

SEXUAL DIMORPHISM IN JURASSIC AMMONITES

by

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THE BENNETT LECTURES

Dr. F. W. Bennett was Chairman of the Geological Section of the Literary and Philosophical Society for nearly twenty-five years. During this period he was also a member of the Museum's Committee, and the outstanding geological collections that are displayed in the Museum owe not a little to his care and enthusiasm. Dr. Bennett died in 1930 and in the following year his two daughters, the Misses Hilda and Rhoda Bennett, endowed a lectureship in geology at the University College (as it then was) in memory of their father. This was a most happy plan, for it is no accident that Leicester has proved such a fertile breeding-ground for both amateur and professional geologists. There can be few other cities in the world with so much geological variety in their immediate neighbourhood. Within twenty miles of the city centre are to be found rocks of Precambrian, Cambrian, Carboniferous, Permian, Triassic, Jurassic and Quaternary age, igneous rocks of many types, and a wealth of mineral veins. The Department of Geology in the University was founded in 1951; a new building, to be called the Bennett Building, which will house the departments of Geology, Geography and Mathematics, is now in course of erection; and the first of a series of "Bennett Lectures," inaugurated in memory of the wisdom and generosity of Dr. F. W. Bennett, was delivered in December 1961 by Dr. T. G. Vallance of the University of Sidney, on "Spilites". Since then Dr. J. H. Callomon of University College, London, and Dr. N. Kawai of the University of Kyoto, have delivered the second and third lectures, and it is with pleasure that the Society is able to publish Dr. Callomon's lecture in this volume of the *Transactions*, for Dr. Callomon, a Lecturer in the Department of Chemistry in University College, London, is himself a distinguished amateur geologist. It is the purpose of the Bennett Lectures to review aspects of geology which are the subject of current controversy, and Dr. Callomon's lecture on sex in ammonites admirably fulfils our expectations.

P. C. Sylvester-Bradley.

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ABSTRACT. The hypothesis of sexual dimorphism in ammonites is based on the presence of secondary sexual characters, which are thought to be reflected in certain (often considerable) differences in size, peristome and sculpture of their shells. It receives its strongest support from the recognition of what are apparently parallel lineages evolving in pairs with the repeated and simultaneous appearance of new characters in the ornamentation of both members of the pairs. The evidence, especially in the Middle and Upper Jurassic ammonites, is now strongly in support of the hypothesis. Certain difficulties remain, but it is not necessary to postulate any behaviour in ammonites differing from what has already been demonstrated to occur in recent cephalopoda. Taxonomic consequences are briefly considered; no major changes in procedure are called for.

I. INTRODUCTION

The hypothesis that ammonites were sexually dimorphic has a long history, and reached the height of its popularity at the beginning of the present century, notably amongst the French school of palaeontologists. Since then it has suffered something of a decline. Not so, however, the study of ammonites in general. Our knowledge of these cephalopods has made great advances during the last fifty years as more and more material has come to be collected all over the world, and we are now in many cases in a position to deduce the phylogenies of ammonite families over considerable ranges of the geological column with some confidence. In tackling problems of classification and phylogeny it has been my experience that the hypothesis of dimorphism often provided a vital clue, and it is in the hope of reviving

*Delivered in the Department of Geology in the University of Leicester on 31st May 1962.

interest in it that the following brief review has been written. A hypothesis it must always remain, for of the organic parts of ammonites, wholly extinct, we know next to nothing. However it has shown itself to have two important properties: it leads to simplifications in our arrangements of facts; and it has, in my own experience a number of times, predicted new discoveries which were subsequently verified. My own direct knowledge being confined largely to the Middle and Upper Jurassic, the review which follows makes no claim to being exhaustive, and the more general considerations should not be taken necessarily to apply outside this range.

II. HISTORICAL

Among the first to consider the possibility of sexual dimorphism in ammonites appears to have been de Blainville (1840, p. 8) in a short general work, the forerunner of a more comprehensive treatise which never appeared. He quoted no specific examples, but stated that ammonites were almost certainly bisexual, and that, by analogy with the living *Nautilus*, any dimorphism in the hard parts was to be sought in differences of inflation of the body chamber, the female being expected to be the larger.

The first mention of an actual case of dimorphism in ammonites seems to be by d'Orbigny (1847). In describing his *Am. anceps* (pp. 462-3) he distinguishes two types of shells, differing in inflation and ornament, the thicker-whorled forms being the one "que je regarde comme ayant appartenu à des femelles". (However, the distinction he quotes do not coincide with those on the basis of which the genus *Reineckeia* is recognized to be dimorphic today).

In his classical paper of 1869 Waagen made the first attempt at a phylogenetic classification of an ammonite group, in trying to arrange the then known forms of the family Oppeliidae in lineages ('Formenreihen'). He found that there were apparently two such lineages developing in parallel throughout the Middle and Upper Jurassic, and was struck by the great similarities of more or less contemporary members of the two series. Thus, for example, in comparing (p. 235) the parent members *Am. subradiatus* Sowerby and *Am. genicularis* Waagen, he found the nuclei of both to be indistinguishable, becoming differentiated only with increasing age. (It is to be noted however that he neither specified his criterion of age—p. 196—nor considered the shapes of peristomes as systematically significant). He examined (p. 236), but firmly rejected, the idea that his two series were merely dimorphic forms of a single lineage for a number of reasons which will be considered again, with others, below.

A claim to have recognized dimorphism quite generally was made by Reynès (1879, p. 26; but written before 1867—see Donovan 1955). Among the distinguishing features he mentions are differences in sizes of shells similarly ornamented, associated with differences of inflation of the whorls and with minor differences, in some cases, of ornamentation and septal sutures. "In making a general study of the ammonites one is easily convinced that most species have two distinct forms, whenever material is sufficient. To what to attribute this difference . . . if not to sex?" Unfortunately, owing to Reynès' death, the Introduction to his projected monograph was the only part ever to be published, and his remarks were limited to generalities. In the absence of systematic text we have little idea how broad his concept of

species was, and hence whether his diagnosis of dimorphism coincided with present ideas.

Quenstedt in his later years considered the problem, but did not commit himself to a definite opinion. He comments in at least two cases (1886, pp. 445, 560) on the simultaneous occurrence of forms which differ only in size and peristome, the smaller forms bearing lappets never found in the larger.

A succinct exposition of the hypothesis was made by Munier-Chalmas (1892). He selected a group of ammonites which had certain features in common. These he termed "formes scaphitoides". In them, the last whorl was more or less bent back (elliptical coiling); peristomes were equipped with lappets; they were of relatively small size; and the ontogenetic development of the septal sutures was rapidly arrested. These forms were commonly found associated with other forms, closely similar in appearance but of larger size, and which, according to the taxonomic scale of the time, were mostly placed in separate genera. Munier-Chalmas postulated that these two groups were merely a reflection of sexual dimorphism and proceeded to pair off examples, both at generic and specific levels. More generally, he stated that similar dimorphism existed in other, non-scaphitoid, genera, ranging from Lower Bajocian to Neocomian. The small forms he thought to be the males. Later (1897, p. 107) he labelled the small forms "formes statives", and the larger ones "formes progressives"; and added to the general list of genera in which he recognised dimorphism. Other examples were added by Haug (1892, 1897) and Glangeaud (1897), bringing the number of genera to twenty-two; no new principles were introduced, although Glangeaud was led to examine closely the taxonomic value of peristomes in classification. Also, the list now included examples from Lias and Cretaceous and Haug mentioned a previous reference to an example in the Permian. Little of all this was supported by detailed systematic or stratigraphic work, and most of it is now largely outmoded.

Somewhat later, Rollier (1913) found further support for the hypothesis in the Opeleds of the Upper Jurassic, again comparing small lappeted forms with larger companions having simple peristomes. Like Munier-Chalmas he paired off a number of species, but went a stage further to consider the taxonomic and nomenclatural consequences: thus (e.g. p. 269) "*Am. subclausus* Opper est le mâle d'*Ochetoceras canaliculatum* v. Buch, tous deux de l'Argovien inférieur. C'est le nom du mâle qui doit disparaître . . .". The success of such procedure would depend entirely upon the ability to arrange all the ammonite groups in pairs, and in this respect he was rather optimistic, not to say dogmatic.

Rollier was followed by his student Loczy (1915, pp. 276, 349) who claimed success in detecting dimorphism in only one, but very interesting, additional genus: *Phylloceras*. This will be referred to again later.

Thereafter, interest in the whole subject waned. Spath, who, in his time, handled and worked on probably a wider range of ammonites than any other author before him or since, was aware of the theory but almost totally ignored it. Writing of *Distichoceras* and *Horioceras* (1928, p. 92) he says "Rollier . . . like Munier-Chalmas before him, even held that they were merely the female and the male of the same species, but there is little concrete evidence in favour of this view". Roman, in his "Essai des Genera" (1938) makes no mention of the matter at all, and there is but a brief summary,

without references, by Mme. Basse (1952, p. 551) in Piveteau's "Traité de Paléontologie".

The hypothesis was not without its critics, and many objections were raised, some relating to matters of fact, others of theory. Starting with the latter, a number of the objections centred around Munier-Chalmas' morphological diagnosis of males. Thus it was widely realised that lappets were in some way significant, but there was no agreement as to what the significance was. Many authors believed, implicitly or explicitly, that lappets were merely transient features of the growing shells, continually resorbed during growth (e.g. Waagen, 1869, p. 196; Buckman, 1888, p. 36, and afterwards); although this was refuted by Pompeckj (1894) who showed in an exhaustive work that lappets were exclusively features of maturity. Even so, some groups have lappets, others not at all. In those groups having them, lappets were taken by Buckman and Bather (1894) to indicate phylogerontism, ". . . the old age of a race, when it is in a sense retrogressive". The fact that most ammonites do not have lappets at any stage was thought to cast doubt on the theory of dimorphism as a whole. Thus Buckman and Bather, reviewing Munier-Chalmas' paper, asked why there was no reference in it to anything from the Lower Inferior Oolite (in fact there is), or Lias. Were "secondary sexual characters a comparatively latterday Jurassic invention?" Pompeckj (1894, p. 282) in a similar review, raised the same question about Triassic ammonites, in which lappets were unknown. However, the logic of such objections seems questionable, for, outside the limited group which he was considering, Munier-Chalmas never insisted on lappets as an essential or universal sexual character.

Then there were objections called forth by analogies with living cephalopods, especially *Nautilus*, which had guided the earlier authors, e.g. d'Orbigny, and which had led to the general identification of the small, lappeted scaphitoid forms as males. The distinctions was supposed to be between thin whorled (male) and more inflated (female) shells. Against this, Buckman and Bather pointed out that "the thick and thin forms of a "species" are replaced in modern collections by a great number of forms in all stages of compression" although here, as they themselves imply, it all depends on what you mean by "species". Subsequently, opinions as to which sex of *Nautilus* has the larger body-chamber changed, and Coëmme (1917) pointed out that there were in fact living cephalopods of both types, in which either the females (e.g. *Argonauta*) or the males (*Octopus vulgaris*) were the bigger; while in others again, e.g. *Sepia*, secondary sexual characters were inconspicuous. There was therefore no positive guidance to be expected from this direction.

Finally, the hypothesis of dimorphism has been repeatedly rejected on phylogenetic grounds. If a parallel development among a group of species was to be attributed merely to differences of sex, then it seemed that the separate sexes followed their own different evolutionary paths; they started and terminated at different points, and, it was claimed, branched independently. Thus, for instance, although Brinkman (1929) found that all the Kosmoceratids he collected at Peterborough did fall into two sharply divisible groups, small-with-lappets and large-without-lappets, the interpretation of this as a reflection of sexual dimorphism conflicted with the more detailed arrangement of his species into lineages, the supposed objectivity of which he preferred. Arguments based on phylogeny depend, however, on the concept of species used to construct the lineages, and are

at best no less hypothetical than dimorphism; and in many of the cases in which dimorphism has been rejected on grounds of phylogeny, recourse had to be made to other much more dubious concepts, such as "phylogerontism", "short-lived off-shoots", and "convergence" to "explain" parallel courses of development among different groups. This matter will be discussed again below.

Objections based on facts were more concrete, and some, although not insuperable, remain. They were pointed out by most authors, and are usually combinations of, or lie between, two extreme cases:

(a) geographical separation of sexes, in which forms thought to be sexual dimorphs are known from beds of the same age, but are not found together at one locality; and

(b) stratigraphical separation, in which the dimorphs are found at one locality but in closely adjacent strata rather than together.

