Ontogenetic development and functional morphology in the early growth-stages of *Calceola sandalina* (LINNAEUS, 1771)

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Abstract: At the earliest ontogenetical stages, *Calceola sandalina* has corallum in the form of hemispheric cup provided with peculiar tube-like outgrowths and attachment scar to the substrate; it lacks septa and external growth lines on the wall. At the next stage operculum appears with a pair of submedially situated, relatively large hinge lists. Succesively, large central septum and two lateral septa appear. Attachment scars of desmocytes arranged in double or single rows are present in the calice and inner side of the operculum. Phylogenetic relationships of operculate corals with the Cambrian *Cothonion* are discussed.

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THE LACK of living organisms with a skeleton similar to *Calceola* has caused taxonomical speculations lasting more than two centuries. *Calceola* was considered to be a rugosan coral, a brachiopod, or a pelecypod - see synonymy in LINDSTRÖM (1882) and KOWALSKI (1983). In the second half of the XIXth century, the systematic position of *Calceola* was fixed within the operculate Rugosa especially by KUNTH (1869). RICHTER (1929) interpreted the morphogeny of operculate corals in terms of rugosan specialization and proposed a functional model of the two parts of the skeleton. Up to now only adult specimens of *C. sandalina* were investigated. DZIK (1992) was the first who illustrated corallum and operculum of juvenile specimens. The purpose of this paper is the description of details of the early ontogeny of *C. sandalina,* the functional analysis of particular skeletal elements as well as the consideration of taxonomical and phylogenetical questions.

Material

The specimens come from the Holy Cross Mts, from the *Microcyclus* Shale (Givetian) of the Skaly Formation [with abundant fauna consisting of brachiopods, bryozoans, echinoderms, ostracodes and trilobites; see ADAMCZAK (1976), and references in DZIK (1981)]. The rock was macerated with Glauber's salt, washed, and skeletons were cleaned with ultrasonic cleaner. The collection numbers about 2000 specimens, housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw (acronym ZPAL). The specimens are generally very well preserved, some of them are partly recrystallized. Most frequent are coralla without opercula, while separate opercula and specimens with fixed opercula (Figs. 1.13, 1.15; 2.5-2.6; 4.3) are rare. Juvenile forms predominate (size frequency, see Fig. 6).

Ontogeny of the skeleton of *Calceola sandalina*

The growth stages are as follows: 1. initial, 2. juvenile, and 3. adult stage. Only the initial stage is morphologically distinct and generally delimited from the next stage by a slight constriction of the calicular diameter.

1. Initial stage: The skeleton is undivided. The initial corallum is cup-like and hemispherical in shape (Figs. 1.3, 1.14; 2.10). It is provided with a tubular outgrowth and a substrate attachment scar, but there are no traces of a substrate preserved. The shape of the attachment surface is very often elongate (Figs. 1.4; 2.13; 4; length ca. 0.7-1.0 mm, width ca. 0.3 mm), occasionally subcircular (Figs. 1.5, 1.11; diameter about 0.3 mm). The external diameter of the hemispherical part is mainly 0.5-0.6 mm. At the internal wall (Fig. 2.10) of an undamaged hemispherical part in one of the calices, there was observed a single row of minute pits. There is, at least, one of two single rows present in this stage.

