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CENOMANIAN AMMONITES FROM SOUTHERN ENGLAND

BY

W. J. KENNEDY

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With 64 plates and 5 tables

THE PALAEONTOLOGICAL ASSOCIATION
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ABSTRACT. About a hundred named ammonite species are recorded from the Lower Chalk (Cenomanian) and contiguous deposits of southern England. Important species based on type material from this area described by Mantell, J. and J. de C. Sowerby, Sharpe, Jukes-Browne, and others are re-described, and the types of important species such as *Mantelliceras mantelli* (J. Sowerby), *M. costatum* (Mantell), and *Acanthoceras hippocastanum* (J. de C. Sowerby) are figured photographically for the first time.

The stratigraphic ranges of all species discussed is given, and the faunal sequence suggested previously for the Lower Chalk (Kennedy 1969, 1970) is reviewed and compared with subdivisions proposed by Spath (1923*b*, 1926*b*), and successions erected elsewhere in the world.

INTRODUCTION

PARTLY as a result of lack of knowledge of detailed stratigraphy, little detailed taxonomic work has been carried out on ammonites from the English Cenomanian. Most authors have relied on the classic sources of Mantell (1822), James Sowerby (1812–1822), his son J. de C. Sowerby (1823–1846), and Sharpe (1853–1857). The chief subsequent workers have been Jukes-Browne (1896), Crick (1896, 1899, 1919), Spath (1923–1943, 1926*a*, *b*, 1937, 1938), C. W. and E. V. Wright (1949, 1951), Wiedmann (1965), and Kennedy and Hancock (1970, 1971).

Important works are available on Cenomanian faunas from other countries, e.g. Collignon (1928–1929, 1931, 1933, 1937, 1939, 1964, etc.) and Wiedmann (1959, 1964). There is an extensive American literature which unfortunately frequently ignores European sources (Stephenson 1952, 1955; Clark 1965). All these works suffer from the lack of good figures and descriptions of classic species from the English succession, e.g. *Mantelliceras mantelli* (J. Sowerby) and *Schloenbachia varians* (J. Sowerby), or those described in the classic French literature, e.g. *Acanthoceras rhotomagense* (Brongniart) and *Schloenbachia coupei* (Brongniart).

It would be premature to attempt a full revision of any group of Cenomanian ammonites from this country. This account is particularly intended as an aid to the detailed stratigraphic account of the Lower Chalk of southern England (Kennedy 1969, 1970). It is therefore concerned primarily with a revision of type material, and such other specimens as are necessary to interpret the species concerned.

Detailed notes are also given for other previously named ammonite species and genera, many of them not previously described from England. The present study is thus complementary to the work of C. W. and E. V. Wright (1951). Many undescribed forms await attention.

No review of the over-all classification of Cenomanian ammonites is intended. I have used the *Treatise* classification of Wright (1952, 1957) as a basis, with some modifications.

STRATIGRAPHIC SUCCESSION

The zonal divisions of the English Cenomanian used here correspond to those proposed by Hancock (1959) for the type Cenomanian of Sarthe. The detailed evidence for this scheme is to be found elsewhere (Kennedy 1969, 1970).

Within the 3 zones proposed, certain restricted ammonite assemblages can be recognized, as indicated in Table 1. These are not subzones; they are a reflection of the restricted and discontinuous nature of the Chalk ammonite sequence (Jefferies 1962, 1963; Kennedy 1969, 1970).

This sequence is discussed after the systematic descriptions, and compared with other faunal sequences proposed for the Cenomanian stage.

TABLE 1. Zonal division and assemblages in southern England.

MIDDLE CHALK	*Mammites nodosoides*	
plenus MARLS (Cenomanian)	*Metoicoceras gourdoni* *Metoicoceras geslinianum*	
LOWER CHALK (Cenomanian)	*Calycoceras naviculare*	
	Acanthoceras rhotomagense	*Acanthoceras jukes-brownei* assemblage *Turrilites acutus* assemblage *Turrilites costatus* assemblage
	Mantelliceras mantelli	*Mantelliceras* gr. *dixoni* assemblage *Mantelliceras saxbii* assemblage *Hypoturrilites carcitanensis* assemblage
GAULT/UPPER GREENSAND (Albian)	*Stoliczkaia dispar*	*Stoliczkaia dispar* and *Mortoniceras* (*Durnovarites*) *perinflatum* Subzone *Arrhaphoceras substuderi* Subzone

AMMONITE PRESERVATION

Ammonite shells were originally wholly aragonitic, with a calcitic aptychus (Hall and Kennedy 1967). In all the facies of the English Cenomanian, aragonite has disappeared, and originally aragonitic fossils occur in three modes of preservation (Jefferies 1962, 1963), of which only the first two are important here.

(i) *Normal chalk preservation.* Here the shell has disappeared, the internal mould has been coated by iron sulphide, and the external mould crushed on to this film to produce a composite internal mould (McAlester 1962; Yates 1962, p. 401, pl. 58). Oysters, serpulids, and other epizoans with calcite shells thus appear cemented to internal moulds.

(ii) '*Pebble*' *preservation.* Ammonites occur as phosphatized and glauconitized internal moulds, sometimes retaining traces of shell and patches of phosphatized sediment. In the Chalk Basement Beds of south-west England, exquisite preservation of this type leaves shells perfectly preserved in phosphate although still sometimes retaining traces of the original nacreous lustre.

(iii) *Oyster cast preservation.* Moulds of ammonites are preserved on oyster attachment areas, occurring even in beds where ammonites are otherwise absent.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of material:

BMNH	British Museum (Natural History), London
GSM	Geological Survey Museum, Institute of Geological Sciences, London
OUM	Oxford University Museum
SMC	Sedgwick Museum, Cambridge
WW	C. W. and E. V. Wright Collection
JMH	J. M. Hancock Collection

SYSTEMATIC PALAEONTOLOGY

Dimensions are given in millimetres, in the following order: Diameter (*D*), Whorl breadth (*Wb*), Whorl height (*Wh*), and breadth of umbilicus (*U*). C and IC refer to costal and intercostal measurements. Figures in parentheses refer to dimensions as a percentage of the diameter.

Phylum MOLLUSCA
Class CEPHALOPODA
Order AMMONOIDEA Zittel 1884
Suborder PHYLLOCERATINA Arkell 1950
Superfamily PHYLLOCERATACEAE Zittel 1884
Family PHYLLOCERATIDAE Zittel 1884
Subfamily PHYLLOCERATINAE Zittel 1884
Genus PHYLLOCERAS Suess 1865
Subgenus HYPOPHYLLOCERAS Salfeld 1824

Phylloceras (*Hypophylloceras*) cf. *seresitense* Pervinquière

Plate 4, figs. 15*a*, *b*

1910 *Phylloceras seresitense* Pervinquière, p. 9, pl. 1, figs. 1–3.
1951 *Phylloceras seresitense* Pervinquière; Wright and Wright, p. 12.
1963 *Phylloceras* (*Hypophylloceras*) *seresitense seresitense* Pervinquière; Wiedmann, pp. 221–224, pl. 15, fig. 4; pl. 21, fig. 1; text-fig. 52 (with synonymy).

Discussion. The only 2 phylloceratid ammonites recorded from the English Cenomanian appear to belong to Pervinquière's species.

Occurrence. The specimen figured by Sharpe (1857, pl. 19, fig. 6; GSM Geol. Soc. 7760) from Ventnor, Isle of Wight, and the specimen from the Cenomanian Limestone in the British Museum (BMNH C73148, Grimsdale Collection) are both of Lower Cenomanian age.

Order LYTOCERATINA Hyatt 1889
Superfamily LYTOCERATACEAE Neumayr 1875
Family TETRAGONITIDAE Hyatt 1900
Subfamily GAUDRYCERATINAE Spath 1927
Genus MESOGAUDRYCERAS Spath 1927

Type species. Ammonites leptonema Sharpe (1855, p. 32, pl. 14, fig. 3), by the original designation of Spath (1927*a*, p. 66).

Diagnosis. Moderately evolute, early whorls compressed, later whorls rather less so, with flat sides and narrowly rounded venter. Internal mould smooth, shell with many fine flexuous lirae. Suture line with shallow external lobe.

Discussion. Only the type species is at present referable to this genus, no other species having been described. *Mesogaudryceras* differs from genera such as *Anagaudryceras* and *Zelandites* in lacking constrictions, whilst compressed early whorls separate it from *Gaudryceras*. Generic differences in the Gaudryceratinae seem to be small, as in many leiostracous groups.

A good discussion of genera closely related to *Mesogaudryceras* is given by Matsumoto (1938) and Wright and Matsumoto (1954).

Occurrence. Rare; Lower Cenomanian of southern England, Greenland, Middle (and Lower?) Cenomanian, southern France.

Mesogaudryceras leptonema (Sharpe)

Plate 1, figs. 10*a*, *b*, 11*a*, *b*

1855 *Ammonites leptonema* Sharpe, p. 32, pl. 14, fig. 3.
1895 *Gaudryceras leptonema* (Sharpe); Kossmat, p. 115.
1896 *Ammonites? leptonema* Sharpe; Jukes-Browne and Hill, p. 163.
1927*a* *Mesogaudryceras leptonema* (Sharpe); Spath, p. 66.
1951 *Mesogaudryceras leptonema* (Sharpe); Wright and Wright, p. 12.
1954 *Mesogaudryceras* cf. *leptonema* (Sharpe); Donovan, p. 23.
1957 *Mesogaudryceras leptonema* (Sharpe); Wright, p. L200, fig. 232, 1.
1961*b* *Mesogaudryceras leptonema* (Sharpe); Thomel, pp. 8, 9.
1965*a* *Mesogaudryceras leptonema* (Sharpe); Thomel, pp. 140, 145.

Holotype. By monotypy, the original specimen figured by Sharpe (1855, p. 32, pl. 14, fig. 3), GSM Geol. Soc. 7762 from the 'Grey Chalk of Ventnor', Isle of Wight, and probably of Lower Cenomanian age.

Diagnosis. *Mesogaudryceras* with about 80 flexuous lirae per whorl.

Description of holotype. The holotype is a well-preserved wholly septate composite mould in grey limestone, in which the ornament of the outer shell surface is particularly well preserved.

The shell is moderately evolute, about half the previous whorl being covered. The whorl section is compressed, with flattened, convergent rounded sides and a rounded, arched venter. The umbilicus is moderately broad, the umbilical shoulder and wall are well rounded.

There are about 80 fine, sharp, flexuous lirae per whorl on the test. They are much narrower than the interspaces. The lirae arise at the umbilical seam, sweep backwards across the umbilical wall, pass straight up the inner part of the whorl sides, flex gently backwards across the middle and outer parts of the flank, and then flex forwards across the ventro-lateral shoulder to form a narrow, forwardly directed, rounded, chevron-like curve over the venter. The suture line is poorly seen, but is moderately sub-divided and moss-like.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
GSM Geol. Soc. 7762, holotype	44	21·5 (48·9)	18·0 (40·9)	14·0 (31·8)	76–78
	33	14·5 (43·9)	12·0 (36·3)	10·0 (30·3)	—

Discussion. As the only described *Mesogaudryceras*, the diagnostic features of the genus (especially lack of constrictions and lirae) distinguish this species from all others. As well as the holotype, there are 3 other specimens from Britain. All are internal moulds, and all show that the mould is quite smooth (Pl. 1, figs. 11*a*, *b*).

Occurrence. The holotype is from the 'Grey Chalk of Ventnor' (Sharpe 1855, p. 32) and is probably of Lower Cenomanian age. Other undoubted Lower Cenomanian specimens are WW 23819 from the *carcitanensis* assemblage fauna of the Glauconitic Marl of Rocken End, Isle of Wight; BMNH C25657 from the Cenomanian Limestone of the Devon coast (probably Bed A_2, of *saxbii* assemblage age); and GSM

31579, from the Lower Chalk of Dorking (Surrey) (in a preservation suggesting a Lower Cenomanian age). Jukes-Browne and Hill (1896) recorded this species from Bed C of Upper Cenomanian (*naviculare* Zone) age on the Devon coast.

Thomel (1961*b*, 1965*a*) recorded the species from the Middle Cenomanian of the Basse-Alpes, France, whilst Donovan (1953, 1954) recorded it from eastern Greenland, associated with Lower Cenomanian *Schloenbachia*. I have a single example from the Banc des Lombards, Cassis, France (Fabre-Taxy and Thomel 1964), which may belong to this species.

Subfamily TETRAGONITINAE Hyatt 1900
Genus TETRAGONITES Kossmat 1895
Tetragonites spp.

Plate 1, figs. 9*a–c*

Discussion and occurrence. This genus is represented by 2 specimens only, WW 22316 from the Chalk Basement Bed at Ringstead (Dorset) and a fragment, BMNH C76360, from the Basement Bed at Sutton Poyntz (Dorset). Both specimens are of Middle Cenomanian, *rhotomagense* Zone age, and represent the first records of the genus from the English Cenomanian.

Superfamily TURRILITACEAE Meek 1876

This superfamily includes most of the Cenomanian heteromorphs, the following genera of which occur in Britain. (I have followed Wiedmann (1965) in treating the scaphitids as a family not a superfamily, and transferring *Worthoceras* to the Ptychoceratidae, although Wright [*in litt.*] doubts the validity of the latter.)

PTYCHOCERATIDAE:	*Worthoceras*
HAMITIDAE:	*Stomohamites*
	Plesiohamites
BACULITIDAE:	*Lechites*
	Sciponoceras
ANISOCERATIDAE:	*Anisoceras*
	Idiohamites
TURRILITIDAE:	*Ostlingoceras*
	Mariella
	Hypoturrilites
	Turrilites
	Carthaginites
SCAPHITIDAE:	*Scaphites*

Family PTYCHOCERATIDAE Meek 1876
Genus WORTHOCERAS Adkins 1928
Worthoceras sp.

Plate 63, fig. 3

Discussion. Several small fragments of smooth or finely ribbed, evolute scaphitoid heteromorphs all belong to this genus, not previously recorded from England. They are specifically indeterminate at present.

Occurrence. Rare; Chalk Basement Bed, Snowdon Hill, Chard (Somerset) (*rhotomagense* Zone, *costatus* assemblage fauna) and elsewhere (author's collection, Wrights' Collection). The genus also occurs in the Lower Cenomanian of Wiltshire (BMNH 88725, Cunnington Collection), and the Isle of Wight (BMNH C16252).

Family HAMITIDAE Hyatt 1900
Genus STOMOHAMITES Breistroffer 1940

Type species. *Hamites virgulatus* Brongniart (1822), by original designation (Breistroffer 1940, p. 85).

Discussion. *Stomohamites* was introduced by Breistroffer as a subgenus of *Hamites*, for *H. virgulatus* and its allies. Spath (1941), Wright and Wright (1951), and Wright (1963*a*) treated it as a subgenus. Wright (1957) and Clark (1965) gave it generic status.

Hamitids of this group differ from *Hamites* [*sensu stricto*] in having denser ribbing, and a suture line with the third lateral saddle nearly as big as the others, and symmetrically bifid. Some have a collared and constricted aperture. Whereas *Hamites* has a known range from the *mammillatum* Zone (Lower Albian) to the *dispar* Zone (Upper Albian), *Stomohamites* ranges from Upper Albian to Upper Cenomanian or Lower Turonian. It is known from Europe, North Africa, Madagascar, and Australia.

Stomohamites duplicatus (Pictet and Campiche)

Plate 5, fig. 12

1941 *Hamites* (*Stomohamites*) *duplicatus* Pictet and Campiche; Spath, pp. 640–642, pl. 72, figs. 12–16; text-fig. 232 (with synonymy).

Discussion. Fragments referred to this species are not uncommon in the phosphatized fauna of the Glauconitic Marl of the western part of the Isle of Wight, also occurring at Stour Bank and in the lower levels of the Lower Chalk in the Lewes region (Southerham). The original of Mantell's *Hamites attenuatus?* (Mantell 1822, pl. 23, fig. 8, *non* Sowerby), BMNH 8607, belongs to this species.

Occurrence. This species is known in the uppermost Albian, *dispar* Zone (Spath 1941). It also occurs in the lowest Cenomanian *carcitanensis* assemblage faunas of southern England, and occurs elsewhere at similar levels (e.g. Madagascar; Collignon 1964, p. 34).

Stomohamites simplex (d'Orbigny)

Plate 1, figs. 1–8

1842 *Hamites simplex* d'Orbigny, p. 550, pl. 134, figs. 12–14.
1951 *Hamites* (*Stomohamites*) *simplex* d'Orbigny; Wright and Wright, p. 14.
1956 *Hamites simplex* d'Orbigny; Sornay, no. 18.
1963*a* *Hamites* (*Stomohamites*) *simplex* d'Orbigny; Wright, pp. 597–599, pl. 81, figs. 1*a–c*.

Discussion. The syntypes of this species have been refigured, and a lectotype designated (Sornay 1956, fig. 1), whilst better material is described by Wright (1963*a*). The English specimens compare well with both these accounts. The species is characterized by an oval-rounded whorl section and fairly strong radial ribs, $4\frac{1}{2}$

in a distance equal to the major costal diameter. Several English specimens show characteristic collared apertures.

As noted by Sornay, the *Hamites simplex* described by Collignon (1928, p. 55, pl. 7, figs. 1–3) is too finely ribbed and probably belongs to another species, as may some of his later examples (Collignon 1964, pl. 318, fig. 1358; pl. 319, figs. 1370–1372) although topotype specimens show up to 6 ribs in a distance equal to the major whorl diameter. The specimen figured by Cieśliński (1959, p. 35, pl. 3, fig. 7) has distinctly oblique ribbing, suggesting that it belongs to another species.

Re-examination of one of Mantell's figured specimens of *Hamites attenuatus?* (Mantell 1822, p. 122, pl. 23, fig. 13, *non* Sowerby) shows that the original of his fig. 13, BMNH 36573, probably belongs to the present species. It bears the label 'Hamsey'.

Occurrence. S. simplex is a persistent but never common constituent of Middle Cenomanian faunas, occurring all over south-east England, especially in *acutus* and *costatus* assemblage faunas. It also occurs in the Basement Bed faunas of the same age and slightly younger in the south-west. A slightly phosphatized example from Bed C, Humble Point (south Devon), of Upper Cenomanian (*naviculare* Zone) age, may belong to this species, although the ribbing is considerably weakened across the dorsum.

The lectotype of *S. simplex* is from the Craie Chloritée of Mont Saint-Catherine, Rouen, France, which yields a rich *costatus* assemblage fauna. The examples discussed by Wright (1963*a*) are from a slightly higher horizon in the Middle Cenomanian.

Genus PLESIOHAMITES Breistroffer 1947

Type species. Hamites multicostatus (Brown 1837), by original designation (Breistroffer 1947, p. 77).

Discussion. This name was introduced by Breistroffer (1947, p. 77) as follows:

> *Plesiohamites* Breistr. nov. subgen.-S.G.-T. *Hamites multicostatus* Brown 1837 ex Spath 1941 (Amm. Gault, part 14, 648, pl. 71, fig. 16). Sous-genre de *Stomohamites*, caractérisé par ses cloisons lytocératiformes et son port de *Diplomoceras*. Une prémutation de l'Hystérocératien super. d'Entrèves-en-Bagues annonce déjà l'espèce du Vraconien d'Angleterre.

According to the *International Code of Zoological Nomenclature* (Stoll 1964), a nominal species, once selected as type of a genus remains the type, even if the specimen used as example is subsequently referred to another species. The type species, and hence the genus is thus based on the original of *Hamites* sp. Mantell 1822, p. 123, pl. 23, fig. 5, BMNH 36572, = Brown 1837, p. 3, pl. 2, fig. 9, refigured here as Plate 3, fig. 10. As Casey has shown (1961, p. 92, footnote), Mantell's specimen is quite different from other material referred to this species by Spath (1941, p. 648, fig. 236) in its finer, denser, sharper, more oblique ribbing, whilst it is from the Lower Chalk of Hamsey, and probably of Lower Cenomanian age. It is quite indeterminate generically, so that *Plesiohamites* is a *nomen dubium* at present.

Plesiohamites multicostatus (Brown)

Plate 3, fig. 10

1822 *Hamites* sp. Mantell, p. 123, pl. 23, fig. 5.
1837 *Hamites multicostatus* Brown, p. 3, pl. 2, fig. 3.
1898 *Hamites* sp.; Crick, p. 62.
non 1921 . . . a species indistinguishable from the Maastrichtian *Diplomoceras cylindraceum*; Spath, p. 251.
1941 *Hamites* (*Stomohamites? multicostatus* Brown; Spath, pp. 648–650 (pars), fig. 236*a*, *b* (*non c–f*, *non* pl. 71, figs. 15–17).
1961 *Hamites multicostatus* Brown; Casey, p. 92, footnote.
non 1962 *Hamites* (*Plesiohamites*) *multicostatus* (Brown); Wiedmann, p. 183, fig. 41.

The quite different Cambridge Greensand material with a lytoceratid suture (Wiedmann 1962, p. 183) has been renamed *Lytohamites similis* Casey (1961, p. 92, footnote). The nature of '*H.*(*P.*). *multicostatus*' Brown of Wiedmann (1962, p. 183, fig. 41) and of *H.*(*P.*). *sulcatostriata* Wiedmann (1962, p. 182, pl. 10, figs. 4, 5; pl. 13, figs. 5, 6; text-figs. 42, 43) remain to be established. They appear to be *Lytohamites*.

Family BACULITIDAE Meek 1876

Two baculitid genera occur in the British Cenomanian: *Lechites*, which is a survivor from the Upper Albian, and *Sciponoceras*.

Lechites is rare. Most examples from south-west England are derived from the underlying Albian, but a few undoubted Lower Cenomanian specimens are known.

Sciponoceras is more important; there seems no doubt that it is derived from *Lechites*; indeed, intermediates occur in the *dispar-perinflatum* Subzone of Dorset. A number of undescribed species occur in England, the genus ranging throughout the Cenomanian and up into the Turonian. *Baculites* appears in the Chalk Rock (Upper Turonian), and is probably directly descended from *Sciponoceras* (Wright, *in litt.*).

In general, *Sciponoceras* is an uncommon genus, except at one level in the Middle Cenomanian. Here, at the top of the *costatus* assemblage fauna, the type species, *S. baculoide*, occurs in vast numbers. This occurrence parallels those reported for *Baculites*, for which a colonial existence on the sea floor has often been suggested (Wright 1957, p. L218).

Genus SCIPONOCERAS Hyatt 1894

(= *Cyrtochilus* Meek 1876 (*non* Jakowlew 1875), *Cyrtochilella* Strand 1929)

Type species. *Hamites baculoide* Mantell (1822, p. 123, pl. 23, figs. 6, 7), by original designation (Hyatt 1894).

Diagnosis. Small or medium-sized baculitids with strong prorsiradiate constrictions. Ornamented by prorsiradiate ribs which are strongest across the venter but weaken and become effaced across the dorsum. The body chamber has strong ventral folds. The aperture is variable. It may be constricted, collared, and lateral lappets and a ventral rostral process occur in some species. The suture is moderately subdivided, with squarish bipartite lobes and saddles.

Discussion. The systematics of this group are in an unfortunate state of confusion. Most material, including that of the type species is fragmentary, crushed, and almost invariably in the form of internal moulds. Such material is difficult to interpret.

The following features have been thought to have systematic importance in the genus: whorl section, frequency and form of constrictions, ribbing and apertural modifications (an important feature according to Wright (*vide* Matsumoto 1959, p. 103)) and, to a lesser extent, sutural pattern. Of these features, the sutures and aperture are lost in most specimens.

Occurrence. Sciponoceras has a world-wide distribution, and ranges from the uppermost Albian to the Upper Turonian.

Sciponoceras baculoide (Mantell)

Plate 1, figs. 12–18; Plate 2, figs. 1*a*, *b*, 2*a*, *b*, 3*a*, *b*, 4*a*, *b*, 5*a*, *b*; Plate 3, figs. 1*a*, *b*, 2, 8, 11; Plate 4, fig. 14

1822 *Hamites baculoide* Mantell, p. 123, pl. 23, figs. 6, 7.
1828 *Baculites obliquatus* J. de C. Sowerby, p. 186, pl. 592, figs. 2, 3.

Types. When introducing this species, Mantell (1822, p. 123) was clearly in possession of, or had examined many specimens, of which he figured 3, a single straight fragment (pl. 23, fig. 7) and a small block with fragments of 2 individuals, one a straight portion, the other an apertural fragment (pl. 23, fig. 6). The large specimen on this block, BMNH 8612, is here designated lectotype.

Diagnosis. A slowly expanding species of *Sciponoceras*, with a laterally compressed oval whorl section, tapering slightly ventrally. There are strong, oblique prorsiradiate constrictions, deepest across the venter and effaced dorsally. There is one constriction in a distance equal to 1·5 or 2 major diameters. The aperture is constricted, with strong oblique ribs developed across the ventral part of the body chamber.

Description. (i) *Lectotype* (Mantell 1822, pl. 23, fig. 6), the larger specimen on BMNH 8612 (Pl. 2, fig. 5*a*). This is of moderate size, expanding slowly, with a compressed, rounded whorl section. The ventral part is ornamented by faint, oblique, prorsiradiate ribs and striae; there are no well-marked constrictions. The last 22 mm of the specimen show accentuated ribbing across the venter, approximately 5 ribs per cm at a whorl height of 8·2 mm. The ribs arise at mid-flank, and pass obliquely across the sides, curving in an adoral direction and then passing straight across the venter. The ribs are projected on the venter, with a gentle adapical slope and a steep adoral slope, giving the ribs a characteristically asymmetric profile.

(ii) *Paralectotype 1*, the other specimen on the same slab as the lectotype. This is a small fragment, with the aperture preserved. It differs from the lectotype in lacking coarse ribbing. The aperture is very finely ribbed and hooded, thus agreeing with fragments figured by Matsumoto and Obata (1963, pl. 2, figs. 1, 3).

(iii) *Paralectotype 2* (Mantell 1822, pl. 23, fig. 7), BMNH 36576*a*, bearing Mantell's original label (Pl. 3, fig. 11). This is a typical composite mould. The specimen is of moderate size, slowly expanding, with a compressed whorl section and rather weak constrictions, one in a distance equivalent to just under twice the major whorl diameter. The most obvious constriction is at the anterior end. It is broad, oblique,

prorsiradiate, shallow across the flanks, weakened across the dorsum, and accentuated across the venter. The diameter behind the constriction is slightly greater than in front, producing a scale-like projection. The adoral part of the specimen bears faint, oblique ribs and striae, 25 per cm, with 4 ventral ribs in a distance equal to the major diameter.

Discussion. The fine ribbed apertures discussed above are not typical of this species, as is clear from many specimens from what I take to be the same horizon as the types. Thus a coarse apertural ribbing, similar to that seen on the lectotype and paralectotype 2 is common (e.g. Pl. 2, figs. 3*a*, *b*; Pl. 3, fig. 2; Pl. 4, fig. 14). I have examined about 100 specimens from this horizon, both Chalk specimens and phosphatized material from Buckland Newton (Dorset) (Pl. 1, figs. 17, 18), and coarse ornament predominates.

As well as a ventral hood, there is a pronounced ventral constriction, as can be seen from one of Sowerby's syntypes of *Baculites obliquatus*, a synonym (J. de C. Sowerby 1828, pl. 592, fig. 2) (Pl. 1, fig. 12; Pl. 2, fig. 3*a*, *b*).

I have not attempted a synonymy of this species other than for material I have examined. The most extensive published synonymy is that given by Matsumoto (1959; see also Matsumoto and Obata 1963).

Sciponoceras baculoide differs from other species of the genus as follows:

S. roto Cieśliński (1959, p. 39) has a subcircular whorl section, and is smooth between rather distant constrictions (1 per 3 diameters).

S. glaessneri Wright (1963*a*, p. 599) has closer-spaced constrictions, is more inflated, and lacks distinct ventral ribs.

S. subbaculoides (Geinitz) (1875, p. 281, pl. 63, fig. 1) is probably best regarded as a *nomen dubium*; the specimen actually figured by Geinitz is a compressed, obliquely ribbed fragment, perhaps belonging to *S. gracile* (Shumard) (1861; Wright 1963*a*, p. 600).

Other, later, species are discussed by Matsumoto (1959) and Matsumoto and Obata (1963); there is a striking similarity between specimens of *S. kossmati* (Nowak) and large individuals of *S. baculoide*.

Occurrence. With fragments it is difficult to name species with certainty, but true *S. baculoide* occurs mainly in the lower part of the *rhotomagense* Zone, especially in the *costatus* assemblage fauna, often in large numbers. The species possibly occurs earlier. Several other species occur in the English Cenomanian, with different apertures, whorl sections, and ornament (cf. Wright 1963*a*, p. 599; Crick 1896).

Sciponoceras roto Cieśliński

Plate 3, fig. 7

1960 *Sciponoceras roto* Cieśliński, pp. 39, 75, 89, fig. 14, pl. 4, figs. 10*a–c*.
1963*a* *Sciponoceras roto* Cieśliński; Wright, p. 599.

Discussion. This species is distinctive in its circular whorl section and 1 constriction in a distance equal to about 3 diameters.

Occurrence. S. roto is rather scarce in *carcitanensis* assemblage faunas, especially the phosphatic faunas of the Glauconitic Marl of the Isle of Wight. The types are from the Lower Cenomanian of Poland.

Family ANISOCERATIDAE Hyatt 1900
Genus ANISOCERAS Pictet 1854

Type species. Hamites saussureanus Pictet (1847), by the original designation of Pictet (1854, p. 70).

Diagnosis. The shell is irregularly coiled, initially helical, but with later parts coiled in the same plane. There is a final hook and straight shaft. Ornament consists of transverse ribs which connect ventral and lateral tubercles (which may bear septate spines) in a characteristic 'button and loop' fashion. These are separated by non-tuberculate ribs.

Discussion. Anisoceras differs from *Protanisoceras* Spath (1925*a*) *sensu* Casey (1961, p. 98) in that the latter genus, which is upper Lower Albian to lower Middle Albian, lacks the characteristic looped ribs. *Heteroclinus* Casey (1961, p. 98, footnote), type species *Hamites nodosus* J. Sowerby (1818, p. 430, pl. 216, fig. 3), proposed for Middle Albian anisoceratids (*H. nodosus*, *H. splendens* Spath, and *H. flexuosus* d'Orbigny), is closer to *Anisoceras* but still has rather distinctive ribbing and lacks lateral tubercles.

In Britain, *Anisoceras* ranges from Upper Albian to Middle Cenomanian. Adkins (1931) recorded this genus from the Upper Turonian of west Texas, whilst Clark (1965) suggested that *Allocrioceras hazzardi* Young (1963, p. 44, pl. 6, figs. 1, 4, 9) may be an *Anisoceras*. This species is from the Upper Turonian, and reference to *Anisoceras* seems unlikely; the type figures and descriptions are insufficient for comment.

Occurrence. Anisoceras has a world-wide distribution in the Upper Albian and Cenomanian.

Anisoceras auberti (Pervinquière)

Plate 3, figs. 3*a*, *b*, 4*a*, *b*, 9*a*, *b*

1907 *Hamites* (*Anisoceras?*) *auberti* Pervinquière, p. 85, pl. 3, fig. 32.
1939 *Anisoceras auberti* (Pervinquière); Spath, p. 558.
1951 *Anisoceras auberti* (Pervinquière); Wright and Wright, p. 14.

Holotype. By monotypy, the original of Pervinquière 1907, pl. 3, fig. 32, from the Cenomanian of Toukabeur, Tunisia.

Diagnosis. This is a compressed, finely ribbed *Anisoceras* with 12–13 fine, sharp ribs in a distance equal to the whorl height. 1–4 ribs are connected across the venter by low, clavate, ventral tubercles separated by 2–4 non-tuberculate ribs.

Description. The whorl section is compressed, with rounded dorsum, broadly rounded flattened sides and a rounded, arched venter. There are 12–13 fine, rather sharp ribs in a distance equal to the whorl height. The ribs are approximately the same width as the interspaces. They are weak, and curved slightly forwards across the dorsum,

passing slightly obliquely forwards across the flank and then straight across the venter. There are long, low, clavate ventro-lateral tubercles along each side of the venter. These join 2, 3, or sometimes 4 ribs, and are connected across the venter by a similar number of ribs, in typical *Anisoceras* 'button and loop' fashion.

Between each tuberculate group there are between 1 and 4 non-tuberculate simple ribs, which are continuous across the venter.

Dimensions.

	Breadth	*Height*	*Ribs*
BMNH 89099:	12·0 mm	15·5 mm	12
	12·5 mm	17·0 mm	13

Discussion. As pointed out by Spath (1939, p. 558), the English material differs from the type in the presence of fine, non-tuberculate ribs. Pervinquière's specimen appears to be part of the final hook, and shows simplification of ribbing in the largest preserved portion, so that reference of the present material to this species appears reasonable.

This is a very distinctive species, differing from *Anisoceras plicatile* (J. Sowerby) in the finer ornament, more compressed whorl section, absence of lateral tubercles and arched venter. *A. plicatile* retains a helicoid element in its coiling to a much greater size. *A. auberti* differs from *Anisoceras* sp. nov. (Spath 1939, p. 55) in having finer ribbing and a more compressed whorl section.

Occurrence. A. auberti is rare in the Lower Cenomanian *carcitanensis* assemblage phosphatized faunas of the Glauconitic Marl of the western part of the Isle of Wight, Warminster (Wilts.), and Stour Bank (Dorset).

Anisoceras plicatile (J. Sowerby)

Plate 3, figs. 12, 13; Plate 4, figs. 1–3

1819 *Hamites plicatilis* J. Sowerby, p. 281, pl. 234, fig. 1.
1822 *Hamites plicatilis* J. Sowerby; Mantell, p. 121, pl. 23, fig. 2.
1822 *Hamites armatus* J. Sowerby; Mantell, p. 122, pl. 23, figs. 3, 4.
1939 *Anisoceras plicatile* (J. Sowerby); Spath, p. 558, fig. 196*e–h*.
1951 *Anisoceras plicatile* (J. Sowerby); Wright and Wright, p. 14.
1959 *Anisoceras plicatile* (J. Sowerby); Cieśliński, p. 36, pl. 4, fig. 2.
1964 *Anisoceras plicatile* (J. Sowerby); Collignon, p. 8, pl. 319, figs. 1363, 1364.
?1965 *Anisoceras* aff. *plicatile* (J. Sowerby); Clark, p. 27, pl. 1, figs. 15, 16.

Lectotype. Here designated, the specimen figured by J. Sowerby (1819, p. 23, pl. 234, fig. 1) from the 'Chalk Marl at Bishopstow, near Warminster'. This specimen is lost (cf. Spath 1939, p. 557). Another specimen, BMNH 44000, referred by Sowerby to this species is available for lectotype designation, but according to Spath (1939, p. 557) this is transitional to *A. pseudoelegans* Pictet and Campiche. The present interpretation is based on Sowerby's figure, and the closely similar specimens figured by Mantell (1822, pl. 23, figs. 1–4), refigured (in part) as Plate 4, figs. 1–3, and numerous uncrushed specimens.

Diagnosis. A medium-sized *Anisoceras*, torticone to an advanced state, with circular whorl section and ornament of fine, dense, rounded ribs, 12 in a distance equal to the whorl height. These join up in twos and threes to mid-lateral and ventral spines. The

spines are septate, and appear as flat-topped tubercles on internal moulds. These grouped ribs are separated by 2 or 3 non-tuberculate ribs.

Description. The whorl section is circular, with 12 ribs in a distance equal to the whorl height. The ribs are fine, rounded, and narrower than the interspaces. They curve forwards across the dorsum, sweep backwards across the flank, and pass straight across the venter. There are 4 rows of septate spines. The mid-lateral and ventral spines appear as flat-topped tubercles on internal moulds. 2 or sometimes 3 ribs join to each lateral tubercle, and a similar number connect in 'button and loop' fashion to the ventral tubercle, and connect these across the venter. Sometimes a broad, low, rounded swelling connects the ventral tubercles. There are from 1 to 3 non-tuberculate ribs between each tuberculate group.

Discussion. The flattened summits of tubercles seen on internal moulds are the scar left at the base of the long, adorally inclined ventral spines, and the blunter lateral spines. As noted by Spath (1939, p. 557), torticone coiling is present to a larger diameter than in most species of *Anisoceras*. After this coiled portion, at least 2 straight shafts are present. This species is quite distinct from any other occurring in the British Cenomanian.

Occurrence. A. plicatile is frequent in the lower part of the *rhotomagense* Zone Lower Chalk of south-east England, and in the Basement Beds of this age in south-west England.

Anisoceras aff. *picteti* Spath

Plate 3, fig. 6; Plate 7, figs. 10*a–c*

cf. 1939 *Anisoceras picteti* Spath, p. 554, fig. 194, pl. 59, fig. 4; pl. 62, fig. 8; especially pl. 63, figs. 3, 4, 8 (with synonymy).

Discussion. Fragments of a coarsely ornamented Lower Cenomanian *Anisoceras* agree most closely with Spath's Upper Albian species. They are most like forms from the *dispar* Zone, but differ in the complete absence of intermediate ribs and looping. They clearly represent the result of a continuation of a trend seen in *dispar–perinflatum* Subzone material. I have referred to these specimens as *A.* aff. *picteti* rather than *A.* aff. *perarmatum* Pictet and Campiche because of their greater compression, narrower venter, and more prominent tuberculation than is seen in that species.

Occurrence. Rare in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight. GSM 108810 is from the *saxbii* assemblage fauna of the Wilmington Sands Basement Bed.

Anisoceras armatum (J. Sowerby)

Plate 5, fig. 11

1817 *Hamites armatus* J. Sowerby, p. 153, pl. 168.
1939 *Anisoceras armatum* (J. Sowerby); Spath, pp. 543–548, pl. 59, fig. 1; pl. 61, figs. 9–11; pl. 62, fig. 5; text-fig. 191 (with synonymy).

Discussion. Occasional *Anisoceras* fragments from the Lower Chalk belong to Sowerby's species, comparing well with the type in the Oxford University Museum (OUM K675*a*, counterpart K675*b*, ex. Buckland Collection).

Occurrence. Rare in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl, Isle of Wight.

Genus IDIOHAMITES Spath 1925

Type species. Hamites tuberculatus J. Sowerby (1818, p. 50, pl. 216, fig. 5), by original designation (Spath 1925*a*).

Diagnosis. The shell is coiled in a single plane, initially an open spiral, followed by 2 sub-parallel shafts in some forms. The ornament consists of straight or slightly oblique ribs, effaced on the dorsum, with paired septate ventral spines. These appear as tubercles on internal moulds, and are present on some or all ribs. They are connected across the venter by a broad rib, sometimes showing incipient looping. Lateral tubercles may be developed. The suture is simple, with broad bifid elements.

Discussion and occurrence. Idiohamites appears in the Upper Albian and ranges into the Lower Cenomanian.

Idiohamites is readily separated from *Anisoceras* by the association of only 1 lateral rib with the tubercles, although some specimens of *Idiohamites* show incipient looping across the venter. *Allocrioceras* has helically coiled early and sometimes later whorls. *Algerites* has closely coiled early whorls, but is so poorly known that further material is needed for a full discussion. It is very densely ribbed, but may not prove separable from *Idiohamites*.

Previous workers on *Idiohamites* have used whorl section, ribbing density, and relations of tuberculate and non-tuberculate ribs as criteria of interspecific importance. In one of the few cases where large numbers of specimens have been studied, Swensen (1963, see also Clark 1965, pp. 29, 30) found that individuals of *Idiohamites varians* (Scott) have very different combinations of tuberculate and non-tuberculate ribs at different growth stages. Thus some specimens had tubercles on every rib, whilst others had up to 6 non-tuberculate ribs between each tuberculate rib.

Most other species are based on small fragments. Available material from England is usually less than 5 cm long, so that introduction of new taxa on the basis of ribbing and tuberculation is of little value. The distinctions within the group of *I. collignoni*, *I. ellipticus*, and *I. ellipticus radiatus* or the group of *I. alternatus* and *I. alternatus vectensis* are thus probably of little real value.

Idiohamites ellipticus ellipticus (Mantell)

Plate 4, fig. 12

1822 *Hamites ellipticus* Mantell, p. 122, pl. 23, fig. 9.
non 1840 *Hamites ellipticus* Mantell; Geinitz, p. 41.
non 1841 *Hamites ellipticus* Mantell; Roemer, p. 93, pl. 14, fig. 5.
non 1843 *Hamites ellipticus* Mantell; Geinitz, p. 9, pl. 1, fig. 7.
non 1872 *Hamites ellipticum*; Schlüter, p. 100, pl. 30, figs. 11, 12; pl. 43, figs. 1, 2.
non 1874 *Helicoceras ellipticum* (Mantell); Geinitz, p. 194, pl. 35, figs. 13–16.
non 1896 *Crioceras ellipticum* (Mantell); Woods, p. 84, pl. 3, figs. 8–10 (= *Allocrioceras woodsi* Spath).
1939 *Idiohamites ellipticus* (Mantell); Spath, pp. 595, 598.
1951 *Idiohamites ellipticus* (Mantell); Wright and Wright, p. 14.
?1959 *Idiohamites ellipticus* (Mantell); Cieśliński, p. 36, pl. 4, figs. 3*a*, *b*.

Holotype. By monotypy, the original specimen figured by Mantell (1822, pl. 23, fig. 9), from the Chalk Marl (Lower Cenomanian) of Middleham, Ringmer, near Lewes (Sussex); BMNH 8611. This is refigured as Plate 4, fig. 12.

Diagnosis. A compressed *Idiohamites* with rounded, flexuous ribs, weakened across the dorsum. There are 7 ribs in a distance equal to the whorl height. Most bear small rounded or transversely elongate tubercles.

Description. The holotype is a well-preserved composite internal mould in grey chalk marl. It is part of the initial flat open spiral. The whorl section is compressed, with flat sides, a rounded dorsum and a rounded venter in intercostal section. There are 7 flexuous ribs in a distance equal to the whorl height. These ribs are rounded, narrower than the interspaces, and slightly weakened across the dorsum. They flex gently forwards across the lower flank, and sweep backwards across the upper flank and ventro-lateral shoulder, to the ventral tubercles. Most ribs bear tubercles. At first these are rounded, but with increasing size they become transversely elongate. Occasional ribs are non-tuberculate. The tubercles are joined across the dorsum by a broad, subdued rib.

Dimensions of holotype.

	Wh	*Wb*	*Ribs*
(*a*)	12·0 mm	7·0 mm	7
(*b*)	7·0 mm	4·0 mm	7

Discussion. This is a rather rare species of *Idiohamites*, differing from *I. alternatus* in having finer, more flexuous ribs, few of which are non-tuberculate. It is also more compressed. *I. ellipticus ellipticus* differs from *I. collignoni* Spath (see below) in having flexuous ribbing, and tubercles on most ribs.

I. vohipalensis Collignon (1964, p. 8, pl. 319, figs. 1366, 1367) is rather more inflated than *I. ellipticus ellipticus* with coarser ribbing (5 ribs in a distance equal to the whorl height) and a siphonal groove, where the ribbing is interrupted. The figures of Cieśliński (1959) are too poor for comment.

Occurrence. I. ellipticus ellipticus is rare in the phosphatized *carcitanensis* assemblage fauna of the Glauconitic Marl of the Isle of Wight, Stour Bank (Dorset), and Warminster (Wilts.). It also occurs in the Glauconitic Marl and basal Chalk Marl around

Lewes (Sussex). It (or a closely related form) is an extremely rare member of the *saxbii* assemblage fauna of the Basement Bed of the Wilmington Sands at Hutchin's (Waterworks) Pit, Wilmington (south Devon).

Idiohamites ellipticus radiatus Spath

Plate 4, figs. 6, 13*a*, *b*, 17

1910 *Hamites alternatus* Mantell, var.; Pervinquière, p. 181, pl. 1, fig. 27 only.
1939 *Idiohamites ellipticus* var. *radiatus* Spath, p. 598.
1951 *Idiohamites ellipticus* var. *radiatus* Spath; Wright and Wright, p. 14.
1955 *Idiohamites ellipticus* var. *radiatus* Spath; Sornay, p. 11.

Lectotype. The specimen figured by Pervinquière (1910, pl. 1, fig. 27 only). This variety was erected by Spath (1939, p. 598) as follows: 'A variety of *I. alternatus*, on the other hand, figured by Pervinquière (1910, p. 18, pl. 1, fig. 27) with tubercles at the extremity of all the ribs and also found at Ventnor (BM no. 36627*b*), is probably a distantly-ribbed variety of *I. ellipticus* Mantell; it may be named var. *radiata* nov.'

This is a common way of introducing new species used by Spath (e.g. 1926*b*, pp. 430–432), involving the citation of a previously figured specimen (usually from outside England) and material in the British Museum or Survey Collection. The figured specimen and the other, usually unfigured specimen or specimens, rank as syntypes, and lectotype designation is necessary.

Diagnosis and description. This is a variety of *I. ellipticus* with straight ribs rather than the flexuous ribs of *I. ellipticus ellipticus*. There are 5 ribs in a distance equal to the whorl height. Each rib bears clavate ventral tubercles.

Discussion. Features separating this variety from the typical form are contained in the diagnosis. The presence of tubercles on every rib separates this form from *I. collignoni*. *I. vohipalensis* (Collignon 1964, p. 8, pl. 319, figs. 1366, 1367) is very closely related, but is slightly more inflated and has a siphonal depression cutting the ribs. None of the American species of *Idiohamites* resemble *I. ellipticus radiatus* or the typical form.

Occurrence. The lectotype is from the Lower Cenomanian of Berrouaghia or Aumale (Algeria), associated with '*Acanthoceras*' *martimpreyi*. The Ventnor paralectotype is a phosphatic internal mould from the *carcitanensis* assemblage fauna of the Glauconitic Marl, where the species is rare. It also occurs at the same horizon at Stour Bank (Dorset), accompanying the typical form.

Idiohamites collignoni Spath

Plate 4, figs. 4, 16*a*, *b*

1931 *Hamites alternatus* Mantell; Collignon, p. 53, pl. 5, fig. 27 (*non* Mantell).
1939 *Idiohamites collignoni* Spath, p. 598.
1955 *Idiohamites collignoni* Spath; Sornay, p. 11.
1964 *Idiohamites collignoni* Spath; Collignon, p. 9, pl. 219, figs. 1368, 1369.

Lectotype. The lectotype, here designated, is the original of Collignon 1931, pl. 5, fig. 7, from the Cenomanian (probably Lower Cenomanian) of Diego Suarez, Madagascar.

Diagnosis. A compressed species of *Idiohamites* with 6–7 rursiradiate ribs in a length equivalent to the whorl height. Alternate ribs are tuberculate.

Description. The whorl section is compressed, with flat sides, a rounded dorsum, convergent ventro-lateral shoulders, and a tabulate venter. The greatest breadth is close to the dorsum.

There are 6–7 ribs in a distance equal to the whorl height. The ribs are rounded, and narrower than the interspaces. They are very weak across the dorsum, and pass adapically across the flanks. Some ribs bear rounded to transversely elongate ventral tubercules, connected across the dorsum by a broad rib. Between these tuberculate ribs are 1 (or rarely 2) non-tuberculate ribs, which weaken across the venter.

Discussion. I. collignoni differs from *I. ellipticus* in the regular alternation of tuberculate and non-tuberculate ribs, and from *I. alternatus* in being more compressed and having finer ornament. English specimens differ from the Madagascan material in having only 1 non-tuberculate rib between tuberculate ribs.

Occurrence. The lectotype is from the '"Champs de Tir" de Diego', a locality from which Collignon (1931) recorded Lower, Middle, and probably Upper Cenomanian ammonites. Subsequently (1964, p. 9) Collignon recorded this species from the Lower Cenomanian Zone of '*Mantelliceras martimpreyi*'. In England, this species occurs as a rarity in the *carcitanensis* assemblage fauna of the Glauconitic Marl of the Isle of Wight, Warminster (Wilts.), and Stour Bank (Dorset).

Idiohamites alternatus alternatus (Mantell)

Plate 4, figs. 9*a*, *b*; Plate 5, figs. 4*a*, *b*, 6, 7*a*, *b*, 10*a*, *b*

1822 *Hamites alternatus* Mantell, p. 122, pl. 23, figs. 10, 11.
non 1840 *Hamites alternatus* Mantell; Geinitz, p. 41.
non 1842 *Hamites alternatus* Mantell; Geinitz, p. 68, pl. 17, fig. 36.
non 1861 *Anisoceras alternatus* Pictet and Campiche, p. 71, pl. 2, figs. 1*a–d* (*non* Mantell) (= *I. dorsetensis* Spath).
1939 *Idiohamites alternatus* (Mantell); Spath, p. 598.
1951 *Idiohamites alternatus* (Mantell); Wright and Wright, p. 14.
1955 *Idiohamites* sp. ind. gr. *alternatus* (Mantell); Sornay, p. 11, pl. 1, fig. 12.

Holotype. By monotypy, the specimen figured by Mantell (1822, pl. 23, figs. 10, 11) from Middleham, Ringmer, near Lewes (Sussex). It is now lost (cf. Spath 1939, p. 597).

Diagnosis. A coarsely ornamented species of *Idiohamites*, compressed, with 6 alternately tuberculate and non-tuberculate ribs in a length equal to the whorl height. These ribs are effaced across the dorsum.

Description. The whorl section is compressed, with a rather broad, rounded dorsum, and broadly rounded sides. The venter is rounded intercostally and across non-tuberculate ribs, but tabulate across tuberculate ribs. The ribs are strong, rounded, and narrower than the interspaces. The ribs are strongly developed across the flanks, where they are rectiradiate to slightly prorsiradiate. Alternate ribs bear rounded or clavate tubercles, joined across the venter by a broad, flattened rib. Non-tuberculate ribs are continuous across the venter.

Discussion. The coarse ornament of this form is very distinctive. As Spath (1939, pp. 597, 598) noted, this species is closely related to, and probably derived from the *dispar* Zone form *I. dorsetensis* Spath. There is some variation in ornament in *I. alternatus alternatus*. Occasional specimens show incipient looping of ribs across the venter, and a tiny lateral tubercle may be present, indicating the close affinity of *Idiohamites* and *Anisoceras*.

I. fremonti (Marcou) (Clark 1965, p. 28) has less regular tuberculation, generally having 2 or 3 non-tuberculate ribs between tuberculate ribs. *I. varians* (Scott) has more distant ribs (4 in a distance equal to the whorl height) and less regular ribbing. *I. alternatus catenatus* Collignon (1964, p. 8, pl. 319, fig. 1365) has 2 non-tuberculate ribs between tuberculate ribs. This form is based on a single fragment and is only doubtfully separable from *I. alternatus alternatus*.

I. alternatus rigida Sornay (1955, p. 10, pl. 1, figs. 5, 9, 13) is a synonym of *I. alternatus vectensis* Spath (see below), which differs from the typical form in having 4, as opposed to 6 ribs in a length equal to the whorl height. The fragment of *I. alternatus* figured by Sornay (1955, pl. 1, fig. 12) from Djebel Hameima, Tunisia, may be a pathological specimen of this species. The horizon is said to be Upper Albian.

Occurrence. I. alternatus alternatus is uncommon in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight. It also occurs at Stour Bank (Dorset), Lewes (Sussex), and Selborne (Hants), at the same horizon. It (or a closely related form) occurs as a great rarity in the *saxbii* assemblage fauna of the Basement Bed of the Wilmington Sands at Hutchin's (Waterworks) Pit, Wilmington (south Devon).

Idiohamites alternatus vectensis Spath

Plate 4, figs. 5, 7, 8, 10, 11; Plate 5, figs. 1*a*, *b*, 2*a*, *b*, 3, 5, 8, 9

1939 *Idiohamites alternatus* var. *vectensis* Spath, p. 598.
1951 *Idiohamites alternatus* var. *vectensis* Spath; Wright and Wright, p. 14.
1955 *Idiohamites alternatus* var. *rigida* Sornay, p. 10, pl. 1, figs. 5, 9, 13.
?1959 *Idiohamites* sp. B., Cieśliński, pp. 37, 88, pl. 4, figs. 6*a–c*.

Lectotype. Spath based this species on four syntypes, figured here as Plate 5, figs. 1*a*, *b*, 2*a*, *b*, 3, 5; BMNH 36585*a–d*. The best of these, BMNH 36585*a* (Pl. 5, figs. 2*a*, *b*) is here designated lectotype. All the types are phosphatic internal moulds of body chambers from glauconitic sandstone; the locality is given as Warminster (Wilts.). They are probably from the sands and phosphate beds below the Glauconitic Marl of this region, and of low Lower Cenomanian age.

Diagnosis and description. A variety of *I. ellipticus* with 4 ribs in a distance equal to the whorl height.

Discussion. This variety differs from *I. alternatus alternatus* in having 4 instead of 6 ribs in a distance equal to the whorl height. Differences from other *Idiohamites* species are clear from the discussion under *I. alternatus alternatus*. *I. alternatus rigida* Sornay is indistinguishable from this variety. *Idiohamites* sp. B. Cieśliński has a rib-density close to that of *I. alternatus vectensis*. The irregular ornament of the Polish material suggests that it is pathological.

Occurrence. Scarce, accompanying the typical form of the species in *carcitanensis* assemblage faunas all over southern England.

Family TURRILITIDAE Meek 1876

This important heteromorph group appears in the early Middle Albian, and has a world-wide distribution in the Cenomanian. It forms an important element of Lower and Middle Cenomanian faunas, but is rare above this. There have been two extensive discussions of the Turrilitidae, those of Dubourdieu (1953) and Clark (1965).

7 generic or subgeneric taxa have been recorded from the English Cenomanian: *Carthaginites*, *Hypoturrilites*, *Mariella* (*Mariella*), *Ostlingoceras* (*Ostlingoceras*), *Turrilites* (*Turrilites*), *T.* (*Euturrilites*), and *T.* (*Mesoturrilites*). Some of the subgenera are of dubious value.

The origin of the Cenomanian forms is fairly simple. 2 genera, *Ostlingoceras* and *Mariella*, range up from the Albian into the Lower Cenomanian. *Hypoturrilites* arises from some species of *Mariella* around the Albian–Cenomanian boundary (I regard *Hypoturrilites primitivus* Clark as a doubtful antecedent). *Turrilites* (*Turrilites*) arises from another species of *Mariella*, perhaps *M. cenomanensis* (Schlüter) in the middle or upper parts of the Lower Cenomanian. *Carthaginites* is simply a descendant of the Albian genus *Raynaudia*.

Genus CARTHAGINITES Pervinquière 1907

Type species. *Turrilites* (*Carthaginites*) *kerimensis* Pervinquière (1907, p. 101), by original designation.

Diagnosis. Small, smooth turrilitids with reduced sutures. The siphuncle is at the upper, inner angle of the whorl. There is a spiral groove at mid-flank, with a row or rows of tubercles present in some species.

Discussion. *Carthaginites* is an extremely rare genus, and is derived from the Upper Albian genus *Raynaudia*, known only from the type species, *Raynaudia raynaudianus* (Collignon) (1932, p. 19, pl. 1, figs. 22–25, text-figs. 24–26), based on 18 individuals from Mont Raynaud, Madagascar. *Raynaudia* differs from *Carthaginites* in lacking a spiral groove at mid flank and in having the siphuncle at the outer upper whorl angle.

In addition to the type species Dubourdieu (1953, pp. 66–68, pl. 4, figs. 49–52; text-fig. 20) described another species, *C. krorzaensis*, from the Upper Cenomanian of Djebel Ouenza, Algeria, whilst *Turrilites inornatus* (Collignon) (1931, pp. 50, 51, pl. 5, figs. 18, 19; text-fig. 22) based on 2 specimens from the Cenomanian of northern Madagascar also belongs to this genus. Records from Texas are unsubstantiated (Clark 1965, p. 56).

Carthaginites cf. *inornatus* (Collignon)

Plate 8, fig. 3

cf. 1931 *Turrilites inornatus* Collignon, pp. 50, 51, pl. 5, figs. 18, 19; text-fig. 22.

Description. A single small phosphatized internal mould appears to belong to Collignon's species. The specimen is 12 mm high and has a maximum diameter of 8·7 mm. $1\frac{1}{2}$ whorls are continuously preserved, with a further $\frac{1}{2}$ whorl above these. The apical angle is low, the sides are flat, with a prominent spiral median groove and a distinctively flattened lower outer whorl angle. The specimen is wholly septate, but much of the detail of the rather simple sutures has been destroyed by corrosion and abrasion.

Discussion. This fragment is identical with the specimens figured by Collignon, the most complete of which is here designated lectotype (Collignon 1931, pl. 5, fig. 18). In particular, the flattening of the lower outer whorl angle and the spiral groove (best seen on the lectotype) are very similar, as is the suture, so far as these are preserved on my specimen. *C. inornatus* differs from both *C. krorzaensis* and *C. kerimensis* in the absence of tuberculation.

Occurrence. Phosphatized Upper Cenomanian *naviculare* Zone fauna of Bed C, Humble Point (south Devon).

Genus HYPOTURRILITES Dubourdieu 1953

(= *Hypoturrilites* Shimizu 1935, p. 195; Spath 1937, p. 598 [both *nom. nud.*]; *Turrilites* Wright and Wright [1951, p. 17; pars])

Type species. Turrilites gravesianus d'Orbigny, by original designation (Dubourdieu 1953, p. 44).

Diagnosis. Turriliticones, generally sinistrally coiled, with a low spiral angle. The whorls are in contact, the siphuncle is on the upper side of the whorl, the outer faces of the whorls are ornamented by 3–4 rows of tubercles, which may bear hollow, septate spines. The upper row tubercles are larger and fewer than those in the lower rows, which are 2–3 times as abundant. Ribs are developed in some forms, especially when adult. The whorl contacts are generally ornamented by strong grooves and ridges, the latter corresponding to the lowest row of tubercles.

Discussion. Dubourdieu (1953) wrote of 'la rangée inférieur étant formée des tubercles plus gros et moins nombreuse'. For the purpose of description I have followed Sharpe (1857) and Wright (1957, 1963*a*), naming tubercles with respect to the presumed life position of the animal.

Wright (1963*a*, p. 601) described Australian material with long spines. Similar specimens occur occasionally in this country, where the spines are seen to be hollow, with a basal septum, as in *Cheloniceras* (Casey 1961, p. 197, fig. 59) and many other ammonites. The only significance of this modification would seem to be as an aid to flotation. It is still difficult to understand how the mantle could fill these spines and then move out of them as growth proceeded, unless they were never tissue-filled,

being wholly a product of the mantle margin, which secreted the partition as soon as the spine was complete.

Hypoturrilites may reach a large size. Several turrilitids have been described which have ribs and *Hypoturrilites*-like tubercles; this feature seems to have no major systematic importance, for it is developed in some specimens of *H. carcitanensis* (Matheron) and *H. mantelli* (Sharpe). Collignon (1964, p. 13, pl. 315, figs. 1386, 1387) has described a variety of *H. gravesianus* (d'Orbigny) showing this feature.

Occurrence. Hypoturrilites has a world-wide distribution, is most abundant in the Lower Cenomanian, but also occurs in the Middle and Upper Cenomanian.

Hypoturrilites gravesianus d'Orbigny

Plate 6, figs. 11 (pars), 12; Plate 10, figs. 4, 5

1814 *Turrilites tuberculatus* J. Sowerby, p. 169, pl. 74 (*non* Bosc).
1822 *Turrilites tuberculatus* Mantell, pl. 24, fig. 6 (*non* Bosc).
1842 *Turrilites gravesianus* d'Orbigny, p. 596, pl. 144, figs. 3–5.
1857 *Turrilites gravesianus* d'Orbigny; Sharpe, p. 62, pl. 25, figs. 7*a*, *b*; pl. 26, fig. 14.
1878 *Turrilites gravesianus* d'Orbigny; Sowerby *in* Dixon, pl. 60, fig. 6 (= Mantell 1842, pl. 24, fig. 6).
?1937 *Turrilites waterloti* Collignon, p. 61, pl. 6, figs. 7, 7*a*.
?1937 *Turrilites boulei* Collignon, p. 67, pl. 6, fig. 20.
1951 *Turrilites gravesianus* d'Orbigny; Wright and Wright, p. 17.
1953 *Hypoturrilites gravesianus* (d'Orbigny); Dubourdieu, p. 44.
1957 *Hypoturrilites gravesianus* (d'Orbigny); Wright, p. L222, fig. 248, 5.
1959 *Turrilites gravesianus* (d'Orbigny); Cieśliński, p. 42, fig. 18.
1963 *Hypoturrilites gravesianus* (d'Orbigny); Renz, p. 1091, pl. 1, figs. 1*a*, *b*.
1963*a* *Hypoturrilites gravesianus* (d'Orbigny); Wright, p. 600, pl. 81, figs. 5*a*, *b*; text-fig. 2.
1964 *Hypoturrilites gravesi* d'Orbigny; Collignon, p. 13, pl. 320, fig. 1386; p. 42, pl. 327, fig. 1462.

Lectotype. D'Orbigny's figured specimen, from Oise, France (Graves Collection), is here designated lectotype.

Discussion. This well-known species is readily distinguished from *H. tuberculatus* (Bosc) by its fewer, larger, uppermost tubercles (10–12 per whorl as against 20 in *H. tuberculatus*), paired lowest rows of tubercles, larger apical angle, and suture line. The suture has a large, asymmetric first lateral saddle (Sharpe 1857; Wright 1963*a*) (Pl. 10, fig. 4).

In small fragments, *H. gravesianus* has 2 large and 4 small tubercles in a distance equal to the exposed whorl height. *H. tuberculatus* has 3 large and 5–6 small tubercles in the same distance. Wright (1963*a*) stated that the lower tubercles are 4–5 times as numerous as those in the upper row in *H. gravesianus*. This is an error.

H. schneegansi Dubourdieu (1953, p. 63, pl. 4, figs. 34–41), based on minute pyritic fragments, is close to *H. gravesianus*. It differs mainly in the disposition of the lower rows of tubercles. The sutures of the two species are similar, but the great difference in size makes comparison difficult.

H. gravesi betaitrensis Collignon (1964, p. 13, pl. 320, figs. 1387, 1388) has ribs on the upper part of the exposed part of the whorl, arising from the larger tubercles, and also occurring between them.

H. waterloti (Collignon) (1937, p. 61, pl. 6, figs. 7*a*, *b*), based on the unique holotype, is close to *H. gravesianus*, and may indeed be identical, the differences being due to its small size.

H. boulei (Collignon) (1937, p. 67, pl. 6, fig. 20) has initial whorls close to the present species but lacks the lower rows of tubercles. The peculiar ornament of later parts of this species suggests that it is a pathological *Hypoturrilites* of the *gravesianus* group. It is best treated as a *nomen dubium*.

Occurrence. *H. gravesianus* is common in the Lower Cenomanian, especially in the *carcitanensis* faunas of the Glauconitic Marl of the Isle of Wight. Occasional specimens occur at higher levels, e.g. I have 1 specimen from the Upper Cenomanian Chalk Basement Bed at Askerswell (Dorset). Peake and Hancock (1961, p. 301) recorded this species from the Totternhoe Stone of Norfolk and Cambridge (*rhotomagense* Zone). *H. gravesianus* has a wide distribution outside England (Europe, India, Madagascar, North America, Australia).

Hypoturrilites mantelli (Sharpe)

Plate 7, figs. 1, 5*a*, *b*

1857 *Turrilites mantelli* Sharpe, p. 63, pl. 25, figs. 5, 6*a*, *b*.
1862 *Turrilites mantelli* Sharpe; Pictet and Campiche, p. 155.
1876 *Turrilites mantelli* Sharpe; Schlüter, p. 134, pl. 37, fig. 9; pl. 38, figs. 11, 12.
1951 *Turrilites mantelli* Sharpe; Wright and Wright, p. 17.
1959 *Turrilites mantelli* Sharpe; Cieśliński, p. 43, fig. 19.
1963 *Hypoturrilites mantelli* (Sharpe); Renz, p. 1092, pl. 1, figs. 4, 9*a*, *b*.
?1964 *Hypoturrilites mantelli* Sharpe; Collignon, p. 42, pl. 329, fig. 1472.

Lectotype. By subsequent designation of Wright and Wright (1951, p. 39), BMNH 32568, the original of Sharpe 1857, p. 63, pl. 25, fig. 5, from the Lower Chalk (probably *mantelli* Zone), near Lewes (Sussex).

Diagnosis. A *Hypoturrilites* with about 30 tubercles in the uppermost row and about 35 tubercles in 3 lower rows.

Description. The lectotype is a well-preserved composite internal mould in grey limestone. It is sinistral, turriliticone, with the whorls in contact throughout. The upper part of the whorl face is slightly convex and inclined, the outer face is flattened to somewhat concave.

There are 4 rows of tubercles, 30 in the uppermost row and 35 in the lower 3 rows. The tubercles in the upper row are transversely elongate, and lie just above mid-flank. They are separated by a spiral depression from 2 rows of smaller, clavate tubercles, with a third tubercle at the whorl contact. The tubercles are connected and separated by oblique transverse striae.

The basal surface of each whorl is ribbed, the ribs corresponding to the lowest series of tubercles; each rib fits into a groove on the succeeding whorl.

Discussion. This species is readily distinguished from other *Hypoturrilites* by the many tubercles in the upper row and only slightly more in the lower rows. The specimen figured by Renz (1963) with an equal number of tubercles in all rows

may be transitional to *Mariella*; the specimen figured by Collignon (1964) has more tubercles in the lower 3 rows, and may be closer to, or transitional to, *H. tuberculatus*.

Occurrence. Scarce in the lower part of the *mantelli* Zone all over southern England. Also known from France, Germany, Switzerland, Poland, and Madagascar.

Hypoturrilites carcitanensis (Matheron)

Plate 6, figs. 1, 2, 4–10

1842 *Turrilites carcitanensis* Matheron, p. 267, pl. 12, fig. 4.
1857 *Turrilites morrisii*; Sharpe, p. 65, pl. 26, figs. 4–8.
?1866 *Turrilites tuberculatus* Stoliczka, p. 187, pl. 87, figs. 6–8 (*non* Bosc).
1876 *Turrilites morrisii* Sharpe; Schlüter, p. 134, pl. 38, fig. 10.
1910 *Turrilites morrisii* Sharpe; Pervinquière, p. 56, pl. 5, figs. 18–20.
1928–1929 *Turrilites morrisii* Sharpe; Collignon, p. 59, pl. 6, figs. 4, 5.
1940 *Turrilites carcitanensis* Matheron; Fabre, p. 242, pl. 5, fig. 7.
1951 *Turrilites carcitanensis* Matheron; Wright and Wright, p. 17.
?1953 *Hypoturrilites oberlini* Dubourdieu, p. 39, pl. 4, figs. 27–30.
1964 *Hypoturrilites carcitanensis* (Matheron); Collignon, p. 12, pl. 320, figs. 1382–1385.
1964 *Hypoturrilites* aff. *carcitanensis* (Matheron); Collignon, p. 52, pl. 321, fig. 1486.
?1964 *Hypoturrilites morrisiformis* Collignon, p. 53, pl. 331, fig. 1490.
?1964 *Hypoturrilites dubourdieui* Collignon, p. 53, pl. 331, fig. 1491.

Holotype. By monotypy, Matheron's specimen (1842, pl. 12, fig. 4), refigured by Fabre (1940, pl. 5, fig. 7), from the Banc des Lombards, Cassis, France. This specimen is in the Natural History Museum, Marseilles, and is probably of Lower Cenomanian age.

Discussion. *H. carcitanensis* is readily distinguished from other species of *Hypoturrilites* by its low (15°) apical angle, concave sides, few, rather distant tubercles in the uppermost row, and the crenulate suture at whorl contacts.

As here interpreted, this species is quite variable. There are from 8 to 11 tubercles in the uppermost row (2–4 in a distance equal to the exposed whorl height) and about twice this number in the lower 3 rows. The uppermost tubercles vary from massive and rounded ('*morrissii*') to fine and pointed ('*carcitanensis*'), and are occasionally linked by a spiral ridge. The lower rows of tubercles show much variation.

In some specimens there is an upper row of elongate tubercles and 2 lower closely spaced rows, the lowest row concealed beneath the whorl contact. In other specimens there is a single transversely elongate tubercle, extending from the lower flank to beneath the whorl contact.

A complete range of transitions between these 2 forms occurs in material from the Glauconitic Marl of the Isle of Wight, and several distinct forms can be recognized. Thus *Turrilites morrisii* Sharpe is a coarsely ornamented form of this species. *Hypoturrilites oberlini* Dubourdieu (based on a single crushed fragment) is merely a specimen of this species with 3 rows of lower tubercles. Large specimens of *H. carcitanensis* tend to develop ribs between, and arising from the large tubercles; *H. morrisiformis* Collignon is such a specimen. *H.* aff. *carcitanensis* Collignon and *H. dubourdieui* Collignon both fall within the variation range of this species as interpreted here. *T. morrisii* Sharpe var. *carcitanensis* Matheron of Collignon (1928–1929, p. 59, pl. 6, fig. 6) = *Turrilites carcitanensis* Matheron var. *antsiramensis*

Breistroffer (Breistroffer *in* Fabre 1940, p. 242) is merely a form with rather more tubercles than usual (18). It is based on 4 small fragments.

English material is chiefly from the condensed Glauconitic Marl. In a fully developed succession, *H. oberlini*, *morrisiformis*, and *dubourdieui* may be recognizable as chronological subspecies (*sensu* Wright and Wright 1949) of *H. carcitanensis*. Specimens from the *saxbii* assemblage faunas of Wilmington (south Devon) and Warminster (Wilts.) (Pl. 7, fig. 2) differ from typical *carcitanensis* in details of ornament, and indicate a higher horizon.

Occurrence. *H. carcitanensis* is frequent in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of Eastbourne (Sussex), the Isle of Wight, and Stour Bank (Dorset). It is widely distributed in Europe, Madagascar, North Africa, and perhaps India.

Hypoturrilites tuberculatus (Bosc)

Plate 6, fig. 11 (pars); Plate 42, fig. 2

1801 *Turrilites tuberculatus* Bosc *in* Buffon, p. 18, pl. 42, fig. 8.
1812 *Turrilites tuberculatus* Bosc; J. Sowerby, p. 169, pl. 74.
1822 *Turrilites tuberculatus* Bosc; Mantell, p. 124, pl. 24, fig. 7.
1842 *Turrilites tuberculatus* Bosc; d'Orbigny, p. 593, pl. 144, figs. 1, 2.
1853 *Turrilites tuberculatus* Bosc; Pictet and Roux, p. 150, pl. 15, fig. 10.
1857 *Turrilites tuberculatus* Bosc; Sharpe, p. 61, pl. 25, figs. 1 (pars), 2,4 (*non* 3); pl. 26, figs. 15, 16.
?*non* 1865 *Turrilites tuberculatus* Bosc; Stoliczka, p. 187, pl. 87, figs. 6–8.
1876 *Turrilites tuberculatus* Bosc; Schlüter, p. 132, pl. 37, figs. 1, 2; pl. 44, fig. 11.
1895 *Turrilites tuberculatus* Bosc; Kossmat, p. 141, pl. 20, figs. 2*a–c*.
?1928–1929 *Turrilites tuberculatus* Bosc; Collignon, p. 64, pl. 6, fig. 14.
1951 *Turrilites tuberculatus* Bosc; Wright and Wright, p. 17.
1959 *Turrilites tuberculatus* Bosc; Cieśliński, p. 44, text-fig. 20.
1963 *Hypoturrilites tuberculatus* (Bosc); Renz, p. 1092, pl. 1, fig. 5.
1964 *Hypoturrilites tuberculatus* (Bosc); Collignon, p. 42, pl. 327, fig. 1463.
1965 *Hypoturrilites tuberculatus* (Bosc); Clark, pp. 50, 51, figs. 18, 19; pl. 19, fig. 9 (?*non* figs. 5, 8).

Discussion. Differences between this species and *Hypoturrilites gravesianus* are discussed on p. 21.

Occurrence. This well-known species is common in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight and elsewhere, and also occurs at higher horizons in the *mantelli* Zone. The geographic range of *H. tuberculatus* includes north-west Europe, southern India (?), and Madagascar. The Texas example figured by Clark (1965, = *Turrilites roemeri* Whitney; for synonomy see Clark) seems only doubtfully referable to this species.

Hypoturrilites tenouklensis (Pervinquière)

1910 *Turrilites tuberculato-plicatilis* Seguenza var. *tenouklensis* Pervinquière, p. 57, pl. 5, fig. 3.

Discussion. A single specimen from the richly fossiliferous ammonite bed at the base of Band 4 (Kennedy 1969), Abbotscliff, Folkestone (Kent), is identical with Pervinquière's figure.

Occurrence. The specimen is from the *Mantelliceras* gr. *dixoni* assemblage, at the top of the Lower Cenomanian. The holotype is from the Cenomanian of Tenoukla, Algeria.

Genus OSTLINGOCERAS Hyatt 1900

Type species. Turrilites puzosianus d'Orbigny (1842, pl. 143, figs. 1, 2), by original designation (Hyatt 1900).

Diagnosis. Tightly coiled turrilitids with a low apical angle, the sides ornamented by dense ribs, with up to 3 rows of fine tubercles at the lower end.

Discussion. Ostlingoceras covers a readily identifiable group of turrilitids, characterized by their delicate ornament and low apical angle, which first appear in the Upper Albian. It is quite distinct from *Turrilites*, and the relationship suggested by Spath (1937, pp. 522, 523) should be rejected.

Occurrence. The genus is known from north-west Europe, north Africa, North America (Texas), and Madagascar. It occurs commonly in the Upper Albian, but is very rare in the Cenomanian.

Ostlingoceras bechii (*Sharpe*)

Plate 8, figs. 9, 11, 13

1857 *Turrilites bechii* Sharpe, p. 66, pl. 26, figs. 13*a*, *b* (as *bechei*).
1861 *Turrilites bechei* Sharpe; Pictet and Campiche, p. 153.
1951 *Ostlingoceras bechei* (Sharpe); Wright and Wright, p. 18.

Holotype. By monotypy, the original of *Turrilites bechii* Sharpe (1857, p. 67, pl. 26, figs. 13*a*, *b*), BMNH 88, from the 'Chalk with siliceous grains at Lyme Regis'.

Diagnosis. Ostlingoceras with a rounded, slightly inflated whorl face, bearing dense, prorsiradiate, slightly flexuous ribs, 6 or 7 in a distance equal to the exposed whorl height. The ribs terminate in a transversely elongate bullate tubercle. There are 3 rows of spirally elongate tubercles beyond the lower termination of each rib; the lowest row lies at the lower whorl contact.

Description. The holotype is a well-preserved internal mould in sandy limestone, partially developed from the matrix. 4 whorls are preserved. The earliest parts of the specimen are septate. It is sinistral, turriliticone, and the whorls are in contact throughout. The outer whorl face is rounded, slightly inflated, and ornamented by numerous faint, transverse, prorsiradiate flexuous ribs, 6 or 7 in a distance equal to the exposed whorl height.

