Two abnormal pygidia of the trilobite *Toxochasmops* from the Upper Ordovician of the Oslo Region, Norway

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Two pygidia of the trilobite *Toxochasmops* from the Upper Ordovician (Katian) of the Oslo Region, Norway, display different types of abnormalities. A juvenile pygidium, treated in open nomenclature as *Toxochasmops* sp. A, has a partially developed axial ring restricted to the right side of the axis which is interpreted as a teratology. The other pygidium, treated in open nomenclature as *Toxochasmops* sp. B, shows a local fusion of two pleural ribs with a poorly developed furrow crossing the fused area; this may either represent a teratology or regeneration after an injury. In the latter case, it could represent a rare example of metaplasia in trilobites with replacement of a pleural furrow by an interpleural furrow during regeneration. The posterior position of the partially developed axial rings, without corresponding pleural ribs, indicates that the posterior part of the axis possibly represents non-functional somites, and abnormalities in this part probably did not significantly affect the vital organs of the trilobite.

Keywords: Abnormalities, teratology, injury, metaplasia, *Toxochasmops*, trilobites, Katian, Ordovician, Oslo Region, Norway.

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Abnormalities and malformations potentially offer a unique insight into the palaeobiology and regenerative abilities of extinct animals, in this case the trilobites. Owen (1985) reviewed and categorised the abnormalities seen in fossil trilobites into three types based on their inferred causes: injuries, pathologies, and teratologies. Babcock (1993, 2007) extensively reviewed the literature on abnormalities in trilobites as well as the effects and causes of some of these. Injuries are generally interpreted as resulting from damage during ecdysis or through predation and are easiest identified by evidence of scars on the exoskeleton (Babcock 1993, p. 220). Pathologies such as swellings (neoplasms) and borings are caused by parasites and disease (e.g. Rushton 1967; Šnajdr 1978, 1981a). Teratologies are genetic or developmental abnormalities. They may be difficult to distinguish from the other types, but if evidence of injuries or pathologies is absent, an abnormal development may represent a teratology (Owen 1985). One phenomenon that is generally accepted as teratological in origin is the partial development of segments in the thorax or pygidium (e.g., see examples cited by Owen 1985; also see Owen & Tilsley 1996). According to Owen (1985), the tagma that most commonly shows teratological abnormalities is the pygidium, and some trilobite groups display a relatively high frequency of abnormal pygidial pleural ribs (Hughes 1969; Šnajdr 1990). Abnormalities in the marginal parts of the pygidium are much more common than in the axial region, which has been explained by a possible higher mortality rate for the latter defects (Owen 1985, p. 267).

The present study describes deformities in two pygidia assigned to the yet undescribed species *Toxochasmops* spp. A and B. The pygidia are part of a larger collection of Chasmopinae from the Oslo Region, Norway, housed at the Natural History Museum, Oslo (collection acronym PMO), and recently studied by the first author. The two specimens are from Katian (Upper Ordovician) strata in the Ringerike and Oslo–Asker districts.

Descriptions

***Toxochasmops* sp. A**
Figure 1A–B

Description: The pygidium (PMO 69440) is 12.8 mm long and represents a juvenile holaspid. The outline is triangular and the left half of the pygidium is normally developed with 17 axial rings (excluding terminal piece and anterior half-ring) and 16 clearly defined pleural ribs. On the right side, between the 15th and 16th axial ring, there is a partially developed ring with a slightly reniform shape that occupies about two-fifths of the axial width. The 15th axial furrow divides just beyond the sagittal line; its posterior branch is very shallow behind the adaxial part of the partially developed axial ring but deepens very abruptly distally to become of similar depth to the anterior branch. The six axial rings anterior to the partially developed ring show a stronger forward deflection abaxially on the right side relative to the left side, and, similarly, the posterior two rings show a stronger rearward deflection abaxially. The number of discernible pleural ribs is equal on both pleural areas and the pleural furrows show no irregularities.