The second of these might be expected as an immediate corollary of the first. It was considerations of this type which deterred Waagen and Pompeckj, for, even allowing for the vagaries of collection-failure, the relative abundances of apparent males and females in a lineage seemed subject to wide fluctuations.

III. THE PRESENT POSITION: DIAGNOSIS

The present position was briefly summarized on a previous occasion (Callomon 1957). The argument proceeds best in a series of steps based entirely on observation, leaving theory and speculation to the end.

(1) The final stage in the ontogeny of ammonites was one of usually well-defined maturity. It appears that ammonites did not continue to grow uniformly until death but attained a mature stage (often called *senile* in the literature) at which growth slowed down and then stopped. Maturity is usually easily recognizable, indicated by one or more of the following signs:

(a) Uncoiling of the umbilical seam, sometimes with marked contraction of the body-chamber. Munier-Chalmas' scaphitoids, and Pompeckj's "ammonites with abnormal body-chamber" are extreme cases of this, but with a practiced eye it can be discerned even in such regular planulates as the *Perisphinctids*. It is a matter of degree, and in a broad sense all mature ammonites seem to have a more or less "abnormal" body-chamber.

(b) Modification of sculpture near the peristome; usually a coarsening and re- or degeneration of ribbing, but often with terminal constrictions, ventral collars, flares, horns, rostra, lateral lappets etc.

(c) Approximation and degeneration of the last few septal sutures.

Individually these features have of course been well known for a long time and to record them once again may seem trivial; yet strangely their significance as signs of maturity was not always recognized, even by notable authorities like Buckman and Spath. More often than not they may be seen together in the same specimen. The significance of lateral lappets as indications of maturity was often particularly contested. Being found usually in relatively small shells, an alternative hypothesis was preferred in which, on the contrary, lappets were regarded as transient features of juveniles, to be continually resorbed during growth. However, the main force of Pompeckj's argument was that lappets are often found in individuals which at the same time show all the other signs of maturity, confined not solely to

the aperture but extending over considerable portions of whorl. Thus, if resorption was limited to lappets only, large shells should commonly show a succession of extensive "abnormal" growth stages in their inner whorls, which is not the case. Conversely, if resorption extended to whole "abnormal" body-chambers so as to leave no trace on inner whorls, the hypothesis would be of little value, for its correctness or otherwise would be wholly undemonstrable.

(2) On applying the foregoing tests, by far the majority of intact shells in most beds are found to be adults. In fact shells which are complete but demonstrably immature are often quite rare. Thus e.g. Westermann (1954, p. 67) did not find a single example in a collection of "several thousand specimens" of Bajocian Otoitidae; and neither did Brinkmann among 3,000 *Kosmoceras* (1929, p. 43). We may call such assemblages *normal faunas*. In marked contrast are the micromorphic, *abnormal faunas* sometimes found, consisting of swarms of complete but young ammonites, a notable example being the small pyritic faunas of parts of the Oxford Clay. Another case seems to be found in the *Aulacostephanus* of the Lower Kimmeridge Clay of Dorset (Ziegler 1962, p. 154). These abnormal faunas appear often to be reflections of peculiar (bio) facies. The conclusion seems inescapable that ammonites normally spent an appreciable part of their lives in the adult stage; and hence the distinction in the previous section between maturity and senility. Hölder (1955, p. 61, 1960) makes the same point, emphasized by his conclusion that in the material before him (*Taramelliceras*), an appreciable proportion in fact died immature. Another pointer in this direction is the fact that the place in the shell at which septation ceased usually coincides more or less with the onset of the "abnormal" part of the conch: *the size of the fully-grown ammonite was predetermined long before septation ceased*.

(3) In a normal fauna, the end-diameters of complete mature shells seem to be often quite closely defined in any one species or even subgenus. They may be expressed in terms of variability about a mean, and standard deviations of as little as 10% seem not uncommon. The correctness of this statement depends of course on the interpretation of "species", both "horizontally" and "vertically". While there is room for considerable divergence of view in the former, choice in the latter may be almost completely eliminated by taking the statement to apply only to assemblages which are *strictly contemporaneous*. This means in practice preferably assemblages collected from the *same bed in the same area* (and conclusions based, for example, on material brought together from old collections in different museums should be treated in the first instance with caution). This constancy of size in adults is abundantly illustrated in Brinkmann's statistical treatment of *Kosmoceras* (1929), and Arkell's monograph of the Corallian ammonites (1935-48; see also Callomon, 1960, p. 188); and is found even in such dwarfs as Liassic *Cymbites* (Donovan, 1957). I know of several other personally (e.g. Fig. 1), but statistics published so far are few. (See also Howarth, 1959, p. xviii for details of certain Amaltheidae, and Ziegler, 1962, p. 41, for *Aulacostephanus*). Westermann (1956, p. 21) claims that "Variabilität" in the size of ammonites is usually around 50%, but he appears to use the word to denote the full range between the smallest and the largest forms found, which does not seem a very useful quantity to measure as it depends upon the chance properties of a few, extreme individuals even when material is plentiful. Dr. Howarth has pointed out that in a reasonably numerous

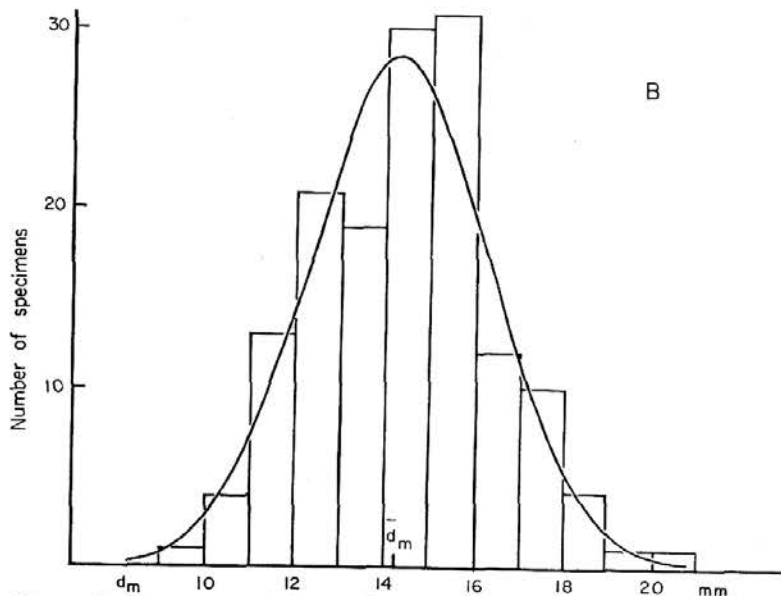
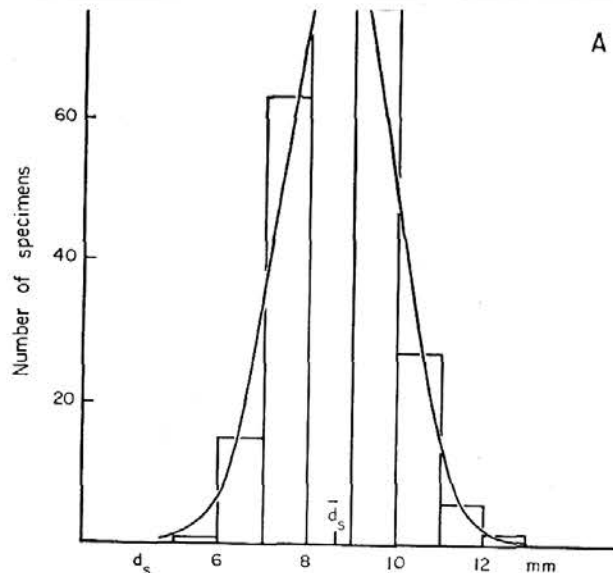


Fig. 1. *Creniceras renggeri* (Oppel), Lower Oxfordian, Mariae Zone of Woodham (Arkell, 1939). A normal assemblage: material wholly mature; highly modified body-chambers.

A. Variation of the diameter d_s at which septation ceased in mature shells, measured in millimeter intervals.

Material:	271 individuals
Mean value, \bar{d}_s :	8.67 mm.
Standard deviation	14.1%

B. Variation of the maximum diameter d_m of mature shells with complete body-chambers, measured in millimeter intervals.

Material	147 individuals
Mean value \bar{d}_m :	14.30 mm.
Standard deviation:	13.8%

Gaussian distribution curves with these values of the standard deviation centred on the mean value obtained have been superposed, normalized arbitrarily.

assemblage assumed to follow a normal distribution, smallest and largest individuals will usually encompass a range of about $m(\text{mean}) \pm 2\sigma$, and that hence Westermann's findings are compatible with a standard deviation σ of 10% or even less. Constancy of size of Palaeozoic species is mentioned by Miller, Furnish and Schindewolf (*Treatise*, 1957, p. L14).

The length of the mature body-chamber is also closely constant in most species, and so the foregoing remarks apply equally well to the diameter of the shell at which septation ceased. This is useful in incomplete material with only part of the body-chamber preserved; or, if the last few septa are approximated etc., when even the whole body-chamber is missing.

(4) When mature shells of a normal, strictly contemporaneous fauna belonging to one genus come to be divided into species, it frequently happens that they fall into two distinct groups. The most obvious distinction is usually the size of the mature shells: those of the one group may be as much as between two and four times as large as the other. Other differences are:

(a) Peristomes: lappets, long rostra etc. if present, are found *only* on the smaller forms, the larger shells having simple sinuous peristomes.

(b) Body-chambers: contraction of the body-chamber with uncoiling of the umbilical seam can occur in both groups, but its extreme scaphitoid manifestation is usually confined to the smaller group.

(c) Ribbing: many ammonites are *variocostates*, i.e. the ribbing on the outer whorl(s) differ markedly in style from that on the inner. This term was introduced by Arkell (1935-48, p. xiii) to describe the morphology of Oxfordian Perisphincts. These include *P. variocostatus* (Buckland) which shows variocostation in extreme form. Variocostate shells have in the past been also described as "hybrid" or "dimorphs", but these terms already have well-defined and distinct meanings. Shells that retain the same style of ribbing throughout, as e.g. *Dactylioceras*, we may term *equicostate*. A special case of variocostation is the common feature of complete loss of ribbing to give a smooth shell. Variocostation is confined to the group of larger forms, the small forms usually retaining their ribbing with but little modification to the end. The ribbing on the smaller forms is also usually rather coarser and stronger than on the larger.

(d) Septal sutures: there seems no clear guide here. The suture-lines of a small form will of course bear little resemblance to the later ones of a form three times larger, although at comparable diameters the suture-lines are usually very similar. There seems to be some evidence that the septa in the smaller forms tend to be spaced relatively more closely together than those in the larger.

(5) Dimorphism may be considered established if these two persistently recognizable groups of shells can be shown to be in some way genetically linked. This appears to be the case, for

(a) inner whorls of both groups are often so similar in every respect as to be practically indistinguishable—the *distinctions arise in maturity*;

(b) new characters, e.g. of ornament, appear in both groups of a genus more or less simultaneously as evolving lineages are followed. Examples are now known (see below) in which this may be observed repeatedly in the same lineage.

Such, then, is the evidence which has to be considered in classification, quite independently of whether we believe in sexual dimorphism in ammonites or not. It was clearly recognised by Arkell, a most keen observer and a strong exponent all his life of a balanced appraisal of all characters in

arriving at a classification of the ammonites; and was incorporated by him, e.g. in his systematic treatment of the Corallian ammonites. It stands out equally clearly in Brinkmann's work on *Kosmoceras* (excluding some of his earlier and later species which in fact fall outside the range from which he so carefully collected at Peterborough). My own introduction to ammonites was largely through collection of Callovian and Oxfordian material, and my ideas were consequently greatly influenced by Arkell and Brinkmann's writings. When apparent dimorphism was then revealed in *Macrocephalites* and other genera, I was led (1955) to a more generalized formulation along the lines outlined above, without at the time myself being aware of much of the past history of the subject. The two groups—large and small forms as differentiated above—were labelled *macroconchs* and *microconchs* respectively. These are morphological terms, and it is quite valid to call a species a "microconch species" even if it has been found in isolation.

These terms include Munier-Chalmas' "formes statives" and "progressives", but are more general, for the diagnoses given above allow the dimorphism to be clearly recognized even in cases such as *Macrocephalites*, which has only mildly "abnormal" body-chambers and simple peristomes in both macro- and microconchs.

Hölder's terms "makrogerontisch" and "mikrogerontisch" (1955, p. 62) have a different meaning, and describe what appear to be genuinely different rates of growth of different individuals in the same morphological species (in his examples, probably macroconchs).

