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Septal architecture and palaeoecology of Calceola (Cnidaria, Calceolidae), with comments on the phylogeny of Devonian operculate tetracorals

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with comments on the phylogeny of Devonian operculate tetracorals

Abstract
In Calceola sandalina the full complement of counter major septa was established very low in the calyx,
extending from the counter septum across to the edge of the counter face. At about mid-height of the calyx, a
counter-lateral major septum was generated on either side of and from the counter septum. Serial minor septal
insertion was initiated adjacent to the counter-lateral septa at a slightly later stage and continued throughout
the subsequent ontogeny of the corallite, with minor septa (schizosepta?) arising on the median side of major
septa and bifurcating from them. Alar fossulae are seen in the calyx of mature corallites, on the counter side of
a low ridge near the lateral extremity of the inner surface of the counter face. Insertion of major septa in the
alar fossula has been observed rarely on the external counter face of worn corallites. The median septum in the
operculum of C. sandalina is a compound structure which incorporates adjacent minor septa. In an Emsian(?)
corallite of ?Chakeola sp. minor septa are derived from major septa, new minor septa being generated on the
outer side of major septa. This corallite also exhibits minor septa adjacent to the K septum, thus casting doubt
on Birenheide's generalisation that the counter-lateral septa of C. sandalina are not separated from the counter
septum by minor septa. In the Emsian Chakeola whitehousei minor septa are present adjacent to the counter
septum of the operculum. The distal, anteriorly facing, projecting peg of the K septum of the corallite
articulated within the large socket in the opercular K septum, and subsidiary grooves and plates on the socket
and septum further facilitated interlocking. Knobs and/or small lists are developed along the posterior edge of
the operculum, in the shelf inside the counter edge; septal pegs developed by septa in the corallite were
accommodated within this shelf. The opercular septal blades interlocked loosely between the anteriorly facing,
distal parts of septa of the corallite. Rare opercula show one or more (abortive?) attempts to overcome
damage which led to displacement of the operculum relative to the corallite, and rejuvenescence is exhibited
to various degrees in many opercula. One operculum was apparently broken (bitten?) in half as a juvenile, but
was reconstructed to reach a mature form. Other specimens show epifauna, borings and bioerosion either on
the external surface of the operculum or on the external cardinal surface of the corallite. ‘Galls’ on the inner
opercular surface are interpreted as stereome deposited to seal off some type of internal parasite. In C.
sandalina, tubules containing tabulae are located just inside the counter face, and may have served to house
soft parts associated with the operculum. Changes of opercular septal morphology suggest that the phylogeny
of Devonian genera of the Calceolidae is Rhizophyllum → Savageola → Chakeola → Richtereola and ultimately,
→ Calceola.

Keywords
Calceola, tetracoral, operculum, Devonian, septa, insertion, GeoQUEST

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Septal architecture and palaeoecology of *Calceola* (Cnidaria, Calceolidae), with comments on the phylogeny of Devonian operculate tetracorals

ANTHONY J. WRIGHT

ALTHOUGH the historic coral genus *Calceola* Lamarck, 1799 (the slipper coral, ‘Pantoffelkoralle’ in German) is very familiar to aficionados of the Devonian system, some details of its morphology remain obscure by comparison with knowledge of the morphology of closely related genera such as *Chakeola* Wright, 2001. In studies of operculate tetracorals Wright (2001, 2006, 2007) emphasised the taxonomic importance at the generic level of opercular morphology. In addition to *Calceola* and *Chakeola*, *Savageola* Wright, 2006 and *Richtereola* Wright, 2006 have...
distinctive opercular morphology, especially in the detailed morphology of septa on the inner surface. The four genera belong to the family Calceolidae, and are here referred to informally as calceolids.

No attempt is made here to provide a full revision or description of *Calceola sandalina* Linné, 1771, and certainly not to address the matter of subspecies of *C. sandalina*; a full evaluation of the various European ‘subspecies’ of *C. sandalina* (e.g., Goldfuss 1840; Richter 1916; Lotze 1928; Tsien 1975) awaits documentation of full details of their opercular morphology and other attributes. The designation of a neotype by Richter (1928, p. 172, fig. 1a-b) does not solve the main problem as, although the neotype (the original of Goldfuss 1840, pp. 287-8, pl. 161, fig. 1f) is a corallite with the operculum attached, it does not display the internal surface of the operculum. So the interpretation here of *C. sandalina* follows the traditional one.

