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THE AMMONITE FAMILY  
HILDOCERATIDAE IN THE  
LOWER JURASSIC OF  
BRITAIN

MICHAEL K. HOWARTH

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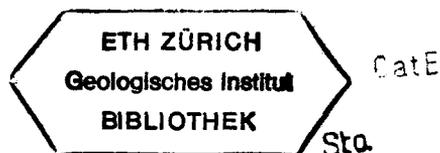
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MICHAEL K. HOWARTH

PART 1

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#### ABSTRACT

Part I includes introductory matter, methods of classification, stratigraphy, biostratigraphy, discussion of the quantitative methods used, and an account of the extent of dimorphism in Hildoceratidae. Species of the harpoceratinid genera *Protogrammoceras*, *Lioceratoides*, *Tiltoniceras*, *Eleganticeras* and *Cleviceras* gen. nov. are described.

#### RÉSUMÉ

La 1ère partie comporte une introduction, les méthodes de classification, la stratigraphie, la biostratigraphie, une discussion des méthodes quantitatives utilisées ainsi qu'un exposé sur l'importance du dimorphisme chez les Hildoceratidae. Des espèces appartenant aux genres Harpoceratinés *Protogrammoceras*, *Lioceratoides*, *Tiltoniceras*, *Eleganticeras* et *Cleviceras* gen. nov. sont décrites.

#### KURZFASSUNG

Teil 1 enthält die Einführung, Methoden der Klassifikation, die Stratigraphie, Biostratigraphie, Diskussion der angewandten quantitativen Methoden und einen Beitrag über das Ausmaß des Dimorphismus bei Hildoceratidae. Beschrieben werden Arten der Harpoceratinae-Gattungen *Protogrammoceras*, *Lioceratoides*, *Tiltoniceras*, *Eleganticeras* und *Cleviceras* gen. nov.

#### РЕЗЮМЕ

Часть I включает вводную часть, методы классификации, стратиграфию, биостратиграфию, дискуссию по использованным количественным методам и рассмотрение степени диморфизма у Hildoceratidae. Описаны виды харпоцератин, принадлежащие родам *Protogrammoceras*, *Lioceratoides*, *Tiltoniceras*, *Eleganticeras* и *Cleviceras* gen. nov.

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# THE AMMONITE FAMILY HILDOCERATIDAE IN THE LOWER JURASSIC OF BRITAIN

## INTRODUCTION

This monograph is based on a large number of ammonites collected bed-by-bed from all the exposures of the Lower Toarcian that existed in England between 1955 and the mid-1980s. The aim was twofold: first, to use the ammonites as the basis for biostratigraphical subdivisions, and secondly to describe the ammonites themselves and to elucidate their phylogeny. A scheme of zones and subzones for the Toarcian existed from work done by earlier authors. This was refined, adapted and checked against the succession of ammonites in all parts of the country, and the final biostratigraphical scheme that evolved was published as the Toarcian correlation chart in the Geological Society's "A correlation of Jurassic rocks in the British Isles" (Cope *et al.* 1980). Some stratigraphical work was found to be necessary, and basic description of the successions or revision of earlier work was published in four papers (Howarth 1962b, 1973, 1978, 1980a).

Apart from a few members of the Phylloceratidae and the Lytoceratidae, the two families of ammonites that dominate the British Lower Toarcian are the Dactylioceratidae and the Hildoceratidae. Specimens occur in abundance, and in the collection as a whole approximately equal numbers of the two families were obtained. However, they rarely occur abundantly together. In most beds one family is usually dominant and the other much less frequent, or even absent. The two families present entirely different problems in classification. Basically, species of Dactylioceratidae are often very variable, sometimes extraordinarily so (e.g. the Yorkshire Tenuicostatum Zone species of *Dactylioceras* (*Orthodactylites*) described by Howarth (1973)), while species of Hildoceratidae are relatively closely defined, exhibiting much less variation. Sexual dimorphism might be present in British Dactylioceratidae, but the evidence is poor, and is entirely absent at most horizons, despite the very large collections that have been obtained from some single beds. In contrast, Hildoceratidae display abundant and marked dimorphism, the description of which is a major feature of this monograph. Some of the more interesting Dactylioceratidae were described in three previous papers (Howarth 1973, 1978, 1980a), and there are others that await description or revision. The Hildoceratidae present less difficult problems of specific classification, and all the British members of the family are described in this monograph, except for the Grammocerotinae and later subfamilies of the Upper Toarcian.

