

Middle Devonian *Calceola sandalina* (Linnaeus, 1771) (Anthozoa, Rugosa) from Moravia (Czech Republic): aspects of functional morphology, gerontic growth patterns, and epibionts

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ABSTRACT

Middle Devonian (lower Givetian) *Calceola sandalina* (Linnaeus, 1771) from Čelechovice Limestone, Moravia, Czech Republic, displays sharply differing ontogenetic stages. Width of ventral side and size/volume of calice steadily increases in juvenile and adult stages but decreases in some specimens in final stages of life: we consider these reductive late stages to be gerontic characters. “Ventral” side of juvenile specimens is flat and straight while in adults this side becomes convex. We suggest that opening of operculum and shifting part of polyp body mass forward would shift centre of gravity so that calicinal part of adult coral could rock down to seabottom. Closing operculum would elevate calice above bottom. Rocking movements could help to free coral from sediment. Operculum positioning could move coral and keep it in optimum feeding position. Single specimen shows predation injury: almost half of the “ventral” side is missing between counter septum and corallite angle but has healed within calice.

KEY WORDS

Anthozoa,
Rugosa,
Calceola,
Givetian,
rugose corals,
gerontic stage,
epibionts,
predation,
regeneration,
ecology.

RÉSUMÉ

Calceola sandalina (Linnaeus, 1771) (Anthozoa, Rugosa) du Dévonien moyen de Moravie (République tchèque) : morphologie fonctionnelle, stade ultime de croissance et épibiontes.

Les spécimens de *Calceola sandalina* (Linnaeus, 1771) du Dévonien moyen (Givétien inférieur) des Calcaires de Čelechovice (République tchèque) montrent des stades ontogéniques bien différenciés. La largeur de la face « ventrale » et la taille et le volume des calices s'accroissent régulièrement au cours des stades juvéniles et adultes mais décroissent chez quelques spécimens lors de la phase ultime du développement. Nous considérons que cette étape à morphologie régressive caractérise un stade sénile ou gérontique. La face « ventrale » des spécimens juvéniles est plane tandis que chez les adultes elle devient convexe. L'ouverture de l'opercule et le déplacement distal des parties molles provoquerait le déplacement du centre de gravité, rapprochant la partie calicinale des coraux adultes du fond marin ; la fermeture de l'opercule entraînerait un mouvement inverse. De tels mouvements de bascule aideraient au désenvasement du polypier. L'angle d'ouverture de l'opercule permettrait le positionnement optimum de l'organisme pour capter la nourriture. Un individu montre des blessures dues à un prédateur ; presque la moitié de la face « ventrale » est manquante entre le septa antipode et l'angle du polypier mais ces dégâts sont cicatrisés du côté calicinal.

MOTS CLÉS

Anthozoa,
Rugosa,
Calceola,
Givétien,
coraux rugueux,
stade gérontique,
épibiontes,
prédation,
régénération,
écologie.

INTRODUCTION

The present paper is a case study concerning the functional morphology of *Calceola sandalina* (Linnaeus, 1771), from the Moravian Devonian. In particular we will comment on the function of flat “ventral” side of *C. sandalina*, on the diminishing of the calice as a manifestation of senility, and on the process of healing of a single injured specimen of *Calceola*.

Our material for this study comes from the Čelechovice Limestone which crops out at Kosíř Hill approximately 7 km NW of Prostějov in the Czech Republic. The locality has been variously mentioned in literature under the names Čelechovice, Kaple, and Rittberg. This limestone outcrops in the Státní lom Quarry and Růžičkův lom Quarry and lies between the villages of Čelechovice and Kaple (Galle & Hladil 1991). *Calceola sandalina* is known from both quarries. The Růžičkův lom Quarry has yielded fewer and smaller specimens than the Státní lom Quarry. Juvenile specimens

and isolated opercula have been found in both quarries. Ficner (1961) published detailed descriptions of both the Čelechovice Limestone and its resident coral *Calceola sandalina*.

Hladil *et al.* (2002) summarized the research history of the Devonian at Čelechovice. They also confirmed the age of the fossiliferous beds as being close to the boundary between the *Polygnathus hemiansatus* and early *Polygnathus varcus* Zones (= lower Givetian). Specimens of *Calceola sandalina* occur in “red beds of the Čelechovice Limestone” (Čelechovice Upper Dark-colored Interval of Hladil *et al.* 2002 comprising beds 117-146 of which beds 136-138 are richly fossiliferous, see Galle & Hladil 1991). The whole unit consists of dark algal limestones, packstones, floatstones, coquinas, and biostromes with typical Čelechovice fauna. It is underlain by dark marlstone of an extremely shallow environment, and overlain by laminated, sometimes siliciferous limestone (Galle & Hladil 1991). Faunal lists and a detailed measured section see also in Galle & Hladil (1991).

ABBREVIATIONS

AG	collection of A. Galle;
FF	collection of F. Ficner;
JS	collection of J. Sedlák;
RL	Růžickův lom Quarry;
SL	Státní lom Quarry.

MATERIAL AND METHODS

The described specimens were a part of the late principal teacher František Ficner's (1903-1985) collection from the Devonian of Čelechovice na Hané in Moravia, Czech Republic. The bulk of F. Ficner's collection is currently in the hands of the Ficner family and is still extant. Large part of it was deposited in the collections of the Czech Geological Service, Prague.

Calceola sandalina is rather rare in the Čelechovice Devonian; the list in Appendix 2 identifies the known specimens.

Calceola sandalina was collected mostly in the quarry scree in both RL and SL. Several specimens are known to originate in the fossiliferous "red bed", but neither their identity nor their position in the bed are known. Most of the small juvenile specimens have been washed out from the soft parts of the "red bed" in both quarries. Several specimens needed minor mechanical preparation.

Specimens were observed and measured under standard binocular microscope. Larger specimens were measured also by calipers. Apical angles were measured on photographs. Only a few specimens have been cut and thin sectioned, the study of inner structures was not in the preview of this project.

