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Abstract

The Upper Lias of Northamptonshire is redescribed from a now obscured exposure of the 3 m of limestones and clays, up to the Upper Cephalopod Bed, that could formerly be seen above the Marlstone Rock Bed in a quarry near Byfield, and from Beeby Thompson's descriptions and collections from the overlying 50 m of clays that were exposed in numerous 19th-century brickpits around Northampton. The three lowest subzones of the Upper Lias occur in the top 1 m of the Marlstone Rock Bed. This is overlain by the Transition Bed of Semicelatum Subzone age and the Abnormal Fish Bed of Exaratum Subzone age. Overlying clays and the Lower Cephalopod Bed belong to the Falciferum Subzone, followed by more clays and the Upper Cephalopod Bed belonging to the Commune Subzone. The latter subzone continues into the basal 5 m of the Unfossiliferous Beds, the middle 15 m do not contain fossils, and the top 5 m and the overlying 27 m of *Leda ovum* Beds belong to the Fibulatum Subzone. The Northampton Sand ironstone of Opalinum Zone age follows after a large non-sequence.

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It is shown that the stratigraphical range of *Zugodactylites braunianus* occurs wholly within the range of *Peronoceras fibulatum*, so the Braunianus Subzone, proposed by Thompson and Buckman as a subzone above the Fibulatum Subzone on the basis of this Northamptonshire succession, has to be abandoned. This relationship between *Peronoceras* and *Zugodactylites* is confirmed by new discoveries in Yorkshire. The Fibulatum Subzone is extended up to include the closely related genus *Porpoceras*, occurring in the Upper *Leda ovum* Beds and in a similar stratigraphical position in Yorkshire. and it is proposed to use *Catacoeloceras crassum* as the index ammonite for the top subzone of the Bifrons Zone.

The Dactylioceratidae of Northamptonshire are described, including the new species *Dactylioceras (Orthodactylites) semiannulatum* from the Exaratum Subzone, the rich faunas of *Peronoceras* and *Zugodactylites*, including the new species *Z. thompsoni*, from the Unfossiliferous and Lower and Middle *Leda ovum* Beds, and *Porpoceras* from the Upper *Leda ovum* Beds. Lectotypes for *Peronoceras fibulatum* (J. de C. Sowerby 1823), *Zugodactylites braunianus* (d'Orbigny 1845) and *Z. pseudobraunianus* (Monestier 1931) are designated. The view is again put forward that a meaningful classification of Dactylioceratidae can only be based on accurate stratigraphical knowledge of the forms and allowance for the wide variation that occurs in some characters, and it is reiterated that no good evidence for sexual dimorphism has yet been found in the family.

Introduction

The closure in 1965 of the old East and West Junction Railway, between Stratford-on-Avon and Towcester, led to the abandonment of the Marlstone Rock Bed iron-ore quarry at Iron Cross Farm, 1·5 km north of Byfield, west Northamptonshire. The tips of overburden were bulldozed back over the whole quarry, thus obliterating the last good exposure of the Upper Lias in Northamptonshire and palaeontologically the most interesting inland exposure of the Upper Lias in England. The main interest lay in the magnificent and well-preserved ammonite fauna of the Abnormal Fish Bed, a 0·15 m (6 in) bed of limestone of Exaratum Subzone age welded to the top of the Marlstone Rock bed. This Bed had been exposed for many years over a length of about 200 m at the side of the mineral railway serving the quarry, and in 1962 and 1963 a collection of about 300 ammonites was made, which included fine specimens of several species that are poorly known elsewhere in Britain. It is a matter for regret that this last good exposure of the Abnormal Fish Bed was not brought to the attention of the Nature Conservancy for possible preservation as a geological Site of Special Scientific Interest.

As well as the Marlstone Rock Bed and its contiguous Transition Bed and Abnormal Fish Bed, the Iron Cross Farm quarry also had good exposures of the overlying Lower Cepahalopod Bed and Upper Cephalopod Bed, which represented horizons up to the Commune Subzone of the Bifrons Zone. Higher beds of the Upper Lias were not seen at Byfield, but they were formerly well exposed in a series of brickpits in and around Northampton. They consist of a thick series of clays up to 50 m (160 ft) thick, the Unfossiliferous Beds below and the *Leda ovum* Beds above, representing horizons up to the top of the Fibulatum Subzone. There have been no exposures from which fossil collections could be obtained for many years, but when the brickpits were worked between 1850 and 1920 they yielded superb collections of ammonites that are still largely undescribed. Interest centres around the *Harpoceras–Zugodactylites* fauna of the *Leda ovum* Beds, a fauna that is very rare anywhere else in the Upper Lias of Britain. In addition, species of *Hildoceras* and *Pseudolioceras* occur in the same beds, and microconch forms of both genera are found, beautifully preserved in the clay facies, forms which are not known from any other British rocks of the same age.

The purpose of this paper is to present a unified description of the Upper Liassic succession and stratigraphical nomenclature, determinations of all the ammonites and the zonal subdivisions, and descriptions of the Dactylioceratidae. The Hildoceratidae will be described separately. Many collections of Northamptonshire Upper Lias ammonites have been examined: the two largest are Beeby Thompson's collection in Northampton Museum and the collection in the British Museum (Natural History) (prefix BM for specimen numbers) which includes good material formerly in the Dorset County Museum. Other collections are in the Geological Survey Museum (GSM) at the Institute of Geological Sciences, London, Oxford University Museum (OUM), the Geology Department of Reading University, Northamptonshire Natural History Society and Leicester City Museum.

The photographs shown in the plates were taken by the author, and the specimens were given a thin coating of ammonium chloride. All figures are natural size unless stated otherwise.

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I wish to thank Mr W. N. Terry and Northampton County Borough Council for the loan of many ammonites from Beeby Thompson's collection; also Mr Gordon Osborne of the Northamptonshire Natural History Society and Field Club, Dr H. C. Ivimey-Cook of the Institute of Geological Sciences, Mr J. M. Edmonds of Oxford University Museum, Dr S. Turner latterly of Reading University and Mr M. D. Jones of Leicester City Museum for ready access to collections in their care.

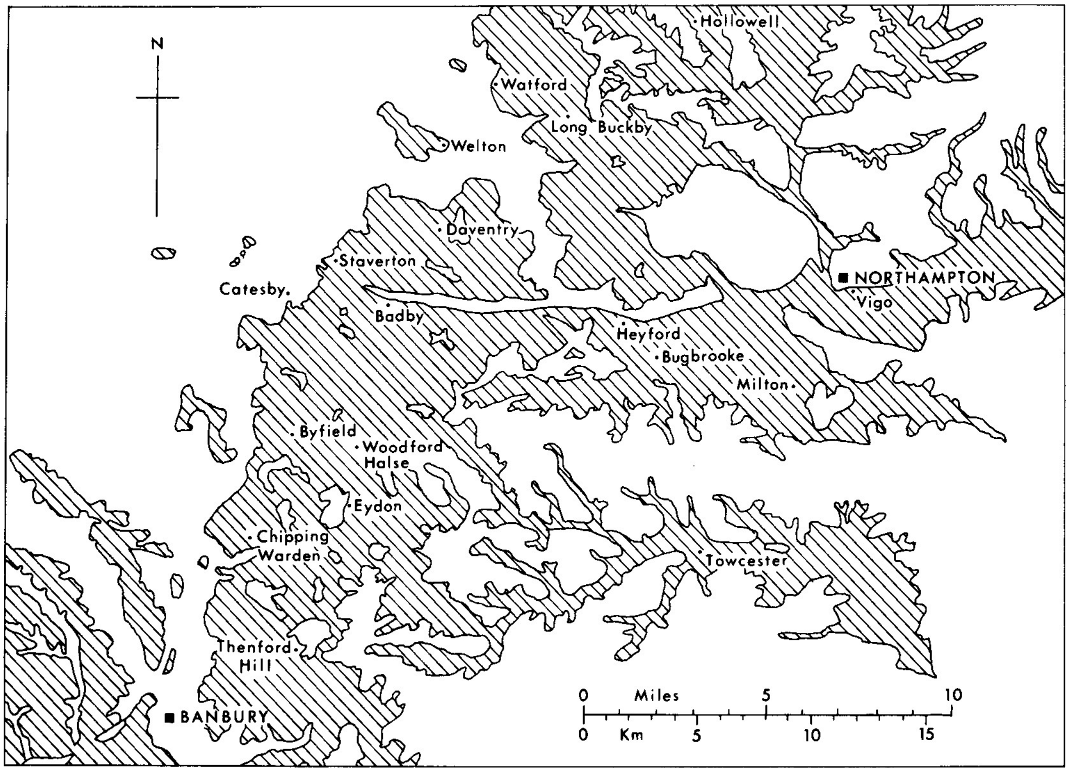


Fig. 1. Map of the outcrop of the Middle and Upper Lias (hatched) in the western half of Northamptonshire, showing all the localities referred to in the text. The Lower Lias occurs to the north-west and the Middle Jurassic to the south-east.

Stratigraphical succession

The stratigraphical succession of the Upper Lias of Northamptonshire was worked out almost single-handed by Beeby Thompson in a long series of papers between 1881 and 1910. Earlier descriptions of the Middle and Upper Lias in the neighbourhood of Banbury by Beesley (1873) and Walford (1878) had included sections at Byfield and Eydon in west Northamptonshire, and it was in their descriptions that the terms Transition Bed, Fish Bed and Cephalopod Bed originated for sections in that area. Nearer Northampton, however, no detailed description existed for the Middle and Upper Lias, and Thompson obtained his information from the numerous quarries in the Marlstone Rock Bed and brickpits in the clay facies of the Upper Lias that existed at that time. His description (Thompson 1881–86) started with the succession revealed by the quarrying of the Marlstone Rock Bed, both as iron-ore and as building stone, at about 30 localities in the western half of the county. The Transition Bed is welded to the top of the Marlstone Rock Bed, followed upwards by a variable sequence of fish beds, then the Lower and Upper Cephalopod Beds, occurring in the lowest 3·0–3·7 m of Upper Lias clays that were removed from the quarries. These represent all horizons of the Upper Lias up to the Commune Subzone of the Bifrons Zone. The beds making up the fish beds were found to be variable in development: in the western part of the county, especially around Byfield and Daventry, they are condensed into a single bed of limestone, 0·15 m (6 in) thick, welded to the top of the Transition Bed, for which Thompson's manuscript name Abnormal Fish Bed is adopted. In several places Thompson (e.g. 1892 : 340; 1910 : 463) referred to this as the 'abnormal' development of the Fish Bed, of which the 'normal' development was found in a relatively small area around Milton and Bugbrooke, 5–8 km south-west of Northampton. In spite of the number of quarries at that time, Thompson had to make excavations at both localities, and the results, presented to the British Association in 1891 (Thompson 1892 : 334–351), showed that at their maximum development the beds consisted of three limestones separated by shales or paper shales, comprising two Fish Beds below and the Inconstant Cephalopod Bed above. They were separated from the Transition Bed by paper shales up to 0·13 m (5 in) thick. The claim that the Abnormal Fish Bed was a condensed lateral equivalent of the Inconstant Cephalopod Bed and both Fish Beds is substantiated by the rich ammonite faunas now known from all of them.

The condensation at the base of the Upper Lias is greater to the south of Byfield: at Middleton Cheney and Thenford, 4–6 km east of Banbury, the Abnormal Fish Bed is thin and the Lower Cephalopod Bed occurs almost immediately above (Beesley 1873 : 23; Walford 1878 : 2; Thompson 1889 : 26–29). West and south of Banbury the Transition Bed and Abnormal Fish Bed are absent: at Wroxton and in the Neithrop cutting (Whitehead *et al.* 1952 : 148, 185; Edmunds *et al.* 1965 : 51, 59) the Lower Cephalopod Bed and clays below, both of Falciferum Subzone age, overlie the Marlstone Rock Bed directly, while at West Bloxham (Hallam 1967 : 421) the Lower Cephalopod Bed with Falciferum Subzone ammonites rests on the Marlstone Rock Bed without intervening shales.

Few descriptions of the Transition Bed to Upper Cephalopod Bed sequence have appeared since Thompson's (1910) review of the succession. Barnard (1950) described foraminifera from the shales above and below one of the Cephalopod Beds at Byfield, though he obtained his samples from new excavations in the railway cutting at Byfield itself, rather than from the excellent exposures that existed in the Iron Cross quarry 1·5 km to the north. Lord (1974 : 604) has described ostracods from the same bed in that railway cutting. The Iron Cross quarry was opened about 1920 and worked until 1965. A photograph of the vertical face, showing the Marlstone Rock Bed and the Lower and Upper Cephalopod Beds, was given by Whitehead (1952 : 159, pl. 8B). In his description of similar quarries on the west side of Byfield and at Upper Catesby (Whitehead 1952 : 177, 179), the succession at the base of the Upper Lias was not properly identified according to Thompson's nomenclature: bed at 5 Upper Catesby (: 177) and bed 4 at Byfield (: 179) are the Abnormal Fish Bed, and beds 3 and 4 at Upper Catesby and bed 3 and the top of bed 2 at Byfield are the Transition Bed. In the Banbury memoir Edmonds (1965 : 56) was equally unsuccessful in using Thompson's stratigraphical nomenclature: while the succession in the Iron Cross quarry was adequately described, the 'cream coloured earthy limestone' immediately above the Transition Bed is the Abnormal Fish Bed, and the two higher limestones are the Lower and Upper Cephalopod Beds. No comment was made on the superb ammonites in the Abnormal Fish Bed. The 'Inconstant Cephalopod Bed' (Edmonds 1965 : 51 (bed 35), 59) does not occur in the Neithrop cutting 2 km north-west of Banbury (the bed is probably the Lower Cephalopod Bed), and at Wroxton (Edmonds 1965 : 59) the two cephalopod limestones are the Lower and Upper Cephalopod Beds.

The expanded sequence of a Fish Bed overlain by the Inconstant Cephalopod Bed was seen again, for the first time since Thompson's days, in excavations below a bridge during construction of the M1 motorway in 1958, 4 km south-west of Northampton (SP 735567). Good Fish Bed and Inconstant Cephalopod Bed ammonites were collected by the author, and also ammonites from the Lower and Upper Cephalopod Beds.

After describing the 3–4 m of beds of the Upper Lias up to the Upper Cephalopod Bed, that were always found in the Marlstone Rock Bed quarries, Thompson turned his attention to the much thicker series of clays that formed the rest of the Upper Lias. They are up to 50 m thick in places, but represent only part of the Commune and Fibulatum Subzones. In Thompson's time there were about 40 pits in the clays (list in Thompson, 1910 : 465–467), though it was unusual for a thickness of more than 6 m of clays, mostly used for brick-making, to be found in any one pit. Several pits were situated within the town of Northampton itself, and a photograph of the best-known one, Vigo brickpit, accompanied Thompson's (1895 : 139–144) description of the method of working the clay. Thompson (1887–88) made four divisions, mainly by means of the different fossil constituents of the clays: the Unfossiliferous Beds at the base overlain by the Lower, Middle and Upper *Leda ovum* Beds. Beautifully preserved ammonites of the genera *Peronoceras*, *Zugodactylites*, *Porpoceras*, *Hildoceras*, *Harpoceras* and *Pseudolioceras* occur in the clay, though

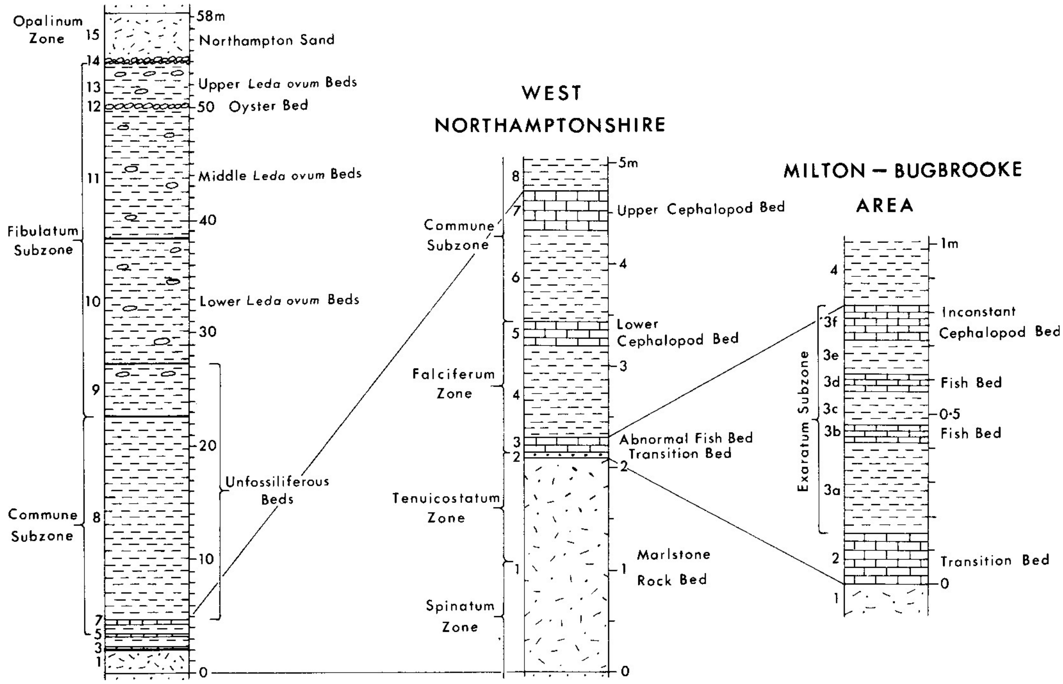


Fig. 2. Vertical sections of the Marlstone Rock Bed and the Upper Lias in Northamptonshire. The general section on the left (partly enlarged in the centre) shows the west Northamptonshire development of bed 3. The expanded bed 3 in the Milton–Bugbrooke area is shown on the right.

perhaps not abundantly, for the total number of specimens found by all collectors in the 40 exposures was only about 700. It was Thompson's discovery in these clays of species of *Peronoceras* apparently overlain by species of *Zugodactylites* that led to the proposal of the Fibulatum and Braunianus Subzones of the Bifrons Zone (Buckman 1910*a* : 86, 87; Thompson 1910 : 462). The *Leda ovum* Beds are overlain by the Northampton Sand, which has a bed of nodules at the base containing derived specimens of *Hildoceras*. Thompson always maintained that in sections undisturbed by any form of slumping the Northampton Sand followed the *Leda ovum* Beds without a break in deposition, so that the succession was complete up to the top of the Upper Lias and into the Inferior Oolite. In support of this contention he advanced innumerable arguments over a period of 40 years (Thompson 1888 : 71–73; 1890; 1893; 1896–1905; 1910 : 467; 1921; 1927), and always rejected the dating and correlations based on the ammonites. Buckman (1890) had shown at an early stage that there are no 'Jurense' Zone ammonites in the Upper *Leda ovum* Beds, and soon afterwards (Buckman 1892) he showed that the ammonites in the Northampton Sand that had been recorded as *Lytoceras jurense* belonged to Lower Bajocian, Opalinum Zone, species.

In fact, all the ammonites of the Upper *Leda ovum* Beds are indicative of the Fibulatum Subzone (as redefined here, p. 245) of the Bifrons Zone. Well-preserved specimens of *Leioceras*, such as *L. thompsoni* Buckman (1899 : xl; suppl. pl. 7, figs 13–16), occur in considerable numbers in the Northampton Sand, together with *Tmetoceras* and *Bredyia* (Thompson 1927 : 62–67), and species of *Pachylytoceras* (Buckman 1905) (Spath also listed determinations of these ammonites in Hollingworth & Taylor, 1951 : 14). This fauna dates the Northampton Sand as Opalinum Zone, probably the upper half (Costosum Subzone), so that, as had been originally pointed out by Buckman and reiterated by Richardson (1926 : 141), the disconformity at the junction of the Upper *Leda ovum* Beds and the Northampton Sand represents the top subzone of the Bifrons Zone, the Variabilis, Thouarsense and Levesquei Zones of the Upper Lias, and probably part of the Opalinum Zone at the base of the Inferior Oolite.

There are now no exposures of any part of the Upper Lias of Northamptonshire from which worthwhile ammonite collections can be obtained. The following succession of the Unfossiliferous Beds and the *Leda ovum* Beds is taken from Thompson's descriptions, and includes redeterminations of all the ammonites found in these beds. The succession for the Upper Cephalopod Bed down to the Marlstone Rock Bed is that measured in 1962 and 1963 in the Iron Cross quarry (SP 519547) 1·5 km north of Byfield, and all the ammonites found in similar quarries by Thompson are included in the determinations. It is closely similar to the section recorded by Thompson (1885 : 301–302) near the railway south-west of Byfield (SP 512528).

15. Northampton Sand. Sideritic limestones of varying type and composition. *Leioceras* spp., *Bredyia* spp., *Tmetoceras scissum* (Benecke), *Alocolytoceras* sp. and *Pachylytoceras* sp. have been obtained from the upper part of the 'ironstone', i.e. the Main Oolitic Ironstone Group (Hollingworth & Taylor 1951 : 39), 2–3 m above the base, indicating the Opalinum Zone, ? Costosum Subzone (see Hollingworth & Taylor 1951 : 14 for determinations, and Thompson 1927 : 65 and Richardson 1926 : 147, 149 for position within the Northampton Sand).

