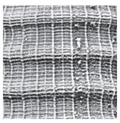
Early ontogeny and distribution of the orthocerid cephalopod *Calorthoceras* Chen, 1981 – taxonomic and palaeoecological implications

Štěpán Manda & Vojtěch Turek



Calorthoceras Chen, 1981 (?Middle Ordovician, Llandovery, to Middle Devonian) is an orthocerid with a straight, annulated shell and a reticulate sculpture. Three slightly curved, endogastric apical parts of shells of *C. butovitzense* Chen, 1981 from the Silurian of Bohemia are described. The most apical part of the shell is blunt and smooth, bordered by a relief fold. The adjacent conical part of the shell shows an accretion structure and is straight or curved. The following part of the shell is straight and slowly expanding. A change in sculpture and shell shape indicating the embryonic conch occurs at shell heights of 1.3–1.6 mm and shell lengths of 4.4–4.7 mm. The first annulus appears at a shell height of 1.6–2.5 mm and a shell length of 5.5–13.5 mm. The dimensions of the embryonic shell indicate a maximum egg size of about 10 mm. The morphology of the juvenile shell agrees with a pelagic habit. *Calorthoceras* is reclassified into the family Dawsonoceratidae Flower, 1962. The morphology of the early ontogenetic stages of the shell demonstrates the affinities of *Calorthoceras* to the Early Devonian *Cyrtoceras pugio* Barrande, 1866 and *Suloceras pulchrum* (Barrande, 1968). The shell of these cephalopods shows morphological convergence with *Spyroceras* Hyatt, 1884 in which the juvenile stages were probably demersal. The distribution of the Silurian *Calorthoceras* is discussed, particularly in the Prague Basin where it represents one of the immigrants from the Baltic–Avalonian area. *Merocycloceras declive* Ristedt, 1968 and *Dawsonoceras multiliratum* Foerste, 1928 are described for the first time from the Silurian of the Prague Basin. • Key words: Cephalopoda, Orthocerida, embryonic shell, palaeoecology, Silurian, Devonian.

Manda, Š. & Turek, V. 2024. Early ontogeny and distribution of the orthocerid cephalopod *Calorthoceras* Chen, 1981 – taxonomic and palaeoecological implications. *Bulletin of Geosciences 99*(*4*), 323–342 (10 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received March 7, 2024; accepted in revised form December 4, 2024; published online December 31, 2024; issued December 31, 2024.

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Orthocerid cephalopods are an important part of the Early Palaeozoic marine faunas. Their adult forms may have been pelagic and demersal, with a relatively simple shell morphology providing only a limited number of morphological characters useful for classification. By contrast, the early ontogenetic development of the shell is important for classification, allowing the orders of Orthocerida and Pseudorthocerida to be separated (*e.g.* Flower 1939, Kröger & Isakar 2006, Kröger & Mapes 2007, King & Evans 2019, Pohle *et al.* 2022). Although several juvenile orthocerids have been described, few have been identified with species established on adult shells limiting their application in classification and phylogenetic concepts. Intraspecific variability in early shell development is equally poorly known (Schindewolf 1933; Ristedt 1968, 1971; Blind 1988; Kröger 2006).

Orthoceras pseudocalamiteum Barrande, 1851 *in* Quenstedt (1951) was one of the first cephalopods described from the Early Palaeozoic of Bohemia, and was successively placed in the genera *Dawsonoceras* Hyatt, 1884, *Spyroceras* Hyatt, 1884 and *Anaspyroceras* Shimizu & Obata, 1935. Finally, *Orthoceras pseudocalamiteum* was established as the type species of the genus *Calorthoceras* Chen, 1981. The holotype of the species comes from the Early Devonian (Pragian). Later, Barrande (1868) described the species from the late Silurian as well as strata between the Pragian and the Givetian (Middle Devonian) (étages E, F, G). This was one of the few species described by Barrande with such a long stratigraphic range (Barrande 1870). The Silurian specimens were later selected as the types of the new species *Calorthoceras illineatum*, *C. multicostatum* and *C. butovitzense* Chen, 1981 *in* Chen *et al.* (1981) (Fig. 1). Some of these species were also recognized in Baltica and China (*e.g.* Chen *et al.* 1981, Kiselev *et al.* 1990).

Due to its distinct shell sculpture (Barrande 1868, Ristedt 1968), *Calorthoceras butovitzense* Chen, 1981 is one of the few Silurian orthocerids in which the embryonic stage can be connected to the adult stage. The aim of this paper is to describe the early shell morphology of *Calorthoceras* and discuss the implications of these findings for the classification and phylogeny of the annulated orthocerids. The distribution of the genus *Calorthoceras* in the Silurian of the Prague Basin is also examined.

Material

The studied *Calorthoceras* specimens originate from the Kopanina Formation, the fourth recognized formation of the marine Silurian strata of Central Bohemia, Czech Republic (Palaeozoic of the Barrandian Area, Prague Basin, Prague Synform). For an overview of the Kopanina Formation, see Kříž (1992, 1998) and Manda & Kříž (2006). Graptolite biozone chart is used as defined by Štorch (2023).

The studied specimens are deposited in the Palaeontological collection of the National Museum, Prague, Museum of Natural History (prefix NM L), in the collection of the Geological Survey, Prague (prefix CGS SM, MŠ) and in the Shary collection in the Museum of Comparative Zoology, Harvard (prefix MCZ).

Results

Early shell of *Calorthoceras butovitzense*

Specimen NM L 10963. – The specimen from the locality Praha-Butovice (Butovitz e1, Barrande 1868, pl. 286, figs 14–16; Fig. 2A, C, D herein; for locality description see Kříž 1992) is a very slightly curved, endogastric shell with a maximum length of 31.8 mm and a diameter of 2.5 mm; the left lateral side is exposed in the mudstone. The apicalmost part of the apex is smooth and irregularly convex (length *c*. 0.5 mm). It is terminated by an oblique and straight, dorsally inclined (9.5°) relief fold (at a shell diameter 0.7 mm).

The early part of the shell is conical with a steeper dorsal side; the angle of expansion is 9°. A slight constriction of the shell is developed just behind the relief fold on the dorsal side. Six fine longitudinal lirae are visible on the dorsal and lateral sides just at the relief fold, three additional lirae appear later on the ventral side. Straight and oblique growth lines adorally inclined to the dorsal side are noticeable just after the appearance of the longitudinal lirae; their inclination decreases with the growth of the shell. A total of 12 growth lines are present in this part of the shell, the first two of which disappear towards the ventral side.

The angle of the shell expansion (point 1) suddenly decreases at a shell diameter of 1 mm (shell length 1.9 mm) and there are three closely spaced growth lines in a narrow portion of the shell. The following portion of the shell is straight and the angle of expansion decreases. The reticulate sculpture consists of equally developed longitudinal lirae and oblique, straight, dorsally inclined growth lines. The distance separating the longitudinal lirae is greater than that of the growth lines – there are 21 growth lines and 8 longitudinal lirae in this part of the shell.

At 1.3 mm shell diameter (shell length 4.6 mm; point 2), the shell expansion rate suddenly decreases while the shell height abruptly increases dorsally. The change in the shell shape coincides with a change in the sculpture: two additional densely spaced growth lines and intercalation of new longitudinal lirae dorsally appear between the prominent lirae. The following portion of the shell up to the appearance of the annuli is straight with a regular reticular sculpture. The growth lines are usually slightly denser than the longitudinal lirae. One or two less pronounced growth lines are locally noticeable between the regular growth lines. Nine longitudinal lirae and 52 growth lines were found in this part of the shell.

At a shell diameter of 1.6 mm (shell length 13.3 mm), the shell is constricted, and the first annuli appear. In total, there are 19 annuli (in the shell length 18.5) and their spacing gradually increases adorally. The distance between the annuli is greater than their width. The sculpture remains reticulate, but the longitudinal lirae are more pronounced than the growth lines. The growth lines are irregularly spaced, their spacing decreases at the top of the annuli. The distance between adjacent growth lines is greatest on the apical side of the annuli. On the last three annuli, they are hardly discernible.

Specimen MCZ 11076. – The specimen (Fig. 2B, E herein) described by Ristedt (1968) comes from the same locality and stratigraphic level as the specimen described above, *i.e.* Praha-Butovice, Na Břekvici, *N. nilssoni* Zone. Note that the inventory number MCZ 10148 and the locality Malá Chuchle given by Ristedt (1968) are incorrect. The specimen partially embedded in the rock shows the right lateral side. The shell is very slightly curved with a maximum length of 20.7 mm and a height of 1.7 mm; the apical part is broken off. The apicalmost part of the apex is blunt and smooth, terminated by a relief fold. The apical part of the shell is conical (angle of expansion is 18.5°), the dorsal side is steeper than the ventral side. Longitudinal lirae appearing close to the relief fold are indistinct.

At a shell diameter of 1.1 mm (shell length 1.5 mm), the shell expansion decreases, and growth lines appear.

