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THE AMMONITE FAMILY  
HILDOCERATIDAE IN THE  
LOWER JURASSIC OF  
BRITAIN

MICHAEL K. HOWARTH

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BRITAIN

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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 Dactyloceratidae 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 Dactyloceratidae are often very variable, sometimes extraordinarily so (e.g. the Yorkshire Tenuicostatum Zone species of *Dactyloceras* (*Orthodactylites*) described by Howarth (1973)), while species of Hildoceratidae are relatively closely defined, exhibiting much less variation. Sexual dimorphism might be present in British Dactyloceratidae, 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 Dactyloceratidae 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 Dactyloceratidae 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 *Dactyloceras* (*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 *Dactyloceras* and *Nodicoeloceras*.

*Commune* Subzone. Base at bottom of bed 49, Whitby, Yorkshire (Howarth, 1962b, p. 398). Characterized by *Dactyloceras 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>Dactyloceras commune</i>	
<i>Harpoceras falciferum</i>	<i>Harpoceras falciferum</i>
<i>Cleviceras exaratum</i>	
<i>Dactyloceras semicelatum</i>	<i>Dactyloceras tenuicostatum</i>
<i>Dactyloceras tenuicostatum</i>	
<i>Dactyloceras 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.

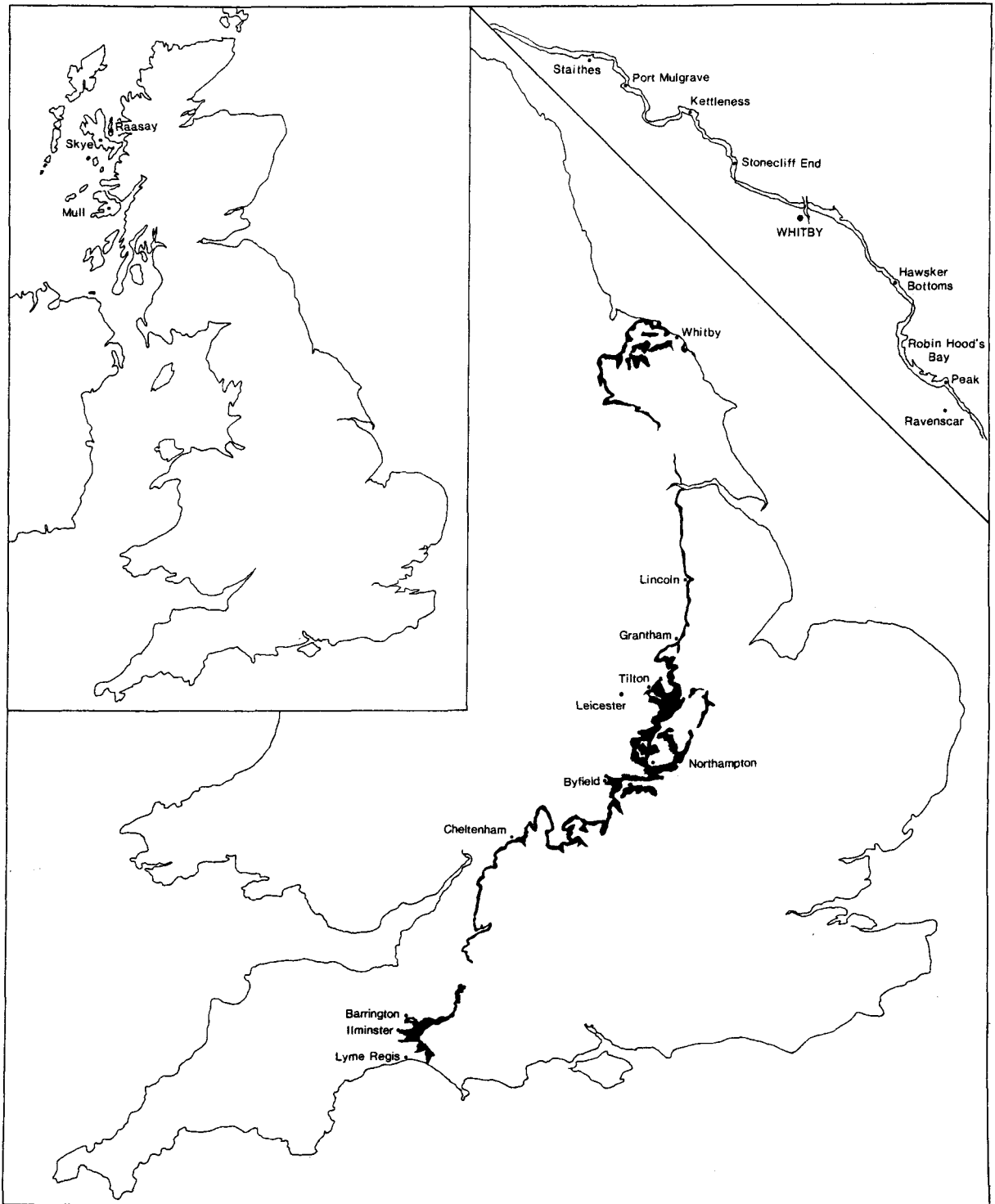
The biostratigraphic ranges of the zone and subzone index ammonites are shown in Text-fig. 2. They are divided into groups and linked to show those that are evolutionary descendents of the immediately preceding index species, or are at least closely connected phylogenetically with the preceding species. It is remarkable that all but two of the 14 subzone index species are confined to the subzone they characterize. In fact some of them are in evolutionary continuity with the index species above and below, which precludes the possibility of their occurrence above or below their subzone. The exceptions are *Pleuroceras apyrenum*, which also occurs in the overlying Hawskerense Subzone, and *Harpoceras falciferum*, which occurs in the Commune Subzone. *Protogrammoceras paltum* is a poor subzonal index and probably occurs both above and below that horizon in other parts of Europe, but it seems to be confined to a single horizon in England, and is used as an index species for lack of any alternative. The zone index species are not as good as infallible indicators of their zones, but none of them actually occur below the zone that they characterize, which would render them of little use as index species. None range through the full biostratigraphical extent of their zones, and this illustrates how stratigraphically confined are most species of ammonites, and how difficult it is to select a common ammonite that has a range as long as the sort of division that makes a useful ammonite zone in this part of the Jurassic.

### STRATIGRAPHY

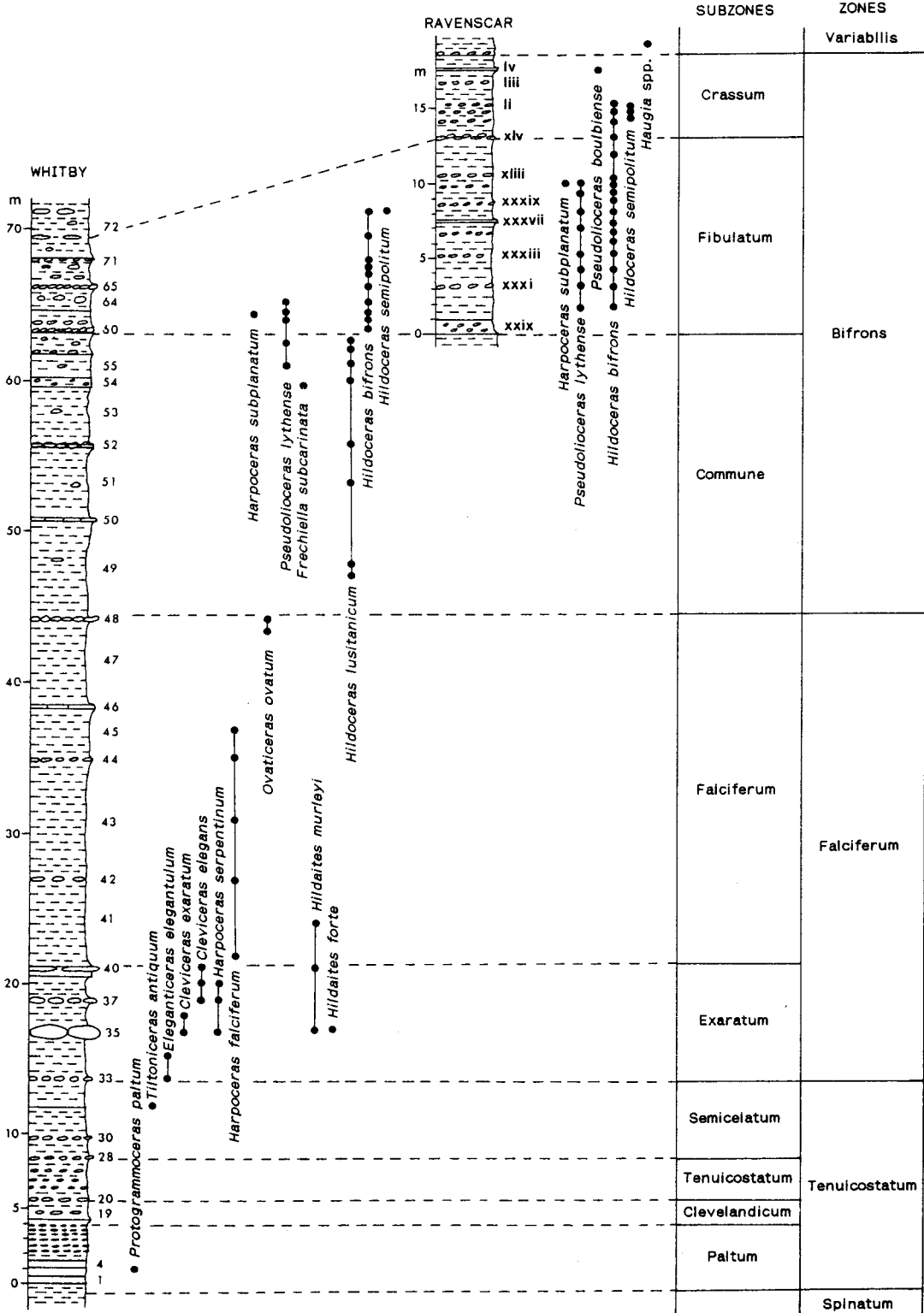
The bulk of the ammonites described in this monograph are from rocks of Lower Toarcian age. A few of them extend up into the Upper Toarcian, but the main ammonites that become abundant in that substage belong to the subfamily Grammocerotinae and the family Phymatoceratidae, and they are not described here. Occasional representatives of Hildoceratidae occur in the Upper Pliensbachian, but they are scattered occurrences and they are always subordinate to the Amaltheidae. Detailed stratigraphy of the British Upper Pliensbachian can be found in three papers by Howarth (1955; 1956; 1957), and there is a summary in the monograph describing the Amaltheidae (Howarth, 1958). Up-to-date correlations of the British Upper Pliensbachian can be found in a more recent synthesis by Howarth (1980b, pp. 48–52, fig. 9). This incorporated (in fig. 9) the results of work on the Cleveland Ironstone Formation in north Yorkshire by Chowns (1966), which resulted in slightly different nomenclature and correlations from those originally given by Howarth (1955, p. 170, pl. 13).

The account that follows is confined to Lower Toarcian rocks. Some of it is a summary of stratigraphy already published in four papers (Howarth, 1962b; 1973; 1978; 1980a), but there are also revised stratigraphical accounts, and new determinations of ammonites collected by previous workers, especially from localities in Somerset and Dorset. A map showing the chief localities in Britain is given in Text-fig. 3.

*Yorkshire.* Inevitably the Hildoceratidae of the Yorkshire coast play a prominent part in the bed-by-bed collections of ammonites that were made in Britain, in the discovery of the species into which they were divided, and in the biostratigraphy that is derived from them. Not only is the Lower Toarcian succession much thicker and more expanded in Yorkshire than anywhere else in England, but it is laid out on the foreshore as a series of wave-cut platforms, which give large areas of usually clean, sea-eroded exposure. The only drawback to collecting is that almost all the outcrops occur between mid-tide and low-water mark. With this time limitation, the exposures are always available, however, and the area for searching is very large. By comparison, the cliff faces seem almost devoid of fossils at many of the same horizons. The expanded Yorkshire sequence is the key to the succession of ammonites in the Tenuicostatum Zone and the Exaratum Subzone, which could not be determined elsewhere in Britain, and the main description can be found in two papers (Howarth, 1962b; 1973). Some ammonites are rare in Yorkshire, however. One is *Cleviceras serpentinum* (Schlotheim),



TEXT-FIG. 3. Map showing the localities in Britain from which major collections of Hildoceratidae have been obtained. The approximate outcrop of Toarcian rocks is shown from Lyme Regis to Whitby.



TEXT-FIG. 4. The lithological succession in the Lower Toarcian of the north Yorkshire coast, the distribution of the Hildoceratidae, and the correlation between the Whitby and Ravenscar sections in the Fibulatum and Crassum Subzones.

which is common elsewhere in England. Another is the dactylioceratid genus *Zugodactylites*, which was only found after clues to its real biostratigraphical horizon were obtained from its occurrence in Northamptonshire. Searches then revealed specimens in Yorkshire that confirmed the view that the horizon it was thought to characterize (the subzone of *Z. braunianus*) is in fact only part of the Fibulatum Subzone (Howarth, 1978, pp. 243, 245). The distinctive ammonite *Tiltoniceras*, previously considered to be absent from Yorkshire, was eventually found, crushed in very large numbers, in two shell beds near the top of the Tenuicostatum Zone (Howarth, 1973, pp. 265–56). Very large collections of ammonites, that are crucial to the biostratigraphy and description of the family, were obtained from Yorkshire, and they are now preserved as reference collections in the Department of Palaeontology, the Natural History Museum, London.

The stratigraphy of the full sequence from the base of the Upper Pliensbachian to the top of the Toarcian can be found in papers by Howarth (1955; 1962b; 1973) and Dean (1954). There is a summary of the stratigraphy and a detailed chart for the Lower Toarcian in Howarth (1980b, p. 58, figs 10B, 11). The lithostratigraphical nomenclature has been reviewed, and new names proposed, for the whole of the Lower Jurassic in Yorkshire by Powell (1984) and Knox (1984). The following is a summary of the succession for the main Whitby district exposures that lie to the north-west of the Peak Fault at Ravenscar. It has been compiled from data in three papers (Howarth, 1962b; 1973; 1978, p. 243); all occurrences of ammonites are recorded, and the lithostratigraphical nomenclature is from Powell (1984, pp. 54–56). The plate and figure numbers of all the ammonites from known horizons that are figured in this monograph are listed in the detailed stratigraphical sections that follow (e.g. as "Pl. 36, fig. 4" under bed 71 below).

Dogger. Opalinum Zone, Aalenian.

Bed no.	Zone of <i>Hildoceras bifrons</i> Subzone of <i>Catacoeloceras crassum</i>	Thickness (in metres)
Whitby Mudstone Formation		
Alum Shale Member		
The Cement Shales (beds 65–72)		
72 (part).	Shale, with calcareous nodules. <i>Catacoeloceras crassum</i> (Young & Bird), <i>Collina mucronata</i> (d'Orbigny), <i>Hildoceras bifrons</i> (Bruguière), <i>H. semipolitum</i> Buckman .....	2.50
Subzone of <i>Peronoceras fibulatum</i>		
72 (part).	Shale, with calcareous doggers. <i>Porpoceras</i> cf. <i>vortex</i> (Simpson), <i>P. verticosum</i> Buckman, <i>Hildoceras bifrons</i> .....	1.50
71.	Cementstone doggers. <i>H. bifrons</i> (Pl. 36, fig. 4) .....	0.25
70.	Shale. <i>H. bifrons</i> .....	0.25
69.	Scattered cementstone doggers. <i>Phylloceras heterophyllum</i> (J. Sowerby) .....	0.08
68.	Shale. <i>H. bifrons</i> , <i>P. heterophyllum</i> .....	0.30
67.	Scattered cementstone doggers. <i>H. bifrons</i> .....	0.13
66.	Shale .....	0.71
65.	Cementstone doggers. <i>H. bifrons</i> , <i>Lytoceras cornucopia</i> (Young & Bird) .....	0.10
The Main Alum Shales (beds 51–64)		
64.	Shale, rows of doggers 0.3m and 0.9m above base. <i>H. bifrons</i> , <i>Pseudolioceras lythense</i> (Young & Bird), <i>Phylloceras heterophyllum</i> , <i>Lytoceras cornucopia</i> , <i>Peronoceras</i> cf. <i>turriculatum</i> (Simpson) and <i>Zugodactylites braunianus</i> (d'Orbigny) 0.1m above base .....	1.60
63.	Shale, many calcareous nodules. In row of nodules at top: <i>Peronoceras fibulatum</i> (J. de C. Sowerby), <i>P. turriculatum</i> , <i>Zugodactylites braunianus</i> and <i>Harpoceras subplanatum</i> (Oppel). In row of nodules 0.3m below top: <i>Peronoceras turriculatum</i> , <i>Zugodactylites braunianus</i> , <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> (Pl. 27, fig. 3). In lower half: <i>Peronoceras fibulatum</i> , <i>P. turriculatum</i> , <i>P. perarmatum</i> (Young & Bird), <i>P. subarmatum</i> (Young & Bird), <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> , <i>Phylloceras heterophyllum</i> .....	1.22
62.	Scattered cementstone doggers. <i>Peronoceras fibulatum</i> , <i>P. turriculatum</i> , <i>P. perarmatum</i> , <i>P. subarmatum</i> , <i>Zugodactylites braunianus</i> .....	0.10