The tube-like and distally closed outgrowth opens to the hemispherical part of the corallum. The outgrowth is distally narrowed, without any trace of longitudinal sutures. Its wall is proximally thickened (Fig. 4). The longest outgrowth is ca. 1.25 mm in length (distal diameter = 0.25 mm; proximal diameter ca. 0.09 mm). Vestiges of broken outgrowths can also be found in specimens of a size of some centimeters. The outgrowth is straight (Figs. 1.5, 1.11) or curved (Figs. 1.1, 1.12). The angle between the flat side of the corallum and the outgrowth varies from 180 to 90 degrees. Specimens with two outgrowths (Figs. 1.6, 1.9; 4.1) or with a flattened outgrowth (Fig. 2.13) are extremely rare. Diaphragms can cut the lumen of the outgrowth (Fig. 4.4). A few similar tabular diaphragms can be observed in the proximal part of the calice.
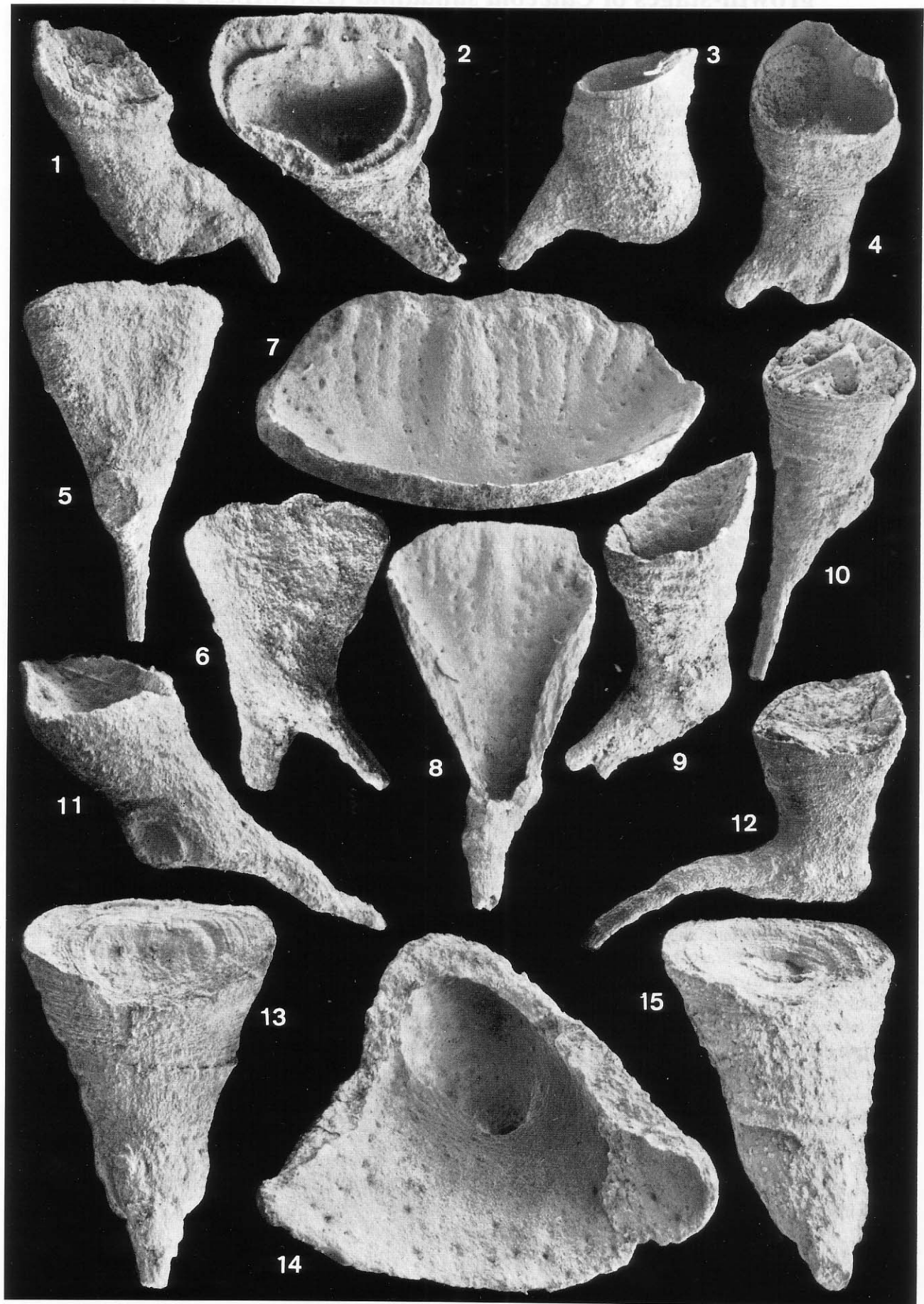
2. Juvenile stage: The beginning of this stage is marked on the surface by prominent, dense growth lines and often by a narrowing of the diameter. Of this stage, opercula are first recorded. The flattening of the coralla and the differentiation of a hinge side of the operculum take place simultaneously. The outgrowth is situated on the convex side, extremely rarely on the flat side of the corallum (Fig. 1.6). Generally, an attachment scar is observed on the flat side, but its position occasionally can be different (Figs. 1.4, 1.11; 4.2).

Corallum. - The edge of the flat side generally is higher than the edge of the convex side (Figs. 1.1, 1.13). The external surface shows dense growth lines (Figs. 1.10, 1.13). At the internal wall vertical rows of pits are developed, which differentiate into: a) Double rows, which are developed on the flat side of the calice in very distinct rows; they appear symmetrically and initiate from the calicular angles (Figs. 1.7, 1.8). b) Single rows, including two rows at the calice angles (which continue from the hemispherical part) and some rows on the convex side. These pits seem to be less deep than that of the flat side (Figs. 1.14; 2.11).

Of the flat side faint septal ridges rise between double rows of pits. A distally swollen central ridge appears for the first time (Figs. 1.7, 1.8). In the subsequent development, the calice morphology doesn't differ considerably from that of the adult forms. In adult skeletons the central septal ridge is named counter-septum, and its swollen part - columella (HILL & JELL, 1969).

