VARIATION AND ONTOGENY OF SOME OXFORDIAN AMMONITES: *TARAMELLICERAS RICHEI* (DE LORIOL) AND *CRENICERAS RENGGERI* (OPPEL), FROM WOODHAM, BUCKINGHAMSHIRE

by D. F. B. PALFRAMAN

ABSTRACT. Statistical and ontogenetic studies of *Taramelliceras richei* (de Loriol) and *Creniceras renggeri* (Oppel) have shown identity in their early stages. Variation in protoconch size is consistent and small, as is the diameter of the nepionic constriction. Divergence in shell form occurs only at the onset of maturity, which in *C. renggeri* begins at about 8·4 mm. and in *T. richei* at about 18·8 mm. It is concluded that the two 'species' are a sexually dimorphic pair. The name *C. renggeri* has priority.

A COLLECTION of Lower Oxfordian ammonites was made from the Woodham Brick Company's Pit, with the objective of studying the variation and ontogeny of selected species. The pit is situated almost midway between Bicester and Aylesbury, near Akeman Street Station, Buckinghamshire (Grid. Ref. 707186), and exposes some seventy feet of Oxford Clay (Arkell 1939). A lithological unit 'The Lamberti Limestone', a bed one foot thick, separates the lowermost forty feet of clay (Athleta Zone) from the uppermost thirty feet (Mariae Zone).

The Mariae Clays, as the beds of the Mariae Zone are here named, furnished the material studied. Both 'species' examined in this paper occur, together, throughout the Mariae Clays at Woodham; they are commonest in the lower ten feet of the Mariae Zone (generally pyritized), becoming rare in the upper twenty feet of beds (generally limonitized). They are both found together at all levels at Woodham. There is no evidence to suggest that either *Taramelliceras richei* (de Loriol) or *Creniceras renggeri* (Oppel) occurs outside the Mariae Zone in this country. However, both species appear to have arisen in the Upper Lamberti Zone, being found in Haute-Saône (Maire 1908). They are both found together in the Renggeri Marls (Mariae and Cordatum Zones) of the Jura Mountains, where they are fairly common (de Loriol 1898–9, 1900 and Arkell 1939). As far as the author is aware they are not recorded above the Cordatum Zone; though, as Arkell (1939) says '. . . exact details of range [are] usually not available'.

All the specimens collected are preserved as internal moulds, pyritic near the base of the zone becoming limonitic towards the top. No original shell material has been found among the collection of several thousand ammonites. In a few individuals the innermost whorls are calcified, but rarely to a diameter of more than 3–4 mm. Some, which are otherwise completely pyritized or limonitized, were found to have a calcareous protoconch.

Very few specimens were found preserved as pyrite or limonite moulds above a maximum diameter of 2 or 3 cm. and it seems that there is a maximum size above which ammonites were not pyritized or limonitized. Internal moulds composed of clay, seen *in*

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situ, showed that some ammonites must have had a diameter of not less than forty centimetres (see Pl. 48, fig. 1); often in the centre of such moulds were to be seen pyritized or limonitized nuclei of familiar dimensions.

Nearly five hundred specimens of *Taramelliceras richei* (de Loriol) and over two hundred specimens of *Creniceras renggeri* (Oppel) have been examined in this work. All specimens collected by, or given to, the author are in the University Museum, Oxford and are prefixed by OUM, those borrowed from the British Museum (Natural History) by BM. The following abbreviations are also used throughout the text: D = diameter, W = whorl width, HH = whorl height, U = umbilical diameter.

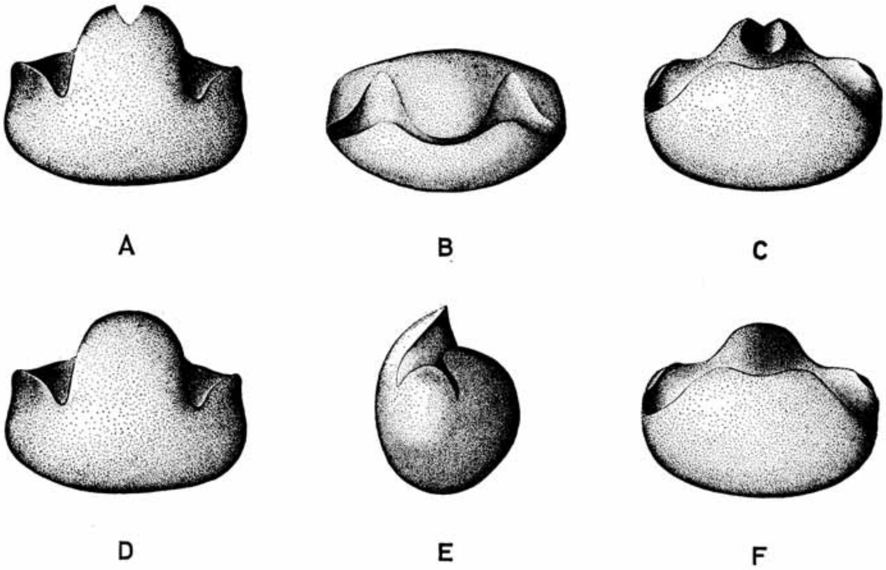
VARIATION AND ONTOGENY OF *TARAMELLICERAS RICHEI* (DE LORIOL)

Due to the conditions of preservation, the most frequently occurring form in which *Taramelliceras richei* (de Loriol) was found at Woodham, was as internal moulds of the phragmocone. The type material of *T. richei* is based largely on internal moulds of phragmocones (de Loriol 1898). In the author's collection of nearly five hundred specimens less than 10 per cent. have any part of the body chamber preserved, and in none of these is it complete. The species is a typical oppelid, being compressed and involute with a small umbilicus. Whorl height is approximately half the diameter, whorl width is approximately quarter the diameter. Coiling is regular in the phragmocone, but on the body chamber of adults the umbilical seam begins to uncoil.

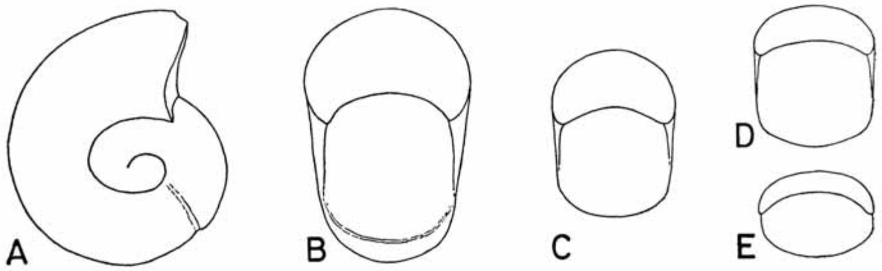
Protoconch. Less than 5 per cent. of the specimens of *T. richei* available were found to have protoconchs preserved; in all some eight protoconchs were dissected out. These are beautifully preserved as smooth pyritic moulds, showing details of the prosuture (text-fig. 1 and Pl. 48, fig. 4). In all cases the protoconchs are barrel-shaped with a width greater than the diameter. The largest recorded diameter of a protoconch of *T. richei* is 0·30 mm., the smallest 0·25 mm. (see Table 1). In one specimen (OUM J25230) the caecal mould is visible (text-fig. 1A, C).

Phragmocone. Just as the surface of the protoconch internal mould is smooth, so also is the first whorl of growth. The nepionic constriction occurs after one complete whorl of growth from the proseptum, at a diameter of about 0·53 mm., or roughly twice that of the protoconch (Table 1).

The nepionic constriction is well-defined, especially in the ventral and ventro-lateral regions, fading on the flanks and almost imperceptible near the umbilicus (text-fig. 2A, B; Pl. 48, fig. 6). In *T. richei* there is no ornamental difference, on the internal mould, between the whorl preceding the nepionic constriction and that immediately succeeding. In some ammonites, *Kosmoceras* and *Garantiana*, Makowski (1962) noted that the ornamentation characteristics of the full-grown shell appeared after the nepionic constriction. Ontogenetic features of note are: a decrease in the W/D ratio from the protoconch to a diameter of 0·8–1·0 mm. and a similar decrease in the U/D ratio to about the same diameter. From a diameter of 0·8–1·0 mm. onwards, growth is almost isometric until the onset of maturity which occurs at a diameter of about 18–20 mm. This is graphically represented here (text-figs. 3 and 4). From a diameter of 0·8–1·0 mm. until the onset of maturity the HH/D ratio shows almost isometric growth (text-fig. 5).



TEXT-FIG. 1. Protoconchs of *Taramelliceras richei* (de Loriol); Mariae Zone, Woodham, Bucks., England. A and D, ventral view; B, inclined apertural view; C and F, apertural view; E, side view. A and C based on OUM J25230; B, D, E, and F based on OUM J25228. All ×100.



TEXT-FIG. 2. Diagram of the innermost whorls of *Taramelliceras richei* (de Loriol); Mariae Zone, Woodham, Bucks., England. A and B, showing the position of the nepionic constriction; E, protoconch. A, B, C, and D, drawn from OUM J25038; E, drawn from OUM J25234. All ×50.

Ribbing is completely absent until a diameter of about 4 mm.; at this diameter radial umbilical swellings begin, strongly near the umbilicus but fading on the flanks. The ribs are shallow and distant and are initially eight to ten per whorl. It is not until a diameter of about 8–10 mm. that ribbing is differentiated into primaries and intercalatories (Pl. 50, fig. 1*a*, *c*).

TABLE 1. Measurements in millimetres of the dimensions of protoconchs and the diameter of the nepionic constriction in specimens of *Taramelliceras richei* (de Loriol). All specimens from University Museum, Oxford (OUM). All specimens from the Mariae Zone, Woodham.