Changes of the L/W ratio during ontogeny were recorded by measuring corallite width along the corallite flat counter side. Measurements were executed at marked points along the corallite length. This was done at every 1 mm close to the apex to document abrupt increase of the corallite width in early growth stages, in later growth stages of the corallite it was done every 5 mm. Data are presented in Figures 1 and 2, these figures illustrate clearly ontogenetic changes in the corallite outlines, particularly

gerontic decrease in corallite diameter. These data are also available on line at <http://www.gli.cas.cz/home/galle/default.htm>

SYSTEMATICS

Family CALCEOLIDAE King, 1846

Weyer (1996) called attention to the fact that Goniophyllidae Dybowski, 1873 is a junior synonym of Calceolidae King, 1846. The family includes Araeopomatinae Lindström, 1883 with genera *Araeopoma* Lindström, 1866 and *Rhytidophyllum* Lindström, 1883, and Calceolinae King, 1846 with *Goniophyllum* Milne-Edwards & Haime, 1866, *Rhizophyllum* Lindström, 1866, and *Calceola* Lamarck, 1799.

Genus *Calceola* Lamarck, 1799

TYPE SPECIES. — *Anomia sandalium* [sic] Gmelin in Linnaeus 1791: 33-49 = *Anomia sandalinum* Linnaeus, 1771: 547. Devonian, Eifel Hills, Germany. By monotypy (Lang *et al.* 1940).

DIAGNOSIS. — See Hill 1981.

Calceola sandalina (Linnaeus, 1771)
(Figs 1-6)

Synonymy: see Pedder & Feist 1998: 973.

MATERIAL EXAMINED. — Specimens 1/1RL (Ficner 1961: pl. IV, fig. 1); 2/13SL (Ficner 1961: pl. III, fig. 2); 4RL; 3/16SL; 5/17SL; 6/2RL; 7/9; 8/23; 9/15SL; 10/18SL; 11/14SL; 12/19SL; 4/11; 13/3RL; 14/6RL; 15/22; 16/20; 17/21; 18/10; 19/24; 20/28SL; 21/103SL; 102SL; 104; 22/7; 23/5RL; 24/8; 109RL; 2/2SL; 2/3RL; thin sections AG 932 A-C, 2 transverse and 1 longitudinal sections; AG 1387 A-B, 1 transverse and 1 longitudinal sections; and opercula 12SL (Ficner 1961: pl. IV, fig. 2); 25; 101SL; 108RL; 26; 27; 106; 107; 105; all specimens except those marked AG are from FF, Čelechovice, Čelechovice Limestone; latex cast of specimens ICh 3482, ICh 3483 from Eifelian(?) Stínava-Chabíčov Formation, Petrovice, collection of I. Chlupáč, Czech Geological Service Prague; specimen 29 (Strnad 1960: figs 1, 2), Eifelian, Horní Benešov, Strnad collection, Silesian Museum Opava; and single specimen AG 1436 A-C, an

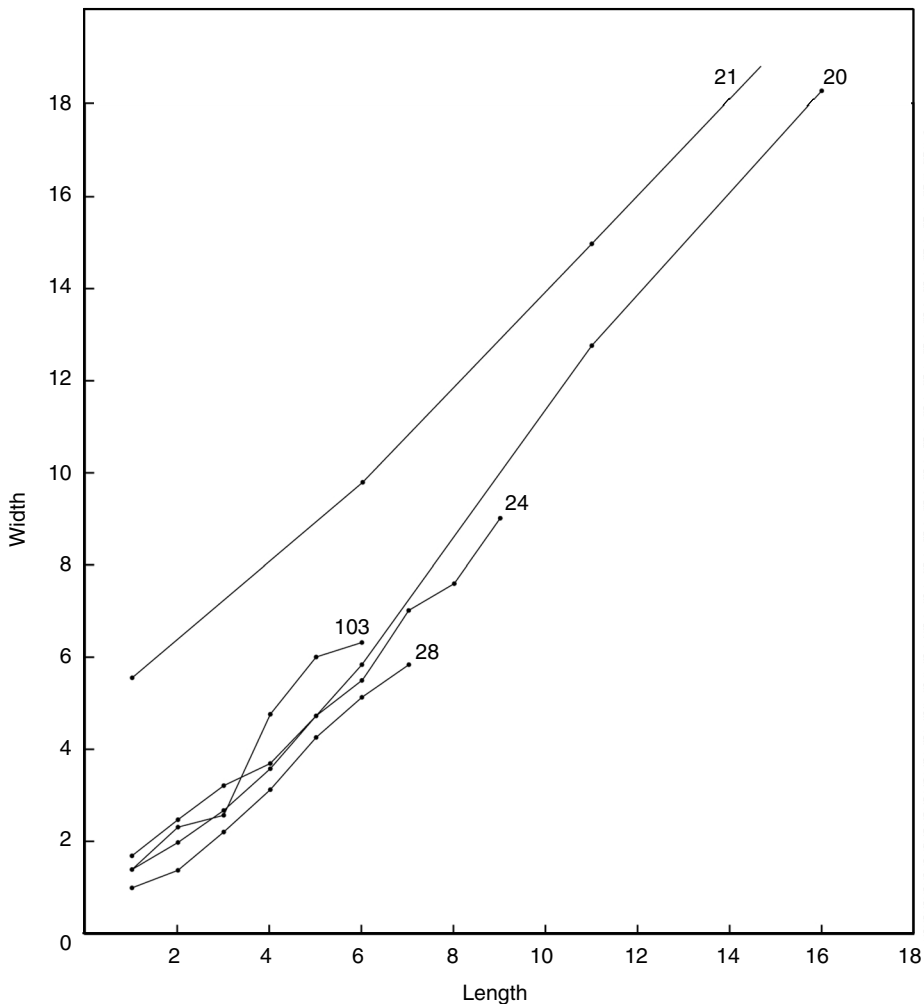


FIG. 1. — Corallite growth of juvenile specimens (20, 21, 24, 28, 103SL) expressed as L/W ratio (L and W in mm), Čelechovice, measurements begin 1 mm after the preserved apex of the corallite; this caused the beginnings of respective lines at various widths. Abbreviation: **SL**, Státní lom Quarry.

incomplete specimen with 3 incomplete oblique sections, Eifelian or Givetian, borehole KDH-9, depth 187.4 m; figured in Galle (1995: pl. 4, figs 1-3, and here on Fig. 6O).

