TWO NEW GENERA OF SILURIAN PHACOPID TRILOBITES

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ABSTRACT. *Delops* and *Struveria*, two new genera of trilobites, are defined. Certain species hitherto placed in the genus *Dalmanites* s.l. are referred to these genera and to the subfamily Zeliszkellinae Delo 1935. The evolutionary relationships are briefly discussed. The following are described: *Delops obtusicaudatus* (Salter), *D. nobilis nobilis* (Thomas), *D. n. marri* subsp. nov., and *Struveria howgillensis* sp. nov.

THE species *Delops obtusicaudatus* (Salter) was first recorded by Sedgwick (1845, p. 446) as *Asaphus caudatus*. Its phacopid affinities, however, were quickly appreciated by Salter (1849) and M'Coy (1851) who described it respectively as *Phacops obtusicaudatus* and *Phacops (Odontochile) obtusicaudata*. M'Coy (1851) was the first worker to figure the species. Salter, in his Monograph of British Trilobites (1864), provided further and better figures of the species under the name *Phacops (Odontochile) obtusicaudatus*. It is here considered the type of *Delops* gen. nov.

At this time the only known locality for this form was Coldwell Quarry in the Lake District but recordings from further afield were later made by Aveline (in Aveline and Hughes 1872, 1888) and Marr (1878). In this last paper Marr (pp. 883, 885) also recorded, and briefly described, *Phacops obtusicaudatus*, var. from the Upper Coldwell Beds. A specimen of this form, placed by Marr in the Sedgwick Museum, Cambridge (specimen number A38594), clearly shows that it is referable to *Dalmanites* s.s. Marr (1892, p. 537) recorded *P. obtusicaudatus* from Troutbeck (Lake District) and Helm Knott (south of Sedbergh) in addition to the type locality. Furthermore, he listed '*Phacops torvus* Wyatt-Edgell, M.S.' from Troutbeck and Helm Knott. The form which Marr recorded from Helm Knott as *P. obtusicaudatus* is conspecific with his '*Phacops torvus* Wyatt-Edgell, M.S.' and the two are here considered to form a new subspecies, *Delops nobilis marri*.

Thomas (1900) described *Phacops (Dalmania) nobilis* from the Wenlock Shale near Builth.

Following this date the Sedbergh forms received mention in several works. Thus, from Cautley (north of Sedbergh), Marr (1913, pp. 12, 17) recorded the following: *Phacops (Dalmannites) obtusicaudatus, Phacops (Dalmannites*?) sp. 1, and *Phacops (Dalmannites)* sp. 2. These forms are conspecific and also belong to the subspecies *D. nobilis marri* subsp. nov.

A form related to *Delops* gen. nov. and hitherto overlooked is described herein as *Struveria howgillensis* gen. et sp. nov.

The writer considers that *Delops* and *Struveria* show affinities with Zeliszkellinae Delo 1935. The glabellar lobation of *Struveria* is distinctly primitive and of the *Dalmanitina* type. *Struveria* is, therefore, placed alongside *Dalmanitina* and *Eudolatites* in the *Dalmanitina*-group of the Zeliszkellinae. In the case of *Delops* the frontal glabellar lobe when viewed from above transgresses the anterior cephalic border, a feature common

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in the Zeliszkellinae but absent in the Dalmanitinae. *Delops*, however, has a peculiar combination of biocharacters, some of which are typical of older genera and others of younger genera, which make its systematic emplacement more difficult. The glabellar lobation in particular distinguishes *Delops* from members of the *Dalmanitina*- and *Zeliszkella*-groups, and it is best considered as a separate group within the Zeliszkellinae. By contrast, the *Zeliszkella*-group contains two genera and the *Dalmanitina*-group three.

It is thought probable that *Delops* has been derived from a member of the *Dalmanitina*-group by the development of some typically Silurian and Devonian phacopid features and partial retention of earlier characters.

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Abbreviations associated with catalogue numbers of specimens are as follows: BM, British Museum (Nat. Hist.); SM, Sedgwick Museum; OUM, Oxford University Museum; HUR, Hull University, Rickards Collection.

SYSTEMATIC DESCRIPTIONS

Class trilobita Walch 1771 Order Phacopida Salter 1864 Family dalmanitidae Vogdes 1890 Subfamily zeliszkellinae Delo 1935 Delops-group nov.

Representatives. The group is monotypic.