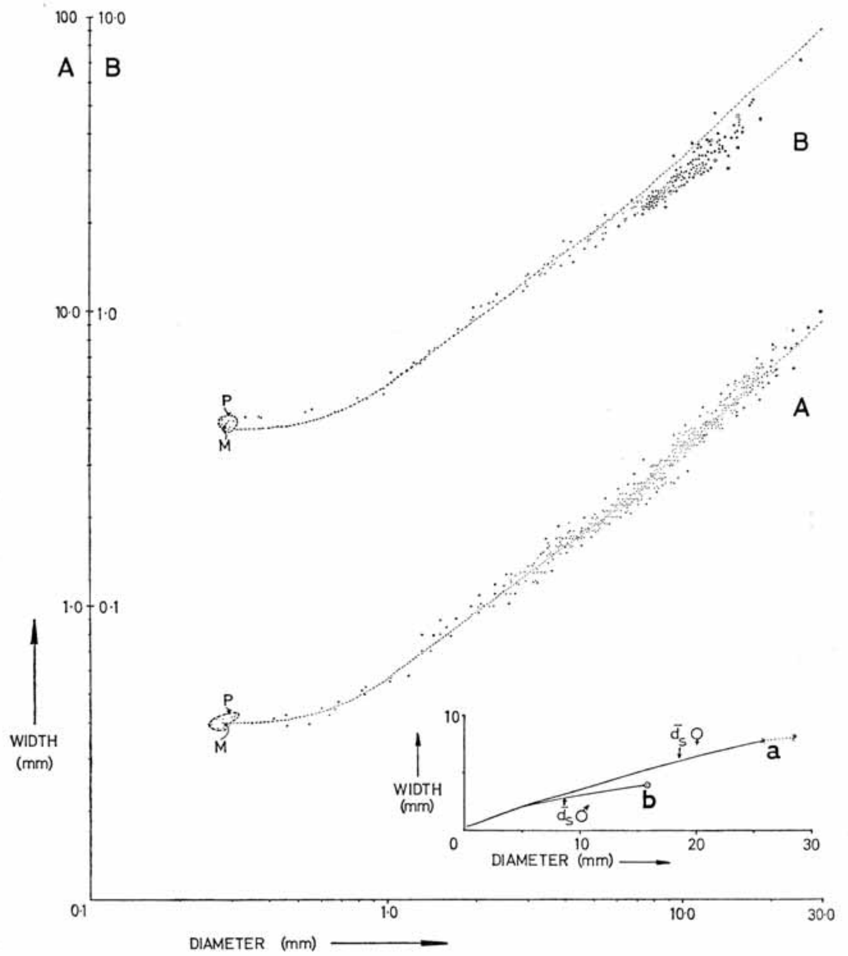
Specimen Number	*Protoconch* D	*Protoconch* W	*Nepionic Constriction* D
J25024			0·53
J25038			0·54
J25040	0·28	0·40	0·54
J25042			0·54
J25045	0·27	0·38	
J25046	0·25	0·40	0·56
J25228	0·30	0·42	0·53
J25230	0·30	0·42	0·53
J25231	0·28	0·41	0·52
J25232	0·27	0·41	0·52
J25234	0·28	0·38	0·53

Differentiated ribbing is undoubtedly a characteristic of *T. richei*, all specimens showing this feature to some degree, with a variation from relatively coarse ribbing to fine (Pl. 49, figs. 1*a*, *b*, 2*a*, *c*). On the final whorl of all adult specimens there are two series of ribs; primaries and intercalatories. The primary ribs generally number ten to twelve per whorl, developing initially as radial umbilical swellings then fading on the flanks and finally becoming relatively sharp and distinct on the ventro-lateral area. They are slightly sinuous with marked ventro-lateral prorsiradiation (Pl. 48, fig. 2*a*; Pl. 49, figs. 1*a*, 2*a*, 4*a*; Pl. 50, fig. 1*a*). Ribs always fade on the venter of internal moulds, but may not do so on the actual surface of the shell. In some cases the venter is smooth (see Pl. 49, fig. 1*b*), whereas in most instances the ribbing simply becomes weaker in the ventral region (Pl. 49, fig. 2*b*). On the last quarter of the adult phragmocone whorl, nearly all specimens develop feeble ventral tubercles, which become stronger adorally (Pl. 49, fig. 4*a*, *b*; Pl. 50, fig. 1*a*, *b*). The tubercles coincide at the point at which opposing ribs, on either side of the venter, both primaries and intercalatories, would meet had they continued uninterrupted across the venter.

The intercalatory ribs, on the final whorl of adult specimens, generally number about forty. They are restricted to the ventro-lateral area and are identical in form with the primary ribs in this region, by way of amplitude, sharpness and direction, for each particular specimen. Between each primary rib are three to four intercalatories (Pl. 48, fig. 2*a*; Pl. 49, figs. 2*a*, 4*a*; Pl. 50, fig. 1*a*).

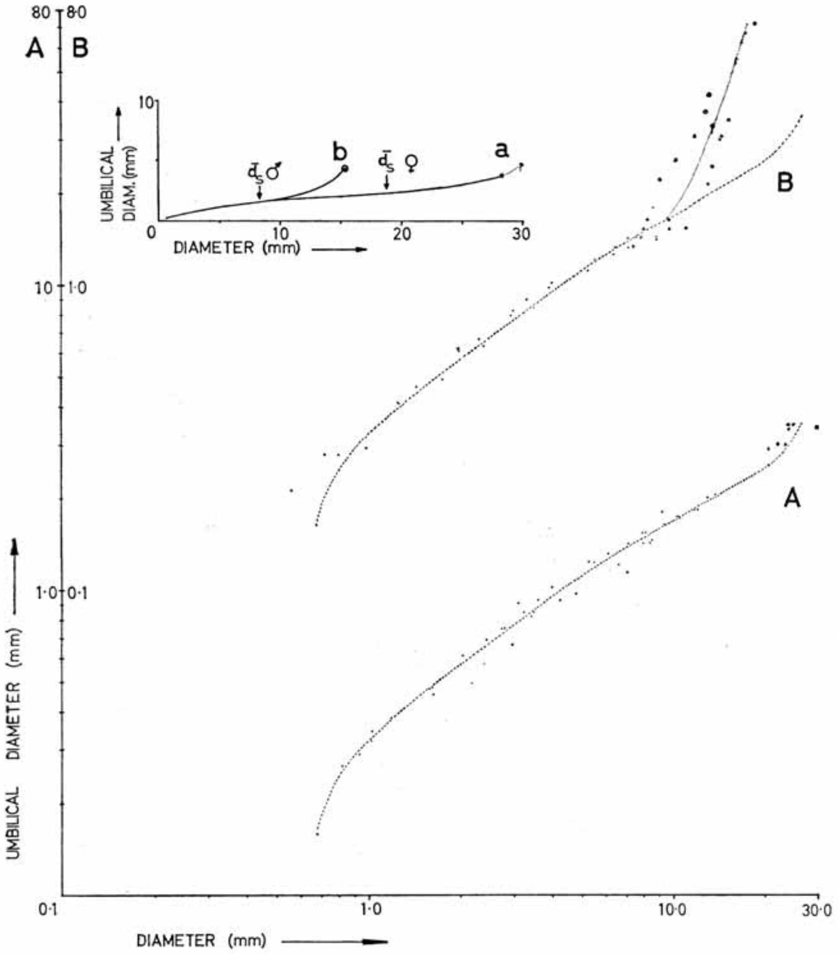
The mean maximum diameter of the phragmocone, of more than two hundred adult specimens, was found to be 18·8 mm., with a standard deviation (σ) of 1·51. The coefficient of variation ($V = 100\sigma/m$, where m is the mean maximum diameter, $\bar{d}_s$, of the adult phragmocones) is 8·02. The greatest diameter at which the septa are approximated was found to be 27 mm., the smallest 14 mm. (text-fig. 6). The phragmocone generally comprised 6¼–7 whorls from the proseptum. Variation in the whorl-shape is here shown diagrammatically (text-fig. 7 and Pl. 48, fig. 2*a*).

The sutural ontogeny of *T. richei* develops in a way which, in Jurassic ammonites, is beginning to appear fundamental (Schindewolf 1954). The prosuture is significantly



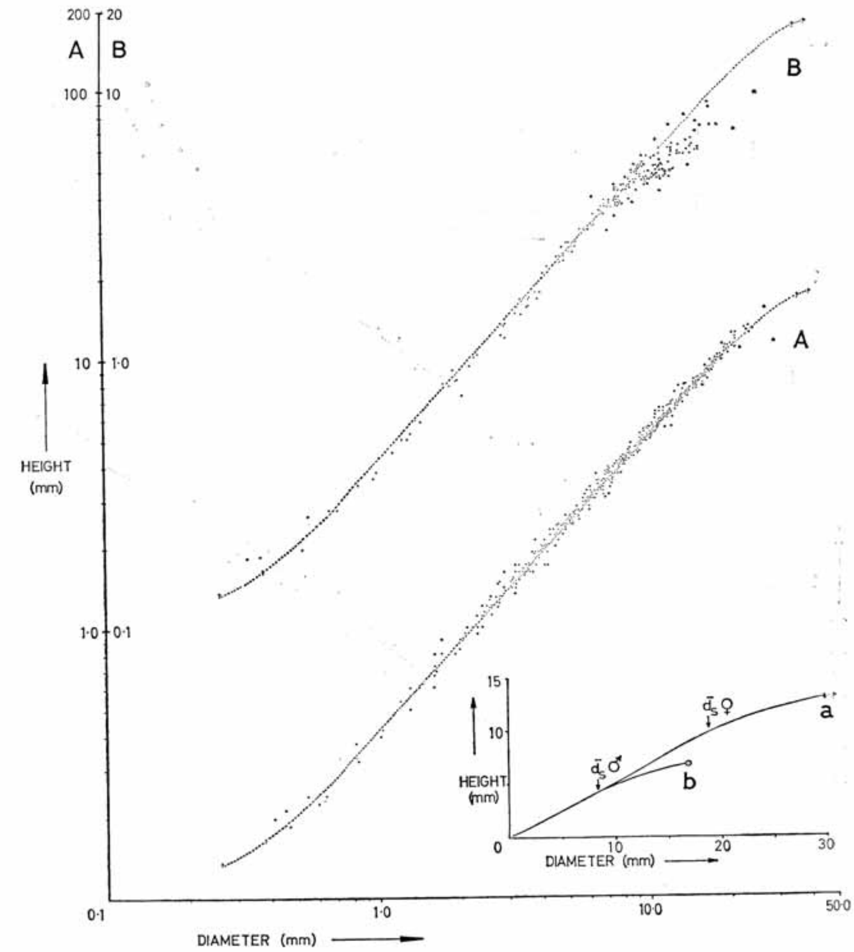
TEXT-FIG. 3. Graphs showing the relationship between diameter and whorl width of *Taramelliceras richei* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the *diameter* axis is common, the *width* axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (W/D for *T. richei*) is controlled by the A scale, graph B (W/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). The areas denoted by P (coarse dashed line) enclose measurements made on the protoconchs: M is the mean of these measurements. Encircled dots represent measurements made at the maximum diameter of complete adults: asterisks—measurements made on adult body-chambers: crosses—measurements made at the adoral end of adult phragmocones: dots—measurements made on immature phragmocones.

