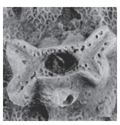
Prokopius, a new name for "*Hippocystis sculptus*" Prokop, 1965, and the status of the genus *Hippocystis* Bather, 1919 (Echinodermata; Diploporita)

Christopher R.C. Paul



Bather proposed the genus *Hippocystis* for some Czech diploporites with horseshoe-shaped diplopores first described by Barrande. Bather cited *Aristocystites subcylindricus* Barrande as the type species and identified a lectotype, but no specimen accepted by Bather as *A. subcylindricus* preserved the oral area. Bather believed *Aristocystites* had irregular haplopores and *Hippocystis* horseshoe-shaped diplopores without intermediates. In 1965 Prokop redescribed one of Barrande's original specimens of ?*A. subcylindricus* as *Hippocystis sculptus* (Barrande). Its oral area has four ambulacral facets, whereas *Aristocystites* is unique among the Aristocystitidae in having only two. A complete specimen of *A. subcylindricus* with the oral area preserved shows only two ambulacral facets. Thus, the type species of *Hippocystis* belongs to *Aristocystites*, of which *Hippocystis* becomes a junior synonym. This leaves '*Hippocystis*' *sculptus* without a valid generic name. The new name *Prokopius* is proposed for it. Parsley has shown that horseshoe-shaped diplopores also occur in *A. bohemicus*, type species of *Aristocystites*. Functional analysis of horseshoe-shaped diplopores suggests they are likely to have evolved repeatedly and so make a poor generic criterion. Characteristic oral areas are much more reliable. *Prokopius* is distinguished by having an oval mouth, surrounded by eight plates, as in all other aristocystitids, with four vertical ambulacral facets, a zigzag hydropore aligned parallel to the oro-anal line and all these features on a raised oral prominence. • Key words: Diploporita, *Hippocystis*, Aristocystitidae, *Prokopius* gen. nov., Ordovician, Sandbian.

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Barrande (1887) described the new genus *Aristocystites*, type species *A. bohemicus* Barrande, 1887. *Aristocystites* is characterized by a large, oval to pyriform theca, usually with a distinct basal attachment scar. The mouth is elongated perpendicular to the oro-anal line and bears two weak ambulacral facets at either end. An elongate hydropore and circular gonopore lie between the mouth and the large, angular periproct. The hydropore is nearer the mouth. Plates are covered with irregular diplopores, but are smooth and plate sutures very difficult to distinguish.

In table 2, Barrande (1887, p. 65) listed seven other specific names doubtfully attributed to *Aristocystites*. These included '?*A. sculptus* Barrande, 1887' and '?*A. subcylindricus* Barrande, 1887, *var. de bohemicus*'. Barrande (1887, p. 113, pl. 6, figs 28, 29) described and illustrated the unique example of ?*A. sculptus* and stated its only distinguishing character was the presence of tumid plates. He also described and illustrated (Barrande 1887, p. 114, pl. 6, figs 26, 27, pl. 13, figs 1–21) '?*A. subcylindricus* Barrande, 1887, *var. de bohemicus*'. The single example illustrated on plate 6 came from the same locality (Chrustenitz) as ?*A. sculptus* and clearly shows the oral area. The distinguishing characters of ?*A. subcylindricus* were a rounded base lacking an attachment scar and horseshoe-shaped diplopores.

Bather (1919a, p. 72) erected the genus *Hippocystis* in one of a series of notes (Bather 1918a, b; 1919a–e) commenting on F.R.C. Reed's monograph describing Ordovician cystoids from Yunnan, China (Reed 1917). Bather (1919a) compared *Sinocystis* Reed, 1917, with other genera in the family Aristocystitidae and in doing so pointed out that some specimens of *Aristocystites* Barrande, were characterized by horseshoe-shaped diplopores. He considered these diplopores to differ sufficiently from those of *Aristocystites* proper to justify characterizing a new genus. Bather (1919a, p. 72) designated *A. subcylindricus* Barrande as the type species of *Hippocystis* and specified the original of Barrande's (1887, pl. 13, figs 1–4) as the 'holotype' (Bather 1919a, p. 73). We would now designate the specimen as a lectotype, but it established the validity of both *Hippocystis* Bather, 1919a, and the type species ?*Aristocystites subcylindricus* Barrande, 1887. The type specimen shows an incomplete theca, lacking the oral region, a rounded base and tumid plates with horseshoe-shaped diplopores.

Chauvel (1941, p. 65) recognized Barrande's species *Aristocystites subcylindricus* as distinct from *A. bohemicus*, but confined it to two specimens illustrated by Barrande (1887, pl. 13, figs 14–16 and 19–21). Neither specimen shows the oral area, but they have relatively smooth plates without impressed sutures. Chauvel thought they could be distinguished from *A. bohemicus* by the rounded aboral extremity. He specifically stated (1941, p. 66) that the two species had plates of the same size and shape bearing identical diplopores. Personally, I would attribute both of Chauvel's examples to *A. bohemicus*, but without seeing the oral areas it is virtually impossible to identify incomplete aristocystitid cystoids (see Paul, 1973, p. 57). Chauvel (1941, p. 70) also recognized *Hippocystis* based on specimens illustrated by Barrande (1887, pl. 6, figs 26, 27 as ?*A. subcylindricus*; pl. 6, figs 28, 29 as ?*A. sculptus*; pl. 13, figs 1–13, 17, 18 as ?*A. subcylindricus*; and pl. 14, figs 14–16 and 17–19 as *A. bohemicus*), but he attributed them to a new species, *H. batheri* Chauvel, 1941. Nevertheless, if the specimens Chauvel grouped together under *Hippocystis batheri* are a valid taxon, the oldest available name for it is *Hippocystis sculptus* (Barrande, 1887) and *H. batheri* Chauvel is a junior synonym. Chauvel (1941, p. 72, fig. 26) stated that *Hippocystis* had four ambulacral facets, strongly convex plates and horseshoe-shaped diplopores. Chauvel's figure of the oral area (1941, fig. 26a) shows an oval mouth from which two ambulacral grooves extend left and right and divide to give four ambulacral facets.

