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Mid-Carboniferous ammonoids from the Shannon Basin, western Ireland: identification of crushed material

Anthea R. Lacchia[1] · George D. Sevastopulo[1] · John R. Graham[1]

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Abstract In the Carboniferous Shannon Basin, Western Ireland, the majority of ammonoids spanning the Serpukhovian-Bashkirian Stages (E_1–R_2 biozonal indices) are preserved as flattened, partial 2D impressions, for which identification is problematic. Ammonoid ornament changes through successive developmental stages of the animal, but the changes of ornament with ontogeny have not been studied for many of the taxa that occur in the Shannon Basin. An approach involving the ontogenetic study of all available 3D material from concretions and museum collections can be used to improve the confidence of identification of flattened material. This is described here for the following Bashkirian ammonoid species: *Phillipsoceras circumplicatile, Vallites henkei* and *Reticuloceras subreticulatum*. Systematic ontogenetic changes in ornament are described here for these taxa for the first time. This represents a first step towards advancing 2D ammonoid taxonomy, which will improve biostratigraphic resolution, with implications for large-scale ammonoid diversity and evolutionary studies.

Keywords Ammonoidea · Carboniferous · Serpukhovian · Bashkirian · Taxonomy · Shannon Basin

✉ Anthea R. Lacchia
lacchiaa@tcd.ie

[1] Department of Geology, Trinity College Dublin, Dublin 2, Ireland

Introduction

Ammonoids are the organisms of choice for many biostratigraphic, evolutionary and global diversity studies. Ammonoid taxonomy is based on knowledge of the morphology of the conch, and generally involves the study of conch shape and size, suture line outline and shell ornament.

Most Irish Serpukhovian and Bashkirian ammonoids are preserved as flattened impressions of the shell (2D preservation): in this case, taxonomic information necessarily comes mostly from the ornament. Not only is 2D preservation of external moulds the dominant mode of preservation at outcrop, where concretions with three-dimensionally preserved ammonoids (3D preservation) are generally rare, but this is also the case for most borehole material. However, the taxonomy of ammonoids preserved as flattened moulds presents significant challenges.

It is argued here that even where concretions (bullions: Hodson 1954a) are available in the outcrop, flattened ammonoids from surrounding strata record valuable information (in terms of assemblages, biostratigraphy, palaeocommunities, etc.) that ought not to be neglected despite the associated taxonomic problems.

Ammonoid ornament changed through successive developmental stages of the animal, but the changes of ornament with ontogeny have not been studied for many taxa. The systematic study of these changes requires good-quality 3D material with shell preserved (e.g., Saunders and Swan 1984). However, type specimens of many taxa of Serpukhovian and Bashkirian age are preserved as 2D impressions, resulting in incomplete morphological descriptions and diagnoses. Furthermore, whether type specimens are flattened or solid, type descriptions are commonly based on a single growth stage: this is the case

for most ammonoid taxa present in the Serpukhovian and Bashkirian strata of Ireland. For instance, within the genus *Reticuloceras*, a thorough ontogenetic study has been published only for *Reticuloceras reticulatum* (Phillips, 1836) (Korn 1997, p.72).

Changes in ornament through ontogeny have been studied in the following taxa with associated description (this list refers to taxa that are pertinent to the Shannon Basin):

- *Homoceras undulatum* (Brown, 1841); Bisat 1924, p.105.
- *Baschkirites/Hudsonoceras ornatus* (Foord and Crick, 1897); Bisat 1924, p.98.
- *Hudsonoceras proteus* (Brown, 1841); Bisat 1924, p.110.
- *Homoceratoides prereticulatus* Bisat 1924; Bisat 1924, p.112.
- *Reticuloceras reticulatum* (Phillips, 1836); Korn 1997, p.72.
- *Anthracoceras paucilobum* (Phillips, 1836); Gordon 1964, p.245.
- *Hodsonites magistrorum* (Hodson, 1957); Hodson 1957, p.21.

Changes in ornament through ontogeny have not been studied in the following taxa (pertinent to the Shannon Basin):

- *Phillipsoceras circumplicatile* (Foord, 1903)
- *Vallites henkei* (Schmidt, 1925)
- *Reticuloceras pulchellum* (Foord, 1903)
- *Reticuloceras subreticulatum* (Foord, 1903)
- *Phillipsoceras paucicrenulatum* (Bisat and Hudson, 1943)
- *Homoceratoides varicatus* Schmidt, 1934
- *Homoceras beyrichianum* (de Koninck, 1844)
- *Isohomoceras subglobosum* (Bisat, 1924)
- *Homoceras smithii* (Brown, 1841)

Clearly, a thorough study of ontogenetic changes of ornament would greatly benefit the taxonomy of Irish Serpukhovian and Bashkirian ammonoids and, in turn, would result in more precise biostratigraphic schemes and information about the structure of palaeocommunities. Until this kind of study is accomplished, identification of 2D material to the species level remains problematic, especially where only fragments are preserved. Here, new data on the changes of ornament through ontogeny of three taxa of ammonoids are presented in order to demonstrate the value of this approach.

Issues in the taxonomy of crushed material

Basic conch parameters such as conch diameter, whorl width and whorl height (Korn 2010) cannot be obtained from 2D material. Improvements in 2D taxonomy can be made only through morphological and ontogenetic analysis of 3D material. Typically, the minimum requirement to make a diagnosis is a portion of the flank from the umbilicus to the venter (Bouckaert 1961); however, even having satisfied this prerequisite, the taxonomist can run into a series of pitfalls when dealing with 2D crushed material.

