Fossils explained 64

Goniatites

Most people are familiar with ammonites (see *Fossils Explained 62*, this issue), with their beautiful, logarithmically spiralled shells, but not everyone has heard of goniatites. They too were fascinating dwellers of past oceans. Goniatites are extinct cephalopods ranging from the middle of the Devonian to the end of the Permian. Although, in the strictest definition, goniatites are those ammonoids that belong to the order Goniatitida, the term goniatite is commonly used as a synonym for all Palaeozoic ammonoids. In the course of this article, the looser definition will apply.

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The cephalopods are remarkable molluscs, sharing features such as a well-developed nervous system and brain, and a mobile, carnivorous lifestyle. The class includes six subclasses, three of which are commonly fossilized: the Ammonoidea, the Nautiloidea and the Coleoidea. The subclass Ammonoidea comprises cephalopods with an external shell, generally coiled, ranging from Lower Devonian to Upper Cretaceous; it includes goniatites, ammonites and ceratites.

After a severe decline in number of taxa at the end of the Devonian period, the Carboniferous period saw the proliferation and diversification of ammonoids up until the Mid Carboniferous boundary, when another crisis in ammonoid evolution took place. Notwithstanding these two crises, an unusually rapid evolutionary rate allowed the Carboniferous goniatites to become the richest and most diverse of all Palaeozoic ammonoid faunas. While goniatites proliferated during the Carboniferous, ammonites thrived in Mesozoic times.

There is general agreement that ammonoids evolved from bactritids, another cephalopod subclass with small, orthoconic (straight) to cyrtoconic (slightly curved) shells. Bactritids were themselves derived from orthoconic nautiloids.

Shell structure

Goniatites were very diverse in terms of size, shape and sculpturing (Fig. 1). They possessed an external shell, also known as conch, made of aragonite, but this mineral is rarely preserved as it is easily altered during burial within the sediment. If the shell is dissolved, the remaining mould is commonly filled by calcite. The conch consisted of three main layers: periostracum, ostracum and hypostracum.

The external shell was divided internally into several chambers, secreted sequentially by the organism as it grew. The animal itself resided in the last formed chamber, the body chamber. As the animal grew, it vacated the previously formed body chamber, or *camera*, and secreted a chamber-dividing wall, or *septum*, behind it. The body chamber is always the largest and it is located in the anterior of the shell. The remaining chambers contained fluid and gas, which are thought to have served a function in buoyancy control. The open end of the body chamber is termed the aperture and the mouth border, or peristome, is located at the edge of the aperture. Goniatite shells are always coiled in a single horizontal plane (planispirally), with each complete coil of 360° being termed a whorl or volution. The initial chamber is known as the protoconch and the portion of shell divided into camerae is known as the phragmocone. Goniatite shells can be evolute, where the whorls overlap little or not at all, or involute, where the whorls overlap considerably. In general, involute forms were prevalent and most goniatites had a globose (roughly spherical or globular) shell. In apertural view (viewed facing the aperture) shells vary from narrow discs to broad, globose shapes (Fig. 2).

A membranous tube, called the siphuncle, extended back through all the chambers of the shell, from the protoconch to the body chamber. It originated as a small bulb, known as the caecum, within the protoconch, and consisted of organic and mineral components. The siphuncle was used to regulate fluid levels in the chambers.

The outer surface of a goniatite, where the shell has been removed, commonly displays zig-zag lines:

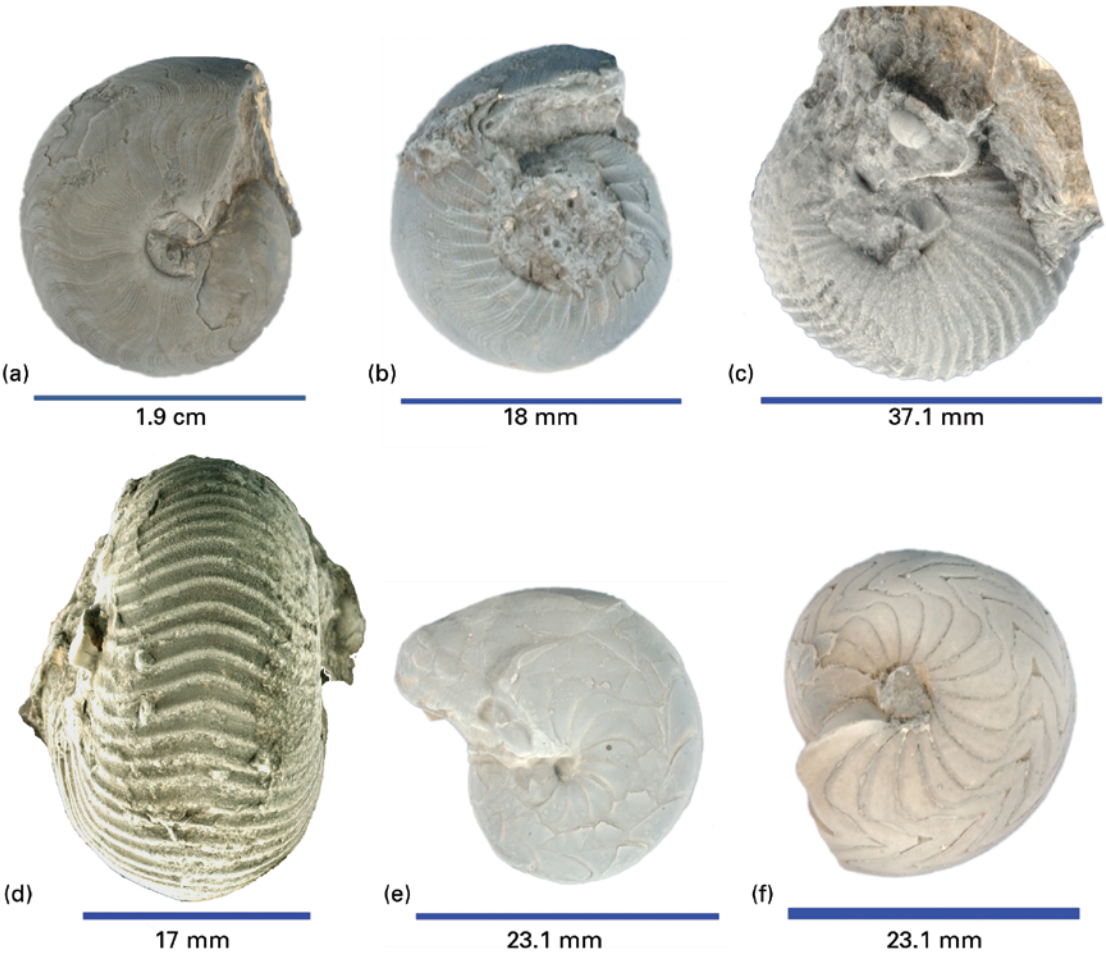

Fig. 1. a. *Reticuloceras subreticulatum* (Foord), Foynes Island, Co. Limerick, Ireland, Lectotype. **b.** *Reticuloceras circumplicatile* (Foord), Lisdoonvarna, Co. Clare, Ireland. Lectotype. **c.** Pericyclus sp., Locality unknown. Note associated small goniatite with prominent constriction. **d.** Same specimen in dorsal view. **e.** *Goniatites*, Rush Slates, Lower Carboniferous, Co. Dublin, Ireland. **f.** Goniatite, Locality unknown.

these are known as suture lines. It is the angular pattern of these lines that gives goniatites their name: in fact, the Greek word γωνια means angle. Suture lines mark the position where the internal chamber-dividing walls (septa) join to the inner side of the external shell. Hence they are only visible once the external shell has been removed (Fig. 3).

There are several terms associated with the description of suture lines. For example, saddles are deflections of the suture line in the adoral direction (towards the aperture), whereas lobes are deflections in the adapical direction (away from the aperture). The oldest suture line is called prosuture and it is defined as the part of the septum that partitions off the protoconch. The next suture to be formed is the primary suture, which is generally regarded as the first true suture. Within the suture line, external (ventral), lateral and internal (dorsal) lobes are known as the primary lobes, since they appear first in ontogeny and phylogeny. A lateral lobe is nearly always present on the flank of ammonoid shells. Additional lobes may form by division of the saddles.

Suture lines are generally represented with an arrow pointing in the direction of growth and, when illustrated, they are projected as a line on a plane. Usually only half is represented.

