AMMONITES OF TETHYAN ANCESTRY IN THE EARLY LOWER CRETACEOUS OF NORTH-WEST EUROPE

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ABSTRACT. Early Lower Cretaceous (Berriasian–Hauterivian) ammonite faunas in north-west Europe were predominantly of boreal origin. However, during Valanginian and Hauterivian times there was strong Tethyan influence. The most sharply defined immigration horizons (earliest Valanginian, early late Valanginian and mid Hauterivian) coincide with significant transgressions. Some species came singly or in small numbers, while others migrated in large numbers to evolve into thriving populations which sometimes gave rise to endemic genera. All the following genera are of Tethyan origin and are reviewed here; species descriptions are given for those genera marked with an asterisk: _Phylloceras_, _Phyllopachyceras_, _Lytoceras_ s. l., _Juddiceras_*, _Aegocrioceras_, _Crioceratites_* (subgenera _Crioceratites_* and _Paracrioceras_*), _Bochianites_*, _Protaconeceras_*, _Olcostephanus_, _Subastieria_, _Parastieria_, _Valanginites_, _Saynoceras_*, _Platylenticeras_, _Thurmanniceras_?*, _Neocomites_ (subgenera _Neocomites_* and _Teschenites_*), _Varlheideites_, _Karakaschiceras_*, _Neohoploceras_*, _Dicostella_*, _Endemoceras_, _Distoloceras_, _Acanthodiscus_, _Leopoldia_, _Saynella_, _Oosterella_*, _Subsaynella_* and _Spitidiscus_. Two new species are described: _Crioceratites_ (_Paracrioceras_) _spathi_ and _Dicostella germanica_. In conjunction with records of boreal ammonites in France, these occurrences allow close correlation of north-west European and Tethyan zonal schemes.

THE early Cretaceous basins of north-west Europe were connected to both the Boreal Ocean to the north and Tethys to the south (text-fig. 1). Their ammonite faunas were predominantly of boreal origin and because of the long history of research in the area are quoted as a standard for the Boreal Realm. Yet there is a strong Tethyan influence in the Valanginian and Hauterivian, appreciated by early workers in the area but often overlooked by specialists further afield. The Tethyan elements facilitate correlation with the standard Lower Cretaceous stages defined in France and Switzerland, and this correlation in turn provides a key for comparison between Tethyan and boreal faunas elsewhere.

The significance of some Tethyan or Tethyan-derived elements in England and Germany was reviewed by Kemper (1971, 1973), Rawson (1973), and Rawson and Kemper (1978), but many of the ammonites remain poorly known and the present paper is the first comprehensive review attempted. It complements the description of boreal ammonites from south-east France (Thieuloy 1973, 1977_a_), and these papers together provide the basis for a much firmer inter-regional correlation than has been achieved previously.

Our own collections and field observations have provided the basis for the research, but we have consulted all the more important public and private collections: a full list is given before the systematic discussions. Unfortunately, many of the best German collections were destroyed during the Second World War, including much of the material figured by Koenen (1902). Many of the ammonites from old collections can be assigned to a horizon in the modern stratigraphical schemes either because accurate and interpretable information was recorded or because some of the famous old German localities were in the thick basin facies clays of Lower Saxony, where a single clay pit in some cases exposed only a single zone. The localities mentioned in the text are shown in text-fig. 2 and are discussed briefly below.

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HISTORICAL REVIEW

The term 'Neocomian' was proposed for strata in the region of Neuchâtel (= Neocom), Switzerland; the stage names Valanginian (Desor 1854) and Hauterivian (Renevier 1874) were erected for part of the Neocomian, again with type localities near Neuchâtel. However, south-east France was the centre of research on strata of this age and the French faunas became the standard for correlation with other regions. As early as 1838, Agassiz recognized the Neocomian age of fossils from the Speeton Clay, and Roemer (1840) made a similar correlation with his Hils faunas.

Ammonite species in England and Germany first became known through the descriptions of Sowerby (1827), Young and Bird (1828), Phillips (1829), and Roemer (1840), so that by the middle of the century the general sequence of faunas was established, the importance of some Tethyan elements had been recognized and broad correlations with France and Switzerland attempted (e.g. Strombeck 1849, 1855; Judd 1868, 1870; Coquand 1869). Subsequently, Neumayr and Uhlig (1881) and Weerth (1884) monographed important German faunas, though little stratigraphical information was given.

A more precise phase of stratigraphical work commenced with the publication of a detailed lithological description of the Speeton Clay by Lamplugh (1889). This provided a firm foundation for the faunal description by Pavlow (1892) in which a detailed account of the faunal sequence facilitated correlations with Germany, France, Switzerland, and the Soviet Union. Then Koenen (1901, 1902) published a detailed zonation for north Germany and monographed the faunas. In this work the stage names Valanginian and Hauterivian were introduced to north-west Europe. Koenen's zonation, with minor amendment (e.g. Stolley 1937), has remained in use almost to the present day (e.g. Muller and Schenck 1943). Koenen (1901) achieved also an impressive correlation between north Germany and Tethys. Spath (1924*a*) compiled a bed-by-bed list of Speeton and Lincolnshire ammonites and proposed a zonation for north-west Europe: the zonation was hypothetical and the ammonite records not always accurate (Rawson 1971*b*, pp. 63–64) but the general picture was valuable and provided further detail for correlation with Tethyan faunas (Spath 1924*a*, table). In 1935, Stolley discussed the occurrence and stratigraphical significance of Tethyan-derived ammonites and belemnites in north Germany and of boreal forms in Tethys, but unfortunately none of the specimens were figured.

Since 1960, monographs on German *Platylenticeras* (Kemper 1961), *Endemoceras* (Thiermann 1963), *Simbirskites* (Bähr 1964) and the dichotomitids (Kemper 1978), and on the English *Simbirskites* (Rawson 1971*a*) and *Aegocrioceras* (Rawson 1975*b*), accompanied by renewed stratigraphical work (summarized in Kemper 1973, 1976; Rawson *et al.* 1978), have provided the basis for a refined subdivision of the Valanginian and Hauterivian stages. The zonal schemes currently in use, together with the main lithostratigraphical terms, are summarized in text-fig. 3.

LOCALITIES

All localities mentioned in the text are shown in text-fig. 2. Below we give brief stratigraphical information on all those from which we have examined specimens; text-fig. 2 also includes a few localities which yielded specimens now lost.

England

Nettleton, Lincolnshire. A series of ironstone quarries (now filled in) along the western slopes of Nettleton Valley provided excellent sections, which have yet to be described in detail. Kaye (1964) published a generalized section and Penny and Rawson (1969, p. 198 and table I) gave some additional information. The top calcareous beds of the Claxby Ironstone yielded an important ammonite fauna (Rawson collection) indicating that these beds, less than 1 metre thick, are condensed representatives of much of the Valanginian and early Hauterivian. The fauna includes *Bochianites*, *Neohoploceras submartini*, *Karakaschiceras* cf. *heteroptychus*, *Endemoceras* spp., *Distoloceras* spp., and *Olcostephanus* spp. (all discussed below) with boreal *Polyptychites*, *Prodichotomites* and *Dichotomites*.

A sand quarry at Top Barn now exposes the overlying Claxby Ironstone; the basal bed of the ironstone has yielded *Neocomites*? cf. *trezanensis*.

Speeton, Yorkshire. This is the type locality of the Speeton Clay; the lithostratigraphy and biostratigraphy are reviewed by Rawson *et al.* (1978). There is a remanié, phosphatised fauna of late Valanginian age in the nodule bed at the base of bed D2D, which contains *Bochianites*, *Olcostephanus*, *Karakaschiceras*, and *Neohoploceras*. Tethyan or Tethyan-derived ammonites in the Hauterivian include *Phylloceras*, *Spitidiscus*, *Protaconeceras* and *Crioceratites*, and the zonal genus *Endemoceras*.

Germany

The German localities occur in five regions in the Lower Saxony Basin, outlined below. Most are old sections, no longer visible, and few stratigraphical details are available.

Emsland. Close to the Dutch border, sediments here form the western marginal facies of the basin. Boreholes in the Georgsdorf and Lingen oilfields and near Nordhorn and Lathen have yielded *Bochianites neocomiensis*, *Karakaschiceras* cf. *inostranzewi* and *Neohoploceras submartini*. Temporary exposures in the Gildehauser Sandstein at Gildehaus yielded *Spitidiscus* and *Crioceratites*. (For details and illustrations see Kemper 1976.)

Osning Edge. The Osning Sandstein (Valanginian–Barremian) of the Osning Edge is the littoral to shallow neritic facies of the southern margin of the basin and was formerly extensively quarried. Ammonites were described by Weerth (1884). Localities:

Brackwede, near Bielefeld:	*Leopoldia* sp.
Ehberg, near Bielefeld:	*Bochianites neocomiensis*.
Hohnsberg, near Osnabrück:	*Neocomites* (*Teschenites*) sp.

Minden region. The dark shales of the basin depocentre crop out north of the Wiehengebirge and the Bückeberge (text-fig. 2). Numerous clay-pits worked the shales but most have disappeared. Localities:

Bückeburg:	*Valanginites* (new pit worked in 1971–1972).
Diepenau:	*Neocomites* sp. c, *Dicostella*. This section is still worked and exposes the *triptychoides* and *bidichotomoides* Zones (see Kemper 1978, fig. 5).
Hasslage:	*Juddiceras*.
Heisterholz:	*Leopoldia leopoldi*. This early Hauterivian section is still worked (see Thiermann 1963, p. 351).
Hollwede:	*Olcostephanus*, *Valanginites*, *Saynoceras*, *Karakaschiceras* (*hollwedensis* Zone fauna).
Mindener Wald:	*Dicostella* sp. nov. a.
Ottensen:	*Dicostella tuberculata*, *D.* aff. *houdardi*, berriasellid gen. uncertain. This was one of the classic 'Arnoldien' Schichten (= *tuberculata* Zone) localities.
Sachsenhagen:	*Platylenticeras*. Abandoned in 1978; section in Kemper (1961).
Stadthagen (Ziegelei Kuhlmann):	*Olcostephanus* and *Acanthodiscus*. Latest Valanginian and early Hauterivian (see Thiermann 1963, pp. 351, 389).
Stadthagen (Ziegelei Möller):	*Phyllopachyceras*, *Juddiceras*, *Crioceratites*, *Olcostephanus*, *Neocomites*? sp. D. Late Valanginian.
Twiehausen:	*Valanginites*, *Saynoceras*, *Karakaschiceras*: *hollwedensis* Zone. Still working (see Kemper 1978).
Varlheide (Hasslage Süd):	*Varlheideites*, *Oosterella*: *crassus* Zone. A new section (see Rawson and Kemper 1978).
Wiedenbrügge:	*Juddiceras*, *Valanginites*, *Saynoceras*: *triptychoides* and *bidichotomoides* Zones (Kemper 1978, fig. 5).

Hannover–Hildesheim–Hils region. Here, outcrops of the shallower-water clays ('Hilsthon') were formerly extensively worked, but of those localities listed below only Sarstedt is still open; many of the remainder were abandoned several decades ago. Localities:

Barsinghausen:	*Valanginites*.
Bredenbeck:	*Valanginites*, *Leopoldia* spp.
Elligser Brink:	*Olcostephanus* of early Hauterivian type.
Hilsbornsgrund:	*Olcostephanus*.
Hoheneggelsen:	*Bochianites*, *Karakaschiceras*, etc. of the *hollwedensis* Zone. Younger strata may have been exposed too. Koenen (1902) figured a number of ammonites from here.
Hollingskopf:	*Dicostella*.
Sarstedt (Ziegelei Moorberg):	*Olcostephanus*, *Acanthodiscus*, *Crioceratites*. Hauterivian (and Barremian)—see sections in Mutterlose (1978).
Schulenburg:	*Leopoldia leopoldi*.
Wintjenberg:	*Lytoceras*.

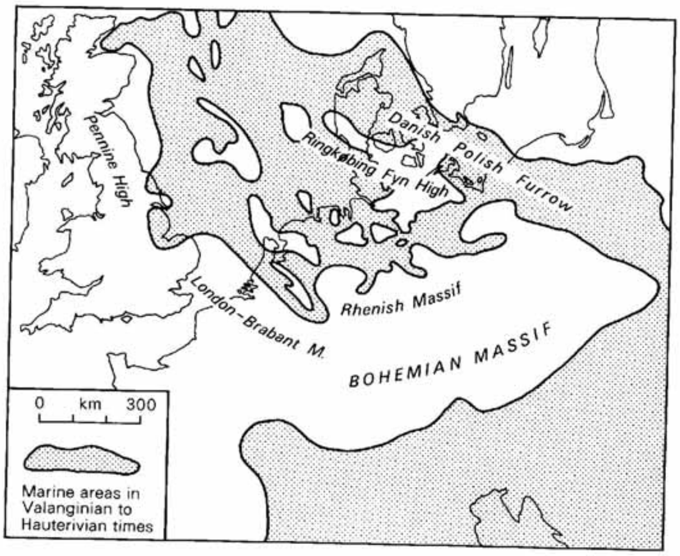
Salzgitter area. Here the marginal facies of the south-eastern part of the basin includes ironstones: ammonites from this area were figured by Neumayr and Uhlig (1881) and Koenen (1902).

Heligoland

In addition to the German onshore localities reviewed above, the North Sea island of Heligoland is an important German locality. Here, clays are exposed on the sea floor and ammonites are occasionally washed ashore. In recent years rich faunas have been collected by skin-divers and reviewed by Kemper, Rawson, Schmid and Spaeth (1974) and Rawson (1974). *Crioceratites* of both Hauterivian and Barremian types occur, and two phylloceratids are recorded.

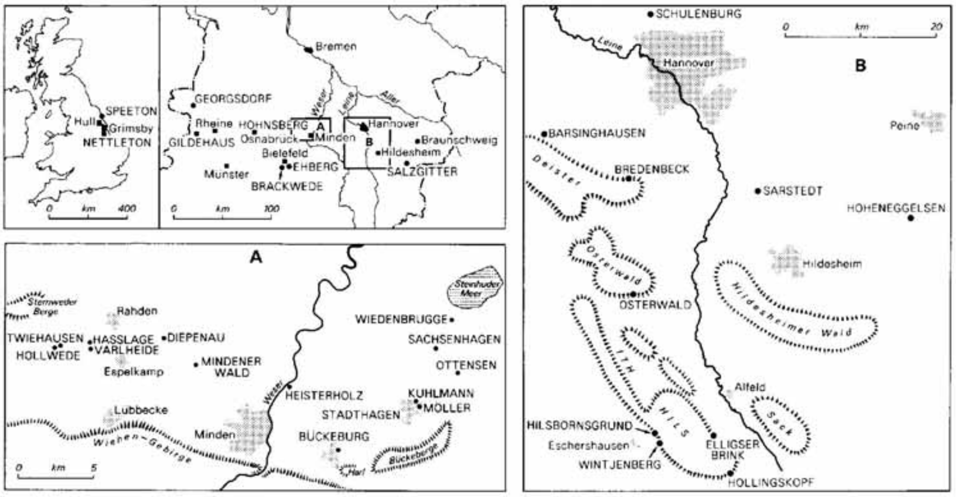
EARLY CRETACEOUS PALAEOGEOGRAPHY AND MARINE CONNECTIONS

The interconnecting basins occupying eastern England, the North Sea region and north Germany during the early Cretaceous essentially formed a southern shelf-sea extension from the 'Boreal Sea', and were separated from western Tethys by a central European landmass (text-fig. 1). There was a marine connection between them via the Danish-Polish Furrow, probably a second connection round the west of Britain (Rawson 1973) and possibly a third directly from the Lower Saxony Basin to South Germany following the line of the Jurassic 'Hessian Straits' (Middlemiss, 1980): the last is impossible to prove because of the absence of sediments, but is indicated by close similarities in brachiopod faunas and in certain ammonite distributions.



TEXT-FIG. 1. Early Cretaceous palaeogeography and marine connections in western Europe.

During the Berriasian (≃ Ryazanian) the Lower Saxony Basin was a non-marine region in which sediments of Wealden facies (the Bückeberg Formation) accumulated, while eastern England remained marine but was open only to boreal influence: the ammonites are related closely to Russian forms (Casey 1973). An early Valanginian transgression reintroduced a marine regime to the Lower Saxony Basin without much extending the area of deposition, while in England the same event is marked by facies change from a brief brackish interval at Speeton (Bed D5) to fully marine conditions and from sandstone to clay ironstone deposition in Lincolnshire.



TEXT-FIG. 2. General locality maps with: A, details of the area around Minden; B, details of the area around Hannover.

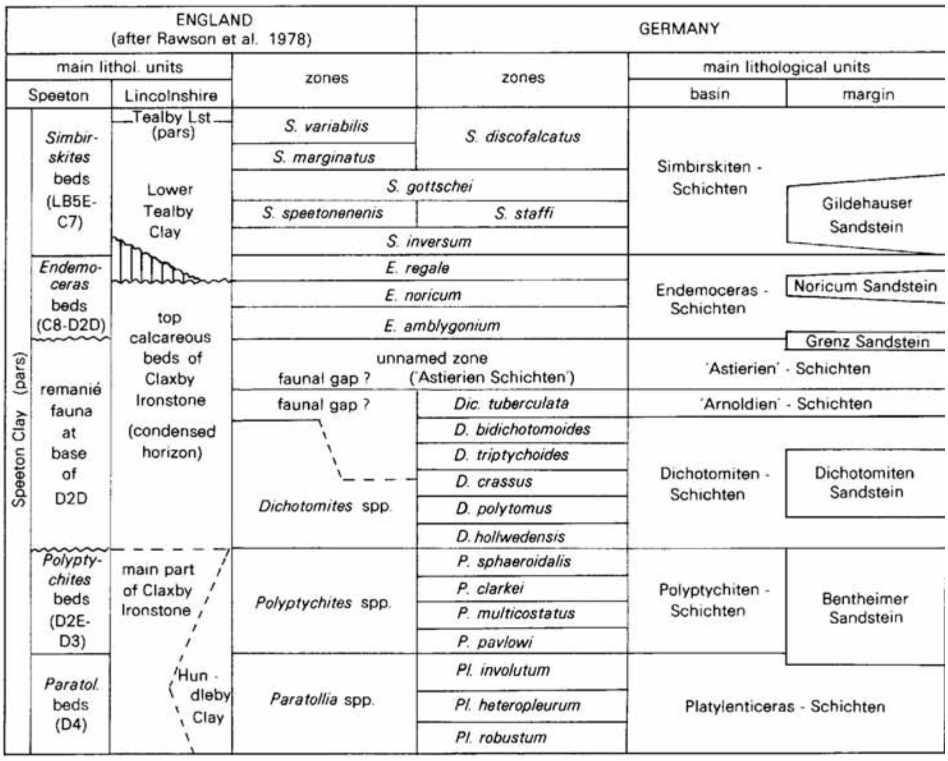
One of the most important transgressions in Europe took place at the beginning of the late Valanginian: its sedimentary and faunal effects are apparent in the Jura, Poland, north Germany, the Netherlands and England. There was an enlargement in the area of the Lower Saxony Basin, especially its eastern part, and the establishment of a direct connection between here and the Polish Furrow via the South Mecklenburg–Brandenburg Basin. Elsewhere, the late Valanginian is represented typically by condensed facies, especially in the Jura where the thin '*Astieria-* und Bryozoënmergel' and equivalents represent the whole late Valanginian (Donze and Thieuloy 1975), and in eastern England where condensed, remanié faunal horizons are the sole representative (Rawson *et al.* 1978). In some areas the condensed facies includes faunas of the earliest late Valanginian and latest Valanginian only, the bulk of the late Valanginian not being represented. Sometimes, earliest Hauterivian faunas also occur in the same condensed beds.

While latest Valanginian/early Hauterivian sea-level changes are difficult to unravel in north-west Europe, there is clear evidence of a mid-Hauterivian (*inversum* Zone) transgression. This is indicated by sharp facies changes in eastern England and overstep in some marginal areas of the Lower Saxony Basin: ammonite faunal changes occurred at the same time. Regression commenced at about the end of the Hauterivian and the Danish–Polish Furrow closed at its southern end during the Barremian. Exchange of ammonites between north-west Europe and Tethys ceased, with the exception of some crioceratitids (see page 261).

AMMONITE DISTRIBUTIONS AND MIGRATION

The stratigraphical distribution of dominant ammonite groups

The zonal sequences for north-west Europe shown in text-fig. 3 are based on a group of genera which dominated the faunas at successive periods of time: the change from one genus to another is sometimes an evolutionary progression but usually a sharp break reflecting immigration. The



TEXT-FIG. 3. Zonal schemes and lithostratigraphy in England and north Germany

majority of genera are of boreal origin but some are derived from Tethys so that the zonal scheme cannot be regarded as a standard for the Boreal Realm. The probable origin of the zonal genera is shown in text-fig. 4.

Patterns of migration

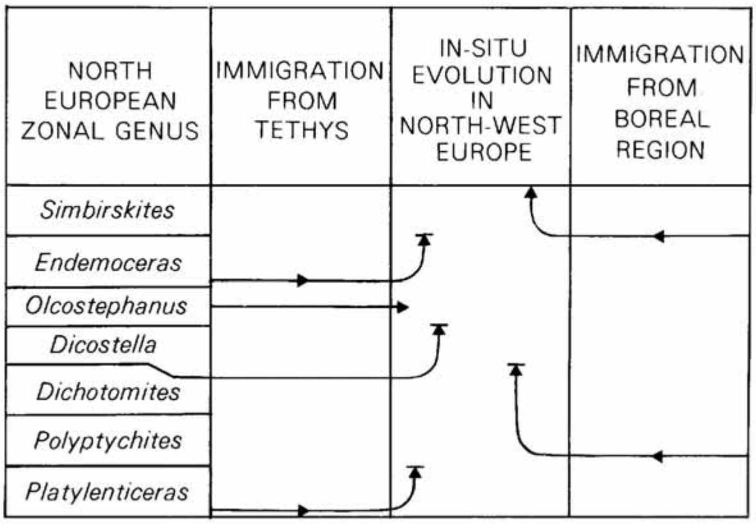
Rawson (1973) distinguished two groups of migrants from Tethys to north-west Europe, those which came singly or in small groups (isolated 'strays') and those which migrated in considerable numbers to form evolving populations which normally temporarily displaced boreal faunas ('mass migrations'). Although there are gradations between them the distinction of the two categories remains useful and we now recognize a third, the 'inter-regional mass occurrence'.

