

SPECIAL PAPERS IN PALAEOLOGY · 53

**Mid-Dinantian ammonoids
from the Craven Basin,
north-west England**



THE PALAEOLOGICAL ASSOCIATION

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MID-DINANTIAN AMMONOIDS FROM
THE CRAVEN BASIN,
NORTH-WEST ENGLAND

BY
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with 8 plates and 51 text-figures

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ABSTRACT. A major new ammonoid-bearing sequence is described from the Worston Shale Group, which spans the late Tournaisian (early Chadian) to mid-Viséan (early Asbian) interval in the Craven Basin of north-west England. The faunas are referable to the *Fascipericyclus-Ammonellipsites* (FA), *Bollandites-Bollandoceras* (BB) and lower part of the *Beyrichoceras* Zone (B1) ammonoid zones. Particularly significant are the early Viséan assemblages from the FA Zone, which are the most diverse known, apart from faunas described previously from the northern Urals of the former Soviet Union. The described assemblages comprise: *Ammonellipsites clitheroensis* sp. nov., *Beyrichoceras* aff. *obtusum*, *Beyrichoceratoides inflatus* sp. nov., *B.* sp. aff. *komiorum*, *B.* sp. 1, *B.* sp. 2, *Bollandites varians* sp. nov., *Bo.*? sp., *Bollandoceras hodderense* Bol. *micronotum*, Bol. sp. 1, Bol. sp. 2, *Dimorphoceras leagramense* sp. nov., *Dzhaprakoceras bellmanense* sp. nov., *D. catena* sp. nov., *D. deflexum*, *D.* cf. *djaprakense*, *D. flexum* sp. nov., *D. hispanicum*, *D. levis* sp. nov., *D. paracatena* sp. nov., *D. subglobosum*, *D. undulatum* sp. nov., *D. westheadi* sp. nov., *Economismoceras planum* sp. nov., *Helicocyclus divergens* sp. nov., *Merocanites* cf. *applanatus*, *M. quadrilobus* sp. nov., *Michiganites* sp., *Nomismoceras rotiforme*, *Parahammatocyclus chaigleyensis* gen. et sp. nov. and *Rotopericyclus postremus* sp. nov. Existing suprageneric classification is modified; the new superfamily Girtyocerataceae is erected together with two new subfamilies: the Ammonellipsitinae and Pericyclinae. Several genera are reclassified, including *Beyrichoceras*, transferred from the Anthracoceratidae to the Girtyoceratidae, and *Bollandites*, transferred from the Muensteroceratidae to the Pericyclinae.

THE mid-Dinantian ammonoid assemblages described in this account, from the Worston Shale Group in the Craven Basin of north-west England, are the most prolific known, apart from those described by Kusina (1973, 1974, 1980, 1983) from the northern Urals in that part of the Commonwealth of Independent States (CIS, formerly the USSR) now known as the Russian Federation. They are also the most accurately dated mid-Dinantian assemblages known, being well constrained in terms of both foraminiferal and conodont biostratigraphies (Riley 1990b).

Dinantian ammonoids were first described from the Craven Basin of north-west England in the classic publication of Phillips (1836). Subsequent publications include those of Bisat (1924, 1934, 1950, 1952) and Moore (1930, 1936, 1939, 1946, 1950, 1952); both authors dealt with late Viséan faunas.

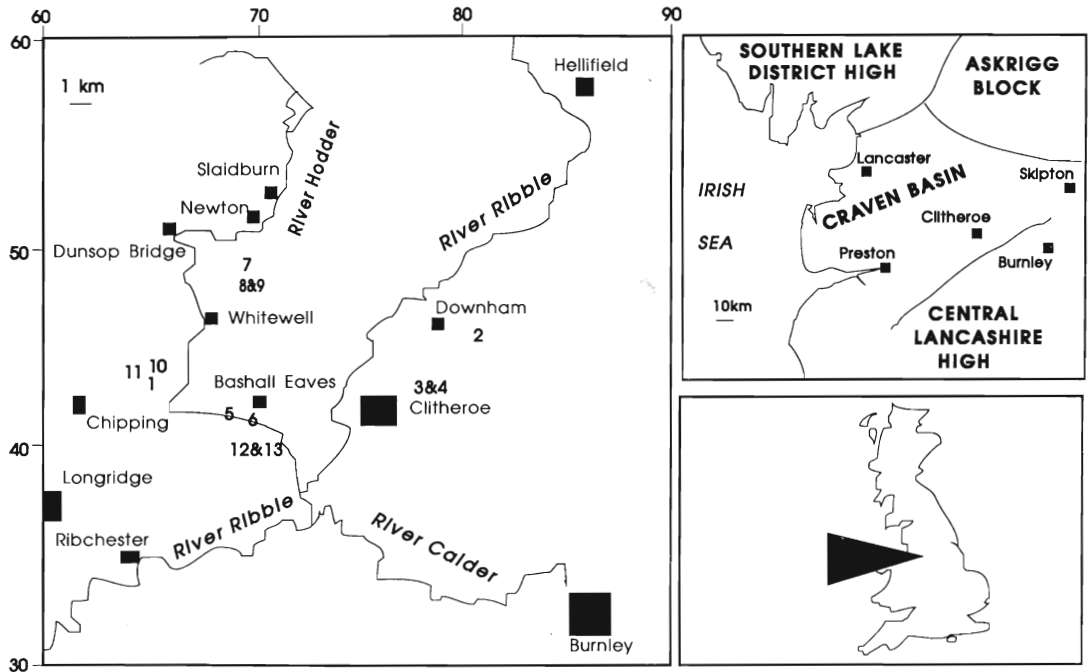
Mid-Dinantian assemblages were first referred to in Earp *et al.* (1961) but these were not described in detail and were only referred to a few species; the only described material was *Merocanites similis* (Crick, 1895), from the late Tournaisian, Chatburn Limestone Group. Further brief reference to mid-Dinantian assemblages from this district was made by Riley (1990a, 1990b, 1991).

STRATIGRAPHY OF THE WORSTON SHALE GROUP

This group, with its component formations and members, has been defined and described recently by Riley (1990b). The location and lithostratigraphy is summarized in Text-figures 1–2. The Dinantian sequence in the Craven Basin is very thick (over 6 km) and accumulated in an actively extending asymmetrical rift basin, trending east-north-east to west-south-west. Marine sedimentation in the early Dinantian began on a carbonate ramp which subsequently fractured and rifted into a series of intra-basinal highs and lows. The rift basin is bounded by the Askrigg Block and Southern Lake District High to the north, and the Central Lancashire High to the south. Because the base of the sequence is unexposed, the age and nature of the oldest Dinantian is unknown; however, seismic evidence (Aitkenhead *et al.* 1992) suggests that around 3 km are concealed.

The oldest strata exposed underlie the Worston Shale Group and comprise the Chatburn Limestone Group, of late Tournaisian age. These strata are developed in a shallow marine, clastic-influenced, carbonate ramp facies. About 1.2 km of Chatburn Limestone has been proved from outcrop and boreholes. At the basin margin there is lateral passage into red beds and evaporites (Stockdale Farm Formation).

The onset of deposition of the Worston Shale Group (Clitheroe Limestone Formation) coincided with the progressive steepening of the ramp. A variable and complex stratigraphy resulted, reflected

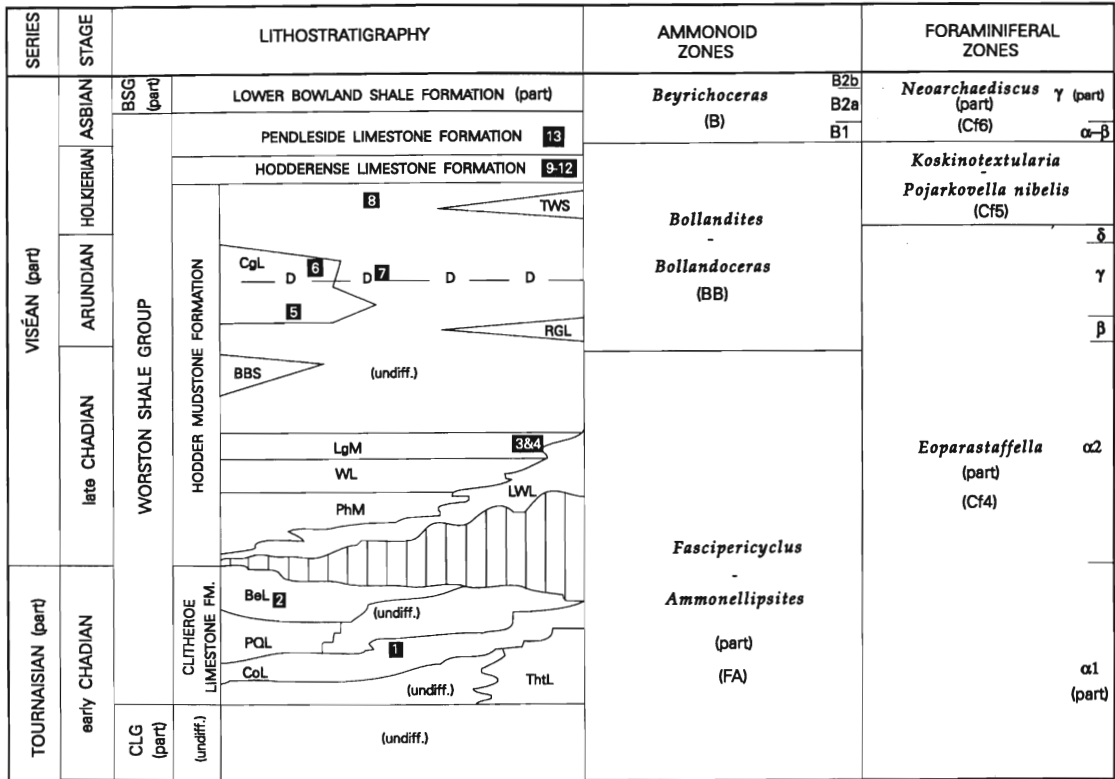


TEXT-FIG. 1. Sketch map of ammonoid localities; for explanation of locality numbers see text.

initially by the development of deeper water Waulsortian limestones and associated facies (Coplw and Bellman Limestone members) in the late Tournaisian. These biohermal limestones, of possible microbial origin (Lees and Miller 1985), display remarkable lateral thickness changes, ranging from a few metres to *c.* 400 m.

By the earliest Viséan (late Chadian) the steepened ramp had fractured, by tectonic rifting, into a series of intra-basinal highs and lows, resulting in a complete reorganization of depositional style. The base of the Viséan (Hodder Mudstone Formation) is therefore associated with widespread submarine erosion and unconformity, marking the switch from a carbonate ramp to a hemipelagic depositional regime. Boulder beds, derived from the underlying formation, accumulated locally, as did thin Waulsortian limestones (Limekiln Wood Limestone Member). Carbonate production within the basin soon ceased and the background dysaerobic accumulation of terrigenous mudstone was interrupted by repeated limestone turbidite influx (Whitemore, Rain Gill, Embsay and Chaigley limestone members) until early Holverian times. These turbidites were derived from the surrounding carbonate ramps and platforms which now developed on the newly submerged Askrigg Block, Southern Lake District High and Central Lancashire High. Minor sandstone turbidite influx also occurred (Buckbanks and Twiston sandstone members) as the surrounding carbonate source areas were by-passed during lowstands. The Hodder Mudstone Formation varies in thickness from less than 100 m up to 900 m, depending on the relief of the basal surface and the relative proportion of turbidites to hemipelagic mudstones.

During the Holverian the basin became progressively starved of sediment, culminating in the widespread deposition of pelagic cephalopod limestones (Hodderense Limestone Formation) of 4–15 m thickness. By early Asbian times limestone turbidite deposition resumed; the Pendleside Limestone Formation has a local thickness of up to 300 m. These turbidites represent the youngest Worston Shale Group stata. By late Asbian times the basin changed from a predominantly dysoxic environment to a euxinic one, represented by the black shales of the overlying Bowland Shale Group. This change is thought to have resulted from stratification of the basin water column as the



TEXT-FIG. 2. Stratigraphical distribution of ammonoids in the Worston Shale Group around Clitheroe; for explanation of locality numbers (in the lithostratigraphy column) see text; lithostratigraphical abbreviations as follows: BBS, Buckbanks Sandstone Member; BeL, Bellman Limestone Member; BSG, Bowland Shale Group; CgL, Chaigley Limestone Member; CLG, Chatburn Limestone Group; CoL, Coplow Limestone Member; LgM, Leagram Mudstone Member; LWL, Limekiln Wood Limestone Member; PhM, Phynis Mudstone Member; PQL, Peach Quarry Limestone Member; RGL, Rain Gill Limestone Member; TWS, Twiston Sandstone Member; ThtL, Thornton Limestone Member; WL, Whitmore Limestone Member. Vertical hatching denotes unconformity; (undiff.) = undifferentiated.

surrounding carbonate platforms became fringed by bioherms, interrupting circulation between the basin and the platform interiors.

AMMONOID ZONATION

Mid-Dinantian ammonoid zonation has recently been revised by Riley (1990a, 1991) and is summarized in Text-figure 3. Riley (1993) has also reviewed Dinantian classification in the British Isles. Problems with the definition and correlation of the Chadian Stage, which has its stratotype in the Craven Basin, have been investigated in detail by Riley (1995). Riley (1990a, 1991) redefined the *Fascipericyclus-Ammonellipsites* (FA) and *Beyrichoceras* (B) ammonoid zones; and proposed a new intervening zone, the *Bollandites-Bollandoceras* Zone. These zones are represented on all continents except Antarctica and South America. A range chart showing the distribution of ammonoid genera through the mid-Dinantian is given in Text-figure 3. As with late Viséan and Namurian ammonoid zones, international correlation is best achieved at the generic level. Few species are distributed internationally, and the sporadic nature of individual ammonoid occurrences in the mid-Dinantian renders the absolute stratigraphical range of individual species difficult to assess.

SERIES FORAM. ZONES GENERA	TOURNAISIAN (part)		VISÉAN (part)				
	Cf3 (part)	Cf4 α 1	Cf4 α 2	Cf4 β - δ	Cf5	Cf6 α - β	Cf6 γ
<i>Protocanites</i>	←	-					
<i>Pericyclus</i>	←						
<i>Rotopericyclus</i>	←	—————					
<i>Muensteroceras</i>	←	—————					
<i>Eurites</i>	←	—————					
<i>Muensteroceratoides</i>	←	—————					
<i>Winchelloceras</i>	←	—————					
<i>Dzheprakoceras</i>	←	—————			---		
<i>Irinoceras</i>	←	—————					→
<i>Merocanites</i>		—————					
<i>Fascipericyclus</i>		-	—————				
<i>Neopericyclus</i>		---	—————				
<i>Ammonellipsites</i>		---	—————				
<i>Beyrichoceratoides</i>		—————					→
<i>Polaricyclus</i>		———					
<i>Stenocyclus</i>		---	—————				
<i>Quasintoceras</i>			-	—————			
<i>Aquilonites</i>			-	———			
<i>Intoceras</i>			-	———			
<i>Michiganites</i>			—————				→
<i>Eonomismoceras</i>			—————				
<i>Helicocyclus</i>			—————				
<i>Kozhimites</i>			—————				
<i>Rhiphaeocyclus</i>			—————				
<i>Hammatocyclus</i>			—————				
<i>Bollandites</i>			—————				→
<i>Bollandoceras</i>			—————				→
<i>Simmonoceras</i>				—————			
<i>Parahammatocyclus</i>				—————			
<i>Oxintoceras</i>				———			
<i>Dimorphoceras</i>					—————		→
<i>Nomismoceras</i>					—————		→
<i>Beyrichoceras</i>					—————		→
<i>Entogonites</i>						---	
<i>Girtyoceras</i>							→
<i>Goniatites</i>							→
<i>Prolecanites</i>							→
<i>Metadimorphoceras</i>							→
<i>Pronorites</i>							→
<i>Praedarellites</i>							→
<i>Arnsbergites</i>							→
AMMONOID ZONES	Pe	FA		BB		B	Go

Fascipericyclus-*Ammonellipsites* (FA) Zone

This is an assemblage zone and is defined at the first entry of *Merocanites*. It overlies the *Pericyclus* Zone. The base lies within the late Tournaisian; however, its precise position in relation to conodont biostratigraphy remains to be proven. *Fascipericyclus* enters low in the zone, followed by *Ammonellipsites* in the latest Tournaisian. The zone extends across the Tournaisian-Viséan boundary. *Fascipericyclus* becomes extinct in the early Viséan prior to the entry of *Helicocylus*, *Michiganites* and *Eonomismoceras* in the uppermost part of the zone. The top of the zone corresponds closely with the base of the Arundian Stage, but still lies within the late Chadian. It is marked by the extinction of *Ammonellipsites* and *Helicocylus*.

Bollandites-Bollandoceras (BB) Zone

The base of this assemblage zone directly overlies the FA Zone and coincides with the first entry of *Bollandites*. Near the base, *Bollandoceras* enters and these two genera persist into the overlying *Beyrichoceras* Zone. *Parahammatoicyclus* gen. nov. occurs in the middle part, with *Dimorphoceras* and *Nomismoceras* entering in the upper part of the zone. The top of the zone lies in the latest Holkerian and corresponds with the base of the overlying *Beyrichoceras* Zone.

Beyrichoceras (B) Zone

This is a genus zone based on the total range of *Beyrichoceras*. The zone is subdivided into three subzones (Riley 1990a), termed successively the *Entogonites* (B1), *Goniatites hudsoni* (B2a) and *Goniatites globostriatus* (B2b) subzones. The B2a and B2b subzones lie within the late Asbian. The *Beyrichoceras* Zone is succeeded directly by the *Goniatites* Zone.

AMMONOID DISTRIBUTION

This section summarizes the stratigraphical distribution of ammonoids within the local succession. The areal distribution of localities is illustrated in Text-figure 1, and the stratigraphical occurrence of the assemblages is summarized in Text-figure 2. Where relevant, BGS specimen numbers are quoted in parentheses. Locality numbers are listed in the locality index at the end of this section.

Unlike the late Viséan and Namurian ammonoids in northern England, Worston Shale Group assemblages are not restricted to discrete marine black shale bands, known as marine bands, but occur in a variety of lithologies in a totally marine sequence. Ammonoids are rare in the Clitheroe Limestone Formation and are always associated with Waulsortian limestones. Ammonoids become abundant at the base of the Hodder Mudstone Formation, thus complementing the change from a carbonate ramp to the dysoxic hemipelagic environment associated with this formation. Despite their abundance, material preserved well enough for identification is sparse and limited to only a few localities where early diagenesis favoured uncrushed preservation. Such occurrences are associated with early pyrite replacement, and with carbonate-rich environments such as in boulder beds and limestone turbidites. The most widespread horizon where uncrushed faunas abound is in the cephalopod limestones represented by the succeeding Hodderense Limestone Formation. The following account documents the occurrence of identifiable faunas in the Worston Shale Group.

Clitheroe Limestone Formation

The ammonoid assemblages in this formation lie in the middle part of the FA Zone, the early part of the zone being indicated in the upper part of the underlying Chatburn Limestone Group by the

TEXT-FIG. 3. Composite range chart for mid-Dinantian ammonoid genera adapted from Riley (1991). The genera *Atratoceras*, *Terektytes* and *Torulites* are omitted since their stratigraphical ranges are poorly known. Abbreviations; *Gon.* = *Goniatites* Zone, *Peri.* = *Pericyclus* Zone. Arrows indicate extension of ranges; broken horizontal lines denote uncertainty.

occurrence of *Merocanites similis*. Several genera have not yet been recorded, including *Ammonellipsites*, *Fascipericyclus* and *Merocanites*. Their absence is attributed to the rarity of ammonoids in this formation.

Coplow Limestone Member. This is the oldest fauna known in the western part of the Craven Basin. Archival material in the BGS collection includes a badly corroded example of *Dzhaprakoceras* sp. (BGS 86246) from Coplow Quarry, Clitheroe and a fragmentary body chamber of a gerontic *Rotopericyclus* cf. *rotuliformis* (BGS W 551) collected during the last century from the River Hodder at Knowlemere, near Newton. *Dzhaprakoceras* cf. *djaprakense* was recovered during the present study from Leagram Knott (locality 1) near Chipping.

Bellman Limestone Member. The strata between the Coplow and Bellman Limestone members have not yielded ammonoids. Ammonoids were noted from Sykes Knoll (locality 2), near Downham (Ramsbottom in Earp *et al.* 1961); the revised fauna comprises *Beyrichoceratoides* aff. *komiorum*, *Dzhaprakoceras hispanicum* and *D. subglobosum*. *Muensteroceratoides* cf. *aksuensis* has been found from The Ridge (SD 7690 4330), near Worston, and at Whitemore Knott (SD 6442 4755), near Whitewell, by A. Cronshaw (Keele University, pers. comm. 1981) and J. Saville (Airton, pers. comm. 1983), respectively.

Hodder Mudstone Formation

This formation encompasses the upper part of the FA Zone through to the upper part of the BB Zone. Crushed merocanitids and muensteroceratids *sensu lato* are common throughout the formation; the following account is restricted to identifiable faunas.

Phynis Mudstone Member. Ammonoids are poorly preserved in this member, but include a specimen of *Fascipericyclus* sp. from a temporary exposure (1977) at Downham Mill (SD 7895 4530) collected by R. F. Grayson, P. W. Phillips and the late S. Westhead (pers. comm. 1977).

Whitemore Limestone Member. As in the underlying Phynis Mudstone Member ammonoids are common but poorly preserved. Faunas have been recovered from several localities including Barn Gill (SD 7210 5355), Slaidburn and an unnamed stream (SD 6480 4793) near Whitemore Knott. *Ammonellipsites* sp. ex gr. *kochi* is encountered for the first time and is accompanied by indeterminate muensteroceratids, *Merocanites* sp. and *Eonomismoceras* sp.

Limekiln Wood Limestone Member. Ramsbottom in Earp *et al.* (1961, p. 179) recorded *Muensteroceras* cf. *eurymphalum* from Bellman Quarry, near Clitheroe; this specimen (BGS 86247) is too corroded for specific identification, but may possibly represent a species of *Eurites* or *Muensteroceratoides*. *Ammonellipsites* cf. *clitheroensis* sp. nov., large fragments of *Dzhaprakoceras* sp., *D. deflexum* and *Merocanites* sp. occur in the adjacent Salthill Quarry (locality 3a).

Leagram Mudstone Member. A temporary exposure (1978–79) of a boulder bed at the base of the Leagram Mudstones at Bellman Quarry (locality 4a) yielded the following ammonoids: *Ammonellipsites clitheroensis* sp. nov., *Beyrichoceratoides inflatus* sp. nov., *Dzhaprakoceras bellmanense* sp. nov., *D. deflexum*, *D. levis* sp. nov., *D. paracatena* sp. nov., *D. undulatum* sp. nov., *D. westheadi* sp. nov. *Merocanites* sp. and *Rotopericyclus postremus* sp. nov. The overlying 3 m of mudstone at Bellman and Salthill quarries (localities 4b and 3b respectively) yielded the following components, in addition to those above; *Dzhaprakoceras catena* sp. nov., *Eonomismoceras planum* sp. nov., *Helicocyclus divergens* sp. nov., and *Michiganites* sp. Higher beds in the Leagram Mudstone are often crowded with poorly preserved merocanitids ('*compressus* beds' of Parkinson 1926) and indeterminate muensteroceratids. Poorly preserved specimens of *Ammonellipsites* sp. ex gr. *kochi* have been recovered from the Leagram Mudstones in Standen Brook, at Primrose Bridge (SD 7390 4070) near Clitheroe, by R. F. Grayson (pers. comm. 1977), and several specimens, possibly of *Helicocyclus* sp. have been recorded from Worston Brook (Parkinson 1926, p. 211; later

identified as *Pericyclus djaprakensis* and *P. trapezoidalis* by Ramsbottom in Earp *et al.* 1961, p. 178). Crushed, poorly preserved *Helicocyclus* sp. occur also in a stream section (SD 6945 4835) at Ashnott, 25 m below the first entry of primitive archaetid foraminiferans; this section is thought to overlie directly the Leagram Mudstone Member.

Chaigley Limestone Member and equivalent strata. Well preserved ammonoid faunas have been recovered from two levels at approximately 30 m and 100 m above the base of the Chaigley Limestone Member. Both these occurrences coincide with Arundian foraminiferal assemblages dominated by *Uralodiscus* spp. The lower fauna, from an exposure in the River Hodder at Papermill Wood (locality 5), consists of *Parahammatocyclus chaigleyensis* sp. nov. and *Dzhaprakoceras hispanicum*. The higher fauna, from an exposure in the River Hodder near Buck Hill (locality 6), contains *Parahammatocyclus chaigleyensis* sp. nov. and *Bollandoceras* sp. 2., *Beyrichoceratoides* sp. 2 and *Bollandites?* sp. At Bonstone Brook (locality 7), *P. chaigleyensis* sp. nov. occurs also in the Dunbarella Bed. In Leagram Brook (SD 6333 4512), near Chipping, indeterminate nomismoceratids (with arched venters) occur some 5 m below the Dunbarella Bed. In the upper part of the Hodder Mudstone Formation, identifiable faunas have been recovered from Crag Beck at Ashnott (locality 8), and include *Beyrichoceratoides* sp. 1, *Bollandoceras* sp. 1 and *Merocanites* sp. At Lower Hodder Bridge (SD 7045 3920), near Stonyhurst, crushed *Bollandoceras* sp. and *Dimorphoceras* sp. are scattered through the upper 50 m of the formation.

Hodderense Limestone Formation

This formation lies in the upper part of the BB Zone. Ammonoids are abundant and widespread; the most diverse fauna so far recovered has come from Leagram Brook (locality 11), near Chipping, and includes *Bollandites varians* sp. nov., *Bollandoceras hodderense*, *Dimorphoceras leagramense* sp. nov., *Nomismoceras rotiforme* and *Merocanites applanatus*.

Pendleside Limestone Formation

Much of this formation corresponds to the B1 Subzone, with only the basal part lying within the underlying BB Zone. The only identifiable fauna comes from the Mearley Limestone Member at locality 13; it includes poorly preserved *Merocanites* sp., together with *Bollandoceras micronotum* and *Nomismoceras rotiforme*, but the most significant component is the first *Beyrichoceras*, *B.* aff. *obtusum*.

LOCALITY INDEX

Clitheroe Limestone Formation

Locality 1. Leagram Knott, north-west corner of quarry (SD 6387 4473), 2.2 km north-east of Chipping Parish Church; coarse crinoidal grainstones in the upper part of the Coplow Limestone Member; early Chadian.
 Locality 2. Sykes Knoll, Quarry (SD 7993 4417), 0.7 km south-east of Hey House Farm, Downham; coarse packstones near the base of the Bellman Limestone Member; early Chadian.

Hodder Mudstone Formation

Locality 3. Salthill Quarry, south side (SD 7560 4254), 1.6 km east-north-east of Clitheroe Castle. Locality 3a is in coarse crinoidal packstones and mudstones in the upper 3 m of the Limekiln Wood Limestone Member. Locality 3b is in pyritic mudstones in the lower 4 m of the Leagram Mudstone Member; late Chadian.
 Locality 4. Bellman Quarry, south side, temporary exposure (1979) in a sewer trench (SD 7585 4260), 1.9 km east-north-east of Clitheroe Castle. Locality 4a is a boulder bed at the base of the Leagram Mudstone Member and locality 4b is in the overlying 3 m of these mudstones; late Chadian.
 Locality 5. River Hodder, east bank (SD 6803 4310), 1.5 km west-south-west of Bashall Eaves; coarse bioclastic packstone (limestone turbidite) about 30 m above the base of the Chaigley Limestone Member; Arundian.

Locality 6. River Hodder, north bank (SD 6828 4275), 1.9 km south-west of Bashall Eaves; coarse erosive-based bioclastic packstone (limestone turbidite) about 100 m above the base of the Chaigley Limestone Member; Arundian.

Locality 7. Ashnott, Bonstone Brook, north bank (SD 6917 4876), 1.7 km south-west of Newton; nodules 2–3 m below the Dunbarella Bed; Arundian.

Locality 8. Ashnott, Crag Beck, west bank (SD 6912 4862), 1.95 km south-west of Newton; wackestone band in the upper 100 m of the Hodder Mudstone Formation; Holkerian.

Hodderense Limestone Formation

Locality 9. Ashnott, Crag Beck, both banks (SD 6896 4817), 2.4 km south-west of Newton; in the upper 3 m of the formation; Holkerian.

Locality 10. Leagram, Hell Clough, east bank (SD 6358 4630), 3.25 km north-north-east of Chipping Parish Church; wackestones and mudstones in lowest 2 m of the section; Holkerian.

Locality 11. Leagram Brook, both banks (SD 6322 4515), 2.05 km north-north-east of Chipping Parish Church; collections made throughout the section; Holkerian.

Locality 12. River Hodder, Great Falls, both banks (SD 7035 3999), 4.2 km south-west of Clitheroe Castle; collections made throughout the section; Holkerian.

Pendleside Limestone Formation

Locality 13. River Hodder, Great Falls, east bank, 50 m upstream from locality 12; coarse packstone in the basal leaf of the Mearley Limestone Member; ?Holkerian or earliest Asbian.

SYSTEMATIC PALAEOLOGY

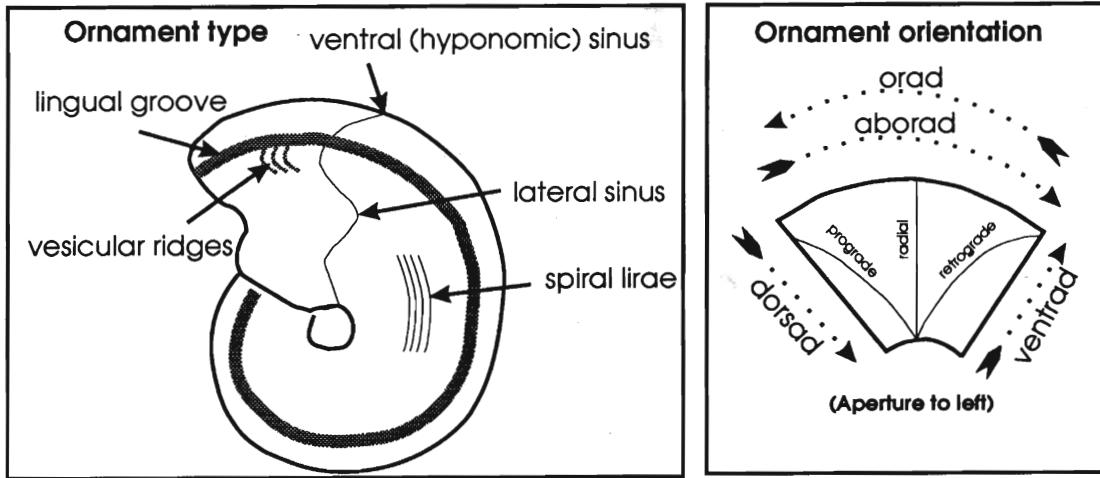
Unless stated otherwise all material is held with the British Geological Survey, Keyworth. Repositories of specimens referred to below are abbreviated as follows; BMNH, The Natural History Museum, London; PIN, Russian Academy of Sciences, Palaeontological Institute, Moscow, Russia; TSNIGR, All Russian Geological Research Institute, St Petersburg, Russia. Dimensions are given in millimetres. Dimensions marked with an asterisk are estimated. Scale bars on figures represent 1 mm. Terminology of the conch form follows Ruzhencev (1962); ornament terminology is summarized in Text-figure 4. The abbreviations D, H, U and W are standard for conch diameter, whorl height, umbilical diameter and conch width, respectively. Lithostratigraphical information on previously described species is given where known.

Because of the difficulties in recognition of the base of the Chadian Stage, discussed in Riley (1990b, 1993, 1995), stratigraphical intervals which may be of early Chadian or late Courceyan age are referred to as late Tournaisian. For the purposes of this account the base of the late Tournaisian is taken to correspond with the base of the *Scaliognathus anchoralis* Conodont Zone (Groessens 1975) or its equivalents. The base of the late Chadian corresponds to the base of the Viséan Series and follows Riley (1990b, 1993, 1995).

Order AGONIATIDA Ruzhencev, 1957
Suborder PROLECANITINA Miller and Furnish, 1954
Superfamily PROLECANITACEA Hyatt, 1884
Family PROLECANITIDAE Hyatt, 1884

Diagnosis (emended). The conch is evolute with moderate whorl expansion and rounded to rectangular whorls in axial section. The suture has 8–14 or more lobes, with a simple ventral lobe, except in gerontic *Dobaracanites* Ruzhencev, 1949. The other lobes are simple with acute or rounded bases. The dorsal lobe is simple and is bounded by an internal lobe, which may protrude ventrad of the umbilical margin.

Range. Tournaisian to Arnsbergian



TEXT-FIG. 4. Conch ornament terminology.

Remarks. The prolecanitids, in comparison with many contemporary ammonoids, show slow species turn-over and, because the conch form is conservative, classification is based on sutural characters. The scheme proposed by Weyer (1972*b*) is adopted here, with minor modification.

Subfamily PROLECANITINAE Hyatt, 1884

Diagnosis. Prolecanitids with a bell-shaped ventral lobe which is constricted orad. A siphuncular notch is present.

Range. Late Chadian to Brigantian.

Genus MICHIGANITES Ruzhencev, 1962

Type species. *Goniatites marshallensis* Winchell, 1862, p. 362.

Diagnosis. Prolecanitins with ten-lobed sutures.

Range. Late Chadian to late Asbian.

Remarks. The following species are included:

M. asiaticus (Karpinsky, 1896); Tien-Shan, Kirgizya, CIS, late Tournaisian.

M. discus (M'Coy, 1844); Clane, Ireland, late Tournaisian.

M. europaeus (Kullmann, 1963); 'Marbre Griotte, CuII)', Cantabria, northern Spain, late Tournaisian or early Viséan.

M. greeni (Miller in Miller and Faber, 1892); Indiana, USA, late Tournaisian or early Viséan.

M. hesteri (Moore, 1952); Pendleside Limestone Formation, Barnoldswick, north-west England, late Asbian.

M. marshallensis (Winchell, 1862); Marshall Sandstone, USA, mid-Dinantian.

M. rhipaeus Kusina, 1980; Nortnichsky Horizon, north Urals, Russian Federation, CIS, ?Arundian.

M. serpentinus (Phillips, 1836); Lower Bowland Shale Formation, Black Hall, Chipping, north-west England, late Asbian.

Michiganites sp. juv.

Plate 2, figure 3; Text-figure 5

Material. BGS Ro 5186; septate, adolescent, pyritic, internal mould; locality 3b.

Range. Late Chadian, upper FA Zone, Hodder Mudstone Formation, Leagram Mudstone Member.

Description. The conch is sub-platyconic with moderate whorl expansion and a wide umbilicus. The whorls are subquadrate in transverse section with flat flanks, a sharply rounded ventro-lateral region, and a feebly convex venter. The external ornament is not preserved. Internally, the conch surface is smooth. The ventral lobe is bell-shaped. Lobes U and U1 are acute and spatulate. Lobe U2 is feeble, acute, narrow and divergent-sided (orad).

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5186	18.0	6.7	7.6	4.5	0.25	0.42	0.37

Remarks. This specimen is closest to *M. marshallensis* and was the only *Michiganites* found during the study.

Subfamily PROTOCANITINAE Weyer, 1972a

Diagnosis. Prolecanitids with a divergent-sided (orad), V-shaped ventral lobe.

Range. Tournaisian to Arnsbergian.

Genus MEROCANITES Schindewolf, 1922

Type species. *Ellipsolites compressus* Sowerby, 1813, p. 84, plate 38.