In the case of *Ph. circumplicatile* (Foord, 1903), it is clear, from study of the type material and from literature descriptions, that the variable ornament of the adult shell makes identification problematic. This problem is exacerbated by the close similarity of *Ph. circumplicatile* to the allied species *Phillipsoceras paucicrenulatum* (Bisat and Hudson, 1943). In the case of the syntypes of *Ph. circumplicatile* utilised by Foord (Fig. 1), it is impossible to ascertain from museum records whether the specimens all came from the same horizon or from different stratigraphic levels at the same locality (which might result in some morphological change). If one accepts Foord's syntype illustrated in Fig. 1c (NMING : F23972), which is very different in ornament (prorsiradiate direction of the ornament, more delicately crenulated growth lines) and in conch shape (more moderate umbilicus and higher whorl section), as *Ph. circumplicatile,* then there is extreme intraspecific variation. It is perhaps more likely that these specimens include more than one species.

Geological setting

The Shannon Basin (Fig. 2), which also has been called West Clare Basin (Gill 1979), Western Irish Namurian Basin (Martinsen 1989) or Clare Basin (Haughton et al. 2009), is located in Western Ireland. It developed during latest Devonian and Early Carboniferous times as a result of crustal extension (Collinson et al. 1991). During the Serpukhovian and Bashkirian, the basin fill followed an overall shallowing-upward trend, starting with deep-water shales and siltstones (Clare Shale Formation), followed by a sand-rich, deep-water, fan system (Ross Sandstone Formation), which is in turn overlain by muddy slope deposits (Gull Island Formation) and cyclothemic deltaic deposits (Central Clare Group). The lithostratigraphy of the Shannon Basin succession was set up by Rider (1974), and a biostratigraphic framework was first established by Hodson (1954a, b) and Hodson and Lewarne (1961), whose work was fundamental in proving the existence of a mid-Carboniferous trough with an axis roughly aligned with the present-day Shannon estuary (Fig. 2). Early biostratigraphic work focused on the Clare Shale Formation, but taxa discussed in the present paper were recovered both from the Clare Shale Formation and from the laterally equivalent deep-water turbidites of the Ross Sandstone Formation (Rider 1974; Collinson et al. 1991; Elliot 2000a, b; Lien et al. 2003).

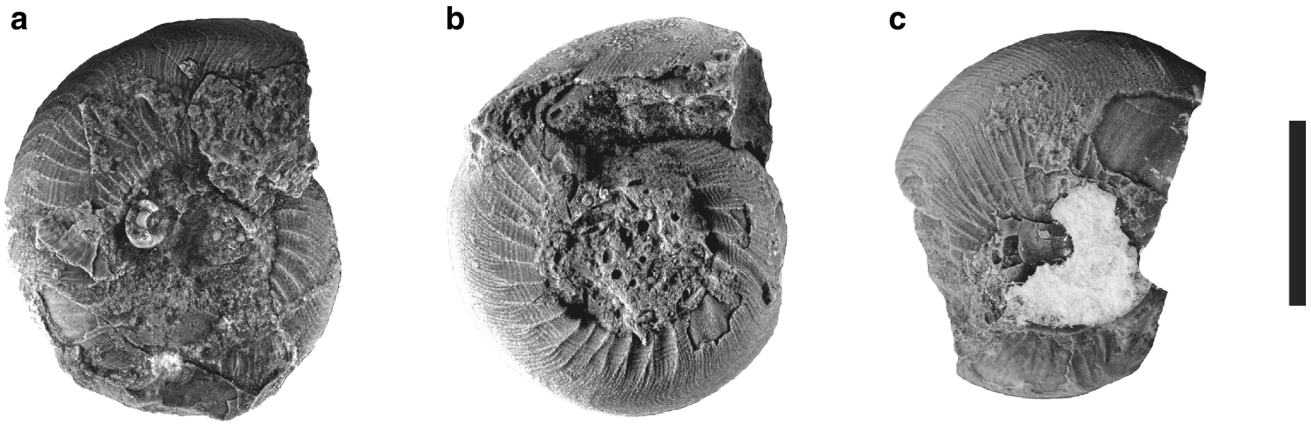

Fig. 1 *Phillipsoceras circumplicatile* (Foord, 1903) syntypes, **a** Paralectotype (NMING : F23969), **b** Lectotype (NMING : F23968), **c** Syntype (NMING : F23972, *partim*). Note that specimen **c** is probably not attributable to this species (see text for discussion) but it is included as it is one of the syntypes designated by Foord. Specimens are from Lisdoonvarna, Co. Clare, Ireland. *Scale* is 10 mm

Fig. 2 Geological map of the study area in Western Ireland and simplified stratigraphic section of the basin fill succession; after Martinsen et al. (2000) and Obradors-Latre et al. (2014, pers. comm.)

Because the basin offers superb cliff exposure and serves as an instructive onshore analog for younger hydrocarbon-bearing successions elsewhere, it is visited by numerous geologists from both industry and academia.

Ammonoid bands

Ammonoids in the Shannon Basin are mostly concentrated in thin intervals of black shale referred to as "condensed sections" or "ammonoid bands", which are thought to represent intervals of sediment starvation. The ammonoids are the dominant faunal component and are accompanied by bivalves, orthoconic nautiloids, conodonts and plant material.

Thick-shelled ammonoids are particularly useful in providing a high-resolution biostratigraphic framework for the late Mississippian to Pennsylvanian Subsystems (Waters et al. 2011). Serpukhovian and Bashkirian ammonoid biostratigraphy for Northwestern Europe was set up by Bisat (1924, 1928) and Bisat and Hudson (1943), and later developed by Ramsbottom (1969, 1971), largely resulting from work in the Central Pennine Basin of northern England (Waters et al. 2011).

