UPPER CENOMANIAN AMMONITES FROM ANJOU AND THE VENDÉE, WESTERN FRANCE

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ABSTRACT. Revision of the Upper Cenomanian ammonites from Anjou and the Vendée in Western France, including those described by A. de Grossouvre (1912), shows that two faunas are present. A lower assemblage including *Pseudocalycoceras*? cf. *lattense* (Thomel), *Thomelites* aff. *sornayi* (Thomel), and rare *Calycoceras naviculare* (Mantell) comes from the Marnes à Ostracées, and can be correlated with similar faunas in Sarthe, the Paris Basin, and southern England. Above, the Sables à *Catopygus obtusus* yields *Sciponoceras gracile* (Shumard), *Metengonoceras dumbli* (Cragin), *Proplacenticeras* cf. *memoriaschloenbachi* (Laube and Bruder), *Forbesiceras* group of *largilliertianum* (d'Orbigny), common *Calycoceras naviculare* and *Metoicoceras geslinianum* (d'Orbigny). This latter fauna can be traced widely in north-western Europe and is equivalent to that of the Plenus Marls of the Anglo-Paris Basin. Elsewhere it is known from Africa and Japan and matches the fauna of the North American *Sciponoceras gracile* Zone. A complete revision of the European species of *Metoicoceras* is given; *M. gourdoni* and four other species described by de Grossouvre are shown to be synonyms of *M. geslinianum*, as are five of the North American species, including the zonal index *M. whitei* Hyatt.

IN 1912 A. de Grossouvre published a short paper entitled '*Le Crétacé de la Loire-Inférieur et de la Vendée*', in which he discussed the stratigraphy and age of the most westerly outliers of Upper Cretaceous sediments in France, north, south, and west of Palluau in the Vendée, and relations within the area around Angers in Anjou, at the western edge of the main outcrop of the Upper Cretaceous in the western margins of the Paris Basin, where the Cretaceous transgresses over the Armorican basement (text-fig. 1). De Grossouvre provided what was for many years the most extensive description and discussion of the ammonite faunas of the zone of *Actinocamax plenus*, the Tuffeau de Saumur and their equivalents (which, together, he equated with Saumurien (Salmurien) substage of the Turonian (de Grossouvre 1901, pp. 779, 783)) and described a series of *Metoicoceras* (as '*Mammites*'), *Metengonoceras*, and *Placenticeras* species from Touvois, Briollay, and Commequiers.

This paper, which is a contribution to the Mid-Cretaceous Events project (sponsored by UNESCO and the IGCP), stems from the confusion and conflicting data at present in circulation over the nature of the sequence across, and position of, the Cenomanian–Turonian boundary (Jefferies 1962–1963; Thomel 1965, 1972*a–b*, 1973*a–b*; Cobban and Scott 1972; Magné and Polvêche 1968; Berthou and Lauverjat 1974*a–b*; Kennedy and Juignet 1973; Juignet, Kennedy, and Wright 1973; Rawson, Curry, Dilley, Hancock, Kennedy, Neale, Wood, and Worssam 1978; Cooper 1978*a–b*, 1979). A revision of the stratigraphy and ammonites described by de Grossouvre was clearly necessary. The Briollay and Touvois material proved to be far more extensive than suggested by published work, for it allows a complete revision of the European species of the widespread late Cenomanian genus *Metoicoceras* Hyatt, 1903, demonstrating clearly the stratigraphic and systematic relationship between the *Metoicoceras* faunas of the Old and New Worlds. It clarifies certain confusing supposed faunal associations and provides ammonite evidence for the age of the lower parts of the Upper Cretaceous in the region.

PREVIOUS WORK

Angers. The higher parts of the Cenomanian in the Angers region, and in particular those around Briollay, were first described in detail by de Grossouvre (1889, p. 503) who noted a level rich in

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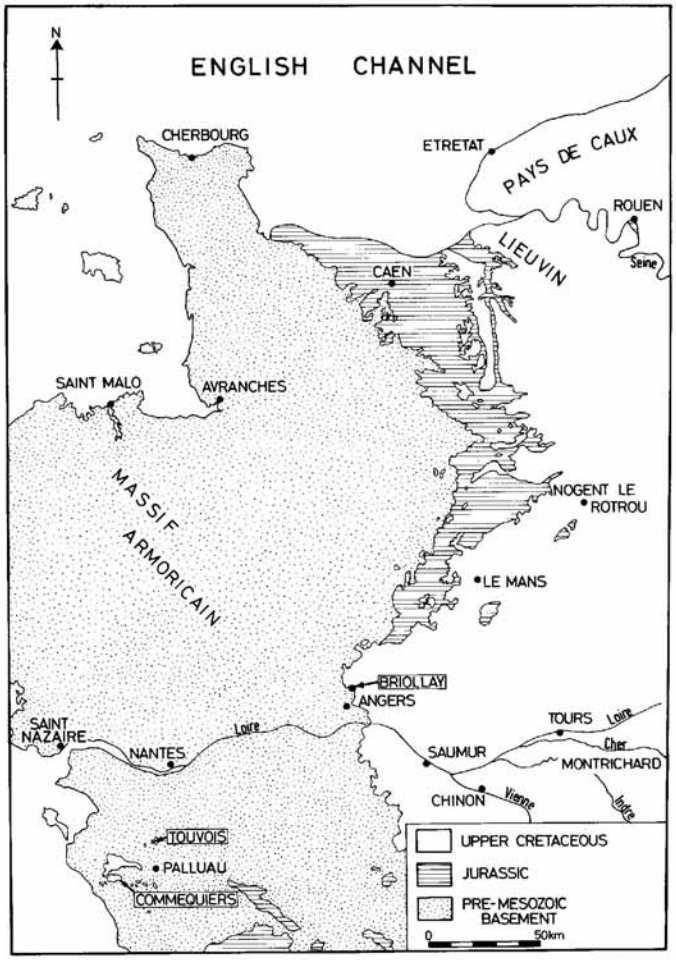


TEXT-FIG. 1. Simplified geological map of north-west France showing the position of the more important localities mentioned in the text.

echinoids (horizon de la Dionière), overlain by Marnes à Ostracées yielding rudists, and a sandy unit with *Pecten guerangeri* d'Orbigny, in turn overlain by a tuffeau containing *Inoceramus labiatus* and thus of Turonian age. Subsequently (1912) he studied and described the ammonites preserved in the Musée d'Histoire Naturelle at Angers as noted in our introductory remarks.

In his synthesis on the Cretaceous of Anjou, Couffon (1936; see also the earlier English Summary of the 'Geology of Maine-et-Loire' published by Couffon and Dollfus in 1928) gave (loosely translated) the following succession in the Angers–Briollay region:

4. Glauconitic sands with *Protocardia hillana*, *Pecten guerangeri*, *Mammites dumasi*, *M. gourdoni*, *Metengonoceras douvillei* . . . traced northwards these pass into cross-bedded sandstones.

3. Marnes à Ostracées.
2. Marnes glauconieuse (= Sables du Maine).
1. Black lignitic and pyritic sands and shaly clays with vegetable debris.

The sands and clays at the base of the sequence rest on Precambrian schists.

Above this Cenomanian sequence, Couffon recorded the presence of Marnes à *Terebratella carantonensis* and Craie à *I. labiatus*, attributed to the Lower Turonian. His work includes lengthy faunal lists for the Cenomanian of the region, notably of the echinoids for which Briollay had become famous.

On the 1/80 000 Geological Map of the region Denizot (1953) recognized the same divisions and emphasized the development of sandstones in the Couches à *Protocardia hillana* in the Morannes region. More recently Louail (1969) has interpreted the clays and sands at the base of this sequence as fluviatile in origin and related them to the Late Cenomanian marine transgression in this region.

The Vendée and Loire-Atlantique. The first stratigraphic accounts of the Cretaceous in the Vendée and Loire-Atlantique (formerly Loire-Inférieure) were given by Rivière (1842) and Bureau (1900). In the Touvois region Bureau recognized the following succession:

3. Three beds of grey fossiliferous limestone, separated by beds of ferruginous sand; approx. 1·3 m.
2. Blue lignitic and pyritic clay; approx. 3 m.
1. Ferruginous sands; approx. 5 m.

The limestones at the top of this sequence yielded the rich faunas preserved in the Cailliaud and Bertrand-Geslin collections now at the Musée de Nantes, whilst Geslin sent some material to d'Orbigny, including one of the syntypes of *Metoicoceras geslinianum*. There are also collections at Nantes from other outliers in this area, notably Commequiers and Bois de Cené, in part described by de Grossouvre in 1912. Other workers in this region have included Ganichaud (1922) who recorded '*Fagesia superstes*' from Montbert (Loire-Atlantique); Gillard (1942) recorded '*Sphenodiscus*' aff. *pedernalis*, *Metengonoceras* cf. *arnaudi*, *Neolobites vibrayei*, *N.* aff. *bedoti*, and '*Stoliczkaia*' sp. from Touvois, whilst Louail (1975) has recorded *Metoicoceras geslinianum*, *Proplacenticeras orbignyanum*, and *Mammites* from Commequiers. Ters (1959) and Louail (1975) have proposed palaeogeographic and stratigraphic syntheses of this area.

PRESENT OUTCROPS

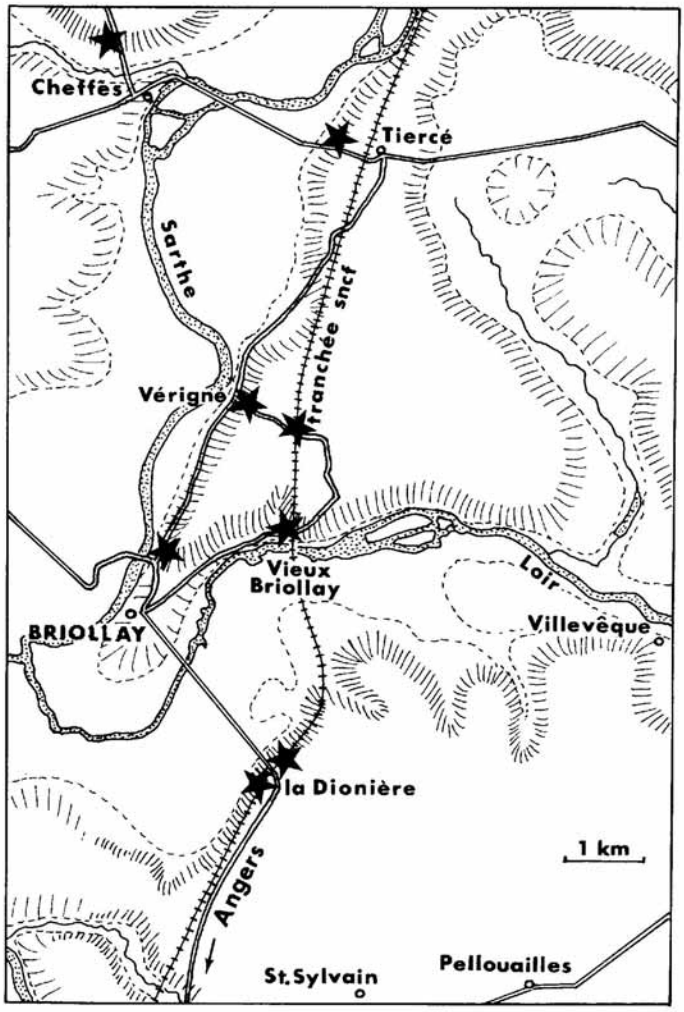
In Vendée and Loire-Atlantique sections are now very poor and there is little to be seen at Touvois. The ammonites described here were probably collected during the excavation of a temporary quarry to supply building stone for the nearby mansion. In the environs of Briollay, however, it is still possible to piece together a succession from scattered outcrops, many of a temporary nature. Text-fig. 2 shows the location of sections in the area, and text-fig. 3 gives a composite succession.

The lowest units visible are of fluvial origin and consist of grey flakey clays with vegetable debris; perhaps a dozen metres are visible in degraded cuttings alongside the road from Briollay to Verigné, close to the bridge across the Sarthe. Towards the top of this sequence are intercalations of greenish ochreous and rusty quartzose sands and gravels up to a metre in thickness, with lenticles of beige clay. This sequence is believed to be of Middle Cenomanian age and to be equivalent to the Sables du Maine to the north.

The sequence is terminated by a sharp discontinuity surface above which are from 12 to 15 m of Marnes à Ostracées. The lower part of this unit is visible at Tiercé, Verigné, and Vieux Briollay; it consists of grey-beige silty marls with *Pycnodonte biauriculata* and *Exogyra columba*, alternating with shell beds and shelly bioclastic limestones, made up of the same species, up to a few tens of centimetres in thickness. The upper part of the Marnes à Ostracées is visible at Cheffes, Verigné, and La Dionière. Limestones are more conspicuous, and at La Dionière the base of the section is a lumachelle of *E. columba* and *P. biauriculata* with a greenish-white limestone matrix. This is terminated by a thin massive limestone, the upper surface of which is interpreted as a minor discontinuity. Above is a sequence of poorly stratified, bioturbated marls and nodular limestone crowded with *Neithea*, *Chlamys*, oysters and other calcitic fossils. This unit is terminated by a poorly exposed limestone. This limestone is also visible in the railway cutting north of Vieux Briollay, on the hillsides around Matheflon, and on the left bank of the Loir around Seiches. Here it is a hard calcarenitic limestone crowded with

fossils. (*Exogyra*, *Neithea*, *Chlamys*, echinoids, brachiopods, bryozoans, serpulids); the bed is riddled by ramifying empty arthropod burrows (Thalassinoides), whilst the top surface is a striking green-stained hardground with borings and cemented epizoans.

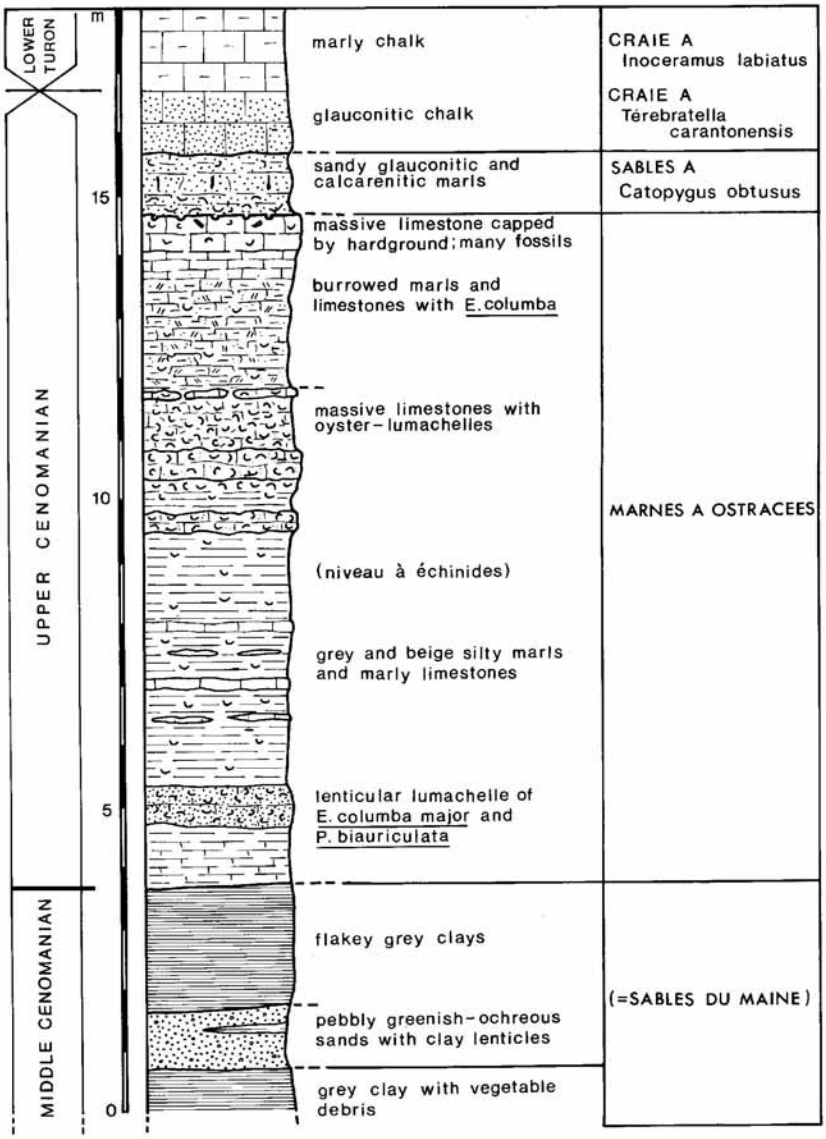
The succeeding Sables à *Catopygus obtusus* consists of sandy, glauconitic marls, sometimes calcarenitic, locally cemented into limestone lenticles; there is a rich shelly fauna, dominated by oysters and pectinids. Early workers give a maximum thickness to this unit of no more than a metre or so, but to the north their



TEXT-FIG. 2. Location of sections in the Briollay region, north of Angers, Maine-et-Loire.

lateral equivalents, the Grès de Morannes and Sables de Bousse, expand to 5 to 15 m, consisting of interbedded sands and gaize lenticles.

Above there is a thin representative of glauconitic Craie à *Terebratella carantonensis*, succeeded by typical marly Craie à *Inoceramus labiatus*.



TEXT-FIG. 3. Generalized stratigraphic succession in the Briollay region.

PROVENANCE OF SPECIMENS

We have collected only fragmentary ammonites from the Briollay sequence, but, thanks to the distinctive lithologies and locality data available, specimens in older collections can be allocated to the formations present in the area as follows:

1. From the lower parts of the Marnes à Ostracées: *Pseudocalycoceras*? cf. *lattense* (Thomel) (two specimens), *Thomelites* aff. *sornayi* (Thomel) (two specimens).
2. From the hardground at the top of the Marnes à Ostracées: *Calycoceras naviculare* (Mantell) (one specimen).
3. From the Sables à *Catopygus obtusus*: *Sciponoceras gracile* (Shumard) (three specimens), *Metengonoceras* cf. *dumbli* (Cragin) (two specimens), *Metengonoceras* sp. (two specimens), *Proplacenticeras* cf. *memoria-schloenbachi* (Laube and Bruder) (one specimen), *Forbesiceras* sp. group of *largilliertianum* (d'Orbigny) (two specimens), *Euomphaloceras septemseriatum* (Cragin) (one specimen), *Calycoceras naviculare* (Mantell) (six specimens), *Metoicoceras geslinianum* (D'Orbigny) (eleven specimens).

Many of these specimens have distinctive green-stained and coated exteriors, suggesting that they come from the base of the Sables à *Catopygus obtusus* immediately above the hardground capping the Marnes à Ostracées.

The Touvois material, consisting of two specimens of *Metengonoceras dumbli*, two of *Calycoceras naviculare*, and eight of *Metoicoceras geslinianum*, occurs in calcarenitic limestones as moulds, some of which have broken surfaces encrusted by serpulids, suggesting reworking. All are believed to be from the limestones at the top of the sequence.

Finally a specimen of *C. naviculare* from Saint-Cyr-en-Bourg (A5) is preserved in coarse, calcarenitic, slightly glauconitic chalk and appears to come from the Craie à *Terebratella carantonensis* or base of the Craie de Fretvou of this area.

SYSTEMATIC DESCRIPTIONS

Location of specimens. The following abbreviations are used to indicate the repositories of specimens cited in the text.

BMNH—British Museum (Natural History), London. MNHP—Muséum d'Histoire Naturelle, Paris. A—Musée d'Angers. N—Musée de Nantes. EMP—École des Mines, Paris (collections now housed at Lyon).

Conventions. All dimensions of specimens are given in millimetres. D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus. Figures in parenthesis are dimensions as a percentage of total diameter. U = number of umbilical bullae per whorl; R = number of ribs per whorl. In describing suture lines: E = external lobe, L = lateral lobe, U = umbilical lobe, I = internal lobe.

Suborder ANCYLOCERATINA Wiedmann, 1966
Superfamily TURRILITACEAE Meek, 1876
Family BACULITIDAE Gill, 1871
Genus SCIPONOCERAS Hyatt, 1894
(*Cyrtochilus* Meek, 1876 (*non* Jakowlew, 1875); *Cyrtochilella* Strand, 1929)
Sciponoceras gracile (Shumard)

Plate 8, figs. 9, 10; Plate 10, figs. 1–4

Synonymy and description. See Cobban and Scott 1972, p. 47; Wright and Kennedy in Juignet *et al.* 1973, p. 21.

Material. Three specimens from the Sables à *Catopygus obtusus*: A23 and A35 (the latter in the aperture of a *Proplacenticeras*) from La Dionière (Maine-et-Loire) and A24 from Matheflon near Seiches-sur-Le-Loir (Maine-et-Loire).

Discussion. The specimens from La Dionière agree closely with the authoritative redescription of *S. gracile* by Cobban and Scott (1972, pp. 47–49, pl. 17, figs. 9–29), and with specimens from the type region of north Texas figured by Wright and Kennedy in Juignet *et al.* (1973, pl. 1, figs. 5–6).

Occurrence. This widely distributed species is best known from the United States where it characterizes the terminal Cenomanian zone named after it. Cobban and Scott (1972) record it from Montana, Wyoming, Utah, Colorado, New Mexico, Arizona, and Kansas. The lost type came from north Texas, where it is moderately common. In England the species occurs in the Plenus Marls (Beds 4–8 of Jefferies 1963 in particular) and the base of the Melbourn Rock where it is locally abundant. In northern France the range is similar. On the Normandy coast it occurs as green-coated moulds in Niveau T_2 of Juignet (1970) and in the chalk above this horizon at Rouen (Bucaille collection). In Sarthe it is found in the Sables à *Catopygus obtusus*.

