Lower Devonian dalmanitid trilobites of the Prague Basin (Czech Republic)

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ABSTRACT: A revision of the Lower Devonian dalmanitid trilobites of the Prague Basin (Czech Republic) is presented. The subfamily Odontochilinae Šnajdr is considered a synonym of Dalmanitidae Vogdes. Twenty-one previously and five newly described (three in open nomenclature) species and subspecies occur in the Prague Basin from the lowermost Pragian (one problematic specimen possibly comes from the uppermost Lochkovian) to the Lower Emsian; the last questionable record is from the Upper Emsian. The species have been assigned to four genera and subgenera: *Odontochile* Hawle & Corda, *Reussiana* Šnajdr, *Zlichovaspis* (*Zlichovaspis*) Přibyl & Vaněk and *Zlichovaspis* (*Devonodontochile*) Šnajdr. These trilobites are considered as scavengers or opportunistic predators, living most of their lives as vagrant benthos burying in the muddy substrate to find organic remains. The first undoubted adult-like meraspid specimens are described.

KEY WORDS: Bohemia, Dalmanitidae, Devonian, Trilobita

Dalmanitid ('odontochilinid') trilobites are amongst the most characteristic fossils of the Bohemian type (or Hercynian) facies development of the Lower Devonian in European peri-Gondwanan terranes. This facies development is characterised by prevailing carbonate sedimentation (see Paris & Robardet 1990; Robardet 2003; Slavík 2004; Valenzuela-Ríos & Slavík 2004). However, dalmanitid trilobites are known not only from carbonate but also from fine clastic sequences deposited in a number of basins that developed in the northern peri-Gondwanan realm, Kazakhstania, Laurentia, South America and Australia. In their typical area of occurrence, the Prague Basin (Fig. 1), dalmanitids range from the base of the Pragian (Praha Formation) up to the Lower Emsian (Zlíchov Formation) (Fig. 2). At the base of the Upper Emsian Daleje–Třebotov Formation they abruptly disappear, with only two questionable fragments known from the Daleje Shale (Upper Emsian; see also Šnajdr 1987a).

1. Historical review

Lower Devonian dalmanitid trilobites have been thoroughly studied in Bohemia for more than 200 years. Zeno (1770) described specimens that probably belonged to *Odontochile* Hawle & Corda, 1847 but these can no longer be traced. A few years later, Born (1775) described a specimen that he related to *Entomolithus* of Linnaeus (1759). This specimen, a pygidium of *Odontochile hausmanni* (Brongniart, 1822), has been found in the palaeontological collections of the Natural History Museum, London. It is the oldest surviving trilobite specimen from the Barrandian area, and was briefly redescribed by Budil & Fortey (2004). Šnajdr (1987a) pointed out that *Asaphus hausmanni* [=*Odontochile hausmanni* (Brongniart, 1822)] is also the first validly described trilobite species from Bohemia, followed by *Asaphus auriculatus* [=*Zlichovaspis auriculata auriculata* (Dalman, 1827)], described on the basis of illustrations published by Sternberg (1825). In 1846, Barrande described *Phacops reussi* [=*Reussiana reussi* (Barrande, 1846)]. Of particular importance is the revision by Hawle & Corda (1847). These authors described the genus *Odontochile* and several new species, of which only two, *Odontochile cristata* and *Odontochile rugosa*, are now regarded as valid. Barrande (1852, 1872) rejected *Odontochile* as invalid but accepted the above-mentioned species, which he assigned to *Dalmania* (in 1852) or *Dalmanites* (in 1872). From his 'Etage G' Barrande figured and described a total of nine species, three of them new – *Dalmania spinifera*, *Dalmania Fletcheri* and *Dalmania MacCoyi*); however, *Dalmania Fletcheri* was included by Šnajdr (1984) in the synonymy of *Zlichovaspis rugosa rugosa* Hawle & Corda. Almost a hundred years after Barrande's last work, Přibyl & Vaněk (1971) revised the Bohemian dalmanitids, supported the validity of *Odontochile*, and described a new subgenus *Odontochile* (*Zlichovaspis*). However, Campbell (1977) considered this subgenus as of doubtful utility. Extensive investigations by Šnajdr (1984, 1985, 1987a, b) substantially improved knowledge of this trilobite group. Šnajdr (1984) carefully revised the type specimens of Hawle & Corda (1847) and subsequently (Šnajdr 1985) erected the new subfamily Odontochilinae, as well as two new genera, *Spinodontochile* and *Devonodontochile,* and five new species and subspecies. In an extensive and very detailed study (Šnajdr 1987a), another five species and subspecies were described. Šnajdr (1987b) also replaced the generic name *Reussia* Maksimova, 1972 with *Reussiana* because of homonymy.

The results of Šnajdr's investigations were complex and detailed, and not easily understood. Some, mostly non-Czech, palaeontologists accepted the results (Edgecombe & Ramsköld 1994; Basse 2003), in some cases with reservations (Ramsköld 1985). However, Šnajdr's taxonomic concepts were strongly criticized by the majority of Czech palaeontologists and several parallel models were used by Chlupáč (1999, 2000, 2002a, b),

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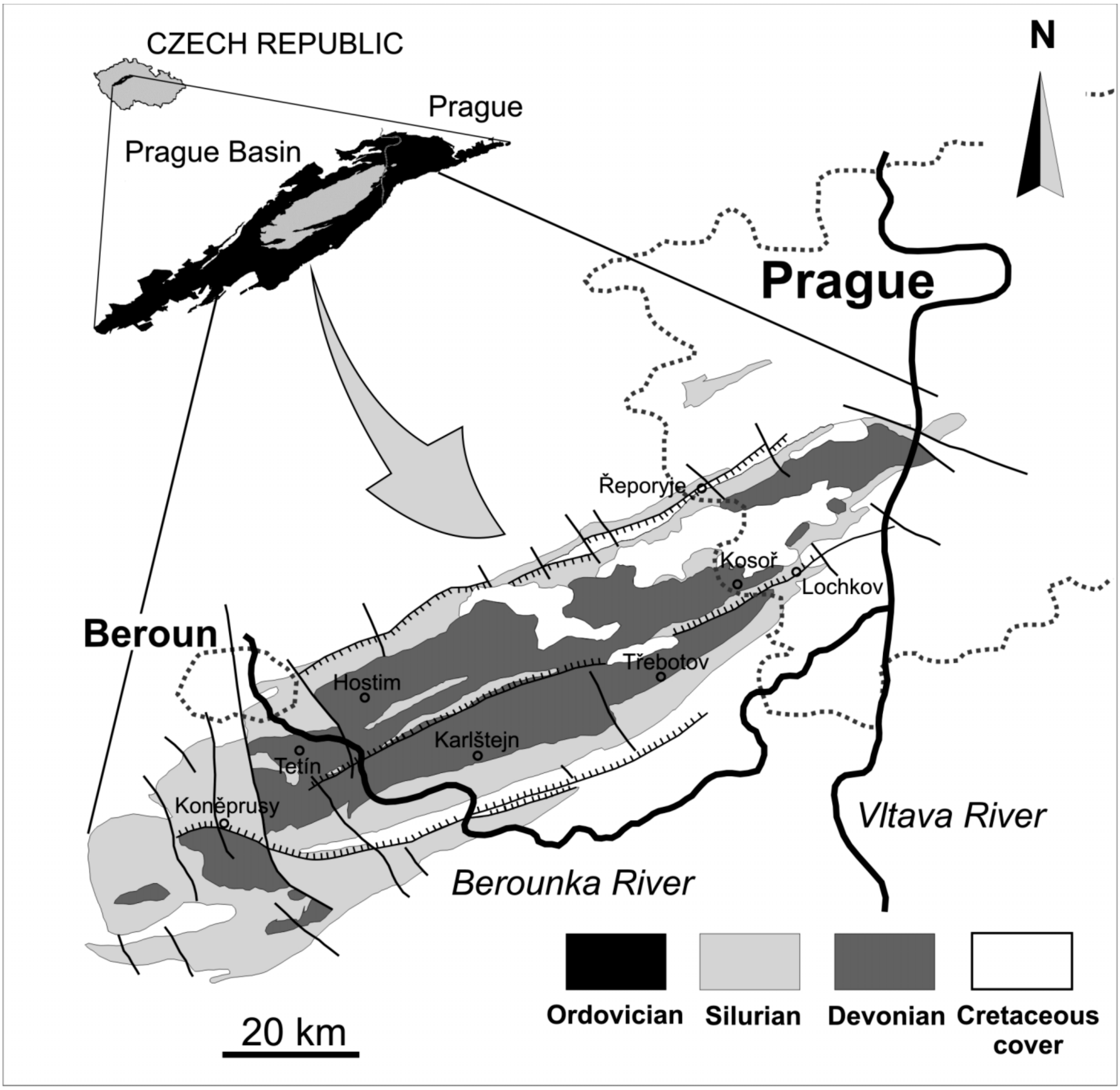

Figure 1 Distribution of Ordovician, Silurian and Devonian rocks in the Prague Basin (including the position of selected important localities discussed in the text). After Chlupáč (1993), modified.

Chlupáč *in* Chlupáč *et al.* (1998), Havlíček & Vaněk (1998), Pek & Vaněk (1989), Vaněk & Valíček (2002) and Vaněk (2002a, b). Some species and subspecies described by Šnajdr (1985, 1987a) were based on minor differences in morphology, or were poorly defined on insufficient material, and in many cases they are scarcely determinable in the field. Some of Vaněk & Valíček's (2002) opinions were shared by Jell and Adrain (2003) who regarded both *Devonodontochile* and *Spinodontochile* as junior synonyms of *Zlichovaspis*. New data on the stratigraphical occurrence of some species were published by Havlíček & Vaněk (1998), Hörbinger (2000) and Vaněk (1999). However, doubts about the validity of many taxa persisted, and a new revision is highly desirable, as these trilobites have often been compared in detail with related species from other European countries, North Africa, North America, Asia and Australia. The new data from this revision surprisingly support a major part (but not all) of Šnajdr's (1985, 1987a) conclusions.

2. Geological setting

The Prague Basin (Figs 1 and 2) is situated in Bohemia, part of the Czech Republic. Marine sedimentation in the basin commenced in the early Tremadocian and persisted into the Middle Devonian (Chlupáč *et al.* 1998). In the Early Devonian, as a part of the Perunica microcontinent (Havlíček *et al.* 1994), the Prague Basin was situated in low southern latitudes (Cocks 2000; Robardet 2003). This, together with minimal supply of terrigenous material into the basin and the probable absence of volcanic activity, resulted in the deposition of almost entirely carbonate sediments during the Lochkovian, Pragian and Early Emsian. In the Lochkovian, grey to white-grey bioclastic limestones of the Kotýs Limestone facies accumulated on elevated parts of the sea floor (mostly in the SW and W part of the basin), whereas dark grey biomicritic limestones with intercalations of dark grey shales, representing the Radotín Limestone facies, are typical of the

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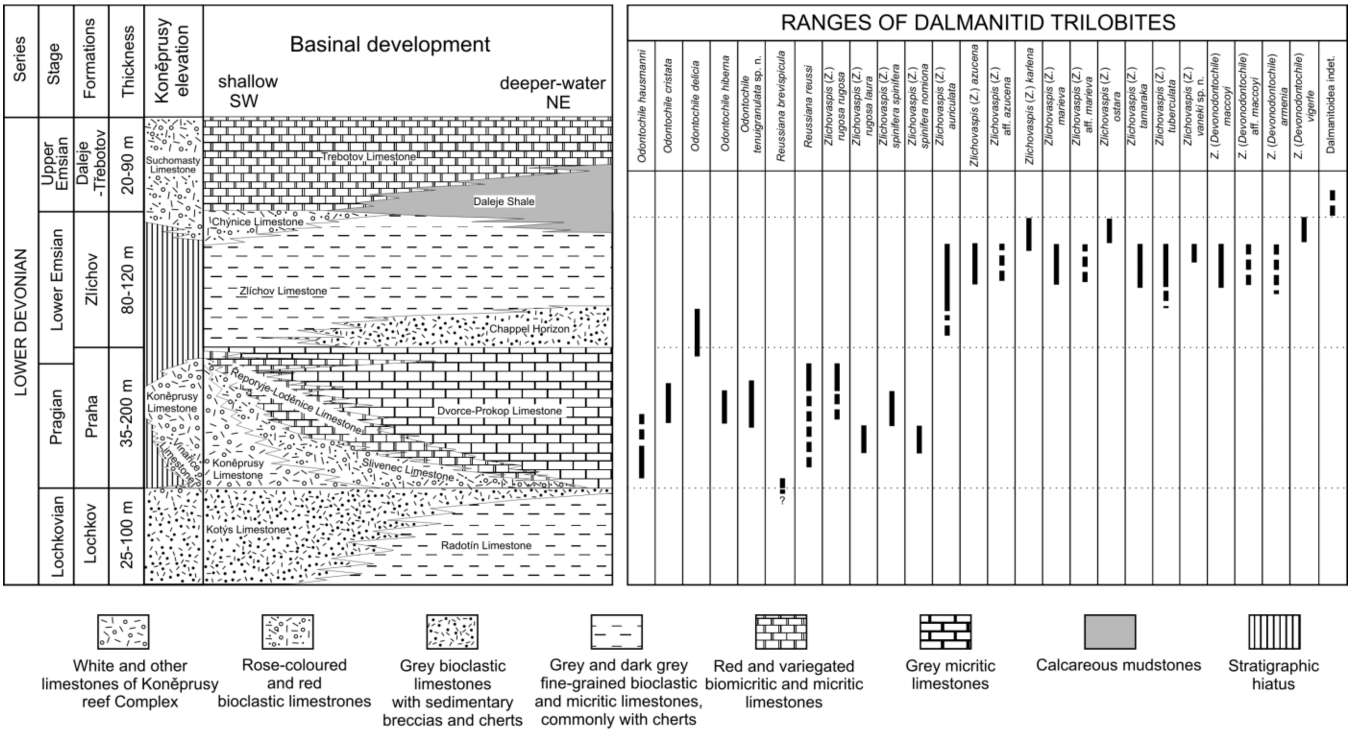

Figure 2 The facies distribution of the Lower Devonian strata (after Chlupáč in Chlupáč *et al.* 1998, modified) and stratigraphic ranges of Lower Devonian dalmanitid trilobites in the Prague Basin.

deeper, NE part of the basin. At the beginning of the Pragian, a global regressive event (Chlupáč & Kukal 1988) caused shallowing of the basin. This drop in sea level coincided with the tectonic upheaval of the present Koneprusy area (see Fig. 1), which strongly affected conditions of sedimentation in the SW part of the basin. During the Pragian a reef formed here, probably with at least a local hiatus during the regression maximum. Abundant bioclastic material was deposited in the neighbourhood of this reef structure and formed the white bioclastic Koněprusy Limestone facies with an abundant, shallow-water fauna (corals, stromatoporoids, crinoids, etc.). On the reef periphery, or in its lower and upper parts (alternative models; see Hladil 1995, 1997; Hladil & Slavík 1997; Havlíček & Vaněk 1998; Vaněk 1999; cf. with Chlupáč 1998, 2003), the red-purple Vinařice Limestone was deposited, containing an abundant shallow-water fauna including sporadic dalmanitids. The stratigraphic and palaeogeographic relations between the elevated Koněprusy area and the deeper parts of the basin are partially hidden owing to a major tectonic structure, the Očkov Thrust, which separates the Koněprusy area from the remaining parts of the basin. Nevertheless, along a NW–SE transect, a gradual facies change is observed from the Koněprusy–Vinařice and Loděnice limestone (Chlupáč 1998). However, knowledge of the faunal content here is relatively poor. The Koněprusy Limestone facies also occurs outside the Koněprusy area, in the lowermost part of the Pragian sequence in the SW part of the basin. In deeper parts of the basin there are many outcrops with well-documented vertical and lateral facies changes, forming continuous lithological series from white bioclastic Koněprusy limestone at the base of the sequence, through purple bioclastic Slivenec (with abundant stromataktis cavities, see Hladil *et al.* 2006), variegated Loděnice, pink micritic Řeporyje and grey micritic Dvorce–Prokop limestones (e.g. Chlupáč 1957, 1998, 2003). The lithological character of the Koněprusy limestones outside the Koněprusy area is almost identical with the 'true' Koněprusy Limestone but their faunal content is different, being comparable rather with the Slivenec Limestone (cf. Havlíček & Vaněk 1998; Vaněk 1999). Whether the Koněprusy Limestone is a diachronous unit or not lies outside the scope of this paper and therefore is omitted in Figure 2, as no determinable dalmanitid remains are known from this rock type outside the Koněprusy area (with the exception of Branžovy near Loděnice, where a special facies development of Lower Pragian occurs). Also, evaluation of the reinstated division of the Dvorce–Prokop Limestone facies (see Havlíček & Vaněk 1998; Vaněk 1999; Hörbinger 2000) into Dvorce Limestone (massive micrites forming mostly the lower part of the member) and Prokop Limestone (thin-bedded micrites common in the upper parts) is beyond the scope of this systematic revision. The two facies sometimes alternate, and therefore the terms lower and upper parts of the Dvorce–Prokop Limestone facies are used here. In the Early Emsian (=Zlichovian regional stage) Zlíchov Formation, the facies relations are simpler. At the base of the formation, in the NE part of the basin, thick layers of breccias and coarse bioclastic limestones form the so-called Chappel Horizon. This horizon gradually disappears towards the SW. It probably represents a destroyed reef structure SE of the preserved sedimentary outcrop. The Zlíchov Limestone (biomicritic platy limestones alternating with platy biosparitic limestones and calcareous shales) represents the main part of this formation. In the upper part of the Zlíchov Formation, the red biodetritic Chýnice Limestones are typical in the SW part of the basin, whereas in the NE part a diachronous onset of rather deeper-water Daleje calcareous shales is characteristic. These shales are typical of the lower part of the Upper Emsian Daleje–Třebotov Formation and are succeeded by micritic Třebotov Limestone (which locally represents entire sequence of the formation).

The complicated facies development and variation in faunal content of the formations reflect several independent and mostly conflicting controls: the synsedimentary tectonics causing sometimes prominent differences in the subsidence rate of the sea floor, and sea-level fluctuations with regression and transgression events causing changes in the sea-current regime, but possibly also in salinity, temperature and nutrient content.

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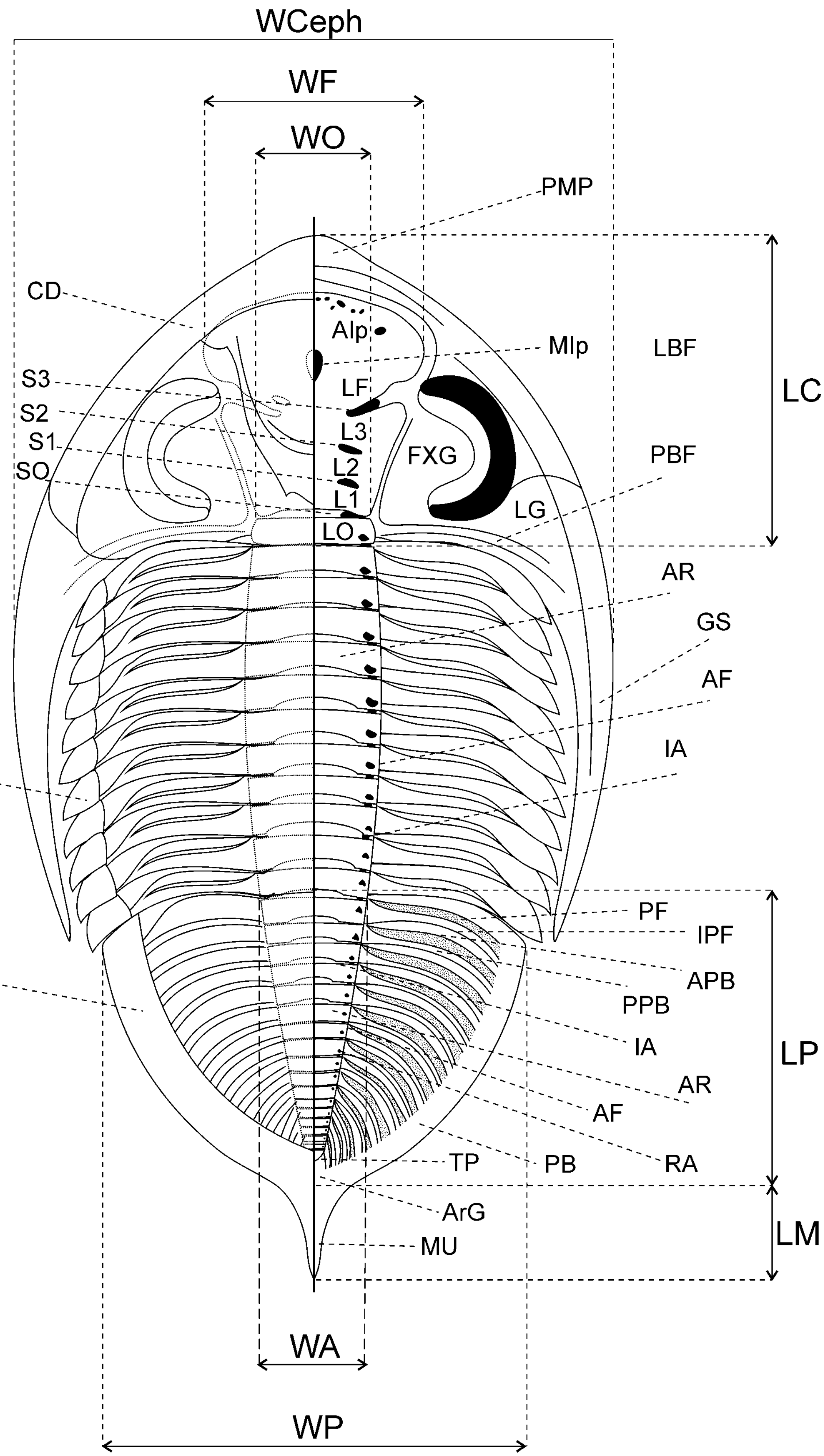

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There are several uncertainties, especially in the detailed conodont and tentaculite biostratigraphy within the thick Praha and Zlíchov formations; however, the boundary intervals are mostly well documented (Chlupáč *et al*. 1998; Chlupáč 1999; Slavík 2004). In addition, locally intensive tectonic deformation of the Lower Devonian rocks often obscures the original sedimentary structures (see Röhlich 2007).

The classical facies scheme of Chlupáč (Chlupáč 1957, 1977; Chlupáč *et al*. 1998) is considered here as essentially valid but requiring some modification in the future. For the purpose of the present work, this scheme was modified mainly in the relationship of the shallow-water and tectonically separated Koněprusy area to the deeper parts of the basin. In particular, the time and space relations of the Vinařice Limestones to the Loděnice and Slivenec limestones are crucial for the correlation of the dalmanitid assemblages. In the Zlíchov Formation, the space and time relations between the occurrences of the biodetritic Chýnice and biomicritic Zlíchov formations, together with the onset of the calcareous shales of the Daleje–Třebotov Formation (Daleje Shale Facies), are important for dating the last extensive radiation and abrupt disappearance of dalmanitids in the Prague Basin.

3. Systematic palaeontology

3.1. Remarks on morphology

Morphological terminology (see Fig. 3) generally follows Whittington & Kelly (1997), supplemented by some terms defined by Šnajdr (1987a, 1990) that are considered more appropriate for precise description of the dalmanitid exoskeleton (for example, precranial median process). Similarly, in the description of sculpture the terminology of Šnajdr (1987a) is preferred rather than that used by Størmer (1980) for phacopid and chasmopinid trilobites. The term ‘granule’ is used in accordance with Whittington & Kelly (1997) to refer to minute protuberance of the exoskeleton, smaller than tubercles or pustules *sensu* Størmer (1980). ‘Thorn-like granule’ and ‘small vertical spine’ have no analogy in the terminology of Størmer (1980); ‘hollow spine’ roughly corresponds to his ‘spine tubercle’, and ‘megagranule’ to his ‘large globular tubercle’. The term ‘tubercle’ is used here to refer to a large, knob-like prominence of the external surface of the exoskeleton, slightly perceptible also on internal moulds as a slight elevation.

Several indices based on body measurement and biometrics are used in the diagnoses and descriptions (Fig. 3). These indices include especially the ratios of cephalic length to width, pygidial length (excluding mucro) to width, and axial width to pygidial width. They were also used by Šnajdr (1987a) and Rábano (1990). However, these indices are of limited usefulness because of variation due partly to tectonic deformation that commonly affects large exoskeletal parts. Because of this deformation, length/width diagrams and more sophisticated biometrical methods were not used, although they were attempted during an early stage of investigation.

More than 80 complete and/or almost complete specimens were examined, showing a wide range of exoskeletal configurations ranging from almost fully extended to partially enrolled. These observations, as well as more detailed remarks on the hypostomal morphology and exoskeletal structures, were discussed by Budil *et al*. (2008) and Budil & Hörbinger (2007).

3.2. Generic and subgeneric features

For the generic and suprageneric classification, the following features were used: vaulting of the exoskeleton (mostly affected by deformation but characteristic for some genera; e.g. *Reussiana*); outline of the cephalon; presence or absence of the precranial median process; outline of the pygidium; length and shape of the mucro; depth and width of pleural furrows and interpleural furrows; width and vaulting (tr.) of the pygidial axis; width of the pygidial doublure – possibly correlated with width of the axis, as pointed out by Campbell (1977); shape of the hypostome; and presence or absence of megapores. Megapores are typically present only in *Zlichovaspis* (*Devonodontochile*), though fine pores are common also in *Reussiana*. However, most of the larger sculptural elements are also perforated (large perforated granules, perforated short spines and perforated spines).

Several features are almost invariable within Bohemian Lower Devonian dalmanitids (e.g. long genal spines reaching the pygidium; shape of the occipital, S1 and S2 apodemes; LF with distinct median, anterolateral and frontal auxiliary impressions; facial suture circumscribing the LF at some distance; large eyes (almost reaching posterior border furrow); large multi-segmented pygidium with anterior pleural bands generally more vaulted and broader than posterior pleural bands). These features were regarded by Šnajdr (1985) as diagnostic of his subfamily Odontochilinae, but they also appear independently in other Silurian and Devonian dalmanitid trilobites (see discussion of the family Dalmanitidae in section 3.5).

3.3. Specific features

A total of 72 features were considered during this present study, but those found to be most important taxonomically are: outline of the cephalon; length and shape of the precranial median process; shape of the anterior and lateral borders, numbers of dorsoventral files and lenses in the eye; position of the omega point of the facial suture; details of hypostomal morphology (e.g. granulation; length of the posterior and posterolateral spines); vaulting of the anterior and posterior pleural bands; length/width ratios of cephalon and pygidium; and details of the sculpture. These features show variation of some kind and the range of this variability is discussed for each species. The numbers of pygidial axial rings and pleural ribs, commonly used to distinguish species of trilobites, are so variable in Bohemian Lower Devonian dalmanitids that in most cases they could not be used as useful diagnostic features, though they are distinctive for few species, for

Figure 3 The morphology of a dalmanitid exoskeleton. Abbreviations: (AF) axial furrows; (AIp) auxiliary impressions on the LF; (APB) anterior pleural bands; (AR) axial ring; (ArG) axial ridge; (CD) cephalic doublure; (FXG) fixigena; (GS) genal spine; (IA) interring apodemes; (IPF) interpleural furrow; (LBF) lateral border furrow; (LO) occipital lobe; (LF) frontal glabelar lobe; (L1), (L2), (L3) lateral glabelar lobes; (LG) librigena; (MIp) median cephalic impression; (MU) mucro; (PB) pygidial border; (PBF) posterior border furrow; (PD) pygidial doublure; (PF) pleural furrow; (PMP) precranial median process; (PPB) posterior pleural bands; (RA) Ring apodemes; (S1), (S2), (S3) lateral glabelar furrows; (SO) occipital furrow; (TP) terminal piece; (TPD) thoracic pleural doublure. Length and width measurements: (LC) length (sag.) of the cephalon; (LM) length of the mucro; (LP) length of the pygidium (without spine); (WA) width of the pygidial axis; (WCeph) width of the cephalon (transv.); (WF) width of the LF; (WO) width of the LO; (WP) width of the pygidium.

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example *Zlichovaspis* (*Z.*) *azucena* (Šnajdr, 1987a). The sculpture of the dorsal exoskeleton proved to be a good diagnostic feature at the specific level. Although variable, the distribution and number of sculptural elements (for example, the number of large granules or thorn-like granules on axial rings, anterior pleural bands and posterior pleural bands and their spatial distribution) are usually characteristic for every species. From this point of view, the main results of Šnajdr (1987a), although slightly re-interpreted, may be considered as supported by the present study.

3.4. Remarks on descriptions

Past difficulties in differentiating some of the species discussed in the present paper have arisen because the differences between many of them are rather subtle, and many (not all, see Šnajdr 1985) lacked concise, informative diagnoses. Such diagnoses are presented here for all species, accompanied by discussions of the differences between them. To reduce the length of the text, detailed descriptions are given only for *Odontochile hausmanni* (Brongniart, 1822), for the new species, or if these descriptions substantially supplement older data. In other cases, the new observations are presented under the heading 'Remarks'.

All figured and cited specimens are housed in the following institutions: National Museum in Prague (NML); Czech Geological Survey (CGS; public collections of M. Šnajdr – MŠ, J. Vaněk – JV and P. Budil – PB); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); and Museum of Bohemian Karst in Beroun (MB). Most figured specimens were coated with ammonium chloride before photography, but a few specimens, as indicated, were not coated for reasons of conservation.