Operculum. - The primordial operculum is oval; the growth direction is centripetal; its external surface is covered with concentric growth lines (Fig. 1.15). The operculum diameter fits well to the external distal diameter of the initial part of the corallum at the level from which growth lines initiate (Fig. 1.13), but occasionally it can be smaller (Fig. 1.15). In the subsequent development, the operculum becomes semicircular (Fig. 6) as a result of the formation of the straight hinge. Two ridges are visible at the internal surface of the youngest opercula (Fig. 2.1). The ridges form the first pair of hinge lists bordering a socket for the columella (Figs. 2.5, 2.6). Successively, the central septum develops in the plane of operculum symmetry, followed by the two "lateral" septa (Figs. 2.2, 2.3). Then, the next pair of "lateral" septa is formed simultaneously with septa of second order, which appear at the arched edge (Figs. 2.4, 2.5, 2.7-2.9). The first pair inserts between the central septum and the first pair of lateral septa; the next second-order septa appear in the same way, between the following lateral septa (Fig. 5.2). The septal pattern is fountain-like; by the straight edge of the operculum the septa are near-ly parallel (Fig. 2.9). Near the arched edge, the septa divide into "trabecular segments" (Fig. 5.2). In the interseptal grooves, double pit rows are visible (ca. 6-7/mm). The rows continue at the flat side of the calice (Figs. 2.5, 2.6). The completion of a hinge is characterized by the development of the additional lists parallel to the first pair, as well as of the sockets of the septal ridges in the calice (Fig. 5.2). Later, on the operculum, a relative height decrease of "lateral" septa (especially on the arched edge) and an increase of the central septum can be observed.

3. Adult stage (Figs. 3.1-3.5): The morphology of adult specimens of *Calceola* was described by many authors, e.g. KUNTH (1869), LINDSTRÖM (1882), TERMIER & TERMIER (1948), HILL & JELL (1969), BIREN-HEIDE (1974) and HILL (1981).

Functional interpretation

1. Initial corallum: The initial skeleton (with its outgrowth) was formed in a single secretion act, growth lines at its surface are lacking. The skeleton is equivalent to the basal plate of scleractinians. The proximal thickening of the outgrowth wall and the formation of diaphragms and tabulae were connected with a gradual withdrawal of the soft body.

The initial stage of *Calceola sandalina* differs from the earliest growth stages of other Rugosa, even from those which differ morphological sharply in their initial (brephic) and post-brephic stages, e.g. in *Cyathaxonia tantilla*. In this species, the brephic skeleton is spirally coiled, with its surface transversely striated, without external longitudinal septal grooves and interseptal ridges, which appear in later ontogenetical stages (SANDO, 1977). Normally developed protosepta and transverse striations at the wall surface in *C. tantilla* are signs of evident differences between the early development of its polyp and that of *C. sandalina*.

In contrast to the initial skeleton of *C. sandalina* the earliest observed part of skeleton of *C. tantilla* was produced by gradual growth. Aseptate, initial coralla of some Rugosa (e.g. *Protomacgeea dobruchnensis* ROZ-KOWSKA, 1956: 287) resemble aseptate, hemispheric parts of *C. sandalina* coralla. As a matter of fact, it is not clear from literature, whether the surfaces of skeleton at aseptate stage of other rugosans were covered with growth lines.