Materials and methods

For the purpose of this study, 3D ammonoids were either extracted from concretions in the Clare Shale Formation, Co. Clare, Ireland, or accessed in museum collections: Geological Museum, Trinity College Dublin (catalogue numbers prefixed TCD); National Museum of Ireland (catalogue numbers prefixed NMING); British Geological Survey, Keyworth, UK (catalogue numbers prefixed GSM); and Geological Sciences Museum of the University of Göttingen (catalogue numbers prefixed GZG.INV). Three taxa were selected to demonstrate the value of using 3D material to establish changes of ornament through ontogeny which can then be applied to crushed material. There is a current lack of published information regarding their ontogeny and diagnostic features, with which to identify crushed material. Well-preserved specimens were chosen and changes in ornament through ontogeny are described and illustrated diagrammatically (Figs. 3, 4, 5; Tables 1, 2, 3).

Systematic palaeontology

Suborder Goniatitina Hyatt, 1884

Superfamily Gastrioceratoidea Hyatt, 1884

Family Homoceratidae Spath, 1934

Subfamily Homoceratinae Spath, 1934

Genus *Vallites* Ruzhencev and Bogoslovskaya, 1971

***Vallites henkei* (Schmidt, 1925); Fig. 3; Table 1.**

1925 *Eumorphoceras subreticulatum* Foord; Schmidt, p. 585, pl. 22, fig. 1, pl. 25, fig. 4–6.

v*1934 *Homoceras henkei* Schmidt; p. 456, p. 453, fig. 70–72.

1943 *Homoceras henkei* Schmidt; Bisat and Hudson, p. 406, pl. 25, fig. 4–7, pl. 30, fig. 2.

v*1957 *Homoceras henkei* Schmidt; Hodson, pl. C fig. 2, pl. E, fig. 4–6.

Also refer to Patteisky (1959), Bouckaert (1960, 1961), Chalard (1960), Ruzhencev and Bogoslovskaya (1971, 1978); Manger, Weyant and Pareyn (1985); Lemosquet, Conrad and Manger (1985); and Korejwo (Korejwo 1986).

Type locality Neheim, Germany (former Emde brickworks quarry).

Type material Syntypes GZG.INV.48185, GZG.INV.48186, GZG.INV.48184 (see Fig. 3a–c).

Other material Specimens of *V. henkei* from the Aille River, Co. Clare, associated with *Hod. magistrorum* (Hodson, 1957), allow juvenile growth stages to be studied. Late adolescent and adult growth stage features were seen in beautifully preserved Irish specimens collected by F. Hodson.

Diagnosis *Vallites* with nodes, also called "beading", decorating the umbilical margin. The umbilical margin forms a pronounced rim and the growth lines do not dichotomize. The ribs gradually decrease in strength through ontogeny until they give way to the very elegant, biconvex growth lines.

Description In all juvenile specimens (NMING : F23971 and Hodson material from the river Aille), growth lines are delicate, radial and c.6 per mm. The umbilical edge is raised, with gently sloping walls; at 8–9-mm diameter (in the Hodson material from the River Aille), growth lines are c.7 per mm and the elevated umbilical rim is still raised (Fig. 3d–e). The growth lines thicken as they cross the rim, but umbilical nodes are absent. A syntype (GZG.INV.48185, Fig. 3a, d) at 7.1-mm diameter has strong, radial growth lines. It has very faint umbilical nodes at this early developmental stage.

A specimen from Slieve Elva from Hodson's Irish collection (TCD.60610) at 18.5-mm diameter illustrates well the biconvex growth lines, which are slightly bent forward immediately after exiting the umbilicus past the nodes, and then turn back slightly, before pushing forward again on the ventrolateral projection (Fig. 3f). The ventral sinus is extremely faint. Growth lines are spaced 5 per mm on the ventrolateral projection. A syntype (GZG.INV.48186, Fig. 3b) is an adult specimen with diameter 21.9 mm, showing beading of growth lines (i.e., nodes) on the umbilical margin, and both ventrolateral projection (with 5 growth lines per mm) and ventral sinus (which is more developed in other specimens). The nodes, which give the appearance of several closely set, pseudo-spiral lines that are formed where the transverse growth lines become slightly crenulated, appear in adolescence. An internal cast (GZG.INV.48184, Fig. 3c) with a diameter of 30.7 mm with faint impressions of the ornament shows both ventrolateral projection and ventral sinus. A specimen with a diameter of 41 mm (from Hodson's Irish collection reposited in the Geological Museum of Trinity College Dublin) has growth lines spaced 2 per mm and both ventrolateral projection and ventral sinus pronounced. The umbilical edge is broad and rounded, and the walls are shallowly sloping. There are no nodes, as is the case in other very mature specimens.

Comparisons The umbilical rim is more pronounced and the shell is narrower in *V. henkei* than in *V. schmidti* (Ruzhencev and Bogoslovskaya, 1971). The umbilical rim is more pronounced in *V. henkei* than in *V. kullmanni* (Korn, 1997). Growth lines in *V. henkei* are coarser than in *V. striolatus* (Phillips, 1836). Lack of dichotomy in the