Differential diagnosis. Distinguished from Zeliszkella-group by the frontal lobe protruding beyond the cephalic margin; by the prominent genal spines; by the relatively large pygidium and by the glabellar lobation. The large, centrally situated eyes, non-mucronate pygidium, and large genal spines distinguish the Delops-group from the Dalmanitina-group of the Zeliszkellinae.

Genus DELOPS gen. nov.

Type species. Phacops obtusicaudatus Salter 1849.

Other species. Delops nobilis nobilis (Thomas) and D. nobilis marri subsp. nov.

Derivation of name. In honour of D. M. Delo.

Diagnosis. Exoskeleton moderately large and tuberculate; cephalon semicircular in outline with prominent genal spines; border furrow well developed except anteriorly where it, and the margin, is transgressed by a swollen frontal lobe; eyes large, crescentic, close to glabella and extending from 3p to region of 1p furrows; glabella club-shaped, axial furrows moderately diverging, 1p furrows with traces of adaxial bifurcation; 2p furrows transversely straight, deep, but do not reach axial furrows, resulting in fusion of the 2p and 3p lobes; 3p furrows well defined, straight, diverging anteriorly; facial suture cuts

the lateral cephalic margin approximately opposite the 2p furrows; pygidium in the shape of an obtuse-angled isosceles triangle, non-mucronate, pygorachis strongly convex, nine to thirteen axial rings, six to nine pygidial pleurae; pygidial margin either entire or with slight lateral denticles seen both on internal and external moulds; doublure either rounded or flat.

Remarks. The peculiar association of biocharacters is sufficient to distinguish Delops from other described genera. Delops almost certainly represents a specialized late offshoot from the Dalmanitina-group. It differs from Dalmanitina (Dalmanitina), D. (Chattiaspis), and Eudolatites in the lobation of the glabella. Thus in D. (Chattiaspis) the frontal lobe is contained within the cephalic margin, whilst in D. (Dalmanitina) the adaxial bifurcation of the 1p grooves and the convergence of the 1p and 2p grooves is more pronounced than in Delops. In both D. (Dalmanitina) and Eudolatites the axial furrows widen more prominently than in Delops where they are slightly re-entrant at the 3p grooves. Delops has deeper 3p furrows than Eudolatites in which the frontal lobe is scarcely detached from the central area. There are superficial resemblances to several other genera, but the complete lack of an anterior border makes for easy distinction from Dalmanites and Odontochile, whilst the pygidial characters are quite unlike any of the Dalmanitinae. Some of the later genera such as Greenops, Neometacanthus, &c., have similar posterior lobation of the glabella but the nature of the frontal lobe in Delops, as well as the unusual pygidium, is sufficient to distinguish it from these forms.

Delops obtusicaudatus (Salter 1849)

Plate 84, figs. 1, 2

1845 Asaphus caudatus Sedgwick, p. 446.

1849 Phacops obtusicaudatus Salter, p. 7.

1851 Phacops (Odontochile) obtusi-caudata Salt. sp.; M'Coy in Sedgwick and M'Coy, p. 161, pl. 1G, figs. 15, 16.

1852 Phacops (Odontochile) obtusicaudatus Salter; Salter in Sedgwick and M'Coy, appendix A, p. ii.

1864 Phacops (Odontochile) obtusicaudatus Salter; Salter, pp. 45-46, pl. 1, figs. 42-45.

Lectotype (here selected). Headshield figured by M'Coy 1851, pl. 16, fig. 15 and refigured herein as Plate 84, fig. 1. The specimen is now housed in the Sedgwick Museum, Cambridge, SM A38682.

Horizon and locality of lectotype. Coldwell Beds, Coldwell, Westmorland.

Dimensions of lectotype. Length of glabella 15 mm.; max. width, glabella 13 mm., postero-lateral cephalic margin 15 mm.

Other material. Specimens in Sedgwick Museum, Geological Survey Museum, British Museum (Nat. Hist.).

Horizon and localities. Middle Coldwell Beds, Upper Coldwell Beds, Lake District; Coldwell Quarry; west of Hundreds Road, near Skelgill; Troutbeck, Westmorland; Coniston, Lancashire.