REMARKS

Tables 1 and 2 give the dimensions of the Čelechovice adult (OR adult) and juvenile (OR juv.) specimens of *C. sandalina* (Table 1), and the differences in dimensions between the specimens from Čelechovice, Horní Benešov, Petrovice,

and Konice KDH-9 (Table 2). Further dimensions of the Čelechovice specimens are given in Appendix 1.

Terminological note: The term “counter septum” is used here for a distinct septum in the central axis of flat “ventral” side of *C. sandalina* which developed from central septal ridge of Stolarski (1993) as septal insertion in *Calceola* is not clear. The same applies on terms “K” and “counter side”.

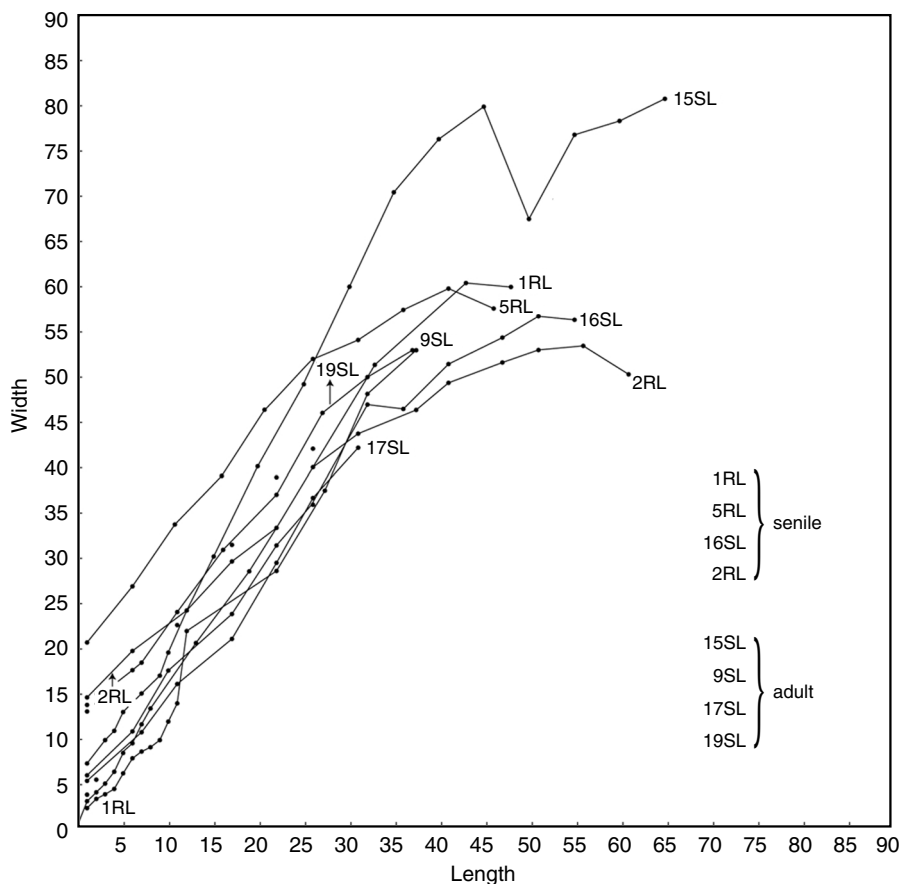


FIG. 2. — Corallite growth of adult (15SL, 19SL, 9SL, 17SL) and gerontic (1RL, 2RL, 5RL, 16SL) specimens expressed as L/W ratio (L and W in mm), Čelechovice, note width decrease on the curve of the specimen 15SL (= rejuvenation, see Fig. 5E-H). For further explanations see Fig. 1. Abbreviations: **RL**, Růžickův lom Quarry; **SL**, Státní lom Quarry.

DISCUSSION

The Moravian material fits well within the accepted width variations of the species (Birenheide 1978). There are obvious variations in the dimensions and degree of stereoplastic thickening among the Čelechovice specimens and those from other Moravian localities. The adult specimens from Čelechovice are large and strongly thickened, but specimens from Horní Benešov, Petrovice, and from borehole KDH-9, near Konice, are smaller and relatively less thickened. There are also differences in the apical angles which increase through ontogeny and are clearly visible in the

Čelechovice material. Presence or absence of tabulae or tabellae also varies: longitudinal section C through the specimen AG 932 (Fig. 6N) shows three successive tabulae or tabellae of various shape and thickness. However, they are usually missing in most of Čelechovice specimens.

Ontogeny of *Calceola sandalina* has been recently discussed by Stolarski (1993). He studied rich material from the Givetian Microcyclus Shale, Holy Cross Mountains, Poland that included all of its ontogenetic stages. He recognized initial, juvenile, and adult stages. Juveniles in the initial stage are not

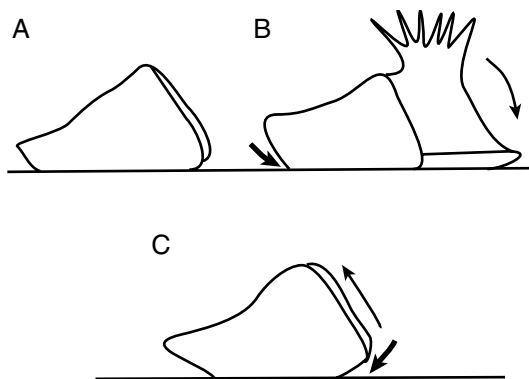


FIG. 3. — Freeing of *Calceola* out of the sediment; **A**, coral deep in sediment; **B**, center of gravity shifts forward and calice moves downward by opening the operculum, apex moves upward and sediment particles pour under apical part; **C**, operculum close, center of gravity shifts backward, calice moves upward and sediment particles pour under calicinal part. Animal moved upward.

observed in Moravian specimens but juvenile stages with growth lines, operculum, and flattened counter side, as well as adult stages, are represented in the Čelechovice material.

