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A REAPPRAISAL OF THE NORTH AMERICAN SPECIES OF THE SILURO-DEVONIAN TRILOBITE GENUS *SCOTIELLA*

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ABSTRACT

The type material of *Scotiella* Delo 1935 is redescribed and the generic diagnosis emended to include trilobites in which the anterior and median lateral glabellar furrows are both strongly and poorly defined. The genus now embraces the species *Scotiella logani* (Hall 1860), ***S. conservatrix*** (McLearn 1924) new combination, *S. minor* (M'Coy 1851), *S. samsonowiczi* Tomczykowa 1962b and *S. opatowiensis* Tomczykowa 1962b. *Scotiella obsoleta* Ulrich and Delo 1940 is reclassified as ***Kloucekia (Kloucekia) obsoleta*** new combination.

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Introduction

The genus *Scotiella* Delo 1935 has a geographical distribution which extends from Nova Scotia across the Atlantic to Poland. It is of importance in that it has a limited stratigraphical range, being confined to the passage beds between the Silurian and Devonian Systems.

The species now referred to *Scotiella* show considerable variation in characteristics associated with the furrowing of the glabella and pygidium and with the axial structures of the latter. These variations have been incorporated into an emended generic diagnosis.

Scotiella is closely related to *Acastella* Reed 1925, a genus existing contemporaneously during the late Silurian and early Devonian in northwest Europe. *Scotiella* is differentiated on the character complex diagnosed below. Trends found in *Scotiella,* but not in *Acastella,* include a tendency towards obsolescence of the anterior glabellar furrowing and a mesial interruption of the posterior axial rings of the pygidium. The similarities between *Scotiella* and *Acastella* suggest a common ancestry which may be found in *Acaste* Goldfuss 1843.

During the research necessary for this short paper I have had the opportunity to study at first hand types and other specimens from collections in the Peabody Museum of Natural History, Yale University, New Haven, Connecticut; plaster casts of type specimens from the collections of the Geological Survey of Canada, Ottawa; material recently collected from the type section at Arisaig, Nova Scotia, by Professor A. J. Boucot, Division of Geological Sciences, California Institute of Technology, Pasadena, California; and also material deposited in the collections of the Geological Institute, Warsaw, from approximately contemporaneous strata in Poland.

In the following text YPM indicates specimens from the collections of the Peabody Museum of Natural History; GSC those from the Geological Survey of Canada and USNM those from the U.S. National Museum, Washington.

When referring to the morphogenesis of the species considered the terms "early" and "late" holaspid are constantly mentioned. These terms are applied to differentiate the smallest and largest groups of holaspid instars. In the Acastinae and related trilobites

the smallest (earliest) holaspides frequently possess genal and caudal mucronations which may be resorbed during the succession of holaspid instars. The largest (latest) holaspides, the adults of the species, may be completely non-mucronate, e.g. the development of *Acastocephala macrops* (Salter 1864) (see Shergold, 1966).

The species primarily concerned in this paper were originally described by Hall (1860, pp. 156-7) as *Dalmania logani* and referred to *Dalmanitina logani* (Hall) and *D. logani* (Hall) var. *conservatrix* by McLearn (1918a, 1918b, 1924). The genus *Scotiella* was erected by Delo (1935, p. 409) with *Dalmania logani* (Hall) as the type species.

Systematic Descriptions

family DALMANITIDAE Vogdes 1890
subfamily ACASTINAE Delo 1935
genus *SCOTIELLA* Delo 1935

TYPE SPECIES. *Dalmania logani* Hall, 1860, p. 156, text-fig. 18.

OTHER SPECIES. *Scotiella conservatrix* (McLearn 1924) (McLearn, 1918a, p. 33; 1918b, p. 129; 1924, p. 168, pl. XXVII, figs. 1, 2, 5). *Scotiella samsonowiczi* Tomczykowa 1962 (Tomczykowa, 1962b, pp. 193-5, pl. XXXIV, figs. 1-6, pl. XXXV, fig. 2). *Scotiella opatowiensis* Tomczykowa 1962 (Tomczykowa, 1962b, pp. 195-6, pl. XXXIV, figs. 7-9, pl. XXXV, figs. 1, 3). *Scotiella minor* (M'Coy 1851) (M'Coy, 1851, p. 161 and Shergold, 1967, pl. 25, figs. 1-3). *Scotiella* cf. *minor* (M'Coy 1851) (Shergold, 1967, pl. 24, figs. 9-11).

AGE. Late Silurian to early Devonian

DISTRIBUTION. North America: Nova Scotia, Arisaig coast sections (Moydart Formation, Stonehouse Formation, zones a-c, common in zone c). North West Europe: Poland, Holy Cross Mountains (Rzepin Beds); United Kingdom, Westmorland (Kirkby Moor Flags) and Prior's Frome, Herefordshire (?Downtonian, basal Rushall Beds).