Goniatites are almost always less than 15 cm and commonly smaller than 5 cm in diameter. Goniatite shells can be smooth or can present varying degrees of ornamentation. Examples of ornamentation include ribs, which are radially directed ridges, sometimes referred to as costae or pilae, riblets, which are small ribs, furrows or depressions, and striae, which are minute grooves on the shell surface. In addition to these, constrictions, defined as depressions encircling the whorl, and plications, defined as coarse radial folds, are common examples of ornamentation found in goniatites. Growth lines, which usually run parallel to the ribs, are defined as striae encircling the whorl and mark repeated minor halts in shell growth.

Growth and ontogeny

Goniatites grew incrementally, via periodical secretion of new septa. A record of their growth is thus retained in their shells, facilitating ontogenetic studies. The following growth stages have been recognised: ammonitella, which is essentially the embryo; neanoconch, or early juvenile; juvenile and adult. If one traces the ontogenetic development of the suture line in a single shell, it is clear that it becomes more complex during the individual's life. In turn, this is paralleled in the phylogenetic development of ammonoids as a whole: while goniatites had relatively simple suture lines, ammonites evolved complex patterns.

Taxonomy

Overall ammonoid classification is based upon differences in suture line pattern, whereas classification of lower systematic units, within goniatites for instance, such as families, genera and species, is based on characteristics such as shell size, sculpturing, shell shape and umbilical width.

The typical goniatitic suture line pattern has undivided, curved saddles and undivided, pointed lobes. In contrast, ceratitic suture lines have denticulate or frilled lobes and rounded, unbroken saddles, while ammonitic suture lines have frilled saddles and lobes.

On this basis, ammonoids with few simple saddles and lobes, such as in the genus *Goniatites* from the Lower Carboniferous, are known as goniatites, and, following the same line of thought, ammonoids can be divided into three groups: goniatites, ceratites and ammonites. However, goniatitic sutures are not exclusive to Palaeozoic goniatites, nor do all goniatites have a goniatitic suture line pattern. So caution must be exercised when using suture lines as a means of classification. To obviate some of the problems posed by this simplistic classification, Wedekind, in 1918, introduced the terms palaeo-, meso- and neoammonoids to classify ammonoids better. In this scheme, all ammonoids of the Palaeozoic are termed palaeoammonoids and so on. Palaeoammonoids can be divided into three orders: Goniatitida, Clymeniida and Prolecanitida. The clymenids are characterised by a dorsal siphuncle, in contrast to the ventral siphuncle of all other ammonoids. The prolecanitids are characterised by a lateral lobe, which is displaced towards the venter; notably, this order gave rise to all ammonoids of the Mesozoic.

Thirdly, goniatites (Order Goniatitida) have a small lateral lobe, close to the umbilical seam, which in turn is the helical line of overlap of successive whorls. In addition, at least one adventitious lobe is present, following division of the saddle between the lateral lobe and the external lobe.

One might wonder why ammonites evolved complex sutures in the first place, but this is a question that is still not fully understood. Having said this, one of the most popular suggestions is that this adaptation served to strengthen the shell and could therefore enable the animal to withstand greater hydrostatic pressure.

Importantly, the simple suture line in nautiloids is in stark contrast to the complex sutures found in ammonoids. But other morphological differences are also important in distinguishing these two subclasses. Ammonoids have a thin siphuncle on the outer region of the whorl, while nautiloids have a thick siphuncle with no fixed position. The septa are concave toward the body chamber in nautiloids, but convex in ammonoids. Furthermore, the shell was generally thicker in nautiloids.

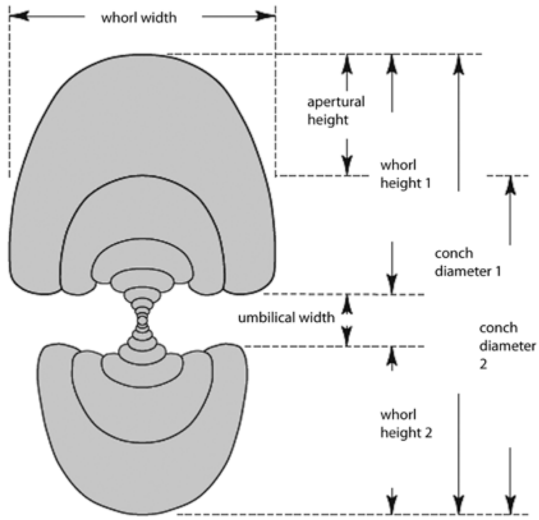

Fig. 2. Palaeozoic ammonoid conch morchology (after Korn, 2010).

