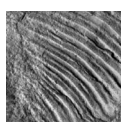


Unusual occurrence of dalmanitid trilobites in the Lochkovian (Lower Devonian) of the Prague Basin, Czech Republic

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Rare remains of *Reussiana* cf. *brevispicula* Hörbinger, 2000 have been collected near the Praha-Lochkov, together with a rich faunal association characteristic of the upper part of the Lochkov Formation (Lower Devonian, Lochkovian, *Monograptus hercynicus* graptolite Biozone). This occurrence confirms the earlier assumption that large Devonian dalmanitids (“odontochilinids”) appear in the Prague Basin below the Basal Pragian Regressive Event. The unique discovery represents one of the earliest occurrences of Devonian dalmanitids worldwide and sheds light on the migration and early radiation of dalmanitids within the Rheic Ocean realm during the Early Devonian. • Key words: Lower Devonian, Lochkovian, Prague Basin, *Reussiana*, Trilobita.

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Large dalmanitid (“odontochilinid”) trilobites are amongst the most characteristic fossils of Bohemian-type (or Hercynian) facies development of the Lower Devonian in European peri-Gondwanan terranes. This facies development is characterised by predominantly carbonate sedimentation (see Paris & Robardet 1990, Robardet 2003, Slavík 2004, Slavík *et al.* 2012). In the typical area of their occurrence, the Prague Basin (Fig. 1), dalmanitids are common in the Lower Devonian from the lower Pragian (basal parts of the Praha Formation) to the top of the lower Emsian (uppermost levels of the Zlíchov Formation). The sudden disappearance of dalmanitids at the top of the lower Emsian, corresponding stratigraphically with the onset of the Daleje Event (Chlupáč & Kukul 1988), is an important biostratigraphical marker for at least the Northern peri-Gondwanan region (Chlupáč 1994a, b).

The appearance of large dalmanitids (“odontochilinids”) in the Prague Basin was traditionally considered to coincide with the onset of the Praha Formation (*e.g.*, Chlupáč 1983, Chlupáč *et al.* 1998, Šnajdr 1987a, Hörbinger 2000), see Fig. 2. However, an incomplete pygidium of *Reussiana* cf. *brevispicula* Hörbinger, 2000

(Fig. 4C) apparently coming from older rocks at Lochkov was briefly discussed by Budil *et al.* (2009, p. 75). The specimen (MCZ 172827) was discovered in the Scháry collection (collected in the 19th century, stored in the Harvard University collections, Massachusetts, USA). On the basis of the particular rock type (grey bioclastic limestone containing fragments of small proetids of the *Lepidoproetus* group), a late Lochkovian age for the specimen was established but with doubts. A new found of a pygidium (CGS PB 300) of *Reussiana* cf. *brevispicula* from a biostratigraphically well-dated stratigraphical level now shows with certainty that dalmanitids were already present in the Prague Basin in the late Lochkovian, though they were uncommon at that time.

Geological settings

In 2009, during construction of a highway between Sliveneč and Lahovice, a new auxiliary route (an extension of “Za Ovčínem” Street) commenced at the hillside 400 m S of Lochkov Village (geographic co-ordinates: 49.997029 N,

