THE EVOLUTION OF THE JURASSIC AMMONITE FAMILY CARDIOCERATIDAE

by J. H. CALLOMON

ABSTRACT. The beginnings of the Jurassic ammonite family Cardioceratidae can be traced back rather precisely to the sudden colonization of a largely land-locked Boreal Sea devoid of ammonites by North Pacific *Sphaeroceras* (*Defonticeras*) in the Upper Bajocian. Thereafter the evolution of the family can be followed in great detail up to its equally abrupt extinction at the top of the Lower Kimmeridgian (*sensu anglico*). Over a hundred successive assemblages have been recognized, spanning some four and a half stages, twenty-eight standard ammonite zones and sixty-two subzones, equivalent on average to time-intervals of perhaps 250,000 years. Material at most levels is sufficiently abundant to delineate intraspecific variability and dimorphism. Both vary with time and can be very large. They point strongly to an important conclusion, that the assemblages found at any one level and place are monospecific. Morphological overlap between successive assemblages then identifies phyletic lineages. Evolution was on the whole gradualistic, with noise, although the principal lineage can be seen to have undergone phylogenetic division at least twice, followed by a major geographic migration of one or both branches. At other times, considerable migrations, which could be geologically instantaneous, did not lead to phylogenetic speciation. The habitat of the family remained broadly Boreal throughout, local endemisms being infrequent and short-lived. Morphologically, the family evolved through almost the complete spectrum of coiling and sculpture to be found in ammonites as a whole, excluding heteromorphs. The nature of the selection-pressure, if any, remains totally obscure.

An appendix by Callomon and Birkelund describes three new taxa: *Arcticoceras cranocephaloide*, *Cadoceras apertum*, and *C. nordenskjoeldi*.

THE profusion and diversity of the Jurassic ammonites, and the rapidity with which they changed with time, have made them favourite guide-fossils for chronostratigraphy since the time of d'Orbigny and Oppel. They have given us a finesse of chronology that has few rivals. The realization that, conversely, this implied rapid evolution in the Darwinian sense, and that the ammonites might thus provide particularly favourable opportunities for evolutionary studies, was not long in following the appearance of the *Origin of Species*. Yet despite the enormous amount of activity in the years since, the impact of the ammonite record on our modern views of evolution as a whole has so far been muted.

The primary task is to arrange the fossils into time-ordered sequences that can be plausibly identified as evolutionary lineages. There arose almost simultaneously two fundamentally different approaches to this problem. The first was espoused by Waagen (1869), biostratigrapher and pupil of Oppel, who stressed the need to collect material carefully bed by bed, as closely together as possible, to the point at which morphological overlap between successive assemblages makes lineal, genetic relationship probable (p. 185). The second was followed by Hyatt (1866, 1889; see review by Donovan 1973), pupil of Agassiz, who was much impressed by ideas deriving from the study of living organisms, particularly vertebrates: that ontogeny of the individual recapitulates the phylogeny of its ancestors (palingenesis). Theories based on such hypotheses have the great attraction that they circumvent the laborious step of detailed collecting. It suffices to recognize the appropriate biogenetic law, and dissection of individuals then allows them to be arranged in phyletic order. As more and more stratigraphical information came to hand, it was a trivial matter to modify, add to, or even reverse the relevant 'law' (proterogenesis); the teleological pursuit of an irreversible evolutionary trend remained, however, undiminished. While inflating the literature, all this did little to fulfil the earlier promises; and in his discussion of evolution in the ammonoid volume of the *Treatise*, Arkell (1957, p. L113) found himself able to cite only four examples of Jurassic lineages at the species-group level as illustration (Liparoceratidae, Amaltheidae, Macrocephalitidae-

Kosmoceratidae, and Macrocephalitidae–Cardioceratidae). Even these cannot survive without more or less serious modification.

Since that time there has been great progress, based almost entirely on the Waagenian prescription of careful field-work. The comprehensive phylogenetic classification at suprageneric level of the Jurassic ammonites, at least, can now be viewed with some confidence (Donovan *et al.* 1981), and many of the uncertainties in the *Treatise* of 1957 involving relationships within and between family-group taxa that could at the time only be regarded as cryptogenic or polyphyletic have been resolved. At the level of the basic unit of phylogeny, the evolving species, the picture still seems rather less certain, however. There have been numerous highly detailed, monographic studies of individual families based largely on carefully collected new material, often running into thousands of specimens. The list, by no means exhaustive, includes in the Jurassic the Glochiceratidae (Ziegler 1958), the Aulacostephaninae (Ziegler 1962), Graphoceratidae (Spiegler 1966, phylogeny reproduced in Lehmann 1976, 1981, fig. 65), Pectinatitinae (Cope 1967), Oppeliidae (Elmi 1967), Lithacoceratinae (Zeiss 1968), Zigzagiceratinae and Pseudoperisphinctinae (Mangold 1971), Berriasellinae (Le Hégarat 1973), Macrocephalitidae (Thierry 1978), and Reineckeiidae (Cariou 1980). Although all members of but four closely related superfamilies having a common root in the Toarcian, no general conclusions concerning ammonite evolution seem to have emerged. About all these groups have in common is a bewildering and apparently random complexity: not so much a family tree as a family bush. Is it true, or still an artefact of taxonomy?

In marked contrast stands another family about whose history much has been learned in recent years, the Cardioceratidae. The circumstances of its distribution make it perhaps an exceptionally favourable candidate for evolutionary studies. It was restricted during much of its career to a circum-polar Boreal habitat in which it was often the sole ammonoid occupant, and over most of which it left abundant remains. The record can therefore be sampled closely in time and widely in space, largely unobscured by the presence of other groups that might confuse through homeomorphisms or rapidly fluctuating abundances. Conversely, it gives unusually clear insights into the basic problems: what does the fossil record of the fundamental unit of evolution, the ammonite biospecies, look like? Hence, what was the true diversity of ammonite species in the same habitat? How quickly could the areal extent of the habitat change? And hence, how closely does the fossil succession have to be sampled for an evolving lineage to be identified?
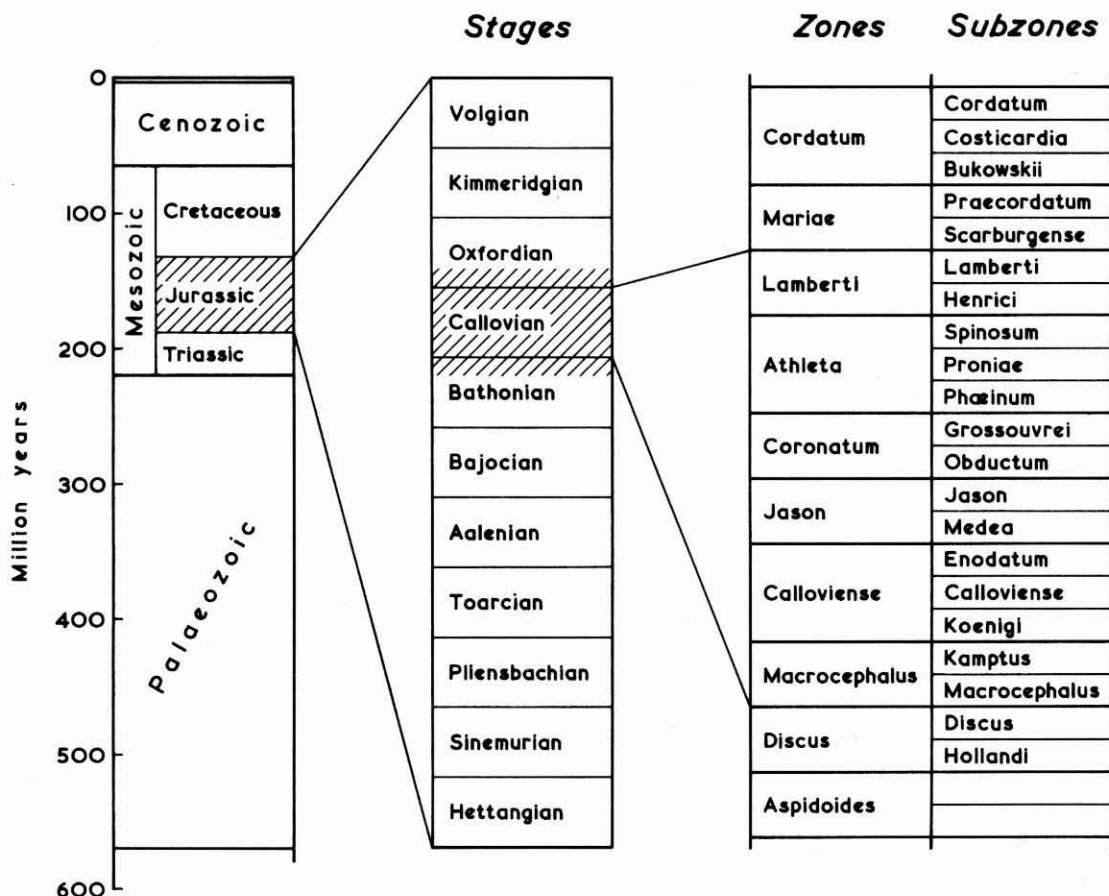
The position of the family Cardioceratidae in the general framework of Jurassic ammonites has been discussed in the recent review by Donovan *et al.* (1981). Its position within the superfamily Stephanocerataceae is shown in text-fig. 1.

CHRONOLOGY

The subdivision of the geological column down to the level of the standard subzone, the lowest unit in the current chronostratigraphical hierarchy, is shown around the top of the Middle Jurassic in text-fig. 2. Zones and subzones are defined by time-planes at their bases and are therefore the rock-equivalents of time-*duration*. Subzones do not in general represent the smallest time-*intervals* that can be geologically distinguished, however. In a typical section a subzone will span a range of beds, several of which will be fossiliferous. Moreover, given enough material, the fossil assemblages will be distinguishable not only in composition but also in the morphological aspect of the chronometric guide-fossils, e.g. successive assemblages of an evolving ammonite lineage. We are therefore interested in the smallest faunal change that can be detected, the closest stratigraphical levels that can be palaeontologically distinguished. These levels we may refer to simply and generally as faunal *horizons* (Callomon 1964; see also Mouterde *et al.* 1971, and, for example, Gabilly 1976, Hantzpergue 1979, Cariou 1980, Callomon and Birkelund 1982). A faunal horizon will often be represented by a single bed; and a subzone will in general span a number of horizons. It is then important to distinguish between the time-duration of formation of a horizon, and the time-intervals between horizons. The time-duration represented by a horizon may be highly variable and will usually not be closely determinable. There may be independent evidence of *condensation* indicating long durations, extending perhaps even to the whole of the interval between successive horizons. It is useful to distinguish two types of condensation (Callomon 1971a): *homogeneous*, in which fossils accumulated over a period of time as sediment was lacking or was subsequently redispersed
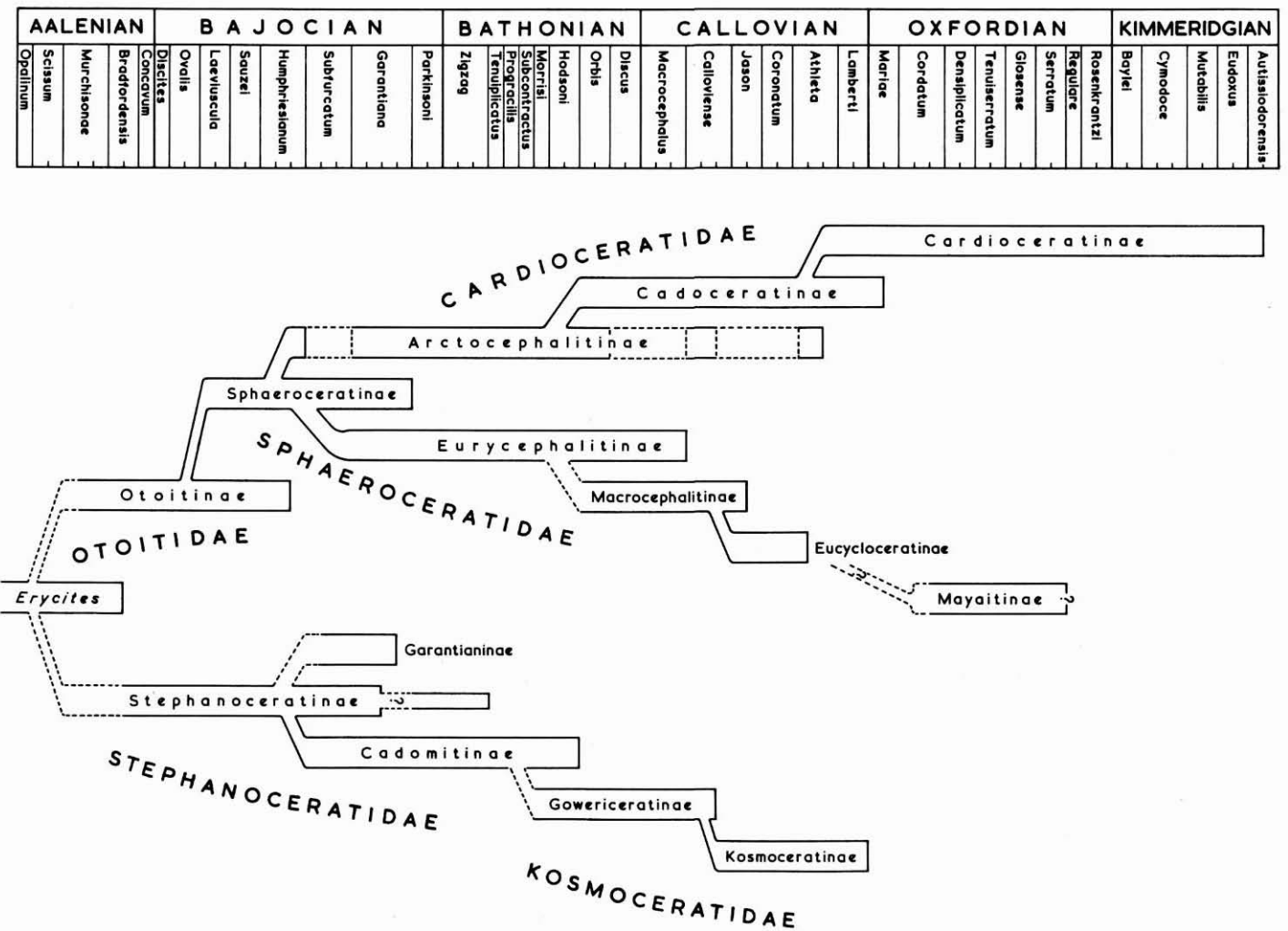
TEXT-FIG. 1. The schematic position of the Cardioceratidae within the superfamily Stephanoceratacae. Side-steps are there purely for artistic convenience and do not imply accelerated morphological changes.

AALENIAN				BAJOCIAN									BATHONIAN									CALLOVIAN						OXFORDIAN								KIMMERIDGIAN				
Opalinum	Scissum	Murchisonae	Bradfordensis	Concavum	Discites	Ovalis	Laeviuscula	Sauzei	Humphriesianum	Subfurcatum	Garantiana	Parkinsoni	Zigzag	Tenuiplicatus	Progracilis	Subcontractus	Morrisi	Hodsoni	Orbis	Discus	Macrocephalus	Calloviense	Jason	Coronatum	Athleta	Lamberti	Mariae	Cordatum	Densiplicatum	Tenuiserratum	Glosense	Serratum	Regulare	Rosenkrantzi	Baylei	Cymodoce	Mutabilis	Eudoxus	Autissiodorensis-

CARDIOCERATIDAE

Cardioceratinae

Cadoceratinae

Arctocephalitinae

Sphaeroceratinae

SPHAEROCERATIDAE

Eurycephalitinae

Macrocephalitinae

Otoitinae

Eucycloceratinae

OTOITIDAE

Mayaitinae ?

Erycites

Garantianinae

Stephanoceratinae

Cadomitinae

STEPHANOCERATIDAE

Gowericeratinae

Kosmoceratinae

KOSMOCERATIDAE

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TEXT-FIG. 2. The chronostratigraphical subdivision of the standard geological column in the Jurassic.

(examples: phosphatic nodule-beds in clay facies, primary greensands); and *heterogeneous*, in which originally well-stratified deposits were subsequently mechanically mixed, for example, by bioturbation, or subsolution followed by wave-action (examples: some Tethyan nodular limestones). Conversely, there may be evidence of very short durations. Unbroken, delicate shells such as ammonites in a bed of heavily cross-bedded clastic sediment may suggest a time-sampling of the instant of current-deposition of the bed as now preserved, perhaps a storm or a tide, the last and only instant recorded in what may well have been a long time spent in accumulating the sediment. Yet elsewhere, a section may yield fossils that are indistinguishable over a range of levels or even separable beds; these would then be treated collectively as a single faunal horizon. Either way, excluding demonstrably condensed deposits, a horizon thus defined is a unit in which no further evolutionary change is discernible (cf. Howarth 1958, p. xxii) and one that may therefore be treated for all practical purposes as of negligible duration. The ultimate basis of chronology is thus 'event stratigraphy', and our view of an evolving lineage is like a succession of snapshots, frames in a moving picture (cf. Bather 1927, p. xcvii).