Prokop (1965) redescribed and illustrated under the name *Hippocystis sculptus* (Barrande, 1887) Barrande's only original specimen with horseshoe-shaped diplopores that preserved the oral area. Prokop (1965) regarded the two specimens illustrated on Barrande's plate 6 as conspecific, adopted the name *Hippocystis sculptus* (Barrande, 1887) for them and maintained that the species was restricted to the Nučice Ore Horizon, in the Černín "Beds" (Caradoc; late Sandbian International Stage, see Bergström *et al*. 2009, Gutiérrez-Marco *et al*. 2017). Specimens of both *A. bohemicus* and *A. subcylindricus* came from slightly younger strata, the Zahořany Formation, from Lodenitz and Straschnitz (Barrande 1887, explanations of pls. 9, 13; see Prokop & Petr 1999, tab. 1).

Prokop (1965) illustrated the gonopore and zigzag hydropore of *Hippocystis sculptus* (Barrande) for the first time and stressed that four ambulacral grooves, which terminated in almost vertical ambulacral facets, arose separately from the edge of the mouth. Prokop thought *H. batheri* Chauvel might be a valid species because it had branched ambulacra. However, Chauvel, (1941, p. 71) expressly stated that only the original specimen of Barrande (1887, pl. 6, fig. 26) showed the oral area. Thus, both Prokop's and Chauvel's descriptions and figures are based on the same specimen. Chauvel (1941, p. 71) also expressly stated that the oral area was poorly preserved, whereas Prokop (1965, p. 305) said: 'By a new preparation the oral part of theca of Barrande's *Aristocystites*? *sculptus* was uncovered which enabled me … to study the hitherto unknown morphology of ambulacra…'. Thus, it seems Prokop was able to see morphological details that were hidden from Chauvel. Recent, good quality latex casts available to me through the courtesy of Bertrande Lefebvre confirm Prokop's observation that the four ambulacral grooves are separate along their entire length from mouth edge to ambulacral facets. *Hippocystis batheri* Chauvel, 1941, is an objective junior synonym of *Hippocystis sculptus* (Barrande, 1887) as validated by Prokop (1965), since both names were established on the same specimen.

Up to this point the situation was simple. *Aristocystites* Barrande had an elongate mouth with two ambulacral facets; *Hippocystis* had an oval mouth with four ambulacral facets. Nevertheless, *Hippocystis* was based on the type species ?*Aristocystites subcylindricus* Barrande, 1887, as originally designated by Bather (1919a). Subsequently, Chauvel (1966, p. 38) introduced a new subfamily, the Hippocystinae, and Parsley (1990) has given a thorough, modern description of *A. bohemicus* and interpreted its mode of life. Furthermore, Makhlouf *et al*. (2017) and Paul (2017) have introduced a new interpretation of the homologies of the oral plating in aristocystitid diploporites, which is thought to characterize the entire family (see below).

Recently, I rediscovered some photographs taken in the late 1960s of a specimen of *Aristocystites subcylindricus* in the United States National Museum, which preserves the oral area. One photograph showed that the oral area and principal orifices of *A. subcylindricus* are virtually identical to those of *A. bohemicus*. The specimen strongly resembles the lectotype of ?*Aristocystites subcylindricus* Barrande, chosen by Bather (1919a, p. 73). Thus, the type species of *Hippocystis* Bather can be shown to have the characters of *Aristocystites* Barrande, 1887, as Barrande originally suspected, and *Hippocystis* becomes a subjective junior synonym of *Aristocystites*. Nevertheless, "*Hippocystis sculptus* (Barrande, 1887)" as described by Prokop (1965) has a distinctly different, oval mouth with four ambulacral grooves and facets, and is genuinely distinct from *Aristocystites*. Thus, "*H. sculptus*" needs a new generic name for which *Prokopius* is proposed here.

The purposes of this paper are to redescribe and define the new genus *Prokopius*, to confirm its systematic position within the Aristocystitidae and the taxonomic significance of different morphological features within the family. Diploporites described in this paper are deposited in the National Museum, Prague (NMP) and the United States National Museum of Natural History (USNM), Washington, DC.

Ambulacral terminology follows Carpenter's system (Carpenter 1884, 1891) in which the ambulacrum opposite the anus is labelled A and the others B–E in a clockwise direction as viewed looking at the mouth. Oral plate terminology in the Aristocystitidae follows Paul (2017, p. 589, fig. 7).

Characters of the genus *Aristocystites*

Parsley (1990) provided a detailed account of *Aristocystites* and its likely mode of life. He synonymized four of Barrande's original species in *A. bohemicus* and described a new species, *A. metroi* Parsley & Prokop *in* Parsley (1990). Parsley (1990, p. 286, fig. 7.2) established for the first time that the elongate mouth was surrounded by eight thecal plates with three arranged along both the anterior and posterior edges and two at each end that bear relatively large, but weakly developed ambulacral facets. All oral frame plates bear numerous diplopores, even beneath the ambulacral facets. Two of the posterior oral frame plates share an elongate, slit-like hydropore, with a complex structure of irregularly pinnate lateral branches (Parsley 1990, p. 286, fig. 8). The gonopore is a prominent structure like the frustrum of a cone, with a countersunk tip that Parsley believed was for the insertion of cover plates forming a small, gonal pyramid. It is usually entirely within a single plate and varies in position from almost touching the periproct margin to halfway between the periproct and hydropore (Parsley 1990, p. 284, figs 6.6, 6.8; p. 289, figs 10.1, 10.2). The periproct itself is large, polygonal and surrounds a circular anus with a ledge for the insertion of triangular anal plates that form an anal pyramid (Parsley 1990, p. 287, fig. 9; p. 289, figs 10.1, 10.2).