Figure 1. Juvenile specimens of *Calceola sandalina* (LINNAEUS, 1771). Middle Devonian, *Microcyclus* shale; Poland, Holy Cross Mts. - 1.1-1.15, ZPAL V.XXI/11-25 (respectively). - Figs. 1.1-1.13, 1.15 × 30; 1.14 × 100.
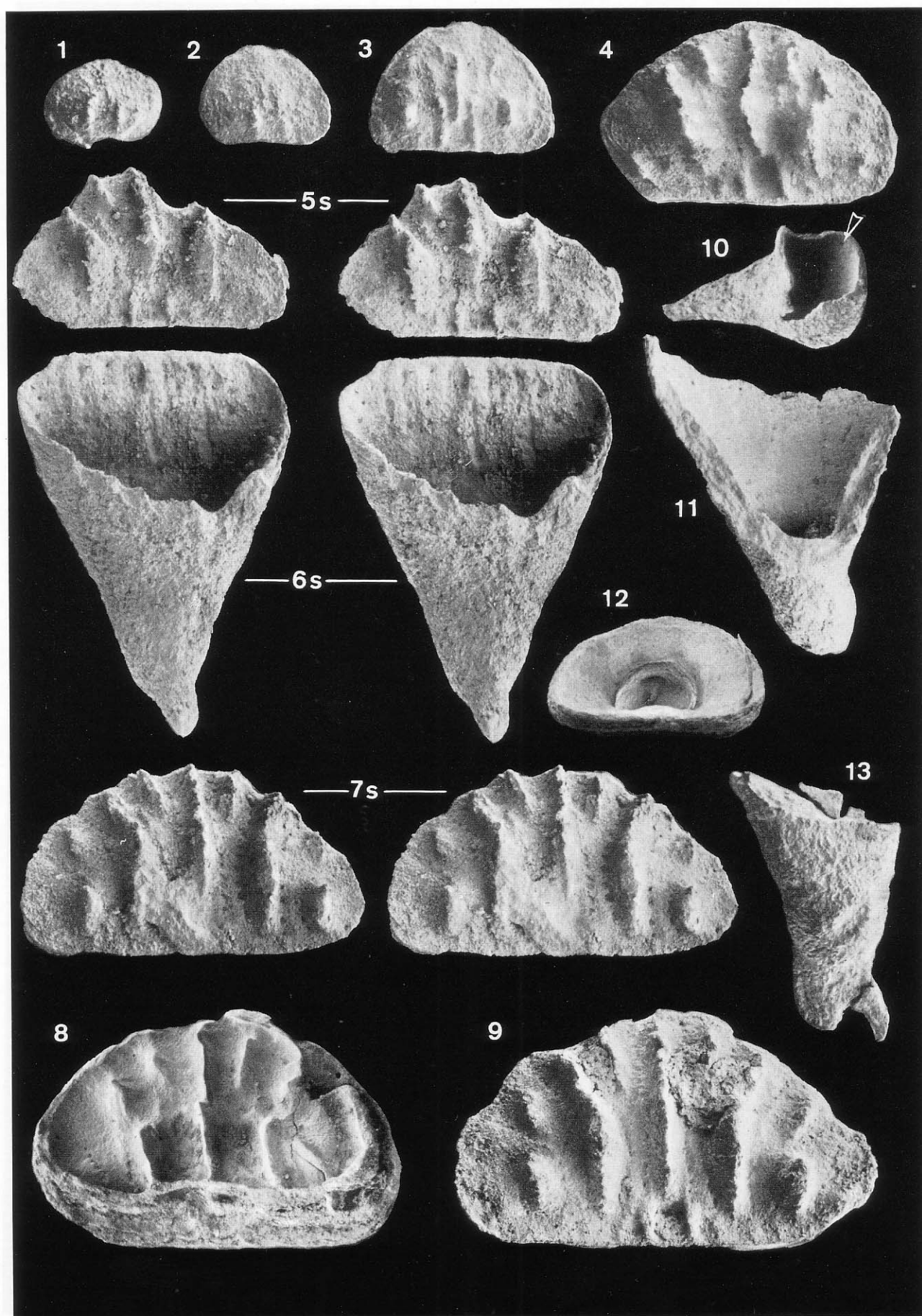
Attachment scars to some protruding substrate (not preserved in fossil condition), are known among different solitary Scleractinia and Rugosa. Their position can be (i) lateral (e.g. in *Metriophyllum gracile* a groove, slightly oblique to the growth direction can be developed; HOLWILL, 1963) or (ii) apical (e.g. in *Ankhelasma typicum* or in *Flabellum*). The scars are interpreted as traces of attachment to the soft stem of sea-weed or algae. It seems that larvae of *C. sandalina* selected only such objects for settlement (Fig. 6).

Outgrowths are known only in initial skeletons of *C. sandalina*. They generally lie at the convex side of the calice. Irregularities in outgrowth shape (flattened outgrowth or two unequal outgrowths, with attachment scar located between them: corallum riding the tube-like substrate, Figs. 4.1-4.2) show evidence of some environmental control of their development. Rhizoidal outgrowths are present in some operculate corals. In specimens of the Silurian operculate coral *Rhizophyllum* irregular rhizoids with diaphragms are developed at the flat side of calice (LINDSTRÖM, 1882: Pl. 4: 1, 4). Such structures are known also in other Rugosa. NEUMAN (1988) suggests that not-tabulated rhizoid holdfasts in the genus *Dokophyllum* were formed as a result of ectodermal secretion of tentacle-like processes. The lack of sutures in the outgrowths of *C. sandalina* are evidence of a formation of these skeletal parts by similar processes. It might be a rudimentary organ inherited from rhizoid-bearing ancestors. If the outgrowth had functional significance, this was limited only to the initial stage. In the following growth stages, when specimens lay at the bottom, the outgrowth probably broke off.