3.5. Systematics

Class Trilobita Walch, 1771
Order Phacopida Salter, 1864
Suborder Phacopina Struve *in* Richter *et al.*, 1959a
Superfamily Dalmanitoidea Vogdes, 1890
Family Dalmanitidae Vogdes, 1890
Subfamily Dalmanitinae Vogdes, 1890

Remarks. Conservation of the subfamily Odontochilinae Šnajdr, 1985 is considered here as very problematic and unmaintainable. Most features used in the definition of this subfamily cannot be considered adequate, as they are shared with other dalmanitid groups. Although some of these features are distinctive (e.g. long genal spines reaching pygidium, facial suture lying outside the preglabellar furrow, detailed hypostomal morphology), the taxonomic importance of these features, in our opinion, does not exceed the generic level (see discussion by Ramsköld 1985). Major problems persist even in the generic assignment of some Upper Silurian and Lower Devonian dalmanitids, especially of Laurentian and current Australian origin, and in finding unambiguous distinguishing features between *Dalmanites* and *Odontochile* (see discussion of *Odontochile* below). It seems that evolution of the 'odontochilinid' features took place at least to a certain degree gradually and independently in several phylogenetic lineages. Many of these features appear randomly, at different times. In addition, the present authors cannot entirely dismiss the possibility of the polyphyletic origin of taxa originally included in this subfamily by Šnajdr (1985, 1987a). Two main evolutionary lineages can be distinguished:

1. *Odontochile–Reussiana*, which appears at the base of the Pragian Stage and disappears in the lower Emsian. According to Maksimova (1972), this lineage is ancestral to *Kasachstania*, and a detailed study of Maksimova's material in the VSEGEI collections, Saint Petersburg, may cautiously support this idea because of some shared features (see discussion of *Reussiana*). However, Edgecombe & Ramsköld (1994) proposed instead that '*Reussiana*-like' features evolved independently in the two separate dalmanitid lineages Dalmanitinae and Odontochilinae.
2. *Zlichovaspis* (*Zlichovaspis*) and *Zlichovaspis* (*Devonodontochile*), ranging from the Lochkovian (or possibly upper Silurian) to the lower Emsian; i.e. they are contemporaneous with the phylogenetically more conservative *Kasachstania*.

Because of all these uncertainties, we regard the Odontochilinae as a junior synonym of Dalmanitinae.

Genus *Odontochile* Hawle & Corda, 1847

Type species. *Asaphus Hausmanni* Brongniart, 1822, Lower Pragian, Praha Formation, Dvorce–Prokop Limestone Facies, *Turkestanella acuaria* dacryoconarid zone.

Diagnosis. Exoskeleton large (maximum sag. length may exceed 150 mm), moderately vaulted. Length/width index approximately 1·6. Cephalon semicircular, with long genal spines reaching pygidium. Anterior cephalic margin semicircular to parabolic, no precranial median process. Facial suture lying outside the preglabellar furrow. S1 and S2 apodemes deeply incised, no longitudinal glabellar furrow. Eyes very large, almost reaching axial furrows at γ and almost reaching posterior border furrow at ε. Doublure wide, flat. Hypostome elongated subtriangular, with three prominent posterior and two smaller posterolateral denticles. Pygidium large, subtriangular, length/width index 0·65–0·75. Axis approximately 0·22 times maximum pygidial width, with 16 to 20 rings. Pleural furrows 13 to 14 in number, deep and wide, flat, interpleural furrows narrow but prominent in some species. Anterior pleural bands more vaulted and broader than posterior pleural bands. Mucro generally short and broad-based, but longer and narrower in stratigraphically younger species. Sculpture of fine and coarse granules.

Remarks. Some recent authors (e.g. Alberti 1967, 1969, 1970, 1983; Přibyl & Vaněk 1971; Pek & Vaněk 1989; Hörbinger 2000; Vaněk & Valíček 2002) regarded the name *Odontochile* as of neuter gender. However, we consider it to be feminine, as did the original authors Hawle & Corda (1847), who used it in conjunction with adjectival species-group names with feminine endings. According to Dr D. Muchnová (Institute of Greek and Latin Studies, Charles University), use of this name as neuter is not well supported, and Dr D. Holloway has advised that, although 'cheilos' from which it is derived is neuter, by changing the ending to e the gender is also changed.

The systematic value of some features distinguishing *Odontochile* and *Zlichovaspis*, as discussed by Přibyl and Vaněk (1971) and Šnajdr (1984, 1987a), are doubtful if *Odontochile* includes *O. delicia* Šnajdr, 1987a. A detailed discussion of these features is given in the remarks on *Zlichovaspis*. Distinguishing *Odontochile* from *Dalmanites* (e.g. see Delo 1935; Richter & Richter 1943; Richter *et al.* 1959b; Maksimova 1972; Campbell 1977; Ramsköld 1985; and in some respects also Edgecombe & Ramsköld 1994) also presents some problems, especially in regard to species from outside the Prague Basin. The following main distinguishing features are considered important here: (1) larger size of *Odontochile*; (2) long genal spines reaching pygidium; (3) facial suture lying outside the preglabellar furrow; (4) absence of precranial median process or spine; (5) hypostome with three prominent posterior and two less expressed posterolateral

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denticles; and (6) thoracic pleurae equally curved at front of thorax and at wide (tr.), multi-segmented pygidium. Some of the above-mentioned features are present also in other dalmanitid genera (for example, the large, multi-segmented pygidium is characteristic of *Bessazoon* Curtis & Lane, 1998), but it is the combination of all of the characters that the present authors regard as diagnostic of *Odontochile*.

Maksimova (1972) described two new subgenera of *Odontochile*, *O.* (*Kasachstania*) and *O.* (*Reussia*) (= *Reussiana*), both now regarded as independent genera. Later, Maksimova (1978) proposed a third subgenus, *O.* (*Pacifina*), based on *Odontochile arcuata* Maksimova, 1968 from the Lower Devonian of central Kazakhstan. The type species is poorly preserved in fine-grained sandstones but can easily be distinguished from all other representatives of the Dalmanitinae by the sharply parabolic outline of its cephalon and pygidium, the very narrow, almost non-existent pygidial border, the prominently keel-like elevation of the postaxial ridge, etc. Despite these distinctive characters, the original diagnosis of *Pacifina* and the species included overlap somewhat with *Forillonaria* Lespérance, 1975.

Species assigned. *Odontochile hausmanni* (Brongniart, 1822); *O. cristata* Hawle & Corda, 1847; *O. delicia* Šnajdr, 1987a; *O. hiberna* Šnajdr, 1985; *O. magrebiana* Alberti, 1983, *O. tenuigranulata* sp. n.

Occurrence. Pragian and Lower Emsian of Perunica, Iberia, northern peri-Gondwana and possibly also Laurentia.

Odontochile hausmanni (Brongniart, 1822)
Figs 4a–j; 12d

1822 *Asaphus Hausmanni* Brgt.; Brongniart, p. 21; pl. 2, figs 3A, B.

For older synonymy, see Šnajdr (1987a).

? 1961 *Odontochile hausmanni* (Brongniart); Mirouse & Pillet, p. 477, pl. 16, figs 6–8.

1987a *Odontochile hausmanni* (Brongniart); Šnajdr, pp. 20–23, pl. 1, figs 1–7, pl. 19, figs 2–4, text-fig. 4–1.

1989 *Odontochile* (*Odontochile*) *hausmanni* (Brongniart); Pek & Vaněk, p. 14.

1998 *Odontochile* (*Odontochile*) *hausmanni* (Brongniart); Chlupáč in Chlupáč *et al*., pl. L, fig. 6.

2000 *Odontochile* (*Odontochile*) *hausmanni* (Brongniart); Hörbinger, pp. 10–11.

2002 *Odontochile hausmanni* (Brongniart); Vaněk & Valíček, p. 10.

2002a *Odontochile* (*Odontochile*) *hausmanni* (Brongniart); Chlupáč, pp. 33–34.

Neotype. Designated Šnajdr (1984); an almost complete specimen with exoskeleton preserved in limestone (eyes broken off), NML 15015. Figured by Barrande (1852, pl. 24, fig. 1), Šnajdr (1987a, pl. 1, fig. 5); Fig. 4a–b. This specimen was selected as lectotype by Chlupáč (in Horný & Bastl 1970) but, as it is not a syntype, that designation is invalid (Vaněk & Valíček 2002, p. 10).

Type horizon and locality. Lower Devonian, Pragian Stage, Praha Formation, Dvorce–Prokop Limestone, exact horizon unknown; Praha–Dvorce.

Other material. Barrande's twelve original specimens stored in the National Museum, Prague, 70 complete and nearly complete specimens, including one entirely enrolled specimen from the Schary collection (MCZ 172821), 25 hypostomes and about 800 selected cephala and pygidia. All specimens are preserved with exoskeleton and/or as internal moulds with relics of exoskeleton.

Diagnosis. A species of *Odontochile* with semicircular or very slightly parabolic anterior cephalic margin. Pygidium with 16 to 17, rarely 18 to 19 axial rings plus terminal piece. LF with dense, large granules finer anteriorly. L2, L3, palpebral lobes and median part of occipital ring with prominent sculpture of sparse, thorn-like, large granules. Eyes with lenses arranged in 50–59 (rarely 60–62) dorsoventral files of up to 14–15 lenses each. Axis of thorax and pygidium with large granules unequal in size. First few pygidial axial rings bear about 10–15 (rarely up to 18–20) granules. Anterior pleural bands of pygidium and thoracic segments bear a row of sparse granules, becoming finer and densier abaxially; small granules occur sporadically on posterior pleural bands.

Description. Exoskeleton macropygous. Cephalon semicircular, with length/width index approximately 0·5. Anterior margin subcircular to very slightly parabolic, but in some specimens curvature of margin is interrupted by a shallow, indistinct concave deflection in line with anterolateral projection of axial furrow (see Barrande 1852, pl. 24, figs 2–5; Fig. 4a). No precranial median process is present and median part of margin is well rounded. Anterior cephalic border is slightly convex, with shallow epiborder furrow. Distinct ridge runs along anterior cephalic margin. Epiborder furrow well rounded in cross-section but sharper on fixigena and genal spine. Robust and long genal spines elliptical in cross-section, reaching second pygidial rib. Posterior border narrow (exsag.), expanding distally. Posterior border furrow not reaching lateral border furrows. Occipital lobe strongly convex (tr.) medially. Median node large, prominent, but relatively low. Occipital furrow moderately deep medially; occipital apodemes narrow (exsag.) and deep. Axial furrows wide, shallow, slightly deeper posteriorly. Preglabellar furrow shallow. Sl and S2 furrows transglabellar, shallow but with very deep, narrow apodemes directed obliquely backwards. S3 furrows deep with distal portion strongly expanded exsagittally. L1, L2 and L3 lobes slightly convex, L2 and L3 lobes with inflated abaxial part. LF lobe wide, convex, with pronounced median impression, and with several auxiliary impressions in its anterior part. Two of these auxilliary impressions, situated towards lateral extremities of LF lobe, are more distinct than others and are visible on internal moulds (see Barrande 1852, pl. 24, figs 2, 3, 5). Pustular, vaulted genal field. Palpebral lobes large, with deep but tiny pits along facial suture. Palpebral furrow deepest opposite δ. Very large eyes with steep visual surface. Prominent, deep furrow is developed beneath visual surface. Dense, fine granulation on anterior and lateral borders, genal field and spines. LF granulose becoming finer forwards. Sparse thorn-like granules on L3, palpebral lobes and near occipital node. Hypostome (see Šnajdr 1987a, pl. 1, figs 6–7, pl. 19, fig. 2) elongated (sag.), with slightly vaulted middle body. Maculae faintly perceptible. Lateral border narrow, lateral and posterior border furrows distinct. Posterior margin with three short spines (one median and two lateral) and two less expressed posterolateral denticles. Outer surface of hypostome granulose; inner surface bears sparse and tiny muscle scars.

Thoracic axis moderately vaulted (tr.), increasing slightly in width on segments 1 to 4 and decreasing in width on segments 5–11. Rings slightly vaulted, with weak lateral lobes, posterior margin arched anteriorly. Pleural furrows deep, wide, lanceolate in outline; anterior and posterior pleural bands narrow (exsag.). Pleural tips curve backwards distally to sharp point. Axial rings covered by thorn-like granules unequal in size. Finer thorn-like granules on anterior and posterior pleural bands.

Pygidium subtriangular, with posterolateral margin rounded in outline. Length/width index approximately 0·70–0·75. Axis about 0·22–0·23 times maximum pygidial width,

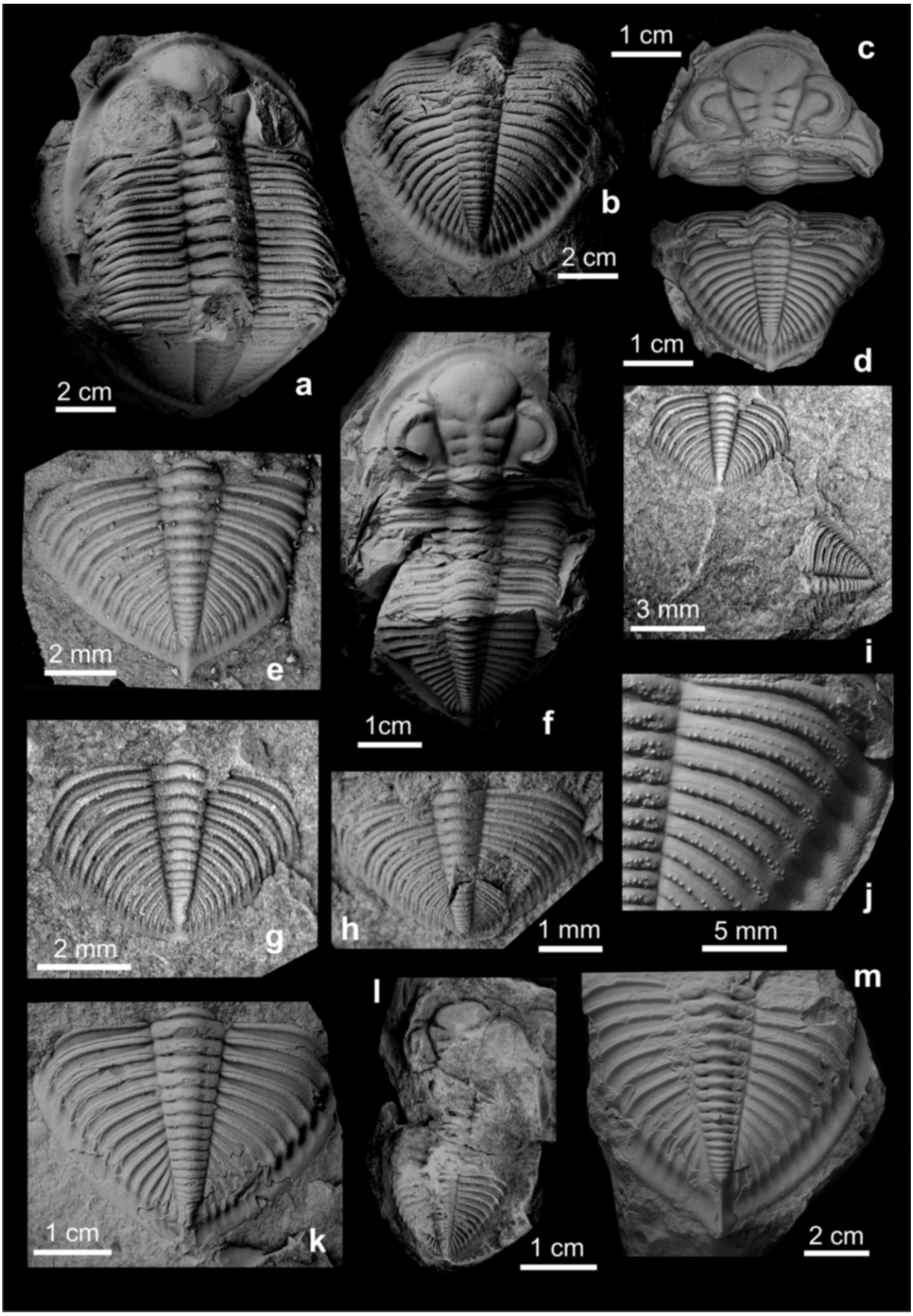

Figure 4 (a–j) *Odontochile hausmanni* (Brongniart, 1822). Praha Formation, Pragian Stage, Dvorce–Prokop Limestone facies: (a) A nearly complete specimen, neotype, NML 15015, Praha–Dvorce, dorsolateral view; (b) The same, posterior view showing pygidium; (c–d) Entirely enrolled specimen, MCZ 172821. Locality unknown: (c) cephalon, dorsal view; (d) pygidium, dorsal view; (e) An early holaspid pygidium, latex cast of CGS PB 152, Radotín; (f) A nearly complete specimen, AD Barrande pl. 2A, fig 13, NML 17012, Lochkov, dorsal view; (g) An early holaspid pygidium, MCZ 172822, Radotín; (h) Late meraspid to early holaspid pygidium, CGS PB 453, Radotín; (i) Two early holaspid pygidia, dorsal view, MCZ 172823, Lochkov; (j) A detail of the pygidium of incomplete specimen, NML 38252, Praha–Hlubočepy. (k–m) *Odontochile cristata* (Hawle & Corda, 1847), Praha Formation, Pragian Stage, Dvorce–Prokop Ls facies: (k) Pygidium, internal mould with exoskeleton, CGS MŠ 14381, Černá rokle near Kosoř, dorsal view; (l) Incomplete specimen, internal mould with relics of exoskeleton, MCZ 172854, Lochkov?; (m) Large pygidium, internal mould with exoskeleton, lectotype NML 19799, Praha (exact locality unknown).

narrowing uniformly backwards, rounded posteriorly. Vaulted (tr.) postaxial ridge extends onto mucro; combined length of postaxial ridge and mucro about 0·2 times axial length. Apodemes present in lateral parts of at least inter-ring furrows 1 to 11. Pseudo-articulating half-ring well developed on second ring, less distinct on rings 3 to 6. Pygidial ribs curved on anterior part of pygidium but almost straight near postaxial ridge. Thirteen to 14 deep and wide pleural furrows; interpleural furrows weak; both pleural and interpleural furrows extend weakly onto border. Anterior pleural bands vaulted. They are higher and wider than posterior pleural bands and widen abaxially to a point above inner margin of doublure. Posterior pleural bands low, narrowing abaxially. Pygidial border weakly vaulted, narrow. Border furrow wide and shallow. Thorn-like granules on axial rings and anterior pleural bands (10–15 granules forming row adaxially, becoming finer and densier abaxially). Small granules occur on posterior pleural bands. Pygidial border and mucro densely and finely granulose. Broad doublure, excluding steeply inclined inner flange, gently convex, finely granulose; inner flange smooth, without sculpture.

Ontogeny. Pygidia of early holaspides differ from larger pygidia in the following features:

1. The mucro is longer and narrower, and more sharply pointed distally. At its base it is more convex (tr.) with a slight sagittal keel-like ridge.
2. Anterior pleural bands are more strongly vaulted. In the smallest specimens they slightly overlap the pygidial outline, forming indistinct spinose processes.
3. Pleural furrows are narrower than in larger specimens, relatively deep and distinctly perforated by dense, fine pores.
4. Interpleural furrows are deeper and also contain a row of pores.
5. The granular sculpture is sparser and weaker on the axial rings and anterior pleural bands, on the latter forming an irregular row along the posterior margin. Granules are rare on the posterior pleural bands, where they are also smaller.

There are no clear differences between large and small pygidia in the number of segments. Šnajdr (1987a) stated that a pygidium 4·5 mm long (from Praha–Braník) has $12\frac{1}{2}$ ribs and 18 axial rings plus a terminal piece. The present authors have recorded similar numbers in several pygidia 4–8 mm long in the collections of CGS, NM and MCZ. These specimens include CGS PB 453 (4 mm long) with 17(18) axial rings and 13–14 pleural furrows (Fig. 4h), and CGS PB 152 (6·5 mm) with 16(17) axial rings and 13 comparatively wider pleural furrows (Fig. 4e).

Very large pygidia (50 to 60 mm in sagittal length) are slightly wider (smaller length/width index) than other specimens and have coarser granules on posterior pleural bands; however, the difference in proportions may be due to deformation.

Measurements. The neotype, a complete specimen, is 61 mm long. The largest known pygidium is 95 mm in overall length, and other fragments of pygidia and cephala of large specimens indicate that the exoskeleton reached a length of up to 250 mm.

Remarks. Several discrepancies concerning the synonymy of this species were solved by Šnajdr (1984, 1987a) and the present authors agree with most of his conclusions. However, an incomplete pygidium (specimen CGS JV 1758) that was figured by Přibyl & Vaněk (1971, pl. 7, fig. 2) as *O.* (*O.*) *cristatum* Hawle & Corda, and regarded by Šnajdr (1987a) as a gerontic pygidium of *O. hausmanni,* is now assigned to the new species *O. tenuigranulata*.

Occurrence. The species is very abundant in the lower part of the Praha Formation (lower *Nowakia* (*Turkestanella*) *acuaria* biozone, lower layers of the Dvorce–Prokop Limestone Facies) at Prague (Dvorce, Braník, Hlubočepy Valley, Barrandova skála Rock, Malá and Velká Chuchle, Lochkov, Klukovice, Požáry II quarry near Řeporyje, Kosoř–Černá rokle gorge and quarry opposite the mouth of Černá rokle gorge) and Karlštejn. It is rare in the transitional layers between the Slivenec and Dvorce–Prokop limestones in Prague (Dvorce, Cikánka near Slivenec), and in the Řeporyje–Loděnice Limestone Facies at Prague – Dívčí hrady and Řeporyje. The upper limit of the stratigraphical range of *O. hausmanni* is not clear. It has commonly been reported as occurring together with *O. cristata* and *Platyscutellum formosum* (e.g. Chlupáč 1957, 1983a, 1993; Šnajdr 1987a), but the present study of the sections suggests instead that these species probably occur at slightly different stratigraphical levels. *O. cristata* appears about slightly above *O. hausmanni* (Hörbinger 2000) or the occurrence of both species overlaps partially (they commonly occur in the rock debris at the classic localities Černá rokle near Kosoř, Praha–Dvorce, etc.). The large gerontic specimens commonly identified as *O. hausmanni* from the middle and upper parts of the Dvorce–Prokop Limestone in St Prokop quarry where *O. cristata* and *Zlichovaspis* (*Z.*) *spinifera* occur, are now assigned to *O. tenuigranulata* sp. n. One questionable finding (CGS MŠ 13401) comes from Vinařice Limestone facies, Měňany, U hájovny quarry (neighbourhood of Koněprusy).

Odontochile cristata Hawle & Corda, 1847
Figs 4k–m; 5a–e

1847 *Odontochile cristata* nobis; Hawle & Corda, p. 94.
For older synonymy, see Šnajdr (1987a).
1987a *Odontochile cristata* Hawle & Corda; Šnajdr, pp. 24–26, pl. 2, figs 1–4, text-fig. 4–2.
1989 *Odontochile* (*O.*) *cristatum* Hawle & Corda; Pek & Vaněk, p. 14.
2000 *Odontochile* (*O.*) *cristatum* Hawle & Corda; Hörbinger, pp. 10–11.
2002 *Odontochile cristatum* Hawle & Corda; Vaněk & Valíček, p. 10.
2002a *Odontochile* (*Odontochile*) *cristatum* Hawle & Corda; Chlupáč, pp. 34–35.

Lectotype. Designated Šnajdr (1984); a deformed incomplete pygidium, NML 19799, preserved as internal mould in grey micritic limestone. Figured by Šnajdr (1984, pl. 2, fig. 2); Fig. 4m.

Type horizon and locality. Lower Devonian, Pragian Stage, Praha Formation, Dvorce–Prokop Limestone, exact horizon unknown; Prague, exact locality unknown.

Other material. NML 15025, 15026, 15027, 15120, 15121, 15122, used by Barrande (1852) for idealised reconstructions. In addition the present authors had at their disposal one damaged complete (Fig. 5f) and one incomplete (Fig. 4l) specimen (both in MCZ collections), 40 incomplete cephala, 15 hypostomes and about 120 mostly incomplete pygidia. All specimens are preserved with exoskeleton and/or as internal moulds with relics of exoskeleton, in some cases (in decalcified limestones) with well-preserved dorsal sculpture. Several sections of various exoskeletal parts were used for study by electron microscopy.

Diagnosis. A species of *Odontochile* with parabolic anterior cephalic margin, anterior cephalic border narrow.

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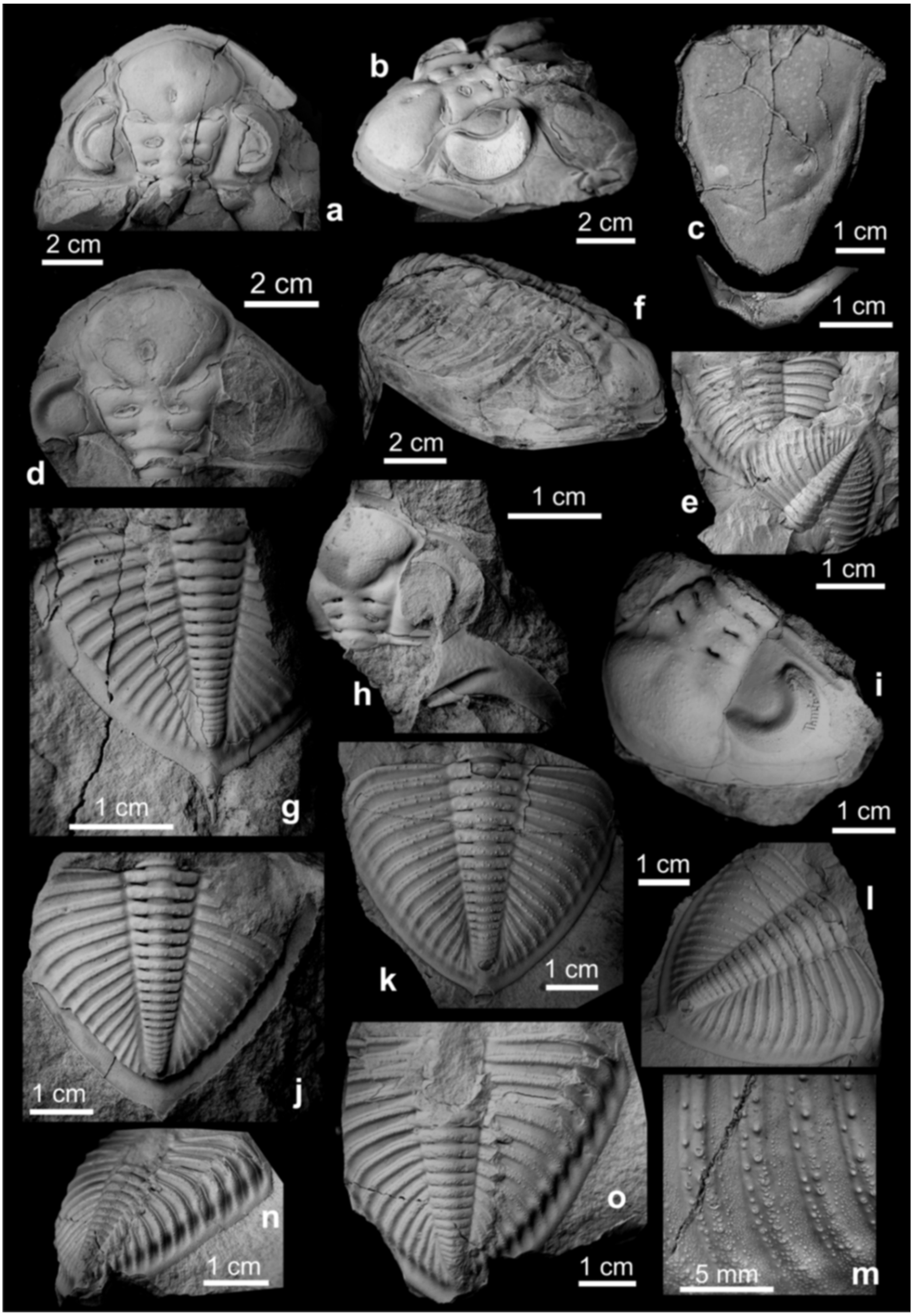

Figure 5 (a–e) *Odontochile cristata* (Hawle & Corda, 1847), Praha Formation, Pragian Stage, Dvorce–Prokop Limestone facies: (a–b) Incomplete cephalon, internal mould with relics of exoskeleton, NML 29651, Lochkov?; (c) Hypostome CGS JV 3509, latex cast, Praha–Konvářka, ventral view and detail of doublure with spines, dorsal view; (d) Incomplete cephalon with relics of exoskeleton, NML 13268, Černá Rokle near Kosoř, dorsal view; (e) Two pygidia, CGS PB 209, Praha–Kosoř. (f) *Odontochile* cf. *cristata* Hawle & Corda, 1847. Almost complete, poorly preserved specimen, Lochkov, MCZ 172828, lateral view. (g–m) *Odontochile delicia* Šnajdr, 1987a, Zlichovian Regional Stage (=lower Emsian), Zlíchov Formation, basal layers, Praha–Hlubočepy, U Kapličky quarry: (g) Damaged pygidium, internal mould, holotype, CGS MŠ 13162, dorsal view; (h) Damaged cephalon, internal mould, CGS MŠ 13282, dorsal view; (i) Incomplete cephalon, internal mould, paratype CGS MŠ 13163, dorsolateral view; (j) Pygidium, internal mould, CGS MŠ 13278; (k–m) Pygidium, internal mould with partly exfoliated exoskeleton, Tomáškův lom quarry, PB 153: (k) dorsal view; (l) dorsolateral view; (m) detail of left anterior pleural ends, lateral view. (n–o) *Odontochile* cf. *hiberna* Šnajdr, an incomplete broken pygidium, CGS PB 210: (n)–lateral view; (o) dorsal view.