Parsley (1990, p. 283, fig. 4) also illustrated horseshoe-shaped diplopores in *Aristocystites bohemicus*, as well as (p. 283, fig. 5) showing the manner by which the diplopores grew as the thecal plates enlarged. Actual specimens (Parsley 1990, figs 6, 10) illustrate the varying states of preservation in different individuals of *Aristocystites*. For example, in figure 6.3 the surface is almost smooth and the epistereom complete. Figures 6.6 and 6.8 show extensive areas where the epistereom is worn revealing the characteristic external outlines of the diplopores, whereas figure 6.11 shows the base of a theca where the transition from smooth epitheca to deeply weathered pore canals can be seen on different parts of the same specimen. Some broadly horseshoe-shaped diplopores show on figure 6.8 among other irregular, crowded diplopores. Finally, most specimens of *A. bohemicus* have an obvious attachment scar, which when deeply weathered shows that all parts of plates forming the scar are densely penetrated by diplopore canals.

Thus, the type species of *Aristocystites* possesses an elongate mouth, whose frame is composed of eight plates and the two at each end bear a single, weak ambulacral facet. Two more mouth frame plates share a complex, slit-like hydropore. A conical gonopore lies further posterior towards the periproct, which is large, polygonal and covered by a simple anal pyramid. Well preserved *A. bohemicus* plates are smooth, but bear numerous diplopores, which in life, opened just below the surface in irregular, sometimes horseshoe-shaped peripores.

Aristocystites metroi Parsley & Prokop *in* Parsley (1990) differs primarily in being larger and having a smooth external surface. No pores show on the external surface due to a lack of weathering. The oral area of *A. metroi* is unknown.

Characters of *Aristocystites subcylindricus* Barrande, 1887

This whole paper depends on the fact that *A. subcylindricus* belongs in the genus *Aristocystites*. Thus, it is imperative to establish its characters before defining *Prokopius* gen. nov. *Aristocystites subcylindricus* was mainly illustrated on plate 13, figures 1–21. These specimens show typical aristocystitid diploporites up to about 50 mm long by 40 mm wide, with distinctly tumid plates, especially adorally, covered with horseshoe-shaped diplopores. Barrande thought that the absence of an attachment surface aborally was significant, but nowadays we regard the presence or absence of an attachment scar as the result of individual growth, not a taxonomic character. For example, Thomka & Brett (2014, p. 184) have recorded well-developed attachment scars in the diploporite *Paulicystis* Frest & Strimple *in* Frest *et al*. (2011) when it grew on a Silurian hardground surface, but their absence in examples preserved in the overlying shale.

Recently, Parsley rediscovered and photographed the specimen of *A. subcylindricus* in the USNM (Reg. no. 436969A, Fig. 1). It shows an elongate ambulacral groove (AG in Fig. 1C) extended at right angles to the oro-anal line (AG–Pe in Fig. 1C). The plates at both ends of the mouth are damaged, so the shape of the facets cannot be seen entirely. Nevertheless, this specimen clearly did not have four facets. Part of the outline of the right

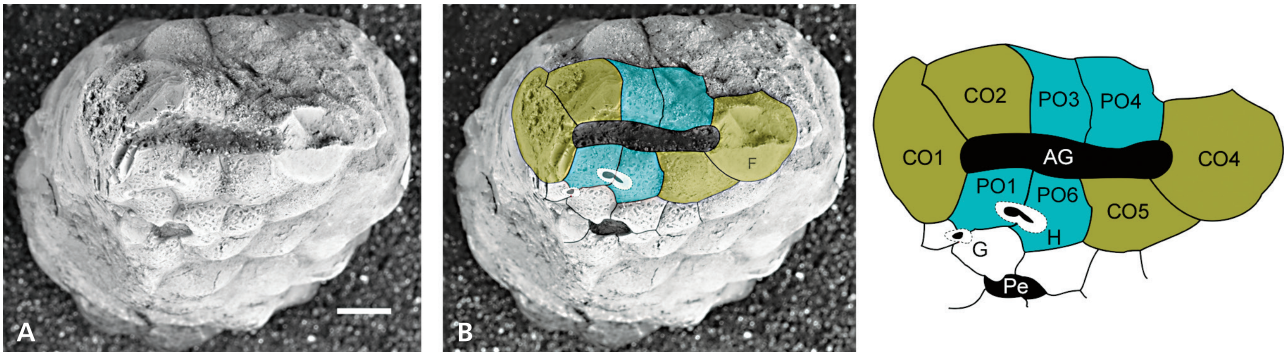

Figure 1. *Aristocystites subcylindricus* Barrande, 1887, USNM 436969A; A – oral view to show ambulacral groove and main thecal orifices; B – the same with interpretation of the thecal plates around the mouth; C – line drawing of the oral plating and main thecal orifices (black). Abbreviations: AG – ambulacral groove; CO1–CO5 – circum-oral plates; F – ambulacral facet; G – gonopore; H – hydropore; Pe – periproct; PO1–PO6 – peri-oral plates. Although damaged only CO1 and CO4 appear to have supported ambulacral facets. Scale bar = 5 mm.

