MANTELLICERAS SAXBII, AND THE HORIZON OF THE MARTIMPREYI ZONE IN THE CENOMANIAN OF ENGLAND

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Abstract. Synonyms of Mantelliceras saxbii (Sharpe) include M. hyatti Spath and M. martimpreyi (Coquand) sensu Pervinquière. In England this species occurs at a recognizable horizon that is in the middle, not at the base of the Lower Cenomanian.

Specific names for Cenomanian ammonites have often been erected haphazardly, ignoring the possibility that specimens of different size may be no more than different growth stages of the same species. The problem is acute in the Cenomanian stage because the ammonites are usually preserved in two quite distinct facies: (i) in limestones (e.g. South Africa, Utatur division of southern India, Chalk of north-west Europe) they occur as moulds preserving the adult body chamber and the later septate portions; (ii) in clays and marls (e.g. Texas, Algeria, and Tunisia) they occur as pyritic or limonitic internal moulds, only preserving minute nuclei or the adults of genuinely tiny species. In southern England the basement beds of Chalk contain ammonites preserved as phosphatic internal moulds and casts, and this preservation sometimes bridges the gap in growth stages between the pyritic nuclei and limestone body chambers. Hence it is possible to demonstrate the equivalence of Ammonites saxbii Sharpe (1857, p. 45, pl. 20, figs. 3a, b). Mantelliceras martimpreyi (Coquand) sensu Pervinquière (1910, p. 41, pl. 4, figs. 3-9), Mantelliceras hyatti Spath (Sharpe 1857, pl. 18, figs. 4a, b), and one of the syntypes of Mantelliceras batheri Spath (Mantell 1822, pl. 22, fig. 1).

It has been pointed out that 'aff.' in this paper is given a different meaning from the interpretation of some other writers. By prefixing a specific name with 'aff.' we mean that the specimen(s) referred to differs rather clearly in some respect(s) from the holotype (or lectotype or neotype) of the species but is still within the limits of variation of the species. It is a notation which allows one to indicate qualitative variation within the pre-evolutionary convention of Linnean nomenclature. This usage was discussed by Trueman and Weir (1946, pp. xx-xxi). We do not mean by 'aff.' that the specimen is necessarily specifically different.

SYSTEMATIC DESCRIPTION

Family ACANTHOCERATIDAE Hyatt 1900 Genus Mantelliceras Hyatt 1903

Mantelliceras saxbii (Sharpe)

Plate 79, figs. 1-5; Plate 80, figs. 1-4; Plate 81, figs. 1, 4, 6, 7, 8; Plate 82, figs. 2, 4, 5

- ? 1814 Ammonites mantelli J. Sowerby, p. 119 (pars.), pl. 55, upper figure only.
 - 1822 Ammonites mantelli var. costata Mantell, p. 114 (pars.), pl. 22, fig. 1 only.
 - 1857 Ammonites saxbii Sharpe, p. 45, pl. 20, figs. 3a, b.
 - 1857 Ammonites mantelli Sowerby; Sharpe, p. 40, pl. 18, figs. 4a-b only (non Sowerby).
 1860 Ammonites saxbii Sharpe; Pictet and Campiche, p. 320.

[Palaeontology, Vol. 14, Part 3, 1971, pp. 437-454, pls. 79-82.]

- 1864 Ammonites saxbii Sharpe; Stoliczka, p. 85.
- 1862 Ammonites martimpreyi Coquand, p. 172, pl. 1, figs. 7-8.
- Ammonites mantelli Sowerby; Schlüter, p. 12, pl. 6, figs. 1, 2, 11. ? 1871
- 1903 Mantelliceras couloni (d'Orbigny); Hyatt, p. 114.
- 1907 Acanthoceras martimpreyi Coquand; Pervinquière, p. 289, pl. 16, figs. ?2-3 only.
- 1910 Acanthoceras martimpreyi Coquand; Pervinquière, p. 41, pl. 4, figs. 3-8 only; fig. 9?
- Mantelliceras hyatti Spath, p. 197. 1925
- 1926 Mantelliceras batheri Spath, p. 431 (pars.).
- ? 1929 Acanthoceras (Mantelliceras) martimpreyi Coquand; Collignon, p. 10, pl. 3, figs. 4-5.
- non 1937 Mantelliceras hyatti Spath; Collignon, p. 55, pl. 4, fig. 5, pl. 9, fig. 9 (=? Eucalycoceras
 - 1937
 - Mantelliceras saxbii (Sharpe); Spath, p. 279. Mantelliceras batheri Spath; Wright and Wright, p. 24. 1951
 - 1951 Mantelliceras hyatti Spath; Wright and Wright, p. 24.
 - 1951 Mantelliceras saxbii (Sharpe); Wright and Wright, p. 25.
 - 1963 Mantelliceras (Mantelliceras) hyatti Spath; Renz, p. 1102, pl. 5, figs. 4-5.
 - 1963 Mantelliceras (Mantelliceras) sp. aff. saxbyi (Sharpe); Renz, p. 1103, pl. 5, fig. 1.
- non 1963 Mantelliceras (Mantelliceras) saxbyi (Sharpe); Renz, p. 1104, pl. 4, fig. 1.
 - ? 1963 Mantelliceras (Mantelliceras) batheri Spath; Renz, p. 1107, pl. 5, fig. 3. 1964
- Mantelliceras hyatti Spath; Collignon, p. 71, pl. 340, figs. 1518, ?1520.
- non 1964 Mantelliceras saxbyi Sharpe; Collignon, p. 98, pl. 341, fig. 1558.
 - ? 1967 Mantelliceras albanense Busnardo et al., p. 222, pl. 12, figs. 1-2.
 - ? 1967 Mantelliceras cf. hyatti Spath; Busnardo et al., p. 222
 - ? 1967 Mantelliceras (Couloniceras) cressierense Renz; Busnardo et al., p. 223, pl. 12, figs. 3-4.
 - ? 1967 Mantelliceras (Couloniceras) cf. cressierense Renz; Busnardo et al., p. 223.

Lectotype. GSM Geol. Soc. coll. 7763, the original of Ammonites saxbii Sharpe 1857, pl. 20, figs. 3a-b, from the Lower Chalk of Ventnor, Isle of Wight; designated by Wright and Wright (1951, p. 38).

This specimen is a small, well-preserved, wholly septate, phosphatic internal mould, retaining traces of matrix which is grey, slightly glauconitic chalk. It is moderately involute, just under half the previous whorl being covered. The intercostal whorl section is compressed, with flat sides and a narrowly rounded venter. The costal section is rather similar, with the greatest breadth at the umbilical bulla. The umbilicus is small and shallow, with a rounded umbilical wall.

There are 28 ribs on the outer whorl. Up to a diameter of 18 mm these ribs are very weak; long, flat

EXPLANATION OF PLATE 79

All figures are of natural size. Specimens are coated with ammonium chloride.

Figs. 1a-b. Mantelliceras saxbii (Sharpe) (the holotype of Mantelliceras hyatti Spath, from the Chalk Marl (Mantelli Zone) of Bonchurch, Isle of Wight. Side and ventral views of BMNH 50288; figured by Sharpe 1857, pl. 18, figs. 4a-b.