EMENDED DIAGNOSIS. *Scotiella* is defined by an association of characteristics some of which are shared with other Acastinae but

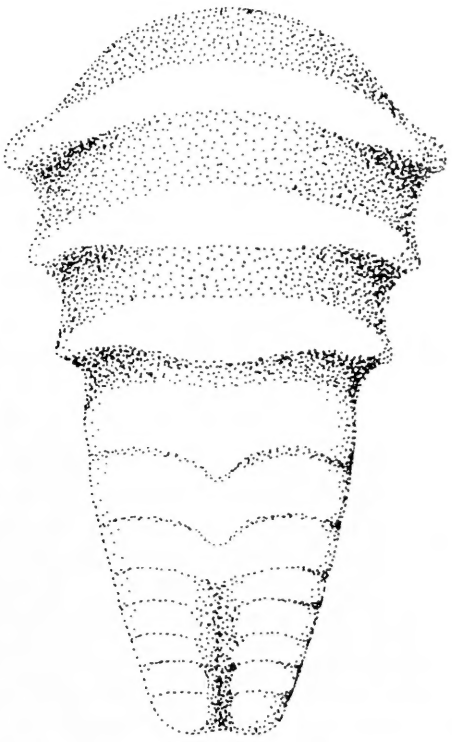
which differ in degree. The following are deemed diagnostic: glabellar furrows incised to varying depths, there being apparent gradations between species with well-defined furrows and those in which the anterior and median lateral furrows are faint or obsolescent; convexities of associated lateral side lobes correspondingly variable; preoccipital lobes approximately one-fourth as wide (exsagittal) as median lateral lobes; a narrow (transverse), upraised, longitudinal glabellar ridge flanked by shallow depressions joining anterior lateral and preoccipital furrows always present but varyingly distinct; long genal spines in young holaspides, short spinules in adults; pygidium with five to six strongly furrowed pleural segments, up to 11 axial rings; posterior axial rings may be uniformly entire throughout morphogenesis or mesially interrupted in the adults; margin entire in late holaspides, possibly denticulate on the shell of early holaspides; short, delicate, often inflected, caudal spinule, as in *Acastella*.

RELATIONSHIPS. In emending the diagnosis of *Scotiella* an attempt has been made to bring the genus into direct comparison with *Acastella*. It seems most closely related to those species of *Acastella*, similar to *A. spinosa* (Salter 1864), the type species, which have non-denticulate late holaspid pygidial margins. Species of *Scotiella* may be readily distinguished from those of the *Acastella spinosa* species-group by their longer glabellar furrows, reduced preglabellar furrow and shorter genal mucronations.

Scotiella conservatrix (McLearn 1924) new combination
pl. 1, figs. 1-7, text-fig. 1.

Dalmanitina logani var. *conservatrix*, n. var.; McLearn, 1918a, p. 33 (*nomen nudum*).
Dalmanitina logani var. *conservatrix*, n. var.; McLearn, 1918b, p. 129 (*nomen nudum*).
Dalmanitina logani var. *conservatrix* McLearn; McLearn, 1924, p, 168, pl. XXVII, figs. 1 (YPM 472), 2 (GSC 5999).
Dalmanitina logani (Hall); McLearn, 1924, pl. XXVII, fig. 5 (GSC 5998).
Scotiella logani var. *conservatrix* (McLearn, 1918); Delo, 1940, p. 34, pl. 2, figs. 18 (GSC 5999), 19 (YPM 472), non fig. 20 (proetid, YPM 25656).

Scotiella logani conservatrix (McLearn); Tomczykowa, 1962b, p. 192.



Text-figure 1. *Scotiella conservatrix* (McLearn 1924) new combination ×10.

TYPES. Lectotype: cephalon, YPM 472. Paratypes: cranidium, GSC 5999; pygidium, GSC 5998.

DISTRIBUTION. *Scotiella conservatrix* (McLearn 1924) occurs in the Moydart Formation, zone a, and in the Stonehouse Formation, zones a-c, of the Arisaig coast section, Nova Scotia. It is not a common trilobite (McLearn, 1924, p. 20).

AGE. Siluro-Devonian passage beds, probably equivalent to marine Downtonian. Copeland (1964, p. 7) has considered the age of the Stonehouse Formation, on the basis of ostracod faunas, to be post-Ludlovian, similar ostracods occurring in the Obere Oesel-

Gruppe on the island of Oesel, previously assigned a Downtonian age.

DIAGNOSIS. A species of *Scotiella* Delo 1935 with the following characteristics: glabella moderately convex (sag.); three well-defined pairs of lateral glabellar furrows, with a tendency for the anterior lateral and preoccipital furrows to converge adaxially; frontal-lobe anteriorly gently angled, with irregularly dispersed tubercles; anterior and median lateral glabellar lobes gently convex (tr. and sag.); preoccipital lobes one-fourth as wide (exsag.) as the median lateral lobes, with stronger convexity (tr.); preglabellar furrow very narrow (sag.), barely present; very short genal mucronations in the adult; pygidium with nine to ten axial rings; rings 5-6 often with very low mesial tubercle; rings 6-10 (more usually 7-10) interrupted mesially; five pleural segments, strongly furrowed; short, delicate caudal spine; border smooth, moderately wide; margin entire in adults.

DESCRIPTION. Cephalic outline pentagonal, postero-laterally rounded-truncate with short genal mucronations. Surface of frontal lobe of glabella with irregular rows of tubercles.