hand facet is preserved (F in Fig. 1B) and shows that the facet extended across the large terminal plate at that end (CO4 in Fig. 1C). The ambulacral groove has three plates along both the anterior and posterior sides. Two along the posterior edge (PO6, PO1) share an elongate, slit-like hydropore (H) in a raised tubercle. A rounded gonopore (G) with a weak rim lies at the junction of PO1 and two plates below it. Finally, a relatively large originally pentagonal periproct (Pe) lies almost directly below the hydropore (Fig. 2). Horseshoe-shaped diplopores can be seen in the plates adjacent to the hydropore and periproct (Fig. 2). All the plates are considerably more tumid and the sutures more obvious than those of either *A. bohemicus* or *A. metroi*.

Aristocystites is the only known genus within the family Aristocystitidae, which has just two ambulacral facets. USNM 436969A shows that *A. subcylindricus* is indeed a species of *Aristocystites*. It shares all the essential details of the oral area with the type species, *A. bohemicus*, except that the gonopore opens at the junction of three plates, instead of within a single plate. The principal difference is the tumidity of the plates.

Systematic palaeontology

Class Diploporita Müller, 1854
Family Aristocystitidae Neumayr, 1889

Diagnosis. – Directly attached diploporites with an elongate oral area surrounded by at least eight plates [four inter-radial peri-orals (POO) and four radial circum-orals (COO)], and covered by a double biseries of cover plates; with 2–5 ambulacra bearing 1–4 brachioles each; with a large hydropore across the PO1 : PO6 suture and often a spout-like gonopore usually within a single plate near the periproct; with thecal plates densely covered with diplopores that are frequently sealed externally by a thin epistereom and sometimes extended into spine-like projections (McDermott & Paul 2018).

Remarks. – This diagnosis is significantly different from preceding diagnoses (*e.g.* Kesling 1968, p. S250) largely because the arrangement of plates in the oral area was not previously fully appreciated, but also because genera that would now be included in the family Holocystitidae were previously included within the Aristocystitidae. All aristocystitid genera where the oral plating and ambulacra are known have a mouth elongated perpendicular to the oro-anal axis and surrounded by eight plates, interpreted by Paul (2017, p. 589, fig. 7) as four, central, peri-oral plates (PO1, PO2, PO4 and PO5) and four distal circum-oral plates (CO1, CO2, CO4 and CO5) (Figs 3, 4 herein). In *Aristocystites* (Fig. 3A) only two, weakly developed ambulacral facets occur. Paul (2017, fig. 7.1) interpreted the two ambulacra as B and D because the facets were developed on plates CO1 and CO4. In *Calix* Rouault, 1851, the ambulacra divide at each end and give rise to four ambulacral facets, one on each circum-oral plate. In the type species, *Calix sedgwicki* Rouault, 1851, (Fig. 3B) each facet gives rise to four long brachioles (see Chauvel 1977, pl. 1, fig. 6). Although numerous species of *Calix* have been described (see Gutiérrez-Marco & Colmenar 2011, p. 190), the only other species of which I am aware in which the oral area is known is '*Calix*' *inornatus* (Meléndez 1958). This also has four ambulacra, but each ends in a distinct pair of facets each mounted on a single circum-oral plate, giving eight facets in all (see Gutiérrez-Marco & Aceñolaza 1999; McDermott & Paul 2018, figs 5b, c). In addition, Chauvel (1978, p. 39, fig. 5b, pl. 3, fig. 1) has illustrated, under the name *Phlyctocystis* sp. another aristocystitid with four divided ambulacra, giving a total of eight facets, but in *Phlyctocystis* Chauvel, 1966, the ambulacral branches are much longer and apparently each facet arises from a separate 'facetal' plate and two other thecal plates. From the published illustrations it seems these two aristocystitids with eight facets have different oral plate arrangements and represent two different genera. I am reluctant to describe a new genus for '*Calix*' *inornatus* without examining the material myself. As the name implies, '*Calix*' *inornatus* has a smooth external surface, whereas *Phlyctocystis* has many tumid plates with deep sutures that are often ornamented with tubercles.

Personally, I prefer to restrict the genus *Calix* to include only those species which have what Chauvel (1977, p. 314) called 'bouquets of brachioles'. The only other genus to share such 'bouquets of brachioles' is *Oretanocalix* Guttiérrez-Marco, 2000, which differs from *Calix s.s.* in having all five ambulacra developed (Gutiérrez-Marco 2000, p. 83, fig. 1e, p. 84). Photographs kindly supplied by Gutiérrez-Marco suggest that *Oretanocalix* has an extra circum-oral plate (CO3) bearing the extra ambulacral facets in ambulacrum A. *Glaphocystis* Chauvel, 1966 (Fig. 3C); *Lepidocalix* Termier & Termier, 1950; *Sinocystis* Reed, 1917; and *Prokopius* nom. nov. (Fig. 4) all have four ambulacral facets. In *Glaphocystis* only a single, biserial brachiole arose from each facet (Chauvel, 1966, p. 39, pl. 4, fig. 1e, pl. 9, figs 2a, b), but the details of the ambulacral appendages in the other genera remain unknown.