The records from Madagascar are dubious (Boule, Lemoine, and Thévenin 1907, p. 44; Collignon 1931, p. 94, pl. 9, fig. 28; text-fig. 26), as is that from the Cameroons (Solger 1904; see Reyment 1955, p. 15). However, the species does occur at Salinas, Angola (Cooper 1978).

Suborder AMMONITINA Hyatt, 1889
Superfamily HOPLITACEAE H. Douvillé, 1890
Family PLACENTICERATIDAE Hyatt, 1900
Genus PROPLACENTICERAS Spath, 1926

Type species. *Placenticeras fritschi* de Grossouvre, 1894, p. 124, pl. 5, figs. 1, 2, by the original designation of Spath 1926*a*, p. 79.

Proplacenticeras cf. *memoriaschloenbachi* (Laube and Bruder)

Plate 14, figs. 4, 5; text-figs. 11F

Compare
1887 *Placenticeras Memoria-Schloenbachi* Laube and Bruder, p. 221, pl. 23, fig. 1.

Material. A single fragment, A35, from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine et Loire).

Description. The specimen is a wholly septate internal mould. The umbilicus is small, deep, and funnel-shaped, with a flat wall and abruptly rounded to subangular shoulder. The flanks are gently inflated, with a whorl breadth : height ratio of 0·5, the maximum breadth being well down on the flanks. The outer flanks are flattened, converging to a narrow, tabulate venter with abrupt angular shoulders. The ornament consists of faint rounded bullae at the umbilical shoulder (five in the fragment preserved); there is no trace of flank ornament on the mould, nor are ventrolateral clavi developed. The suture, although too poorly preserved for complete description or illustration, is typically placenticeratid, with deep, much subdivided, narrow-necked lobes and saddles.

Discussion. The work of Wolleben (1967) on Santonian-Campanian *Placenticeras* of the *P. syrtale* (Morton) group, Paulcke's work on Campanian *Hoplitoplacenticeras* (1907), and unpublished work by H. C. Klinger and W. J. Kennedy on Coniacian *Proplacenticeras* of the *umkwelanense* (Etheridge)—*kaffrarium* (Etheridge)—*subkaffrarium* (Spath) group has demonstrated that placenticeratid species are extremely variable. Each population shows a gradation from smooth oxyconic individuals with narrow tabulate venters to robust, ribbed, and tuberculate individuals (e.g. *Stantonoceras* Johnston, 1903), and that evolutionary changes consist in large part of a shift in population mode and proportion of morphotypes within successive species, as now widely documented in other ammonite groups, e.g. *Neogastroplites* (Reeside and Cobban 1960). No large *Proplacenticeras* populations of late Cenomanian to early Turonian age have been documented to date, but we suspect that the several names introduced for forms at this level in North America, including *P. pseudoplacenta* (Hyatt) (1903, p. 216), *P. pseudoplacenta occidentale* (Hyatt) (1903, p. 217), and *P. cumminsi* (Cragin) (1893, p. 237), represent but a single species, as do the approximately contemporaneous European forms, including perhaps *P. kharesmenense* (Lahusen) (in Romanowsky 1884, p. 134, pl. 2; pl. 3, fig. 1), *P. memoriaschloenbachi* Laube and Bruder (1887, p. 221, pl. 23, fig. 1), and *P. kysylcumense* (Arkhanguelsky) (1916, p. 45, pl. 7, figs. 4–7; text-fig. 16).

Our single specimen cannot resolve these problems; by virtue of its weak umbilical bullae and tabulate venter, lacking ventrolateral tubercles, it most strongly resembles *P. memoriaschloenbachi*.

Occurrence. Apart from the present occurrence in the Sables à *Catopygus obtusus* of Briollay, we have seen poor fragments from the same horizon in Sarthe which may belong here. *P. memoriaschloenbachi* was first described from the Zone of *Inoceramus labiatus* near Prague, but this zone in Czechoslovakia includes the *gracile* Zone. The various records from Saxony in East Germany are all from the *gracile* Zone.

Family ENGONOCERATIDAE Hyatt, 1900
Genus METENGONOCERAS Hyatt, 1903

Type species. *Metengonoceras inscriptum* Hyatt 1903, p. 180, pl. 25, figs. 5–9; pl. 26, figs. 1–4, by the subsequent designation of Diener (1925).

Diagnosis. Very compressed involute engonoceratids with a narrow venter, concave and bicarinate or tabulate during early and middle growth stages but rounding on adult whorls and body chambers. Weak radial ribs and ventrolateral tubercles are rarely present; flexuous growth lines are generally the sole ornament. Internal moulds may lack ornament and have acute peripheries. The suture line is pseudoceratitic, with numerous auxiliary and adventive elements; saddles are entire, lobes moderately frilled.

Discussion and occurrence. Spath (1924) introduced the genus *Epengonoceras* for 'Hyatt's "*Metengonoceras*" from the Eagle Ford Shales', that is for the Cenomanian species; those from the Albian he left as *Metengonoceras*. By 1931 (p. 340) Spath himself doubted this generic distinction. Stephenson (1953), in the most extensive review of the type species, *Epengonoceras dumbli*, concluded that it was inseparable from *Metengonoceras*. We agree: the sutures are similar; the only difference in ornament between *M. inscriptum* and *E. dumbli* are broad plicate ribs on the inner flank of the former.

Metengonoceras dumbli (Cragin)

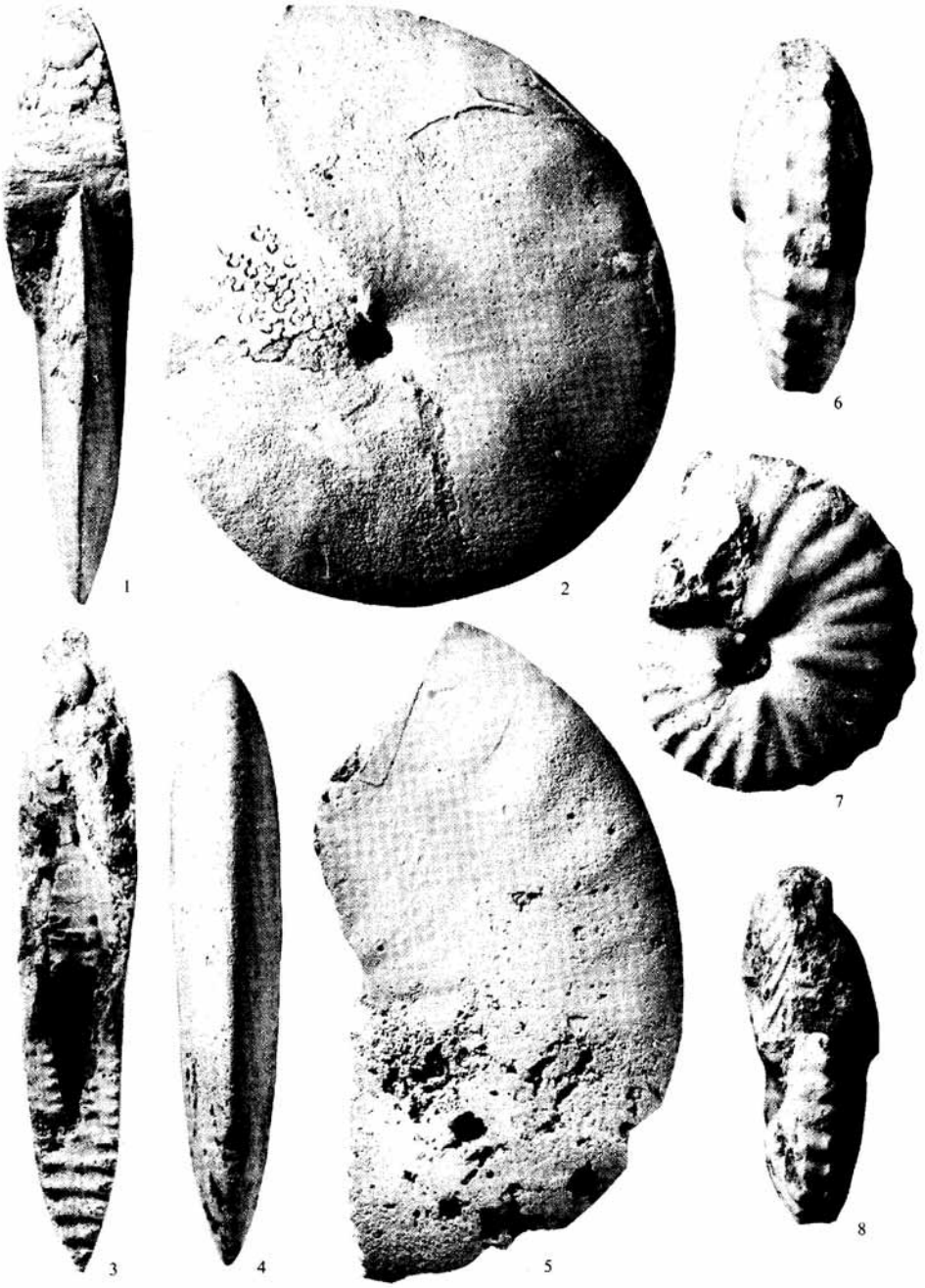
Plate 3, figs. 1–5; Plate 7, figs. 4–6; text-figs. 4A–G; 5B–F

1893	*Sphenodiscus dumbli* Cragin, p. 243, pl. 44, fig. 6.
1894	*Sphenodiscus* cf. *pedernalis* de Grossouvre (*non* von Buch), p. 140, text-fig. 58.
1903	*Metengonoceras dumbli* (Cragin); Hyatt, p. 185, pl. 27, figs. 3–14.
non 1904	*Engonoceras dumbli* (Cragin); Lasswitz, p. 232, pl. 13, fig. 2*a–b*.
?1908	*Metengonoceras* sp. de Grossouvre, p. 10, text-fig. 1.
1908	*Metengonoceras* sp. de Grossouvre, p. 10, text-fig. 2.
?1912	*Metengonoceras* sp. de Grossouvre, p. 33, text-fig. 5.
1912	*Metengonoceras Douvillei* de Grossouvre, p. 34, pl. 3, fig. 3; text-fig. 6.
1912	*Metengonoceras tolveiense* de Grossouvre, p. 36, pl. 3, fig. 4; text-fig. 8.
1924	*Epengonoceras dumbli* (Cragin); Spath, p. 508.
1925	*Metengonoceras Douvillei* Grossouvre; Diener, p. 229.
1925	*Metengonoceras Dumblei* (*sic*) Cragin; Diener, p. 229.
1925	*Metengonoceras tolociense* (*sic*) Grossouvre; Diener, p. 229.
?1925	*Metengonoceras* sp. ind. Grossouvre; Diener, p. 229.
1928	*Epengonoceras dumbli* (Cragin); Adkins, p. 264.
1931	*Epengonoceras dumbli* (Cragin); Reeside and Weymouth, p. 14.
1935	*Metengonoceras dumbli* (Cragin); Furon, p. 55.
?1935	*Metengonoceras nigeriensis* Furon, p. 55, pl. 3, fig. 1*a–b*; text-fig. 16.

EXPLANATION OF PLATE 3

Figs. 1–5. *Metengonoceras dumbli* (Cragin). 1, 2. N5; 3–5. N4 from Touvois (Loire-Atlantique). These two specimens are the syntypes of *Metengonoceras tolveiense* de Grossouvre.

Figs. 6–8. *Metoicoceras geslinianum* (d'Orbigny). N3 from Touvois (Loire-Atlantique); the holotype of *Mammites pervinquierei* de Grossouvre.



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1942 *Epengonoceras dumbli* (Cragin); Moreman, p. 217.
1943 *Metengonoceras dumbli* (Cragin); Schneegans, p. 136, text-fig. 17.
1951 *Metengonoceras dumblei* (*sic*) (Cragin); Adkins and Lozo, pl. 2, fig. 5.
1953 *Metengonoceras dumbli* (Cragin); Stephenson, p. 206, pl. 55, figs. 1–4.
1957 *Epengonoceras dumbli* (Cragin); Barber, p. 9, pl. 25, figs. 9, 10.
1960 *Metengonoceras douvillei* de Grossouvre; Hancock, p. 250.
?1972 *Epengonoceras dumbli* (Cragin)?; Cobban and Scott, p. 59, pl. 8.
1978 *Metengonoceras dumbli* (Cragin); Kennedy and Hancock, pl. 13, fig. 5*a–c*.

Types. Cragin (1893, p. 243) based this species on twenty specimens: one figured by Hyatt (1903, pl. 27, figs. 3–14) and Stephenson (1953, pl. 55, fig. 1) from the Templeton Member of the Woodbine Formation, four miles east of Whitsboro, Grayson County, Texas, is referred to as the 'type' by both authors, but no formal lectotype designation has been made. We therefore designate this specimen, USNM 29403 as lectotype of Cragin's species.

Material. Three specimens: N4 and N5, the syntypes of *M. tolveiense* de Grossouvre, from Touvois (Loire-Atlantique), and the holotype of *M. douvillei* de Grossouvre (École des Mines, Paris) from the Upper Cenomanian of the Carrière Sainte-Croix, Le Mans (Sarthe). Two fragments, A30 from the Sables à *Catopygus obtusus* of the Fosse Hubért, Morannes (Maine-et-Loire), and A32 from the Sables à *C. obtusus* of La Dionière, Briollay (Maine-et-Loire), may also belong here.

Dimensions

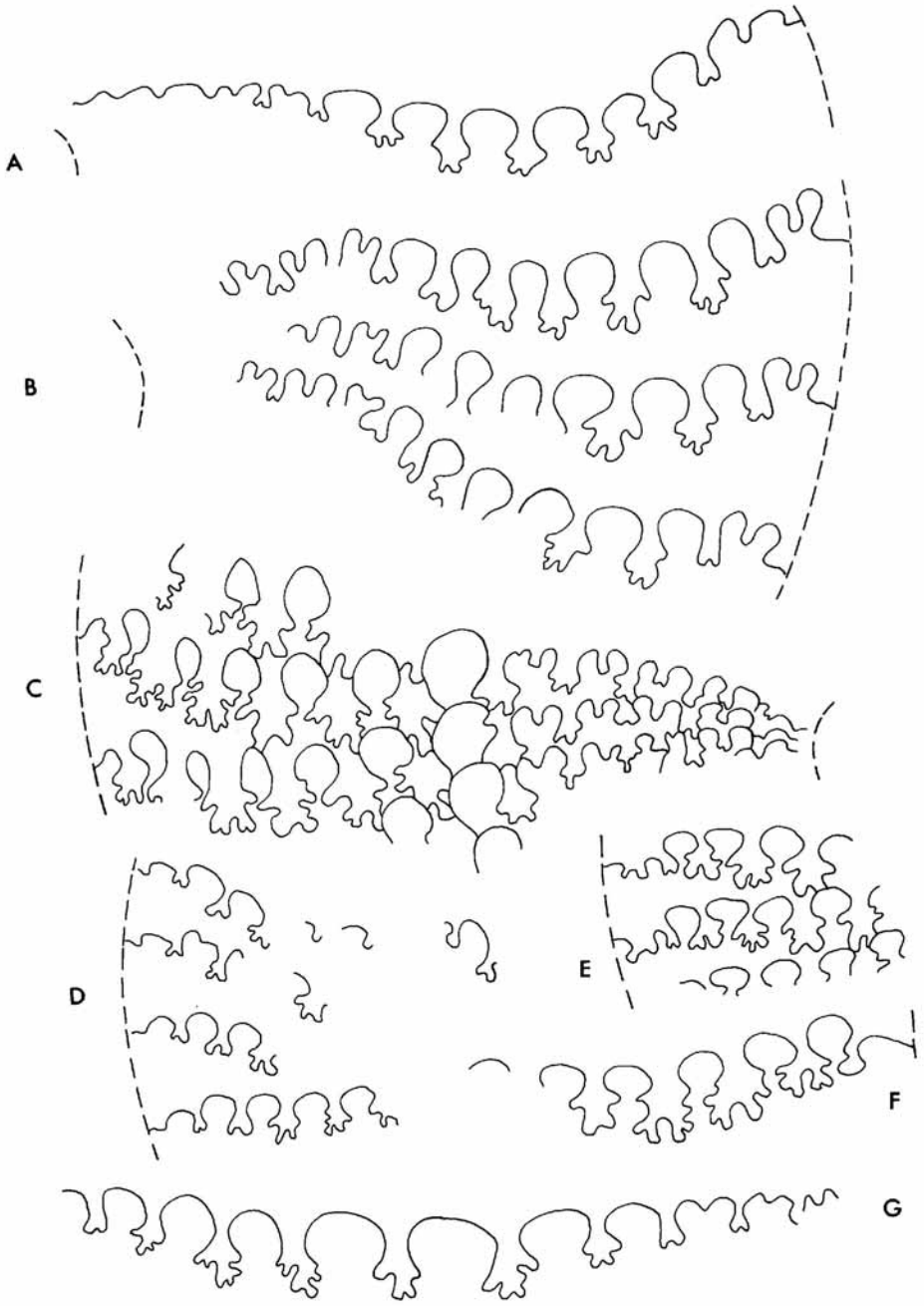
	D	*Wb*	*Wh*	*Wb/Wh*	*U*
The holotype of *M. douvillei*	88·0	17·0(19)	45·0(51)	0·38	6·0(7)
N5	94·0	18·0(19)	49·0(52)	0·37	5·5(7)

Description. The material consists entirely of internal moulds and all specimens retain their body chamber. The coiling is very involute, compressed (whorl breadth to height ratio is 0·37 to 0·38), with a very narrow tabulate or acute venter on internal moulds of the phragmocone, rounding on the body chamber.

Ornament, best preserved on the body chamber, consists of flexuous biconcave striae, prorsiradiate and distinctly but shallowly concave across the lower flank, and markedly convex at mid-flank; they are again distinctly concave, on the outer flank and project slightly on the venter. The outer part of the striae is periodically accentuated into a low, broad, flat, plicate rib, producing a style of ornament similar to that seen in many Oppeliidae.

The sutures are closely spaced and interlock throughout (text-fig. 4A–F). In the adult suture there are approximately fourteen saddles which vary from squat and flat to distinctly rounded or phylloid; the necks are equally variable in degree of constriction. The auxiliary saddles on the suspensive lobe are bifid, tending to simplify towards the umbilical shoulder. De Grossouvre's figure of the suture of *M. tolveiense* is based on the inner whorls of specimen N4; it is redrawn in text-fig. 4E; the adult sutures tend to show somewhat greater elongation of the saddles.

TEXT-FIG. 4. External sutures of European *Mentengonoceras*. A. *Metengonoceras douvillei* de Grossouvre. A copy of de Grossouvre's (1912) figure of the suture of the holotype (École des Mines, Paris), from the Upper Cenomanian of Le Mans (Sarthe) ×3. B. *M. arnaudi* de Grossouvre. A copy of de Grossouvre's (1912) figure of the suture of the holotype, from the Cenomanian of Charentes. ×3. C. *Metengonoceras* sp. Specimen A33 from the Marnes à *Ostrea biauriculata* of Morannes (Maine-et-Loire). ×1·5. D. *M. douvillei* de Grossouvre. Parts of three successive sutures of the holotype. ×1·5. (See also fig. A.) E. *M. tolveiense* de Grossouvre. Parts of three successive sutures of the inner whorls of syntype N4, from the Cenomanian of Touvois (Loire-Atlantique). ×3. F. *M. tolveiense* de Grossouvre. Partial suture of syntype N5, from the Cenomanian of Touvois (Loire-Atlantique). ×3. G. *M.* sp. Copy of de Grossouvre (1912) from the Cenomanian of Sarthe (precise horizon unknown). ×3.


A
B
C
D
E
F
G

Discussion. De Grossouvre (1912) said that *M. tolveiense* could be distinguished from *M. douvillei* by the narrow base and slimmer body of the saddles. We doubt if this is sufficient to justify specific separation between ammonites of such closely similar proportions and ornament. The two fragments from Briollay may also belong to the same species.

When this material is compared with figures and specimens of the North American *M. dumbli*, the similarities are striking. The sutures of *M. dumbli* are also rather variable (compare text-figs. 4A, D, E with 5B–F and Stephenson 1953, p. 206), but show a similar number of elements, a similar ventral saddle, proportion and degree of division of lobes, variation in outline of saddle terminations, and a rather similar subdivision of elements on the suspensive lobe. The venter is similarly flattened on the phragmocone and rounded on the body chamber, although the European material is mature at diameters from 88 to 105 mm, whereas Stephenson (1953, p. 206) records individuals up to 185 mm, and Cobban and Scott (1972) figure an individual 250 mm in diameter. The course of growth striae in both species is similar, although perhaps a little less flexuous in many *M. dumbli*, some of which develop low, broad, crescentic ribs on the outer flank. The available material of *M. tolveiense-douvillei* thus appears to be within the range of variation of *M. dumbli*, which has priority.

The *Metengonoceras* sp. of de Grossouvre (1912, p. 33, text-figs. 5), from an unknown horizon in Sarthe, has a rather similar suture to *M. dumbli* (text-fig. 4G), and may also be a synonym, as may *M. nigeriensis* Furon (1935, p. 55, pl. 3, fig. 1*a–b*) (*fide* Cobban and Scott, p. 59).

M. arnaudi de Grossouvre, from an unknown horizon in the Cenomanian of Charentes, has never been adequately illustrated; de Grossouvre gave only a figure of the suture line (1912, text-fig. 4B). This is rather distinctive, with pincer-like auxiliary saddles on the suspensive lobe and a pincer-like outermost adventive saddle, whilst the saddles are in general more elongate. For these reasons we would tentatively retain it as a separate species.

The final Cenomanian species is *M. acutum* Hyatt (1903, p. 184, pl. 26, fig. 8; pl. 27, figs. 1–2), the suture of which is reproduced here as text-fig. 5A. We have been unable to locate this specimen, but according to Hyatt, it differs from *M. dumbli* in retaining an acute venter in adults and has larger lobes and saddles in a straight instead of curved suture trace. Without further material, it remains difficult to assess this species fully. The type locality, Elm Fork, Dallas County, Texas, suggests it came from the Britton Member of the Eagle Ford Shale (*Sciponoceras gracile* Zone), and is thus later than typical *M. dumbli*, although a contemporary of the specimens described here.