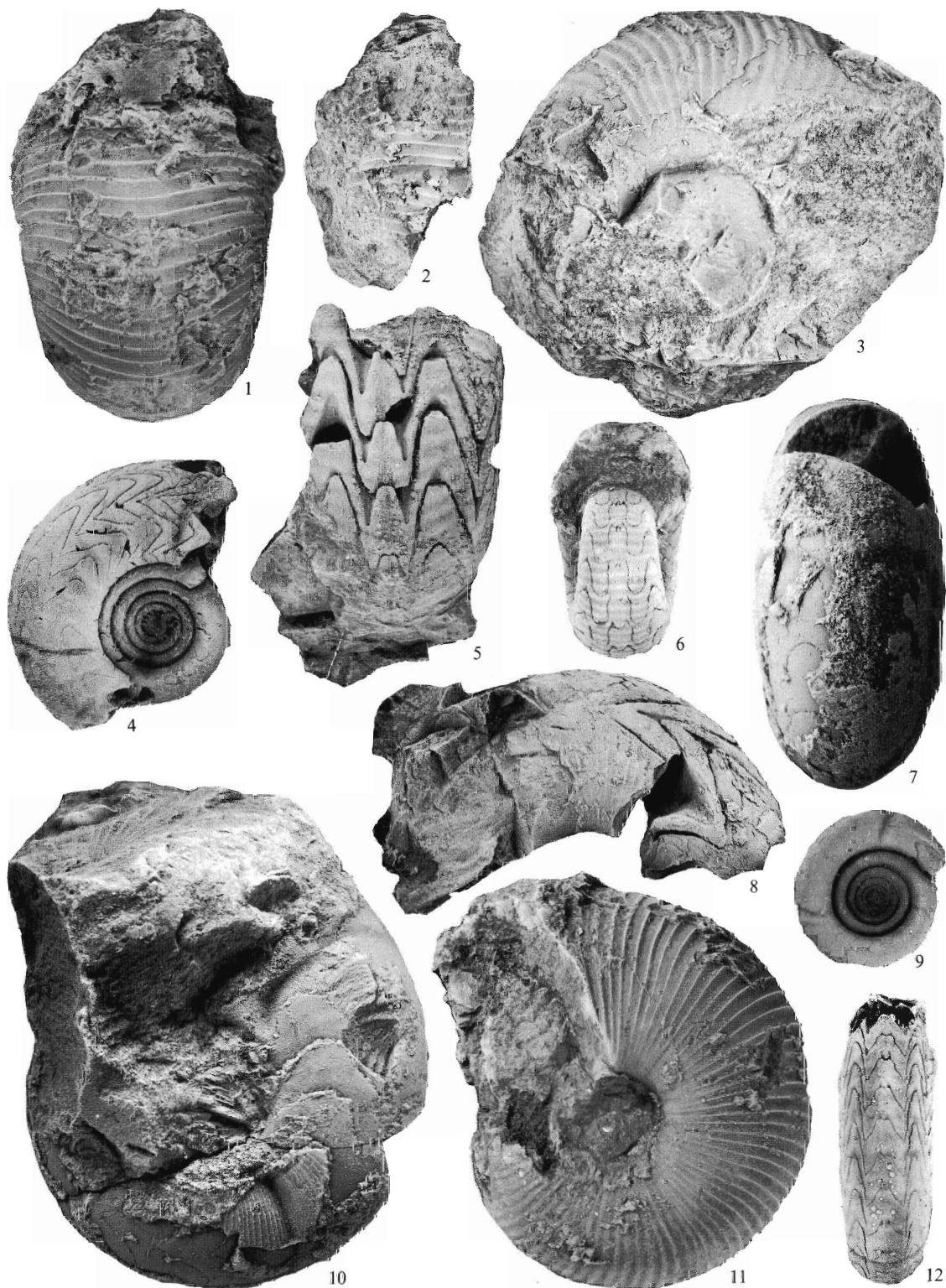
Remarks. *Erdbachites* Weyer, 1965, is a junior synonym of *Merocanites* because the type species of *Merocanites* has a divergent-sided ventral lobe (this can be seen on the type if immersed in silicone oil and illuminated with a strong light). Many species are inadequately described, or based on such

EXPLANATION OF PLATE I

Figs 1–3, 5–6, 8, 11. *Ammonellipsites clitheroensis* sp. nov. (see also Pl. 2, fig. 4). 1, 11, holotype, Ro 864; locality 4a; ventral and lateral views of exfoliated adolescent conch; $\times 3$. 2, paratype, Ro 867; locality 4a; ventral view of fragmentary, testiferous adult conch showing constriction; $\times 1$. 3, paratype, Ro 863; locality 4a; lateral view of exfoliated adult conch; note loss of ribs low on flanks; $\times 1.5$. 5, 8, paratype, Ro 865; locality 4a; ventral and lateral views of fragmentary, exfoliated adult conch; $\times 2$. 6, paratype, Ro 866; locality 3b; oral view of exfoliated early adolescent conch; $\times 5$.

Figs 4, 9, 12. *Heliocyclus divergens* sp. nov.; locality 3b. 4, 12, holotype, LZA 9422; lateral and ventral views of fragmentary, exfoliated adult conch; $\times 3$. 9, paratype, LZA 9445; lateral view of exfoliated adolescent conch; $\times 3.25$.

Figs 7, 10. *Rotopericyclus postremus* sp. nov.; locality 4a; holotype, Ro 933; ventral and lateral views of partly testiferous adolescent conch; $\times 3$.



RILEY, *Ammonellipsites*, *Helicocyclus*, *Rotopericyclus*

poorly preserved material that it is impossible to apply the name to anything other than the type. Little is known about their variation, hence many species names may be synonyms. The following species are included:

- M. applanatus* (Frech, 1899); Erdbach Limestone, Germany, mid-Dinantian.
M. compressus (Sowerby, 1813); 'Blackrock Limestone', Cork, Ireland, mid-Dinantian.
M. djaprakensis (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.
M. drostei (Collinson, 1955); Broadhead Formation, Kentucky, USA, late Tournaisian.
M. henslowi (Sowerby, 1821); Carboniferous Limestone, Isle of Man, UK, Asbian.
M. houghtoni (Winchell, 1862); Marshall Sandstone, USA, mid-Dinantian.
M. ogivalis (Pareyn, 1961); Banc de Mazzer, Sahara, north Africa, late Asbian.
M. planorbis Delépine, 1941; Carboniferous slates, Morocco, N. Africa, Dinantian.
M. similis (Crick, 1895); Haw Bank Limestones, Skipton, north-west England, late Tournaisian.
M. subapplanatus (Smyth, 1951); Tober Colleen Formation, Rush, near Dublin, Ireland, late Chadian.
M. subhenslowi (Wagner-Gentis, 1964); 'griotte limestone', Cantabria, northern Spain, late Tournaisian or early Viséan.
M. tenuis (Sheng, 1984); middle of Donggulubasitao Formation, north-west China, Viséan.

Merocanites cf. *applanatus* (Frech, 1899)

Plate 2, figure 1, Text-figures 6–8

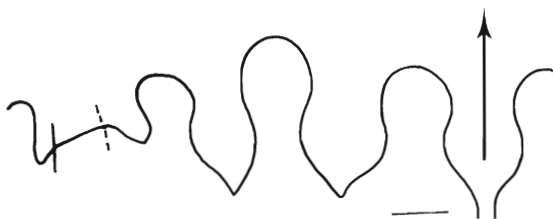
- 1889 *Prolecanites ceratitoides* (von Buch); Holzapfel, p. 240, pl. 3, figs 13–14.
 1889 *Prolecanites Henslowi* (Sowerby); Holzapfel, p. 43, pl. 3, fig. 5.
 1897 *Prolecanites ceratitoides* (von Buch); Foord and Crick, p. 251, fig. 120.
 1899 *Prolecanites applanatus* Frech, pl. 46a, fig. 9.
 1922 *Merocanites Holzapfeli* Frech; Schindewolf, p. 15, fig. 2b.
 1925 *Merocanites applanatus* (Frech); Schmidt, p. 539, pl. 19, fig. 15.
 1934 *Merocanites applanatus* (Holzapfel); Bisat, p. 305, pl. 24, fig. 1; text-fig. 22.
 1935 *Prolecanites (Merocanites) applanatus* Frech; Böhm, pp. 126, 136, pl. 7, figs 1–4, 15; text-figs 17–18.
 1941 *Merocanites applanatus* (Frech); Delépine, p. 45, pl. 3, figs 5–6; text-fig. 6B.
 1941 *Prolecanites (Merocanites) applanatus* (Frech); Schmidt, p. 150, pl. 19, fig. 1.
 1951a *Merocanites applanatus* (Frech); Schindewolf, p. 49, pl. 3, figs 3–5.

EXPLANATION OF PLATE 2

- Fig. 1. *Merocanites* cf. *applanatus* (Frech, 1899); Ro 5196; locality 9; lateral view of exfoliated, slightly crushed adult conch; $\times 1$.
 Fig. 2. *Nomismoceras rotiforme* (Phillips, 1836) (see also Pl. 6, fig. 15); Ro 2028; locality 13; lateral view of exfoliated adult conch; $\times 3.5$.
 Fig. 3. *Michiganites* sp.; Ro 5182; locality 4b; lateral view of exfoliated early adolescent conch; $\times 2$.
 Fig. 4. *Ammonellipsites clitheroensis* sp. nov. (see also Pl. 1, figs 1–3, 5–6, 8, 11); holotype, Ro 864; locality 4a; oral view of exfoliated adolescent conch; $\times 2$.
 Figs 5–8. *Eonomismoceras planum* sp. nov. 5, paratype, Ro 876; locality 3b; lateral view of exfoliated juvenile conch; $\times 3.25$. 6, paratype, Ro 894; locality 4b; lateral view of exfoliated, slightly crushed adult conch; $\times 2$. 7–8, holotype, Ro 874; locality 3b; lateral and ventral views of exfoliated adult conch; $\times 3.5$.
 Fig. 9. *Merocanites quadrilobus* sp. nov. (see also Pl. 3, fig. 5); paratype, Ro 5174; locality 4a; fragmentary, exfoliated late adolescent conch; $\times 1$.
 Figs 10–11. *Dimorphoceras leagramense* sp. nov.; holotype, Ro 895; locality 11; lateral and ventral views of fragmentary, exfoliated adult conch; $\times 5$.



RILEY, mid-Dinantian ammonoids



TEXT-FIG. 5. *Michiganites* sp.; Ro 5186; ventral and dorsal suture (part), $D = 17.1$, $H = 6.2$, $U = 7.5$, $W = 4.5$.

non 1961 *Merocanites applanatus* (Frech) var. *bicarinatus* Pareyn, pl. 2, figs 1–3, pl. 3, figs 6–9.
1963 *Merocanites applanatus* (Frech); Kullmann, p. 274, pl. 17, figs 1–2; text-fig. 2b.

Type specimen. *Prolecanites applanatus*, figured by Frech (1899, pl. 46a, fig. 9).

Material. More than 30, mainly distorted internal moulds preserved in micrite; from localities 4a, 9–12.

Range. Holkerian, Upper BB Zone; Hodderense Limestone Formation. Known also from the Erdbach Limestone, Germany and from the upper part of the Milldale Limestones, Staffordshire (Riley 1991).

Diagnosis. A *Merocanites* with rapid whorl expansion, early development of a subquadrate whorl section (trans.) and a deep, broad umbilical lobe (U2).

Description. The conch is serpenticonic with rapid whorl expansion. The flanks are flat, which together with the narrow ventrolateral shoulder and narrow, feebly convex venter, give a subquadrate appearance to the whorl in axial section after $H = 10$ mm. The external ornament is not preserved and the internal ornament is smooth. The ventral lobe is narrow and V-shaped with sides that diverge orad. It is deep in juveniles, but becomes shallower in the adult, when it is not as deep as the umbilical lobe, U2, or the lateral lobe. The lateral lobe and the umbilical lobes, U3 and U2, are spatulate; U2 is comparatively broad and deep for this genus. All the saddles are rounded.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5263	81.0	26.5	33.0	17.0	0.21	0.41	0.33
Ro 5293	70.0	26.5	27.0	15.5	0.22	0.39	0.39
Ro 5257	25.5	8.7	9.9	6.8	0.27	0.39	0.34
Ro 5270	18.5	7.5	8.6	5.5	0.3	0.46	0.41
Ro 5281	12.2	4.5	5.1	3.7	0.3	0.42	0.37

Remarks. The types of *M. applanatus* were destroyed during World War Two, hence no adequate modern description is available. The Craven material appears to belong to this species on account of the early deepening of lobe U2, the relatively rapid whorl expansion and the early presence of a subquadrate axial whorl section.

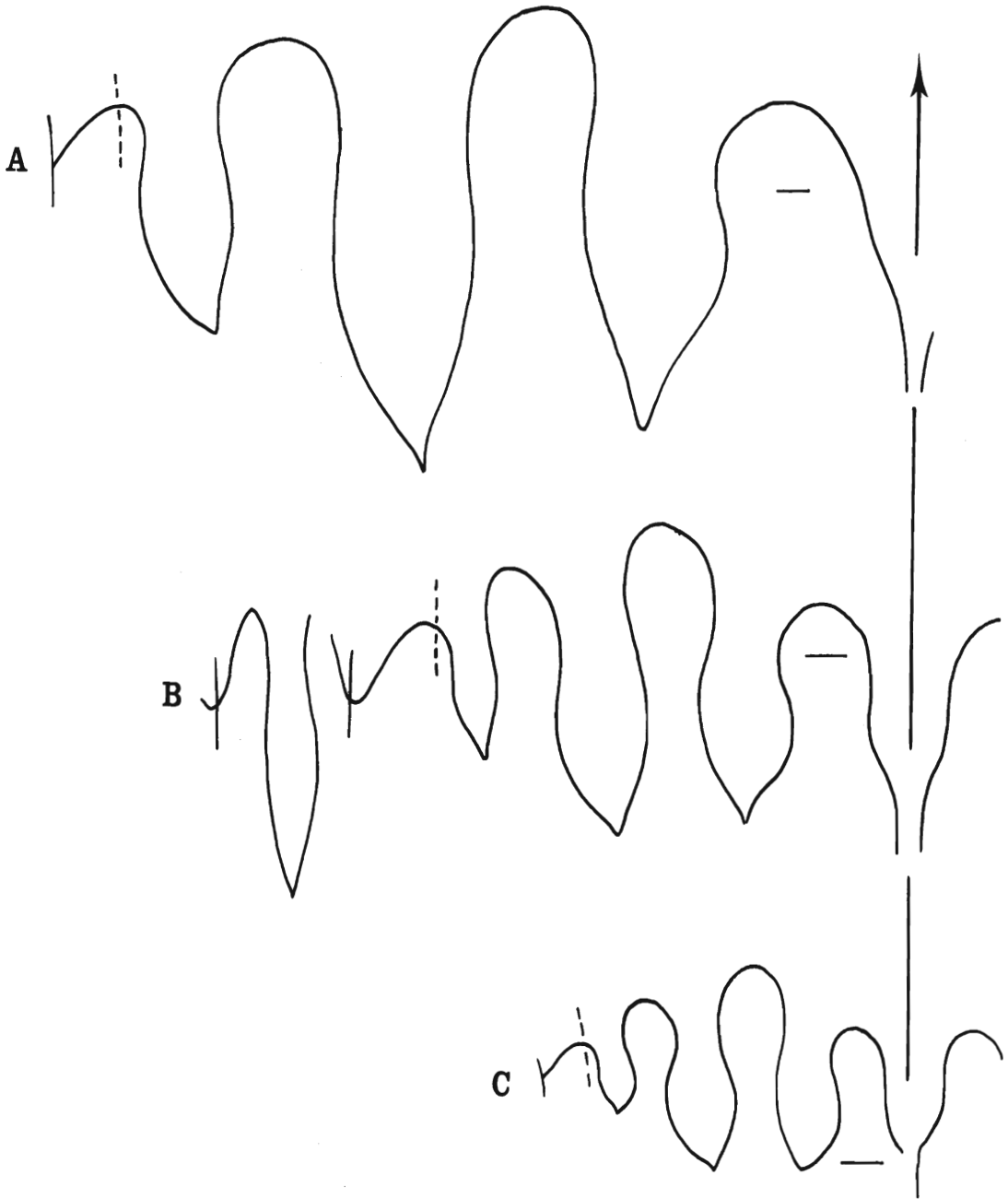
Merocanites quadrilobus sp. nov.

Plate 2, figure 9; Plate 3, figure 5; Text-figures 7–8

Derivation of name. For the four exposed lobes on the conch sides.

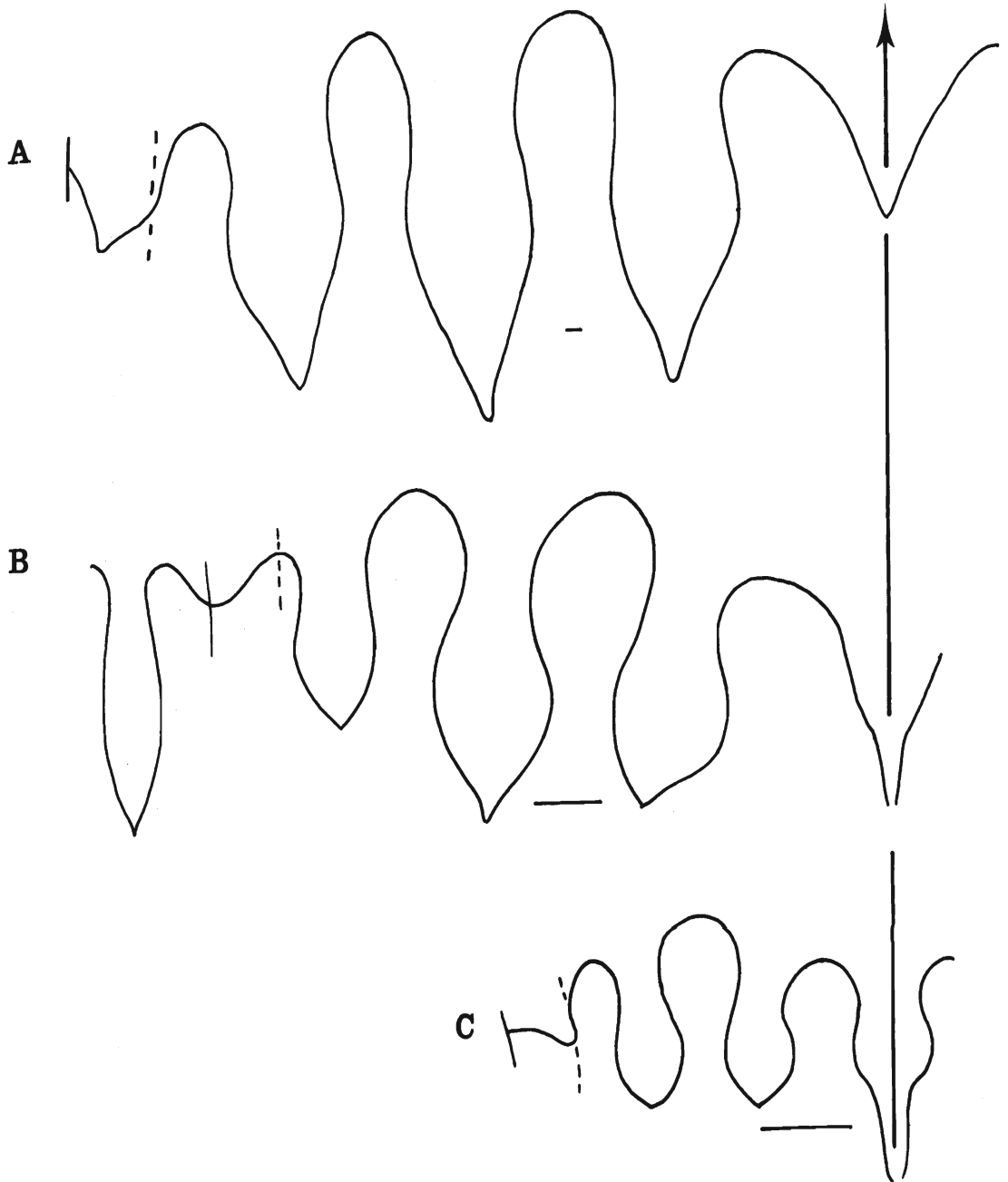
Material. Holotype Ro 5173 and paratypes Ro 5174–5175, all mainly exfoliated, fragmentary, septate conches preserved in micrite; from locality 4a.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation, Leagram Mudstone Formation.



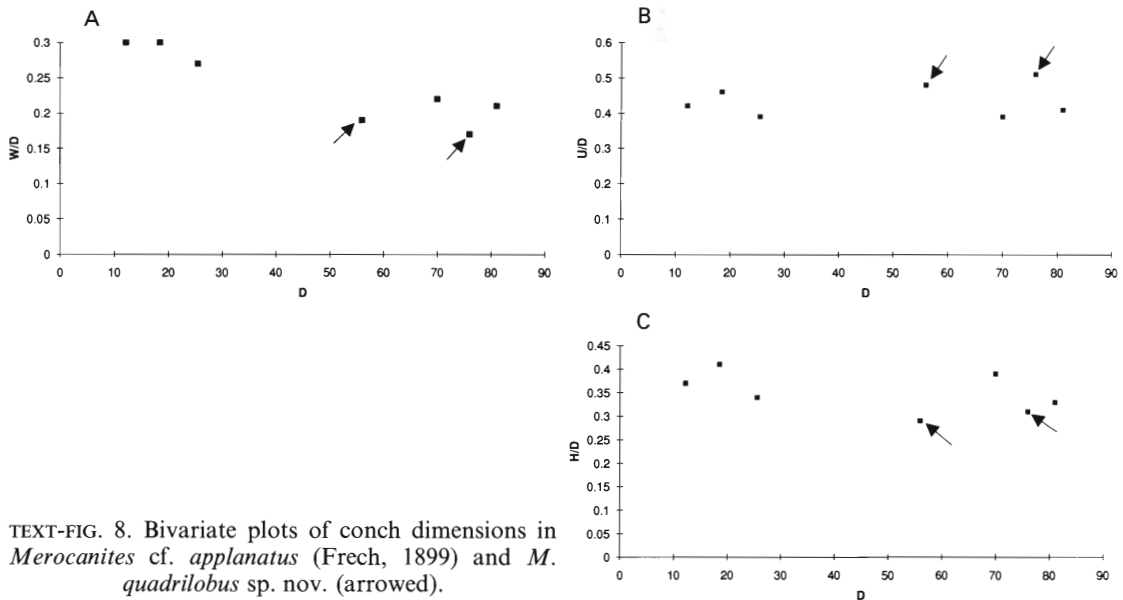
TEXT-FIG. 6. *Merocanites* cf. *applanatus* (Frech, 1899). A, Ro 5196; ventral suture, H = 23.0 (reversed image). B, Ro 5224; ventral suture, H = 9.5, W = 6.7. C, Ro 5218; ventral suture, H = 6.9, W = 5.0.

Description. The conch is serpenticonic with moderate whorl expansion. Initially the flanks are rounded, but they are nearly flat after H = 15 mm. The venter is narrow and convex. The external ornament is not preserved and the internal ornament is smooth, without constrictions. The external suture shows a broad ventral lobe



TEXT-FIG. 7. *Merocanites quadrilobus* sp. nov. A, holotype, Ro 5173; ventral suture, H = 52.8, W = 26.9. B, paratype, LZA 9378; ventral and dorsal suture, H = 7.9 (reversed image). C, paratype, LZA 9373; ventral suture, D = 9.1, H = 3.4, U = 4.2, W = 2.5.

which is relatively shallow with sides that diverge orad. Both the lateral lobe and the umbilical lobes, U2 and U3, are deep, spatulate and broad. Characteristically, the umbilical lobe, U1, is exposed ventrad of the whorl suture during late ontogeny and has a concave dorsad wall.



TEXT-FIG. 8. Bivariate plots of conch dimensions in *Merocanites* cf. *applanatus* (Frech, 1899) and *M. quadrilobus* sp. nov. (arrowed).

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5173	—	52.0	—	30.2	—	—	—
Ro 5174	76.0	23.5	39.0	13.0	0.17	0.51	0.31
Ro 5175	56.0	16.5	27.0	10.5	0.19	0.48	0.29

Remarks. It is possible that forms referred to *Prolecanites compressus* by Parkinson (1926), from the lower part of the Hodder Mudstone Formation, belong to this species; however, none of his material is available for comparison. Crushed merocanitids abound in the lower part of the Hodder Mudstone Formation, but they do not show sutural details. The type of *Merocanites compressus* is distorted and the nature of the suture in the umbilical region is obscure. Only *M. djaprakensis*, *M. drostei* and *M. houghtoni* have an umbilical lobe, U1, with a concave ventrad wall. The possibility that these species are immature *M. quadrilobus* sp. nov. is discounted because they are described from conches of similar diameter to the new species. The presence of an exposed umbilical lobe, U1, is unique and converges with the eocanitid genus *Cantabrianites* Weyer, 1965, which is known from Brigantian and Pendleian strata. In *Cantabrianites*, however, the four exposed lobes are produced by insertion of a new umbilical lobe, U4, rather than ventrad migration of umbilical lobe, U1.

Order GONIATITIDA Hyatt, 1884

Suborder GONIATITINA Hyatt, 1884

Superfamily DIMORPHOCERATAEAE Hyatt, 1884

Diagnosis (emended). The conch is involute, with a small umbilicus, and varies from suboxyconic to pachyconic. The early whorls lack a serpenticonic stage. The external ornament is feeble and consists of bisinuous transverse striae with well developed linguae. Spiral ornament is sometimes present. The ventral lobe is wide and divergent-sided (orad) and usually has subdivided prongs. The lateral lobe is often subdivided, and is sometimes serrate.

Range. Holkerian to Langsettian.

Remarks. The following families are included:

Anthracoceratidae Plummer and Scott, 1937; Pendleian to Langsettian.

Berkoceratidae Librovitch, 1957; Brigantian to Arnsbergian.

Dimorphoceratidae Hyatt, 1884; Holkerian to Kinderscoutian.

The Girtyoceratidae Wedekind, 1918 and Gonioloboceratidae Spath, 1934, formerly placed in the Dimorphocerataceae, are transferred herein to the newly erected superfamily Girtyocerataceae; hence the diagnosis has been emended.

Family DIMORPHOCERATIDAE Hyatt, 1884
Subfamily DIMORPHOCERATINAE Hyatt, 1884
Genus DIMORPHOCERAS Hyatt, 1884

Type species. *Glyphioceras gilbertsoni* Phillips, 1836.

Diagnosis. Dimorphoceratins with bipartite ventral lobe prongs.

Range. Holkerian to mid-Brigantian.

Remarks. The following species are included:

D. algens Gordon, 1957; Alapah Limestone, Kiruktagiak River Alaska, Asbian or Brigantian.

D. brancoi Holzapfel, 1889; Erdbach Limestone, Germany, mid-Dinantian.

D. dneperense Kusina in Kusina and Poletaev, 1991; Zone XIIa, Solochovskaya Suite, Donets Basin, Ukraine, CIS, ?Asbian.

D. gilbertsoni (Phillips, 1836); Bolland, north-west England, Viséan.

D. leagramense sp. nov.; Great Falls Limestone Formation, Leagram, north-west England, late Holkerian.

D. leitriemense Moore, 1958; Dough Mountain, Co. Leitrim, Ireland, Brigantian.

D. kathleenae Moore, 1936; Lower Bowland Shale Formation, Dinckley, north-west England, Brigantian.

Dimorphoceras leagramense sp. nov.

Plate 2, figures 10–11; Text-figures 9–10

Derivation of name. From Leagram, the type locality.

Material. Holotype, Ro 895, paratypes Ro 896–905, internal micritic casts; from locality 11.

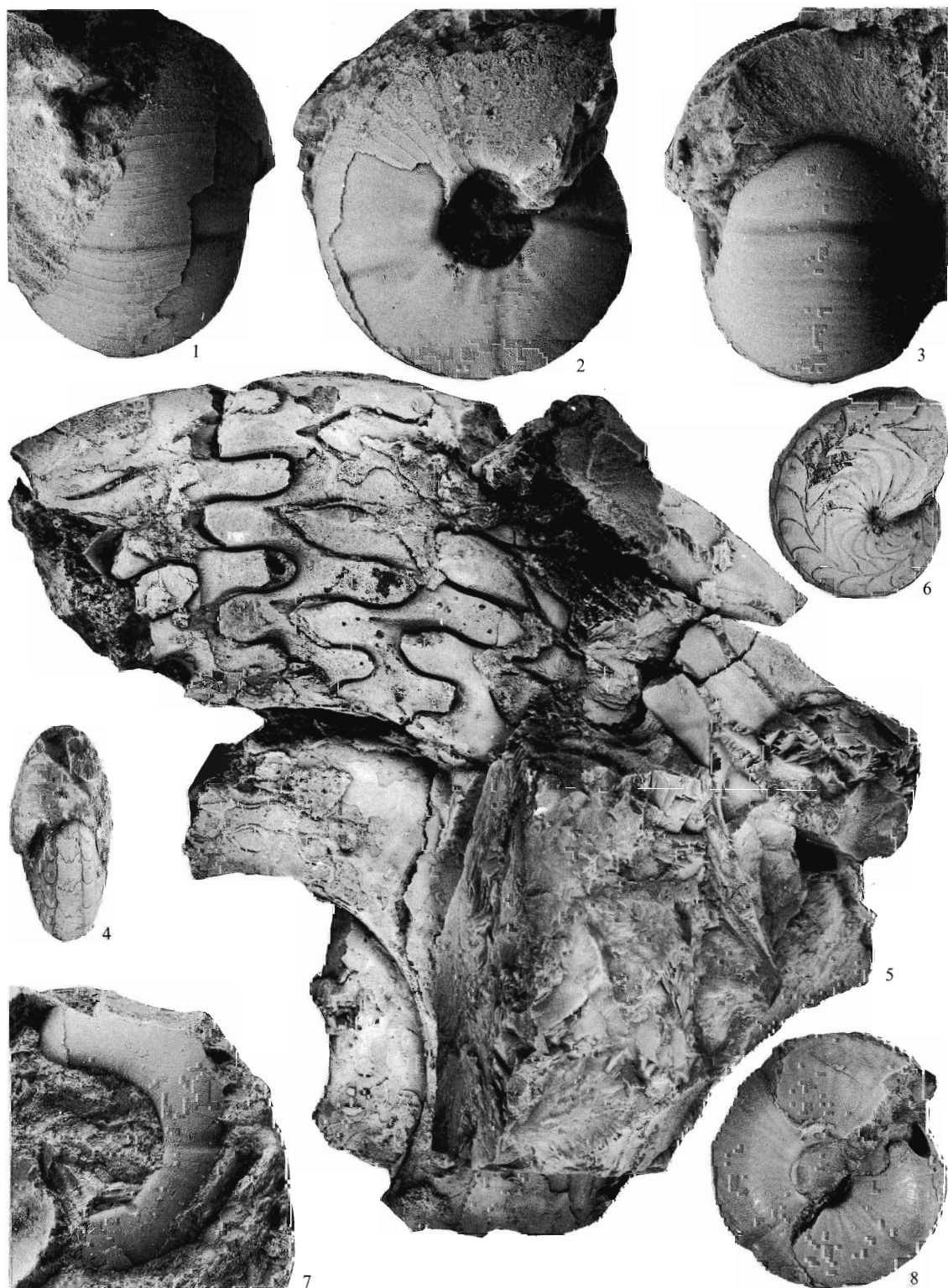
EXPLANATION OF PLATE 3

Figs 1–3, 8. *Parahammatocyclus chaigleyensis* gen. et sp. nov. (see also Pl. 6, figs 1, 4, 12; Pl. 7, fig. 8). 1–3, holotype, Ro 5127; locality 6; lateral, oral and ventral views of partly testiferous, late adolescent conch; × 4. 8, paratype, Ro 3723; locality 7; exfoliated, partly crushed adolescent conch; × 2.75.

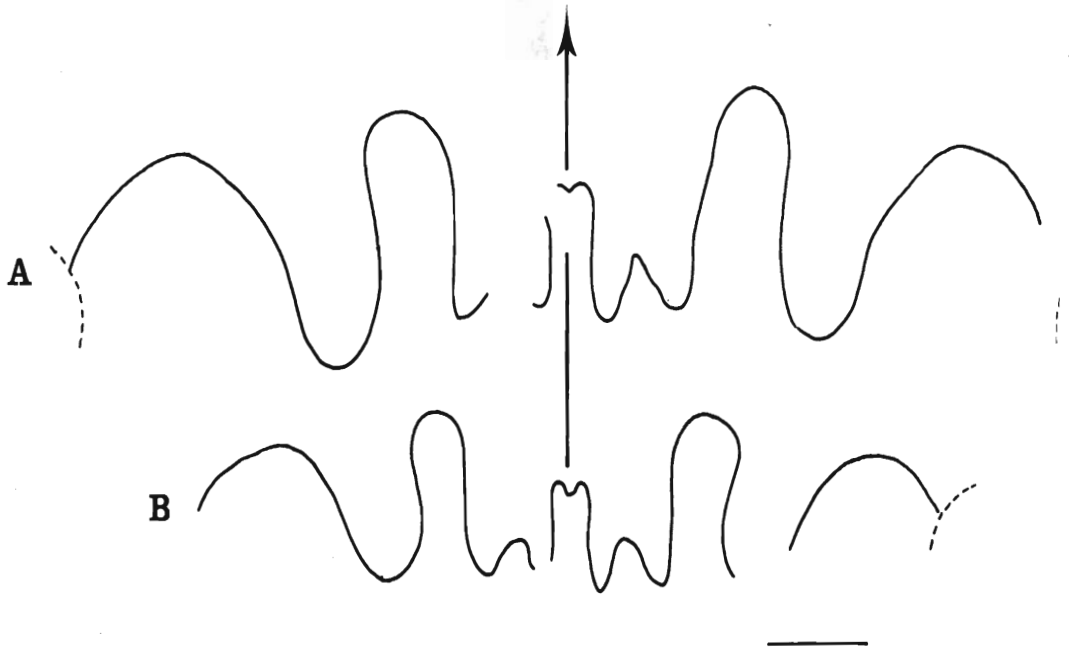
Figs 4, 6. *Dzhaprakoceras levis* sp. nov. (see also Pl. 4, figs 2, 4); holotype, LZA 9399; oral and lateral views of exfoliated adolescent conch; × 2.75.

Fig. 5. *Merocanites quadrilobus* sp. nov. (see also Pl. 2, fig. 9); holotype, Ro 5173; locality 4a; lateral view of fragmentary exfoliated adult conch; note exposure of umbilical lobe U1; × 1.

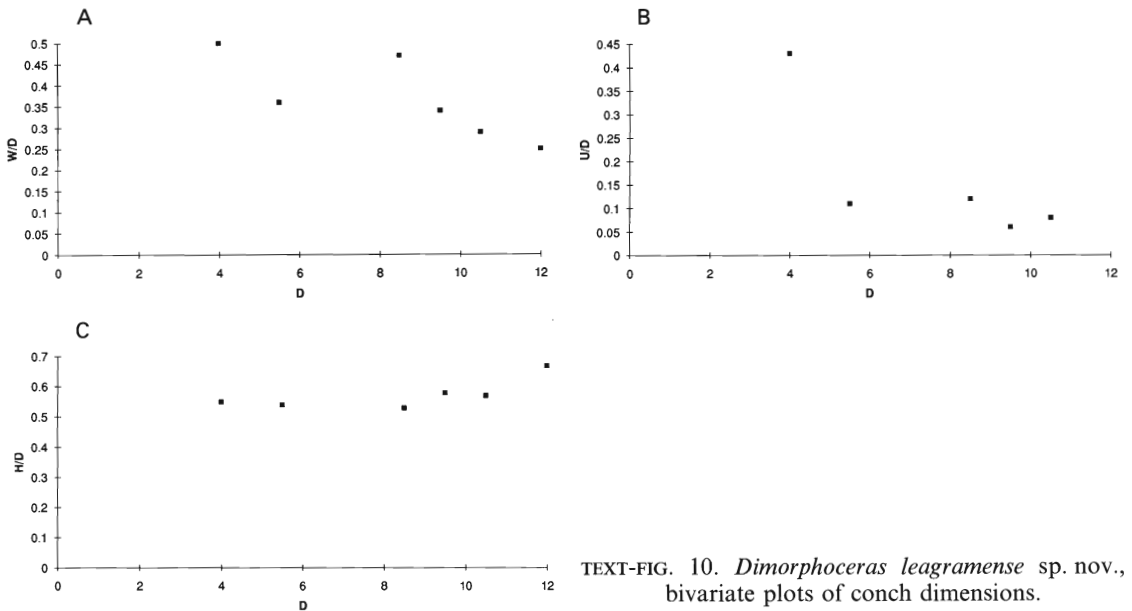
Fig. 7. *Bollandites?* sp.; Ro 5076a; locality 6; lateral view of fragmentary, exfoliated late adolescent conch; × 4.



RILEY, mid-Dinantian ammonoids



TEXT-FIG. 9. *Dimorphoceras leagramense* sp. nov.; holotype, Ro 895. A, ventral suture, $D = 8.2$, $H = 4.4$, $U = 1.8$, $W = 3.9$. B, ventral suture, $H = 2.9$, $W = 3.1$.



TEXT-FIG. 10. *Dimorphoceras leagramense* sp. nov., bivariate plots of conch dimensions.

Range. Holkerian, upper BB Zone; upper part of the Hodder Mudstone Formation and Hodderense Limestone Formation.

Diagnosis. A *Dimorphoceras* with rounded lobes and a high, narrow median saddle.

Description. The conch is suboxyconic and laterally compressed, but pachyconic below the third whorl. The umbilicus is very small. The conch flanks are broad and slightly convex, converging into a narrow, rounded venter. The external ornament is not preserved, but the internal ornament shows feeble, bisinuuous undulations with well developed lateral and hyponomic sinuses and linguae, sometimes forming a shallow lingual groove high on the flanks. The external suture shows a ventral lobe which is bipartite, with rounded lobes and subacute subsidiary saddles. There is a narrow, high median saddle, about half the ventral lobe depth and twice the subsidiary saddle height. The lateral saddle is rounded and inflated, especially in juveniles ($H = 3$). The lateral lobe is deep and rounded with steep walls. The umbilical saddle is high and broad.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 889	12.0	8.0	0.0	3.0	0.25	—	0.67
Ro 898	10.5	6.0	0.8	3.0	0.29	0.08	0.57
Ro 902	9.5	5.5	0.6	3.2	0.34	0.06	0.58
Ro 895	8.5	4.5	1.0	4.0	0.47	0.12	0.53
Ro 903	5.5	3.0	0.6	2.0	0.36	0.11	0.54
Ro 905	4.0	2.2	0.5	2.0	0.50	0.43	0.55

Remarks. *D. leagramense* sp. nov. is most similar to *D. gilbertsoni* from which it differs by its more laterally compressed conch and higher median saddle.

Superfamily GIRTYOCERATACEAE superfam. nov.

Diagnosis. Goniatitiniids with oxyconic to subsphaeroconic conches and serpenticonic early whorls. The external ornament usually has both spiral and transverse elements; often with a well developed lingua and sometimes a lingual groove. Simple or dichotomous ribs may be present on the flanks and/or umbilical region. The ventral lobe is broad and divergent-sided (orad) and often has a well developed median saddle. The lateral saddle is rounded to subacute. The lateral lobe is acute.

Range. Late Chadian to Arnsbergian.

Remarks. The following families are included:

Girtyoceratidae Wedekind, 1918; Holkerian to Arnsbergian.

Eogonioloboceratidae Ruzhencev and Bogoslovskaya, 1978; late Chadian to Arnsbergian.

Family GIRTYOCERATIDAE Wedekind, 1918

Diagnosis (emended). The conch is oxyconic to subsphaeroconic. The external ornament has transverse and often spiral elements. The transverse ornament is usually strongly bisinuuous. Simple or dichotomous ribs, which may fail during late ontogeny, are present in some stratigraphically young species, as is a lingual groove. The ventral lobe is broad and divergent-sided (orad). The lateral saddle is usually sub-acute and may be rounded. The lateral lobe is acute.