The unique Silurian genus, *Triamara* Tillman, 1967, has three ambulacral grooves, each of which ends in a double facet. It also has a much smaller mouth, almost certainly surrounded by only the four peri-oral plates. Recently, McDermott & Paul (2018) have described another Ordovician aristocystitid genus, *Binocalix*, which has paired ambulacral facets set above a smooth ambulacral platform. The monotype is incomplete, so the exact number of ambulacral facets is uncertain, but it probably had four pairs. The oral area is unknown in other possible aristocystitid genera, such as *Baculocystites* Barrande, 1887; *Pachycalix* Chauvel, 1936; *Campylostoma* Dreyfus, 1939; *Magrebocystis* Chauvel, 1966; and *Atlasocystis* Chauvel, 1978.

Genus *Prokopius* gen. nov.

1887 *Aristocystites* Barrande, (*partim*) pp. 113, 114, pl. 6, figs 26–29.
1965 *Hippocystis* Prokop, p. 303 (*non* Bather, 1919a).
1999 *Hippocystis* Prokop. – Prokop & Petr, p. 64.
? 2014 *Hippocystis* Prokop. – Noailles *et al*., 2014, p. 457.

Type species. – *Hippocystis sculptus* (Barrande, 1887) *sensu* Prokop (1965).

Diagnosis. – An aristocystitid genus with a relatively small, oval mouth surrounded by a prominent oral rim such that the four ambulacral facets are orientated vertically, with oral pores in the peristome; hydropore a zigzag slit set in an oval tubercle elongate parallel to the oro-anal axis and across the suture PO1:PO6; conical gonopore within a single plate below the hydropore; with a theca composed of strongly tumid plates covered with diplopores that are often horseshoe shaped.

Figure 2. *Aristocystites subcylindricus* Barrande, 1887, USNM 436969A. Lateral view of the area between the ambulacral groove and the periproct showing several horseshoe shaped diplopores. Scale bar = 5 mm.

Remarks. – Bather (1919a, p. 72) did not give a diagnosis of *Hippocystis*, but following Barrande (1887, p. 102) he accepted that the pores in the various forms of *Aristocystites* recognized by Barrande fell into two categories. In the first they were irregularly shaped and not obviously united in pairs. In the second the pores were 'far more obviously in pairs, and those of each pair are connected by a rather narrow channel of horse-shoe shape, at the ends of which they lie' (Bather 1919a, p. 72). Furthermore, Bather added 'The adoral region of the theca in the latter specimens is unknown, but the pore-character warrants their separation as a genus for which I propose the name *Hippocystis* in allusion to the horse-shoe.' (Bather 1919a, p. 72). Thus, the possession of horseshoe-shaped diplopores was the prime character on which Bather based the genus *Hippocystis*. Unfortunately, the type species of *Aristocystites s.s*. also sometimes bears horseshoe-shaped diplopores (see Parsley 1990, p. 283) and so this character is not diagnostic of the genus described by Prokop (1965) as *Hippocystis*.

Calix, Sinocystis, Lepidocalix, and *Glaphocystis* are all aristocystitids with four ambulacra. *Prokopius* (Figs 4, 5) differs from all these genera in having a relatively small, oval mouth (M in Fig. 4) surrounded by a raised oral rim and in having its hydropore as a zigzag slit aligned parallel to the oro-anal axis of the theca. Furthermore, it differs from *Calix* (as here restricted) in lacking the bouquets of brachioles; it has a single facet in each ambulacrum. The other three genera also have only a single facet per ambulacrum, but the facets are orientated parallel to the oral surface, not vertically. *Sinocystis* and *Lepidocalix* typically have their diplopores raised in spines on the plate

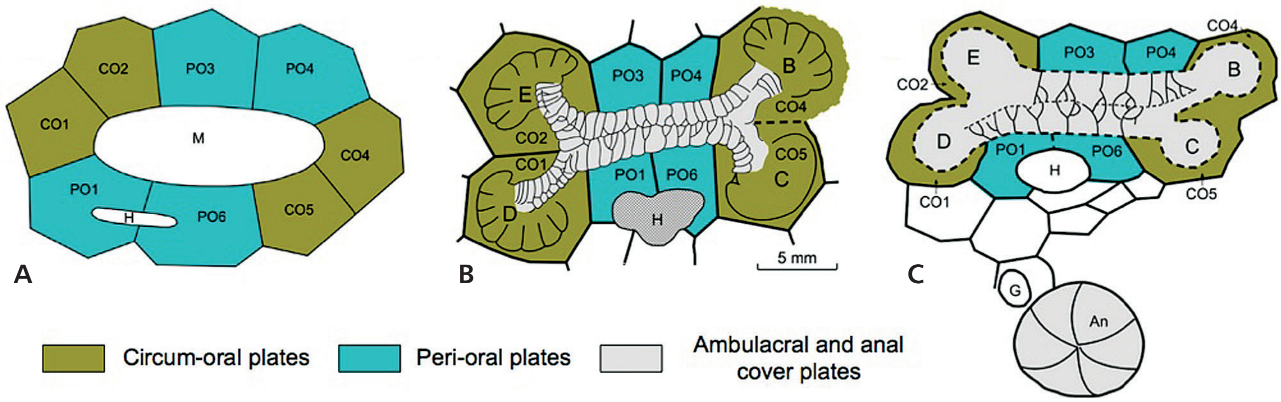

Figure 3. Ambulacra and oral plating in aristocystitid diploporites. • A – *Aristocystites* Barrande, 1887. • B – *Calix sedgwicki* Rouault, 1851. • C – *Glaphocystis* Chauvel, 1966. In aristocystitids the mouth (M) lies within a broad food groove, which extends left and right. The food grooves are covered with a double biseries of cover plates (B, C). In *Aristocystites* (A) a single large facet lies at each end of the food groove. In *Calix* (B) both food grooves divide to give four large facets from which up to four brachioles arise. In *Glaphocystis* (C) the four facets gave rise to a single brachiole. Abbreviations: An – anus; B–E – ambulacra; CO1–CO5 – circum-oral plates; G – gonopore; H – hydropore; M – mouth; PO1–PO6 – peri-oral plates. Notes: A – redrawn from Parsley (1990, fig. 2, p. 286); B – redrawn from Chauvel (1977, fig. a, p. 315); C – redrawn from Chauvel (1966, pl. 4, fig. 1e). Scale applies to B only.

