Chapter 2
Ammonoid Color Patterns

Royal H. Mapes and Neal L. Larson

2.1 Introduction and Background

Mapes and Davis (1996) provided an extensive overview of preserved ammonoid color patterns. Their report covered the general history of reported occurrences and listed three genera from the Triassic, six genera from the Jurassic, and six genera from the Cretaceous (Tab. 2.1). They also discussed the possible kinds of color patterns (transparency, achromatism, monochromatism, irregular and regular spot patterns, transverse zigzag, chevron and radial stripes and longitudinal stripes or bands), geographic occurrences, and ways to recognize biological patterns vs. false patterns produced by shell thickening and diagenetic processes. Included was a comparison of the color pattern in *Nautilus* (and *Allonautilus*), the only known externally shelled cephalopods living today. In addition to the above, they speculated on the functions of patterns and on the possible different mechanisms of taphonomic destruction of the ammonoid color patterns to explain why such patterns are so rarely preserved.

Mapes and Davis (1996) were puzzled that orthoconic and coiled nautiloids and bactritoids with color patterns had been recovered from the Late Paleozoic (Carboniferous), but none of the ammonoids co-occurring with those cephalopods retained any trace of a color pattern even though in some cases many thousands of ammonoid specimens had been recovered from the same locations and strata. This problem remains unresolved. Since 1996, some new information has come to light and is reported herein. This includes the recognition of iridescent color patterns, some new false color patterns, and some limited information on the development of specific color patterns associated with habitat and mode of life.

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Table 2.1 Occurrences of ammonoids with color patterns, modified after Mapes and Davis (1996)

Taxon	Author	Pattern	Quality	Country
Triassic				
Arctoceras sp.	This report	M	M	USA
Dieneroceras knechti	This report	L	D on L	USA
Dieneroceras spathi	Mapes and Sneck 1987	L	D on L	USA
Dieneroceras subquadratum	Mapes and Davis 1996	L	D on L	USA
Flemingites russelli	This report	M	M	USA
Juvenites septentrionalis	This report	R	D on L	USA
Juvenites thermarum	This report	R	D on L	USA
Kashmirites sp.	This report	L	D on L	USA
Owenites koeneni	Tozer 1972; Mapes and Sneck 1987	R	D on L	USA
Owenites sp. *cf. 0. koeneni*	Mapes and Sneck 1987	R	D on L	USA
Owenites sp.	Mapes and Sneck 1987	C	D on L	USA
Paranannites aspensis	This report	R	D on L	USA
Paranannites mulleri	This report			
Prosphingites slossi	Keupp 2000	R	D on L	USA
Preflorianites toulai	Keupp 2000	R	D on L	USA
Xenoceltites sp.	This report	L	D on L	USA
Jurassic				
Amaltheus stokesi	Spath 1935	L pathologic	D on L	England
Amaltheus subnodosus	Pinna 1972	L	D on L	Germany
Amaltheus gibbosus	Pinna 1972	L	D on L	Germany
Amaltheus margaritatus	Mapes and Davis 1996	L	D on L	England
Androgynoceras lataecosta	Spath 1935; Arkell 1957	L	D on L	England
Asteroceras stellare	Arkell 1957	L	L on D	France
Asteroceras stellare	Manley 1977	S	D on L	England
Cadoceras sp.	This report	L	I on N	Russia
Eboriceras sp.	This report	L	I on N	Russia
Kosmoceras jason	This report	L	I on N	Russia
Leioceras sp.	Greppin 1898; Arkell 1957	L	L on D	Switzerland
Pleuroceras spinatum	Schindewolf 1928, 1931; Arkell 1957	R	D on L	Germany
Pleuroceras salebrosum	Pinna 1972; Lehmann 1990	S	D on L	Germany
Pleuroceras transiens	Pinna 1972	S	D on L	Germany
Pleuroceras sp. aff. *solare*	Heller 1977	L	D on L	Germany
Proriceras sp.	This report	L	I on N	Russia
Quenstedtoceras (*Lamberticeras*) *lamberti*	This report	L	I on N	Russia

