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A new Early Devonian operculate tetracoral genus from eastern Australia

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Abstract – *Chakeola*, a solitary latest Lochkovian to late Emsian (Early Devonian) new genus of the operculate tetracoral family Calceolidae, is characterised by: opercular septa that are present from adjacent to the median septum to the lateral extremities of the operculum; a lack of rootlets on the counter face of the corallite; a weak counter opercular face in mature specimens; and eccentric growth increments on the external opercular surface. The type species, *C. johnsoni* new species, is described from latest Lochkovian *pesavis* Zone), early Pragian (*sulcatus* Zone) and late Pragian (*pireneae* Zone) strata of the Garra Formation, Wellington, NSW. *C. whitehousei* new species is described from the Ukalunda Beds (*perbonus* Zone, mid-Emsian), near Ukalunda, Queensland. Specifically indeterminate occurrences of the genus from the Mudgee district in New South Wales are in: the Taylors Hill Formation (*?kindlei* Zone, late Pragian); the Sutchers Creek Formation (*serotinus* Zone, late Emsian); and possibly the Mullamuddy Formation (*sulcatus* Zone, early Pragian). *Rhizophyllum calceoloides* from the Tabberabbera Formation (Emsian), Victoria also belongs in this new genus. *Calceola sinensis* and *Calceola sandalina acuminata* from Emsian strata in northern Vietnam are also assigned to this genus.

Chakeola thus ranges from the latest Lochkovian (*pesavis* Zone) to the late Emsian *serotinus* Zone; it presumably arose from *Rhizophyllum* or a related form, and probably gave rise to *Calceola* in the Emsian in eastern Australia or SE Asia. The occurrence of the genus in eastern Australia and Vietnam provides further evidence of faunal exchange during the Early Devonian. This study concludes that features of the exterior and interior surfaces of the opercula of genera of the Calceolidae are diagnostic at the generic level.

INTRODUCTION

Chakeola is a new solitary operculate tetracoral from the Early Devonian of eastern Australia and north Vietnam, and is included in the Calceolidae King 1846 along with the three other Devonian solitary operculate genera: *Calceola* Lamarck 1799; *Rhizophyllum* Lindström 1866; and *Pararhizophyllum* Pedder 1997. Apart from the work of Strusz (1967), little taxonomic work has been done on Calceolidae from the Devonian of New South Wales, and none on silicified Devonian material.

Results of ongoing morphological, biostratigraphic and evolutionary studies of some Early Devonian Calceolidae are presented here; those pertaining more directly to *Calceola* will be presented elsewhere (Wright in prep.). Silurian *Goniophyllum* were discussed by Johannessen (1993) and Wright (1997). My studies originally focused on silicified *Calceola* from the Mount Frome Limestone in the Mudgee district, N.S.W. where abundant but mostly poorly preserved *Calceola* opercula and corallites were found at one level in particular. W.B. Clarke (1878) first recognised this genus in the Emsian to Eifelian Mount Frome Limestone (Pickett 1978, Wright 1981). Examination of material from other occurrences of this genus and other genera of operculate corals have led me to the conclusion that morphological features of the internal and external surfaces of the operculum are characteristic taxonomic features at the specific and generic levels. For example, the presence in *Chakeola* of septa across much of the width and the length of the operculum and the mode of opercular growth distinguish this genus from its closest relative, *Calceola*.

TAXONOMY

Phylum Cnidaria

Order Tetracorallia Haeckel 1866

Material studied is deposited in the Australian Museum (AMF), the Queensland Museum (QMF), the Geological Survey of Queensland (GSQF) and the Humboldt Museum für Naturkunde, Berlin (MB.k). Large additional collections of Chakeola are held at MUCEP (Macquarie University Centre for Ecostratigraphy and Palaeobiology) and the Australian Museum.

Family Calceolidae King 1846

As reported by Weyer (1996), the valid name for this family is Calceolidae King 1846 not Goniophyllidae Dybowski 1873. Aspects of the morphological reconstruction of *Calceola* have been discussed by Gudo (1998).

Prior to discussion of the definitive characteristics of the opercula of the several relevant genera, certain features of the operculum, which in this family has a roughly circular to semicircular shape, need to be named and defined. In the 4 coral genera discussed here, the flat face of the corallite is the counter (K) face; the linear extremity (in the counter position) of the operculum may terminate at an edge or a face. For instance, there is a prominent face on the operculum of *Calceola* (Figures 1E, 1G) which is an approximate continuation of the counter face of the corallite; this is here termed the Counter Opercular Face (KOF), enabling its distinction from the counter face of the corallite (although there is normally geometric continuity of the two curved planar surfaces). In other calceoloid genera this counter margin of the operculum consists mostly of a linear edge rather than a well-developed planar surface. Further, in most juvenile and many mature opercula of *Calceola* I have been able to study, the KOF intersects the (curved) K face of the corallite at quite a marked angle; only in supermature specimens is there no discernible angle developed between the 2 planes.

The width of the corallite is measured at the straight edge of the counter face or the operculum; corallite length is measured normal to this, in the plane of junction (commissure) between the operculum and corallite; height is the distance between the corallite apex and the commissure, measured normal to the commissure. The latter term is borrowed from brachiopod terminology to describe the plane or line of junction of the operculum and slipper (corallite). In this paper I refer to the median septum of the operculum rather than the K septum, as this appears to be a composite plate.

The term fossula is used to indicate a locus of septal insertion. Evidence for the presence of alar fossulae near the lateral extremities of the counter face will be presented here, but other aspects of the morphology of these corals will be addressed elsewhere. There is, as yet, limited evidence for the presumed septal insertion in the cardinal fossulae.

The operculum of *Rhizophyllum* has a weakly convex to irregular to weakly concave outer surface, is subcircular to transversely oval in outline (Figure 1B) and has a low median septum and subdued lateral septa (often weak ridges only: see Figure 1C). The KOF of *Rhizophyllum* is generally absent or very low, but some *R. gotlandicum* (F. Roemer 1856) figured by Lindström (1883, pl. 3, fig. 1) and Johannessen (1998, fig. 3L) do exhibit a crude KOF. The operculum of *Pararhizophyllum* is very similar to that of