Diagnosis. Exoskeleton moderately large, tuberculate, and with a prominent doublure; cephalon semicircular, anterior border interrupted by protruding frontal glabellar lobe, genal spines present, border furrow well developed except anteriorly; eyes large, crescentic, lensed surface extending from anterior-most part of 3p lobes to midway between 2p and 1p furrows; cephalic axial furrows widen steadily from occipital ring;

1p, 2p, and 3p lobes graduated and increasing in size anteriorly, 2p and 3p lobes fused abaxially so that 2p furrows do not reach axial furrows; frontal lobe large, swollen, protruding beyond anterior cephalic margin, with a posteriorly positioned pit; whole cephalon ornamented with coarse tubercles; pygidium relatively large, well segmented, pygorachis with eleven to thirteen axial rings, and pleural regions with nine pleurae; pygidial margin entire and doublure rounded.

Description. The cephalon is approximately semicircular in outline, moderately convex, and has free cheeks which slope steeply to the prominent border.

The genal spines are relatively short, reaching a length equal to about half that of the glabella. Both the cephalic margin and the border furrow are transgressed by the frontal lobe of the glabella, but otherwise the border is a distinctive feature and is ornamented by the same kind of large tubercles as the rest of the cephalon. Details of these tubercles are not easily ascertained since they are usually 'streaked out'. The eyes are large and similar to those in *Dalmanites* but are not as centrally situated on the cheeks and are positioned rather more anteriorly. The posterior branch of the facial suture is directed towards the lateral cephalic margin which it cuts at a level midway between the 2p and 3p furrows.

A distinctive feature of *D. obtusicaudatus* is the glabellar lobation. Owing to compression the fusion of the 2p and 3p lobes is only occasionally seen, but the gradation in size from the 1p to 3p lobes is always discernible. The 1p and 2p lobes are quadrangular and the 3p lobes triangular. The 3p furrows diverge anteriorly and bound the swollen frontal lobe. In most of the specimens examined the frontal lobe just transgresses the frontal cephalic margin but the nature of preservation often makes it difficult to assess the part played by distortion. The frontal lobe is collapsed in several instances, and in some of these cases the anterior cephalic margin is visible from above.

Thoracic segments have not been seen.

The pygidium is relatively large, has eleven to thirteen rings on the pygorachis, and about nine pleurae in each of the pygidial pleural fields. Both pleural and interpleural furrows are well developed. An important feature of the pygidium is the entire margin and rounded doublure (see Pl. 84, figs. 2a, b). At the anterior end the pygorachis is approximately one-third of the total width of the pygidium, and its posterior extremity reaches to the margin. None of the specimens examined show any signs of tuberculation

EXPLANATION OF PLATE 84

All specimens whitened with magnesium oxide and all except fig. 2 illuminated from top left.

Figs. 1-2. Delops obtusicaudatus (Salter), Coldwell Beds, Coldwell, Westmorland. 1, Lectotype, SM A38682, internal mould of incomplete cephalon, figured by M'Coy (1851), pl. 1G, fig. 15, $\times 2\frac{1}{2}$. 2a, BM In55901, latex cast of external mould of small, compressed pygidium, showing narrow border, illumination from top right, $\times 2\frac{1}{2}$. 2b, BM In55901, latex cast of external mould of doublure showing broad and rounded nature, illuminated from top right, $\times 2\frac{1}{2}$.

Figs. 3-7. Delops nobilis marri subsp. nov. 3, Holotype, HUR/1D/384, internal mould of almost undistorted cephalon, Cautley, NW. Yorkshire, ×2½. 4, Paratype, SM A38678, Helm Knott, near Sedbergh, NW. Yorkshire; internal mould of well-preserved cephalon, ×2½. 5, Paratype, HUR/1D/6, Cautley, NW. Yorkshire; internal mould of part of cephalon showing glabellar lobation, ×2½. 6, Paratype, HUR/1D/177, Cautley, NW. Yorkshire; latex cast of external mould of pygidium, ×2·1. 7, Paratype, HUR/1D/177a, Cautley, NW. Yorkshire; internal mould of almost complete pygidium, ×2½.

upon either internal or external moulds of the pygidium and may be contrasted in this respect with the cephalon which, in spite of its generally poor preservation, shows the tubercles. This suggests that lack of tubercles on the pygidium is not merely a result of their obliteration by compression. There are nine pygidial pleurae of which the anteriormost five closely correspond to the rings on the pygorachis. Both the pleural and interpleural furrows are well developed and extend to the narrow border of the pygidium.

