Echinoid Skeleton

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Abstract—The skeleton of echinoids is internal and mesodermal, as in other echinoderms. Skeletal elements, including spines, are covered with single-layer epidermis and the skeleton is functionally external relative to the main body of the animal. It is composed of calcite with a high content of magnesium. Skeleton parts vary in the amount of magnesium, depending on the sea water temperature. However, at the relatively low taxonomic level, the major factor in this respect is genetic control. Representatives of different taxonomic groups living in the same temperature conditions differ considerably in the content of magnesium. Spongy or fenestrate microstructure called stereome is rather specific. Other type of microstructure is only characteristic of some elements of the Aristotle's lantern. Cristallographically, each element is a single calcite crystal with definite orientation of optical axes. The formation of larval skeleton begins at the late blastula stage. The larval skeleton is rather specific and sometimes varies in different species of the same genus. The development of definitive skeleton is either connected with elements of larval skeleton or it is formed independently in the amniotic cavity on the left side of the larva.

INTRODUCTION

The skeleton of sea urchins, like that of other echinoderm classes, is always internal, mesodermal in origin. In most cases, including spines, skeletal elements are only covered with a thin epidermal layer and, hence, the skeleton is functionally external relative to the main animal's body (Fig. 1). Particular skeleton parts are always composed of $CaCO_3$. The mineral form is always calcite, while the magnesian component is usually significantly greater than in the majority of invertebrates.

The skeleton consists of many growing elements (ambulacral and interambulacral plates), while new elements appear in the course of ontogeny. Skeletal elements are articulated movably (spines) or form a rigid structure (test).

Except for some structures, skeletal elements are optically a monocrystal.

The endoskeleton of sea urchins is studied within the framework of many scientific fields, following rather various approaches. Biologists are interested in the endoskeleton of sea urchins, since exclusive functional specialization of its parts contrasts, for example, with relative simplicity of functions of shells of bivalve and gastropod mollusks. In echinoderms, including sea urchins, skeletal elements play a role in a wide diversity of physiological processes. In addition, these animals are suitable objects for physiological studies, since this group has provided rather extensive embryological, biochemical, and ecological data. Significant biomedical importance of echinoid endoskeleton is connected with the fact that it is rather similar to mammalian bones and teeth.

On the other hand, the endoskeleton is important for geologists, because it is well preserved in the fossil record, usually retaining the primary crystallographic structure.

The crystallographic structure in itself is of interest for mineralogists, because it displays distinctive features of the crystal growth and orientation which are not observed in other invertebrate groups. Paleoecologists sometimes attempt to use the elemental composition of skeletons of fossil echinoderms (and members of other phyla) as markers of salinity and temperature of marine basins of the geological past.

COMPOSITION

The data on skeletal magnesium are most complete and, hence, they deserve special attention. As indicated above, magnesian component of the echinoderm skeleton is sufficiently high, comparable to that of coralline algae, calcareous sponges, and alcyonarians. It has been shown that magnesium, mainly in the form of $MgCO_3$ is in solid solution with $CaCO_3$. Since substitution of calcium by magnesium influences the size of the calcitic crystal lattice, the amount of magnesium is easy to determine by X-ray structural analysis (on the assumption that the change in lattice size depends exclusively on the replacement by magnesium). This provides a particularly important analyti-
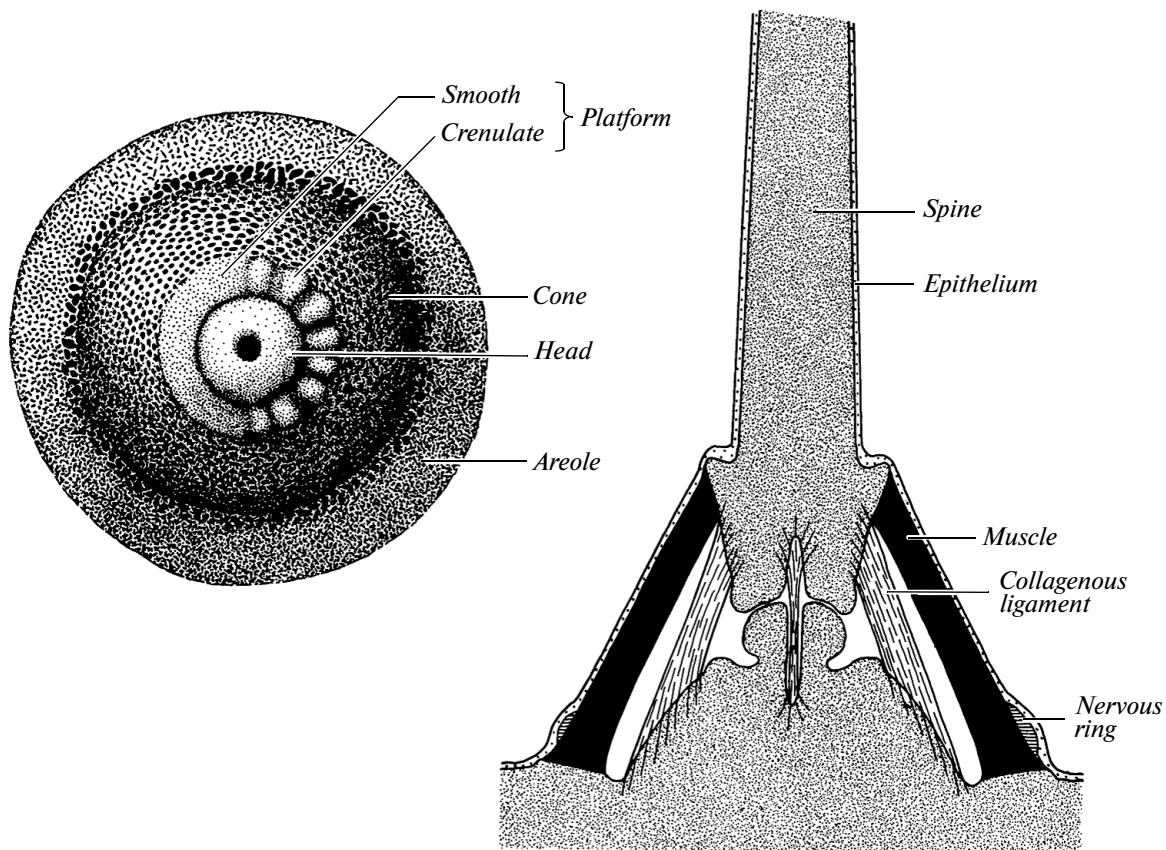
Fig. 1. Tubercle structure in the echinoid test: (a) tubercle, (b) cross section of tubercle and spine fragment with soft connective tissue (single-layer epithelium covering the skeleton is seen) (after Smith, 1964).

cal tool, since the impurity of samples due to organic tissue or extraneous matter is excluded.

Different authors marked for the first time a correlation between the magnesium content in calcitic echinoderm skeleton and temperature of marine water. It has been shown that species inhabiting warmer waters have a greater amount of magnesium. However, all of these studies showed significant variability which could not be explained by the influence of temperature. Raup (1966) noted that the variability in the magnesium content undoubtedly depends on the particular skeleton part. For example, it is shown that spines of sea urchins, particularly large primary spines, contain a smaller amount of magnesium than plates of the main skeleton part.