The subfamily Harpoceratinae includes the bulk of the abundant faunas, one lineage of which starts with *Tiltoniceras* in England and evolves *in situ* through *Eleganticeras* and two successive species of *Cleviceras* in the Exaratum Subzone, while a second lineage consists of four species of *Harpoceras* in the Falciferum and Bifrons Zones (see Text-fig. 44). The rare *Ovaticeras* at the top of the Falciferum Zone is another genus of the subfamily, as are *Pseudolioceras*, which starts in the Commune Subzone, and *Polyplectus* and *Osperlioceras*. The second major subfamily is the Hildoceratinae, starting with *Hildaites* in the Exaratum Subzone, and evolving into the genus *Hildoceras* in the Falciferum Subzone. The subfamilies Arieticeratinae and Bouleiceratinae are represented by rare individuals that are out of their main province (Tethys), or local developments of single species that are much more abundant in the Upper Pliensbachian and Lower Toarcian of southern Europe and the Mediterranean area.

## METHODS OF CLASSIFICATION

Much progress has been made in the decades from the mid-1950s to the end of the 1980s to improve on the morphological methods of classification used by the classical ammonite workers in Britain, notably Buckman, Spath and Arkell. It is now widely acknowledged that single-bed collections of ammonites need to be obtained in order to

determine the amount of variation within a species, and to elucidate the scale of morphological differences between species. Collections from mixed horizons, where the stratigraphical relationships are unknown, are of little use for this basic step in classification. In fact, in the Lower Jurassic it is no longer worth describing extensive collections of ammonites for which original stratigraphical information is not known. These methods have resulted in a new view of ammonite species that admits considerably more intraspecific variation, and results in many fewer species being accepted. It is also likely that these species are a closer approximation to the units that evolved. Such units are the interbreeding populations in one area at one time, and their recognition is the basic aim of ammonite systematics, so that higher taxonomic units can be built on them, and more soundly based phylogenies erected.

The classification of the Hildoceratidae described here is based on about 2,500 ammonites collected from known horizons in the Lower Toarcian in Britain. The main localities newly collected between 1955 and 1987 were the north coast of Yorkshire, the area south of Grantham, Lincolnshire, Tilton, Leicestershire, the area around Byfield, west Northamptonshire, and to a lesser extent the Ilminster and Barrington district of Somerset, and the Dorset coast. Luckily, the latter two areas had been well collected with good stratigraphical control by Mr J. F. Jackson, the British Geological Survey and others. The higher part of the Lower Toarcian in Northamptonshire had also been well recorded and collected by Beeby Thompson when exposures were much more extensive. In all the collections that were examined it was found that it was rare for two or more closely related species to occur at a single horizon. In those few cases where two such species were recognized together (*Hildaites murleyi* and *H. forte*; *Harpoceras soloniacense* and *H. subplanatum*; *Hildoceras laticosta* and *H. lusitanicum*), it was because they were eventually found to differ in overall stratigraphical range, or because the amount of variation was too much to be easily encompassed in a single species. Where two or more less closely related species were recognized at the same horizon, the differences between them were clear and unambiguous, and the variation within each could be quantified easily. That variation could then be used to judge where species divisions should be placed in the evolving lineages, so that the amount of variation of the species in its full stratigraphical range was in keeping with the amount of variation at one horizon. These were the main methods by which existing specific names were arranged in synonymies. The result differs from that obtained by considering morphology alone and disregarding stratigraphy. These methods work well with Hildoceratidae, and are even more applicable to the Dactylioceratidae that accompany them, which present a bewildering mass of morphological variation that defies sensible classification, until single horizon associations are determined. They are also the methods that were used with the British Upper Pliensbachian Amaltheidae (Howarth, 1958; 1959), which also present an amount of morphological variation that cannot be resolved without knowledge of the stratigraphical associations.