Range. Holkerian to Arnsbergian.

Remarks. The following genera are included:

- Beyrichoceras* Foord, 1903; Holkerian to Asbian.
- Cousteauceras* Korn, 1988; late Brigantian to early Pendleian.
- Edmooroceras* Elias, 1956; early Pendleian.
- Eumorphoceras* Girty, 1909; late Brigantian to Arnsbergian.
- Girtyoceras* Wedekind, 1918; Asbian to Brigantian.
- Peytonoceras* Saunders, 1966; Arnsbergian.
- Sulcogirtyoceras* Ruzhencev, 1960; late Brigantian.
- Torulites* Kusina and Yatskov, 1987; ?Arundian.
- Tumulites* McCaleb, Quinn and Furnish, 1964; Pendleian.

Winchelloceras Ruzhencev, 1965 may be a girtyoceratid; however, its taxonomic position is unclear since the early whorls are undescribed. *Pseudogirtyoceras* Wagner-Gentis in Higgins and Wagner-Gentis 1982 is here considered to be a junior synonym of the eogonioloboceratid *Atratoceras* Librovitch, 1957. Kusina (1987) placed *Beyrichoceras* in the Anthracoceratidae Plummer and Scott, 1937, but the presence of spiral ornament, evolute early whorls and sutural characters of *Beyrichoceras* do not support this.

Genus BEYRICHOCERAS Foord, 1903

Type species. *Goniatites obtusus* Phillips, 1836, plate 19, figures 10–11.

Diagnosis. Moderate-sized to large girtyoceratids with subsphaeroconic to pachyconic conches and rounded to rectangular whorls in axial section. The external ornament consists of transverse bisinuous striae, often with a well developed lingua. Spiral ornament is usually limited to the lingua, but may extend over the flanks and venter. Internal constrictions are sometimes present. The ventral lobe is divergent-sided (orad), with flexed sides and acute prongs which diverge abroad. The lateral saddle is acute to subacute. The lateral lobe is acute with flexed sides.

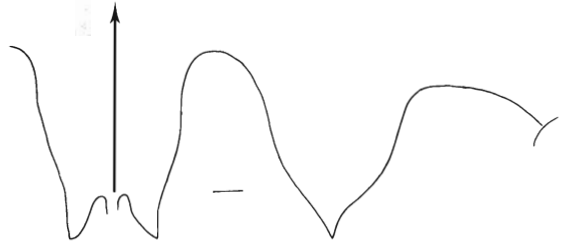
Range. Holkerian to Asbian.

Remarks. The following species are included:

- B. araneum* Nicolaus, 1963; Go α 2, Goniatitenknollen, Eschenberg bei Hillerhausen, Germany, late Asbian.
- B. constans* Kusina, 1987; Viséan Complex, Novaya Zemlya, CIS, Asbian.
- B. delicatum* Bisat, 1924; 'reef limestone', Treak Cliff, northern England, Asbian.
- B. mepeli* Schmidt, 1941; CuII δ , or CuIII α , Herborn, Germany, late Asbian.
- B. obtusum* (Phillips, 1836); Lower Bowland Shale Formation, Black Hall, Chipping, north-west England, late Asbian.
- B. parkinsoni* Bisat, 1934; Pendleside Limestone Formation, Slaidburn, north-west England, Asbian.
- B. rectangularum* Bisat, 1934; ?Malham Formation, Grassington, north-west England, Asbian.
- B. tardum* Ruzhencev, 1966; limestones in Kzyl-Shin Gorge, south Urals, Russian Federation, late Asbian.
- B. tenue* Kusina, 1987; Viséan Complex, Novaya Zemlya, CIS, Asbian.
- B. vesiculiferum* (de Koninck, 1880); Visé, Belgium, Asbian.

Beyrichoceras bashachense Popov, 1965, *B. furiense* Padget, 1952 and *B. mackellari* Campbell, Brown and Coleman, 1983 are here placed in *Bollandoceras*. *Beyrichoceras trevallynense* Brown, Campbell and Roberts 1964, is here transferred to *Bollandites*. The generic status of *Beyrichoceras bootibootiense* Campbell, Brown and Coleman, 1983 is unclear; however, the lack of serpenticonic

TEXT-FIG. 11. *Beyrichoceras* aff. *obtusum* (Phillips, 1836); Ro 2160; ventral suture, H = 14.4.



early whorls excludes it from *Beyrichoceras*. The conch and suture suggest affinity with *Dzhaprakoceras* or *Beyrichoceratoides*.

Beyrichoceras aff. *obtusum* (Phillips, 1836)

Plate 8, figure 12; Text-figure 11

- | | |
|------------------|--|
| 1836 | <i>Goniatites obtusus</i> Phillips, p. 233, pl. 19, figs 10–11, ?13 (<i>non</i> fig. 12, <i>fidé</i> Foord 1903). |
| 1880 | <i>Goniatites obtusus</i> Phillips; de Koninck, p. 104, pl. 47, fig. 10–10a (<i>non</i> pl. 46, fig. 3, <i>fidé</i> Delépine 1940). |
| 1897 | <i>Glyphioceras obtusum</i> (Phillips); Foord and Crick, p. 169, text-fig. 79. |
| 1899 | ? <i>Glyphioceras obtusum</i> (Phillips); Frech, pl. 46a, fig. 3. |
| 1903 | <i>Glyphioceras (Beyrichoceras) obtusum</i> (Phillips); Foord, p. 163, pl. 42, fig. 7a–c (<i>non</i> figs 8a–b, 9a–b). |
| 1924 | <i>Beyrichoceras obtusum</i> (Phillips), Bisat, p. 86, pl. 9, fig. 3. |
| 1940a | <i>Beyrichoceras obtusum</i> (Phillips); Delépine, p. 69, pl. 4, figs 3–8; text-fig. 16. |
| <i>non?</i> 1941 | <i>Beyrichoceras obtusum</i> (Phillips); Delépine, p. 64, pl. 3, figs 33–35. |
| 1952 | <i>Beyrichoceras obtusum</i> (Phillips); Bisat, p. 170, fig. 2d (<i>non</i> 2h) |

Lectotype. Designated by Bisat (1952), BMNH C247a, figured by Phillips (1836, pl. 19, figs 10–11).

Material. Specimen Ro 2160, fragmentary exfoliated, septate late adolescent preserved in packstone; from locality 13.

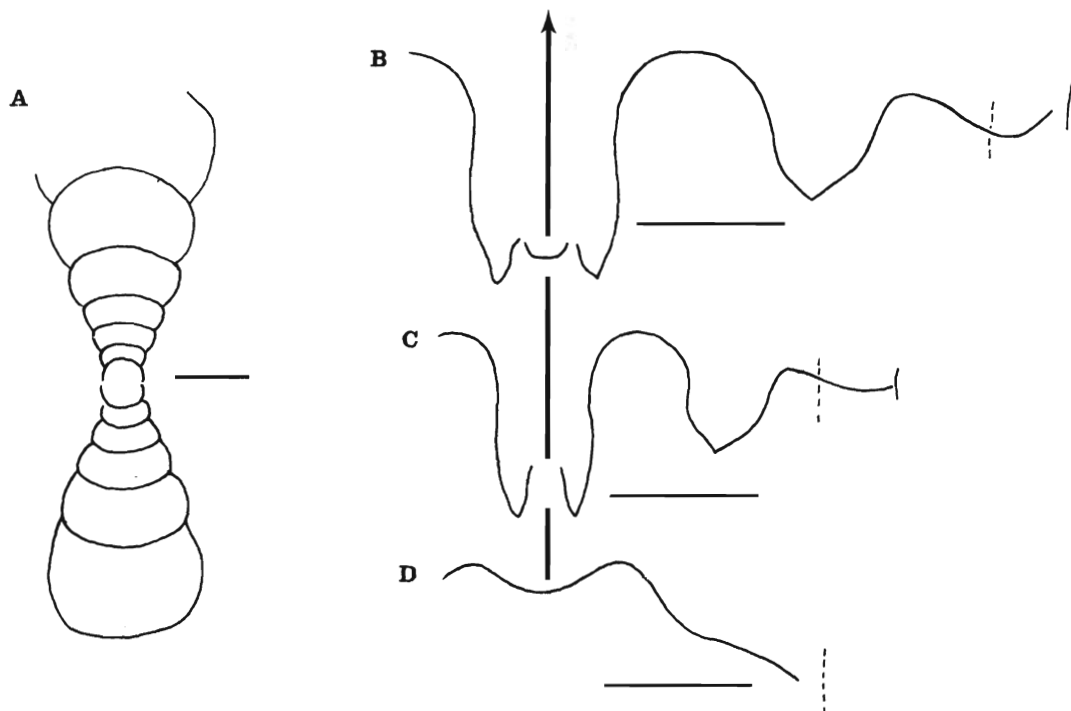
Range. *B. obtusum sensu stricto* occurs only in the B2a and B2b subzones (late Asbian). In the Craven Basin this interval lies in the Lower Bowland Shale Formation. Elsewhere in Europe this species is known from the same subzones.

Description. The conch is pachyconic with feebly convex sides, a sharply rounded ventro-lateral area and a narrow convex venter, giving an almost subquadrate axial whorl section. The external ornament is not preserved. The internal ornament consists of feeble vesicular ridges in the ventrolateral region. Two feeble bisinuous constrictions are present in the quarter of the whorl preserved. The ventral lobe has slightly divergent acute prongs, flexed divergent sides (orad). The lateral saddle is narrow and sharply rounded. The lateral lobe is broad, with flexed sides and is the same depth as the ventral lobe.

Remarks. This specimen is close to the type in the development of constrictions, widely spaced septa and conch form; however, the median saddle is higher than in the type.

Superfamily NOMISMOCERATAEAE Librovitch, 1957

Diagnosis (emended). The conch is small, laterally compressed, serpenticonic to discoconic with slow whorl expansion. The whorls are often arched at maturity, when the venter may be carinate, acute or flattened. Coiling is usually regular, but is quadrangular in the Entogonitidae. The external ornament is transverse and often strongly bisinuous; ribs may be present (Entogonitidae). The ventral lobe is bipartite with simple, rounded to acute prongs and parallel to divergent (orad) sides. The lateral saddle is rounded. The lateral lobe is often narrow and may be rounded or acute.



TEXT-FIG. 12. *Enomismoceras planum* sp. nov. A, paratype, Ro 893; axial section. B, holotype, Ro 874; ventral suture, $D = 11.3$, $H = 2.5$, $U = 6.7$, $W = 2.8$. C-D, paratype, Ro 876; C, ventral suture, $D = 7.9$, $H = 1.5$, $U = 4.9$, $W = 2.3$; D, ventral suture, $D = 7.0$, $H = 1.4$, $U = 4.5$, $W = 2.1$.

Range. Late Chadian to Arnsbergian.

Remarks. Two families are included:

- Nomismoceratidae Librovitch, 1957; late Chadian to Yeadonian.
- Entogonitidae Ruzhencev and Bogoslovskaya, 1971; Asbian.

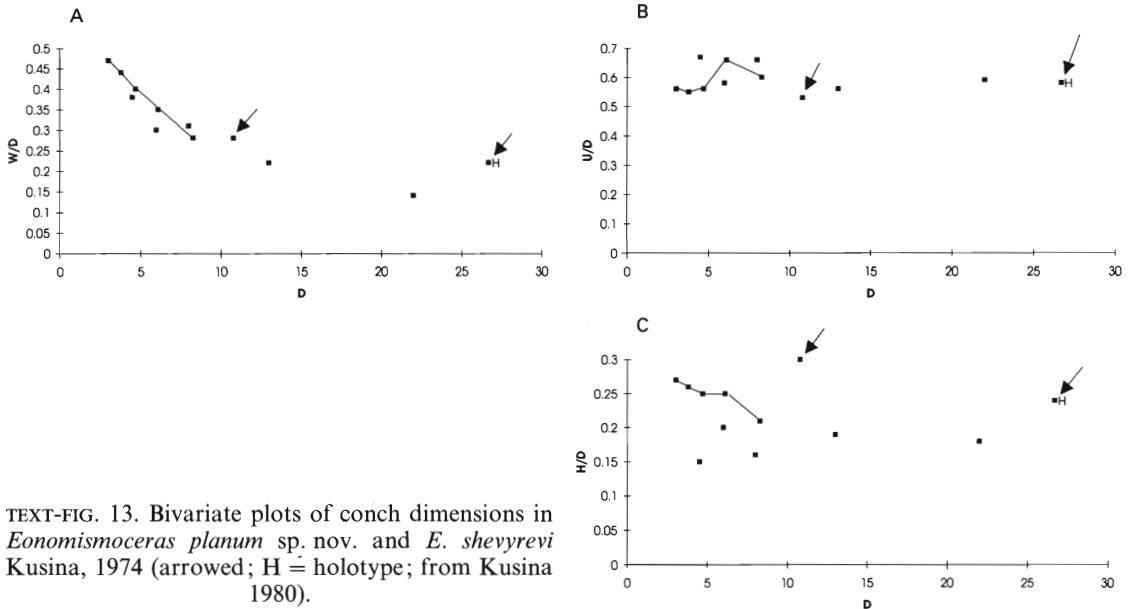
Family NOMISMOCERATIDAE Librovitch, 1957

Diagnosis. Nomismocerataceans with regular coiling.

Range. Late Chadian to Yeadonian.

Remarks. The following genera are included:

- Baschkirites* Librovitch, 1957; Marsdenian to Yeadonian.
- Beleutoceras* Ruzhencev and Bogoslovskaya 1971; Pendleian.
- Cavilentia* Ruzhencev and Bogoslovskaya, 1971; Arnsbergian.
- Enomismoceras* Kusina, 1974; late Chadian.
- Hudsonoceras* Moore, 1946; Alportian to Kinderscoutian.
- Nomismoceras* Hyatt, 1884; Holkerian to Brigantian.
- Pseudonomismoceras* Frech, 1899; ?early Viséan.
- Simmonoceras* Kusina, 1974; Arundian.



TEXT-FIG. 13. Bivariate plots of conch dimensions in *Eonomismoceras planum* sp. nov. and *E. shevyrevi* Kusina, 1974 (arrowed; H = holotype; from Kusina 1980).

Genus EONOMISMOCERAS Kusina, 1974

Type species. Eonomismoceras shevyrevi Kusina, 1974, plate 4, figures 1–2.

Diagnosis (emended). Nomioceratides with serpenticonic, non-carinate conches and strongly bisinuuous transverse ornament. Constructions may be present in early ontogeny. The ventral lobe is narrow with sub-parallel sides, often constricted orad. The lateral saddle is broad and well rounded. The lateral lobe is narrow and acute.

Range. Late Chadian.

Remarks. The following species are included:

E. shevyrevi Kusina, 1974; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

E. planum sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

Eonomismoceras planum sp. nov.

Plate 2, figures 5–8; Text-figures 12–13

Derivation of name. From the Latin *planus* (= flat), with reference to the dorso-ventral flattening of the whorls.

Material. Holotype Ro 874, paratypes Ro 875–894, pyritic internal moulds; from locality 3b.

Range. Late Chadian, Upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. An *Eonomismoceras* with a steep-sided, broad-based, acute lateral lobe.

Description. The conch is serpenticonic with slow whorl expansion, and dorso-ventrally compressed whorls which have narrow, convex flanks and a broad convex venter. The external ornament is unknown. The internal ornament consists of feeble, bisinuuous ridges which show a shallow lateral sinus and a deep, V-shaped hyponomic sinus. Constructions, which follow the external ornament, may be present in juveniles. The ventral lobe is deep, with sub-parallel sides which constrict slightly orad. The lateral saddle is broad and well

rounded. The lateral lobe is shallow, about three-quarters of the ventral lobe depth, broad-based and acute with sub-parallel sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 894	22.0	4.0	13.0	3.0	0.14	0.59	0.18
Ro 874	13.0	2.5	7.3	2.8	0.22	0.56	0.19
Ro 876	8.0	1.3	5.3	2.5	0.31	0.66	0.16
Ro 880	6.0	1.2	3.5	1.8	0.30	0.58	0.20
Ro 878	4.5	0.7	3.0	1.7	0.38	0.67	0.15
Ro 893	8.3	1.8	5.0	2.33	0.28	0.60	0.21
Ro 893	6.1	1.5	4.0	2.16	0.35	0.66	0.25
Ro 893	4.7	1.2	2.6	1.89	0.40	0.56	0.25
Ro 893	3.8	1.0	2.1	1.66	0.44	0.55	0.26
Ro 893	3.0	0.8	1.7	1.4	0.47	0.56	0.27

Remarks. The most obvious feature which distinguishes this species from *E. shevyrevi* is the sub-parallel-sided, broad-based, acute lateral lobe. *E. shevyrevi* is further distinguished by possessing a higher whorl section at comparable diameters.

Genus *NOMISMOCERAS* Hyatt, 1884

Type species. *Goniatites spirorbis* Phillips, 1836, plate 20, figures 51–55.

Diagnosis. (based on Ruzhencev and Bogoslovskaya 1971). The conch is small discoconic and laterally compressed. The whorls are moderately arched at maturity, when the venter may become narrow and flat. The external ornament is transverse and bisinuous with a strong lingua, which may form a lingual groove. The ventral lobe has divergent sides (orad) and rounded prongs. The lateral saddle is broad and well rounded. The lateral lobe is shallow, narrow and rounded.

Range. Holkerian to Brigantian.

Remarks. The following species are included:

N. frechi Schmidt, 1925; Weitengrund, Germany, Viséan.

N. germanicum Schmidt, 1925; Bredelar, Germany, late Asbian.

N. rotiforme (Phillips, 1836); Bolland, north-west England, Viséan.

N. spirorbis (Phillips, 1836); Lower Bowland Shale Formation, Black Hall, Chipping, north-west England, late Asbian.

N. vittigerum (Phillip, 1836); Bolland, north-west England, Viséan.

Nomismoceras? *spiratissimum* Holzapfel, 1889, *N.?* *infracostatum* Schindewolf, 1951a and *N.?* *pseudocycilus* Campbell, Brown and Coleman, 1983 are too poorly known to be certain of their inclusion in this genus.

Nomismoceras rotiforme (Phillips, 1836)

Plate 2, figure 2; Plate 6, figure 15

1836	<i>Goniatites rotiformis</i> Phillips, p. 237, pl. 2, fig. 56–58.
?1844	<i>Ammonites vittiger</i> Phillips; de Koninck, p. 582, pl. 50, fig. 5a–c.
1880	<i>Goniatites rotiformis</i> Phillips; de Koninck, p. 114, pl. 50, fig. 16.
1897	<i>Nomismoceras rotiforme</i> (Phillips); Foord and Crick, p. 215, text-fig. 103.
non 1901	<i>Nomismoceras rotiforme</i> (Phillips); Frech, pl. 46a, fig. 6a–f.

Holotype. BMNH C.271a, Phillips (1836, pl. 20, fig. 56).

Material. More than 30 exfoliated, mainly fragmentary, distorted, micritic conches representing all growth stages; localities 9–13.

Range. Holkerian, upper BB Zone to B1 Subzone; Hodder Mudstone Formation to Pendleside Limestone Formation.

Description. The conch is small, discoconic and laterally compressed, with a carinate venter at maturity. Whorl expansion is slow. The external ornament is not preserved. The internal ornament consists of feeble, regularly spaced, transverse undulations on the middle of the flanks. The details of the suture are unclear; however, the ventral lobe is broad and strongly divergent-sided (orad). The lateral saddle is broad and rounded. The lateral lobe is shallow, narrow and rounded.

Remarks. This species is distinguished from the similar *N. vittigerum* by the presence of radial undulations on the flanks,

Superfamily PERICYCLACEAE Hyatt, 1900
Family MUENSTERCERATIDAE Librovitch, 1957

Diagnosis. The conch is of medium to large size, subsphaeroconic to discoconic, sometimes suboxyconic, with a medium-sized to closed umbilicus. The early whorls are serpenticonic to cadiconic, never involute. The usually feeble external ornament consists of transverse striae, which may lack or have one or more sinuses; weak spiral ornament is rarely present. The ventral lobe has parallel, divergent (orad) or convergent (orad) sides. The lateral saddle is rounded. The lateral lobe is acute.

Range. Courceyan to Pendleian.

Remarks. The following genera are included:

- Beyrichoceratoides* Bisat, 1924; late Chadian to Arnsbergian.
- Bollandoceras* Bisat, 1952; Arundian to Brigantian.
- Dzhaprakoceras* Popov, 1965; late Tournaisian to Arundian.
- Eurites* Kusina, 1973; late Tournaisian.
- Kozhimites* Kusina, 1971; late Chadian.
- Muensteroceras* Hyatt, 1884; Tournaisian.
- Muensteroceratoides* Popov, 1965; late Tournaisian.
- Terektytes* Librovitch, 1957; late Tournaisian or early Viséan.

Kozhimites, originally of the monospecific family Kozhimitidae Kusina, 1971, is close to *Dzhaprakoceras* and therefore separation into a separate family is here considered unjustified. The following genera require further comment.

(1) *Beyrichoceras* Foord, 1903. The combination of well developed spiral ornament, strongly bisinuous transverse ornament, subacute lateral saddles and a prolonged juvenile serpenticonic stage places this genus within the Girtyoceratidae.

(2) *Bollandites* Bisat, 1952. Internal ribbing of the early whorls and in some cases the adolescent whorls, together with sutural characters places *Bollandites* within the Pericyclidae.

(3) *Cluthoceras* Currie, 1954. Examination of type and paratype material reveals that *Cluthoceras* falls within *Beyrichoceratoides* as now defined. This extends the range of *Beyrichoceratoides* beyond the Pendleian (the horizon of *B. invaginatum*) into the Arnsbergian (Calmy Limestone).

(4) *Eoglyphioceras* Brüning, 1923. This genus was given priority over *Beyrichoceratoides* by Korn (1988); however, when originally erected, no type species was given (unlike *Beyrichoceratoides*) and it appears that the genus was defined by amalgamation of *Beyrichoceras* and *Muensteroceras*. This lack of clarity in the original description renders *Eoglyphioceras* invalid.

Genus BEYRICHOCERATOIDES Bisat, 1924

Type species. Goniatites implicatus Phillips, 1836.

Diagnosis. The conch is involute, small to medium-sized and varies from discoconic to subsphaeroconic and lacks a juvenile serpenticonic stage. The umbilicus is of small to moderate size. The venter is rounded, but may become subquadrate late in ontogeny. The external ornament consists of simple transverse striae which become bisinuuous during late adolescence. The internal surface of the conch may develop strong undulations (and more rarely ribs) particularly on the flanks, during late adolescence. Constructions are present; they run parallel with the external ornament but often fail during adolescence. The ventral lobe is narrow, parallel to sub-parallel sided, often constricted orad, sometimes lyre-shaped and may be asymmetrical. It has acute prongs and a low median saddle. The lateral saddle is rounded and often broad, never inflated. The lateral lobe is narrow and acute.

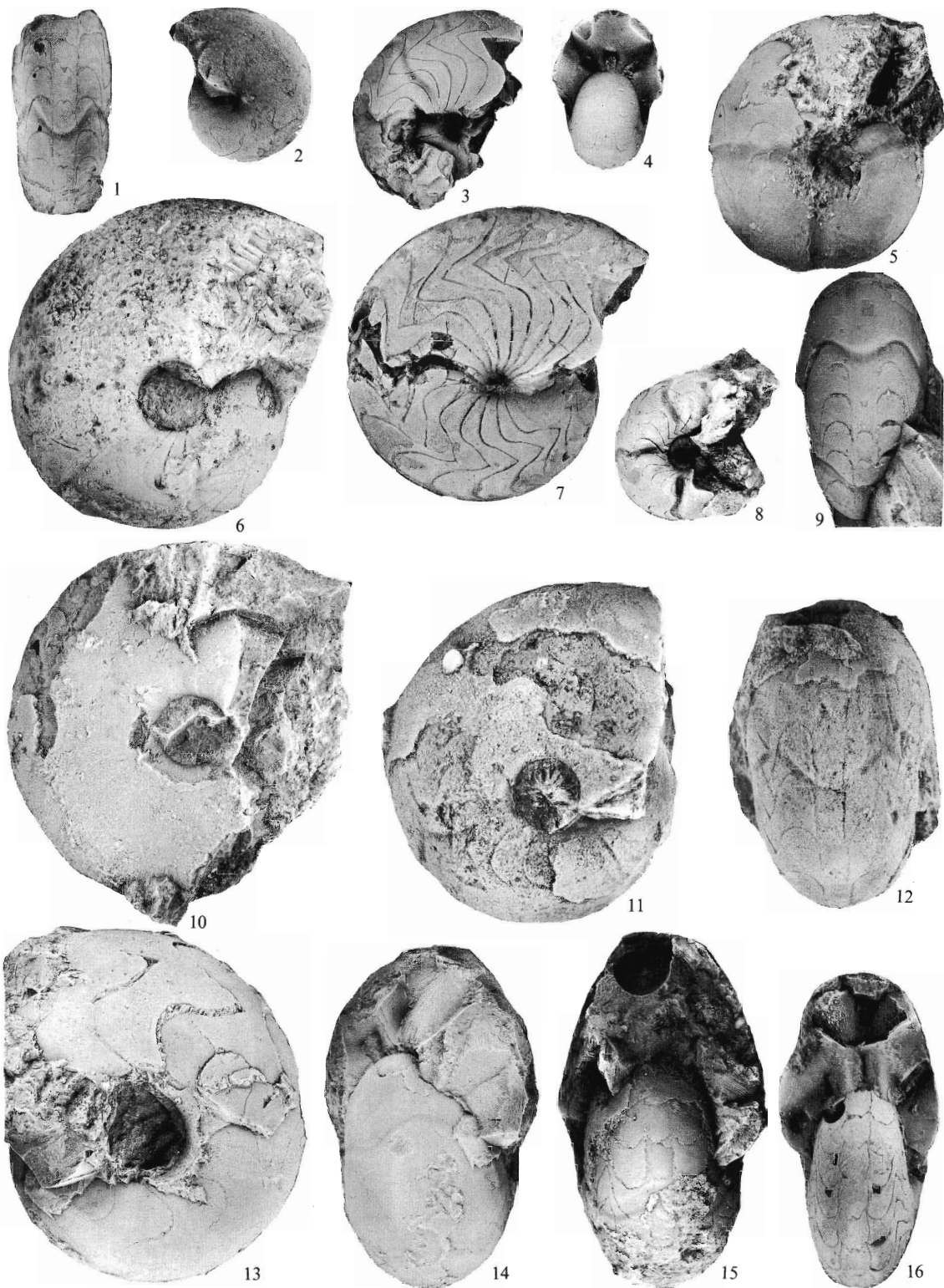
Range. Late Chadian to Pendleian.

Remarks. The following species are included:

- B. fournieri* (Delépine, 1940a); black limestones, near Dinant, Belgium, late Asbian.
- B. glicki* (Gordon, 1964); Fayetteville Shale (upper part), Elkins, Washington County, Arkansas, USA, Pendleian.
- B. implicatus* (Phillips, 1836); Lower Bowland Shale Formation, Black Hall, Chipping, north-west England, late Asbian (B2b).
- B. inflatus* sp. nov.; Clitheroe Limestone Formation, Clitheroe, north-west England, late Chadian.
- B. invaginatus* Bisat, 1924; Upper Bowland Shale Formation, Malham, north-west England, late Pendleian (E1c).
- B. involutus* (Pareyn, 1961); Djenien Series, Djebel Arlal (locality 22), Algeria, late Brigantian or Pendleian.
- B. komiorum* Kusina, 1980; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

EXPLANATION OF PLATE 4

- Figs 1, 3, 7, 16. *Dzhaprakoceras catena* sp. nov.; locality 3b. 1, 3, paratype, Ro 916; ventral and lateral views of exfoliated, fragmentary, adolescent conch; $\times 2.25$. 7, 16, holotype, Ro 5192; lateral and oral views of slightly distorted, exfoliated late adolescent conch; $\times 2.5$.
- Figs 2, 4. *Dzhaprakoceras levis* sp. nov. (see also Pl. 3, figs 4, 6); paratype, Ro 913; locality 3b; lateral and oral views of exfoliated juvenile conch; $\times 6$.
- Fig. 5. *Beyrichoceratoides* sp. 1; Ro 5161; locality 8; lateral view of partly testiferous, exfoliated adolescent conch; $\times 2.5$.
- Figs 6, 15. *Dzhaprakoceras flexum* sp. nov. (see also Pl. 5, figs 3, 5); paratype, LZA 9521; locality 3a; partly testiferous, adolescent conch; $\times 2$.
- Figs 8–9. *Dzhaprakoceras undulatum* sp. nov. (see also Pl. 5, fig. 1; Pl. 7, fig. 2). 8, paratype, Ro 928; locality 3b; lateral view of fragmentary, exfoliated juvenile conch; $\times 2$. 9, paratype, Ro 923; locality 4a; ventral view of exfoliated adolescent conch; $\times 2.25$.
- Fig. 10. *Dzhaprakoceras deflexum* Kusina, 1980 (see also Pl. 6, figs 7–8; Pl. 7, fig. 15); LZA 9522; locality 4a; lateral view of partly testiferous late adolescent conch; $\times 2$.
- Figs 11–12. *Dzhaprakoceras subglobosum* (Librovitch, 1927); Ro 5178; locality 2, lateral and ventral views of partly testiferous adolescent conch; $\times 3$.
- Figs 13–14. *Beyrichoceratoides inflatus* sp. nov. (see also Pl. 7, figs 10, 12–14); holotype, Ro 5170; locality 4a; lateral and oral views of largely exfoliated late adolescent conch; $\times 2$.



RILEY, *Dzhaprakoceras*, *Beyrichoceratoides*

B. neilsoni (Currie, 1954); Index Limestone, Bishopbriggs, Scotland, Pendleian.

B. redesdalensis (Hind, 1918); Redesdale Ironstone, Ridsdale, Northumberland, north-east England, Asbian.

B. stenolobus (Phillips, 1836); Lower Bowland Shale Formation, Black Hall, Chipping, north-west England, late Asbian (B2b).

B. truemani (Currie, 1954); Index Limestone Shales, Bishopbriggs, Scotland, Pendleian.

B. truncatus (Phillips, 1836); Bolland, north-west England, early Brigantian.

Beyrichoceratoides can develop similar ventral lobe shapes to those of *Dzhaprakoceras* and *Bollandoceras*; the latter has a serpenticonic juvenile stage and is therefore easily distinguished from *Beyrichoceratoides*. *Dzhaprakoceras*, like *Beyrichoceratoides*, lacks a juvenile serpenticonic stage, but develops a bisinuous transverse ornament much earlier in ontogeny than *Beyrichoceratoides*.

Beyrichoceratoides inflatus sp. nov.

Plate 4, figures 13–14; Plate 7, figures 10, 12–14; Text-figures 14–15

Derivation of name. From the inflated adult whorls.

Material. Holotype, Ro 5170, paratypes Ro 5164, 5168 (late adolescent and mature conches, partly exfoliated and septate), preserved in packstone; from locality 4a.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

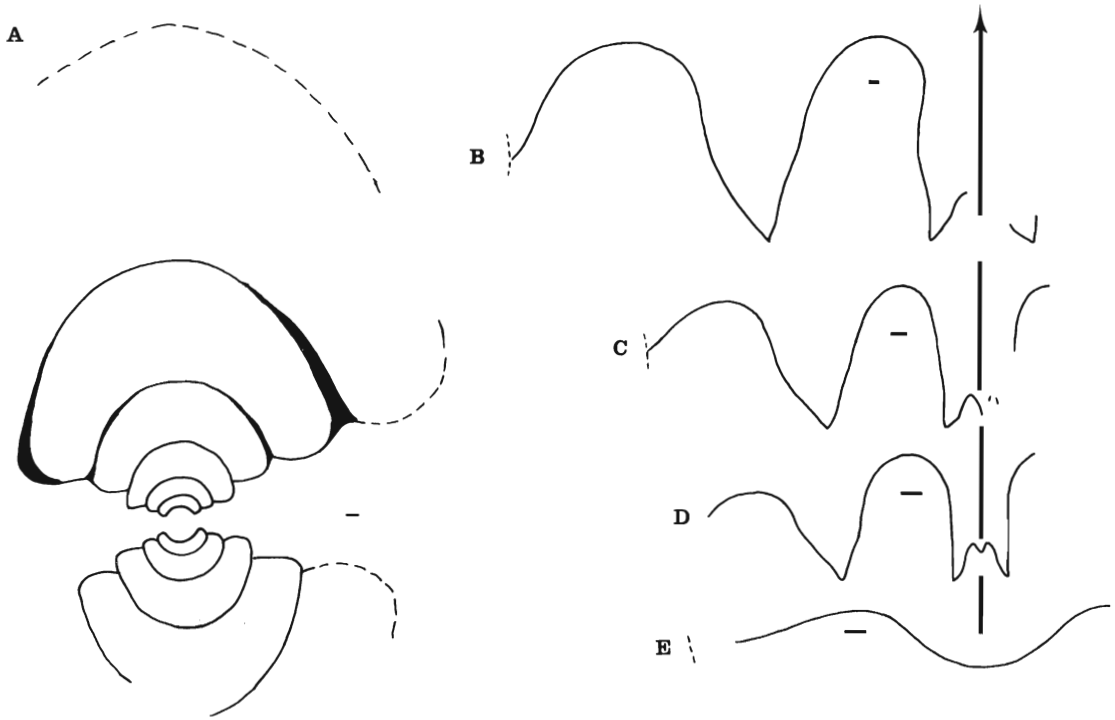
Diagnosis. A large *Beyrichoceratoides* with cadiconic early whorls which become inflated and subsphaeroconic at maturity.

Description. The conch is large and subsphaeroconic with inflated whorls when mature. The earlier whorls are cadiconic. The umbilicus is moderately wide with convex walls. The conch flanks are weakly convex and merge gently with the broad convex venter. The external ornament consists of delicate, bisinuous, transverse striae with a weak lateral sinus and a broad shallow hyponomic sinus. The internal ornament consists of feeble undulations which are parallel to the external striae. About four constrictions per whorl are present until late adolescence ($D = 34$ mm); they are parallel with the external ornament. The ventral lobe is narrow with sub-parallel sides that become increasingly divergent orad. The lateral saddle is broad and rounded. The lateral lobe is narrow and acute with flexed sides.

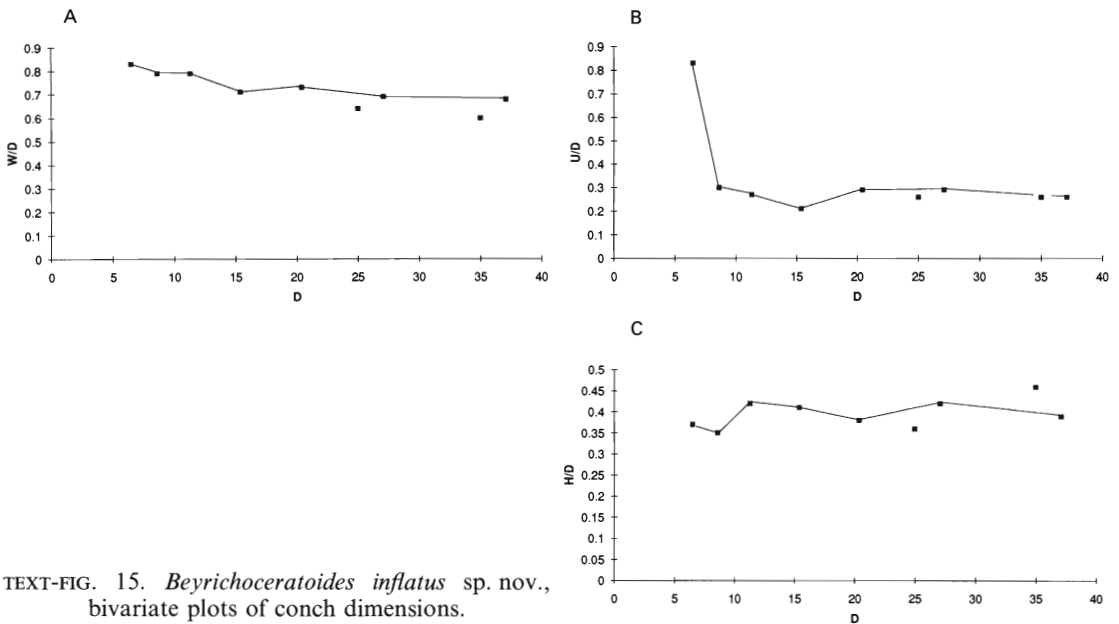
Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5164	—	28.5	18.1	44.4	—	—	—
Ro 5170	35.0	16.0	9.0	21.0	0.60	0.26	0.46
Ro 5168	25.0	9.0	8.0	16.0	0.64	0.32	0.36
Ro 5164	37.1	14.6	9.7	25.4	0.68	0.26	0.39
Ro 5164	27.1	11.4	7.8	18.8	0.69	0.29	0.42
Ro 5164	20.4	7.8	5.9	14.8	0.73	0.29	0.38
Ro 5164	15.4	6.3	3.2	11.0	0.71	0.21	0.41
Ro 5164	11.3	4.8	3.0	8.9	0.79	0.27	0.42
Ro 5164	8.6	3.0	2.5	6.8	0.79	0.30	0.35
Ro 5164	6.5	2.4	2.1	5.4	0.83	0.32	0.37

Remarks. This species resembles superficially *Eurites* Kusina in conch form; however, *Eurites* has retrograde transverse ornament which lacks a lateral sinus.



TEXT-FIG. 14. *Beyrichoceratoides inflatus* sp. nov. A-B paratype, Ro 5164; A, axial section. B, ventral suture, H = 32.8; C, holotype, Ro 5170; ventral suture, H = 14.6; D-E, paratype Ro 5168; D, ventral suture, H = 8.9; E, constriction, H = 9.8.