14. Nodule Bed. Layer of grey argillaceous limestone nodules derived from the Upper Lias, of varying sizes and shapes, and worn and stained a variety of colours, set in a matrix of clay or sand, sometimes phosphatic or calcareous. Many fossils in places, especially brachiopods, and sometimes the matrix is composed of crushed shells; none are diagnostic of age which is probably Opalinum Zone; derived *Hildoceras bifrons* (Bruguière) common . . . . 0·08–0·30 m (3 in–1 ft)

Zone of *Hildoceras bifrons*
Subzone of *Peronoceras fibulatum*

13. Upper *Leda ovum* Beds. Clay, blue or yellow, sandy and micaceous in places, with much iron pyrites, and nodules of grey argillaceous limestone, sometimes in rows. *Nuclana* ['*Leda*'] *ovum* (J. Sowerby) occurs only in small numbers. *Phymatoceras* cf. *iserense* (Oppel) (Buckman 1898 : xvii; suppl. pl. 2, figs 1, 2), *P.* cf. *narbonense* (Buckman 1898 : xiv; suppl. pl. 2, figs 3, 4), *Porpoceras vortex* (Simpson), *Pseudolioceras lythense* (Young & Bird), *Harpoceras subplanatum* (Oppel), *Hildoceras bifrons*, *Phylloceras heterophyllum* (J. Sowerby), *Lytoceras cornucopia* (Young & Bird) . . . 4·50 m (15 ft)

12. Oyster Bed. Continuous row of large grey nodules of argillaceous limestone, white on the outside, bored and often encrusted with oysters and serpulids. Occasional *Hildoceras bifrons* . 0·18 m (7 in)

11. Middle *Leda ovum* Beds. Blue clay, with nodules of grey argillaceous limestone. *Nuculana* ['*Leda*'] *ovum* abundant, no gastropods. *Zugodactylites braunianus* (d'Orbigny), *Z. thompsoni* sp. nov., *Peronoceras fibulatum* (J. de C. Sowerby), *P. subarmatum* (Young & Bird), *P. perarmatum* (Young & Bird), *Pseudolioceras lythense* (Young & Bird), *Harpoceras soloniacense* (Lissajous), *H. subplanatum* (Oppel), *Hildoceras bifrons*, *Phylloceras heterophyllum* . . . . 11 m (35 ft)

10. Lower *Leda ovum* Beds (or *Cerithium* Beds). Blue clay, with nodules of grey argillaceous limestone. *Nuculana* ['*Leda*'] *ovum* common, *Procerithium* (*Xystrella*) *armatum* (Goldfuss) and other gastropods abundant, and distinguish the beds from the Middle *Leda ovum* Beds. *Zugodactylites braunianus* (d'Orbigny) (Buckman 1926 : pl. 658; 1927 : pl. 720), *Z. rotundiventer* Buckman (1927 : pl. 743), *Z. thompsoni* sp. nov., *Z. pseudobraunianus* (Monestier), *Peronoceras turriculatum* (Simpson), *P. fibulatum*, *P. subarmatum*, *P. perarmatum*, *Pseudolioceras lythense*, *Harpoceras soloniacense* (Buckman 1927 : pls 684, 721, 722), *Hildoceras bifrons*, *Phylloceras heterophyllum* . . . . . 11 m (35 ft)

9. Unfossiliferous Beds (part). Blue clay, with a few large nodules of grey argillaceous limestone near the top. *Nuculana ovum* absent. *Peronoceras turriculatum, P. fibulatum, P. subarmatum, P. perarmatum, Harpoceras soloniacense, Hildoceras bifrons* . . . . 4·60 m (15 ft)

Subzone of *Dactylioceras commune*

8. Unfossiliferous Beds (part). Blue clay. *Dactylioceras* cf. *commune* (J. Sowerby) in bottom 3 m, no fossils in top 15 m . . . . 18 m (60 ft)

7. Upper Cephalopod Bed. Limestone, brown, ferruginous, flaggy or rubbly, and shaly in places. Ammonites abundant: *Dactylioceras commune* (Thompson 1886 : 26; pl. 1, figs 3a, 3b, 4; Buckman 1926 : pl. 657), *D. praepositum* (Buckman), *Nodicoeloceras* sp. indet., *Hildoceras sublevisoni* Fucini, *Harpoceras falciferum* (J. Sowerby), *Pseudolioceras lythense, Frechiella subcarinata* (Young & Bird) (Arkell 1951 : pl. 1, fig. 3), *Lytoceras metorchion* (Buckman 1926 : pls 666, 681), *Phylloceras heterophyllum* . . . . 0·38 m (1 ft 3 in)

6. Clay, grey or brown, marly, sandy or ferruginous in patches, with small white limestone nodules. Ammonites small and poorly preserved, but *Dactylioceras commune, Hildoceras sublevisoni* and *Harpoceras falciferum* are common . . . . 0·9 m (3 ft)

Zone and Subzone of *Harpoceras falciferum*

5. Lower Cephalopod Bed. Limestone, hard, pale yellow-brown, blue interior, sometimes sandy, oolitic or shaly, and in three thin layers in places. Ammonites only occasional, but microconchs and large macroconchs of *Harpoceras falciferum* occur (Thompson 1885 : 309, fig. 1), also *Dactylioceras* sp. indet., *Nodicoeloceras crassoides* (Simpson) (Thompson 1885 : 309, fig. 2), and *Ovaticeras ovatum* (Young & Bird) (see below) . . . . 0·23 m (9 in)

4. Clay, blue-grey and brown, marly, with a few small white limestone nodules. Ammonites rare. *Dactylioceras* sp. indet. . . . . 0·9 m (3 ft)

Subzone of *Harpoceras exaratum*

3. Abnormal Fish Bed. Limestone, hard, pale blue-grey, brown when weathered, containing large grey ooliths in places. Separated from the bed below by a parting in most places. Full of tiny black fish fragments, including some whole teeth, and occasional pieces of wood. Well-preserved ammonites abundant. *Harpoceras exaratum* (Young & Bird), *H. elegans* (J. Sowerby), *H. serpentinum* (Schlotheim), *Hildaites murleyi* (Moxon) (Buckman 1928 : pl. 772), *Dactylioceras* (*Orthodactylites*) *semiannulatum* sp. nov., *Dactylioceras* sp. indet., *Nodicoeloceras crassoides* (Simpson), *Lytoceras crenatum* (Buckman) (Thompson 1885 : 200, fig. 6; Buckman 1926 : pls 665, 680), *Phylloceras heterophyllum* . 0·15 m (6 in)

Zone of *Dactylioceras tenuicostatum*
Subzone of *Dactylioceras semicelatum*

2. Transition Bed. Limestone, pale brown, oolitic, ferruginous. Welded to the top of the Marlstone Rock Bed. *Tiltoniceras antiquum* (Wright), *Dactylioceras* (*Orthodactylites*) *directum* (Buckman), *D.* (*O.*) *semicelatum* (Simpson) . . . . 0·05 m (2 in)

Subzones of *Dactylioceras tenuicostatum, D. clevelandicum and Protogrammoceras paltum,*
and Zone of *Pleuroceras spinatum*

1. Marlstone Rock Bed. Limestone, green, red-brown when weathered, full of chamosite ooliths. *Dactylioceras* (*Orthodactylites*) *tenuicostatum* (Young & Bird) rare in top 0·15 m; *Pleuroceras spinatum* (Bruguière) occurs rarely below the top 1 m. *Tetrarhynchia tetrahedra* (J. Sowerby) and *Lobothyris punctata* (J. Sowerby) abundant below the top 1 m. Thickness at Byfield . . . . 2·1 m (7 ft)

The *Ovaticeras ovatum* recorded in the Lower Cephalopod Bed is BM C.79469 (Miss A. E. Baker Collection), a single specimen that came from Gayton, 8 km SW of Northampton. It is a typical example of *Ovaticeras*, 100 mm in diameter, and is the only specimen known from outside Yorkshire and Lincolnshire. Its horizon was not recorded, but the matrix is that of the Lower Cephalopod Bed, which agrees with the Falciferum Subzone age of the species in Yorkshire.

In a small area around the villages of Milton and Bugbrooke, 5–8 km SW of Northampton, the condensed Abnormal Fish Bed (bed 3) expands to form two or three limestones separated by shales. The maximum development is at Milton where the following succession was recorded by Thompson (1892 : 336). It was seen again in 1958 below a motorway bridge at SP 735567.

Bed 3, total thickness 0·67 m (2 ft 2 in):

3f. Inconstant Cephalopod Bed. Limestone, pale brown-grey, fine-grained, slightly oolitic in places. Large specimens of *Harpoceras serpentinum* common, also *H. elegans*, *Hildaites murleyi*, *Dactylioceras* sp. indet. and *Lytoceras* sp. indet. . . . . 0·10 m (4 in)

3e. Shale, grey-brown, marly. Only slightly softer than the Inconstant Cephalopod Bed. Large crushed *Harpoceras serpentinum* . . . . 0·10 m (4 in)

3d. Fish Bed. Brown, crystalline, nodular limestone, oolitic in places, containing small fish fragments. *Harpoceras exaratum*, *Hildaites murleyi* . . . . 0·05 m (2 in)

3c. Shale, pale brown, finely laminated ('paper' shale). *Harpoceras exaratum* . . 0·10 m (4 in)

3b. Fish Bed. Brown crystalline limestone, oolitic in places, in large slabs forming a continuous bed, containing small fish fragments. *Harpoceras exaratum*, *Hildaites murleyi* . . 0·05 m (2 in)

3a. Shale, finely divided at top, passing down into clay with red sandy layers . . 0·27 m (10 in)

2. Transition Bed. Limestone, marly and oolitic. *Tiltoniceras antiquum*, *Dactylioceras* (*Orthodactylites*) *directum* . . . . 0·15 m (6 in)

At Bugbrooke, 6·5 km west of Milton, the thickness of bed 3 has diminished to 0·43 m (1 ft 5 in) and only one Fish Bed is present. The following succession was seen in an excavation made by Thompson (1892 : 337; 1910 : 463–464).

3f. Inconstant Cephalopod Bed. Hard limestone. Large specimens of *Harpoceras serpentinum* 0·20 m (8 in)

3e. Shale, finely laminated. Crushed *H. serpentinum* . . . . 0·10 m (4 in)

3b–d. Fish Bed. Limestone in large slabs. *H. exaratum*, *Hildaites murleyi*, *Lytoceras crenatum* 0·05 m (2 in)

3a. Shale, finely laminated . . . . 0·08 m (3 in)

The examples of *Hildaites murleyi* in the Fish Bed were recorded by Thompson as *Ammonites latescens* Simpson, and later (Thompson 1910 : 462, 463) the term 'Fish Bed, or Latescens Zone' was used. When the holotype of *A. latescens* was figured by Buckman (1913 : pl. 79) it was shown to be a species of *Pseudogrammoceras* from the Thouarsense Zone of Yorkshire.

Thompson's collection also contains specimens of *Harpoceras elegans* and *H. serpentinum* marked 'Inconstant Cephalopod Bed' from quarries at nearby localities at Rothersthorpe, Weedon and Harpole. Finally, in a railway cutting near Watford, about 10 km NW of this area, Thompson (1885 : 191–193) recorded a variable sequence of beds that appears to show a transition between the Inconstant Cephalopod Bed – Fish Bed succession and the Abnormal Fish Bed. In one part of the cutting the Abnormal Fish Bed, Transition Bed and Marlstone Rock Bed form one block of stone, in another part the Abnormal Fish Bed is separated from the Transition Bed by a thin bed of shale or clay, while the thickest development in the cutting consists of the Inconstant Cephalopod Bed (0·15 m), separated by shale (0·06 m) from the Fish Bed (0·08 m), and the latter separated by sandy clay (0·06 m) from the Transition Bed.

At all localities further west and south-west from Welton (Thompson 1886 : 19), Daventry, Staverton and Catesby southwards to Chipping Warden, bed 3 is condensed into the Abnormal Fish Bed and is the same as already described at Iron Cross quarry, Byfield. The only succession which does not conform is one described by Thompson (1896*a* : 426) from excavations for bridge foundations at SP 542534, 0·8 km north of Woodford Halse. Thompson saw a bed which he interpreted as the Inconstant Cephalopod Bed only 0·05 m above the Fish Bed, but which 'often merges into the Fish Bed below'. It contained large ammonites recorded by Thompson as *A. strangewaysi*, which are either *Harpoceras serpentinum* or *H. falciferum*, but more interesting were the two large specimens figured by Buckman (1926 : pls 666, 681) as the holotypes of *Orcholytoceras metorchion* and *O. appropinquans*, which are both now interpreted as *Lytoceras metorchion*. They have a distinctive type of preservation in which parts of the whorls are distorted or broken and displaced, and the matrix does not differ from that of the Lower and Upper Cephalopod Beds. Specimens of *Lytoceras* with this characteristic preservation have been found by other collectors, including the author at Iron Cross quarry, Byfield, only in the Upper Cephalopod Bed, and some doubt must be thrown on Thompson's observations, and on the presence of the Inconstant Cephalopod Bed at Woodford Halse. If present at Woodford Halse, it would be 15 km west of the Milton–Bugbrooke area and would be the only occurrence of the bed outside that area.

The Yorkshire coast

In all previous descriptions of stratigraphically localized collections of ammonites from the Upper Lias of the Yorkshire coast it has been stated that species of *Zugodactylites* do not occur in Yorkshire (Buckman 1915*a* : 102; Dean 1954 : 171; Howarth 1962*b* : 415). So the chance discovery of a complete and beautifully preserved example of *Zugodactylites braunianus* at Whitby in 1968 was surprising enough. More interesting was its horizon in bed 63, at about the middle of the Fibulatum Subzone as then defined (Howarth 1962*b* : 397), and this agreed with the conclusion arrived at from study of the Northamptonshire ammonites, that *Zugodactylites* occurred wholly within the stratigraphical range of *Peronoceras*. Confirmation of this distribution was then sought in Yorkshire: in 1973 a few more *Zugodactylites* were found in beds 62–64 of the main outcrop at Whitby, and the total number known is now six, including the small fragment recorded previously (Howarth 1962*b* : 397, bed 64) as *Peronoceras* cf. *turriculatum*. This compares with 106 specimens of *Peronoceras* collected from beds 60–63, so although *Zugodactylites* is much less common than *Peronoceras* at Whitby, it can be shown to occur in the lower part of the Fibulatum Subzone. At the same time a larger collection of *Zugodactylites* was made from bed xxxi (Howarth 1962*b*: 401) on the foreshore below Ravenscar: 18 specimens are now known, including a poorly preserved *Z. braunianus* recorded previously as *Peronoceras* sp. indet. (BM C.68504), and an excellent *Z. thompsoni* sp. nov. (Pl. 8, fig. 2) recorded previously as *Peronoceras* aff. *subarmatum*. *Peronoceras* occurs only in beds xxix and xxx below and does not accompany these *Zugodactylites*, and this probably represents merely a local variation in their distribution when compared with Whitby. As explained later (p. 245), now that the Braunianus Subzone has to be abandoned, the Fibulatum Subzone is extended upwards in Yorkshire, up to the base of the Crassum Subzone in bed 72 at Whitby and in bed xiv at Ravenscar.

The following is a record of the new ammonites collected in Yorkshire, and includes all the specimens of *Zugodactylites* that are now known (all specimens BM).

1. **Long Bight to Rail Hole Bight,** foreshore east of Whitby (see Howarth 1962*b* : 397; pl. 28).
   Bed 64. *Zugodactylites braunianus* (C.68344) 0·30 m above the base.
   Bed 63, row of scattered doggers at top. *Z. braunianus* C.78218–9; *Peronoceras fibulatum* C.78206–14; *P. turriculatum* C.78215–7.
   Bed. 63, row of doggers 0·30 m below top. *Zugodactylites braunianus* C.78204–5; *Peronoceras turriculatum* C.78198–200; *Hildoceras bifrons* C.78203; *Pseudolioceras lythense* C.78201–2.
   Bed 63, lower half. *Peronoceras fibulatum* C.78178–91; *P. perarmatum* C.78194–7; *Phylloceras herophyllum* C.78192.
   Bed 62. *Zugodactylites braunianus* C.78193; *Peronoceras fibulatum* C.78175–7.
2. **Foreshore below Ravenscar** (see Howarth 1962*b* : 401; pl. 27).
   Bed xliii. *Porpoceras vortex* C.78251–2; *P. verticosum* C.78229–31.
   Bed xlii. *Harpoceras subplanatum* (Oppel) C.75830.
   Bed xxxii. *Hildoceras bifrons* C.78248.
   Bed xxxi. *Zugodactylites braunianus* C.68504, C.78232–47; *Z. thompsoni* C.68503; *Pseudolioceras lythense* C.78249–50.
   Bed xxx. *Peronoceras fibulatum* C.78224–8; *P. perarmatum* C.78253; *Pseudolioceras lythense* C.78254; *Phylloceras heterophyllum* C.78255.

Critical re-examination of the Whitby ammonites also shows that the rich *Porpoceras* fauna in beds xliii and xlii at Ravenscar is also found as poorly preserved ammonites in the basal 1·5 m (5 ft) of bed 72 at Whitby (Howarth 1962*b* : 396). C.68525–6 are two medium-sized fragments of *P.* cf. *vortex* that have alternating fibulate-tuberculate and simple ribs, C.68527 is a small ammonite, apparently complete at 35 mm diameter and possible adult, that is probably a *Porpoceras*, while C.68528 is a fragment showing the typical ornament of *P. verticosum*. The lowest *Catacoeloceras crassum* occur in considerable numbers 1 m (3 ft) higher up, i.e. 1·5 m (5 ft) below the top of bed 72. So beds xliii and xlii at Ravenscar are to be correlated with the lowest 1·5 m of bed 72 at Whitby.

Zonal subdivisions and correlation with Yorkshire

The sequence of ammonite faunas in the Northamptonshire Upper Lias is closely similar to the sequence on the Yorkshire coast (Howarth 1962*b* : 1973), and much of the standard succession of zones and subzones for the basal half of the Upper Lias in north-west Europe is based on these two areas (Dean, Donovan & Howarth 1961). The zonal divisions and a comparison between Yorkshire and Northamptonshire are given in Table 1.

Table 1. Zone and subzone divisions and correlation between Northamptonshire and Yorkshire. The bed numbering for Yorkshire is from Howarth 1962*b* for the Upper Lias, and from Howarth 1955 : 156 for the Middle Lias.

Zone	Subzone	Northamptonshire	Yorkshire
Hildoceras bifrons	*Catacoeloceras crassum*	(absent)	Bed 72 (upper 2·5 m), xlv–lvi (Cement Shales)
	Peronoceras fibulatum	Upper *Leda ovum* Beds Oyster Bed Middle *Leda ovum* Beds Lower *Leda ovum* Beds Unfossiliferous Beds, top 4·6 m	72 (lower 1·5 m), 60–71, xxix–xliii, ? xliv (Cement Shales and Main Alum Shales)
	Dactylioceras commune	Unfossiliferous Beds, bottom 18 m Upper Cephalopod Bed Bed 6	49–59, xvi–xxviii (Main Alum Shales and Hard Shales)
Harpoceras falciferum	*Harpoceras falciferum*	Lower Cephalopod Bed Bed 4	48 (Ovatum Band) 41–47(Bituminous Shales)
	Harpoceras exaratum	Inconstant Cephalopod Bed } Abnormal Fish Bed Fish Beds } Abnormal Fish Bed (bottom of subzone absent)	35–40 (Jet Rock) 33, 34 (Jet Rock)
Dactylioceras tenuicostatum	*Dactylioceras semicelatum*	Transition Bed	28–32 } Grey Shales
	Dactylioceras tenuicostatum	Marlstone Rock Bed, top ? 1 m	20–27 } Grey Shales
	Dactylioceras clevelandicum	Marlstone Rock Bed, top ? 1 m	18, 19 } Grey Shales
	Protogrammoceras paltum	Marlstone Rock Bed, top ? 1 m	1–17 } Grey Shales; 26–28 } Ironstone Series
Pleuroceras spinatum	*Pleuroceras hawskerense*	Marlstone Rock Bed, below top ? 1 m	20–25 } Ironstone Series
	Pleuroceras apyrenum	Marlstone Rock Bed, below top ? 1 m	5–19 } Ironstone Series

Species of *Pleuroceras*, characteristic of the Middle Lias Spinatum Zone, are only rarely found in the Marlstone Rock Bed, and always occur below the top 1 m. The junction between the Middle and Upper Lias occurs about 1 m below the top of the Marlstone Rock Bed, but its exact position is unknown owing to the rarity of ammonites, and there is no lithological break within the ironstone. The lowest two subzones of the Tenuicostatum Zone are not represented by ammonites, but the Tenuicostatum Subzone is represented by a few examples of the index species in the top 0·15 m of the ironstone. Ammonites first become abundant in the Northamptonshire Upper Lias in the Transition Bed with the appearance of *Dactylioceras semicelatum*, *D. directum* and *Tiltoniceras antiquum*. This is the characteristic fauna of the Semicelatum Subzone and correlates with the top beds of the Grey Shales in Yorkshire. There is little or no palaeontological break between the top of the Marlstone Rock Bed and the Transition Bed.

The Abnormal Fish Bed in western Northamptonshire and the Fish Beds and Inconstant Cephalopod Bed near Northampton belong to the upper two-thirds of the Exaratum Subzone of the Falciferum Zone. *Eleganticeras*, which is characteristic of the lower third of the subzone, is absent in Northamptonshire, and this interval is probably the extent of the disconformity between the Transition Bed and the Abnormal Fish Bed. *Eleganticeras* is a close phylogenetic successor of *Tiltoniceras*, so it is less likely that sedimentation was complete, but *Eleganticeras* absent, in Northamptonshire. The abundant ammonites in the Abnormal Fish Bed are the same as those in beds 35–40 of the Yorkshire Jet Rock, but owing to the condensation *Harpoceras exaratum* and *H. elegans* are mixed together. In addition, the bed contains many well-preserved specimens of *H. serpentinum* and *Hildaites murleyi*, two species that are rare in Yorkshire.

In the more expanded sequence near Northampton, *Harpoceras exaratum* occurs in the Fish Beds, while *H. elegans* occurs in the Inconstant Cephalopod Bed, and this is the same as the relative position of the two species in Yorkshire. *Harpoceras serpentinum* appears to be confined to the Inconstant Cephalopod Bed and the shale immediately overlying the Fish Beds, and with *H. elegans* characterizes the top third of the Exaratum Subzone.

The Lower Cephalopod Bed and bed 4 belong to the Falciferum Subzone. Both contain *H. falciferum* and a single specimen of *Ovaticeras ovatum* has been found in the Lower Cephalopod Bed, and they are to be correlated with the Bituminous Shales and the Ovatum Band in Yorkshire. The base of the Commune Subzone of the Bifrons Zone is marked by the incoming of *Dactylioceras commune* and *Hildoceras sublevisoni* in the clays of bed 6. These two species are abundant and better preserved in the Upper Cephalopod Bed, where *D. praepositum* and *Frechiella subcarinata* also occur. This fauna is the same as in the type area of the Commune Subzone, i.e. the Hard Shales and lower part of the Alum Shales in Yorkshire. *H. falciferum* persists in considerable numbers in the Commune Subzone in Northamptonshire, unlike Yorkshire where it dies out before the top of the Falciferum Subzone. *D. commune* also occurs in the basal 3 m of the Unfossiliferous Beds.

The base of the Fibulatum Subzone is drawn at the first appearance of species of *Peronoceras*, 4·6 m below the top of the Unfossiliferous Beds. Species of *Peronoceras* are more abundant throughout the Lower and Middle *Leda ovum* Beds, where they are accompanied by rich faunas of *Zugodactylites*. It was this apparent sequence of *Peronoceras* in the Unfossiliferous Beds followed by *Zugodactylites* in the *Leda ovum* Beds that led to the original proposal of the Fibulatum and Braunianus Subzones by Buckman (1910*a* : 86). Buckman determined the ammonites, but all the stratigraphical details and ammonite collections had been supplied by Thompson, who published the same sequence shortly afterwards (Thompson 1910 : 461, 462). However, in the same paper, as well as much earlier, Thompson (1910 : 465; 1888 : 83) was aware that *Peronoceras* and *Zugodactylites* occurred together in abundance in the *Leda ovum* Beds. In fact in Northamptonshire it appears that the stratigraphical range of *Zugodactylites* occurs wholly within the range of *Peronoceras*, and the new evidence from Yorkshire confirms the substantial coexistence of the two genera. So the Braunianus Subzone has to be abandoned. A similar conclusion was reached by Guex (1970*b* : 623) on the basis of the position of *Zugodactylites* in the succession at Aveyron, south-east France, though the evidence there is not strong, because *Peronoceras* does not occur (or is very rare) in that area, and the position of *Zugodactylites* can only be compared with that of species of *Hildoceras*.

It is now proposed to retain the Fibulatum Subzone for those beds above the Commune Subzone whose base is marked by the first appearance of *Peronoceras*. This subzone will be extended up to include beds that contain the closely related genus *Porpoceras*, i.e. the Upper *Leda ovum* Beds in Northamptonshire, and beds xliii and xlii at Ravenscar in Yorkshire. This is the top of the Lias in Northamptonshire: if the top 1–2 m of the Upper *Leda ovum* Beds belong to the top subzone of the Bifrons Zone (as in Leicestershire, see below), then the diagnostic ammonites of the genus *Catacoeloceras* are not present. These conclusions are not contradicted by the presence of *Phymatoceras* in the Upper *Leda ovum* Beds, a genus that is usually held to be typical of the Variabilis Zone in Britain. In France, *Phymatoceras* first appears immediately below the main *Porpoceras* horizon (Guex 1972 : 619), and mid-Bifrons Zone *Phymatoceras* also occur in Italy (Pinna & Levi-Setti 1973), though with less accurately documented stratigraphical position. The Northamptonshire specimens are not out of place in the Fibulatum Subzone, therefore, and this is the lowest occurrence of the genus in Britain. *Harpoceras* is present in considerable numbers in the Northamptonshire Fibulatum Subzone: *H. soloniacense* occurs in the Unfossiliferous and Lower and Middle *Leda ovum* Beds, and is the phylogenetic successor of *H. falciferum* of the Commune Subzone; the more involute *H. subplanatum* (Oppel) occurs in the Middle and Upper *Leda ovum* Beds. The latter species is the highest occurrence of *Harpoceras* in Britain, after which the genus became extinct. In Yorkshire, *Harpoceras* disappeared much earlier, at about the middle of the Falciferum Subzone, but a single large specimen of *H. subplanatum* (BM C.75830) has been found in bed xlii at Ravenscar (the *Porpoceras* horizon) since the succession was described previously (Howarth 1962*b*).