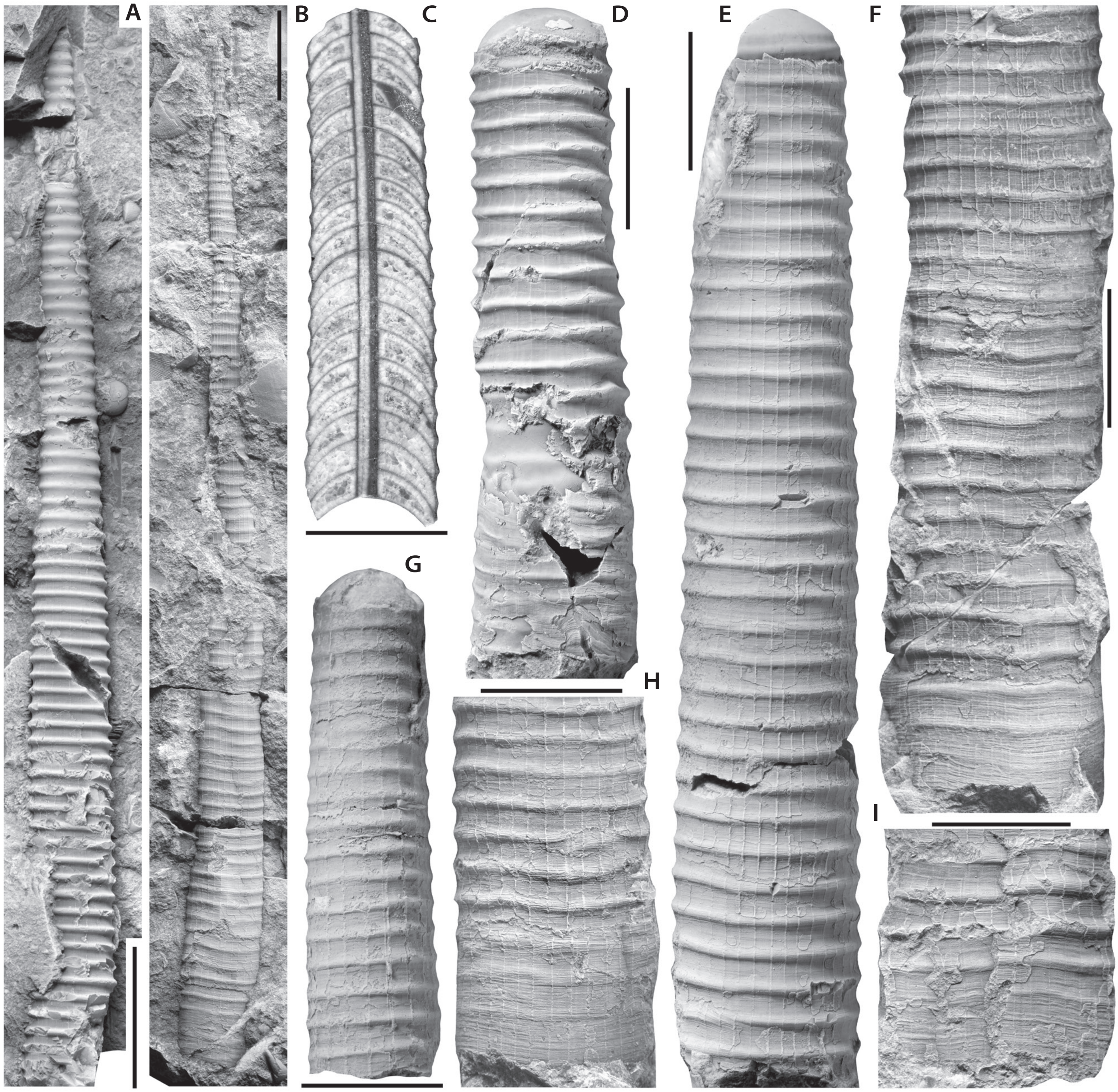

Figure 1. *Calorthoceras butovitzense* Chen, 1981, Ludlow Series, Kopanina Formation, Bohemia, Prague Basin. A – holotype, lateral view, NM L 10916 (Barrande 1868, pl. 278, fig. 33), Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. B – an almost complete flattened shell with juvenile stage and adult modification, SM 434, Praha-Řeporyje, Mušlovka quarry, bed no. 0, Ludfordian Stage, lowermost *S. leintwardinensis* Zone. C, G – median section and lateral view, specimen NM L 15373 (Barrande 1868, pl. 278, figs 24, 25), a type of *C. illineatum* Chen, 1981, Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. D – dorsal view, NM L 10960 (Barrande 1868, pl. 286, figs 11–13), a type of *C. multicostatum* Chen, 1981, Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. E – lateral view, NM L 10915 (Barrande 1868, pl. 278, figs 29, 30), a type of *C. multicostatum* Chen, 1981, Praha-Zadní Kopanina, Ludfordian Stage, *S. leintwardinensis* Zone. F – a flattened specimen with mature modification, lateral view, SM 436, Praha-Řeporyje, Mušlovka quarry, bed no. 0, Ludfordian Stage, lowermost *S. leintwardinensis* Zone. H – a flattened shell with mature modification, lateral view, SM 435, Praha-Řeporyje, Mušlovka quarry, bed no. 0, Ludfordian Stage, lowermost *S. leintwardinensis* Zone. I – a flattened shell with mature modification, lateral view, SM 437, Praha-Řeporyje, Mušlovka quarry, bed no. 0, Ludfordian Stage, lowermost S. *leintwardinensis* Zone. Scale bar: 10 mm.

Longitudinal lirae become visible around the whole shell circumference (point 1). The next part of the shell is conical with an angle of expansion of 10°, the dorsal side remaining steeper. The growth lines are oblique, inclined towards the dorsum and slightly curved adaperturally in the middle of the lateral side; the curvature becomes progressively flatter adaperturally. Longitudinal lirae gradually thicken. The distance between adjacent growth

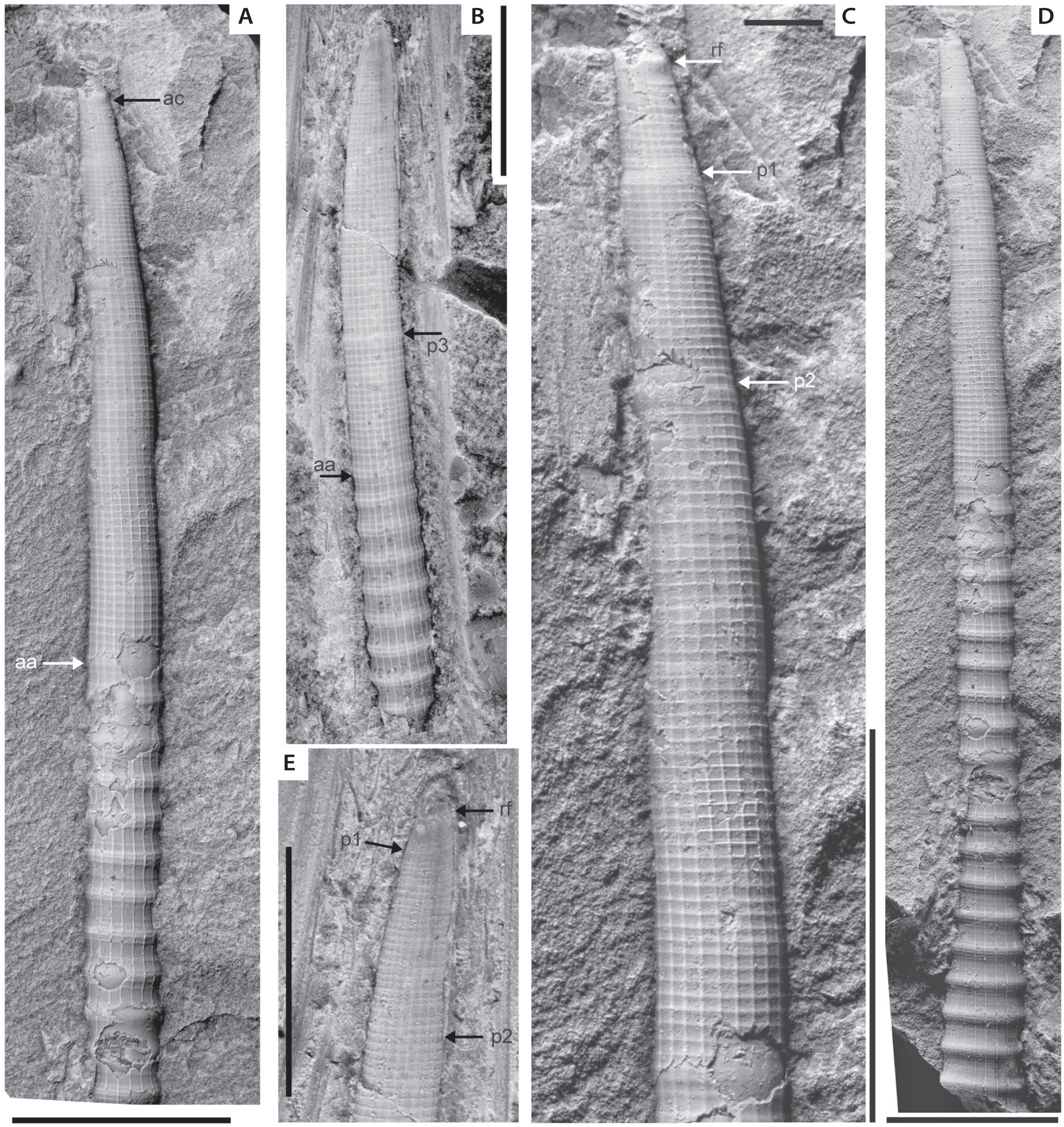

Figure 2. Specimens with preserved embryonic shell of *Calorthoceras butovitzense* Chen, 1981, Ludlow Series, Kopanina Formation, Bohemia, Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. A, C, D – holotype, lateral view, NM L 10963 (Barrande 1868, pl. 286, figs 13–15), p1 and p2 mean point 1 and point 2, see description, point 2 corresponds to hatching. B, E – lateral view, MCZ 11076 (Ristedt 1968: pl. 1, fig. 13), p1–3 refer to the point given in the description, point 2 corresponds with hatching**.** Abbreviations: aa – annulation appearance; ac – apical constriction; rf – relief fold. Scale bar: 5 mm.

lines is slightly less than the distance between longitudinal lirae. There are 27 growth lines present in this shell part.

At a shell diameter of 1.5 mm (shell length 4.7 mm), the angle of expansion decreases and the growth lines become straight (point 2). A reticular sculpture is present as the growth lines cross the longitudinal lirae at fairly equal intervals. Twenty growth lines and 11 longitudinal lirae are recorded in this portion of the shell.

At a shell diameter of 1.7 mm (point 3, shell length 9.2 mm), there are three densely spaced growth lines and the shell expands abruptly on the dorsal side. The next part of the shell is again straight with a reticulate sculpture, but