Figs. 2a-b. Mantelliceras aff. saxbii (Sharpe) (the syntype of Mantelliceras batheri Spath figured by Mantell 1822, pl. 22, fig. 1, as Ammonites mantelli var. costata), from the Lower Chalk of Lewes, Sussex. Side, front, and ventral views of BMNH 5694.

Fig. 3. Mantelliceras saxbii (Sharpe); phosphatized internal mould from the phosphate bed (Mantelli Zone, M. saxbii assemblage horizon) above the Glauconitic Marl of Gore Cliff, Isle of Wight. Side view of WJK 8761.

Figs. 4a-b. Mantelliceras aff. saxbii (Sharpe); limonitic internal mould from the Lower Cenomanian 700 m north-east of Koudiat el Assel, 11 km north-north-east of Bou Khadra village, eastern Algeria (9865.2971). Side and front views of authors' collection M6; differs from M. saxbii in possessing fewer ribs although the ribbing on the venter is stronger and the tubercles on the shoulders are

Figs. 5a-b. Mantelliceras aff. saxbii (Sharpe); phosphatized internal mould from the Glauconitic Marl (Mantelli Zone, H. carcitanensis assemblage horizon) at Gore Cliff, Isle of Wight. Side and front views of WJK 9958; more inflated than M. saxbii.

ribs arise at the umbilical shoulder, each with a very faint umbilical bulla, and pass straight up the flank; where the whorl starts to contract the ribs turn gently forwards to meet the shoulder at small, pointed, ventro-lateral tubercles. These long ribs are separated by two or three shorter ribs which arise just below mid-flank, but are otherwise similar to the long ribs.

Beyond 18 mm the ribbing becomes much stronger, each long rib bears a distinct umbilical bulla, small lower ventro-lateral tubercles appear, whilst the upper ventro-lateral tubercles become stronger and clavate as the diameter increases.

In the suture line the first lateral saddle is moderately broad and evenly bipartite; the accessory lobe here is as large as the second lateral lobe (U2). The first lateral lobe is not as long as the external lobe, but has a narrow stem and the end is divided into four narrow and elongate accessory lobes.

Discussion. Sharpe's figure is good, although reversed and somewhat restored.

This species is clearly based on a juvenile specimen. A good idea of the middle growth stages of the species can be gained from the following descriptions of the holotype of *Mantelliceras hyatti* Spath, BMNH 50288 (Pl. 79, figs. 1a-b). This specimen cannot be separated specifically from the lectotype of *M. saxbii* at comparable diameters; it also is a phosphatized, wholly septate, internal mould.

The shell is involute, about half the previous whorl being covered. The whorl section is compressed, the greatest breadth being just above the umbilical bulla. The intercostal section is rounded, and there is a broadly rounded venter in costal section; the whorl sides are slightly inflated.

The umbilicus is small and rather deep, the umbilical wall is steep and undercut, the umbilical shoulder is quite sharply rounded.

There are 36–37 ribs at a diameter of 55 mm. Up to a diameter of 30 mm there are 2 short ribs separating the longer ribs, and such pairs of short ribs sometimes occur up to a diameter of 45 mm. The longer ribs arise at the umbilical seam, with an umbilical bulla, developed to varying degrees on successive ribs. Up to 40 mm diameter the ribs are faintly flexed, swinging forwards across the inner part of the flank, backwards across mid-flank and forwards across the ventro-lateral shoulder, where they broaden slightly. There is an angular change in the costal whorl section a little below the shoulder without lower ventro-lateral tubercles, but strong sharp clavate upper ventro-lateral tubercles are developed on all ribs. The venter is flat with a width about half the whorl thickness, and the upper ventro-lateral tubercles are connected by broad, slightly elevated ribs.

The intercalated short ribs are similar to the long ribs except that they arise at various positions on the sides, from just above the umbilical bulla to the mid-flank, and occur in ones or twos between the long ribs.

Over the last part of the outer whorl, at diameters greater than 45 mm, the long and short ribs alternate regularly.

On some ribs there is a faint indication of a mid-lateral swelling, but never a pronounced tubercle. A later growth stage of *Mantelliceras saxbii* is illustrated by one of the syntypes of *M. batheri* Spath (BMNH 5694, the original of Mantell 1822, pl. 22, fig. 1, from the Lower Chalk of Sussex, bearing Mantell's original label 'xxii, i') although it is slightly more inflated than the type of *M. hyatti*.

This specimen is a well-preserved, slightly worn and distorted, wholly septate, composite internal mould ('normal' chalk preservation of Jefferies 1962) in hard limestone.

The shell is moderately evolute, about half the previous whorl being covered. The whorl section is compressed, and the greatest breadth is at the umbilical bullae. The intercostal section is rounded; the costal section is also approximately rounded, but there is an angular change on the upper part of the sides and a flattened, broadly convex venter. The umbilicus is narrow and deep, the umbilical wall is overhanging and the umbilical shoulder rounded.

There are 37 ribs at a diameter of 92 mm, alternately long and short; up to a diameter of 50 mm there are sometimes 2 short ribs together. The long ribs arise at the umbilical seam, and develop strong umbilical bullae immediately above the umbilical shoulder. These ribs are flat and rounded, the same width as, or slightly narrower than the interspaces. The ribs pass straight across the sides, developing clavate ventro-lateral tubercles on each side of the narrow venter. The ribs are connected across the venter by a low rounded rib. The shorter, intercalated ribs arise about a third of the way up the sides, and are similar to the long ribs.

The adult body-chamber of M. saxbii appears at about 100 mm diameter in British material, and extends for over half a whorl. A crushed chalk example is figured as Pl. 80, figs. 1a-b; a phosphatic

example (slightly more inflated than the type would be, and better referred to as M. aff. saxbii) is figured as Plate 81, fig. 1. The ribs are broad and rounded, and one long rib alternates with one (rarely two) shorter ribs. The venter is flattened between distinct, rounded and faintly clavate, ventro-lateral tubercles. Close to the aperture (traces are preserved in the specimen shown in Pl. 80, fig. 2), the ribs weaken and approximate; there are many coarse striae which become distinctly inclined forwards. The aperture itself is simple.

TABLE 1. Measurements in mm of *Mantelliceras saxbii* (Sharpe). The last three specimens are from the phosphate bed above the Glauconitic Marl (Mantelli Zone, *M. saxbii* faunal horizon), Gore Cliff, Isle of Wight.

Collection key: GSM = Geological Survey Museum, Institute of Geological Sciences, London; BMNH = British Museum (Natural History); WJK and JMH = authors' collection.

Measurements of diameter, whorl height, and whorl width have been made between ribs.