Indeed, there is much inconsistency in the taxonomic levels at which taxa are cited in the literature, and many other ‘subspecies’ have been proposed but are not discussed here (e.g., Yoh & Yü 1957; You 1988; Chi 1933; Yu & Liao 1974). Detailed descriptions of *C. sandalina* have been given by Hill & Jell (1969) and Zhen & Jell (1996) among others. This paper does, however, attempt a detailed analysis of certain morphological aspects of this bizarre coral (see Fig. 1 for illustrations of full details of their opercular morphology and other attributes. The designation of a neotype by Richter (1928, p. 172, fig. 1a-b) does not solve the main problem as, although the neotype (the original of Goldfuss 1840, pp. 287-8, pl. 161, fig. 1f) is a corallite with the operculum attached, it does not display the internal surface of the operculum. So the interpretation here of *C. sandalina* follows the traditional one.

3. Good calceolid moulds are relatively rare but can yield significant data (Wright 2001), nicely complementing calcareous material. A clear preservational bias, however, tends to occur with larger silicified calceolide specimens being less common than smaller specimens.

Material and abbreviations for material examined is from: the Kunth collection from the Humboldt Museum, Berlin (MBK); the Senckenberg Museum, Frankfurt (SMF); the Institut für Paläontologie, Universität Bonn (STIPB Anth); the Australian Museum, Sydney (AM F); the Sedgwick Museum, Cambridge (CAMS A); the University of Queensland, School of Earth Sciences (UQ F); and the Queensland Museum, Brisbane (QM F). The Kunth collection includes most of his illustrated specimens (e.g. MBK 870) as well as 20 additional specimens catalogued as 623.1-20; none of the
623 series was illustrated by Kunth, but many are illustrated here (see also Appendix).

TERMINOLOGY
As calceolides are in many morphological respects unusual corals, some aspects of their morphology need to be described in a framework that is unconventional for corals (see Wright 2001, p. 22) but appropriate for brachiopods because of the similarity in shape between the calceolide operculum and some strophic brachiopods. Of course, morphological features seen in thin sections of calceolides can be described with conventional coral terminology, but some important features in these corals are only seen in 3D specimens; the focus of this study is on the surface expression of structures, and far less on their appearance in thin section.

In Figure 1, illustrations are annotated where appropriate with abbreviations used here. The straight line of contact between corallite and operculum (Fig. 1) in calceolides is here termed the hingeline, and it is here taken to be in the posterior position; it marks the distal edge of the counter face of the corallite, and width is measured along the hingeline. The transversely flat (but curved from proximal to distal) counter ‘plate’ of the corallite (Figs 1-2) has an outer surface (KEF) and inner surface (KIF); after Wright (2001) the term KOF is the posterior face of the operculum. OIF and OEF are the internal and external faces of the operculum respectively.

Conventional terminology is used for most skeletal elements with the adoption of the terms: ‘list’ (after Stolarski 1993, p. 171, fig. 5.2) for the small plates (Figs 3, 7) that are developed normal to the opercular hingeline on what is here called the posterior shelf (Fig. 3A, C-F), the space between the posterior edge of the operculum and the posterior ends of the septal blades; ‘knobs’ for the low rounded dimples (mostly) on the shelf; and ‘pegs’ for the dilated distal tips of both major and minor septa in the corallite. Stolarski (1993) used the term ‘columella’ for the distal swelling of the K septum of the corallite, after Hill & Jell (1969, p. 547) who used the term ‘columella-like’; this terminology is not used here.

OBSERVATIONS ON CALCEOLA SANDALINA
Septal Features
Septa. As Calceola lacks dissepiments and (except for rare, mostly early ontogenetic specimens) tabulae, septa are the important skeletal elements. Septal blades (Wright 2006) are variably developed on the inner surface of the operculum in Savageola, Chakeola, Richtereola and Calceola.

Corallite. The convex external cardinal face exhibits in some (usually worn or weathered) specimens (Fig. 1A-B) pinnate septal traces indicating normal insertion in the cardinal fossulae. The inner surface of the cardinal ‘plate’ occasionally exhibits low septal ridges also indicating insertion but most septal detail is seen on the KIF and the KEF (in the latter case, where slight weathering, etching or wear has
occurred).

Major and minor septal grooves are variably developed on the KEF but are usually obscured by prominent growth ridges; the trace of the counter septum on the KEF is located in a prominent ridge (Figs 1E, 4B, 11C), normally with a single central groove (Zhen & Jell 1996, pl. 3, fig. 4; Wright et al., this volume, fig. 3E). Septal insertion on the KEF has been observed on a Belgian specimen (Wright et al., this volume, fig. 2F, H) and a Queensland specimen (Fig. 4B-C), both of which show recently inserted (major?) septa arising next to the alar septum and rapidly becoming parallel to other septa and the median ridge.

In the calyx, septa are normally low ridges except for the distal extremity of the K and other septa on the KIF. The strongly developed K septum (Hill & Jell 1969) is strongly modified.