'Stray' occurrences. Almost throughout the Valanginian and Hauterivian, Tethyan species are found in north-west Europe, either as single specimens or as small, short-lived populations. Some obviously represent the chance migration of a single animal penetrating an unfavourable environment (or an empty shell drifting in) and occur randomly through the sequence (e.g. phylloceratids). Others (e.g. *Spitidiscus*) occur in small numbers, usually at clearly defined horizons and often associated with other immigrants. Their immigration period was brief and they did not evolve into new species: such

forms are thus of exceptional value in correlation and include many of the 'inter-regional' markers discussed by Kemper (1971).

Regional mass occurrences (= 'mass migrations' of Rawson 1973). Some genera originated in Tethys but migrated northward either to occupy newly formed niches (e.g. *Platylenticeras*) or to compete successfully against pre-existing forms and thus evolve *in situ* to form endemic species or even genera (e.g. *Endemoceras*, *Distoloceras*).

Inter-regional mass occurrences. In some instances a fairly long-ranged genus suddenly expanded dramatically in numbers in both north-west Europe and parts of Tethys: all known examples are of Tethyan origin. The most spectacular is *Olcostephanus* (see p. 268), which increased on two occasions (latest early Valanginian and latest late Valanginian). *Bochianites* expanded briefly in the early late Valanginian (p. 266). *Saynoceras* and *Valanginites* show a similar rapid inter-regional expansion but the genera are short-ranged. Some of the occurrences again provide important inter-regional markers (Kemper 1971; Thieuloy 1977*a*).

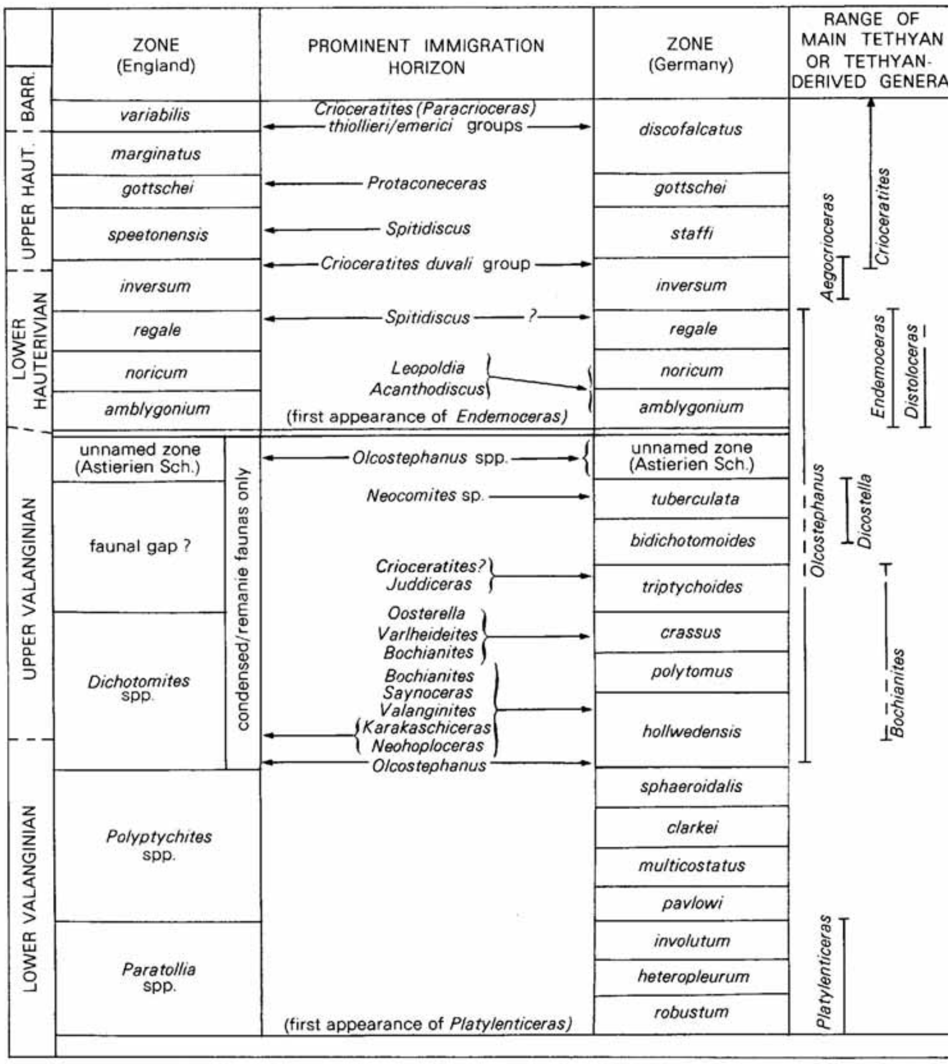


TEXT-FIG. 4. Origin of zonal genera

Relationships between migrations and transgressions

While single occurrences appear to be randomly scattered in time, ammonites that immigrated from Tethys to form small, short-lived populations or dominant groups show a significant distributional pattern (text-fig. 5) which is often related to transgressions. The replacement of Tethyan-derived forms by boreal genera does not show such a relationship and doubtless reflects the probability that environmental conditions generally suited boreal faunas more than Tethyan ones.

The early Valanginian transgression which flooded the previously non-marine Lower Saxony Basin and parts of the North Sea (e.g. Heligoland) was accompanied by the immigration from Tethys of *Platylenticeras*, which evolved rapidly to occupy the whole Lower Saxony Basin. Marine conditions had continued from Ryazanian times in eastern England, and here the sparse early Valanginian faunas are dominantly boreal. The more widespread transgression at the beginning of



TEXT-FIG. 5. Occurrence of Tethyan-derived ammonites in England and north Germany (excluding single occurrences).

the late Valanginian coincided approximately with the evolutionary change in north-west Europe from *Polyptychites* to *Dichotomites*, and polyptychitids continued to dominate the faunas until almost the end of the Valanginian. However, the transgression created significant faunal changes ('Faunenschnitte') through

(i) An increase in diversity and rate of evolution within the Polyptychitinae, including the change from *Polyptychites* to *Prodichotomites* and *Dichotomites* (Kemper 1978); this was presumably because of the increase in variety of available biotopes.

(ii) Increased migration in both directions between western Tethys and north-west Europe (e.g. *Karakaschiceras*, *Valanginites*, *Saynoceras*, *Bochianites*, etc. to north-west Europe).

The later successive immigrations of *Dicostella*, *Olcostephanus* and *Endemoceras* are less obviously related to sea-level changes, but the appearance of *Endemoceras* at Speeton is accompanied by renewed sedimentation after a period of phosphatization and reworking of late Valanginian ammonites. In general, the early Hauterivian is a period of significant Tethyan influence with the occurrence of such genera as *Olcostephanus*, *Acanthodiscus*, *Leopoldia* and *Spitidiscus*: it is also a time when the belemnite *Hibolites* migrated northward in large numbers, to replace *Acroteuthis*.

In the mid-Hauterivian, *Simbirskites* abruptly replaced *Endemoceras*; almost immediately afterwards there was a brief immigration of the heteromorph *Aegocrioceras* of presumed Tethyan ancestry. In marginal areas of the north-west European basins the *Aegocrioceras* beds (*inversum* Zone) are clearly transgressive. In late Hauterivian times the ammonite faunas are almost exclusively boreal with the exception of some heteromorphs. However, the systematics and taxonomy of the heteromorphs is unsatisfactory and it remains uncertain how closely related are the late Hauterivian and Barremian Tethyan and boreal forms (see p. 261).

COLLECTIONS

Material has been examined from the following collections (abbreviations used in the text are shown in parentheses).

British Museum (Natural History)	(BM)
Geologisches-Paläontologisches Institut, Georg-August Universität, Göttingen	(GPIG)
Geologisches-Paläontologisches Institut, Universität Hamburg	(GPIH)
Geologisches-Paläontologisches Institut und Museum, Universität Münster	(GPIM)
Private collection of Herrn R. Gröver, Kemperweg 73, 4400 Münster/Westfalen	(GC)
Hull University Geology Department	(HU)
Institut Dolomieu, Université de Grenoble (Thieuloy colln.)	(ID)
Institute of Geological Sciences, London	(IGS)
Private collection of Dipl.-Geol. J. Mutterlose, Geologisches-Paläontologisches Institut, Universität Hannover	(MC)
Naturkunde-Museum, Bielefeld	(NMB)
Niedersächsisches Landesamt für Bodenforschung/Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover	(NLFB)
Sedgwick Museum, Cambridge	(SM)
Private collection of Herrn H. Stühmer, Wasser- und Schiffahrtsamt Tönning, Zweigstelle Helgoland, Südhafen, 2192 Helgoland	(SC)
Private collection of Messrs C. W. and E. V. Wright, The Old Rectory, Seaborough, Beauminster, Dorset	(Wrights' colln.)
Yorkshire Museum, York	(YM)
Zentrales Geologisches Institut, Berlin	(ZGI)

SYSTEMATIC PALAEONTOLOGY

Notes. In the synonomy of species, only the first description plus subsequent north-west European records are listed.

In the small number of cases where original specimens are in private collections, a set of casts has been deposited in the NLFB and a duplicate set in the BM.

Superfamily PHYLLOCERATACEAE Zittel, 1884
Family PHYLLOCERATIDAE Zittel, 1884
Subfamily PHYLLOCERATINAE Zittel, 1884

Discussion. There are two specimens of *Phylloceras serum* Oppel from the English Hauterivian and a single *Phyllopachyceras* from north Germany. The *Phylloceras serum* are from the Speeton Clay beds C8, *regale* Zone (figured Rawson 1966*a*, pl. 72: HU. C/Rn.460), and C6, *speetonensis* Zone (recorded Rawson 1971*a*, p. 36: BM. C75852). Originally, they were recorded as *Hypophylloceras* cf. *perlobatum* (Sayn) but we follow Wiedemann and Dieni (1968, p. 20) and Kennedy and Klinger (1977, p. 353) in placing this species in synonymy with *P. serum*.

Koenen (1902, p. 39) recorded '*Phylloceras* aff. *winkleri*' from Ziegelei Möller, Stadthagen. The specimen has not been traced, but the description accords well with *Phyllopachyceras winckleri* (Uhlig), a species which first appears in the *trinodosum* Zone of the upper Valanginian. The horizon of the Stadthagen specimen was quoted as *radiatus* Zone; it is not clear whether this is the same example that Koenen (1907) later recorded from the 'Astierien'-Schichten.

Two phylloceratids from Heligoland (SC) are of either Hauterivian or Barremian age (Rawson 1974, p. 56).

Superfamily LYTOCERATACEAE Neumayr, 1875
Family LYTOCERATIDAE Neumayr, 1875
Subfamily LYTOCERATINAE Neumayr, 1875

Discussion. Poorly-preserved, fragmentary lytoceratids referred to *Lytoceras* s.l. occur in the Hauterivian of the Speeton Clay, beds D1, C8 (Wrights' colln: Rawson 1971*b*, pp. 69, 70) and C6 (SM. B53081). The last specimen was recorded by Whitehouse and Brighton (1924, p. 360) as *Lytoceras* cf. *subfimbriatum* d'Orbigny, but is too poorly preserved for satisfactory identification, though the lytoceratid suture is visible. Spath's (1924*a*, p. 79) *Lytoceras* aff. *vogdti* Karakasch from the Tealby Limestone (basal Barremian) of Lincolnshire is at Cambridge, Sm B.11128.

There are two lytoceratids from north Germany, one recorded by Koenen (1902, p. 35) as *Lytoceras* cf. *phestus* Matheron from the lower Hauterivian(?) of Wintjenberg, and one mentioned by Stolley (1935) as '*Lytoceras*' from Ottensen (?*tuberculata* Zone). Both the specimens appear lost. Weerth's (1884, p. 20, pl. IV, fig. 1) '*Ammonites* (*Lytoceras*) *seebachi*' (holotype in ZGI) from the Osning Sandstein of Tönsberg is a Barremian *Paracrioceras*, probably an inflated member of the *denckmanni*/*muelleri* group.

Superfamily ANCYLOCERATACEAE Meek, 1876
Family ANCYLOCERATIDAE Meek, 1876

Discussion. The Ancyloceratidae are a heteromorph family of varying shell shape, usually with either regular, crioceratitid coiling throughout growth, or an early crioceratitid stage followed by a hooked or straight body chamber. They are generally split into subfamilies according to the type of coiling, but it is possible that some of the smaller Ancyloceratinae are dimorphs of members of the Crioceratitinae (Rawson 1975*a*, p. 282; Gaida, Kemper and Zimmerle 1978, p. 52).

Subfamily PROTANCYLOCERATINAE, Breistroffer 1947
Genus JUDDICERAS Spath, 1924*a*

Type species. Crioceras curvicosta Koenen 1902, by original designation.

Diagnosis. Moderately large (estimated diameter at least 220 mm), probably with a loose crioceratitid coiling, but known only from gently curved body chamber fragments. Whorls moderately compressed with sub-oval section, dorsum almost flat. Ribs strong, simple, or rarely bifurcating close to the dorsum, of uniform strength, curving forwards strongly near to and across the rounded venter. Suture crioceratitid.

Discussion. *Juddiceras* is known from the type species only. It was not defined by Spath (1924*a*) and was incorrectly interpreted by Wright (*in* Arkell *et al.* 1957) and, in part, by Immel (1978, p. 24) for reasons discussed below.

Juddiceras is probably more loosely coiled than *Aegocrioceras* and is distinguished from that genus by the strong forward curvature of the ribs towards and over the venture.

Juddiceras curvicosta (Koenen, 1902)

Plate 34, figs. 1, 2

1902 *Crioceras curvicosta* Koenen, p. 326, pl. 50, fig. 1 (non figs. 2, 3).
non 1957 *Juddiceras curvicostum* (Koenen); Wright *in* Arkell *et al.*, p. 207, fig. 236, 3.

Lectotype. Spath (1924*a*, p. 84) designated the original of Koenen's pl. 50, fig. 1 as 'genotype' of *Juddiceras* and thus as lectotype of *J. curvicosta*. The specimen has not been traced.

Material. Twelve fragmentary specimens from the *triptychoides* Zone (upper Valanginian) of north Germany: Hasslage 5, Ottensen 2, Stadthagen (Z. Möller) 4, Wiedenbrugge 1 (all in NLFB).

Diagnosis. As for genus.

Discussion. Koenen (1902) figured 2 fragmentary body chambers from Stadthagen (Z. Möller) as *Crioceras curvicosta*: the larger (plate 50, fig. 1) was designated by Spath (1924*a*, p. 84) as genotype of *Juddiceras* but the smaller (pl. 50, figs. 2, 3) was figured by Wright (in Arkell *et al.* 1957) and formed the basis for the *Treatise* diagnosis of *Juddiceras*. The latter specimen differs from the lectotyoe of *J. curvicosta* in having less strongly curved ribs, some of which are larger and bear ventro-lateral tubercles; it is here transferred to *Crioceratites*? sp. (Immel 1978 recognized the two morphotypes but retained both in *Juddiceras*).

We have located twelve whorl fragments of *J. curvicosta*, all with similar ornament and whorl proportions to the lectotype. All are body chamber fragments of varying size, and the smallest specimen is figured here. This presumably immature individual suggests that the characteristic *Juddiceras* ribbing occurs from diameters of about 70 mm upward, but earlier (septate) whorls are not known; it appears likely that *Juddiceras* had a loose, crioceratitid coiling like that of *Himantoceras*.

Subfamily CRIOCERATITINAE Wright, 1952

Discussion. The Crioceratitinae had an essentially Tethyan distribution, but at times they migrated into adjacent areas such as north-west Europe where they first appeared in the late Valanginian (*Crioceratites*? spp.) and formed thriving populations in the Hauterivian and Barremian. The north-west European forms are difficult to compare with Tethyan species because of preservational differences; the former are either pyritized, septate early whorls or large body-chamber steinkerns, while the latter are pyritized nuclei or calcareous intermediate whorls, often distorted. Furthermore, the monographs of Koenen (1902) on German faunas and Sarkar (1955) on French ones have resulted in a plethora of 'local' names which further obscure possible relationships.

Among the north-west European genera, the mid-Hauterivian form *Aegocrioceras* is endemic to the area (Rawson 1975*b*). In contrast, the mid Hauterivian to early Barremian *Crioceratites* sequence is very close to the French lineage; from *Crioceratites* of the *nolani* and *duvali* group (see below) in the mid Hauterivian through *C.* (*Paracrioceras*) *spathi* (= '*Emericiceras*' of the *thiollierei* group) and *C.* (*P.*) *strombecki* (= '*E.*' *emerici* group) of the *variabilis*/*discofalcatus* Zones to *Hoplocrioceras fissicostatum* (= '*Binelliceras*' *binelli* group). The first appearance of '*Emericiceras*' in France is a reliable indicator for the base of the Barremian, and hence the occurrence of comparable forms in the basal *variabilis* Zone at Speeton and the uppermost part of the *discofalcatus* Zone in north Germany is significant in the local definition of the Hauterivian/Barremian boundary (p. 307).

Genus AEGOCRIOCERAS Spath, 1924

Type species. Hamites capricornu Roemer 1840, by original designation.

Discussion. Aegocrioceras is a distinctive crioceratitid with strong, simple ribs which usually bear small, ventro-lateral tubercles to a varying diameter; mid-lateral tubercles may occur also on the earliest whorls. It occurs in the north German and English mid-Hauterivian: German (including Heligoland) occurrences were reviewed by Rawson (1974, 1975*b*) and the English fauna is monographed (Rawson 1975*b*). The sudden appearance of *Aegocrioceras* marks a well-defined immigration horizon, but there are no obvious immediate ancestors anywhere. *Bejucoceras* Cantú Chapa (1976) from the Lower Hauterivian of Mexico has simple ribs and in lateral view the type species resembles *Aegocrioceras raricostatum* (Phillips), but *Bejucoceras* has a smooth ventral region. Despite the time gap, *Aegocrioceras* may have descended from *Juddiceras*.

A single *Aegocrioceras*? sp. has been collected from the base of the *sayni* Zone at Bellegarde-en-Diois (Drôme) (Thieuloy colln). The specimen is flattened, but appears to have more strongly developed, almost spinose, ventro-lateral tubercles than typical *Aegocrioceras*.

Genus CRIOCERATITES Léveillé, 1837
Subgenus CRIOCERATITES Léveillé, 1837

Type species. C. duvali Léveillé 1837, by original designation.

Crioceratites spp. (*nolani* and *duvali* groups)

Plate 34, figs. 3, 4

Discussion. Crioceratites of the *nolani* and *duvali* groups appear suddenly in the English and German successions in the upper part of the *inversum* Zone, where they occur with the last species of *Aegocrioceras*, *A. spathi* Rawson. From this level upward *Crioceratites* occurs throughout the Hauterivian but specimens are generally flattened and the species poorly known. Early authors (e.g. Judd 1868) recognized the identity of some specimens with Tethyan forms but a number of species

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EXPLANATION OF PLATE 34

All figs. × 1 except fig. 13.

Figs. 1, 2. *Juddiceras curvicosta* (Koenen), incomplete body chamber, *triptychoides* Zone, Ziegelei Möller, Stadhagen. GPIG.

Figs. 3, 4. *Crioceratites duvali* Léveillé, bed C7A, *inversum* Zone, Speeton. BM. C. 82456 (Rawson colln).

Figs. 5, 6. *Subsaynella* cf. *sayni* (Paquier), Speeton (horizon not known). BM. C. 72677 (Lamplugh colln).

Figs. 7, 8. *Spitidiscus* cf. *rotula* (J. de C. Sowerby), Speeton (horizon unknown). YM. 418, supposedly the original of Phillips (1829, pl. 2, fig. 45), though the specimen differs considerably from Phillips' diagrammatic figure.

Figs. 9, 10. *Spitidiscus* cf. *subcassida* (Spath), bed C8B mid, upper *regale* Zone, Speeton. BM. C. 82465 (Rawson colln).

Figs. 11–15. *Spitidiscus rotula* (J. de C. Sowerby). 11–13, holotype, Speeton (horizon unknown), BM. 43885 (Sowerby colln), previously figured by Sowerby (1827) (fig. 13 × 1·5); 14, 15, bed C5L, *speetonensis* Zone, Speeton. BM. C. 82466 (Rawson colln).

Figs. 16, 17. *Crioceratites*? sp., *triptychoides* Zones, Ziegelei Möller, Stadthagen. GPIG.

Figs. 18, 19. *Paracrioceras spathi* sp. nov., holotype, bed C2C, *variabilis* Zone, Speeton. BM. C. 82457 (Rawson colln).

Figs. 20, 21. *Bochianites neocomiensis* (d'Orbigny), Osning Sandstein, Ehberg, near Bielefeld. NMB.

Figs. 22, 23. *Bochianites* cf. *goubechensis* Mandov, remainé horizon, base of bed D2D, Speeton. BM. C. 82460 (Rawson colln).

PLATE 34

KEMPER *et al.*, Lower Cretaceous ammonites

names have since been proposed for the mid-Hauterivian species. Subsequently both Rawson (1973, p. 138) and Sarkar (*in* Casey and Rawson 1973, p. 429) have reaffirmed the occurence in north-west Europe of typical Tethyan species, and here we figure (Pl. 34, figs. 3, 4) *C.* (*C.*) *duvali* Léveillé from the top *inversum* Zone (Bed C7A) of the Speeton Clay. All the *Crioceratites* of the top *inversum* and lower *speetonensis/staffi* Zones belong to the *duvali* or *nolani* groups:

duvali group	*nolani* group
hildesiensis Koenen 1902, pl. 22, fig.5	*beani* Young and Bird 1828, pl. 15, fig. 9 (refigured Howarth 1962, pl. 19, fig. 7)
tenuilobatum Koenen 1902, pl. 18, figs 1-3	*hildesiensis* Koenen 1902, pl. 22, fig. 6
wermbteri Koenen 1902, pl. 43, fig. 4	ex gr. *hildesiense* Koenen: Kemper 1976, pl. 2, fig. 1; pl. 27, figs 3, 4, 10

These conclusions are the opposite of those reached by Immel (1978), who regarded the north-west European forms as specifically distinct from Tethyan ones.

