable because ordinarily there is no pore here. This specimen shows that disorders in the development of the test do not influence the position and number of gonoducts, i.e., there are no places on the test surface predisposed for gonopore formation. In the place indicated by the developing genital ring resorption of the plate takes place and a perforation is formed.

An identical anomaly (L-) in the living *Clypeaster rosaceus* has been illustrated by Koehler (1924: pl. 28: 1, 4).

R- anomaly (lack of zone II or I)—4-ray symmetry.—The presented case shows, like the previous example, an incomplete pattern reflected by the lack of one growth zone. The periproct is displaced to the right of the Lovén axis (R- anomaly). The growth zones building the anterior (III) and posterior right (I) or anterior right (II) are present, which means that zone II (specimen with the periproct in its normal position) or I (specimens with the periproct in an abnormal position) is lacking. Its lack may be the result of disorders taking place in ocular II (Fig. $10E_1$) or ocular I (Fig. $10E_2$) of the apical system. Thus, growth zone IV and V occur on the left, and only one growth zone on the right side of the bilateral symmetry axis. The development of a larger number of growth zones on one

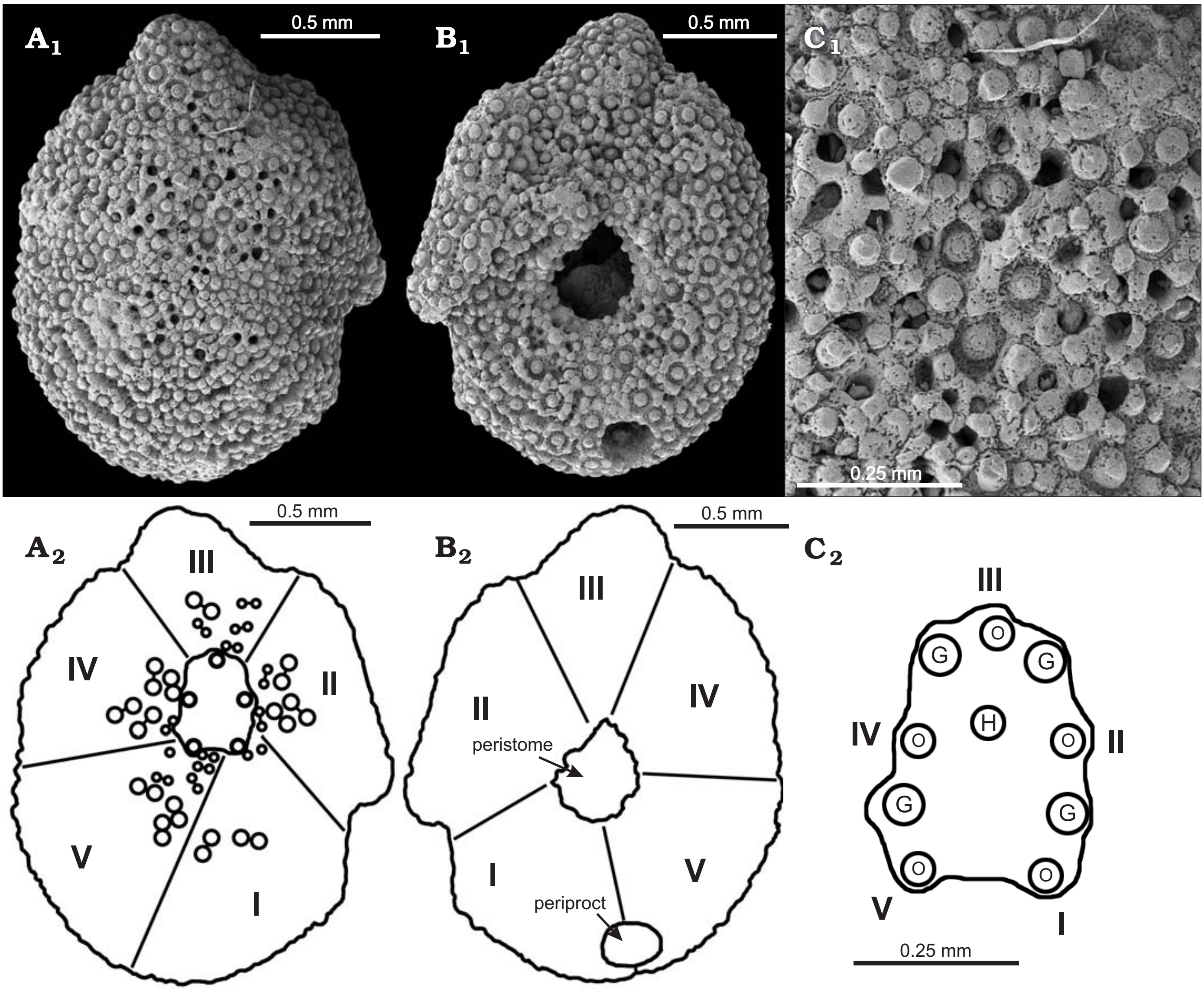

Fig. 11. Example of "second type" deformity formed on the pentamerous system (*Echinocyamus apicatus* Mortensen, 1948, MWG/E/13) from Korytnica, Badenian. **A**. Aboral side. **B**. Oral side. **C**. Close-up of apical system. A_1, B_1, C_1, photos of the specimen; A_2, B_2, C_2, explanatory drawings of the same. I–V, growth zone; O, ocular pore; G, gonopore (genital pore); H, hydropore.

side of the axis results in the relative migration of the zone with the periproct to the right (view from the aboral side).