**Figure 2.** Views of calices of *C. sandalina* corallites, Middle Devonian, Eifel region, Germany, showing well preserved major and minor septa separated by desmocyte scars, K septum and counter-lateral septa, and development of minor septa on the KIF. E and F probably prepared (by Richter?) to remove cardinal corallite walls, exposing KIF. A-B, ‘*C. sandalina* L. n. mut. alpha’ Richter, SMF160/1, Richter collection, Duppach, Stringocephalen-Stufe, Givetian; A, view of corallite; B shows derivation of minor septa clearly. C, MBK 869.1 (figured by Kunth 1869, fig. XIX.5), see Fig. 1F: insertion of minor septa again shown clearly. D, MBK 869.2, E, SMF 56359, with cardinal plate and lateral walls removed, showing insertion of minor septa. F, SMF 56358, Gondelsheim; as for Fig. 2E, showing formation of minor septa and ridges marking alar fossulae. Scale bars 5 mm.
distally, producing a highly inflated, prominent, pointed or rounded projection which articulated with the socket excavated into the K septum on the operculum. The anterior face of this distally inflated structure normally exhibits a groove in which the K opercular septum articulated.

On the KIF, major septa are wider than minor septa, and all are separated by rows of pits (desmocyte scars of Stolarski 1993) in the depressions between septa (Fig. 2B-C). Only single rows of desmocyte scars have been observed in mature Calceola; Rhizophyllum, Chakeola, Savageola, Richtereola and Goniophyllum also exhibit desmocyte scars.

Operculum. A particular feature of Calceola relates to the obvious fact that septa are developed on both the corallite and the operculum, as in other operculate corals. Whereas septa in the corallite develop more or less as is normal for tetracorals, septa on the operculum are compelled (in a sense) to conform to the septal insertion pattern of the counter plate of the corallite (see, for instance, Termier & Termier 1948, fig. 11) and, at the same time, to match the septal topography and morphology of the distal cardinal edge to ensure that a tight fit was achieved at the calical edge between the operculum and corallite. So, in a sense, the opercular septa obeyed a cardinal plan as well as a counter plan.

Figure 3. Opercula of Calceola sandalina (Linné, 1771), Middle Devonian, Eifel region, Germany. A, D, internal surface (IOF) of mature specimen, MBK 623.2, with marked change in convexity of floor. B, worn external surface (EOF) showing septa, MBK 868.1 (figured by Kunth 1869, fig. XIX.11). C, CAMSMA 5866 with few septal blades, strongly deflected septa laterally, and posterior face (KOF). E-F, MBK 623.8, two views of internal surface showing septa, changes in convexity of valve floor, striking changes in septal patterns (Fig. 3F), and knobs and lists in posterior shelf.
Septal traces are occasionally seen on the worn OEF, with septal traces appearing dark when wet, and interseptal stereome appearing white to grey. The OEF of several specimens (Figs 1C, 3B, 11A-B) clearly show that the straight median (K) septum is flanked two major septa which are initially directed at a high angle to the hingeline but rapidly straighten; lateral major septa arise at a high angle to, and along, the hingeline but all these septa are more or less straight, rather than being curved as on the OIF. Septal insertion in opercula has not been investigated in this paper.

On the OIF, major septa are mostly wider than minor septa, and both orders are present close to the hingeline as well as at the anterior margin. Medially the septa are straight, but lateral septa curve slightly (Fig. 3A, C-F) at about half their length. Septa arise normal to and along the hingeline, rather than being radially arranged about the median point of the operculum. There are about 24 major septa.

Some mature *C. sandalina* opercula (Fig. 3A, C-D, F) show a marked change in convexity of the OIF at about midlength, accompanied by widening of septa. This is possibly contemporaneous with the initiation of minor septal insertion in the corallites even though minor septa occur at the hingeline in opercula.

All opercula have a median K ‘septum’ which is a composite, complex structure formed by the amalgamation of the true K septum with adjacent septa (Fig. 4A). At least two septa form the lateral borders of the socket but become fused to the K septum anteriorly (Fig. 4A), and become detached from it towards the distal (anterior) margin of the operculum. The posterior portion of this K septum exhibits a large excavation which functioned as a socket for the reception of the modified tip of the K septum on the corallite. The K septum is blade-like, being thickest posteriorly, and reaches the anterior margin; its maximum height is at about one-third its length. The K septum of a silicified specimen from a late Emsian level in the Mount Frome Limestone (near Mudgee, NSW: Pickett 1978; Wright 1981; Percival et al. 2010) shows a maximum height of 7.7 mm at a width of 53 mm and length of 24 mm. Birenheide (1974, pl. 1, fig. 1) illustrated an operculum in which the septa flanking the K septum at the margin of the operculum were interpreted by him as major septa, so he considered that minor septa were absent adjacent to the K septum (but see below).