It is interesting to estimate these geological time-intervals in absolute terms. Average values are collected in Table 1. The distinction between zones and subzones is to some extent arbitrary and historically determined, for subzones are created by subdivision of zones. Their number is also somewhat subjective and increasing as knowledge grows: in Oppel's time the total was thirty-three. An average of three ammonite horizons in a subzone seems to be about typical in the current state of Jurassic stratigraphy. In favourable cases it may be higher: in the Oxford Clay of Peterborough, Brinkmann recorded some twenty-five distinguishable horizons of *Kosmoceras* in six subzones (Callomon 1968; see also fuller discussion, 1984a), four per subzone. (For those

TABLE 1. Estimates of time-intervals.

Unit	Number of units	Average duration, $<\Delta t>$
STANDARD JURASSIC, NORTH-WEST EUROPE		
System: Jurassic	1	55·0 Ma (135–190 BP)
Stages	11	5·0 Ma
Zones	76	720,000 a
Subzones	154	350,000 a
Horizons	say, 450	120,000 a
Cf. S. S. Buckman (1893–1929)		
Ages	47	
Hemerae	375	
STANDARD APTIAN–ALBIAN, SOUTHERN ENGLAND		
System: Lower Cretaceous	$\frac{1}{4}$	17·0 Ma (98–115 BP)
Stages	2	8·5 Ma
Zones	14	1·2 Ma
Subzones	39	440,000 a
STANDARD UPPER CRETACEOUS, NORTH AMERICA		
System: Upper Cretaceous	$\frac{1}{2}$	34·0 Ma (64–98 BP)
Stages	$6\frac{1}{2}$	5·2 Ma
Zones	60	570,000 a

who like tidyness in stratigraphical nomenclature, the time-equivalent of 'horizon', as chron is to zone, could well be taken to be Buckman's 'hemera' (1893, 1902) stripped of all references to 'acme' of 'species', both of which would need a great deal of separate definition in this context. We shall have come full circle.) The table also includes analogous figures for parts of the Cretaceous in which comparable stratigraphical refinement has been achieved; the convention in North America is not to differentiate between zones and subzones. The absolute ages are still those of the 'Geological Society of London' scale (Harland *et al.* 1964, 1971), for various modifications proposed more recently (Harland *et al.* 1982; Odin 1982) seem to be questionable improvements, in the Jurassic at least.

The succession of faunal horizons of Cardioceratidae is shown in text-fig. 3. The family lived for most of the time in a restricted Boreal faunal province (see below) in much of which the standard European zonation cannot be recognized. A separate Boreal standard zonation has therefore had to be worked out, shown on the right, with the standard European scale on the left for comparison. Where the two scales are shown separated, correlation at zonal level is still only tentative (Upper Jurassic) or quite impossible (Middle Jurassic). The scales are drawn essentially on the assumption of equal durations at subzonal level. Representing as they do the integrated synthesis of a vast amount of detailed stratigraphical work over a wide area and at all levels, this approximation is certainly to be preferred to the equal-stage approximation of Harland *et al.* (1982). Since the figure was drawn (1980) more faunas of Cardioceratidae have been distinguished, and the number now stands at over a hundred. The family thus lived through four and a half stages, about twenty-eight zones, and sixty-two (European) subzones. The figures in Table 1 indicate for this a duration of twenty-two million years, sampled in faunal horizons at intervals on average of 200,000–250,000 years.

TAXONOMY

The basic units: biospecies. It is not fifty years since there appeared a still comprehensive monograph (Maire 1938) describing a section of the Cardioceratidae in what has come to be commonly called 'conventional' form. The taxonomy at specific and generic levels is purely descriptive in terms of selected morphological characters, the stratigraphical discrimination is barely at zonal level, and the value of it all is today not much more than that of a picture-book. This work was soon followed by Arkell's monograph of the Cardioceratidae of the English Corallian Beds (1941–1943, 1946–1948), which was to have a very strong influence on his views of ammonoid taxonomy generally. The material was abundant and there was now a great deal of precise

TEXT-FIG. 3. The faunal horizons of the Cardioceratidae. Only stratigraphically well-localized assemblages sufficiently numerous to give an indication of variability have been included. With the exception of one in the Coronatum Zone, all the assemblages indicated came from the region between north-west Europe and the Barents Shelf. Those indicated by full black circles are illustrated in text-figs. 4, 5, and 8. Note separate zonations in different faunal provinces.

stratigraphical information, certainly down to subzonal level. Nevertheless, few, if any, of the available collections from single localities and horizons were sufficiently large immediately to strike the eye as obviously natural, variable biospecific assemblages: the fundamental units of evolution, the species, were not apparent. Arkell's taxonomy at specific level was therefore also primarily morphological, but it improved on previous attempts by taking into account a wider range of characters. This included the all-important recognition of the adult stage in ontogeny, so that such discontinuities in the morphological spectrum that exist, those that we ascribe today to dimorphism, were in almost all cases picked up correctly. The vexing question of phyletic relationships between 'species' was then elevated to the discussion of classification at higher, generic levels. Arkell explicitly recognized the possibility of a choice here between the two extremes of a 'horizontal' or a 'vertical' classification (1940, p. lxxii; 1948, pp. 380–382). Nevertheless he could not come to any firm conclusions. The specific diversity at every stratigraphical level appeared to be large; somehow, there seemed to be a complex 'tangled skein' of lineages evolving in parallel, successively passing through the same 'evolutionary grades' (1935, p. xx; a residual throwback to Hyattian teleology due to Bather); and the end-note was one of despair (1948, p. 380): '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.'

My own introduction to the study of ammonites was through some of the same groups as those described by Arkell, but I had the good fortune to happen on a number of temporary exposures that yielded very large collections from very narrowly defined horizons. The most famous of these was perhaps the Lamberti Limestone of Woodham (Arkell 1939), packed with ammonites amongst which the Cardioceratidae were dominant. Faced with such an abundance of material I was forced to the exact opposite of Arkell's conclusion. The contradiction was resolved through the realization that all the Cardioceratidae at one level were merely members of a single genetically linked assemblage, that is, variants of one species—genetic species or *biospecies*. Nor was this just an extreme manifestation of the hallowed division of palaeontologists into 'lumpers' or 'splitters' depending on their inclination. Given enough material, it shows only one morphological discontinuity, the one that divides it into its dimorphic components of macro- and microconchs. Since putting forward this view in 1963 (p. 48), a vast amount of new material has served only to support it. Much of this new material lies in the Cardioceratidae. Thus, in at least thirty of the first forty-one faunas shown in text-fig. 3, material is sufficiently plentiful—from between a dozen to over a hundred complete adults in either or both dimorphs—to leave the monospecific character of the assemblage in no doubt. In the interval between Jason and Athleta Zones the record is still rather patchy, but it resumes in strength in the Lamberti Zone, mentioned above. Monospecific assemblages can also be demonstrated at various levels in the Oxfordian (Sykes and Callomon 1979, p. 858), and become unmistakeable again in the Kimmeridgian (Birkelund and Callomon, in press; Callomon 1971b, p. 159).

Monospecific assemblages within the family appear therefore to be the rule whenever material is plentiful. There are, however, exceptions. In the Nordenskjoeldi Zone of East Greenland, typical *Cadoceras* differing little from those above and below is temporarily reduced to the status of a minority by another group of Cardioceratidae differing so strongly in morphology that it was originally identified as a perisphinctid *?Olcostephanus* by Madsen (1904) (see below, p. 84). This group is as similarly dimorphic and monospecific as the associated *Cadoceras*, but there is no morphological overlap between the two. It is also known only from East Greenland, where it is abundant at several horizons, and the conclusion must be that it was a local endemic element. Yet the fact that it, too, was clearly monospecific within itself serves only to underline the rule.

Some other examples are known. In England and East Greenland, *Cadoceras* in the Calloviense Zone is accompanied at three horizons by another Cardioceratid of the genus *Chamoussetia* Douvillé (discussed further below), raising the specific diversity to two. The Russian Platform was inhabited at about the same time by what was clearly another distinct endemic group, *Cadoceras surense* and *C. subpatruum* Nikitin, 1885. To judge by collections in the British Museum, members of this group very occasionally found their way into the Kellaways Rock of Wiltshire. The specific diversity of the Cardioceratidae at this horizon has thus risen to barely three, the highest value I know.

It seems that in deciding what taxonomic approach to follow in classifying a group of Cardioceratidae, the safest working hypothesis (prejudice?) is to assume that it is monobiospecific until proven otherwise. There is then nothing in the Corallian faunas described by Arkell to refute this hypothesis.

The corollary to these conclusions is the recognition of the enormous range of morphological variability that an ammonite biospecies could accommodate. The classic example continues to be the successive assemblages of late Albian *Gastroplites* so beautifully described by Cobban and Reeside (1960). They too are monospecific. There is independent sedimentological evidence for their close synchroneity in the way they were packed into
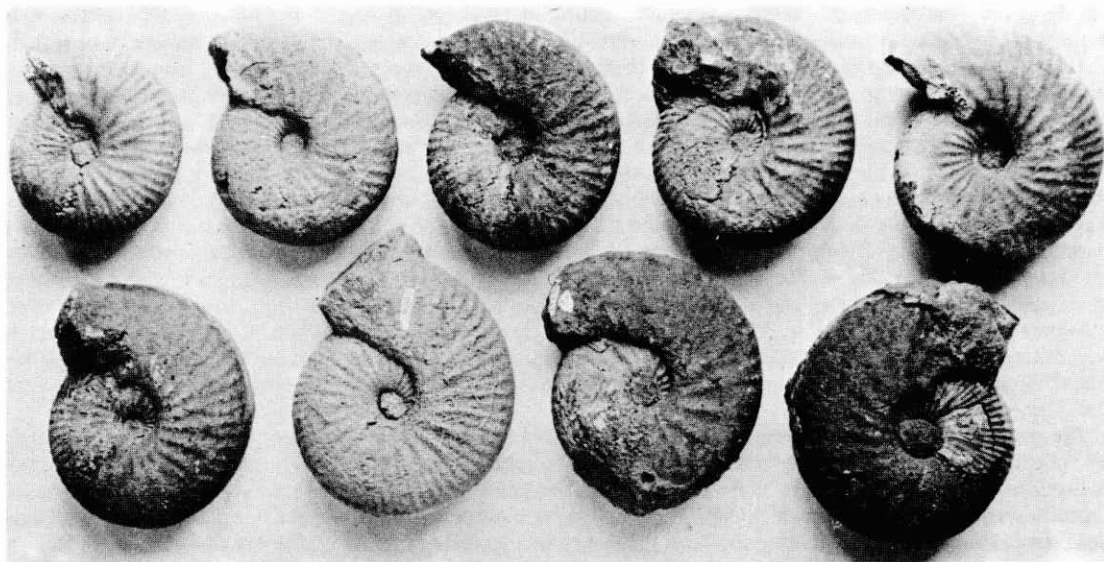
TEXT-FIG. 4. The variability of *Cranocephalites pompeckji* (Madsen, 1904) bsp., including *C. vulgaris* Spath, 1932. Boreal Bathonian, Pompeckji Zone and Subzone, Katedralen, Jameson Land, East Greenland; all adult macroconchs, × 0·50. An assemblage of low variability.

single concretions. The only remaining taxonomic uncertainty arises from the lack of any indication whether the material was adult or juvenile, complete or fragmentary; and hence there is no way of discerning from the descriptions alone the dimorphism that almost certainly existed in the group at maturity. Other examples of wide variability that have been recognized are reviewed by Kennedy and Cobban (1976, p. 38), although the most impressive they cite, that of Bajocian *Sonninia*, has to be modified to meet the stratigraphical requirements enumerated above. The majority of the sixty-four 'species' reunited by Westermann (1966) came from a manifestly homogeneously condensed bed incorporating three readily separable faunal horizons, falling into two zones (Concavum, Discites), and were combined under the name of a species, *S. adicra*, whose type series came from yet another level, in the Ovalis Zone, at least three faunal horizons higher still. The grounds for the suggestion (Callomon 1963, p. 36) that the high specific diversity at some levels claimed by Brinkmann in *Kosmoceras* may have been a subjectively imposed artefact, arising from a failure to grasp the full range of intraspecific variability, have only been strengthened in the years since; and it is disappointing to see, in the recent reworking of Brinkmann's original data (Raup and Crick 1981), a resolution of this question neither achieved nor even attempted.

The range of variability of an ammonite species was not constant, and the way it could change is also well illustrated by the Cardioceratidae. Two examples are shown here: *Cranocephalites pompeckji* (Madsen), in which the variability is quite small (text-fig. 4); and *Quenstedtoceras lamberti*, in which it is extreme (text-fig. 5).

Nomenclature. In its initial stages, the classification of a group of fossils has inevitably to be primarily morphological. It divides a collection of individuals into subsets according to whatever morphological characters the classifier regards as important, and the emphasis tends naturally to lean more heavily on differences than on similarities. Classification is in its analytical phase (Wright 1981). The subsets are given rank and are named according to the rules of nomenclature. The basic unit is the Linnéan typological *morphospecies*. As knowledge grows there is built up a set of two-dimensional arrays or matrices of morphospecies, morphological gradation (horizontal) against change with time (vertical), describing the full range of forms found. There comes a point when differences between some species vertically are less than those between others horizontally; and it is a logical step to signify what are now seen as vertical similarities by combining such species into taxa of next higher rank, genera with vertical ranges. The criteria are still purely morphological, so these genera are also still morpho- or *form-genera*; and so on. The mode of growth of such conventional, vertical classification is of course well known. The number of nominal species and higher taxa generated in a morphologically

diverse group can be considerable, and the Cardioceratidae are no exception. Starting with *Ammonites cordatus, lamberti, serratus* and four others described already by Sowerby in the *Mineral Conchology* (1813–1819), the family has grown to encompass today five subfamilies, sixty-one genera or subgenera, and over 600 nominal species. Such a profusion of names is widely regarded as the 'burden of palaeontology', serving mainly to obscure the 'real' relationships of interest, namely the phylogenetic connections; but regarded merely as labels for morphological objects, their number is largely unavoidable.

In contrast, a horizontal classification that regards all the members of a contemporaneous, morphologically diverse assemblage as merely variants of a single biospecies, possibly bisexually dimorphic, interchanges the criteria of a conventional classification. Such a biospecific assemblage may have effectively little or no vertical range in time. Any stratigraphically adjacent assemblage that can be morphologically distinguished as a whole from its predecessor has undergone a perceptible evolutionary change and is thus a separate entity requiring a label, no matter how this may be indicated in formal, nomenclatural terms. In a horizontal classification, presumed genetic cohesion within the assemblage is given precedence over morphological dissimilarities between variants; and discernible evolutionary changes between stratigraphically neighbouring assemblages, no matter how slight, take precedence over what morphological overlap remains, even if still great.

To convert from a vertical classification of parallel ranging morphospecies and morphogenera to a phyletic classification in terms of a succession of horizontal biospecies—the transition from the analytic to the synthetic phase in classification—therefore calls for the recognition of intertaxial relationships beyond those needed for a purely morphological classification, relationships likely to become apparent only after much work has been done and material is plentiful. It is therefore likely to call also for a comprehensive and radical reorganization of existing nomenclature, within the unchanging framework of the *Rules*. On the one hand, many specific names may disappear, with little loss, as their types are demoted to status of infrasubspecific variants within a biospecific assemblage. On the other hand, however, labels have to be found for all the distinguishable assemblages that are regarded as biospecific—the *transients* of Bather (1927) (*nomen novum* for 'Mutation' of Waagen 1869; *non* de Vries 1905), if in supposed phyletic succession—and this can cause problems and lead to confusion. The labels have to take the form of Linnéan binomina and to be chosen as far as possible from among the names of existing nominal species according to priority and the *Rules*, as in any other exercise of reclassification. If the locality, horizon, and hence assemblage of the type of an existing nominal species are precisely known, then the labelling of that assemblage/biospecies with the name of the species solves the problem.