The ribs extend from the upper, crenulate whorl suture to just above the lower suture, where they terminate in a row of faint, transversely elongate tubercles, 1 tubercle corresponding to each rib. Below this tubercle, and displaced slightly apically, are 3 rows of small, rather weak, spirally elongate, rounded, equidistant tubercles. The rows are separated by smooth spiral bands. The lowest of the 3 rows of tubercles lies at the lower whorl suture.

The base of the whorls is convex, rounded, and ornamented by slightly prorsiradiate

rounded ribs, equal in number to those on the outer face of the whorl. The upper surface of the whorl is smooth, with grooves to accommodate the ribs on the base of the preceding whorl.

Differences between *O. bechii* and *O. puzosianum* (d'Orbigny) are well known (see Spath 1937, p. 525). It differs from *O. puzosiforme* Spath in having more inflated sides and 4 as opposed to 3 rows of tubercles. Both *O. davisense* Young (1958*b*, p. 287, pl. 40, figs. 4, 5, 7) and *O. conlini* Clark (1965, p. 37, pl. 8, fig. 4; pl. 9, figs. 2, 6) have a much coarser ornament.

Occurrence. O. bechii is rare in the Lower Cenomanian; the holotype is probably from bed A_2 of the Cenomanian Limestone, probably from Humble Point (south Devon) or close by. There are several other specimens from this area (e.g. BMNH C11721, SMC B35792), probably from the same bed. I have collected this species from the phosphatized *carcitanensis* assemblage fauna of the Glauconitic Marl at Stour Bank (Dorset), and from low in the Lower Cenomanian at Folkestone (Kent).

Ostlingoceras puzosiforme Spath

Plate 7, fig. 6

1857 *Turrilites puzosianus* d'Orbigny var.?; Sharpe, p. 68, pl. 27, fig. 11 (*non* d'Orbigny).
1926*b* *Ostlingoceras puzosiforme* Spath, pp. 429, 431.
1951 *Ostlingoceras puzosiforme* Spath; Wright and Wright, p. 18.

Holotype. By monotypy, the original of *Turrilites puzosianus* d'Orbigny, var., of Sharpe 1857, p. 68, pl. 27, fig. 11 (*non* d'Orbigny), BMNH 50283, from the Chloritic Marl of Bonchurch, near Ventnor, Isle of Wight.

Diagnosis. Ostlingoceras with about 30 fine ribs per whorl, weakened on the middle parts of the outer whorl face, with a row of small tubercles just below mid-flank and 2 rows closer to the lower whorl contact.

Description. The holotype is an indifferently preserved, part-phosphatized internal mould of a single, apparently non-septate whorl. The shell is sinistral, and the whorls are in contact. The outer whorl face is flat, the upper whorl face rounded. There are an estimated 30–33 ribs per whorl. These ribs are distinct on the upper part of the flank, but weaker on the middle parts of the outer face, giving the impression of a shallow spiral groove. Below this, each rib bears a sharp, transversely elongate tubercle, separated by a smooth spiral band from a second set of smaller tubercles, which lie close to a third, rather more rounded set. The ribs continue over the lower face.

Discussion. The differences between *O. puzosiforme*, *O. bechii*, and *O. puzosianum* (d'Orbigny) are discussed by Spath (1937, p. 525). The fine, very flexuous ribs of *O. puzosiforme* are distinctive, as is the spacing of the tubercles, especially the highest, almost at the mid-point of the outer whorl face.

Occurrence. Rare in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight, Wiltshire, and north Dorset.

Ostlingoceras gallienii (Boule, Lemoine, and Thévenin)

Plate 7, figs. 3, 4

1906 *Turrilites puzosianum* d'Orbigny, var. *gallienii* Boule, Lemoine, and Thévenin, p. 60, pl. 14, figs. 4, 5.
1931 *Turrilites gallienii* Boule, Lemoine, and Thévenin; Collignon, p. 47, pl. 5, figs. 15, 16.
1964 *Paraturrilites gallienii* (Boule, Lemoine, and Thévenin); Collignon, p. 12, pl. 315, figs. 1379–1380.

Occurrence. Very rare in the phosphatized *carcitanensis* assemblage fauna of the Glauconitic Marl of Stour Bank, Shillingstone (Dorset). Also known from a unique specimen from the Rifle Butt's pit, Market Weighton (Yorkshire) (WW 23352). The species is best known from Madagascar.

Genus MARIELLA Nowak 1916

Type species. Turrilites bergeri Brongniart (1822), by original designation (Nowak 1916).

Diagnosis. Turrilitids with many low oblique ribs, bearing up to 4 rows of small tubercles.

Discussion. It is quite clear from the *International Code of Zoological Nomenclature* (Art. 57(*d*)) that *Mariella* is not invalidated by *Mariaella* Gray (1833), and the views of Breistroffer (1947), Dubourdieu (1953), and Wiedmann (1962) should be rejected, as should the taxa *Paraturrilites* Breistroffer (= *Mariella* Nowak) and *Paraturrilites* (*Bergericeras*) Wiedmann (= *M.* (*Mariella*) Nowak).

3 subgenera are recognized: *M.* (*Mariella*), with the characters of the genus; *M.* (*Wintonia*), with an uncoiled initial portion, known only from a few examples from Texas (Clark 1965, pp. 49 et seq.); and *M.* (*Plesioturrilites*) (Clark 1965, p. 45), with a prominent spiral groove and a loosely coiled adult whorl.

Only the restricted subgenus *M.* (*Mariella*) occurs in England, where it is known from the Upper Albian and Lower Cenomanian. There are 4 well-established species of this group recorded from the Cenomanian, and several other undescribed forms also occur.

My interpretation of *Mariella* is rather different from that of some previous authors. Thus Dubourdieu (1953) placed *M.* (*M.*) *cenomanensis* (Schlüter) and *M.* (*M.*) *essenensis* (Geinitiz) in *Turrilites* [*sensu stricto*]. This is quite reasonable, as these 2 species are rather different from *M. bergeri*, and, indeed, in terms of ornament *M. cenomanensis* is transitional to *Turrilites*, while *M. essenensis* is transitional to *Hypoturrilites*.

Occurrence. Mariella has a world-wide distribution in the Upper Albian and Lower Cenomanian.

Mariella (*Mariella*) *lewesiensis* (Spath)

Plate 8, figs. 1, 4, 5, 8

1857 *Turrilites bergeri* Brongniart; Sharpe, p. 65, pl. 26, fig. 10 only (*non* Brongniart).
1926*b* *Turrilites lewesiensis* Spath, pp. 429, 431.

1937 *Mariella lewesiensis* (Spath); Spath, p. 512.
1951 *Paraturrilites lewesiensis* (Spath); Wright and Wright, p. 17.
1956 *Paraturrilites lewesiensis* (Spath); Benavides-Cáceres, p. 436, pl. 40, figs. 8, 9.
1964 *Paraturrilites lewesiensis* (Spath); Collignon, p. 51, pl. 321, fig. 1484.

Holotype. By the original designation of Spath (1926*b*, p. 431), the original of *Turrilites bergeri* Brongniart (Sharpe 1857, p. 65, pl. 26, fig. 10) (*non* Brongniart), BMNH 33558, from the 'Chalk Marl, Lewes'.

Diagnosis. Mariella with 4 equidistant rows of tubercles on about 20 slightly oblique ribs per whorl. The tubercles in the uppermost row are larger than those in the other rows; the tubercles of the lowest row are smaller and slightly clavate, and lie at the contact with the whorl below.

Description. The holotype is a slightly distorted composite internal mould in grey chalk. 2 whorls are preserved. The shell is sinistral, turriliticone, with the whorls in contact. The upper, outer face of the whorl is smooth, broad, flat, and gently inclined. The outer face is gently curved, and ornamented by 3 spiral rows of rather large tubercles, 21 per whorl. These are arranged on faint, oblique ribs, so that the tubercles in alternate rows of successive ribs correspond.

The tubercles in the upper 2 rows are rounded, those in the uppermost row being slightly larger than all the others. The tubercles in the third row, the lowest exposed on the outer whorl face, are smaller, and slightly elongate spirally (i.e. clavate). A fourth row of similarly elongate smaller tubercles is present at the lower suture, partially covered, producing crenulations along the whorl contact. The lower whorl surface bears faint radial ribs, each rib corresponding to one of the tubercles in this lowest row.

Discussion. The holotype of this species, not listed by Crick (1898), which Wright and Wright (1951) regarded as missing, is preserved in the British Museum (Natural History). Sharpe's figure is excellent.

The sub-equal tuberculation readily distinguishes *M. lewesiensis* from *M. cenomanensis* and *M. essenensis*. Spath (1937, pp. 512, 513) distinguished *M. lewesiensis* from *M. dorsetensis* (Spath) in that '*M. dorsetensis* (Spath) lacks the uppermost row of tubercles, and is smooth on the concave area covered by the previous whorl'. The type of *M. dorsetensis* appears to be lost, but Sharpe's figure (1857, pl. 26, fig. 11) shows that it also has 4 rows of tubercles. At present I am inclined to regard *dorsetensis* as uninterpretable (but see Collignon 1964, p. 51, pl. 331, figs. 1482, 1483, and Renz 1963).

Occurrence. Frequent in the lower part of the Lower Cenomanian, especially the basal part of Chalk Marl in Sussex. The species also occurs in the Lower Cenomanian of Madagascar and Peru.

Mariella (*Mariella*) *cenomanensis* (Schlüter)

Plate 8, fig. 10

1857 *Turrilites tuberculatus* Sharpe, p. 61, pl. 14, fig. 3 (*non* Bosc).
1876 *Turrilites cenomanensis* Schlüter, p. 131, pl. 37, figs. 6–8.
1926*b* *Turrilites cenomanensis* Schlüter; Spath, p. 429.

?1929 *Turrilites* cf. *cenomanensis* Schlüter; Collignon, p. 62, pl. 6, fig. 10.
1951 *Paraturrilites cenomanensis* (Schlüter); Wright and Wright, p. 16.
1953 *Paraturrilites cenomanensis* (Schlüter); Dubourdieu, p. 52 etc.
1959 *Paraturrilites cenomanensis* (Schlüter); Cieśliński, p. 40, fig. 15.
?1964 *Paraturrilites cenomanensis* (Schlüter); Collignon, p. 54, pl. 331, fig. 1492.

Lectotype. The larger of the 2 specimens figured by Schlüter (1876, pl. 37, fig. 6) is designated as lectotype of this species.

Discussion. The large size of the tubercles in the uppermost row, and the close spacing of the tubercles in the lowest 2 rows, together with their pronounced elongation, characterize this species.

Occurrence. Frequent in the lower part of the *mantelli* Zone all over southern England; Lower Cenomanian of western Europe, North Africa, and Madagascar.

Mariella essenensis (Geinitz)

1849–1850 *Turrilites essenensis* Geinitz, p. 122, pl. 6, figs. 1, 2.
1857 *Turrilites bergeri* Sharpe, p. 65, pl. 26, fig. 9 only (*non* Brongniart).
1858–1864 *Turrilites essenensis* Geinitz; Pictet and Campiche, p. 153.
1876 *Turrilites essenensis* Geinitz; Schlüter, p. 10, pl. 37, figs. 3–5.
1926*b* *Turrilites essenensis* Geinitz; Spath, p. 429.
1951 *Paraturrilites essenensis* (Geinitz); Wright and Wright, p. 16.
1959 *Paraturrilites essenensis* (Geinitz); Cieśliński, p. 41, fig. 16.

Discussion. Geinitz's figure shows a *Mariella* with 3 rows of tubercles on the exposed whorl face, as do Schlüter's. There are indications of a strongly crenulate suture at the whorl contact, and strong ribbing on the upper and lower whorl surfaces, with a tubercle-like development at the outermost part of these ribs.

Schlüter's figures also show the uppermost row of tubercles to be larger than those in the other rows. The main difference from *M. lewesiensis* is thus the presence of 3 rather than 4 distinct rows of tubercles.

Occurrence. This species is not uncommon in the phosphatized *carcitanensis* faunas of the Glauconitic Marl of the Isle of Wight, and Stour Bank (Dorset).

Genus TURRILITES Lamarck 1801
(including EUTURRILITES Breistroffer 1953)

Type species. Turrilites costatus Lamark 1801, by original designation.

Diagnosis. Closely coiled turrilitids with low apical angle. There are strong ribs on the upper part of the exposed whorl side, and several rows of tubercles below, corresponding to the ribs.

Discussion. As well as *T.* (*Turrilites*), 2 other subgenera have been recognized. *T.* (*Euturrilites*) Breistroffer (1953) (type species *T. scheuchzerianus* Bosc = *Turbinites* Dubourdieu (1953) [*non* Martin 1809]), is ornamented by ribs only. As far as I am aware, only the type species is referred to this subgenus, which appears to be rather

superfluous (cf. Reyment 1955, p. 13). *T.* (*Mesoturrilites*) Breistroffer (1953) differs from the restricted subgenus in the suppression of the ribbing and a tendency for the tubercles to become linked into a spiral ridge.

The range of *Turrilites* is from the upper part of the Lower Cenomanian to the 'Lower Turonian' (Roman and Mazerin 1913).

Turrilites (*Turrilites*) *costatus* Lamarck

Plate 6, fig. 3; Plate 8, figs. 12, 14

1799 corne d'ammon turbineé; Montfort, p. 147, figs. 1, 3, 4.
1801 *Turrilites costata* Lamarck, p. 102.
1904*a* *Turrilites costata* Lamarck; Douvillé, pp. 54, 54*a*, 54*b*.
1925 *Turrilites costatus* Lamarck; Diener, p. 81 (with synonymy).
1962 *Turrilites costatus* Lamarck; Wiedmann, p. 192 (with synonymy).
1963*a* *Turrilites costatus* Lamarck; Wright, p. 601, pl. 81, fig. 4.
1965 *Turrilites* (*Turrilites*) *costatus* Lamarck; Clark, p. 53, figs. 20*a*, *b*; pl. 20, figs. 1, 2, 7, 8.

Discussion. Douvillé (1904*a*, p. 54*a*, fig. 1) figured a specimen from the Lamarck Collection as 'type' of this species; since Lamarck mentioned the species from several localities and several collections, this specimen is here designated lectotype.

Extensive synonymies have been given by Diener (1925) and others. *Turrilites triplicatus* J. Sowerby (for synonymy see Diener 1925) is simply a pathological specimen of *T. costatus* (Pl. 8, fig. 12).

Occurrence. T. costatus first appears in England high in the Lower Cenomanian, as part of the fauna of 'Grizzle' at Wilmington (south Devon). It also occurs in the lower part of the Middle Cenomanian above, and, in England at least, reaches a maximum abundance in the lower part of the *rhotomagense* Zone as the nominal species of the *costatus* assemblage. This is the same horizon as the source of the lectotype, which is the 'Craie Chloritée', Rouen. At higher levels in the Middle Cenomanian it becomes rather scarce, if not rare, being replaced suddenly by the successional species *T. acutus* Passy.

T. costatus extends to a high horizon in the Upper Cenomanian in North Africa and is known from a single specimen from the remanié Upper Cenomanian *naviculare* Zone fauna at the base of Bed C, Humble Point (south Devon). It is recorded from the 'Turonian' by Roman and Mazerin (1913, p. 11, pl. 4, fig. 9), and has a world-wide distribution in the Middle and Upper Cenomanian.

Turrilites (*Turrilites*) *acutus Passy*

Plate 7, figs. 7, 8

1832 *Turrilites acutus* Passy, p. 334; Atlas, p. 7, pl. 16, figs. 3, 4.
1925 *Turrilites acutus* Passy; Diener, p. 79 (with synonymy).
1951 *Turrilites acutus* Passy; Wright and Wright, p. 17 (with synonymy).
1965 *Turrilites* (*Turrilites*) *acutus* Passy; Clarke, p. 54, pl. 19, fig. 7 (with synonymy).

Discussion. Like *T. costatus*, this is a very familiar species. I have examined the types of *Turrilites wiestii* Sharpe (1857) and *T. tevesthensis* Coquand (1862), both of which

are synonyms of Passy's species (see Diener 1925). *T. acutus* differs from *T. costatus* in its tendency towards development of an upper row of tubercles rather than the ribs seen in *T. costatus*. Stratigraphically separated populations of these 2 species are quite distinct, although individuals with intermediate features undoubtedly occur.

Turrilites dearingi Stephenson (1952; Clark 1965) is close to this species, differing only in that the lowest row of tubercles is exposed on the outer surface of the whorl. This species is based on a single specimen, which may merely be an aberrant *T. acutus*.

Occurrence. *T. acutus* first appears in the Middle Cenomanian, and is the nominal species of the *acutus* assemblage faunas. It extends into the Upper Cenomanian, although not, so far as is known, in England. The species has a wide distribution elsewhere (Europe, Africa, Madagascar, North America).

Turrilites (*Turrilites*) *scheuchzerianus* Bosc

1925 *Turrilites scheuchzerianus* Bosc; Diener, p. 84 (with synonymy).
1965 *Turrilites* (*Euturrilites*) *scheuchzerianus* Bosc; Clarke, p. 56, pl. 20, figs. 3, 5, 6.
1966 *Euturrilites scheuchzerianus* Bosc emend. Sharpe; Collignon, p. 24, pl. 12, fig. 1 (with synonymy).

Occurrence. *T. scheuchzerianus* first appears in England as a rarity at the top of the Lower Cenomanian. It is a persistent if rare member of Middle Cenomanian faunas although always much rarer than *T. costatus* and *T. acutus*. The species is widespread elsewhere in the world.

Turrilites (*Turrilites*) *borssumensis* Schlüter

Plate 8, fig. 6

1857 *Turrilites costatus* Lamarck, var.; Sharpe, p. 66, pl. 27, fig. 12 (*non* Lamarck).
1876 *Turrilites borssumensis* Schlüter, p. 129, pl. 38, figs. 6, 7.
1951 *Turrilites* cf. *borssumensis* Schlüter; Wright and Wright, p. 17.

Discussion and occurrence. Sharpe's somewhat doubtful specimen (Pl. 8, fig. 6) is from Ventnor, Isle of Wight (GSM Geol. Soc. 7778).

Subgenus MESOTURRILITES Breistroffer 1953
Turrilites (*Mesoturrilites*) *aumalensis* Coquand

Plate 7, fig. 9; Plate 8, fig. 15

1862 *Turrilites aumalensis* Coquand, p. 323, pl. 35, fig. 5.
1951 *Turrilites aumalensis* Coquand; Wright and Wright, p. 17.

Discussion and occurrence. Wright and Wright (1951, p. 18) recorded this species from Dorset; at Swanage it occurs in fissure fillings of Lower Cenomanian age in the top of *dispar* Zone Upper Greensand. I have another Lower Cenomanian specimen from Southerham, near Lewes (Sussex) (Pl. 7, fig. 9). The specimen of '*Turrilites costatus* var.' figured by Sharpe (1857, pl. 27, fig. 13) is only doubtfully referable to this species (Pl. 8, fig. 15; see also Wright and Wright 1951).

Family SCAPHITIDAE Meek 1876
Genus SCAPHITES Parkinson 1811

Type species. Scaphites equalis J. Sowerby, by the subsequent designation of Meek (1876).

Diagnosis. The shell is scaphitoid; early whorls coiled in close contact, with a short, straight, non-septate shaft, recurved to form a hook, not in contact with the phragmocone. The whorls are inflated or compressed; the ornament consists of simple ribs on the inner whorl side which branch and cross the venter, together with shorter intercalated ribs. The aperture is constricted, collared, with additional processes sometimes present. Some species bear umbilical and ventro-lateral tubercles.

Discussion. As well as *S.* (*Scaphites*), Wiedmann (1965) has introduced 2 subgenera: *S.* (*Metascaphites*) and *S.* (*Hyposcaphites*). He also included *Pteroscaphites* Wright and *Otoscaphites* Wright as subgenera.

Scaphites has a world-wide distribution, but species occurring in England seem to have been largely restricted to the Northern Hemisphere.

Scaphites (*Scaphites*) *equalis* J. Sowerby

Plate 64, figs. 5*a*, *b*, 6*a*, *b*

1813 *Scaphites equalis* J. Sowerby, p. 53, pl. 18, figs. 1–3.
1965 *Scaphites* (*Scaphites*) *equalis* J. Sowerby; Wiedmann, p. 417, pl. 56, figs. 1–4; text-figs. 3*a*, *b* (with synonymy).

Holotype. BMNH 43986, figured by Sowerby (1813, pl. 18, figs. 1–3). This specimen is unlocalized, but preservation (it is a phosphatic mould) indicates that it is probably from the Chalk Basement Bed of south-west England.

Discussion. Wiedmann (1965) provided an extensive synonymy, description, and discussion of this species. *S. equalis* is highly variable, and specimens may be inflated and coarsely ribbed or compressed with quite subdued ornament (cf. Wright and Wright 1951). However, *S. equalis* can usually be separated from *S. obliquus*, from which it evolves in the Lower Cenomanian. On the basis of this species alone, it is possible to recognize successively higher horizons in the Chalk Basement Beds of south-western England. The most obvious changes are towards increasing effacement of the primary ribs on the inner part of the whorl-sides of the hook and the development of more pronounced lateral tubercles.

Occurrence. S. equalis is common in the Middle and Upper Cenomanian in England, especially in the Basement Bed facies and in Bed C of the Cenomanian Limestone. It occurs only sporadically in the main mass of the Lower Chalk.

Jefferies (1963) recorded *S. equalis* from the *plenus* Marls; *S. equalis* var. *turonensis* Roman and Mazerin (1913, p. 12, pl. 4, figs. 10–14) from the 'Turonian' of Uchaux, France, belongs to this species. It is also recorded from low in the Lower Cenomanian of Dorset and Wiltshire (e.g. Mottram *et al.* 1956).

Scaphites obliquus J. Sowerby

Plate 63, figs. 2*a*, *b*; Plate 64, figs. 2, 3*a*, *b*, 4

1813 *Scaphites obliquus* J. Sowerby, p. 54, pl. 18, figs. 4–7.
1965 *Scaphites* (*Scaphites*) *obliquus* J. Sowerby; Wiedmann, p. 415, pl. 56, figs. 5, 6; text-fig. 3*c*.

Lectotype. Here designated, BMNH 43987*a*, figured by J. Sowerby 1813, pl. 18, figs. 4–6, from Hamsey (Sussex).

Discussion. This species is amply treated by Wiedmann (1965). Previous authors have considered this species to be based on a unique holotype. In fact, Sowerby figured 2 specimens, and lectotype designation is thus necessary.

Phosphatized scaphitids of the *obliquus* group from the Middle Cenomanian Basement Beds of south-west England fall within the limits of *Scaphites yokoneurae* Yabe as defined by Wiedmann (1965), because they possess a pronounced umbilical bulge. This alone does not warrant their separation from the associated *S. obliquus*, and indeed there are intermediates.

Forms figured by Guéranger (1867, pl. 5, fig. 8) and Collignon (1929, pl. 5, fig. 6) are rather distinctive, and Wiedmann's view that *S. yokoneurae* represents part of a separated lineage of *Scaphites*, parallel to the *equalis-obliquus* stock, seems reasonable.

Occurrence. In England, *S. obliquus* first appears commonly in the *saxbii* assemblage faunas of the *mantelli* Zone; below this level scaphitids are very rare. It accompanies *S. equalis* in Middle Cenomanian faunas, but has died out by Upper Cenomanian times, being absent from the *naviculare* Zone faunas of Bed C on the Devon coast and elsewhere.

Scaphites hilli Adkins and Winton

1965 *Scaphites* (*Scaphites*) *hilli* Adkins and Winton; Wiedmann, p. 421 (with synonymy).

Discussion and occurrence. A few doubtful fragments from the phosphatized Lower Cenomanian *carcitanensis* assemblage fauna of the Glauconitic Marl of the Isle of Wight may belong to this species (Wright, *in litt.*).

Suborder AMMONITINA Hyatt 1889
Superfamily DESMOCERATACEAE Zittel 1895
Family DESMOCERATIDAE Zittel 1895
Subfamily DESMOCERATINAE Zittel 1895
Genus DESMOCERAS Zittel 1884
Subgenus DESMOCERAS (DESMOCERAS) Zittel 1884

Type species. Ammonites latidorsatus Michelin (1838) by the subsequent designation of Boule, Lemoine, and Thévenin 1907–1907.

Desmoceras (*Desmoceras*) *latidorsatum* (Michelin)

Plate 45, figs. 4*a*, *b*

1838 *Ammonites latidorsatus* Michelin, p. 101, pl. 12, figs. 9, 9*a*.
1923 *Desmoceras latidorsatum* (Michelin); Spath, p. 39, pl. 2, figs. 2*a*, *b*; text-fig. 9.
1951 *Desmoceras latidorsatum* (Michelin); Wright and Wright, p. 18.

Discussion and occurrence. This species is very rare in the English Cenomanian. I have collected the species from the Chalk Basement Bed, Snowdon Hill, Chard (Somerset) (*rhotomagense* Zone, *acutus* assemblage); a specimen from Beaminster Down (Dorset) from the same horizon may be a remanié Lower Cenomanian form. Other specimens are: GSM Zb 1293 (a doubtful individual from the top of the Glauconitic Marl, Melbury Down (Dorset) (Pl. 10, fig. 7) (low *mantelli* Zone)), and WW 20809 from Bed C (*naviculare* Zone), Humble Point (south Devon).

Desmoceras (*Desmoceras*) cf. *inane* (Stoliczka)

Plate 10, figs. 1*a*, *b*, 2*a*, *b*

cf. 1865 *Ammonites inanis* Stoliczka, p. 121, pl. 59, fig. 13 only.
1895 *Desmoceras inane* (Stoliczka); Kossmat, p. 107, pl. 19, figs. 6, 7.
1923 *Desmoceras inane* (Stoliczka); Spath, p. 42, footnote.

Discussion and occurrence. The specimen from Warminster, BMNH 37279, mentioned by Spath (1923) appears to belong to Stoliczka's species. It is of Lower Cenomanian age.

Subfamily PUZOSIINAE Spath 1922
Genus PUZOSIA Bayle 1878

Type species. Ammonites planulatus J. de C. Sowerby, by the original designation of Bayle (1878) (= *Ammonites subplanulatus* Schlüter 1871). Bayle introduced this generic name in explanation of his plates 45 and 46, without description or diagnosis.

Ammonites planulatus J. de C. Sowerby is, however, not available, due to the prior usage of the combination *Ammonites planulatus* by Schlotheim (1820, p. 59) and *Ammonites planulatus ellipticus* by Schuebler (in von Zieten 1830, p. 14). The lectotype (J. de C. Sowerby 1827, pl. 570, fig. 5; Sharpe 1855, p. 29, pl. 12, fig. 3) of *Ammonites planulatus* J. de C. Sowerby (Pl. 9, fig. 2) is extremely poorly preserved, and I cannot reasonably separate it from *Puzosia subplanulata* of Schlüter (1871, p. 4, pl. 2, figs. 5–7). The difficulties of interpreting the type species of the genus are discussed by Matsumoto (1954).

Diagnosis. Evolute, many-whorled, whorl section compressed, with flattened sides and a rounded, arched venter. There are periodic flexuous constrictions, directed forwards across the venter as a chevron. Inner part of flanks usually smooth, outer parts bearing many fine costae which parallel the constrictions (see also Matsumoto 1954, Wright 1957).

Discussion. The limits of *Puzosia* are ably discussed by Matsumoto (1954). 2 subgenera, *P.* (*Puzosia*) and *P.* (*Anapuzosia*) are at present recognized.

Occurrence. Lower Albian to Upper Turonian, worldwide.

Puzosia (*Puzosia*) *subplanulata* (Schlüter)

Plate 9, figs. 1, 2; Plate 10, figs. 3*a*, *b*; Plate 50, fig. 5

1827 *Ammonites planulatus* J. de C. Sowerby, pl. 570, fig. 5.
1855 *Ammonites planulatus* J. Sowerby; Sharpe, p. 29, pl. 12, fig. 3.
1871 *Ammonites subplanulatus* Schlüter, p. 4, pl. 2, figs. 5–7.
1951 *Puzosia planulata* (J. Sowerby); Wright and Wright, p. 18.

Discussion. Because of the problems of interpreting this species, I describe the lectotype of Sowerby's *Ammonites planulatus* in detail. It is a very poorly preserved composite internal mould, partially embedded in grey glauconitic chalk. A thick coating of badly discoloured brown varnish hides most of the fine detail of the surface ornament of the specimen.

It is evolute, about one-seventh of the previous whorl being covered. The whorl section is compressed, with flat sides, convergent ventro-lateral shoulders, and a narrowly arched venter, in part accentuated by crushing. The umbilicus is broad and shallow; the umbilical wall and shoulder are rounded. There are 5 narrow, flexuous, and deep constrictions per whorl. These constrictions arise at the umbilical seam, sweep forwards across the umbilical shoulder and the flank, sweep backwards across the lower part of the ventro-lateral shoulder and forwards across the venter, to form a chevron over the siphuncle. On the ventro-lateral shoulder, between each constriction, there are delicate, curved, rounded ribs which are concave towards the aperture. The preservation of the lectotype is too poor to determine the number between each constriction; the suture is not visible.

Dimensions.

D	*Wb*	*Wh*	*U*
50	14·5 (29)	19 (38)	19 (38)

The large size of Schlüter's specimen and the poor preservation of Sowerby's makes comparison difficult, but I am at present inclined to regard them as the same form.

P. subplanulata is liable to be confused with several other species, and I am unhappy about the rather subtle differences between *Puzosia* species as conceived by Spath (1923) and Matsumoto (1954). According to Spath (1923, p. 44), '*P. planulata*' (i.e. *subplanulata*) is more compressed and more evolute than *P. sharpei* Spath. *P. communis* Spath (1923, p. 47, pl. 2, figs. 3*a*–*e*; text-fig. 11*a*) is said to have a smaller umbilicus, less acute chevrons, and less distinct costation than '*P. planulata*' (i.e. *subplanulata*). It also has more constrictions (6–7 per whorl). *P. crebrisulcata* Kossmat has more constrictions per whorl (8), as have forms such as *P. octosulcata* (Sharpe). This latter species is more inflated, and seems to be mature at much smaller diameters. Other contemporary species are discussed by Kossmat (1898) and Matsumoto (1954).

Occurrence. Rare in *mantelli* and *rhotomagense* Zones in southern England and western Europe.

Puzosia (*Puzosia*) *sharpei* Spath

Plate 10, figs. 6*a*, *b*; Plate 14, fig. 6

1855 *Ammonites planulatus* J. de C. Sowerby; Sharpe, p. 29, pl. 12, fig. 4 (*non* Sowerby).
1923 *Puzosia sharpei* Spath, p. 46, pl. 1, figs. 11, 12; text-fig. 11*b*.
1951 *Puzosia sharpei* Spath; Wright and Wright, p. 19.

Discussion and occurrence. This species was recorded by Spath (1923, p. 47) from the Lower Cenomanian of Warminster (Wilts.) and Bonchurch, Isle of Wight. His specimens are illustrated as Plate 10, fig. 6*a*, *b*, and Plate 14, fig. 6. Wright and Wright (1951, p. 19) also recorded the species from Devon.

Puzosia (*Puzosia*) cf. *crebrisulcata* Kossmat

Plate 14, figs. 5, 7*a*, *b*

cf. 1898 *Puzosia crebrisulcata* Kossmat, p. 116, pl. 17, fig. 4; pl. 18, fig. 2.

Discussion and occurrence. A number of small, compressed *Puzosia* with wide, acute constrictions may belong to Kossmat's species. Specimens from the Chalk Basement Bed (*rhotomagense* Zone, *acutus* assemblage), Snowdon Hill, Chard (Somerset) (Pl. 14, fig. 5), and from the Chalk Marl, of Ventnor, Isle of Wight (Pl. 14, figs. 7*a*, *b*) are figured.

Puzosia (*Puzosia*) *octosulcata* (Sharpe)

Plate 13, fig. 3; Plate 14, figs. 1*a*, *b*, 2*a*, *b*, 3

1857 *Ammonites octo-sulcatus* Sharpe, p. 42, pl. 19, figs. 3*a*, *b*.
1923 *Puzosia octosulcata* (Sharpe); Spath, pp. 45, 46.
1951 *Puzosia octosulcata* (Sharpe); Wright and Wright, p. 19.
1964 *Puzosia octosulcata* (Sharpe); Collignon, p. 18, pl. 321, figs. 1400, 1401.

Lectotype. By subsequent designation of C. W. and E. V. Wright (1951, p. 37), the original of Sharpe 1857, pl. 19, figs. 3*a*, *b*, GSM 7761 from the 'Grey Chalk of Ventnor', Isle of Wight.

Diagnosis. A small, rather involute and round-whorled *Puzosia* with 8 almost straight shallow constrictions per whorl, the outer parts of the sides bearing very fine flexuous ribs between constrictions.

Description of lectotype. The lectotype is a small, well-preserved composite internal mould with traces of a limonitic coating. The shell is moderately involute, about half the previous whorl being covered. The whorl section is slightly compressed, with rounded, flattened sides and a rounded, arched venter. The greatest breadth is just above mid-flank.

There are 8 constrictions on the outer whorl. These are narrow and only moderately incised, passing forwards across the sides, with only a slight flexure, to produce a gentle, rounded forwards sweep over the siphonal region. Between the constrictions are fine, rounded, flexuous ribs, sweeping gently forwards across the venter. They are

best developed on the ventro-lateral shoulders. It is not possible to count the numbers of ribs between constrictions owing to poor preservation.

The umbilicus is shallow; the umbilical wall and shoulder are sharply rounded. The sutures are not visible.

Dimensions.

	D	*Wb*	*Wh*	*U*
GSM 7761, lectotype	24·6	9·2 (37·4)	10·2 (41·5)	6·4 (26·0)

Discussion. Small size, involution, rounded whorl section, faint, straight constrictions, and weak chevron across the venter make this a readily recognizable form, although Pervinquière (1907) regarded it as a mere variety of *P. mayoriana* (d'Orbigny). All the specimens I have seen are small, suggesting the lectotype is adult.

Occurrence. As well as the lectotype, there are several other specimens from Ventnor in museum collections (BMNH, GSM, SMC), a specimen from Bed A_2 of the Cenomanian Limestone (GSM Wood Collection Zn9068), and a phosphatized specimen from the Chalk Basement Bed at Beaminster Down (Dorset) (H. G. Owen Collection). The species thus seems to occur in both Lower and Middle Cenomanian. Collignon (1964) recorded the species from the Lower Cenomanian of Madagascar.

Genus AUSTINICERAS Spath 1922

Type species. Ammonites austeni Sharpe (1855), by the original designation of Spath (1922, p. 127).

Diagnosis. Medium-sized to large puzosiids with a compressed, convergent whorl section and a narrowly arched venter. Moderately evolute, with 2 distinct orders of ribbing; distant, long flexuous main ribs with many shorter, flexuous intercalated ribs.

Discussion. There is some variation in the treatment of *Austiniceras*, which has been regarded as a separate genus or as a subgenus of *Parapuzosia*, from which it shows only slight differences (Spath 1922; Wright and Wright 1951; Matsumoto 1954; 1966; Wright 1957; Collignon 1961).

According to Matsumoto (1954, 1966) the 2 genera may be separated in that *Parapuzosia* has

> an evenly rounded venter and an oval or subelliptical whorl section. Its flanks are gently inflated (often in the outer whorl) or subparallel (often in the inner whorl). *Austiniceras* has a remarkably narrow, if not fastigate, venter and a convergent whorl section.

I agree with Matsumoto that the types of the 2 genera differ, notably in the flexuous major and intercalated ribs of *Austiniceras austeni* as opposed to the rectilinear major and intercalated ribs of *Parapuzosia daubréei* (de Grossouvre). *Austiniceras* (mainly Cenomanian–Turonian) is earlier than *Parapuzosia* (essentially Senonian), although Collignon (1961) has described Campanian *Austiniceras*. *Parapuzosia* is undoubtedly descended from *Austiniceras*, and is the intermediate form of some species which introduces difficulties in assessing the generic status of *Austiniceras*.

Occurrence. The time range of *Austiniceras* can now be extended to the lower part of the Lower Cenomanian (see below); the geographic distribution extends over north-west Europe, north Africa, Madagascar, and Japan.

Austiniceras austeni (Sharpe)

Plate 11, fig. 1; Plate 12, figs. 1*a*, *b*

1855 *Ammonites austeni* Sharpe, p. 28, pl. 12, figs. 1*a*, *b* only (*non* fig. 2 = *A. dibleyi* Spath).
1922 *Austiniceras austeni* (Sharpe); Spath, p. 127.
1951 *Austiniceras austeni* (Sharpe); Wright and Wright, p. 19.

Lectotype. By subsequent designation of Spath (1922, p. 127), the original of *Ammonites austeni* Sharpe 1855, pl. 12, figs. 1*a*, *b* only, BMNH C3382, from the Lower Chalk of Guildford (Surrey).

Diagnosis. A very large species of *Austiniceras*, with 5 narrow, straight constrictions per whorl in the early growth stages. In middle growth stages there are 5 long, strong, flexuous major ribs per whorl, separated by numerous (over 30) shorter, flexuous intercalated ribs. Major ribs becoming increasingly dense, with fewer intercalated ribs, on the body chamber.

Description. The lectotype is a large, composite internal mould in grey chalk. More than half the last whorl is probably body chamber.

The shell is very large, involute, with about three-fifths of the previous whorl being covered. The whorl section is compressed, the sides are flat, converging towards the rather narrow, arched, and rounded venter. The umbilicus is rather small and shallow, the umbilical wall is flat and vertical, the umbilical shoulder is narrowly rounded.

The inner whorls, so far as can be seen, are smooth, with 5 narrow, straight constrictions per whorl.

Major ribs first appear at a diameter of between 90 and 100 mm, and between this and a diameter of 270 mm there are 5 major ribs per whorl. These ribs are strong, narrow, rounded, and flexuous. Arising at a weak umbilical bulla, they sweep gently backwards across the lower and middle parts of the whorl side and then sweep forwards across the venter, broadening slightly at mid-flank. Between these major ribs there are between 27 and 35 intercalated ribs. Arising at mid-flank, these are at first very faintly developed, mere striae in places (as is very clear from Sharpe's figure). They follow the same course as the major ribs. The intercalated ribs strengthen across the outer two-thirds of the whorl, crossing the venter parallel to, and only slightly weaker than, the major ribs.

At diameters greater than 270 mm (i.e. the last third of the outermost whorl) there is a marked increase in the density of the major ribs, and a consequent decrease in the number of intercalated ribs. This change in ornament is presumably associated with maturity in the species. There are thus 12 major ribs on the last third of the outer whorl, separated by only 3 or 4 intercalated ribs, which are developed on the outer part of the whorl side only. Passing inwards, towards the umbilicus, these intercalated ribs are completely lost between the last few major ribs, which are themselves effaced on the venter. Sutures not seen.

Dimensions.

	D	*Wb*	*Wh*	*U*
BMNH C3382, lectotype	410	133 (32·4)	168 (40·9)	116 (28·3)
BMNH C569	419	136 (32·5)	156 (37·2)	99 (23·6)

Discussion. Sharpe's figures of the lectotype of this species are very good, but reversed. The suture, as seen on phosphatized material from south-west England, is very complicated and subdivided, as in other puzosiids.

Rather poor fragments, perhaps belonging to this species, suggest that internal moulds may be completely smooth at small diameters, except for the constrictions. The siphuncle is close to the ventral shell wall in this species, and because of this the constrictions are very weak across the venter.

A. austeni differs from *A. dibleyi* Spath in its flatter sides, fewer major ribs (5–6 as opposed to 8–9 in *A. dibleyi*), more numerous intercalated ribs (generally over 30 as opposed to 6–9 in *A. dibleyi*), and generally weaker ornament.

A.? curvatisulcatum (Chatwin and Withers) (= *Desmoceras curvatisulcatum* Chatwin and Withers 1909, p. 68, pl. 2, figs. 1–4; Spath 1922, p. 128) is much smaller, more inflated, and has stronger constrictions.

Occurrence. A. austeni occurs all over southern England in the Cenomanian. It first appears as a great rarity in the unphosphatized fauna of the Glauconitic Marl of the Isle of Wight, low in the *mantelli* Zone. It is frequent in higher parts of the Lower Cenomanian and in the Middle Cenomanian.

In the Basement Bed facies of south-west England, this species is rare in the phosphatized faunas, but not uncommon unphosphatized just above the Basement Bed.

It is the commonest Upper Cenomanian ammonite in the Lower Chalk facies, and is common and widespread in the Melbourn Rock (Lower Turonian, *nodosoides* Zone). Wright and Wright (1951, p. 19) also recorded it from the *lata* Zone (Middle Turonian).

Austiniceras dibleyi Spath

Plate 13, figs. 1, 2; Plate 14, fig. 4

1855 *Ammonites austeni* Sharpe, p. 28, pl. 12, fig. 2 only.
1922 *Austiniceras dibleyi* Spath, p. 127.
1931 *Puzosia matheroni* (d'Orbigny); Douvillé, p. 39, pl. 2, figs. 5*a*, *b* (*non* d'Orbigny).
1931 *Puzosia* (*Austiniceras?*) *dibleyi* (Spath); Spath, p. 316.
1951 *Austiniceras dibleyi* Spath; Wright and Wright, p. 19.

Holotype. By original designation of Spath (1922, p. 127), BMNH C13912, *subglobosus* Zone, Betchworth (Surrey) (Dibley Collection). This is not the original of *Ammonites austeni* Sharpe (1855, p. 28, pl. 12, fig. 2 only), Lower Chalk (Sussex); this specimen is lost.

Diagnosis. A medium-sized, rather coarsely ornamented *Austiniceras*, with 9 flexuous major ribs per whorl, separated by between 6 and 9 flexuous intercalated ribs, which arise one-third to half-way up the whorl side.

Description. The holotype is a well-preserved, flattened chalk specimen with the shell replaced by limonite (probably after pyrite), partially developed from matrix. It is

rather involute, just over half the previous whorl being covered. The whorl section is compressed, with broadly rounded sides, convergent ventro-lateral shoulders, and a narrowly rounded venter. The umbilicus is shallow and rather narrow; the umbilical wall and shoulder are rounded.

There are 9 strong, narrow, rounded flexuous ribs on the outer whorl. Arising at the umbilical shoulder, these ribs pass gently forwards across the lower part of the flank, backwards across mid-flank, and thence gently forwards across the venter, where they are most strongly developed, projecting with a steep adoral and gently inclined adapical face.

Between these major ribs are between 6 and 9 weaker, flexuous, intercalated ribs. These arise between one-third and half-way up the flank, and are at their strongest development across the venter. The exposed parts of the inner whorls are smooth except for the major ribs. Suture not seen.

Dimensions.

	D	*Wb*	*Wh*	*U*
BMNH C13912, holotype	130	— (—)	54 (41·5)	42 (32·3) (specimen slightly distorted)

Discussion. A. dibleyi differs from *A. austeni* in its smaller size, coarser ornament, and different number of major and intercalated ribs (see p. 39). Douvillé's specimens of *Puzosia matheroni* (d'Orbigny) are conspecific with the present form, as is clear from a fine specimen in the British Museum, BMNH C52616 (O'Donnell Collection) from the same locality (Pl. 13, fig. 1). There is only a superficial similarity to d'Orbigny's Lower Cretaceous species (d'Orbigny 1840, p. 497, pl. 122).

Occurrence. Rare; in addition to the holotype I have seen the following specimens:

BMNH C10618; basal *subglobosus* Zone, Bluebell Hill, Burham (Kent) (Dibley Collection).
BMNH unregistered specimen; *plenus* Marls, Merstham (Surrey) (Jefferies Collection).
SMC F17845; *plenus* Marls, Cap Blanc Nez, France (Jefferies Collection).

This species is recorded by Jefferies (1962, 1963) from the *geslinianum* Zone of the *plenus* Marls (Cenomanian–Turonian). The specimens from the Upper *forbesiana* Beds of Salinas, Angola, generally regarded as Upper Cenomanian (Howarth 1965) could equally be of Lower Turonian age. The associated *Kanabiceras* and '*Protacanthoceras*' characterize a horizon close to the Cenomanian/Turonian boundary which is not represented in either type area.

Superfamily HOPLITACEAE H. Douvillé 1890

For a discussion of the Hoplitaceae see Casey 1965, pp. 458–460, whose restriction of this group to the Hoplitidae, Schoenbachiidae, Placenticeratidae, and Engonoceratidae, with a separate Superfamily Douvilleiceratacеae (including the Douvilleiceratidae, Deshayesitidae, and Parahoplitidae; see Casey 1957) is accepted here. The views of Wiedmann (1966) should also be consulted.

Family HOPLITIDAE H. Douvillé 1890
Subfamily HOPLITINAE H. Douvillé 1890

Dominating the fauna of the English Gault, this group is represented in the Cenomanian by a solitary genus, *Hyphoplites*.

Genus HYPHOPLITES Spath 1922

Type species. Ammonites falcatus Mantell (1822, pp. 117, 118, pl. 21, figs. 6, 12), by the original designation of Spath (1922).

Diagnosis. See Wright and Wright 1949, p. 481.

Discussion. Wright and Wright (1949) reviewed the origin and evolution of *Hyphoplites* in detail, and their work has become a classic on ammonite evolution. I have accepted their species limits, but regard them, and their varieties, as being morphological units only, although their chronological subspecies (e.g. *H. falcatus aurora*) may have some greater value. Examination of *Hyphoplites* populations from the Chalk facies suggests that there is every intermediate within the 2 branches of the *Hyphoplites* stock, the diphyletic origin of *Hyphoplites* thus apparently being a simple derivation of 2 'good' *Hyphoplites* species from 2 *Discohoplites* species. One wonders if the existence of a good *dispar–perinflatum* Subzone *Discohoplites* assemblage might simplify the position further.

Occurrence. Hyphoplites is, *par excellence*, a boreal genus, with a distribution largely confined to north-west Europe, although also known from southern France (Fabre 1940) and Transcaspasia (Semenow 1899). Avnimelech (1965) recorded a single specimen of *Hyphoplites falcatus* from Israel.

Discohoplites, the antecedent of *Hyphoplites*, has a similar, largely north-west European distribution, but is also known from Transcaspasia (Semenow 1899) and northern Spain (*dispar* Zone; *Discohoplites* cf. *falcatus* (Semenow); Wiedmann 1959, p. 717; 1964, p. 113). The genus also occurs in north Africa, e.g. several individuals from the uppermost Albian marls on the northern slopes of Gadet Chi, 3 km east of Bou Khadra in the Ouenza region of eastern Algeria (specimens collected with J. M. Hancock, 1965).

Stratigraphically, *Hyphoplites* first appears in the uppermost Albian (Wright and Wright 1949) and extends throughout the Lower Cenomanian.

Hyphoplites falcatus falcatus (Mantell)

Plate 15, figs. 2*a*, *b*

1949 *Hyphoplites falcatus falcatus* (Mantell); Wright and Wright, p. 484, pl. 30, figs. 1*a–c*, 3, 4 (with synonymy).
1951 *Hyphoplites falcatus falcatus* (Mantell); Wright and Wright, p. 21.
1957 *Hyphoplites falcatus* (Mantell); Wright, p. L396, fig. 516, 1*a*, *b*.
1959 *Hyphoplites falcatus* (Mantell); Cieśliński, pp. 53, 54, fig. 7.

1963 *Hyphoplites falcatus falcatus* (Mantell); Renz, p. 1096.
1965 *Hyphoplites falcatus* (Mantell); Avnimelech, p. 160.

Occurrence. The restricted form of this species first occurs as a rarity in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight and Stour Bank (Dorset).

It is very common in some *saxbii* assemblage faunas, especially in the Isle of Wight (the '*falcatus*' Zone of Spath (1923*b*, p. 144)). It occurs higher in the Lower Cenomanian, in the *Mantelliceras* gr. *dixoni* assemblage fauna at Folkestone (Kent), and at the base of Bed B on the Devon coast (BMNH, Grimsdale Collection; C. W. Wright, pers. comm.). The species also occurs in the remanié Lower Cenomanian fauna of the Middle Cenomanian Chalk Basement Bed in south-west England, and in the conglomerate at the top of the Eggardon Grit west of Maiden Newton (Dorset).

Elsewhere, it occurs in the Lower Cenomanian of Germany (Schlüter 1871–1872, etc.), France (Hancock 1959, etc.), Switzerland (Renz 1963, p. 1096), Transcaspasia (Semenow 1899), and Israel (Avnimelech 1965).

Hyphoplites falcatus interpolatus Wright and Wright

1949 *Hyphoplites falcatus interpolatus* Wright and Wright, p. 485, pl. 30, figs. 2, 6, 7.
1951 *Hyphoplites falcatus interpolatus* Wright and Wright; Wright and Wright, p. 21.
1963 *Hyphoplites falcatus interpolatus* Wright and Wright; Renz, p. 1096, pl. 1, fig. 11.

Occurrence. Rare in the *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight and Stour Bank (Dorset). It occurs more frequently above, in some *saxbii* assemblage faunas, e.g. in the hard limestones on top of Gore Cliff in the Isle of Wight, and 3 m above Glauconitic Marl at Eastbourne (Sussex). Also known from the Lower Cenomanian of Switzerland (Renz 1963) and France (Hancock 1959).

Hyphoplites falcatus aurora Wright and Wright

1949 *Hyphoplites falcatus aurora* Wright and Wright, p. 485, pl. 29, figs. 3*a*, *b*, 9; pl. 30, figs. 5*a–c*.
1951 *Hyphoplites falcatus aurora* Wright and Wright, p. 21.

Occurrence. This form appears in the Upper Albian, and survives into the Lower Cenomanian, where it is rare in the *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight, and, doubtfully, above (Gore Cliff).

Hyphoplites campichei Spath

1949 *Hyphoplites campichei* Spath; Wright and Wright, p. 483, pl. 29, figs. 1, 5, 6, 8 (with synonymy).
1951 *Hyphoplites campichei* Spath; Wright and Wright, p. 21.

Occurrence. Rather uncommon in the phosphatized *carcitanensis* faunas of the Glauconitic Marl of the Isle of Wight and Stour Bank (Dorset). Frequent in some *saxbii* assemblage faunas, especially the phosphate band above the Glauconitic Marl in the Isle of Wight, and at Eastbourne (Sussex). A single specimen comes from 11 m

above the Glauconitic Marl, Folkestone (Kent). Hancock (1959) recorded the species from the Lower Cenomanian of Sarthe, France.

Hyphoplites curvatus (Mantell)

Plate 15, figs. 1, 3*a–c*

1949 *Hyphoplites curvatus* (Mantell); Wright and Wright, p. 488, pl. 31, figs. 1–4 (with synonymy).
1951 *Hyphoplites curvatus* (Mantell); Wright and Wright, p. 21.

Occurrence. Fairly common in *carcitanensis* and *saxbii* assemblage faunas, e.g. the Glauconitic Marl of the Isle of Wight, Stour Bank (Dorset), and the phosphatic nodule bed above the Glauconitic Marl in the western part of the Isle of Wight and Eastbourne (Sussex). It also occurs in Beds A_1 and A_2 of the Cenomanian limestone, and in the Lower Cenomanian of western Europe.

Hyphoplites arausionensis arausionensis (Hébert and Munier-Chalmas)

Plate 15, fig. 4

1949 *Hyphoplites arausionensis* (Hébert and Munier-Chalmas); Wright and Wright, p. 491 (with synonymy).
1949 *Hyphoplites crassofalcatus crassofalcatus* (Semenow); Wright and Wright, p. 490, pl. 32, figs. 1, 5, 6, 8 (with synonymy).
1951 *Hyphoplites crassofalcatus crassofalcatus* (Semenow); Wright and Wright, p. 21.
1951 *Hyphoplites arausionensis* (Hébert and Munier-Chalmas); Wright and Wright, p. 21.

Discussion. The syntypes of this species are in the collections of the Sorbonne; casts are figured as Plate 15, figs. 1 and 4. The smaller specimen has been designated lectotype (Wright and Wright 1949, p. 491) and is clearly not separable from *Hyphoplites crassofalcatus*. Hébert and Munier-Chalmas's figures are deceiving, and this led the Wrights to treat *arausionensis* as a separate species from *crassofalcatus*.

Occurrence. Common in the phosphatized *carcitanensis* assemblage faunas of the Glauconitic Marl of the Isle of Wight, also occurring above in *saxbii* assemblage faunas. It occurs in Beds A_1 and A_2 of the Cenomanian Limestone, and the basement bed of the Wilmington Sands (south Devon). Widely distributed in western Europe, Transcaspasia (Semenow 1899).

Hyphoplites arausionensis horridus Wright and Wright

1949 *Hyphoplites crassofalcatus horridus* Wright and Wright, p. 49, pl. 31, fig. 10; pl. 32, fig. 7 (with synonymy).
1951 *Hyphoplites crassofalcatus horridus* Wright and Wright; Wright and Wright, p. 21.

Occurrence. Rare, accompanying the typical form.

Hyphoplites costosus Wright and Wright

1949 *Hyphoplites costosus* Wright and Wright, p. 484, pl. 29, figs. 7*a*, *b*.
1951 *Hyphoplites costosus* Wright and Wright, p. 21.

Occurrence. Rare in *carcitanensis* and ?*saxbii* assemblage faunas in Devon, Dorset, Wilts. and Hants; France (Hancock 1959).

Hyphoplites pseudofalcatus (Semenow)

1949 *Hyphoplites pseudofalcatus* (Semenow); Wright and Wright, p. 49, pl. 23, figs. 5–9.
1951 *Hyphoplites pseudofalcatus* (Semenow); Wright and Wright, p. 21.

Occurrence. Rare in the lower parts of the *mantelli* Zone all over southern England; France (Hancock 1959).

Family SCHLOENBACHIIDAE Parona and Bonarelli 1897

Euhystrichoceras, which first appears in the upper Albian of north Africa, is the earliest member of this group. Two genera are definitely referred to the family: *Euhystrichoceras* and *Schloenbachia*. Both occur in England, the former as a great rarity, the latter as the most abundant Cenomanian ammonite. I am uncertain of the systematic position of *Prionocycloides*, *Tropitoides*, and *Prohauericeras*. *Pseudacompsoceras* Spath 1925*a*, usually placed in this family, is a synonym of *Acompsoceras* Hyatt 1903 (cf. Casey 1965, p. 462), and should be transferred to the Acanthoceratacеae. The origin of the family lies in Upper Albian hoplitids of the *Callihoplites–Lepthoplites–Pleurohoplites* group.

Spath's view (1926, pp. 241 et seq.) of a polyphyletic origin for the Lower Cenomanian species of *Schloenbachia* from these Albian 'genera' may be more reasonable than at first seems apparent, for the range of morphological variation seen in *Schloenbachia varians* (J. Sowerby) in the Lower Cenomanian is as great as that seen in all 3 of these hoplitid 'genera' at the top of the Albian.

Although the types are lost, I have no doubt that *Ammonites salteri* Sharpe (1857, p. 50, pl. 23, figs. 3*a–c*, 5*a*, *b*) is a pathological *Schloenbachia*, and not a *Pleurohoplites*.

Genus SCHLOENBACHIA Neumayr 1875

Type species. Ammonites varians J. Sowerby (1817), by the subsequent designation of H. Douvillé (1890).

Diagnosis. A highly variable group of medium-sized ammonites; involute and compressed to evolute and highly inflated, carinate, the keel being strong to weak. Compressed forms may be smooth and constricted, although most forms bear umbilical, or umbilical and lower lateral tubercles, which may or may not be connected by fine striae or ribs to about twice as many ventro-lateral clavi. More inflated forms usually have strong umbilical and lower lateral tubercles, each lower lateral tubercle giving rise to a pair of flexuous ribs, with strong ventro-lateral clavi at the end of each rib.

With increasing inflation the ribbing breaks down into tubercles only. Very inflated forms bear huge upper lateral tubercles or septate spines. There is a long rostrum in some forms. The suture is rather simple.

Discussion. The diagnosis expresses some of the enormous variation seen in this genus, which is, however, quite readily recognizable. Most specimens are internal moulds, so that the extremes of ornament are rather reduced.

In life, inflated forms bore very long delicate lateral spines and had a high, delicate keel projecting forwards at the aperture as a long rostrum. Other variations within the genus are the compressed, completely smooth forms with a fastigate venter, forms

with puzosiid-like constrictions and yet others with looped hoplitid-like ribs. Cope (*in litt.*) has demonstrated dimorphism in this genus.

There are numerous records of *Schloenbachia* from the uppermost Albian, most of which are unsatisfactory. Thus Wright (1947) and Spath (1938) recorded the genus from the *dispar–perinflatum* ammonite bed at Punfield Cove (Dorset). This bed is overlain by a similar glauconitic Cenomanian sediment, which is piped down into it in burrows and fissures (Wright 1959, p. 766; cf. Smart 1955). The fillings of these burrows are the source of the *Schloenbachia*, which thus represent contamination from younger deposits. I have seen *Schloenbachia* occurrences of this type from several localities in north Dorset.

Thomel (1961*a*) recorded Upper Albian *Schloenbachia* from what appears to be a similar occurrence in the Alpes-Maritimes, France. Breistroffer (1936, pp. 65–67; 1940, p. 96; 1947, pp. 63, 66 (47 and 50 in reprinted copies)) recorded *Schloenbachia* from the Upper Albian of La Fauge, Vercours, France.

Follet (1954) recorded the genus from Saint-Amand-des-Hautes-Terres, northern France, but all records require critical reappraisal before the possibility of mixture of faunas by burrowers, etc., can be dismissed and a definite Upper Albian age admitted for *Schloenbachia*.

Schloenbachia extends throughout the English Cenomanian, and at many levels forms 90% and more of the ammonite fauna. From an examination of large populations from the Lower and Middle Cenomanian Chalk facies it is clear that there is every transition from compressed, smooth forms to strongly ornamented inflated spinose ones, with a peak (in terms of abundance) at the mid-point.

Upper Cenomanian *Schloenbachia* are rare, except as phosphatized specimens from the base of Bed C in south-west England. Here it seems that the genus has undergone definite divergence, and that several distinct species (albeit undescribed at present) are represented at this level.

Dr. J. M. Hancock is preparing a complete revision of *Schloenbachia*, and the unravelling of the complex synonymies of many species must wait until the publication of this work. Species are not discussed further here.

Occurrence. *Schloenbachia* is a characteristic 'boreal' genus. It is unknown in the New World, extending no further west than eastern Greenland (Donovan 1953, 1954). It occurs in England, extends into western Europe (Germany, Switzerland, Poland, etc.) and eastwards into Transcaspasia (Semenow 1899). In France, the genus occurs in the north, in the type Cenomanian and extends down the Rhone as far south as the Alpes-Maritimes and the Mediterranean coast.

The genus is not known, however, from the western Mediterranean, or from Spain, or from points south, i.e. the well-known north African and Madagascan faunas. The only exotic occurrence of *Schloenbachia* is that noted by Spath (1926, p. 242) from central Persia; I have not been able to examine these specimens or otherwise confirm the record.

Genus EUHYSTRICHOCERAS Spath 1933

Type species. Ammonites nicaisei Coquand, by original designation.

Discussion. Only 4 specimens of this genus are known from England; the holotypes of *E. simplex* Spath (BMNH 37276) and *E. constrictum* Spath (BMNH 88694) are from 'Warminster' (Wilts.), the other 2 specimens are phosphatized examples from the Isle of Wight (Wrights' Collection, H. G. Owen Collection). All occurrences are of low Lower Cenomanian age. This genus is to be revised by Dr. H. G. Owen, and is not further discussed here.

Family LYELLICERATIDAE Spath 1921

Transferred from the Hoplitaceae to the Acanthocerataceae by Casey (1965) as a result of the discovery of the Upper Albian genus *Paradolphia*, ancestral to *Forbesiceras* and probably descended from *Neophlycticeras* (*Eotropitoides*), the Forbesiceratinae are here incorporated into the Lyelliceratidae.

Genus FORBESICERAS Kossmat 1897
(= DISCOCERAS Kossmat 1895)

Type species. Ammonites largilliertianus d'Orbigny, by the subsequent designation of Diener (1925, p. 180).

Diagnosis. Medium-sized, very involute, compressed, high-whorled ammonites with flat or slightly convex sides, and a narrow tabulate to subfastigate venter with 1 or 3 weak, sometimes crenulate, keels.

The sides are ornamented either by very fine flexuous to falcate ribs, terminating in small sharp ventral tubercles, or by straight ribs on the inner part of the flank and rounded mid-lateral tubercles giving rise to one or several strongly rursiradiate ribs on the outer flank. The suture is finely divided, with subphylloid folioles.

Discussion and occurrence. This group of ammonites was originally named *Discoceras* by Kossmat (1895), but subsequently replaced by *Forbesiceras* (1897) because of the prior usage of *Discoceras* by Barrande in 1867 for Ordovician nautiloids.

Forbesiceras ranges throughout the English Cenomanian, but is always very rare. Elsewhere, the genus is also restricted to the Cenomanian, and is known from Europe, Africa, Madagascar, southern India, and Texas. In all these places it is rare, and as a result most species are based on only a few specimens, with but slight interspecific differences. Species limits and synonymy are also complicated by the introduction of names based on 2 differing groups of material, limestone specimens of large size, and minute pyritic nuclei. The latter mainly come from north Africa and Madagascar. *Neopulchellia* is thus almost certainly a synonym of *Forbesiceras* (Casey 1965). The problem of correlating pyritic nuclei and limestone casts is acute in several other Cenomanian genera, e.g. *Acanthoceras*, *Mantelliceras*, and *Hypoturrilites*.

Forbesiceras largilliertianum (d'Orbigny)

1841 *Ammonites largilliertianus* d'Orbigny, p. 320, pl. 95.
1925 *Forbesiceras largilliertianum* (d'Orbigny); Diener, p. 180 (with synonymy).
?1940 *Forbesiceras largilliertianum* (d'Orbigny); Fabre, p. 221, pl. 6, fig. 9.
1951 *Forbesiceras largilliertianum* (d'Orbigny); Wright and Wright, p. 23.
1964 *Forbesiceras largilliertianum* (d'Orbigny); Collignon, p. 19, pl. 321, fig. 1409; p. 60, pl. 324, fig. 1499.

Discussion. This is a rather rare species. I have examined specimens in the d'Orbigny Collection, the figured specimens of *Ammonites complanatus* (Mantell) (a synonym) and the specimen figured by Crick (1907, p. 180, pl. 11, fig. 6). *F. beaumontianum* (d'Orbigny 1841, p. 328, pl. 98, figs. 3–5) is close to this species, but has a wider umbilicus, stronger ornament, and a broader, flatter venter.

Occurrence. Rare in the Lower and Middle Cenomanian of southern England; occurring widely in Europe, Africa, Asia, and India.

Forbesiceras beaumontianum (d'Orbigny)

1841 *Ammonites beaumontianus* d'Orbigny, p. 328, pl. 98, figs. 3–5.
1965 *Forbesiceras beaumontianum* (d'Orbigny); Casey, p. 460, text-fig. 173.

Discussion. I have examined the type specimens in the d'Orbigny Collection. This species is very similar to *F. largilliertianum* (see above).

Occurrence. Very rare, basement bed of Wilmington Sands, Wilmington (south Devon) (Lower Cenomanian); Lower Cenomanian of France (Hancock 1959, etc.).

Forbesiceras obtectum (Sharpe)

Plate 16, fig. 3; Plate 9, figs. 3*a*, *b*; Plate 46, fig. 3

1853 *Ammonites obtectus* Sharpe, p. 20, pl. 7, figs. 4*a–c*.
1896 *Ammonites obtectus* Sharpe; Jukes-Browne and Hill, p. 156.
1907 *Forbesiceras obtectum* (Sharpe); Pervinquière, p. 108, pl. 6, figs. 7–11; text-figs. 31–34.
1910 *Forbesiceras obtectum* (Sharpe); Pervinquière, p. 23.
1925 *Forbesiceras obtectum* (Sharpe); Diener, p. 181.
1928 *Forbesiceras obtectus* (Sharpe); Collignon, p. 27, pl. 2, figs. 13, 13*a*.
1940 *Forbesiceras obtectum* (Sharpe); Basse de Menorval, p. 222, pl. 5, fig. 14.
1951 *Forbesiceras obtectum* (Sharpe); Wright and Wright, p. 24.
?1965 *Forbesiceras obtectum* (Sharpe); Wood, p. 302.

Discussion. The holotype of this species, from Chardstock (Devon) (Sharpe 1853, pl. 7, figs. 4*a–c*) is lost. At larger dimensions than the holotype, this species develops strongly rursiradiate ribbing on the outer part of the flank. This accentuates the trend seen on the last part of the holotype, so that this species comes to resemble *F. subobtectum* Kossmat, although the ornament is very faint (Pl. 46, fig. 3).

Several species which are very close to *F. obtectum* have been described. *F. subobtectum* has a much coarser ornament on the whorl sides and transverse ribbing on

the venter at small sizes, although this is lost in large specimens (see Collignon 1964, pl. 335, fig. 1501, top figure). *F. pseudobtectum* Collignon (1964, p. 60, pl. 334, fig. 1500) lacks ribbing on the inner part of the flank and has no keel. *F. conlini* Stephenson (1952, p. 205, pl. 56, fig. 1; pl. 57, figs. 2–5) lacks strongly rursiradiate ribbing on the outer part of the flank, but is otherwise very similar.

Occurrence. Rare; Middle Cenomanian, Chalk Basement Bed of Chardstock and Snowdon Hill, Chard (Somerset); 'Lower Chalk', Ventnor, Isle of Wight (GSM 37878, etc.). This species is recorded by Meyer (1874) from bed 11 (= Bed A) of the Cenomanian Limestone of Lower Cenomanian age of the Devon coast. Wood (1965) recorded it from a horizon close to the Lower–Middle Cenomanian boundary at Folkestone (Kent).

Forbesiceras sculptum Crick

Plate 15, figs. 5, 6*a*, *b*; Plate 16, figs. 1*a*–*c*, 2*a*, *b*; Plate 45, figs. 5*a*, *b*

1907 *Forbesiceras sculptum* Crick, p. 182, pl. 11, figs. 7, 7*a*.
1907 *Forbesiceras nodosum* Crick, p. 182, pl. 11, figs. 8–8*c*.
1931 *Forbesiceras sculptum* Crick; Basse de Menorval, p. 39.
1951 *Forbesiceras sculptum* Crick; Wright and Wright, p. 24.
1955 *Forbesiceras sculptum* Crick; Reyment, p. 21, fig. 8*b*.
?*non* 1964 *Forbesiceras nodosum* Crick; Collignon, p. 63, pl. 336, fig. 1503.
1964 *Forbesiceras clarki* Collignon, p. 64, pl. 336, fig. 1505.
?1964 *Forbesiceras furnishi* Collignon, p. 63, pl. 336, fig. 1504.

Discussion. The holotype of *Forbesiceras sculptum* (Pl. 15, figs. 6*a*, *b*), described in detail by Crick (1907), is a fragment of a small individual. It can be matched with the inner whorls of a medium-sized individual in the Sedgwick Museum (Pl. 16, figs. 1*a*–*c*), which demonstrates a transition into the distinctive lateral and ventral ornament of the holotype of *F. nodosum* Crick (Pl. 15, fig. 5), indicating that the types of *nodosum* and *sculptum* are the same species.

F. furnishi Collignon (1964, p. 63, pl. 336, fig. 1504) differs from this species only in having much finer ribbing, and is probably a mere variant. *F. clarki* Collignon (1964, p. 64, pl. 336, fig. 1505) can be matched with the specimen shown in Plate 16, figs. 1*a*–*c*, and is also a synonym of *F. sculptum*. *F. nodosum* Crick of Collignon (1964, p. 63, pl. 336, fig. 1503) appears to belong to a more finely ornamented and distinct form, but the figure is poor. *F. conlini* Stephenson (1952, p. 205, pl. 56, fig. 1; pl. 57, figs. 2–5) is differentiated from *F. sculptum* mainly by the presence of mid-lateral nodes at small diameters, and scarcely merits specific separation, so far as can be seen from the figures.

Occurrence. Extremely rare; English specimens are from unknown horizons in the Lower Chalk near Ventnor, Isle of Wight (SMC B3527, Pl. 16, figs. 1*a*–*c*; GSM 88283, Wood Collection, Pl. 45, figs. 5*a*, *b*), and a specimen from the *M. saxbii* assemblage fauna of Bed A_2 of the Cenomanian Limestone, Chardstock (Devon) (Pl. 16, figs. 2*a*, *b*). Elsewhere, the species is recorded from Zululand (the types), Madagascar, and the Calabar Province of Nigeria (Reyment 1955).

Forms best referred to as *F.* aff. *sculptum* occur in the *T. acutus* assemblage fauna of the Chalk Basement Bed at Snowdon Hill, Chard (Somerset).

Superfamily ACANTHOCERATACEAE Hyatt 1900
Family ACANTHOCERATIDAE Hyatt 1900

This coarsely ornamented group of ammonites forms an important part of the Cenomanian ammonite fauna. 3 genera, *Mantelliceras*, *Acanthoceras*, and *Calycoceras* are of great stratigraphic value, and individual species often have world-wide distribution. The group thus forms a striking contrast to the largely boreal hoplitids.

The family Acanthoceratidae is at present divided into 4 subfamilies, Mantelliceratinae, Acanthoceratinae, Metoicoceratinae, and Mammitinae (Wright 1957). All are intimately related.

The Mantelliceratinae appear close to the Albian/Cenomanian boundary, with *Mantelliceras* as a direct descendant of *Stoliczkaia* (Lyelliceratidae), as are an unnamed group of '*Paracalycoceras*'-like forms. Accompanying *Mantelliceras* in the Lower Cenomanian are *Sharpeiceras*, *Graysonites*, *Utaturiceras*, and *Paracalycoceras* (for an examination of these genera see below), as are genera and subgenera based on minute pyritic nuclei, i.e. *Submantelliceras* and *Cottreauites*, both of which are of doubtful validity. In Madagascar there are consistent records (summarized by Collignon 1959) of the association of *Mantelliceras* and *Calycoceras*, not seen elsewhere in the world. On strictly morphological grounds, there can be little doubt that *Calycoceras* [*sensu lato*] is derived from *Mantelliceras*.

Closely related to *Calycoceras* are *Eucalycoceras* and *Tarrantoceras*; *Hourcquiceras* seems to me to be of doubtful status. Other genera referred to the Mantelliceratinae by Wright (1957) are *Neopulchellia*, probably based on forbesiceratid nuclei (compare Casey 1965). *Acompsoceras* (= *Pseudacompsoceras*) probably belongs here too. I am uncertain of the affinities of *Tunesites*.

The Acanthoceratinae are believed to arise from the Mantelliceratinae via *Calycoceras*, but there is no good stratigraphic evidence for this. *Acanthoceras* is the parent stock of the subfamily, giving rise to *Protacanthoceras* and *Euomphaloceras* in the Middle Cenomanian, and probably *Romaniceras*, *Yubariceras*, and *Dunveganoceras* at higher levels.

Protacanthoceras gives rise to *Neocardioceras* and, perhaps, via an unnamed Upper Cenomanian genus, to *Metoicoceras*, and hence the Metoicoceratinae. *Euomphaloceras* gives rise to *Kanabiceras*. '*Paracanthoceras*' (= *Plesiacanthoceras*) is of doubtful status and value, whilst the Lower Cenomanian micromorph *Neosaynoceras* is difficult to place in any group.

The Mammitinae are derived from several acanthoceratinid stocks.

Subfamily MANTELLICERATINAE Hyatt 1900
Genus MANTELLICERAS Hyatt 1900

Type species. Ammonites mantelli J. Sowerby (1814), by the original designation of Hyatt (1900, p. 113).

Diagnosis. Medium-sized (rarely large) ammonites, evolute and inflated to involute and compressed, usually with umbilical, lower lateral, lower and upper ventro-lateral tubercles on long ribs, alternating with short ribs with lower lateral and lower and upper ventro-lateral tubercles at some stage in the ontogeny. Some forms lose

all but the upper ventro-lateral tubercles early in their ontogeny and may become non-tuberculate when adult. Venter typically raised, but a siphonal tubercle is never developed. Suture-line relatively simple, with moderately subdivided rectangular bifid elements.

Discussion. From *Mantelliceras mantelli*, the type species of the genus, there is a considerable range of morphological variation. Thus with an increasing degree of inflation, the ribbing and tuberculation tends to become stronger, as in *M. tuberculatum* (Mantell) and *M. cantianum* (Spath). Both these and other inflated species have a full set of tubercles early in development, although these weaken and may be lost in the adult. In other forms of *Mantelliceras*, e.g. *M. costatum* (Mantell), although the degree of inflation is similar to that of *M. mantelli*, all but the upper ventro-lateral tubercles are lost early in ontogeny. This feature is also seen in the more compressed *Mantelliceras*, e.g. *M. saxbii* (Sharpe), where the middle and later growth stages have lost all but the upper ventro-lateral tubercles, which are often lost on the adult body chambers although they may reappear irregularly close to the aperture. The lateral tubercle is absent throughout most, if not all, of the ontogeny of some species of *Mantelliceras*.

There are a number of genera related to *Mantelliceras*, and they can be distinguished as follows:

1. *Acanthoceras* (Middle and Upper Cenomanian). This genus differs from *Mantelliceras* in its larger size, square whorl section, and the absence of a mid-lateral tubercle, but has a siphonal tubercle, which is never developed in *Mantelliceras*. Long ribs only are developed on the body whorl of many species of *Acanthoceras*.

2. *Calycoceras* (Middle Cenomanian to Lower Turonian). *Calycoceras* [*sensu stricto*] (i.e. *C. naviculare* (Mantell) and closely related forms) is readily separable from *Mantelliceras* by its highly inflated whorl section, and the presence of a siphonal tubercle during the early stages in ontogeny. When adult, or when the siphonal tubercle has been lost, it becomes extremely difficult to separate the 2 genera, although in general, inflated species can often be separated in that the greatest whorl breadth is at the umbilical tubercle in *Calycoceras* and at the lateral tubercle in *Mantelliceras* (I am grateful to Mr. C. W. Wright for pointing out this useful fact).

Calycoceras is a Middle to Upper Cenomanian/Lower Turonian genus over most of the world; reported associations of *Calycoceras* and *Mantelliceras* together in Europe (Renz 1963, Busnardo *et al.* 1966) are based on dubious species of '*Calycoceras*', although Collignon (1937, 1959, 1964) consistently recorded the 2 genera together in Madagascar.

3. *Sharpeiceras* (Lower Cenomanian). This genus is usually readily separable from *Mantelliceras* by its extremely flat sides, a depressed siphonal region and ribs that are all long in the middle and later growth stages, with umbilical, mid-lateral, lower and upper ventro-lateral tubercles, as in the type species, *S. laticlavium* (Sharpe).

