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THE EARLIEST *CYRTINA* (BRACHIOPODA, CYRTINIDINA) IN THE DEVONIAN OF THE BARRANDIAN (CZECH REPUBLIC)

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Abstract: *The earliest known Cyrtina in the Prague Basin has been discovered in the Kotýs Limestone of the Lochkov Formation (Lochkovian) among a rich brachiopod-coral fauna at Branžovy ridge near Bubovice (Beroun District, Czechia). Rare and imperfectly preserved silicified shells are assigned to Cyrtina praecedens Kozłovski, 1929, a species originally described from Podolia, Ukraine. The species is known also in north-eastern Russia (Tajmyr and Sette-Daban Mts) and likely also in New South Wales, Australia. Its distribution provides evidence of the rapid spread of Cyrtina across the shallow shelves of Laurussia, Siberia and Gondwana in the Early Devonian. The Devonian and Carboniferous distribution of Cyrtina is restricted to the agitated, shallow-water carbonate environment in tropical and temperate climatic belts.*

Key words: *Cyrtina*, Brachiopods, Devonian, Lochkovian, Barrandian.

INTRODUCTION

The cyrtinidines are a small but characteristic group of rhynchonellate brachiopods in the Devonian. The eponymous family Cyrtinidae comprises only five genera: *Cyrtina* Davidson, 1859 (including the subgenus *Hystricocyrtina* Havlíček & Vaněk 1998), *Cyrtinaella* Frederiks, 1916, *Moniellocyrtina* Garcia-Alcalde, 2001, *Squamulariina* Frederiks, 1916, and *Tecnocyrtina* Johnson & Norris, 1972 (Johnson 2006). The cosmopolitan genus *Cyrtina* appeared at the beginning of the Devonian. So far, indisputed Silurian ancestors of cyrtinidines are uncertain (Boucot *et al.* 1960) while there are hundreds of papers describing the cyrtinids from the Devonian and the Carboniferous.

In the Barrandian area of Czechia, the genus was first recognized by Barrande (1879). The specimens from the Koněprusy Limestone were assigned by him to *Cyrtina heteroclita* (Defrance, 1824). Almost eighty years later, Havlíček (1956) described four species. He distinguished *Cyrtina kazi* Havlíček, 1956 (with two subspecies *C. kazi* kazi Havlíček, 1956 and *C. kazi vltavana* Havlíček, 1956) and *C. vlasta* Havlíček, 1956 from the Pragian (Praha Formation), and *Cyrtina morana* Havlíček, 1956 and *C. teta* Havlíček, 1956 from the Early Emsian (Zlíchov Formation). Subsequently, Havlíček & Vaněk (1998) erected two new species, *Cyrtina morosa* Havlíček & Vaněk, 1998 and *C. prateta* Havlíček & Vaněk, 1998, both from the Pragian (Koněprusy Limestone). The same authors (Havlíček & Vaněk, 1998) erected *Hystricocyrtina*, with the type species *Cyrtina kazi* and synonymized the subspecies *C. kazi kazi* and *C. kazi vltavana*. Havlíček (in Havlíček & Kukal 1990) erected *Cyrtina platypleura* Havlíček, 1990 from the upper Emsian (Suchomasty Limestone). Two different specimens from the Suchomasty Limestone were determined as *Cyrtina* aff. *morana* Havlíček, 1956.

Previously, no cyrtinid species has been reported from the Lochkovian, Eifelian and Givetian beds of the Prague Basin. Recently, a cyrtinid has been discovered in the Kotýs Limestone of Lochkovian age. This is the oldest cyrtinid know from the Prague Basin and is described herein. Thanks to the silicified mode of preservation by silicification the shape of the spiralium is visible which is still uknown in other species from the Prague Basin.

GEOLOGICAL SETTING

The locality all the specimens are from is situated at the northern limb of the Devonian infil of the Prague Basin in Central Bohemia of Czechia (Czech Republic) approximately 7 km NE of the

Beroun town (Figure 1A, B). The Devonian succession of the Prague Basin starts with the carbonate deposits of the Lochkov Formation (Lochkovian) and continues to the Srbsko Formation (Givetian). The Lochkovian to Eifelian succession is characterised by shallow water biodetrital mostly crinoidal limestones. It also comprises reef bioskeletal accumulations of Pragian, Emsian and Eifelian age which are located predominantly along the today preserved north-western limb of the basin. Deeper pelagic lithofacies of the same age are situated more south-eastward. These are represented mostly by dark coloured calcisiltites. The overlying siliciclastic Givetian succession indicates the beginning of the Variscan orogeny (Chlupáč 1998, Vacek & Žák 2019).