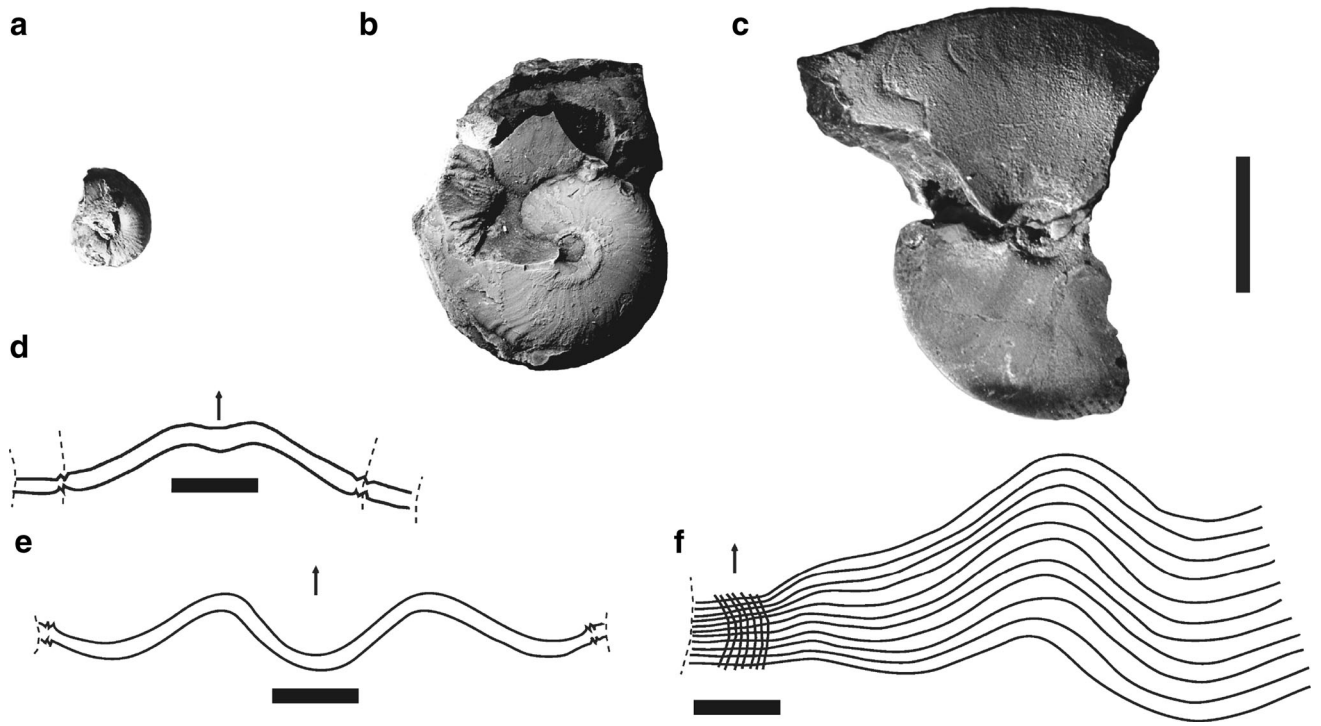

Fig. 3 Changes in ornament in *Vallites henkei* (Schmidt, 1925). **a** Syntype GZG.INV.48185, **b** Syntype GZG.INV.48186, **c** Syntype GZG.I. NV.48184. Specimens are from Neheim, Germany. *Scale bar* is 10 mm long. **d** Growth lines (NMING : F23971) at 7 mm with *dashed lines* at edges of umbilical wall, **e** Growth lines of TCD.60608 at 10-mm diameter, **f** Growth lines of TCD.60608 at 15-mm diameter. Specimens are from Lisdoonvarna, Ireland. *Scale bars* are 2 mm long