**Septal insertion and fossulae in calceolides: a review of published opinions**

Before discussing new data it may be useful to review briefly some published facts about septal...
insertion in calceolide corals. In *Goniophyllum pyramidale* Hisinger, 1829 (Llandovery-Wenlock: Silurian), septal insertion can be seen on three external surfaces faces (not the counter face) of the pyramidal corallite (Johannessen 1993; Wright 1997), so the cardinal and the two alar fossulae can be identified. In the calyx, insertion of major septa can be clearly seen in the cardinal fossula and alar fossulae (Wright 1997, fig. 1A-B, D); on the internal counter face (Wright 1997, fig. 1K-L), minor septa are generated near to the counter septum by bifurcation on the median side of the major septum. *Rhizophyllum* and *Pararhizophyllum* are not discussed here as their dissepiments largely prevent observation of septal insertion on the corallite, although Johannessen (1998, fig. 3A, H, J) showed specimens wherein septa are visible on the KIF.

Conventional wisdom dictates that no insertion takes place at the counter fossula in tetracorals. Certainly septal insertion associated with the counter ‘plate’, as described here, is far more complex than insertion in the cardinal region, but what is the nature of septal insertion? On the KIF, parallel major and minor septal grooves are present, almost invariably meeting the edge of the KIF at an acute angle. Two specimens are now known which exhibit septal insertion at an edge, with one apparently showing the trace of the alar septum along which a few septa arise but very soon become parallel to earlier septa on the KIF; one specimen from Belgium is illustrated by Wright *et al.* (this volume, fig. 2E-G). A second specimen, *C. ?sandalina* (QMF 21882) from the Givetian Papilio Mudstone, Broken River Province, Queensland (see Jell *et al.* in Withnall *et al.* 1993), is remarkable in that the early stages of several recently inserted and somewhat irregular major septa are clearly visible on the KIF, before they become parallel to other septa. No insertion of minor septa has yet been observed on the KIF.

The alar fossulae of *C. sandalina* are shown by septal patterns in well preserved mature corallites (Fig. 2A, F) to be located near the corners of the inner surface of the KIF of the mature corallites (as also stated by Hill & Jell 1969, p. 544), on the counter side of well defined low ridges. These fossulae are not indicated by any septal traces on the external surface of the operculum.

**Septal insertion on the counter face**

Several well preserved corallites from the Eifel provide new data on the development of septa on the KIF. On the KIF low in the calyx, the K septum is flanked by numerous major septa extending out to the angle of the calyx (Fig. 2C, E-F); no details of insertion below this level have been observed.
A counter-lateral septum then arises by branching from either side of the K septum (Fig. 2B-C); none of the excellent views of *Calceola* figured by Birenheide (1974) shows the derivation of counter-lateral septa from the K septum low in the calyx as illustrated herein.

At a slightly later stage, insertion of minor septa commences, by bifurcation from the median side of each major septum in succession (Fig. 2B-C, F). This bifurcation commences from the first major septum lateral to the counter-lateral septum, and progressively involves all lateral major septa almost to the corner of the corallite and produces a (narrow) minor and a (wide) major septum separated by desmocyte scars (Fig. 2B-C). These new minor septa, although appearing serially, can be called schizosepta after Weyer (2007).

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Traditionally (Kunth 1869; Hill 1935; Scrutton 1997), insertion should be achieved by new major septa being added on the counter side of the alar septum, with minor septa being inserted between the new major septum and the previously inserted major septum. Material illustrated here demonstrates that, in the corallite, insertion of minor septa occurred serially in a locus which

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**Figure 6.** Calical mould of *Chakeola* (?) sp. showing septal insertion on KIF; Sutcher Creek Formation, Snake Creek, Mudgee district, NSW, Emsian (see Wright 2001, fig. 4C); AM F104352. **A-B.** mould and sketch, with black lines for septa; scale bars 5 mm. **C.** enlargement showing minor septa adjacent to K septum, scale bar 2 mm.

**Figure 7.** Operculum of *Rhizophyllum* sp., AM F104349; basal limestone of the Mandagary Park Formation, *eurekaensis* Zone, Lochkovian, Early Devonian, south of Manildra, N.S.W. (Savage 1973; Wright 2006; previously figured by Wright 2001, fig. 1B-C). **A.** whole specimen; **B.** enlargement of posterior region. This specimen shows lists on the posterior shelf and the apparent derivation of two lists from each major septum; minor septa just visible posteriorly and peripherally. Scale bars 2 mm.
was further and further away from the K septum as the corallite grew.