A new index ammonite is required for the top subzone of the Bifrons Zone. The best choice is *Catacoeloceras crassum* (Young & Bird), which was first used as a zonal index by Corroy & Gérard (1933) in south-east France (see Dean, Donovan & Howarth 1961 : 482–483). It is abundant in the upper half of the Cement Shales in Yorkshire, and first appears not far above the *Porpoceras* horizon (Howarth 1962*b* : 396, 400, 402). The upper limit of the subzone, and of the Bifrons Zone, is marked by the first appearance of *Haugia* at the base of the Variabilis Zone. *Catacoeloceras crassum*, other species such as *C. dumortieri* Maubeuge, and species of *Collina* form a distinct group of ammonites, easily distinguished from *Peronoceras* and *Porpoceras* of the Fibulatum Subzone.

Correlations with other areas

England

The *Leda ovum* Beds used to be well exposed in Northamptonshire as far north as the Kettering – Corby – Thrapston area, and they could still be seen recently in the bottom of a gravel pit near Thrapston, where the uppermost beds yielded *Hildoceras bifrons*, indicating the Fibulatum Subzone. Ammonites obtained from former exposures in the north-east of the county and in Leicestershire and Rutland as listed by Woodward (1893 : 280–284) cannot now be checked, except for a typical *H. bifrons* from Helpston, north-west of Peterborough, which again indicates the Fibulatum Subzone. There is, however, a good example of *Catacoeloceras crassum* (Young & Bird) in the collections of the Institute of Geological Sciences (GSM 22519) whose locality is merely recorded as 'Leicestershire'. It is preserved in typical *Leda ovum* Beds grey clay matrix with a white chalky shell, and must indicate that the clays in the area from which it came extend up into the base of the Crassum Subzone. It compares closely (Pl. 8, fig. 6) with many of the specimens of *C. crassum* from the Cement Shales at Ravenscar, Yorkshire. It was presented to the Geological Survey before 1865 by Lady Exeter (of Burghley House, Stamford), and the most likely locality from which it could have come is the top of the Lias beneath the Northampton Sand that caps the hill at Nevill Holt (SP 815935), near Medbourne, south-east Leicestershire. This is only 10–13 km north of the Kettering – Corby exposures, and details of some of the former exposures in the area were given by Judd (1875 : 82; the *Amm. crassus* Phillips recorded by Judd was apparently a determination given to ammonites low in the Upper Lias clays and from the Commune Subzone, and it is unlikely to refer to the true *Catacoeloceras* of the Crassum Subzone). A less likely area for the specimen is the Buckminster – Sproxton – Croxton Kerrial area of north-east Leicestershire where the junction between the Lias and the Northampton Sand also occurs.

The is no evidence for the presence of the Crassum Subzone anywhere else, for near Grantham nine specimens of *Porpoceras vortex* and *P. verticosum* have been obtained from the top part of the Bifrons Zone clays, some only 1–2 m below the top of the Lias, others perhaps 6 m below (see p. 280). These show that the top of the Lias at Grantham is near or at the top of the Fibulatum Subzone. They are accompanied by specimens of *Hildoceras bifrons* and *Pseudolioceras lythense*. At Lincoln the Lias was formerly exposed in two brickpits described by Ussher (1888 : 33–35) and Trueman (1918 : 103–107). The Bifrons Zone clays are about 15 m thick and have yielded many ammonites (mainly British Museum (Natural History) collections) preserved as pyritic or septarian nodules. There are many *Dactylioceras commune*, including variants with thick and massive whorls, and some *Hildoceras sublevisoni*, of the Commune Subzone. Also there are large well-preserved examples of *H. bifrons*, several *Peronoceras fibulatum*, *P. subarmatum* and *P. perarmatum*, and a single very large (110 mm diameter) and coarsely ribbed *Porpoceras vortex* (BM C.19857), all from the Fibulatum Subzone, and the last species from near the top of that subzone. Throughout Northamptonshire, and at Grantham and Lincoln, the ammonities show that the highest beds of the Lias beneath the Northampton Sand ironstone belong to the top of the Fibulatum Subzone, because the diagnostic genus *Porpoceras* is known from each area. Only at one poorly-defined area of eastern Leicestershire is there any evidence for the overlying Crassum Subzone, and the single known *C. crassum* requires the presence of only an extra 1 m or thereabouts of beds at the base of that subzone. So the top of the Lias maintains an almost constant horizon between Northamptonshire and Lincoln, and there is disconformity, but no regional or angular unconformity, between it and the Northampton Sand. Trueman's (1918 : 110, fig. 5) diagram (redrawn by Arkell 1933 : 177, fig. 31), which shows a substantial angular unconformity resulting in the overstep of the Lias by the Northampton Sand between Northampton and Lincoln, is not correct. It was based on wrong age determinations of the Dactylioceratidae. The Bifrons Zone clays disappear quickly north of Lincoln and are not are seen again until the Yorkshire basin north of Market Weighton.

South-westwards from Northamptonshire the clays of the Bifrons Zone extend into Oxfordshire and steadily diminish in thickness. The ammonites from the Hook Norton railway cuttings listed by Woodward (1893 : 268–269) can be seen in many collections, and include many well-preserved *Peronoceras fibulatum* and other species. No new information has been obtained about the exposures farther south in Gloucestershire, Somerset or Dorset.

Southern France, the Alps and Italy

The succession of Dactylioceratidae in the Bifrons Zone at Aveyron, southern France, worked out in detail by Guex (1972), is closely similar to that of Northamptonshire and Yorkshire, though a major difference is the rarity of the genus *Peronoceras* at Aveyron. The Commune Subzone is represented in horizons I and II (see Table 2) of Guex (1972 : 618) which contain *Dactylioceras* cf. *commune* and *Hildoceras sublevisoni*. In horizon III the latter species is replaced by the first *H. bifrons*, and *Peronoceras* is probably represented by small inner whorls of *P. turriculatum* (Simpson) (Guex 1972 : pl. 8, figs 5, 7–9). This is the lowest fauna of the Fibulatum Subzone. Rich faunas of *Zugodactylites* appear in horizon IV. It was this close appearance of *Z. braunianus* above the first *H. bifrons* (which marks the base of the Bifrons Subzone (=Fibulatum Subzone) in France), that led Guex (1970*b*) to reject the use of *Z. braunianus* as an index species for a subzone above the Bifrons (=Fibulatum) Subzone. Guex inferred that *Zugodactylites* must occur in the Bifrons Subzone, though he did not recognize *Peronoceras* at Aveyron, and so he could not work out the relative distribution of the two genera. The coincidence of the ranges of *Peronoceras* and *Zugodactylites* has now been demonstrated in England, so it is possible to correlate horizons III and IV at Aveyron with the lower part of the Fibulatum Subzone. *Porpoceras vortex* appears in abundance in horizon VII, which correlates with the English *Porpoceras* horizon, then other species of *Porpoceras* occur higher up in horizon IX and in the lower part of horizon X. Thus, horizons III–lower X are equivalent to the Fibulatum Subzone. As in Northamptonshire *Harpoceras soloniacense* and *H. subplanatum* occur throughout this subzone at Aveyron, and the first *Phymatoceras* appear about the middle of the subzone (horizon VI). The base of the Crassum Subzone is marked by the incoming of *Catacoeloceras* in the upper part of horizon X, and it appears in abundance in horizon XI. *Catacoeloceras* remains an abundant ammonite at Aveyron up to the top of the Crassum Subzone (horizon XIII) and throughout the Variabilis Zone (horizons XIV–XVIII), and it is accompanied by many other Dactylioceratidae, mainly belonging to the genus *Collina*, that are rare in England. *Harpoceras* became extinct at the top of the Fibulatum Subzone, and does not occur in the Crassum Subzone at Aveyron. Table 2 gives a summary of the horizons and the main diagnostic ammonites at Aveyron, and their English subzonal equivalents. At the left of the table are the different subzonal divisions used at Aveyron (after Gabilly *et al.* 1971), which are based on the succession of species of *Hildoceras*, and they are exactly equivalent to the three English subzones. The same sequence of *Hildoceras* species occurs in England, but it would be very difficult to apply subzones based on them to the English succession, especially in the upper two subzones, because *Hildoceras* is less common in England, and the species are much more alike and more difficult to identify than the Dactylioceratidae that accompany them. In particular *H. bifrons* and *H. semipolitum* are merging or overlapping species. They are distinct when fully developed, but confusing when the considerably variable *H. bifrons* is slowly evolving into the equally variable *H. semipolitum*. This is also the case at Aveyron, where the population of *Hildoceras* in horizon VIII already contains specimens determined as

Table 2. Ammonite faunas and subdivisions of the Bifrons and Variabilis Zones at Aveyron, and the equivalent English subzones.

Divisions at Aveyron	Horizons	Main ammonites	English equivalents
Variabilis Zone	XVIII XVII XVI XV XIV	*Haugia* spp. *Catacoeloceras* spp.	Variabilis Zone
Hildoceras semipolitum Subzone	XIII XII XI upper X	*Catacoeloceras*, *Hildoceras semipolitum*, *H. bifrons*	*Catacoeloceras crassum* Subzone
Hildoceras bifrons Subzone	lower X IX VIII VII	*Porpoceras* spp., *Harpoceras*, *Hildoceras bifrons* and spp.	*Peronoceras fibulatum* Subzone
	VI V	*H. bifrons*, *Harpoceras*	
	IV	*Zugodactylites*, *H. bifrons*	
	III	*H. bifrons*, *Peronoceras*	
Hildoceras sublevisoni Subzone	II I	*Hildoceras sublevisoni* *Dactylioceras* sp.	*Dactylioceras commune* Subzone

H. semipolitum as well as *H. bifrons*, and other forms intermediate between the two, yet Guex does not draw the base of the Semipolitum Subzone until the middle of horizon X. On the other hand, the population in horizon XII still contains specimens determined as *H. bifrons* as well as *H. semipolitum*. Either the ranges of the two species overlap a great deal, or there is really only one slowly evolving species. Undoubtedly subzones based on Dactylioceratidae could be applied to the Aveyron succession within the Bifrons Zone, and they would be more distinctive, more precise and easier to use. In fact it appears that the boundary between the Bifrons and Semipolitum Subzones was placed by Guex in a position that accorded with a change in the Dactylioceratidae, rather than a change in the two species of *Hildoceras* that he used as subzonal indexes.

In Austria and Italy the succession of ammonites in the Bifrons Zones appears to be largely in accordance with the English and French successions. The faunas at Kammerker, Austria, have been described by Fischer (1966) and those in Italy by Pinna & Levi-Setti (1971). There are many discrepancies in the determination of individual ammonites that could not be sorted out without examination of the whole collections, and the stratigraphical relationships of the Italian forms is not known in sufficient detail for bed-by-bed comparisons to be made with England. It is to be noted, however, that *Porpoceras* and *Catacoeloceras* are abundant in some parts of Italy in the equivalent of the upper part of the Bifrons Zone and in the Variabilis Zone, but the presence of *Peronoceras* and *Zugodactylites* is more problematical.

North-eastern Siberia, northern Alaska, arctic Canada, Greenland, Spitzbergen

The new evidence for the zonal ranges for the Northamptonshire Bifrons Zone Dactylioceratidae has considerable bearing on the dating of the *Zugodactylites, Porpoceras* and *Pseudolioceras* faunas that are widespread over a very large area from north-eastern Siberia eastwards to Spitzbergen. The succession in Siberia has been described in detail by Dagis (1968 : 70–98; 1974 : 65–79) and that in Canada, Greenland and Spitzbergen by Frebold (1975 : 18–21, table 1), who summarized all previous work. Throughout much of this vast area the Commune Subzone is represented by *Dactylioceras commune*, accompanied by other species in Siberia. The next higher fauna consists of *Zugodactylites braunianus* and other species, which are abundant in Siberia (Dagis 1968 : 39–56) and closely comparable with those in Northamptonshire, and less common but still characteristic *Zugodactylites* in the Canadian Arctic. Hitherto this fauna has been placed at the top of the Bifrons Zone in the 'Braunianus Subzone', with a gap below representing the missing Fibulatum Subzone. However, it is now clear that this is a Fibulatum Subzone fauna, and there is no need for a gap between it and the underlying Commune Subzone.

The next higher fauna consists of species of *Porpoceras* and *Pseudolioceras.* It occurs over the whole area, has been referred to as a widespread Arctic marker bed, and contains *Porpoceras polare* (Frebold), *P. spinatum* (Frebold), *Pseudolioceras* cf. *compactile* (Simpson) and other species of *Pseudolioceras.* In Siberia *Porpoceras polare* follows closely above the *Zugodactylites* fauna, then *Pseudolioceras rosenkrantzi* Dagis occurs higher up (Dagis 1968 : 76). A summary of all the occurrences and the reasons for correlating the bed with the Thouarsense Zone, Striatulum Subzone, in Europe, was given by Frebold (1975 : 19–20). This correlation relies entirely on the dating of *Pseudolioceras compactile* (Simpson) in Europe. Species of *Pseudolioceras* are poor age indicators, however, for they are very difficult to determine, even with large European collections of known stratigraphy, in which single-horizon collections show considerable variation. On the other hand, the two Arctic species of *Porpoceras*, though not known in Europe, are definitely species of *Porpoceras*, showing the characteristic mixture of fibulate and single ribs at larger sizes. All the evidence from Northamptonshire, Yorkshire, south-east France and Italy shows that *Porpoceras* occurs in what is now called the Fibulatum Subzone, before the incoming of *Catacoeloceras* of the Crassum Subzone. *Porpoceras* disappears with the advent of *Catacoeloceras.* Therefore, a better correlation of the Arctic *Porpoceras – Pseudolioceras* bed is with the top of the Fibulatum Subzone in Europe. All the specimens of *Pseudolioceras* in that bed could be accommodated in, or are closely allied to, *P. lythense* (Young & Bird), a highly variable species that occurs in the Bifrons Zone of western Europe, so there is no need to postulate a younger age for the Arctic bed because of the *Pseudolioceras* fauna that it contains. This correlation does not necessarily apply to the higher horizon in Siberia (i.e. bed 11 of Dagis 1968 : 76–77), where *Porpoceras* is absent and *Pseudolioceras rosenkrantzi* occurs, which may belong to a higher zone.

Palaeontology

Family **DACTYLIOCERATIDAE** Hyatt 1867

Many studies of Dactylioceratidae have been made in recent years since the stratigraphical sequence of most of the Yorkshire coast Upper Liassic species was worked out in an earlier paper (Howarth 1962*b*). The main descriptions are by Dagis (1968), Fischer (1966), Géczy (1966), Guex (1971, 1972, 1973*a*, 1973*b*, 1974), Howarth (1973), Pinna & Levi-Setti (1971), Sapunov (1963) and Schmidt-Effing (1972). Stratigraphical knowledge of the relationships between the forms described was very variable, and in cases where it was, of necessity, poor in detail, as in the Italian faunas described by Pinna & Levi-Setti (1971), then a classification based mainly on morphological divisions had to be adopted. Where the stratigraphy was better known, it has been used as a guide to the generic and specific divisions to varying degrees, and many conflicting opinions have been expressed.

When a single-bed collection of Dactylioceratidae is obtained, one of the most striking features often seen is the wide variation, usually in whorl breadth, rib-density and amount of tuberculation. In this respect they are often many times more variable than the Hildoceratidae that accompany them in equal abundance at many localities. Three different methods can be used for classification of such a collection – (1) reference to a single variable species, (2) division into two or more species or (3) division into two genera and several species. Method (3) is inevitable with small collections of indifferently preserved specimens, or where the stratigraphy is not accurately known. However, where collections are larger, better preserved and include adults, and where the stratigraphy is accurately known, then the variation at a single horizon is often seen to be continuous, and any specific or generic divisions are arbitrary divisions of that variation. A factor of more significance is that when enough single-bed collections from several zones have been examined, it becomes apparent that diagnostic characters are often held in common by all the specimens from a single bed, regardless of their wide variation in other characters. For example, in the collections from the Tenuicostatum Zone Grey Shales of Yorkshire (Howarth 1973) all the specimens at each horizon possess the mixture of single and bifurcating ribs at some growth stage that is characteristic of the subgenus *Orthodactylites*, regardless of whether the whorls are compressed or broad, the ribbing dense or sparse, or tubercles present or absent; in the Northamptonshire *Zugodactylites* described herein, all the specimens, whether compressed or depressed, possess the characteristic sharp ventrolateral tubercles at the end of single ribs, at least at some stage of growth; in *Peronoceras* both compressed and depressed forms have fibulate ribs that are retained on the adult whorl; in the slightly stratigraphically younger *Porpoceras*, both compressed and depressed forms have the characteristic mixture of single and fibulate ribs with ventrolateral tubercles at intervals; and in Lincolnshire the population of *Dactylioceras commune* in the Commune Subzone contains a significant proportion of individuals with a remarkably large whorl breadth, which all, nevertheless, have the widely spaced, single, non-tuberculate primary ribs that are so characteristic of *D. commune*. The conclusion to be drawn is that the depressed-whorled forms are more closely related to the compressed-whorled forms that they accompany, than they are to the depressed-whorled forms in other zones. To maintain that the compressed and depressed-whorled types belong to two different lineages that are separate from the Tenuicostatum to the Variabilis Zones requires that a remarkable series of parallel evolutionary changes had to take place, with the same diagnostic characters evolving simultaneously in both lineages. This seems to be most unlikely, and it is much more probable that there is a close genetic relationship between the compressed and depressed forms at each horizon. In those cases where two different lineages do coexist at one horizon, such as the presence of *Peronoceras* and *Zugodactylites* in abundance in the Northamptonshire Fibulatum Subzone, then the differences between them are quite clear – each has its own diagnostic characters, there is no overlap in morphology, and there are no specimens that are intermediate between the two.

The classification adopted in each case depends on the quantity and state of preservation of the material. With the Grey Shales *Orthodactylites*, the abundant, well-preserved material allowed the continuity of the variation between very different end-forms to be demonstrated, so only one specific name was applied to each single-bed assemblage, and specific distinctions were used for significant changes from bed to bed. One of these changes involved severe restriction of the amount of variation in one species, *D. tenuicostatum*, which does not have the depressed forms of the preceding or succeeding species. Inevitably such a classification received severe criticism from Guex (1974), who would divide the assemblage at each horizon into *Dactylioceras* and *Nodicoeloceras*, thus arbitrarily splitting the continuous variation into two. In fact Guex's method is to decide in advance the scale and type of characters that are to be used for classification of Dactylioceratidae, then apply them to the Grey Shales collections, without taking account of proper analysis of the morphology of those collections. The different amount of variation in one of the Grey Shales species does not alter the basic reasons for treating each assemblage as a single species. Nor can the methods used be criticized because, according to Guex, *Nodicoeloceras* survived in the Bifrons Zone long after the disappearance of *Dactylioceras* – the depressed-whorled forms in the upper half of the Bifrons Zone are not *Nodicoeloceras*, they belong to *Porpoceras* or *Catacoeloceras*, or perhaps an unnamed genus. Another analysis that revealed a large amount of variation in a single species was Hirano's (1971 : 104–108) study of *Dactylioceras helianthoides* Yokoyama in Japan, where rib-density ranges at a given diameter were found to be as high as 3 : 1 between the most densely and most sparsely ribbed individuals from the same horizon. In the case of the *Peronoceras* and *Zugodactylites* faunas described here, the collections are not large enough to prove the continuity of the variation in each genus, and thus to refer all the forms at one horizon to a single species. Several species are used in each genus, this being the most practicable classification to adopt in this case. British collections of *Porpoceras* are treated in the same way.

After close examination of all the main occurrences of Dactylioceratidae in Britain, there seems no reason to change the basic classification of seven genera put forward previously (Howarth 1962*b* : 408), which is still the best expression of the sequence of changes that takes place in the Dactylioceratidae. The purely morphological approach of Buckman (1926–27 : 41–46) only confuses a relatively simple sequence of genera, as does the addition of a new generic name like *Rakusites* Guex (1971 : 232), which is based on a specimen of *Dactylioceras anguiforme* (Buckman), from the Falciferum Zone of Somerset, that has feebly tuberculate inner whorls. The total amount of variation in *D. anguiforme* is much more than the difference between the holotype (Buckman 1928 : pl. 763) and the specimen used as holotype of *Rakusites* (Guex 1971 : pl. 1, fig. 1). Such a morphological approach has led Guex (1973*b* : 575–581) to put forward a classification for Dactylioceratidae that is greatly at variance with the views expressed here. He separates all the depressed-whorled forms from the compressed-whorled forms that they accompany, then splits them up further so that there are long parallel lineages of *Catacoeloceras*, *Porpoceras* and *Nodicoeloceras*, all starting in the Tenuicostatum and Falciferum Zones. In my opinion *Catacoeloceras* starts in the Crassum Subzone, *Porpoceras* starts in the upper half of the Fibulatum Subzone and *Nodicoeloceras* starts in the Exaratum Subzone, and all Guex's records of these genera in older beds are based on misidentifications, as are also his records of *Collina* before the Fibulatum Subzone. The upper limits of these depressed-whorled genera are also clear in Britain and at Aveyron – the Commune Subzone for *Nodicoeloceras* and the top of the Fibulatum Subzone for *Porpoceras*, while *Catacoeloceras* ranges well up into the Variabilis Zone. However, it is not certain that all the depressed forms high in the Bifrons and Variabilis Zones in southern France and Italy can be satisfactorily accommodated in *Catacoeloceras* or *Collina*. *Transicoeloceras* Pinna (1966 : 124) has been applied to the most depressed forms in the Bifrons Zone in Italy, and *Platystrophites* Levi-Setti & Pinna (1971 : 476) is also available, though the latter may be a synonym of *Porpoceras*.

The Northamptonshire Dactylioceratidae do not provide any evidence for the recognition of dimorphism in the family, and the position remains as stated previously (Howarth 1973 : 249) – no collection from a British population contains adults that can be divided into two distinct groups which differ in size or any other morphological character. The evidence put forward by Guex (1973*b*) in support of dimorphism was obtained from collections of ammonites from the Bifrons Zone of the Aveyron area. All the specimens are pyritized phragmocones, mostly small and immature, in which the body chambers and mouth borders are not preserved. None of the specimens used (including those figured in the plates) show any adult features. The measurements given in a later paper (Guex 1974 : 423–425), as detailed evidence in support of dimorphism in one particular case, do not demonstrate that two groups were present. When the measurements are plotted as graphs, it can be seen that this collection of separate whorls shows continuous variation, and it has been split arbitrarily by Guex into two parts that do not represent natural groups. Again no adults are present. At other localities in many different parts of Europe all the genera present at Aveyron attain much larger sizes before they show adult features, which usually consist of a contracted or constricted mouth border to the adult body chamber. The proof of dimorphism in Dactylioceratidae cannot be obtained from collections of small, pyritized, septate inner whorls like those at Aveyron. The least that is required to demonstrate dimorphism satisfactorily is a substantial collection of complete adult specimens from one horizon, that are provably adult because they have constricted mouth borders and approximated suture-lines, and which can be shown to be divisible into two distinct groups on the basis of the diameter at the adult mouth border, or on other major differences such as the shape of the mouth border. There are many such collections of Hildoceratidae, but none of Dactylioceratidae are known so far.

Genus *DACTYLIOCERAS* Hyatt 1867

TYPE SPECIES. *Ammonites communis* J. Sowerby 1815, designated ICZN Opinion 576, 1959.