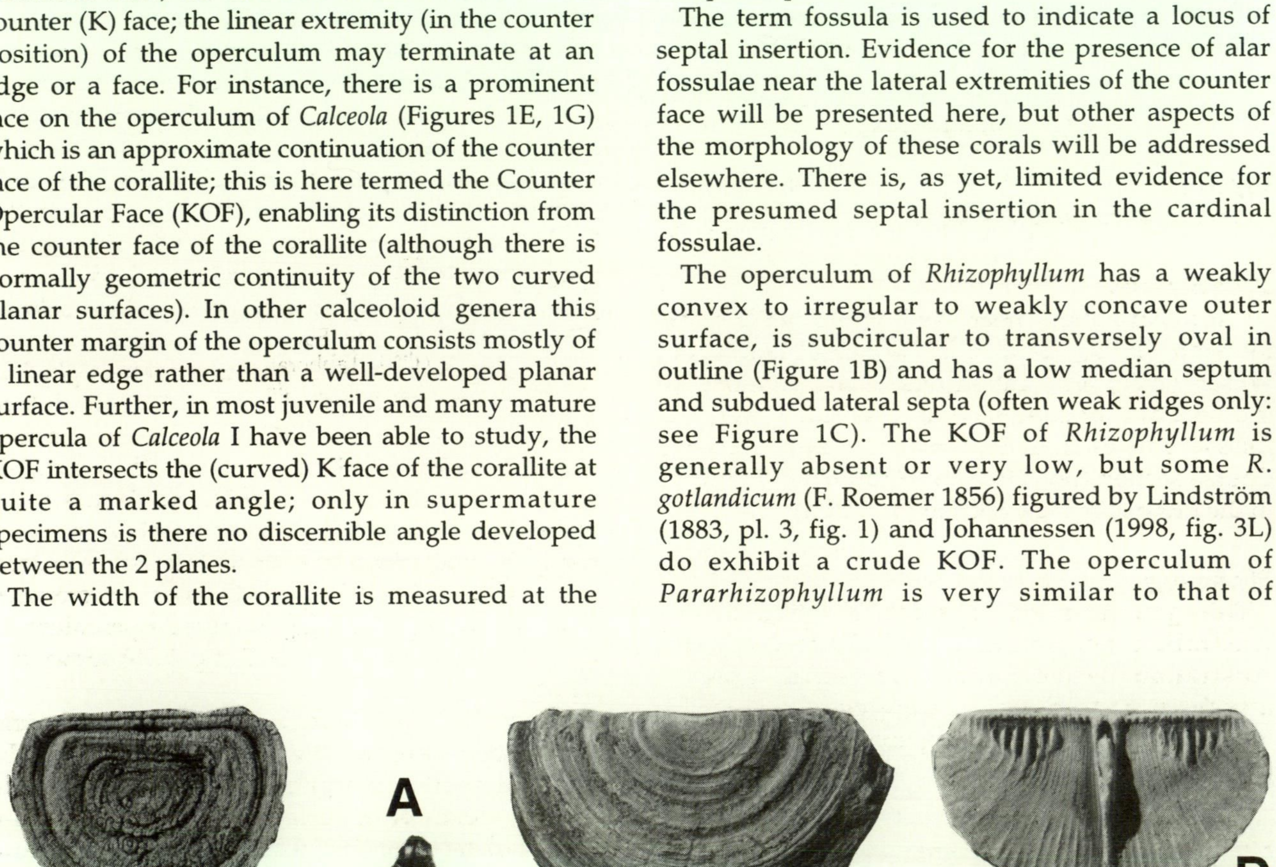


Figure 1 A–C. *Rhizophyllum*? sp. nov., Garra Formation, Manildra, N.S.W., *eurekaensis* Zone, Early Devonian (Lochkovian). **A**, AMF 104347, counter face of corallite showing talons, x 2. **B**, AMF 104348, external surface of juvenile operculum, x 4. **C**, AMF 104349, internal surface of mature operculum showing very subdued septa, x 2. **D–G**, *Calceola sandalina sandalina* (Linnaeus 1771), all from the Middle Devonian of the Eifel district, Germany. **D–E**, internal views of opercula: **D**, MB.k 866 (illustrated by Kunth 1869, pl. XIX, fig. 5), x 2.5; **E**, MB.k 869, x 1.5 showing large KOF; **F**, AMF 11696, external view of an operculum, x 2 approximately; **G**, specimen viewed from the counter direction, showing the K face of the corallite and (arrowed) the counter opercular face (KOF) (University of Bonn specimen, from Pelm, Eifel district).

Rhizophyllum, except that the K septum tends to be relatively large; a KOF is not known in this genus. *Calceola* has a semicircular operculum with a prominent planar KOF (Figure 1E) and a low number of relatively short septa located laterally at maturity (Figures 1d–e). *Chakeola* has a very prominent suite of long, high and numerous septa and lacks a KOF except in the mature growth stage; septa developed at the lateral extremities of the operculum are low and short, so an accurate count of septa is often difficult. The 2 latter genera lack the rootlets seen in *Rhizophyllum?* (Figure 1A), and mature corallites probably rested on their counter face (as suggested by Richter 1928).

Chakeola new genus

Type Species

Chakeola johnsoni new species.

Type Stratum

Garra Formation, near Wellington, N.S.W.; see Johnson (1975), Lenz and Johnson (1985) and Wilson (1989) for location of sections. In terms of the sections documented by Wilson (1989), *C. johnsoni* ranges from 31.5 m to 111 m in the Golf Course section (revisited), and from 73 m to 130 m in the Mountain View Section (revisited).

Etymology

This generic name is a modification of the Australian aboriginal name *Chakola* for the Australian native Superb Lyre-bird (*Menura novaehollandiae*), to draw an analogy between the fan-like arrangement of the opercular septa and the tail feathers of the male bird.

Diagnosis

Solitary Calceolidae lacking rootlets and dissepiments, but exhibiting rare tabellae; the slipper tends to have a flat counter face. The operculum has long, high septa developed across the width and length of the inner surface; a counter opercular face (KOF) which is absent in juveniles but imperfectly developed in some mature specimens; and eccentric growth lines in mature individuals.

Species assigned

C. johnsoni sp. nov. from the latest Lochkovian and Pragian of the Garra Formation, Wellington district, N.S.W.; *C. whitehousei* sp. nov. from the late Emsian Ukalunda Beds of the Ukalunda district, Queensland; *Calceola sinensis* Mansuy 1908, and *Calceola sandalina acuminata* Mansuy 1916, both from the Early Devonian of Vietnam; *Rhizophyllum calceoloides* Talent 1963 from the Emsian Tabberabbera Formation of Victoria; and possibly *Calceola sandalina* (Linnaeus 1771) of Jell and Hill (1969, p. 17) from the Emsian of Ukalunda, Queensland. Many other reports of *Calceola* might be more properly termed *Chakeola* but, in the absence of definitive opercular material, these must remain unsubstantiated.

Remarks

External and internal features of the operculum immediately distinguish this new genus from *Calceola*, *Rhizophyllum* and *Pararhizophyllum*. This is most strongly demonstrated by the well-developed septa and the lack of the KOF (except in mature specimens) in *Chakeola*. Both mature and immature opercula of *Calceola* show septa restricted to a small number of grouped well lateral of the median septum, in contrast to the operculum-wide development of septa in *Chakeola*. Another important distinction is the development of the KOF: this flattened surface on the K edge of the operculum is absent in juvenile *Chakeola*, but is pronounced in both immature and mature *Calceola* (Figure 1e).

In distinguishing his new genus *Pararhizophyllum* from *Rhizophyllum*, Pedder (1997) stated that *Calceola* is distinctive (*inter alia*) in having "anisometric" opercular growth as reflected by the growth lines on the exterior surface of the operculum (Figure 1F). However, all opercula of corals in this group are, to at least some extent, anisometric in that the growth lines are crowded towards the K edge; the paratype operculum of *Pararhizophyllum* (Pedder 1997, fig. 3.18) shows this clearly.