2. Juvenile and adult skeleton: A constriction of the corallum diameter and the appearance of growth lines determinate, respectively, the end of the initial and the beginning of juvenile ontogenetic stages. Differences between the stages were caused by morphological transformations of the polyp (probably connected with the formation of an operculum beyond the oral disc) and in changes of its mode of life.

Juvenile opercula with uniformly high septa contrast with adult opercula which show a high central septum and small septal ridges. The near-hinge parts of the latter are much higher than their peripheral parts. During the ontogeny, septal function changed. Being uniform at early stages, the function became differentiated at later stages. The function of "lateral" septa could change from the function of withdrawing the operculum to the polyp -
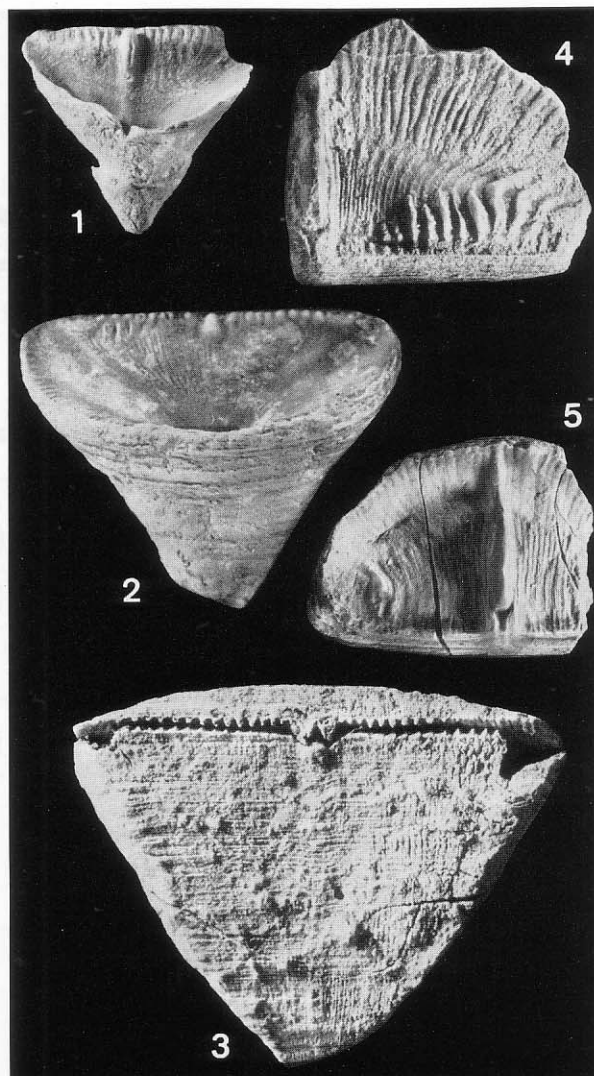

Figure 3. *Calceola sandalina* (LINNAEUS, 1771), Middle Devonian, *Microcyclus* shale; Poland, Holy Cross Mts. Adult coralla and opercula. - 3.1. ZPAL V.XXI/1; 3.2. ZPAL V.XXI/2; 3.3. ZPAL V.XXI/3; 3.4. ZPAL V.XXI/4; 3.5. ZPAL V.XXI/5. All figures × 2.

to that of fixing the operculum in the hinge. The latter function influenced morphological changes of septa near the hinge observed in adult stages. It seems that the function of the central septum did not change during ontogeny. The increase of its dimensions could the consequence of a complete taking over of the draw function, which it previously shared with the neighbouring septa.

