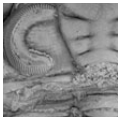# Exoskeletal architecture, hypostomal morphology and mode of life of Silurian and Lower Devonian dalmanitid trilobites

PETR BUDIL, ALAN TREVOR THOMAS & FRANTIŠEK HÖRBINGER

The overall exoskeletal architecture and hypostomal morphology of Silurian *Dalmanites* and Lower Devonian *Odontochile*, *Reussiana* and *Zlichovaspis* are compared and discussed. All four genera were benthic. However, a gradual shift from predator-scavenger to a scavenging feeding habit is inferred from the evolution of these dalmanitids in the Upper Silurian and Lower Devonian. In the more conservative, probable predator-scavenger *Dalmanites*, the posterior hypostomal doublure has a group of robust denticles: these would have been effective shredding structures, enabling milling or cutting of food into smaller particles, and allowing *Dalmanites* to deal with mechanically relatively robust prey. Lower Devonian dalmanitids from the Prague Basin possess a comparable denticulate structure on the posterior hypostomal doublure. However, although overall exoskeletal dimensions are larger, the denticles are significantly finer and denser. The whole exoskeleton of these younger dalmanitids, with a large multi-segmented pygidium, is considered well adapted for close approximation to the sediment surface. Shallow burrowing in a soft substrate, and scavenging with opportunistic predation, is therefore considered to be their main feeding habit. *Odontochile*, *Reussiana* and *Zlichovaspis* characteristically occur in micritic limestone facies, where the sediment surface is likely to have been soft. The shift from a more predatory to a dominantly scavenging mode of life may have occurred independently in several unrelated dalmanitid groups, with "odontochilid" characteristics developing at different stratigraphical levels. • Key words: Dalmanitidae, trilobite, mode of life, body morphology, hypostomes.

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Dalmanitids form an important part of the trilobite faunas found in Silurian and Lower Devonian carbonate and fine clastic sequences in Avalonia, Kazakh terranes, Australia and Laurentia. After significant late Ordovician extinctions, they occur in early Silurian strata (*e.g.*, El Chair *et al.* 1985, Curtis & Lane 1997) albeit relatively rarely, but their acme started in middle Silurian times. In the late Lochkovian and earliest Pragian, they are found widely in the northern peri-Gondwana realm (see Budil *et al.* submitted). Silurian and Devonian dalmanitids show an evolutionary tendency toward forms with large, multi-segmented and flat pygidia. This morphological shift is associated with increased cephalic convexity (see Campbell 1977), increased genal spine length, and by the changes in hypostomal morphology described below. Discussion of these changes, and assessment of their importance for changes in mode of life, is the focus of this contribution.

Figured and cited specimens are housed in the following institutions: National Museum, Prague (NM), Czech Geological Survey (CGS), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ), Natural History Museum, London (NHM) and Lapworth Museum, University of Birmingham (BU).

Systematic palaeontology

Order Phacopida Salter, 1864
Suborder Phacopina Struve *in* Richter *et al*., 1959
Superfamily Dalmanitoidea Vogdes, 1890
Family Dalmanitidae Vogdes, 1890

Genus *Dalmanites* Barrande, 1852

Type species. – *Trilobus caudatus* Brünnich, 1781, from the Coalbrookdale Formation (Wenlock) of England.
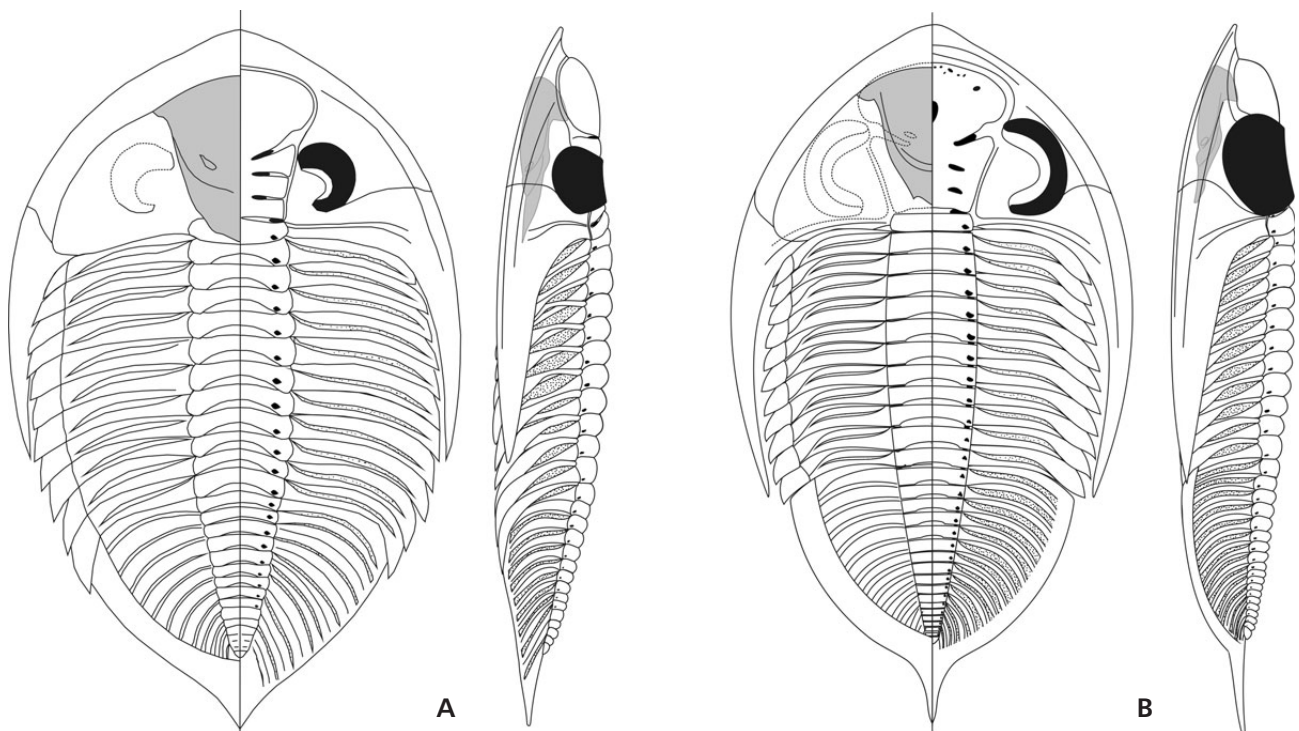
Figure 1. A – schematic drawing of the ventral, dorsal and lateral general body morphology of *Dalmanites* Barrande, 1852, based on NHM It20991, *Dalmanites myops* (König, 1825), Silurian, Wenlock, Much Wenlock Limestone, Dudley. • B – sketch of the dorsal and ventral general body morphology in *Zlichovaspis* Přibyl & Vaněk, 1972 (after Budil *et al.* in press). The inferred position of the hypostome is indicated.