Calceola sandalina was also studied recently in detail by Gudo (1998, 2001, 2002). He reconstructed its polyp and speculated on its functional and constructional anatomy, ontogeny, and ecology.

Occurrence: *Calceola sandalina* in Moravia: in addition to the Čelechovice locality the species occurs in five localities: Horní Benešov (lower part of the Middle Devonian, Eifelian?, Strnad 1960), Vratíkov (lower Middle Devonian, Špinar 1951; the specimen has been reported in, but has not been located in the Charles University collections), Petrovice (?Eifelian, coll. I. Chlupáč in the Czech Geological Survey Prague), and Konice, borehole KDH-9, depth 187.4 m (Eifelian-Givetian; Galle 1995).

Slightly metamorphosed coarse quartzitic conglomerate of Middle (?) Devonian age from the locality Kozí brada near Tišnov NW of Brno yielded relatively abundant but poorly preserved coral and brachiopod fauna. Among rugosans, several specimens of *C. sandalina* are preserved both as isolated corallites and opercula.

DISCUSSION

JUVENILE AND ADULT STAGES

As stated above, the apical angle varies broadly during ontogeny of *Calceola sandalina* specimens from Čelechovice. It further supports the opinion that this feature is not a valid taxobasis to define species of *Calceola* (see Pedder & Feist 1998). Variation of the apical angle expressed as W/L ratio is illustrated in the diagram on Figure 1. The entire width of the flat ventral side of the corallite has been measured in defined length intervals and recorded in the graph (Fig. 1) so that the graph curve illustrates an entire width of the corallite. The W/L ratio of the individuals changes from small to large and to small again. The “ventral” side of the juvenile specimens is always flat and straight both transversally and longitudinally.

Table 1 gives the measurements of both adult and juvenile individuals of *C. sandalina* from Čelechovice. It lists the maximum measured apical angles in represented individuals. The smallest juvenile apical angles are as low as 22–23°. Adult specimens, on the other hand, always show apical angles greater than 25°; they are usually 70–80°, and they are only rarely as acute as 50°.

GERONTIC STAGE

The graph of the length/width ratio of the “ventral” side of adult *C. sandalina* (Fig. 2) shows that it steadily increased during the individual’s life. In some Čelechovice specimens it decreases in very late growth stages. Similar late growth stages decrease is also illustrated by Termier & Termier (1948: text-fig. 6). We consider such narrowing in these specimens as a gerontic character. Unfortunately, the operculum is never preserved in situ on any of the specimens discussed, so its reaction (resorption?) to the decrease in calice width has not been documented. Other characters, calice shape and size, change distinctly during the gerontic stage. Calice size decreases during gerontic changes of the corallite (Fig. 5A–D, Y). With the changes in calice size, the calice shape also changes. In juveniles and adults the calice more or less copies the

TABLE 1. — Comparison of the dimensions of adult and juvenile specimens of *Calceola sandalina* (Linnaeus, 1771), from Čelechovice. Abbreviations: **juv.**, juvenile; **OR**, observed range. Length, width, height and calice depth in mm; apical angle in degrees.

	Length	Width	Height	Number of septa	Calice depth	Apical angle
OR adult	19.2-9.0	24.5-80.9	13.0-30.9	38-121	13.6-29.0	52-114
OR juv.	5.6-16.8	5.8-21.2	2.6-11.4	16-30	5.0-12.1	56-95

TABLE 2. — Comparison of dimensions of all studied Moravian specimens (adults and juvenile). Abbreviation: **sp.**, specimen. Corallite width in mm; max. apical angle in degrees.

	Corallite width	Number of septa	Max. apical angle
Čelechovice			
Observed range	5.8-80.9	10-48	56-114
Number of specimens	24	17	9
Mean	45.9292	31.4706	90
Horní Benešov (1 sp.)	34.0	—	75
Petrovice (1 sp.)	30.4	29	87
Konice KDH-9 (1 sp.)	21.8-23.5	—	—

outer half-cone shape of the corallite, but in gerontic specimens the calice differs distinctly, it is commonly funnel-shaped, with the shallow distal (close to operculum) end, and the proximal end of the calice (close to apex) modified into a relatively long and narrow channel (Fig. 6L, M). We do not believe above mentioned changes to be caused environmentally as they occur in large adult specimens and are unknown in juveniles. Environment would influence all specimens (and probably not only *C. sandalina*) in a respective time horizon.

REJUVENATION

Rejuvenation is common in most rugosan genera including *Rhizophyllum* Lindström, 1866, which is closely related to *Calceola*. The phenomenon is rather rare in *Calceola sandalina*, as well as, in other species of *Calceola*. Of the specimens of *C. sandalina* from Čelechovice listed in Appendix 2 below plus those discussed herein from the FF, only three show rejuvenations or calicinal budding: two from SL (one specimen from FF, one from JS) and one from RL). A specimen from West Sahara, figured in Termier & Termier (1948: text-fig. 6) shows

rejuvenations and two juvenile specimens figured in Stolarski (1993: figs 1.2, 2.12) are rejuvenated within the calice.

One of the specimens discussed here, 9/15SL (Fig. 5E-H) shows clear asymmetric rejuvenation. The specimen's left side (when observed from its cardinal side) decreases in width from 79.8 mm at the corallite length 44 mm to a width of 67.5 mm (specimen length 49 mm). Following the next 5 mm of growth length which is 54 mm, the width is 76.8 mm, and at 64 mm in length it grown to a width of 80.9 mm (see also Fig. 2). The calice of the specimen is perfectly symmetrical and no signs of rejuvenation are manifest on the interior. The septal number on the counter side is somewhat asymmetric, being 57-K-63 of both majors and minors, but such asymmetry appears also in *C. sandalina* corallites without signs of rejuvenations. However, the course of the cardinal-counter plane has changed somewhat due to asymmetric rejuvenation.