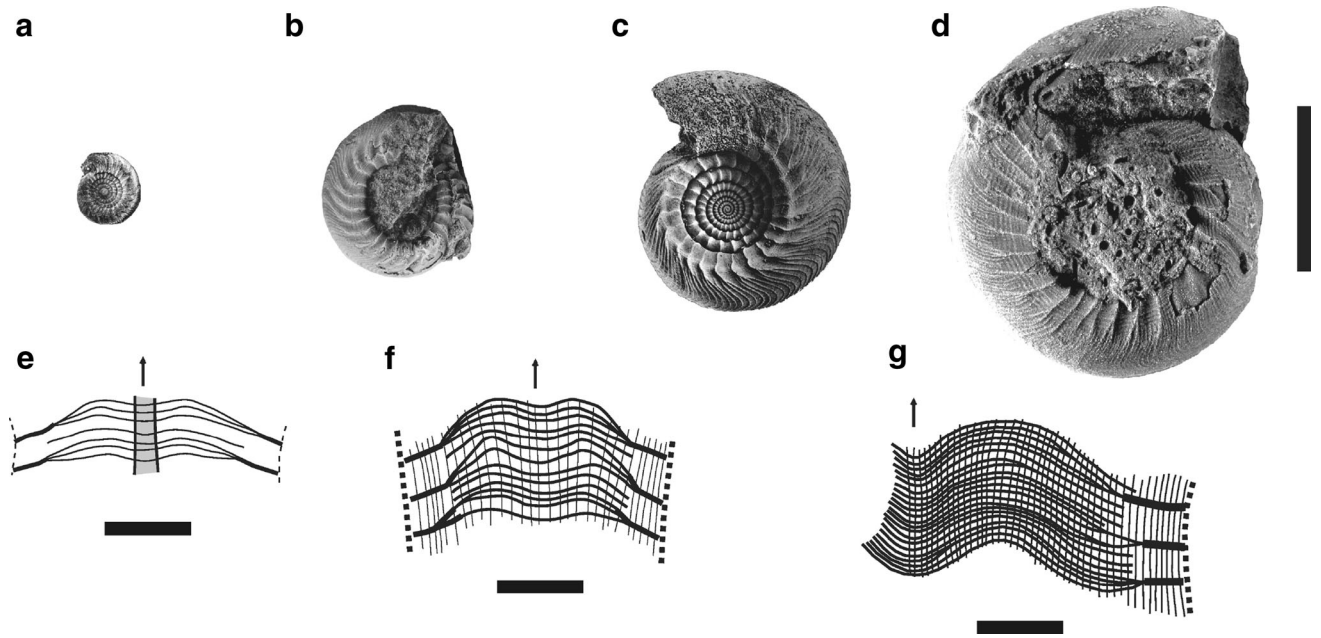

Fig. 4 Changes in ornament in *Phillipsoceras circumplicatile* (Foord, 1903). **a** Paralectotype (NMING : F23972 *partim*), Lisdoonvarna, Ireland, **b** TCD.60601, Murphy's Bridge, Ireland, **c** GSM 86917, Neheim, Germany, **d** Lectotype (NMING : F23968), Lisdoonvarna, Ireland. *Scale* is 10 mm long. **e** Growth lines in paralectotype (NMING : F23972 *partim*) at 4-mm diameter with *shaded ventral* sulcus, **f** Growth lines in TCD.60601 at 9-mm diameter, **g** Growth lines in lectotype (NMING : F23968). *Scale bars* are 2 mm long

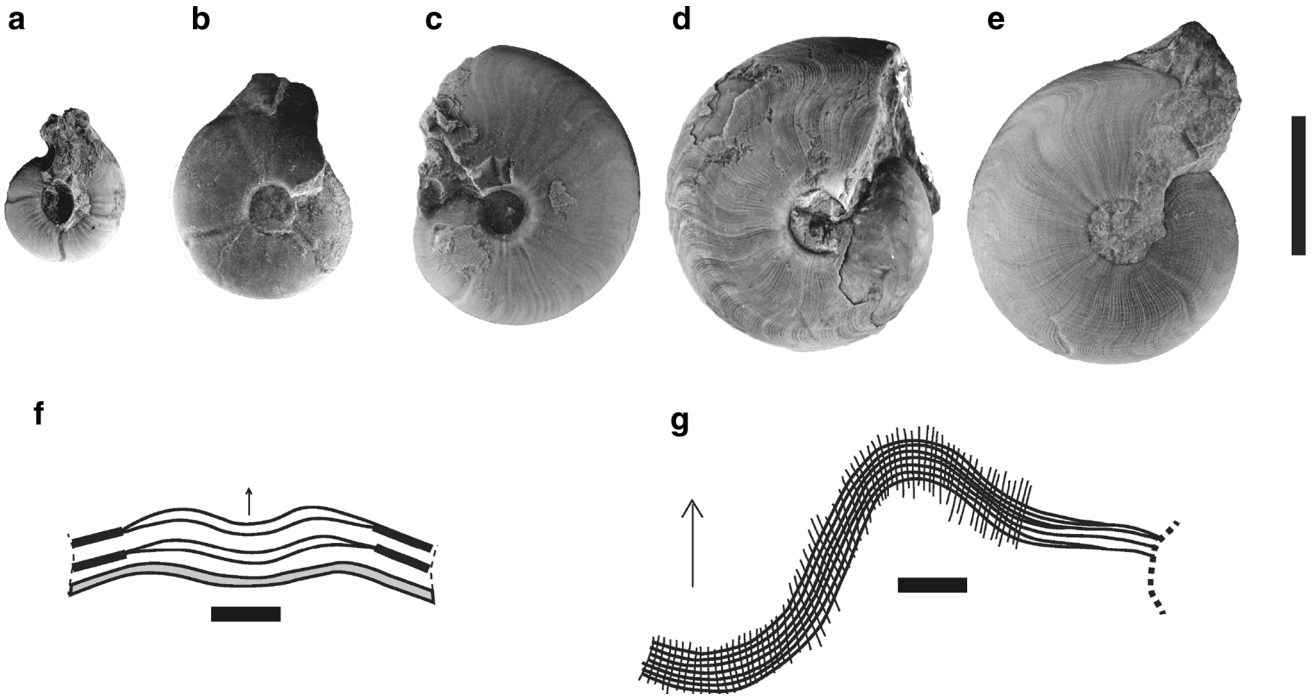

Fig. 5 Changes in ornament in *Reticuloceras subreticulatum* (Foord, 1903). **a** TCD.60602, Blake's Bridge, **b** TCD.60603, Blake's Bridge, **c** TCD.60604, Blake's Bridge, **d** Lectotype (NMING : F23964), Foynes Island, Co. Limerick, Ireland, **e** TCD.60605, Blake's Bridge. *Scale bar* is 10 mm long. **f** Growth lines of TCD.60602, Blake's *Bridge*, and *shaded constriction*, **g** Growth lines in lectotype (NMING : F23964), Foynes Island, Co. Limerick, Ireland. *Scale bars* are 2 mm long

Table 1 Conch measurements for *Vallites henkei* (Schmidt, 1925)

Species	Specimen number	D (mm)	WW (mm)	WW/D
Vallites henkei (Schmidt, 1925)	GZG.INV.481-85	7.1	4.4	0.61971831
	GSM.81006	8.5	5	0.588235294
	NMING : F23971	9	4.8	0.533333333
	GSM.89946	10	6	0.6
	Zi4688	10.9	5.5	0.504587156
	Zi4690	11.5	6.9	0.6
	Zi4489	11.6	8.9	0.767241379
	GSM.86934	17.8	9.5	0.533707865
	GSM.86936	11.8	7.7	0.652542373
	NMING : F23974	21.8	10.4	0.47706422
	GZG.INV.481-86	21.9	8.6	0.392694064
	GSM.86931	27.8	12.8	0.460431655
	GZG.INV.481-84	30.7	14	0.456026059

Measurements include: diameter (D), whorl width (WW) and (WW/D). Specimens were either collected from the Clare Shale Formation, Co. Clare, Ireland, or accessed in museum collections. Measurements of diameter (D) and whorl width (WW) are in mm

growth lines of *V. henkei* distinguishes this species from *Ht. varicatus* and *Hod. magistrorum.*

Family Reticuloceratidae Librovitch, 1957

Subfamily Reticuloceratinae Librovitch, 1957

Genus *Phillipsoceras* Ruzhencev and Bogoslovskaya, 1975

***Phillipsoceras circumplicatile* (Foord, 1903); Fig. 4; Table 2**

v*1903 *Gastrioceras circumplicatile* Foord, p.200, pl.49, fig. 12a, b, 13.

v1924 *Reticuloceras inconstans* Bisat, p.118, pl.3, fig. 6.