SYNONYMS. *Arcidactylites* Buckman 1926 (type species: *A. arcus*[1]); *Microdactylites* Buckman 1926 (type species : *Ammonites attenuatus* Simpson 1855); *Anguidactylites* Buckman 1926 (type species : *A. anguiformis*); *Leptodactylites* Buckman 1926 (type species: *L. leptum*); *Peridactylites* Buckman 1926 (type species: *P. consimilis*); *Toxodactylites* Buckman 1926 (type species: *T. toxophorus*); *Vermidactylites* Buckman 1926 (type species: *Ammonites vermis* Simpson 1855); *Xeinodactylites* Buckman 1926 (type species: *Dactylioceras helianthoides* Yokoyama 1904); *Athlodactylites* Buckman 1927 (type species: *Ammonites athleticus* Simpson 1855); *Curvidactylites* Buckman 1927 (type species: *C. curvicosta*); *Koinodactylites* Buckman 1927 (objective synonym); *Nomodactylites* Buckman 1927 (type species: *N. temperatus*); *Parvidactylites* Buckman 1927 (type species: *P. parvus*); *Simplidactylites* Buckman 1927 (type species: *S. simplicicosta*); *Rakusites* Guex 1971 (type species: *R. pruddeni*); *Eodactylites* Schmidt-Effing 1972 (type species: *Dactylioceras pseudocommune* Fucini 1935).

DIAGNOSIS. Evolute planulates or serpenticones, in which the whorl section varies between compressed and highly depressed and typically has flat sides. Ribs single or bifurcating, either annular or passing over the venter with forwards inclination. Ventrolateral tubercles absent or small, but larger tubercles or spines and occasional fibulate ribs occur on the inner whorls of some species.

REMARKS. The earliest species occur in the Mediterranean area, perhaps first in the upper part of the Spinatum Zone and definitely in the Tenuicostatum Zone; thereafter species are common or abundant up to the top of the Commune Subzone, where the genus evolves into *Peronoceras*. In north-west Europe examples do not occur in the Spinatum Zone, *Dactylioceras* s.s. occurs rarely low in the Tenuicostatum Zone (e.g. Howarth 1973 : 253), then the subgenus *Orthodactylites* becomes abundant higher in the Tenuicostatum Zone and survives to at least the middle of the Falciferum Subzone. *Dactylioceras* s.s. first occurs again in Britain in the Exaratum Subzone, and becomes abundant in the Falciferum and Commune Subzones. The restricted subgenus *Dactylioceras* consists of those species in which single, annular ribs are absent or only occasional, and they do not have the depressed whorls of some examples of *Orthodactylites*. The well-known type species *D. commune* has characteristically widely-spaced primary ribs on a flat whorl side, and ventrolateral tubercles are absent or only rudimentary. The morphology of *D. pseudocommune* Fucini, the type species of *Eodactylites*, is so similar to that of *D. commune* that *Eodactylites* has to be placed in synonymy with the subgenus *Dactylioceras*, even though the age difference between the two is considerable, i.e. basal Tenuicostatum Zone and Commune Subzone. In fact *D. pseudocommune* has only slightly more angular whorls, straighter ribs, a lower rib-density and slightly more prominent ventrolateral tubercles than *D. commune*. The sequence of species of *Dactylioceras* in Yorkshire has already been described (Howarth 1962*b* : 408–409), and a particularly rich and variable fauna is present at Barrington, Somerset. This variation is in the tuberculation and rib-density of the inner whorls, and includes fibulate ribs and ventrolateral tubercles and spines of varying sizes. Several forms are worthy of specific but not generic names.

In addition to the species described below, the following Dactylioceratidae also occur in Northamptonshire:

1. *Dactylioceras* cf. *anguiforme* (Buckman) in the Abnormal Fish Bed. The material obtained is insufficient and too poorly preserved for accurate identification. It represents a normal species

[1] All type species are by original designation, unless stated otherwise.

of *Dactylioceras* s.s., and those characters that can be seen agree with *D. anguiforme* (Buckman 1928 : pl. 763) from the Exaratum Subzone of Barrington, Somerset. It is not the same as *D.* (? *Orthodactylites*) *vermis* (Simpson) which occurs at this horizon in Yorkshire (Buckman 1913 : pl. 68), at Grantham, Lincolnshire, and at Barrington, Somerset (Buckman 1927 : pl. 68A). *D. crassiusculosum* (Simpson) in the Exaratum Subzone of Yorkshire (Buckman 1912 : pl. 62) is also different.

2. *Dactylioceras* also occurs in the Lower Cephalopod Bed, but no specimens were obtained that are specifically determinable.

3. *Dactylioceras* spp. in the Upper Cephalopod Bed. *D. commune* (J. Sowerby) is abundant, and specimens agree exactly with the Yorkshire holotype (Dean, Donovan & Howarth 1961 : pl. 72, fig. 5) and topotypes (Buckman 1927 : pls 707, 708). An example of small inner whorls from King's Sutton, Northamptonshire, was figured by Buckman (1926 : pl. 657) as *Arcidactylites arcus*. It agrees exactly with the inner whorls of *D. commune* and must be considered a synonym. Specimens with considerably greater rib-density, especially at diameters of more than 30 mm, also occur in the Upper Cephalopod Bed, and they agree with *D. praepositum* (Buckman 1927 : pl. 701). The Northamptonshire specimens of *D. commune* and *D. praepositum* are mostly incomplete and not so well preserved as the abundant and well-known Yorkshire population of the two species. *Nodicoeloceras* sp. indet. occurs rarely in this bed, but those obtained were too small and too poorly preserved to identify accurately.

Subgenus *ORTHODACTYLITES* Buckman 1926

TYPE SPECIES. *O. directum* Buckman 1926.

SYNONYMS. *Kryptodactylites* Buckman 1926 (type species: *Ammonites semicelatus* Simpson 1843); *Tenuidactylites* Buckman 1926 (type species: *Ammonites tenuicostatus* Young & Bird 1822); ? *Kedonoceras* Dagis 1968 (type species: *K. asperum*).

DIAGNOSIS. *Dactylioceras* with annular, rectiradiate or prorsiradiate ribs. Single as well as bifurcating ribs occur commonly at some growth stage. Rib-density moderate to high, occasionally distantly ribbed on inner whorls. Whorl shape varies from compressed to highly depressed. Ventrolateral tubercles or spines may occur on depressed whorls and ribs may be looped to them in fibulate style.

REMARKS. Species of *Dactylioceras* with a mixture of single and bifurcating annular ribs on at least their outer whorls occur throughout much of the Tenuicostatum Zone, and the rich faunas in the Grey Shales of Yorkshire have been described previously (Howarth 1973). Although they are largely superseded by *Dactylioceras* s.s. in the Falciferum Zone, some species of *Orthodactylites* remain, and one of them, the new species *D.* (*O.*) *semiannulatum*, occurs in the Exaratum and Falciferum Subzones of Northamptonshire. It has a wide distribution from Yorkshire to Somerset, and those specimens in the Falciferum Subzone are probably the youngest *Orthodactylites* in England.

Dactylioceras* (*Orthodactylites*) *semiannulatum sp. nov.

Pl. 1, figs 1–9

1927 *Xeinodactylites helianthoides* (Yokoyama); Buckman : pl. 699.
1927 *Dactylioceras annulatum* (J. Sowerby); Buckman : pl. 700.
1962*b* *Dactylioceras* sp. nov. Howarth : 387, bed 37.
? 1973*a* *Dactylioceras aequistriatum* (Zieten); Guex : 508; pl. 11, fig. 7; pl. 14, fig. 13.

DIAGNOSIS. A species with rounded whorls, annular ribs and no tubercles that occurs in the Falciferum Zone. The whorl section is nearly circular and the whorl breadth slightly exceeds the height. The ribs are straight, annular and radial or slightly rursiradiate; many bifurcate at the ventrolateral position, but at diameters of more than 40 mm single ribs are also common.

HOLOTYPE. BM C.71280 from the Abnormal Fish Bed, Exaratum Subzone, 1·5 km north of Byfield, Northamptonshire.

OTHER MATERIAL. Paratypes from the same bed and locality as the holotype are C.70856–59 and C.71281–83. Other paratypes from Somerset, Leicestershire and Yorkshire are listed below.

DIMENSIONS. These are given in the following order. Diameter: whorl height, whorl breadth, umbilical width; the figures in brackets express the last three dimensions as proportions of the diameter.

C.71280	– 52·0:	15·3 (0·29), 16·4 (0.32), 24·0 (0·46)
C.70856	– 59·0:	16·6 (0·28), 17·5 (0·30), 28·7 (0·49)
C.70858	– 37·4:	12·0 (0·32), 13·0 (0·35), 16·3 (0·44)
C.71924	– 30·0:	10·3 (0·34), 14·0 (0·47), 12·5 (0·42)

DESCRIPTION. The known material of this species comes from the Abnormal Fish Bed at Byfield, Northamptonshire; a bed of nodules 12 m above the Marlstone Rock Bed, 1·3 km south of Harston, Leicestershire (SK 840305); bed 37 at Port Mulgrave, Yorkshire coast (Howarth 1962*b* : 387); and bed 6 at Barrington, Somerset (Pringle & Templeman 1922 : 451); all are of Exaratum Subzone age. It also occurs in bed 18/19 at the latter locality, of lower Falciferum Subzone age. The specimens from Byfield include one that is 75 mm in diameter at the broken aperture of its body chamber which is one whorl in length, and it may have been a complete adult. The other specimens are smaller, but better preserved, and they show the inner whorls down to about 10 mm diameter (Pl. 1, figs 1–3, 9). The Harston specimen (Pl. 1, fig. 6) is a small individual of 30 mm diameter with fairly thick whorls. The Port Mulgrave specimens are those recorded previously (Howarth 1962*b*) as *Dactylioceras* sp. nov. (C.50206, C.50210–18). They are also small specimens of up to 50 mm diameter, and include the three inner whorls figured here (Pl. 1, figs 4, 5, 7), which show variation in whorl thickness at 28 mm diameter from 0·37 to 0·43 of the diameter. The holotype has 62 ribs on its last whorl at 56 mm diameter. Some specimens (e.g. Pl. 1, fig. 1) have slightly more ribs, and the Port Mulgrave specimens' inner whorls are fairly fine-ribbed, but there is no large variation in the rib-density of this species, as in some others (Howarth 1973). The specimen from bed 6 at Barrington figured by Buckman (1927 : pl. 699) is similar in most respects, though it has slightly fewer ribs on its innermost whorls. The Falciferum Subzone example from bed 18/19 at Barrington (Buckman 1927 : pl. 700) is 78 mm in diameter, with a body chamber of just less than one whorl in length, and compares closely with the Byfield specimens in whorl dimensions and rib-density. Another specimen (Pl. 1, fig. 8) from the same district, from Moolham, Ilminster, and probably from the Falciferum Subzone, is similar. It has a body chamber exactly one whorl in length ending in a constricted and flared mouth border at about 93 mm diameter, showing it to be an adult. The species is referred to the subgenus *Orthodactylites* because of the substantial number of single ribs, especially at diameters of more than 40 mm; it is the youngest known species of that subgenus.

Nodicoeloceras crassoides occurs in the same beds at all the localities, and can be distinguished from *D. semiannulatum* by its much larger whorl breadth and by the tubercles that are usually present on its inner whorls. The greatest resemblance, however, is with *D. semicelatum* (Simpson) in the top subzone of the Tenuicostatum Zone. *D. semicelatum* has a very large variation in whorl breadth, rib-density and presence or absence of tubercles, and the ribs are prorsiradiate or occasionally radial. In *D. semiannulatum* the ribs vary between radial and rursiradiate, and specimens are not continuously variable into the depressed-whorled contemporaneous species *Nodicoeloceras crassoides*. *D. helianthoides* Yokoyama, with which Buckman identified one of the Barrington ammonites, has been redescribed by Hirano (1971 : 104; pl. 14, figs 1–10); it belongs to the

Plate 1 ×1

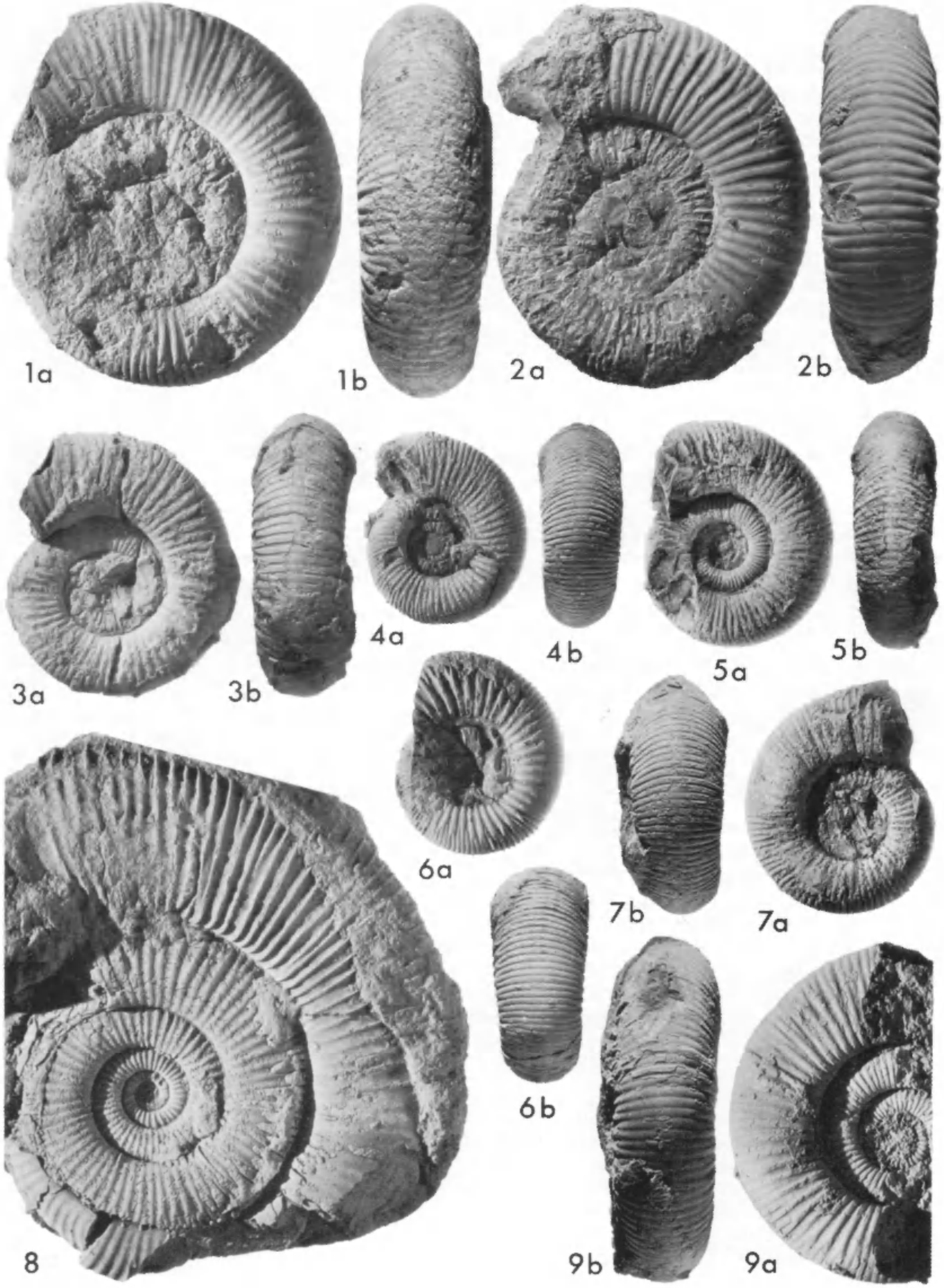
Dactylioceras (*Orthodactylites*) *semiannulatum* sp. nov., Exaratum Subzone

Figs 1–3, 9. Abnormal Fish Bed, quarry at Iron Cross Farm, 1·5 km north of Byfield, Northamptonshire. Fig. 1, BM C.70856. Fig. 2, holotype, BM C.71820. Fig. 3, BM C.70858. Fig. 9, BM C.70857.

Figs 4, 5, 7. Bed 37, Jet Rock, Rosedale Wyke, Port Mulgrave, Yorkshire. Fig. 4, BM C.50214. Fig. 5, BM C.50218. Fig. 7, BM C.50212.

Fig. 6. Nodules 12 m (40 ft) above Marlstone Rock Bed, quarry (SK 840305), 1·2 km south of Harston, Leicestershire; BM C.71924.

Fig. 8. Moolham Farm, Ilminster, Somerset; BM C.72558.


1a
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subgenus *Dactylioceras* s.s., has few or no single ribs, and has ventrolateral tubercles on the inner whorls. The specimen from Morocco figured by Guex (1973*a* : 508; pl. 11, fig. 7) as *D. aequistriatum* (Zieten) appears to be very close to *D. semiannulatum*. Its identification cannot be upheld until a suitable type specimen is obtained for Zieten's species.

Genus *NODICOELOCERAS* Buckman 1926

TYPE SPECIES. *Ammonites crassoides* Simpson 1855.

SYNONYMY. *Crassicoeloceras* Buckman 1926 (type species: *C. pingue*); *Lobodactylites* Buckman 1926 (type species: *L. lobatum*); *Multicoeloceras* Buckman 1926 (type species: *M. multum*); *Spinicoeloceras* Buckman 1926 (type species: *S. spicatum*); *Mesodactylites* Pinna & Levi-Setti 1971 (type species: *M. annulatiforme*).

DIAGNOSIS. Whorls always depressed, with wide flat or arched venter, and inner whorls often cadicone. Ribs usually bifurcate at ventrolateral edge, occasionally single, and sometimes fibulate in tuberculate specimens. Rib-density moderate to low. Development of ventrolateral tubercles or spines on inner whorls very variable, tubercles absent in some species.

REMARKS. The type species occurs in the upper half of the Exaratum Subzone, and others occur in the Falciferum and Commune Subzones, especially in the Barrington area of Somerset. The development of tubercles is particularly variable in this genus: in some cases they occur as intermittent spines with non-tuberculate ribs between, or they may be developed on every rib, or ribs may be looped in pairs to them (fibulate), while in other species tubercles are present in some individuals but absent in others. The combination of variable tuberculation and highly depressed whorls makes the genus distinctive and worthy of separation from *Dactylioceras*. Some complete adults are known in which the final whorl contracts in breadth up to the mouth border (e.g. Pl. 3, fig. 1), but they do not become compressed as in *Dactylioceras*. The depressed whorls are, therefore, a feature of all growth stages of *Nodicoeloceras*.

Nodicoeloceras crassoides (Simpson 1855)

Pl. 2, figs. 1, 4, 5; Pl. 3, fig. 1

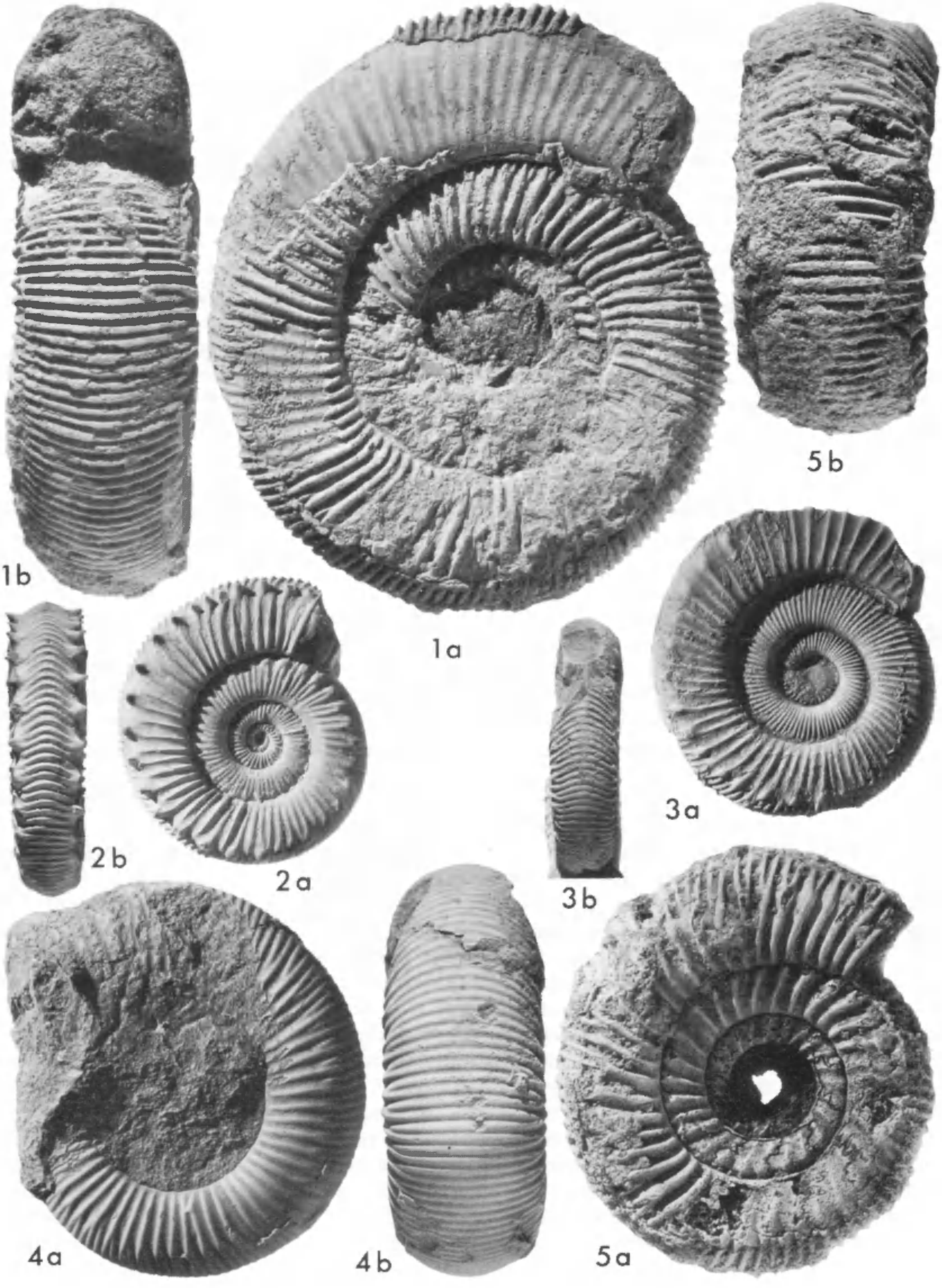
1819 *Ammonites annulatus* J. Sowerby : 41; pl. 222, fig. 5 (*non* figs 1–4) (*non Ammonites annulatus* Schlotheim 1813).
1855 *Ammonites crassoides* Simpson : 55.
1855 *Ammonites fonticulus* Simpson : 57.
1884 *Stephanoceras subarmatum* (Young & Bird); Wright : 477; pl. 85, figs 2, 3.
1884 *Stephanoceras raquineanum* (d'Orbigny); Wright : 478; ? pl. 86, figs 5–7; pl. 87, figs 7, 8.
1885 *Stephanoceras raquineanum* (d'Orbigny); Thompson : 307; pl. 1, figs 2, 2a.
1912 *Coeloceras fonticulum* (Simpson) Buckman : pl. 59.
1913 *Coeloceras crassoides* (Simpson) Buckman : pl. 89.
1927 *Nodicoeloceras crassoides* (Simpson) Buckman : pl. 89A.

Plate 2 ×1

Nodicoeloceras crassoides (Simpson), Exaratum Subzone
Figs 1, 4, 5. Abnormal Fish Bed. Fig. 1, Catesby, 6·5 km south-west of Daventry, Northamptonshire; Northampton Museum, B. Thompson collection. Fig. 4, quarry at Iron Cross Farm, 1·5 km north of Byfield, Northamptonshire; BM C.70862. Fig. 5, Byfield, Northamptonshire; BM C.69088, W. E. Cutler Colln.

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone
Fig. 2. Lower *Leda ovum* Beds, Thenford Hill, 7 km north-east of Banbury, Northamptonshire; OUM J.20184, T. Beesley Colln.