IV. ILLUSTRATIONS AND RECOGNIZABLE EXTENT OF DIMORPHISM

It is impossible to give more than a brief outline here, with selected examples, and what follows should therefore not be interpreted too literally from the systematic point of view but regarded more as a general guide.

We may take as a starting-point the phylogenetic scheme of evolution of the Middle and Upper Jurassic ammonites adopted in the *Treatise* (Arkell, in Arkell, Kummel and Wright, 1957, p. L106-7, fig. 150), separating out, as there, the Phylloceratina and Lytoceratina, and confining our attention to the Ammonitina. Many generic and subgeneric names are currently used to embrace both macro- and microconch species, but we will here use subgenera to include species all of one category or the other only. To avoid ambiguity, any particular species will be interpreted as macro- or microconch wherever possible on the basis of its type-specimen. This includes subgeneric type-species, and hence the interpretation of sub-genera. In the examples that follow, names are arranged in pairs or pairs of groups joined by a hyphen, representing complementary macro- and microconchs, always in that order. Macroconchs are also indicated by the letter [M] in brackets; microconchs by [m].

1. *Hildocerataceae*. The lowest point in the succession at which dimorphism becomes clearly recognizable by the diagnoses given above is in two sub-families in the Upper Toarcian: the Grammocerotinae, so abundantly illustrated in Buckman's monograph (1887-1907), and the Hammatoceratinae, which are thought to be ancestral to the majority of the higher Jurassic Ammonitina.

Fig. 2 shows an example of dimorphic *Grammoceras* from the Toarcian, Thouarsense Zone, of England. Upwards, in the Graphoceratidae, the

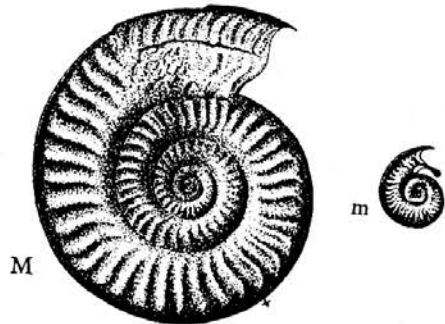


Fig. 2. M: *Grammoceras audax* Buckman (1887-1907, pl. xxviii, fig. 4). m: *Grammoceras arenaceum* (Buckman) (= *Canavarella? arenacea* Buckman, 1887-1907, pl. xxviii, fig. 20). Both specimens from the Striatulum Beds, Cotteswold Sands, Gloucestershire, $\times 0.5$

macro- and microconch forms of *Leioceras opalinum* were amongst the first to be noticed as possible dimorphs (Quenstedt; see also Hoffman, 1913, p. 62), and are still as clear-cut a case as I know. A name available for the macroconch is *Cypholioceras* (Buckman, 1899). Equally clear-cut is the dimorphism in the Murchisonae and Sowerbyi Zones, e.g. *Ludwigia* [M]-*Ludwigina* [m] Buckman; *Graphoceras* [M]-*Ludwigella* [m] Buckman (see Fig. 3) and to judge from Buckman's monograph, it is possible to follow this up through the Middle Bajocian.

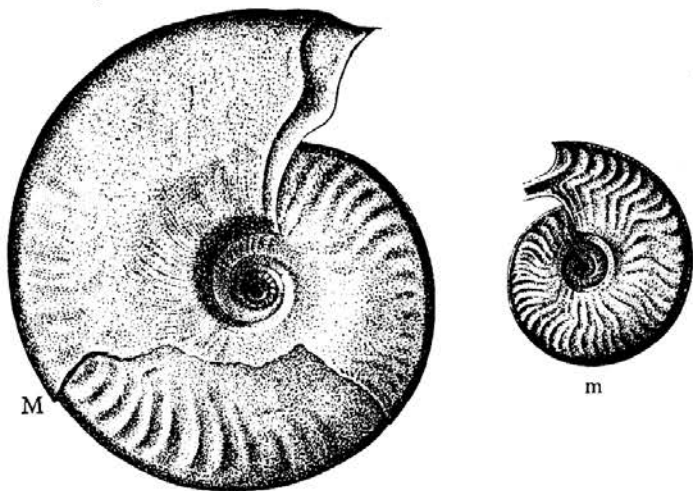


Fig. 3. M: *Graphoceras cavatum* (Buckman) (= *Lioceras concavum* var. *v-scriptum* Buckman, = *Lucya cavata* Buckman, 1887-1909, pl. ix, fig. 1). m: *Ludwigina cornu* (Buckman) (= *Ludwigella cornu* Buckman, 1887-1909, pl. iv, fig. 3). Both specimens from the Concavum Zone, Bradford Abbas. $\times 0.5$

In the closely related Sonniniidae, macro- and microconchs can to some extent also be recognised, e.g. *Witchellia* [M]-*Pelekodites* [m] Buckman (and their synonyms as listed in the *Treatise*), and *Fontannesia* [M]-*Nannina* [m] Buckman. In *Sonninia* itself (i.e., forms with tuberculate inner whorls) there is still some uncertainty, for in this group maturity of growth seems hard to establish beyond doubt. Body-chambers do not markedly uncoil, final septa do not seem to approximate, and for some reason final peristomes seem rarely, if ever, preserved (Oechsle, 1958; Hölder, 1960). Many species are large and variocostate, but of the numerous small figures in Buckman's and Oechsle's monographs some at least give the impression of being adults and not just nuclei.

The Hammatoceratidae are of particular interest because of their position intermediate between Hildoceratid ancestors and the proliferation of Middle Jurassic descendants which then dominate the field up to the Cretaceous. The relation between *Hammatoceras* (macroconch) and *Erycites* (microconch) has been discussed by Donovan (1958, p. 57). There is some doubt in the interpretation of the type-figure of the type-species of *Hammatoceras* itself (*Treatise*, p. L267), but Donovan and Arkell follow most authors in regarding the species as large and variocostate (e.g. *Pachammatoceras* Buckman, *Planammatoceras* Buckman).

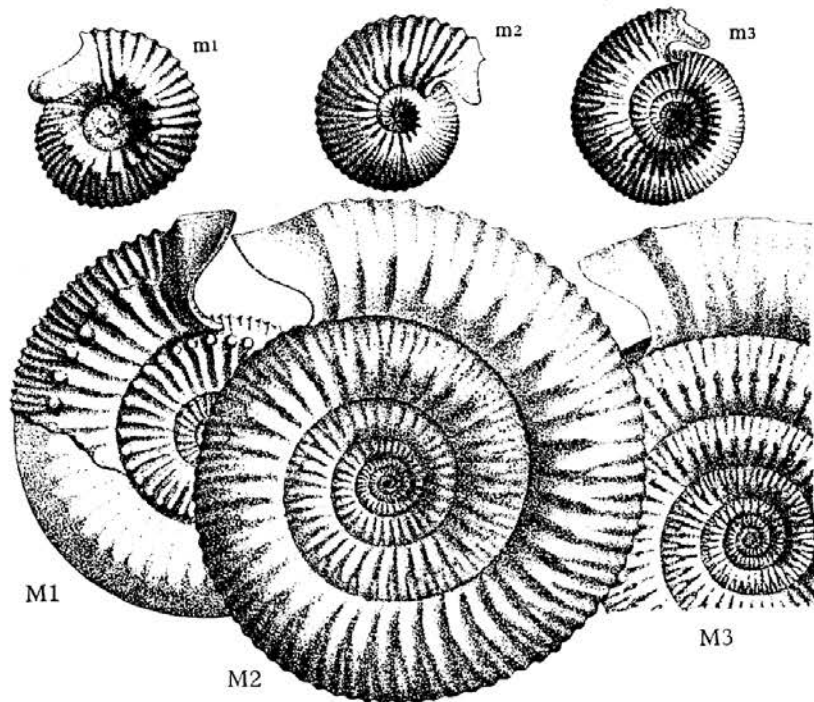


Fig. 4. *Stephanoceras-Otoites*/Normannites. M1: *Amm. Humphriesianus pinguis* Quenstedt, 1886-7, pl. 65, fig. 12. M2: *Amm. Humphriesianus* Quenstedt, *ibid.*, fig. 9. M3: *Amm. Humphriesianus macer* Quenstedt, *ibid.*, fig. 10. Middle Bajocian, Bayeux. m1, 2: *Ammonites contractus* Quenstedt, 1886-7, pl. 64, fig. 16, pl. 65, fig. 1. m3: *Amm. Braikenridgii* Quenstedt, 1886-7, pl. 65, fig. 6. Brown Jura δ , Swabia, $\times 0.5$.

2. *Stephanocerataceae*. The boundary between these and the *Hammatoceratidae* is to some extent arbitrary, but the earliest members of the superfamily, in the Sowerbyi Zone or even earlier, continue to be divisible: *Docidoceras* (*cylindroides*), *Labyrinthoceras*, *Emileia* [M]-*Abbasites*, *Frogdenites*, *Docidoceras* partim (*planulatum*, *biforme* Buck.) [m]. These groups lead upwards into the maze of *Stephanoceratidae*, *Sphaeroceratidae* and *Otoitidae* of the Sauzei-Humphriesianum Zones in the Middle Bajocian, which largely remain to be worked out systematically and of which I can claim no close personal knowledge. However, it seems a safe prediction that they, too, will be generally divisible into complementary macro- and microconchs, for this is already possible in a number of particular cases, e.g. *Stephanoceras* s.s. [M]-*Normannites* [m]. Other forms usually referred to *Stephanoceras* s.l. (*Skirroceras*, *Gibbistephanus* Buckman) have inner whorls practically indistinguishable from *Otoites* (see Fig. 4). The division is clearest where isolated faunas occur at well-defined horizons, as for example, in *Pseudotoites* [M]-*Otoites* [m] of Western Australia (Arkell and Playford, 1954). A well-known example in the Upper Bajocian is *Cadomites* [M]-*Polyplectites* [m], already quoted by Munier-Chalmas (and see Arkell, 1954, p. 81).

In the Middle or Upper Bajocian the *Stephanoceratidae* seemed to branch more than once, to generate several families which withdrew to rather restricted areas (faunal provinces) in which they then evolved independently. As is now well known, this ecological differentiation reached its peak in the Bathonian, and as a result stratigraphic correlation of beds of this age round the world still presents major difficulties today. One group, native to North Africa and Arabia, seemed to revert to the keeled style of earlier ancestors, with the retention of dimorphism. The first stage is the reappearance of a ventral smooth band: *Ermoceras* (*Telermoceras*) [M]-*Kosmermoceras* [m] (Arkell, 1952); and, if Arkell is right, the last stage was *Clydoniceras* [M]-*Delecticeras* [m] of the Upper Bathonian.

In Europe the dominant family were the "bullati" (*Tulitidae*). The position in these is still not quite clear, despite the recent monograph by Arkell; paucity of material, peculiarities of facies, and extremities of form combine to make them difficult to unravel. Macro- and microconchs can however still be detected. In the Bathonian we have *Tulites*, *Morrisiceras* [M]-*Krumbeckia*, *Schwandorfia* [m]; and *Bullatimorphites* [M]-an unnamed form [m] (*A. microstoma* d'Orb.? and spp. aff.; cf. Arkell, 1954, p. 108-9). In the Callovian there is *Kheraiceras* [M]-*Bomburites* [m]. The *Tulitidae* are thought to have given rise to the *Macrocephalitidae*, which suddenly proliferated at the beginning of the Callovian and, except in the Boreal realm, achieved world-wide distribution. The division of *Macrocephalites* into macro- and microconchs was fully dealt with previously (Callomon, 1955) (Fig. 5). They were of special interest in that dimorphism could be clearly detected in forms in which there are no modified peristomes. Macro- and microconchs differ only in size and in the variocostation of the former.

The *Pachyceratidae* are probably also descended from the *Tulitidae* of the Bathonian, and are also clearly dimorphic. In the Middle Callovian there is *Erymnoceras* [M]-*Rollierites* [m]; in the Upper Callovian, *Pachyceras* [M]-*Pachyerymnoceras* [m]. The Oxfordian macroconch is

OK.