Specimen	Diameter	Whorl height	Whorl width	Width of umbilicus	No. of ribs on last whorl	No. of primaries	No. of secondaries
Lectotype							
GSM Geol. Soc.							
coll. 7763	25.9	11.7	8.6	5.4	28	8 a.	20 a.
M. 'hyatti'							
BMNH 50288	56.0	26.4	19.4	11.6	36 a.	14	22 a.
M. 'batheri'							
BMNH 5694	92.4	44.4	37.7 a.	19.8	36	17 a.	19
= M. aff. saxbii							
WJK 8761	68.3	28-8	23.7	19-3	37	18	19
JMH CC761	43.8 a.	22·1 a.	14.8 a.	8.4			
WJK 8938	54.0	24.8	20.6	13.0			

Characters of Mantelliceras saxbii. The distinctive characters of M. saxbii are: (i) when young, a markedly compressed whorl section with flat parallel sides; (ii) when young, the mid-flank decoration is weak, but there are markedly sharp ribs on the shoulders and sharp upper ventro-lateral tubercles; (iii) in youth there are numerous short ribs, and pairs of short ribs are maintained to middle age; (iv) numerous ribs—some 28 on nuclei, increasing to 35–38 in the middle stages, but decreasing again to approximately

EXPLANATION OF PLATE 80

All figures are of natural size. Specimens are coated with ammonium chloride.

Figs. 1a-b. Mantelliceras saxbii (Sharpe); composite chalk mould from the upper part of the phosphate bed (Mantelli Zone, M. saxbii assemblage horizon) above the Glauconitic Marl, Gore Cliff, Isle of Wight. Side and ventral views of JMH CC760; note the retention of tubercles on the shoulders although the whorl compression and probably the clavateness of the tubercles have been exaggerated by crushing.

Fig. 2. Mantelliceras saxbii (Sharpe); composite chalk mould from the phosphate bed (Mantelli Zone, M. saxbii assemblage horizon) 3 m above the Glauconitic Marl, Eastbourne, Sussex. Side view of WJK 2689; an adult showing striae between ribs on the body chamber.

Figs. 3a-d. Mantelliceras saxbii (Sharpe); the lectotype from the Lower Chalk (Mantelli Zone) of Ventnor, Isle of Wight. GSM Geol. Soc. coll. 7763 (Institute of Geological Sciences photograph).

Figs. 4a-b. Mantelliceras saxbii (Sharpe); limonitic internal mould from the Lower Cenomanian 700 m north-east of Koudiat el Assel, 11 km north-north-east of Bou Khadra village, eastern Algeria (9865.2971). Side and front views of authors' collection M5.

Figs. 5a-b. Copies of Coquand's original figures of Ammonites martimpreyi (1862, pl. 1, figs. 7-8). Figs. 6a-c. Mantelliceras ventnorense Diener; the holotype from the Chalk Marl (Mantelli Zone) of Ventnor, Isle of Wight. Ventral, side and front views of GSM Geol. Soc. coll. 7759.

30 on an adult; (v) short ribs and ventro-lateral tubercles are maintained on to the adult body-chamber.

The ratio of the whorl height: whorl width is 1.36 in both the lectotype and the holotype of M. 'hyatti', and this compression immediately distinguishes the species from M. mantelli (J. Sowerby). Only occasionally does one get more compressed specimens with a ratio as high as 1.5, but less-compressed specimens ranging away from M. saxbii s.s. are common (e.g. Plate 81, figs. 1a-b; ratio 1.17-1.18). Up to diameters of about 25 mm, as in the lectotype itself, the width of the venter is around 0.5 of the whorl width; with further growth the whorl section widens faster than the venter, and the venter width may be as low as 0.34 of the whorl width. In M. mantelli the width of the venter is more constant at almost exactly half the whorl width.

THE STATUS OF MANTELLICERAS MARTIMPREYI

The most important synonym of *Mantelliceras saxbii* is *M. martimpreyi* (= *Ammonites martimpreyi* Coquand 1862, pp. 172–173, pl. 1, figs. 7–8) because it has been adopted by many authors as the zonal ammonite for the lowest part of the Cenomanian.

The original description and figures of this species are in a rather obscure publication; they are therefore reproduced here as Pl. 80, figs. 5a-b. Coquand's original description is as follows:

Ammonites Martimpreyi H. Coq. pl. 1, fig. 7 et 8.
 Diamètre 21 millimètres.

Coquille comprimée, ornée, en travers et par tours, de 28 à 30 petites côtes inégales, dont les unes un peu plus saillantes que les autres, et au nombre de 6 à 8, partent de l'ombilic et viennent se terminer à la périphérie: chacune de ces côtes renferme dans l'intervalle qu'elles laissent entre elles, un nouveau système de côtes, au nombre de 3 à 5, moins nettement accusées et qui vont en s'atténuant vers l'ombilic, où elles se montrent bijugées; chaque côte porte vers son extrémité supérieure deux tubercules, dont l'un, plus saillant, est limité franchement vers le dos, et dont l'autre est placé à deux millimètres en dessous. Dos formé par une carène, s'élevant sensiblement au-dessus des tubercules terminaux; ombilic peu ouvert.

Cette espèce, par ses côtes inégales, par les deux tubercules dont elles sont ornées, ainsi que par sa carène, se distingue des autres Ammonites du terrain crétacé.

Elle a été découverte par M. Ville, à Bérouaguia, province d'Alger, dans l'étage rhotomagien. Je me suis fait un devoir de la dédier au général de Martimprey, sous-gouverneur de l'Algérie, qui m'a fourni les plus grandes facilités pour pénétrer dans les parties les moins connues des possessions françaises.

In the summer of 1965, one of us (W. J. K.) was able to examine Coquand's collection in the Geological Institute, Nepstadion Korut, Budapest (part of Coquand's collection is in the National Museum, but none of that material is relevant here).

The specimens are uncatalogued, and are stored by locality. There are nine specimens in one tray bearing the following label:

'Ammonites martimpreyi Coquand.

Roth'. [indecipherable symbol] 'Berrouaghia' [indecipherable word] 'Aumaule'.

This presents an immediate problem, for Coquand does not mention more than one specimen in his description, and figures only one, which would thus be the holotype by monotypy. Pervinquière figured seven of these nine ammonites in 1910 and considered one of them (Pervinquière 1910, pl. 4, figs. 7a, 7b; Pl. 81, figs. 7a-b herein) as 'trés

probablement le type figuré dans "Geol. Pal. S. Constantine", pl. 1, fig. 7–8'. Pervinquière's figure shows this ammonite to have a diameter of about 21 mm (allowing for the over-pyritization visible) which would agree with Coquand's measurement, but Pervinquière failed to state that his figures are appreciably reduced: the original is larger; moreover, it does not agree with Coquand's description of the decoration.

The main difficulty is that Coquand stated, indeed emphasized, that his specimen had a keel, and this is clearly shown in his figure. If this was an original feature of the shell, Ammonites martimpreyi could hardly be a Mantelliceras, but it could be referred to Cottreauites, a genus with close affinities to Mantelliceras (see Sornay 1955). It is true that the smoothly keeled species of Cottreauites that have been described from north Africa only possess a mere trace of a keel (e.g. C. subboulei Sornay) but the Malagasy species C. boulei Collignon is more distinctly keeled. There are also ammonites with a similar Mantelliceras-type decoration on the sides but possessing a tuberculated keel which have been referred to Acompsoceras, e.g. A. dubourdieui Sornay. But the keel may not have been genuine: in our experience limonitic ammonites from clays in north Africa have quite often developed a 'keel' from being crushed, and, as discussed below, several of the 'co-types' of A. martimpreyi have such false keels.