Remarks. – The British Wenlock species of *Dalmanites* have not been revised in detail since they were originally described in the nineteenth and early twentieth centuries: there has been some taxonomic and nomenclatural confusion as a consequence (Dean 1960, Morris 1988). Delo (1935) selected *D. caudatus* (Brünnich, 1781) as type species of the genus. The same species was later called *longicaudatus* by Murchison (1839). However, what Brongniart (1822) called *caudatus* is a different species: it is the same as what Salter (1864) called 'var.' α *vulgaris*, and which was previously named *myops* by König (1825). Salter's figures of these taxa remain the best available: his (1864, pl. 3, figs 19–21 and 5) respectively show typical specimens of *D. caudatus* and *D. myops*. The latter species differs from *caudatus* most obviously in having only a short anterior mucro on the cephalon, a smaller eye that does not indent the posterior border furrow, a glabella that does not narrow so strongly posteriorly, and a pygidium with only a short posterior spine.

Description. – Exoskeleton ovoid in outline, moderately vaulted. Length/width index approximately 1.5. Cephalon semicircular, with robust genal spines reaching to 7–8th (rarely to 9th) thoracic segment. Anterior cephalic margin semicircular to parabolic, mucronate or with simple precranial process. Facial suture lying inside or close to preglabellar furrow. Glabella strongly expanding anteriorly. S1 and S2 apodemes deeply incised; no longitudinal glabellar furrow. L1, L2, L3 and LF vaulted. Eye large, lying between S3 and S1 or S0. Doublure wide, with deep and wide pseudovincular (antennal) and shallow vincular furrows perceptible laterally. Hypostome slightly vaulted, posteriorly elongated, subtriangular in outline; three prominent posterior denticles, the median one most prominent.

Short, robust, irregularly arranged spines occur on the posterior hypostomal doublure; in some specimens, they are visible on the posterior hypostome margin in posterior external view. Eleven thoracic segments; pleural furrows post-facetal, deeply impressed, lanceolate in outline. Pleural tips pointed, with wide articulating facets, moderately curved backward at front of thorax but more prominently inclined and shorter (tr.) posteriorly. Pygidium subtriangular, length/width index 0.70–0.74. Axis vaulted, approximately 0.35 of pygidial width. Twelve to fifteen axial rings. Nine to ten deep and wide pleural furrows, with flat or only slightly concave bottoms, almost reaching pygidial margin; interpleural furrows narrower. Anterior pleural band more vaulted and broader than posterior. Mucro vaulted, prolonged into broad-based spine. Doublure relatively wide, inner flange of posterior part upturned towards dorsal exoskeleton. Sculpture of fine and coarse granules.
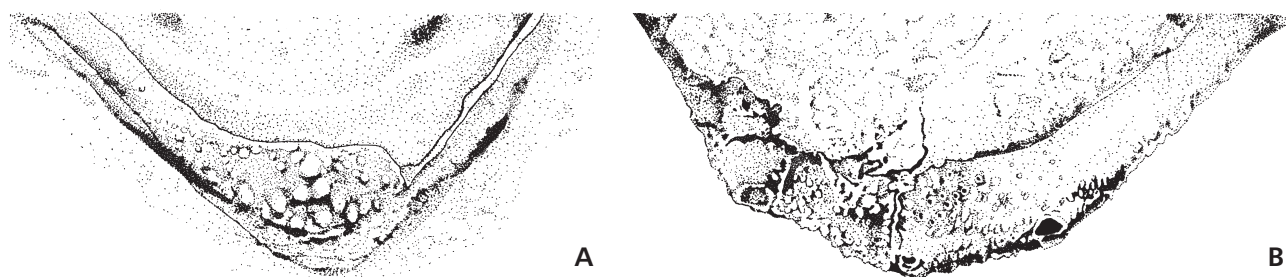
Figure 2. Line drawing of the differences in the spatial distribution of minute denticles on the posterior hypostomal doublures. • A – *Dalmanites myops* (König, 1825). Silurian, Wenlock, Much Wenlock Limestone Formation, Dudley, BIRUG 3366. • B – *Odontochile cristata* Hawle & Corda, 1847. Lower Devonian, Pragian Stage, Praha Fm., Dvorce-Prokop Limestone, Praha-Konvářka, latex cast of the specimen CGS JV 3509.