61. Shale .....	0-23
60. Limestone nodules. <i>Peronoceras fibulatum</i> , <i>P. turriculatum</i> , <i>P. perarmatum</i> , <i>P. subarmatum</i> , <i>Hildoceras bifrons</i> .....	0-08
Subzone of <i>Dactylioceras commune</i>	
59. Shale. <i>Dactylioceras athleticum</i> (Simpson), <i>D. praepositum</i> Buckman, <i>Hildoceras</i> cf. <i>lusitanicum</i> Meister, <i>Pseudolioceras</i> cf. <i>lythense</i> .....	0-91
58. Limestone nodules and siderite mudstone lenses. <i>Dactylioceras athleticum</i> , <i>D. praepositum</i> , <i>Hildoceras lusitanicum</i> , <i>Lytoceras cornucopia</i> .....	0-15
57. Shale .....	0-15
56. Limestone nodules. <i>Dactylioceras athleticum</i> , <i>D. praepositum</i> .....	0-05
55. Shale. <i>D. athleticum</i> , <i>D. praepositum</i> , <i>D. temperatum</i> (Buckman), <i>D. crassescens</i> (Simpson), <i>Hildoceras lusitanicum</i> , <i>Pseudolioceras lythense</i> , <i>Phylloceras heterophyllum</i> .....	1-52
54. Shale, with limestone nodules. <i>Dactylioceras commune</i> , <i>D. praepositum</i> , <i>D. temperatum</i> , <i>Hildoceras lusitanicum</i> (Pl. 35, fig. 1), <i>Frechiella subcarinata</i> (Young & Bird) .....	0-61
53. Shale, with row of nodules 0-91m above base. <i>Dactylioceras commune</i> , <i>Phylloceras heterophyllum</i> .....	3-81
52. Lenses of red siderite mudstone. <i>Dactylioceras commune</i> , <i>Hildoceras lusitanicum</i> .....	0-15
51. Shale, with row of nodules 0-61m below top. <i>Dactylioceras commune</i> , <i>D. temperatum</i> , <i>Hildoceras lusitanicum</i> , <i>Phylloceras heterophyllum</i> .....	4-88
The Hard Shales (beds 49, 50)	
50. Red siderite mudstone. <i>Dactylioceras commune</i> .....	0-13
49. Shale, with doggers and pyritic masses 1-22m below top. <i>Hildoceras lusitanicum</i> , <i>Dactylioceras commune</i> and <i>D. temperatum</i> in upper half .....	6-30
Zone of <i>Harpoceras falciferum</i>	
Subzone of <i>Harpoceras falciferum</i>	
Jet Rock Member	
The Ovatum Band	
48. Double row of large red doggers. <i>Ovaticeras ovatum</i> (Young & Bird) (Pl. 24, figs 3-5; Pl. 25, fig. 1), <i>Dactylioceras</i> cf. <i>toxophorum</i> (Buckman), <i>D.</i> cf. <i>consimile</i> (Buckman), <i>Phylloceras heterophyllum</i> .....	0-30
The Bituminous Shales (beds 41-47)	
47. Shale. <i>Ovaticeras ovatum</i> 0-75 m below top, <i>Dactylioceras</i> sp. indet .....	5-60
46. Red siderite mudstone .....	0-13
45. Shale. <i>Harpoceras falciferum</i> (J. Sowerby), <i>Dactylioceras</i> sp. indet., <i>Phylloceras heterophyllum</i> .....	3-35
44. Row of scattered doggers. <i>Harpoceras falciferum</i> , <i>D.</i> cf. <i>consimile</i> .....	0-15
43. Shale. <i>Harpoceras falciferum</i> (Pl. 20, figs 1, 7), <i>Dactylioceras gracile</i> (Simpson), <i>D. consimile</i> , <i>Nodicoeloceras incrassatum</i> (Simpson) .....	7-67
42. Row of scattered pyritized doggers. <i>Harpoceras falciferum</i> (?Text-fig. 33; ?Pl. 18, fig. 3; ?Pl. 20, fig. 5) ...	0-13
41. Shale. <i>Harpoceras falciferum</i> , <i>Hildaites murleyi</i> (Moxon), <i>Dactylioceras</i> sp. indet. ....	5-88
Subzone of <i>Cleviceras exaratum</i>	
The Jet Rock (beds 33-40)	
40. The Millstones. Limestone doggers up to 4.5 m diameter. <i>Cleviceras elegans</i> (J. Sowerby), <i>Hildaites murleyi</i> , <i>Dactylioceras</i> sp. indet. ....	0-30
39. Top Jet Dogger. Limestone. <i>Cleviceras elegans</i> , <i>Dactylioceras</i> sp. indet. ....	0-23
38. Shale. Lines of large irregular doggers, the Upper Pseudovertebrae, and occasional doggers similar to the Curling Stones occur 0-3m above base. <i>Cleviceras elegans</i> (Pl. 15, fig. 1), <i>H. serpentinum</i> (Schlotheim) (Pl. 16, fig. 2), <i>Phylloceras heterophyllum</i> .....	1-52
37. The Curling Stones. Large oblate-spheroidal pyritized doggers up to 0.45m diameter. <i>Cleviceras elegans</i> (Pl. 12, figs 6-8; Pl. 14, fig. 2), <i>Harpoceras serpentinum</i> , <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semiannulatum</i> Howarth, <i>Nodicoeloceras crassoides</i> (Simpson), <i>Phylloceras heterophyllum</i> ...	0-30
36. Shale. <i>Cleviceras exaratum</i> .....	1-52
35. The Whale Stones. Large ovoid doggers up to 3m long and 1 m thick, and many smaller doggers, including lines of irregular doggers, the Lower Pseudovertebrae. <i>Cleviceras exaratum</i> (Text-fig. 10; Pl. 9, figs 2-6; Pl. 10, figs 3, 4; Pl. 11, figs 9-17; Pl. 12, figs 1-5; Pl. 13, figs 1, 2), <i>Harpoceras serpentinum</i> , <i>Hildaites murleyi</i> (Pl. 31, figs 1-4, 6, 7), <i>H. forte</i> (Buckman) (Pl. 32, fig. 2), <i>Phylloceras heterophyllum</i> , <i>Lytoceras crenatum</i> (Buckman), <i>L. nitidum</i> (Young & Bird) .....	0-91
34. Shale, with many limestone nodules. <i>Eleganticeras elegantulum</i> (Young & Bird) (Pl. 8, figs 11-17) .....	2-60
33. The Cannon Ball Doggers. Spherical limestone doggers up to 0.18m diameter. <i>Eleganticeras elegantulum</i> (Pl. 7, figs 4, 8; Pl. 8, figs 2-10, 18-21; Pl. 9, fig. 1) .....	0-15

Zone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*  
Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*

Grey Shale Member

32.	Shale. <i>Tilloniceras antiquum</i> (Wright) (Text-fig. 13; Pl. 6, fig. 7; Pl. 7, figs 2, 3) and <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i> (Simpson) in shell beds at base, 0.1m above base and 0.3m below top..	1.83
31.	Shale. <i>D. (O.) semicelatum</i> , <i>Meneghiniceras lariense</i> (Meneghini) (Howarth, 1976, p. 773, figs 1, 2) .....	2.13
30.	Row of pyritized limestone doggers up to 0.2m diameter. <i>D. (O.) semicelatum</i> .....	0.10
29.	Shale. <i>D. (O.) semicelatum</i> .....	1.07
28.	Double row of limestone doggers up to 0.15m diameter. <i>D. (O.) semicelatum</i> .....	0.23

Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*

27.	Shale. <i>D. (O.) tenuicostatum</i> .....	0.61
26.	Red limestone nodules. <i>D. (O.) tenuicostatum</i> .....	0.05
25.	Shale. <i>D. (O.) tenuicostatum</i> .....	0.61
24.	Row of small limestone nodules. <i>D. (O.) tenuicostatum</i> .....	0.08
23.	Shale. <i>D. (O.) tenuicostatum</i> .....	0.38
22.	Row of small limestone nodules.....	0.08
21.	Shale. <i>D. (O.) tenuicostatum</i> .....	0.76
20.	Red limestone lenses up to 0.25m diameter. <i>D. (O.) tenuicostatum</i> .....	0.15

Subzone of *Dactylioceras* (*Orthodactylites*) *clevelandicum*

19.	Shale. <i>D. (O.) clevelandicum</i> Howarth in limestone nodules 0.45m above base .....	1.27
18.	Shale. <i>D. (O.) crosbeyi</i> (Simpson) in row of nodules in middle of bed.....	0.38

Subzone of *Protogrammoceras paltum*

17.	Sixth Red Nodules. Row of red limestone doggers .....	0.08
16.	Shale .....	0.20
15.	Fifth Red Nodules. Row of red limestone doggers .....	0.08
14.	Shale .....	0.23
13.	Fourth Red Nodules. Row of red limestone doggers .....	0.05
12.	Shale .....	0.30
11.	Third Red Nodules. Row of red limestone doggers .....	0.05
10.	Shale .....	0.25
9.	Second Red Nodules. Row of red limestone doggers.....	0.05
8.	Shale .....	0.41
7.	First Red Nodules. Row of red limestone doggers.....	0.08
6.	Shale .....	0.53
5.	Row of limestone nodules .....	0.05
4.	Shale .....	0.36
3.	Red calcareous mudstone. <i>Protogrammoceras paltum</i> ( Buckman) (Text-fig. 11; Pl. 1, fig. 1), <i>Dactylioceras</i> sp. indet.....	0.08
2.	Shale. <i>Lytoceras</i> sp. indet. ....	0.53
1.	Shale .....	0.51

Cleveland Ironstone Formation (bed numbers from Howarth, 1955, p. 156)

28.	Row of round limestone nodules. <i>Pholadomya ambigua</i> (J. Sowerby) and <i>Pseudopecten aequivalvis</i> (J. Sowerby) .....	0.05
27.	Shale, sandy.....	0.46
26.	Sulphur Band. Shale, close-bedded, bituminous.....	0.15

Zone of *Pleuroceras spinatum*

Subzone of *Pleuroceras hawskerense*

25.	Shale. <i>Pleuroceras hawskerense</i> (Young & Bird) in nodules at base .....	0.33
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At the top of this section a disconformity between the incomplete Cement Shales and the Dogger cuts out the top part of the Crassum Subzone and all higher horizons in the Toarcian. The only succession in north Yorkshire where the Toarcian is complete is at Peak, below Ravenscar, on the east side of the Peak Fault. Here the Cement Shales are overlain without a significant break by the Peak Mudstone Member (formerly the Peak Shales) of Variabilis Zone age. The *Catacoeloceras*, *Porpoceras* and *Zugodactylites* faunas are much more abundant than at Whitby, and the succession is considerably thicker. The following section gives the complete sequence of the Fibulatum and Crassum subzones at Peak. Bed numbers

of the Whitby succession are given in brackets where they are considered to be exact equivalents. A comparison between the two successions is shown in Text-fig. 4.

Bed no.	m
<i>Zone of Haugia variabilis</i>	
Whitby Mudstone Formation	
Peak Mudstone Member (base only)	
lviii. Shale. <i>Haugia</i> sp., <i>Catacoeloceras dumortieri</i> (Maubeuge) .....	1.00
lvii. Limestone nodules .....	0.08
<i>Zone of Hildoceras bifrons</i> Subzone of <i>Catacoeloceras crassum</i>	
Alum Shale Member	
The Cement Shales	
lvi. Shale. <i>Catacoeloceras dumortieri</i> .....	0.91
lv. Large flat nodules or continuous bed of red limestone. <i>Catacoeloceras crassum</i> (Young & Bird), <i>C. dumortieri</i> , <i>Pseudolioceras boultiense</i> (Young & Bird) (Pl. 27, fig. 6), <i>Phylloceras heterophyllum</i> (J. Sowerby) .....	0.10
liv. Shale. <i>Catacoeloceras dumortieri</i> .....	0.84
liiii. Row of scattered nodules. <i>Catacoeloceras crassum</i> .....	0.08
lii. Shale .....	1.30
li. Large flat limestone nodules. <i>Hildoceras bifrons</i> (Bruguière) .....	0.10
l. Shale. <i>Catacoeloceras crassum</i> , <i>Hildoceras semipolatum</i> Buckman .....	0.46
xlx. Small limestone nodules. <i>Catacoeloceras crassum</i> , <i>Collina mucronata</i> (d'Orbigny) <i>Hildoceras bifrons</i> (Pl. 38, fig. 2), <i>H. semipolatum</i> .....	0.08
xlvi. Shale. <i>Catacoeloceras crassum</i> , <i>Collina</i> cf. <i>mucronata</i> , <i>Hildoceras semipolatum</i> .....	0.46
xlvi. Small nodules. <i>Catacoeloceras crassum</i> , <i>Hildoceras bifrons</i> .....	0.08
xlvi. Shale. <i>Catacoeloceras</i> cf. <i>crassum</i> .....	0.91
xliv. Double row of large cementstone nodules. <i>Catacoeloceras crassum</i> , <i>Hildoceras bifrons</i> .....	0.30
Subzone of <i>Peronoceras fibulatum</i>	
xliv. Shale, with many cementstone nodules. <i>Porpoceras</i> aff. <i>vortex</i> (Simpson) near base; <i>Hildoceras bifrons</i> .....	2.30
xl. Large cementstone nodules .....	0.13
xl. Shale, with many cementstone nodules .....	0.66
Ammonites in beds xli and xlii: <i>Porpoceras vortex</i> (Simpson), <i>P. verticosum</i> Buckman, <i>P. vorticellum</i> (Simpson), <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> , <i>Harpoceras subplanatum</i> (Opper) (Pl. 22, fig. 5).	
xli (=Whitby bed 71). Small cementstone nodules. <i>Hildoceras bifrons</i> .....	0.08
xl. Shale. <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	1.14
xxxix. Small nodules. <i>Hildoceras bifrons</i> .....	0.08
xxxviii. Shale. <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	0.91
xxxvii. Red cementstone bed .....	0.10
xxxvi. Shale. <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	0.81
xxxv. Small nodules. <i>Hildoceras bifrons</i> .....	0.08
xxxiv. Shale. <i>Hildoceras bifrons</i> .....	1.22
xxxiii. (=Whitby bed 65). Band of cementstone. <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	0.15
The Main Alum Shales	
xxxii. Shale, with many nodules. <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	2.00
xxx. Large limestone doggers. <i>Peronoceras subarmatum</i> (Young & Bird), <i>Peronoceras</i> sp. indet., <i>Zugodactylites braunianus</i> (d'Orbigny), <i>Z. thompsoni</i> Howarth, <i>Hildoceras bifrons</i> , <i>Pseudolioceras lythense</i> .....	0.15
xxx. Shale, with few nodules. <i>Peronoceras fibulatum</i> , <i>P. perarmatum</i> (Young & Bird), <i>Hildoceras</i> <i>bifrons</i> (Pl. 27, fig. 2), <i>Pseudolioceras lythense</i> , <i>Phylloceras heterophyllum</i> .....	2.13
xxix. Shale, with many small nodules. <i>Peronoceras fibulatum</i> , <i>P. turriculatum</i> (Simpson), <i>P. subarmatum</i> (Young & Bird) .....	0.91
Subzone of <i>Dactylioceras commune</i>	
xxviii. Shale. <i>Dactylioceras athleticum</i> (Simpson) .....	1.07

*Lincolnshire.* In north Lincolnshire the Upper Pliensbachian and the lower part of the Lower Toarcian were well exposed until recently in quarries at Kirton-in-Lindsey and Roxby. Accounts of the succession were given by Howarth & Rawson (1965), Penny & Rawson (1969, pp. 194–97) and Howarth (1980a, p. 645). Ammonite faunas of all the subzones of the Tenuicostatum Zone occur in shales and in a calcareous mudstone above the Marlstone Rock Bed. Considerably higher up well-preserved examples of *Cleviceras elegans* occur in a row of doggers. These are of Exaratum Subzone age and the sequence ends before the top of that subzone is reached. The following summary is taken from the previously published accounts listed above.

<i>Zone of Harpoceras falciferum</i>	
Subzone of <i>Cleviceras exaratum</i>	
	m
Shale .....	0·10
Flat limestone doggers. <i>Cleviceras elegans</i> (J. Sowerby), <i>H. serpentinum</i> (Schlotheim), <i>Dactylioceras vermis</i> (Simpson), <i>Phylloceras heterophyllum</i> (J. Sowerby) .....	0·15
Shale .....	0·92
Limestone. <i>Cleviceras</i> cf. <i>exaratum</i> (Young & Bird) .....	0·23
Shale .....	3·05
Limestone doggers .....	0·15
<i>Zone of Dactylioceras (Orthodactylites) tenuicostatum</i>	
Subzone of <i>Dactylioceras (Orthodactylites) semicelatum</i>	
Shale, close-bedded. <i>Tiltoniceras antiquum</i> (Wright), <i>Dactylioceras</i> sp. indet. ....	3·20
Shale, sandy. <i>Tiltoniceras antiquum</i> , <i>Dactylioceras</i> sp. indet. ....	0·30
Shale, with a few limestone nodules. <i>Dactylioceras (Orthodactylites) semicelatum</i> (Simpson) .....	1·70
Subzone of <i>Dactylioceras (Orthodactylites) tenuicostatum</i> (part)	
Shale. <i>Dactylioceras (Orthodactylites)</i> cf. <i>tenuicostatum</i> .....	1·30
Subzones of <i>D. (O.) tenuicostatum</i> (part), <i>D. (O.) clevelandicum</i> and <i>Protogrammoceras pallum</i>	
Hard calcareous mudstone, with some limestone nodules. <i>D. (O.) tenuicostatum</i> , <i>D. (O.) clevelandicum</i> Howarth, <i>Protogrammoceras pallum</i> Buckman .....	0·40–1·10
<i>Zone of Pleuroceras spinatum</i>	
Marlstone Rock Bed. <i>Pleuroceras</i> sp. ....	3·00

The clay-pit exposures in Lincoln itself that were described by Ussher (1888, pp. 33–35), Woodward (1893, p. 285) and Trueman (1918), have long since disappeared. The only exposures seen recently are those in Bracebridge brickpit, 5km south of Lincoln, where the succession of the Upper Pliensbachian and the overlying Tenuicostatum Zone was given by Howarth (1958, p.xi). *Tiltoniceras* occurs in the Lincoln succession, as shown by specimens in older collections, which proves the presence of the Semicelatum Subzone, but there are no ammonites from any of the lower subzones of the Tenuicostatum Zone. Many ammonites from higher horizons occur in older collections: there are several *Ovaticeras* (e.g. Pl. 24, fig. 1) from the top of the Falciferum Subzone, and good faunas of ammonites in the Bifrons Zone, especially *Dactylioceras commune*, *Hildoceras bifrons*, and several species of *Peronoceras*; and highest of all, a good specimen of *Porpoceras vortex* (Simpson) from near the top of the Fibulatum Subzone.

In south Lincolnshire the Lower Toarcian used to be well-exposed in Rudd's Brickyard (SK 913344) immediately south of Grantham. The junction with the overlying Northampton Sand Ironstone (Aalenian, Opalinum Zone) was exposed in excavations for waterworks 1·5km south of Grantham, and the Marlstone Rock Bed was seen in brickpits at Gonerby, north of Grantham. From these exposures Trueman (1918, pp. 107–08) pieced together an almost complete section of the Lower Toarcian at Grantham. The highest horizons contain species of *Porpoceras*, and the high Fibulatum Subzone date that this indicates has been confirmed by the discovery of more examples of that genus in clays 1–2m below the

Northampton Sand Ironstone in quarries at Harlaxton (Howarth, 1978, pp. 280–01, pl. 9, figs 1, 2). In the following section, taken from Trueman (1918, p. 107), redeterminations are given of the ammonites in his collection (most of them obtained from H. Preston), which are now in the Geology Department of Nottingham University, as well as many other ammonites from Grantham.