Glabella strongly pentagonal in outline, anteriorly gently angled (the apparently strongly angled anterior contour of the frontal lobe of the lectotype is due to slight lateral distortion), laterally subparallel-sided, the enclosing axial furrows diverging anteriorly at approximately 15-20 degrees. Frontal lobe large, moderately convex in lateral profile, extending slightly across the line of the axial furrows, occupying an anteriorly marginal position with regard to the front of the cephalon, bearing roughly five rows of tubercles radiating anteriorly from a point midway between the axial extremities of the anterior lateral glabellar furrows. Anterior lateral lobes subtriangular in shape, very narrow adaxially (exsag.) where they encroach backwards towards the axial ends of the median lateral furrows. Median lateral lobes subrectangular with posterior curvature to the back, narrow adaxially. Anterior and median lateral lobes are fused abaxially. Preoccipital lobes very narrow (exsag.) being merely a narrow ridge about one-fourth as wide (exsag.) as the median lateral lobes, with appreciably greater transverse convexity than the latter so that the abaxial ends slope to a lower level.

Anterior lateral glabellar furrows strong, wide, deep, slightly sigmoidal, posteriorly oblique, almost reaching backwards to the ends of the median lateral furrows. The latter are short, equally deep and wide (exsag.), linear or gently curved, failing to reach the axial furrows abaxially. Preoccipital furrows very wide (exsag.), deep, slightly curved to anterior at abaxial ends, strongly curved to the anterior at the adaxial ends, with a tendency to converge towards the posterior extremities of the anterior lateral furrows, there being a shallow tract along the proposed line of confluence between on the one side the anterior and median lateral lobes, which are very slightly raised above it, and on the other a narrow (tr.) median longitudinal field raised to an equal level.

Occipital furrow curving slightly forward mesially. Occipital ring considerably wider (sag. and exsag.) than the preoccipital lobes, having a similar transverse convexity, rising above the level of the glabellar side lobes.

Genae laterally extensive, without marginal furrow, without an area of librigena anterior to the frontal lobe such as that present in species of *Acaste* and *Acastella*. Postocular section of the facial suture cutting the lateral cephalic margins opposite the median lateral lobes; preocular section marginal immediately anterior to and defining the limits of the frontal lobe. The preglabellar furrow is represented merely by a slight marginal break in the slope of the convexity of the frontal lobe. Adult genae are provided with minute genal spinules; young holaspides have somewhat longer, more delicate, spines. Eyes moderately large and extending from the anterior lateral to the preoccipital glabellar furrows.

Nature of visual surface, hypostome and thorax unknown.

Pygidium subtriangular in outline, the lateral margins culminating posteriorly in a caudal spine which is long in young holaspides but considerably shorter in adults. Axis strongly convex (tr.), raised throughout its length above the pleurae, terminating abruptly before the posterior spine without trace of a post-axial ridge. There are nine clearly defined rings and a trace of a tenth. Rings 1-3, forming the anterior third of the axis, are clearly defined, being separated by deep transverse furrows. The remaining rings are separated by poorly-defined furrows. Ring 4 is entire, similar to 1-3. Rings 5 and 6 are broadly V-shaped (sag.), the apex pointing posteriorly, bearing, in well-preserved material, a

small tubercle which appears to lie sagittally within the fifth and sixth transverse furrows. Rings 7-10 are mesially interrupted by a smooth band or groove running longitudinally along the axis from the sixth transverse furrow. Whereas the halves of rings 7 and 8 are directed sagittally to the posterior, those of rings 9 and 10 point forwards. There are four well-defined pleurae, deeply grooved and separated by extremely weak interpleural furrows; a fifth is faintly indicated and there is sufficient space for a sixth in the smooth area at the posterior end of the pleural field. Border moderately wide, separated from the furrowed pleurae by a weak marginal furrow. Lateral margins entire in adults.

Scotiella logani (Hall 1860)
pl. 2, figs. 1-8; pl. 3, figs. 1-8.

Dalmania logani. n. sp.; Hall, 1860, pp. 156-7, text-fig. 18 (untraced).
Dalmanites logani Hall; Bassler, 1915, p. 385.
Dalmanitina logani (Hall); McLearn, 1918a, p. 32.
Dalmanitina logani (Hall); McLearn, 1918b, p. 130.
Dalmanitina logani (Hall); McLearn, 1924, pp. 167-8, pl. XXVII, fig. 3 (GSC 6211), 4 (GSC 6210), 6 (YPM 481), non fig. 5 (GSC 5998).
Scotiella logani (Hall); Delo, 1935, pp. 406-7, text-figs. 12 (untraced), 13 (untraced), 14 (GSC 6211).
Scotiella logani (Hall, 1860); Delo, 1940, pp. 33-4, pl. 2, figs. 14 (untraced), 15 (untraced), 16 (YPM 481), 17 (YPM 25102).
Phacopina (Scotiella) logani (Hall); Struve, 1959, p. 0489, text-fig. 386, 5 a-c.
Scotiella logani (Hall); Tomczykowa, 1962b, p. 192

TYPES. It has not been found possible to trace with certainty either of the specimens used by Hall (1860, p. 156, text-fig. 18) to illustrate *Scotiella logani*. All the specimens figured by McLearn (1924, pl. XXVII) were labeled as plesiotypes and none of these can be accurately matched with the original syntypes. I have, therefore, selected from among McLearn's plesiotypes, GSC 6210, as neotype of the species.