Crioceratites? spp.

Plate 34, figs. 16, 17

1902 *Crioceras curvicosta* Koenen, p. 326, pl. 50, figs. 2, 3 (non fig. 1).
1957 *Juddiceras curvicostum* (Koenen); Wright *in* Arkell *et al.*, p. L207, fig. 236, 3.

Material. Thirty fragmentary specimens from the *triptychoides* Zone (Upper Valanginian) of north Germany: Hasslage 3, Stadthagen (Z. Möller) 8, Wiedenbrugge 19 (all in NLFB).

Discussion. Associated with *Juddiceras* are numerous body chamber fragments of a *Crioceratites*-like heteromorph characterized by an almost circular whorl section and occasional stronger, generally trituberculate, ribs. The suture is crioceratitid. The specimens show some variation and more than one species may occur. They are provisionally placed in *Crioceratites* together with Koenen's (1902) smaller syntype of '*Crioceras*' *curvicosta*.

The relationship between *Crioceratites*? spp. and *Juddiceras curvicosta* is not clear: both are represented by body chamber fragments of various sizes, though the largest specimen known is a *Juddiceras* and theoretically it is possible that *Crioceratites*? body chambers are immature growth stages of *Juddiceras* (just as the French *Himantoceras acuticostatum* Thieuloy has inner whorls with *Crioceratites*-like ribbing and a body chamber with strong simple ribs comparable with those of *Juddiceras* except that they are stronger and curve forward only slightly). However, the smallest *Juddiceras* is smaller than most *Crioceratites*? spp., is moderately compressed instead of circular in section, and the ribs bend forward much more strongly.

Crioceratites? spp. are of similar age to *Himantoceras* and are thus one of the earliest known Crioceratitinae. They differ from *Himantoceras* in having a more rapidly expanding whorl height and may not be as loosely coiled.

Subgenus PARACRIOCERAS Spath, 1924

Type species. *Ammonites* (*Crioceras*) *occultus* Seeley 1865, by original designation.

Discussion. At the base of the Barremian the *Crioceratites* faunas of Europe developed more closely spaced tuberculate ribs with fewer fine, non-tuberculate ribs between, and occasional looped ribs. In north-west Europe the name *Paracrioceras* is used for these and some related descendant forms while in France *Emericiceras* Sarkar 1954 is employed. Rawson (1975*a*) regarded *Emericiceras* as a junior subjective synonym of *Paracrioceras* though this is disputed (Sarkar 1978).

Paracrioceras spathi sp. nov.

Plate 34, figs. 18, 19

non 1924*a* *Paracrioceras statheri* Spath, p. 77.
1924*b* *Paracrioceras statheri* Spath; Spath, p. 173, figs. 1–4.

Holotype. BM. C. 82457 (Rawson colln) from bed C2C (*variabilis* Zone), Speeton.

Paratypes. Three fragments BM. C. 82458–9 (Rawson colln) from bed C2C, Speeton; BM. C. 35037 (Lamplugh colln), horizon not known, Speeton.

Diagnosis. *Paracrioceras* with whorl breadth slightly greater than whorl height; only two or three fine, non-tuberculate ribs between the strong trituberculate ones. Some of the finer ribs loop to the major ones, especially over the venter.

Discussion. Howarth (1962, p. 129) suggested that the holotype of *P. statheri* Spath (the specimen figured by Phillips 1829 as *Hamites beani* Young and Bird) was the same specimen as that figured by Young and Bird (1828) as the holotype of *Hamites beani*, and that *P. statheri* is therefore a junior objective synonym of *Crioceratites beani* (Young and Bird). There is only one '*Hamites*' *beani* in the Yorkshire Museum collections that has been recorded as a figured specimen (YM. 422); it was referred to by both Spath (1924*b*) and Melmore (1947, p. 235) as Phillips' original, but closely matches Young and Bird's diagrammatic figure too. Thus we follow Howarth's interpretation.

Spath (1924*b*) subsequently figured 2 ammonites as *P. statheri*; these do not match the specimen which Spath thought was Phillips' original and which he made holotype of *P. statheri*, but they are conspecific with the larger specimen figured here as holotype of *P. spathi*. One (BM. C. 35037) is from the Lamplugh collection, labelled 'Zone B, lower part'. The other (formerly BM. 89105*a*) is lost.

P. spathi is close to the Tethyan species '*Emericiceras*' *thiollierei* (Astier), differing only in having a broader whorl section.

Family BACULITIDAE Meek, 1876
Subfamily BOCHIANITINAE Spath, 1922
Genus BOCHIANITES Lory, 1898

Type species. *Baculites neocomiensis* d'Orbigny 1842, by original designation.

Bochianites neocomiensis (d'Orbigny, 1842)

Plate 34, figs. 20, 21

1884 *Baculites neocomiensis* d'Orbigny; Weerth, p. 25, pl. 3, figs. 5, 6.
1902 *Bochianites* cf. *neocomiensis* d'Orbigny? a nov. sp.; Koenen, p. 397, pl. 15, fig. 3.
?1904 *Bochianites* cf. *neocomiensis* d'Orbigny; Andrée, pp. 23, 33.
1950 *Bochianites* cf. *neocomiensis* Koenen; Stolley, p. 125.
1950 *Bochianites neocomiensis* d'Orbigny; Riedel, pp. 133–136.
1951 *Bochianites* sp. Bartenstein and Brand, pl. 22.
1969 *Bochianites neocomiensis* d'Orbigny; Witkowski, pl. 19, fig. 4.
1976 *Bochianites neocomiensis* d'Orbigny; Kemper, p. 36, pl. 31, figs. 21–24.

Material. One block of several specimens from the base of Bed D2D, Speeton (Wrights' colln 24592); two fragments from the Claxby Ironstone of Nettleton (Wrights' colln 12724, 14329); numerous specimens from north Germany (horizons and localities discussed below).

Discussion. All the German *Bochianites* that we have seen apparently belong to this species, but a critical examination is difficult because all are compressed and/or small fragments only. With the exception of some doubtful records of early later Valanginian age, the species is confined to the middle of the late Valanginian, and there is a mass occurrence in the middle of the Dichotomiten Schichten (*polytomus*? to *triptychoides* Zones).

The geographical distribution is interesting. The mass occurrence is at the western margin of the Lower Saxony Basin (Georgsdorf and Lingen oilfields and boreholes near Nordhorn and Lathen) where core samples show the species occurring in large numbers on bedding planes (Kemper 1976, p. 36). In the sandy facies (Osning Sandstein) of the southern margin it is much rarer but specimens have been recorded by Weerth (1884) and Andrée (1904) and a specimen from Ehberg is figured here (Pl. 34, figs. 20, 21). A specimen is also recorded from Hoheneggelsen, further east (Koenen 1902), but none are known from the dark shales of the central basin facies.

The English examples are from condensed levels.

Bochianites cf. *goubechensis* Mandov, 1971

Plate 34, figs. 22, 23

cf. 1971 *Bochianites goubechensis* Mandov, p. 97, pl. 3, figs 1-9.
1971*b* *Bochianites neocomensis* d'Orbigny; Rawson, p. 67.

Material. One body chamber fragment (Rawson colln., BM. C. 82460) found in a phosphatized steinkern of *Polyptychites* from the basal D2D nodule bed, Speeton.

Discussion. The specimen has two strong and sinuous constrictions and thus accords closely with *B. goubechensis*. It remains doubtful whether Mandov's species should be kept separate from *B. neocomiensis* with only one constriction.

Superfamily HAPLOCERATACEAE Zittel, 1884
Family OPPELIIDAE Bonarelli, 1894
Subfamily ACONECERATINAE Spath, 1923
Genus PROTACONECERAS Casey, 1954

Type species. Oppelia patagoniensis Favre 1908, by original designation.

Protaconeceras sp. nov.

Plate 37, figs. 1-3

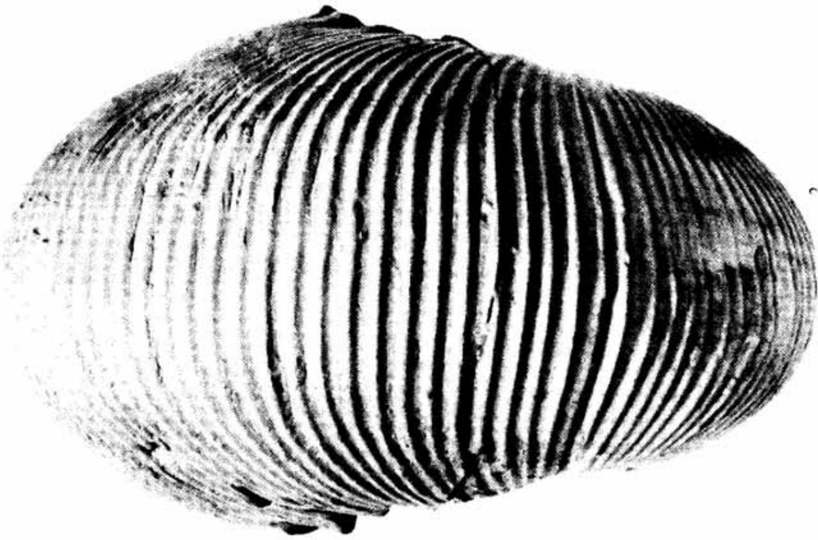
1954 *Protaconeceras* sp. nov. Casey, p. 270, pl. 7, fig. 7.

Discussion. Knowledge of the distribution and origin of early Cretaceous oppeliids is fragmentary, and *Protaconeceras* is recorded only from Patagonia and Speeton. At Speeton, small, septate specimens of *Protaconeceras* sp. nov. are moderately common in bed C4; they were described and a single specimen figured by Casey (1954). Additional specimens have since been collected but advanced growth stages are still not known. The additional material includes one specimen (Pl. 37, figs. 1-3) which has the slightest suggestion of an angularity in the ventro-lateral region. This provides a link with the only aconeceratid of comparable age from France, a whorl fragment of *Protaconeceras*? sp. from the *sayni* Zone of Chamaloc (Pl. 37, fig. 4). This is larger (probably 70-80 mm diameter) than the Speeton examples with a more clearly defined serrated keel and a well-marked ventro-lateral shoulder reminiscent of that in *Aconeceras austronisoides* Brunnschweiller from the early Albian of Australia.

EXPLANATION OF PLATE 35

Figs. 1, 2. *Olcostephanus* (*Olcostephanus*) sp. ('*Proastieria*' Stolley), *hollwedensis* Zone, Hollwede. NLFB kv 207 (Hapke colln), × 1.

PLATE 35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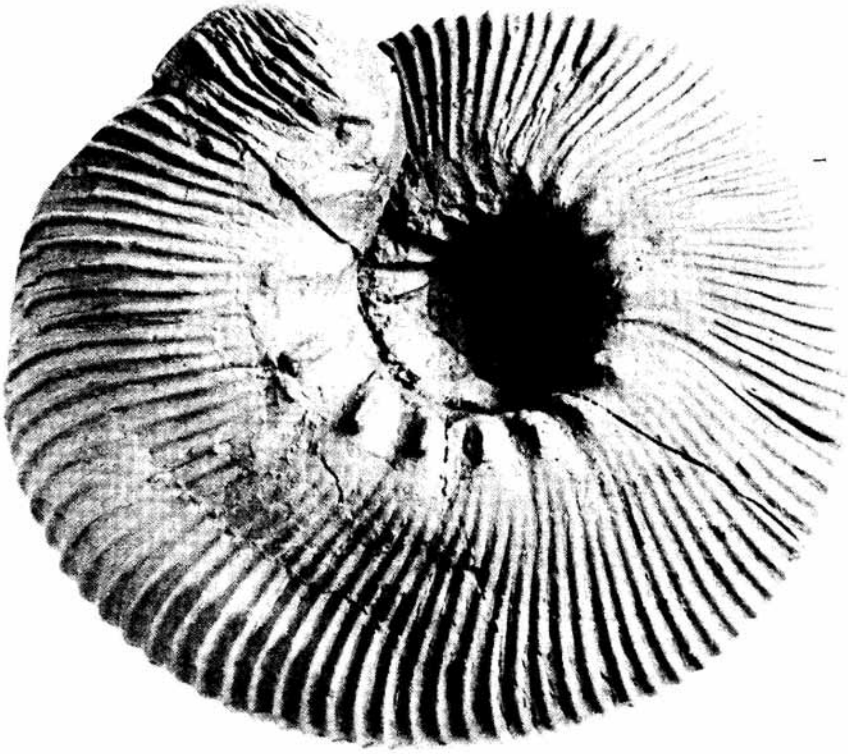
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KEMPER *et al.*, Lower Cretaceous ammonites

Superfamily PERISPHINCTACEAE Steinmann, 1890
Family OLCOSTEPHANIDAE Haug, 1910
Subfamily OLCOSTEPHANINAE Haug, 1910

Discussion. The Olcostephaninae are a very typical Tethyan assemblage, with a broad geographical distribution and a remarkable morphological homogeneity (with the exception of *Saynoceras*). From a sub-mediterranean area of dispersal, the subfamily spread not only to the two extremities of Tethys (abundantly to the west, from Mexico down to the Andean Province in Peru and Argentina, and more diffusely to the east to the Japanese Province) but also to the south to populate the seas bordering Gondwanaland (Salt Range, Tanzania, Madagascar, and southern Africa).

Northwards, more or less prospering populations became established in the most southerly expansion of the Boreal Realm in north-west Europe. The stratigraphical occurrence and affinities of English and German forms are reviewed here and some are figured for the first time: a full palaeontological description of the fauna is still awaited.

Genus OLCOSTEPHANUS Neumayr, 1875

Discussion. In north Germany there are two clearly defined *Olcostephanus* horizons in the Valanginian, whereas English Valanginian *Olcostephanus* occur only in condensed horizons. In both countries the genus is moderately common through the Lower Hauterivian

The 'Proastieria' fauna

This fauna occurs at the base of the Dichotomiten-Schichten, at about the Lower/Upper Valanginian boundary (see Kemper, Ernst and Thiermann 1978). It yields the inflated, large forms which Stolley (1937) called 'astierioiden Polyptychiten' or '*Proastieria*'. At Hollwede, these are associated with the last *Polyptychites* (*P. sphaeroidalis* etc.) and with the first dichotomitids (*Prodichotomites hollwedensis* Kemper, index species of the lowest Upper Valanginian zone). It is only at the summit of the range of '*Proastieria*' that *Saynoceras verrucosum* and *Valanginites nucleus* appear. These two species are elements of the former '*nucleus* Zone', in which Stolley (1935) noted the occurrence of smaller and flatter *Olcostephanus* identified, probably erroneously, as closely approaching *O.* (*R.*) *psilostomus*; they were not figured.

The *Olcostephanus* ('*Proastieria*') figured here (Pl. 35, figs. 1, 2) is the first to be illustrated. Although it does not compare exactly with Tethyan species of similar age, it is noteworthy that in the south-east of France the top beds of the Lower Valanginian furnish abundant populations of inflated olcostephanids—*O. perinflatus* (Matheron), *O. stephanophorus* (Matheron) and a rare, undescribed

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EXPLANATION OF PLATE 36

All figs. × 1.

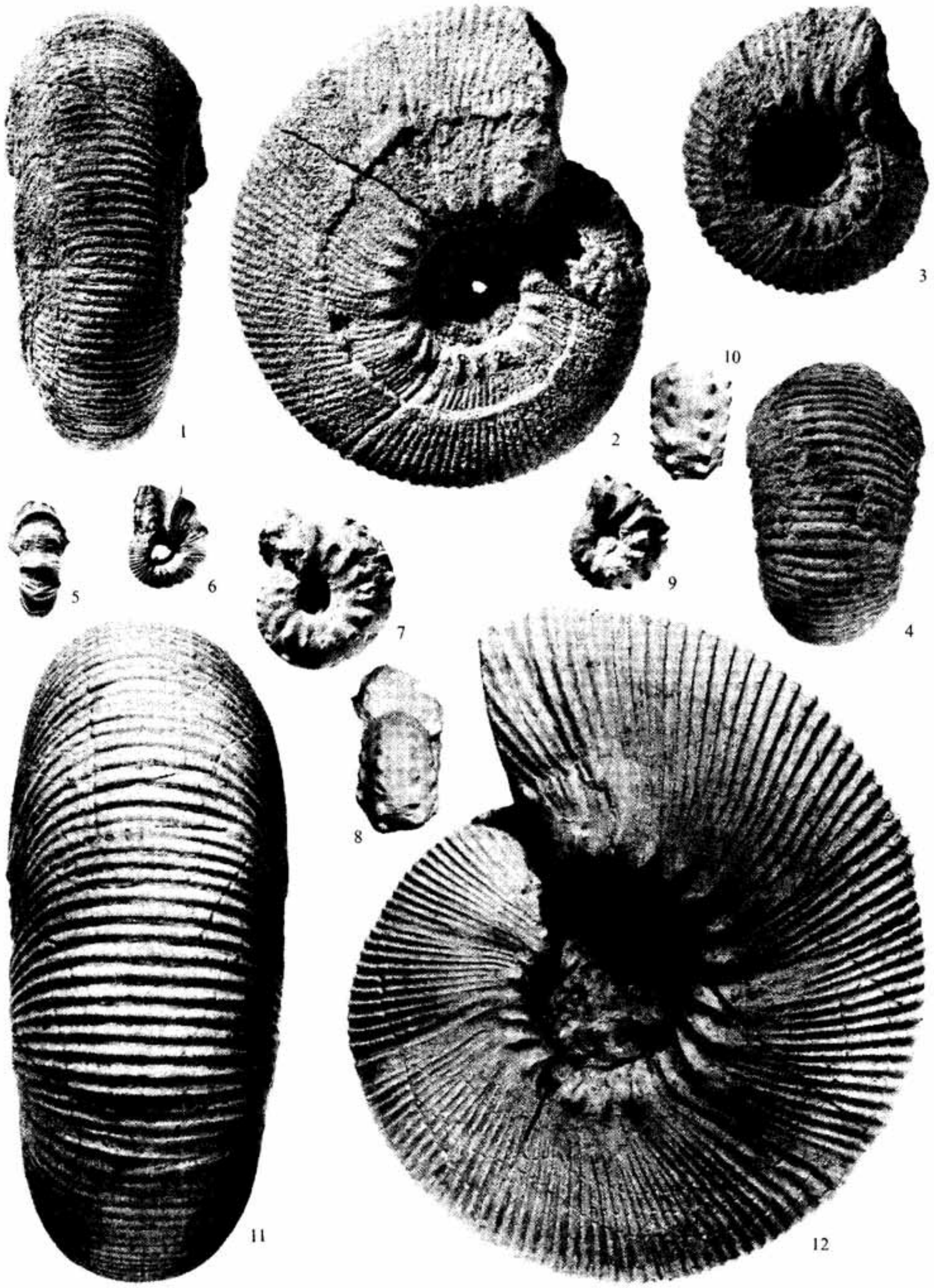
Figs. 1, 2. *Olcostephanus* (*Olcostephanus*) aff. *atherstoni densicostatus* (Wegner), top calcareous beds of Claxby Ironstone, Nettleton. BM. C. 82467 (Rawson colln).

Figs. 3, 4. *Olcostephanus* (*Rogersites*) sp. (*psilostomus* group), top calcareous beds of Claxby Ironstone, Nettleton. BM. C. 82468 (Rawson colln).

Figs. 5, 6. *Parastieria* sp. nov., Speeton (probably bed C8). Wrights' colln 24563.

Figs. 7–10. *Saynoceras verrucosum* (d'Orbigny), *hollwedensis* Zone, Twiehausen. Petsch colln, casts NLFB kv 225, kv 229.

Figs. 11, 12. *Olcostephanus* (*Olcostephanus*) sp. (*atherstoni* group), 'Astierien'-Schichten, Stadthagen (Kuhlmann). NLFB kv 208 (Hapke colln).



KEMPER *et al.*, Lower Cretaceous ammonites

species (*O. polyptychoides* Sayn MS) in which the ribs recall in certain aspects those of the polyptychitids.

Between this first *Olcostephanus* horizon and the 'Astierien'-Schichten rare and crushed *Olcostephanus* occur only in the upper part of the Dichotomiten-Schichten (Möller, Stadthagen).

Some of the rare, indeterminate fragments of *Olcostephanus* from the basal D2D remanié bed at Speeton may represent the '*Proastieria*' fauna.

The 'Astierien'-Schichten fauna

These beds, at the top of the German Valanginian, are rich in olcostephanids, but specimens are often crushed and none have been figured previously. The two illustrated here (Pl. 36, figs. 11, 12; Pl. 37, figs. 7, 8) belong to the *O. atherstoni* group. The level is exactly homologous with the 'couche de Villers-le-Lac' (French Jura) and the thin, marly 'Astieriaschicht' of the stratotype section at Valangin (Neuchâtel Jura). There the *Olcostephanus* populations are abundant and varied: *O. astieri* (d'Orbigny), *O. sayni* Kilian (= *O. scissus* Baumberger), *O. actinotus* (Baumberger) (= group of *atherstoni* Sharpe). The Astierien-Schichten horizon is equally well represented in the Sub-mediterranean Province, especially in the south-east of France (Thieuloy 1977*b*); it corresponds to the lower part of the *callidiscus* Zone, where *O. sayni* and *O. astieri* are abundant and *O. psilostomus* is rather rare.

The 'Astierien-Schichten fauna may also be represented in England (see below).