More often than not, however, the horizons of existing nominal species as defined by their types are not precisely known; or assemblages are recognized from which no species have yet been named. One practice has been in such cases to use an existing specific name for a range of successive transients and to distinguish the levels within the range by means of additional specific adjectives, i.e. to give the transients the rank of chronological subspecies (see, for example, Brinkmann's classification of *Kosmoceras* (1929)). I think such procedures are, however, best avoided. As Sylvester-Bradley pointed out (1951, p. 92), in practice it will never be possible to distinguish absolutely in fossils between geographical and chronological subspecies. Of these, the former have a precise, largely objective, neontological definition, whereas the latter can never be other than subjective in the same sense as that of conventional classification. But in discussions of modes of evolution, the distinction between them is important. As soon as the concept of chronospecies is introduced in any form, so is the need for the concept of 'pseudoextinction' at the subjectively drawn transition between chronospecies, and the temptation to regard the duration of chronospecies thus defined as some sort of natural, objective measure of rates of evolution. The labelling of successive transients can be accommodated under the same specific name simply by the addition of some further non-Linnéan symbol, such as $\alpha, \beta, \gamma \ldots$; or as was done by Cobban (1969), who labelled six North American transients of *Scaphites* as *S. leei* Reeside I–III and *S. hippocrepis* DeKay I–III.

If the claims summarized above were correct, that the evolution of the Cardioceratidae was with minor exception monophyletic, then the need for more than a single genus group or a single family group name to represent the main lineage would, strictly speaking, disappear: the genus *Cardioceras*, represented by the succession of biospecific transients in text-fig. 3, one Linnéan specific name for each level, would say it all. In practice, however, there always remains a need for an easy shorthand method of referring to forms of a particular morphology, for instance when comparing new material with what has already been described. It is therefore convenient to retain the historical classification informally, carrying as it does the popular and often well-entrenched concept of a group. It may then become necessary to be able to distinguish between the use of the same Linnéan name in two distinct senses, e.g. *Q. lamberti* (J. Sowerby 1819) biospecies, incorporating the full range of forms shown in text-fig. 5, and *Q. lamberti* morphospecies, to be distinguished from *Q.*
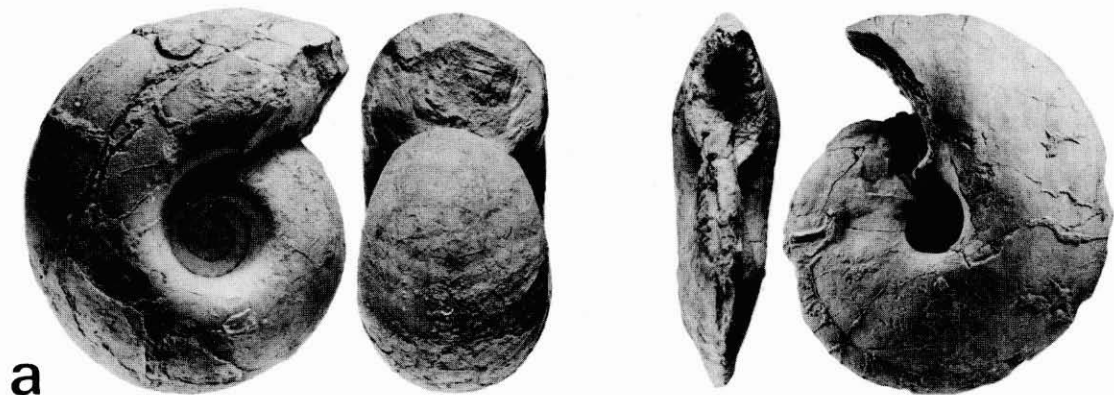
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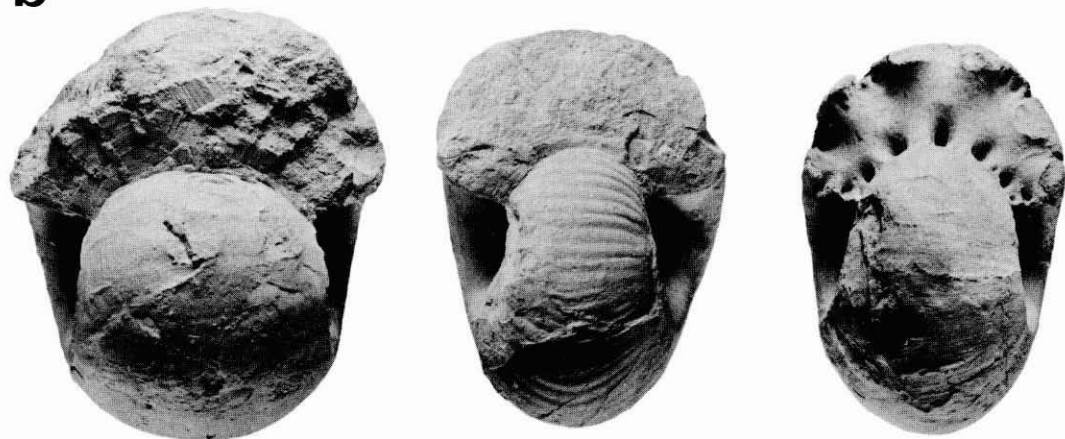
sutherlandiae, Q. henrici, Q. grande, etc., auctt., the other members of *Q. lamberti* biospecies. The *Rules* give us no convenient mechanism for indicating such distinctions formally, short of the full cumbersome procedure of demoting and writing out the names in full infrasubspecific form, i.e. *Q. lamberti* var. *sutherlandiae, Q. lamberti* var. *henrici*, etc. But, in practice, little confusion should arise from a mixed nomenclature, the sense being apparent from the context. The use of a name in the sense of biospecies is likely to occur much the less frequently, and a simple way to emphasize the point might be to follow it where necessary with the abbreviation 'bsp.', much as open nomenclature already often refers to taxa as 'sp.' or 'spp.'. Analogous remarks apply to names of the genus group: it continues to be simple and convenient to refer to *Cadoceras* and *Quenstedtoceras* as well as to *Cardioceras* even if the boundaries between them are wholly arbitrary. But no evolutionary significance should be attached to such usage.

TEXT-FIG. 5. The variability of *Quenstedtoceras lamberti* (J. Sowerby, 1819) bsp. Upper Callovian, Lamberti Zone and Subzone, Woodham, England; an assemblage of high variability.

a, morphological end-forms in the inflation of the shell, *Q.* (*Eboraciceras*) *grande* Arkell, 1939 (inflated); *Q.* (*Lamberticeras*) *lamberti* (Sowerby, 1819) (compressed). Complete adult macroconchs, × 0·25.

b, the full range with intermediate variants, including *Q.* (*E.*) *cadiforme* Buckman, 1923, *ordinarium* (Leckenby, 1859), *subordinarium* Buckman, 1920, *dissimile* (Brown, 1849), *henrici* Douvillé, 1912. A second series in the degree of involution of the shell would lead from *Q. lamberti* via *Q.* (*Prorsiceras*) *gregarium* (Leckenby, 1859) to *Q.* (*E.*) *sutherlandiae* (J. de C. Sowerby, 1827). All complete adult phragmocones, in some cases with incipient body-chambers, × 0·50. Microconchs range from *Q.* (*L.*) *flexicostatum* (Phillips, 1829) to *Q.* (*Quenstedtoceras*) *leachi* (J. Sowerby, 1819) (not shown).
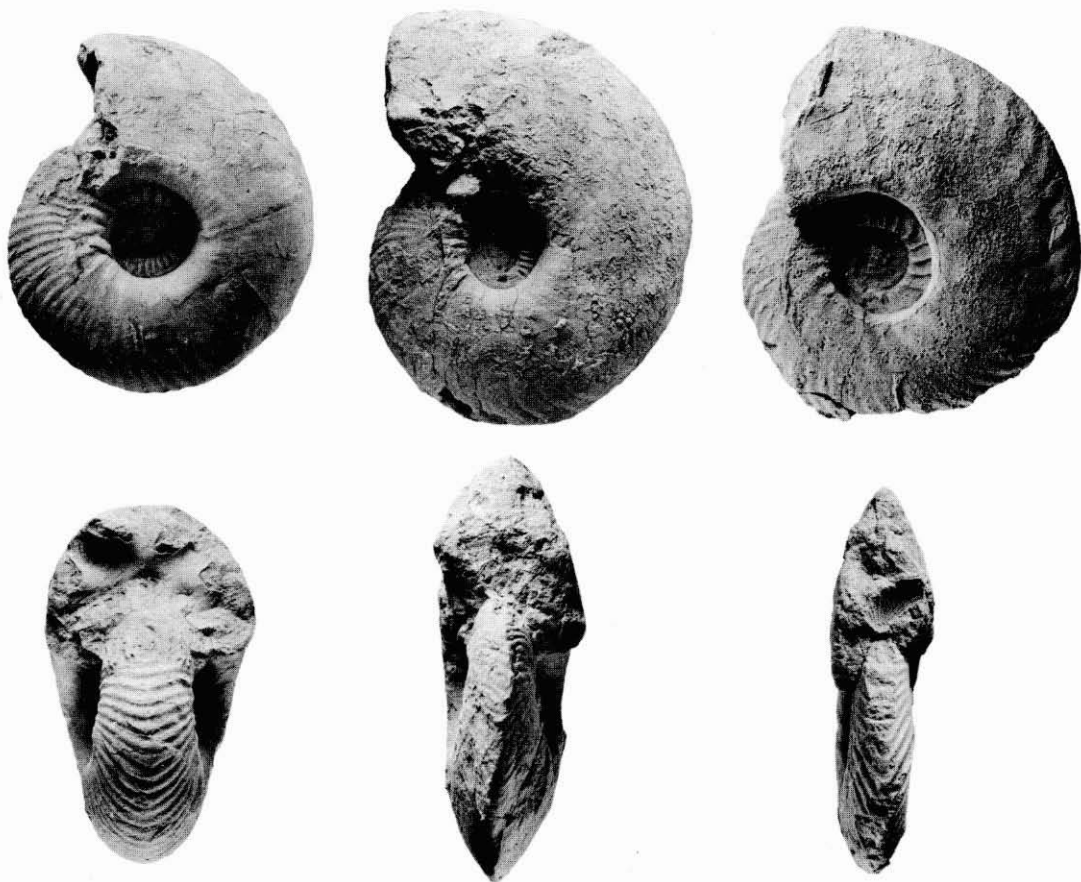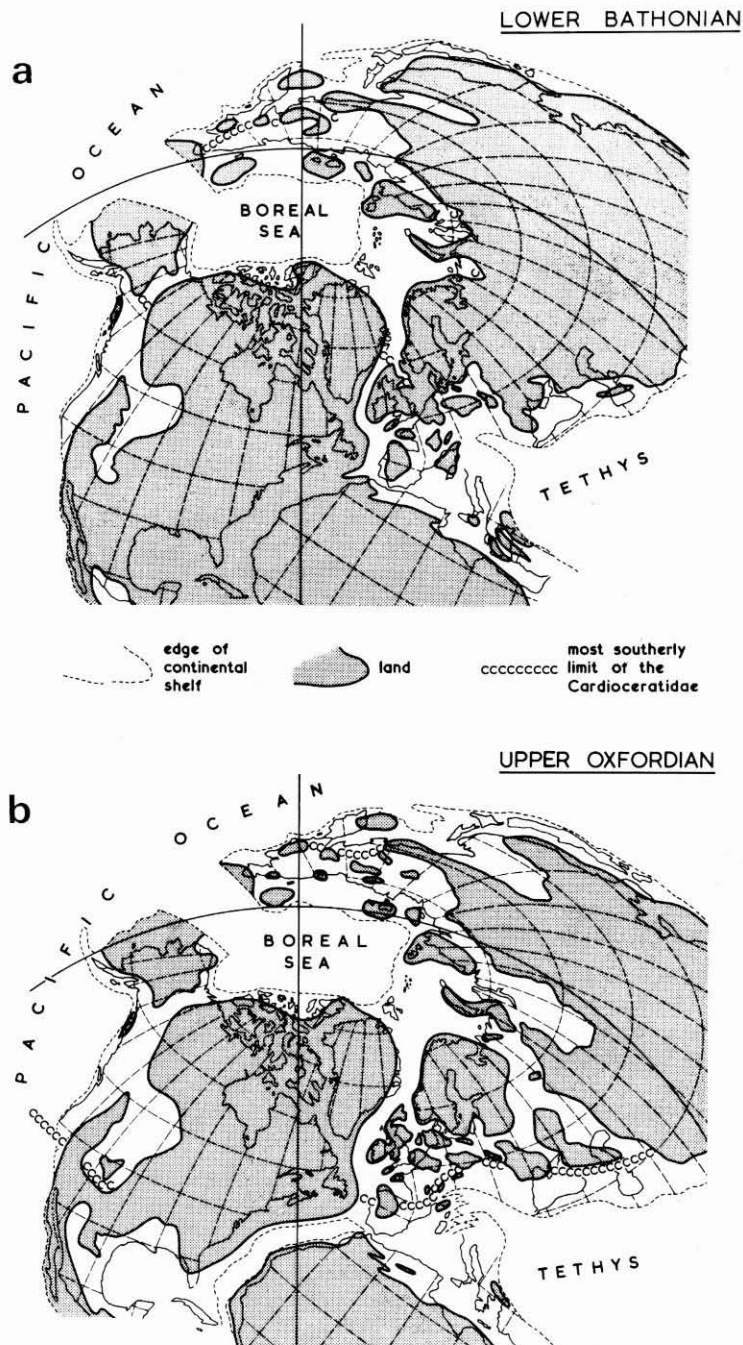
BIOGEOGRAPHY

The role of biogeography in discussions of modes of evolution is crucial. Are two successive fossil assemblages at one locality related by lineal descent, or are they immigrants, the centre of evolution lying somewhere else? Are two fossil assemblages at two localities some distance apart slightly different because they differ slightly in age or because they are contemporaneous geographical subspecies?

We may take as starting-point some of the categories discussed by Kennedy and Cobban (1976) in their excellent review of ammonite biogeography. It is necessary to distinguish between localities at which the fossil shells are now found and the region in which they lived, bred, and hence evolved. We observe the former and attempt to deduce the latter. Kennedy and Cobban differentiated five possible patterns of distribution: (1) pandemic; (2) latitudinally limited; (3) endemic and provincial; (4) disjunct; and (5) post-mortem.

Distribution. The distribution of the Cardioceratidae falls under the headings (2) and (3). The family was confined to the circum-polar regions of the northern hemisphere and constituted one of the main faunal elements that characterized the Boreal Realm. The southern limits of its distribution varied widely in space and time. They are shown in two palaeogeographic maps in text-fig. 6: at the time of maximum confinement (6a) in about the Lower–Middle Bathonian; and at the time of maximum extension (6b) in the Upper Oxfordian—at the height of the Boreal Spread of Arkell (1956).

These limits could be very sharp. Sometimes they may be ascribed to identifiable physical barriers. Thus, the principal factor restricting the Cardioceratidae to the relatively small area shown in text-fig. 6a was the almost completely land-locked extent of the Bathonian Boreal Sea. The Bathonian ammonites of, for instance, East Greenland and of southern Britain have not a single element in common, making correlations still impossible (see lower third of text-fig. 3). The Arctic forms have been followed down the Viking Straits between Norway and Greenland into the Viking Graben of the northern North Sea as far as a point about 170 km south-east of the Shetlands (Callomon 1976, 1979). This brings them to within 1,000 km of the nearest European–Tethyan faunas in southern England from which they were then still separated by a local barrier now represented by brackish or non-marine sediments. Elsewhere, the boundaries could be equally sharp in shelf seas known to have been otherwise free of bathymetric barriers. The transition from faunal dominance to insignificance could be complete in distances also between 500 and 1,000 km, e.g. in the Upper Bathonian, between the northern Yukon and the Alaska Peninsula (Callomon 1984b); in the Lower Callovian, between Normandy and the Aquitaine Basin (cf. Cariou 1980); in the Upper Oxfordian, between England and the Paris Basin; and in the Lower Kimmeridgian, between Scotland and eastern England. In contrast, within the Boreal Realm closely similar if not identical faunas can be recognized over very large distances. Thus, the earliest Cardioceratidae of the Borealis Zone, the highly characteristic *Cranocephalites borealis*, have been found in central East Greenland, in the northern Yukon, and in the Anabar region of northern Siberia, a triangle of sides 5,000 km; while the equally characteristic forms close to *Cardioceras martini* Reeside from the Lower Oxfordian Cordatum Zone, Bukowskii Subzone, occur in Britain, France as far south as the Ardèche, Switzerland, Poland, Lithuania, the Moscow and Volga Basins, trans-Caspian Turkmenistan, the Anabar region of northern Siberia, Franz Josef Land, the Canadian Arctic Archipelago, the Alaska Peninsula, British Columbia, Oregon and Wyoming, over distances greater than 10,000 km.