Table 2.1 (continued)

Taxon	Author	Pattern	Quality	Country
Quenstedtoceras henrici	This report	L	I on N	Poland
Tragophylloceras loscombi	Pinna 1972	L	D on L	England
Xipheroceras sp.	This report	R	D on L	Germany
Cretaceous				
Beudanticeras ambanjabese	This report	L	I on N	Madagascar
Beudanticeras beudanti	This report	L	I on N	Madagascar
Beudanticeras caseyi	This report	L	I on N	Madagascar
Calliphylloceras sp. aff. *C. demedoffi*	Bardhan et al. 1993	R	D on L	India
Cleoniceras sp.	This report	L	I on N	Madagascar
Desmoceras media	This report	L	I on N	Madagascar
Desmoceras inflatum	This report	L	I on N	Madagascar
Hoploscaphities nicolletii	This report	L	I on N	USA
Hoploscaphities (Jeletz-kytes) reesidei	This report	L	I on N	USA
Libycoceras afikpoense	Reyment 1957	s	D on L	Nigeria
Placenticeras meeki	This report			USA
Paratexanites (Parabe-vahites) serratomarginatus	Matsumoto and Hirano 1976	L	D on L	Japan
Protexanites (Protexanites) botanti shimizui	Matsumoto and Hirano 1976	L	D on L	Japan
Protexanites (Anatexanites) fukazawai	Matsumoto and Hirano 1976	L	D on L	Japan
Pseudouhligella sp.	This report	L	I on N	Madagascar
Puzosia malandiandrensis	This report	L	I on N	Madagascar
Hoploscaphites nicolletii	This report	L	I on N	USA
Submortoniceras woodsi	Kennedy et al. 1981	L	D on L	South Africa
Tetragonites glabrus	Tanabe and Kanie 1978	L	D on L	Japan
Tetragonites sp.	Tanabe and Kanie 1978	R	D on L	Japan

S spots, *L* longitudinal, *R* radial/transverse, *C* combined, *M* monochrome, *D* on *L* dark on light, *L* on *D* light on dark, *I* on *N* iridescent on nacre color

2.2 Additional Reports of Ammonoid Color Patterns

Mapes and Davis provided a relatively complete documentation of the known color patterns that had been described up to 1996. However, because there is no comprehensive listing of this biological condition for fossil cephalopods, inevitably some reports and specimens in museum collections were missed. One missed report is by Klinger and Kennedy (1981) where a specimen of *Submortoniceras woodsi* (Spath 1921) from the Cretaceous of South Africa was described and illustrated with traces of longitudinal banding. According to these authors, similar banding was described by Matsumotoi and Hirano (1976) on a stratigraphically older specimen of *Protexanites (P.) bontanti shimizui* Matsumoto 1970 from Hokkaido, Japan.

We know of only three new reports since Mapes and Davis (1996) summarized the known occurrences of ammonoids with color patterns. Probably the most significant new information is the report by Ebbighausen et al. (2007) of a Devonian goniatite with a color pattern from Morocco. The single specimen has dark transverse bands that follow the sinuous growth lines on a specimen of *Tornoceras* sp. This color-banded taxon is limited to a single specimen at this time. We accept this report with some reservation because of the limited number of specimens reported. However, presuming that this report is valid, this specimen would represent the oldest color pattern known in the ammonoid lineage, the only specimen of a goniatite with a color pattern, and it is the only ammonoid specimen with a color pattern known from the Paleozoic.

A Jurassic specimen of *Xipheroceras* sp. from Germany has been brought to our attention as having multiple longitudinal color bands (Klug, personal communication 2012). The specimen is approximately 185 mm in diameter and the relatively thin bands are dark on a light background on the outer shell. The bands are present on both the lateral, ventrolateral, and venter of the conch (Fig. 2.1). These color bands are similar to those described and illustrated by Lehman (1990, Fig. 2.1) on *Pleuroceras* sp. from the Jurassic of Germany.

