Frontal auxiliary impressions in the Ordovician trilobite *Dalmanitina* Reed, 1905 from the Barrandian area, Czech Republic

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Fossils preserved in Cambrian to Devonian sediments of the Barrandian area (Czech Republic) have contributed significantly to our knowledge of numerous invertebrate groups. With respect to trilobites, important data has been discovered on the construction of eyes, healing of exoskeletal injuries, as well as on the morphology of soft parts. The generally rarely preserved frontal auxiliary impressions (FAIs) on the glabellar surface of trilobites were first described in Devonian examples from this area in the mid-nineteenth century by Barrande. Such impressions have only rarely been documented in a few trilobite species in the Lower Palaeozoic of the Barrandian area. Here we describe twelve exceptionally preserved holaspid cephalic shields of *Dalmanitina socialis* Barrande, 1846. These specimens are internal moulds and were collected at three localities in the Upper Ordovician Letná Formation. These materials document a high level of variability in the disposition of FAIs within the glabella. However, the FAIs show a common pattern at the anterior glabellar margin and are arranged in two pairs around a medial impression and are also associated with a third pair situated more posterolaterally. This current study is the first to focus on the distribution of FAIs within the Dalmanitidae. *Dalmanitina socialis* specimens with FAIs from the Letná Formation indicate that the depositional environment at the several localities in that unit was favourable to exceptional preservation. Excellently preserved cephalic shields of *Dalmanitina* demonstrate the presence of the posterior median impression (pmi) of Eldredge (1972) and enable new terminology to be proposed for other FAIs. • Key words: Trilobites, frontal auxiliary impressions, soft-tissue preservation, Letná Formation, Upper Ordovician, Czech Republic.


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Trilobites from the Cambrian to Devonian sediments of the Barrandian area (Czech Republic) have contributed significantly to our knowledge of their palaeobiology, such as the construction of their eyes, the nature of their exoskeletal injuries and their soft-part morphology, for instance their digestive system (see e.g. Budil & Fatka 2020). With respect to auxiliary glabellar impressions, it was Barrande (1852, pp. 111, 112) who first noticed and figured in several trilobites the presence of these, and twenty years later he (1872, pp. 150, 151) described the occurrence of "impressions auxiliaires" in greater detail. In the present contribution, we describe twelve exceptionally preserved late holaspid cephalic shields of the abundant species *Dalmanitina socialis* (Barrande, 1846), all collected from three localities in the lower Sandbian Letná Formation. This study represents the first detailed analysis of frontal auxiliary impressions (FAIs) in the Dalmanitidae.

Geological setting

Havlíček & Vaněk (1966) compiled a comprehensive list of species from the Ordovician of the Prague Basin, including taxa from the Letná Formation. Earlier data on the geological setting, skeletal fossils and faunal assemblages of the Letná Formation has been recently summarized by Fatka *et al.* (2013) and Drage *et al.* (2018). At several outcrops containing the *Dalmanitina–Deonaspis* Association of Havlíček & Vaněk (1990), rare remains of non-mineralized to slightly mineralized fossils have been discovered, including rare trilobites with the remains of their alimentary tract (Jahn 1893; Chlupáč 1988, 1999a, b; Rak *et al.* 2013; Fatka *et al.* 2013).

*Dalmanitina* Reed, 1905 in the Prague Basin. – In the Prague Basin, *Dalmanitina* is found exclusively in sediments...
ments of the Berounian Regional Stage (Fig. 1C), which corresponds to the Sandbian to lower to middle Katian of the international stratigraphic standard (see Havlíček & Marek 1973, Bergström et al. 2009, Fatka et al. 2013). The systematics of Dalmanitina in Bohemia has been studied especially by Šnajdr (1956, 1982a, b, 1987, 1990) and more recently also by Vaněk & Vokáč (1997). Two informal groups can be distinguished within Dalmanitina in the Barrandian area, the Dalmanitina socialis group [this includes D. socialis (Barrande, 1846) and D. citinen-sis Šnajdr, 1956] and the D. proaeva group [this includes D. proaeva proaeva (Emmrich, 1839), D. proaeva elfrida Šnajdr, 1982a and D. proeva asta Šnajdr, 1982a] (see also Drage et al. 2018).