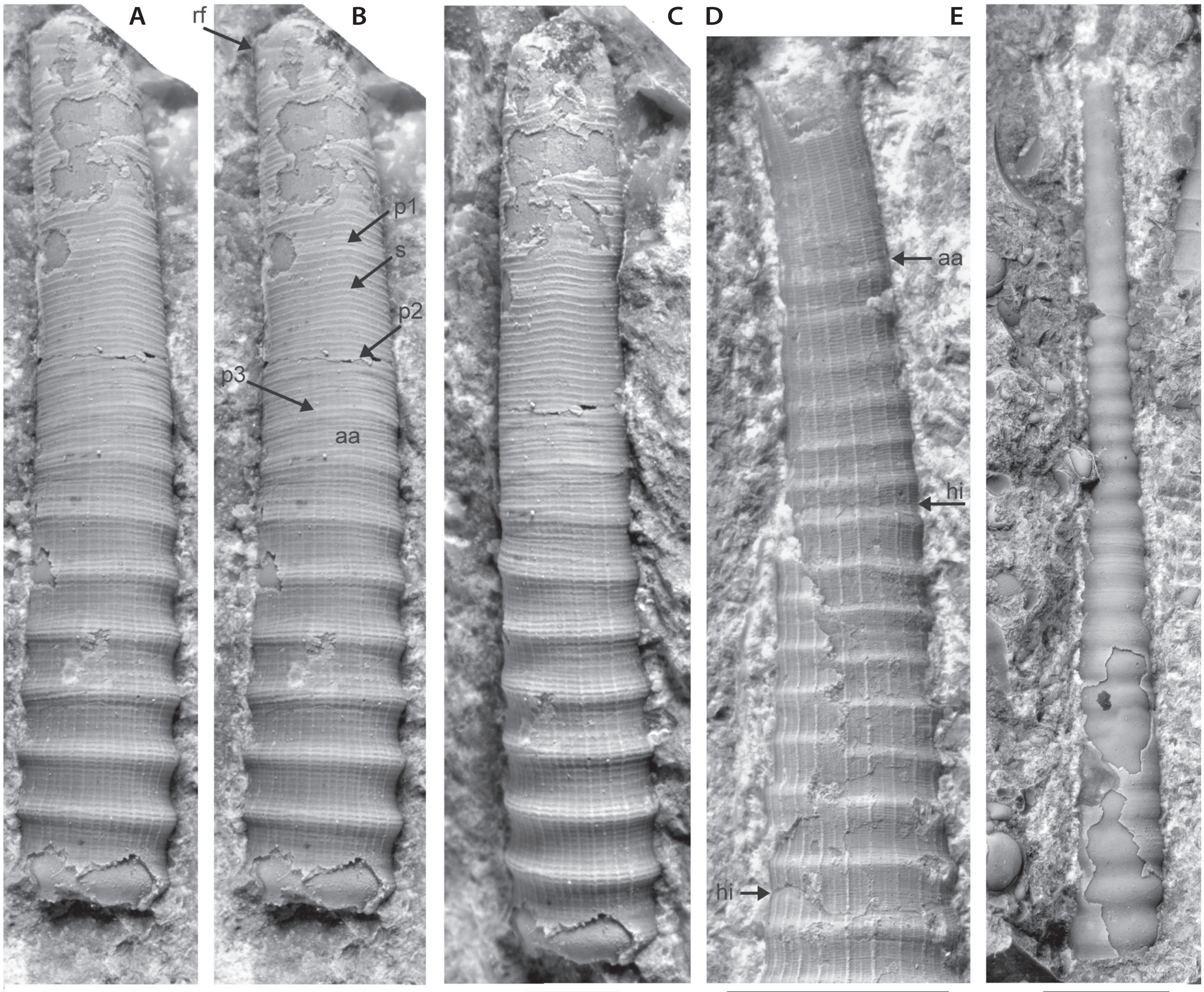

Figure 3. A–C – A juvenile shell of *Calorthoceras butovitzense* Chen, 1981, dorsolateral (A, B) and dorsal view, NM L 63649, Ludlow Series, Kopanina Formation, Bohemia, Praha-Řeporyje, road-cut section, Gorstian Stage, *L. progenitor* Zone; p1–3 refer to the point giving in the description, point 2 corresponds with hatching. D – detail of the adapical part of *Calorthoceras butovitzense* Chen, 1981, lateral view, NM L 15485 (see explanation of Fig. 4A). • E – *Orthoceras lynx* Barrande, 1868, holotype by monotypy, lateral view, NM L 10963 (Barrande 1868, pl. 336, figs 21–26), Lochkov locality, Ludlow Series, Ludfordian Stage, Kopanina Formation, for detail see Fig. 5A. Abbreviations: aa – annulation appearance; hi – healed injury; rf – relief fold; s – dorsolateral sinus in the growth lines. Scale bars: A–C (1 mm), B (5 mm), C (3 mm).

the sculpture is not as regular as prior to point 3. Twenty growth lines are visible in this portion of the shell, the number of visible longitudinal lirae is the same as in the preceding shell portion.

At a shell height of 1.8 mm (shell length 13.5 mm), the first annulus is indicated by a slight decrease in the shell diameter. At this point, 11 longitudinal lirae are visible on the shell surface. A total of eight annuli are developed on the shell. They are regular in shape and annuli are narrower than interspaces between them. Three growth lines are visible on the elevated part of the annuli and there are one or two less distinct growth lines between the raised parts of two adjacent annuli.

Specimen NM L 15485. – The specimen (Řeporyje-cesta Section, bed no. 13, Ludlow Series, Gorstian Stage, *L. progenitor* Zone, Kopanina Formation, Manda & Turek 2019; Fig. 3A–C herein) is a complete and slightly curved juvenile shell with a maximum height of 1.8 mm and a length of 10.6 mm. Left lateral side is embedded in the rock. The apex is hemispherical, without constriction. The ventral side is nearly straight, the shell expands dorsally. The angle of expansion gradually decreases from 11° to 4°. The apicalmost part of the apex is blunt, slightly convex and smooth, inclined towards the dorsal side. The margin of the apicalmost part of the apex is marked by a relief fold and a faint groove moderately inclined towards the dorsum (SH = 1.1 mm). Well-developed growth lines appear at a shell height of 1.2 mm, *i.e.* at a distance of 0.7 mm from the apex. A total of 38 growth lines are present up to the point of change in sculpture (point 2). The distance between growth lines is irregular; the distance between the fourth and fifth line (counted from the apex) is unusually high (0.2 mm). The growth lines are convex towards the apex, the maximum depth of the flexure is localized dorsolaterally. The depth of the flexure gradually decreases with the growth of the shell. Twenty growth lines were detected before point 1.

At a shell width of 1.5 mm (shell length 3.1 mm), the relatively regular sculpture is disrupted by the insertion of a less pronounced growth line (point 1). Beyond this point, fine longitudinal lirae appear on the dorsal side. There are approximately 14 growth lines in the shell portion between points 1 and 2.

At a shell height of 1.6 mm (shell length 4 mm), the sculpture changes abruptly (point 2). The growth lines become more densely spaced, irregular and straight, the longitudinal lirae are more elaborate and present around the entire circumference of the shell.

At a shell height of 1.6 mm (shell length 4.4 mm; point 3), two more elaborate growth lines appear. The shell is slightly constricted dorsally (initial annulus). The first transverse annulus appears at a shell height of 1.6 mm (shell length of about 5.5 mm). There is a total of eight, regularly spaced annuli. The annuli are narrower than the interspaces between them. The sculpture is reticulate, the growth lines and the longitudinal lirae are equally elaborate. The distance between the growth lines varies; they are denser at the tops of the annuli. In the interspace between the annuli, the course of the growth lines is slightly irregular; the lines sometimes converge or diverge or are slightly bent. Sixteen longitudinal lirae are visible on the first annulus and 19 at the aperture owing to the gradual intercalation of new longitudinal lirae. The aperture is straight. A very thin shell wall is visible on the internal mould at the aperture.

Specimen NM L 15485. – Barrande (1868) assigned the specimen NM L 15485 from the locality Beroun, Dlouhá hora hill (Dlauha hora, figured by Barrande 1868, pl. 260, fig. 25; Figs 3D, 4A herein) to the species *Orthoceras electum*. The specimen, however, exhibits a sculpture characteristic of *Calorthoceras butovitzense*. The trilobite *Eophacops bulliceps*, preserved on a slab of light-coloured skeletal limestone along with specimen NM L 15485, indicates the upper *leintwardinensis* Biozone of the lowermost Ludfordian Stage (Vokáč *et al.* 2019). The specimen NM L 15485 is a 40.8 mm long fragment of the slightly curved apical part of the shell. It has a maximum height of 6.3 mm; only the left lateral side is exposed on the slab.

The apical-most part of the shell is missing, having broken off, and its minimum diameter is 2.3 mm. In the first four millimetres, the shell is straight and very slowly expanding. The sculpture consists of longitudinal lirae (of which nine are visible) and densely packed transverse growth lines, that are slightly irregular in spacing. At the intersections of the growth and longitudinal lirae, the growth lines are deflected apically forming a shallow V-shape.

The first annulus appears at a shell diameter of 2.5 mm. The angle of expansion increases (5°). The distance between regular annuli varies slightly but generally increases. The annuli are straight or very slightly curved. Behind the first annulus, fine lirae are inserted between the more prominent longitudinal ones, these lirae rapidly conform to others as the shell growth. The number of longitudinal lirae gradually increases from 9 to 27. The first five annuli are less pronounced than those that follow. The sculpture remains reticulate, the course of the growth lines becomes more irregular. The adapical deflection of the growth lines at the intersection with the longitudinal lirae disappears. The longitudinal lirae gradually thicken into longitudinal ridges.

At a shell height of 3.1 mm, there is a transversely healed shell injury across the shell. A second combined shell injury is located ventrally at a shell height of 4.35 mm. It consists of a ventral U-shaped damage of the shell followed by a break in the sculpture parallel to the growth lines.

Discussion

Embryonic and juvenile shell

The apical part of the shell of *Calorthoceras* is slightly curved and endogastric. The shape of the apical shell is variable. Each studied specimen has its own specific characters. The apicalmost part of the shell apex is blunt and smooth, bordered by a relief fold. The following part of the shell shows an accretion structure and is curved or conical in shape. Thus, minor changes in the shape of the shell should better not be considered a species-specific character. The following part of the shell is straight and slowly expanding.

Although there are several changes in the sculpture and shape in the apical part of the shell, neither a shell constriction (*e.g.* Ristedt 1968) indicating hatching, nor any uniform morphological feature that could be used to determine the hatching phase was found. Considering the coincidence of certain changes in shell morphology and their presence in the studied specimens, we suppose that the onset of the post-hatching phase is manifested by changes in shell sculpture, shape and expansion rate. These

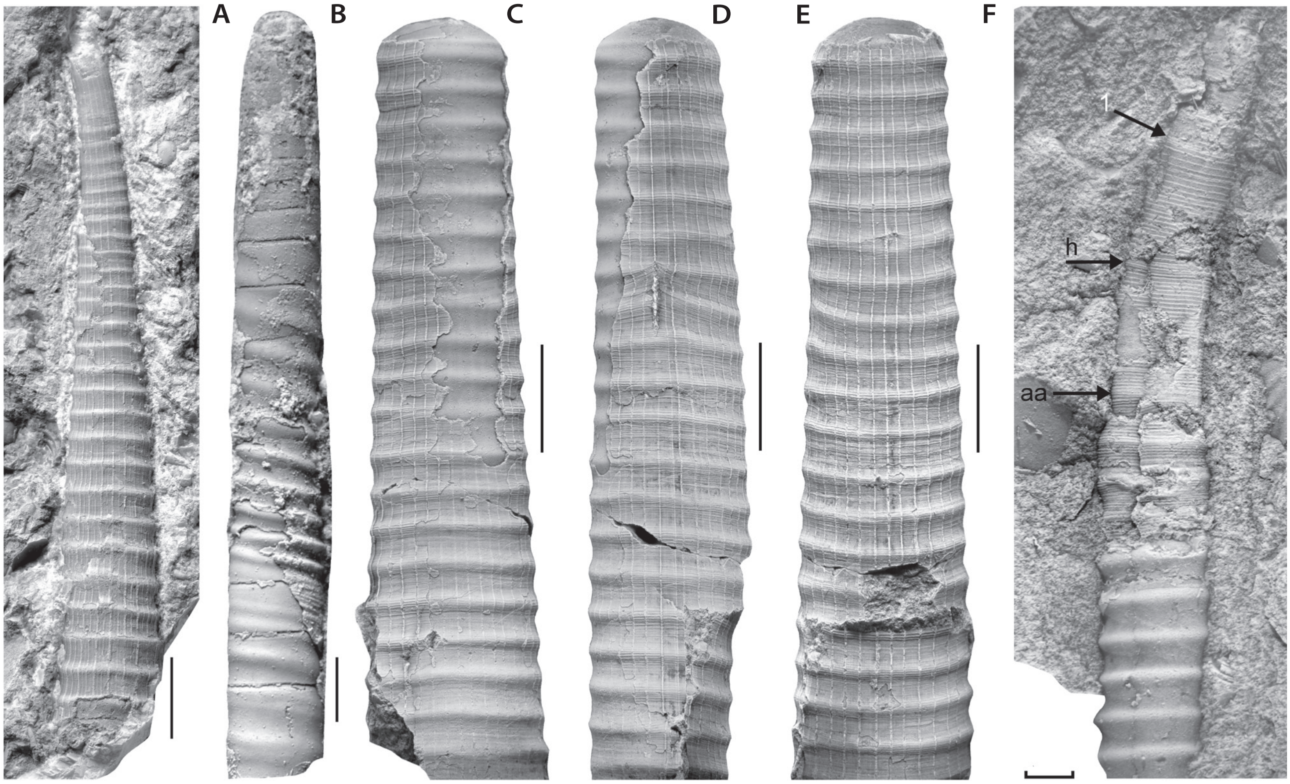

Figure 4. A, C–E – *Calorthoceras butovitzense* Chen, 1981. A– lateral view, NM L 15485 (figured as *Orthoceras electum* by Barrande 1868, pl. 260, fig. 25), for detail see Fig. 3D, Kopanina Formation, Bohemia, locality Dlouhá hora, Ludfordian Stage, *leintwardinensis* Zone. C–E – body chamber of sub-adult specimen showing a shallow hyponomic sinus and a shell repair, ventral, lateral and dorsal view, the body chamber is not figured completely, the actual length is 40 mm, SM439, Kopanina Formation, Bohemia, Praha-Řeporyje, Mušlovka quarry, bed no. 0, Ludfordian Stage, lowermost *S. leintwardinensis* Zone. • B – *Merocycloceras declive* Ristedt, 1968, lateral view, SM 438, Kopanina Formation, Bohemia, Praha-Butovice, Na Břekvici, Ludlow Series, Gorstian Stage, *N. nilssoni* Zone; this is the first record of the species in the Prague Basin, the species was described from the early and middle Ludlow of Sardinia and Carnic Alps (see Gnoli 2003). • F – *Dawsonocerina caelebs* (Barrande, 1868), lateral view, NM L 42964, Kopanina Formation, Bohemia, SW part of Prague, ?Praha-Lochkov, lowermost Přídolí Series. Abbreviations: aa – annulation appearance; h – hatching indication; 1 – a narrow shell portion with densely spaced growth lines in mid embryonic shell. Scale bars: A, C–E (5 mm), B, F (1 mm).

changes occur at a shell height of 1.3–1.6 mm and a shell length of 4.4–4.7 mm (Figs 2, 3). If the determination of the hatching stage based on these criteria is correct in the specimens studied, the shell height and length of the hatchlings varied between 0.3 mm and 0.25 mm (about 10% of hatchling size).