According to Collignon (1928–1929, p. 37), *Sharpeiceras piveteaui* (Collignon) has alternately long and short ribs when young, although the generic position of the specimen is perhaps a little uncertain. Adult specimens of *Sharpeiceras* have a tendency to develop modest ventro-lateral horns by the fusion of the lower and upper ventro-lateral tubercles.

4. *Eucalycoceras* (Middle/Upper Cenomanian to Lower Turonian?). This genus can be separated from *Mantelliceras* by the presence of a siphonal tubercle on a high arched venter and a high, flat-sided whorl section.

5. *Tarrantoceras*. This upper Cenomanian genus (Pl. 17, figs. 2*a*, *b*) is a striking homeomorph of *Mantelliceras*. The distinctive features, as Stephenson (1955) demonstrated when describing the genus, is the presence of a siphonal tubercle in the juveniles, some of which (Stephenson 1955, pl. 6, figs. 10–12, etc.) have a distinct *Protacanthoceras*-like appearance. The suture line is also distinctive (Stephenson 1955, p. 59).

6. *Budaiceras*. Like *Mantelliceras*, this is a Lower Cenomanian genus, known, however, only from the southern United States (Wright 1957). The 2 genera differ in that *Budaiceras* has distinctly flexuous ribbing, and siphonal clavi, which are twice as numerous as the ribs on the outer whorl.

7. *Acompsoceras* (Lower and Middle Cenomanian). This highly variable genus is separated from *Mantelliceras* by the suture line, which has distinctly sub-rounded and sometimes phylloid folioles. The ornament is also distinctive; thus in coarsely ornamented *sarthense*-type species there are strong ribs which branch from an umbilical tubercle, and although the ribs also bear lateral, lower and upper ventro-lateral tubercles, as in *Mantelliceras*, the upper ventro-lateral tubercles are pronouncedly clavate. There is a very smooth ventral area in *Acompsoceras*, often subcarinate, whilst the adult whorls may be almost unornamented (Schlüter 1871, pl. 3, figs. 4, 5).

Some nuclei (i.e. *Acompsoceras melleguense* Sornay, *A. dubourdieui* Sornay; Sornay 1955, pp. 20–23, pl. 2, figs. 5, 7, 11) appear to have a siphonal tubercle (Sornay 1955, pl. 2, fig. 7), although both Sornay (1955, p. 22) and Collignon (1928–1929, p. 42) commented on the difficulties of recognizing nuclei of the genus.

8. *Graysonites*. This genus, described by Young (1958*a*) from the Lower Cenomanian of Texas, has also been recorded from California (Matsumoto 1959, 1960), Japan (Matsumoto 1960), and Spain (Wiedmann 1959, 1964). *Graysonites* have 'submantellicerine' nuclei (see below), but in the adult have enormous ventro-lateral horns developed from the fusion of the upper and lower ventro-lateral tubercles.

9. *Utaturiceras*. This Lower Cenomanian genus has been revised very completely by Matsumoto, Sastry, and Sarkar (1966). The chief distinguishing feature is a much more deeply divided suture line than that in typical *Mantelliceras*. Otherwise, the ornament is very similar to that of *Mantelliceras* of the *ventnorense* and *saxbii* group in general style of ribbing (discussed in Kennedy and Hancock 1971).

Utaturiceras is another genus with 'submantellicerine' nuclei, and subsequent work may show that it should be treated as a subgenus of *Mantelliceras*.

10. *Stoliczkaia* (Upper Albian to Lower Cenomanian). This genus gives rise to *Mantelliceras*, and is particularly difficult to separate under some circumstances. 3 subgenera are recognized:

S. (*Faraudiella*) is readily separated from *Mantelliceras*. It is compressed, with a very small umbilicus, a sharp venter, and a row of siphonal tubercles which persist onto the body chamber.

S. (*Villoutreysia*) is closer to *Mantelliceras*, but Casey (1965) characterized it as

a *Stoliczkaia* with a broad, square venter and strong persistent ribbing, which differs from *Mantelliceras* in a much earlier loss of ventral tubercles, squarer whorls, and a narrower and shallower umbilicus.

S. (*Stoliczkaia*) can usually be separated from *Mantelliceras* in the middle and later stages because of the rounding of the venter, the general lack of tubercles and the strange, subdued, distant ribbing on the body chamber. Nuclei (Pl. 17, figs. 1*a*, *b*, 5*a*–*c*, 6*a*, *b*, 7*a*, *b*) are often distinct (Pl. 17, figs. 1*a*, *b*, 6*a*, *b*) in being very involute, compressed, having only ventro-lateral tubercles and a raised venter. Others (Pl. 17, figs. 5*a*–*c*, 7*a*, *b*) are distinctly submantellicerine, and cannot be safely separated from nuclei of *Mantelliceras* such as *M. saxbii*, which lack good lateral and umbilical tubercles at this diameter. This close resemblance is not surprising considering the close affinities of the 2 genera; *Mantelliceras* probably develops from *S.* (*Stoliczkaia*) by some sort of proterogenesis.

11. *Paracalycoceras* (Lower Cenomanian) differs from *Mantelliceras* in having a raised siphonal region when young, and developing very strong, non-tuberculate, flexuous, backwards directed ribs when adult. These ribs are of several lengths.

All of these genera are well known from small, medium-sized, and large specimens, and with knowledge of ontogeny, are fairly readily separated from *Mantelliceras*, each other, and related genera (*Mammites*, *Metoicoceras*, *Neophlycticeras*). However, when only juveniles are known (as in the case of some genera and many species from the thick marl successions of north Africa), it becomes difficult to separate these nuclei into the genera discussed above. As a result, several 'genera' have been introduced for these nuclei. 2 are particularly important here; a third, *Neopulchellia* is (according to Casey 1965) a forbesiceratid nucleus, and does not require further discussion.

12. *Cottreauites*. This genus has been recorded from the Lower Cenomanian of Madagascar and north Africa, the chief accounts being those of Collignon (1928–1929) and Sornay (1955); Wright (1957) regarded this form as a subgenus of *Mantelliceras*. *Cottreauites* covers a very distinctive group of ammonites, with a strikingly subcarinate venter, distinct ventro-lateral tubercles, and a suture line with largely undivided, almost pseudoceratitic, elements.

13. *Submantelliceras*. This 'genus' or 'subgenus' is one of the chief headaches of Cenomanian ammonite systematics. The name was introduced by Spath (1923*b*) as follows: '*Submantelliceras* gen. nov. (type: *Acanthoceras aumalense* (Coquand) Pervinquière: "Ammon. Cret. Alger.," *Mem. Soc. Geol. France, Pal.*, (**42**), 1910, p. 42, pl. 4, fig. 11.' The specimen referred to is described by Pervinquière (1910, explanation of pl. 4) as 'paraît être le type figuré par Coquand, pl. 1, fig. 27–28'. This specimen is taken by Pervinquière as one of a number of 'cotypes' of Coquand's species, a species which Pervinquière discussed at length 3 years previously (1907, pp. 296–298, pl. 16, figs. 6*a*, *b*–11*a*–*c*). The 'cotype' series shows considerable variation, and at present little can be said other than that they are a series of generically unassignable nuclei.

The specimen specifically referred to by Spath (Pervinquière's figure is reproduced as Pl. 17, fig. 4) is figured in side view only; it is moderately involute, with (apparently) very flat sides, and very faint ribs, which bear distinct lower and upper ventro-lateral tubercles. When examining Coquand's collection in Budapest in 1964, I was unable

to locate this specimen. The British specimens of '*Submantelliceras*' (Spath 1923*a*; Wright and Wright 1951, p. 24) are figured as Plate 17, figs. 3*a*, *b*, 8*a–d*.

Subsequent authors have shown that nuclei of this general type occur in several genera, e.g. *Graysonites* (Young 1958*a*) and *Utaturiceras* (Matsumoto *et al.* 1966), although in no instance have adults with early whorls which correspond to the specimen cited by Spath been described. Wright (1957) considered that '*Submantelliceras* includes merely inner whorls of compressed species of this (*Mantelliceras*) and other genera'; as Young (1958*a*) noted, *Graysonites* is one of these 'other genera'.

Submantelliceras is thus a *nomen dubium* at present, and should not be used. If, however, subsequent work shows that it has distinctive outer whorls, it may become a desirable, and indeed useful generic or subgeneric name for the '*Acanthoceras*' *villei* (Coquand) or '*Acanthoceras*' *suzannae* (Coquand) group of ammonites, if these are separable from *Graysonites* (see Young 1958*a*); it may even have priority over this latter genus.

One name remains to be discussed at this point; Busnardo *et al.* (1966, pp. 223–225) introduced the subgenus *Mantelliceras* (*Couloniceras*) as follows:

> Remarques au sujet du genre *Mantelliceras*.
>
> Ce genre ubiquiste est abondamment représenté dans le Cénomanien inférieur par de nombreuses espèces. La plupart d'entre elles ont une section subquadratique et 4 tubercules par côte, ainsi que le montre le générotype: *M. mantelli* (Sow.).
>
> Mais il existe un petit nombre de formes dont les caractères sont suffisamment différents du groupe *M. mantelli* pour permettre leur rangement au sein d'un sous-genre nouveau: *Couloniceras* dont le subgénérotype est: *Ammonites couloni* d'Orb., 1840, p. 340, pl. 104, seulement, et M. Collignon, 1937, p. 32, pl. XI, fig. 1.
>
> Diagnose. — Section étroite, flancs plats ou à peine incurvés; ombilic assez ouvert; côtes radiales, les unes partant de l'ombilic, les autres régulièrement alternantes avec les premières, débutant vers le milieu des flancs. Elles s'atténuent fortement ou s'interrompent sur le bord externe.
>
> Tubercule ombilical à peine sensible, tubercules latéraux absents, sauf sur les tours jeunes, fort tubercule périsiphonal. La représentation la plus exacte de ce groupe est donnée par la figuration de M. Collignon 1937, *Acanthoceras couloni* d'Orb., p. 32, pl. XI, fig. 1, 1*a*, 1*b*, qui représente le véritable néotype de l'espèce, et en conséquence le subgénérotype de *Couloniceras*. Les espèces suivantes peuvent être rangée dans ce nouveau sous-genre:
>
> *M.* (*Couloniceras*) *biroi* Collignon 1964
> *M.* (*Couloniceras*) *agrawali* Collignon 1964
> *M.* (*Couloniceras*) *cressierense* Renz 1963
> *M.* (*Couloniceras*) *planum* Renz 1963
> *M.* (*Couloniceras*) *rouqueti* n. sp. 1966
>
> Toutes appartiennent au Cénomanien inférieur.

There is every *morphological* transition from this 'subgenus' to *Mantelliceras* of the *mantelli* type; thus there are inflated *Mantelliceras* without lateral tubercles (*M. costatum*), and those which are compressed with lateral tubercles (*M. tenue* Spath), while the stage at which the lateral and other tubercles are lost is highly variable between species, and between individuals of the same species.

Couloniceras is not used here.

Occurrence. *Mantelliceras* has a world-wide distribution in the Lower Cenomanian and seems to be restricted to this part of the stage, although Collignon (1939, 1959, 1964, etc.) consistently recorded it associated with *Calycoceras* in his Madagascan

Zone of *Mantelliceras mantelli* and *Calycoceras newboldi*. *Calycoceras newboldi* (Kossmat) is normally regarded as a Middle to Upper Cenomanian form elsewhere in the world. In England the 2 species do occur associated; i.e. in the Chalk Basement Bed of south-west England, and Wright (*in* Arkell 1947, p. 197) has referred the Chalk Basement Bed of the Isle of Purbeck (Dorset) to Collignon's *M. mantelli* and *C. newboldi* Zone. However, this 'association' (Wright, *in litt.*) consists of a Middle Cenomanian phosphatized and unphosphatized fauna with much older remanié and derived Lower Cenomanian and Upper Albian material, with a distinct preservation (see also Hancock *in* Smith 1957, pp. 141, 142).

Mantelliceras mantelli (J. Sowerby)

Plate 17, figs. 9*a–c*, 10*a–c*; Plate 20, fig. 2; Plate 23, figs. 2*a*, *b*

1814 *Ammonites mantelli* J. Sowerby, p. 119, pl. 55, lower figure only.
non 1822 *Ammonites mantelli* J. Sowerby; Mantell, p. 113, pl. 21, fig. 9; pl. 22, fig. 1.
non 1841 *Ammonites mantelli* J. Sowerby; d'Orbigny, p. 340, pls. 103, 104.
1857 *Ammonites mantelli* J. Sowerby; Sharpe, p. 40, pl. 18, figs. 7*a–c* only.
?1863 *Ammonites mantelli* J. Sowerby; Pictet and Campiche, p. 200 (pars), *non* pl. 26.
1863 *Ammonites mantelli* J. Sowerby; Pictet, p. 22.
1864 *Ammonites mantelli* J. Sowerby; Stoliczka, p. 81, pl. 41, figs. 2, 3; pl. 42, fig. 2, *non* 1, 3.
?1871 *Ammonites mantelli* J. Sowerby; Schlüter, p. 12, pl. 5, figs. 1, 2, 5–8.
non 1875 *Ammonites mantelli* J. Sowerby; Geinitz, p. 279, pl. 62, figs. 1, 2.
1897 *Acanthoceras mantelli* (J. Sowerby); Kossmat, p. 23, pl. 4, figs. 4*a–c*.
non 1898 *Acanthoceras* cf. *mantelli* (J. Sowerby); Choffat, p. 73, pl. 5, fig. 1.
1903 *Mantelliceras mantelli* (J. Sowerby); Hyatt, p. 114.
non 1907 *Acanthoceras mantelli* (J. Sowerby); Boule, Lemoine, and Thévenin, p. 29, pl. 8, fig. 3.
non 1907 *Acanthoceras mantelli* (J. Sowerby); Pervinquière, p. 288, pl. 16, fig. 18.
?1910 *Acanthoceras mantelli* (J. Sowerby); Pervinquière, p. 41, pl. 4, fig. 1.
1911 *Mantelliceras mantelli* (J. Sowerby); H. Douvillé, p. 299.
non 1920 *Acanthoceras mantelli* (J. Sowerby); Taubenhaus, p. 13, pl. 1, fig. 1.
?1937 *Mantelliceras mantelli* (J. Sowerby); Collignon, p. 53, pl. 7, fig. 1; pl. 9, fig. 7.
?1940 *Mantelliceras* cf. *mantelli* (J. Sowerby); Fabre, p. 236.
1951 *Mantelliceras mantelli* (J. Sowerby); Wright and Wright, p. 24.
1959 *Mantelliceras mantelli* (J. Sowerby); Cieśliński, p. 63, fig. 33.
1963 *Mantelliceras mantelli* (J. Sowerby); Renz, p. 1100, pl. 2, figs. 3*a*, *b*; pl. 4, figs. 5, 6.
1964 *Mantelliceras mantelli* (J. Sowerby); Collignon, p. 27, pl. 333, fig. 1436; pl. 337, figs. 1506–1508; ?pl. 338, figs. 1509, 1510.

Lectotype. Here designated, the original of the smaller, lower left-hand figure of Sowerby's (1814) plate 55, BMNH 43940*a*, from the Lower Chalk of Ringmer, near Lewes (Sussex).

Diagnosis. A moderately involute *Mantelliceras* with characteristically octagonal whorl section. There are about 37 alternately long and short ribs per whorl. The long ribs have umbilical, mid-lateral, lower and upper ventro-lateral tubercles. The shorter ribs lack an umbilical tubercle and sometimes lack the lateral tubercle. On the outer whorls there is a tendency for all but the upper ventro-lateral tubercles to disappear.

Description. The lectotype is a medium-sized, somewhat damaged, crushed composite internal mould in hard limestone. Fragments of *Inoceramus* are embedded in the umbilicus of the unfigured side. It is involute, about two-thirds of the previous

whorl being covered. The whorl section is slightly depressed and wider than high, rounded in intercostal section, and octagonal in costal section. The umbilicus is relatively narrow and deep, the umbilical wall steep, rounded and undercut, and the umbilical shoulder is rounded.

There are 36 ribs per whorl at a diameter of 45 mm; 18 of these ribs are long, arising at the umbilical seam and passing weakly up the umbilical wall. At the umbilical shoulder, most produce a small bullate umbilical tubercle. The ribs are strong across the flank, rounded and slightly narrower than the interspaces. A small bullate tubercle is present at mid-flank. On the upper flank, the ribs slope gently forwards and connect to weak transversely elongate lower ventro-lateral tubercles. From this tubercle the ribs sweep slightly forwards to a slightly clavate upper ventro-lateral tubercle. The upper ventro-lateral tubercles lie on either side of a rather narrow venter, across which they are connected by a broad, slightly swollen, rounded rib. Some of the ribs, especially towards the largest preserved parts of the specimen, lack an umbilical or lateral tubercle.

Shorter, intercalated ribs alternate with the long ribs. These intercalated ribs arise at mid-flank, and bear lower and upper ventro-lateral tubercles only; otherwise they are identical with the corresponding portions of the long ribs.

In some cases the long and short ribs alternate regularly; in other cases, long ribs, with a full complement of tubercles, are separated by a short rib and a long rib with only ventro-lateral tubercles. The 8 tubercles on each long rib lie at the corners of an octagon, and this gives the shell a characteristic appearance. The sutures are not visible.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 43940*a*, lectotype	45·0	22·8 (50·7)	21·5 (47·8)	10·5 (23·3)	36
BMNH 50161*a*	44·3	22·5 (50·8)	22·0 (49·7)	11·0 (24·8)	32

Discussion. The octagonal whorl section of small and medium-sized specimens, together with the rather dense ribbing, is diagnostic of this species, and separates it from all other described forms occurring in the English Cenomanian.

Collignon (1964, p. 66) showed that adult specimens of *M. mantelli* lose their tubercles, and have alternately long and short ribs. *M. mantelli* var. *percostata* (Collignon) (1964, p. 68, pl. 338, fig. 151*a*) differs from the type in having 50 as opposed to about 40 ribs per whorl.

Occurrence. This is a rather scarce species of *Mantelliceras*, most frequent in the lowest part of the Lower Cenomanian, i.e. *carcitanensis* assemblage faunas, but also occurring in *saxbii* and *M.* gr. *dixoni* assemblage faunas. *M. mantelli* occurs at this general level all over southern England, and is also known from the Lower Cenomanian of Europe, north Africa, India, Madagascar, and the U.S.S.R.

Mantelliceras cantianum Spath

Plate 18, figs. 1*a–c*; Plate 20, figs. 1*a–c*; Plate 26, figs. 1, 5

1857 *Ammonites navicularis* Mantell; Sharpe, p. 39, pl. 18, figs. 1, 2 (*non* Mantell).
1926*a* *Mantelliceras cantianum* Spath, p. 82.

1931 *Mantelliceras budaense* Adkins, p. 41, pl. 2, fig. 3; pl. 4, fig. 10.
1937*a* *Mantelliceras cantianum* Spath, p. 279.
1951 *Mantelliceras cantianum* Spath; Wright and Wright, p. 24.
1964 *Mantelliceras cantianum* Spath; Collignon, p. 80, pl. 344, fig. 1532, fig. 1533 (var. *unituberculata*), fig. 1534 (var. *abrupta*).
1969 *Mantelliceras cantianum* Spath; Matsumoto *et al.*, p. 256, pl. 27, fig. 3; pl. 28, fig. 7.

Holotype. By the original designation of Spath (1926*a*, p. 82), the original of *Ammonites navicularis* Mantell (Sharpe 1857, pl. 18, fig. 1) (*non* Mantell), BMNH 36834, from Dover (Kent), probably from the lower part of the *mantelli* Zone.

Diagnosis. A moderately evolute coarsely ribbed *Mantelliceras* with an inflated, depressed whorl section, and strong, closely spaced umbilical and lower lateral tubercles which are retained to a large diameter.

Description. The type is a well-preserved chalk specimen, a composite internal mould with a blue-black iron sulphide coat. Part of one side of the specimen is worn smooth. Just under half the last whorl is body chamber.

The shell is evolute, about one-fifth of the previous whorl being covered. The whorl section is inflated, much wider than high, with the greatest breadth at the lower lateral tubercle. The intercostal whorl section is oval to rounded; the costal section is depressed and polygonal. The umbilicus is broad and deep, the umbilical wall steep, and the umbilical shoulder broadly rounded.

There are 32 ribs at a diameter of 117 mm, alternately long and short. The long ribs arise at the umbilical shoulder, and are broad, coarse and rounded, and approximately the same breadth as the interspaces. These ribs are gently flexed across the sides, and each bears a large, strong, rounded umbilical tubercle, and a very strong transversely elongate lower lateral tubercle, the 2 tubercles being connected by a very strong, high rib.

Up to a diameter of about 100 mm there is a small but distinct lower ventro-lateral tubercle. Beyond this diameter there is a slight angulation in the costal whorl section at this point. There are small rounded to transversely elongate upper ventro-lateral tubercles on each side of the broadly rounded venter. The upper ventro-lateral tubercles are connected across the venter by a broad, strong, rounded rib.

These long ribs alternate very regularly with much shorter, intercalated ribs. These intercalated ribs arise just below mid-flank, and rapidly reach a comparable strength to the long ribs, with which they are identical in their upper lateral, ventro-lateral, and ventral development. The sutures are not visible.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 36834, holotype					
costal	117	—	49 (41·9)	37 (31·6)	32

Discussion. The inflated section, coarse, rursiradiate ribbing, and very strong development of closely spaced umbilical and lower lateral tubercles distinguish this from all other described species of *Mantelliceras*. *M. cantianum* var. *unituberculata* Collignon (1964, p. 80, pl. 344, fig. 1533) differs from the typical form of the species in lacking a lower lateral tubercle. *M. cantianum* var. *abrupta* Collignon (1964, p. 80, pl. 344, fig. 1534) is merely a very coarsely and distantly ribbed form.

Occurrence. Lower Cenomanian, common in *carcitanensis* assemblage faunas, also occurring in the overlying *saxbii* assemblage faunas all over southern England. An important specimen in the British Museum (Natural History) is from Hunstanton (Norfolk) (BMNH C29622). It is preserved in a gritty chalk full of *Inoceramus*, suggesting derivation from the *Inoceramus* Bed.

The species also occurs in the Lower Cenomanian of Madagascar, perhaps western Europe (Thomel 1965*a*, *b*; ?Schlüter 1871, pl. 5, figs. 3, 4), Japan (Matsumoto *et al.* 1969), and North America (Matsumoto 1959, p. 71).

Mantelliceras costatum (Mantell)

Plate 19, figs. 1*a*, *b*, 2*a–c*; Plate 24, fig. 1

1822 *Ammonites mantelli* var. *costata* Mantell, pp. 113, 114, pl. 21, fig. 9 only.
1926*b* *Mantelliceras costatum* (Mantell); Spath, p. 431.
1951 *Mantelliceras costatum* (Mantell); Wright and Wright, p. 24.

Lectotype. Here designated, the original of *Ammonites mantelli* var. *costata* Mantell 1822, p. 113, pl. 21, fig. 9 (BMNH C5028). The specimen bears Mantell's original green label, now faded and illegible.

Diagnosis. A moderately inflated and strongly ribbed *Mantelliceras* characterized by early loss of all but the upper ventro-lateral tubercles.

Description. The lectotype is a well-preserved, septate, composite internal mould in grey limestone. The specimen is slightly distorted, and one side is rather badly abraded. The shell is involute, about half the previous whorl being covered. The whorl section is moderately inflated, as wide or slightly wider than high. It is rounded to oval in intercostal section, and rounded in costal section with a flattened venter. The umbilicus is deep and rather narrow, with a steep rounded umbilical wall, and a rounded umbilical shoulder.

There are 38 ribs at a diameter of 60 mm; 20 of these ribs are long, each arising just above the umbilical seam. They are strong, rounded, narrower than the interspaces, passing straight across the whorl sides, with maximum strength at mid-flank. Up to a diameter of 30 mm there are weak bullate umbilical tubercles, lower and upper ventro-lateral tubercles. Beyond this diameter there are only upper ventro-lateral tubercles, one on each side of a rather wide tabulate venter. They are connected across the venter by a strong rounded rib.

The long ribs are separated by 1, or rarely 2 shorter, intercalated ribs. These are of quite irregular length; some arise about a third of the distance up the flank, others do little more than cross the venter, where all the ribs are equally developed. The sutures of the lectotype are not wholly visible, but seem to be of normal *Mantelliceras* type.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH C5028, lectotype	62·7	— (—)	29·0 (46·3)	14·9 (23·8)	38
BMNH 5693, paralectotype					
costal	100	42·5 (42·5)	39·0 (39·0)	23·6 (23·6)	35
intercostal	93·2	38·7 (41·5)	37·0 (39·7)	23·6 (25·3)	35

Discussion. Early loss of umbilical, lateral and lower ventro-lateral tubercles, inflated sides, coarse, very regularly long and short ribs, and retention of upper ventro-lateral tubercles are the distinctive features of this species. It is thus quite distinct from all other named forms occurring in the English Cenomanian.

One of the syntypes of *Mantelliceras batheri* Spath, i.e. *Acanthoceras martimpreyi* Coquand of Pervinquière 1907, pl. 16, fig. 18 (*non* Coquand), may belong to this species.

Occurrence. This species is not uncommon in *carcitanensis* and *saxbii* assemblage faunas all over southern England.

Mantelliceras dixoni Spath

Plate 20, figs. 3*a–c*, 4, 5; Plate 21, figs. 3, 5*a*, *b*; Plate 22, figs. 2*a–c*

1850 *Ammonites milletianus?* J. de C. Sowerby, *in* Dixon, p. 359, pl. 29, fig. 15 (*non* d'Orbigny).
1926*b* *Mantelliceras dixoni* Spath, pp. 427, 430.
1951 *Mantelliceras dixoni* Spath; Wright and Wright, p. 25.

Holotype. By original designation of Spath (1926*b*, p. 430), the original of *Ammonites milletianus?* J. de C. Sowerby *in* Dixon 1850, pl. 29, fig. 15 (*non A. milletianus* d'Orb.), BMNH 33630, from the Lower Chalk of 'Sussex'.

Diagnosis. A small, evolute species of *Mantelliceras*, with strong umbilical, lower lateral and ventro-lateral tubercles when young. All tuberculation is lost at a diameter of 30 mm (?based on a pathological type-specimen).

Description. The holotype is a small, crushed, and distorted composite internal mould in grey chalk. The shell is moderately evolute, just under half the previous whorl being covered. The whorl section appears to have been compressed, and rounded, but the true form has been destroyed by post-burial crushing. The umbilicus is quite broad and shallow. The umbilical wall is sharply rounded.

At a diameter of 30 mm the type had an estimated 30 alternately long and short ribs per whorl. The long ribs arise at the umbilical seam and pass straight across the flank. There are umbilical, lower lateral and upper ventro-lateral tubercles, all of which are present up to a diameter of 20 mm. Clavate upper ventro-lateral tubercles are present on each side of the narrow arched venter up to a diameter of 30 mm.

Intercalated between the long ribs are short ribs, arising just below mid-flank. At first these short ribs bear upper and lower ventro-lateral tubercles, and then upper ventro-lateral tubercles only. These short ribs are as strong as the long ribs on the ventro-lateral shoulders and across the venter.

Beyond 30 mm there is a distinct change in ornament. All the tubercles are lost, other than a small umbilical bulla, whilst the ribs are strong across the venter and flexed at mid-flank, giving the shell a *Stoliczkaia*-like appearance.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 33630, holotype	42·5	16·0 (37·7)	15·0 (35·3)	12·8 (30·1)	30–32

Discussion. Dixon's figure of this species is quite good. I find *M. dixoni* a difficult

form to interpret. The sudden change in ornament could be interpreted as associated with maturity; unfortunately, the position of the last suture is not clear, whilst the specimen is small for an adult *Mantelliceras*.

Alternatively, this may be a pathological specimen, the change being the result of damage during life; however, changes in ornament of this type characterize *Mantelliceras* from the highest parts of the Lower Cenomanian.

Because of the peculiar changes in ornament seen on the type of *M. dixoni*, I have been unable to refer any other specimens to the species with complete certainty.

However, *Mantelliceras* specimens occurring at the top of the Lower Cenomanian at Folkestone (Kent) (Pl. 20, fig. 4; Pl. 21, figs. 3, 5*a*, *b*; Pl. 22, figs. 2*a–c*), in the Medway Valley (= *Metacalycoceras guerangeri* Spath (pars) 1926*b*, p. 431; BMNH C13534–13535, Pl. 20, fig. 5), and Bed B of the Cenomanian Limestone (Wrights' Collection), resemble *Mantelliceras dixoni* in general appearance, but have a tabulate venter and only weakly tuberculate inner whorls. I refer to these as *Mantelliceras* group of *dixoni* (Kennedy 1969, 1970).

These specimens show some resemblance to a number of Madagascan species. Thus *M. pseudohyatti* Collignon (1964, p. 73, pl. 341, fig. 1525) is more densely ribbed and lacks a strikingly tabulate venter. *M. betiokyense* Collignon (1964, p. 78, pl. 343) has a similar ribbing style, although the ribs are finer. *M. birroyi* Collignon (1964, p. 84, pl. 346, figs. 1540, 1541) is very close, but is more densely ribbed, whilst *M. thomeli* Collignon (1964, p. 91, pl. 348, fig. 1551) seems to be more inflated.

Occurrence. Rare in the upper part of the *mantelli* Zone, Kent (?), Sussex (?).

Mantelliceras aff. *souaillonense* (Renz)

Plate 21, figs. 2, 4; Plate 22, figs. 1*a–c*

1963 *Calycoceras souaillonense* Renz, p. 1111, pl. 4, figs. 1–3.

Description. The shell is moderately evolute, about half the previous whorl being covered. The whorl section is inflated, rounded in costal and intercostal section, the greatest breadth being at the lower lateral tubercle. There are 27–29 ribs per whorl.

Up to diameters of about 50 mm the ribs are very variable. Some ribs arise at the umbilical seam and are very strong, with a strong bituberculate umbilical bulla. Of these 2 tubercles, the lower lateral tubercle is the stronger, so that the maximum breadth is at this point. From the bulla, strong, rounded ribs extend across the broad venter, with lower and upper ventro-lateral tubercles, which are lost at diameters of about 35 mm. Beyond this size the ribs pass across the venter without tubercles at the shoulders.

The long ribs are separated by short ribs, arising at, or below, mid-flank, sometimes even extending from the umbilical seam. These short ribs lack an umbilical bulla, and sometimes a lower ventro-lateral tubercle. Beyond 50 mm all tuberculation is lost, except for an occasional umbilical bulla. The ribs are almost all long, and in 2 specimens, show approximation, indicating maturity, at diameters of about 70 mm. Suture not seen.

Discussion. The English material described above differs from the holotype of *M. souaillonense* in having coarser ribbing, and losing tuberculation at much smaller diameters.

The holotype of *M. souaillonense* is unique; further specimens may show that the present material falls within the range of that species.

M. aff. *souaillonense* most closely resembles *M. cantianum*, from which it is almost certainly descended. *M.* aff. *souaillonense* is, however, more inflated, adult at smaller diameters, coarser ribbed, and loses its bituberculate umbilical bulla at a much smaller diameter than *M. cantianum*.

Occurrence. Rare in the *M.* gr. *dixoni* assemblage faunas at Folkestone (Kent), and in Bed B of the Cenomanian Limestone (Wrights' Collection).

Mantelliceras lymense (Spath)

Plate 21, fig. 1; Plate 23, figs. 1*a*, *b*

1907 *Acanthoceras martimpreyi* (Coquand); Pervinquière, p. 289, pl. 16, figs. 16*a*, *b* only (*non* Coquand).
1926*b* *Eucalycoceras lymense* Spath, pp. 427, 431.
non 1939 *Calycoceras* (*Eucalycoceras*) *lymense* Spath; Collignon, p. 72, pl. 2, fig. 2.
1951 *Eucalycoceras lymense* Spath; Wright and Wright, p. 26.

Discussion. A re-examination of the specimen figured by Pervinquière (1907, pl. 16, figs. 16*a*, *b* only) shows that this is in fact a Lower Cenomanian *Mantelliceras*, and not an *Eucalycoceras*.

Occurrence. Very rare; the specimen recorded from the Cenomanian limestone (preservation suggests bed B), BMNH C8002*a*, mentioned by Spath (1926*b*) may belong here (Pl. 23, figs. 1*a*, *b*), as does a single specimen, BMNH C76412 from the *M.* gr. *dixoni* assemblage fauna at Folkestone (Kent) (Pl. 21, fig. 1). Pervinquière's specimen is from Algeria, and is preserved in the École des Mines, Paris.

Mantelliceras saxbii (Sharpe)

1855 *Ammonites saxbii* Sharpe, p. 45, pl. 20, fig. 3.
1971 *Mantelliceras saxbii* (Sharpe); Kennedy and Hancock, p. 437.

Discussion. This species is fully dealt with elsewhere (Kennedy and Hancock 1971).

Mantelliceras tenue Spath

Plate 20, fig. 6; Plate 23, fig. 3

1859 *Ammonites mantelli* Sowerby; Pictet and Campiche, p. 200, pl. 26, figs. 3*a*, *b*.
1903 *Mantelliceras picteti* Hyatt, p. 114 (pars).
1926*b* *Mantelliceras tenue* Spath, pp. 427, 430.
1963 *Mantelliceras tenue* Spath; Renz, p. 1108, pl. 2, figs. 4*a*–*c*.

Discussion. M. tenue is a distinctive compressed form; it has well-developed umbilical,

lateral, lower and upper ventro-lateral tubercles on long ribs, which alternate with shorter ribs.

English specimens are rather more densely ribbed than the type or the specimen figured by Renz (1963).

Occurrence. Common in the lower part of the *mantelli* Zone (*carcitanensis* and *saxbii* assemblage faunas); also occurring in the Lower Cenomanian of western Europe.

Mantelliceras tuberculatum (Mantell)

Plate 24, figs. 2*a*, *b*, 3, 4, 5*a*, *b*, 7; Plate 25, figs. 1*a–c*

1822 *Ammonites mantelli* var. *tuberculatus* Mantell, p. 114.
1857 *Ammonites mantelli* var. A. Sharpe, p. 40, pl. 18, figs. 6*a*, *b*.
1859 *Ammonites mantelli* Sowerby; Pictet and Campiche, p. 209, pl. 26, figs. 5*a*, *b* (*non* Sowerby).
?1871 *Ammonites mantelli* Sowerby; Schlüter, p. 12, pl. 5, figs. 1, 2 (*non* Sowerby).
1903 *Mantelliceras picteti* Hyatt, p. 114 (pars).
?1910 *Acanthoceras martimpreyi* Coquand; Pervinquière, p. 42 (pars), pl. 5, figs. 10*a*, *b*.
1926*a* *Mantelliceras tuberculatum* (Mantell); Spath, p. 82.
1928–1929 *Mantelliceras mantelli* (Sowerby); Collignon, p. 33, pl. 3, figs. 2, 2*a*.
1937 *Mantelliceras tuberculatum* (Mantell); Collignon, p. 54, pl. 7, fig. 3.
1951 *Mantelliceras tuberculatum* (Mantell); Wright and Wright, p. 24.
1963 *Mantelliceras tuberculatum* (Mantell); Renz, p. 1102, pl. 2, figs. 1*a*, *b*.
1964 *Mantelliceras tuberculatum* (Mantell); Collignon, pp. 65, 69, pl. 337, figs. 1511 (var. *umbilicata*), 1512; pl. 339, figs. 1516, 1517 (var. *pinguis*).

Lectotype. Here designated, BMNH 32542. This specimen is from the Mantell Collection, and as is shown below, is available for lectotype designation. The specimen is labelled '*Calycoceras* aff. *naviculare* (Sharpe *non* Mantell?) Lower Cenomanian, Lower Chalk, Lewes, Sussex. Mantell Collection 1853 (32542)'. An addition in L. F. Spath's handwriting reads 'labelled by Crick "*Acanthoceras mantelli*"'.

Diagnosis. An evolute, inflated *Mantelliceras*, with coarse, alternately long and short ribs. The long ribs bear large and prominent umbilical, lateral, lower and upper ventro-lateral tubercles. The short ribs have ventro-lateral tubercles only. The tubercles are retained to a large diameter.

Description. The lectotype is a perfectly preserved composite internal mould in hard grey chalk. About half the last whorl is body chamber. The shell is evolute, about a third of the previous whorl being covered. The whorl section is depressed, the greatest breadth being at the lateral tubercle. The intercostal whorl section is rounded, the costal section is polygonal. The umbilicus is broad and deep, the umbilical wall is steep and rounded, the umbilical shoulder is also rounded.

There are 26–27 ribs per whorl at a diameter of 83 mm. These ribs are alternately long and short. The long ribs arise at the umbilical seam and are broad, rounded, and narrower than the interspaces; they pass straight across the flanks. There are strong, sub-spinose umbilical, mid-lateral, lower and upper ventro-lateral tubercles on all these ribs. The shorter ribs arise at mid-flank, and become as strong as the long ribs by the ventro-lateral shoulder, and are equally developed across the venter. These ribs bear upper and lower ventro-lateral tubercles only.

The sutures of the lectotype are not fully visible, but appears to be of normal *Mantelliceras* type.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 32542, lectotype	83·5	— (—)	37·0 (44·3)	25·9 (31·0)	26
	69·0	40·5 (58·7)	30·6 (42·9)	20·5 (29·7)	26

Discussion. The inflated whorl section, coarse ribbing, and retention of strong tubercles to a large size, separate *M. tuberculatum* from all other described *Mantelliceras* occurring in England. The most similar species are *M. indianense* Hyatt and *M. ampakabense* Collignon; distinguishing features of these forms are given by Collignon (1964).

In introducing this varietal name, Mantell (1822, p. 114) stated:

> Var. *tuberculata*: with eight rows of tubercles. The two additional sets which distinguish this variety, are placed on each side, midway between the margin and the ambit, and the second row of tubercles from the umbilicus. These intermediate tubercles occur on every rib, each of the larger costae being ornamented with eight, while the shorter ones have but four. From the numerous tubercular projections on this variety the outer volution is somewhat pentagonal.

Mantell did not figure examples of his 'var. *tuberculata*', for, as he stated in a footnote, the plates of the work (Mantell 1822) were completed before any 'illustrative specimens' had been discovered.

The interpretation of *M. tuberculatum* is clear from Mantell's description, and I have selected a fine specimen from Mantell's Collection as lectotype, this specimen being an undoubted syntype of his 'variety'. Most authors have taken Sharpe's specimen (Sharpe 1857, pl. 18, figs. 6*a*, *b*), as type, for example Renz (1963, p. 1102), but this is quite invalid. With designation of a lectotype it is quite clear that Collignon's vars. *pinguis* and *umbilicata* (1964) do not bear separation from the typical form.

Occurrence. M. tuberculatum occurs in *carcitanensis* assemblage faunas all over southern England and is often frequent. It is also present in *saxbii* assemblage faunas, but is rare. It is also known in western Europe, Spain (Wiedmann 1959, 1964; Renz 1963), Madagascar, and north Africa.

Mantelliceras ventnorense Diener

Plate 26, figs. 2*a–c*

1857 *Ammonites feraudianus* Sharpe, p. 51, pl. 23, figs. 6*a–c* (*non* d'Orbigny).
1860 *Ammonites feraudianus* Sharpe; Pictet and Campiche, p. 338.
1925 *Mantelliceras ventnorense* Diener, p. 170.
1925*a* *Mantelliceras subcostatum* Spath, p. 197.
1940 *Mantelliceras ventnorense* Diener; Fabre, p. 236, pl. 8, fig. 8.
1951 *Mantelliceras ventnorense* Diener; Wright and Wright, p. 25.
1964 *Mantelliceras ventnorense* Diener; Collignon, p. 87, pl. 347, fig. 1547.

Holotype. By original designation of Diener, GSM 7759, from the Lower Chalk of Ventnor, Isle of Wight, figured by Sharpe 1857, pl. 22, figs. 6*a–c*.

Diagnosis. A compressed, moderately involute *Mantelliceras*, with faint umbilical bullae and clavate ventro-lateral tubercles only on long flexuous ribs, alternating with shorter flexuous ribs. There are 32–36 per whorl.

Description. The holotype is a small composite internal mould in hard chalk, with a limonitic coat. The specimen is distorted into an ellipse, and the venter is abraded over the last third of a whorl. The shell is moderately evolute, about a third of the previous whorl being covered. The whorl section is compressed, the greatest breadth being at the umbilical bulla. The sides are flat, with slightly convergent ventro-lateral shoulders, and a rounded venter in intercostal section. The costal section is rather similar but with a slightly more arched venter. The umbilicus is narrow, rather shallow, with a steep umbilical wall and a narrowly rounded umbilical shoulder.

There are 32 ribs on the outer whorl; 11 of these are long. The long ribs are rather sharply rounded and narrower than the interspaces. They arise at the umbilical seam, pass straight up the umbilical wall, and develop a strong prorsiradiate umbilical bulla on the umbilical shoulder. The ribs are flexuous, passing forwards to mid-flank, back across the upper flank, and finally forwards across the ventral shoulder to the ventro-lateral tubercle. The ribs tend to broaden across the ventral shoulder, and at the smallest diameter visible there is some indication of a lower ventro-lateral tubercle.

The ventral tubercles are pointed, slightly clavate, and are connected across the venter by a rounded, forward-directed rib. In the siphonal region, this rib is elevated above the level of the ventral tubercles.

Between these long ribs there are from 1 to 3 shorter, intercalated ribs, which arise about a third of the way up the flank. Initially faint, these intercalated ribs strengthen across the ventro-lateral shoulder, and are similar to the long ribs across the venter. The short ribs have the same flexuous form on the flanks as the long ribs. A few of them join up to the umbilical bullae by faint growth striae. The sutures are not distinct but appear to be of *Mantelliceras* type.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
GSM 7763, holotype	28·7	12·0 (41·8)	14·2 (49·5)	6·8 (23·7)	32

Discussion. The absence of lower ventro-lateral and lateral tubercles and compressed whorl section separates the holotype of *M. ventnorense* from other described *Mantelliceras* occurring in the English Cenomanian. The closest species is *M. saxbii*, the lectotype of which has straighter ribs and a definite lower ventro-lateral tubercle when young.

These 2 species are, however, very closely related. Specimens of what I take to be adult *M. ventnorense* as figured by Fabre (1940) and Collignon (1964) have much more flexuous ribs than specimens of *M. saxbii* of the same size. For the present, therefore, I have separated these 2 species. Subsequent work may well show that differences are of subspecific or varietal significance only (Kennedy and Hancock 1971).

Occurrence. Infrequent in the lower part of the *mantelli* Zone all over southern England; also occurring in Europe and Madagascar.

Genus SHARPEICERAS Hyatt 1903

Type species. Ammonites laticlavius Sharpe 1855, p. 31, pl. 14, figs. 1*a*, *b*, by original designation of Hyatt (1903).

Diagnosis. Large acanthoceratid ammonites characterized by high, flattened whorls, the whorls only slightly embracing in the early and middle stages. There are numerous long, straight ribs with umbilical, mid-lateral, lower and upper ventro-lateral tubercles. When adult, the ventro-lateral tubercles tend to develop into a horn-like process, whilst a fifth tubercle, between the mid-lateral and lower ventro-lateral, may appear.

Discussion. The most obvious features of this genus are the high flat sides, with dense, long ribs, all of which bear umbilical, mid-lateral, lower and upper ventro-lateral tubercles. There is a tendency to develop horns when adult.

Most species are based on unique holotypes or a few specimens only; several available names may fall into synonymy when more is known of intra-specific variation in the genus.

Graysonites Young (Young 1958*a*, Matsumoto 1959, 1960) is very close to *Sharpeiceras*. The inner whorls of this genus are 'submantellicerine', with upper and lower ventro-lateral and umbilical tubercles; the outer whorls of the type species, *G. lozoi* Young develop huge spines by the fusion of the ventro-lateral tubercles.

Species such as *Sharpeiceras florencae* Spath and *S. vohipalense* Collignon are transitional, and *Graysonites* may eventually be shown to be merely a subgenus of *Sharpeiceras*. *Tlahualitoceras* Kellum and Mintz (1962), type species *T. tlahualitoense* Kellum and Mintz, is a synonym of *Sharpeiceras*; the type species may be conspecific with *S. florencae* Spath.

Occurrence. This genus is extremely rare, although recorded from the Lower Cenomanian of western Europe, North America, north Africa, the Middle East, west Africa, southern India, and Madagascar. As well as the named forms recorded here, several unnamed or indeterminate forms occur in England.

Sharpeiceras laticlavium (Sharpe)

Plate 27, figs. 1*a–c*; Plate 28, fig. 1

1855	*Ammonites laticlavius* Sharpe, p. 31, pl. 14, figs. 1*a*, *b*.
non 1871	*Ammonites laticlavius* Sharpe; Schlüter, p. 18, pl. 7, figs. 4–8 (= *S. schlueteri* Hyatt).
1878	*Acanthoceras laticlavium* Sharpe; Bayle, pl. 114.
?1896	*Ammonites laticlavius* Sharpe; Jukes-Browne and Hill, pp. 155, 163.
1903	*Sharpeiceras laticlavium* (Sharpe); Hyatt, p. 111.
1903	*Acanthoceras laticlavium* var. *Moçambiquensis* Choffat, p. 25, pl. 4, figs. 3*a*, *b*; pl. 7, figs. 2*a*, *b*.
non 1904*b*	*Acanthoceras laticlavium* (Sharpe); Douvillé, p. 239, pl. 31, fig. 3 (= *S. florencae* Spath).
1925*a*	*Sharpeiceras laticlavium* (Sharpe); Spath, p. 198.
?1937	*Acanthoceras* (*Sharpeiceras*) *laticlavium* (Sharpe); Basse de Menorval, p. 179.
1951	*Sharpeiceras laticlavium* (Sharpe); Wright and Wright, p. 25.
1964	*Sharpeiceras laticlavium* (Sharpe); Collignon, p. 102, pl. 353, figs. 1562, 1563.

Holotype. By monotypy, the original of Sharpe 1855, pl. 14, figs. 1*a*, *b*, GSM 7755, from the Lower Chalk of Bonchurch, Isle of Wight.

Diagnosis. A high-whorled *Sharpeiceras* with 35 ribs per whorl on the inner whorls, ribbing on the outer whorls tending to coarsen and to develop a fifth, upper lateral tubercle.

Description of holotype. The holotype is a well-preserved, wholly septate composite internal mould in grey limestone with a thin limonitic coat. About a fifth of the previous whorl is covered. The whorl section is compressed, with flattened sides, flattened ventro-lateral shoulders, and a flattened venter, raised slightly over the siphonal area.

There are 36 ribs on the outer whorl. These arise as faint swellings at the umbilical seam, strengthen and pass straight across the umbilical wall, and straight across the whorl sides, where they are approximately as wide as the interspaces. There is a well-developed, bullate umbilical tubercle, a stronger, slightly bullate mid-lateral tubercle, and a much stronger lower ventro-lateral tubercle on each rib. The lower ventro-lateral tubercle is connected to a strong, clavate upper ventro-lateral tubercle by a broad, subdued, forward-directed rib.

The venter between the ventro-lateral tubercles is depressed during the earliest visible stages, but at larger diameters a low, broad siphonal swelling is developed, perhaps a reflection of the position of the siphuncle. The sutures are not visible.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
GSM 7755, holotype	135	48·8 (36·2)	59·0 (43·7)	34·5 (25·6)	36

Discussion. The holotype is an individual showing the middle growth stages only. A number of large specimens from the Glauconitic Marl at Eastbourne (Sussex) show what I take to be the adult form; the best of these is figured in Plate 28, fig. 1. These specimens show that the ribbing becomes gradually coarser as size increases, with rib density dropping to 22 or 23 per whorl. The mid-lateral tubercle becomes elongated radially, a faint fifth tubercle appears between the lower ventro-lateral and mid-lateral tubercles, whilst the ventro-lateral tubercles become much strengthened. Some specimens show approximation of ribbing close to the aperture.

These specimens suggest that *S. laticlavium moçambiquensis* Choffat is no more than an adult *S. laticlavium*.

Sharpeiceras schlueteri Hyatt (1903, p. 111 = *S. laticlavium* Sharpe; Schlüter 1871, p. 18, pl. 7, figs. 4–9 (*non* Sharpe)) differs from *S. laticlavium* in having a much more quadrangular, lower whorl section, a far wider umbilicus, and about 28 ribs per whorl at a diameter of about 300 mm. The tuberculation also appears to be far more delicate than in Sharpe's species.

Sharpeiceras florencae Spath (1925*a*, p. 198, pl. 37) has only 25 ribs at a diameter of 120 mm, 10 less than *S. laticlavium*, and is very coarsely ribbed on the body chamber.

Sharpeiceras vohipalense Collignon (1964, p. 104, pl. 354, fig. 1565) is an even more coarsely ribbed species, with 17 ribs per whorl at a diameter only slightly greater than the type of *laticlavium*. The lower ventro-lateral tubercles are exaggerated and horn-like, whilst the upper ventro-lateral tubercles are reduced.

Acanthoceras laticlavium var. *byzancea* Pervinquière (1907, p. 302, pl. 14, fig. 4) does not appear to be a *Sharpeiceras* (see Spath 1925*a*, p. 199).

Sharpeiceras laticlavium var. *indica* Kossmat (1895, p. 103, pl. 10, figs. 5, 6) has slightly fewer ribs than *S. laticlavium* at a comparable diameter to Sharpe's specimen, and has lost the mid-lateral tubercle at this size (see also Collignon 1964, p. 82).

Sharpeiceras occidentale Benavides-Cáceres (1956, p. 465, pl. 54, figs. 5, 6) has a more quadrangular whorl section than *S. laticlavium* and has coarser ribs. It is based on a single fragment.

Mantelliceras falloti Collignon (1931, p. 41, pl. 4, figs. 9–12) appears to be a *Sharpeiceras*. It has only 20 ribs at a diameter of 60 mm and is thus much more coarsely ornamented than *S. laticlavium*.

Mantelliceras corroyi Fabre (1940, p. 237, pl. 7, figs. 5, 6) may also be a *Sharpeiceras*. It differs from *S. laticlavium* in having a very wide umbilicus and an almost serpenticone mode of coiling. Like *M. falloti* it is very coarsely ornamented.

Sharpeiceras goliath Haas (1942, p. 7, figs. 5–7) from Angola, is based on a large, very poorly preserved mould, which is probably not separable from *S. laticlavium*.

Sharpeiceras laticlavium var. *mexicana* (Böse) from the Buda Limestone (Böse 1927–1928, p. 253, pl. 10, fig. 6; pl. 11, fig. 1) is said to be more compressed than *S. laticlavium*, and to have twice as many ventro-lateral as umbilical tubercles, the ribs arising in twos from the umbilical tubercles.

Acanthoceras (*Sharpeiceras*) *piveteaui* Collignon (1928–1929, p. 37, pl. 3, figs. 18, 18*a*) is based upon a specimen less than 20 mm in diameter, and cannot be compared with present material of *S. laticlavium* or other species.

Sharpeiceras congo Matsumoto, Muramoto, and Takahashi (1969, p. 261, pl. 29, fig. 1; pl. 30, fig. 1; text-figs. 3, 4) is a Japanese form, best distinguished from *S. laticlavium* in that it has only 15 or 16 very coarse strongly tuberculate ribs on the body whorl.

Occurrence. Very rare. As well as the holotype, there is an unlocalized specimen, BMNH C3677, probably from Folkestone (Kent), several specimens from the *carcitanensis* assemblage fauna at Eastbourne (Sussex) (GSM Zn3155, 3156, also author's collection), whilst the species is recorded from chalk above the Totternhoe Stone at Speeton (Yorks.) (Hill 1888, p. 351). This last occurrence seems unlikely. The species also occurs in France (Thomel 1965*a*, *b*, etc.), Africa (Mozambique), and Madagascar.

Sharpeiceras schlueteri Hyatt

1871 *Ammonites laticlavius* Sharpe; Schlüter, p. 18, pl. 7, figs. 4–8 (*non* Sharpe).
1903 *Sharpeiceras schlüteri* Hyatt, p. 111.
1951 *Sharpeiceras schlüteri* Hyatt; Wright and Wright, p. 25.
1964 *Sharpeiceras schlüteri* Hyatt; Collignon, p. 102, pl. 353, fig. 1564.

Discussion and occurrence. This rare species is known from a doubtful fragment in Wrights' Collection (WW 20524) from the remanié Lower Cenomanian fauna of the Chalk Basement Bed at Ringstead (Dorset), and a specimen from the *carcitanensis* assemblage fauna of the Glauconitic Marl of Ventnor, Isle of Wight (J. Parmenter Collection). The species also occurs in Germany and Madagascar.

Sharpeiceras florencae Spath

Plate 25, fig. 2

1904 *Acanthoceras laticlavium* (Sharpe); Douvillé, p. 239, pl. 31, fig. 3.
1925*a* *Sharpeiceras florencae* Spath, p. 198, pl. 37.
1933 *Sharpeiceras florencae* Spath; Collignon, p. 67, pl. 6, fig. 5.

Discussion and occurrence. This species is characterized by coarse ribbing (25 ribs per whorl in the type at a diameter of 200 mm), as discussed above (p. 65). A number of specimens can be referred to the species; one, GSM Zb4754, from Folkestone (Kent) (Osman Collection) was identified by Spath as *S.* aff. *florencae*; other specimens are from the unphosphatized fauna of the Glauconitic Marl at Eastbourne (Sussex) (author's collection), and a specimen from Ringmer (Sussex) (GSM 100738, Pl. 25, fig. 2). All occurrences are Lower Cenomanian. The species also occurs in Africa, Madagascar, and perhaps North America (Matsumoto 1959, pp. 69, 70, fig. 28).

Genus ACOMPSOCERAS Hyatt 1903
(= PSEUDACOMPSOCERAS Spath 1926*b*)

Type species. Ammonites bochumensis Schlüter 1871, p. 1, pl. 1, figs. 1–4; pl. 2, fig. 1; by original designation of Hyatt 1903.

Diagnosis. Medium-sized to large acanthoceratids, moderately evolute to moderately involute, usually compressed. Inner whorls ornamented by strong to weak umbilical tubercles and twice as many clavate ventro-lateral tubercles, connected by low, broad ribs in weakly ornamented species. Coarsely ornamented species develop 1 or 2 sets of lateral tubercles. Venter smooth, sometimes subcarinate. Adult whorls often smooth. Suture complex, sometimes with subphylloid folioles.

Discussion. A useful discussion by Casey (1965, p. 462) has shown that *Pseudacompsoceras* is the coarsely ornamented division of *Acompsoceras* species, and that these 2 genera do not bear separation.

Acompsoceras reaches a very large size, and there are problems in relating limonitic nuclei, such as Sornay (1955) described from north Africa, to giant limestone moulds. This is a rare genus in Britain, known only from about 20 specimens. None is known from the Basement Beds of south-west England.

Occurrence. Rare in the Lower and Middle Cenomanian of south-east England; occurring widely in western Europe, north Africa, Madagascar, and North America.

Acompsoceras sarthense (Guéranger)

Plate 26, fig. 3; Plate 29, figs. 1*a–c*

1857 *Ammonites coupei* var., Sharpe, pl. 19, figs. 1*a–c*.
1867 *Ammonites sarthensis* Guéranger, p. 5, pl. 4, fig. 1; pl. 8, fig. 2.
1871 *Ammonites inconstans* Schlüter, p. 7, pl. 3, figs. 1–5.
1907 *Acompsoceras sarthense* (Guéranger); Pervinquière, p. 303, pl. 17, figs. 1–3.
1925*a* *Pseudacompsoceras vectense* Spath, p. 197.
1951 *Pseudacompsoceras vectense* Spath; Wright and Wright, p. 24.

?1963 *Pseudacompsoceras bifurcatum* Powell, p. 311, pl. 31, figs. 1, 7, 11; text-fig. 31*r*.
1964 *Acompsoceras sarthense* Guéranger; Collignon, p. 106, pl. 355, figs. 1566, 1567 (var. *bituberculata*).

Diagnosis. *Acompsoceras* with coarsely ornamented inner whorls bearing 23–24 ribs per whorl, most arising in twos from strong umbilical tubercles and bearing strong lateral, lower and upper ventro-lateral tubercles. Adult whorls almost smooth.

Discussion. It would not seem possible to separate *A. vectense* from the smaller specimen of *Acompsoceras inconstans* figured by Schlüter (1871, pl. 3, fig. 1), which at a diameter of 150 mm has about 23 ribs on the outer whorl, nor these specimens from Guéranger's originals. The large specimens figured by Schlüter (pl. 3, fig. 4) and Guéranger (1867, pl. 4, fig. 1; pl. 8, fig. 2) show that this species reaches a large size and becomes almost smooth.

The coarse ornament of the inner whorls of this species separates it from other described forms of *Acompsoceras*. *Pseudacompsoceras bifurcatum* Powell (1963, p. 311, pl. 31, figs. 1, 7, 11; text-fig. 31*r*) is said to differ from *A. vectense* in having bifurcating ribs and a nodose keel; it is probably a synonym.

Occurrence. Very rare in the Lower and Middle Cenomanian of southern England, Middle and Upper Cenomanian of France (Hancock 1959); also known from Germany, north Africa, Madagascar, and perhaps North America.

Acompsoceras renevieri (Sharpe)

Plate 30, figs. 1*a–c*

1857 *Ammonites renevieri* Sharpe, p. 44, pl. 20, figs. 2*a–c*.
1860 *Ammonites renevieri* Sharpe; Pictet and Campiche, p. 310.
non 1867 *Ammonites renevieri* Sharpe; Guéranger, pl. 7, fig. 4 (= *A. pseudorenevieri* Spath (genus uncertain).
1871 *Ammonites renevieri* Sharpe; Schlüter, p. 1.
?1871 *Ammonites bochumensis* Schlüter, p. 1, pl. 1, figs. 1–4; pl. 2, fig. 1.
?1903 *Acompsoceras bochumense* (Schlüter); Hyatt, p. 111.
1903 *Acompsoceras renevieri* (Sharpe); Hyatt, p. 112.
1951 *Acompsoceras renevieri* (Sharpe); Wright and Wright, p. 27.

Lectotype. By subsequent designation of Wright and Wright (1951, p. 38), the original of Sharpe 1857, pl. 20, figs. 2*a–c*, GSM 7753. The label of this specimen gives the locality as 'above Gore Cliff, Isle of Wight'; Sharpe gives the locality as Blackdown, Isle of Wight. A Lower Cenomanian horizon is indicated.

Diagnosis. Compressed *Acompsoceras* with about 12 long, broad subdued ribs with umbilical and ventro-lateral tubercles in middle growth stages, alternating with short ribs with only ventral tubercles. Outer whorls almost smooth.

Description of lectotype. The lectotype is a rather badly preserved composite internal mould in grey limestone, broken into 3 pieces, with traces of the former presence of another, outer whorl. It is wholly septate.

The shell is moderately involute, about half the previous whorl being covered. The whorl section is high, compressed, with broadly rounded, flattened sides, and a faintly ridged venter. The greatest breadth is at about mid-flank. The umbilicus is small and shallow with a broadly rounded umbilical wall and shoulders.

There are about 12 very broad, long, low ribs on the outer whorl, as broad or slightly narrower than the interspaces, and effaced on the outer parts of the flank. The ribs arise as broad swellings on the umbilical shoulder, developing into strong, slightly bullate tubercles on the outer parts of the shoulder. There is a broad swelling on each rib at mid-flank, and at the smallest diameter visible, a weak tubercle. There are small distinct and slightly clavate lower ventro-lateral tubercles at the smallest diameter visible, but these are soon lost.

Well-developed long, clavate upper ventro-lateral tubercles are present on all long ribs. Between the long ribs there are 1 or rarely 2 faint swellings (barely ribs) on the outer part of the flank, each associated with a clavate ventro-lateral tubercle. The venter is smooth with a faint median ridge. The suture has been inked in on the lectotype; such as is visible is of normal *Acompsoceras* type, with subphylloid folioles.

Dimensions.

	D	*Wb*	*Wh*	*U*
GSM 7753, lectotype	115	34·5 (30·0)	54·0 (46·9)	26·5 (23·0)

Discussion. The broad, low, subdued ornament and the few ribs separates *A. renevieri* from forms such as *A. sarthense*, *A. tenue*, *A. sahnii*, *A. catsigrasae*, *A. antsatrama-havelonense*, and *A. pseudosarthense* as described by Collignon (1964). *A. viottii* Collignon (1966, p. 26, pl. 16, fig. 1) is a much more densely ribbed form.

A. bochumense Schlüter (1871, p. 1, pl. 1, figs. 1–4; pl. 2, fig. 1) appears to be a synonym. *A. essendiense* Schlüter (1871, p. 3, pl. 1, figs. 5–7; pl. 2, fig. 2) is closely related to Sharpe's species. It is, however, almost completely unornamented, other than having faint ribs on the inner parts of the flank up to a diameter of about 16 cm and ventro-lateral clavi to about the same size. The 2 varieties described by Pervinquière (1907) are also less strongly ornamented than *A. renevieri*, as is *A. essendiense* var. *madagascariensis* Collignon (1964, pp. 108, 109, pl. 356, fig. 1569; pl. 357, fig. 1570).

Occurrence. Very rare in the Lower Cenomanian, Isle of Wight; *saxbii* assemblage fauna, Eastbourne (Sussex). Also Lower Cenomanian, Germany?, France.

Acompsoceras aff. *essendiense* (Schlüter)

Plate 31, fig. 2

1871 *Ammonites essendiensis* Schlüter, p. 3, pl. 1, figs. 5–7; pl. 2, fig. 2.
1903 *Acompsoceras essendiense* (Schlüter); Hyatt, p. 110.
1907 *Acompsoceras essendiense* (Schlüter); Pervinquière, p. 306, pl. 17, figs. 4, 5 (var. *mrhilensis*); pl. 17, figs. 6, 7 (var. *mardjeurensis*).
1964 *Acompsoceras essendiense* (Schlüter) var. *madagascariensis* Collignon, pp. 108, 109, pl. 356, fig. 1569; pl. 357, fig. 1570.

Discussion and occurrence. A large, well-preserved *Acompsoceras* from the *M.* gr. *dixoni* assemblage fauna at Folkestone (Kent). It has rather more ventro-lateral clavi than the type, but is otherwise very similar. The species also occurs in Germany, north Africa, and Madagascar.

Genus CALYCOCERAS Hyatt 1900

Type species. Ammonites navicularis Mantell (1822, p. 198, pl. 22, fig. 5), by original designation of Hyatt 1900. There has been considerable confusion associated with the type species of this genus (see Wright and Wright 1951, and Wright 1959*b*, ICZN Opinion 551).

Diagnosis. Medium-sized to large acanthoceratid ammonites, typically moderately evolute with rounded, depressed whorl sections. Ribs strong, alternately long and short, with umbilical-lateral, lower and upper ventro-lateral, and siphonal tubercles early in ontogeny, all of which may disappear with age. Some species referred to this genus are spinose, and high-whorled forms are also known.

Discussion. As at present conceived, *Calycoceras* is a very broadly based genus. Several subgeneric names are needed, but until detailed relationships within this highly polymorphic group are known, no divisions should be made.

Several groups can be recognized within the genus; the 5 given below may represent fairly natural groupings (see also Matsumoto *et al.* 1957):

(i) *Calycoceras* [*sensu stricto*]–*C. naviculare*, *C. boulei* (Collignon), *C. bruni* (Fabre). Distinct inflated high Cenomanian forms.

(ii) *C. newboldi* (Kossmat), *C. newboldi spinosum* (Kossmat), *C. orientale* (Matsumoto). Spinose Middle and Upper Cenomanian forms, homeomorphic with some species of *Acanthoceras*.

(iii) *C. gentoni* (Brongniart), *C. paucinodatum* (Crick), *C. bathyomphalum* (Kossmat). Small forms with strongly tuberculate inner whorls and strongly ribbed non-tuberculate outer whorls. Largely Middle Cenomanian.

(iv) *C. choffati* (Kossmat), *C. coleroonense* (Stoliczka), *C. sinuosum* (Collignon). Compressed, densicostate forms with tabulate venters. High Middle Cenomanian and Upper Cenomanian.

(v) *C. lotzei* (Wiedmann), *C. aberrans* (Kossmat), *C. barruei* (Pervinquière). *Cheloniceras*-like forms with strongly developed, close-spaced spinose umbilical and lower ventro-lateral tubercles, and a depressed whorl section. Known largely from nuclei. High Middle Cenomanian and Upper Cenomanian.

Only one of these groups, (v), has been named, as *Lotzeites* Wiedmann (1959, p. 731). The introduction of this subgenus for small *Cheloniceras*-like nuclei is unfortunate. Some species, e.g. *C. bathyomphalum*, referred to *Lotzeites* by Wiedmann (1959, p. 372) have outer whorls of *C. subgentoni* type (i.e. group (iii) above), as shown by Collignon (1964, pl. 362, fig. 1527) who referred the species to *Eucalycoceras*, which it certainly is not. In addition, there is every transition from *bathyomphalum* type nuclei to *subgentoni* type nuclei in contemporary populations from the Middle Cenomanian of southern England.

Differences between *Calycoceras* and other genera are discussed on p. 50. *Calycoceras* [*sensu stricto*] is readily separable from *Acanthoceras*, but forms such as *C. spinosum* and *C. orientale* have intermediate features.

Inflated *Calycoceras* and *Mantelliceras* are homeomorphs. They can usually be separated by the absence of a siphonal tubercle at any stage in *Mantelliceras*, and the fact that the umbilical tubercle is more prominent than the lateral tubercle in *Calycoceras* whilst the reverse is usually true in *Mantelliceras* (p. 50).

Occurrence. Middle Cenomanian to Lower Turonian; world-wide.

Calycoceras naviculare (Mantell)

Plate 33, figs. 1*a*, *b*; Plate 34, figs. 1*a*, *b*; Plate 35, figs. 1, 2; Plate 36, figs. 1, 2*a–c*, 3*a–c*, 4; Plate 37, figs. 1*a*, *b*, 2, 3; Plate 47, figs. 1*a–c*, 3*a*, *b*, 5*a*, *b*

1822 *Ammonites navicularis* Mantell, p. 198, pl. 22, fig. 5.
non 1827 *Ammonites navicularis* Mantell; J. de C. Sowerby, p. 105, pl. 555, fig. 2.
non 1841 *Ammonites mantelli* Sowerby; d'Orbigny, p. 340, pls. 103, 104.
non 1857 *Ammonites navicularis* Mantell; Sharpe, p. 39, pl. 18, figs. 1, 2, 3, 8.
1864 *Ammonites navicularis* Mantell; Stoliczka, p. 73, pl. 39, figs. 2–4.
?1867 *Ammonites navicularis* Mantell; Guéranger, p. 6, pl. 5, fig. 5 (*non* pl. 5, fig. 3).
1897 *Acanthoceras naviculare* (Mantell); Kossmat, p. 11.
1898 *Acanthoceras naviculare* (Mantell); Choffat, p. 72, pl. 4, figs. 6*a*, *b*; pl. 6, figs. 1, 2.
non 1907 *Acanthoceras naviculare* (Mantell); Boule, Lemoine, and Thévenin, p. 10, pl. 8, figs. 1, 2.
?1907 *Acanthoceras naviculare* (Mantell); Pervinquière, p. 281.
1912 *Fagesia navicularis* (Mantell); de Grossouvre, p. 26, pl. 3, fig. 1.
1919 *Ammonites navicularis* Mantell; Crick, p. 154, pl. 4.
non 1921 *Calycoceras naviculare* (Mantell); Spath, p. 315, footnote.
1926*a* *Ammonites navicularis* Mantell; Spath, p. 83 (pars).
1926*b* *Metacalycoceras grossouvrei* Spath, p. 431.
?1926*b* *Metacalycoceras boehmi* Spath, p. 431.
1931 *Acanthoceras borgesi* H. Douvillé, p. 32, pl. 2, figs. 3, 4.
1931 *Metacalycoceras borgesi* (H. Douvillé); Spath, p. 316.
1937 *Ammonites navicularis* Mantell; Collignon, p. 44 (pars).
1937 *Calycoceras* (*Metacalycoceras*) *stoliczkai* Collignon, p. 48.
1937*a* *Ammonites navicularis* Mantell; Spath, p. 277.
1951 *Calycoceras naviculare* (Mantell); Wright and Wright, p. 26.
1951 *Calycoceras borgesi* (H. Douvillé); Wright and Wright, p. 26.
?1951 *Calycoceras boehmi* (Spath); Wright and Wright, p. 26.
1957 *Calycoceras obrieni* Young, p. 1171, pl. 150, figs. 1–4; text-figs. 1*f*, *h*.
?1957 *Calycoceras* cf. *stoliczkai* Collignon; Matsumoto *et al.*, p. 19, pl. 6, figs. 1*a*, *b*.
1957 *Calycoceras naviculare* (Mantell); Wright, p. L431, fig. 531, 6, fig. 532.
1958 *Calycoceras* (*Metacalycoceras*) *auspicum* Anderson, p. 243, pl. 20, fig. 8.
1958 *Mantelliceras oregonense* Anderson, p. 244, pl. 8, fig. 4; pl. 14, fig. 1.
1959 *Calycoceras stoliczkai* Collignon; Matsumoto, p. 78, pl. 21, fig. 1; text-figs. 33–35.
?1964 *Calycoceras* cf. *boehmi* (Spath); Collignon, p. 114, pl. 359, fig. 1580.
?1964 *Calycoceras* cf. *stoliczkai* Collignon; Collignon, p. 124, pl. 364, fig. 1593.
1964 *Calycoceras* cf. *naviculare* (Mantell); Collignon, p. 126, pl. 365, fig. 1596.
?1964 *Calycoceras* cf. *borgesi* (H. Douvillé); Collignon, p. 128, pl. 366, fig. 1599.
1965 *Calycoceras grossouvrei* (Spath); Collignon, p. 10, pl. 3, fig. 2.

Holotype. By monotypy the specimen figured by Mantell 1822, pl. 22, fig. 5, BMNH 5681. This specimen was described by Mantell as being from the 'Upper Chalk' of Offham (Sussex). It is undoubtedly of Cenomanian or basal Turonian age; Mantell's 'Upper Chalk' in fact encompasses our present Middle and Upper Chalk.

Diagnosis. Inflated, depressed evolute *Calycoceras* with many (usually about 30 or more) ribs per whorl. Siphonal and lateral tubercles lost early in ontogeny. Umbilical tubercle very strong. Ventral tubercles rounded.

Body chamber with strong, coarse, alternately long and short ribs, venter tabulate between strong rounded ventro-lateral tubercles.

Description. The holotype (Pl. 33, figs. 1*a*, *b*) is poorly preserved, and has been well-described by Crick (1919, pp. 154–160). The following description is based upon

a series of specimens kindly loaned to me by Mr. C. W. Wright; they are all from Bed C of the Cenomanian Limestone. From a comparison with better preserved chalk material (e.g. Pl. 36, fig. 1, and specimens in my own collection), it can be shown that these are undoubtedly conspecific with the holotype.

1. 20–40 mm. The shell is moderately evolute, well under half the previous whorl being covered. The whorl section is depressed, with the greatest breadth at the umbilical tubercle on many ribs, but at the lateral tubercle on others. The intercostal section is rounded. Up to a diameter of about 25 mm the costal whorl section is angular, but beyond this diameter the ventral part of this section tends to become rounded. The umbilicus is deep, the umbilical wall rounded.

There are 25–32 ribs per whorl. Long ribs arise at the umbilical seam, are strong across the umbilical wall, and develop a strong umbilical tubercle, which in some individuals strengthens with increasing size. From this tubercle arise strong, slightly rursiradiate ribs. These are about as wide as the interspaces, and bear a strong lateral tubercle up to a diameter of about 25 mm. There is a small, rounded to transversely elongate ventro-lateral tubercle and a siphonal tubercle. The siphonal tubercle disappears, or is present as only a faint swelling on the rib, by about 30–35 mm. The ventro-lateral tubercles also disappear, their site being marked only by a change in slope of the rib at the ventro-lateral shoulder.

The long ribs alternate with 1 or 2 intercalated ribs. Some of these arise at mid-flank, others extend down to the umbilical seam, but are weak in this region, and lack an umbilical and, usually, a lateral tubercle. These intercalated ribs are similar to the long ribs across the venter. Occasionally, ribs arise in twos from the umbilical tubercle.

2. 40–120 mm. Whorl section and coiling remain similar. On the 2 specimens available there are 37 ribs on the outer whorl. The umbilical tubercle is strong (the greatest breadth is at this point) and ribs bearing this tubercle alternate with 1 or 2 shorter or non-tuberculate ribs. In a fragmentary specimen (WW 19159) the ribs branch from the umbilical tubercle.

There is a pronounced rounded tubercle on the ventro-lateral shoulder, apparently developing from the slight angulation present at diameters of 40–50 mm. On one specimen (WW 22431), traces of a faint siphonal swelling are present at diameters of more than 100 mm.

3. At larger diameters, the ribbing becomes increasingly coarse and strong; the ribs are alternately long and short, narrower than the interspaces, with strong ventro-lateral tubercles, a strong transversely elongate umbilical tubercle, and a flattened venter. Specimens reach diameters of 300 mm.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
WW 22650 (costal)	31·0	22·0 (71)	12·0 (39)	9·6 (31)	24/25
WW 19217 (costal)	31·5	24·0 (76)	14·0 (44)	10·0 (32)	26/27
WW 22438	39·0	—	16·5 (42)	14·0 (36)	32/33
WW 22431	119·0	—	—	41·5 (35)	35

Discussion. This species is figured at length because of its great importance, world-wide distribution, frequent misinterpretation, and difficulties of interpretation of

Mantell's unsatisfactory type. As a result of the previous poor knowledge of this species, a number of names now fall into synonymy:

1. *Calycoceras borgesi* (H. Douvillé) (1931, p. 32, pl. 2, figs. 3, 4) cannot be separated from *C. naviculare*, as is clear from topotype specimens in the British Museum (Natural History) (O'Donnell Collection, BMNH C52618–52620).

2. *Calycoceras grossouvrei* (Spath) (= *Fagesia navicularis* (Mantell); Grossouvre 1912, pl. 3, fig. 1) is simply a rather densely ribbed variant of *C. naviculare*, with about 40 ribs per whorl.

3. *Calycoceras obrieni* Young (1957, p. 1171, pl. 150, figs. 1–4; text-figs. 1*f*, *h*), as Matsumoto (1959, p. 81) suggested, is not separable from *C. naviculare*; details of inner whorls (Young 1957, p. 1173) appear to differ in such trivial details as to be dismissed.

4. *Calycoceras stoliczkai* Collignon (1937, p. 48, = *Ammonites navicularis* Stoliczka 1864, pl. 39, figs. 2–4) would seem to be a synonym of *C. naviculare*, differences suggested by Collignon (1937) and Matsumoto (1959) being insufficient for separation at present.

Calycoceras boulei Collignon (see below) is a Middle Cenomanian species which gives rise to *C. naviculare*, to which it is very similar. There are differences, but these seem to be slight.