Table 2 Conch measurements for *Phillipsoceras circumplicatile* (Foord, 1903)

Species	Specimen number	D (mm)	WW (mm)	WW/D
Phillipsoceras circumplicatile (Foord, 1903)	NMING : F23972	4	2	0.5
	TCD.60601	9.6	5.5	0.572916667
	GSM.95233	11.8	7.7	0.652542373
	GSM.95234	12.5	6.2	0.496
	GSM.86939	13.6	8.6	0.632352941
	GSM.86917	14.5	7.3	0.503448276
	GSM.95231	14.8	8	0.540540541
	GSM.85388	14.9	7.9	0.530201342
	GSM.95236	16	9.6	0.6
	GSM.95232	16.3	8.6	0.527607362
	NMING : F23968	21	12.5	0.5952381
	NMING: F23969	21.6	12.8	0.59259259

Measurements include: diameter (D), whorl width (WW) and (WW/D). Specimens were either collected from the Clare Shale Formation, Co. Clare, Ireland, or accessed in museum collections. Measurements of diameter (D) and whorl width (WW) are in mm

Table 3 Conch measurements for *Reticuloceras subreticulatum* (Foord, 1903)

Species	Specimen number	D (mm)	WW (mm)	WW/D
Reticuloceras subreticulatum (Foord, 1903)	Zi7113	6.7	4.2	0.626865672
	Zi7112	7.3	4	0.547945205
	Zi7115	8.2	4.6	0.56097561
	Zi7118	8.8	6.2	0.704545455
	Zi7116	11.9	6.3	0.529411765
	LZ1988	13.7	8.3	0.605839416
	Zi7114	15.5	9.2	0.593548387
	Zi7117	15.7	8.2	0.522292994
	Zi7123	16.8	9.8	0.583333333
	Zi7119	18.5	8.9	0.481081081
	TCD.60604	19.6	10.1	0.515306122
	NMING : F23964	22.9	12	0.524017467

Measurements include: diameter (D), whorl width (WW) and (WW/D). Specimens were either collected from the Clare Shale Formation, Co. Clare, Ireland, or accessed in museum collections. Measurements of diameter (D) and whorl width (WW) are in mm

1925 *Eumorphoceras inconstans* Schmidt, p.586, pl.22, fig. 3, pl.25, fig. 7–10.

1934 *Reticuloceras inconstans* Phillips; Schmidt, p.453, fig. 68, 69.

1943 *Reticuloceras inconstans* Phillips; Bisat and Hudson, p.424.

1943 *Reticuloceras circumplicatile* Foord; Bisat and Hudson, 425, pl.24 fig. 1, 2, pl.29 fig. 2a, b.

v1954a *Reticuloceras circumplicatile* Foord; Hodson, p.157.

v1954b *Reticuloceras circumplicatile* Foord; Hodson, p.277, pl.11 fig. 4.

v*1957 *Reticuloceras circumplicitale* Foord; Hodson, p.10, pl.A, pl.B fig. 1, 2, 4.

Also refer to Patteisky (1959); Bouckaert (1960); Chalard (1960); and Ruzhencev and Bogoslovskaya (1975).

Type locality Lisdoonvarna (erroneously labelled Cliffs of Moher), Co. Clare (see discussion in Hodson 1954b).

Type material Lectotype (NMING : F23968, Fig. 4d), Paralectotype (NMING : F23972, Fig. 4a), Paralectotype (NMING : F23969, Fig. 1a), Paralectotypes (NMING : F23971, NMING : F23973).

Other material Adolescent characters, which are missing from the type series, can be ascertained from material identified by Hodson: TCD.60601, GSM 86917 (Fig. 4b–c).

Diagnosis Phillipsoceras with prorsiradiate, strongly marked plications branching suddenly into "bunches" of usually three or four crenulate growth lines at the same point along the flank.

Description The juvenile paralectotype (NMING : F23972, Fig. 4a), 4 mm in diameter, with 5 whorls preserved, has radial or very slightly prorsiradiate plications, spaced c.6 per mm, regularly branching into growth lines at a similar point along the flank. The ornament is non-crenulate at this stage and occasional intercalations are present in the outer whorls. The number of growth lines to emerge from the plications is normally 3, in some cases 4, with secondary branching present. Growth lines are c.8–10 per mm on the venter and, while no ventral sinus is developed, there is a slight ventrolateral projection and ventral sulcus. Very faint spirals traverse plications at this diameter, but they are much more obvious at later stages of growth.

Adolescent characters can be ascertained from material identified by Hodson (TCD.60601, GSM 86917, Fig. 4b–c): in these specimens, spirals are strong on the flank, with ventral spirals starting to develop at c.9 to 10-mm diameter, although these are more clearly marked in certain specimens than others. The ventrolateral projection is pronounced, while the ventral sinus is present but less pronounced. The plications are prorsiradiate and spaced 3 to the mm; they thicken on emerging from the umbilical margin and split into three or four growth lines. Secondary branching of the growth lines is common. One or two intercalations are inserted in between the plications on the flank but they do not extend down to the umbilical margin. Growth lines are spaced 10 per mm on the ventrolateral projection. The umbilical margin is rounded with wide umbilical diameter (3.6 mm in NMING : F23968, Fig. 4d).