The dimensions of the embryonic shell indicate an egg size that, when compared to modern coleoids, falls in a field occupied by both pelagic and demersal cephalopods (see De Baets *et al.* 2012). Compared to other members of the Orthocerida, the embryonic shell in *Calorthoceras* would be amongst the largest in that order. The morphology of the slowly expanding, conical juvenile shell is more consistent with a pelagic habit; even the juvenile shell could easily have been transported by currents.

The aperture of the embryonic shell was oblique with a shallow sinus on the ventral side, which likely indicates the position of the hyponome. A prominent dorsolateral sinus may represent the ocular sinus (Fig. 3B). The sinus gradually disappears in the late embryonic stage, perhaps as a result the head complex protruding from the aperture.

The development of annuli is preceded by a portion of the shell with irregular sculpture. The annuli appear on the shell immediately after hatching (similar to lechritrochocerids, Turek 2010, Manda & Turek 2019) or with a considerable delay. In a distance of 5 mm after the appearance of the annuli, six or seven annuli are developed. The number of growth lines per unit length of the shell is similar or lower in the annulated stage to that of the preceding non-annulated stage. The first annulus appears at a point where the shell height decreases or, alternatively (specimen NM L 63649), at the hatching point where the shell height increases (Fig. 3A–C). The shell height at the point of the first annulus varies between 1.6–2.5 mm and at shell lengths of 5.5–13.5 mm (Figs 2, 3). The difference in the timing of the annulation onset may be under environmental control. In the Pragian species *Suloceras pulchrum* (Barrande, 1868), which is probably closely related to *Calorthoceras*, annulations are well developed in individuals from reef limestones, but poorly developed or absent in specimens from deeper mudstone facies (Manda & Turek 2011). The specimen of *C. butovitzense* (Fig. 3A–C) with the ontogenetically earliest appearance of annuli comes from a shallow-water environment with corals. Two specimens of *Calorthoceras* from Butovice show only slightly different timing of annulation, although one specimen comes from a cephalopod limestone and the other from a mudstone with associated graptolites and juvenile molluscs.

The internal structures of the embryonic and early juvenile shells of *Calorthoceras* are unknown, the septa of the early juvenile shells are very slightly convex, and the convexity of the septum increases during ontogeny. The siphuncle in ontogenetically earliest specimens is slightly subcentral; the ratio between the shell height and siphuncle diameter is about seven (Fig. 10F, G).

Taxonomic implications

Species presently classified under the genus *Calorthoceras* were previously placed in *Anaspyroceras* Shimizu & Obata, 1935*, Metaspyroceras* Foerste, 1932 or *Spyroceras* Hyatt, 1884 (Babin 1966, Ristedt 1968, Kiselev 1984). Kröger & Isakar (2006) argued for the validity of *Calorthoceras* and assigned it to the family Orthoceratidae McCoy, 1844. The Silurian representatives of the family Orthoceratidae, exhibit, however, a straight, spherical apex. Annuli are developed in some Silurian orthoceratids, but the timing of their appearance/disappearance during ontogeny differs between individual taxa. In *Kopaninoceras fluminese* (Meneghini, 1857), annulation appears in later ontogenetic stages (Barrande 1868, Manda *et al.* 2023). In *Orthocycloceras*? *lynx* (Barrande, 1868), relatively low and wide annulations appear in the juvenile stage, but the species is known only from the holotype (Figs 3E, 5A). Well-developed annuli are restricted to the late embryonic/early juvenile stage in *Merocycloceras declive* Ristedt, 1968 (Fig. 4B); this is also confirmed by a change in septal spacing only slightly preceding annulation in the specimen figured here. The annuli of Orthoceratidae are usually lower and wider than those of *Calorthoceras.* Where the shells of orthoceratids are weakly curved, they are rather exogastric than endogastric as in *Calorthoceras*. The exogastric character of the shell is evidenced by the presence of the hyponomic sinus on the convex side of the shell as in, *e.g.* the Ordovician *Ctenoceras schmidti* Noetling, 1884 (Sweet 1964) and the Silurian *Kopaninoceras cavum* (Barrande 1877) as well as *Kentronites transiens* (Barrande, 1866).

The early embryonic shell of *Calorthoceras* is conical or slightly curved with a blunt apex. The curved apex corresponds in size and shape to the apex of *Dawsonoceras* Hyatt, 1884 or *Dawsonocerina* Horný, 1955 (Kröger & Isakar 2006). The post-juvenile shell of these genera is straight but may also be slightly curved and endogastric. In *Calorthoceras*, however, the longitudinal lirae appear already in the embryonic stage. The formation of growth lines in a specimen with suppressed longitudinal lirae in the embryonic shell corresponds to that in the early stage of *Dawsonocerina* (Barrande 1868, 1877). The embryonic shell of *Dawsonocerina caelebs* (Barrande, 1868) exhibits shortening of the growth line spacing in embryonic shell mid-length; hatching is manifested by a change in the shell curvature and sculpture and the early appearance of annuli (Fig. 4F). The siphuncle of *Calorthoceras* is thin with tubular connecting rings and simple, short, orthochoanitic septal necks (Fig. 1C, Fig. 10), similar to those of *Dawsonocerina* (Horný 1955). The septal neck of *Calorthoceras butovitzense* may also be nearly loxochoanitic and extending beyond the connecting rings into the siphuncle (Fig. 10E), a character that also appears in *Dawsonoceras* and *Dawsonocerina* (Horný 1955).

Dawsonoceras includes over twenty species from the Late Ordovician and Silurian strata of Laurentia, Avalonia, Baltica, Argentina and Bohemia (Flower 1962, Kröger & Isakar 2006, Cichowolski 2008, Kröger *et al.* 2011, Kröger 2013). The type species, *Dawsonoceras annulatum* (Sowerby, 1816), has an evenly annulated shell with wavy growth lines passing in later growth stages into frills; longitudinal lirae are sometimes weakly indicated (Fig. 5K). However, similar longitudinal structures are developed as fabricational noise between the protruding growth lines in oncocerids (Stridsberg 1988a, Manda & Turek 2009). It is uncertain whether *D. annulatum* shows reduced longitudinal lirae or whether they evolved from an ancestor without longitudinal lirae. Several species of the genus *Dawsonoceras* have well-developed longitudinal lirae and for these species, the genus *Cedarvilloceras* Shimizu & Obata, 1935 was proposed. Unlike *Calorthoceras*, the longitudinal lirae are usually less distinct at the apical part of the annuli in *Dawsonoceras* (Foerste 1928). The shell of *Dawsonoceras multiliratum* Foerste, 1928 (pl. 60) from late Llandovery–early Wenlock of Wisconsin, Illinois and mid-Llandovery of the Prague Basin (Fig. 6) has sparse, narrow annuli and a sculpture reminiscent of *Calorthoceras*. The shell of *Calorthoceras* is considerably smaller (maximum height *c.* 20 mm) than the shell of *Dawsonoceras* (maximum height *c.* 50 mm) and the body chamber of *Calorthoceras* is proportionally longer. *Calorthoceras* and *Dawsonoceras* are probably closely related.

The early ontogenetic appearance of annulation is a diagnostic character of the Dawsonoceratidae. In *Dawsonoceras*, the annuli and interspaces between them are regular, sinusoidal in cross section, whereas the annulation of *Calorthoceras* differs in that the annuli are