DISTRIBUTION. All the available material is from the Arisaig coast sections of Nova Scotia, the species occurring there in zones a-c

of the Stonehouse Formation and being most common in the last (McLearn, 1924, p. 20).

AGE. As for *Scotiella conservatrix* cited above.

DIAGNOSIS. A species of *Scotiella* Delo 1935 with faint to very faint anterior and median lateral glabellar furrows occasionally represented by fine upraised ridges; preoccipital furrows deep and wide (exsag.); anterior and median lateral glabellar lobes fused abaxially; frontal lobe anteriorly depressed, gently angled, not encroaching laterally across the courses of the axial furrows; genae with minute posterolateral points; eye moderately large; seven lenses at the maximum height (vert.) of the visual surface; pygidium with eight to ten axial rings, mesially interrupted in the posterior two-thirds of the axis; five pleural segments; border moderately wide especially along the lateral margins, without distinct marginal furrow; margin entire in adults, denticulate in young holaspides.

DESCRIPTION. The description is based on cranidia, glabellae and pygidia. There is one specimen in which the eye is preserved. The geometry of outline of the cephalon, the nature of the hypostome and the thorax remain unknown.

Glabella trapezoidal, laterally subparallel-sided, anteriorly gently angled. The axial furrows diverge at about 25-30 degrees in small specimens, about 20 degrees in large adults. Anterior lateral and median lateral glabellar side furrows faint to very faint on internal moulds or represented by weak elevated ridges; very faint to obsolete on casts taken from external moulds. The relief of the anterior part of the glabella is uniformly convex (tr. and sag.). When visible the anterior lateral furrows are long, very shallow, narrow (exsag.), and slightly sigmoidal, with a weak posterior median deflection; as in *Scotiella conservatrix* (McLearn) they tend to converge towards the adaxial ends of both the median lateral and preoccipital furrows. The median lateral furrows are rather wider (exsag.), shallow and considerably shorter, linear or gently curved and failing abaxially to reach the axial furrows. The preoccipital furrows are deep and wide (exsag.) in all specimens regardless of preservation; they curve slightly to the anterior at both their abaxial and adaxial ends, this curvature being most strongly emphasized in small specimens. There is apparent

on some specimens a narrow (tr.) median longitudinal field, slightly upraised, and separated from the equally raised anterior and median lateral glabellar lobes by a faint, discontinuous furrow lying along the proposed line of confluence between the anterior lateral and preoccipital furrows.

Frontal lobe, when viewed in lateral profile, with lower convexity than that of *S. conservatrix,* falling anteriorly to a very narrow (sag.), dorsal intramarginal rim, running concentrically to the anterior contour of the frontal lobe and representing the preglabellar furrow; not extending laterally across the courses of the axial furrows; bearing up to five rows of very faint tubercles, radiating from a point between the adaxial extremities of the anterior lateral furrows. Anterior lateral glabellar lobes subtriangular, fused distally with the subrectangular median lateral lobes. Preoccipital lobes very narrow (exsag.), about one-fourth the width of the median lateral lobes but having a slightly greater transverse convexity.

Occipital furrow deep, especially abaxially, wide (sag.). Occipital ring raised above the general surface of the glabellar side lobes, with a somewhat stronger transverse convexity than that of the preoccipital lobes.

Genae postero-laterally provided with very small mucronate points, similar to those of *Acastella prima* Tomczykowa 1962a. Eyes moderately large, extending from the anterior lateral glabellar furrows to the preoccipital furrows; sited a little closer to the glabella than to the cephalic margins; rising to about the level of the top of the glabella. The visual surface at hand is incomplete, the posterior third being broken off, but the remainder contains at least 73 lenses (giving an estimated total for the surface of approximately 120) contained in at least 15 dorso-ventral files (an estimated 22 for the complete surface) with rows of six lenses alternating with seven at the maximum vertical height of the surface.

Pygidium with subtriangular outline, laterally evenly rounded, culminating in a short, sharp, inflected caudal point. There are eight to ten axial rings and five pleural segments. The axis is moderately convex (tr.), raised above the pleurae and abruptly terminating before the posterior border without a marked postaxial ridge. Rings 1-3 separated by deep and wide (sag.) trans-

EXPLANATION OF PLATES

PLATE 1

Scotiella conservatrix (McLearn 1924), Stonehouse Formation, Arisaig coast section, Arisaig, Nova Scotia.

Figs. 1, 2. YPM 472, holotype, exfoliated cephalon; fig. 1, dorsal view showing minute genal spine, ×4; fig. 2, lateral view, ×4.
Figs. 3, 4. YPM 25111, exfoliated pygidium largely masked by matrix; fig. 3, dorsal view, ×4; fig. 4, axis showing mesially interrupted posterior rings, ×12.
Fig. 5. YPM 25113, early holaspid cranidium, exfoliated, dorsal view, ×4.
Figs. 6, 7. YPM 25112, exfoliated pygidium; fig. 6, dorsal view, ×5; fig. 7, lateral view, ×5.