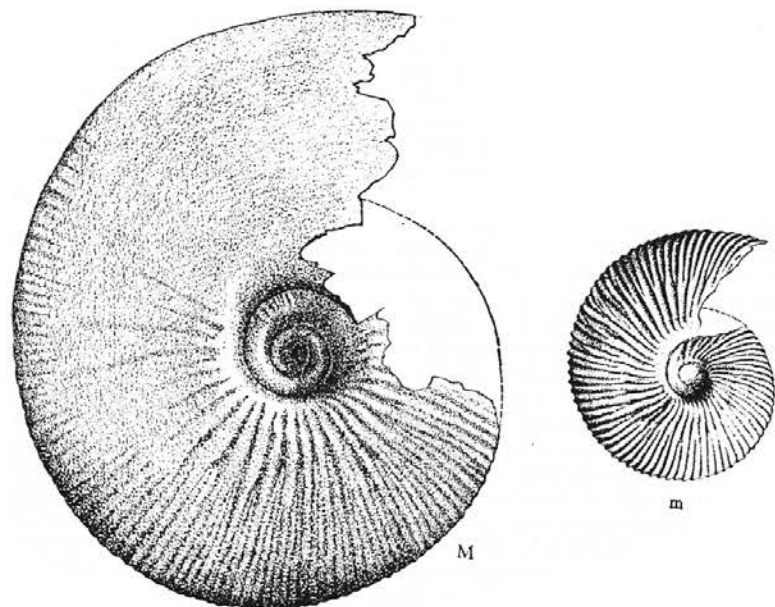


Fig. 5. M: *Macrocephalites* (*Macrocephalites*) cf. *sceptifer* (Buckman) (Jeannot (1951, pl. xxvii). m: *Macrocephalites* (*Dolikephalites*) *Uhligi* Lemoine (Jeannot (1951, pl. xxii, fig. 1) (= *subcompressus* Waagen var.). Herznach, bed A5, Calloviense Zone, Enodatum Subzone, $\times 0.4$.

Tornquistes: the microconchs have yet to be recorded, unless the specimen figured by Haas (1955, pl. 18, figs. 22-25) as "*?Quenstedtoceras ?mariae*" is one of them. The Indo-Tethyan descendants show complete homeomorphism with *Macrocephalites*, and *Mayaites* [M] can be equated with *Epimayaites* [m], *Paryphoceras* [m], and *Dhosaites* [m].

The Boreal realm first became clearly differentiated in about the Upper Bajocian, with the establishment in North America, Russia, Siberia and the Arctic of yet another *Stephanoceratid* offshoot, the great family *Cardioceratidae*. We have seen that when trying to trace lineages from the fossil record the theory of dimorphism introduces a new principle: the lineages must develop in pairs, in parallel, like railway lines. New characters must appear more or less opposite each other. The *Cardioceratidae* provide an elegant demonstration of this, for as result of new collecting by Lauge Koch's expeditions in East Greenland during the summers 1957-58, the macro- and microconch branches of this family can now be followed uninterruptedly over at least 24 full ammonite zones, commencing in what is probably Upper Bajocian with early *Sphaeroceratid*-like ancestors and leading up to *Amoeboceras* of the Lower Kimmeridgian. New features occur in both branches at least eight times. Details of some of the earlier forms will be published in due course (see Callomon 1959), but the succession may be briefly summarized here (Table 1) and is illustrated in Plate I, Figs. A-H. The names and figures have been selected to illustrate leading features and cannot

TABLE I

Horizon	Macroconch	Microconch	Description	
Callovian	?Upper Bajocian (Greenland)	<i>Cranoecephalites</i> group of <i>borealis</i> (Spath)	sphaeroceratid, blunt coarse ribs	
	Bathonian (Arctic)	<i>Cranoecephalites</i> } <i>Arctoecephalites</i> }	involute, ribbing fine and dense	
	Macrocephalus-Jason Zones	<i>Cadoceras</i>	round venter, evolute, sharp umbilical margin	
	Coronatum-Athleta Zones	<i>Longaeviceras</i>	sharp venter, with accentuated secondary ribbing	
	Lamberti Zone	<i>Lamberiticeras</i>	incipient keel	
	Mariae-Cordatum Zones	<i>Cardioceras</i> } <i>Goliathiceras</i> }	keel	
	Plicatilis Zone	<i>Maltoniceras</i>	keel and secondary ribbing differentiated	
	Bimammatum Zone	<i>Priondoceras</i>	isolated crenulate keel	
	Oxfordian	Lower Kimmeridgian	<i>Euprionoceras</i>	
			<i>Amoeboceras</i> s.s.	
		<i>Amoebites</i>		
		<i>Scarburgiceras</i> } <i>Vertebriceras</i> }		
		<i>Cawtoniceras</i>		
		<i>Amoeboceras</i> s.s.		
		<i>Quenstedtoceras</i> s.s. and subgen. nov.		
		<i>Pseudocadoceras</i> partim		
		<i>Pseudocadoceras</i>		
		<i>subgen. nov.?</i>		
		<i>Cranoecephalites</i> group of <i>pygmaeus</i> Donovan		

of course represent the great range of forms to be found together at any one level. The sudden appearance and profusion of the *Cardioceratidae* in Europe in the Calloviense Zone reflects a faunal migration and not an "evolutionary burst", for the evidence from the Arctic shows the family to have had a long and continuous pre-Callovian history. Origin of the *Cardioceratidae* in the *Macrocephalitidae* (a wholly Tethyan family) as usually postulated (cf. *Treatise*, p. L116, after Schindewolf) must definitely be abandoned.

A picture which is even more detailed if not as extensive in time can now also be constructed for the *Kosmoceratidae* (Pl. I, Figs. I-Q). Being more elaborately ornamented than the *Cadoceratinae* they show the appearance of new features more clearly, and are at all stages dimorphic. They too are a boreal family, which made its first appearance in Greenland in the Variable Zone, and spread across Europe like the *Cadoceratinae* in masses two zones later, in the Calloviense Zone. The earliest forms are very much like *Stephanoceras* and the first new character to appear is flattening of the venter with development of sharp ventrolateral edges. Thus in the Variable and *Macrocephalus* Zones we have *Kepplerites* [M]-*Toricelliceras* [m]. Next lateral tubercles develop, and in the Calloviense Zone there is *Govericeras* [M]-*Toricelliceras* [m]. The shells become compressed in *Sigaloceras* [M]-*Gulielmina* [m]. The venter becomes smooth, the ventro-lateral margins develop rows of tubercles, and the flanks a double row of lateral tubercles in the Jason and Coronatum Zones, with *Gulielmites* [M] and *Zugokosmokeras* [M]-*Gulielmiceras* [m]. In some shells the ribbing becomes very widely spaced, strong and coarse, so that in the Coronatum Zone we have the group of *Kosm. pollucium* Teiss [M]-*Spinikosmokeras* (*castor*, *pollux*) [m]. The secondary ribs, which furcate at the lateral tubercles, reunite in pairs at ventro-lateral tubercles ("bundling") to give as fine-ribbed forms in the Lower Athleta Zone, *Lobokosmokeras* (*proniae* etc.) [M]-*K. rimosum* (Quenstedt) [m]; and as coarse-ribbed forms, *Hoplikosmokeras* (*gemmatum* etc.) [M]-*K. aculeatum* group (incl. *Spinikosmokeras acutistriatum* Buckman) [m].

In some shells the secondary ribs fuse in threes or fours at the ventro-lateral margin into elongated clavi, and in the Middle Athleta Zone *Kosmoceras duncani* (Sowerby, neotype, Arkell, 1939, pl. xi, fig. 6) is the macroconch and *K. sp. nov.* (Arkell, 1939, pl. xi, fig. 7; Teisseyre, 1884, pl. iii, fig. 20) is the microconch. The primary and secondary ribbing become divorced, irregular, with widely-spaced ventro-lateral tubercles in the Upper Athleta and Lamberti Zones, with *Kosmoceras* s.s. (*spinosum*) [M]-*K. arkelli* Makowski [m]. Over the middle range (Jason-Lower Athleta Zones) the family has been studied in great detail statistically in the classical work of Brinkmann (1929). He showed that the dimorphic lineages developed in parallel with a most remarkable degree of correlation: the most prominent examples are the sudden decrease in size at the Jason-Coronatum Zone boundary (level 135 cm at Peterborough), and the sudden appearance of "bundling" at the Coronatum-Athleta boundary (level 1093 cm). He dismisses the possibility that this parallel development is merely a reflection of dimorphism (p. 212) because it conflicts with his phylogenetic arrangement of what he considered to be separate species on statistical evidence. Thus, he claimed to have found two lineages of macroconchs—*Zugokosmokeras* and *Kosmoceras* sensu stricto; and three of microconchs—*Gulielmiceras* (his *Anakosmokeras*), with two "short-lived off-shoots", and *Spinikosmokeras* in two branches. I have myself spent a considerable time

studying the Kosmoceratidae, particularly outside the range treated by Brinkmann, and have come to doubt the reality of his phylogenetic scheme. Thus, *Spinikosmokeras* and his "*Kosmoceras sensu stricto*" do have the same ranges; and his statistics do not do justice to the great variability of forms in fact found. There is also reason to doubt whether his treatment was in fact as objective as he claimed; for in describing his "method of work" (p. 27) he says that the order of procedure was to collect a shell and record its horizon; then to ascribe it to *genus and species*; to measure it; and then (in all except a few cases) to throw it away. He also comments that rarely did this preliminary sorting into species present difficulties. Having thus imposed a classification on his material, perhaps it is not surprising that the statistics confirmed it. Most of the shells in fact belong to only two of Brinkmann's subgenera, *Zugokosmokeras* and *Gulielmiceras*; and the impression in the field that the rarer shells of other types belong to quite separate species is certainly hard to resist. However, in cases where material was plentiful, I have found the opposite hypothesis, that all the macroconchs and microconchs in one bed each form a single highly variable and non-Gaussian population, equally hard to refute. Certainly Brinkmann's samples were statistically quite inadequate to do so, and in no case does he establish branching of lineages in terms of actual bi- or polymodal distributions. To my mind the most telling single piece of evidence in favour of the genetic unity of the whole group lies in the onset of bundling of secondary ribs in all forms simultaneously at the base of the Athleta Zone (level 1094 cm. at Peterborough). It is too striking to be coincidental; and if we abandon Brinkmann's phylogenetic scheme the hypothesis of dimorphism does, as he himself points out, provide a simple explanation of the rigorous divisibility of the family at all levels into macro- and microconchs, and the remarkable parallel development occurring among them, both of which are undoubtedly real.

The Kosmoceratidae have until recently commonly been thought to be descendants of the Macrocephalitidae (*Treatise*, fig. 154, after Schindewolf) because of the strong resemblance between certain of the oldest European representatives [*Keplerites kepleri* (Oppel), including *Am. macrocephalus evolutus* (Quenstedt) and *Macrocephalites (Dolikephalites) e.g. typicus* Blake.] However, it is now clear that the resemblance is close only between the macroconch of the Kosmoceratidae and a microconch of the Macrocephalitidae. Once dimorphism is recognized we should infer phylogenetic relationship between two groups only if both dimorphic components show great similarity: this requirement introduces another criterion of continuity when constructing lineages. In the present example phylogenetic relation must be rejected on other grounds as well, stratigraphic, ecological and morphological; but it serves to show how recognition of dimorphism can provide insight into problems of phylogeny.

The Kosmoceratidae also demonstrate another interesting point, that although new characters always ultimately appeared in both dimorphic groups, they did not always do so simultaneously: the microconchs sometimes led the macroconchs by a whole ammonite zone. Thus, the earliest microconchs in the Variable Zone already had tabulate venters, whereas the inner whorls of *Keplerites* acquired them only in the Macrocephalus Zone. Double rows of lateral tubercles, with smooth venter, were present in microconchs already in the Calloviense Zone, whereas *Gulielmites*, by and large,

did not acquire them until the Jason Zone. Similar behaviour is found in other families.

3. *Perisphinctaceae*. The dimorphism of this great superfamily seems to me to be the most impressive, for it is here most consistently discernible and can be followed not only up the main stem but also into the numerous side branches, major and minor, which separated repeatedly, and from faunal province to province.

Unmistakable Perisphinctids first appear in quantity in the Upper Bajocian, and macro- and microconchs are so similar in their inner whorls that even Buckman retained them in the same genera, despite the fact that adults have widely different sizes, macroconchs are varicosate, and microconchs have lappets (*Leptosphinctes* Buckman [M]-*Cleistosphinctes* Arkell [m]). In their range of morphological forms they show extensive homeomorphism with many *Choffatia* of the Upper Bathonian-Lower Callovian; *Perisphinctes* of the Middle-Upper Oxfordian, and *Dorsoplanites* of the Volgian.

The first major side-branch, the Parkinsoniidae, also appear in the Upper Bajocian. The forms of *Garantiana* [M]-*Strenoceras* [m] show an astonishingly complete range of homeomorphs with the Kosmoceratidae (see Douvillé, 1915), with the same phenomenon, that the smooth venter with ventral tubercles is fully developed in the microconchs (*Strenoceras*) a zone earlier (Subfurcatum) than in the macroconchs (*Garantiana*). *Parkinsonia* s.s. itself, a macroconch, is accompanied by lappeted microconchs (Arkell, 1956, pl. xix, fig. 7).