Remarks. – This general description of typical *Dalmanites* morphology is based on *D. caudatus* (Brünnich, 1781), *D. myops* (König, 1825) and *D. corrugatus* (Reed, 1901), all from the British Wenlock. These form part of a closely related group of European and North American Wenlock–early Ludlow species (Ramsköld 1985), which also includes *D. nexilis* Salter, 1864, *D. limulurus* (Green, 1832), *D. obtusus* (Lindström, 1885) and *D. platycaudatus* Weller, 1907. All these share especially prominent lateral nodes on the first, sixth and seventh thoracic axial rings, and nodes on the pygidial pleural ribs (for discussion see also Sandford & Holloway 2006).

However, there are other species sometimes assigned to *Dalmanites*, which differ in a variety of ways (Ramsköld 1985). Some were removed from *Dalmanites* by Campbell (1977) and Holloway (1981). Others were assigned by Curtis & Lane (1998, pp. 62, 63) to *Bessazoon*, which is known from the British and Australian Llandovery and Wenlock. In the context of the present study, the relatively large and wide multi-segmented pygidium of *Bessazoon*, somewhat reminiscent of Lower Devonian dalmanitids, is notable because although unrelated, it shares some of the "odontochilid" features discussed below. There are other early Silurian (*e.g., Dalmanites? fezzanensis* El Chair, Hammann & Thiedig, 1985) and late Ordovician dalmanitids (*e.g., Eudolatites* Delo, 1935 and *Mucronaspis* Destombes, 1963; see detailed discussion by Lespérance 1975 and Holloway 1981), with comparable morphologies. As well as similar pygidia, these taxa share a generally flat exoskeleton, with moderate to large rather posteriorly positioned eyes, which often form the most elevated part of the exoskeleton.

Genus *Odontochile* Hawle & Corda, 1847

Type species. – *Asaphus Hausmanni* Brongniart, 1822. Lower Devonian, Pragian Stage, Praha Formation, Dvorce-Prokop Limestone Facies, *Turkestanella acuaria* Zone.

Description. – Exoskeleton elongate, ovoid in outline, large (maximal sagittal length can exceed 150 mm), moderately vaulted. Length/width index approximately 1.6. Cephalon semicircular, with long genal spine extending back to pygidium. Anterior cephalic margin semicircular to parabolic, without anterior process. Facial suture lying outside preglabellar furrow. Glabella strongly expanding anteriorly. S1 and S2 apodemes deeply incised, no longitudinal glabellar furrow. LF vaulted, with distinct median, anterolateral and frontal auxiliary impressions. Eye very large, almost reaching axial furrow at γ and posterior border furrow at ε. Palpebral lobe much elevated above glabella. Doublure wide and flat, with deep and wide pseudovincular (antennal) furrow. Hypostome elongated, subtriangular; with three prominent spines posteriorly, and two weaker ones posterolaterally. Robust anterolateral wings. Posterior part of hypostomal doublure vaulted, especially medially, bearing a dense cluster of small denticles. Eleven thoracic segments, with deeply impressed postfacetal pleural furrows lanceolate in outline. Pleural tips pointed, with wide articulating facets, equally curved at front of thorax and at wide (tr.) pygidium. Pygidium large, subtriangular, length/width index 0.70–0.75. Axis vaulted, approximately 0.22 of pygidial width. Sixteen to twenty axial rings; 13–14 deep and wide pleural furrows, with flat or only slightly concave bottom. Interpleural furrows very narrow. Anterior pleural band more vaulted and broader than posterior. Mucro vaulted, generally prolonged into short broad-based spine; in derived species this spine is longer, and more narrowly based. Doublure relatively wide, flat, with inner flange upturned to dorsal exoskeleton. Sculpture of fine and coarse granules.

Remarks. – This brief description of *Odontochile* morphology is based on the modified diagnosis of Budil *et al.* (submitted). *Reussiana* Šnajdr, 1987 strongly resembles *Odontochile*, but has a very flat exoskeleton, and an exceptionally high number of pygidial segments (17–21 rings and 15–18, possibly 19, wide and flat-bottomed pleural furrows). The pygidium of *Reussiana* bears only a very short, blunt posterior process, and lacks a posterior spine.
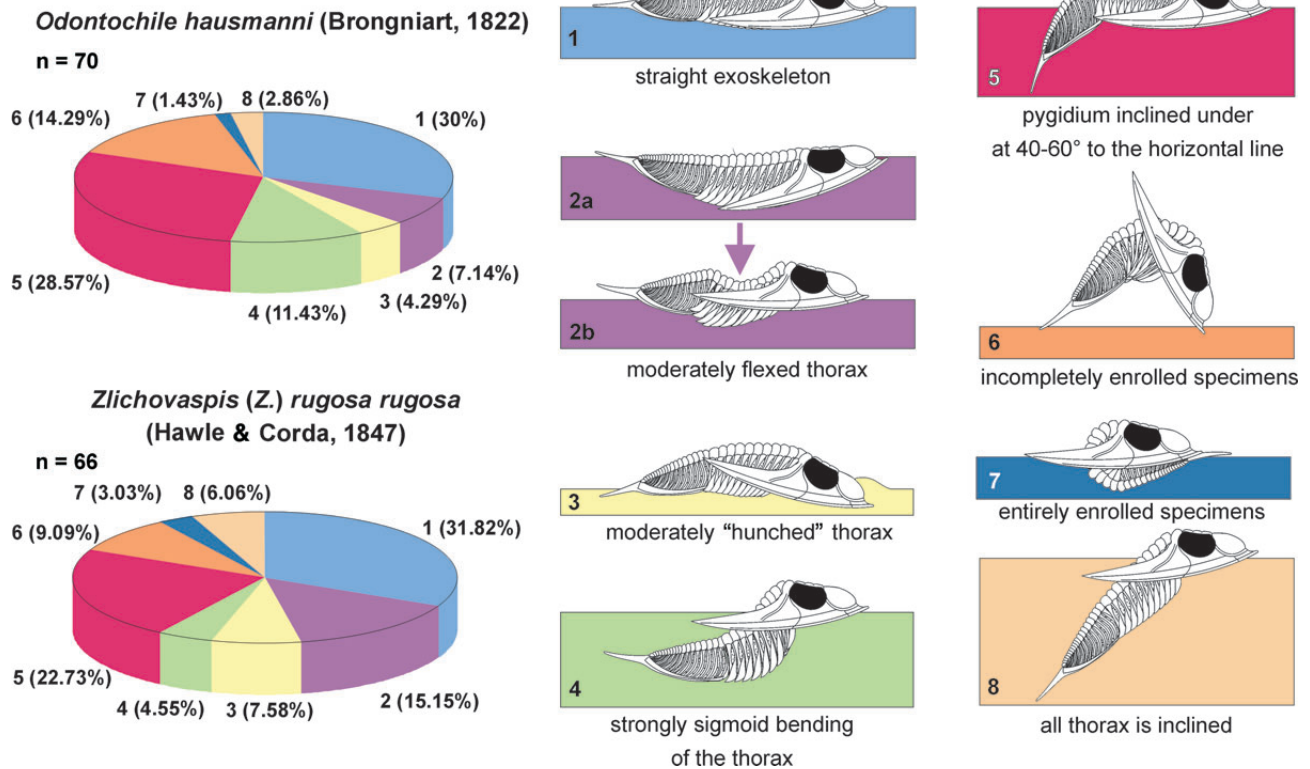
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Odontochile hausmanni (Brongniart, 1822)