Early Hauterivian Olcostephanus

Olcostephanus occur scattered through the *Endemoceras* beds of England and north Germany; they are generally of *amblygonium* or *noricum* Zone age in Germany (approximately the *radiatus* Zone of earlier authors) and *regale* Zone age in England. The difference in horizons is simply a reflection of poor development of the lower zones in England and rarity of fossils in the *regale* Zone in Germany (see Rawson 1971*b*).

A number of forms have been figured and show that at least five species occur:

Olcostephanus ventricosus (Koenen 1902) (= *O. multiplicatus* Neumayr and Uhlig 1881, pl. 33, fig. 2, 2*a*, *non* Roemer).

The horizon of this species is the early Hauterivian of Elligser Brink and not the Valanginian of Hoheneggelsen as indicated by Koenen. There are strong analogies between the figured syntype (believed lost) and examples of the *atherstoni* group with semi-elliptical section (*O. actinotus* and *O. rigidus* (Baumberger)). A specimen from the basal Hauterivian at Ziegelei Moorberg, Sarstedt, figured by Kemper (1976, pl. 31, fig. 14) as *O.* cf. *ventricosus* belongs to the *atherstoni–ventricosus* group.

EXPLANATION OF PLATE 37

All figs. × 1 except figs. 1, 4, 11, 12.

Figs. 1–3. *Protaconeceras* sp. nov., bed C4, *gottschei* Zone, Speeton. BM. C. 82461 (Rawson colln). Fig. 1 × 1·5.

Fig. 4. *Protaconeceras*? sp., *sayni* Zone, Chamaloc (Drôme). ID 10280 (Thieuloy colln). × 1·33.

Figs. 5, 6. *Olcostephanus* (*Rogersites*) sp. (*psilostomus–schencki* group), top calcareous beds of Claxby Ironstone, Nettleton. BM. C. 82469 (Rawson colln).

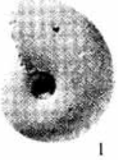
Figs. 7, 8. *Olcostephanus* (*Olcostephanus*) sp. (*atherstoni* group). 'Astierien'-Schichten, Stadthagen (Kuhlmann). NLFB kv 209 (Hapke colln).

Figs. 9, 10. *Oosterella* aff. *cultrata* (d'Orbigny), *crassus* Zone, Varlheide (Süd). NLFB kv 223 (colld Krause).

Fig. 11. *Platylenticeras* sp. juv. a. Platylenticeras-Schichten, Sachsenhagen. NLFB kv 210.

Fig. 12. *Platylenticeras* sp. juv. b, Platylenticeras-Schichten, Suddendorf. NLFB kv 211.

PLATE 37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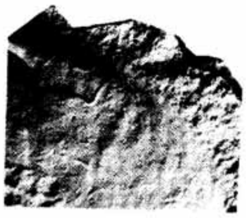
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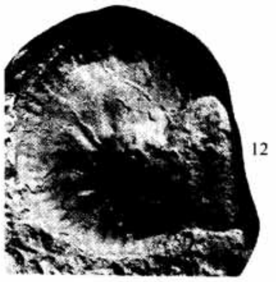
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KEMPER *et al.*, Lower Cretaceous ammonites

Olcostephanus convolutus (Koenen 1902, pl. 39, figs. 4*a*, *b*).

This species, from the Hilsbornsgrund and Elligser Brink, is less typically Tethyan. It differs from *O. ventricosus* by its more inflated section and the more obtuse peri-umbilical tubercles. These characteristics occur to a lesser extent in a specimen figured by Baumberger (1908, pl. 25, fig. 3) as '*Astieria*' *guebhardti* Kilian from the 'Hauterivienmergel' of Cressier.

Olcostephanus ovalinus (Koenen 1902).

This species, from Elligser Brink, was not figured but its described characteristics evoke those of *O. atherstoni* var. *densicostatus* (Wegner).

Olcostephanus subfilosus Spath 1924*a* (= *O.* (*Astieria*) *astieri* in Pavlow 1892, pl. 17 (10), fig. 15; also includes pl. 18 (11) fig. 17, and *O.* (*A.*) *astieri* in Danford 1906, pl. 16, fig. 7).

This is a finely-ribbed, slightly inflated form of the group of *filosus* Baumberger–*multistriatus* Zwierzicki: the holotype (text-fig. 6*a*, *b*) resembles particularly one of the Tanzanian forms (Zwierzicki 1914, pl. 6, figs. 6, 7). *O. subfilosus* is moderately common in the upper part of the *regale* Zone at Speeton (beds C8B and C8A).

Olcostephanus (*Rogersites*) cf. *ambikyi* (Besairie 1936).

A specimen from the condensed *amblygonium–noricum* horizon (bed D1) at Speeton (Rawson colln) and a second individual recorded by Spath (1924*a*, p. 75) as *O.* (*R*?) cf. *convolutus* (SM. B. 11137: possibly from the D2D remanié horizon) are close to the inner whorls of *O.* (*R.*) *ambikyi* (Besairie) from the Upper Valanginian of Madagascar.

Olcostephanus *of uncertain age*

Several north-west European *Olcostephanus* cannot be dated accurately because either they are from condensed horizons and belong to species that apparently cross the Valanginian/Hauterivian boundary or there is doubt about their recorded horizon. The latter is particularly pertinent to the commonly recorded *Olcostephanus* (*Rogersites*) *psilostomus* (Neumayr and Uhlig 1881, pl. 32, figs. 2, 2*a*). The original authors and Koenen (1902, p. 151) indicated that the figured syntype was from Hoheneggelsen, i.e. from the '*Proastieria*' horizon (*hollwedensis* Zone): however, this could be erroneous (or the Hoheneggelsen section may have exposed higher beds too) for there is considerable evidence that the species occurs at the top of the Valanginian and base of the Hauterivian:

(*a*) The varieties *koeneni* Wegner 1909 (for Koenen 1902, pl. 54, figs. 2*a*, *b*) and *picteti* Wegner 1909 (for Pictet and Campiche 1858–60, pl. 43, fig. 1) from Stadthagen are early Hauterivian morphotypes.

(*b*) The type of *O. leptoplanus* (Baumberger 1908), a subjective synonym of *O. psilostomus* var. *picteti*, is from the Astieriamergel of Neuchâtel.

(*c*) The uppermost Valanginian beds of the Vocontian region have yielded several *O. psilostomus* (see p. 270).

(*d*) The population from Neuquen province, Argentina, studied by Riccardi, Westermann and Levy (1971), includes several specimens (e.g. pl. 13, fig. 2) readily attributable to *O. psilostomus*. The fauna is of late Valanginian or early Hauterivian age.

(*e*) Neumayr and Uhlig (1881, p. 22) had another syntype from the Hilsbornsgrund, which is probably early Hauterivian.

Several *Olcostephanus* occur in the condensed late Valanginian—early Hauterivian top calcareous beds of the Claxby Ironstone of Nettleton. A well-preserved specimen (Pl. 36, figs. 1, 2) of the *atherstoni* group has constrictions which are lacking at this stage of development in Tethyan forms: it shows affinity with a young individual figured by Kilian (1902, pl. 57, fig. 1) and interpreted by Wegner (1909) as *O. atherstoni* var. *densicostatus*. It is interesting that such forms are from condensed levels on the neritic platform of the Arc de Castellane. The Lincolnshire specimen also approaches closely *O. rigidus* (Baumberger) from the base of the Hauterivian marls of Landeron (Swiss Jura).

From the same locality and horizon, an *O*. (*Rogersites*) sp. (Pl. 36, figs. 3, 4) is a microconch of the *psilostomus* group, differing from typical examples only in its thicker whorl. It thus approaches *O. psilostomus* var. *crassus* (Roch). A more coarsely ribbed specimen (PL 37, figs. 5, 6) has deep, oblique constrictions reminiscent of *O. psilostomus* var. *koeneni* (Wegner).

Genus SUBASTIERIA Spath, 1923*a*

Type species. Olcostephanus (*Astieria*) *sulcosus* Pavlow 1892, by original designation.

Discussion. The original figure of the holotype of *S. sulcosus* is reproduced in text-fig. 6*c*, *d*. Spath (1923*a*) did not define the genus but he later (Spath 1924*a*) noted that it is characterized by its highly coronate whorls, and placed two further species in it: *S. decipiens* (a nom. nov. for *O. atherstoni* in Pavlow 1892, pl. 10, fig. 14) and *S. trisulcosus* (Phillips). All three species are from Speeton; the fragmentary holotype of *S. decipiens* (formerly in the Scarborough Museum) is lost, and *S. trisulcosus*, based on an unfigured specimen of Phillips', is lost and uninterpretable (Howarth 1962, p. 132).

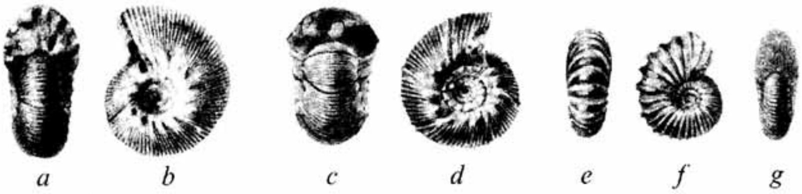
S. sulcosus is a rare element in bed C9A (*regale* Zone) at Speeton and a less coronate, only slightly constricted form, *S.* cf. *decipiens* Spath, occurs in C8 (*regale* Zone). These Speeton *Subastieria* are probably derived from early Hauterivian *Olcostephanus*. The genus is not known from Germany but is quoted in the Tethyan Realm (e.g. *S. inordinatus* (Tzankov) from Bulgaria and *S. dacquei* (Krenkel) from Tanzania): however, these records could represent parallel morphological grades in other *Olcostephanus* lineages. Further investigation may show that *Subastieria* should not be retained as a distinct genus.

Genus PARASTIERIA Spath, 1923*b*
(? = CAPELOITES Lisson, 1937)

Plate 36, figs. 5, 6; text-fig. 6*e*–*g*

Type species. Acantoceras? *peltoceroides* Pavlow 1892, by original designation.

Discussion. Parastieria is a microconch olcostephanid previously recorded only from Speeton, where it is represented by the type species and an undescribed form. *P. peltoceroides* (text-fig. 6) is not uncommon in beds C9C and C9A (*regale* Zone): the German ammonite ('*Acanthoceras* n. f.' in Neumayr and Uhlig 1881, pl. 15, fig. 6) which Pavlow included in *P. peltoceroides* is not a *Parastieria*. *P.* sp. nov. (Pl. 36, figs. 5, 6) is represented by two specimens, probably from C8. While the inner whorls of *P. peltoceroides* are close to those of *Olcostephanus*, the body chamber ornamentation suggests an affinity with *Capeloites* Lisson 1937, and this is reinforced by the looped ribbing of *P.* sp. nov. which closely matches that of *Capeloites*. *P.* sp. nov. is very close to *C. perelegans* (Matheron)



TEXT-FIG. 6. Type specimens of Speeton Clay olcostephanids. *a*, *b*, *Olcostephanus subfilosus* Spath, holotype, BM. C. 34964 (reproduced from Pavlow 1892, pl. 17, fig. 15*a*, *b*). *c*, *d*, *Subastieria sulcosus* (Pavlow), holotype, formerly in the BM but now decomposed (reproduced from Pavlow 1892, pl. 18, fig. 18*a*, *b*). *e*–*g*, *Parastieria peltoceroides* (Pavlow), lectotype here designated, YM 742 (reproduced from Pavlow 1892, pl. 18, fig. 21*a*–*c*). All × 1.

(see Thieuloy 1969 for figures) which Thieuloy has now found in the *nodosoplicatum* Zone of the Arc de Castellane. Further investigation of the relationships of the two genera is required.

Parastieria is represented from the Tethyan Realm by *P. hispanica* (Mallada), *P*? *betica* (Mallada) and an undescribed species from the early Hauterivian of Muret (Chartreuse).

Genus VALANGINITES Kilian, 1910

Plate 38, figs. 1-8, 11-12

Type species. Ammonites nucleus Roemer 1840 (*non* Phillips 1829), subsequently designated by Spath (1939).

Discussion. Valanginites is an important and widely distributed genus which cannot be fully revised here, though important observations have been made by Thieuloy (1977*a*). There are three outstanding problems to be resolved despite the numerous publications on the genus (e.g. Charles 1948; Imlay 1937; Karakasch 1902; Matheron 1878-80; Mayer-Eymar 1887; Nikolov 1963; Riccardi and Westermann 1970; Roch 1930; Sayn 1889; Thieuloy and Gazay 1967; Thieuloy 1977*a*; Tzankov 1943).

The type species

Although the species name *A. nucleus* is generally attributed to Roemer, it was actually introduced by Phillips (1829, p. 174, pl. 2, fig. 43) for a very small (5 mm diameter), indeterminate nucleus from the Speeton Clay. The holotype, formerly believed lost (Howarth 1962, p. 133), is in the Yorkshire Museum (YM. 415: see Pyrah 1978). Roemer (1840, pl. 13, fig. 2) figured a much larger ammonite as '*A. nucleus* Phillips?' and the species has subsequently been interpreted from this. Unfortunately, the figure is poor and inaccurate and the specimen lost, so that *A. nucleus* Roemer *non* Phillips has become a source of uncertainty and misinterpretation. However, we figure a cast of Roemer's lost original (Pl. 38, figs. 1, 2), and an application to the International Commission for Zoological Nomenclature to stabilize the usage of *A. nucleus* sensu Roemer is in preparation.

Infraspecific/specific variation and taxonomy

There is strong variation in shell form and coarseness of ribbing in *Valanginites* and a number of specific names are available for distinctive morphotypes. Unfortunately, it has never proved possible to obtain enough material from any one locality and horizon to assess possible infraspecific variation. We have examined about 200 *Valanginites* from north Germany (mainly adults) but the exact horizon of most is unknown. Roemer's (1840) original of *V. nucleus* was an unusually small adult interpreted here as a variant of those *Valanginites* with much reduced or no sculpture (Pl. 38, figs. 1-6). In this sense, *V. nucleus* may form little more than 30% of the German fauna. A similar percentage is attained by specimens with coarse primary ribs and mid-lateral swellings typical of *V. wilfridi* (Karakasch) (Pl. 38, figs. 7-8). However, there are transitions between the *nucleus* and *wilfridi* morphologies for in some forms the characteristic lateral swellings of *wilfridi* appear later in ontogeny and may even be confined to the last quarter whorl (Pl. 38, figs. 11-12).

EXPLANATION OF PLATE 38

All figs. × 1.

Figs. 1-6. *Valanginites nucleus* (Roemer *non* Phillips). 1, 2, cast of the lost original of Roemer (1840), from Bredenbeck, GPIG (duplicate in NLFB, kv 212); 3, 4, complete, almost smooth adult, GPIM B6.704; 5, 6, complete adult with slight mid-lateral strengthening of primary ribs, Petsch colln (cast in NLFB, kv 213).

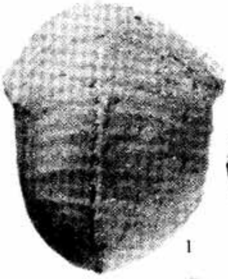
Figs. 7, 8. *Valanginites wilfridi* (Karakasch), adult body chamber showing characteristic coarse primary ribs and mid-lateral swellings. GPIM B6.702.

Figs. 9, 10. *Saynoceras verrucosum* (d'Orbigny). Petsch colln (cast in NLFB, kv 214).

Figs. 11, 12. *Valanginites* intermediate between *nucleus* and *wilfridi*. GPIM B6.703.

Specimens shown in figs. 3-12 are from the *hollwedensis* Zone of Ziegelei W. Flörke, Twiehausen.

PLATE 38


1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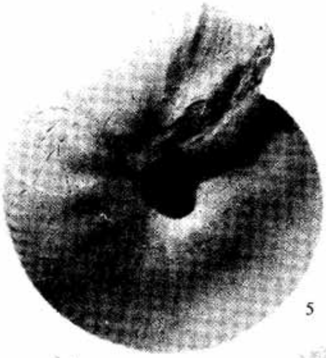
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12

KEMPER *et al.*, Lower Cretaceous ammonites

Previously figured German *Valanginites* belong either to *nucleus* (Struckmann 1890, pl. 11, fig. 5; non pl. 12, figs. 1, 2 = *Olcostephanus*) or a *nucleus/wilfridi* intermediate (Koenen 1902, pl. 4, figs. 6–7; Kemper 1976, pl. 29, fig. 4). However, other morphotypes (species?) occur in north Germany. The shell forms range from small, narrow and *utriculus*-like to wide, *dolioformis*-like shells. An undescribed globular and rather smooth species attained a maximum shell diameter of about 70 mm and is the largest *Valanginites* known. Specimens with ventral nodes—'*Dobrodgeiceras wilfridi ventrotuberculatum*' (Nikolov)—do not occur; they apparently represent a geographical subspecies limited to Tethys.

Because of the difficulties of bed-by-bed collecting the evaluation of the sculptural phylogeny of *Valanginites* is impossible at present, but new observations in the south-east of France (Thieuloy 1977*a*) indicate that the oldest specimens are near to an individual figured by Thieuloy (1977*a*, pl. 9, figs. 19, 20) as *V. psaephoides paludensis* Thieuloy. Thus the smooth *Valanginites* of the *nucleus* group could be the most advanced forms after which the stock became extinct.

Taxonomic problems in *Valanginites* are compounded by the problem of poor figures and lost types, as for example in *V. bachelardi* (Sayn) and *V. psaephoides* (Mayer-Eymar) which may be synonyms of *V. nucleus*, or *V. simplus* (d'Orbigny) whose holotype was tiny (8 mm diameter) and is now lost.

Biology

The biological aspects of *Valanginites* are interesting and require further study. The shell wall is extremely thick on the flanks of some specimens (up to 3 mm at shell diameters of about 35 mm). The shell is tightly coiled except at the adult chamber which contracts with markedly excentric coiling. The end of growth is marked by a prominent flared collar (Pl. 38, figs. 2, 4, 5, 12). The shell at the apertural side of the collar turns back and as it also encircles the whorl it forms a channel which extends from umbilicus to umbilicus. Specimens are generally adult at 35–70 mm diameter.

Dimorphism may occur though it is less obvious and clear than supposed by Kemper (1976, explanation to pl. 29, fig. 4).

Stratigraphical and geographical distribution

Valanginites appeared early in the late Valanginian (*verrucosum* Zone in Tethys, *hollwedensis* Zone in Germany). Because of its short stratigraphical range and wide lateral distribution it is a remarkably useful index fossil. North German localities (estimated specimen numbers in brackets) are: Barsinghausen (2), Bredenbeck (1), Bückeburg (6), Feldbergen borehole 16 (1), Hoheneggelsen (3), Hollwede (30), Twiehausen (80), Wiedenbrügge (80). Elsewhere it occurs in Bulgaria, France, Morocco, Mexico, Peru, Poland, and the USSR (Crimea).

Genus SAYNOCERAS Munier-Chalmas, 1893

Type species. Ammonites verrucosus d'Orbigny 1841, by original designation.

Discussion. In addition to the type species, the genus includes *S. hirsutum* Fallot and Termier and *S. americanum* Imlay. All are micromorphs (maximum diameter *c.* 25 mm) with an inflated shell and a broad, subpentagonal or elevated trapezoidal section. The distinctive ornament consists of two tubercles on each flank (mid-lateral or peri-umbilical and ventral, the latter alternating with or opposite the other ventral tubercle) joined by bundled or zig-zag ribs. The narrow to broad ventral region is crossed by blunt ribs, arranged in zig-zag or in loops. The suture line is of olcostephanid type, with the E/L saddle either broad, shallow and with superficial incisions, or narrow, high and with deep incisions.

S. verrucosum is the only species of this typically Tethyan genus which became adapted to the boreal region.

Saynoceras verrucosum (d'Orbigny, 1841)

Plate 36, figs. 7–10; Plate 38, figs. 9, 10

1841 *Ammonites verrucosus* d'Orbigny, p. 191, pl. 58, figs. 1–3.
1902 *Saynoceras verrucosum* d'Orbigny; Koenen, p. 408, pl. 15, fig. 2.
1937 *Saynoceras verrucosum* (d'Orbigny); Stolley, p. 452.
1950 *Saynoceras germanicum* Stolley, p. 131.
1951 *Saynoceras* sp. Bartenstein and Brand, pl. 22.
1971 *Saynoceras verrucosum* (d'Orbigny); Kemper, p. 52.
1976 *Saynoceras verrucosum* (d'Orbigny); Kemper, p. 36.
1978 *Saynoceras verrucosum* (d'Orbigny); Kemper, Ernst and Thiermann, p. 17.

Material. About twenty specimens from north Germany; Hollwede, Twiehausen, Hoheneggelsen, Wiedenbrügge, and the Georgsdorf oilfield.

Description. Saynoceras of maximum diameter about 25 mm, with rounded to broadly subpentagonal section, broadest at the level of the mid-lateral tubercles. Flanks clearly divisible into two parts (the inner subvertical, the outer oblique and converging towards the venter) separated by thorn-like mid-lateral tubercles. These lie at the summit of a subdued, slightly forwardly-bending, internal rib. Ventro-lateral tubercles thick and transverse at their apex, then form pinched, distant clavi, adorally thorn-like and narrowing. External lateral ribs project only slightly and zig-zag between mid-lateral and ventro-lateral tubercles (i.e. across the outer flank). Venter broad, feebly convex, crossed by blunt zig-zag ribs. Peristome preceded by deep constrictions between two drawn-out, slender lappets. Suture characterized by a broad, shallow, feebly incised E/L saddle.

Discussion. D'Orbigny's figure is largely erroneous: the spacing of the ventro-lateral tubercles near the aperture is exaggerated, because at this stage these are notably more dense; this is as clear in Tethyan specimens as in boreal ones. The ventral region is never so narrow, and the breadth of the outer flank is generally less. In addition, the whorl is never depressed as indicated in d'Orbigny's figure 2. The body chamber of the holotype is crushed, as is often the case in specimens from the vocontian facies.