Shallow-water biodetrital and peri-reefal accumulations of Lochkovian age, with abundant crinoid limestones of the Kotýs Limestone are exposed along the northwestern limb of the Prague Basin (Chlupáč 1998). This member is characterised by grey bioclastic well-bedded limestones with common cherts in the middle part of the sequence. The limestone is rich in brachiopods and crinoidal detritus, with fauna referred to the *Coniproetus-Decoroscutellum* Trilobite Assemblage (Chlupáč 1983). This SW-NE strip of shallow-water Kotýs Limestone subsides towards the south-east, where the Radotín Limestone represents the Lochkovian stage. The Radotín Limestone is distinguished by dark-grey to black bituminous platy limestone beds rhythmically alternating with black calcare-

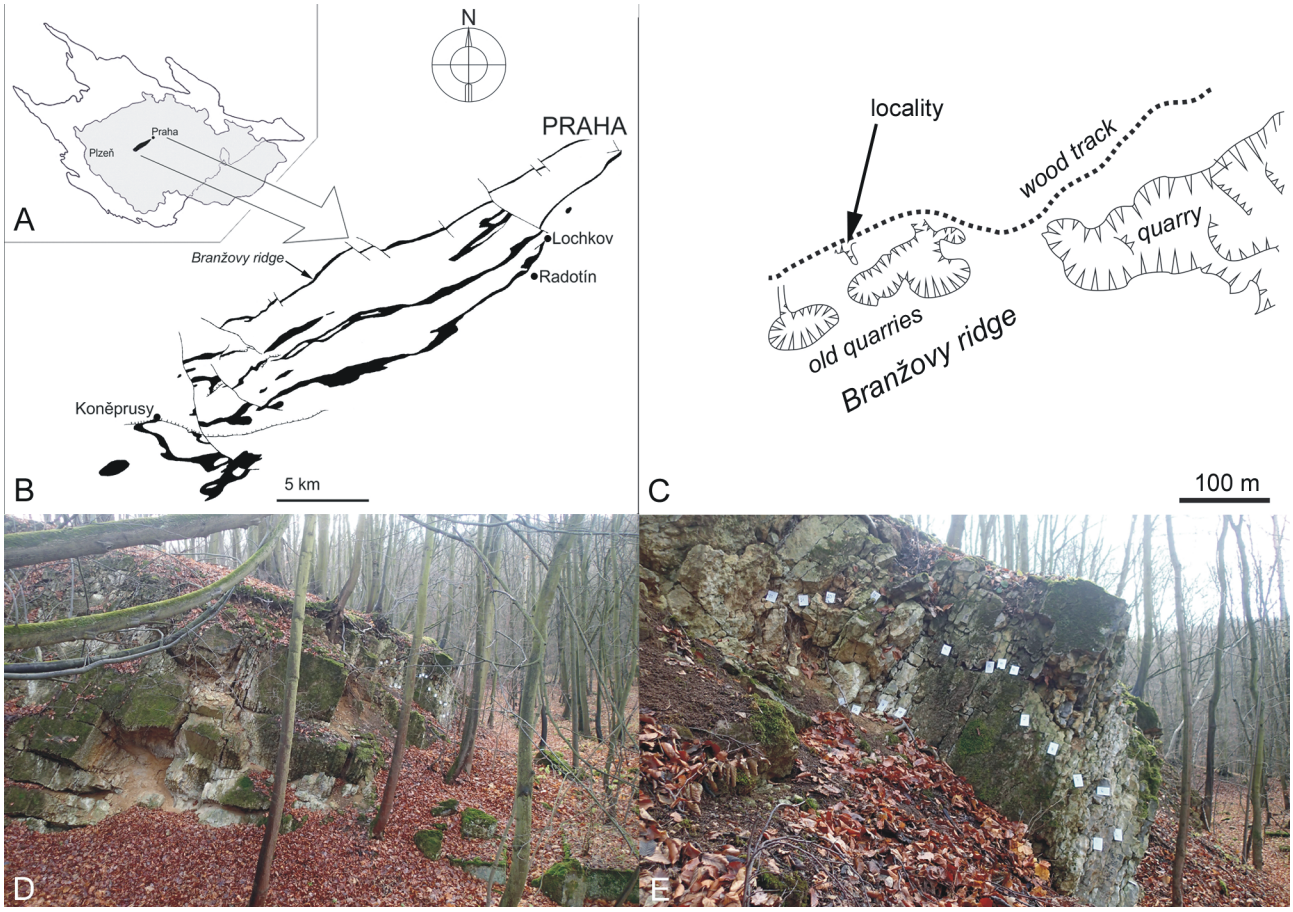


Figure 1. *Geographical setting of the Barrandian area (A) and distribution of the Lochkov Formation in the Prague Basin with marked locality of Cyrtina praecedens Kozłowski, 1929 (B), location of quarries and the sampled section in old trench (indicated by arrow) at the Branžovy ridge (C), and the richly fossiliferous outcrop of the lowest exposed limestone beds (E) from which specimens of Cyrtina praecedens came.*

ous shales. Its fauna contains many planktonic and nektonic organisms including graptolites and dacryoconaride tentaculites. An excellent survey of the Lochkov Formation has been given by Chlupáč (1998).

Detailed data about the locality of the earliest *Cyrtina* in the Prague Basin were published by Mergl (2003, 2021). The locality is situated between the villages Bubovice and Loděnice, in a short survey trench at the northern side of a small abandoned quarry in the Kotýs Limestone (Figure 1C). Grey platy limestone beds exposed in the trench are steeply dipping toward the south (Figure 1D). Limestone beds contain chert nodules and accumulations of bioskeletal material, mainly brachiopod shells. The lowest exposed beds yielded a highly diversified association with more than forty brachiopod species, corals and diverse epibiont organisms. The genera *Navispira*, *Parmorthina*, *Isorthis*, *Dalejina*, *Resserella*, *Iridistrophia*, *Spinatrypa*, *Lissatrypa*, *Gypidula* and strophomenide brachiopods are distinctive. The middle part of the sequence contain abundant *Spinatrypa* and *Spinatrypina*, associated mostly with *Dalejina* and *Skenidioides*. The highest limestone beds in the trench are poor in brachiopods carrying mainly smooth-shelled representatives of *Lissatrypa*. Conodonts indicate a level near the base of the middle Lochkovian (*Lanea omoalpha-Ancyrodelloides carlsi* conodont zones (Slavík 2011, Slavík *et al.* 2012).

SYSTEMATIC PART

Order Spiriferinida Ivanova, 1972
Suborder Cyrtinidina Carter & Johnson, 1994
Superfamily Cyrtinoidea Frederiks, 1911
Family Cyrtinidae Frederiks, 1911

Genus ***Cyrtina*** Davidson, 1859
Type species: *Calceola heteroclita* Defrance, 1824; Pragian, Lower Devonian, France.

Cyrtina praecedens Kozłowski, 1929
Plate 1

1929 *Cyrtina praecedens* sp. n. Kozłowski, p. 207, pl. 11, figs 8–23; text-figs 68, 10–75.
1954 *Cyrtina praecedens* Kozłowski; Nikiforova et al., p. 150, pl. 15, fig. 9.
1960 C*yrtina praecedens* Kozłowski; Ivanova in Sarycheva, p. 279, text-figs 403, 404.
1962 *Cyrtina praecedens* Kozłowski; Ivanova, p. 109.
1964 ? *Cyrtina praecedens* Kozłowski, 1929; Drot, p. 91, pl. 11, fig. 3a, b, pl. 24, fig. 2.
1967 *Cyrtina praecedens* Kozłowski; Ivanova, p. 79, text-figs 6, 7.
1967 *Cyrtina praecedens* Kozłowski; Alekseeva, p. 102, pl. 15, fig. 9–13, text-fig. 64.
1968 *Cyrtina praecedens* Kozłowski; Modzalevskaya, pl. 27, figs. 20–24.
cf. 1969 *Cyrtina praecedens* Kozłowski, 1929; Savage, p. 483, pl. 92, figs 1–44, text-fig. 5.
1971 *Cyrtina praecedens* Kozłowski; Ivanova, p. 24, text-fig. 8.3; p. 37, text-fig. 18; p. 46, text-fig. 23; p. 710, text-fig. 39.1; pl. 6, fig. 1, pl. 11, figs 1–6; pl. 12, fig. 10.
1985 *Cyrtina praecedens* Kozłowski, 1929; Nikiforova et al., p. 52, pl. 12, figs 3, 4, pl. 15, fig. 9.
1994 *Cyrtina praecedens* Kozłowski, 1929; Tcherkesova et al., p. 78, pl. 9, figs 5, 6.
2012 *Cyrtina praecedens* Kozłowski, 1929; Baliński, p. 922, fig. 20B, C.