n = 70

Zlichovaspis (Z.) rugosa rugosa
(Hawle & Corda, 1847)

n = 66

1 straight exoskeleton

2a
2b moderately flexed thorax

3 moderately "hunched" thorax

4 strongly sigmoid bending of the thorax

5 pygidium inclined under at 40-60° to the horizontal line

6 incompletely enrolled specimens

7 entirely enrolled specimens

8 all thorax is inclined

Figure 3. Summary of the main complete exoskeletal configurations in *Odontochile hausmanni* (Brongniart, 1822) and *Zlichovaspis* (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda, 1847).
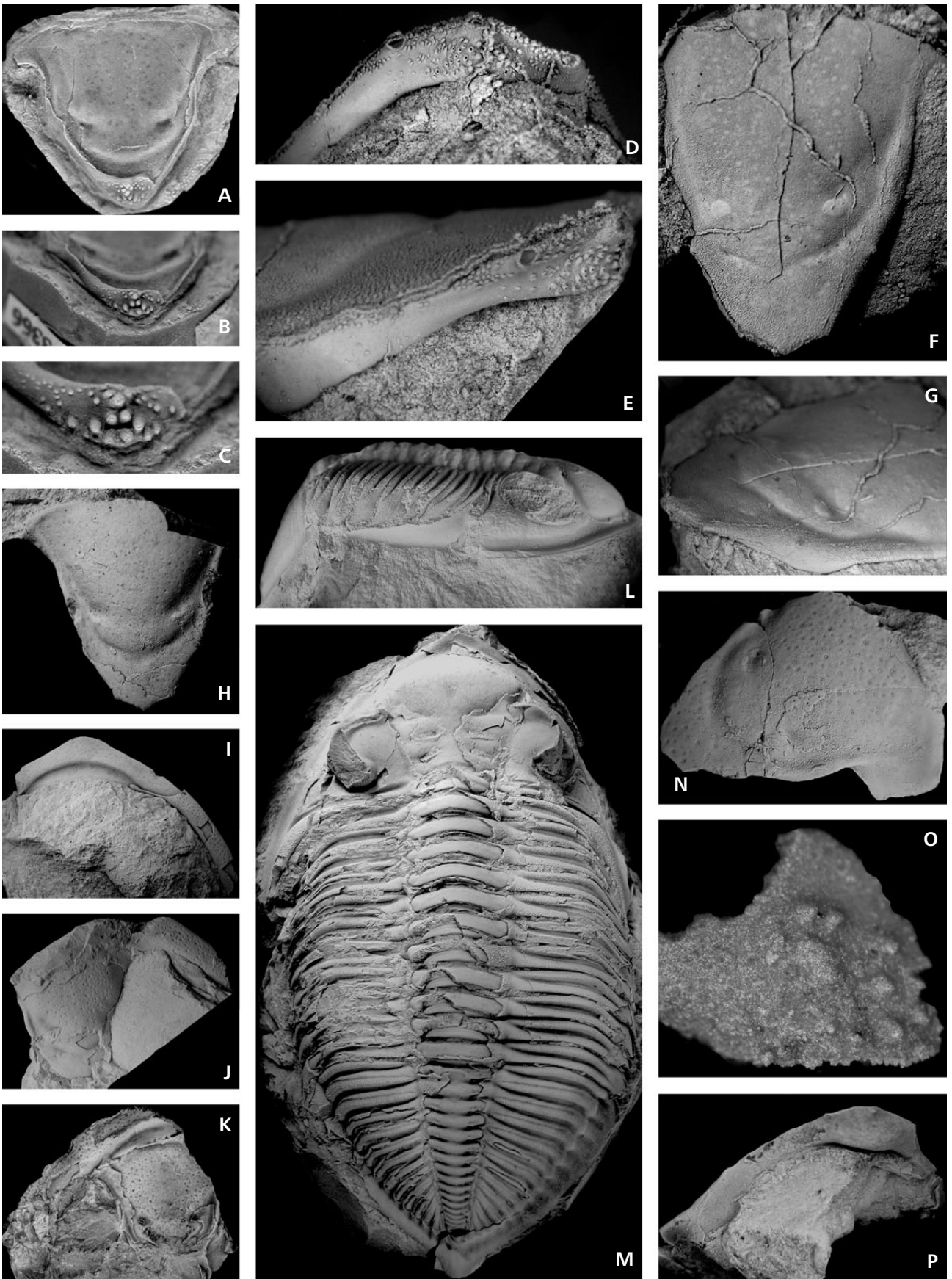
Zlichovaspis (*Zlichovaspis*) Přibyl & Vaněk, 1971 differs from *Odontochile* particularly in having a subtriangular cephalon with a parabolic anterior margin, and by the presence of a short median process. The pygidium of *Zlichovaspis* (*Zlichovaspis*) is more subtriangular in outline, with 16–21 axial rings plus a terminal piece, and with a long terminal spine. *Zlichovaspis* (*Devonodontochile*) Šnajdr, 1985 shares these features, but has a more pronounced anterior cephalic process of linguoid outline, a long but narrower terminal pygidial spine with a less robust base, and is especially distinguished by the prominent perforation of all elevated exoskeletal parts by mega-pores. The hypostomes of all these genera are still relatively poorly known, but they seem to share a similar morphology, which differs in several respects from that of *Dalmanites* (see below).