Remarks. D. obtusicaudatus does not seem to occur outside the Lake District, and the headshields obtained from Coldwell, &c., and contained in the various museums, are not well preserved. Nevertheless, the general pattern of a coarsely tuberculate semicircular cephalon can usually be ascertained and in occasional better-preserved specimens the nature of the various biocharacters can be seen.

The specimen originally figured by M'Coy (1851, pl. 1G, fig. 15), and designated here as the lectotype, was not included by Salter in his 1873 catalogue of the fossils contained in the then Cambridge Museum. As a result the fossil was missing for many years and in fact was only found by Dr. Forbes and the writer in 1963. The pygidium figured at the same time as the headshield could not be found and it may be either a composite drawing or an idealized drawing.

Delops nobilis nobilis (Thomas)

Plate 85, figs. 7, 10

1900 Phacops (Dalmania) nobilis Thomas, pp. 617-18, pl. 34, figs. 1-3.

Holotype. The specimen figured by Thomas (1900), pl. 34, fig. 1, now housed in the Oxford University Museum, specimen number C24–25, and refigured herein as Plate 85, figs. 7 and 10; internal and external moulds of almost complete specimen.

Dimensions of holotype. Length of glabella 25 mm.; approximate width of cephalon 38 mm.

Horizon and locality of holotype. Wenlock Shales, 1 mile east of Builth, 150 yards from bank of R. Wye. Other material. Specimens in the University Museum, Oxford.

Diagnosis. Exoskeleton moderately large, tuberculate, and with a prominent, rounded doublure; cephalon semicircular, anterior border interrupted by protruding frontal glabellar lobe, border furrow well developed except anteriorly; eyes large, crescentic, extending from top of 3p lobes to midway between 1p furrows and occipital furrow; cephalic axial furrows widen steadily to top of 3p lobes and then widen more rapidly to produce a club-shaped glabella; 1p, 2p, and 3p lobes graduated and increasing in size anteriorly, 2p and 3p lobes abaxially fused so that 2p furrows do not reach axial furrows; frontal lobe large, swollen, protruding beyond anterior cephalic margin, with a posteriorly positioned pit; whole cephalon ornamented with coarse tubercles elongated parallel to length of fossil; pygidium well segmented, pygorachis with nine to eleven axial rings; pygidial margin showing faint tendency to denticulation of the anterior-most segment.

Description. This species was thoroughly described and reconstructed by Thomas and it remains only to note that the 2p furrows do not extend to the axial furrows as depicted by him (pl. 34, fig. 3). This interpretation is clearly based upon the holotype, which has the 2p furrow crushed. Other specimens contained in the University Museum, Oxford

(e.g. C558), show the deep 2p furrows typical of *Delops* which fade out before the axial furrows are reached. Finally, the pygidia examined by the writer show a slight denticulation of the anterior-most pleural segment of the pygidium.

Remarks. Delops nobilis nobilis differs from D. obtusicaudatus mainly on the characters of the pygidium, which in the case of the former species has fewer axial rings, a denticulation of the margin, and numerous tubercles similar to those on the rest of the exoskeleton.

Delops nobilis marri subsp. nov.

Plate 84, figs. 3-7; Plate 85, figs. 8, 9; text-fig. 1a

1892 Phacops torvus Wyatt-Edgell, M.S.; Marr, p. 537.

- ?1911 Phacops obtusicaudatus Watney and Welch, pp. 217, 223, 227, 228, 234.
- 1913 Phacops (D.) obtusicaudatus Marr, pp. 12, 17.
- 1913 Phacops (Dalmannites?) sp. 1, Marr, p. 17.
- 1913 Phacops (Dalmannites) sp. 2, Marr, p. 17.

Holotype. HUR/1D/384, the headshield figured on Plate 84, fig. 3, internal mould of almost complete cephalon.

Dimensions of holotype. Width of cephalon 35 mm.; length of glabella 19 mm.; max. width of glabella 16 mm.

Horizon and locality of holotype. Basal Ludlow limestone, Zone of nilssoni-scanicus, Bluecaster.

Horizon. Rare in the top few feet of the Brathay Flags (Wenlock Series) and common in the bipartite limestone immediately overlying the Brathay Flags; rare in the Upper and Middle Coldwell Beds of

Localities. Bluecaster, and mouth of Backside Beck, Cautley, north of Sedbergh; Troutbeck, Westmor-

Material. Over 100 specimens.