Figure 2. Juvenile specimens of *C. sandalina* (LINNAEUS, 1771). Middle Devonian, *Microcyclus* shale; Poland, Holy Cross Mts. - 2.1-2.4, opercula, ZPAL V.XXI/26-29. - 2.5S-2.6S, stereo view of corallum and operculum, the same specimen ZPAL V.XXI/30. - 2.7S, stereo view of juvenile operculum, ZPAL V.XXI/31. - 2.8-2.13, ZPAL V.XXI/32-37. All figures × 30.
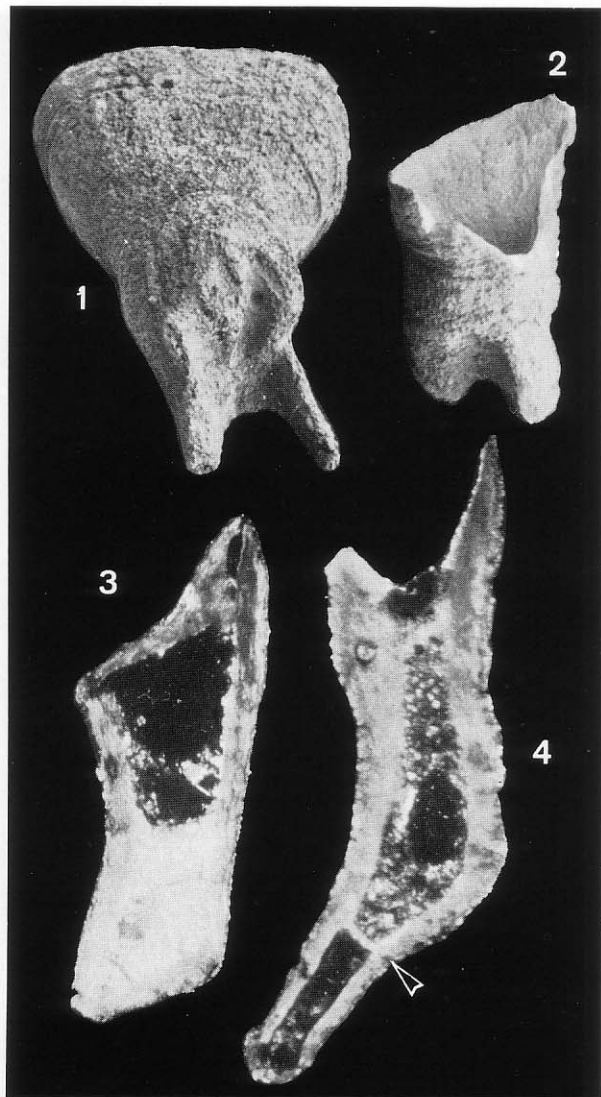
Figure 4. *Calceola sandalina* (LINNAEUS, 1771). Middle Devonian, *Microcyclus* shale; Poland, Holy Cross Mts. - 4.1, corallum with two outgrowths, riding the tube-like substrate, ZPAL V.XXI/6. - 4.2, ZPAL V.XXI/7. - 4.3, longitudinal section of a specimen with fixed operculum, ZPAL V.XXI/8. - 4.4, longitudinal section of a specimen with an outgrowth. Note the diaphragm cutting the lumen of the outgrowth (arrow), ZPAL V.XXI/9. All figures × 30.

Figure 5. *Calceola sandalina* (LINNAEUS, 1771). Middle Devonian, *Microcyclus* shale; Poland, Holy Cross Mts. - 5.1, single pit interpreted as a place of desmocyte attachment. ZPAL V.XXI/10, × 300. - 5.2, fragment of a juvenile operculum. ZPAL V.XXI/10, × 30. Note the first pair of hinge lists bordering the socket for the columella (arrow), additional sockets for calicular septal ridges and "trabecular segments" visible at peripheral part of septa.

Occasionally, evidence of rejuvenescence can be observed within the calice and at the internal surface of the operculum (Fig. 1.2; Fig. 2.12). This phenomenon is connected with a rapid reduction of the polyp body, widely known in Rugosa and in some scleractinian corals.

Rows of pits present in the initial stage and later stages were interpreted as desmocyte attachment scars. In Recent Scleractinia they correspond to the position of mesenteria (WISE, 1970). They were recorded also in Rugosa (FEDOROWSKI, 1985, 1989). Presence of desmocyte attachments already in initial skeletons show evidence of the development of mesenteria already in the earliest ontogenetical stages. Their exact continuation in calices as well as in opercula show evidence of the continuation of the same mesenteria throughout the "dorsal" and opercular part of the soft body. In adults, the
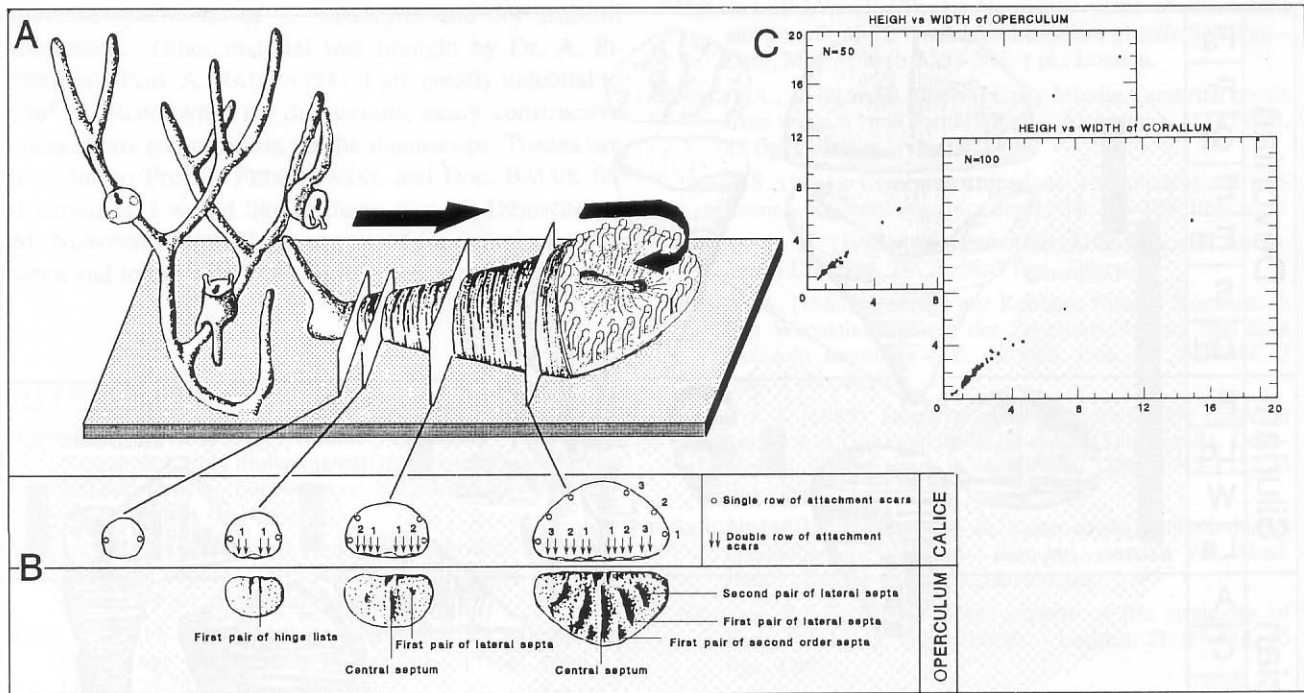
Figure 6. A. Reconstruction showing the mode of life of initial and juvenile specimens of *Calceola sandalina*. The initial skeletons of *C. sandalina* appear to have been attached to stalks of algae. - B. Ontogenetical changes of operculum and calice. - C. Size frequency.