Much less conspicuous rejuvenation is visible also on the specimen 10/18SL (Fig. 5K, M). It is an injured specimen described below; however, its rejuvenation is not connected with its injury: injury is post rejuvenation.

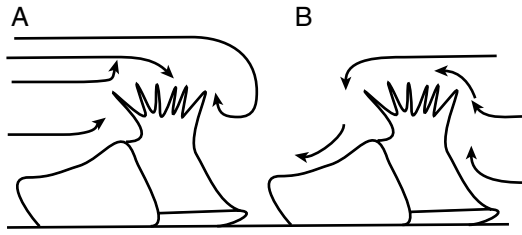


FIG. 4. — *Calceola* with calice facing downstream (A) and upstream (B).

CONVEX COUNTER SIDE OF THE CORALLITE, FEEDING AND CURRENT ORIENTATION

The counter side of the corallite can be geometrically defined as triangular sector of cylinder surface with long axis parallel to cylinder base in adult specimens, as illustrated here in Figure 3A, H and M, and Gudo 2002: pl. 2, text-fig. 6 (see also Hill & Jell 1969). This is not the case in juvenile specimens; their counter sides are straight in both directions, as seen here on Fig. 5R, and lie horizontally on the sea floor. The curvature of the corallite longitudinal axis changes dramatically during ontogeny, in the adult stage specimens are strongly convex longitudinally on their “ventral” side and are slightly concave longitudinally on their “dorsal” side. The curved “ventral” side strongly resembles the profile of the rockers on a rocking chair and, as discussed below, it functioned similarly.

Gudo (2001) compared the shape of *Calceola* corallite to snowshoe. He also suggested that the individuals of *Calceola* could free themselves from the sediment by pushing down their opercula. Gudo (2002: 685) further suggested that “by means of opening and closing their operculae these corals were able to compensate for the effects of sedimentation and lift themselves out of the sediment when[...] the lid was pushed into the sediment during the opening process”. We suggest that opening of operculum and shifting of part of the polyp body mass forward would shift the centre of gravity so that the calicinal part of coral could rock down to the bottom and its apex would move upwards (Fig. 3A, B), while closing the operculum would cause the contrary

(Fig. 3C). Such rocking movements could help to free the coral from the sediment.

Convex “ventral” side would also enable movements of coral over the sea bottom when pushed by operculum movements. Straight corallite would easily embed into the bottom.

Operculum positioning could push or drag the coral over the seabottom and by such means it could have, besides freeing the coral from the sediment as suggested in Gudo (2001), move the coral into and keep it within optimum position, facing into and favorably deflecting the current for food, oxygen, and waste removal.

Stolarski (1993) reconstructed the current-oriented mode of life of *C. sandalina* with apex oriented toward the current. Such currents would bring added food and oxygenated water in contact with the tentacles. Parsley (pers. comm., May 2002) commented on Stolarski’s hypothesis by suggesting that with the calice facing downstream the tentacles are catching prey in the backeddies in a manner described for *Aristocystites* (Parsley 1990). The tentacles are feeding in a reduced energy situation, energy being dissipated by the corallite by placing drag on the currents as they flow over it. This mode of life seems to work well for echinoderm brachioles. *Calceola* is a recumbent coral and the current close to the bottom is reduced through drag along the bottom. The profile of the coral creates a hydrofoil when the calice faces into the current and would accelerate current over the top of the calice. By extending the lower corallite surface to force the current to accelerate (Bernoulli Principle) the more typical higher energy regimen typical of corals is, more or less, restored across the upper surface of the polyp and the tentacles. The flow through mode of food capture, typical of corals is thereby retained. However, evidence on the orientation of *C. sandalina* upstream or downstream is missing (Fig. 4A, B).

PREDATION

Specimen 10/18SL (Fig. 5J-M) shows severe injury on its right side when observed from its “dorsal” (= cardinal) side. Approximately one