It is also evident that the magnesium content is under genetic control, probably at a rather low taxonomic level.

Table 1 shows the data on the sea urchin fauna of Eniwetok Atoll. All forms dwell under essentially the same temperature conditions. Note that echinometrids are distinguished by their high magnesium content. In all cases, only interambulacral plates were analyzed to minimize the variations connected with the position of samples in the skeleton. For these purpose X-ray structural analysis was used.

Thus, it is possible to recognize at least three factors that correlate with chemical composition: temperature of marine water, position in the skeleton, and individual genetic component. However, as Raup noted, none of these cases is possible to explain this correlation by relationships with particular metabolic processes. Consequently, the situation is undoubtedly more complex; certain other internal and external factors probably also play a role. This problem is typical for similar problems arising in the study of all organisms secreting calcareous skeleton. Dorofeeva and Solovjev (1987) examined the ratio of magnesium and calcium in the skeleton of several extant echinoid species on the material stored in the Borissiak Paleontological Institute and Institute of Oceanology of the Russian Academy of Sciences. The data obtained are reported below.

Accumulation of magnesium in the echinoid skeleton, which consists of high-magnesian calcite, is determined primarily by biological factors. The effect of ambient temperature is insignificant and it is only manifested in comparisons of the magnesium content in homologous parts of the skeleton: ambulacral and interambulacral plates and spines (Table 2). For example, a decrease in temperature by 1°C in the habitats of members of the genera *Pourtalesia*, *Urechinus*, *Brisaster*, and *Kamptosoma* is accompanied by a decrease in

Table 1. Percent by weight of $MgCO_3$ in interambulacral plates of 15 echinoid species from Eniwetok Atoll (Raup, 1966)

Family, genus, species	$MgCO_3$, %
Spatangidae	
Maretia planulata (Lamarck)	8.4
Toxopneustidae	
Tripneustes gratilla (Linnaeus)	9.8, 9.7
Temnopleuridae	
Mespilia globulus (Linnaeus)	10.4
Diadematidae	
Echinothrix calamaris (Pallass)	10.4
E. diadema (Linnaeus)	10.6
Diadema savignyi (Audouin)	10.8
Brissidae	
Metalia spatangus (Linnaeus)	10.4
M. dicrana Clark	11.8
Rhinobrissus hemiasteroides A. Agassiz	11.3
Cidaridae	
Eucidaris metularia (Blainville)	11.6
Parasaleniidae	
Parasalenia gratiosa A. Agassiz	12.2
Echinometridae	
Echinometra mathaei (Blainville)	13.5
Heterocentrotus trigonarius (Lamarck)	14.0
Echinostrephus aciculatus A. Agassiz	14.3
Echinoneidae	
Echinoneus cyclostomus Leske	14.9

magnesium concentration in ambulacral and interambulacral plates and spines by on average 0.05–0.08%. Weber (1973) revealed similar values of the temperature gradient of the magnesium content in homologous parts of the skeleton of tropical sea urchins.

Physiological features of echinoids have a more significant effect on the magnesium content of the skeleton than temperature. In the overwhelming majority of cases, the greatest concentration of magnesium is characteristic of ambulacra; that of the interambulacra is somewhat lower and, in spines, it is 1.3–2 times lower. It is noteworthy that the concentration of magnesian in interambulacra relative to that in ambulacra is constant in members of one family (for example, in Pourtalesiidae or Schizasteridae).

In general, in members of different Euechinoidea taxa, the magnesium content in ambulacra varies within a very wide range (1.2–3.7%); in members of the same family, variations are significantly lower, at most 0.4%. The sole exception is provided by the species *Kamptosoma abyssale*, in the ambulacra of which the magnesium content is by 1.5–2.0% lower than in other species examined of Diadematidae. By the way, some researchers believe that the genus *Kamptosoma* should be assigned to the family Echinothuriidae.

The comparison of data on the orders Echinoida and Clypeasteroida suggests that the magnesium content in the skeleton of extant members of younger genera is lower than in earlier taxa. In particular, in the order Echinoida, the magnesium content in members of the genus *Echinometra* (Paleocene–Recent) is higher than in the skeleton of *Strongylocentrotus* (Miocene–Recent). The strictest genetic control of magnesium concentration in calcite of sea urchins is probably characteristic of the generic level. However, this assumption requires further investigation. Thus, the distribution of magnesium in echinoid skeletons is useful for taxonomic purposes.

The magnesium content in biogenic carbonate marine invertebrates positively correlates with the temperature in water habitats. For some groups, the quantitative ratios between these parameters, which provide the basis for the method of determination of water temperatures in ancient seas, were established.

However, the use of skeletons of sea urchins and other echinoderms for these purposes is unsuitable, because fossilization may result in an increase (towards dolomite) or, more often, decrease (towards pure calcite) in magnesium content.

Other components of echinoderm skeleton remain almost unexplored. In many cases, it was impossible to separate the skeleton from soft tissues; therefore, it is difficult and even impossible to treat the results of analyses. Another important problem is pollution. For example, Clarke and Wheeler (1922) reported that a skeleton sample of *Lytechinus anamensis* contained 9.93% of silicon; however, they rejected these data because of high probability of attachment and penetration of quartz grains into skeletal fragments. This admixture of sediments is rather usual because of the porous nature of the overwhelming majority of echinoderm calcite.

MICROSTRUCTURE

In the majority of skeletal elements of sea urchins and other echinoderms, the texture is spongy or fenestrate (stereome), which is distinctly seen at ×20 or greater magnification; it frequently resembles the internal texture of vertebrate bones (Fig. 2). In echinoderms, the pore spaces are connected with each other and sometimes occupy more than 50% of the total volume of a skeletal element. In a living animal, pores are mostly filled with fibrous connective tissue. Many authors have described cellular texture in connection with other studies. Smith (1980) provided the most detailed analysis of stereome types.

The simplest cellular structure is two-dimensional lattice of optically continuous calcite. The primary element is usually a triradiate spicule. The spicule has calcite projections, which branch and join each other, gradually forming the porous texture. In a plate of sea urchins, as in the majority of massive parts of echinoderms, further deposition of calcite inevitably results in the formation of a three-dimensional lattice. The growth by peripheral accretion continues and adds

Table 2. Mean magnesium content in the ambulacral (A), interambulacral (IA) plates and spines (S) of extant sea urchins (from collections of A.N. Solovjev and A.N. Mironov) (after Dorofeeva and Solovjev, 1987)