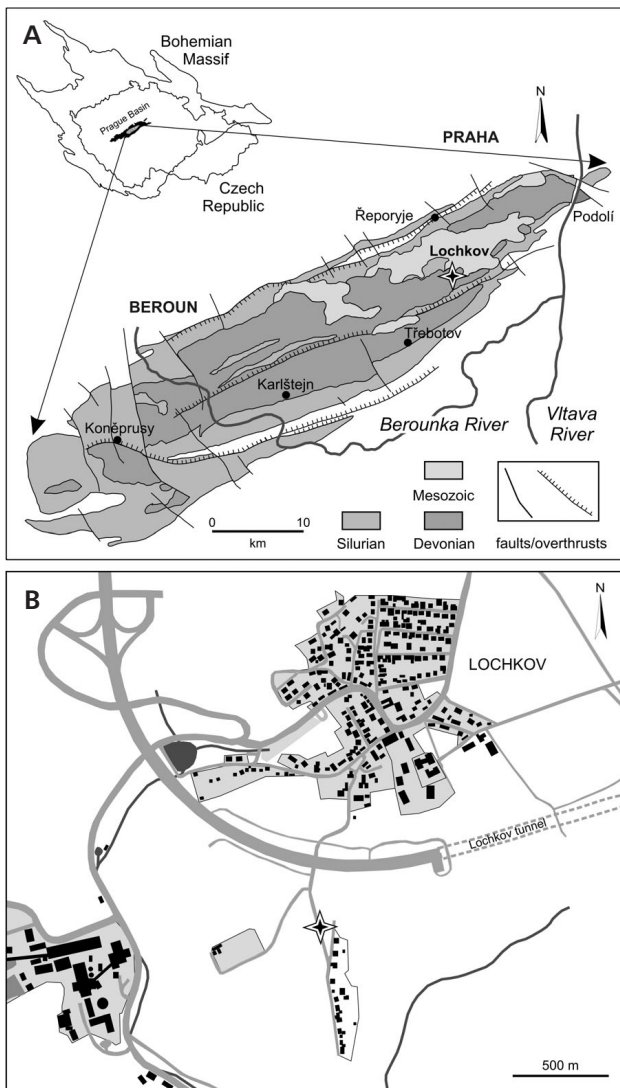


Figure 1. A – simplified geological map of the Prague Basin (after Budil *et al.* 2009, 2013). • B – map of the Lochkov district. The locality where the pygidia of *Reussiana cf. brevispicula* were collected indicated by a star in both maps.

14.350473 S). In the road cutting, heavily weathered calcareous shales and thin-layered, biosparitic limestones of the upper part of the Lochkov Formation, Radotín Limestone Member (Lower Devonian, Lochkovian) were exposed. A section approximately 30 m thick, moderately affected by tectonics (several minor faults) was documented (Fig. 3). The beds are generally inclined at approximately 20–30° to the north-west. Intensive weathering and decalcification (see Suchý 2002) has strongly affected the original character of the rocks. Traces of solifluction that originated during the Quaternary and the typical downslope bending of limestone layers were also observed at several places in the section.

An extremely rich fossil assemblage (see also Figs 4 and 5) was collected from the road cutting, including abundant and relatively well-preserved disarticulated speci-

mens of the brachiopods “*Howellella*” *digitatoides* Havlíček, 1959 and *H. inchoans* (Barrande, 1879), and uncommon *Plectodonta* sp., *Bleshidium?* sp., *Gypidula* sp., smooth atrypid, *Orthida* indet. and *Chonetida* indet. Of the other taxa represented, the cornulitid *Cornulites* sp., and the bivalves *Actinopteria cf. migrans* Barrande, 1881 and *Hercynella?* sp. are common; and the graptolite *Monograptus hercynicus* Perner, 1899, the gastropod *Platyceras?* sp., the trilobites *Leonaspis lochkovens* Prantl & Přibyl, 1949 and *Spiniscutellum* sp., and the phyllocarid crustacean *Ceratiocaris* sp. are rare. “*Orthoceras*” aff. *deletum* Barrande, 1868 and the bryozoan *Hederella?* sp. are also present. The occurrence of *Reussiana cf. brevispicula* Hörbinger, 2000 among this rich association is rather exceptional. The general character of the fossil assemblage corresponds well with that of the upper but not uppermost levels of the Lochkov Formation (mass occurrence of *Howellella* and *Cornulites*, common *Actinopteria cf. migrans*, index graptolite *Monograptus hercynicus* and trilobite *Leonaspis lochkovens*). The assemblage can be assigned to the well-known and widespread *Lochkovella-Lochkothele* Community *sensu* Havlíček & Štorch (1999) and the *Antipleura-Hercynella* Community group *sensu* Kříž (1999) on the basis of the species composition, though the index (nominotypic) genera are missing. Dalmanitid trilobites have not been recorded previously from these communities. This part of the Lochkov Formation lies within the *Paranowakia intermedia* dacryoconarid Biozone. The apparent absence of dacryoconarids in the exposure can possibly be explained by taphonomic bias due to the dissolution of the minute thin walled shells of dacryoconarids during the decalcification and heavy weathering of the limestone and shale.

Systematic palaeontology

Superfamily Dalmanitoidea Vogdes, 1890
 Family Dalmanitidae Vogdes, 1890
 Subfamily Dalmanitinae Vogdes, 1890

Remarks. – Early Devonian dalmanitids of Bohemian-type (or Hercynian) facies development were included in the subfamily Odontochilinae Šnajdr, 1985 by Šnajdr (1985, 1987a, b). Budil *et al.* (2009) considered the discrimination of this subfamily as problematic, because most features regarded as diagnostic by Šnajdr (1985) are shared with other dalmanitid groups and are not of taxonomic importance above the generic level (see also discussion by Ramsköld 1985). There are major problems even in the generic assignment of some “late” Silurian and Early Devonian dalmanitids, especially of Laurentian and current Australian origin, and in finding unambiguous distinguishing features between *Dalmanites* Barrande, 1852 and *Odontochile*