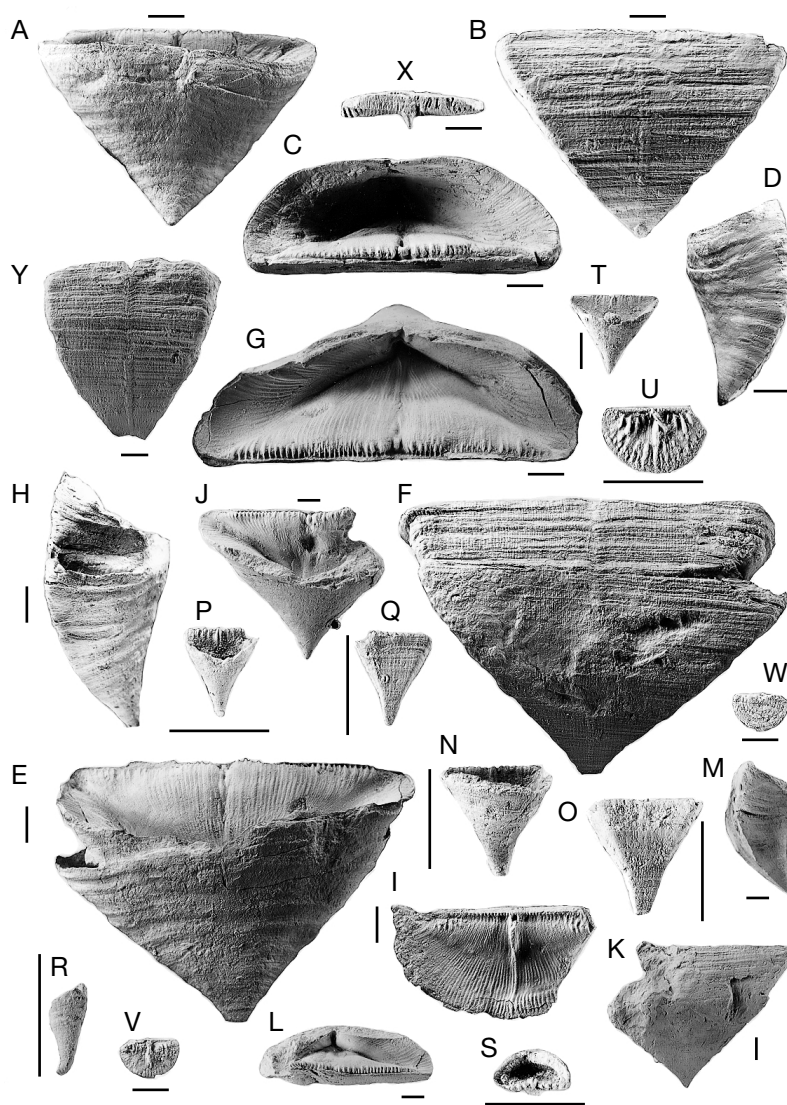


FIG. 5. — *Calceola sandalina* (Linnaeus, 1771), coll. F. Ficner, Čelechovice, all specimens are whitened with ammonium chloride prior the photographing; **A-D**, specimen 1/1 (1RL), RL, well developed specimen with somewhat closing (senile) calice; **A**, "dorsal" side; **B**, "ventral" flat counter side; **C**, calicinal view; **D**, lateral view with convex "ventral" counter and concave "dorsal" cardinal sides; **E-H**, specimen 9/15 (15SL), SL, rejuvenated adult specimen; **E**, "dorsal" view; **F**, "ventral" view; **G**, calicinal view; **H**, lateral view; **I**, specimen 12SL, SL, adult operculum; **J-M**, specimen 10/18 (18SL), SL, injured specimen; **J**, "dorsal" view with damaged but healed septa and counter side of the calice; **K**, "ventral" view unhealed conical traces; **L**, calicinal view; **M**, lateral view; **N, O**, specimen 19/24 (24), unknown locality in Čelechovice, juvenile specimen; **N**, "dorsal" view; **O**, "ventral" view; **P-S**, specimen 20/28 (28SL), SL, juvenile specimen; **P**, "dorsal" view; **Q**, "ventral" view; **R**, lateral view with straight "ventral" side; **S**, calicinal view; **T**, specimen 16/20 (20), unknown locality in Čelechovice, young adult specimen, "dorsal" view; **U**, specimen 27, unknown locality in Čelechovice, juvenile(?) operculum; **V, W**, specimen 26, unknown locality in Čelechovice, juvenile(?) operculum; **V**, inner side; **W**, outer side; **X**, specimen 25, unknown locality in Čelechovice, adult operculum, view from the hinge line; **Y**, specimen 6/2 (2RL), RL, senile specimen with closing calice, "ventral" view. Abbreviations: **RL**, Růžickův lom Quarry; **SL**, Státní lom Quarry. Photos by Mrs. Hana Vršťalová (Central Geological Survey, Prague). Scale bars: 10 mm.

half of the “ventral” side is missing between the counter septum and the alar corallite angle. The injury is healed within the calice and is also visible on deformed septa close to the injury, while the outer flat ventral side shows no marks of healing. (The adjacent dorsal part has been broken off after diagenesis). The operculum is not preserved but because of the extent of the damage it clearly must have been involved. Such mechanical damage is hardly imaginable in the rather low-energy environment where the sedimentary particles are silt sized. It seems likely that the injury is the result of a predatory attack. The nature of the injury, unhealed or poorly healed marks on both the flat outer corallite and inside the calice, suggests a quick short violent action of a durophagous animal (probably vertebrate) larger than *Calceola* rather than a prolonged attack of a small invertebrate predator or slow destruction of the part of the corallite by a parasite. As the traces of durophagous predation start in Devonian (Wood 1999), we consider the specimen worth mentioning. Injury caused to discussed specimen 18SL of *Calceola* seems to be severe, as almost entire alar quadrant of the polyp has been removed. The specimen survived at least for some time; septa on the hinge side of the calice are deformed but healed while the calice floor recovered only in part. At least part of the operculum was probably removed in the attack and thereby the wounded tissues were open to secondary predation and enhanced probability for bacterial infection. The survival of the injured specimen is remarkable and testifies to an amazing regeneration capacity.

In speculating on what sort animal was capable of bringing about such injury, one must preferentially consider strong jawed vertebrate (Signor & Brett 1984). Durophagous placoderms and chondrichthyans appeared in the Devonian (Signor & Brett 1984). Nevertheless, such animals are not known from Čelechovice or from other Givetian localities in Moravia. Hladil (1991) mentioned fish scrapings among ichnofossils from the bed 10 (Frasnian, late *Palmatolepis rhenana* [Upper *Palmatolepis gigas*] Zone) of Lesní lom Quarry.

Both internal and external sides of the “ventral” (counter) side of the calice bear conical depressions close to the edge of the injury. The healing process started within the calice but, naturally, not on the outer “ventral” side. There, the depressions could have originated after death and possibly after fossilization of the specimen (most probably during, or shortly after, the quarrying activities). However, we consider it more probable, that they originated during the predator attack, and that they are the traces of teeth or beak opposite to those within calice. Even if we would suppose that original calcitic (or Mg-calcitic) skeleton of *C. sandalina* was both softer and more brittle than its current post diagenetic state, a nearly 10 mm thick calcitic plate must have been impressive challenge for any animal. The ichnological aspect of the case is recently been dealt with by Galle & Mikuláš (2003).

For the injured coral data see Appendix 3.

EPIBIONTS

Epibionts are common among Čelechovice fauna; almost all sessile forms are host animals for other benthic faunas. *Calceola sandalina* is not among the most sought hosts. The material at hand comprises 19 adult specimens; nine of them are epibiont-infested, 21 epibionts have been counted, some of the hosts bear multiple epibionts. None of the seven juvenile specimens bears an epibiont; neither do any of 10 isolated opercula. Among epibionts, tabulate corals predominate (“*Favosites*”, alveolitid, *Heliolites*, and auloporoid[s]), stromatoporoids and spiral worm-like tubes (“*Spirorbis*”) occur more than once, and other organisms occur only in one specimen (Table 3).