Order	Family	Species	Locality, depth, m	Water temperature, °C	Mg, mass. % A	Mg, mass. % IA	Mg, mass. % S	S/A
Diadematoida		*Diadema* sp.	Tropical region, Atlantic, 1–2	26–29	3.42	–	2.07	0.61
	Diadematidae	*Echinotrix calamaris* (Pallas)	Bismarck Archipelago, 1	24–28	2.98	2.77	1.80	0.61
	Diadematidae	*Kamptosoma abissale* Mironov	Maskarenskaya Depression, 4375	0.5–1.0	1.47	1.35	–	–
		Kamptosoma abissale Mironov	Kurily–Kamchatka Trench, 5220	1.0–1.5	1.54	1.42	–	–
		Kamptosoma abissale Mironov	Nansei Islands, 5600	1.0–1.5	1.50	1.41	–	–
Temnopleuroida	Toxopneu-stidae	*Tripneustes gratilla* (Linné)	New Guinea, 1.5	26–29	2.53	2.39	–	–
	Echinometridae	*Echinometra mathaei* (Blainville)	Tonga Islands, 1	26–29	3.58	3.56	–	–
Echinoida	Strongylocentroidae	*Mesocentrotus nudus* (Agassiz)	Sea of Japan, 2–3	4–24	1.76	1.66	1.13	0.64
		Strongylocentrotus intermedius (Agassiz)	Sea of Japan, 2	4–24	1.39	1.25	0.67	0.49
Clypeasteroida	Laganidae	*Laganum laganum* (Leske)	New Hannover Island, 0.5	26–29	3.67	3.56	–	–
	Dendrasteriidae	*Scaphechinus mirabilis* (A. Agassiz)	Sea of Japan, 3	4–24	2.10	1.92	–	–
	Loveniidae	*Echinocardium cordatum* (Pennant)	Sea of Japan, 10	4–24	2.49	2.39	–	–
Spatangoida	Schizasteridae	*Brisaster* sp.	Gulf of Alaska, 292	5	2.42	2.35	1.25	0.51
		Brisaster sp.	Bering Sea, 525	4	2.34	2.25	1.17	0.50
		Brisaster sp.	Falkland Islands, 720	2–3	2.25	2.20	1.08	0.47
		Brisaster sp.	Japanese Trench, 1260	1–2	2.20	2.09	1.01	0.46
Holasteroida	Urechinidae	*Urechinus naresianus* (Agassiz)	Peru–Chile Trench, 1680	2.5–3.0	2.18	2.13	1.63	0.75
		Urechinus naresianus (Agassiz)	Kurily–Kamchatka Trench, 2800	1.5–2.0	2.15	2.04	1.61	0.74
	Pourtalesiidae	*Pourtalesia vinogradovae* Mironov	South Antilles Trench, 5800	0.2–0.5	1.25	1.20	0.88	0.73
		P. heptneri Mironov	Banda Sea, 7350	0.5–1.5	1.30	1.23	0.93	0.75
		P. laguncula beringiana Baranova	Bering Sea, 2800	1–2	1.38	1.34	1.04	0.75
		Echinocrepis rostrata Mironov	Aleutian Trench, 5020	1.0–1.5	1.32	1.26	0.93	0.75
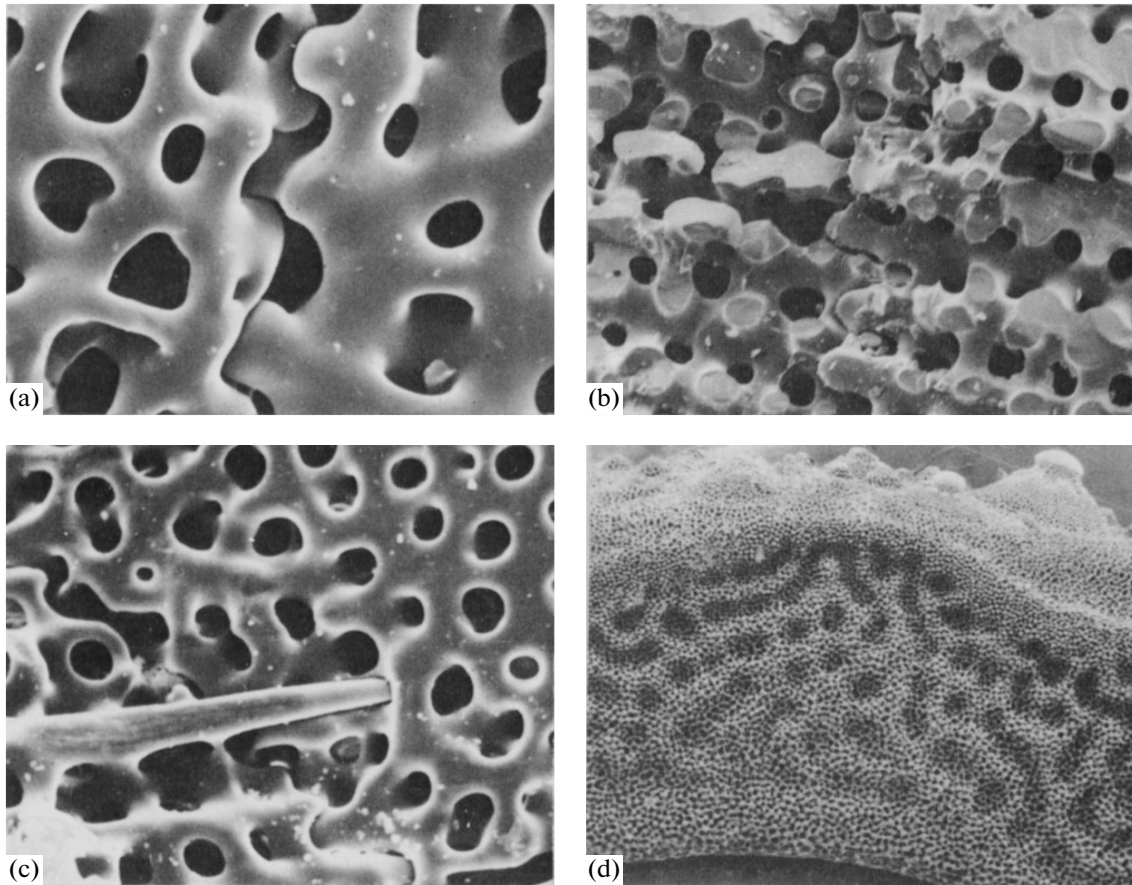
Fig. 2. Various stereome types of sea urchins (SEM microphotographs): (a) ×475, (b) ×300, (c) ×300, (d) ×30 (after Smith, 1984).

calcite to the plate throughout the animal's life, although varying in rate.

The teeth in the lantern of sea urchins are complex, distinguished in structure from other skeleton parts; they are formed of many various elements (Fig. 3). In the upper, relatively soft apex of the tooth (plumula), primary paired plates are formed. During the growth, they fall downwards, changing in shape from triangular to more elongated. Subsequently, lateral plates, i.e., adaxial expansions of primary plates start to be formed. Between the primary and lateral plates, prisms and laths of the stereome appear, forming the prism zone. As the growth continues, the tooth plates become fused in the shape of columns and prisms to form polycrystalline calcite, i.e., high-tensile multifibrous tissue. The "stone zone" located between the primary dental plates and prism zone, which is the region of very narrow acicular crystals, forms an extremely firm polycrystalline matrix. The primary and lateral plates are inclined towards the center and form a series of cones built in each other (cone-in-cone). This is functionally analogous to a self-sharpening structure, such as a chisel, so that a tooth always remains sharp. A very firm narrow stone zone forms the cutting edge of tooth, which is supported on either side by primary and lateral plates. As the stone zone is worn, the pressure is applied to the lowermost pair of plates, which are also gradually worn, completely exposing a new cutting edge.