Material and methods

The specimens used in this study are all internal moulds and they belong to three historical collections: that of Joachim Barrande in the National Museum, Prague (NM L 59867, 59868), that of the Czech Geological Survey, Prague (ČGS MŠ 7212, 7229, 1237, 7244, 7253, 7255 and XA 023a-b) and that of the Museum für Naturkunde, Berlin (MFN T 1638.1 and T 1638.3). These specimens were collected from three localities: from Veselá and Děd near Beroun, and from the Ostrý hills (Fig. 1B). All specimens are preserved as internal moulds in light to dark yellow or pale brown quartzose sandstone (Figs 3–5). They are more than 32 mm in sagittal length and correspond to a late holaspis growth stage. Only the internal moulds were studied, as the external moulds were not usually collected in the 19th century and are mostly absent in the historical collections. Photographs were taken using a NIKON D 300 digital camera, and specimens were coated with ammonium chloride sublimate beforehand. Drawings were made from the photographs using Corel Draw X3 and Photoshop CS5.

Terminology of frontal auxiliary impressions

The morphological term ‘Frontal Auxiliary Impressions’ (FAIs) was proposed by Lerosey-Aubril et al. (2011, p. 167) to distinguish glabellar muscle scars located on
the frontal glabellar lobe only. FAIs were interpreted as related to the extrinsic musculature of the foregut, distinct from the muscle scars associated with the glabellar furrows and likely representing insertion sites for the musculature of the appendages. FAIs refer to a specific subset of muscle scars borne by the glabella, whereas other terms such as ‘auxiliary impressions’ (= impressions auxiliaires) of Barrande (1852, 1872), Harrington (1959), Šnajdr (1990) and Budil et al. (2009, pp. 65, 67, fig. 3), ‘auxiliary musculature’ of Born (1919), ‘auxiliary muscle impressions’ of Eldredge (1972, p. 143), or ‘auxiliary impression system’ of Eldredge & Braniša (1980, p. 190), Edgecombe (1993), Ramsköld & Edgecombe (1993, p. 275), Edgecombe & Fortey (2000, pp. 334, 337, 340) referred to all of them. Lerosey-Aubril et al. (2011) and Lerosey-Aubril & Peel (2018, p. 748) hypothesized that all trilobites might have possessed muscles associated with the foregut, at least as suspensor muscles, but in most taxa this musculature was too delicate to leave external marks on the dorsal exoskeleton. These authors also supposed a limited use of the distribution pattern of FAIs for the study of phylogenetic relationships between major trilobite groups.

Analysis of impressions preserved in specimens of Dalmanitina socialis examined in the current study shows a common pattern in the disposition of at least eight FAIs (Fig. 2). Two more or less prominent, non-paired pits are placed medially, one situated anteriorly to S3 glabellar furrows (= pmi of Eldredge 1972, see below), the other at the anterior glabellar margin. Four other arrangements are arranged in two pairs situated around the non-paired anterior median impression. The third pair of impressions is located more posterolaterally. In well-preserved specimens, the following types of FAIs may be distinguished:

1) Posterior median impression (pmi) – is a deep elongate pit sometimes forming a sagittal groove located on the inner surface of the posterior part of the frontal glabellar lobe anterior to S3; the pmi was first used and discussed by Eldredge (1972, p. 149, text-fig. 6c) in the calmoniid Bouleia.

2) Anterior median impression (ami) – is a conspicuous, transversally elongate elliptical pit located sagittally in the preglabellar furrow. A similar impression developed as a pad and located sagittally near the anterior border furrow in Calyptaulax holstenensis was discussed and figured by Eldredge (1971, p. 58, fig. 3).

3) Anterior lateral impressions (ali) – are represented by four impressions arranged in two pairs flanking the ami laterally.

4) Abaxial impressions (abi) – are a pair of large impressions placed posteriorly from the anterolateral margin of the glabella; they are positioned abaxially opposite the mid-distance between ami and pmi. They represent the most abaxial FAIs and delimit a diamond-shaped area where most of the more minor FAIs are located.

The main abaxial rows commonly become obsolescent as they converge posteriorly at the midline.