Suture lines cannot help because Coquand did not figure one.

This matter can probably never be fully resolved without neotype designation. We therefore select the original in the Coquand collection figured by Pervinquière 1910, pl. 4, figs. 7a-b (reproduced here as Pl. 81, figs. 7a-b) as neotype of Ammonites martim-preyi Coquand.

Of the seven surviving figured specimens, the originals of figs. 4, 6, 7, and 8 are all specifically inseparable from M. saxbii, although there is some variation amongst them for instance in the stage at which ribs become prominent across the venter, and the stage where the lower ventro-lateral tubercle begins to weaken. The original of fig. 8 has faint mid-lateral swellings on the long ribs, although no true tubercle is developed; crushing has produced false keels on the originals of figs. 4 and 8.

The neotype (fig. 7) is a perfectly preserved, wholly septate, limonitic internal mould. It is almost the same size as the lectotype of *M. saxbii*, but loses the lower ventro-lateral tubercles earlier, although the costal whorl section continues to be markedly angular at this level on the side. There are up to three short ribs between any two full length ribs.

The original of fig. 9 is very close to *M. saxbii* but differs in having stronger ribbing on the sides (and the venter?), in having a higher ratio of long to short ribs, develops lower ventro-lateral tubercles earlier (and possibly retains them longer), and possesses faint mid-lateral swellings on some of the long ribs.

EXPLANATION OF PLATE 81

- All figures are of natural size. Specimens in figs. 1, 11-13 are coated with ammonium chloride.
- Figs. 1a-b. Mantelliceras aff. saxbii (Sharpe); uncrushed and partly phosphatized specimen from the Glauconitic Marl/Popple Bed junction (Mantelli Zone), Dead Maid Pit, Mere, Wiltshire. Side and ventral views of WJK 5341.
- Figs. 2-10. Copies of Pervinquière 1910 pl. 4, figs. 2-10, the 'cotypes' of *Mantelliceras martimpreyi* (Coquand). Pervinquière's original figure numbers are retained; figs. 7a-b are the neotype; figs. 10a-b are a specimen of *Mantelliceras* gr. tuberculatum (Mantell); fig. 4 is generically indeterminate. Originals in the Geological Institute, Nepstadion Korut, Budapest.
- Figs. 11a-13b. Stoliczkaia (Stoliczkaia) spp. juv.; phosphatic specimens from the Dispar Zone ammonite bed, Upper Greensand, south Dorset. C. W. Wright collection, nos. 7450 (11a-c), 7145 (12a-b), 231 38 (13a-b). These specimens show the similarities of nuclei of S. (Stoliczkaia) and M. sayhii

The original of fig. 2 has a genuine notched keel and may be a *Cottreauites*. The original of fig. 10 is better judged from Pervinquière's figures and, as Pervinquière noted, can be compared with *M. mantelli*.

The other three specimens preserved in Budapest do not correspond with figs. 3 or 5, and were thus not figured by Pervinguière.

TABLE 2. Measurements in millimetres of the syntypes of *Ammonites martimpreyi* Coquand in the Geological Institute, Budapest, figured by Pervinquière 1910, pl. 4; reproduced here in Plate 81, figs. 2–10.

Fig. No.	Identification	Diameter	Whorl height	Whorl width	Width of umbilicus	No. of ribs					
2	Cottreauites?	10	4.5	3							
3	original not found in museum										
4	M. saxbii	20	11	7							
5	original not found in museum										
6	M. saxbii	22	11	8	4						
7	M. saxbii (neotype										
	of A. martimpre	yi) 25	12	11	5	34-35					
8	M. saxbii crushed and distorted										
9	M. aff. saxbii	36	19	11	7	34-35					
10	now in decomposing fragments										

There are many ammonites figured as Mantelliceras martimpreyi but not all of them are synonymous with M. saxbii. Pervinquière (1907) discussed M. martimpreyi at length and with discernment; he stressed the similarity with Sharpe's var. B of Ammonites mantelli which from Sharpe's description would appear to be represented by Sharpe 1856, pl. 18, fig. 4, i.e. the holotype of M. hyatti. Pervinquière also explains correctly the differences from M. mantelli which is more inflated and has mid-lateral tubercles. However, Pervinquière at this time figured a variety of species under the name Acanthoceras martimpreyi (1907, pl. 16).

Fig. 1 is closer to Mantelliceras ventnorense Diener because the ribbing is flexuous.

Figs. 2 and 3 are juveniles, probably not specifically determinable, but belong to the M. saxbii group.

Figs. 4 and 5 are more inflated and probably belong to another species.

Fig. 16 was renamed *Eucalycoceras lymense* by Spath (1926). We have examined the original in the École des Mines in Paris and it is a true *Mantelliceras*, but too inflated for *M. saxbii*.

Fig. 17 is difficult to determine.

Fig. 18 was made a syntype of *Mantelliceras batheri* by Spath (1926). We have examined the original in the École des Mines in Paris: it is close to *M. costatum* (Mantell) and only differs from Mantell's species in having abrupt beginnings to the long ribs on the umbilical edge, and a sulcate venter at the tuberculate stage.

Proper assessment of all the small pyritic and limonitic specimens from Madagascar, North Africa and Texas must await detailed study of the plentiful material that we have collected stratigraphically from Algeria and Tunisia. As far as can be judged at present not a single limonitic or pyritic ammonite figured by Collignon (1929, 1964) from Madagascar belongs exactly to *M. saxbii*; this is possibly only a reflection of the variability of nuclei, and need not mean that the species is absent from Madagascar. 'Submantelliceras' worthense (Adkins) as figured by Adkins (1928, pl. 20, fig. 11) appears inseparable from *M. saxbii* at comparable diameters; Scott (1926) actually called some of Adkins' specimens *Acanthoceras martimpreyi*.

SPECIES COMPARABLE TO MANTELLICERAS SAXBII

Mantelliceras ventnorense Diener

This is the most puzzling relative of Mantelliceras saxbii. The holotype, by the original designation of Diener (1925, p. 170) is the original of Ammonites feraudianus Sharpe (1857, p. 51; pl. 23, figs. 6a-c) non d'Orbigny, GSM 7759, from the 'Grey Chalk at Ventnor' (figured here as Pl. 80, fig. 6). This specimen is a small composite internal mould in hard chalk with a limonitic coat. It is distorted into an ellipse (major diameter 28.7 mm), and the venter is abraded over the last third of a whorl. This poor preservation makes comparison with M. saxbii difficult, but the decoration is similar. The chief distinctions of M. ventnorense appear to be: (i) the much earlier loss of a distinct lower ventro-lateral tubercle (there is the merest trace of such a tubercle at the smallest diameter visible-12 mm?); (ii) the much more flexuous ribbing. Both these features could be exaggerated in the type by the abrasion, crushing and distortion; the apparently greater inflation is almost certainly artificial. However, examples of Mantelliceras which are compressed and have flexuous ribbing are known (e.g. Pervinquière 1907, pl. 16, fig. 1a-b); several authors have described what are probably larger specimens of this species (e.g. M. ventnorense in Fabre 1940, p. 236, pl. 8, fig. 8; and M. ventnorense in Collignon 1964, p. 87, pl. 347, fig. 1547). We leave M. ventnorense here as a separate species, but further work may well indicate that it would be better treated as a subspecies (or variety) of M. saxbii.