In order to classify goniatites, ornamentation is often important. For instance, the shape of the growth lines can vary from species to species and can often be used as a diagnostic feature. In general, growth lines are known as linear when they are straight or nearly straight on the flank and venter of the conch. They are known as convex if they form a single, broad salient, also known as lingua, on the lateral area and a hyponomic sinus (reentrant notch) on the venter. They are biconvex if salients are formed on both the umbilical margins and ventrolateral areas of the conch.

Goniatites can be preserved as flattened or three-dimensional specimens and different identification methods must be applied to these different modes of preservation. The character of the ornament is the main means of identification of flattened specimens. The strength, character and general direction of the ornament are important features. For instance, goniatites of the genus *Reticuloceras* possess reticulate ornamentation: in other words, both tranverse (radial) and spiral (in the direction of coiling) ornament. In contrast, goniatites of the genus *Homoceras*, with a

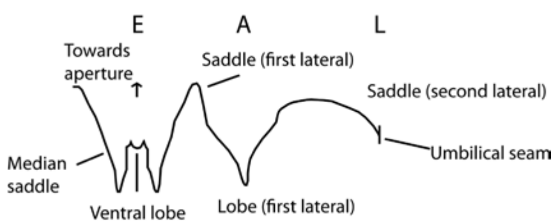

Fig. 3. Generalized terminology of the Suture line.

few exceptions, do not possess spiral striae. In some taxa, extra striae are interpolated between two existing striae, or a single rib may dichotomize, trichotomize or quadrichotomize. These are all important features in identification.

Solid, three-dimensional specimens are often found in hard, calcareous concretions and, by splitting these apart, it is often possible to examine the cross sectional view of the whorls (Fig. 4). This allows the three basic conch diameters to be measured: these are whorl width, whorl height and conch diameter. Starting from these, it is possible to calculate features such as umbilical width, apertural height and imprint zone width. If the external shell is preserved on the three-dimensional specimens, it can sometimes be carefully peeled off to reveal the suture line on the internal mould.

Mode of life

Goniatites are extinct, so any interpretation of their mode of life is by inference. Indeed, the distribution of goniatites in space and time is much better known than their biology. The pearly *Nautilus* is the only known living descendant of externally shelled cephalopods. But, however tempting it may be to draw palaeoecological inferences from *Nautilus*, it must be noted that it is not phylogenetically closely related to ammonoids.

Nevertheless various approaches can be used, from synecological studies, which look at the associations and occurrences of ammonoids in the field, to autoecological studies, which focus on the morphology of the individual shell in order to obtain physical constraints on the living organism. Most palaeoecological studies focus on ammonoids as a whole, rather than on goniatites in particular. Therefore any discussion is based on the assumption that the conclusions reached are valid for all ammonoid taxa, including goniatites. As such, the reader is referred to *Fossils Explained 62: Ammonites*, also in this issue, for further information on mode of life.

The world-wide distribution of goniatites indicates a nekto-pelagic habit and the ability to invade various habitats. While neanic and most small juveniles were quasiplanktic, at maturity they became more mobile. Having said this, swimming ability remains controversial in ammonoids and the drag associated with the shell would certainly hinder high-speed swimming.

Lenticular shells with bilateral symmetry are generally associated with mobility, while prominent ornamentation is associated with reduced locomotion. In goniatites, the growth lines are generally fine and not very prominent, which is consistent with a nektonic habit. However, the globose shape of most goniatites suggests they were poor swimmers.

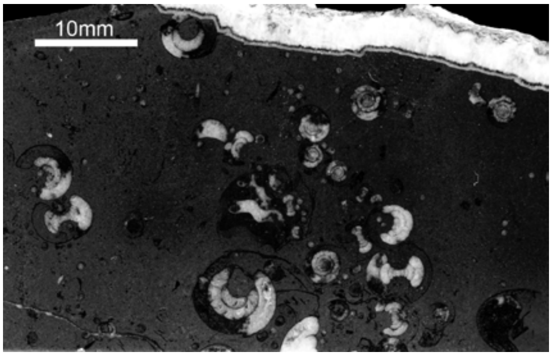

Fig. 4. Close-up of a polished section through a bullion. Goniatites in cross-sectional view, showing inner whorls. From St Brendan's Well, Lisdoonvarna, Co. Clare, Ireland.