Figure 2. Frontal auxiliary impressions on the glabella of Dalmanitina socialis. A – the general pattern of frontal auxiliary impressions (FAIs) and terminology proposed herein, the dashed boundary lines indicate the posterolateral limits of the area where FAIs occur, the dotted area covers the surface where small FAIs are commonly arranged in two oblique rows; B – distribution of FAIs in all herein studied specimens of Dalmanitina socialis (Barrande, 1846).
Frontal auxiliary impressions in *Dalmanitina socialis* were only observed on internal moulds, being expressions of pads (positive reliefs) on the visceral surface of the glabella. No evidence of the presence of FAIs was found on the external surface of the glabella in this species, despite the study of ca 600 cephala.

**Description**


ČGS MŠ 7212 (Figs 3A, A1; 6A). – About thirty-five more or less symmetrically disposed, small FAIs are preserved on the frontal glabellar lobe (Fig. 6A). A pmi is developed as a sagittally elongate pad, composed of a deeper posterior part and a rounded and shallower anterior part (see Fig. 3A). Five other impressions are conspicuous; a large, elliptical medial imprint (ami; Fig. 3A1) is associated with two other deep, more lateral pits (ali2, ali2´; Fig. 3A1), all situated near the anterior glabellar margin. Two other rounded imprints lie more posterolaterally (abi, abi´; Fig. 3A1). About fifteen fine, rounded elliptical imprints are more posterolaterally (abi and abi´; Fig. 3B). About thirty-five symmetrically disposed FAIs are preserved, those on the left side arranged in a row connecting the anterior glabellar margin with the pmi (Figs 4A, 6E). Two pairs of anterior impressions are deep and slightly elliptical (Fig. 4A1). Posterolateral impressions are present but weakly developed.

ČGS MŠ 7237 (Figs 3B, B1; 6B). – A distinct pmi is developed as a deep, sagittally elongate pad (see Fig. 3B). A set of about thirty symmetrically disposed FAIs is seen on the anterior glabellar lobe. Seven FAIs are conspicuous; five of these pits occur at the anterior margin of the glabella, where a deep triangular ami is bounded by two sagittally elongate imprints on the left side (ali1 and ali2 in Fig. 3A1) and by two rounded imprints on the right side (ali1´ and ali2´; Fig. 3A1). Two rounded pmi is composed of two rounded pads. There is a well-developed, elliptical ami associated with ali1, ali1´ and ali2; both abi and abi´ are also present (Fig. 3D1).

ČGS MŠ 7229 (Figs 3D, D1; 6D). – About twenty fine and shallow FAIs are preserved. Only four very weak impressions are visible on the left side of the glabella; about fifteen impressions are developed on the right side, the most prominent in the right lateral sector. A distinct, ellipsoidal pmi is composed of two rounded pads. There is a well-developed, elliptical ami associated with ali1, ali1´ and ali2; both abi and abi´ are also present (Fig. 3D1).

ČGS MŠ 7253 (Figs 4A, A1; 6E). – A distinct, ellipsoidal pmi is composed of two rounded pads. There is a weakly developed, elliptical ami. About thirty shallow FAIs are preserved, those on the left side arranged in a row connecting the anterior glabellar margin with the pmi (Figs 4A, 6E). Two pairs of anterior impressions are deep and slightly elliptical (Fig. 4A1). Posterolateral impressions are present but weakly developed.

ČGS MŠ 7244 (Figs 4B, B1; 6F). – Small, slightly elliptical, deep pmi; ami small and shallow, both pairs of anterior impressions well developed and elliptical in outline (ali1, ali1´ and ali2, ali2´; Fig. 4B1). Posterolateral impressions very weakly developed (see Fig. 4B1). Only four small FAIs are preserved on the surface of the porous internal mould of the frontal glabellar lobe (Fig. 6F).

ČGS XA 23b (Figs 4C, C1; 6G). – Small, deep pmi, subrounded in outline. Three anterior impressions are indistinctly developed (ali1´, ali2 and ali2´; Fig. 4C1). Posterolateral impressions are developed as shallow, smooth surfaces. About ten small, shallow FAIs are irregularly dispersed on the frontal glabellar lobe (Fig. 6G).

ČGS XA 23a (Figs 4D, D1; 6H). – The pmi is rounded and deep; ami, ali1, ali1´ and both abi1, abi1´ are poorly developed; ali2 and ali2´ relatively deep and distinct (Figs 4D, D1). About thirty small and shallow FAIs are irregularly distributed (Fig. 6H).