Discussion: Reports of partially developed axial rings without associated disruptions of other parts of the pygidium are rare, but examples have been illustrated by Šnajdr (1981b, pl. 11, fig. 4) and Hahn *et al.* (1982, fig. 2). In the former case, the other axial rings are not significantly affected except for a bend in the posterior part of the axis. The latter case shows two partially developed axial rings in the posterior region where they are developed on each side of the sagittal line with two intervening fully developed S-shaped rings. The pleural regions do not seem to be particularly affected in either of these specimens. These abnormalities are unlikely to represent healed injuries as there is no indication of the highly irregular, radiating furrows suggestive of a 'point' injury such as those illustrated by e.g. Ormiston (1967, pl. 10, fig. 8) and Rudkin (1985, fig.1c, d). Partially developed axial rings were also described from a trilobite opistothorax by Pocock (1974). Here, two partially developed rings are present on each side of the sagittal line, both having corresponding pleural ribs, and most of the rings are disrupted to varying degrees. This specimen stands out from the other cases in being associated with a longitudinal fracture which was taken to indicate that the disruption was caused by an injury (Pocock 1974).

PMO 69440 lacks borings of any kind whilst the well-impressed furrows delimiting the axial ring suggest that the observed abnormality is not a neoplastic swelling, which could have indicated a parasitic origin. Hence, it is likely that the abnormality represents a teratological condition.

The partially developed axial ring in PMO 69440 shares some general features with the specimens described by Šnajdr (1981b) and Hahn *et al.* (1982), such as: 1) the partially developed axial rings appear to be fully developed at the abaxial margin; 2) they occur in the posterior region of the pygidium (post-apodemal sector); 3) the pleural region is not particularly affected in any of the specimens. The last mentioned feature may be related to the position of the abnormal axial ring in the posterior region. In contrast, two pygidia illustrated by Šnajdr (1981a, fig. 8) and Ebbestad (1999, fig. 82E), which have a laterally V-shaped dichotomy on the apodemal sector (fourth and first axial ring, respectively), both exhibit pleural ribs corresponding to the teratological axial rings. This is also the case in the opistothorax discussed by Pocock (1974). Likewise, the poorly developed right pleural region illustrated by Rushton (1967, fig. 2a) is also associated with the effacement of an axial rib, probably relating to a swelling on the first axial ring, which may represent a parasitic infestation (Owen 1985, p. 266).

The development of axial rings from the abaxial margin indicates that the primary mechanical function of the axial ring was positioned near the axial furrow, likely related to the apodemal pits (attachment of muscles). The posterior position (i.e. in the post-apodemal sector) of the partially developed axial rings in a couple of described specimens (present case; Šnajdr 1981b), without corresponding pleural ribs, suggests that the posterior part of the axis represents non-functional somites (cf. Hessler 1962) and thus such abnormalities may not have affected the vital organs of the trilobite.

Other types of reported abnormalities on the pygidial axis also include partially developed axial rings (Jell 1975, pl. 18, fig. 3; Evitt & Tripp 1977, pl. 11, fig. 11) but are found in association with more complex disruptions and are not relevant for comparison with PMO 69440.

***Toxochasmops* sp. B**
Figure 1C–D

Description: This subtriangular pygidium (PMO 64328) is 20.7 mm long and represents a late holaspis specimen. The axis has 15 rings (excluding terminal piece and anterior half-ring). The pleural region has 14 clearly defined pleural ribs with small scattered pits, weakly incised narrow interpleural furrows and wide, well-impressed pleural furrows. The 11th and 12th pleural ribs on the right side of the pygidium fuse near the axis and the pleural furrow is correspondingly effaced adaxially. The furrow is normally impressed for five-sevenths of its course. As the ribs merge, the pleural furrow is replaced by a narrow, rather poorly defined furrow similar in appearance to the interpleural furrows. The two pleural ribs diverge again close to the axial furrow, such that the pleural furrow is visible as a small indention (Fig. 1D). The furrow in

