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Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications

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Taxonomy of Sexual Dimorphism in Ammonites: Morphogenetic Evidence in Hecticoceras brightii (Pratt)

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With Plates 6–8 and 11 Text-figures

Abstract. A variational and ontogenetic study of the Oxford Clay ammonite *Hecticoceras brightii* (PRATT), indicates that the species is dimorphic. The two forms (one large, the other small) have identical juvenile stages suturally, dimensionally, and ornamentally. Differences in size and ornament at maturity are interpreted as being expressions of sexual dimorphism. It is considered that the partners of a sexually dimorphic pair should have the same name and be differentiated by the zoological symbols ♂ and ♀.

Introduction

From the studies of BONARELLI (1893), DE TSYTOVITCH (1911), LEMOINE (1932), and ZEISS (1956) it is clear that there is enormous variation within the genus *Hecticoceras*: intraspecific variation is also great. In this article, a collection of the species *Hecticoceras brightii* (PRATT), largely from a single locality, is examined from a variational and ontogenetic viewpoint.

Throughout the text the following abbreviations are used: BCM = Bristol City Museum; BM = British Museum (Natural History); LU = Leicester University; OUM = Oxford University Museum; D = diameter; W = whorl width; UD = umbilical diameter; HH = whorl height. Measurements are recorded in millimetres.

Material

Localities. During the present study of *H. brightii* (PRATT) about one hundred specimens were examined. The majority of these came from Woodham, Buckinghamshire. Sixty from this locality were collected by the writer (OUM J25689–OUM J25739 and OUM J25748–OUM J25756) and eight by the late Dr. W. J. ARKELL (OUM J20505–OUM J20512; OUM J20505–6 are figured in ARKELL, 1939, pl. VIII, figs. 20a–b, 21a–b). Two small collections from Oxford contributed to the total; one collected by Canon L. W. GRENSTED from a temporary exposure in Charlbury Road (GRENSTED, 1954, OUM J10180–OUM J10182 and OUM J10221), the other (OUM J23253–OUM J23257) coming from St. Gile's Pit, Sum-

mertown (collector not recorded). A further ten specimens were collected by the author from Peckondale Hill, Yorkshire (OUM J25740–OUM J25747 and LU 289–LU 290). The type material (PRATT, 1841) has been examined in the Bristol City Museum.

Preservation. All the specimens examined are small internal pyritic/limonitic moulds, rarely exceeding 20 mm. in diameter. One individual from Charlbury Road, Oxford (OUM J10221) is still partially embedded in a clay matrix. Though not complete, a large part of the adapical portion of the body chamber is preserved as a clay mould contiguous with the pyritic mould of the phragmocone and very early part of the body chamber.

Variation and ontogeny of Hecticoceras brightii (Pratt)

Family OPPELIIDAE BONARELLI, 1893
Subfamily HECTICOCERATINAE SPATH, 1925
Genus *Hecticoceras* BONARELLI, 1893, p. 77
Type species: *Ammonites hecticus* REINECKE, 1818
(figured REUTER, 1908, p. 106)
Subgenus *Brightia* ROLLIER, 1922 (p. 360)
Type species *Hecticoceras nodosum* (QUENSTEDT) BONARELLI, 1893 (p. 94)
Hecticoceras (Brightia) brightii (PRATT)
Pl. 6–8; Text-figs. 1–11

1841. *Ammonites Brightii* PRATT (pars), p. 164, pl. VI, fig. 4.
1893. *Hecticoceras (Lunuloceras) Brighti* PRATT, BONARELLI, p. 98.
1911. *Hecticoceras Brighti* PRATT (pars), DE TSYTOVITCH, p. 66, pl. VI, figs. 4, 4b, 7–10.
1924. *Lunuloceras rursicostatum* ROBSON MS., BUCKMAN, (vol. V) pl. DI, figs. 1–3.
1932. *Hecticoceras Brighti* PRATT, LEMOINE, p. 207, pl. XI, figs. 1–25.
1939. *Hecticoceras (Brightia) glyptum* (BUCKMAN), ARKELL, p. 144, pl. VII, figs. 20a–b, 21a–b.
1951. *Brightia Brighti* PRATT (pars), JEANNET, p. 61, pl. 13, figs. 18, 20.
1951. *Brightia sveva* BONARELLI (pars), JEANNET, p. 62, pl. 13, figs. 22, 24.

General remarks and brief description

The general preservation of this species renders it suitable for ontogenetic studies. Unfortunately, the body chamber of the majority of specimens examined occurred at greater diameters than are commonly preserved among pyritic ammonites from the above mentioned localities. Indeed no peristome has been seen even on otherwise complete specimens with a maximum diameter which cannot have exceeded 15 mm. (OUM J25739, Pl. 7, fig. 7 and OUM J25726, Pl. 7, fig. 9).

The early whorls are smooth and rather evolute, the degree of involution/evolution remaining almost constant throughout ontogeny. The whorls of mature stages of this species are high and laterally compressed. The UD/D ratio is about 40 %. At a diameter of 4–7 mm. lateral nodes and a ventral keel develop during the final one or two phragmocone whorls as does a sharpening of the umbilical wall. In the adult stages two forms are found: a small form in which the body

chamber ornament differs little from that of the immediately preceding phragmocone, and a large form in which a series of fine ventro-lateral ribs is developed in the final stages of the mature phragmocone; these persist on to the body chamber. Differences between large and small forms do not appear to exist in the early ontogenetic stages.

The lectotype. In his diagnosis of the new species "*Ammonites Brightii*", PRATT (1841, p. 164) does not mention which of his two illustrated specimens (op. cit. pl. VI, figs. 3 and 4) is the holotype. The specimen illustrated in PRATT's fig. 3 (now catalogued BCM C 1803) is a crushed, but mature, specimen with lappet (herein pl. 8, fig. 7). Its maximum diameter is 42 mm. This specimen has been chosen by BUCKMAN (1925, vol. V, pl. DXLIX) as the "holotype" of the species "*Lunuloceras brighti*, PRATT sp." (loc. cit.). PRATT's diagnosis of the species (1841, p. 164) indicates that there are lateral nodes "... which in the young shell ... are hardly visible, and also become obsolete near the aperture". The specimen chosen by BUCKMAN as the "holotype" has very feeble radial swellings on the lower flank, according to PRATT's original drawn illustration (op. cit. fig. 3). The refigured lectotype (BUCKMAN 1925, vol. V, pl. DXLIX) is virtually uninterpretable: whatever evidence there may have been of lateral ornament has gone, due to flaking of the shell (the specimen, as seen by the present author in June 1966, is in a similar state as indicated by BUCKMAN's illustration of more than thirty years ago: the specimen is now coated with a layer of preservative. See herein pl. 8, fig. 7).

PRATT's second specimen of "*A. Brightii*" (1841, pl. VI, fig. 4) has been refigured by BUCKMAN (1924, vol. V, pl. DI). The latter author considers this specimen (BCM C 1804) to be a paratype of "*A. Brightii*" and refers it to "*Lunuloceras rursicostatum*, ROBSON MS". The present writer considers that this second, uncrushed specimen of PRATT's is much closer to his diagnosis (loc. cit.) than the crushed lappetted specimen[1]. Laterally nodose Woodham forms accord reasonably well with this second specimen.

Some of the specimens figured by QUENSTEDT (1886–7, pl. 82, figs. 10–14) as "*Ammonites hecticus nodosus*" are extremely similar to the Woodham forms examined herein. Most of the specimens figured by DE TSYTOVITCH (1911) and LEMOINE (1932) (see synonomy herein for details) as "*Hecticoceras Brighti*", are virtually identical to Woodham examples of this species.

Probably encompassed within the specific name *H. brightii* (PRATT) is the holotype of "*Lunuloceras glyptum*, nov." (BUCKMAN 1926, vol. VI, pl. DCXLVI: catalogued BM C41705). This is wholly septate with a diameter of 38 mm. and, according to BUCKMAN (loc. cit.), comes from "Shotover [Summertown][2], near Oxford; Oxfordian; J. W. T.[3] Coll. 'Purch. ex. Carter'."

Remarks. There is some uncertainty about assigning the laterally nodose, finely ribbed *Hecticoceras* of Woodham to the species *H. brightii* (PRATT). From the works of BONARELLI (1893), DE TSYTOVITCH (1911), and LEMOINE (1932) it is

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[1] Ed.: The author informed me that a request will be made to ICZN on this issue.
[2] The square brackets are BUCKMAN's.
[3] J. W. TUTCHER.

evident that there is much variation in the position and frequency of lateral nodes and in the frequency and form of ventro-lateral ribs. The precise determination of specific boundaries is clearly impossible.

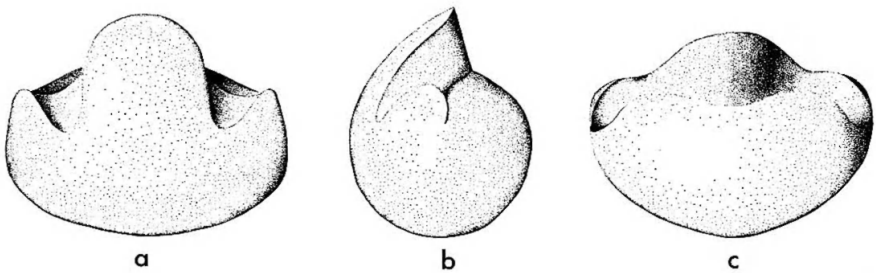
Protoconch

Some twenty-two protoconchs (Text-fig. 1) have been dissected out; all are internal moulds, generally of pyrite but not uncommonly of calcite. The pyrite/calcite junction often occurs at the proseptum. When the calcitic proseptum has been dissolved away, it is a relatively easy matter to remove early chambers from the protoconch.

The protoconch is smooth and globular (Text-fig. 1), with the following parameters (Text-fig. 2):

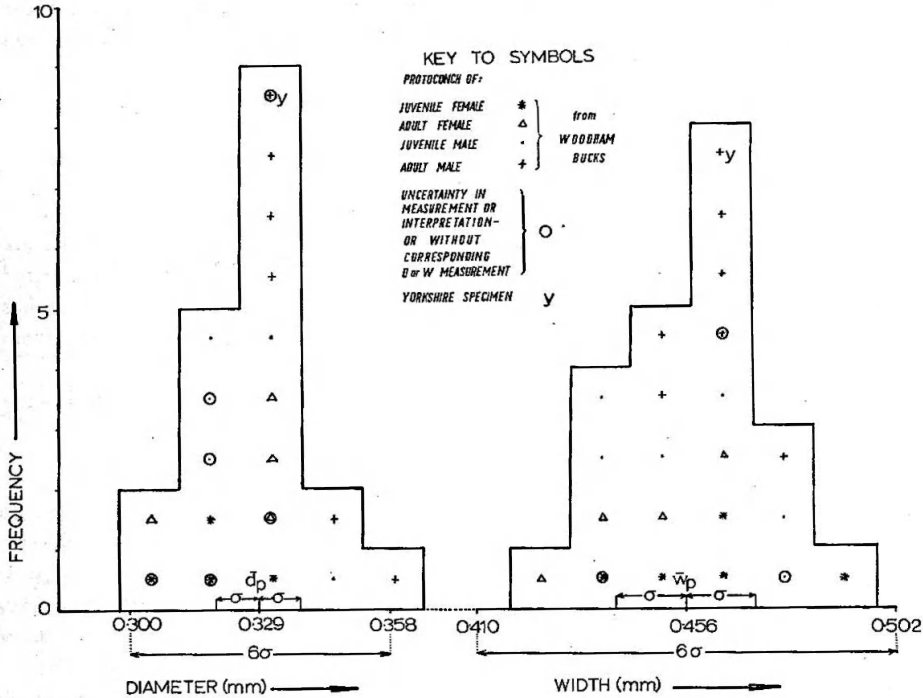
	specimens	mean	σ	range	V
diameter (D)	19	.329 mm.	.009 mm.	.30– .36 mm.	2.89
width (W)	22	.456 mm.	.015 mm.	.41– .50 mm.	3.40
W/D ratio	22	1.385	–	1.33–1.42	–

The ventral saddle of the prosuture is large and rounded: the lateral lobe is smaller and more acute (Text-figs. 3f–g; Pl. 6, figs. 1a–c). In many protoconchs can be seen, in a ventral position, the caecal mould or the early siphuncle (Pl. 6, figs. 1a–c).