Eyes with lenses arranged in 54–56 dorsoventral files of up to 14 lenses each. Pygidium subtriangular in outline, length/width index about 0·65–0·70. Postaxial ridge strong, keel-like, extending along short mucro with narrow base. Axis composed of 17–18 rings plus subtriangular terminal piece; median parts of rings inflated, strongly vaulted in sagittal section. There are 13 to 14 (rarely 15) deep, flat-bottomed, very wide pleural furrows that narrow (exsag.) above interior margin of doublure. Interpleural furrows distinct. Anterior pleural bands narrow, keel-like in cross-section, more inflated and expanded (exsag.) above inner margin of doublure. Posterior pleural bands low, narrow. Pygidial border slightly vaulted. Sculpture of dense, fine granules on most of dorsal exoskeleton; anterior pleural bands of thorax and pygidium also with irregular row of slightly coarser granules in some specimens; posterior pleural bands with fine granules arranged in a single row.

Description. For detailed descriptions see Barrande (1852) and Šnajdr (1987a, 1990). These descriptions are supplemented here by remarks on the hypostomal morphology, based on several newly collected and well-preserved specimens (see also Budil *et al*. 2008). Hypostome prolonged (sag.), with a slightly vaulted middle body and inflated maculae. Lateral border expands backwards (tr.), border furrow distinct. Lateral part of doublure narrow, widening posteriorly, strongly vaulted; posterior part of doublure prominently vaulted, especially medially where it bears a cluster of very fine, short, irregularly arranged spines (Fig. 5c). Posterior margin with three short spines; lateral margin with a smaller spine opposite posteriormost part of middle body. Outer surface of hypostome excluding posterior doublure densely granulose, with weak larger granules also present on anterior lobe of middle body; inner surface with sparse muscle scars.

Ontogeny. Several small holaspid pygidia have been found, the smallest one 9 mm long (NML 30357). These differ from larger holaspides especially in having deeper pleural and interpleural furrows, both containing a row of distinct, dense and fine pores, and slightly coarser sculpture on the anterior pleural bands (which also have prominently vaulted distal ends) and on the axial rings.

Measurements. The lectotype, an incomplete large pygidium, is 58 mm long. The largest known pygidia are more than 65 mm long (sag.), with 17 axial rings, and $14\frac{1}{2}$–15 ribs; the smallest pygidium is 9 mm long.

Remarks. The main differences which enable *O. hausmanni* and *O. cristata* to be easily distinguished are: their different cephalic anterior margin outlines (subcircular to very slightly parabolical in *O. hausmanni* but relatively prominently parabolical in *O. cristata*); prominently coarser and less dense granulation on LF lobe in *O. hausmanni*; anterior pleural bands and postaxial ridge on pygidium of *O. cristata* are prominently keel-like in cross-section; and the sculpture on pygidial and thoracic anterior pleural bands and axis of *O. hausmanni* consists of prominently coarser granules.

Occurrence. Šnajdr (1987a) and Chlupáč (1983a, 1993, 1999) stated that *O. cristata* occurs in the lower part of the Praha Formation together with *O. hausmanni*. The present study of measured sections suggests, however, that *O. cristata* occurs in the lower (but not lowermost) and middle parts of the Praha Formation. It is not possible to confirm whether *O. cristata* occurs with or immediately above *O. hausmanni*, though the discovery of both species together in rock debris may indirectly support their co-occurrence. Higher in the Praha Formation, *O. cristata* occurs in association with *O. tenuigranulata* sp. n. and with *Zlichovaspis spinifera spinifera*. *O cristata* is probably restricted to the region of Prague (Černá rokle, Radotín, Konvářka, Řeporyje, St Prokop Quarry) where its stratigraphical range lies within the *Turkestanella acuaria* biozone.

Odontochile delicia Šnajdr, 1987a
Fig. 5g–m

1987a *Odontochile karabosa delicia* subsp. n., Šnajdr; pp. 28–29, pl. 3, figs 4–6, text-fig. 5.
1989 *Odontochile* (*O.*) *karabosa delicia* Šnajdr; Pek & Vaněk, p. 14.
2000 *Odontochile* (*O.*) *karabosa delicia* Šnajdr; Hörbinger, pp. 10–11.
2002 *Odontochile karabosa delicia* Šnajdr; Vaněk & Valíček, p. 10.

Holotype. An incomplete pygidium (internal mould with relics of exoskeleton), CGS MŠ 13162, preserved in decalcified very fine-grained biosparitic limestone. Figured by Šnajdr (pl. 3, fig. 5); Fig. 5g.

Type horizon and locality. Lowermost Emsian, Zlíchov Formation, basal layers (Coral Horizon of the Chapel), Praha–Hlubočepy – Lom u kapličky quarry.

Other material. Cephalon with part of the thorax, four incomplete cephala and eight incomplete pygidia from the type locality, preserved in fine-grained biosparitic to biomicritic limestone; one extremely well preserved pygidium with remains of the exoskeleton, from a slightly decalcified limestone of uncertain stratigraphic position at Tomáškův lom (Fig. 5k–m).

Diagnosis. A species reminiscent of *Odontochile cristata*, but with these specific features: (1) sparse thorn-like granules on L1+L2 lobes and fixigena; (2) eyes with lenses arranged in dorsoventral rows of up to 11–12 lens each; (3) with 17–20 axial rings plus terminal piece. Rings 14–17 plus terminal piece often vaulted, inflated; (4) axial rings with sparsely distributed thorn-like granules along posterior margin and on sagittal portion; (5) anterior pleural bands with about 12–15 sparsely distributed thorn-like granules; posterior pleural bands with sparse, tiny granules in a row; (6) the entire exoskeleton in the interspaces between large granules finely and densely granulated, including pleural furrows.

Description. See Šnajdr (1987a)

Measurements. The holotype is 29 mm in sag. length, and the largest pygidium is about 70 mm long.

Remarks. *O. delicia* was proposed by Šnajdr (1987a) as a subspecies of a new species, *O. karabosa*. The holotype of the nominotypical subspecies, *O. karabosa karabosa,* is an incomplete large, pathological pygidium with partly exfoliated exoskeleton and missing mucro, preserved in micritic limestone (Šnajdr 1987a, pl. 2, figs 5–6, pl. 19, fig. 5), and the only other specimen mentioned was an incomplete pygidium, which was not illustrated. Despite extensive searches for them, neither of these specimens can be found in the collections of the Czech Geological Survey, and they may never have been lodged there with Šnajdr's other material; both specimens are therefore presumed lost. No other specimen was mentioned by Šnajdr (1987a) and no new material supporting the existence of this species has been found so far. Thus, with the present state of knowledge, the most reasonable solution is to consider the name *Odontochile karabosa karabosa* nomen dubium. However, the differences between *O. karabosa karabosa* and *O. karabosa delicia* in Šnajdr's original concept were very minute, including e.g. the density of granulation.

O. delicia shows closest affinities to *O. cristata* and *O. hiberna*. With the first, it shares a parabolic outline of the cephalic margin; all three species having a subtriangular pygidium outline with similar length/width indexes and a longer mucro with a narrower base (shorter mucro with

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broader base in *O. hausmanni* and *O. tenuigranulata* sp. n.). There are also similarities in the number of wide, flat-bottomed pleural furrows (13–15 in *O. delicia* and 13–14, rarely 15 in *O. cristata* and *O. hiberna*). However, *O. cristata* and *O. hiberna* differ in the number of axial rings (17–18 to compare with 17–20 rings in *O. delicia*), and their axis is slightly wider, uniformly tapering backwards. Nevertheless, the best features distinguishing *O. delicia* from *O. cristata* and *hiberna* are its lesser vaulting of anterior pleural bands on the pygidium and its markedly different sculpture, consisting of a combination of fine granulation and larger sparsely distributed thorn-like granules.

Occurrence. Lowermost Emsian, uppermost part of the Praha Formation (Dvorce–Prokop Limestone) to lowermost Zlíchov Formation (lower Zlíchov Limestone). The species is so far known almost exclusively from Prague and surrounding areas – Praha–Hlubočepy (Lom u Kapličky quarry) and Dvorce – but it has been found also in Tomáškův lom near Srbsko. One, very poorly preserved incomplete pygidium of uncertain systematic position was found in the lower part of the Praha Formation (lower Dvorce–Prokop Limestone facies) in Prague–Velká Chuchle, Přídolí section (mentioned by Chlupáč (2000) as *O.* cf. *karabosa*).

Odontochile hiberna Šnajdr, 1985
Fig. 6a–c

1985 *Odontochile hiberna* sp. n.; Šnajdr, pl. 2, figs 3–4.
1987a *Odontochile hiberna* Šnajdr; Šnajdr, pp. 26–27, pl. 3, figs 1–3, text-fig. 4–3.
1989 *Odontochile* (*O.*) *hibernum* Hawle & Corda; Pek & Vaněk, p. 14.
2002 *Odontochile cristatum* Hawle & Corda; Vaněk & Valíček, p. 10 [*partim*].

Holotype. An incomplete pygidium with exoskeleton, CGS MŠ 13154, preserved in partly decalcified micritic limestone ('white beds'). Figured by Šnajdr (1985, pl. 2, fig. 3; 1987a, pl. 3, fig. 1); Fig. 6a.

Type horizon and locality. Pragian Stage, Praha Formation; Prague – Konvářka (a road cutting N of Dívčí Hrady, lower part of Dvorce–Prokop Limestone facies lying immediately above the Slivenec and Loděnice limestones).

Additional material Two incomplete pygidia from the type locality, five other incomplete pygidia.

Diagnosis. A species similar to *O. cristata* but with the following distinguishing features: (1) distal parts of anterior pleural bands extremely vaulted, prominently keel-like in cross-section; (2) keel-like postaxial ridge less distinct; (3) markedly different sculpture on pygidial axial rings and ribs: Axial rings with densely crowded granules of unequal size (some thorn-like) on median part of axial rings only, lateral parts of rings almost smooth. Distal parts of anterior pleural bands with densely crowded granules of unequal size (markedly larger than in *cristata*), some of them thorn-like, one row of sparse granules on adaxial part of anterior pleural bands. Posterior pleural bands with sparsely distributed small granules.

Description. See Šnajdr (1987a).

Remarks. This species was considered as of doubtful validity by Vaněk & Valíček (2002), who placed it in synonymy with *O. cristata*. Although *O. hiberna* may be difficult to distinguish from the latter, no specimens that are clearly intermediate between the two species in the main diagnostic features were observed. Both taxa occur together (*O. hiberna* rather sporadically), so it is unlikely that *hiberna* is a subspecies of *cristata*. *O. tenuigranulata* sp. n. also resembles *O. hiberna* in some respects, but the former differs in the less vaulted pygidium, the moderately vaulted and wider anterior pleural bands, the complete absence of a keel-like postaxial ridge, and the larger number of axial rings and ribs. It is possible that the two species groups *hausmanni*+*tenuigranulata* and *cristata*+*hiberna* (with possibly also *delicia*), each living in the same environment, showed some patterns of convergence or mimicry. *O. hiberna* and *O. tenuigranulata* represent the extremes in the range of morphological variation in each group, whereas *O. hausmanni* and *O. cristata* are easily differentiated.

Measurements. Incomplete pygidium of holotype 30 mm long. The largest incomplete pygidium known is about 50 mm in sag. length.

Occurrence. Dvorce–Prokop Limestone, high in the lower Pragian sequence; Prague – Konvářka, Kosoř (Černá rokle gorge).

Odontochile tenuigranulata sp. n.
Fig. 6d–g

1971 *Odontochile* (*Odontochile*) *cristatum* Hawle & Corda; Přibyl & Vaněk, pl. 7, fig. 2.
1987a *Odontochile hausmanni* (Brongniart); Šnajdr, p. 23.

Derivation of name. From the Latin words *tenuis* – fine, slight, feeble; *granum* – grain. The name emphasises the finer sculpture of the new species compared to the type species.

Holotype. Incomplete pygidium, CGS PB 154, preserved as an internal mould with relics of exoskeleton in decalcified limestone, figured in Figure 6d.

Paratypes. Incomplete cephalon, CGS PB 155; young holaspid pygidium, CGS PB 156; holaspid pygidium, CGS PB 157; and young holaspid pygidium, CGS PB 158; all preserved as internal moulds with relics of exoskeleton in decalcified limestone.

Type horizon and locality. Lower Devonian, Pragian Stage, Praha Formation, middle part of the sequence; Dvorce–Prokop Limestone facies, Prague – Malá Chuchle.

Other material. Twenty pygidia, a cephalon and possibly an associated hypostome, all from a decalcified micritic limestone exposed in the W part of the St-Prokop Quarry.

Diagnosis. A species similar to *O. hausmanni* but with the following distinguishing features: (1) vaulting of exoskeleton weaker; (2) greater number of pygidial axial rings (18–20, rarely 21); (3) cephalic sculpture finer and sparser in young holaspides, with thorn-like granules appearing only in large, gerontic specimens; (4) larger granules forming row on anterior pleural bands smaller and sparser, increasing in number on elevated distal parts of bands; (5) posterior pleural bands with only sparse granules abaxially, except on first segment; (6) axis of small and large, gerontic pygidia with sparse, large granules medially and sparser granules laterally.

Discussion. Recognition of this species resolves some of the problems in the specific assignment of material (mostly large, gerontic specimens) common in old collections made from St-Prokop quarry by Hanuš (1923). Přibyl & Vaněk (1971) assigned these specimens mostly to *O. cristata*, whereas Šnajdr (1987a, p. 23) regarded them as gerontic individuals of *O. hausmanni. O. tenuigranulata* shares most features with *O. hausmanni* and is probably most closely related to it. However, the sculpture of even very small holaspides of *O. tenuigranulata* is more reminiscent of that of *O. cristata* than that of *O. hausmanni* (see also '*Odontochile*' sp. of Šnajdr 1987a, pl. 20, fig. 4, which probably belongs to *tenuigranulata*). It is possible that *tenuigranulata* is a subspecies of *O. hausmanni*, but it is not certain whether the two taxa occur together. The present authors have several specimens possibly belonging to *O.*

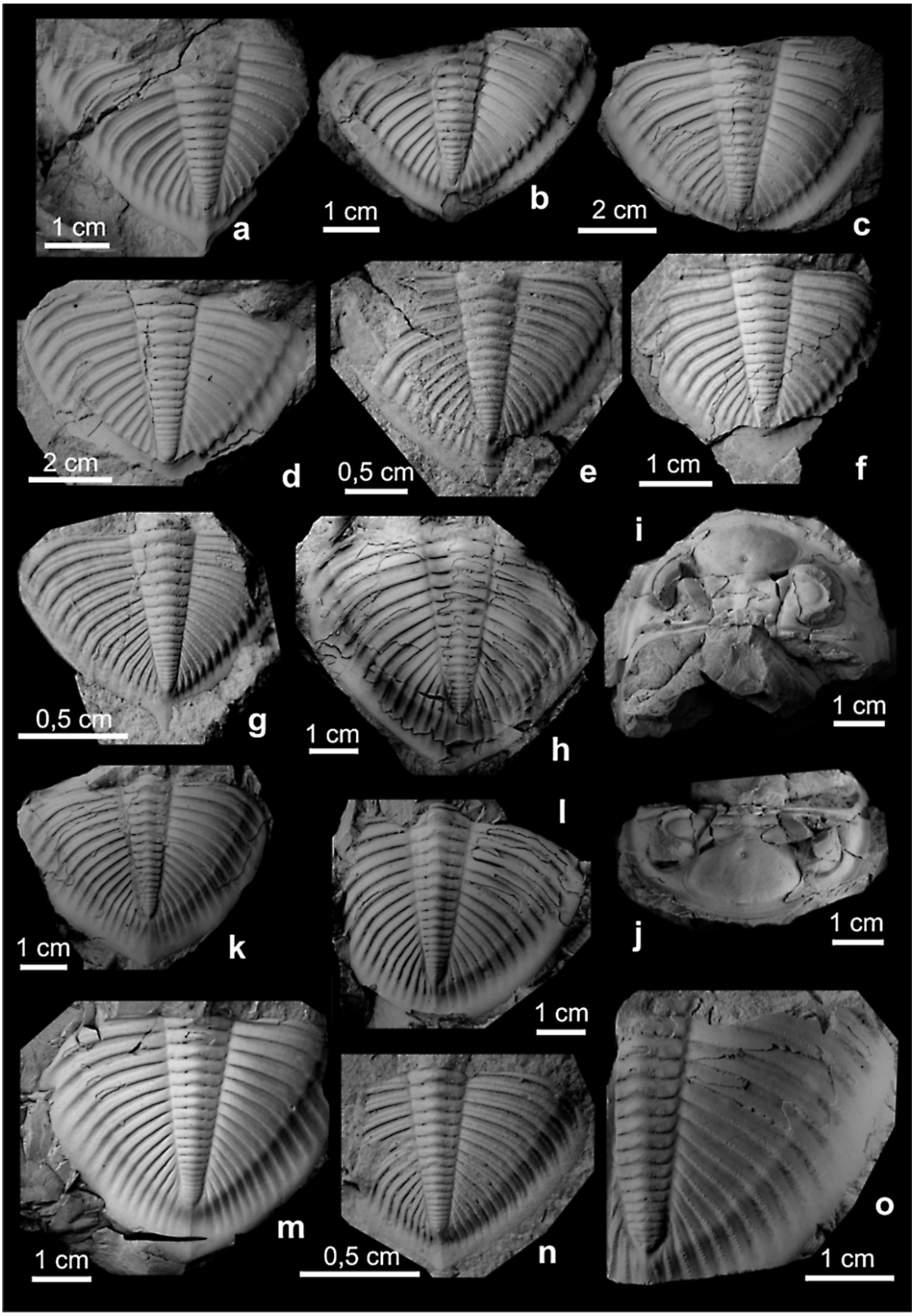

Figure 6 (a–c) *Odontochile hiberna* Šnajdr, 1985. Pragian Stage, Praha Formation: (a) Incomplete pygidium, holotype CGS MŠ 13154., Praha–Konvářka; (b) Incomplete pygidium, CGS MŠ 13273. Praha–Lochkov, Černá rokle gorge; (c) Incomplete pygidium, CGS MŠ 13275. Praha–Lochkov, Černá rokle gorge. (d–g) *Odontochile tenuigranulata* sp. n. Pragian Stage, Praha Fm, Praha–Malá Chuchle: (d) Incomplete pygidium, holotype CGS PB 154; (e) Incomplete holaspid pygidium, CGS PB 156; (f) Incomplete pygidium, CGS PB 157; (g) Incomplete young holaspid pygidium, CGS PB 158. (h–o) *Reussiana reussi* (Barrande, 1846). Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, Damil hill near Tetín (with exception of m): (h) Lectotype, incomplete pygidium NML 15038, dorsal view; (i, j) Cephalon, NML 30364, Tetín: (i) dorsal view; (j) frontal view; (k) Almost complete pygidium, NML 17636, lectotype of *O. hausmanni* Hawle & Corda, 1847, dorsal view; (l) Pygidium, NML 29852, dorsal view; (m) Pygidium with exoskeleton, CGS PB 211, dorsal view. Černá rokle near Kosoř; (n) Early holaspid pygidium, PB159, dorsal view; (o) Part of pygidium, NML 30267, dorsal view.

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hausmanni from St-Prokop Quarry, and a few specimens of *O. tenuigranulata* of uncertain stratigraphical position from Černá rokle gorge where *O. hausmanni* is common. At present it seems best to regard *O. tenuigranulata* as an independent species.

O. tenuigranulata can be easily distinguished from *O. cristata* by the subcircular outline of the cephalon, the larger (though sparse) granules on the LF lobe, the narrower pleural furrows, the lack of strong, keel-like vaulting of the anterior pleural bands, and the absence of a keel-like postaxial ridge.

Measurements. The holotype, CGS PB 154, is about 45 mm long (sag.). The smallest pygidium is about 10 mm long, and the largest ones from St. Prokop quarry may be more than 100 mm long.

Occurrence. *O. tenuigranulata* sp. n. is typical of the micritic facies of the middle part of the Praha Formation (Dvorce–Prokop Limestone): Prague – Malá Chuchle and St. Prokop quarry. It occurs with *O. cristata* and *Zlichovaspis spinifera spinifera*, and its distribution may be related to the development of mud-mount structures. Questionable remains come from Černá rokle gorge (rock debris of uncertain age).

Genus *Reussiana* Šnajdr, 1987b

Type species. *Phacops Reussii* Barrande, 1846. Pragian Stage, Prague Formation, Dvorce–Prokop Limestone facies (upper part), Prague Basin.

Occurrence. Upper Silurian (?Přídolí) to Lower Devonian (Pragian); Prague Basin, Kazakhstania, Laurentia, questionably also northern peri-Gondwana (Morocco).

Diagnosis. Exoskeleton large, broadly oval in outline, weakly vaulted; length/width index approximately 1·2. Cephalon semioval, with wide, flat anterior border lacking precranial median process. Thoracic axial rings with robust vertical median node. Pygidium wide, weakly vaulted, length/width index approximately 0·65–0·77. Axis narrow, 0·18–0·19 of maximum pygidial width, with 17–21 rings that are strongly elevated medially. Pleurae with 15–18 (rarely 19) pleural furrows; pleural and interpleural furrows extend distally onto broad, concave border. Postaxial ridge long, keel-like; mucro very short, broad. Doublure wide, flat. Sculpture of fine granules only.

Remarks. There are several species that are strongly reminiscent of *R. reussi* in pygidial morphology, but which are not known from their cephala. These include most of the species assigned by Maksimova (1972) to the new genus *Reussia* (a name replaced by *Reussiana* by Šnajdr 1987b because of homonymy), such as *R.* ? *batymarginata* (Maksimova, 1968); *R.* ? *kailensis* (Maksimova, 1969), *R.* ? *idonea* (Maksimova, 1968) and *R.* ? *schischkatensis* (Balashova, 1968). Even in the material stored in VSEGEI, St Petersburg, no cephala of these species could be found, and the present authors therefore agree with Šnajdr (1987a) that their generic assignment is uncertain. *R. thuringica thuringica* (Alberti, 1967) and *R. thuringica franconica* (Alberti, 1969) are also known only from pygidia but the specimens illustrated by Alberti (1969), although fragmentary, are comparatively well preserved, and strongly resemble the type species in the vaulting of the pygidium, the extremely narrow axis, the wide postaxial part of the pygidial border, the wide pleural furrows and the very fine granulation.

Also assigned to *Reussiana* by Maksimova (1972) was *Odontochile kiikbaica* (Maksimova, 1968), but we agree with Edgecombe and Ramsköld (1994) that this species belongs to *Kasachstania* Maksimova, 1972.

Species assigned. *Reussiana reussi* (Barrande, 1846); *R. brevispicula* (Hörbinger, 2000); *R.* ? *batymarginata* (Maksimova, 1968); *R.* ? *hassaica* (Kayser, 1896); *R.* ? *kailensis* (Maksimova, 1969); *R.* ? *idonea* (Maksimova, 1968); *R* ? *occidentalis* (Bureau, 1900); *R.* ? *schischkatensis* (Balashova, 1968); *R.* ? *taffi* (Ulrich & Delo *in* Delo, 1940); *R. thuringica thuringica* (Alberti, 1967); *R. thuringica franconica* (Alberti, 1969), *R.* ? sp. (*Odontochile* cf. sp. A. of Richter & Richter 1943, pl. 5, figs 8–9).

Reussiana reussi (Barrande, 1846)
Fig. 6h–o; 7a–b

1846 *Phacops Reussii* Barrande; Barrande, p. 83.
For older synonymy, see Šnajdr (1987a).
1987a *Reussiana reussi* (Barrande); Šnajdr, pp. 52–53, pl. 9, figs 1–3, pl. 19, fig. 6.
1989 *Odontochile* (*Reussiana*) *reussi* (Barrande); Pek & Vaněk, p. 14.
2000 *Odontochile* (*Reussiana*) *reussi* (Barrande); Hörbinger, pl. 1, fig. 7.
2002 *Reussiana reussi* (Barrande); Vaněk & Valíček, p. 11.
2002a *Reussiana reussi* (Barrande); Chlupáč, pp. 34–35.

Lectotype. Designated Chlupáč in Horný & Bastl (1970); an incomplete large pygidium (exoskeleton partly exfoliated), NML 15038, preserved in micritic limestone. Figured by Barrande (1852, pl. 25, figs 8–9); Šnajdr (1987a, pl. 9, fig. 1); Fig. 6h.

Type horizon and locality. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, exact horizon unknown (probably upper part of the Pragian sequence); Damil near Tetín.

Other material. Paralectotypes NML 15039, 15040, 15007. One cephalon, a few incomplete cranidia and cephalic fragments and about 120 selected pygidia.

Diagnosis. A species of *Reussiana* with pygidium with 17–19 backwards swollen axial rings plus terminal piece. Pseudoarticulating halfrings at least on rings 2–10. There are 15 to 16 wide, flat-bottomed pleural furrows. Anterior pleural bands vaulted, steeply inclined to pleural furrow, inflated above inner margin of the doublure. Posterior pleural bands low. Pygidial border narrow, slightly vaulted. Dorsal exoskeleton very finely perforated.

Description. See Šnajdr (1987a). The genal spines hardly reach the 9–10th thoracic segment.

Ontogeny. Several small holaspid pygidia were studied (8–15 mm long). They have axial rings with strongly inflated posterior margins, forming a pseudonode medially as discussed by Šnajdr (1987a). Pleural furrows are narrower than in larger specimens, relatively deep and distinctly perforated by dense, fine pores. Interpleural furrows are shallow but marked by a distinct row of pores. The margins and other parts of the pygidium are also perforated. The keel-like postaxial ridge is more distinct than in larger specimens.

Variability. The numbers of axial rings and ribs vary slightly (see diagnosis), and the granulation on the exoskeleton also varies slightly in diameter.

Measurements. The length of the holotype is 52 mm, largest pygidium 64 mm long, two smallest pygidium 8 mm long. They posses 18 axial rings and $16\frac{1}{2}$ ribs.

Occurrence. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, middle to upper part (about upper third of the Pragian sequence): Tetín (Damil), Koda near Beroun; Prague – Lochkov and Prague – Kosoř, approximately middle to upper third of the Pragian sequence. Two pygidia from Lochkov and Kosoř were found 10 mm and 12·5 m above the base of the Pragian, respectively. Abundant at type locality, rare at other localities. Specimens of *Reussiana* from the Řeporyje and Slivenec limestone facies (?basal

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Pragian sequence) belong to *R. brevispicula* (see also Hörbinger 2000). An indeterminable fragment of pygidium with comparatively coarser sculpture comes from Vinařice Limestone, Na Telíně locality.

Reussiana brevispicula Hörbinger, 2000
Fig. 7c–e, g, h

2000 *Odontochile* (*Reussiana*) *brevispiculum* n.sp.; Hörbinger, pp. 10–12, pl. 1, figs 1–6.
2002 *Reussiana brevispiculum* Hörbinger; Vaněk & Valíček, p. 11.

Holotype. Pygidium with partly exfoliated exoskeleton, CGS FH 1. Figured by Hörbinger (2000, pl. 1, fig. 1); Fig. 7c.

Type horizon and locality. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, basal layers. Prague – Kosoř, Černá rokle gorge.

Other material. Eight pygidia with remains of exoskeleton in grey micritic limestone, one doubtful, strongly deformed pygidium in dark grey, thin-bedded limestone.

Diagnosis. *Reussiana* with elongated pygidium, slightly more vaulted than in type species. Length/width index approximately 0·77. Axis with 19–21 (rarely 22) rings plus terminal piece. Pleurae with 17–18 (rarely 19) narrow pleural furrows. Anterior pleural bands with sharply steep posterior margin. Pleural ribs extend almost to lateral and posterior margins of pygidium. Pygidial border very narrow, slightly vaulted, border furrow indistinct. Axial rings, pleural bands and pygidial border densely and finely granulated.

Remarks. *Reussiana brevispicula* differs from the type species by its narrower pygidium outline, larger number of rings and pleural furrows, sharply steep posterior margin of anterior pleural bands and especially by its narrower pleural furrows. Also the lateral border is narrower in this species.

Of the species described from outside the Prague Basin, *Reussiana* ? *batymarginata* (Maksimova, 1968) is strongly reminiscent of *R. brevispicula*, both having distinctly narrow pleural furrows and a rather elongated pygidium, but differs in having fewer pygidial segments. *R.* ? *schischkatensis* (Balashova, 1968) shares a large number of pygidial segments and narrow pleural furrows with *R. brevispicula*, but differs from it especially in the distinctly wider pygidial outline and coarser sculpture on the axial rings and pleural bands.

Ontogeny. Two small holaspid pygidia are relatively wider than in larger specimens, having length/width index of 0·6–0·69. A small pygidium 11 mm long shows relatively distinct median pseudonodules or short robust spines on the axial rings. The smallest pygidium, CGS PB 211 (5·5 mm long), has axial rings that are distinctly swollen medially but which lack distinct sculpture.

Measurements. Holotype is 35 mm long, the largest known pygidium is ca. 90 mm long.

Occurrence. Lower Pragian Stage, Praha Formation, lowermost part of the Dvorce–Prokop Limestone facies (micritic facies): Prague – Kosoř (Černá rokle Gorge), Lochkov and Radotín. One strongly deformed pygidium (Fig. 7f) in the Schäry Collection (MCZ 172827), stated to be from Lochkov, is preserved in dark grey, bituminous, thin-bedded biosparitic limestone characteristic of the upper part of the Lochkov Formation (Lochkovian Stage). This specimen is probably the stratigraphically oldest record of dalmanitid trilobites in the Lower Devonian of the Prague Basin. Alternatively, the specimen may come from a shale intercalation in the lowermost Dvorce–Prokop Limestone, though this is considered less likely.