As the Cardioceratidae expanded southwards, other groups spread to the north. From about the Callovian till the time of their extinction in the Kimmeridgian, the Cardioceratidae overlapped with these other groups in a broad circle, leading to a subdivision of the Boreal Realm into various shifting, more restricted areas or provinces (see, for example, Sykes and Callomon 1979 for the Upper Oxfordian). These other groups included notably the Kosmoceratidae in the Upper Bathonian and Callovian, and a branch of the Perisphinctidae in the Oxfordian, later to become the Aulacostephanidae of the Kimmeridgian. Yet although many of these Sub-Boreal Provinces at

TEXT-FIG. 6. Palaeobiogeographic maps of the distribution of the Cardioceratidae. *a*, Lower Bathonian; *b*, Upper Oxfordian. Continental reconstructions after Smith and Briden (1977), modified. Distributions of land and sea around the Bering Straits highly uncertain, pending satisfactory microcontinental reconstructions of north-east Siberia. Positive evidence for any oceanic basin in the Jurassic Boreal Sea is lacking.

times reached very high latitudes, rarely did they penetrate the innermost polar regions, and there thus remained a restricted Boreal Province of about the extent shown in text-fig. 6a, in which the Cardioceratidae reigned supreme and unchallenged throughout the whole of their phylogeny.

Habitat. Most ammonites, even if not all, were free swimmers during much of their life-cycle; and the fossils that are our sole source of information are the remains of what were very effective buoyancy apparatuses. The connection between living habitat and fossil distribution could therefore have been blurred both by migrational patterns in the living animals and by post-mortal dispersion of the empty shells (category (5) above). Conversely, to deduce the location of centres of evolution from observed fossil distributions requires additional information. How important the difference might be is hard to judge at the outset. Analogy with living *Nautilus* suggests that migrational amplitudes may have been small but that post-mortal dispersal could have been considerable. The fact that the extremes of dispersal of *Nautilus* from its 'home' in the Philippines, once postulated to account for the observed distribution of shells, are being repeatedly refuted by the discovery of widely distributed living populations, e.g. off the shores of Burma, Japan, and south-west Australia, merely reinforces the need at least to consider the problem explicitly. In other living cephalopods, mainly squids, the opposite pattern is observed: migrational amplitudes during life can be considerable, certainly of the order of 1,000 km, whereas post-mortal remains are concentrated in highly restricted hatching and dying grounds in shallow shelf environments. Finally, yet other cephalopods are entirely pelagic in open oceans, the distinction in this sense between ocean and seas generally being not primarily the physical one of bathymetry so much as the secondary one of trophic environment—the food-chains characteristic of oceanic currents. The overall diversity of the ammonites strongly suggests that they may in themselves have spanned the whole spectrum of habitats found in living cephalopods. Certainly the distribution of the largest group falling into Kennedy and Cobban's category (1), pandemic—the Phyllocerataceae and many of the Lytocerataceae—would find its simplest explanation in terms of a pelagic, oceanic habitat (a view apparently already expressed by Nikitin and Pompeckj *teste* Salfeld 1924, p. 4, and explored a little further with some graphic examples in Callomon 1984b).

Fortunately, in many groups of ammonites, the Cardioceratidae among them *par excellence*, extra information is available (cf. Callomon 1963, p. 26). It lies in the composition of the fossil assemblages. In its clearest form it manifests itself in the following observations.

(a) Abundance: ammonites are common in a bed or a succession of beds thought not to be significantly condensed in the sense previously discussed above.

(b) Dominance: leaving aside trace-fossils, ammonites outnumber all other groups of macrofossils, e.g. bivalves; and amongst the ammonites, one group predominates.

(c) Preservation: a majority of shells is unbroken, and a significant fraction retains delicate apertural structures such as lateral lappets or ventral rostra.

(d) Maturity: the assemblage consists almost exclusively of adults (a 'normal fauna' in the sense of Callomon 1963).

(e) Sexual segregation: the sex ratio may be significantly polarized in the direction of either dimorph, macroconch or microconch. Examples are known in which the polarization can be almost total (Callomon 1981, p. 261).

(f) Specific diversity: this has been discussed above, leading to the conclusion that many if not all ammonite assemblages of the type being considered here were genetically monospecific.

(g) Geographical stasis: ammonite assemblages conforming to (a)–(f) occur not just once in an area at one horizon, but are found in a succession of faunal horizons in that area—horizons in the sense also previously discussed, of levels characterized by morphologically distinguishable assemblages, reflecting evolutionary change.

Assemblages combining features (a)–(f) to varying degrees are common, almost always found in the sediments of epicontinental seas of shallow to moderate depths so widespread in the Jurassic.

They include most of the famous cephalopod beds of the Inferior Oolite of Dorset and many other examples too numerous to list, from the Lias (see, for example, Howarth 1973) to the Albian (e.g. Kemper 1982, p. 560; see also the examples given by Kennedy and Cobban 1976, p. 32). Any one of the factors by itself might perhaps be passed over without too much further comment, but the combination of several or all of them in the remains of what were once nektonic organisms can only have a special explanation, rooted in the life-cycle of the animals. The observations would be consistent with a mode of life in which the ammonites, like many modern cephalopods, were gregarious; undertook some migration during growth with, at times, at least partial segregation of the sexes; and were bound to well-defined geographical areas of relatively shallow water as breeding, spawning, hatching, and, finally, for the female macroconchs at least, dying grounds—where we now find them (Callomon 1981, p. 262).

The implication is that within the whole of the area of distribution of the fossils, those more restricted areas in which their assemblages conform to factors (a)–(f) were at or close to the breeding grounds and hence, at any instant, the true centres of evolution. If now to these instantaneous factors is added in one area the feature (g), geographical stasis over a succession of horizons and period of time, the presumption grows into fair certainty that this area represented a fixed centre of evolution of a segment of a whole lineage—genus, family, or other supraspecific taxon in a phylogenetic classification. The best-known example of such a lineage conforming to all the factors enumerated above must be Brinkmann's succession of *Kosmoceras* at Peterborough. (And, in contrast, few if any assemblages like them of Jurassic Nautilida are known at all.)

To emphasize these points, I suggest the introduction of a new term. The adjective *endemic* applied to fossil distribution patterns has been borrowed from neontological usage and is usually taken to signify the whole of the area, albeit geographically restricted, in which a species or higher taxon of fossils is now found, irrespective of the sense in which the taxa are defined. To state the area in which a 'species' or 'genus' was endemic does not by itself identify for us within that area the locus of any evolving unit, biospecies, geographical biosubspecies, race, or whatever other entity we invoke in discussions of speciation. As I have indicated above, the 'true home' of ammonites can in many cases be identified with some confidence, both at isolated horizons and over periods of time. It might therefore be useful to refer to an area in which an ammonite biospecies probably lived and bred, as indicated by factors (a)–(f), and an area in which a succession of biospecies forming a lineage evolved, (g), as areas in which the (bio)species and (phylo)genus were *eudemic*.

The areas in which the Cardioceratidae were eudemic can be identified in the majority of the horizons indicated in text-fig. 3, i.e. during most of the duration of the lineage. Where and when will be indicated in the historical summary that follows.

EVOLUTIONARY HISTORY

The succession of the Cardioceratidae is illustrated in text-fig. 8, taking samples at the levels shown as full black circles in text-fig. 3. One macro- and one microconch is shown wherever possible from the same horizon, but in some cases the segregation is so strong that good adult specimens with complete body chambers are not yet available. With rare exceptions, all the material came from eudemic assemblages in the region between southern Britain and Spitsbergen.

Origins. The beginning of the family is sharply defined by what appears to have been a near-instantaneous colonization of the Boreal Sea, whose extent at the time was much as shown in text-fig. 6a. This followed a considerable period during which it had been vacant of ammonites. Barely distinguishable assemblages of the earliest form, *Cranocephalites borealis* (Spath), have been found in three widely dispersed areas already alluded to above: in the northern Yukon and adjacent Richardson Mountains (Frebold 1961, as *C. borealis* and *C. warreni* nov.) (eudemic, criteria (b)–(f)); the Anabar region of northern Siberia (Voronets 1962, as *Xenocephalites kononovae*, *Morrisiceras* [sic] *sibiricum, laptinskayae* nov., and Meledina 1967, as *Boreiocephalites pseudoborealis* nov.); and central East Greenland (Spath 1932; Donovan 1953, as *Arctocephalites kochi*
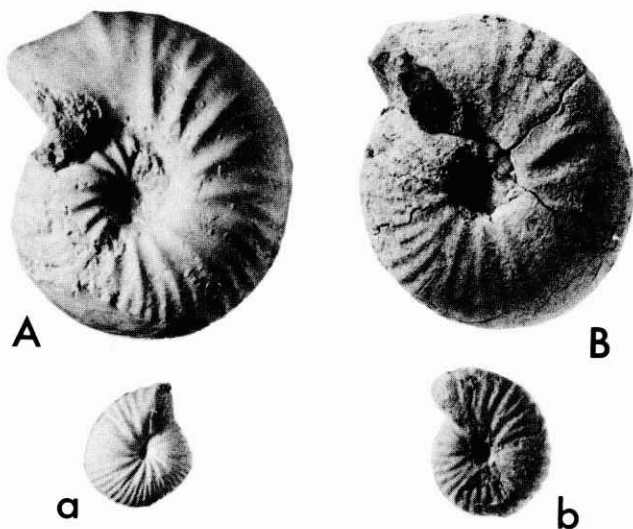
TEXT-FIG. 7. The earliest Cardioceratidae and their probable ancestors. A, *a*, *Sphaeroceras* (*Defonticeras*) *oblatum* (*Whiteaves*), Oblatum Zone (equivalent to the upper Humphriesianum Zone of the European standard), Canada. A, macroconch, Alberta, figured in Hall and Westermann 1980, pl. 14, fig. 3*a*, *b*; *a*, microconch, Queen Charlotte Island, ibid., fig. 8. B, *b*, *Cranocephalites borealis* (Spath), Borealis Zone, East Greenland. B, macroconch, more than usually strongly ribbed variant retaining ribbing on the mature body chamber; *b*, microconch, typical—note how much more subdued and coarser the ribs are than in *S. defontii*. Both JHC coll. (Reduced × 0·75).

nov.; and Callomon 1959) (eudemic, all criteria: sex ratio at least 20 : 1 in favour of macroconchs—text-figs. 7B, 8A). In the Yukon, the last previous ammonite occupant was *Arkelloceras* of Lower Bajocian, Sauzei Zone age. In northern Siberia, it appears to have been late *Pseudolioceras* of the Upper Aalenian; and nowhere in the Viking Straits nor on the Barents Shelf is anything known definitely younger than Toarcian. Yet sediments of the intervening period are present, often with characteristic bivalves, notably Inoceramids. Where, then, did these invaders come from?

The immediate predecessors of *C. borealis* can be plausibly identified in a subgenus *Defonticeras* of *Sphaeroceras* eudemic in the north-east Pacific, found today in the Cordillera from the Alaska Peninsula to Oregon and in the Rockies of Alberta and Montana (see descriptions and stratigraphy in Hall and Westermann 1980, and review of the systematics in Callomon 1984*b*). A typical pair is compared with *C. borealis* in text-fig. 7. The Pacific forms have some stratigraphical range, for at least three faunal horizons can be distinguished; and although they have not yet been found in concentrated cephalopod beds like those with *C. borealis* in East Greenland, the overall impression is that they were eudemic at least somewhere in the region. They generally occur in association with typical pandemic *Stephanoceras* of the Humphriesianum Zone, so that their age is firmly established. They differ from their European counterparts, *Sphaeroceras* s.s. (including *Chondroceras* auctt.), in relatively minor but quite consistent and easily recognized details of the style of ribbing, and may well have been no more than geographical subspecies at the extremes of a distribution ranging from the western Tethys eastwards along and across the northern shelf seas of the Pacific. Entry into the Boreal Sea must then have been somewhere in the region of the Bering Strait, perhaps along a corridor into the Yukon as shown in text-fig. 6*a*, even though the palaeogeographic reconstructions in this part of the world are still perforce more than usually conjectural (including the land mass shown as covering most of Alaska, which may not have been there at all). The close overall resemblance between *Defonticeras* of the Humphriesianum Zone and *Cranocephalites borealis* then suggests that the age difference between them could not have been great, i.e. that the age of the latter, and hence the root of the Cardioceratidae, is early Upper Bajocian. This remains the only way of estimating it, for as text-fig. 3 indicates, direct correlations are still impossible.

Bajocian–Bathonian. Once established, the Cardioceratidae continued to evolve in isolation in the Boreal Sea. Up to the Callovian the succession is best developed in Jameson Land, East Greenland, represented by some thirty faunal horizons in each of which the assemblages were clearly eudemic by all the criteria. The preponderance of macroconchs is particularly prominent. The material that

could be collected at some levels is almost limitless, illustrated in Rosenkrantz's famous photograph (1929, p. 146) with its caption, 'in the foreground thousands of ammonites lie spread over the ground'.

The first morphological changes that occurred led away from the sphaeroconic coiling of *Sphaeroceras* and *C. borealis* to more evolute, round-whorled shells (text-fig. 8B–C) of *Cranocephalites* at its most typical. Blunt ribbing was retained on the body-chambers, but the ribbing on the inner whorls was transmuted by proterogenesis (the first appearance of new characters in the early stages of ontogeny), becoming progressively more fine, dense, and sharp. The six faunas in the Pompeckji Zone are particularly instructive in this respect, for they show that the evolutionary 'progress' was by no means rectilinear: there was much to and fro in the correlation between characters. Thus, there is a strong homeomorphism in overall shell form between the first and fifth of the faunas (text-fig. 4) and between the second and the sixth, but the third (8c) and fourth are quite distinct. Morphological variability became quite low (text-fig. 4), particularly in whorl thickness at values around 50% of whorl diameter. Assemblages closely similar to some of those in Greenland, in part perhaps identical, are again known from the Canadian Arctic (Frebold 1958) and northern Siberia (Meledina 1973).

The next major change occurred in the Arcticus Zone. Modification was now in the adult stages of ontogeny, i.e. the opposite of proterogenesis. In the macroconchs, the shells became predominantly compressed, with arched external edge and wholly smooth body-chamber (text-fig. 8E, F). These are the characteristics of the morphogenus *Arctocephalites* Spath, 1928. The microconchs (8e, f) assumed a morphology that was then to remain almost unchanged to the top of the Callovian, generally encompassed by the traditional name *Pseudocadoceras* Buckman, 1918. At the same time there set in an enormous range of variability in the inflation of the adult macroconch shell. Thus, in the first of the assemblages, that of *A. arcticus* itself (text-fig. 8E), there is a continuous range between *A. elegans* Spath (1932, pl. 10, fig. 4) at *c.* 35%, and *A. sphaericus* Spath (1932, pl. 17, fig. 1) at up to 85%. The distribution is, however, not symmetrical, compressed forms predominating. All other characters are also highly variable, and there remains a considerable morphological overlap with the predecessors in *Cranocephalites*. Besides Greenland, rich faunas of *Arctocephalites* have been found in Franz Josef Land (the type area of *A. arcticus*) and in the Yukon (Poulton 1984).

The characters of *Arctocephalites* were slowly transformed into those of *Arcticoceras* Spath, 1924, in the Ishmae Zone (text-fig. 8H) by sharpening of the external edge of the shell with pronounced forward projection and accentuation of the ribbing, in some variants almost up to the sharpness of a carina. Were the subsequent history unknown, one would be tempted to discern here a prophetic forerunner of *Cardioceras* itself. Maximum diameters are up, but the high variability of inflation remained as it had been before, with a minority of sphaerocones at each level. The area of distribution became slightly enlarged, *A. ishmae* making its appearance now also in the transgressive sediments of the Petchora Basin of northern Russia (Keyserling 1846; see lectotype refigured in Saks (ed.) 1976, pl. 9, fig. 1) and the lower reaches of the R. Lena (Meledina, 1977).