Hill and Jell (1969) showed considerable insight when they noted that "this group" (referring to the group characterised by *Rhizophyllum calceoloides*, which they transferred to *Calceola*) "lies morphologically between *Rhizophyllum* and *Calceola*". The assignment of the latter species here to *Chakeola* serves to stress the correctness of their assessment of the distinctive nature of this new taxon, albeit based on development of stereome and tabellae. Hill and Jell listed several other species as possibly belonging to this group; the original illustrations given for these taxa are mostly inadequate for further decisions on their generic assignments at this time. Hill and Jell (1969) suggested that tabellae occur in a number of calceoloid taxa, and these have been reported in both *Calceola* and the new genus described here. For only one of the species which they assigned to *Calceola* (*Calceola sandalina* var. *acuminata* Mansuy 1916) is there opercular information (Mansuy 1916; pl. 1, fig. 5e), and this certainly looks like a good *Chakeola* as its septa extend from the median septum to the lateral extremities of the operculum. There is little point in attempting to re-assess the other taxa without further information on the operculum.

Occurrences of genus

The Early Devonian genus is known extensively from N.S.W. from: the Garra Formation, Wellington area; the Taylors Hill Formation, the Sutchers Creek Formation and possibly the Mullamuddy Formation, Queens Pinch, Mudgee area; and the Sutchers Creek Formation, Snake Creek Road, Mudgee area. It also occurs in the Ukalunda Beds, Ukalunda, Queensland; in the Tabberabbera Formation, Gippsland, Victoria; and in Tonkin (north Vietnam).

Garra Formation. Much of the studied silicified *Chakeola* material was extracted by Brian Johnson during his PhD studies at Macquarie University (Johnson 1975) from 2 sections through the early Pragian part of the Garra Formation near Wellington, N.S.W.: the G (Golf Course) section and the M ("Mountain View") section. Significant additions to the store of material have subsequently been made by members of MUCEP, especially from the revisited Golf Course section (GCR) and revisited "Mountain View" section (MV). The relationships between these different generations of measured sections, and the completeness of the sequence studied have been brought into focus by Wilson (1989). He concluded that remeasurement of sections, and conodont data which have accrued since Johnson's studies, indicate that the rich silicified faunas have been almost all extracted from *sulcatus* Zone strata.

Mudgee district (N.S.W.). Chakeola is known from early(?) and late Pragian, and late Emsian clastic strata of several formations in the Mudgee district, mostly in the Queens Pinch area. In the Mudgee district, correlations of strata yielding this genus have been summarised by Garratt and Wright (1988) and Colquhoun *et al.* (1997). The lowest occurrence of calceoloid material is in the early Pragian Mullamuddy Formation, where non-diagnostic moulds have been found at the level where the stropheodontid brachiopod *Nadiastrophia* appears. The next youngest occurrence is in the Taylors Hill Formation (probably *kindlei* Zone, middle Pragian). Higher in the sequence, a fragmentary mould from the Sutchers Creek Formation (*serotinus* Zone, late Emsian) has been recognised.

The only other occurrence in the district is from exposures of the Sutchers Creek Formation (Wright 1995; Colquhoun *et al.* 1997) in the road cutting known as the Snake Creek Road section, N of Mudgee.

Queensland. Calceoloid material, some of which is described below, has been known from the Ukalunda district since the pioneering work of Jack (1889), Reid (1929, 1930) and Whitehouse (1929). Some material was described as *Calceola s. sandalina* by Jell and Hill (1969), and in a thesis by Bennedick (1993). Brachiopods from the Ukalunda Beds were described by Parfrey (1989) and Brock and Talent (1993); in both studies the age assigned to the fauna was Emsian on the basis of *perbonus* Zone conodonts.

Victoria. This genus is known from Tabberabbera, Victoria, whence Talent (1963) described *Rhizophyllum calceoloides* from the Tabberabbera Formation. This species is poorly known, despite being known both calcareous specimens and moulds. Material illustrated by Talent (1963, pl. 11) clearly includes both *Chakeola* (pl. 11, figs 1–5; text-fig. 11) and, from a different locality, *Rhizophyllum* (pl. 11, figs 6–7). Further illustrations of the holotype of *Chakeola calceoloides* were given by Hill and Jell (1969, text-fig. 2.4a–c). Talent considered that specimens which Etheridge (1899) described from this locality as *Rhizophyllum interpunctatum* de Koninck 1876 are conspecific with *C. calceoloides.*

Vietnam and South China. Calceola sinensis Mansuy (1908 pl. 2, figs 20–26) has a strongly septate operculum, and is here interpreted as a species of *Chakeola.* Mansuy assigned only material from his figures 20–1, 24 and 26 to his new species from Ban-Gioc, but the opercula illustrated in his figures 23 and 25, and the calical mould in his Fig. 22 are, by comparison with Australian material from clastic strata, very likely also to belong to *Chakeola.* Nevertheless, this material is in need of careful restudy. According to Mansuy (1908) the Vietnamese occurrences are in strata characterised by "*Orthis vespertilio* and *Spirifer crispus*". I have been informed by Professors Tong Dzuy Thanh and Art Boucot that these fossils are from the Emsian *tonkinensis* beds.

A second species from Vietnam, *C. sandalina acuminata*, appears to have an operculum characteristic of *Chakeola* (Mansuy 1916, pl. 1, fig. 5e). Mansuy (1916, pl. 1, figs 4a–c) illustrated as *Calceola sandalina* material which may also belong to the new genus as it is indistinguishable from Australian *Chaleola* material; a serious problem in this regard is that we have little knowledge of internal moulds of good *Calceola.* Wang *et al.* (1974, pl. 2, figs 4–11) illustrated material from south China which they assigned to the above subspecies; the operculum (pl. 2, figs 10–11) is similar to that of *Chakeola* internally, but there appears to be a strongly developed KOF suggesting that this group is in need of restudy to clarify its generic affinities. The shared occurrence of *Chakeola* highlights affinities between the Early Devonian shallow marine faunas of SE Asia and eastern Australia; this has already been emphasised for corals (e.g., Packham 1953; Fontaine 1961; Zhen 1998; Zhen *et al.* in prep.) and vertebrates (e.g., Rich and Young and 1996, Young and Janvier 1999). Therefore, the occurrence of *Chakeola* in both northern Vietnam and southern China is not unexpected.

Other illustrations of calceoloid corals from

Vietnam (Fontaine 1961, p. 200, pl. XII, fig. 5: Nguyen *et al.* 1980, p. 94, pl. 22, fig. 1, pl. 23, fig. 2, pl. 24, fig. 1) do not permit conclusive assignment. However, the last of these illustrations shows what appears to be a good *Chakeola* operculum. This material is left in open nomenclature as the full morphological and stratigraphic relationships of the material are not known.

"*C. sandalina sinensis* Mansuy 1908" has been reported widely from SW China (Yu and Zhang. 1963, pl. 57, figs 15–16 especially; these illustrations were reproduced in Yu and Liao 1974, pl. 104); the illustrated opercula are strongly reminiscent of *Chakeola*, but there are no short major septa visible adjacent to the K septum. Yoh and Yu (1957) described a number of new subspecies of *Calceola sandalina*, but included illustrations of opercula for only *C. s. subsinensis* Yoh and *C. s. naningensis* Yoh. Illustrations of the former by Yoh and Yu (1957) and Jia *et al.* (1977, pl. 57, fig. 6a) are inadequate for thorough comment on their possible relationships to *Chakeola*, although both species clearly possess numerous opercular septa. Yoh (1988) described a number of new and old species of *Calceola*, most of which appear to need further evaluation.