Text-fig. 1a–c. Protoconch of *Hecticoceras brightii* (PRATT). Diagram based on male from the Oxford Clay, Woodham, Buckinghamshire (OUM J25709). a, ventral view; b, lateral view; c, apertural view. All figs. x 80.

Remarks. As far as can be assessed from the small sample, there is no significant difference between the protoconchs from small and large forms of this species, nor between specimens from Woodham and a single individual from Peckondale Hill, Yorkshire.



Text-fig. 2. Histogram of diameter and width of the protoconch of *Hecticoceras brightii* (Pratt). Specimens from Woodham, Buckinghamshire, except one (labelled 'y') which is from Peckondale Hill, Yorkshire. Abbreviation: $\overline{d}_p$ = mean diameter, $\overline{w}_p$ = mean width of protoconch.

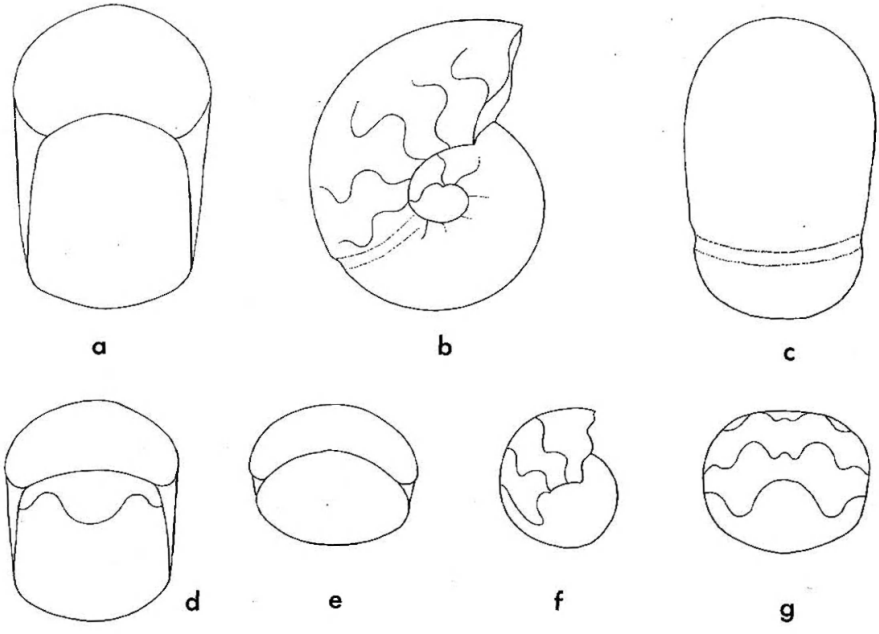
Phragmocone

Early whorls and general growth pattern

The whorl shape of the early growth stages is extremely tumid and quite smooth (Text-figs. 3e–g). Seven eighths to one whorl from the proseptum is the nepionic constriction: it is strongest ventrally, slightly fading on the flanks (Text-figs. 3b–c). The mean diameter of the nepionic constriction is 0.657 mm. with a range of 0.60–0.70 mm.: the standard deviation is 0.036 mm., and the coefficient of variation 5.554.

The very early whorls after the nepionic constriction are smooth and unornamented. The whorl shape alters from being tumid in the juvenile stages (Text-fig. 3a, d, e) becoming quadrate at a diameter of 3–5 mm. (Pl. 6, fig. 3f), and eventually, in the late phragmocone stages, laterally compressed (Text-figs. 7a–c). The W/D ratio decreases from the protoconch to a diameter of 0.6–0.8 mm. and from this stage remains fairly constant until the onset of maturity (Text-fig. 4). From a diameter of 0.6–0.8 mm. the UD/D and HH/D growth curves also reflect almost isometric growth until the onset of maturity (Text-figs. 5, 6).

In the juvenile stages the umbilical area is rounded, passing laterally on to the flanks without perceptible differentiation. At a diameter in the order of 4–7 mm., the umbilical area is differentiated from the flank by a moderately sharp umbilical angle: the umbilical area becoming sufficiently steep to warrant being called an umbilical wall. The umbilical wall and umbilical angle are, in most specimens, well-defined (Pl. 6, figs. 5a, 6a; Pl. 7, figs. 1a, 2a, 3, 9a; Pl. 8, figs. 1c, 4); in others there is but slight differentiation (Pl. 7, figs. 3a, 4a).



Text-fig. 3. The innermost whorls of *Hecticoceras brightii* (PRATT) from the Oxford Clay, Woodham, Buckinghamshire. b and c show the position of the nepionic constriction; b, d, f, and g show the position of the prosuture, primary suture, and other early sutures; a, d, and e show the changes in whorl shape during one whorl of growth. a–d, based on male (OUM J25700); e–g, based on juvenile female (?) (OUM J25731). All figs. x 40.

Among small forms of *H. brightii* the umbilical angle and wall retain their strength throughout phragmocone growth, weakening but slightly near the phragmocone/body chamber junction of mature specimens (Pl. 7, figs. 4, 7, 9a–b). In mature specimens of large forms of this species, the umbilical angle often weakens to become rounded as much as one whorl before the phragmocone/body chamber junction, at a diameter of 7–9 mm. (Pl. 6, figs. 8a, 9a; Pl. 7, figs. 8d, 10a): this is best observed in OUM J20505 (Pl. 8, fig. 4).

Remarks. The W/D, UD/D, and HH/D ratios of large and small forms of this species are identical up to diameters of about 10 mm. and, at comparable diameters, there is no difference in the strength of the umbilical angle between large and small forms. The adoral weakening of the umbilical angle near the

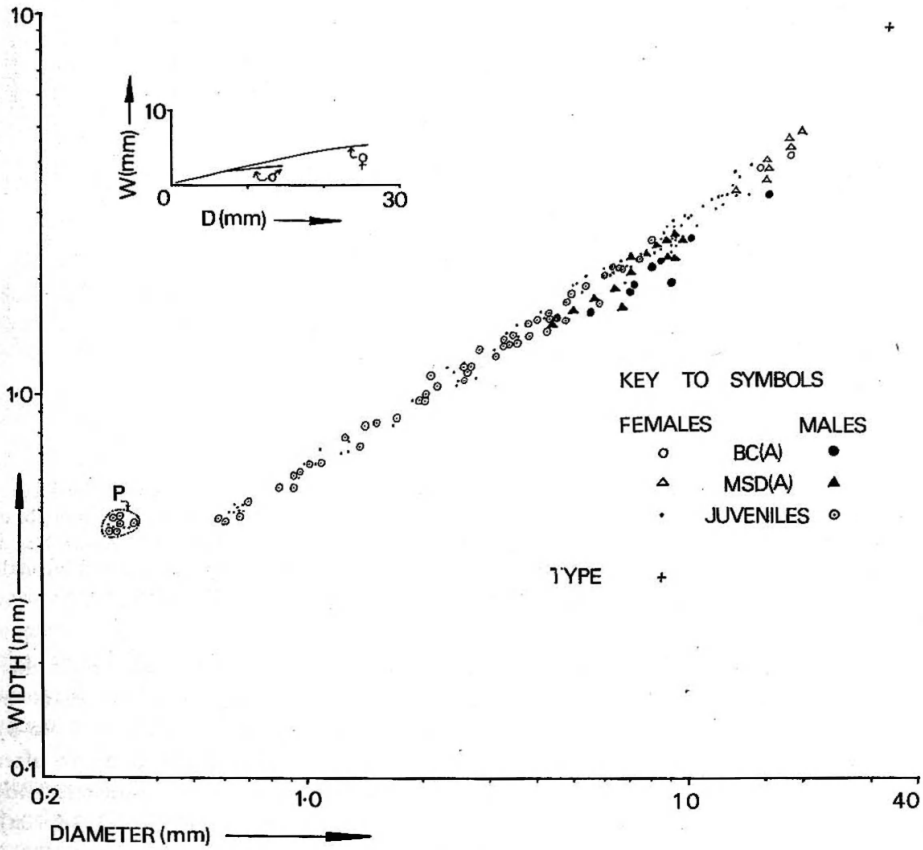
phragmocone/body chamber junction of adults appears to be a function of maturity in small forms. Among some large forms the weakening of the umbilical angle appears to be related to maturity, in others to size.

Ornament

The various types of ornament shown by *H. brightii* are: a ventral keel, lateral nodes, and ventro-lateral ribs. Ribs are developed only on large forms of this species. In a few specimens lateral spiral sculpture is present.

Keel

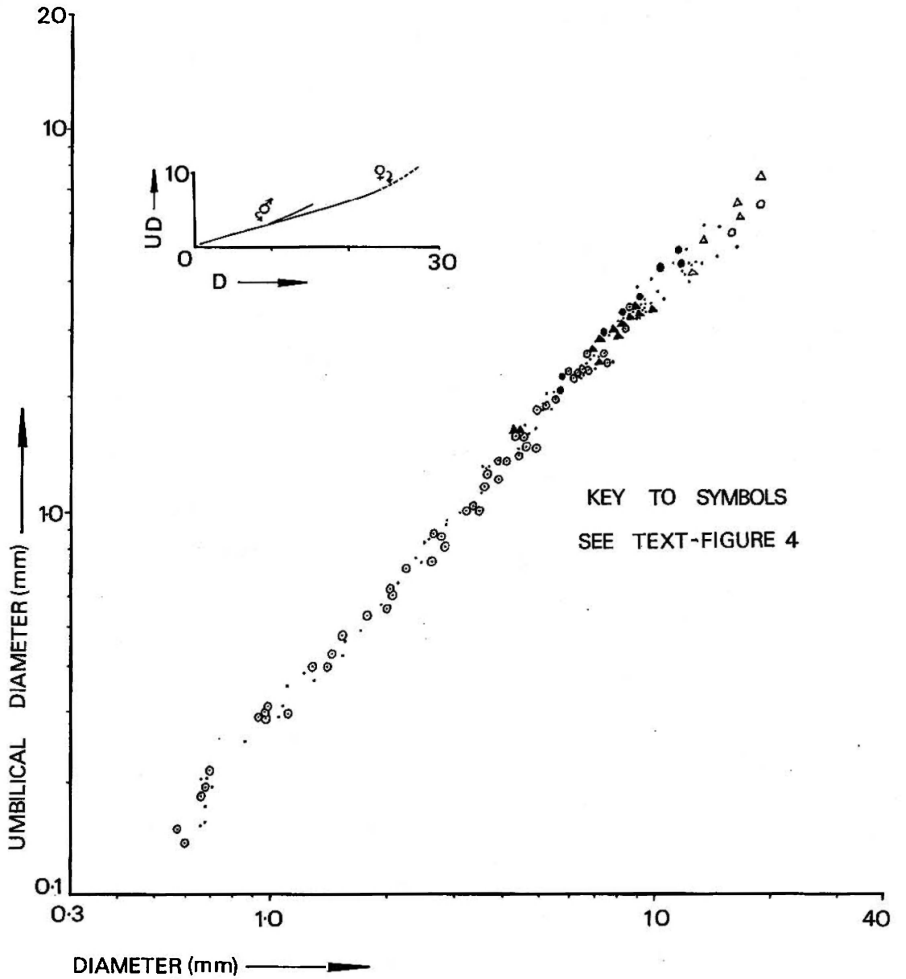
The development of a keel occurs at about the same diameter as the whorl section becomes quadrate, between 4–7 mm. In no specimen is the keel very strong, and in many cases the venter is but slightly arched (Pl. 6, figs. 3c, d, f). Typical ex-



Text-fig. 4. Graph on log/log scale for diameter and width of *Hecticoceras brightii* (Pratt) ♂ and ♀. Dashed line encloses measurements made on the protoconch (area 'P'). 'Type' refers to the holotype of "*Lunuloceras glyptum*" Buckman (1926, vol. VI, pl. DCXLVI). Inset: same graph on linear/linear scale showing position of approximate best-fit line.

amples are illustrated (Pl. 6, figs. 5b, 6b–c). At the onset of development, the keel is always very weak: in all cases it becomes progressively stronger adorally throughout phragmocone growth, as shown by the large form LU 289 (Pl. 7, figs. 8c, b, e). In both large and small forms of this species, there is comparable variation in the diameter of keel-origin and in general strength. Feeble keels of large and small forms, respectively, are shown by specimens LU 290 (Pl. 6, fig. 9b) and OUM J25698 (Pl. 6, figs. 3c, d): strong keels of large and small forms, respectively, are shown by specimens OUM J25702 (Pl. 8, fig. 5a) and OUM J25740 (Pl. 7, fig. 6b).