surface (see Makhlouf *et al*. 2017 and Paul *et al*. 2017, respectively). Finally, *Glaphocystis* is most similar in general appearance to *Prokopius* in having similar, tumid plates with deep sutures, covered in abundant irregular diplopores. Hydropores in aristocystitids vary, but the hydropore in *Prokopius* is unique in my experience in being a zigzag slit set perpendicular to the long axis of the mouth. *Aristocystites* has a similar slit-like hydropore within a tubercle across the suture PO1:PO6, but it is not obviously zigzag and is orientated parallel to the long axis of the mouth.

Other species. – None. *Hippocystis batheri* Chauvel, 1941 is regarded as a junior synonym of *P. sculptus*.

Occurrence. – According to Prokop (1965, p. 303, 305) both specimens originated from the Nučice ore horizon in the Černín "Beds", at Chrustenice, near Prague. According to Gutiérrez-Marco *et al*. (2017) this correlates with the lower middle Berounian Regional Stage and thus the late Sandbian International Stage.

Prokopius sculptus **(Barrande, 1887)**
Figures 4, 5

1887 ?*Aristocystites sculptus* Barr., Barrande, p. 113, pl. 6, figs 28, 29.
1887 ?*Aristocystites subcylindricus* var. de *bohemicus* Barr., Barrande, p. 114, pl. 6, figs 26, 27.
1965 *Hippocystis sculptus* (Barrande). – Prokop, p. 303, pls 1, 2, text-fig. 1.
1990 *Hippocystis sculptus* (Barrande). – Parsley, p. 292.
1999 *Hippocystis sculptus* (Barrande). – Prokop & Petr, p. 64, tab. 1.

Lectotype. – NMP L13003, the original of Barrande, 1887, pl. 6, figs 26, 27.

Material. – Two examples, the lectotype and the original of Barrande, 1887, pl. 6, figs 28, 29 (NMP L13004).

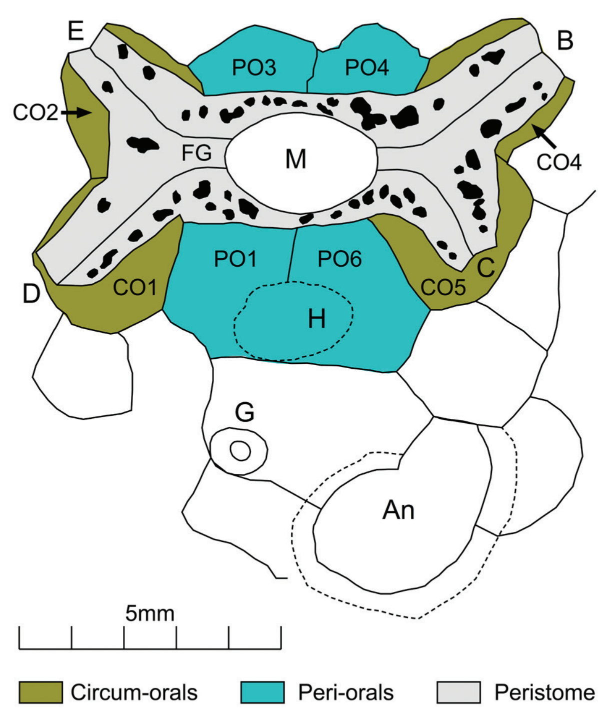

Figure 4. *Prokopius sculptus* (Barrande, 1887) Lectotype NMP L13003. Camera lucida drawing of plate arrangement around the mouth. Abbreviations: An – anus; B–E – ambulacra; CO1–CO5 – circum-oral plates; FG –food grooves; G – gonopore; H – hydropore; M – mouth; PO1–PO6 – peri-oral plates. Ambulacral pores black. One plate is missing from the upper right side of the anus.