Peronoceras turriculatum (Simpson), Fibulatum Subzone
Fig. 3. Bed 63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.68125.


1b
1a
5b
2b
2a
3b
3a
4a
4b
5a

1927 *Crassicoeloceras pingue* Buckman : pl. 728.
1963 *Nodicoeloceras crassoides* (Simpson); Zanzucchi : 117; pl. 14, figs 8, 8a.
1963 *Catacoeloceras crassoides* (Simpson) Sapunov : 126; pl. 5, fig. 2; pl. 6, fig. 1.
1963 *Catacoeloceras fonticulum* (Simpson) Sapunov : 126; pl. 6, fig. 2.
1968 *Nodicoeloceras crassoides* (Simpson); Lehmann : 53; pl. 17, fig. 4.
1971 *Nodicoeloceras crassoides* (Simpson); Pinna & Levi-Setti : 99; pl. 4, figs 1, 2.
1972 *Nodicoeloceras crassoides* (Simpson); Schmidt-Effing : 122; pl. 13, fig. 4; pl. 14, fig. 2.
? 1973 *Nodicoeloceras crassoides* (Simpson); Weitschat : 38; pl. 1, fig. 4.

HOLOTYPE. Whitby Museum no. 126 (Buckman 1913 : pl. 89), from the Exaratum Subzone of the Yorkshire coast.

DIMENSIONS.

Holotype	–	76·0: 19·0 (0·25), 27·4 (0·36), 39·5 (0·52)
Pl. 2, fig. 1	–	92·5: 23·7 (0·25), 26·6 (0·29), 46·1 (0·50)
	–	60·5: 19·1 (0·32), 26·3 (0·43), 27·8 (0·46)
C.69088	–	64·5: 18·6 (0·29), 27·2 (0·42), 31·4 (0·49)
BM 43894	–	103·0: 24·5 (0·24), 30·0 (0·29), 56·0 (0·54)
	–	70·0: 21·6 (0·31), 32·8 (0·47), 32·2 (0·46)

DESCRIPTION. *Nodicoeloceras crassoides* occurs commonly in the Abnormal Fish Bed and in the Inconstant Cephalopod Bed, associated with *Dactylioceras* (*Orthodactylites*) *semiannulatum* described above. There is some resemblance between the two species, but *N. crassoides* always has a much larger whorl breadth, and ventrolateral tubercles are usually developed on its inner whorls. No specimens transitional between the two species have been found. The Northamptonshire population of *N. crassoides* shows considerable variation in whorl dimensions, rib-density and size of tubercles, and the presence or absence of the shell accounts for the entirely different appearance of the sharp, high ribs and tubercles of the shell and the low almost effaced ribs on the internal mould (Pl. 2, fig. 1) (Howarth 1975). A specimen with its shell complete, from the Abnormal Fish Bed of Chipping Warden, Northamptonshire, was figured by Wright (1884 : pl. 85, figs 2, 3); it has widely-spaced ribs, ventrolateral tubercles on its inner whorls, a particularly large whorl breadth and some fibulation on the inner whorls. A similar Byfield specimen is figured in Pl. 2, fig. 5, although this has no fibulate ribs. Every gradation exists between this coarse-ribbed, wide-whorled type and the median form figured in Pl. 2, fig. 1. Specimens obtained from the unweathered Abnormal Fish Bed at Iron Cross quarry, Byfield, rarely have any shell attached; such a specimen, with relatively slender whorls and no tubercles at the smallest diameter seen, is figured in Pl. 2, fig. 4, to illustrate the opposite end of the morphological range. Specimens also occur in the Lower Cephalopod Bed, such as the example from Watford, west Northamptonshire, figured by Thompson (1885 : 309; pl. 1, figs 2, 2a), showing that the species occurs in both subzones of the Falciferum Zone in Northamptonshire. On the Yorkshire coast *N. crassoides* occurs in bed 37 (Howarth 1962*b* : 387) in the upper part of the Exaratum Subzone, associated with *D. vermis* (Simpson), *D. crassiusculosum* (Simpson) and *D. semiannulatum* sp. nov. The holotypes of *N. crassoides* itself and of its synonym *Ammonites fonticulus* Simpson came from this bed; both specimens have a large whorl breadth and tubercles on their inner whorls, and others collected from the same bed show a morphological range similar to that of the Northamptonshire specimens.

At Barrington, Somerset, *N. crassoides* occurs in bed 7, at about the middle of the Exaratum Subzone, and also in beds 16 and 18/19 (Pringle & Templeman 1922 : 451) in the Falciferum Subzone. The best specimens are from bed 18/19: two of them were figured by Buckman (1927 : pls 89A, 728), and one (pl. 728) was made the holotype of the new genus and species *Crassicoeloceras pingue*. They both are very closely comparable with the Yorkshire and Northamptonshire specimens and are in fact conspecific. Another specimen that is conspecific is the lectotype of *Ammonites annulatus* (J. Sowerby 1819 : 41; pl. 222, fig. 5), also from the Ilminster–Barrington succession. Oppel (1856 : 255), Tate & Blake (1876 : 299) and Wright (1884 : 473) all restricted Sowerby's species to his fig. 5 of pl. 222, and excluded his figs 1–4, but none of these was a formal selection of the lectotype, which must be attributed to Sylvester-Bradley (1958 : 67). The other three figured paralectotypes of Sowerby's *A. annulatus* are an example of *Dactylioceras semicelatum* (Simpson) from the top of the Marlstone Rock Bed at Copredy, Northamptonshire (Sowerby 1819 : pl. 222, fig. 1), another of the same species from the Grey Shales of the Yorkshire coast (pl. 222, fig. 2), and a *D. anguiforme* (Buckman) from the Falciferum Zone, ? Exaratum Subzone, of Ilminster, Somerset (pl. 222, figs 3, 4). As was mentioned in an earlier paper (Howarth 1973 : 257), the lectotype agrees exactly in matrix with other ammonites from bed 18/19 at Barrington, and it is a large specimen with a complete adult body chamber 1¼ whorls long (Pl. 3, fig. 1). On its outer whorl there is a mixture of single and bifurcating ribs, while on the penultimate whorl down to a diameter of about 45 mm all the ribs bifurcate and ventrolateral tubercles are present on most of them. It has a high whorl breadth throughout.

A. annulatus J. Sowerby 1819 cannot be used as the specific name instead of *N. crassoides* Simpson 1855, because it is preoccupied by *Ammonites annulatus* Schlotheim 1813. Tate & Blake (1876 : 168) and Wright (1884 : pl. 84, figs 7, 8) both interpreted Sowerby's species as an important index-species for the lowest zone of the Upper Lias, a mistake that was corrected by Buckman (1910*a* : 85), who pointed out that the correct determination for that completely different compressed-whorled index-species was *Dactylioceras tenuicostatum*. Another *Nodicoeloceras* that occurs in the Falciferum Zone is *N. spicatum* (Buckman 1928 : pl. 777) in bed 23 at Barrington, and *N. lobatum* (Buckman 1927 : pl. 730) and *N. multum* (Buckman 1928 : pl. 785) occur in the overlying Commune Subzone; they all differ in details of ribbing or tuberculation.

Genus *PERONOCERAS* Hyatt 1867

TYPE SPECIES. *Ammonites fibulatus* J. de C. Sowerby 1823, subsequently designated by Buckman (1911 : *v*).

DIAGNOSIS. Gradational from compressed ellipsocones to depressed cadicones. Whorls quadrangular with flat sides and venter. Ribs fine to distant; regular fibulation to ventrolateral tubercles or spines always present at some growth stage, but may be absent on small whorls of fine-ribbed species.

DISTRIBUTION. Fibulatum Subzone, lower and middle parts. Northamptonshire: Unfossiliferous Beds (top 4·6 m), Lower and Middle *Leda ovum* Beds. Yorkshire: Whitby beds 60–63, Ravenscar beds xxix and xxx.

REMARKS. *Peronoceras* is best known from its development on the Yorkshire coast. At Whitby it occurs in large numbers in a restricted group of beds (Howarth 1962*b* : 397, beds 60–63) that directly overlie the Commune Subzone containing *Dactylioceras athleticum* (Simpson) and *D. praepositum* (Buckman). In Northamptonshire it has similar relationships with the highest species of *Dactylioceras*, and again there is no overlap between the two genera. Fibulation combined with compressed whorls is the diagnostic feature of *Peronoceras*, but fibulation is by no means confined to *Peronoceras*, for many depressed-whorled Dactylioceratidae in other parts of the Upper Lias have ribs looped to tubercles or spines on their inner whorls. *Porpoceras* also has fibulate ribs in species that have depressed or approximately square whorls, but in that genus the mixture of fibulate and single ribs is distinctive, and in Britain it occurs at a higher horizon.

Large collections from single horizons in the Yorkshire Fibulatum Subzone show many intermediates between entirely different end-forms. The series between compressed fine-ribbed and depressed coarse-ribbed runs from *P. turriculatum* to *P. fibulatum* and then *P. subarmatum*. Unlike the Tenuicostatum Zone fauna of *Dactylioceras* (*Orthodactylites*) described earlier (Howarth 1973), these species of *Peronoceras* retain differences up to the end of the adult body chamber. Complete specimens of the three species differ from each other at all growth stages, so there is justification for maintaining that three species coexisted at the same horizon. Placing them all under one specific name would unite specimens that are always different; 'splitting' or 'lumping' has no stratigraphical significance for the full range of morphologies occurs throughout the stratigraphical range of the genus in Yorkshire and probably in Northamptonshire. *P. perarmatum* (including *P. andraei*) differs in having widely-spaced ribs at all growth stages and a whorl section that varies from square to depressed. There is, however, no justification for dividing off those species with depressed whorls as a different genus, because the complete range from compressed to depressed occurs together, they evolve and die out at the same horizons, and they have characters of consistent fibulation in common that unite them and mark them off from other older and younger genera. The link with the ancestral species *D. praepositum* (Buckman) in the beds directly below is through the fine-ribbed compressed species *Peronoceras turriculatum*, which differs only slightly in possessing fibulate ribs.

As in other Dactylioceratidae, adult *Peronoceras* have a constriction at the mouth border. Occasional examples have an earlier constriction in the last half whorl of the adult body chamber (e.g. Pl. 3, fig. 2; Pl. 5, fig. 3), and these are probably individuals that grew again after the first onset of sexual maturity. The mean diameter at the adult mouth border in 15 specimens of *P. fibulatum* is 81 mm, the range being 65–100 mm. The other species become adult within the same range, though the mean adult diameter may be slightly larger in *P. turriculatum*, and slightly smaller in *P. subarmatum* and *P. perarmatum*. All complete adults have body chambers between $\frac{13}{16}$ and 1 whorl in length. Only one much smaller specimen has been found so far: an example of *P. subarmatum* (Pl. 4, fig. 4) which is complete and apparently adult at 23 mm diameter. It has some injuries and irregular ornament on the outer whorl, and it is not proposed to claim that dimorphism can be recognized in *Peronoceras* on the evidence of this specimen alone.

Peronoceras fibulatum (J. de C. Sowerby 1823)

Pl. 2, fig. 2; Pl. 3, fig. 2; Pl. 4, figs 1, 2

1823 *Ammonites fibulatus* J. de C. Sowerby : 147; pl. 407, fig. 2.
1830 *Ammonites bollensis* Zieten : 16; pl. 12, fig. 3.
1885 *Ammonites bollensis* Zieten; Quenstedt : 370; pl. 46, fig. 14.
1926 *Peronoceras fibulatum* (J. de C. Sowerby) Buckman : pl. 683.
1961 *Peronoceras fibulatum* (J. de C. Sowerby); Dean, Donovan & Howarth : pl. 73, fig. 2.
1963 *Peronoceras fibulatum* (J. de C. Sowerby); Sapunov : 128; pl. 6, fig. 3.
1966 *Peronoceras fibulatum* (J. de C. Sowerby); Fischer : 36; pl. 1, fig. 15; pl. 5, fig. 11.
? 1968 *Peronoceras fibulatum* (J. de C. Sowerby); Lehmann : 54; pl. 17, fig. 2.

LECTOTYPE. BM 43911 from Whitby, Yorkshire (figured Sowerby 1823 : pl. 407, fig. 2; Dean, Donovan & Howarth 1961 : pl. 73, fig. 2), is one of three syntypes in Sowerby's collection. Although is it the specimen Sowerby figured, it is a syntype and not the holotype. It is here designated lectotype. The other two syntypes, now paralectotypes, are also both *P. fibulatum* from Whitby: C.79626 is 80 mm in diameter and is a complete adult, but most of the venter is worn away on the whole of the outer whorl, so it would not be suitable as a lectotype; C.79627 is only 27 mm in diameter.

DIAGNOSIS. Whorl section compressed to approximately square. Ribs of moderate density and looped in pairs to ventrolateral tubercles, though occasional single ribs may occur on outer whorls. Two ribs issue from each ventrolateral tubercle and are projected forwards on the venter.

DESCRIPTION. *P. fibulatum* is the commonest species of *Peronoceras* in Britain, and is characterized by evolute, square to compressed whorls, moderate rib-density, and a high proportion of ribs looped in pairs (fibulation) to ventrolateral tubercles. Other species of *Peronoceras* have different whorl proportions and rib-densities, and less consistent fibulation. The Yorkshire coast lectotype is an evolute, almost serpenticone, and densely-ribbed specimen, and is fibulate throughout. The other end of the variation in the species is illustrated by another Yorkshire specimen, figured in Pl. 4, fig. 1, which has more massive whorls and more widely spaced ribs. Many other Yorkshire

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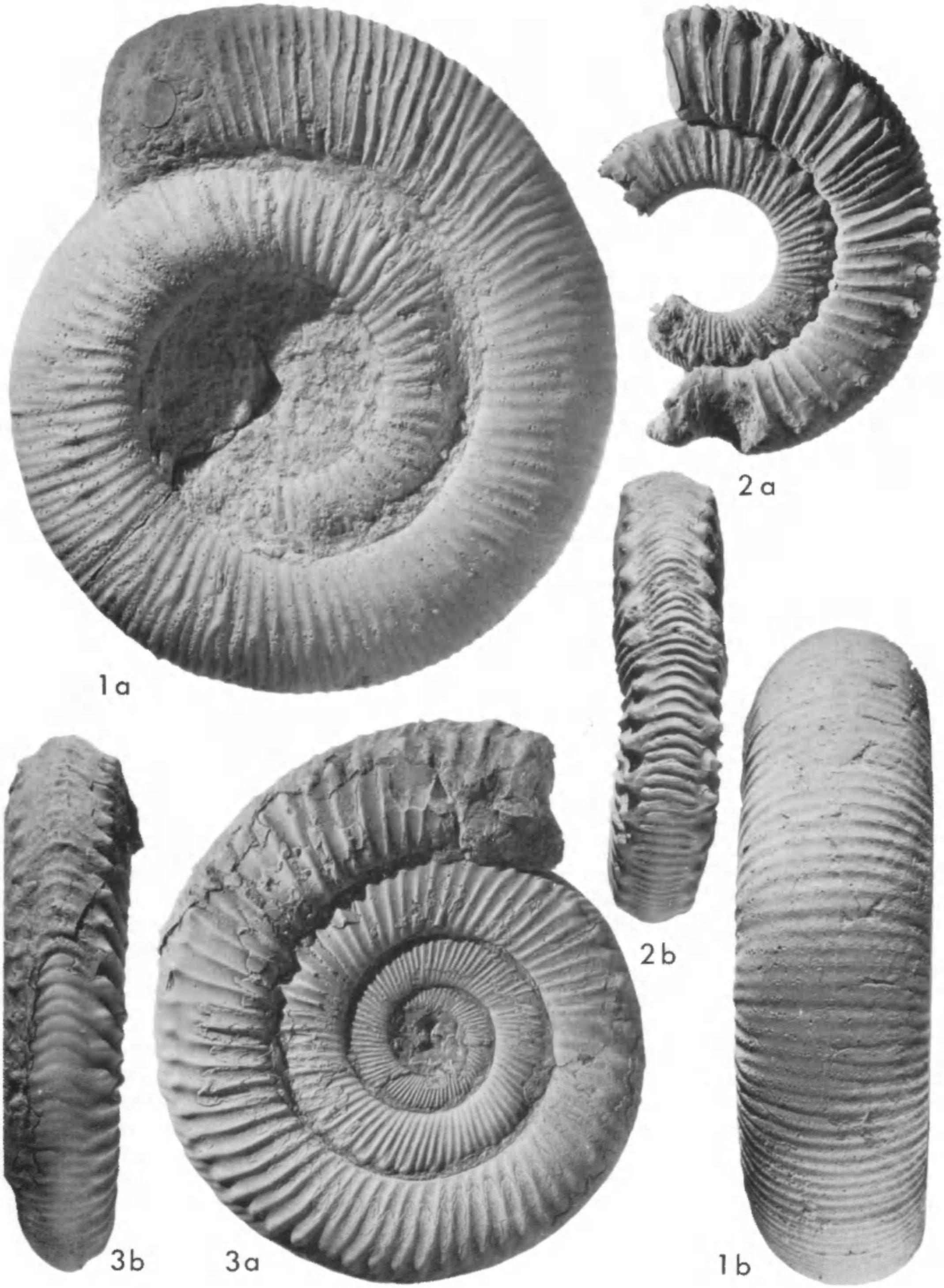
Plate 3 ×1

Nodicoeloceras crassoides (Simpson), [Falciferum Subzone]
Fig. 1. [Bed 18/19, Barrington], Ilminster, Somerset; BM 43894 (lectotype of *Ammonites annulatum* J. Sowerby, 1819 : 41; pl. 222, fig. 5).

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone
Fig. 2. *Leda ovum* Beds, Northampton; BM C.67519.

Peronoceras turriculatum (Simpson), Fibulatum Subzone
Fig. 3. Bed 63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.56567.


1a
2a
2b
3a
3b
1b

specimens fall within this range of variation, including the example figured by Buckman (1926 : pl. 683).

In Northamptonshire *P. fibulatum* occurs in the top 4·6 m of the Unfossiliferous Beds and in the Lower and Middle *Leda ovum* Beds. Specimens were fairly common at some localities, especially former brickpits in Northampton. The range of morphology they exhibit is similar to those from the Yorkshire coast: Pl. 3, fig. 2 shows a specimen of average whorl dimensions and rib-density, and Pl. 4, fig. 2 an example with more widely-spaced ribs. Most specimens are preserved as internal moulds or with only the inner shell intact (Howarth 1975), and the relief of the ribs and especially the ventrolateral tubercles is much reduced. On the adoral half of body chambers, however, the inner shell is not developed, and the tubercles are seen to be sharply pointed spines when the main shell is preserved (Pl. 2, fig. 2).

Ammonites bollensis Zieten (1830 : 16; pl. 12, fig. 3), including the specimen figured under that name by Quenstedt (1885 : pl. 46, fig. 14), is a synonym of *P. fibulatum. Ammonites youngi* Reynès (1879 : pl. 3, figs 13–18) is probably also a synonym, but it will be necessary to select and figure a type specimen before that specific name can be definitely interpreted.

Peronoceras turriculatum (Simpson 1855)

Pl. 2, fig. 3; Pl. 3, fig. 3; Pl. 4, figs 3, 6, 8

1855 *Ammonites turriculatus* Simpson : 59.
1911 *Peronoceras turriculatum* (Simpson) Buckman : pl. 30.
? 1968 *Dactylioceras attenuatum* (Simpson); Lehmann : 49; pl. 17, fig. 8.
? 1972 *Dactylioceras* sp. indet. 2, Guex : 618; pl. 8, figs 5, 8, 9.
? 1972 *Microdactylites attenuatus* (Simpson); Guex : 618; pl. 8, fig. 7.

HOLOTYPE. Whitby Museum no. 152, figured by Buckman (1911 : pl. 30).

DIAGNOSIS. Whorls compressed with flat sides and arched venter. Ribs fine and dense up to 40 mm diameter, and occasionally looped in pairs to ventrolateral tubercles; at larger diameters ribs are stronger and fibulation becomes more prominent, but some single ribs without tubercles remain. Most ribs bifurcate at the ventrolateral shoulder, and are projected forwards on the venter and sometimes raised in the middle.

DESCRIPTION. *P. turriculatum* differs from *P. fibulatum* in having fine dense ribs on the inner whorls, and only a few fibulate ribs. The dense ribs occur up to about 40 mm diameter, and there are occasional small ventrolateral tubercles to which the ribs are looped. The ribs bifurcate at the ventrolateral shoulder and form secondary ribs that are projected forwards over the arched venter. At larger sizes the ribs become more widely spaced, and fibulation is more frequent. On the body chamber ventrolateral tubercles are sometimes developed on each rib, and specimens have the appearance of a large, thick-whorled and coarsely-ribbed *Zugodactylites braunianus*. *P. turriculatum* shows considerable variation in development of tubercles and fibulation, but rib-density is greater throughout than in most examples of *P. fibulatum*.

In Yorkshire *P. turriculatum* is fairly common throughout the *Peronoceras*-bearing part of the Fibulatum Subzone, and the holotype is a median member of the species in all characters. A more complete adult Yorkshire specimen that shows the single ribs with ventrolateral tubercles on the body chamber is figured in Pl. 3, fig. 3, and an example of the densely-ribbed inner whorls is figured in Pl. 2, fig. 3. Specimens are somewhat smaller and usually less complete in Northamptonshire, where they occur in the top part of the Unfossiliferous Beds and in the Lower *Leda ovum* Beds. Two examples of densely ribbed inner whorls are figured in Pl. 4, figs 3 and 6, one almost without tubercles, the other with small sharp tubercles, and a larger specimen with more widely-spaced ribs and much larger tubercles on the outer whorl is figured in Pl. 4, fig. 8.

Peronoceras subarmatum (Young & Bird 1822)

Pl. 4, figs 4, 5, 7

1822 *Ammonites subarmatus* Young & Bird : 250; pl. 13, fig. 3.
1855 *Ammonites semiarmatus* Simpson : 60.

1962*a* *Peronoceras subarmatum* (Young & Bird) Howarth : 117; pl. 17, fig. 5.
1962*a* *Peronoceras semiarmatum* (Simpson) Howarth : 117; pl. 17, fig. 6.
1966 *Peronoceras subarmatum* (Young & Bird); Fischer : 37; pl. 1, figs 16, 17; pl. 5, fig. 12; pl. 6, figs 1–3.

NEOTYPE. Whitby Museum no. 521 was described, figured and designated neotype by Howarth (1962*a* : 117; pl. 17, fig. 5), though it is possible that this specimen is the holotype.

DIAGNOSIS. Whorls depressed, with whorl height/whorl breadth ratio of 0·65–0·85 at 35–50 mm diameter. On the coronate inner whorls almost all ribs are looped in pairs to large ventrolateral tubercles or spines. A few single ribs without tubercles occur on the outer whorl. Two ribs issue from each tubercle and cross the venter with only slight forwards projection.

DESCRIPTION. Specimens with slightly to much depressed whorl sections, and coronate inner whorls where the ribs are looped to long ventrolateral spines, also often accompany *P. fibulatum*. The depressed whorl section remains in the adult body chamber, and so these forms are referred to a separate species, *P. subarmatum*. The neotype from Whitby has approximately average depressed whorls in which the ratio of whorl height to whorl breadth is 0·85 at 50 mm diameter. Another Whitby specimen, the neotype of *Ammonites semiarmatus* Simpson (Howarth 1962*a* : 117; pl. 17, fig. 6), has slightly less depressed whorls, but is similar in all other characters, and is therefore placed in synonymy with *P. subarmatum*. *P. perarmatum* has more widely-spaced ribs throughout growth.