Remarks on exoskeletal morphology

The exoskeleton of most Silurian and Devonian dalmanitids is dorsoventrally flattened, but with the axial region (including the glabella) elevated. The ventral side of the exoskeleton is flat, with a relatively wide doublure. The

Figure 4. A–C – *Dalmanites myops* (König, 1825). Ventral side of hypostome, internal mould with exoskeleton with preserved denticles on posterior doublure, BU 3366. Silurian, Wenlock, Much Wenlock Limestone Formation, Dudley. • A – ventral view, × 2. • B – posterior view, × 2. • C – detail of denticles, × 3.5. • D–G – *Odontochile cristata* Hawle & Corda, 1847. Latex cast of the hypostome, CGS JV 3509, Lower Devonian, Pragian Stage, Praha Formation, Dvorce-Prokop Limestone, Praha-Konvářka. • D – posteroventral view of hypostomal doublure, × 3. • E – posterolateral view, × 2.5. • F – ventral view, × 1.5. • G – oblique ventral view on sculpture of hypostomal margin and maculae, × 1.8. • H–I, N–P – *Zlichovaspis* (*Devonodontochile*) *vigerle* (Šnajdr, 1987b). Lower Devonian, Lower Emsian (Zlichovian Regional Stage), Zlíchov Formation, Zlíchov Limestone, Praha-Žvahov. • H – incomplete hypostome CGS JV 3533, internal mould, × 1.5. • I – cephalic doublure, CGS PB 189 (coll. F. Hörbinger), internal mould with relics of exoskeleton, × 1. • N – incomplete hypostome, CGS JV 3523, dorsolateral view showing robust anterolateral wings, × 1.5. • O – detail of denticles on posterior hypostomal doublure, ex CGS JV 3533, × 5. • P – incomplete hypostome, internal mould with relics of exoskeleton, CGS JV 3533, × 1.5. • L – *Odontochile hausmanni* (Brongniart, 1822), neotype, almost complete specimen NM L 15015, lateral view. Lower Devonian, Pragian Stage, Praha Formation, Dvorce-Prokop Limestone, Praha-Dvorce, × 0.8. • J–K, M – *Zlichovaspis* (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda, 1847). Lower Devonian, Pragian Stage, Praha Formation, Dvorce-Prokop Limestone, Damil Hill near Tetín. • J – incomplete cephalic doublure with hypostome *in situ*, NML 30261, × 1. • K – ditto, MCZ 172840, × 1. • M – almost complete specimen, NML 15001, dorsal view, × 1.3.

ventral side of the hypostome is wide and relatively flat also, extending only very slightly below the plane of the cephalic doublure or lying at the same level. The prominent, strongly elevated schizochroal eyes with steep visual surfaces contain hundreds of individual lenses, arranged in regular dorso-ventral files. Their field of view is predominantly lateral, being limited anteriorly by the peripheral part of the cheek and by the frontal glabellar lobe. These various characteristics vary in detail between different Silurian and Devonian dalmanitid groups. However, they are generally more pronounced in *Odontochile* than in *Dalmanites,* being accompanied in *Odontochile* by the large, wide, and multi-segmented pygidium. The doublure of *Odontochile* and *Zlichovaspis* is prominently pitted: the fine pores probably represent sites of sensor attachment, perhaps comparable with the bothria of arachnids (*e.g.*, Meslinger 1987) and some other arthropod groups. The Lower Devonian *Reussiana* and *Kazachstania* Maksimova, 1972 are extreme examples of this morphological type.

General hypostomal architecture is very similar in *Dalmanites*, *Odontochile* and *Zlichovaspis*; no hypostome is known for *Reussiana* so far. Representatives of these genera share the wide, rounded but elongated subtriangular hypostomal outline, with a moderately vaulted middle body and prominent maculae. The anterolateral wings are very robust (Fig. 4N), suggesting firm attachment of the conterminant hypostome (Fortey & Owens 1999a, b). The anterior wings probably also developed a small process like that seen in at least some phacopids (see Bruton & Haas 2003a).