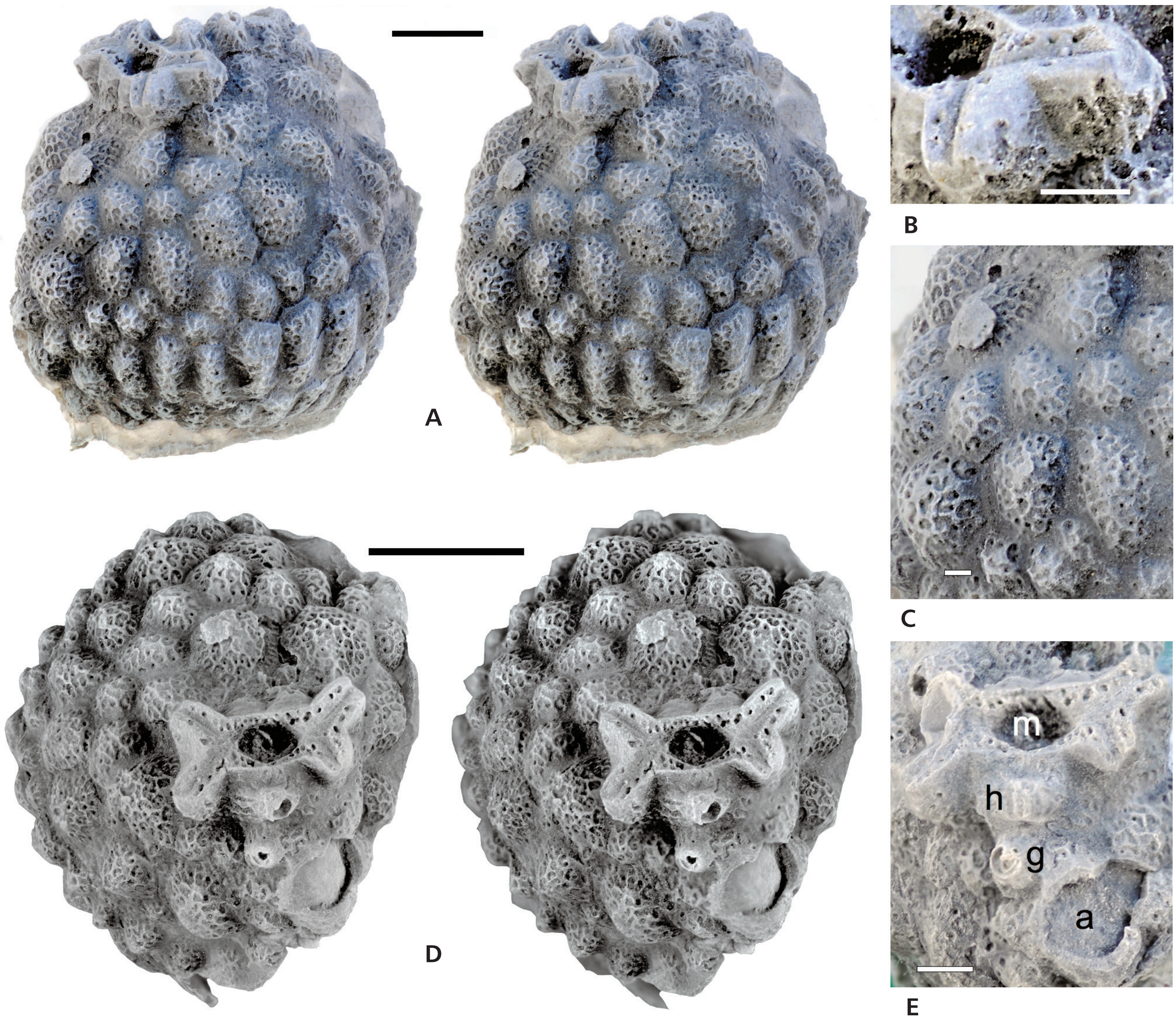

Figure 5. *Prokopius sculptus* (Barrande, 1887), lectotype NMP L13003. Photographs of latex casts. A – stereo photographs of oblique lateral view to show plate arrangement, tumid plates covered with diplopores and oral prominence; B – enlargement of ambulacra D and E to show facets perpendicular to food grooves; C – detail of several plates to show horseshoe-shaped diplopores; D – stereo photographs to show tumid plates, raised oral prominence and main thecal orifices; E – enlargement of area between mouth and anus to show main thecal orifices. Note plate missing from upper right side of anus. Abbreviations: a – anus; g – gonopore; h – hydropore; m – mouth. Latexes coated with white fingerprint powder. Scales bars = 5 mm (A, D); 2 mm (B); 1 mm (C, E).

Diagnosis. – As for the genus, which is monotypic.

Description. – Theca: more or less globular (Fig. 5A, D), composed of numerous strongly tumid plates with deep sutures and of two generations in the lectotype. Plates of the lectotype clearly arranged in circlets aborally (Fig. 5A), but more irregularly arranged approaching the oral prominence. At least 10 primary plates preserved in one incomplete circlet and 15 and 16 secondaries in adjacent circlets. These comprise approximately half the circumference of the theca, so about double the number in a complete theca. Theca at least 25 mm high in the lectotype, where the base is not seen and 60 mm maximum dimension in a second specimen.

Plates: strongly tumid with deep sutures and covered with irregular diplopores (Fig. 5A, C, D). Plates reach up to 5 mm in the lectotype and 7 mm in the second specimen. In the lower two preserved circlets of the lectotype the plates are distinctly elongate, primaries reaching 5 mm high by 2.5 mm across. All plates of the second specimen are more or less equant in plan view. No clear indication of circlets can be recognized nor is there any way to orientate the specimen except that at one end of the oval preserved part of the theca the plates are less well preserved. This may represent an attachment area.

Diplopores: developed over the entire surface of the plates when well preserved. Often irregular in shape, but also commonly horseshoe shaped (Fig. 5C). Perpendicular canals are 0.125 mm in diameter in both specimens and are separated by about 0.425–0.500 mm in the lectotype and by 0.550–0.625 mm in the second example, both measured centre to centre. The separation of the pores is not really significant and most peripores follow very irregular paths between the two perpendicular canals. Peripores are distinctly sunken into the plate surface, about 0.25 mm wide, but variable.

Mouth (M in Fig. 4, m in Fig. 5E): oval with the long axis more or less perpendicular to the oro-anal axis, 2.8 mm wide by 2.0 mm, and surrounded by a prominent raised peristome measuring 9.7 mm by 5.3 mm and with obvious oral pores (Figs 4, 5D). Four food grooves radiate from the lateral ends of the mouth and end in vertical ambulacral facets 1.1 mm wide by 1.1 mm high (Fig. 5B). Ambulacra are of unequal length, with D the longest (3.8 mm), then B (3.6 mm) and C (3.2 mm), and E (3.1 mm) the shortest (Figs 4, 5D). Mouth frame composed of eight plates (Fig. 4); four central peri-orals and four lateral circum-orals. The narrow food grooves are separate along their entire lengths and more or less central in the circum-oral plates (Fig. 4).