Inset. The same graphs plotted on a linear scale and having both axes common. *a*, W/D for *T. richei*; *b*, W/D for *C. renggeri*. The arrowed points, $\bar{d}_s$ ♀ and $\bar{d}_s$ ♂, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 4. Graphs showing the relationship between diameter and umbilical diameter of *Taramelliceras richei* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the *diameter* axis is common, the *umbilical diameter* axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (U/D for *T. richei*) is controlled by the A scale, graph B (U/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). Conventions as for text-fig. 3.

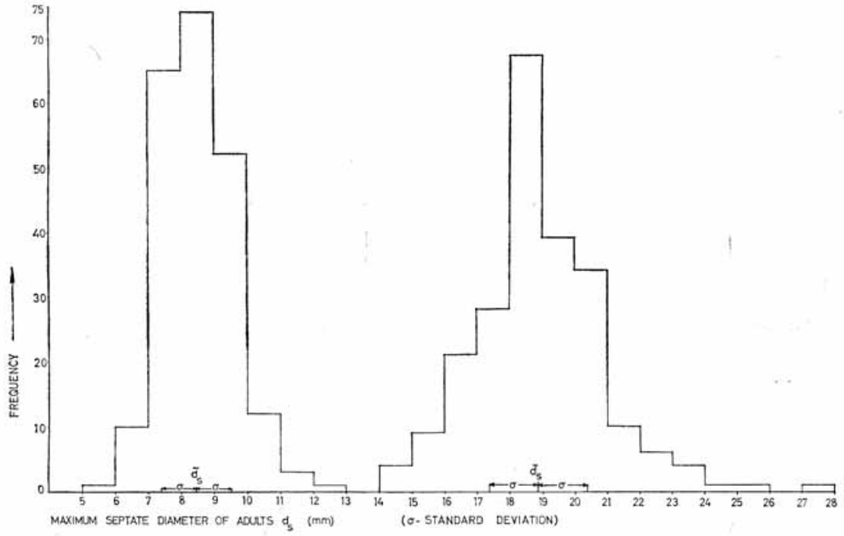
Inset. The same graphs plotted on a linear scale and having both axes common. *a*, U/D for *T. richei*; *b*, U/D for *C. renggeri*. The arrowed points, $\bar{d}_s$ ♀ and $\bar{d}_s$ ♂, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 5. Graphs showing the relationship between diameter and whorl height of *Taramelliceras richei* (de Loriol), and of *Creniceras renggeri* (Oppel). The two graphs are superimposed: the *diameter* axis is common, the *height* axis is divided into A and B scales, the B scale being one log cycle behind the A scale. Graph A (HH/D for *T. richei*) is controlled by the A scale, graph B (HH/D for *C. renggeri*) is controlled by the B scale. The fine dashed line on graph B is that superimposed from graph A (approximate best-fit line). Conventions as for text-fig. 3.

Inset. The same graphs plotted on a linear scale and having both axes common. *a*, HH/D for *T. richei*; *b*, HH/D for *C. renggeri*. The arrowed points, $\bar{d}_s$ ♀ and $\bar{d}_s$ ♂, mark the position of the mean septate diameter of mature specimens of supposed female and male respectively. All specimens from the Mariae Zone, Woodham.

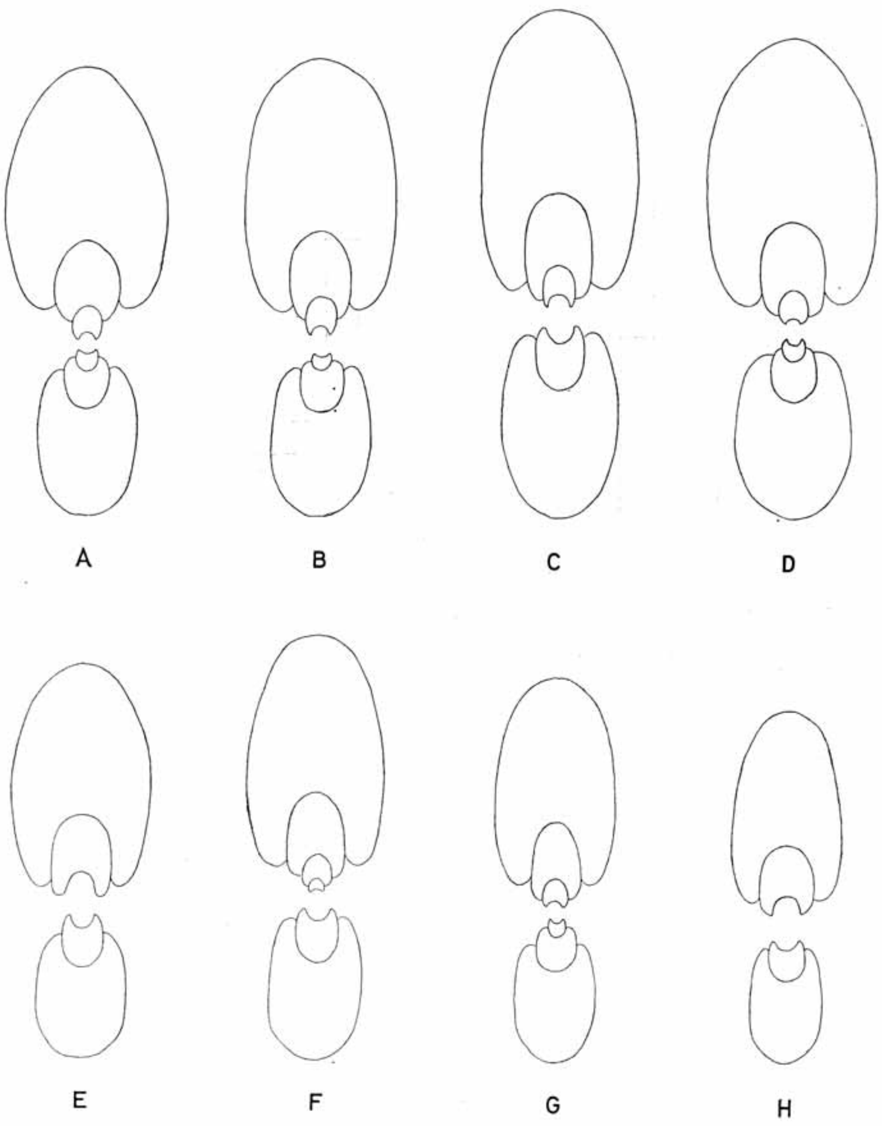
different from the primary suture, having a very large ventral saddle. The primary suture (text-figs. 1 and 8) is divided into: external (or ventral), lateral, U_2, U_1, and dorsal lobes, with corresponding saddles between. These first-formed lobes have been called 'protolobes' by Schindewolf (1954): subsequent works (Schindewolf 1960, 1962, and 1963) have shown that these basic protolobes are common to all Jurassic ammonites so far investigated. Addition of successive sutural elements in *T. richei* occurs at the



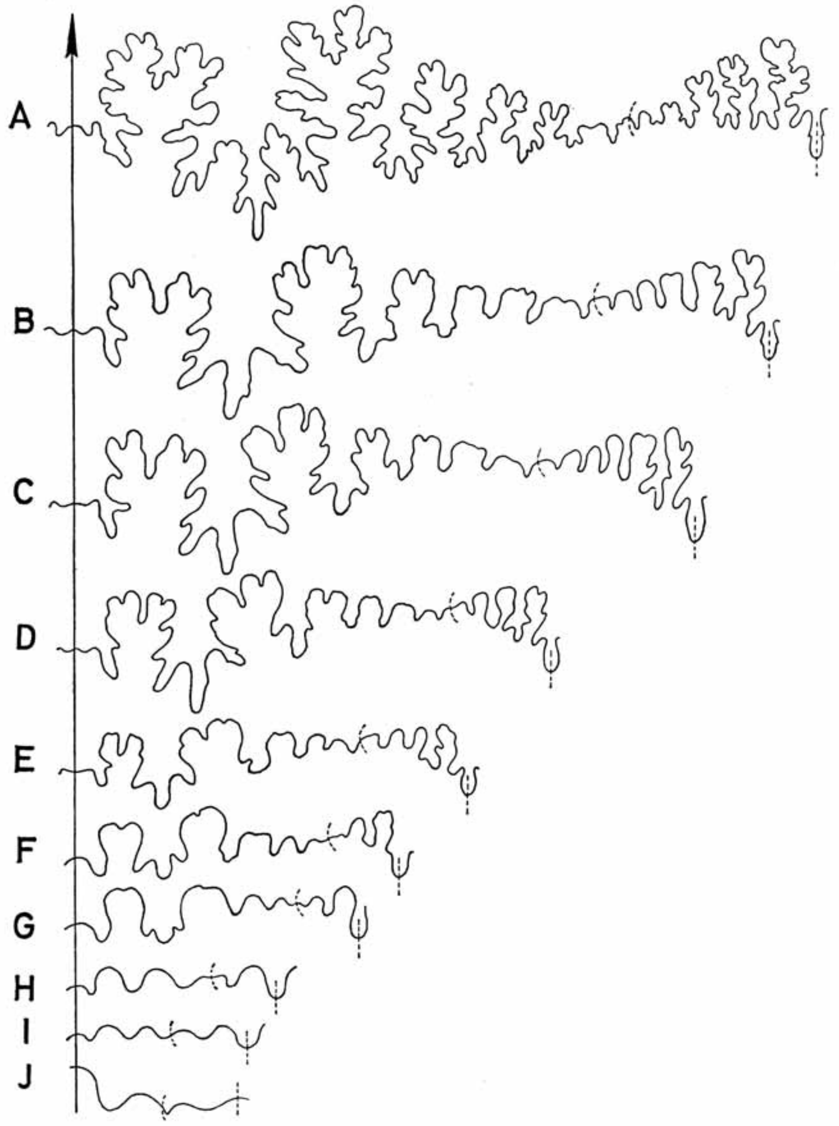
TEXT-FIG. 6. Histogram showing the variation in the diameter at which septation ceases (d_s) in mature specimens of *Taramelliceras richei* (de Loriol) and in *Creniceras renggeri* (Oppel). The *T. richei* range is from 14–28 mm., the *C. renggeri* range from 5–13 mm. All specimens from the Mariae Zone, Woodham.

umbilical seam; this is the 'U-type' ontogeny of Schindewolf (1954). The final sutures of adult specimens are greatly differentiated into several complex saddles and lobes (text-fig. 8A). Sutural approximation, generally regarded as a feature of maturity, is commonly to be seen in most specimens with a phragmocone diameter of 18–19 mm. (Pl. 48, fig. 2*a*; Pl. 49, figs. 2*a*, 4*a*, 4*b*; Pl. 50, fig. 1*a*).