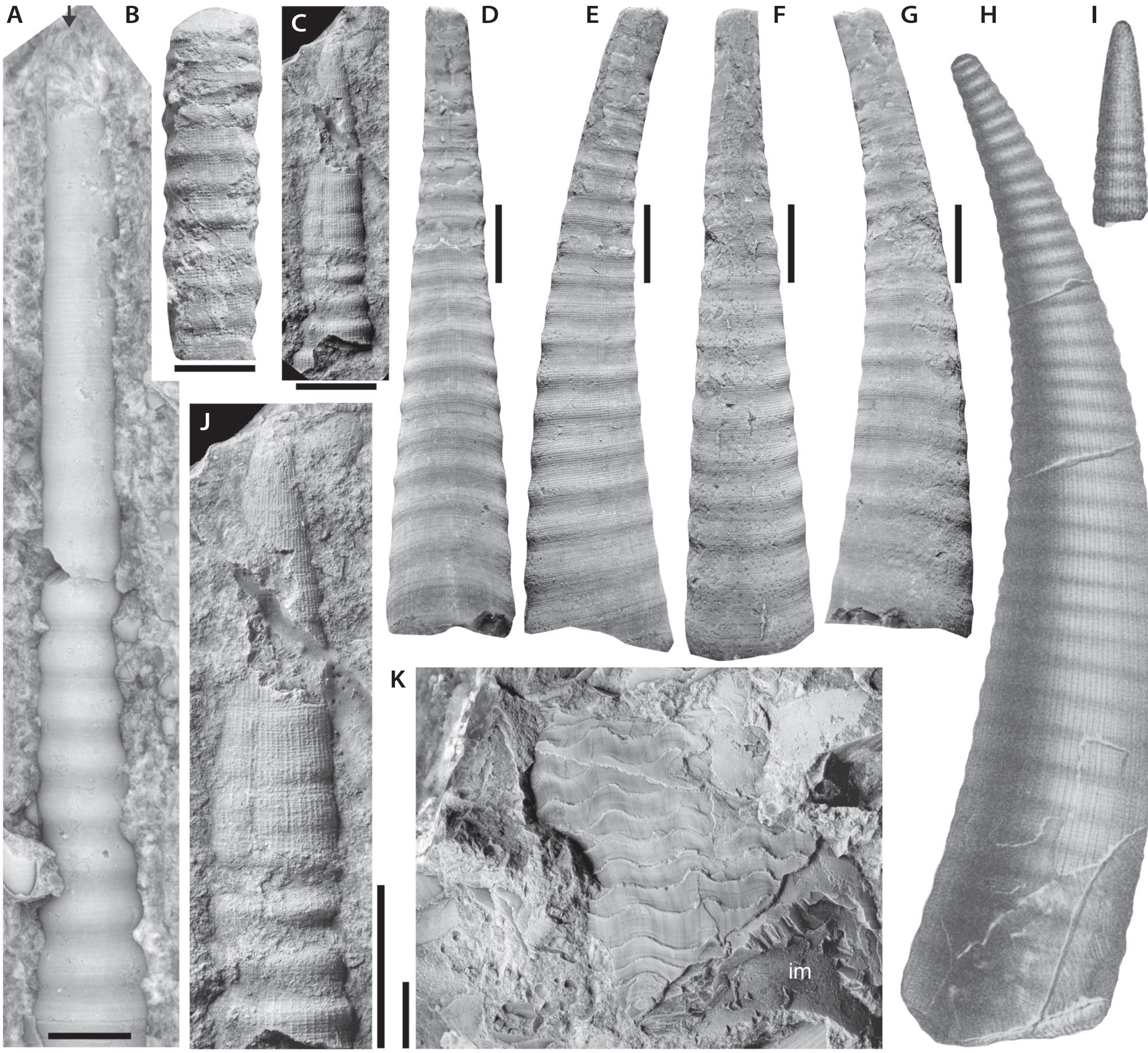

Figure 5. A – detail of apex of *Orthocycloceras*? *lynx* (Barrande, 1868), lateral view, NM L 10963 (see explanation of Fig. 3F); arrow shows top of the apex with the broken off part of the shell. • B – juvenile shell of *Suloceras pulchrum* (Barrande, 1868), lateral view, SM 444, Praha-Barrandov, Lower Devonian, Pragian Stage, Dvorec-Prokop Limestone (white beds). • C–J – *Cyrtoceras pugio* Barrande, 1866, Lower Devonian, upper Lochkovian, Radotín Limestone, locality Lochkov, Central Bohemia; C, I, J – flattened apical shell (C, J), NM L 10268 (Barrande 1866, pl. 156, fig 23; I). D–G – early part of shell with broken embryonic shell showing appearance of annulation and hyponomic sinus, ventral right lateral, dorsal and left lateral view, NM L 65267. H – reproduction of the Barrande's illustration (1866, pl. 156, fig. 18, specimen NM L 10267), idealized view of slightly flattened shell, length of the shell 137 mm. K – sculpture of *Dawsonoceras annulatum* (Sowerby, 1816), SM 445, im means internal mould, Praha-Malá Chuchle, Ludlow Series, Gorstian Stage, *L. scanicus*–*S. chimaera* Zone, Kopanina Formation. Scale bars: A (1 mm), B–K (5 mm).

shorter than interspaces separating them. The shell of *Dawsonoceras annulatum* (Sowerby, 1816) sometimes exhibits ontogenetic changes in the growth lines spacing; the growth lines are densely spaced on the top of the annuli, which is a character common to *Calorthoceras* but unknown in annulated orthoceratids such as, *e.g.* *Kopaninoceras fluminese* (Meneghini, 1857) and *Orthocycloceras*? *lynx* (Barrande, 1868) (Figs 3E, 5A).

The newly observed mature modification in *Calorthoceras* (Fig 1B, F, H, I) is manifested by densely spaced, fine growth lines, a sudden suppression and disappearance of annuli close to the aperture in a fully-grown shell (length of mature modification is 7 to 11 mm, height about 12 mm). This type of shell modification is characteristic of representatives of the family Dawsonoceratidae (*e.g.* the type species of *Dawsonoceras* and *Dawsonocerina*, Barrande, 1868; Blake 1882, Horný 1955) and is not known in annulated representatives of the family Orthoceratidae. An unusual adult modification of the shell is a narrowing of the shell and a change in the arrangement of the annuli. This narrowing is not present immediately at the aperture of the shell, but some short distance away. In one specimen of *Calorthoceras butovitzense*, the shell wall is exfoliated, and the internal mould shows a constriction (Fig. 1D) followed by less developed and more densely spaced annuli. Similar constrictions of the shell occur in the genus *Dawsonocerina*, most commonly in *D. dulce* (Barrande, 1868) from the latest Ludlow and earliest Přídolí Series (Barrande 1868, pl. 295, figs 6, 9, 12).

Among the morphologically similar types of annulated orthocerids is also the species *Cyrtoceras pugio* Barrande, 1866 (pl. 156, figs 18–28 including var. *juncea*) from the late Lochkovian of the Prague Basin. It is characterized by an endogastrically curved, annulated shell and dense, reticulate sculpture with unequally developed longitudinal lirae (Fig. 5D–H). The apex is spherical, the ontogenetically early part of the shell is slowly expanding with regular and fine reticulate sculpture appearing already in the embryonic shell (Fig. 5C, I, J). Annulation also appears very early in ontogeny, but the timing is variable. The morphology of the early growth stages of the shell and its size resembles that of the genus *Calorthoceras*; the two taxa are probably closely related.

The sculpture and annulation of *Cyrtoceras pugio* has a strong resemblance to that of the stratigraphically younger species *Suloceras pulchrum* (Barrande, 1868) from the Pragian of the Prague Basin, which has been placed (Manda 2001, Kröger 2008) in the family Spyroceratidae Shimizu & Obata, 1935. It is worth mentioning that the species is known also from France and probably occurs in other regions, too (Babin 1966). The apex of *S. pulchrum* is unknown, but the juvenile shell has regularly developed annulation and a dense, regular reticulate sculpture like the juveniles of *Calorthoceras* (Manda & Turek 2011, fig. 10; Figs 5B, 9F). *Suloceras* Manda, 2001 may thus be related to *Calorthoceras.* This is additionally supported by the slowly expanding shell, absence of cameral deposits, tubular siphuncle with orthochoanitic to suborthochoanitic septal necks and of finer and coarser longitudinal ornament elements (Figs 9F, 10C). The genus *Suloceras* is therefore reclassified in the family Dawsonoceratidae.

The Devonian species of *Calorthoceras* [e.g. *C. pseudocalamiteum* (Barrande, 1851), *C. subtubicinella* (Whitborne, 1890), *C. tubicinella* (Sowerby, 1840)] and some related taxa (e.g. *S. pulchrum*) were previously placed in the pseudorthocerid family Spyroceratidae (Babin 1966, Zhuravleva 1978, Kröger 2008) due to the similar character of sculpture and annulation. Spyroceratids differ from *Calorthoceras* in having well-developed cameral deposits and a relatively thick siphuncle. The embryonic shell of *Spyroceras* (Niko 1996, Kröger & Isakar 2006; Manda & Turek unpubl. data) is cup-shaped with a cicatrix. In contrast, the apical-most part in *Calorthoceras* is expanded ventrally and the embryonic shell is more than twice as large. Although the shells of spyroceratids and *Calorthoceras* (and related taxa) are similar, the large embryonic shell of *Spyroceras* may indicate demersal juveniles; both convergent groups may thus differ in the early ontogenetic habitat and mode of life.

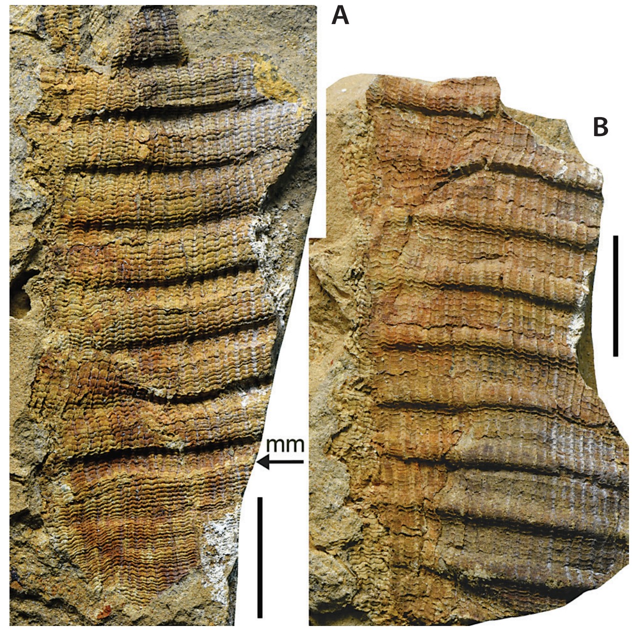

Figure 6. Part (B) and counterpart (A) of *Dawsonoceras multiliratum* Foerste, 1928; specimen MŠ 11772; Llandovery Series, Aeronian Stage, *D. convolutus* Zone; Bohemia, Prague Synform, Hýskov, V Jakubince, pit DB226 (see Štorch 2001). This is the first report of the species outside Wisconsin and Illinois. Abbreviation: mm – mature modification. Scale bar: 10 mm.

Occurrence and mode of life of *Calorthoceras* in the Silurian of the Prague Basin

In the Prague Basin, the species *Calorthoceras butovitzense* (Fig. 1) ranges from the earliest Homerian to earliest Ludfordian stages, Ludlow Series (Fig. 7, interval embracing about 12 Ma, for the list of localities, see Taxonomic note). The separate single record comes from the earliest Lochkovian Stage, Early Devonian.

The range record of *Calorthoceras butovitzense* is discontinuous; at nine localities, the species occurs in a narrow time interval represented by one or only a few beds. In most faunas it is one of the rarest straight-shelled cephalopods. However, this species is relatively abundant at two localities (Praha-Butovice, Na Břekvici and Praha-

Řeporyje, Mušlovka Quarry). The successions of both localities were deposited below wave base on the upper slope of a volcanic elevation. The species is therefore not common in most of the shallow deposits preserved in the Prague Basin. All growth stages are present at both sites, but only one individual with an adult modification was found at the Butovice site. Thus, there is only one locality in the Prague Basin with a more or less balanced population, where different growth stages occur.

The distribution of *C. butovitzense* in the Silurian strata of the subtropical Prague Basin represents only part of the total range of the species recorded in Baltica, Avalonia and the South China palaeoblock (Fig. 7). The species represents an immigrant to the Prague Basin. The earliest Ludlowian, when the species first appeared in the Prague Basin, is a period when other immigrants of Baltic-Avalonian origin also first appeared in the Basin (Stridsberg 1985, 1988b; Stridsberg & Turek 1997; Manda 2008). The youngest occurrence precedes a small extinction event after which many cephalopods of Baltic-Avalonian origin no longer occur (Štorch *et al.* 2014). The distribution pattern of *Calorthoceras* in the Prague Basin (small number of localities with temporally narrow occurrences) does not provide a clear evidence of stable local populations and may rather indicate a repeated immigration during the period of open faunal communication between the Prague Basin and the northern marine basins. An indication of a low faunal differentiation in peri-Gondwana is the absence of *C. butovitzense* in the Přídolí strata of the Prague Basin (Gnoli 2003).