The main differences between the hypostomes of *Dalmanites* and *Odontochile* lie in the shape of the posterior and posterolateral margin. In *Dalmanites*, the general outline of the hypostome is more subtriangular, with three robust posterior spines. By contrast, in *Odontochile* and *Zlichovaspis*, the hypostome has a more elongate subpentagonal outline, with three prominent posterior and one pair of additional posterolateral spines. These are seen only in the best preserved specimens however (Fig. 4D; for discussion see Budil *et al.* submitted). Šnajdr (1987b, p. 14, fig. 2) neither discussed nor figured these features, while Barrande (1852, 1872) overemphasized the prominence of the posterolateral spines.

The major contrast between *Dalmanites* and *Odontochile/Zlichovaspis* hypostomes is seen on the posterior

doublure (Fig. 2). In all the genera discussed, the medial part of this doublure is vaulted, but this is more distinct in *Odontochile* and *Zlichovaspis* (Fig. 4F). In *Dalmanites*, this part of the doublure possesses a cluster of irregularly arranged short, sparse but relatively robust spines (see Fig. 4A–C). In *Odontochile* and *Zlichovaspis*, a comparable structure is developed, but the spines are smaller in size and larger in number. The spines are shorter, denser, narrower in diameter, and their arrangement is more regular (see Fig. 4E–G). Both structures could have functioned in a rasp-like way, shredding, milling and cutting food. Very similar groups of tiny spines on the vaulted median part of the hypostome doublure were found by Bruton & Haas (2003a, pl. 2, fig. 4–6) in the phacopid *Geesops*. Broadly comparable structures have been described in some odontopleurids Chatterton & Perry (1983; see also Fortey & Owens 1999a, b), in *Asaphus* (Ivantsov 1990), *Isotelus* (Fortey & Owens 1999b) and lichids (see also Kaesler *et al.* 1997).

Asymmetrically arranged small denticles on the posterior hypostome margin (lying mainly between three larger posterior spines) are visible in external view in some specimens of *Dalmanites caudatus* (*e.g.*, NHM 59069, BU 56 figured by Salter 1864, pl. 3, fig. 8). In contrast, such structures are very rarely visible in Bohemian Lower Devonian dalmanitids, commonly having been destroyed during preparation from indurated biomicritic limestones. After three years of searching, they have been found only in two specimens briefly discussed also by Budil *et al.