Stolley (1950) was misled by d'Orbigny's figures into placing the German forms in a new species, *S. germanicum*. He defined the distinctive features as: more numerous ventro-lateral tubercles on the last third of the shell; a rounded ventral region, broader than the space between the mid-lateral and ventro-lateral tubercles; and an apertural constriction. However, these are all characteristic of *S. verrucosum* and a comparison of the German and Tethyan populations shows that they are conspecific. (It should be noted that *S. germanicum* is not a *nomen nudum*, as Kemper (1971) suggested, because Stolley defined the distinctive characteristics of his species.)

There is a fairly clear dimorphism in *S. verrucosum* (Thieuloy, in preparation). In the microconch the tubercles appear earlier, the section is pentagonal and the width of the ventral region is less than or about the same as the outer flank (two of the German specimens may belong to this dimorph). On the contrary, the macroconch has a broader, more rounded section, the tubercles appear later and the breadth of the ventral region exceeds that of the outer flank.

Stratigraphical and geographical distribution. The horizon is clearly defined: in Tethys *S. verrucosum* occurs in a thin horizon (several metres thick in the pelagic facies, several decimetres in the neritic facies) at the very base of the late Valanginian, always in an argillaceous lithofacies probably corresponding with an important transgression. It is associated with numerous *Valanginites* and some *Prodichotomites* and almost smooth *Dichotomites* ('*Neocraspedites*'). In north Germany it is again associated with *Valanginites* and *Prodichotomites* in the upper part of the *hollwedensis* Zone (where it is generally preserved in the body chambers of large polyptychitids). It occurs at a similar horizon in the Polish Lowland (Witkowski 1969).

Subfamily uncertain

Genus PLATYLENTICERAS Hyatt, 1900

Plate 37, figs. 11, 12

Type species. Oxynoticeras heteropleurum Neumayr and Uhlig 1881, by original designation.

Discussion. Platylenticeras has been extensively discussed (Kemper 1961, 1971; Thieuloy 1973, 1977*a*) with particular emphasis on its inter-regional distribution, and the north-west European forms are monographed (Kemper 1961). Kemper (1975, fig. 9) and Thieuloy (1977*a*, pp. 397–398) stressed its derivation from olcostephanid ancestors and rejected Casey's (1973, p. 260) proposal to place it in a new subfamily Platylenticeratinae within the family Berriasellidae. Of particular importance are the figures of early whorls (Kemper 1961, pl. 7, fig. 3; Pl. 37, figs. 11, 12 here) which clearly show olcostephanid features. The earliest species have circum-umbilical nodes ('*Tolypeceras*' Hyatt 1903; a separate generic name seems unnecessary, though *Tolypeceras* could be used as a subgenus). These are presumably nearest to the ancestral form, but the definite ancestral stock (Polyptychitinae or Spiticeratinae?) remains unknown and we regard the subfamily assignment of *Platylenticeras* as uncertain.

Species of *Platylenticeras* are of outstanding importance for inter-regional correlation, even though the main evolutionary radiation was in the Lower Saxony Basin and in other areas the genus is less well represented by slightly different subspecies or even species (*gevrilianum* group in southern France and the '*Pseudogarnieria*' group on the Russian Platform). There are several *Platylenticeras* localities in north Germany (including Heligoland) and the genus occurs also in south-east France (where it apparently originated), Switzerland, Czechoslovakia (Teschen area) and Poland (Tomaszow). Crushed fragments are recorded from D4 at Speeton. The Spitsbergen (Frebold 1929, pp. 5–6; Sokolov and Bodylevsky 1931, p. 26) and Russian Platform (Sasonova 1971, pp. 93–94, pl. 22, fig. 1) occurrences are doubtful and require reinvestigation.

Family BERRIASELLIDAE Spath, 1922

[= PALAEOHOPLITIDAE Roman, 1938, pro parte]

Discussion. The blossoming of the Berriasellidae makes a dominant mark on the early Cretaceous ammonite faunas of the Tethyan Realm and adjacent areas. The planulate forms of perisphinctid aspect have a smooth or grooved tabulate venter, and show a tendency for advanced growth stages to develop trituberculation on some ribs (e.g. *Endemoceras*). The planulates constitute a root stock which repeatedly gave rise to genera of more diverse morphology. Curiously, these various derivatives exhibit a recurrence of evolutionary trends:

(*a*) early whorls with strong primary ribs, later whorls more-or-less smooth (e.g. *Karakaschiceras, Leopoldia, Dicostella*);

(*b*) precocious development of strong trituberculation (often spinose) on some ribs; later whorls either trend towards smooth (e.g. *Acanthodiscus*) or remain strongly ribbed while becoming loosely coiled (e.g. *Varlheideites*) or uncoiled (e.g. *Distoloceras*);

(*c*) sutural modification by development of an asymmetric lateral lobe (L) and undivided lobe U1.

There is also a general tendency for the shell to become slightly to strongly inflated.

Few berriasellid phylogenies have been documented in detail, and because of the large number of apparent homeomorphs there are great difficulties in interpreting fragments alone. Indeed, many species and some genera are known only from incomplete growth stages (inner whorls, or body chamber fragments) and the number of genera recognized may well be reduced when ontogenies and phylogenies become better known.

Three early Cretaceous subfamilies are distinguished: Berriasellinae Spath, 1922; Neocomitinae Spath, 1925; and Endemoceratinae Schindewolf, 1966 (= Leopoldiinae Thieuloy, 1971). Contrary to the opinion of Spath (1924*a*), who derived the Berriasellinae and Neocomitinae from different perisphinctid stocks, these three subfamilies developed naturally from one another and each rapidly replaced its forerunner in time.

The palaeogeographical distribution of the Berriasellidae is primarily in Tethys and the region margining Gondwanaland, but our study illustrates the sub-boreal development of the younger subfamilies and their notably increased emplacement through time.

Subfamily NEOCOMITINAE Spath, 1922

Discussion. After reintegrating into this group the genera *Thurmanniceras*, *Kilianella*, and *Sarasinella* (included by Roman (1938) in his Berriasellinae) and excluding the forms now placed in the Endemoceratinae, one can define the Neocomitinae as a very homogeneous group, dominated by a central stock of compressed forms with high whorls and a rounded or tabulate venter, though in the Andean Province this is more commonly grooved. The suture line has a radial orientation with a symmetrical lateral lobe and a lobe U_1 divided into two lobules, U_1v and U_1d.

Genus THURMANNICERAS Cossmann, 1901

Type species. Ammonites thurmanni Pictet and Campiche 1860, by original designation.

Thurmanniceras? cf. *campylotoxum* (Uhlig, 1902)

1976 *Neocomites* sp. Kemper, pl. 30, fig. 10.

Discussion. A neocomitid fragment (NLFB Kv 221) from the Bentheim Sandstein of the Georgsdorf 6 borehole (depth 525 m), figured in lateral view only by Kemper (1976), has the following characteristics: prominent umbilical bullae; bifurcation of some secondary ribs after an earlier stage where intercalated ribs of variable lengths dominate, accompanied by the development of falcoid curvature of the ribs with a well-accentuated mid-lateral convexity; marginal swelling of the external ribs; a smooth and feebly arched venter.

These features characterize the group of *Thurmanniceras*? *campylotoxum*, with which the German specimen is compared. The stratigraphical horizon is in accord as *T*? *campylotoxum* is zonal index of the upper part of the early Valanginian.

Genus NEOCOMITES Uhlig, 1905
Subgenus NEOCOMITES Uhlig, 1905

Type species. Ammonites neocomiensis d'Orbigny, 1841, by subsequent designation (Sayn 1906, not Roman 1938 as stated by Wright *in* Arkell *et al.* 1957).

Diagnosis. Whorls moderately involute to involute; section rectangular with very feebly convex flanks and truncated venter. Ribbing fine, homogeneous and more or less flexuous, dividing at a variable height and often bidichotomous. Primary ribs arise at unbilical bullae and secondary ribs rise at the ventral margin into little oblique tubercles. Constrictions and juvenile trituberculation in some forms.

Suture line characterized by the breadth of the ventral saddle and the symmetrical lateral lobe.

Neocomites (*Neocomites*) spp.

Plate 39, figs. 1-9, 11, 12

Discussion. Rare fragments and nuclei of *Neocomites* have been found at various levels in the German Valanginian. Most are too incompletely preserved for firm identification or differ slightly from well-known Tethyan forms, but at least four species are represented. *Neocomities* (*N.*) sp. a (Pl. 39, figs. 1, 2) and *N.* (*N.*) sp. b (Pl. 39, figs. 5, 6) are distinguished from typical *Neocomites* by their broad umbilicus, and both probably lie towards the end of the *Neocomites* lineage. *N.* sp. a has fine, closely spaced ribs bundled in twos and threes in the inner whorls but mainly single on the last two thirds of a whorl (body chamber). *N.* sp. B is slightly more coarsely ribbed than A, the ribs generally arising in pairs at an umbilical tubercle and branching again higher on the flank. *Neocomites N.* sp. C (Pl. 39, figs. 3, 4) has moderately fine ribbing but is without an exact equivalent in Tethys; at the same growth stage, *N.* (*N.*) *neocomiensis* has finer, denser ribs with much rare bidichotomous ribbing. *Neocomites*? sp. D (Pl. 39, figs. 11, 12) has moderately fine ribbing in which occasional ribs are slightly stronger and have well-developed mid-lateral tubercles.

Subgenus TESCHENITES Thieuloy, 1971

Type species. Hoplites neocomiensiformis Uhlig 1901, by original designation.

Diagnosis. Whorls moderately involute; section rectangular to oval, with venter flattened on the phragmocone and rounded on the body chamber. Ornament neocomitinid on the chambered whorls, more irregular on the living chamber, as much in the distribution of the primary and secondary ribs as in their relief. Sporadic or general strengthening of the umbilical tubercles and of the corresponding primary ribs. Secondary ribs bending forward, forming projecting convexities on the venter which they cross without weakening. Lateral ribs sometimes obliterated. Lateral lobe very feebly asymmetric.

Neocomites (*Teschenites*) sp.

Plate 39, fig. 10

Discussion. A specimen from the Osning Sandstein of Hohnsberg (GPIG) has a rib pattern which in the inner and middle whorls (to 60 mm diameter) is comparable in density and style to vocontian individuals. However, the German specimen has one unusual feature, the occurrence of sporadic bifurcations on the outer quarter of the flank. On the last one third of a whorl the ribbing is a little stronger, but there are several vocontian examples with this characteristic (Thieuloy colln).

The specimen compares with individuals from the region of the Valanginian/Hauterivian boundary of south-east France.

Neocomites? cf. *trezanensis* Sayn, 1907

Plate 39, figs. 7–9

cf. 1907 *Neocomites trezanensis* Sayn, p. 34, pl. 3, figs. 20, 25; pl. 4, fig. 15.

Discussion. This specimen (GSM. CJW. 9104) was found by Mr. C. J. Wood, associated with *Menjaites* at the base of the Claxby Ironstone at Woods Hill Quarry, Nettleton. Because it is so small (*c.* 13·5 mm diameter) slight doubt remains about its specific identification, but the ornament is of vocontian type. The feeble swelling at the mid-lateral bifurcation is clearly visible. This tuberculate stage appears very fleetingly in the Nettleton specimen and this also happens in specimens of *N*? *trezanensis*, where there is considerable individual variation.

EXPLANATION OF PLATE 39

All figs. × 1 except fig. 9.

Figs. 1, 2. *Neocomites* (*Neocomites*) sp. a, *pitrei* Zone, Ottensen. GPIG.

Figs. 3, 4. *Neocomites* (*Neocomites*) sp. c, middle or upper Dichotomiten-Schichten, Diepenau. NLFB kv 215.

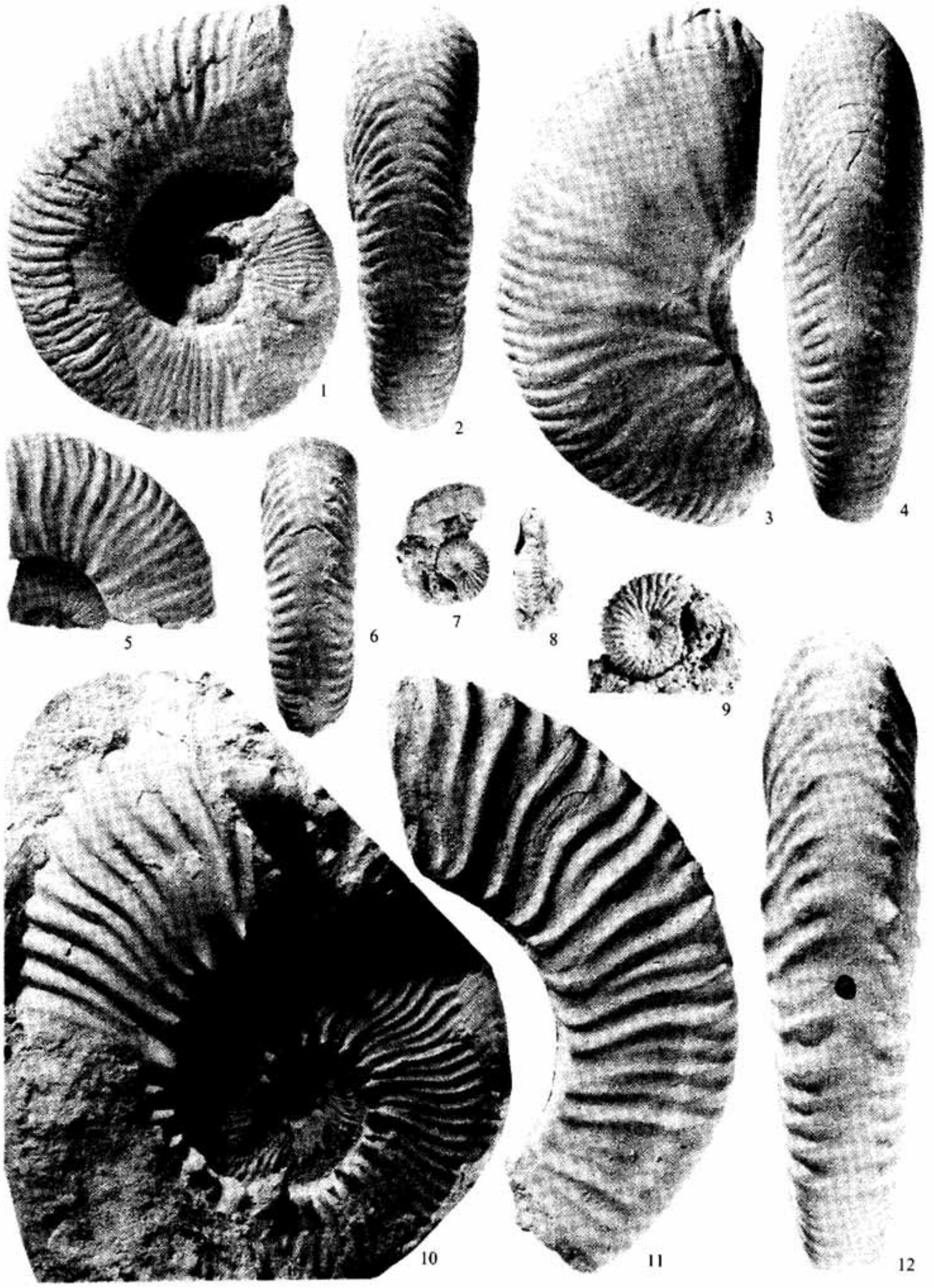
Figs. 5, 6. *Neocomites* (*Neocomites*) sp. b, *pitrei* Zone, Ottensen. GPIG.

Figs. 7–9. *Neocomites* cf. *trezanensis* Sayn, *Paratollia* Zone, basal Claxby Ironstone, Woods Hill Quarry, Nettleton. IGS CJW. 9104 (colld C. J. Wood). Fig. 9 × 2.

Fig. 10. *Neocomites* (*Teschenites*) sp., Osning Sandstein, Hohnsberg. Cast (NLFB kv 216) from an external mould in GPIG.

Figs. 11–12. *Neocomites*? sp. D, Ziegelei Möller, Stadthagen (probably Dichotomiten-Schichten). GIPG.

PLATE 39



KEMPER *et al.*, Lower Cretaceous ammonites

Genus VARLHEIDEITES Rawson and Kemper, 1978

Plate 44, figs. 3-5

Type species. V. peregrinus Rawson and Kemper 1978, by original designation.

Discussion. Varlheideites was proposed for a dimorphic neocomitid in which nearly all growth stages are known. The microconch is *Neocomites*-like but has a lateral lappet, while the macroconch passes from *Neocomites*-like inner whorls into a more loosely coiled stage with *Distoloceras*-like ornament. It is known only from the Varlheide (= Hasslage Süd) claypit, near Lübbecke, where it occurs with abundant *Dichotomites* in the *crassus* Zone (early late Valanginian). *Varlheideites* was regarded as a possible derivative of early *Neocomites*, but we now suggest that it evolved from the late early Valanginian *Thurmanniceras*? *campylotoxum*. It shares certain characteristics with *Neocomites*? of the *platycostatus* Sayn group, for which Nikolov (1966) created the genus *Eristavites*; the relationship requires further investigation.

Subfamily ENDEMOCERATINAE Schindewolf, 1966

Discussion. This subfamily includes both 'central stock' genera and more tuberculate, often somewhat inflated, derivatives. All have the same sutural structure; an undivided U_1, more-or-less marked asymmetry of the lateral lobe (L) with a reduction of the internal lobule resulting in an almost bicuspid lobe (text-fig. 7), and a flattening of the ventral saddle.

Genus KARAKASCHICERAS Thieuloy, 1971

Type species. Hoplites biassalensis Karakasch 1889, by original designation.

Emended Diagnosis (modified from Thieuloy 1971, p. 229). Slightly involute to involute, slightly to moderately compressed with almost triangular whorl section; umbilical wall steep; flanks feebly to moderately convex; venter narrow, flat at first but becoming gently arched during growth. Umbilical bullae give rise to a bundle of 2 or 3 ribs, some of which may branch higher on the flank; ribs project radially on to ventro-lateral shoulder where they may swell slightly; ribs on one shoulder may terminate opposite, or alternate with, those on the other shoulder, but are always separated by a smooth band along mid-venter. With growth, ribs diminish and may disappear from the flanks (often well before the adult body chamber); eventually the umbilical bullae and vestigial ribs or slight bullae in the ventro-lateral region may also disappear and the shell become smooth or retain sparse plicae on the lower part of the flank. Suture very denticulate with asymmetric lobes and an E/L saddle divided by a deep median lobule.

Discussion. In addition to the type species, Thieuloy (1971) placed the following in *Karakaschiceras*: *Hoplites inostranzewi* Karakasch, *Hoplites pronecostatus* Felix 1891 (= *Hoplites leenhardti* Kilian 1895), *Hoplitides brandesi* Koenen, *Hoplitides gibbosus* Koenen, *Leopoldia quadristrangulata* Sayn, and *Hoplites karakaschi* Uhlig. We now add *Hoplites heteroptychus* Pavlow from Speeton and the group of *Amaltheus*? *attenuatus* Behrendsen (revised by Riccardi *et al.* 1971) from Argentina. Most of these species at some time or other have been placed in *Leopoldia*, but *Karakaschiceras* is distinguished from that genus by its radially arranged ventro-lateral ribs (sometimes swollen into small bullae), by a narrower venter and by stronger ribbing in the inner whorls of most species. *Karakaschiceras* species form a natural group of late early Valanginian to early late Valanginian age; true *Leopoldia* is early Hauterivian.

Karakaschiceras is widely distributed in the shallower water facies of Tethys (though it is rarely common) and species have also been described from north Germany, England and Argentina. The north-west European material is highly variable, sparse and fragmentary; more specimens might reduce the number of species currently recognized.

Karakaschiceras biassalense (Karakasch, 1889)

Plate 40, figs. 1, 3

1889 *Hoplites biassalensis* Karakasch, pp. 8–9, pl. 1, figs. 4, 5.

Material. One specimen from bed D2D (basal nodules), Speeton. BM. C. 82462 (Rawson colln).

Diagnosis. An involute, compressed *Karakaschiceras* with smooth flanks from an early growth stage; closely spaced, slight ventro-lateral bullae which gradually disappear; and a ventral region which becomes rounded by about 60 mm diameter.

Discussion. The Speeton specimen is a phosphatized, somewhat corroded individual from the phosphatic nodules at the base of D2D. It matches closely specimens figured from the Crimea (e.g. Karakasch 1907) and the Jura (Baumberger 1903–10).

K. biassalense has often been collected from condensed horizons, but individuals from the more expanded vocontian facies of south-east France are from two horizons, the middle *campylotoxum* Zone (late early Valanginian) and the *verrucosum* Zone (early late Valanginian) (Thieuloy colln).

Karakaschiceras cf. *inostranzewi* (Karakasch, 1889)

Plate 40, figs. 2, 4

cf. 1889 *Hoplites inostranzewi* Karakasch, pp. 434–435, pl. 1, figs. 1–3.

Material. One fragment from Speeton, probably base of bed D2D (Danford colln, IGS 17805): three fragments from north Germany; Hollwede (NLFB), Hoheneggelsen (GPIG), Georgsdorf borehole 174 (NLFB kv 217).

Discussion. The broad, flat venter, the fasciculate and forwardly curving ribs and the periodic, oblique constrictions closely approach the corresponding characteristics of the phragmocone of the Crimean species. In the absence of a body chamber in our specimens we can only compare them with the Crimean forms. *K. inostranzewi* is common in the *campylotoxum* Zone, but also occurs as a rare element in the basal late Valanginian.

Karakaschiceras brandesi (Koenen, 1902)

Text-fig. 7*c*, *d*

1902 *Hoplitides brandesi* Koenen, p. 226, pl. 7, figs. 1–3; non? pl. 30, fig. 4.

Type. Three of the four figured syntypes (formerly Brandes colln) are in the GPIH collections; the original of Koenen's pl. 7, fig. 2 (GPIH type-cat. no. 23) is here selected as lectotype (text-fig. 7). All are from Hoheneggelsen.

Other material. Four fragments from Hoheneggelsen (GPIG, one specimen, GPIH, three specimens).

Diagnosis. A moderately involute *Karakaschiceras* which is smooth from an early growth stage: the rounded venter develops early in ontogeny. The first lateral lobe is so asymmetrical that it is almost bifid.