The type species of the genus, *Calorthoceras pseudocalamiteum*, occurs in the Koněprusy Limestone of the Koněprusy area. There, the Koněprusy Limestone consists of deposits of a tropical, shallow-water, skeletal debris accumulation with reef build-ups in the uppermost part. The species is found in most facies of the Koněprusy Limestone (Hladil & Slavík 1997), but is usually uncommon or rare (Chlupáč 1955, Manda 2001). Its abundance is associated with reef build-ups and coquinas deposited in cavern fills

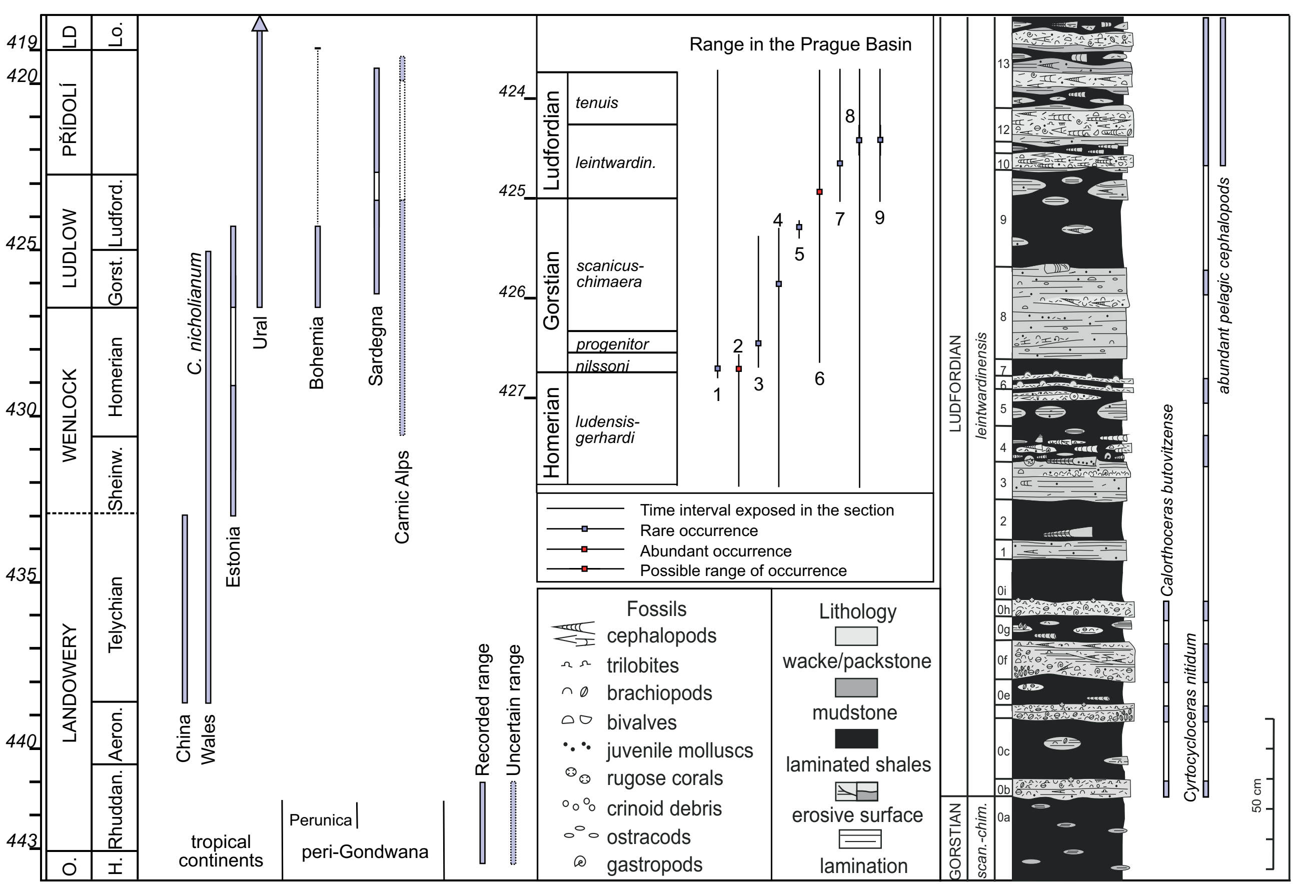

Figure 7. Stratigraphic range and latitudinal distribution of *C. butovitzense* and closely related or conspecific *C. nicholineatum* and detailed rage of the *C. butovitzense* in the middle Silurian of the Prague Basin (box on the middle), numbers indicate localities: 1 – Tachlovice locality; 2 – Butovice, Na Břekvici; 3 – Praha–Řeporyje, road-cut section; 4 – Praha-Malá Chuchle, Vyskočilka section; 5 – Loděnice-Sedlec; 6 – Praha-Řeporyje, Mušlovka Quarry; 7 – Kozolupy Section 927; 8 – Barrande's locality Dlauha hora; 9 – Barrande's locality Hinter Kopanina. Box on the right shows range of the *C. butovitzense* and another annulated demersal orthocerid *Cyrtocycloceras nitidum* (Barrande, 1866) in the NW wall of the Mušlovka Quarry.

Figure 8. *Calorthoceras pseudocalamiteum* (Barrande, 1851) *in* Quenstedt (1851) in a coquina of molluscs, trilobites, phyllocarids and trilobites; Lower Devonian, Pragian Stage; Koněprusy Limestone, Praha Formation; Koněprusy, Zlatý kůň hill area, most probably Houbův lom Quarry; NM L 65268. Scale bar 50 mm.

between stromatactids (Fig. 8; Chlupáč 1955, Manda 2001, Košan 2004). There, together with the orthocerid *Dawsonocerina discretum* (Barrande, 1868), it represents the most abundant cephalopod. Pelagic cephalopods are not known from coquinas in the Koněprusy reef. The species *C. pseudocalamiteum* does not occur in the more distal equivalents of the Koněprusy Limestone. *Calorthoceras* is one of the few cephalopod species exclusively associated with the Koněprusy Limestone. *Calorthoceras* is also known from the reef limestones of the Carnic Alps (Bandel 1969, Schönlaub & Flajs 1975) and the Armorican Massif (Babin 1966), *i.e.* areas with palaeobiogeographical affinity with the Prague Basin.

Calorthoceras has a slowly expanding, straight or very weakly curved, endogastric shell, relatively short phragmocone chambers and a thin, subcentral siphuncle. Shells of this type are usually characteristic of pelagic orthocerids. However, the well-developed sculpture and annulation of *Calorthoceras* rather resembles that of the demersal orthocerid *Cyrtocycloceras* (Marek 1971); the shell of pelagic orthocerids is mostly smooth. The functional morphology of annulated shells with complex sculpture is a matter of discussion and a general consensus is yet to be reached – the possible explanations include shell strength improvement, anti-predatory adaptation, shell hydrodynamics/buoyancy refinement, and camouflage (*e.g.* Ward 1981, Chamberlain 1993, Barskov 2018, Jaitly *et al.* 2022, Thakor *et al.* 2023). The autecology of *Calorthoceras* is thus based on indirect observations discussed below.

The distribution pattern of *Calorthoceras* in the Prague Basin indicates that it was probably a demersal cephalopod inhabiting a strictly delimited environment (*cf.* Watkins & Berry 1977, Hewitt & Watkins 1980). More than half

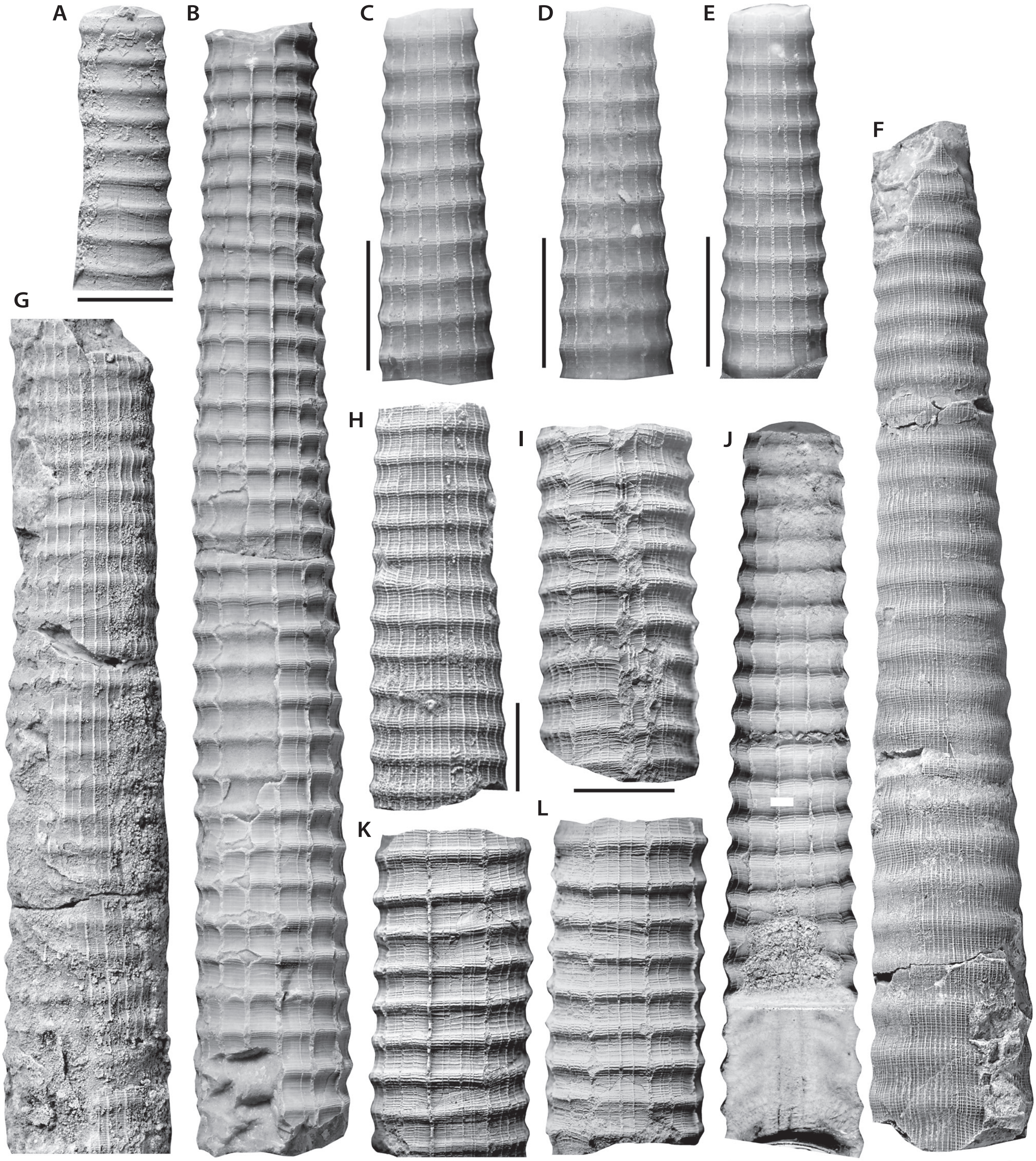

Figure 9. A – *Calorthoceras butovitzense* Chen, 1981, lateral view, juvenile shell with a healed injury, sculpture is indistinct because outer shell layer is exfoliated, SM440, Ludlow Series, Kopanina Formation, Bohemia, Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. • B–E, G–J – *Calorthoceras pseudocalamiteum* (Barrande, 1851) *in* Quenstedt (1951), Lower Devonian, Pragian Stage; Koněprusy Limestone, Praha Formation; B – specimen with a low number of longitudinal ridges, lateral view, NM L 19912 (Barrande 1868, pl. 278, fig. 3), Koněprusy; C–E – lateral, dorsal and ventral view, ontogenetically earliest known specimen, Houbův lom Quarry; G – specimen with high number of longitudinal lirae, lateral view, NM L 15375 (Barrande 1868, pl. 278, fig. 27), Koněprusy; H – lateral view, SM441, Koněprusy, Císařský lom Quarry, western wall, skeletal coquina; I, K, L – ventral, lateral and dorsal view, SM442, Koněprusy, Houbův lom; J – lateral view, NM L 10921, Koněprusy. • F – *Suloceras pulchrum* (Barrande, 1868), lateral view, NM L 10355, lectotype SD Manda (2001) (Barrande 1868, pl. 276, fig. 7); Lower Devonian, Pragian Stage; Koněprusy Limestone, Praha Formation. Scale bars: 10 mm (B, G, F, I, J, K, L), 5 mm (C–E, H), 3 mm (A).