COMMENTS ON AUSTRALIAN CHAKEOLA

*Chakeola whitehousei*. Minor septa are present adjacent to the counter septum (Fig. 5, large arrows) in the extremely well preserved holotype operculum internal mould of the Emsian (*perbonus* conodont zone: see Wright 2001, p. 24) *Chakeola whitehousei* (Wright 2001, fig. 4E). Minor septa are visible as faint, narrow grooves in the mould (emanating from the articulatory pit in the counter septum), and as marginal crenulations. Other points that need to be made about the morphology of this unique specimen are:

1. The anterior face of the articulatory pit in the K septum clearly shows grooves (small arrow) which presumably acted as a muscle attachment site (as did the striated cardinal process or ctenophoridium of some spiriferid brachiopods; see Carter *et al.* 1994). Even well preserved calcareous *C. sandalina* opercula only rarely show any vestige of this sort of feature, but silicified *C. sandalina* opercula from the late Emsian Mount Frome Limestone (near Mudgee, NSW) show that the K septum of the corallite did possess such grooves and furrows (Wright, unpublished data).

2. The posterior shelf of this specimen shows short lists normal to the hinge line (see below for discussion of articulatory structures) and knobs (see below).

3. Several major septa flanking the counter septum are unusually thickened and high anterior of midlength (Fig. 5). In the holotype, this is asymmetrical but affects at least four major septa on one side and two or three on the other. This is not considered a pathological feature, as other Queensland material of this species (Wright 2001, fig. 4T, Q) show suggestions of this condition.
?Chakeola sp. A mode of septal insertion similar to that of C. sandalina is present in a unique Australian Emsian(?) corallite of ?Chakeola sp. (see Wright 2001, fig. 4C; Fig. 6A-C herein) where minor septa are derived from major septa which, as in C. sandalina, appear early in ontogeny; the locus of insertion of minor septa (?alar fossula) ‘migrates’ laterally towards the corner of the corallite. Each major septum gives rise to a new minor septum on its outer side (Fig. 4A-B).

Most importantly, this corallite also exhibits minor septa adjacent to the K septum (Fig. 4C, arrows), demonstrating that minor septa existed adjacent to the counter septum of some calcereoid corals in both corallite and operculum. This casts serious doubt on Birenheide’s (1974) conclusion that the counter-lateral septa lie adjacent to the counter septum throughout the ontogeny of the corallite and are not separated from it by minor septa in C. sandalina.

ARTICULATORY STRUCTURES
Superficially, it appears that articulation of the corallite with the operculum along the hingeline is achieved by essentially tooth-and-socket structures, in basically the same way as stropheodontid brachiopods are constructed. Certainly, in well preserved complete Calceola the fit between the operculum and corallite can be so perfect that, at least on the counter face, the contact between the two pieces is hard to locate accurately (e.g. Fig. 1E).

Most Calceola and Chakeola corallites have a well defined cleft or slit on the front of the swollen K septum (see Fig. 2A-B, D-F); this clearly had an articulatory function, accommodating the blade-like end of the counter septum of the operculum. Silicified Australian Rhizophyllum from the Early Devonian (Savage 1973; Wright 2001; Percival et al. 2010) Mandargery Park Formation lack this cleft or slit, as do Rhizophyllum corallites illustrated by Lindstrom (1866, pls 30-31; 1883, pls 3-4; but not pl. 9, fig. 4 [R. tennesseense Roemer]). Rhizophyllum illustrated by Johannessen (1998, fig. 3A, F, J) and Pararhizophyllum (Pedder in Pedder & Murphy 1997, fig. 3.13, 3.15) show this feature, as does the ?Rhizophyllum sp. illustrated by McLean (1974, pl. 6, figs 10-12).

**Corallite.** The K septum is dilated at its distal end, where it clearly articulated with the pit in the counter septum on the operculum. One of the striking features of the hingeline of Calceola corallites is the series of dilated septal ends (pegs) on either side of the K septum; these would normally be considered the distal ends of major septa, but in most cases it is difficult to trace the septa (even though the major and minor septa can be so clearly differentiated by the desmocyte scars) to these projections. The illustrations of Birenheide (1974, pl. 2, figs 1-2) suggest strongly that these processes arise from both major and minor septa, but in many corallites major septa alone appear to give rise to these septal pegs. These septal pegs articulated within the posterior shelf of the operculum (Fig. 8); this figure also shows clearly that the opercular septal blades articulated with the spaces between the lateral septa of the corallite. The width of the opercular counter shelf is about 1.5 mm, and the distance between the distal edge of the KEF and the anterior edge of the septal blades of the corallite (measured normal to the counter plate) is approximately 1.0 mm.

‘Canalicules’. Thin sections (UQ F4811a and UQ F4815a) located just inside the KEF show tabulate vertical tubes, about 0.1 mm in diameter, filled with clear calcite (Fig. 9). These structures were studied by Lafuste & Semenoff-Tian-Chansky (1968, text-figs C-E, plate 1, figs 1-3) in material from the Spanish Sahara, and they concluded that the biological significance of the tubes (or ‘canaliclues’ as they called them) was unknown. Longitudinal sections of Eifelian Calceola studied by Hill & Jell (1969), one normal to the KEF (Fig. 9B) and the other just inside and parallel to the KEF (Fig. 9A), show these clearly. The latter view clearly indicates that they lie a short distance to the posterior of the dilated major septal ends (pegs) and are located close inside and about 0.25 mm from the KEF. The tubes have a diameter of about 0.1 mm. Lafuste & Semenoff-Tian-Chansky (1968) indicated a maximum diameter of 0.17 mm.