PLATE 2

Scotiella logani (Hall 1860), Stonehouse Formation, Arisaig coast section, Arisaig, Nova Scotia.

Figs. 1, 2. YPM 481, plesiotype, internal mould cranidium; fig. 1, dorsal view, ×4; fig. 2, lateral view, ×4.
Fig. 3. YPM 25106A, early holaspid, exfoliated cranidium, dorsal view, ×4.5.
Fig. 4. YPM 25104A, cranidium, latex cast from external mould, dorsal view, ×4; YPM 25104B, early holaspid pygidium, latex cast, oblique view, ×4.
Fig. 5. GSC 5999, plesiotype, plaster cast cranidium, dorsal view, ×4.
Fig. 6. YPM 25114, internal mould glabella, lateral view frontal lobe, ×8.
Fig. 7. YPM 25109, exfoliated cranidium, dorsal view, ×4.
Fig. 8. GSC 6210, neotype, plaster cast cranidium, dorsal view, ×3.

PLATE 3

Scotiella logani (Hall 1860), Stonehouse Formation, Arisaig coast section, Arisaig, Nova Scotia.

Fig. 1. YPM 25108, internal mould cranidium, dorsal view, ×5.
Fig. 2. YPM 25106B, internal mould, visual surface, ×10.
Fig. 3. YPM 25103, internal mould pygidium, dorsal view, ×4.
Fig. 4. YPM 25105, internal mould pygidium, dorsal view, ×4.
Fig. 5. YPM 25104B, early holaspid pygidium, latex cast from external mould, showing entire axial rings and denticulate margin, ×10.
Fig. 6. YPM 25107, pygidium, latex cast from external mould, dorsal view, ×4.
Fig. 7. YPM 25102, plesiotype, exfoliated pygidium, dorsal view, ×5.
Fig. 8. YPM 25101, internal mould pygidium, dorsal view, ×4.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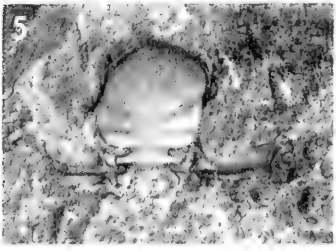
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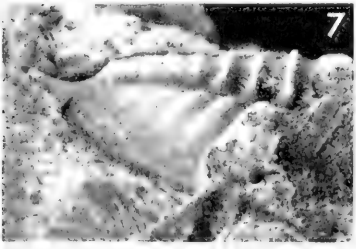
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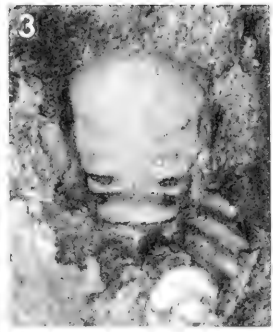
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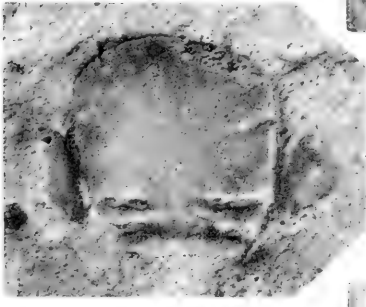

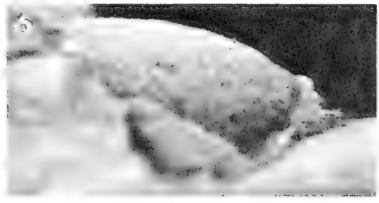
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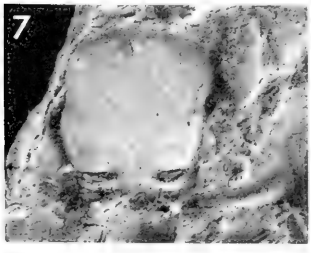
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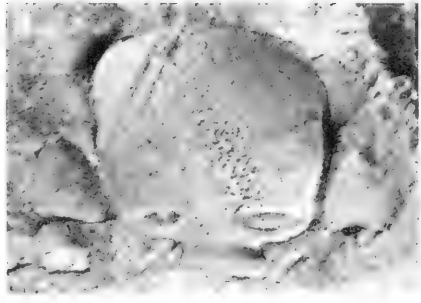