Bed	m
9. Shale. No fossils .....	5.50
<i>Zone of Hildoceras bifrons</i>	
<i>Subzone of Peronoceras fibulatum</i>	
8. Grey shale. <i>Harpoceras subplanatum</i> (Oppel) (Pl. 22, fig. 7), <i>Hildoceras bifrons</i> (Bruguière), <i>Pseudolioceras lythense</i> (Young & Bird), <i>Porpoceras vortex</i> (Simpson), <i>P. verticosum</i> Buckman, <i>Peronoceras</i> cf. <i>turriculatum</i> (Simpson) .....	1.52
<i>Subzone of Dactylioceras commune</i>	
7. Grey shale, with scattered limestone nodules. <i>Dactylioceras commune</i> (J. Sowerby), <i>Nodicoeloceras</i> sp. indet. ....	9.10
6. Limestone. <i>Dactylioceras commune</i> , <i>Hildoceras lusitanicum</i> Meister, <i>Frechiella subcarinata</i> (Young & Bird) (Pl. 29, fig. 5) .....	0.30
<i>Zone of Harpoceras falciferum</i>	
<i>Subzone of Harpoceras falciferum</i>	
5. Grey shale, with scattered limestone nodules. <i>Harpoceras falciferum</i> (J. Sowerby) in lower part .....	6.10
4. The Oolite Bed. Rubbly limestone and clay with scattered oolite grains. <i>Ovaticeras ovatum</i> (Young & Bird) (a single specimen) (Pl. 24, fig. 2) in the upper part, <i>Harpoceras falciferum</i> , <i>Nodicoeloceras</i> cf. <i>crassoides</i> (Simpson), <i>Dactylioceras gracile</i> (Simpson), <i>Dactylioceras</i> sp. indet. ....	0.15
3. Grey shale, with limestone nodules. <i>Harpoceras falciferum</i> .....	2.75
<i>Subzone of CleVICeras exaratum</i>	
2. Grey shale, with blue limestone nodules. <i>CleVICeras elegans</i> (J. Sowerby) (Pl. 12, figs 10–12, 14, 17, 18; Pl. 14, figs 4, 5), <i>Dactylioceras verme</i> (Simpson) .....	4.60
1. Paper shales with flat nodules. Age unknown .....	4.60

In Trueman's time the top of the Marlstone Rock Bed and the basal beds of the overlying shales were not exposed near Grantham, so it is particularly fortunate that these horizons were well-exposed in recent years in two quarries at Harston and Denton, 12km SW of Grantham, until they were filled-in in 1975. Ammonites of the Tenuicostatum Zone were especially abundant, and it was possible to show that that zone occurs wholly within the Marlstone Rock Bed, there being ammonite evidence for the presence of all the subzones except the lowest, the Paltum Subzone. The succession and the dactylioceratid ammonites were described in detail by Howarth (1980a, pp. 643–44, pl. 81, figs 8–10; pl. 82, figs 1, 2, 9–12, 17–18). Of particular interest in the Harston and Denton quarries is the horizon of nodules 11.4–11.5m above the Marlstone Rock Bed, which contains an abundant fauna of *CleVICeras elegans*. Sufficient well-preserved and complete specimens were obtained to show that Buckman's (1922b, pp. 452–53, tables 6, 7; 1925a, p. 76; 1930a, p. 40) "Grantham ammonite", which was also referred to as "a new species of *Eleganticeras*" by Spath (1942, p. 268), is in fact the microconch of *CleVICeras elegans*. This is the best fauna in England for demonstrating that *C. elegans* is dimorphic. The following summary of the Harston/Denton succession is taken from Howarth (1980a, pp. 643–44).

<i>Zone of Harpoceras falciferum</i>	
<i>Subzone of Harpoceras falciferum</i>	
Clay. <i>Harpoceras falciferum</i> , <i>Dactylioceras</i> sp. indet. ....	2.00
Limestone. <i>Harpoceras falciferum</i> .....	0.20
<i>Subzone of CleVICeras exaratum</i>	
Shale .....	1.20

Scattered flat nodules of blue limestone. <i>Cleviceras elegans</i> (J. Sowerby) (Pl. 12, figs 9, 15, 16, 19; Pl. 14, fig. 6), <i>Dactylioceras anguiforme</i> Buckman, <i>Nodicoeloceras crassoides</i> (Simpson), <i>Phylloceras heterophyllum</i> (J. Sowerby) .....	0-10
Shale .....	10-00
Hard calcareous clay, with a row of scattered limestone nodules at the top. <i>Cleviceras elegans</i> , <i>H. serpentinum</i> (Schlotheim), <i>Hildaïtes murleyi</i> (Moxon) .....	1-30
Shale, with row of thin flat limestone nodules at the top. <i>Cleviceras elegans</i> , <i>H. serpentinum</i> .....	0-05
Scattered lenses of coarse sandstone. <i>Cleviceras</i> cf. <i>exaratum</i> (Young & Bird) .....	0-05
Zone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i>	
Marlstone Rock Bed (part) .....	1-20
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i>	
In top 0-08m of Marlstone Rock Bed: <i>Tiltoniceras antiquum</i> (Wright), <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i> (Simpson).	
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i>	
0-08-0-13m below top of Marlstone Rock Bed: <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i> (Young & Bird).	
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>clevelandicum</i>	
0-23m below top of Marlstone Rock Bed: <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>crossbeyi</i> (Simpson) (one specimen).	
Zone of <i>Pleuroceras spinatum</i>	
Marlstone Rock Bed (part). <i>Pleuroceras spinatum</i> (Bruguière) .....	3-00

*Leicestershire.* Interest in Leicestershire centres on the Tilton railway cutting, and the quarries that existed until the early 1970s in the surrounding area. The railway cutting is still a good exposure and shows the Marlstone Rock Bed and the overlying shales up to the *Falciferum* Subzone. It is the best section for demonstrating that the so-called "Transition Bed" is the diagenetically altered or weathered top of the Marlstone Rock Bed. It was not originally lithologically distinct, nor is it separated from the rest of the Marlstone Rock Bed by any discernable break or disconformity. *Tiltoniceras* is abundant and *Dactylioceras* (*Orthodactylites*) *semicelatum* is common in the top of the Marlstone Rock Bed, showing that as at Harston and Denton, the *Tenuicostatum* Zone occurs within that bed. However, at Tilton there are no ammonites from the lower subzones of the *Tenuicostatum* Zone. Again as at Harston, *Harpoceras serpentinum* and *Cleviceras elegans* occur in the overlying shales and doggers, but there are no longer the abundant well-preserved faunas of the latter species. Former exposures in Leicestershire (Judd, 1875) showed the presence of horizons up to the base of the *Crassum* Subzone, as proved by a single example of *Catacoeloceras crassum* (Young & Bird) (Howarth, 1978, p. 246, pl. 8, fig. 6). The following summary of the section exposed in the Tilton railway cutting (SK 762055) is taken from Howarth (1980a, p. 643).

Zone of <i>Harpoceras falciferum</i>	
Subzone of <i>Harpoceras falciferum</i> m	
Shale, with rows of limestone nodules 0-5m and 0-6m below top. <i>Harpoceras falciferum</i> (J. Sowerby) .....	5-50
Clay containing large calcite oolites. <i>Harpoceras falciferum</i> , <i>Phylloceras heterophyllum</i> (J. Sowerby) .....	0-70
Subzone of <i>Cleviceras exaratum</i>	
Clay with oolites. <i>Harpoceras serpentinum</i> (Schlotheim) .....	0-80
Oolitic limestone. <i>Harpoceras serpentinum</i> , <i>Cleviceras elegans</i> (J. Sowerby), <i>Dactylioceras</i> sp. indet. ....	0-20
Shale and Clay. <i>Harpoceras serpentinum</i> in top 0-5m .....	1-80
Zone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i>	
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i>	
Marlstone Rock Bed (part). Dark green oolitic limestone, weathered brown at top. <i>Tiltoniceras antiquum</i> (Wright) (Pl. 5, figs 3; Pl. 6, figs 1-6; Pl. 7, figs 1, 9) in top 0-2m, <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i> (Simpson) in top 0-9m .....	2-50
Zone of <i>Pleuroceras spinatum</i>	
Marlstone Rock Bed (part). Green oolitic limestone in top 1m, calcareous sandstone below. <i>Pleuroceras</i> cf. <i>hawskerense</i> (Young & Bird) in top part .....	ca. 3-00

*Northamptonshire.* The description of the stratigraphy and the collection of the magnificent ammonite faunas of the Lower Toarcian of Northamptonshire formed a substantial part of the geological work of Beeby Thompson. Some of the ammonites were determined and figured by Buckman (1909a–30a), who used their apparent succession in constructing relevant parts of his many schemes of zones and hemerae. The stratigraphy was reviewed and partly redescribed, and the Dactylioceratidae were described, by Howarth (1978). Horizons are present up to near the top of the Fibulatum Subzone. As usual outside Yorkshire, the lower half of the Lower Toarcian is much condensed, but the Bifrons Zone is represented by unusually thick clays. There are many features of considerable interest in the ammonite fauna:

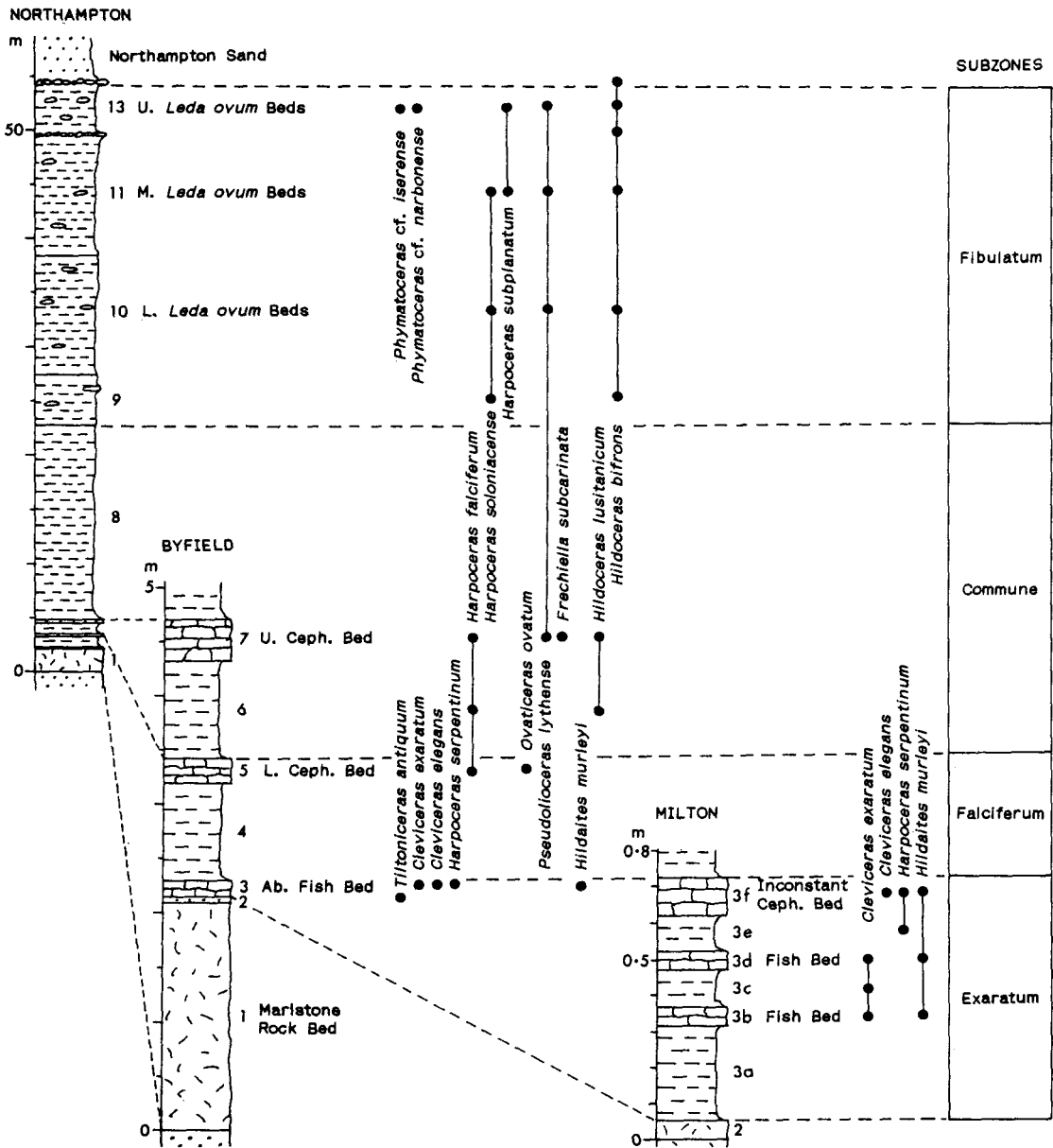
(1) As in Leicestershire and south Lincolnshire the Tenuicostatum Zone lies in the top part of the Marlstone Rock Bed. *Tiltoniceras* and *Dactylioceras* (*Orthodactylites*) *semicelatum* are abundant and prove the presence of the Semicelatum Subzone. There are rare ammonites from the Tenuicostatum Subzone, but none from the two lower subzones of that zone.

(2) The last remaining exposure of the Abnormal Fish Bed, a 0.15m bed of limestone of mid- and upper Exaratum Subzone age, was seen in the early 1960s at Iron Cross quarry, 1.5km north of Byfield, in the west of the county, and more than 300 of its beautifully-preserved ammonites were obtained. The most interesting of these is *Harpoceras serpentinum* (Schlotheim), which is represented by many fine specimens and is much more abundant than anywhere else in Britain. *Cleviceras exaratum* and *C. elegans* occur together in this condensed bed, and another major feature is the splendid specimens of *Hildaites murleyi* (Moxon) and *H. forte* (Buckman), once again the best development of these species in Britain.

(3) The clays of the so-called Unfossiliferous Beds and the *Leda ovum* Beds, that overlie the Lower and Upper Cephalopod Beds, contain many fine ammonites of the Fibulatum Subzone. The shell preservation in white aragonite, which is sometimes iridescent, is especially noteworthy, and these clays furnished all the material used in the description of the remarkable and unique shell structure of the Dactylioceratidae (Howarth, 1975). *Peronoceras* is well represented, with the same species as in Yorkshire, but nearly unique to England is the splendid fauna of another Dactylioceratid genus, *Zugodactylites*. These were described by Howarth (1978), and elsewhere in England they occur only as the much rarer examples in Yorkshire. As well as some fine microconchs of *Hildoceras bifrons* (Bruguière), the only ones in Britain, these beds are also notable for the development of two further species of *Harpoceras*, *H. soloniacense* (Lissajous) and *H. subplanatum* (Oppel). The former species is highly dimorphic, and is represented by some beautifully preserved ammonites, unique to the British fauna. Finally, microconchs of the genus *Pseudolioceras* are preserved in the clays, another unique occurrence in the British fauna.

The following succession (Text-fig. 5) is taken from the earlier description of Howarth (1978, pp. 240–241):

Bed no.	m
15. Northampton Sand. <i>Leioceras</i> spp. &c. Aalenian, Opalinum Zone.	
14. Nodule bed. Many derived ammonites, especially <i>Hildoceras bifrons</i> (Bruguière). Probable age: Opalinum Zone .....	0.08 – 0.30
Zone of <i>Hildoceras bifrons</i> Subzone of <i>Peronoceras fibulatum</i>	
13. Upper <i>Leda ovum</i> Bed. Clay. <i>Porpoceras vortex</i> (Simpson), <i>Pseudolioceras lythense</i> (Young & Bird), <i>Hildoceras bifrons</i> , <i>Harpoceras subplanatum</i> (Oppel) (Pl. 22, fig. 6; Pl. 23, fig. 3), <i>Phymatoceras</i> cf. <i>iserense</i> (Buckman), <i>P. cf. narbonense</i> (Buckman), <i>Phylloceras heterophyllum</i> (J. Sowerby), <i>Lytoceras cornucopia</i> (Young & Bird) .....	4.50



TEXT-FIG. 5. The lithological succession and distribution of Hildoceratidae in the Lower Toarcian of Northamptonshire. The lower part of the succession at Byfield and the expanded succession at Milton are shown on larger scales.

- |  |       |
|--|-------|
| 12. Oyster Bed. Large limestone nodules. <i>Hildoceras bifrons</i> .....   | 0-18  |
| 11. Middle <i>Leda ovum</i> Beds. Clay. <i>Zugodactylites braunianus</i> (d'Orbigny), <i>Z. thompsoni</i> Howarth, <i>Peronoceras fibulatum</i> (J. de C. Sowerby), <i>P. subarmatum</i> (Young & Bird), <i>P. perarmatum</i> (Young & Bird), <i>Pseudoloceras lythense</i> , <i>Harporoceras soloniacense</i> (Lissajous) (Pl. 21, figs 2, 9), <i>H. subplanatum</i> (Oppel) (Pl. 23, fig. 1), <i>Hildoceras bifrons</i> , <i>Phylloceras heterophyllum</i> .....   | 11-00 |
| 10. Lower <i>Leda ovum</i> Beds. Clay. <i>Zugodactylites braunianus</i> , <i>Z. rotundiventer</i> Buckman, <i>Z. thompsoni</i> , <i>Z. pseudobraunianus</i> Monestier, <i>Peronoceras turriculatum</i> (Simpson), <i>P. fibulatum</i> , <i>P. subarmatum</i> , <i>P. perarmatum</i> , <i>Pseudoloceras lythense</i> (Pl. 25, figs 3, 5; Pl. 27, figs 1, 4), <i>Harporoceras soloniacense</i> (Pl. 21, figs 3, 5, 6-8; Pl. 22, figs 1-3), <i>Hildoceras bifrons</i> (Pl. 37, figs 2, 4; Pl. 38, fig. 3), <i>Phylloceras heterophyllum</i> ..... | 11-00 |
| 9. Unfossiliferous Beds (part). Clay. <i>Peronoceras turriculatum</i> , <i>P. fibulatum</i> , <i>P. subarmatum</i> , <i>P. perarmatum</i> , <i>Harporoceras soloniacense</i> , <i>Hildoceras bifrons</i> .....   | 4-60  |