The Cranocephaloide Zone saw a major change in the direction of evolution of the Cardioceratidae (text-fig. 8I; and see Appendix). The coiling of the shells became evolute and round-whorled again, maximum diameters were reduced, and ribbing persisted on the body-chambers, all reminiscent of *Cranocephalites*. But most remarkably, the range of variability became narrow in almost all characters (cf. Birkelund and Perch-Nielsen 1976, p. 304) and thenceforth remained so to the top of the Middle Callovian. In the Variabile Zone further modification took place, again in the adult stages of ontogeny. The coiling became evolute and inflated on the outer whorls, and the deep open umbilicus developed steep sides with sharp edges—the generic characters of *Cadoceras* Fischer, 1882. *C. variabile* (text-fig. 8J) retains many of the features of *Arcticoceras* on its inner whorls, but in the Calyx Zone (text-fig. 8K), the transition to *Cadoceras* is complete. Various assemblages of such early forms of *Cadoceras* are also known from widely dispersed but scattered localities elsewhere, including the Lena–Anabar region of northern Siberia, the Canadian Arctic Archipelago, and the northern Yukon in which at least one of them, that of *C. barnstoni* (Meek,
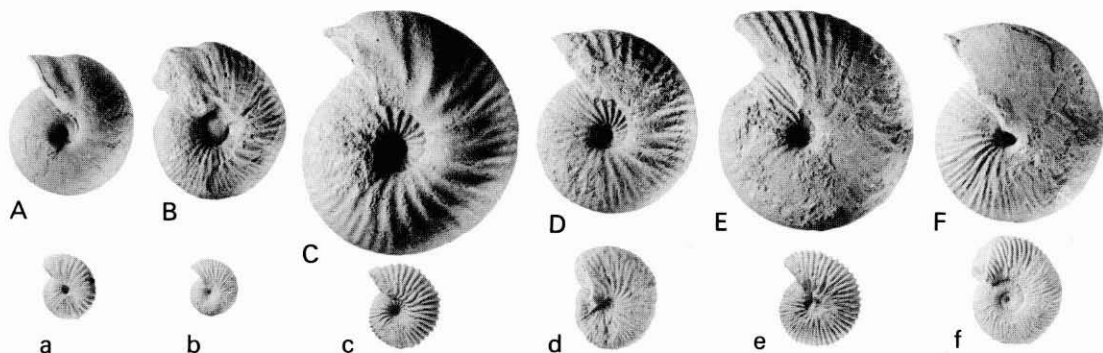
TEXT-FIG. 8. Illustrations of the Cardioceratidae, sampled at the levels indicated by full black circles in text-fig. 3. Capital letters, macroconchs; lower-case letters, microconchs. Complete adults except where indicated. All photographs of casts, × 0·33.

(i) BAJOCIAN-BATHONIAN

A, a, *Cranocephalites borealis* (Spath); topotypes, Borealis Zone, Jameson Land, East Greenland.

B, b, *C. indistinctus* Callomon (1959); holo- and topotypes, Indistinctus Zone, same area.

C, c, *Cranocephalites* sp. nov. A; middle Pompeckji Zone, same area (see also Callomon 1976).

D, d, *C. pompeckji* (Madsen); topotypes, Pompeckji Zone, same area (see also text-fig. 4).

E, e, *Arctocephalites arcticus* (Newton and Teall); lower Arcticus Zone, Jameson Land.

F, f, *Arctocephalites* sp. nov. B; upper Arcticus Zone, same area.

1859), was eudemic (Poulton 1984). Occasional representatives have also been found as far south now as Cook Inlet in southern Alaska (*C. moffiti* Imlay; Callomon 1984*b*).

The Cranocephaloide Zone saw also the arrival in some parts of the Boreal Sea of a second but closely related groups of ammonites, the genus *Kepplerites* of the family Kosmoceratidae (see text-fig. 1). This appeared suddenly in East Greenland at the bottom of the zone as the first of a succession of eudemic assemblages ranging in parallel with the Cardioceratidae up into the Upper Callovian. At some levels, both families are found together in the same bed in comparable numbers; at others, either of the two families occurs to the virtual exclusion of the other. Two families could therefore coexist eudemically in the same area; but the overall distribution of Cardioceratidae and Kosmoceratidae was quite different. In the Upper Bathonian, the Kosmoceratidae extended from the Western Interior of North America as far north as the Yukon, just; and from East Greenland as far north as Spitsbergen. Yet they did not penetrate the inner reaches of the Boreal Sea, being unknown both in the Canadian Arctic Archipelago and in northern Siberia. Their endemism thus defined a separate and disjointed Sub-Boreal Province within the Boreal Realm. How the two halves of the province communicated with each other, as they clearly did, is not obvious in terms of the fossil distributions found today. There may be yet another pointer here to the importance of migration during the life-cycle, along routes leaving little trace in the record. Furthermore, *Kepplerites* appeared to be able to follow some routes not taken by the Cardioceratidae. *K. keppleri* (Oppel) managed to penetrate briefly along the only possible corridor leading into north-west Europe through the North Sea as soon as this became open at the very beginning of the Callovian, appearing at a single horizon in the Upper Cornbrash of England and in the Macrocephalenoolith of Swabia (Callomon 1959, 1984*b*). Conversely, this intercommunication provided the first means of correlating the Boreal and Tethyan succession since the Aalenian, and hence of identifying the Bathonian–Callovian boundary in the whole of the Arctic.

Callovian. The Lower Callovian saw the beginning of the 'Boreal spread' of Arkell, the general southerly extension of the limits of distribution of the Cardioceratidae. In part this was simply an invasion of already existing seas, as in North America. Elsewhere it marked marine transgression
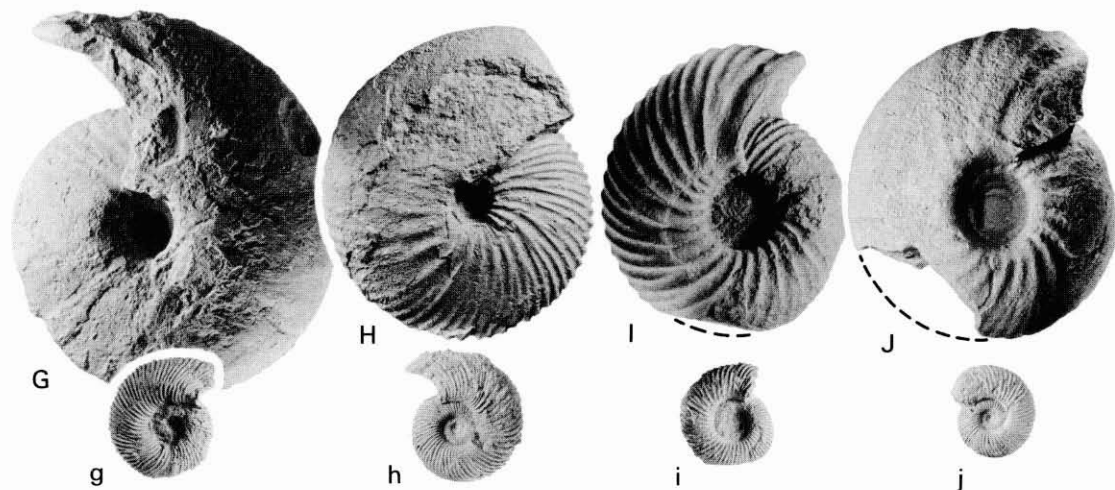
TEXT-FIG. 8, *continued* (ii)

G, g, *Arctocephalites greenlandicus* Spath; topotypes, Greenlandicus Zone, Jameson Land.
H, h, *Arcticoceras ishmae* (Keyserling); middle Ishmae Zone, same area. (The [M] is adult but incomplete; only the last quarter whorl is body-chamber.)
I, i, *A. cranocephaloide* sp. nov. (see Appendix); holo- and allotypes, lowest Cranocephaloide Zone, same area. (The [m] is a complete adult phragmocone only.)
J, j, *Cadoceras variabile* Spath; chorotypes, Variabile Zone, same area.

over what had previously been land, as on the Russian Platform. In Greenland a change in sedimentary regime reduced the quality of the fossil record, making it necessary to piece together evidence from more widely scattered localities. And there occurred the first clearly identifiable phylogenetic divisions within the family.

The general morphology of early Callovian *Cadoceras* was one of relatively small forms of low variability, evolute, with inflated smooth adult body-chambers and wide umbilici, usually referred to as *Paracadoceras* Crickmay, 1930. This group now became eudemic in southern Alaska (profusely illustrated by Imlay 1953; see review in Callomon 1984b) and extended as far south as southern British Columbia. Very similar forms occur in northern Siberia (Meledina 1977); and two specimens are even known from the Upper Cornbrash of southern England (*P. breve* (Blake 1905)). In East Greenland *Paracadoceras* was briefly abundant but poorly preserved at the top of the Apertum Zone. It then almost disappeared, its place taken by a new form known only from this area, *C. nordenskjoeldi* sp. nov. (see Appendix). This occurs in typically eudemic assemblages over a range of beds, and at least two morphologically distinguishable faunal horizons can be recognized. The end-forms look more like Perisphinctids than *Cadoceras*, and were first tentatively identified as such. The group dominates the assemblages, but ordinary *Paracadoceras* also occurs, rarely, as does *Kepplerites*. It terminated at the top of the Nordenskjoeldi Zone, leaving no successors.

During this period a second corridor into western Europe became open, across the Russian Platform from the north-east. Its former presence is today attested by eudemic assemblages intermediate in morphology between *Paracadoceras* and *Cadoceras* s.s. in the Petchora and Moscow Basins (*C. elatmae* (Nikitin): cf. Sazonov 1957 and Meledina 1977; index of the Elatmae Zone) and in the Swabian Alb and northern Jura (*C. quenstedti* Spath: Quenstedt 1886, pl. 79, figs. 5–6, 7 (type); in the 'Hauptbank' of the Macrocephalenoolith of Dietl (1981), associated with *Macrocephalites macrocephalus* (Schlotheim et Zittel) and lying above *K. keppleri*). These Cadoceratids did not get as far as Britain, although the Tethyan Macrocephalitids show that the seas were open; and nowhere along this route have any contemporaneous Keppleritids been found, supporting the idea that the
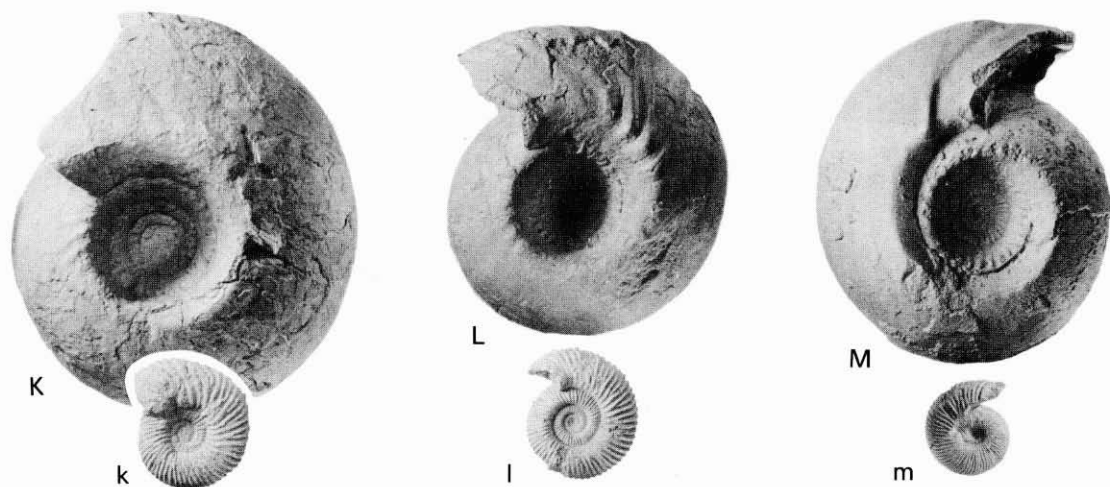
TEXT-FIG. 8, *continued* (iii)

K, k, *Cadoceras calyx* Spath; topotypes, Calyx Zone, same area. (The [M] is adult but incomplete; only the last fifth whorl is part of the body-chamber which probably extended over another three-quarters of a whorl.)
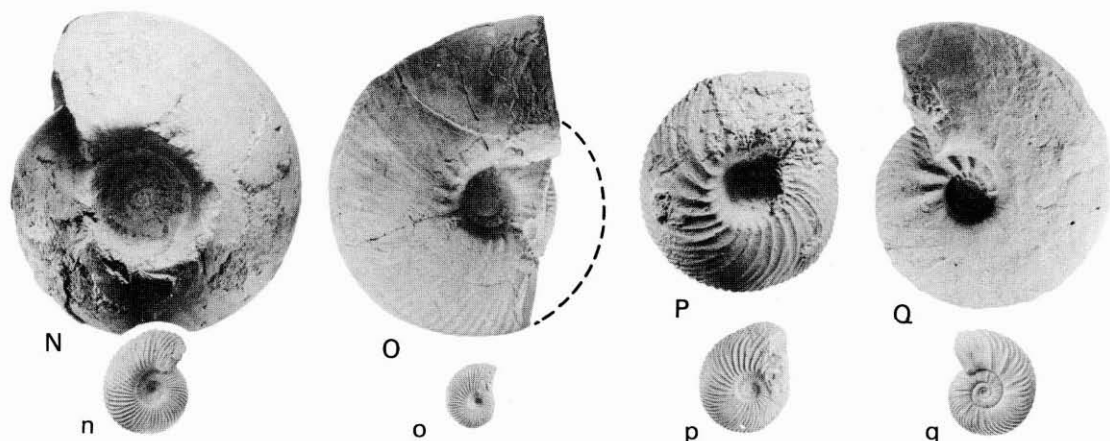
CALLOVIAN

L, l, *C. apertum* sp. nov. (see Appendix); holo- and allotypes, Apertum Zone, same area.

M, m, *C. septentrionale* Frebold, 1964; Jameson Land. Known so far only from the Arctic, predating the earliest forms found in the Calloviense Zone of Britain.

source of the invading Cadoceratids had been the *Kepplerites*-free inner Boreal Province north of Siberia.

Free communication along an open seaway between Norway and Greenland, connecting the Boreal Sea with the shelf seas of western Europe and thence the Tethys, was finally established at the beginning of the Calloviense Zone and stayed open well into the Cretaceous. It was sharply marked by the arrival in Britain of the Cardioceratidae and Kosmoceratidae in great numbers but in comparable proportions, preserved today as the spectacular fossils for which the Kellaways Beds have long been famous. Four successive eudemic and monospecific faunal horizons can be recognized: *C. tolype* Buckman, 1923 (Kellaways Clay of southern England and Normandy, Calloviense Zone, lower Koenigi Subzone); *C. rubrum* Spath, 1932 (Kelloway Rock of the Yorkshire coast, upper Koenigi Subzone); *C. sublaeve* (Sowerby 1814) (text-fig. 8N; Kellaways Rock of Wiltshire Calloviense Subzone); and *C. durum* Buckman, 1922 (Kellaways Rock, south Yorkshire, Enodatum Subzone). These differ in relatively minor aspects of coiling and ribbing, but the remarkable feature is the constancy throughout of their sphaeroconic cross-section. The degree of inflation is around 90% of the shell diameter at the end of the macroconch phragmocone, with very little variation. This morphology represents one of the major landmarks in the evolution of the lineage. Closely similar forms are found throughout the Boreal Realm, notably in East Greenland (*C. sublaeve*), the Canadian Arctic and Alaskan North Slope (*C. voronetsae* Frebold, 1964), and the Lena–Anabar region of northern Siberia (*C. emelianzevi* Voronets, 1962).

But even more remarkable is a second example of phylogenetic branching within the Cardioceratidae. Simultaneously with the arrival of *Cadoceras* in Britain at the base of the Calloviense Zone there appeared the genus *Chamoussetia* Douvillé (illustrated in the *Treatise* (Arkell 1957, p. L303). Size, dimorphism, ribbing, and septal sutures all point unambiguously to its position in the Cardioceratidae, yet nothing could be greater than the contrast between its predominantly discoidal, involute shells and open-coiled, sphaeroconic *Cadoceras*: its cross-section has developed a sharp

TEXT-FIG. 8, *continued* (iv)

N, *n*, *Cadoceras sublaeve* (J. Sowerby, 1814); lectotype [M] (not quite complete, the final quarter-whorl of body-chamber not preserved) and allo-topotype [m], Kellaways Rock, Kellaways, Wiltshire, Calloviense Zone and Subzone.

O, *o*, *Stenocadoceras stenoloboide* (Pompeckji; [M], holotype of *S. iniskinense* Imlay (1953, pl. 46, figs. 7, 9); [m], topo- or chorotype of *S. stenoloboide* s.s. (1953, pl. 47, figs. 7, 8); both from southern Alaska, presumed Middle Callovian.

P, *p*, *Longaeviceras nikitini* (Sokolov, 1912); middle Athleta Zone, Peterborough, England. (Both adults, but only the beginnings of the body-chambers preserved.)