of the specimens of *C. butovitzense* from the Mušlovka Quarry exhibit one or more shell repairs, which are small to large in extension (as defined by Bond & Saunders 1989). The injuries are of various types including U- and V-shaped shell breaks (*e.g.* Figs 1F; 4D; 9H, K). A healed injury was also observed in a juvenile shell (Fig. 9A). Healed injuries are extremely rare in pelagic orthocerids in the Silurian of the Prague Basin (Manda & Turek, unpubl. data). Thus, the presence of healed injuries rather indirectly supports a demersal habit and life of the cephalopod in a close contact with the sea floor (for discussion and another explanation Klug 2007). The absence of deposits in the phragmocone and the siphuncle (although the internal structures of the apical part of the phragmocone are poorly known) indicates that the shell was vertically oriented during life, at least when resting (*e.g.* Peterman *et al.* 2019). The shallow hyponomic sinus (Fig. 4C–E), if detectable, suggests a low physical activity of the animal. Occurrence in local and geographically restricted populations (in one or few beds with distinct fauna and limited lateral extension) precludes significant vertical migration in a relatively shallow water settings. The shell was relatively long during life, perhaps up to 20 centimetres with a small diameter of 12 mm (Fig. 1B) but there is no evidence of truncation of any part of the shell. The demersal habit of the cephalopod is also supported by the fact that no adult or juvenile *Calorthoceras* shells have been found in the pelagic sediments (shales) surrounding the volcanic archipelagos in the Prague Basin. However, the biogeography of *Calorthoceras* demonstrates the ability of these cephalopods to transverse long distances between continents via surface currents.

Conclusions

The species assigned to the genus *Calorthoceras* range from the Telychian up to the Givetian; an occurrence in the Middle Ordovician is not excluded. The species of this genus usually inhabited shallow, tropical seas. An occasional migration to peri-Gondwanan basins during the Silurian is documented. The record of C. *butovitzense* in the Prague Basin is discontinuous, with limited evidence of local populations of this perhaps demersal orthocerid.

The ontogenetically early part of the shell is weakly curved, endogastric and the apical part of the shell is non-accretionary and smooth, terminating in a relief fold. Hatching is manifested by a change in the sculpture and shape of the shell. The embryonic shell with a length of slightly below 5 mm is among the largest in orthocerids, but the early stages may have been pelagic. The wide paleobiogeographic dispersion in combination with local populations is consistent with a pelagic juvenile stage. Despite limited material, variability in embryonic shell shape (conical or weakly curved hemispherical apex) and sculpture are documented. Longitudinal lirae appear already in the embryonic shell while annulation of the shell appears soon after hatching or with a relatively long delay.

The embryonic shell in the species of the genus *Calorthoceras* supports its placement in the family Dawsonoceratidae. The morphology of the adult shell modifications and the structure of the siphonal tube in *Calorthoceras* are also consistent with this family assignment. The early ontogenetic development indicates an affinity of *Calorthoceras* with the Lochkovian "*Cyrtoceras*" *pugio* (Barrande 1866) and the Pragian genotype *Suloceras pulchrum* (Barrande, 1868). *Calorthoceras* and the above-mentioned taxa were previously placed in the family Spyroceratidae on the basis of similar sculpture. However, spyroceratids have an apex with a cicatrix and a phragmocone with well-developed cameral deposits and thus belong to the pseudorthocerids.

Taxonomic note

Subclass Orthoceratoidea Teichert, 1967
Order Orthocerida Kuhn, 1940
Family Dawsonoceratidae Flower, 1962

Genus *Calorthoceras* Chen, 1981 *in* Chen *et al.* (1981)

Type species. – *Orthoceras pseudocalamiteum* Barrande, 1851 *in* Quenstedt (1851), Pragian, Early Devonian, Central Bohemia.

Diagnosis. – Emended. Dawsonocerid with a slender, very slowly expanding shell, straight or very slightly curved and endogastric; shell height not exceeding 20 mm; annulation appears in the juvenile stage; annulations symmetrically arched, spaces between annuli usually slightly greater than the width of the annuli, spaces between the annuli shallow or straight; annuli low and their height corresponds to less than one tenth of the shell height. Prior to the appearance of annulation, the sculpture of the juvenile shell is reticulate, longitudinal lirae/ridges equal in thickness or differentiated, more distinct than growth lines; number of longitudinal lirae/ridges is variable but moderately increases during the shell growth.

Remarks. – The species of *Calorthoceras* differ from type species of *Dawsonoceras* (*D. annulatum*) in the presence of longitudinal ridges/lirae on the shell surface, lirae appear already on the embryonic shell. Distinguishing the species of *Calorthoceras* from the species of *Dawsonoceras* with longitudinal lirae is difficult (*e.g.* Upper Ordovician

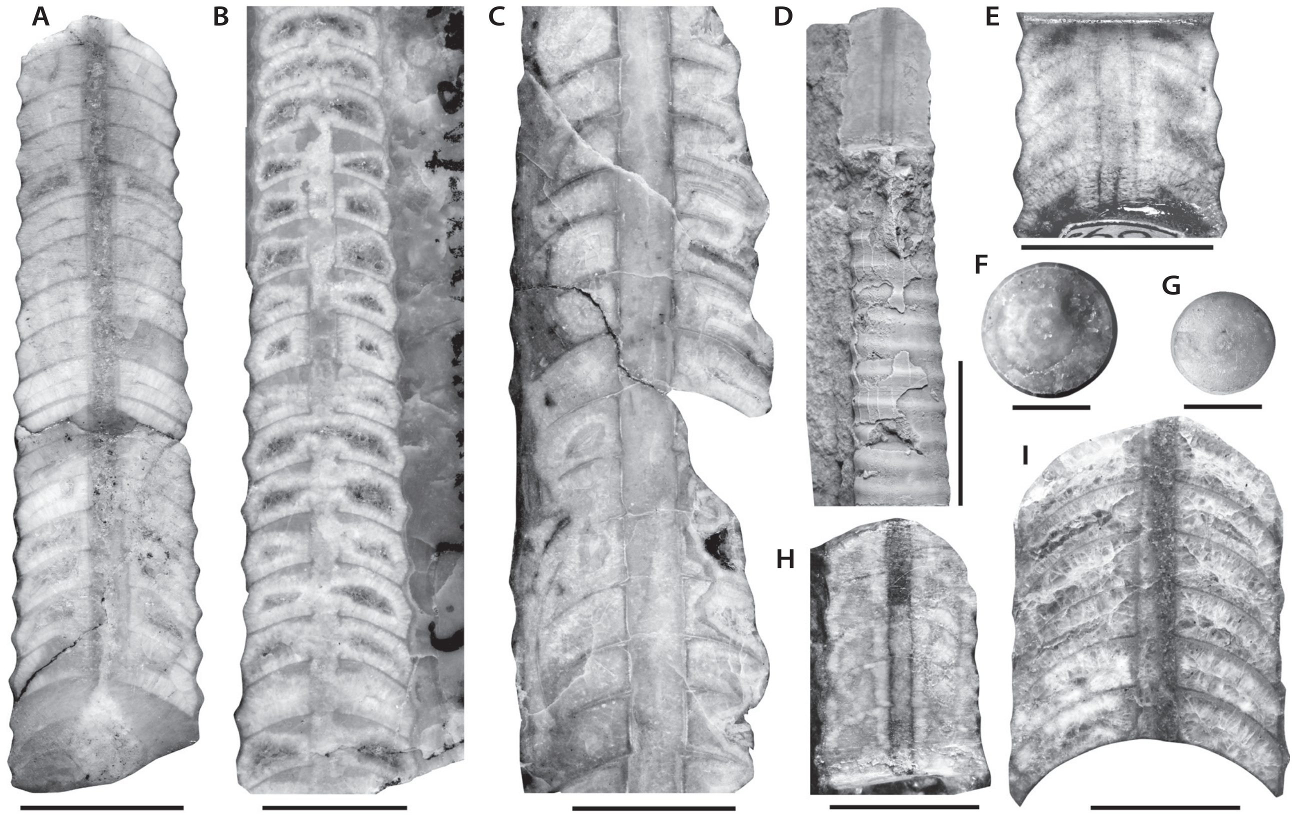

Figure 10. A, B, E, F – *Calorthoceras pseudocalamiteum* (Barrande, 1851) *in* Quenstedt (1851), Lower Devonian, Pragian Stage; Koněprusy Limestone, Praha Formation; A – median section, specimen NM L 10917 (Barrande 1868, pl. 278, fig. 16), Koněprusy; B – median section, specimen NM L 15366 (Barrande 1868, pl. 278, fig. 18), Koněprusy; E – median section of the specimen illustrated as Fig. 9J; F – cross section of the specimen illustrated as Fig. 9C–E. • C – *Suloceras pulchrum* (Barrande, 1868), median section, NM L 15353, paratype (Barrande 1868, pl. 276, fig. 14); Lower Devonian, Pragian Stage; Koněprusy Limestone, Praha Formation. • D, H, G, I – *Calorthoceras butovitzense* Chen, 1981; D, H – lateral view (D) and median section (H), NM L 15374 (Barrande 1868, pl. 278, fig. 26); Tachlovitz, Kopanina Formation, Ludlow Series, Gorstian Stage, *N. nilssoni* Zone; G – cross section of the specimen illustrated as Fig. 9A; I – median section, SM 443 Ludlow Series, Kopanina Formation, Bohemia, Praha-Butovice, Na Břekvici, Gorstian Stage, *N. nilssoni* Zone. Specimen 10D coated by ammonium chloride, median section photographed in water. Scale bars: 10 mm (A, C, D, E), 5 mm (B, G, I), 2 mm (F, G).

Dawsonoceras fenestratum (Eichwald, 1860) and Silurian *Dawsonoceras nodocostatum* (McChesney, 1861). The shells in the species of *Dawsonoceras* are larger in size, the maximum height is greater, and the siphuncle is wider. Further research has to show whether some of *Dawsonoceras* species with longitudinal lirae may belong to the genus *Calorthoceras* or whether it would be convenient to again use the genus *Cedarvilleoceras* Shimizu & Obata, 1935 for them.

The genus *Suloceras* (Fig. 9F, 10C) differs from *Calorthoceras* in having dense and finer reticulate sculpture, low and wider annulation, which is sometimes reduced in later ontogenetic stages, relatively thicker siphuncle; in addition, the shell height is three times greater.

Chen *et al.* (1981, p. 98) distinguished two groups of *Callorthoceras* species. The group of *C. pseudocalamiteum* ("longitudinal sharp-edged lirae, more than one longitudinal striae between two lirae"), and the group of *C. illineatum* ("surface with longitudinal lirae and straight transverse striae, without subordinate longitudinal striae"). Kiselev (1988) established a new subgenus *Calorthoceras* (*Hornyceras*) based on *C. illineatum* (= *C. butovitzense*), which we consider unjustified due to only minimal differences (less elaborated sculpture and a greater average number of longitudinal lirae).

The shell morphology of a Middle Ordovician orthocerid from the Ordos area described as *Anaspyroceras beauportense* Whiteaves, 1906 (Chen & Zou 1984) resembles species of *Calorthoceras*, but a revision is needed. If this species belongs to *Calorthoceras*, the record of this genus would be considerably longer than that of the phylogenetically related *Dawsonoceras*. The stratigraphically oldest unambiguous species of the genus is *C. nicholianum* (Blake, 1882) from the late Llandovery–early Ludlow series of Wales.