Genus *Zlichovaspis* Přibyl & Vaněk, 1971

Type species. *Odontochile rugosa* Hawle & Corda, 1847.

Diagnosis. Exoskeleton large, moderately to strongly vaulted, with length/width index ca. 1·8–2·0. Cephalon subtriangular to moderately subtriangular, anterior margin parabolic with mostly short precranial median process. Pygidium of subtriangular to rounded subtriangular outline, with long mucro, length/width index 0·65–0·8. Axis with width (tr.) 0·22–0·23 of maximum pygidial width (sag.), well delimited posteriorly, with 16–21 rings plus terminal piece. Postaxial region gently to strongly vaulted. Pleurae with 12 to 17 deep, commonly narrow pleural furrows and elevated ribs. Doublure narrow. Sculpture of fine to large granules, some thorn-like, and singular, sharp spines.

Remarks. *Zlichovaspis* was proposed by Přibyl & Vaněk (1971) as a subgenus of *Odontochile*, distinguished from the nominotypical subgenus by the presence of an anterior cephalic process, lateral glabellar furrows that are better defined medially, the greater length of ε–ω on the facial suture, differences in the hypostomal morphology, and the narrower interpleural furrows (actually the pleural furrows, as noted by Šnajdr 1987a, p. 30). Campbell (1977) considered these features as variable within the Dalmanitidae and not of subgeneric significance; however, *Zlichovaspis* was accepted by later authors either as an independent genus (Šnajdr 1985, 1987a; Vaněk & Valíček 2002) or as a subgenus of *Odontochile* (Pek & Vaněk 1989). Šnajdr (1987a) regarded the diagnostic characters of *Zlichovaspis* as the subtriangular cephalon with parabolic anterior margin, the short anterior cephalic process, the deeply impressed and narrow pleural furrows, the long mucro and the highly differentiated sculpture. He also noted that the hypostomal morphology does not differ greatly from that of *Odontochile*. The present authors agree with Šnajdr on the main diagnostic characters of *Zlichovaspis*, but their concept of the genus differs from his in that they consider it to include two subgenera, *Z.* (*Zlichovaspis*) and *Z.* (*Devonodontochile*). A few species assigned here to *Zlichovaspis* show a similarity to *Odontochile* in one of their characters. For example, *Z.* (*Z.*) *auriculata* (Dalman, 1827) almost lacks an anterior cephalic process, and *Z.* (*Z.*) *vaneki* sp. n. has relatively wide pleural furrows. Conversely, *O. delicia* Šnajdr, 1987a has a long, narrow pygidial mucro like that of *Zlichovaspis*, and *O. cristata* Hawle & Corda, 1847 and *O. delicia* Šnajdr, 1987a has a parabolic anterior cephalic margin. The presence of these characters, that are not typical of the respective genera, may be explained by convergence.

Subgenus *Zlichovaspis* (*Zlichovaspis*) Přibyl & Vaněk, 1971
(=*Spinodontochile* Šnajdr, 1985)

Type species. As for genus.

Diagnosis. A subgenus of *Zlichovaspis* with the following subgeneric characters: anterior margin parabolic with short to almost non-existent precranial median process; pygidium with robust mucro; axis with 16–21 rings plus terminal piece; pleurae with 12 to 16 deep, commonly narrow pleural furrows and elevated ribs; interpleural furrows distinct; distal pleural ends moderately vaulted; sculpture of fine to large granules, some thorn-like, in several species also with sharp robust spines or megagranules; no megapores but common fine pores.

Remarks. *Spinodontochile* was compared with *Odontochile* by Šnajdr (1985, 1987a), and was regarded as subgenus of the latter by Pek & Vaněk (1989). However, the present authors agree with Vaněk & Valíček (2002) and Jell & Adrain (2003) that it is a junior synonym of *Z.* (*Zlichovaspis*). *Spinodontochile* differs slightly from *Z.* (*Zlichovaspis*) in the length/width index

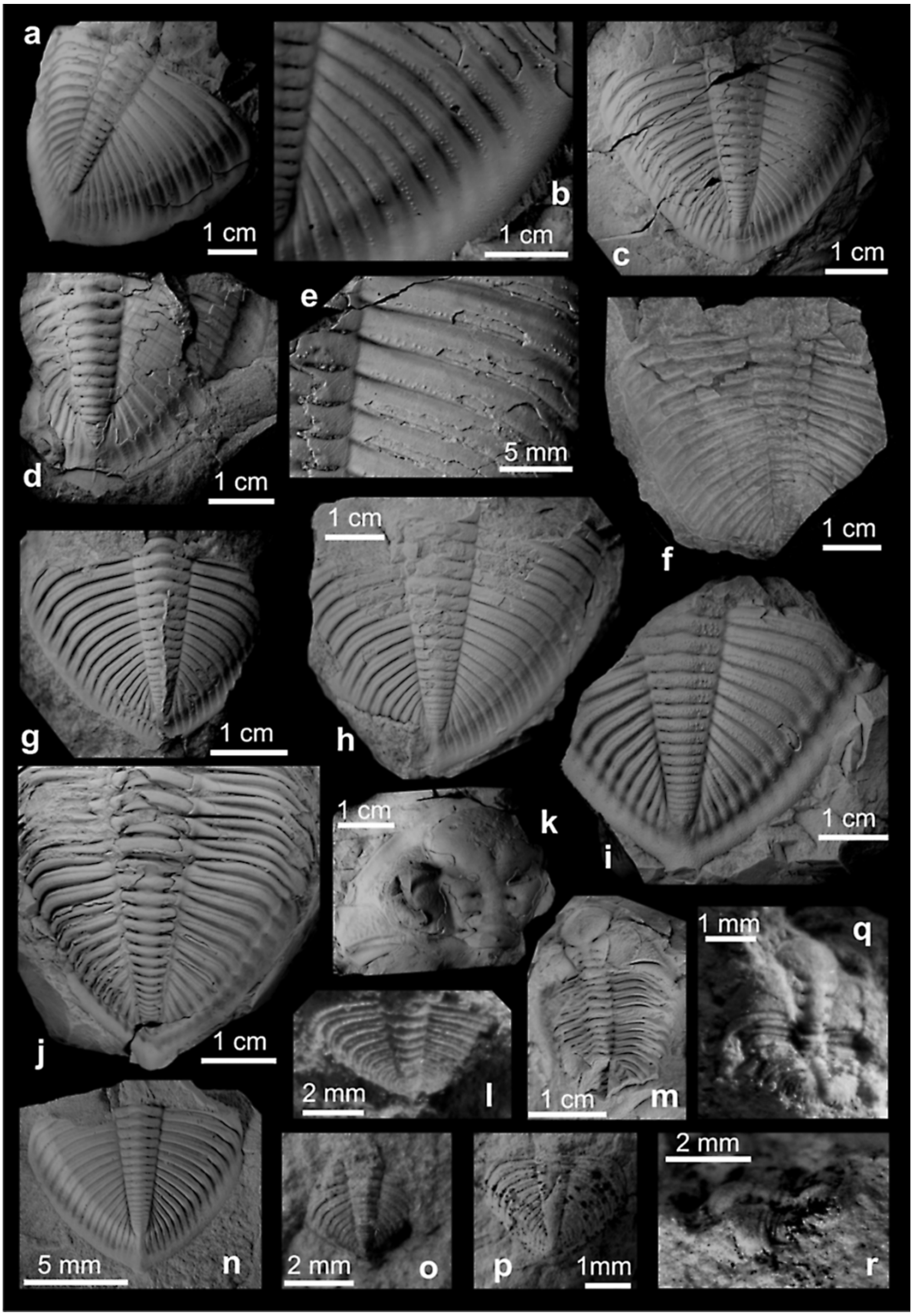

Figure 7 (a–b): *Reussiana reussi* (Barrande, 1846), Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies. Damil hill near Tetín: (a) Almost complete pygidium, NML 17636, lectotype of *O. hausmanni* Hawle & Corda, 1847, lateral view; (b) Detail of right pleural field of the pygidium, NML 29852, figured on Fig. 6l. (c–e), (g–h) *Reussiana brevispicula* (Hörbinger, 2000), Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies (lower part), Černá rokle near Kosoř: (c, e) Pygidium, holotype CGS PB159: (c) dorsal view, (e) detail of the right pleural field. (d) Pygidium CGS PB 160, dorsal view. (g) Pygidium CGS PB 161, dorsal view; (h) Pygidium, CGS PB 162, dorsal view. (f) *Reussiana* cf. *brevispicula* (Hörbinger, 2000). Incomplete pygidium preserved in the dark grey bioclastic limestone (? upper part of Lochkov Formation), MC 172827 (Schary coll.), Lochkov, dorsal view. (i–r) *Zlichovaspis* (*Z.*) *rugosa rugosa* (Hawle & Corda, 1847). Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, Damil hill near Tetín. Specimens (o) and (l–r), preserved in soft decalcified limestone, were not coated by ammonium chloride: (i) Incomplete pygidium with exoskeleton, CGS MŠ 13200, dorsal view; (j) Detail of the pygidium of almost complete specimen NML 15001; (k) Incomplete cephalon, lectotype, NML 18379, dorsal view; (l) Meraspid pygidium, MCZ 172820, Praha–Bráník; (m) Lectotype of invalid species *Dalmania Fletscheri* Barrande, 1846, NML 15007, dorsolateral view; (n) Early holaspid pygidium, assigned by Barrande (1852) to the invalid species *Dalmania Fletscheri* Barrande, 1846, NML 15006, dorsal view; (o) Meraspid pygidium, MCZ 172818, dorsal view; (p) Late meraspid–early holaspid pygidium, MCZ 172819; (q–r) Almost complete meraspid specimen (free cheeks displaced), MCZ 172817, Praha–Bráník: (q) dorsal view; (r) lateral view.

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of the exoskeleton, short but prominent precranial median process, the slightly rounded subtriangular outline of the pygidium, and different sculpture in most (not all) representatives. These features are not considered here as sufficient even for subgeneric status of *Spinodontochile*. The genus *Roncellia*, considered as a synonym of *Zlichovaspis* by Šnajdr (1987a), is considered here as an independent genus, distinguished by the length of the genal spines (reaching the fifth thoracic segment only in *Roncellia*), a very narrow, steeply declined anterolateral cephalic border of different outline than in *Zlichovaspis*, and a very narrow pygidial border. Some of these features are shared by *Roncellia* and *Gamonedaspis* (see Edgecombe 1993).

Many species of *Z.* (*Zlichovaspis*) are known from regions outside the Prague Basin. The first representatives probably appeared in eastern Gondwana, where *Z.* (*Z.*) *formosa* (Gill, 1948) occurs in the lowermost Devonian. During the Lochkovian and especially the Pragian, the subgenus spread within the Rheic Ocean realm. Its extensive radiation continued up to the mid Emsian when it abruptly decreased in abundance, only sporadic records of late Emsian age being known. The first representatives in the Prague Basin appeared in the early (but not earliest) Pragian, at a time when rich *Odontochile* already inhabited the basin and *Reussiana* communities were already present. This evidence suggests that there were two separate migrations of dalmanitid trilobites into the Prague Basin during the Early Devonian.

Species assigned. *Z.* (*Z.*) *rugosa rugosa* (Hawle & Corda, 1847); *Z.* (*Z.*) *rugosa laura* Šnajdr, 1985; *Z.* (*Z.*) *auriculata* (Dalman, 1827); *Z.* (*Z.*) *azucena* Šnajdr, 1987a; *Z.* (*Z.*) *? formosa* (Gill, 1948); *Z.* (*Z.*) *karlena* (Šnajdr, 1987a); *Z.* (*Z.*) *marieva* (Šnajdr, 1985); *Z.* (*Z.*) *ostara* Šnajdr, 1987a; *Z.* (*Z.*) ? *perceensis* (Clarke, 1905); *Z.* (*Z.*) ? *orientalis* (Haas, 1968); *Z.* (*Z.*) ? *paraspinifera* (Alberti, 1983); *Z.* (*Z.*) *rhenana* (Kayser, 1880); *Z.* (*Z.*) ? *seillouensis* (Morzadec, 1976); *Z.* (*Z.*) *spinifera spinifera* (Barrande, 1846); *Z.* (*Z.*) *spinifera nomiona* (Šnajdr, 1987a), *Z.* (*Z.*) ? *syncrama* (Campbell, 1977), *Z.* (*Z.*) ? *litchfieldensis* (Delo, 1940); *Z.* (*Z.*) *tamaraka* (Šnajdr, 1985); *Z.* (*Z.*) *tuberculata* (Hawle & Corda, 1847); *Z.* (*Z.*) *vaneki* sp. n.

Occurrence. Lower Devonian, Lochkovian to Emsian, Perunica, Iberia, northern peri-Gondwana, eastern Gondwana (present-day Australia) and Laurentia.

Zlichovaspis (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda, 1847)
Fig. 7i–r

1847 *Odontochile rugosa* nobis; Hawle & Corda, p. 94.
For older synonymy, see Šnajdr (1987a).
1987a *Zlichovaspis rugosa rugosa* (Hawle & Corda); Šnajdr, pp. 30–33, pl. 12, figs 1–5; pl. 15, fig. 3; text-fig. 5–1.
1989 *Odontochile* (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda); Pek & Vaněk, p. 14.
2000 *Odontochile* (*Zlichovaspis*) *rugosum rugosum* (Hawle & Corda); Hörbinger, p. 11, pl. 1, figs 8–9.
2002 *Zlichovaspis rugosa rugosa* (Hawle & Corda); Vaněk & Valíček, pp. 11–12.
2002a *Odontochile* (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda); Chlupáč, pp. 33–34.
2002a *Zlichovaspis rugosum rugosum* (Hawle & Corda); Vaněk, p. 3.

Lectotype. Designated Šnajdr (1984); an incomplete cephalon, NML 18379, preserved as an internal mould with relics of exoskeleton in grey micritic limestone. Figured by Šnajdr (1984, pl. 11, fig. 4); Fig. 7k.

Type horizon and locality. Pragian, Praha Formation, Dvorce–Prokop Limestone facies, exact horizon unknown (probably upper part of Praha Formation). Exact locality unknown, probably Tetín–Damil. The species was reported by Hawle & Corda (1847) from the Prague area and Damil.

Other material. Paralectotypes NML 15001, 15029, 15030, 15031; 67 complete and nearly complete specimens; about 220 selected cephala, cranidia and pygidia; three incomplete specimens and one damaged cephalon with articulated, or almost *in-situ* hypostome.

Diagnosis. A species of *Z.* (*Zlichovaspis*) with these characteristic features: cephalon moderately subtriangular, length/width index approximately 0·55; anterior cephalic border with prominent concave (sag.) precranial median process; eyes with lenses arranged in 48–55 dorsoventral files of up 10–12 lenses each; thoracic and pygidial pleural furrows deep, flat-bottomed; pygidium rounded subtriangular, length/width index approximately 0·7; axis with 16–18 rings plus subtriangular terminal piece; postaxial ridge vaulted, crossing border furrow; mucro robust and long; 13–14(15) pleural furrows; anterior pleural bands strongly vaulted, inflated distally above inner margin of doublure; posterior pleural bands vaulted; whole exoskeleton excluding apodemal pits covered by dense granules, coarsest on axial rings (especially their posterolateral parts) and postaxial region; pleural furrows very densely granulated.

Description. See Šnajdr (1987a).

Ontogeny. An almost complete but partly disarticulated meraspis (degree M4) in the Schary collection probably belongs to this species (Fig. 7q–r). It is poorly preserved in soft decalcified limestone from Praha–Bráník, is 3·3 mm long, and lacks the free cheeks. The cranidium is prominently large with a strongly vaulted glabella and long genal spines reaching almost to the pygidium. Occipital furrow deep; S1–S2 short, transverse, very deep; S3 deep, almost straight, expanding anterolaterally. Cephalic border flat and narrow, fixigena vaulted, without visible granulation. Eyes large, reaching from S3 to L2, palpebral furrow distinct. Posterior border furrow distinct. Four thoracic segments with distinct and wide (exsag.) pleural furrows. Pygidium small, short but wide, moderately vaulted. The first protothoracic segment is almost isolated. Moderately vaulted axis composed of 9–10 rings. There are 8–9 pleural furrows deep and wide on first 2–3 segments, narrow and line-like on posterior segments. No visible perforations. Interpleural furrows narrow but deep. Distal parts of pygidial segments overlap the pygidial outline, forming isolated, rounded processes on lateral margin, similar to those on meraspid transitory pygidia of '*Dalmanites*' *puticulifrons* Whittington & Campbell (1967, pl. 15, figs 8, 9, 12, 13, 16). There is no mucro; the posterior pygidial margin is broadly rounded. The specimen represents the youngest ontogenetic stage of Dalmanitinae known from the Prague Basin. Despite its differences from larger holaspides, its adult-like shape (*sensu* Speyer & Chatterton 1989) is apparent.

In the same collection, there are three other late meraspid to very early holaspid pygidia of *Z.* (*Z.*) *rugosa rugosa*, coming from the same locality. In all of them, the pleural ends slightly overlap the margin (Fig. 7l, o–p).

Measurements. Lectotype cephalon 26 mm in length (sag.). The largest complete specimens are 115 mm long. Fragments of large pygidia indicate that the exoskeleton reached a length of up to 220 mm.

Remarks. In the collections of the National Museum, Prague, there are three cephala and one incomplete specimen of *Z.* (*Z.*) *rugosa rugosa* with articulated hypostomes in-situ. Another poorly preserved cephalon from Tetín–Damil, in the

Schary collection, also has an attached hypostome (see Budil *et al.* 2008).

The present authors agree with Šnajdr (1987a), Pek & Vaněk (1989) and Vaněk & Valíček (2002) that *Dalmania fletcheri* Barrande, 1852 is a junior synonym of *Z.* (*Z.*) *rugosa rugosa*. Šnajdr stated that characters used by Barrande as the basis for erecting *fletcheri* are characteristic of small holaspides of *rugosa rugosa*. These features include the distinct perforations in the pleural furrows, now shown to be present also in early holaspides of *Zlichovaspis* (*Z.*) cf. *tuberculata*, *Odontochile hausmanni*, *O. tenuigranulata* sp. n. and *Reussiana reussi*.

Occurrence. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies, higher part (probably from the *Guerichina infundibulum* to *Guerichina strangulata* dacryoconarid biozones). The species is very abundant in the vicinity of Beroun but rare in the Prague district: Tetín–Damil, Srbsko, Hostím, Karlštejn, Solway quarries near Bubovice, Prague–Dvorce (rare), Bráník (rare), Hlubočepy – Barrande's rock quarry, Velká Chuchle–Přídolí (?), Zadní Kopanina. Šnajdr (1987a) reported several specimens from the Řeporyje Limestone in Prague – Klukovice (Červený lom quarry) and Prague – Cikánka. The stratigraphic position of these specimens is not entirely clear, but at the localities in question the Řeporyje Limestone facies occupies a relatively large stratigraphic interval comprising from one- to two-thirds of the Pragian sequence. A pygidium from the Koněprusy Limestone facies in Homolák quarry at Měňany was questionably assigned to *rugosa rugosa* by Šnajdr (1987a). This specimen cannot be located at present in the collections of either the Czech Geological Survey or the National Museum, but its original discovery was confirmed by R. Horný (pers. comm. 2004).

Zlichovaspis (*Zlichovaspis*) *rugosa laura* Šnajdr, 1985
Fig. 8a–h

1985 *Zlichovaspis rugosa laura* subsp. n.; Šnajdr, p. 167.
1985 *Zlichovaspis rugosa sitta* subsp. n.; Šnajdr, p. 167.
1987a *Zlichovaspis rugosa laura* Šnajdr; Šnajdr, p. 33, pl. 13, figs 1–3; text-fig. 5–3.
1987a *Zlichovaspis rugosa sitta* Šnajdr; Šnajdr, pp. 33–34, pl. 13, figs 4,5; pl. 15, figs 1,2; text-fig. 5–2.
1989 *Odontochile* (*Zlichovaspis*) *rugosa laura* Šnajdr; Pek & Vaněk, p. 14.
1989 *Odontochile* (*Zlichovaspis*) *rugosa sitta* Šnajdr; Pek & Vaněk, p. 14.
2002 *Zlichovaspis rugosa laura* Šnajdr; Vaněk & Valíček, p. 11.
2002 *Zlichovaspis rugosa sitta* Šnajdr; Vaněk & Valíček, p. 12.

Holotype. An incomplete pygidium, CGS MŠ 11674, preserved as an internal mould with relics of exoskeleton, in pink to white biodetritic Lodĕnice Limestone. Figured by Šnajdr (1985, pl. 2, fig. 5; 1987a, pl. 13, fig. 1); Fig. 8a.

Type horizon and locality. Pragian, Praha Formation, intermediate layers between Řeporyje and Lodĕnice Limestone facies; Branžovy near Lodĕnice, Záloženský lom quarry.

Other material. Lodĕnice Limestone: 28 incomplete cephala and cranidia, several thoracic segments, an incomplete and disarticulated thorax and about 70 incomplete pygidia. Wide range of exoskeleton fragments, including parts of cephalic (one almost complete) and pygidial doublures. All specimens are preserved in pink to grey biodetritic to biomicritic limestone, often with partly exfoliated exoskeleton or as internal and external moulds. Additional eight incomplete cephala and cranidia and ten incomplete pygidia, originally assigned to *Zlichovaspis* (*Z.*) *rugosa sitta* Šnajdr, 1985, come from pink to grey biodetritic to biomicritic Vinařice Limestone (Pragian, Praha Formation). Most of these specimens are poorly preserved, corroded internal moulds, rarely with relics of exoskeleton.

Diagnosis. A subspecies of *Zlichovaspis* (*Z.*) *rugosa*, differing from the nominotypical subspecies in the following features: (1) precranial process more rounded; (2) sparser and prominently coarser granules to thorn-like granules strongly differentiated in diameter cover occipital lobe, L1–L3, LF and palpebral lobes; (3) thoracic segments with rare granules close to axial furrows and sparse granules irregularly distributed on anterior pleural bands; (4) coarser and sparser granulation on pygidium; these granules are strongly differentiated in diameter and shape, ranging from large granules to thorn-like granules; (5) axial rings with dense granulation adaxially, but lateral axial lobes with sporadic granules only; (6) pleural furrows covered by fine, sparse granules.

Description. See Šnajdr (1987a).

Remarks. The above-mentioned differences are sufficient to distinguish the subspecies. Distinctive of *Z.* (*Z.*) *rugosa laura* as conceived here (i.e. *Z. rugosa* from the biodetritic limestone) is the coarse, differentiated granulation, though this varies randomly in shape, average diameter and distribution (see Fig. 11). *Z.* (*Z.*) *rugosa sitta* Šnajdr, 1985 is therefore included in the synonymy of *Z.* (*Z.*) *rugosa laura*. The former was considered by Šnajdr (1985, 1987a) to differ from *Zlichovaspis* (*Z.*) *rugosa laura* in having slightly wider pleural furrows, and slightly larger coarse granules and thorn-like granules, sparsely distributed on the glabella, occipital lobe and pleural bands of the pygidium. However, abundant new material from the collection of J. Vaněk, coming from the Branžovy–Záloženský lom and Čeřinka quarries, offers a large spectrum of specimens showing wide and continuous variability in density, diameter and space arrangement of granules, and also in the depth and width of the pleural furrows. In many specimens, it is almost impossible to distinguish the subspecies *laura* and *sitta* with certainty. In addition, they co-occur in some cases (e.g. in Čeřinka quarry), suggesting that the existence of two subspecies is biologically improbable. Even in the holotype of *Z.* (*Z.*) *rugosa sitta* – an incomplete cranidium with corroded exoskeleton, figured by Šnajdr (1985, pl. 2, fig. 2; 1987a, pl. 13, fig. 5) – a strong size differentiation of the granules, regarded as the characteristic feature of *Z.* (*Z.*) *rugosa laura*, is perceptible. The subspecies were distinguished in practice mostly by their different origin: *Z.* (*Z.*) *rugosa laura* in the Lodĕnice Limestone from Branžovy quarry, and *Z.* (*Z.*) *rugosa sitta* from the Vinařice Limestone at Měňany near Koněprusy. The variability of sculpture depending on local environment has been described by Chlupáč (1977) in Bohemian phacopid trilobites and discussed by Kácha & Petr (1995). The present authors propose to preserve the name of the well-documented subspecies *Z.* (*Z.*) *rugosa laura* and suppress the name of the comparatively poorly known *Z.* (*Z.*) *rugosa sitta*. Occurrences of *Zlichovaspis* (*Z.*) *rugosa laura* are probably restricted to areas of biodetritic limestone facies, deposited on elevated parts of the sea floor in relatively shallow-water environments (see also Chlupáč & Šnajdr 1989; Chlupáč *et al.* 1998). Several specimens show a prominent vaulting of the pygidial axial rings and pleural bands, forming weak keel-like elevations on the posterior part of rings and on the anterior pleural bands. The adaxial depth and width of S3 also varies slightly between some specimens.

Measurements. Length of holotype 28 mm (mucro broken off). Length of largest pygidium exceeds 70 mm (without mucro). No young holaspid specimens were available; smallest pygidium c. 15 mm long; average length of studied specimens 40–55 mm.

Occurrence. Pragian, Praha Formation, Koněprusy, Slivenec and Řeporyje–Lodĕnice limestone facies; Branžovy near Loděnice, Záloženský lom quarry and Čeřinka quarry near Bubovice. These layers represent roughly the middle part of the Pragian sequence in this area. *Zlichovaspis* (*Z.*) *rugosa laura* is locally very abundant at these localities, associated with *Zlichovaspis* (*Z.*) *spinifera nomiona* Šnajdr (1987a). Rare in Vinařice Limestone facies; Plešivec hill near Měňany. Probably lower to middle part of the Pragian sequence rather than lower as stated by Šnajdr (1987a).

Zlichovaspis (*Zlichovaspis*) *auriculata* (Dalman, 1826)
Fig. 8i–p

1827 *Asaphus auriculatus* Dalman; Dalman, p. 66.
For older synonymy, see Šnajdr (1987a).
1987a *Zlichovaspis auriculata auriculata* (Dalman); Šnajdr, pp. 35–38.
1989 *Odontochile* (*Zlichovaspis*) *auriculata auriculata* (Dalman); Pek & Vaněk, p. 14.
1998 *Odontochile auriculata auriculata* (Dalman); Chlupáč in Chlupáč *et al*., pl. LII, fig. 6.
2000 *Odontochile* (*Zlichovaspis*) *auriculatum auriculatum* (Dalman); Hörbinger, p. 11.
2002 *Zlichovaspis auriculata auriculata* (Dalman); Vaněk & Valíček, p. 11.
2002a *Odontochile* (*Zlichovaspis*) *auriculata auriculata* (Dalman); Chlupáč, p. 34.
2002a *Zlichovaspis auriculatum auriculatum* (Dalman); Vaněk, p. 3.

Holotype (by monotypy). A nearly complete dorsal exoskeleton (eyes and left librigena damaged), NML 18728, preserved in grey biomicritic to fine biodetritic limestone as internal moulds with relics of exoskeleton. Figured by Sternberg (1825, pl. 2, fig. 2), Šnajdr (1987a, pl. 11, figs 3,4); Fig. 8i.

Type horizon and locality. Zlichovian Stage, Zlíchov Formation, exact horizon unknown, Karlštejn (exact locality unknown).

Other material. Specimens discussed and figured by Barrande (1852), specimens in Hawle and Corda and J. Barrande collections deposited in the National Museum, Prague and Museum of Comparative Zoology, Harvard University, Massachusetts (about 50 cephala and 600 pygidia in total).

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) anterior cephalic margin parabolic in dorsal view. No precranial median process; (2) eyes with 44–46 dorsoventral files of up to 11 lenses each; (3) LF with dense granulation becoming finer forwards; (4) pygidium elongated subtriangular, length/width index approx. 0·7–0·8; (5) postaxial ridge moderately vaulted, dorsal part slightly keel-like in cross-section, mucro long, robust; (6) axis with 17–19 (rarely 20–21) rings plus terminal piece; (7) 13 to 14 narrow pleural furrows (width less than or equal to that of pleural bands); (8) thorn-like granules on rings and pleural bands uneven in size. Rings bear granules especially along posterior margin; two or three largest granules form irregular exsagittal rows on adaxial part of axis. Anterior pleural bands with 6–8 large granules spaced unevenly, but forming irregular row on whole band surface.

Description. See Šnajdr (1987a).

Remarks. Because doubts still persist concerning the validity of some species occurring together with *Zlichovaspis* (*Z.*) *auriculata* in the Zlíchov Formation, brief comparisons with the last mentioned species are presented here. *Zlichovaspis* (*Z.*) *ostara* Šnajdr, 1987a differs especially in its pygidial sculpture of dense, minute granules between more sporadic larger granules, and in having narrower pleural furrows. *Zlichovaspis* (*Z.*) *tuberculata* differs especially in the cephalic border having a prominent precranial median process (absent in *Zlichovaspis* (*Z.*) *auriculata*) and the more pronounced pygidial sculpture, even in small specimens. In small holaspides of *Zlichovaspis* (*Z.*) *tuberculata* the large granules on the distal portions of the pleural bands are more closely spaced; in larger specimens prominent large, thorn-like granules or spines comparable with *Zlichovaspis* (*Z.*) *spinifera* (Barrande, 1846) are developed. *Zlichovaspis* (*Z.*) *azucena* Šnajdr, 1987a differs from *Z.* (*Z.*) *auriculata* especially in the distinctly narrow, subtriangular outline of the pygidium, the larger number of axial rings and pygidial ribs, the large granules closely spaced on the distal portions of the pleural bands, and the absence of granules on the proximal parts of the pleural bands. *Zlichovaspis* (*Z.*) *marieva* Šnajdr, 1985 differs especially in its short precranial median process, distinctly narrower pleural furrows and more vaulted pleural bands, and smaller, more abundant granules on both anterior and posterior pleural bands. *Zlichovaspis* (*Z.*) *karlena* Šnajdr, 1987a differs especially in its regularly arranged, large megagranules or spines comparable in diameter with the width of the anterior pleural bands. *Zlichovaspis* (*Z.*) *tamaraka* (Šnajdr, 1985) differs in its prominent megagranules irregularly arranged on the axial rings and anterior pleural bands. *Zlichovaspis* (*Z.*) *vaneki* sp. n. differs especially in the broader outline of its pygidium, the wide pleural furrows, the sculpture of large but sparse thorn-like granules on the axial rings, and the smaller, more abundant granules on the pleural bands.