Modifications of the shell at maturity include the formation of lappets, which are projections of the peristome in the ventral area. This particular modification probably served to streamline the shell and facilitate swimming. It has been recorded in goniatites of the genus *Eumorphoceras*.

The genus *Entogonites* is characterised by a tetrangular coiling of its inner whorls, a unique feature in Palaeozoic ammonoids. Even though it is unclear what the functional properties of this type of coiling were, the horizontally orientated aperture (calculated from the opening rate of the whorl spiral) in *Entogonites* suggests a planktonic lifestyle.

In general, a combination of autoecological and synecological approaches is best in any comprehensive palaeoecological study. One thing is certain: goniatites still leave mysteries to be uncovered.

Use in biostratigraphy—a case study from the Irish Carboniferous

Because of their high evolutionary rates, their broad geographic distribution and relatively easy recognition, goniatites are a prime tool in biostratigraphy. In many intervals, international ammonoid zones provide time resolution in the order of a few hundred thousand years.

Having said this, ammonoid faunas become more provincial during the Mississippian series of the Carboniferous. In fact, in two papers in 2002–2003, Korn and colleagues showed that Middle and early Late Tournaisian faunas from Morocco closely resemble time-equivalent faunas from the United States, Europe, the Urals and Central Asia, but, during the late Visean, ammonoid provinces were formed. The genera *Entogonites* and *Goniatites* have wide palaeogeographical distribution, indicating cosmopolitism at the genus level at least until the end of the middle Visean.

Even when provincial, goniatites are extremely useful in more local studies. In Europe, goniatites have been used to subdivide and zone the Carboniferous (see Waters & Condon for a table summarizing the ammonoid zones and subzones of the Namurian regional stage).

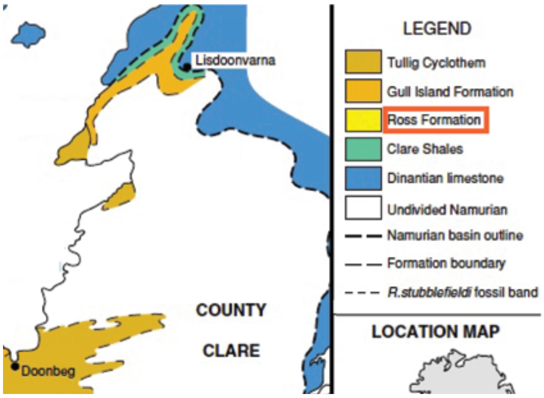

Fig. 5. Northern part of Western Irish Namurian Basin (after Martinsen & Collinson, 2002).

For example, the stratigraphy and sedimentology of the Western Irish Namurian Basin relies on the biostratigraphic framework that only goniatites can provide. This basin developed in latest Devonian and Early Carboniferous time as a result of crustal extension. Carboniferous limestone floors the basin and the basin fill succession begins with the deep water Clare Shales. These are overlain by various turbidite facies of the Ross Formation. The Ross Formation is in turn overlain by the muddier Gull Island Formation, which grades up into shallow marine and continental deposits of the Central Clare Group (Fig. 5).

Hodson and Lewarne established the biostratigraphy of the basin in the 1950s. Goniatites are largely restricted to laterally extensive marine bands, which are organic-rich shales with a mixed fauna, including goniatites and bivalves. Each band has a distinctive faunal assemblage, usually with a dominant goniatite species, that allows correlation within the basin.

For instance, the index fossils employed in the biostratigraphy of the Ross Sandstone, which crops out mainly in the Loop Head Peninsula, Co. Clare, Ireland, are: *Reticuloceras paucicrenulatum*, *Reticuloceras circumplicatile*, *Homoceras henkei* and *Homoceratoides prereticulatus*.

These taxa were described in key papers by Bisat in 1923 and Bisat & Hudson in 1943. Behind-outcrop coring, coupled with sedimentary logging and other techniques have helped elucidate the depositional environment of the Ross Sandstone, but there is still considerable uncertainty regarding detailed correlation across the peninsula. Current research is re-examining the biostratigraphy and attempting to solve some of these outstanding issues.

Acknowledgements

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Suggestions for further reading

The online database GONIAT (www.goniat.org) is a very useful biostratigraphical tool: it includes biostratigraphical range and palaeogeographical distribution of Palaeozoic ammonoids.

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