The ribbing of *C. boulei* seems to be more delicate, whilst the whorl section is more angular during the middle growth stages, with distinct lateral tubercles (Matsumoto 1959, fig. 31 clearly shows this). It is also less depressed, with a proportionately smaller umbilicus, than *C. naviculare*.

Calycoceras boehmi (Spath) (= *Ammonites navicularis* Mantell; Guéranger 1867, pl. 5, fig. 5) is based on a side view only of an ammonite from the Cenomanian of Le Mans. Hancock (1959) recorded the species from the Marnes à *Ostrea biauriculata*, and it may be a synonym of *C. naviculare*. It appears to lack strong umbilical tubercles, but until better topotype material is described, this must remain a doubtful name. The specimen figured by Collignon (1964, pl. 359, fig. 1580) is less depressed than *C. naviculare*.

Calycoceras letullieri Collignon (1964, p. 131, pl. 367, figs. 1603, 1604) is a spinose depressed species, separated from *C. naviculare* by the presence of lateral tubercles to a much greater diameter.

Calycoceras thieuloyi Collignon (1964, p. 133, pl. 368, figs. 1605–1607) is an extremely depressed species, described as bearing only a single tubercle at the umbilical shoulder. This may be a *Mantelliceras*; until the inner whorls are known the true generic position seems uncertain.

Acanthoceras naviculare as described by Boule, Lemoine, and Thévenin (1907) does not seem to belong to the genus *Calycoceras*. Their pl. 8, fig. 1, is perhaps a *Fagesia* or *Vascoceras*, and fig. 2 may be a *Mantelliceras* (Collignon 1937), as may the specimen figured by Collignon (1931, pl. 5, fig. 4; see Collignon 1937, p. 48).

Occurrence. Upper Cenomanian, Bed C, of the Devon coast; top 10 m of Lower Chalk at Eastbourne (Sussex); top of Lower Chalk elsewhere in Sussex, Surrey, and Kent; *plenus* Marls (Jefferies 1963). Widespread outside England in the Upper

Cenomanian; France, Portugal, Africa, India, Middle East, North America, and Japan; 'Lower Turonian' of France and perhaps Angola.

Calycoceras bathyomphalum (Kossmat)

Plate 38, figs. 1*a*, *b*, 2*a*, *b*

1895 *Acanthoceras bathyomphalum* Kossmat, p. 197, pl. 25, figs. 4*a–c*.
1939 *Calycoceras* (*Eucalycoceras*) *bathyomphalum* (Kossmat); Collignon, p. 71, pl. 2, fig. 1.
1951 *Calycoceras bathyomphalum* (Kossmat); Wright and Wright, p. 24.
1959 *Calycoceras* (*Lotzeites*) *bathyomphalum* (Kossmat); Wiedmann, p. 732.
1964 *Calycoceras* (*Lotzeites*) *bathyomphalum* (Kossmat); Wiedmann, p. 121.
1964 *Eucalycoceras bathyomphalum* (Kossmat); Collignon, p. 73, pl. 341, fig. 1527.
?non 1966 *Calycoceras* (*Lotzeites*) cf. *bathyomphalum* (Kossmat); Thomel *in* Porthault *et al.*, p. 427, pl. 8, figs. 6, 7.

Discussion. The original figure of this species (Kossmat 1895, pl. 25, figs. 4*a–c*) is of a small, wholly septate specimen 30 mm in diameter. There are 27–28 ribs on the outer whorl, alternately long and short, the long ribs with small umbilical tubercles, very strong lower ventro-lateral spines, weak upper ventro-lateral tubercles, and a small siphonal tubercle up to a diameter of about 20 mm. The short ribs lack an umbilical tubercle, and usually a lower ventro-lateral tubercle.

Wiedmann (1959, 1964) referred this species to the subgenus *Calycoceras* (*Lotzeites*) Wiedmann on the basis of the strong lateral spines.

Nuclei identical with the type figure occur widely in south-west England (Pl. 38, figs. 2*a*, *b*), but are associated with strongly ribbed, non-tuberculate body chambers of *Calycoceras paucinodatum* (Crick) type (Pl. 38, figs. 1*a*, *b*). Collignon (1964, pl. 341, fig. 1527) figured a similar specimen from Madagascar, and on the basis of the change in ornament referred *C. bathyomphalum* to *Eucalycoceras*, which it certainly is not.

Furthermore, there are specimens of the *C. paucinodatum* group which have nuclei transitional towards the *bathyomphalum* type of ornament, and it may prove possible to treat *C. paucinodatum* as a mere variant of *C. bathyomphalum* (Pl. 41, fig. 3; Pl. 46, figs. 2*a–c*). The adult ornament of *C. bathyomphalum* would seem to preclude its reference to *C.* (*Lotzeites*). The specimen figured by Thomel (*in* Porthault *et al.* 1966, pl. 8, figs. 6, 7) is from the Upper Cenomanian, above the horizon of the English material, and retains *Lotzeites*-like ornament to a somewhat larger diameter.

Occurrence. Not uncommon in *rhotomagense* Zone, *acutus* assemblage Basement Bed faunas in south-east England; represented at higher horizons by related forms. Also known in Madagascar, India, and perhaps France.

Calycoceras boulei Collignon

Plate 42, fig. 3

1937 *Calycoceras* (*Metacalycoceras*) *boulei* Collignon, p. 43, pl. 5, figs. 2–4; pl. 8, figs. 9–11.
1951 *Calycoceras boulei* Collignon; Wright and Wright, p. 26.
1959 *Calycoceras boulei* Collignon; Matsumoto, p. 75, pl. 20, figs. 1*a*, *b*; text-figs. 31, 32.
1964 *Calycoceras boulei* Collignon; Collignon, p. 126, pl. 365, fig. 1594.

Discussion and occurrence. This species is closely related to *C. naviculare*, to which it

gives rise at some time in the late Middle Cenomanian or Upper Cenomanian. Differences are discussed on p. 73. *C. boulei* occurs as a rarity in the poorly phosphatized or unphosphatized faunas of the Chalk Basement Bed at Bincombe (Dorset), and perhaps other localities. It is thus of high Middle Cenomanian age, also perhaps occurring later. The species also occurs in Madagascar, North America, and France (Porthault *et al.* 1966, etc.).

Calycoceras bruni Fabre

1940 *Calycoceras bruni* Fabre, p. 230, pl. 7, figs. 1, 2.
1951 *Calycoceras bruni* Fabre; Wright and Wright, p. 26.

Discussion. The puzzling record of this Upper Cenomanian *Calycoceras* from Dorset given by Fabre (1940) is based on a mis-labelled specimen in the collections of the Geological Department of the University of Lyon (Reg. No. 14011). The matrix and preservation of this specimen suggests that it is in fact from the Marnes à *Ostrea biauriculata* of Sarthe (J. M. Hancock, pers. comm.).

Calycoceras aff. *choffati* (Kossmat)

Plate 38, figs. 5*a*, *b*; Plate 39, figs. 1*a–c*, 3*a–c*

cf. 1897 *Acanthoceras choffati* Kossmat, p. 12, pl. 4, fig. 1.
cf. 1907 *Acanthoceras choffati* Kossmat; Crick, p. 205, pl. 12, figs. 5*a*, *b*.

Discussion and occurrence. Compressed, finely ribbed *Calycoceras*, differing from the holotype of *C. choffati* in having a lower rib density, a tabulate venter, whilst retaining their upper ventro-lateral tubercles, occur in *jukes-brownei* assemblage faunas of the Weald (Burnham, Lower Froyle, Glynde, Eastbourne) and Chalk Basement Beds of similar age in south-west England. The most closely comparable figured and described specimens are those noted by Crick (1907) from a high Middle Cenomanian horizon. English specimens also show resemblances to *Calycoceras* of the *newboldi planecostata* group.

Calycoceras newboldi newboldi (Kossmat)

Plate 39, figs. 2*a–c*; Plate 40, figs. 2*a*, *b*

1897 *Acanthoceras newboldi* Kossmat, p. 111, pl. 12, figs. 2, 3; pl. 14, fig. 2.
1951 *Calycoceras newboldi* (Kossmat); Wright and Wright, p. 25.

Discussion. Calycoceras of the *newboldi* group are common and widely distributed in the Middle and Upper Cenomanian. These forms are centred on *C. newboldi* and vary towards stronger tuberculation (*C. newboldi spinosum* (Kossmat)) and towards flat-sided, non-tuberculate forms (*C. newboldi planecostata* (Kossmat)). Several names have been introduced for this variable group, and these divisions have been variously regarded as species and subspecies or varieties. The proper interpretation of these forms must await a detailed knowledge of variation in contemporary populations and changes in populations with time; this is not yet possible.

3 forms can be recorded from England with confidence, *C. newboldi newboldi*, *C. newboldi spinosum*, and *C. newboldi planecostata*.

C. newboldi madagascariensis Collignon (1937, p. 40, pl. 3, figs. 6, 6*a*; pl. 8, fig. 7) differs from *C. newboldi newboldi* in having flatter sides, a section higher than wide, more ribs (45 as opposed to 35), and persistent ventro-lateral and umbilical tubercles.

C. newboldi ankomakaensis Collignon (1937, p. 40, pl. 3, figs. 7, 7*a*; pl. 8, fig. 6) differs from *C. newboldi* in its evolute coiling, flat sides, high whorls, many ribs (42), and loss of tuberculation (Pl. 42, figs. 4*a*, *b*).

C. newboldi germaini Fabre (1940, p. 228, pl. 8, figs. 3, 4) differs from *C. newboldi* in its stronger tuberculation. It is separated from *C. newboldi spinosum* because of displacement of the umbilical tubercle on to the lower part of the flank, the backwards flexure of the ribs between the ventro-lateral tubercles, and the presence at large diameters of a siphonal tubercle.

English specimens of *C. newboldi* usually vary a little around Kossmat's figures.

Occurrence. Frequent in Chalk Basement Beds of *acutus* and *jukes-brownei* assemblage age in south-west England and chalk facies of the same age; also surviving into the *naviculare* Zone. Elsewhere, widespread in the Middle and Upper Cenomanian of western Europe, north Africa, Japan, and India.

Calycoceras newboldi planecostata (Kossmat)

Plate 41, figs. 1*a*, *b*, 2*a*, *b*

1897 *Acanthoceras newboldi planecostata* Kossmat, p. 116, pl. 13, figs. 1*a–c*.

Discussion and occurrence. This form is rather rare in England, and such specimens as I would refer to the subspecies come from high *rhotomagense* Zone Basement Beds and the *naviculare* Zone Basement Bed fauna of Askerswell (Dorset). It also occurs in India and Madagascar. A specimen apparently transitional to *ankomakaensis* is figured (Pl. 42, figs. 4*a*, *b*).

Calycoceras newboldi spinosum (Kossmat)

Plate 38, figs. 3, 4*a*, *b*; Plate 40, fig. 3; Plate 42, fig. 1; Plate 43, figs. 3, 5

1897 *Acanthoceras newboldi* var. *spinosa* Kossmat, p. 114, pl. 13, figs. 2*a–c*, 3*a*, *b*; pl. 14, figs. 1*a*, *b*.
1951 *Calycoceras newboldi* var. *spinosum* (Kossmat); Wright and Wright, p. 26.

Discussion and occurrence. Spinose *Calycoceras* or the *newboldi* group are frequent in Chalk Basement Beds of *acutus*, *jukes-brownei*, and low *naviculare* Zone age, and also occur in the Chalk facies of similar age. These specimens are nearly all rather small, and show much variation (Pl. 38, figs. 3, 4*a*, *b*; Pl. 40, fig. 3).

Larger specimens (Pl. 43, figs. 3, 5) show the strong similarity of this species to *Acanthoceras*, as is clear from the large (220 mm) specimen described and figured by Matsumoto *et al.* (1957).

Wright and Wright (1951, p. 26) commented on the convergence of this species towards *Acanthoceras hippocastanum* (J. de C. Sowerby). This convergence is seen in Upper Cenomanian specimens from Bed C of the Cenomanian Limestone.

C. newboldi spinosum is widely recorded from north-west Europe, India, Africa, Madagascar, and North America.

Calycoceras paucinodatum (Crick)

Plate 9, figs. 4*a–c*; Plate 40, fig. 4; Plate 41, fig. 3; Plate 43, figs. 2, 4*a*, *b*; Plate 44, figs. 1*a–c*, 2*a–c*; Plate 45, figs. 1, 2, 3*a*, *b*; Plate 46, figs. 1*a–c*, 2*a–c*; Plate 47, figs. 6*a*, *b*, 7, 8*a*, *b*

?1822 *Ammonites gentoni* Brongniart, pp. 183, 392, pl. 6, fig. 6.
1857 *Ammonites navicularis* Mantell; Sharpe, p. 39, pl. 18, figs. 3, 5 only (*non* Mantell).
1900 *Calycoceras naviculare* Sharpe; Hyatt, p. 589.
1907 *Calycoceras paucinodatum* Crick, p. 203, pl. 13, figs. 3, 3*a*.
?1911 *Ammonites gentoni* Brongniart; R. Douvillé, pp. 223, 223*a*.
1925 *Calycoceras gentoni* (Brongniart); Diener, p. 167 (pars).
1925 *Calycoceras paucinodatum* (Crick); Diener, p. 167.
1926*a* *Metacalycoceras subgentoni* Spath, p. 83.
1937*a* *Calycoceras subgentoni* (Spath), p. 279.
1951 *Calycoceras subgentoni* (Spath); Wright and Wright, p. 25.
?1951 *Calycoceras gentoni* (Brongniart); Wright and Wright, p. 25.
1951 *Calycoceras paucinodatum* (Crick); Wright and Wright, p. 26.

Discussion. The holotype of *C. paucinodatum* was well described by Crick (1907, p. 203) and is figured here (Pl. 44, figs. 2*a–c*). Crick also discussed the original of Sharpe's (1857, pl. 18, figs. 3*a*, *b*) *Ammonites navicularis* (Sharpe, *non* Mantell) designated by Spath (1926*a*, p. 83) as type of *Calycoceras subgentoni* (Pl. 44, figs. 1*a–c*), and concluded that both specimens were conspecific. I agree with Crick's view; both specimens are from the same general horizon (*rhotomagense* Zone, *acutus* assemblage, or thereabouts), and apparent differences are only those of individuals. Specimens from England which I refer to this species are highly variable.

Inner whorls may bear very strong umbilical and lower ventro-lateral spines, thus being transitional towards *C. bathyomphalum* (Pl. 41, fig. 3; Pl. 46, figs. 2*a–c*); others lose all but the weak umbilical and lower ventro-lateral tubercles at diameters of 20–30 mm.

Adult whorls are also variable. Strength of ribbing, diameter at which tubercles disappear, and strength of umbilical tubercles are the most obvious variables, as is rib density. Two striking variants in this last respect are a distantly ribbed form with about 32 ribs on the outer whorl (Pl. 45, fig. 1; Pl. 47, figs. 8*a*, *b*) and a form in which the ribs are crowded and number about 36 on the outer whorl (Pl. 45, figs. 3*a*, *b*; Pl. 46, figs. 1*a–c*). The whorl section is also more depressed in the latter, and the ribbing weaker. Some specimens probably belonging to this species retain traces of ventro-lateral tubercles when adult.

The considerable range of variation admitted in this species is a result of the scores of specimens available for study; this is the commonest acanthoceratid in the *acutus* assemblage faunas of Chalk Basement Beds in south-west England.

The species most likely to be confused with *C. paucinodatum* is *C. gentoni* (Brongniart), casts of the types of which are figured (Pl. 23, figs. 4*a–c*; Pl. 40, figs. 1*a*, *b*). The types fall within the limits of *C. paucinodatum* as here conceived, although as individuals they do not find a precise match in *paucinodatum* populations.

It is known that the Rouen ammonite bed, the source of the holotype of *C. gentoni*,

is of *costatus* assemblage age, i.e. older than the typical *C. paucinodatum* to which it doubtless gives rise. Furthermore, the few topotype specimens of *C. gentoni* I have seen are all less spinose than some members of *C. paucinodatum* populations and lose their ventral tuberculation at small diameters. Pictet (1863, pl. 6, figs. 3*a–c*) figured 1 medium-sized spinose specimen. Subsequent work may show that *C. gentoni* is a synonym of *C. paucinodatum*, and that it has priority, although I remain undecided at present.

Occurrence. Common in the upper parts of the *rhotomagense* Zone in south-west England, although somewhat scarcer in the south-east. Also recorded from Europe, the Middle East, southern Africa, and Madagascar.

Subgenus LOTZEITES Wiedmann 1959

Type species. Acanthoceras aberrans Kossmat (1895, p. 202, pl. 14, fig. 4).

Diagnosis. See Wiedmann (1959, p. 731; 1964, p. 121).

Discussion. Wiedmann introduced this subgenus for medium-sized *Calycoceras* with ventro-lateral spines and straight ribs which homeomorph *Cheloniceras*. He referred three species, *C.* (*L.*) *aberrans*, *C.* (*L.*) *bathyomphalum*, and *C.* (*L.*) *lotzei* Wiedmann to the subgenus.

C. bathyomphalum has outer whorls which show it to be a *Calycoceras* of the *paucinodatum* group, and must be removed. *C.* (*L.*) *lotzei* may be based on a nucleus, but *C.* (*L.*) *aberrans* is a most distinctive form, with characteristically looped ribs across the venter between the ventro-lateral spines. Another species referable to this genus is *C.* (*L.*) *barruei* (Pervinquière).

Occurrence. Rare in high Middle and Upper Cenomanian of England, Spain, north Africa, Madagascar, and India.

Calycoceras (*Lotzeites*) *aberrans* (Kossmat)

Plate 37, figs. 4*a–c*; Plate 47, figs. 2*a*, *b*

1895 *Acanthoceras aberrans* Kossmat, p. 202, pl. 24, figs. 4*a–c*.
1951 *Euomphaloceras aberrans* (Kossmat); Wright and Wright, p. 29.

Discussion and occurrence. This species occurs rarely in Britain, as part of the phosphatized *naviculare* Zone fauna of Bed C, on the south Devon coast (BMNH, GSM, SMC B35528, Wrights' Collection WW20660, 20611, 19797). Outside England this species is also rare. The type is from India; Collignon (1964, p. 14, pl. 371, fig. 1617) recorded 2 specimens of his var. *madagascariensis* from the Cenomanian of Madagascar.

Calycoceras (*Lotzeites*) aff. *barruei* (Pervinquière)

Plate 47, figs. 4*a*, *b*; Plate 59, figs. 7*a*, *b*

cf. 1907 *Acanthoceras barruei* (Pervinquière), p. 284, pl. 15, figs. 7*a–c*.

Discussion. '*Acanthoceras*' *barruei* is based on a poor, crushed specimen, and it is thus difficult to interpret. A number of ammonites from England are close to this species and are best referred to as *C.* (*L.*) aff. *barruei*.

Occurrence. Chalk Basement Bed, Ringstead (Dorset) (WW22955, 22956) (high Middle Cenomanian); Bed C, Lyme Regis (Dorset) (SMC B35529) (*naviculare* Zone); Chalk Basement Bed, Askerswell (Dorset) (BMNH C76378) (basal *naviculare* Zone).

Genus PARACALYCOCERAS Spath 1925

Type species. Ammonites wiestii Sharpe (1857, p. 47, pl. 21, figs. 3*a–c*), by original designation of Spath (1925*a*, p. 197).

Diagnosis. Medium-sized, somewhat involute ammonites. Inner whorls slightly compressed, with long ribs bearing umbilical bullae, and lower and upper ventro-lateral tubercles separated by 1, 2, or sometimes more shorter ribs. There is a distinctly raised siphonal area, and an incipient siphonal tubercle on all ribs.

Outer whorl with a broad venter, and broad, distant, flexuous rursiradiate ribs, irregularly long and short.

Discussion. The remarkable ornament of the outer whorls separates *Paracalycoceras* from most acanthoceratids, although some *Stoliczkaia* species are superficially similar.

The type specimen of *P. wiestii* is lost, and I know of only 1 other specimen (WW 3556), described below. The nature of the inner whorls of this specimen raises some problems, as it resembles a number of 'submantellicerine' forms known from pyritic nuclei only.

Occurrence. Lower Cenomanian, *saxbii* assemblage fauna of Bed A_2 of the Cenomanian Limestone. Doubtful specimens occur in the Grizzle (high *mantelli* Zone) at Wilmington (south Devon). The genus also occurs in North America (C. W. Wright, pers. comm.).

Paracalycoceras wiestii (Sharpe)

Plate 32, figs. 1*a–d*

1857 *Ammonites wiestii* Sharpe, p. 47, pl. 21, figs. 3*a–c*.
1860 *Ammonites wiestii* Sharpe; Pictet and Campiche, p. 343.
1925*a* *Ammonites wiestii* Sharpe; Spath, p. 197.
1937*a* *Paracalycoceras wiestii* (Sharpe); Spath, p. 280.
1951 *Paracalycoceras wiestii* (Sharpe); Wright and Wright, p. 27.

Holotype. By monotypy, the original of Sharpe 1857, pl. 21, figs. 3*a–c*, from 'the chalk with siliceous grains' of Chardstock (Devon).

Diagnosis. As for genus.

Description and discussion. I know of only 1 specimen other than the type which can be referred to this species (WW 3556, Pl. 32, figs. 1*a–d*). This consists of a nucleus 30 mm in diameter and most of the body chamber. The early whorls are involute, slightly compressed, with flattened sides, and a rounded venter. There are 11 long ribs per whorl at a diameter of 30 mm. These ribs bear an elongate umbilical bulla, and pass straight across the flanks to a rather faint lower ventro-lateral swelling, and thence forwards to a small, rounded upper ventro-lateral tubercle. These longer ribs are separated by 2 or 3 shorter, intercalated ribs.

The ribs do not at first cross the venter, but there is a distinct siphonal ridge, which at a diameter of about 15 mm becomes broken by depressions corresponding to interspaces between ribs, those parts of the ribs which cross the venter thus bearing a suggestion of a siphonal tubercle.

On the body chamber, the whorl section is still slightly compressed, but with a broader, rounded venter, whilst the coiling has become more evolute. There are 12 ribs on the third of a whorl preserved. Long ribs rise at the umbilical shoulder, and are strong and broad, flexing backwards across flanks and venter. These ribs are very widely spaced and separated by 1, 2, or more shorter ribs. The peculiar ornament of the body chamber of *P. wiestii* readily separates it from other species.

The nucleus, however, shows an identical style of ribbing to several species of *Cottreauites*, e.g. *C. subvicinale* (Boule, Lemoine, and Thévenin) and *C. waterloti* Collignon (Collignon 1929). *Cottreauites* (Collignon 1929; Sornay 1955) is known only from nuclei, but as well as a comparable style of ribbing, the available *Paracalycoceras* specimen has a distinctly subcarinate venter at a comparable diameter.

The suture line of *Cottreauites* as figured by Collignon (1929) is simple; at the smallest diameter visible on *P. wiestii* (Pl. 32, fig. 1*a*) it is relatively simple, yet still more subdivided than in *Cottreauites* figured by Collignon, more closely resembling those figured by Sornay (1955). My present view is that more material is needed, but that there is a strong possibility that *Cottreauites* may be wholly or partly a synonym of *Paracalycoceras*.

Occurrence. The Wrights' specimen is from Bed A_2 of the Cenomanian Limestone at Whitecliff, Seaton (Devon). Sharpe's specimen is from Chardstock (Devon), where Bed A_2 is also present, and I infer that it is from this horizon also. Both occurrences are thus Lower Cenomanian, *mantelli* Zone, approximately *saxbii* assemblage age. Possibly comparable *Cottreauites* species are all of low Lower Cenomanian age.

Genus EUCALYCOCERAS Spath 1923

Type species. Ammonites pentagonus Jukes-Browne (*in* Jukes-Browne and Hill 1896, p. 156, pl. 5, figs. 1, 1*a*), by original designation of Spath (1923*b*, p. 144).

Diagnosis. Medium-sized compressed, involute, high-whorled ammonites, with dense ribbing, umbilical tubercles (sometimes projected into the umbilicus), and lower ventro-lateral, upper ventro-lateral, and siphonal tubercles, closely spaced across a high arched venter. Most, or all, of the tubercles may disappear on the body chamber, which shows approximated ribbing and a broad venter.

Discussion. As originally conceived, Spath (1923*b*) included a variety of species in

this genus which are better placed in *Calycoceras* [*sensu lato*], i.e. *C. spinosum* (Kossmat) and *C. choffati* (Kossmat).

Subsequently (1937*a*, p. 279), he restricted the genus to the *pentagonum* group, with 'compressed often almost smooth adult whorls or with the ribbing fine and degenerate'.

The subgenera *Proeucalycoceras* and *Subeucalycoceras* of Thomel (1969) were published without diagnosis, and are thus *nomina nuda*. They are a heterogeneous assortment, including the Lower Cenomanian *Mantelliceras lymense* (Spath).

Pseudocalycoceras Thomel 1969 has *Ammonites harpax* Stoliczka as type species. It is separated from *Eucalycoceras* in having a larger umbilicus; on average, fewer (25 as opposed to 35–50), coarser, flexuous rursiradiate ribs; and a strong umbilical bulla, twisted into an S. There are 3–5 rows of tubercles across the venter, closely spaced in the early stages, the upper ventro-lateral and siphonal tubercules surviving in adults.

Eucalycoceras has its origin in a compressed Middle Cenomanian group of *Calycoceras* [*sensu lato*] such as occur in the middle part of the *rhotomagense* Zone. The earliest English *Eucalycoceras* appear at the top of the *rhotomagense* Zone.

Occurrence. Eucalycoceras is known from north-west Europe, Africa, Madagascar, North America, and southern India, ranging from Middle Cenomanian to Lower Turonian.

Eucalycoceras pentagonum (Jukes-Browne)

Plate 48, figs. 1*a*, *b*, 2, 3*a*, *b*, 4*a*, *b*, 5*a*, *b*, 6*a*, *b*; Plate 49, figs. 1*a–c*

1864 *Ammonites harpax* Stoliczka, p. 72 (pars), pl. 37, fig. 2.
1896 *Ammonites pentagonus* Jukes-Browne; *in* Jukes-Browne and Hill, p. 156, pl. 5, figs. 1*a*, *b*.
1898 *Acanthoceras pentagonum* Jukes-Browne; Kossmat, p. 14, pl. 4, figs. 4*a–c*.
1923*b* *Eucalycoceras pentagonum* (Jukes-Browne); Spath, p. 144.
?1940 *Eucalycoceras* cf. *pentagonum* (Jukes-Browne and Hill); Fabre, p. 229.
1951 *Eucalycoceras pentagonum* (Jukes-Browne); Wright and Wright, p. 26.
1964 *Eucalycoceras pentagonum* Jukes-Browne and Hill; Collignon, p. 138, pl. 370, fig. 1610, ?fig. 1611, fig. 1612 = var. *tazoalavensis* Collignon.
1965 *Eucalycoceras* aff. *pentagonum* Jukes-Browne and Hill; Collignon, p. 12.

Holotype. Jukes-Browne's original specimen, GSM 53481, from Bed C of the Cenomanian Limestone near Lyme Regis (Dorset), by monotypy.

Diagnosis. A moderately involute, compressed *Eucalycoceras*, with slab-like sides bearing many long straight ribs which are effaced at mid-flank. These long ribs alternate with shorter, intercalated ribs. The long ribs are projected into the umbilicus as a transversely elongate tubercle; all the ribs bear 5 rows of tubercles across the venter on the phragmocone. The body chamber lacks ventral tubercles and has approximated ribs close to the aperture.

Description. The holotype is a poorly preserved, corroded, phosphatic internal mould, bearing traces of glauconitic and phosphatic chalk. Just under half the final whorl is body chamber. The shell is moderately involute, about two-thirds of the previous whorl being covered. The whorl section is compressed, with flat sides and a high, arched venter on the phragmocone, becoming broadly rounded on the body chamber.

The greatest width is at mid-flank. The umbilicus is rather small, full of phosphatic sediment, and not fully visible. The umbilical wall is fairly steep.

There are 18–20 long ribs per whorl, arising from bullate umbilical tubercles which project into the umbilicus. The ribs pass across the flanks with only a gentle flexing. They are rounded and about the same width as the interspaces. At the middle growth stage they are effaced at mid-flank. The long ribs are separated by 1 or sometimes 2 shorter, intercalated ribs, which arise just below mid-flank. All the ribs on the phragmocone strengthen across the venter, and bear 5 rows of tubercles. The lower ventro-lateral tubercles are weakest and show slight spiral elongation, as do the slightly stronger upper ventro-lateral tubercles. The siphonal tubercles are strongest and show a slight transverse elongation.

On the body chamber there is a marked change in ornament. All the ventral and ventro-lateral tuberculation is lost, and the venter becomes broadly rounded. At first, the ribs weaken considerably, but they strengthen at the aperture, becoming approximated, with a distinct flexure at mid-flank, so that they are slightly rursiradiate across the venter. These ribs have a very steep adoral face, a flattened outer face, and a steep adapical face, and are as wide or wider than the interspaces. This gives the specimen a very distinctive appearance. The sutures are not visible.

Discussion. Jukes-Browne's figures are highly restored. A fine specimen in the Wrights' Collection (WW 22644, Pl. 49, figs. 1*a–c*) shows the middle growth stages, especially effacement of the ribs and mid-flank. The nature of the adult body chamber ornament is best seen on a specimen in J. M. Hancock's Collection (JMH CC740, Pl. 48, figs. 1*a*, *b*).

The early stages in development are illustrated by a series of specimens in the Wrights' Collection. Thus at the smallest diameter available (WW 2977, 18 mm, Pl. 48, figs. 4*a*, *b*) the whorl section is high, compressed, with flattened sides, flattened ventro-lateral shoulders, and a flat venter. There are about 28 ribs which run straight across the sides, but details of the umbilical region are not visible. There is a sharp lower ventro-lateral tubercle, connected to a strong, high, sharp upper ventro-lateral tubercle by a broad forwardly directed rib. The upper ventro-lateral tubercles increase in strength and at 18 mm rise high above the ventral region. The ribs cross the venter, and there is a hint of a clavate siphonal tubercle.

A larger specimen (WW 22478, Pl. 48, figs. 5*a*, *b*) shows that at diameters of about 30–35 mm the ribs nearly all extend down to the umbilicus, but that only 1 in every 2 or 3 develops an umbilical bulla. By this diameter the venter has broadened, become arched, and the siphonal tubercle is becoming increasingly prominent.

A larger fragment (WW 20799, Pl. 48, figs. 6*a*, *b*) links these small specimens with the holotype.

I know of no described species likely to be confused with *E. pentagonum*. The umbilical tubercles of *E. gothicum* project deeply into the umbilicus. *E. besairei* Collignon (1937, p. 13, pl. 3, figs. 1–4; pl. 7, fig. 5) develops very distant ribbing on its body chamber. *E. spathi* Collignon (1937, p. 17, pl. 4, fig. 2; pl. 9, fig. 3) has distinctive ribbing, not effaced at mid-flank, and is much more evolute and less compressed than *E. pentagonum*.

E. (?)shastense (Reagan) (Matsumoto 1959, p. 94, pl. 23, figs. 1*a–c*; pl. 24, figs.

2*a*, *b*, 3*a*, *b*; text-figs. 47–50) is a Lower Turonian species, which Matsumoto has discussed in detail. It has an *Eucalycoceras*-like venter, with 5 rows of tubercles, but does not show the crowded ribs of *Eucalycoceras*, whilst tending to develop a lateral tubercle. It is more evolute, more coarsely ribbed, and less elevated than typical *Eucalycoceras*. Other Lower Turonian species of the same group are '*Eucalycoceras*' *dentonense* Moreman (1942, p. 205, pl. 33, figs. 4, 5; text-fig. 21) and '*Eucalycoceras*' *indianense* Moreman (1942, p. 206, pl. 33, figs. 9, 10; text-fig. 21). A new generic or subgeneric name is needed for these forms, but their phylogeny is at present obscure (compare Matsumoto 1959, pp. 97, 98). Some of the '*Romaniceras*' described by Jones (1938) may also belong here. '*Romaniceras*' *coahuilense* Jones (1938, p. 118, pl. 6, fig. 1; pl. 8, fig. 5; see Matsumoto 1959, p. 98) is very close to *Eucalycoceras*, but this species too develops a lateral tubercle.

Occurrence. Most English specimens of *E. pentagonum* come from the phosphatized *naviculare* Zone fauna of Bed C of the Cenomanian Limestone of the Devon coast. The species also occurs at the same horizon at Wilmington (south Devon). Another specimen is from the *naviculare* Zone of the Lower Chalk at Eastbourne (Sussex), collected by Mr. J. Parmenter, whilst there is a specimen in the Institute of Geological Sciences (GSM RLS453), from 'a pit 750 yards SSW of Great Kimble Church, Bucks', 3–4 m below the *plenus* Marls.

The species occurs widely in southern France, Spain, Portugal, north Africa, India, Madagascar, and perhaps North America (C. W. Wright, pers. comm.).

Eucalycoceras gothicum (Kossmat)

Plate 50, figs. 1, 2*a*, *b*

1865 *Ammonites rotomagensis* var. *compressa* Stoliczka, p. 69, pl. 34, fig. 5.
1895 *Acanthoceras gothicum* Kossmat, p. 69, pl. 25, figs. 3*a–c*.
?1907 *Acanthoceras* cf. *gothicum* Kossmat; Pervinquière, p. 261.
1923*b* '*Acanthoceras*' *gothicum* Kossmat; Spath, p. 144.
1925 *Acanthoceras gothicum* Kossmat; Diener, p. 161.
?1940 *Eucalycoceras* cf. *gothicum* (Kossmat); Fabre, p. 228.

Discussion. This species is readily identifiable by the characteristic projection of the umbilical tubercles into the umbilicus.

Occurrence. Upper part of *rhotomagense* Zone and low *naviculare* Zone of south-west England. Also occurs in western Europe, north Africa, Madagascar, and India.

Eucalycoceras rowei (Spath)

Plate 49, figs. 2, 3, 4*a*, *b*, 5*a*, *b*, 6*a*, *b*, 7*a*, *b*; Plate 50, figs. 3, 4*a*, *b*, 6*a*, *b*, 7*a*, *b*

1867 *Ammonites couloni?* d'Orbigny; Guéranger, p. 6, pl. 5, fig. 1 (*non* d'Orbigny).
1926*b* *Mantelliceras rowei* Spath, p. 431.
1951 *Mantelliceras rowei* Spath; Wright and Wright, p. 24.
1959 *Eucalycoceras rowei* (Spath); Hancock, p. 251.

Lectotype. Here designated, BMNH C7285, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Diagnosis. Compressed, densely ribbed *Eucalycoceras* in which outer whorls bear umbilical tubercles, but with only 3 rows of tubercles across the venter.

Description. The lectotype is a phosphatized internal mould, retaining traces of phosphatized shell. Only the outer whorl is visible. The shell is rather evolute, about a quarter of the previous whorl being covered. The whorl section is compressed, the greatest breadth being at the umbilical tubercle. The sides are flat and the venter rounded in intercostal section; the costal section is polygonal to rounded. The umbilicus is quite wide and moderately deep. The umbilical wall is sharply rounded and undercut and the umbilical shoulder is rounded.

There are 38 ribs per whorl at a diameter of 50 mm, and all are long, arising from an umbilical bulla which is developed to a varying degree and is occasionally absent. The ribs are strong, sharp, acutely rounded, and narrower than the interspaces. Most pass straight up the sides, although some ribs are gently flexed. Each rib bears a small bullate lower ventro-lateral tubercle and a clavate upper ventro-lateral tubercle on each side of a narrow, flat venter. Between the upper and lower ventro-lateral tubercles the ribs are broader than on the flanks. The upper ventro-lateral tubercles are connected across the venter by a broad, sharp, rounded rib, depressed immediately against the upper ventro-lateral tubercle, but raised to just above or just below the level of the ventro-lateral tubercle in the mid-ventral region. A siphonal tubercle is present up to a diameter of 25–30 mm; it weakens at greater diameters.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH C7285, lectotype	51·6	—(—)	19·8( )	15·3( )	38

Discussion. Topotypes in the Wrights' Collection (WW 20644, 20774, 20775, 20777, 21889, 22001, 22663, 22670) show the development of this species (Pl. 49, figs. 2–7) and indicate some variation in ornament, and in the strength of the tuberculation. The largest available specimens show that a good siphonal tubercle is present, and that short ribs separate the long ribs.

The compression of this species, many ribs, and trituberculate venter when adult, separates it from other named *Eucalycoceras*. The specimen figured by Guéranger (1867) may well be an adult of this species, but is shown in side view only. It is apparently lost (J. M. Hancock, pers. comm.).

Mantelliceras sellardsi Adkins (1928, p. 239, pl. 25, fig. 1; pl. 26, fig. 4) seems to be an *Eucalycoceras*, but is poorly figured and described. It appears to differ from *E. rowei* in having lower and upper ventro-lateral tubercles and fewer ribs (Adkins 1928, pp. 239, 240).

I had originally thought the present species to be a *Tarrantoceras* (Stephenson 1955, p. 59), but although the inner whorls are very similar, *Tarrantoceras* seems invariably to lose its siphonal tubercle and to be adult at small diameters. It is very closely related to *Eucalycoceras* of the *rowei* group.

Occurrence. Rare; Bed C, Cenomanian Limestone, Devon coast; Upper Cenomanian of Sarthe, France.

Subfamily ACANTHOCERATINAE Hyatt 1900
Genus ACANTHOCERAS Neumayr 1875

Type species. Ammonites rhotomagensis Brongniart *in* Cuvier and Brongniart 1822, p. 391, pl. N, figs. 2*a*, *b*, by subsequent designation of de Grossouvre (1894).

Diagnosis. Medium-sized or large evolute or moderately involute ammonites, often with quadrate whorl section. Typically strongly ribbed, with straight, rarely flexuous strong rounded ribs, usually alternately long and short on the inner whorls although this may change on the outer whorl where all the ribs may be long.

Strongly tuberculate, with umbilical, lower and upper ventro-lateral, and siphonal tubercles. The siphonal tubercles are often lost early in ontogeny. The ventro-lateral tubercles often combine to form a transverse tubercle, or the upper ventro-lateral tubercle may be absorbed into a ventro-lateral horn. The aperture is simple. The suture is simple, with broad, squarish bifid or trifid elements.

Discussion. Acanthoceras at present covers a number of groups of rather similar ammonites which require subgeneric separation when the groups have been fully described and discussed. The restricted genus is a group of square-whorled, rather involute ammonites, with alternately long and short simple ribs when young, and long ribs only when adult.

Haas (1963) introduced the genus *Paracanthoceras*, later (1964) renaming it *Plesiacanthoceras* due to prior usage of *Paracanthoceras*, with *P. wyomingense* (Reagan) as type species. Matsumoto and Obata (1966) questioned the separation of *Plesiacanthoceras* and *Acanthoceras*; this view is upheld here.

Acanthoceras [*sensu stricto*] is quite distinct from *Calycoceras* [*sensu stricto*] (i.e. *sensu C. naviculare*). *Calycoceras* [*sensu stricto*] has an inflated, fat whorl section, losing all but the upper ventro-lateral tubercles at an early stage, with close, fat, rounded ribbing.

Acanthoceras is clearly separated from *Euomphaloceras* by the presence of multiple siphonal tuberculation, intercalated ventral ribs, and ventral constrictions in the latter. *Romaniceras* is characterized by the presence of a further row of lower lateral tubercles. *Yubariceras* has 1 or 2 more rows of lateral tubercles. A fuller discussion of *Acanthoceras* and a revision of the *rhotomagense* group is given elsewhere (Kennedy and Hancock 1970).

I regard the following species of '*Acanthoceras*' previously recorded from Britain as *nomina dubia*, being based on insufficient or idealized representation, and I prefer not to use the names until the type material is refigured and redescribed.

(i) *Acanthoceras deciduum* Hyatt (1903, p. 107) = *Ammonites rhotomagensis* Defrance (d'Orbigny 1841, p. 345, pl. 106). This is based on a typical d'Orbigny synthetograph without scale. I have been unable to trace the figured specimen in the d'Orbigny Collections in France.

(ii) *Acanthoceras sherborni* Spath (1926*a*, p. 82) = *Ammonites cenomanensis* d'Archiac (Sharpe 1857, p. 34, pl. 17, figs. 1*a*, *b* (*non* d'Archiac)). The holotype is lost. Sharpe's figure is of a remarkably paucicostate *Acanthoceras*, possibly a specimen of *A. rhotomagense confusum* Guéranger.

(iii) *Acanthoceras diadema* Spath (1926*b*, pp. 426, 431) = *Ammonites cunningtoni* Pictet (1863, p. 32, pl. 5, fig. 1) is an *Euomphaloceras*.

(iv) *Acanthoceras simulans* Spath (1926*a*, p. 82) = *Ammonites rotomagensis* Defrance (Schlüter 1871, p. 15, pl. 7, fig. 3 only). This is based on a ventral view only of a single ammonite which shows multiple siphonal tuberculation. It is probably an *Euomphaloceras* of the *inerme* group.

Occurrence. Middle and Upper Cenomanian; world-wide.

Acanthoceras rhotomagense rhotomagense (Brongniart)

1822 *Ammonites rhotomagensis* Brongniart; Cuvier and Brongniart, p. 391, pl. N, figs. 2*a*, *b*.
1970 *Acanthoceras rhotomagense rhotomagense* (Brongniart); Kennedy and Hancock, p. 466, pl. 88, figs. 1–5; pl. 89, fig. 1; text-figs. 2, 6*b*, 7.

Occurrence. Very rare in *costatus* and *acutus* assemblage faunas.

Acanthoceras rhotomagense subflexuosum Spath

1826 *Ammonites rhotomagensis* Defrance; J. de C. Sowerby, vol. 6, p. 25, pl. 515, fig. 1.
1923*b* *Acanthoceras subflexuosum* Spath, p. 144.
1970 *Acanthoceras rhotomagense subflexuosum* Spath; Kennedy and Hancock, p. 469, pl. 90, figs. 1–4; text-fig. 8.

Occurrence. Quite frequent in *costatus* and *acutus* assemblage faunas.

Acanthoceras rhotomagense sussexiense (Mantell)

1822 *Ammonites sussexiensis* Mantell, p. 114, pl. 20, fig. 2.
1970 *Acanthoceras rhotomagense sussexiense* (Mantell); Kennedy and Hancock, p. 472, pl. 89, fig. 2; pl. 91, figs. 1, 2; pl. 92, figs. 1, 2; text-figs. 3–5, 6*b*.

Occurrence. Frequent in *costatus* assemblage faunas; common in the succeeding *acutus* assemblage faunas.

Acanthoceras rhotomagense confusum (Guéranger)

1867 *Ammonites confusus* Guéranger, pp. 5, 6, pl. 2, fig. 4; pl. 3, fig. 1; pl. 8, fig. 1.
1970 *Acanthoceras rhotomagense confusum* (Guéranger); Kennedy and Hancock, p. 478, pl. 94, figs. 1–4; pl. 95, fig. 1.

Occurrence. Frequent in the middle part of the *rhotomagense* Zone.

Acanthoceras rhotomagense clavatum Kennedy and Hancock

1970 *Acanthoceras rhotomagense clavatum* Kennedy and Hancock, p. 479, pl. 96, figs. 2, 3; pl. 97, fig. 5.

Occurrence. Not uncommon in *costatus* and *acutus* assemblage faunas.

Acanthoceras basseae Kennedy and Hancock

1970 *Acanthoceras basseae* Kennedy and Hancock, p. 481, pl. 97, figs. 1*a*, *b*, 2*a*, *b*, 5*a*, *b*.

Occurrence. A single specimen from the middle part of the *rhotomagense* Zone, Eastbourne (Sussex).

Acanthoceras hippocastanum (J. de C. Sowerby)

Plate 51, figs. 1*a–d*, 2*a*, *b*, 3*a–c*, 4*a–c*, 5*a*, *b*

1826 *Ammonites hippocastanum* J. de C. Sowerby, p. 23, pl. 514, fig. 2.
non 1857 *Ammonites hippocastanum* J. de C. Sowerby; Sharpe, p. 37, pl. 17, figs. 3, 4.
non 1907 *Acanthoceras hippocastanum* (J. de C. Sowerby); Crick, p. 194, pl. 13, figs. 4, 4*a*.

non 1910 *Acanthoceras rhotomagense* Defrance var. *hippocastanum* (J. de C. Sowerby); Pervinquière, p. 44, pl. 4, figs. 32–36.
?1923*b* *Protacanthoceras hippocastanum* (J. de C. Sowerby); Spath, p. 144.
non 1929 *Acanthoceras hippocastanum* (J. de C. Sowerby); Collignon, p. 32, pl. 3, figs. 1, 1*a*.
non 1931 *Acanthoceras hippocastanum* (J. de C. Sowerby); Collignon, p. 38, pl. 4, figs. 1, 2.
1937*a* *Acanthoceras hippocastanum* (J. de C. Sowerby); Spath, p. 279.
non 1940 *Acanthoceras hippocastanum* (J. de C. Sowerby); Fabre, p. 232, pl. 5, figs. 10, 11.
non 1951 *Acanthoceras hippocastanum* (J. de C. Sowerby); Wright and Wright, p. 28.

Lectotype. The lectotype, by subsequent designation of Kennedy and Hancock (1970), is the original of *Ammonites hippocastanum* J. de C. Sowerby 1826, p. 23, pl. 514, fig. 2, GSM 37667. From Sowerby's description, and from the preservation, the lectotype is clearly from Bed C of the Cenomanian Limestone. The locality is almost certainly Humble Point, south Devon, or close by.

Diagnosis. A small, inflated, depressed, involute *Acanthoceras*, with the greatest breadth at a strong umbilical tubercle. Ornament consists of about 22 strong ribs, alternately long and short. The long ribs bear huge umbilical tubercles, very strong, pointed lower ventro-lateral tubercles, and strong clavate upper ventro-lateral and siphonal tubercles. The short ribs are weaker, without tubercles, or with weak, clavate upper ventro-lateral and siphonal tubercles.

Description. The lectotype is a medium-sized phosphatized internal mould, septate for all but the space of the last few ribs. The phosphate is a pale cream colour with a thin glauconitic coat in patches. The umbilicus is full of phosphatized sediment.

The shell is moderately evolute, and the whorl section is depressed. The intercostal section is inflated, with rounded sides, converging towards a broadly rounded venter. The costal section is depressed, polygonal, and highly angular; the greatest breadth is at the umbilical tubercle. The umbilicus is rather small, deep, with a steep umbilical wall and a rounded umbilical shoulder.

There are 22 ribs on the outer whorl, of which 11 are long, and arise at the umbilical seam. They pass straight up the umbilical wall and are produced at the umbilical shoulder into a very prominent, sharp, slightly bullate, umbilical tubercle. The ribs are as wide as the interspaces and pass straight up the sides, weakening at mid-flank. They connect to a strong, pointed, lower ventro-lateral tubercle and a strong clavate upper ventro-lateral tubercle. There are clavate siphonal tubercles, slightly weaker than the upper ventro-lateral tubercles, to which they are connected by a broad rounded rib.

The shorter ribs alternate very regularly with the long ribs. Arising at mid-flank, they are at first weak, passing straight up the flank and across the ventro-lateral shoulder, without developing lower ventro-lateral tubercles, but with clavate upper ventro-lateral and siphonal tubercles, although these are weaker than those on the long ribs. Occasionally, the long ribs are separated by much weaker non-tuberculate ribs, arising at mid-flank, passing straight up the sides and across the venter.

The suture is not fully visible but appears to be of normal *Acanthoceras* type.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
GSM 37667, lectotype, costal	64·0	53·0 (82·6)	29·6 (46·3)	17·0 (26·6)	22
intercostal	59·3	44·6 (75·2)	27·6 (46·5)	17·0 (28·6)	22

Discussion. The small size of adult specimens, their inflated form, coarseness of ribbing, and strong tuberculation are the key features of *A. hippocastanum*. The

short ribs, lacking lower ventro-lateral tubercles, and the occasional presence of non-tuberculate ribs, separate this species from almost all other described *Acanthoceras*. *A. jukes-brownei* has slightly fewer ribs and lacks the striking umbilical and lower ventro-lateral tubercles of *A. hippocastanum*. It also reaches a much larger size.

As Wright and Wright (1951, p. 26), noted, some contemporary *Calycoceras* of the *spinosum* group are superficially similar to this species and are often difficult to separate when poorly preserved.

Only Sowerby's original figured specimen can be referred to this species; all other previous descriptions refer to other inflated species of *Acanthoceras*. The other syntype specimen referred to by Sowerby is of Middle Cenomanian age (Kennedy and Hancock 1970).

Occurrence. Upper Cenomanian, *naviculare* Zone, Bed C of the south Devon coast.

Acanthoceras jukes-brownei (Spath)

Plate 52, figs. 1*a*, *b*, 2, 3*a*–*c*; Plate 53, fig. 1; Plate 54, fig. 1; Plate 55, figs. 1*a*–*c*, 2

1857 *Ammonites hippocastanum* Sowerby; Sharpe, p. 37, pl. 17, fig. 2 only (*non* Sowerby).
1926*a* *Protacanthoceras jukes-brownei* Spath, p. 82.
1951 *Acanthoceras jukes-brownei* (Spath); Wright and Wright, p. 28.

Holotype. By original designation of Spath (1926*a*, p. 82), the original of *Ammonites hippocastanum* Sowerby (Sharpe 1857, pl. 17, fig. 2 only (*non* Sowerby)), BMNH 50162, from the Lower Chalk Basement Bed, Man o' War Cove (Dorset).

Diagnosis. Large *Acanthoceras* in which alternation of long and short ribs, about 17 per whorl, is retained to maturity. Long ribs with strong bullate umbilical tubercles and strong transversely elongate ventro-lateral tubercles. Short ribs with ventro-lateral tubercles only.

Description. The holotype is a small, part-phosphatized internal mould, in hard, sandy glauconitic chalk. The whole of one side and the whole of the venter, apart from the final part, extending for only 4 ribs, has been destroyed. Only the outermost whorl is visible. The specimen is septate to 36·5 mm.

The shell is moderately evolute, about a third of the previous whorl being covered. The whorl section is depressed. The intercostal section is flat-sided, with broadly rounded ventro-lateral shoulders and a rather narrow, flat venter. The costal section is polygonal, the greatest breadth being at the umbilical tubercle. The umbilicus is rather small and deep. The umbilical wall is steep and rounded.

There are 20 ribs on the outer whorl, 8 long ribs and 12 shorter intercalated ribs. The long ribs arise at the umbilical bullae on strong, slightly flexed, prorsiradiate rounded ribs. These ribs are narrower than the interspaces and are weakened on the upper part of the flank. They bear strong, sharply pointed lower ventro-lateral tubercles which are connected by a low broad rib to strong clavate upper ventro-lateral tubercles. The ribs are broad and rounded across the rather narrow venter, bearing a clavate siphonal tubercle, only slightly less prominent than the upper ventro-lateral tubercles.

Intercalated between the long ribs are 1 or 2 shorter ribs. Some of these ribs arise at the umbilical seam; lacking an umbilical tubercle, and only faintly developed

across the flank, they bear a weak lower ventro-lateral tubercle and have a ventral development similar to the long ribs. Other short ribs arise at mid-flank and these lack a lower ventro-lateral tubercle. The sutures are poorly visible but of normal *Acanthoceras* type.

Dimensions.

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 50162, holotype	47	— (—)	23·0 (48·9)	15·0 (31·9)	19

Discussion. From a study of dozens of specimens it has become apparent that the indifferently preserved holotype is, in fact, the nucleus of the giant acanthoceratids with coarse, alternately long and short ribs which are abundant in the upper part of the English Middle Cenomanian (Pl. 52, fig. 2; Pl. 53, fig. 1).

These specimens show that the later whorls are evolute, with a depressed whorl section, trapezoidal in intercostal and costal section; the sides are flattened, the umbilical shoulder and venter broadly rounded. There are about 17 ribs per whorl, alternately long and short. The long ribs arise at the umbilical seam as a broad low swelling, produced into a very strong bullate umbilical tubercle. These are connected to a strong, transversely elongate ventro-lateral tubercle by strong rounded ribs. These ribs are narrower than the interspaces, and are depressed at mid-flank.

The ventro-lateral tubercles are connected across the venter by a low rounded rib, considerably narrower than the interspaces. The short ribs arise at about mid-flank and develop ventro-lateral tubercles like those on the long ribs, connected across the venter by a similar rib.

There is much variation in this species. Some nuclei are relatively compressed (Pl. 55, figs. 1*a–c*), whilst a few large specimens develop enormous horns (Pl. 54, fig. 1; Pl. 55, fig. 2).

The alternately long and short ribs of adults distinguish this from most named *Acanthoceras*. Differences from *A. hippocastanum* are discussed under that species. *Ammonites hudani* Fric (1911, p. 10, fig. 33) may be a related ammonite, but the holotype appears to lack such a regular alternation of long and short ribs as *A. jukes-brownei*.

Occurrence. Common in the upper part of the *rhotomagense* Zone in southern England.

Acanthoceras latum Crick

Plate 56, figs. 1*a*, *b*; Plate 57, figs. 1*a*, *b*

1907 *Acanthoceras latum* Crick, p. 195, pl. 12, figs. 2, 2*a*.

Lectotype. Crick based this species on 3 specimens; the one described in detail and figured (1907, pl. 12, figs. 2, 2*a*) is here designated lectotype.

Discussion. This species belongs to the *rhotomagense* group, but individuals of *latum* type do not occur in the type population at Rouen; the English and African examples come from a somewhat higher horizon.

Occurrence. Middle Cenomanian, *rhotomagense* Zone, *acutus* assemblage faunas of the Chalk Basement Bed, Snowdon Hill, Chard (Somerset). The types are from Zululand.

Acanthoceras tunetana Pervinquière

Plate 40, fig. 5

1907 *Acanthoceras confusum* (Guéranger) var. *tunetana* Pervinquière, p. 268, pl. 13, fig. 4.

Discussion and occurrence. A remarkable ammonite from the Chalk Basement Bed, Snowdon Hill, Chard (Somerset), of *rhotomagense* Zone, *acutus* assemblage age would seem to belong to this species. There are 8 distant ribs on the last half whorl, with a strong rounded umbilical tubercle, a very strong rounded lower ventro-lateral tubercle on each side of a broad venter, which bears weak, clavate upper ventro-lateral and siphonal tubercles.

The type is a much larger specimen, but shows a comparable venter, distant ribs, and peculiar lower ventro-lateral tubercles.

Acanthoceras whitei Matsumoto

Plate 58, figs. 1*a*, *b*

1959 *Acanthoceras whitei* Matsumoto, p. 82, pl. 22, figs. 1*a–c*; pl. 39, fig. 1; text-fig. 36 (with synonymy).

Discussion and occurrence. This species is well described and figured by Matsumoto (1959). Occasional specimens from *jukes-brownei* assemblage faunas of south-east and south-west England seem to belong here.

Genus EUOMPHALOCERAS Spath 1923
(= CUNNINGTONICERAS Collignon 1937)

Type species. Ammonites euomphalus Sharpe 1855, p. 31, pl. 13, figs. 4*a–c*, by original designation of Spath (1923*b*, p. 144, footnote 2).

Diagnosis. Medium-sized to large acanthoceratids characterized by the exaggerated development of umbilical and/or ventro-lateral horns or spines. Ventral constrictions are present in some species, as are short intercalated ventral ribs, all of which bear a siphonal tubercle. There are always more rows of siphonal tubercles than other tubercles at some stage in development.

Discussion. This striking genus appears in the Middle Cenomanian (*E. inerme* (Pervinquière), *E. cunningtoni* (Sharpe)) and extends to the top of the stage (*E. euomphalum*). It is derived from *Acanthoceras* of the *sussexiense* (Mantell) group by loss of ribbing and development of intercalated ventral ribs and constrictions. Specimens showing this multiple siphonal tuberculation appear in the *costatus* assemblage faunas of the Craie Chloritée, Rouen, France, and are figured by Kennedy and Hancock (1970).

Kanabiceras Reeside and Weymouth (1931) is very close to *Euomphaloceras*, but the siphonal tubercles form a definite serrated keel (sometimes seen in *E. euomphalum*), whilst the ventro-lateral tubercles are oblique, not transverse (see Matsumoto 1959, pp. 98 et seq.). The 2 genera are connected by intermediates. In England, *Kanabiceras* occurs at a higher horizon than *Euomphaloceras*, in the *plenus* Marls, Melbourn Rock, and as part of the indigenous fauna of Bed C in south Devon (Jefferies Collection; Sedgwick Museum, Cambridge; Wrights' Collection).

Occurrence. *Euomphaloceras* has a world-wide distribution in the Middle and Upper Cenomanian.

Euomphaloceras euomphalum (Sharpe)

Plate 43, fig. 1; Plate 59, figs. 1*a*, *b*, 2*a*–*c*, 3*a*, *b*, 4*a*–*c*, 5*a*, *b*

1855 *Ammonites euomphalus* Sharpe, p. 31, pl. 13, figs. 4*a*–*c*.
1899 *Douvilleiceras euomphalum* (Sharpe); Crick, pp. 251, 256, figs. 1, 2.
1907 *Acanthoceras giltarei* Pervinquière, p. 285, pl. 15, figs. 8*a*–*c*, 9*a*, *b*.
1923*b* *Euomphaloceras euomphalum* (Sharpe); Spath, p. 143, footnote 4.
1951 *Euomphaloceras euomphalum* (Sharpe); Wright and Wright, p. 29 (pars).
1963*a* *Euomphaloceras euomphalum* (Sharpe); Wright, p. 609.

Holotype. By monotypy, Sharpe's specimen BMNH 50185 (= Sharpe 1855, p. 31, pl. 13, figs. 4*a*–*c*) from 'Man o' War Cove' (Dorset). This locality is wrong (see below).

Diagnosis. *Euomphaloceras* with distinct constrictions in front of the long ribs, ventro-lateral tubercles never fusing, and developing ventro-lateral spines when adult.

Description. The holotype is a well-preserved wholly septate internal mould. The shell is very evolute, about one sixth of the previous whorl being covered. The whorl section is depressed, the greatest breadth being at the lower ventro-lateral spine; it is oval in intercostal section, polygonal in costal section. The sides are inflated, with a broad venter. The umbilicus is broad, the umbilical wall rounded, and impressed to accommodate the lower ventro-lateral spines of the preceeding whorl.

There are 20 long ribs on the outer whorl. These arise at the umbilical seam as faint swellings, pass forwards across the umbilical wall, connecting to sharp prorsiradiate umbilical bullae on the umbilical shoulder. These are connected in turn by a sharp rib to a strong outward-pointing lower ventro-lateral spine. This spine is joined by a slightly broadened prorsiradiate rib to a transversely elongate upper ventro-lateral tubercle.

The upper ventro-lateral tubercles are joined across the venter by a narrow rib, depressed medially, with a faint siphonal tubercle. There is a strong constriction across the venter in front of each of these ribs, so that the ribs have an asymmetric profile, with a steep adoral face and a gentle adapical face. The ribs are narrower than the interspaces.

Between each long rib there are 1 or 2 short intercalated ribs. These arise at the level of the lower ventro-lateral tubercle and extend across the venter, bearing faint upper ventro-lateral tubercles. There are thus 2–3 times as many ribs on the venter as on the flanks. Some, but not all, of the shorter ribs extend down on to the flanks as faint striae.

The suture has a long narrow first lateral saddle, a wide lateral lobe with a short, broad central element, and a small umbilical saddle.

Discussion. Sharpe's specimen is clearly mis-localized, and is from Bed C of the Devon coast. Another specimen, BMNH C26307, from 'Chardstock' is also mis-localized.

Material from Bed C is quite variable at diameters larger than the holotype (Pl. 43, fig. 1; Pl. 59, figs. 3*a*, *b*, 4*a*–*c*, 5*a*, *b*). As Wright (1963*a*, p. 609) has discussed, at least 2 very distinct forms occur. In some specimens the upper ventro-lateral

tubercles are transversely elongate and are developed on many of the intercalated ribs.

In other forms there is a stronger tendency towards spinosity. The upper ventro-lateral tubercles are projected strongly normal to the venter, with 3–4 non-spinose ribs between spinose ones. The development of long lower ventro-lateral spines and their accommodation in depressions in the umbilical wall of the preceding whorl produces a polygonal umbilicus.

My largest specimen has a whorl breadth of 50 mm, an estimated diameter of 120 mm, and appears to be adult.

E. euomphalum differs from *E. cunningtoni* (Sharpe) in its much lower long rib density and the development of constrictions, which I have never seen in English specimens of *cunningtoni*. *E. cunningtoni* and all other described forms (discussed below) are very coarsely ornamented and unlikely to be confused with *E. euomphalum*.

Acanthoceras giltarei Pervinquière (1907, p. 285, pl. 15, figs. 8*a–c*, 9*a*, *b*) is a synonym of *E. euomphalum*, although the types are poor.

Occurrence. Upper Cenomanian, *naviculare* Zone, Bed C, Devon coast and Bovey Lane Sandpit, Beer (south Devon), also the same horizon at Wilmington (south Devon). The species is also known from the Upper Cenomanian of Algeria and occurs in Tunisia.

Euomphaloceras cunningtoni (Sharpe)

Plate 60, figs. 1*a*, *b*; Plate 61, figs. 2*a*, *b*

	1855	*Ammonites cunningtoni* Sharpe, p. 35, pl. 15, figs. 2*a–c*.
	?1863	*Ammonites cunningtoni* Sharpe; Pictet, p. 32, pl. 5.
	1864	*Ammonites meridionalis* Stoliczka, p. 76, pl. 41, figs. 1*a–c*.
	1897	*Acanthoceras cunningtoni* var. *cornuta* Kossmat, p. 11, pl. 5, figs. 1*a–c*.
?*non*	1904*b*	*Acanthoceras cunningtoni* Sharpe; H. Douvillé *in* Morgan, p. 241, pl. 31, figs. 2*a*, *b*.
	1907	*Acanthoceras cunningtoni* Sharpe; Pervinquière, p. 277, pl. 15, figs. 1*a–c*.
	1907	*Acanthoceras meridionale* Stoliczka; Pervinquière, p. 278, pl. 15, figs. 2–6.
	1933	*Acanthoceras cunningtoni* (Sharpe); Collignon, p. 63, figs. 2, 3.
non	1940	*Cunningtoniceras cunningtoni* Sharpe; Fabre, p. 234, pl. 8, fig. 5.
	1944	*Cunningtoniceras höltkeri* Erni, p. 479, pl. 11.
	1951	*Euomphaloceras euomphalum* (Sharpe); Wright and Wright, p. 29 (pars).
	1952	*Acanthoceras? eulessanum* Stephenson, p. 201, pl. 47, fig. 5; pl. 48, figs. 3, 4.
	1957	*Euophaloceras* cf. *euomphalum* (Sharpe); Matsumoto *et al.*, p. 34, pl. 15, fig. 3, *non* fig. 13.
	1963*a*	*Euomphaloceras cunningtoni* (Sharpe); Wright, p. 607, pl. 88, fig. 2; pl. 89, fig. 9 (with synonymy).
	1964	*Euomphaloceras euomphalus* Sharpe var. *pervinquierei* Collignon, p. 145, pl. 373, fig. 1619.
	?1966	*Euomphaloceras cornutum* Kossmat; Collignon, p. 28, pls. 14, 15.
	1966	*Euomphaloceras pervinquierei* Collignon, p. 29.
	1969	*Euomphaloceras meridionale* (Stoliczka); Matsumoto *et al.*, p. 272, pl. 33, figs. 1, 2; pl. 34, fig. 1; text-fig. 6.

Holotype. By monotypy, the original specimen figured and described by Sharpe 1855, p. 29, pl. 15, figs. 2*a–c*, from the Lower Chalk of Upton Scudamore (Wilts.), BMNH 88704.

Description. The holotype is a large, somewhat damaged limonite-coated composite internal mould. The inner whorls are not preserved. The shell is very evolute. The whorl section is depressed, oval in intercostal section, with the greatest breadth at

mid-flank, and rounded, convergent sides. The costal section is angular-polygonal, the greatest breadth being at the umbilical tubercle. The umbilicus is wide and deep, the umbilical wall high, sloping outwards.

At a diameter of 150 mm there are 11 long ribs. These arise as broad gentle swellings at the umbilical seam, pass straight up the umbilical wall and connect to large, strong, bullate umbilical tubercles just outside the umbilical shoulder. These tubercles are connected to the prominent ventro-lateral horns by broad rounded ribs which run straight up the sides, and are slightly wider than the interspaces. The ventro-lateral horns are large, clavate, and directed outwards and upwards to a level just above the venter.

At the smallest diameter visible there are 2 strong clavate upper ventro-lateral tubercles and 1 or 2 small rounded tubercles on a spirally elongate siphonal swelling, connected to the upper ventro-lateral tubercles by a broad low rib.

Between the long ribs there are 1 or 2 short intercalated ribs, extending across the venter only. These bear a rounded siphonal tubercle, or, in some cases, 2 smaller tubercles. With increasing size the intercalated ventral ribs disappear, as do the siphonal tubercles, whilst the ventro-lateral horn and upper ventro-lateral tubercle combine to form a large bituberculate horn. The siphonal region between the horns is depressed.

The dorsum is notched to accommodate the spines of the preceding whorl, which are visible, part embedded in the umbilical wall of the outer whorl.

The suture is poorly exposed; Sharpe's figure is composite and restored. In addition to the figured part there is a further badly damaged part of the outer whorl.

Discussion. Wright (1963*a*) has discussed this species at length and his conclusions are accepted here.

E. cunningtoni cunningtoni differs from *E. cunningtoni* var. *meridionale* (Stoliczka) including *E. meridionale africana* (Pervinquière) in that the latter variety has as many upper ventro-lateral tubercles as siphonal, connected by strong ribs, whereas in *E. cunningtoni cunningtoni* there are more siphonal than upper ventro-lateral tubercles.

E. cunningtoni tuberculata (Pervinquière) is simply another variant with rather fewer siphonal tubercles than in *E. cunningtoni cunningtoni*. This form is transitional towards an inflated *Acanthoceras* in this respect.

E. cunningtoni must be separated from *E. euomphalum*; differences are discussed under that species.

E. inerme (Pervinquière) (= *A. evolutum* Spath) is, together with *E. cunningtoni*, an early Middle Cenomanian *Euomphaloceras*, and intermediates between the 2 species occur (Pl. 63, fig. 1). The chief differences are the more normal *Acanthoceras*-type ribbing of *inerme*, whilst *cunningtoni* has fewer ribs and more exaggerated tuberculation.

E. cunningtoni has more inflated sides and coarser ventro-lateral tuberculation than *E. alvaradoense* (Moreman) (1942, p. 205, pl. 32, fig. 6), although this may be partly a preservation effect.

E. euomphalus var. *pervinquierei* Collignon (1964, p. 145, pl. 372, fig. 1619 = *E. pervinquierei* Collignon 1966) cannot be separated from *E. cunningtoni*.

E. lonsdalei (Adkins) (Wright 1963*a*, p. 609, pl. 87, fig. 2; pl. 88, fig. 1; pl. 89,

fig. 2) is a close relative of *E. cunningtoni* and again perhaps merits only varietal separation. It is more densely ribbed than *cunningtoni*, less depressed, with weaker tuberculation and a lesser tendency towards multiple ventral ribbing and tuberculation.

E. asura Matsumoto and Muramoto (Matsumoto *et al.* 1969, p. 277, pl. 35, fig. 1; pl. 36, fig. 1; text-fig. 7) has many minor ribs on the inner part of the whorl side, which serves to differentiate it from other described *Euomphaloceras* species.

E. lehmanni Collignon (1966, p. 28, pl. 13, figs. 1, 2) is a more densely and coarsely ribbed (20 per whorl) species than *E. cunningtoni*, whilst between each long rib there is only 1 shorter, ventral rib with upper ventro-lateral and siphonal tubercles.

E. salvani Collignon (1966, p. 29, pl. 17, figs. 2, 2*a*) differs from *E. cunningtoni* in having more ribs (24) and intercalated ribs on the early part only. It also has a very faint or almost effaced umbilical tubercle and a squarer whorl section.

There are so few specimens of *Euomphaloceras* of the *cunningtoni* group available that no real conclusions can be drawn. I suspect that more material would enable the reduction of the total number of species considerably. These are coarsely ornamented ammonites; in related acanthoceratids the range of variation discussed above often occurs in a single contemporary population.

Occurrence. The holotype is from Upton Scudamore (Wilts.). Several brachiopods are present in the matrix, e.g. *Orbirhynchia mantelliana* (J. Sowerby) and *Kingena* sp. These indicate that the specimens are from the *Orbirhynchia mantelliana* Band (Kennedy 1969), of *rhotomagense* Zone age, from the top of the *costatus* assemblage.

In addition to this specimen, BMNH C75906, from Calne (Wilts.), BMNH 88706 from Norton, near Warminster (Wilts.) (with a slightly glauconitic matrix), and ?BMNH C824, an unlocalized specimen (ex. Gardiner Coll.), belong to this species. The preservation of these specimens suggests a horizon in the lower part of the Middle Cenomanian.

I have collected a few specimens from the *costatus* assemblage fauna at Holborough (Kent). *E. euomphalum* also occurs in western Europe, north Africa, Japan, and Madagascar.

Euomphaloceras inerme (Pervinquière)

Plate 59, figs. 6*a*, *b*; Plate 61, figs. 1*a*, *b*; Plate 62, figs. 1*a*, *b*; Plate 64, fig. 1

1826 *Ammonites rhotomagensis* J. de C. Sowerby, p. 25, pl. 515, fig. 7 only.
1855 *Ammonites sussexiensis* Mantell; Sharpe, p. 34, pl. 15, figs. 1*a–d* (*non* Mantell).
1907 *Acanthoceras cunningtoni* var. *inermis* Pervinquière, p. 277.
1923*b* *Acanthoceras sussexiense* (Mantell); Spath, p. 144, footnote.
1926*a* *Acanthoceras evolutum* Spath, p. 83.
1951 *Acanthoceras evolutum* Spath; Wright and Wright, p. 28.
1957 *Acanthoceras* aff. *evolutum* Spath; Matsumoto *et al.*, p. 33, pl. 14, fig. 2.

Holotype. By monotypy, the specimen figured by Sharpe 1855, pl. 15, figs. 1*a–d*, GSM Geol. Soc. Coll. 7754, from the Lower Chalk, Lewes (Sussex), bearing the label '*A. sussexiensis* Mantell, Grey Chalk, Lewes, fig'd Chalk Moll. 15, f. 1'.

Description. The holotype is a large, limonite-coated composite internal mould, somewhat distorted, and badly broken into 5 pieces, with many of the tubercles missing. The shell is evolute, about a sixth of the previous whorl being covered. The

whorl section is depressed, rounded to pentagonal in intercostal section, the greatest breadth being at the umbilical shoulder. The sides are flat, the venter broadly rounded. The costal section is polygonal to trapezoidal, with the greatest breadth at the umbilical shoulder. The umbilicus is wide and moderately deep, and the umbilical wall quite steep and rounded.

There are 19–20 ribs at a diameter of 140 mm, the number decreasing slightly at greater diameters. These ribs arise at the umbilical seam and pass across the umbilical wall in a slightly rursiradiate fashion, developing into strong, bullate umbilical tubercles at the umbilical shoulder. These tubercles are connected to the lower ventro-lateral tubercles by a strong rounded rib, the same breadth as the interspaces, directed slightly backwards.

The lower ventro-lateral tubercles are strong, tending to be clavate. They are connected to strong clavate upper ventro-lateral tubercles by a broad, forward-directed rib. There are 2 or 3 small rounded siphonal tubercles corresponding to each pair of upper ventro-lateral tubercles, situated on a low, rounded, spirally elongate siphonal mound.

Between the long ribs there are 2 or 3 short, intercalated ribs extending across the venter. Each bears a weak, rounded siphonal tubercle.

This type of ventral ornament disappears quite suddenly at a diameter of 70 mm. The ventro-lateral tubercles coalesce, until, at the largest diameter preserved, the ornament consists of distant ribs with a siphonal depression.

The dorsum is notched to accommodate the lower ventro-lateral tubercles of the preceding whorl, and these tubercles are visible, part embedded in the umbilical wall of the succeeding whorl. The suture is simple, of normal *Acanthoceras* type, so far as can be seen.

Discussion. The type is very poorly preserved, and Sharpe's figure is good, although restored and reversed. His figure of the suture is composite.

Euomphaloceras evolutum (Spath 1926*a*) has the same type specimen as *E. inerme*. Presumably Spath overlooked Pervinquière's earlier designation.

The two species of *Euomphaloceras*, *E. salvani* and *E. lehmanni*, described by Collignon (1966) from Morocco show some resemblance to the present form. In both these species, however, 1 long rib alternates very regularly with 1 short rib and the ornament is coarse. These may merely be differences of individuals rather than species or varieties.

E. inerme is widely referred to the genus *Acanthoceras* (Spath 1926*a*; Wright 1951; Matsumoto *et al.* 1957), and is indeed intermediate between *Acanthoceras* and *Euomphaloceras* in some respects. However, the multiple siphonal tuberculation and the presence of intercalated ventral ribs suggest *Euomphaloceras*, although the lateral ribbing is of *Acanthoceras* type.

Spath (1923*b*, p. 144) referred *Ammonites rhotomagensis* J. de C. Sowerby (1826, pl. 515, fig. 2) to *Acanthoceras sussexiense* (Mantell). Examination of this specimen, BMNH 439836 (bearing the label 'Such with Sussex on the (Coombes)'), figured Plate 61, figs. 1*a*, *b*, shows the presence of multiple siphonal tuberculation and intercalated ventral ribbing at the smallest diameter visible. Thus there are 1 or 2 tubercles and an associated intercalated rib between the long ribs up to a diameter of about

55 mm; after this, the *Euomphaloceras*-like ornament is replaced by normal *Acanthoceras* ribbing.

In addition to the type, I have seen the following specimens of *E. inerme*, BMNH C73637, Lower Chalk, Hamsey (Sussex), labelled *A. sussexiense* in Spath's writing (Pl. 61, figs. 1*a*, 1*b*); ?BMNH C55821, Lower Chalk, north-west of Reigate (Surrey), (G. W. Butler Collection); BMNH C73636, Lower Chalk, near Calne (Wilts.); BMNH 5690, 'Sussex' (Mantell Collection); and BMNH C75907–75909, Devizes (Wilts.).

There are, in addition, transitional specimens between *E. inerme* and *E. cunningtoni* (Pl. 63, fig. 1); the specimen of *E. euomphalum* figured by Matsumoto *et al.* (1957, fig. 13) belongs here.

Occurrence. As with *E. cunningtoni*, it is difficult to decide the horizon of the type. The only chalk specimens I have collected are from the *costatus* assemblage faunas of Holborough (Kent). The preservation of the other material from the Weald, including the type, suggests this horizon or a slightly higher level in the Middle Cenomanian.