Although separable from the above-named species, *Zlichovaspis* (*Z.*) *auriculata* still shows a wide range of variation, especially in the sculpture on its pleural bands. Specimens form a continuous morphological series from those with coarse thorn-like granules to those that are almost entirely smooth, with only weak large granules on the anterior pleural bands and none on the posterior bands. There is variation also in the cephalic and pygidial outlines, and the width and depth of the pleural and interpleural furrows. Despite this remarkable variability, which was briefly discussed by Šnajdr (1987a), it is not considered useful to differentiate subspecies of *Zlichovaspis auriculata* based mostly on minor differences, especially in view of the uncertainties in the stratigraphical occurrence of the different morphs represented in old museum collections.

Ontogeny. Several early holaspid cephala and pygidia were observed. The pygidia up to 10–15 mm are characterised by deeper interpleural furrows and distinctive perforations in the pleural furrows. In addition, the granulation on the anterior and posterior pleural bands is more prominent. Three cephala 8–10 mm long possess relatively coarse but dense granulation on LF, L3 and L2. LF, L1–L3 and the fixigenal fields are perforated by fine pores less than 0·1 mm in diameter. These fine pores, which differ from the megapores of *Zlichovaspis* (*Devonodontochile*) Šnajdr, 1985 in lacking peripheral mounds, occur in the interspaces between granules on LF and disappear during ontogeny.

Measurements. Length of holotype 50 mm. Smallest cephala and pygidia are 6–10 mm. Largest complete specimens probably exceed 210 mm in length.

Occurrence. Zlíchov Formation, lower (?), middle to upper part (not only upper part as stated by Šnajdr, 1987a). Very abundant species. Hostim (with *Viriatellina* cf. *pseudogeinitziana*), Lužce, Čeřinka quarry near Bubovice, relatively lower (with *Nowakia* (*Dmitriella*) *praesulcata*) to upper part of Zlíchovian sequence plus one questionable finding coming from the Chýnice Limestone, Boubová, Karlštejn, Choteč (Kozákův mlýn hill), Praha (Řeporyje–Zabitá rokle gorge, Hlubočepy Valley near Klukovice, Zlíchov (with *Viriatellina*

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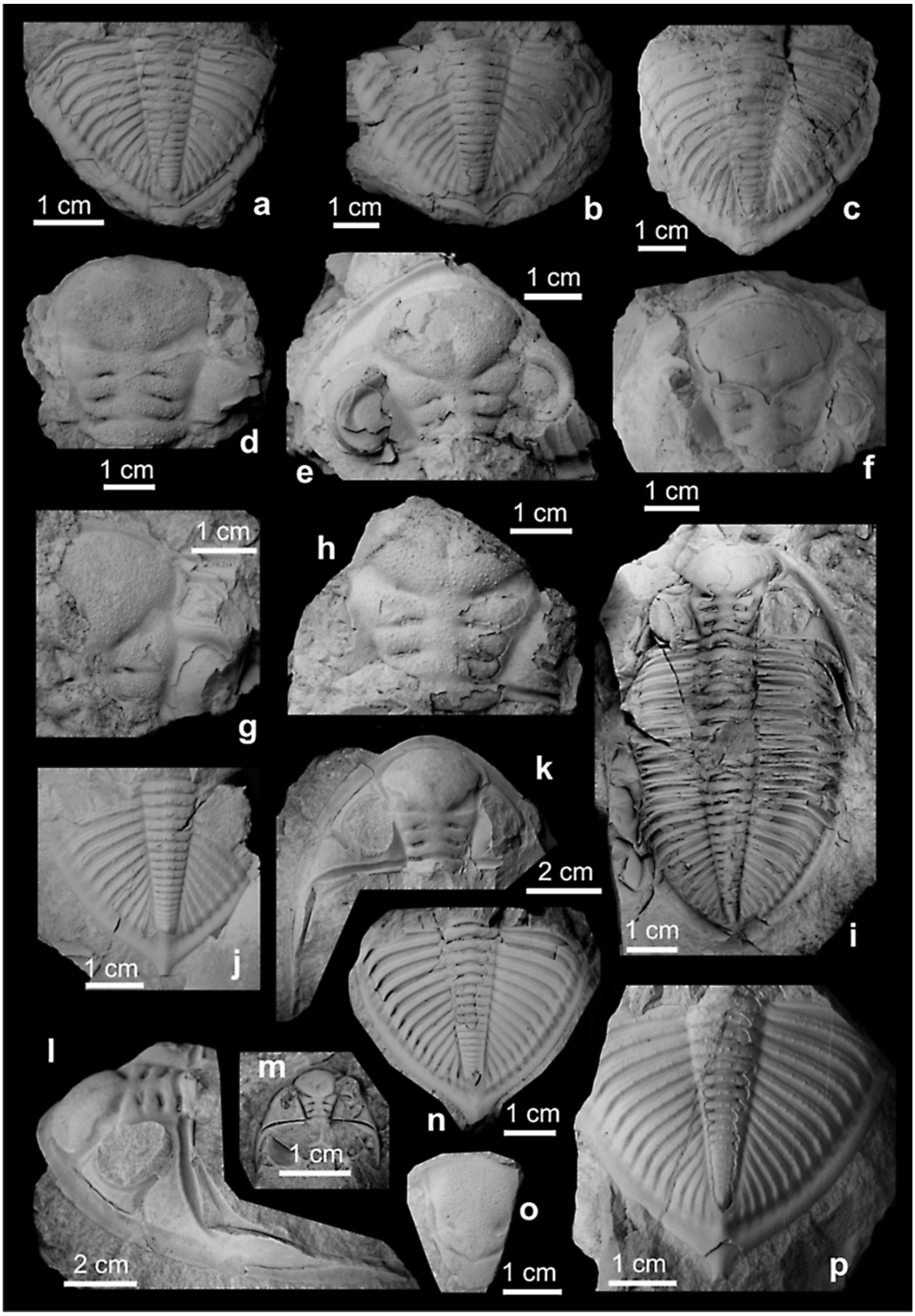

Figure 8 (a–h) *Zlichovaspis* (*Z.*) *rugosa laura* Šnajdr, 1985. Pragian Stage, Praha Formation: (a–b) Loděnice Limestone facies, Záloženský lom quarry: (a) Holotype, incomplete pygidium with damaged exoskeleton, CGS MŠ 11674, dorsal view; (b) Incomplete pygidium with damaged exoskeleton, CGS MŠ 13307, Lužce, dorsal view; (c–d) Vinařice Limestone facies, Měňany, quarry near gamekeeper's lodge: (c) Pygidium NML 22579, paratype of invalid subspecies *Zlichovaspis* (*Z.*) *rugosa sitta* Šnajdr, 1985; (d) Incomplete cephalon CGS MŠ 13153, holotype of invalid subspecies *Zlichovaspis* (*Z.*) *rugosa sitta* Šnajdr, 1985, dorsal view; (e–h) Loděnice Limestone facies, Záloženský lom quarry: (e) Incomplete cranidium, CGS JV 3514, dorsal view; (f) Incomplete cephalon, internal mould with relics of exoskeleton, CGS JV 3561, dorsal view; (g) Incomplete cranidium, CGS JV 3512, dorsal view; (h) Incomplete cranidium with prominent coarse granulation, CGS JV 3513, dorsal view. (i–p) *Zlichovaspis* (*Z.*) *auriculata* (Dalman, 1827), Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (i) Holotype, a nearly complete specimen NML 18728, Karlštejn, internal mould, dorsal view; (j) Incomplete pygidium with coarse sculpture, CGS PB 164, Čeřinka quarry near Bubovice, dorsal view; (k–l) Incomplete cephalon, internal mould, CGS PB 165, Praha–Holyně: (k) dorsal view; (l) lateral view; (m) Early holaspid cephalon, MCZ 172845 (Schary collection), Hostim; (n) pygidium, internal mould with relics of exoskeleton, showing almost entirely effaced sculpture, NML 29759, Hostim, dorsal view; (o) Hypostome, internal mould, CGS PB 163, Holyně–Opatřilka; (p) Incomplete pygidium with typical sculpture, lectotype of *Odontochile subdepressa* Hawle & Corda, 1847, NML 19801, Hostim, dorsal view.

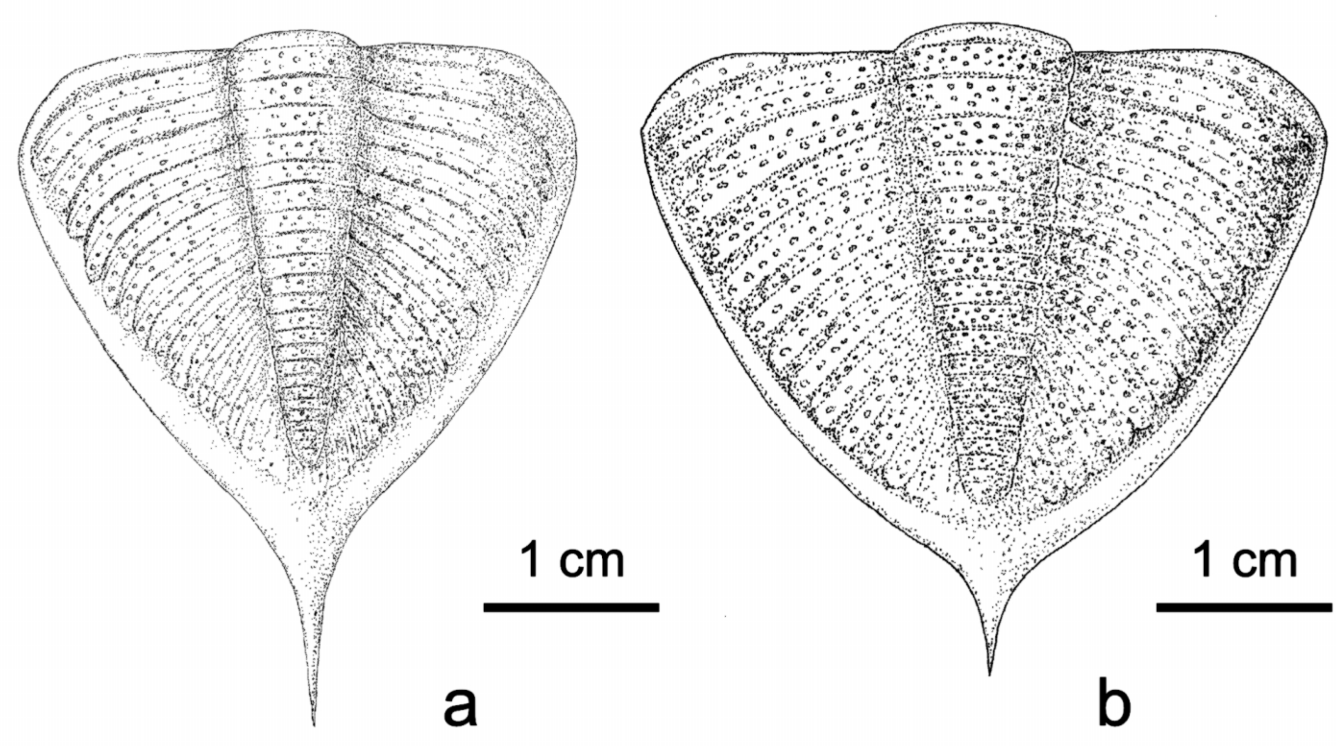

Figure 9 (a) *Zlichovaspis* (*Z.*) *azucena* Šnajdr, 1985. Reconstruction of the pygidium. (b) *Zlichovaspis* (*Z.*) *marieva* Šnajdr, 1985. Reconstruction of the pygidium.

cf. *pseudogeintziana*), Holyně–K Dobré vodě, Požáry II quarry (lower to middle part of the sequence). Two specimens strongly resembling this species come from the lower part (Coral Horizon of the Chappel) of the Zlichovian sequence near Praha–Barrandov. This species is dominant among the museum and field material from the Zlíchov Formation, forming at least 60% of all specimens available.

Zlichovaspis (*Zlichovaspis*) *azucena* Šnajdr, 1987a
Fig. 9a; 10a–h

1987a *Zlichovaspis azucena* sp. n.; Šnajdr, pp. 35–38, pl. 18, figs 2–4, text-figs 5–6.
1989 *Odontochile* (*Zlichovaspis*) *azucena* Šnajdr; Pek & Vaněk, p. 14.
2000 *Odontochile* (*Zlichovaspis*) *azucena* Šnajdr; Hörbinger, pp. 10–11.
2002 *Zlichovaspis azucena* Šnajdr; Vaněk & Valíček, p. 11.

Holotype. An incomplete pygidium (exoskeleton partly exfoliated), CGS MŠ 13184, preserved in grey bisparitic limestone. Figured by Šnajdr (1987a, pl. 18, fig. 4); Fig. 10a.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, upper part, Hostim.

Other material. Twenty-five incomplete pygidia, mostly preserved as internal moulds with relics of exoskeleton.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) pygidium distinctly elongated sagittally, subtriangular in outline, length/width index slightly more than 0·8; (2) mucro robust, broadly based, comprising one-quarter of the pygidial length; (3) axis with 19–21 rings (rarely 22 and more) plus terminal piece; (4) 15–16 (rarely 17) narrow and deep pleural furrows, widening abaxially; (5) anterior pleural bands with 5–6 (rarely 7–8) larger granules, interspaces vary; distal parts with dense granules of uneven size ranging from minute to thorn-like, granules rare or absent on proximal part.

Description. See Šnajdr (1987a).

Remarks. *Zlichovaspis* (*Zlichovaspis*) *azucena* is one of the most distinctive species proposed by Šnajdr (1985, 1987a). It is easily distinguishable from all other *Zlichovaspis* species by the extremely elongate outline of its pygidium, the greater number of pygidial segments, and its mucro with a very broad base. Šnajdr (1987a) suggested that this species is rare, but new discoveries by one of the present authors (RM) from the neighbourhood of Hostim suggest that it may be common at least locally.

Ontogeny. Several young holaspid pygidia were studied. These have a broader subtriangular outline and narrower border than larger pygidia, but like the latter have 20–21 axial rings, 15–16 pleural furrows, a more elongated pygidial outline in comparison with other species, very narrow pleural furrows, and comparable sculpture and vaulting of the pleural bands.

Measurements. Length of holotype 56 mm, that of the largest pygidia more than 70 mm.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, upper part, Hostim, Praha–Hlubočepy (St. Prokop quarry), Švagerka, Řeporyje–Ve skále quarry. Infrequent species.

Zlichovaspis (*Zlichovaspis*) aff. *azucena* Šnajdr, 1987a
Fig. 10i–j

Material. Almost complete pygidium (exoskeleton partly exfoliated), NML 29758, preserved in grey biosparitic limestone of Zlichovian Stage; Zlíchov Formation, Zlíchov Limestone facies (?upper part). Hostim (exact locality unknown), Collected by Zeidler.

Remarks. This pygidium differs from those of most representatives of *Zlichovaspis* (*Zlichovaspis*) in its distinctly elongated outline. In this respect it is reminiscent of *Zlichovaspis*

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(*Z.*) *azucena* Šnajdr, 1987a but it differs from that species in the smaller number of pygidial ribs, more rounded posterolateral outline, and details of the sculpture. The sculpture is more like that of *Zlichovaspis* (*Zlichovaspis*) *marieva* (Šnajdr, 1985) in lacking thorn-like granules on the distal parts of the ribs, but compared to the latter species the pygidium is more elongated in outline and the postaxial ridge is keel-like. The present pygidium resembles both *Z.* (*Z.*) *azucena* and *Z.* (*Z.*) *marieva* in having narrow pleural furrows and comparable vaulting of the pleural bands, but it differs from these species in the density of its large granules, and in having dense and very fine granulation on the distal ends of the pleural ribs and on the border. The narrow pleural furrows, narrow border, more elongate outline and markedly different sculpture easily distinguishing the present pygidium from *Z.* (*Z.*) *auriculata* (Dalman, 1827). As the single pygidium offers no possibility to evaluate the variability of the above-mentioned distinguishing features, and as the precise locality and horizon are uncertain, the specimen is left in open nomenclature.

Measurements. The pygidium is 62 mm long.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies (probably upper part), Hostim (exact locality unknown).

Zlichovaspis (*Zlichovaspis*) *karlena* (Šnajdr 1987a)
Fig. 10k–m

1987a *Spinodontochile karlena* sp. nov.; Šnajdr, pp. 46–47, pl. 8, figs 1–3
1989 *Odontochile* (*Spinodontochile*) *karlena* Šnajdr; Pek & Vaněk, p. 14
1996 *Odontochile* (*Zlichovaspis*) *karlena* (Šnajdr); Havlíček & Vaněk, pp. 2, 11.
2002 *Zlichovaspis karlena* Šnajdr; Vaněk & Valíček, p. 11

Holotype. A damaged complete specimen (exoskeleton partly exfoliated), NML 16924, preserved in grey micritic limestone. Figured by Barrande (1872, pl. 13, figs 24, 25), Šnajdr (1987a, pl. 8, figs 1, 2); Fig. 10k–l.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone Facies, upper layers. Choteč (stated on original label of Barrande); according to Chlupáč (1983b, 2002a), locality is probably situated NW of the former Kalinův mlýn mill.

Other material. Five incomplete pygidia with partly exfoliated exoskeleton and vertical spines broken off.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) glabella (except L1) covered with coarse, randomly distributed megagranules and smaller granules; (2) thorax with axial rings covered by densely distributed megagranules; (3) anterior pleural bands with a row of 6–9 closely spaced megagranules; (4) pygidium rounded subtriangular in outline, length/width index approx. 0·75; (5) axis with 17–19 rings plus terminal piece, rings narrow with 2–6 vertical megagranules, deep apodemal pits in inter-ring furrows; (6) 13–14 (rarely 15) wide pleural furrows; (7) anterior pleural bands with row of 8–9 vertical, irregularly spaced megagranules of slightly larger diameter than width of bands. Interspaces finely granulose.

Description. See Šnajdr (1987a).

Remarks. The species is poorly known. The holotype, assigned by Barrande (1872, pl. 13, figs 24–25) to *Dalmanites spinifera* Barrande, 1846 differs significantly from other Lower Devonian dalmanitid trilobites of the Prague Basin in having prominent, large megagranules to spines developed even in the young holaspid stage. These megagranules are very robust, comparable with those in large holaspides of *Z.* (*Z.*) *spinifera* or *Z.* (*Z.*) *tuberculata*. They are even larger in diameter than the width (exsag.) of the anterior pleural bands, and their dimensions increase during ontogeny. In addition, although slightly irregularly arranged, they form relatively well developed and densely spaced rows on pleural bands, compared with the rather sporadic arrangement of spines in the other two mentioned species.

Measurements. Length (sag.) of holotype 52 mm (deformed incomplete specimen), length of largest pygidium 80 mm.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone: Choteč. Chýnice Limestone facies: Bubovice, Čeřinka quarry. Very rare. The species is the only dalmanitid known with certainty from the Chýnice Limestone facies.

Zlichovaspis (*Zlichovaspis*) *marieva* (Šnajdr, 1985)
Fig. 9b; 11a–c

1852 *Dalmanites spinifera* Barrande (partim); Barrande, pl. 25, fig 2.
? 1852 *Dalmanites spinifera* Barrande (partim); Barrande, pl. 27, figs 4–5, 7.
1985 *Spinodontochile marieva* sp. n.; Šnajdr, p. 167, pl. 1, figs 1–3.
1987a *Spinodontochile marieva* Šnajdr; Šnajdr, pp. 43–44, pl. 7, figs 1–6, text-fig. 4–7.
1989 *Odontochile* (*Spinodontochile*) *marieva* Šnajdr; Pek & Vaněk, p. 14.
2002 *Zlichovaspis marieva* Šnajdr; Vaněk & Valíček, p. 11.
2002a *Odontochile* (*Zlichovaspis*) *auriculatum auriculatum* (Dalman) (partim); Chlupáč, p. 34 (Barrande's plate 25, fig. 2).
? 2002a *Odontochile* (*Spinodontochile*) *spinifera spinifera* (Barrande) (partim); Chlupáč, p. 34 (Barrande's pl. 27, figs 4, 5, 7).
? 2002a *Odontochile* sp.; Vaněk p. 4.

Holotype. An incomplete pygidium with partly exfoliated exoskeleton, CGS MŠ 13174, preserved in grey biosparitic limestone. Figured by Šnajdr (1985, pl. 1, fig. 1; 1987a, pl. 6, fig. 6,); Fig. 11a.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation (probably upper part), Hostim.

Other material. Fifteen incomplete cephala, about 65 selected pygidia (mostly newly collected material). All specimens are preserved as internal moulds with relics of exoskeleton but several of the best specimens have the exoskeleton almost entirely preserved.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) cephalon subtriangular. Anterior margin parabolic with short but prominent precranial median process. Cephalon densely granulose. Glabella, genal field and palpebral lobe covered with prominent thorn-like granules of unequal size; (2) pygidium semioval to subtriangular in outline, length/width index 0·7–0·75; (3) axis with 17–19 rings plus elevated terminal piece, mucro subtriangular in cross-section; (4) 13 to 14 deep pleural furrows, narrower than anterior pleural bands. Interpleural furrows well defined; (5) both the anterior and posterior pleural bands almost equivalent in vaulting, steeply inclined downward into pleural furrows, their distal ends vaulted, knob-like; (6) pygidial border narrow; (7) axial rings covered with randomly distributed larger granules of equal size. Anterior pleural bands with 8–12 granules, distal parts with dense smaller granules increasing in number. Posterior pleural bands with 12 larger granules almost equivalent

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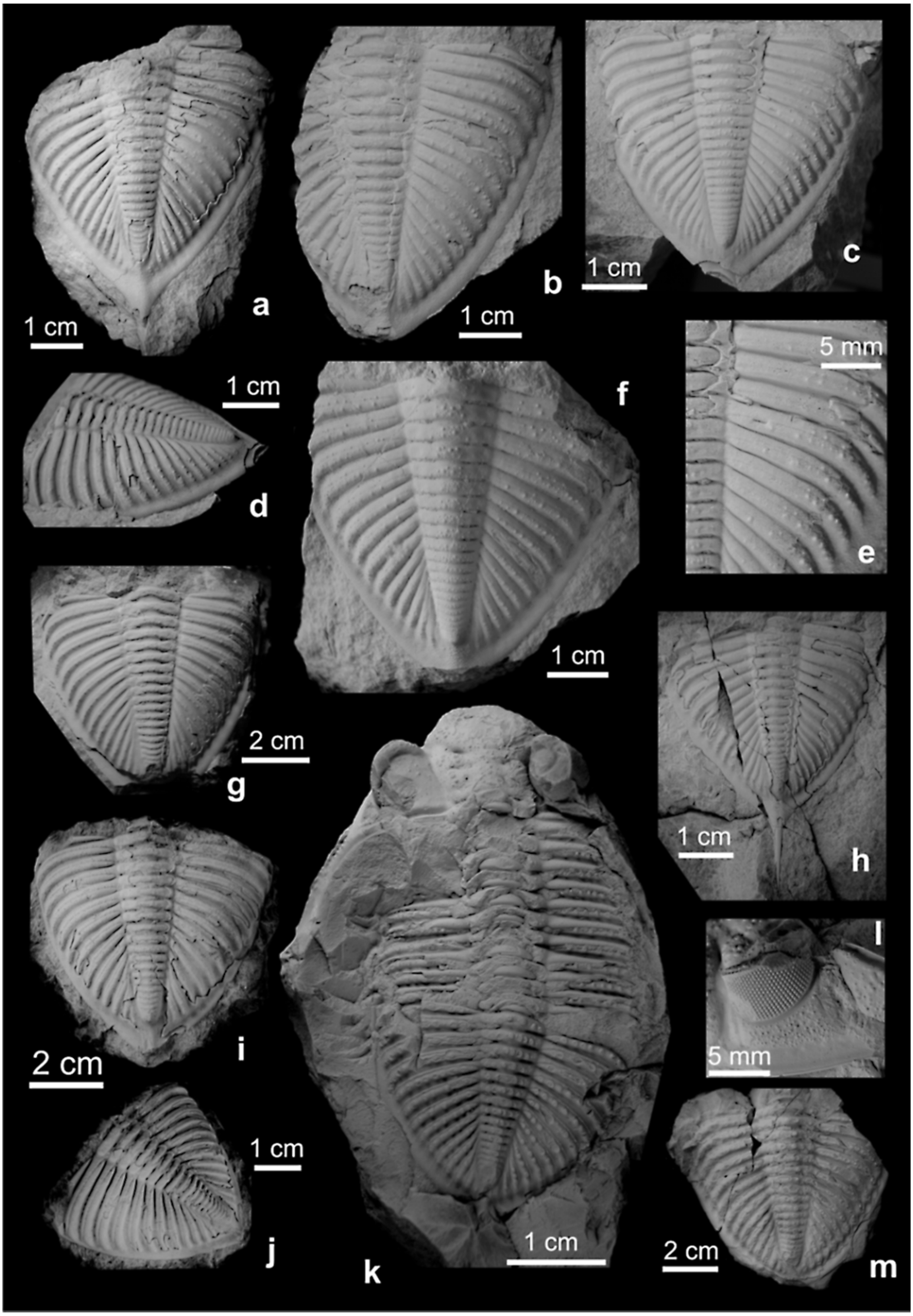

Figure 10 (a–h) *Zlichovaspis* (*Z.*) *azucena* Šnajdr, 1985. Zlichovian (lower Emsian), Zlíchov Formation: (a) Holotype pygidium CGS MŠ 13184, internal mould with exoskeleton partly exfoliated, Hostim, dorsal view; (b) Incomplete pygidium, internal mould with exoskeleton, paratype CGS MŠ 13186, dorsal view; (c–e) Well-preserved pygidium, internal mould with exoskeleton, CGS PB 166, Hostim, Boubová: (c) dorsal view; (d) lateral view; (e) detail of right pleural field; (f) Incomplete pygidium, internal mould with exoskeleton, NML 29888, dorsal view; (g) Incomplete pygidium, internal mould, CGS PB 167, dorsal view; (h) Pygidium, internal mould with exoskeleton, CGS MŠ 13186, dorsal view. (i–j) *Zlichovaspis* (*Z.*) aff. *azucena* Šnajdr, 1985. Zlichovian regional stage (lower Emsian), Zlíchov Formation Pygidium NML 29758, internal mould with partly exfoliated exoskeleton, Hostim: (i) dorsal view; (j) dorsolateral view. (k–m) *Zlichovaspis* (*Z.*) *karlena* Šnajdr, 1985. Zlichovian regional stage (lower Emsian), Zlíchov Formation: (k–l) Holotype, incomplete specimen, internal mould with exoskeleton, NML 16924, Choteč: (k) dorsal view; (l) detail of the eye, lateral view; (m) Incomplete large pygidium, internal mould, uppermost Zlíchov Limestone, Praha–Holyně, CGS JV 3515, dorsal view.

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in diameter to the granules on anterior pleural band, distal parts with crowded small granules.

Description. See Šnajdr (1987a).

Remarks. This species is fairly easily differentiated from others in the Lower Devonian of the Prague Basin. The most similar species is *Zlichovaspis* (*Z.*) *tuberculata* (Hawle & Corda, 1847), which differs in its more subtriangular outline of the pygidium, the smaller number and larger size of the thorn-like granules on the axial rings and pleural bands, and the wider pleural furrows. *Zlichovaspis* (*Z.*) *auriculata* (Dalman, 1827) differs in lacking a precranial median process, its flatter pygidium of more subtriangular outline, the different granulation on the anterior and posterior pleural bands, and the wider pleural furrows and pygidial border.

The present authors questionably assign to *Z.* (*Z.*) *marieva* an incomplete cephalon figured by Barrande (1852, pl. 27, figs 4, 5, 7) as *Dalmanites spinifera*. The specimen was not mentioned by Šnajdr (1987a). Chlupáč (2002a) assigned it to *Odontochile* (*Spinodontochile*) *spinifera* Barrande, whereas Vaněk (2002a) determined it as *Odontochile* sp. The specimen is preserved in a grey micritic limestone without tentaculitid remains, and the locality 'Hostin' (Hostim) mentioned by Barrande (1852) suggests an age of Pragian to Zlichovian. Barrande's reconstruction of the cephalon is idealised, and the preservation is poor, but the specimen resembles *Z.* (*Z.*) *marieva* especially in the prominent precranial median process and type of sculpture.

Z. (*Z.*) *marieva* shows considerable variability in the number and diameter of the large granules on the anterior and posterior pleural bands. In some specimens, between the first-order granules, sparse, irregularly arranged finer granules are also present. The number of first-order granules on the axial rings varies from 10–12 up to 25–35 on the first three rings. The arrangement of the granules also varies: in some specimens they are more common on the posterior part of the rings. Pseudo-articulating half rings may also be more prominent in some specimens than in others.

Ontogeny. The smallest pygidium, 9 mm long, was described by Šnajdr (1987a).

Measurements. Length (sag.) of holotype 30 mm (deformed incomplete specimen); length of largest pygidium 62 mm; length of largest cephalon 42 mm.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, upper part: Hostim, Lužce, Karlštejn, Choteč, Praha–Řeporyje (Zabitá rokle), Švagerka. The species is quite abundant at these localities, except for the last two.