Q, *q*, *Quenstedtoceras lamberti* (J. Sowerby, 1819). [M], Lamberti Limestone, Woodham (adult phragmocone with a tenth of a whorl of body-chamber; for a complete adult, see text-fig. 5). [m], Tidmoor Point, Weymouth. Upper Lamberti Zone.

carina, making it closely homoeomorphic with *Cardioceras* itself. Among earlier forms, those most closely resembling it, and hence the most plausible ancestors, are found at the top of the Ishmae Zone. An indication of the resemblance may be obtained already in the slightly older *A. kochi* Spath (1932, pl. 14, figs. 2, 3; pl. 15, figs. 1, 4, and 5, compressed variants of *A. ishmae*). The phylogenetic branching-point is therefore indicated at about this level in text-fig. 1. One of the other characteristics apparently inherited unchanged from *Arcticoceras*, in contrast to *Cadoceras*, is the wide variability in whorl thickness. In *Chamoussetia lenticularis* (Phillips, 1829), it ranges from 40 to 100% of the diameter (Buckman 1914, pl. 98). But most mysterious are the stratigraphical range and geographic distribution of the genus. It has been found in an area extending from East Greenland through Britain to the Jura and thence across the Russian Platform as far as the Volga. Yet although tolerably common at some levels in the Calloviense Zone in East Greenland and in Britain (three horizons), nowhere has it been found in assemblages that could be described as eudemic. It always occurs only as a minor constituent of the total ammonite fauna or, if alone, as a rarity. And no trace has been found anywhere of the intermediate forms between Ishmae and Calloviense Zones, in a region in which the Cardioceratidae are otherwise so well documented. Even more mysterious is the disappearance of the genus during the whole of the Middle Callovian, only to reappear abruptly and briefly for a second time in Britain and Normandy in the Athleta Zone of the Upper Callovian, as *C. galdrynus* (d'Orbigny) (cf. text-fig. 1). Perhaps the moral of all this is to remind us how fragmentary the fossil record can be even in circumstances in which it otherwise seems particularly close to complete.

In the Middle Callovian the Cardioceratidae largely retreated into the inner recesses of the Boreal Province and our knowledge of them is very patchy. Occasional eudemic faunas are known from Alaska (*Stenocadoceras*: text-fig. 8O) and from the Russian Platform (*Cadoceras milaschevici*
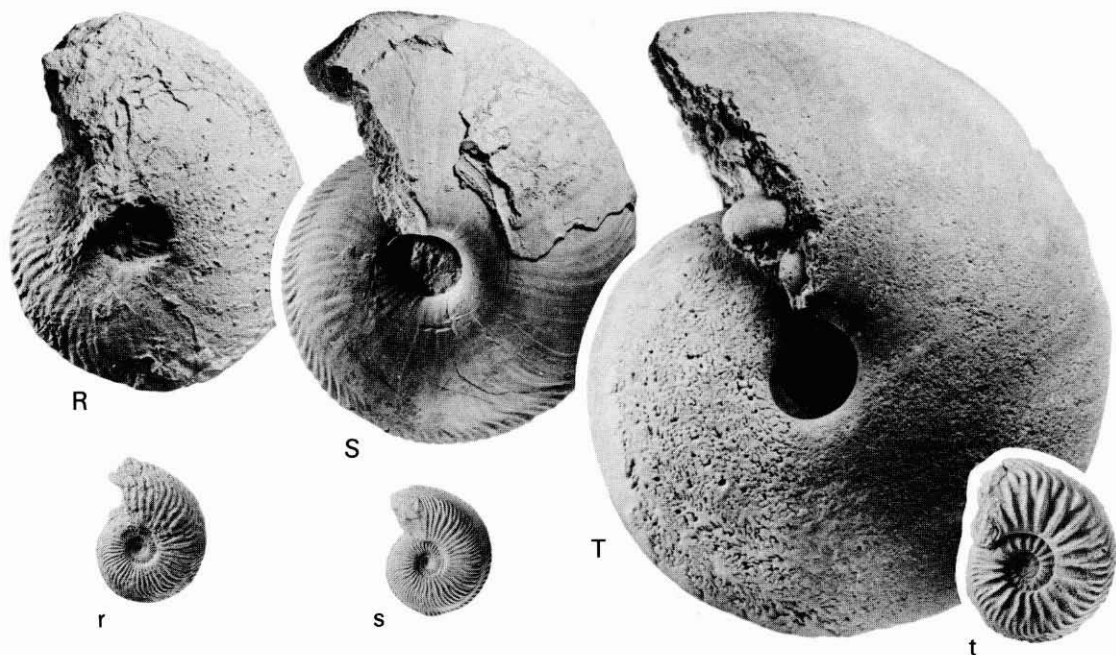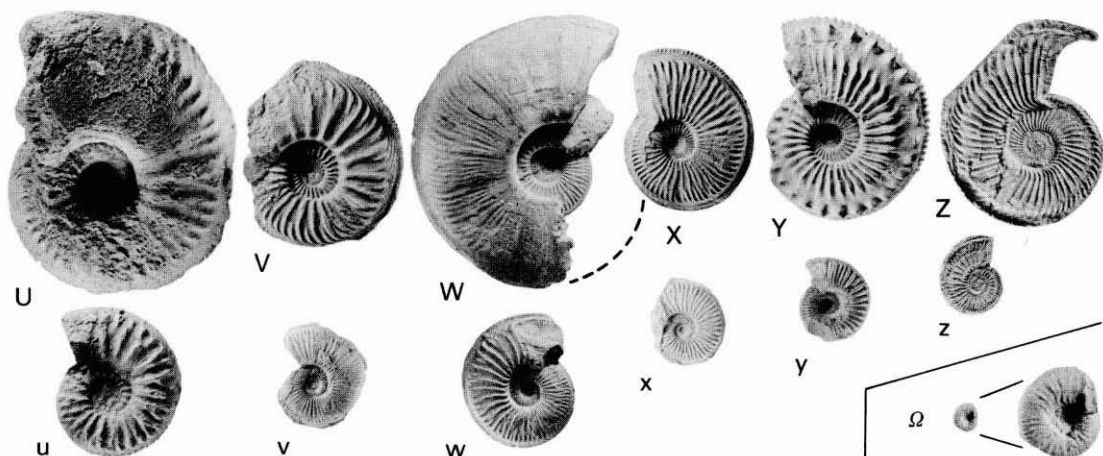
TEXT-FIG. 8, *continued* (v)

OXFORDIAN

R, r, *Cardioceras praecordatum* Douvillé; eastern England, Warboys and St. Ives, Mariae Zone, Praecordatum Subzone. (Incomplete adults; [M], body-chamber just beginning, former extent a further half-whorl; [m], last quarter-whorl body-chamber).

S, s, *C. bukowskii* Maire, 1938; Lower Calcareous Grit, Tenants Cliff Member (formerly Ball Beds: see Wright 1983), Yorkshire coast, Cordatum Zone, Bukowskii Subzone. (Possibly a junior synonym of *C. martini* Reeside, 1919, from southern Alaska. [M]: wholly septate, the uncoiling umbilical seam indicating the former presence of almost another whole whorl, maximum diameter *c.* 320 mm, greater than that of fig. 8T).

T, t, *C. excavatum* (J. Sowerby, 1815) [M]/*C. densiplicatum* Boden, 1911 [m]; Densiplicatum Zone, Vertebrale Subzone, Corallian Beds, southern England.

(Nikitin)), but in most of the more accessible regions of Europe and Greenland their place was taken by the Kosmoceratidae. In the early Upper Callovian they became more common and widespread again as the genus *Longaeviceras* (text-fig. 8P, *p*). Inner whorls are now compressed with acute external margins, developed in extreme variants as a sharp carina. Variability of inflation has again increased, and the cadoceratid characters of sloping umbilical walls with sharp edge have been pushed back proterogenetically to the last stages of ontogeny, on the inflated adult body-chamber. These were undoubtedly the first steps in the direction of *Cardioceras*. Eudemic assemblages of *L. stenolobum* (Keyserling, 1846) (including *L. keyserlingi* (Sokolov) and spp.) are known from the Petchora and the Olenek–Anabar region of Siberia (Sokolov 1912; Bodylevsky 1960; Knyazev *et al.* 1973; Meledina 1977) and characterize the Keyserlingi Zone of the standard Soviet Boreal zonation. More scattered records come from many places within the Boreal Province: from Franz Josef Land, Spitsbergen, Novaya Zemlya, the lower Lena River, and the Alaskan North Slope (see review in Callomon 1984b). In all of this region these were the only ammonites present. Further south, in East Greenland, *Longaeviceras* occurs with *Kosmoceras* in comparable numbers; and in Britain it has become a very minor but persistent component of the ammonite faunas dominated by eudemic Sub-Boreal *Kosmoceras* or, increasingly, Sub-Tethyan invaders such as *Peltoceras* (Athleta Zone).

TEXT-FIG. 8, *continued* (vi)

U, u, *Cardioceras maltonense* (Young and Bird, 1822) [M]/*C. cawtonense* (Blake and Hudleston, 1877) [m] (lectotype, only the last quarter-whorl body chamber). Densiplicatum Zone, Maltonense Subzone, Wiltshire and Yorkshire.

v, v, *Amoeboceras glosense* (Bigot and Brasil); Glosense Zone, Dorset and eastern England.

w, w, *A. serratum* (J. Sowerby, 1813); glacial drift *ex* Ampthill Clay of Lincolnshire, Serratum Zone ([M], neotype).

x, x, *A. regulare* Spath; [M], holotype and [m], topotype, Regulare Zone, Novaya Zemlya.

KIMMERIDGIAN

Y, y, *Amoeboceras kitchini* (Salfeld, 1915) [M]/*A. rasenense* Spath, 1935 [m]; topotype [M], Scotland, and holotype [m], Market Rasen, Lincolnshire; upper Cymodoce Zone.

z, z, *A. kochi* Spath; topotypes, lower Eudoxus Zone, Milne Land, East Greenland.

(Offset)

Ω, *Nannocardioceras anglicum* (Salfeld, 1915); topotype, uppermost Eudoxus Zone, Ringstead, Dorset. The last of the Cardioceratidae: only one specimen is shown, an almost complete adult at ×0·33 and ×1·0, as dimorphism has so far not been recognized in this species.

It survived there with little change to the top of the Callovian and perhaps into the basal Oxfordian (*L. staffinense* Sykes, 1975) (text-fig. 1).

Meanwhile, yet another phylogenetic division of the Cardioceratidae occurred in the Boreal Province, leading to the genus *Quenstedtoceras*. This differs from *Longaeviceras* in three principal respects (see text-figs. 5, 8Q). Oxycone coiling with sharp carina became common; umbilical margins became rounded; and ribbing became strongly differentiated, accentuated primaries standing well apart from largely disjointed, intercalated secondaries (text-fig. 8Q, q). The range of variability became extreme (text-fig. 5). These new faunas formed a second wave of the Boreal Spread, sweeping into the Sub-Boreal provinces in enormous numbers. In Europe north of the Alps and Carpathians this sudden invasion characterizes the base of the Lamberti Zone, and appears to have been synchronous and complete in less than the time of an ammonite subzone. It extended as far south as the Ardèche and Jura, Swabia, southern Poland, the northern Caucasus, and trans-Caspian Turkmenistan. In North America, a similar surge southwards took the new faunas into the Western Interior, as far as Montana (*Q. collieri* Reeside). These new limits were close to the widest achieved by the family (text-fig. 6*b*). At the same time, Tethyan ammonites spread northwards in a profusion not seen since the early Lower Callovian (Callomon 1968, p. 276), so that the time of the maximum Boreal Spread was also one of maximum overlap of faunal provinces. In the Lamberti Zone of

Britain, at least, the phylogenetic separation of *Quenstedtoceras* from *Longaeviceras* was already complete: there are no intermediates. The division must therefore have taken place a little earlier, before the great migration. What appear almost certainly to have been eudemic intermediates have now been described from the Anabar region of northern Siberia (Meledina 1977: *Eboraciceras taimyrense* nov., *E. nikolajevi* (*non* Bodylevsky), *E. subordinarium* (*non* Buckman) [M]; *L. insolitum* nov.; *Q. angustatum* nov. [m]—all 'Subordinarium' Zone). The locus of phylogenesis appears therefore to have lain again within the inner recesses of the Boreal Province proper, and the great migration played little if any part in the process. Neither was the wide range of morphological variability the family had by then assumed associated with it, for it had set in before and remained unchanged thereafter until well into the Oxfordian.

Oxfordian. The Oxfordian Cardioceratidae have been described in profusion from Europe, Asia, and North America. Two recent works add significantly to our knowledge of the Cordatum Zone (Gygi and Marchand 1982; Wright 1983). Distributions stayed wide, reached their maximum (text-fig. 6*b*) and oscillated relatively little. The main conclusions may be summarized as follows. Morphologically, there was a general progress from carinate forms of ogival section with rather simply curved ribbing (*Quenstedtoceras*, text-fig. 8Q, *q*) via keeled forms of sagittate section (*Cardioceras*, 8R, *r*, S, *s*) with more or less strongly differentiated ribbing (8*t*, *u*), to subquadrate forms with wholly differentiated ribbing and vestigial crenulate keel (*Amoeboceras*, 8W, *w*, X, *x*). Variability of inflation remained high up to the Densiplicatum Zone, varying from 30% (*C. excavatum*, text-fig. 8T) to over 80% (*Goliathiceras titan* Arkell, same horizon). It then dropped, and the *Goliathiceras*-like sphaeroconic morphology is not found again. Differentiation of the ribbing reached an extreme in microconchs in the Cordatum and Densiplicatum Zones as *Vertebriceras* or *Sagitticeras*; and in macroconchs in late *Amoebites* (text-fig. 8Y). New characters appeared proterogenetically in at first a minority of variants and subsequently spread through a population gradually before becoming dominant. Thus, in the lower Lamberti Zone, carinate forms are in a minority. In the upper Lamberti Zone they constitute about 50% of the population. In the lowest Mariae Zone, Scarburgense Subzone, carinate forms dominate (*Q. mariae–woodhamense*: Arkell 1939), but the first keeled forms appear (*C. scarburgense*), perhaps 10% of the population. In the upper Scarburgense Subzone, the proportion of keeled forms has risen to 70%; in the lower part of the overlying Praecordatum Subzone (text-fig. 8R, *r*), to 90%. In the upper Praecordatum Subzone, the first *Vertebriceras*-like forms appear; in the lowest Cordatum Zone, these form perhaps 20% of the fauna; and in the middle Cordatum Zone, Costicardia Subzone, they make up at least 50% (*C. quadrarium* Buckman). Progress was, however, far from smooth, and there were numerous reversals. Thus, in the lowest Densiplicatum Zone, there was a temporary reversion to homeomorphs (*C. tenuicostatum*) of forms in the lowest Cordatum Zone without *Vertebriceras*, while the faunas of the middle Densiplicatum Zone, with *Vertebriceras*, are closely homeomorphic with those of the middle Cordatum Zone. Similarly, the *praecordatum*-like forms are recapitulated in the lower Glosense Zone of the Upper Oxfordian (*Amoeboceras ilovaiskii*) (cf. text-fig. 8v, *v*), and *Vertebriceras*-like styles of tuberculate ribbing reappear at various isolated levels, one in the Rosenkrantzi Zone (*A. marstonense* partim), another in the Cymodoce Zone (text-fig. 8Y), and a final one high in the Eudoxus Zone (*Hoplocardioceras decipiens* Spath). Thus, locally there was much oscillation in time between styles of morphology. Significantly, however, the overall progress involving almost exactly the same succession, ranges, and extremes of morphology, often within a single eudemic assemblage, has been recorded in Britain (Arkell 1941–1948; Sykes and Callomon 1979), North America (Reeside 1919; Imlay 1982; Callomon 1984*b*), and northern Siberia (Pavlow 1914; Knyazev 1975). Such close, parallel homotaxis shows that there was effectively complete and instantaneous genetic communication among the Cardioceratidae in all parts of the Boreal Realm throughout at least the whole of the Oxfordian.

Some examples of the distribution of the Cardioceratidae in the Oxfordian are also interesting palaeoecologically. In much of north-west Europe the Lower Oxfordian was widely developed in what seems to have been a specialized biofacies as far as ammonites were concerned. In England it

includes much of the Upper Oxford Clay (cf. Arkell 1939; Spath 1939), and in the eastern Paris Basin and the Jura, the so-called Renggeri Marls (cf. de Loriol 1898–1900; Maire 1908, 1938). The ammonite collections are voluminous and the Cardioceratidae among them consist almost exclusively of beautifully preserved but small pyritic phragmocones. It has therefore been widely assumed that this reflects merely the accidents of preservation and selective weathering, the middle and outer whorls of what would otherwise have been perfectly 'normal', mature ammonites being crushed, decalcified, and hence lost. Excavation of fresh material shows, however, that this is not so. In the great majority of cases the pyritic phragmocones were preserved complete, up to the commencement of the body-chamber. An appreciable fraction of the pyritized specimens even retain traces of the initial parts of the body-chamber. It follows that the shells must have been less than fully grown at death, i.e. juveniles, which is confirmed by the absence of all signs of maturity in fresh specimens with the crushed body-chamber preserved. An analysis of the assemblages in the Mariae Zone at Woodham and Warboys (cf. Callomon 1968) shows that they consisted at most levels exclusively of juveniles, microconchs outnumbering macroconchs by at least 10 to 1. The ammonites are also relatively rare, scattered randomly through the beds and never concentrated at any one bedding-plane. The assemblages therefore have a totally different aspect from that usually met with, especially that of assemblages characterized above as eudemic. This antithesis therefore strengthens the conclusion that the composition of ammonite fossil assemblages is significant. At Woodham and Warboys it is emphasized even further by the observation that the Perisphinctidae in the beds with 'abnormal', juvenile cardioceratids are similarly immature. In contrast, the associated oppeliid Taramelliceratinae (*Taramelliceras richei* [M]–*Creniceras renggeri* [m]: cf. Palframan 1966) are quite mature and consist wholly of adults. Finally, at isolated levels even the Cardioceratidae and Perisphinctidae are again mature. At Woodham, this is the case in a thin limestone bed in Arkell's Selenitic Mariae Clays, bed A, and at Warboys, in bed 4 (text-fig. 8R, *r*).