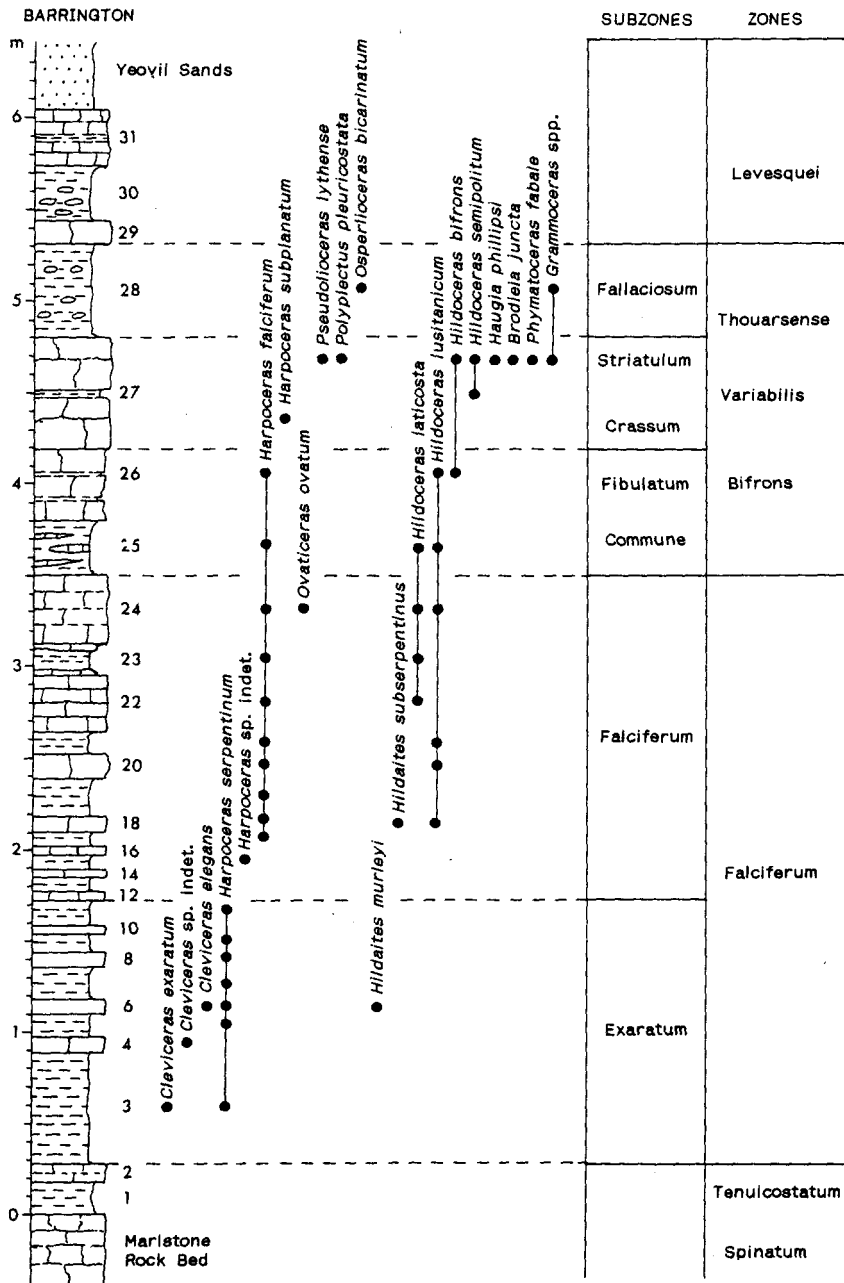
Subzone of <i>Dactylioceras commune</i>	
8. Unfossiliferous Beds (part). Clay. <i>Dactylioceras</i> cf. <i>commune</i> (J. Sowerby) in bottom 3m .....	18.00
7. Upper Cephalopod Bed. Limestone. <i>Dactylioceras commune</i> , <i>D. praepositum</i> (Buckman), <i>Nodicoeloceras</i> sp. indet., <i>Hildoceras lusitanicum</i> Meister (Pl. 35, fig. 2), <i>Harpoceras falciferum</i> (J. Sowerby) (Text-fig. 32), <i>Pseudoloceras lythense</i> (Pl. 25, fig. 4), <i>Frechiella subcarinata</i> (Young & Bird) (Pl. 29, fig. 4), <i>Lytoceras metorchion</i> (Buckman), <i>Phylloceras heterophyllum</i> .....	0.38
6. Clay. <i>Dactylioceras commune</i> , <i>Hildoceras lusitanicum</i> , <i>Harpoceras falciferum</i> .....	0.90
Zone of <i>Harpoceras falciferum</i>	
Subzone of <i>Harpoceras falciferum</i>	
5. Lower Cephalopod Bed. Limestone. <i>Harpoceras falciferum</i> , <i>Dactylioceras</i> sp. indet., <i>Nodicoeloceras crassoides</i> (Simpson), <i>Ovaticeras ovatum</i> (Young & Bird) (two specimens; Pl. 25, fig. 2) ..	0.23
4. Clay. <i>Dactylioceras</i> sp. indet. ....	0.90
Subzone of <i>Cleviceras exaratum</i>	
3. Abnormal Fish Bed. <i>Cleviceras exaratum</i> (Young & Bird) (Pl. 10, fig. 8; Pl. 11, figs 1-6), <i>C. elegans</i> (J. Sowerby) (Pl. 12, fig. 13; Pl. 14, figs 3, 7), <i>H. serpentinum</i> (Schlotheim) (Text-fig. 26; Pl. 15, fig. 5; Pl. 17, figs 5-7; Pl. 18, figs 1, 2; Pl. 19, fig. 1), <i>Hildaites murleyi</i> (Moxon) (Pl. 31, figs 5, 8; Pl. 32, fig. 4), <i>H. forte</i> (Buckman) (Text-fig. 41; Pl. 32, fig. 1), <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semiannulatum</i> Howarth, <i>Dactylioceras</i> sp. indet., <i>Nodicoeloceras crassoides</i> , <i>Lytoceras crenatum</i> (Buckman), <i>Phylloceras heterophyllum</i> .....	0.15
Zone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i>	
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i>	
2. Marlstone Rock Bed (part). Limestone, oolitic, ferruginous, weathered pale brown. <i>Tiloniceras antiquum</i> (Wright), <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i> (Simpson) .....	0.05
Subzones of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i> , <i>D. (O.) clevelandicum</i> and <i>Protogrammoceras paltum</i> , and Zone of <i>Pleuroceras spinatum</i>	
1. Marlstone Rock Bed (part). Limestone, full of green chamosite ooliths. <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i> in top 0.15 m (Tenuicostatum Subzone); <i>Pleuroceras spinatum</i> (Bruguière) below the top 1m (Spinatum Zone) .....	2.10

The basal one-third of the Exaratum Subzone, characterized by *Eleganticeras*, is missing in Northamptonshire, and the remainder of the subzone is developed as the Abnormal Fish Bed, as in the section above, over most of the outcrops in the western half of the county. However, in a small area around Milton and Bugbrooke, 5-8km SW of Northampton, the Exaratum Subzone expands up to a maximum of 0.67m (Text-fig. 5). The bottom one-third of the subzone is still absent, but the following is the maximum development seen at Milton (Howarth, 1978, p. 242):

Subzone of <i>Cleviceras exaratum</i>	
3f. Inconstant Cephalopod Bed. Limestone. <i>Harpoceras serpentinum</i> (Schlotheim), <i>Cleviceras elegans</i> (J. Sowerby), <i>Hildaites murleyi</i> (Moxon), <i>Dactylioceras</i> sp. indet., <i>Lytoceras</i> sp. indet. ....	0.10
3e. Shale. <i>Harpoceras serpentinum</i> .....	0.10
3d. Fish Bed. Limestone. <i>Cleviceras exaratum</i> , <i>Hildaites murleyi</i> .....	0.05
3c. Shale. <i>Cleviceras exaratum</i> .....	0.10
3b. Fish Bed. Limestone. <i>Cleviceras exaratum</i> , <i>Hildaites murleyi</i> .....	0.05
3a. Shale, with clay and red sandy layers in lower half .....	0.27

*South Somerset.* One of the most important and fossiliferous ammonite successions in the Toarcian in Britain occurs in the area around Barrington and Stocklinch in south Somerset. Exposures of the beds are now poor and intermittent, but when they were well-exposed in the early 1920s a splendid bed-by-bed collection of ammonites was obtained, which still contributes greatly to our knowledge of the Lower Toarcian sequence of species. The main part of the succession was seen in a quarry, re-opened for building stone in 1920 after long disuse, in the middle of fields to the west of the cross roads on Winsmoor Hill, half way between Barrington and Stocklinch (ST 385178). At the same time a new quarry was opened about 300m to the north on the west side of Shelway Lane (ST 385180), which exposed the same beds though in a much-disturbed condition. The Marlstone Rock Bed was worked in

the bottom of both quarries, and was overlain by 4.2m of thin limestones, marls and clays that contained abundant ammonites indicating horizons up to the top of the Bifrons Zone. In the same year excavations for a reservoir close to the second quarry, but on the east side of Shelway Lane (ST 386181), revealed a section that extended the succession upwards for a further 3.7m and contained ammonites up as far as the Dispansum and perhaps the Levesquei Subzones.



TEXT-FIG. 6. The lithological succession and the distribution of Hildoceratidae in the Lower Toarcian at Barrington, Ilminster, Somerset. Ammonites of five successive zones and subzones are mixed in the condensed beds 26 and 27, so clear divisions cannot be drawn between the zones and subzones in this part of the column.

The full lithological sequence was recorded by J. Pringle of the Geological Survey and was published by Hamlet (1922, pp. 72–75). Professor D. M. S. Watson collected 170 ammonites from the sections in January 1921, and submitted them to Spath who published a list of determinations and horizons, and a lithological description and a set of bed numbers (Spath 1922, pp. 449–450) that were completely different from those of Hamlet. Watson's ammonites are in the Natural History Museum. In February 1921 A. Templeman collected about 385 ammonites for the Geological Survey, and a summary succession (with Hamlet's bed numbers) with some ammonite determinations made by Buckman, was published by Pringle & Templeman (1922, pp. 450–451). There are also a few specimens from known horizons in Buckman's own collection that were obtained at the same time. More recently, Wilson collected about 35 ammonites from beds 22–26 in 1946, and Spath's determinations of these are listed in Wilson *et al.* (1958, p. 55). The sections revealed by the reservoir excavation and the quarry on the west side of Shelway Lane are now completely obscured. The quarry on Winsmoor Hill is badly overgrown, but beds 24–26 were reached by the author in 1964 and yielded 25 ammonites.

The quarry on the west side of Shelway Lane (ST 385180) is not known to have yielded any of the ammonites collected by Watson, Templeman, and Buckman, all of which came from the two excavations that are here called Water Works Quarry (ST 386181) and Winsmoor Hill Quarry, Barrington (ST 385178). Hamlet (1922) called them Water Works and Barrington Quar [sic] respectively; Spath (1922) (after Watson) called them Barrington and Stocklinch respectively; Pringle & Templeman (1922) called them Shelway Lane, Barrington, and Barrington Quarry respectively; Wilson *et al.* (1959) called the second one Winsmoor Hill Quarry. All these confusingly different names refer to the two excavations only.

In 1971 a new reservoir was constructed at ST 392170 on top of a hill 1 km south-east of Winsmoor Hill Quarry. Beds 25–29 were well-exposed in the excavations; the upper half of bed 27 was developed as a shell bed and many large well-preserved ammonites were collected. The Marlstone Rock Bed and beds 1–20 were exposed in a deep trench at ST 391171. Ammonites were collected from beds 5, 6 and 10, those of bed 6 being of particular interest, this being the horizon of *Cleviceras elegans* (J. Sowerby), found for the first time in the Barrington succession.

More than 650 ammonites have been collected from known horizons in the Barrington succession. A number of the best specimens collected by Templeman were figured by Buckman in volumes 6 and 7 of *Type Ammonites* (1926a–27a), but determinations of the majority of Templeman's ammonites have never been published. In the following succession new determinations are given for all the ammonites collected by Watson, Templeman, Pringle, Buckman, Wilson and the author up to the top of bed 27, and references are given to all the figured specimens. The bed numbers used are those of Hamlet (1922), and a somewhat fuller description of the lithology can be found in his paper. Spath's (1922, pp. 449–450) bed numbers are equated with those of Hamlet (1922) and Pringle & Templeman (1922) in the following way:

<i>Spath</i>	<i>Hamlet</i>	<i>Spath</i>	<i>Hamlet</i>
15	= 32	7	= 15–17
14	= 28	6	= 9–14
13	= 27	5	= 8
12	= 24–26	4	= 6
11	= 22, 23	3	= 3 (part), 24
10	= 20, 21	2	= 3 (part)
9	= 19	1	= Marlstone Rock Bed, ?1–2
8	= 18		

Zone of <i>Dumortieria levesquei</i>	
Subzones of <i>Phlyseogrammoceras dispansum</i>	
and ? <i>Dumortieria levesquei</i>	
Bed	m
no.	
32. Yeovil Sands (base). Yellow Sands. <i>Phlyseogrammoceras dispansum</i> (Lycett), ? <i>Dumortieria</i> sp. indet. ....	1.83
31. Limestone with central parting .....	0.30
30. Clay, with a few calcareous nodules .....	0.30
29. Limestone .....	0.13
Zone of <i>Grammoceras thouarsense</i>	
Subzone of <i>Pseudogrammoceras fallaciosum</i>	
28. Dark grey clay with some limestone nodules. <i>Pseudogrammoceras</i> spp., <i>Grammoceras</i> spp., <i>Hammatoceras</i> sp., <i>Ospertioceras bicarinatum</i> (Zieten) (Pl. 29, fig. 2) .....	0.51
Subzone of <i>Grammoceras striatulum</i> , Zone of <i>Haugia variabilis</i>	
and Zone of <i>Hildoceras bifrons</i> , Subzone of <i>Catacoeloceras crassum</i>	
27. Two beds of massive grey limestone separated by thin clay. The upper limestone is sometimes crowded with large ammonites crushed together in a shell bed. It contains the following species indicative of the three horizons listed above: <i>Grammoceras</i> spp., <i>Polyplectus pleuricostata</i> (Haas) (Pl. 28, fig. 10), <i>Brodieia juncta</i> Buckman (Pl. 5, fig. 4), <i>Haugia phillipsi</i> (Simpson) (abundant), <i>Phymatoceras fabale</i> (Simpson), <i>Hildoceras semipolitum</i> Buckman (Pl. 38, fig. 4), <i>H. bifrons</i> (Bruguière), <i>Pseudolioceras lythense</i> (Young & Bird). The clay parting contains <i>Hildoceras semipolitum</i> Buckman. The lower limestone contains <i>Harpoceras subplanatum</i> (Oppel) .....	0.61
Subzones of <i>Peronoceras fibulatum</i> and	
<i>Dactylioceras commune</i> (upper part)	
26. Grey limestone, with 2 or 3 partings of clay. <i>Hildoceras bifrons</i> (Pl. 37, fig. 6), <i>H. lusitanicum</i> Meister (Pl. 35, fig. 6), <i>Dactylioceras commune</i> (J. Sowerby), <i>D. cf. praepositum</i> (Buckman), <i>Nodicoeloceras multum</i> (Buckman 1927a, pl. 785, holotype), <i>Harpoceras falciferum</i> (J. Sowerby) .....	0.38
Subzone of <i>Dactylioceras commune</i> (lower part)	
25. Clay, with thin beds of grey limestone. <i>Hildoceras laticosta</i> Bellini (Pl. 34, figs 4, 5), <i>H. lusitanicum</i> (Pl. 34, fig. 7), <i>Dactylioceras commune</i> , <i>Nodicoeloceras</i> sp. indet., <i>Harpoceras falciferum</i> (Buckman 1927a, pl. 742) .....	0.30
Zone of <i>Harpoceras falciferum</i>	
Subzone of <i>Harpoceras falciferum</i>	
24. Pale grey limestone, with 3 partings of clay. <i>Hildoceras laticosta</i> (Pl. 34, fig. 6), <i>H. lusitanicum</i> , <i>Harpoceras falciferum</i> (Pl. 20, fig. 4; Buckman 1927a, pl. 764A), <i>Ovaticeras ovatum</i> (Pl. 23, fig. 4), <i>Dactylioceras consimilis</i> (Buckman 1927a, pl. 778, holotype), <i>D. toxophorum</i> (Buckman), <i>Nodicoeloceras lobatum</i> (Buckman 1927a, pl. 730, holotype) .....	0.38
23. Red-brown clay, with thin limestones at top and bottom. <i>Hildoceras laticosta</i> (Pl. 34, fig. 7-? or from bed 22), <i>Harpoceras falciferum</i> (abundant; Pl. 20, fig. 8; Buckman 1926a, pl. 682; 1927a, pls 775A, 775B), <i>Dactylioceras simplicicosta</i> (Buckman 1927a, p. 43, paratype, BGS GSM 38303), <i>D. leptum</i> (Buckman 1926a, p. 42, holotype, BGS GSM 38018, figured Clark, 1982, p. 16, pl. 1, fig. 10), <i>Nodicoeloceras spicatum</i> (Buckman 1927a, pl. 777, holotype) .....	0.18
22. White marly limestone. <i>Hildoceras laticosta</i> , <i>Harpoceras falciferum</i> (Buckman 1927a, pl. 741), <i>Dactylioceras toxophorum</i> (Buckman 1927a, pl. 776, holotype), <i>Nodicoeloceras</i> sp. indet. ....	0.30
21. Olive-grey clay, with <i>Crania</i> . <i>Hildoceras</i> cf. <i>lusitanicum</i> , <i>Harpoceras falciferum</i> , <i>Dactylioceras</i> sp. indet. ....	0.13
20. Pink-grey marly limestone. <i>Hildoceras lusitanicum</i> (Pl. 36, figs 1, 2), <i>Harpoceras falciferum</i> (Pl. 19, fig. 4), <i>Dactylioceras verme</i> (Simpson) (Buckman 1927a, pl. 68A), <i>Dactylioceras</i> spp. indet., <i>Nodicoeloceras</i> sp. indet. ....	0.13
19. Brown-grey clay. <i>Harpoceras falciferum</i> abundant (Text-fig. 30), especially in a layer of large specimens at middle of bed; <i>Nodicoeloceras crassoides</i> (Simpson) .....	0.20
18. Grey limestone. <i>Hildoceras lusitanicum</i> , <i>Harpoceras falciferum</i> common (the ammonite from this bed recorded by Spath (1922, p. 450, bed 8) as " <i>Hildaites</i> cf. <i>chrysanthemum</i> Yokoyama sp." is labelled "Moolham" in Watson's writing (i.e. Moolham Farm, Ilminster); it is <i>Hildaites subserpentinus</i> Buckman (see Pl. 33, fig. 2)) .....	0.08
Templeman and Buckman collected the following ammonites from beds 18 and 19 combined: <i>Harpoceras falciferum</i> (Pl. 19, figs 3; Pl. 20, fig. 2), <i>Hildaites subserpentinus</i> (Pl. 32, fig. 5; Pl. 33, fig. 3), <i>Dactylioceras verme</i> , <i>D. toxophorum</i> , <i>Dactylioceras</i> sp., <i>D. (Orthodactylites) semiannulatum</i> Howarth (Buckman 1927a, pl. 700), <i>Nodicoeloceras crassoides</i> (Simpson) (Buckman 1927a, pls 89A, 728).	