Material: One complete shell, three ventral valves, and one dorsal valve stored in the palaeontological collection of the West Bohemia University at Plzeň (PCZCU 2481–2485).

Description: Shell is small, 7.8 mm wide in the largest specimen examined, pauciplicate, thin-walled, with slightly asymmetrical ventral valve, transverse in outline. Anterior commissure is serrate, slightly emarginate in dorsal view.

The dorsal valve is semicircular, gently convex in axial profile, with acute cardinal extremities. The fold is prominent, rapidly expanding anteriorly. Lateral slopes are low with two to three (Pl. 1, figs 9, 16) strong rounded plications separated by deep and broad interspaces. Interior of dorsal valve shows small cardinal platform with very small cardinal process, likely of two or more plates, large dental sockets and short subparallel crura. Jugal process and jugum are unknown.

The ventral valve is hemipyramidal, with deep rounded sulcus bounded by prominent, weakly curved and rounded plications. Apart from a sulcus-bounding plication, each lateral slope bears up to three rapidly diminishing rounded plications separated by broad interspaces. Ventral apex is prominent, directed posteriorly to posterolaterally. Ventral interarea is high triangular, gently curved in side view, divided by narrow delthyrium which

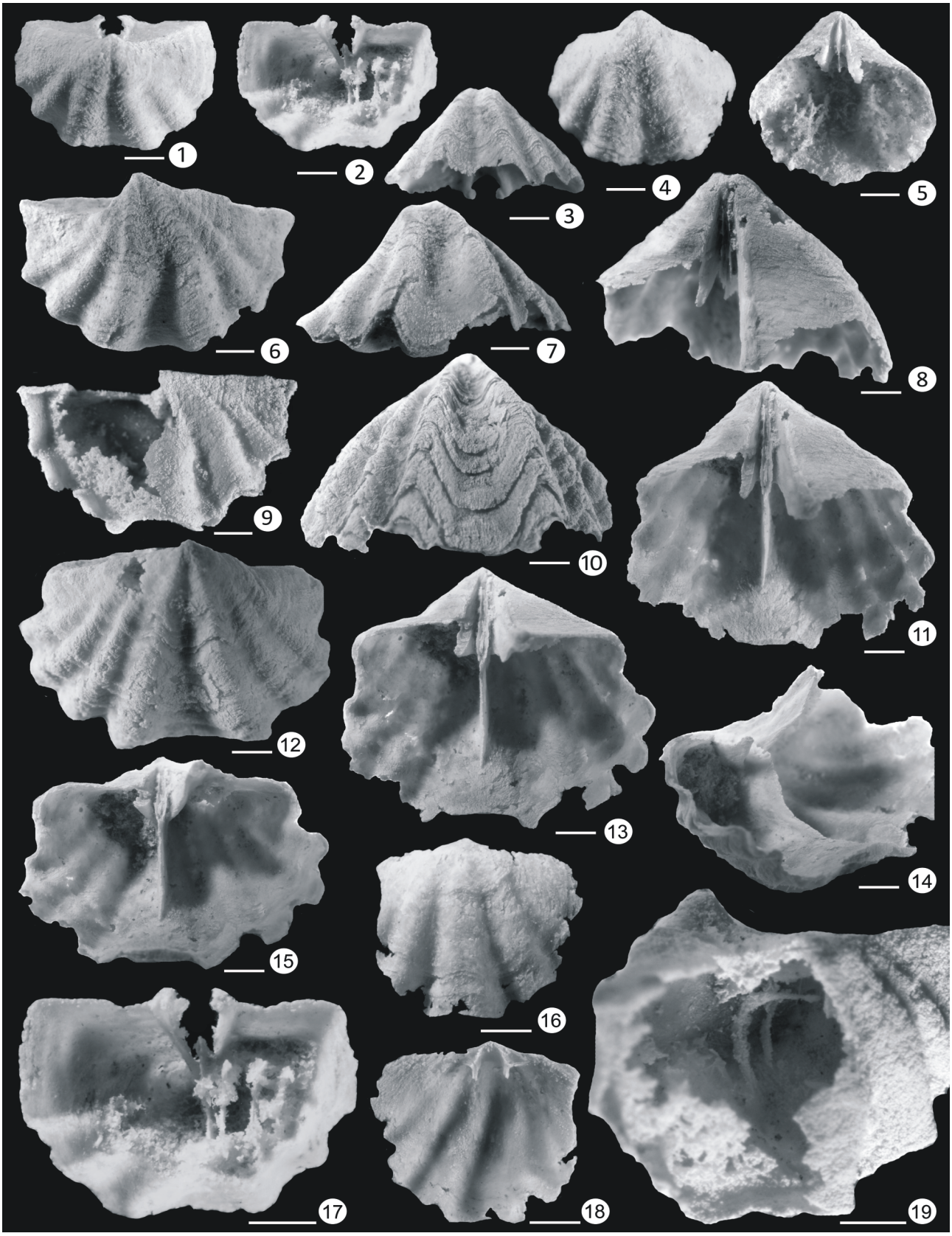
occupies less than 20 % of the hinge line. Lateral slopes are low with two (Plate I, figs 1, 6) to four (Plate I, fig. 12) strong rounded plications separated by deep and broad interspaces. Deltidium is unpreserved. Dental plates form a shallow long spondylium supported by a prominent median septum, which abruptly disappears anterior to shell midlength. Teeth are large. Tichorhinum is long and thin. Along its corroded axis (Plate I, figs 11, 13) the dorsal crest of the median septum is well visible. The spiralia are partially preserved in three specimens. Descending dorsal portions of spiralia are less curved and more laterally deviating than the ventral portions of spiralia, which are much more elongate ventrally (Plate I, figs 17, 19). Arrangement and spacing of spiralia follow the courses of shell plications.