Mantelliceras couloni (d'Orbigny)

A neotype for this species was designated by Collignon (1937, p. 56, pl. 11) who distinguished it from M. hyatti (i.e. M. saxbii) in that: (i) the ribs do not reach the centre of the venter so that between the high ventro-lateral tubercles there is a sinus; (ii) the narrowness of the venter combined with the gentle convexity of the flanks produces a perfectly oval intercostal whorl section.

One of us (J. M. H.) has re-examined the neotype (from Lamnay, Sarthe, France), several topotypes and a number of other examples from the Sarthe. They show that up to moderate diameters (50 mm, possibly more) M. couloni is not easily distinguished

EXPLANATION OF PLATE 82

All figures are of natural size. Specimens are coated with ammonium chloride.

Figs. 1a-b. Mantelliceras aff. couloni (d'Orbigny); internal mould with traces of cast of shell from the basement bed of the Wilmington Sands (Mantelli Zone), Hutchins' Pit, Wilmington, south Devon. Ventral and side views of JMH CC337.

Fig. 2. Mantelliceras saxbii (Sharpe). Front view of specimen figured in Plate 79, fig. 3.

Figs. 3a-b. Utaturiceras vicinale (Stoliczka); internal mould from the Utatur Group, southern India.

Side and front views of Oxford University Museum KY 311.

Fig. 4. Mantelliceras aff. saxbii (Sharpe); phosphatized internal mould from the phosphate bed (Mantelli Zone, M. saxbii assemblage horizon) above the Glauconitic Marl, Gore Cliff, Isle of Wight. Front view of WJK 8763; the nucleus is close to the lectotype but the whorl section in the middle stage is appreciably more inflated.

Fig. 5. Mantelliceras aff. saxbii (Sharpe); phosphatized internal mould with traces of phosphatized shell from the Popple Bed (Mantelli Zone), Dead Maid Pit, Mere, Wiltshire. Ventral view of JMH CC739; angular shoulders with strong tubercles have been retained to a middle growth

stage.

from *M. saxbii*: in *M. couloni* there is a narrow venter in relation to the inter-costal whorl thickness (1:4), and umbilical bullae are absent. Around diameters of 70 mm *M. couloni* develops exaggerated ventro-lateral tubercles whilst retaining a narrow venter; the tubercles are only slightly clavate. In some individuals these great tubercles are continued to diameters of 135 mm; in others the adult body chamber begins around 100–110 mm diameter, on which the ventro-lateral tuberculation rapidly disappears and thereafter the venter merely shows a slight flattening.

Not only are the younger stages possibly indistinguishable, but there are all gradations between *M. couloni* and *M. saxbii*. However, the two extremes have not yet been found together at the same horizon, and one is probably the descendant of the other. The exact horizon of the neotype is not recorded, but its lithology combined with the locality of Lamnay suggests that it was from the top third of the Lower Cenomanian.

Wright and Wright (1951) recorded *M. couloni* from south-west England, correctly noting that the English examples are less compressed than the type. Moreover, the tuberculation is probably never so strong. We figure an example (Pl. 82, figs. 1*a-b*) from Wilmington which is less compressed than the types of both *M. couloni* and *M. saxbii*, but in other features is intermediate between the two species. This specimen has a venterwidth 0·36 of the whorl-width.

Utaturiceras vicinale (Stoliczka)

This ammonite has had a somewhat chequered history. Spath (1926) used 'Acanthoceras' vicinale as a zonal index for the top of the Cenomanian, as did Collignon (1959) and Wright (1957). In 1956 Wright made it the type species of a new genus—Utaturiceras. As Casey (1960) notes, this Upper Cenomanian age is erroneous (it probably originated with Kossmat's inference of horizon from the matrix), and it is a Lower Cenomanian genus. He concluded that Utaturiceras was a synonym of Mantelliceras, and Ammonites vicinalis could be matched with Mantelliceras of the group of M. saxbii.

We had been inclined to follow the view of Casey until the revision of *Utaturiceras vicinale* by Matsumoto *et al.* (1966) combined with the features seen in a specimen in the Oxford University Museum (Pl. 82, figs. 3a-b) showed that the species are slightly different. In particular, juveniles of *U. vicinale* have more flexuous ribbing, whilst the middle and adult stages are more compressed, high whorled and with more numerous subdued ribs (40:35) which are very weak across the venter, whilst the width of the venter is less than a third of the inter-costal whorl thickness. These subtle but important differences give *Ammonites vicinalis* a quite distinct appearance. We are still uncertain whether it merits generic or even subgeneric separation from *Mantelliceras*; it could still be an extreme variant of the *M. saxbii* group. Matsumoto and Sarkar were unfortunate in being dependent on specimens from the Isle of Wight for suture lines of *Mantelliceras*. The suture line differences they list are not so distinct when one compares *U. vicinale* with well preserved *Mantelliceras* limestone internal moulds from Devon (text-fig. 1). For these reasons we are sorry that Matsumoto (1969, p. 291) should have felt it necessary to place *Utaturiceras* in a separate subfamily (Utaturiceratinae) from *Mantelliceras*.

Other species described from Europe

Mantelliceras cressierense Renz (1963, p. 1105, pl. 4, figs. 3a, 3b), from the Swiss Jura, is based on a single crushed specimen; it differs from M. saxbii in its coarser, fewer ribs

(29:37 per whorl at 70 mm diameter), but is probably a closely allied species. Renz's *M. saxbii* (pl. 4, fig. 1) differs from that species by its possession of a marked mid-lateral tubercle, but his *M.* aff. saxbii and *M. hyatti* are both *M. saxbii*, as is possibly his *M. ventnorense* (pl. 4, fig. 2).

Busnardo (in Busnardo et al. 1966) has figured several Mantelliceras from the French Jura whose preservation is rather poor and which are therefore difficult to assess properly. His M. albanense (pl. 12, figs. 1, 2) resembles the adult of the more inflated M. saxbii such as we figure as Plate 81, fig. 1, but the inner whorls of M. albanense are said to have ribs of equal length.

TEXT-FIG. 1. External suture-lines above the umbilical shoulder of *Mantelliceras* and *Utaturiceras*. All \times 2. Figs. b, d-f drawn by J. M. H.