MFN T1638.3 (Figs 5A, A1; 6I). – Deep pmi, elliptical in outline; ami is narrow; ali1, ali1´, ali2´ and both abi1, abi1´ are well developed; ali2 is not preserved (Figs 5A, A1). Seven small FAIs are preserved on the left side of the glabella (Fig. 6I).

MFN T1638.1 (Figs 5B, B1; 6J). – Relatively shallow pmi is composed of two rounded imprints. All other FAIs are well preserved, including about twelve small imprints, all arranged in two longitudinal rows on the anteriormost glabellar lobe (Fig. 6J).

NM L 59867 (Figs 5C, 6K). – The pmi is rounded. Small ami associated with poorly preserved ali2 and ali2´.
Figure 3. Internal moulds of cephalon of *Dalmanitina socialis* (Barrande, 1846) with FAIs, Upper Ordovician Letná Formation, Berounian Regional Stage (Sandbian to lower to middle Katian), Prague Basin. A, A₁ – well-vaulted internal mould of cephalon with both genal spines, showing slightly damaged eyes, Děd Hill near Beroun, ČGS MŠ 7212; B, B₁ – strongly vaulted internal mould of cephalon with both genal spines missing and with well-preserved eyes, Veselá Hill, Beroun, ČGS MŠ 7237; C, C₁ – three-dimensional cephalon with left genal spine in situ and with excellently preserved eyes, Beroun – Veselá Hill, ČGS MŠ 7255; D, D₁ – incomplete vaulted cranidium with partially preserved genae and left eye, right eye and occipital ring missing, Beroun – Ostrý Hill, ČGS MŠ 7229.
Figure 4. Internal moulds of cephalon of *Dalmanitina socialis* (Barrande, 1846) with FAIs, Upper Ordovician Letná Formation, Berounian Regional Stage (Sandbian to lower to middle Katian), Prague Basin. A, A<sub>1</sub> – complete vaulted cephalon with both eyes and both genal spines, Veselá Hill, Beroun, ČGS MŠ 7253; B, B<sub>1</sub> – complete well-vaulted cephalon with the left genal spine and slightly damaged eyes, Veselá Hill, Beroun, ČGS MŠ 7244; C, C<sub>1</sub> – incomplete highly vaulted cranidium with both eyes and partially damaged right anterolateral cephalic margin, Veselá Hill, Beroun, ČGS XA 23b; D, D<sub>1</sub> – nearly complete vaulted cephalon with both eyes and left genal spine, Veselá Hill, Beroun, ČGS XA 23a.
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The right abi’ is poorly developed. About five small FAIs are present in the anteriormost part of the glabella (Fig. 6K).

**NM L 59868 (Figs 5D, 6L).** – The pmi and ami are shallow; ali₁ and ali₁’ not preserved; ali₂, ali₂’ and both lateral impressions (abi and abi’; Fig. 5D) are shallow and rounded. Other FAIs are tiny and very poorly visible (Fig. 6L).

**Discussion**

Frontal auxiliary impressions (FAIs)

Frontal auxiliary impressions are usually interpreted as attachment sites for strong extrinsic muscles enabling suspension and dilatation of the anterior part of the...
digestive system (for detail discussion see Lerosey-Aubril et al. 2011, pp. 172–178). FAIs are regarded as indicative of a major modification of the foregut: its differentiation into a well-developed pouch-like organ (i.e. a crop) comparable to the stomach of modern spiders or the proventriculus of crabs, the function of which (e.g. pumping, chewing/filtering) required a powerful musculature (see Dunlop et al. 1992, Marples 1983, Lerosey-Aubril et al. 2011).

**Frontal auxiliary impressions in Dalmanitina**

In Dalmanitina, the preservation of FAIs is exceedingly rare, but a given specimen may exhibit several tens of them, typically subcircular and faint. Of the ca 600 cephalia of this taxon investigated in the course of this study, FAIs were found in twelve specimens only; these structures are preserved exclusively on internal or composite moulds (see Figs 3–5). The FAIs of Dalmanitina are arranged in...
a characteristic triangle, which reaches its maximal width along the anterior margin of the frontal glabellar lobe.