Jensen (1981) studied in detail the ultrastructure of teeth of different echinoid groups under a scanning electron microscope and provided excellent photographs of the central lamellae—needles—prisms (CLNP) system (Fig. 4). She used these data in her classification of the class Echinoidea.

CRYSTAL OPTIC FEATURES OF THE SKELETON

Each skeletal element of the echinoid test (ambulacral, interambulacral plate, plate of the apical system, or spine) is a calcite monocrystal, although it lacks faces. In some cases, a skeletal element or its parts consist of submicroscopic crystallites, which are positioned rather regularly and uniformly relative to the optical axis C (Figs. 5, 6). In the crown plates, the optical axes are positioned perpendicularly, obliquely, or tangentially relative to the plate surface (Fig. 6). The primary tubercles of sea urchins apparently consist of mosaic, relatively large crystals (Raup, 1965) and, thus, they differ crystallographically from the plate which bears these tubercles. Raup (1956, 1960,
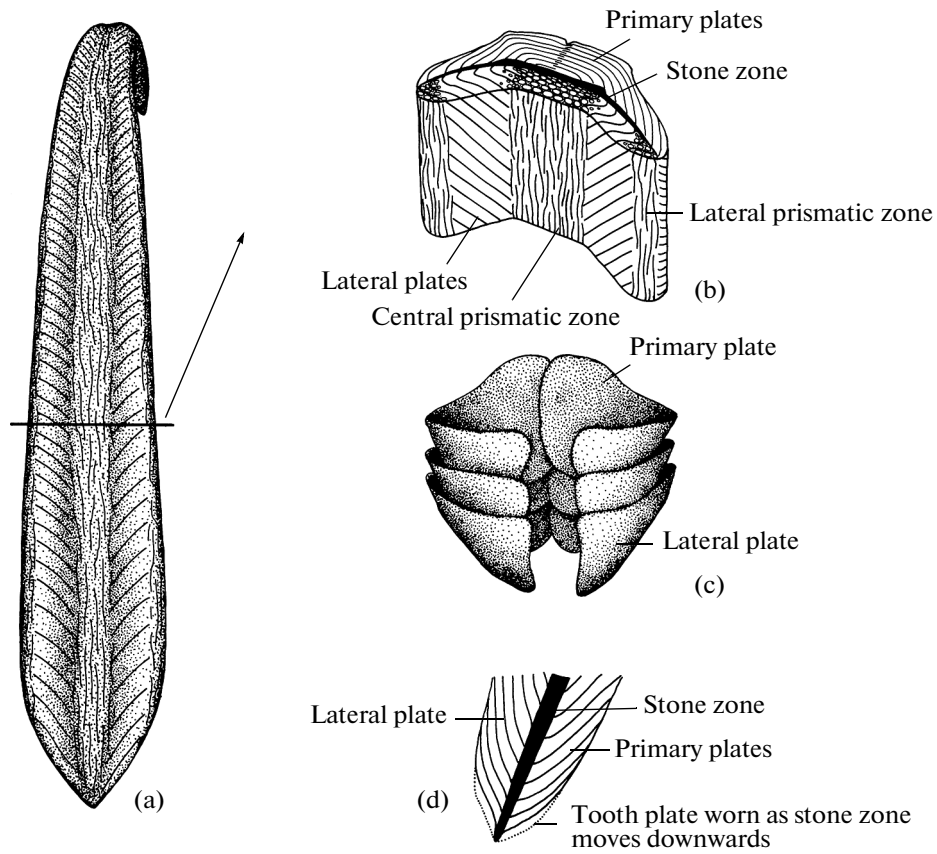
Fig. 3. Structure of tooth and its self-sharpening design: (a–c) Early Jurassic pedinoid sea urchin *Diademopsis*: (a) axial view of a grooved tooth, (b) block-diagram showing cross section in the specified direction, (c) slightly "broken" view of three pairs of tooth plates; (d) cross section of masticatory tooth end, showing the process of "sharpening," as the tooth goes down (after Smith, 1964).
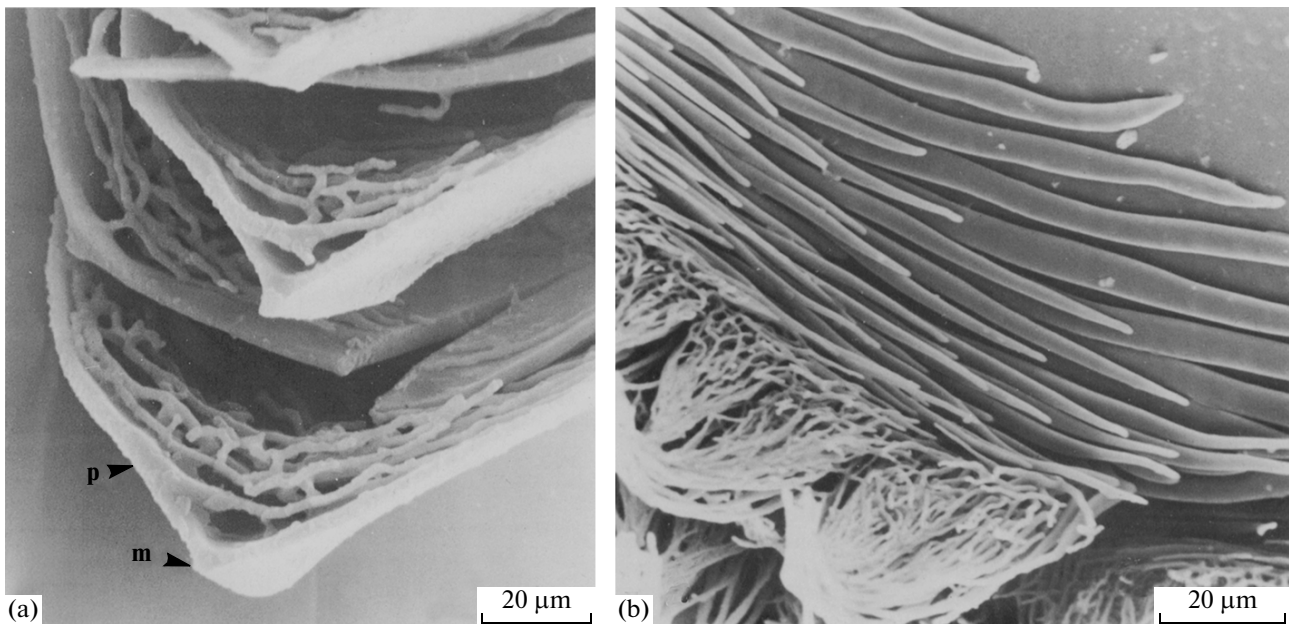
Fig. 4. SEM microphotographs of central lamellae–needles–prisms (CLNP) systems of tooth plates in (a) *Phormosoma placenta* and (b) *Eucidaris metularia* (after Jensen, 1981).
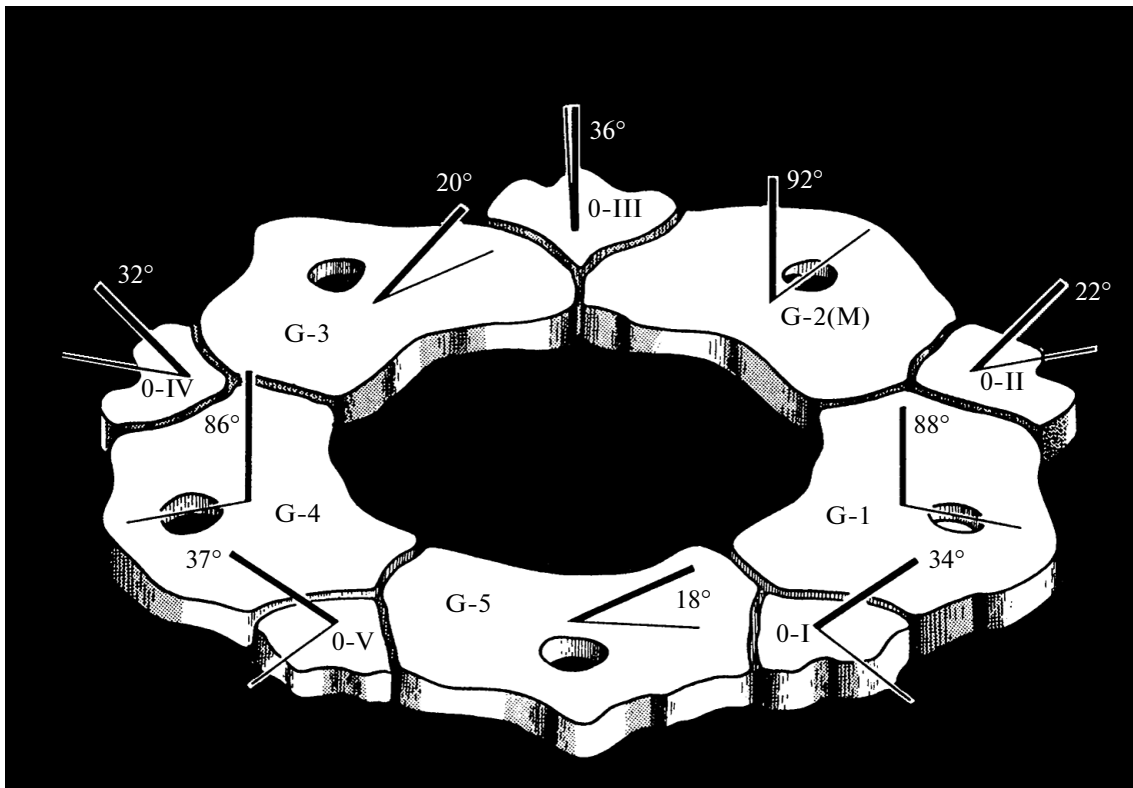
Fig. 5. Structural scheme of the apical system of *Echinus esculentus*; directions of axes C are shown by thick lines; figures (in degrees) concern the angle between the axis C and plate surface (after Raup, 1965).
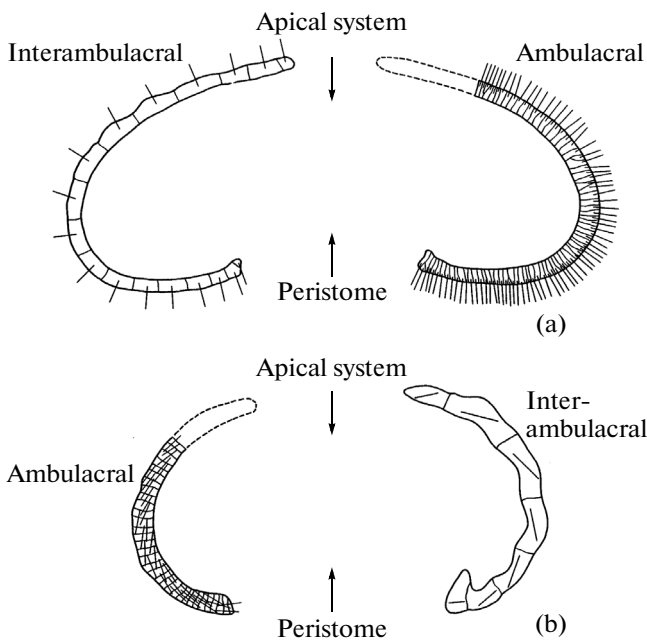
Fig. 6. Cross section of the test (crown) of (a) *Srtongylo-centrotus purpuratus* and (b) *Eucidaris thouarsii*; plate boundaries and orientation of optical axes C are shown; axes C (straight lines) are in the diagram plane (after Raup, 1962).