Most of the epibionts occur on the longitudinally slightly concave “dorsal” (cardinal) side (17 of 21); it is likely, but cannot be proved, that at least some if not most grew on living specimens. Specimens were bottom-heavy and so were quite stable. After their death they probably rested on the sea bottom in their life position with their flat side down. Other epibionts, as those growing inside the calice (two, and probably also the specimen figured in Remeš 1929:

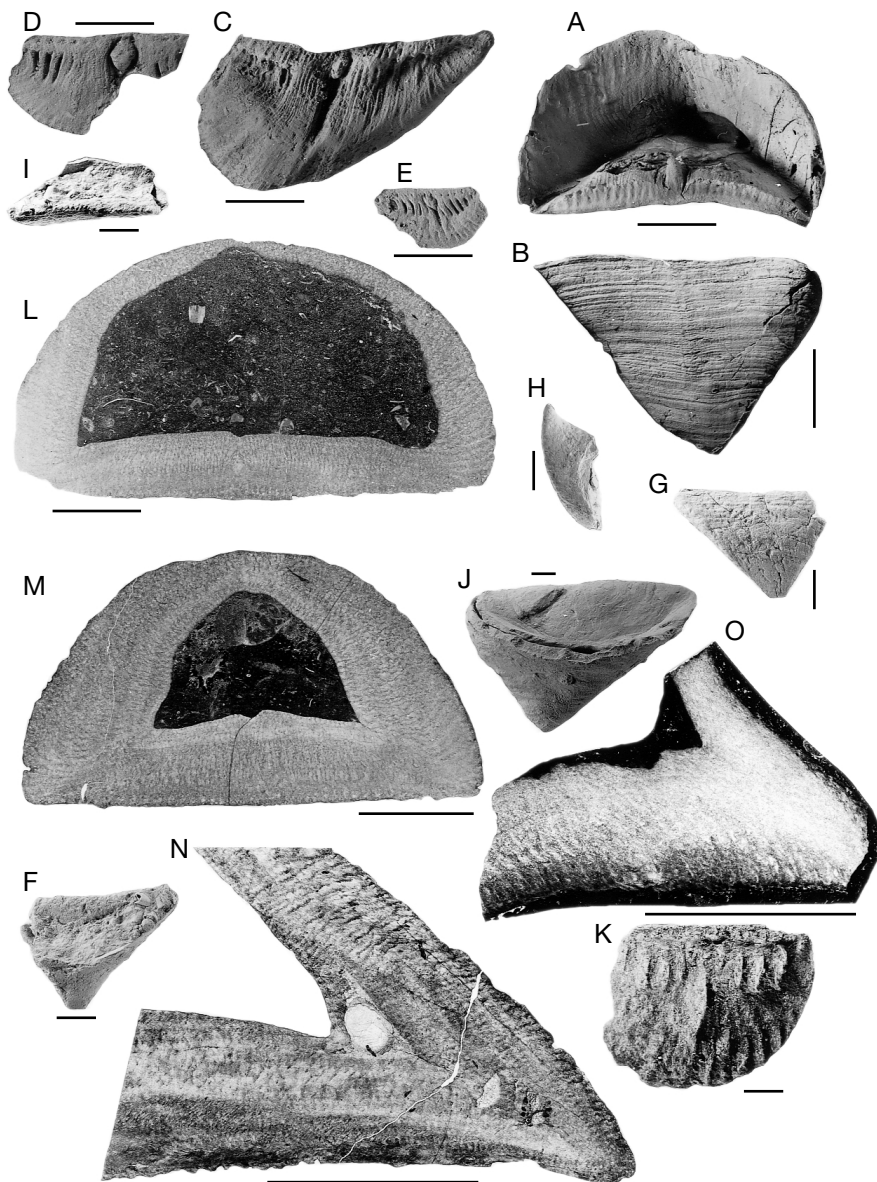


FIG. 6. — *Calceola sandalina* (Linnaeus, 1771), all specimens are whitened with ammonium chloride prior the photographing except the thin sections; **A, B**, specimen ICh 3483, Chlupáč collection, Czech Geological Survey, Eifelian, Petrovice, latex cast; **A**, calicinal view; **B**, "ventral" view; **C-E**, three specimens ICh 3482 A-C, same collection and locality, steinkerns of opercula; **F-I**, specimen 29, Strnad collection, Silesian Museum Opava (figured in Strnad 1960: figs 1, 2); Eifelian, Horní Benešov; **F**, "dorsal" view; **G**, "ventral" view; **H**, lateral view; **I**, calicinal view; **J**, specimen 2/13 (13SL), Givetian, Čelechovice, SL, adult specimen with operculum in situ; **K**, specimen 107, unknown locality in Čelechovice (Givetian), juvenile operculum; **L-N**, specimen AG 932 A-C, coll. Galle, Geological Institute Academy of Science, unknown locality in Čelechovice (Givetian); **L**, transverse section nearer to calice; **M**, transverse section nearer to apex, senile closing of the calice is visible; **N**, longitudinal section through counter-cardinal plane; free spaces under the tabulae or tabellae; **O**, specimen AG 1436 C, coll. Galle, Geological Institute Academy of Science (figured in Galle 1995: pl. 4, figs 1-3); Borehole KDH-9, vicinity of Konice, close to Eifelian/Givetian boundary; transverse section through deformed specimen. Abbreviations: **RL**, Růžickův lom Quarry; **SL**, Státní lom Quarry. Photos by Mrs. Hana Vršťalová, thin sections by Mrs. Dana Hejdová (Central Geological Survey, Prague). Scale bars: A-J, L-O, 10 mm; K, 1 mm.

TABLE 3. — Distribution of epibionts over the corallites of *Calceola* in Čelechovice. Abbreviations: first column refers to locations on *Calceola* corallite (dorsal [cardinal], ventral [counter], operculum inside and outside, inside calice); “Fav.”, “*Favosites*”; Alv., alveolite; Hel., *Heliolites*; Aul., aulopod; Str., stromatopod; Rug., rugosan; “Spi.”, spiral worm-like tube, like *Spirorbis*; Bry., bryozoan; ?Hf., base or holdfast of unknown affinity; ?, problematic organic remain; Σ, sum.