mesenteria at the flattened side of the body were very numerous. Judging from the desmocyte attachment scars, in the mesenterial pairs, the mesenteria were closely spaced (in youngsters at ca. 0.1 mm in adults at ca. 0.3 mm), so their entocoels were verry narrow. Septa in *Calceola,* although rudimentary, are developed markedly at the calicular margin, fainting proximally, and continuing down only as narrow spaces between double rows of mesenterial attachment scars. The material under study doesn't allow for any statement concerning the mesenterial development at the convex side of the body.

Mode of life. - The proposed scenario of ontogenetical development assumes an attachment of larvae (planula) to any protruding substrate (algae) and forming an initial hemispherical skeleton with a (?) stabilizating outgrowth. Larger specimens fell down from the filamentous substrate by their own weight and took this position at the muddy bottom (lying on the flat side). It seems that the apical part of the corallum was oriented currentwards and that the opening of the operculum could provoke turbulence of water current (Fig. 6). That could be an advantage in food supply.

Hunting for the ancestors - Conclusions

The Silurian-Devonian operculate corals of the fa-

mily Goniophyllidae DYBOWSKI, 1873 (HILL, 1981) contain forms with a single operculum (*Calceola, Rhizophyllum, Rhizophylloides* and *Rhytidophyllum*) as well as with four opercula (*Goniophyllum* and *Araeopoma*).

Microstructural data obtained by LAFUSTE (1983) show that skeletons of *Goniophyllum* and *Calceola* are, in general, similar. In both, sclerenchyme is made of microlamellae but they differ in the shape of the latter: In *Goniophyllum* there are microlamellae of a cupular form, usually encountered in Rugosa, whereas in *Calceola* microlamellae are thinner, broader and sometimes pincers-shaped. As a result, LAFUSTE (1983) considered *Calceola* as a genus incertae sedis, but with some resemblance to the family Goniophyllidae.