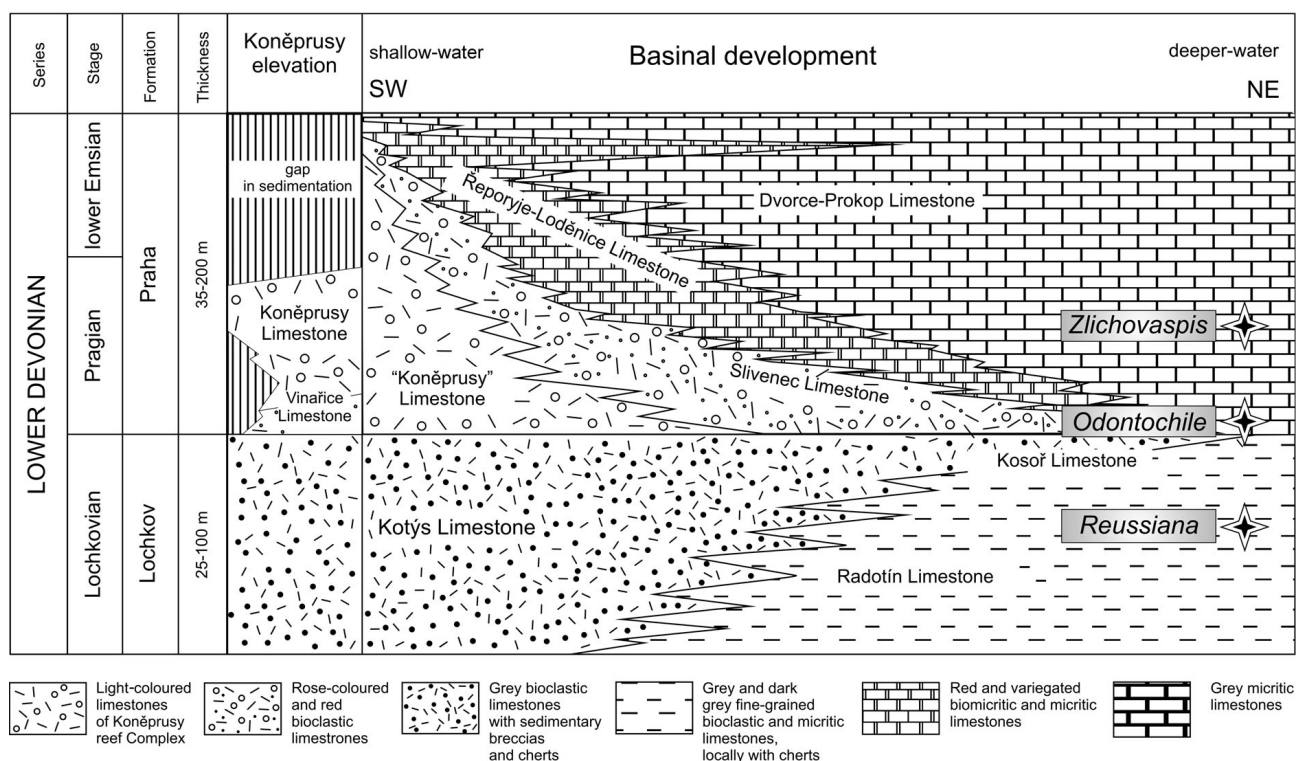


Figure 2. Lochkovian to lowermost Emsian stratigraphy of the Prague Basin (after Chlupáč 1977 and Chlupáč in Chlupáč et al. 1998, modified by Budil et al. 2009, 2013). Stars show the stratigraphic position of the currently known FADs of *Reussiana*, *Odontochile* and *Zlichovaspis*.

Hawle & Corda, 1847. It seems that evolution of the “odontochilid” features occurred at least to a certain degree gradually and independently in several phylogenetic lineages. Many of these features appear randomly, at different times. In addition, Budil et al. (2009) also discussed the possibility of the polyphyletic origin of taxa originally included in this subfamily by Šnajdr (1985, 1987a), with two main lineages – *Reussiana*-*Odontochile* and *Zlichovaspis*-*Zlichovaspis* (*Devonodontochile*). The similar body shape of these large dalmanitids can be explained by their similar feeding habit; i.e. a change from the predation-dominated to the scavenging-dominated mode of life (see Budil et al. 2008) within the scavenger-predator feeding habit *sensu* Fortey & Owens (1999).

Genus *Reussiana* Šnajdr, 1987b

Type species. – *Phacops reussii* Barrande, 1846; Pragian Stage, Praha Formation, Dvorce-Prokop Limestone (upper part), Prague Basin, Barrandian area, Czech Republic.

Reussiana cf. *brevispicula* Hörbinger, 2000

Figure 4A–C

Description of specimen CGS PB 300. – Pygidium elongated, length/width index altered to about 0.63 by strong flat-

tening of the specimen, with a very short, indistinct mucro. Axis with 19–20 rings plus terminal piece. Pleurae with 17 deep pleural furrows. More posterior ribs tend to develop an imbricate profile – resulting from anterior pleural bands having very steep posterior slopes and less steep anterior slopes. Pleural ribs extend almost to lateral and posterior margin of pygidium. Pygidial border wide, border furrow indistinct. Inner part of doublure margin coinciding with the line of pygidial border but the pleural furrows and ribs extend for virtually the entire width of the border. Axial rings, pleural bands and border densely granulated.