1962, 1965) showed that the optical axes are uniformly oriented within a family or genus. Therefore, this character is useful for the establishment of the taxonomic position of particular taxa.

It should be noted that, in the case of rapid burial in carbonate rocks, the echinoid test sometimes has no time to be filled by with deposits and remains empty. In this case, each skeletal plate can become the center of crystallization of the secondary, so-called syntaxial calcite, the crystals of which form sides retaining the orientation of optical axes of this skeletal plate.

LARVAL AND DEFINITIVE SKELETONS

Larvae of the majority of extant echinoderms (except for the bipinnaria of starfishes) have skeletal elements developed to a greater or lesser extent, but the internal supporting skeleton is particularly strongly developed in the ophiopluteus of ophiuroids and echinopluteus of sea urchins.

Larvae of different echinoid groups considerably differ in morphology, primarily in the number and length of projections (arms) and the larval skeleton. The calcitic skeleton appears for the first time as small granules at the stage of late blastula before gastrulation. These granules are tightly connected with primary mesenchymal cells. However, opinions differ as to whether they are formed intracellularly or in the
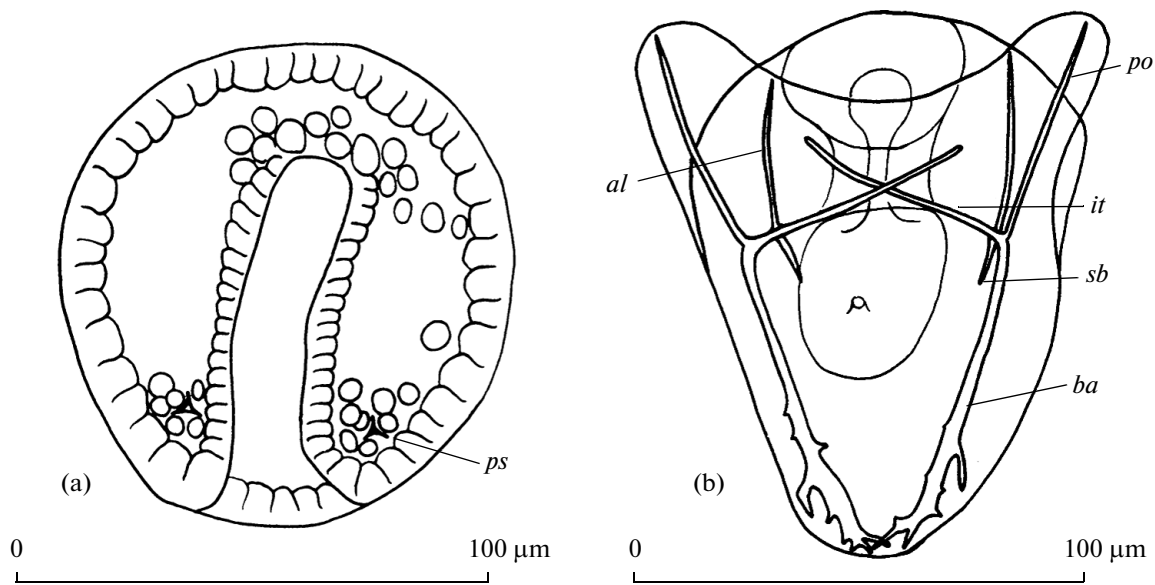
Fig. 7. *Mesocentrotus nudus:* (a) gastrula and (b) early pluteus. Designations: (*al*) anterolateral spine, (*ba*) basal spine (*it*) internal transverse spine, (*po*) postoral spine, (*ps*) primary spicule, (*sb*) secondary basal spine (after Kryuchkova, 1984).