Occurrence. M. dumbli is recorded from horizons as low as the Middle Cenomanian but ranges up to the highest Cenomanian where it is associated with *Metoicoceras whitei*. In the United States the chief occurrences are in Texas, although the species occurs in the Western Interior (Colorado). There are records from the 'Lower Turonian' of Niger and Nigeria, whilst the French material ranges through the higher parts of the Upper Cenomanian.

Metengonoceras sp.

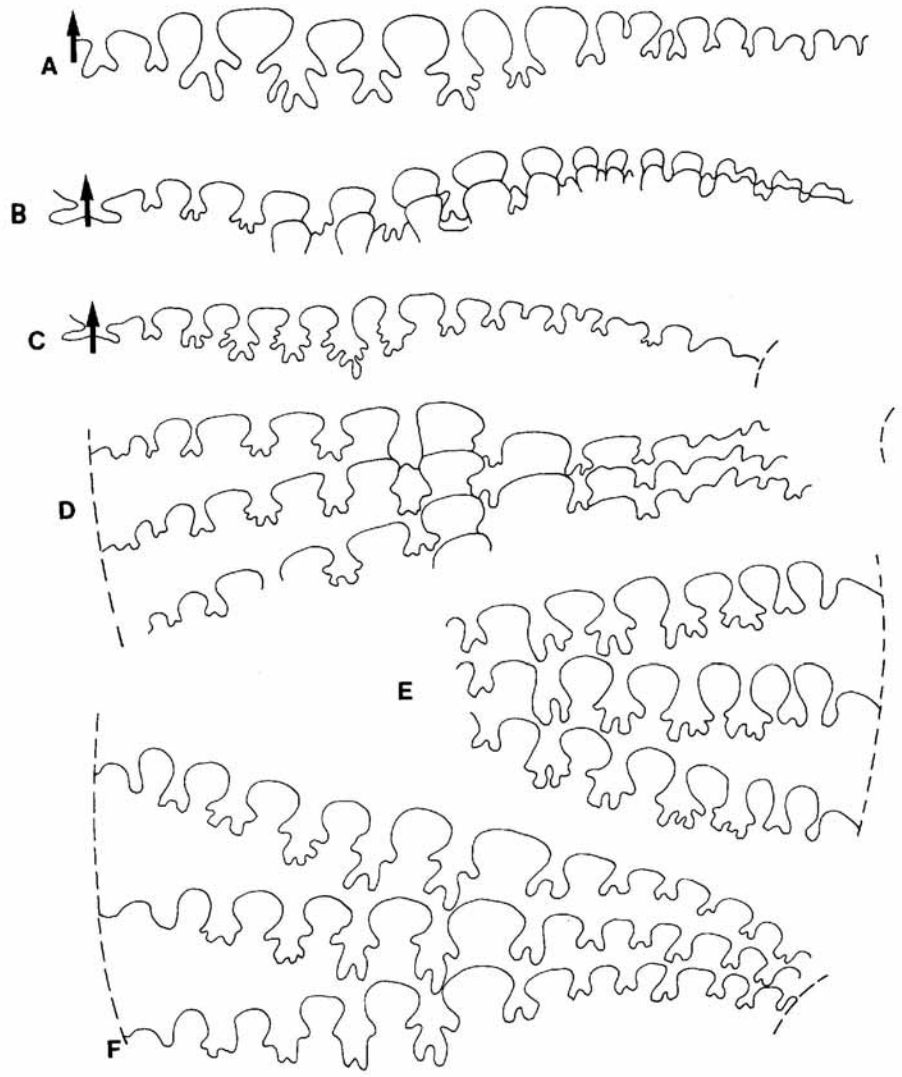
Text-figs. 4C, 6

Material. Two specimens: A33 from Morannes (Maine-et-Loire) probably from the Sables à *Catopygus obtusus*, and A31 from the Sables à *C. obtusus* of La Dionière, Briollay (Maine-et-Loire).

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
A33	123·0	25·2(20)	72·5(59)	0·35	—(—)

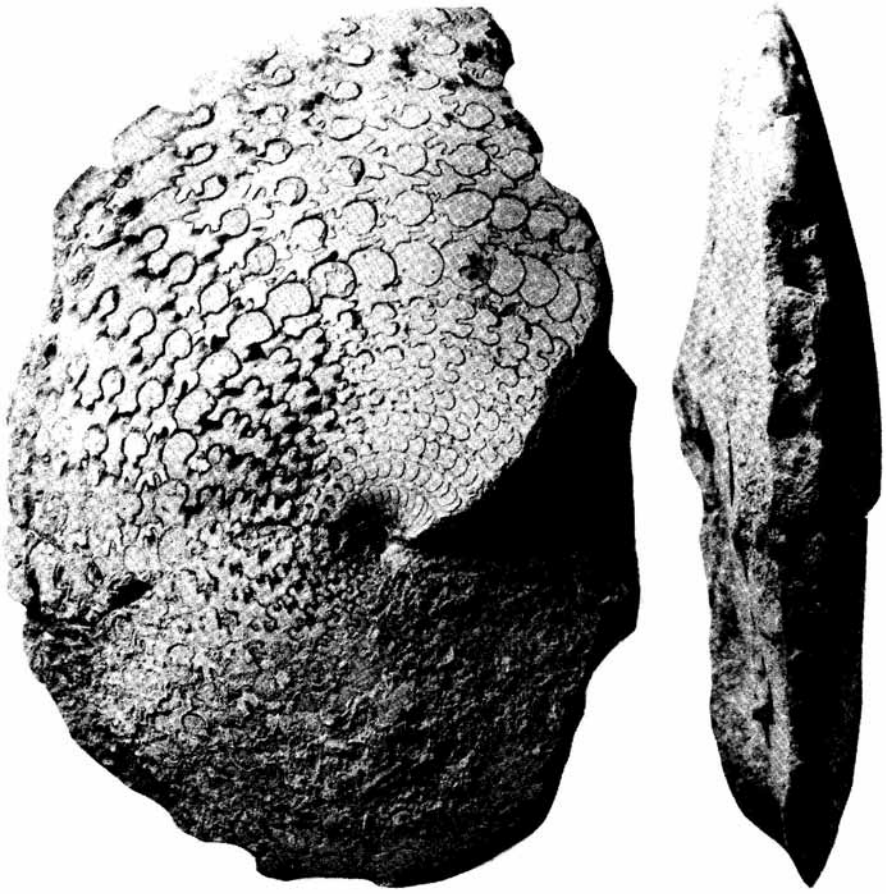
Description and discussion. What appears to be a rather different *Metengonoceras* from those discussed above is represented by a large, wholly septate, specimen and a small fragment. The proportions are similar to those of *M. dumbli* but the suture is very distinctive (text-fig. 4C). The outer adventive lobes are more deeply subdivided and asymmetrically bifid. The ventral saddle appears distinct from that of other *Metengonoceras*, whilst all the larger saddles are far more



TEXT-FIG. 5. External suture lines of North American *Metengonoceras* species. All figures are × 3. A. *Metengonoceras acutum* Hyatt (after Hyatt 1903, pl. 27, fig. 1) from the Eagle Ford Shale (?Britton Member) Elm Fork, Dallas Co., Texas. B–F. *M. dumbli* (Cragin). B–C are taken from the proposed lectotype, USNM 29403 from the Templeton Member of the Woodbine Formation 4 miles east of Whitsboro, Grayson Co., Texas (USGS Mes. Loc. 150). D–F are taken from three specimens in the authors' collections from the Templeton Member of the Woodbine Formation at its type section on the Templeton Branch of Cornelius Creek near Bells, Grayson County, Texas (USGS Mes. Loc. 164).

elongate and phylliform than in other species. The outer four adventive saddles terminate in an asymmetric, narrow-necked, expanded, elongate foliole; the next two have a rather more symmetrical, broader, and larger terminal foliole (although still with a narrow neck); whilst the largest has a broad, subcircular foliole. The auxiliary saddles on the suspensive lobe are bifid, simplifying towards the umbilical seam; and the auxiliary lobes are also bifid and simplify towards the seam.

The rounding of the venter on the phragmocone and particularly the sutures in these specimens set them apart from other available material. These differences may merely be a reflection of greater size, but the sutures are equally distinct from those of the large *M. dumbli* figured by Stephenson (1953, pl. 55, figs. 2–3) so that a further species may indeed be represented.



TEXT-FIG. 6. *Metengonoceras* sp. A33 from Morannes (Maine-et-Loire), probably from the Sables à *Catopygus obtusus*.

SUPERFAMILY ACANTHOCERATACEAE de Grossouvre, 1894
FAMILY LYELLICERATIDAE Spath, 1921
Genus FORBESICERAS Kossmat, 1897
(= DISCOCERAS Kossmat, 1895, *non* Barrande, 1867)

Type species. Ammonites largilliertianus d'Orbigny 1841, p. 320, pl. 95 by the subsequent designation of Diener (1925, p. 180).

Forbesiceras sp. aff. *largilliertianum* (d'Orbigny)

Text-figs. 7, 10A

Compare
1841 *Ammonites largilliertianus* d'Orbigny, p. 320, pl. 95.
1925 *Forbesiceras largilliertianum* (d'Orbigny); Diener, p. 180 (with synonymy).
1971 *Forbesiceras largilliertianum* (d'Orbigny); Kennedy, p. 47 (with synonymy).

Material. Two specimens, A 34 from the Sables à *Catopygus obtusus* of Cheffes-sur-Sarthe and an unregistered specimen in the Palaeontological collections of the University at Rennes, apparently from the same horizon and locality.

Dimensions

	D	*Wb*	*Wh*	*Wb/Wh*	*U*
A34	241·0	73·0(30)	146·0(60)	0·5	—(—)

Description and discussion. These two huge discs are far larger than the majority of previously described *Forbesiceras* and with the absence of inner whorls their identification poses a problem. The coiling is very involute, with a compressed whorl section, the flanks wholly lacking ornament on the mould. The shoulders are accentuated into keels between which the venter is distinctly concave at the smallest diameter visible, slowly flattening around the early parts of the outer whorls, and becoming somewhat rounded at the largest preserved diameter. The sutures show the deeply incised lobes and constricted saddles bearing the sub-phylloid folioles typical of other *Forbesiceras* species (e.g. Stoliczka 1864, pl. 49, fig. 1*b*; Kossmat 1895, p. 180, pl. 22, fig. 6*c*) developed to an extraordinary degree. Although still septate at 240 mm, the suture lines are crowded and overlapped at the smallest diameters visible (text-fig. 7).

Lack of ornament on our specimens suggests they are best compared with *Forbesiceras* of the *largilliertianum* group, which may lack ornament on internal moulds. There are a number of undescribed Upper Cenomanian *Forbesiceras* of this group present in the phosphatic faunas of division C of the Cenomanian Limestone of south Dorset and Devon (Kennedy 1970, p. 658) known only as fragments (authors', C. W. Wright and Orval Bayliss collections) and the present material may well belong to one of these. The two specimens represent the first record of *Forbesiceras* from such a high level in the Cenomanian.

Occurrence. Division C of Cenomanian Limestone (Upper Cenomanian) of south Devon, Sables à *C. obtusus* of Briollay (Maine-et-Loire).

Family ACANTHOCERATIDAE Hyatt, 1900
Subfamily MANTELLICERATINAE Hyatt, 1903
Genus CALYCOCERAS Hyatt, 1900

Type species. Ammonites navicularis Mantell (1822, p. 198, pl. 22, fig. 5), by original designation.

Discussion. Calycoceras has been diagnosed in modern terms by Matsumoto, Saito, and Fukada (1957) and by Kennedy (1971), who recognized groupings within the genus, but refrained from giving subgeneric names to these groups. Full discussion of the nomenclature within *Calycoceras* is to be found in Juignet and Kennedy (1976), who reviewed the various subgenera proposed by Thomel (1972*a*).

Occurrence. The genus is limited to the Middle and Upper Cenomanian. Records of *Calycoceras* from the Lower Cenomanian (e.g. Renz in Renz, Luterbacher, and Schneider 1963; Busnardo, Enay, Latreille, and Rouquet 1966) are based upon *Mantelliceras* specimens that have lost their tuberculation on the outer whorls. The distribution is nearly world-wide: western Europe, U.S.S.R., Middle East, north Africa, Angola, Madagascar, South Africa, southern India, Japan, the western interior of the U.S.A.

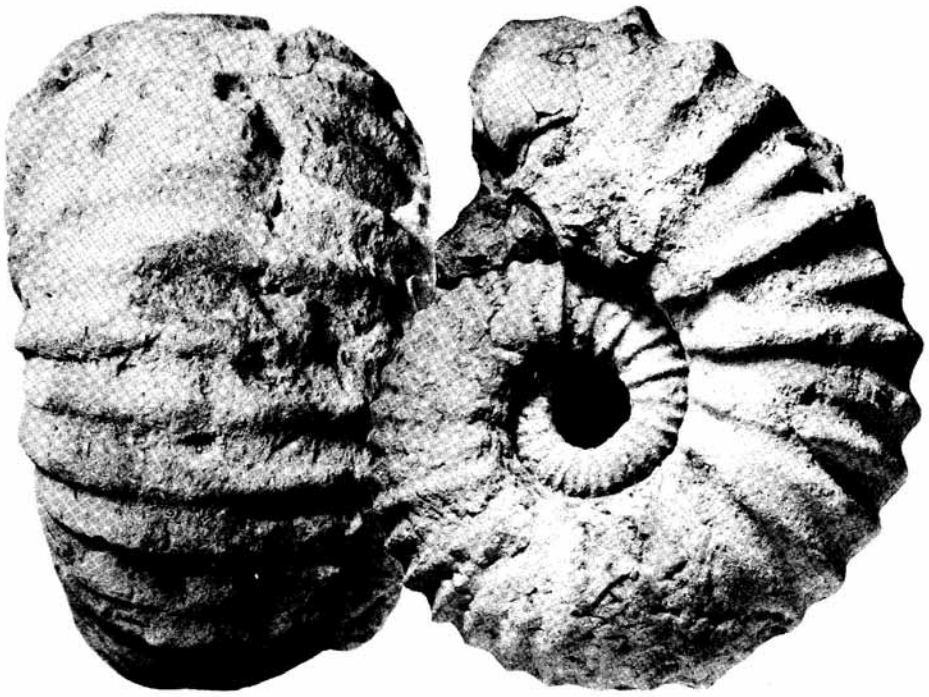
Calycoceras naviculare (Mantell)

Plates 4, 5, 6; Plate 7, figs. 1–3; Plate 15, figs. 4–6; Plate 17, fig. 4; text-figs. 8, 9, 10C, 11A–C

Synonymy. See Kennedy (1971) and Cobban (1971)

Type. Holotype, by monotypy, Mantell's original specimen, BMNH 5681, figured by him (1822) as pl. 22, fig. 5. This specimen is said to be from Offham, 3 km north-west of Lewes (Sussex) and since the work of Crick (1919) there has been discussion as to its precise provenance. The matrix is comparable with the Plenus Marls of this part of Sussex and we suggest this was the source of the holotype.

TEXT-FIG. 7. *Forbesiceras* sp. group of *largilliertianum* (d'Orbigny) from the Sables à *Catopygus obtusus* of Cheffes-sur-Sarthe (Maine-et-Loire). A34. Reduced ×0·55. Actual diameter is 241 mm.

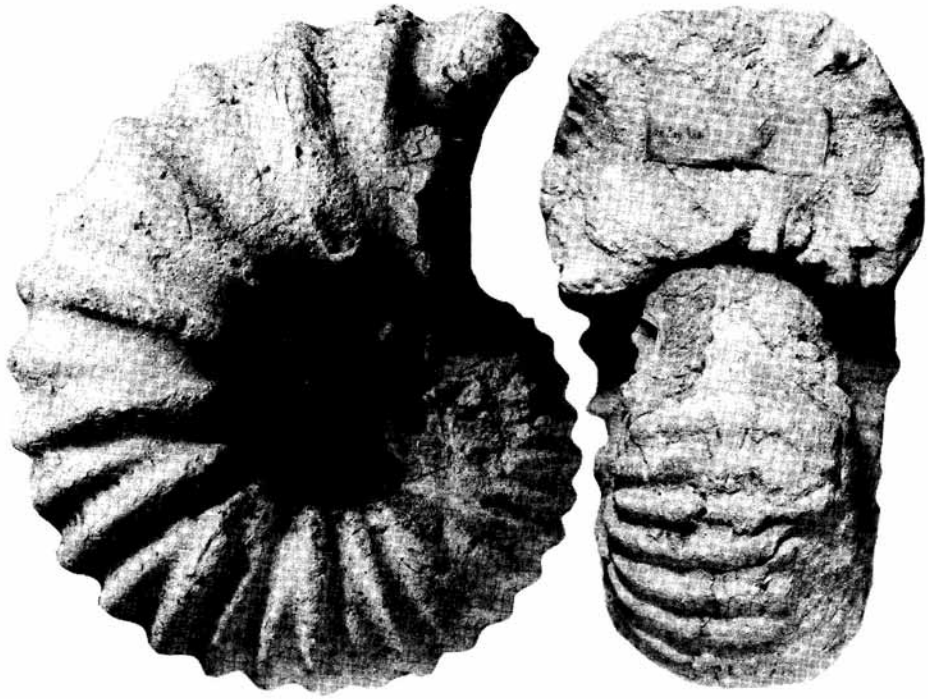


TEXT-FIG. 8. *Calycoceras naviculare* (Mantell). A1, Extreme depressed variant from the hardground at the summit of the Marnes à *Ostrea biauriculata* of Briollay (Maine-et-Loire). The figured side of the specimen is heavily glauconitized, and appears to have formed part of the actual hardground surface. Note specimen of *O. biauriculata* in aperture. The last two thirds of the outer whorl are body chamber. ×0·55.

Material. Eleven specimens: N1, the holotype of *C. grossouvrei* (Spath) and N2 (= *Acanthoceras rhotomagense* of de Grossouvre 1912, p. 4) from Touvois (Loire-Atlantique); A1 from the hardground at the top of the Marnes à *Ostrea biauriculata* at Briollay (Maine-et-Loire); A5 from the base of the Craie Marneuse or Craie à *Terebratella carantonensis* at Saint-Cyr-en-Bourg (Maine-et-Loire). From the Sables à *Catopygus obtusus* in Maine-et-Loire; A2 from Le Puy Notre Dame, A3 from Blaison, A4 from La Motte, Chaumont, A6 from Briollay, A7 from Le Puy Notre Dame, A8 from La Dionière, Briollay, A11 from Blaison (tranchée de la Chemin de Fer).

Dimensions

	D	*Wb*	*Wh*	*Wb*: *Wh*	*U*	*B*	*R*
A5	133	—(—)	54(40)	—	43·5(33)	21	43–44
	at 107·5	69(64)	43·5(40)	1·58	34·5(32)	21	43–44
A8	105	60(57)	42(40)	1·43	35(33)		36
A11	64	41·3(64)	29·5(46)	1·4	16·2(25)	14	33–34
A4	97·5	68·5(70)	39·5(40)	1·7	31(32)	22	44
A7	155	—(—)	56(36)	—	53·5(35)		35–36
A3	151	—(—)	56(37)	—	54(36)	18	32
A2	190	106·3(56)	71·8(38)	1·5	64·5(34)	?14	32
A1	—	97(—)	60( )	1·6	( )		—
N1	85	—(—)	38( )	—	24·3( )	?20	?40+

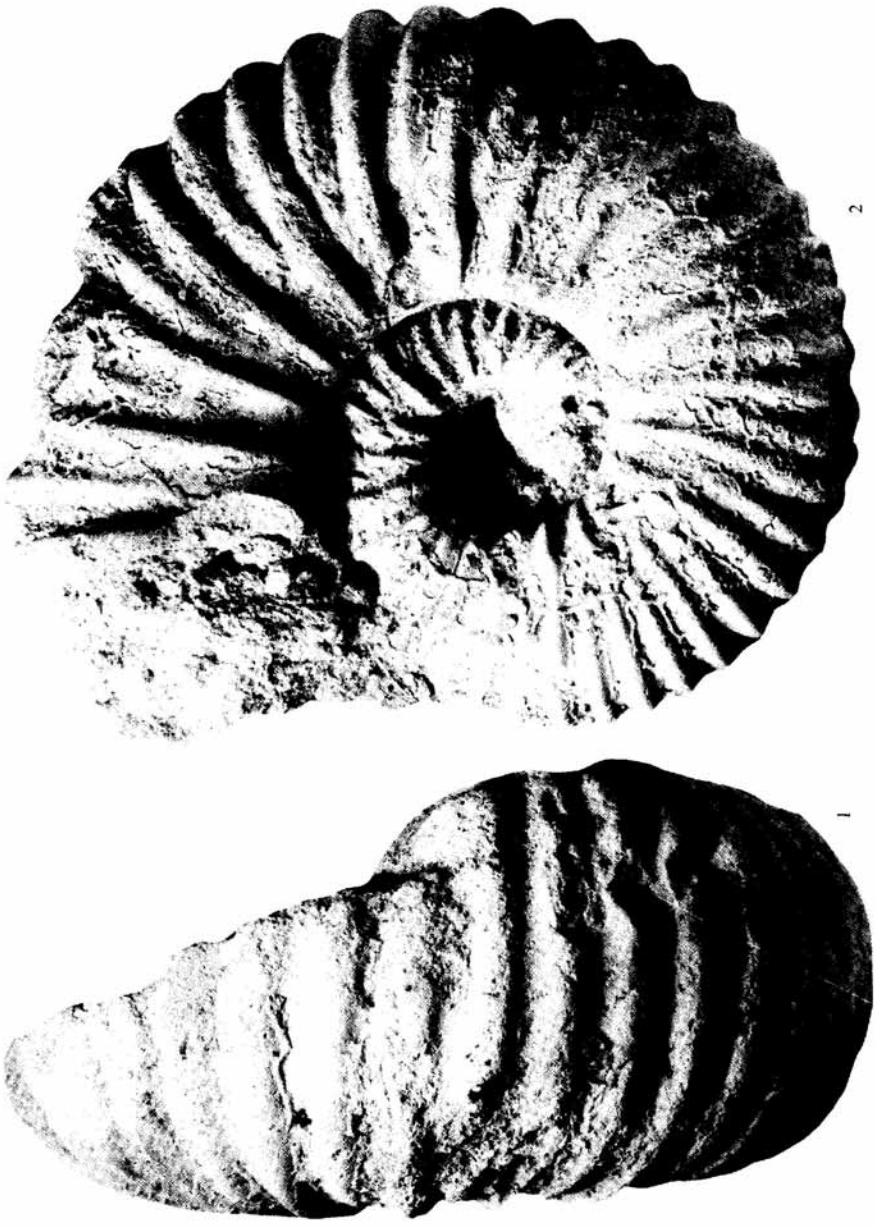


TEXT-FIG. 9. *Calycoceras naviculare* (Mantell). A2, depressed coarse-ribbed variant showing distinctive paired ribs arising from umbilical bullae on the inner whorls. From the Marnes à *Ostrea biauriculata* of Le Puy Notre Dame (Maine-et-Loire). ×0·6.