Kimmeridgian. The Kimmeridgian Cardioceratidae have never been comprehensively described. The record is very patchy both in space and in time, apparently partly due to the exclusive dominance of other groups in the Sub-Boreal Provinces, such as the Aulacostephanidae in northern Europe. But in many areas of the Boreal Realm biofacies developed that seemed to be inimical to ammonites of any kind. Most of those parts of North America in which the Cardioceratidae had flourished were lost to an almost unbroken succession of shales with nothing but *Buchia*. Even the northern North Sea, Viking Straits, and Barents Shelf succumbed to prolonged deposition of black shales, often laminated, indicative of anoxic environments. In these, the genus *Amoeboceras* occurs at isolated, well-spaced but widespread horizons, suggesting infrequent and highly episodic colonization of an otherwise hostile environment; and it seems likely that for much of the time the centres of evolution may have been displaced more towards the peripheral areas of the Boreal Realm. It becomes difficult at times, therefore, to recognize a single phyletic thread through the disjointed record, and a more complicated pattern of phylogenetic divisions than hitherto may one day emerge.

The Kimmeridgian succession begins at a sharp faunal discontinuity. The last Oxfordian forms of the Rosenkrantzi Zone were still of considerable size (*c.* 100 mm), the macroconchs with involute, compressed body-chambers on which the ribbing was subdued or faded altogether, as in *Cardioceras* (Sykes and Callomon 1979, pl. 120). Their southerly limits barely stretched to southern England. They were almost immediately succeeded in the Baylei Zone by a whole new generation of small, evolute, strongly ribbed forms only a quarter of the size, belonging to a species *A. bauhini* (Oppel) (Sykes and Callomon 1979, pl. 121, figs. 1, 4, 5, abundant material in Stuttgart) that was eudemic in areas as far apart as Swabia and Scotland. Thereafter the genus retreated to the north, from East Greenland via Spitsbergen to Franz Josef Land and northern Siberia, where the succession can be clearly followed well into the Mutabilis Zone (Spath 1932; Shulgina 1960; Mesezhnikov and Romm 1973; Mesezhnikov and Shulgina 1982). There was a fairly rapid increase in size and accentuation of the ventrolateral ribbing (Sykes and Callomon 1979, pl. 121, figs. 2, 3) via *A. subkitchini* Spath (1932) to the spectacularly tuberculate *A. kitchini* (Salfeld) (text-fig. 8x, *x*), recalling the sculpture

of *Vertebriceras*, and finally to *A. spathi* Shulgina, 1960 or *A. pulchrum* Mesezhnikov and Romm, 1973. In the Eudoxus Zone, three faunas have been characterized throughout the same region: *A. kochi* Spath (text-fig. 8Y, *y*), *A.* (*Hoplocardioceras*) *decipiens* Spath, and *A. elegans* Spath (1932; Callomon and Birkelund 1982, faunas 20–22). Although more or less tuberculate, they resemble the previous forms in size, dimorphism, and style of ribbing. They are the last Cardioceratidae found in the Arctic.

Finally, the end of the lineage. The youngest faunas known anywhere occur in Britain. They belong to the genus *Nannocardioceras* Spath, of which there appear to be only two species: *N. anglicum* (Salfeld) and *N. krausei* (Salfeld) (text-fig. 8Ω). These are remarkable in two respects: they are minute—complete adults rarely exceed 20 mm in diameter; and they have so far defied all attempts to recognize dimorphism. They appear suddenly in the upper Eudoxus Zone and come to an equally abrupt end in the lower Autissiodorensis Zone (Callomon 1971*b*; Cope 1974; Cox and Gallois 1981). Over this range they underwent little change and occur at many levels, concentrated at some in southern England into veritable shell-breccias. They were therefore truly eudemic in this region, which seems to have been the last outpost of a long lineage. Some other very small species have been described from the Eudoxus Zone of East Prussia (*C. borussicum* and *volgae*, Krause 1909) and the Volga Basin (*C. subtilicostatum* and *volgae*, Pavlow 1886), but seem still to be a little older. There is no discernible evidence whatever in the rocks of anything that could have been associated with this demise.

MODES OF EVOLUTION

The fossil record of the Cardioceratidae, although extensive, continues to be highly punctuate. The evidence consists of discontinuous successions of morphologically distinguishable assemblages A_1, B_1, C_1 . . .; A_2, B_2, C_2 . . .; A_3, B_3, C_3 . . . at widely separated localities 1, 2, 3 . . . within the Boreal Realm, such as East Greenland (1), North America (2), and northern Siberia (3) in particular. The basic problem is that of arranging the assemblages into evolutionary sequences, of attempting to reconstruct their phylogram. Did B_1 evolve from A_1, or from A_2, or from A_3 (sym- or allopatric speciation)? Or what in fact are the genetic relations between roughly contemporaneous but morphologically distinguishable B_1, B_2, and B_3: separate species, or geographical subspecies, and/or phyletic transients (chronosubspecies)? Could $\{B_1, B_2, B_3\}$ be merely a monophyletic descendant of $\{A_1, A_2, A_3\}$?

The earlier discussions in this paper have demonstrated the basic features of these assemblages. (1) They were almost all genetically monospecific, even when morphologically highly variable. This removes much of the impenetrable microdendritic structure of previous phylogenetic reconstruction. (2) They were frequently eudemic: where now found is close to where they bred, and hence to where they were evolving at the time. (3) The time-intervals between them were of the order of 100,000 years. (4) The time-durations they represent are only small fractions of the intervals between them. It immediately follows that even in such a favourable case as the present one, the record continues to be highly incomplete (10% would be a very generous estimate).

Microevolution. The geographical questions are hard to answer unambiguously. If we examine two geographically distant but chronologically close assemblages in detail, we can almost always discern small differences. For example, the very first member of the lineage found in East Greenland (A_1), the Yukon (A_2), and northern Siberia (A_3) are so similar that one would not hesitate to put them into the same species, *Cranocephalites borealis*; yet they differ in small ways that make them distinguishable. In East Greenland A_1 has some stratigraphical range A_1, A_1', A_1'' . . . over which no change can be recognized ('stasis'—at least, as reflected in shell morphology; evolution may well have been occurring in other characters). The next assemblage, belonging to *C. indistinctus* and found in East Greenland (B_1) and the Canadian Arctic (B_2), is similarly close. Yet there is a large morphological jump from A to B.

One could therefore propose either, or a mixture, of two extreme interpretations. In the first, A_1, A_2, A_3, B_1, B_2 represent samples of a single, smoothly evolving lineage taken at different times and places—phyletic gradualism. The implications would be that genetic communication was everywhere instantaneous, and that the discontinuities in the morphological sequence are due to accidents of preservation in a highly incomplete record. Even if the fraction preserved were as high as the

10% quoted above, distributed randomly, the chances of ever finding an assemblage identical with A_1 a second time in another section of beds spanning a similar time range would be 10 to 1 against in any given case. The quasi-stasis in A_1 observed in Greenland could still have been for a very small fraction of the time between A_1 and B_1—probably correct—and be only approximate, because of limited material—also quite likely. The difficulty would be the manifestly non-random bunching of the samples $(A_1, A_2, A_3), (B_1, B_2), \ldots$ which indicates a strong statistical correlation in space-time; but in view of the much greater mystery of why so little of the record is preserved anyway, i.e. why so few at all of the rocks contain ammonites, the non-random distribution of what there is should not worry us too much. One could make up various quite respectable explanations for strong regional and temporal correlations, some of which might even be testable independently.

In the second interpretation, assemblages (A_1, A_2, A_3) and (B_1, B_2) represent samples of an evolving plexus of demes (local populations) in a state of stasis on either side of an effectively instantaneous speciation event, precise moment and place unknown, that occurred at some time between A and B—the model of punctuated equilibria. In this model (B_1, B_2) would be replacements of (A_1, A_2), extinct, by allopatric modification from A_3, or some yet other invisible root. In such a model (A_1, A_2, A_3) need not be chronologically closely correlated. On the other hand, one would expect on random sampling of the plexus to find more evidence of stasis locally, e.g. (A_1, A_1', C_1), $(B_2, C_2, C_2') \ldots$ rather than $(A_1, B_1, C_1), (A_2, B_2, C_2)$. The degree of genetic differentiation achieved in the plexus could, moreover, not have risen much above subspecific level, for the morphological differences between different geographical demes $(C_1, C_2, C_3 \ldots)$ issuing from a common speciation event are usually less than those between extreme variants within the same deme. (If one takes the view that morphology of the shell need be no guide at all to former genetic relationships, then that is the end of the discussion anyway.)

Thus, examining the evidence of the Cardioceratidae at the level of relations between successive assemblages alone, i.e. over time-spans of the order of 100,000 years, one cannot really distinguish between the two models that have been popularly invoked. Even if one could, the difference would not be very interesting, for it would have little bearing on the questions of real interest—see below. One important feature the models do share, however, is the need for complete genetic intercommunication across the breadth of the Boreal Realm within the time-interval between two or at most a very few faunal horizons, say an ammonite subzone, either by direct migration or, less strenuously, through an interbreeding relay. That this was possible can be demonstrated independently, e.g. in the second Boreal Spread at the base of the Lamberti Zone described previously. (The direct distance from Anabar in Siberia to Tidmoor Point in Dorset is 5,000 km. A migration taking 250,000 years need therefore not have progressed faster than 2 km a century—hardly a catastrophic event from an ecological point of view.)

Mesoevolution. The picture becomes clearer when we examine the evidence in the longer term. As also pointed out already, if we compare successive assemblages over longer ranges in widely separated regions, e.g. in twenty or more horizons of the Bajocian-Bathonian, or Oxfordian, of East Greenland, North America, and northern Siberia, the most striking feature is the almost perfect homotaxial correlation between them. This can now have only one interpretation, that of a single gene-pool evolving with time, $\{A_1, A_2, A_3\} \to \{B_1, B_2\} \to \{C_1, C_2, C_3\} \to \ldots$. Segregation into subspecies there may have been, but total separation into reproductive isolation was at best rare. When it did occur we could tell, as in *Chamoussetia* or *Cadoceras nordenskjoeldi*. Partial segregation could well have been followed by rehybridization—and we arrive at Sylvester-Bradley's third model (1977), that of reticulated speciation. Punctuated gradualism (Malmgrem *et al.*, 1983; see also Hallam 1982): punctuated in the short term, gradualistic in the medium to long term, with noise. On balance, it fits the Cardioceratidae best.

Macroevolution. It seems, then, that the complete family tree of the Cardioceratidae is not much more complicated than as it is shown in text-fig. 1. A few twigs need to be added, particularly in the crown of the tree, but the main branches of supraspecific taxa are all there. Evolution there certainly has been, both within the family as reflected in its morphology, and with respect to all the

neighbouring families shown in text-fig. 1, such as the Kosmoceratidae, from which reproductive isolation was complete. But what was the driving force? To what selection pressure, if any, was this evolution an adaptive response?

I have no idea. We have only the morphology of the shells and the circumstances of their fossilization to guide us. The central mystery lies in the great intraspecific variability of morphology. The conventional wisdom associates form with hydrodynamic potential, oxycones are streamlined, adapted for rapid locomotion, sphaerocones the converse, good for quasi-benthonic hovering. Such explanations can hardly fit the assemblage shown in text-fig. 5. Moreover, the range of variability could, as we have seen, persist for long periods of time almost unchanged: from *Lamberticeras-Eboraciceras* in the Lamberti Zone to *Cardioceras-Goliathiceras* in the Densiplicatum Zone. Finally, it could survive without modification a major faunal migration, as in the Lamberti Zone. The idea central to many models of speciation, that high variability is associated with high geographical mobility during faunal migrations and changes of habitat, low variability with evolutionary stasis in equilibrium, seems therefore also not to apply. The coupling between shell and environment, physical or biological, appears to have been negligible. And lithofacies provides no clue either. The variability of eudemic *Cardioceras* in the typical Oxford Clay of the Cordatum–Densiplicatum Zones of Staffin in the Isle of Skye appears to be identical with that found in the limestones and calcareous sandstones of the Corallian Beds of Oxfordshire.

And what of the long-term trends? It is perhaps true in a very broad sense to say, as has been said, that the Cardioceratidae saw an overall transition from early round-whorled sphaerocones to late oxycones with keels. But this by itself means little. If we follow the ancestors of the Cardioceratidae back, as it is perfectly possible to do so today in almost as great detail as we have followed them forward, we come to *Erycites* at the base of the Aalenian (text-fig. 1) and, not much further, to *Hammatoceras* in the Toarcian, with splendid keels and a general style of ribbing and coiling not so very different from some *Amoeboceras* in the Upper Oxfordian. But the main point is that whereas it may be possible to recognize a 'trend' in the lineage *post hoc*, it would have been rash to predict the direction of future development at any single point along the lineage. Thus, as was pointed out previously, the first attempt at a change from sphaerocones to oxycones began in the Bathonian, in the Arcticus Zone. It had progressed a long way in *Arcticoceras* at the end of the Ishmae Zone. Faced at this point with the choice, forwards or backwards, the ammonites took both. The lineage split. One branch completed the process and turned into *Chamoussetia*. The other reverted to perfect sphaerocones in *Cadoceras*. In the Calloviense Zone there was no telling which branch would survive the longest. In the event it was the sphaerocones, who lived to make *Cardioceras* another day. Cope's Rule does not apply here either, other than in the trivial sense that in a lineage the size of whose members goes up and down (text-fig. 8), there must be times when it goes up. And we need shed few tears for the pathetic dwarfs that terminated the lineage. Until the very last day, they were flourishing.

What about relationships between ontogeny and phylogeny? Again, it is hard to discern any of significance. The change from round-whorled to carinate or to keeled coiling might seem a clear example of proterogenesis, in which a change of character first observed in the earlier (but not the earliest) stages of ontogeny subsequently spreads to the later stages. Yet here it depends, for instance, even on which of the dimorphs is being considered. While perhaps true for the isocostate microconchs, it is at best only partly true in the variocostate macroconchs, in which adult variants with carinate to non-carinate body chambers occur together from the Upper Callovian to the Middle Oxfordian. Carination as one character is strongly coupled to inflation as another; and in comparing ontogenetic stages it depends on the choice of criterion, whether equality of shell diameter or degree of maturity. Conversely, the appearance for instance of strong tuberculation on the adult macroconch body chamber of *Amoebites* in the Lower Kimmeridgian (text-fig. 8y) could be construed as an example of palingenesis, in which new characters first appear in the adult stages of ontogeny and the earlier stages recapitulate the morphologies of the ancestors. Yet it is a transient phyletic development, found only in the macroconchs over a range of perhaps four faunal horizons, and is itself homoeomorphic with sculpture found previously only in the adult stages of some

variants among microconchs in the Lower and Middle Oxfordian (*Vertebriceras*). And none of these characters is visible in the earliest ontogenetic stages, at shell diameters between 0·5 and 5·0 mm, anywhere from Bathonian to Kimmeridgian. So, again, much depends on the arbitrary delimitation of ontogenetic stages. All that it seems safe to say therefore is that, phylogenetically, morphological characters come and go, that they may do so at various stages of ontogeny, that they are often strongly coupled, and, perhaps in part because of this, that they may be more or less persistent. The use of terms such as paedomorphosis, with its connotations of the evolution of that part of the genotype controlling ontogenetic development and onset of sexual maturity, seems best avoided in the present context.

The Cardioceratidae therefore provide us with no grounds for invoking any concept of 'macroevolution' distinct from that of micro- or mesoevolution. Of 'species selection' there is no sign.