Most of the Northamptonshire specimens are less complete, and consist mainly of inner whorls or immature examples with body chambers. Two such immature specimens are figured (Pl. 4, figs 5, 7), both with one whorl of body chamber, but the mouth borders are missing. In both, the fibulate tuberculate ribs of the inner whorls give way to a mixture of fibulate, single tuberculate and single non-tuberculate ribs on the last $\frac{1}{4}$ whorl. These are modifications usually associated with an adult body chamber, so the complete adult diameter of these specimens would probably have been about 60–70 mm. A much smaller complete adult specimen is also known from Bugbrooke, Northamptonshire, which is one of the main localities from which *P. subarmatum* has been obtained (Pl. 4, fig. 4). It is only 23 mm in diameter at the constricted mouth border, the body chamber is $\frac{3}{4}$ whorl in length and the final two closely approximated septa occur at 16 mm diameter. Whorl dimensions (mm) just before the mouth border are 22·0: 6·4 (0·29), 8·1 (0·37), 11·0 (0·50) (whorl height/breadth ratio 0·74); at smaller sizes the whorls are more depressed, e.g. at 14 mm diameter whorl height/breadth ratio is 0·51. On the small parts of the penultimate whorl that are exposed, large ventrolateral tubercles with some single and some fibulate ribs can be seen. On the final $\frac{3}{4}$ whorl the ribs and tubercles become irregular, most of the tubercles on one side of the whorl do not correspond with those on the other side, and there are signs of injury on the early part of the body chamber. It is possible that this specimen stopped growing or became prematurely adult because of its injuries.

Peronoceras perarmatum (Young & Bird 1822)

Pl. 5, figs. 1–4

1822 *Ammonites perarmatus* Young & Bird, 1–3 May 1822[2] : 249; pl. 14, fig. 11 (*non Ammonites perarmatus* J. Sowerby, 1 June 1822)
1828 *Ammonites subarmatus* Young & Bird : 263; pl. 14, fig. 8.
1843 *Ammonites andraei* Simpson : 23.
1855 *Ammonites andraei* Simpson; Simpson : 59.
1912 *Porpoceras perarmatum* (Young & Bird) Buckman : pl. 50.
1912 *Porpoceras andraei* (Simpson) Buckman : pl. 57.
1963 *Peronoceras andraei* (Simpson); Sapunov : 128; pl. 6, fig. 4.

[2] Evidence for the publication date of Young & Bird's *Geological Survey of the Yorkshire Coast* can be found in the *Monthly Magazine*, London, **53** (368) : 446, for 1 June 1822, where it was included in a review of books published during May 1822, and also in a paper by Young (1822, *Mem. Wernerian Soc.*, Edinburgh, **4** : 262) on the Kirkdale Caves, read to the Wernerian Natural History Society of Edinburgh on 4 May 1822, where he said that his book was 'just published'. The publication date was, therefore, 1, 2 or 3 May 1822, and *Ammonites perarmatus* Young & Bird has priority over *A. perarmatus* J. Sowerby published on 1 June 1822 (Sowerby 1822 : 72; pl. 352; for date of publication see Cleevely 1974 : 443), and now known to be an Oxfordian *Euaspidoceras* (Arkell 1940 : 193).

HOLOTYPE. Whitby Museum no. 180, figured by Buckman (1912 : pl. 50).

DIAGNOSIS. Whorl section varies between square and depressed. Ribs of low density and widely spaced throughout growth; though mainly single and bearing prominent ventrolateral tubercles, some are looped in pairs to the tubercles. Most ribs bifurcate at the tubercles, and secondaries are projected forwards and widely spaced on the venter.

DESCRIPTION. Specimens in which the primary ribs are considerably more widely spaced than in *P. fibulatum*, and in which the whorl section varies between square and much depressed, frequently accompany the more compressed and densely ribbed *P. fibulatum*. The holotype of *P. perarmatum* from Yorkshire is an extreme type, in which the whorl breadth is very large, the ribs are very widely spaced and there is only occasional fibulation on the inner whorls which have large ventrolateral tubercles. The venter is badly worn by erosion on most of the outer whorl as is shown in Buckman's figure (1912 : pl. 50). A less extreme Yorkshire specimen is figured here (Pl. 5, fig. 1) that has its ventral ribs intact. All gradations exist between this and the square-whorled type exemplified by the holotype of *Ammonites andraei* (Buckman 1912 : pl. 57). Regular fibulation in the latter specimen extends up to 40–50 mm diameter, after which the ribs are mainly single, with small to moderate ventrolateral tubercles.

In Northamptonshire *P. perarmatum* also has the same vertical range as *P. fibulatum*, for it occurs in the Unfossiliferous Beds and in the Lower and Middle *Leda ovum* Beds. A portion of an adult body chamber that has a much depressed whorl section is figured in Pl. 5, fig. 2, and although both ends of it are missing the whorl can be seen to become rapidly more compressed towards the aperture, which must have been at about 65 mm diameter. Another specimen with a less strongly depressed whorl section is figured in Pl. 5, fig. 4, and a nearly complete adult body chamber with a square whorl section in Pl. 5, fig. 3. The latter specimen shows an example of a constriction at a former mouth border followed by a further short period of growth (less than $\frac{1}{4}$ of a whorl), and it is interesting to note that the single ribs and ventrolateral tubercles after the first constriction bear great resemblance to those of *Zugodactylites*, and are considerably different from the widely-spaced fibulate ribs of the previous half whorl.

Genus *ZUGODACTYLITES* Buckman 1926

TYPE SPECIES. *Ammonites braunianus* d'Orbigny 1845.

SYNONYMY. *Omolonoceras* Dagis 1967 (type species: *O. manifestum*); *Gabillytes* Guex 1971 (type species: *G. larbusselensis*).

DIAGNOSIS. Characterized by single, straight primary ribs that bifurcate at small sharp ventrolateral tubercles, and form forwardly projected secondary ribs on the venter. Some single ribs occur on the adult body chamber. Whorl shape varies from compressed to depressed, and the

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Plate 4 × 1 (Fig. 4, × 1·5)

Peronoceras fibulatum (J. de C. Sowerby), Fibulatum Subzone

Fig. 1. Bed 62, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.56539.

Fig. 2. Top part of Unfossiliferous Beds, railway cutting 1·2 km south of Long Buckby, Northamptonshire; Northampton Museum, B. Thompson Colln.

Peronoceras turriculatum (Simpson), Fibulatum Subzone

Fig. 3. Unfossiliferous Beds, Hollowell, 13 km north-west of Northampton; Northampton Museum, B. Thompson Colln.

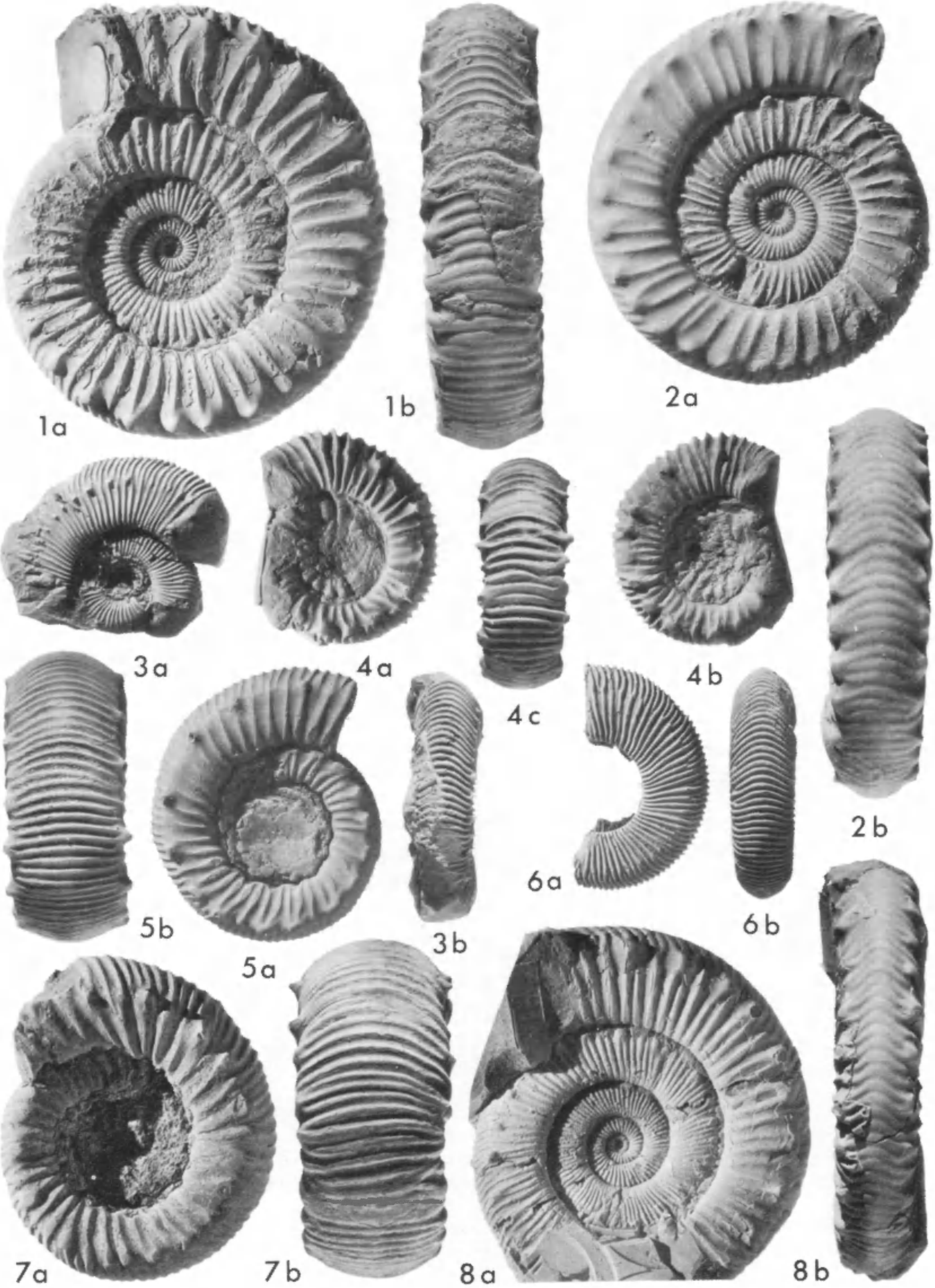
Fig. 6. Lower or Middle *Leda ovum* Beds, Badby, 3 km south of Daventry, Northamptonshire; Northampton Museum, B. Thompson Colln.

Fig. 8. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20138*a*, E. A. Walford Colln.

Peronoceras subarmatum (Young & Bird), Fibulatum Subzone

Figs 4, 7. [? Lower] *Leda ovum* Beds, Bugbrooke, Northamptonshire; Miss A. E. Baker Colln. Fig. 4, BM 20843, × 1·5. Fig. 7, BM 20135.

Fig. 5. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20146, ? E. A. Walford Colln.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depressed whorls may be coronate with large ventrolateral tubercles. A blunt ventral keel is formed in one species. Complete adults have a strong constriction immediately before the adult mouth border.

DISTRIBUTION. Fibulatum Subzone, lower (but not basal) and middle parts. Northamptonshire: Lower and Middle *Leda ovum* Beds. Yorkshire: Whitby beds 62–64, Ravenscar bed xxxi.

REMARKS. The sharp ventrolateral tubercles that occur at the ends of all the primary ribs are characteristic of all species of *Zugodactylites*. In this respect they differ from the accompanying species of *Peronoceras* which have fibulate ribs. The most likely ancestor for *Zugodactylites*, the fine-ribbed species *Peronoceras turriculatum*, always has some fibulate ribs. Like *Peronoceras*, *Zugodactylites* shows a wide range of whorl shapes occurring in the same bed. The compressed- and depressed-whorled forms remain considerably different up to the end of the adult body chamber, so they are considered to be specifically distinct. They do not change to much more similar morphology on the body chamber, as was found in species of *Orthodactylites* in the Tenuicostatum Zone (Howarth 1973), where the depressed and compressed forms were considered to be conspecific. *Zugodactylites* with complete adult body chambers are, in fact, remarkably frequent, and although the rib-density shows wide variation, there is much less variation in final size, and species are fairly closely defined.

The variation in whorl shape in *Zugodactylites* led Dagis (in Dagis & Dagis 1967) to propose the generic name *Omolonoceras* for those forms with depressed whorls. Dagis (1968 : 52–56, 73, 84) showed that these depressed forms occur in north-eastern Siberia in the same beds as *Zugodactylites*. The difference in whorl shape is not considered here to be worthy of generic distinction, because compressed and depressed forms of Dactylioceratidae that are clearly related by other distinctive characters often occur together in the same bed, and in some cases (*Orthodactylites* of the Tenuicostatum Zone) they may even be conspecific. *Omolonoceras* has the same sharp ventrolateral tubercles on single ribs that are the main characteristic of *Zugodactylites*.

Generic distinction of a different sort was put forward by Guex (1971) when he proposed the name *Gabillytes* for the small keeled species *Zugodactylites pseudobraunianus* (Monestier) (*G. larbusselensis* is a synonym). Sexual dimorphism was the real basis claimed for the proposal of the genus. If *Z. pseudobraunianus* and *Z. braunianus* could be shown to be sexual dimorphs, then they should be referred to the same species, rather than made generically different. However, *Z. pseudobraunianus* is much less common than *Z. braunianus* in England and it has not been found at all in Yorkshire. The ventral keel occurs most prominently on the last whorl of the phragmocone before the adult body chamber, and is lost on the adult. Such a prominent keel is not found in *Z. braunianus* at any growth stage, although the venter may be raised in some individuals at much larger sizes into a pseudo-keel. So the keel of *Z. pseudobraunianus* is a morphological feature that is not associated with the adult body chamber. The case for dimorphism seems to be unproved, and the two forms are here kept as different species.

Plate 5 ×1

Peronoceras perarmatum (Young & Bird), Fibulatum Subzone

Fig. 1. Beds 60–63, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.76486.

Fig. 2. *Leda ovum* Beds, railway cutting, Eydon, Northamptonshire; OUM J.20139, E. A. Walford Colln.

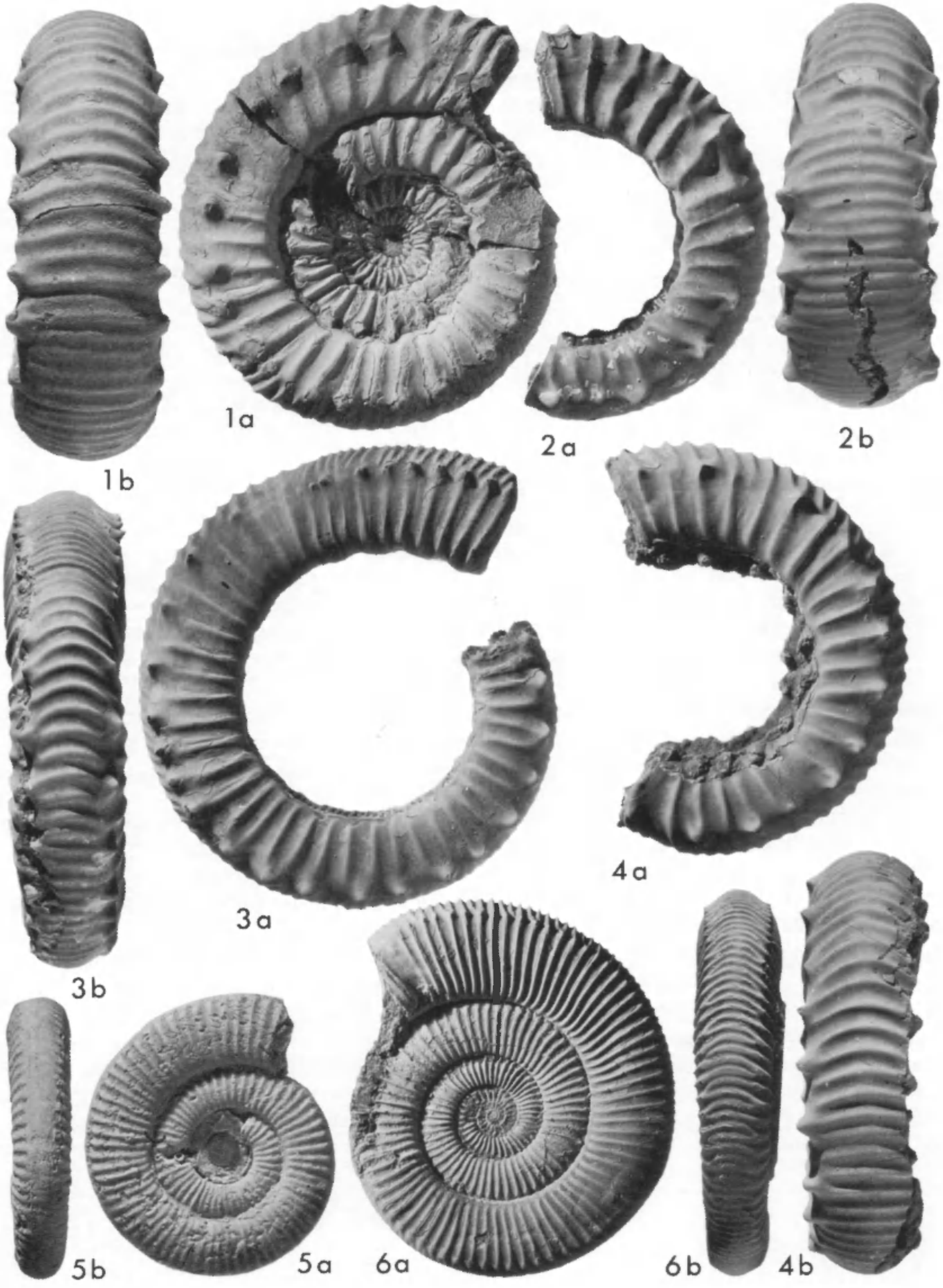
Fig. 3. *Leda ovum* Beds, Northampton; BM C.67507.

Fig. 4. Lower *Leda ovum* Beds, Thenford Hill, 7 km north-east of Banbury, Northamptonshire; OUM J.20199.

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

Fig. 5. Le Clapier, Aveyron, France; lectotype, Inst. Pal. Mus. Hist. Nat. Paris, d'Orbigny Colln. no. 1936.

Fig. 6. *Leda ovum* Beds, Northampton; OUM J.16288, C. Upton Colln.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Zugodactylites braunianus (d'Orbigny 1845)

Pl. 5, figs 5, 6; Pl. 6, figs 1–6; Pl. 7, figs 1–4; Pl. 8, fig. 5

1845 *Ammonites braunianus* d'Orbigny : 327; pl. 104, figs 1–3.
1874 *Ammonites braunianus* d'Orbigny; Dumortier : 103; pl. 28, fig. 5.
1885 *Ammonites braunianus* d'Orbigny; Quenstedt : 373; pl. 46, fig. 18.
1926 *Zugodactylites braunianus* (d'Orbigny) Buckman : pl. 658.
1927 *Zugodactylites braunianus* (d'Orbigny); Buckman : 44.
1927 *Zugodactylites mutatus* Buckman : pl. 720.
1931 *Coeloceras* (*Dactylioceras*) *braunianum* (d'Orbigny) Monestier : 53; pl. 3, figs 10, 13–19, 24.
1959 *Coeloceras* (*Dactylioceras*) *braunianum* (d'Orbigny); Théobald & Duc : 21; pl. 2, figs 9, 9*a*.
1961 *Zugodactylites braunianus* (d'Orbigny); Dean, Donovan & Howarth : pl. 73, fig. 1.
? 1966 *Zugodactylites braunianus* (d'Orbigny); Fischer : 43; pl. 2, fig. 6; pl. 5, fig. 9.
1966 *Zugodactylites sapunovi* Géczy : 440; pl. 1, fig. 3.
1967 *Zugodactylites moratus* Dagis : 63; pl. 1, figs 3, 4.
1968 *Zugodactylites braunianus* (d'Orbigny); Dagis : 41; pl. 8, figs 4–6.
1968 *Zugodactylites moratus* Dagis; Dagis : 49; pl. 8, figs 7, 8.
1970*a* *Zugodactylites braunianus* (d'Orbigny); Guex : 342; pl. 1, fig. 2.
1970*b* *Zugodactylites braunianus* (d'Orbigny); Guex : 623; pl. 1, figs 1–7.
1973*b* *Zugodactylites braunianus* (d'Orbigny); Guex : 552; pl. 3, figs 10, 11.
1975 *Zugodactylites* cf. *braunianus* (d'Orbigny); Frebold : 15; pl. 5, figs 3–5, ? 6.

LECTOTYPE. The best specimen in d'Orbigny's collection (Inst. Pal., Mus. Hist. Nat. Paris) is no. 1936 from Le Clapier, Aveyron, and is here designated lectotype (Pl. 5, fig. 7 – it was figured previously by Guex 1970*b* : pl. 1, figs 5–7). It is the largest of the syntypes on which d'Orbigny based his description, and the specimen from which he obtained his measurements (his value of 0·12 for the whorl thickness is evidently an error, and his figure of a 58 mm diameter specimen, said to be natural size, is either idealized or enlarged). Dimensions (mm) of the lectotype are – 43·0: 10·6 (0·24), 9·5 (0·22), 22·8 (0·53).

DIAGNOSIS. A finely-ribbed, compressed species of *Zugodactylites*. The whorl height exceeds the whorl breadth at sizes of more than about 20 mm diameter. The whorl section is rounded, with a rounded or arched venter. The ribs are generally fine, but show wide variation in density; they are straight and bifurcate at small sharp ventrolateral tubercles; the secondary ribs are arched forwards on the venter, and are sometimes raised and sharp in the middle of the venter. Maximum size of complete adults varies between 43 and 90 mm diameter, and a strong constriction occurs immediately before the mouth border.

DISTRIBUTION. Fibulatum Subzone. Lower and Middle *Leda ovum* Beds of Northamptonshire; beds 62–64 at Whitby, and bed xxxi at Ravenscar, Yorkshire.