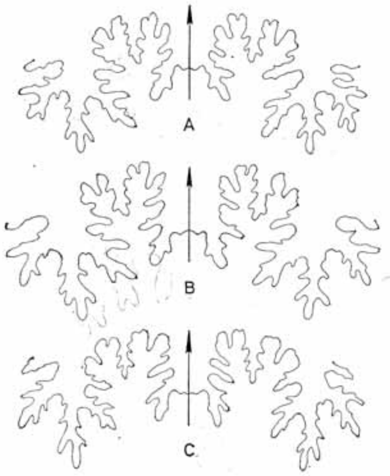
In the adult sutures the largest saddles are the first and second lateral and the largest lobes the ventral and lateral. These major sutural elements show the greatest range of variation and have been compared on either side of the venter in the same specimen, and on the same side of the venter at similar diameters, in different specimens. Comparing the same sutural elements, on either side of the venter for any single specimen, shows remarkably little variation (text-fig. 9). The greatest difference recorded is in the frilling of the most adapical accessory lobe: even so this difference is somewhat subtle and does not compare with the wide intraspecific sutural variation shown by *Morrisiceras morrisi* (Oppel) and *Clydoniceras discus* (Sow.) mentioned by Arkell (1957).



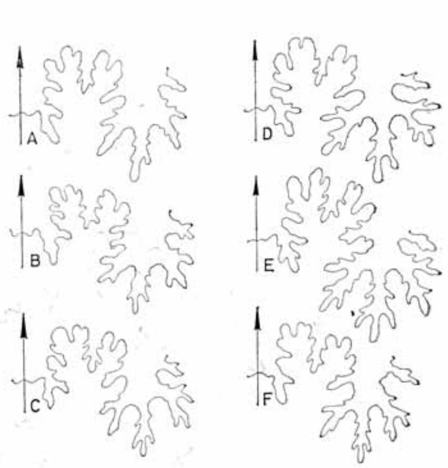
TEXT-FIG. 7. Cross-sections through the phragmocone of *Taramelliceras richei* (de Loriol). A, OUM J25041; B, OUM J25021; C, OUM J25010; D, OUM J25239; E, OUM J25241; F, OUM J25236 G, OUM J25005; H, OUM J25238. All ×4. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 8. Sutural ontogeny of *Taramelliceras richei* (de Loriol). A, OUM J25013, ×9 (D = 15 mm.); B, OUM J25036, ×15 (D = 8·7 mm.); C, OUM J25036, ×18 (D = 6·4 mm.); D, OUM J25036, ×20 (D = 4·6 mm.); E, OUM J25036, ×25 (D = 3·13 mm.); F, OUM J25036, ×30 (D = 2·13 mm.); G, OUM J25036, ×35 (D = 1·53 mm.); H, OUM J25036, ×50 (D = 0·85 mm.); I, OUM J25040, ×50 (D = 0·32 mm.); J, OUM J25040, ×50 (D = 0·28 mm.). I, primary suture. J, prosuture. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 9.



TEXT-FIG. 10.

TEXT-FIG. 9. Sutural variation in *Taramelliceras richei* (de Loriol). A, OUM J25230 (D = 12·2 mm.); B, OUM J25228 (D = 12·0 mm.); C, OUM J25229 (D = 12·1 mm.). All × 7·5. All specimens from the Mariae Zone, Woodham.

TEXT-FIG. 10. Sutural variation in *Taramelliceras richei* (de Loriol). A, OUM J25029 (D = 12 mm.); B, OUM J25028 (D = 12·4 mm.); C, OUM J25009 (D = 11·8 mm.); D, OUM J25035 (D = 12 mm.); E, OUM J25024 (D = 12 mm.); F, OUM J25026 (D = 12 mm.). All × 7·5. All specimens from the Mariae Zone, Woodham.

Variation between the same sutural elements of different specimens, at approximately the same diameter, shows relatively marked differences (text-fig. 10). These differences are generally of size, however, the disposition of the elements being essentially the same. The most marked differences are between the specimens OUM J25029 and OUM

EXPLANATION OF PLATE 48

Fig. 1. Internal clay mould of a large *Peltoceras*(?) *sp.*; basal Mariae Zone (about 5 ft. above the Lamberti Limestone), Woodham, Bucks. $\times \frac{1}{10}$.

Fig. 2. *Taramelliceras richei* (de Loriol, OUM J25571. Adult phragmocone. *a*, side view; *b*, apertural view. Both × 3.

Fig. 3. *T. richei*, BM C. 39588; Oxford Clay, Scarborough, Yorkshire. × 1.

Fig. 4. *T. richei*, OUM J25234 (lost); Mariae Zone, Woodham, Bucks. Protoconch. × 50.

Fig. 5. *T. richei*, OUM J25672. Adult specimen. *a*, side view; *b*, ventral view. The body-chamber occupies about $\frac{1}{3}$ of the final whorl. Both × 3.

Fig. 6. *T. richei*, OUM J25038. Innermost whorls showing the nepionic constriction. × 40.

Fig. 7. *T. richei*, BM 39642; Oxford Clay, Scarborough, Yorkshire. Stereopair of adult specimen showing the nature of the peristome and ventro-lateral spines. × 1.

Fig. 1—unwhitened; Figs. 2*a*, *b*, 3, 5*a*, *b*, and 7—whitened with ammonium chloride; Figs. 4 and 6—whitened with magnesium oxide. All specimens from the Mariae Zone, Woodham, Bucks., unless otherwise stated.

J25024 (text-fig. 10A, E). Generally speaking it seems fairly safe to say that the intra-specific sutural variation in *T. richei* is extremely small.

Body-chamber. The body-chamber of adult specimens of *T. richei* is quite different from the phragmocone. The most marked change is in the development of ventral and ventro-lateral spines. In some specimens spines develop quite suddenly after the last septum in both positions. Specimen OUM J25676 shows the ventral spines beginning first, the ventro-lateral spines developing later (Pl. 49, fig. 3*a*, *b*). The ventro-lateral spines are paired and alternate with those on the venter, relative to the median plane. Not all body-chambers, of specimens which are otherwise identical, become spinose: they merely retain the ventral tubercles of the adult phragmocone (Pl. 48, fig. 5*a*, *b*). However, there is probably a whole range between tuberculate venters only, and spinose venters and ventro-lateral regions: this is supported by a collection of specimens from the Oxford Clay of Warboys, Hunts. (BM C.4333, C.10651, C.15960, C.16009, C.16010, C.19286, and C.19296), which shows precisely this range.

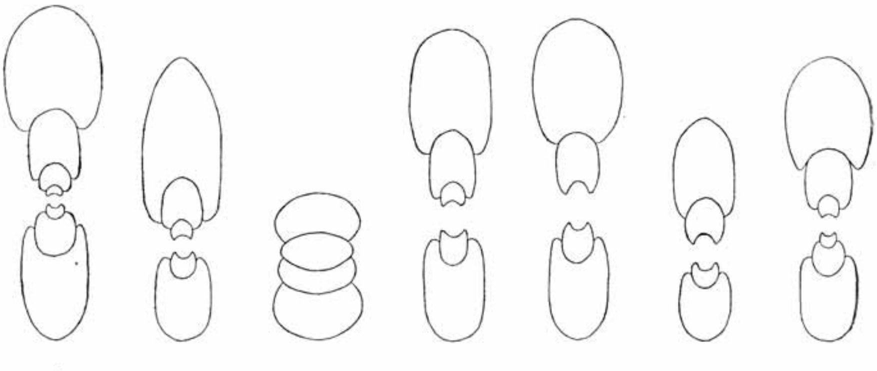
Ribbing on the body-chamber appears to be weaker than on the phragmocone, but the very poor preservation of the body-chambers of Woodham specimens may affect this feature. Some of the better preserved specimens from Warboys show well-defined ribs, both primaries and intercalatories, even on the flanks of the body-chamber (BM C.4333 and C.15960). The phragmocones of these specimens are otherwise identical with those from Woodham.

As would be expected in the final stages of adult specimens, the body-chamber uncoils at the umbilical seam (Pl. 49, fig. 3*b* and text-fig. 4). Among the Woodham specimens the author was unable to find an adult which showed the nature of the peristome. However, among three specimens from the Oxford Clay of Scarborough, Yorkshire (BM 39642, C.39588, and C.39589), labelled *Proscaphites oculatus* (Phillips), is one specimen (BM 39642) which shows the nature of the peristome (Pl. 48, fig. 7). These specimens are almost certainly conspecific with *T. richei*, developing ventral and ventro-lateral spines (Pl. 48, figs. 3 and 7): unfortunately the phragmocone is not preserved and the body-chamber of the specimens is crushed. The peristome of BM 39642 is fairly simple, its outline coinciding with the course of the primary ribs. The diameter of the almost complete specimen (45 mm.), which has a body-chamber of three-quarters of a whorl, is in agreement with the predicted size of complete adults from Woodham, assuming that the Woodham specimens have a body-chamber of about three-quarters of a whorl. If this is so, the total number of whorls from the proseptum is from $7–7\frac{3}{4}$ in *T. richei*.