Discussion. The ontogeny of this species has been described in some detail by Kennedy (1971), whilst Cobban (1971) has illustrated a magnificent series of specimens from the Upper Cenomanian Greenhorn Limestone of the western interior of the United States, although his material is almost all slightly crushed or distorted. The material from Touvois and Briollay is thus of great interest since it allows, for the first time, illustration of the range of variation in contemporaneous European material of this important species. Ribbing varies greatly in strength and density, with from 32 to 44 ribs and from 14 to 21 umbilical bullae per whorl. Ribs may be rursi- or rectiradiate; in some cases springing in pairs from bullae, in other cases alternating far more regularly, long and short. Pairs of ribs may loop from one umbilical tubercle to the equivalent tubercle on the opposite flank, or ribs may zigzag, only one rib of a pair linking with the corresponding tubercle.

EXPLANATION OF PLATE 4

Figs. 1–2. *Calycoceras naviculare* (Mantell). A4, a finely and rursiradiately ribbed variant from the Sables à *Catopygus obtusus* of Chaumont sur le Loire (La Motte), Maine-et-Loire. Two-thirds of the outer whorl is body chamber.



KENNEDY *et al.*, Upper Cenomanian ammonites

Bullae vary from strong to weak. Some specimens bear distinct ventrolateral tubercles throughout ontogeny; in others there is merely a slight change in rib profile marking the site of the tubercle; and some have an evenly rounded venter throughout middle and late growth stages. In adults the whorl breadth varies from 56 to 70% of total diameter, height from 36 to 40%, umbilical diameter from 25 to 36%, and whorl breadth to height ratio from 1·4 to 1·7. There seems to be no difference between the variation in specimens from the Marnes à *Ostrea biauriculata* and those from the Sables à *C. obtusus*.

On the basis of the present material, there is no reason to separate *Calycoceras borgesi* (Douvillé), *C. stoliczkai* Collignon and *C. grossouvrei* Spath from *C. naviculare* (contrary to the views of Thomel 1972*a*).

C. obrieni Young (1957, p. 1171, pl. 150, figs. 1–4; text-fig. 1*f*, *h*) is widely thought to be a synonym of *C. naviculare* (Matsumoto 1959*b*; Kennedy 1971; Juignet *et al.* 1973), although Dr. W. A. Cobban tells us that it is older than the *C. naviculare* that he has described from the *gracile* Zone of the western interior of the United States.

C. boehmi (Spath) (= *Ammonites navicularis* Guéranger (*non* Mantell) 1867, pl. 5, fig. 5) is an allied but slightly earlier species which is more compressed and lacks distinct umbilical bullae; Hancock (1960) recorded it from the Middle Cenomanian and the Upper Cenomanian Sables du Perche.

Occurrence. *C. naviculare* is an Upper Cenomanian species. The examples from the Vendée and Maine-et-Loire described in this paper are mostly from the *gracile* Zone. In Sarthe it is rare in any one member, but first appears below the *gracile* Zone, in the Sables du Perche (Hancock 1960; Juignet 1977) and ranges to the Sables à *Catopygus obtusus*/Sables de Bousse (Juignet *et al.* 1973).

In southern England it is best known from the phosphatic fauna of Bed C on the coast of Devon (Kennedy 1970, 1971), but it is also one of the widespread ammonites of the slightly later Plenus Marls whilst *Calycoceras* close to *Calycoceras naviculare*, mostly transitions from *C. boulei* Collignon, occur earlier.

In south-east France *C. naviculare* (also recorded as *C. borgesi* and *C. grossouvrei*) is better known from the *gracile* Zone, but is also listed from the underlying *crassum* Zone of Thomel under the name of *C. stoliczkai* (Thomel 1972*a*). Thomel also records *C. boehmi* and *C. boulei* from this Zone.

In the western interior of the United States it has a more limited range: all the records of Cobban (1971) and Cobban and Scott (1972) are from the basal part of the Bridge Creek Limestone in the Zone of *Sciponoceras gracile*, but *C. naviculare* does not appear to range to the top of the zone.

The geographic range of *C. naviculare* is wide: France (Normandy, Sarthe, Vendée, Maine-et-Loire, Provence), southern England (Devon, Dorset, Sussex, Surrey), Spain (Burgos, Soria), Portugal (Ourem), Algeria, Tunisia ?, Angola, Madagascar (Manera), southern India (Trichinopoly), Japan (central Hokkaido), United States (Kansas, Arizona, Colorado, California, Oregon).

Genus PSEUDOCALYCOCERAS Thomel, 1969

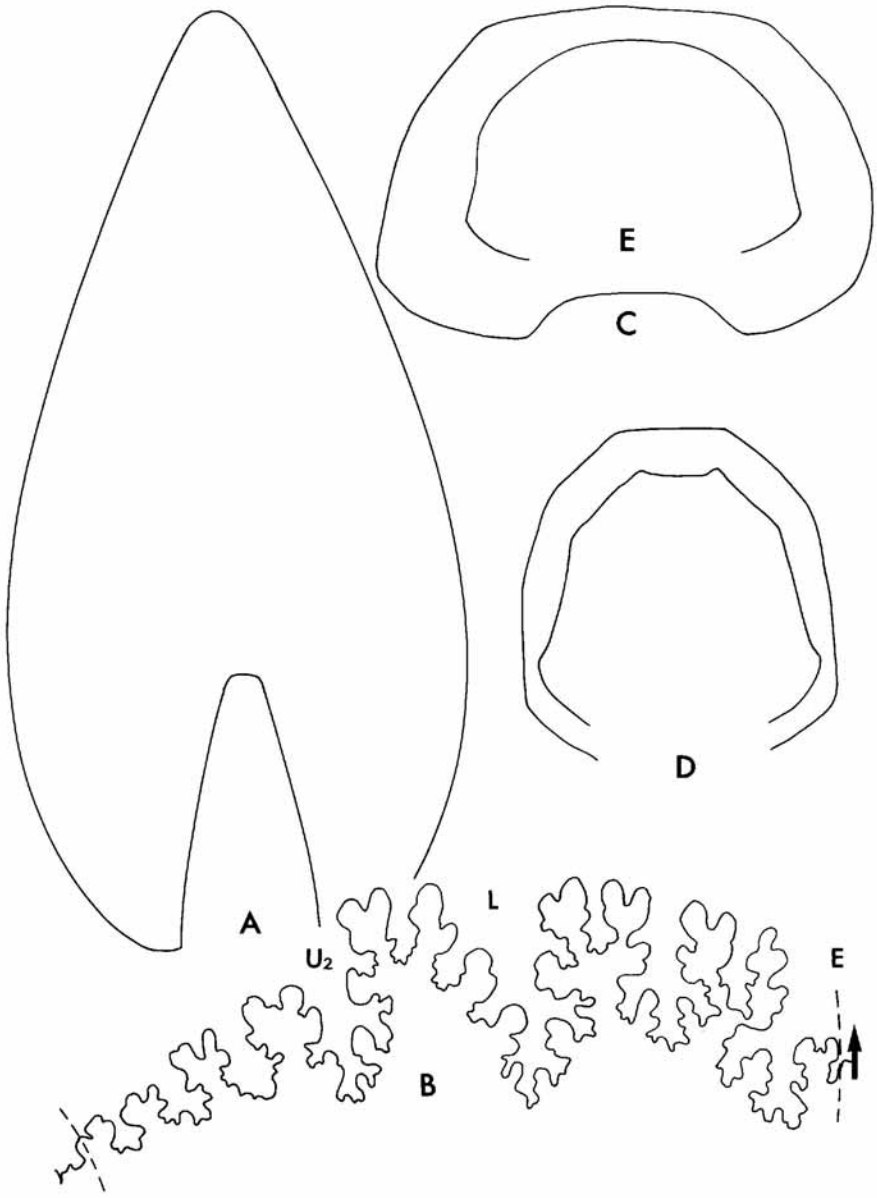
Type species. *Ammonites harpax* Stoliczka, 1865, p. 72, by original designation. A lectotype has been designated, described, and refigured by Matsumoto and Kawano (1975).

Diagnosis. Moderately compressed to moderately inflated with dense ribs in middle growth, arising from strong, in many but not all cases S-shaped umbilical bullae, and bearing generally clavate inner and outer ventrolateral and siphonal tubercles rather close together on a well-arched venter. On the body chamber the ribs may be distant and tend to be markedly rursiradiate and the ventral tubercles weaken.

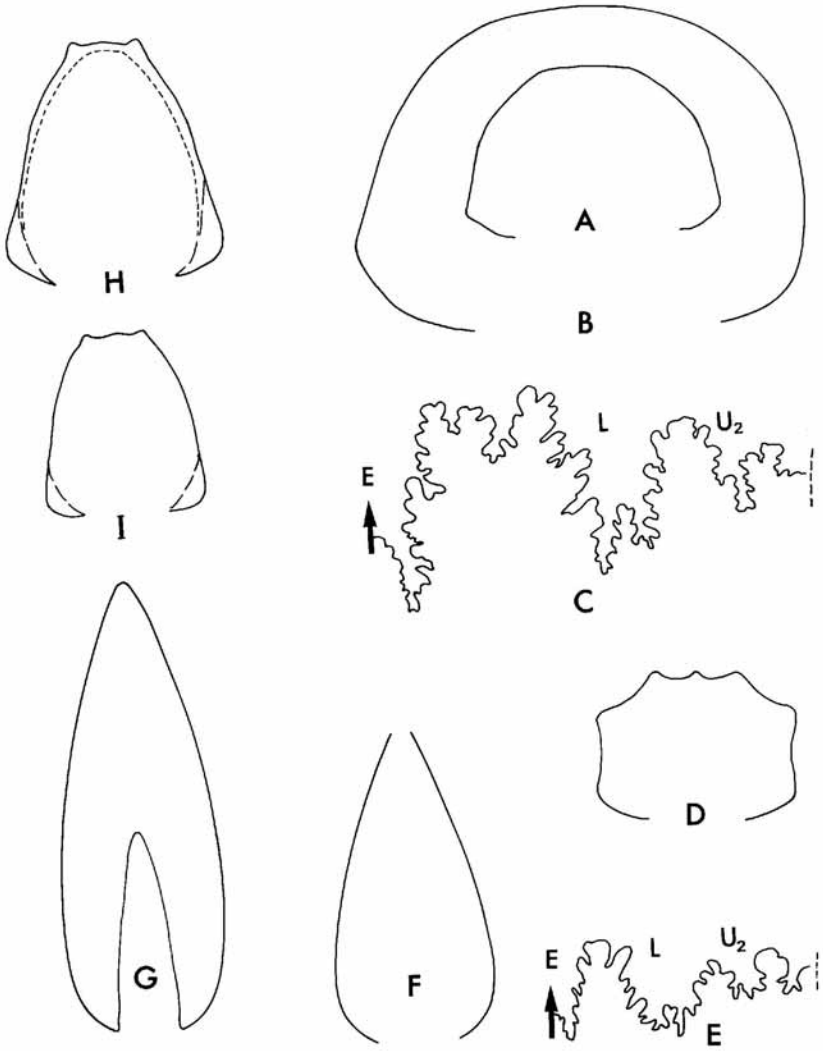
EXPLANATION OF PLATE 5

Figs. 1–2. *Calycoceras naviculare* (Mantell). Densely ribbed variant with strong umbilical bullae and retaining distinct angular shoulders. A5, from the glauconitic chalk at the base of the Craie Marneuse, Saint-Cyr-en-Bourg (Maine-et-Loire).

KENNEDY *et al.*, Upper Cenomanian ammonites



TEXT-FIG. 10. A. Whorl section and B external suture of *Forbesiceras* sp. group of *largilliertianum* (d'Orbigny). A34, ×1. C. Whorl sections of *Calycoceras naviculare* (Mantell). A5, ×1. D. Whorl sections of *Pseudocalycoceras* sp. A36, ×1.



TEXT-FIG. 11. A, B, C. Whorl sections and external suture of *Calycoceras naviculare* (Mantell). A, C specimen A3, B, A11, ×1. D, E. Whorl section and suture line of *Euomphaloceras septemseriatum* (Cragin). A22, ×2·5. F. Whorl section of *Proplacenticeras* cf. *memoriaschoenbachi* (Laube and Bruder). A35, ×1. G. Whorl section of *Metengonoceras* sp. A33, ×1. H. Whorl section of *Pseudocalycoceras* cf. *lattense* (Thomel). A26, ×1. I. Whorl section of *Thomelites* aff. *sornayi* (Thomel). A25, ×1.

Discussion. *Pseudocalycoceras* is close to *Eucalycoceras* but is distinguished by the more distant, curved ribs on the body chamber and the more clavate ventral tubercles.

Thomel included a wide range of forms in *Pseudocalycoceras*. He (1972*a*, p. 96) made *Acanthoceras haugi* Pervinquière (1907, p. 270, pl. 14, fig. 1*a–b*) type species of a subgenus *Haugiceras* (and previously—1969, p. 651—of a subgenus *Neocalycoceras*, a *nomen nudum* for lack of description), distinguished by a more inflated whorl section, straighter and weaker ribs, untwisted umbilical tubercles, and rounded ventral tubercles. Given the range of variation in *P. harpax*, we do not think that *haugi* needs to be separated subgenerically.

P. flandrini Thomel (1966, p. 430, pl. 10, figs. 3–5), *P. eguituriense* Thomel (1972*a*, p. 92, pl. 29, figs. 6–7; pl. 30, fig. 7; pl. 31, fig. 6), and *P. planum* Thomel (1972*a*, p. 93, pl. 30, figs. 1–6) appear to be crushed *Thomelites*. *P. harpax lattense* Thomel is discussed below. *P. dromense* Thomel (1972*a*, p. 94, pl. 30, figs. 8–9) appears to be a *Calycoceras*. *P. pseudoorbignyi* Thomel (1972*a*, p. 95) seems not to be a *Pseudocalycoceras*.

Barroisiceras trinodosum Moreman (1942, p. 212, pl. 33, figs. 1–2; text-fig. 2*a*), referred to *Pseudocalycoceras* by Thomel is a pathological *Metoicoceras*. *Pulchellia bentoniana* Cragin (1893, p. 239), similarly referred, is a *Tarrantoceras* (*Sumitomoceras*) and *Eucalycoceras lymense* Spath (1926*b*, pp. 427, 431) is a *Mantelliceras* (Kennedy 1971, p. 60).

We are left with the following:

1. *Pseudocalycoceras harpax* (Stoliczka): synonyms *P. harpax tulearensis*, *ankomakensis*, *ramondaense*, and *talinorensis* Collignon (1937, p. 34, pl. 1).
2. *P. morpheus* (Stoliczka), the type of which is pathological (see Matsumoto and Kawano 1975 for discussion).
3. *P. dentonense* (Moreman) (see Cobban and Scott 1972) of which *E. indianense* (Moreman, 1942), *E. lewisvillense* (Moreman 1942), and *E. underwoodi* Powell, 1963, are synonyms.
4. *P. angolaense* (Spath 1931, p. 316): possibly a senior synonym of *P. dentonense* (see Cooper 1978).
5. *P. haugi* (Pervinquière 1907): possible synonyms are *A. judaicum* Taubenhaus, 1920, *A. palastinense* Taubenhaus, 1920, *Protacanthoceras batnense* Collignon, 1937, *P. jullienei* Collignon, 1937, *Calycoceras alaouitense* Basse, 1940, *C. paralouitense* Basse, 1940, and *Pseudocalycoceras robustum* Thomel, 1972*a*.
6. ?*Pseudocalycoceras lattense* Thomel, 1966.

Occurrence. Upper Cenomanian of western Europe (England, France, Spain), Romania, north Africa (Morocco, Algeria, Tunisia), Middle East (Syria, Israel), Malagasy, southern India, Angola, central and west Texas, the western interior of the United States, California, and Japan (Hokkaido).

Pseudocalycoceras? cf. *lattense* (Thomel)

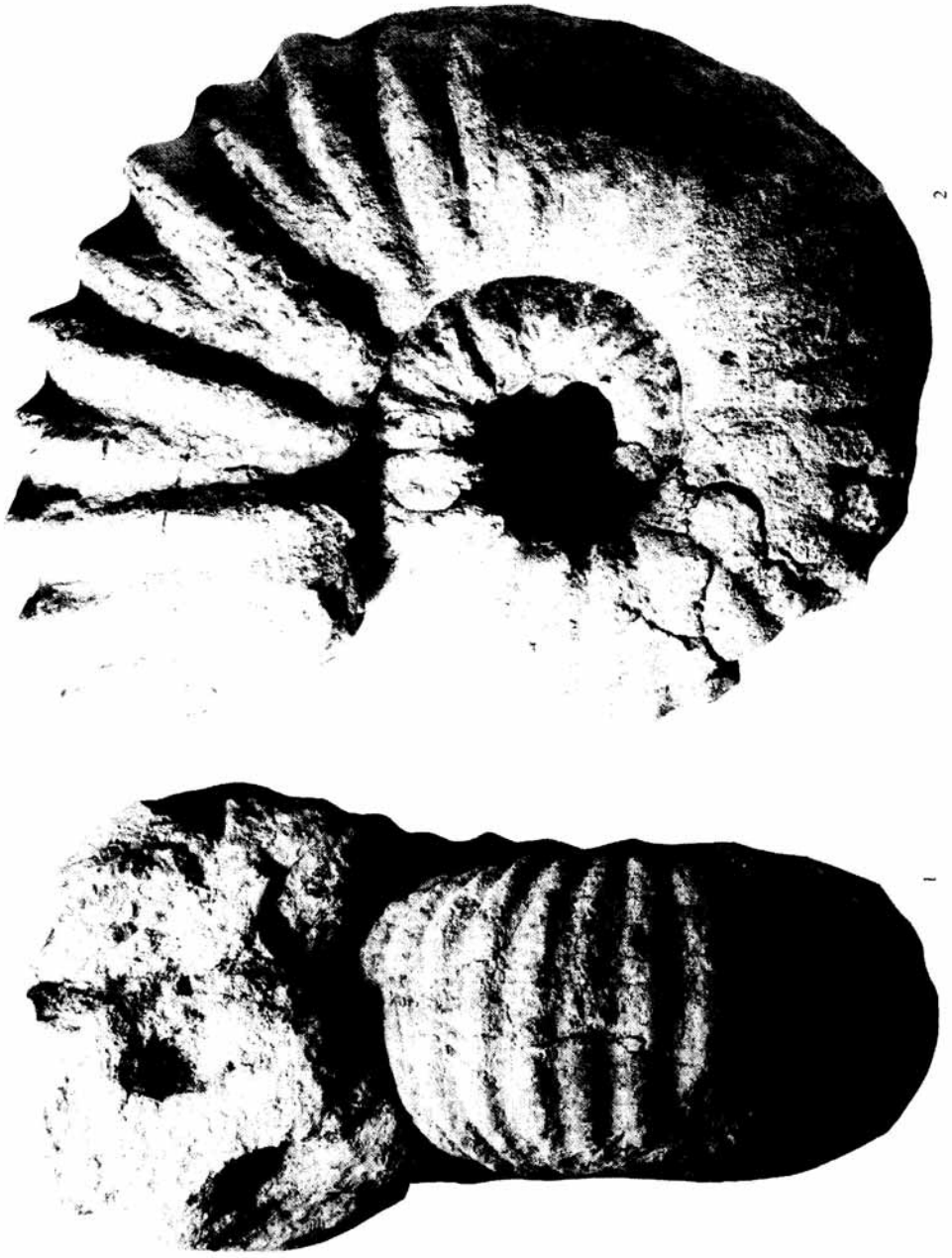
Plate 8, figs. 5–8; text-fig. 11H

Compare

1966 *Eucalycoceras harpax* (Stoliczka) var. *lattensis* Thomel, p. 429, pl. 9, figs. 1–3.
1972*a* *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax lattense* (Thomel); Thomel, p. 89, pl. 32, figs. 1–2.
?1972*a* *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax talinorensis* (Collignon); Thomel, p. 90 (*pars*), pl. 31, figs. 1–3 only.

EXPLANATION OF PLATE 6

Figs. 1–2. *Calycoceras naviculare* (Mantell). Evolute, slender-whorled, coarsely ribbed variant, A7, from the Marnes à *Ostrea biauriculata*, Le Puy Notre Dame (Maine-et-Loire). Identified as *Fagesia navicularis* by de Grossouvre.