TEXT-FIG. 15. *Beyrichoceratoides inflatus* sp. nov., bivariate plots of conch dimensions.

Beyrichoceratoides sp. aff. *komiorum* Kusina, 1980.

Plate 5, figures 2, 6

1980 *Beyrichoceratoides komiorum* Kusina, p. 62, pl. 5, fig. 3.*Holotype*. Figured by Kusina (1980, p. 62, pl. 5, fig. 3); specimen PIN 2775/347.*Material*. Ro 5128, exfoliated, non-septate, mid-adolescent preserved in sparry calcite; from locality 2.*Range*. Late Tournaisian, middle FA Zone; Clitheroe Limestone Formation (Bellman Limestone Member). The holotype comes from the base of the BB Zone, near the top of the Kosvinsky Horizon, north Urals, Russian Federation.*Description*. The conch is small and subdiscoconic with a well rounded venter and a small umbilicus. The external and internal ornament are not preserved. Weak, radial constrictions are present. The suture is not visible.*Dimensions*.

Specimen	D	H	U	W	W/D	U/D	H/D
Holotype (Kusina)	44.1	20.4	6.4	21.4	0.48	0.15	0.51
Ro 5182	17.0	8.0	2.0	10.0	0.59	0.12	0.47

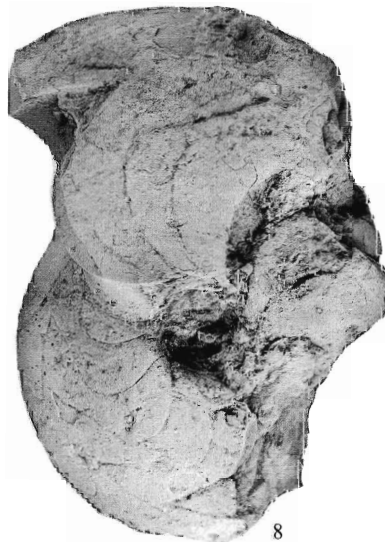
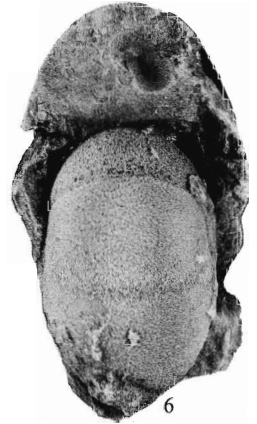
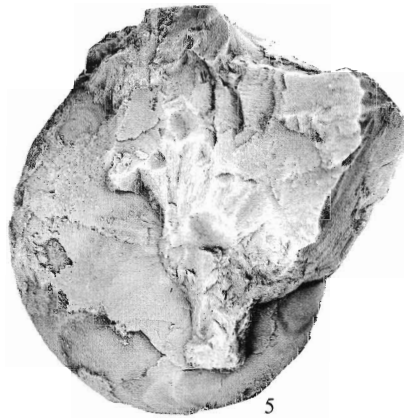
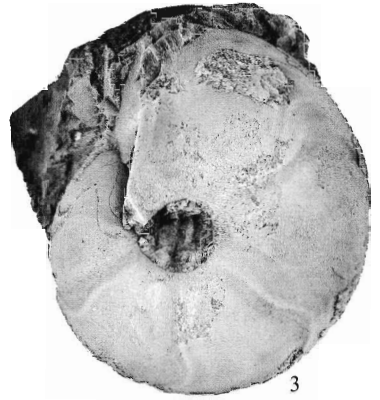
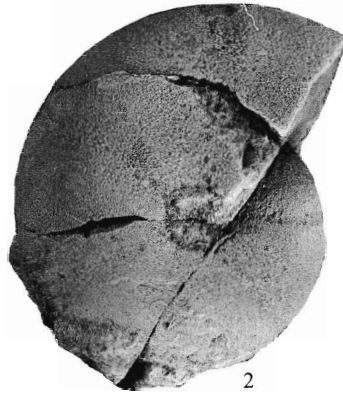
Remarks. The radial constrictions exclude this ammonoid from being assigned to *Dzhaprakoceras*.*Beyrichoceratoides* sp. 1

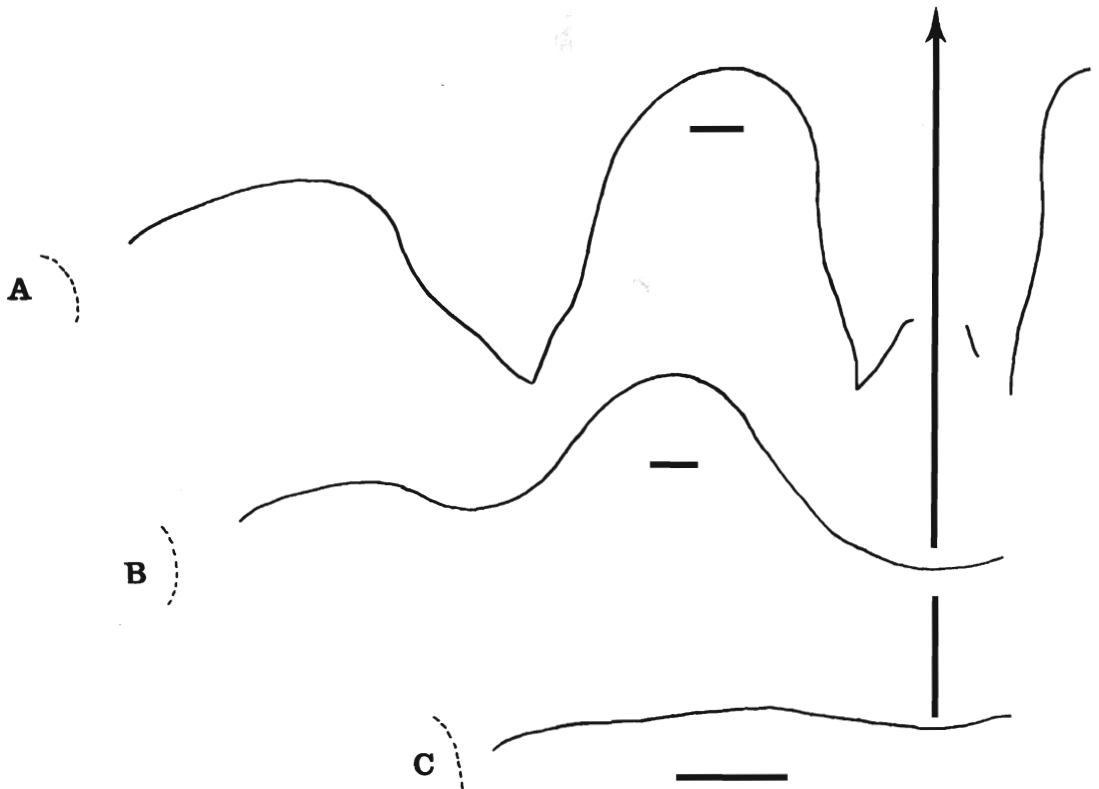
Plate 4, figure 5; Text-figure 16

Material. Ro 5160–5162, fragmentary, mid-adolescent conches preserved in sparry calcite; from locality 8.*Range*. Holkerian, upper BB Zone; Hodder Mudstone Formation.*Description*. The conch is subdiscoconic and relatively evolute with a well rounded venter. The external ornament is transverse and delicate, radial in juvenile whorls but, in later whorls, slightly bisinuuous with a lateral and hyponomic sinus. An internal ornament is not present. There are four constrictions per whorl, which run parallel to the ornament. The ventral lobe is divergent-sided in juveniles but becomes increasingly lyrate with age. The lateral saddle is rounded. The lateral lobe is narrow and acute.

EXPLANATION OF PLATE 5

- Figs 1, 4. *Dzhaprakoceras undulatum* sp. nov. (see also Pl. 4, figs 8–9; Pl. 7 fig. 2); holotype, Ro 925; locality 4a; lateral views of fragmentary, partly testiferous late adolescent conch; $\times 2$.
- Figs 2, 6. *Beyrichoceratoides* sp. aff. *komiorum* Kusina, 1980; Ro 5182; locality 2; lateral and ventral views of exfoliated adolescent conch; $\times 3$.
- Figs 3, 5. *Dzhaprakoceras flexum* sp. nov. (see also Pl. 4, figs 6, 15); holotype, Ro 1009; locality 4a; lateral views of partly exfoliated late adolescent conch; $\times 2$.
- Fig. 7. *Dzhaprakoceras hispanicum* (Foord and Crick, 1897); Ro 3720; locality 5; lateral view of exfoliated adult conch; $\times 1.5$.
- Figs 8–9. *Dzhaprakoceras bellmanense* sp. nov. (see also Pl. 7, figs 12, 14); holotype, Ro 915; locality 4a; lateral and oral views of fragmentary, exfoliated adult conch; $\times 1$.

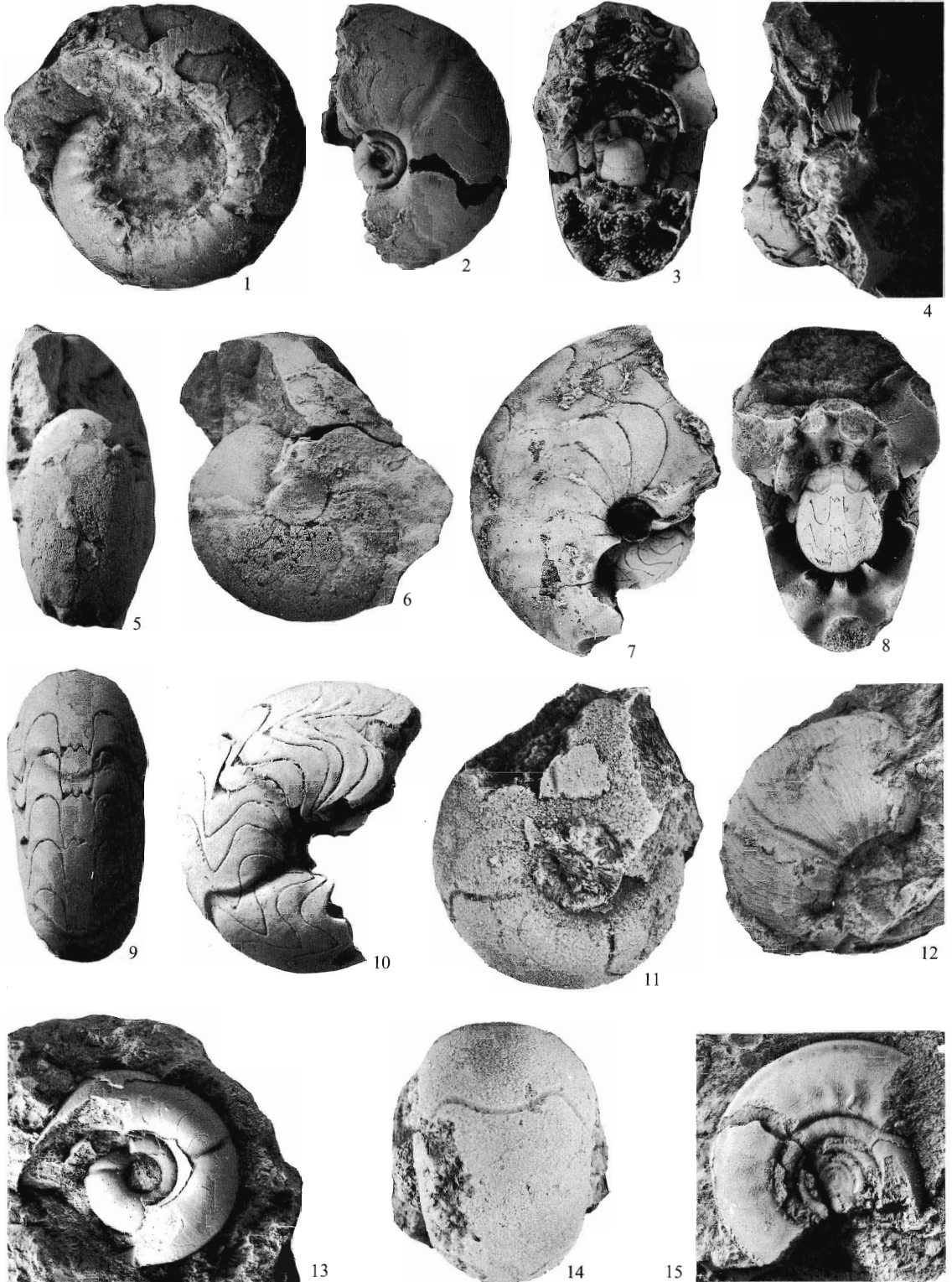




TEXT-FIG. 16. *Beyrichoceratoides* sp. A, C, Ro 5161; A, ventral suture, H = 13.5. C, constriction, H = 2.9. B, Ro 5160; constriction, H = 12.0;

EXPLANATION OF PLATE 6

- Figs 1, 4, 12. *Parahammatocyclus chaigleyensis* gen. et sp. nov. (see also Pl. 3, figs 1–3, 8; Pl. 7, fig. 8). 1, paratype, Ro 5137; locality 6; lateral view of mainly exfoliated adolescent conch; note failure of tubercles toward aperture; $\times 4$. 4, paratype, Ro 5105; locality 5; lateral view of fragmentary, partly testiferous adolescent conch; note failure of tubercles in final whorl; $\times 4$. 12, paratype, Ro 3721; locality 5; lateral view of fragmentary, testiferous adolescent conch; $\times 3.5$.
- Figs 2–3. *Dzhaprakoceras westheadi* sp. nov. (see also Pl. 7, figs 4–6); holotype, LZA 9407; locality 3b; lateral and oral views of fragmentary, exfoliated adolescent conch; $\times 2$.
- Figs 5–6. *Bollandoceras hodderense* (Bisat, 1924) (see also Pl. 8, figs 2–3, 8–9, 11); lectotype (here designated), BMNH C25732; locality 12; oral and lateral views of fragmentary, exfoliated late adolescent specimen; $\times 2$.
- Figs 7–8. *Dzhaprakoceras deflexum* Kusina, 1980 (see also Pl. 4, fig. 10); Ro 1007; locality 4a; lateral and oral views of fragmentary, exfoliated late adolescent conch; $\times 2$.
- Figs 9–10. *Dzhaprakoceras paracatena* sp. nov.; holotype, LZA 9391; locality 3b; ventral and lateral views of fragmentary, exfoliated adolescent conch; $\times 4$.
- Figs 11, 14. *Dzhaprakoceras djaprakense* (Librovitch, 1927); Ro 5193; locality 1; lateral and ventral views of exfoliated adolescent conch; $\times 3$.
- Fig. 13. *Beyrichoceratoides* sp. 2 (see also Pl. 18, figs 13, 15); Ro 5076b; locality 6; lateral view of fragmentary, partly testiferous juvenile conch; $\times 4$.
- Fig. 15. *Nomismoceras rotiforme* (Phillips, 1836) (see also Pl. 2, fig. 2); holotype, BMNH C271a; precise locality unknown, 'Bolland'; lateral view of fragmentary, exfoliated conch; $\times 4$.



RILEY, mid-Dinantian ammonoids

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5161	—	13.0	—	12.0*	—	—	—
Ro 5162	18.5	9.0	6.0*	9.5	0.51	0.32	0.49

Remarks. This form probably represents a new species; further description awaits the discovery of more material.

Beyrichoceratoides sp. 2

Plate 6, figure 13; Plate 8, figures 13, 15

Material. Specimen Ro 5076b, juvenile, partly testiferous conch, embedded in packstone; Ro 5056, exfoliated slightly crushed testiferous adolescent conch; RH 1638, fragmentary, testiferous, slightly crushed adult conch. All the material is from locality 6.

Range. Arundian, lower BB Zone; Hodder Mudstone Formation (Chaigley Limestone Member).

Description. The adult conch is subdiscoconic, but juveniles are cadiconic. The external ornament consists of straight, transverse striae in juveniles, which become progressively bisinuuous during growth. In the adult the striae are prosiradiate from the umbilical edge, which is raised slightly, but then deflect into a gentle lateral sinus on the mid-flank. There is a broad lingua and, apparently, a well developed hyponomic sinus, which is incompletely preserved. The venter is still rounded. The internal ornament shows feeble undulations which follow the path of the external ornament. Constrictions are present, at least until mid-adolescence; there are three per whorl and they also follow the external ornament. The suture is incompletely preserved but shows a rounded lateral saddle and an acute lateral lobe.

Remarks. These specimens are placed in *Beyrichoceratoides* on account of the cadiconic juvenile stage and the late development of strongly bisinuuous ornament. *Beyrichoceratoides* sp. 1 is more laterally compressed with a less steep umbilical wall.

Genus BOLLANDOCERAS Bisat, 1952

Type species. *Beyrichoceras submicronotum* Bisat, 1934.

Diagnosis. The conch is of small to moderate size, subsphaeroconic to discoconic with a small umbilicus. Juveniles are serpenticonic, but by early adolescence the conch is cadiconic. The venter may be rounded or subquadrate. The external ornament is transverse, radial in juvenile specimens but later bisinuuous with a lateral and hyponomic sinus. Constrictions, if present, are parallel to the ornament. The ventral lobe has flexed, divergent (orad) sides. The lateral saddle is rounded. The lateral lobe is acute, often with flexed sides.

Range. Arundian to Asbian (possibly early Brigantian).

Remarks. The following species are included:

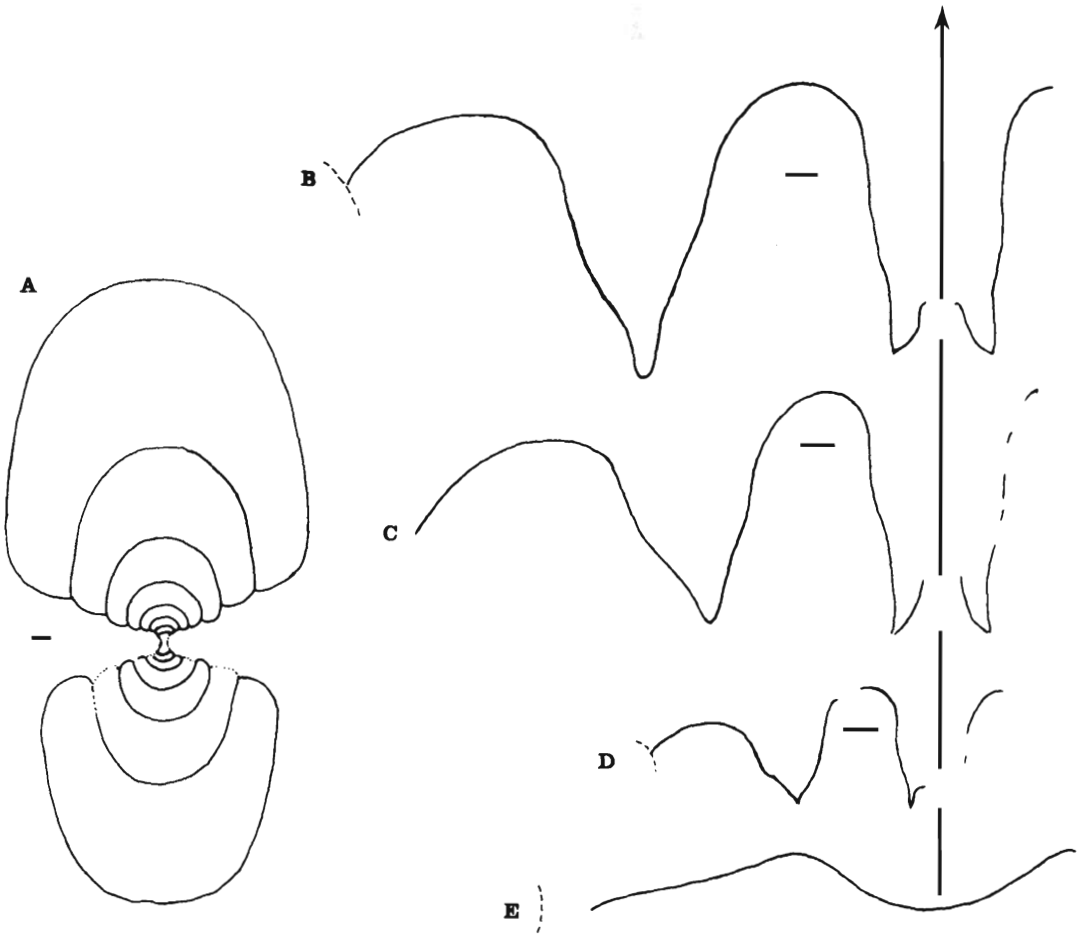
B. bashachense (Popov, 1965); Kara-Kiya Suite, Tien-Shan, Kirgizya, CIS, Arundian.

B. excavatum (Phillip, 1836); Carboniferous Limestone, Bowes, north-west England, Asbian.

B. furiense (Padget, 1952); Fury River, Co. Tyrone, Northern Ireland, Asbian.

B. globosum Bisat 1952; Lower Bowland Shale Formation, Barnoldswick, north-west England, late Asbian.

B. hodderense (Bisat, 1924); Great Falls Limestone Formation, Stonyhurst, north-west England, late Holkerian.



TEXT-FIG. 17. *Bollandoceras hodderense* (Bisat, 1924) A-B, Ro 5190; A, axial section; B, ventral suture, H = 12.2, W = 13.6; C, E, Ro 5191; C, ventral suture, D = 24.4, H = 11.2, U = 4.9, W = 13.0; E, constriction, H = 8.2, W = 10.1 (same scale as C). D, lectotype, BMNH c25732; ventral suture, H = 6.8.

- B. librovitchi* (Popov, 1965); base of Kara-Kiya Suite, Tien-Shan, Kirgizya, CIS, Arundian.
B. mackellari (Campbell, Brown and Coleman, 1983); Caswell Creek Group, Queensland, Australia, Asbian or Brigantian.
B. micronotoides (Bisat, 1934); 'reef limestone', Swinden Quarry, Cracoe, northern England, Asbian.
B. micronotum (Phillips, 1836); Bolland, north-west England, Asbian (preserved in reef limestone).
B. minusculum (Kusina, 1980); Kosvinsky Suite, Kozhim River, north Urals, Russian Federation, CIS, ?Arundian.
B. stylense Kusina, 1991; zone C₁V_e base of Stylsky Horizon, Donets Basin, Ukraine, CIS, ?Arundian.
B. submicronotum (Bisat, 1934); 'reef limestone', Cow Low Nick, Castleton, northern England, Asbian.

Dzhapraceras? minusculum Kusina, 1980, belongs here on account of its serpenticonic early whorls and divergent-sided (orad), flexed ventral lobe. *Beyrichoceras* (*Bollandites*) *bashachensis*

Popov, 1965 should also be placed in *Bollandoceras* since its constrictions are bisinuuous, a feature not present in *Bollandites* as redefined herein (p. 75).

Bollandoceras hodderense (Bisat, 1924)

Plate 6, figures 5–6; Plate 8, figures 2–3, 8–9, 11; Text-figures 17–18

- 1924 *Beyrichoceras hodderense* Bisat, p. 84, pl. 9, figs 6–7
 non 1940a *Beyrichoceras hodderense* Bisat var. *vallense* nov. var. Delépine, p. 63, pl. 3, figs 13–18.
 1961 *Bollandoceras hodderense* (Bisat); Ramsbottom in Earp *et al.*, pl. 11, fig. 9a–b.
 non 1961 *Beyrichoceras hodderense* Bisat; Pareyn p. 114, pl. 9, figs 8–16; text-fig. 14.

Type specimen. Lectotype here designated, BMNH C. 25732, no original figure.

Material. Ro 5188–91, RH 1536–1566, adolescent and mature conches, exfoliated and preserved in micrite; from localities 9 (Ro 5189–91), 11 (RH 1536–1566) and 12 (topotype, Ro 5188).

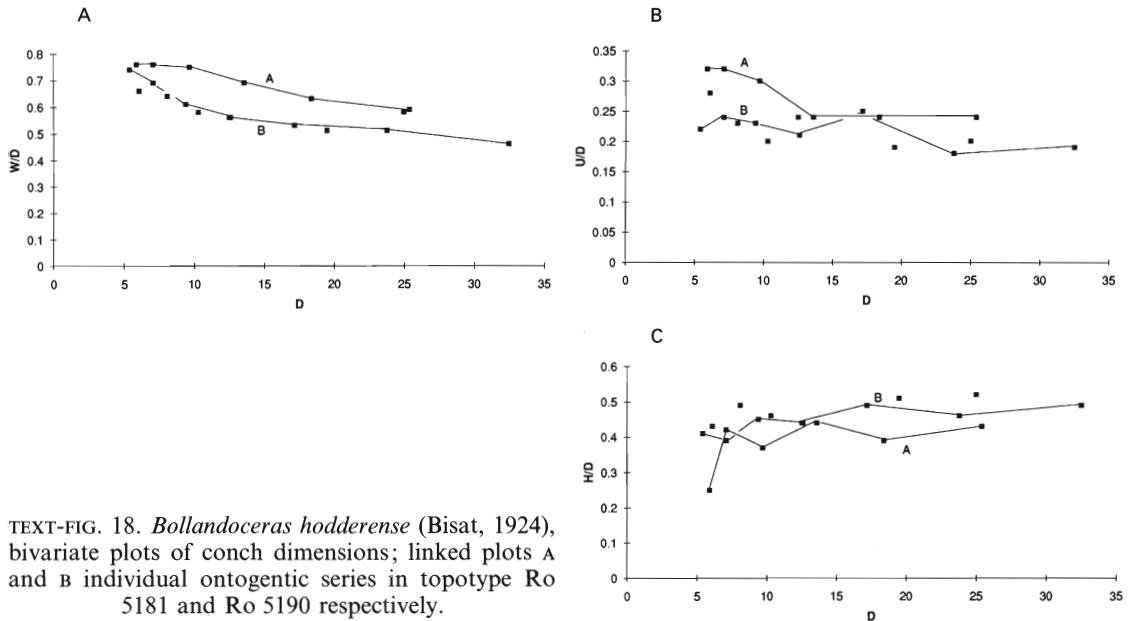
Range. Holkerian, upper BB Zone; Hodderense Limestone Formation. Known also from the Milldale Limestones in Staffordshire. Records from Belgium and the Sahara are incorrect.

Diagnosis. A *Bollandoceras* with a stout subdiscoconic conch which maintains constrictions and an expanding umbilicus throughout ontogeny.

Description. The conch is variable from discoconic to subpachyconic, involute, with moderate whorl expansion. The umbilicus expands throughout growth. The external ornament consists of weak, gently bisinuuous transverse striae, three to four per mm at H = 7 mm. The internal ornament shows feeble undulations which follow the external ornament. There are up to six constrictions per whorl, these run parallel to the external ornament and are retained throughout growth. The suture consists of a deep, narrow ventral lobe with flexed sides which diverge orad, a rounded lateral saddle and a relatively narrow lateral lobe with an acuminate termination.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5190	32.5	16.0	6.0	15.0	0.46	0.19	0.49
Ro 5191	25.0	13.0	5.0	14.5	0.58	0.20	0.52
Ro 1536	19.5	9.9	3.7	10.0	0.51	0.19	0.51
Ro 5188	12.5	5.5	3.0	7.0	0.56	0.24	0.44
Ro 1550	10.3	4.7	2.1	6.0	0.58	0.20	0.46
Ro 1555	8.1	4.0	1.9	5.2	0.64	0.23	0.49
Ro 1564	6.1	2.6	1.7	4.0	0.66	0.28	0.43
Ro 5181	25.4	11.0	6.0	14.9	0.59	0.24	0.43
Ro 5181	18.4	7.1	4.4	11.5	0.63	0.24	0.39
Ro 5181	13.6	6.0	3.3	9.4	0.69	0.24	0.44
Ro 5181	9.7	3.6	2.9	7.3	0.75	0.30	0.37
Ro 5181	7.1	3.0	2.3	5.4	0.76	0.32	0.42
Ro 5181	5.9	1.5	1.9	4.5	0.76	0.32	0.25
Ro 5190	23.8	10.9	4.3	12.2	0.51	0.18	0.46
Ro 5190	17.2	8.4	3.6	9.2	0.53	0.25	0.49
Ro 5190	12.6	5.6	2.7	7.1	0.56	0.21	0.44
Ro 5190	9.4	4.2	2.2	5.7	0.61	0.23	0.45
Ro 5190	7.1	2.8	1.7	4.9	0.69	0.24	0.39
Ro 5190	5.4	2.2	1.2	4.0	0.74	0.22	0.41



TEXT-FIG. 18. *Bollandoceras hodderense* (Bisat, 1924), bivariate plots of conch dimensions; linked plots A and B individual ontogenetic series in topotype Ro 5181 and Ro 5190 respectively.

Remarks. *Bol. hodderense* is distinguishable from other subdiscoconic to discoconic *Bollandoceras* since the umbilicus does not contract and constrictions are retained during ontogeny.

Bollandoceras micronotum Phillips (1836)

Plate 8, figures 5, 7; Text-figures 19–20

- 1836 *Goniatites micronotus* Phillips, p. 234, pl. 19, figs 22–23.
- 1889 *Glyphioceras micronotum* (Phillips); Holzapfel, pl. 2, fig. 1.
- 1897 *Glyphioceras micronotum* (Phillips); Foord and Crick, p. 173, text-fig. 81.
- 1924 *Beyrichoceras micronotum* (Phillips); Bisat, p. 46, pl. 9, figs 4–5.
- 1934 *Beyrichoceras micronotum* (Phillips); Bisat, pp. 289, 291, pl. 24, fig. 2, text-fig. 18.
- 1940a *Beyrichoceras micronotum* (Phillips); Delépine, p. 68, pl. 4, figs 9–12.
- 1941 *Beyrichoceras micronotum* (Phillips); Delépine, p. 62, pl. 3, figs 25–32.

Holotype. BMNH C262a, figured by Phillips (1836, pl. 19, figs 22–23).

Material. Specimens Ro 4316, 4320, 4322–3, 4328–31, 4333, 4336, 4346, 4350, 4351–3, 4357 and 4362–80, solid partly exfoliated conches, some septate and fragmentary, representing all growth stages, preserved in micrite and silicified packstone; from localities 11 (uppermost beds) and 13.

Range. Asbian, B Zone; Pendleside Limestone to Lower Bowland Shale Formation. Widespread in this zone in western Europe.

Diagnosis. A laterally compressed, discoconic *Bollandoceras* in which the umbilicus contracts during late ontogeny.

Description. The conch is discoconic with moderate whorl expansion. The umbilicus expands until late ontogeny when it reduces in diameter. The external ornament consists of bisinuous transverse striae. The internal ornament shows feeble undulations which correspond with the external ornament. There are four constrictions per whorl; the constrictions also follow the path of the external ornament, but become weak during ontogeny.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 4322	19.0	10.6	3.1	10.4	0.55	0.16	0.56
Ro 4353	12.4	5.7	—	6.7	0.54	—	0.50
Ro 4330	9.8	5.4	1.2	5.4	0.55	0.12	0.55
Ro 4330	6.8	3.2	1.3	4.3	0.63	0.19	0.47
Ro 4330	4.8	2.2	1.2	3.4	0.71	0.25	0.46
Ro 4330	3.5	1.4	1.2	2.6	0.74	0.34	0.40
Holotype	24.5	12.3	4.0	12.0	0.49	0.16	0.50

Remarks. *Bol. micronotum* is close to *Bol. minusculum* (Kusina, 1980) which, however, lacks constrictions. *Bol. micronotum* differs from other discoconic *Bollandoceras* with laterally compressed conches and progressively contracting umbilici, in that the venter is not sub-quadrate at maturity.

Bollandoceras sp. 1

Plate 8, figure 4; Text-figure 21

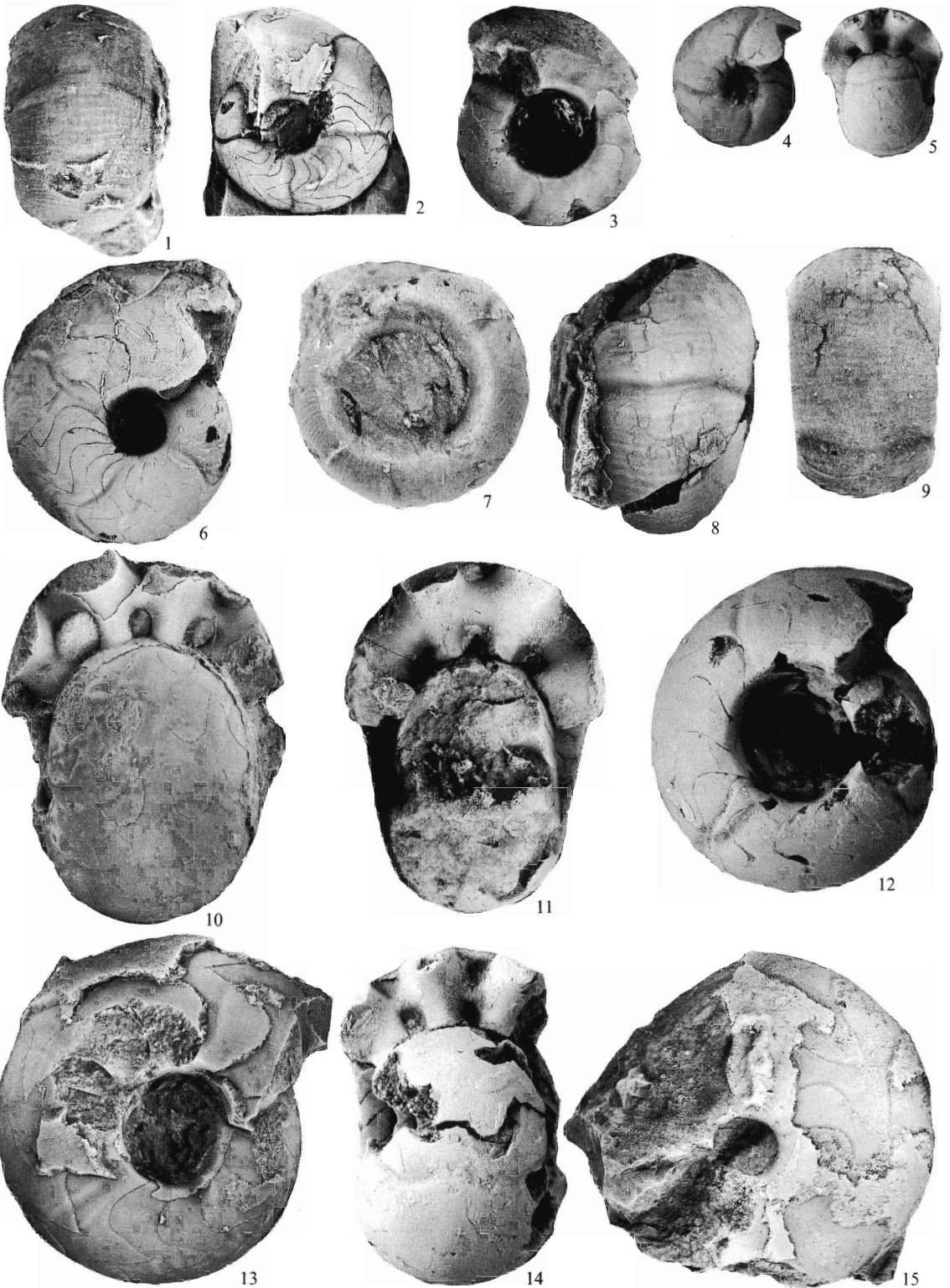
Material. One, exfoliated, septate early adolescent specimen, Ro 5163, preserved in sparry calcite; from locality 8.

Range. Holkerian, upper BB Zone; Hodder Mudstone Formation.

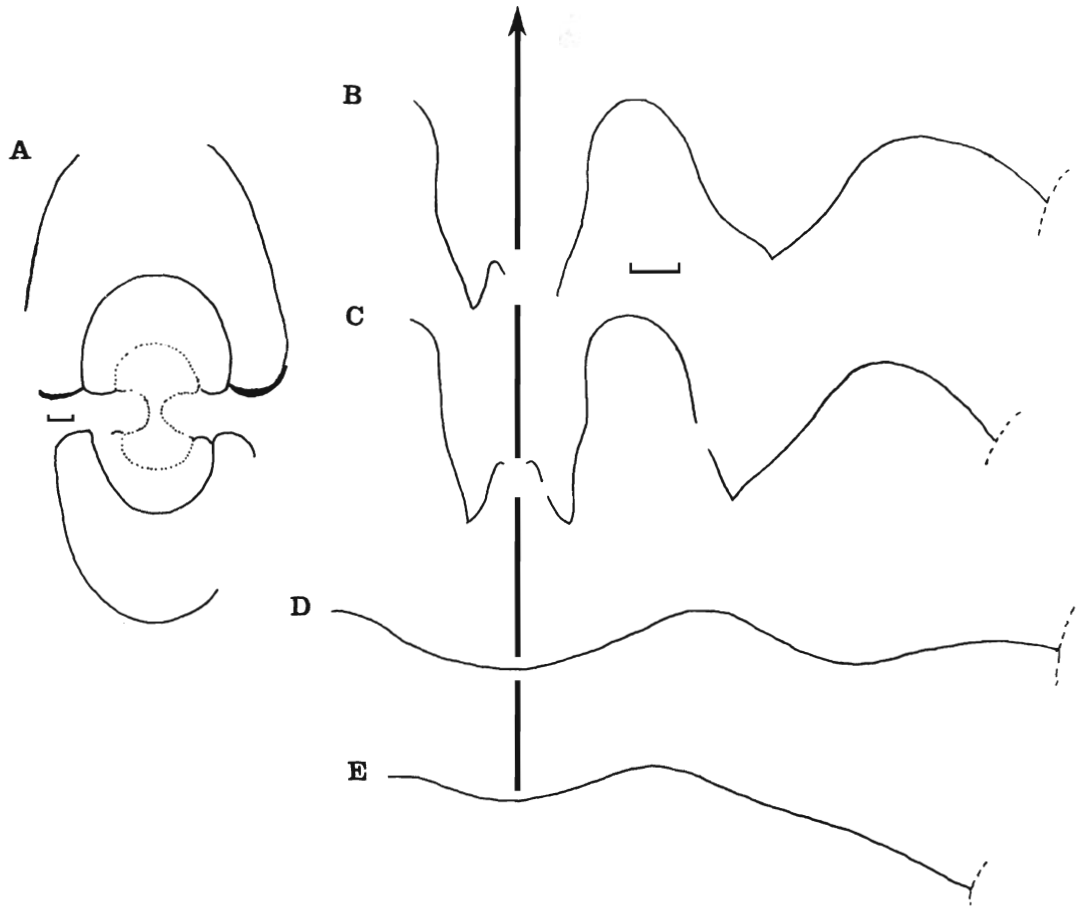
Description. Conch compressed, involute, but with an open umbilicus and rounded venter. The ornament, which is only partly preserved, consists of frail transverse bisinuuous striae, with a lateral sinus and a strong hyponomic sinus, separated by a feeble lingua. Three strong constrictions occur, and these apparently follow the external ornament; the internal ornament is apparently smooth. The suture, although not well preserved, shows a flexed, divergent sided (orad) ventral lobe with flexed walls and a rounded lateral saddle.