Among the better preserved specimens from Woodham, the phragmocone is a dull black colour, whereas that of the body-chamber is a golden reflective (if pyritic) mould. The dull black colour extends just on to the body-chamber, and in many cases a well-defined line can be traced between the black and golden parts of the body-chamber. The line is almost co-incidental with the course of the primary ribs but with slightly greater ventral prorsiradiation. This line may represent the annulus (Crick 1898): however, no muscle-scars were recorded from any specimen of *T. richei* from Woodham.

VARIATION AND ONTOGENY OF *CRENICERAS RENGGERI* (OPPEL)

Creniceras renggeri is a smaller 'species' than *Taramelliceras richei*, complete adults rarely attaining a diameter of more than 20 mm. It appears that because of its small size *C. renggeri* is generally to be found complete, or nearly so, as it rarely exceeds the optimum size for complete preservation as a pyritic or limonitic mould in the Oxford Clay of Woodham.



TEXT-FIG. 11. Cross-sections through *Creniceras renggeri* (Oppel) A, OUM J25294; B, OUM J25378; C, OUM J25378 (inner whorls of B); D, OUM J25298; E, OUM J25305; F, OUM J25322; G, OUM J25272. All except fig. C are ×4; fig. C ×30. All specimens from the Mariae Zone, Woodham.

TABLE 2. Measurements in millimetres of the dimensions of protoconchs and the diameter of the nepionic constriction in specimens of *Creniceras renggeri* (Oppel). All specimens from the University Museum, Oxford (OUM). All specimens from the Mariae Zone, Woodham.

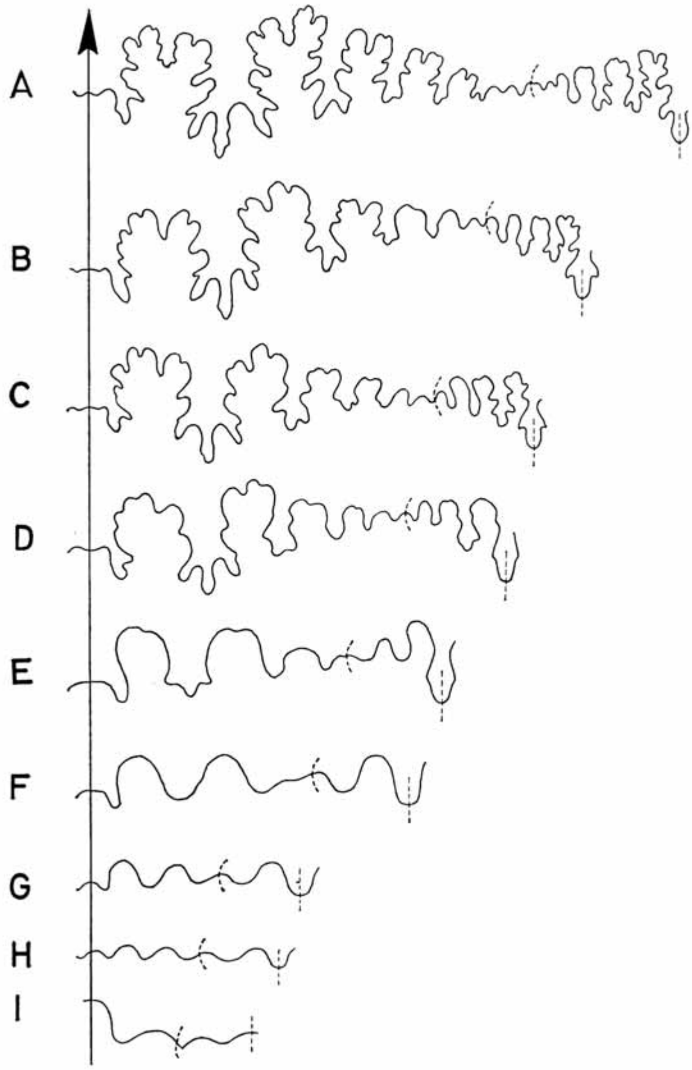
Specimen Number	*Protoconch*		*Nepionic Constriction*
	D	W	D
J25305	0·29	0·40	
J25308	0·30	0·42	
J25347	0·29	0·42	
J25364	0·28	0·41	0·54
J25368	0·28	0·42	0·53
J25378	0·29	0·41	0·56

Protoconch. Ontogenetically *C. renggeri* goes through identical stages as *T. richei* until the onset of maturity. Protoconchs are identical in shape to, and vary within almost the same limits as, those of *T. richei* (Table 2, cf. Table 1).

EXPLANATION OF PLATE 49

Taramelliceras richei (de Loriol). All specimens are from the Mariae Zone of Woodham, Bucks. and have been whitened with ammonium chloride. All ×3.

Fig. 1. OUM J25482. Adult phragmocone. *a*, side view; *b*, ventral view. Fig. 2. OUM J25617. Adult phragmocone. *a*, side view; *b*, ventral view. Fig. 3. OUM J25676. Adult specimen; the body-chamber occupies the last half-whorl; ventral and ventro-lateral spines are developed. *a*, ventral view; *b*, side view. Fig. 4. OUM J25455. Adult phragmocone. *a*, side view; *b*, ventral view.



TEXT-FIG. 12. Sutural ontogeny of *Creniceras renggeri* (Oppel). A, OUM J25244, ×12 (D = 10·61 mm.); B, OUM J25364, ×15 (D = 8·03 mm.); C, OUM J25364, ×16 (D = 6·08 mm.); D, OUM J25364, ×25 (D = 3·18 mm.); E, OUM J25364 ×50 (D = 1·43 mm.); F, OUM J25364, ×50 (D = 0·99 mm.); G, OUM J25364, ×50 (D = 0·38 mm.); H, OUM J25364, ×50 (D = 0·33 mm.); I, OUM J25364, ×50 (D = 0·28 mm.). H, primary suture. I, prosuture. All specimens from the Mariae Zone, Woodham.

Phragmocone. The nepionic constriction occurs at a diameter of between 0·53 mm. and 0·56 mm., compared with 0·52–0·56 mm. in *T. richei*. However, only three measurements of the nepionic constriction were available for *C. renggeri*, compared with ten for *T. richei*. The whorl shape (text-fig. 11) and sutural ontogeny (text-fig. 12) of *C. renggeri* vary within very similar limits to those of *T. richei* (text-figs. 7 and 8).

A complete lack of ornament occurs until a diameter of about 4 mm., where shallow, distant, radial, umbilical swellings develop. These swellings fade on the flanks and do not re-form on either the venter or ventro-lateral regions. These features are consistent with those recorded in *T. richei* at comparable diameters. The W/D, U/D, and HH/D ratios are identical to those of *T. richei* at similar growth stages (text-figs. 3, 4, and 5).

The final whorl of the phragmocone is, in most cases, seen only on removal of the body-chamber. Septation generally ceases at a diameter of 8–9 mm. The mean diameter at which septation ceases, in over two hundred adults, is 8·4 mm.: standard deviation (σ) is 1·1: coefficient of variation (V) is 12·8 (text-fig. 6). Specimen OUM J25246, with a maximum septate diameter of 17 mm., is almost certainly a very large adult *C. renggeri* (Pl. 50, fig. 5). However, variation in over two hundred specimens of *C. renggeri* is not continuous to such a large diameter, the range of continuous variation being 5–13 mm. (text-fig. 6), and it seems that the specimen in question is an extreme form.

The final whorl of the mature phragmocone is typically oppelid in character, being compressed and involute and with a narrow umbilicus. There are 4½–5½ complete whorls from the proseptum to the end of the phragmocone in adult specimens.

Radial umbilical swellings are developed, which fade on the flanks. These generally number about ten per whorl and are comparable with those, in number, direction, and nature, of *T. richei* at a similar diameter (Pl. 50, fig. 2*a*, *c* and cf. Pl. 50, fig. 1*c*). The ventro-lateral area is smooth, as is the venter, except on the final quarter whorl of adults, where feeble ventral tubercles are almost always developed. The tubercles become well-defined immediately before the beginning of the body-chamber (Pl. 50, figs. 2*a*, 3; Pl. 51, figs. 1*a*, 2*a*, *b*). Uncoiling of the umbilical seam in adults begins before the final septa are deposited (Pl. 50, figs. 2, 4, 5; and Pl. 52, figs. 2*b*, 3, 5), becoming markedly so on the body-chamber (Pl. 50, figs. 2*a*, 3; Pl. 51, figs. 2*a*, 3; Pl. 52, figs. 1, 3, and text-fig. 13).

Sutures were drawn at a diameter of approximately 8 mm. from nine specimens, showing the first and second lateral saddles and the ventral and lateral lobes. Differences in the same suture on either side of the venter are decidedly small (text-fig. 14); whereas

EXPLANATION OF PLATE 50

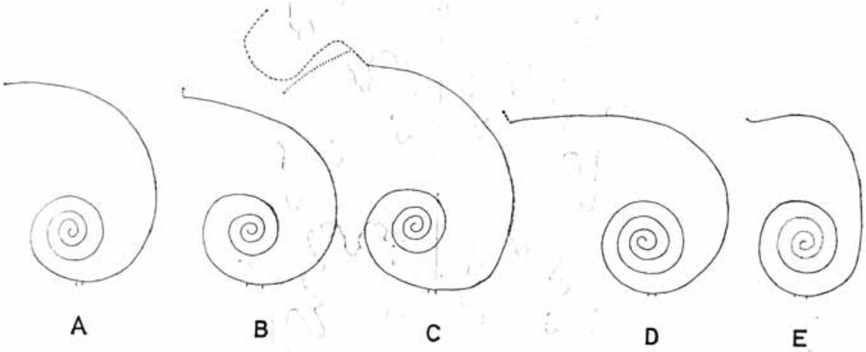
Fig. 1. *Taramelliceras richei* (de Loriol), OUM J25430. *a*, side view of adult phragmocone; *b*, ventral view of adult phragmocone; *c*, preparation of the inner whorls.

Figs. 2–4. *Creniceras renggeri* (Oppel). Fig. 2. OUM J25244. *a*, side view of adult specimen; *b*, ventral view of adult body-chamber; *c*, preparation of the inner whorls. Fig. 3. OUM J25360. Rostrate adult specimen. Fig. 4. OUM J25282. Body-chamber with almost complete peristome. *a*, side view; *b*, ventral view; *c*, apertural view.

Fig. 5. *C. renggeri* (?), OUM J25246. Giant adult male?