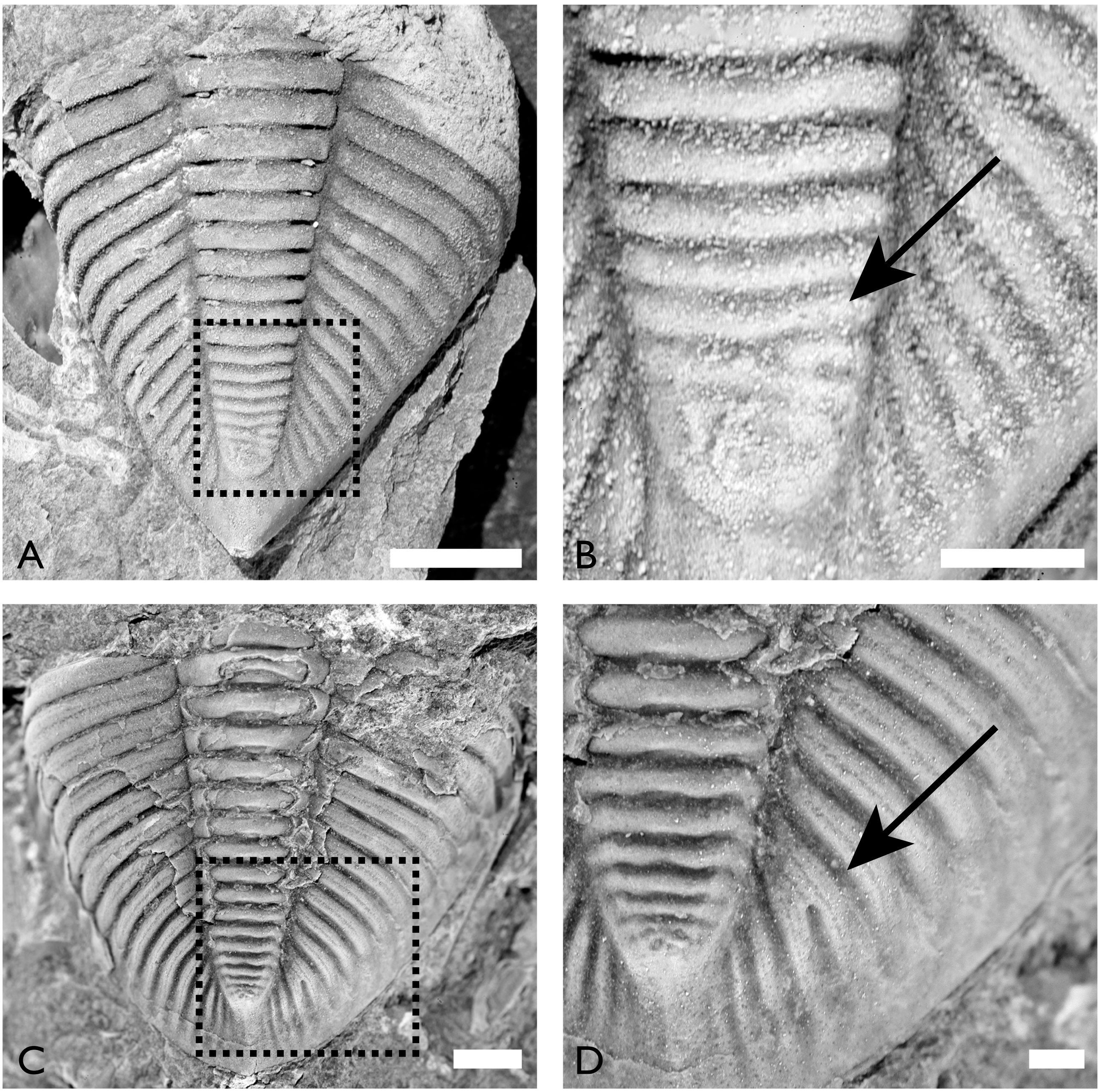

Fig. 1. **A**: *Toxochasmops* sp. A, pygidium displaying a partially developed axial ring between the 15th and 16th rings on the posterior right side of the axis. Nakkholmen Formation, Vestbråten, Ringerike district, PMO 69440. Scale bar 3 mm. **B**: Same specimen as in A, close-up of the posterior part of the axis showing the partially developed axial ring. Scale bar 1 mm. **C**: *Toxochasmops* sp. B, pygidium showing a local fusion of the 11th and 12th pleural ribs in the posterior part of the right pleural area. Solvang Formation, Kalvøya, Oslo–Asker district, PMO 64328. Scale bar 3 mm. **D**: Same specimen as in C, close-up of the fused area showing the replacement of the pleural furrow with a vague furrow resembling an interpleural furrow. Scale bar 1 mm. See Størmer (1953) for locations.