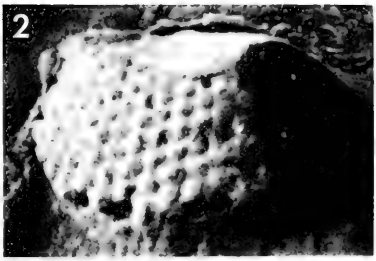

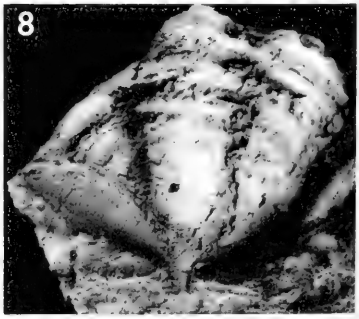

verse furrows, rings 4-10 by weak furrows. Rings 7-10 appear to be mesially interrupted as in *S. conservatrix*. Pleurae bear deep and wide (exsag.) pleural furrows and are separated by very weak interpleural furrows. Border moderately wide, smooth, without marked marginal flattening, save posteriorly. Margin in late holaspides apparently entire. One very small external mould (YPM 25104b), approximate width 2.90 mm, approximate length 1.40 mm, associated with a cranidium of *S. logani* (YPM 25104a), shows clearly eight uninterrupted axial rings and five pleural segments. The margin bears small denticulations which must also have been present on the shell. During the ontogeny of the species there appears to be a definite increase with size in the number of posterior rings becoming mesially interrupted. Rings 5-10 may have this characteristic in large specimens.

SUBFAMILY ZELISZKELLINAE Delo 1935
GENUS *KLOUCEKIA* Delo 1935
SUBGENUS *KLOUCEKIA* Delo 1935

Kloucekia (Kloucekia) obsoleta (Ulrich and Delo 1940) new combination

Scotiella obsoleta Ulrich & Delo n. sp.; Ulrich and Delo 1940 *in* Delo, 1940, pp. 34-5, pl. 2, figs. 21, 22 (USNM 79128, both specimens).

TYPES. Cotypes (designated Delo, 1940, p. 34): USNM 79128, 79130.

OCCURRENCE. The species occurs in the Whiteoaks Sandstone of Tennessee.

AGE. Lower Silurian, ? Llandoverian.

COMMENTS. The species *obsoleta* Ulrich & Delo 1940 is rejected from *Scotiella*. Although photographs sent to me by Dr. C. Harper, Jr., of the original syntypes show faint anterior and median lateral glabellar furrows they also show a slight bifurcation at the adaxial ends of the preoccipital furrows, where these are overdeepened. In addition the pygidium of this species as described by Delo (1940, pp. 34-5) is small, semicircular, non-spinose and has only three well-defined pleural segments. All these characteristics dif-

ferentiate it from other species of *Scotiella* described above, but ally it with species of the zeliszkellinid subgenus *Kloucekia (Kloucekia)* Delo 1935 to which it may be referred.

K. (K.) obsoleta is not the only representative of its genus to have been confused with *Scotiella. Kloucekia (Phacopidina) major* (Harper 1947) was originally placed in the same genus. These assignations serve to underline the relationships between zeliszkellinid trilobites of the *Kloucekia* type and the Acastinae.

The trend towards obsolescence of both the anterior and median lateral glabellar furrows appears to be operative at more than one time during the history of the Dalmanitidae and especially among those genera close to *Acaste*. The trend is observable in *Kloucekia, Calmonia* and *Phacopina* as well as in *Scotiella.* In each case there is considerable variation in the depth of furrow impression. In *Phacopina braziliensis* (Clarke) (1890, pl. 1, fig. 2) and *P. devonica* (Ulrich 1892) (see Kozlowski, 1923, pl. 4, figs. 7-11) these furrows are present, though faint. In *P. anceps* (Clarke) (1890, pl. 1, fig. 3) and *P. nylanderi* (Clarke) (1907, pl. 22, fig. 1) they are completely absent.

The Relationships of the North American Species of *Scotiella*

Some of the observations made by Hall (1860, pp. 156-7) in his original definition of *Scotiella logani* differ from those given above. Hall noted the presence of strong genal spines but these cannot be confirmed in the material presently available. He further noted (p. 157) six segments in the pleural field of the pygidium and his text-figure shows seven, possibly eight, though on all the material at hand only five are present.

The type-species, *Scotiella logani,* is in the majority of its characteristics most closely related to *S. conservatrix* (McLearn), differing mainly in the weakness of the anterior and median lateral glabellar furrows and the lower convexities (exsag.) of the frontal and lateral lobes. The tubercles prominent on the frontal lobe of *S. conservatrix,* are also present but less distinct on that of *S. logani.* The glabellar furrows in both species extend adaxially to a similar distance but the rather distinctive, slightly upraised, and narrow, median longitudinal ridge of *S. conservatrix* is very

much less prominent in *S. logani*. The pygidia are almost inseparable.

In cephalic characteristics *S. logani* is very nearly homeomorphic with *S. opatowiensis* Tomczykowa 1962b, save that the eyes of the latter are a little further distant from the posterior border furrow and the frontal lobe is a little more anteriorly rounded. The pygidium of *S. opatowiensis* is unknown but is possibly identical to that of *S. samsonowiczi* Tomczykowa 1962b, which occurs at the same localities and in the same beds.

Scotiella conservatrix is most closely related on cephalic characteristics to *S. minor* (M'Coy 1851). Both species have strong glabellar furrows, but in the latter they are somewhat shorter. In *S. minor* the frontal lobe of the glabella is decidely anteriorly angled (Shergold, 1967, pl. 2, fig. 1). The same comments also apply to *S.* cf. *minor* with its distinctly pentagonal glabella (ibid., pl. 1, fig. 9).