Measurements. – Length (*sag.*) 49 mm; estimated maximum with about 80 mm.

Remarks. – The pygidium is strongly reminiscent of *R. brevispicula* in general morphology, including the outline, the very short and robust mucro, and the very steep posterior slopes of the anterior pleural bands. In size it is comparable with the largest known specimens of *R. brevispicula* (the holotype is 35 mm long and the largest known pygidium is about 90 mm long). The specimen differs from pygidia of the type species *Reussiana reussi* (Barrande, 1846) in its narrower outline, higher number of axial rings and pleural furrows, very steep posterior slopes of the anterior pleural bands, and especially in the narrower pleural furrows. The surface sculpture is very poorly preserved, hindering

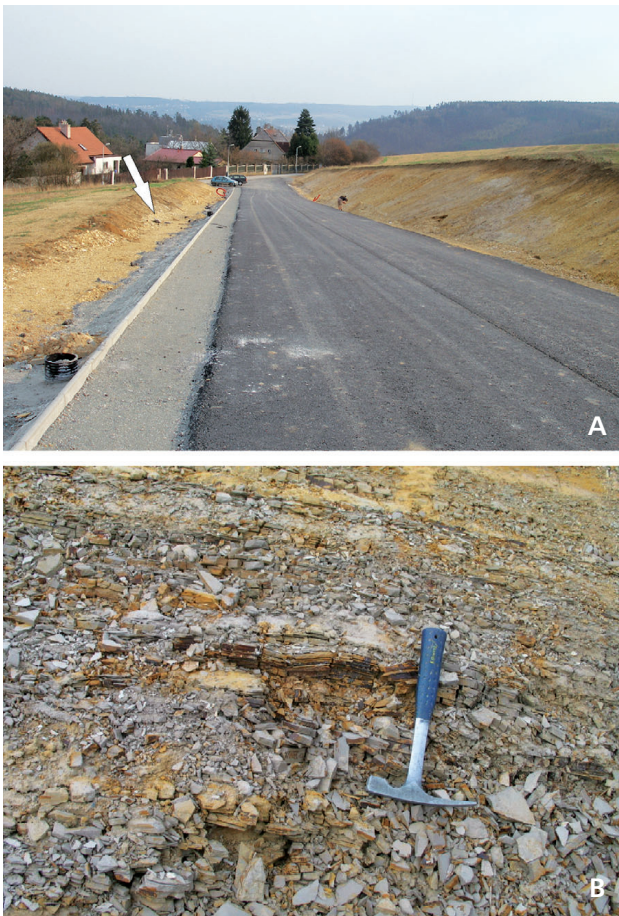


Figure 3. The road cutting at Praha-Lochkov. • A – general view of the outcrops from the north; arrow indicates the locality of *Reussiana* cf. *brevispicula*. • B – platy limestones intercalating with shales.

comparison with better-preserved specimens from unweathered limestones. Nevertheless, it is apparent that very dense granulation is present on the pleural bands, and is probably more prominent than in Pragian representatives of the genus (cf. Fig. 4B, E, F). In the number of segments and the shape of the pleural furrows this specimen is similar to the pygidium of *Reussiana* housed in the Scháry collection (see above) and apparently coming from a similar stratigraphic horizon, and both specimens are considered to belong to the same species. It is uncertain whether their differences from *R. brevispicula* could justify the erection of a new subspecies for them.

As for species described from outside the Prague Basin, *Reussiana? batymarginata* (Maksimova, 1968), from the upper Silurian (Přídolí?) or lowermost Devonian of Kazakhstan, closely resembles *R. cf. brevispicula* in the rather elongated pygidium with distinctly narrow pleural furrows, but has fewer pygidial segments (see Budil *et al.* 2009). *R.? schischkatensis* (Balashova, 1968), from strata of possible Pragian age in Tajikistan, shares the large number of pygidial segments and narrow pleural furrows with *R. cf.*

brevispicula, but differs especially in the distinctly wider pygidial outline and coarser sculpture on both axial rings and pleural bands.

Remarks on palaeogeography and possible migrations of Early Devonian dalmanitids

The newly discovered specimens of *Reussiana* indicate the relatively early migration of this genus into the Prague Basin, whereas *Odontochile* and *Zlichovaspis* appeared here slightly later (in Pragian; Budil *et al.* 2009; see also Fig. 2). All three genera were very significant members of the Pragian *Reedops-Odontochile* Assemblage *sensu* Chlupáč (1983) and/or the *Odontochile-Prokopia* Biofacies *sensu* Havlíček & Vaněk (1998). It is unlikely that *Reussiana* had its evolutionary origins in the Prague Basin, where dalmanitids are absent in the Silurian except for the rare pauci-segmented forms *Struveria orba* (Barrande, 1852) and *Delpops? dermolac* Šnajdr, 1981 in the uppermost Wenlock. Neither of these forms is closely related to *Reussiana*, and there is a considerable time difference between their occurrence and that of *Reussiana* in the Lochkovian. The oldest known representatives of *Reussiana* are in the upper Silurian (Přídolí?) or lowermost Devonian of Kazakhstan (Maksimova 1968, T.N. Koreň – personal communication) and we consider that this region was probably the evolutionary centre for the genus.