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Material. Two fragments, A26, from the Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire), and A29, from the same horizon at Chevir-le-Rouge (Maine-et-Loire).

Description. Both specimens are composite internal moulds. The smaller fragment (A29) shows a compressed whorl section, with long rursiradiate ribs arising singly or in pairs from umbilical bullae, separated by shorter, intercalated ribs. There are strong clavate outer ventrolateral tubercles on either side of a concave venter, connected by a broad rounded rib with a trace of a clavate siphonal tubercle. A26, a larger, better-preserved fragment, has a whorl breadth:height ratio of 0·89, and is ornamented by low, broad flat ribs, ten of which are present on the specimen. They are slightly rursiradiate, arising in twos or threes from umbilical bullae, and separated by intercalated ribs. There are well-developed clavate ventrolateral tubercles on either side of a slightly arched venter, connected by low broad ribs which bear a distinct clavate siphonal tubercle. The sutures are not seen.

Discussion. These two poor fragments appear to belong to the same species, and the larger piece compares well with the earlier parts of the outer whorl of the holotype of *P. harpax lattense* as figured by Thomel. That form, however, is not certainly a *Pseudocalycoceras*; its venter suggests that it may be a *Thomelites*.

Occurrence. Upper Cenomanian of Les Lattes (Alpes-Maritimes) and of Briollay (Maine-et-Loire).

Pseudocalycoceras sp.

Text-figs. 10D, 12

Material. One specimen only, A36, from the Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire).

Description. This specimen is rather battered, but preserves two-thirds of a whorl of body chamber. The dimensions are as follows:

D	*Wb*	*Wh*	*Wb*/*Wh*	*U*
151	45·7(30)	54(36)	0·85	56·8(38)

The coiling is evolute, with a wide umbilicus. The whorl section is compressed. On the early parts of the outer whorl, ornament consists of strong umbilical bullae, which give rise to pairs of strong distant, convex rursiradiate ribs, with a single short rib intercalated. On the body chamber, strong long ribs with bullae alternate regularly with short ribs or with long ribs lacking bullae. There is an indication of conical inner ventrolateral tubercles at the smallest diameters visible, strong clavate outer ventrolateral tubercles retained to the aperture, connected across the venter by a strong rib which bears a clavate siphonal tubercle, lost at the beginning of the body chamber. The sutures are not seen.

Discussion. The poorly preserved specimen may be no more than an adult individual of the preceding species. It differs, however, from the holotype of *P. lattense* in a number of respects; notably a wider umbilicus (38% vs. 29%), although the umbilical seam of the type is clearly egressing. The other dimensions are nearly identical. Ornament is also different, the ribbing of our specimen being

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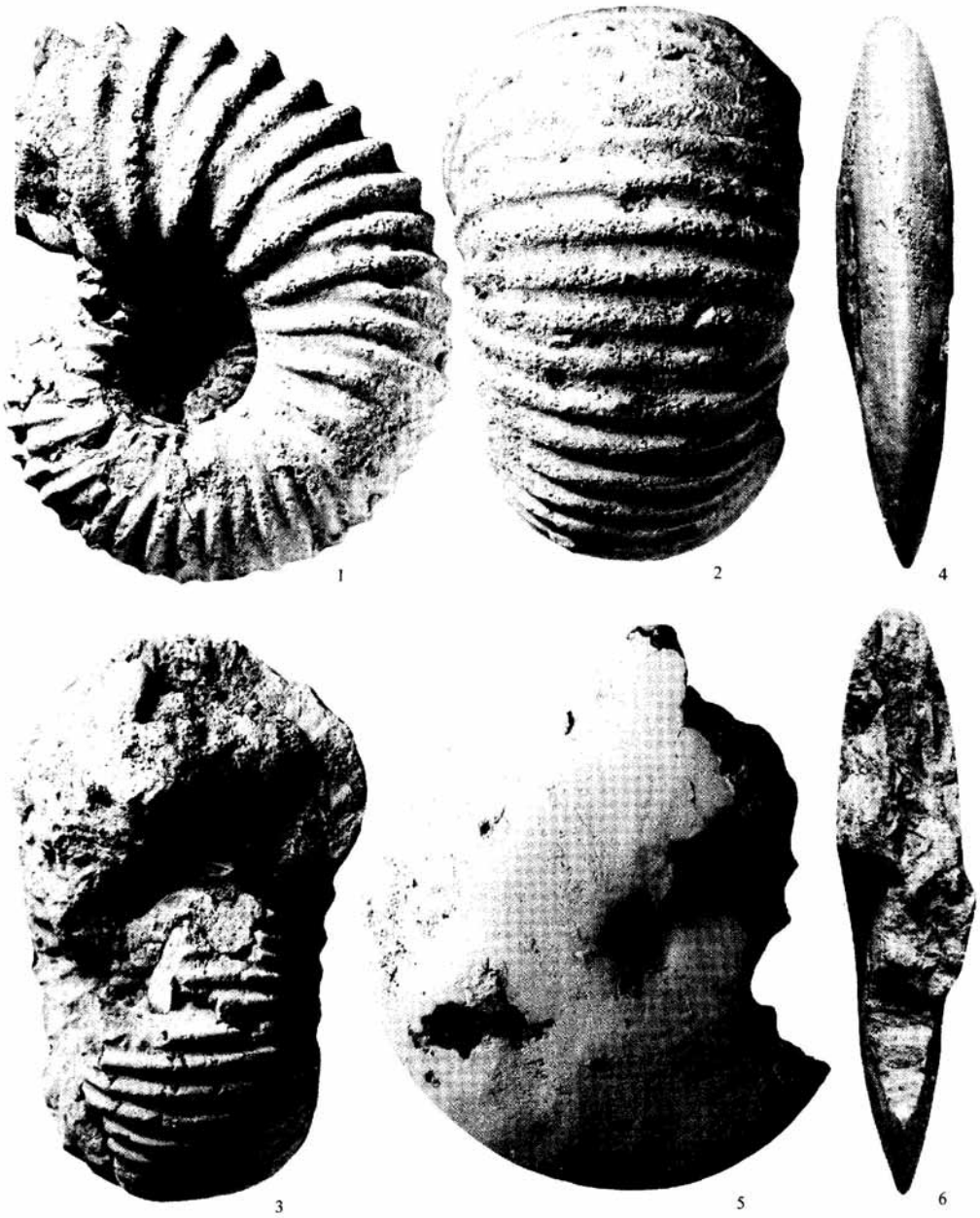
EXPLANATION OF PLATE 7

Figs. 1–3. *Calycoceras naviculare* (Mantell). N1, the holotype of *Calycoceras grossouvrei* (Spath) from Touvois (Loire-Atlantique).

Figs. 4–6. *Metengonoceras dumbli* (Cragin). The holotype of *Metengonoceras douvillei* de Grossouvre from the Upper Cenomanian, Carrière Sainte-Croix, Le Mans (Sarthe). The specimen was in the École des Mines, Paris (collections now at Lyon).



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coarse and distant. In these respects it compares more closely with *Pseudocalycoceras? pseudoorbigny* Thomel (1972, p. 95, pl. 29, figs. 1–2), although the dimensions of that species are a little different (at D = 81·3 mm, Wb = 31%, Wh = 39%, Wb/Wh = 0·79, U = 32%).

Occurrence. Marnes à *O. biauriculata* of La Dionière, Briollay (Maine-et-Loire). The most closely comparable forms are from the Upper Cenomanian of south-east France.

TEXT-FIG. 12. *Pseudocalycoceras* sp. A36, from the Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire). ×0·67.

EXPLANATION OF PLATE 8

Figs. 1–4. *Thomelites* aff. *sornayi* (Thomel). 1, 2. A28, from the Marnes à *Ostrea biauriculata* of Chevir-Le-Rouge (Maine-et-Loire); 3, 4. A25, from Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire).

Figs. 5–8. *Pseudocalycoceras* cf. *lattense* Thomel. 5, 6. A26, from the Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire); 7, 8. A29, from the Marnes à *Ostrea biauriculata* of Chevir le Rouge (Maine-et-Loire).

Figs. 9, 10. *Sciponoceras gracile* (Shumard). A24, from the Sables à *Catopygus obtusus* of Matheflon, Seiches-sur-le-Loir (Maine-et-Loire).

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Genus THOMELITES Wright and Kennedy, 1973

Type species. Jeanrogericeras sornayi Thomel 1966 (p. 431, pl. 11, figs. 1–3).

Diagnosis. See Wright and Kennedy 1973, p. 25.

Discussion. Thomelites was erected by Wright and Kennedy in 1973 for Upper Cenomanian species previously confused with *Utaturiceras* (Wright 1956), a Lower Cenomanian homoeomorph (Casey 1960; Matsumoto, Sastry, and Sarkar 1966). In 1973 it was suggested that *Thomelites* might be ancestral to *Metoicoceras* (Wright and Kennedy, p. 25). The description of a host of ammonites of this group by Thomel (1972*a*) and further work on early *Metoicoceras* from the United States have improved our knowledge of the status and relationships of the genus.

Thomelites differs from typical *Metoicoceras* in having weaker ribs and stronger tuberculation; there is more of a tendency for ribs to spring in groups from massive umbilical bullae, whilst the clavi on the shoulders are more pronounced; a siphonal tubercle is present until the outermost whorls. The sutural elements are frequently less reduced. However, a number of forms show intermediate features. Thus the earliest North American Western Interior species of *Metoicoceras*, *M. praecox* Haas (1949, p. 15, pls. 5–7; text-figs. 5–9), has some juveniles which possess siphonal clavi at small diameters, whilst the Texas species *Metoicoceras latoventer* Stephenson (1953, p. 209, pl. 53, figs. 1–9; pl. 54, figs. 9–11) also possesses a siphonal tubercle up to diameters of 20–25 mm. These species probably post-date the earliest (undescribed) European *Thomelites*, but are approximately contemporaneous with the type species and other known forms, suggesting that the two genera coexisted in time but not in space.

Thomelites can be readily separated from the later Turonian genus *Jeanrogericeras* Wiedmann, 1960 (type species *Ammonites reveliereanus* Courtiller 1860) which invariably lacks siphonal clavi.

We should refer the following species to *Thomelites*:

1. *Thomelites sornayi* (Thomel) (1966, p. 431, pl. 11, figs. 1–3).
2. *T. prerusticum* (Thomel) (1966, p. 431, pl. 11, fig. 4).
3. *T. flandrini* (Thomel) (1966, p. 430, pl. 10, figs. 3–5).
4. *T. eguituriense* (Thomel) (1972*a*, p. 92, pl. 29, figs. 6–7; pl. 30, fig. 7; pl. 31, fig. 6).
5. *T. planum* Thomel (1972*a*, p. 93, pl. 30, figs. 1–6).
6. *T. hancocki* Juignet and Kennedy (1976, p. 123, pl. 34, fig. 2*a–c*).
7. *T.* sp. (*Acanthoceras compressum* Jukes-Browne (*pars*) in Jukes-Browne and Hill, 1896, pl. 5, fig. 2–2*a* only).

?8. *T. bethlehemensis* Avnimelech and Shoresh (1962, p. 533, pl. 15, fig. 3*a–c*, text-fig. 3).

Occurrence. Upper Cenomanian of southern England (Bed C in Devon, top of Lower Chalk in Dorset), remanié faunas on hardground Antifer no. 2 in Normandy, Marnes à *Ostrea biauriculata* of Verneil-le-Chétif (Sarthe) and Briollay (Maine-et-Loire), Upper Cenomanian of Basses-Alpes and Alpes-Maritimes, and the Middle East.

Thomelites aff. *sornayi* (Thomel)

Plate 8, figs. 1–4; text-fig. 16*i*

Compare

1966 *Jeanrogericeras sornayi* Thomel *in* Porthault, Thomel, and de Villoutreys, p. 431, pl. 11, figs. 1–3.
1973 *Thomelites sornayi* (Thomel); Wright and Kennedy, p. 26, pl. 2, fig. 1*a–c*; pl. 3, figs. 3*a–c*, 5*a–b*, 6*a–c*.

Material. Two specimens, A25, from the Marnes à *Ostrea biauriculata* of La Dionière, Briollay (Maine-et-Loire), and A28, from the same horizon at Chevir-le-Rouge (Maine-et-Loire).

Description. The smaller specimen A28 is a composite mould of just under half a whorl with an estimated maximum diameter of 50 mm, most of which is septate. The umbilicus is of moderate size and depth with a

rounded wall and shoulder. The whorl section is compressed, with gently inflated inner flanks, the maximum breadth at the umbilical bullae, upper flanks which are rather more flattened and convergent, and a flattened venter. On the preserved fragment there are four umbilical nodes which vary from subspinose and conical to bullate. From these arise groups of two or three recti- to prorsiradiate ribs, with one or two shorter, intercalated ribs between each group. There are also a few long ribs without bullae, a total of twenty ribs in all, eleven of which begin at the umbilical shoulder. The rather narrow venter bears strong, persistent, subequal ventral and siphonal clavi, borne on low broad ribs.

The second specimen, A25, again a composite mould, appears to be an adult with at least half a whorl of body chamber. Slightly distorted, the specimen has the following dimensions:

D	*Wb*	*Wh*	*Wb/Wh*	*U*
104·5	36(34)	38·5(37)	0·93	31·5(30)

The phragmocone is too damaged for useful description. The body chamber bears massive conical umbilical bullae whence arise groups of three or four rursiradiate ribs, with two or three intercalated ribs, arising low on the flank (and connected tenuously to bullae in some cases), separating each group. In all twenty-one ribs correspond to four bullae. At the aperture, the ornament is modified into a series of long, weaker, rursiradiate, flexed convex ribs. There are strong clavate shoulder tubercles and a clavate siphonal tubercle borne on a low broad rib. The siphonal tubercle declines on the later parts of the body chamber and the venter, slightly concave on the phragmocone, rounds towards the aperture. The sutures are not seen.

Discussion. These two *Thomelites* show a style of ribbing and umbilical tuberculation corresponding closely to that of the type species, *T. sornayi*. They differ, however, in their lack of inner ventrolateral tubercles and retention of a siphonal tubercle. Lack of an inner ventrolateral tubercle also precludes reference to the coarsely ornamented *T. prerusticum* (Thomel 1966, p. 43, pl. 11, fig. 4) where tubercles dominate over ribbing (Thomel originally referred this species to *Metasigaloceras*). Retention of an inner ventrolateral tubercle also characterizes the species *Pseudocalycoceras eguituriense* (Thomel) and the diminutive *T. hancocki* Juignet and Kennedy (1976). *T. flandrini* (Thomel) bears lateral tubercles on long ribs. There are also similarities to *T. planum* (Thomel): the holotype, and only specimen referred to the species by Thomel, is badly crushed, but shows strong umbilical bullae on the inner whorls and a style of ribbing (so far as is preserved) which matches our specimens. There is, however, a trace of inner ventrolateral tubercles on the nucleus and an early loss of siphonal clavi. The differences between *T. sornayi*, *T. flandrini*, *T. planum*, and *T. eguituriense* are all slight and no more than a single variable species may be represented.

Occurrence. Upper Cenomanian, Marnes à *O. biauriculata* at La Dionière (Maine-et-Loire) and Verneil-le-Chétif (Sarthe). *T. sornayi* occurs at the same level in southern England (phosphatic fauna of Bed C of the Cenomanian Limestone in Devon) and in Thomel's *crassum* Zone in south-eastern France.

Subfamily EUOMPHALOCERATINAE Cooper, 1978
Genus EUOMPHALOCERAS Spath, 1923
(= *Kanabiceras* Reeside and Weymouth, 1931; *Cunningtoniceras* Collignon, 1937)

Type species. Ammonites euomphalus Sharpe, 1855, pl. 13, fig. 4*a–c*, by monotypy.

Remarks. Cooper (1978) reduced *Kanabiceras* to a subgenus of *Euomphaloceras*, separating it from the restricted form on the basis of the siphonal tubercles joining to form a prominent keel and the outer ventrolateral tubercles more or less oblique to the keel. Specimens of *E. euomphalum* in the C. W. Wright collection show that this species is extremely variable in its ventral ornament and includes individuals with typical *Kanabiceras* features at some stages in development. Even subgeneric separation is regarded as unnecessary, following Dr. Wright's observations.

Occurrence. Euomphaloceras has a virtually world-wide distribution in the Middle and Upper Cenomanian.

Euomphaloceras septemseriatum (Cragin)

Plate 9, figs. 3–5; text-fig. 11D–E

1969 *Kanabiceras septemseriatum* (Cragin); Matsumoto, Maramoto, and Takahashi, p. 279, pl. 37, figs. 1–3 (with synonymy).
1972 *Kanabiceras septemseriatum* (Cragin); Cobban and Scott, p. 72, pl. 12, figs. 5–27 (with synonymy).
1978 *Euomphaloceras* (*Kanabiceras*) *septemseriatum* (Cragin); Cooper, p. 106, figs. 4N–O, 10A–E, 12E–H, 18G–H, 19G–L, 26A–B, 28.

Holotype. Cragin's original specimen from the Eagle Ford Formation of Dallas County, Texas, refigured by Cobban and Scott (1972) as their pl. 12, figs. 24–25.

Material. One specimen only, A22, from the Sables à *Catopygus obtusus* of Seiches-sur-le-Loir (Maine-et-Loire), labelled 'tranchée du Chemin de Fer'.

Description. The specimen is a well-preserved, wholly septate internal mould, with a green glauconitic veneer. The dimensions are as follows:

D	*Wb*	*Wh*	*Wb*/*Wh*	*U*
30·0	20(67)	11·9(40)	1·68	10·2(34)

It bears eighteen umbilical bullae, some of which develop into conical tubercles at the largest diameter preserved. Low, narrow, distant prorsiradiate ribs arise from the bullae, connecting them to a similar number of inner ventrolateral tubercles, which are alternately strongly and feebly developed. Approximately twice as many outer ventrolateral tubercles are obliquely placed on the venter and are connected to the rounded clavi on the low keel.

The umbilical wall is distinctly notched in places to accommodate the long ventrolateral spines (Moreman 1927, pl. 13, fig. 5).

Discussion. Full descriptions of this species are given by Matsumoto (1959*b*), Matsumoto *et al.* (1969), Cobban and Scott (1972) and Cooper (1978). Study of European, North American, and Angolan material has convinced us that *E. septemseriatum* is a rather variable species, and that densely ribbed variants intergrade with the coarsely ornamented *E. echinatum* (Douvillé) (1931, p. 34, pl. 3, figs. 1–5; pl. 4, figs. 1, 2) and *E. stanislausense* (Anderson) (1958, p. 247, pl. 8, figs. 5, 5*a*).

Occurrence. This species occurs widely in the upper part of the Plenus Marls of the Anglo-Paris Basin and their equivalents (the *Kanabiceras* sp. of Jefferies, 1962, 1963 represent poorly preserved *Kanabiceras septemseriatum*). In Normandy we have seen specimens in the green-coated faunas of niveau T_2 of Juignet (1970) on the coast, and indigenous material from slightly higher horizons, associated with *Sciponoceras gracile*, at Rouen. It also occurs in the Sables à *C. obtusus* of Sarthe (Juignet *et al.* 1973). The species is frequent and widespread in the North American *Metoicoceras whitei*/*Sciponoceras gracile* Zone of the western interior from the Black Hills uplift southwards, in north and west Texas. It also occurs in California, Japan (Hokkaido), and Angola (Salinas).

EXPLANATION OF PLATE 9

Figs. 1–2. *Metoicoceras geslinianum* (d'Orbigny). A13, the holotype of *Metoicoceras gourdoni* (de Grossouvre), a green-coated glauconitized internal mould from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire). Arrows indicate those parts of the specimen which have been repaired with plaster.

Figs. 3–5. *Euomphaloceras septemseriatum* (Cragin). A22, a green-coated glauconitized mould from the Sables à *Catopygus obtusus* of Seiches sur le Loir (Maine-et-Loire).

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Subfamily MAMMITINAE Hyatt, 1900
(= Metoicoceratidae Hyatt, 1903; Fallotitinae Wiedmann, 1960)
Genus METOICOCERAS Hyatt, 1903

Type species. Ammonites swallovii Shumard (1860, p. 591) by the subsequent designation of Shimer and Shrock (1944).

Diagnosis. Typical *Metoicoceras* are compressed, moderately involute acanthoceratids, in which the body chamber may uncoil slightly. The normal ornamentation is dominantly of straight to flexuous ribs which are alternately long and short, the longer sometimes branching from umbilical bullae. These ribs are low and broad and in later growth stages characteristically have steeper flanks in the rear and slope gently forwards in cross-section; the crests of the ribs are flat in some species.

Umbilical bullae, inner ventrolateral tubercles, clavate or not, and outer ventrolateral clavi occur in most species in earlier ontogeny, but later the tuberculation may weaken, leaving only the outer ventrolateral clavi or no tubercles at all, on angular or rounded shoulders. The venter is typically narrow, smooth, and tabulate or depressed between the clavi on the shoulders. On body chambers the venter may broaden and ribs or gentle undulations cross it without interruption or tubercles.

There is a tendency towards sutural simplification.

Some evolute square-whorled robustly ornamented species are also referred to *Metoicoceras*, as are a few transitional forms with siphonal tubercles during early ontogeny.

Discussion. As noted above, typical *Metoicoceras* probably represent an offshoot from early *Thomelites* by loss of siphonal clavi, reduction of umbilical bullae, inner and outer ventrolateral tubercles, and a tendency for ribbing to dominate over tuberculation, although there are predominantly tuberculate species and much variation within species.

The earliest *Metoicoceras* occur in North America; the earliest Western Interior species, *M. praecox* Haas and the approximately contemporaneous *M. latoventer* Stephenson, show intermediate features such as the possession of a siphonal tubercle at very small diameters. The work of Cobban (1953) demonstrated a succession of *Metoicoceras* species in the U.S. Western Interior, and as already noted, these early *Metoicoceras* are contemporaries of typical European *Thomelites*; only in the latest Cenomanian did *Metoicoceras* spread beyond the United States in numbers.