The adult growth lines are coarsely crenulated and, as already noted by Bisat and Hudson (1943), irregularly spaced: for instance, the lectotype (NMING:F23968, Fig. 4d) has 4–5 growth lines per mm, but a paralectotype (NMING:F23969, Fig. 1a) has 1–2 growth lines per mm on the venter. In adult specimens, the plications and the growth lines are prorsiradiate and a ventrolateral projection is present. Quadrichotomy and trichotomy are the common mode of branching. Interpolated growth lines appear between the primary plications at the branching point along the flank and these vary in number from 2 to about 6. In adult specimens (NMING : F23968, NMING : F23969, Fig. 4) described here, the umbilical plications are 2 (in some cases 3) per mm and a ventral sulcus is no longer present. Spirals are strongly marked all over the test, resulting in a strongly reticulate ornament. While the pattern of branching, namely trichotomy and quadrichotomy, is conserved, the number of intercalations grows through ontogeny.

Remarks A confident diagnosis of this species where preserved flattened can be made where a combination of the following features is present: trichotomy and quadrichotomy; strong spirals between the umbilical plications; forward projection of these plications; obviously reticulate nature of the growth lines. All diagnostic features of the ornament for this species are already present in the early adolescent growth stages and continue into maturity.

Comparisons As opposed to many other species in the genus, such as *Ph. nodosum* (Bisat and Hudson, 1943), *Ph. stubblefieldi* (Bisat and Hudson, 1943), *Ph. regularum* (Bisat and Hudson, 1943), *Ph. umbilicatum* (Bisat and Hudson, 1943) and *Ph. samlesburyense* (Bisat and Hudson, 1943), dichotomy is not the main mode of branching in *Ph. circumplicatile*. The Russian species *Ph. alpharipaeum* (Ruzhencev and Bogoslovskaya, 1975) is closely similar to *Ph. circumplicatile* (see discussion in Ruzhencev and Bogoslovskaya 1975, p.54) and they are likely to be synonyms, but this merits further investigation.

Genus *Reticuloceras* Bisat, 1924

***Reticuloceras subreticulatum* (Foord, 1903); Fig. 5; Table 3**

v*1903 *Glyphioceras (Beyrichoceras) subreticulatum* Foord, p.184, pl.49 fig. 6a, b, 7a–d.

1925 *Eumorphoceras subreticulatum* Foord; Schmidt, p.585, pl.22 fig. 1, pl.25, fig. 4–6.

v1943 *Reticuloceras subreticulatum* Foord; Bisat and Hudson, p.423, pl.26, fig. 3.

Also refer to Bouckaert (1960, 1961); Hodson (1954a, b); Patteisky (1959); and Calver and Ramsbottom (1961).

Type locality Foynes Island, Co. Limerick, Ireland.

Type material Lectotype (NMING : F23964, Fig. 5d), and associated paralectotypes (NMING : F23965, NMING : F23966, NMING : F23967) with greater diameter than the lectotype, showing features of the ornament and internal cast.

Other material Irish specimens collected by Hodson from Blake's Bridge and Fisherstreet Bay, Co. Clare, and reposited in the collections of Trinity College Dublin (TCD.60602, TCD.60603, TCD.60604, TCD.60605, Fig. 5a–c, e).

Diagnosis Ellipsocone shell with narrowly rounded umbilical edge and closely set, clearly crenulated growth lines, which dichotomize narrowly in a regular fashion one-third of the way up the flank. The spirals are less pronounced than the growth lines but still clearly visible. Trichotomy and quadrichotomy are absent and there is early development of a ventrolateral projection, which is

not pronounced. In adult specimens, growth lines are slightly rursiradiate at the dichotomizing point, which is about one-third of the distance from umbilicus to venter, before bending in a prorsiradiate direction.

Description The inner whorls are ribbed (except in the first whorl). Juvenile specimens (TCD.60602, Fig. 5a, and other specimens from Hodson's collection) at c.8-mm diameter have ribs spaced c.10 per mm and projected slightly forward into a ventrolateral projection. Three well-marked constrictions are present on the internal cast (Fig. 5a). At 9-mm diameter, umbilical plications dichotomise into growth lines, which are accompanied by intercalated growth lines (Fig. 5a, f). As adolescence is reached, the plications degenerate into growth lines which bifurcate along the flank. A ventrolateral projection is present, becoming gradually more pronounced through ontogeny. At 15-mm diameter (TCD.60603, Fig. 5b), the growth lines are spaced 8–10 per mm on the ventrolateral projection; the same is true for a specimen at 19.5-mm diameter (TCD.60604, Fig. 5c). Dichotomy is always narrow and in rare cases intercalations are present. Spiral growth lines cross the shell in the ventral area and around the ventrolateral projection.

In the lectotype (NMING : F23964, Fig. 5d, g), at 23-mm diameter, growth lines bifurcate at the point where they start to become slightly rursiradiate on the flank, about one-third of the distance from umbilicus to venter, before bending in a prorsiradiate direction. Dichotomy is narrow and growth lines are closely spaced, averaging 16 per mm on the umbilical margin and 10 per mm on the ventrolateral projection. No ventral sulci are observed on the type material. Spiral growth lines decorate several areas of the flank. Constrictions (three to the whorl) remain well marked through ontogeny. As observed in the adult paralectotypes (NMING : F23965, NMING : F23966, NMING : F23967), the growth lines tend to form bundles on the ventrolateral projection in more mature specimens and these bundles form indentations or grooves on the internal cast. The small ridges on the test produced by slightly raised growth lines mentioned by Foord (1903) are visible on the lectotype (NMING : F23964, Fig. 5d, g) and are also present in adult specimens from Blake's Bridge, Co. Clare, Ireland (Fig. 5e). Umbilical walls shallow in gradient and suture line with parallel-sided external lobe, typical of *Reticuloceras* (see Ruzhencev and Bogoslovskaya 1978).