A possible color pattern on *Placenticeras meeki* from an unknown locality in the Cretaceous of North America has also been discovered (Fig. 2.2). There are two types of dark bands on the specimen. One is expressed as dark bands that are widely spaced and that follow the growth lines of the specimens. These widely spaced bands are interpreted as a false color pattern and probably result from shell thickening like that seen in other false color patterns (see below). The other set of transverse bands are closely spaced, slightly darker bands than that of the shell material and are only observed on the right side of the conch on an internal whorl of

Fig. 2.1 Longitudinal color bands (see *arrows*) on a specimen of *Xipheroceras* sp. *SNMS* (= Staatliches Museum fuer Naturkunde, Stuttgart, Germany) 70085 from the Arietenkalk Formation, basal late Sinemurian, Obtusum-Zone, at Schwäbisch-Gmünd-Unterbettringen, Germany. Scale Bar = 3.0 cm

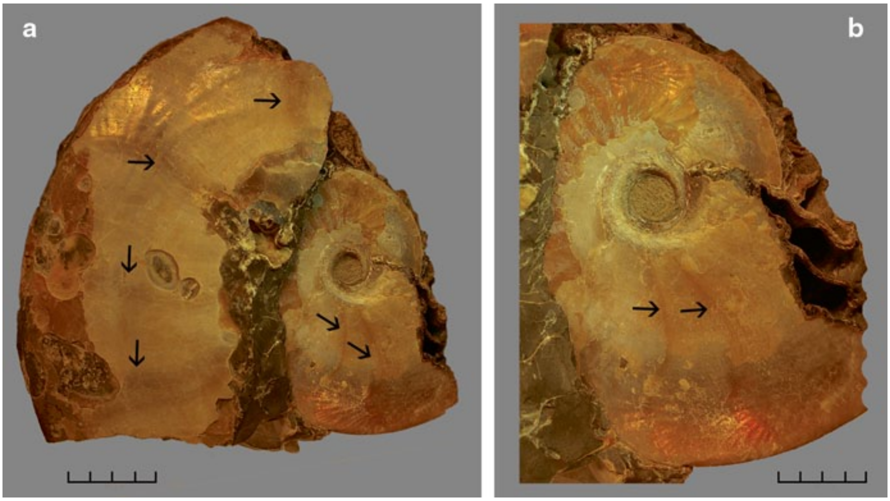

Fig. 2.2 *Placenticeras meeki,* late Campanian, Late Cretaceous, Pierre Shale, most likely South Dakota with a possible pigment emplaced color pattern. **a**. Overall view of the specimen showing several dark transverse bands that follow the growth lines on the outer whorl (at *arrows*) that are interpreted as false color patterns. Scale bar=4.0 cm. **b**. Enlarged view of the exposed inner whorl showing approximately seven closely spaced transverse dark bands on the exposed shell near the venter that are interpreted as possible color bands. Also, on this part of the specimen there are several (see *two arrows*) of the more widely spaced dark transverse false color bands similar to those seen at the arrows on the outer whorl as shown in **a**

the phragmocone. These dark bands are on a lighter surface of the external shell and appear to be confined to the outer shell layer. That this case is a legitimate biologically emplaced color pattern is uncertain because bilateral symmetry of the bands cannot be observed and the pattern is not expressed any other places on the testiferous conch. Thus, we believe that additional specimens are necessary to confirm that these are biologically emplaced color bands.