Stratigraphic and evolutionary relationships

As currently known, *Chakeola* appeared in the latest Lochkovian *pesavis* Zone and ranged up into the late Emsian *serotinus* Zone. Its ancestral stock most probably is *Rhizophyllum* or *Pararhizophyllum*, or some undescribed form. Morphologically, there are some major, fundamental differences between *Rhizophyllum* (which exhibits rootlets, subdued to absent opercular septa, and abundant dissepiments and generally lacks a KOF) and *Chakeola* so the immediate ancestor of *C. johnsoni* might well be an intermediate between *Rhizophyllum* and *Chakeola*, such as *Pararhizophyllum*. Although *Rhizophyllum* ranges up into the late Emsian, *Chakeola* is very much more similar to, and is probably ancestral to, *Calceola*. The only solitary operculate tetracoral known from strata younger than the *serotinus* Zone is *Calceola*, which ranges through the Eifelian and Givetian.

Chakeola johnsoni n. sp.

Figures 2A–V, 3A–Z

Type Material

AMF 104320 (holotype operculum), Golf Course section, Johnson locality G 506; paratypes: AMF 104321–104346, 104350. Paratypes, with locality numbers following, are: AMF 104321, from locality M 81; AMF 104322, AMF 104337, M 96; AMF 104323–4, AMF 104330, M 102; AMF 104325, M 89; AMF 104326–7, AMF 104332, AMF 104342, M 83; AMF 104328, M 73; AMF 104329, MV 130; AMF 104331, M 143; AMF 104333, GCR 64; AMF 104334, M 99; AMF 104335, GC 145; AMF 104336, AMF 104338–9, GCR 34.5; AMF 104340, M 98; AMF 104341, M 100; AMF 104343, M 141; AMF 104344, MV 130; AMF 104345, GCR 31.5; AMF 104346, G 506; AMF 104350, M 87.

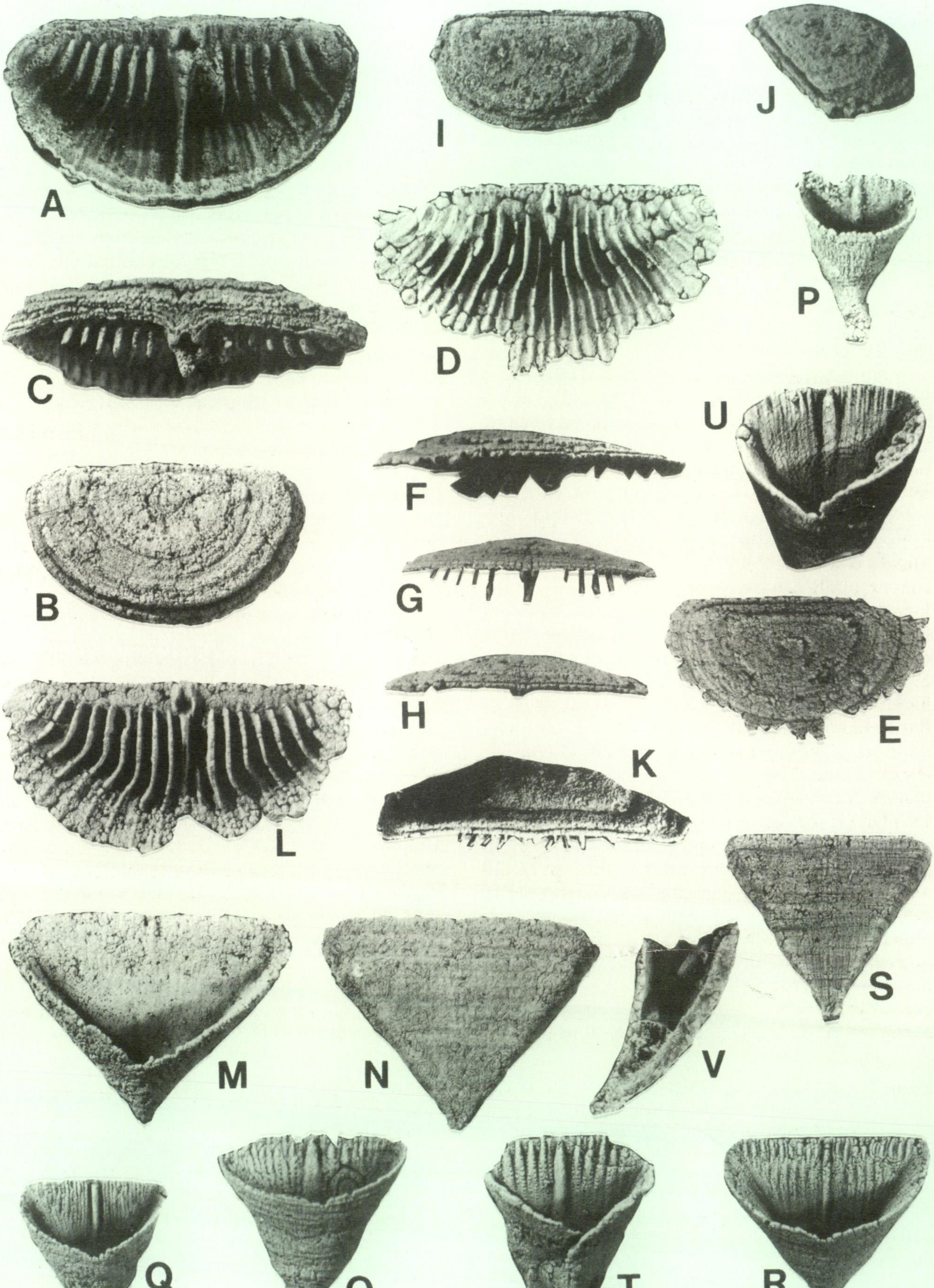
Occurrence

All material is from the Wellington Golf Course and Mountain View sections through the Garra Formation (Johnson 1975), Wellington, N.S.W. (mostly Pragian: see Wilson 1989). In the Golf Course section, *C. johnsoni* occurs more rarely (at G506, GC 145 and GCR 31.5, GCR 34.5 and GCR 64); *Rhizophyllum* is much more common in this section than *C. johnsoni*. In the Mountain View section, *C. johnsoni* occurs at M 73–143, with some very rich horizons; *Rhizophyllum* is not present in silicified residues from this section. Current data suggest that the Golf Course section is latest Lochkovian to early Pragian (*pesavis* to *sulcatus* zones) and the Mountain View section is younger (*kindlei* Zone and, at least in part, possibly *pireneae* Zone: Wilson 1989, p. 147). Some brief comments on locality numbers are given below.

Johnson's (1975, figure 1, 2; 1981) collections from two sections were the primary source of much of the material studied here. His sections (Golf Course [G and GC] and Mountain View [M]) have been further sampled by staff and students from Macquarie University as GCR and MV sections; as resampling of the 2 sections was carried out using Johnson's sampling numbers painted on the rocks, direct correlation is possible between the original and "revisited" sections. However, Johnson's original G samples cannot be not equated with certainty with the measured sections. On this basis, *C. johnsoni* ranges from 31.5 m to 111 m in the GCR section (Wilson 1989, Table 1), in which the top of the *pesavis* Zone has been located at about 35 m (Wilson 1989, p. 124, fig. 3). In the Mountain View section, *C. johnsoni* ranges from M 73 to M 143 and in the MV section from MV 120c to MV 130, yielding a range of at least 60 m; Wilson (1989, p. 147) concluded that conodonts indicative of the *pireneae* Zone first appear in the MV section at 81.3 m. The disjunct occurrence of the species in latest *pesavis* and *sulcatus* age strata in the Golf Course section and *kindlei* and *pireneae* age strata in the Mountain View section may simply reflect non-representation in Wellington samples studied. This is to some extent supported by the occurrence of the new genus in probable *kindlei* age strata of the Taylors Hill Formation near Mudgee.