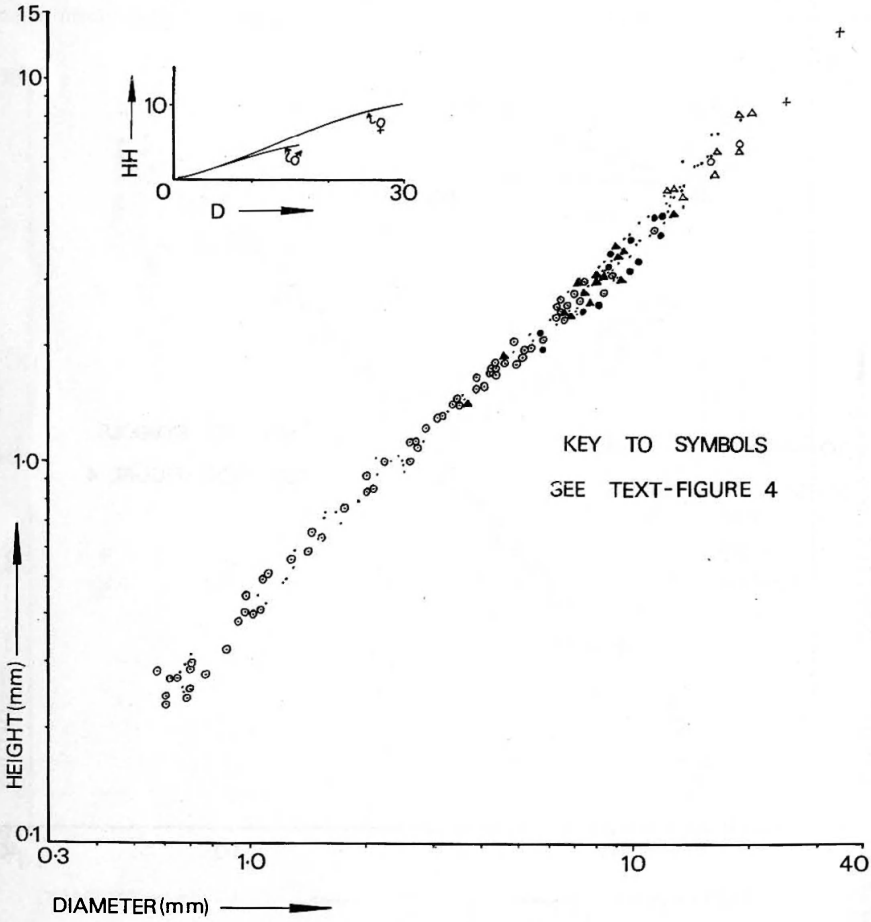
Remarks. At comparable diameters there is no difference between the keels of large and small forms.



Text-fig. 5. Graph on log/log scale for diameter and umbilical diameter of *Hecticoceras brightii* (Pratt) ♂ and ♀. 'Type' refers to the holotype of "*Lunuloceras glyptum*" Buckman (1926, vol. VI, pl. DCXLVI). Inset: same graph on linear/linear scale showing position of approximate best-fit line.

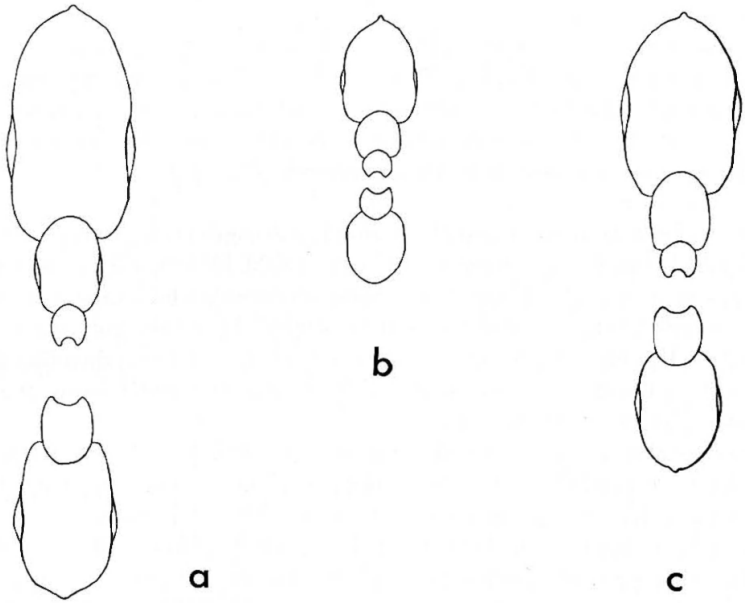
Ribs

Not all specimens develop ribbing. Ribbing is, in fact, confined to only the large form of *H. brightii*. The smallest diameter at which ribs begin is about 10 mm. (OUM J25716, not illustrated) and the largest 12.6 mm. (OUM J25702, Pl. 8, fig. 5c). Ribbing is concave and entirely restricted to the ventro-lateral area. In nearly all ribbed specimens, the ribs are not seen until obliquely illuminated, and, in many cases, it is difficult to decide at precisely which point they commence. The Woodham and Peckondale Hill individuals are usually ribbed for about one third to three quarters of a whorl (Pl. 8, fig. 4; Pl. 7, fig. 8d), but in many of these cases there is little evidence to suggest that the specimens are mature. Ribbing never encroaches on to the venter proper. Variation in rib-strength is from very feeble (Pl. 8, fig. 5c) to relatively strong (Pl. 7, fig. 8d).



Text-fig. 6. Graph on log/log scale for diameter and whorl height of *Hecticoceras brightii* (Pratt) ♂ and ♀. 'Type' refers to the holotype of "*Lunuloceras glyptum*" Buckman (1926, vol. VI, pl. DCXLVI). Inset: same graph plotted on linear/linear scale showing position of approximate best-fit line.

Remarks. Ribbing appears to be a useful distinction between large and small forms of *H. brightii*. Specimens which have ribbed body chambers, but do not show typical features of maturity (OUM J25723, Pl. 7, fig. 2a, and OUM J25689, Pl. 6, fig. 4a) are herein considered to be juveniles of the large form. However, the diameter at which the ribbing of the phragmocone occurs in large forms is never attained by the phragmocone of mature small forms. In no case did even almost complete small forms of this species show evidence of ribbing on the body chamber (Pl. 6, fig. 3a; Pl. 7, fig. 7).



Text-fig. 7a–c. Cross-sections of *Hecticoceras brightii* (PRATT) from the Oxford Clay. a, juvenile female from Woodham, Buckinghamshire (OUM J25733); b, male from Peckondale Hill, Yorkshire (OUM J25740); c, juvenile female from Peckondale Hill, Yorkshire (OUM J25741). All figs. x 5.

Lateral ornament

Characterising the subgenus *Brightia* to which the species *H. brightii* belongs, is the presence of ". . . distant bullate ribs or submesial nodes . . ." (ARKELL, KUMMEL & WRIGHT, 1957). Lateral nodes, as observed in this species, do not develop until a diameter of about 5 mm. Among small forms, the nodes begin at a diameter of 4.8–6.0 mm. with a mean of 5.3 mm. (six specimens) compared with large forms in which the diameter at which nodes develop is 4.8–6.9 mm. with a mean of 5.5 mm. (four specimens). The diameters at which the nodes of juvenile individuals develop, fall within the range 4.8–6.9 mm. Preparations of specimens show that the first three whorls of growth are smooth-flanked (Pl. 6, figs. 3e, 4b).

The number of nodes on each phragmocone whorl remains remarkably

constant for both forms, varying between 7 and 8. In the small form, because of the diameter of the mature phragmocone, there is usually only one, or less, nodose phragmocone whorl (Pl. 6, figs. 3a–b; Pl. 7, figs. 6a, 9a–b). Among the mature smaller examples of the small form, in which the complete phragmocone is less than 6 mm., lateral phragmocone nodes may be entirely absent (Pl. 7, fig. 7). It therefore appears that the origin of lateral nodes is a function of absolute size rather than of maturity, as the body chamber of these very small specimens becomes laterally nodose within the diameter range 4.8–6.9 mm. In large forms there are commonly two laterally nodose phragmocone whorls (Pl. 7, figs. 8a, d; Pl. 8, figs. 2a, c).

Node strength varies appreciably in both large and small forms. Some small forms are almost smooth-flanked (Pl. 6, fig. 3b; Pl. 7, fig. 4) whereas others bear well-developed nodes with a marked degree of lateral projection (Pl. 7, figs. 9a–d). Similar variation is to be seen among large forms, in which almost smooth examples with weakly nodose flanks are present (Pl. 8, fig. 5c) to fairly strongly so (Pl. 7, figs. 8d–e).

The nodes of large forms usually retain their strength throughout phragmocone growth (Pl. 7, figs. 8a–e), though in one case, OUM J25693, adoral degeneration of nodes can be seen (Pl. 8, figs. 2a–e). Some specimens, which cannot be reliably ascribed to either large or small forms of *H. brightii*, have very pronounced lateral nodes (Pl. 6, figs. 6a–c, 7a–b). In all cases nodes are elongate in a direction parallel to the venter. Between adjacent nodes of both large and small forms, the flanks are weakly concave (Text-figs. 7a–c).