I have seen no specimens from the Basement beds of south-west England. Peake and Hancock (1961) recorded this species from the Totternhoe Stone (*rhotomagense* Zone); a phosphatized specimen from this level is figured (Pl. 59, figs. 6*a*, *b*). The preservation of specimens from Devizes (Wilts.) is identical with that of specimens of *E. cunningtoni* from this locality.

The Japanese material discussed by Matsumoto *et al.* (1957) is from 'the Upper Palaeogyliakian, approximately Upper Cenomanian'. (These authors do not recognize a middle division of the Cenomanian stage.)

Genus PROTACANTHOCERAS Spath 1923*b*

Type species. Ammonites bunburianus Sharpe (1853, p. 25, pl. 9, figs. 3*a*–*c*), by original designation of Spath (1923*b*, p. 144).

Diagnosis. Micromorphs, typically involute, compressed or inflated, with flat sides, prominent umbilical tubercles, lower ventro-lateral tubercles, and closely spaced clavate upper ventro-lateral and siphonal tubercles. The upper and lower ventro-lateral tubercles and sometimes the siphonal tubercles fuse as a prorsiradiate clavus in the adult, forming a chevron-like ornament. Ribs normally present. Suture simple, of normal *Acanthoceras* type.

Discussion. Protacanthoceras has been too widely interpreted by previous authors. The name should be applied only to micromorph ammonites which are adult at diameters of a few centimetres. Larger specimens, with virtually identical nuclei, belong to an unnamed but closely related genus (see below).

Protacanthoceras first appears in the Middle Cenomanian, and at this level juveniles are identical with some normal *Acanthoceras* nuclei; distinction is only possible when adult features appear. The Middle Cenomanian species are usually fairly inflated; several undescribed species are present, whilst *Ammonites triserialis* J. de C. Sowerby (*in* Fitton 1836), referred to *Protacanthoceras* by Spath (1923*b*) and Wright and Wright (1951), appears to be of Middle Cenomanian age.

The acme of *Protacanthoceras* development in Britain is in the Upper Cenomanian,

as represented by the phosphatic fauna of Bed C and its equivalents in south Devon. Here, compressed members of the genus are abundant; in addition to *P. compressum* (Jukes-Browne) and *P. bunburianum*, several new species are present.

Ammonites harpax Stoliczka, referred to *Protacanthoceras* by some authors (e.g. Collignon 1937, Basse 1940), and *Protacanthoceras collignoni* Fabre (1940, p. 225, pl. 7, figs. 7, 8) are *Pseudocalycoceras* Thomel (1969).

Occurrence. *Protacanthoceras* occurs mainly in north-west Europe. *Ammonites tropicus* Stoliczka may be a *Protacanthoceras*, and occurs in southern India and Madagascar. '*Protacanthoceras* sp. nov?' (Matsumoto *et al.* 1957) from Hokkaido, Japan, belongs here, whilst Collignon (1965, p. 12) recorded the genus from north Africa, without illustration. '*Acanthoceras*' *cuspidum* Stephenson (1952) from Texas is a *Protacanthoceras* (Wright, *in litt.*). The genus ranges from Middle to Upper Cenomanian.

Protacanthoceras bunburianum (Sharpe)

Plate 31, figs. 1*a–c*

1853 *Ammonites bunburianus* Sharpe, p. 25, pl. 9, figs. 3*a–c*.
1860 *Ammonites bunburianus* Sharpe; Pictet and Campiche, p. 315.
1923*b* *Protacanthoceras bunburianum* (Sharpe); Spath, p. 144.
1925 *Ammonites bunburianus* Sharpe; Diener, p. 24.
1951 *Protacanthoceras bunburianum* (Sharpe); Wright and Wright, p. 28.

Holotype. The original specimen figured by Sharpe (1853, pl. 9, figs. 3*a–c*), BMNH 50155, said by Sharpe to be from Chardstock (Devon) (see below).

Diagnosis. A compressed, flat-sided *Protacanthoceras*, with weak, flat ribs, weak umbilical and lower-lateral tubercles, and delicate clavate upper ventro-lateral and siphonal tubercles.

Description. The holotype is a small, perfectly preserved brown phosphatic internal mould, retaining traces of glauconitic chalky matrix. Just over half the last whorl is body chamber. The shell is rather involute, about half the previous whorl being covered. The whorl section is compressed, considerably higher than wide, the greatest breadth being just below mid-flank. The whorl sides are flat, parallel, with a broadly rounded ventral shoulder and narrow arched venter which is rounded intercostally, but slightly angular in costal section. The umbilicus is small and shallow, with a vertical umbilical wall and a broadly rounded umbilical shoulder.

On the phragmocone the ribs are broad and flat, and are separated by very narrow interspaces. All the ribs are long; every other rib bears a faint umbilical bulla. The ribs are at first weak, passing straight across the whorl sides. Ribs and interspaces become strongly differentiated at the ventro-lateral shoulder, where the ribs swing forwards towards the aperture and the interspaces become deeper, and as wide as the ribs.

There is a faint lower ventro-lateral swelling on most ribs, whilst each rib bears a delicate clavate upper ventro-lateral tubercle on each side of the narrow venter. The upper ventro-lateral tubercles are connected across the venter by a broad, low, swollen rib, bearing a delicate clavate siphonal tubercle. Each of these ribs is separated from its neighbours by a narrow interspace.

On the body chamber, the ribs are very broad across the ventro-lateral shoulder, with a gentle adoral face and a steep adapical face. As the aperture is approached transverse striae appear on all the ribs, the umbilical tubercle disappears, and the ventro-lateral and siphonal tubercles weaken, suggesting that the specimen is adult.

The type has suffered damage during the latter part of its life, for the last quarter whorl is slightly malformed, the ventral ornament becoming slightly asymmetric. The suture is of normal acanthoceratid type with broad, plump, slightly subdivided elements.

Dimensions

	D	*Wb*	*Wh*	*U*	*Ribs*
BMNH 50155, holotype	32·8	11·0	14·8	8	27–28 on outer whorl

Discussion. Sharpe's figures of this species are rather poor. The locality given by Sharpe, i.e. Chardstock, is doubtful; I have never found the species at this locality, whilst it is common in the phosphatic faunas of Bed C of the Cenomanian Limestone in south Devon.

Sharpe's locality may thus be erroneous, unless a local equivalent of Bed C is present at Chardstock (Mr. C. W. Wright tells me that this is his opinion too). Sharpe received his specimen from Mr. Bunbury, and several other specimens from this collector are obviously mis-localized, i.e. the holotype of *Ammonites euomphalus*, and the original of *Ammonites navicularis* Mantell (Sharpe 1857, pl. 17, fig. 1 (*non* Mantell)).

P. bunburianum is a readily recognizable species, differing from *P. compressum* in its altogether weaker ornament and the broadening and flattening of the ribs on the outer part of the flank. '*Protacanthoceras* sp. nov.' (Jukes-Browne *in* Jukes-Browne and Hill 1896, pl. 5, figs. 2, 2*a*) is more inflated with much coarser tuberculation. *P. tropicum* is more inflated, with distinctly rounded ribs.

The closest species are '*Protacanthoceras* sp. nov.' (Matsumoto *et al.* 1957) and '*P.* sp. nov.' (Jukes-Browne *in* Jukes-Browne and Hill 1896, pl. 5, figs. 3*a*, *b*), both of which can be separated by their fewer ribs and weaker tubercles.

Occurrence. Upper Cenomanian, *naviculare* Zone fauna of Bed C of the Cenomanian Limestone of the Devon coast, and the same horizon at Wilmington and around Beer (south Devon).

Protacanthoceras compressum (Jukes-Browne)

Plate 32, figs. 2*a–d*

1896 *Ammonites hippocastanus* var. *compressus* Jukes-Browne; *in* Jukes-Browne and Hill, p. 157, pl. 5, figs. 4, 4*a* only (*non* figs. 1*a*, *b*, 3*a*, *b*, = '*P.*' spp. nov.).
1923*b* *Protacanthoceras compressum* (Jukes-Browne); Spath, p. 144.
1951 *Protacanthoceras compressum* (Jukes-Browne); Wright and Wright, p. 28.
1957 *Protacanthoceras compressum* (Jukes-Browne); Wright, p. L414, figs. 534, 4*a*, *b*.
non 1965 *Protacanthoceras* aff. *compressum* (Jukes-Browne); Avnimelech and Shoresh, p. 532, pl. 15, figs. 2*a*, *b*; text-fig. 2.

Lectotype. By subsequent designation of C. W. and E. V. Wright (1951, p. 28), GSM 53484, the original of Jukes-Browne's (1896) pl. 5, figs. 4, 4*a*.

Diagnosis. Compressed *Protacanthoceras* with about 22 ribs per whorl, most ribs

bearing small umbilical and lower ventro-lateral tubercles. Upper ventro-lateral and siphonal tubercles closely spaced on a narrow, arched venter.

Description of lectotype. The lectotype is a well-preserved phosphatic internal mould, apparently of an adult specimen, with most of the body chamber preserved. The umbilicus is plugged by phosphatized sediment and the following description is thus incomplete.

The shell is moderately evolute, compressed, with flat sides and a narrowly arched venter. There are approximately 22 ribs on the outer whorl. Most of the ribs arise at the umbilical seam and bear a small bullate umbilical tubercle. The ribs flex gently forwards and then backwards across the flat, parallel sides, to a sharp, rounded, lower ventro-lateral tubercle, which is connected by a broad, forward-directed rib to an upper ventro-lateral tubercle. These, and the siphonal tubercle, are strongly clavate and closely spaced across the high, narrow venter. The siphonal tubercle is displaced slightly forwards so that the venter has a chevron-like appearance. The suture line is simple and of normal *Protacanthoceras* type.

Discussion. Reference by Wright to GSM 53484 as the original of Jukes-Browne's fig. 3 is an error (Wright, *in litt.*); this specimen is in fact the original of fig. 4.

This species shows a range of variation in terms of degree of inflation, strength and number of ribs and tubercles, but is nevertheless readily recognizable.

Of the other specimens referred to *P. compressum* by Jukes-Browne, the original of his fig. 2 (GSM 43482) is probably the inner whorls of an ammonite of the '*Jeanrogericeras*' *sornayi* Thomel type (see below). The other specimen, Jukes-Browne's fig. 3 (GSM 43483), differs from *P. compressum* in having only about half the total number of ventral tubercles per whorl as are present in *P. compressum*.

Of other species of *Protacanthoceras*, *P. bunburianum* is rather similar, but has weaker umbilical and lateral tubercles and more ribs.

'*P.* sp. nov.' of Matsumoto *et al.* (1957) is very close to *P. compressum* and may be a synonym; unfortunately the figures are poor. '*P.*' *tropicum* which has stronger ribs, is more inflated, has squarer ventro-lateral shoulders, and lacks the high, arched venter of *P. compressum*.

Occurrence. The lectotype is from the phosphatic *naviculare* Zone fauna of Bed C of the Devon coast, where the species is not uncommon. It occurs at the same horizon inland, at Wilmington (south Devon). I have been unable to confirm the Dorset, Wilts., and Surrey records noted by Wright and Wright (1951).

Protacanthoceras triseriale (J. de C. Sowerby)

1836 *Ammonites triserialis* J. de C. Sowerby *in* Fitton, pp. 239, 344, pl. 18, fig. 27.
1923*b* *Protacanthoceras triseriale* (J. de C. Sowerby); Spath, p. 144.
1951 *Protacanthoceras triseriale* (J. de C. Sowerby); Wright and Wright, p. 29.

Discussion. Sowerby's figured specimen appears to be lost, and no locality is given, although the species is said to be from 'the sands of Blackdown and of some other places in Devonshire'. This appears to be a *Protacanthoceras*, of Middle Cenomanian type, but I have seen no other specimens I would refer to the species.

Genus UTATURICERAS Wright 1956 (pars)

Discussion. Wright introduced this genus for a group of Upper Cenomanian acanthoceratid ammonites, unfortunately selecting as type species a Lower Cenomanian form closely allied to *Mantelliceras*. The Upper Cenomanian group, including forms such as *Protacanthoceras* aff. *compressum* of Avnimelech and Shoresh (1962), thus remains unnamed.

Members of this group which occur in England are '*Jeanrogericeras*' *sornayi* Thomel (*in* Porthault *et al.* 1966, p. 431, pl. 11, figs. 1–3), and '*Metasigaloceras*' *prerusticum* Thomel (*in* Porthault *et al.* 1966, p. 431, pl. 11, fig. 4). There are, in addition, several unnamed forms. All come from Dorset or Devon and are of *naviculare* Zone age, mostly from Bed C of the Cenomanian Limestone.

THE FAUNAL SEQUENCE IN SOUTHERN ENGLAND

The detailed stratigraphy of sections of the Lower Chalk of south-east England and the Lower Chalk and contiguous deposits of south-west England have been described elsewhere (Kennedy 1969, 1970). The evidence from these works, and subsequent studies, are combined below as a series of zonal lists, which are in turn sub-divided into assemblages. This ammonite stratigraphy is then compared with previous attempts at subdividing the English Cenomanian.

Faunal sequences from other parts of the world for rocks of this age are also discussed and compared with the English succession.

UPPER ALBIAN

Stoliczkaia dispar Zone

Stoliczkaia dispar and *Mortoniceras* (*Durnovarites*) *perinflatum* Subzone

Spath (1923–1943) and Wright (1947, 1963*b*, 1965) listed the faunas of the Subzone; relevant species are: *Puzosia* spp., *Callihopites seeleyi* Spath, *C. tetragonus* (Seeley), *C. vraconensis* (Pictet and Campiche), *Arrhaphoceras studeri* (Pictet and Campiche), *A. substuderi* Spath and vars., *A. transitorium* Spath, *Lepthoplites cantabrigiensis* Spath, *L. falcoides* Spath, *Discohoplites simplex* Wright and Wright, *D. subfalcatus* (Semenow), *D. valbonnensis* (Hébert and Munier-Chalmas) *dorsetensis* Wright and Wright, *D. daedelus* Wright and Wright, *D. transitorius* Spath, *Hyphoplites costosus* Wright and Wright, *H. campichei* Spath, *H. falcatus aurora* Wright and Wright, *Stoliczkaia dispar* (d'Orbigny), *S. dorsetensis* Spath, *S. notha* Seeley, *S. rhamnonotus* (Seeley), *S. africana* (Pervinquière), '*Submantelliceras*' spp. (*Stoliczkaia* nuclei), *Engonoceras iris* Spath, *Mortoniceras* (*Durnovarites*) *perinflatum* Spath, *M.* (*D.*) *postinflatum* Spath, *M.* (*D.*) *quadratum* (Spath), *M.* (*D.*) *subquadratum* Spath, *M.* (*Cantabrigites*) spp., *Mariella bergeri*, *M. miliaris*, *M.* sp. nov., *Anisoceras armatum*, *A. campichei*, *A. exoticum* Spath, *A. perarmatum* Pictet and Campiche, *A.* spp., *Idiohamites* spp., *Stomohamites duplicatus*, *S.* spp., *Lechites gaudini*, *L.* spp., *Sciponoceras*? sp., *Scaphites* spp.

CENOMANIAN

Mantelliceras mantelli Zone

Characteristic genera are *Mantelliceras*, *Sharpeiceras*, *Hypoturrilites*, and *Hyphoplites*.

Hypoturrilites carcitanensis assemblage

Inflated *Mantelliceras*, frequent *H. carcitanensis*, and the occurrence of *Idiohamites* species are the most notable features of this assemblage:

Anisoceras armatum, *A.* aff. *picteti* (rare), *Acompsoceras* spp. nov. (rare), *Austiniceras austeni* (occasional), *Desmoceras* spp. (very rare), *Euhystrichoceras* spp., *Forbesiceras* spp., including *F. largilliertianum* and *F. beaumontianum* (rare), *Hyphoplites arausionensis arausionensis* and transitions to var. *horridus*, *H. arausionensis horridus*, *H. campichei*, *H.* cf. *falcatus*, *H. pseudofalcatus* (all occur occasionally), *Hypoturrilites gravesianus*, *H. tuberculatus*, *H. carcitanensis* (frequent), *H. mantelli* (scarce), *Idiohamites alternatus alternatus*, *I. alternatus vectensis*, *I. ellipticus ellipticus*, *I. ellipticus radiatus*, *I. collignoni*, *I.* spp. nov.? (all scarce but persistent), *Lechites* sp.? (very rare), *Mesogaudryceras leptonema* (very rare), *Mariella cenomanensis* (locally frequent), *M. essenensis* (scarce), *M. lewesiensis* (locally frequent), *M.* spp. nov. (occasional but persistent), *Mantelliceras costatum*, *M. cantianum*, *M. tenue*, *M.* aff. *saxbii*, *M.* aff. *ventnorense* (all frequent), *M. mantelli* (scarce to uncommon), *Puzosia* spp. (rare), *Scaphites* sp. (?*hilli*, very rare), *Schloenbachia varians subvarians*, *S. v. subtuberculata* and intermediates (very common), *S. v. varians*, *S. v. subplana* and *S. v. ventriosa* (scarcer, with transitional forms), *S. nodulosa*, *S.* spp. nov. (constricted; rare), *Sciponoceras roto* (rare), *S.* sp. nov. (rare), *Stomohamites duplicatus* (scarce but persistent), *Sharpeiceras laticlavium* (rare), *S. schlueteri* (very rare), *S.* cf. *florencae* (very rare), *Ostlingoceras bechii*, *O. puzosiforme*, *O. gallienii*, *Turrilites* (*Mesoturrilites*) spp. (very rare).

Mantelliceras saxbii assemblage

Inflated *Mantelliceras* are relatively uncommon, being replaced by *Mantelliceras* of the *saxbii* group. *Idiohamites* has disappeared. *Hyphoplites falcatus* is locally common:

Acompsoceras sarthense, *A. renevieri*, *A.* spp. (all scarce), *Austiniceras austeni* (frequent), *Desmoceras* spp. (rare), *Forbesiceras* spp. (rare), *Hyphoplites campichei*, *H. falcatus falcatus*, *H. falcatus interpolatus* and intermediates (locally common), *H. curvatus*, *H. arausionensis* (locally frequent), *Hypoturrilites* aff. *carcitanensis* (scarce), *H. mantelli* (scarce), *H. gravesianus*, *H. tuberculatus* (sometimes frequent), *Mantelliceras mantelli*, *M. costatum*, *M. cantianum* (occasional), *M. saxbii*, *M. ventnorense*, *M. tenue* and related forms (frequent), *M.* spp. nov. (rare), *Mariella cenomanensis* (locally frequent), *M.* spp. (occasional), *Mesogaudryceras leptonema* (very rare), *Ostlingoceras bechii* (rare), *Paracalycoceras wiestii* (very rare), *Phylloceras* (*Hypophylloceras*) cf. *seresitense* (very rare), *Puzosia octosulcata*, *P.* spp. (rare), *Scaphites obliquus* (locally common), *S.* aff. *equalis* (scarce), *Sciponoceras* spp. (scarce), *Stomohamites* sp., *Schloenbachia varians subplana*, *S. v. subvarians*, *S. v.*

subtuberculata and intermediates (common), *S. v. varians*, *S. v. ventriosa* and intermediates (scarce), *S. nodulosa*, *S. glabra* (rare), *Sharpeiceras laticlavium* (very rare).

Mantelliceras gr. *dixoni* assemblage

Hypoturrilites tenouklensis (rare), *H.* spp., *Austiniceras austeni* (scarce), *Acompsoceras* aff. *essendiense* (rare), *Mantelliceras* gr. *dixoni* (scarce), *M.* aff. *souaillonense* (scarce), *M. lymense* (rare), *M.* cf. *mantelli* (rare), *Paracalycoceras*? spp., *Schloenbachia varians subplana*, *S. v. subvarians*, *S. v. subtuberculata* and transitions (common), *S. v. varians*, *S. v. ventriosa* and intermediates (scarcer), *S. nodulosa*, *S.* spp. (rare), *Scaphites equalis* (rare), *S.* sp. (rare), *Turrilites costatus*, *T. scheuchzerianus*.

Acanthoceras rhotomagense Zone

Acanthoceras of the *rhotomagense* and *jukes-brownei* groups, *Calycoceras newboldi*, *C. paucinodatum*, abundant *Turrilites costatus*, *T. acutus*, and *Scaphites equalis* characterize this Zone.

Turrilites costatus assemblage

Turrilites costatus, *Sciponoceras baculoide*, and *Acanthoceras* of the *rhotomagense* group are especially common. *Acanthoceras* aff. *rhotomagense rhotomagense*, *A. rhotomagense subflexuosum*, *A. rhotomagense sussexiense*, *A. rhotomagense clavatum*, *A. rhotomagense confusum*, intermediates and related forms (all frequent), *Austiniceras austeni*, *Acompsoceras* cf. *essendiense*, *A. sarthense*, *A.* spp., etc. (all rare), *Anisoceras plicatile* (frequent), *A.* sp. nov. (scarce), *Calycoceras* spp. (rare), *Euomphaloceras inerme*, *E. cunningtoni* and intermediates (rare), *Forbesiceras* sp. (rare), *Hypoturrilites gravesianus* (very rare), *Scaphites obliquus* (scarce), *S. equalis* (rare), *Sciponoceras baculoide* (abundant), *Schloenbachia* aff. *varians varians*, *S.* aff. *v. ventriosa* and intermediates (scarce), *S.* aff. *v. subplana*, *S. costata*, *S.* aff. *v. subvarians*, *S.* aff. *v. subtuberculata* and intermediates (common), *S. nodulosa* (scarce), *Stomohamites simplex* (occasional), *Turrilites costatus* (common), *T. scheuchzerianus* (occasional).

Turrilites acutus assemblage

Acanthoceras aff. *rhotomagense rhotomagense*, *A. rhotomagense sussexiense*, *A. rhotomagense confusum*, *A. rhotomagense subflexuosum*, *A. rhotomagense clavatum* and related forms (common), *A. latum* (rare), *Austiniceras austeni* (frequent), *Anisoceras plicatile* (frequent), *A.* spp. nov. (frequent), *Acompsoceras* spp. (rare), *Calycoceras newboldi newboldi*, *C. newboldi spinosum* and related forms (frequent), *C. paucinodatum* and related forms (common), *C. bathyomphalum* and transitions to *C. paucinodatum* (frequent), *Euomphaloceras* of the *cunningtoni-inerme* group (rare), *Forbesiceras obtectum*, *F.* aff. *obtectum* (rare), *F. largilliertianum* (scarce), *Protacanthoceras* spp. nov. (rare), *Eucalycoceras?* spp. (rare), *Puzosia subplanulata*, *P.* aff. *crebrisulcata*, *P.* spp. (all scarce), *Scaphites equalis* (common, sometimes abundant), *S. obliquus* (common), *Sciponoceras* aff. *baculoide*, *S.* spp. nov. (rare), *Stomohamites simplex* (scarce), *Schloenbachia* aff. *varians varians*, *S.* aff. *v. ventriosa* and intermediates (scarce), *S.* aff. *v. subplana*, *S. v. costata*, *S.* aff. *v. subvarians*, *S.*

aff. *v. subtuberculata* and intermediates (common), *S. nodulosa*, *S.* spp. nov. (scarce), *Turrilites acutus* (common), *T. costatus* (scarce), *T. scheuchzerianus* (scarce), *Worthoceras* sp. (rare).

Acanthoceras jukes-brownei assemblage

Acanthoceras jukes-brownei and related forms (common), *A. whitei* (rare), *A.* spp. (scarce), *Austiniceras austeni* (occasional), *Acompsoceras sarthense* (rare), *Calycoceras* aff. *choffati* (scarce), *C. boulei* (rare), *C.* group of *paucinodatum* (scarce), *C.* sp., *newboldi-spinosum* group (scarce), *C. newboldi planecostata* (scarce), *C.* aff. *bathyomphalum* (scarce), *C.* (*Lotzeites*) *barruei* (rare), *Protacanthoceras* spp. nov. (scarce), *Eucalycoceras gothicum* (rare), *Scaphites equalis* (frequent), *S. obliquus* (rare), *Schloenbachia* spp. (frequent), *Stomohamites simplex* (scarce), *Turrilites costatus*, *T. acutus*, *T. scheuchzerianus* (all scarce), *Sciponoceras* sp. nov. (rare).

Calycoceras naviculare Zone

Acanthoceras hippocastanum (rare), *Austiniceras austeni* (frequent), *Calycoceras naviculare* (occasional), *C.* aff. *newboldi spinosum* (frequent), *C. newboldi planecostata* and related forms (scarce), *C.* (*Lotzeites*) *aberrans* (rare), *C.* (*L.*) spp. (rare), *Carthaginites* cf. *inornatus* (very rare), *Euomphaloceras euomphalum* (rare), *Forbesiceras* spp. nov. (rare), *Protacanthoceras compressum*, *P. bunburianum*, *P.* spp. nov. (frequent), *Turrilites costatus* (rare), '*Utatur*iceras' spp. including '*Jeanrogericeras*' *sornayi*, '*Metasigaloceras*' *prerrusticum* (all rare), *Scaphites equalis* (common), *Sciponoceras* sp. nov. (rare), *Schloenbachia lymense* (occasional), *S.* spp. nov. (frequent), *Stomohamites* sp. (rare).

plenus Marls

Metoicoceras geslinianum Zone

Metoicoceras geslinianum (d'Orbigny), *Austiniceras dibleyi*, *Pachydiscus* sp., *Calycoceras naviculare*, *C.* spp.? indet., *Sciponoceras* sp., *Scaphites equalis*.

Metoicoceras gourdoni Zone

Metoicoceras gourdoni (de Grossouvre), *Allocrioceras pariense* (White), *A.* sp., *Stomohamites?* sp., *Calycoceras* sp., *Sciponoceras* sp., *Kanabiceras* sp., *Sumitomoceras* spp.

MIDDLE CHALK
(lower part)

Mammites nodosoides (Schlotheim), *M.* spp., *Kanabiceras* sp., *Watinoceras* sp., *Neocardioceras* sp., *Metoicoceras* cf. *dumasi* (de Grossouvre) (Hancock *in* Smith and Drummond 1963), *Lewesiceras peramplum* (Mantell), *Metasigaloceras rusticum* (J. Sowerby), *Fagesia pachydiscoides* Spath, *Austiniceras austeni*, *Sciponoceras gracile*, *Allocrioceras* spp., including *A. pariense*.

COMPARISON WITH PREVIOUS WORK

There have been only two previous attempts to devise an ammonite succession for the English Cenomanian, both by Spath (1923*b*, 1926*b*). Wright (1947) tentatively suggested that Collignon's (1937) Madagascan zonal scheme might be applied. Hancock (1967) applied his three-fold division as used in the type Cenomanian.

Spath's 1923*b* scheme is as follows:

Upper Cenomanian (Acanthoceratan) (*subglobosus* Zone of authors)	*Metoicoceras pontieri* *Acanthoceras cenomanense* *Calycoceras baylei*
Lower Cenomanian (Schloenbachian) (*varians* Zone of authors)	*Euomphaloceras euomphalum* *Hyphoplites falcatus* *Mantelliceras martimpreyi*

From the remainder of the paper dealing with the Cenomanian, it is clear that this scheme is the product of an early stage of Spath's work, and in 1926*b* further observations led him to the following scheme.

vicinale *subflexuosum*	*subglobosus*
rhotomagense *diadema* *vectense*	upper *varians* (= *euomphalus*)
costatus *cantianum*	*lower varians* (= *falcatus*)
martimpreyi (pre-*martimpreyi*)	*Stauronema carteri* and *Pecten asper* (?)

As with some of Spath's other zonal schemes, this is a combination of guesswork and intuition; it bears no relationship to an actual succession.

Since this scheme forms the basis of much subsequent discussion (for instance, Dubourdieu 1953, Müller and Schenk 1943, Jeletzky 1968, etc.), and is the basis of the *martimpreyi* Zone, I review it at length.

1. The pre-*martimpreyi* Subzone.

'Apart, possibly from certain undescribed Warminster ammonites of the genera *Submantelliceras* and *Euhystrichoceras*, the exact horizon of which is unknown, the only British forms that can be ascribed to the (provisional) pre-*martimpreyi* Zone belong to a curious fauna of uncoiled types—Anisoceratids, etc., known only from Gore Cliff, Isle of Wight. These comprise undescribed Algeritids, notably *Idiohamites*, distinguished from *Anisoceras* by ornamentation and simple suture line, with bifid dorsal lobe. They are partly derivatives of *Idiohamites dorsetensis* nov., referred to below, and developments of forms like *Anisoceras picteti* nov. and *A. compichei* nov., all from the earlier *dispar* Zone' (Spath 1926*b*, p. 424).

This is indeed the earliest extensive Cenomanian fauna found in Britain, and although Spath recorded it only from Gore Cliff, this, the *carcitanensis* assemblage fauna, also occurs elsewhere in the Isle of Wight, around Lewes (Sussex), Selborne (Hants.), and in south-west England.

2. The *martimpreyi* Subzone.

'*Mantelliceras martimpreyi* is easily confused with the flattened forms of the (probably later) *couloni* type; and Pervinquière identified with it some Tunisian forms that are here referred to *Mantelliceras batheri* nov., and *Eucalycoceras lymense* nov. Since at Berrouaghia in Algeria, *Mantelliceras martimpreyi* occurs in the lowest ('*Algerites*') and highest beds (above *Eucalycoceras constrictum* nov. which cannot be very low in the Cenomanian), it is, perhaps a somewhat doubtful fossil, but *Mantelliceras saxbii* (Sharpe) is a closely allied British species' (Spath 1926*b*, p. 424).

Previous discussions (Kennedy and Hancock 1971) have already shown that the original *martimpreyi* Zone of Spath is above the base of the Cenomanian stage, and since Spath gave Ventnor (Isle of Wight) and Warminster (Wilts.) as localities for the Zone, there seems no doubt that, as originally conceived, the *martimpreyi* Zone corresponds to the *saxbii* assemblage.

Subsequent usage of *M. martimpreyi* as an index for the basal Cenomanian is thus to be blamed elsewhere.

3. *costatum* and *cantianum* Subzones.

These divisions are not supported by field evidence; both species range down to the bottom of the *mantelli* Zone. Of more interest is the equation of this part of the Cenomanian with a '*falcatus*' Zone, for *Hyphoplites* is abundant above the *saxbii* assemblage in the Isle of Wight. Spath's suggestion that *Hyphoplites* ranges into beds with '*Protacanthoceras* of the *hippocastanum* group', is based on remanié specimens from Middle Cenomanian Chalk Basement Beds.

4. The *euomphalum* Zone.

Use of *E. euomphalum* as a zonal index for such a low level in the Cenomanian is puzzling, as this is a very high Cenomanian species. Two explanations seem possible; firstly Spath may have considered *E. cunningtoni* to be a synonym of *euomphalum* (as some subsequent workers have), or he may have been misled by specimens of *E. euomphalum* in the British Museum and Geological Survey Collections which are mis-labelled, and said to come from Middle Cenomanian Basement Beds at Evershot (Dorset) and Chardstock (Devon) (which they certainly do not), or the type, which is also mislocalized (Wright and Wright 1951).

Spath's subdivisions of the Upper Cenomanian are not valid, *Acanthoceras vectense* (= *A. sussexiense*), *A. rhotomagense* (Spath *non* Brongniart?), and *A. subflexuosum* being contemporaries. This division seems to be pure speculation.

5. *vicinale* Subzone.

Casey (1960) and Matsumoto, Sastry, and Sarkar (1966) successfully demonstrated the unsatisfactory nature of *Ammonites vicinalis* as an index for the top of the Cenomanian. In spite of these inadequacies Spath made several good guesses on the basis of very little real evidence.

Wright (1947, p. 197) tentatively suggested that the South Dorset Chalk Basement Bed was to be equated with Collignon's (1937) Zone of *Mantelliceras mantelli* and *Calycoceras newboldi*; subsequently it has become clear that similarities between Basement Bed faunas and Collignon's Zone are the result of remanié Lower Cenomanian fossils being mixed with a Middle Cenomanian Basement Bed (Wright 1965, *in litt.*).

COMPARISON WITH WORK OUTSIDE ENGLAND

1. EUROPE. Cenomanian faunas have been described widely in Europe (Schlüter 1871–1876; Noetling 1885; Renz *et al.* 1963; Choffat 1898; Seguenza 1881–1882), and these faunas can be compared in detail with the English succession.

Faunas rather than stratigraphies have been described, and no detailed discussion is therefore given. In only 2 areas, France (especially the south-east) and northern Spain and Portugal, have detailed stratigraphies been proposed. These are discussed below.

France. Sornay (1959) reviewed early work on the stratigraphy of the French Cenomanian, admitting a two-fold division into Lower and Upper Cenomanian—'Mantelliceran' and 'Acanthoceratan' of Spath and Collignon. Faunal lists quoted by him often contain species which normally occur at widely separated horizons, and misidentification seems to have been widespread, especially where classic species (*Schloenbachia varians*, *Calycoceras naviculare*) are concerned.

My own work suggests that in northern France at least, there is an exactly comparable succession to that present in southern England. In particular, the famous Craie Chloritée at Rouen can be dated as equivalent to the *Turrilites costatus* assemblage of the *rhotomagense* Zone (Kennedy and Hancock 1970).

In Sarthe, the ammonite stratigraphy of the type Cenomanian has been reviewed by Hancock (1959). The approximate correlation with the English succession is shown in Table 2. Hancock recognized 3 zones, which form the basis of the subdivision of the English succession. Faunas are:

LOWER CENOMANIAN

Mantelliceras mantelli Zone

1. *Argile glauconieuse à minerai de fer: Hypoturrilites schneegansi* Dubourdieu, *Hyphoplites campichei*, *H. costosus*, *H. crassofalcatus*, *Stoliczkaia* sp. juv., *Euhystrichoceras nicasei* (Coquand).

2. *Craie glauconieuse à* Pecten asper*: Hypoturrilites tuberculatus*, *Mariella lewesiensis*, *M.* cf. *cenomanensis*, *Hyphoplites curvatus*, *H.* aff. *curvatus*, *H. falcatus falcatus*, *H. falcatus interpolatus*, *H. pseudofalcatus*, *Mantelliceras couloni*, *M.* aff. *batheri* (? = *M. saxbii*), *M.* cf. *saxbii* (*hyatti*), '*Stoliczkaia*' sp. nov. (*Stoliczkaia*), *Forbesiceras beaumontianum.*

3. *Marnes à* Orbitolites *de Ballon: Mantelliceras saxbii* (*hyatti*).

MIDDLE CENOMANIAN

Acanthoceras rhotomagense Zone

1. *Sables et grès de la Trugalle et Lamnay à* Perna lanceolata *et* Anorthopygus orbicularis*: Austiniceras* cf. *austeni*, *Acompsoceras sarthense* (*Pseudacompsoceras vectense*), *Forbesiceras beaumontianum*, *Acanthoceras rhotomagense confusum* (*Acanthoceras confusum*).

TABLE 2. Zonal divisions in Europe and North Africa

SOUTHERN ENGLAND (This paper)	SARTHE (Hancock 1959)	S.E. FRANCE (Thomel *et al.* 1960, etc.)	SPAIN AND PORTUGAL (Wiedmann 1959, 1964)	ALGERIA–TUNISIA (Dubourdieu 1953)
plenus Marls		*Metoicoceras geslinianum*		Zone V
	No ammonites		*Metoicoceras mulleri*	
		Calycoceras (Lotzeites) crassum	*Neolobites choffati*	Zone IV
Calycoceras naviculare	*Calycoceras naviculare*			
		Calycoceras naviculare	'*Protacanthoceras*' *choffati*	
			Euomphaloceras africanum	Zone III
Acanthoceras rhotomagense	*Acanthoceras rhotomagense*	*Acanthoceras rhotomagense*	?	
Mantelliceras mantelli	*Mantelliceras mantelli*	*Mantelliceras mantelli*	*Mantelliceras mantelli*	Zone II
		Mantelliceras martimpreyi	*Graysonites*	*Hypoturrilites schneegansi*
No ammonites				
Stoliczkaia dispar		*Stoliczkaia dispar*	*Stoliczkaia dispar*	*Mariella bergeri*

2. *Craie de Théligny: Scaphites obliquus.*

3. *Sables et grès du Mans à* Scaphites equalis *et* Turrilites costatus*: Scaphites equalis, S. obliquus, Sciponoceras* cf. *baculoide, Turrilites costatus, T. scheuchzerianus, Acanthoceras rhotomagense rhotomagense* and vars., *A.* aff. *latum*?, *Euomphaloceras* aff. *cunningtoni* (*A.* (subgen. nov.) sp. nov.), *Calycoceras sarthacense, C. newboldi, C. gentoni, C. cenomanense, Eucalycoceras* aff. *choffati.*

UPPER CENOMANIAN

Calycoceras naviculare Zone

1. Zone à Crustacés à la base des sables du Perche*: Acanthoceras* aff. *rhotomagense confusum, A.* cf. *rhotomagense sussexiense* (*A.* cf. *vectense*), *Calycoceras* between *newboldi planecostata* and *paucinodatum, C.* between *newboldi paucinodatum* and *boehmi, C. sarthacense, C.* aff. *gentoni?*

2. *Sables du Perche à* Rhynchonella compressa*: Calycoceras* aff. *gentoni, C. paucinodatum, C.* aff. *newboldi, C. ?boehmi, C.* aff. *guerangeri, C. vergonsense* Collignon, *C. bruni, C.* aff. *cottreaui, C. newboldi planecostata, C. cenomanense* and vars., *Acompsoceras sarthense.*

3. *Marnes à* Ostrea biauriculata*: Forbesiceras largilliertianum, Calycoceras* aff. *newboldi planecostata, C. newboldi spinosum, C.* cf. *gentoni, C.* aff. *naviculare*, (*C.* between *naviculare* and var. *borgesi* and *cenomanense*), *C.* cf. *naviculare, C. bruni, C. guerangeri, C.* ?aff. *vergonsense, C. guerangeri, C.* aff. *sarthacense, Eucalycoceras rowei.*

The Sarthe faunas are poor, but resemblances between the fauna of the Argile Glauconieuse à Minerai de Fer and the *carcitanensis* assemblage and higher parts of the *mantelli* Zone are obvious. The Sables et Grés de Mans are clearly equivalent in part at least to the English *costatus* assemblage, perhaps going higher.

The faunas from the base of the *naviculare* Zone in Sarthe do not match any of the English faunas very well, and there is a suggestion that they may be part equivalent to the *jukes-brownei* assemblage.

The *naviculare* Zone faunas of Bed C in Devon agree well with those of the Marne à Ostrea *biauriculata* (Basse de Menorval 1959, pp. 802, 803, etc.).

In southern France, papers by Thomel (1961*a*, *b*, 1962, 1965*a*, *b*, 1967, 1968), Fabre-Taxy and Thomel (1964), and Porthault *et al.* (1966) have revised the work of Fabre (1940) in this region, which is an important one linking the faunas of northern Europe with those of north Africa.

The zonal scheme proposed is shown in Table 2. Relevant details are:

UPPER ALBIAN

Stoliczkaia dispar Zone

Stoliczkaia dispar, Schloenbachia sp., *Mantelliceras martimpreyi, Anisoceras perarmatum, Mariella bergeri, Ostlingoceras puzosianum, Pervinquieria quadrata, P. rostrata, Hyphoplites campichei.*

LOWER CENOMANIAN

Mantelliceras martimpreyi Zone

Submantelliceras suzannae, *Sciponoceras baculoide*, *Hypoturrilites tuberculatus*, *H. carcitanensis*, *H. oehlerti* (Pervinquière), *H. gravesianus*, *Mariella cenomanensis*, *Hyphoplites campichei*, *H. arausionensis*, *H. costosus*, *H. falcatus*, *Schloenbachia subvarians*, *S. subtuberculata*, *S. varians*, *Mantelliceras couloni*, *M. hyatti*, *M.* cf. *latetuberculatum*, *M.* cf. *biroi*.

Mantelliceras mantelli Zone

Hypoturrilites mantelli, *Hyphoplites falcatus*, *H. arausionensis*, *H. pseudofalcatus*, *Acompsoceras bochumense*, *Mantelliceras cantianum*, *M. mantelli*, *M. tuberculatum*, *M. hyatti*, *M. batheri*, *M. ventnorense*, *M. couloni*, etc., *Sharpeiceras laticlavium*, *Stomohamites simplex*, *Anisoceras saussurei*, *Sciponoceras baculoide*, *Turrilites scheuchzerianus*, *Hypoturrilites carcitanensis*, *H. tuberculatus*.

MIDDLE CENOMANIAN

Acanthoceras rhotomagense Zone

Mesogaudryceras leptonema, *Turrilites acutus*, *T. costatus*, *T. scheuchzerianus*, *Scaphites obliquus*, *S. equalis*, *Stomohamites simplex*, *Anisoceras saussurei*, *Puzosia subplanulata*, *Austiniceras austeni*, *Schloenbachia* spp., *Forbesiceras obtectum*, *Acompsoceras sarthense*, *Calycoceras gentoni*, *C. subgentoni*, *C.* cf. *haugi*, *C. newboldi* and vars., *C. paucinodatum*, *C. baylei*, *C. boulei*, *C. vergonsense*, *C. choffati*, *Acanthoceras rhotomagense sussexiense* (*vectense*), *A. r. rhotomagense*, *A. sherborni*, *A. discoidale* (Kossmat), *A. hippocastanum*, *A. confusum*, *Euomphaloceras inerme* (*Acanthoceras evolutum*), *E. cunningtoni* and vars., *E. medlicotti*, '*Utaturiceras*' *bethlehemensis* Avnimelech and Shoresh, *Dunveganoceras liguriense* (nom. nud).

UPPER CENOMANIAN

Calycoceras naviculare Zone

Scaphites decaryi Collignon, *Turrilites costatus*, *Austiniceras austeni*, *Schloenbachia* spp., *Calycoceras orbignyi*, *C. brunei* and vars., *C. besairiei*, *C. gentoni*, *C. newboldi* and vars., *C. bathyomphalum* and var. *nicaenensis*, *C. subwiestii*, *Eucalycoceras jeanneti* var. *nicaensis*, *E. pentagonum*, *E. harpax*, *Acanthoceras jukes-brownei* (*Protacanthoceras*), *Dunveganoceras liguriense* (nom. nud.).

Calycoceras (*Lotzeites*) *crassum* Zone

Calycoceras cf. *stoliczkai*, *C.* cf. *morpheus*, *C. bathyomphalum*, *C.* (*L.*) *crassum*, *Eucalycoceras harpax*, *E. harpax* vars. *tulearensis* and *lattensis*, *E. baylei*, *Protacanthoceras bunburianum*, '*Utaturiceras*' *flandrini*, '*U.*' *sornayi*, '*U.*' *prerusticum*.

Metoicoceras geslinianum Zone

Metoicoceras gourdoni, *M. geslinianum*, *Worthoceras vermiculum* (Shumard), *Otoscaphites* sp.

The *dispar* Zone faunas compare well with those of southern England, save for the precocious appearance of *Schloenbachia* and *Mantelliceras martimpreyi*.

The possibility of mixing cannot be overlooked in the former case (see Thomel 1961*b*), whilst the latter could well be a *Stoliczkaia* nucleus, as nuclei of '*martimpreyi*' type occur in our *dispar* Zone (see p. 100).

The succeeding *martimpreyi* and *mantelli* Zones do not compare sufficiently well with the English succession for detailed correlation, whilst the absence of *Idiohamites* is noteworthy. The *only* element of the *martimpreyi* Zone which cannot be matched in England (other than leiostracans) is '*Submantelliceras*' *suzannae*. This is also the only 'characteristic' form of the *martimpreyi* Zone.

The *rhotomagense* Zone is broadly comparable to that of southern England, although records of forms such as *Schloenbachia lymense*, '*Utaturiceras*' *bethlehemense*, and *Acanthoceras hippocastanum*, if confirmed, suggest that the Middle to Upper Cenomanian boundary is drawn higher than I have taken it in England.

Both *naviculare* and *crassum* Zones are to be equated with the English *naviculare* Zone; diagnostic forms of the *crassum* Zone such as *C. stoliczkai* (= *C. naviculare*?), *C. bathyomphalum*, *P. bunburianum*, and '*Utaturiceras*' spp. all occur (or have close relatives) in Bed C faunas.

The Cenomanian faunas from Cassis described by Fabre (1940) and revised by Fabre-Taxy and Thomel (1964) are of considerable interest. The essential features of this sequence are a basal ferruginous remanié horizon yielding Aptian, Lower and Middle Cenomanian ammonites overlain by Upper Cenomanian silts and sandstones with indigenous Upper Cenomanian forms such as *Eucalycoceras pentagonum* and '*Protacanthoceras*' *harpax*.

Fabre-Taxy and Thomel recognized *martimpreyi* Zone forms in the remainé horizon, but a re-examination of the collections of the Universities of Marseilles and Lyon, and collecting at Cassis failed to reveal any trace of a fauna earlier than the English lowest Cenomanian.

Spain and Portugal. The classic study in this area is that of Choffat (1898). Wiedmann (1959, 1964) gave a stratigraphy for the Upper Cretaceous. Relevant parts of his succession are shown in Table 2. Details are:

UPPER ALBIAN

Stoliczkaia dispar Subzone

Stoliczkaia dispar, *Discohoplites* cf. *subfalcatus*, *M.* (*Mortoniceras*) *rostratum*, *Durnovarites* sp. nov. ?, *Puzosia* cf. *crebrisulcata*, *Tetragonites balmensis*, *M.* (*Mariella*) cf. *bergeri*.

CENOMANIAN

I. Zone of *Graysonites* ('*Submantelliceras*')

Graysonites sp.

II. *Mantelliceras mantelli* Zone

No separate fauna given. The following (Wiedmann 1959, p. 718; 1964, p. 114) are listed from Zones II and III: *Forbesiceras largilliertianum*, *? Sharpeiceras indicum*,

Mantelliceras mantelli, *M.* cf. *mantelli*, *M. mantelli tuberculatum*, *M.* cf. *menabense* Collignon, *M.* (?) sp., *Gaudryceras multiplexum* (Kossmat).

III. *Euomphaloceras africanum* Zone

Euomphaloceras africanum, *Calycoceras* cf. *boulei*, *Eucalycoceras* cf. *pentagonum*, *Turrilites* (*Euturrilites*) *scheuchzerianus*, *Paracalycoceras* (?) sp.

IV. '*Protacanthoceras*' *jacobi* Zone

Calycoceras sp. nov., cf. *paucinodatum*, *C. newboldi spinosum*, *C. paucinodatum*, *C.* cf. *jeanneti*, *C. orientalis*, '*Protacanthoceras*' *harpax*, '*P.*' cf. *jacobi*, '*P.*' sp. nov., *Eucalycoceras pentagonum*, *E. choffati*, *Paracalycoceras* cf. *alouitoense* (Basse de Menorval), *Acanthoceras* cf. *quadratum*, *Mantelliceras* (?) sp. nov., *Hypoturrilites laevis*.

V. *Neolobites choffati* Zone

Neolobites choffati, *N. brancai*, *N.* cf. *vibreyanus*, *N.* cf. *schweinfurthi*, *Calycoceras naviculare*, *C.* cf. *subgentoni*, *C.* aff. *orbignyi*, *C. cottreaui*, *C.* cf. *newboldi spinosum*, *C.* (*Lotzeites*) *lotzei*, *Eucalycoceras gothicum*.

VI. *Metoicoceras mulleri* Zone

Metoicoceras mulleri

These zonal faunas are somewhat sparse. The fauna of the zone of *Graysonites* consists of only a few doubtful fragments of that genus, whilst Wiedmann (1964, p. 117) considered that the lowest beds of the Cenomanian (the subzone of *M. aumalense*) are not proven by cephalopods. The *mantelli* Zone fauna can be correlated with the Lower Cenomanian, whilst above, the *africana* Zone yields some species, *Eucalycoceras* cf. *pentagonum* for example, which suggest the *naviculare* Zone, and others, i.e. *Euomphaloceras africanum*, which suggest the Middle Cenomanian.

The *jacobi* and *choffati* Zones are to be correlated with the English *naviculare* Zone. The *mulleri* Zone finds no obvious parallel in England.

2. SOVIET UNION. Moskveen and Naidin (1959) reviewed the stratigraphy of the Upper Cretaceous of European Russia. From their account it seems that cephalopods are scarce, and they admit only a lower (*Mantelliceras*, etc.) and upper (*Acanthoceras rhotomagense*, etc.) division of the Cenomanian.

The most interesting cephalopod fauna from the Soviet Union was described by Semenow (1899) from Transcaspasia. He recorded *Karamanites grossouvrei* (Semenow), *Schloenbachia* spp., *Hyphoplites* spp., *Acanthoceras rhotomagense*, and '*A.*' *cunningtoni*. This record represents the south-eastern limit of the boreal genera *Schloenbachia* and *Hyphoplites*.

The chief point to arise from the European Cenomanian is thus the possibility of a horizon of '*Submantelliceras*' *aumalense* at the base of the stage, which is not represented in England.

3. THE MIDDLE EAST. Basse de Menorval (1937, 1940), Douvillé *in* Morgan (1904), Taubenhaus (1920), and Avnimelech and Shoresh (1962) are the chief sources on the Cenomanian of the Middle East.

Douvillé (1904) recorded Lower and Middle Cenomanian ammonites from Persia. Basse de Menorval (1937, 1940) recorded more extensive faunas from Syria, Lebanon, and Israel (Palestine); specimens associated at various localities have clearly come from different horizons, but Lower (*Sharpeiceras laticlavium*, *Mantelliceras* spp.), Middle (*Acanthoceras sussexiense*), and Upper Cenomanian ammonites ('*Protacanthoceras*' *angolaense*) are all present.

Avnimelech (1965) recorded a Lower Cenomanian *Hyphoplites falcatus* from Carmel (Israel), whilst Avnimelech and Shoresh (1962) redescribed Cenomanian faunas from the environs of Jerusalem. The Calcairé à *Acanthoceras*, 70–100 m thick, yielded *Turrilites costatus*, *?T. undulatus*, '*Protacanthoceras*' *judaicum*, '*P.*' *angolaense*, '*P.*' cf. *compressum* (Avnimelech and Shoresh, *non* Jukes-Browne), *Calycoceras harpax*, *C. haugi*, *C. boulei*, *C. newboldi*, *C. ?paucinodatum*, '*C.*' *africanum*, and '*Utaturiceras*' *bethlehemense*, and is referred to the Middle Cenomanian, although in my view it extends into the base of the Upper Cenomanian in our sense. The overlying 75–150 m yielded *Neolobites vibreyanus*, and are possibly to be correlated with the higher parts of the Upper Cenomanian.

4. NORTH AFRICA. Classic accounts of north African faunas are given by Pervinquière (1907, 1910); subsequent studies are by Dubourdieu (1953, 1956), Sornay (1955), and Collignon (1965, 1966). Specimens figured in these works suggest that faunas comparable to those in England occur in North Africa, although some exotic genera have appeared. Unpublished work with J. M. Hancock suggests a detailed correlation will eventually be possible.

Morocco. Collignon (1966) recognized 3 divisions in the Tarfaya region:

(i) A lower niveau à *Euturrilites scheuchzerianus*, also yielding *Acompsoceras viottii* Collignon, and *Tarrantoceras* cf. *rotatile* Stephenson, considered to be of Lower Cenomanian age. The only evidence for this is its position at the base of the succession; the *Tarrantoceras* suggests a horizon very high in the stage.

(ii) A higher niveau à *Calycoceras* et *Euomphaloceras*, with *Turrilites ougnanensis* Collignon, *Puzosia* cf. *subplanulata*, *Pachydesmoceras maroccanum* Collignon, *Calycoceras choffati*, *C.* cf. *newboldi*, *Acanthoceras* aff. *rhotomagense*, *A. haugi*, '*Protacanthoceras*' *harpax*, *Euomphaloceras salvani* Collignon, *E. lehmanni* Collignon, *E. cornutum*, *Tarrantoceras wrighti* Collignon, *T. marchesinii* Collignon, and *T. stephensoni* Collignon. This is referred to the Middle Cenomanian *Calycoceras newboldi* Zone; in fact some species are probably Middle Cenomanian, but the *Tarrantoceras* species all suggest a horizon high in the Upper Cenomanian.

(iii) A niveau à *Pachydesmoceras marrocanum*, also yielding *Acompsoceras viottii*, which cannot be definitely placed.

Algeria. Algeria and Tunisia (discussed below) represent classic areas of anomaly in Cenomanian ammonite studies, with minute limonitic specimens in the marl facies and large moulds in limestones. Correlation of the two preservations is still in an early stage, and many names for limonitic nuclei may eventually fall into synonymy.

The classic study is by Pervinquière (1910) who revised work by Coquand, Peron, Thomas, and others. Pervinquière recognized a number of zones, based on ammonites,

bivalves, echinoids, and gastropods. From his lists it seems that ammonites from several horizons are mixed in some cases; thus '*Acanthoceras*' *martimpreyi* is recorded from both low in the Cenomanian and at a higher level, above beds with *Acanthoceras* and *Calycoceras*.

The most important species, '*Acanthoceras*' *aumalense*, is recorded from Zone 3 at Aumale and Zone 1 at Berrouaghia, low in the Cenomanian. The precise locality and horizon of the 'cotypes' of that species are unfortunately unknown.

Collignon (1965) described *Neolobites vibreyanus*, *N. fortaui*, *N. peroni*, *N. bussoni*, *Calycoceras naviculare* (*grossouvrei*), *C. boulei*, *Eucalycoceras* aff. *pentagonum*, and a *Protacanthoceras* sp. from Tinhret (Algerian Sahara); all indicate a *naviculare* Zone age for the fauna.

Dubourdieu (1953, 1956) described faunas from the Algero-Tunisian border; these are discussed below.

Tunisia. The classic study is by Pervinquière (1907), from whose figures it is clear that correlation with England is possible; unfortunately a precise stratigraphy is lacking. A more detailed account is given by Dubourdieu (1953, 1956) and Sornay (1955) for the Mont du Melligue region. The general succession is given in Table 2; the details are:

UPPER ALBIAN (VRACONNIEN)

II. *Mariella bergeri* Zone

Hysteroceras sp., *Pervinquieria* (*Durnovarites*) *spinosa* Pervinquière, *P.* (*D.*) aff. *spinosa*, *Stoliczkaia* cf. *dispar* d'Orbigny (*in* Pervinquière), *Spathiceras tunisiense*, *Prionocycloides numidicus* Sornay, *Cottreauites africanus* Sornay, *C. subboulei* Sornay, *Submantelliceras suzannae*, *S.* gr. *aumalense suzannae*, *Protacanthoceras* (?) sp., *Ficheuria peroni*, *F.* sp., *Flickia* (?) *rudelli* Dubourdieu, *Scaphites bassei*, *Turrilitoides* cf. *hungardianus* and vars., *Mariella bergeri*, *M. kerkourensis* Dubourdieu, *M. hillyi* Dubourdieu, *Ostlingoceras puzosianum* (d'Orbigny), *Hamites intermedius* Sowerby, *Stomohamites subvirgulatus* Spath (?), *S.* sp. (?), *Lechites moreti* Breistroffer, *Anisoceras* cf. *jacobi* Breistroffer, *Sciponoceras* sp. (*Cyrtochilus*), *Hemiptychoceras* sp.

LOWER CENOMANIAN

I. *Hypoturrilites schneegansi* Zone, 200–250 m

Stoliczkaia sp., *Submantelliceras suzannae*, *S.* aff. *aumalense*, *S.* sp., *Mantelliceras* gr. *martimpreyi*, *M.* spp., *Cottreauites africanus* Sornay, *C. melleguensis* Sornay, *Prionocycloides zrissensis* (Pervinquière), *Acompsoceras dubourdieui* Sornay, *Flickia simplex* Pervinquière, *Scaphites bassei*, *Ostlingoceras* sp., *Hypoturrilites tuberculato plicatilis*, *H. schneegansi* Dubourdieu, *H. carcitanensis* (*oberlini*), *H. betieri* Dubourdieu, *Mariella cenomanensis* (*Turrilites*), *M.* cf. *essenensis* (*Turrilites*), *M? boukhadrensis* (Dubourdieu) (*Turrilites*), *Turrilites pervinquierei* Diener, *T. harchaensis* Dubourdieu, *Idiohamites alternatus*, *Stomohamites* aff. *subvirgulatus*, *Sciponoceras pervinquierei* Breistroffer (*Cyrtochilus*).

Three horizons are recognized in this Zone:

Horizon A. Close to the Vraconnian, with *Submantelliceras*, *Cottreauites*, and

Prionocycloides surviving from the beds below, and *Acompsoceras*, *Turrilites*, and *Hypoturrilites* appearing. *Mantelliceras* of the *martimpreyi* group are absent.

Horizon B. Characterized by the disappearance of the last *Stoliczkaia*, and the appearance of the first *Mantelliceras* (*martimpreyi* group). *Submantelliceras* and *Hypoturrilites* are abundant, whilst *Acompsoceras* also occurs. 2 turrilitids, *Hypoturrilites betieri* and *H. oberlini* (= *H. carcitanensis*) are characteristic.

Horizon C. Submantelliceras disappears, *Hypoturrilites* becomes extinct; the last *Cottreauites* appear at this level. Characteristic forms are: *Cottreauites melleguense*, *Flickia simplex* Pervinquière, *Hypoturrilites tuberculato plicatilis*, *Mariella cenomanensis* (*Turrilites*), *Turrilites pervinquierei*, *T. harchensis*, *T. asselensis*, *Sciponoceras pervinquierei* (*Cyrtochilus*).

Zone II

Puzosia sp., *Mantelliceras* sp., *Scaphites bassei*, *Ostlingoceras*, *Prionocycloides proratum* (Coquand), *Acompsoceras melleguense*, *Euhystrichoceras nicasei*.

UPPER CENOMANIAN

Zone III, 200–350 m

Calycoceras cottreaui (*Mantelliceras*), *Acompsoceras* sp. (group of *renevieri*), *Protacanthoceras* (?) sp., *Acanthoceras rhotomagense*, *A. hippocastanum* var., *A.* gr. *haugi*, *Calycoceras* gr. *newboldi* (Kossmat *in* Pervinquière), *C.* cf. *gothicum*, *C.* cf. *barruei*, *Euomphaloceras* gr. *meridionale*, *Forbesiceras obtectum*, *Scaphites africanus* Pervinquière, *S. peroni* Pervinquière and vars., *Turrilites* aff. *borssumensis*, *Euturrilites scheuchzerianus*, *Carthaginites krorzaensis*, *Sciponoceras* sp. (*Cyrtochilus*).

Zone IV, 180–300 m

Acompsoceras dubourdieui, *Calycoceras* cf. *gothicum*, *C.* cf. *barruei*, *Acanthoceras hippocastanum*, *A.* sp., *Euomphaloceras* gr. *meridionale*, *Forbesiceras obtectum* and related forms, *Neolobites* sp., *Scaphites peroni* and vars., *S.* group of *equalis-obliquus*.

Zone V, 60–100 m

Terminal part of Cenomanian, with *Inoceramus* cf. *concentricus*.

This succession is of considerable importance. The faunas from the top of the 'Vraconnian' and Horizon A at the base of the *schneegansi* Zone yield faunas with an intermediate character between those of the uppermost Albian and Cenomanian.

Dubourdieu refers his Horizon A to the 'pre-*martimpreyi*' Subzone, but this is clearly not in the sense intended by Spath. *Submantelliceras* of the *aumalense* group ranges from the 'Vraconnian' into the Lower Cenomanian, and there is thus evidence for Wiedmann's '*aumalense*' Subzone, although it is not definitely shown to be Cenomanian.

Hypoturrilites oberlini, which I regard as a synonym of *H. carcitanensis*, characterizes Horizon B, and since this also characterizes the English *carcitanensis* assemblage, suggests that Horizon A represents a part of the Cenomanian unknown

in Britain. *H. schneegansi* is recorded by Hancock (1959) from the base of the type Cenomanian, but none of the associated fauna can be used to identify a precise level within Dubourdieu's succession. The *schneegansi* Zone and Zone II can thus be correlated with most of the *mantelli* Zone in England.

The fauna of Zone III probably corresponds to part of the English *rhotomagense* Zone, but records of *Calycoceras* of *barruei* type suggest it may be also equal to the base of the *naviculare* Zone. The fauna of Zone IV is Upper Cenomanian; records of *Neolobites* recall the widespread occurrence of this genus in the *naviculare* Zone faunas of many parts of southern Europe and the Near East.

5. WEST AFRICA. *Nigeria.* Reyment (1955) reviewed Cretaceous ammonite occurrences in Nigeria, recording a *dispar* Zone fauna comparing well with that of England. Cenomanian faunas are poor; *Euhystrichoceras occidentale* Reyment and *Desmoceras* (*Pseudouhligella*) *calabarense* Reyment are recorded from the lower parts of the Odukpani formation, below a fauna with *Metoicoceras* aff. *ornatum* Moreman, *M.* sp., *Phylloceras* cf. *velledae*, *Desmoceras latidorsatum*, *Turrilites scheuchzerianus*, *Forbesiceras sculptum*, and *Calycoceras* sp. indet., suggesting a very high Cenomanian age.

Angola. Howarth (1965) reviewed literature on the Cretaceous of Angola. Cenomanian faunas are well known, but no detailed stratigraphy is available. Haas (1942) described a Lower Cenomanian *Sharpeiceras* and a *?Mantelliceras*, whilst Thiele (1933) recorded a Cenomanian *Acanthoceras*.

The most important fauna is that from Salinas, described by H. Douvillé (1931) and Spath (1931), yielding '*Protacanthoceras*' *angolaense* (= *Acanthoceras lyelli* Douvillé (*non* Leymerie)), *Calycoceras naviculare* (= *C. borgesi* Douvillé), *Kanabiceras echinatum* (Douvillé), *Austiniceras dibleyi* (= *Puzosia matheroni* Douvillé (*non* d'Orbigny)), *Stoliczkaia dispar* var. *attenuata* Douvillé; '*Knemiceras*' *uhligi* Choffat, and '*Pulchellia*' *caicedoi* Karsten.

Of these, all but the '*Stoliczkaia*' and '*Pulchellia*' indicate a high Cenomanian or basal Turonian age. The *Stoliczkaia* is taken by Spath (1931) and Howarth (1965) to be of Cenomanian age, but must surely be Lower Cenomanian, whilst the '*Pulchellia*' seems a misidentified acanthoceratid (Spath 1931).

6. SOUTHERN AFRICA. *Mozambique.* Upper, Middle, and Lower Cenomanian ammonites were described by Choffat (1903).

South Africa. Cenomanian faunas are well known from False Bay, Zululand. Collignon (1931) recorded Lower Cenomanian *Sharpeiceras*, whilst Crick (1907) and Venzo (1936) described a rich fauna from higher in the Cenomanian. Species are: *Turrilites scheuchzerianus*, *T. costatus*, *T. acutus* (common), *Hypoturrilites nodiferus* (Crick), *Forbesiceras largilliertianum* (d'Orbigny), *F. sculptum*, *Acanthoceras flexuosum* Crick, *A. crassiornatum* Crick, *A. munitum* Crick, *A. expansum* Crick, *A. robustum* Crick, *A. quadratum* Crick, *A. latum* Crick, *A. hippocastanum* Crick (*non* Sowerby), *A. gortanii* Venzo, *Calycoceras newboldi* Crick (?*non* Kossmat), *C. newboldi spinosum* Crick (?*non* Kossmat), *C. newboldi planecostata* Crick (?*non* Kossmat), *C. nitidum*

(Crick), *C. paucinodatum* (Crick), *C. choffati* Crick (*non* Kossmat), '*Acanthoceras*' *cornigerum* Crick, etc.

The abundant *Acanthoceras* all belong to the *rhotomagense* group, but the population structure (possibly only one 'good' species is represented) differs from that of the Rouen ammonite bed (Kennedy and Hancock 1970). This, together with the *Calycoceras*, common occurrence of *T. acutus*, and scarcity of *T. costatus*, lead me to place this assemblage higher in the *rhotomagense* Zone, above the *acutus* assemblage as developed in this country because of the presence of *C. choffati*, but below the *jukesbrownei* assemblage, on the basis of the style of ornament of the *Acanthoceras*. Spath (1925*a*) and Venzo (1936) both recorded Lower Cenomanian ammonites from isolated localities in this general area.

7. MADAGASCAR. More Cenomanian (and indeed Cretaceous) ammonite species have been described from Madagascar than any other part of the world, chiefly as a result of the monographic researches of Collignon (1928–1929, 1931, 1933, 1937, 1939, 1964), Boule, Lemoine, and Thévenin (1907), and Basse de Menorval (1931). Other sources on the Cenomanian are Besairie (1930, 1936, 1953), Collignon (1954, 1959, 1964), and Besairie and Collignon (1956, 1960) (all with bibliographies).

Extensive faunal lists are not reproduced here; rather, it should be pointed out that most work has been on *assemblages* from individual localities rather than on a stratigraphic succession. This has led to the production of zonal assemblages (Table 3) which indicate that either localities yield, and zones are based on, assemblages spanning considerable parts of the Cenomanian stage, or that the distribution of Cenomanian ammonites in Madagascar differs from that elsewhere in the world.

TABLE 3. Zonal divisions of the Cenomanian of Madagascar

Collignon 1937	Besairie and Collignon 1956	Collignon 1959	Besairie and Collignon 1960	Collignon 1964
Mantelliceras vicinale	*Acanthoceras vicinale*	*Utaturiceras vicinale*	*Hourcquiceras*	
Acanthoceras rotomagense	*A. rotomagense*	*A. rotomagense*	*A. rotomagense*	*A. rotomagense*
Acanthoceras cenomanense and *A. cunningtoni*	*Protacanthoceras harpax*	*Euomphaloceras cunningtoni*	*Euomphaloceras cunningtoni*	*Euomphaloceras euomphalum*
Mantelliceras mantelli and *Eucalycoceras newboldi*	*M. mantelli* and *Calycoceras newboldi*	*M. mantelli* and *Calycoceras newboldi*	*M. mantelli* and *Calycoceras newboldi*	*M. mantelli* and *E. newboldi*
Mantelliceras martimpreyi	*M. martimpreyi*	*M. martimpreyi*	*M. martimpreyi*	*M. martimpreyi*

Examples are:

Mantelliceras martimpreyi Zone

Whilst many undoubted low Cenomanian ammonites are listed, including various '*Submantelliceras*' of *suzannae* and *martimpreyi* type, *Cottreauites*, *Hypoturrilites*, etc., *Acanthoceras hippocastanum* is also recorded from this zone.

Mantelliceras mantelli and *Calycoceras newboldi* Zone

The following are only some of the forms described by Collignon (1964) from this Zone: *Hypoturrilites gravesianus*, *H. tuberculatus*, *H. carcitanensis*, *Turrilites scheuchzerianus*, *T. costatus*, *T. acutus*, etc., '*Paraturrilites*' *lewesiensis*, '*P.*' *dorsetensis*, *Forbesiceras largilliertianum*, *F. obtectum*, etc., *Mantelliceras mantelli*, *M. tuberculatum*, *M. saxbii*, *M. cantianum*, *M. couloni*, *M. indianense*, *M. vicinale*, *M.* spp. nov., *Sharpeiceras laticlavium*, *S. schlueteri*, '*Eucalycoceras*' *bathyomphalum*, *Calycoceras subgentoni*, *C. gentoni*, *C.* cf. *boehmi*, *C. paucinodatum*, *C. newboldi* and var. *spinosa*, *C.* cf. *borgesi* (= *C. naviculare*), *C. stoliczkai* (= *C. naviculare*), *C. baylei*, *Acompsoceras sarthense*, *A. essendiense*, *Eucalycoceras besairei*, *E. pentagonum*, *Metoicoceras swalloviforme* Collignon, *M. besairei* Collignon, *M. sakarahense* Collignon, *M. fasciculatum* Collignon.

Euomphaloceras euomphalum Zone

The use of *E. euomphalum*, an Upper Cenomanian form, for index species of the Middle Cenomanian of Madagascar stems from Collignon's regard of *E. euomphalum* and *E. cunningtoni* as synonyms; his '*euomphalum*' all belong to the latter species.

Details are: *Euomphaloceras cunningtoni* (*euomphalum*), '*Protacanthoceras*' *harpax* and vars., '*P.*' *tropicum*, *Calycoceras sinuosum* Collignon, *C. coleroonense* Stoliczka var. *percostata* Collignon, *C. newboldi planecostata*, *C. newboldi ankomakaensis*, *C. newboldi madagascariensis*, *C. choffati* and vars., *C. boulei*, *C. multicostatum*, *C.* cf. *naviculare*, *C.* (*Lotzeites*) *aberrans madagascariensis* Collignon, *Eucalycoceras pentagonum*, *Metasigaloceras trituberculatum* Collignon.

Acanthoceras rotomagense Zone

Calycoceras cenomanense Collignon (*non* d'Archiac), *Acanthoceras rotomagense* Collignon (*non* Brongniart).

Hourcquiceras Zone

Hourcquiceras latelobatum Collignon, *H. hourcqui* Collignon, *H. andranovoritelense* Collignon, '*Mammites*' *menabensis* Collignon, *M. subnodosoides* Collignon, *M. prenodosoides* Boule, Lemoine, and Thévenin.

One is forced to conclude that, whilst a sensible sequence of faunas can be found in the Madagascan Cenomanian, each zonal assemblage contains elements from several horizons, and that as a result correlation between Madagascar and the rest of the world is still not fully possible.

Two important points arise from the Madagascan faunal work. Firstly, in the pyritic marls near the base of the stage there is a level with '*Submantelliceras*' of

suzannae and *aumalense* type. Secondly, towards the top of the stage there are beds with *Hourcquiceras*, and '*Mammites*' with *Dunveganoceras*-like inner whorls.

A peculiar feature of the area seems to be the absence of good *Acanthoceras rhotomagense* faunas. The *A. rhotomagense* figured by Collignon (1964, pl. 372) does not belong to Brongniart's species, and indeed may not be an *Acanthoceras*, whilst '*A.*' *cottreaui* Collignon, '*A.*' *breistrofferi* Collignon, and '*A.*' *guggenbergi* seem dubious members of that genus.

8. INDIA. Classic accounts of the Cretaceous faunas of southern India are given by Stoliczka (1863–1866) and Kossmat (1895–1898), now being revised by Matsumoto and others (1966 onwards). Unfortunately, no detailed stratigraphy is available, nor does it seem likely that one will be produced in the foreseeable future. It is, however, clear that the Utatur Group spans the Upper Albian to the Lower Turonian. Many species are common to the Indian and English successions, and correlation seems eminently possible.

9. JAPAN. Cenomanian ammonites from Japan have been described by Matsumoto and others in a series of papers (Matsumoto 1938 onwards). Faunas are rather sparse, whilst *Inoceramus* and desmoceratids or puzosiids are widely used as zonal indices. The Infragyliakian *Desmoceras kossmati* Zone corresponds to part of the Upper Albian and Lower Cenomanian. *Graysonites* aff. *adkinsi*, *Stoliczkaia* aff. *dorsetensis*, *S.* aff. *africana*, *Euhystrichoceras nicasei*, and *Prionocycloides proratum* occur below, *Graysonites* cf. *fountaini*, *G.* spp. indet., *Acompsoceras* sp. nov., *Mariella*, and *Desmoceras kossmati* occur above.

The Lower Gyliakian *Desmoceras* (*Pseudouhligella*) *japonicum* Zone corresponds to the rest of the Cenomanian stage. In the lower *Mantelliceras japonicum* Subzone, *Mantelliceras japonicum* Matsumoto, Muramoto, and Takahashi, *M. cantianum*, *M.* spp., *Sharpeiceras kongo*, *Desmoceras poronaicum* Yabe, *D.* (*P.*) *japonicum* Yabe, *Zelandites inflatus* Matsumoto, *Parajaubertella imlayi* Matsumoto, *Turrilites costatus*, *Hypoturrilites komatoi* Yabe, and *Sciponoceras baculoide* are recorded; this is an essentially Lower Cenomanian assemblage. The succeeding *Calycoceras orientale* Subzone yields *Acanthoceras cornigerum*, *A. amphibolum*, *A.* aff. *latum*, *Euomphaloceras cunningtoni meridionale*, and *E.* cf. *lonsdalei* below, and *Calycoceras* of the *newboldi-spinosum* and *orientale* groups above. This is a Middle Cenomanian assemblage.

The highest Cenomanian yields *Calycoceras naviculare*, *Eucalycoceras pentagonum*, *Protacanthoceras* sp., *Pachydesmoceras*, and *Austiniceras*.

Similarities to the English Cenomanian sequence are obvious, whilst the lowest 'Turonian' of this area yields *Kanabiceras septemseriatum*, *Sumitomoceras faustum* Matsumoto and Muramoto, and *Sciponoceras kossmati*.

10. AUSTRALASIA. Cenomanian faunas are poorly known. Casey and Glaessner (*in* Glaessner 1958) described a new genus and species *Chimbuites sinuosocostatus* Casey and Glaessner from New Guinea, originally considered to be an Aptian *Deshayesites*, then regarded as Albian, and later (Wright 1963*a*) as of Cenomanian age. Erni (1944) described a Middle Cenomanian *Euomphaloceras* (*Cunningtoniceras höltkeri* Erni = *E. euomphalum*) from New Guinea.

Wright (1963*a*) described two Cenomanian faunas from Bathurst Island, Northern Australia:

(i) An *in situ* fauna with *Stomohamites simplex*, *Sciponoceras glaessneri* Wright, *Hypoturrilites gravesianus*, *Turrilites costatus*, *Borissiakoceras* (?) sp., *Acanthoceras tapara* Wright, and *A. mirialampiense* Wright.

(ii) A fauna collected from beach boulders, with: *Sciponoceras* sp., *Hypoturrilites gravesianus*, *Scaphites dailyi* Wright, *Chimbuites mirindowensis* Wright, *Euomphaloceras cunningtoni*, and *E. lonsdalei*.

Both these faunas seem to be of Middle Cenomanian age. The *Acanthoceras* species are of the *rhotomagense* group, and *E. cunningtoni* is a *rhotomagense* Zone species, although *E. lonsdalei* is said to occur above *E. euomphalum* in the United States.

11. SOUTH AMERICA. Cretaceous rocks are widely distributed in South America, but little is known of detailed stratigraphy. The best account in this respect is the work of Benavides-Cáceres (1956) in northern Peru. 4 zones are recognized in the Cenomanian:

Acanthoceras chasca Zone
Exogyra africana Zone
Exogyra cf. *ponderosa* Zone
Paraturrilites lewesiensis Zone

The *lewesiensis* Zone yields *Mariella lewesiensis* (4 specimens) and *Sharpeiceras occidentale* (1) and is thus of Lower Cenomanian age.

The *ponderosa* Zone yields no ammonites, whilst the *africana* Zone yields only indeterminate acanthoceratids.

The *chasca* Zone yields *Forbesiceras* sp. indet. (1), *Acanthoceras chasca* Benavides-Cáceres (4), *A. sangalense* Benavides-Cáceres (4), *A. pollocense* Benavides-Cáceres (4), and *Neolobites kummeli* Benavides-Cáceres (14).