Zlichovaspis (*Zlichovaspis*) aff. *marieva* (Šnajdr, 1985)
Fig. 11d–e

Material. Incomplete pygidium, internal mould with relics of exoskeleton from the dark grey fine biosparitic limestone of the upper part of the Zlíchov Formation, Hostim. One additional pygidium (CGS PB 230) from the same locality.

Remarks. These pygidia appear to be most closely related to *Zlichovaspis* (*Z.*) *marieva*, but lie outside the variability of that species by the more triangular outline of their pygidium, the very narrow pleural furrows, the narrower axis, and the entirely different type of sculpture on the pygidial ribs, with fewer large granules arranged chaotically on the anterior pleural bands. In the chaotic arrangement of granules there is a resemblance to *Z.* (*Z.*) *tamaraka* (Šnajdr, 1985) but in that species large megagranules are present on the axis and pleural bands. These two pygidia appear to belong to a new species, but in view of the limited material available it has been left in open nomenclature.

Measurements. The incomplete pygidium figured is 21 mm long; the other, larger pygidium is 40 mm long.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, upper part: Hostim–Boubová (nad křížem).

Zlichovaspis (*Zlichovaspis*) *ostara* Šnajdr, 1987a
Fig. 11g–l

1987a *Zlichovaspis auriculata ostara* subsp. n.; Šnajdr, pp. 35–38, pl. 11, figs 5–6, text-fig. 5–5.
1989 *Odontochile* (*Zlichovaspis*) *auriculata ostara* Šnajdr; Pek & Vaněk, p. 14.
2000 *Odontochile* (*Zlichovaspis*) *auriculatum ostara* Šnajdr; Hörbinger, p. 11.
2002 *Zlichovaspis auriculata ostara* Šnajdr; Vaněk & Valíček, p. 11.

Holotype. Pygidium with exoskeleton intact (except on part of pleural band and mucro), CGS MŠ 13177, preserved in fine sparitic limestone. Figured by Šnajdr (1987a, pl. 11, figs 5–6); Fig. 11g.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, probably from the upper part of the Zlichovian sequence (fine, grey sparitic limestone with *Chondrites* sp. burrows), Choteč.

Other material. Eleven incomplete pygidia with remains of the exoskeleton.

Diagnosis. Species strongly reminiscent of *Zlichovaspis* (*Z.*) *auriculata* with the following specific features: (1) 12–14 pleural furrows, distinctly narrower than pleural bands; (2) entire surface of axial rings covered with granules of unequal size (they are concentrated on the posterior margin of the rings in *Z.* (*Z.*) *auriculata*); (3) anterior pleural bands with 3–4 large, thorn-like granules, interspaces covered by densely distributed minute granules and perforated granules, slightly perceptible also on internal moulds. Band more inflated above the inner margin of the doublure; (4) posterior pleural bands with a row of densely spaced granules of unequal size.

Remarks. This species, described by Šnajdr (1987a) as a subspecies of *Zlichovaspis* (*Z.*) *auriculata* was poorly known, being based on the holotype only. Its validity at species level is supported by the discovery of additional specimens which conform comparatively well with the slightly modified original diagnosis. All the specimens share very narrow pleural furrows, and anterior pleural bands with only a few large sporadic granules between which are coarse granules. Almost all of the specimens are from the uppermost Zlíchov Limestone. Several specimens that are considered by the present authors to belong to *Zlichovaspis* (*Z.*) *ostara* were found by one of them (RM) occurring together with *Zlichovaspis* (*Z.*) *auriculata* in the high part of the Zlichovian sequence near Hostim–Boubová. Because the co-occurrence of subspecies is unlikely, and with evaluation of the above-mentioned differences from *Zlichovaspis* (*Z.*) *auriculata*, it is preferred to regard *ostara* as a separate species.

All of the specimens show considerable variability in number of axial rings and pleural furrows. There is some variability also in the length/width index of the pygidium, which may reach 0·7–0·8, and in the depth of the pleural furrows and vaulting of the pleural bands, these being especially pronounced in large specimens (Fig. 11o–p). Specimen CGS PB 157 has a broader pygidial outline and wider axis than others. All of these differences are considered to be due to intraspecific variability. There is a noticeable tendency towards effacement of the sculpture near the axial furrows, both on the axis and on the adjacent part of the rib. In this respect,

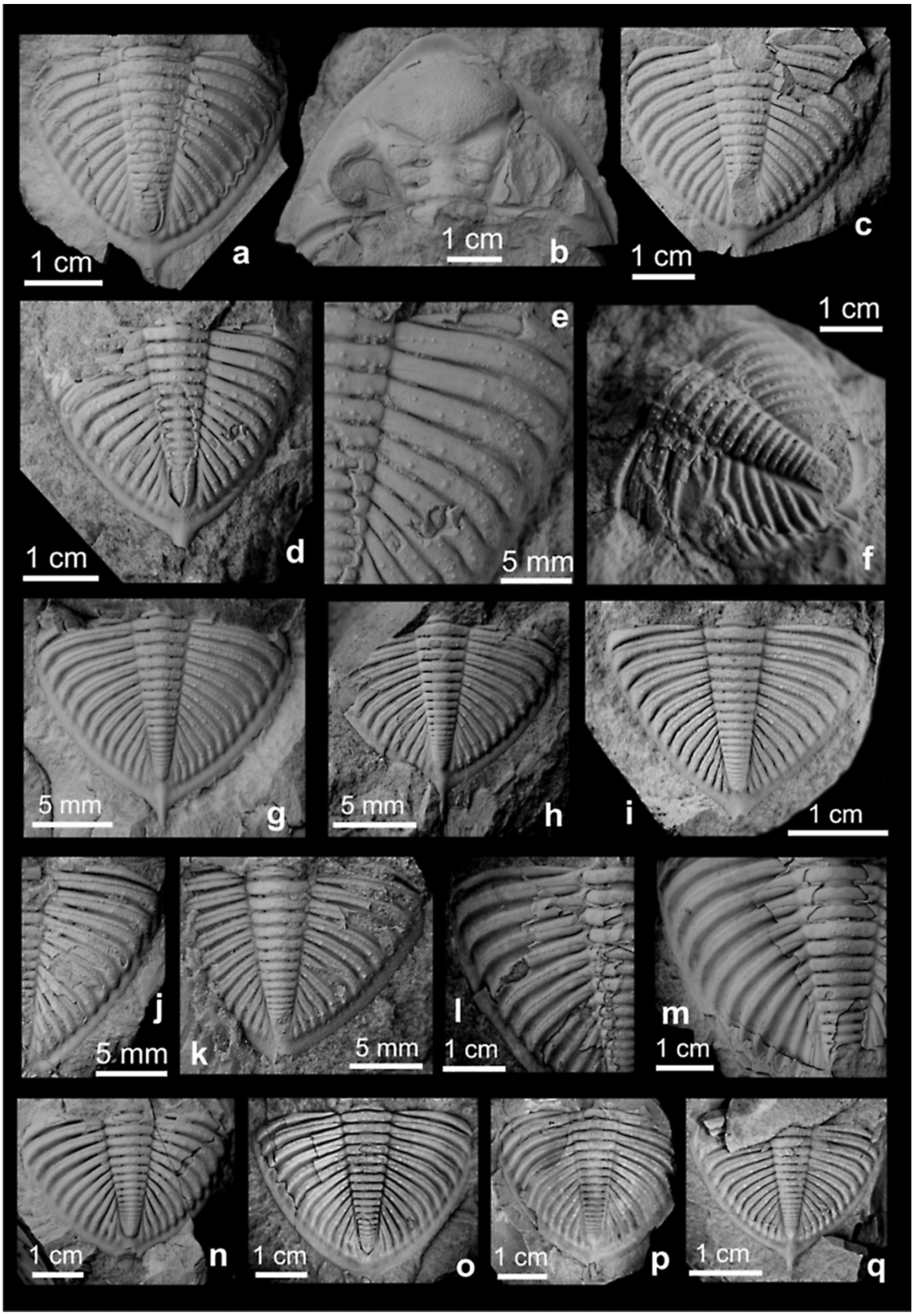

Figure 11 (a–c): *Zlichovaspis* (*Zlichovaspis*) *marieva* (Šnajdr, 1985). Zlichovian (lower Emsian), Zlíchov Formation: (a) Holotype, pygidium CGS MŠ 13174, Hostim, dorsal view; (b) Large cephalon, CGS MŠ13361, Hostim, dorsal view; (c) Incomplete pygidium CGS PB 168, internal mould with exoskeleton, Praha–Řeporyje (Zabitá rokle gorge). (d–e) *Zlichovaspis* (*Z.*) aff. *marieva* (Šnajdr, 1985). Zlichovian regional stage (lower Emsian), Zlíchov Formation. Incomplete pygidium CGS PB 169, Hostim, Boubová: (d) dorsal view; (e) detail of right pleural field, dorsal view. (f) *Zlichovaspis* (*Z.*) cf. *marieva* (Šnajdr, 1985), incomplete pathologic pygidium with coarse granulation, internal mould with remains of exoskeleton, MB 315/77/16, Hostim, dorsolateral view. (g–l) *Zlichovaspis* (*Z.*) *ostara* Šnajdr, 1987a. Zlichovian regional stage (lower Emsian), Zlíchov Formation: (g) Holotype, complete pygidium with exoskeleton, CGS MŠ 13177, Choteč, dorsal view; (h) Incomplete pygidium, internal mould with remains of exoskeleton, CGS PB 170, Karlštejn, Kněží Hora, dorsal view; (i) Incomplete pygidium, internal mould with exoskeleton, NML 30218, Hostim, dorsal view; (j) Incomplete pygidium, internal mould with exoskeleton, CGS PB 169. Karlštejn, Kněží Hora, detail of right pleural field, dorsal view; (k) Incomplete early holaspid pygidium, internal mould with exoskeleton, CGS PB 172, Karlštejn, Kněží Hora, dorsal view; (l) Damaged pygidium, internal mould with exoskeleton, CGS PB 171, detail of left pleural field. (m–q) *Zlichovaspis* (*Z.*) cf. *ostara* Šnajdr, 1987a: (m) Damaged pygidium, internal mould with exoskeleton, CGS PB 173, Karlštejn, Kněží Hora, detail of axis and left pleural field; (n) Pygidium, internal mould with exoskeleton, Čeřinka quarry near Bubovice, CGS PB 174, dorsal view; (o) Incomplete pygidium, MCZ 17826, Choteč, dorsal view; (p) Incomplete pygidium, MCZ 17836 location unknown, dorsal view; (q) Incomplete early holaspid pygidium, MCZ 172857, dorsal view.

Zlichovaspis (*Z.*) *ostara* strongly resembles *Zlichovaspis* (*Z.*) *azucena*, but the former differs, e.g., in its broader pygidial outline.

Measurements. Length of holotype 14 mm; largest pygidia more than 50 mm long.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, higher and uppermost parts (biomicritic to biosparitic limestone): Choteč, Čeřinka quarry near Bubovice (?), Hostim, Karlštejn-Kněží hora, Praha–Žvahov.

Zlichovaspis (*Zlichovaspis*) *spinifera spinifera* (Barrande, 1846)
Fig. 12a–c, e

1846 *Phacops spinifer* Barrande; Barrande, p. 82.
? 1957 *Odontochile spinifera* Barr.; Coma & Villalta, p. 22, text-fig. 3.
1958 *Odontochile spinifera* (Barr.); Struve, pl. 3, fig. 15.
For older synonymy, see e.g. Šnajdr (1987a).
1987a *Spinodontochile spinifera spinifera* (Barrande); Šnajdr, pp. 40–42, p. 4, figs 1–5, pl. 5, figs. 1–5, pl. 18, figs 5–7, pl. 19, fig. 1.
1989 *Odontochile* (*Zlichovaspis*) *spinifera spinifera* (Barrande); Pek & Vaněk, p. 14.
? non 1990 *Spinodontochile spinifera* (Barrande); García-Alcalde *et al*., fig. 12/1.
non 1993 *Odontochile spiniferum* Barrande; Levi-Setti, p. 306, pl. 215.
2000 *Odontochile* (*Spinodontochile*) *spiniferum spiniferum* (Barrande); Hörbinger, p. 11.
2002 *Zlichovaspis spinifera spinifera* (Barrande); Vaněk & Valíček, p. 12.
2002a *Odontochile* (*Spinodontochile*) *spinifera spinifera* (Barrande); Chlupáč, p. 34.
2002a *Zlichovaspis spiniferum* (Barrande); Vaněk, p. 3.

Lectotype. Subsequent designation of Přibyl (*in* Horný & Bastl 1970, p. 294); a large, incomplete pygidium (internal mould with relics of exoskeleton), NML 15041, preserved in grey biomicritic limestone. Figured by Barrande (1852, pl. 25, figs 15–18), Šnajdr (1987a, pl. 4, fig. 5); Fig. 12a.

Type horizon and locality. Pragian, Praha Formation, Dvorce–Prokop Limestone, upper layers (*Guerichina strangulata* dacryoconarid biozone); Praha–Hlubočepy (exact locality unknown).

Other material. Twenty incomplete cephala, one incomplete thorax with part of cephalon and pygidium (negative counterpart) and about 55 incomplete pygidia. All specimens are preserved in biomicritic limestone as internal and external moulds with relics of exoskeleton.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) anterior margin parabolic, with short concave (sag., exsag.) precranial median process in late holaspid specimens; (2) sculpture of entire cephalon (especially occipital lobe and glabella) consisting of dense, coarse granules of unequal size in small specimens, becoming thorn-like granules varying in size in large specimens; (3) pygidium semioval in outline, length/width index ca. 0·8. Axis robust, wide, about 0·27 times as wide as pygidium, consisting of 16–18 rings plus terminal piece; (4) axis covered with coarse, dense, thorn-like granules of unequal size in small specimens, in large specimens with up to two (rarely three) large, vertical spines on every ring, forming two exsagittal rows. Numerous smaller spines surround these large spines; (5) 12 to 14 deep, narrow pleural furrows; (6) anterior pleural bands vaulted, covered by thorn-like granules in small holaspid specimens, in large specimens with up to six or seven large vertical spines surrounded by smaller spines. Interspaces smooth; (7) posterior pleural bands with sparse coarse granules or small spines forming a row.

Description. See Šnajdr (1987a). His description can be supplemented with new information on the thoracic morphology, based on the small holaspid specimen CGS PB 158 (Fig. 12e): Axis wide, low, entire surface including lateral portions equally covered by very dense but coarse thorn-like granules of unequal diameter. Their density in places exceeds 20 granules per 1 mm^2. Thoracic pleurae relatively narrow (trans.). Pleural furrows narrow, deep. Both anterior and posterior pleural bands vaulted. Anterior pleural bands covered with dense, thorn-like, irregularly arranged granules of unequal diameter. Posterior pleural bands with one row of thorn-like granules, their distal portions with crowded granules.

Remarks. The older synonymy of this species was discussed in detail by Šnajdr (1987a). The present authors support his concept of the species and the separation from it of *Z.* (*Z.*) *tuberculata*, *Z.* (*Z.*) *tamaraka* (Šnajdr, 1985) and *Z.* (*Z.*) *karlena* (Šnajdr, 1987a) as independent though probably related species. Šnajdr (1987a) also described prominent allometry in the ontogenetic development of *Zlichovaspis* (*Z.*) *spinifera spinifera*. His observations, which we can be supported and supplemented by the present investigations, include changes in the cephalic outline with the precranial median process being absent in small specimens. In small pygidia there are slightly fewer axial rings (16–17), the number of pleural furrows varies from 12 to 13, and the distal portions of the pleural bands are prominently vaulted. However, the most important ontogenetic changes are in the sculpture. In the smallest specimens it consists of dense, coarse granulation uniformly covering the entire exoskeleton, especially the median part of the pygidial axial rings and the posterior part of the anterior pleural bands. In small holaspid specimens (with pygidia 10–15 mm long), dense, thorn-like granules replace the granulation, covering the entire dorsal surface but being most prominent on the glabella and the pygidial axis and pleural bands. In the largest specimens (150–120 mm long), the thorn-like granules are strongly differentiated and some develop into long, robust, sub-vertical spines, forming irregular rows on the axis and pleural bands. Other spines are substantially smaller but also prominent in comparison with younger specimens. This prominent sculpture was used by Šnajdr (1985) as a basis for establishing the genus *Spinodontochile*. In fact, no other distinguishing features support the existence of this genus. *Zlichovaspis* (*Z.*) *tuberculata* (Hawle & Corda, 1847) has a somewhat similar sculpture but that species differs from *Z.* (*Z.*) *spinifera spinifera* in its ontogenetic development (see discussion of the former species).

Many dalmanitids from Morocco, Spain and Turkey have been assigned to *Z.* (*Z.*) *spinifera*, but the determinations are often erroneous, mainly because of poor preservation. *Odontochile spinifera orientalis* Haas, 1968, from the Upper Emsian of Turkey, probably belongs to an independent species. Records of *Z.* (*Z.*) *spinifera* from Morocco, reported especially by G. Alberti (1969, 1970) and Hollard (1978), represent the related *Zlichovaspis* (*Z.*) *paraspinifera* (Alberti, 1983). Most newer records from Morocco can be attributed to the latter species. The specimen from the SE Anti-Atlas Mountains assigned by Schraut (2000) to *Odontochile* cf. *paraspiniferum* resembles *Z.* (*Z.*) *spinifera* in sculpture and in the broad outline of the pygidium, but differs in having a narrower pygidial border. A complete dorsal exoskeleton from the Pragian Hamar Laghdad Formation of the Alnif area, attributed to *Odontochile spiniferum* Hawle & Corda, 1847 by Levi-Setti (1993), differs in its more prominent precranial

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median process, shorter genal spines, distinctly wider pygidial pleural furrows, and sculpture of fine to coarse granules. It probably represents a new species. Specimens described as *Odontochile spinifera* by Arbizu (1986) from the Pyrenees and the Cantabrian Mountains, Spain, resemble *Zlichovaspis* (*Z.*) *karlena* Šnajdr, 1987a, but the preservation does not allow reliable comparison. *Dalmanites* (*Odontochile*) *rhenanus* Kayser, 1880 resembles *Z.* (*Z.*) *spinifera* but its preservation is poor. Also poorly preserved are specimens from Gerona (Spain) assigned to *Odontochile spinifera* by Coma & Villalta (1957), and those from the Cantabrian region (NW Spain) assigned to *Spinodontochile spinifera* by García-Alcalde *et al.* (1990, pl. 12, fig. 1).

Measurements. Length of lectotype (not holotype as stated by Šnajdr 1987a, p. 42) 84 mm, excluding articulating half ring and mucro. Largest pygidium 90 mm long without mucro; smallest pygidium (CGS MŠ 13158) 5·5 mm long. The length of the exoskeleton of the largest specimens probably exceeded 250 mm.

Occurrence. Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies. Middle and upper part of the sequence. Praha–Bráník, Řeporyje, Konvářka, Malá Chuchle, Hlubočepy (quarry north of Barrandova skála Rock and St-Prokop quarry, Cikánka quarry near Slivenec, Kosoř (Černá rokle gorge).

Zlichovaspis (*Zlichovaspis*) *spinifera nomiona* Šnajdr, 1987a
Fig. 12f

1987a *Spinodontochile spinifera nomiona* subsp. nov.; Šnajdr, pp. 42–43, pl. 5, figs 6–7.
1989 *Odontochile* (*Zlichovaspis*) *spinifera nomiona* Šnajdr; Pek & Vaněk, p. 14.
2002 *Zlichovaspis spinifera nomiona* Šnajdr; Vaněk & Valíček, p. 12.

Holotype. An incomplete pygidium with partly exfoliated exoskeleton, CGS MŠ 11675, preserved in bioclastic limestone. Figured by Šnajdr (1987a, pl. 5, fig. 6); Fig. 12f.

Type horizon and locality. Pragian, Praha Formation, Loděnice Limestone facies, Branžovy near Loděnice, Založenský lom quarry.

Other material. Three incomplete pygidia with partly exfoliated exoskeleton, originally described by Šnajdr, and two other incomplete pygidia (internal moulds with partly preserved exoskeleton) from the Vaněk collection, stored in the Czech Geological Survey.

Diagnosis. A subspecies of *Zlichovaspis* (*Z.*) *spinifera* with the following specific features: (1) thorn-like granules on axial rings strongly differentiated in size, even in small holaspid specimens; (2) anterior pleural bands with sparse thorn-like granules of varying sizes; (3) posterior pleural bands with a row of sparse, thorn-like granules of unequal size (in nominotypical subspecies they are denser, smaller and more irregularly arranged); (4) pleural furrows covered by tiny granules; (5) apodemal pits in inter-ring furrows more distinct; (6) exoskeleton thick.

Remarks. *Zlichovaspis* (*Z.*) *spinifera nomiona* can be differentiated from the nominotypical subspecies by the characters listed in the diagnosis. However, distinguishing it from *Zlichovaspis* (*Z.*) *rugosa laura*, which is dominant in the assemblages from the Branžovy and Čeřinka quarries, is not as easy. Šnajdr (1985) originally did not discriminate the two taxa, but subsequently (Šnajdr 1987a) he separated *Zlichovaspis* (*Z.*) *spinifera nomiona* on the basis of four pygidia selected from the original material of *Zlichovaspis* (*Z.*) *rugosa laura*. The differences between the two taxa are minor. In *Zlichovaspis* (*Z.*) *spinifera nomiona*, prominent, thorn-like granules are distributed evenly over the entire surface of the pygidial axial rings, whereas in *Z.* (*Z.*) *rugosa laura* they are smaller and sparse on the lateral part of the rings. The granules on the pleural bands are coarser and the pleural furrows are narrower in *Z.* (*Z.*) *spinifera nomiona*. All specimens of *Z.* (*Z.*) *spinifera nomiona* are poorly preserved, so the status of the subspecies should be considered as provisional.

Measurements. Length of holotype 40 mm; other pygidia 35–50 mm long.

Occurrence. The subspecies is very rare and insufficiently known, being limited to the Pragian Koněprusy, Slivenec and Loděnice Limestone facies at the type locality. Its occurrence in a similar sedimentary succession in the Čeřinka quarry (J. Vaněk, pers. comm. 2004) is considered here as doubtful; all of these specimens that are available represent *Zlichovaspis* (*Z.*) *rugosa laura* with coarse sculpture.

Zlichovaspis (*Zlichovaspis*) *tamaraka* (Šnajdr, 1985)
Fig. 12g–j

1852 *Dalmania spinifera* Barrande (partim); Barrande, pl. 27, fig. 6.
For older synonymy, see Šnajdr (1987a).
1987a *Spinodontochile tamaraka* Šnajdr; pp. 47–48, pl. 9, figs 4–5.
1989 *Odontochile* (*Spinodontochile*) *tamaraka* (Šnajdr); Pek & Vaněk, p. 14.
2002 *Zlichovaspis tamaraka* (Šnajdr); Vaněk & Valíček, p. 12.
2002a *Odontochile* (*Spinodontochile*) *tamaraka* (Šnajdr); Chlupáč, p. 35.
2002a *Zlichovaspis tamaraka* (Šnajdr); Vaněk, p. 3.

Holotype. A pygidium with exoskeleton (distal part of mucro broken off), damaged by calcite veinlet, CGS MŠ 13179. Figured by Šnajdr (1985, pl. 1, fig. 5), Šnajdr (1987a, pl. 9, fig. 4); Fig. 12g.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, probably the upper part of the sequence, Hostim.

Other material. Pygidium, paralectotype of *Dalmania spinifera* Barrande, 1846, figured by Barrande (1852, pl. 27, fig. 6). Nineteen other, incomplete pygidia preserved as internal moulds in limestone.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) wide axis with 16–17 rings plus terminal piece; (2) 12 to 13 narrow pleural furrows, widening abaxially; (3) axial rings with sculpture of haphazardly distributed granules of uneven size; some rings also with solitary, irregularly spaced vertical megagranules to short robust spines; (4) each anterior pleural band bears up to four (rarely five) megagranules with diameter equal to or greater than width (exsag.) of band. Megagranules arranged chaotically, interspaces finely granulose.

Description. See Šnajdr (1987a).

Remarks. This species is easily distinguishable from all others by its distinct sculpture and wide axis. It is very rare but is represented in newly collected material that supports a late Zlichovian age. The variability in the diameter of the megagranules and space arrangement is noticeable; every specimen has its own pattern of sculpture.

Measurements. Length of holotype 25 mm; other pygidia 35–50 mm long.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, upper part of the sequence, Hostim, Holyně, Opatřilka. Rare.

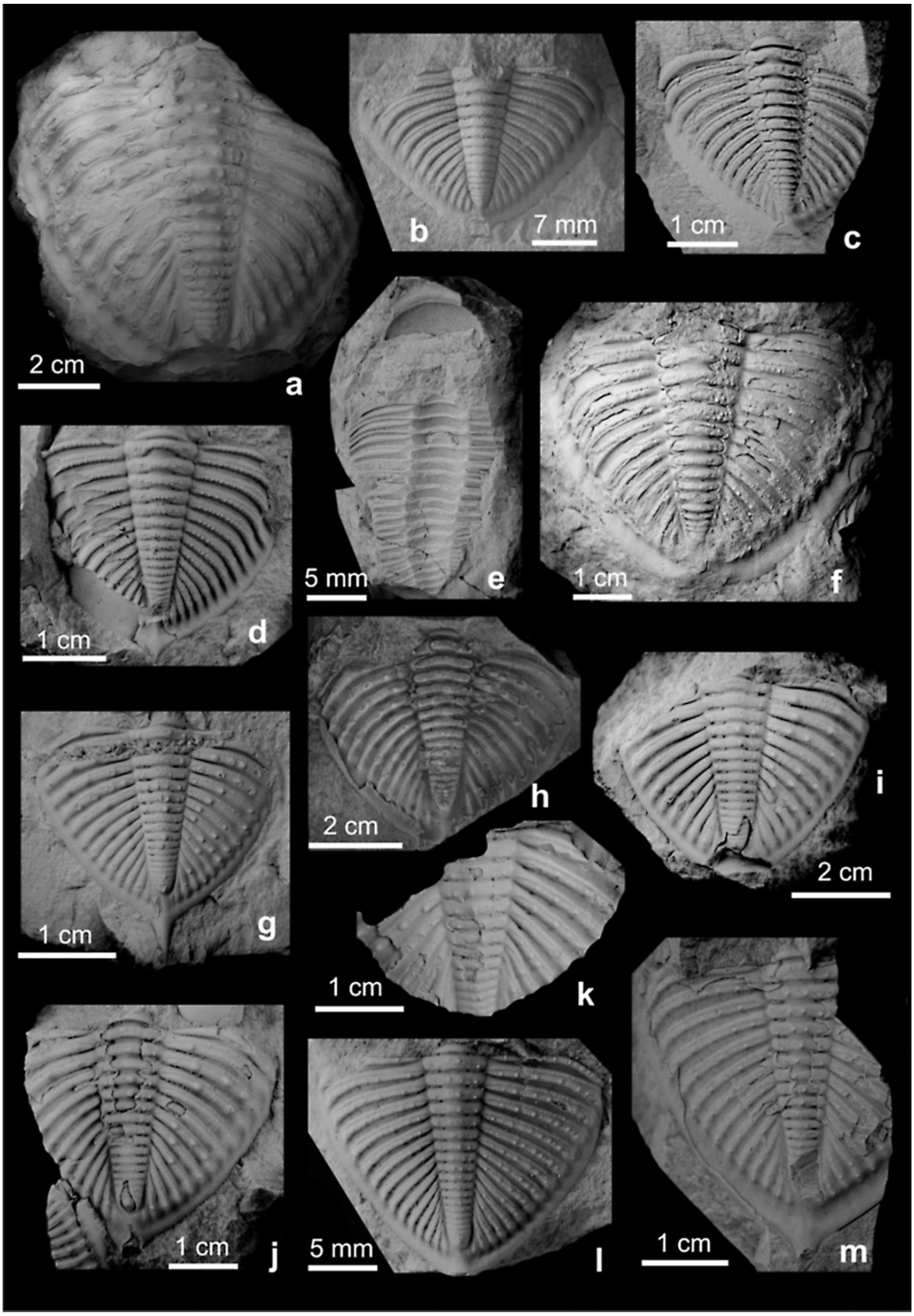

Figure 12 (a–c), (e) *Zlichovaspis* (*Z.*) *spinifera spinifera* (Barrande, 1852). Pragian Stage, Praha Formation, Dvorce–Prokop Limestone facies: (a) Holotype, incomplete large pygidium, internal mould with relics of exoskeleton, NML 15041, Praha–Hlubočepy, dorsal view. (b) Early holaspid pygidium, CGS PB 176, Praha–Konvářka, dorsal view. (c) Early holaspid pygidium, NML 30237, Kosoř–Černá rokle. (e) Incomplete early holaspid specimen, negative counterpart in decalcified limestone, CGS PB 175, Praha–Konvářka, dorsal view. (d) *Odontochile hausmanni* (Brongniart, 1822), incomplete early holaspid pygidium, NML 15024, Praha–Podolí, dorsal view. (f) *Zlichovaspis* (*Z.*) *spinifera nomiona* (Šnajdr, 1987a). Pragian Stage, Praha Formation, Loděnice Limestone facies. Holotype pygidium CGS MŠ 11675, Branžovy near Loděnice, dorsal view. (g–j) *Zlichovaspis* (*Z.*) *tamaraka* (Šnajdr, 1985). Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (g) holotype, pygidium CGS MŠ 13179, Hostim, dorsal view; (h) Incomplete pygidium, MCZ 172834; (i) Incomplete pygidium, NML 29884, Hostim, dorsal view; (j) Incomplete pygidium, NML 29883, Hostim, dorsal view, Hostim, dorsal view. (k) *Zlichovaspis* (*Z.*) cf. *tuberculata* (Hawle & Corda, 1847) fragment of pygidium, internal mould, NML 37412, pebble in Cenozoic sandstones, Karlštejn–Liteň brickyard. (l–m) *Zlichovaspis* (*Z.*) *tuberculata* (Hawle & Corda, 1847). Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (l) Holotype, incomplete pygidium, internal mould with exoskeleton, NML 19800, Praha–Hlubočepy, dorsal view; (m) Incomplete pygidium, internal mould with relics of exoskeleton, CGS PB 177, Karlštejn.