Specimens have been whitened with ammonium chloride. All from the Mariae Zone, Woodham, Bucks. All figs. ×3.

differences between sutures of different specimens, drawn at approximately the same diameter, are more marked (text-fig. 15). The range of variation, qualitatively assessed, appears to be similar to that shown by *T. richei* (cf. text-figs. 9 and 10). Sutural approximation can clearly be seen in a large number of specimens (Pl. 50, figs. 2*a*, 3; Pl. 51, figs. 1*a*, 3*a*, 12; Pl. 52, figs. 2*a*, *b*, 3, 4, 5, 6).

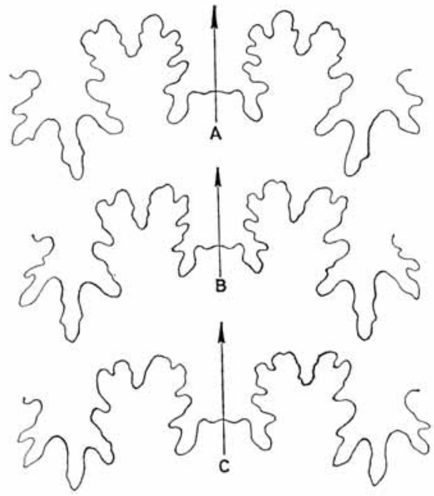


TEXT-FIG. 13. Diagrams of the umbilical seam of *Creniceras renggeri* (Oppel). The positions of the last two sutures are indicated. C, position of venter and lappet indicated. A, OUM J20662; B, OUM J20673; C, OUM J25364; D, OUM J20675; E, OUM J25377. All ×10. All specimens from the Mariae Zone, Woodham.

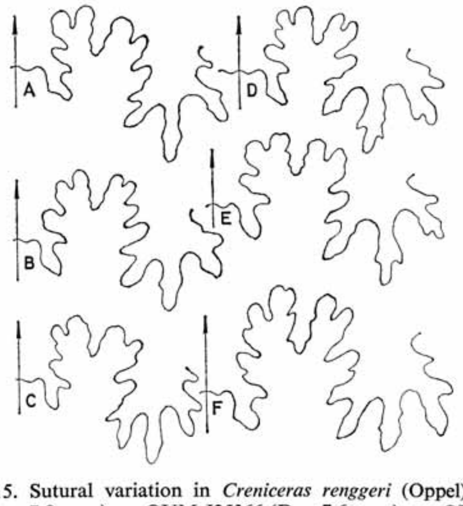
Body-Chamber. In nearly all specimens of *C. renggeri* a large proportion of the final whorl is body-chamber: in complete specimens the body-chamber occupies two-thirds to three-quarters of a volution (Pl. 51, figs. 2*a*, 4; Pl. 52, figs. 1–3, 5, 6). In complete adult specimens the total number of whorls, counting from the proseptum, is from $5\frac{1}{2}$–$6\frac{1}{2}$. Morphology apart, the most striking difference between the body-chamber and phragmocone is that of colour. When pyritized the body-chamber is preserved as a golden reflective internal mould, whereas the phragmocone is a dull black colour. The body-chamber is frequently well preserved and some specimens have almost complete apertures.

Spiral striae are developed on the body-chamber of all adult specimens: this feature is particularly well seen on specimens OUM J25248, J25265 and J25392 (Pl. 51, fig. 3*a*; Pl. 52, figs. 2*a*, 6). The striation is only feebly developed on the phragmocone (Pl. 51, fig. 3*a*), if at all.

The ventral tubercles of the phragmocone give rise to large truncated spines on the venter of the adult body-chamber. A great deal of variation is to be seen between specimens concerning the spines. At one extreme a few specimens have perfectly smooth venters (Pl. 52, figs. 2, 4), while others develop enormous spines (Pl. 52, figs. 1, 5). Among the Woodham population, however, a complete range from smooth venters to coarsely spined ones is to be seen (Pl. 51, figs. 5–12 and Arkell 1939, pl. 9, figs. 15–27). The majority of specimens have spines similar to those of OUM J25392 (Pl. 52, fig. 6). In complete adults there are generally nine to twelve spines on the body-chamber; however, the total number depends largely on the size of the spines: specimens with finely denticulate venters having as many as twenty-four (Pl. 51, fig. 11).



TEXT-FIG. 14. Sutural variation in *Creniceras renggeri* (Oppel). A, OUM J25335 (D = 8·5 mm.); B, OUM J25327 (D = 8·0 mm.); C, OUM J25329 (D = 8·3 mm.). All ×15. All specimens from the Mariae Zone, Woodham.



TEXT-FIG. 15. Sutural variation in *Creniceras renggeri* (Oppel). A, OUM J25367 (D = 7·8 mm.); B, OUM J25366 (D = 7·6 mm.); C, OUM J25326 (D = 7·8 mm.); D, OUM J25341 (D = 8·2 mm.); E, OUM J25345 (D = 8·2 mm.); F, OUM J25355 (D = 8·1 mm.). All ×15. All specimens from the Mariae Zone, Woodham.

The general inclination of the spines is slightly rursiradial (Pl. 51, fig. 1*a*; Pl. 52, fig. 6); rectiradial direction is fairly common (Pl. 51, fig. 2*a*) and prorsiradial direction rare and, at best, very slight.

In all adult specimens which have a complete body-chamber the ventral spines fade out completely just before the aperture (Pl. 50, figs. 2*a*, 3, 4*a*; Pl. 51, figs. 2*a*, 4 and Pl. 52, figs. 3, 6). Spines may not develop near the aperture, or, if they do, they are formed as solid shell, a mould of which would not reflect their original shape. The final spine of OUM J20695, an incomplete adult, is truncated near the base (Pl. 51, fig. 5); obviously not broken, the spine may have formed as solid shell with only the lowermost part hollow.

On well-preserved spines, fine ridges can be seen parallel to the edge of the spine (Pl. 51, figs. 1*a*, *d*). Arising from the ventral spines in many individuals are sinuous ventro-lateral ribs, which often fade on the flanks and may, or may not, reappear weakly in the umbilical region (Pl. 51, fig. 1*a*). In specimens with a denticulate venter, these shallow ribs are better defined in the ventro-lateral region, weakening on the flanks and umbilical region (Pl. 51, fig. 11). Individuals with no spines rarely develop ribs; at best they are very feeble and atypically weakest in the ventro-lateral position (Pl. 52, figs. 2*a*, *b*, 4). Because of the shallowness and large width of the ribs, they are only seen in well-preserved specimens.

The peristome of adult specimens of *C. renggeri* develops constrictions, flares, lappets and rostra and is considerably more ornate than that of *T. richei*. Constrictions in adults vary from feebly developed to quite strongly so (Pl. 51, fig. 2*a*; Pl. 50, fig. 4*a*). In the case of well-developed constrictions the peristome is flared (Pl. 50, fig. 4*a*, *c*): however, the conditions of preservation may have been unfavourable for faithfully recording the true shape of both lappets and rostra in this species. Lappets are generally short, close to the umbilical seam and triangular to elongate in shape (Pl. 51, figs. 2*a*, 4; Pl. 52, figs. 2*b*, 3). Flattened specimens labelled *Ammonites cristatus* Sowerby, from the Oxford Clay of Scarborough, Yorkshire, though poorly preserved, show the lappets to be considerably more elongate than shown by the Woodham specimens (Pl. 52, figs. 7, 8). The preserved part of the lappet of OUM J25325 (Pl. 51, fig. 4) is identical to the early part of the lappet of BM C.27545 (Pl. 52, fig. 8): the lappet of the former is obviously broken and may well have been the same shape and size as that of the latter. The two forms (*A. cristatus* and *C. renggeri*) are probably conspecific, the Yorkshire individuals giving a truer outline of the lappet. In some cases the Woodham specimens have lappets which, in cross-section, are concave relative to the median plane (Pl. 50, fig. 4*c*; Pl. 51, fig. 2*b*). The rostra of Woodham specimens (Pl. 50, figs. 3, 4*a*; Pl. 51, figs. 2*a*, 4; Pl. 52, fig. 3) are almost identical with those of the Yorkshire specimens (Pl. 52, figs. 7, 8) in both size and inclination.

As on *T. richei* a line appears on the body-chamber of *C. renggeri* immediately after the last septum on adult specimens, possibly representing the position of the annulus (Crick 1898). The course of this line is almost identical with that recorded for *T. richei* (Pl. 51, figs. 10, 12). Faint muscle scars were seen on the venter of several individuals: they are particularly prominent in a smooth-ventered specimen, OUM J25376, where they occur immediately either side of the mid-ventral line in the earliest part of the body-chamber and extend adorally for about 50° of a volution (Pl. 52, fig. 4*a*, *b*).

DISCUSSION ON SEXUAL DIMORPHISM

De Blainville (1840) was the first author to point out the possibility of separate sexes in the ammonites. More recent work (Callomon 1955 and 1963; Makowski 1962) has shown that among synchronous large and small forms of initially identical ammonites, there is sound reason for accepting de Blainville's claim. By analogy with living cephalopods, the large form is thought to be the female and the small form the male: these are the macroconchs (M) and microconchs (m), respectively, of Callomon (1955 and 1963).

The present author accepts the criteria of Makowski (1962) relating to sexual dimorphism in ammonites:

(1) identical initial stages of ontogeny in both (large and small) forms, and identity of their phylogeny,

(2) lack of intermediate forms in adult (gerontic) stages,

(3) presence of both forms in the same strata,

(4) numerical ratio of the supposed sexes (sex ratio), comparable to that observed in living forms.

In the foregoing account it has been shown that *T. richei* and *C. renggeri* agree in early ontogenetic stages but it has yet to be shown that they can be 'phylogenetically identified'. As Callomon (1963) has pointed out; '[*Taramelliceras* and *Creniceras*] both commence together at the base of the Oxfordian, basal Mariae Zone (Renggeri Marls); both are there already very variable (see Arkell 1939), and I [Callomon] have the feeling that they are merely dimorphic companions thence throughout the rest of

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EXPLANATION OF PLATE 51

Creniceras renggeri (Oppel) from the Mariae Zone, Woodham, Bucks.