All the material described in this monograph is housed in museum collections, for which the following abbreviations are used in this monograph: **BGS** – British Geological Survey, Keyworth, Nottingham; **BM** – The Natural History Museum, London; **MM** – Manchester University Museum; **NMW** – National Museum of Wales, Cardiff; **OUM** – Oxford University Museum; **SM** – Sedgwick Museum, Cambridge; **WM** – Whitby Museum, Yorkshire.

Ammonite whorl measurements are in mm and are quoted in the following order: diameter, whorl height, whorl breadth, umbilical width. Figures in brackets express the preceding measurement as a proportion of the diameter. Note that the dimension "Radius" (R), measured for calculating the spiral constant (as described on p. 31) is not included in the sequence of quoted measurements.

## ACKNOWLEDGEMENTS

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## BIOSTRATIGRAPHY

The ammonite succession in England is the basis of most of the zones and subzones of the Pliensbachian and Toarcian stages in north-west Europe. Those in the Lower Pliensbachian and the Upper Toarcian were based on the Dorset coast and the Cotswolds sequences respectively. The subdivisions of the Upper Pliensbachian and the Lower Toarcian, from which came most of the ammonites described in this monograph, were based on the ammonite succession on the Yorkshire coast. Early work by Buckman (1910a, p. xvi; 1910b; 1915b; 1918b; 1922b) and others was brought together in a zonal scheme for the whole Lower Jurassic by Spath (1942). An expanded and more detailed account by Dean, Donovan & Howarth (1961) included the results of investigations on the Upper Pliensbachian part of the succession by Howarth (1955; 1956; 1957; 1959, p. xv). Changes to some of the subzonal nomenclature as a result of more work on the Lower Toarcian by Howarth (1973, p. 266; 1978, p. 244) were incorporated in the most recent summary of the subdivisions and correlations of the Pliensbachian and Toarcian stages by Howarth (*in Cope et al.*, 1980, pp. 48–59). The latter scheme is followed here without change, and the zones and subzones from the base of the Pliensbachian to the top of the Toarcian that are used in this monograph are given in Text-fig. 1. Detailed history of the reasons for arriving at this scheme can be found in the papers already listed, and correlations between the different outcrops in Cope *et al.* (1980).

Problems that were not discussed in Cope *et al.* (1980) are the division of the Pliensbachian and the Toarcian into formal Lower and Upper divisions, the status of the substage names that have been proposed, and the status of the terms Lower, Middle and Upper Lias. The division of both Pliensbachian and Toarcian into Lower and Upper parts was given in the table in Dean, Donovan & Howarth (1961, p. 441), and this is followed here without change. There have never been any alternatives proposed for the position of the Lower/Upper Pliensbachian boundary, which has always approximated to a change in the lithology in some areas in Britain, and is based on a major change in the ammonite faunas in north-west Europe, where members of the ammonite family Liparoceratidae evolved into the Amaltheidae. Alternatives to the division of the Toarcian into Lower and Upper parts have been discussed by Howarth (1964, pp. 190–1), but the proposal to use a formal Middle Toarcian division has not gained acceptance, and is abandoned in favour of the two-fold division into Lower and Upper Toarcian.