Diagnosis. Exoskeleton moderately large with a flattened doublure; cephalon semicircular, anterior border interrupted by protruding frontal glabellar lobe; genal spines long and robust; border furrow well developed except anteriorly; occipital ring with mesial tubercle; eyes large, crescentic, extending from top of 3p lobes to 1p grooves; cephalic axial furrows widen steadily from occipital ring; 1p, 2p, and 3p lobes graduated

EXPLANATION OF PLATE 85

All specimens whitened with magnesium oxide.

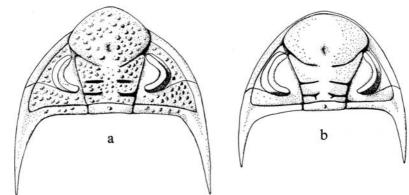
Figs. 1-6. Struveria howgillensis sp. nov. Cautley, NW. Yorkshire. 1, Holotype, HUR/1D/260, latex cast of external mould, ×2½. 2, Paratype, HUR/1D/1, latex cast of external mould showing frontal cephalic margin, $\times 2\frac{1}{2}$. 3, Paratype, HUR/1D/208, internal mould of headshield of young specimen, $\times 2\frac{1}{2}$. 4, Paratype, HUR/1D/161a, internal mould of somewhat flattened pygidium, $\times 2\frac{1}{2}$. 5, Paratype, HUR/1D/383, almost undistorted pygidium, internal mould, $\times 2\frac{1}{2}$. 6, Paratype, HUR/1D/197, internal mould of small, compressed pygidium, $\times 2\frac{1}{2}$

Figs. 7, 10. Delops nobilis nobilis (Thomas). 1 mile east of Builth. 7, Holotype, OUM C25, latex cast of external mould of almost complete well-preserved specimen, ×1. 10, Holotype, OUM C24,

counterpart of OUM C25, internal mould of part of thorax and cephalon, ×1.

Figs. 8, 9. Delops nobilis marri subsp. nov. Cautley, NW. Yorkshire. 8, Paratype, HUR/1D/19, internal mould of small cephalon, ×2½. 9, Paratype, HUR/1D/7, latex cast of external mould of glabella of a young specimen showing nature of tuberculation, $\times 2\frac{1}{2}$.

and increasing in size anteriorly, 2p and 3p lobes fused abaxially so that 2p furrows do not reach axial furrows; frontal lobe large, swollen, protruding beyond the cephalic margin, and having a posteriorly positioned pit; whole cephalon ornamented with large tubercles interspaced with more numerous smaller ones; pygidium tuberculate, pygorachis with nine to ten axial rings and pleural regions with six to eight pleurae; pygidium margin showing at least three lateral denticles, doublure flat; hypostome tuberculate, with three denticles along posterior margin, anterior wings and maculae similar to *Chattiaspis*.



TEXT-FIG. 1. a, Delops nobilis marri gen. et subsp. nov.; reconstruction of cephalon, approx. ×1·5. b, Struveria howgillensis gen. et sp. nov.; reconstruction of cephalon, approx. ×1·5.

Description. In all its biocharacters the subspecies marri differs only in relative proportions from the type subspecies. The cephalon is of similar shape and size but the eyes are situated rather more anteriorly than in nobilis s.s. and extend from the top of the 3p lobes to the level of the 1p furrows. In nobilis s.s. the frontal lobe is more swollen than in marri and thus the axial furrows widen steadily in the latter, but the rate of widening increases suddenly after the 3p lobes in the former. The tubercles are rounded and not elongated parallel to the axis as in the case of the type subspecies.

The pygidium has nine or ten axial rings but no specimens have been found having eleven axial rings. In the cases of those specimens with eight pygidial pleurae the anterior-most five correspond with axial rings. The interpleural furrows reach the pygidial margin whilst the pleural furrows reach only three-quarters of the way to the margin. The denticulation of the anterior pygidial margin is a distinctive feature of the subspecies, there being three distinct denticles and other less distinct ones posteriorly. As in *nobilis* s.s. the doublure is broad but in *marri* it is flat and not rounded.