Concentric ornamentation consists of numerous low lamellae arranged in anteriorly increasing intervals (Plate I, fig. 10). Punctation has not been observed due to the silicification but micro-spines are discernible on external surface of lateral slopes.

Remarks: The Bohemian specimens from the Lochkov Formation are indistinguishable from *Cyrtina praecedens* Kozłowski, 1929 from the Lower Devonian of Podolia, Ukraine. Apart from the formal description, Kozłowski (1929) commented extensively on the morphologic variability of the species. Nikiforova (1954) again commented on its occurence in Podolia. She remarked on differences between *C. praecedens* and *C. heteroclita* (Defrance, 1824) to which the specimens from Podolia previously were assigned by Siemiradzki (1906). Following on observations by Kozłowski (1929), she stressed that the main differences comprise the presence of small micro-spines densely covering the shell surface, the smaller shell size, and incorrectly, the fewer radial plications in *C. praecedens*. She also emphasized the different age of *C. praecedens*. Its first appearance has been reported from the Skala Formation (Nikiforova 1954, p. 151) of Silurian age, but this occurrence seems dubious because there are no reliable data about the presence of this genus in pre-Devonian strata. The greatest abundance of *C. praecedens* was in the Mytkiv Beds of the Borshchiv Horizon (Nikiforova 1954; p. 151). Subsequently, Ivanova (1971) reported its FAD in the Tajna Beds and its maximum occurrence in the overlying Mytkiv Beds. These data were adopted by Nikiforova *et al.* (1985). The precise distribution of brachiopods across the Silurian/Devonian in Podolia was presented by Baliński (2012). Acoording to worker, the FAD of *Cyrtina praecedens* in the measured Dnistrove section in bed No. 48, some 14 metres above the S/D boundary. This level falls to the Khudykivtsi Beds (= Tajna Beds) but the species is much more common in the subsequent Mytkiv Beds (both of Lochkovian age). All figured specimens from Podolia (Kozłowski 1929, Nikiforova 1954, Nikiforova *et al.* 1985, Baliński 2012) are rather small, showing a high apsacline, subplanar to distinctly curved ventral interarea, and several lateral plications on the shell flanks. Its cardinal extremities range from acute to rounded as stated already by Kozłowski (1929). The great phenotypic plasticity of *C. praecedens* is also evident from its illustrations: the neotype (Nikiforova *et al.* 1985; pl. 12, fig. 3) and specimens figured by Baliński (2012; fig. 20, figs B, C) have rounded cardinal extremities while the specimen figured by Nikiforova (1954; pl. 15, fig. 9) clearly displays acute extremities. The same plasticity is apparent in Bohemian specimens. They show rounded (Plate I, figs 1, 12) or acute (Plate I, fig. 6) extremities. Size and spacing of