**Figure 10.** Opercula of Calceola sandalina, Middle Devonian, Eifel region, Germany, showing rejuvenescence, injury, galls and epifauna. A, internal view showing two galls, MBK 623.11. B, internal view showing a single gall, CAMSM A.9121a. C, internal view showing small-scale epifauna, STIPB-Anth 4, Pelm. D-E, posterior and opercular views respectively, showing several phases of attempted recovery from dislodgement of the operculum, as well as a gall and asymmetrical septa, MBK 867 (figured by Kunth 1869, fig. XIX.13). F, internal view showing several phases of rejuvenescence, STIPB-Anth 3, Gerolstein. G-H, external and internal views of damaged operculum MBK 623.6, showing asymmetrical septal development; G, external surface, showing incomplete juvenile stage, and some later irregularity; H, internal view of operculum, with markedly asymmetrical septal development. I, internal view showing some rejuvenescence on OEF, STIPB-Anth 1, Gerolstein. J, external view (see also Fig. 11D-E) showing epifauna, STIPB-Anth 2, Gerolstein. Scale bars all 5 mm.
Figure 11. Calceola sandalina (Linné, 1771), Middle Devonian, Eifel region, Germany. A-B, external surfaces of two opercula photographed wet, showing septa. A, MBK 623.14, B, MBK 623.15. C, KEF of worn corallite showing septal grooves and median septum, SMF 56360, Dachsberg. D-E, epifauna on OEF: small shells (some in post-mortem erosional depressions) and other bioerosional features, as well as fine calcareous (?) threads (possibly algal), STIPB Anth2 (see Fig. 10K), Gerolstein. F, view of KEF of corallite, AM F136638 with borings. Scale bars A-C, F, 5 mm; D-E, 2 mm.

wall thickness of 0.02 mm, and a lateral spacing of generally 0.7-0.8, varying from 0.5-1 mm for the tubes. The tubes have not been seen in calcareous hand specimens. The vertical continuity (as far as can be determined) of these tubes suggests that, if they were not parasitic in nature, they may have been pits in which specialised muscles for holding the operculum were located; this perhaps tenuous explanation could in turn explain the presence of the low rounded knobs within the opercular posterior shelf, which could have been the area of attachment of these muscles on the operculum. Thus, these ‘tubes’ would have been sealed off with tabulae and eventually filled with diageneric calcite as upward growth progressed, just as occurs in the normal ‘abandoned’ coral.
skeleton.

**Operculum.** Near the posterior edge of the operculum of *Calceola*, between the septal blades and the posterior face (KOF), is a narrow transverse shelf (the posterior shelf) with an array of small spaces or depressions occupied by small rounded knobs or short paired plates, occasionally both (Fig. 3D-E). Most knobs are continuous with the (major) septal blades, but knobs between these major septa can occupy a minor septal position (Fig. 3D). Occasionally a major septum gives rise to a very short linear array of knobs (Fig. 3D) normal to the hingeline. This diverse configuration could eventually prove to have some taxonomic significance, particularly when the observed differences in convexity of opercula are also considered. As stated above, the septal pegs of the corallite articulated within the shelf on the operculum. The septal blades have a loose articular relationship with the septa on the distal region of the KIF (Fig. 8). *Rhizophyllum*, as illustrated here, differs in lacking any sign of knobs, although numerous lists are developed on the posterior shelf on the illustrated specimen (Wright 2001, fig. 1C; and herein Fig. 7A-B). Two such lists arise from each major septum; this specimen does show faint minor septa posteriorly but their relationship to the lists is unclear.

In most *Calceola* opercula there is a marked space between the septal blades and the K septum, occupied by subdued septal traces (Fig. 2A-B). Lists and knobs are still developed just inside the distal extension of the KOF, but there is clearly no articulation in this region.

In many cases, as in *Rhizophyllum* (Wright 2001, fig. 1C) and *C. johnsoni* (Wright 2001, fig. 3H, O, T) small plates trend posteriorly from the posterior ends of major septal blades; this can be also seen clearly in some *Calceola* opercula (Fig. 3D-F). In *Richtereola* there is a flattish posterior area without any structures between the posterior ends of the major septal blades and the KOF; this is clearly seen, but to a lesser extent, in *Chakeola* (Wright 2001, fig. 3P). The septal pegs of the *Rhizophyllum* corallite clearly articulated within the space between these plates.