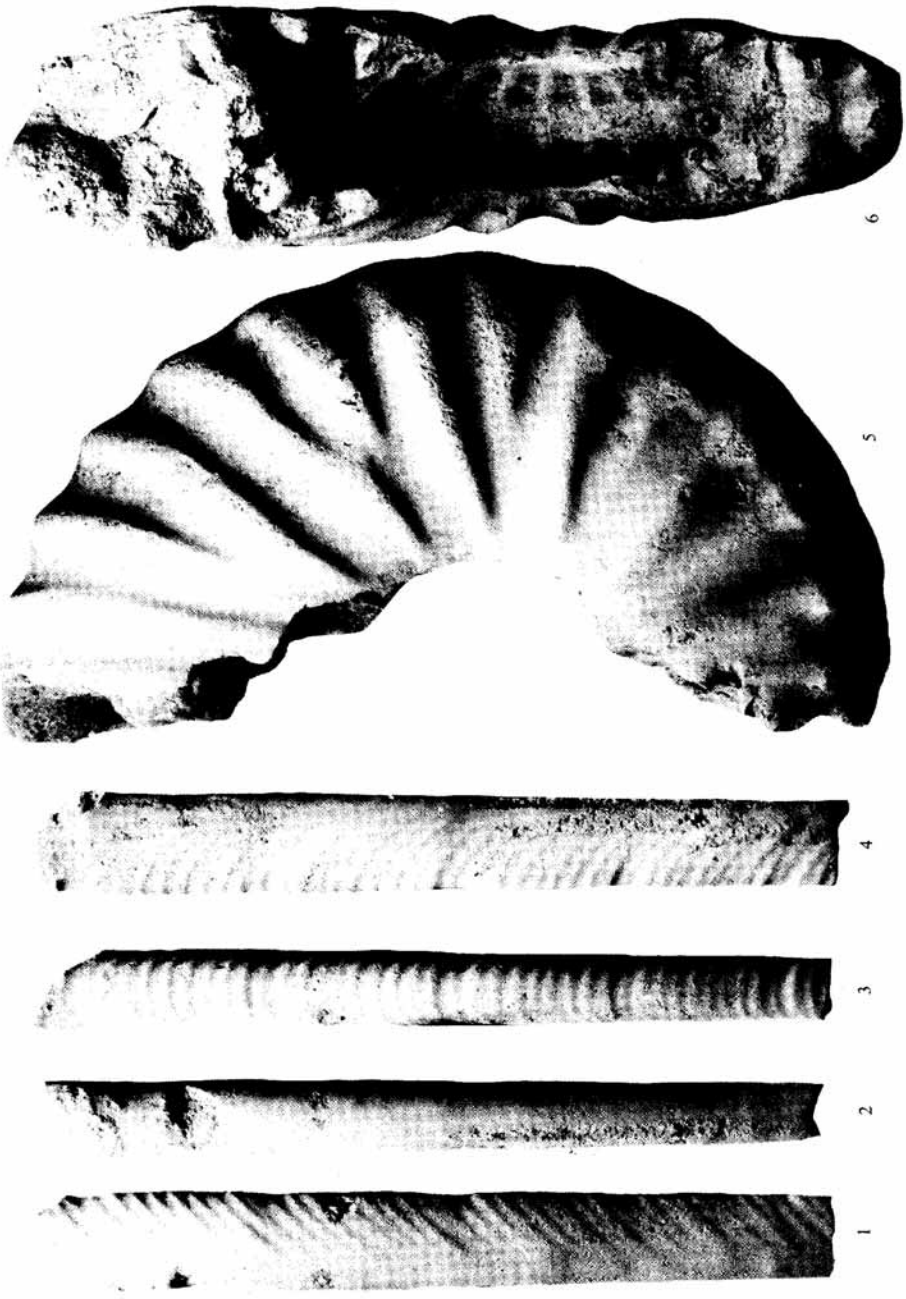
More than twenty *Metoicoceras* species have been described, of which we recognize:

1. *M. swallovi* (Shumard) (1860, p. 591): *M. swallovi macrum* Stephenson (1953, p. 209, pl. 51, figs. 4–7), based on juveniles, does not deserve separation.
2. *M. geslinianum* (d'Orbigny) (1850, p. 146) of which *M. gourdoni* (de Grossouvre), *M. bureaui* (de Grossouvre), *M. petraschecki* (de Grossouvre), *M. dumasi* (de Grossouvre), *M. pervinquierei* (de Grossouvre), *M. gibbosum* Hyatt, *M. kanabense* Hyatt, *M. whitei* Hyatt, *M. pontieri* Leriche, *M. ornatum* Moreman, *M. irwini* Moreman, and *M. boesei* Jones are all synonyms (see below).
3. *M. praecox* Haas (1949, p. 15, pls. 5–7; text-figs. 5–9).
4. *M. mosbyense* Cobban (1953, p. 48, pl. 6, figs. 1–14; pl. 7, figs. 1–3) (of which *M. muelleri* Cobban (1953, p. 49, pl. 6, figs. 15–16; pl. 8, figs. 1–7; pl. 9) may be a synonym).
5. *M. defordi* Young (1957, p. 1169, pl. 149, figs. 1–8; text-fig. 1*a*, *e*, *g*, *i*).
6. *M. latoventer* Stephenson (1953, p. 209, pl. 53, figs. 1–9; pl. 54, figs. 9–11) of which *M. crassicostae* Stephenson is a synonym.
7. *M. acceleratum* Hyatt (1903, p. 127, pl. 14, figs. 11–14).

EXPLANATION OF PLATE 10

Figs. 1–4. *Sciponoceras gracile* (Shumard). A23, a body chamber mould from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire).

Figs. 5–6. *Metoicoceras geslinianum* (d'Orbigny). A14, a green coated, glauconitized body chamber from the Sables à *Catopygus obtusus* of Péllonalles (Maine-et-Loire).



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A number of other forms referred to *Metoicoceras* appear to represent other genera. *Buchiceras swallovi* var. *puercoensis* Herrick and Johnson (1900, p. 213, pl. 27, figs. 3–4) is a *Spathites*.

M. antiquum Karrenberg (1935, p. 139, pl. 31, fig. 13) is a Lower Cenomanian mantellicerine.

M. stoliczkai Sastry and Matsumoto (1967, p. 2, pl. 1, fig. 1*a–f*) is a *Spathites* (*Jeanrogericeras*), synonymous with *S.* (*J.*) *revelierеanus* (Courtiller).

Five *Metoicoceras* species are listed and described from the Lower Cenomanian of Madagascar by Collignon (1964). *M. swalloviforme* (1964, p. 149, pl. 375, fig. 1627) and *sakarahense* (ibid., p. 150, pl. 375, figs. 1630–1632) occur associated at one locality, Collines Vohipaly (Mancra), *M. besairiei* (ibid., p. 149, pl. 375, figs. 1628–1629) and *M. sakarahense* at a second locality, Chutes de Mahaboboka (Sakaraha), and *M. fasciculatum* (ibid., p. 151, pl. 375, fig. 1633) at a third locality, Antanimanga 1 (Mandabe). All the specimens are small and the assemblage may form only one variable species. A number of features of the illustrated material suggest these may be Lower Cenomanian homoeomorphs of *Metoicoceras*. The style of ribbing in all of them strongly recalls *Mantelliceras* or *Utaturiceras*. The smooth, raised venter of the juvenile *M. sakarahense* (Collignon 1964, pl. 375, fig. 1632) is a feature of compressed Mantelliceratinae and is seen in no other species of *Metoicoceras*, whose venter is either undulose and irregularly elevated between upper ventrolateral clavi (e.g. Cobban 1953, pl. 6, figs. 8, 11) or concave (ibid., pl. 6, fig. 15) at similar diameters. The ribbing style of species such as *M. besairiei* and *sakarahense* is reminiscent of *Cottreauites subvicinalis* (Boule, Lemoine, and Thévenin). The specimen of *M. sakarahense* figured by Collignon as his pl. 375, fig. 1631 has chevron-ribbing on the venter, and possibly a siphonal tubercle. This interpretation is supported by the age of the specimens which is said to be Lower Cenomanian, confirmed by the recognition of one species, *M. besairei*, in Israel (Lewy and Raab 1978).

Occurrence. Excluding the Malagasy material discussed above, the earliest *Metoicoceras* occur in the lower part of the Upper Cenomanian of north Texas and Montana–Wyoming. Most records of the genus are from high in the Upper Cenomanian in the Zone of *Sciponoceras gracile* (= *Zone* of *M. whitei*) and equivalents: western interior of the United States, Texas, Mexico, Columbia, Brazil; north Africa (Morocco), Nigeria, Angola; Europe (England, France, Germany, Spain, Portugal); Iran. We know of no *Metoicoceras* younger than the *gracile* Zone, above which it is replaced by its descendant *Spathites* (*Jeanrogericeras*).

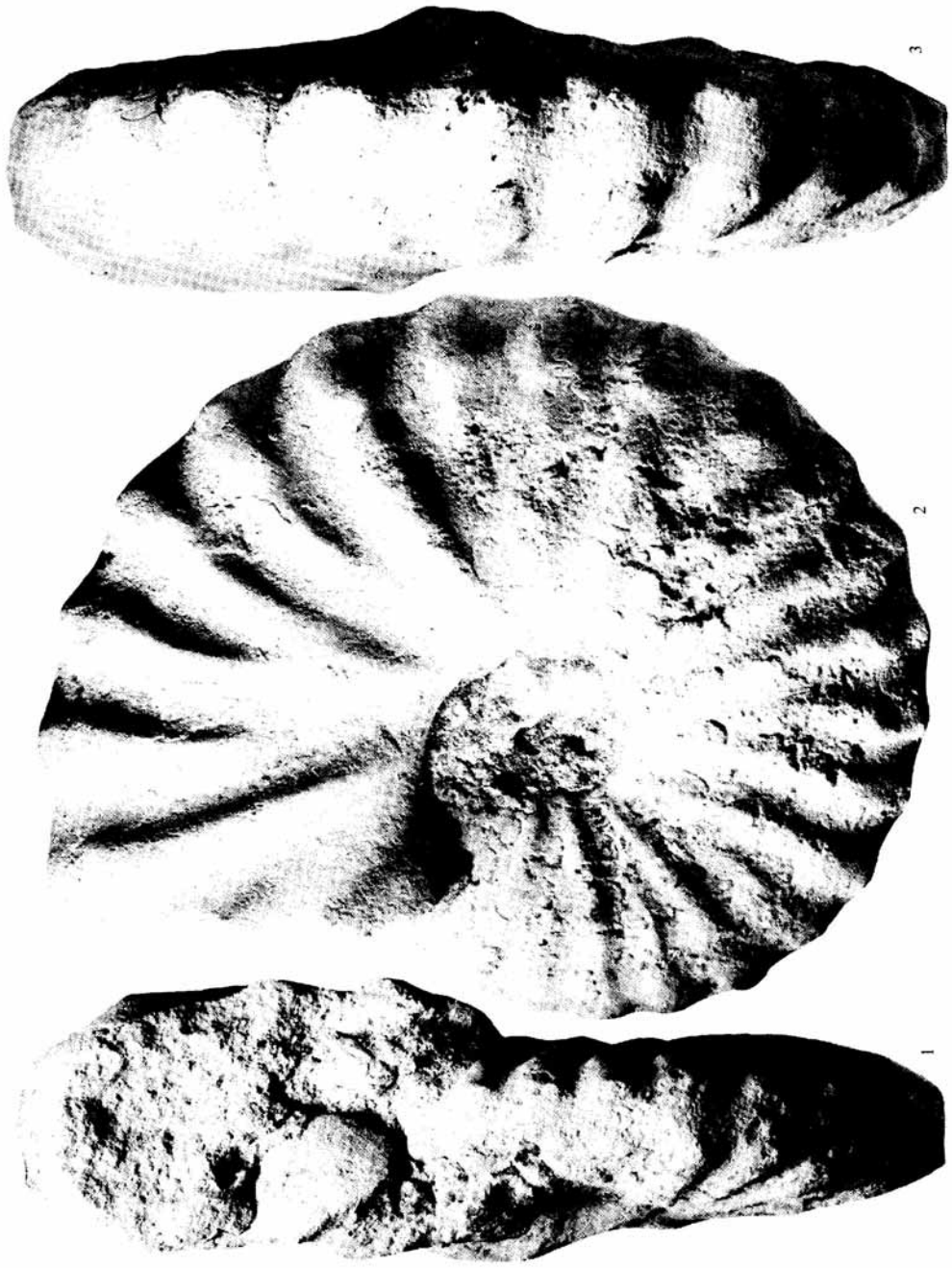
Metoicoceras geslinianum (d'Orbigny)

Plate 3, figs. 6–8; Plate 9, figs. 1–2; Plate 10, figs. 5–6; Plates 11–13; Plate 14, figs. 1–3; Plate 15, figs. 1–3; Plate 16; Plate 17, figs. 1–3; text-figs. 13–17.

1841 *Ammonites catillus* Sowerby; d'Orbigny, p. 235, pl. 97, figs. 1–2.
1850 *Ammonites Geslinianus* d'Orbigny, p. 146.
1854 *Ammonites Geslinianus* d'Orbigny; Millet, p. 103.
1867 *Ammonites Geslinianus* d'Orbigny; Guéranger, p. 6, pl. 5, fig. 2.
non 1872 *Ammonites* cf. *Geslinianus* d'Orbigny; Schlüter, p. 9, pl. 3, figs. 6–7.
?1875 *Ammonites* cf. *Geslinianus* d'Orbigny; Geinitz, p. 280, pl. 62, fig. 3.
1877 *Buchiceras swallovi* (Shumard); White, p. 202, pl. 20, fig. 1*a–c*.
1894 *Buchiceras swallovi* (Shumard); Stanton, p. 168, pl. 37, fig. 1; pl. 38, figs. 1–3.
1901 *Buchiceras swallovi* (Shumard); Hill, pl. 40, fig. 2.
1902 *Pulchellia Gesliniana* d'Orbigny; Petrascheck, p. 140, pl. 7, figs. 3*a–b*, 4 *a–b*, 5*a–b*.
1903 *Metoicoceras gibbosum* Hyatt, p. 121, pl. 15, figs. 5–8.
1903 *Metoicoceras whitei* Hyatt, p. 122, pl. 13, figs. 3–5; pl. 14, figs. 1–10, 15.
1903 *Metoicoceras kanabense* Hyatt, p. 282, pl. 15, figs. 9–11.

EXPLANATION OF PLATE 11

Figs. 1–3. *Metoicoceras geslinianum* (d'Orbigny). A12, a green-coated, glauconitized internal mould from the Sables à *Catopygus obtusus* of Chavagnes (Maine-et-Loire).



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1905 *Metoicoceras Pontieri* Leriche, p. 120, pl. 2, figs. 1 3.
1910 *Metoicoceras whitei* Hyatt; Grabau and Shimer, p. 197, text-fig. 1457*c–e*.
1912 *Mammites Pervinquierei* de Grossouvre, p. 19, pl. 2, fig. 3.
1912 *Mammites Gourdoni* de Grossouvre, p. 20, pl. 1, fig. 1.
1912 *Mammites Geslini* d'Orbigny; de Grossouvre, p. 21.
1912 *Mammites Petrashecki* de Grossouvre, p. 22, pl. 2, fig. 2.
1912 *Mammites Bureaui* de Grossouvre, p. 22, pl. 1, fig. 2.
1912 *Mammites Dumasi* de Grossouvre, p. 23, pl. 2, fig. 1.
1912 *Mammites Pontieri* Leriche; de Grossouvre, p. 23.
1912 *Mammites Whitei* Hyatt; de Grossouvre, p. 24.
1912 *Mammites Kanabensis* Hyatt; de Grossouvre, p. 24.
1912 *Mammites Gibbosus* Hyatt; de Grossouvre, p. 25.
1918 *Metoecoceras* aff. *whitei* Hyatt; Bose, p. 203, pl. 12, figs. 4, 7.
1926*a* *Metoicoceras pontieri* Leriche; Spath, Table facing p. 80.
1926*b* *Metoicoceras whitei* Hyatt; Spath, p. 428.
1927 *Metoicoceras whitei* Hyatt; Scott, p. 142.
1927 *Metoicoceras irwini* Moreman, p. 92, pl. 13, figs. 3–4.
1927 *Metoicoceras whitei* Hyatt; Moreman, p. 94, pl. 15, fig. 1.
1927 *Metoicoceras swallovi* (Shumard); Moreman, p. 95, pl. 15, fig. 3.
1927 *Metoicoceras gibbosum* Hyatt; Moreman, p. 96, pl. 14, fig. 4.
1928 *Metoicoceras gibbosum* Hyatt; Adkins, p. 248.
1928 *Metoicoceras whitei* Hyatt; Adkins, p. 249, pl. 26, figs. 1 2.
1928 *Metoicoceras irwini* Moreman; Adkins, p. 249.
1931 *Pulchellia caicedoi* Karstan; Douvillé, p. 26, pl. 2, fig. 1*a–b*.
1935 *Metoicoceras swallovi* (Shumard); Karrenberg, p. 137, pl. 31, fig. 11, pl. 33, fig. 9.
1935 *Metoicoceras* aff. *swallovi* (Shumard); Karrenberg, p. 138, pl. 31, fig. 12, pl. 33, fig. 10.
1935 *Metoicoceras* aff. *whitei* Shumard; Karrenberg, p. 138.
1938 *Metoicoceras boesei* Jones, p. 127, pl. 10, figs. 1–3.
1939 *Pulchellia gesliniana* d'Orbigny; Dacqué, p. 88, pl. 6, figs. 3 4.
1942 *Metoicoceras whitei* Hyatt; Moreman, p. 210.
1942 *Metoicoceras gibbosum* Hyatt; Moreman, p. 211.
1942 *Metoicoceras irwini* Moreman; Moreman, p. 211.
1942 *Metoicoceras kanabense* Hyatt; Moreman, p. 211.
1942 *Metoicoceras ornatum* Moreman, p. 211, pl. 32, fig. 4, text-fig. 2*c*.
1942 *Barroisiceras trinodosum* Moreman, p. 212, pl. 33, figs. 1, 2, text-fig. 2*a*.
1942 *Barroisiceras brittonense* Moreman, p. 212, pl. 33, fig. 3, text-fig. 2*b*.
1944 *Metoicoceras whitei* Hyatt; Shimer and Shrock, p. 591, pl. 245, figs. 8–10.
1951 *Metoicoceras* Adkins and Lozo, pl. 6, fig. 13.
1951 *Metoicoceras pontieri* (Leriche); Wright and Wright, p. 27.
1951 *Metoicoceras whitei* Hyatt; Wright and Wright, p. 27.
1955 *Metoicoceras* aff. *ornatum* Moreman; Reyment, p. 47, pl. 9, fig. 6–7.
1955 *Ammonites* (*Mammites*) *geslinianus* d'Orbigny; Sornay, fiche 11, figs. 1 4.
?1960 *Metoicoceras swallovi* (Shumard); Wiedmann, pp. 714, 720.
1960 *Metoicoceras gourdoni* (de Grossouvre); Wiedmann, pp. 716, 726.
1960 *Metoicoceras*(?) *petrascheki* (de Grossouvre); Wiedmann, p. 716.
1960 *Metoicoceras whitei* Hyatt; Easton, text-figs. 1132–1135*a–c*.
1960 *Protacanthoceras brittonense* (Moreman); Matsumoto, p. 44.
1960 *Barroisiceras trinodosum* Moreman; Matsumoto, p. 44.

EXPLANATION OF PLATE 12

Figs. 1–9. *Metoicoceras geslinianum* (d'Orbigny). 1–3 is A16; 4–6 is A19; 7–9 is A27; all are green-coated glauconitized internal moulds from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire).

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1962 *Metoicoceras geslinianum* (d'Orbigny); Jefferies, p. 609, pl. 77, fig. 19.
1962 *Metoicoceras gourdoni* (de Grossouvre); Jefferies, p. 609, pl. 77, fig. 20.
1963 *Metoicoceras geslinianum* (d'Orbigny); Jefferies, p. 4.
1963 *Metoicoceras gourdoni* (de Grossouvre); Jefferies, p. 5.
1964 *Metoicoceras swallovi* (Shumard); Wiedmann, p. 112.
1964 *Metoicoceras*(?) *petrasheki* (de Grossouvre); Wiedmann, p. 112.
1964 *Metoicoceras gourdoni* (de Grossouvre); Wiedmann, p. 112.
1966 *Metoicoceras* sp. aff. *ornatum* Moreman; Collignon, p. 34, pl. 19, figs. 1, 2.
1966 *Metoicoceras* sp. aff. *mosbyense* Cobban; Collignon, p. 35, pl. 19, fig. 3.
1966 *Metoicoceras gourdoni* (de Grossouvre); Porthault *et al.*, p. 426.
1966 *Metoicoceras geslinianum* (d'Orbigny); Porthault *et al.*, p. 426.
1970 *Metoicoceras geslinianum* Kennedy, p. 613.
1970 *Metoicoceras gourdoni* (de Grossouvre); Kennedy, p. 613.
1971 *Metoicoceras geslinianum* (d'Orbigny); Kennedy, p. 103.
1971 *Metoicoceras gourdoni* (de Grossouvre); Kennedy, p. 103.
1971 *Metoicoceras whitei* Hyatt; Cobban, pp. 5, 18.
1972 *Metoicoceras whitei* Hyatt; Cobban and Scott, p. 74, pl. 14, figs. 3–4, 9–11; pl. 16, figs. 1 2; text-fig. 34.
1972*a* *Metoicoceras gourdoni* (de Grossouvre); Thomel, p. 10.
1972*a* *Metoicoceras geslinianum* (d'Orbigny); Thomel, p. 10.
1973 *Metoicoceras geslinianum* (d'Orbingy); Wright and Kennedy, p. 234, pl. 1, fig. 7; pl. 3, fig. 1*a–c*.
1973 *Metoicoceras gourdoni* (d'Orbigny); Wright and Kennedy, p. 236, pl. 2, fig. 2*a–c*.
1973*b* *Metoicoceras geslinianum* (d'Orbigny); Thomel, p. 16.
1973*b* *Metoicoceras gourdoni* (de Grossouvre); Thomel, pp. 15–16.
1975 *Metoicoceras whitei* Hyatt; Hattin, p. 32, pl. 6, figs. K, M.
1977 *Metoicoceras geslinianum* (d'Orbigny); Mojica and Wiedmann, p. 748, figs. 3, 4.
1977 *Metoicoceras whitei* Hyatt; Kauffman, p. 19, fig. 7.
non 1977 *Metoicoceras* aff. *whitei* Hyatt; Chancellor, Reyment, and Tait, p. 91, fig. 5 (= *Quitmaniceras* cf. *brandi* Powell).
1978*a* *Metoicoceras geslinianum* (d'Orbigny); Cooper, p. 117, text-fig. 29.
1978*a* *Metoicoceras gibbosum* (Hyatt, 1903); Cooper, p. 117, text-figs. 21*a–c*, 30.
1978 *Metoicoceras geslinianum* (d'Orbigny); Kennedy and Hancock, p. v. 16, pl. 13, figs. 3, 6; pl. 14, figs. 1A B.
1978 *Metoicoceras whitei* Hyatt; Young and Powell, pl. 4, figs. 3–4.
1978 *Metoicoceras* ex. gr. *geslini* (d'Orbigny); Viaud, pl. 8, fig. 3, 3*a–b*.
1978 *Metoicoceras geslinianum* (d'Orbigny); Wiedmann and Kauffman, pl. 6, figs. 4, 5.