EXPLANATION OF PLATE 7

- Figs 1, 3, 7, 9, 11. *Bollandites varians* sp. nov. (see also Pl. 8, fig. 14). 1, 7; paratype, Ro 951; locality 11; ventral and lateral views of testiferous juvenile; $\times 8$. 3, paratype, Ro 5187; locality 11; lateral view of exfoliated adolescent conch; $\times 2$. 9, paratype, Ro 953; locality 11; ventral view of exfoliated juvenile conch; note ribbing; $\times 8$. 11, holotype, LZA 7865; locality 12; oral view of fragmentary, exfoliated adult conch; $\times 1.75$.
- Fig. 2. *Dzhaprakoceras undulatum* sp. nov. (see also Pl. 4, figs 8–9; Pl. 5, fig. 1); paratype, Ro 923; locality 4a; lateral view of partly testiferous, adolescent conch; $\times 2.25$.
- Figs 4–6. *Dzhaprakoceras westheadi* sp. nov. (see also Pl. 6, figs 2–3); locality 3b. 4–5, paratype, LZA 9407; lateral and oral views of exfoliated juvenile conch (dissected); $\times 4$. 6, paratype, Ro 920; lateral view of exfoliated, partly crushed adolescent conch; $\times 2.5$.
- Fig. 8. *Parahammatoicyclus chaigleyensis* gen. et sp. nov. (see also Pl. 3, figs 1–3, 8; Pl. 6, figs 1, 4, 12); paratype, Ro 3723; locality 7; ventral view of fragmentary exfoliated adolescent conch; $\times 2.75$.
- Figs 10, 13. *Beyrichoceratoides inflatus* sp. nov. (see also Pl. 4, figs 13–14); paratype, Ro 5168; locality 4a; oral and lateral views of largely exfoliated, late adolescent conch; $\times 2$.
- Figs 12, 14. *Dzhaprakoceras bellmanense* sp. nov. (see also Pl. 5, figs 8–9); paratype, LZA 9419; locality 3b; fragmentary, exfoliated adolescent conch; $\times 4$.
- Fig. 15. *Dzhaprakoceras deflexum* Kusina, 1980 (see also Pl. 4, fig. 10; Pl. 6, figs 7–8); LZA 9522; locality 4a; lateral view of fragmentary, partly testiferous adolescent conch; $\times 2$.



RILEY, mid-Dinantian ammonoids



TEXT-FIG. 19. *Bollandoceras micronotum* (Phillips, 1836). A, Ro 4330; axial section. B, D, holotype, BMNH C262a; B, ventral suture, H = 9.7; constriction at D = 19.7, H = 9.4; C, E, Ro 4322; C, ventral suture, H = 8.4; E, constriction at H = 8.4.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5163	12.0	5.5	2.5	6.5	0.54	0.21	0.46

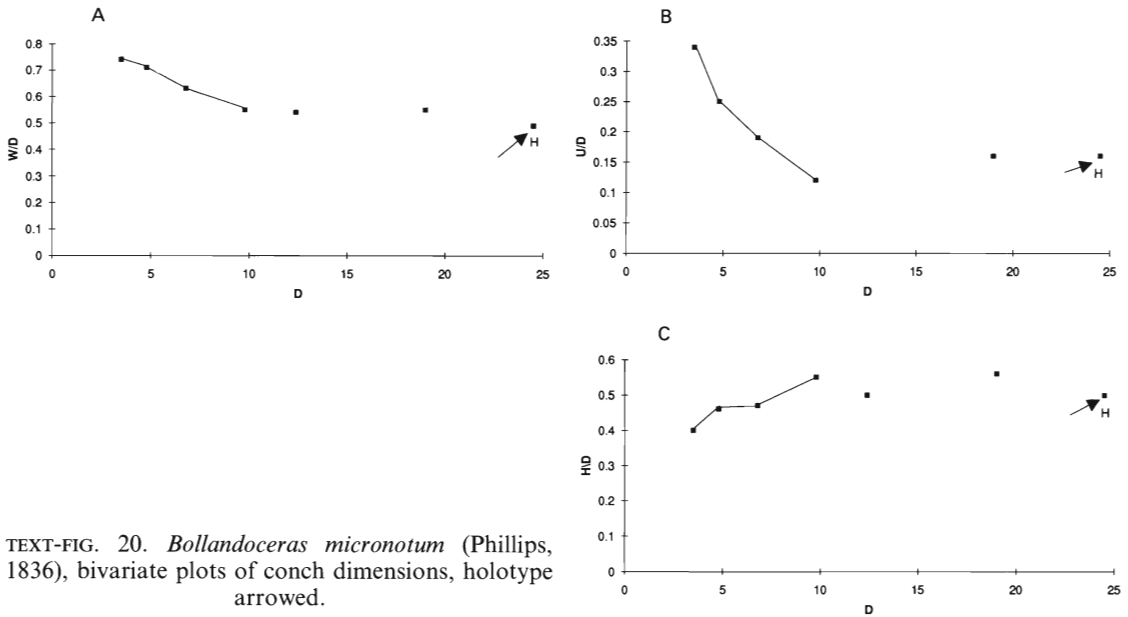
Remarks. Because the ontogenetic development is taxonomically important in the recognition of *Bollandoceras* species, this specimen has been left in open nomenclature pending discovery of further material.

Bollandoceras sp. 2

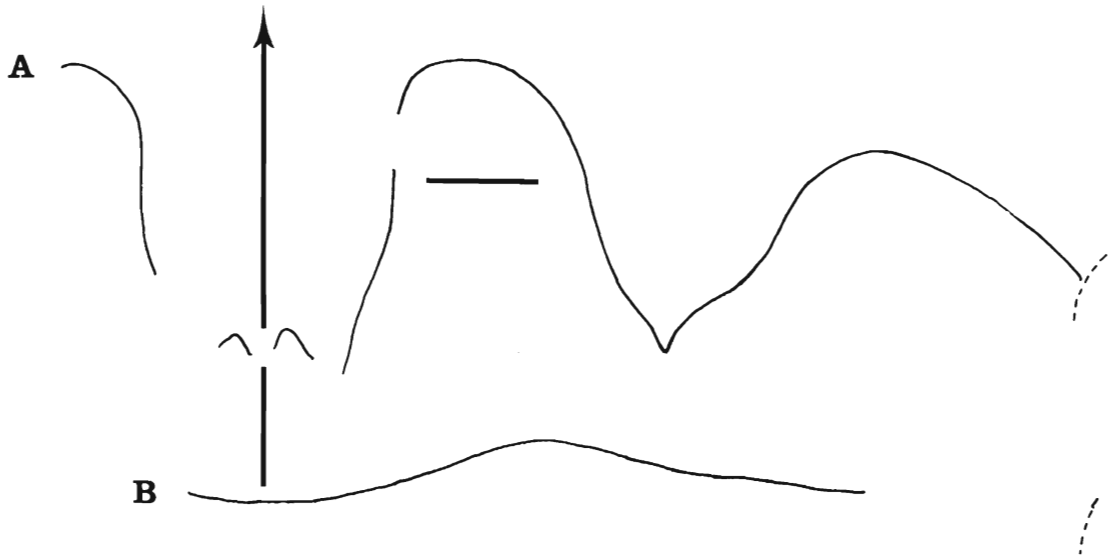
Plate 8, figures 6, 10; Text-figure 22

Material. Ro 5136, solid, mostly exfoliated, partly septate adolescent conch; from locality 6.

Range. Arundian, lower BB Zone; Hodder Mudstone Formation (Chaigley Limestone Member).



TEXT-FIG. 20. *Bollandoceras micronotum* (Phillips, 1836), bivariate plots of conch dimensions, holotype arrowed.



TEXT-FIG. 21. *Bollandoceras* sp. 1; A, Ro 5163; ventral suture, D = 11.0, H = 5.5; B, constriction, D = 11.0, H = 5.5.

Description. The conch is small, subdiscoconic, laterally compressed and relatively involute with rapid whorl expansion. The internal ornament consists of feeble transverse striae (five per mm on the ventro-lateral shoulder at H = 3.4), which are radial over the flanks, but curve aborad over the venter to form a broad hyponomic sinus. There are three constrictions per whorl, which have a slight lateral and a deeper hyponomic sinus (the external ornament is not preserved at comparable diameters). The ventral lobe is divergent-sided (orad) with slightly flexed sides. The lateral saddle is broad and rounded. The lateral lobe is shallow, broad and acute, with a flexed dorsal side.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5136	11.0	6.8	2.1	6.2	0.56	0.19	0.62

Remarks. The ornament style, broad nature of the lateral lobe and the divergent-sided (orad) ventral lobe are consistent with *Bollandoceras*. Specific identification awaits discovery of more material, so that the ontogeny can be elucidated. The adolescent conch of this species is more compressed than *Bol.* sp. 1, and the transverse ornament develops a lateral and hyponomic sinus much later in ontogeny.

Genus DZHAPRAKOCERAS Popov, 1965

Type species. *Muensteroceras tianshanicum* Librovitch, 1927.

Diagnosis (emended). The conch varies from mainly pachyconic to discoconic, but cadiconic to subsphaeroconic forms are also represented. A juvenile serpenticonic stage is absent. The external ornament consists of weak, bisinuuous, transverse striae which are present from the late juvenile stage. Constrictions occur commonly and follow the external ornament, but may fail during adolescence. The internal ornament, if present, follows the external ornament and consists of feeble undulations, particularly in the lingual region; weak spiral undulations may also occur. The ventral lobe is lyrate. The lateral saddle is rounded. The lateral lobe is acute.

Range. (?Courceyan) Chadian to Arundian.

Remarks. The following species are included:

D. bellmanense sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

D. catena sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

EXPLANATION OF PLATE 8

Figs 1, 14. *Bollandites varians* sp. nov. (see also Pl. 7, figs 1, 7, 9). 1, paratype, Ro 5187; locality 11; oral view of exfoliated adolescent conch; $\times 2$. 14, holotype, LZA 7865; locality 12; lateral view of fragmentary, exfoliated adult conch; $\times 1.75$.

Figs 2-3, 8-9, 11. *Bollandoceras hodderense* (Bisat, 1924) (see also Pl. 6, figs 5-6). 2-3, topotype, Ro 5181; lateral and ventral views of fragmentary, exfoliated adult conch; locality 12; stout variant, $\times 1.6$. 8-9, 11, Ro 5191; locality 13; oral, lateral and ventral views of exfoliated adult conch; $\times 2$.

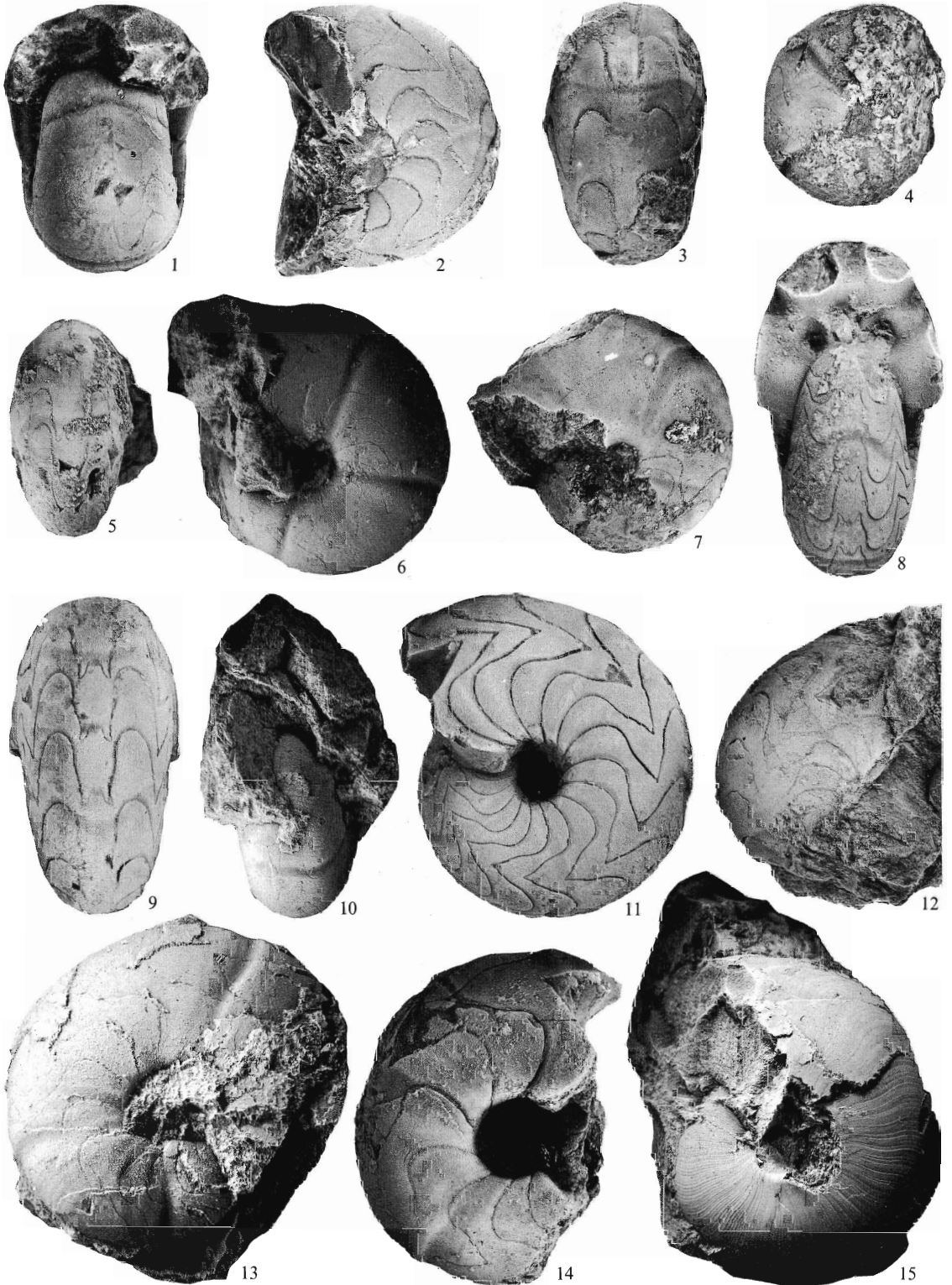
Fig. 4. *Bollandoceras* sp. 1; Ro 5163; locality 8; lateral view of exfoliated, early adolescent conch; $\times 2$.

Figs 5, 7. *Bollandoceras micronotum* (Phillips, 1836); Ro 4322; locality 13; ventral and lateral views of exfoliated adolescent conch; $\times 2$.

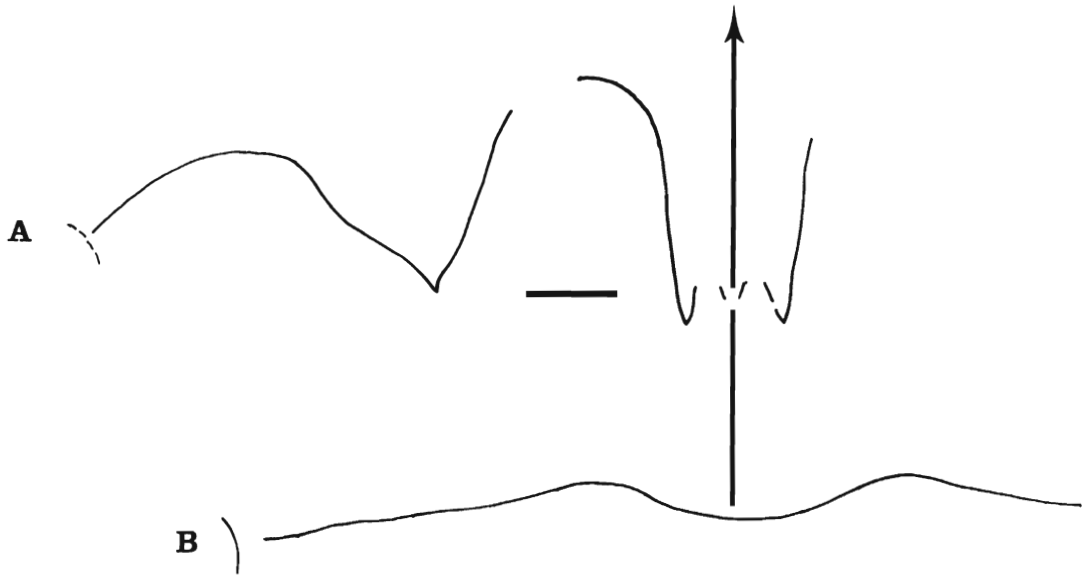
Figs 6, 10. *Bollandoceras* sp. 2; Ro 5136; locality 6; lateral and oral views of exfoliated, early adolescent conch; $\times 4$.

Figs 13, 15. *Beyrichoceratoides* sp. 2 (see also Pl. 6, fig. 13); locality 6. 13, Ro 5056; lateral view of exfoliated, slightly crushed adolescent conch; $\times 4$. 15, RH 1638; lateral view of fragmentary, testiferous, slightly crushed adult conch; $\times 2$.

Fig. 12. *Beyrichoceras* aff. *obtusum* (Phillips, 1836); Ro 2160; locality 13; lateral view of fragmentary exfoliated conch; $\times 2$.



RILEY, mid-Dinantian ammonoids



TEXT-FIG. 22. *Bollandoceras* sp. 2; Ro 5136; A, ventral suture, $D = 10.3$, $H = 5.2$, $U = 1.8$, $W = 6.1$; B, constriction, same conch dimensions as A.

D. chermnykhi Kusina, 1980; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

D. deflexum Kusina, 1980; ?Nortnichsky Horizon, Chernaya River, north Urals, Russian Federation, CIS, ?Arundian.

D. djaprakense (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.

D. duponti (Delépine, 1940a); Waulsortian, Drehance, Belgium, late Tournaisian.

D. flexum sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

D. gracile Kusina, 1980; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

D. grande Kusina, 1980; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

D. hibernicum (Delépine, 1940b); Waulsortian, St Doughlas, Dublin, Ireland, late Tournaisian.

D. hispanicum (Foord and Crick, 1897); Carboniferous, Asturias, Spain, Dinantian.

D. improcerum Kusina, 1980; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, Chadian.

D. kokdzhareense (Popov, 1965); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.

D. koninckianum (Schindewolf 1951a); Waulsortian, Pauquays, Belgium, late Tournaisian.

D. latilobatum Kusina, 1983; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

D. latumbilicatum (Kullmann, 1961); 'Marbre Griotte', Cantabria, north Spain, late Tournaisian or ?early Viséan.

D. levis sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

D. narynense (Popov, 1965); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.

D. paracatena sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

D. planum Kusina and Yatskov, 1987; Milin Suite, Novaya Zemlya, CIS, 'mid-Viséan'.

- D. pseudoparallelum* (Delépine, 1941); 'Green Slates', Erfoud, Morocco, mid-Dinantian.
D. quantulum Kusina and Yatskov, 1987; Milin Suite, Novaya Zemlya, CIS, 'mid-Viséan'.
D. shabyrense (Popov, 1968); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.
D. sonkulica (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.
D. subglobosum (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.
D. subtile Kusina, 1980; Nortnichsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, Arundian.
D. tianshanicum (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.
D. westheadi sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.
D. undulatum sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

D. grande, *D. latiumbilitatum* and *D. undulatum* sp. nov. may belong to *Beyrichoceratoides*, since their early whorls are unknown. *D.?* *minusculum* Kusina, 1980 is transferred to *Bollandoceras* on account of its serpenticonic early whorls and divergent-sided (orad) ventral lobe. *Dzhaprakoceras* was originally intended to include muensteroceratids with lyrate ventral lobes; however, this ventral lobe form is not restricted to *Dzhaprakoceras*, occurring also in *Beyrichoceratoides* and *Kozhimites*. In this study *Dzhaprakoceras* is interpreted as including muensteroceratids with a combination of bisinuuous ornament (present from the late juvenile stage), lyrate ventral lobes, and absence of a juvenile serpenticonic stage. It is unfortunate that the ontogeny of the type species of *Dzhaprakoceras* is unknown. *Muensteroceras pseudaganides* George and Ponsford, 1935 is too poorly known for definite inclusion in *Dzhaprakoceras*; the holotype is probably an *Irinoceras*, but the paratypes are *Dzhaprakoceras* sp.

Dzhaprakoceras (Akeshakoceras) longilobatum Liang and Wang, 1991 does not belong to *Dzhaprakoceras*. The holotype (Liang and Wang 1991, pl. 14, figs 11–12) shows spiral ornament and an acute lateral saddle. It is clearly a goniatitid and not a muensteroceratid.

Dzhaprakoceras bellmanense sp. nov.

Plate 5, figures 8–9; Plate 7, figures 12, 14; Text-figures 23–24

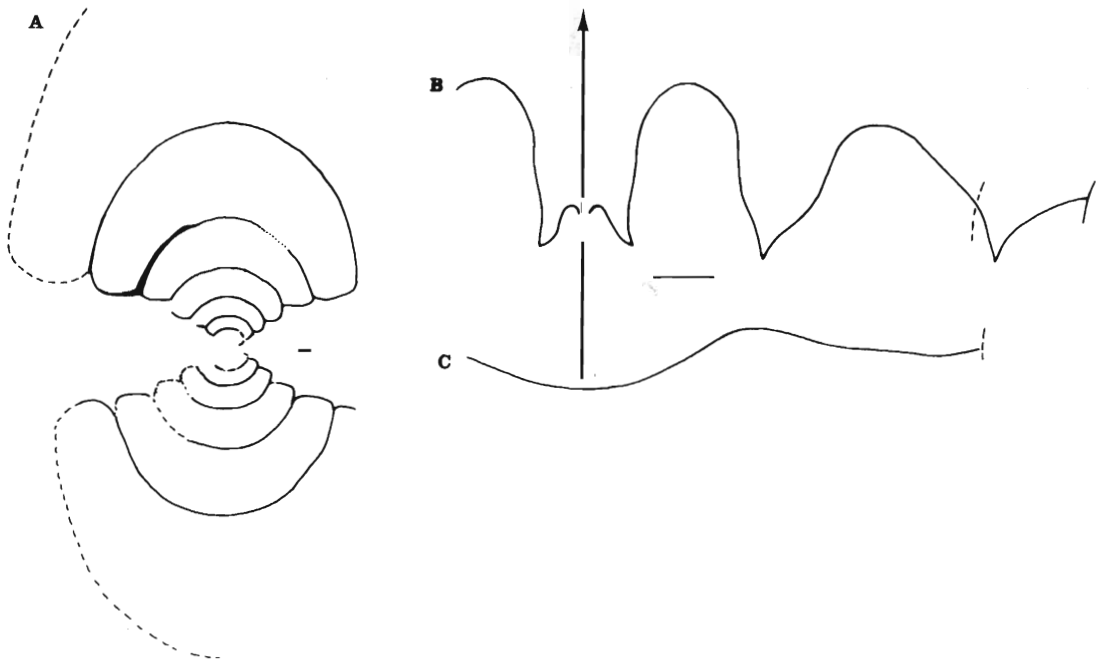
Deviation of name. From the type locality, Bellman Quarry.

Material. Holotype, Ro 915, fragmentary, exfoliated, late adolescent, septate conch preserved in micrite; from locality 4a; and paratype, LZA 9419, exfoliated, septate, pyritic conch; from locality 3b.

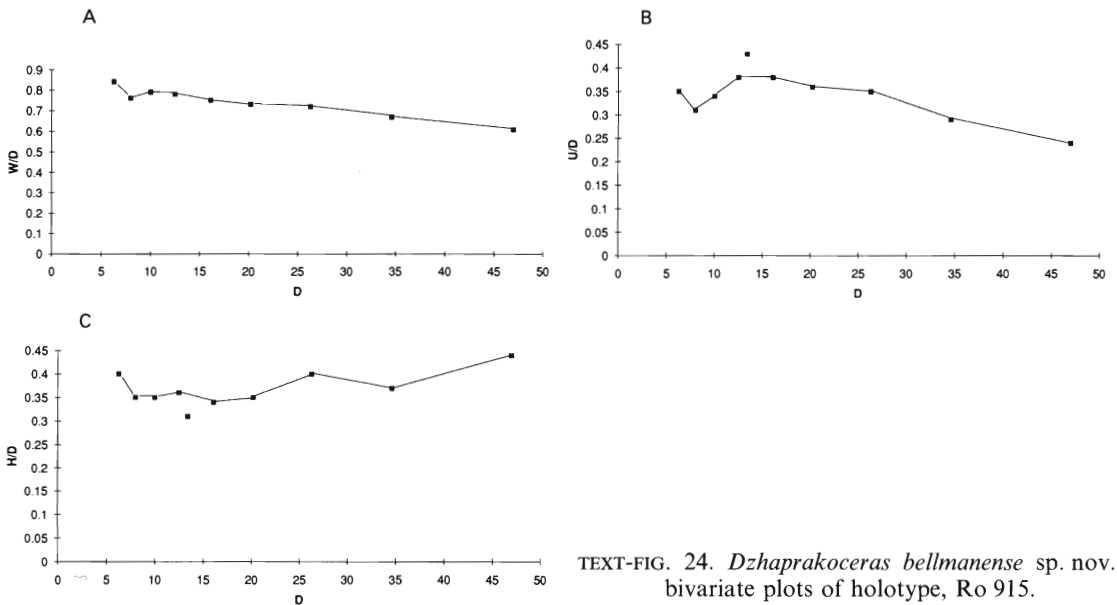
Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A large subdiscoconic *Dzhaprakoceras* which develops a lyrate ventral lobe during late adolescence.

Description. The conch is large ($D = 70+$), subdiscoconic and has an umbilicus of moderate width. Whorl expansion is moderate, but slow below $D = 35$, when the conch is cadoconic. The external ornament is unknown. The internal ornament consists of very weak transverse ridges with a shallow broad lateral and hyponomic sinus. Constrictions are present below $D = 13$ and run parallel with the external ornament. There are four per whorl. The suture is only clearly seen in the adolescent specimen, where the ventral lobe is slightly divergent-sided (orad), narrow and deep. In the holotype it is lyrate, but poorly preserved. The lateral saddle is narrow and rounded. The lateral lobe is deep and narrow and has flexed, subparallel sides, with an acute termination.



TEXT-FIG. 23. *Dzhaprakoceras bellmanense* sp. nov. A, holotype, Ro 915; axial section. B-C, paratype, LZA 9419; B, ventral suture, $D = 13.4$, $H = 4.2$, $U = 5.8$; C, constriction, same dimensions as B.



TEXT-FIG. 24. *Dzhaprakoceras bellmanense* sp. nov., bivariate plots of holotype, Ro 915.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 915	47.0	20.7	11.4	28.6	0.61	0.24	0.44
Ro 915	34.6	12.8	9.9	23.2	0.67	0.29	0.37
Ro 915	26.3	10.4	9.2	18.9	0.72	0.35	0.40
Ro 915	20.2	7.0	7.2	14.7	0.73	0.36	0.35
Ro 915	16.1	5.5	6.1	12.0	0.75	0.38	0.34
Ro 915	12.5	4.5	4.8	9.7	0.78	0.38	0.36
Ro 915	10.0	3.5	3.4	7.9	0.79	0.34	0.35
Ro 915	8.0	2.8	2.5	6.1	0.76	0.31	0.35
Ro 915	6.3	2.5	2.2	5.3	0.84	0.35	0.40

Remarks. This species is closest to a form incorrectly attributed to *D. hispanicum*, by Kusina (1980, pl. 4, fig. 5), but differs in its more inflated whorls and larger umbilicus.

Dzhaprakoceras catena sp. nov.

Plate 4, figures 1, 3, 7, 16; Text-figures 25–26

Derivation of name. From the Latin *catena* (= chain), with reference to the chain-like appearance of the coalesced ventral lobes.

Material. Holotype, Ro 5192, exfoliated, septate, pyritic late adolescent; from locality 3b; paratypes, LZA 9396, 9389, exfoliated, pyritic septate juveniles; from locality 3b; LZA 9395, pyritic, septate early adolescent; from locality 4b; Ro 916, exfoliated, septate adolescent preserved in micrite; from locality 4a.

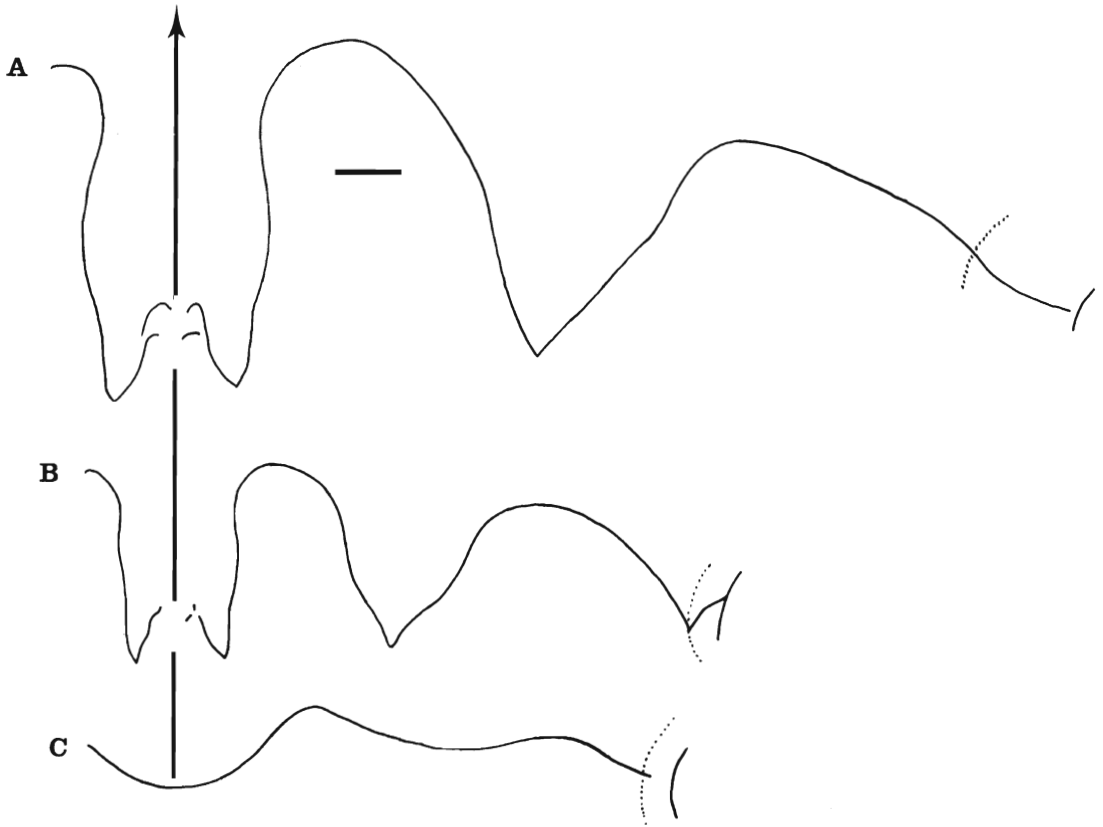
Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A small involute, discoconic *Dzhaprakoceras* with coalescent ventral lobes present by early adolescence and a relatively broad lateral lobe. Constrictions occur in the juvenile whorls, but fail by mid-adolescence.

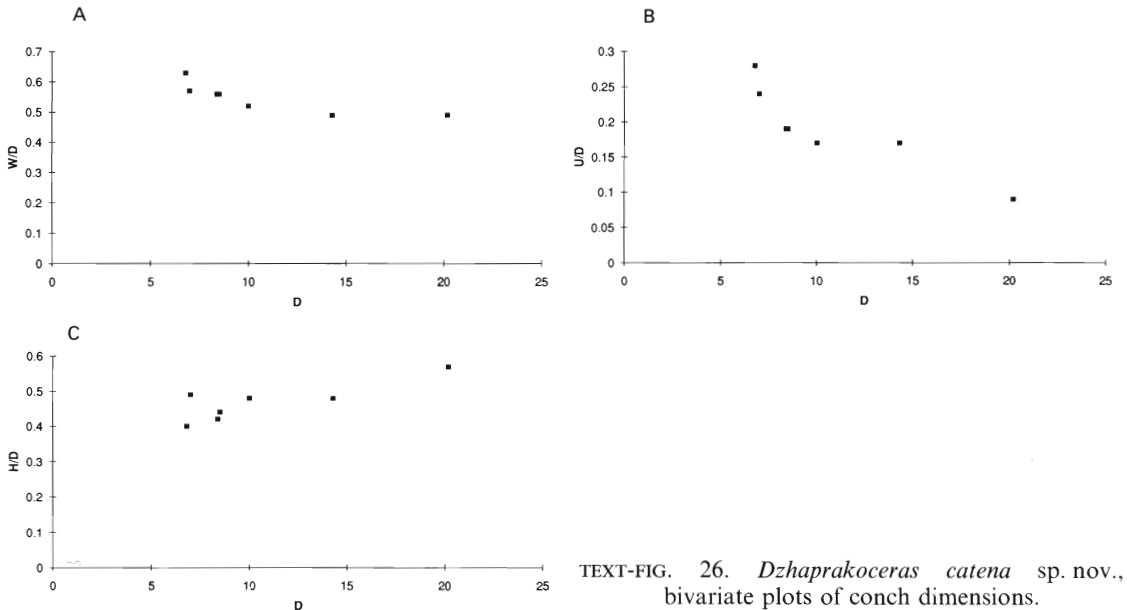
Description. The conch is small, discoconic, laterally compressed and involute with pachyconic early whorls, rapid whorl expansion and a small umbilicus. The external ornament is unknown. The internal ornament consists of weak transverse ridges on the flanks, corresponding with the position of the lateral sinus and lingua; these characters appear to be absent below H = 8. Constrictions are present below H = 5 (about four per whorl), they are bisinuuous with a nearly V-shaped hyponomic sinus and a shallow, broad lateral sinus. The ventral lobe is lyrate and deep; it becomes coalescent with adjacent lobes by early adolescence. The lateral saddle is broad and rounded. The relatively broad lateral lobe is nearly as deep as the ventral lobe and is acute, with flexed sides.

Dimensions.

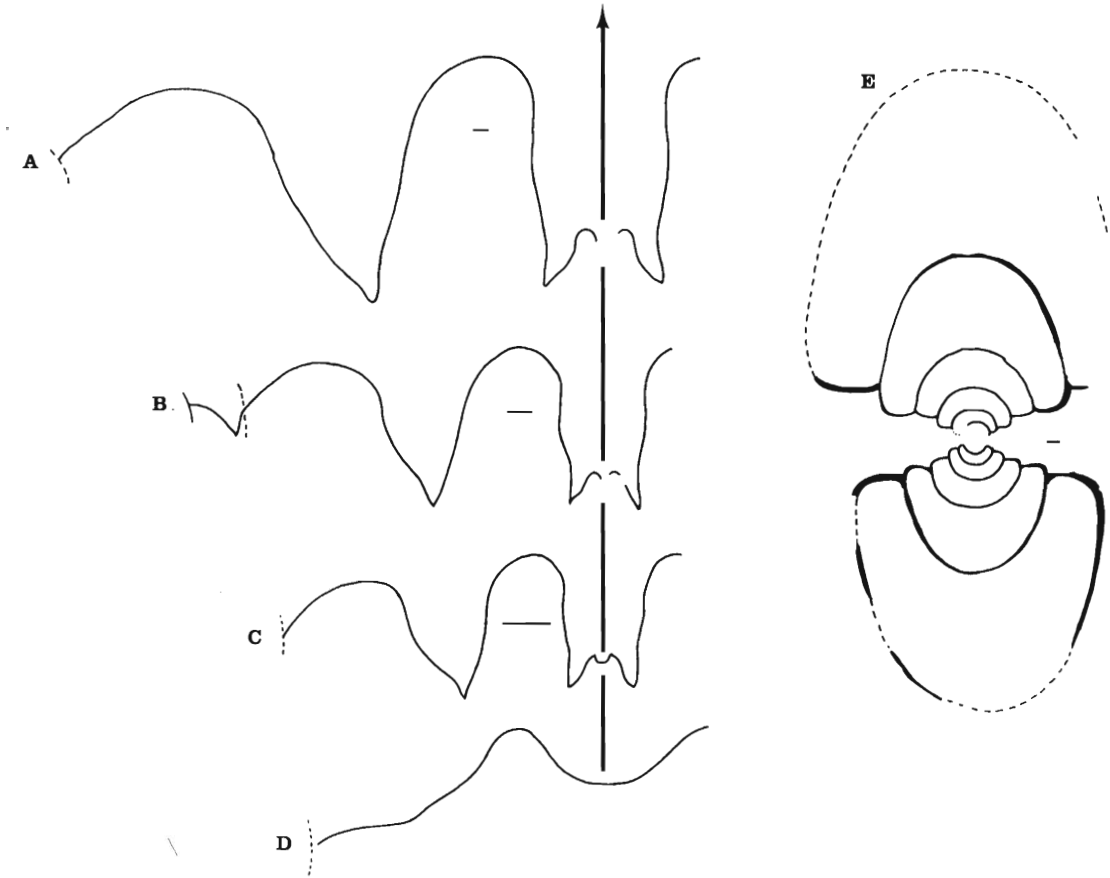
Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5192	20.2	11.5	1.9	9.9	0.49	0.09	0.57
LZA 9405	14.3	6.8	2.5	7.0	0.49	0.17	0.48
LZA 9409	10.0	4.8	1.7	5.2	0.52	0.17	0.48
LZA 9398	8.5	3.7	1.6	4.8	0.56	0.19	0.44
LZA 9394	8.4	3.5	1.6	4.7	0.56	0.19	0.42
LZA 9384	7.0	3.4	1.7	4.0	0.57	0.24	0.49
Ro 929	6.8	2.7	1.9	4.3	0.63	0.28	0.40



TEXT-FIG. 25. *Dzhaparakoceras catena* sp. nov. A, holotype, Ro 5192; ventral suture, $D = 18.4$, $H = 9.7$, $U = 2.3$, $W = 9.1$. B-C, paratype, LZA 9405; B, ventral suture, $D = 12.9$, $H = 6.2$, $U = 2.8$, $W = 6.4$; C, constriction, $D = 12.6$, $H = 6.0$, $U = 2.5$, $W = 5.0$.