Early Devonian palaeogeographic reconstructions, with Siberia in the Northern Hemisphere, Kazakhstan north of the equator, and Perunica between Western Gondwana in the south and Laurussia in the west, suggest that several migration routes may have been possible (Fig. 6). The recognition of possible migration routes must consider the dispersal abilities of dalmanitid larvae. Budil *et al.* (2009) suggested that the metaprotaspides of dalmanitids, though preferring rather medium-deep shelf environments rather than extremely shallow waters, probably had limited possibilities to migrate across wider, open ocean regions. The anaprotaspid stage (see Whittington & Kelly 1997, cf. Laibl *et al.* 2014) is not known in dalmanitids, the youngest documented specimens of which belong to early metaprotaspid stages possess a typically adult-like body plan *sensu* Speyer & Chatterton (1989) (*i.e.* considered to be benthic).

The migration of *Reussiana* into the Prague Basin may be most easily explained *via* a possible connection with regions to the south of Kazakhstan, accounting for the dispersal of the genus in both the southern and northern hemispheres along the south and north equatorial currents. This migration route (A in Fig. 6) is consistent with the suggested course of the South Equatorial Current (*sensu* Wilde 1991) as well as the South Tropical Current along the NE margin of Laurussia (see Scotese & McKerrow 1990,