In some specimens, FAls are disposed in two very slightly diverging rows (Fig. 6A, B, I, J) associated with a wide row of usually larger, elliptical or irregularly shaped and deeper impressions along the anterior glabellar margin. Such a configuration agrees well with the dalmanitid distribution pattern of FAls (sensus Eldredge 1971, 1979). The distribution pattern of FAls was used as diagnostic for the higher systematics of Phacopina by Eldredge (1971, 1979), Edgecombe (1993, 1994) and Carvalho et al. (2003). However, it is noteworthy that the FAls in Dalmanitina seem to show variability in both shape and outline (Fig. 2A), and this does not seem to be solely explained by taphonomy. FAls in some specimens do not form a triangular configuration but a rather irregular cluster of impressions that occupies a large part of the anterior half of the anterior glabellar lobe (Fig. 6D, E, H, L). Such distribution pattern of FAls may indicate some limited taxonomic importance for FAls in Ordovician dalmanitids. It is also necessary to point out that, although the faint FAls are rarely preserved, at least one or more of the more conspicuous FAls (ali, abi, ami) have been observed in numerous specimens of Dalmanitina examined during this study. These more conspicuous marks form a polygonal field in which faint FAls are irregularly scattered. A comparable arrangement of deep and shallow FAls in a slightly modified form was discussed by Šnajdr (1987) and Budil et al. (2008, 2009) in Odontochile and Zlichovaspis (see also Richter 1923). At the anteriormedial tip of the glabella, a large impression (ami) was observed in about 70% of specimens of Dalmanitina. This large impression also belongs, most probably, to the same system (see also Barrande 1852, 1872). The posterior median impression (pmi) is characteristic of many other dalmanitids; e.g. Chattiaspis, Crozonaspis, Dalmanites, Daytonia, Eodalmanitina, Francovichia, Guichenia, Morgatia, and Zelischkella (see Henry 1965, 1968, 1980, 1989; Nion & Henry 1966; Henry & Morzade 1968; Wolfart 1968; Henry et al. 1974; Eldredge 1971; Robardet et al. 1972; Hammann 1972, 1974; Chatterton & Ludvigsen 2004; see also Lerosey-Aubril & Peel, 2018 and Gutiérrez-Marco et al. 2019).

In two articulated specimens of Dalmanitina [Fatka, unpublished data, specimens NM L 51954 (National Museum, Prague) and MB 1965.2.13 (Museum für Naturkunde, Berlin)], the anteriormost portion of the glabella collapsed while the hypostome was still in situ. This collapsed cavity clearly represents the space enclosed between the hypostome and dorsal exoskeleton rather than the remains of the crop (see Fatka et al. 2013 and Lerosey-Aubril & Peel 2018, p. 752, for similar interpretations). This is confirmed by the absence of a connection between this cavity and the remains of the digestive tract visible under the trunk axis as well as in the posterior portion of the glabella. In support of this, Fatka (unpublished data) concluded that in Dalmanitina, the crop occupied only the posterior portion of the frontal glabellar lobe (see Lerosey-Aubril & Peel 2018 and Wendruff et al. 2020).

The presence of characteristic FAls in some specimens of Dalmanitina clearly indicates the existence of strong extrinsic muscles connecting the foregut to the dorsal exoskeleton. Such morphology suggests possible differentiation of a well-developed crop. Both the presence of a crop in Dalmanitina and the fact that it did not occupy the whole cavity underneath the frontal glabellar lobe finds support in the recent illustration of specimens of an undescribed Silurian dalmanitid from the Waukesha Lagerstätte showing digestive structures, including a crop and paired digestive glands (Wendruff et al. 2020, figs 3d, f).

Conclusions

Study of twelve excellently preserved cephalic shields of Dalmanitina allows the recognition of prominent FAls in this taxon (pmi, ami, ali and abi) circumscribing an area bearing much fainter FAls. FAls in this taxon were only present on the visceral surface of the dorsal exoskeleton (glabellar frontal lobe). The configuration of FAls in Dalmanitina may vary from somewhat regular and triangular to irregular and somewhat oval in outline, questioning the use of the distribution patterns of FAls for taxonomic purposes. This supports the claim of Lerosey-Aubril & Peel (2018, p. 751) that the distribution pattern of FAls might be of limited use for study of phylogenetic relationships between major trilobite groups.

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