* (submitted). Both specimens were found among specimens coming from soft, white decalcified limestones. The best specimen (Fig. 4D–G) is an almost complete internal and counterpart external mould of a hypostome of *Odontochile cristata* Hawle & Corda, 1847 (CGS JV 3509), from the lower part of the Dvorce-Prokop Limestone Facies (Praha Formation, Pragian Stage) from Praha-Konvářka. The rasp-like structure can be seen on a latex cast taken from the external mould. The second specimen is a comparatively poorly preserved fragment of the posterior hypostomal doublure belonging to *Zlichovaspis* (*Devonodontochile) vigerle* (Šnajdr, 1987b; CGS JV 3533), found in the decalcified parts of the uppermost Zlichov Limestone from Praha-Žvahov (see Fig. 4H, O–P). Cavities after dissolved fine denticles were seen in the rock matrix surrounding this specimen. However, the whole structure was so fragile that, despite conservation, it was
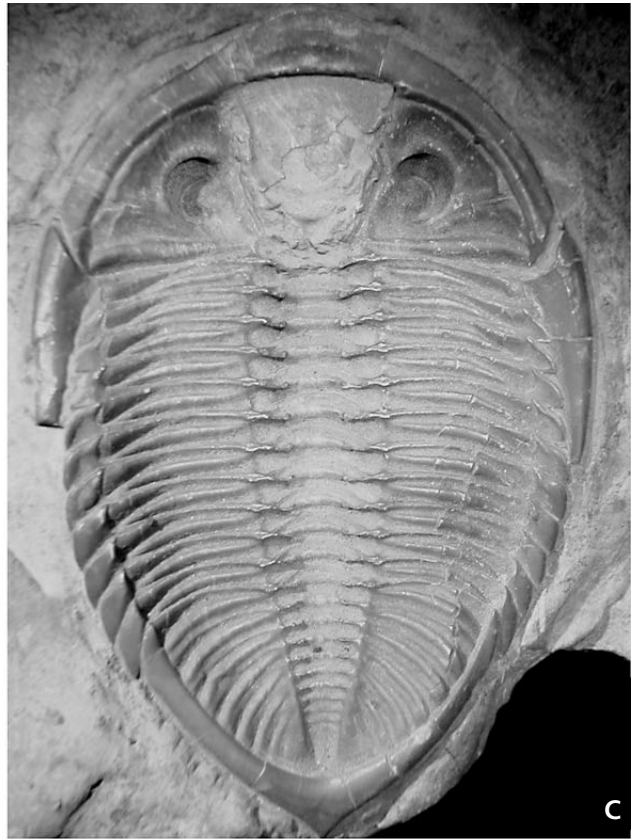
Figure 5. A, B – *Odontochile hausmanni* (Brongniart, 1822). Entirely enrolled specimen, a representative of exoskeleton configuration 7 (Fig. 3), MCZ 172821. Lower Devonian, Pragian Stage, Praha Formation, Dvorce-Prokop Limestone. Locality unknown. A – dorsal view, B – lateral view. × 2.8. • C – *Dalmanites myops* (König, 1825). Complete specimen with hypostome *in situ*, ventral view. NHM It 20991, Silurian, Much Wenlock Limestone., Wenlock, Dudley, × 0.9. • D, E – *Zlichovaspis* (*Zlichovaspis*) *auriculata* (Dalman, 1826), Lower Devonian, Zlichovian regional stage (lower Emsian), Zlíchov Formation, Zlíchov Limestone. Representatives of the exoskeleton configuration 1 (Fig. 3). • D – holotype, a nearly complete specimen NML 18728, Karlštejn, internal mould, dorsal view, × 1.7. • E – almost complete, dorsally flattened specimen in shale, NML22577, Praha-Řeporyje, dorsal view, × 1.5.
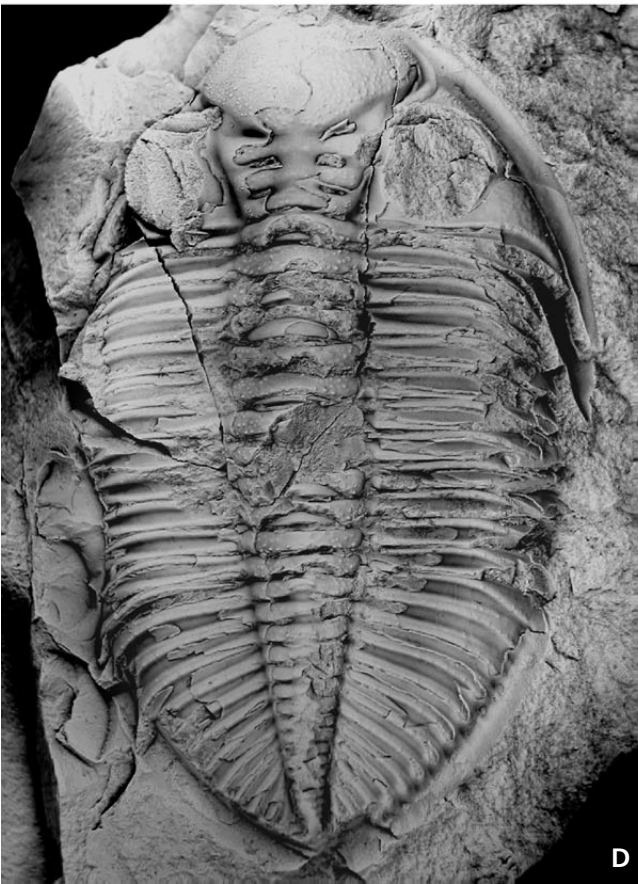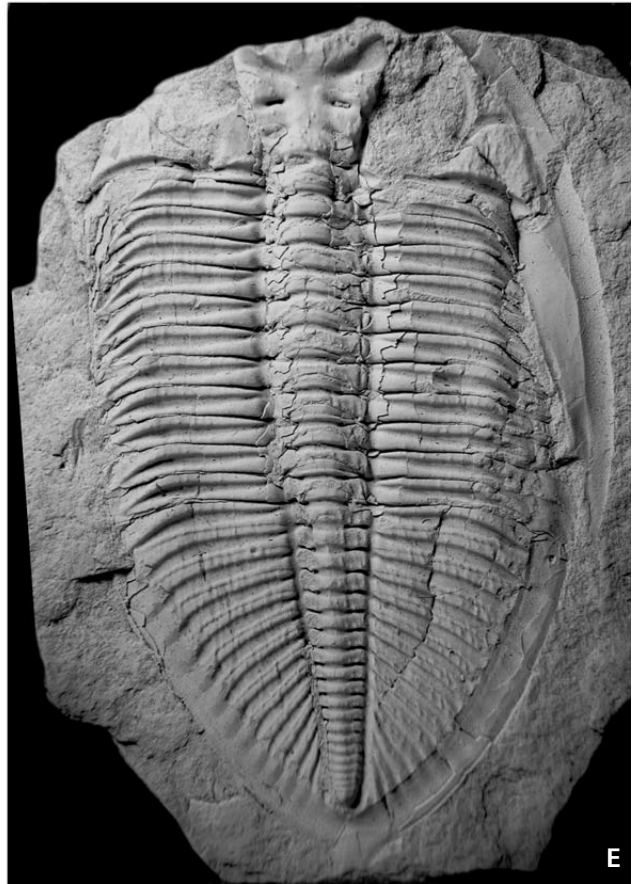
broken during preparation, and only the small fragment figured on Fig. 4O remained. It comes from the median, most elevated part of the posterior doublure, well seen in Fig. 4P.