**PALAEOECOLOGY: PATHOLOGICAL SPECIMENS, REJUVENESCENCE AND EPIFAUNA**

Several opercula show evidence of aberrant growth; two (Fig. 10A-B, E) exhibit one or more swellings (galls) on the inner surface of the operculum. There is no sign on these opercula of the galls being caused by boring from the outer surface of the operculum. The development of galls was discussed by Morris (1990, p. 379) and it seems that such putative ‘pearls’ are best explained by an infestation by an internal parasitic larva which has provoked encapsulation with stercome by the coral mantle.

Galle & Mikuláš (2003) and Galle & Ficner (2004) discussed material of *C. sandalina* from the Czech Republic. One Givetian specimen (Galle & Mikuláš 2003) showed severe predator damage to the corallite, with healing of the injury and regrowth of damaged septa visible inside the calyx but not on the outer (K) surface; no operculum was available for study.

Largely post-mortem borings, excavations, and epifauna such as spirorbid snails on various parts (internal and external surfaces) of the skeleton (Fig. 10C, 11F) show no consistent location on the *Calceola* skeleton. There is general agreement about the life position of *Calceola*, which lay on the sea floor on its convex KEF, exposing the KOF and the cardinal face to epifauna and, perhaps, parasites; many authors have discussed the palaeoecology of the genus (e.g., Richter1929; Birenheide 1990; Godo 2000). Holes are bored into several corallites (e.g. Fig. 11F); Mottequin & Sevastopulo (2008) reported holes (≤1 mm in diameter) drilled into brachiopods, and these were attributed to a predator or parasite. Rare, faint circular markings on the KEF of *Calceola* corallites may indicate abortive attempts to drill into the corallite.

Often the OIF and the cardinal face of the corallite exhibit what appear to be *Clionolithes* (see Wright et al., this volume, fig. 3G). A large operculum shows an abundant epifauna of small shells on the OEF (Fig. 10K, 11D-E); in itself this is not remarkable, but much of this epifauna is clearly attached in post mortem cavities in the surface of the operculum, indicating that disarticulated opercula were available at the interface (and convex up in this case) for some time prior to burial. Dr Alex Cook has commented that these epifaunal shells resemble the parasitic organism *Microconchus* from the Devonian-Jurassic of Europe which has an initially bulbous shell form such as in the Eifel material, and that the thin calcareous stringers (Fig. 11E) resemble the calcified expression of algal thalli, perhaps associated with endolithic algae.

A specimen from Wellin, Belgium (see Wright et al., this volume, fig. 3E-F) is preserved with the operculum intact but considerably displaced; this specimen must have been buried not just rapidly after death but while there was still some attachment of the operculum to corallite by soft parts.

Several opercula show abnormal posterior faces (KOF: Fig. 10E, H, J) and internal faces (OIF) recording rejuvenescence (Fig. 10E-F,
J). One specimen (Fig. 10D-E) has undergone several phases of this, as well as showing a gall on the opercular floor; this multiple rejuvenescence seems to have been a response by the coral to repeated or even permanent but partial detachment or displacement of the operculum. Another operculum (Fig. 10F) from the Kunth collection, as well as Givetian specimens from Queensland illustrated by Zhen & Jell (1996, pl. 3, figs 2, 5), show less striking rejuvenescence. It seems such interruptions to the normal growth of the operculum were not unusual, as they are already known from corallites; for example Galle & Ficner (2004, p. 23, fig. 5E-F) described and illustrated Czech material that shows striking rejuvenescence of the corallite. Little is yet known about possible stratigraphic restriction of specimens showing such rejuvenescence.

A further operculum (Fig. 10G-H) retains only half of its juvenile outer surface and KOF, with a further irregularity in the external growth pattern; this fragmentation is most likely to have been caused by a predator. The development of septa in this specimen is quite asymmetrical (Fig. 10H), suggesting that the soft parts of the coral were damaged, but not fatally.

**PHYLOGENY OF CALCEOLIDE GENERA**

Figure 12 illustrates a possible scenario, initially presented at the St Petersburg congress (Wright 2007), for the evolutionary relationships of some common Devonian calceolide genera, based on opercular characters, suggesting that the generic evolutionary sequence is *Rhizophyllum* → *Savageola* → *Chakeola* → *Richtereola* and, ultimately, → *Calceola*. *Rhizophyllum* appears in the Llandovery of Gotland (Lindström 1883) and Australia (Munson & Jell 1999; McLean 1974) and ranges well into the Emsian (e.g. Pedder & Feist 1999), and lacks septal blades. *Savageola* (Early Devonian, Lochkovian: *eurekaensis* Zone, Manildra, NSW) probably evolved from *Rhizophyllum* with the loss of dissepiments and the development of primitive low, paired septal blades extending to the anterior margin. The Early Devonian *Chakeola*, from eastern Australia and Vietnam, ranges from the latest Lochkovian *pesavis* conodont zone into the late Emsian.