The species *Anaspyroceras cultellus* Talent & Philip, 1956 is very similar to *C. butovitzense* and is therefore formally transferred to the latter genus. The Devonian species *Orthoceras dolatum* Whitborne, 1890, *O. subtubicinella* Whitborne, 1890 and *O. tubicinella* Sowerby, 1840 are formally placed in the genus *Calorthoceras*; both species are very similar to the type species of *Calorthoceras*. All species of the genus *Calorthoceras*, whether Silurian or Devonian, are very similar, but the type and stratigraphically younger species have more complex sculpture and lower average number of longitudinal lines.

The species "*C. choteczense*" Chen, 1981 *in* Chen *et al.* (1981) is inadequately described and the name is thus a *nomen nudum*. Only one specimen (Barrande 1870, pl. 361, figs 15–17) attributed to this taxon is from the locality Chotecz g1; the locality embraces collecting sites of the Emsian–Eifelian interval, Central Bohemia. There is no relevant reason to separate the single specimen at the species level; the individual is the stratigraphically youngest representative of the type species from which it cannot be distinguished.

Species included. – *Calorthoceras butovitzense* Chen, 1981, Telychian–Lochkovian; *C. cultellus* comb. nov. (Talent & Philip, 1956), Silurian–Devonian boundary interval, Victoria (Australia). *C. dolatum* comb. nov. (Whitborne, 1890), Middle Devonian, Givetian, South England. *C. pseudocalamiteum* (Barrande, 1851) *in* Quenstedt (1851), Pragian, Central Bohemia, Massif Armorican (Babin 1966), Carnic Alps (Bandel 1969, Schönlaub & Flajs 1975, listed, not illustrated); *C. nicholianum* (Blake, 1882) comb. nov., Telychian–Gorstian, Wales; *C. subtubicinella* (Whitborne, 1890) comb. nov., Middle Devonian, Givetian, South England. *C. tubicinella* (Sowerby, 1840) comb. nov., Middle Devonian, Givetian, South England (Whitborne 1890), Germany (Sandberger & Sandberger 1851).

Calorthoceras butovitzense Chen, 1981 *in* Chen *et al.* (1981)

Figures 1, 2, 3A–D, 4C–E

partim 1868 *Orthoceras pseudocalamiteum* Barr.; Barrande, pl. 278, figs 22–26, 29–33, pl. 286, figs 11–16.
1968 *Anaspyroceras pseudocalamiteum* (Barrande 1852). – Ristedt, p. 249, 50, pl. 1, fig. 13, text-fig. 3–4c.
partim 1874 *Orthoceras pseudo-calamiteum* Barr.; Barrande, p. 261–264.
1977 *Anaspyroceras pseudocalamiteum* (Barrande, 1852). – Serpagli & Gnoli, p. 176, 178, pl. 5, figs 3, 4.
1981 *Calorthoceras illineatum* Chen sp. nov.; Chen *et al.*, p. 23.
1981 *Calorthoceras multicostatum* Chen sp. nov.; Chen *et al.*, p. 23, pl. 7, fig. 16.
1981 *Calorthoceras butovitzense* Chen sp. nov.; Chen *et al.*, p. 23, 24, pl. 7, fig. 17.
1984 *Metaspyroceras pseudocalamiteum* (Barrande, 1866). – Kiselev, p. 22, 23, pl. 3, figs 20, 22.
1988 *Calorthoceras* (*Hornyoceras*) *illineatum* Chen, 1981. – Kiselev, p. 81, 82, fig. 1(1–4).
1990 *Calorthoceras* (*Hornyoceras*) *illineatum* Chen, 1981. – Kiselev *et al.*, p. 40, pl. 12, fig. 7.
1991 *Anaspyroceras pseudocalamiteum* (Barrande). – Gnoli & Serpagli, p. 190, 194, pl. 3, fig. 3.
? 1998 *Anaspyroceras* cf. *pseudocalamiteum* (Barrande, 1852). – Gnoli & Histon, p. 320, pl. 5, fig. 4.
? 1999 *Calorthoceras* cf. *pseudocalamiteum* (Barrande, 1852). – Histon, p. 248, Heritsch pl. 6, figs 625–627, Stache pl. 9, fig. 1.
? 1999 *Calorthoceras* aff. *pseudocalamiteum* (Barrande, 1851). – Histon, p. 248, Heritsch pl. 7, figs 683, 689, Stache pl. 8, fig. 8, pl. 9, figs 4, 5.
2006 *Calorthoceras pseudocalamiteum* (Barrande, 1866). – Kröger & Isakar, p. 144, fig. 6a.

Holotype. – SD Chen (1981). Specimen NM L 10916 (Barrande 1868, pl. 278, fig. 33), locality Butovitz e1, Silurian, Ludlow Series, *N. nilssoni* Zone, Kopanina Formation (Fig. 1A).

Diagnosis. – Emended. *Calorthoceras* with a variable number of longitudinal lirae, which are usually densely packed and more distinct than growth lines; the distance between adjacent longitudinal lirae is roughly twice the distance between adjacent anulations; annulation reduced or missing close to the aperture of adult specimens; the apex is usually slightly curved.

Remarks. – Based on Barrande's figured specimens, Chen *in* Chen *et al.* (1981) established three new Silurian species: *C. multicostatum* (holotype, Barrande 1868, pl. 278, figs 27, 28; other specimens: pl. 278, figs 29–32, pl. 286, figs 11–16), *C. illineatum* (Barrande 1868, pl. 278, figs 21–26) and *C. butovitzense*. All three species occur in the early Ludlow *nilssoni* Zone and most of them originate from the Butovice. There is no reason to separate the three taxa. Formally, the best-defined species is *C. butovitzense* with a designated holotype, which is a well-preserved specimen; thus, the name *butovitzense* is preferred. Kiselev (1988) preferred the name *C. illineatum*, which is, however, inadequately defined (nomen nudum, name formalised by Kiselev in 1988).

Calorthoceras butovitzense differs from the type species in having a higher average number of longitudinal elements, lirae are lower and less elaborate, prominent lirae are intercalated by secondary finer lirae only occasionally, protruding longitudinal ridges are absent. The annuli are usually slightly lower relative to shell height and reduced close to the aperture of fully-grown specimens. Specimens with a higher number of longitudinal lirae (*e.g.* Fig. 1E) co-occur with specimens with a reduced number of ridges (Figs 1G, 10D).

Calorthoceras pseudocalamiteum is characterised by 14 to 17 protruding longitudinal ridges occasionally intercalated by one or three finer lirae in post-juvenile shells (Fig. 9B, J). Longitudinal lirae in the juvenile shell of *C. pseudocalamiteum* are undifferentiated as in *C. butovitzense* (Fig. 9C–E). The seven shells of *C. pseudocalamiteum* from the reef core facies do not have protruding longitudinal ridges, but a greater number of finer lirae, thus resembling the Silurian *C. butovitzense* (Fig. 9G, H, "*C. multicostatum*" in Chen *et al.* 1981). Based strictly on the shell morphology, they could be placed in the latter species, but they are more likely to represent morphological extremes of *C. pseudocalamiteum*. This is attested by one specimen showing a combination of multiple finer longitudinal lirae and few protruding ridges (Fig. 9I–L); the longitudinal lirae in *C. butovitzense* are finer than in *C. pseudocalamiteum*.

Orthoceras nicholianum Blake, 1882 (p. 88, pl. 3, figs 7, 7a, 8, 15) from the late Llandovery–early Ludlow series of Wales exhibits all characters of *Calorthoceras* and it is difficult to separate from *C. butovitzense*; both taxa may be conspecific but a revision of the Welsh material is needed.

Occurrence. – Bohemia, Prague Basin, Kopanina Formation, Gorstian–lowermost Ludfordian (*nilssoni–leintwardinensis* zones). *N. nilssoni* Zone: Tachlovice locality, several specimens, tuffitic limestone with corals. Praha-Butovice, Na Břekvici (Barrande's locality Butovitz), bed no. 10, 11, cephalopod limestones and mudstones (Kříž 1992), more than thirty specimens, six specimens collected by the author (ŠM). *Lobograptus progenitor* Zone: Praha-Řeporyje, road-cut section, bed no. 13, skeletal limestone, three specimens. *S. chimaera–L. scanicus* Biozone: Praha Malá Chuchle, Vyskočilka section, bed no. 6, cephalopod limestone (lower part of the biozone), two specimens, less than one percent of the collected cephalopods (Manda & Kříž 2007). Loděnice-Sedlec, bed no. 3, cephalopod limestone (upper part of the biozone), one specimen (Kříž 1999). Lower *S. leintwardinensis* Zone: Praha-Řeporyje, Mušlovka Quarry, bed no. 0 just above base of the Ludfordian (Manda & Budil 2007), grey skeletal brachiopod-trilobite-cephalopod limestone, 36 specimens (most abundant cephalopod, species reported by Bouček 1937). Upper *S. leintwardinensis* Zone: Barrande's locality Dlauha hora, skeletal brachiopod-trilobite limestone, few specimens. Barrande's locality Hinter Kopanina, yellow weathered cephalopod limestone, few specimens. Kozolupy Section 927, lowermost part of the bed no. 1, rusty crinoidal limestone, five specimens.

Lochkovian, Lochkov Formation. Černá rokle near Malá Chuchle, lowermost *U. uniformis* Zone (Chlupáč *et al.* 1972, Frýda & Manda 1997), one subadult specimen collected in a platy limestone intercalated with shale. An occurrence in the middle–upper Lochkovian Radotín Limestone (Barrande's etage Ff1, Barrande 1874, Novák 1886) has not been confirmed.

Carnic Alps, occurrence uncertain, Homerian, upper Přídolí (Bogolepova 1998, Histon 1999, Gnoli & Histon 1998). Central and Southwest China, Telychian (Chen *et al.* 1981, Chen & Holland 2002). Estonia, Sheinwoodian–lower Homerian, Gorstian–early Ludfordian (Kiselev *et al.* 1990). North Ural, Ludlow–Lochkovian (Kiselev 1984). ?Pyrenees, Homerian, upper Přídolí (Barrois 1883, Gourdon 1889). Sardegna, lower Gorstian–middle Ludfordian, Přídolí (Gnoli & Serpagli 1991). ?Tajmyr, Gorstian (Kříž & Bogolepova 1995).

Acknowledgements

This research was supported by the Czech Grant Agency through the project GA20-23363S (Biostratigraphy and faunal dynamics of the Silurian (ŠM), the Strategic Research Plan of the Czech Geological Survey (DKRVO/ČGS 2023–2027; internal task No. 311410) and Ministry of Culture of the Czech Republic (IP DKRVO 2024-2028/2.IIIa) (VT). The authors thank Jessica Cundiff for her help during our stay in the Museum of Comparative Zoology in Harvard, Lenka Váchová (National Museum, Prague) for making photographs. Martina Aubrechtová (Czech Academy of Sciences, Prague) kindly improved the English and made a number of suggestions to improve the manuscript. Reviewer's comments by David H. Evans (Somerset, England) and Alexander Pohle (Ruhr Universität, Bochum, Germany) were important for the final form of the manuscript, as well as comments by the associate editor Christian Klug (Paläontologisches Institut und Museum der Universität Zürich, Switzerland).

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