Plate I. *Cyrtina praecedens* Kozłowski, 1929; Lochkovian, Lochkov Formation, Kotýs Limestone, lower fossiliferous beds with silicified fauna at Branžovy ridge near Bubovice, Czechia.
1–3, 17. Small ventral valve, (1) exterior in ventral view, (2) interior showing median septum and partly broken three loops of spiralium, (17) the same enlarged, and (3) exterior in anterior view, PCZCU 2481;
4, 5. Small ventral valve, (4) exterior and (5) interior showing tichorhinum, PCZCU 2482;
6, 7, 9, 19. Complete shell, (6) exterior of ventral valve and (7) the same in anterior view, (9) exterior of incomplete dorsal valve, and (19) oblique view inside the shell showing two loops of the right spiralium, PCZCU 2483;
8, 10–15. The ventral valve, (8) exterior in posterior view showing high ventral interarea and narrow delthyrium, (10) exterior in anterior and (12) ventral views, (11) the shell interior in posterodorsal, (13) dorsal, (14) oblique, and (15) anterodorsal views, showing median septum, tichorhinum, dental plates and teeth, PCZCU 2484;
16, 18. Small dorsal valve, (16) exterior and (18) interior showing small cardinal process and crura, PCZCU 2485.
Bar length equals to 1 mm.

Plate I



concentric lamellae are comparable in Bohemian and Ukrainian specimens.

Apart from Podolia and Bohemia, *C. praecedens* or a closely related species was recorded from the New South Wales, Australia, where the species has been found in abundance in the Mandagery Park Formation of "Siegenian" (=Pragian) age (Savage 1969). Savage noted the presence of right-angular cardinal extremities and figured (Savage 1969; pl. 92, figs 35 to 38) the spiralia preserved by silicification. He pointed out the smaller size of the specimens and disconnection of the median septum from the tichorhinum. Savage (1974) kept the material of "Gedinnian" (= Lochkovian) age in open taxonomy but stressed their similarity to *C. praecedens*. However, the presence of *C. praecedens* in Australia, New South Wales, was doubted by Brock (2003), who referred the specimens described by Savage (1969) to *Cyrtina wellingtonensis* Dun, 1904. According to the concept of Savage (1969), the Australian specimens of *C. praecedens* are smaller and have fewer plications than *C. praecedens* from Podolia. The size differences between *C. wellingtonensis* from the Garra Limestone at Eurimbla (Brock 2003) and *C. praecedens* from the Mandagery Park Formation at Manildra (Savage 1969) are very subtle and there is size overlap. Either way, the species from New South Wales, Australia, are closely related to *C. praecedens* and confirm the morphological resemblance of the Early Devonian cyrtinids.

Alekseeva (1967) mentioned occurrence of *C. praecedens* in the Lower Devonian (Lower Settedabanskoy Horizon) of the Sette-Daban Mountains in north-eastern Russia (Verkhoyansk-Kolymian Fold Belt). Tcherkesova *et al.* (1994) referred specimens of Lochkovian age (Usttareyskiy Horizon) from the Tajmyr peninsula of North-eastern Russia to *C. praecedens*. Both occurrences are located near the margin of the Siberia terrane and confirm the presence of *C. praecedens* or closely related species outside Laurussia and Gondwana in the Early Devonian time.