Scotiella samsonowiczi is in its cephalic form intermediate between *S. conservatrix* and *S. logani* and also between *S. conservatrix* and *S. minor*. The glabellar furrows are present but weak in the type specimens although other material from the same locality shows considerable diversity in strength (Dr. Ewa Tomczykowa, pers. comm.). The genal spines are somewhat longer than in other species of *Scotiella* at the equivalent morphogenetic stage. The frontal lobe is anteriorly angled and the preocular section of the facial suture is marginal as in *S. minor*. In the pygidium there are six pleural segments as against five in *S. logani* and *S. conservatrix* and the posterior axial rings are entire, as in young holaspides of *S. logani,* not mesially interrupted.

The interruption of the posterior axial pygidial rings in adults of *S. logani* and *S. conservatrix* is paralleled in other dalmanitid genera only in *Acastoides henni* (R. Richter 1916), affecting rings 5-8 in both *A. henni posthuma* R. & E. Richter 1952 and *A. henni henni* (R. Richter 1916) (see R. & E. Richter, 1952, pl. 2, figs. 8, 13). The reason for this development is unknown.

Young holaspides of *Scotiella logani* and/or *S. conservatrix* appear to have pygidia with lateral marginal denticulations, these appearing in *Scotiella* contemporaneously with similar structures in young holaspides of species of *Acastella*. In the latter genus these denticulations appear in the adult ontogenetic stages at a

later date, e.g. *Acastella tiro* R. & E. Richter 1954. They are also present in young holaspides of species of *Acastocephala* Shergold 1966 but, as in *Scotiella* they do not persist into the adult morphogenetic stages.

Discussion

The type material for *Scotiella* originally described by Hall (1860) has not been traced though it is possible that the two specimens concerned (Hall, 1860, p. 158, text-fig. 18) were unknowingly refigured by McLearn (1924). The specimens of this latter author now constitute the type series. In this there are no complete specimens with articulated cephala and pygidia; and no such specimens have been observed in the recently collected material. All the specimens available to date are isolated heads or tails, these being preserved either as moulds or are exfoliated, with the greater part of the shell usually missing.

Within the material at his disposal McLearn (1918a, 1924) was able to differentiate two cephalic types, one referred to *Scotiella logani, sensu stricto,* and the other to the variety *conservatrix*. The *logani* type of cephalon (McLearn, 1924, pl. XXVII, figs. 3, 4, 6) is characterized by having a rather smooth glabella with low sagittal convexity and faint, weakly impressed, anterior and median lateral glabellar furrows. The axial furrows of early holaspides diverge anteriorly at a greater angle than do those of late holaspides (see pl. 2, figs. 1, 3, 5, 7, 8). The *conservatrix* type of cephalon (McLearn, 1924, pl. XXVII, fig. 1) has a greater glabellar convexity (sag.) and there are three pairs of clear, well-defined glabellar furrows, as in the genus *Acastella*. Throughout morphogenesis the axial furrows appear to diverge at an angle similar to that of the early holaspides of *Scotiella logani, sensu stricto,* (see pl. 1, figs. 1, 5). The greater anterior angle to the frontal lobe of the *conservatrix* cephalon figured by McLearn (1924, pl. XXVII, fig. 1; YPM 472) is due to slight lateral distortion. In this characteristic there is very little difference between the two cephalic types on undistorted material.

McLearn (1924, p. 168) considered there to be every gradation between the strongly furrowed cephalic form *(conservatrix)* and the pauci-furrowed type *(logani),* this presumably influencing his contention that the *conservatrix* type of cephalon should be

regarded as having no higher taxonomic status than that of a variety. His opinion was supported by Delo (1940, p. 34).

In originally assessing only the type material the present author was inclined to disagree with the above stated view. Large holaspid cephala appear to be quite distinct, though the number of characteristics in common between the two cephalic types certainly establishes their close relationship. Small holaspides, however, show greater affinity and are often difficult to separate, the one diagnostic difference being a slightly greater lobar convexity in the *conservatrix* forms, which have as a result somewhat deeper furrows. On examining additional material, recently collected and kindly loaned by Professor A. J. Boucot, however, the differences between specimens of large holaspid cephala gradually became reduced. The statement, "in the distinctness of the anterior two pairs of furrows . . . the *logani* form . . . grades more or less indistinguishably into the variety *conservatrix*" (Delo, 1940, p. 34), is justifiable, the *conservatrix* and *logani* cephalic forms being interpreted as the end members of this morphological gradation.

McLearn made no differentiation between the two taxa he recognised on pygidial characteristics. Delo (1940, p. 34), however, referred to *S. logani* a pygidium with a short, inflected, rather incongruous, caudal mucronation (Delo, 1940, pl. 2, fig. 17; YPM 25102) and to *conservatrix* a non-mucronate pygidium (pl. 2, fig. 20; YPM 25656). The latter has been re-examined by the writer who concludes that it belongs not to *Scotiella* but to a proetid trilobite.