A. chasca is an *Acanthoceras* of the *rhotomagense* group, and suggests a Middle Cenomanian horizon. The other 2 *Acanthoceras* species are not comparable with any other *Acanthoceras*, with the possible exception of *A. basseae*, and are thus of little use for dating the fauna. The *Neolobites* is also of little value. A Middle Cenomanian age thus seems the most probable.

12. UNITED STATES. Rocks of Cenomanian age are widely developed in the United States, and there is an enormous literature, both stratigraphic and palaeontological. One of the best-known areas is Texas, and this is discussed in most detail, together with the significance of the high Cenomanian faunas with *Metoicoceras* and *Dunveganoceras* known from the Western Interior.

Texas and adjacent areas. The best stratigraphic summary comes from Adkins (1933), whilst the main faunal accounts are given by Adkins (1928, 1931), Böse (1927–1928), Moreman (1942), Young (1958*a*, *b*), Powell (1963), Clark (1965), and others.

TABLE 4. Formations and stages in the Middle Cretaceous of Texas and the Gulf Coast

	Eagle Ford Group	Arcadia Park Britton Bluebonnet	Turonian
GULF SERIES (part)			Upper Cenomanian
	Woodbine Group	Templeton Lewisville	Middle Cenomanian
		Red Branch/Euless Dexter	(No ammonites)
	Washita Group	Buda Grayson/Del Rio Mainstreet Paw Paw	Lower Cenomanian
COMANCHE SERIES		Weno Denton Fort Worth Duck Creek	Albian

The classification of the Texas mid-Cretaceous is shown in Table 4. Faunal details are:

Paw Paw

As Clark (1965) suggested, the Albian/Cenomanian boundary possibly lies at or close to the top of the Paw Paw.

Main Street

Stoliczkaia sp. nov. Adkins, *Graysonites adkinsi* Young, *G. fountaini* Young, *G. wooldridgei* Young, *Scaphites worthensis* Adkins and Winton, *S. hilli* Adkins and Winton, *Anisoceras perarmatum*, *Ostlingoceras conlini* Clark, *Graysonites lozoi* Young, '*Submantelliceras*' *brazoensis* (Böse), '*S.*' *wacoense* (Böse), *Stoliczkaia* aff. *dispar* Böse (*non* d'Orbigny), *S. texana* Craigin, *S. uddeni* Böse, *Tetragonites brazoensis* Böse, *Adkinsia bosquensis* Böse, *A. adkinsi* Böse, *A. semiplicata* Böse, *A. sparcicostata* Böse, *A. tuberculata* Böse, *Engonoceras bravoense* Böse, *E. uddeni* Craigin, *E. retardum* Hyatt, *E.* spp., *Mariella* (*Plesioturrilites*) *brazoensis brazoensis* and var. *pecosensis* Clark, *M.* (*P.*) *rhaciformis*, *M.* (*P.*) *bosquensis* Böse, *M.* (*Wintonia*) *graysonensis* (Adkins), *Scaphites bosquensis* Böse, *S. subevolutus* Böse, *Lechites comanchensis* (Adkins).

Buda

Budaiceras (7 species), *Stoliczkaia adkinsi* Böse, *S. texana*, *S.* spp., *Sharpeiceras laticlavium* var. *mexicana* Böse, *Euhystrichoceras remolinense* Böse, *Hypoturrilites tuberculatus*, *Mariella* (*Mariella*) *wysogorskii* Lasswitz, *M.* (*Plesioturrilites*) *brazoensis brazoensis*, *Sciponoceras baculoide* (Clark *non* Mantell?).

Woodbine Formation

No ammonites are recorded by Stephenson (1952) from the Dexter and Red Branch/Euless members.

Lewisville

Turrilites aff. *acutus* [*T. dearingi*], *Acanthoceras tarrantense tarrantense* (Adkins), *A. tarrantense nitidum* Stephenson, *A. wintoni* Adkins, *A. adkinsoni* Stephenson, *A. hazzardi* Stephenson, '*A*' *barcusi* (Jones), *Euomphaloceras cunningtoni* (*Acanthoceras eulessanum* Stephenson), *Forbesiceras conlini* Stephenson, *Metengonoceras dumbli* (Craigin).

Templeton

Protacanthoceras cuspidum (Stephenson) [*Acanthoceras*], *Dunveganoceras? bellsanus* (Stephenson) [*Mammites*], *Metengonoceras swallovi swallovi* Shumard, *M. swallovi macrum* Stephenson, *M. latoventer* Stephenson, *M. crassicostae* Stephenson.

Eagle Ford Group
Base of Eagle Ford Shale (Stephenson 1955)

Acanthoceras johnsonianum Stephenson, *Euomphaloceras lonsdalei*, *E. alvaradoense*, *Tarrantoceras rotatile* Stephenson, *T. stantoni* Stephenson, *T. lilianense* Stephenson, *T. multicostatum* Stephenson, *Borissiakoceras orbiculatum* Stephenson.

Clark (1965) recorded *Turrilites acutus* and *T. costatus* from the Tarrant Formation. Relations within the Eagle Ford Group are complicated by the fact that the Tarrant Formation of Moreman (1942), as developed in Tarrant County and classed by him as basal Eagle Ford, is in fact a local equivalent of the top of the Lewisville Member of the Woodbine (Stephenson 1955).

It is, however, apparent that the Moreman's overlying Britton Member yields ammonites which have been regarded as of Lower Turonian age:

'*Eucalycoceras*' *bentonianum* (Craigin), '*E.*' *dentonense*, '*E.*' *lewisvillense*, *Allocrioceras* spp., including *A. pariense*, *Metoicoceras whitei* Hyatt, *M. gibbosum* Hyatt, *M.* spp., *Kanabiceras kanabense* (Hyatt), *Kanabiceras septemseriatum*, *Worthoceras* spp., *Sciponoceras gracile*, etc.

The Texas faunal succession is undoubtedly incomplete, but is nevertheless of extreme interest. Thus the occurrence of *Submantelliceras* (some surely *Graysonites* nuclei), *Stoliczkaia*, and *Graysonites* in the Grayson–Del Rio recalls the basal part of Dubourdieu's *schneegansi* Zone in the Algero-Tunisian border region, although these beds cannot be directly correlated with England.

Few species from the Buda occur in England, but the *Sharpeiceras* and *Hypoturrilites* suggest the lower part of the *mantelli* Zone, perhaps the *carcitanensis* assemblage.

The fauna of the Lewisville Member of the Woodbine, dominated by *Acanthoceras* of the *rhotomagense* group, but also yielding *Euomphaloceras cunningtoni* and *Turrilites* aff. *acutus*, is to be correlated with the lower parts of the *rhotomagense* Zone in England.

The fauna of the Templeton Member is less readily compared with the English succession, although *Protacanthoceras cuspidum* is close to some Bed C *naviculare* Zone species.

An important Templeton form for correlation within the United States is *Mammites? bellsanus* Stephenson. The highly characteristic whorl section of this species, ribbing, and especially the attitude of the upper ventro-lateral tubercles, recalls the inner whorls of *Dunveganoceras* species, especially specimens of *D. albertense* (Warren) *montanense* Cobban as figured by Cobban (1953, pl. 10, figs. 1–6). I would therefore tentatively refer Stephenson's species to *Dunveganoceras*.

The basal Eagle Ford fauna is very high in the Cenomanian, probably corresponding to a part of the *naviculare* Zone in England, if records of *Tarrantoceras* from Bed C (Casey 1960) are confirmed.

The fauna of the Britton member indicates a correlation with part of the *plenus* Marls, and perhaps the base of the Middle Chalk.

Pacific Coast. Matsumoto and Popenoe (1960) reviewed the stratigraphy of this region; the best faunal account is given by Matsumoto (1959), who revised the Cretaceous ammonites from California described by Anderson (1958). As Matsumoto and Popenoe (1960) commented, many years of fieldwork are needed to decipher the complex stratigraphic and structural relations within this region; and present comments are therefore scanty.

In south-west Oregon and northern California the base of the Hornbrook formation (Peck, Imlay, and Popenoe 1956) is of Cenomanian age, with *Mantelliceras* (Lower Cenomanian), *Acanthoceras* cf. *turneri* White (*non* Sowerby, = *A. whitei* Matsumoto) (Middle Cenomanian), and *Calycoceras* cf. *stoliczkai* (= *C. naviculare*) (Upper Cenomanian).

Further south, on the north-west side of the Sacramento Valley, *dispar* Zone ammonites are known from units ii or iii of Matsumoto and Popenoe (1960, p. 30). Unit iii yields *Graysonites wooldridgei*, *G*? sp., and *Desmoceras kossmati* Matsumoto (Lower Cenomanian), whilst units iv and v are of Middle or Upper Cenomanian age, yielding *Calycoceras newboldi*, *Sciponoceras baculoide*, etc.

To the west of the Sacramento, the Antelope Shale yields Middle to Upper Cenomanian ammonites, i.e. *Calycoceras* cf. *spinosum*, *C. boulei*, and *C. stoliczkai* (= *C. naviculare*).

On the west of the San Joaquin Valley an interesting Middle Cenomanian fauna comes from the so-called Lower Waltham Shale (Matsumoto and Popenoe 1960, p. 56). Species are *Forbesiceras* cf. *obtectum*, *Acanthoceras* cf. *evolutum* (= *Euomphaloceras inerme*), *A.* cf. *sherborni*, *Turrilites* cf. *costatus*, and *T.* (*E.*) cf. *scheuchzerianus*.

Lower, Middle, and Upper Cenomanian ammonites are known from the San Francisco Bay area, including *Mantelliceras* (= *Acanthoceras*) *lecontei* Anderson (1958, p. 242, pl. 13, figs. 1, 1*a*), *Turrilites* cf. *costatus*, *T. scheuchzerianus*, *Acanthoceras whitei*, and *Calycoceras orientale*. Alcatraz Island is of Cenomanian age.

The Western Interior. The Cretaceous stratigraphy of this area was reviewed by Cobban and Reeside (1952), and the zonal stratigraphy discussed by Cobban

TABLE 5. Subdivisions of the Middle Cretaceous of the Western Interior of the U.S.A.

Stages	*Zones*	*Other ammonites*
'Turonian'	*Sciponoceras gracile*	*Scaphites delicatus* Warren, *Worthoceras* sp., *Tragodesmoceras scotti* Moreman, *Metoicoceras whitei*, *Watinoceras* sp., *Kanabiceras kanabense*, *Borissiakoceras* cf. *orbiculatum*
	Dunveganoceras albertense	*Metoicoceras mosbyense* Cobban, *M. mulleri* Cobban, *Dunveganoceras albertense montanense*, *D. parvum* Cobban
Cenomanian	*Dunveganoceras conditum*	*Metoicoceras* sp. nov. (Cobban 1952)
	Dunveganoceras pondi	*Calycoceras canitaurianum* (Haas), *Metoicoceras praecox* Haas
	Acanthoceras wyomingense (= *Acanthoceras*? sp. A. of Cobban and Reeside).	*Eucalycoceras* sp. A. (Hattin 1968), *Borissiakoceras* sp., *B. reesidi*, *B. orbiculatum* Stephenson, *Stomohamites* sp.
	Acanthoceras amphibolum	*Borissiakoceras reesidi*
	Borissiakoceras reesidi	*Borissiakoceras compressum* Cobban, *Johnsonites sulcatus* Cobban, 'acanthoceratids' (Cobban 1961)
Albian	*Neogastroplites* McLearn	

(1961). Relevant details are shown in Table 5, together with the ammonite species present.

This sequence cannot be readily correlated directly with Europe, except for the *albertense* Zone, which corresponds to Wiedmann's *mulleri* Zone, and the *gracile* Zone, which corresponds to part of the *plenus* Marls and basal Middle Chalk.

Lower in the sequence the large acanthoceratids and the Binneyitidae which are so widely distributed in the Western Interior are unknown in western Europe, and comparison can be made only via the Texas strata.

Thus *Borissiakoceras orbiculatum* occurs in the basal Eagle Ford and the *Acanthoceras wyomingense* Zone, suggesting a very high Cenomanian age for most of the Western Interior succession, but Cobban (1961) recorded *B.* cf. *orbiculatum* from the *gracile* Zone, whilst the *Dunveganoceras*-like features of *Mammites? bellsanus* from the Templeton suggests that the *wyomingense* Zone is probably Middle Cenomanian. No undoubted Lower Cenomanian ammonites seem to be recorded from this region.

13. CANADA. Jeletzky (1968) reviewed the stratigraphy of the Cretaceous of the Western Interior of Canada. Ammonite faunas are very poor, whilst Jeletzky compared the succession with Cobban and Reeside's (1952) preliminary suggestions for a division of the United States Western Interior succession and a series of untenable ammonite, belemnite, *Inoceramus* and echinoid Zones and Subzones purported to represent the European succession.

The Western Interior succession is:

Cenomanian
- *Dunveganoceras hagei* Zone
- *Dunveganoceras parvum* Zone
- *Dunveganoceras albertense* Zone
- *Dunveganoceras* cf. *conditum* Zone
- *Acanthoceras athabascense* Zone
- 'Zone H'

The *albertense* and *conditum* Zones can presumably be correlated with the same nominal zones in the United States. 'Zone H' yields no diagnostic index fossils.

14. GREENLAND. Donovan (1953, 1954) recorded a small Cenomanian fauna from East Greenland, interesting for the record of *Schloenbachia*. Species are: *Schloenbachia* aff. *subplana*, *S. subtuberculata*, *S. subvarians*, *S.* cf. *varians* and var. *tetrammata*, *S.* spp., *Mesogaudryceras* cf. *leptonema*, *Phylloceras* cf. *velledae*, *Lytoceras* sp. nov. cf. *vicinum*.

CONCLUSIONS

From the description of Uppermost Albian to Lower Turonian faunas given in the preceding pages, a number of broad conclusions can be drawn.

1. An Upper Albian *dispar* Zone ammonite fauna can be recognized in many parts of the world.

2. In north Africa, Madagascar, Texas, and possibly southern France, marls spanning the Albian to Cenomanian boundary yield faunas with elements of both stages, *Stoliczkaia* and '*Submantelliceras*' apparently representing a high Albian or very low Cenomanian horizon.

Above, again in a marl facies, come beds with *Hypoturrilites*, *Submantelliceras* of the *suzannae* and *aumalense* type, and *Stoliczkaia*. What appears to be this horizon is represented in limestone facies in Texas, California, Japan (and possibly Spain and Portugal) by beds with *Graysonites*.

3. These faunas are absent in England. This may be due to (i) a non-sequence at the Albian/Cenomanian boundary, as in many areas (Kennedy 1969, 1970); (ii) the absence of ammonites at this level (several metres and more of virtually unfossiliferous sediment occur between the highest Albian and lowest Cenomanian faunas at some localities); or (iii) confinement of *Graysonites* and the '*Submantelliceras*' *suzannae* and *aumalense* group ammonites to the Tethyan region.

4. A general Lower to Middle to Upper Cenomanian ammonite succession comparable to that seen in England can be recognized over wide areas of the world, locally modified by the presence of forms with restricted distribution, i.e. *Pseudocalycoceras* of the *harpax* group, *Borissiakoceras*, *Budaiceras*, *Adkinsia*, *Neolobites*, and *Engonoceras*, and the absence of largely boreal forms such as *Schloenbachia* and *Hyphoplites*.

5. Individual species have great geographical ranges, including key stratigraphic indicators such as *Mantelliceras mantelli* (Europe, Africa, Madagascar, India), *Calycoceras naviculare* (Europe, north Africa, Middle East, Madagascar, Japan,

India, U.S.A.), *Eucalycoceras pentagonum* (Europe, north Africa, Madagascar, India, U.S.A.), and many others, so that detailed world-wide correlation of most of the Cenomanian will eventually be possible.

6. In the Western Interior of North America a peculiar, restricted Upper Cenomanian fauna occurs, characterized by *Borissiakoceras* (also known in the U.S.S.R., Texas, and ?Australia), *Dunveganoceras* (also possibly occurring in Texas and Madagascar), hypernodose *Acanthoceras*, and *Metoicoceras*.

7. The base of the Turonian stage is best drawn at the base of a *Mammites nodosoides/Mytiloides labiatus* Zone. The *Sciponoceras gracile–Metoicoceras whitei* Zone, the *plenus* Marls, and those parts of the Middle Chalk below the appearance of *Mammites* and *Mytiloides labiatus*, yielding *Sciponoceras gracile*, *Kanabiceras*, and *Neocardioceras* should thus be considered Cenomanian.

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Explanation of Plate 1

All figures natural size.

Figs. 1–8. *Stomohamites simplex* (d'Orbigny). 1, BMNH C76361, phosphatic internal mould, *T. costatus* assemblage fauna, Chalk Basement Bed, Buckland Newton (Dorset); the aperture is partially preserved. 2, SMC B21350; 3, B21351; 4, B21353; 5, B21347; 6, B21352; 7, B21348; 8, B21349; all are composite internal moulds; 2 shows the aperture, 3 a former apertural position, 5 is pathological for a part of its length; Lower Chalk, Ventnor, Isle of Wight, probably of *A. rhotomagense* Zone age.

Figs. 9*a–c*. *Tetragonites* sp. BMNH C76360, phosphatic internal mould, *A. jukesbrownei* assemblage fauna, Chalk Basement Bed, Sutton Poyntz, near Weymouth (Dorset).

Figs. 10*a, b*. *Mesogaudryceras leptonema* (Sharpe). Holotype, GSM Geol. Soc. 7762, 'Grey Chalk', Ventnor, Isle of Wight; probably of Lower Cenomanian age; the ornament of the outer surface of the shell is preserved (I.G.S. photograph).

Figs. 11*a, b*. *Mesogaudryceras* cf. *leptonema* (Sharpe). BMNH C25657, internal mould, retaining traces of test, *M. saxbii* assemblage age, Bed A_2, Cenomanian limestone, Devon coast.

Figs. 12–18. *Sciponoceras baculoide* (Mantell). 12–14, syntypes of *Baculites obliquatus* J. de C. Sowerby; 12, BMNH 44005*a*; 13, BMNH 44005*c*; 14, BMNH 44005*b*; all are composite internal moulds, Lower Chalk, Hamsey (Sussex), all probably of *T. costatus* assemblage age; 12, apertural fragment. 15–18, BMNH C76362–65, phosphatic internal moulds, *T. costatus* assemblage fauna, Chalk Basement Bed, Buckland Newton (Dorset); 15, 16 show constrictions; 17, 18 show the strong ventral ribbing typical of mature specimens.

Explanation of Plate 2

All figures natural size.

Figs. 1*a*, *b*, 2*a*, *b*, 3*a*, *b*, 4*a*, *b*, 5*a*, *b*. *Sciponoceras baculoide* (Mantell). 1*a*, *b*, SMC B21323; 2*a*, *b*, SMC B251; 3*a*, *b*, SMC 21311; 4*a*, *b*, SMC 21315; all are composite internal moulds; Lower Chalk, Ventnor, Isle of Wight; 3*a* retains part of the apertural margin, and ventral constriction. 5*a*, *b*, lectotype (larger specimen) and paralectotype 1, on block BMNH 8612, Lower Chalk, Sussex, probably of *T. costatus* assemblage age; both specimens are composite internal moulds; the paralectotype is an apertural fragment; figured by Mantell 1822, pl. 23, fig. 6.

Explanation of Plate 3

All figures natural size.

Figs. 1*a*, *b*, 2, 8, 11. *Sciponoceras baculoide* (Mantell). 1*a*, *b*, SMC B21313, composite internal mould showing the constrictions; Chalk Marl, Ventnor, Isle of Wight, probably of *T. costatus* assemblage age. 2, SMC B21316, crushed apertural fragment, same horizon and locality. 8, BMNH C76366, weakly ornamented specimen, phosphatic *T. costatus* assemblage fauna, Chalk Basement Bed, Buckland Newton (Dorset). 11, BMNH 36576*a*, paralectotype 2, Lower Chalk, Sussex; composite internal mould, probably of *T. costatus* assemblage age; figured by Mantell 1822, pl. 23, fig. 7.

Figs. 3*a*, *b*, 4*a*, *b*, 9*a*, *b*. *Anisoceras auberti* (Pervinquière). 3*a*, *b*, BMNH 36586*a*, Warminster (Wilts.); 4*a*, *b*, BMNH C49, Isle of Wight; 9*a*, *b*, BMNH 89099, Warminster (Wilts.); all specimens are phosphatic internal moulds, of *H. carcitanensis* assemblage age, and were mentioned by Spath 1939, p. 558.

Figs. 5*a*, *b*. *Anisoceras* aff. *auberti* (Pervinquière). Phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Ventnor, Isle of Wight; listed by Jukes-Browne and Hill (1903, p. 86) as *Anisoceras pseudoelegans* Pictet and Campiche. SMC B35784 (Jukes-Browne collection).

Fig. 6. *Anisoceras* aff. *picteti* Spath. BMNH C76420, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Fig. 7. *Sciponoceras roto* Cieśliński. BMNH C76421, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Fig. 10. *Plesiohamites multicostatus* (Brown). Holotype, BMNH 36572, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by Mantell 1822, pl. 23, fig. 5.

Figs. 12, 13. *Anisoceras plicatile* (J. Sowerby). 12, BMNH C76381, *T. acutus* assemblage fauna, Chalk Basement Bed, Toller Porcorum, near Maiden Newton (Dorset); 13, BMNH C76390, same horizon, Snowdon Hill, Chard (Somerset); both specimens are phosphatic internal moulds.

Explanation of Plate 4

All figures natural size.

Figs. 1–3. *Anisoceras plicatile* (J. Sowerby). 1, BMNH 4842; 2, BMNH 36567*b*; 3, BMNH 36568; all composite internal moulds, Lower Chalk, Hamsey (Sussex); figured by Mantell 1822, pl. 23, figs. 1, 2, 4.

Figs. 4, 16*a*, *b*. *Idiohamites collignoni* Spath. 4, BMNH C76422, phosphatic internal mould, *H. carcitanensis* fauna, Glauconitic Marl, Gore Cliff, Isle of Wight. 16*a*, *b*, paralectotype, BMNH 36586*a*, internal mould, Lower Cenomanian, Warminster (Wilts.); mentioned by Spath 1939, p. 598.

Figs. 5, 7, 8, 10, 11. *Idiohamites alternatus* (Mantell) *vectensis* Spath. BMNH C76423–27, a series of variants, phosphatic *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Figs. 6, 13*a*, *b*, 17. *Idiohamites ellipticus* (Mantell) *radiatus* Spath. 6, BMNH C76428, Gore Cliff, Isle of Wight; 13*a*, *b*, paralectotype mentioned by Spath 1939, p. 598, BMNH 36627*b*, Ventnor, Isle of Wight; both are phosphatic internal moulds, *H. carcitanensis* fauna, Glauconitic Marl. 17, copy of Pervinquière 1910, pl. 1, figs. 26, 27; 27*a*, *b*, is the lectotype.

Figs. 9*a*, *b*. *Idiohamites alternatus alternatus* (Mantell). BMNH 36627*a*, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Ventnor, Isle of Wight; mentioned by Spath 1939, p. 598.

Fig. 12. *Idiohamites ellipticus ellipticus* (Mantell). Holotype, BMNH 8611, composite internal mould, Lower Chalk, Lewes (Sussex), probably of *H. carcitanensis* assemblage age; figured by Mantell 1822, pl. 23, fig. 9.

Fig. 14. *Sciponoceras baculoide* (Mantell). BMNH C76409, composite internal mould of an apertural fragment, *T. costatus* assemblage fauna, Band 9, Lower Chalk, Folkestone (Kent).

Figs. 15*a*, *b*. *Phylloceras* (*Hypophylloceras*) cf. *seresitense* Pervinquière. BMNH C73148, *M. saxbii* assemblage fauna, Bed A_2, Cenomanian Limestone, Axmouth (Devon).

Explanation of Plate 5

All figures natural size.

Figs. 1*a*, *b*, 2*a*, *b*, 3, 5, 8, 9. *Idiohamites alternatus* (Mantell) *vectensis* Spath. 1*a*, *b*, BMNH 36585*b*; 2*a*, *b*, 36585*a*; 3, 36585*c*; 5, 36585*d*; Cenomanian, Warminster (Wilts.); mentioned by Spath 1939, p. 598. 36585*a*, lectotype; remainder are paralectotypes. 8, BMNH C76429; 9, BMNH C76430, phosphatic internal moulds, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Figs. 4*a*, *b*, 6, 7*a*, *b*, 10*a*, *b*. *Idiohamites alternatus alternatus* (Mantell). 4*a*, *b*, BMNH C457*b*; 6, BMNH 36628; 7*a*, *b*, BMNH C457*a*; all internal moulds, phosphatic *H. carcitanensis* fauna, Glauconitic Marl, Ventnor, Isle of Wight; mentioned by Spath 1939, p. 598. 10*a*, *b*, copy of Mantell 1822, pl. 23, figs. 10, 11, the holotype of *Hamites alternatus*, Middleham, Ringmer (Sussex), now lost.

Fig. 11. *Anisoceras armatum* (J. Sowerby). BMNH C76431, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Fig. 12. *Stomohamites duplicatus* (Pictet and Campiche). BMNH C76432, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Explanation of Plate 6

All figures natural size.

Figs. 1, 2, 4–10. *Hypoturrilites carcitanensis* (Matheron). BMNH C76433–41; phosphatic *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Fig. 3. *Turrilites* (*Turrilites*) *costatus* Lamarck. BMNH C76391, phosphatic body chamber fragment, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Fig. 11. *Hypoturrilites gravesianus* (d'Orbigny) and *Hypoturrilites tuberculatus* (Bosc). BMNH 5762, Ringmer (Sussex), figured by Sharpe 1857, pl. 25, fig. 1, as *Turrilites tuberculatus*. This specimen is a chimaera (D. Phillips, in litt.); the upper whorls are the specimen of *H. gravesianus* figured by Mantell 1822, pl. 24, fig. 6, as *Turrilites tuberculatus*; the lower whorls are *Hypoturrilites tuberculatus* (Bosc).

Fig. 12. *Hypoturrilites gravesianus* (d'Orbigny). BMNH C76459, composite internal mould, *H. carcitanensis* assemblage fauna, Lower Chalk, near Upper Beeding (Sussex); note the well-preserved spines.

Explanation of Plate 7

All figures natural size.

Figs. 1, 5*a*, *b*. *Hypoturrilites mantelli* (Sharpe). 1, lectotype, BMNH 32568; 5*a*, *b*, paralectotype, BMNH 32551; both composite internal moulds, Lower Chalk, Lewes (Sussex); figured by Sharpe 1857, pl. 25, figs. 5, 6*a*, *b* respectively.

Fig. 2. *Hypoturrilites* aff. *carcitanensis* (Matheron). BMNH 37409, phosphatic internal mould, Cenomanian Upper Greensand, Warminster (Wilts.).

Figs. 3, 4. *Ostlingoceras gallienii* (Boule, Lemoine, and Thévenin). 3, BMNH C76386; 4, BMNH C76387; both are phosphatized internal moulds; *H. carcitanensis* assemblage fauna, Glauconitic Marl, Stour Bank, Shillingstone (Dorset).

Fig. 6. *Ostlingoceras puzosiforme* Spath. Holotype, BMNH 50283, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Bonchurch, near Ventnor, Isle of Wight; figured by Sharpe 1857, pl. 27, fig. 11.

Figs. 7, 8. *Turrilites* (*Turrilites*) *acutus* Passy. 7, BMNH C76404; 8, BMNH C76300; both are phosphatized specimens, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Fig. 9. *Turrilites* (*Mesoturrilites*) *aumalensis* Coquand. BMNH C76458, composite internal mould, ? *M. saxbii* assemblage fauna, Band D, Lower Chalk, Eastwoods Cement Co. Pit, Southerham, near Lewes (Sussex).

Figs. 10*a*–*c*. *Anisoceras* aff. *picteti* Spath. BMNH C76448, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Woody Point, St. Lawrence, Isle of Wight.

Explanation of Plate 8

All figures natural size.

Figs. 1, 4, 5, 8. *Mariella* (*Mariella*) *lewesiensis* (Spath). 1, BMNH C76462; 5, BMNH C76463; composite internal moulds, unphosphatized *H. carcitanensis* fauna, Band 1*b*, Lower Chalk, Eastbourne (Sussex). 4, BMNH 33558, holotype figured by Sharpe 1857, pl. 26, fig. 10, composite internal mould, Chalk Marl, Lewes (Sussex). 8, BMNH C76444, phosphatic internal mould, *M. saxbii* assemblage fauna, Band 2*a*, Lower Chalk, Gore Cliff, Isle of Wight.

Fig. 2. *Ostlingoceras* aff. *gallienii* (Boule, Lemoine, and Thévenin). GSM Zn9067, *M. saxbii* assemblage fauna, bed A_2, Cenomanian Limestone, Humble Point (south Devon).

Fig. 3. *Carthaginites* cf. *inornatus* (Collignon). BMNH C76469, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Fig. 6. *Turrilites* (*Turrilites*) *borssumensis* Schlüter. GSM Geol. Soc. 7778, composite internal mould, Lower Chalk, Ventnor, Isle of Wight.

Fig. 7. *Hypoturrilites* cf. *tuberculatus* (Bosc). BMNH C76443, phosphatic internal mould, *M. saxbii* assemblage fauna, Band 2*a*, Lower Chalk, Gore Cliff, Isle of Wight.

Figs. 9, 11, 13. *Ostlingoceras bechii* (Sharpe). 9, holotype, BMNH 88, figured by Sharpe 1857, pl. 26, figs. 13*a*, *b*; 11, SMC B35792; both internal moulds, Bed A_2, Cenomanian Limestone; 9 is from near Lyme Regis; 11 from Axmouth, Devon. 13, BMNH C76410, composite internal mould, lower part of *M. mantelli* Zone Folkestone (Kent).

Fig. 10. *Mariella* (*Mariella*) cf. *cenomanensis* (Schlüter). BMNH C76445, same horizon and locality as figs. 7, 8.

Figs. 12, 14. *Turrilites* (*Turrilites*) *costatus* Lamarck. 12, BMNH 33619, composite internal mould, Lower Chalk, Sussex. This specimen is the holotype of *Turrilites triplicatus* J. de C. Sowerby, figured by J. de C. Sowerby *in* Dixon 1850, pl. 29, fig. 16; Sharpe 1857, pl. 27, fig. 15. 14, BMNH C76367, phosphatic internal mould, *T. costatus* assemblage fauna, Chalk Basement Bed, Buckland Newton (Dorset).

Fig. 15. *Turrilites* (*Mesoturrilites*) cf. *aumalensis* Coquand. GSM Geol. Soc. 7779, composite internal mould, Lower Chalk, Ventnor, Isle of Wight; figured by Sharpe 1857, pl. 27, fig. 13.

Fig. 16. *Ostlingoceras* aff. *puzosiforme* Spath. GSM Zb 692, phosphatic internal mould, Lower Cenomanian, Norton Ferris (Wilts.).

Explanation of Plate 9

All figures natural size.

Figs. 1, 2. *Puzosia subplanulata* (Schlüter). 1, BMNH C76392, phosphatic internal mould, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset). 2, BMNH 9381, lectotype of *Puzosia planulata* J. de C. Sowerby, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by J. de C. Sowerby 1827, pl. 570, fig. 5, and Sharpe 1855, pl. 12, fig. 3.

Figs. 3*a*, *b*. *Forbesiceras* aff. *obtectum* (Sharpe). BMNH C76393, phosphatic specimen retaining much of the test, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Figs. 4*a–c*. *Calycoceras paucinodatum* (Crick). BMNH C76394, phosphatic specimen, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Explanation of Plate 10

All figures natural size, except figs. 2*a*, *b*.

Figs. 1*a*, *b*, 2*a*, *b*. *Desmoceras* (*Desmoceras*) cf. *inane* (Stoliczka). 1*a*, *b*, BMNH 37279, phosphatic internal mould, Lower Cenomanian, Warminster (Wilts.); mentioned by Spath 1923, p. 42. 2*a*, *b*, same, enlarged ×2.

Figs. 3*a*, *b*. *Puzosia subplanulata* (Schlüter). OUM K1278, phosphatic internal mould, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Figs. 4, 5. *Hypoturrilites gravesianus* (d'Orbigny). 4, GSM Geol. Soc. 7777*a*, phosphatic internal mould, Bonchurch, Isle of Wight; figured by Sharpe 1857, pl. 26, fig. 14. 5, BMNH 33557, composite internal mould, Lower Chalk, near Lewes (Sussex); figured by Sharpe 1857, pl. 25, figs. 7*a*, *b*.

Figs. 6*a*, *b*. *Puzosia* (*Puzosia*) cf. *sharpei* Spath. GSM Zb342, phosphatic internal mould, *M. saxbii* assemblage fauna, Popple Bed, Mere (Wilts.); identified by L. F. Spath.

Fig. 7. *Desmoceras* sp. GSM Zb1293, phosphatic internal mould, Lower Cenomanian Glauconitic Marl, Melbury Down, near Shaftesbury (Dorset).

Explanation of Plate 11

Fig. 1. *Austiniceras austeni* (Sharpe). Lectotype, BMNH C3382, composite internal mould, Lower Chalk, Guildford (Surrey); figured by Sharpe 1855, pl. 12, figs. 1*a*, *b*. Reduced; actual diameter 410 mm; (BMNH photograph).

Explanation of Plate 12

Figs. 1*a*, *b*. *Austiniceras austeni* (Sharpe). Ventral and apertural views of lectotype, BMNH C3382, composite internal mould, Lower Chalk, Guildford (Surrey); figured by Sharpe 1855, pl. 12, figs. 1*a*, *b*. Reduced; actual diameter 410 mm; (BMNH photographs).

Explanation of Plate 13

All figures natural size.

Figs. 1, 2. *Austiniceras dibleyi* Spath. 1, BMNH C52616, Cenomanian/Turonian, Salinas, Angola; the specimen retains its test. 2, BMNH C10618, composite internal mould, 'basal *subglobosus* zone', Bluebell Hill, Burnham (Kent), probably of high Middle Cenomanian age.

Figs. 3*a–c*. *Puzosia* (*Puzosia*) *octosulcata* (Sharpe). Lectotype, GSM Geol. Soc. 7761, composite internal mould, from 'the Grey Chalk of Ventnor', Isle of Wight; figured by Sharpe 1857, pl. 19, figs. 3*a*, *b*; probably of Lower Cenomanian age; (I.G.S. photographs).

Explanation of Plate 14

All figures natural size, except figs. 2*a*, *b*.

Figs. 1*a*, *b*, 2*a*, *b*, 3. *Puzosia* (*Puzosia*) *octosulcata* (Sharpe). 1*a*, *b*, BMNH 37275, composite internal mould from Ventnor, Isle of Wight. 2*a*, *b*, same, enlarged ×2. 3, BMNH C76368, phosphatic internal mould, *T. acutus* assemblage fauna, Chalk Basement Bed, Beaminster Down, Beaminster (Dorset).

Fig. 4. *Austiniceras dibleyi* Spath. Holotype, BMNH C10618 (Dibley Collection), *H. subglobosus* Zone, Lower Chalk, Betchworth (Surrey).

Figs. 5, 7*a*, *b*. *Puzosia* (*Puzosia*) cf. *crebrisulcata* Kossmat. 5, BMNH C76395, phosphatic specimen, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset). 7*a*, *b*, SMC B241, Chalk Marl, Ventnor, Isle of Wight.

Fig. 6. *Puzosia* (*Puzosia*) *sharpei* Spath. GSM 31551, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Bonchurch, Isle of Wight; mentioned and determined by Spath 1923, p. 47.

Explanation of Plate 15

All figures natural size.

Figs. 1, 3*a–c*. *Hyphoplites curvatus* (Mantell). 1, Photograph of cast of paralectotype of *H. arausionensis* (Hébert and Munier-Chalmas), figured by Hébert and Munier-Chalmas 1875, pl. 4, fig. 4; Cenomanian, Uchaux, France; in collections of the Sorbonne, Paris, unregistered. 3*a–c*, Holotype, BMNH 5739, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by Mantell 1822, pl. 19, fig. 18; (BMNH photographs).

Figs. 2*a*, *b*. *Hyphoplites falcatus falcatus* (Mantell). Lectotype, BMNH 5737, composite internal mould, Lower Chalk, Middleham, near Lewes (Sussex); figured by Mantell 1822, pl. 21, fig. 6.

Fig. 4. *Hyphoplites arausionensis arausionensis* (Hébert and Munier-Chalmas). Photograph of cast of lectotype figured by Hébert and Munier-Chalmas 1875, pl. 4, fig. 5; Cenomanian, Uchaux, France; in collections of the Sorbonne, Paris, unregistered.

Figs. 5, 6*a*, *b*. *Forbesiceras sculptum* Crick. 5, Holotype of *F. nodosum* Crick, BMNH C18172; 6*a*, *b*, BMNH C18171, holotype of *F. sculptum* Crick; both specimens from the Middle Cenomanian, False Bay, Zululand.

Explanation of Plate 16

All figures natural size.

Figs. 1*a–c*, 2*a*, *b*. *Forbesiceras sculptum* Crick. 1*a–c*, SMC B35276, composite internal mould, Chalk Marl, Ventnor, Isle of Wight; this specimen, although poorly preserved, serves as a link between the holotype of *F. nodosum* (Pl. 15, fig. 5) and that of *F. sculptum* (Pl. 15, figs. 6*a*, *b*). 2*a*, *b*, BMNH C431, *M. saxbii* assemblage fauna, Bed A_2, Cenomanian Limestone, Chardstock (Devon).

Fig. 3. *Forbesiceras obtectum* (Sharpe). SMC B62796, composite internal mould, showing the rursiradiate ribbing on the outer part of the flank typical of adults of this species; Chalk Marl, Ventnor, Isle of Wight.

Explanation of Plate 17

All figures natural size.

Figs. 1*a*, *b*. *Stoliczkaia* cf. *rhamnonotus* (Seeley). WW 24473, phosphatic internal mould, *dispar-perinflatum* Subzone ammonite bed, Durdle Cove (Dorset).

Figs. 2*a*, *b*. *Tarrantoceras?* sp. JMH CC329, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Figs. 3*a*, *b*, 8*a–d*. '*Submantelliceras*' spp. 3*a*, *b*, BMNH C9733; 8*a–d*, BMNH 88719; both are phosphatic internal moulds, Lower Cenomanian, Warminster (Wilts.); mentioned by Spath 1923*b*, p. 145.

Fig. 4. *Acanthoceras aumalense* (Coquand), a copy of Pervinquière 1910, pl. 4, fig. 11, cited by Spath (1923*b*) as type of the genus *Submantelliceras*.

Figs. 5*a–c*. *Stoliczkaia* cf. *dispar* (d'Orbigny). WW 23138, phosphatic internal mould, *dispar-perinflatum* Subzone ammonite bed, White Nothe (Dorset).

Figs. 6*a*, *b*. *Stoliczkaia* sp. juv., cf. *rhamnonotus* (Seeley). WW 4854, phosphatic internal mould, *dispar-perinflatum* Subzone ammonite bed, Durdle Cove (Dorset).

Figs. 7*a*, *b*. *Stoliczkaia* cf. *dorsetense* Spath. Same preservation, horizon, and locality as figs. 6*a*, *b*.

Figs. 9*a–c*, 10*a–c*. *Mantelliceras mantelli* (J. Sowerby). 9*a–c*, BMNH 50161*a*, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Bonchurch, Isle of Wight; figured by Sharpe 1857, pl. 18, fig. 7. 10*a–c*, BMNH 43940*a*, lectotype, Chalk Marl, Ringmer (Sussex); figured by J. Sowerby 1814, pl. 55, lower figure only.

Explanation of Plate 18

All figures natural size.

Figs. 1*a–c*. *Mantelliceras cantianum* Spath. Holotype, BMNH 36834, composite internal mould, Lower Chalk, Dover (Kent), probably from the lower part of the *M. mantelli* zone; figured by Sharpe 1857, pl. 18, fig. 1 as *Ammonites navicularis* Mantell.

Explanation of Plate 19

All figures natural size.

Figs. 1*a*, *b*, 2*a*–*c*. *Mantelliceras costatum* (Mantell). 1*a*, *b*, paralectotype, BMNH 5693; 2*a*–*c*, lectotype, BMNH C5028; both are composite internal moulds, probably of Lower Cenomanian age. The lectotype is labelled 'Hamsey' (near Lewes, Sussex), and bears Mantell's original label indicating that it corresponds to his pl. 21, fig. 9; the paralectotype is from Middleham, near Lewes (Sussex).

Explanation of Plate 20

All figures natural size.

Figs. 1*a–c*. *Mantelliceras cantianum* Spath. BMNH C5027, composite internal mould, Lower Chalk, near Lewes (Sussex); figured by Sharpe 1857, pl. 18, fig. 2.

Fig. 2. *Mantelliceras* aff. *mantelli* (J. Sowerby). BMNH C76446, phosphatic internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Gore Cliff, Isle of Wight.

Figs. 3*a–c*. *Mantelliceras dixoni* Spath. Holotype, BMNH 33630, composite internal mould, Lower Chalk, Sussex; figured by J. de C. Sowerby *in* Dixon 1850, pl. 29, fig. 15.

Figs. 4, 5. *Mantelliceras* gr. *dixoni* Spath. 4, BMNH C76411, composite internal mould, *M.* gr. *dixoni* assemblage fauna, Band 4*a*, Lower Chalk, Abbotscliff, Folkestone (Kent). 5, BMNH C13535, composite internal mould, Lower Chalk, Burham (Kent); mentioned by Spath 1926*b*, p. 431, as *Metacalycoceras guerangeri* Spath.

Fig. 6. *Mantelliceras tenue* Spath. BMNH C76457, composite internal mould, ?*M. saxbii* assemblage fauna, Band J, Lower Chalk, Novington Farm, Plumpton (Sussex).

Explanation of Plate 21

All figures natural size.

Fig. 1. *Mantelliceras lymense* (Spath). BMNH C76412, composite internal mould, *M.* gr. *dixoni* assemblage fauna, Band 4*a*, Lower Chalk, Abbotscliff, Folkestone (Kent).

Figs. 2, 4. *Mantelliceras* aff. *souaillonense* (Renz). 2, BMNH C76413; 4, BMNH C76414; preservation, horizon, and locality as for fig. 1.

Figs. 3, 5*a*, *b*. *Mantelliceras* gr. *dixoni* Spath. 3, BMNH C76415; 5*a*, *b*, BMNH C76416; preservation, horizon, and locality as for fig. 1.

Explanation of Plate 22

All figures natural size.

Figs. 1*a–c*. *Mantelliceras* aff. *souaillonense* (Renz). BMNH C76417, composite internal mould, *M*. gr. *dixoni* assemblage fauna, Band 4*a*, Lower Chalk, Abbotscliff, Folkestone (Kent).

Figs. 2*a–c*. *Mantelliceras* gr. *dixoni* Spath. BMNH C76418; preservation, horizon, and locality as for fig. 1.

Explanation of Plate 23

All figures natural size.

Figs. 1*a*, *b*. *Mantelliceras lymense* (Spath). BMNH C8002*a*, internal mould, Cenomanian Limestone, Whitelands, Pinhay Bay (south Devon); matrix suggests the specimen is from Bed B; mentioned by Spath 1926*b*, pp. 427, 431.

Figs. 2*a*, *b*. *Mantelliceras* aff. *mantelli* (J. Sowerby). BMNH C76464, composite internal mould, *H. carcitanensis* assemblage fauna, Glauconitic Marl (Band 1*b*), Eastbourne (Sussex).

Fig. 3. *Mantelliceras tenue* Spath. BMNH C76447, crushed composite internal mould, unphosphatized *M. saxbii* assemblage fauna, phosphate bed above the Glauconitic Marl, Woody Point, Isle of Wight.

Figs. 4*a–c*. *Calycoceras gentoni* (Brongniart). Photograph of a cast of the 'cotype' from the Cenomanian of Westphalia, figured by R. Douvillé 1911, figs. C1–4. In Sorbonne collections, Paris; unregistered. The original is an internal mould.

Explanation of Plate 24

All figures natural size.

Fig. 1. *Mantelliceras costatum* (Mantell). BMNH C76455, internal mould, *M. saxbii* assemblage fauna, basement bed of the Wilmington Sands, Hutchin's (Waterworks) Pit, Wilmington (south Devon).

Figs. 2*a*, *b*, 3, 5*a*, *b*, 7. *Mantelliceras tuberculatum* (Mantell). 2*a*, *b*, BMNH C76450; 5*a*, *b*, BMNH C76451; 7, BMNH C76452; all are phosphatic internal moulds, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Rocken End, Isle of Wight. 3, BMNH C76442, composite internal mould, *M. saxbii* assemblage fauna, Band 3, Lower Chalk, Gore Cliff, Isle of Wight.

Fig. 4. *Mantelliceras* aff. *tuberculatum* (Mantell). BMNH C76449, slightly less spinose internal mould, phosphatic *H. carcitanensis* assemblage fauna, Glauconitic Marl, Ventnor, Isle of Wight.

Fig. 6. *Mantelliceras* sp., between *mantelli* (J. Sowerby) and *tuberculatum* (Mantell). BMNH C76453, same horizon and locality as for figs. 2, 5, 7.

Explanation of Plate 25

All figures natural size.

Figs. 1*a–c*. *Mantelliceras tuberculatum* (Mantell). Lectotype, BMNH 32542, composite internal mould, probably from the *M. mantelli* zone, Lower Chalk, Lewes (Sussex).

Fig. 2. *Sharpeiceras florencae* Spath. GSM 100738, composite internal mould, probably from the *M. mantelli* Zone, Lower Chalk, Ringmer (Sussex).

Explanation of Plate 26

All figures natural size.

Figs. 1, 5. *Mantelliceras cantianum* Spath. 1, OUM K1274, Lower Chalk, Ringmer (Sussex); probably of *M. mantelli* Zone age. 5, BMNH C76460, *H. carcitanensis* fauna, Lower Chalk, near Upper Beeding (Sussex); both specimens are composite internal moulds.

Figs. 2*a–c*. *Mantelliceras ventnorense* Diener. GSM Geol. Soc. 7759, composite internal mould, Lower Chalk, Ventnor, Isle of Wight; figured by Sharpe 1857, pl. 23, figs. 6*a–c* as *Ammonites feraudianus*.

Fig. 3. *Acompsoceras sarthense* (Guéranger). Ventral view of specimen in Plate 29, figs. 1*a–c*; (I.G.S. photograph).

Fig. 4. *Acompsoceras* sp. BMNH C76465, composite internal mould, lower part of *A. rhotomagense* Zone, Lower Chalk, Eastbourne (Sussex).

Explanation of Plate 27

All figures natural size.

Figs. 1*a–c*. *Sharpeiceras laticlavium* (Sharpe). Holotype, GSM Geol. Soc. 7755, composite internal mould, Lower Chalk (probably *M. mantelli* Zone), Bonchurch, Isle of Wight; figured by Sharpe 1855, pl. 14, figs. 1*a*, *b*; (I.G.S. photograph).

Explanation of Plate 28

Fig. 1. *Sharpeiceras laticlavium* (Sharpe). BMNH C76466, composite internal mould of an adult specimen, *H. carcitanensis* assemblage fauna, Glauconitic Marl, Head Ledge, Eastbourne (Sussex); reduced, actual diameter 380 mm.

Explanation of Plate 29

All figures natural size.

Figs. 1*a–c*. *Acompsoceras sarthense* (Guéranger). GSM Geol. Soc. 7757, holotype of *Pseudacompsoceras vectense* Spath, figured by Sharpe 1857, pl. 19, figs. 1*a–c*, as *Ammonites coupei* var.; composite internal mould, Lower Chalk, Ventnor, Isle of Wight; (I.G.S. photograph). See also Plate 26, fig. 3.

Explanation of Plate 30

All figures natural size.

Figs. 1*a–c*. *Acompsoceras renevieri* (Sharpe). Lectotype, GSM Geol. Soc. 7753, composite internal mould, Lower Chalk, near Blackdown, Isle of Wight; figured by Sharpe 1857, pl. 20, figs. 2*a–c*; (I.G.S. photograph).

Explanation of Plate 31

All figures natural size.

Figs. 1*a–c*. *Protacanthoceras bunburianum* (Sharpe). Holotype, BMNH 50155; figured by Sharpe 1853, pl. 9, figs. 3*a–c*; phosphatic internal mould, said to be from Chardstock (Devon); probably from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone (see p. 98).

Fig. 2. *Acompsoceras* aff. *essendiense* (Schlüter). BMNH C76419, composite internal mould, *M.* gr. *dixoni* assemblage fauna, Band 4*a*, Lower Chalk, Abbotscliff, Folkestone (Kent).

Explanation of Plate 32

All figures natural size, except fig. 2*d*.

Figs. 1*a–d*. *Paracalycoceras wiestii* (Sharpe). WW 3556, internal mould, *M. saxbii* assemblage fauna, Bed A_2, Cenomanian Limestone, White Cliff, Seaton (south Devon).

Figs. 2*a–d*. *Protacanthoceras compressum* (Jukes-Browne). Lectotype, GSM 53484, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Devon coast; figured by Jukes-Browne *in* Jukes-Browne and Hill 1896, pl. 5, figs. 4, 4*a*. 2*d*, magnified $\times 2$, to show the suture; (I.G.S. photographs).

Figs. 3*a–c*, 4*a–c*. *Protacanthoceras* aff. *compressum* (Jukes-Browne). 3*a–c*, GSM 53482; 4*a–c*, GSM 53483; both paralectotypes, internal moulds, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Devon coast; figured by Jukes-Browne *in* Jukes-Browne and Hill 1896, pl. 5, figs. 2, 3*a*; (I.G.S. photographs).

Explanation of Plate 33

Figs. 1*a*, *b*. *Calycoceras naviculare* (Mantell). Holotype, BMNH 5681, composite internal mould, figured by Mantell 1822, pl. 22, fig. 5, and said to be from the Upper Chalk of Offham (Sussex); probably from the top of the Lower or base of the Middle Chalk; slightly reduced, maximum length 149 mm.

Explanation of Plate 34

Both figures natural size.

Figs. 1*a*, *b*. *Calycoceras naviculare* (Mantell). WW 22431, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Humble Point (south Devon).

Explanation of Plate 35

Both figures natural size.

Figs. 1, 2. *Calycoceras naviculare* (Mantell). 1, apertural view of WW 22431 (see Pl. 34); 2, WW 22432; both internal moulds, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Humble Point (south Devon).

Explanation of Plate 36

All figures natural size.

Figs. 1, 2*a–c*, 3*a–c*, 4. *Calycoceras naviculare* (Mantell). 1, SMC B76783, composite internal mould, uppermost Lower Chalk or basal *plenus* Marls, Betchworth (Surrey). 2*a–c*, WW 22650; 3*a–c*, WW 19217; 4, WW 22657; all internal moulds, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Humble Point (south Devon).

Explanation of Plate 37

All figures natural size, except fig. 3.

Figs. 1*a*, *b*, 2, 3. *Calycoceras naviculare* (Mantell). 1*a*, *b*, WW 20662 (part of inner whorl only); 2, WW 19159; 3, apertural view of WW 22438 (see Pl. 47, figs. 5*a*, *b*), ×1·2; all internal moulds, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Humble Point (south Devon).

Figs. 4*a–c*. *Calycoceras* (*Lotzeites*) *aberrans* (Kossmat). WW 19797, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Humble Point (south Devon).

Explanation of Plate 38

All figures natural size.

Figs. 1*a*, *b*, 2*a*, *b*. *Calycoceras bathyomphalum* (Kossmat). 1*a*, *b*, BMNH C76396; 2*a*, *b*, BMNH C76397; both phosphatic internal moulds retaining traces of test, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Figs. 3, 4*a*, *b*. *Calycoceras* aff. *newboldi spinosum* (Kossmat). 3, BMNH C76375; 4*a*, *b*, BMNH C76376; both phosphatic internal moulds, basal *C. naviculare* Zone fauna, Chalk Basement, Askerswell (Dorset).

Figs. 5*a*, *b*. *Calycoceras* aff. *choffati* (Kossmat). BMNH C76456, crushed composite internal mould, *A. jukes-brownei* assemblage fauna, Lower Chalk, Glynde (Sussex).

Explanation of Plate 39

All figures natural size.

Figs. 1*a–c*, 3*a–c*. *Calycoceras* aff. *choffati* (Kossmat). 1*a–c*, BMNH C76389, internal mould, *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Storridge Hill, Chardstock, on the Devon/Somerset border. 3*a–c*, BMNH C18216, Middle Cenomanian, False Bay, Zululand; figured by Crick 1907, pl. 12, figs. 5, 5*a* as *Acanthoceras choffati* Kossmat; the specimen retains recrystallized test.

Figs. 2*a–c*. *Calycoceras* aff. *newboldi newboldi* (Kossmat). BMNH 37574, phosphatic internal mould, *A. rhotomagense* Zone fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset); mentioned by Kossmat 1897, p. 113.

Explanation of Plate 40

All figures natural size.

Figs. 1*a*, *b*. *Calycoceras gentoni* (Brongniart). Photograph of a cast of the 'holotype', phosphatic internal mould, *T. costatus* assemblage fauna, Craie Chloritée, Rouen, France; figured by Brogniart 1822, pl. 6, fig. 6, and R. Douvillé 1911, figs. H_1–H_4.

Figs. 2*a*, *b*. *Calycoceras newboldi newboldi* (Kossmat). WW 24800 (ex author's collection), phosphatic internal mould, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Fig. 3. *Calycoceras* aff. *newboldi spinosum* (Kossmat). BMNH C76385, phosphatic internal mould, *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, White Nothe (Dorset).

Fig. 4. *Calycoceras paucinodatum* (Crick). BMNH C76369, phosphatic internal mould of medium-sized specimen, *T. acutus* assemblage fauna, Chalk Basement Bed, Beaminster Down, near Beaminster (Dorset).

Fig. 5. *Acanthoceras tunetana* Pervinquière. JMH CC168, phosphatic internal mould retaining traces of test, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowden Hill, Chard (Somerset).

Explanation of Plate 41

All figures natural size.

Figs. 1*a*, *b*, 2*a*, *b*. *Calycoceras newboldi planecostata* (Kossmat). 1*a*, *b*, BMNH C76382; 2*a*, *b*, BMNH C76383; both partly phosphatic internal moulds, *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Bincombe (Dorset).

Fig. 3. *Calycoceras paucinodatum* (Crick). Ventral view of BMNH C76370, phosphatic specimen, *T. acutus* assemblage fauna, Chalk Basement Bed, Beaminster Down, Beaminster (Dorset). This specimen bears strong umbilical and lower lateral tubercles, and is thus transitional towards *Calycoceras bathyomphalum* (Kossmat).

Explanation of Plate 42

All figures natural size.

Fig. 1. *Calycoceras newboldi spinosum* (Kossmat). OUM KY310, topotype retaining traces of test, Utatur Group, Southern India.

Fig. 2. *Hypoturrilites tuberculatus* (Bosc). BMNH C76461, composite internal mould of specimen retaining the aperture, *H. carcitanensis* assemblage fauna, Lower Chalk, near Upper Beeding (Sussex).

Fig. 3. *Calycoceras* cf. *boulei* Collignon. BMNH C76384, partly phosphatized internal mould of body chamber, *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Bincombe (Dorset).

Figs. 4*a*, *b*. *Calycoceras* aff. *newboldi ankomakaensis* Collignon. BMNH C76377, phosphatic internal mould, basal *C. naviculare* Zone fauna, Chalk Basement Bed, Askerswell (Dorset).

Explanation of Plate 43

All figures natural size.

Fig. 1. *Euomphaloceras euomphalum* (Sharpe). Apertural view of GSM 36933, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Figs. 2, 4*a*, *b*. *Calycoceras paucinodatum* (Crick). 2, BMNH C76398, phosphatic specimen of densely ribbed variant of this species; strong umbilical tubercles are retained throughout; *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset). 4*a*, *b*, BMNH C76400, medium-sized phosphatic specimen of compressed, distantly ribbed variant of this species; horizon and locality as for fig. 2.

Figs. 3, 5. *Calycoceras newboldi spinosum* (Kossmat). 3, BMNH C76399; 5, BMNH C76401; both are phosphatized; *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Explanation of Plate 44

All figures natural size.

Fig. 1*a–c*, 2*a–c*. *Calycoceras paucinodatum* (Crick). 1*a–c*, BMNH 50287, holotype of *Calycoceras subgentoni* (Spath); phosphatic specimen from the *A. rhotomagense* Zone fauna, Chalk Basement Bed, Storridge Hill, Chardstock, on the Somerset/Devon border. 2*a–c*, BMNH C18214, holotype of *C. paucinodatum*, Middle Cenomanian, False Bay, Zululand; figured by Crick 1907, pl. 13, figs. 3, 3*a*.

Figs. 3*a–c*. *Calycoceras nitidum* (Crick). Holotype, BMNH C18211, Middle Cenomanian, False Bay, Zululand; figured by Crick 1907, pl. 12, figs. 4, 4*a*.

Explanation of Plate 45

All figures natural size.

Figs. 1, 2, 3*a*, *b*. *Calycoceras paucinodatum* (Crick). 1, BMNH C76402, distantly ribbed, evolute variant; phosphatic internal mould; the last third of the outer whorl is body chamber. 2, BMNH C76403, phosphatized closely ribbed form, retaining the test. Both from the *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset). 3*a*, *b*, BMNH 76475, phosphatic internal mould of finely ribbed, fat-sided variant, *T. acutus* assemblage fauna, Chalk Basement Bed, Toller Porcorum, near Maiden Newton (Dorset).

Figs. 4*a*, *b*. *Desmoceras* (*Desmoceras*) *latidorsatum* (Michelin). BMNH C76371, phosphatic internal mould, Chalk Basement Bed, Beaminster Down, Beaminster (Dorset); probably a remanié Lower Cenomanian specimen.

Figs. 5*a*, *b*. *Forbesiceras sculptum* Crick. GSM 88283, composite internal mould from an exposure of *M. mantelli* Zone, Lower Chalk, north of Nansen Hill, Ventnor, Isle of Wight; this specimen closely resembles the type of *F. nodosum* Crick (Pl. 15, fig. 5), and links it with the specimen of *F. sculptum* figured in Pl. 16, figs. 1*a*–*c*; note the distinctive ventral ornament and occasional mid-lateral nodes.

Explanation of Plate 46

All figures natural size.

Figs. 1*a–c*, 2*a–c*. *Calycoceras paucinodatum* (Crick). 1*a–c*, BMNH C76372, phosphatic internal mould of densely ribbed variant, *T. acutus* assemblage fauna, Chalk Basement Bed, Beaminster Down, Beaminster (Dorset). 2*a–c*, BMNH C76373, spinose variant transitional towards *Calycoceras bathyomphalum* (Kossmat); phosphatic specimen, same horizon and locality as for figs. 1*a–c*.

Fig. 3. *Forbesiceras obtectum* (Sharpe). SMC B35266, phosphatic topotype specimen retaining the test, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset); note the fine growth striae and faint rursiradiate ribs on the outer part of the flank.

Explanation of Plate 47

All figures natural size.

Figs. 1*a–c*, 3*a*, *b*, 5*a*, *b*. *Calycoceras naviculare* (Mantell). 1*a–c*, WW 20662, perhaps transitional towards *C.* (*Lotzeites*) sp.; 3*a*, *b*, WW 23253; 5*a*, *b*, WW 22438 (for apertural view see Pl. 37, fig. 3); all from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Figs. 2*a*, *b*. *Calycoceras* (*Lotzeites*) *aberrans* (Kossmat). SMC B35528, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Lyme Regis (south Devon).

Figs. 4*a*, *b*. *Calycoceras* (*Lotzeites*) aff. *barruei* (Pervinquière). BMNH C76378, phosphatic internal mould, basal *C. naviculare* Zone, Chalk Basement Bed, Askerswell (Dorset).

Figs. 6*a*, *b*, 7, 8*a*, *b*. *Calycoceras paucinodatum* (Crick). 6*a*, *b*, BMNH C76374, phosphatic internal mould, basal *C. naviculare* Zone, Chalk Basement Bed, Beaminster Down, Beaminster (Dorset); 7, BMNH C76467, composite internal mould, lower part of the *A. rhotomagense* Zone (*T. acutus* or *T. costatus* assemblage), Eastbourne (Sussex); 8*a*, *b*, BMNH C76405, phosphatic specimen of compressed, sparsely ribbed variant, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Explanation of Plate 48

All figures natural size.

Figs. 1*a*, *b*, 2, 3*a*, *b*, 4*a*, *b*, 5*a*, *b*, 6*a*, *b*. *Eucalycoceras pentagonum* (Jukes-Browne). Series of specimens from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon). 1*a*, *b*, adult body chamber, JMH CC740. 2, 3*a*, *b*, 4*a*, *b*, 5*a*, *b*, 6*a*, *b*, are a series showing progressively larger diameters; 2, WW 21891; 3*a*, *b*, WW 21890; 4*a*, *b*, WW 20776; 5*a*, *b*, WW 22478; 6*a*, *b*, WW 20799.

Explanation of Plate 49

All figures natural size.

Figs. 1*a–c*. *Eucalycoceras pentagonum* (Jukes-Browne). WW 22644, medium-sized, wholly septate specimen; phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Figs. 2, 3, 4*a*, *b*, 5*a*, *b*, 6*a*, *b*, 7*a*, *b*. *Eucalycoceras rowei* (Spath). Series showing variation throughout ontogeny; 2, WW 20777; 3, WW 21891; 4*a*, *b*, WW 22663; 5*a*, *b*, WW 24801; 6*a*, *b*, WW 20774; 7*a*, *b*, WW 20644; all from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Explanation of Plate 50

All figures natural size.

Figs. 1, 2*a*, *b*. *Eucalycoceras gothicum* (Kossmat). 1, BMNH C76406, part-phosphatized internal mould, *A. jukes-brownei* assemblage fauna immediately above the Chalk Basement Bed, Snowdon Hill, Chard (Somerset). 2*a*, *b*, BMNH C76379, phosphatic fragment, basal *C. naviculare* Zone fauna, Chalk Basement Bed, Askerswell (Dorset).

Figs. 3, 4*a*, *b*, 6*a*, *b*, 7*a*, *b*. *Eucalycoceras rowei* (Spath). 3, copy of Guéranger 1867, pl. 5, fig. 1; paralectotype, Upper Cenomanian, *C. naviculare* Zone, Marne à *Ostrea biauriculata*, Sarthe; it appears to be lost (J. M. Hancock, pers. comm.); the original size is unknown. 4*a*, *b*, BMNH C76470; 6*a*, *b*, lectotype, BMNH C7285; 7*a*, *b*, WW 21889; all from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Fig. 5. *Puzosia* (*Puzosia*) *subplanulata* (Schlüter). SMC B240, composite internal mould, Lower Chalk, Ventnor, Isle of Wight; matrix suggests the specimen is from the *M. mantelli* Zone.

Explanation of Plate 51

Figs. 1*a–d*, 2*a*, *b*, 3*a–c*, 4*a–c*, 5*a*, *b*. *Acanthoceras hippocastanum* (J. de C. Sowerby). 1*a–d*, Lectotype, GSM 37667, figured by J. de C. Sowerby 1826, pl. 514, fig. 2; 2*a*, *b*, BMNH C76471; 3*a–c*, WW 21899; 4*a–c*, WW 21900; 5*a*, *b*, WW 21898; all from the phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Explanation of Plate 52

All figures natural size, except fig. 2.

Figs. 1*a*, *b*, 2, 3*a–c*. *Acanthoceras jukes-brownei* (Spath). 1*a*, *b*, Holotype, BMNH 50162, part phosphatized internal mould, *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Man o' War Cove (Dorset); figured by Sharpe 1857, pl. 17, fig. 2. 2, BMNH C76468, composite internal mould of body chamber fragment, *A. jukes-brownei* assemblage fauna, Band 10, Lower Chalk, Eastbourne (Sussex); reduced ×0·67. 3*a–c*, BMNH 76476, internal mould of a nucleus from the unphosphatized *A. jukes-brownei* assemblage fauna immediately above the Chalk Basement Bed, Beaminster Down, Beaminster (Dorset).

Explanation of Plate 53

Fig. 1. *Acanthoceras jukes-brownei* (Spath). BMNH C76454, composite internal mould of medium-sized individual, *A. jukes-brownei* assemblage fauna, Band 12, Lower Chalk, Compton Bay, Isle of Wight; slightly reduced, actual diameter 230 mm.

Explanation of Plate 54

Fig. 1. *Acanthoceras* aff. *jukes-brownei* (Spath). BMNH C76473, hypernodose specimen, phosphatic *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Furley, near Membury (south Devon); reduced, ×0·67.

Explanation of Plate 55

All figures natural size, except fig. 2.

Figs. 1*a–c*, 2. *Acanthoceras jukes-brownei* (Spath). 1*a–c*, OUM 1277, phosphatic internal mould of juvenile specimen, Chalk Basement Bed, Membury (south Devon). 2, ventral view of BMNH C76473, reduced, ×0·67; for details, see explanation of Plate 54.

Explanation of Plate 56

Both figures natural size.

Figs. 1*a*, *b*. *Acanthoceras latum* Crick. Lectotype, BMNH C18197, Middle Cenomanian, False Bay, Zululand; figured by Crick 1907, pl. 12, figs. 2, 2*a*.

Explanation of Plate 57

Figs. 1*a*, *b*. *Acanthoceras latum* Crick. BMNH C76407, partly phosphatized specimen, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset); slightly reduced.

Explanation of Plate 58

Both figures natural size.

Figs. 1*a*, *b*. *Acanthoceras whitei* Matsumoto. BMNH C76474, phosphatic *A. jukes-brownei* assemblage fauna, Chalk Basement Bed, Furley, near Membury (south Devon).

Explanation of Plate 59

All figures natural size, except figs. 2*a–c*.

Figs. 1*a*, *b*, 2*a–c*, 3*a*, *b*, 4*a–c*, 5*a*, *b*. *Euomphaloceras euomphalum* (Sharpe). 1*a*, *b*, 2*a–c*, Holotype, BMNH 50158, figured by Sharpe 1855, pl. 13, figs. 4*a–c*; this specimen is phosphatized, and is recorded by Sharpe to be from Man o' War Cove (Dorset); this locality is undoubtedly wrong, and the specimen is probably from the *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Devon coast; 2*a–c* are magnified ×2. 3*a*, *b*, BMNH C7287, figured by Crick 1899, fig. 2; 4*a–c*, BMNH C76472; 5*a*, *b*, JMH CC741; all internal moulds, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, Humble Point (south Devon).

Figs. 6*a*, *b*. *Euomphaloceras inerme* (Pervinquière). BMNH C76388, phosphatic internal mould, remanié *T. costatus* assemblage fauna, lower part of Totternhoe Stone, Houghton Regis, near Dunstable (Bedfordshire).

Figs. 7*a*, *b*. *Calycoceras* (*Lotzeites*) aff. *barruei* (Pervinquière). SMC B35529, internal mould, phosphatic *C. naviculare* Zone fauna, Bed C, Cenomanian Limestone, near Lyme Regis (Dorset).

Fig. 8. *Calycoceras* (*Lotzeites*) sp. BMNH C76380, phosphatic internal mould, basal *C. naviculare* Zone fauna, Chalk Basement Bed, Askerswell (Dorset).

Explanation of Plate 60

Both figures natural size.

Figs. 1*a*, *b*. *Euomphaloceras cunningtoni* (Sharpe). Holotype, BMNH 88704, composite internal mould, Lower Chalk, Upton Scudamore (Wilts.), probably of *T. costatus* assemblage age; figured by Sharpe 1855, pl. 15, figs. 2*a–c*. A further portion of outer whorl is not figured.

Explanation of Plate 61

All figures natural size.

Figs. 1*a*, *b*. *Euomphaloceras* aff. *inerme* (Pervinquière). BMNH 43983*b*, composite internal mould, figured by J. de C. Sowerby 1826, pl. 515, fig. 2, as *Ammonites rhotomagensis*, and referred to by Spath (1923*b*, p. 144) as *Acanthoceras sussexiense* (Mantell). The specimen bears the label 'Such with Sussex on the (Coombes)'.

Figs. 2*a*, *b*. *Euomphaloceras cunningtoni* (Sharpe). OUM K1275, composite internal mould, Lower Chalk, Sussex.

Explanation of Plate 62

Both figures natural size.

Figs. 1*a*, *b*. *Euomphaloceras inerme* (Pervinquière). BMNH C73637, composite internal mould, Lower Chalk, Sussex.

Explanation of Plate 63

All figures natural size, except fig. 1.

Fig. 1. *Euomphaloceras* sp. between *inerme* (Pervinquière) and *cunningtoni* (Sharpe). Composite internal mould, *A. rhotomagense* Zone, Lower Chalk, Newtimber, near Brighton (Sussex); H. Doust Collection; reduced, ×0·9.

Figs. 2*a*, *b*. *Scaphites obliquus* J. Sowerby. BMNH C76408, large phosphatic internal mould, *T. acutus* assemblage fauna, Chalk Basement Bed, Snowdon Hill, Chard (Somerset).

Fig. 3. *Worthoceras* sp. BMNH 88725, composite internal mould, Lower Cenomanian, Wilts.

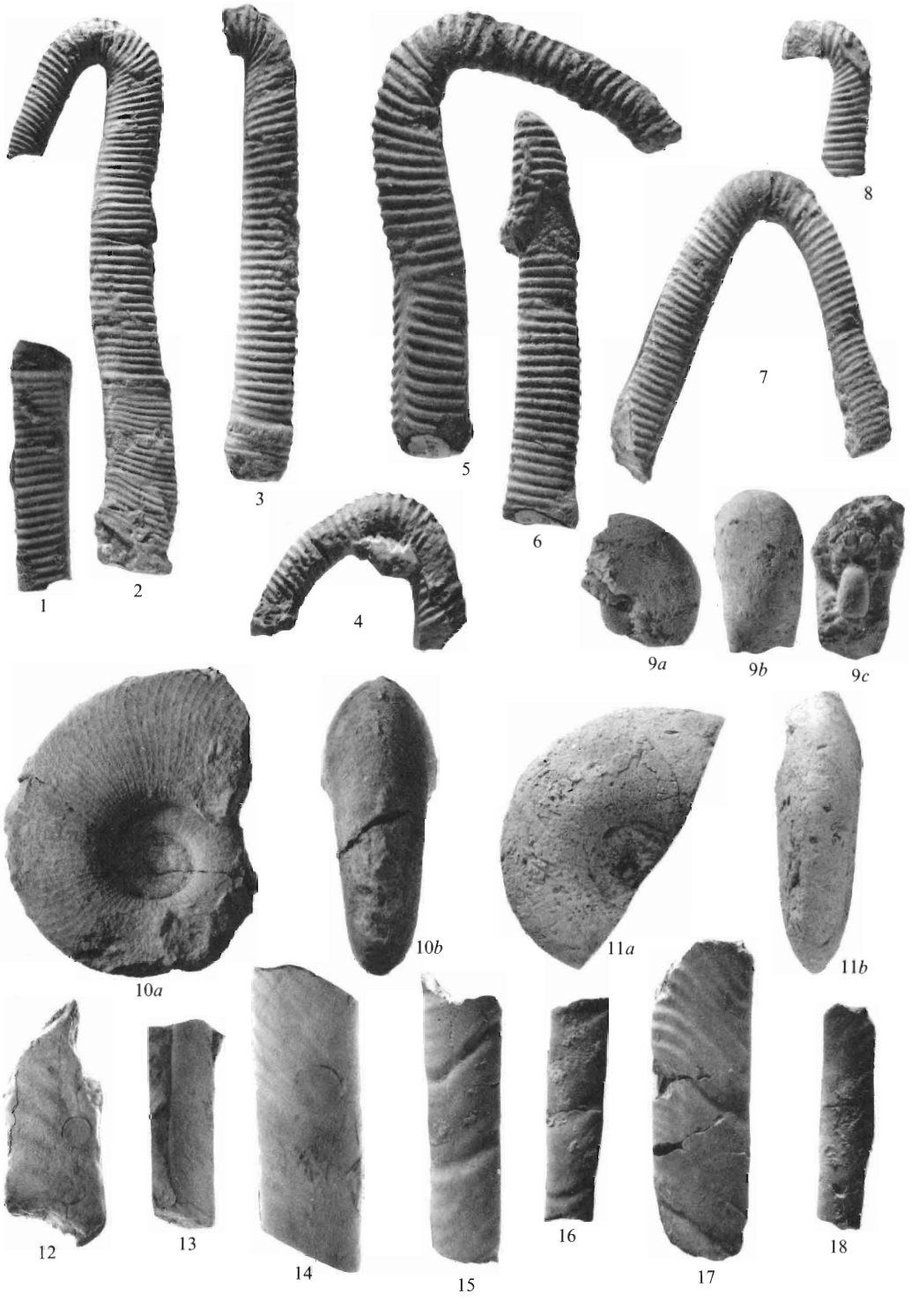
Explanation of Plate 64

All figures natural size.