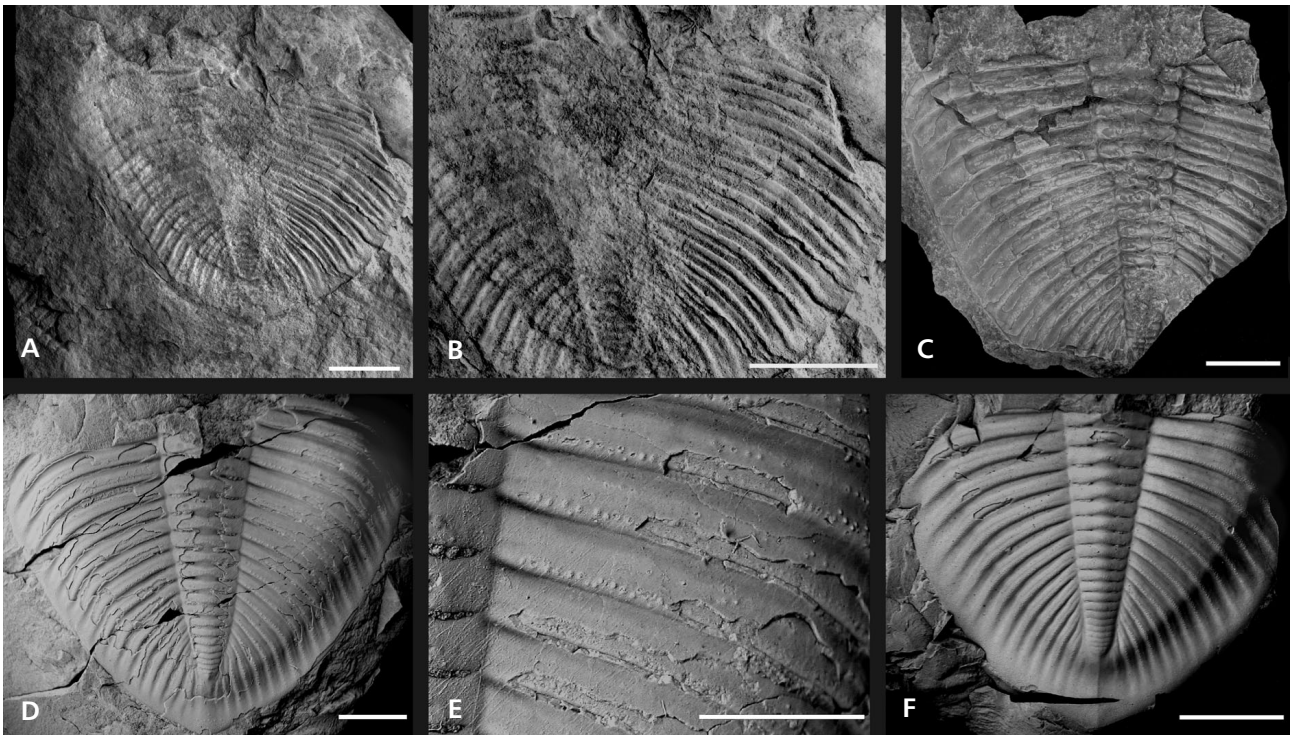


Figure 4. A, B – *Reussiana cf. brevispicula* Hörbinger, 2000. Strongly flattened pygidium, external mould and fragment of another pygidium (left lower corner), CGS PB 300. Lochkov Formation (Lower Devonian, Lochkovian Stage, *Monograptus hercynicus* Biozone) exposed at Praha-Lochkov. A – dorsal view; B – detail. • C – *Reussiana cf. brevispicula* Hörbinger, 2000; incomplete pygidium preserved in dark grey bioclastic limestone (?upper part of Lochkov Formation, Lochkovian Stage), MC 172827 (Scháry coll.), Lochkov, dorsal view. • D, E – *Reussiana brevispicula* Hörbinger, 2000. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies (lower part), Černá rokle near Kosof. Pygidium, holotype CGS PB 159. D – dorsal view; E – detail of the right pleural field. • F – *Reussiana reussi* Barrande, 1846. Pragian Stage, Praha Formation, Dvorce-Prokop Limestone facies. Pygidium with exoskeleton, CGS PB 211, dorsal view. Černá rokle near Kosof. Scale bars represent 10 mm.

Cocks & Torsvik 2006). The migration of *Reussiana* into the Prague Basin together with other, more common elements (warburgellid trilobites – see Chlupáč 1983, brachiopods – see Havlíček & Štorch 1999, bivalves – see Kříž 1999 and cephalopods – see Manda 2001) was already possible in the early Lochkovian. Later Lochkovian faunas became rather endemic in the Prague Basin (for further discussion of Lochkovian faunas in peri-Gondwana and Northern Gondwana areas, see especially Gnoli 1985, Gnoli et al. 1988, Manda & Frýda 2010, Frey et al. 2014 a.o.). In the latest Lochkovian there was another, minor influx of new trilobite elements – e.g. *Reedops* Richter & Richter, 1925 and *Pragoproetus* Šnajdr, 1977 – into the Prague Basin. This influx is notable worldwide, even within offshore realms (see Chlupáč 1994b, p. 489), and preceded the later evolution of Pragian and Emsian trilobite communities. It is uncertain whether the appearance of *Reussiana* in the Lochkovian of the Prague basin is related to the first or the second event. Rare and fragmentary remains of *Reussiana* (*R. thuringica thuringica* Alberti, 1967 and *R. thuringica franconica* Alberti, 1969) are known in the Pragian of Saxo-Thuringia (Alberti 1967, 1969) but these occurrences very probably reflect subsequent dis-

persal of *Reussiana* within the Rheic Ocean, possibly starting in the Prague Basin.

Exchange of dalmanitid trilobites may also have been possible between Laurussia and European peri-Gondwana (B in Fig. 6). However, Laurussian dalmanitoids include the almost endemic synphoriids, which are absent in the Devonian of Perunica (Lespérance 1975, Holloway 1981). To explain the migration of *Reussiana* (unknown in Laurussia), *Odontochile* and the related but probably separate *Zlichovaspis* evolutionary lineage (uncertain occurrence in Laurussia) to Perunica via this connection would be highly speculative. The rare occurrence of *Zlichovaspis* in the Emsian of the Rheinische Schiefergebirge (Eastern Avalonia, after Linnemann 2000) most likely represents a later dispersal of the genus.

The rare occurrence of certain early Silurian dalmanitids, such as *Dalmanites? fezzanensis* El Chair et al., 1985 in North Africa, and the rich dalmanitid fauna there of “Bohemian type” (including *Reussiana*, *Odontochile* and *Zlichovaspis* since the Pragian; see Budil et al. 2009) indicates the exchange of invertebrate fauna, including trilobites, within Western Gondwana in the Early Devonian (C in Fig. 6). On the other hand, migration of *Reussiana*