Growth zone III marks the anterior of the mature individual, the periproct is displaced along the suture between developing growth zones V and I (Fig. 10E_1) or II (Fig. 10E_2). The process of development of the posterior part of the test with the periproct took place following a delay, which is illustrated by specimens in Fig. 6. The delay can be measured by the position of the periproct—the closer it is to the apical system (on the aboral side—Fig. 6C, or on the margin—Fig. 6B), the larger is the delay in the time of its switch onto the test and the larger disorders in the petal pattern. The specimen presented in Fig. 6C has more than one pair of interambulacral plates between the peristome and periproct. This is a proof linking this anomaly with an early stage of ontogeny. The development of the petals has not been subject to deformations—the number of pore pairs is typical of a normal individual.

Deformations of the test outline around the periproct can be linked with disease-induced changes caused by infection under the test leading to dwarfing (atrophy?) of the soft tissues, the lack of which defined the test shape. The origin of such deformations should be explained on the basis of living specimens.

L-R+ anomaly (appearance of zone I', lack of zone V)—changed 5-ray symmetry.—The interpretation of this case is much more complex. The periproct lies on the aboral side. For some reason it began its "relocation" quite late (after third? pair of interambulacral plates) and did not finish its developmental move to the oral side. Thus, it can be assumed that the anomaly took place near the periproct (growth zone V). The disorder can be explained as the effect of the lack of ocular V (Fig. 10F). This may the cause of deformations in the rear part of the test, in this case the abnormal position of the periproct.

An additional zone occurs on the right side of the test. Deformation of the two growth zones on the right side in the rear of the test suggest that the most posterior growth zone is the additional growth zone (I'). The disorder can be explained as the effect of doubling of the area associated with ocular I (Fig. 10F). The posterior ambulacral zones should be interpreted as two growth zones (two ocular pores in the apical system in Fig. 7C) without their halves of interambulacral zones in between (zones I and I') (see Jackson 1927; Hotchkiss 2000b for examples). In the examples discussed hitherto, the growth zone was a part of the test, in which the particular elements were not changed. This case is, however, different, because two zones display malformations. It is difficult to point to the cause which only in one case resulted in malformations of the pattern of ambulacral and interambulacral plates.

The anomalies observed in this specimen can be interpreted differently. The test possesses five growth zones correctly distributed with regard to 2-ply symmetry (i.e., II and I to the left and IV and V to the right). According to Saucède et al. (2003) it is a constraint that extraxial elements do not penetrate axial modules. The periproct can only migrate between adjacent growth zone modules (interradius of an interambulacrum). The cause of the observed periproct position could be its abnormal migration or displacement from the apical system (location at the suture boundary between zones IV and V, instead of at the suture boundary between zones I and V) and a considerably delayed incorporation of the periproct (extraxial element) within the surface of the developing test (axial part). The posterior ambulacral zones are in this interpretation two growth zones without their halves of interambulacral zones in between (zones I and V). What could have caused the disappearance of the interambulacral plates between these ambulacra? It is possible that the periproct "relocation" to the posterior part (via "gateway" see Saucède et al. 2003) was blocked by a twin ocular (zones V and I), and the exocyclic migration was forced to an adjacent interradial suture. Its lack in the V/I position is due to the lack of a seam (i.e., columns of interambulacral plates). The position taken by the migrating periproct in this specimen (and in this interpretation) coincides with von Ubisch's axis and is the ancestral location of the periproct in Eleutherozoa (see Hotchkiss 1998, Fig. 2).

L+R- anomaly (appearance of zone IV', lack of zone II)—changed 5-ray symmetry.—In these cases two processes have been disrupted: symmetry placement and, for the first time to such a degree, formation of the genital system. The first disorder can be explained as the effect of the lack of ocular II area by simultaneous doubling of the area associated with ocular IV (Fig. 10G). The consequence of such anomalies (L+R-) is the lack of growth zone II and the appearance of growth zone IV'. Three zones developed (IV, IV', V) to the left of the bilateral symmetry axis and only one (I) to the right (Figs. 8A_2, B_2 and 9A_2, B_2). Therefore, the area with the periproct has been relocated towards the side with the smaller number of developing zones.

The genital system has not been subject to disorders in the other examples. There is no evidence linking this anomaly with symmetry disorders.

All the discussed anomalies can be attributed only to deformations in the growth zones at the ends of the developing hydrocoel torus (between IV and V and located on von Ubisch's axis; Hotchkiss 1998). This interpretation is simpler, but it does not explain why only some anomalies cause delay in the incorporation of the periproct into the axial part of the test.

"Second type" deformities.—The Miocene specimen of *Echinocyamus apicatus* (MWG/E/13; see Fig. 11) from the MGW collection is an example of a deformity formed on the pentamerous system (Jackson 1927).