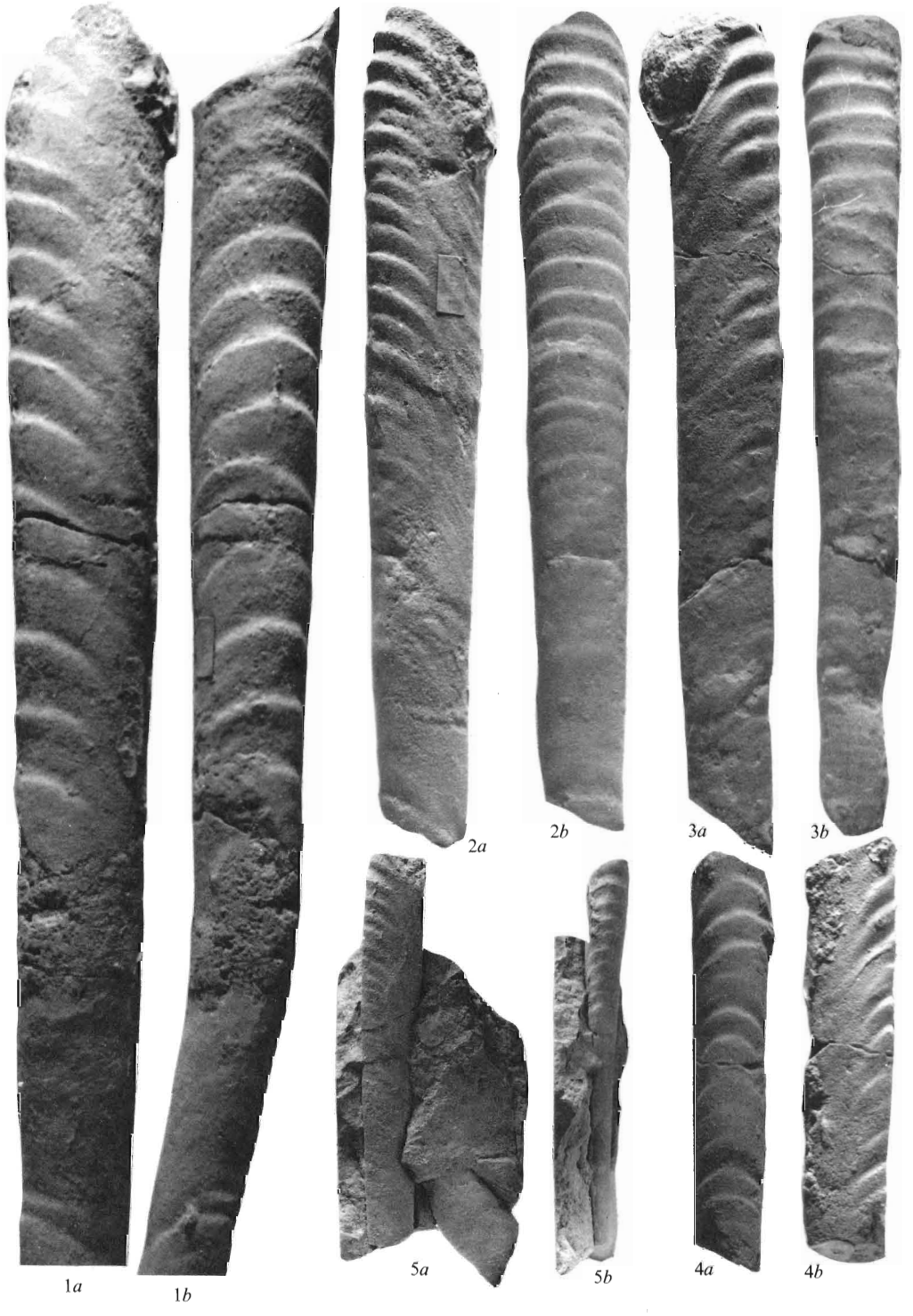
Fig. 1. *Euomphaloceras inerme* (Pervinquière). Holotype, GSM Geol. Soc. 7754, composite internal mould, Lower Chalk, Lewes (Sussex); figured by Sharpe 1855, as pl. 15, figs. 1*a–d*.

Figs. 2, 3*a*, *b*, 4. *Scaphites obliquus* J. Sowerby. 2, BMNH 4799*a*, lectotype of *Scaphites striatus* Mantell, Chalk Marl, Hamsey (Sussex); figured by Mantell 1822, pl. 22, figs. 9, 11. 3*a*, *b*, lectotype of *S. obliquus*, BMNH 43987*a*, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by J. Sowerby 1813, pl. 18, figs. 4–6. 4, BMNH C72200, paralectotype, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by J. Sowerby 1813, pl. 18, fig. 7.

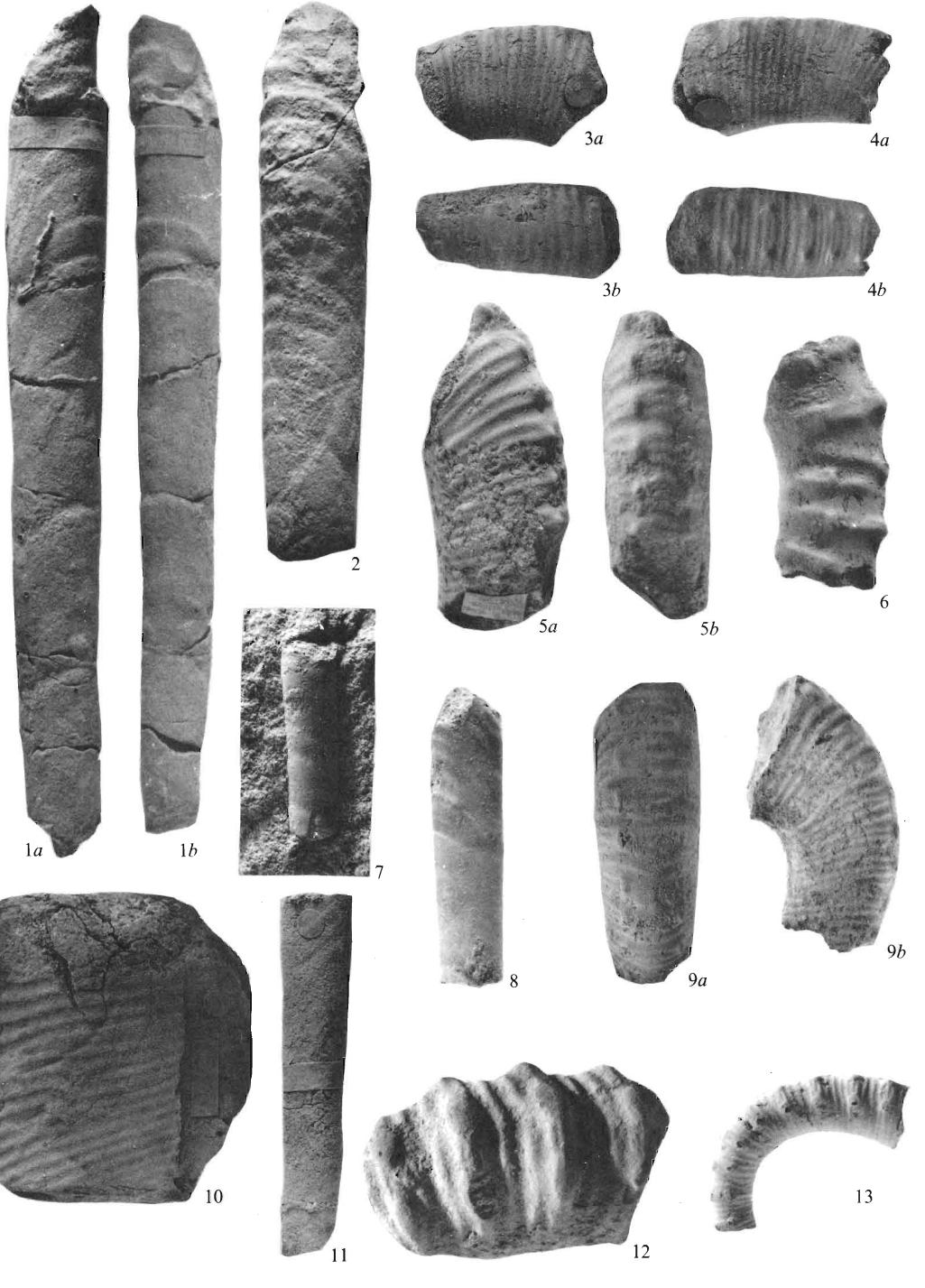
Figs. 5*a*, *b*, 6*a*, *b*. *Scaphites* (*Scaphites*) *equalis* J. Sowerby. 5*a*, *b*, Holotype, BMNH 43986, phosphatized mould, probably from the Chalk Basement Bed, south-west England; figured by J. Sowerby 1813, pl. 18, figs. 1–3. 6*a*, *b*, BMNH 4798, composite internal mould, Lower Chalk, Hamsey (Sussex); figured by Mantell 1822, pl. 22, figs. 8, 12, as *Scaphites costatus*.



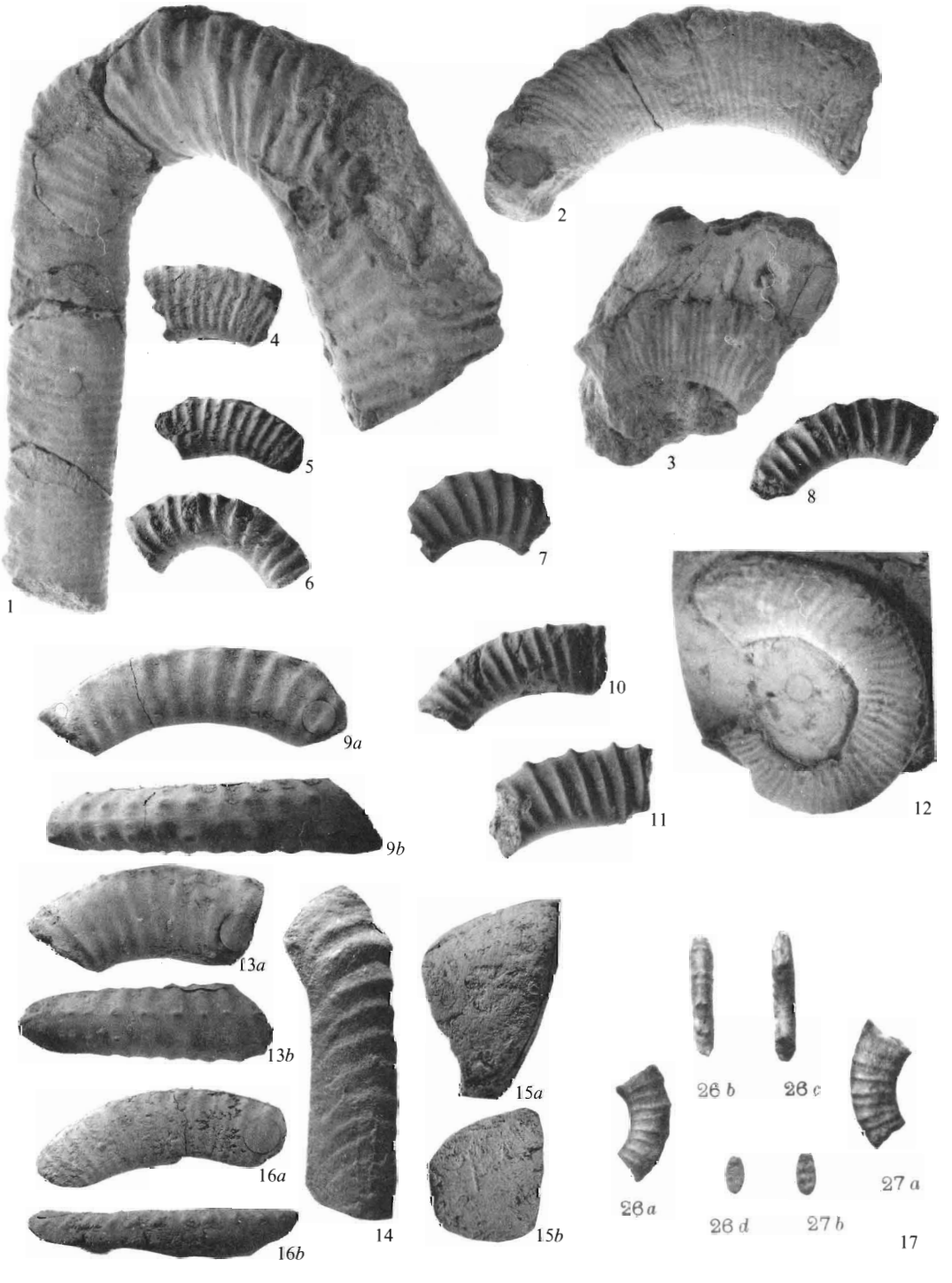
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

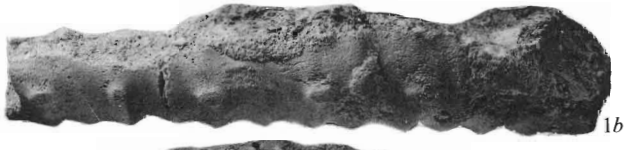


KENNEDY, Cenomanian ammonites

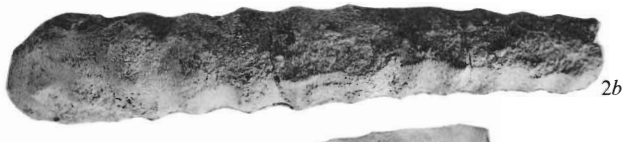


KENNEDY, Cenomanian ammonites


1*a*


1*b*


2*a*

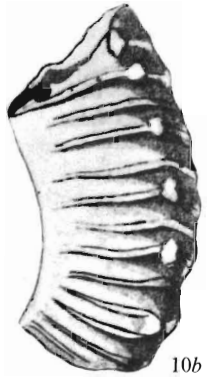

2*b*


6


7*a*


7*b*


10*a*


10*b*


3


4*a*


4*b*


5

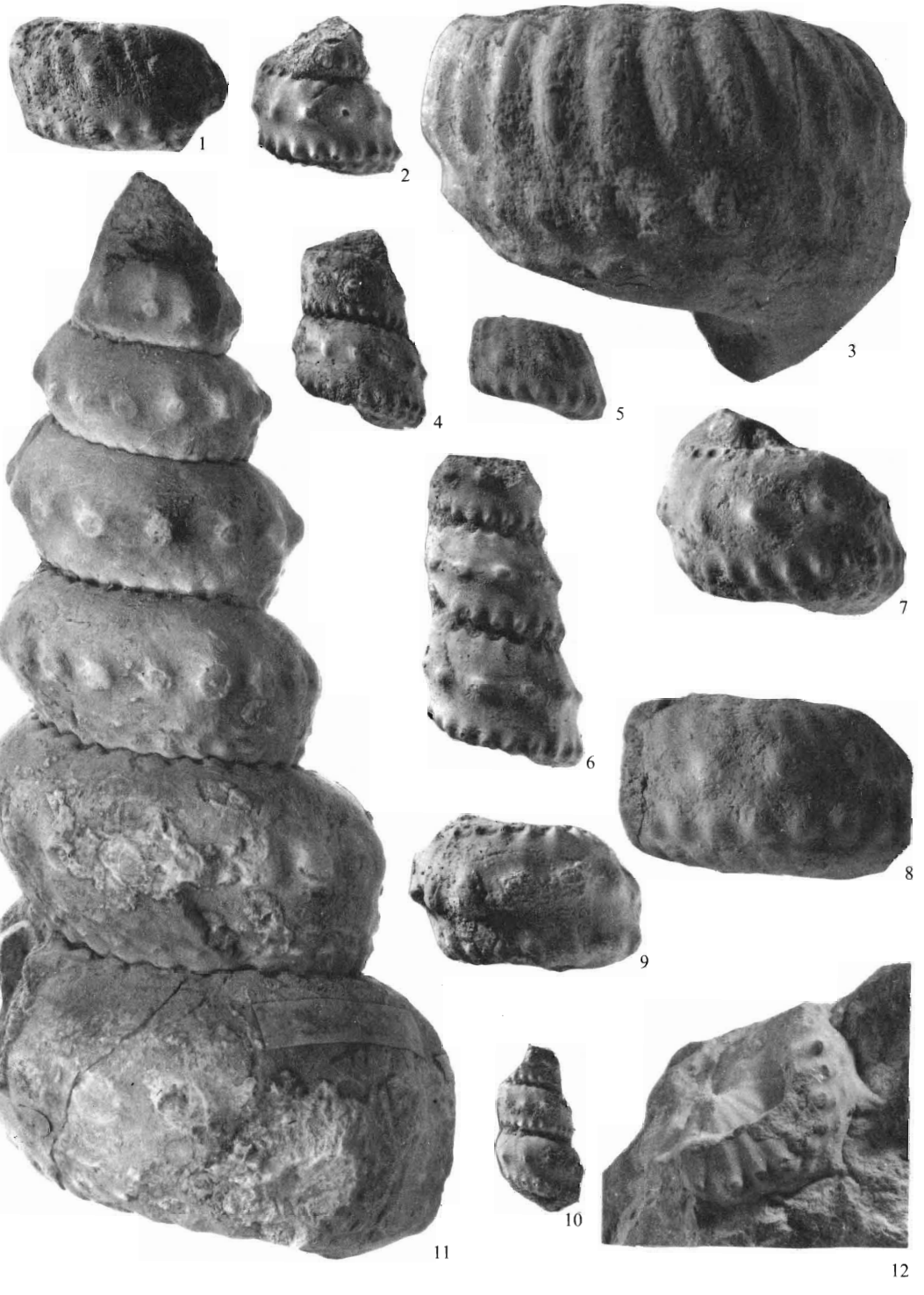

8


12


9

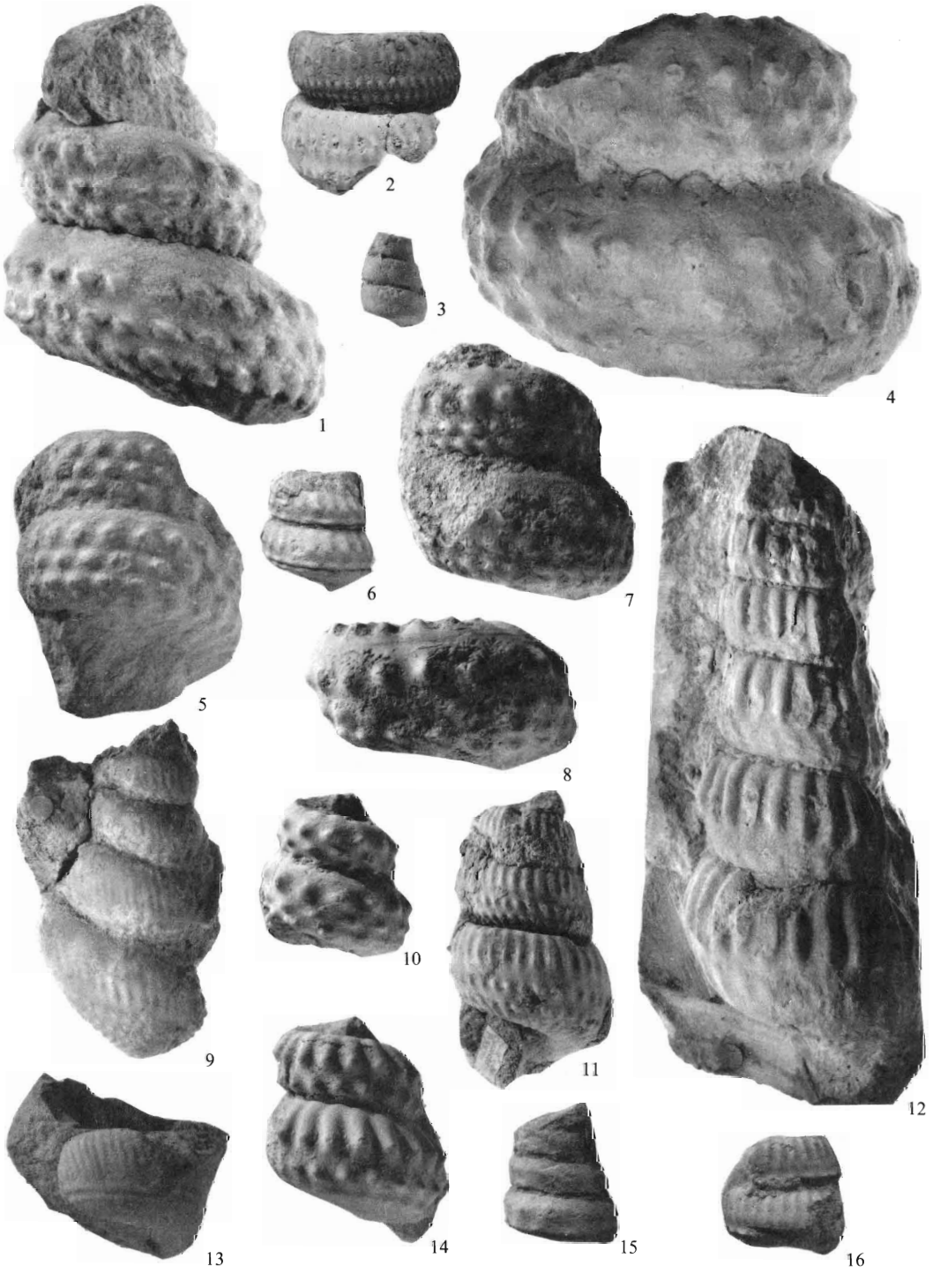

11

KENNEDY, Cenomanian ammonites

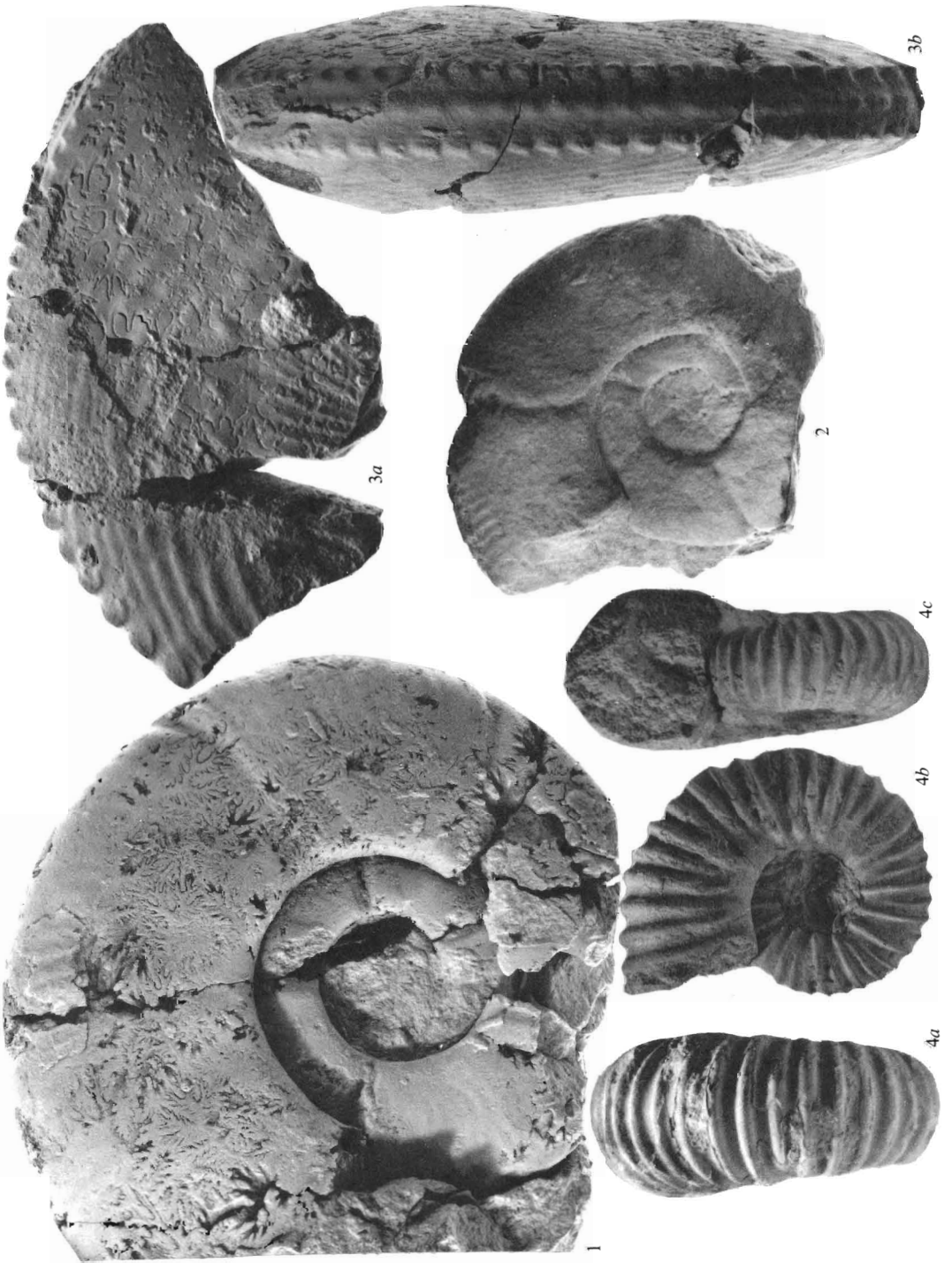


KENNEDY, Cenomanian ammonites

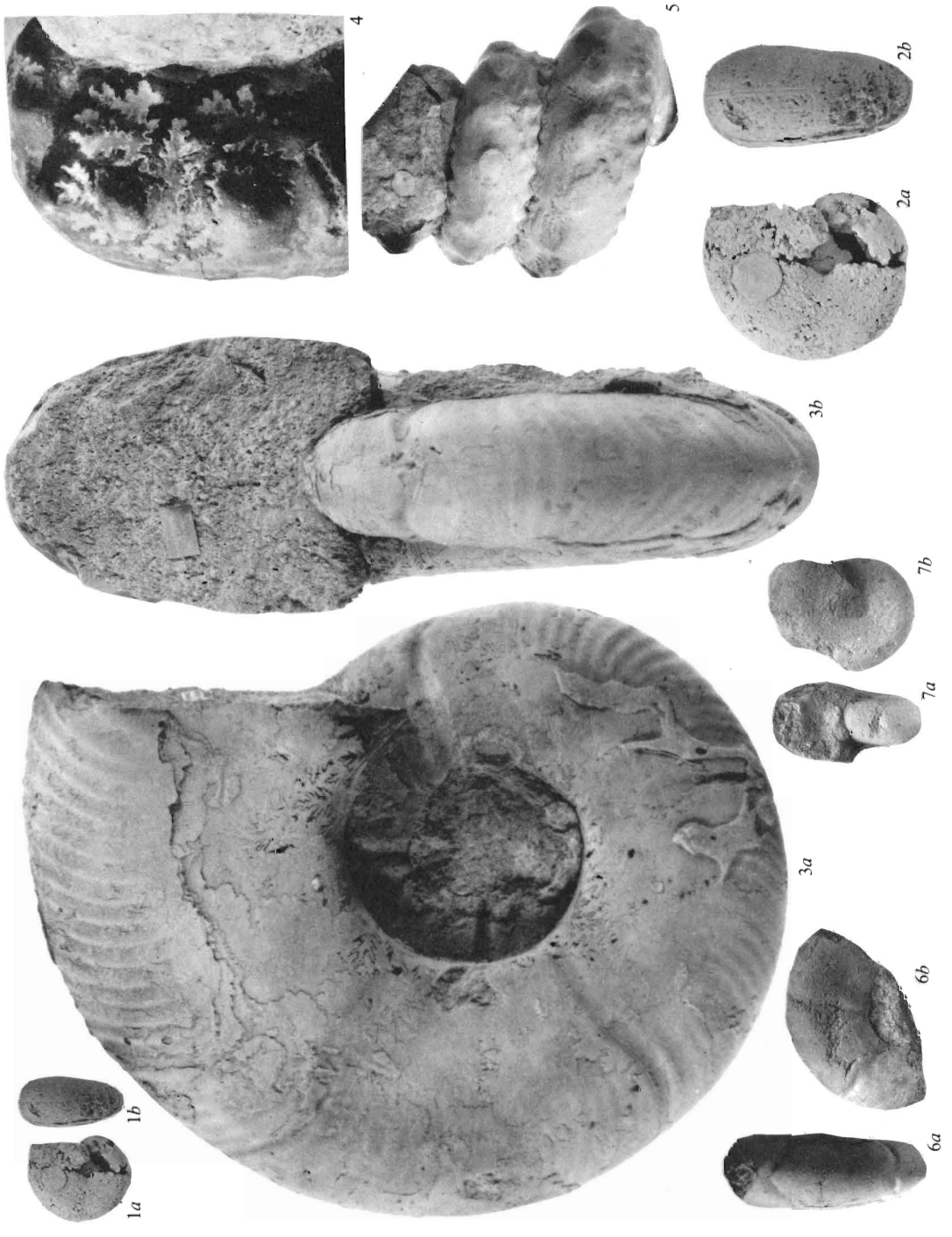
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

1

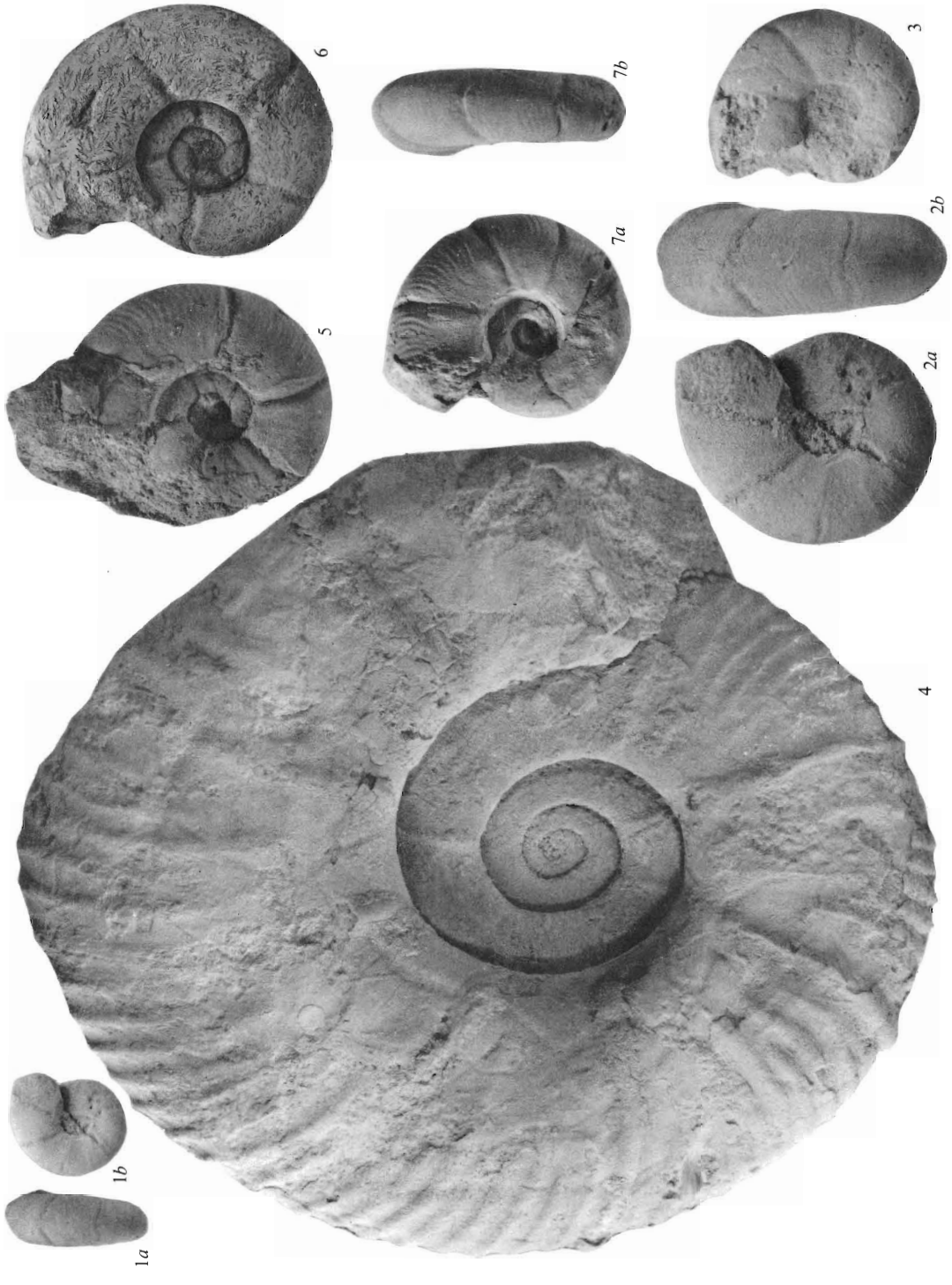
KENNEDY, Cenomanian ammonites

1*a*

1*b*

KENNEDY, Cenomanian ammonites

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites


1


2*a*


2*b*


3*a*


3*b*


3*c*

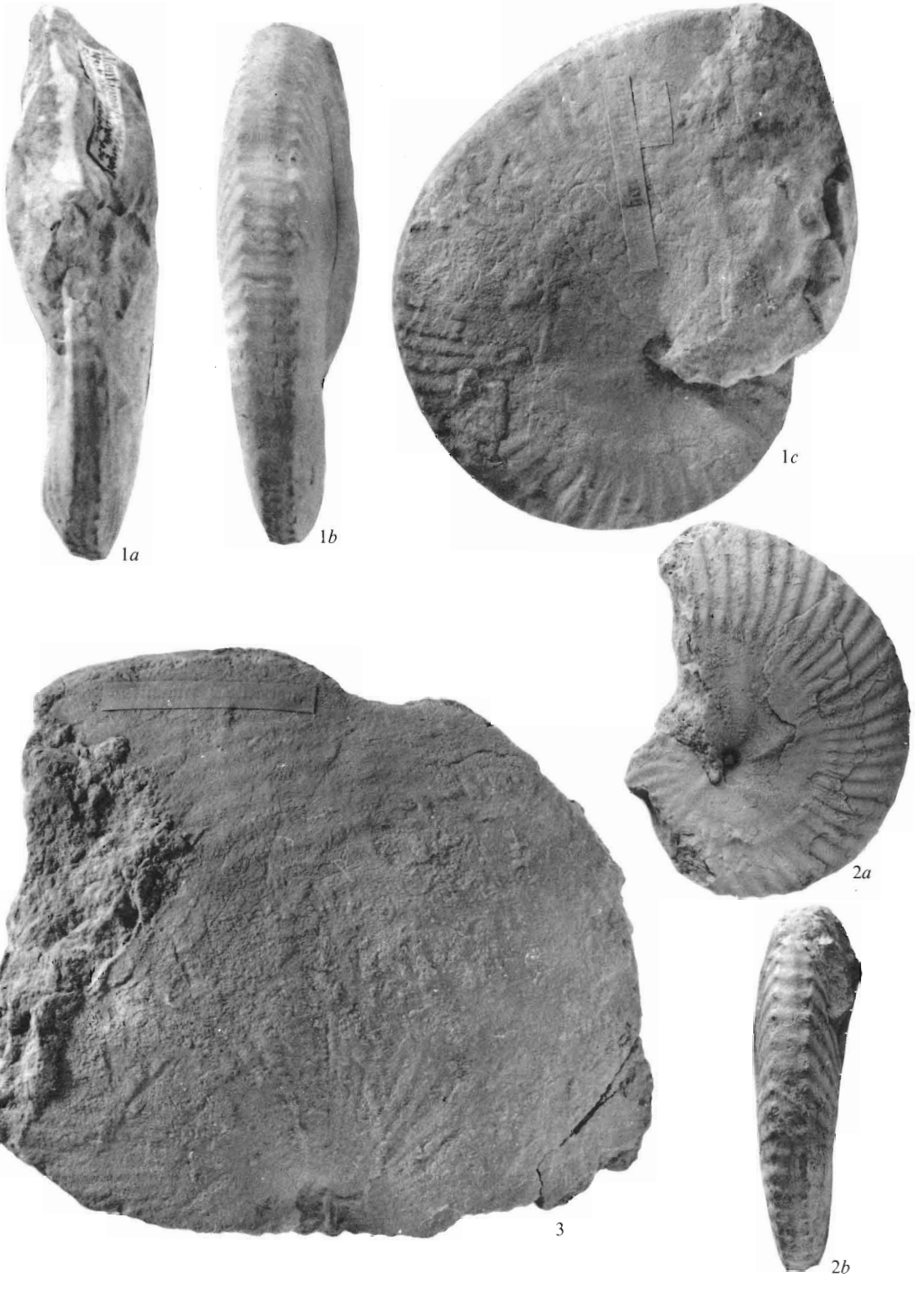

4


5


6*a*


6*b*

KENNEDY, Cenomanian ammonites



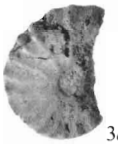
KENNEDY, Cenomanian ammonites


1*a*


1*b*


2*a*

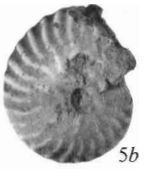

2*b*


3*a*


3*b*


4


5*a*


5*b*


5*c*


6*a*


6*b*


7*a*


7*b*


9*a*


9*b*


9*c*


8*a*


8*b*


8*c*

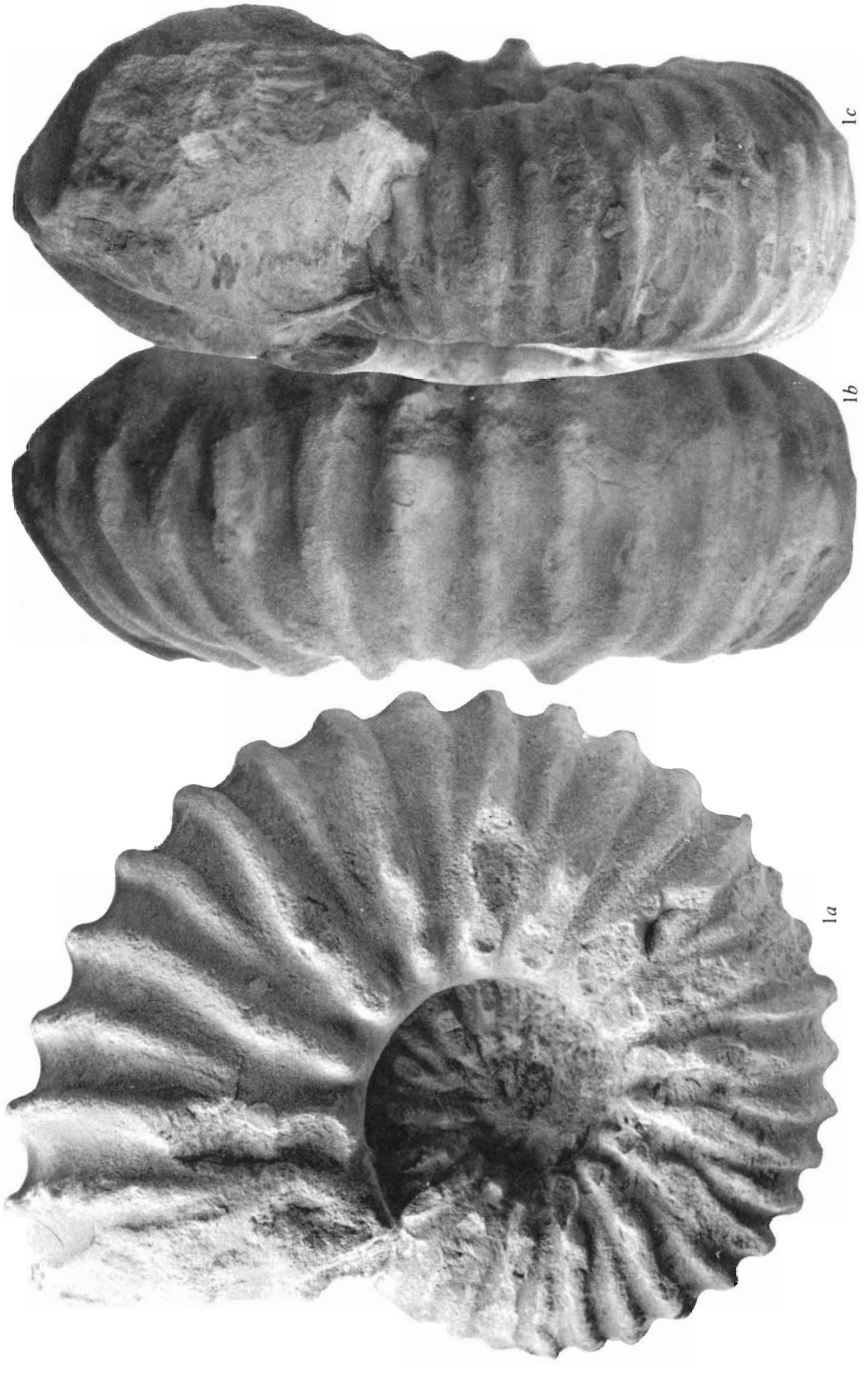

8*d*


10*a*


10*b*


10*c*

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

1*a*

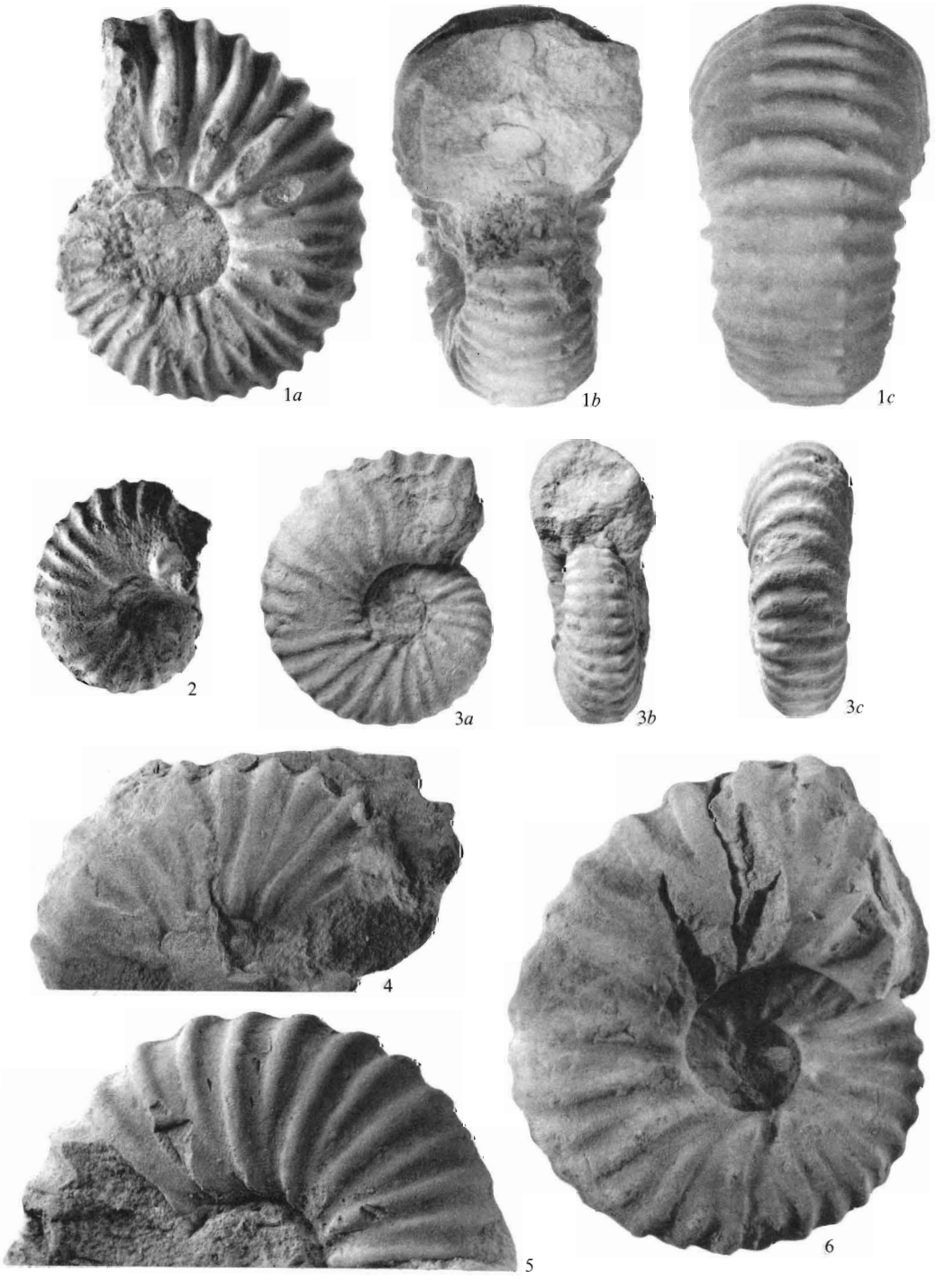
1*b*

2*a*

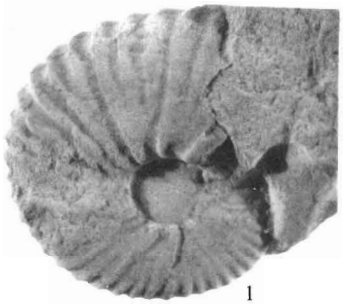
2*b*

2*c*

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



1

2

3

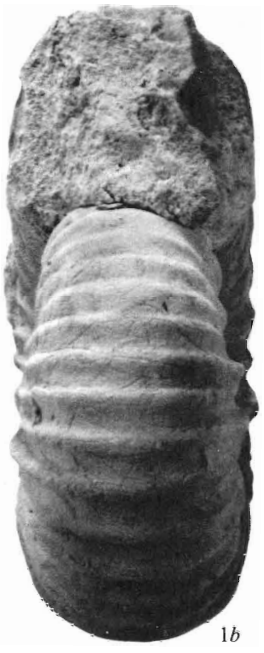
4

5*a*

5*b*

KENNEDY, Cenomanian ammonites

1*a*



1*b*

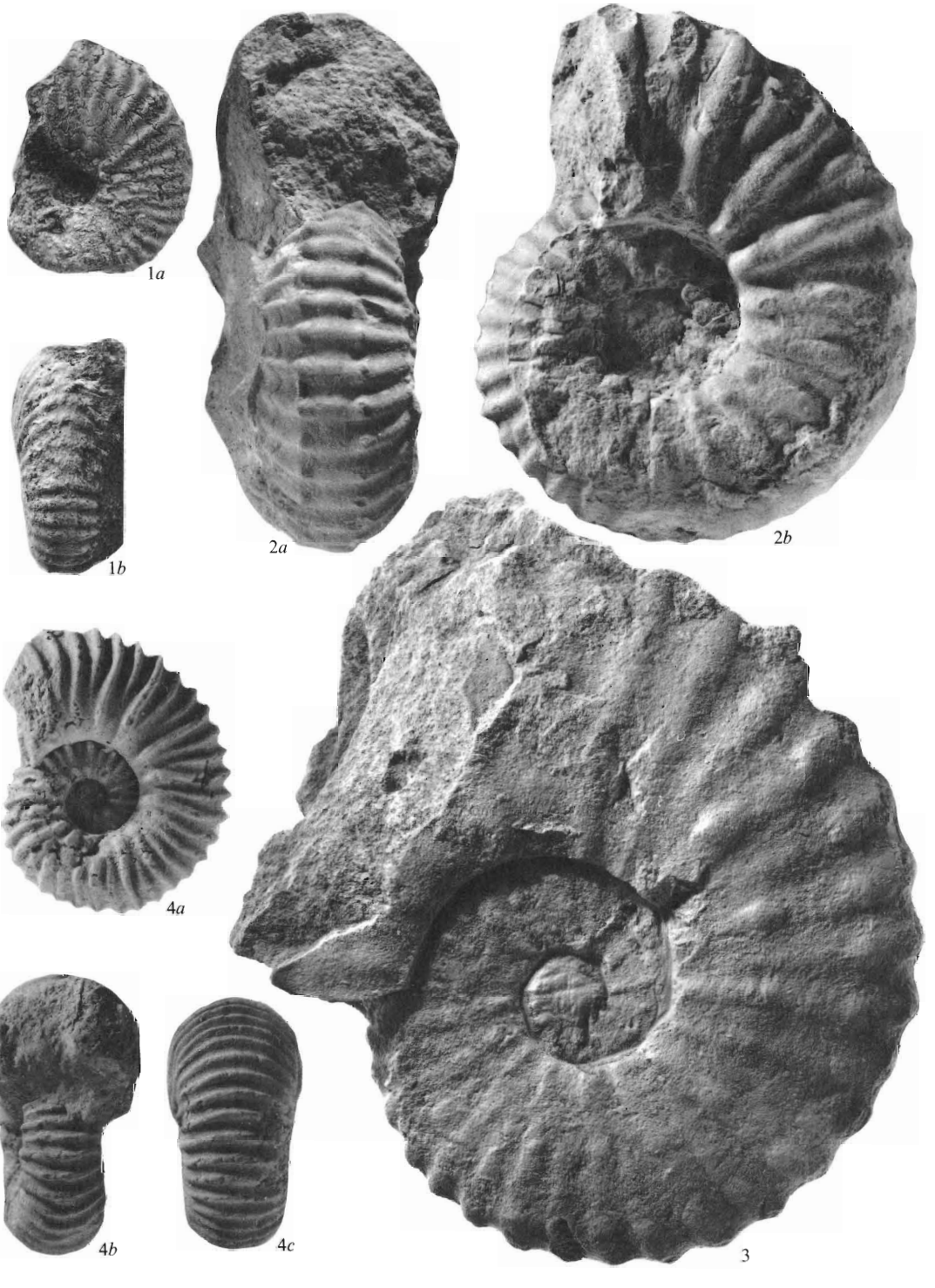
1*c*

2*a*

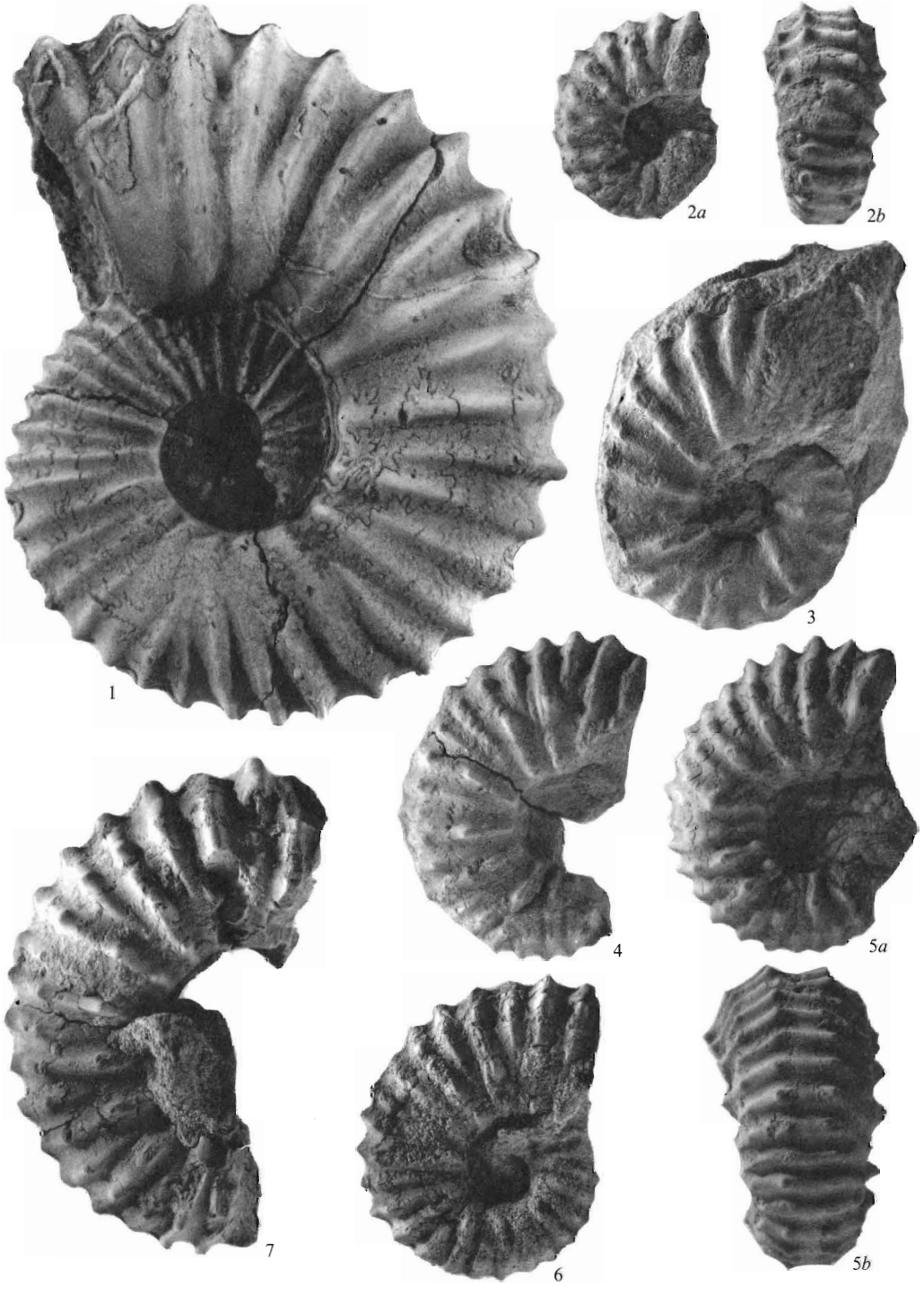
2*b*

2*c*

KENNEDY, Cenomanian ammonites

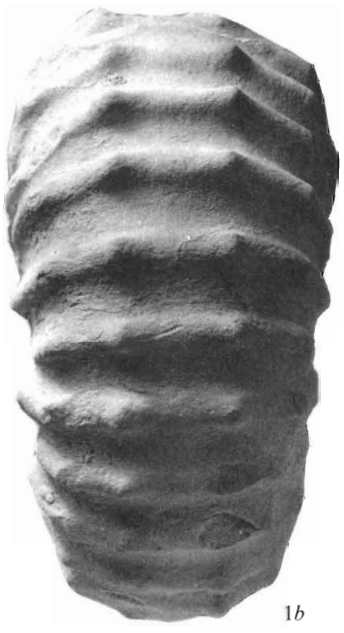


KENNEDY, Cenomanian ammonites



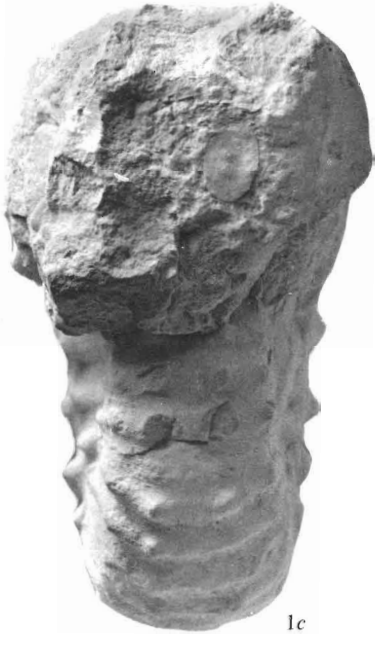
KENNEDY, Cenomanian ammonites

1*a*



1*b*

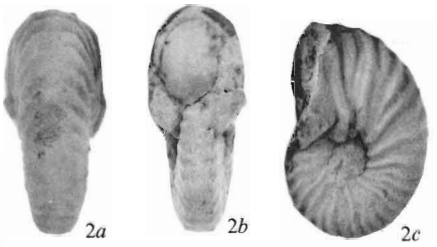
2



1*c*

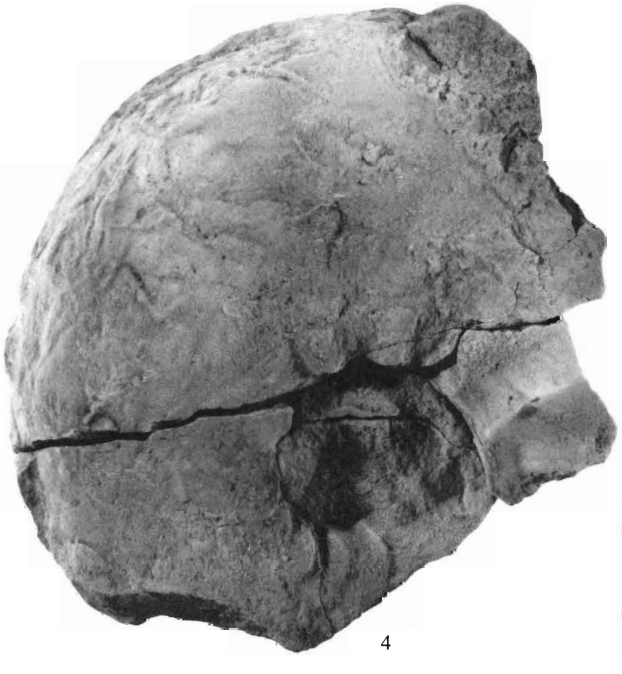
KENNEDY, Cenomanian ammonites

1



2*a* 2*b* 2*c*

3



4

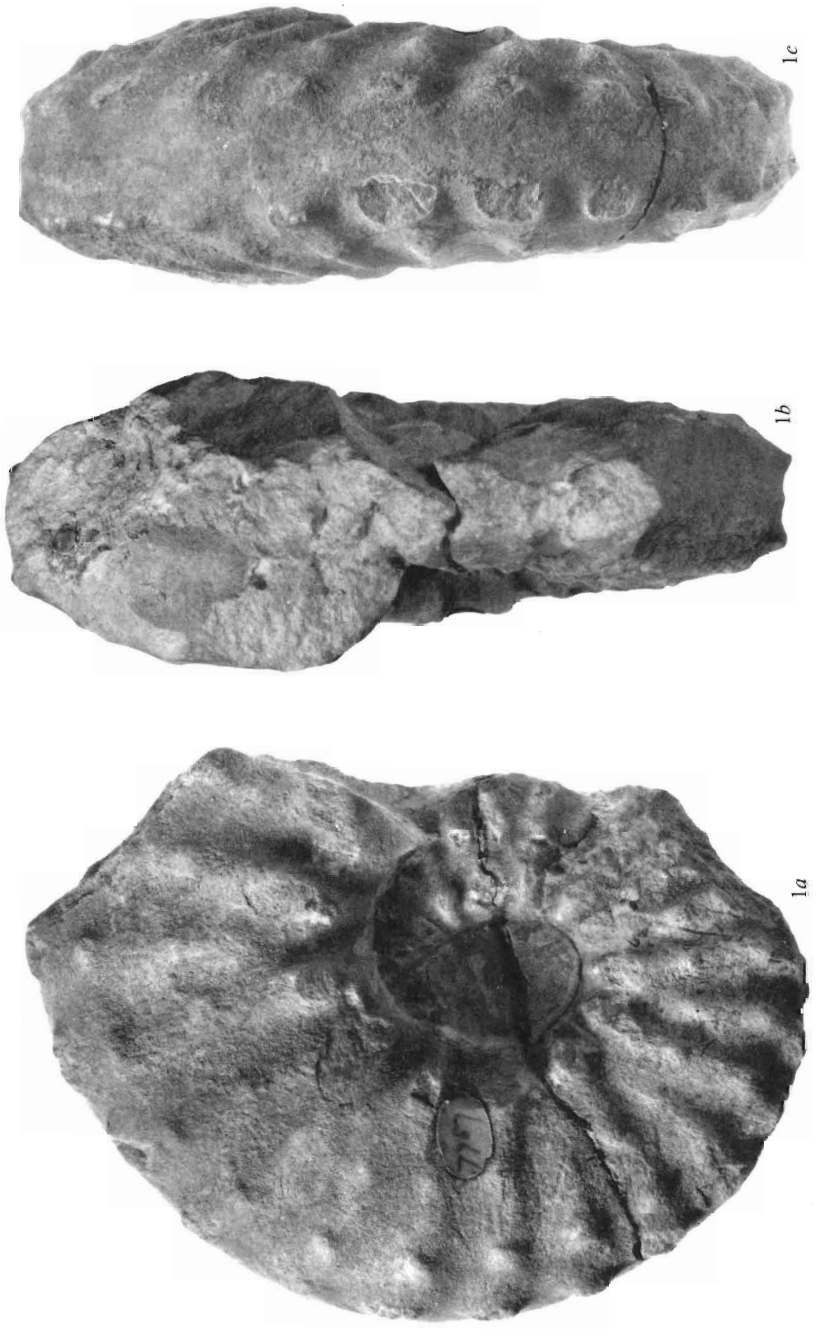
5

KENNEDY, Cenomanian ammonites

KENNEDY, Cenomanian ammonites

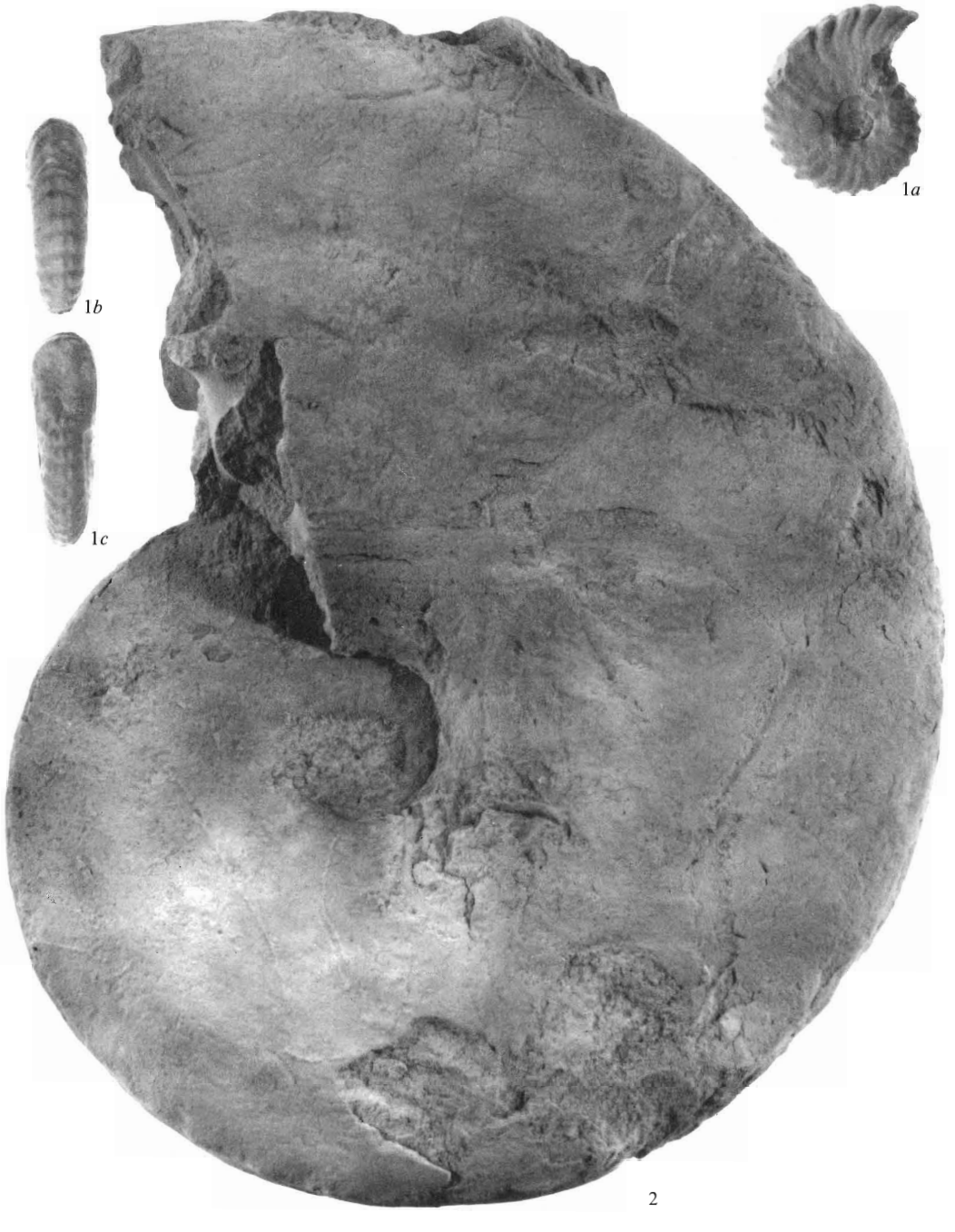
1

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

KENNEDY, Cenomanian ammonites



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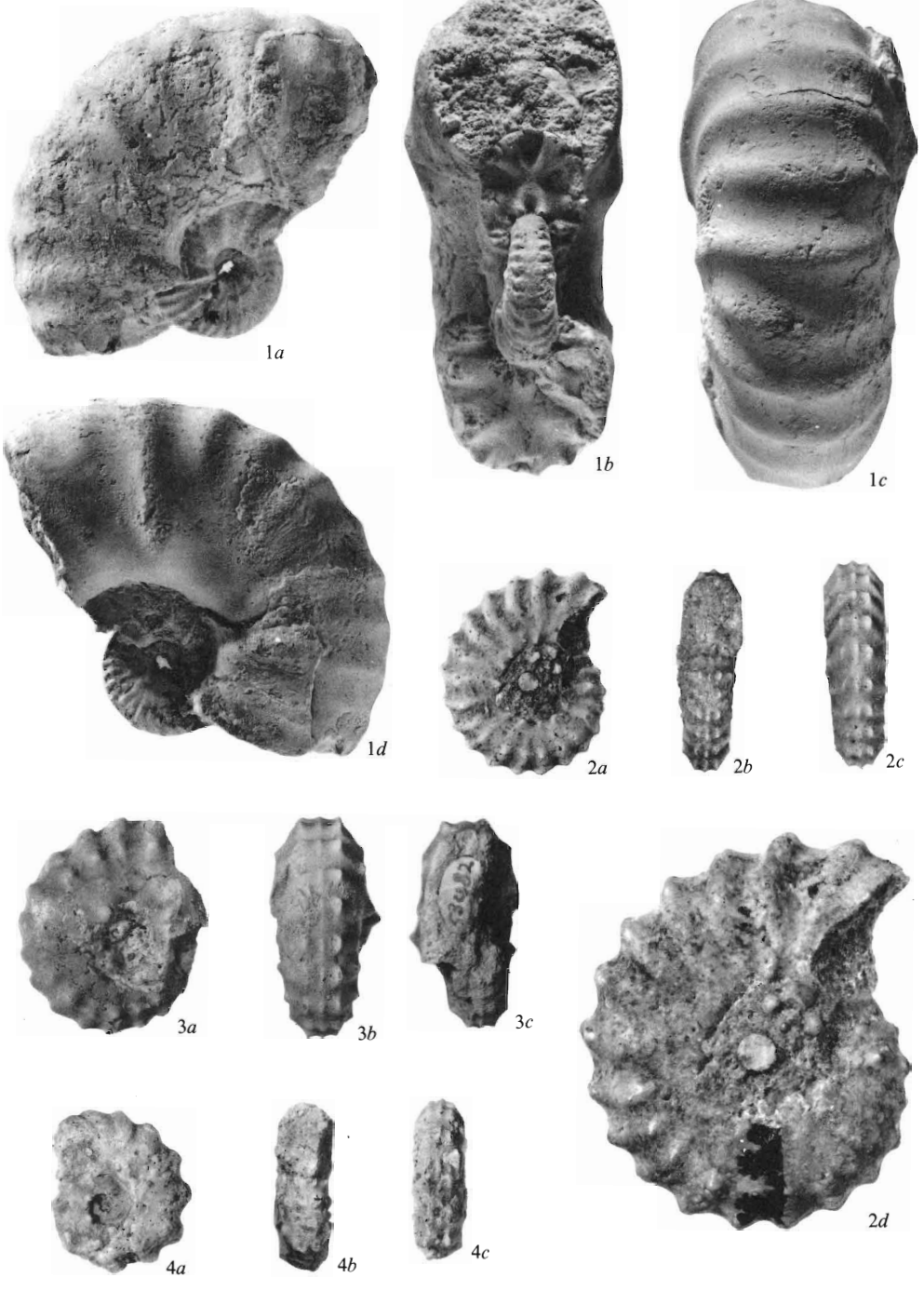
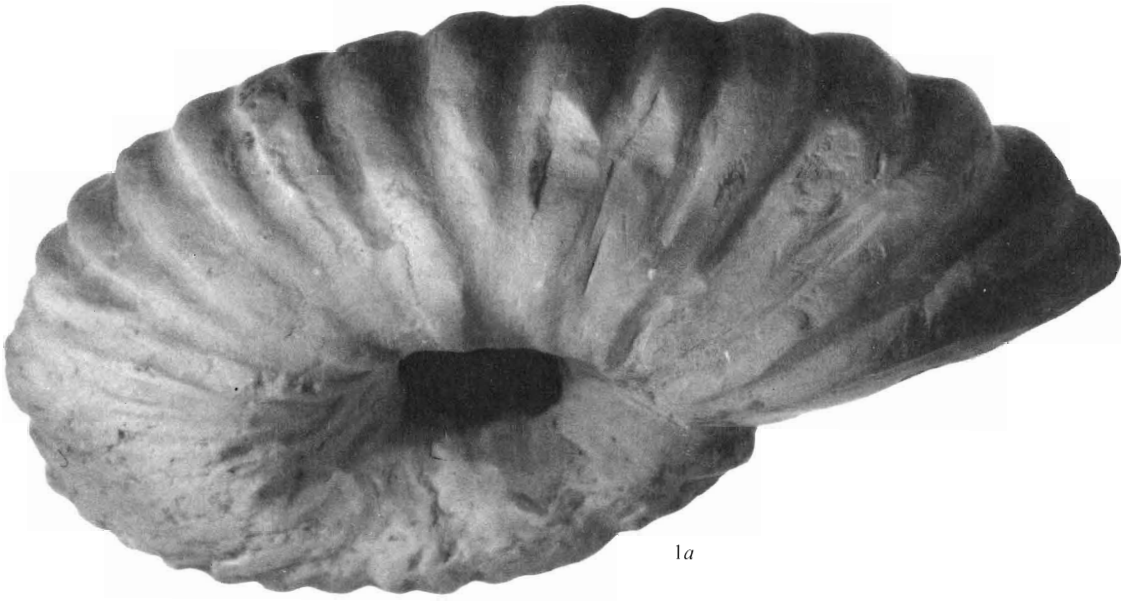


KENNEDY, Cenomanian ammonites



1*a*

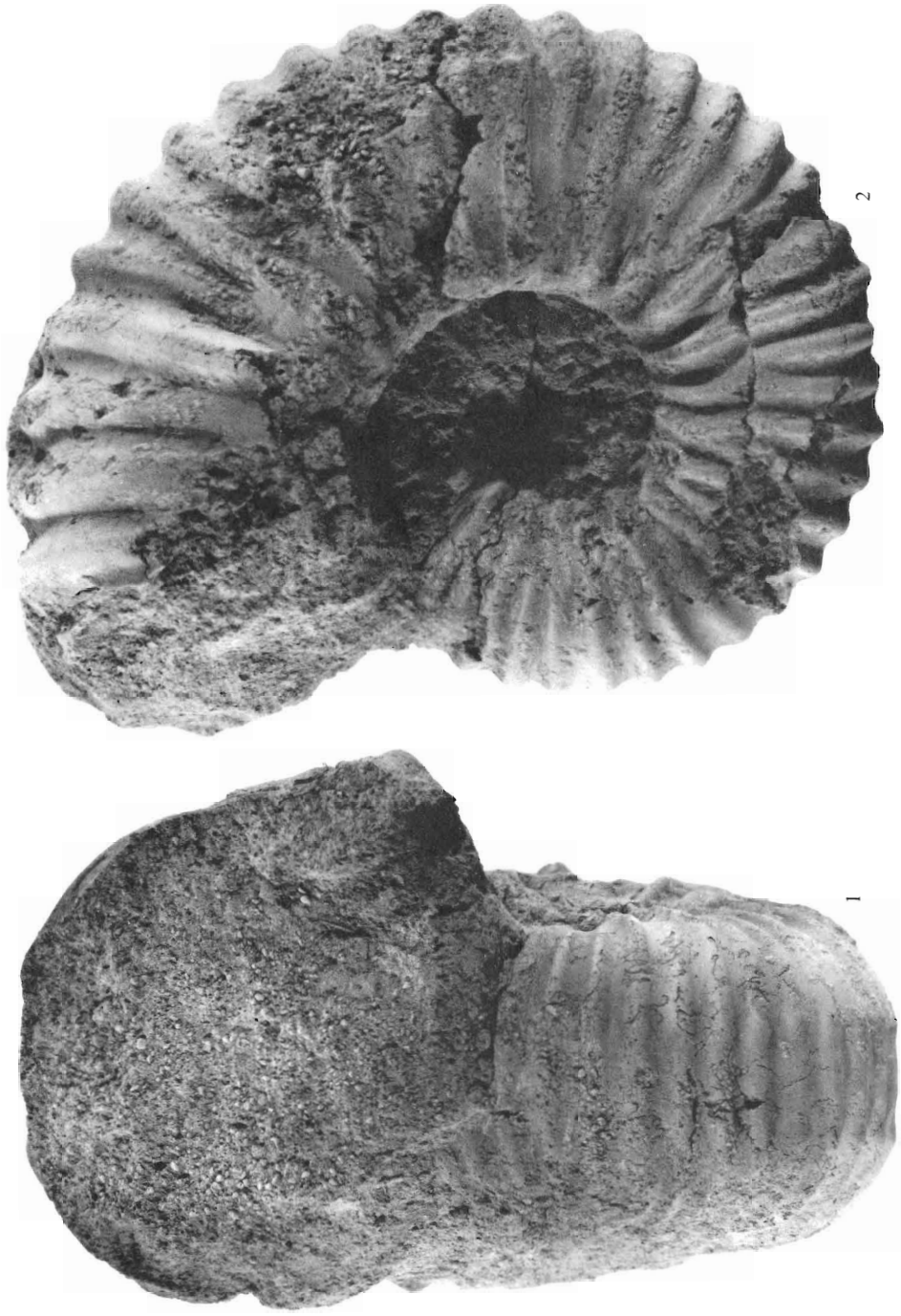
1*b*

KENNEDY, Cenomanian ammonites

1*b*

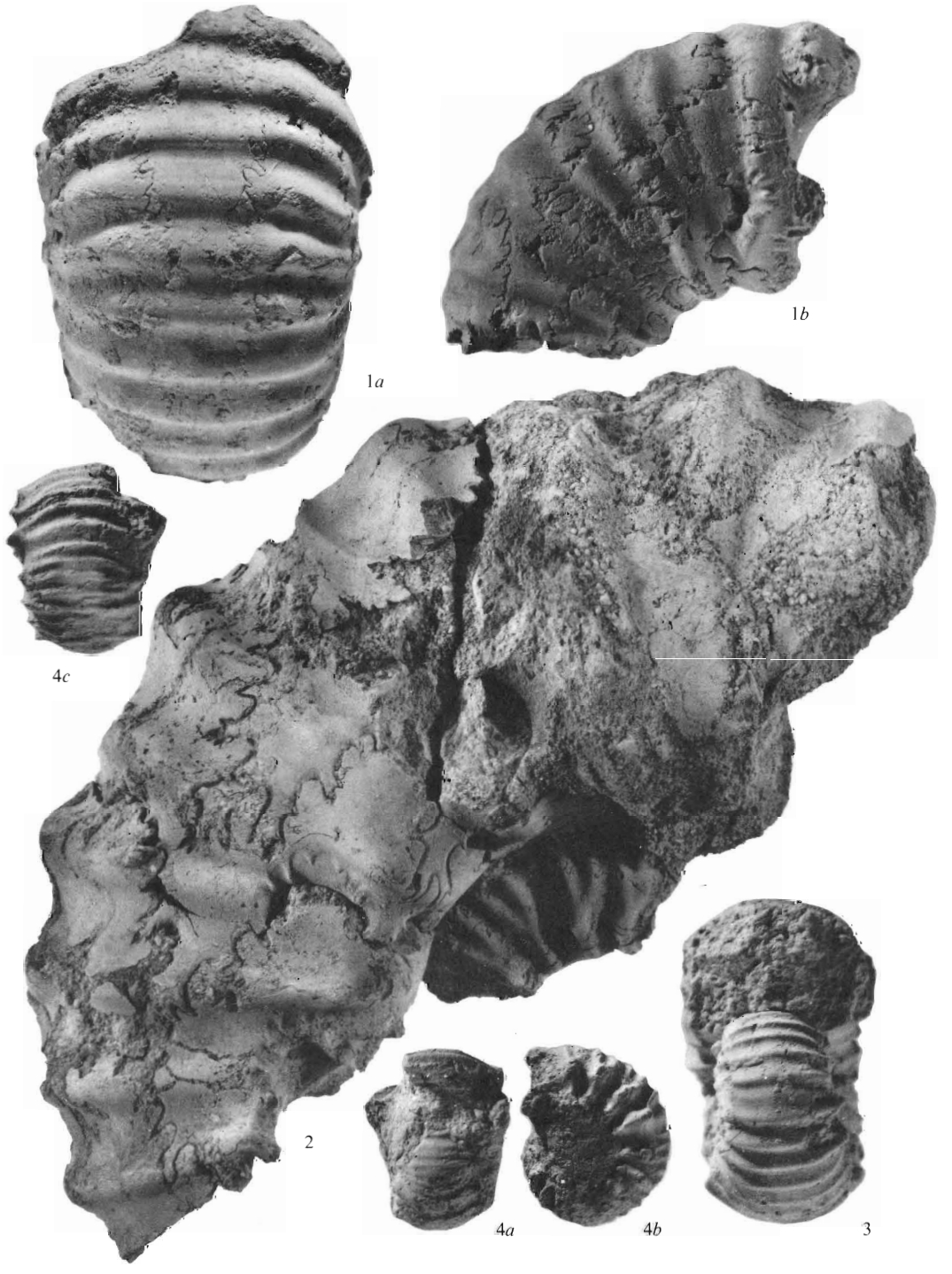
1*a*

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

KENNEDY, Cenomanian ammonites



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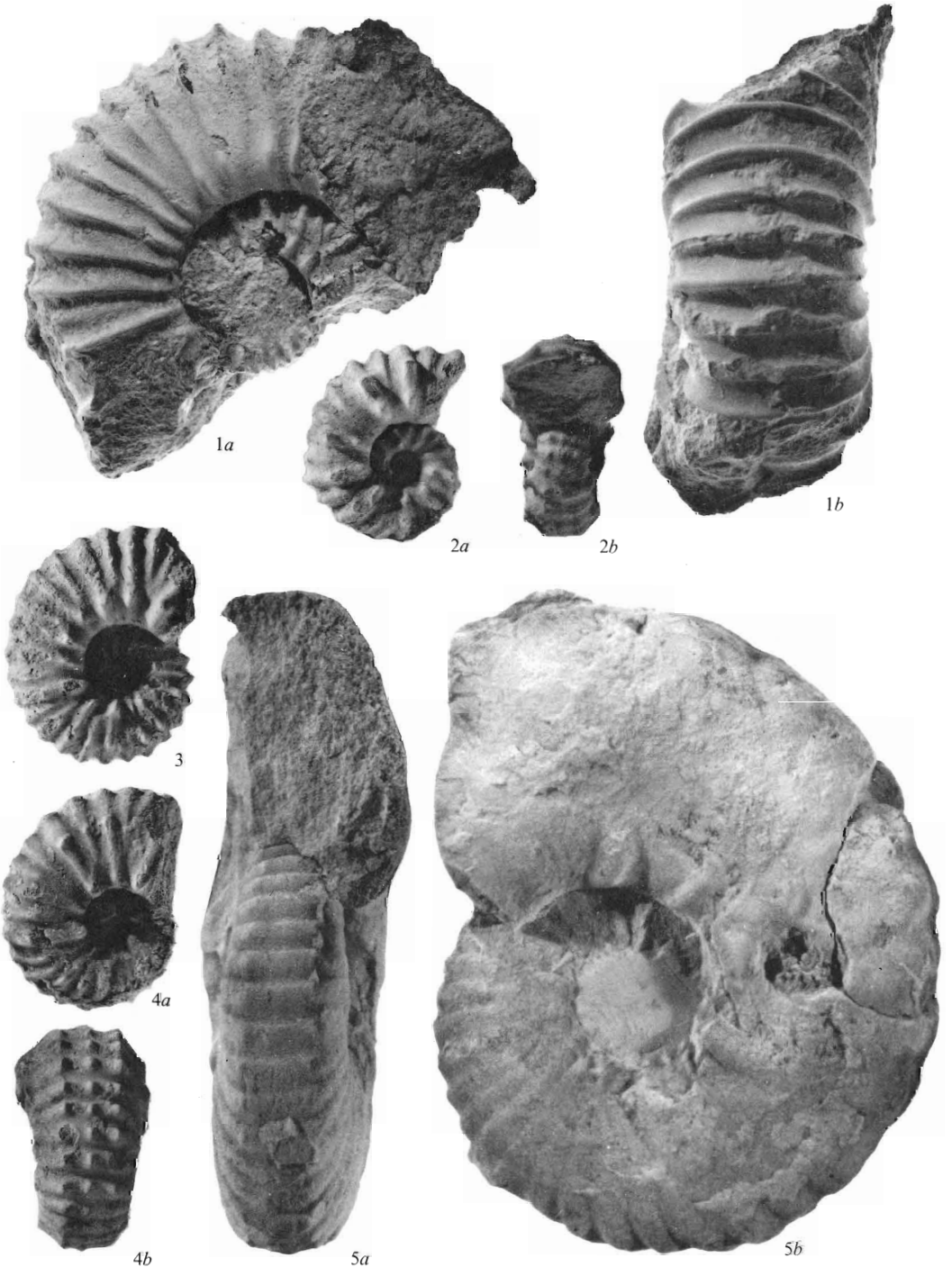
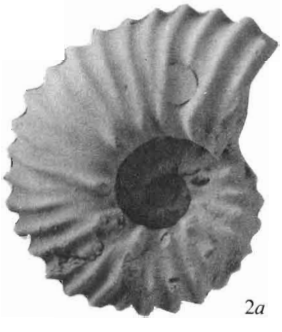