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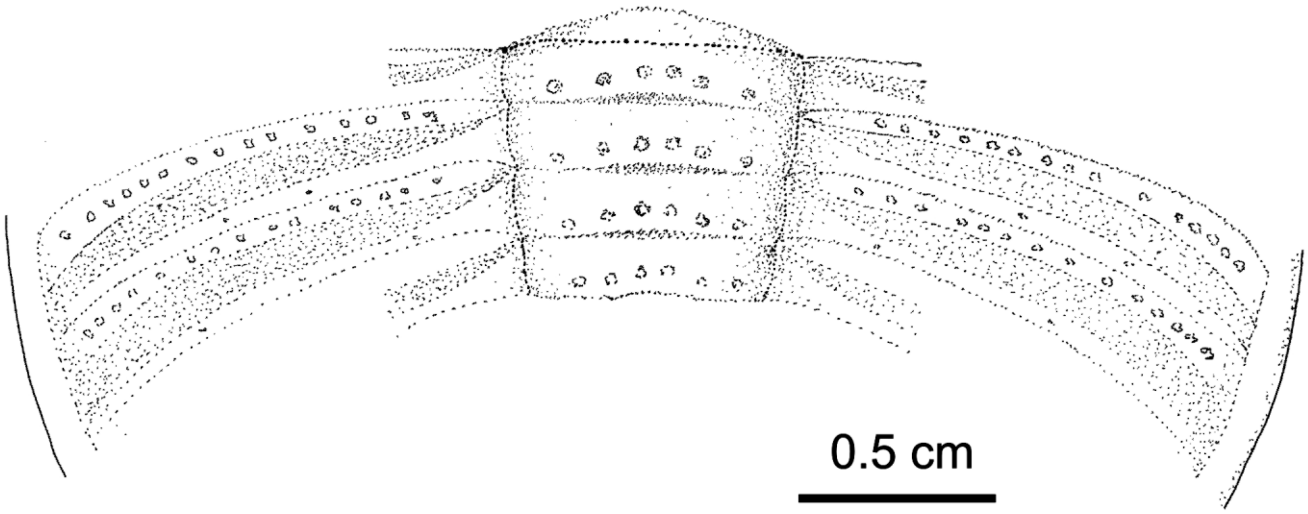

Figure 13 *Zlichovaspis* (*Z.*) *vaneki* sp. n, a reconstruction of the first two pleural bands.

Zlichovaspis (*Z.*) *tuberculata* (Hawle & Corda, 1847)
Figs 12l–m; 14a–e

1847 *Odontochile tuberculata* nobis; Hawle & Corda, p. 211.
For older synonymy, see Šnajdr (1987a).
1987a *Spinodontochile tuberculata* (Hawle & Corda); Šnajdr, pp. 43–44, pl. 7, figs 1–6, text-fig. 4–7.
1989 *Odontochile* (*Spinodontochile*) *tuberculata* (Hawle & Corda); Pek & Vaněk, p. 14.
1998 *Odontochile* (*Spinodontochile*) *tuberculata* (Hawle & Corda); Chlupáč in Chlupáč *et al*., pl 52, fig. 12.
2000 *Odontochile* (*Spinodontochile*) *tuberculatum* (Hawle & Corda); Hörbinger, p. 11.
2002 *Zlichovaspis tuberculata* (Hawle & Corda); Vaněk & Valíček, p. 12.

Lectotype. Designated by Chlupáč (*in* Horný & Bastl 1970, p. 314; pygidium (mucro broken off) with exoskeleton), NML 19800, preserved in grey biosparitic limestone. Figured by Šnajdr (1984, pl. 16, fig. 1), Šnajdr (1987a, pl. 7, fig. 3); Fig. 12l.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation. Exact horizon unknown. Praha, exact locality unknown, as that originally stated is unreliable (see also Šnajdr 1984, 1987a).

Other material. About 30 incomplete pygidia and six cephala preserved as internal moulds with relics of exoskeleton, rarely with partly exfoliated exoskeleton only.

Diagnosis. A species resembling *Zlichovaspis* (*Z.*) *spinifera*, but with the following specific features: (1) precranial median process present from small holaspid stage; (2) prominent, spinose occipital node; (3) surface of cephalon densely, finely granulose. Thorn-like granules of varying size sparsely distributed on glabella; (4) pygidial axis slightly vaulted, roof-shaped in transverse section, with 19–20 rings plus terminal piece; (5) three to five large granules situated asymmetrically on each ring forming irregular rows (exsag.) on axis; (6) 14 to 15 deep pleural furrows, widening abaxially. Anterior pleural bands vaulted, with 5–6 (up to 8 in large specimens) sparsely distributed, thorn-like granules or spines. Interspaces finely granulose. Density of granulation increases abaxially; (7) posterior pleural bands narrow, lower than anterior bands, bearing one row of tiny granules; (8) pygidial border narrow (exsag.); (9) pygidia of larger specimens (50 mm and more in length) bear spines strongly increasing in size, resembling *Zlichovaspis* (*Z.*) *spinifera* (Barrande, 1846).

Description. See Šnajdr (1987a).

Remarks. The concept of *Zlichovaspis* (*Z.*) *tuberculata* published by Šnajdr (1987a) is supported by the present study. The species is distinguished from *Zlichovaspis* (*Z.*) *spinifera* (Barrande, 1846) by the features mentioned in the diagnosis. In addition, larger pygidia have finely granulose interspaces between the large granules and spines on the anterior pleural bands, whereas in *Zlichovaspis* (*Z.*) *spinifera* spinose granules or tiny spines surround the larger spines but fine granulation is absent.

Measurements. Length of lectotype 17 mm (mucro broken off). Pygidia of largest specimens exceed 120 mm, suggesting length of complete specimens more than 300 mm.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, upper part of the sequence: Praha–Hlubočepy, Řeporyje (Zabitá rokle), Hostim, Boubová, Čeřinka near Bubovice, Karlštejn.

Zlichovaspis (*Zlichovaspis*) *vaneki* sp. n.
Figs 13; 14f–r

Derivation of name. In honour of Dr J. Vaněk (1939–2005), the eminent Czech trilobite specialist, who kindly offered the type material for the present study.

Holotype. A complete pygidium with remains of exoskeleton, CGS JV 3516 (Fig. 14f), preserved in decalcified fine-grained biodetritic limestone.

Type horizon and locality. Uppermost lower Emsian, upper Zlíchov Formation; uppermost layers of the Zlíchov Limestone facies below the Chýnice Limestone, *Nowakia elegans* dacryoconarid Biozone. Čeřinka quarry near Bubovice.

Other material. Five incomplete cephala, one fragment of thoracic segment and 23 pygidia, all preserved with partly exfoliated exoskeleton in decalcified fine-grained biosparitic to biomicritic limestone.

Diagnosis. A species of *Zlichovaspis* (*Z.*) with the following specific features: (1) obliquely subtriangular pygidium with broad border behind axial terminus, border furrow shallow; (2) mucro with broad base, but posteriorly narrow and long (ca. 30% total pygidial length); (3) axis with 19–20 axial rings plus terminal piece; (4) 13–14 very wide (more than 1·5 times

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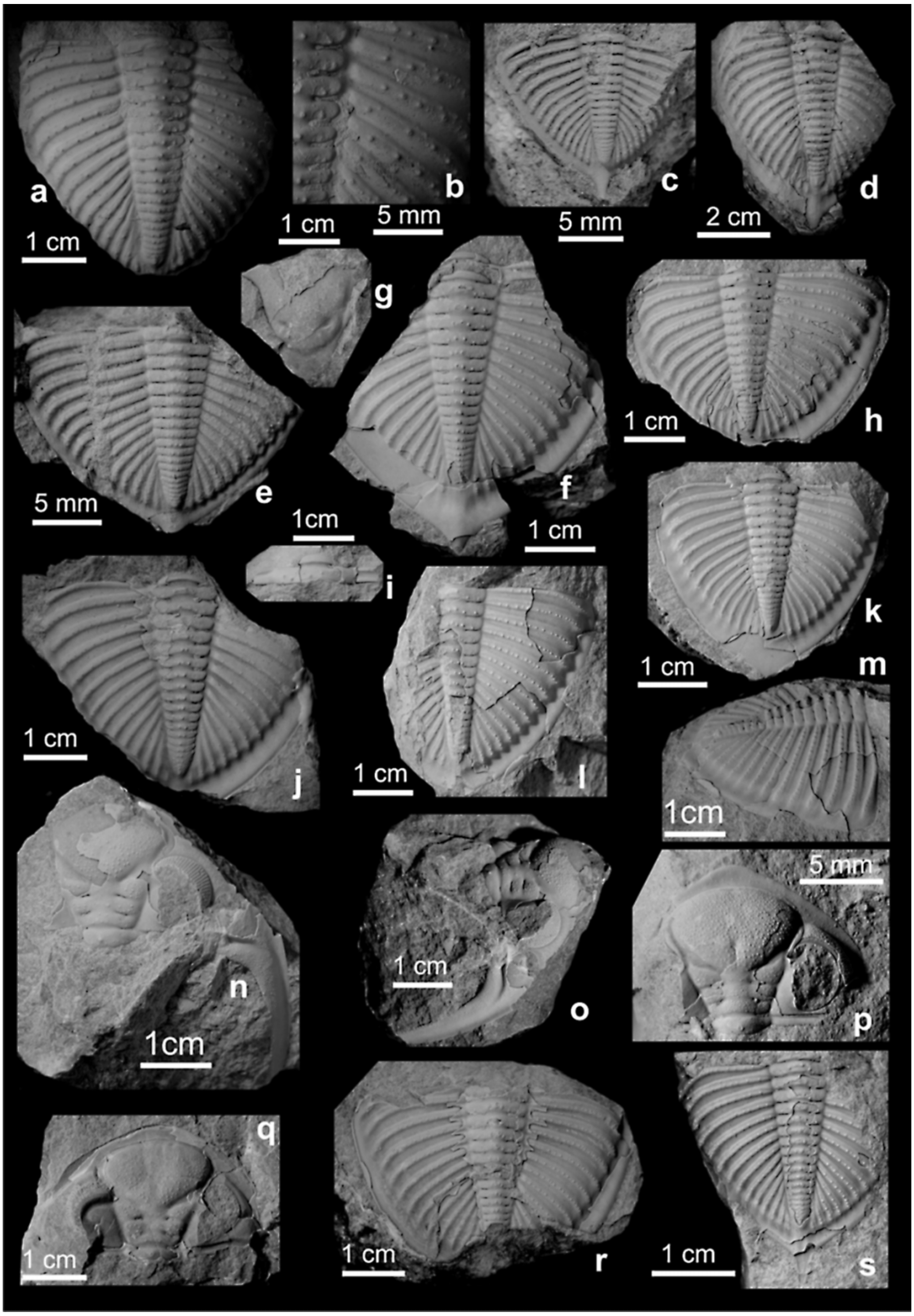

Figure 14 (a–e) *Zlichovaspis* (*Z.*) *tuberculata* (Hawle & Corda, 1847). Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (a–b) Incomplete pygidium, internal mould with relics of exoskeleton, NML 17680, Hostim: (a) dorsal view; (b) detail of right pleural field, dorsal view; (c) Incomplete early holaspid pygidium, internal mould with exoskeleton, CGS PB 180, Hostim, dorsal view; (d) Incomplete pygidium, internal mould with relics of exoskeleton, CGS PB 178, Karlštejn, dorsal view; (e) Incomplete early holaspid pygidium, internal mould with exoskeleton, CGS PB 179, Hostim, dorsal view. (f–r) *Zlichovaspis* (*Z.*) *vaneki* sp. n. Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies, uppermost part. Čeřinka quarry near Bubovice: (f) Holotype, incomplete pygidium with partly exfoliated exoskeleton, CGS JV 3516, dorsal view; (g) Paratype, incomplete hypostome, internal mould, CGS JV 3528, dorsal view; (h) Paratype, incomplete pygidium with partly exfoliated exoskeleton, CGS JV 3517, dorsal view; (i) Incomplete thoracic segment, CGS JV 3523, dorsal view; (j) Paratype, incomplete pygidium with partly exfoliated exoskeleton, CGS JV 3518, dorsal view; (k) Paratype, incomplete pygidium with partly exfoliated exoskeleton, CGS JV 3519, dorsal view; (l–m) Paratype, incomplete pygidium with partly exfoliated exoskeleton, CGS JV 3520: (l) Dorsal view; (m) lateral view; (n–o) Paratype, incomplete cephalon with partly exfoliated exoskeleton, CGS JV 3522: (n) Dorsal view; (o) lateral view; (p) Paratype, incomplete young holaspid cephalon with partly exfoliated exoskeleton, CGS JV 3527, dorsal view; (q) Paratype, incomplete holaspid cephalon, internal mould, CGS JV 3529, dorsal view; (r) Paratype, incomplete pygidium, internal mould with remains of exoskeleton, CGS JV 3526, dorsal view. (s) *Zlichovaspis* (*Z.*) cf. *tuberculata* (Hawle & Corda, 1847). Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies, uppermost part. Čeřinka quarry near Bubovice. Incomplete pygidium, CGS JV 3521, dorsal view.

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width of pleural bands), flat-bottomed pleural furrows; (5) exoskeleton almost smooth but large, sparsely distributed granules present on abaxial part of glabella, occipital ring and axis. Pygidial axial rings with 5–9 large, thorn-like granules. Vaulted anterior pleural bands with 10–14 (rarely 15–17) larger granules forming an irregular row along band margin. Dense coarse granules cover adaxial part of genal spines, abaxial portions of pleural bands (arranged in row on posterior pleural bands) and pygidial border only.

Remarks. The generic assignment of the new species is somewhat problematic. The widely subtriangular outline of the pygidium, the wide pleural furrows, and the broadly-based mucro are features shared with *Odontochile*. However, the parabolic outline of the anterior cephalic margin, the presence of a short precranial median process, and the long mucro instead support assignment to *Zlichovaspis*, and this is consistent with the stratigraphic occurrence of the species. *Z.* (*Z.*) *vaneki* is characterised especially by its wide pleural furrows, broad pygidial outline and sparsely distributed, large thorn-like granules without intervening fine granulation. The new species resembles both *Z.* (*Z.*) *tuberculata* (Hawle & Corda, 1847) and *Z.* (*Z.*) *auriculata* (Dalman, 1827). *Z.* (*Z.*) *tuberculata* differs in having a more prominent precranial median process, sparser granulation on the glabella, narrower pygidial pleural furrows, a shorter (sag.) postaxial region of the pygidium, and more robust but sparser thorn-like granules or spines on the pygidial axis and especially on the anterior pleural bands. In *Z.* (*Z.*) *tuberculata* the anterior pleural bands bear 6–8 large granules or spines whereas in *Z.* (*Z.*) *vaneki* sp. n. there are 10–15 (rarely 17) granules of smaller diameter. *Z.* (*Z.*) *auriculata* differs from *Z.* (*Z.*) *vaneki* in the absence of a precranial median process, the narrower pygidial outline and pygidial border, the narrower and deeper pleural furrows, and the finer, denser granulation on the axial rings. In *Z.* (*Z.*) *vaneki* and *Z.* (*Z.*) *auriculata*, the larger granules on the anterior pleural bands of the pygidium are similar in size, but the number of these granules in *auriculata* is similar to that in *Z.* (*Z.*) *tuberculata*. *Z. karlena* Šnajdr, 1987a differs from *Z.* (*Z.*) *vaneki* especially in having narrower pleural furrows and distinctly larger, regularly arranged and denser hollow spines on the anterior pleural bands. The posterior pleural bands bear a row of tiny granules in *Z. karlena* but in *Z.* (*Z.*) *vaneki* sp. n. they are almost smooth. *O. delicia* Šnajdr, 1987a differs from *Z.* (*Z.*) *vaneki* in having narrower pleural furrows, a narrower pygidial border, smaller thorn-like granules on the axis and pleural bands, and in having a dense sculpture of fine granules covering the entire external surface including the pleural furrows.

Ontogeny. One fragment of a very young holaspid or late meraspid pygidium, ca. 3mm long, with marginal spiny prolongations of the pygidial ribs, has been observed. Several young holaspid pygidia show general resemblance to young pygidia of *Z.* (*Z.*) *tuberculata*.

Measurements. The holotype pygidium is 39 mm long, and most other pygidia and cephala are 10–40 mm in sagittal length.

Occurrence. The type locality and horizon, where it is quite common. Three other pygidia from Choteč were found in old collections (CGS, MCZ).

Subgenus *Zlichovaspis* (*Devonodontochile*) Šnajdr, 1985

Type species. *Dalmania MacCoyi* Barrande, 1852. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, Prague Basin.

Occurrence. Lower Devonian, lower Emsian (Zlichovian regional stage), Prague Basin.

Diagnosis. A subgenus of *Zlichovaspis* with the following characteristic features: (1) prominent, lingulate, slightly anteriorly upturned precranial median process; (2) axis vaulted, with 17–19 (rarely 20) rings plus terminal piece; (3) mucro with robust base but otherwise slender, vaulted and long; (4) 13–14 deep, narrow pleural furrows; (5) pleural ribs strongly elevated, distal ends distinctly vaulted, knob-like; (6) megapores up to 0·35 mm cover all elevated parts of exoskeleton.

Remarks. Šnajdr (1985, 1987a) did not compare his genus *Devonodontochile* with *Zlichovaspis*, but in fact it resembles the latter in many features noted above, as does *Spinodontochile* (see remarks on *Z.* (*Zlichovaspis*)). The most important distinguishing feature of *Devonodontochile* is the presence of distinct megapores on all elevated parts of the exoskeleton. However, in the present authors' opinion this is not a sufficient basis for retaining *Devonodontochile* as an independent genus. Nevertheless, this feature represents a unique apomorphy within dalmanitids, although similar perforations are present in some Laurentian asteropygines (e.g. *Bellacartwrightia*, *Greenops* and some others; see Whiteley *et al*. 2002). Because of the presence of megapores and other characteristic features of the exoskeletal architecture discussed in the diagnosis, it is preferable to regard *Devonodontochile* as a subgenus of *Zlichovaspis*. In any case, both taxa are probably closely related and *Devonodontochile* should be considered as an advanced dalmanitid.

Species assigned. *Zlichovaspis* (*Devonodontochile*) *maccoyi* (Barrande); *Z.* (*D.*) aff. *maccoyi* (Barrande); *Z.* (*D.*) *armenia* (Šnajdr); *Z.* (*D.*) *vigerle* (Šnajdr).

Zlichovaspis (*Devonodontochile*) *maccoyi* (Barrande, 1852)
Figs 15a–k, o; 16a–c, f–g

1852 *Dalmania MacCoyi* Barrande; Barrande, p. 548; pl. 23, figs. 18, 19.
For older synonymy, see Šnajdr (1987a).
1987a *Devonodontochile maccoyi maccoyi* (Barrande); Šnajdr, pp. 49–50, pl. 14, fig. 1–6 and pl. 16. fig. 1.
1989 *Odontochile* (*Devonodontochile*) *maccoyi maccoyi* (Barrande); Pek & Vaněk, p. 14.
2000 *Odontochile* (*Devonodontochile*) *maccoyi maccoyi* (Barrande); Hörbinger, p. 11.
2002 *Zlichovaspis maccoyi maccoyi* (Barrande); Vaněk & Valíček, p. 11.
2002a *Devonodontochile maccoyi maccoyi* (Barrande); Chlupáč, pp. 33–34.
2002b *Devonodontochile maccoyi maccoyi* (Barrande); Chlupáč, p. 32.
2002a *Zlichovaspis maccoyi maccoyi* (Barrande); Vaněk, p. 3.
2002b *Zlichovaspis maccoyi* (Barrande); Vaněk, p. 3.

Lectotype. Designated by Chlupáč (*in* Horný & Bastl 1970, p. 196; an incomplete large pygidium (internal mould with relics of exoskeleton), NML 15002, preserved in biosparitic limestone. Figured by Barrande (1852, pl. 23, figs 18–19), Šnajdr (1987a, pl. 14, fig. 1).

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies. Exact horizon unknown. Lužce (exact locality unknown).

Other material. Paralectotypes NML 15003 (Fig. 15b), 150028, 15033 (Fig. 15o), 16927, 16928, 16929, 16930, 16931, 16932, 16933. Fifteen incomplete cephala and about 150 selected pygidia, larger number of broken exoskeletal parts (genal spines, pleurae). Mostly internal moulds with relics of the exoskeleton, preserved in grey biosparitic to biomicritic limestone.

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Diagnosis. A species of *Zlichovaspis* (*Devonodontochile*) with the following specific features: (1) eyes with 42–45 dorsoventral files of up to 11 lenses; (2) glabella, genal field, posterior border and occipital lobe covered with randomly distributed megapores and sparse, low, thorn-like granules of unequal size; (3) pygidium elongate (sag.), length/width index approx. 0·75–0·8; (4) axis roof-like in transverse section anteriorly, strongly elevated posteriorly, with 17(16)–19(20) rings plus terminal piece; (5) (12)13–14 narrow (narrower than posterior pleural bands), flat-bottomed pleural furrows; (6) anterior pleural bands strongly vaulted, sloping steeply into pleural furrows. Posterior bands wide, moderately vaulted; (7) rings and pleural bands bear densely crowded megapores. Large perforated granules of unequal size present on distal part of anterior bands.

Description. See Šnajdr (1987a).

Ontogeny. The smallest pygidium described by Šnajdr (1987a) is 10 mm long. It has 19 axial rings, 13 pleural furrows, deeply impressed, line-like interpleural furrows, and prominent granulation especially on the distal part of the anterior bands. Megapores are less than 0·1 mm in diameter and indistinct. Many small pygidia (8–15 mm in length) from the vicinity of Hostim were collected by one of the present authors (RM) and are also present, though rare, in museum collections (NM, MCZ). These pygidia resemble *Zlichovaspis* (*Devonodontochile*) *maccoyi* in most features, but differ in the absence of perceptible megapores. The specimens cannot be assigned to any other dalmanitid species, and so they are regarded as belonging to early holaspides of *Zlichovaspis* (*Devonodontochile*) *maccoyi*. The absence of megapores may be secondary, caused by recrystallisation of the rock.

Measurements. Length of lectotype 44 mm (mucro incomplete). Length of largest pygidium 61 mm (mucro broken off).

Occurrence. Zlíchov Formation, middle to upper (but not uppermost) part: Lužce, Hostim, Karlštejn, Tachlovice–Chýnice, Stydlé vody, Praha–Holyně. Chlupáč (1957) reported the occurrence of *Z.* (*Devonodontochile*) *maccoyi* in the intermediate layers between the Zlíchov and Chýnice Limestone facies at Praha–Klukovice. This report is supported by the discovery of the species by L. Ferová at a similar stratigraphical horizon in Čeřinka quarry near Bubovice. *Z.* (*D.*) *maccoyi* occurs together with *Z.* (*Z.*) *vaneki* sp. n. in the uppermost part of the Zlíchov Limestone at the same locality.

Zlichovaspis (*Devonodontochile*) aff. *maccoyi* (Barrande, 1852)
Fig. 15l–m

Material. An incomplete corroded pygidium (internal mould with relics of exoskeleton), CGS PB 215, preserved in white-grey, coarse biosparitic limestone.

Horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies. Srbsko.

Remarks. This pygidium is similar to that of *Zlichovaspis* (*Devonodontochile*) *maccoyi* but differs in these features: (1) pygidium more elongated, length/width index greater than 0·8; (2) there are 17–18 axial rings but only 12 pleural furrows; (3) pleural furrows very narrow adaxially but distinctly wider abaxially, very deep; (4) interpleural furrows distinct; (5) sparse, poorly defined megagranules of diameter greater than or equal to width of posterior pleural bands, irregularly arranged on posterior pleural bands and also on anterior pygidial margin. First anterior pleural band with four megagranules, second to fourth (?) bands with three megagranules. Posterior pleural bands with 8–10 distinct coarse granules that increase slightly in diameter adaxially. Distal part of pleural bands covered with dense fine granulation and sporadic larger granules; (6) prominent large megapores sporadically dispersed on axis and pleural bands. The specimen does not closely resemble any other known representative of *Zlichovaspis* (*Devonodontochile*) and may belong to a new species.

Measurements. Length of incomplete pygidium (mucro broken off) approximately 32 mm.

Occurrence. Zlíchov Formation, middle to upper (not the uppermost) part: Srbsko.

Zlichovaspis (*Devonodontochile*) *armenia* Šnajdr, 1987a
Fig. 15n, p–r

1987a *Devonodontochile maccoyi armenia* subsp. nov.; Šnajdr, p. 51, pl. 16, fig. 4, pl. 17. figs 4–6.
1989 *Odontochile* (*Devonodontochile*) *maccoyi armenia* (Šnajdr); Pek & Vaněk, p. 14.
2000 *Odontochile* (*Devonodontochile*) *maccoyi armenia* (Šnajdr); Hörbinger, pp. 10–11.
2002 *Zlichovaspis maccoyi armenia* (Šnajdr); Vaněk & Valíček, p. 11.

Holotype. An incomplete large pygidium (internal mould with relics of exoskeleton), CGS MŠ 13167, preserved in biosparitic limestone. Figured by Šnajdr (1987a, pl. 17, figs 5–6); Fig. 15n.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies. Srbsko (Petzold quarry).

Other material. One incomplete pygidium with exoskeleton, paratype, figured by Šnajdr (1987a, pl. 16, fig. 4); Fig. 15p. Four other pygidia, internal moulds with relics of the exoskeleton, preserved in grey biosparitic to biomicritic limestone.

Diagnosis. A species reminiscent of *Zlichovaspis* (*Devonodontochile*) *maccoyi* with the following specific features: (1) pygidial outline more elongated sagittally, length/width index greater than 0·8; (2) megapores very sparsely distributed on axial rings and pleural bands; (3) sparse, thorn-like granules on axial rings; (4) numerous perforated thorn-like granules of irregular size on anterior pleural bands (rare adaxially); sparse granules on posterior bands.

Remarks. This species is poorly known, being based on limited material. Although several new specimens can be assigned to it, its systematic value is still doubtful. The features regarded by Šnajdr (1987a) as distinctive are relatively consistent but very minor, and consequently Šnajdr considered *armenia* to be only a subspecies of *Z.* (*Devonodontochile*) *maccoyi*. However, as *armenia* occurs at Hostim–Boubová together with *maccoyi*, the present authors prefer to regard them as separate species. In the vicinity of Prague, *Z.* (*D.*) *armenia* is known from a slightly lower stratigraphical level than the type species (Hörbinger 2000).

Ontogeny. Some of the small holaspid pygidia referred to in the discussion of *Zlichovaspis* (*Devonodontochile*) *maccoyi* differ from the others in their greater elongation. In this respect they resemble *Z.* (*D.*) *armenia* and they may in fact belong to the latter species.

Measurements. Length of holotype approximately 39 mm, length of other specimens 20–40 mm.

Occurrence. Zlíchov Formation, middle to upper (but not uppermost) part: Srbsko, Tachlovice–Chýnice, Hostim–Boubová.

Zlichovaspis (*Devonodontochile*) *vigerle* (Šnajdr, 1987a)
Fig. 16d–e, h–j

1987a *Devonodontochile maccoyi vigerle* subsp. nov.; Šnajdr, p. 50, pl. 16, fig. 1, pl. 17. figs 1–3.