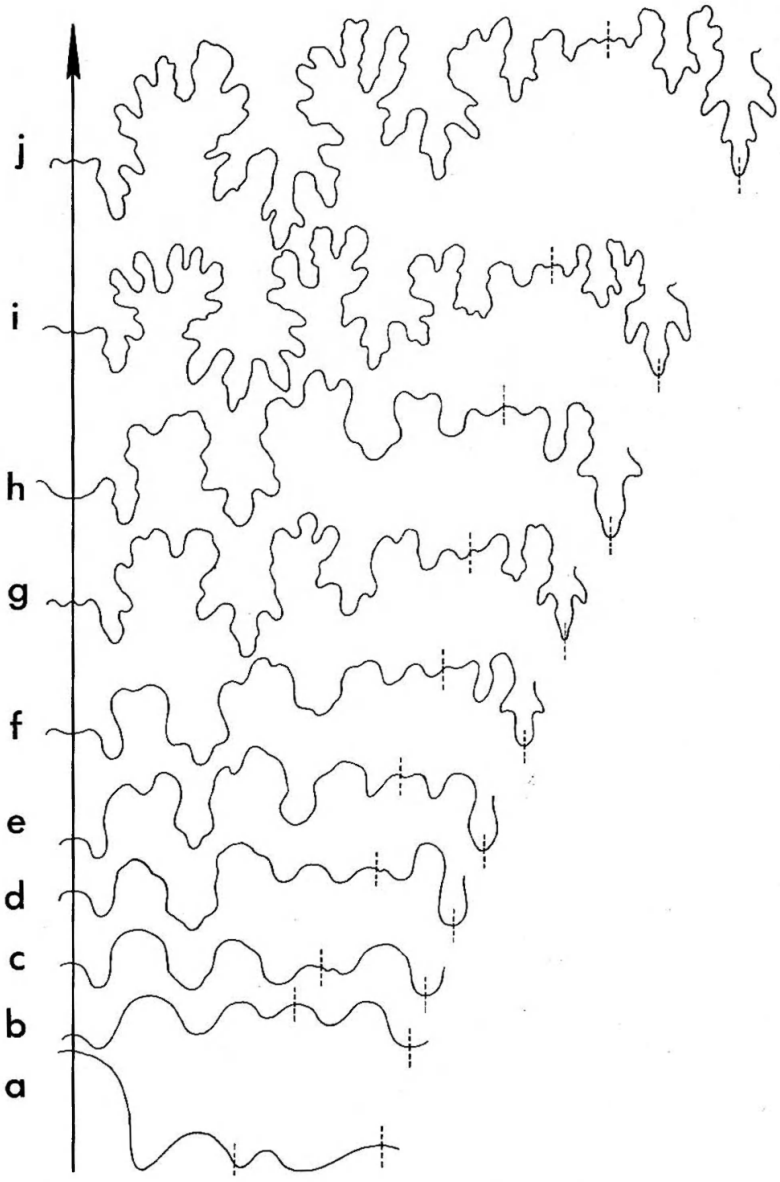
Occasionally nodes are not the only form of lateral ornament. Between the ventro-lateral ribs and lateral nodes of some specimens of the large form, various types of spiral sculpturing are present. A feeble fillet can be seen on each of two specimens from Peckondale Hill, LU 289 and OUM J25741 (Pl. 7, fig. 8d and Pl. 8, fig. 1c, respectively); whereas a shallow, but distinct groove is present, in a similar position, on a specimen from Woodham, OUM J20505 (Pl. 8, fig. 4). Spiral ornament is only present on large forms at greater phragmocone diameters than are attained by small forms.

Due to the type of preservation of all specimens examined here (internal moulds), there is little evidence of growth lines, which are generally confined to the exterior of the ammonite shell. The well-preserved inner whorls of a presumed juvenile large form of *H. brightii* show faint traces of what are herein interpreted as growth lines. These are closely spaced, sinuous, and pass uninterrupted over a feeble lateral fillet (Pl. 6, fig. 4b). No other examples of this feature have been seen.

Sutures

Sutural ontogeny

Ten sutures, including the prosuture and primary suture, have been drawn at varying diameters ranging from 0.35 mm. to 19 mm. The sutures, taken from six different specimens, have been assembled according to increasing diameter (Text-fig. 8a–j). The resulting "ontogeny" shows a gradual increase in complexity of sutural elements such as typifies the sutural ontogeny of a single specimen.

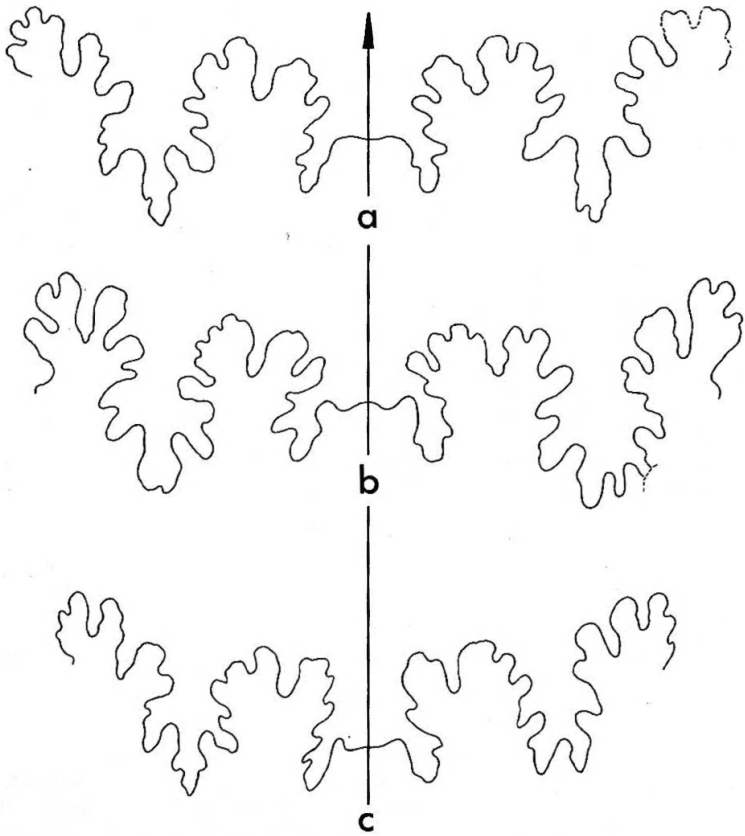


Text-fig. 8a–j. Sutural ontogeny of *Hecticoceras brightii* (PRATT) from the Oxford Clay, Woodham, Buckinghamshire. a, prosuture, male, D = 0.35 mm, (OUM J25709) x 80; b, primary suture, juvenile, D = 0.40 mm, (OUM J25695) x 75; c, male, D = 1.06 mm, (OUM J25709) x 47; d, juvenile female (?), D = 2.60 mm, (OUM J25711) x 28; e, juvenile, D = 4.07 mm, (OUM J25701) x 20; f, juvenile, D = 4.60 mm, (OUM J25695) x 21; g, female, D = 7.2 mm, (OUM J25693) x 15; h, juvenile, D = 7.8 mm, (OUM J25695) x 15; i, female, D = 16 mm, (OUM J25697) x 8; j, female, D = 19 mm, (OUM J25693) x 8. Arranged according to diameter at which suture was drawn (cf. PALFRAMAN, 1968).

In Text-fig. 8, h and g are slightly anomalous in that h, drawn at a larger diameter than g (7.7 mm. and 7.2 mm. respectively), is slightly simpler than g. The probable reasons for this anomaly have previously been pointed out by the author (PALFRAMAN, 1967, p. 71). At comparable diameters the sutures of large and small forms of *H. brightii* are identical.

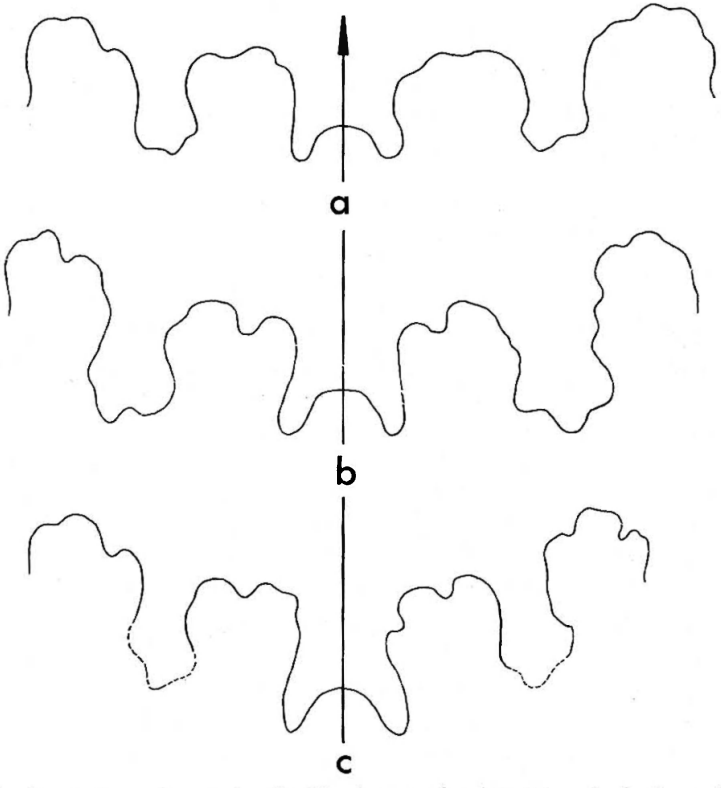
Sutural variation

The sutures of the large and small forms of this species are figured separately (Text-figs. 9, 10). Sutures chosen for variation studies in both forms are 'normal' (i. e. not approximated). In the large form, sutures have been drawn from three randomly chosen specimens at a diameter of about 15 mm., and in the small form from three randomly chosen specimens at a diameter of about 6 mm. The sutural elements figured are the ventral and lateral lobes and the first and second lateral saddles. These elements are the most complex and variable at any diameter in both large and small forms.



Text-fig. 9a–c. Sutural variation of *Hecticoceras brightii* (PRATT) ♀, from the Oxford Clay. a, at D = 14.7 mm, (OUM J25733) from Woodham, Buckinghamshire; b, at D = 15.6 mm, (OUM J25702) same loc.; c, at D = 14.8 mm, (LU 289) from Peckondale Hill, Yorkshire. All figs. x 12.

The variation of a single suture, either side of the venter, in both large and small forms, is almost negligible. The most adapical element of the lateral saddle shows greatest variation in all cases, especially so with the more complex suture of the large form (Text-figs. 9a–c) compared with the relatively simple suture of the small form (Text-figs. 10a–c). Sutural variation within the three examples given for each form, is greater than variation of a single suture either side of the venter. Sutural variation within each form is, nonetheless, very small.



Text-fig. 10a–c. Sutural variation in *Hecticoceras brightii* (PRATT) ♂, from the Oxford Clay. a, at D = 6.1 mm, (OUM J25700) Woodham, Buckinghamshire. b, at D = 6.1 mm, (OUM J25698) same loc.; c, at D = 6.0 mm, (OUM J25740) from Peckondale Hill, Yorkshire. All figs. x 30.

Remarks. Species of the Cretaceous ammonite genus *Neogastroplites* show enormous intraspecific morphological variation; at least as great as that shown by *H. brightii*. The suture of any single species of *Neogastroplites*, drawn at a prescribed diameter is, however, remarkably consistent (REESIDE & COBBAN, 1960, figs. 11, 14, 15, 18–20). In these examples the most adapical element of the lateral lobe is the most variable (loc. cit., figs. 14 H, 19 C). The present author has already described sutural variation in some Jurassic ammonites (PALFRAMAN, 1966, p. 300 and 304; 1967, pp. 71, 79).

The mature phragmocone

The familiar criteria of maturity (CALLOMON, 1957) are not always applicable to *H. brightii.* In no case is a peristome preserved, and uncoiling of the body chamber at the umbilical seam is difficult to detect because of the large size of the umbilicus and small amount of whorl involution. Therefore, the only criterion which can be used here is that of approximation of the sutures. Among small forms, this is often easy to detect, especially as preservation commonly permits the retention of the body chamber and last formed chambers. The diameter of the mature phragmocone of the large form is, however, in the region of the maximum preservational size of pyritic Oxford Clay ammonites; hence the body chamber and perhaps the last few chambers (so critical for determining sutural approximation) are lacking. There is no evidence to show that the pyrite mould/clay mould transition coincides with the phragmocone/body chamber junction (HUDSON & PALFRAMAN, 1969).