organic matrix connected with mesenchyma. Raup (1966) adheres to the latter point of view. At the stage of gastrula, triradiate spicules are usually already well visible (Fig. 7a). In the course of further development, they become complicated and form the larval framework, which consists of simple or three-edged perforated spines with projections and thorns and are variously articulated with each other (Figs. 8–11).

The differences in the structure of larva and larval skeleton are manifested not only in large echinoid taxonomic groups, but also at the species level, as was repeatedly indicated (Mortensen, 1921, 1931, 1937, 1938, etc.). This was confirmed by our studies of larvae belonging to six species from the Sea of Japan (Kryuchkova and Solovjev, 1975), the specificity of which is shown below.

The greatest number of arms and the most complex skeleton are characteristic of members of the order Spatangoida, one of the most specialized echinoid groups. A typical larva of this group was investigated using the example of *Echinocardium cordatum* (Pennant).[1] Figure 8 shows the general appearance of this larva and the middle skeleton part with designation of the main elements. At the early pluteus stage, *E. cordatum* has two pairs of arms and one unpaired aboral projection. Subsequently, the number of arms increases and reaches six pairs in a completely formed larva; the unpaired projection increases in length (Fig. 8a). The skeleton consists of simple and three-

edged perforated spines. The larval body is supported by lateral projections of the aboral spine, basal and secondary basal spines having projections. At the base of postoral spines, there are perforated plates (Fig. 8b).

Larvae of flat echinoids (order Clypeasteroida) have fewer skeletal elements than Spatangoida, but form a characteristic element, such as basal "basket," which supports the larval body from below. It is formed by fusion of branched ends of two basal spines. The basal and secondary basal (additional) spines support the pluteus body from lateral sides. The arms are supported by simple and perforated spines (Fig. 9). Species distinctions of the skeleton structure of pluteuses are manifested in structural features of the basal "basket." In particular, the basal basket of *Scaphechinus griseus* (Mortensen) is formed of one plate with large cells (Fig. 9a). The "basket" of *Scaphechinus mirabilis* Agassiz consists of two relatively massive plates with small thorns (Fig. 9b). Perforated spines differ to a lesser extent; the character of interlacing varies in places.

In contrast to Spatangoida and Clypeasteroida, larvae of other echinoid groups not always have distinct diagnostic characters typical of particular groups. Apparently, it is difficult to provide uniform characteristics for larvae of the order Camarodonta.

Essential differences in the morphology of pluteuses at different developmental stages were observed by us in members of two genera of this order, *Strongylocentrotus* and *Mesocentrotus*. Larval skeletons of the two species of these genera differ in general design.

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[1] Recent studies have shown that *E. cordatum* occurs near the Atlantic coasts of Western Europe and Mediterranean. *Echinocardium* from the Sea of Japan must be referred to the other species.
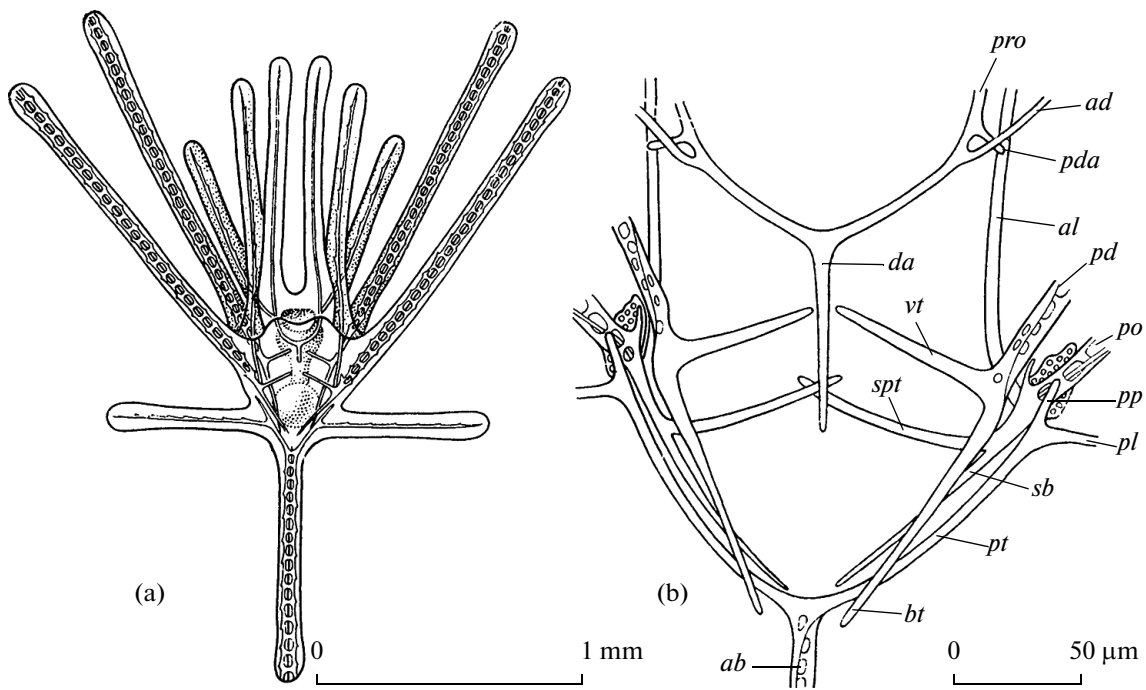
Fig. 8. Larval *Echinocardium cordatum* (Pennant) before the beginning of metamorphosis: (a) general appearance, (b) central part of skeleton. Designations: (*pro*) preoral spine, (*ad*) anterodorsal spine, (*al*) anterolateral spine, (*da*) dorsal arch, (*pd*) posterodorsal spine, (*po*) postoral spine, (*pl*) posterolateral spine, (*pp*) perforated plate, (*pt*) posterior transverse spine, (*ab*) aboral spine, (*vt*) ventral transverse spine, (*spt*) secondary posterior transverse spine, (*bt*) basal transverse spine, (*sb*) secondary basal spine, (*pda*) process of dorsal arch (after Kryuchkova and Solovjev, 1975).