Name

The species is named for Dr Brian Johnson who first made significant collections of this coral in his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palaeoecological studies of the Garra Formation (Johnson 1975).

Diagnosis

A species of *Chakeola* with up to 11 major septa on each side of the median septum on a mature operculum. Maximum opercular width more than 17 mm, and known length about 9–10 mm; corallite height up to 20 mm. Median opercular septum flanked by one short major septum towards the C edge, especially in mature specimens; apical angle of mature corallite about 75°.

Description

External features

Corallite Juvenile slippers are essentially tubular to elliptical in cross section over a length of about 1–2 mm, and are slightly irregularly curved (Figures 2O–P, 3W–Y) before the flat counter face develops with its initial apical angle of 40°. Some early rejuvenescence is displayed; only 3 specimens with the operculum in place have been observed, and 2 of them are very early juveniles (e.g., Figure 3W–Z). The K face varies from gently concave to gently convex, rarely being strongly curved, and bears fine longitudinal traces of septa and prominent growth lines; rare specimens suggest that there was a delicate plate-like distal extension of the K face (as in *Calceola*), but this has been mostly destroyed. In larger specimens the angle enclosed by the edges of the K face is about 70°. The maximum observed width is 17 mm, the length 13 mm and the height about 20 mm. The C edge is smoothly curved, so that its edge makes an angle of less than 90° with the plane of the K face.

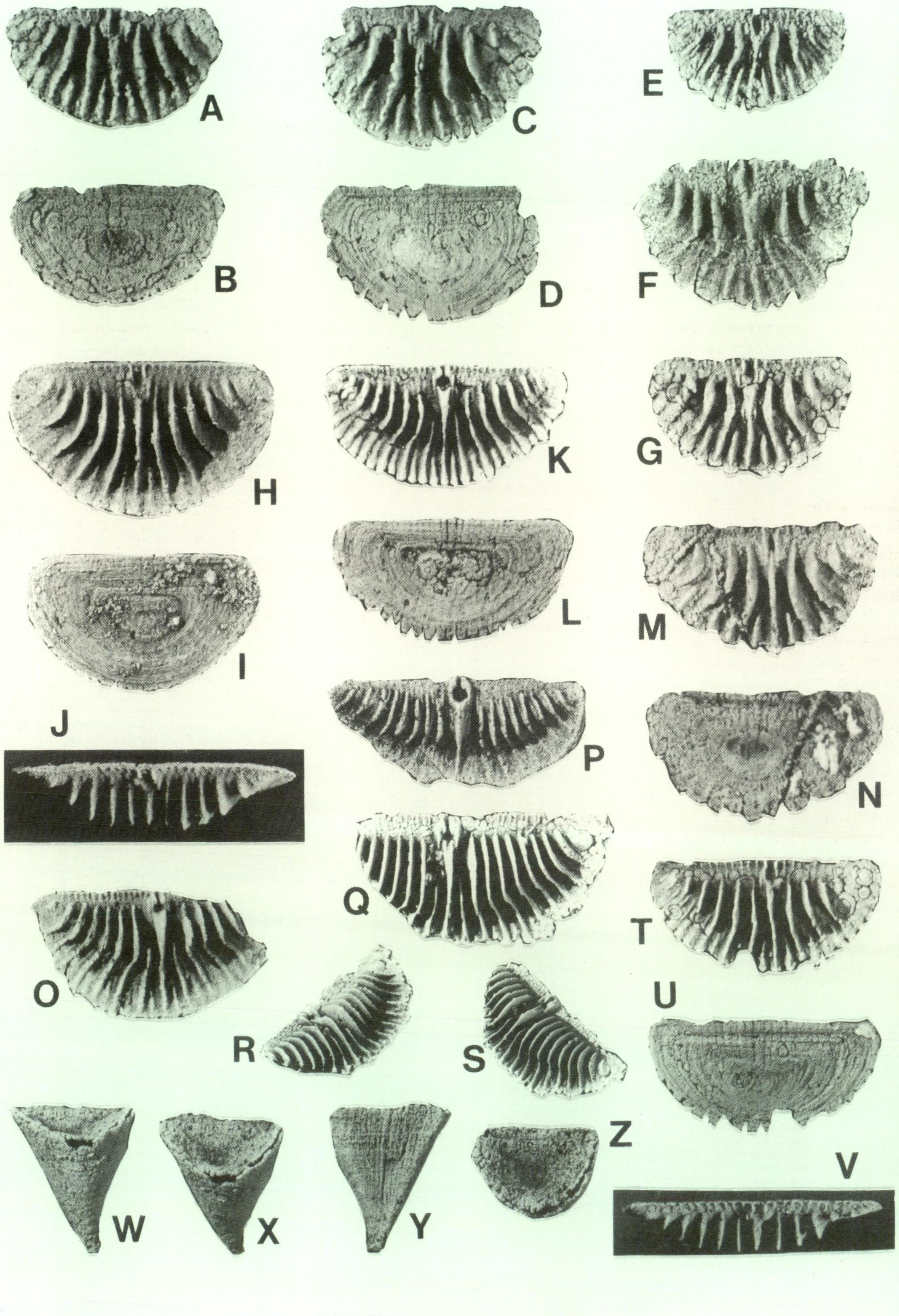
Operculum The outer opercular surface is flat to gently convex through most of growth, commonly with a central (juvenile) depression or irregularity (see juvenile specimen with attached operculum in Figure 3W–Z), and becoming very convex in late growth stages. Growth lines on the external surface are initially concentric but become strongly eccentric in larger specimens, so that the operculum is slightly more transverse at maturity. A juvenile operculum is semi-oval, with width/length ratio of about 1.6:1 at a width of about 1.2 mm, having strongly rounded lateral extremities. At a width of 7.5 mm the ratio is 1.7:1. The largest flat operculum has a ratio of 1.8:1 at a width of 13 mm. At a width of 13.5 mm, the holotype, a strongly convex specimen, still has a ratio of 1.8:1. The growth lines indicate that, following the initial rounded growth stage, a more rounded-triangular form developed, with rounded acute corners at the counter edge; the corners become generally rounded-rectangular in mature specimens. A KOF is absent initially but becomes more apparent throughout ontogeny; when developed, KOF *generally* shows a low angle to the commissure and is a rough, irregular surface as opposed to the smooth planar face seen in *Calceola.* The holotype shows a rather strongly developed but roughly layered KOF at a high angle to the commissure, and is clearly a mature or gerontic feature.

Internal features

Corallite On the inner K face of the slipper, the median (K) septum is always marked by its greater width than other septa and its prominent, projecting distal tip (usually more so in mature specimens with a width of >10 mm) and is flanked by about 11 variably developed major septa, on either side (Figure 2D, 3P–Q). The septa generally are separated at the K edge by shallow furrows and minor septa are always present distally (e.g., Figure 2A, 2D, 3Q). The distal tips of these lateral major (and minor) septa articulated in depressions between the denticulations on the K edge of the operculum. Septa are weakly developed on the curved C rim opposite the K face. The maximum width of the hinge line is 13.5 mm. In smaller specimens, the lateral septa are more obvious, and rows of both trabecular granules along the septa and desmocyte scars are apparent (Figure 2T). Longitudinally broken slippers occasionally show the expected development of tabellae, but no dissepiments (Figure 2V).