The recent monographs of the Bathonian ammonites clearly reveal dimorphism more or less throughout the Perisphinctidae, in the Zigzagiceratinae, e.g. *Procerites* [M]-*Phaulozigzag* [m] (cf. Arkell, 1958, p. 175) and the even more specialized *Procerozigzag* [M]-*Zigzagiceras* [m]; and in the Pseudoperisphinctinae (cf. Arkell, 1958, pp. 211, 235): *Choffatia* [M]-with *Homeoplanulites* [m], *Siemiradzka* [m] and *Planisphinctes* [m]. It is perhaps significant that Westermann has also come to recognize the dimorphism in these groups (1958, pp. 12-13, 76, 89), thereby reversing his previous opinion on the matter (1954, p. 69).

The Perisphinctidae of the Callovian are in need of systematic revision, but the pattern is clear: *Choffatia* (partim), *Indosphinctes*, *Subgrossowria* and *Poculisphinctes* are macroconchs corresponding to *Grossowria* [m]. Specialized minor offshoots include two similar but probably not closely related groups of Proplanulitinae: in Europe we have *Crassiplanulites* Buckman [M]-*Proplanulites* [m], and in India *Kinkelinceras* [M]-*Hubertoceras* (*hubertus* Spath, 1931, p. 320 and figs.) [m]. A major Callovian side-branch constitutes the Reineckeidae, probably descendants of the Morphoceratidae, as follows: in the Bathonian, *Morphoceras* [M]-*Ebrayiceras* [m]; in the Lower Callovian, *Reineckeia* [M]-*Reineckeites* [m]; and in the Upper Callovian, *Collotia* [M]-*Reineckeites* pars, cf. *R. brasili* (Gérard & Contaut) [m]. The Callovian Perisphinctids are also interesting because they seem to be one of the rare cases in which one can observe at all closely what appears to be genuinely the branching of a lineage: usually our postulates of branching are inferential, based on the more or less sudden appearance of two types of shell where there was only one before. The branching family in this case are the Peltoceratinae, distinguished above all else by the unusual feature of retroradial secondary ribbing. This character appears first in some of the *Choffatia* [M]-*Homeoplanulites* [m]-like forms

of the Lower Callovian (e.g. *P. submutatus* Nikitin). Accompanied by exceedingly evolute ribbing on the inner whorls it dominates in the Perisphinctids of the Middle Callovian of extra-Tethyan Europe and Russia: cf. *Am. convolutus* Quenstedt, 1887, pl. 81, fig. 36 [M]-*Am. convolutus auritulus* Quen. ibid. figs. 30-34 [m]; and even more markedly in the Lower Athleta Zone: *Am. fluctuosus* Pratt [M]-*Am. comptoni* Pratt [m] (refigured by Buckman, 1925, pl. 615; 1924, pl. 455). These forms include the groups of *P. mosquensis* and *scopinensis*. The Peltoceratinae are then distinct from the Middle Athleta to Cordatum Zones: *Peltoceras*, *Peltoceratoides*, *Peltomorphites* [M]-*Rursiceras*, *Parapeltoceras* auctt., *Parawedekindia* [m]. Descendants, e.g. *Gregoryceras* and *Epipeltoceras* are still relatively little known, and the macroconchs appear not yet to have been identified.

The derivation of the Peltoceratinae therefore follows the railway-line analogy closely: dimorphic lineages must branch in pairs. The Peltoceratinae have almost always been regarded as the ancestors of the Aspidoceratinae, mainly because of the strong resemblance between certain quadrate *Peltoceras* and *Euaspidoceras*. The latter appears and becomes common suddenly in the Upper Callovian, Lamberti Zone, and although adult and complete material is now plentiful, in England from the Lamberti-Plicatilis Zones, the usual diagnoses failed until recently to reveal any obvious subdivision into macro- and microconchs. Only careful and prolonged search has brought to light a few specimens which appear to be adult and complete microconchs, although none shows the final peristome. I have collected two specimens from the Lamberti Limestone of Woodham (in which large *Euaspidoceras* abounds); another specimen from an old collection is of the same age, from Normandy; a third, from Oxford Clay, probably Mariae Zone, is in the British Museum (no. C70567), which also has two specimens from the Ball Beds of Yorkshire, Cordatum Zone. They are all small (50 mm.), and except for slight degeneration of the ornament, and in some cases approximation of the final sutures, indistinguishable from inner whorls of the large forms, which usually attain 300 mm. when complete. Perhaps the scarceness of microconchs is only apparent, due to this great similarity and the lack of prominent signs of maturity: large *Aspidoceras* is never variocostate and seems to show very little modification of coiling on the mature body-chamber. The innermost whorls of these early *Euaspidoceras* are hard to distinguish from *Grossouwia* and bear no resemblance to *Peltoceras*. However, they are already tuberculate in the Lamberti Zone, and cannot therefore be descended from Pseudoperisphinctinae via forms like *Mirosphinctes*, as has been suggested, for these flourished later, in the Lower Oxfordian (Haas, 1955).

In the Kimmeridgian, the Aspidoceratinae branch at least once, into a globose branch (*Physodoceras*, *Aspidoceras* s.s.) and a modified planulate branch (*Clambites*, *Hybonotoceras*); and, most interestingly, dimorphism is again recognizable in at least the latter (microconch *Hybonotoceras mundulum* (Oppel) subsp. Berckhemer & Hölder, 1959, p. 33, with lappets). The Aspidoceratinae appear therefore to be dimorphic throughout, the dimorphism being mostly inconspicuous but considerable. It is interesting to note that the only mention which Jeannot (1951) makes of possible dimorphism in any of the rich Callovian-Oxfordian faunas from Herznach which he studied refers to just this family: he distinguishes two varieties of

Euaspidoceras ferrugineum (p. 202) which, he claims, however, differ only in suture line.

There is here then a great contrast between the dimorphism as found in the Aspidoceratinae and either the Perisphinctidae or Peltoceratinae. There are other consistent differences: the Aspidoceratinae are commonly found at all levels (starting in the Lamberti Zone) with thick apyrychi, which are practically unknown in both Perisphinctidae and Peltoceratinae; and they also seem to have consistently thicker tests. All in all, the differences between Aspidoceratinae on the one hand, and Perisphinctidae or Peltoceratinae on the other, outnumber the similarities, and I am not averse to the view, hinted by Spath (1931, p. 593), that Aspidoceratinae were directly derived from Lytoceratidae, via intermediates such as *Aspidoceras antiquum*, *amplexum* and *rollieri* Loczy 1915. This would make them the greatest single innovation in Ammonitina since *Productylioceras* of the Lower Lias. It would also make the "successive replenishment of stock" indicated in fig. 150 of the *Treatise* unnecessary; it is the last remaining alleged case in the Jurassic of what used to be a popular mechanism for joining morphologically similar groups (Salfeld's theory of iterative evolution in part) which however has not stood the test of time. (The Simoceratinae of the *Treatise* contain many extraneous Perisphinctids, e.g. *Nebroditis*).

Continuing upwards with the Perisphinctidae, the situation is again exceptionally clear in the Oxfordian as a result of Arkell's monograph of the English Corallian ammonites (1935-48) (fig. 6). The material from the Plicatilis Zone available to him and collected subsequently (Callomon, 1960) is unusually favourable for study, for it is plentiful—there are now some hundreds of specimens—and well preserved; moreover it is mature and mostly complete, including peristomes. Arkell's classification was based on a conscious attempt to appraise all the characters of the shells, and he was thus led to divide them into macro- and microconchs without any consideration of whether dimorphism was involved. The important conclusions which can be drawn from this work are threefold. Firstly, the division into macro- and microconchs is here quite rigorous, as much so as in Brinkmann's *Kosmoceras*. Secondly, the variability of contemporaneous members of a genus is very great. Thirdly, and as a consequence, the amount of complete material which has to be available before it can be claimed that a contemporaneous population has been fully characterized is enormous: less than a hundred specimens seems scarcely adequate. These points will be discussed further below.

In the Upper Oxfordian ecological fragmentation becomes extreme, making the Perisphinctids proverbially difficult to classify. One branch can be pursued upwards in Northern Europe to *Rasenia* and *Aulacostephanus* of the Kimmeridgian (the latter recently monographed by Ziegler, 1962). Both genera seem to be divisible into large variocostate macroconchs and small lapped microconchs as elsewhere. Thus we have *Zonovia* Sasonov, *Eurasenia* Geyer, *Involuticeras* Salfeld [M]-*Rasenia* s.s. Salfeld, *Prorasenia* Schindewolf, *Rasenioides* Schindewolf [m]; *Aulacostephanoides* Schindewolf, *Aulacostephanus* Tornquist, *Pararasenia* Spath [M]-*Aulacostephanoceras* Ziegler, *Aulacostephanites* Ziegler [m]; *Xenostephanus* Arkell & Callomon [M]-*Xenostephanoides* Arkell & Callomon [m]. However, Ziegler considers (p. 153) and rejects the existence of dimorphism, again on the grounds that it would conflict with his phylogenetic arrangement of species.

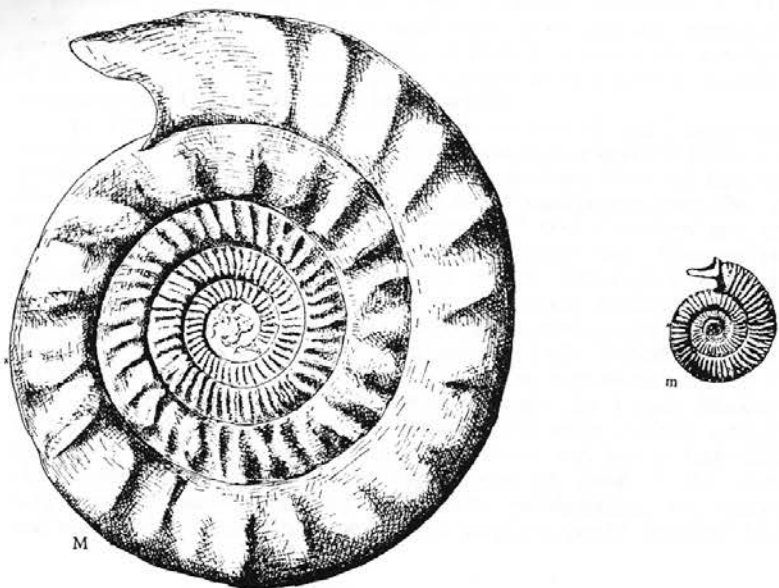


Fig. 6. M: *Perisphinctes (Arisphinctes) ingens* (Young & Bird). Complete adult, figured by Arkell (1935-48), pl. 23, fig. 5; a varicostate macroconch, max. size 483 mm. m: *Perisphinctes (Dichotomosphinctes) rotoides* Ronchadzc. Complete adult, figured by Arkell (1935-48), pl. 16, fig. 1; a microconch with lappet, max. size 98 mm. Commencement of body-chambers shown by crosses. Both specimens from one of the Corallian Shell-beds east of Oxford; Oxfordian, Plicatilis Zone, Antecedens Subzone. Both figures reduced, to $\times 0.2$ original size.

On the other hand, this arrangement leads to what seems to me to be other embarrassments. Ziegler duly notes (p. 145) that many of his species, which he considers to be not directly related, nevertheless show striking similarities. He therefore introduces the concept of evolutionary trend ("Entwicklungstendenz"), a sort of phylogenetic driving-force, which directs successive lineages along similar lines, leading to repeated convergences. There are at least five of these trends: towards increasing size, steepening of umbilical walls, narrowing of the umbilicus, deepening of the ventral groove, and coarsening of the ornament. He cites several examples of the first, lineages starting with small microconchs and terminating with large macroconchs, and discusses specifically the case of *A. autissiodorensis*, macroconch and undoubtedly the most singularly ornamented species of the genus. It is accompanied in the Autissiodorensis Zone by specimens of *A. volgensis*, as close a microconch companion as could be wished for. Yet *volgensis* seems to precede *autissiodorensis* by a zone, so that the latter must have evolved from the former and cannot simply be its dimorphic companion. He makes no comment however on the fact that in each of the cited cases the lineage seems at some point to cross the dotted line: the small, equicostate lappeted forms suddenly lose their lappets and simultaneously change to large varicostates. Finally, when discussing the derivation of *Aulacostephanus* as a

whole from *Rasenia* (p. 143), he remarks on the appearance of the characteristic ventral smooth band in several lineages simultaneously. "Diese Gleichzeitigkeit ist überraschend, erklären lässt sie sich nicht". He concludes that the genus is polyphyletic. The only conclusion I would feel inclined to draw from all these observations is, once again, that all the species and apparently separate lineages were in fact not genetically independent, and if this is admitted, most of the difficulties disappear.