Remarks. The headshields and pygidia from the Howgill Fells described here as D. n. marri are regarded as conspecific on the grounds of identical ornamentation and association, in the absence of other ornamented forms. Marr (1913) recorded P. obtusicaudatus from the same beds but all the specimens collected by the writer, together with those examined in museum collections, show that only one tuberculate phacopid occurs at this horizon in the Howgill Fells. The forms listed by Marr (1892, pp. 537, 538) as

Phacops torvus (respectively SM A38617 and A38596) are conspecific with his specimens briefly described as P. (Dalmannites?) sp. 1 and P. (Dalmannites) sp. 2 (Marr 1913, p. 17) and which are now contained in the Sedgwick Museum, Cambridge (respectively numbers A38995a-b and A38996). The Sedgwick Museum specimens show, therefore, that D. n. marri occurs in the Troutbeck area as well as in the Howgill Fells. Of P. (Dalmannites) sp. 2 Marr wrote: 'A form was recorded by me from the Obtusicaudatus Beds of Lakeland, under the name Ph. torvus Wyatt-Edgell. This form is common at Narthwaite. I cannot find the specimen of Ph. torvus of Wyatt-Edgell which led me to make this identification.' In view of this doubt concerning the nature of Wyatt-Edgell's original specimen it is better to adopt a different specific name and for this reason marri is used here. D. n. marri differs from D. obtusicaudatus mainly in the characters of the pygidium. In the former case the pygidium has a denticulate margin, a broad, but flat doublure, and only nine to ten axial rings on the pygorachis, whilst the latter has an entire pygidial margin, a broad, rounded doublure, and eleven to thirteen axial rings on the pygorachis. D. n. marri is the form from Sedbergh usually listed as P. obtusicaudatus, but as has been shown it differs from this species and has closer affinities with P. nobilis Thomas.

All the forms of *Delops* described in this work are found in impure limestones. *D. n. marri* is absent, in the Howgill Fells, from the graptolitic mudstones immediately above and below, except at one locality where these are unusually calcareous and where a single specimen has been obtained. By contrast, the subspecies is extremely abundant in the basal limestones of the Ludlow Series (*nilssoni-scanicus Zone*) where it occurs with *Struveria howgillensis*, *Miraspis* sp., *Decoroproetus* sp., and *Encrinurus* sp.

Dalmanitina-group Genus Struveria gen. nov.

Type and only known species. Struveria howgillensis sp. nov. Derivation of name. In honour of W. Struve.

Diagnosis. Cephalon semicircular, genal spines long and robust; border furrow distinct but unlike cephalic margin does not pass in front of frontal glabellar lobe; eyes large and positioned near the antero-lateral border furrow; posterior branch of facial suture cuts lateral cephalic margin opposite 2p furrows, and anterior portion can be seen passing round front of glabella in suitably preserved specimens; glabellar lobation very similar to Dalmanitina (Dalmanitina), D. (Chattiaspis) and Eudolatites with 1p furrows adaxially bifurcating; 1p and 2p furrows converge towards axial furrows; axial furrows only slightly divergent until 2p furrows reached when they flare suddenly to produce a club-shaped glabella; 1p and 2p lobes of similar size but 3p lobes much larger and frontal lobe dominant, but not transgressing anterior cephalic margin; pygidium relatively large, moderately convex, very similar to Eudolatites, margin entire, non-mucronate; nine to ten (? eleven) axial rings on pygorachis, seven or eight pygidial pleurae.

Remarks. From Dalmanites and Odontochile, Struveria can be distinguished on the characters of both the pygidium and cephalon. It lacks the ornate cephalic features of the other genera in the Dalmanitinae. Struveria differs from Dalmanitina (Dalmanitina) in having larger eyes, a non-mucronate pygidium and in having the whole of its frontal lobe contained within the cephalic margin. The glabella of Dalmanitina (Chattiaspis) is

not club-shaped and the pygidium is mucronate. The pygidium of *Struveria* is very similar in appearance to that of *Eudolatites* but has a smaller number of axial rings and pleural segments. The glabellae of the two genera are also similar in general shape but the frontal lobe of *Eudolatites* transgresses the anterior cephalic margin. In spite of these differences the writer considers that *Eudolatites* Delo is the closest genus. If there is a tendency in later representatives of the Dalmanitidae to enclose the frontal lobe within the anterior border of the cephalon then it is conceivable that *Struveria* has evolved from *Eudolatites*, which ranges from the Ordovician to ? Middle Silurian. Such a change would also involve a fall in the number of pygorachial segments from a minimum of eleven (in *Eudolatites*) to nine or ten.

Struveria howgillensis gen. et sp. nov.