Lectotype. An unregistered specimen in the collection of the Musée d'Histoire Naturelle, Paris, figured by Sornay (1955, figs. 3–4), refigured here as text-fig. 13, is herein designated as lectotype of *M. geslinianum*.

The exact status of the type material of *Ammonites geslinianus* is confused. The species is no. 18 of d'Orbigny's Vingtième Étage—the Cenomanian– in the second volume of the *Prodrome de Paléontologie Stratigraphique Universelle* (1850, p. 146), and the name was introduced as follows: '18. *Geslinianus*, d'Orb., 1847. *Am. catillus*, d'Orb., 1841, Pal., 1, p. 325, pl. 97, fig. 1, 2 (non *catillus*, Sowerby). Vibrayes (Sarthe), Touvois (Loire-Inferieur). M. Bertrand Geslin.'

The first author to revise d'Orbigny's species fully, de Grossouvre (1912, p. 21) discussed what he described as 'L'echantillon qui a été figuré comme type par d'Orbigny est porte sur le catalogue de sa collection comme provenant des marnes du grès vert supérieur, de la ferme de la Mairie, près le village de Lamenais, aux environs de Vibraye (Sarthe). Une vieille étiquette porte l'inscription suivante: "du grès vert du canton et des

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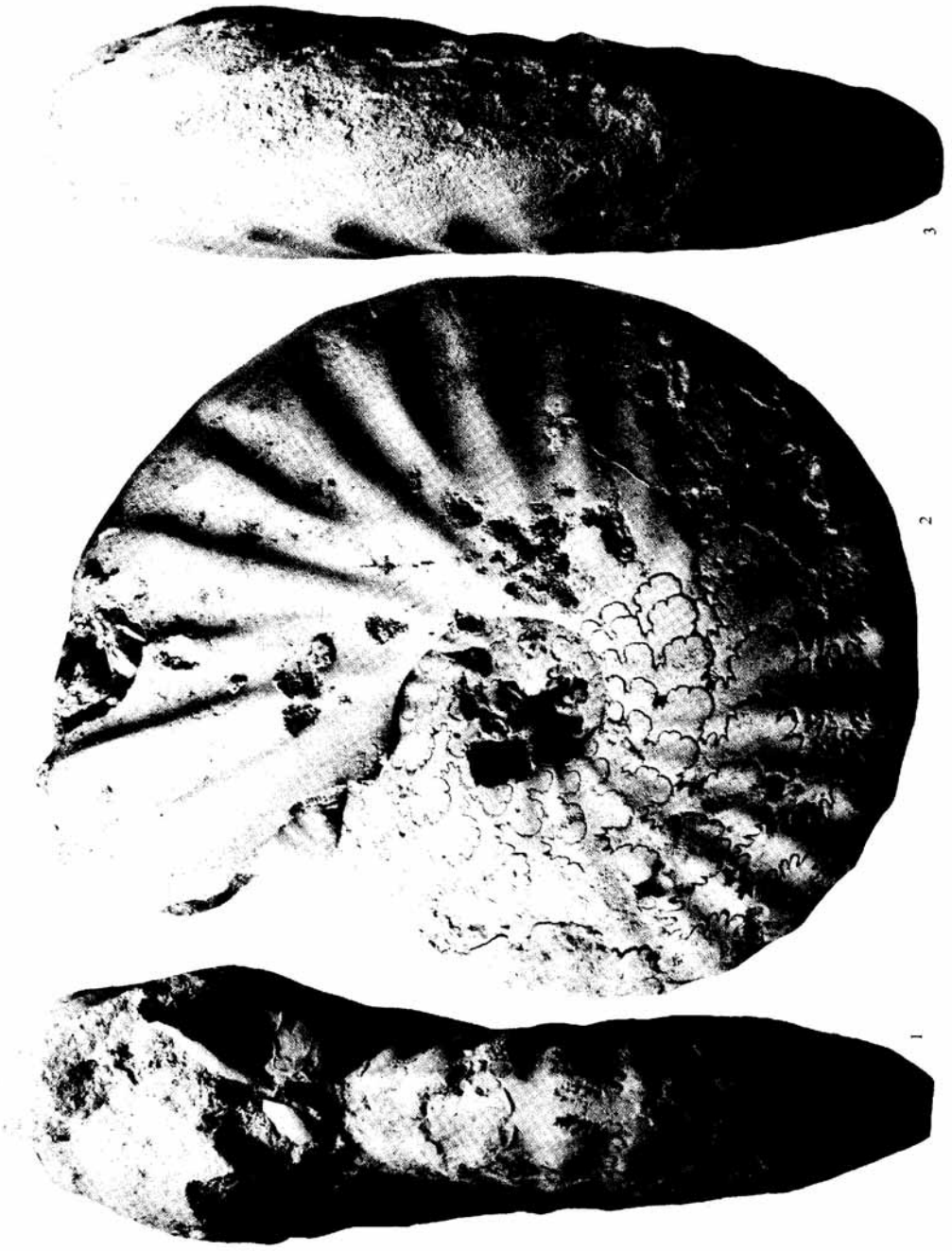
EXPLANATION OF PLATE 13

Figs. 1–3. *Metoicoceras geslinianum* (d'Orbigny). A18, a green-coated glauconitized internal mould from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire).



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TEXT-FIG. 13. *Metoicoceras geslinianum* (d'Orbigny). The lectotype, an unregistered specimen in the collections of the Muséum d'Histoire Naturelle, Paris. This specimen is said to be from Lamnay, Sarthe, but probably comes from the Saumur region (see p. 70).

EXPLANATION OF PLATE 14

Figs. 1–3. *Metoicoceras geslinianum* (d'Orbigny). A20. The holotype of *Mammites petrashecki* de Grossouvre, a glauconitized, green-coated internal mould from the Sables à *Catopygus obtusus* of Briollay (Maine-et-Loire).

Figs. 4–5. *Proplacenticeras* cf. *memoriaschloenbachi* (Laube & Bruder). A35, a septate fragment from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire).

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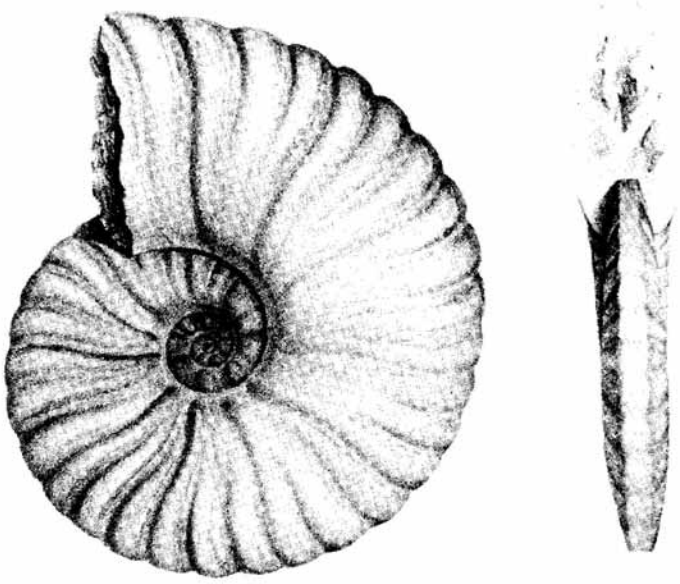

TEXT-FIG. 14. Copies of d'Orbigny's original protographs of *Metoicoceras geslinianum* (*Ammonites catillus*) reproduced from *Paléontologie Française, Terrains Crétacés*, volume 1, pl. 97 (1840).

environs de Vibraye (Sarthe), d'une ferme appelée la Maitrie ou l'on a tiré de la marne, ou bien du village de Lamenais (Lamenay) ou l'on a tiré de la castine pour la forge."

'La carte d'Etat-Major n'indique pas de village de la Mairie ou de la Maitrie aux environs de Lamenais.

'La gangue de cet échantillon est un calcaire gris-verdâtre. D'après les indications de la carte géologique ce calcaire appartiendrait au Cénomanien inférieur: son niveau serait au-dessous des Sables du Perche.

'Cet échantillon se distingue par sa taille, car, détail important, qui parait être passé inaperçu le plus souvent, la figure donnée par d'Orbigny le représente réduit de 1/4: son diametre est de 130 mm et celui de son ombilic, relativement large de 54 mm.

'D'Orbigny a encore cité cette espèce de Touvois, mais aucun des échantillons de cette localité que nous avons examinés et qui présentent des caractères analogues ne peuvent lui être exactement identifiés.'

Subsequently, Sornay (1955) notes that only a single fragment, registered as no. 6110, from Touvois, now remains in the d'Orbigny collection, and that the specimen described by de Grossouvre has now disappeared, and may not, in fact, have been d'Orbigny's original, in that the catalogue of the d'Orbigny collection, drawn

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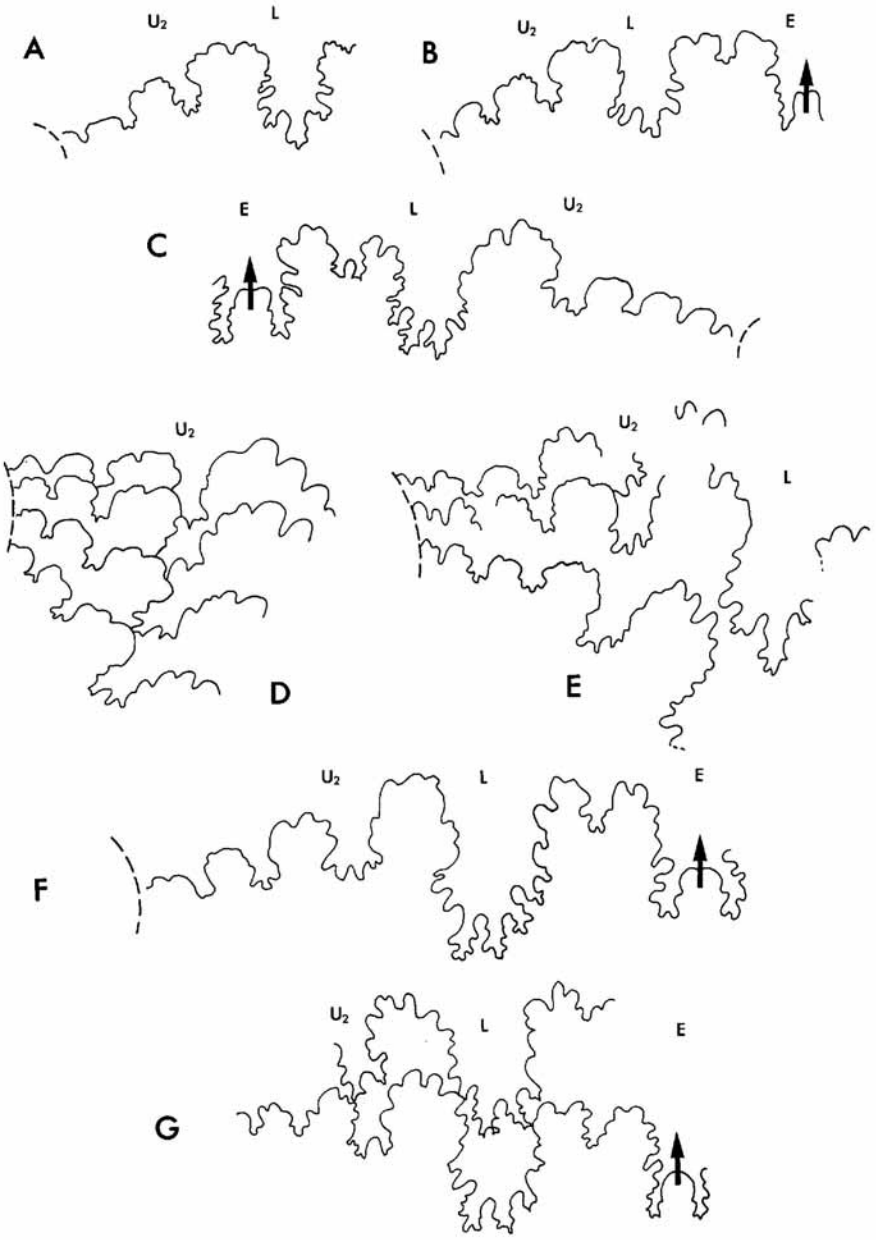
TEXT-FIG. 15. External sutures of *Metoicoceras geslinianum* (d'Orbigny). A–B. From the holotype of *Mammites pervinquierei* de Grossouvre, from the Cenomanian of Touvois (Loire-Atlantique). ×3. C. From specimen N9, also from Touvois. ×1·5. D. Details of the suspensive lobe on four successive sutures of specimen A13 from the Sables à *Catopygus obtusus* of Briollay (Maine-et-Loire). ×1·5. E. Parts of the last three sutures of specimen N7, from the Cenomanian of Touvois (Loire-Atlantique). ×3. F. From the holotype of *Mammites bureaui* de Grossouvre, also from Touvois. ×3. G. From specimen N8, also from Touvois. ×1·5.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up prior to Grossouvre's work, makes no mention of it, whilst de Grossouvre's measurements do not correspond to those of d'Orbigny's type.

Sornay notes, however, the presence of a specimen in the general collections of the Muséum d'Histoire Naturelle in Paris, probably from the Vibraye Collection, bearing the label 'type', which he invalidly designated neotype ('Je propose en tout cas de la prendre comme néotype en l'absence d'un meilleur echantillon dans la collection Vibraye').

Now d'Orbigny was clearly possessed of more than one specimen, the remaining fragment from Touvois and the Comte de Vibraye's specimen, which is said to have come from Lamenais, near Vibraye, Sarthe. It seems very likely to us that the specimen designated as 'neotype' by Sornay may, in fact, be both d'Orbigny's original, and the specimen discussed by de Grossouvre, in spite of the differences in measurement given by various authors. De Grossouvre was in error in suggesting that d'Orbigny had designated a type; Sornay's designation of a 'neotype' is invalid so long as any of d'Orbigny's type series remained in existence. The Touvois fragment 6110 can be presumed to be the Touvois specimen mentioned by d'Orbigny and we regard the unregistered Vibraye specimen as being that referred to by d'Orbigny. The latter we have designated lectotype above, but, even if this specimen were to be proved not to have been d'Orbigny's, the Touvois fragment 6110 is still available for lectotype designation.

There remains the problem of horizon. The lectotype's horizon and locality given by d'Orbigny (1841, p. 326) is 'les marnes du grès vert supérieur a la ferme de la Mairie, près du villiage de Lamanais, aux environs de Vibraye (Sarthe)'. As de Grossouvre noted (see above), and as Thomel (1973*b*) has reaffirmed, this locality suggests a Lower Cenomanian age for the species, since the outcropping Cretaceous in this area consists of Craie Glauconieuse à *Pecten asper* and Sables et Grès de Lamnay (Juignet 1974). In consequence, Juignet *et al.* (1973) suggested that the specimen in fact came from the farm Les Metairies, near Lamnay, on the road to Vibraye, where there is a hill capped by Upper Cenomanian sediments, the inference being that the specimen came from the Sable à *Catopygus obtusus*. The matrix of the lectotype of *M. geslinianum* is a fine, grey, micaceous calcareous silt, and the specimen is preserved as a very crushed composite internal mould. This is quite clearly not a lithology matching Lower Cenomanian outcrops in the area whilst it is quite different from the Sables à *C. obtusus* of the region. There is, however, a series of specimens, including *M. geslinianum*, *Euomphaloceras septemseriatum*, *Calycoceras*, and *Neolobites* species from Saumur, preserved in the keep of the Château de Saumur which are a precise match with the lectotype in preservation and lithology, and we suggest that this region is the source of the lectotype, and, as is frequently the case with nineteenth-century collections, d'Orbigny's specimen was mis-labelled or became associated with the label of some other specimen.

Material. Twenty-one specimens: a paratype specimen, MNHP, d'Orbigny collection, no. 6110; N3, the holotype of *Mammites pervinquierei* de Grossouvre, N5, the holotype of *M. bureaui* de Grossouvre, and five other specimens, N7–11, all from Touvois (Loire-Atlantique). A13 (the type of *M. gourdoni* de Grossouvre), A15 (the type of *M. dumasi* de Grossouvre), from Briollay; A16–19, A20 (the type of *M. petraschecki* de Grossouvre), and A27 from La Dionière, Briollay; A21 from Chevir-sur-Sarthe (all Maine-et-Loire) all from the Sables à *Catopygus obtusus*; A21 from Chevir-sur-Sarthe; A12 from Chanvagnes and A14 from Pellouailles (all Maine-et-Loire). All specimens are green coated and are from the base of the Sables à *C. obtusus*.

EXPLANATION OF PLATE 15

Figs. 1–3. *Metoicoceras geslinianum* (d'Orbigny). A17, a green-coated glauconitized internal mould from the Sables à *Catopygus obtusus* of La Dionière, Briollay (Maine-et-Loire).

Figs. 4–6. *Calycoceras naviculare* (Mantell). A11, a juvenile showing pairs of ribs arising from umbilical bullae and well-developed ventrolateral tubercles. From the Sables à *Catopygus obtusus* of Blaison (tranchée de la Cimitière) (Maine-et-Loire).

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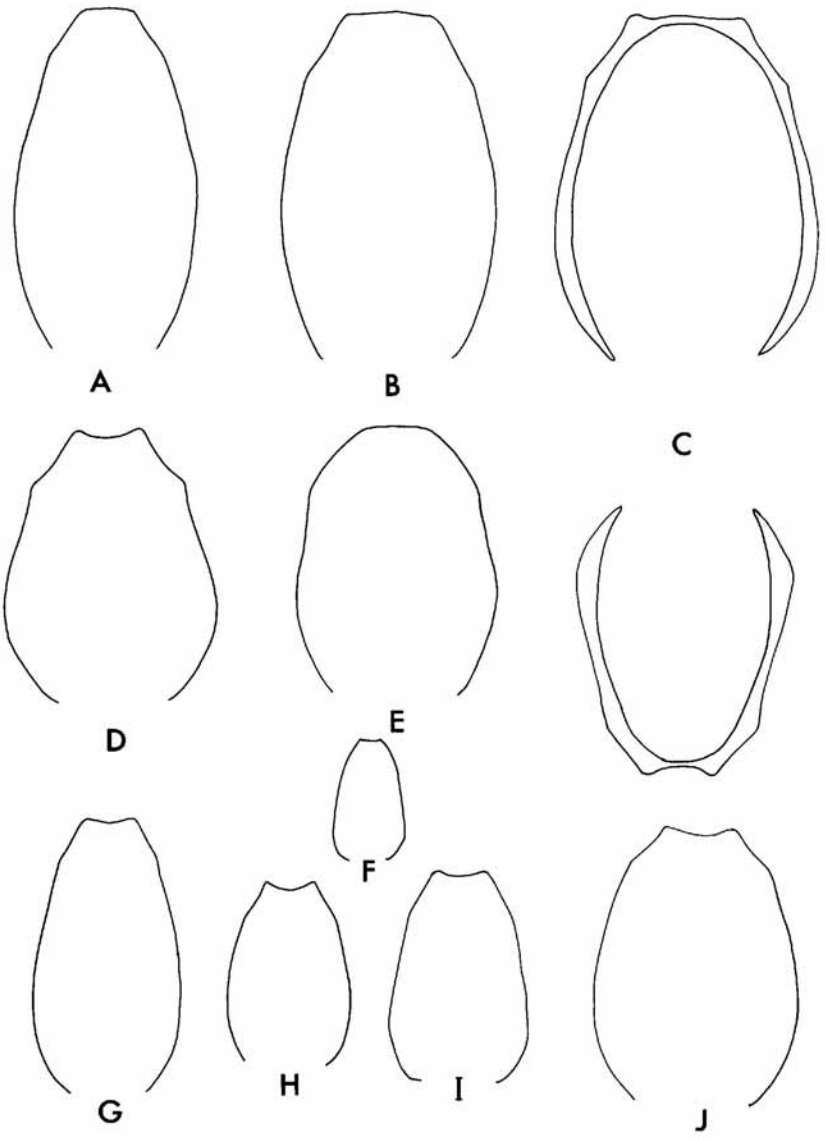
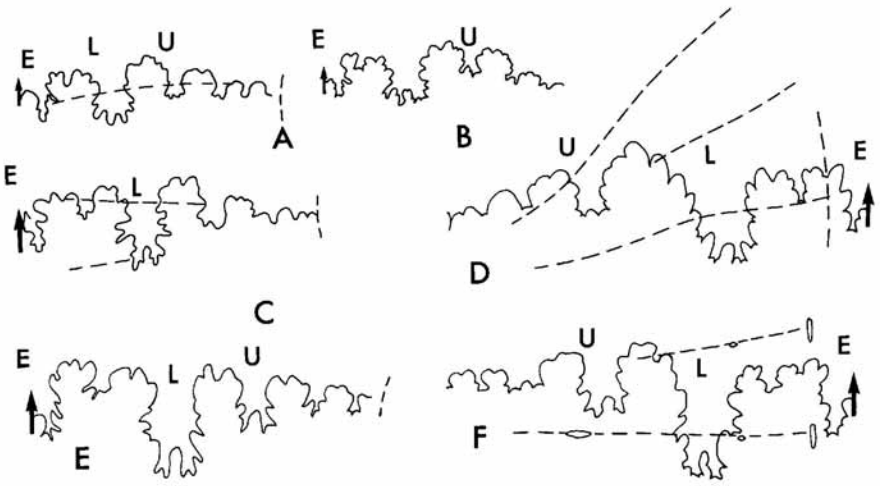


TEXT-FIG. 16. Whorl sections of *Metoicoceras geslinianum* from the Briollay region. A: A18; B: A12; C: A13, the types of *Mammites gourdoni*; D: A17; E: A14; F: A27; G: A15; H: A19; I: A20, the type of *M. petrashecki*; J: A16.