Other examples of Boreal Perisphinctids that may be briefly mentioned include the continuation of what might be regarded as the central stock in the Middle Kimmeridgian, *Sphinctoceras* [M]-*Subdichotomoceras* [m], which leads on to the Dorsoplanitinae, *Dorsoplanites* spp. both macro- and microconchs (illustrated by Spath, 1936, from East Greenland, and widely homeomorphic with *Choffatia*), and the Pavlovids, including the giants of the Portlandian, e.g. *Titanites* [M]-*Crendonites* [m] etc. Even such localized peculiarities as *Virgatites* are duly dimorphic (Michalski, 1890, pl. iii, fig. 1—varicostate macroconch; and pl. i, fig. 1, microconch), as are the even more localized Greenland equivalents (*Epipallasiceras praecox* Spath [M]-*E. pseudaperta* Spath [m]). The microconchs in these later forms no longer have lappets.

In more southerly regions other groups flourished. New features appeared, e.g. the characteristic alternation of single and biplicate ribs of *Idoceras* and *Nebrodités*, both dimorphic (Ziegler, 1959, p. 54), and the virgatome ribbing first seen in *Ataxioceras* (cf. *Am. lictor* Fontannes [M]-*Am. Lothari* Opper [m]), figured together from Crussol by Dumortier and Fontannes, 1876, pl. xii). Donze and Enay (1961, p. 65) mention the

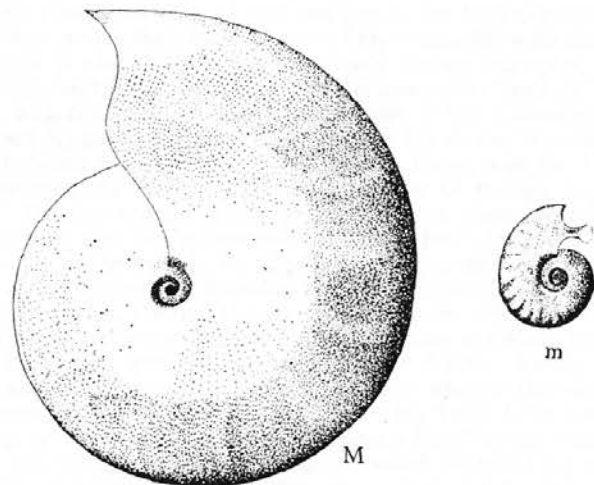


Fig. 7. M: *Oppedia aspidoides* (Opper) Waagen, 1869, pl. 18, fig. 1. Bathonian, near Niort. m: *Oecotraustes serrigerus* Waagen, 1869, pl. 20, fig. 8. Balin. Both specimens from the Aspidoides Zone, $\times 0.5$.

dimorphism in later forms from the Lower Tithonian (*Lithacoceras*). One could go on with examples almost indefinitely: practically any monograph on Perisphinctidae has but to be opened. A point of interest is that a number of Jurassic subfamilies continue into the Cretaceous, and there is no reason to suppose that they then cease to be dimorphic.

4. *Haplocerataceae*. The Opeiliidae are one of the longest-lived branches of Ammonitina. Macro- and microconchs can again be picked out at most levels, although the possible relations between them are here not always as clear as in other families. The family incorporates more than its fair share of oddities with highly "abnormal" body-chambers and the dimorphism seems repeatedly to assume extreme proportions. However, the overall impression that it is consistently present stems again from the observation that new characters of ornament appear repeatedly in both groups. The early forms in the Bajocian (*Opeilia*, *Amblyoxyites*, *Oxycerites* [M]-*Oecotraustes*, *Toxamblyites*, *Cadomoceras* [m]) include Waagen's original pair, *Opeilia subradiata* [M]-*Oecotraustes genicularis* [m] (fig. 7). They persist with minor modifications through the Upper Bajocian-Bathonian, and lead in the Upper Bathonian to more evolute, strongly and coarsely-ribbed *Hecticoceras* of the Callovian and Lower Oxfordian. Unfortunately, the types of the type-species of most of the many subgenera are incomplete, and their status problematical, but macro- and microconchs representing most of the various types of ornament have

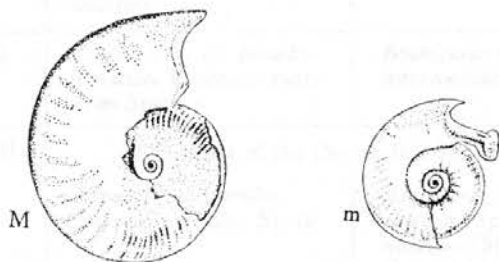


Fig. 8. M: *Hecticoceras lonsdalii* (Pratt), 1842, pl. v, fig. 2. m: *Hecticoceras brightii* (Pratt), 1842, pl. vi, fig. 3. Both specimens from the Lower Oxford Clay, Christian Malford, probably uppermost Coronatum Zone. $\times 0.5$.

been figured, e.g. the "typical" biphlicate forms, *H. punctatum* (Stahl) [M] Douvillé, 1914, pl. i, fig. 1 - *H. (Putealicerias) puteale* (Leckenby) Buckman [m] (type figured in *Treatise*, known with lappets); the nodose forms with fine secondaries: *Am. hecticus nodosus* Quenstedt, 1887, pl. 82, fig. 39 [M]-*Am. hecticus* Quenstedt *ibid.*, figs. 29-30 [m]; and the forms with fine secondaries and no primaries at all: *H. nodosulcatum* (Lahusen) Douvillé, 1914, pl. v, fig. 8 [M]-*Am. hecticus parallelus* Quenstedt, 1887, pl. 82, figs. 24-25. Characteristically, a temporary excursion into bicarination in the Upper Callovian produced two groups, *Distichoceras* [M]-*Horioceras* [m] (fig. 9). In the Oxfordian a whole series of forms appear which repeat extraordinarily closely the morphology of the Bajocian ancestors, except that

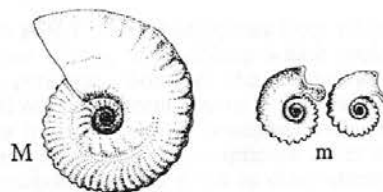


Fig. 9. M: *Distichoceras bicostatum* (Stahl), Quenstedt, 1886-7, pl. 85, fig. 7. m: *Horioceras baugieri* (d'Orbigny), Quenstedt, 1886-7, pl. 85, figs. 17, 18. Spinosum Clays, Swabia, $\times 0.5$.

they are now tricarinate: compare *Am. Arolicus* Oppel (1862-3, pl. 51, fig. 2) [M]-*Am. stenorhynchus* Oppel (pl. 52, fig. 1) [m]. In the Lower Tithonian there is an impressive parallelism between macroconchs (*Taramelliceras*) and microconchs (*Glochiceras*), from, for example, the Solenhofen beds, as also figured by Oppel, including *T. prolithographicum* (Font.) [M]-*G. lithographicum* (Oppel) [m] (see also Berkhemer and Hölder, 1959, p. 86), although Ziegler regards this as yet another case of convergence (1962, p. 145). *Glochiceras*-like forms (*Creniceras*) and *Taramelliceras* (subgenus *Proscaphites*) 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 have the feeling that they are merely dimorphic companions thence throughout the rest of the Upper Jurassic.

5. *Ammonites of the Lias*. The question concerning these remains. I can claim close knowledge of only one group, the Liparoceratidae of the Pliensbachian, and in these the evidence is fully compatible with dimorphism. Three types of shell (considering again only mature examples, here also readily diagnosed) are found: (a) pure sphaerocones; (b) "hybrids" (= variocostates), with capricorn inner whorls and more or less Liparoceratid outer whorls; and (c) pure capricorns. The interest lies in the "hybrids", intermediate between two otherwise highly diverse forms, and the family has figured prominently in the literature in support of various phylogenetic theories. The first was the theory of recapitulation, championed by Hyatt, who concluded that the sphaerocones (a) must have descended from the capricorns (c) via the hybrids (b). Spath (1938) reversed the order, and with the help of the stratigraphical studies and careful collecting of W. D. Lang on the Dorset coast, claimed to have shown that the capricorns forms had evolved from sphaerocone ancestors by proterogenesis in the late Ibex-Davoei Zones. This thesis was however open to grave doubts. Firstly, with the material available to him, Spath could not show whether the variocostates in fact preceded the capricorns as implied in his Table I, for beds of the critical age on the Dorset coast are only poorly fossiliferous, condensed or absent. Most of the early variocostates on which he based his arguments were in old collections from unrecorded sections in the Midlands, particularly Napton-on-the-Hill, Warwickshire, and his dating of these as from the Ibex Zone, Centaurus Subzone was pure supposition unsupported by records. Secondly, both the earliest variocostates, and what Spath regarded as the earliest "true" capricorns, were admittedly preceded by small capricorn-like forms (*Beaniceras*), but the alternative possibility, that variocostates and capricorns could equally well have evolved from these was dismissed by

stating, quite arbitrarily, that *Beaniceras* was a dwarf off-shoot "... which was short-lived and left no descendants" (Spath, 1938, pp. 14, 25). (He himself began to doubt this later, however; see Spath, 1956). Thirdly, having defined, characterized and described all the species, the attempt to arrange them in true phylogenetic order met with defeat, for Spath was forced to write (p. 23): "... whichever way evolution went, the forms must be closely interrelated, and in my opinion, they are a uniform plastic stock that defies classification except on a purely morphological basis".

Much new information has become available in recent years from exposures in the Midlands, in particular the brick-pit at Blockley station, 23 miles S.W. of Napton, and cuttings for the London-Birmingham motorway at Kilsby, 8 miles N.E. of Napton. Four successive faunas can be clearly distinguished. The forms in succession differ only so slightly, but systematically, that there is little doubt that we have a nearly continuous record. From below:

	Sphaerocones and Variocostates	Capricorns
Horizon I	<i>Liparoceras cheltiense</i> (<i>Acanthopleuroceras valdani</i> and spp. common)	<i>Beaniceras centaurus, costatum</i>
Horizon II	<i>Liparoceras cf. pseudo-striatum</i> Trueman, <i>rusticum</i> Spath	<i>Beaniceras aff. centaurus</i> intermediate to <i>luridum</i>
Horizon III	The fauna of the Dorset Belemnite Stone:	
	<i>Liparoceras pseudo-striatum, elegans</i> Spath	<i>Beaniceras luridum</i> vars. <i>atavum</i> (Spath), <i>intermedium</i> (Spath), <i>wrightii</i> (Fucini), <i>involutum</i> (Spath)
Horizon IV	The Napton fauna:	
	<i>Liparoceras kilsbyense</i> Spath, <i>Androgynoceras naptonense</i> (Spath)	<i>Beaniceras luridum</i> (Simpson), <i>Aegoceras sparsicosta</i> (Trueman), aff. <i>maculatum</i> (small)

According to current zonal classification (Dean, Donovan and Howarth, 1961), all are in the Ibx Zone; Horizon I represents the Valdani Subzone, and Horizons II-IV the Luridum Subzone, equivalent roughly to Spath's Maugelesti and Centaurus Subzones, which were however never closely defined.

The picture that emerges is one of two groups, sphaerocones and capricorns, evolving smoothly side by side. The available material of sphaerocones from II—some 150 complete adults—includes not a single "hybrid", nor anything transitional to *Beaniceras*. (The mean adult diameter is 97 mm.

standard deviation 16%). The sphaerocones from III contain a few examples with planulate inner whorls, with ribbing which could in one or two cases be described as capricorn. Some of the *Beaniceras* in the same bed are already close in all respects except size to *A. maculatum* of the Davoei Zone. The sphaerocones from IV (eleven examples) include all degrees of varicosation, five examples having truly capricorn inner whorls.