DESCRIPTION. About 60 solid and well-preserved specimens from the *Leda ovum* Beds of the Northampton area have been examined; most of the best specimens came from the former brickpits, especially Vigo brickpit, which were within the town itself. In addition many crushed and fragmentary specimens occur in the cores of the numerous boreholes that have penetrated that clay formation. Of the 30 specimens that belong to Beeby Thompson's collection, 23 came from the Lower *Leda ovum* Beds and 7 from the Middle *Leda ovum* Beds, and the species is not known from lower or higher horizons. About half the specimens are complete adults, each with a deep constriction immediately before the mouth border. The constriction affects both inside and

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Plate 6 ×1

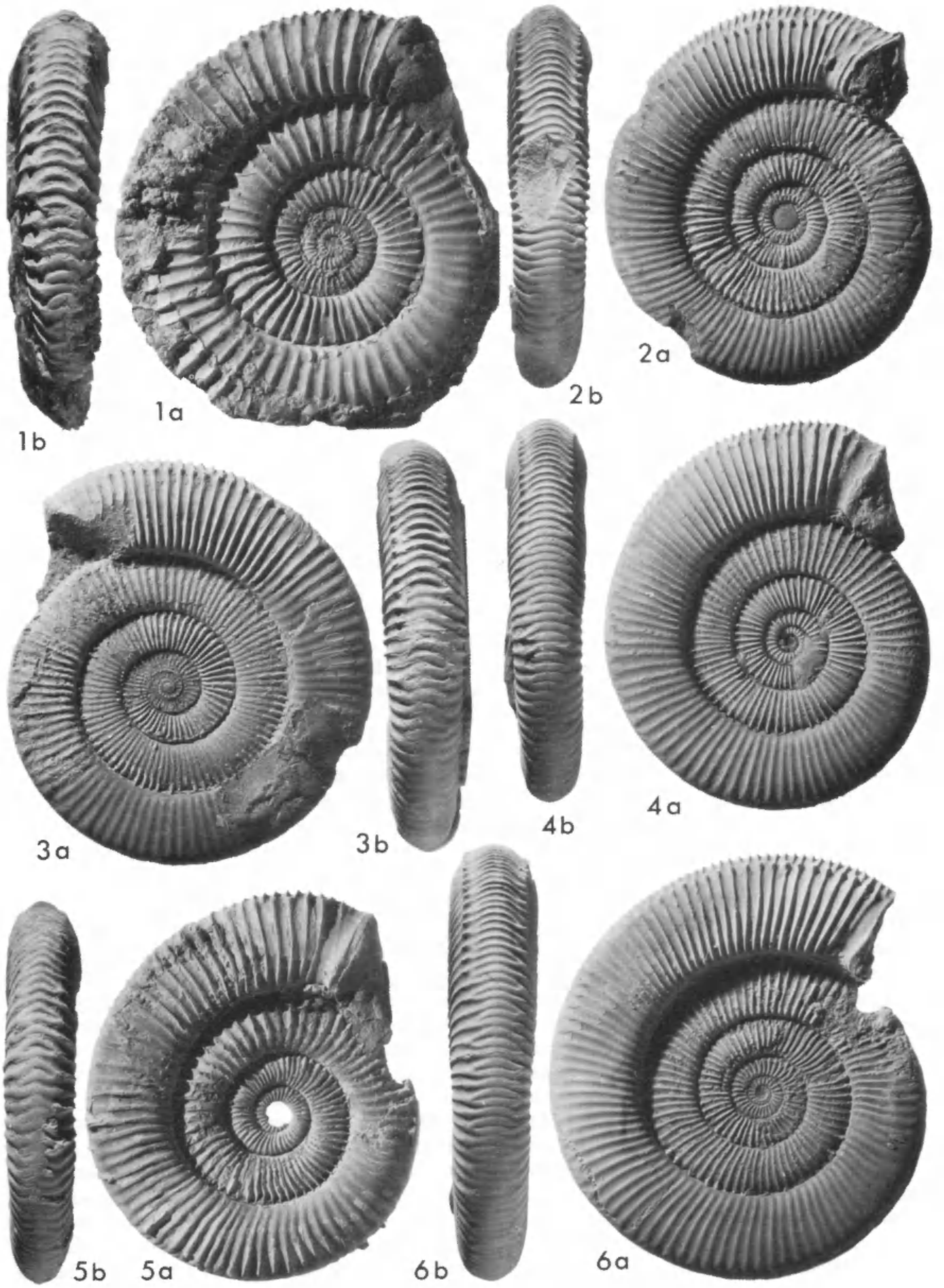
Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

Figs 1, 3, 5. Lower *Leda ovum* Beds, Heyford, 10·5 km west of Northampton. Fig. 1, BM C.67525. Fig. 3, BM C.67524. Fig. 5, BM C.56068.

Fig. 2. Lower or Middle *Leda ovum* Beds, Vigo brickpit, Northampton; Northampton Museum, B. Thompson Colln.

Fig. 4. Lower or Middle *Leda ovum* Beds, Northampton; BM C.67521.

Fig. 6. Middle *Leda ovum* Beds, Racecourse brickpit, Northampton: BM C.67533.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outside surfaces of the shell, in it the ribs are much reduced or absent, and it is followed by one or two swollen ribs before the mouth border itself. Such constrictions can be seen in all the specimens figured here, and in the one figured by Buckman (1927 : pl. 720); none of them have constrictions before the final mouth border. In 31 specimens the diameter at the adult mouth border varies between 43 and 70 mm; the mean value (M) is 57·8 mm, the standard deviation (s) is 7·0 mm and the range spanned by $M \pm 2s$ is 43·8–71·8 mm. The histogram (Fig. 3) confirms that the distribution is unimodal with a peak frequency between 55 and 60 mm. Similarly the diameter at the last suture-line in 23 adult specimens varies between 31 and 47·5 mm, the mean being 39·2 mm and the standard deviation 4·5 mm. The length of the adult body chamber in 22 adults varies between $\frac{11}{16}$ and $\frac{15}{16}$ whorl, the mean being $\frac{13}{16}$ whorl.

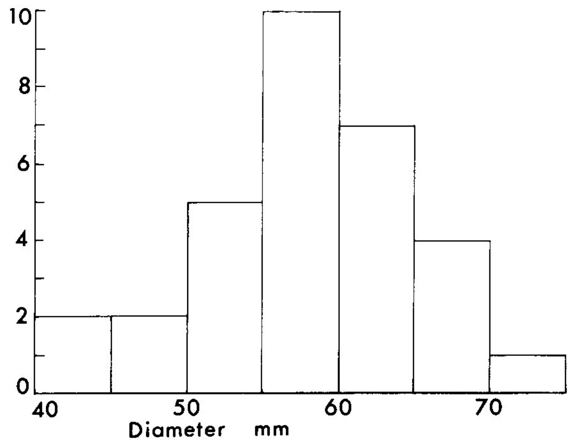


Fig. 3. Histogram of the diameter at the mouth border of 31 specimens of *Zugodactylites braunianus* from Northamptonshire.

Z. braunianus has compressed whorls, and in the Northampton population it can be seen (Fig. 4) that the height of the whorl always exceeds the breadth at sizes of more than 6 mm whorl height (*c*20 mm diameter). On the largest whorls the height/breadth ratio may reach 1·4. There is wide variation in rib-density, and the full range can be seen in the series of specimens figured in Pl. 5, fig. 6, Pl. 6, figs 1–3, 5, 6, Pl. 7, fig. 1 and in Dean, Donovan & Howarth (1961 : pl. 73, fig. 1). These eight form a continuously grading series, though the end-members, Pl. 6, figs 1 and 3, look considerably different. The rib-density of the 48 measurable specimens is expressed graphically in Fig. 5A, and that of the eight figured specimens in Fig. 5C. These are conventional graphs, in which the number of ribs in a complete whorl is plotted against the diameter of that whorl at its larger end. Close inspection of the ribbing reveals many instances of uneven rib spacing over short lengths of a whorl, so in order to express the changes in rib-density more accurately, 90° quadrants were marked on the specimens and counts of the number of ribs per quarter whorl were made. The relatively high rib-density of the species allows this to be done without appreciable errors. Graphs can now be plotted of the number of ribs in a quarter of a whorl against the whorl diameter at its larger end. The results are shown in Fig. 5B for the 48 Northamptonshire specimens and Fig. 5D for the eight figured specimens. The general unevenness of the ribbing is much more clearly displayed, and the rib-curves of the eight figured specimens are interlaced to such an extent that the apparent separation of the rib-curves in the ribs per whorl graph (Fig. 5B) is seen to be largely spurious. The wide range of variation observed in rib-density appears to be a genuine character of the species, and not due to the mixing of specimens from different horizons, because specimens of widely differing rib-densities occur in both the Lower and the Middle *Leda ovum* Beds; e.g. four of the specimens in Figs 5C and 5D (nos 3, 5, 6, 8), including the most densely and the most coarsely ribbed individuals, came from the Heyford brickpit, where only the Lower *Leda ovum* Beds were exposed, whilst the densely ribbed specimen from the

Racecourse brickpit, Northampton, and the coarsely ribbed Abington Park sewer trench specimen (Figs 5C, 5D, nos 2 and 7) both came from the Middle *Leda ovum* Beds. A graph of the rib-density of the Vigo specimens alone occupies 90% of the variation shown by the whole fauna. The Vigo specimen figured by Buckman (1927 : pl. 720) as the holotype of *Zugodactylites mutatus* is a typical *Z. braunianus* in all respects.

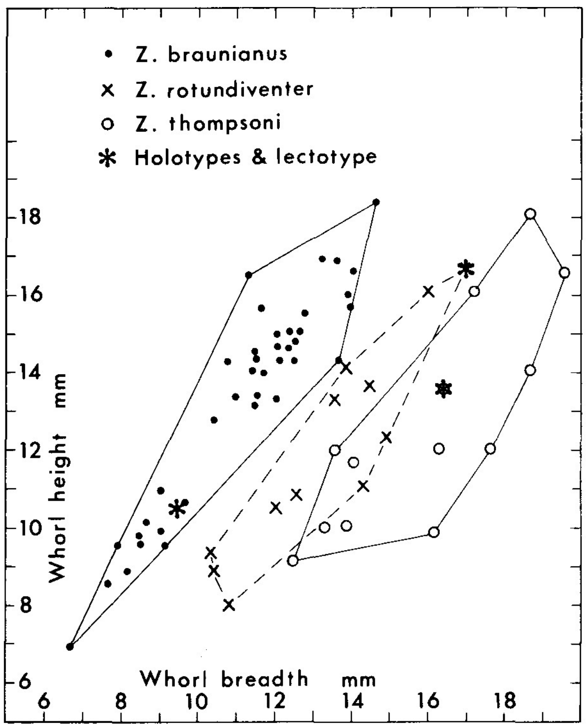


Fig. 4. Graph of whorl height plotted against whorl breadth for 35 specimens of *Zugodactylites braunianus* from Northamptonshire and four from Yorkshire, nine specimens of *Z. rotundiventer* from Northamptonshire, and eight specimens of *Z. thompsoni* from Northamptonshire and one from Yorkshire.

Examples of *Zugodactylites* have now been found in the lower and middle part of the Fibulatum Subzone of the Yorkshire coast (see p. 243). Six specimens are known from beds 62–64 of the main outcrop at Whitby, and 17 specimens were obtained from bed xxxi at Ravenscar. The Whitby examples include the large complete specimen figured in Pl. 7, fig. 3, whilst those from Ravenscar include those figured in Pl. 8, fig. 5, which is an exact match for the Northamptonshire specimen figured by Dean, Donovan & Howarth (1961 : pl. 73, fig. 1), Pl. 7, fig. 2, which has thicker whorls than average and is transitional to *Z. rotundiventer*, and Pl. 7, fig. 4, which is the most densely ribbed Yorkshire specimen. Although the Yorkshire population is morphologically close to that of Northamptonshire and the two are clearly conspecific, there are some differences. The main one is the larger sizes attained by the Yorkshire adult specimens: nine complete adults ranged from 61 to 86 mm in diameter at the mouth border, the mean being 73·8 mm and the standard deviation 7·3 mm; this larger size probably reflects the more advantageous ecological conditions in which the Yorkshire population lived. The only other significant difference is in the rib-density: the Yorkshire specimens all fall in the lower two-thirds of the range of variation of the Northampton specimens shown in Fig. 5A.

The ventrolateral tubercles are small and sharp when seen on the outer surface of the main shell or as moulds of the inner surface of the main shell, but the 'inner shell' (Howarth 1975) cuts across the base of the tubercles, so that they are hardly visible on the surface of the inner shell or

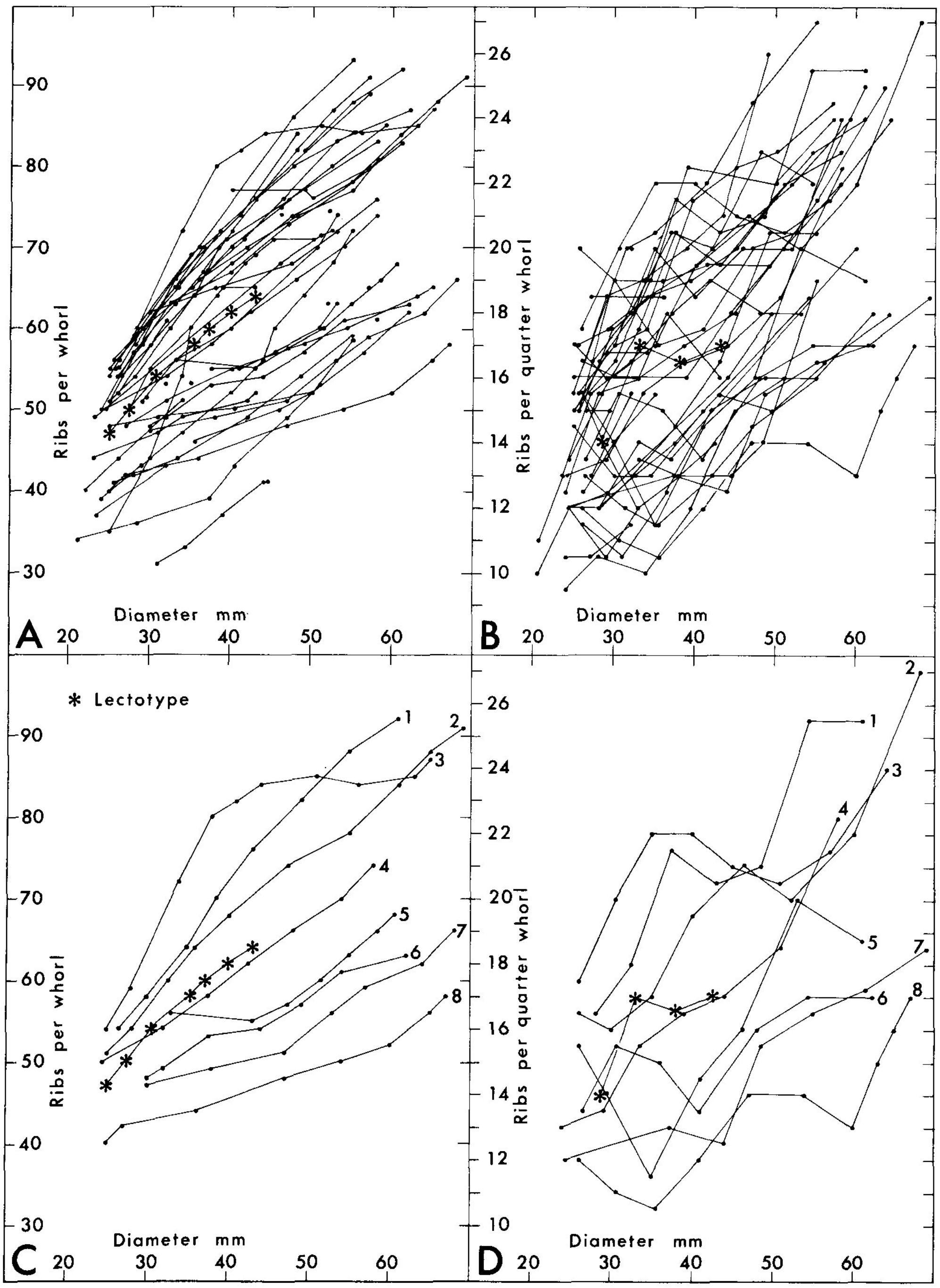


Fig. 5. Graphs of rib-density of *Zugodactylites braunianus*. Figs 5A and 5B each contain about 225 points obtained from 48 specimens from Northamptonshire. Figs 5C and 5D are plots of eight specimens selected to show almost the full range of rib-density. 1 = Northampton Museum specimen, Pl. 6, fig. 2; 2 = BM C.67533, Pl. 6, fig. 6; 3 = BM C.67524, Pl. 6, fig. 3; 4 = OUM J.16288, Pl. 5, fig. 6; 5 = BM C.56068, Pl. 6, fig. 5; 6 = BM C.56067, figured Dean, Donovan & Howarth 1961 : pl. 73, fig. 1; 7 = Northampton Museum, Pl. 7, fig. 1; 8 = BM C67525, Pl. 6, fig. 1.

on the internal mould. Some ribs bifurcate while others remain single at the ventrolateral tubercles, and the proportion of ventral to primary ribs is about 1·5 in many specimens, but varies between 1·3 and 1·8 and is independent of the variations in rib-density. The ventral ribs sometimes zigzag across the venter between tubercles that are not opposite each other on the sides of the venter. In some specimens the middle of the venter is slightly raised into a pseudo-keel, and the secondary ribs across it are raised and sharp in the middle, accentuating the effect.

The lectotype, from Le Clapier, Aveyron, was previously figured by Guex (1970*b* : pl. 1, figs 5–7). In whorl height and breadth, and in rib-density, it occupies a position in the centre of the variation of the Northamptonshire population (Figs 4 and 5). Guex's (1970*b* : 625) opinion, that the specimen figured by Dean, Donovan & Howarth (1961 : pl. 73, fig. 1) (Fig. 5C, no. 6) differed significantly from the lectotype and might have come from a different horizon, is not borne out by the analysis given here, for both are well within the ranges of variation of both the Northamptonshire and Yorkshire specimens, the latter being known to have come from a more restricted horizon. Other Aveyron specimens were figured by Dumortier, Monestier, Theobald & Duc and Guex as listed in the synonymy. Dumortier's (1874 : 103, pl. 28, fig. 5) specimens of 90 and 99 mm diameter are bigger than many English specimens, but they agree closely otherwise, and Monestier's (1931 : 53) specimens appear to be rather more compressed, but further specimens and analysis are needed before convincing differences could be established.

A single specimen from the manganese mine of Urkut, Hungary, was made the type of the new species *Z. sapunovi* by Géczy (1966 : 440) because it had partly bifurcating ribs and a raised pseudo-keeled venter. Partly bifurcating ribs with a secondary/primary ratio of between 1·3 and 1·8 are typical of *Z. braunianus*, and a raised venter with a pseudo-keel occurs in about one-third of the Northamptonshire collection (Pl. 6, fig. 5 shows the feature well). Many of them have a cross-section like that given by Géczy, whose specimen is a *Z. braunianus*, probably adult at about 70 mm diameter and with about 100 ribs on the final whorl. The specimens described by Dagis (1968 : 41) from north-eastern Siberia are also very similar to the Northamptonshire fauna. They include the new species *Z. moratus* Dagis (1968 : 49) which was used for those examples with a slightly greater whorl breadth. They are not as broad as *Z. rotundiventer*, and they are best accommodated in *Z. braunianus*, of which they appear to be slightly broader-whorled immature examples.

Zugodactylites rotundiventer Buckman 1927

Pl. 7, figs 5, 6

1927 *Zugodactylites rotundiventer* Buckman : pl. 743.
1966 *Zugodactylites rotudiventer* Buckman; Fischer : 44; pl. 2, fig. 17; pl. 5, fig. 8.
1967 *Zugodactylites latus* Dagis : 65; pl. 1, fig. 5.
1968 *Zugodactylites latus* Dagis; Dagis : 51; pl. 8, fig. 9.

HOLOTYPE. BM C.71443 (Buckman 1927 : pl. 743) from the *Leda ovum* Beds at Vigo brickpit, Northampton. Dimensions (mm) – 73·5: 16·7 (0·23), 17·0 (0·23), 42·5 (0·58).

DIAGNOSIS. Differs from *Z. braunianus* in the larger whorl breadth, which equals or exceeds the whorl height at all growth stages. Ribbing similar to *Z. braunianus*, with small sharply-pointed ventrolateral tubercles.

DISTRIBUTION. Fibulatum Subzone, Lower *Leda ovum* Beds of Northamptonshire.

DESCRIPTION. The collection consists of the holotype and eight other specimens, all from the *Leda ovum* Beds of Northamptonshire. One is from Heyford brickpit, 10 km west of Northampton, while the remainder are from Vigo brickpit, and six of them were labelled by Beeby Thompson as coming from the Lower *Leda ovum* Beds. Unfortunately the holotype was not so labelled, but there is no evidence that it or any others came from a horizon other than the Lower *Leda ovum* Beds. The species has a broad arched venter at all sizes, and a considerably larger whorl breadth than *Z. braunianus* (Fig. 4). At diameters of 40 mm and larger the whorl height and breadth may be approximately equal, but at smaller sizes the whorl breadth always exceeds the height. The primary ribs, sharp ventrolateral tubercles and secondary ribs on the venter are similar to those in *Z.*

braunianus, and the rib-density is the same as the lower half of the range of variation in *Z. braunianus*. The primary ribs bifurcate or remain single at the ventrolateral tubercles, and the ratio of secondary/primary ribs is about 1·5.

Four of the specimens are adults. The holotype has a constriction immediately preceding a flared mouth border at 75 mm diameter; its body chamber occupies exactly one whorl, but only small parts of the final suture-lines can be seen. A second, fragmentary specimen has a similar constriction and mouth border at 65 mm diameter and the body chamber occupies slightly more than one whorl. Two much smaller specimens (Pl. 7, figs 5, 6) have constrictions and mouth borders at 34 and 35 mm diameter preceded by $\frac{7}{8}$ and $\frac{13}{16}$ whorl of body chamber respectively and crowded final suture-lines in both cases.

Dagis (1968 : 51) referred specimens with the same whorl height/breadth ratio and the same rib-density as the Northamptonshire specimens to his new species *Z. latus*, which appears to be a synonym.

Zugodactylites thompsoni sp. nov.

Pl. 8, figs 1–4

HOLOTYPE. BM C.67529 from the Lower *Leda ovum* Beds at Heyford brickpit, Northamptonshire. Dimensions (mm) – 48·5: 13·6 (0·28), 16·4 (0·34), 24·3 (0·50).

PARATYPES. BM C.79468 from Hollowell, Northamptonshire; OUM J.20213 from Eydon, Northamptonshire; four specimens in Northampton Museum, three of them from Vigo brickpit and one from Greenough's brickpit, Northampton; one specimen from Vigo brickpit in the collections of the Northamptonshire Natural History Society and Field Club; BM C.68503 from bed xxxi at Ravenscar, Yorkshire.

DIAGNOSIS. A cadicone species of *Zugodactylites*, in which the whorl breadth exceeds the whorl height at all growth stages. The venter is wide and arched especially at sizes below 50 mm diameter. Ribs on the inner whorls are widely spaced, and each bears a moderate to large ventro-lateral tubercle, giving a coronate whorl shape.

DISTRIBUTION. Fibulatum Subzone. Lower and Middle *Leda ovum* Beds of Northamptonshire, and bed xxxi at Ravenscar, Yorkshire.

DESCRIPTION. The holotype (Pl. 8, fig. 1) and seven of the paratypes of this species come from the *Leda ovum* Beds of Northamptonshire. Four of the paratypes are in Beeby Thompson's collection: two were definitely found in the Lower *Leda ovum* Beds, while one came from the Middle *Leda ovum* Beds, so that its stratigraphical range is the same as that of *Z. braunianus*. The specimen figured in Pl. 8, fig. 4 is a complete adult with a mouth border at 47 mm diameter preceded by a strong constriction, and its body chamber is $\frac{7}{8}$ whorl long. The largest paratype (Pl. 8, fig. 3) is incomplete at its aperture at 65 mm diameter, but there are indications that it was an adult and about 75 mm in diameter when complete up to its mouth border. The holotype and most of the other Northamptonshire paratypes have adult, but incomplete, body chambers, and they would all have been between 45 and 70 mm in diameter when complete.