TEXT-FIG. 17. External sutures of *Metoicoceras geslinianum* from the Briollay region. A: A20, the type of '*Mammites*' *petrashecki* de Grossouvre; B: A15, the type of '*M.*' *dumasi* de Grossouvre; C: A17; D: A18; E: A16; F: A13, the holotype of '*M.*' *gourdoni* de Grossouvre. All ×1.

Dimensions	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*	*R*
Lectotype						
(*a*) after d'Orbigny	125	28(22)	54(43)	0·52	0·36(29)	
(*b*) after de Grossouvre	130	—(—)	—(—)	—	0·54(41)	—
(*c*) after Sornay	128	—(—)	55(43)		0·37(29)	—
(*d*) herein	134	28(21)	54(43)	0·52	35·5(29)	32
A20 Type of *M. petrashecki*	101	26·8(27)	40·3(40)	0·67	23·8(23)	32
A18	160					
at	128	36(28)	59(46)	0·60	22·3(17)	28
A15 Type of *M. dumasi*	113·5	30·8(27)	47·5(42)	0·65	20·5(18)	27/28
A12	144·5	40(28)	61(42)	0·66	33·9(23)	26/27
A14	—	30	42·5	0·67	—	—
A17	103	35·2(34)	53·8(52)	0·65	18·5(18)	25
A16	103·8					
at	91·5	32·4(35)	45·8(50)	0·70	15·5(17)	27/28
A19	60·0	21·4(35)	31·2(52)	0·68	7·7(13)	26
A27	39·5	12·7(32)	21·5(54)		2·9(7)	—
N5 Type of *M. bureaui*	98·5	—(—)	51(52)		11(11)	30
N3 Type of *M. pervinquierei*	50·5	21·2(42)	26·4(52)		9·3(16)	24/25
A13 Type of *M. gourdoni*	138	41·5(30)	58·5(42)	0·70	30·5(22)	22
USNM 29408 = *M. whitei* Hyatt (Hyatt 1903, pl. 13, figs. 3–5)	137	41·3(30)	67·2(49)	0·62	22·9(17)	30
USNM 27409 Type of *M. kanabense*	39·4	11·4(29)	20·6(52)	0·55	3(8)	28
UT 19809 Holotype of *M. ornatum*	109·5	33·2(30)	47·8(44)	0·69	22·0(20)	23
Paratype, UT 21243	131·5	—(—)	56·0(43)	—	30·5(23)	22

Diagnosis. A medium-sized *Metoicoceras* with 25–33 ribs per whorl. The distinctive features are the retention of both inner and outer ventrolateral tubercles and a large umbilicus (17–29% of diameter) through middle and into late growth stages.

Description of lectotype (text-fig. 13). This is a crushed composite internal mould. Because of the crushing, the ornament is artificially subdued.

The coiling is moderately involute, although the umbilical seam egresses over the last half whorl, which is body chamber. The umbilical wall is low, with a rounded shoulder. The inner whorls, partly obscured, bore strong, blunt distant bullae, giving rise to pairs of low, broad, flattened ribs. At the beginning of the last whorl, these branch from the bullae in pairs, with some intercalated ribs. On the body chamber this pattern becomes irregular, long ribs with weak bullae alternating with one or two short ribs. Long ribs are prorsiradiate across the inner flank, flexing backwards (and rarely branching) at mid-flank and widening into spatulate terminations on the ventrolateral shoulder. The short ribs arise at or below mid-flank, sometimes seemingly branched at their inception, and rapidly widen into spatulate terminations. Broad, band-like ribs cross the venter. There is a suggestion of an effaced lower lateral tubercle on some ribs, and of ventrolateral clavi on either side of the narrow venter.

Discussion. The fifteen specimens of *Metoicoceras* from Briollay and Touvois belong to a single species. The considerable variation they show led de Grossouvre (1912) to erect five new specific names for these whilst still retaining eight other names for approximately contemporaneous *Metoicoceras* from other localities. It seems to us that the Briollay–Touvois populations show a complete gradation between two extremes. At one end ribbing is dominant over tubercles, as in *M. bureaui* with thirty ribs on the adult and rapid loss of ventrolateral tubercles to leave a nearly smooth venter (holotype Pl. 16). *M. petraschecki* with thirty-two ribs is even more densely ribbed but retains the ventrolateral tubercles for slightly longer (Pl. 13 and juvenile in Pl. 12, figs. 4–6). At the opposite extreme is *M. gourdoni* (holotype Pl. 9, figs. 1–2) with only twenty-two broad ribs on the outer whorl and both inner and outer ventrolateral tubercles retained on the body chamber; similar robust inner whorls are seen in A17 (Pl. 15); *M. pervinquierei* (holotype Pl. 3, figs. 6–8) is a juvenile of this sort. The lectotype of *M. geslinianum* is an intermediate, similar to *M. gourdoni* but does not retain such strong ornament. *M. dumasi* (holotype Pl. 17, figs. 1–3) is another intermediate with slightly flexuous ribs. Juveniles vary from nearly smooth (Pl. 12, figs. 1–3) to coarsely ribbed and tuberculate (Pl. 3, figs. 6–8), whilst strength of ribbing and tuberculation may increase during growth or decline. This variation is well within that known in other acanthoceratids.

A further complicating factor in this group of specimens is that ontogenetic changes occur at differing rates in different individuals, so that the adult of one specimen may resemble the juvenile of another; adult body chamber modifications, or modifications of the terminal parts of the phragmocone, especially loss of tubercles, occur at small diameters in some specimens. We have only eight definite adult specimens (as indicated by approximated sutures and ornament changes) and these fall into two distinctive size classes, suggestive of sexual dimorphism. The types of *M. bureaui*, *petraschecki*, and *dumasi* together with specimen N10 thus appear to be microconchs, mature at 90 to 110 mm diameter; the type of *M. gourdoni*, specimens A12, A14, and A18 (all of which are damaged) appear to be macroconchs, mature at 140 to 160 mm diameter, an approximately 1:1·5 size ratio.

M. pontieri Leriche (1905, p. 120, pl. 2, figs. 1–3; text-fig. 1) from the 'Turonian' of Lumbres, Pas de Calais, is simply a feebly ornamented *M. geslinianum*, the style of ribbing, with spatulate rib terminations matching that developed in the type of *M. bureaui*, but accentuated by crushing. *Pulchellia caicedoi* Douvillé (*non* Karsten) (1931, p. 26, pl. 2, fig. 1*a–b*) from the Cenomanian of

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EXPLANATION OF PLATE 16

Figs. 1–6. *Metoicoceras geslinianum* (d'Orbigny). 1–3 is N6, the holotype of *Mammites bureaui* de Grossouvre; 4–5 is MNHP 6110 (d'Orbigny collection), the paralectotype; 6 is N10. All specimens are from Touvois (Loire-Atlantique).

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Salinas, Angola, is also within the range of variation of *M. geslinianum*, and is a strict contemporary (Cooper 1972, 1978). Karrenberg's (1935) *M. swallovi* (p. 137, pl. 31, fig. 11; pl. 33, fig. 10) with rather strongly ornamented large shells, should also be referred to *M. geslinianum*, closely resembling the lectotype if allowance is made for the crushed state of the latter. The various juvenile or fragmentary *Metoicoceras* recorded from Nigeria by Reyment (1955, p. 47, pl. 9, figs. 6–7) and from Morocco by Collignon (1966, pp. 34–35, pl. 19, figs. 1–3) also appear to belong to d'Orbigny's species as here interpreted.

The rich *Metoicoceras* faunas of the Kanab Valley, Utah, and the Britton member of the Eagle Ford Shale in Texas, are contemporaneous with the Touvois–Briollay material, and large collections from both areas in the United States show the type of *M. whitei* to be a rather typical member of a very variable population. The feebly ornamented members of these collections are typified by *M. irwini* Moreman (1927, p. 92, pl. 13, figs. 3–7). The type of this form is compressed and involute with thirty-two irregularly long and short gently flexed prorsiradiate ribs per whorl. The ribs are virtually effaced on the inner flank, but develop broad spatulate ends on the ventrolateral shoulders. There are feeble, rounded inner and clavate outer ventrolateral tubercles which are rapidly lost on the body chamber. As inflation increases, ribs and tubercles strengthen; the type of *M. gibbosum* Hyatt is an inflated individual where ribbing predominates over tuberculation; there are approximately twenty-six ribs on the outer whorl. The type of *M. whitei* lies between *M. irwini* and *gibbosum* in terms of rib strength and inflation, but has somewhat stronger tuberculation. The coarsely ornamented variant of this group, equivalent to *M. gourdoni*, is represented by the type of *M. ornatum* Moreman (1942, p. 211, pl. 32, fig. 4; text-fig. 3*c*). This range extends from juveniles (e.g. *M. kanabense* Hyatt, 1903, p. 44, pl. 15, figs. 9–11) to adults, which show considerable size variation. The variation matches that of *M. geslinianum* in every respect, though coarsely ornamented forms tend to dominate. These American varieties are exact contemporaries of *M. geslinianum* and we consider them to be synonyms of it.

Furthermore, the contemporaneous species of '*Barroisiceras*', '*B.*' *trinodosum* Moreman (1942, p. 212, pl. 33, figs. 1–2; text-fig. 2*a*) and '*B.*' *brittonense* Moreman (1942, p. 212, pl. 3, fig. 3; text-fig. 2*b*) are malformed *Metoicoceras*; additional pathological specimens in the J. P. Conlin collection, at the U.S. Geological Survey in Denver, confirm this. *M. boesei* Jones (1938, p. 127, pl. 10, figs. 1–3) is a further North American species which falls within the range of variation of *M. geslinianum*.

Discussion of older American species of *Metoicoceras* is deferred for another paper.

Occurrence. Under various guises, *M. geslinianum* has a range from the U.S. Western Interior south to Texas and north-central Mexico, Columbia, Brazil, Morocco, Nigeria, and Angola. In Europe it occurs widely in southern England, Germany, northern Spain, Portugal, and across France from the Pas de Calais to Basses-Alpes. The stratigraphic range of the species spans the *Plenus* Zone of western Europe—the *M. gourdoni*/*geslinianum* Zones of Jefferies (1962–1963). The American occurrences are associated with similar faunas in the classic *M.* '*whitei*'/*S. gracile* Zone, and a similar restricted stratigraphic range is indicated.

STRATIGRAPHICAL CONCLUSIONS

Table 1 summarizes correlation of the faunas discussed in this paper with those known from the other areas in northern France and southern England. The few ammonites from the Marnes à *Ostrea biauriculata* of Briollay can be matched in the rather more diverse assemblages from the

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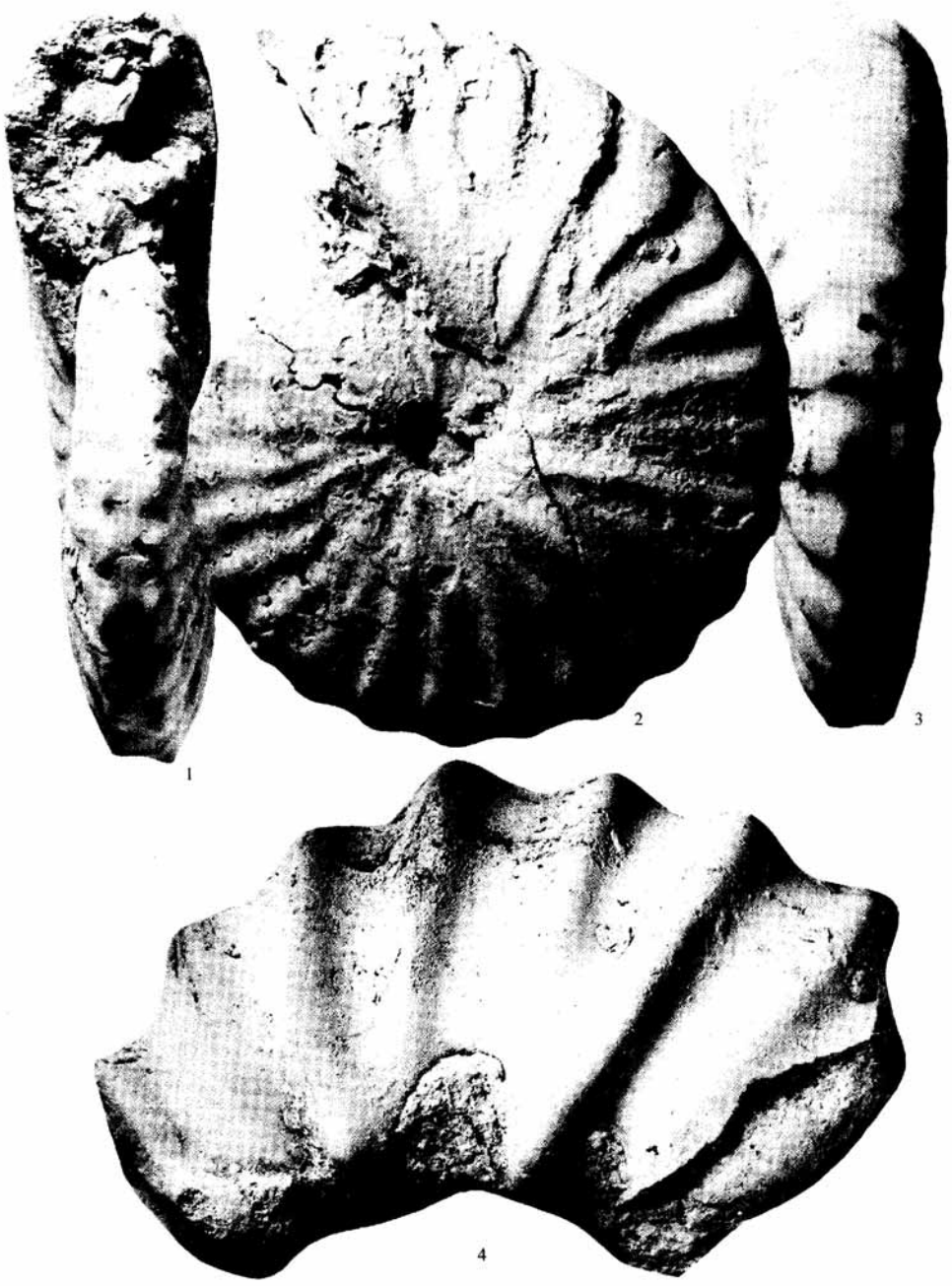
EXPLANATION OF PLATE 17

Figs. 1–3. *Metoicoceras geslinianum* (d'Orbigny). A15, the holotype of *Mammites dumasi* de Grossouvre, a green-coated internal mould from the Sables à *Catopygus obtusus* of Briollay (Maine-et-Loire).

Fig. 4. *Calycoceras naviculare* (Mantell). N2 from Touvois (Loire-Atlantique); original of de Grossouvre's (1912, p. 4) *Ammonites rotomagensis* Defrance.



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same unit in Sarthe, which has also yielded numerous *Calycoceras* of the *guerangeri* (Spath)—*bruni* (Fabre) group and *Acanthoceras hippocastanum* (J. de C. Sowerby) (Juignet *et al.* 1973; Juignet, Kennedy, and Lebert 1978). Further north, in Normandy, a similar association is known at the top of the Craie de Rouen (niveau 11 of Juignet 1970; Juignet and Kennedy 1976) and at the top of the Lower Chalk in southern England (Kennedy and Hancock 1978). The association of *Thomelites* and *Calycoceras naviculare* is also characteristic of the well-known phosphatic faunas of Division C of the Cenomanian Limestone of south-west England.

To the east of Briollay, in Touraine, Marnes à *O. biauriculata* are exposed along the Canal du Berry in the valley of the Cher (Butt 1966; Hancock, Kennedy, and Wright 1977). They have yielded only poorly preserved acanthoceratids to us, but correlation with the same unit in the Briollay region seems highly likely. Above, the nodular and glauconitic base of the Craie de Fretevou has yielded specimens of *Sciponoceras* suggesting a correlation with either the Sables à *Catopygus obtusus* or the base of the Craie à *Terebratella carantonensis*. In the Saumur region, the occurrence of Cenomanian fossils has been documented for many years, and indeed some were recorded and described by d'Orbigny in *Paléontologie française*. The collections of the Château de Saumur include specimens of *Neolobites vibrayeanus* (d'Orbigny), *Pseudocalycoceras*? cf. *lattense*, *Calycoceras* (*Lotzeites*?) sp., *C. naviculare* and *M. geslinianum* which indicate the presence of equivalents of the Marnes à *O. biauriculata* and Sables à *Catopygus obtusus* in a silty calcareous clay facies in the vicinity (Juignet and Kennedy in preparation).

The fauna of the Sables à *C. obtusus* at Briollay is clearly equivalent to the Touvois fauna described here. It also matches that of the same unit in Sarthe, and its lateral equivalent, the Sables de Bousse. In the Paris Basin it matches that of the Plenus Marls (Jefferies 1962, 1963; Amedro, Bidar, Damotte, Manivit, Robaszynski, and Sornay 1978) and the unphosphatized fauna of Bed C of the Cenomanian Limestone in Devon.

In terms of zonal nomenclature, both faunas can be referred to the upper part of the *Calycoceras naviculare* Zone in the sense in which is was used by Arkell, Kummel, and Wright (1957). As we have shown, *C. naviculare* has a long range and is an excellent index species for such a broad zone. Considering subsequent zonations, the lower fauna is correlated with the *C. naviculare* Zone in

TABLE 1. Suggested correlation of the Briollay faunas with adjacent areas in northern France and southern England

Saumur	Canal du Berry	Briollay	Sarthe	Northern France/ Southern England
Metoicoceras geslinianum fauna	Base of Craie de Fretevou with *Sciponoceras* and *Inoceramus pictus*	Sables à *Catopygus obtusus* with *M. geslinianum*, *S. gracile*, *E. septemseriatum*, *Proplacenticeras* sp., *C. naviculare*, *F.* gr. *largilliertianum*, *M.* cf. *dumbli*	Sables à *Catopygus obtusus* with *M. geslinianum*, *S. gracile*, *E. septemseriatum*, *Proplacenticeras* sp., *Ps. lewisvillense*, etc.	Plenus Marls with *M. geslinianum*, *E. septemseriatum*, *S. gracile*, *C. naviculare*, etc.
Pseudocalycoceras–Neolobites fauna	Marnes à *Ostrea biauriculata*	Marnes à *Ostrea biauriculata* with *C. naviculare*, *P.* cf. *lattense*, *P.* sp., *Thomelites* aff. *sornayi*	Marnes à *Ostrea biauriculata* with *C. naviculare*, *C. bruni*, *C. guerangeri*, *Pseudocalycoceras* sp., *Thomelites sornayi*, *Acanthoceras hippocastanum*	Top of Lower Chalk/Craie de Rouen with *C. naviculare*, *Thomelites*, *Acanthoceras hippocastanum*, *Schloenbachia lymense*, etc.

the more restricted sense that was used by Hancock (1960), Kennedy (1969, 1971), and Amedro *et al.* (1978) and the *Eucalycoceras pentagonum* Zone of Juignet and Kennedy (1976) and Juignet *et al.* (1978). The upper fauna is correlated with the *M. geslinanum* and *M. gourdoni* Zones of Jefferies (1962, 1963), the *M. geslinianum* Zone of Amedro *et al.* (1978), and the greater part of the *Sciponoceras gracile* Zone as used by Kennedy and Hancock (1977), Kennedy and Hancock (1978), Juignet and Kennedy (1976), and Juignet *et al.* (1978).

Outside northern France and England, the higher *Metoicoceras* fauna can be recognized in Germany and Czechoslovakia (Dacqué 1939; Petrascheck 1902), Angola (Cooper 1978), and in the rich *S. gracile* Zone assemblages of the Bridge Creek Member of the Greenhorn Limestone of the U.S. Western Interior (Cobban and Scott 1972) and the Britton Member of the Eagle Ford Group in Texas (Moreman 1927, 1942). Elements of the fauna can also be recognized in California, Nigeria, and Japan. The *M. geslinianum*/*S. gracile*/*Euomphaloceras septemseriatum* association is emerging as a world-wide datum for correlation in the Upper Cenomanian.

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