Sutural approximation of small forms can clearly be demonstrated (Pl. 6, figs. 3a–b; Pl. 7, figs. 4, 6a, 7, 9a–b). It is difficult to show this for many large forms, although some undoubtedly have approximated sutures (Pl. 6, fig. 8; Pl. 7, fig. 8d). The final suture of specimen OUM J20505 (Pl. 8, fig. 4) is quite different from all preceding ones. The saddles and lobes are displaced towards the umbilicus, due to the formation of a disproportionately large ventral lobe. In order to accommodate all the sutural elements, the dorsal aspect of the septum is "rursiradial" compared with its predecessors.

In all, ten phragmocones of the large form are considered as having approximated sutures and thirteen of the small form. Other specimens are considered either immature, as OUM J25723 which is probably a juvenile large form (Pl. 7, figs. 2a–b), or merely small phragmocones without approximated sutures which may be the juvenile stages of either the large or small form of *H. brightii.*

The diameter at which septation ceases on the phragmocones of mature small forms is from 4.3–9.2 mm. with a mean ($\bar{d}_s$) of 7.27 mm. The corresponding range for the large form is 15.0–20.0 mm. with a mean of 17.98 mm. The mature phragmocone of large forms has a high whorl section (Pl. 6, figs. 2b, 8b, 9c; Pl. 8, figs. 2e, 5b), that of the small form is relatively depressed (Pl. 6, fig. 3d; Pl. 7, fig. 6c) and is similar to the whorl section of preparations of the large form at comparable diameters (Pl. 7, fig. 8c). Whorl section is therefore related to absolute size rather than maturity.

The total number of whorls of growth, from the proseptum, varies in the small form from $3^1/_2$ (OUM J25700, Pl. 7, fig. 4) to $3^3/_4$ (OUM J25699 – not figured). The total number of phragmocone whorls in some very tiny small forms, such as OUM J25739 (Pl. 7, fig. 7) may be even less than $3^1/_2$, but poor preservation or absence of inner whorls does not allow an accurate count to be made. In the large forms the total number of whorls is in the order of 5 (OUM J25697, Pl. 6, figs. 2a, 2d; OUM J25693 and OUM J20505, Pl. 8, figs. 2e and 4, respectively). Because of inferior preservation a more accurate range cannot be given. No original shell material has been seen on either large or small forms of *H. brightii.*

Remarks. One of PRATT's syntypes of "*Ammonites Brightii*" (1841, pl. VI, fig. 4) agrees well with Woodham forms in ornament. It is not possible to be certain that the sutures of the syntype are approximated; however, the maximum septate diameter of the specimen is 20 mm. and there is about half a whorl of body chamber (maximum diameter = 26.5 mm.). The phragmocone size of this syntype is in keeping with those recorded on Woodham specimens.

BUCKMAN's holotype of "*Lunuloceras glyptum*" (1926, vol. VI, pl. DCXLVI) is very similar, ornamentally, to Woodham forms, but with rather more distinct nodes and ribs. It is wholly septate with a diameter of 38 mm.; clearly much larger than the Woodham forms. However, it may reasonably be considered to be at the upper end of a 'normal' size range. In a normally variable assemblage of *Creniceras renggeri* (OPPEL) ♀ from Woodham, the range of mature phragmocones is 14–27 mm. (PALFRAMAN, 1966). It is to be borne in mind that specimens from Woodham and Peckondale Hill are unlikely to exceed 20 mm. and that mature specimens comprising the large form of *H. brightii* from these localities are likelier to be at the 'smaller' end of a normally variable assemblage due to preservational factors. The difference in size between "*Lunuloceras glyptum* BUCKMAN" and the Woodham/Peckondale Hill specimens of *H. brightii* may also be due to geographical or chronological variation.

The implication here is that "*L. glyptum*" is probably conspecific with *H. brightii* (PRATT), though without intermediate forms this is impossible to prove (Text-figs. 4–6).

Body chamber

Although the body chamber of the small form of this species is commonly preserved, that of the large form is rare and its description is based on but few, and incomplete, examples. In no specimen is the peristome preserved.

General growth

The general growth pattern of the small form of *H. brightii* is influenced at the onset of body chamber development: the W/D and HH/D ratios reflect negative allometry and can be seen deviating from otherwise isometric growth at a diameter of 7–9 mm. (Text-figs. 4, 6). A similar pattern is also true for large forms, which deviate from isometric growth at a diameter of 18–20 mm.

The length of the body chamber of small forms is at least half to two thirds of a whorl (Pl. 6, fig. 3c, Pl. 7, fig. 7; Text-figs. 11b–d, g), and that of the large form at least half a whorl (Pl. 7, fig. 10a; Text-fig. 11a). As no body chamber is complete it is not possible to give an accurate total number of whorls of growth from the proseptum. The minimum total number of whorls for small forms must be $4^1/_4$–$4^3/_4$, and for large forms $5^1/_2$ plus.

Uncoiling of the body chamber of adult specimens at the umbilical seam is difficult to assess visually in view of the open umbilicus and small degree of whorl involution (Pl. 6, fig. 3a). In the small form of *H. brightii* this feature is best represented graphically (Text-fig. 5). Among large forms there is insufficient body chamber preserved to note this development.

Ornament

Keel

The keel of both large and small forms continues uninterrupted across the phragmocone/body chamber junction and becomes progressively stronger, in both forms, on to the mature body chamber. In the small forms this increase in keel strength compares with the keel strength of the inner whorls of large forms at the same diameter (small form: Pl. 7, figs. 9c–d; inner whorls of the large form at comparable diameter: Pl. 7, figs. 8b–c). The keel on the body chamber of the large form is relatively very strong (Pl. 7, fig. 10b).

Lateral ornament

The lateral ornament characterising the phragmocone of this species continues on to the body chamber but is, in many cases, slightly modified. Among small forms the lateral nodes of the body chamber become proportionately stronger than on the phragmocone (Pl. 6, figs. 3a–b; Pl. 7, figs. 9a–d). As no body chamber is complete it is not possible to see whether the ornament degenerates near the peristome, as in the cases of mature individuals of many species.

Among the large forms of *H. brightii* the lateral nodes persist on to the body chamber. In two cases there is little modification, OUM J25734 (Pl. 8, fig. 3) and OUM J10221 (not illustrated); in another example, OUM J25724, the body chamber nodes become less raised from the flanks and convexly crescentic, with adjacent nodes merging into one another (Pl. 7, fig. 10a).

Remarks. It is significant that large forms of *H. brightii* which have body chambers preserved, have phragmocones smaller than the mean of the Woodham collection of this species. This emphasises the critical part played by preservation.

Ribbing

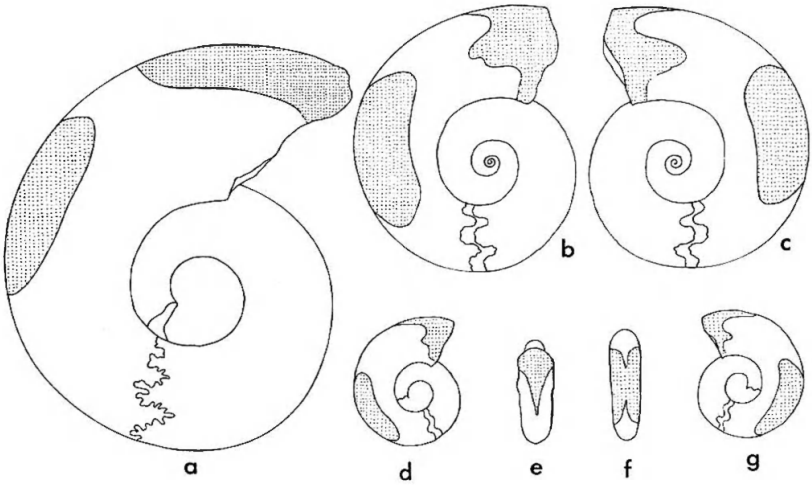
Even the most adapical part of the body chamber of small forms is not ribbed. The body chamber of large forms is more sharply ribbed than the phragmocone (Pl. 7, fig. 10; Pl. 8, fig. 3), but the number of ribs per whorl remains about the same, varying from 60–80. The clay mould of the body chamber of specimen OUM J10221, from Oxford, shows that ribbing of the ventro-lateral area continues to a diameter of at least 35 mm.

Possible muscle scars

On several specimens of both large and small forms, the body chamber is commonly a black colour, as is the phragmocone, but with well-defined areas of golden pyrite. The black/gold junction is generally very sharp. Among several body chambers the golden areas are always in the same relative position and bilaterally symmetrical about the median plane. Two areas are present, both crossing the venter: a ventro-lateral one, normally occurring after one quarter of a whorl of body chamber growth, and a second larger area extending from the umbilical seam across the flank and over the venter. This second area occurs one third to one half a whorl beyond the body chamber/phragmocone junction (Text-fig. 11). Because of the constancy, in shape and position, of these areas, in both

large and small forms, it would appear that this feature is not simply due to the whims of preservation.

Remarks. CRICK (1898) has already speculated that areas such as these are probably related to the musculature of ammonites. The present author is in agreement with this interpretation with respect to the differentiated areas of the body chamber of *H. brightii*. STENZEL (1964, p. K69–70) shows that between the



Text-fig. 11a–g. Possible muscle scars of *Hecticoceras brightii* (PRATT) from the Oxford Clay, Woodham, Buckinghamshire. a, female, (OUM J25724) (see Pl. 7, fig. 9a); b, c, male, (OUM J25698) (see Pl. 6, fig. 3a); d–g, male, (OUM J25739) (see Pl. 7, fig. 7). d, g, lateral views; e, f, ventral views. The stippled area is that of possible muscle attachment. All figs. x 3.

muscles of living *Nautilus* and their point of attachment to the shell of the body chamber, a thin layer of conchiolin is secreted by the epithelium. If a similar layer were formed between the muscles and the shell of ammonites, this may account for a difference in the colour of the pyrite infilling, i. e. the colour of the pyrite being influenced by the composition of the abutting shell/conchiolin layer. Similar differentiated areas have previously been noted on *Creniceras renggeri* (OPPEL) (PALFRAMAN, 1966).

General remarks

One specimen of *H. brightii*, OUM J25692, in which the sutures are not approximated, has a body chamber of two thirds of a whorl in length. The specimen is probably a small form in which phragmocone growth has almost ceased, but in which the final two or three septa have not been secreted. The adoral end of the preserved body chamber is constricted; the specimen is undamaged. This probably indicates that the individual is mature, as constrictions have not previously been encountered at the same diameter among preparations of undamaged specimens of this species.

Coexisting individuals of the genus *Hecticoceras* are to be found among which are large and small forms. "*Ammonites Lonsdalii*" (PRATT) [large form] and "*Ammonites Brightii*" (PRATT)[4] [small form] from the Oxford Clay of Christian Malford, Wiltshire, occur side by side (PRATT, 1841). CALLOMON (1963a), though retaining separate specific names for the two species, interprets them as sexual dimorphs, of which "*A. Brightii*" is considered to be the microconch [m] and "*A. Lonsdalii*" the macroconch [M]. The microconch "species" has an ornate lappetted peristome; the macroconch peristome is simple.

At the present time there is no evidence to prove that the small form of *H. brightii* (as interpreted herein) is lappetted, nor that the large form has a simple peristome. There is, however, abundant evidence to show that among coexisting large and small forms of ammonites which have identical inner whorls, the small form has a more highly ornate peristome than the large form.