Morphology of the young stages of *Calceola* show some similarities to the morphology of early middle Cambrian *Cothonion sympomatum* (JELL & JELL, 1976; JELL, 1984), which allow for considering the latter as a presumable relative of operculate corals. Juvenile stages of *Calceola* resemble that of *Cothonion* in the disproportional development of large septa at opercula, in contrary to the small septal ridges in calices. The operculum of *Cothonion* is circular to semicircular, with septa radiating from the central aseptate area. The opercula of *Calceola* are in the earliest stages almost elliptical and change shape with the development of a straight hinge. Thus, differences between these forms could be
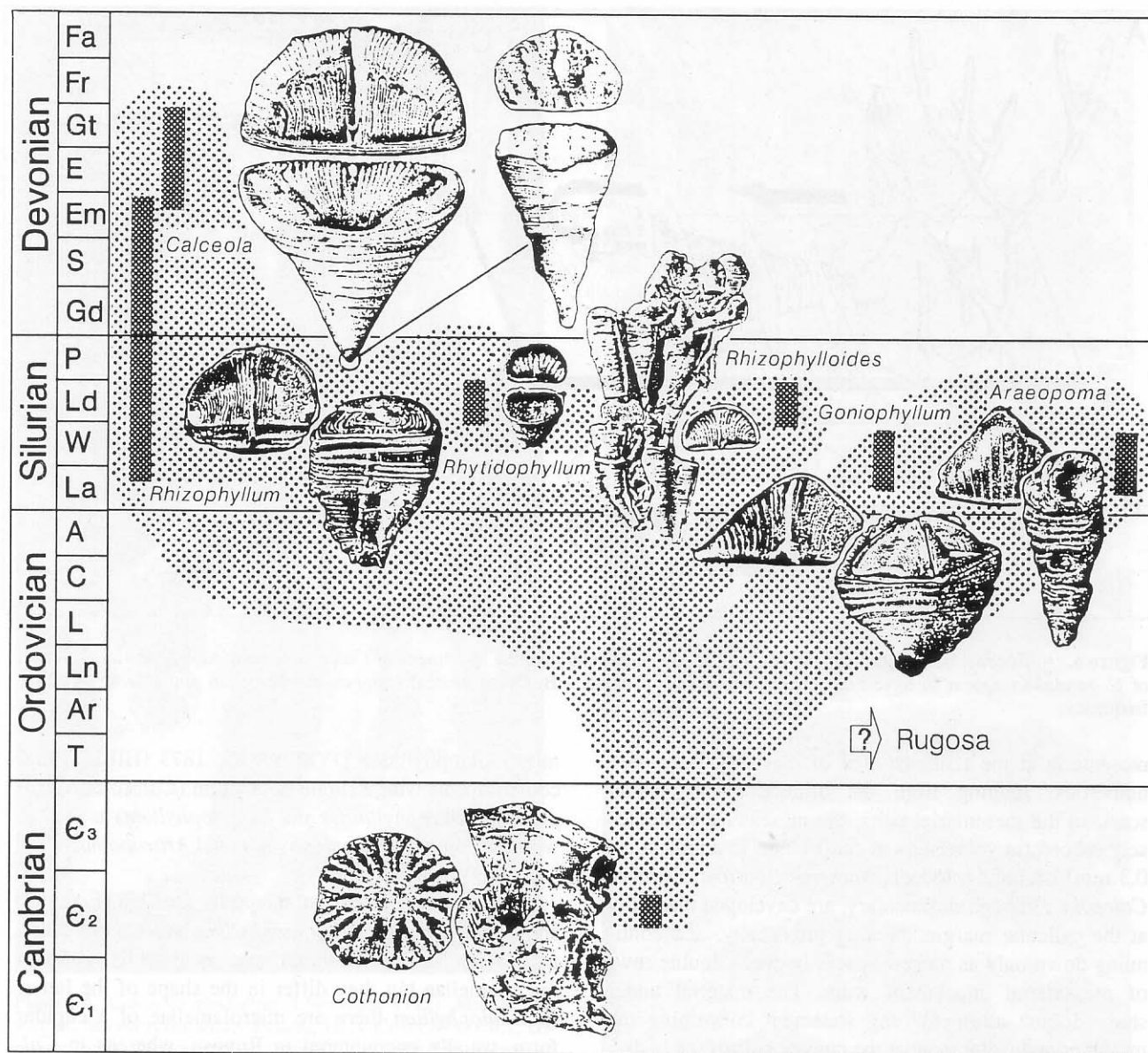
Figure 7. Presumed relationships of operculate corals (Cothoniida) and Rugosa.

considered as a result of their different functional specialization.

Let us presume that the operculum was a primeval feature inherited from their Cambrian ancestors. This peculiar feature separates the operculate forms as a monophyletic group (Cothoniida) from other corals which also derived from the *Cothonion* group but developed independently. The latter lineage, evolving into the rugosan stock (Fig. 7), lost their opercula and developed a septal apparatus of the monacanthid type. Perfectioning of the hinge mechanism (*Calceola* evolutionary lineage) or losing of its role (*Araeopoma* evolutionary lineage) could be a matter of specialization; RICHTER (1929) suggested, that the losing of a regular quadrangle corallum shape in the late ontogeny of *Araeopoma*, could

be connected with the losing of touch between corallum and movable opercula up to their possible reduction and complete disappearance. In this scenario the gap in documentation between Cambrian and Silurian is embarassing. The absence of operculate forms in Ordovician time should be explained by a poor representation of this group in the earliest Palaeozoic. The second unknown point in the assumed history of operulate and rugose coral stocks is the appearance of the serial septal insertion.

Acknowledgments

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