Rather significant distinctions are already observed at early stages. Basal club-shaped spines of *Strongylocentrotus intermedius* (Agassiz) are connected by two thorns at the club ends (Fig. 10b), whereas the ends of
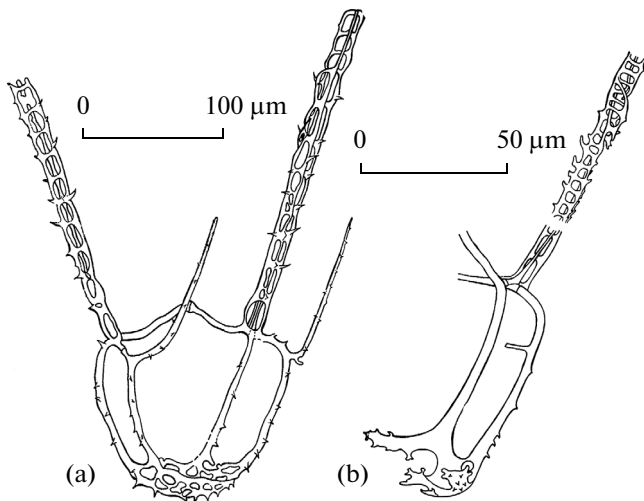

Fig. 9. Basal "basket" of larvae: (a) *Scaphechinus griseus* (Mortensen), (b) *S. mirabilis* Agassiz (4—5 day of development) (after Kryuchkova and Solovjev, 1975).

narrow simple spines of *Mesocentrotus nudus* (Agassiz) have projections, forming a complex lock (Fig. 10a). At the late stages, larval *M. nudus* has ciliary "epaulettes" (Fig. 11a), which are absent in *S. intermedius* (Fig. 11b). The formation of definitive skeletons follows different ways. The first plates of the skeleton of juvenile *S. intermedius* develop on the postoral and posterodorsal spines and dorsal arch (Fig. 12a). The formation and development of the definitive skeleton of *M. nudus* follows the same way as in the majority of other echinoids, for example, *Scaphechinus mirabilis* (Fig. 12b), i.e., it is initiated in the shape of separate spicules (future primary plates of imago, formed on the left side of larva) in the amniotic cavity. An important difference of juvenile stages of the two species considered is the presence of primary pedicellariae, which develop in *M. nudus* at the stage of planktonic larva (Fig. 13) and are never formed at this stage in *S. intermedius*.

Thus, we have briefly considered distinctive developmental features of the definitive skeleton in certain species inhabiting the Sea of Japan. A thorough examination of the metamorphosis and development of skeleton in juvenile echinoids was performed by Gordon (1926a, 1926b, 1928).

The presence of calcareous skeleton in larval echinoids allows transition to the fossil condition. The
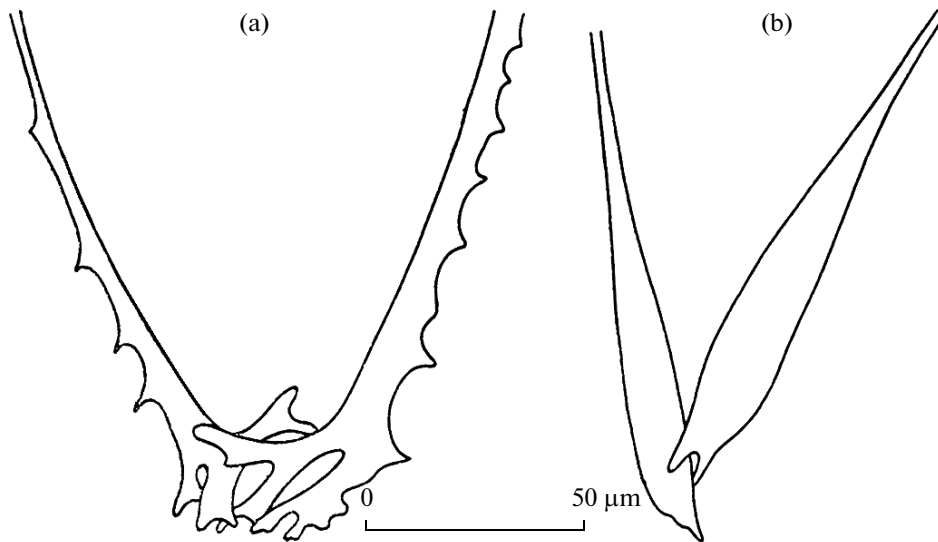
Fig. 10. Basal part of larval skeleton: (a) *Mesocentrotus nudus* (Agassiz), (b) *Strongylocentrotus intermedius* (Agassiz) (3–4 day of development) (after Kryuchkova and Solovjev, 1975).
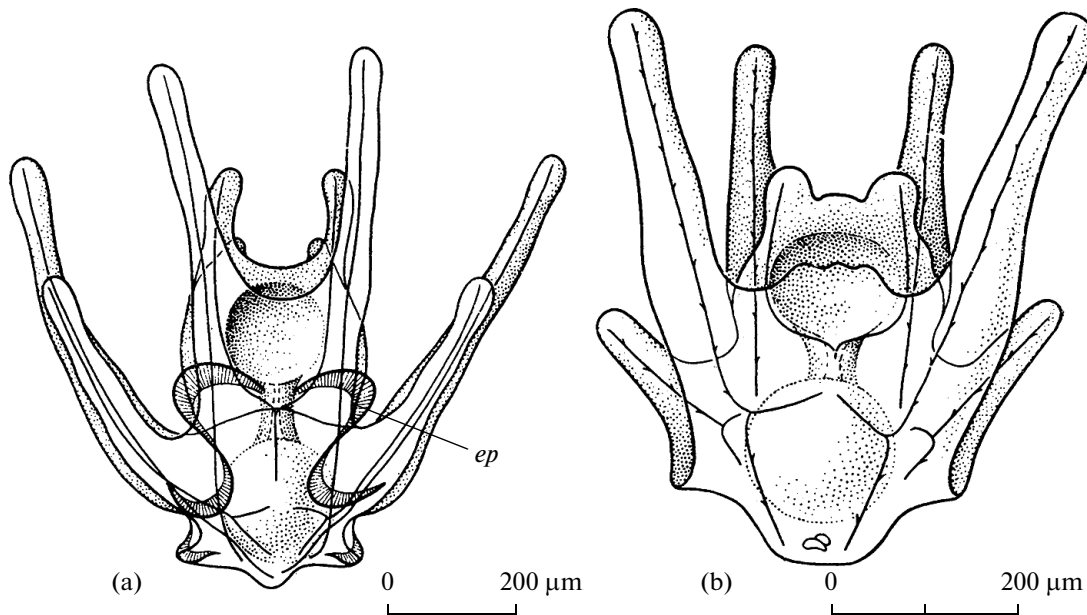

Fig. 11. General view of a larva before the beginning of a metamorphosis: (a) *Mesocentrotus nudus*, (b) *Strongylocentrotus intermedius;* (*ep*) epaulettes (after Kryuchkova and Solovjev, 1975).

records of fossil larval skeletons are rather scarce. Deflandre-Rigaud (1946) described a number of specimens from the Oxfordian of France, which are undoubted fragments of the echinopluteus skeleton and small definitive spines and valves of pedicellariae of juveniles (Fig. 14). The presence of tests of the species *Nucleolites scutatus* in the same beds suggests that these fragments probably belong to the same species.