The status of the Charmouthian, Carixian, Domerian, Whitbian and Yeovilian substages was also discussed by Dean, Donovan & Howarth (1961, pp. 441, 461–61, 468, 473), Donovan & Howarth (1964a; 1964b) and Howarth (1964). Charmouthian has been used inconsistently by different authors. Its best definition probably makes it a synonym of Pliensbachian, and it is better abandoned in favour of the latter stage name. Carixian and Domerian are exact equivalents of Lower and Upper Pliensbachian respectively, but neither are in common use, though they are occasionally seen as more convenient “shorter” versions of the substage names. Whitbian and Yeovilian were proposed to reflect the lithological difference

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STAGES	ZONES	SUBZONES
Upper Toarcian	<i>Dumortieria levesquei</i>	<i>Pleydellia aalensis</i> <i>Dumortieria moorei</i> <i>Dumortieria levesquei</i> <i>Phlyseogrammoceras dispansum</i>
	<i>Grammoceras thouarsense</i>	<i>Pseudogrammoceras fallaciosum</i> <i>Grammoceras striatulum</i>
	<i>Haugia variabilis</i>	
Lower Toarcian	<i>Hildoceras bifrons</i>	<i>Catacoeloceras crassum</i> <i>Peronoceras fibulatum</i> <i>Dactyloceras commune</i>
	<i>Harpoceras falciferum</i>	<i>Harpoceras falciferum</i> <i>Cleviceras exaratum</i>
	<i>Dactyloceras tenuicostatum</i>	<i>Dactyloceras semicelatum</i> <i>Dactyloceras tenuicostatum</i> <i>Dactyloceras clevelandicum</i> <i>Protogrammoceras paltum</i>
Upper Pliensbachian	<i>Pleuroceras spinatum</i>	<i>Pleuroceras hawskerense</i> <i>Pleuroceras apyrenum</i>
	<i>Amaltheus margaritatus</i>	<i>Amaltheus gibbosus</i> <i>Amaltheus subnodosus</i> <i>Amaltheus stokesi</i>
Lower Pliensbachian	<i>Prodactyloceras davoiei</i> <i>Tragophylloceras ibex</i> <i>Uptonia jamesoni</i>	

TEXT-FIG. 1. Ammonite zones and subzones for the Pliensbachian and Toarcian in Britain (subzones are not listed for the Lower Pliensbachian).

between the argillaceous facies of the Lower Toarcian in the Whitby area of Yorkshire, and the arenaceous facies of the Upper Toarcian in the Yeovil district in Somerset and Dorset. However, the Whitbian/Yeovilian boundary is at the top of the Variabilis Zone, whereas the Lower/Upper Toarcian boundary is at the base of that zone. Whitbian and Yeovilian are not, therefore, equivalents of the Lower and Upper Toarcian, and the formal substage names are not useful terms for this reason.

In recent years much progress has been made towards the complete separation of lithostratigraphical and biostratigraphical nomenclature. In the Jurassic System, Lias and its divisions Lower, Middle, and Upper Lias are terms of undoubted lithostratigraphic origin that have been widely used until recently in a biostratigraphical sense. Lias has been used as synonymous with Lower Jurassic: Lower Lias as an exact equivalent of Hettangian, Sinemurian and Lower Pliensbachian; Middle Lias for Upper Pliensbachian; and Upper Lias for Toarcian. Lias has often been incorporated in the titles of papers on Lower Jurassic zones and subzones (e.g. Spath, 1942; Dean, Donovan & Howarth, 1961). "Lias" originated as a descriptive term for the alternating shale and limestone 'layers' that are typical of the Lower Lias in England.

The three-fold division was originally made by giving the name Middle Lias to the more arenaceous central part, which separates the Lower Lias from the Upper Lias, both of which are more argillaceous or calcareous. Increasing knowledge of the distribution of the ammonites led to the conclusion that the arenaceous beds of the Middle Lias have different biostratigraphical ranges in different parts of Britain, and for about 100 years until recently Middle Lias was used as a biostratigraphical term by most authors, exactly equivalent to Upper Pliensbachian. This led to the complaint by some authors that the arenaceous beds started at lower horizons in many areas. However, to use a different "Middle Lias" in each area would destroy the usefulness of the term, because the different areas (or basins) of deposition were not connected, and each had its own separate history of arenaceous deposition occurring at different times in the middle of the Lower Jurassic (e.g. the arenaceous beds of the Scalpay Sandstone start within the Margaritatus Zone in Mull (Oates, 1978, p. 149), and this would be local the base of the Middle Lias, but in Yorkshire Hemingway (1974, p. 165) placed the base of the Middle Lias at the base of the Staithes Formation, which is one zone lower, in the Davoei Zone). When used like this Middle Lias becomes meaningless anywhere outside its type area, which would have to be in Somerset. So the terms Lower Lias, Middle Lias and Upper Lias have little relevance in Lower Jurassic biostratigraphy, and they are not used in this monograph. The term Lias is also no longer useful as a biostratigraphical term, because the base of the Jurassic no longer coincides with the base of the Lias in many parts of Britain (Cope *et al.*, 1980, pp. 17–22).