- a. Mantelliceras saxbii (Sharpe) Kyushu University no. 9307, T. Matsumoto collection from the Glauconitic Marl, St. Catherine's Point, Isle of Wight. After Matsumoto in Matsumoto, Sastry, and Sarkar 1966.
- b. Utaturiceras vicinale (Stoliczka) Oxford University Museum KY 311 from the Utatur Group of southern India.
- c. Utaturiceras vicinale (Stoliczka) Lectotype, Geological Survey of India 190, from the Utatur Group, Odium, southern India. After Matsumoto in Matsumoto, Sastry, and Sarkar 1966.
- d. Mantelliceras aff. saxbii (Sharpe) JMH CC461 from the Mantelliceras-rich bed, Mr. Hutchins' pit, Wilmington. Devon.
- e. Mantelliceras saxbii (Sharpe) WJK 8761 from the upper phosphate bed, Gore Cliff, Isle of Wight.
- f. Mantelliceras ventnorense Diener JMH CC459 from the Mantelliceras-rich bed, Mr. Hutchins' pit, Wilmington, Devon.

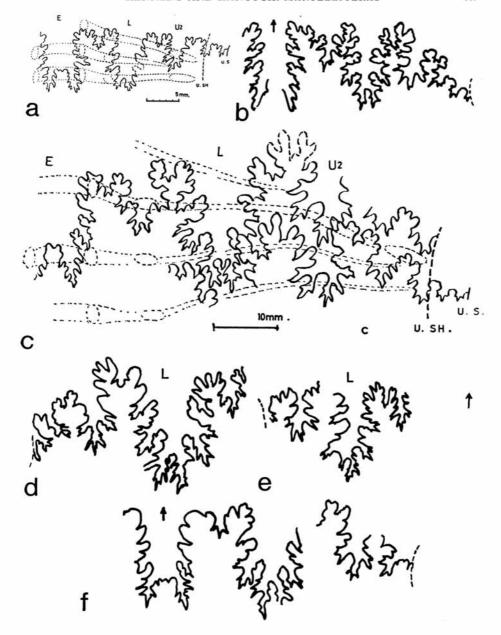
In the list below of the features which Matsumoto and Sarkar (1966) say distinguish the sutures of *Utaturiceras* from those of *Mantelliceras*, the exceptions are noted afterwards in brackets:

- (1) They are fairly deeply incised (also seen in fig. d);
- (2) There are numerous descending auxiliaries (also seen in fig. d).

In addition they note in the suture lines of Utaturiceras:

- (3) The deeply bipartite external saddle (also seen in fig. e);
- (4) The first lateral lobe is deeper than broad and is bipartite at the bottom; its median foliole is much lower than and overhung by the adjacent lateral folioles (also seen in fig. f);
- (5) The first lateral lobe is deeper than the external lobe E (also seen in fig. e but not shown by the *Utaturiceras* in fig. b);
- (6) The inner (i.e. dorsal) branch of the external saddle is slightly taller than the outer, and narrowed by deeply incised lobes (also seen in fig. f);
- (7) The saddle between the lateral lobe L and the second lateral lobe U2 is higher than that between the external lobe and the lateral lobe (also seen in fig. d and fig. f, but barely shown by the *Utaturiceras* in fig. b);
- (8) The saddle inside the second lateral lobe U2 and the auxiliary saddles are arranged on a descending line (also seen in fig. d);
- (9) The second lateral lobe U2 is much smaller than the lateral lobe L (if anything this is less marked in the *Utaturiceras* fig. b).

It has also been our experience that: (a) the first lateral saddle (= external saddle) in *Mantelliceras* of the *saxbii* group is broader than in the specimen figured by Matsumoto and Sarkar (fig. a); (b) the outer side of the lateral lobe is lower on the side than the lower ventro-lateral tubercles.



Species described from Madagascar

Collignon (1964) has figured several forms which belong here, or are closely related. His *Mantelliceras hyatti* (p. 71, pl. 340, figs. 1518–1520) is carefully compared with the type and is therefore synonymous with *M. saxbii*; fig. 1519 illustrates the slightly more inflated form such as we figure as Plate 79, fig. 5. This greater inflation is also characteristic of *M. hyattiforme* Collignon (p. 71, pl. 340, figs. 1521–1524) but the chief distinction of this species is the greater number of ribs (42–45).

Mantelliceras pseudohyatti Collignon (1964, p. 73, pl. 341, fig. 1525) also has more ribs than M. saxbii (43 at a diameter of 92 mm); apart from this rib density, its only other marked distinctions from the English syntype of M. batheri described on p. 439, are the slight forward twist of the ribs above the lower ventro-lateral tubercle and the

considerable strength of the ribs on the venter.

Mantelliceras biroi Collignon (1964, p. 84, pl. 346, figs. 1540, 1541; pl. 351, fig. 1540) is characterized by its broad ribs which lose their ventro-lateral tubercles comparatively early (around 40–60 mm diameter). However, it is doubtful if the form identified as M. saxbyi (pl. 351, fig. 1558) really belongs there: the figure is poor but one can see midlateral tubercles and markedly strong lower ventro-lateral tubercles.

Eucalycoceras spp.

Eucalycoceras is an Upper Cenomanian genus, type species E. pentagonum (Jukes-Browne & Hill), and therefore not likely to give rise to confusion if the horizons of the specimens are known. However, the middle stages and particularly the nuclei of compressed species are superficially similar to M. saxbii. They can be distinguished by (a) the possession of a strong umbilical tubercle (usually bullate) on every rib at the umbilical shoulder; (b) the sharpness of the ribbing, particularly noticeable on the venter where it is stronger than in M. saxbii.

Graysonites spp.

Wiedmann (in Basse 1959, p. 807) remarked that he did not believe that nuclei of M. 'martimpreyi' could be equated with true Mantelliceras; it would be necessary to prove that they were not really nuclei of Graysonites, a genus which occurs in the basal Cenomanian of Texas.

This genus, as described by Young (1958), shows great variation in the suture lines. Although that of the type species, G. lozoi Young (1958, text-fig. 1f), is distinct in possessing an exceptionally wide first lateral saddle with two strong, but unequal, accessory lobes, all the suture lines are drawn at diameters too large to compare with nuclei from either England or north Africa. The decoration of the young of G. lozoi (Young 1958, pl. 27, figs. 1, 2, 6, 7, 9, and 10) show it to have stronger and longer ribbing on the sides than is to be found in Mantelliceras of the saxbii group, and possibly stronger than in any old world Mantelliceras. Mature Graysonites have great horns on the shoulders reminiscent of a compressed Euomphaloceras.

STRATIGRAPHY

A Zone of Mantelliceras martimpreyi has long been widely quoted as the lowest zone of the Cenomanian stage, e.g. Wright 1957, Collignon 1959, Thomel 1965. There have

been occasional authors who have referred to a bottom pre-Martimpreyi subzone, e.g. Spath 1926, Muller and Schenk 1943, although generally only as a subzone of the Martimpreyi Zone. Always this Martimpreyi Zone has been placed below a Zone of M. cantianum (Spath 1926), or M. mantelli (Collignon 1937, 1959; Wright 1957; Thomel 1965), or Schloenbachia varians (Muller and Schenk 1943). Although we do not suggest that any of these authors were basing their zonation on single species, there can be no doubt that they considered M. martimpreyi itself to occur at, or very close to, the base of the Cenomanian. Because M. martimpreyi had supposedly not been found in northern Europe, it was believed that there was a zone missing at the base of the Cenomanian in this region. We contend that M. martimpreyi itself is a synonym of M. saxbii (as described above) and that its horizon in northern Europe is well above the base of the Cenomanian. This conclusion is not entirely novel; Dubourdieu (1956), in a penetrating analysis of the ammonite succession in the Cenomanian of the Ouenza region on the borders of Algeria and Tunisia, showed that M. martimpreyi did not enter the succession until above the occurrence of Idiohamites alternatus and Hypoturrilites of the groups to which H. gravesianus and H. carcitanensis belong. The same is true of the English succession as was foreshadowed by Spath (1926).