2.3 False Color Patterns

2.3.1 Background

According to Mapes and Davis (1996), false color patterns can have several different appearances ranging from random blotches to longitudinal and transverse bands on the shell. These different patterns are caused by a variety of different mechanisms. The false color pattern that Mapes and Davis (1996) indicated as most common is where thickening of the shell is present. Such places are at constrictions, pseudo-constrictions, and varices. Additional places not noted by Mapes and Davis (1996) include ribs, falcations, nodes and other places where shell thickening can occur. In any case, it appears that these false color patterns are associated with growth halts, during which megastriae or similar growth-related structures were formed (see Klug et al. 2007 for a discussion and references).

2.3.2 Reports

Since 1996, several new reports of false color patterns have been made. Klug et al. (2007) indicated that they had observed dark areas where the shell was thickened on several Carboniferous and Triassic ammonoid genera. These transversely placed bands were at regular intervals where an interim aperture position was located (megastriae). They concluded that these dark bands were the remnants of black organic material like that seen on the dorsal shell and at some injury sites on modern *Nautilus*, and that these bands were the product of some form of stress or adverse conditions during the animals growth in a broad sense. We are not confident that this explanation is adequate or correct; however, we do agree that these "color" bands are not an organic pigment emplaced like the brown transverse stripes seen on modern *Nautilus*. Thus, until additional study is done on these phenomena, we will consider them to be, with reservation, in the general category of "false color bands".

In another report Klug et al. (2012) described a situation where 17 specimens of the ammonite *Baculites* sp. (Late Cretaceous) from Germany were recovered with exceptional soft tissue preservation. One of the specimens is reported to have 11–12 false color bands on the shell. Klug et al. (2012) correctly determined that the bands were a false color pattern and indicated that these dark bands were places where growth of the animal had slowed or temporarily halted and faint ribs were deposited.

A report on a false color pattern not mentioned by Mapes and Davis (1996) is by Branson (1964). He described a specimen of *Goniatites choctawensis* (now considered to be *G. multiliratus*) from the Delaware Creek Member of the Caney Formation in south central Oklahoma as an internal mold with dark and light bands in the spaces between the septa. He considered the infilling material to be calcite with "internal mineral color". He also noted that similar specimens from the Early Carboniferous of Derbyshire, England had similar brown patterns. We agree that this coloration is a false color pattern although it could even be post mortem (i.e. diagenetic); however, little study has been done on why the calcite in the cameral chambers is colored. Under normal circumstances, one would assume that the coloration is a result of trace mineral elements in the calcite. However, sliced specimens of various Carboniferous goniatites (including ones from the Delaware Creek Member of the Caney Formation in Oklahoma), Permian prolecanitids, and Cretaceous ammonites that had colored calcite in the phragmocone chambers received some limited study (RHM, new observations). These specimens were very slowly (weeks) dissolved in very dilute acetic acid, and it was discovered that when the calcite was removed from the cameral chambers, the colored cameral filling was a fibrous-like gel that dried into a fibrous mat similar to the pelical lining seen in the chambers of modern *Nautilus*. Significantly, the goniatite specimens with clear calcite in the same acid containers with specimens that had the colored calcite did not have this fibrous gel material in the cameral spaces. The significance of this fibrous gel remains unstudied, but it is here speculated that this fibrous gel material is a remnant of the original cameral fluid and that the original cameral fluid in ammonoids was more of a gel, rather than a liquid as is seen in modern *Nautilus.* Additional study of this phenomenon is recommended.

Another kind of false color pattern is known from two cases, one is in the Devonian of Germany (Richter 2002; Richter and Fischer 2002) (Fig. 2.3), and the other is from the Early Jurassic of England (Paul 2011). In all cases, the specimens are extremely well preserved pyritized internal molds. On the surface of these molds, there are regular patterns of dark areas on the brilliant shiny surface of the internal mold of the specimen. These patterns can form transverse bands that follow the septa in phragmocones or as bilaterally symmetrical dark patches (Fig. 2.3). Richter (2002) and Richter and Fischer (2002) provided a convincing discussion as to the origin of these patterns. They observed that the darkening of these areas on the internal mold of the shell are places where the shell was rough-textured with micropyrite crystals. These rough textured areas are without the polish seen on the smooth surfaces of the internal mold of the rest of the specimens. They concluded that these dark patches are attachment scars and interpreted them as soft tissue attachment structures (Richter 2002; Richter and Fischer 2002). Paul (2011), in his analysis of the English specimens, concluded that the transverse bands he observed represented pauses in the growth of the animals he analyzed. In all of these cases, the dark bands are on the internal mold, and therefore, they are not biologically emplaced pigments in the shell of these animals. Also, these authors were convinced that the repetition of the bands is directly related to the episodic growth of the animal.