Fig. 1. OUM J25245. Adult specimen. *a*, side view; *b*, apertural view; *c*, ventral view; *d*, ridges on ventral spines (×10). Fig. 2. OUM J25249. Adult with almost complete peristome. *a*, side view; *b*, apertural view. Fig. 3. OUM J25248. Adult specimen. *a*, side view; *b*, apertural view; *c*, ventral view. Fig. 4. OUM J25325. Adult specimen with almost complete peristome. Fig. 5. OUM J20695. Adult specimen showing truncated spine. Fig. 6. OUM J25252. Adult specimen. Fig. 7. OUM J25254. Adult specimen. Fig. 8. OUM J20662. Adult specimen. Fig. 9. OUM J25250. Adult specimen. Fig. 10. OUM J25250. Unwhitened adult specimen showing the course of the annulus (?). Fig. 11. OUM J25253. Adult specimen. Fig. 12. OUM J25255. Unwhitened adult specimen showing the course of the annulus (?). Specimens have been whitened with ammonium chloride, except figs. 10 and 12. Photographs by the author. All ×3, except 1*d* which is ×10.

EXPLANATION OF PLATE 52

Figs. 1–8. *Creniceras renggeri* (Oppel), from the Mariae Zone, Woodham, Bucks.

Fig. 1. OUM J25247. Adult specimen. Fig. 2. OUM J25265. Adult specimen with almost complete peristome. *a*, side view, showing spiral striae; *b*, side view, showing lappet. Fig. 3. OUM J25364. Complete adult specimen showing lappet and rostrum. Fig. 4. OUM J25376. Incomplete adult showing muscle scars. *a*, side view; *b*, ventral view. Fig. 5. OUM J25356. Almost complete adult specimen. Fig. 6. OUM J25392. Almost complete adult specimen.

Fig. 7. BM 39644; Oxford Clay, Yorkshire. Complete specimen, probably an adult.

Fig. 8. BM C.27545; Oxford Clay, Yorkshire. Complete specimen, probably an adult.

Fig. 9. *C. renggeri* ♂ and ♀. Reconstruction: ♂ based on OUM J25392 and BM C.27545 (see figs. 6 and 8); ♀ based on OUM J25660 and BM 39642 (see Pl. 48, fig. 7). ×1. Specimens have been whitened with ammonium chloride. Photographs by the author. All ×3, except fig. 9 which is natural size.

the Upper Jurassic.' Both *Taramelliceras* and *Creniceras* extend into the Kimmeridgian (Arkell 1957, p. L125; see Arkell, Kummel and Wright 1957; Hölder 1955 and Ziegler 1957 and 1959). As far as the author is able to determine, neither genus is found at higher levels than the Kimmeridgian.

Among the Woodham oppelids there are certainly no intermediates between *T. richei* and *C. renggeri*; there is a 'morphological hiatus' (Makowski 1962) of about one whorl of growth and the largest adult *C. renggeri* is not as large as the smallest *T. richei* (text-fig. 6). The two 'species' occupy the same strata, and, as far as can be determined, both begin at the same level, basal Mariae Zone, at Woodham.

The ratio of the large to small forms, *T. richei* to *C. renggeri*, is two to one. This can only be an approximate ratio as specimens from Woodham with a diameter of less than 8–9 mm. cannot reliably be differentiated into large and small forms. By analogy with living cephalopods, which show sexual dimorphism (Sweet 1964, p. K9; Makowski 1962, pp. 56–58), it is not unreasonable to contend that the two forms, *T. richei* and *C. renggeri*, are sexual dimorphs: they show sexual differences, both size and sex ratio, comparable with those displayed by living cephalopods. A reconstruction of the dimorphic pair has been produced (Pl. 52, fig. 9). It is to be inferred that the larger is the female.

TAXONOMY

The taxonomic problems, which acceptance of the sexual dimorphism theory bring, have been discussed at length by Callomon (1955 and 1963) and Makowski (1962). The present author is of the opinion that sexual dimorphs of the same species should have the same specific name (Makowski 1962), being differentiated by the zoological symbols ♂ and ♀. The specific name accepted for a dimorphic pair should be that of the first named 'species' (following the law of priority) and, as far as the author can assess, there should be no more complication in ammonite taxonomy than in, say, ostracod taxonomy where sexual dimorphs of the same species are given the same specific name.

Jeannet (1951) does not include the genus *Creniceras* Munier-Chalmas in the family Taramelliceratinae Spath 1928. The genus, along with *Bukowskites* nov. and *Popanites* Rollier, is classified by Jeannet as: 'Incertae Sedis', family Oppeliidae Bonarelli 1894. As the present results show, *C. renggeri* and *T. richei* are sexual dimorphs of the same species (= *C. renggeri*) and on this basis the author agrees with Arkell, Kummel and Wright's (1957) classification in which the genus *Creniceras* is included in the subfamily Taramelliceratinae.

SUMMARY AND CONCLUSIONS

Creniceras renggeri (Oppel) and *Taramelliceras richei* (de Loriol) from Woodham are identical in every feature up to a diameter of about 8 mm. In the late stages of the adult phrgmocone, both 'species' develop feeble ventral tubercles which become ventral spines on the body-chamber. *T. richei* differs from *C. renggeri* in that ventro-lateral spines may be developed on the body-chamber.

The variation shown by the sutures at diameters of 8 mm. and 12 mm., in *C. renggeri* and *T. richei* respectively, is small and qualitatively similar. Sutural ontogeny is identical throughout: the sutures of *T. richei* become more complex in the adult stages, but always at larger diameters than are recorded for adult phragmocones of *C. renggeri*.

In adults the body-chamber of both 'species' uncoils at the umbilical seam. The peristome of *T. richei* is relatively simple; that of *C. renggeri* is ornate, developing flares, constrictions, rostra, and lappets.

Recent work has added substance to de Blainville's theory of sexual dimorphism in ammonites. By analogy with living cephalopods it seems probable that the large form is the female and the small form the male.

It is concluded that *Creniceras renggeri* (Oppel) and *Taramelliceras richei* (de Loriol) are really male and female respectively of the same species, and that the specific name of the dimorphic pair should be that of the earliest named form. It is finally considered that the inclusion of the genus *Creniceras* in the subfamily Taramelliceratinae is correct.

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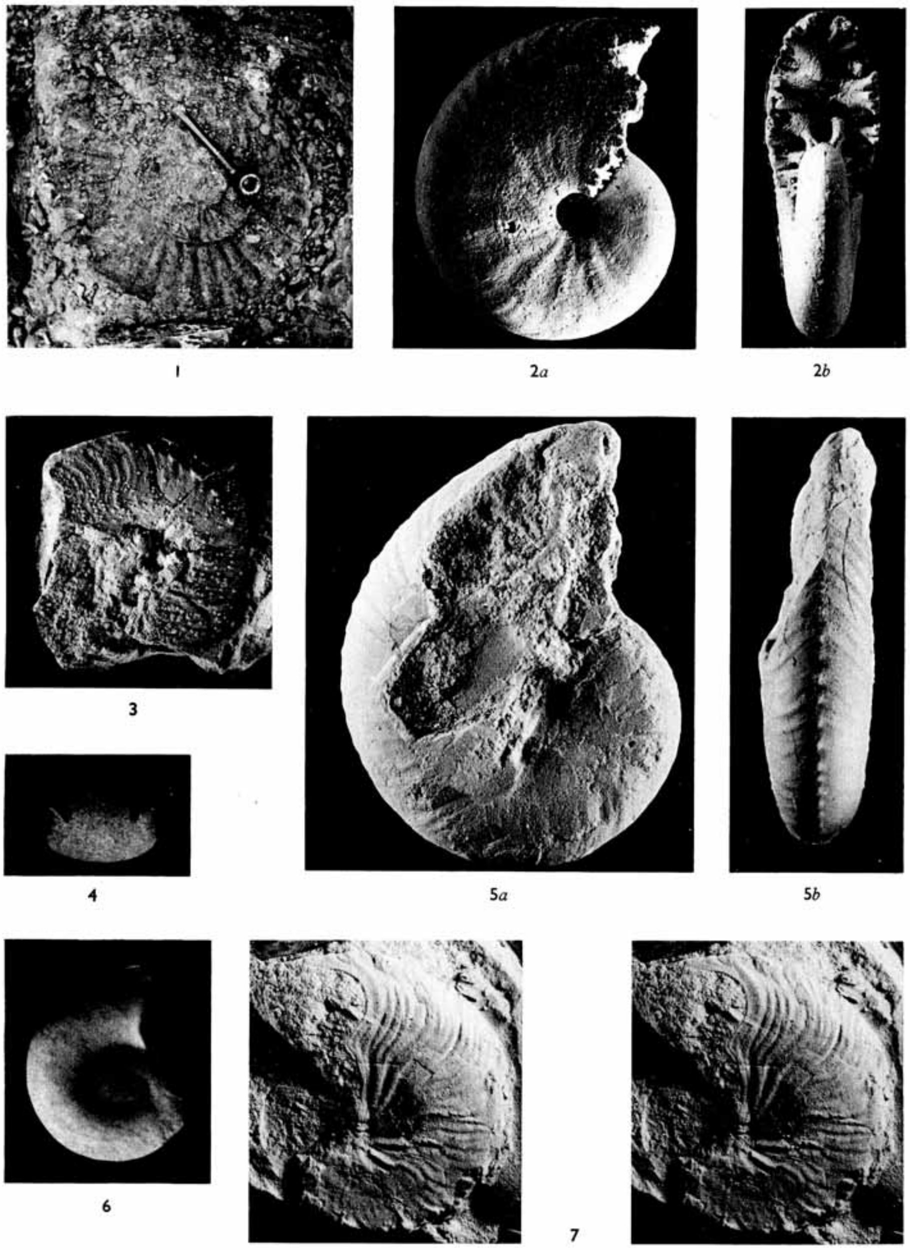
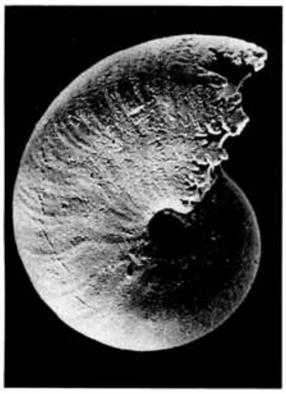