THE MANTELLI ZONE IN SOUTHERN ENGLAND

Subdivisions of the Lower Cenomanian. Recent fieldwork in southern England (Kennedy 1969, to which reference should be made for full faunal lists) has shown that it is possible to divide the Lower Chalk into three Zones of Mantelliceras mantelli, Acanthoceras rhotomagense, and Calycoceras naviculare. These divisions correspond to those recognized by one of us (Hancock 1959) in the type Cenomanian of the Sarthe.

Within the lowest zone (Mantelli Zone) occur three distinctive and widely recognizable ammonite assemblages. It would be premature to call these subzones because the faunas are largely concentrated at discrete horizons separated by relatively unfossiliferous beds which may correspond to levels which elsewhere yield other distinctive assemblages.

(i) At the base is a *Hypoturrilites carcitanensis* assemblage. In this the commonest ammonites are *Schloenbachia* which probably outnumber all other ammonites put together. But the characteristic, and still common, members of the assemblage are various inflated *Mantelliceras* such as *M. mantelli* (J. Sowerby), *M. tuberculatum* (Mantell), and *M. cantianum* Spath; and *H. carcitanensis* (Matheron). Particularly characteristic but infrequent are *Idiohamites collignoni* Spath, *I. alternatus* (Mantell), *I. alternatus* var. *vectensis* Spath, *I. ellipticus* (Mantell), *I. ellipticus* var. *radiatus* Spath, several possible new species of *Idiohamites*, *Anisoceras auberti* (Pervinquière), *A. armatum* (J. Sowerby), and *A.* aff. *picteti* Spath.

Other frequent finds are *Hypoturrilites gravesianus* (d'Orbigny), *H. tuberculatus* (Bosc), *Mariella cenomanensis* (Schlüter), *Mar. lewesiensis* (Spath), *Mantelliceras costatum* (Mantell), *M. tenue* Spath, *M.* aff. *saxbii*, *M.* aff. *ventnorense*—the last two both more inflated than the types (see Pl. 79, figs. 5a-b, with a whorl height: whorl width ratio of 1.09).

(ii) In the middle is the *Mantelliceras saxbii* assemblage. In this *Schloenbachia* is still a common genus but not so markedly as in the *carcitanensis* assemblage, and the inflated

forms have become still less common. Amongst the *Mantelliceras*, compressed species, e.g. *M. saxbii*, *M. ventnorense*, *M. tenue*, and related forms, are now dominant over inflated species, but some inflated species still survive, e.g. *M. cantianum*, *M. mantelli*, and *M. tuberculatum*. The *Idiohamites* and *Anisoceras* so typical of the *carcitanensis* assemblage have disappeared. *Hyphoplites falcatus* (Mantell) and other *Hyphoplites* spp. become locally common. *Hypoturrilites* is, in general, scarcer, although *H. tuberculatus* is sometimes frequent and *H. carcitanensis* is replaced by forms best referred to as *H.* aff. *carcitanensis* which differ from the earlier form in details of ornament. *Austiniceras austeni* (Sharpe) and *Scaphites obliquus* J. Sowerby can be common here, but are not characteristic.

(iii) Near the top is the *Mantelliceras dixoni* assemblage. This is not a rich assemblage and the most abundant ammonites are compressed forms of *Schloenbachia*. This level is characterized by the appearance of *Mantelliceras* of the group of *M. dixoni* Spath and *M.* aff. souaillonense (Renz), which are accompanied by *M. lymense* and *M.* cf. mantelli.

Occurrence of Mantelliceras saxbii. M. saxbii is common in the middle assemblage horizon, to which it lends its name, over the whole of south-east England, including the Chilterns (Childrey, Chinnor) and the Mere-Warminster region (especially from the Popple Bed). It occurs also in the remanié Lower Cenomanian faunas of the Chalk basement beds of the south-west, whilst this and related forms are also to be found in the phosphatic conglomerate of the top of the Eggardon Grit of the Hooke Valley; in Bed A2 of the Cenomanian Limestone on the Devon coast and at Storridge Hill (Chardstock); and in the basement bed of the Wilmington Sands. It must not be assumed from these records that all these fossiliferous beds in south-west England are exactly on the M. saxbii assemblage-horizon.

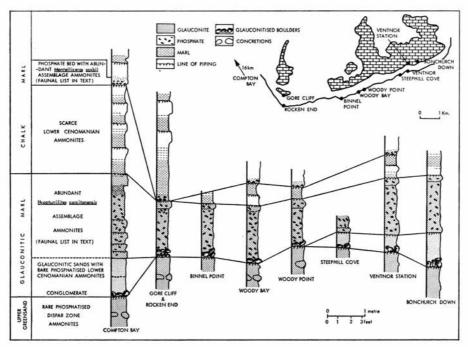
Related forms, which differ from the type chiefly in their greater inflation, occur in both the *saxbii* and *carcitanensis* assemblages over the whole of southern England.

Horizon of the types of M. saxbii and M. hyatti. In describing Ammonites saxbii, Sharpe (1857, p. 45) recorded that his figured specimen (now the lectotype) came from the Grey Chalk of Ventnor, Isle of Wight. He recorded that the original of pl. 18, fig. 4 (the holotype of M. hyatti) came from the Grey Chalk of Bonchurch, also in the Isle of Wight.

Both specimens are preserved as phosphatic internal moulds and retain traces of grey-buff, silty glauconitic chalk. This preservation might suggest that they were from the Glauconitic Marl, but it should be noted that Sharpe was very careful to state which specimens were actually from this horizon, e.g. explanation of pl. 18, figs. 6 and 7 (Mantelliceras mantelli and M. tuberculatum). Recent field work in the Isle of Wight has shown that there is a phosphate bed above the Glauconitic Marl (i.e. in the 'Grey Chalk') which is identical in lithology with the sediment that adheres to the two types, which yields M. saxbii in a preservation identical with that of the two types, and is clearly the source of both of them. The relationship of this saxbii assemblage-bed to the base of the Chalk as it is traced across the Isle of Wight is summarized in text-fig. 2.

Whilst the horizon of the two types is resolved, the actual locality is far from certain. Glauconitic Marl and the overlying Chalk Marl have been exposed at several localities at Ventnor; thus there is a section 300–400 m west of the promenade (National Grid reference SZ 559772) and a large pit next to the old station (SZ 561779). Bonchurch is immediately east of Ventnor, and Lower Chalk fossils could well be from landslipped

boulders on the beach (see Middlemiss and Bromley 1962, p. 450), from a small pit below Bonchurch Down (SZ 572782), or possibly from a pit below Nansen Down, north of the A3055 (SZ 578790). S. Saxby, the collector of both types, lived at Bonchurch, and therefore might even have got them from a temporary exposure.