2.4 Iridescent Color Patterns

2.4.1 Background

In the last decade, hundreds of ammonite specimens with undescribed iridescent color patterns have been discovered. Keupp (2005) was the first to describe and illustrate this occurrence, although Reyment (1957) indicated he had seen such a color pattern but did not adequately document this phenomenon. It must be noted that photography of this phenomenon is difficult because this feature is usually more evident as the specimen is moved in the light, and it may for this reason that Reyment could not adequately document it in his 1956 report.

These newly recognized color patterns are preserved as iridescent longitudinal bands parallel to the venter on the external surface (presumably the outer prismatic layer) of the shell. These bands are probably the result of the prismatic shell ultrastructure selectively breaking down light into different wavelengths (i.e., different colors), but this phenomenon needs additional study to confirm this assumption and to test in how far the appearance of the color patterns was altered by diagenesis.

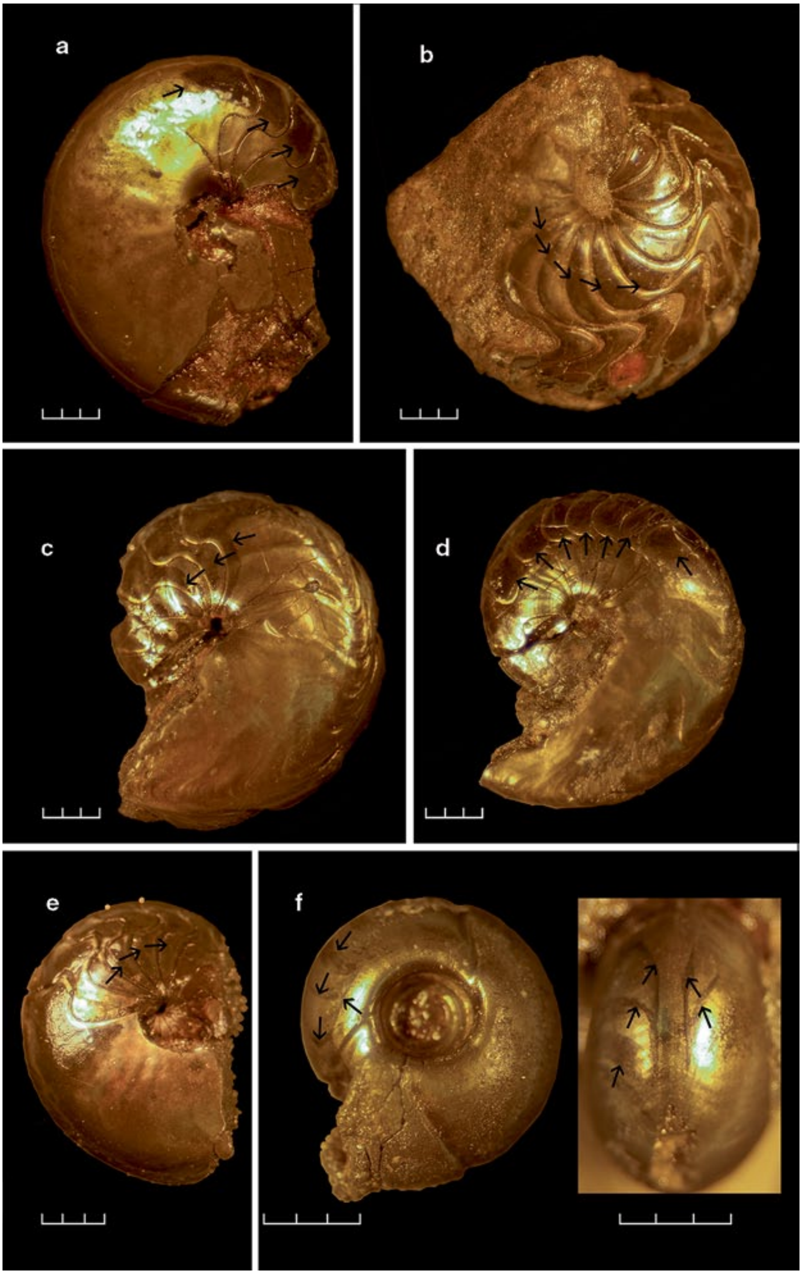

Fig. 2.3 **a–e** Pyritized internal molds of six Devonian ammonoid genera from Germany with false color patterns. The false color patterns are bilateral *black* areas on the golden pyrite of the phragmocones and sometimes the apical parts of body chambers (see *arrows*). All specimens are reposited at the Institut für Geologie und Paläeontologie der Universtät Münster (MB.C). **a** Left lateral view of *Armatites* aff. *planidorsatus* specimen MB.C 2910(272,E54), **b** Right lateral view of *Linguatornoceras haugi* specimen MB.C 3087 (265,E38), **c** Left lateral view of ? *Truyolsoceras* sp. specimen MB.C 3071 (2614,E410), **d** Left lateral view of *Cheiloceras (Puncticeras) longilobum*