The subdivisions of the Upper Pliensbachian and Lower Toarcian substages are so dependent on the English succession of ammonites, that it is useful to give brief definitions of critical points. In this part of the Jurassic, stages are based on their constituent zones, and zones on their constituent subzones. The most important definitions, therefore, are the bases of the subzones, because the appropriate ones then form the definitions of the zones, and in turn of the substages and stages. Short definitions of the bases of the subzones are given below, with indications of the characteristics of each.

*Stokesi Subzone.* Base at bottom of bed 1, Hawsker Bottoms, or bed 12, Staithes, Yorkshire (Howarth, 1955, pp. 155, 158). Characterized by the appearance of *Amaltheus stokesi* (J. Sowerby), which is confined to the subzone.

*Subnodosus Subzone.* Base at bottom of bed 18, Hawsker Bottoms, or bed 26 Staithes, Yorkshire (Howarth, 1955, pp. 155, 158). Characterized by the appearance of *Amaltheus subnodosus* (Young & Bird), which is confined to the subzone. *Amaltheus margaritatus* de Montfort also appears, and persists into the Apyrenum Subzone.

*Gibbosus Subzone.* Base at bottom of bed 21, Hawsker Bottoms, or bed 32, Staithes, Yorkshire (Howarth, 1955, pp. 155, 157). Characterized by the appearance of *Amaltheus gibbosus* (Schlotheim), which is confined to the subzone.

*Apyrenum Subzone.* Base at bottom of bed 25, Hawsker Bottoms, Yorkshire (Howarth, 1955, p. 155; 1980b, p. 52, fig. 9). Characterized by the appearance of species of *Pleuroceras*, especially *P. transiens* Frentzen at the base, and *P. solare* (Phillips), *P. apyrenum* (Buckman) and *P. spinatum* (Bruguière) higher up. The latter species persists to the top of the Hawskerense Subzone.

*Hawskerense Subzone.* Base at bottom of bed 38, Hawsker Bottoms, or bed 55, Staithes, Yorkshire (Howarth, 1955, p. 154, 157). Characterized by the presence of *Pleuroceras hawskerense* (Young & Bird) and other species of *Pleuroceras*. Amaltheidae become extinct at or before the top of the subzone.

*Paltum Subzone.* Base at bottom of bed 26, the Sulphur Band, Kettleless, or bed 58, Staithes (Howarth, 1955, p. 157; 1973, p. 242; 1980b, p. 52, fig. 9). *Protogrammoceras paltum* (Buckman) is confined to this horizon in England, and the early species of *Dactylioceras*, that are characteristic in southern Europe, are virtually absent. Not a satisfactory subzone index species, but there are no others (Howarth, 1973, pp. 267–68). The absence of Amaltheidae is an important feature.

*Clevelandicum Subzone.* Base at bottom of bed 18, north Yorkshire coast (Howarth, 1973, p. 241). Characterized by the appearance in England of the first fine-ribbed species of *Dactylioceras* (*Orthodactylites*), of which *D. (O.) crosbeyi* (Simpson) is the earliest, then *D. (O.) clevelandicum* Howarth appears soon afterwards. Both species are confined to this subzone.