Discussion. The species was exhaustively described by Koenen, but as his description was based on whorl fragments only and the additional material is also fragmentary, the ontogeny of the species remains poorly known, especially in the early (to 60 mm diameter) growth stages. A small specimen which Koenen (1902, pl. 30, fig. 4) assigned to the species is difficult to compare with the other material and we reidentify it as *K.* sp.

K. brandesi is slightly more involute than *K. gibbosum* and becomes smooth at a much earlier stage. Compared with *K. biassalense* it is less involute and less compressed but smoother, with a rounded venter from a much earlier growth stage. Furthermore, the tubercles of *K. brandesi* are more bulky and continue for longer, and the dorso-lateral ribs are more conspicuous than in *K. biassalense*.

K. brandesi is known only from the '*verrucosum* Zone' (*hollwedensis* Zone) of Hoheneggelsen, and we do not know any examples from the Tethyan Realm.

Karakaschiceras heteroptychum (Pavlow, 1892)

Plate 41, figs. 10, 11, 16, 17

1892 *Hoplites heteroptychus* Pavlow, p. 109, pl. 18 (11), fig. 22.
non 1902 *Hoplites heteroptychus* Pavlow; Koenen, p. 217, pl. 7, fig. 10.
non 1906 *Hoplites* ? *heteroptychus* Pavlow; Danford, p. 106, pl. 14, fig. 2.

Type. Pavlow included in the synonymy of his species *Hoplites arnoldi* Sayn (1889, pl. 17, figs. 6, 7) non Pictet and *Hoplites botelae* Toucas (1890, pl. 18, fig. 10) non Kilian. These syntypes are not conspecific with the English example which Pavlow figured and which has been taken as characteristic of the species (e.g. Danford 1906; Spath 1924*a*). This specimen is in the Yorkshire Museum, YM 425, as indicated in Pavlow's caption, and not at Cambridge as indicated in his text. It is formally designated as lectotype to stabilize usage of the species name; the specimen has almost completely decomposed but is readily interpretable from Pavlow's figure (reproduced here, Plate 41, figs. 10, 11).

Pavlow's other syntypes are reidentified as follows:

H. arnoldi sensu Sayn: fig. 6 = holotype of *Neohoploceras provincialis* (Sayn 1907)
fig. 7 = *Neohoploceras* sp.
H. botelae sensu Toucas = *Dalmasiceras toucasi* Mazenot 1939.

Material. Speeton; 1 fragment (BM. C. 82463, Rawson colln) from the basal nodules of bed D2D: Nettleton; 1 fragment (Rawson colln) from the top calcareous beds of the Claxby Ironstone: Hoheneggelsen; 1 fragment (GPIG).

Diagnosis. A slightly evolute, slightly inflated *Karakaschiceras* which remains strongly ribbed to at least 100 mm diameter, eventually becoming more compressed and almost smooth. Rib pattern irregular; ribs normally either rise in pairs at the umbilical tubercle, or branch just above; one (or, rarely, both) branches again at a varying position higher on the flank. Thus there are normally three, rarely, two or four, ribs per bundle.

Karakaschiceras gibbosum (Koenen, 1902)

Plate 40, figs. 5, 6; text-fig. 7*a*, *b*

1881 *Hoplites* cf. *neocomiensis* d'Orbigny; Neumayr and Uhlig, p. 167, pl. 48, fig. 3.
1902 *Hoplitides gibbosus* Koenen, p. 214, pl. 7, figs. 7–9.

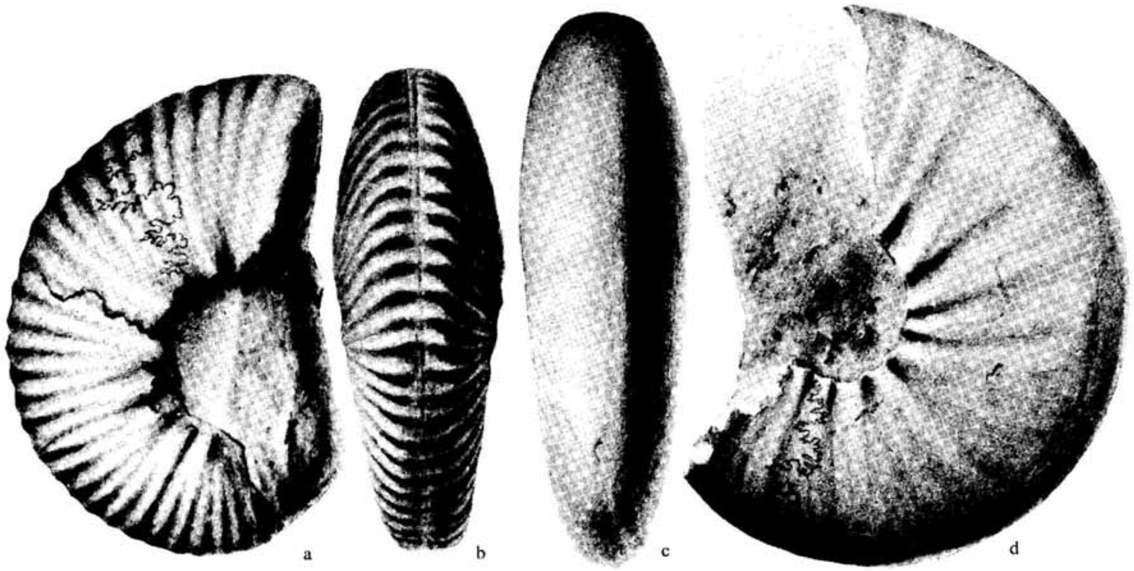
Type. Koenen referred to 2 ammonites, Neumayr and Uhlig's original (see synonomy) and a specimen in the Brandes colln (GPIH, type-cat. no. 24) which Koenen figured. The latter (text-fig. 7) is here designated lectotype. Both were from Hoheneggelsen.

Material. Two specimens; Hoheneggelsen (GPIG) and Twiehausen (Gröver colln—cast NLFB kv 218).

Diagnosis. A slightly evolute, slightly inflated *Karakaschiceras* which is strongly ribbed to about 75 mm diameter when the ribs reduce and almost disappear, and the venter becomes more arched.

Discussion. The two specimens closely match the lectotype but one (Pl. 40, figs. 5, 6) shows a more advanced growth stage where at about 75 mm diameter the ribs reduce in strength and almost disappear, the umbilical bullae reduce and the venter becomes more arched. This change coincides with the beginning of the body chamber but may not be simply an adult character since other *Karakaschiceras* show similar changes often well before the adult body chamber.

K. gibbosum is close to *K. heteroptychum* in general proportions but has more ribs per bundle and becomes smooth at an earlier diameter; there is insufficient material of either species for closer comparison.



TEXT-FIG. 7. Lectotypes (designated here) of north German *Karakaschiceras*. *a*, *b*, *K. gibbosum* (Koenen), GPIH, type-cat. no. 24; *c*, *d*, *K. brandesi* (Koenen), GPIH type-cat. no. 23. (Photographs reproduced from Koenen 1902, pl. 7.) Both specimens × 1, from Hoheneggelsen. The suture lines show a strongly asymmetric, almost bicuspid lateral lobe.

Karakaschiceras sp. a

Plate 41, figs. 18, 19

Discussion. A small, fragmentary specimen from Hoheneggelsen has bundles of four or five ribs associated with each umbilical bulla. In this it approaches *K. gibbosum* but is apparently more involute than that form.

Karakaschiceras sp. b

Plate 41, figs. 1–3, 8, 9

Discussion. A specimen from Twiehausen (*hollwedensis* Zone) is close in general proportions to *K. heteroptychum* but the rib pattern is even more irregular; widely spaced, strong umbilical bullae give rise to one or two primary ribs which may branch again higher on the flank; above about 25 mm diameter additional ribs are intercalated occasionally, either at the umbilical edge or higher on the flank. At this stage there are three or four ribs per bundle. The ribs are continuous over the venter, though slightly depressed; there is no clear, slightly raised smooth area along mid-venter as in other *Karakaschiceras*. During growth the flanks flatten slightly.

The innermost whorls are reminiscent of *Neohoploceras* but lack the strong constrictions and smooth ventral band of that genus.

A form comparable to *K.* sp. b occurs in the *verrucosum* Zone of south-east France, and we figure an example here (Plate 41, figs. 12, 13).

Genus NEOHOPLOCERAS Spath, 1939

Type species. Ammonites submartini Mallada 1887, by original designation.

Discussion. Neohoploceras is known mainly by inflated, strongly ribbed, deeply constricted and tuberculate inner whorls, but in more advanced growth stages (60–100 mm diameter) the tubercles and constrictions weaken or disappear and the shell becomes slightly compressed (e.g. *N. dubisiensis* [Baumberger 1906, pl. 12, fig. 1]; *N. ambikyensis* Collignon [1962, pl. 192, fig. 874]). The largest known specimen is a *N. submartini* from Nettleton which is still septate at 280 mm diameter; at this stage it is almost discoidal and closely approaches large *Karakaschiceras*.

Neohoploceras submartini (Mallada, 1887)

Plate 41, figs. 4–7

1887 *Ammonites submartini* Mallada, p. 17, pl. 10, figs. 7–9, pl. 11, figs. 12–14.
1902 *Hoplitides* aff. *arnoldi* Pictet; Koenen, p. 218, pl. 33, fig. 5.
1976 *Kilianella* (*Neohoploceras*) *submartini* (Mallada); Kemper, pl. 29, fig. 3.

EXPLANATION OF PLATE 40

All figs. × 1.

Figs. 1, 3. *Karakaschiceras biassalense* (Karakasch), phosphatised steinkern, base of bed D2D, Speeton. BM. C. 82462 (Rawson colln).

Figs. 2, 4. *Karakaschiceras* cf. *inostranzevi* (Karakasch), early Upper Valanginian, Georgsdorf borehole 174 (891–894 m). NLFB kv 217.

Figs. 5, 6. *Karakaschiceras gibbosum* (Koenen), *hollwedensis* Zone, Twiehausen. Cast (NLFB kv 218) of example in GC.

PLATE 40

KEMPER *et al.*, Lower Cretaceous ammonites

Material. Twelve specimens. Speeton, four fragments from the base of bed D2D (Yorkshire Museum; Raws colln.); Nettleton, six fragments from the top calcareous beds of the Claxby Ironstone (BM. C. 82464 a Rawson colln); Hoheneggelsen, Koenen's figured specimen (GPIH, type cat. no. 20); Georgsdorf borehole (433 m), Kemper's figured specimen (NLFB kv 220).

Discussion. This distinctive species is widely distributed in the Tethyan Realm and is one of t commoner immigrants in the English late Valanginian: English specimens have not been figur before but the inner whorls, showing typical *submartini* ornament, are illustrated on Plate 4 figs. 4, 6. The larger, almost discoidal growth stage (see above) will be fully illustrated elsewhe (Rawson, in preparation). We also refigure Kemper's (1976) specimen from Georgsdorf borehole 1

Neohoploceras sp.

Plate 41, figs. 14, 15

1906 *Hoplites* ? *heteroptychus* Pavlow; Danford, p. 106, pl. 14, fig. 2.
1924*a* *Hoplitides* aff. *submartini* Sayn; Spath, p. 75.

Discussion. The specimen figured by Danford (1906) and reidentified by Spath (1924*a*) is phosphatised internal mould of identical preservation to other remanié Valanginian ammonites fro the base of bed D2D at Speeton. Danford presumably erred in recording it from a higher level in D

Compared with similar growth stages of *N. submartini*, this specimen is less inflated and mo sparsely ribbed, only three or four secondaries being associated with each primary on the last who the rib pattern is indistinct on the last half whorl but exhibits an irregular pattern, two primary ri sometimes arising at an umbilical tubercle before branching higher on the whorl. In gener proportions it compares with *N. jacobi* (Besairie) but the holotype of that species has occasional fin ribs between the strong primaries.

Genus DICOSTELLA Busnardo, 1966

Type species. D. pitrei Busnardo 1966 (= *D. tuberculata* Roman 1933) by original designation. We rega *D. pitrei* as a junior subjective synonym of *Hoplites* (*Neocomites*) *houdardi* var. *tuberculata* Roman; the variety here raised to specific rank and placed in *Dicostella*.

EXPLANATION OF PLATE 41

All figs. × 1.

Figs. 1–3, 8, 9. *Karakaschiceras* sp. b, *hollwedensis* Zone, Twiehausen. 1, rubber cast from external mould; 2, natural internal mould of body chamber; 8, 9, rubber cast from external and internal moulds. NLFB kv 21 (Krause colln).

Figs. 4–7. *Neohoploceras submartini* (Mallade). 4, 6, inner whorl fragment of a large specimen from the to calcareous beds of the Claxby Ironstone, Nettleton, BM. C. 82464 (Rawson colln); 5, 7, Dichotomiten Schichten, Georgsdorf borehole 10 (433 m), NLFB kv 220 (previously figured by Kemper 1976).

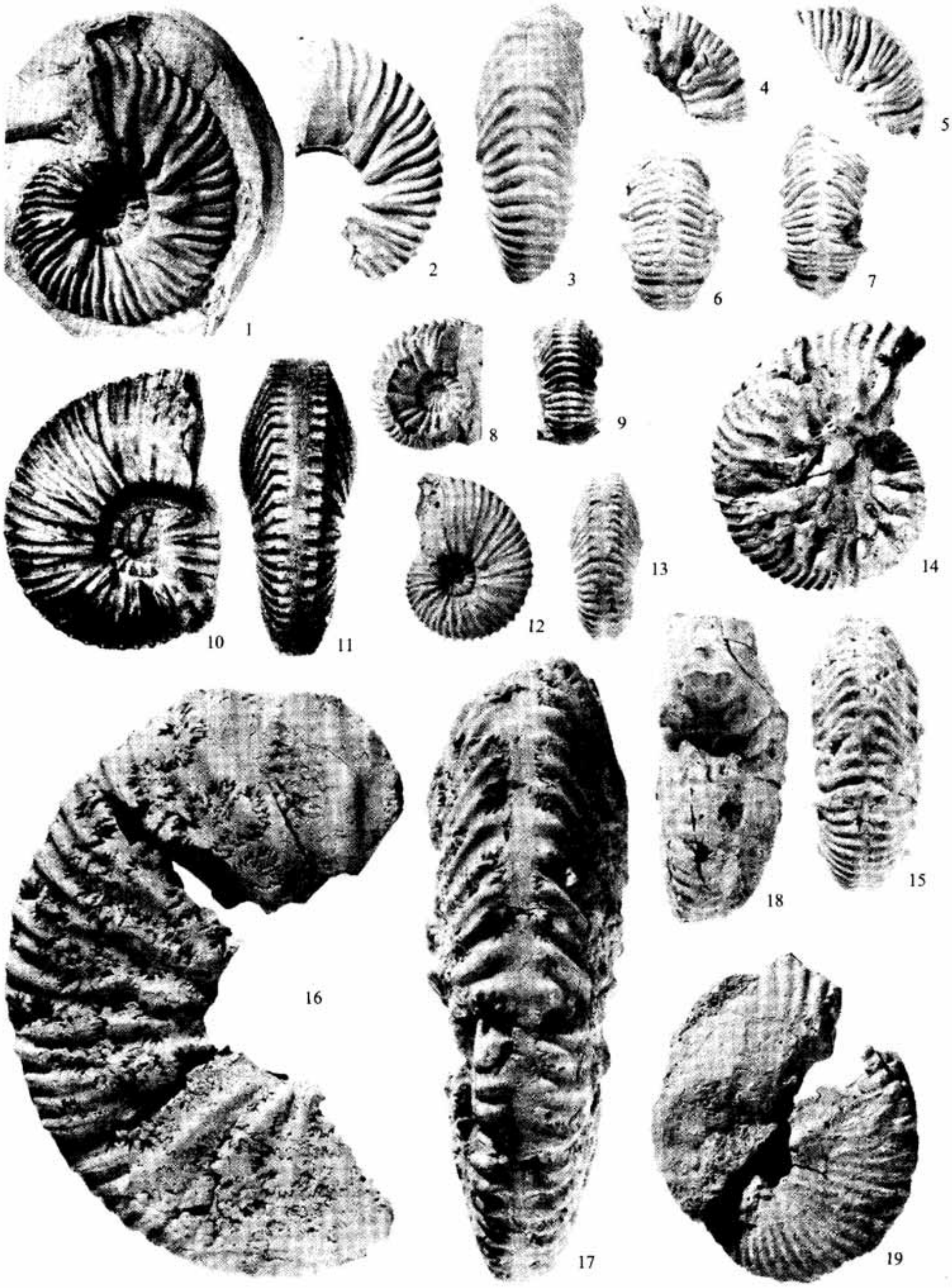
Figs. 10, 11, 16, 17. *Karakaschiceras heteroptychum* (Pavlow). 10, 11, lectotype, reproduced from Pavlow 1892 pl. 18, fig. 22 (YM. 425, now almost completely decomposed); 16, 17, phosphatized steinkern, remanié nodule at base of bed D2D, Speeton, BM. C. 82463 (colld G. Pinckney).

Figs. 12, 13. *Karakaschiceras* cf. sp. b, *verrucosum* Zone, Barrett-le-Bas (Hautes-Alpes). ID 10287 (Thieulo colln).

Figs. 14, 15. *Neohoploceras* sp., Speeton (presumably base of D2D). IGS 17939 (previously figured by Danfor 1906).

Figs. 18, 19. *Karakaschiceras* sp. a, Hoheneggelsen (presumably *hollwedensis* Zone). GPIG.

PLATE 41



KEMPER *et al.*, Lower Cretaceous ammonites

Emended diagnosis. Large (to at least 230 mm diameter); early members with moderately thick, evolute whorls, later members more compressed and approaching discoidal. Venter flattened, smooth. Ribbing rather uniform on early growth stages; on middle and adult whorls development of short and sinuous primaries separated by one or more secondaries. Ribs strongly prorsiradiate especially on the ventral part of the whorls and the ventro-lateral shoulder.

Discussion. *Dicostella* is a late Valanginian form first described from France and Switzerland but later recognized as the characteristic ammonite of the north German 'Arnoldien' Schichten (Kemper 1971). Stolley (1937) thought the German forms were conspecific with *Ammonites arnoldi* Pictet and Campiche and proposed a new genus, *Arnoldia*, for them. This name was preoccupied but is not a synonym of *Neohoploceras* as indicated in the *Treatise*.

Earlier species of *Dicostella* (*D. germanica* sp. nov. and allies) are now known from the Dichotomiten Schichten of Diepenau and are crucial for the interpretation of the genus. Unfortunately the Diepenau ammonites are rare and fragmentary, so that for a long time their real character remained unknown and they were placed in *Luppovella* by Kemper (1973); they include some strongly spinose forms which Stolley (1937) misinterpreted as *Acanthodiscus*. Other Diepenau specimens show that the enigmatic *Hoplites teutoburgensis* Weerth (1884) from the Osning Sandstone is another early *Discostella*.

A diagnostic feature of *Dicostella* is the sculpture of the middle and adult stages, with its short primaries and the prorsiradiate bend of all ribs. The primaries are sinuous on the older species (e.g. *D. germanica*—Plate 45, figs. 5–6), but in the course of evolution they become shorter, straighter, and stronger (*D. tuberculata*—Plates 46, 47). The secondaries start at different levels on the flank, often at an umbilical swelling on the primaries. They may also be intercalated, in which case they may have their own feeble swelling on the umbilical edge, or they may be confined to the ventral half of the whorl. The primaries also swell at the mid flank, though only in a few examples, mainly in the adult, are they really spinose. All ribs bear slight, almost clavate, swellings on the ventro-lateral shoulder; sometimes these become stronger, resulting in trispinose primaries. Such variants somewhat resemble *Acanthodiscus*, but the ventro-lateral, clava-like spines on the primaries of *Dicostella* are much stronger than the feeble ventro-lateral swellings of the secondaries (in contrast with the uniform swellings in *Acanthodiscus*). The ribs are interrupted by a smooth band along the venter, but their imaginary prolongation forms a marked angle where in superficially similar *Neohoploceras* the ribs are practically perpendicular to the venter. Although the primaries are strongly swollen on the dorsal part of the flanks, they are slightly stronger than the secondaries on the ventral part of the whorls too.

Thus the resemblance of some spinose fragments to *Acanthodiscus* is a matter of homeomorphy. This may also be the case with *Jabronella*, where the primaries are straight and the lateral spine is nearer the venter than in *Dicostella* (see Riccardi 1977). However, ammonites such as *Jabronella* and the '*Thurmannites*' figured by Imlay (1937)—if they are really Valanginian—could be interpreted alternatively as having a common ancestry with *Dicostella*. A derivation of *Dicostella* from forms such as '*Hoplites*' *zitteli* Uhlig (1901, pl. 7, fig. 5) is possible, but again the age of the species is unknown.

EXPLANATION OF PLATE 42

All figs. × 1.

Figs. 1, 2, 6, 8, 9, 10. *Lyticoceras cryptoceras* (d'Orbigny), *nodosoplicatum* Zone, Chabrières (Alpes-de-Haute-Provence). Thieuloy colln, ID. 10285 (figs. 1, 2), ID. 10286 (figs. 6, 8), ID. 10283 (figs. 9, 10).

Figs. 3, 4. *Endemoceras regale* (Pavlow), C8B, *regale* Zone, Speeton. BM. C. 82470 (Rawson colln).

Figs. 5, 7. *Endemoceras* aff. *noricum* (Roemer), bed D2A (*amblygonium* Zone), Speeton. BM. C. 82471 (Rawson colln).

PLATE 42


1


2


3


4


5


6


7


8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10

KEMPER *et al.*, Lower Cretaceous ammonites

Dicostella tuberculata (Roman, 1933)

Plate 43, figs. 5, 6; Plate 46, figs. 1–3, 6–7, Plate 47, figs. 1, 4–5

1933 *Hoplites (Neocomites) houdardi* var. *tuberculata* Roman, p. 19, pl. 1, figs. 2, 3.
1937 *Hoplites (Arnoldia) arnoldi* Pictet; Stolley, pp. 497–498.
1950 *Arnoldia* sp., Seitz, p. 142.
1966 *Dicostella pitrei* Busnardo, pp. 236–238, pl. 15, figs. 1–4.
1971 *Dicostella pitrei* Busnardo, Enay and Pitre; Kemper, pp. 53, 55.
1973 *Dicostella pitrei* Busnardo, Enay and Pitre; Kemper, pp. 335, 337.
1976 *Dicostella pitrei* Busnardo, Enay and Pitre; Kemper, pp. 36, 38.