It is indeed difficult to make a differentiation on pygidial characteristics because all the pygidia represented in the collections examined, and referable to an acastinid genus, have the same segmentation, five pleural segments and nine to eleven axial rings, depending on the morphogenetic stage attained. All the pygidia observed are further characterized by a mesial interruption in the posterior rings of the axis. Nevertheless there are pygidia similar to that figured by Delo (1940, pl. 2, fig. 17) as *S. logani*. In addition there are others with lateral margins a little more sharply drawn in, very slightly narrower borders and slightly longer mucronations. These may belong to the *conservatrix* type of cephalon. Just as the head of this species is closely similar to that of *Acastella,* so is the narrower, more triangular pygidium.

It must be stressed, however, that the pygidia of *logani* and *conservatrix* are very similar and as such cannot be used confidently as a basis for differentiation, a problem which may only be resolved by the discovery of a completely articulated specimen of either species.

Thus among the type material of *Scotiella* there are two distinct cephalic types, which may be end members of a gradational morphological series, accompanied by scarcely distinguishable pygidia. There can be no question of the observed differences being attributed to preservation or to morphogenesis, for specimens, quite distinct and of comparable size, occur together at the same localities in both calcareous and argillaceous matrices. That sexual dimorphism may account for these differences might be considered but cannot be proved. It is interesting to note in this respect that Tomczykowa (1962b) has recently described two species of *Scotiella* from the Holy Cross Mountains, southern Poland: *S. samsonowiczi,* having glabellar furrows present but incised to varying depths, and *S. opatowiensis,* having weak anterior and median lateral furrows. Only one type of pygidium is known and this is articulated with the *samsonowiczi* type of cephalon. Both species occur on a similar horizon in the Rzepin Beds (Podlasian = ? Downtonian) at Lezyce-Belcz near Opatów and at Lipniczek near Sandomierz (Tomczykowa, 1962b, p. 203).

The inclusion of both strongly and weakly furrowed cephala within the single genus raises certain taxonomic points. Delo (1935, p. 409) in erecting *Scotiella* originally confined the genus to the type species, *S. logani* (Hall), the generic diagnosis thus incorporating the observation "anterior glabellar furrows faint to obsolescent." This diagnosis was left largely unmodified in a later paper (Delo, 1940) though in considering the pygidium the earlier definition "rounded, with short spine" was altered to "rounded, with or without short spine" (p. 33), presumably to reconcile the differing species which Delo attributed to the genus at this time. The variety *conservatrix* was included in *Scotiella* in his paper, in spite of the original definition which excluded trilobites with strongly defined glabellar furrows. No emendation was made to the diagnosis to account for this inclusion.

Disregarding the latter assignation later authors have come to regard the faintness of the anterior glabellar furrows as absolutely

diagnostic of *Scotiella*. Struve (*in* Moore, 1959, p. 0489) for example has considered *Scotiella* as representing a subgenus of *Phacopina* Clarke 1913, in which the anterior and median lateral furrows may be similarly faint. His diagnosis retains Delo's (1940) statements concerning the nature of the pygidium of *Scotiella*. If these authors are to be followed strictly, then only such species as *S. logani* with the anterior two pairs of furrows faintly defined, can be classed within the genus.

With respect to the differences and similarities between the cephalic forms noted above, this situation is somewhat unsatisfactory. Until it can be conclusively proven that the *logani* and *conservatrix* forms are conspecific or otherwise, I would prefer to regard them as separate species, thus following the procedure adopted by Tomczykowa (1962b) in dealing with the Polish species. The generic diagnosis of *Scotiella* has been emended here to embrace both strongly and weakly furrowed glabellar forms. Some allowance has also been made for the differing pygidial characteristics between North American and European species. The species thus included in the genus are: *Scotiella logani* (Hall 1860), *S. conservatrix* (McLearn 1924), *S. samsonowiczi* Tomczykowa 1962b, *S. opatowiensis* Tomczykowa 1962b and *S. minor* (M'Coy 1851).

Conclusions

1. The exact taxonomic status of *Scotiella* must remain in doubt until fully articulated specimens of either *S. logani* or *S. conservatrix* are discovered, in which event the correct assignment of the pygidium may be facilitated.

2. McLearn (1924) and Delo (1940), impressed by the apparent morphological transition between the *logani* and *conservatrix* cephalic types and being unable to distinguish associated pygidia readily, referred both species to *Scotiella,* a procedure followed here.

3. It is suggested that the poorly furrowed cephalon represents a derivation from the strongly furrowed type, though there is a possibility that this difference is the result of sexual dimorphism.

4. The strongly furrowed *Scotiella* of the Stonehouse Formation probably represents a rapidly evolved branch of Acastinae

derived from a parent species of *Acaste* at a time when *Acastella* was evolving from a similar source in northwest Europe.

5. *Acastella,* present in Europe and north Africa from Ludlovian to Siegenian time, has not been reported from North America. *Scotiella,* present from Ludlovian to Lower Gedinnian time in North America, is only sparsely represented in Europe, where its range is confined to beds about the Siluro-Devonian passage (late Ludlovian to early Downtonian). *Scotiella* may thus be interpreted as the temporal equivalent in North America of the genus *Acastella* in Europe and north Africa.

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