Comparisons This species shares many features of the ornament with *Reticuloceras pulchellum* (Foord, 1903), but the cone-shaped umbilicus of the latter, with nearly vertical umbilical walls, is a distinguishing feature since *R. subreticulatum* has a narrowly rounded umbilical edge. Furthermore, the rursiradial projection of growth lines is far slighter in *R. pulchellum,* if present at all. Both species possess a ventrolateral projection, but in *R. pulchellum* the overall course of the growth lines appears to be more radial. As mentioned by Bisat and Hudson (1943, p. 424), in *R. subreticulatum* the ventral sinus is not very pronounced, in contrast to species such as *Ph. paucicrenulatum*. *Reticuloceras melanum* (Korn, 1997) has more delicate growth lines and less obvious spirals. Compared to *Reticuloceras bisorsale* (Phillips, 1836), the ornament is more subdued in *R. subreticulatum*.

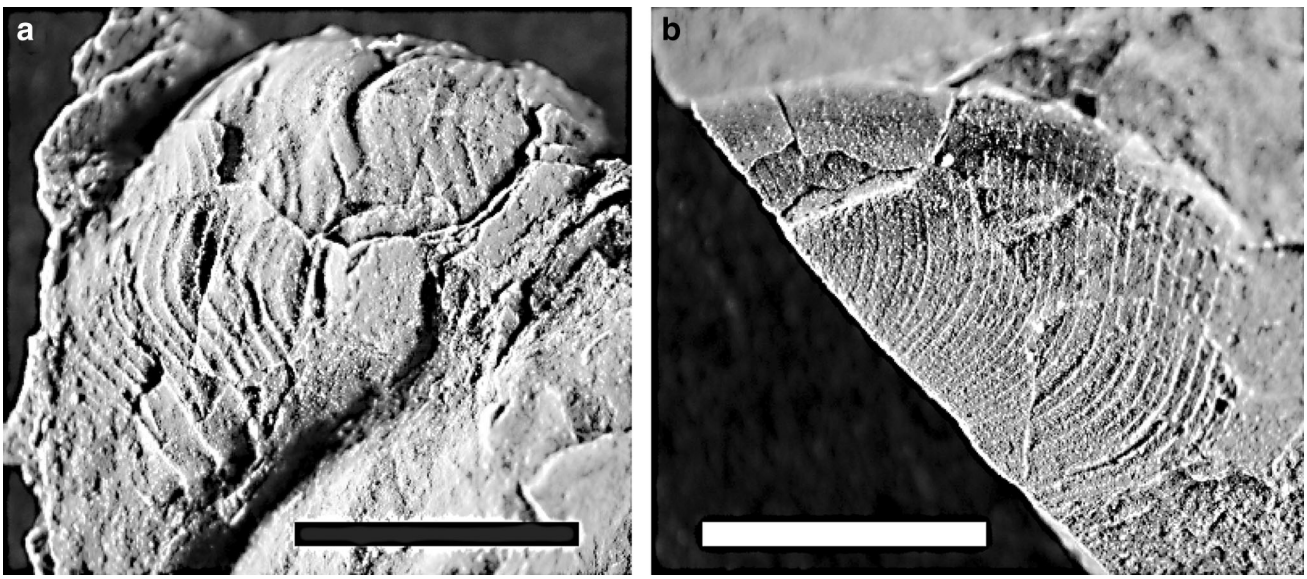

Fig. 6 Irish ammonoids preserved in 2D **a** *Ph. circumplicatile* (TCD.60606). **b** *V. henkei* (TCD.60607). Specimens are from Loop Head, Co. Clare, Ireland. *Scale bars* are 5 mm long

Discussion

For the three taxa above (namely *V. henkei, Ph. circumplicatile* and *R. subreticulatum*), changes in ornament are described systematically here for the first time. This kind of detailed description leads to more confident identifications and acts as an aid to taxonomists working on crushed material, who can refer to the ornament description for a given growth stage. For instance, *V. henkei* is usually diagnosed by features at or close to the umbilical edge (such as the presence of "beading" and an umbilical ridge). However, when these features are absent due to incomplete preservation, information such as the spacing (5 per mm in Fig. 6b) and strength of the growth lines can be used to make a determination (Fig. 6b). Similarly, *Ph. circumplicatile* shares many features of the ornament with *Ph. paucicrenulatum*, which leads to uncertainty in identifications. However, even incomplete 2D specimens can be identified where diagnostic features of the ornament are combined: for example, a crushed specimen from Co. Clare (TCD.60606, Fig. 6a) was identified as *Ph. circumplicatile* because of the presence of trichotomy and quadrichotomy as primary mode of branching, spirals along the flank and spacing of the growth lines (5 per mm).

Conclusions and further work

New data on three Bashkirian ammonoids for which ontogenetic information was previously incomplete or lacking are presented here. This information not only furthers knowledge of the ontogeny of these ammonoids but also leads to more confident specific identification of ammonoids preserved as flattened external moulds.

Further work is needed to resolve the taxonomy of 2D ammonoids. Within the R1 biozone, outstanding issues include the degree of variation within the group *Ph. circumplicatile-Ph. paucicrenulatum.* In order to make large-scale advances in 2D ammonoid taxonomy, future ontogenetic studies based on 3D shells should encompass details of changes of ornament as well as basic conch parameters.

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