Operculum Juvenile opercula have an essentially flat inner surface on which the septa are located; in

◀ **Figure 2** A–V. *Chakeola johnsoni* n. sp., all silicified paratypes (except for the holotype operculum shown in Figures A–C) from the Pragian Garra Formation at Wellington, N.S.W. **A–C**, holotype AMF 104320: **A**, internal view, x 5; **B**, external view x 4; **C**, view of counter edge showing KOF, x 5. **D–H**, AMF 104322: **D**, internal view, x 4; **E**, external view, x 3; **F**, oblique view of counter edge; **G–H**, 2 counter views of counter edge, both x 3. **I–J**, AMF 104321: **I**, external view, x 4; **J**, oblique counter view of mature specimen, x 4 approx. **K**, AMF 104336, view of counter edge of operculum, x 4. **L**, AMF 104337, internal view of operculum, x 4. **M–N**, AMF 104340, cardinal and counter views respectively of large corallite, x 3. **O**, AMF 104341, cardinal view of corallite showing major and minor septa on inner counter face, and irregular initial stage, x 8. **P**, AMF 104342, juvenile corallite showing irregular initial stage, x 8. **Q**, AMF 104343, cardinal view of corallite showing subdued development of major and minor septa on inner counter face, x 3. **R–S**, AMF 104344, cardinal and counter views of corallite, also showing initial stage, x 3. **T**, AMF 104345, cardinal view of corallite showing major and minor septa on inner counter face, x 5. **U**, AMF 104346, cardinal view of corallite showing major and minor septa on inner counter face, x 3. **V**, AMF 104328, longitudinally broken corallite showing tabellae, x 3.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mature specimens the operculum is thickened towards the K edge so that the base on which the septa are located is elevated. In mature specimens, there is a prominent concave area inside the C edge where all septa are low but still reach the C edge; this area is less concave in juvenile specimens. A median septum (the K septum) is developed throughout ontogeny. In the smallest available specimens, with a width of 4 mm, there are 3 flanking long (major) septa and, peripherally, 3 small minor septa alternating with the major septa. New septa are added at the lateral extremities of the operculum. In early growth stages the septa are straight but the 2 or 3 major septa adjacent to the median septum are curved laterally through about 30° at about mid-length in larger specimens. Mostly the septa are vertical, but occasionally slope outwards. In lateral profile, the major septa arise just inside the flat denticulate K surface, rapidly become high and less rapidly reduce in height to cross the cardinal flange as low ridges; thus the top edge of these major septa is very strongly curved. The K septum is somewhat higher than other major septa, and tends to have a steep swollen edge descending into the articulating pit. Invariably there is one relatively short major septum between the K septum and the next major septum of "normal" length; the septa are short in not extending far towards the K edge. At maturity there are up to 11 well-defined high, long curved major septa extending to the lateral extremities of the operculum. These septa are progressively shorter and lower towards the lateral extremities of the opercula. Minor septa normally reach less than halfway to the K edge (although rare specimens show minor septa extending from near the K ends of the major septa to the C edge), and appear to increase in length throughout ontogeny but, in mature specimens, may be less prominent laterally.

Denticulation in the form of fine longitudinal ridges along the K edge forms sockets which accommodate the tips of both major and minor septa along the K edge of the slipper, as is well shown by AMF 104320 and AMF 104350, as well as by smaller specimens like AMF 104329, AMF 104330 and AMF 104334. The sockets are located on a distinct flat area where the septa do not reach the K edge. In juvenile opercula, there are as many short longitudinal ridges producing these very shallow "sockets" as there are major plus minor septa, but there is no clear continuity between the septa and the ridges bounding these sockets; in juveniles, irregular, rather abrupt bending of the septa where they cross the flat area (discussed below) makes it uncertain whether the septa continue to from boundaries to the sockets. In mature specimens like the holotype the counter ends of the major septa clearly terminate in front of the wide shallow sockets which are separated by a reduced number of wide, low ridges (Figure 2A). There are thus sufficient sockets in juveniles to accommodate both the major septal tips and the minor septal tips (rarely observed on available slippers), but in mature specimens there are sufficient sockets for only the major septa.

The articulating pit for the distal tip of the K septum (on the slipper) is deep and rounded, with a small longitudinal slit-like extension towards the K edge; this pit is essentially restricted to and raised above the flat region on the K side of other major septa. The complex pit consists of the K septum which extends as a blade into the C end of the socket, and two (minor?) septa which wrap around and form the socket, and extend in the C direction to fuse with the sides of the K septum. These minor(?) septa which form the sides of this socket often leave a pair of fine grooves on the exterior of the operculum (Figures 3H, 3K, 3R). The K septum is reduced in height and width progressively towards the C edge, but is higher and longer than other major septa, almost reaching the C edge. The flat area between the K edge and the ends of the major septa tends to become slightly longer towards the K septum; in other words, the K ends of septa near the K septum are located further from the K edge than those of the lateral major septa.

Corallite Little can be seen by way of structure inside the slipper, although the strength of development of the septa inside the K face varies considerably; septa are weakly developed on the C face. Several Garra corallites show that the alar fossulae are located on the K face, close to the angle of the corallite. Tabellae are present on one longitudinally broken specimen (Figure 2V).

◀ **Figure 3** **A–Z**. *Chakeola johnsoni* n. sp., paratype silicified specimens (all opercula except for **W–Z**) from the Pragian Garra Formation at Wellington, N.S.W. **A–B**, AMF 104323, internal and external views, x 10. **C–D**, AMF 104324, internal and external views, x 10. **E**, AMF 104326, internal view, x 10. **F**, AMF 104338, internal view, x 8. **G**, AMF 104327, internal view, x 8. **H–J**. AMF 104329: **h**, internal view, x 7; **I**, external view, x 6; **J**, counter view of opercular edge, x 7 approx. **K–L**, AMF 104330, internal and external views, x 5. **M–N**, AMF 104331, internal and external views, x 5. **O**, AMF 104333, internal view, x 5. **P**, AMF 104335, internal view, x 4. **Q–S**, AMF 104325: **Q**, internal view, x 4; **R–S**, oblique internal views showing height of septa and worn or broken rim. **T–V**, AMF 104334: **T–U**, internal and external views, x 6; **V**, counter view of opercular edge, x 7 approx. **W–Z**, AMF 104339, tiny corallite with operculum in place, in cardinal, dorso-cardinal, counter and opercular views respectively, all x 10.

Ontogenetic changes To summarise, significant ontogenetic changes in the operculum, as described above are:

1. progressive development of the KOF;
2. increase in the convexity of the external surface;
3. increased development of convex floor beneath highest parts of septa;
4. growth lines on external surface of operculum are initially oval to concentric but become strongly eccentric in larger specimens, largely due to crowding of growth lines and development of straight counter edge;
5. increase in number of septa flanking the K septum;
6. in mature specimens the region adjacent to the K edge lacking septa becomes relatively shorter, and minor septa become less prominent towards the K region; and
7. in mature opercula the septa are directly continuous with the "sockets" immediately inside the K edge, whereas in well-preserved juvenile specimens fine longitudinal ridges, not certainly continuous with the major septa, form the margins of the sockets.