Fig. 2.4 World map showing the locations around the world where ammonoids with iridescent color patterns have been recovered. In North America: *1* north-central South Dakota and *2* Coon Creek, Tennessee; Europe: *3* Normandy, France, *4* Łuków, Poland, and *5* Saratov, Russia, and Africa: *6* Mahajanga province, Madagascar

2.4.2 Locations, Description, and Ages of Specimens

Ammonoid sites that preserve an iridescent color pattern have been collected from around the world (Fig. 2.4) in the Jurassic (Fig. 2.5), the Early Cretaceous (Fig. 2.6), and the Late Cretaceous (Fig. 2.7). The locations and ages are as follows: Late Jurassic, Callovian Stage of Saratov, Russia and Łuków, Poland (Fig. 2.5); the Early Cretaceous, Albian Stage of Mahajanga Province, Madagascar and Normandy, France (Fig. 2.6); the Late Cretaceous, late Campanian Stage of south-central Tennessee, USA and the Late Cretaceous, late Maastrichtian Stage of north-central South Dakota, USA (Fig. 2.7).

2.4.2.1 Russian Occurrence – Late Jurassic

At the Saratov site (Russia, Late Jurassic) ammonoids were collected from the Dubki Quarry, a site that quarries a hard-clay used in the production of bricks. The Dubki Quarry lays in the *Quenstedtoceras* (*L.*) *lamberti* Zone – latest late Callovian of the Late Jurassic. This zone contains clays and marls deposited under oxygen

specimen MB.C 2908 (15,E66), **e** *Right* lateral view of *Falcitornoceras korni* (MB.C 3073 (2606, E402), **f–g** *Right* lateral and ventral views, respectively, of *Paratorleyoceras globosum* (MB.C 3086 (661,E33). Scale bars = 3.0 mm