The specimen has five growth zones. In contrast to the examples discussed above, the growth zones are in positions typical of individuals without anomalies (Fig. 11A_2, B_2). The apical system is located on the test apex and possesses four gonopores and five ocular pores (Fig. 11C). The periproct is correctly developed both with regard to its shape and location in relation to the bilateral symmetry axis. Only the rear part of the test of this individual has the specific characteristics: oval outline, loaf-like shape, oral side flat. The growth zones II and III have prominent swellings of the test (Fig. 11A_1, B_1). The peristome shape is changed, attaining an irregular outline. On the aboral side of the test all five ambulacra have anomalies linked with the varied sizes and irregular arrangment of the isopores of the petals (Fig. 11A_2).

The growth malformations appeared after establishment of symmetry (5-ray) and test habit (bilateral). This is evidenced by the preserved test symmetry. The anomaly is linked with the incomplete development of the water-vascular system (?disorders of the third phase of distal-less gene expression, see Lowe et al. 2002). Additional, in growth zones II and III, the anomaly is linked with loss of shape control.

Conclusions

The 5-ray symmetry of the echinoid test seems to be a stable feature. Disorders occur extremely rarely. As a result, there are hardly any examples and analyses of this topic in the literature. Therefore, Miocene fossils illustrating symmetry disorders are a unique find.

Disorders of 5-ray symmetry are not lethal; moreover, the resulting individuals have a specific ontogeny. The anomalies are observed in three species of genus *Echinocyamus*. Analysis of the studied material allows formulation of several general opinions, referring to the influence of anomalies in early ontogenic stages on the test and different soft parts of irregular echinoids of the genus *Echinocyamus*.

Test symmetry.—The determination of the number of growth zones takes place within the soft tissues of the rudiment (pri-

Table 1. Possible symmetry anomalies of the echinoid test, based on the studied material.

Ocular plate	Type of anomaly	Symmetry	Result in test	Material	Source
ocular II doubled	R+	6	appearance of II’	*Clypeaster rosaceus*	Koehler 1924
ocular IV doubled	L+	6	appearance of IV’	*Echinocyamus apicatus*	this study
lack of ocular IV	L-	4	lack of IV	*Clypeaster rosaceus* *Echinocyamus apicatus* *Echinocyamus calariensis*	Koehler 1924 this study this study
lack of ocular II	R-	4	lack of II	*Echinocyamus apicatus*	this study
lack of ocular V, ocular I doubled	L-R+	5	appearance of I’, lack of V	*Echinocyamus apicatus*	this study
lack of ocular II, ocular IV doubled	L+R-	5	appearance of IV’, lack of II	*Echinocyamus apicatus* *Echinocyamus pusillus*	this study this study

mary lobes of the hydrocoel), and the number of ocular plates. This is the key moment in the origin of symmetry disorders.

The paper presents cases of an anomalous test plan resulting from disorders taking place in the apical system, which causes the ocular plates either to not develop or become doubled. As a consequence, tests can be observed which lack (L- or R- anomaly) or have too many growth zones (L+ or R+ anomaly). Cases of complex anomalies (L+R- or L-R+) are also possible. The relationship between the anomaly in the apical system and the morphology of the test based on the analysed material is shown in Table 1.

Test shape.—The von Ubisch axis regime is compulsory in regular echinoids until the moment that the genital area G4 docks into place (Fig. 10A$_1$ *versus* Fig. 10B$_1$), although this does not apply to clypeasteroids (monobasal apical system). Later, in irregular echinoids, the periproct becomes exocyclic and other processes forming bilateral symmetry commence. Each growth zone is formed “individually” to develop the test of the irregular individual (due to this it is possible to observe which zone is lacking), i.e., III—anterior, which is relocated (5- or 6-ray symmetry) or forms the anterior (4-ray symmetry), IV—left anterior, etc. The individuality of the ambulacral growth zones justifies looking for ray homologies among different classes of echinoderms (Hotchkiss 1998).

Genital system.—The process of genital ring formation, although linked with the test surface, took place without distinct disorders. Each part of the genital ring developed two gonoducts: on the right gonopores 3 and 4, and on the left gonopores 2 and 1, which are always correctly oriented in relation to the anterior of the organism and the hydropore position. Despite an additional ambulacral growth zone that creates extra border to the apical system (L+ anomaly), the genital system is not able to re-create the ancestral structure, a fifth gonopore.

Digestive tract and periproct.—Disorders in test symmetry, when occurring in zones not connected with the periproct, do not influence the development of the digestive tract. Disorders near the periproct cause delay in the process of its exocyclic migration. Evidence of this delay is the accelerated number of interambulacral plates between the peristome and periproct. As a consequence, the periproct attains an abnormal position on the interambulacrum (at the test margin, on the aboral side or, in a different interpretation, even on another interambulacrum), which occurs only in individuals with symmetry anomalies (5 specimens out of 14). In individuals with a correct structure (ca. 60 000), no specimens with this anomaly have been observed. Therefore, symmetry disorders can cause vast disorders of the time-clock of early ontogenic stages in a given individual.

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