However, there are also other Lower Devonian species of the genus *Cyrtina*. *Cyrtina heteroclita* (Defrance, 1824) has three plications on lateral slopes as the maximum (Gourvennec 1989), with markedly stronger sinus-bounding plications. The shells from Branžovy locality exhibits tree to four plications on lateral slopes and sinus-bounding plications in all four sampled valves are not conspicuously larger than other plications. According to Kozłowski (1929) the ventral median septum of *C. heteroclita* is formed by two plates ("lamelles externes du septum") and lack the internal lamella ("lamelle intraseptale"). Kozłowski (1929) stressed that the internal lamella is the characteristic feature of *C. praecedens*. The examined ventral septa of specimens from the Branžovy locality show a differently silicified internal lamella laterally enclosed by wider and weaker silicified side lamellae (Plate I, figs 11, 13, 15). The structure of the median septum is therefore more similar to the structure of *C. praecedens* than this in *C. heteroclita*. *Cyrtina intermedia* (Oehlert, 1887) from the Pragian (Gourvennec 1989) differs from specimens from Branžovy locality by more transverse shell, acute cardinal extremity in adults and four to seven plications in lateral slopes. The cardinal process of *C. intermedia* is simple while in *C. praecedens* consists from more lamellae (Gourvennec 1989). One dorsal valve from Branžovy exhibits two lamelae but this may be artifact of preservation by silicification. *Cyrtina utrimquesulcata* Fuchs, 1919 is weakly known (Fuchs 1919; Dahmer 1931, 1942, 1951) and Gourvennec (1989) suggested its identity with *C. intermedia*. *Cyrtina pauciplicata* Oehlert, 1887 differs from Bohemian specimens by very weak plications on lateral slopes (Gourvennec 1989).

DISCUSSION

Cyrtina praecedens Kozłowski, 1929 represents the earliest member of the cyrtinidid evolutionary clade. This Early Devonian species is followed by numerous subsequent species which have an extensive distribution in the temperate to tropical seas from the Lochkovian to the Viséan. Many Early to Late Devonian species of the genus *Cyrtina* are known from numerous sites of temperate to tropical Gondwana (Barrande 1879; Havlíček 1956, 1998; Savage 1969, 1974; Talent 1963; Drot 1964; Benedetto 1985; Gourvennec 1989; Havlíček & Vaněk 1998; García-Alcalde 2001; Brock 2003), Laurussia (Billings 1863; Clarke 1900; Fuchs 1919; Kozłowski 1929; Dahmer 1931, 1951; Biernat 1954, 1966; Nikiforova 1954; Amsden 1958; Boucot 1959, 1960; Amsden & Ventress 1963; Ehlers 1963; Johnson 1966, 1970, 1978, 1990; Lenz 1977; Havlíček & Ficner 1978; Johnson *et al.* 1980; Cooper & Dutro 1982; Perry 1984; Nikiforova *et al.*

1985; Brice 1988; Baliński 2012) and Siberia and associated terranes (Gratsianova 1967; Alekseeva 1967; Anderson *et al.* 1969; Alekseeva *et al.* 1970, 1981; Kulkov 1963; Bublitchenko 1974; Tcherkesova *et al.* 1994). The clade continues into the Carboniferous (Carter 1967; Brunton 1984, 1987; Mottequin & Brice 2016).

Brachiopod associations with abundant cyrtinids (Havlíček & Ficner 1978, Johnson & Trojan 1982, Brunton 1987, Johnson 1990, Havlíček 1998, Brice 2003) are often situated in agitated, shallow-water carbonate environments. The common development of *Cyrtina* and allied genera took place in the reef and forereef biotopes, often within a crinoid "gardens" and corals, but the genus is almost ubiquitous. It is also common in near-shore and neritic siliciclastic biofacies (Dahmer 1931, 1948; Boucot 1973) sometimes related with a deep and calm environment. Sea bed within the photic zone, with abundant brachiopods, corals and crinoids is suggested already for the Lochkovian members of the genus, including *C. praecedens*, *C. wellingtonensis*, and C. sp. (*sensu* Johnson 1990). Suggested fixosessile mode of life of *Cyrtina* (Bassett 1984) was confirmed by a direct observation by Głuchowski (2005) who described *Cyrtina* shell attached to crinoid pluricolumals. Twisted apex of herein figured ventral valves (Plate I, figs 6, 12) may be indicative of attachment to a crinoid stem.

CONCLUSION

The earliest member of the cyrtinid clade, *Cyrtina praecendes* Kozłowski, 1929 has been currently discovered among a taxonomically rich brachiopod and coral association of Lochkovian age in the Prague Basin of Central Bohemia, Czechia. The Bohemian specimens cannot be distinguished from the topotypic specimens from Podolia, Ukraine. Its occurrence in Bohemia confirms the rapid distribution of cyrtinids along shallow tropical and subtropical shelves of Gondwana, Laurussia and Siberia in the Lochkovian.

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