Analysis of complete exoskeletons of Lower Devonian dalmanitids from the Prague Basin

Relatively abundant museum material has been available for this analysis (n = 144 complete exoskeletons). Most of the specimens are stored in the National Museum, Prague, but others have been studied in the collections of the Museum of Comparative Zoology, Harvard University, Massachusetts and the Czech Geological Survey. Additional material in several private collections, especially those of the third author, P. Kolář and J. Valíček, has been used also. Only two species – *Odontochile hausmanni* (Brongniart, 1822) and *Zlichovaspis* (*Zlichovaspis*) *rugosa rugosa* (Hawle & Corda, 1847) – were sufficiently common to be used; other taxa, especially *Zlichovaspis* (*Zlichovaspis*) *auriculata* (Dalman, 1827), are comparatively little represented. Seventy specimens represent the first species and sixty-six specimens the second (Fig. 3).

Eight main configurations of the articulated exoskeleton have been recognized, but some are rare. Their occurrence ratios are relatively similar in both analysed species, despite their being generically distinct and of different stratigraphical age. A predominance of extended, moderately flexed or "hunched" exoskeletons is as expected (41.43% in *O. hausmani* and 54.55% in *Zlichovaspis* (*Z.*) *rugosa* respectively).

More surprising is the abundance of specimens with the pygidium, or the pygidium and the last few thoracic segments, inclined downwards at approximately 45° to the horizontal plane (typical example see Fig. 4L; 28.57% and 22.73%). Relatively rare are specimens with a slightly sigmoidally bent thorax (11.43% and 4.55%). Conversely, partially enrolled specimens are quite common (14.29% and 9.09%) but only three completely enrolled examples have been found so far (one of *Odontochile hausmanni* and two of *Zlichovaspis* (*Z.*) *rugosa rugosa*). Similarly, the specimens with straight thorax but with cephalon inclined at some angle are relatively rare (2.86% and 6.06%, respectively). Šnajdr (1987b, p. 12) briefly, but largely correctly, discussed the main exoskeleton configurations identified here. He considered the most commonly preserved configurations to represent the pre-mortem attitudes of the animals, partially buried in sediment. We agree with this suggestion with some reservation, because taphonomic processes such as local transport of dead animals by currents could influence the different types of body flexing.

The sampling bias has been usually conceived as an additional factor affecting the analysis. In our case, the selection made by collectors is certainly insignificant, because the articulated remains, particularly of large dalmanitids of Devonian age, are generally very rare in the Barrandian area and they belong to the forefront of every collection. Thus the collection studied represents a relatively good basis for the analysis presented.

Active burrowing by asaphid trilobites, living in comparable lithofacies, was discussed by Cherns *et al.* (2006). Those authors interpreted *Asaphus* as the trace-maker of the *Thalassinoides* ichnofossil, producing limestone "nodules" characterized by Y- and T- shaped branching. The Lower Devonian dalmanitids of the Prague Basin occur in nodular limestones also, but there is no direct proof that the nodules originated in a similar way. The general body morphology of dalmanitids, although having a conterminant hypostome, is different from that of *Asaphus*, being more flattened, with elevated eyes, a different glabellar lobation and so on. Rather shallow burrowing or ploughing is more likely in dalmanitids. Despite their common occurrence as body fossils, there are no trilobite-related traces known from the Praha and Zlíchov formations. The probability of their preservation is very low because of taphonomic conditions (R. Mikuláš, pers. comm.). The number of complete dalmanitids is too few to enable a study of the occurrence and variation of exoskeletal configurations in individual beds.

Discussion and interpretation

Dalmanitids are among those trilobites with a supposed predator-scavenger mode of life (Fortey & Owens 1999a, b). All the observations made here accord generally with this interpretation. However, the morphology of *Dalmanites* and particularly that of *Odontochile*, is not what would be expected for active predators of relatively large mobile animals. In particular, the situation of the eyes does not facilitate the effective anterior vision necessary for active pursuit of prey. However, Clarkson (1966) clearly showed that the visual fields of some Wenlock dalmanitids do overlap at front and rear. There is also at least some degree of binocular vision in these areas. However, the visual field in *Dalmanites* forms a relatively narrow latitudinal belt, inclined very slightly upwards from the horizontal line.

We interpret this shape of visual field as effective more for the identifying the predators rather than for catching of the prey. As Bruton & Haas (2003b, pp. 356–358) suggested for *Phacops*, the large schizochroal eyes, with their vertical files of lenses, may have functioned primarily as motion detectors, to identify the presence of enemies. On the other hand, Schoeneman (2007) has recently presented a new, detail analysis of the schizochroal eyes, presenting

evidence, that this eye type was a neural superposition visual system, capable of producing a good overall image. The common traces of injuries described by Šnajdr (1987b) and Budil *et al.* (submitted) show that dalmanitids, even those of large size, were commonly attacked.

We consider all the characteristic morphological features of late Silurian–early Devonian dalmanitids as adaptations for rather shallow burrowing or ploughing in the superficial layers of the sediment. The flattened body morphology with elevated eyes would have enabled the animal to see its surroundings even when partly buried in sediment (Thomas & Lane 1984). The animals may have fed using a combination of grazing, scavenging and predation of small burrowing animals. The differences in general exoskeletal and hypostomal morphologies described here suggest some variations in life-mode and feeding strategy. The more primitive condition is seen in *Dalmanites*, which may have relied more on predation and/or have taken more mechanically robust prey.

The "odontochilid" morphology is characterized by: a generally flat body shape; longer genal spines, offering improved stability during the flexing of exoskeleton to burrow into the sea floor; larger, more elevated, but rather posteriorly placed eyes; a hypostome with smaller and denser fine denticles on the posterior doublure; a large, flat and multi-segmented pygidium. These may be adaptations for greater reliance on scavenging and/or grazing.

Shallow burrowing near the surface of the sediment is inferred, the thoracic and pygidial appendages being used to collect food and transport it towards the mouth in the manner suggested by Eldredge (1971). Stürmer & Bergström (1973) suggested a raptorial mode of feeding in Devonian dalmanitids, but argued that this was probably combined with suction of material into a food groove, without true filtering. The vaulted "odontochilid" glabella, lying above the flat, wide hypostome, and surrounded by tightly embracing genal spines, invites a comparison with the filtering chamber inferred by Fortey & Owens (1999a, b) for harpetids and trinucleids, and seen also in some aulacopleurids. Filter feeding was proposed for *Phacops* by Bruton & Haas (2003a), and this interpretation represents an interesting alternative to the generally accepted concept of Fortey & Owens (1999a, b). We do not consider filter feeding likely in dalmanitids, but suction into a food groove could have been very effective, especially on a soft, muddy sea-floor. Shallow burrowing in search of food could explain also the prevalence of straight and moderately flexed specimens among articulated remains, and the extreme rarity of enrolled specimens.

The "odontochilid" features discussed here appeared several times, and in several combinations, in independent evolutionary lineages of dalmanitids. The mosaic emergence of these features in dalmanitid evolution may thus reflect repeated, relatively minor, changes in feeding strategies in the evolutionary lineage. These morphological changes therefore do not constitute a robust basis for recognition of the Odontochilinae Šnajdr, 1985 as an independent subfamily.

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