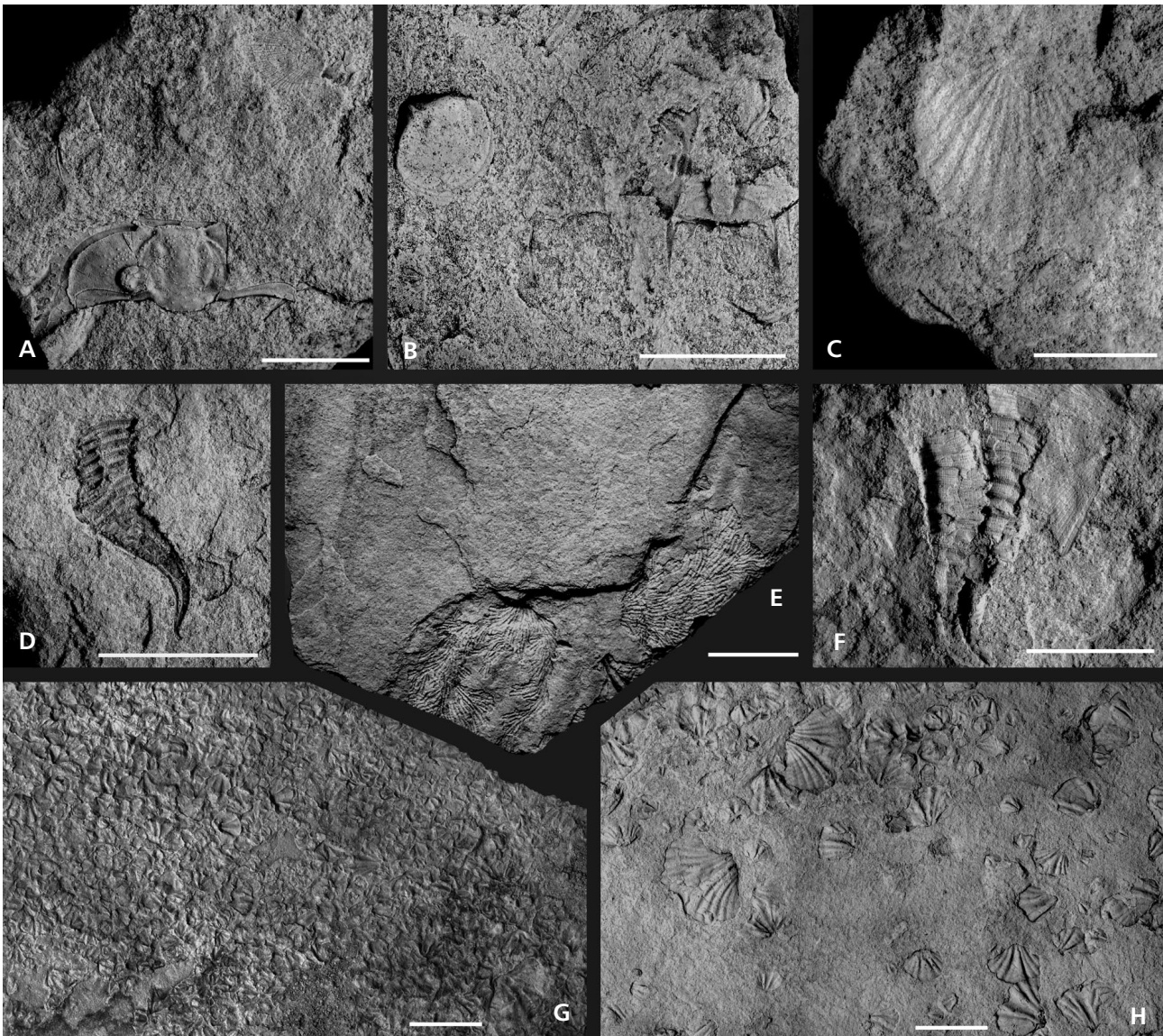


Figure 5. Fauna of the upper part of the Lochkov Formation (Lower Devonian, Lochkovian Stage, *Monograptus hercynicus* Biozone) exposed at Praha-Lochkov. • A, B – *Leonaspis lochkovensis* Prantl & Přibyl, 1949. A – incomplete cephalon CGS PB 307, dorsal view; B – two incomplete pygidia (internal and external moulds), dorsal view, CGS PB 308. • C – *Spiniscutellum?* sp., poorly preserved pygidium, CGS PB 313. • D, F – *Cornulites* sp. D – specimen CGS PB 304, dorsal view; F – specimens CGS PB 302, dorsal view. • E – *Hederella?* sp. coating the shell of “*Orthoceras*” aff. *deletum* Barrande, 1868, CGS PB 323. • G – *Howellella digitatoides* Havlíček, 1959, specimen CGS PB 337. • H – *Howellella inchoans* (Barrande, 1879), specimen CGS PB 336. Scale bars represent 10 mm.

from present-day North Africa into the Prague Basin is less probable, as the genus is not known in the Lochkovian of North Africa.

The evolutionary origin of *Odontochile* remains somewhat obscure, as representatives of the genus appear almost contemporaneously in the lower Pragian of the Prague Basin and in the Pragian of North Africa.

The extension of the Perunica – Western Gondwana migration route to the east (D in Fig. 6) was considered by Budil *et al.* (2009) to be responsible for the migration of *Zlichovaspis* from Eastern to Western Gondwana.