Plate 7 ×1

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone

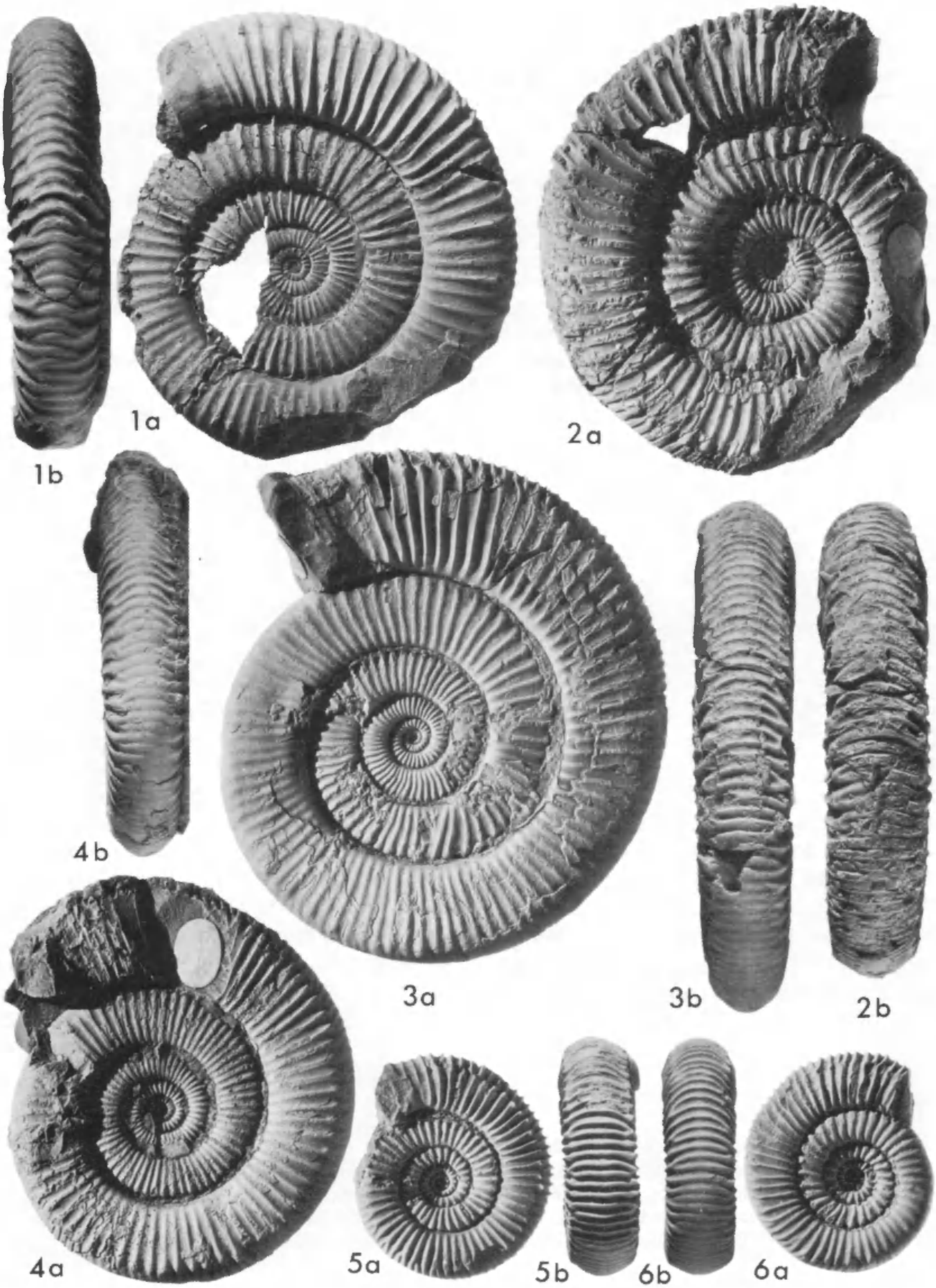
Fig. 1. Middle *Leda ovum* Beds, sewer trench, Abington Park, Northampton; Northampton Museum, B. Thompson Colln.

Figs 2, 4. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire. Fig. 2, BM C.78232. Fig. 4, BM C.78234.

Fig. 3. Bed 63, 0·30 m (1 ft) below top, Alum Shales, foreshore 0·8 km east of Whitby, Yorkshire; BM C.78205.

Zugodactylites rotundiventer Buckman, Fibulatum Subzone

Figs 5, 6. Lower *Leda ovum* Beds, Vigo brickpit, Northampton. Fig. 5, BM C.79467. Fig. 6, BM C.79466.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The single Yorkshire specimen (Pl. 8, fig. 2) is from bed xxxi at Ravenscar where *Z. braunianus* also occurs commonly. It is probably an adult but the final part of the body chamber and the mouth border are missing. The body chamber preserved is $\frac{3}{4}$ whorl long and ends at 61 mm diameter; when complete with a body chamber one whorl long, it would have been about 70 mm in diameter. The ribs are rather more widely spaced throughout than in the holotype, and the large ventrolateral tubercles on the inner whorls become considerably smaller on the outer whorl.

The main distinguishing feature from *Z. braunianus* and *Z. rotundiventer* is the whorl shape, which is always depressed, with the whorl breadth exceeding the height, but there is considerable variation depending on the growth stage reached (Fig. 4). Another difference is the development of moderate to large ventrolateral tubercles on whorls up to about 35 mm diameter, which diminish in size at larger diameters to become not much larger than those in the other two species. The ribs generally bifurcate at the ventrolateral tubercles except on the final part of the adult body chamber where some single ribs occur (Pl. 8, fig. 3).

This is the only species of *Zugodactylites* in England that has a much depressed whorl shape and large ventrolateral tubercles on the inner whorls. The only other species of *Zugodactylites* with such depressed whorls are those from north-eastern Siberia described by Dagis (1967 : 48; 1968 : 52) as two species of his new genus *Omolonoceras*. Both have whorls similar in shape to those of *Z. thompsoni*, but they differ in having considerably smaller ventrolateral tubercles.

Zugodactylites pseudobraunianus (Monestier 1931)

Pl. 9, figs 4–7

1931 *Coeloceras* (*Dactylioceras*) *pseudobraunianum* Monestier : 54; pl. 3, figs 2, 4, ? 6, 7; pl. 9, fig. 15.
1971 *Gabillytes larbusselensis* Guex : 234, 239; pl. 2, figs 2a–d; pl. 3, fig. 3.
1972 *Gabillytes larbusselensis* Guex; Guex : pl. 8, figs 1, 2.
1973*b* *Gabillytes larbusselensis* Guex; Guex : 551; pl. 3, figs 9, 12–14.

LECTOTYPE. Monestier had three syntypes and one doubtful example. The largest figured syntype (Monestier 1931 : pl. 3, fig. 4; pl. 9, fig. 15) is here designated lectotype; it is from Guilhomard, Aveyron.

DIAGNOSIS. A small species of *Zugodactylites*, in which complete adults are 22–30 mm in diameter at the mouth border. The venter of whorls up to 18–20 mm diameter has a blunt keel, which is progressively lost on the final half whorl of the adult body chamber. Ribs fine and dense, bifurcating at small ventrolateral tubercles, and generally similar to the ribs in *Z. braunianus* at similar sizes.

DISTRIBUTION. Fibulatum Subzone. Lower *Leda ovum* Beds in Northamptonshire.

DESCRIPTION. The collection consists of 10 almost complete specimens and fragments of 15 further specimens from the Lower *Leda ovum* Beds at Vigo brickpit, Northampton. The largest example (Pl. 9, fig. 5) is 25 mm in diameter at its broken aperture, and it has $\frac{11}{16}$ whorl of body chamber with the last suture-lines (which are not approximated) at 16·5 mm diameter. It appears

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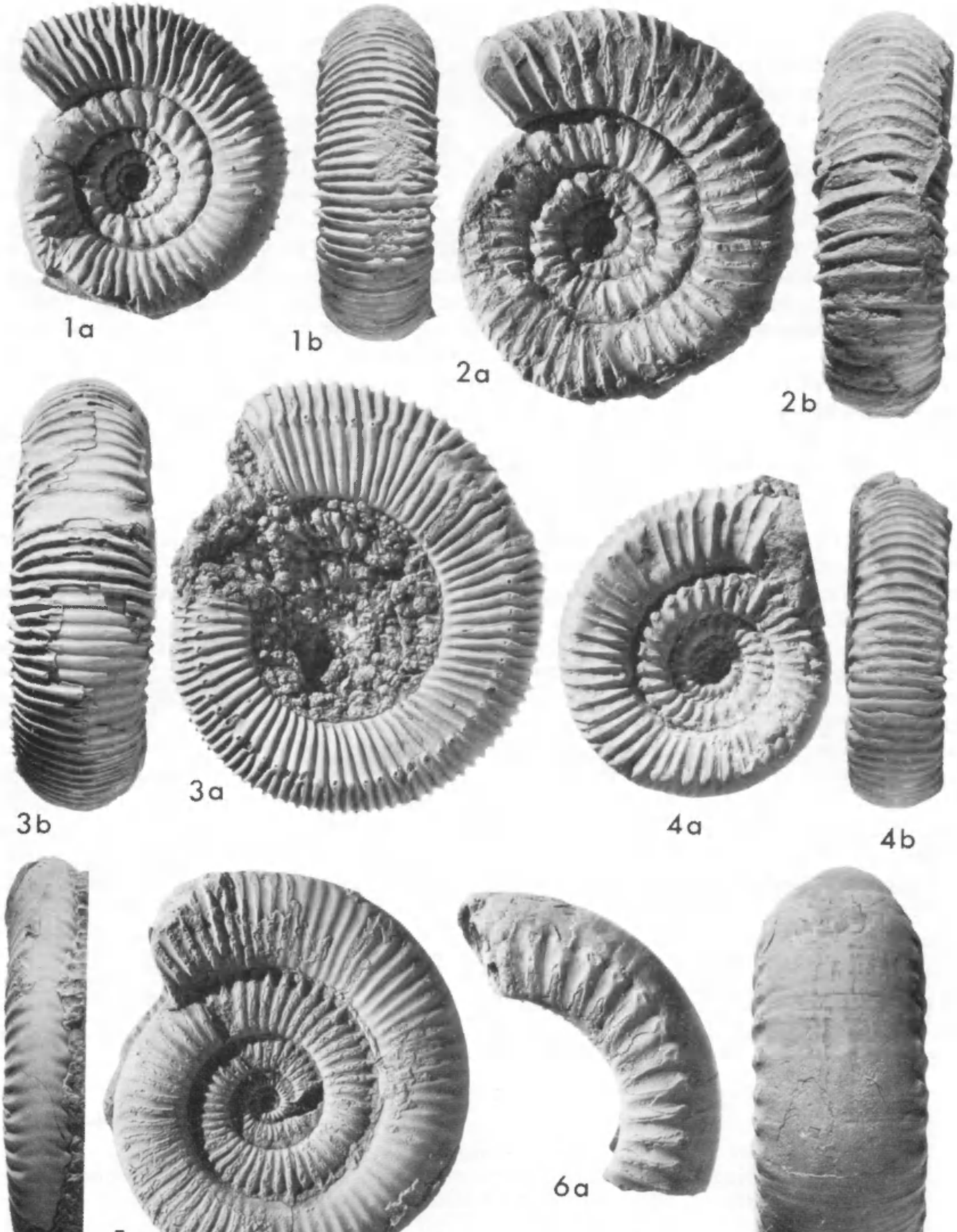
Plate 8 ×1

Zugodactylites thompsoni sp. nov., Fibulatum Subzone
Fig. 1. Lower *Leda ovum* Beds, Heyford, Northamptonshire; holotype, BM C.67529.
Fig. 2. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire; BM C.68503.
Fig. 3. Middle *Leda ovum* Beds, Eydon, Northamptonshire; OUM J.20213.
Fig. 4. *Leda ovum* Beds, Hollowell, 13 km north-west of Northampton; BM C.79468.

Zugodactylites braunianus (d'Orbigny), Fibulatum Subzone
Fig. 5. Bed xxxi, Alum Shales, foreshore below Ravenscar, Yorkshire; BM C.78246.

Catacoeloceras crassum (Young & Bird), Crassum Subzone
Fig. 6. [? Upper] *Leda ovum* Beds, [? Nevill Holt area, Medbourne], Leicestershire; GSM 22519, Lady Exeter Colln. (collected pre-1865) (see p. 246).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6b

to be nearly complete and would have had its adult mouth border before reaching 30 mm diameter. One of the fragments has septa up to 16 mm diameter, and in all the others septation ceases at smaller sizes. A rather smaller, but complete, adult is figured in Pl. 9, fig. 4. This is 22·2 mm in diameter at the mouth border, has $\frac{13}{16}$ whorl of body chamber, and final approximated suture-lines at 14 mm diameter; it also shows that the keeled venter becomes progressively rounded on the last half whorl of the adult body chamber. Two more specimens (Pl. 9, figs 6, 7) are nearly adult, but neither is quite complete; they both have $\frac{3}{4}$ whorl of body chamber and the blunt keel on the venter is beginning to be lost just before the aperture.

The angled or keeled venter on all whorls except the final half whorl of the adult body chamber is accentuated by the raised sharp secondary ribs in the middle of the venter. It is a unique feature of this species that is not found in whorls of *Z. braunianus* of the same size, where the ribs may sometimes be raised and sharp in the middle of the venter, but no prominently keeled venter is formed. The ribs are variable in strength and density; they are often fairly strong and widely spaced at 7–15 mm diameter, then become smaller and dense on the last half whorl of the body chamber. Small, sharp ventrolateral tubercles are usually formed on the final whorl, but they may be feeble or absent on the earlier whorls with ventral keels.

The type specimens of *Z. pseudobraunianus* were described by Monestier (1931 : 54) from the Bifrons Zone at Aveyron. The lectotype is the largest of them and has a maximum size of 21 mm diameter; it is similar in shape and ornament to the Northampton specimen of Pl. 9, fig. 7. Another Aveyron specimen was made the type of the new genus and species *Gabillytes larbusselensis* by Guex (1971 : 239). It does not differ from *Z. pseudobraunianus* in having stronger ribs, as claimed by Guex, because it is only 10·7 mm diameter (Guex's figure (1971 : pl. 2, fig. 2) is enlarged to approximately × 2·4); in fact it agrees very closely in rib strength and density with the lectotype of *Z. pseudobraunianus* at the same size. It also agrees closely with the penultimate whorls of several of the Northampton specimens. Guex's specimen appears to be a juvenile, and not an adult as he claims, because its strongly ribbed and keeled final half whorl is characteristic of the penultimate whorl of the Northampton specimens, which become adult at 22–30 mm diameter after further growth of about one whorl on which the ribs become more dense and the keel is progressively lost. The notion also put forward by Guex (1971 : 235) that this species and the genus *Gabillytes* are microconchs, for which the corresponding macroconchs are represented by *Z. braunianus*, is not thought to be correct. *Z. pseudobraunianus* has a keeled venter that is mainly characteristic of the last septate whorl. Such a keel is not found in *Z. braunianus*, and it seems difficult to substantiate a claim that a pair of forms are dimorphic, when there are morphological differences at similar growth stages that do not include the adult body chambers of either form.

Genus *PORPOCERAS* Buckman 1911

TYPE SPECIES. *Ammonites vortex* Simpson 1855.

SYNONYM. *Telodactylites* Pinna & Levi-Setti 1971 (type species: *Ammonites desplacei* d'Orbigny 1844).

Plate 9 **× 1 (Figs 4–7, × 1·5)**

Porpoceras verticosum Buckman, Fibulatum Subzone

Fig. 1. 1–2 m below top of Bifrons Zone Clays below Northampton Sand ironstone, ironstone quarry (SK 878309), Harlaxton, 6 km south-west of Grantham, Lincolnshire; BM C.69564.

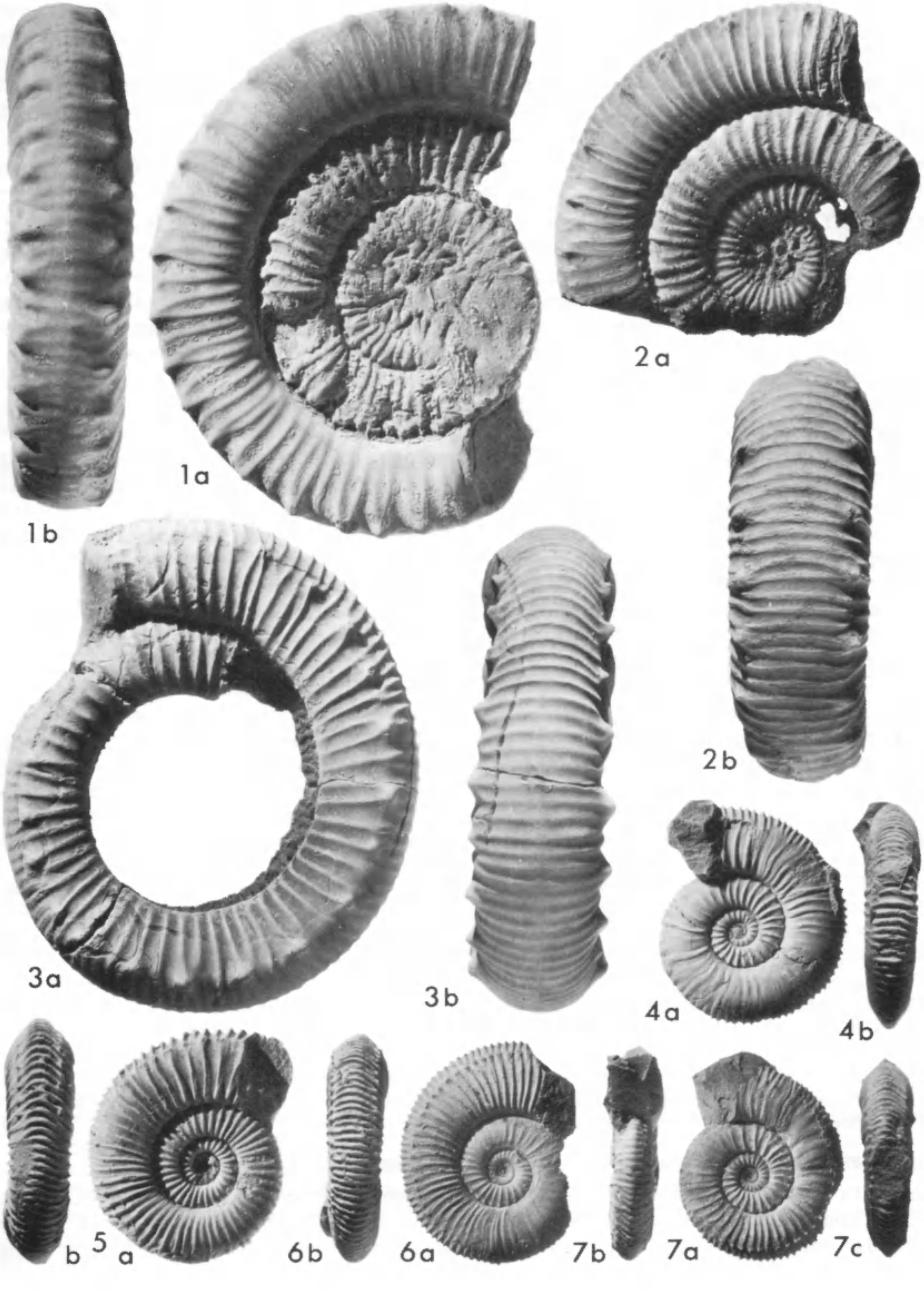
Porpoceras vortex (Simpson), Fibulatum Subzone

Fig. 2. Same horizon and locality as Fig. 1; BM C.69565.

Fig. 3. Upper *Leda ovum* Beds, Corby, Northamptonshire; Northampton Museum, B. Thompson Colln.

Zugodactylites pseudobraunianus (Monestier), Fibulatum Subzone

Figs 4–7. Lower *Leda ovum* Beds, Vigo brickpit, Northampton; all × 1·5. Fig. 4, BM C.79465. Fig. 5, BM C.67531. Fig. 6, BM C.79463. Fig. 7, BM C.79464.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4b
b
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a
6b
6a
7b
7a
7c

DIAGNOSIS. Whorl section varies between square and depressed. Ventrolateral tubercles occur on every second, third or fourth rib. The primary ribs on the side of the whorl are sometimes looped in pairs to tubercles, but this character is not constant as in *Peronoceras*. One to three non-tuberculate ribs occur between each tuberculate rib. Ribs on the venter are continuations of the non-tuberculate primary ribs, or issue in pairs from the ventrolateral tubercles, or a few are intercalated.

DISTRIBUTION. Fibulatum Subzone, upper part. Northamptonshire: Upper *Leda ovum* Beds. Yorkshire: Whitby bed 72 (lower 1·5 m), Ravenscar beds xlii and xliii.

REMARKS. Three British species are known, *P. vortex* (Simpson), *P. verticosum* Buckman (1914 : pl. 91) and *P. vorticellum* (Simpson) (Buckman 1913 : pl. 90), which occur at a single horizon in Yorkshire, Lincolnshire and Northamptonshire. This is near the top of the Fibulatum Subzone, well above the range of *Peronoceras* and *Zugodactylites*, and below the lowest *Catacoeloceras* at the base of the Crassum Subzone. The three species are commonest at Ravenscar, Yorkshire, in beds xlii and xliii (Howarth 1962*b* : 400). From a study of the considerable numbers of specimens present it seems that the three species are closely related, all having the special fibulation and tuberculation characters of *Porpoceras* as distinct from *Peronoceras*. They differ from each other mainly in the much-depressed whorls of *P. vortex*, the less depressed, almost square whorl section of *P. verticosum*, and the closely similar whorls, but denser, weaker ribs and weaker tubercles, of *P. vorticellum*. If a much larger collection were available with more complete adults it might be possible to suggest that all three were variants of a single species. Pinna & Levi-Setti's (1971 : 107, 121) separation of *P. verticosum* and *P. vorticellum* from *P. vortex*, by referring the two former to *Nodicoeloceras*, is not correct. Species of *Peronoceras* with square or depressed whorls, such as *P. subarmatum* and *P. perarmatum*, are distinguished by having much more consistent fibulation on at least their inner whorls, where the ventrolateral tubercles are larger and developed as spines when the shell is complete. The alternating nature of the tubercles and single ribs in *Porpoceras* and the varying amount of fibulation make the genus distinctive.

In addition to the two Northamptonshire examples of *P. vortex* from the Upper *Leda ovum* Beds that are described below, several specimens are known from the Grantham area. *P. vortex* and *P. verticosum* were collected by Trueman (1918 : 107) from his bed 8, about 6 m below the top of the Lias, immediately south of Grantham. Three *P. vortex* and one *P. verticosum* were collected many years ago by the Institute of Geological Sciences at Grantham (GSM 22515–18). More recently two fine specimens (Pl. 9, figs 1, 2) have been found 1–2 m below the top of the Lias in ironstone quarries at Harlaxton (SK 878309), 6 km SW of Grantham.

Porpoceras vortex (Simpson 1855)

Pl. 9, figs 2, 3

1855 *Ammonites vortex* Simpson : 60.
1905 *Coeloceras* (*Peronoceras*) *desplacei* (d'Orbigny); Joly : 10; pl. 2, figs 1–5.
1911 *Porpoceras vortex* (Simpson) Buckman : pls 29A, 29B.
? 1966 *Peronoceras vortex* (Simpson) Pinna : 118; pl. 6, figs 16, 18.
? 1966 *Peronoceras vortex* (Simpson); Fischer : 42; pl. 2, fig. 5.
1971 *Peronoceras vortex* (Simpson); Pinna & Levi-Setti : 121; pl. 11, fig. 7; pl. 12, fig. 9.
1972 *Porpoceras vortex* (Simpson); Guex : pl. 8, fig. 16.

HOLOTYPE. Whitby Museum no. 153a, figured by Buckman (1911 : pl. 29A).

DESCRIPTION. There are two examples of this species from the Upper *Leda ovum* Beds at Corby in Beeby Thompson's collection. The better-preserved specimen (Pl. 9, fig. 3) consists of slightly more than one whorl which is a complete adult body chamber with a marked constriction at the mouth border at 76 mm diameter. Almost all the whorl is crushed laterally so that the whorl breadth appears to be too small for this species, but there is a short length of uncrushed whorl just after the final suture-line, which has a whorl height of 13·0 mm and a whorl breadth of 21·0 mm at about 45 mm diameter. Comparing these dimensions with those of the type specimens of the three Yorkshire species (Buckman 1914 : 91*b*), it is clear that the specimen can only belong to

P. vortex. The second Corby specimen consists of half a whorl of about 70 mm maximum diameter and is not well preserved. Both specimens have a ventrolateral tubercle on approximately every third rib and some of the primary ribs are looped in pairs to the tubercles.

A specimen from an ironstone quarry at Harlaxton, Lincolnshire, is figured for comparison (Pl. 9, fig. 2). It has final suture-lines at about 47 mm diameter, and the aperture after nearly a whorl more is close to the adult mouth border at about 70 mm diameter. *P. verticosum*, which also occurs at Harlaxton (Pl. 9, fig. 1) and other localities near Grantham, differs in its square whorl section. *P. vortex* is common in beds xlii and xliii at Ravenscar, Yorkshire, where complete adults range between 70 and 110 mm maximum diameter.

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