Lectotype (here designated) Roman 1933, pl. 1, fig. 2.

Material. Twelve specimens from the 'Arnoldien' Schichten (= *tuberculata* Zone); Ottensen 11 (NLFB kv 230, 243–246), Hollingskopf 1 (GPIG).

Diagnosis. Large *Dicostella* with high, slender whorls and very strong and blunt but short primaries on the dorsal part of the flanks only—they do not reach mid-flank.

Description. Shell discoidal, with high, slender whorls and weakly convex flanks. Venter flattened. Width of umbilicus moderate, variable (25–35 %). Umbilicus shallow and umbilical wall low, steeply dipping and slightly convex. Umbilical shoulder rounded. Largest diameter of shell estimated at about 180 mm.

The sculpture is very typical; primaries short (not reaching the mid-flank line), very strong and blunt (e.g. Plate 46, fig. 1). Their highest elevation is at the ventral-most end, but the dorsal extremity (on the umbilical shoulder) is also strongly elevated. At first (to diameters of about 30 mm) the primaries and secondaries may be of equal thickness (Pl. 46, figs. 2), the primaries being distinguished by swelling slightly in mid-flank. The ribs bifurcate only. Other specimens of similar size may have already strong primaries (Pl. 46, figs. 6, 7). The ratio of secondary to primary ribs is fairly constant, but in the inner whorls most secondaries join the primaries in bundles of 2 or 3 (Pl. 46, figs. 6, 7; Pl. 47, fig. 5) whereas with growth the degree of bundling diminishes (Pl. 46, fig. 1; Pl. 47, fig. 1) and more secondaries are intercalated. In some instances one secondary may be connected to the dorsal-most swelling of the preceding primary (Pl. 47, fig. 5); other intercalated secondaries may be shorter (Pl. 47, fig. 5).

On the ventral half of the whorl the ribs are strongly prorsiradiate and moderately uniform, though those originating from primaries may be slightly higher than intercalated ones. All are slightly elevated on the ventro-lateral shoulder; the ribbing is interrupted on the flattened venter (Pl. 43, fig. 6; Pl. 46, figs. 3, 7; Pl. 46, fig. 4).

Discussion. The German material is represented mainly by body chambers of varying size. Although this ammonite is a first class guide fossil for part of the late Valanginian (*tuberculata* Zone) and its old name '*Arnoldia*' was the origin of the term 'Arnoldien' Schichten, the species has never been described or illustrated from Germany. The German specimens match closely both the lectotype and the specimen figured by Busnardo (1966, pl. 15, fig. 1).

D. tuberculata represents the discoidal end member of the genus. It occurs in the Lower Saxony Basin, Switzerland and south-east France.

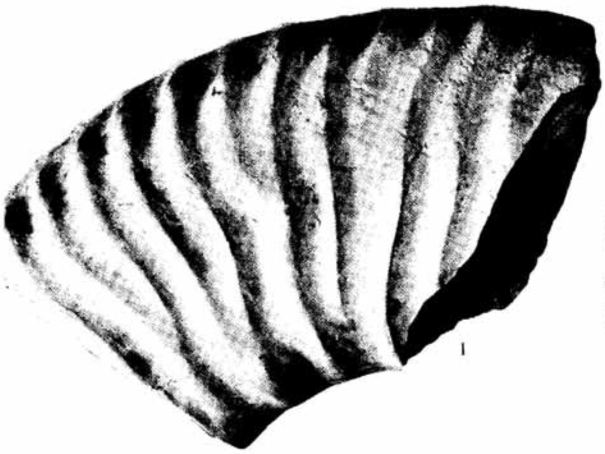
EXPLANATION OF PLATE 43

All figs. × 1.

Figs. 1, 2. *Dicostella* sp. nov. b, *bidichotomoides* Zone?, Mindener Wald. GPIH (colld A. Thiermann).

Figs. 3, 4. *Dicostella teutoburgensis* (Weerth), *bidichotomoides* Zone, Diepenau. Cast (NLFB kv 235) of a specimen in a private collection.

Figs. 5, 6. *Dicostella tuberculata* (Roman), *tuberculata* Zone, Hollingskopf. GPIG.


1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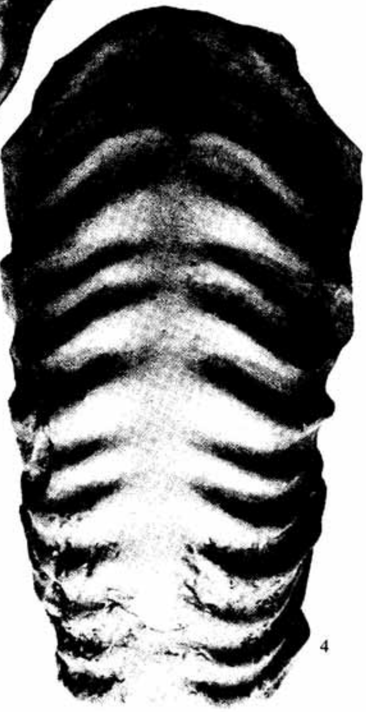
4


5


6

KEMPER *et al.*, Lower Cretaceous ammonites

Dicostella houdardi (Roman, 1933)

1905 *Hoplites* sp. nov. Baumberger, p. 61, pl. 11, fig. 3.
1933 *Hoplites* (*Neocomites*) *houdardi* Roman, pp. 16–19, fig. 5, pl. 1, fig. 1.
? 1966 *Dicostella* cf. *pitrei* Busnardo, pl. 15, fig. 4.

Lectotype. Roman 1933, pl. 1, fig. 1, designated herein.

Discussion. *D. houdardi* is close to *D. tuberculata* but has only slightly elevated primaries which are less spinose, less thick, more numerous and with a longer elevated part. The species is known from the south-east of France, the Swiss Jura and adjacent part of the Paris Basin. Its extension into the Boreal Realm is indicated by a specimen from Ottensen (NLFB kv 224) which differs from typical specimens in having weaker primaries and a stronger prorsiradiate bend of the ribs: it is figured (Pl. 11, figs. 1, 2) as *D.* aff. *houdardi*.

Dicostella germanica sp. nov.

Plate 45, figs. 5, 6; Plate 47, figs. 2, 3

Holotype. NLFB kv 234, from the *bidichotomoides* Zone, Diepenau.

Paratypes. Three specimens (NLFB kv 233, 238, 239) from the *bidichotomoides* Zone, Diepenau.

Diagnosis. Large *Dicostella* with wide umbilicus. Whorls low, moderately thick, with slightly convex flanks. Primary ribs on middle and adult growth stages elevated on the dorsal part of the whorl, clearly sinuous on the middle growth stages and with nodelike swellings on the umbilical edge and near the middle flanks.

Description. The material is fragmentary. The holotype (Pl. 45, figs. 5, 6) has a diameter of 200 mm. It is adult or nearly so; the shell has a wide umbilicus and low, only moderately thick whorls. The specimen figured on Plate 47, figs. 2, 3, gives an impression of the sculpture of the middle growth stages; here the primaries bear swellings on the middle of the flanks and on the umbilical shoulder. All ribs are slightly elevated on the ventrolateral shoulder and have a prorsiradiate bend. The holotype shows a later stage in sculptural ontogeny. The primaries now have a fairly strong dorsal elevation but are more strongly elevated in mid-flank and on the umbilical shoulder. This elevated part of the primaries extends to a point slightly ventral from the mid-flank line (contrast with *D. tuberculata*). They have a slight sinusoidal bend. In the middle of the last whorl the primaries remain single, but elsewhere they bifurcate. The number of intercalated secondaries varies. All ribs have a prorsiradiate bend and are raised on the ventro-lateral shoulder into almost clavate swellings. The variability increases on the body chamber where the sculpture is more spinose.

Discussion. The typical sculpture of *D. germanica* indicates a close relationship to the younger *D. tuberculata*, which probably evolved from *D. germanica*.

EXPLANATION OF PLATE 44

All figs. × 1.

Figs. 1, 2. *Dicostella* aff. *houdardi* (Roman), *tuberculata* Zone?, Ottensen. NLFB kv 224 (Hapke colln).

Figs. 3–5. *Varlheideites peregrinus* Rawson and Kemper, *crassus* Zone, Varlheide: previously unfigured paratypes. 3, 4, microconch showing the beginning of a lappet, NLFB kv 249; 5, immature macroconch showing the commencement of the trituberculate stage, NLFB kv 250.

KEMPER *et al.*, Lower Cretaceous ammonites

Dicostella teutoburgensis (Weerth, 1884)

Plate 43, figs. 3, 4; Plate 45, figs. 1, 2

1881 *Hoplites* n. f. ind. Neumayr and Uhlig, p. 176, pl. 40, fig. 1, pl. 41, fig. 1.
1884 *Ammonites* (*Hoplites*) *teutoburgensis* Weerth, p. 20, pl. 5, fig. 1.
1902 *Hoplites acuticosta* Koenen, p. 198 (pars).
1966 *Neocomites* aff. *dubisiensis* Baumberger; Busnardo, p. 231, pl. 14, figs. 2, 3.

Holotype. Weerth 1884, pl. 5, fig. 1. The specimen has not been traced.

Material, Four body chamber fragments from Diepenau: NLFB kv 377 (colld. P. F. Rawson) and three in a brickworker's collection (casts NLFB kv 235–237).

Discussion. *D. teutoburgensis* includes those large members of the early group of *Dicostella germanica* which have less curved ribs, a less regular arrangement and development of the ribs on the penultimate growth stage and irregular ribbing on the broad, large body chamber (see Weerth's figure). Plate 45, figs. 1, 2 give an idea of a late growth stage. As the sculpture of early and middle stages is unknown, a diagnosis cannot be formulated.

The holotype was from the Osning Sandstein of Tönsberg, near Oerlinghausen. The species also includes a specimen figured by Neumayr and Uhlig (see synonymy) from the Hils ironstones at Grube Helene near Salzgitter which Koenen (1902, p. 198) cited as a syntype of his *Hoplites acuticosta*.

Dicostella sp. nov. a

Plate 46, figs. 4, 5

1902 *Hoplites* cf. *longinodus* Neumayr and Uhlig; Koenen, p. 188, pl. 51, fig. 2.

Material. Three short fragments from the *bidichotomoides* Zone, Diepenau; GPIH (two specimens), NLFB kv 232.

Discussion. These fragments are almost homeomorphic with *Acanthodiscus*. The primaries are raised throughout their length and slightly flattened in the ventro-lateral region; they end in a broad, low, almost clavate elevation (Pl. 46, fig. 4, 5). The secondaries are much weaker but form a marked angle at the ventro-lateral shoulder, though this is weaker than the swelling of the primaries. Most other features are unknown.

Dicostella sp. nov. b

Plate 43, figs. 1, 2

Material. Two fragments, from the Mindener Wald (horizon not known: GPIH) and Diepenau (*bidichotomoides* Zone: NLFB kv 240, collected by Kemper).

Discussion. Again the material is too incomplete for formal naming, but the two fragments cannot be attributed to one of the described species. They are evolute with clear *Dicostella* features. The

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EXPLANATION OF PLATE 45

Figs. 1, 2, 5, 6 × ½, figs. 3, 4 × 1.

Figs. 1, 2. *Dicostella teutoburgensis* (Weerth), *bidichotomoides* Zone, Diepenau. NLFB kv 377 (colld P. F. Rawson).

Figs. 3, 4. Genus uncertain, *tuberculata* Zone?, Ottensen. GPIG.

Figs. 5, 6. *Dicostella germanica* sp. nov., holotype, *bidichotomoides* Zone, Diepenau. NLFB kv 234 (colld E. Kemper).

PLATE 45

KEMPER *et al.*, Lower Cretaceous ammonites

primaries are elevated on the umbilical shoulder and in mid-flank. Secondaries generally split from the raised area on the umbilical shoulder, and are also elevated in mid-flank. All the ribs swell on the ventro-lateral shoulder, where they are almost clavate.

Genus ENDEMOCERAS Thiermann, 1963

Type species. *Hoplites amblygonius* Neumayr and Uhlig 1881, by original designation.

Discussion. *Endemoceras* was proposed for a distinctive and abundant group of north-west European ammonites which had previously (e.g. Spath 1924*a*) been placed in *Lyticoceras* Hyatt, 1900 (type species *A. cryptoceras* d'Orbigny 1840). Wright (1975) declared the two genera to be synonymous after studying the lectotype of *L. cryptoceras*. However, the specimen is worn and Wright had no other material; nor did he mention the preliminary conclusions of Thieuloy (1971), who had already examined and cleaned the specimen, suggested its exact horizon and referred to additional material in pointing out differences between the two genera. Thieuloy (1977*b*) has now discussed the differences in greater detail and stressed that although advanced growth stages of the two genera may be comparable in some ways, the juvenile and intermediate whorls are significantly different:

(*a*) The ribs of *Lyticoceras* cross the venter with a forward convexity, though always very reduced over the siphonal line. The venter is rounded. In *Endemoceras* there are ventral chevrons and the venter is more or less tabulate, with a narrow smooth or slightly pinched line along the siphonal line.

(*b*) In *Lyticoceras* the ventro-lateral tuberculation is homogeneous; every external rib is raised at the ventro-lateral shoulder into a small isometric spine. *Endemoceras* has small clavi, which sometimes become spinose in later growth stages.

(*c*) The primary ribs of *Lyticoceras* are generally less sinuous than those of *Endemoceras*, though there is some overlap in this feature.

(*d*) The lateral lobe (L) of *Lyticoceras* is less asymmetrical and has a deeper median lobule than in *Endemoceras*.

Two *Endemoceras* and three *Lyticoceras* as figured in Plate 42 to exemplify some of the differences, which are apparent under varying conditions of preservation.

Hence we regard *Endemoceras* as a distinct genus so far known only from north-west Europe (where German forms were monographed by Thiermann 1963, and English occurrences reviewed by Rawson 1971*b*). *Lyticoceras* faunas are still inadequately described, but their stratigraphy is now known. The lectotype of *L. cryptoceras* came from La Lagne, near Castellane, and Thieuloy (1971, 1977*b*) showed that it is from the *nodosoplicatum* Zone at the top of the lower Hauterivian. The *Lyticoceras* fauna of this zone is widespread in south-east France and is stratigraphically well separated from the last *Teschenites* of the early lower Hauterivian; no Berriasellidae are known from the intervening *loryi* and *jeannoti* Zones. Thus *L. cryptoceras* is of similar age to *E. regale* and not to the *E. noricum* group which it superficially resembles.

Endemoceras shows similar evolutionary trends to the almost contemporary *Neocomites* (*Teschenites*) lineage of south-east France and both forms could be derivatives of earlier *Neocomites*. Conversely, *Lyticoceras* probably migrated southward from north-west Europe as a derivative of late *Endemoceras* (Thieuloy 1977*b*).

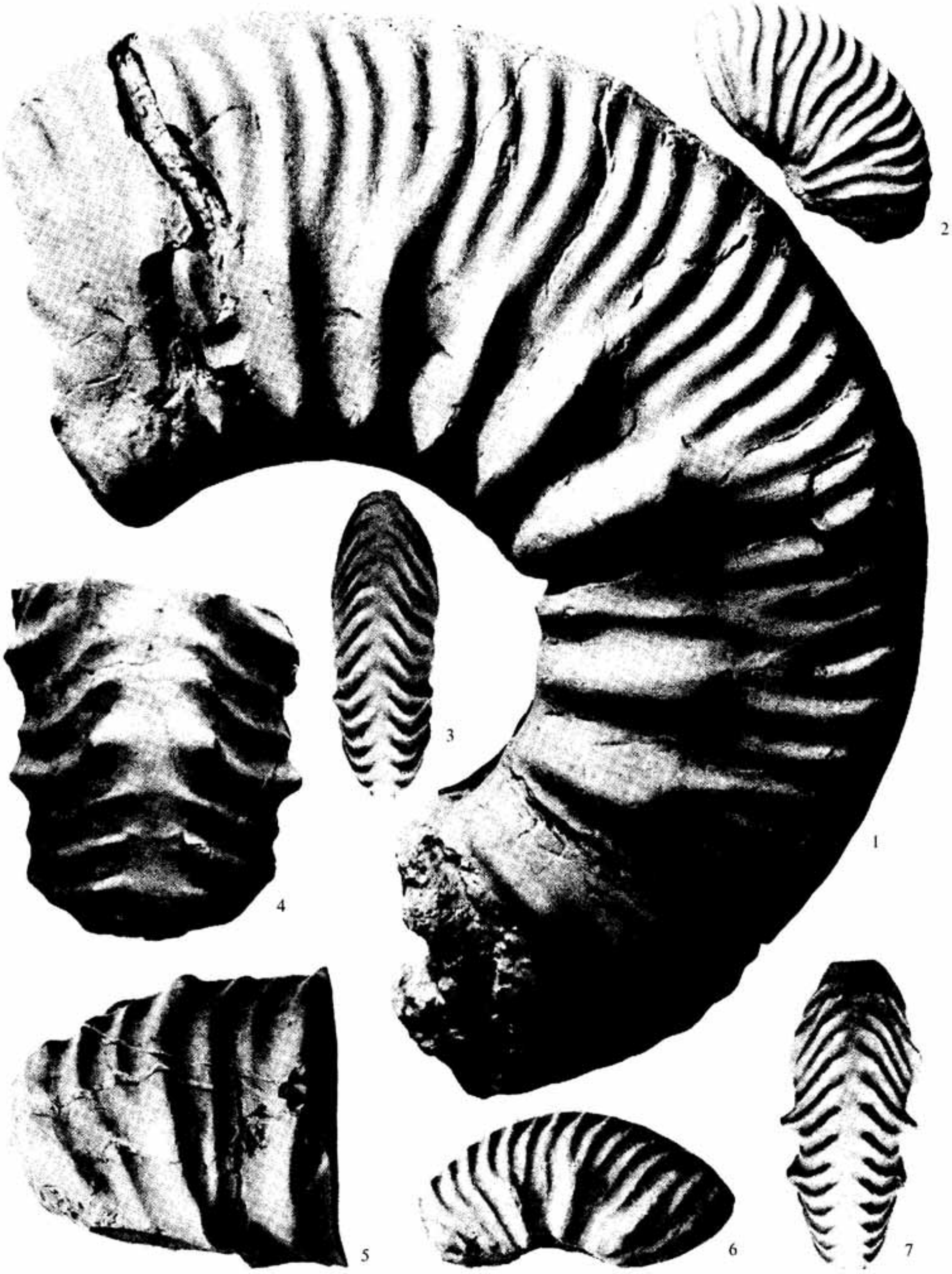
EXPLANATION OF PLATE 46

All figs. × 1.

Figs. 1-3, 6, 7. *Dicostella tuberculata* (Roman), *tuberculata* Zone, Diepenau: 1, adult (?) body chamber, NLFB kv 243 (Hapke colln); 2, 3, variety in which strong primaries have not yet developed, NLFB kv 24 (Pfaff colln); 6, 7, NLFB kv 245 (Pfaff colln).

Figs. 4, 5. *Dicostella* sp. nov. a, *bidichotomoides* Zone, Diepenau. GPIH (colld A. Thiermann).

PLATE 46



KEMPER *et al.*, Lower Cretacious ammonites

Genus DISTOLOCERAS Hyatt, 1900

Type species. Ammonites hystrix Phillips 1829, by original designation.

Discussion. '*Distoloceras*' is recorded from Valanginian and lower Hauterivian strata in various parts of the Boreal and Tethyan Realms, and thus appears important for inter-realm correlation. However, the generic name has been used in a broad sense for uncoiled berriasellids of varied ancestry. The type species is from the Speeton Clay, where it and related species (*D. pavlowi* Spath, *D. curvinodus* (Phillips) etc.) form a discrete generic group in the lower part of the *Endemoceras* beds (Rawson 1971*b*, p. 69, fig. 3). The fauna is now being monographed (Rawson, in preparation). *Distoloceras* also occurs in the Claxby Ironstone of Lincolnshire and in the *amblygonium* and *noricum* Zones of north Germany (specimens figured by Roemer 1840; Koenen 1902; Neumayr and Uhlig 1881). It is derived from *E. amblygonium* through the earliest species, *D.* sp. nov. (Rawson, unpublished thesis, 1966*b*), and reached a peak in uncoiling in *D. roemeri* whose outer whorls closely resemble *Crioceratites* (Neumayr and Uhlig 1881, pl. 55).

'*Distoloceras*' from other areas do not appear to be related to this discrete north-west European group. For example, Collignon's (1962) records from Madagascar may be derivatives of contemporary *Sarasinella* (*D. spinosissimum* Haussman; Collignon, pl. 194) and 'kilianellids' (*D. hirtzi* Collignon, pl. 185), while Thieuloy (1973, p. 298) noted that the majority of French '*Distoloceras*' belong to a lower Valanginian (*campylotoxum* Zone) 'kilianellid' and to upper Valanginian *Eleniceras*. He has not recorded a single true *Distoloceras* among the French 'boreal' ammonites (Thieuloy 1977*a*). However, the juvenile '*Acanthodiscus*' *lamberti* Sayn, probably from the *trinodosum* Zone, is like *Distoloceras*, but because of its rarity its affinities remain uncertain.

genus uncertain

Plate 45, figs. 3, 4

Material. One whorl fragment from Ottensen (probably *tuberculata* Zone), GPIG.

Discussion. The characters of this fragment (coarse ribs, sometimes primaries and short secondaries, sometimes almost bifurcating; more or less convex ventral region) are reminiscent of *Breistrofferella varappensis* (Baumberger) which has strong, widely spaced ribs. However, the probable horizon does not correspond as *Breistrofferella* first appears in the basal Hauterivian.