	“Fav.”	Alv.	Hel.	Aul.	Str.	Rug.	“Spi.”	Bry.	?Hf.	?	Σ
Dorsal (C)	4	2	2	3	2	1	1	0	1	1	17
Ventral (K)	0	0	0	0	1	0	0	0	0	1	2
Operculum	0	0	0	0	0	0	0	0	0	0	0
Inside calice	0	0	0	0	0	0	1	1	0	0	2
Σ	4	2	2	3	3	1	2	1	1	2	21

pl. III, fig. 4) and probably also those on the flat “ventral” (counter) side (two) grew after death and disruption of their respective hosts.

CONCLUSIONS

Specimens of *Calceola* from Čelechovice display the following growth characteristics:

- the juvenile stage has its “ventral” side both transversally and longitudinally flattened and with small apical angle. Adult and gerontic stages have a marked convex “ventral” side, a large apical angle, and a diminishing corallite diameter and calice size in gerontic specimens;
- the convex “ventral” side of adult and gerontic specimens together with operculum movements could have served to position the coral with its apex or calice into the current, and to free the coral from the sediment;
- an injured specimen testifies to the presence of a durophagous predator in the Čelechovice Givetian, and to the amazing regeneration capacity of *Calceola*;
- epibionts preferred the “dorsal” side of *Calceola* in the Čelechovice section; it is probable that at least some of them grew on living specimens.

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APPENDIX 1

Dimensions of *Calceola sandalina* (Linnaeus, 1771), from Moravia. Abbreviations: **L**, corallite length (in mm); **W**, corallite width (in mm); **H**, corallite height (in mm); **nl + ll**, number of major + minor septa; **CD**, calice depth (in mm); **A**, apical angle (in degrees); **Čelech.**, Čelechovice; **H. Benešov**, Horní Benešov; **Ich**, collection of I. Chlupáč. Čelechovice specimens are arranged according to decreasing W.

Specimen No.	L	W	H	nl + ll	CD	A
Čelech. 9/15	62.0	80.9	28.5	48	36.8	103
Čelech. 2/13	54.9	80.8	28.4	–	–	–
Čelech. 10/18	50.0	73.4	20.0	41	29.5	100
Čelech. 11/14	66.9	72.3	25.0	41	–	114
Čelech. 1/1	45.2	66.7	22.6	40	29.0	90
Čelech. 4/11	40.1	62.0	–	41	26.1	–
Čelech. 22/7	54.5	61.0	23.7	25	–	–
Čelech. 13/3	52.5	61.0	31.5	–	–	86
Čelech. 23/5	55.0	59.4	29.3	–	–	–
Čelech. 24/8	46.0	58.0	23.0	38	33.9	–
Čelech. 3/16	54.0	57.8	25.2	44	19.0	85
Čelech. 5/17	47.6	56.0	18.0	43	24.7	76
Čelech. 6/2	69.0	53.5	30.9	–	–	73
Čelech. 7/9	43.0	53.0	16.5	37	29.5	–
Čelech. 14/6	36.0	40.5	13.0	38	23.8	–
Čelech. 12/19	33.0	40.0	15.0	–	17.4	83
Čelech. 15/22	19.2	29.9	16.6	–	15.6	–
Čelech. 8/23	19.0	24.5	13.1	–	13.6	–
Čelech. 17/21	16.7	21.2	11.4	29	12.1	–
Čelech. 16/20	16.8	18.3	8.3	22	10.0	74
Čelech. 18/10	10.1	11.0	3.2	15	–	95
Čelech. 19/24	8.8	9.0	5.0	13	5.0	62
Čelech. 21/103	5.6	6.3	3.1	10	–	72
Čelech. 20/28	6.9	5.8	2.6	10	–	56
H. Benešov 29	23.0	34.0	13.0	–	–	75
Petrovice Ich	21.4	30.4	17.9	29	–	87

APPENDIX 2

List of the Čelechovice specimens of *Calceola sandalina* (Linnaeus, 1771) in fossil collections. Abbreviations: **FF**, F. Ficner coll.; **JS**, J. Sedlák coll.

- Czech Geological Service, Prague, 3 specimens (2 FF, 1 JS);
- Masaryk University, Brno, 3 specimens (1 FF, 2 JS);
- collection of late Prof. Kalabis, Brno, 1 specimen (1 JS);
- Museum of Natural History, Prostějov, 3 specimens + 1 isolated operculum (2 + operculum FF, 1 JS);
- collection of Mr. Souček, Prostějov, 1 specimen (1 FF);
- collection of Mr. Remeš, Olomouc, 4 specimens + isolated operculum (2 + operculum coll. Remeš, 1 FF, 1 JS);
- National Museum Cardiff, Great Britain, 1 specimen (1 FF);
- Purkyně University, Olomouc, 1 specimen (1 JS);
- collection of R. Jiříček, Brno, 2 specimens (collected by Jiříček);
- Moravian Museum, Brno, 1 specimen (old collection);
- Natural History Museum, Olomouc, 1 specimen (old collection);
- National Museum, Prague, 2 specimens (1 JS from coll. Plas, 1 coll. F. Smyčka);
- Vienna, Austria, 1 specimen (coll. Smyčka); 1 specimen from the Smyčka collection is missing and probably lost.

APPENDIX 3

Data of the injured specimen 10/18SL, Státní lom Quarry, Čelechovice.

Length = 50.0 mm

Width = 36.7 mm is half width from counter septum to calice edge, restored width = 72.0-74.0 mm

Height = c. 20.0 mm

Major septa = 20 + K major septa (left half of the corallite)

Major + minor septa = 31 + K (left half of the corallite + counter septum; some septa split on the hinge line)

Calice depth = 25.9 mm

Apical angle = 60° at the apex, increases up to 100°

Epibionts: small rugosan on the left corallite side, its calice is directed upward; trace of “*Spirorbis*”; embedded star-like structures (see Galle & Mikuláš 2003).