*Tenuicostatium Subzone.* Base at bottom of bed 20, north Yorkshire coast (Howarth, 1973, p. 241). Characterized by *Dactylioceras* (*Orthodactylites*) *tenuicostatium* (Young & Bird), which is confined to the subzone.

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*Semicelatum* Subzone. Base at bottom of bed 28, north Yorkshire coast (Howarth, 1973, p. 240). Characterized by *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson), which probably does not extend into the overlying subzone. *Tiloniceras antiquum* occurs in the upper half of the subzone in Britain.

*Exaratum* Subzone. Base at bottom of bed 33, north Yorkshire coast (Howarth, 1962b, p. 388; 1973, p. 240). Characterized by three successive ammonites: *Eleganticeras elegantulum* (Young & Bird) in the lower part, *Cleviceras exaratum* (Young & Bird) in the middle part, and *C. elegans* (J. Sowerby) in the upper part. *Harpoceras serpentinum* (Schlotheim) and *Hildaites* also occur.

*Falciferum* Subzone. Base at bottom of bed 41, north Yorkshire coast (Howarth, 1962b, p. 392). Characterized by *Harpoceras falciferum* (J. Sowerby), which persists into the overlying Commune Subzone, and by *Orthildaites* and early species of *Hildoceras*. Species of *Ovaticeras* and *Hildaites* also occur, as do several species of *Dactylioceras* and *Nodicoeloceras*.

*Commune* Subzone. Base at bottom of bed 49, Whitby, Yorkshire (Howarth, 1962b, p. 398). Characterized by *Dactylioceras commune* (J. Sowerby), which is confined to the subzone. *Hildoceras laticosta*, *H. lusitanicum* Fucini, *Harpoceras falciferum* and *Nodicoeloceras* also occur.

*Fibulatum* Subzone. Base at bottom of bed 60, Whitby, Yorkshire (Howarth, 1962b, p. 397). Characterized by species of *Peronoceras*, especially *P. fibulatum* (J. de C. Sowerby), throughout the subzone; *Zugodactylites* is also common in some areas, and *Porpoceras* occurs in the upper part of the subzone. All three genera are confined to the subzone. *Harpoceras soloniacense* (Lissajous) and *H. subplanatum* (Oppel) are present in some areas. The first *Phymatoceras* occurs in this subzone.

*Crassum* Subzone. The base starts 1.5m above the bottom of bed 72, Whitby, or at the bottom of bed xliv, Ravenscar, Yorkshire (Howarth, 1962b, pp. 396, 400; 1978, pp. 243-44; 1980b, p. 58, fig. 11). Characterized by *Catacoeloceras*, which replaces *Porpoceras* of the Fibulatum Subzone. *Phymatoceras* occurs occasionally, but *Haugia* does not appear until the overlying Variabilis Zone.

SUBZONES	ZONES
<i>Catacoeloceras crassum</i>	<i>Hildoceras bifrons</i>
<i>Peronoceras fibulatum</i>	
<i>Dactylioceras commune</i>	
<i>Harpoceras falciferum</i>	<i>Harpoceras falciferum</i>
<i>Cleviceras exaratum</i>	
<i>Dactylioceras semicelatum</i>	<i>Dactylioceras tenuicostatum</i>
<i>Dactylioceras tenuicostatum</i>	
<i>Dactylioceras clevelandicum</i>	
<i>Protogrammoceras paltum</i>	
<i>Pleuroceras hawskerense</i>	<i>Pleuroceras spinatum</i>
<i>Pleuroceras apyrenum</i>	
<i>Amaltheus gibbosus</i>	<i>Amaltheus margaritatus</i>
<i>Amaltheus subnodosus</i>	
<i>Amaltheus stokesi</i>	

TEXT-FIG. 2. Stratigraphical ranges of the zone and subzone index species in the Upper Pliensbachian and Lower Toarcian in Britain. Solid linking lines indicate direct phylogenetic descent of one species from the other, while broken lines show close phylogenetic affinity.































































































































































































































































































































































































































































































































