**Figure 12.** A proposed phylogeny for five calceolide genera, from *Rhizophyllum* (oldest) to *Calceola* (youngest); see text for discussion of ranges of genera. *Rhizophyllum* sp. (AM F104347); *Savageola unicus* Wright, 2007, holotype (AM F104351); *Chakeola johnsoni* Wright, 2001, holotype (AM F104320); *Richtereola disruptus* Wright, 2007, holotype (AM F104352); and *Calceola* sp. (Kunth collection, MBK 866). Specimens are not to scale.
serotonin conodont zone (Wright 2001); its septal blades do not reach to the anterior margin. Further reduction in number and arrangement of septal blades appears to have led progressively (although details are not available) to Richtereola (late Emsian: Montagne Noire, Taemas area of N.S.W., south China and north Vietnam), and to Calceola ranging from late Emsian (Werner 1968; Truyols et al. 1990) to late Givetian (e.g., Lotze 1928; Truyols et al. 1990; Stolarski 1993). Apart from the loss of dissepiments and rootlets in the presumed transition from Rhizophyllum to Savageola, there appears to be no significant structural change in the nature of the corallite.

SUMMARY
The pattern of septal insertion in the Devonian tetracoral Calceola sandalina is shown to differ in detail from that in other tetracorals. The full complement of counter major septa was established low in the calyx, before counter-lateral septa appeared, extending from the counter septum across to the edge of the counter face, as in Chakeola. At about mid-height of the calyx, one counter-lateral (major) septum was generated on either side of and from the counter septum. Serial minor septal insertion was initiated from the major septa adjacent to the counter-lateral septa at a slightly later stage and continued throughout the subsequent ontogeny of the corallite, with minor septa arising on the median side of major septa and bifurcating from them; these minor septa can be classified as schizosepta after Weyer (2007). The alar fossulae are best seen in the calyx of mature corallites, on the counter side of a low ridge near the lateral extremity of the inner surface of the counter face where major septa abut the alar septum at an acute angle but rapidly became parallel to earlier major septa. Major septal insertion in the alar fossula has been observed rarely on the external counter face of worn corallites. The median septum in the operculum of C. sandalina is a compound structure which incorporates the adjacent minor septa.

Somewhat similar insertion is present in an Australian Emsian (?) corallite of ?Chakeola sp. where minor septa are derived from major septa which, as in C. sandalina, appeared early in ontogeny; however, this form differs from C. sandalina in that each major septum gives rise to a new minor septum on its outer side. This corallite also has minor septa adjacent to the K septum, thus casting doubt on Birenheide’s (1974) generalisation that the counter-lateral septa of C. sandalina are not separated from the counter septum by minor septa. In the holotype operculum of Chakeola whitehousei (Emsian, Australia), minor septa are present adjacent to the counter septum, and delicate articular plate-like extensions arise from the posteriorly directed face of the articular socket which is located near the posterior end of the counter septum.

The distal, anteriorly facing projection from the K septum of the corallite articulated within the large socket in the opercular K septum, and subsidiary grooves and plates on the socket and septum further facilitated interlocking. Knobs and/or small lists are developed along the posterior edge of the operculum, in the shelf inside the counter edge; the septal pegs developed by septa in the corallite were accommodated within this shelf. The opercular septal blades interlocked loosely between the anteriorly facing distal parts of septa of the corallite.

Opercula show one or more attempts to overcome various types of damage including displacement of the operculum relative to the corallite, and breakage and rejuvenescence are exhibited to various degrees in many opercula. Other specimens show epifauna, borings and bioerosion either on the external surface of the operculum or on the external cardinal surface of the corallite. ‘Galls’ on the inner opercular surface are interpreted as stereome deposited to seal off some type of internal parasite. Tabulate tubules filled with diagenetic calcite are located just inside the KEF in C. sandalina, and may have housed soft parts concerned with anchoring of the operculum.

Changes of opercular septal morphology suggest that the Devonian evolutionary sequence at the generic level is Rhizophyllum → Savageola → Chakeola → Richtereola and ultimately, → Calceola.

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**APPENDIX**

This list summarises catalogue numbers for specimens in the Humboldt Museum, Berlin (MBK) illustrated by Kunth (1869, tafel XIX), as far as can be determined:

Figure 1, MBK 870; figure 2, MBK 871; figure 3, MBK 870; figure 4, MBK 869/2; figure 5, MBK 869/1; figure 6, uncertain, possibly 869/1; figure 7, 868/2; figures 8-9, both uncertain; figure 10, MBK 866; figure 11, MBK 868/1; figure 12, MBK 872; figure 13, MBK 867. None of the 623 series in the Kunth collection was figured by him.