Comparison of the two forms examined

Among adult *Hecticoceras brightii* (PRATT), there are large and small forms without intermediates. The protoconch of both forms varies within almost identical limits, as does the diameter of the nepionic constriction. The first $2^1/_2$–3 whorls of both forms are smooth, after which lateral nodes develop at a diameter of 4.8–6.0 mm. in the small form and 4.8–6.9 mm. in the large form. The umbilical area steepens to form an umbilical wall, with a sharp umbilical angle, at a diameter of 4–7 mm. in both forms. At this same diameter, and in both forms, a ventral keel is developed which continues throughout growth. The whorl section of both forms is identical at comparable diameters.

Graphical plots of the W/D, UD/D and HH/D ratios show that the early stages of both forms are identical up to a diameter of about 7 mm., at which size the onset of adulthood in the small forms leads to differing growth proportions, i. e. they deviate from otherwise isometric growth. A similar deviation from isometric growth occurs at the same relative stage of growth, the onset of adulthood, in the large form, but at a greater absolute diameter than in the small form (about 18 mm.).

Only the large form is ribbed, but the diameter at which ribs develop on the phragmocone of the large form is greater than is ever attained by the phragmocone of the small form.

Both forms have identical sutures at comparable diameters. Sutural variation across the venter, in both forms, is very small, as is variation of sutures drawn at the same diameter from three individuals within each form. Sutural approximation in small forms occurs at a diameter of about 7.3 mm. and in the large form at about 18 mm.

The body chamber of large and small forms is at least half a whorl in length and bears a keel and lateral nodes. The body chamber of the large form is ventro-

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[4] This is one of PRATT's syntypes of his species "*Ammonites Brightii*" (1841, pl. VI, fig. 3) reproduced herein (Pl. 8, fig. 7).

laterally ribbed. The number of whorls, from the proseptum, in the small form is 4 1/2–4 3/4, that of the large form at least 5 1/2. There is a "morphological hiatus" (MAKOWSKI, 1962) of at least one whorl between the two forms.

The 'muscle scars' on the body chamber are symmetrical about the venter of both forms and in exactly the same relative positions. Nothing is known about the peristome of either form.

Stratigraphic distribution

England

The type material came from a railway cutting near Christian Malford, Wiltshire. To judge from the other ammonites figured by PRATT (1841), also from this locality, it would appear that the Oxford Clay here is of uppermost Coronatum age, as earlier suggested by CALLOMON (1963a, p. 42). Specimens of *H. brightii* from the Oxford Clay of Peckondale Hill, Yorkshire, are from the Athleta/ Lamberti Zone.

Only two specimens of this species were collected *in situ* at Woodham, Buckinghamshire, both coming from the "Lower Spinosum Clays" [Athleta Zone]. Specimens of *H. brightii* collected from tip heaps were most commonly associated with pyritic nuclei of *Kosmoceras spinosum* (SOWERBY), the latter almost certainly coming from the "Spinosum Clays" [Athleta Zone]. ARKELL (1939, p. 144) recorded seven specimens of this species *(H. brightii)* from Woodham "... in preservation of Bed B [lower "Mariae Clays"]" (loc. cit.). The preservation of finely ornamented oppeliid ammonites from the "Spinosum" and lower "Mariae Clays" of Woodham is, however, very similar. CALLOMON's collecting at Woodham suggests that *H. brightii* is restricted to the "Spinosum Clays" and "Lamberti Limestone" [mainly Lamberti Zone] (CALLOMON, personal communication).

The collection of ammonites recorded by GRENSTED (1954) from the drainage ditch in Charlbury Road, Oxford, indicates a fauna characteristic of the Athleta Zone (ammonite fauna identified by Dr. J. H. CALLOMON).

Other occurrences

The species *H. brightii* is recorded from the Callovian of France (Chaine du Mont-du-Chat) by LEMOINE (1932) and from the Callovian of Chézery by DE TSYTOVITCH (1911). The former author maintains that its zonal range is "Macrocephalus Zone – Mid. Athleta Zone". Forms closely resembling *H. brightii* from Braunen Jura of the Swabian Jura Mountains are figured by QUENSTEDT (1886–7) and similar forms are recorded by LAHAUSEN (1883) from the Rjäsan area of Russia. According to JEANNET (1951), the range of *H. brightii* at Herznach, Switzerland, is Upper Callovian to Middle Oxfordian. In his studies of the ammonite fauna of Kutch, India, SPATH (1928, part. II, p. 121) records only one unidentifiable fragment of "the genus *Brightia*", which probably came from the Athleta Zone.

Remarks. Little is known about the stratigraphic and geographic distribution of *H. brightii*; it appears to be commonest in the Upper Callovian of Europe, but its exact range is not known. One of the problems involved in

establishing the distribution of *H. brightii* concerns its identification. Very many authors give only faunal lists and in many cases *H. brightii* may be reposing under a different name.

Conclusions

Hecticoceras brightii (PRATT) of Woodham and Peckondale Hill exhibits dimorphism: the two forms are identical in their early ontogenetic stages but differ in their "mature" stages. Little is known about the distribution of this species.

The observed dimorphism is tentatively regarded as being sexual in nature. Some taxonomic considerations follow.

Taxonomy of dimorphic ammonites

Taxonomic assignments of members of dimorphic ammonite pairs have been many and varied. ARKELL, although clearly appreciating frequent cases of concomitance of large and small forms with similar inner whorls (1935–48, 1951–59) "... especially in the Middle and Upper Jurassic ..." (1957, p. L87), assigned large and small forms to different taxa, and regarded lappets (characteristic of many small forms) "... as of at least subgeneric rank ..." in his classification (1957, p. L90).

Many authors have used a similar taxonomic procedure to that of ARKELL; among them DJANÉLIDZÉ (1922, p. 28) who suggested that the only practical solution was to include supposed sexual dimorphs in the same genus but not in the same species. The recent works of CALLOMON (1955, 1957, 1963a, 1963b) on sexual dimorphism in ammonites, include a similar taxonomic approach to that of ARKELL (loc. cit.), and DJANÉLIDZÉ (loc. cit.). Partners of a dimorphic pair are included in the same genus but assigned to separate subgenera. The large form of a dimorphic pair has the appellation "macroconch" (designated by "M"), the small form, "microconch" (designated by "m"). Thus, the genus *Aulacostephanus* is divided into four subgenera (CALLOMON, 1963b), two of which are "microconchs" (*Aulacostephanites* and *Xenostephanoides*) and two "macroconchs" (*Aulacostephanoides* and *Xenostephanus*).

This procedure of giving the partners of a dimorphic pair separate names, and using the expressions "macroconch" and "microconch", has also been used by WESTERMANN (1964) as an interim taxonomic solution. In this work the "microconch" also has the symbol '♂' appended, and the "macroconch" '♀' [e. g. *Kumatostephanus (Kumatostephanus)* – Ma. ♀, and *Kumatostephanus (Gerzenites)* – Mi. ♂].

The first author to propose the use of zoological symbols to descriminate between large and small forms of a dimorphic ammonite pair, appears to have been GLANGEAUD (1897). In this work he also advocated the inclusion of the two forms in the same species, "On conserverait celui de l'espèce (mâle ou femelle) le

plus ancien, par exemple, et on le ferait suivre du signe ♂ ou ♀..." (loc. cit., p. 106). This taxonomic procedure has been followed by MAKOWSKI (1962), and PALFRAMAN (1966, 1967), and, in part, by HOWARTH & DONOVAN (1964), COPE (1967), and GUEX (1967), who include the partners of each dimorphic pair in the same species, but distinguish between them by the expressions "macroconch" and "microconch".

Clearly taxonomic procedures for naming dimorphic ammonites are disharmonious. Since the likeliest explanation of the observed dimorphism is sexual, as has been pointed out by many authors, then it would appear to be most logical to include both forms in the same species, using as the specific name the older (or oldest) available [see International Code of Zoological Nomenclature, Article 24, (b), (ii)[5] (1961, p. 27)]. The concept of "monosexuelle Parataxa" used by WESTERMANN (1964) as a temporary measure, an example of which has been given and a nomenclatural technique applied by many, is invalid under the rules of zoological nomenclature. Hence, conspecific dimorphic ammonites are included in the same species by the present writer, the specific name of the pair being the oldest available irrespective of the sex of the "species" from which the name is derived.

A further point to be considered is the question of labelling the different sexes of a dimorphic pair. CALLOMON's (1963a, p. 29) "macroconch" and "microconch" expressions are not wholly satisfactory, especially in the context in which he proposes: "These are morphological terms, and it is quite valid to call a species a 'microconch species' even if it has been found in isolation". As has been shown (PALFRAMAN, 1966), the peristome of the "macroconch" of *Creniceras renggeri* (OPPEL) [= *Taramelliceras richei* (DE LORIOL)] is less ornate than that of the "microconch" of this species. Even so, the peristome of the "macroconch" *C. renggeri* is more ornate than the peristome of some of CALLOMON's "microconchs", as in the case of the "microconch" species *Aulacostephanus (Aulacostephanites)* cf. *eulepidus* and *A. (A.) ebrayoides* (1963b, pl. 32, figs. 1–8 and 9–10, respectively). Not only this, but among many groups the "microconchs" are clearly larger than the "macroconchs" of other groups [some of the "microconchs" figured by DJANÉLIDZÉ (1922) and MAKOWSKI (1962) are very much larger than the "macroconch" *Creniceras renggeri* (OPPEL) (PALFRAMAN, 1966)].

The conclusion to be drawn here, is that, in some cases at least, a dimorphic pair is required in order to assess whether one has a "microconch" or "macroconch" form.

Among dimorphic ammonite pairs, the smaller forms with ornate peristomes have almost always been considered as males by previous authors. The precise function of lappets, a feature of many "microconchs", is not known: whether they were to protect delicate organs, ova, or the young of females, as suggested by ARKELL (1957), as arm supports for swimming organs (GILLET, 1937), or as indicators of gerontism (BUCKMAN & BATHER, 1894), are speculations based on scant evidence. It seems likely that small forms of *Pectinatites* with ventral horns

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[5] Article 24, (b), (ii) states: The law of priority applies when two or more generations, forms, stages, or sexes of a species are named as different taxa; ...

(Cope, 1967, p. 17) may have been males, the horn housing the male sex organ thought to be analogous with the spadix of the extant male *Nautilus*.

The present author considers that palaeontological findings, when interpeted in the light of knowledge of living cephalopods, suggest that the smaller form of a dimorphic ammonite pair is probably the male, and hence tentatively differentiates the partners of such a pair by the use of the zoological symbols ♀ and ♂. It should be understood, therefore, that the use of the male and female symbols by this author in the present context, is a convention implying no more than that this is considered the most likely, rather than proven, interpretation. However, as Callomon (1963a, p. 47) has written "The question of which of a dimorphic pair should be identified with a particular sex . . . lies wholly with the unobservable [and] . . . can never rise above speculation".

Since the labelling of palaeontological material is to produce a useful system, it would seem that to include the partners of a sexually dimorphic ammonite pair in separate taxa, in view of the evidence available, is without basis. It implies that, while many recognise sexual dimorphism in ammonites, the evidence on which it is based is less reliable than that on which the present monomorphic taxonomic system is based.

Perhaps the major reason why many authors do not incorporate the partners of a sexually dimorphic ammonite pair in the same species is the magnitude of the observed dimorphism. If it were as subtle as that suggested by Clarkson (1966) among some Silurian acastid trilobites, or as small as that seen in living *Nautilus* (Willey, 1902), this author has little doubt that dimorphic ammonites would always have been placed in the same species.