Remarks

Despite the lack of evidence suggesting current sorting and transportation, separate opercula and slippers occur in more or less equal numbers. This material is generally coarsely silicified and worn, broken or abraded, so that some features like the height of septa, the exact shape of the operculum, and (in particular) the length of the septa flanking the K septum is uncertain in some specimens. One specimen was encrusted by a heliolitid coral, so sedimentation rates were, at least occasionally, slow. The most obvious taphonomic(?) effect on the opercula is on the cardinal edge which may, in some specimens, be removed right back to the descending edges of the septa, which then appear to maintain their reduced height right to the rim of the operculum (e.g., Figures 2A, 3H, 3P, 3Q, 3S). However, well preserved large opercula exhibit low septal ridges right to the cardinal edge. Nevertheless, as with many silicified faunas, it is not certain that the largest specimens have been silicified, although the crowding of growth lines strongly suggests that mature specimens have been studied.

Comparisons

C. johnsoni differs from *C. whitehousei* (see below) in having only one short major septum adjacent to the K septum; in lacking well-developed septa on the internal C face (although this may only reflect the relatively smaller nature of *C. johnsoni* corallites examined); and in lacking the prominent furrow (siphonoglyph?) medially on the internal C face of the corallite.

Rhizophyllum calceoloides Talent 1963 (especially paratype operculum pl. 11, fig. 5 and text-fig. 11; not pl. 11, figs 6–7) from the Emsian Tabberabbera Formation, Victoria, is congeneric with *C. johnsoni*. At least 2 taxa may be represented by material figured by Talent. The holotype and the paratype operculum are from the same locality. The latter specimens are probably generically distinct from the specimen in Plate 11, fig. 7, which shows clearly the moulds of dissepiments and is therefore probably a *Rhizophyllum*. Thin sections of the holotype figured by Hill and Jell (1969, fig. 2.4a, 4b, 4c) showed tabellae in the corallite. Hill and Jell noted that Talent's species was morphologically intermediate between *Calceola* and *Rhizophyllum* and suggested that the best method for distinguishing the genera was not only the development of dissepiments and abundant tabellae in *Rhizophyllum*, but also the lack of distortion of the lamellar schlerenchyme around the trabeculae. The figured specimen showing the opercular septa has about 9 lateral septa on either side of the median septum plus 2 shorter septa developed closer to the C edge. Detailed comparison of this Victorian material with the new species described herein is frustrated as the very large operculum (width of 23 mm; width/length ratio impossible to calculate due to the incomplete illustrated specimen) is too poorly preserved in the crucial region adjacent to the K septum to be evaluated.

Several occurrences are noted here of opercula and corallites of this genus of *Chakeola* in clastic strata in the Mudgee district; mostly these are too poorly preserved for specific identification:

1. Several opercula and corallites have been collected from Taylors Hill Formation at Queens Pinch, south of Mudgee, N.S.W. (probably *kindlei* Zone, Pragian): this material has 7–8 lateral major septa, at a width of ca. 15 mm, on each side of the median septum (Figure 4A: AMF 104351). Other, poorly preserved material from this formation suggests some variation in the relative lengths of these septa. This material shows a width/length ratio of more than 2.4, so may be a different species.
2. From the Mullamuddy Formation underlying the Taylors Hill Formation at Queens Pinch, indeterminate calical moulds but no opercula have been found in these Pragian beds.
3. From the Sutchers Creek Formation, also at Queens Pinch SW of Mudgee (*serotinus* Zone, late Emsian), this fragmental specimen (Figure 4B: AMF 104353) has about 8 well-developed lateral major septa at a width of about 12 mm. The width/length ratio for this specimen is approximately 1.6. There do not appear to be any short major septa adjacent to the K septum, as in both species described here. Minor septa are very subdued, and appear as low peripheral

ridges; as this specimen is sheared along the K edge, it can only be noted that it seems to be very distinctive.

4. A single, unexpectedly well-preserved (most fossils from the locality being extremely deformed) specimen is from the road cutting known as the Snake Creek Road section, N of Mudgee, probably from the Sutchers Creek Formation (Wright 1995; Colquhoun *et al.* 1997). This calical internal mould, which is similar in gross morphology to specimens from the Mullamuddy Formation and the Taylors Hill Formation, is a very important specimen as it shows clearly that the CLF is located on the inner surface of the K face, very close to the angle of the corallite (Figure 4C: AMF 104352), as well as details of septa on the K face. The specimen also shows very clearly developed minor septa extending well down the inner surface of the K face to the alar fossula, and a prominent swelling high on the K septum.

Chakeola whitehousei n. sp.
Figures 4D–O, ?P–T

?1930 *Calceola* sp. nov. Reid: 27, 29.

Material

QMF 40760 (holotype operculum); note that the partly calcareous specimen (Figure 4D) was photographed before etching the shell material away with dilute acid to produce an internal mould (Figure 4E); from QM locality L 1008 (Pyramid area). Paratypes: QMF 40761–40769, also from QM locality L 1008. Several specimens in an old GSQ collection from GSQ L 850 (probably Gordon Gully) are GSQ F 9518, 13489–13491 are not certainly conspecific with the other material. All material from the Ukalunda Beds, Ukalunda district, Queensland. Although calcareous material occurs in the Ukalunda Beds, the most informative material is in the moulds.

Material is from 2 localities, one in Gordon Gully (QM L 1008) and another in the Pyramid area (GSQL 580); these localities may represent different horizons. The material from GSQ 580 is preserved in a blue-grey hard mud rock, as opposed to the fine buff sandstone from QM L 1008 from which the holotype and other material were collected. The material is not certainly conspecific as the material from GSQL 580 has fewer septa than the holotype; they do, however, share the 2 short major septa adjacent to the K septum.

Name

The species is named for Dr F. Whitehouse who first (Whitehouse 1929) made a meaningful assessment of collections of Devonian fossils from Ukalunda.

Diagnosis

A species of *Chakeola* with at least 12 high major septa on a mature operculum on both sides of the K septum, reaching almost to the cardinal edge. Two short major septa occur adjacent to the K septum peripherally on the operculum.