17. Blue-grey clay. <i>Harpoceras falciferum</i> , <i>Dactylioceras</i> cf. <i>anguiforme</i> (Buckman), <i>D. verme</i> .....	0.08
16. Grey limestone. <i>Nodicoeloceras crassoides</i> .....	0.05
15. Clay with small phosphatic nodules. <i>Harpoceras</i> sp. indet. ....	0.08
14. Grey marly limestone .....	0.05
13. Brown marl. <i>Dactylioceras anguiforme</i> .....	0.08
12. Grey marly limestone .....	0.05
Subzone of <i>Cleviceras exaratum</i>	
11. Grey marl. <i>Harpoceras serpentinum</i> (Schlotheim) (Pl. 17, figs 1, 2, specimens transitional to <i>Harpoceras falciferum</i> ), <i>Dactylioceras anguiforme</i> (Buckman 1927a, pl. 763, holotype) .....	0.13
10. Grey marly limestone. <i>Harpoceras serpentinum</i> , <i>Dactylioceras anguiforme</i> .....	0.05
9. Grey marl. <i>Harpoceras</i> cf. <i>serpentinum</i> .....	0.10
8. Grey Limestone. <i>Harpoceras serpentinum</i> .....	0.08
7. <i>Rhynchonella bouchardi</i> Bed. Grey marl, with many phosphatic nodules. <i>Harpoceras serpentinum</i> (Pl. 17, figs 3, 4), <i>Dactylioceras</i> sp. indet., <i>Nodicoeloceras crassoides</i> .....	0.18
6. Grey limestone. <i>Harpoceras serpentinum</i> (Pl. 16, fig. 5; Buckman 1927a, pl. 739), <i>Cleviceras elegans</i> (J. Sowerby), <i>Hildaites murleyi</i> , ? <i>Hildaites wrightii</i> (Spath) (Pl. 30, fig. 7 – possibly from bed 4 below), <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semiannulatum</i> Howarth (Buckman 1927a, pl. 699), <i>Phylloceras heterophyllum</i> (J. de C. Sowerby) .....	0.08
5. Brown shaly clay. <i>Harpoceras serpentinum</i> .....	0.13
4. Fish Bed. Row of flat limestone nodules. <i>Cleviceras</i> sp. indet. ....	0.08
3. <i>Leptaena</i> Clay. Pale green-brown clay, shaly at top, iron-stained at middle. <i>Cleviceras exaratum</i> (Young & Bird), <i>Harpoceras</i> cf. <i>serpentinum</i> abundant but crushed .....	0.61
Zone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i>	
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>semicelatum</i>	
2. Grey marly limestone. <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) cf. <i>semicelatum</i> (Simpson) .....	0.10
Subzone of <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) <i>tenuicostatum</i> and Zone of <i>Pleuroceras spinatum</i>	
1. Sandy Marl. <i>Dactylioceras</i> ( <i>Orthodactylites</i> ) cf. <i>tenuicostatum</i> (Young & Bird), <i>Pleuroceras</i> cf. <i>spinatum</i> (Bruguière), <i>P. apyrenum</i> (Buckman) .....	0.18
Marlstone Rock Bed. Blue-grey oolitic limestone. <i>Pleuroceras spinatum</i> , <i>P. apyrenum</i> , <i>P. solare</i> (Phillips), <i>Amaltheus margaritatus</i> de Montfort, <i>Leptaenoceras leptum</i> Buckman (Pl. 30, fig. 3) below the top 0.3 m (?Apyrenum Subzone) .....	2.13

In addition to the specimens listed in the succession above, several other Barrington ammonites have been figured for which horizons were not recorded accurately. The holotype of *Dactylioceras parvum* (Buckman, 1927a, pl. 779) possibly came from bed 26. The holotype of *Dactylioceras simplicicosta* (Buckman, 1927a, p. 43) is a Barrington specimen (BGS GSM 38304) of unknown horizon that probably came from bed 23, the same horizon as the paratype (BGS GSM 38303). The lectotype of *Ammonites annulatum* J. Sowerby, 1819 (*non* Schlotheim 1813) is a large example of *Nodicoeloceras crassoides* (Simpson, 1855). It was figured by Howarth (1978, pp. 258–59, pl. 3, fig. 1), and its horizon can be definitely identified as bed 18/19 from its distinctive matrix. The matrix of the large specimen of *Harpoceras serpentinum* figured by Buckman (1927a, pl. 740) matches that of bed 6 exactly, and there can be little doubt that it came from that bed (cf. Buckman 1927a, pl. 739). Notable features of the Barrington succession of ammonites are:

1. The presence of many specimens of *Harpoceras serpentinum* in the Exaratum Subzone, including examples at the top that are transitional to *Harpoceras falciferum*. Species of *Cleviceras* are not as abundant as in Yorkshire or Northamptonshire, and the absence of *Eleganticeras* probably indicates that the lower part of the Exaratum Subzone is cut out by a non-sequence.

2. The ammonites of the Falciferum Subzone are more varied and abundant than anywhere else in Britain. Microconchs of *Harpoceras falciferum* are especially common and well-preserved. The holotypes of the two species *Dactylioceras anguiforme* and *D. toxophorum* (Buckman 1927a, pls 763, 776) come from beds 11 and 22 respectively of the Falciferum

Zone. They are two of the most widespread "normal" species of *Dactylioceras* in that zone, but are often crushed and less well-preserved in most other exposures in Britain.

3. After the relatively expanded sequence in the Falciferum Subzone, the succession is condensed again in beds 24–28, which represent horizons up to the Fallaciosum Subzone. The only horizon for which the ammonite evidence is poor is the Fibulatum Subzone. The diagnostic genera *Peronoceras*, *Porpoceras* and *Zugodactylites* are absent at Barrington, but the presence of *Hildoceras bifrons* suggests that the Fibulatum Subzone is represented in part of bed 26. *Hildoceras semipolitum* shows the presence of the Crassum Subzone in bed 27, where there is also abundant evidence for the Variabilis Zone and the Striatulum Subzone.

*Dorset coast.* The Spinatum Zone and most of the Toarcian occurs in the highly condensed Junction Bed, which varies from 0.4m to 2.5m in thickness, and consists of several distinct layers of different types of limestone. The ammonite faunas, though rich and sometimes well-preserved, contribute little to knowledge of the succession in the British Toarcian because of their fragmentary and highly disjointed stratigraphical history. The Junction Bed was described in detail by Buckman (1910b, pp. 61, 64, 82; 1922b), and by Jackson (1922b; 1926) who excavated several blocks *in situ* and collected many ammonites. Determinations of the ammonites in the Spinatum Zone part of the bed were given by Howarth (1957, p. 193). The stratigraphy of the Junction Bed was put into an entirely new context by the work of Jenkyns & Senior (1977), and finally the stratigraphy, age determinations and correlations were brought together in a short synthesis by Howarth (1980b, p. 48, fig. 8A; pp. 53–54, fig. 10A). Buckman (1910b, 1922b) introduced, and Jackson (1926, pp. 491–92) refined, the lettered nomenclature that is always applied to individual layers in the bed.

The Junction Bed occurs in two cliff developments: in the "Western Cliffs" between Seatown and Eypesmouth it is up to 1m thick, the layers are regularly deposited, and there are representatives of most horizons from the Spinatum Zone up to the Levesquei Subzone. These are layers R to I, but no block of the bed contains all the layers, and there are some highly attenuated blocks that contain only two layers. The layers are separated by erosion planes, though all are cemented together into a solid block. Here the bed overlies sands and clays of the Margaritatus Zone with only slight disconformity, and it is overlain by the Down Cliff Clay containing Levesquei Subzone ammonites.

The second development is the "Watton bed" in Watton Cliff, about 300m east of Eypesmouth, where the bed is very different in lithology, though it has a similar age range. When the bed was first described in detail by Buckman (1922b) and Jackson (1922), severe difficulties were encountered with the ammonite succession because the sequence was obtained from a large loose block, which was unfortunately lying upside-down on the talus. Derivation of older ammonites into younger parts of the bed was the only way they could explain the presence of well-preserved Exaratum Subzone ammonites above Striatulum Subzone ammonites in the same block. That error was rectified after further investigation by Jackson (1926) revealed that the block was indeed upside-down, but considerable numbers of Gibbosus Subzone brachiopods and Falciferum Subzone ammonites remained high in the bed that could only be accounted for by "derivation" from older beds. Much light was thrown on the problem by Jenkyns & Senior (1977) who found that the Watton Bed consisted originally of a coarse arenaceous limestone of Margaritatus Zone, Gibbosus Subzone age, sometimes overlain by a thin development of the P layer (Spinatum and Tenuicostatum Zones), followed by conglomeratic limestones (Mw and Uw layers) containing derived Gibbosus Subzone material and also ammonites of Falciferum and Commune Subzone ages. From Exaratum Subzone times onwards it was adjacent to an active fault, movement along which opened fissures in the now solidified bed, which were infilled with white, fine-grained lithographic limestones (layers D, D<sub>1</sub>–D<sub>5</sub>) of at least Exaratum,

Commune, Variabilis, Striatulum and Fallaciosum Subzone ages. Successive openings of fissures at different levels in the bed led to an irregular stratigraphical sequence of lithographic limestones, all within the older "matrix", and the latter contained the Falciferum and Commune Subzone ammonites and the derived Gibbosus Subzone brachiopods at high levels in the bed.

Jackson's ammonite collection (listed in Jackson 1926, pp. 505-07, 512-21) is preserved in the National Museum of Wales, Cardiff. There are other collections from known horizons in the Natural History Museum (including Buckman's and the author's collections) and in the British Geological Survey. New determinations of all these ammonites are given in the successions below.

### 1. The Junction Bed in the Western Cliffs between Seatown and Eypemouth:

- Layer I. Striatulum Subzone. Pale limestone, rubbly ..... 0-0.08m  
*Grammoceras thouarsense* (d'Orbigny) and *G. striatum* (J. de C. Sowerby) (many specimens in BM and NMW), *Esericeras* sp. indet. (NMW), *Hildoceras* cf. *bifrons* (Bruguière) ? derived (NMW 26.135.G31).
- Layer K. Fibulatum Subzone, Crassum Subzone. White limestone, conglomeratic, rubbly ..... 0-0.08m  
*Catacoeloceras* cf. *crassum* (Young & Bird) (NMW 26.135.G13), *C. dayi* (Reynès) (NMW 26.135.G9-12, G14), *Peronoceras turriculatum* (Simpson) (NMW 26.135.G4, G76-78), *Hildoceras bifrons* (NMW 26.135.G79-81), *H. cf. semipolium* (Buckman) (NMW 26.135.G81.2; 59.410.G129-130), *Hildoceras* sp. indet. (NMW 26.135.G30, G96).
- Layer L. Commune Subzone, Fibulatum Subzone (part). Pink and yellow limestone, rubbly, conglomeratic ..... 0-0.25m  
*Hildoceras lusitanicum* Meister (BM C.30773, 68914-16, 22, 24, 25; NMW 26.135.G88, G89.1, G89.2, G91 (Pl. 36, fig. 3), 59.410.G123), *H. bifrons* (BM C.68892-913, C.68921, 23; NMW 26.135.G89 (Pl. 37, fig. 8), G90, G92, G93, 59.410.G122), *Dactylioceras* cf. *athleticum* (Simpson) (BM C.67689, NMW 59.410.G124), *D. cf. temperatum* (Buckman) (NMW 59.410.G125), *Dactylioceras* sp. indet. (NMW 26.135.G85-87), *Nodicoeloceras spicatum* (Buckman) (BM C.67690).
- Layer M. Falciferum Subzone. Hard, massive limestone, conglomeratic, pink with red patches ..... 0-0.23m  
*Hildoceras laticosta* Bellini (BM C.68917-20), *Orthildaites douvillei* (Haug) (Buckman 1923a, pl. 444, holotype, BGS GSM 37298) (BM C.69040; Pl. 34, fig. 3), *Harpoceras falciferum* (J. Sowerby) (large macroconchs abundant; BM 43946 (the holotype; Pl. 19, fig. 2), BM C.4973, C.2270 (Text-fig. 31), C.30767-68, C.68770-81; BGS GSM 22840-41, 24328-29, 25029; NMW 26.135.G23, G24, G36.1, 59.410.G117-120), *Dactylioceras verme* (Simpson) (BM C.67686), *Dactylioceras* sp. indet. (BM C.67687-88), *Nodicoeloceras* cf. *spicatum* (BM C.67685).
- Layers N and O. Exaratum Subzone (upper part). Nodular limestones, with marly and ferruginous bands ..... 0-0.23m  
 Layers N and N<sub>1</sub> at Thorncombe Beacon are the lateral equivalents of layers O<sub>1</sub>, O<sub>2</sub> and O<sub>3</sub> at Ridge Cliff, and in most exposures N and O<sub>1</sub> pass up into layer M without any disconformity.
- |  |   |                   |
|--|---|-------------------|
| N —earthy ferruginous seam, 0.05-0.08m                               | } | Thorncombe Beacon |
| N <sub>1</sub> —white nodular limestone, 0.08-0.13m                  |   |                   |
| O <sub>1</sub> —grey nodular limestone, 0.03-0.08m                   | } | Ridge Cliff       |
| O <sub>2</sub> —marly clay and limestone, nodules at top, 0.08-0.10m |   |                   |
| O <sub>3</sub> —grey-yellow earthy limestone, 0.03-0.08m             |   |                   |
- Ammonites in layers N, N<sub>1</sub> and O<sub>1</sub>: *Harpoceras serpentinum* (Schlotheim) (NMW 26.135.G25-29, G103-113 (Pl. 15, fig. 3; Pl. 16, figs 3, 4); BM C.30771), *Cleviceras elegans* (SM J38416 (Pl. 13, fig. 3)), *Dactylioceras anguiforme* (Buckman) (NMW 26.135.G3, G102, 59.410.G176). *Calliphylloceras* sp. indet. (NMW 57.487.G12).
- Layer P. Tenuicostatum Zone and Spinatum Zone, Hawskerense Subzone. Brown and grey limestone, with many fine ooliths and occasional sandstone pebbles. .... 0-0.30m  
*Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) (BM 67928, C.17548 (Howarth 1980a, pl. 81, figs 3, 4), C.48752, C.74719; BGS GSM 22475, 22514; NMW 26.135.G123; SM J 44225-26 (Howarth 1957, p. 197, pl. 17, figs 5, 6), *D. (O.) tenuicostatum* (Young & Bird) (NMW 26.135.G5.2 (Howarth 1980a, pl. 81, figs 7,8), G5-8 (8 specimens), G124 (Howarth 1980a, pl. 81, figs 5, 6), *Protogrammoceras pallium* (Buckman) (BM 67939 (Pl. 2, fig. 1), C.2200 (Pl. 1, fig. 3 and Wright 1884, pl. 81, figs 4-6), C.30769, C.68536; BGS GSM 47160 (the holotype, Pl. 2, fig. 2 and

Buckman 1922a, pl. 362A), 47161 (Pl. 1, fig. 2 and Buckman 1923a, pl. 362B); SM J 44798), *Pleuroceras spinatum* (Bruguière), *P. spinatum* var. *buckmani* (Moxon), *P. yeovilense* Howarth, *P. hawkskerense* (Young & Bird), *P. apyrenum* Buckman (see Howarth 1980a, p. 640 for discussion of age range).

Layer Px. Spinatum Subzone, Hawkskerense Subzone. Hard, grey-pink limestone, with scattered ooliths ..... 0-0.25m  
*Pleuroceras* cf. *spinatum*.

Layer R. Spinatum Zone, Apyrenum Subzone. Hard, dark-grey conglomeratic limestone, with coarse ooliths and many sandstone pebbles ..... 0-0.25m  
*Pleuroceras* spp. (characteristic of Apyrenum Subzone (Howarth 1957, 1958)), *Lioceratoides serotinus* (Bettoni) (Pl. 5, fig. 1).

2. The Junction Bed in Watton Cliff, 300m east of Eypesmouth:

Layer Mw. Commune Subzone and Striatulum Subzone. Hard, massive, pink and yellow limestone, conglomeratic, with many derived blocks and fossils ..... 0-0.50m  
*Harpoceras falciferum* (NMW 26.135.G329), *Harpoceras* sp. indet. (NMW 26.135.G313), *Hildoceras lusitanicum* (NMW 26.135.G312), *Dactylioceras* sp. indet. (NMW 26.135.G311), *Grammoceras* sp. (Jackson coll. 6846 (Jackson 1926, p. 519), not in NMW).

Layer Uw. Falciferum Subzone. Sandy, conglomeratic limestone, with many derived sandstone blocks ..... 0.50-1.40m  
*Harpoceras falciferum*, *Dactylioceras* sp. indet.

Layers D<sub>5</sub>—D<sub>1</sub>. Thouarsense Zone, Striatulum Subzone (D<sub>5</sub>—D<sub>3</sub>), and Variabilis Zone (D<sub>1</sub>). Fine-grained, white lithographic limestones, with much false bedding truncated by erosion planes; occurs inside layers Mw, Uw and the brown Gibbosus Subzone sandstone "matrix" ..... 0.25-0.75m

D<sub>5</sub>—band of abundant *Grammoceras striatulum* (J. de C. Sowerby) top 0.08m

D<sub>5</sub> / D<sub>4</sub>—*Hammatoceras* cf. *insigne* (Schubler) (BM C.69951-52).

D<sub>3</sub>—*Grammoceras* sp. indet. (BM C.30770).

D<sub>1</sub>—*Haugia* sp. indet. (BM C.74718—parts of a large specimen).

[D<sub>1</sub>—D<sub>5</sub> (level unknown)—*Grammoceras* sp. indet. (NMW 26.135.G327)]

Layer D. Exaratum Subzone (middle part), and ? Commune Subzone. Finely laminated, white lithographic limestone ..... 0-0.20m  
*Cleviceras exaratum* (Young & Bird) (many microconchs and macroconchs; BM C.27868 (2 specimens; Pl. 10, fig. 6); NMW 26.135.G78-2, G316-325, 57-487.G1-10 (Pl. 10, figs 5, 7; Pl. 11, figs 7, 8)), *Jacobella lugeoni* Jeannet (BGS GSM 47106 (Pl. 30, fig. 1 and Buckman 1923a, pl. 23A); NMW 26.135.G325-1-325-3), *Leukadiella* cf. *ionica* Renz & Renz (NMW 57.487.G11 (Pl. 30, fig. 2)), *Alocolytoceras germaini* (d'Orbigny) (NMW 26.135.G315).

Layer C. ? Exaratum Subzone. Pale limestone, sandy at base ..... 0-0.13m  
Hildoceratid indet. (NMW 26.135.G326).

Layer P. Age and lithology as for the Western Cliffs (Jackson 1926, p. 518) ..... 0-0.20m

*Western Scotland.* Pliensbachian and Toarcian rocks are found in Skye, Raasay, Mull, Ardnamurchan and several other areas in NW Scotland. Correlation of the outcrops was summarized by Howarth (1980b, pp. 51-59), the Pliensbachian of Raasay was revised by Howarth (1957; 1959, p. xv), and the Pliensbachian and lower beds of the whole area were revised by Oates (1978). No determinable Hildoceratidae have been found in the Pliensbachian of western Scotland. The Toarcian is thinner and less well exposed, and it has not been revised recently. It contains many Dactylioceratidae and some Hildoceratidae, though many are crushed and poorly preserved. The successions in Raasay and Skye were described by Lee (1920, pp. 30-41) and Anderson & Dunham (1966, pp. 10-12), and the following summary includes many ammonites collected in recent years by Dr A. B. Smith, which are now in the collections of the Natural History Museum:

Zone of *Dumortieria levesquei*

Subzones of *Dumortieria moorei* and *Pleydellia aalensis*

Dun Caan Shales. Shales, micaceous and sandy. *Dumortieria* spp and *Pleydellia* spp. .... m  
Non-sequence ..... 20.00

Zone of *Harpoceras falciferum*Subzones of *Harpoceras falciferum* and *Cleviceras exaratum* (part)

Raasay Ironstone. Green oolitic limestone, with many shaly bands. *Hildoceras laticosta* Bellini, *Harpoceras falciferum* (J. Sowerby), *Cleviceras elegans* (J. Sowerby), *Dactylioceras toxophorum* (Buckman) and *D. sp.*, *Nodicoeloceras sp. indet.* ..... Up to 2.40

Subzone of *Cleviceras exaratum* (part) andZone of *Dactylioceras (Orthodactylites) tenuicostatum* (part)

Portree Shale. Shales, with limestone nodules. *Cleviceras cf. exaratum* (Young & Bird), *?Eleganticeras elegantulum* (Young & Bird), *Dactylioceras anguiforme* (Buckman) ..... Up to 20.00

Zones of *Dactylioceras (Orthodactylites) tenuicostatum* (part)and *Pleuroceras spinatum*

Scalpa Sandstone. Massive sandstones. Poorly preserved *Dactylioceras (Orthodactylites) tenuicostatum* (Young & Bird) in top 2 m.