TEXT-FIG. 26. *Dzhaparakoceras catena* sp. nov., bivariate plots of conch dimensions.



TEXT-FIG. 27. *Dzhaparakoceras deflexum* Kusina, 1980. A, Ro 1008; ventral suture, H = 26.0, W = 28.4. B, Ro 1007; ventral suture, H = 12.6, W = 13.2. C-D, LZA 9390; c, ventral suture, H = 5.5, W = 7.4; d, constriction, same dimensions as c. E, Ro 1025; axial section.

Remarks. *D. gracile* has a stouter conch than *D. catena* sp. nov. *D. chermnykhi* has a convex (dorsad) ventral side to the lateral lobe whereas in *D. catena* sp. nov. it is concave. *D. latilobatum*, unlike *D. catena* sp. nov., has divergent prongs (aborad) to the ventral lobe. The closest species to *D. catena* sp. nov. is *D. paracatena* sp. nov.; however, in the latter species the lateral lobe is narrower and has less divergent sides.

Dzhaparakoceras deflexum Kusina, 1980

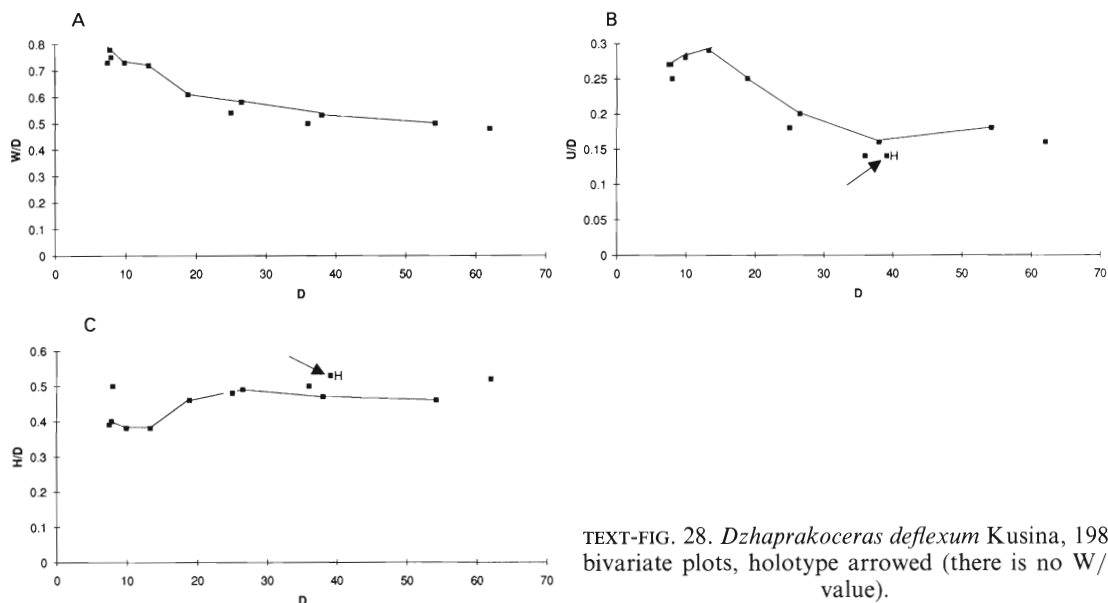
Plate 4, figure 10; Plate 6, figures 7-8; Plate 7, figure 15; Text-figures 27-28

1980 *Dzhaparakoceras deflexum*, Kusina, p. 58, pl. 4, fig. 7.

Holotype. PIN 2775/365, figured by Kusina (1980, pl. 4, fig. 7).

Material. Seven conches, LZA 9522, Ro 1007-8, and Ro 1023-5, partly exfoliated, some septate, representing all growth stages, preserved in micrite; from locality 4a; and Ro 1006, an early adolescent, pyritic internal mould; from locality 3b.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member). The type material is thought to be from the Arundian lower BB Zone, Nornichsky Horizon, north Urals.



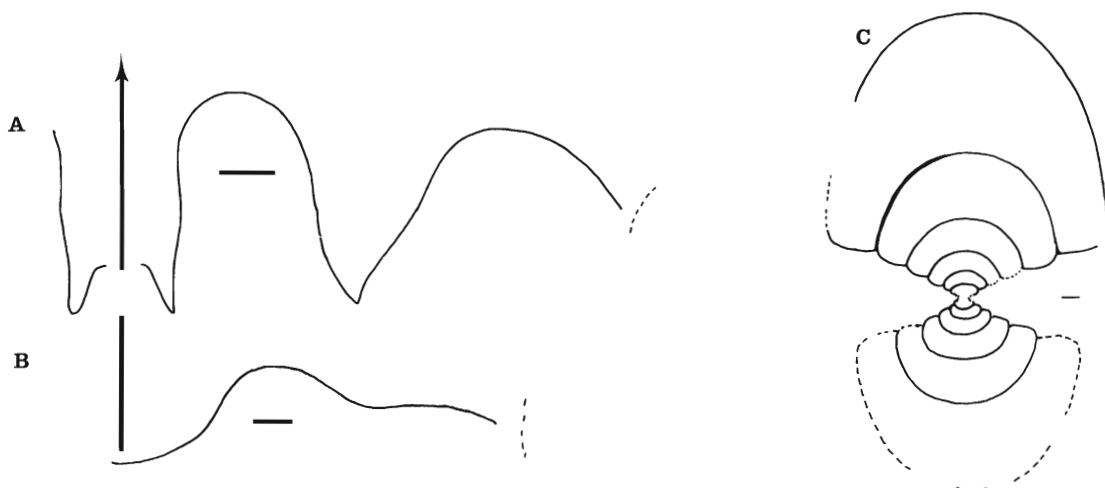
TEXT-FIG. 28. *Dzhaprakoceras deflexum* Kusina, 1980, bivariate plots, holotype arrowed (there is no W/D value).

Diagnosis. A subdiscoconic *Dzhaprakoceras* in which the ventral lobe is slightly divergent-sided (orad).

Description. The conch is subdiscoconic with a small umbilicus which expands constantly until maturity after which the umbilical diameter remains unchanged. The juvenile whorls are cadiconic; whorl expansion is relatively rapid after $D = 13$. The external ornament is only partly preserved (LZA 9522); it is virtually smooth, apart from very weak striae and growth lamellae. These are grouped together at the umbilical margin, giving the appearance of bands, but become virtually imperceptible over the mid-flank and venter. The internal ornament consists of weak bisinuuous ridges, which in adolescence give rise to vesicular ridges over the ventrolateral region corresponding with linguae. Four constrictions, which are bisinuuous, with a deep, broad hyponomic sinus, are present up to late adolescence, after which they fail. The suture shows a narrow deep ventral lobe with lyrate, parallel, flexed sides; the lateral saddle is narrow and rounded; the lateral lobe is deep, with divergent sides (orad) and a subacute termination.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 1008	62.0	32.0	10.0	30.0	0.48	0.16	0.52
Ro 1025	54.2	24.7	10.0	27.0	0.50	0.18	0.46
Holotype	39.1	20.8	5.3	—	—	0.14	0.53
Ro 1007	36.0	18.0	5.0	18.0	0.50	0.14	0.50
LZA 9522	25.0*	12.0	4.5	13.5	0.54	0.18	0.48
Ro 1006	8.0	4.0	2.0	6.0	0.75	0.25	0.50
LZA 9406	7.5	2.9	2.3	5.5	0.73	0.27	0.39
Ro 1025	38.0	17.8	6.4	20.2	0.53	0.16	0.47
Ro 1025	26.5	13.1	5.2	15.3	0.58	0.20	0.49
Ro 1025	18.9	8.7	4.7	11.6	0.61	0.25	0.46
Ro 1025	13.3	5.0	3.8	9.6	0.72	0.29	0.38
Ro 1025	9.9	3.8	2.8	7.2	0.73	0.28	0.38
Ro 1025	7.8	3.1	2.1	6.1	0.78	0.27	0.40



TEXT-FIG. 29. *Dzhapraceras flexum* sp. nov. A, C, paratype, LZA 9521; A, ventral suture, H = 7.9, W = 11.1; C, axial section. B, holotype, Ro 1009; constriction, H = 7.9 (reversed image).

Remarks. The slightly divergent-sided (orad) ventral lobe in adolescents superficially resembles that of *Bollandoceras*, but is not as severe. The lack of a juvenile serpenticonic stage, coupled with the early appearance of bisinuous transverse ornament, clearly places this species in *Dzhapraceras*. Kusina (1980) gave the type horizon as possibly the Nortnichsky Horizon; the presence of this species in the late Chadian in Britain suggests it is more likely that the type horizon is in the Kosvinsky Horizon.

Dzhapraceras sp. juv. cf. *djapracense* (Librovitch, 1927)

Plate 6, figures 11, 14

- 1927 *Muensteroceras djapracense* Librovitch, p. 37, pl. 7, figs 3–4; text-figs 18–19.
 1961 *Muensteroceras djapracense* Librovitch; Kullmann, p. 262, text-fig. 7b.
 1961 *Muensteroceras subglobosum* Librovitch; Pareyn, p. 104, pl. 8, figs 27–28.
 1968 *Dzhapraceras djapracense* (Librovitch); Popov, p. 89, pl. 3, figs 6–7, pl. 14, fig. 6, text-figs 15g, i–m, 16z.
 1980 *Dzhapraceras djapracense* (Librovitch); Kusina, p. 53, pl. 4, fig. 1; text-fig. 13.

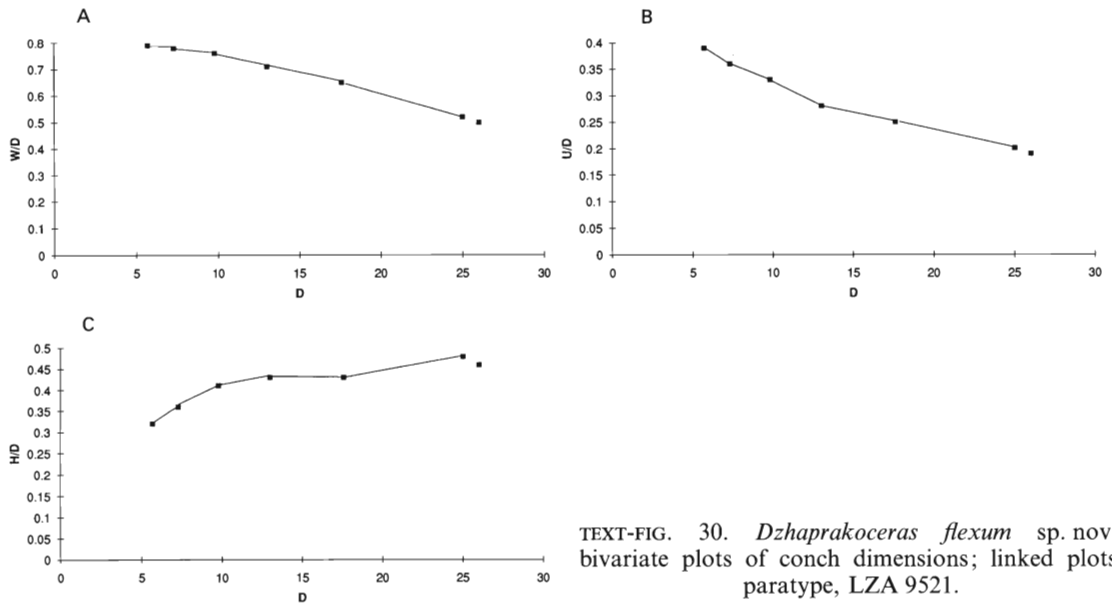
Lectotype. Designated by Kusina 1980, specimen 101/2473, TSNIGR Museum, St Petersburg, figured by Librovitch (1927, pl. 7, figs 3–4).

Material. Ro 5193, mid-adolescent, mostly exfoliated, septate (details of suture unclear), preserved in sparry calcite; from locality 1.

Range. Late Tournaisian, middle FA Zone; Clitheroe Limestone Formation (Coplw Limestone Member). Known also from middle FA Zone assemblages in north Africa, Spain and Tien-Shan (CIS).

Diagnosis. A subglobose *Dzhapraceras* with a relatively wide umbilicus.

Description. The conch is subpachyconic, with a relatively wide umbilicus. The external ornament is poorly preserved and consists of weak bisinuous striae. There are three narrow, deeply incised constrictions per whorl which show through to the exterior of the conch. Both the lateral and hyponomic sinuses are broad and separated by a narrow lingua. The suture is not well preserved, but consists of a rounded lateral saddle with flexed sides and an acute lateral lobe; the rest of the suture is not visible.



TEXT-FIG. 30. *Dzhaprakoceras flexum* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, LZA 9521.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 5193	16.0	6.5	5.0	12.0	0.75	0.31	0.41

Remarks. The ventral lobe is not preserved; identification is based on the conch shape and the early presence of bisinuous ornament. The only other subglobose *Dzhaprakoceras*, *D. subglobosum*, has a smaller umbilicus and a more laterally compressed conch.

Dzhaprakoceras flexum sp. nov.

Plate 5, figures 3, 5; Text-figures 29–30

Derivation of name. From the Latin *flexus* (= sinuosity), with reference to the ornament.

Material. Holotype Ro 1009; from locality 4a; and paratype LZA 9521; from locality 3b. Both conches are late adolescents, partly exfoliated with intact body chambers, preserved in micrite.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A small pachyconic *Dzhaprakoceras* with a wide umbilicus and persistent constrictions.

Description. The conch is small, pachyconic, with cadiconic early whorls, a relatively wide umbilicus and moderate whorl expansion. The external ornament consists of weak, bisinuous, transverse striae with a broad lingua. The internal ornament consists of feeble transverse undulations, more accentuated in the lingual region, giving an impression of a subtle lingual groove. Five constrictions per whorl persist throughout growth and follow the ornament. The ventral lobe is narrow and lyrate. The lateral saddle is broad and rounded. The lateral lobe is acute and broad with flexed sides and is nearly as deep as the ventral lobe.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 1009	26.0	12.0	5.0	13.0	0.50	0.19	0.46
LZA 9521	25.0	12.0	5.0	13.0	0.52	0.20	0.48
LZA 9521	17.6	7.5	4.4	11.5	0.65	0.25	0.43
LZA 9521	13.0	5.6	3.6	9.2	0.71	0.28	0.43
LZA 9521	9.8	4.0	3.2	7.4	0.76	0.33	0.41
LZA 9521	7.3	2.6	2.6	5.7	0.78	0.36	0.36
LZA 9521	5.7	1.8	2.2	4.5	0.79	0.39	0.32

Remarks. This species is closest to *D. subglobosum* from which it differs in its constantly expanding umbilicus and more pachyconic form.

Dzhaprakoceras hispanicum (Foord and Crick, 1897)

Plate 5, figure 7; Text-figures 31–32

- 1897 *Glyphioceras hispanicum*, Foord and Crick, p. 190, text-fig. 91.
 ?1941 *Muensteroceras occidentale* Foord; Delépine, p. 58, pl. 1, figs 7–8; pl. 2, fig. 1.
 1943 *Beyrichoceras hispanicum* (Foord and Crick); Delépine, p. 47, pl. 1, figs 1–2.
 1951 *Nautellipsites difficilis* (Foord); Smyth, p. 298, pl. 11, figs 1–2; text-figs 1h–1.
 1961 ?*Muensteroceras hispanicum* (Foord and Crick); Kullmann, p. 258, pl. 20, fig. 1; text-figs 7a, 8b.
 1960 *Nautellipsites hispanicus* (Foord and Crick); Wagner-Gentis, p. 49, text-figs 1–3, 4a–c.
 non 1980 *Dzhaprakoceras hispanicum* (Foord and Crick); Kusina, p. 56, pl. 4, fig. 5; text-fig. 16.

Type specimen. *Glyphioceras hispanicum*, BMNH 37492, figured by Foord and Crick, 1897, p. 190, text-fig. 91.

Material. Two septate, mature, mostly exfoliated conches, preserved in micrite; Ro 3720, from locality 5; and Ro 5176, from locality 2.

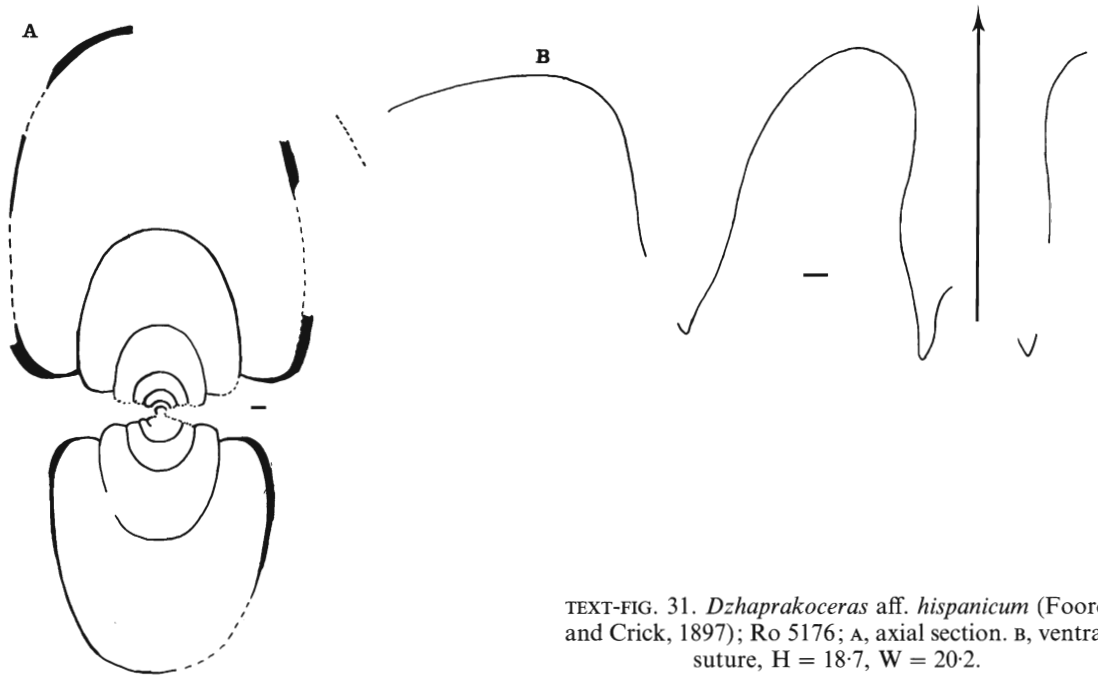
Range. Late Tournaisian to Arundian, middle FA Zone to lower BB Zone; Clitheroe Limestone Formation (Bellman Limestone Member) to Hodder Mudstone Formation (Chaigley Limestone Member).

Diagnosis. A large subdiscoconic *Dzhaprakoceras* with rapid whorl expansion.

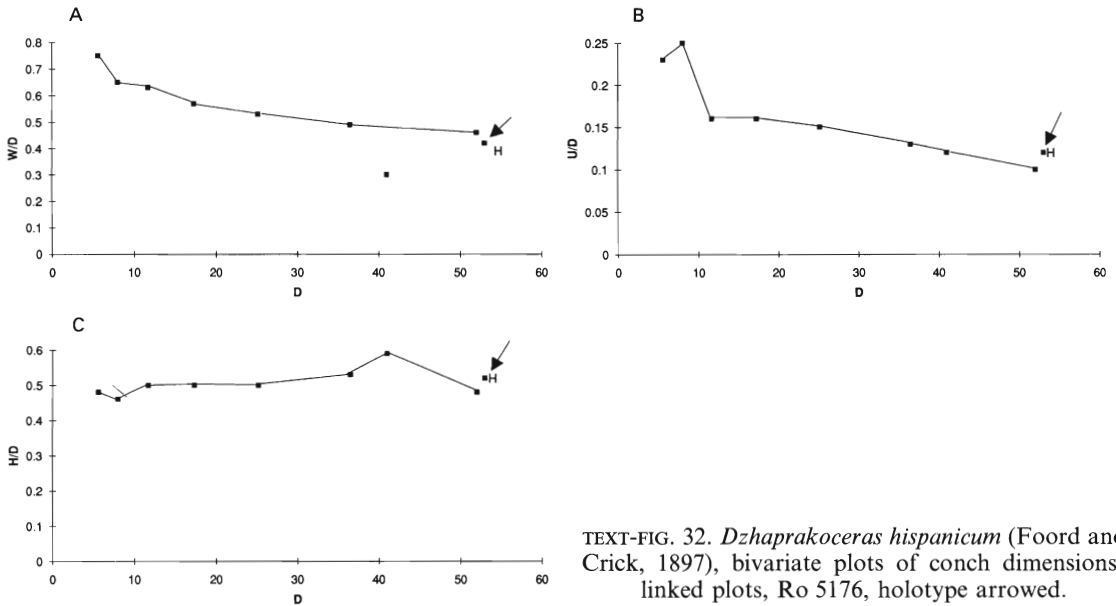
Description. The conch is subdiscoconic with rapid whorl expansion and a small umbilicus. The ornament is very weak and consists of simple, bisinuous, transverse striae with a well developed lingua. There are no constrictions and the internal surface of the conch is smooth. The ventral lobe is lyrate, deep and narrow. The lateral lobe is also deep and narrow with a slightly flexed ventrad wall.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Holotype	53.0	27.5	6.5	22.0	0.42	0.12	0.52
Ro 5176	52.0	25.0	5.0	24.0	0.46	0.10	0.48
Ro 3720	41.0	24.0	5.0	12.4*	0.30	0.12	0.59
Ro 5176	36.5	19.2	4.9	18.0	0.49	0.13	0.53
Ro 5176	25.2	12.7	3.9	13.4	0.53	0.15	0.50
Ro 5176	17.3	8.7	2.7	9.8	0.57	0.16	0.50
Ro 5176	11.7	5.9	1.9	7.4	0.63	0.16	0.50
Ro 5176	8.0	3.7	2.0	5.2	0.65	0.25	0.46
Ro 5176	5.6	2.7	1.3	4.2	0.75	0.23	0.48

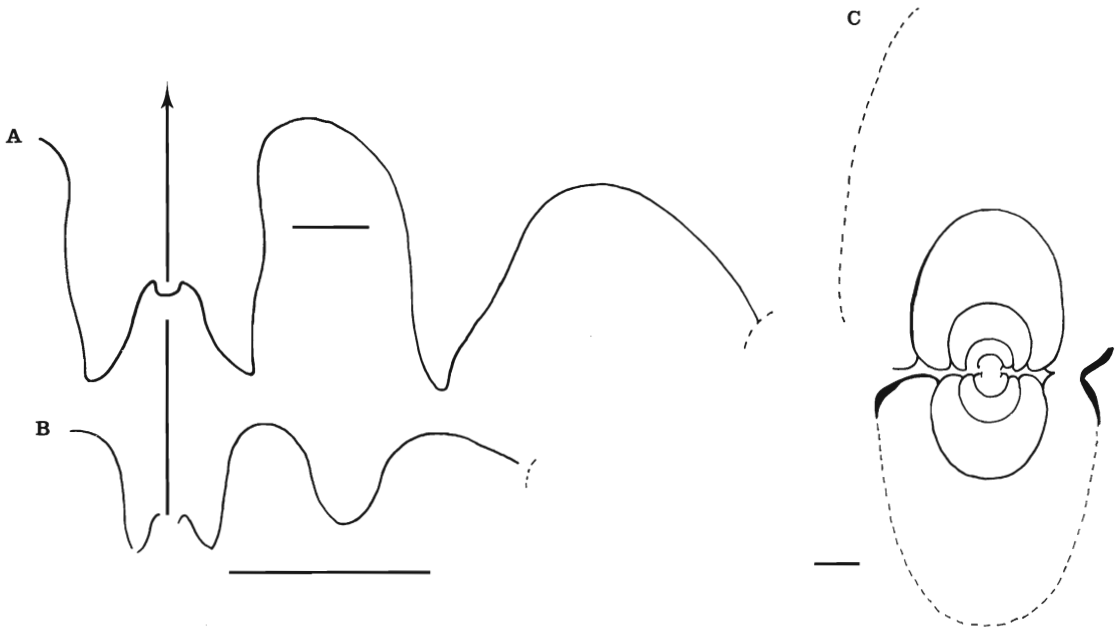


TEXT-FIG. 31. *Dzhaprakoceras* aff. *hispanicum* (Foord and Crick, 1897); Ro 5176; A, axial section. B, ventral suture, H = 18.7, W = 20.2.



TEXT-FIG. 32. *Dzhaprakoceras hispanicum* (Foord and Crick, 1897), bivariate plots of conch dimensions; linked plots, Ro 5176, holotype arrowed.

Remarks. There is a considerable amount of variation in the suture spacing. Characteristics of this species are the rapid whorl expansion, coupled with a relatively narrow ventral lobe and nearly straight sides to the lateral lobe.



TEXT-FIG. 33. *Dzhaparakoceras levis* sp. nov. A, C, holotype, LZA 9399; A, ventral suture, H = 7.3; C, axial section. B, Ro 913; ventral suture, H = 1.0, W = 1.9.

Dzhaparakoceras levis sp. nov.

Plate 3, figures 4, 6; Plate 4, figures 2-4; Text-figures 32-33

Derivation of name. From the Latin *levis* (= smooth), with reference to the smooth internal surface of the conch.

Material. Holotype LZA 9399, mid-adolescent, paratypes Ro 911-4, juveniles; all conches are septate, exfoliated and pyritic; from locality 3b.

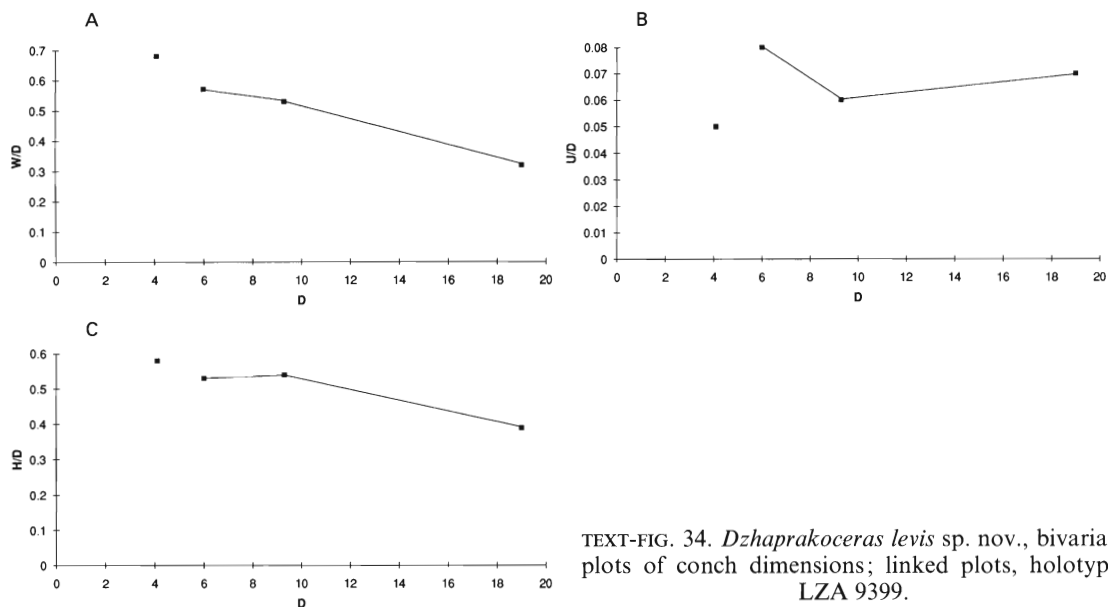
Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A small, involute, discoconic *Dzhaparakoceras* which lacks constrictions, has closely spaced sutures and a broad ventral lobe, with a high median saddle.

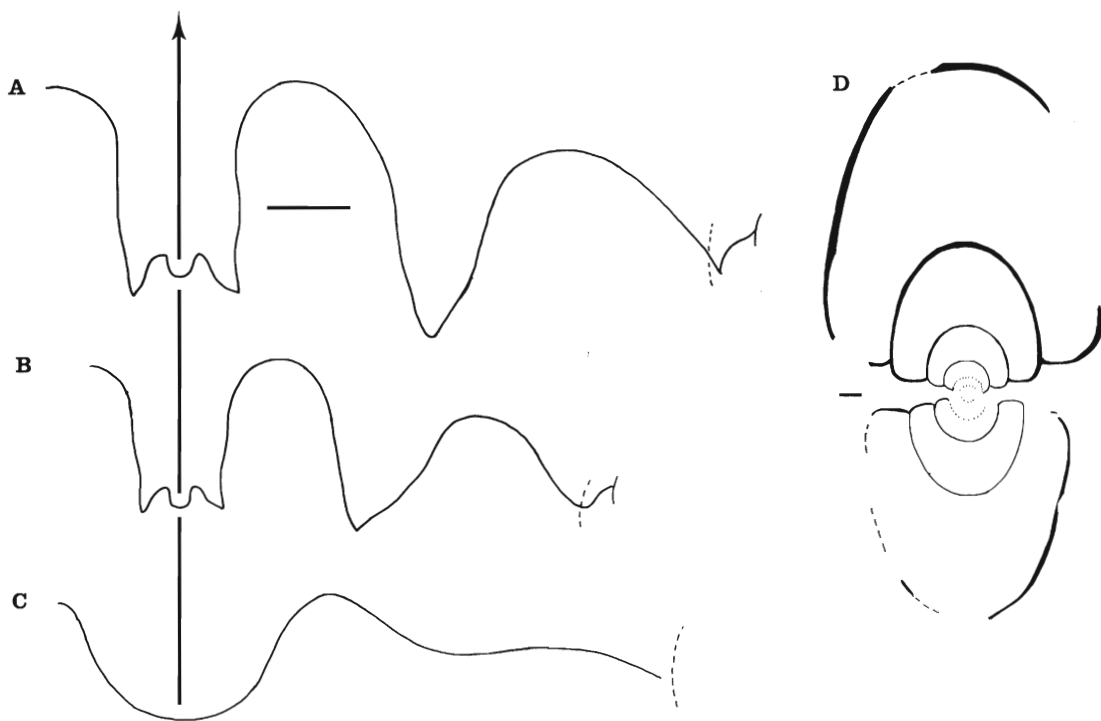
Description. The conch is small, discoconic and involute with rapid whorl expansion and an almost closed umbilicus. Juveniles are sphaeroconic to pachyconic. The external ornament is unknown and the internal surface of the conch is smooth. Constrictions are absent. The ventral lobe is broad and lyrate with a high median saddle (30 per cent. of ventral lobe depth). The lateral saddle is broad and rounded. The lateral lobe is narrow and acute with almost straight sides.

Dimensions.

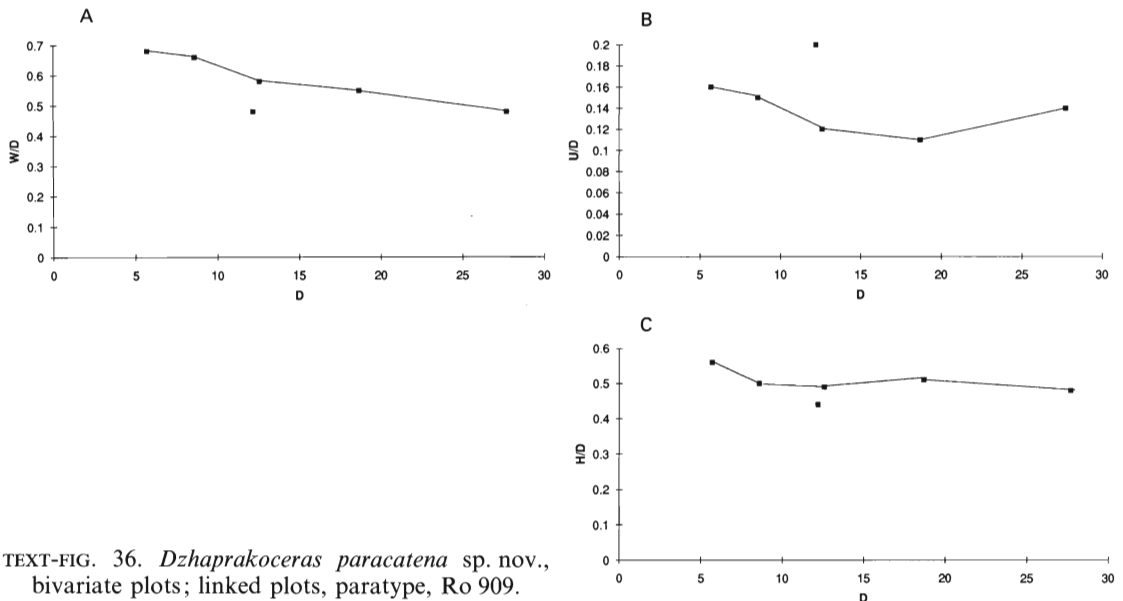
Specimen	D	H	U	W	W/D	U/D	H/D
LZA 9399	19.0	7.4	1.4	6.0	0.32	0.07	0.39
LZA 9399	9.3	5.0	0.6	5.0	0.53	0.06	0.54
LZA 9399	6.0	3.2	0.5	3.4	0.57	0.08	0.53
Ro 913	4.1	2.4	0.2	2.8	0.68	0.05	0.58



TEXT-FIG. 34. *Dzhaprakoceras levis* sp. nov., bivariate plots of conch dimensions; linked plots, holotype, LZA 9399.



TEXT-FIG. 35. *Dzhaprakoceras paracatena* sp. nov. A-C, holotype, LZA 9391; A, ventral suture, D = 12.0, H = 5.9, U = 2.4, W = 5.6; B, ventral suture, H = 4.0, W = 4.7; C, constriction, H = 4.9, W = 5.3. D, paratype, Ro 909; axial section.



TEXT-FIG. 36. *Dzhaparakoceras paracatena* sp. nov., bivariate plots; linked plots, paratype, Ro 909.

Remarks. This species has similarities with *Kozhimites planus* Kusina, 1971, notably in the lateral conch compression and suture form, especially that of the ventral lobe. However, *Kozhimites* has a distinct ornament style displayed by regular constrictions in which the hyponomic salient is placed well forward of the lateral sinus. None of these features is seen in *D. levis* sp. nov.

Dzhaparakoceras paracatena sp. nov.

Plate 6, figures 9–10; Text-figures 35–36

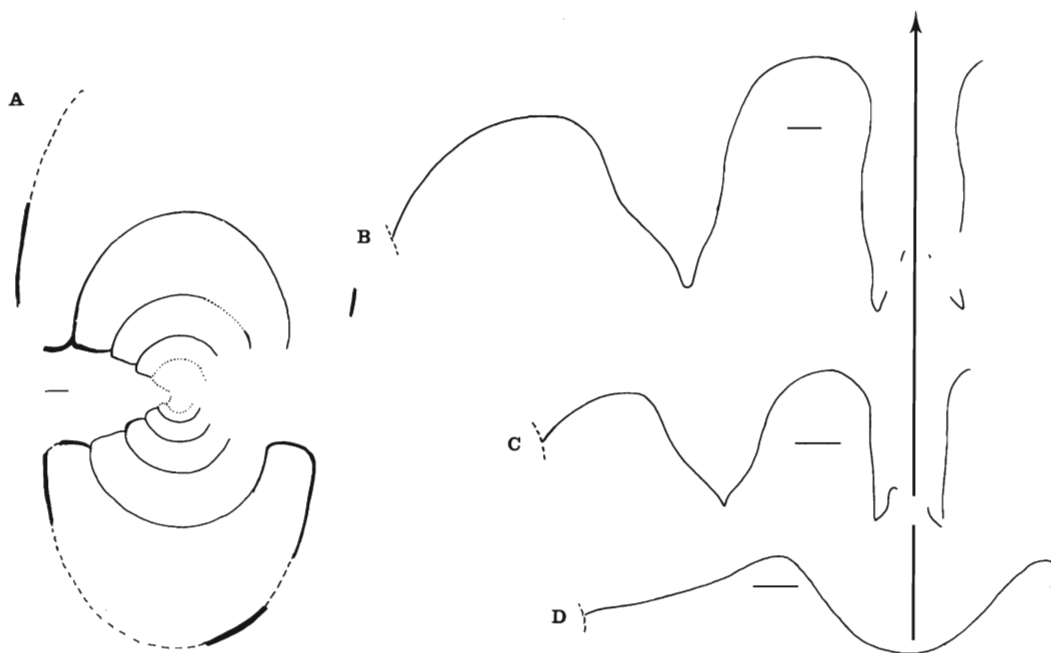
Derivation of name. From the similarity to *D. catena* sp. nov.