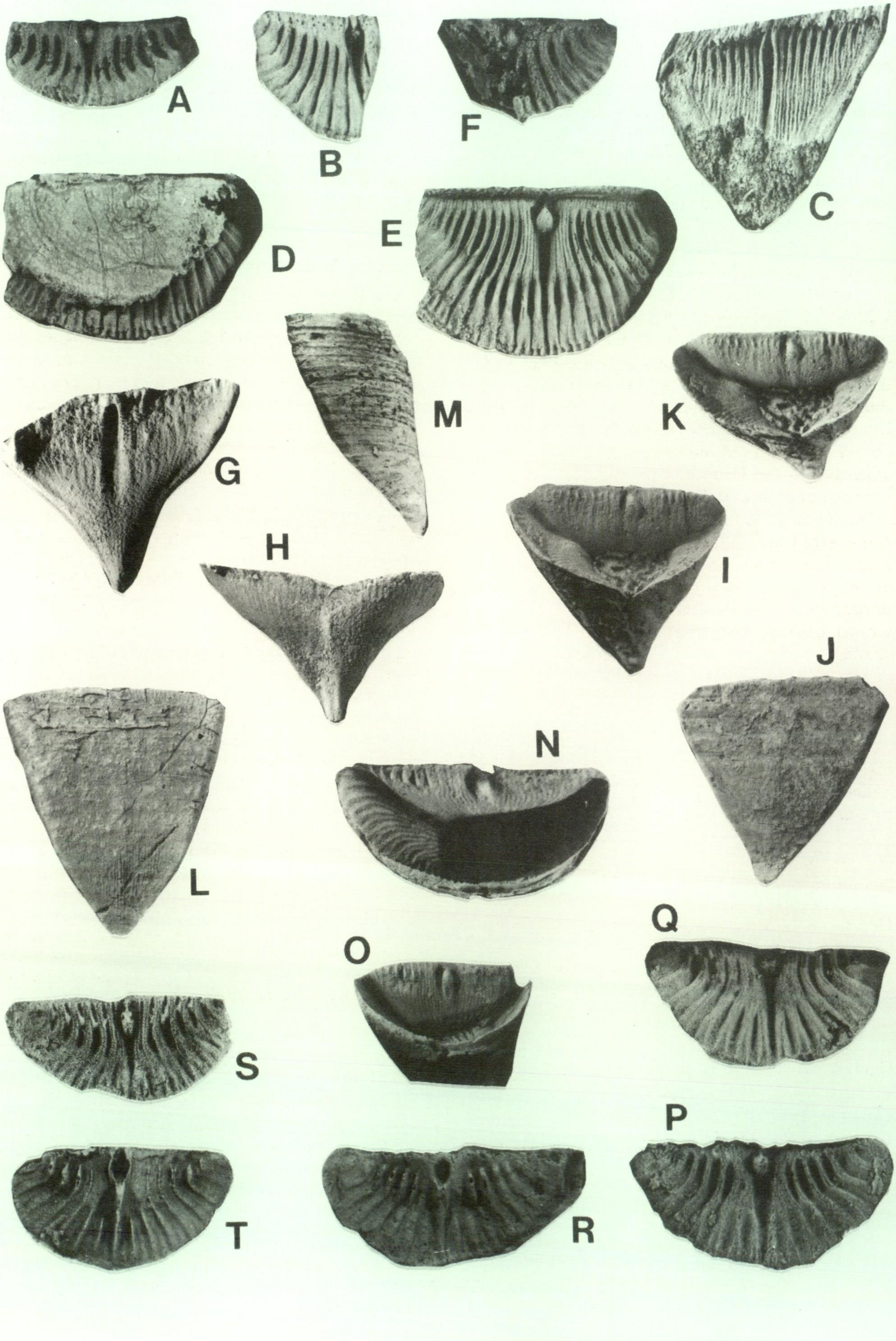
Description

External. Slippers reach up to 23 mm in width and height, and about 24 mm in length, with an apical angle of about from 30° to 60°. The shell material on the slipper is very thick in comparison with the Garra species. The outer surface of the K face bears longitudinal septal striations and growth lines, and varies from flat to slightly convex. Both K and C calical surfaces bear prominent septal traces, and there is a prominent K septum. The outer opercular surfaces are all weathered, so details of growth lines cannot be distinguished; the growth lines do, however, appear to be more strongly eccentric than in *C. johnsoni*. In the holotype a high KOF is present. Calical moulds show a strongly inflated K septum and a prominent C depression low in the calyx. The calyx is almost filled with stereome in mature specimens, so that the calical surfaces in the cardinal quadrants are almost horizontal.

Internal features of operculum and corallite

Operculum The holotype operculum shows at least 12 major septa on each side of the prominent K septum which is markedly thicker than any other septum. The K septum extends to the C edge and displays a prominent pit with a slender extension towards the K edge. All septa are curved, especially those major septa near the K septum. All major septa extend to the C edge, where they are greatly reduced in height from their maximum which is located well towards the K edge. The hingeline is denticulated, with very low remnants of the major septa continuing to the K edge; other faint ridges presumably represent the minor septa. A small node occurs in this denticulate area along the extension of most major septa. As in *C. johnsoni*, the high portion of the major septa is shorter in septa located towards the lateral extremities of the operculum. Minor septa are present as peripheral crenulations, but may also be present between major septa from the K edge to at least mid-length.

Corallites Tabellae have been observed only rarely in longitudinally oriented weathered corallites. Inside the cardinal edges about 24 low rounded septal ridges are seen in well-preserved material; these are apparently alternating major and minor septa which also show bifurcation similar to that of *Goniophyllum* (Wright 1997, fig. 1L). The septa are clearly denticulate and rows of desmocyte attachments scars (Stolarski 1993) also occur between septa.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Remarks

Ukalunda material available for study consists of calcareous slippers and a few opercula, and some moulds of opercula in weathered material. Some bedding planes display numerous disarticulated specimens of slippers and opercula and occasional specimens with the operculum in place. In contrast to material of *C. johnsoni*, specimens of *C. whitehousei* showing the early ontogenetic stages and such abundant septal detail are not available.

Reid (1930) identified an un-numbered figure of a corallite from Ukalunda as *Calceola* sp. nov., presumably basing this identification on Whitehouse's (1929, p. 159) statement that "The present form, however, is not a member of the *C. sandalina* group. It has markedly fewer septa". Although the reader must infer from this ambiguous statement that Whitehouse thought the Ukalunda form had comparatively few septa, this observation is not borne out by the present studies; nevertheless the Ukalunda form described here is very different from *Calceola*.

The holotype is unusual for the genus in that the major septa are thickened and apparently higher well in front of mid-length; this may be pathological or a gerontic feature. It has been deemed undesirable to make a cast of this mould, as this would destroy the fragile details left by acid etching.

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◀ **Figure 4** A–C, *Chakeola* sp. indet. from the Mudgee district, N.S.W. **A**, AMF 104351, Taylors Hill Formation, Queens Pinch area, S of Mudgee, N.S.W.; internal mould of operculum, x 4. **B**, AMF 104353, Sutchers Creek Formation, Queens Pinch area, incomplete internal mould of operculum, x 4. **C**, AMF 104352, from Sutchers Creek Formation, Snake Creek road section, N of Mudgee; internal mould of counter face, showing swollen K septum, major and minor septa, and alar fossulae near edge of K face, x 4. **D–O**, *Chakeola whitehousei* n. sp., all from the Pyramids area, Ukalunda district, Queensland. **D–E**, QMF 40760, holotype operculum: **D**, prior to etching, showing strongly eccentric growth lines, x 2.5; **E**, internal mould after etching, x 2.5. **F**, paratype QMF 40761, fragmental internal mould, x 5. **G–H**, QMF 40762, counter and cardinal views respectively of calical internal mould, x 3. **I–K**, QMF 40764, calcareous corallite in cardinal, counter and calical views respectively, x 3. **L–M**, QMF 40763, counter and lateral views of calcareous corallite, x 3. **N–O**, QMF 40765: **N**, oblique calical view x 2; **O**, calical view x 3. **P–T**, *Chakeola whitehousei?* from GSQ locality 580, Gordon Gully, Ukalunda district, Queensland. **P**, GSQ F 13489, internal mould, x 3; **Q–R**, GSQ F 13490, internal mould and cast, x 3; **S–T**, GSQ F 13491, internal mould and cast, x 3.

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