Some very well-preserved Falciferum Zone *Dactylioceras* occur in the limestone nodules of the Portree Shales on the east coast of Skye, but they have not been described or figured, and most of the other ammonites throughout the Toarcian are poorly preserved or crushed. Part of the Tenuicostatum Zone probably occurs in the bottom few metres of the Portree Shales, but some examples of *Dactylioceras (Orthodactylites)* occur in the top 2m (6 ft) of the Scalpa Sandstone, showing that the zone extends down into that formation. These, and all the other Toarcian ammonites for which there are published identifications, were collected by the Geological Survey before 1918. They were identified by Buckman, and his dating of the beds was published as an appendix to the Applecross, Raasay and NE Skye memoir (Lee, 1920, pp. 64–89). The later memoir of Anderson & Dunham (1966) repeated Buckman's identifications of the ammonites from the Toarcian of Skye, but added no new records of ammonites. So the dating of the Raasay Ironstone as Bifrons Zone, Commune Subzone (=Subcarinatum Subzone of Buckman), stems entirely from Buckman's identification (*in* Lee, 1920, pp. 32, 66, 67) of one or more ammonites from the Raasay Ironstone of Raasay as "*Hildoceras bifrons* (d'Orbigny, *non* Bruguière)". None of the accompanying Dactylioceratidae are distinctive of that subzone, as all of them were given identifications that could be applicable to Falciferum Zone species (few of Buckman's identifications are reliable: for example, some of the ammonites from both the top of the Scalpa Sandstone and the Portree Shales were identified as *Dactylioceras cf. commune*). Buckman's dating of the Raasay Ironstone as Commune Subzone has been repeated by many authors, including Arkell (1933, p. 185; 1956, p. 35), Anderson & Dunham (1966, p. 12), Hallam (1967, p. 424) and Howarth (1980b, p. 59, fig. 10B). However, recent collecting by Dr Andrew Smith does not confirm this dating. The ammonites he obtained from the ironstone on Raasay are:

Ca 120 *Dactylioceras*; mainly *D. toxophorum* (Buckman), and probably one or two other species,

5 *Harpoceras falciferum* (J. Sowerby),

4 *Harpoceras sp. indet.*,

1 *Cleviceras elegans* (J. Sowerby),

2 *Hildoceras laticosta* Bellini.

None of the ammonites are well preserved, but the single *Cleviceras elegans* is distinctive, and shows that the top of the Exaratum Subzone is present, while the Falciferum Subzone is the date indicated by all the other ammonites in the collection. All the many examples of *Dactylioceras* have the appearance of Falciferum Subzone forms, and *D. toxophorum* is the commonest species amongst them, but there are none with the distinctive widely spaced ribbing of *D. commune*. The two specimens of *Hildoceras laticosta* are large and partly crushed, and are identified as this Falciferum Subzone species from the small portions of ribbing that are visible. Buckman (1920) probably based his identification and age assessment on examples that were similar, but there is no evidence for the presence of any Bifrons Zone species of *Hildoceras*. The age of the Raasay Ironstone in Raasay and Skye is Falciferum Subzone and

top Exaratum Subzone, therefore. Ammonites were also collected from the Portree Shales in Berreraig Bay, 10 km north of Portree, Skye, by Dr Smith, and they include two crushed specimens that are probably *Eleganticeras elegantulum*, as well as some probable *Cleviceras exaratum* and *Dactylioceras anguiforme* (Buckman). These ammonites appear to confirm Buckman's identifications of similar specimens from the same locality and horizon, and they show that the middle and lower parts of the Exaratum Subzone are present in the Portree Shales.

The Raasay Ironstone or a similar bed also occurs in Ardnamurchan, and the fauna there includes two specimens of *Grammoceras* indicating a horizon in the Thouarsense Zone, as well as Dactylioceratidae of the Falciferum Zone. They were originally determined by Buckman (in Richey & Thomas, 1930, pp. 43, 44). When they were re-examined in 1960, the *Grammoceras* determination was accepted (Dean, Donovan & Howarth, 1961, p. 487), and both horizons appear to be present in the ironstone at that locality.

### QUANTITATIVE METHODS

Measurements of whorl proportions and other parameters are frequently included in descriptions of ammonites, and a considerable number of such statistics are used in this monograph. Measurements are not often useful in discovering the divisions between species. Rather it is found that after species divisions have been detected by other means (mainly discontinuous variation in single-bed assemblages, combined with a consideration of the likely phylogeny from bed-to-bed), statistics can be used to express those divisions in quantitative terms, and to define more objectively the variation within each species.

(1) *Univariate analysis*. Prominence is given to simple analysis of a single measurement on a series of specimens, such as the diameter of the whole ammonite at the adult mouth-border. Many species described in this monograph are size dimorphic, and many specimens are complete adults. The hundreds of raw measurements are not tabulated in full. Instead, the mean value, the observed range, the standard deviation and the coefficient of variation are given. These are defined as follows:

N = the number of specimens on which the parameter X is measured.

M = the mean value of X, i.e.  $(\sum X/N)$  or  $\bar{X}$

O.R. = the observed range in the values of X, i.e. the lowest and highest values.

s = the standard deviation of X, obtained with the expression<sup>1</sup>

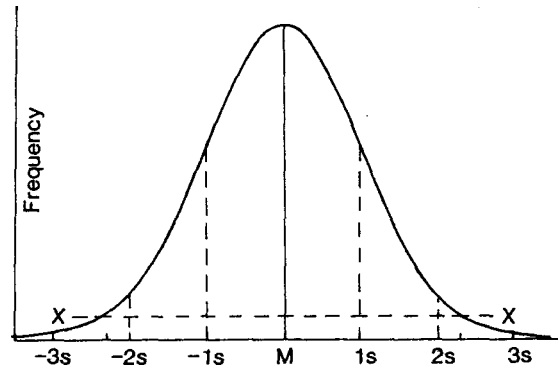
$$s = \sqrt{\frac{\sum(\bar{X}-X)^2}{N-1}} \text{ or } s = \sqrt{\frac{\sum X^2 - [(\sum X)^2/N]}{N-1}}$$

V = the coefficient of variation, i.e.  $(s/M) \times 100$

It has often been stated that the variation in a natural population that has a normal distribution for a given parameter should be definable by the expression  $M \pm ns$ , where M and s are the mean and standard deviation as defined above, and n = 2, 3 or 4 (always a whole

<sup>1</sup>These two expressions are the same. The second one is the basis of electronic calculator or computer operation, from which s is obtained without having to calculate  $\bar{X}$  first. Note that the formula for the standard deviation has (N-1) as the denominator. This is the formula used for the standard deviation of a *sample* from a population.

The alternative formula,  $s = \sqrt{\frac{\sum(\bar{X}-X)^2}{N}}$ , with N as the denominator, is the population standard deviation, and should only be used when a *complete* population is measured. This never happens in palaeontological work. Most electronic calculator or computer programs use the (N-1) formula to derive standard deviation, but some offer the N formula as an alternative. The subject was well discussed by Simpson, Roe & Lewontin (1960, pp. 83, 100). In one of the few works to use statistics on the same ammonites as are described here, Lehmann (1966, p. 35) used the wrong "N" formula for his standard deviation. His values for s should be multiplied by  $\sqrt{(N/N-1)}$  to be compared with those in this monograph. This will increase Lehmann's values of s by 2.5% where his sample size was 20, but by only 1% where his sample size was 50.



TEXT-FIG. 7. The Normal (or Gaussian) Distribution Curve for a population, plotted with frequency (i.e. numbers of individuals) on the y-axis, and a measured parameter (e.g. adult diameter) on the x-axis.  $M$  is the mean value of that parameter in the population, and the scale on the x-axis measures distances from the mean in units of one standard deviation ( $s$ ). The area under the curve is proportional to numbers of individuals: 68% of those individuals fall in the area bounded by the vertical lines at  $1s$  and  $-1s$ , 95.5% are between  $2s$  and  $-2s$ , and 99.7% are between  $3s$  and  $-3s$ . The dashed line  $X-X$  joins the intersection of the curve with the points  $2.3s$  and  $-2.3s$ : it is the position at which the x-axis has to be drawn if the  $M \pm 2.3s$  formula (see p. 30) is accepted as a valid definition of the species in terms of that parameter, and the area between  $X-X$  and the curve then represents 100% of the population.

number) according to which theory is followed. These ideas are derived from the shape of the normal (or Gaussian) distribution curve, which has been shown to be a close approximation to the way in which variable characters are distributed in natural populations. The area under a normal distribution curve can be expressed in terms of multiples of  $s$  (Text-fig. 7). In the theoretical curve, the area under the curve from:

- $M - 1s$  to  $M + 1s$  is 68% of the total area under the curve
- $M - 2s$  to  $M + 2s$  is 95.5% of the total area under the curve
- $M - 3s$  to  $M + 3s$  is 99.7% of the total area under the curve

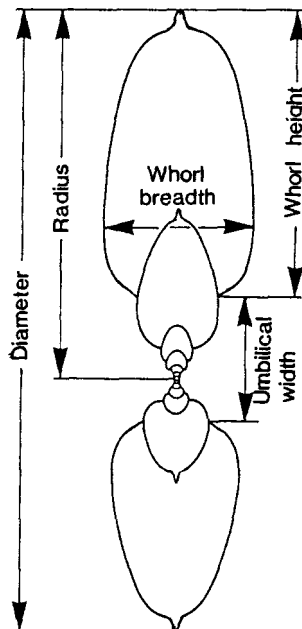
It has been argued by some that even  $M \pm 3s$  will not describe all individuals in the population, because there will still be 0.3% (i.e., 3 in every 1000 individuals) outside that range. However, the normal distribution curve can only be an approximation to a natural distribution because the theoretical curve joins the x-axis only at infinity and at minus infinity, so that infinitely large (and infinitely small) animals are theoretically possible. This is absurd: animals have finite size limits, and there must be a value of  $n$  in the expression  $M \pm ns$  that defines the largest and smallest animals that can physically exist. At that value of  $n$  the area under the curve is 100% by definition for a natural population. This alters the areas for the  $M \pm 1s$  and  $M \pm 2s$  parts of the curve, which will be slightly more than 95.5% and 99.7% respectively for a real natural population. So can a real figure for  $n$ , or at least an estimate of its likely value, be obtained from analysis of real populations? If the observed range (O.R.) and the standard deviation ( $s$ ) are known for a given parameter measured in a population, then O.R. can be compared with the range from  $M - ns$  to  $M + ns$ , and a value obtained for  $n$  in the expression:  $O.R. = (M + ns) - (M - ns)$ , that is  $O.R. = 2ns$ . This will give the value of  $n$  in the formula  $M \pm ns$  which encompasses all the variation in the population. In this monograph 217 values of O.R. and  $s$  have been obtained for measurements on many samples of *Eleganticeras elegantulum*, *Cleviceras exaratum*, *C. elegans*, *Harpoceras serpentinum* and *H. falciferum*. The samples sizes vary from 6 to 146, and Table 1 gives the results of obtaining a value for  $n$  in the expression  $O.R. = 2ns$  for various groups of sizes of the original samples.

Sample size	N	M	s	O.R.
6-9	38	1.47	0.19	0.65-1.80
10-19	77	1.76	0.20	1.35-2.21
20-29	43	1.90	0.22	1.47-2.35
30-39	20	2.03	0.25	1.67-2.48
40-49	12	2.20	0.24	1.93-2.68
50-146	27	2.27	0.29	1.85-2.94
40-146	39	2.32	0.28	1.85-2.94

Table 1. Mean values (M), standard deviations (s) and the observed ranges (O.R.) of n in the expression  $O.R. = 2ns$  for the 217 samples in Tables 6-9, 12-15 and 17-26 for which standard deviations and observed ranges have been calculated.

The mean value of n clearly increases as sample size increases, and does not reach a stable value until the original sample size is more than about 40. Considering the theory that the normal distribution curve is an approximation to the distribution of a natural population, and the values of  $M \pm 2s$ ,  $M \pm 3s$  or even  $M \pm 4s$  that have been used before, it is unlikely that a value for n of 2 or less can be realistic (i.e.  $M \pm 2s$ ). So the four groups of sample sizes below 40 can be discarded. For sample sizes of 40 and above, n is more stable, and it seems that the best estimate for a value for n is 2.3, this being the mean of the 39 values obtained where the original sample sizes were in the range 40-146. This means that in these populations of ammonites size variation in a shell parameter is best described by the expression  $M \pm 2.3s$ , which is equal to all the variation in the shells. It also means that the line of the real distribution curve (cf. Text-fig. 7) meets the x-axis at the two points  $M - 2.3s$  and  $M + 2.3s$ , and all the variation in the measured parameter is between these points. Table 1 also shows that the highest value found for n is 2.94, and this is in a sample where the original sample size was 90. In fact the values for n for the four largest original samples of 103, 104, 120 and 146 readings, are 2.61, 2.89, 2.36 and 2.42 respectively.

(2) *Bivariate analysis.* Whorl proportions and rib-density have been measured and analysed in many published descriptions of ammonites. Whorl proportions measured in this



TEXT-FIG. 8. Ammonite whorl dimensions as measured in this monograph.

monograph are shown in Text-fig. 8, and it will be observed that the radius (R) from the "centre" of the ammonite spiral to the outermost point of the whorl is a measurement that has not often been made before. The "centre" of the spiral is the centre of the protoconch, which can be seen or estimated to well within the accuracy of the measurement taken, when the uncertainties due to shell thickness and preservational distortion are taken into account. Rib-density cannot be measured easily in most Hildoceratidae, and variations in rib-density are expressed in descriptive terms only for most species, except in *Protogrammoceras* where rib counts are shown in Text-fig. 12. In this respect the family is markedly different from the contemporary Dactyloceratidae, in which rib counts assume considerable importance (Howarth, 1973, p. 261, fig. 6; 1978, p. 272, fig. 5).

Whorl dimensions were measured on many hundreds of Hildoceratidae, and in many species they were plotted on graphs as scatter diagrams in the usual pairs of Diameter against Whorl

Height, Diameter against Whorl Breadth, Diameter against Umbilical width, and Whorl Height against Whorl Breadth. This enables an estimate to be made of the amount of variation, and usually reveals any points that were incorrectly measured or abnormal for some other reason. Many such scatter diagrams are included in this monograph, and individual specimens can readily be compared with most of them. A major complication is introduced by dimorphism, and the desire to show both dimorphs of one species on the same diagram for comparison purposes. The amount of difference between small microconchs and the much larger macroconchs leads to highly unbalanced scatter diagrams. By plotting with log-log scales instead of linear scales, the areas occupied by the two dimorphs are made much more comparable with each other. Another complication arises from the desire to combine graphs so that four of the parameters measured (D, Wh, Wb and U) on one species are shown on one diagram, resulting in a large reduction in the number of diagrams. This was done by plotting all the measurements obtained for one species on a single piece of log-log graph paper, the measurements for some parameters (e.g. umbilical width) being multiplied by a constant factor in order to obtain the desired placing on the graph. Multiplication by such common factors does not distort the shapes of groups of points on log-log graphs, it merely alters the position of a group on the graph, while maintaining unaltered the relative position of the points within a group. Single scales are given on these graphs, and the factors by which each point must be multiplied to reproduce the original measurements are given in the text-figure explanations. Regression lines, reduced major axes, or any other "best-fit" lines, would add to the clutter of these already complicated graphs, and they are not given.

(3) *Spiral*. The spiral growth of shells of Mollusca has been described by many authors in dissertations that range from complex mathematics of little practical value (eg Blake, 1878; Burnaby, 1966) to more useful analysis of measurements that can be made on actual specimens (eg Lehmann, 1966). Planispiral ammonites are less complicated than bivalved shells or the helical spirals of gastropods, because their growth can be described as a single equiangular or logarithmic spiral. Much of the earlier work was reviewed by Thompson (1942, pp. 748-849), and the effect that differing spiral forms have on the involution or uncoiling of the ammonite shell was investigated graphically by Raup (1967, p. 43). It is probable that the mid-point of the venter of all planispiral ammonites grows in an equiangular (or logarithmic) spiral expressed by the equation:

$$r_2 = r_1 e^{\theta \cot \alpha}$$

where  $r_1$  and  $r_2$  are radial distances from the centre of the spiral to the mid-point of the venter,  $\theta$  is the angle (in radians;  $360^\circ = 2\pi$  radians) around the spiral between the radii  $r_1$  and  $r_2$ ,  $\alpha$  is the spiral angle (i.e. the smaller angle between the radius and the tangent to the spiral), and  $e$  is the base of natural logarithms. The equation is sometimes used in the alternative form:

$$r_2 = r_1 e^{k\theta}$$

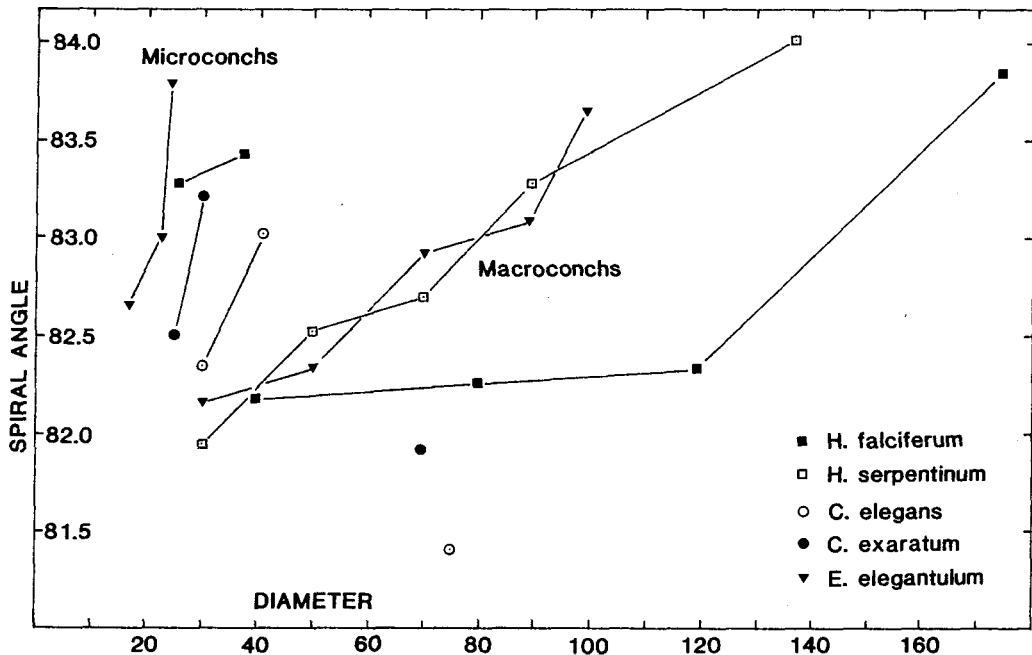
the only difference being the substitution of the "spiral constant"  $k$  for  $\cot \alpha$ , so that  $k = \cot \alpha$ .