Material. Holotype, LZA 9391, fragmentary, pyritic, exfoliated, adolescent conch; from locality 3b; paratype Ro 913, fragmentary, septate, adolescent conch, preserved in micrite; from locality 4a.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A small discoconic, almost lenticular *Dzhaparakoceras* with early ontogenetic constriction loss and a deep narrow lateral lobe.

Description. The conch is discoconic, almost lenticular, with a small umbilicus, which has gently sloping sides. Juveniles are pachyconic; whorl expansion is rapid. The external ornament is not preserved. The internal ornament consists of regularly spaced, weak bisinuous ridges; these become strongly developed in the ventrolateral region where vesicular ridges occur corresponding with the linguae. The hyponomic sinus is relatively narrow, rounded and deep. Constrictions occur up to $D = 11$; it is estimated that there are four per whorl; they are strongly incised and follow the internal ornament. The suture shows a subparallel-sided ventral lobe which is slightly lyrate; the lateral saddle is broad and rounded, but the lateral lobe is very narrow with flexed sides and a subacute termination.



TEXT-FIG. 37. *Dzhaparakoceras subglobosum* (Librovitch, 1927). A, DM 1275; axial section. B, Ro 5177; ventral suture, $D = 24.2$, $H = 10.8$, $U = 3.7$, $W = 13.3$. C–D, Ro 5178; C, ventral suture, $H = 5.9$, $W = 8.6$; D, constriction, $H = 6.2$, $W = 9.1$.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 909	27.7	13.2	3.8	13.3	0.48	0.14	0.48
Ro 909	18.7	9.6	2.0	10.2	0.55	0.11	0.51
Ro 909	12.6	6.2	1.5	7.3	0.58	0.12	0.49
Ro 909	8.6	4.3	1.3	5.7	0.66	0.15	0.50
Ro 909	5.7	3.2	0.9	3.9	0.68	0.16	0.56
LZA 9391	12.2	5.4	2.5	5.9	0.48	0.20	0.44

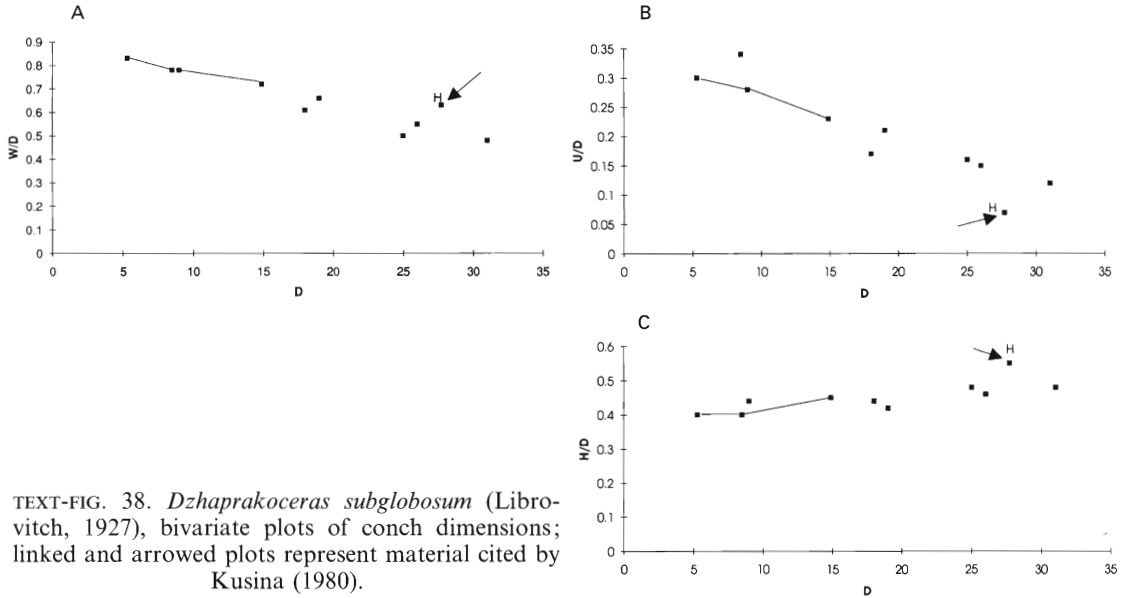
Remarks. This new species is similar to *D. catena* sp. nov. but differs in the early loss of constrictions and the very narrow, deep lateral lobe. Similar also is *D. levis* sp. nov., which has, however, a wider ventral lobe and lacks constrictions.

Dzhaparakoceras subglobosum (Librovitch, 1927)

Plate 4, figures 11–12; Text-figures 37–38

- 1927 *Muensteroceras subglobosum* Librovitch, p. 35, pl. 6, fig. 7; pl. 7, figs 1–2; text-fig. 17.
 1941 *Muensteroceras subglobosum* Librovitch; Librovitch, p. 143, pl. 37, fig. 3; text-fig. 25.
 non 1961 *Muensteroceras subglobosum* Librovitch; Pareyn, p. 104, pl. 8, figs 27–28.
 1968 *Dzhaparakoceras subglobosum* (Librovitch); Popov, p. 88, pl. 3, figs 4–5; pl. 6, fig. 5; text-fig. 16.
 1980 *Dzhaparakoceras subglobosum* (Librovitch); Kusina, p. 57–8, pl. 4, fig. 6.

Lectotype. Designated by Kusina (1980), specimen 100/2473, TSNIGRI Museum, St Petersburg; no reference to original figure.



TEXT-FIG. 38. *Dzhaprakoceras subglobosum* (Librovitch, 1927), bivariate plots of conch dimensions; linked and arrowed plots represent material cited by Kusina (1980).

Material. Twelve conches preserved in wackestone, mostly exfoliated and septate, some fragmentary, representing various growth stages. Specimens Ca 1592, 1863, DM 1265, 1269, 1275 and Ro 5177–8, 5180–1, 5183–5; from locality 2.

Range. Late Tournaisian, middle FA Zone; Clitheroe Limestone Formation (Bellman Limestone Member). Known also from the middle FA Zone in Tien-Shan (CIS) and possibly from the BB Zone in the north Urals (CIS).

Diagnosis. A small, pachyconic, subglobose *Dzhaprakoceras* with a narrow ventral lobe and maintaining a nearly constant umbilical diameter after early adolescence.

Description. The conch is pachyconic, subglobose and of moderate size. The umbilicus is open, of nearly constant diameter, but becomes narrower during the sixth or seventh whorl. The ornament consists of very delicate transverse striae (not well preserved). Constrictions are present; they are regular, about five per whorl, and bisinuous; they show a well developed hyponomic sinus, but a shallower lateral sinus and fail after H = 9 mm. The ventral lobe has slightly divergent sides in the immature conch, but becomes narrow deep and lyrate when mature. The lateral saddle is evenly rounded and slightly inflated orad. The lateral lobe is moderately broad with flexed sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
DM 1265	31.0	15.0	4.0	15.0	0.48	0.12	0.48
DM 1269	—	13.0	4.5	15.0	—	—	—
DM 1275	26.0	12.0	3.8	14.5	0.55	0.15	0.46
Ro 5177	25.0	12.0	4.0	12.5	0.50	0.16	0.48
Ca 1663	19.0	8.0	4.0	12.5	0.66	0.21	0.42
Ca 1592	18.0	8.0	3.0	11.0	0.61	0.17	0.44
Ro 5183	9.0	4.0	2.5	7.0	0.78	0.28	0.44

Remarks. The species is very similar to *D. djaprakense* which, however, is more dorso-ventrally compressed and has a larger umbilicus. Specimens with the specimen number prefix Ca and DM were incorrectly assigned to *Muensteroceras difficile* by Ramsbottom in Earp *et al.* (1961, p. 179).

Dzhaprakoceras undulatum sp. nov.

Plate 4, figures 8–9; Plate 5, figure 1; Plate 7, figure 2; Text-figures 39–40

Derivation of name. From the Latin *undulatus* (= undulated) with reference to the ornament.

Material. Holotype Ro 925, paratypes Ro 921–3, 926–7, partly exfoliated conches at various growth stages preserved in wackestone; from locality 4; Ro 928–9, pyritic septate adolescent moulds; from locality 3.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A small, relatively evolute, subdiscoconic *Dzhaprakoceras* with ontogenetic constriction loss and the progressive development of a strongly bisinuuous transverse ornament.

Description. The conch is small, subdiscoconic and relatively evolute with slow whorl expansion. Juveniles are initially cadiconic but later pachyconic. The external ornament consists of weak transverse bisinuuous striae with well developed lateral and hyponomic sinuses. The internal ornament is also well developed and consists of vesicular ridges which follow the external ornament. There are five constrictions per whorl; they are deeply incised and follow the external ornament, but fail at maturity. The ventral lobe is deep, narrow and lyrate. The lateral saddle is broad and rounded. The lateral lobe is broad and acute with almost straight sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 925	27.5	13.5	5.0	12.0	0.44	0.18	0.49
Ro 928	10.5	4.0	2.5	5.2	0.50	0.24	0.38
Ro 929	6.5	2.5	2.0	3.5	0.54	0.31	0.31
Ro 927	17.5	7.5	3.5	9.0	0.51	0.20	0.43
Ro 927	12.6	5.4	2.8	6.8	0.54	0.22	0.43
Ro 927	9.3	3.7	2.2	5.5	0.59	0.24	0.40
Ro 927	6.9	2.8	1.7	4.5	0.65	0.25	0.41

Remarks. This new species is very similar to *D. deflexum* which, however, is more involute, retains constrictions and has a flexed ventrad side to the lateral lobe.

Dzhaprakoceras westheadi sp. nov.

Plate 5, figures 8–9; Plate 6, figures 2–3; Plate 7, figures 4–5; Text-figures 41–42

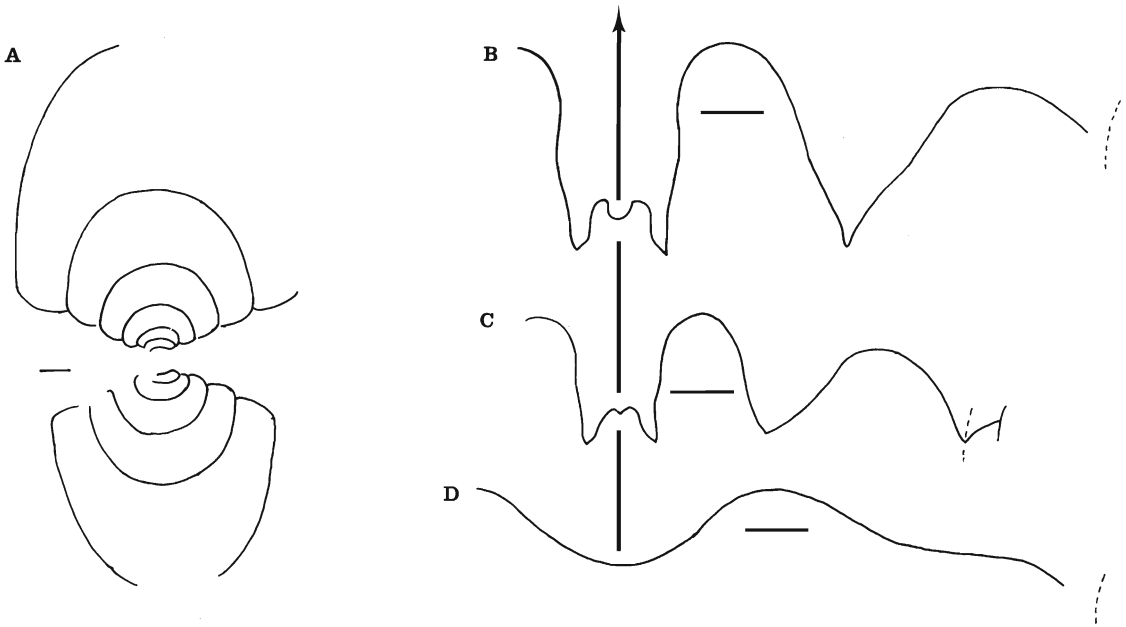
Derivation of name. In honour of the late Mr S. Westhead, a keen amateur geologist from Clitheroe, famous for his excellent collection of local crinoids.

Material. Holotype, LZA 9407, exfoliated, adolescent, pyritic conch; from locality 3b. Paratypes; Ro 917 part exfoliated conch preserved in micrite; from locality 4a; and LZA 9386, 9393, 9401–3, 9407–8, 9410–1, 9414, Ro 919, Ro 5171, exfoliated pyritic conches; from locality 3b.

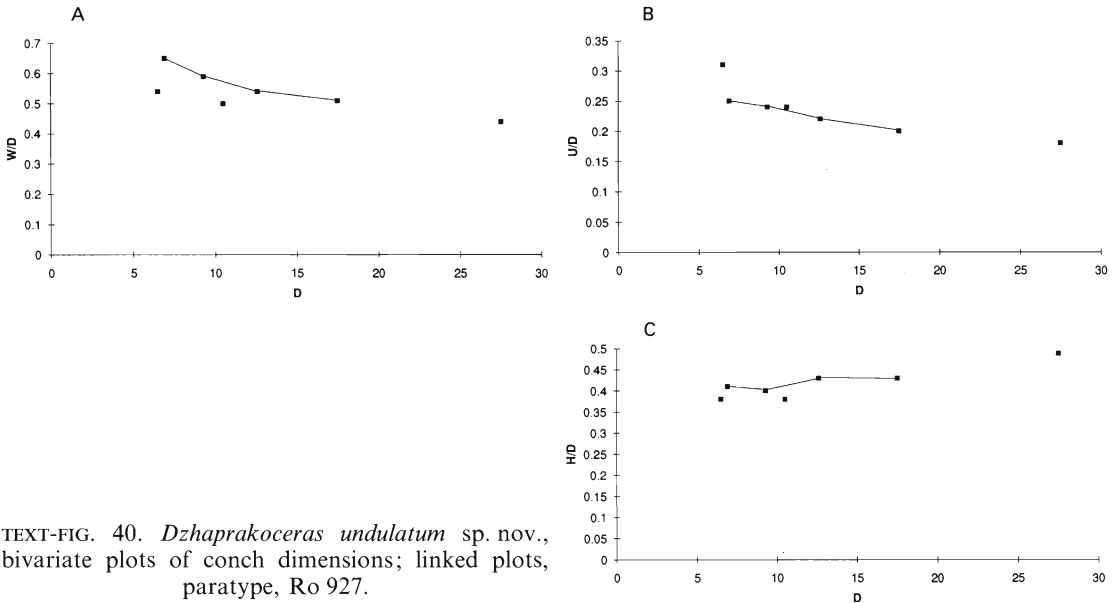
Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation, Leagram Mudstone Member.

Diagnosis. A medium-sized, subdiscoconic *Dzhaprakoceras* with strongly bisinuuous transverse ornament.

Description. The conch is subdiscoconic with moderate whorl expansion and an average-sized umbilicus with steep sides. The juvenile whorls are cadiconic. The external ornament is not preserved, but the internal

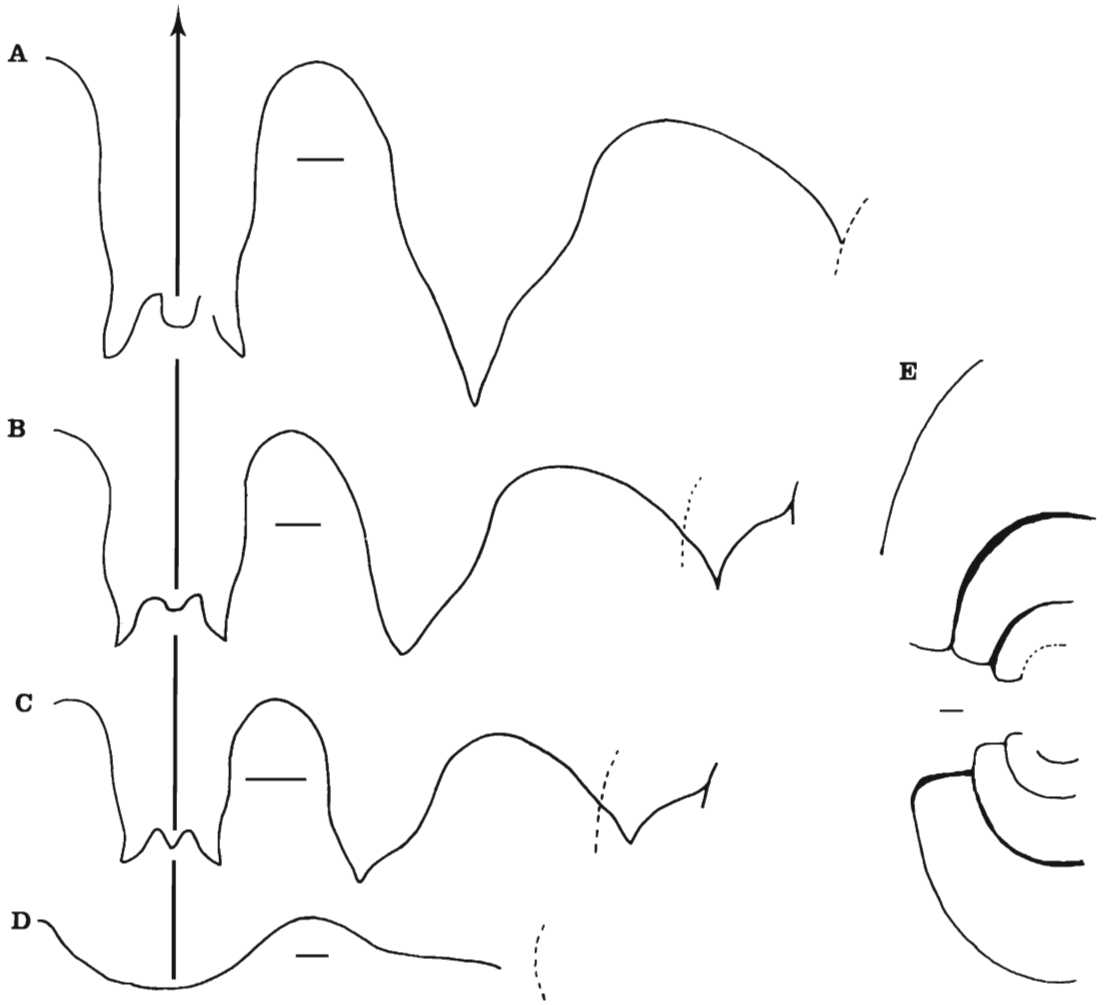


TEXT-FIG. 39. *Dzhaparakoceras undulatum* sp. nov. A, paratype, Ro 927; axial section, B, D, paratype, Ro 923; B, ventral suture, H = 5.8; D, constriction, H = 5.8. C, paratype, Ro 928; ventral suture, H = 4.4, W = 5.6.



TEXT-FIG. 40. *Dzhaparakoceras undulatum* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, Ro 927.

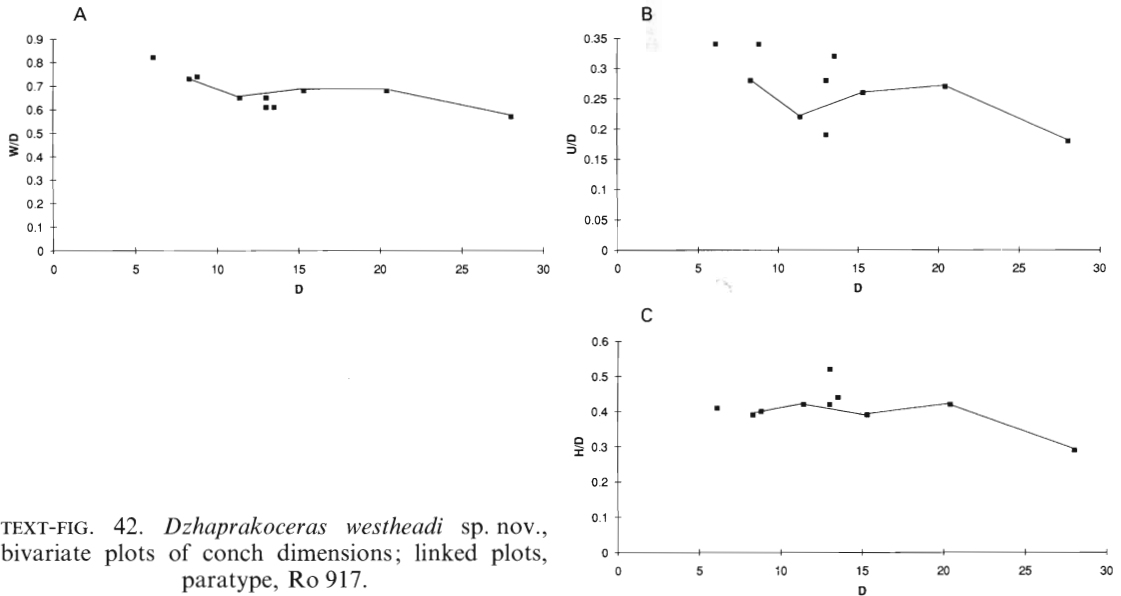
ornament consists of weak, strongly bisinuous transverse ridges which are well developed on the ventrolateral region, giving rise to vesicular ridges which correspond to the linguae. The hyponomic sinus is broad and relatively deep. There are five, well developed constrictions per whorl, which follow the path of the internal ornament. The suture consists of a narrow, lyrate ventral lobe with slightly divergent sides (orad). The lateral saddle is narrow and sharply rounded; the lateral lobe is deeper than the ventral and is narrow with flexed sides and an acute termination.



TEXT-FIG. 41. *Dzhaprakoceras westheadi* sp. nov. A, E, paratype, Ro 917; A, ventral suture, H = 11.4, W = 15.3; E, axial section. B, D, holotype, LZA 9407; B, ventral suture, H = 8.1, W = 12.8; D, constriction, H = 9.1, W = 13.4. C, paratype, LZA 9403; ventral suture, H = 5.7, W = 8.4.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 917	28.0	8.0	5.0	16.0	0.57	0.18	0.29
Ro 917	20.4	8.5	5.5	13.8*	0.68	0.27	0.42
Ro 917	15.3	6.0	4.0	10.4*	0.68	0.26	0.39
Ro 917	11.4	4.8	2.5	7.4*	0.65	0.22	0.42
Ro 917	8.3	3.2	2.3	6.1*	0.73	0.28	0.39
LZA 9402	13.5	5.9	4.3	8.3	0.61	0.32	0.44
LZA 9401	13.0	5.4	3.7	8.5	0.65	0.28	0.42
Ro 919	13.0	6.8	2.5	7.9	0.61	0.19	0.52
LZA 9408	8.8	3.5	3.0	6.5	0.74	0.34	0.40
LZA 9410	6.1	2.5	2.1	5.0	0.82	0.34	0.41



TEXT-FIG. 42. *Dzhaparakoceras westheadi* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, Ro 917.

Remarks. This species is most similar to *D. bellmanense* sp. nov., but differs in having greater whorl inflation, more strongly bisinuous internal ornament and a smaller umbilicus. Juveniles and early adolescents are similar to *D. flexum*, but differ from that species in having a more divergent (orad) ventral lobe at comparable diameters.

Family PERICYCLIDAE Hyatt, 1900

Diagnosis (emended). Small to large ammonoids in which the conch varies from subsphaeroconic to discoconic, rarely oxyconic, and may be involute or evolute. The external ornament is mainly transverse, simple or branched, often strong with ribs and/or tubercles; spiral ornament is sometimes present. The internal ornament is transverse and follows the external. The ventral lobe varies from narrow to moderate width, with parallel, divergent or convergent (orad) sides. The lateral saddle may be rounded, subacute or acute, but the lateral lobe is always acute.

Range. Tournaisian to Asbian.

Remarks. The Pericyclidae can be split into two groups based on the shape of the lateral saddle. The following new subfamilies are introduced below:

Ammonellipsitinae subfam. nov. (lateral saddles acute to subacute); late Tournaisian to late Chadian

Pericyclinae Hyatt, 1900 [*nom. trans.* Riley] (forms with well rounded lateral saddles); Tournaisian to Asbian

Subfamily AMMONELLIPSITINAE subfam. nov.

Diagnosis. Pericyclidae which have acute or subacute lateral saddles, divergent sides (orad) to the ventral lobe and a serpenticonic juvenile stage.

Range. Late Tournaisian to late Chadian.

Remarks. The following genera are included:

Ammonellipsites Parkinson, 1822; late Tournaisian to late Chadian.

Fascipericlyclus Turner, 1948; late Tournaisian to late Chadian.

Helicocyclus Schindewolf, 1951a; late Chadian.

Stenocyclus Schindewolf, 1951a; late Tournaisian.

The erection of the new subfamily restricts *Ammonellipsites* to the species group of which *Ellipsolithes funatus* Sowerby, 1813 is the type. Gordon's (1957, 1964) treatment of the above genera as subgenera of *Ammonellipsites* is not adopted here.

Genus AMMONELLIPSITES Parkinson, 1822.

Type species. *Ellipsolithes funatus* Sowerby, 1813, pl. 32.

Diagnosis. The conch is commonly pachyconic, but may be serpenticonic or cadiconic; juveniles are serpenticonic. The external and internal ornament consists of transverse ribs which are usually simple, but may show irregular bifurcation; spiral lirae may occur externally between the ribs. The ventral lobe has strongly divergent sides (orad) and a high median saddle. The lateral saddle and lateral lobe are acute.

Range. Late Tournaisian to late Chadian.

Remarks. The following species are included:

A. ballardensis Gordon, 1964; Grand Falls Chert Member, Boone Formation, Kansas, USA, late Tournaisian or early Viséan (*texanus* Conodont Zone).

A. clitheroensis sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

A. djaprakensis (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS; late Tournaisian.

A. doohylensis (Foord, 1903); Carboniferous Limestone, Doohyle, Co. Limerick, Ireland, late Tournaisian.

A. funatus (Sowerby, 1813); Blackrock limestones, near Cork, Ireland, mid-Dinantian.

A. kayseri (Schmidt, 1925); Erdbach Limestone, CuII γ , Germany, mid-Dinantian.

A. kochi (Holzapfel, 1889); Erdbach Limestone, CuII γ , Germany, mid-Dinantian.

A. multicostatus (Foord, 1903); Carboniferous Limestone, Middleton, Ireland, late Tournaisian.

A. nikitini (Librovitch, 1927); Dzhaprak Suite, Tien-Shan, Kirgizya, CIS, late Tournaisian.

Ammonellipsites is closest to *Stenocyclus*, a genus which develops ontogenetically a carinate venter, absent even in gerontic specimens of *Ammonellipsites*. Mature *Fascipericyclus* may have a ribbing character similar to that of *Ammonellipsites* with infrequent rib bifurcation; however, the earlier ontogeny of *Fascipericyclus* shows strong, regular rib bifurcation and this feature, coupled with the low median saddle, serves to distinguish the two genera.

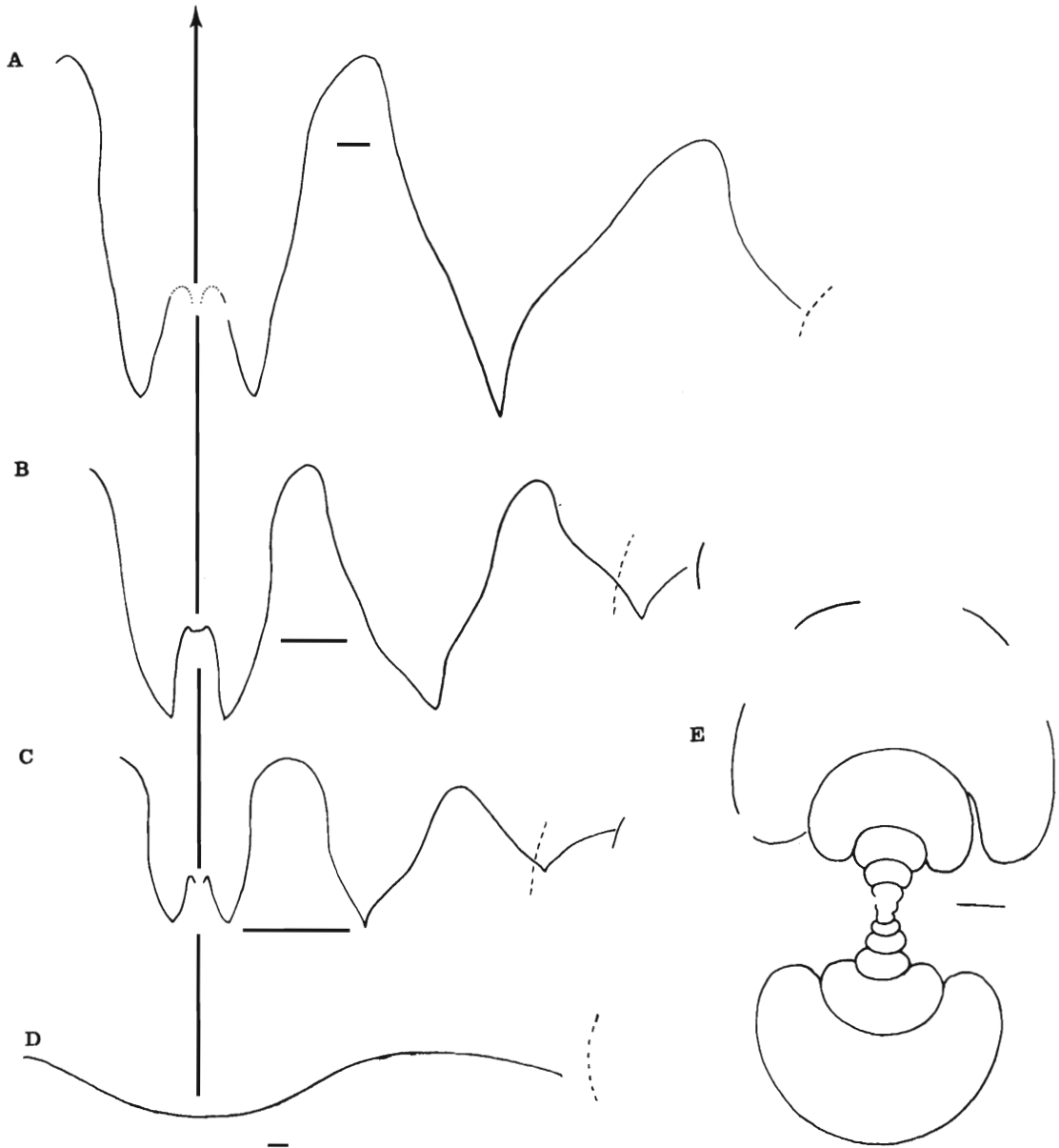
Ammonellipsites clitheroensis sp. nov.

Plate 1, figures 1–3, 5–6, 8, 11; Plate 2, figure 4; Text-figures 43–44

Derivation of name. From Clitheroe, the type locality.

Material. Holotype Ro 864, exfoliated late adolescent, preserved in wackestone; from locality 4a; and paratypes LZA 9404, 9412 and 9452, pyritic, septate, exfoliated adolescents; from locality 3b. Also paratypes Ro 863–9, adolescent and mature conchs, some exfoliated and septate, preserved in wackestone; from locality 4a.

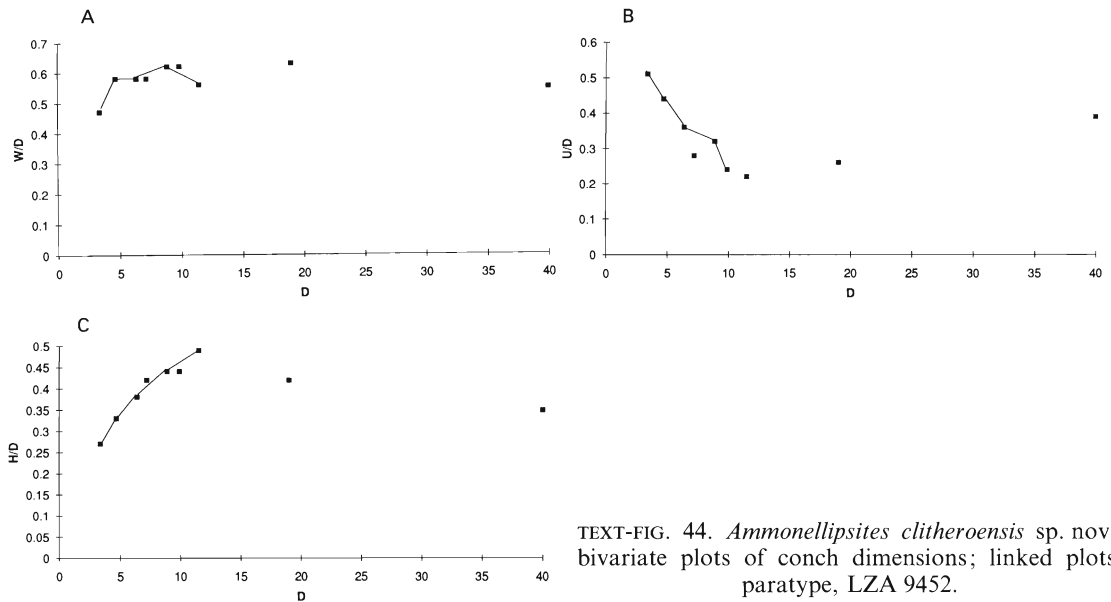
Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Whitemore Limestone and Leagram Mudstone members).



TEXT-FIG. 43. *Ammonellipsites clitheroensis* sp. nov. A, paratype, Ro 865; ventral suture, H = 12.2. B, E, paratype, LZA 9452, B, ventral suture, H = 4.9, W = 6.5; E, axial section. C, paratype, Ro 866; ventral suture, D = 5.7, H = 2.0, U = 2.7, W = 3.6. D, paratype, Ro 863; transverse ornament, H = 14.9, W = 5.1.

Diagnosis. An *Ammonellipsites* with a relatively prolonged juvenile serpenticonic stage and ontogenetic development of constrictions.

Description. The conch is pachyconic with a small umbilicus and slow whorl expansion. Juveniles are serpenticonic until the fourth whorl, when the conch becomes cadiconic. The external ornament consists of flat-topped transverse ribs with a broad, shallow hyponomic sinus. The internal ornament consists of asymmetrical ribs which correspond with the external ornament, but fail low on the flanks, especially at maturity.



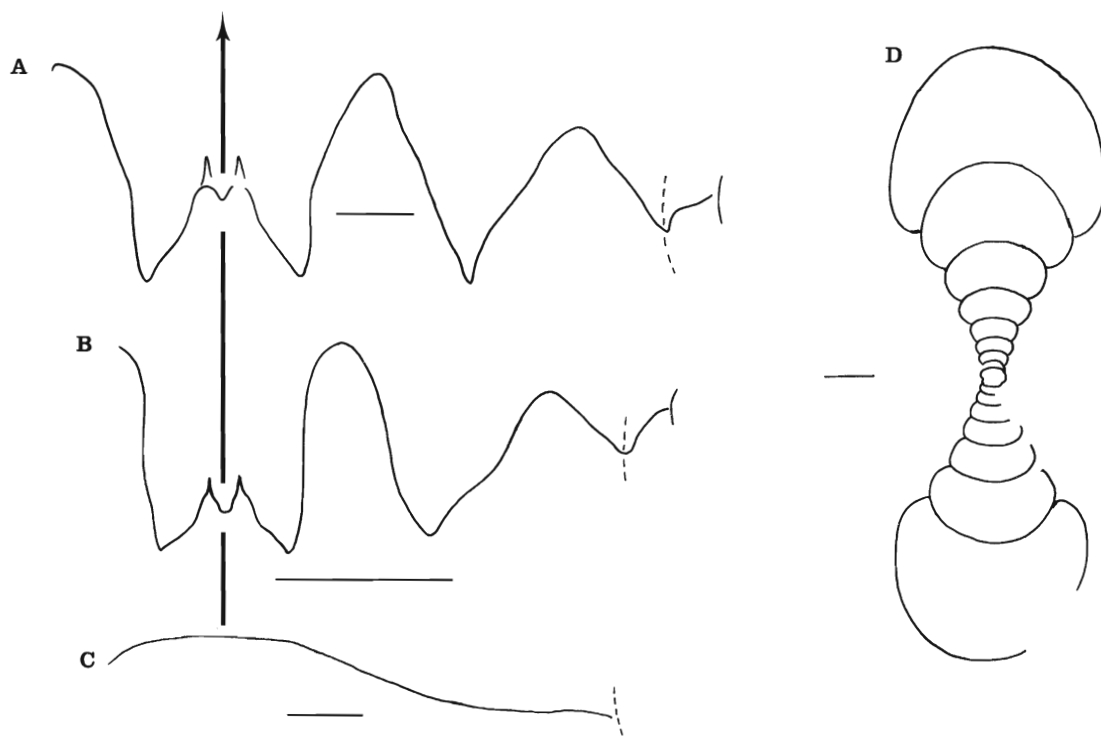
TEXT-FIG. 44. *Ammonellipsites clitheroensis* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, LZA 9452.

Constrictions develop at maturity and have been seen only on fragmentary specimens; they are deeply incised and follow the ornament; they are visible externally and are enhanced by suppression of the adjacent ribs. The ventral lobe is broad and deep, with strongly divergent (orad) sides and a high median saddle. The lateral saddle and lateral lobe are broad and acute with flexed sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 863	40.0	14.0	15.5	22.0	0.55	0.39	0.35
Ro 864	19.0	8.0	5.0	12.0	0.63	0.26	0.42
LZA 9452	11.5	5.5	2.5	6.4	0.56	0.22	0.49
LZA 9452	8.9	3.9	2.8	5.5	0.62	0.32	0.44
LZA 9452	6.4	2.5	2.3	3.7	0.58	0.36	0.38
LZA 9452	4.7	1.5	2.1	2.7	0.58	0.44	0.33
LZA 9452	3.4	0.9	1.7	1.6	0.47	0.51	0.27
LZA 9404	9.9	4.4	2.4	6.1	0.62	0.24	0.44
Ro 866	7.2	3.0	2.0	4.2	0.58	0.28	0.42

Remarks. This new species is very similar to *A. kochi*, which, however, from Holzapfel's (1899) and Schmidt's (1924) descriptions, appears to have a shorter juvenile serpenticonic stage, with spiral lirae, and apparently lacks constrictions when mature. Unfortunately, *A. kochi* has never been adequately described and the type material was destroyed during World War Two, hence comparison is difficult. The form which occurs in the Tober Colleen Formation (Rush Slates) of the Dublin Basin, attributed to *A. kochi* by Smyth (1951), has a much longer serpenticonic juvenile stage than *A. clitheroensis* and differs in ornament strength and sutural characters. The Irish form appears to be a new species.