The earliest questionable representative of *Zlichovaspis*, *Z. (Z.)? formosa* (Gill, 1948), occurs in the Lochkovian of Australia (Jell 1989, Jell & Holloway 1983, Šnajdr 1987a) and it is therefore possible that the genus originated in this area. However, the supposedly opposite direction of the South Subpolar Current and the large distance between Eastern and Western Gondwana, including Perunica, make this migration route questionable. Nevertheless, in the Silurian and Devonian of south-eastern Australia, faunal elements of “Bohemian” character (*e.g.* brachiopods, cephalopods and graptolites, the same gen-

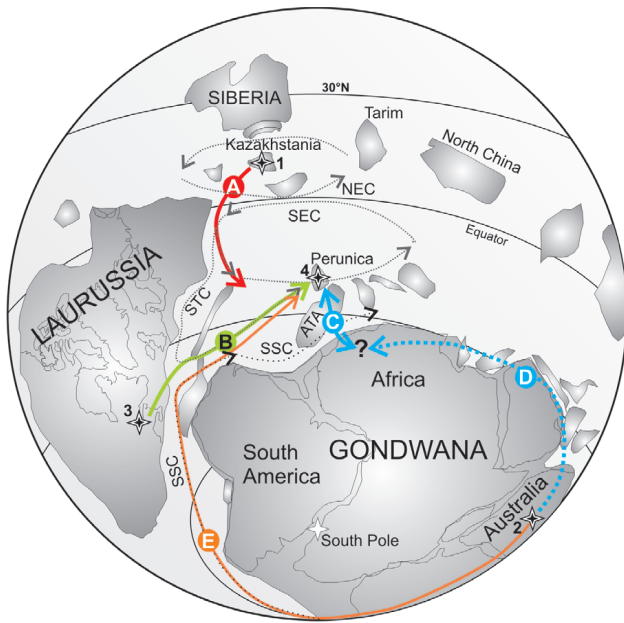


Figure 6. Palaeogeographic map of the world in the Early to Middle Devonian; simplified and modified after Cocks & Torsvik (2006). Stars numbered 1–4 show currently known occurrences of late Přídolí to Lochkovian dalmanitids: 1 – *Reussiana? batymarginata*, Přídolí to Lochkovian of Kazakhstan; 2 – *Zlichovaspis (Z.)? formosa*, Lochkovian of SE Australia, 3 – late Silurian (?) and Early Devonian dalmanitids in Laurussia (e.g., *Forillonaria* Lespérance, 1975; *Huntoniatonia* Campbell in Jell & Adrain, 2003, = *Huntonia* Campbell, 1977; *Neoprobolium* Struve, 1958; *Odontochile* Hawle & Corda, 1847 and *Phalangocephalus* Campbell, 1977), 4 – *Reussiana cf. brevispicula* in the Prague Basin (this contribution). Supposed direction and abbreviations of ocean currents modified after Wilde *et al.* (1991): SEC – South Equatorial Current; STC – South Tropical Current; SSC – South Subpolar Current. For details, see discussion in the text.

era of phacopids and other trilobite groups) occur repeatedly (see Chatterton *et al.* 1979, Holloway & Neil 1982, Jell & Holloway 1983, Chlupáč 1994b, Strusz & Garratt 1999, Sandford 2006, Sandford & Holloway 2006). In addition, brachiopods of Australian type became established in the Prague Basin during the early Emsian (Havlíček 1994). It may be speculated that the Basal Pragian Regressive Event (see Chlupáč & Kukal 1988) and other eustatic changes during the Early Devonian (Johnson *et al.* 1985) temporarily influenced oceanic circulation patterns and temporarily opened new migration routes. This interpretation, however, is not consistent with the recent investigation of magnetic susceptibility and gamma-ray spectrometry by Vacek (2011) who speculated that eustatic sea-level changes played only a subordinate role in the Lochkovian-Pragian boundary interval in the Prague Basin.

Another speculative migration route may have been along the South African and South American margins (E in Fig. 6), utilising the South Subpolar Current (SSC). However, this route is unlikely as dalmanitoids are represented

in the Lower Devonian of these regions (the Malvinokaffric Realm) by endemic forms (see also Budil *et al.* 2009).

Conclusions

The first record of Lower Devonian dalmanitid trilobites in the Prague Basin is in the upper Lochkovian. The time difference between the appearance of *Reussiana* (upper Lochkovian), *Odontochile* (lower Pragian) and *Zlichovaspis* (higher Pragian) suggests that the migration of these trilobites into Perunica was not a single event, as traditionally supposed, but was a rather gradual and multi-source episode (Fig. 2). The rarity of *Reussiana* in the upper Lochkovian of the Prague Basin may be explained by unfavourable living conditions for these trilobites (partial dysoxia, prevailing deposition of bioclastic limestones). Similarly, an abrupt onset of unfavourable living conditions (increased input of siliciclastics) may have caused the disappearance of large dalmanitids (preferring calcareous muddy substrate) in the Prague Basin at the level of Daleje Event, near the base of the upper Emsian.

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