the fused area has a sinuous course broadly similar to that seen in the corresponding pleural area on the left side of the pygidium, and small pits are present on the adjacent area. The two ribs are slightly more inflated than their left counterparts, especially near the fusion.

Discussion: Fused pleural segments as seen in this specimen are much more common than the case discussed for *Toxochasmops* sp. A, although often associated with other types of abnormalities. The abnormality discussed here is distinguished from dichotomising ribs as the fusion is restricted to a local point between two fully developed adjacent ribs. Similar cases, albeit more severe, of locally fused pleural ribs on two pygidia of *Pseudogygites latimarginatus* were illustrated by Babcock (1993, fig. 3.3; 2007, fig. 2H) who surmised the abnormality to be of teratological origin. Kandemir & Lerosey-Aubril (2011, fig. 2) described a pygidium of *Ditomopyge*? sp. indet. showing a local fusion of the 7th and 8th pleural ribs in the left pleural region. They considered it most likely that the abnormality originated from a teratology. However, this fusion differs from the one seen in PMO 64328 in that the pleural furrow is totally absent in the fused area.

Injuries have previously been associated with alterations of the pleural ribs. Budil *et al.* (2010, fig. 3) illustrated a healed rib with a depression developed on the distal third of the rib. This was interpreted to represent a false 'pleural furrow' (*sic*), although it is uncertain whether it has appeared due to repair during subsequent moultings (Šnajdr 1981a, p. 51) or merely represents a depression reminiscent of a furrow caused by deformation.

Some fusions of pleural ribs have been attributed to 'point' injuries (e.g. Ormiston 1967, pl. 10, fig. 8; Rudkin 1985, fig.1c). These abnormalities have been interpreted to represent injuries during ecdysis, when the integument was soft and flexible. The areas of distortion are, however, relatively larger in the specimens described by Ormiston (1967, pl. 10, fig. 8) and Rudkin (1985, fig.1c), and tend to have an irregular appearance. If PMO 64328 represents a healed 'point' injury, the inflicted injury would have been very minor and probably not have caused significant damage outside the area of fusion. The presence of a vague furrow and pits in the fused area could suggest that the animal had repaired the area during several moultings following the injury. Šnajdr (1981a, figs 9, 10) argued that during this type of repair the injured surface would be reconstructed and its function stabilised during the course of subsequent moultings, as opposed to the more jagged appearance of early stage repairs (Ludvigsen 1977). If the abnormality in PMO 64328 indeed represents an injury, it is remarkable that the regeneration of the area has replaced the pleural furrow with a furrow of interpleural type. If so, this may represent a rare case of metaplasia, a process where one type of specialised cells is replaced by another (see Babcock 1993, p. 221). Metaplasia has not yet been determined unambiguously in trilobites but has been suggested for the anomalous development of spines as a response to injury (Babcock 2007, p. 9). It is, however, difficult to confidently determine whether the abnormality in PMO 64328 is a teratology or an injury.

Conclusions

Two pygidia of *Toxochasmops* from the Upper Ordovician (Katian) strata of the Oslo Region show two different types of abnormalities. The pygidium of *Toxochasmops* sp. A has a partially developed axial ring that likely represents a teratology. The pygidium of *Toxochasmops* sp. B displays a local fusion of two ribs. This abnormality may either represent a teratology or regeneration of a small injury. If the pleural furrow in this specimen was replaced by an interpleural furrow during the regeneration of an injury, it could represent a rare example of metaplasia in trilobites.

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