If  $r_1$  and  $r_2$  are  $180^\circ$  (or  $\pi$  radians) apart (i.e.  $r_1 + r_2 = D$ , the diameter of the ammonite), then the equation of the spiral becomes:  $r_2 = r_1 e^{\pi \cot \alpha}$ , or  $\frac{r_2}{r_1} = e^{\pi \cot \alpha}$ , or  $\log_e \frac{r_2}{r_1} = \pi \cot \alpha$ , and  $\alpha = \cot^{-1} (\frac{1}{\pi} \log_e \frac{r_2}{r_1})$ . The alternative form is  $k = \frac{1}{\pi} \log_e \frac{r_2}{r_1}$ . It is only necessary to add one extra measurement (the Radius on Text-fig. 8) to those (Diameter, Whorl Height, Whorl Breadth and Umbilical Width) that are usually made on ammonites, to enable the spiral angle  $\alpha$  or the spiral constant  $k$  to be calculated easily. This is because  $r_1 + r_2 = D$  (the Diameter), so that  $\alpha = \cot^{-1} (\frac{1}{\pi} \log_e \frac{R}{(D-R)})$  (or  $k = \frac{1}{\pi} \log_e \frac{R}{(D-R)}$ ), where  $R$  (the Radius of Text-fig. 8)  $= r_2$ .

Lehmann (1966, p. 37) first used this method to obtain the spiral constant  $k$  of several species of ammonites including *Eleganticeras elegantulum* from the Ahrensburg Drift nodules in north Germany. In this monograph  $R$  has been measured along with the other whorl

dimensions on many examples of *E. elegantulum*, *Cleviceras exaratum*, *C. elegans*, *Harpoceras serpentinum* and *H. falciferum*. The spiral angle  $\alpha$  and the spiral constant  $k$  were calculated (with a hand calculator or computer program) for each specimen, and the results are tabulated in Tables 9, 15, 19, 22 and 25 ( $k$  is included for direct comparison with Lehmann's (1966) results). Plots of the spiral angle  $\alpha$  against the shell diameter (Text-fig. 9), reveal that the trend towards increasing involution in both phylogenies, i.e. *E. elegantulum*  $\rightarrow$  *C. exaratum*  $\rightarrow$  *C. elegans*, and *H. serpentinum*  $\rightarrow$  *H. falciferum*, is reflected in decreasing values of  $\alpha$ , i.e. the shell spirals are becoming more quickly expanding. It also shows that the spiral angle  $\alpha$  does not remain constant, but is continually changing throughout the growth of an individual ammonite.  $\alpha$  decreases in the earliest 1–2 whorls to reach its lowest value, then has a period of slow increase through the main period of growth, before increasing steeply in the adult body-chamber where the rate of increase of the spiral of the venter decreases rapidly. Thus the growth of the mid-point of the venter of the ammonite shell can be described as an equiangular spiral with a continually changing spiral angle  $\alpha$ . The changes in  $\alpha$  are best depicted on a graph (Text-fig. 9) relating it to the shell diameter (or alternatively to the number of whorls of growth). This is a more practical method than the complex mathematical analysis that Burnaby (1966) found was necessary in attempting to derive a single mathematical equation that described the growth of an ammonoid shell. Unfortunately the original measurements on the single ammonoid analysed by Burnaby were well outside the degree of accuracy required to produce a meaningful result. Indeed, it is very difficult to obtain measurements of the spiral growth of a single specimen that are sufficiently accurate to be analysed in that way, when the shell thickness and the distortion that occurred during preservation are taken into account.

(4) *Length of the body-chamber and number of whorls.* The length of the body-chamber was measured in the many complete adults that were available of the commonest species. A complete mouth-border is a complex curve, and the last suture-line is usually angled back-



TEXT-FIG. 9. The spiral angle  $\alpha$  plotted against the shell diameter for macroconchs and microconchs of *Eleganticeras elegantulum*, *Cleviceras exaratum*, *C. elegans*, *Harpoceras serpentinum* and *H. falciferum*.

wards (prorsiradiate) with respect to the radial line, so the length of the body-chamber is an inexact measurement. It was estimated by eye to the nearest  $10^\circ$ , between the top of the second lateral saddle (which is usually close to the mid-point of the side of the whorl) of the final suture-line, and the rear-most point of the curve of the mouth-border on the ventral part of the side of the whorl (cf Text-fig. 10). These estimates, with an error of about  $\pm 7^\circ$ , were converted to proportions of a whorl (e.g.  $210^\circ = 0.58$  whorls) and they have a maximum error of about  $\pm 0.02$  whorls. They are sufficiently accurate to give the average body-chamber length in each dimorph, especially when the error of  $\pm 0.02$  whorls is compared with a typical range of adult body-chamber lengths in one dimorph (e.g. 0.47–0.63 whorls in microconchs of *Eleganticeras elegantulum* (p. 82)).

Counts of the number of whorls up to the adult mouth-border were much more difficult to obtain, because very few adults could be developed sufficiently free of matrix in the umbilicus to reveal the protoconch. In fact the number of whorls could be observed only in one adult microconch *Clevelandia elegans* (and then only up to the adult suture-line, because the body-chamber was incomplete), and one adult macroconch *Har poceras soloniacense* (Pl. 21, fig. 9).

### DIMORPHISM

The possibility that ammonites were sexually dimorphic has been discussed since the first half of the nineteenth century. One of the keys to dimorphism is the recognition that crowded final suture-lines and contracted, constricted or otherwise modified mouth-borders are features of a fully grown, adult ammonite. Such features were often referred to as "gerontic" by Buckman and later workers like Spath and Arkell. In any case, the sort of morphological differences between the dimorphs that might have been associated as a pair, became raised to progressively higher taxonomic categories from the 1850s onwards, in the increasing degree of morphological splitting of the following hundred years. To Buckman, Spath and Arkell small size, lappets, constrictions at mouth-borders, and modified final ornament were characters of specific, subgeneric or even generic rank. By the time the *Treatise* emerged, Arkell (1957, p. L90) wrote that ". . . the theory of sexual dimorphism can only be shelved as unproved". In the *Treatise* there are many instances where small size, the possession of lappets or "gerontic simple ribs" (p. L.322) were accorded subgeneric or generic status. The *Treatise* authors clearly did not find it possible to reverse their own work and the continuing morphological splitting, and recombine in single species the sort of disparate morphologies that had been given higher and higher taxonomic status during the previous 100 years. It needed a new generation of ammonite palaeontologists working more with large ammonite collections obtained from known horizons, to find that pairs of morphologies were so often associated together, and evolved in parallel, that some relationship between them was a probability. That relationship is as sexual dimorphs of a pair, now universally known as macroconch and microconch, and conveniently written in this monograph, as elsewhere, as M and m respectively. In comparison with many Recent cephalopods (though not *Nautilus*), the smaller microconchs are usually supposed to be the males, and the larger macroconchs the females. From the early 1960s more workers recognized the reality of such dimorphic species and lineages, and the whole subject was well summarized by Callomon (1981, p. 257).

During the collecting of Toarcian Hildoceratidae for this monograph it soon became apparent that dimorphic pairs occurred at some horizons. The shales or clays with beds of nodules or thin limestones that are characteristic of the English Toarcian, are particularly suited to single bed collecting, and to the preservation of complete adults in the nodules. Association of the macroconchs and microconchs as sexual dimorphs of single species was not found to be a difficulty, so the problem of which macroconch to pair with which microconch, which has so often been discussed by others and has led to their reference to

different subgenera, does not occur in these Hildoceratidae. Members of this family must be some of the earliest undoubted examples of dimorphism in Ammonitina. Dimorphism has been postulated for earlier members of the superfamilies Psilocerataceae and Eoderocerataceae, but many difficulties of recognition and association remain. Certainly the earliest true lappets appear to be those of *Hildoceras* (e.g. Pl. 37, figs 2–5, 7, 10), and they are probably the origin of all the lappets that occur widely in succeeding families and superfamilies in the Middle and Upper Jurassic. During work for this monograph, many examples of collection and preservation failure were encountered, and of mismatching of numbers of dimorphs in certain beds or areas. These are all summarized below, in a description of the general features of sexual dimorphism that were found in the English Hildoceratidae.

Amongst the species described here, the following were found to be dimorphic: *Eleganticeras elegantulum*, *Cleviceras exaratum*, *C. elegans*, *Harpoceras serpentinum*, *H. falciferum*, *H. soloniacense*, *Pseudolioceras lythense*, and *Hildoceras bifrons*. The most obvious omissions from the list are: *Tiltoniceras antiquum*, of which adults are rarely preserved in Britain and none can be proved to be microconchs; *Harpoceras subplanatum*, which is not known to be dimorphic anywhere in Britain, despite its clear derivation from an older species of *Harpoceras*; similarly, dimorphism is not known in *Pseudolioceras boulbiense*, though it was derived from the dimorphic species *P. lythense*; *Hildaites murleyi* is almost certainly dimorphic in Germany, but no British microconchs are known, despite the abundance of specimens in Northamptonshire; and no microconchs have been found in Britain in species of *Hildoceras* other than *H. bifrons*, though several of the other species are dimorphic in France. Though included in the list above, the evidence for dimorphism in *Harpoceras serpentinum* in Britain consists of only a single microconch amongst about 300 macroconchs.

(a) *Morphological features of adults.* Determination that an ammonite is adult and fully grown is the most important step in the recognition of dimorphism. Signs of maturity are:

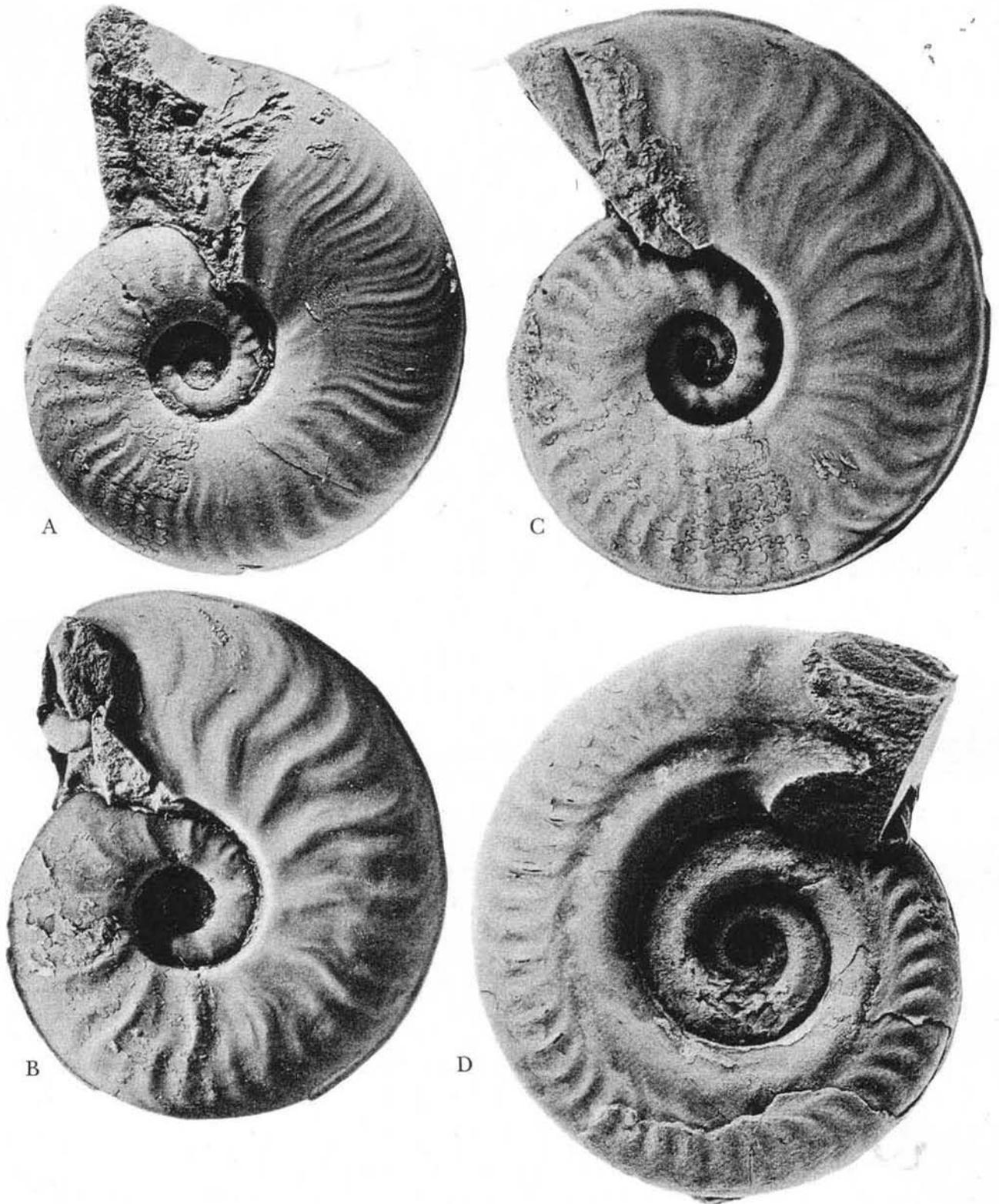
1. Modification of the growth of the body-chamber near the mouth-border. This is often called "uncoiling of the body-chamber", but in fact it rarely actually uncoils away from the previous whorl. Instead, the spirals of both venter and umbilical seam depart from the spirals followed during immature growth, so that the umbilicus widens and the relative whorl height decreases. In some cases the actual whorl height may decrease over the last quarter whorl, and in species with depressed whorls, the real whorl breadth often decreases.

2. Modification of the ribs on the final part of the body-chamber, which become variously striate, coarser, or less strongly curved and angled.

3. Development of lateral lappets in the mouth-border, and a constriction immediately before the mouth-border. Constrictions are diagnostic only when they do not occur regularly on the immature shell, and they may be formed by a thickening of the inside surface of the shell only, so that they are not visible on the outer surface of the shell.

4. Crowding ("approximation") of the last two to four suture-lines. They may become so close together that they interfere with each other.

Lappets are characteristic of microconchs, whereas modifications to the ornament are usually much more obvious in macroconchs. The conclusion that shells with these features are adult depends on the observation that immature shells do not show such modifications in the middle of growth. Alternatively, such shells would need to cast off or resorb long portions of their body-chambers and up to four suture-lines before resuming normal growth to a larger size. There is no evidence that this has ever happened. In ammonites with well developed lappets or in the mature modifications of some heteromorphs, the criteria for adulthood are very clear. The Hildoceratidae described here are mostly at a stage before real lappets evolved, and the adult mouth-borders of the microconchs mainly followed the shape of the ribs. It was only in the later *Hildoceras* that this became modified into the first real lappets seen in ammonites (Text-fig. 10D). The recognition of microconchs in pre-lappeted species can be more difficult, and three complete adult microconchs of *Cleviceras exaratum*



TEXT-FIG. 10. Well-preserved complete adult microconchs. A-C, *Cleviceras exaratum* (Young & Bird, 1828); all are internal casts, and show crowding of the last 3 or 4 suture-lines, adult body-chambers approximately half a whorl long, and slightly flared mouth-borders immediately preceded by slight constrictions; A, B, bed 35, Hawsker Bottoms, Whitby, Yorkshire, both  $\times 3$ ; C, bed 35, Port Mulgrave, Whitby, Yorkshire,  $\times 2.5$ ; A, BM C.53431 (Pl. 12, fig. 2); B, BM C.75613 (Pl. 11, fig. 17); C, SM J46255 (Pl. 9, fig. 2). D, *Hildoceras bifrons* (Bruguère, 1789), BM C.68820, a complete adult with a well-formed lateral lappet, from the Lower or Middle *Leda ovum* Beds, Northampton,  $\times 2.5$  (Pl. 37, fig. 10).

are shown in Text-figs 10A–C, to illustrate most of the adult features that are seen in such forms. Mature modifications are also seen on the much larger adult macroconchs, and there are good examples in Text-figs 25, 42; Pl. 7, fig. 8, Pl. 9, figs 4, 6, Pl. 14, fig. 5, Pl. 19, fig. 1 and Pl. 38, fig. 6.

(b) *Relative abundance of dimorphs.* It might be thought that the “sex-ratio” of numbers found together should be approximately 1:1. The many factors that can upset such a ratio in ammonites include a tendency to form single-sex shoals during various stages of the breeding cycle (as do some modern cephalopods), post mortem sorting by water currents, differential destruction of shells of different sizes during burial and preservation, and various reasons for collection failure. The latter include a disinclination to collect small specimens, that were wrongly thought to be immature, when larger, “better and more complete”, examples could be found. Such bias is clear in the many nineteenth century collections that contain few or no microconchs. This monograph presented the opportunity to discover the sex-ratio in newly collected material, because efforts had been made to avoid the more obvious causes of collection bias, and to compare the results with the sex-ratios in older collections. Table 2 gives the number of macroconchs and microconchs examined for each species, and the resulting macroconch/microconch ratio. It is seen that the figures for that ratio vary from 0.87 up to 8.0. Only two species consist solely of material collected by myself from accurately known horizons: these are *Eleganticeras elegantulum* and *Cleviceras exaratum*, for which the macroconch/microconch ratios are 1.38 and 0.87 for total numbers of 392 and 489 specimens respectively. In *C. elegans* most of the 153 specimens were newly collected, but the macroconch/microconch ratios of 0.74 for 59 specimens from the Grantham area, and 0.82 for 20 specimens from the Northamptonshire Inconstant Cephalopod Bed, were much modified by the 5.0 ratio for 66 specimens from the Yorkshire coast. The ratio of 1.73 for the whole collection is a mixture that reflects the rarity of microconchs in Yorkshire. In *Harpoceras serpentinum* microconchs seem to be genuinely very rare in Britain (though they are more common in France and Germany), and the single Northamptonshire example compares with about 300 macroconchs from Somerset, Northamptonshire and Yorkshire. *H. falciferum* is another species in which microconchs appear to be rare in Yorkshire, from where 190 macroconchs, but only 3 microconchs have been seen. Specimens occur throughout a thickness of 17m of shales and nodules and it is not possible to obtain large numbers from single horizons. The 193 specimens were obtained by many collectors over the last 150 years, and it does appear that microconchs are much less common than macroconchs in Yorkshire. Much larger numbers of *H. falciferum* can be obtained from the Ilminster area of Somerset, where the 520 macroconchs and 130 microconchs give the more realistic ratio of 4:1. Even these figures contain many specimens in older collections, and the real ratio in Somerset is probably nearer to 2:1 judging from the 24 macroconchs and 13 microconchs collected by myself in recent years from an exposure of bed 23 at Barrington.