TEXT-FIG. 45. *Helicocyclus divergens* sp. nov. A, C-D, holotype LZA 9422; A, ventral suture, H = 4.6, W = 4.8; C, constriction; D, axial section. B, paratype, LZA 9388; ventral suture, D = 7.0, H = 1.8, W = 2.9.

Genus HELICOCYCLUS Schindewolf 1951a

Type species. Helicocyclus gracillimus Schindewolf, 1951a.

Diagnosis (emended). Ammonellipsitins with predominantly small ($D < 55$ mm) laterally compressed, evolute, discoconic conches, which are serpenticonic until late adolescence. Whorl expansion is slow. The external ornament consists of simple or branched, relatively weak, transverse ribs which bend orad over the flanks and venter, with consequential loss of a hyponomic sinus. The internal ornament, where present, consists of weak ribs which follow the external ornament. Constrictions occur at all diameters and follow the external ornament. The ventral lobe has divergent sides (orad), acute prongs and a broad, high median saddle. The lateral saddle is acute to subacute. The lateral lobe is acute with flexed sides.

Range. Late Chadian.

Remarks. The following species are included:

H. divergens sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

H. gracillimus Schindewolf, 1951a; Winterberg, Harz, Germany, Viséan.

H. involutus Kusina in Shumansky and Kusina, 1977; Kosvinsky Horizon, Kozhim River, north Urals, Russian Federation, CIS, late Chadian.

This genus was erected using juvenile material and hence the diagnosis has been modified. *Pericyclus*

tianshanicus Librovitch, 1927 and the synonymous *P. evolutus* Librovitch, 1927, although included in *Helicocyclus* by Schindewolf (1951a) and Kusina (1980), have much higher whorl expansion rates than *Helicocyclus*, and have a low median saddle and a subacute lateral saddle. The author therefore follows Popov (1968) in placing *P. tianshanicus* within *Fascipericyclus*.

Helicocyclus divergens sp. nov.

Plate 1, figures 4, 9, 12; Text-figures 45–46

Derivation of name. From the divergent-sided ventral lobe.

Material. Holotype LZA 9422 and paratypes LZA 9383, 9421, 9424, 9426–30, 9433–4, 9445, RH 1525–35 and Ro 5400; all pyritic internal septate moulds representing all growth stages; from locality 3b.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Diagnosis. A *Helicocyclus* with a broad and strongly divergent-sided (orad) ventral lobe.

Description. the conch is subdiscoconic, but serpenticonic below $D = 10$ mm and has a large umbilicus, convex flanks and a narrow, arched, rounded venter. Whorl expansion is slow. The external ornament is unknown. The internal ornament consists of delicate, simple transverse ribs which slope orad over the flanks and venter (spaced at about 0.75 mm on the venter at $D = 12$ mm); a hyponomic sinus is not present. There are four constrictions per whorl throughout growth, these follow the internal ornament. The ventral lobe is broad with strongly divergent sides (orad) and a broad, high (c. 40 per cent. of ventral lobe depth) median saddle. The lateral saddle is narrow and acute. The lateral lobe is acute with slightly flexed sides.

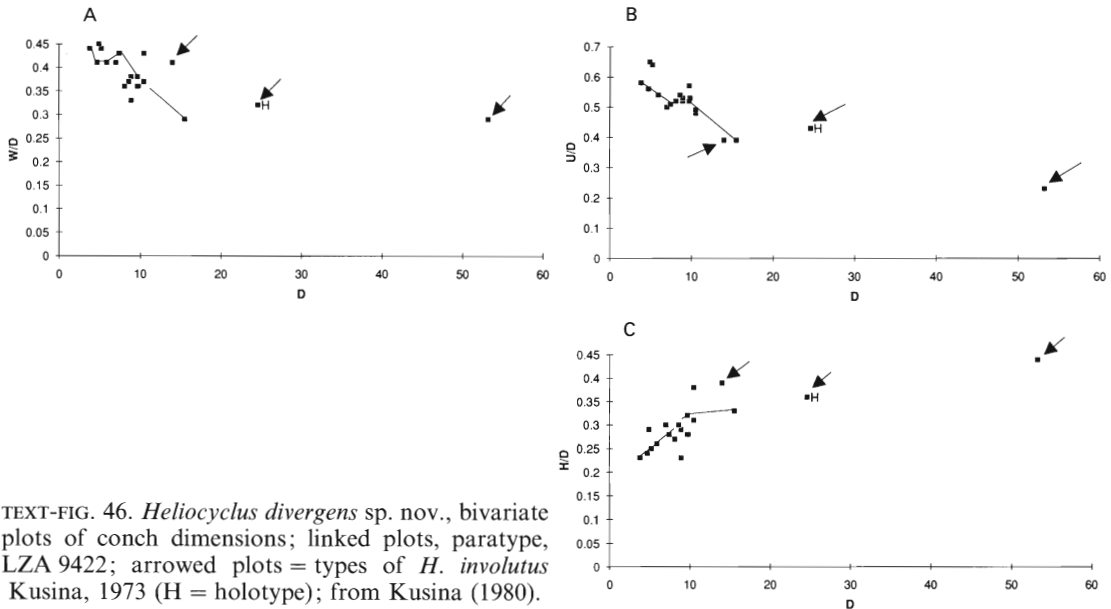
Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
LZA 9426	10.5	4.0	5.0	4.5	0.43	0.48	0.38
LZA 9424	10.5	3.3	5.1	3.9	0.37	0.49	0.31
LZA 9429	9.8	2.7	5.2	3.5	0.36	0.53	0.28
LZA 9428	9.7	2.7	5.5	3.5	0.36	0.57	0.28
RH 1531	8.9	2.6	4.7	3.4	0.38	0.52	0.29
LZA 9445	8.9	2.0	4.7	2.9	0.33	0.53	0.23
LZA 9427	8.6	2.6	4.6	3.2	0.37	0.54	0.30
RH 1534	8.1	2.2	4.2	2.1	0.26	0.52	0.27
LZA 9388	7.0	2.1	3.5	2.9	0.41	0.50	0.30
LZA 9434	5.2	1.3	3.3	2.3	0.44	0.64	0.25
LZA 9383	4.9	1.4	3.2	2.2	0.45	0.65	0.29
LZA 9422	15.5	5.0	6.0	4.5	0.29	0.39	0.33
LZA 9422	9.7	3.1	5.1	3.7	0.38	0.52	0.32
LZA 9422	7.4	2.1	3.8	3.2	0.43	0.51	0.28
LZA 9422	5.9	1.5	3.2	2.4	0.41	0.54	0.26
LZA 9422	4.7	1.2	2.6	2.0	0.41	0.56	0.24
LZA 9422	3.8	0.9	2.2	1.7	0.44	0.58	0.23

Remarks. *H. divergens* sp. nov. is very similar to *H. involutus*; however, the broad divergent-sided ventral lobe of the new species is distinctive. *H. gracillimus* does not show as much whorl arching at comparable diameters and lacks a broad divergent-sided ventral lobe.

Subfamily PERICYCLINAE Hyatt, 1900 [*nom. trans.* Riley]

Diagnosis. Pericyclids with broad, rounded lateral saddles and a ventral lobe with subparallel, parallel or convergent (orad) sides. The ornament sometimes fails during late ontogeny.



TEXT-FIG. 46. *Helicyclus divergens* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, LZA 9422; arrowed plots = types of *H. involutus* Kusina, 1973 (H = holotype); from Kusina (1980).

Range. Tournaisian to Asbian.

Remarks. The division of the pericyclids by previous workers, e.g. Turner (1948), Schindewolf (1951b) and Gordon (1957), was based on the divergence of the ventral lobe sides and is not followed here. Species groups previously treated as subgenera, e.g. *Goniocyclus*, are here treated as genera. The following genera are included:

Asiacyclus Librovitch, 1962; Tournaisian

Bollandites Bisat, 1952; Arundian to Asbian.

Goniocyclus Gordon, 1986; mid-Tournaisian.

Hammatocyclus Schindewolf, 1951b; ?late Tournaisian to Arundian.

Neopericyclus Popov, 1965; late Tournaisian

Parahammatocyclus gen. nov.; Arundian

Pericyclus Mojsisovics von Mojsvár, 1882; Tournaisian.

Polaricyclus Riley, 1991; late Tournaisian.

Rhiphaeocyclus Kusina, 1973; Arundian.

Rotopericyclus Turner, 1948; Tournaisian to late Chadian.

Bollandites, formerly placed in the Muensteroceratidae, is here included with the pericyclins since it has many similarities, particularly in general conch and suture form, with *Hammatocyclus*.

Genus BOLLANDITES Bisat, 1952

Type species. *Beyrichoceratoides castletonense* Bisat, 1924.

Diagnosis. The conch is of variable size (D ~ 15–100 mm), cadiconic, platyconic or subsphaeroconic with serpenticonic early whorls. The external ornament consists of simple, weak, transverse striae with a gentle lateral sinus and a broad feeble hyponomic sinus; the ornament is coarser in juveniles; spiral lirae are rarely present. An internal ornament is present in juveniles and consists of simple transverse ribs which follow the external ornament, usually the internal ornament does not persist into adolescence. Strongly incised constrictions are present in juveniles, but these commonly fail

during late adolescence. The ventral lobe is relatively broad and has divergent (orad), flexed sides. The lateral saddle is rounded and the lateral lobe is acute with flexed sides.

Range. Arundian to Asbian.

Remarks. The following species are included:

B. baoshanensis Liang and Zhu, 1988; Qingshigou Baoshan County, western Yunnan, People's Republic of China, Viséan.

B. castletonensis (Bisat, 1924); 'reef limestone', Treak Cliff, northern England, Asbian.

B. donetsensis Kusina, 1991; Zone C₁V_e, base of the Stylsky Horizon, Donets Basin, Ukraine, ?Asbian.

B. mediocris Kusina, 1991; Zone C₁V_e, base of the Stylsky Horizon, Donets Basin, Ukraine, ?Asbian.

B. phillipsi (Foord and Crick, 1897); Carboniferous Limestone, Yorkshire, northern England, ?Asbian.

B. sulcatus Bisat, 1952; Pendleside Limestone Formation, Barnoldswick, north-west England, late Asbian.

B. tianshanicum (Popov, 1968); base of Kara-Kiya Suite, Tien-Shan, Kirgizya, CIS, Arundian.

B. trevallynensis (Campbell, Brown and Coleman, 1983); Bonnington Siltstone, New South Wales, Australia, Viséan.

B. umbilicatus (Bisat, 1934); 'reef limestones' Newton Gill, Hellifield, north-west England, late Asbian.

B. varians sp. nov.; Hodderense Limestone Formation, Leagram north-west England, late Holkerian.

Bollandites bashatchensis Popov, 1965, should be transferred to *Bollandoceras* (see p. 40). *B. kokdzharensis* Popov, 1965 and *B. narynensis* Popov, 1965, judged by their conch form and suture, fall within *Dzhaprakoceras* (see p. 50). *Bollandites bowsheri* Gordon, 1957, cannot be placed in *Bollandites* since its transverse ornament progrades over the venter; the generic status of this species is at present unclear but it probably represents a juvenile *Goniatites* sp. *Bollandites kiligwae* Gordon, 1957, was based on a suite of juveniles; this species lacks a serpenticonic juvenile stage, thus excluding it from *Bollandites* and it may belong to *Beyrichoceratoides* or *Dzhaprakoceras*. *Bollandites boreus* Kusina, 1980, is similar in conch form to *Bollandites*, but has retrograde constrictions and a ventral lobe without flexed sides, this species is here placed in *Rotopericyclus* (see p. 80). *Bollandites trevallynensis*, originally described under *Beyrichoceras*, has a transverse ornament with feeble sinuses and a suture typical of *Bollandites*.

Bollandites varians sp. nov.

Plate 7, figures 1, 3, 7, 9, 11; Plate 8, figure 14; Text-figures 47–48

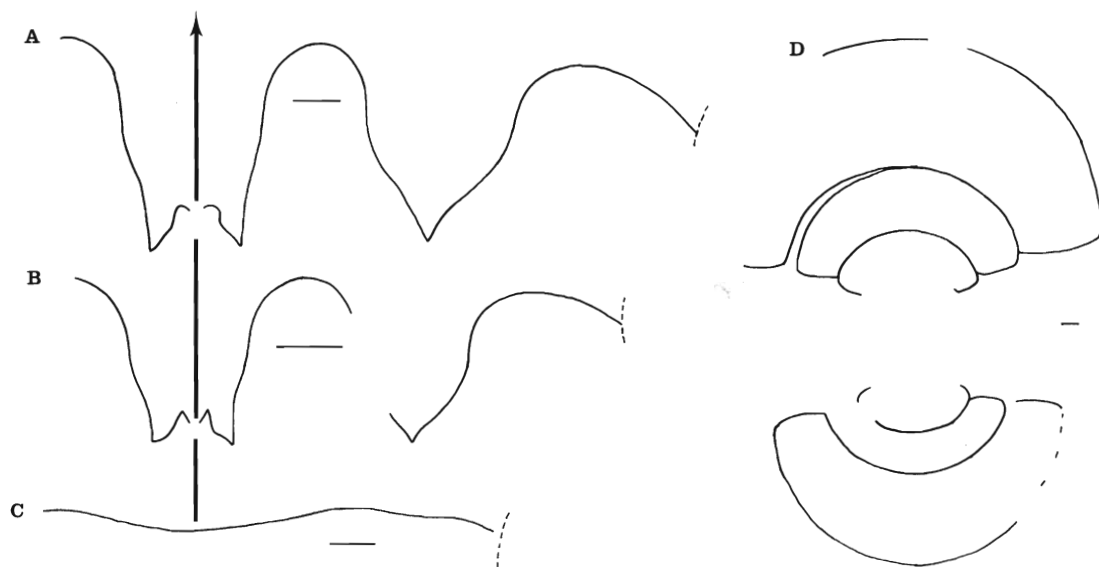
Derivation of name. From the variable shape of the conch.

Material. Holotype Ro 5187, solid septate, exfoliated conch; from locality 11; and paratypes Ro 934–8; from locality 9; Ro 940–53; from locality 10; LZA 7865; from locality 12; solid and fragmentary conches at all growth stages, some juveniles showing ornament.

Range. Late Chadian, upper BB Zone; Hodderense Limestone Formation.

Diagnosis. A subsphaeroconic to pachyconic *Bollandites* with a broad venter and wide umbilicus throughout growth.

Description. The conch is variable, subsphaeroconic to cadiconic at maturity, but always serpenticonic before the fourth whorl; whorl expansion is slow. The venter may broaden considerably above D = 9 mm. The



TEXT-FIG. 47. *Bollandites varians* sp. nov. A, paratype, LZA 7865; ventral suture, H = 6.7, W = 11.8. B-C, holotype, Ro 5187; B, ventral suture, H = 4.0, W = 8.6; C, constriction, same dimensions as B. D, paratype, Ro 940; axial section.

umbilical walls are steep-sided. The external ornament consists of weak, simple, transverse striae, spaced at four per mm at $W = 7$ mm, but is much coarser in juveniles. The hyponomic sinus is broad and very weak; a lateral sinus is present in some adults. Weak transverse ribs are present on internal casts below $D = 6$ mm. Constrictions are retained throughout growth, but are particularly strong in juveniles ($D = < 6$ mm) and run parallel to the external ornament. The suture has rounded saddles and a divergent (orad) ventral lobe with flexed sides; the lateral lobe is deep and relatively narrow, with flexed sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
Ro 940	32.0	13.0	10.0	22.0	0.69	0.31	0.41
LZA 7865	21.0	10.0	4.5	12.0	0.57	0.21	0.48
Ro 941	19.5	6.0	11.0	11.0	0.56	0.56	0.31
Ro 939	16.0	4.5	6.5	12.5	0.78	0.41	0.28
Ro 942	14.0	5.0	6.0	10.0	0.71	0.43	0.36
Ro 951	5.3	1.6	3.3	3.5	0.66	0.62	0.30

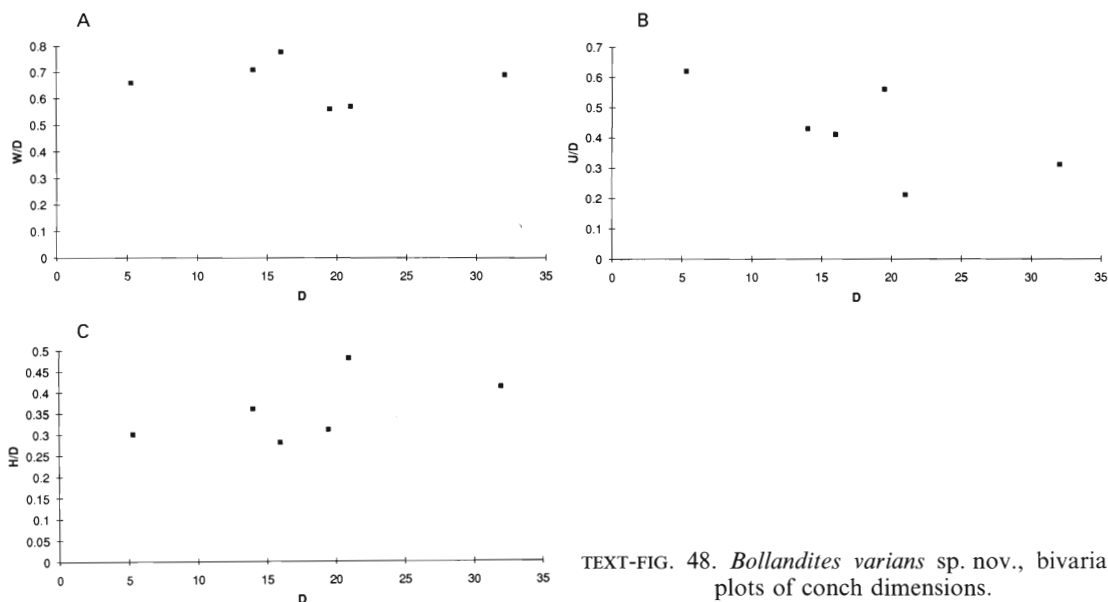
Remarks. The conch form of this stratigraphically early species is in stark contrast to that of late Asbian forms, which show lateral whorl compression, accelerated ontogeny and arched venters.

Bollandites? sp.

Plate 3, figure 7

Material. Ro 5076a, a fragmentary, late adolescent, exfoliated conch; from locality 6.

Range. Arundian, lower BB Zone; Hodder Mudstone Formation (Chaigley Limestone).



TEXT-FIG. 48. *Bollandites varians* sp. nov., bivariate plots of conch dimensions.

Description. The conch is apparently cadiconic with a wide umbilicus and a steep umbilical shoulder. The external ornament is not preserved. The internal ornament, which is preserved only low on the flanks, consists of weak radial undulations. There are no sutures.

Remarks. This specimen is tentatively placed in *Bollandites* on account of the general conch form.

Genus PARAHAMMATOCYCLUS gen. nov.

Type species. *Parahammatocyclus chaigleyensis* sp. nov.

Diagnosis. Conch small, $D = < 20$ mm, subsphaeroconic in the adult, but initially serpenticonic with an intermediate cadiconic stage. During the cadiconic stage, umbilical tubercles are present. The ornament consists of simple, coarse transverse striae; these are nearly radial, with only a weak hyponomic sinus. The external suture has a divergent-sided (orad) ventral lobe, a rounded lateral saddle and a deep, broad lateral lobe, with flexed sides and an acute mammilate termination.

Range. Arundian.

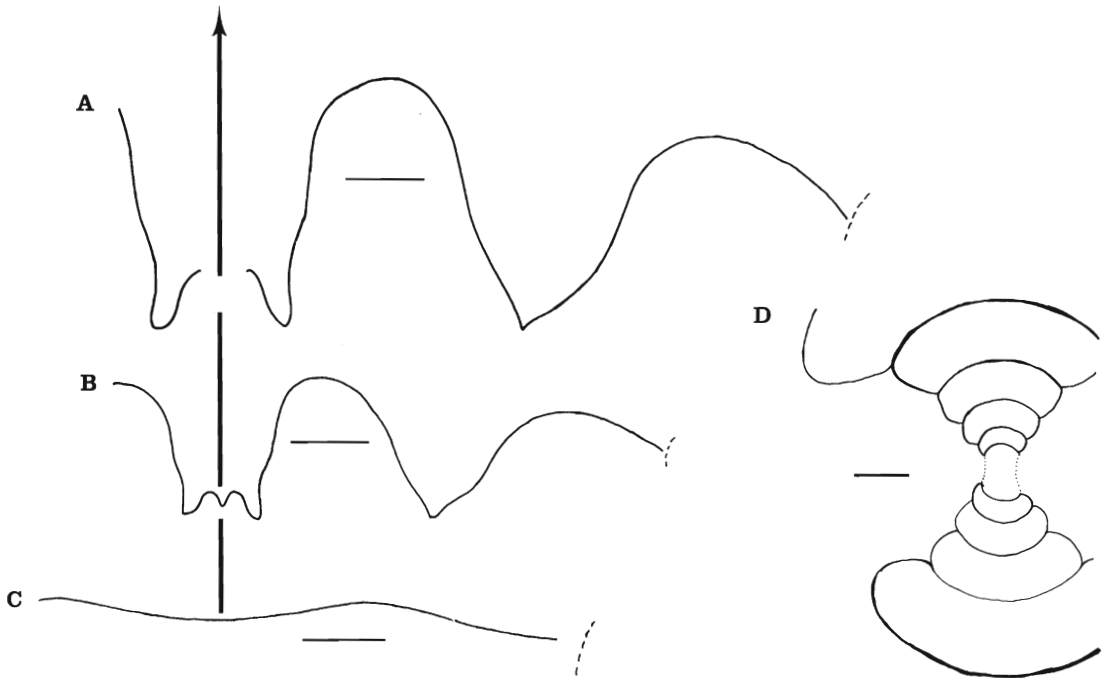
Remarks. This genus is intermediate between *Bollandites* and *Hammatocyclus*. It differs from the former in the presence of umbilical tubercles, and from the latter by ontogenetic loss of tubercles and the presence of a divergent-sided (orad) ventral lobe. Bearing in mind these morphological relationships and the stratigraphical position of *Parahammatocyclus*, it is reasonable to propose that the new genus represents an intermediate in a phyletic lineage between *Hammatocyclus* and *Bollandites*. The new genus is at present monospecific.

Parahammatocyclus chaigleyensis gen. et. sp. nov.

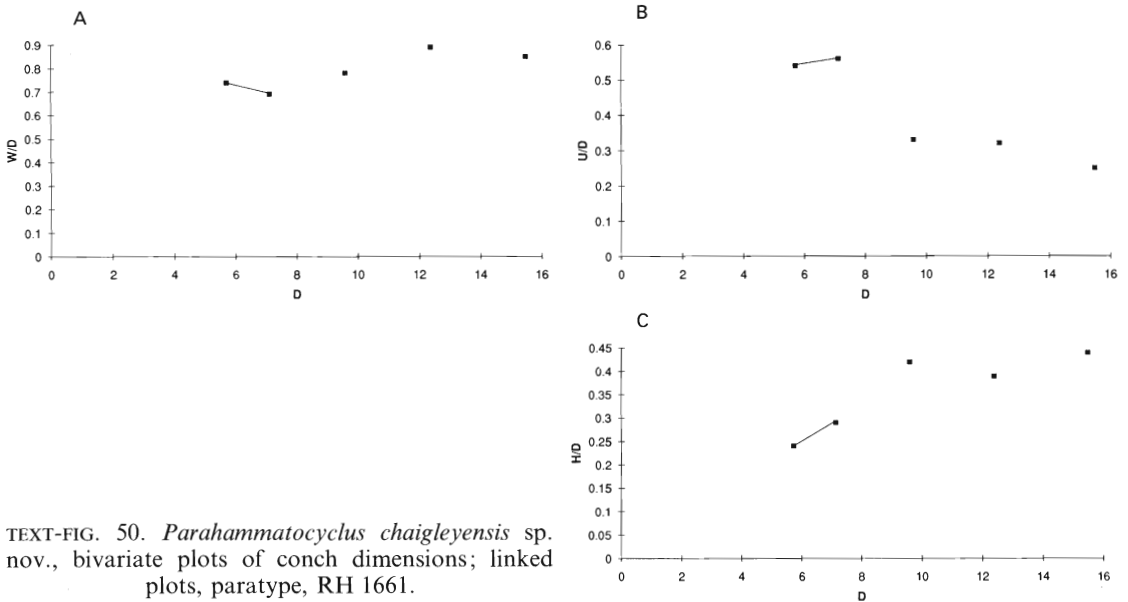
Plate 3, figures 1–3, 8; Plate 6, figures 1, 4, 12; Plate 7, figure 8; Text-figures 49–50

Derivation of name. From Chaigley, the hamlet near where the holotype was found.

Material. Holotype Ro 5127, partly testiferous late adolescent; from locality 6; paratypes, Ro 3721 (fragmentary testiferous adolescent conch; from locality, 5), Ro 3723 (exfoliated, partly crushed adolescent;



TEXT-FIG. 49. *Parahammatocyclus chaigleyensis* sp. nov. A, C, paratype, Ro 1657; A, ventral suture, H = 5.6; C, constriction, H = 3.2. B, paratype, RH 1631; ventral suture (reversed image), H = 3.5, W = 5.8. D, paratype, RH 1661; transverse section.



TEXT-FIG. 50. *Parahammatocyclus chaigleyensis* sp. nov., bivariate plots of conch dimensions; linked plots, paratype, RH 1661.

from locality, 7), Ro 5105 (fragmentary, partly testiferous adolescent; from locality, 5), Ro 5137 (mainly exfoliated adolescent; from locality 6), RH 1631 and 1657 (exfoliated adolescent conches; from locality 6) and RH 1661, juvenile embedded in packstone and sectioned axially. All specimens are ankeritic.

Range. Arundian, lower BB Zone; Hodder Mudstone Formation (Chaigley Limestone Member).

Diagnosis. As for genus.

Description. The conch is small ($D = < 20$ mm), serpenticonic in the early whorls, subsphaeroconic when mature, with an intermediate cadiconic stage. The umbilicus is subquadrate at maturity. The external ornament consists of coarse, simple, transverse striae, which show only a feeble hyponomic sinus. Umbilical tubercles are present during adolescence, but these are lost at maturity. The internal ornament consists of weak transverse undulations which follow the external ornament, except near the umbilical tubercles, where the undulations sometimes branch. The umbilical tubercles are more strongly developed internally than externally. At least four constrictions, moderately incised, are present; they follow the external ornament and are preserved also on the exterior of the conch. The external suture consists of a divergent (orad) ventral lobe, rounded lateral saddle and a deep, broad, acute lateral lobe with strongly flexed sides.

Dimensions.

Specimen	D	H	U	W	W/D	U/D	H/D
RH 1651	15.5	6.8	3.8	13.2	0.85	0.25	0.44
Ro 5127	12.4	4.8	4.0	11.0	0.89	0.32	0.39
Ro 5144	9.6	4.0	3.2	7.5	0.78	0.33	0.42
RH 1661	7.1	2.1	4.0	5.0	0.69	0.56	0.29
RH 1661	5.7	1.4	3.1	4.2	0.74	0.54	0.24

Remarks. The branching of the transverse undulations on the internal ornament further suggests the pericyclid affinities of this new taxon.

GENUS ROTOPERICYCLUS Turner, 1948

Type species. *Pericyclus rotuliformis* Crick, 1899.

Diagnosis. Small to large pericyclinae with subdiscoconic conches. The ornament consists of transverse ribs or striae which pass retrograde over the flanks and venter, giving rise to a deep hyponomic sinus. Subordinate spiral lirae may be present, giving rise to crenulation. Constrictions are deeply incised, regular and numerous, visible both internally and externally. The ventral lobe of the suture has subparallel sides which diverge very slightly orad; the lateral saddle is rounded and the lateral lobe acute.

Range. Tournaisian to late Chadian.

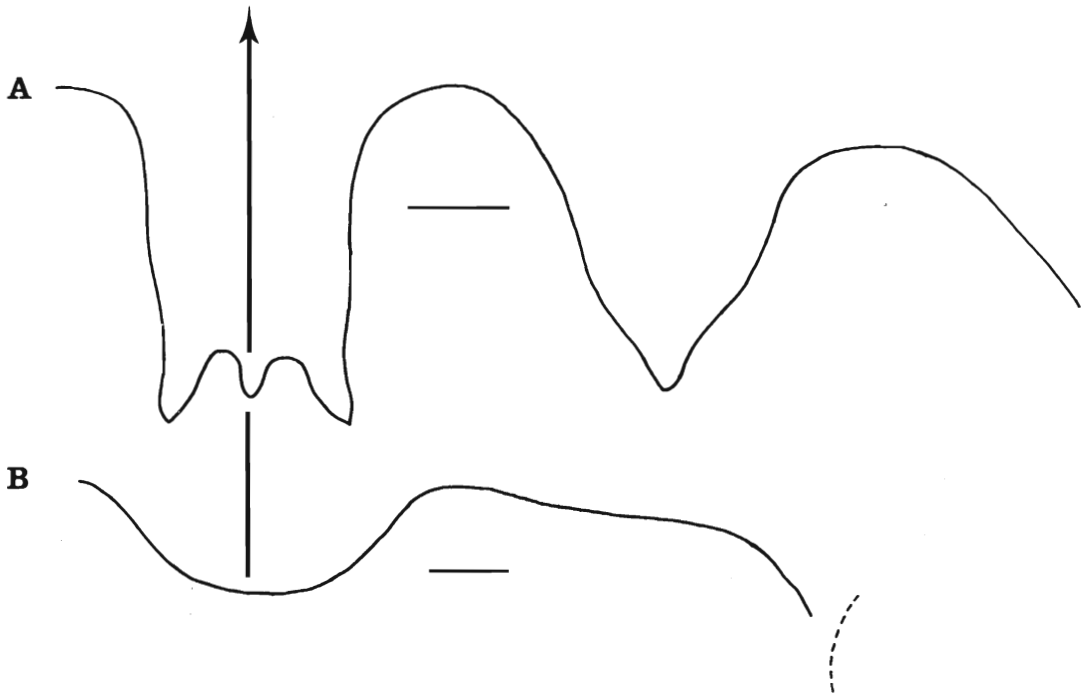
Remarks. The following species are included:

R. boreus (Kusina, 1980); Kosvinsky Suite, Kozhim River, north Urals, Russian Federation, CIS, late Chadian

R. multiplicatus (Delépine, 1940a); ?Calcaire de Vaux, Belgium, late Tournaisian.

R. postremus sp. nov.; Hodder Mudstone Formation, Clitheroe, north-west England, late Chadian.

R. rotuliformis (Crick, 1899); Carboniferous Limestone, Saint Douglas, Ireland, Courceyan.



TEXT-FIG. 51. *Rotopericyclus postremus* sp. nov.; holotype, Ro 933. A, ventral suture, H = 7.2, W = 7.2; B, constriction, same dimensions as A.

Rotopericyclus postremus sp. nov.

Plate 1, figures 7, 10; Text-figure 51

Derivation of name. From the Latin, *postremus* (= last).

Diagnosis. A small *Rotopericyclus*, lacking ribs, but with weak transverse ornament and subordinate spiral lirae.

Range. Late Chadian, upper FA Zone; Hodder Mudstone Formation (Leagram Mudstone Member).

Material. Holotype, Ro 933, partly testiferous conch, presumably mature; from locality 4a.

Description. The conch is subdiscoconic and compressed with a relatively wide, steep-walled umbilicus. The external ornament consists of coarse crenulate transverse striae, which pass retrograde over the flanks, where they are slightly concave (orad), and the venter, resulting in a deep hyponomic sinus (2 mm deep at D = 16 mm). An internal ornament is not developed. Four or five strong constrictions are present; these are deeply incised next to the umbilicus and are clearly visible on the external conch surface. The suture has a slightly divergent-sided (orad) ventral lobe, with slightly flexed sides. The lateral saddle is rounded. The lateral lobe is relatively narrow, nearly as deep as the ventral lobe, and has a subacute, mammillate termination.

Remarks. Despite the abundant and diverse ammonoid fauna present in the lower part of the Hodder Mudstone Formation, there are no other records of *Rotopericyclus*. The new species is the youngest example known and is so distinct, in lacking ribs, that it warrants description as a new species, despite the paucity of material.

DISCUSSION AND CONCLUSIONS

The Worston Shale Group ammonoids are particularly important in relating mid-Dinantian ammonoid stratigraphy to established conodont and foraminiferal zonal schemes. This is possible because of the extremely thick sequence preserved in the Craven Basin which displays a fortuitous interbedding of limestone turbidites within the hemipelagic ammonoid mudstone facies. Despite these advantages, it has only been possible to improve controls on the absolute ranges of a few species. This is a consequence of the nature of ammonoid preservation, the many stratigraphical gaps, a lack of faunas conspecific between separate regions and poor biostratigraphical controls on correlation. These limitations are the main reason for leaving the FA and BB zones undivided into subzones.

The mid-Dinantian assemblages described provide a key insight into this poorly known interval of ammonoid stratigraphy and only the faunas from the CIS surpass them in diversity. Between the CIS and the Craven Basin only a few species are conspecific, namely *Dzhaprakoceras deflexum*, *D. djaprakense*, *D. subglobosum* and *Muensteroceratoides aksuensis*, but there are some apparent differences in stratigraphical distribution. For example, in the northern Urals, *D. deflexum* and *D. subglobosum* were reported to come possibly from the BB Zone, Nortnichsky Horizon (Kusina 1980), whereas in the Craven Basin *D. deflexum* is recorded only from the upper FA Zone, and *D. subglobosum* from the middle FA zone, as in Tien-Shan (Popov 1968). These differences may be real, but it must be stressed that the northern Urals occurrences of *D. deflexum* and *D. subglobosum* were only tentatively located stratigraphically by Kusina (1980). All the genera known from the Worston Shale Group are recorded from the CIS, apart from *Parahammatocyclus* gen. nov. This disparity between distribution at the species and generic levels is typical of ammonoid occurrences documented from younger Carboniferous strata. Species conspecific with those from other regions include *Merocanites applanatus*, recorded from the Erdbach Limestone in Germany, and *Dzhaprakoceras hispanicum*, described from the Genicera Formation in Spain and the Tober Colleen Formation, Ireland. The faunas from the Craven Basin suggest that *D. hispanicum* is a long-ranging form, from middle FA to early BB. Because of the condensed nature of the Erdbach Limestone it is difficult to assess the true stratigraphical range of *M. applanatus*.

Some proposals on ammonoid evolution can also be made. Bisat (1952), when erecting the genus *Bollandites*, suggested an affinity with the pericyclids, particularly *Hammatocyclus*. This seems to be borne out by the discovery of *Parahammatocyclus* gen. nov., which appears to be the direct ancestor of *Bollandites*, resulting in a lineage originating with *Hammatocyclus*. There is still, however, the problem that *Parahammatocyclus* gen. nov. is recorded from above the first entry of *Bollandites*. *Helicocyclus* is likely to have originated from *Ammonellipsites*. Both these genera have similar sutures and a serpenticonic juvenarium, but in *Helicocyclus* the serpenticonic whorl form is maintained throughout ontogeny.

Amongst the muensteroceratids, *Beyrichoceratoides*, *Dzhaprakoceras* and *Muensteroceratoides* are closely related because a serpenticonic juvenarium is lacking. These genera also show oral constriction of the ventral lobe. If *Muensteroceras* is the ancestor, then there is a possible lineage from *Muensteroceratoides* through *Beyrichoceratoides* to *Dzhaprakoceras*, but the stratigraphy of these genera suggests that *Dzhaprakoceras* appears before *Beyrichoceratoides*. Unfortunately, the precise timing of the appearance of genera in the early part of the FA zone is not well enough known to resolve this problem. *Bollandoceras* has a serpenticonic juvenarium; it is therefore unlikely that *Beyrichoceratoides* or *Dzhaprakoceras* are ancestors; upper FA forms referred to *Muensteroceras* by Kusina (1980) seem more probable.

The origin of *Dimorphoceras* remains a mystery, but some juvenile involute *Dzhaprakoceras*, such as *D. levis* sp. nov., show similarity to juvenile *Dimorphoceras*. *Kozhimites*, with its strongly bisinuous ornament, laterally compressed conch and broad ventral lobe, is also a possible candidate as ancestor.

In the nomismoceratids, the lineage *Eonomismoceras*–*Simmonoceras*–*Nomismoceras* reflects the stratigraphical and morphological progression of these genera, although the stratigraphical position of *Simmonoceras* at the base of the BB Zone is not conclusively proven.

Winchelloceras seems to be close morphologically to *Beyrichoceras*, but unfortunately the juvenarium of the former is undescribed. There are no clues in the mid-Dinantian assemblages as to the origin of the important genus *Goniatites*, which appears in the late Dinantian. Some superficial similarity exists between the sutures of *Goniatites* and the ammonellipitins; however, the juvenaria differ dramatically and there is a long stratigraphical gap between the extinction of the ammonellipitins, at the top of the FA Zone, and the appearance of *Goniatites*, in the upper part of the B zone.

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