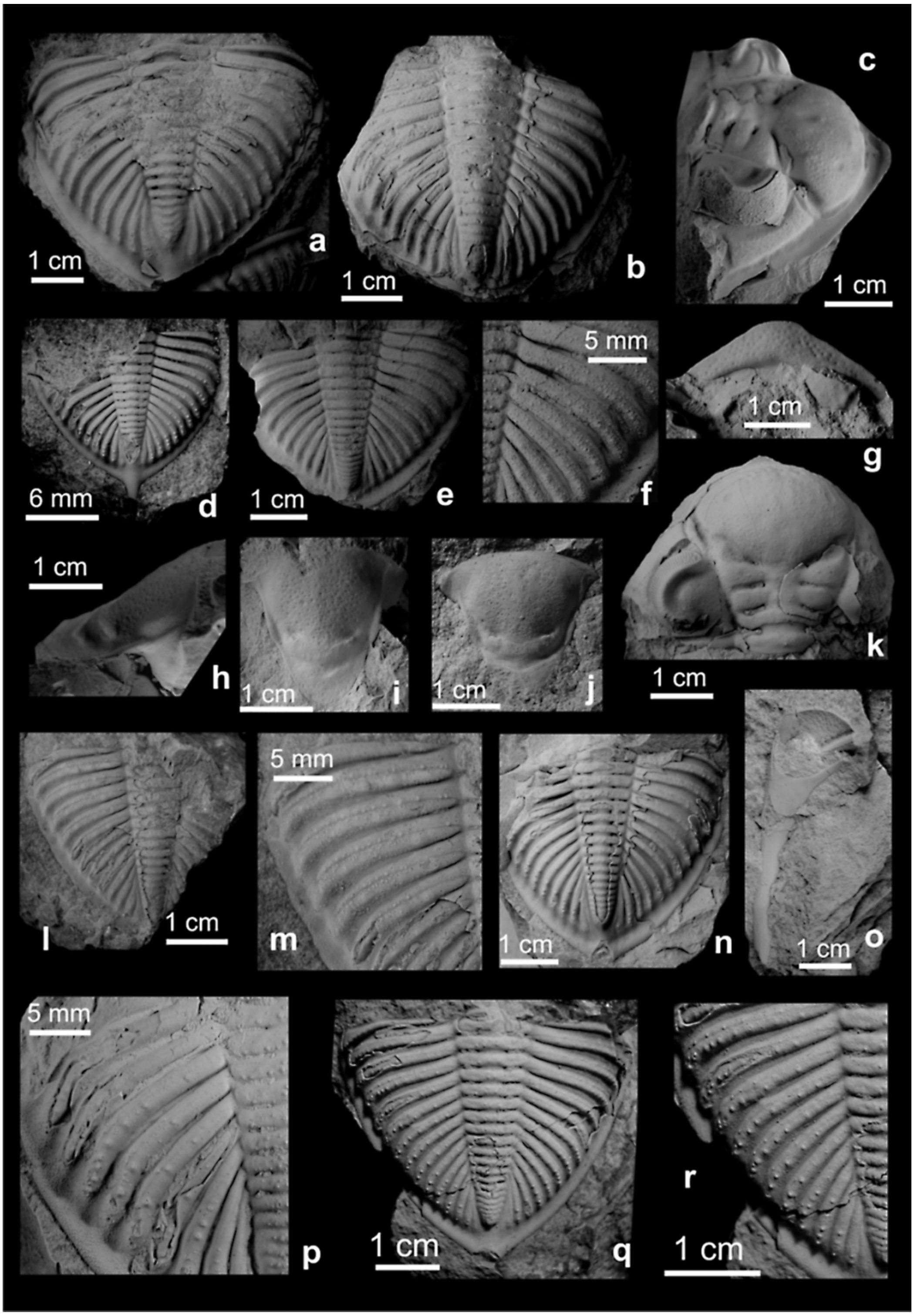

Figure 15 (a–k, (o) *Zlichovaspis* (*Devonodontochile*) *maccoyi* (Barrande, 1852) Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (a) Incomplete large pygidium, internal mould with relics of exoskeleton, CGS PB 182, Hostim, Boubová; (b) Paralectotype, incomplete large pygidium, internal mould with relics of exoskeleton, NML 15003, Lužce; (c), (g) Incomplete cephalon, internal mould with relics of exoskeleton, NML 16929, Lužce: (c) Dorsolateral view; (g) ventral view on the doublure; (d) Incomplete early holaspid pygidium, CGS PB 183, Hostim, Boubová, dorsal view. (e–f) Incomplete large pygidium, internal mould with exoskeleton, NML 22573, Tachlovice: (e) dorsal view; (f) detail of right pleural field; (h–i) Incomplete hypostome, internal mould, NML 16932, Lužce: (h) lateral view showing robust anterior wing; (i) dorsal view; (j) Incomplete hypostome, internal mould, CGS PB 184, dorsal view; (k) Incomplete large cephalon, NML 16927, Lužce, dorsal view; (o) Fragment of genal spine with part of free cheek, NML 15033, Lužce, ventral view. (l–m) *Zlichovaspis* (*Devonodontochile*) aff. *maccoyi* (Barrande, 1852) Zlichovian (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies, Hostim. Incomplete pygidium with remains of exoskeleton, CGS PB 215: (l) dorsal view; (m) detail of left pleural field. (n), (p–r) *Zlichovaspis* (*Devonodontochile*) *armenia* (Šnajdr, 1987a). Zlichovian regional stage (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies: (n) Holotype, incomplete pygidium, internal mould with remains of exoskeleton CGS MŠ 13167, dorsal view; (p) Paratype, incomplete pygidium with exoskeleton, NML 22575, Tachlovice, detail of left pleural field; (q–r) Incomplete pygidium, internal mould with exoskeleton, CGS PB 186, Hostim, Boubová: (q) dorsal view; (r) detail of left pleural field.

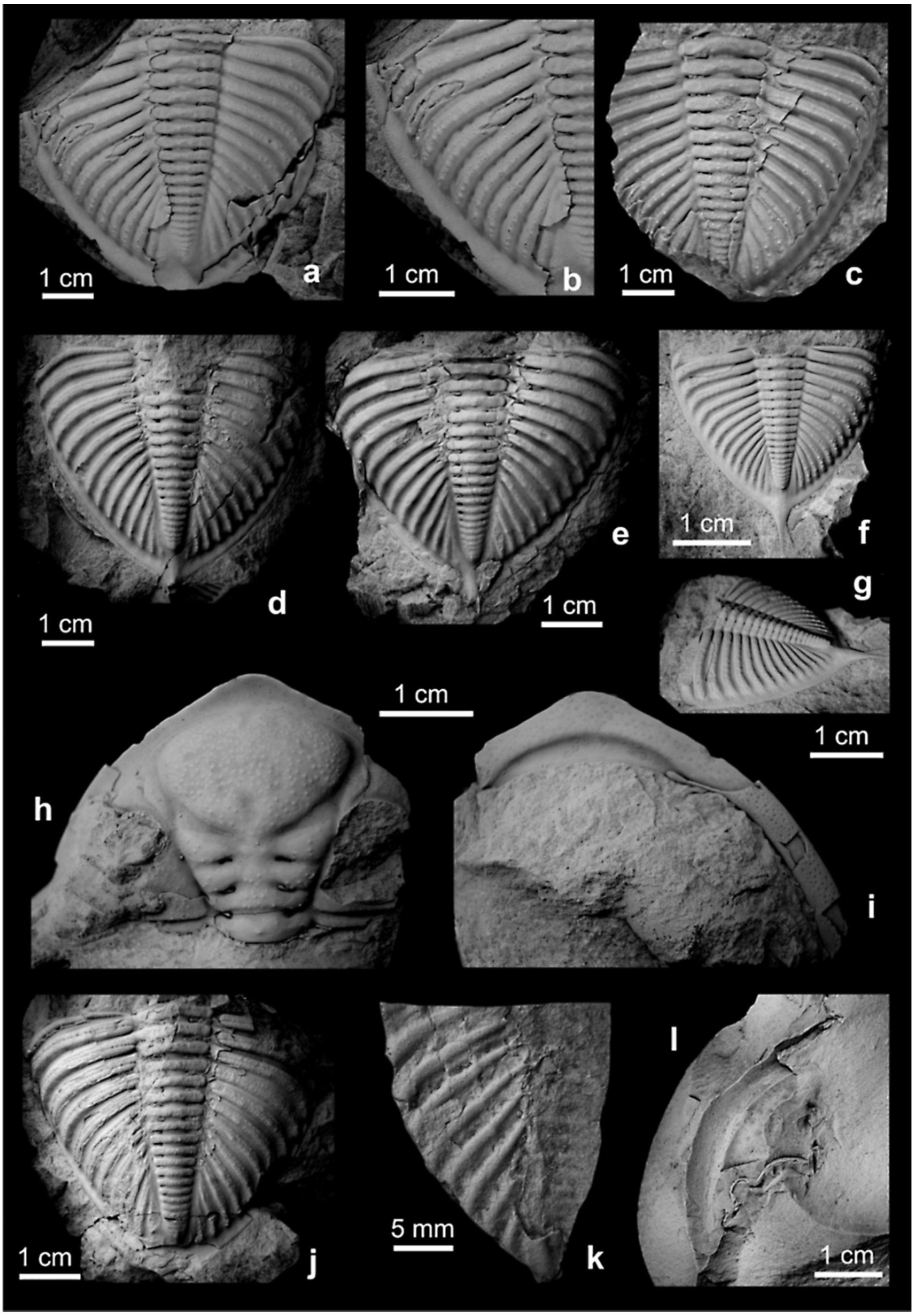

Figure 16 (a–c), *Zlichovaspis* (*Devonodontochile*) *maccoyi* (Barrande, 1852): (a–b) Incomplete pygidium CGS PB 187, internal mould with exoskeleton, Hostim, Boubová: (a) dorsal view; (b) detail of left pleural field, dorsal view; (c) Incomplete pygidium, internal mould with remains of exoskeleton, CGS PB 185, Hostim, Boubová. (d–e) *Zlichovaspis* (*Devonodontochile*) *vigerle* (Šnajdr, 1987a). Zlichovian regional stage (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies, uppermost part: (d) Holotype, damaged pygidium, internal mould with remains of exoskeleton, CGS MŠ 13172, Praha–Hlubočepy, Švagerka, dorsal view. (e) Incomplete pygidium, internal mould with remains of exoskeleton, CGS JV 3532, Švagerka. (f–g) *Zlichovaspis* (*Devonodontochile*) *maccoyi* (Barrande, 1852), Almost complete pathologic pygidum, internal mould with exoskeleton, CGS PB 188, Holyně, Dobrá Voda: (f) dorsal view; (g) lateral view. (h–j): *Zlichovaspis* (*Devonodontochile*) *vigerle* (Šnajdr, 1987a). Zlichovian regional stage (lower Emsian), Zlíchov Formation, Zlíchov Limestone facies, uppermost part: (h–i) Incomplete cephalon, internal mould preserved in decalcified limestone, CGS PB 189, Praha–Švagerka: (h) dorsal view; (i) ventral view; (j) Incomplete pygidium, internal mould with relics of exoskeleton, CGS MŠ 13170, Švagerka. (k) Dalmanitoidea gen. et sp. indet. Daleje–Třebotov Formation, Daleje Shale facies. Incomplete pygidium, CGS PB 212, Pekárkův mlýn quarry. (l) Dalmanitoidea ? gen. et sp. indet. Daleje–Třebotov Formation, Daleje Shale facies. Fragment of left (?) librigena, negative counterpart, CGS MŠ 13187, Praha–Hlubočepy (Ke hřitovu street), dorsal view.

1989 *Odontochile* (*Devonodontochile*) *maccoyi vigerle* (Šnajdr); Pek & Vaněk, p. 14.

2002 *Zlichovaspis maccoyi vigerle* (Šnajdr); Vaněk & Valíček, p. 11.

Holotype. An incomplete pygidium (internal mould with relics of exoskeleton), CGS MŠ 13172, preserved in dark-grey micritic limestone. Figured by Šnajdr (1987a, pl. 17, fig. 1); Fig. 16d.

Type horizon and locality. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, uppermost layers. Praha–Zlíchov (Švagerka).

Other material. About 35 isolated pygidia, three cephala, several thoracic fragments and three isolated hypostomes. Almost all specimens are preserved as internal moulds with remains of exoskeleton. Only a few specimens from the decalcified limestones have well-preserved sculpture.

Diagnosis. A species reminiscent of the *Zlichovaspis* (*Devonodontochile*) *maccoyi*, with the following specific features: (1) Lf coarsely, strongly granulated; (2) pygidial border very narrow, especially anteriorly, where distal ends of pleural ribs extend very close to margin; (3) numerous thorn-like granules of irregular size especially on median part of axial rings; (4) dense smaller perforated granules cover entire surface of distal portions of anterior pleural bands, also abundant adaxially. Posterior pleural bands also with abundant granules; (5) megapores surrounded by distinct swelling.

Remarks. *Z.* (*D.*) *vigerle* was originally described by Šnajdr (1987a) as a subspecies of *Z.* (*D.*) *maccoyi* (Barrande, 1852). Numerous specimens recently collected support the validity of this taxon at the species level. The most important differences between *Z.* (*D.*) *vigerle* and the type species include the distinctly narrow border, different sculpture and shape of the megapores with a peripheral swelling. *Z.* (*D.*) *vigerle* also comes from a slightly higher stratigraphical level, in the uppermost part of the Zlíchov Limestone facies deposited in relatively deeper water. However, *Z.* (*D.*) *maccoyi* has also been found by the present authors and Bc. L. Ferrová in the uppermost Zlíchov Limestone and lower part of the Chýnice Limestone facies at Čeřinka quarry near Bubovice.

Measurements. Length of holotype approximately 48 mm; length of largest pygidium 65 mm.

Occurrence. Lower Emsian (Zlichovian regional stage), Zlíchov Formation, Zlíchov Limestone facies, uppermost part: Praha–Zlíchov (Švagerka), Karlštejn–Kněží hora (immediately below the Daleje Shale).

Dalmanitoidea gen. et sp. indet.
Fig. 16k–l.

1987a Odontochilinae gen. et sp. indet.; Šnajdr, p. 53.

Material. Fragment of pygidium, a negative counterpart with the exoskeleton (inner part), CGS PB 212, collected by Š. Rak at Petzoldův lom quarry. Questionable internal mould of incomplete left (?) librigena with part of doublure, CGS MŠ 13187, discussed by Šnajdr (1987a), from Hlubočepy–U hřbitova street locality.

Remarks. The fragment of the pygidium has 14–15 axial rings and 9–10 relatively narrow pleural furrows. No megapores or sculpture are visible. Although the specimen is fragmentary and deformed, it is apparent that it belongs to a dalmanitid, but cannot be assigned with confidence even to a genus. The fragment of a left librigena, described but not figured by Šnajdr (1987a) as a possible odontochilinid, has a moderately wide, tuberculate genal field somewhat reminiscent of some dalmanitoids. The specimen does not permit a more exact determination. Nevertheless, both specimens suggest the possible rare occurrence of the last dalmanitids in the Upper Emsian strata of the Prague Basin.

Measurements. The fragment of pygidium is 25 mm long (sag.); librigenal fragment about 40 mm long.

Occurrence. Upper Emsian Stage (Dalejan Regional Stage), Daleje–Třebotov Formation, Daleje Shale facies (approximately middle part): Praha–Petzoldův lom quarry; Praha–Hlubočepy, Ke Hřbitovu locality.

4. Dalmanitid associations in the Lower Devonian of the Prague Basin

Dalmanitid trilobites have been included in several faunal assemblages and biofacies by previous authors. Chlupáč (1983a) defined the *Reedops–Odontochile* Assemblage as characteristic of the deeper-water development of the Praha (Dvorce–Prokop and Řeporyje–Loděnice Limestone facies) and the Zlíchov (Zlíchov Limestone facies) formations, but also mentioned the occurrence of large dalmanitid trilobites in the *Platyscutellum–Kolihapeltis* Assemblage. Similarly, Havlíček & Vaněk (1998) defined the *Odontochile–Prokopia* Biofacies for the deeper-water development of the Praha Formation (Dvorce and Prokop Limestone facies in their concept) but also included dalmanitids in several other biofacies.

In the Prague Basin during the Early Devonian, dalmanitid trilobite faunas varied substantially in space and time. Several different dalmanitid associations, differing in the composition of genera and species composition, can be distinguished. They show a strong facies preference for relatively deeper-water, quiet environments (micritic, biomicritic or fine biosparitic limestones). However, in places they also inhabited shallower-water, high energy environments where they formed locally abundant assemblages of distinct of (sub)species composition. Dalmanitids are common here especially in the biomicritic interlayers, and/or their remains (mostly moults) were probably transported (broken or sorted). No remains of dalmanitid trilobites have been found in the Koněprusy reef area, although they do occur rarely around its periphery. Although the sections where important stratigraphic boundaries are exposed are generally well-studied in the Prague Basin, insufficient information is available on the stratigraphical occurrence of faunas outside these intervals. Most museum samples, commonly those of great systematic importance, lack any detailed stratigraphical information, only an approximate locality being mentioned. The considerable changes made by Šnajdr (1985, 1987a) in the taxonomy of many species are largely followed in the present paper. Therefore, the present authors consider some older determinations and published occurrences as unusable. An attempt has been made to supplement previously published data (Chlupáč 1957, 1983a; Přibyl & Vaněk 1971; Šnajdr 1985, 1987a; Hörbinger 2000) with new collections. Specimens from newly measured sections studied during the present revision were mostly determinable at the generic level only. More important findings were found loose. This is a serious problem, because the remains of dalmanitid trilobites are mostly large and their determination from small fragments collected during stratigraphical study is mostly unreliable. Therefore, this analysis of the dalmanitid associations should be considered as preliminary and subject to revision in the future. The data support in many aspects the previous analysis of the Praha Formation by Havlíček & Vaněk (1998) and Vaněk (1999), but with certain differences discussed below (Fig. 17). The following eight associations are distinguished:

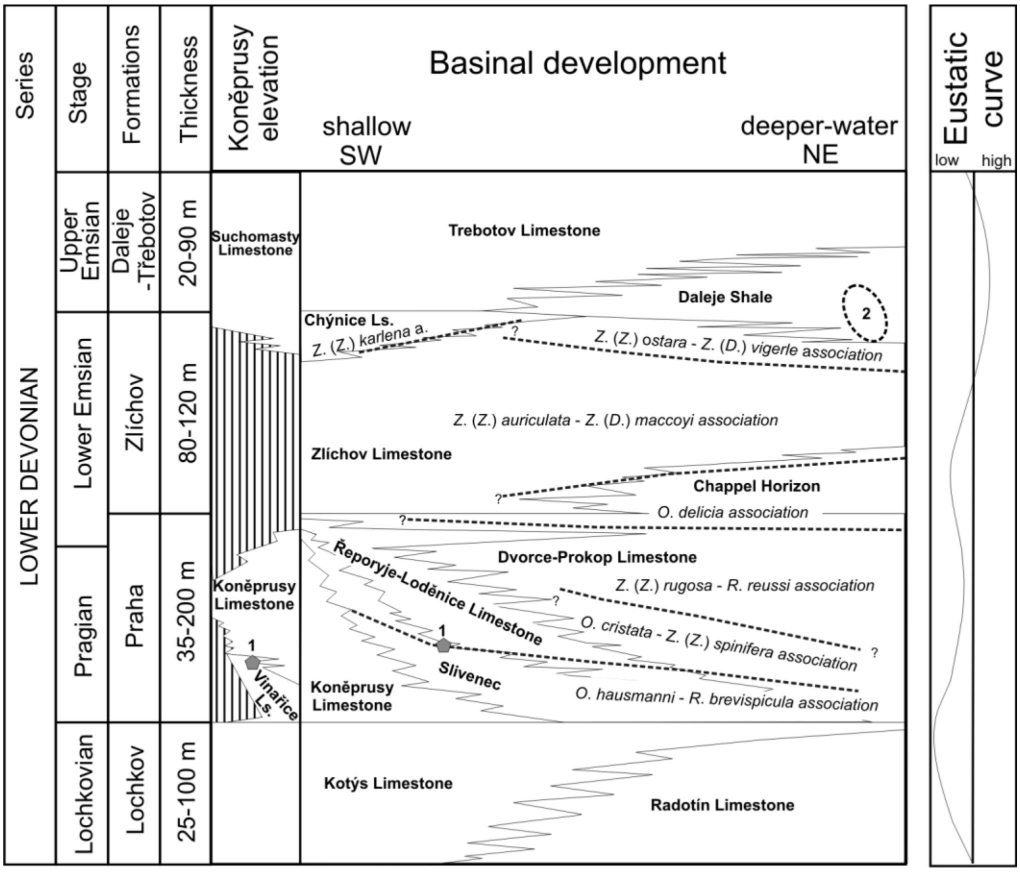

Figure 17 A review of the dalmanitid associations on the Lower Devonian of the Prague Basin. (1) *Zlichovaspis* (*Z.*) *rugosa laura–Zlichovaspis* (*Z.*) *spinifera nomiona* association. (2) Stratigraphic range of Dalmanitoidea indet. For explanation of the lithological units, see Figure 2.

(1) *Reussiana brevispicula–Odontochile hausmanni* association, confined to the lowermost part of the Dvorce–Prokop Limestone facies in areas with micritic development of the Praha Formation (e.g. Kosoř, Lochkov and Velká Chuchle). Both species are also known from the Slivenec and Řeporyje–Loděnice Limestone facies at the base of the Pragian sequence (Cikánka near Slivenec, Praha–Dívčí hrady etc.). However, the occurrence of this association is not entirely isochronous, and *O. hausmanni* in particular is known also from other outcrops at a possibly slightly higher stratigraphical position, especially in the Beroun district (Karlštejn etc.). Hörbinger (2000) reported the occurrence of *Reussiana brevispicula* in the classic Kosoř–Černá rokle section immediately above the base of the Praha Formation. One problematic specimen from Lochkov may come from the upper part of the Lochkov Formation. The first appearance of *Odontochile hausmanni* comes at a slightly higher level, 1·5–4 (or 5) m above the base of the Dvorce–Prokop Limestone Facies. The upper range of the species is not known with certainty. It has been reported by Chlupáč (1957) and Šnajdr (1987a) as occurring together with *Odontochile cristata* at many localities but the present authors did not find them together in the measured sections. However, in rock debris at most of these localities, especially in the Prague neighbourhood, both species occur together. Therefore, their possible overlap cannot be excluded. The previously published records of *O. hausmanni* from the middle to upper part of Pragian sequence refer, however, to *O. tenuigranulata* sp. n.

(2) *Odontochile cristata–Zlichovaspis spinifera spinifera* association, confined to micritic and biomicritic limestones of the lower but not the lowermost part of the Praha Formation up to its middle–upper part, locally corresponding with the Prokop Limestone facies *sensu* Vaněk (1999). The lower and upper ranges of this association are not entirely clear, and in its upper part it may be partly contemporaneous with the *Reussiana reussi–Z.* (*Z.*) *rugosa rugosa* association. In addition to the index species, *Odontochile tenuigranulata* sp. n., and possibly *O. hausmanni*, also occur in areas where mud mound structures are developed.

(3) *Zlichovaspis* (*Z.*) *rugosa laura–Zlichovaspis* (*Z.*) *spinifera nomiona* association, confined to the shallow-water development of the Pragian sequence in its lower to middle part; e.g., the Vinařice, Loděnice and Slivenec Limestone facies. This association has been found at only four localities: Plešivec–Homolák quarry (one fragment), Měňany–U hájovny quarry, Branžovy–Záloženský lom quarry and Čeřinka quarry near Bubovice (probably reflecting the occurrence of sea floor elevations; see Chlupáč and Šnajdr 1989).

(4) *Reussiana reussi–Zlichovaspis* (*Z.*) *rugosa rugosa* association, confined to the upper part (approximately two-thirds) of the Pragian sequence. The index species commonly occur at this level in biomicritic and micritic Dvorce–Prokop Limestone facies (Prokop Limestone facies sensu Vaněk 1999), especially in the SW part of the Prague Basin (Beroun district, e.g. at Damil). However, both taxa also occur sporadically in lower strata in the Prague district (a pygidium of *R. reussi* was found by J. Valíček ca. 10 m above the base of the Pragian at Lochkov–Stěnový lom quarry). *Z.* (*Z.*) *rugosa* has also been confirmed in the Řeporyje Limestone facies at Červený lom near Klukovice and Cikánka quarries, but these occurrences are in a higher part of the lower Pragian sequence.

(5) *Odontochile delicia* association, confined to the boundary beds between the Praha and Zlíchov Formations. This monospecific association occurs in the uppermost few metres of the Praha Formation, developed as grey micritic limestone with

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cherts, and in micritic to fine biosparitic limestone layers at the base of the Zlíchov Formation or in the fine-grained interlayers within the 'Chappel horizon' (intraformation breccias at the base of the Zlíchov Formation in the NE part of the Prague Basin). No specimens were found outside the Prague area, with the exception of one pygidium of doubtful stratigraphical position (CGS PB 153).

(6) *Zlichovaspis* (*Z.*) *auriculata auriculata*–*Z.* (*Devonodontochile*) *maccoyi* association occurs in a wide stratigraphic interval from the lower to the upper part of the Zlichovian sequence. The lowermost occurrences of doubtful *Z.* (*Z.*) *auriculata auriculata* come from the layers immediately above the *O. delicia* association, or even within the range of that association in the SW part of the Prague Basin, where the 'Chappel Horizon' is absent (Stydlé Vody Quarry). The range of *Z.* (*Z.*) *auriculata* is confirmed by the common occurrence of the tentaculites *Nowakia* (*Dmitriella*) *praesulcata,* corresponding to the *Nowakia zlichovensis* Biozone (S. Berkyová and P. Lukeš, pers. comm. 2006), and by the occurrence of *Viriatelina* cf. *pseudogeinitziana*, representing *Nowakia barrandei*, perhaps up to the *N. elegans* Biozone (P. Lukeš, pers. comm. 2005). One questionable occurrence comes from the Chýnice Limestone at Čeřinka quarry near Bubovice. Similarly, a second index species *Z.* (*Devonodontochile*) *maccoyi* together with *Z.* (*D.*) *armenia* is common, especially in the middle to upper part of the Zlichovian sequence. In some sections, especially in the Prague district, *Z.* (*D.*) *armenia* occurs with *Zlichovaspis* (*Z.*) *azucena* slightly lower than *Z.* (*D.*) *maccoyi* (Hörbinger 2000), but near Hostim all three species may occur together in a relatively high part of the Zlichovian sequence. In the upper part of this association, *Zlichovaspis* (*Z.*) *marieva*, *Z.* (*Z.*) *tuberculata* (very common locally, e.g. in Hostim–Boubová), *Z.* (*Z.*) *tamaraka* (rare) and *Z.* (*Z.*) *karlena* (very rare) also occur. *Zlichovaspis* (*Z.*) *vaneki* sp. n. occurs in the upper part of this association, below the onset of Chýnice Limestone facies in the Čeřinka quarry near Bubovice, where it is accompanied by *Z.* (*D.*) *maccoyi*. This species occurs here as high as the intermediate layers between the Zlíchov and Chýnice Limestone facies (observations of L. Ferová).

(7) *Zlichovaspis* (*Z.*) *ostara*–*Z.* (*Devonodontochile*) *vigerle* association, confined to the uppermost part of the Zlichovian sequence in rather deeper-water development, immediately below the onset of the Daleje Shale facies (Daleje–Třebotov Formation). It comprises locally abundant assemblages, especially in the SE and NE part of the Prague Basin. However, rare specimens of *Z.* (*Z.*) cf. *ostara* were found in rock debris together with *Z.* (*Z.*) *auriculata* and *Z.* (*D.*) *maccoyi* in the relatively shallow-water Hostim area below the onset of the Chýnice Limestone facies.

(8) *Zlichovaspis* (*Z.*) *karlena* rarely occurs in the uppermost part of the last-mentioned association. However, it forms a distinct association in the biodetritic Chýnice Limestone facies in the Čeřinka quarry. Only rare and mostly indeterminate specimens of other dalmanitids (cf. *Z.* (*D.*) *maccoyi* and *Z.* (*Z.*) *auriculata*) were found in this facies during recent collecting.

The abrupt extinction of dalmanitid trilobites in the Prague Basin was probably induced by onset of the local Daleje event, characterised by shale sedimentation in a deeper part of the basin (see Chlupáč & Kukal 1988 and Chlupáč in Chlupáč *et al.* 1998). This event probably reflected a global-scale eustatic sea level rise. In the Daleje Shale only two fragments of possible dalmanitids have been found, but these may indicate at least sporadic occurrence of this group in the Upper Emsian. In the purely carbonate facies of the Prague Basin, dalmanitids disappear at the Lower/Upper Emsian boundary (transition from the Chýnice to the Třebotov Limestone facies near Hostim).

5. Remarks on evolution and palaeogeography

The sudden appearance of dalmanitid trilobites in the Prague Basin at the base of the Pragian is noteworthy. Elsewhere these trilobites are known in the Lower Devonian from Lochkovian strata (e.g. Kazakhstan, Australia and North and South America; see Edgecombe & Ramsköld 1994; Jell 1989; Jell & Holloway 1983; Maksimova 1967, 1968, 1969, 1972, 1975, 1977, 1978; Šnajdr 1987a). However, in Perunica (see Havlíček *et al.* 1994), probably due to its relative isolation, there is no record of dalmanitacean trilobites after the Late Ordovician extinction until the base of the Pragian, with the exception of the rare occurrence in the uppermost Wenlock of *Delops* and *Struveria* (see Budil 2005) in rather deep water facies (see Thomas & Lane 1984). Many, if not most, dalmanitoidean trilobites probably had an adult-like protaspis sensu Speyer & Chatterton (1989), specialised for a benthic mode of life (in *Dalmanites*, see Whittington & Campbell 1967, pl. 15; in *Dalmanitina*, see Barrande (1852) and Šnajdr (1990); in *Mucronaspis*, see Temple 1952; Kielan 1960; Budil 1996). The anaprotaspid stage is not known in dalmanitids, the youngest specimens documented being early metaprotaspides. Budil (2005) suggested that the metaprotaspides, though preferring rather deep shelf environments, were not able to migrate across open oceans. However, a widespread fall in sea level during the extensive Lochkovian–Pragian regressive event may have opened new migration routes in regions peripheral to formerly deeper shelf environments. Together with the gradual closing of the Rheic Ocean, this could have made possible the migration of new elements into the peri-Gondwanan area, possibly from the north-east. However, dalmanitids were also present in Laurentia at this time (see Holloway 1981). It is interesting that *Reussiana* first appears in the Prague Basin (with *Odontochile*) in the lowermost Pragian (or perhaps uppermost Lochkovian), and is also questionable known from the Lochkovian and Pragian of Kazakhstan, whereas *Zlichovaspis* appears in the Prague Basin in the lower-middle Pragian but is questionably known from the Lochkovian of Australia (e.g. *Zlichovaspis* (*Z.*) ? *formosa* Gill, 1948; see Jell 1989; Jell & Holloway 1983; Šnajdr 1987a). Dalmanitids also inhabited terrains in the northern peri-Gondwana region (Morocco) and Iberia at about the same time. From the Pragian to the latest Early Emsian, these associations radiated extensively in the Prague Basin. The abrupt extinction of these faunas is probably not restricted to the Prague Basin, but also occurred in northern peri-Gondwana (Morocco) and other areas. Therefore, this extinction is probably a good marker of the Lower/Upper Emsian boundary, at least at the regional (peri-Gondwana) scale but probably also globally.

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