Among ammonite groups in which dimorphism has been reported, dimorphic differences (such as absolute size, and the nature of the peristome) are generally appreciable. It is unacceptable to some authors that the great morphological differences between partners of many dimorphic pairs are not expressed in the species binomium as advocated herin. Indeed, the sexual symbol alone (which suffixes the binomium) entirely denotes the dimorphism. Callomon (1963a) and Arkell (1957) would clearly express morphological differences between dimorphic ammonite pairs at a higher taxonomic level, i. e. the subgenus (or higher).

However, in the juvenile stages, the partners of many dimorphic ammonite pairs show no shell differences (Makowski, 1962; Palframan, 1966, 1967). If an immature specimen of a sexually dimorphic species is discovered, and the taxonomic procedure of Callomon is followed, which of two possible names is given to the specimen? Arkell (1939, p. 167) was clearly confronted by such a situation when he examined two nuclei of *Distichoceras bicostatum* (Stahl) which were "... at a stage indistinguishable from *Horioceras baugieri* (D'Orbigny)". According to this author's interpretation (Palframan, 1967), *D. bicostatum* and *H. baugieri* are partners of a dimorphic pair, and both "species" reside under the name of *D. bicostatum*. If specimens are immature, they are labelled *D. bicostatum* juv.; if sexual features are present then the appropriate symbol is used.

Also, assuming sexually dimorphic ammonites arose from sexually monomorphic ancestors, at what degree of morphological difference would the line be

drawn between giving each dimorph a separate name or the same name? If the taxonomic procedure as advocated herein is followed no such difficulty arises.

It is recommended that when describing new ammonite species exhibiting dimorphism, one describes both sexes. The holotype may be based on either sex, but, following COPE's precedent (1967), the present author recommends basing the holotype of the species on the female ("macroconch"), unless for reasons of poor preservation or incomplete females this is not desirable. Also following COPE (loc. cit.), a specimen of the sexual partner of the holotype may be designated paratype (allotype).

Finally, it is hoped that workers on ammonites will bear in mind the concept of sexual dimorphism; it may well be a useful key for suppressing many unreliable and capriciously erected "species", towards a more complete understanding of the pattern of ammonite evolution, and also towards reducing the number of names and taxonomic complexities of this valuable group.

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Explanation of Plates

Plate 6

Magnification x 3 unless otherwise indicated.

Hecticoceras brightii (PRATT), from the Oxford Clay of Woodham, Buckinghamshire, unless otherwise stated.

Fig. 1a–c. Juvenile female (?): protoconch showing proseptum, prosuture, and early siphuncle; (OUM J25731) x 50. a) ventral view; b) lateral view; c) apertural view.

Fig. 2a–d. Female; mature phragmocone (OUM J25697). a) innermost whorls showing nepionic constriction (arrowed) x 20; b) apertural view; c) ventral view; d) lateral view.

Fig. 3a–f. Male; almost complete adult (OUM J25698). a) lateral view, note approximation of sutures and body chamber extending for about half a whorl; b) preparation of phragmocone; c) ventral view; d) apertural view; e–f) preparation of the inner whorls: e) lateral view; f) apertural view, note quadrate whorl section (cf. d).

Fig. 4a–c. Juvenile female (?) (OUM J25689). a) lateral view of immature phragmocone with a quarter of a whorl of body chamber; b) lateral view of a preparation of the inner whorls, note the growth lines on the flanks x 6; c) same as b.

Fig. 5a–c. Male; almost complete specimen with two thirds of a whorl of body chamber (OUM J25692). a) lateral view, note the constriction near the adoral end of the body chamber; b) ventral view; c) apertural view.

Fig. 6a–c. Male (?); phragmocone only (OUM J25695). a) lateral view; b) ventral view; c) apertural view.

Fig. 7a,b. Juvenile male (?); body chamber only (OUM J25730). a) lateral view; b) ventral view.

Fig. 8a,b. Female, from the Oxford Clay, Peckondale Hill, Yorkshire; mature phragmocone (OUM J25747). a) lateral view, note sutural approximation; b) apertural view, note the siphuncle of the penultimate whorl against the impressed area of the final preserved whorl.

Fig. 9a–c. Female, from the Oxford Clay, Peckondale Hill, Yorkshire; phragmocone only (LU 290). a) lateral view; b) ventral view; c) apertural view.

Specimens have been whitened with ammonium chloride except OUM J25731 (fig. 1) which has been whitened with magnesium oxide. – Photographs by the author.

Plate 7

Magnification x 3 unless otherwise indicated.

Hecticoceras brightii (PRATT), from the Oxford Clay of Woodham, Buckinghamshire, unless otherwise stated.

Fig. 1a,b. Male (?); almost complete adult (OUM J25696). a) lateral view; b) ventral view.

Fig. 2a,b. Juvenile female (?); almost complete juvenile with half a whorl of body chamber (OUM J25723). a) lateral view, note the umbilical wall continuing on to the body chamber, and the ventro-lateral ribbing of the most adapical part of the body chamber; b) ventral view.

Fig. 3. Juvenile male (?); specimen with one third of a whorl of body chamber; lateral view (OUM J25721).

Fig. 4. Male; mature phragmocone; lateral view, note approximated sutures (OUM J25700).

Fig. 5a,b. Juvenile; part of body chamber (OUM J25737). a) lateral view; b) ventral view, note extremely pronounced lateral nodes.

Fig. 6a–c. Male from the Oxford Clay, Peckondale Hill, Yorkshire; mature phragmocone (OUM J25740). a) lateral view, note approximated sutures; b) ventral view; c) apertural view.

Fig. 7. Male; almost complete specimen with approximated sutures and about two thirds of a whorl of body chamber; lateral view (OUM J25739).

Fig. 8a–e. Female from the Oxford Clay, Peckondale Hill, Yorkshire; phragmocone only (LU 289). a–c) preparations of the inner whorls: a) lateral view; b) ventral view; c) apertural view. d–e) outer phragmocone whorls: d) lateral view; e) ventral view.

Fig. 9a–d. Male; adult specimen with one third of a whorl of body chamber (OUM J25726). a–b) lateral views, note sutural approximation; c) ventral view; d) apertural view.

Fig. 10a,b. Female; almost complete specimen with half a whorl of body chamber (OUM J25724). a) lateral view, note sharp ventro-lateral ribs of body chamber and degeneration of the phragmocone nodes as they pass on to the body chamber; b) ventral view, note sharp keel.

All specimens have been whitened with ammonium chloride. – Photographs by the author.

Plate 8

Magnification x 3 unless otherwise indicated.

Hecticoceras brightii (PRATT), from the Oxford Clay of Woodham, Buckinghamshire, unless otherwise stated.

Fig. 1a–c. Juvenile female from the Oxford Clay, Peckondale Hill, Yorkshire; phragmocone only (OUM J25741). a) apertural view; b) ventral view; c) lateral view, note the umbilical wall which continues to the end of the preserved phragmocone.

Fig. 2a–e. Female; phragmocone only (OUM J25693). a–b) preparation of the inner whorls: a) lateral view; b) ventral view. c–e) outer phragmocone whorls: c) lateral view; d) ventral view; e) apertural view.

Fig. 3. Juvenile (?) female; incomplete specimen with a quarter of a whorl of body chamber; lateral view, note the well-developed ventro-lateral ribs (OUM J25734).

Fig. 4. Female; phragmocone only; lateral view showing degeneration of the umbilical wall about one whorl before the end of the preserved phragmocone (OUM J20505).

Fig. 5a–c. Female; final half whorl of phragmocone (OUM J25702). a) ventral view; b) apertural view; c) lateral view, note feeble lateral nodes and weak ventro-lateral ribs.

Fig. 6. Female from the Oxford Clay, Christian Malford, Wiltshire; lateral view of syntype figured by PRATT (1841, pl. VI, fig. 4). (BCM C 1804) x 1.

Fig. 7. Crushed oppeliid ammonite from the Oxford Clay, Christian Malford, Wiltshire; lateral view of specimen with lappet (original to PRATT, 1841, pl. VI, fig. 3). (BCM C 1803) x 1.

All specimens have been whitened with ammonium chloride. – Photographs by the author, except figs. 6 and 7.

Discussion

J. H. CALLOMON:

1. Terms "macro-" and "microconch". It may well be that, in some cases at least, a dimorphic pair is required to assess whether a particular specimen is a microconch or macroconch. But in stating that these were purely morphological terms it was not claimed that all ammonites must be automatically classifiable as one or the other. The point is that some forms, e. g. *Creniceras, Mirosphinctes* or *Sutneria* can immediately be recognized as microconchs on purely morphological grounds (the lappets) without reference to any other groups. Moreover, this labelling stays even if opinion as to what constitutes a dimorphic pair changes.

2. Functions of lappets. What is the point of prolonging the discussions of the possible functions of lappets, horns, constrictions and rostra? They came and went, and cannot therefore be encompassed by any simple generalization which is not tautologous.

3. The specific classification of inner whorls of dimorphic species. The problem of what morphospecific name to give an incomplete nucleus at a stage at which dimorphs cannot yet be separated is surely only a special case of the much wider problem of identifying ammonites on their inner whorls generally. If the choice is between only two names, one is lucky. Supposing Dr. PALFRAMAN had collected a single nucleus of a *Creniceras/Taramelliceras* from a new locality in the Renggeri Marls, and, as sometimes happens, all the other ammonites were also nuclei. What would he call it? *C. renggeri, crenatum, dentatum, richei, minax, pseudoculatum, anar, patturatense*...? Yes, but one could tell if one knew from which subzone the specimen came. But to do this one would first have to name one of the other nuclei: and how does one distinguish *Cardioceras leachi, mariae, scarburgense, praecordatum, bukowskii, pavlowi, omphaloides, goliathum*...? Yes, but one could tell if one knew in which subzone one was... Surely the point has been made often enough: a classification of the ammonites based on nuclei is perfectly possible; it would be delightfully simple, wholly uninteresting, and quite wrong.