Plate 85, figs. 1-6; text-fig. 1b

Holotype. HUR/1D/260 and 260a, internal and external moulds of almost complete cephalon; latex cast of external mould figured (Pl. 85, fig. 1).

Dimensions of holotype. Width of cephalon 30 mm.; length of glabella 13 mm.; max. width of glabella 15 mm.

Horizon of holotype. Basal Ludlow limestone, Zone of nilssoni-scanicus.

Locality. Bluecaster, Cautley.

Material. Over 100 headshields and pygidia.

Horizon and localities. Restricted to the bipartite basal Ludlow limestone, Zone of nilssoni-scanicus; Bluecaster; mouth of Backside Beck; north of Sedbergh.

Diagnosis. As for genus.

Description. The cephalic outline varies somewhat with the direction of compression but is approximately semicircular, with prominent genal spines which are only occasionally longer than the glabella. Immediately in front of the glabella the border is extremely narrow and only rarely can the facial suture be traced in this region (Pl. 85, fig. 2). Large crescentic eyes and palpebral lobes dominate the cheeks. The eyes extend from the most anterior point of the 3p lobes almost down to the level of the 1p furrows, whilst the posterior branch of the facial suture extends in an anterior direction along the base of the sub-vertical lensed surface of the eye to a point level with the 2p furrows, and then curves outwards in an anteriorly convex curve to cut the lateral margin of the cephalon almost opposite the 2p furrows.

The axial furrows diverge only slightly from the occipital groove to the 2p furrows but then diverge strongly, bounding a swollen frontal lobe, and giving the whole glabella a club-shaped appearance. Adaxial bifurcation of the 1p grooves is shown by most of the specimens and in some instances is accentuated by compression (Pl. 85, fig. 1). A more typical instance is shown by the specimen figured on Plate 85, fig. 3. Convergence of the 1p and 2p furrows is usually detectable (Pl. 85, figs. 1–3). The 3p furrows are not straight but convex posteriorly, thus giving a subtriangular shape to the 3p lobes. The sharp contrast in size between the 3p lobes on the one hand, and the 1p and 2p lobes on the other, also serves to distinguish *S. howgillensis* from species included in the Dalmanitinae. The frontal lobe is transversely elliptical in outline. In

neither transverse nor sagittal sections is it strongly convex, whilst most specimens show a shallow pit situated on the sagittal line in a posterior position. The occipital ring is of the same convexity as the glabella except for the presence of a mesial tubercle.

Only fragments of thoracic segments have been found in association with the headshields and pygidia and they are not sufficiently well preserved to warrant description.

The pygidium is relatively large with an entire margin completely devoid of spines or protuberances whilst the broad pygorachis does not reach the posterior margin. Nine or ten axial rings are usually present and possibly eleven in some specimens. At its widest point the pygorachis occupies fractionally less than one-third of the maximum width of the pygidium. Seven or eight pleurae are developed, each with a distinct pleural groove which, however, does not reach as far towards the border as the interpleural furrows. The interpleural furrows reach the pygidial margin.

Hypostomata obtained in association with S. howgillensis are similar to the hypostome of Chattiaspis except that three posterior denticles are developed.

Remarks. The club-shaped glabella and slight convergence of the 1p and 2p furrows are features typical of the Dalmanitina-group of the Zeliszkellinae. The whole appearance of the pygidium, and particularly of the axis, is reminiscent of some species of Dalmanites, but is distinct in having fewer axial rings and more pygopleurae. S. howgillensis is a more common fossil than D. nobilis marri, which occurs at the same horizon, but unlike this latter species has not been obtained from the Wenlock Series.

EVOLUTIONARY NOTES

Thomas (1900) records *D. n. nobilis* from the Wenlock Shales of Builth and the specimens contained in the Oxford Museum are labelled '1 ml. E. of Builth, 150 yards from bank of Wye'. This locality is almost certainly in the Wenlock Shales and may be in the Zone of *C. lundgreni* (Elles 1900, fig. 4, p. 385). *D. n. marri* first appears rarely in the top few feet of the Wenlock Series in beds yielding *Monograptus flemingii* (Salter) (common), *M. pseudodubius* Bouček and *Gothograptus nassa* (Wood). It is, however, extremely common at the base of the Ludlow Series where it occurs in two thin, impure limestones separated by a 4-foot thick bed of non-calcareous graptolitic mudstone.