Hydropore (H in Fig. 4, h in Fig. 5E): in an oval tubercle, 2.0 by 1.5 mm, set across the PO1:PO6 suture line with the long axis parallel to the oro-anal axis. In the centre of the tubercle is a narrow, zigzag groove.

Gonopore (G in Fig. 4, g in Fig. 5E): a small circular pore, 0.4 mm in diameter set in a prominent tubercle that tapers from about 2 mm in diameter at the base to 1.1 mm at the top. Apparently with a distinct concave rim that may have supported a gonal pyramid, but if so the gonal plates are now all missing.

Periproct (An in Fig. 4, a in Fig. 5E): a relatively large, rounded pentagonal opening, now slightly distorted and 3.7 by 2.7 mm; provided with a narrow periproctal margin for the insertion of anal plates, none of which has been preserved. One periproct border plate to the NE is missing in L13003 (Figs 4, 5E).

Remarks. – Prokop (1965) restricted this species to the two specimens illustrated by Barrande on pl. 6, figs. 26, 27, which Barrande attributed to ?*A. subcylindricus*, and pl. 6, figs. 28, 29, which Barrande regarded as ?*A. sculptus*. As first reviser, Prokop chose the name *Hippocystis sculptus* for this species, but selected L13003 as type specimen because it shows the oral area. Barrande attributed other specimens to his species ?*A. subcylindricus* and illustrated several on plate 13. Thus, the original of plate 6, figs 26, 27 is not a monotype and as far as I am aware, Barrande did not specify types of his material. I think the type selected by Prokop for *H. sculptus* can only be a lectotype. The alternative of accepting Barrande's unique monotype for ?*A. sculptus* (L13004) involves accepting a type specimen that does not show the critical oral area.

Occurrence. – As for the genus *Prokopius*.

Taxonomic characters

Bather (1919a) thought that the horseshoe-shaped diplopores of *A. subcylindricus* were sufficiently significant to characterize a new genus, *Hippocystis*. This is potentially a useful character. Paul (1973) and Paul & Bockelie (1984) used the morphology of the diplopores in *Sphaeronites* to characterize subgenera, and the pore density to characterize species within the subgenera. Diplopores were almost certainly respiratory structures (Paul 1972). They consist of a pair of perpendicular canals that open into the thecal interior and were connected by a tangential canal externally. Body fluids flowed up one perpendicular canal, across the tangential canal where oxygen diffused into and carbon dioxide diffused out of the body fluids, and the oxygenated body fluids returned to the thecal interior down the second perpendicular canal. In many diplopores the tangential canal is an oval pit excavated in the external surface of the theca called a peripore and it was covered with soft tissue in life. In many aristocystitids, including *Aristocystites*, the peripores were covered with a calcified 'epistereom' (Parsley 1990).

Any adaptation that increased the residence time of the body fluids in the tangential canal would increase the total amount of exchange. Such adaptations include widening the peripore to increase both its cross-sectional and surface areas or taking an indirect route between the perpendicular canals which effectively lengthens the tangential canal. So, for example, a semicircular route between the perpendicular canals would increase the length by $\pi/2$ compared with a straight route between them. Sinuous, or horseshoe-shaped peripores may increase the length by even more. Thus, irregular peripores, including horseshoe shapes, are an effective way of increasing the amount of gas exchange without increasing the number of diplopores. They are widely distributed among different diploporites. The need to increase the amount of exchange was probably particularly acute in diploporites with calcified peripores, such as the aristocystitids. Gases would only diffuse through the soft tissue, not the calcite. Thus, a calcified peripore with 50% calcite would halve the rate of exchange compared with one entirely composed of soft tissue (Paul 1972, 1978). Hence, it seems likely that different aristocystitids might well have adopted the same solution to increasing their respiratory rate and evolved horseshoe-shaped peripores independently. Diplopores raised in tubercles are another way to increase the effective exchange surface and they appear to have evolved independently in *Lepidocalix*, *Sinocystis* and *Calix*.

Conclusions

The new generic name *Prokopius*, type species *Hippocystis sculptus* (Barrande, 1887) *sensu* Prokop (1965), is proposed to replace the genus *Hippocystis* Bather, 1919a, type species *Aristocystites subcylindricus* Barrande, 1887, by original designation. *Prokopius sculptus* is unique within the Aristocystitidae in having an oval, rather than elongate, mouth, four ambulacral grooves which terminate in vertical ambulacral facets, each of which supported a single appendage (? brachiole) and a zigzag hydropore parallel to the oro-anal line, all of which occur in a prominent, raised oral frame. The new name becomes necessary because a specimen of *Aristocystites subcylindricus* with the oral area preserved shows that this species has only two ambulacral facets, a character unique to the genus *Aristocystites* Barrande, type species *Aristocystites bohemicus* Barrande, 1887. Thus, the type species of *Hippocystis* Bather, 1919a, can be shown to be a species of *Aristocystites* and hence *Hippocystis* becomes a junior synonym of *Aristocystites* Barrande, 1887. The family Aristocystitidae includes directly attached diploporites with an elongate mouth surrounded by eight plates, four central, inter-radial, peri-oral plates and four, more distal, radial, circum-oral plates; a hydropore across the PO6:PO1 suture, plus a gonopore below the oral frame plates and to the left of the periproct. Genera within the family can be distinguished on the details of the plating around the mouth and the number and arrangement of ambulacra. There are, however, too many possible aristocystitid genera in which the oral surface is unknown to define subfamilies reliably at present.

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