D. F. B. PALFRAMAN:

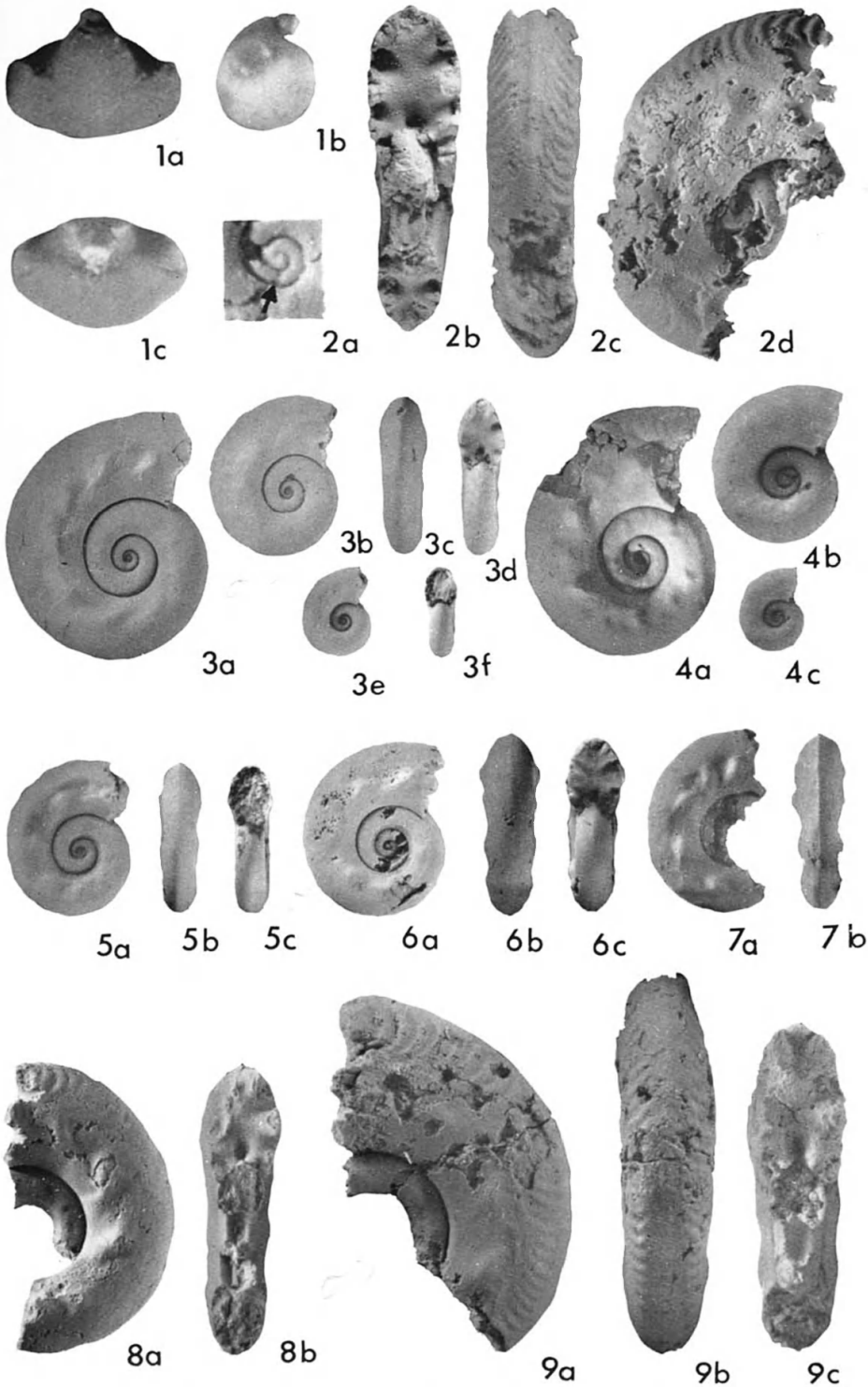
1. The terms "macroconch" and "microconch". My remarks (p. 147) are fully justified: I merely pointed out one of the imperfections of the terms "macroconch" and "microconch". One cannot always reliably label even a complete ammonite as "macroconch"/"microconch" according to the nature of the peristome as my example demonstrates.

2. Function of lappets. Lappets are a feature of the peristome of the small forms among many dimorphic ammonite pairs. Presumably this structure has a function, and a function which may well be related to the sexual activity of the ammonite, and hence is directly relevant to the present discussion. Simply because all small forms do not have lappets does not make a generalisation about them (and I have not made one) or their function tautological.

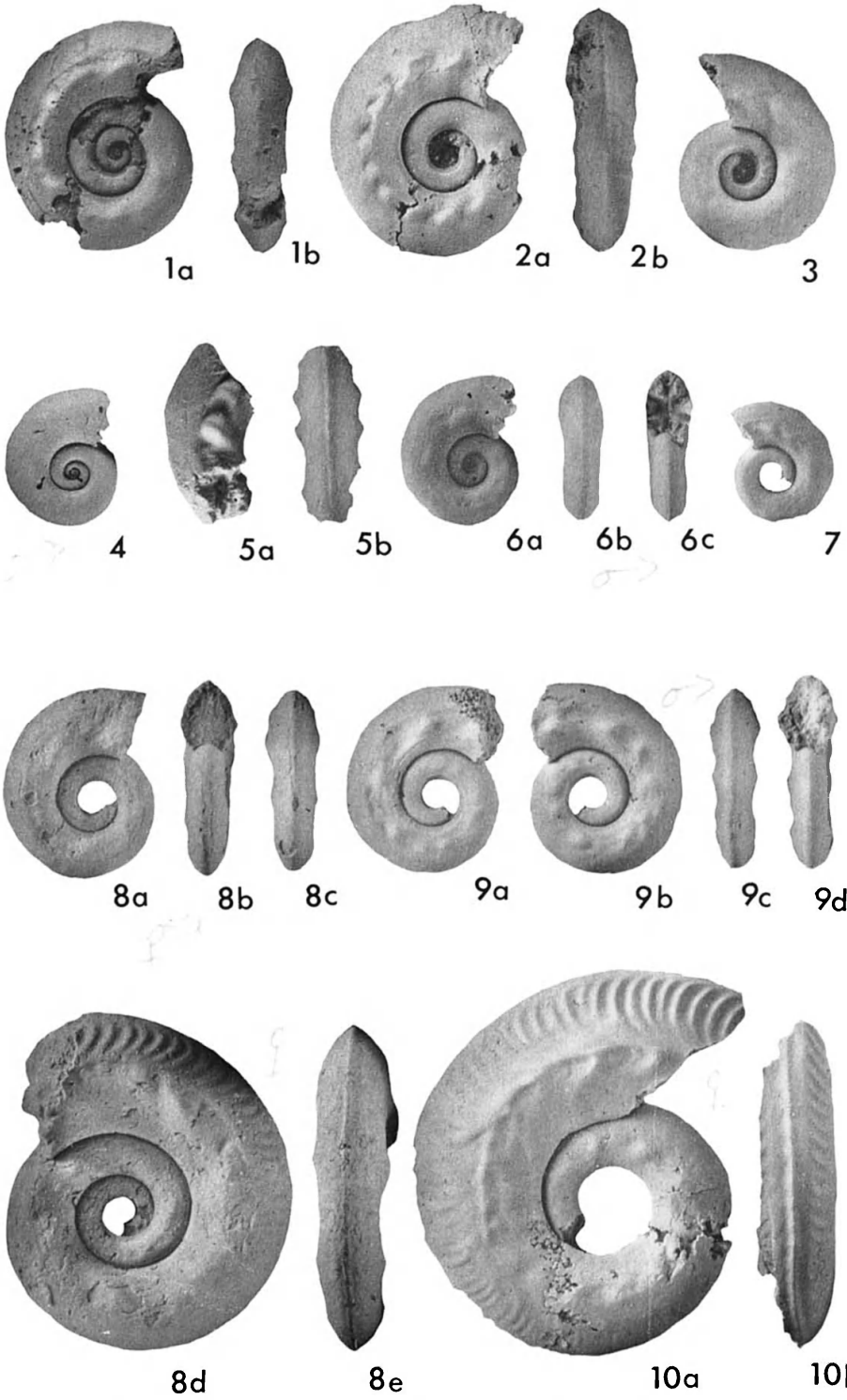
3. The specific classification of the inner whorls of dimorphic species. Not having examined in minute detail the nuclei of other species of *Creniceras/Taramelliceras* I should probably not be able to identify a single nucleus of this group to specific level. However, whatever name I gave to the nucleus would be the same for the nucleus of the large form as for the small. My point is that in the juvenile stages, of the partners of the dimorphic pairs which I have examined at least, there is no difference between the partners: therefore, why try giving separate names to identical nuclei? Some incomplete studies of the nuclei of *Quenstedtoceras mariae* and *Cardioceras scarburgense* show that there are differences between them, even in the size and proportions of the protoconchs.

G. E. G. Westermann:

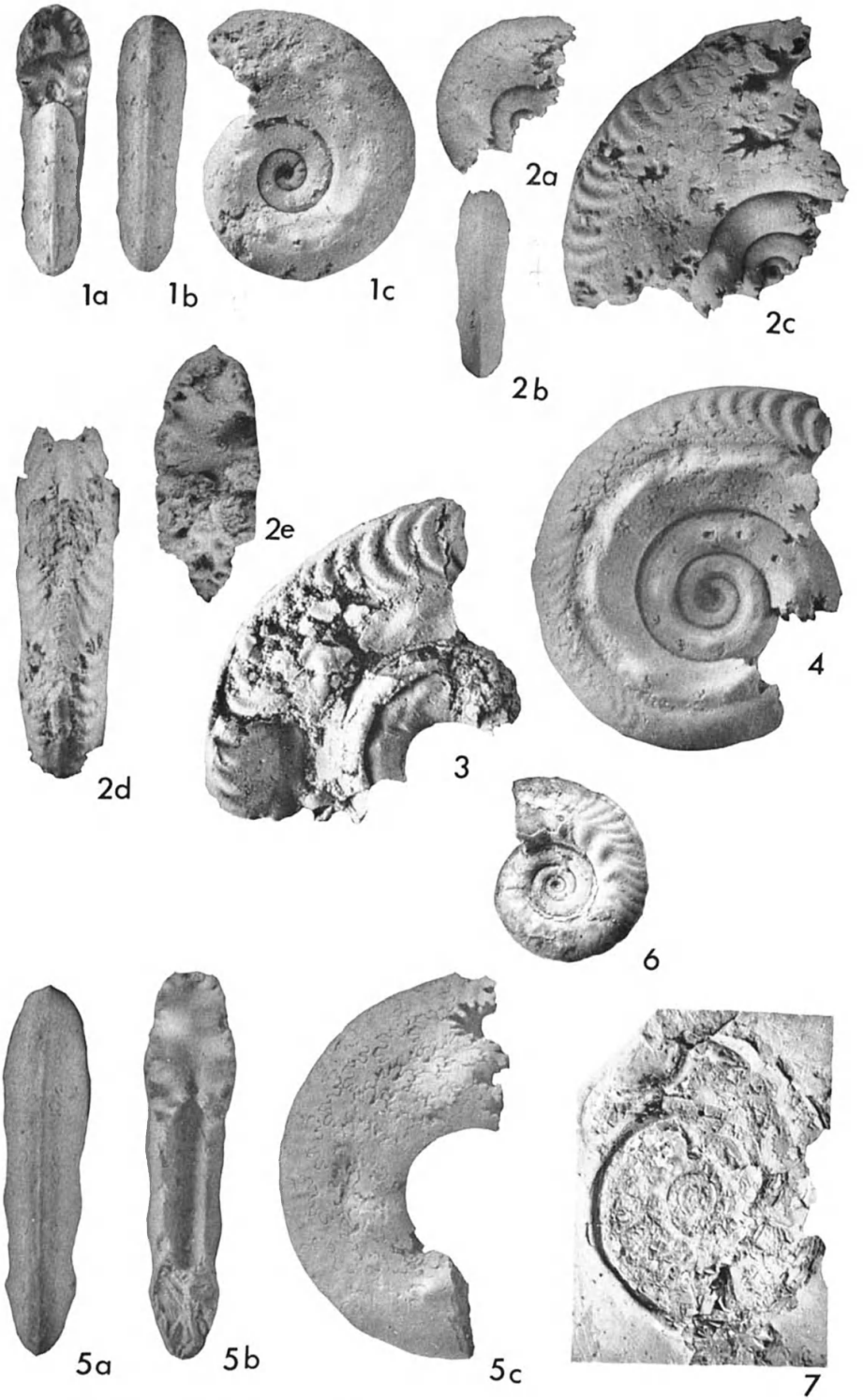
The dispute about whether to use the terms "macroconch" and "microconch" (or their abbreviations) or the sex symbols appears to me partly due to a misunderstanding; both could be employed, each in its context: The descriptive terms 'macroconch/microconch' remain useful in the morphologic description of specimens showing the characteristic body chamber modifications so often discussed; however, in the light of today's knowledge of living cephalopods (p. 18), the symbols of the inferred sex should be suffixed to the formal Linnéan name, at least if both dimorphs are included in the same taxon. Thus, there appears to be an alternative, the use of either suffix depending on the degree of confidence placed on the inference for the sex.



D. F. B. Palframan: Mollusca – Ammonoidea – Jurassic *Hecticoceras*



D. F. B. Palframan: Mollusca – Ammonoidea – Jurassic *Hecticoceras*



D. F. B. Palframan: Mollusca – Ammonoidea – Jurassic *Hecticoceras*