Genus ACANTHODISCUS Uhlig, 1905

Type species. Ammonites radiatus Bruguière 1789, by subsequent designation (Sayn *in* Cossmann 1907, not Spath 1924*a* as indicated by Wright *in* Arkell *et al.* 1957).

Discussion. True *Acanthodiscus* (i.e. sensu Goguel 1940) form a discrete lower Hauterivian assemblage, and are predominantly distributed in the shallower-water, sometimes condensed, facies of Europe, from north-west Germany through the Polish Furrow to the Crimea in the east and the Paris Basin, Jura, and Provence in the west. They are rare in the deeper-water vocontian facies but

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EXPLANATION OF PLATE 47

All figs. × 1.

Figs. 1, 4, 5. *Dicostella tuberculata* (Roman), *tuberculata* Zone, Ottensen: 1, NLFB kv 230 (Pfaff colln); 4, 5, NLFB kv 246 (Pfaff colln).

Figs. 2, 3. *Dicostella germanica* sp. nov., paratype, *bidichotomoides* Zone, Diepenau. NLFB kv 238 (colld E. Kemper).

KEMPER *et al.*, Lower Cretaceous ammonites

occurrences are now documented (Thieuloy 1977*b*). German forms were well illustrated by Neumayr and Uhlig (1881) and Jura and Paris Basin occurrences monographed by Baumberger (1903–10) and Goguel (1940). Goguel showed that the German *A. radiatus* are consistently more inflated than Tethyan forms and our observations confirm this.

The first appearance of *A. radiatus* is taken to mark the base of the 'standard' Hauterivian (Thieuloy 1977*b*), so that its appearance in north-west Germany is crucial for the definition of the Valanginian/Hauterivian boundary there. Unfortunately, although *Acanthodiscus* is quite common in museum collections (at least 100 specimens) this obviously reflects selective collecting; in the field it is rare. Thiermann (1963) obtained a single example each of *A. radiatus*, *A. vacecki* and *A. ottmeri* in the middle of the *noricum* Zone at Stadthagen (Kuhlmann) whereas he collected over 350 *Endemoceras* at the same locality. The genus is a little more common in the shallower-water clays at Z. Moorberg, Sarstedt (Mutterlose colln) where it has been found in the upper part of the *amblygonium* Zone.

Genus LEOPOLDIA Mayer-Eymar, 1887

Type species. *Ammonites leopoldinus* d'Orbigny 1840, by virtual tautonomy.

Discussion. The close relationship between *Leopoldia* and *Acanthodiscus* is well documented (e.g. Neumayr and Uhlig 1881; Goguel 1940; Thieuloy 1977*b*) and the two genera occur together in the Jura, the Paris Basin, Provence, and the Crimea. Most occurrences are in shallow-water, often condensed, facies and the order of appearance (and hence of evolution) of the genera is still uncertain, though in two sections in the vocontian facies, Thieuloy (1977*b*) has recorded rare *Leopoldia* above the first *Acanthodiscus*.

In north-west Germany, *Leopoldia* is extremely rare. Koenen (1902) figured fragments of *L.* cf. *leopoldi* from Bredenbeck (pl. 14, fig. 3; pl. 32, fig. 4) and there are single specimens of *L. leopoldi* from the Endemoceras-Schichten (exact horizon unknown) of Heisterholz, Schulenburg (NLFB kv 247, 248) and the Hannoversche Treue mine near Engesode (Salzgitter district). Two fragmentary specimens from Bredenbeck (Koenen 1902, pl. 32, fig. 2) and the Osning Sandstein of Brackwede are here identified as *L.* sp.; the species is more evolute than *L. leopoldi*.

Genus SAYNELLA Kilian, 1910

Type species. *Ammonites clypeiformis* d'Orbigny 1841, by subsequent designation (Spath 1924*a*).

Saynella sp. nov.

Discussion. A single septate whorl fragment from bed D1 at Speeton (Wrights' colln 16574) of a specimen at least 150 mm in diameter differs from *S. clypeiformis* in having denser, more persistant ribs and a rounded umbilical wall. The ventral-most part of the whorl is broken off, but it is clear that the ribs curved forward less strongly towards the venter than in *S. clypeiformis*.

Family OOSTERELLIDAE Breistroffer, 1940
Genus OOSTERELLA Kilian, 1911

Type species. *Ammonites cultratus* d'Orbigny 1841, by subsequent designation (Roman 1938).

Oosterella aff. *cultrata* (d'Orbigny, 1841)

Plate 37, figs. 9, 10

1881 *Schloenbachia* n. f., cf. *cultrata* d'Orbigny; Neumayr and Uhlig, p. 142, pl. 15, fig. 3.
1902 *Schloenbachia* n. sp., Koenen, p. 56.
1902 *Schloenbachia* n. f. cf. *cultrata* d'Orbigny; Koenen, p. 56.

Material. One body chamber from the *crassus* Zone, Varlheide (NLFB kv 223).

Discussion. Their rare and fragmentary preservation prevent a full analysis of German *Oosterella*, but there are differences between these and the French forms. D'Orbigny's figure (1841, pl. 46, figs. 1, 2) is reasonably accurate and his specimen can be matched with individuals in the Thieuloy colln. In all these forms rib bifurcation is quite common but unequal; sometimes it is distinct, at other times blurred so that one of the outer ribs appears to be intercalated.

The Varlheide specimen has high whorls and a very high, acute and undulating keel. The ribs bend forward very strongly on the ventral half of the flanks and every fourth one is slightly stronger than the others on the dorsal half of the flank. This feature was mentioned by Neumayr and Uhlig (1881, p. 142) as characteristic of their fig. 3 specimen. Both of these have dominantly single ribs.

We have not traced the three specimens referred to by Koenen and Neumayr and Uhlig. They were recorded from Osterwald (older than Varlheide?), Ludwig mine (Salzgitter), and Grenzlerburg. The latter two could be late Valanginian or even early Hauterivian in age. The Varlheide specimen is one of the earliest *Oosterella* known, though there is a record of *O. cultrata* from the 'middle' Valanginian of the Agadir Basin, Morocco (Wiedmann, Butt and Einsele 1978), associated with *Sarasinella longi.*

Superfamily DESMOCERATACEAE Zittel, 1895
Family DESMOCERATIDAE Zittel, 1895
Subfamily EODESMOCERATINAE Wright, 1955
Genus SUBSAYNELLA Spath, 1923

Type species. Desmoceras sayni Paquier 1900, by original designation.

Subsaynella cf. *sayni* (Paquier, 1900)

Plate 34, figs. 5, 6

1896 *Olcostephanus* cf. *carteroni* (d'Orbigny): Lamplugh, table opposite p. 184.
cf. 1900 *Desmoceras sayni* Paquier, pp. v, vi, pl. 8, fig. 2.
1924*a* *Subsaynella* ('*Saynella*') sp. n. (group of '*S.*' *sayni*), Spath, pp. 77, 82.

Material. One specimen (BM. C. 72677) from Speeton, horizon unknown.

Discussion. The Speeton example differs from typical Tethyan *S. sayni* (e.g. Busnardo 1970, figs 2, 3) in being a little less compressed and more coarsely ribbed. However, some French specimens in the Thieuloy collection possess one or the other of these characteristics, and we therefore compare the Speeton form with *S. sayni.*

Spath (1924*a*) recorded the specimen from C6 (p. 77) or C5 (p. 82), but he was probably mislead by the label in Lamplugh's handwriting which is still preserved. This noted that the specimen was collected by Mr. Headley and that its horizon was 'C6 (probably)'. There is no evidence that Headley identified the horizon; Lamplugh apparently suggested it because he believed the ammonite to be a variety of *Simbirskites speetonensis*, a species confined to C6. The Lamplugh identification on the specimen label is clear: '*Amm. speetonensis* var. - - - I believe this is the variety which is labelled *carteroni* in some museums'.

From the correlations that Spath (1924*a*) and we have made, C6 (or C5) was a very appropriate suggestion, albeit for the wrong reason!

Genus SPITIDISCUS Kilian, 1910

Plate 34, figs. 7–15.

Type species. Ammonites rotula J. de C. Sowerby 1827, by original designation.

Discussion. Spath (1924*a*) listed several species from Speeton, but most are difficult to interpret and only dubiously distinct. Their systematics and taxonomy await revision, but our interpretation of previously figured forms is shown in table 1. There are two main horizons: rare, small specimens of *S. rotula* occur in bed C5L (*speetonensis* Zone) while forms of the *S. pavlowi* group are common in bed

TABLE 1. Previously figured *Spitidiscus* from the Speeton Clay

Original reference	Spath 1924*a*	This paper	Location of spec.
Ammonites rotula J. de C. Sowerby 1827, p. 136, pl. DLXX, fig. 4	*Spitidiscus rotula*	*Spitidiscus rotula*	BM. 43885
Ammonites youngi Young and Bird 1828, p. 256, pl. 12, fig. 6	*Spitidiscus youngi*	uninterpretable (after Howarth 1962)	Lost
Ammonites rotula Sow: Phillips 1829, pl. 2, fig. 45	*Spitidiscus subrotula* nom. nov. (holotype)	*Spitidiscus rotula*?	YM 418(?)
Olcostephanus (*Holcodiscus*) *rotula* Sow: Pavlow 1892, pl. XVII, fig. 11		*Spitidiscus pavlowi* (Karakasch) syntype	BM. C. 34970
Ibid. fig. 12	*Spitidiscus inflatiformis* nom. nov. (holotype)	*Spitidiscus pavlowi* (Karakasch) syntype	YM 431
Ibid. fig. 13		*Spitidiscus* cf. *rotula*	Lost (BM. C. 34979
Desmoceras cf. *cassidoides* Uhlig: Pavlow 1892, pl. XVIII, fig. 19	*Barremites subcassida* nom. nov. (holotype)	*Spitidiscus subcassida* Spath	BM. C. 34975
?*Desmoceras* cf. *cassidoides* Uhlig: Danford 1906, pl. XIV, fig. 6	*Spitidiscus youngi*	*Spitidiscus* sp.	IGS 17917

C8A (top *regale* Zone). *S. rotula* has an approximately semicircular whorl section and th constrictions curve forward strongly over the venter, while *S. pavlowi* is more inflated and th constrictions curve forward less strongly. Karakasch (1907, p. 117) pointed these differences ou when he proposed *S. pavlowi* as a new name for the specimens figured by Pavlow (1892, pl. 17, figs. 11 12 only) as *S. rotula*. Karakasch's name was overlooked by Spath (1924*a*) and Rawson (1971*b*), wh used the name *S. inflatiformis* Spath (1924*a*). As *S. inflatiformis* was proposed as a nomen novum fo Pavlow's figure 12 it is a junior objective synonym of *S. pavlowi*.

Lower in C8 (*regale* Zone) a single specimen (Pl. 34, figs. 9, 10) has been found which closel matches the holotype of '*Barremites*' *subcassida* Spath; it is more compressed than *S. pavlowi*, wit almost flat flanks which bear very feeble constrictions. These features characterize a commo Tethyan group (*S. fasciger* Thieuloy, *S. darderi* Fallot and Termier, and *S. deleaui* Busnardo) whic occurs from the top of the *jeannoti* Zone to the early Barremian.

In Germany, *Spitidiscus* sp. (cf. *rotula*?) occurs in the upper part of the Gildehauser Sandstein o Gildehaus (Kemper 1976, pl. 19, figs. 7, 10, 11; pl. 30, figs. 6–8); its exact horizon is not known but i could correlate with the Speeton immigration horizon in the upper *speetonensis* Zone (*S. rotula* level)

CORRELATION WITH THE TETHYAN STANDARD

The standard Lower Cretaceous stages and zones are defined in France, and correlation with borea areas has always been problematic. Even the Jurassic/Cretaceous boundary is defined at differen levels in the two realms (see Casey 1973) and there are corresponding problems in applying standar stage boundaries to north-west Europe (see Rawson *et al.* 1978). Hence the occurrence of Tethya ammonites at various levels in north-west Europe is invaluable for correlation, especially when take in conjunction with Thieuloy's (1977*a*) description of a considerable number of boreal forms fro precisely recorded horizons in south-east France. A small number of forms which Thieuloy regarde as of boreal origin are not so, and their real origin remains dubious. The identification of certain other species is discussed below, mainly in the light of recent work on the German dichotomitids (Kemper 1978).

Polyptychitinae in south-east France. The Polyptychitinae dominate much of the boreal Valanginian, and a few forms occur in south-east France. Comparison is often difficult because the French specimens are all inner whorls whereas boreal individuals are often adult body chambers. However, it is clear that the sequence of morphotypes or species is the same in both realms. In the following discussion, figure references refer to Thieuloy (1977*a*).

The main *Polyptychites* stock is represented by the *P. keyserlingi* group: *P.* cf. *lejanus* Bogoslovsky sensu Thieuloy (pl. 6, fig. 11), which occurs in the middle part of the lower Valanginian. Late lower Valanginian *Polyptychites* of the fine and densely ribbed group near to *P. tscherskii* Pavlow are represented by a specimen of '*P.* aff. *plicatilis*' from the *campylotoxum* Zone (pl. 7, fig. 1).

Neocraspedites-like ammonites appear in the lower/upper Valanginian boundary beds and are offshoots of the early *Prodichotomites* radiation. The earliest (*campylotoxum* or *verrucosum* Zone) were described as *Prodichotomites collignoni* Thieuloy (pl. 6, figs. 12–21); they are closely related to the *P. flexicostata* group of the *hollwedensis* Zone. Early growth stages of apparently more advanced *Neocraspedites*-like *Prodichotomites* were figured as *Dichotomites* ('*Neocraspedites*') cf. *fissuratus* (Koenen), *D.* ('*N.*') cf. *flexicosta* (Koenen), *D.* ('*N.*') *aff. undulatus* (Koenen), *D.* ('*N.*') *vocontius* Thieuloy, and *D.* ('*N.*') sp. inc. A and B (pl. 8, figs. 2–21). All were from the *verrucosum* Zone, and the same assemblage occurs in north Germany with *Saynoceras verrucosum* in the *hollwedensis* Zone.

A more advanced *Prodichotomites* is represented by the *P. ramulosus* (Koenen) group (pl. 7, fig. 10) from the *trinodosum* Zone. This occurrence fits best with boreal forms in the middle part of the Dichotomiten-Schichten. *Dichotomites* s.s. is represented by species generally quoted by early French and Swiss workers as *D. bidichotomus* (Leymerie in d'Orbigny) or *D.* cf. or aff. *bidichotomus*. However, this species cannot be defined with certainty (see Kemper 1978). Thieuloy's (1977*a*) figured specimens are reinterpreted as follows:

pl. 6, fig. 22 *D. petschi* Kemper
pl. 7, fig. 9 *D. petschi*
pl. 7, figs. 11, 12 *D. evolutus* Kemper
pl. 8, fig. 1 *D.* aff. *tardescissus* Koenen

The stratigraphical horizons of the French *D. petschi* and *D.* aff. *tardescissus* are unkown. *D. evolutus* apparently occurs with *Teschenites* and *Dicostella* of the *tuberculata* group, which would indicate a younger age (very late Valanginian) than the German representatives of the species (*hollwedensis* to *crassus* Zones).

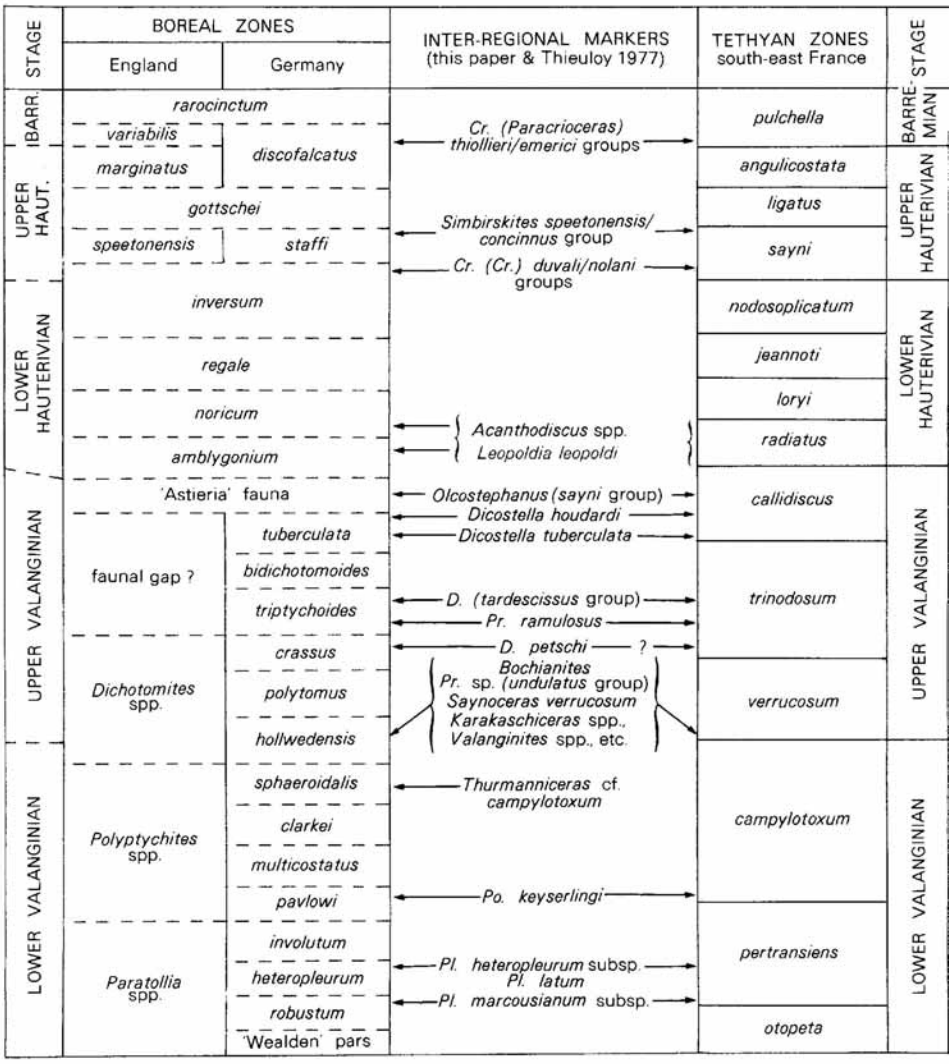
Zonal correlations

The occurrence of a significant number of inter-regional markers facilitates the zonal correlations suggested in text-fig. 8: the stratigraphical reliability of individual species is discussed in the above section and in the systematic descriptions, or in Thieuloy (1977*a*).

Stage and substage boundaries

The base of the Valanginian. Thieuloy (1977*a*, p. 435) lowered the base of the Valanginian in south-east France to include the distinctive faunas of his *otopeta* Zone, which are widely distributed in Tethyan Europe. Earlier, Kemper (1971) had drawn the boundary at the first appearance of *Platylenticeras*, which occurs both in Germany and the northern margin of the pelagic zone in France but is absent from most Tethyan areas. In France, *Platylenticeras* comparable with forms from the lowest Platylenticeras-Schichten appear very high in the *otopeta* Zone, which suggests that the upper part of the German Bückeberg Formation ('Wealden') was already Valanginian *sensu* Thieuloy.

Whichever boundary is eventually agreed upon, the local boundary in England is best drawn at the base of the *Paratollia* spp. Zone, which has yielded very rare *Platylenticeras* and *Pseudogarnieria*.



TEXT-FIG. 8. Inter-regional markers and correlation of zonal schemes for north-west Europe and south-east France.

The lower/upper Valanginian boundary. In the south-east of France the boundary is clearly defined by the appearance of *Saynoceras verrucosum*, which is limited to a thin horizon at the base of the zone (Thieuloy 1977*a*). In Germany, Kemper (e.g. 1978) drew the boundary at the first appearance of *Prodichotomites*, i.e. at the base of the *hollwedensis* Zone. However, the *Olcostephanus* at the base of this zone compare with latest early Valanginian forms from Tethys (p. 268) and *Saynoceras verrucosum* first appears in the upper part of the zone, together with *Valanginites* and *Karakaschiceras*. This suggests that the 'standard' boundary should lie in about the middle of the *hollwedensis* Zone. Supporting evidence lies in the discovery of *Prodichotomites* in south-east France, where the earliest records are near the top of the lower Valanginian (Thieuloy 1977*a*, p. 436, fig. 3).

The base of the Hauterivian. The 'standard' base is defined by the first appearance of *Acanthodiscus*, though this is rare in the vocontian facies. In north-west Europe the appearance of *Endemoceras* is taken to mark the boundary (see Rawson *et al.* 1978, p. 12). As the earliest *Acanthodiscus* so far known from the *Endemoceras* beds is from the upper part of the *amblygonium* Zone (p. 302) it is possible that the lower *amblygonium* Zone is late Valanginian. However, *Acanthodiscus* is too rare in Germany to justify changing the local boundary yet, though the possibility that it is drawn slightly too low exists.

The lower/upper Hauterivian boundary. The base of the *Subsaynella sayni* Zone marks the base of the 'standard' upper Hauterivian. Its correlative horizon in England was taken by Thieuloy (1973) at the base of the *speetonensis* Zone (= base of the *staffi* Zone in Germany). However, *Crioceratites duvali*, which is limited to the *sayni* Zone in France, occurs in the uppermost part of the *inversum* Zone in both England and north Germany (p. 262) and hence we draw the base of the upper Hauterivian within the upper part of the *inversum* Zone.

The base of the Barremian. The 'standard' base lies at the base of the *Nicklesia pulchella* Zone. In the apparent absence of Tethyan ammonites in this part of the north-west European sequence, the boundary here was drawn provisionally at the disappearance of *Simbirskites* (see Rawson 1971*a*, p. 80). The occurrence at Speeton of *Crioceratites* (*Paracrioceras*) *spathi* at the base of the *Simbirskites variabilis* Zone suggests that this zone (and the upper part of the German *discofalcatus* Zone) is already earliest Barremian, as *P. spathi* has the characteristic looped ribs of '*Emericiceras*' from the lowest Barremian of Tethys.

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