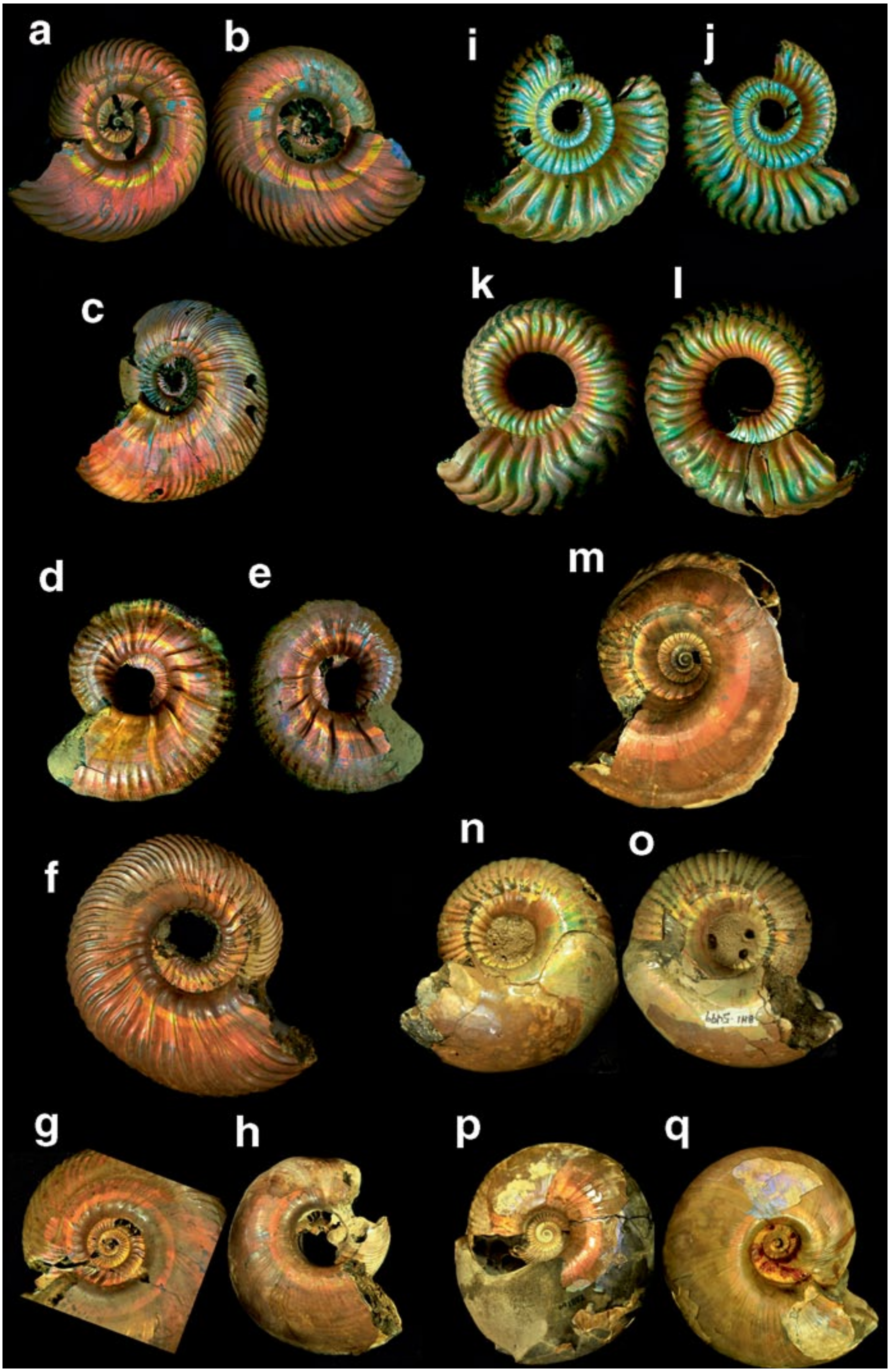

Fig. 2.5 Five ammonoid genera from the Late Jurassic with iridescent longitudinal color bands. Four of the ammonoid genera are from the late Callovian, Late Jurassic, Dubki Quarry near Saratov, Russia (**a–o**) and one genus is from the late Callovian, Late Jurassic in Łuków, Poland (**p–q**).

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