All the remaining dimorphic Hildoceratidae in Britain rely mainly on the clays of the *Leda ovum* Beds in the Fibulatum Subzone of Northamptonshire for preservation of the microconchs. The only exception is in *Hildoceras bifrons*, for which a single microconch is known from Trent, north Dorset. *Harpoceras soloniacense* occurs only in the *Leda ovum* Beds in Northamptonshire, and the high sex-ratio of 8:1 (40 macroconchs and 5 microconchs) probably shows that the small microconchs (average diameter 26.7mm) were overlooked by collectors. The four known English microconchs of *Pseudolioceras lythense* came from the same beds, where they were found with about 25 macroconchs. Nearly 150 macroconchs of *P. lythense* have been seen from Yorkshire, and a similar number of *Hildoceras bifrons* from Yorkshire are also all macroconchs. Both species occur in the same beds in Yorkshire, and it appears that no microconchs have been found due to their failure to be preserved or collected. On the other hand, in the *Leda ovum* Beds of Northamptonshire, 15 microconchs of *H. bifrons* have been found with 40 macroconchs, giving a sex-ratio of 2.7:1. The most

	Macros	Micros	M/m
1. <i>Eleganticeras elegantulum</i>	227	165	1.38
2. <i>Cleviceras exaratum</i>	227	262	0.87
<i>C. elegans</i> , all	97	56	1.73
3. <i>C. elegans</i> , Grantham area	25	34	0.74
4. <i>C. elegans</i> , Northants only	9	11	0.82
<i>Harpoceras serpentinum</i>	300	1	—
<i>H. falciferum</i> , all	710	135	5.26
<i>H. falciferum</i> , south Somerset	520	130	4.00
5. <i>H. falciferum</i> , bed 23 Barrington	24	13	1.85
6. <i>H. soloniacense</i>	40	5	8.00
[ <i>H. subplanatum</i> ]	28	0]	
<i>Pseudoioceras lythense</i>	180	4	—
7. <i>P. lythense</i> , Northants only	25	4	6.25
[ <i>P. boulbiense</i> ]	120	0]	
[ <i>Hildoceras lusitanicum</i> ]	200	0]	
<i>H. bifrons</i>	250	16	—
8. <i>H. bifrons</i> , Northants only	40	15	2.67
Totals for samples 1–8 only	617	508	1.19

Table 2. Number of macroconchs and microconchs obtained, and the macroconch/microconch "sex-ratio" (M/m), for dimorphic Hildoceratidae in England.

surprising species for which no microconchs have been found in Britain is *Tiltoniceras antiquum*, because many good microconchs of *Tiltoniceras* are known from western Canada. In this case the preservation is probably at fault, because almost all the examples of *Tiltoniceras* in the top of the Marlstone Rock bed in Leicestershire are immature showing no adult features, and the only evidence for the presence of much larger specimens that might have been macroconchs are small fragments of large whorls, broken during deposition of that bed. From all these occurrences it is clear that the sex-ratio depends on many factors, the most important being related to preservation and collecting, but when conditions are favourable for giving a relatively unbiased sample the ratio is between about 0.7 and 1.5. Finally, from the average sex-ratio of 1.19 derived from the eight most satisfactory samples in Table 2, it might be conjectured that there is little to suggest that the original sex-ratio in dimorphic Hildoceratidae differed greatly from 1:1.

(c) *Size ranges of the dimorphs.* The diameter of the ammonite shell measured at the adult mouth-border, shows considerable variation in each dimorph. Table 3 gives the average size of complete adults of each dimorph, the sizes of the smallest and largest specimens found, and the ratio of maximum/minimum size for each dimorph. The latter ratio, which is a measure of the size variation in each dimorph, should be interpreted with care, taking into account the number of specimens on which it is based. In the microconchs the low size range of 1.24 in *Harpoceras soloniacense* is based on only 5 specimens, and clearly represents less than the full size range. The figure of 1.73 for 17 microconchs of *Hildoceras bifrons* might be questioned for the same reason, but it is hardly different from the size range of 1.78 of 75 *Harpoceras falciferum* microconchs, which is probably a realistic estimate of the real size range in that species. The three earlier species all have the much larger size ranges of 2.74 (in 90 specimens) for *Eleganticeras elegantulum*, 3.06 (in 146 specimens) for *Cleviceras exaratum* and 3.18 (in 51 specimens) for *C. elegans*, which again are probably realistic figures. In the macroconchs the largest/smallest ratio is based on much smaller numbers because many fewer complete adults have been collected. The ratio is 2.21 in *Eleganticeras elegantulum*, based on 52 specimens, which is much the largest collection. Other significant values are 2.29 (in 21 specimens) in *Cleviceras exaratum*, 2.04 (in 23 specimens) in *Harpoceras serpentinum*, 2.20 (in 14 specimens) in *H. falciferum*, and 1.84 (in 17 specimens) in *Hildoceras bifrons*. So the largest/smallest size-ratio range is about 1.7 to 3.2 in microconchs, and about 1.8 to 2.3 in macroconchs. It is interesting to compare the size ranges with the

	Microconchs					Macroconchs					
	1	2	3	4	5	6	7	8	9	10	11
	Min	Aver(no)	Max	Max/Min	Stdev	Min	Aver(no)	Max	Max/Min	Stdev	M/m
<i>Eleg. elegantulum</i>	14.6	23.7(90)	40.0	2.74	4.3	66	102 (52)	146	2.21	16.4	4.30
<i>Clevic. exaratum</i>	16.0	30.3(146)	49.0	3.06	7.1	85	146 (21)	195	2.29	30.8	4.82
<i>C. elegans</i>	19.5	39.8(51)	62.0	3.18	10.5	125	155 (3)	190	1.52	—	3.89
<i>Harp. serpentinum</i>	—	25.2 (1)	—	—	—	115	166 (23)	235	2.04	31.4	6.59
<i>H. falciferum</i>	28.6	35.8(75)	51.0	1.78	4.0	159	244 (13)	350	2.20	65.0	6.82
<i>H. soloniacense</i>	24.3	26.7 (5)	30.2	1.24	2.3	128	159 (3)	190	1.48	—	5.96
<i>Pseudo. lythense</i>	—	37.0 (4)	—	—	—	>160	—	—	—	—	—
<i>Hild. bifrons</i>	24.0	35.1(17)	41.5	1.73	5.4	95	131 (17)	175	1.84	23.6	3.73

Table 3. Size data for adult specimens of eight species of Hildoceratidae in England. For microconchs, column 1 is the minimum size, 2 is the average (mean) size (based on the number of specimens stated in brackets), column 3 is the maximum size, column 4 is the ratio of maximum/minimum size, and column 5 is the standard deviation. Columns 6–10 give the equivalent data for the macroconchs. Column 11 is the ratio of sizes of average macroconch/average microconch, i.e. the ratio column 7/column 2.

Coefficient of Variation (V%) in the average size of each dimorph. V is the standard deviation (s) expressed as a percentage of the average value (M) of the size of the dimorphs, and it may be used as an estimation of how "sharply defined" a species is for a particular feature. Values of V are given in Table 4, where it is seen, for example, that a Coefficient of Variation in mean size of 16% corresponds to a largest/smallest ratio of 2.21 (in macroconchs of *Eleganticeras elegantulum*). Other values,  $V_1$ , are also given in Table 4: these are the values of V that would give the observed largest/smallest ratio if it is assumed that the species is defined by the expression  $M \pm 2.3s$  (as postulated on p. 30). Most of the values of  $V_1$  agree fairly well with the real values of V, the largest discrepancy being for macroconchs of *Harpoceras falciferum*, where the real V (26%) is much larger than the value  $V_1$  (16%) derived from the  $M \pm 2.3s$  formula; it implies that macroconchs of *H. falciferum* are more variable in size than the maximum/minimum ratio of 2.20 suggests. In general, a Coefficient of Variation of 14.5% results in a size ratio of 2:1 (and 22% in a size ratio of 3:1) if the  $M \pm 2.3s$  formula is used as an approximation to the species definition in that character. If the formula  $M \pm 2s$  is preferred, a value of 17% for V corresponds to a size ratio of 2:1 between the largest and smallest specimen of each dimorph, and a value of 25% for V corresponds to a size ratio of 3:1.

	Microconchs			Macroconchs		
	Max/min	V	( $V_1$ )	Max/min	V	( $V_1$ )
<i>Eleg. elegantulum</i>	2.74	18	(20)	2.21	16	(16)
<i>Clev. exaratum</i>	3.06	24	(22)	2.29	21	(17)
<i>C. elegans</i>	3.18	26	(23)	—	—	—
<i>Harp. serpentinum</i>	—	—	—	2.04	19	(15)
<i>H. falciferum</i>	1.78	11	(12)	2.20	26	(16)
<i>Hildoceras bifrons</i>	—	—	—	1.84	18	(13)

Table 4. Size-range ratios (maximum size/minimum size) for macroconchs and microconchs of six species of Hildoceratidae in England. V is the Coefficient of Variation in the average size of the dimorph.  $V_1$  is the Coefficient of Variation in the average size which would give the observed maximum/minimum ratio if the species is defined on size according to the formula  $M \pm 2.3s$  (see text for further explanation<sup>1</sup>).

<sup>1</sup> $V_1$  is calculated from the formula  $V_1 = \frac{100(R-1)}{2.3(R+1)}$ , where R is the max/min ratio given in the table. If the species is defined by  $M \pm 2.3s$  (see text) and  $V_1 = \frac{100s}{M}$ , then the formula  $\frac{M+2.3s}{M-2.3s} = \frac{\max}{\min}$  can be converted to  $\frac{100+2.3V_1}{100-2.3V_1} = \frac{\max}{\min}$  which can be re-arranged into the formula for  $V_1$  given above.

Finally, figures are given in Table 3 for the ratio of the average sizes of the dimorphs. For the three members of the *Eleganticeras-Cleviceras* lineage the ratio is in the range 3.9–4.8, in the *Harpoceras* lineage it is in the range 6.0–6.8, while for *Hildoceras bifrons* it is 3.7. Similar information is shown graphically on the histograms of Text-figs 16 and 27, where the extent of the gap between the largest adult microconch and the smallest adult macroconch is well seen. No adult specimens of any of the species fall in these size gaps. The species in which there is least difference between largest microconch and smallest macroconch is *Eleganticeras elegantulum*, but even here the ratio  $M_{\min}/m_{\max}$  is 1.65. In the five other species (excluding *Harpoceras serpentinum* for which the size range of microconchs is unknown) that ratio is higher, even as high as 3.1 in *H. falciferum* which has well-documented size ranges for both dimorphs.

#### Conclusions.

1. Most Toarcian Harpoceratinae and Hildoceratinae for which large collections have been obtained are dimorphic in England. The main exceptions are *Tiltoniceras antiquum*, *Harpoceras serpentinum* and *Hildaites murleyi*, which are known to be dimorphic elsewhere, but preservation or collection failure in England produced few or no microconchs. The most important features of dimorphism in Hildoceratidae are lack of lappets in the microconchs of the early forms, large size differences between the dimorphs without any overlap, and size variation of up to more than 3:1 in the adults of each dimorph.

2. The sex-ratio of numbers of macroconchs:microconchs is probably near to 1:1, though it might be up to 2:1 in some species and localities. Major discrepancies are probably due to preservational failure or bias during collecting.

3. The ratio largest:smallest for complete adults is 1.7:1 to 3.2:1 in microconchs and 1.8:1 to 2.3:1 in macroconchs. Ratios of 3:1 and 2:1 correspond to Coefficients of Variation in average adult size of 22% and 14.5% respectively.

4. The size-ratio of average adult macroconch:average adult microconch varies from 3.7:1 to 6.8:1. In all species there is a considerable size gap between the largest adult microconch and the smallest adult macroconch, so that the latter is at least 1.65× as big as, and may be more than 3× as big as, the former.

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## SYSTEMATIC DESCRIPTIONS

Order AMMONOIDEA Zittel, 1884, pp. 355, 392

Suborder AMMONITINA Hyatt, 1889, p. 7

Superfamily HILDOCERATAEAE Hyatt, 1867, p. 99

Family HILDOCERATIDAE Hyatt, 1867, p. 99

*Remarks.* The most recent classification of the family is due to Donovan, Callomon & Howarth (1981, pp. 114–143). Hildoceratidae includes all the earlier representatives of the superfamily, some of which (*Pseudolioceras*) then continue up to the Lower Bajocian. The families Phymatoceratidae, Graphoceratidae and Sonniniidae were derived from various genera of Hildoceratidae in the Toarcian and Aalenian, and make up the remainder of the Hildocerataeae. The constituent subfamilies of the Hildoceratidae are:

Harpoceratinae; Jamesoni Zone, Lower Pliensbachian, to Laeviuscula Zone, Lower Bajocian; relatively involute, with flexuous ribbing.

Arieticeratinae; Margaritatus Zone, Upper Pliensbachian, to Tenuicostatum Zone, Lower Toarcian; more evolute, straighter ribs, tubercles in some forms.

Hildoceratinae; Falciferum to Variabilis Zones, Lower and Upper Toarcian; evolute, quadrate whorl-section, strongly angled ribbing in some forms.

Grammocerotinae; Variabilis Zone, Upper Toarcian, to Lower Bajocian; evolute, straight or flexuous ribbing.

Leiocerotinae; Aalenian; derived from Grammocerotinae, becoming involute.

Bouleiceratinae; Tenuicostatum to Thouarsense Zones, Toarcian; aberrant genera, with reduced suture-lines.

Tmetoceratinae; Upper Toarcian to Aalenian; has a ventral sulcus.

Abundant representatives of the Harpoceratinae and Hildoceratinae are found in Britain and are described in this monograph. Also abundant in Britain are the later subfamilies Grammocerotinae, Leiocerotinae and Tmetoceratinae, which are not described here. Arieticeratinae are Tethyan in distribution and only very rare representatives appear in the Boreal regions of NW Europe; in fact, only five specimens are known in Britain. Bouleiceratinae are a collection of genera that have simplified or degenerate suture-lines. Apart from the occurrence of very rare examples of *Jacobella* and *Leukadiella* in the Junction Bed in Dorset, only one other species, *Frechiella subcarinata*, is present in Britain, and is confined to the Commune Subzone, Bifrons Zone. In the Pliensbachian all representatives of the superfamily originate and evolve elsewhere (usually in the Tethyan or Mediterranean area), and all examples that occur in Britain are individual stragglers or small restricted

populations that penetrated from the south. With the arrival of *Tiltoniceras* in the Tenuicostatum Zone and *Harpoceras* in the Falciferum Zone, large resident evolving populations were established in Britain and other areas of NW Europe, which gave rise to all later genera of the superfamily. Dimorphism is striking and clearly recognizable in some species, from *Eleganticeras* in the basal Falciferum Zone onwards. Its apparent absence in some genera and species might be due to collection failure, or failure to recognize that suitable dimorphs belong to the same species.

*Occurrence.* Lower Pliensbachian, Jamesoni Zone, to Lower Bajocian, Laeviuscula Zone. World-wide.

*Abnormal growth and the Monestieriinae.* A recurrent abnormality in some Hildoceratidae is the growth of some specimens without keels. In such individuals keels are absent from all whorls, and they are not immediately recognizable as abnormal because there are no asymmetric features or monstrous deformations of the sort usually associated with abnormal growth (e.g. the keel displaced on to one side of the shell, which is an occasional abnormality in Amaltheidae and *Hildoceras*, and the frequent rib abnormalities found in Dactyloceratidae). They all lack a ventral keel, and the ribs pass across the venter without interruption. There are several such groups of ammonites that are widely different in whorl proportions and style of ribbing, and in all cases they are identical, except for the absence of a keel, with the normally-keeled ammonites which occur much more commonly in the same beds. Sapunov (1965, pp. 129–133) proposed the subfamily Monestieriinae to accommodate these keel-less Hildoceratidae, basing his new subfamily on the two genera *Monestieria* Cossmann, 1922, and *Praehaploceras* Monestier, 1931. Other genera that should be included are *Phenakoceras* Maubeuge, 1949a, and *Buckmanites* Guex, 1973c. The view taken here is that all these specimens are due to abnormal shell growth, and the superfamily Monestieriinae and the generic and specific names given to them are not necessary. The placing of the Monestieriinae as a synonym of Grammocerotinae Buckman (1905), is due to the recognition that the type specimen of the type species of the type genus is an abnormal *Phlyseogrammoceras* or *Pseudogrammoceras*. The following is an interpretation of all the known examples of abnormal keel-less Hildoceratidae in the Toarcian:

1. *Monestieria errata* (Simpson). The holotype (Buckman, 1920a, pl. 188; refigured here Pl. 13, fig. 2) is from bed 35 at Hawsker Bottoms, Yorkshire. It is 34.5mm diameter, and except for the absence of a keel, it is an exact match for *Cleviceras exaratum*, which is abundant in the same bed. It is an abnormal macroconch of *C. exaratum*, because its whorl proportions agree with those of the macroconchs and its ribbing is of the same bold type. Two more specimens were collected from bed 35 at Hawsker Bottoms (BM C.53535) and Rosedale Wyke (C.50309), which are only 12mm and 22mm diameter respectively, but by far the largest "*Monestieria*" yet found is the magnificent specimen figured in Pl. 13, fig. 1a (left) (SM J38361). It is one of three ammonites on a block from bed 35, Whitby, Yorkshire (probably from Port Mulgrave). The associated specimens are normal examples of *Cleviceras exaratum*: one is an incomplete macroconch (Pl. 13, fig. 1a, right), the other a complete adult microconch (Pl. 13, fig. 1a, lower centre). The 100mm diameter keel-less specimen is exactly like the macroconch, except that the ribs swing forwards and pass uninterrupted across the venter as large folds (Pl. 13, fig. 1b).

2. *Monestieria goslariensis* (Schloenbach). Of the two originals figured by Schloenbach (1865, p. 166, pl. 26, figs 7, 8) the specimen of fig. 7 from Oserfelde, Goslar, Hannover, was designated lectotype by Sapunov (1965, p. 131). It is about 60mm diameter and was said to come from the "Bronni and Serpentinus" Zone, i.e. the Falciferum and Bifrons Zones of modern nomenclature. It has every appearance of being an abnormal *Cleviceras* or *Harpoceras*, probably a *Cleviceras exaratum*, but the drawing and lack of an exact horizon make



































































































































































































































































































































































































































