It becomes necessary at this point to draw attention to two systematic morphological points that Spath wholly ignored, and which make the apparent continuity of phylogenetic development portrayed in his fig. 1 (reproduced in the *Treatise*, p. L115, fig. 153, 1-6 only) misleading. Firstly, adult sizes are once again well-defined, although standard deviations are rather higher than in other cases we have considered. It becomes clear that up to at least the base of the Davoei Zone all the shells again fall into two groups: large sphaerocones and small capricorns. The size-ratio is ca. 4:1. Secondly, the final peristomes of the two groups differ. The sphaerocones terminate with a perfectly straight mouth-border, free of constrictions, appendages or inflexions. The capricorns all terminate with a prolonged rounded ventral rostrum, already cited by Waagen (1869) when founding the genus *Aegoceras*. As far as I can judge from Spath's monograph, and from material I have myself collected, this two-fold divisibility extends upwards throughout the Davoei Zone, and downwards into the Jamesoni Zone (*Beaniceras* can be plausibly led back to *Polymorphites*, as in e.g. Dean, Donovan and Howarth's pl. 68, fig. 4). The important point is that the "hybrids", when adult, appear to be usually as large as pure *Liparoceras* of the same age, and consistently larger than the pure capricorns. The Liparoceratidae may thus be simply arranged in three series:

- Large sphaerocones with simple peristomes: *Liparoceras*, Jamesoni-Margaritatus Zones.
- Large variocostates with simple peristomes: *Liparoceras* pars (*L. naptonense* Spath)-*Androgynoceras* (*A. subcontractum* Spath)-*Oistoceras* pars auctt. (*O. allaeotypum* Trueman). Upper Ibx-lower Margaritatus Zones.
- Small-medium capricorns with ventral rostrum on peristome: *Polymorphites* - *Beaniceras* - *Aegoceras* (= *Androgynoceras* pars auctt., e.g. *A. maculatum*)-*Oistoceras* (*O. figulinum* (Simpson)). Jamesoni-top Davoei Zones.

(It seems useful to revive the name *Aegoceras*, with *Beaniceras* and *Oistoceras* possibly as subgenera; for *Androgynoceras* is much closer to *Liparoceras*, to which it could also be subjugated as subgenus).

Have we here, then, another example of dimorphism, with macroconch sphaerocones and variocostates on the one hand, and capricorn microconchs on the other? Below the Davoei Zone one might well be excused for asking on what grounds *Liparoceras* and the capricorns are thought to be related at all: yet related they clearly are, for the subsequent variocostates show the former to contain the seed of the latter. One might feel that the second appearance of a capricorn stock is coincidental, another case of the homeomorphism so readily invoked elsewhere. However, two other modifications can be observed to occur in parallel. There is a sudden increase in size between faunas II and III of the Ibx Zone as listed above. The sphaerocones increase from 100 to ca. 160 mm. the capricorns simultaneously from ca. 20 mm. to 30-40 mm. More prominently, the modification of the venter

to form *Oistoceras* occurs in both variocostates and capricorns together. Thus, although in a sense both Hyatt and Spath were partly right, the explanation outlined above seems to me to be simpler, more comprehensive, and more in keeping with the facts. It also avoids the inexplicable tangle of Spath's interweaving stocks.

6. *Phylloceratina*, *Lytooceratina*. Surprisingly little, from our present viewpoint, seems to be known about these groups. The nature of the Tethyan point, seems to be known about these groups. The nature of the Tethyan limestones in which they are most often found seems usually to preclude the recovery of complete specimens with peristomes intact. Because of their special positions in the whole scheme of evolution of the ammonites I should place high on the list of priority a thorough investigation in a suitably chosen assemblage from each group of the signs of maturity, and variability of size. The results could not fail to be highly interesting. Dimorphism, if present, may turn out to be slight if Loczy's conclusions concerning two species of *Phylloceras* are sound (1915, pp. 276, 284): *Ph. euphylloides* Till and *Ph. hatzegi* are said to occur each in two varieties, differing only in thickness and shape of constrictions.

V. EVIDENCE FROM RECENT CEPHALOPODA

Many of the objections which have been raised in the past against the theory of sexual dimorphism centre on the extreme variation of the relative numbers of supposed males and females. Thus at certain levels at Peterborough Brinkmann found a 3 to 1 preponderance of Kosmoceratid microconchs (bearing in mind, though, a possible enrichment by selective destruction of large shells due to wave-action); whereas in the *Cranoccephalites pompeckji* beds of East Greenland, yielding a profuse, typically normal fauna, macroconchs preponderate in the ratio of about 100 to 1. These facts, however, do not conflict with a picture in which the ammonites were (?benthic-) nektonic and gregarious, which is to my mind also required to explain the apparent ecology of at least some ammonite species (e.g. Callomon, 1960). They indicate that ammonites changed their immediate habitats at some stage of their development, which is also suggested both by their morphological ontogeny alone (see *Treatise*, p. L14) and the existence of such well-defined normal faunas: and more specifically that the sexes were at least at some stage segregated.

A more general, and implicit rather than explicit, objection in authors' minds has undoubtedly been based on the great difference between forms which the theory unites: dimorphism in the ammonites, if real, is no small effect. Influenced by the slight dimorphism found in the still extant *Nautilus*, effects of comparable magnitude were repeatedly looked for in the ammonites and not found, and the whole theory consequently dismissed.

It is of course fallacious to assume that features of any recent cephalopod must be a guide to the corresponding features in ammonites. It is however valid, when assessing the facts about ammonites, to consider the recent cephalopods as an indication, if not of the actual, at least of the not impossible.

As far as I have been able to find out, relatively little concerning those aspects which interest us here has been published. Judging from shells that I have myself seen, and Willey's account (1902, p. 748), recent *Nautilus* resembles the ammonites (as do Jurassic fossil Nautilids) in attaining a both

morphologically and sexually mature stage with slightly modified body-chamber and approximated final septa; but in adults, sexual dimorphism is slight, the male being the more voluminous (Willey, 1902). (There have been claims to have detected a similar degree of dimorphism in Jurassic Nautili also—Crick, 1898). It would be interesting to have statistics on the final size of mature *Nautilus* shells. The cuttle-fish, to judge from cuttle-bones washed up on the shore, also attain a fairly uniform maximum size; together with many squids, they appear to be gregarious, but otherwise little seems to be known of their habits. The best-known of the modern cephalopods appears to be *Octopus vulgaris* (see e.g. Robson, 1929); but systematic study of all the Octopoda is made difficult by their great variability, and there appears to be no simple relationship between sexual maturity, size and age in either sex. I have been unable to find further substantiation for the statement quoted by Coëmme (1917) that the males were appreciably (five times) bigger than the females. *O. vulgaris* does however seem to provide some evidence of segregation of the sexes (Robson, 1929, p. 16) leading to variations in the relative numbers found in a catch in a given spot.

Similar observations were made by Naef (1923, p. 804) in certain other groups; in particular, the process of spawning in *Abraliopsis scintillans* is preceded by a migration of the wholly segregated, gregarious females to shallow waters, so that catches are entirely free of males.

Extreme sexual dimorphism is found, as is well known, in certain of the Argonautidae: the female of *Argonauta argo* is between 10 and 20 times larger than the male (Naef, 1923, Robson, 1931); and in *Tremoctopus violaceus* the ratio is about the same (Robson, 1931, p. 72). Even so, in the earlier post-larval stages up to sizes approaching that of the fully-grown male, the forms of both sexes are closely similar (Naef, 1923, p. 803).

Thus, the recent cephalopoda cannot be encompassed by any simple generalisation; but the theory of sexual dimorphism in ammonites does not require the postulate of any phenomena not known among living forms. There are certainly no *a priori* grounds for rejecting a dimorphic size-ratio of even five to one.

The question of which of a dimorphic pair should be identified with a particular sex received considerable attention in the past, but as the answer lies wholly with the unobservables it can never rise above speculation. It is in any case quite unimportant for practical purposes.

VI. TAXONOMY

Two arguments that have been adduced to reject the hypothesis of dimorphism are that, if true, apparent species ought at any one level to occur strictly in pairs (which they manifestly do not); and that lineages of species and genera should be found to have evolved strictly in pairs, in parallel (which, as we have seen in a number of cases, has also been claimed not to be the case). There is no denying this conflict, but the question has to be asked, what in fact are these species and genera?

It seems to me that the purposes of a classification are twofold: to label facts, and to arrange them according to their similarities and differences. These two functions are admirably fulfilled by an essentially binomial nomenclature of Linnean type, with rules to impart stability and avoid ambiguity, as in common use. In the case of fossils, the only criteria we

have for the arrangements are the morphology of the hard parts, and there results a classification into *morphological species* and genera which assumes nothing concerning the biology of the former animals.

An entirely separate problem is introduced if we wish to discuss the evolution of the animals, for successive generations are related by breeding habits; and to make progress we have to make resource to some sort of genetic theory, to construct a model to guide us in the arrangements of the facts. We introduce the concept of *genetic species*, defined as the cross-section at any level of the supposedly evolving lineage, and hence comprising at that level all the members of a variable population capable of interbreeding. The questions are, what do genetic species in ammonites look like? Do the morphological species of authors in the literature approach the model of genetic species at all closely? And if not, would it be a practical, or even desirable goal to try to make them do so?

With regard to the second question, my answer would be sceptical: by and large, not very closely. This is based not on a desire to maintain the hypothesis of dimorphism at all cost, but on numerous quite independent grounds. (I am also far from alone in this view: see e.g. the Introduction to "The species concept in palaeontology"; Sylvester-Bradley, 1956). Thus, if the true character of genetic species were at all obvious, the true, final phylogenetic classification of the ammonites would have been deduced long ago. Yet we find leading authorities writing, e.g. of *Beaniceras*, "examination . . . leads to the conviction that . . . all the species (sic) of *Beaniceras* formed one interbreeding population." (Spath, 1938, p. 25). Yet again, of the Corallian ammonites, "The present study has shown again how ammonite material, if sufficiently plentiful, will defeat any attempt at classification, however "natural" and well balanced its author may consider it to be . . . In at least some cases (perhaps all), the possibility of defining species depends on deficiency of material . . ." (Arkell, 1935-48, p. 380). In fact, the common experience that the more the material, the fewer the species; with an equally well-known corollary, that smooth species are few, knobby ones many.

It is also necessary to realise that a lineage of genetic species can diverge and branch with time, but not converge: derivation of a genetic species from its predecessors must be strictly monophyletic. But the results of taxonomic study often lead to the conclusion (e.g. in Arkell's Corallian *Cardioceras* and Ziegler's *Aulacostephanus*) that the genera under consideration are of polyphyletic origin. This can therefore mean only one of two things: either the contained species are genetic species, in which case the *genus* is subjective, morphological, and something whose phylogeny cannot be discussed outside the phylogenies of the individual contained species (unless a whole series of "trends", "off-shoots", "convergences" and coincidences are postulated leading to a complexity which offends against common sense); or that the *species* are in fact morphological, merely subjective components of a single genetic species. In each of three cases that have been studied in detail (*Cardioceras*, *Kosmoceras* and *Aulacostephanus*) I think the second of the two alternatives above applies, for the reasons already discussed: new characters spread repeatedly within short periods of time to all branches ("species") of the genus, indicating that they are in fact genetically not independent, i.e. still members of the same genetic species.

All these points have strong implications on what constituted genetic species in ammonites, in particular their variability. I have slowly come to the conclusion that it was enormous. This conclusion, too, can be supported

on independent grounds, for it becomes almost inescapable whenever one sets out to attempt a classification of a large amount of complete, well-preserved material (measured in hundreds of specimens) of a single family, preferably found together in a single bed and a single locality; and when one frees oneself of all prejudice induced by existing names in the literature. I can mention several examples from personal experience. The most revealing was the fauna of the Pompeckji Zone in East Greenland. This contains a bed a foot or two thick packed with complete adult well-preserved *Cranocephalites* which weather out and lie spread over the ground literally in their thousands. No other ammonites are found—a classical example of what Spath called an "impoverished fauna". He had described wisps of this fauna (1932) collected in small lots by various expeditions at various localities, and found it necessary to use 22 names to characterize it, 9 specific and 13 varietal. Even so, it turns out that he covered only about half of the range of forms found. This stretches from large, globose, smooth, involute shells (homoeomorphs in part of Tethyan *Tulites* or *Morrisiceras*) to much smaller evolute, coarsely-ribbed planulates not unlike some Perisphinctids. Some have a ventral smooth band, others not. When confronted with this profusion of material in Greenland, the choice was clear: every specimen a separate species, or one specific name for the lot. Other examples include the 150 or so *Liparoceras* from a single bed mentioned previously; a splendid collection (C. W. Wright) of uncrushed *Catasigaloceras enodatium* from the Kellaways Rock of South Cave, Yorkshire; all the English Corallian Perisphinctids and Cardioceratidae from each subzone of the Plicatilis Zone (Arkell; Callomon, 1960); and the Cardioceratidae of the Lamberti Zone—a large collection from the Lamberti Limestone of Woodham leaves little doubt that the whole range of macroconchs from discoidal keeled *Quenstedtoceras* (*Lamberticeras*) *lamberti* to cannonball-like *Q. (Eboraceras) grande* Arkell are part of the same genetic species. It is interesting to note that this great variability is also being recognized outside the Jurassic: in Triassic ammonites from the Canadian Arctic (Tozer, 1961, p. 42), and Cretaceous *Neogastrophites* from North America (Reese and Cobban, 1960).