The graptolitic mudstone yields the following fauna, which is indicative of the nilssoni-scanicus Zone: Monograptus nilssoni (Barrande), M. scanicus Tullberg, M. chimaera (Barrande), M. c. salweyi (Lapworth), M. colonus compactus Wood, M. varians Wood, M. vicinus Perner.

Thus, whilst *D. n. nobilis* and *D. n. marri* are separated geographically, the latter also occurs at a higher stratigraphical level. In view of the similarities between the two forms it is likely that *marri* has evolved directly from *nobilis* by an increase in the denticulation of the pygidial margin from slightly denticulate to prominently so, and by a change in shape of the doublure.

The exact relationship of *D. obtusicaudatus* to *D. nobilis* is not certain. If there is a tendency to increased denticulation of the pygidial margin then the former species may represent a survival into the Ludlow Series of the root stock from which *D. nobilis* sprang and in which basic changes are taking place in the pygidia.

Struve (1959, p. 0475) considers that 'with little doubt the Dalmanitinae are descendants of the Dalmanitina-group of the Zeliszkellinae'. If this is the case there has been

a change in the size and position of the eyes, a tendency to enclose the frontal lobe of the glabella within the cephalic margin, an increase in the size of the genal spines and a modification of the glabellar furrows. The *Delops*-group may be regarded as a descendant of the *Dalmanitina*-group in which only a few of these tendencies have become manifested. Thus whilst the 1p furrows retain traces of the adaxial bifurcation typical of members of the Zeliszkellinae, the 2p furrows have become modified and do not reach the axial furrows. Similarly the frontal lobe protrudes beyond the anterior border, but the eyes have become large and have moved away from the anterior border furrow to a more central position.

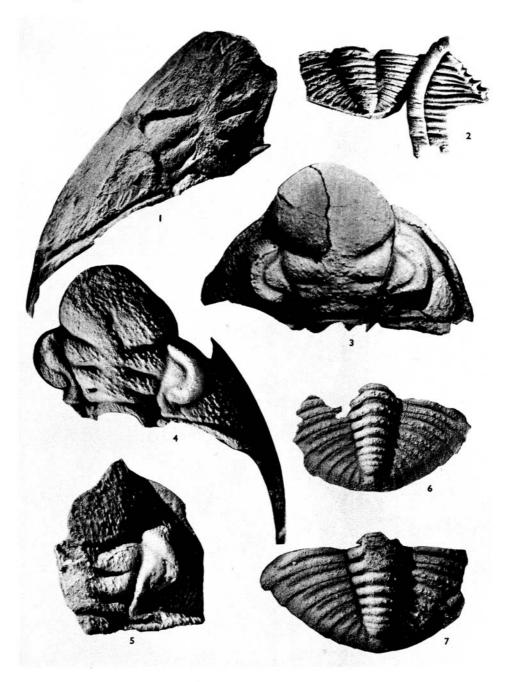
Struveria is a later representative of the Dalmanitina-group reflecting the same tendencies which resulted in Delops but to a degree which merits its retention in the Dalmanitina-group. Thus both the eyes and genal spines are large and more typical of the Dalmanitinae but in other and more fundamental characters, such as glabellar lobation, the genus is typically zeliszkellinid.

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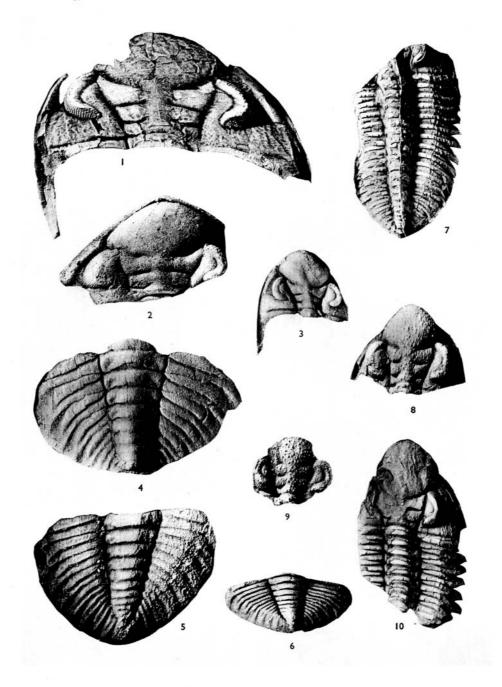
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