PALFRAMAN, Oxford Clay ammonites

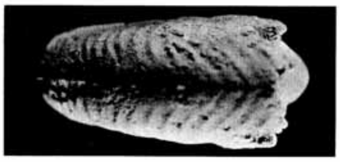


1*a*

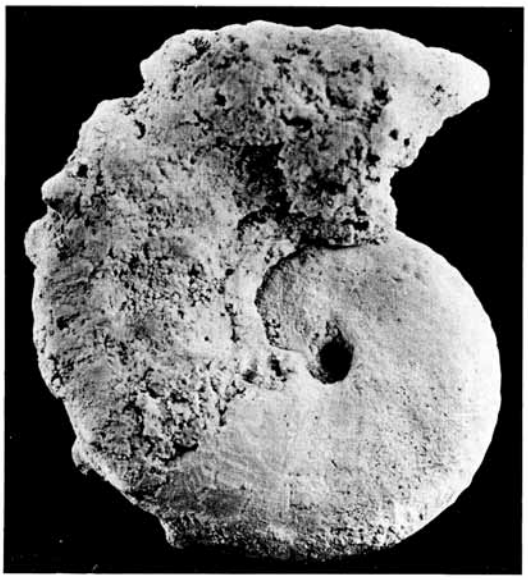
2*a*

3*a*

1*b*

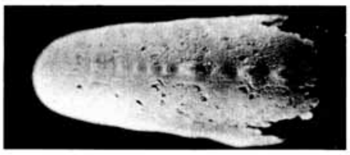


2*b*



3*b*

4*a*



4*b*

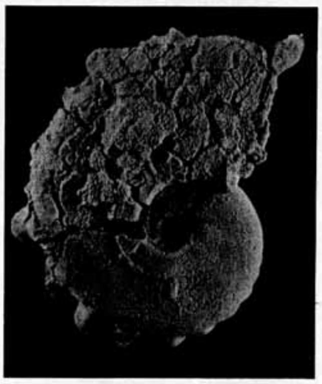
PALFRAMAN, Oxford Clay ammonites


1*a*


2*a*


2*b*


2*c*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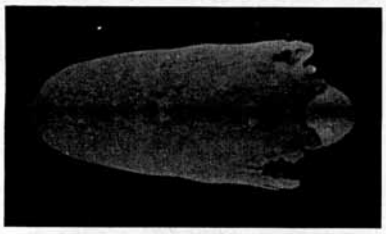
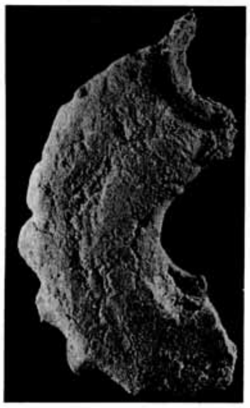

1*b*


1*c*

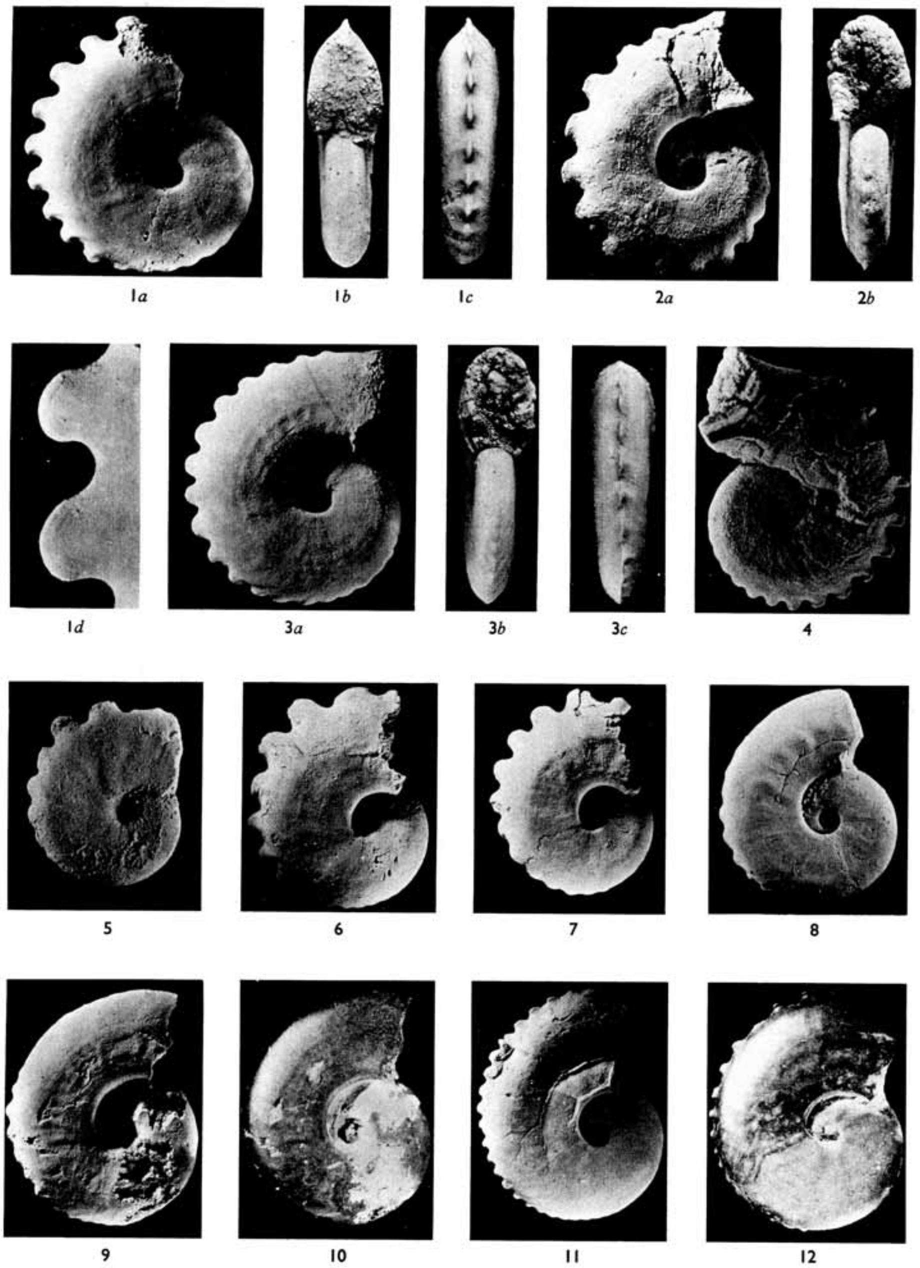

4*a*


4*b*

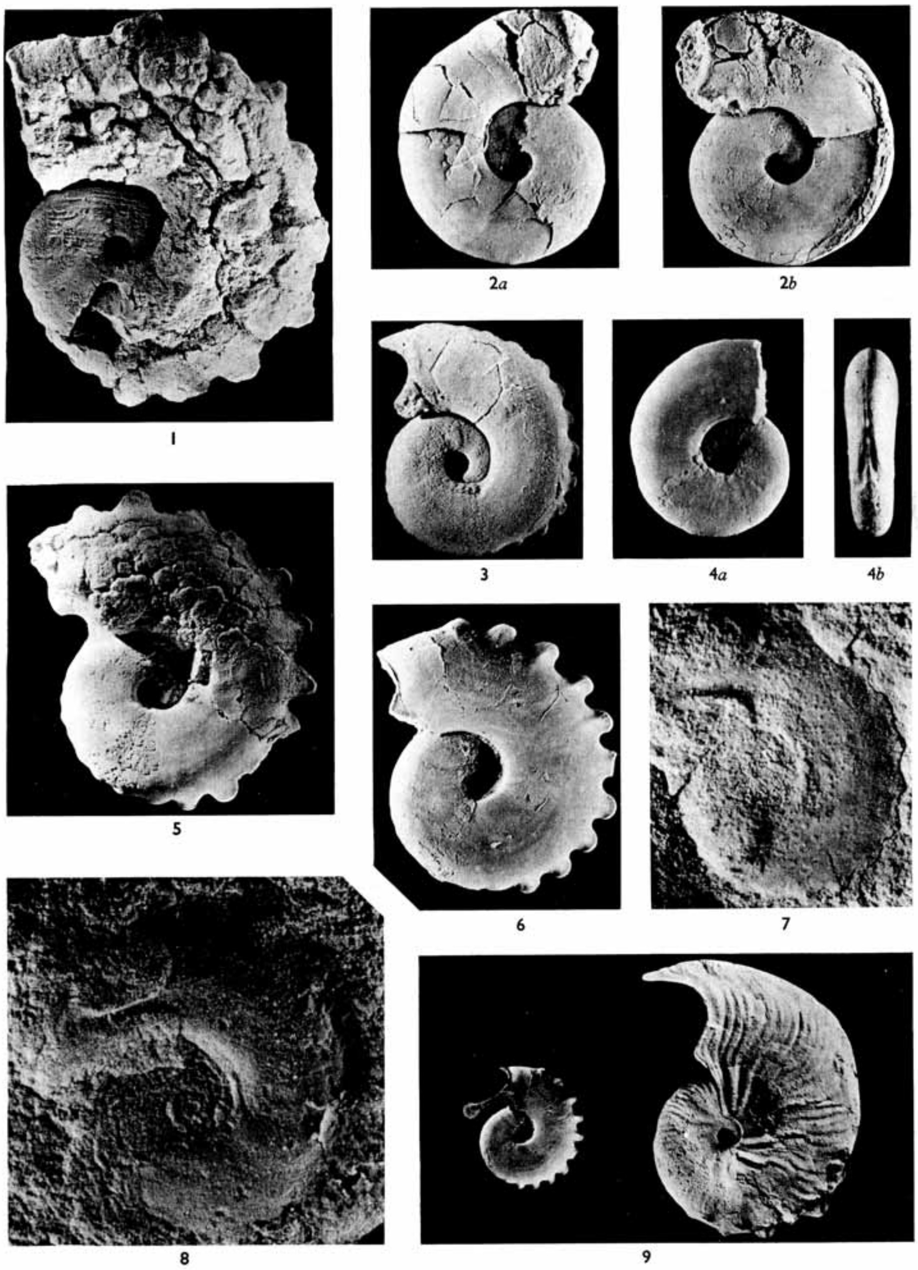

4*c*


5

PALFRAMAN, Oxford Clay ammonites



PALFRAMAN, Oxford Clay ammonites



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