Not only are the genetic species highly variable, but the variability does not seem to be necessarily symmetrical about any sort of average. There seems often to be a tail of fringe-forms, sometimes rather odd-looking and extreme in one or other character of ornament. Sometimes these fringe-forms persist as a minority for long periods of time, as in e.g. Brinkmann's *Kosmoceras* sensu stricto up to the Athleta Zone. At others, they invade the genetic species as a whole, and ultimately become dominant, as with the keel of *Cardioceras*: keeled forms are rare and constitute the "fringe" in *Longaeviceras* of the Athleta Zone. In the Lamberti Zone, they make up perhaps a quarter of the whole assemblage; in the lowest Mariae Zone perhaps a half; and in the upper Mariae Zone non-keeled forms have become a rarity.

Seen against this background, I think the objections against the hypothesis of dimorphism in ammonites based on the non-pairing of "species" lose their force.

Should we strive to cast our taxonomic scale so that specific names are used to denote genetic rather than morphological species? I think not, for practical reasons. The delimitation of genetic species is likely to be successful only when large amounts of material are available; yet if the primary purpose of classification is to label facts, practical palaeontologists often have to name their finds long before their affinities to others are at all clear. In

the first instance, the names provide a language to describe *differences* rather than similarities; and no detectable difference is too minute to be worth recording—the refined state of Jurassic stratigraphy stands as a monument to this.

Similarly, I do not think that we should allow our taxonomy at specific level to be influenced by considerations of possible dimorphism, as Rollier suggested, for practical palaeontologists often have to name species long before subsequent supporting material allows it to be identified as macro- or microconch; and chaos would result if such later judgments, possibly tentative or contested, were allowed to interfere with original specific names. Nevertheless, the morphological facts which allow dimorphism to be recognized are no less worthy of taxonomic recognition than others and to ignore them can lead to confusion, as we have seen in the case of the Liparoceratidae. If we are content to admit a morphological basis for our species, the dimorphism is in my opinion best incorporated at subgeneric level. The subgenus as taxon has many advantages: sub-generic names are easily created, and promoted to or demoted from generic rank without disturbing the original names of species. It might be thought that this gives the subgenus two separate functions: to delimit subgroups of morphologically similar units within a group (genus); and to express a division in one genus which is equally found in other genera. Reflection however shows that basically these two functions are not qualitatively distinct; for the former groups form usually according to their ornament, sculpture, etc. whereas the latter merely according to different features, namely those which we have seen to be signs of maturity. No new taxon is therefore needed; we have stated all that is required if, at the generic point in the classification, we merely draw up two lists of subgenera under the headings of macro- and microconchs. Neither is it necessary to strain to achieve equal numbers opposite each other; for one reason or another one of the dimorphs may cover a far wider range of forms than the other, e.g. when the macroconchs are variocostate, as in the Plicatilis Zone Perisphincts:

macroconchs	microconchs
<i>Perisphinctes</i> s.s.	<i>P. (Dichotomosphinctes)</i>
<i>P. (Arisphinctes)</i>	
<i>(Kraaosphinctes)</i>	
<i>(Liosphinctes)</i>	

There is, however, usually no need to have more than one full generic name at a time; and ammonite nomenclature would stand to gain considerably in simplicity, with no loss in precision, if many of the often bewildering array of generic names used today were reduced back to the rank of subgenera. The scheme outlined above would I think also tend to create more of a balanced and unified taxonomic scale throughout the whole group of ammonoidea than that which exists at present. It is the taxonomic procedure used by Arkell, and broadly adopted in the *Treatise*. It is interesting to see that it has led to the reincarnation at subgeneric level of many names, subsequently fallen into synonymy, unwittingly supplied by Buckman.

This brings us to a most important point concerning type specimens. Every species is potentially the type-species of a genus and is ultimately defined by a single specimen (whether holotype or lectotype). In the past, a deplorable number of species has been created on the basis of immature or insufficiently

complete specimens, which was often understandable and sometimes unavoidable. Endless, and entirely avoidable, confusion has however been created in more modern times by the pernicious practice of making such imperfect species the basis of new genera. Their status as macro- and microconchs is in many cases for ever in doubt; all attempts to resolve the questions were frustrated at birth. Even such well-known genera as *Hecticoceras*, *Kosmoceras*, and *Reineckeia* stand under this cloud and my placings of *Collotia* and *Scarburgiceras* in the examples of section IV above do not follow unambiguously from type-specimens.

I should like therefore to end with a number of pleas to authors: firstly, to restrict the use of new names for ammonite genera and species to material which is sufficiently complete so that a possible question of macro- and microconch is not left in doubt; secondly, when figuring or describing any material, to indicate on the figure or in the legend the point of commencement of the body-chamber, if any; thirdly, to examine such material and state, if possible, whether it is mature or not; and fourthly, when describing plentiful material, to quote data of relative numbers of mature individuals, their maximum sizes and septate diameters etc., even of unfigured specimens. The value of so much of the older literature would have been often enhanced if attention had always been paid to these points.

VII. CONCLUSION

I have tried to show in this brief review that the theory of sexual dimorphism in ammonites has a long history, that the evidence on which it is based has grown rather than melted away, and in many Jurassic ammonites is now very strong. Its recognition leads to simplification and greater order in classification. Much remains to be done; and if nothing else, the theory shows up many places of weakness in the record, places where systematic work is urgently needed.

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EXPLANATION TO PLATE I

(All figures $\times 0.4$)Figs. A—H, *Cardioceratidae*?UPPER BAJOCIAN: *Borealis* Zone

- A. *Cranocephalites borealis* (Spath) a. *Cranocephalites pygmaeus* (Donovan)

BATHONIAN: Pompeckji Zone

- B. *Cranocephalites pompeckji* (Madsen) b. *Cranocephalites* sp. nov.

BATHONIAN: *Nudus* Zone

- C. *Arctocephalites arcticus* (Newton & Teall) c. *Arctocephalites* sp. nov.

LOWER CALLOVIAN: *Calloviense* Zone

- D. *Cadoceras* (*Cadoceras*) aff. *elatmae* Nikitin d. *Cadoceras* (*Pseudocadoceras*) sp. aff. *laminatum* Buckman

UPPER CALLOVIAN: *Lamberti* Zone

- E. *Quenstedtoceras* (*Lamberticeras*) *lamberti* (Sowerby) e. *Quenstedtoceras* (?*Quenstedtoceras*) *gallicum* Arkell

OXFORDIAN: *Plicatilis* Zone

- F. *Cardioceras* (*Cardioceras*) *highmoori* Arkell f. *Cardioceras* (*Subvertebriceras*) *densiplicatum* Boden

OXFORDIAN: *Decipiens* Zone (incl. *Alternans* Zone)

- G. *Amoeboceras* (*Prionodoceras*) *glosense* (Bigot & Brasil) g. *Amoeboceras* (*Amoeboceras*) aff. *alternans* (v. Buch)

LOWER KIMMERIDGIAN: *Mutabilis*-*Pseudomutabilis* Zones

- H. *Amoeboceras* (*Euprionoceras*) *kochi* Spath h. *Amoeboceras* (*Amoebites*) cf. *elegans* Spath

Details: the figures are based on the following:—A: Callomon, 1959, pl. xvii, fig. 1; E. Greenland. a: *Arctocephalites* (*Cranocephalites*) *kochi* sp. nov. var. *pygmaeus* nov. Donovan, 1953, pl. 16, fig. 5a; E. Greenland. B: *Cranocephalites vulgaris* sp. nov. Spath, 1932, pl. 1, fig. 4a; E. Greenland. b: author's coll. no. 1176; E. Greenland. C: *ibid.*, no. 1068; E. Greenland. c: *ibid.*, no. 1002. D: type of *Cadoceras rubrum* Spath, 1932, p. 63, B.M. no. 33591; Kellaways Rock, Yorkshire, England. d: author's coll.; Kellaways Rock, Wiltshire. E: *ibid.*, Woodham, England. e: *ibid.*, Weymouth. Rostra of these forms are well illustrated by Quenstedt, 1887, pl. 90, figs. 1, 2. F: Arkell, 1935-48, pl. xlvi. fig. 3; Corallian, Wiltshire. f: Arkell, 1935-48, pl. liii, fig. 7; Corallian, E. Scotland. G: B.M. no. 89070; Drift, Essex. g: Sokolov, 1912, p. ii, fig. 7; from N. Russia, but also known in England. H: holotype, Spath, 1935, pl. v, fig. 2; E. Greenland. h: Spath, 1935, pl. 3, fig. 1, (but see also pl. 5, fig. 4); E. Greenland.

All figures by the author.

Figs. I—Q, *Kosmoceras*

MACROCEPHALUS ZONE

- I. *Kepplerites keppleri* (Oppel) i. *Toricelliceras* sp.

CALLOVIENSE ZONE

- J. *Sigaloceras calloviense* (Sowerby) j. *Gulielmina quinqueplicata* Buckman

JASON ZONE

- K. *Kosmoceras* (*Gulielmites*) *medea* Callomon k. *Kosmoceras* (*Gulielmiceras*) *gulielmi* (Sow.) anterior Brinkmann
L. *K.* (*Gulielmites*) *jason* (Reinecke) l. *K.* (*Gulielmiceras*) *gulielmi* (Sow.)

CORONATUM ZONE, OBDUCTUM SUBZONE

- M. *K.* (*Zugokosmokeras*) *obductum* (Buckman) m. *K.* (*Gulielmiceras*) *gulielmi* (Sow.) var.

GROSSOUVREI SUBZONE

- N. *K.* (*Zugokosmokeras*) *obductum* (Buckman) posterior Brinkmann n. *K.* (*Gulielmiceras*) *gulielmi* (Sow.) var.
O. *K.* (*Zugokosmokeras*) *grossouvrei* (Douville) o. *K.* (*Gulielmiceras*) aff. *gulielmi* (Sow.)

Lower ATHLETA ZONE

- P. *K.* (*Lobokosmokeras*) *phaeinum* (Buckman) p. *K.* (*Spinikosmokeras*) *acutistriatum* Buckman

Middle ATHLETA ZONE

- Q. *K.* (*Kosmoceras*) *gemmatum* (Phillips) var. q. *K.* (*Spinikosmokeras*) aff. *transitionis* (Nikitin)

Details: I, i: *Amm. macrocephalus evolutus* Quenstedt, 1886-7, pl. 77, fig. 1, pl. 76, fig. 3, Macrocephalenoollit, Swabia. J, j: Brinkmann, 1929, pl. iv, figs. 1, 2; Kellaways Rock, Wiltshire. K: *Kosmoceras* (*Zugokosmokeras*) *enodatum posterior* Brinkmann, 1929, pl. ii, fig. 1; Peterborough, level 30 cms. k: *ibid.*, pl. iii, fig. 1; Peterborough, level 11 cms., which is strictly speaking still in the Enodatum Subzone of the Calloviense Zone. L, l: *ibid.*, pl. ii, fig. 2, pl. iii, fig. 2; Peterborough, levels 132 and 83 cms. M, m: *ibid.*, pl. ii, fig. 3, pl. iii, fig. 3; Peterborough, levels 185 and 170 cms. N, n: *ibid.*, pl. ii, fig. 4, pl. iii, fig. 4; Peterborough, levels 560 and 540 cms. O, o: *ibid.*, pl. ii, fig. 6, pl. iii, fig. 6; Peterborough, levels 992 and 1086 cms. P: *Kosmoceras* (*Zugokosmokeras*) *proniae duplicicosta* Brinkmann, 1929, pl. ii, fig. 7; Peterborough, level 1291 cms. *K. proniae* differs in becoming smooth on the outer whorl; it occurs in the middle Athleta Zone. p: *Amm. Elizabethae* Quenstedt, 1886-7, pl. 83, fig. 27, from the Acutistriatum Band at Christian Malford, Wiltshire. Q: Brinkmann, 1929, pl. iv, fig. 4; Hackness Rock, Scarborough. q: *ibid.*, pl. iv, fig. 6; Popilani; = *Kosm. transitionis* Krenkel non Nikitin, occurring in England in the Middle Athleta Zone.

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