KENNEDY, Cenomanian ammonites

1*a*

1*b*

1*c*



2*a*

2*b*

2*c*

3*a*

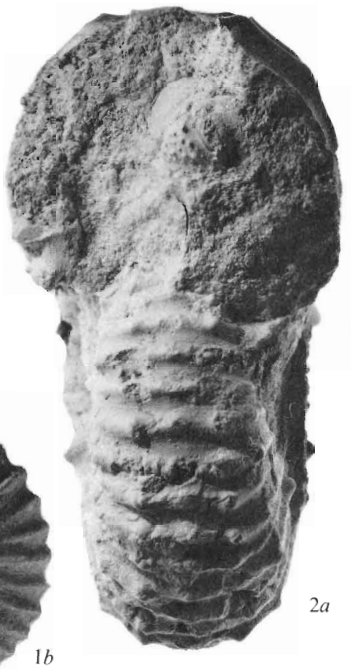
3*b*

3*c*

KENNEDY, Cenomanian ammonites

1*a*

1*b*



2*a*

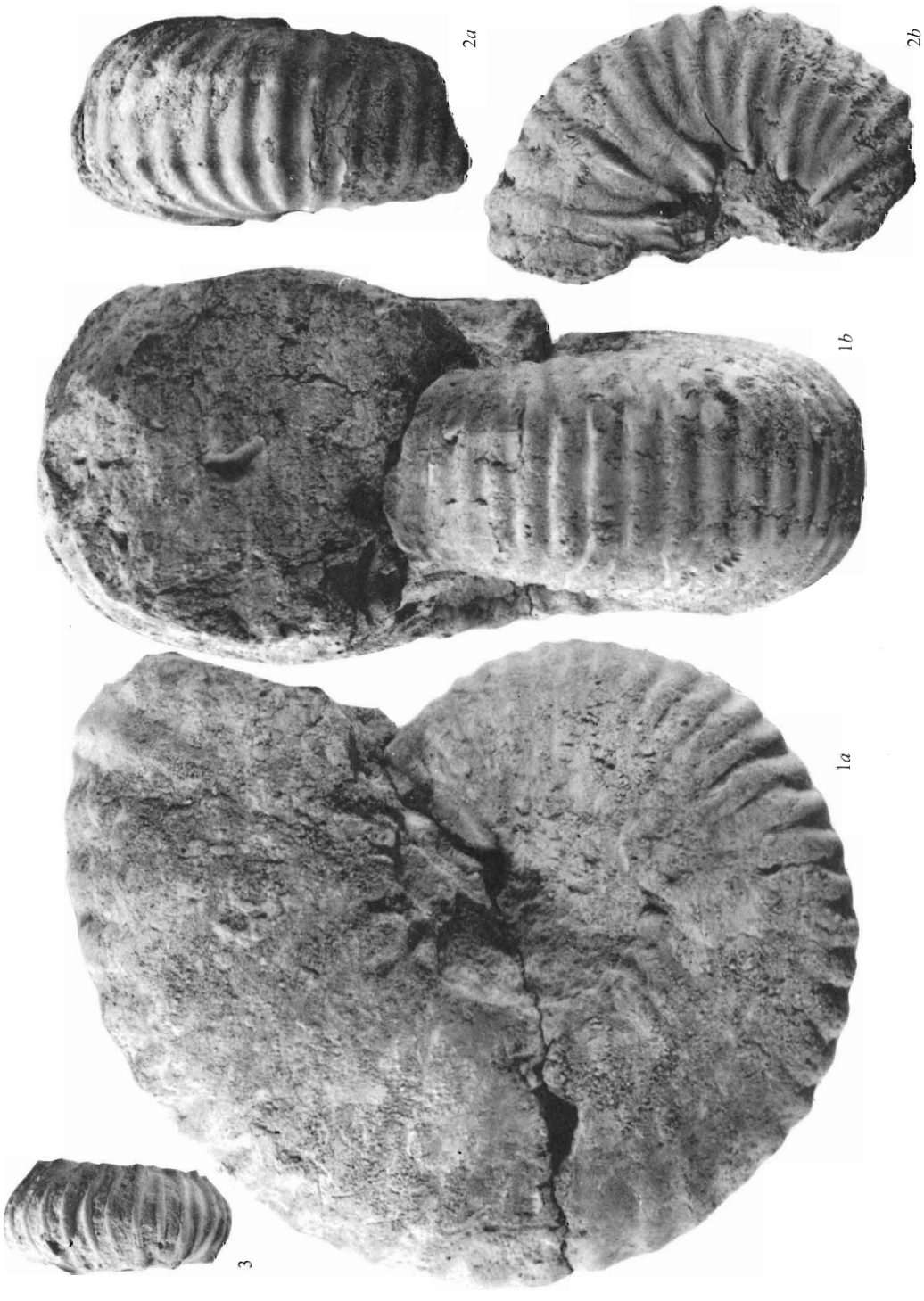
2*b*

3

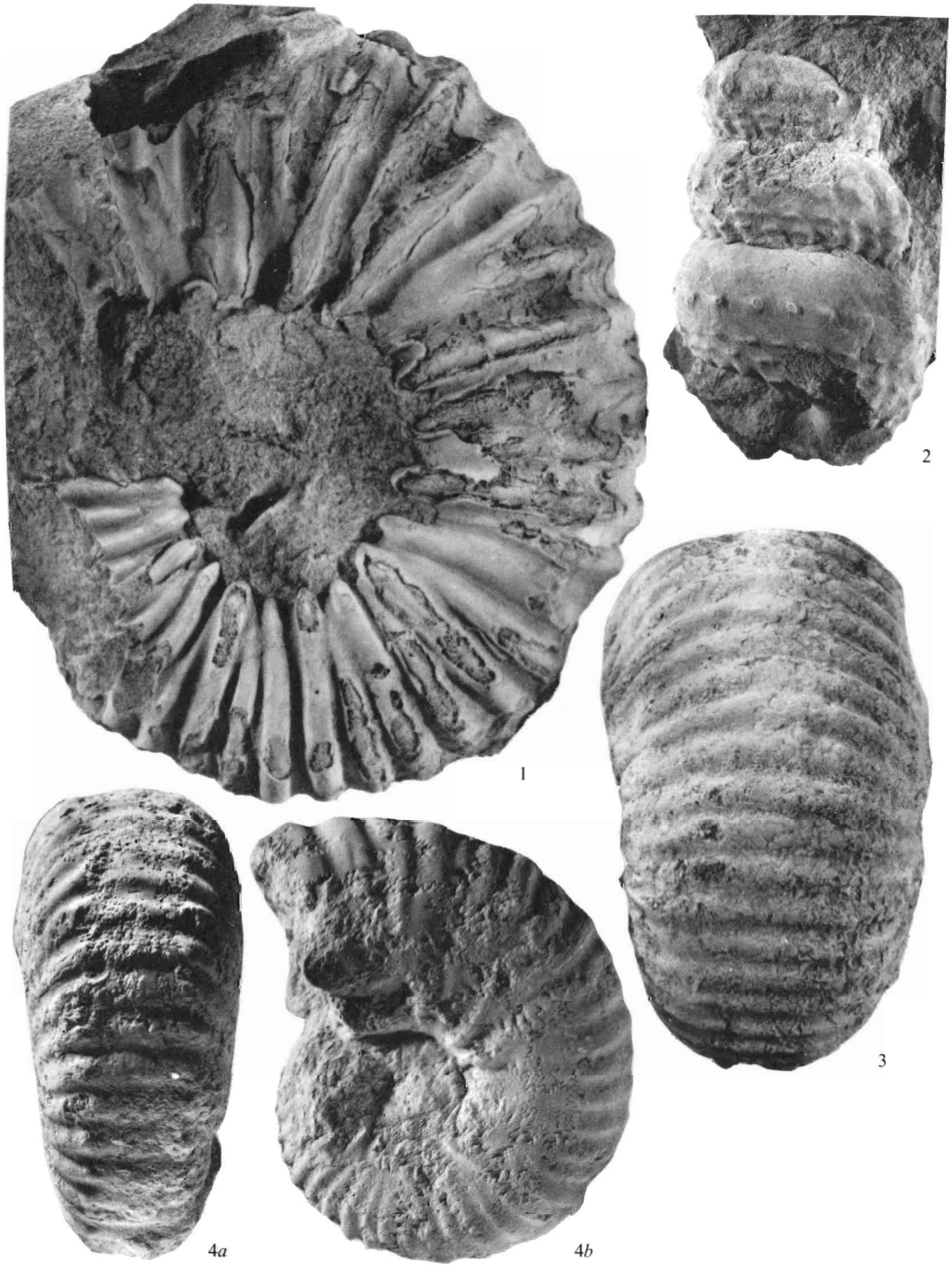
4

5

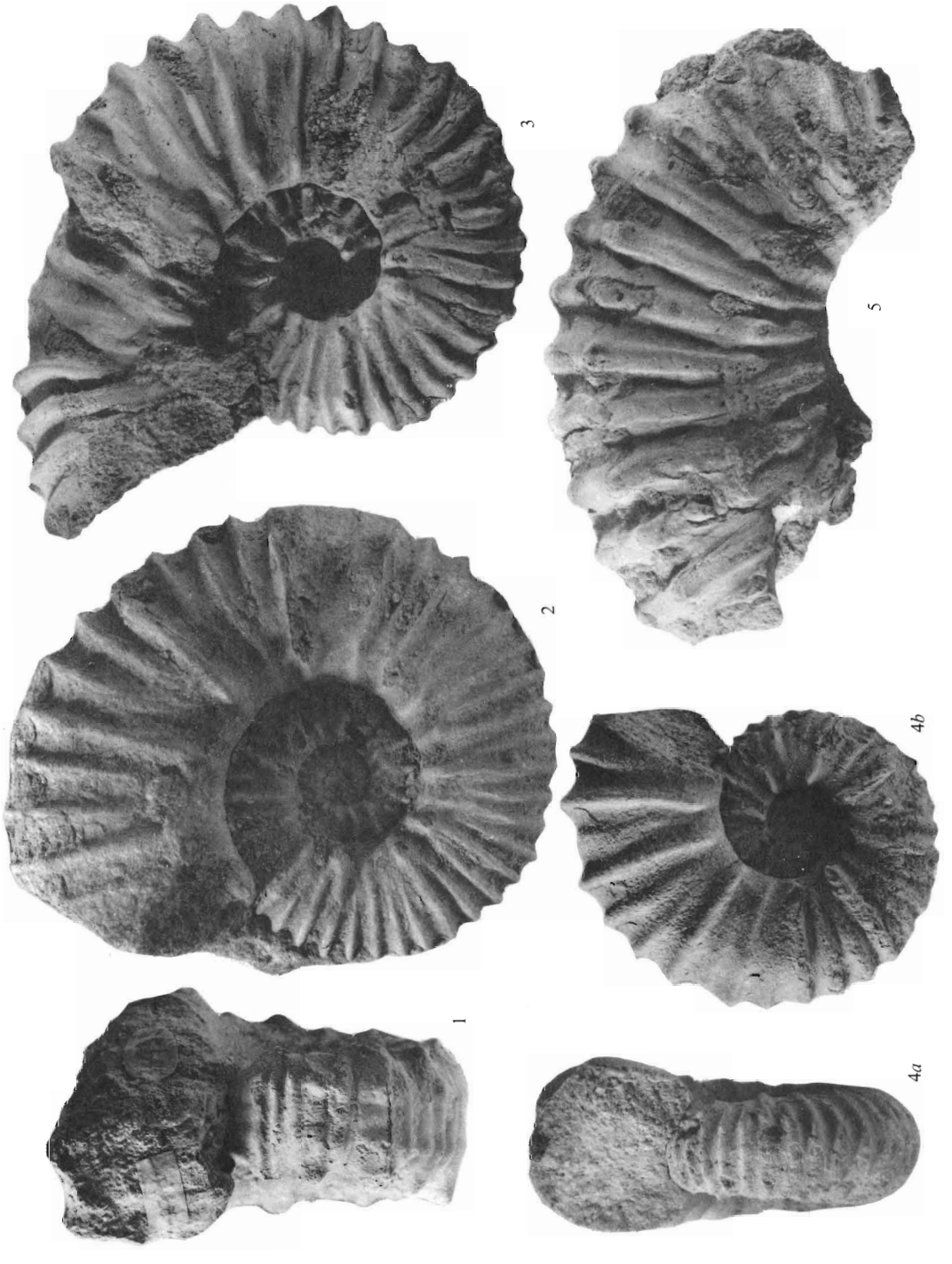
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



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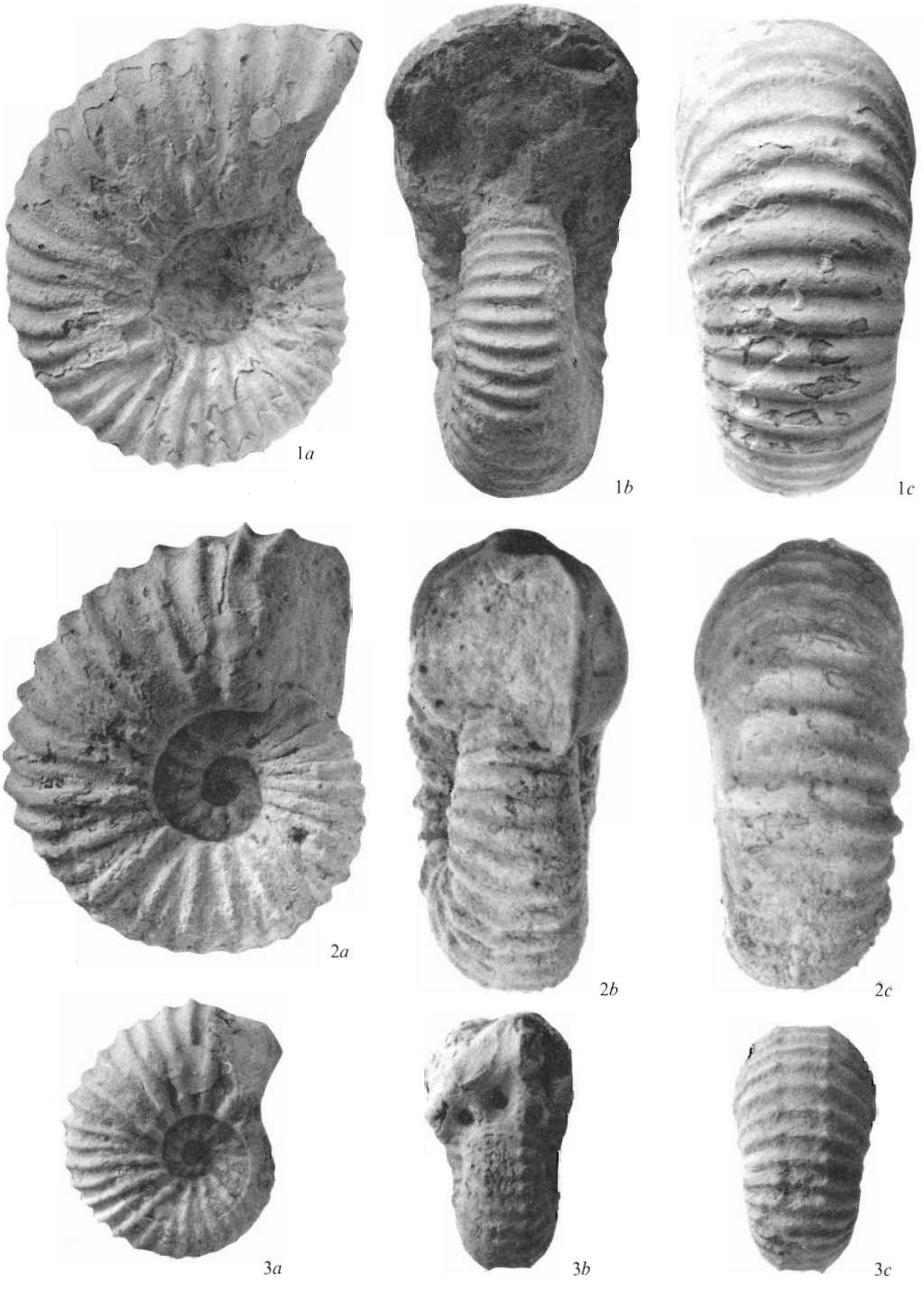

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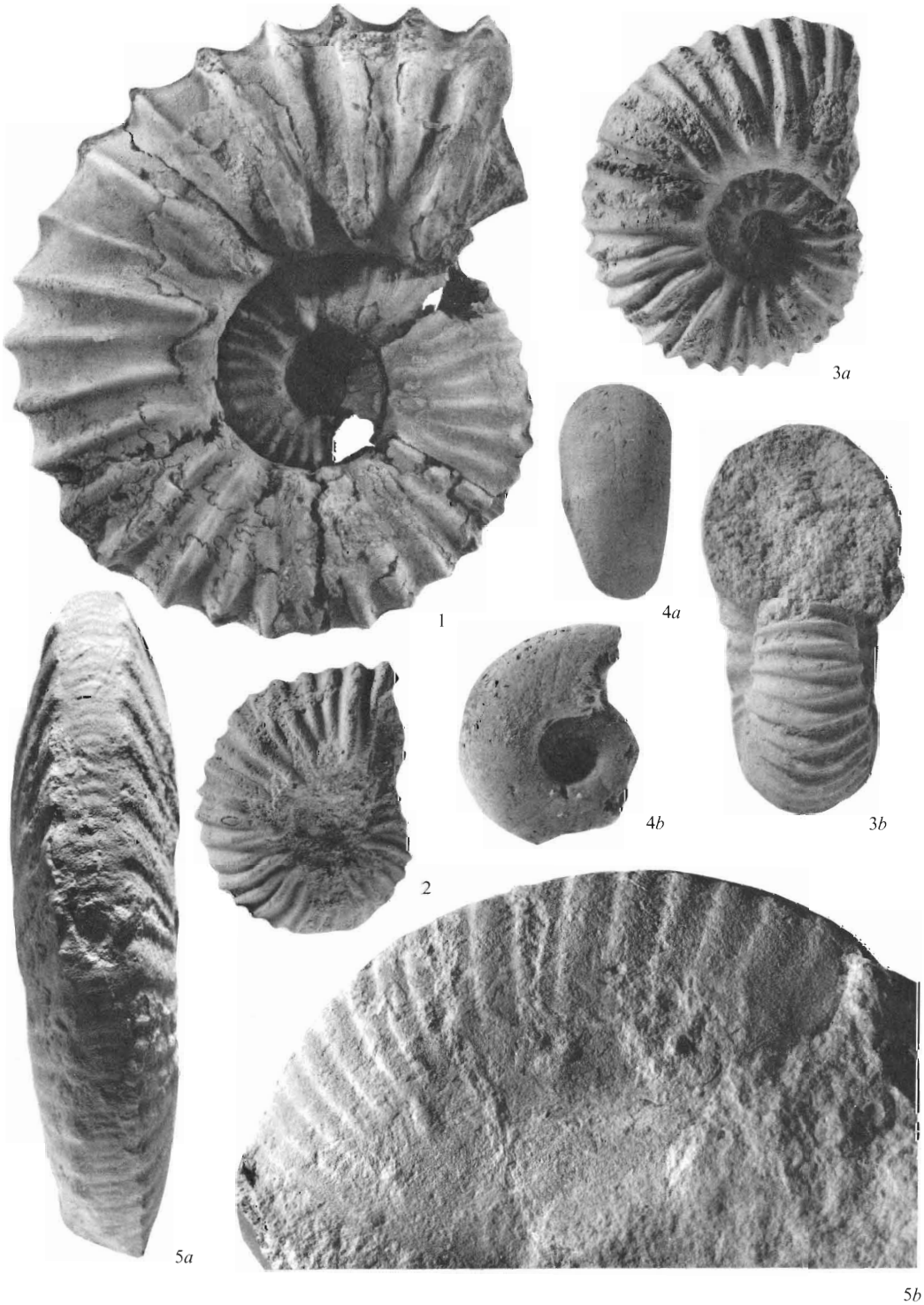
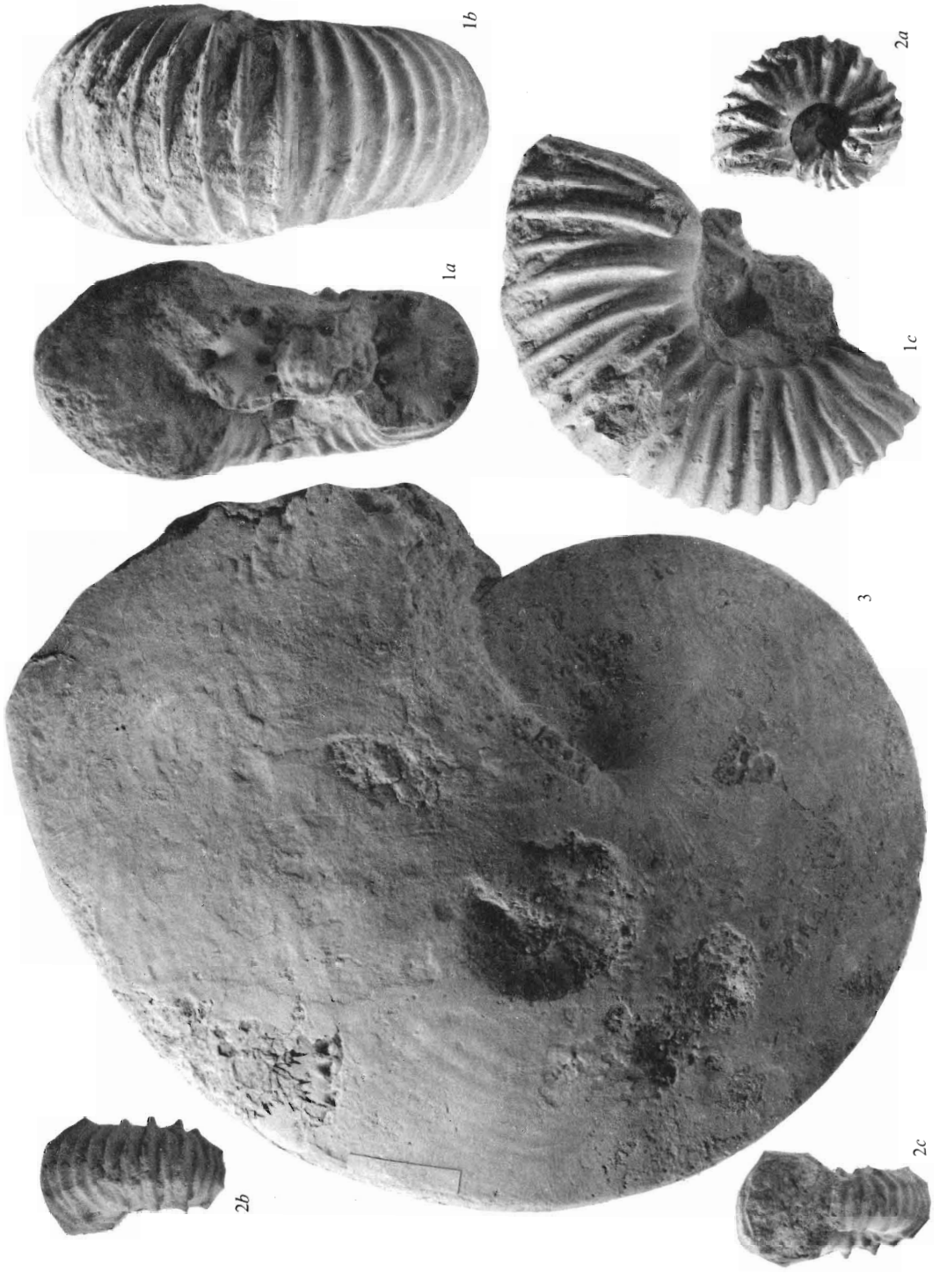


KENNEDY, Cenomanian ammonites



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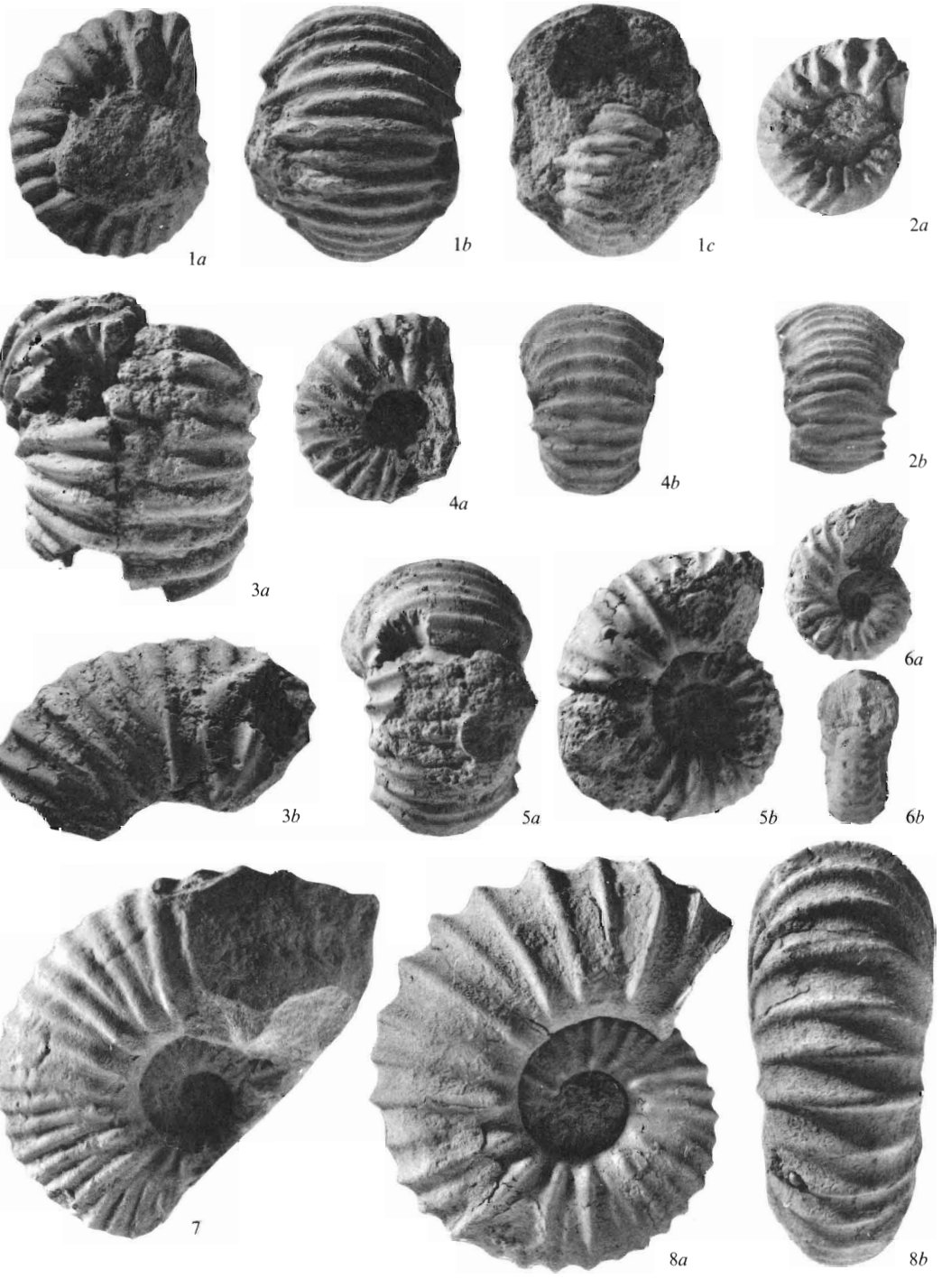
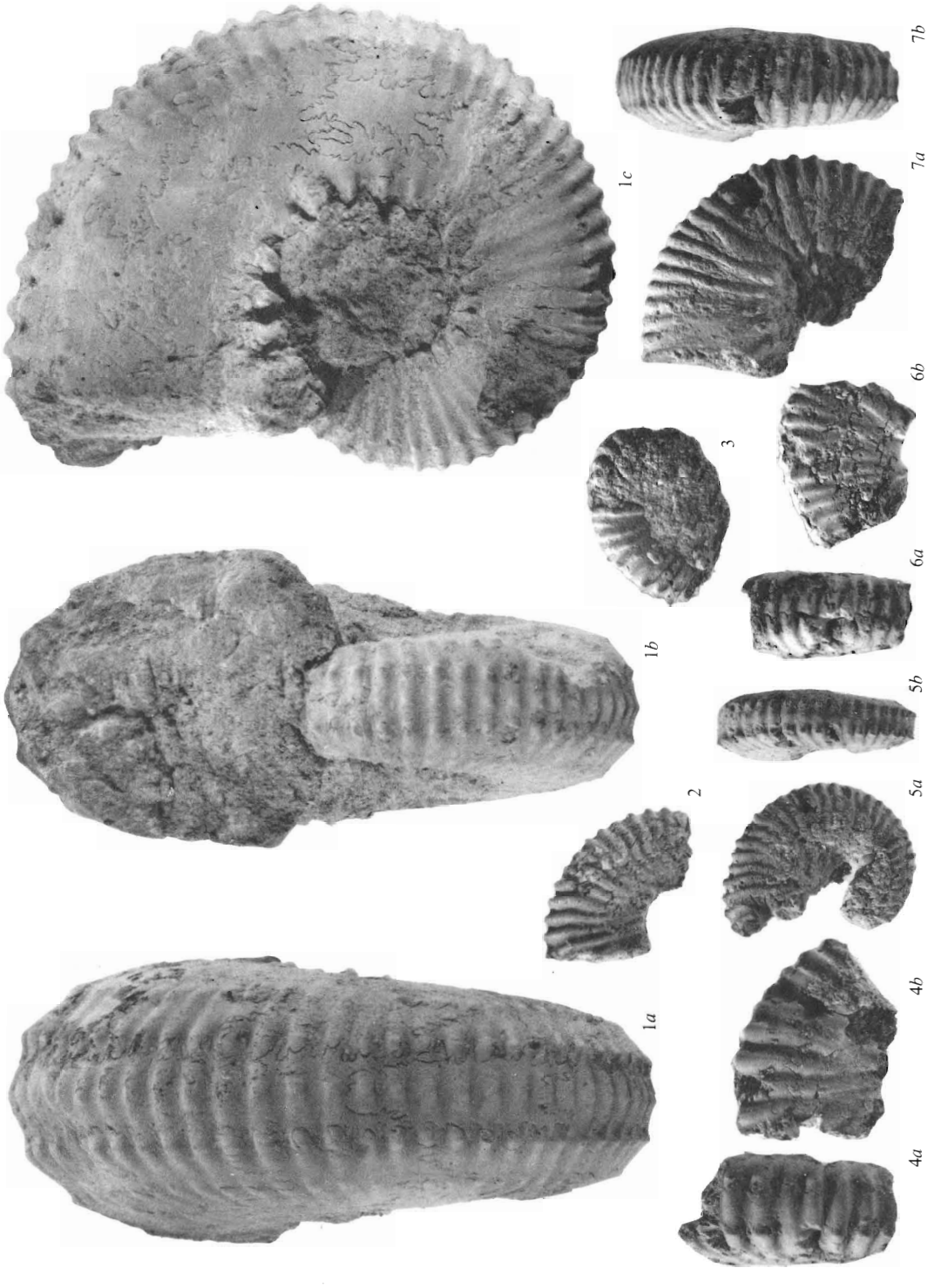
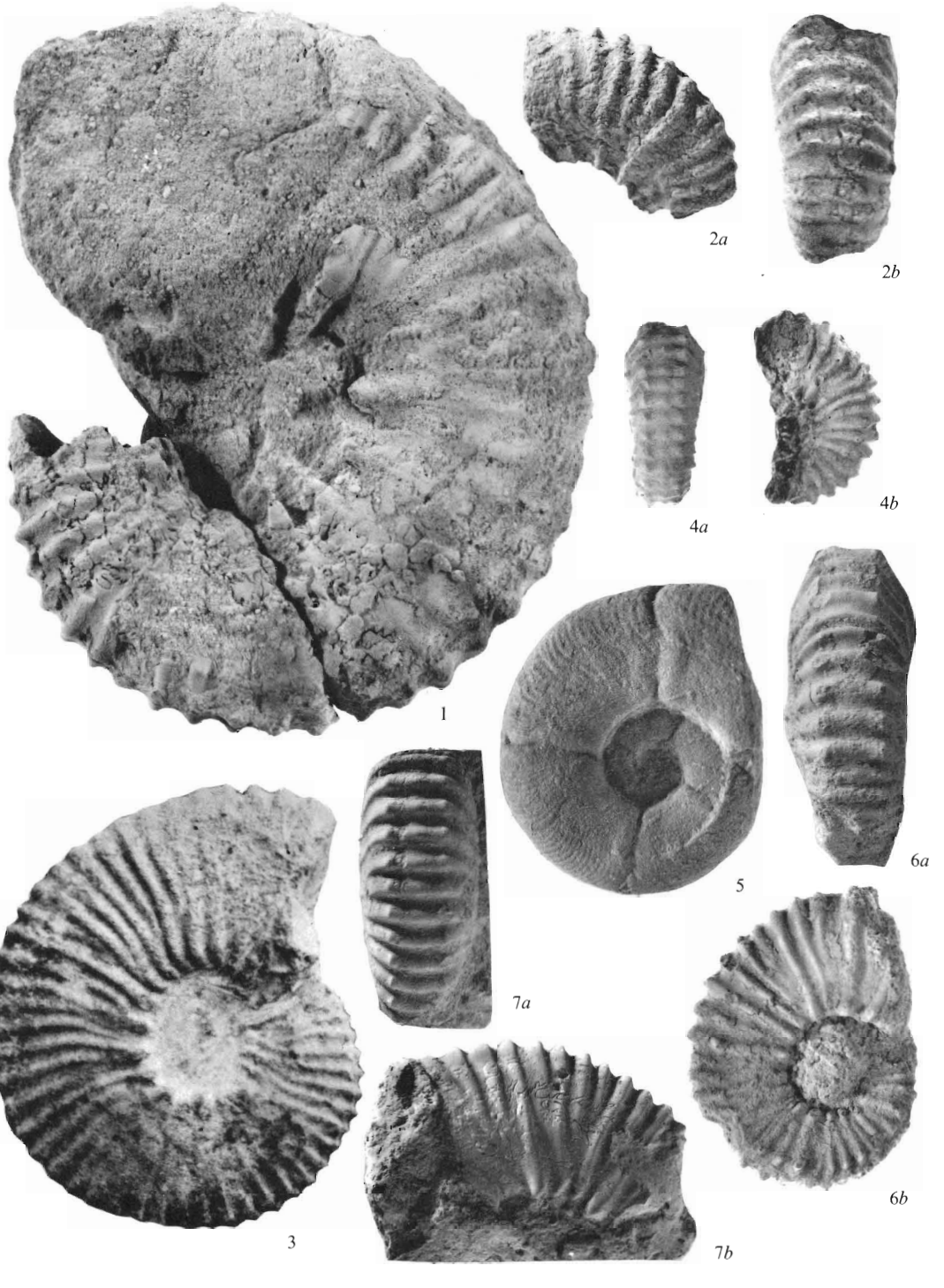


KENNEDY, Cenomanian ammonites

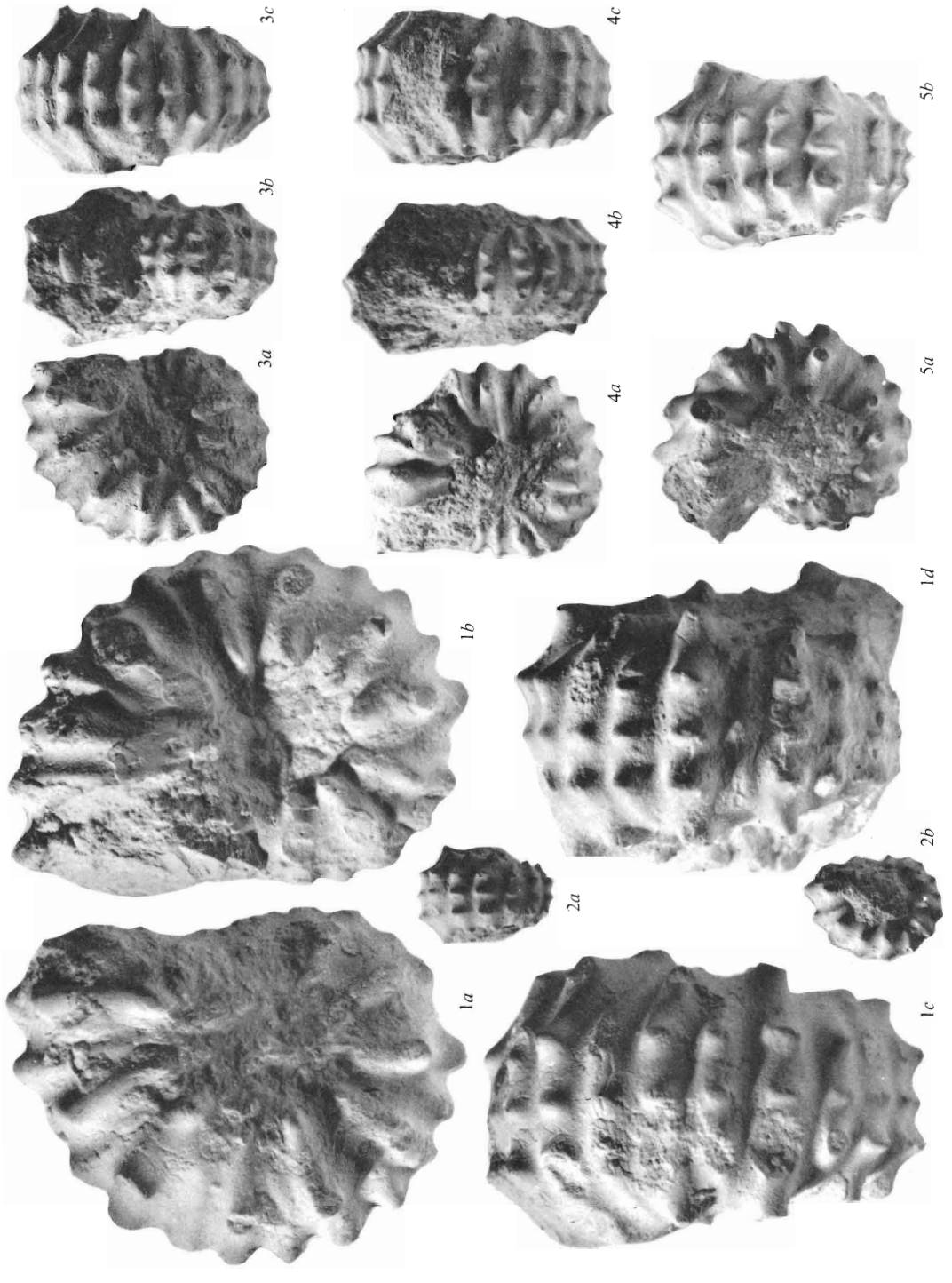
KENNEDY, Cenomanian ammonites



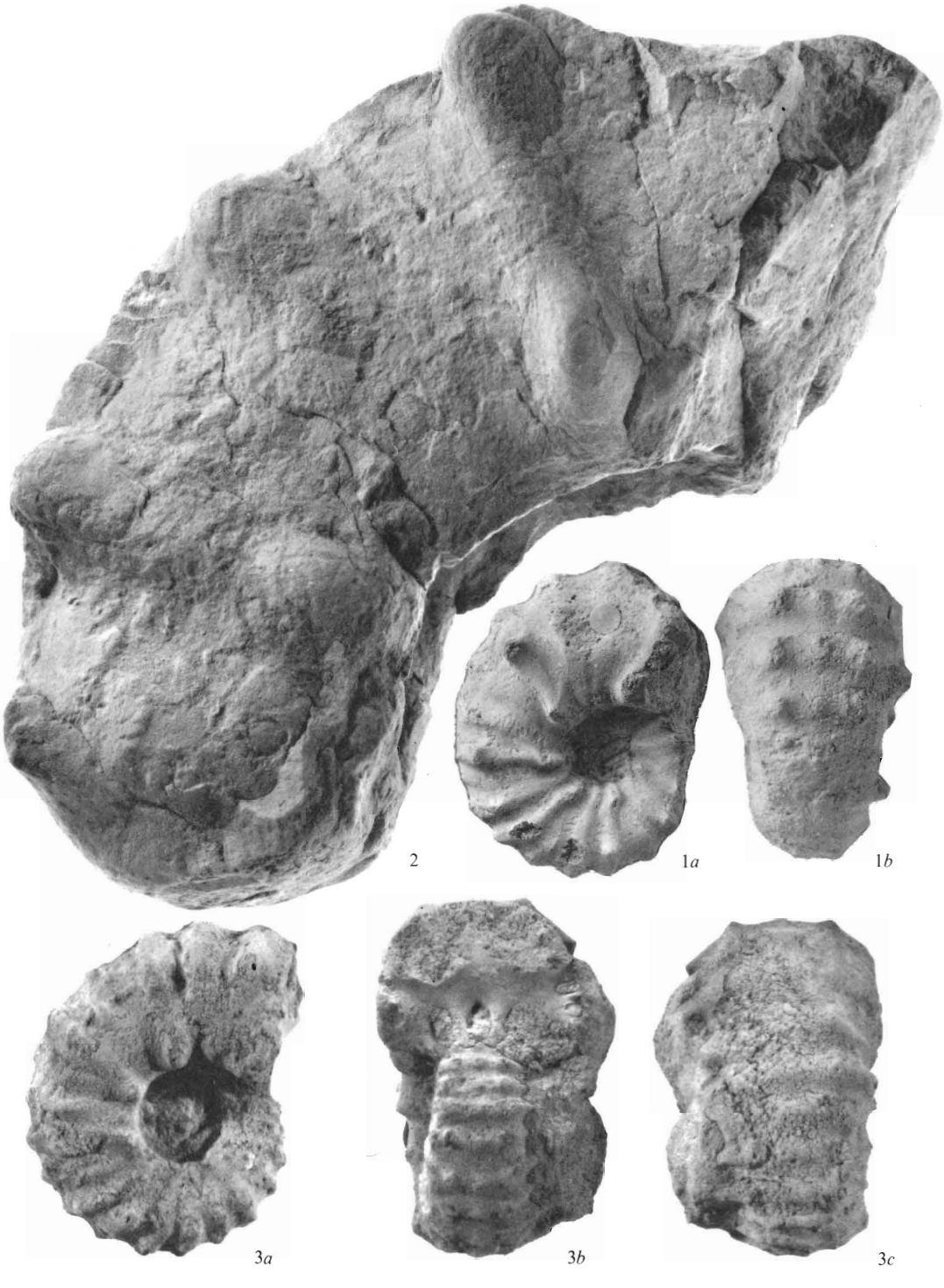
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

1

KENNEDY, Cenomanian ammonites

1

KENNEDY, Cenomanian ammonites

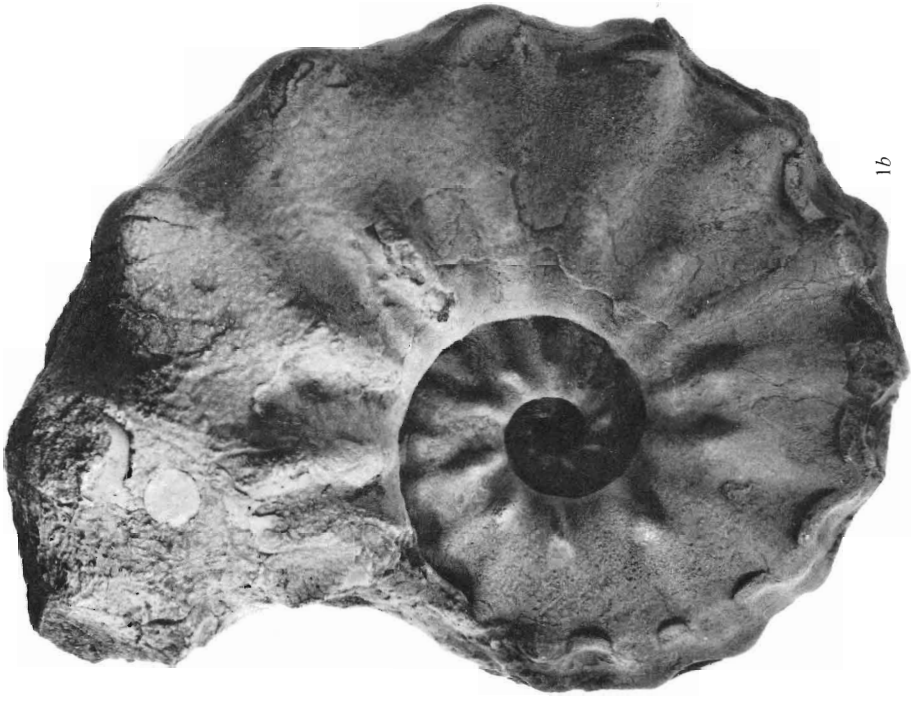
1*a*

1*b*

1*c*

2

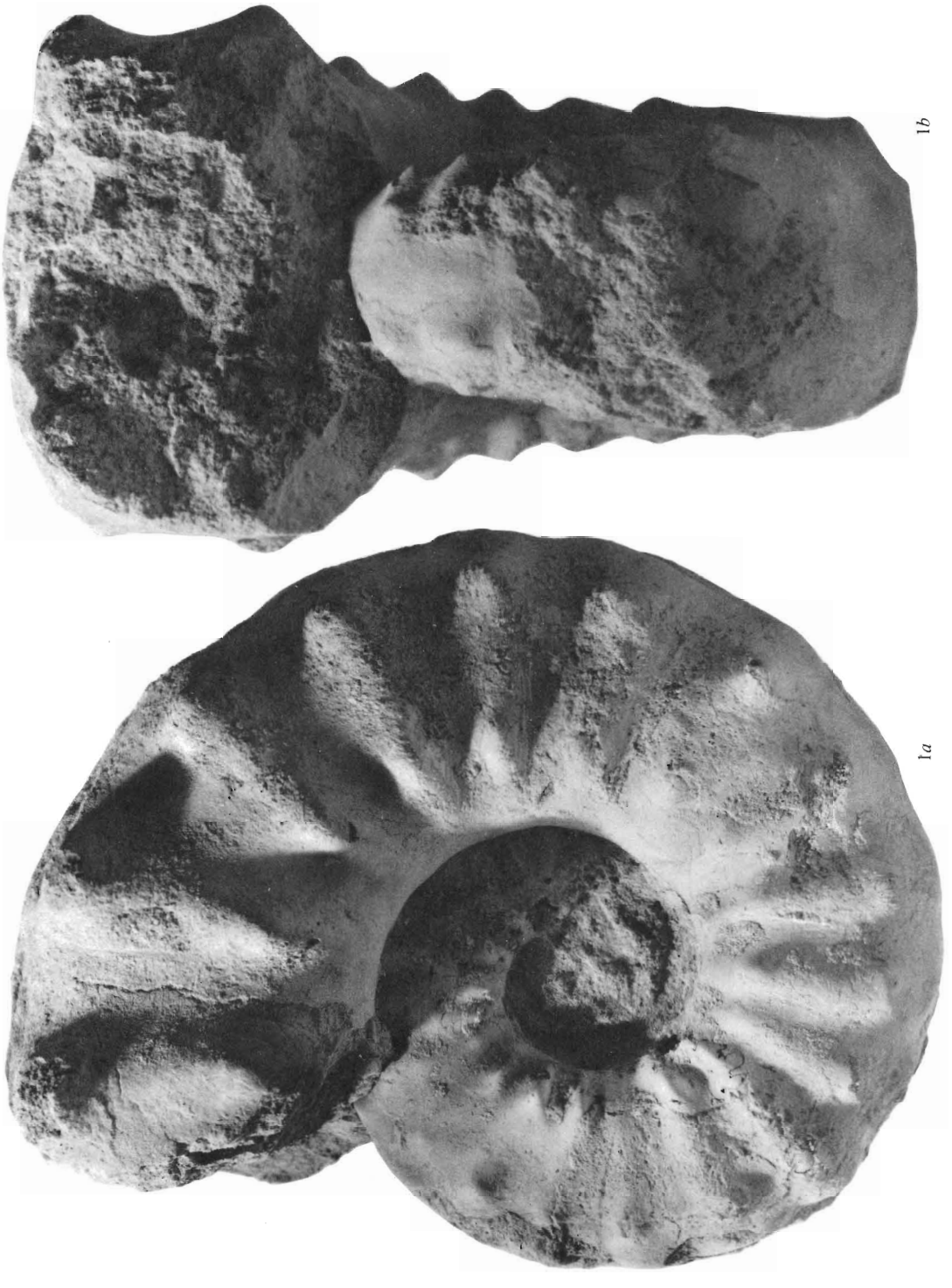
KENNEDY, Cenomanian ammonites



1*b*

1*a*

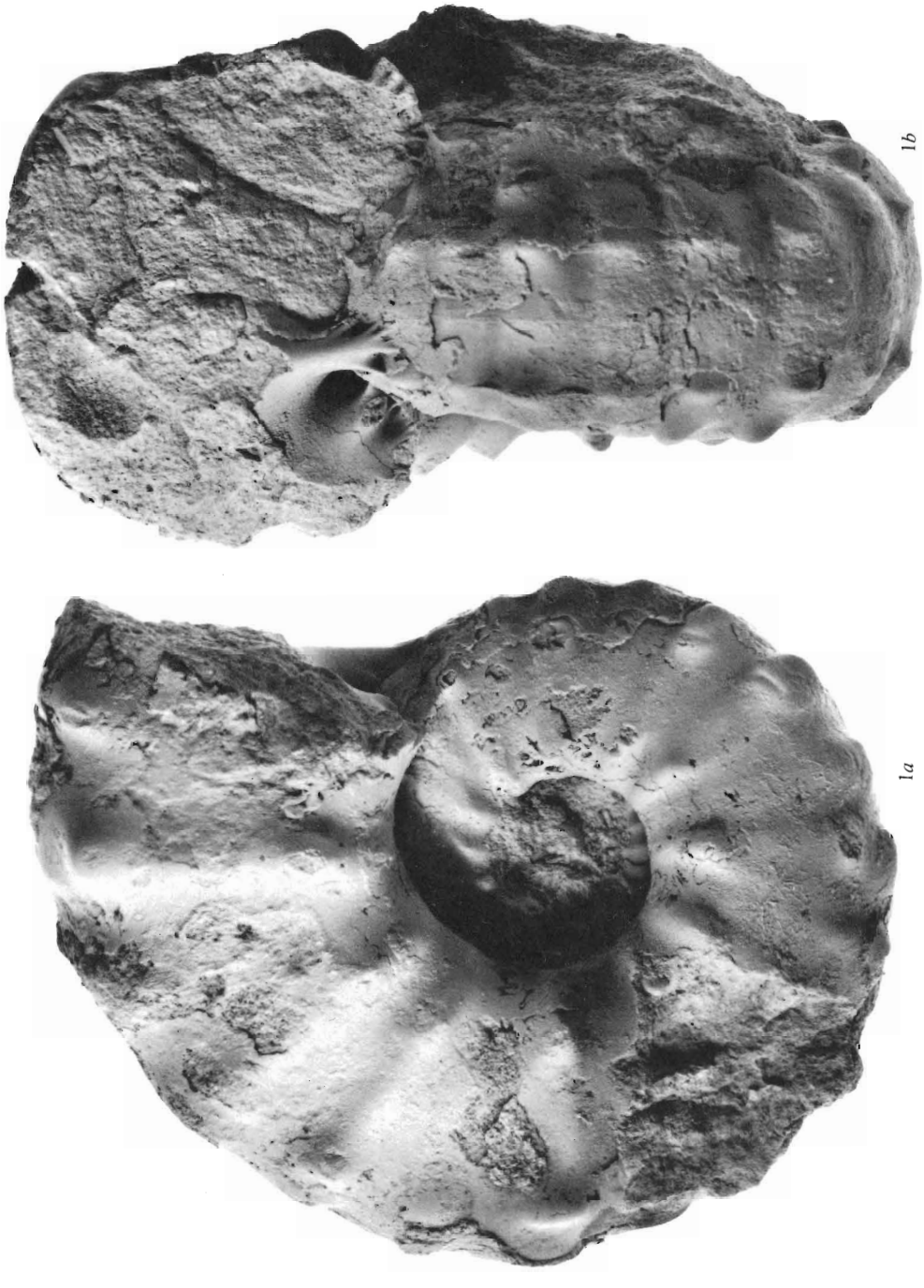
KENNEDY, Cenomanian ammonites



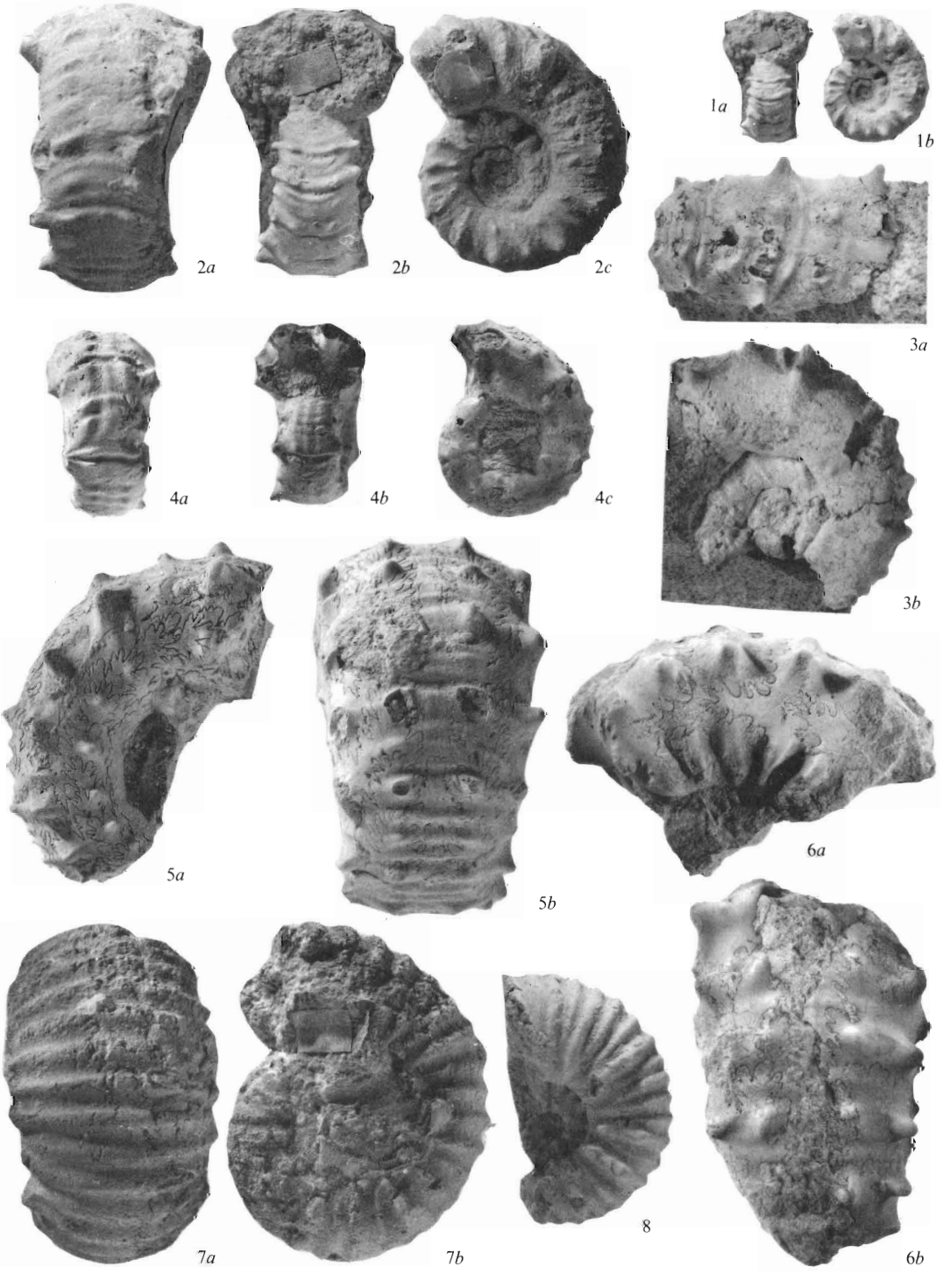
1*b*

1*a*

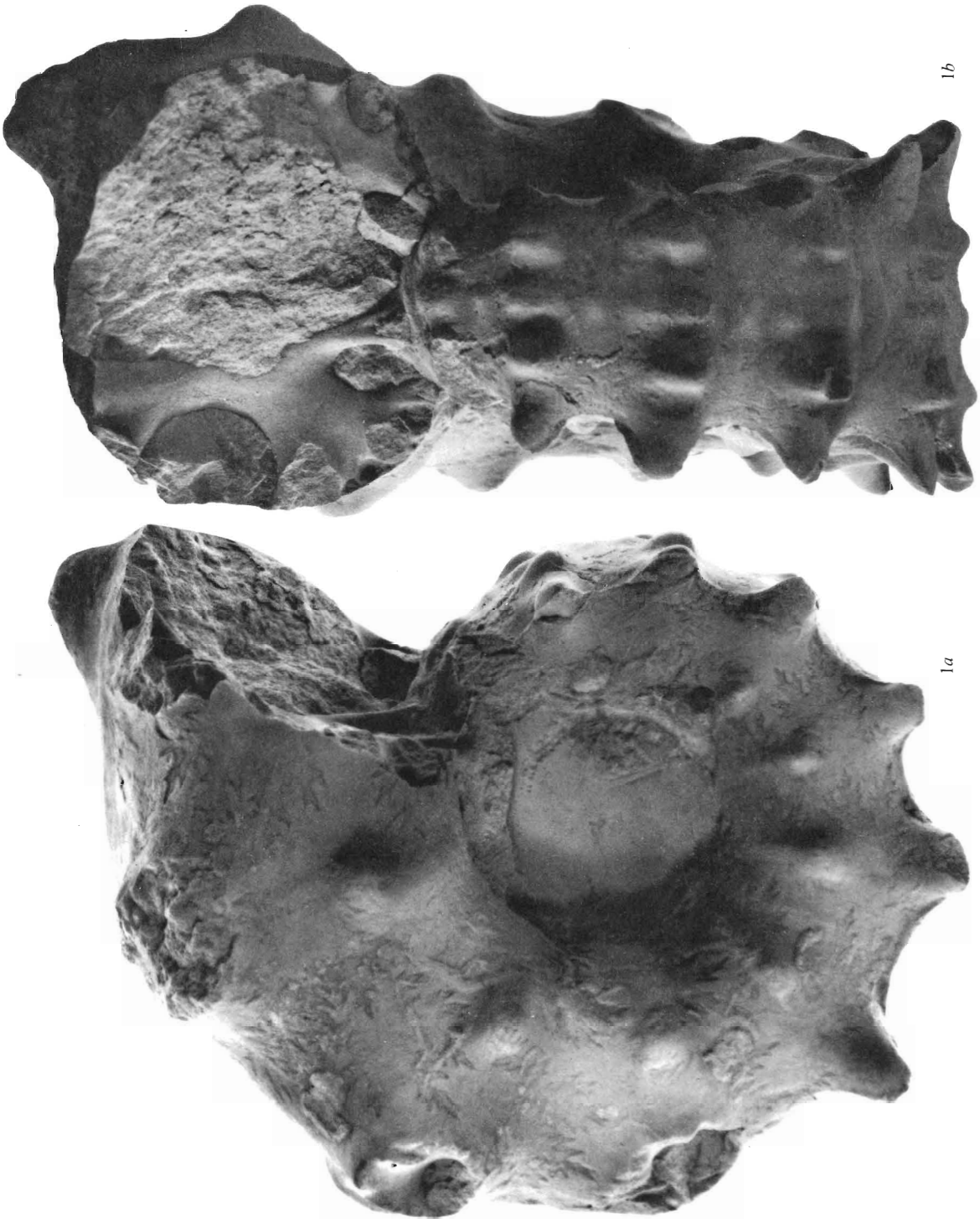
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites



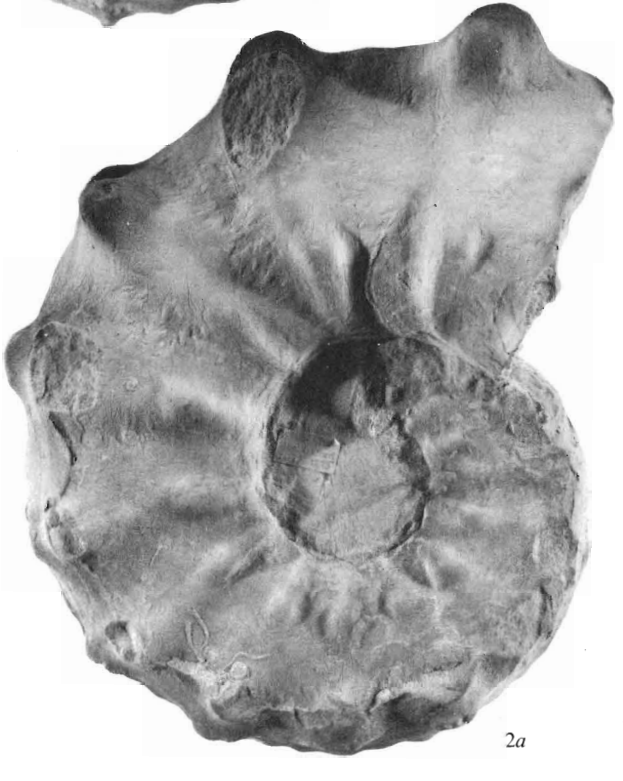
KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites

1*a*

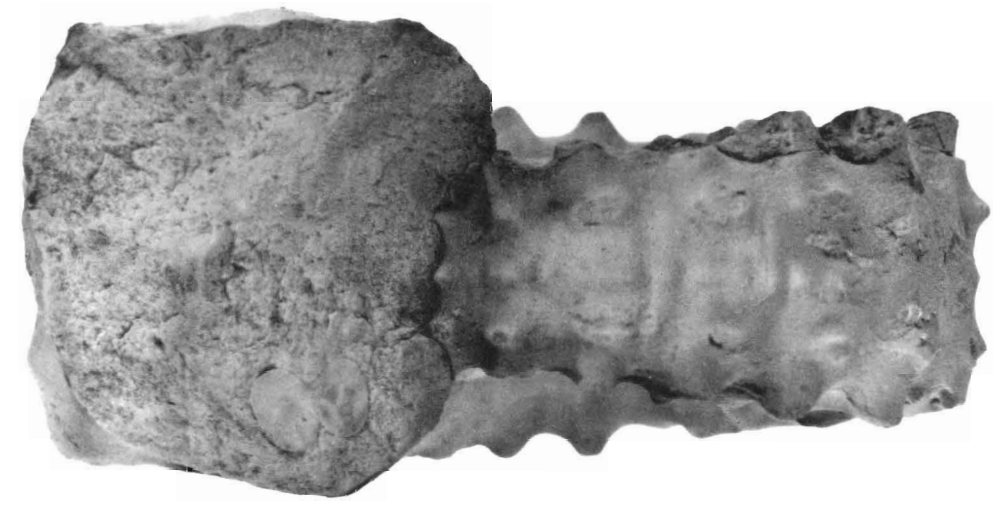
1*b*



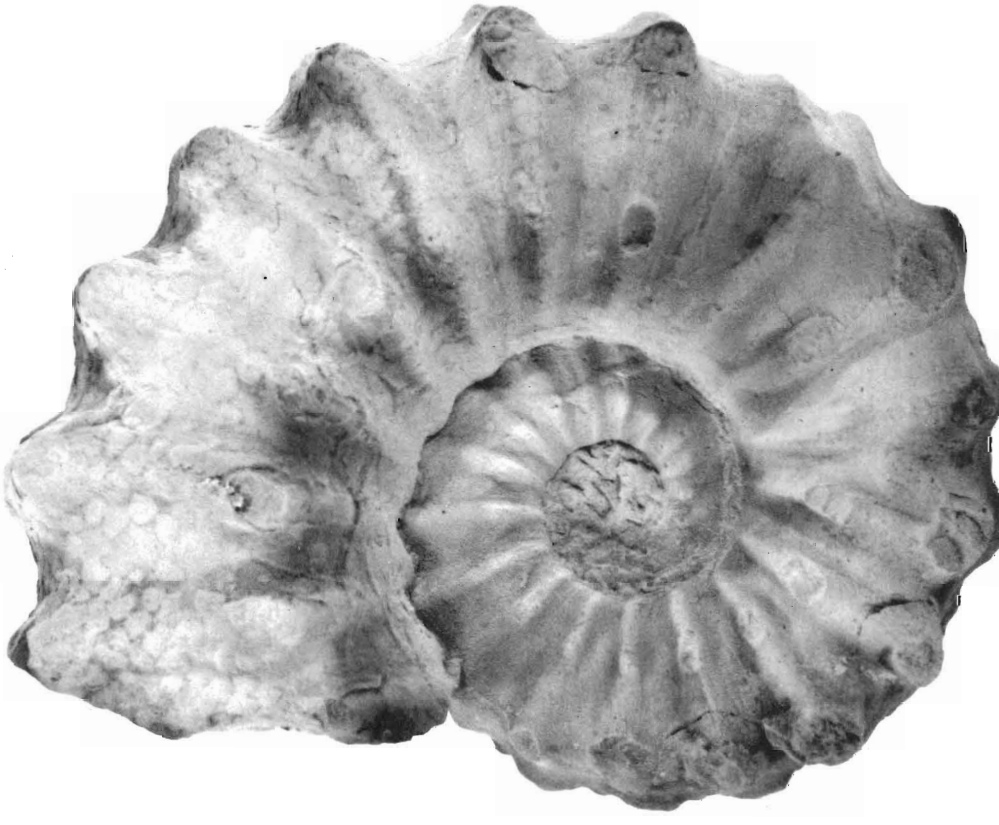
2*a*

2*b*

KENNEDY, Cenomanian ammonites



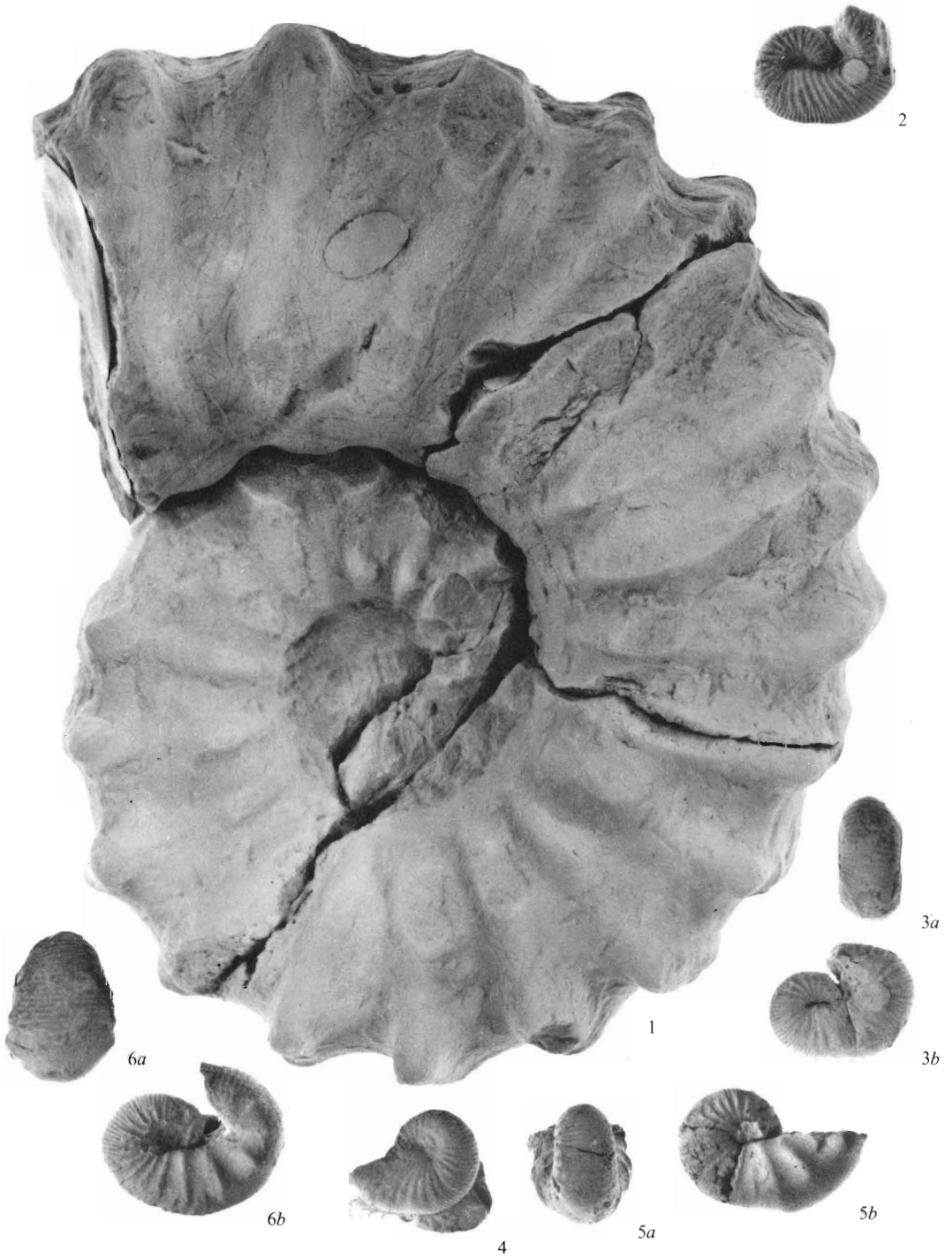
1*b*



1*a*

KENNEDY, Cenomanian ammonites

KENNEDY, Cenomanian ammonites



KENNEDY, Cenomanian ammonites