The number of finds of larval echinoderm skeletons will undoubtedly increase, if micropaleontologists pay special attention to echinoderm remains when picking up microfossils by washing.
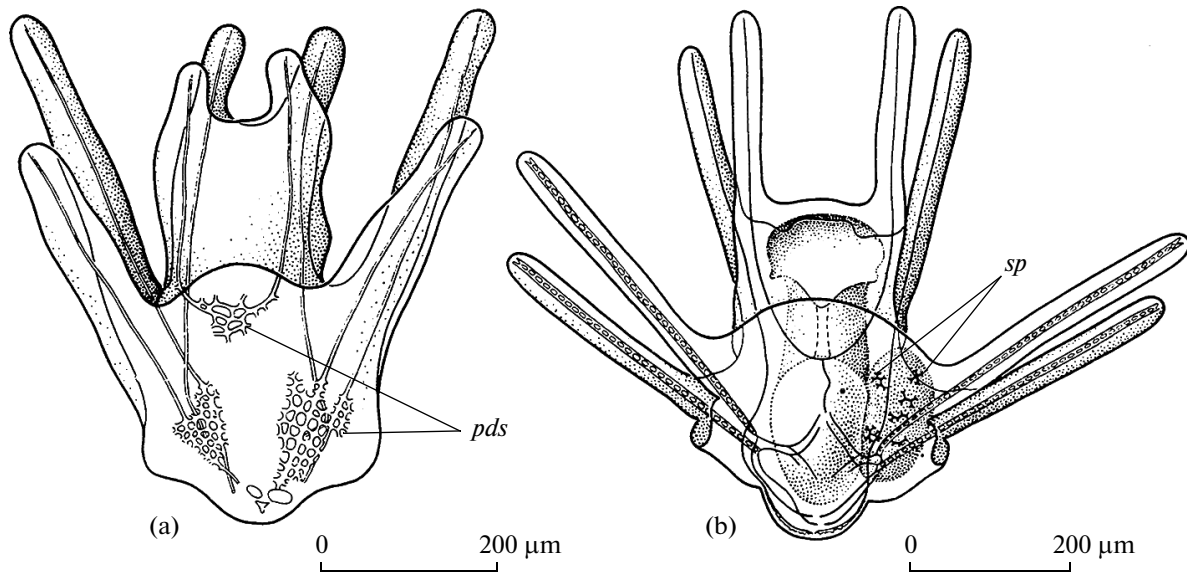
Fig. 12. Formation of the definitive skeleton: (a) initiation of primary definitive plates in *Strongylocentrotus intermedius*, (b) initiation of spicules of primary definitive plates in amniotic cavities of *Scaphechinus mirabilis*; (*pds*) plates of definitive skeleton, (*sp*) spicules of primary definitive plates (after Kryuchkova and Solovjev, 1975).
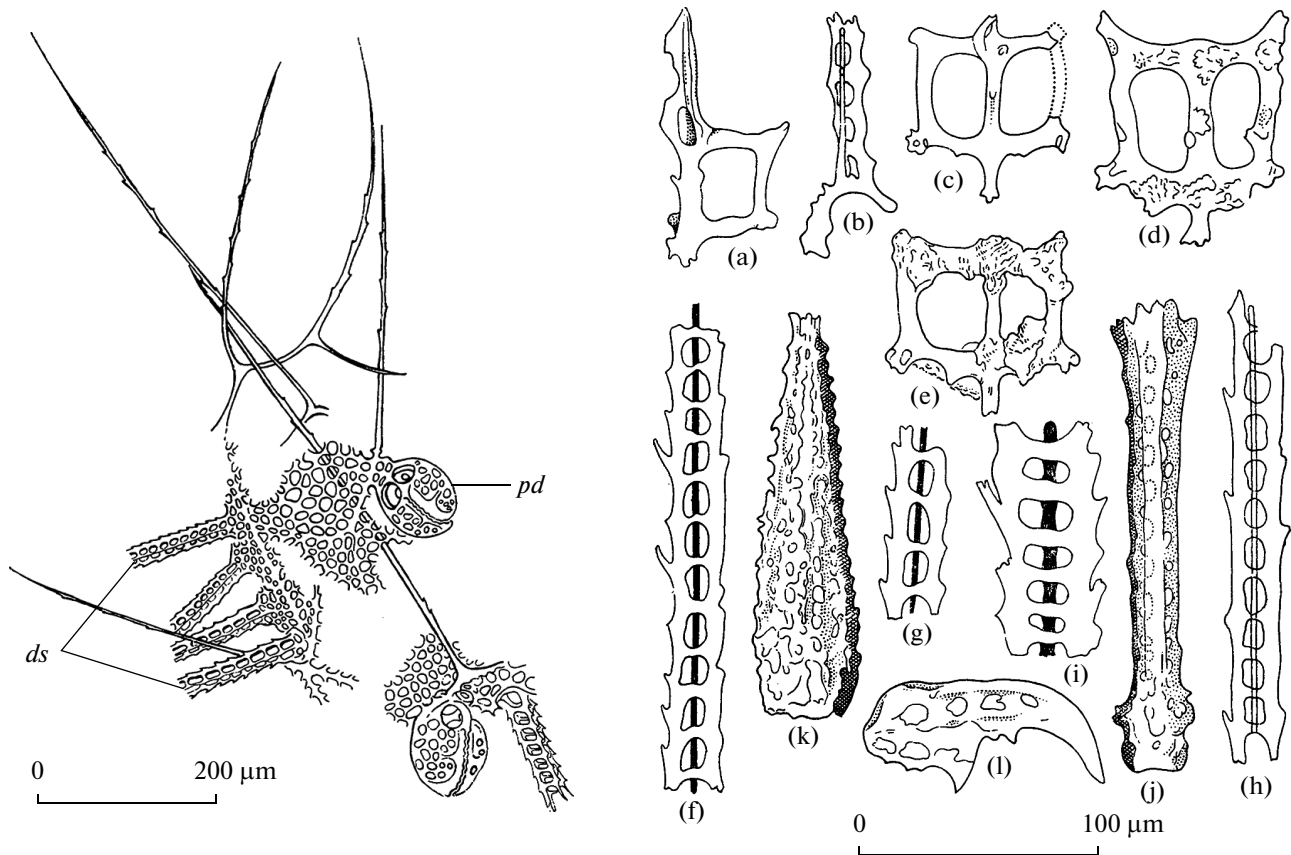
Fig. 13. Remains of larval skeleton, definitive spines and pedicellariae of juvenile *Mesocentrotus nudus*. Designations: (*ds*) definitive spines, (*pd*) pedicellariae (after Kryuchkova and Solovjev, 1975).

Fig. 14. Skeletal elements of larval echinoids from Oxfordian marls: (a, c−e) incomplete skeletons of pluteuses; (b, f−h) fragments of perforated spines of pluteuses; (i−k) skeletal elements of juveniles: (i, j) definitive spines, (k) primary spine, (l) valve of pedicellariae; Calvados, France (after Deflandre-Rigaud, 1946).

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