TEXT-FIG. 2. Stratigraphical occurrences of the Mantelliceras saxbii assemblage in the Isle of Wight.

Horizon of the English syntype of Mantelliceras batheri. Mantell figured his specimen (pl. 22, fig. 1) amongst a group of fossils from 'the chalk and chalk marl, near Lewes'. The preservation suggests an horizon in the lower part of the Lower Chalk, a formation within which both the *carcitanensis* and *saxbii* assemblages are prominent near Lewes.

STATUS OF THE MARTIMPREYI ZONE

We ourselves do not use 'Martimpreyi Zone' in southern England but its equivalent is clearly the *saxbii* assemblage-horizon. Inflated *Mantelliceras*, such as *M. mantelli*, occur both above and below this, and are actually more prominent below. The same is true of the more inflated *Schloenbachia* such as *S. varians*. Therefore if Martimpreyi Zone is used, it should not be placed at the base of the Cenomanian.

Under various names Mantelliceras saxbii or closely related forms have been described from Lower Cenomanian rocks in Europe (Germany, Switzerland, northern and

southern France), north Africa (Algeria, Tunisia), Madagascar, and possibly North America. How is it that collectors have thought that it marked the base of the Cenomanian stage? One of the origins of error has been the mis-identification of the nuclei of other species of *Mantelliceras*, and even of *Stoliczkaia*, as *M. 'martimpreyi'* (as was pointed out by Pervinquière in 1907). We figure here (Pl. 81, figs. 11–13) examples of *Stoliczkaia* nuclei from the Dispar Zone of Dorset which could easily be mistaken in this way. Pervinquière (1907) actually recorded many of his Tunisian specimens of *M. martimpreyi* as Vraconian (= top Albian), but, from our experience in Algeria and Tunisia, *Mantelliceras* never appears until well above the disappearance of such diagnostically Albian genera as *Mortoniceras*.

The careful records of Thomel (1965, 1966) show that the ammonite succession in south-east France probably does not differ from that of southern England, in spite of the fact that Thomel has now listed *M. martimpreyi* from undoubted top Albian (Thomel 1968). His 'zone à *Mantelliceras martimpreyi*' corresponds in large part with the *Hypoturrilites carcitanensis* assemblage-horizon and his 'zone à *Mantelliceras mantelli*' corresponds in large part with the *M. saxbii* assemblage-horizon.

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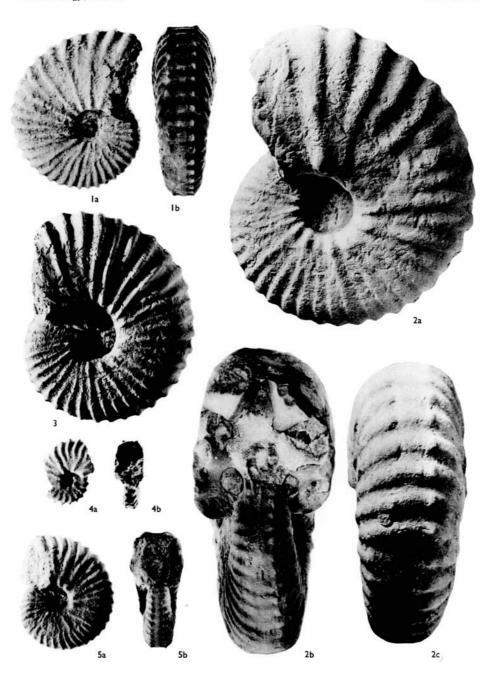
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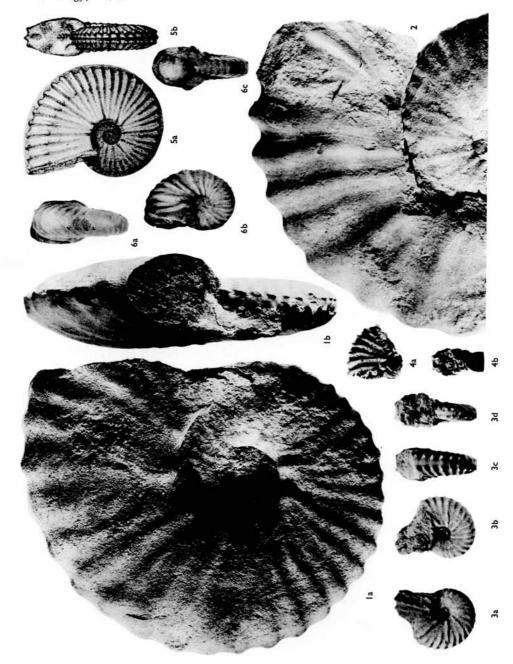
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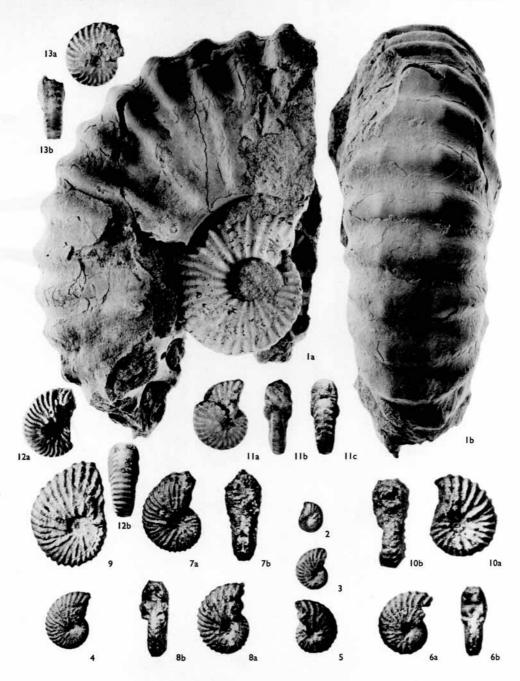


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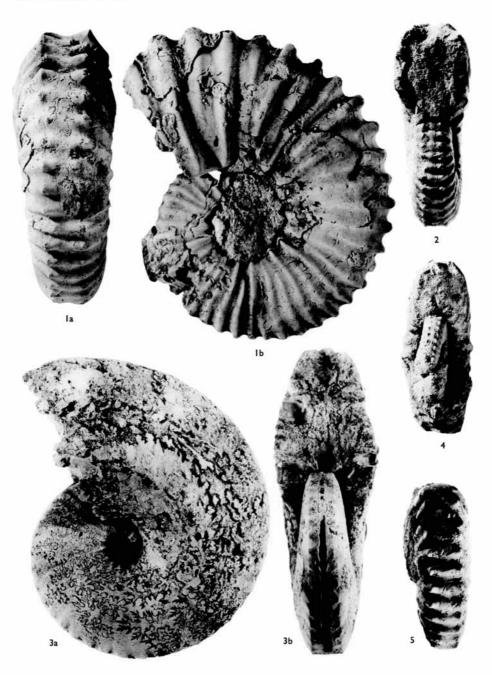




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