CONCLUSIONS

The Cardioceratidae have been recorded so abundantly both in space and in time that they must now be able to tell us as much about their evolution as any group of ammonites ever will. The principal conclusions are that locally most assemblages were monospecific and at times highly variable. On the one hand, this greatly simplifies the reconstruction of their lineages, which turn out to have evolved mainly monophyletically. Phylogenetic branching was infrequent and tended to produce offshoots that were localized and short-lived. Among general models of modes of evolution that have been proposed, that which fits best appears to be the one of reticulated speciation put forward by Sylvester-Bradley. On the other hand, the breadth and persistence of the range of variability of the evolving species makes it hard to discern any close connections between morphology, function, and environment, and hence to imagine the nature of the selection-pressure, if any, to which the evolution of the lineage was the adaptive response. In short, we now know rather precisely how the Cardioceratidae evolved, but not why.

More generally, what is known of other groups of ammonites suggests strongly that the conclusions reached in the Cardioceratidae may apply much more widely. They certainly carry over in full to that other closely studied group, the Kosmoceratidae. It would be interesting to see how some of the other ammonite family trees in the literature would survive the arboreal pruning shears.

APPENDIX

DESCRIPTION OF THREE NEW SPECIES

by J. H. Callomon *and* T. Birkelund

This section validates the names of three species that appear as zonal indices in text-fig. 3. The stratigraphy of the type area, Jameson Land, was described by Surlyk *et al.* (1973). Section and bed numbers refer to detailed logs deposited in the records of the Greenland Geological Survey (GGU), Copenhagen. Specimens are in the collections of the Geological Museum of the University of Copenhagen (MGUH). Localities are shown on the geological map of Carlsberg Fjord (Birkelund and Higgins 1977).

Arcticoceras cranocephaloide sp. nov.

Plate 1, figs. 1–3; text-figs. 8ɪ, *i*, 9ᴀ, ʙ

1976 'Boreal ammonite assemblage (mainly *Arcticoceras*) . . .' Birkelund and Perch-Nielsen, p. 304, fig. 269.

Material. Holotype [M] (Pl. 1, fig. 1; text-fig. 8ɪ) (MGUH 16569 *ex* GGU 185602c), paratypes (Pl. 1, fig. 3, text-fig. 9ᴀ, ʙ) (MGUH 16572–16573 *ex* id., a, b) and twenty other specimens out of the field collection cited in the synonymy; south-west of Fossilbjerg, central Jameson Land, section 42, bed 2. Allotype [M] (Pl. 1, fig. 2; text-fig. 8*i*) (MGUH 16570); west of Olympen, central Jameson Land, section 70, bed 11. Further small collections from numerous localities in the Fossilbjerget–Olympen area.

Etymology. When found as slightly phosphatized adult body-chambers, the usual mode of preservation, these can resemble similarly preserved assemblages of *Cranocephalites* sufficiently closely to be mistaken for them.

Description. Macroconchs medium-sized (adults 90–140 mm); inner whorls fairly evolute (umbilical widths around 30%) and rounded in section as in their descendants, early *Cadoceras*; becoming more involute and compressed on adult body-chamber as in their predecessors in the Ishmae Zone. Ribbing initially dense, bifurcating regularly at little below mid-height, gently projected, 30–40 per whorl, persisting over adult body-chamber with perhaps some coarsening and, in some, additional intercalated secondaries. Adult body-chamber moderately contracted at end, ventrally flattened, occupying 0·6–0·7 whorl, terminated by simple peristome immediately preceded by deep, prominent constriction. Inflation moderate, not very variable, 40–50% of the diameter, although in one it reached 80%. Umbilici open, shallow, with well-rounded edges. Sutures typical for family, moderately incised. Microconchs evolute, almost serpenticone (umbilicus 40% at 40 mm); section slightly compressed, arched; ribbing strong, dense, forty to the whorl, ventrally projected, secondaries becoming somewhat accentuated on external margin; peristome with ventral rostrum. Sex ratio greater than 20 : 1 in the Greenland assemblages, in favour of macroconchs.

Comparisons. The characteristic features are the evolute, adult macroconch body-chamber ribbed to the end, and the deep terminal constriction. Nothing comparable appears yet to have been described from anywhere else.


EXPLANATION OF PLATE 1

Figs. 1–3. *Arcticoceras cranocephaloide* sp. nov. 1, holotype [M] (MGUH 16569), complete adult with peristome. 2, allotype [m] (MGUH 16570), complete adult phragmocone. 3, paratype [M] (MGUH 16573), wholly septate nucleus, presumably [M], showing inner whorls. Boreal Upper Bathonian, Cranocephaloide Zone, basal ammonite bed, section 42, bed 2, south-west of Fossilbjerg (fig. 1), and section 70, bed 11, south-west of Olympen (figs. 2, 3), northern Jameson Land.

Fig. 4. *Cadoceras nordenskjoeldi* sp. nov. Holotype [M] (MGUH 16581), complete adult. Lower Callovian, Nordenskjoeldi Zone, horizon *β*; section 43, bed 20, south-west of Fossilbjerg, Jameson Land.

PLATE 1

CALLOMON, Evolution of the Cardioceratidae
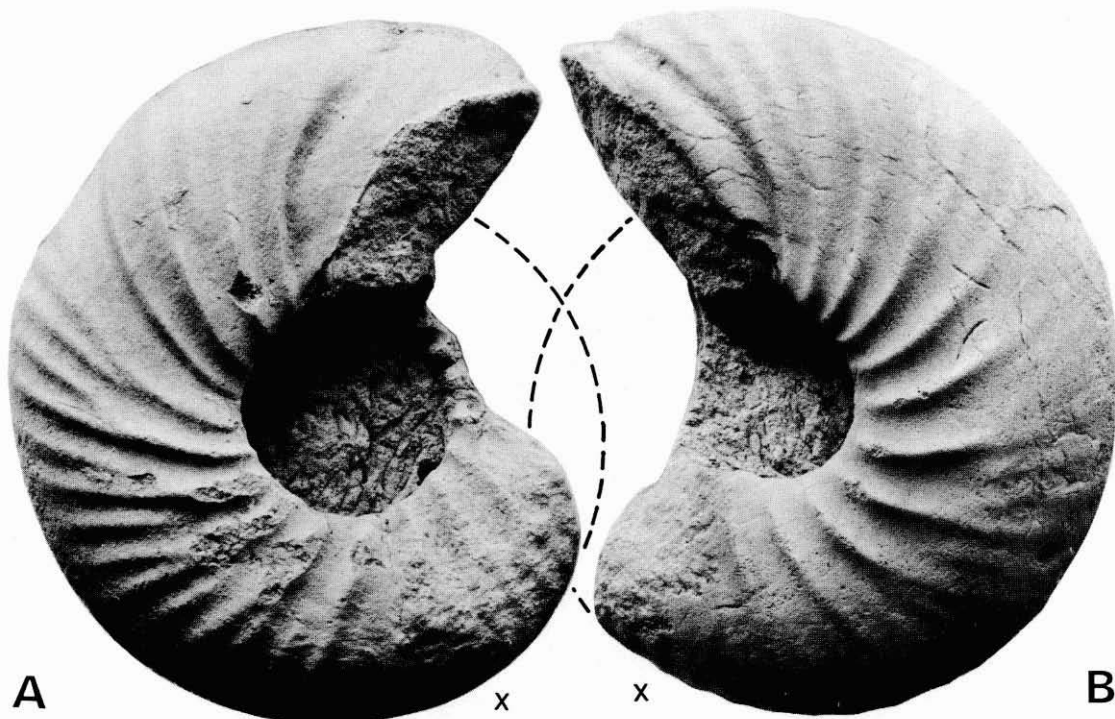
TEXT-FIG. 9. A, B, *Arcticoceras cranocephaloide* sp. nov. Paratypes [M] (MGUH 16571, 16572), body-chambers of two adults with peristomes, × 0·71. Same bed, locality, and sample as the holotype (Pl. 1, fig. 1), Jameson land.

Distribution. Jameson Land, East Greenland, at many localities between the head of Hurry Fjord and the northern slopes of Olympen, always at one concretionary level.

Age. Boreal Upper Bathonian. With it occurs the first of a subsequently uninterrupted succession of Kosmoceratidae, *Kepplerites* sp. nov. (cf. Spath 1932, pl. 26, fig. 6), still round-whorled at all stages of growth both in the macro- and microconchs, six horizons below the *Kepplerites* of the Apertum Zone correlated with the European forms from the basal Callovian (see below).

Cadoceras apertum sp. nov.

Plate 2; Plate 3, figs. 1–6

Material. Holotype [M] (Pl. 2; text-fig. 8L) (MGUH 16574 *ex* JHC2444) and three paratypes (Pl. 3, figs. 2, 3, 6); allotype [m] (Pl. 3, fig. 1; text-fig. 8*l*) (MGUH 16575 *ex* JHC2436) and two paratypes (Pl. 3, figs. 4, 5). The holo- and allotypes came from the southern slopes of Olympen, locality 62, bed 19, collected 1964 by R. C. Whatley and D. M. Brown, the other paratypes from the south-western slopes of Fossilbjerget, locality 43, bed 11. In addition, there are *c.* 100 [M] and 90 [m] from various localities in the same region.

Description. Macro- and microconchs are indistinguishable up to 30 mm: evolute, whorl-section round to slightly compressed and highly arched, whorl-width about 37%, umbilicus 33 to 43% of diameter. Microconchs

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EXPLANATION OF PLATE 2

Cadoceras apertum sp. nov. Holotype [M] (MGUH 16574), complete adult with part of peristome. Lower Callovian, Apertum Zone, horizon *β*; section 62, bed 19, south slopes of Olympen, Jameson Land.

PLATE 2

×
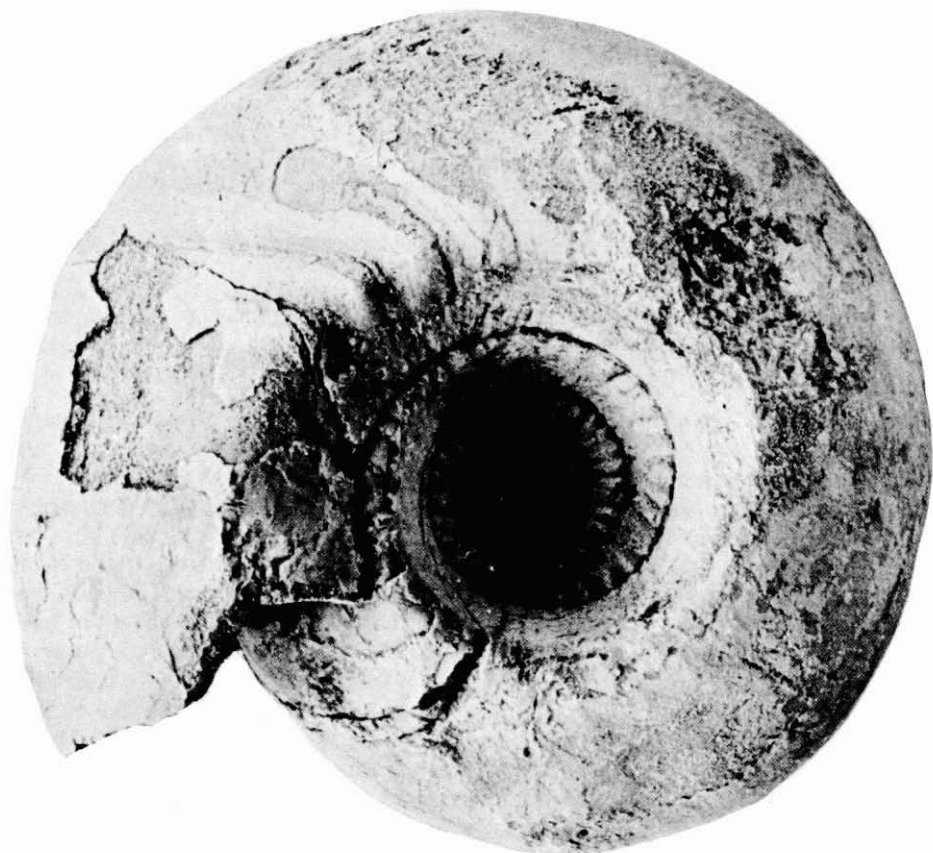
septate to *c.* 35 mm; the adult body-chamber thence increases little in area of cross-section so that umbilicus widens and the outer whorl becomes almost serpenticone. Length of the adult body-chamber *c.* 0.7 whorl; maximum diameter 50–55 mm; peristome with slightly flared collar and strong ventral projection. Ribbing dense, strong, bifurcating about mid-flank with numerous simple ribs and intercalatories; about thirty-three to forty-three primaries per whorl. In the macroconchs the whorl-section begins to inflate, from 45% at 40 mm to 52% at 50 mm, 61% at 60 mm, 65% at 70 mm, 72% at 80 mm, 75% at 90 mm, and 80% at 100 mm (means of five to ten specimens in each case), at about which diameter the mature body-chamber commences. The inflation varies little. The standard deviation of some ten measurements in macroconchs at 90 mm is 9%; in microconchs at 35 mm, 11%. Umbilical width on intermediate whorls ranges from about 30 to 40% of the diameter (see the figured paratypes, which range over the extremes), and whorl-section correspondingly depressed, rounded, or sub-triangular. Ribbing fades around 70 mm and adult body-chamber is smooth, becoming contracted, with some regeneration of ribbing near aperture. Peristome has terminal constriction; maximum diameters between 120 and 150 mm.

Comparisons. The characteristic features of the species are the evolute inner whorls giving a wide, shallow umbilicus with well-rounded edge, followed by the inflated, somewhat more involute adult body-chamber with very steep umbilical walls and sharp umbilical edge, typical of *Cadoceras* s.s.

The nearest forms in the literature appear to be *C. frearsi* (d'Orbigny, 1845), from the Moscow Basin. The specimen figured by d'Orbigny (1845, pl. 37, figs. 1, 2 [M])—probably holotype by monotypy—appears to be lost. It was not among the remaining Russian material from the Keyserling excursion in the Verneuil–d'Orbigny collection when this was redescribed in the *Palaeontologia Universalis* in the first decade of this century. Nikitin (1885, p. 55) also did not see it. He pointed out that the locality cited by d'Orbigny could not have been correct (in common with others), for the oldest rocks occurring there were of Volgian age. He therefore figured a specimen of what he took to be the form closest to d'Orbigny's description, in pl. (*x*) 12, fig. 52, from Elatma on the Oka, south-east of Moscow. This specimen was refigured by Sazonov (1957, pl. 4, fig. 1, 1a [M]) and designated lectotype, but not being a syntype this is technically invalid. To conserve his intention, however, it is now formally redesignated neotype. A number of topotypes (Pl. 3, fig. 2; Pl. 4, figs. 1–3) help to establish the variability. None carries the mature body-chamber, but the general resemblance to *C. apertum* is close as far as they go, particularly in Pl. 4, fig. 1. The ribbing is slightly different, however, in being coarser, blunter, and less regular. What appear clearly to be the associated microconchs were given a new name, *C. mundum* (Sazonov 1957, pl. 6, figs. 2 (holotype) from Elatma, 3–6, from Kostroma), but these do differ significantly from *C. apertum* [m] in being smaller and much less evolute. The horizon is said to lie in the same clays that yield *C. elatmae* and *Macrocephalites*, i.e. the Elatmae Zone of the standard Russian zonation.

There are a few other figures in the literature of isolated forms resembling *C. apertum*, e.g. *C.* cf. *glabrum* Imlay: Meledina (1977, pl. 8, fig. 2; pl. 9, fig. 2), from the Elatmae Zone of the Petshora, and *C. anabarense* Bodylevsky (1960, pl. 4, fig. 3): Meledina (1977, pls. 21–24, fig. 1), from the Elatmae Zone of Anabar Bay in northern Siberia.

Paracadoceras is smaller, more delicately ribbed to smaller diameters, and less inflated. In East Greenland it is also younger.

Distribution. Positively characterized so far only in Jameson Land, it has been found there at many localities around Fossilbjerget and Olympen. The clearest exposures are at locality 43, south-west of Fossilbjerget. Here the species occurs abundantly at three sharply defined concretionary levels (beds 9, 11, 13) in a 1·5 m thick

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Figs. 1–6. *Cadoceras apertum* sp. nov. 1, allotype [m] (MGUH 16575), same bed and locality as the holotype (Pl. 3). 4, 5, paratypes [m] (MGUH 16579, 16580), wholly septate but complete phragmocones. 2, 3, 6, paratypes [M] (MGUH 16576–16578), all wholly septate nuclei, showing the range of variability of coiling and ribbing on the inner whorls. 2–6, section 43, bed 11, south-west slopes of Fossilbjerg, Jameson Land; Apertum Zone, horizon β.

PLATE 3
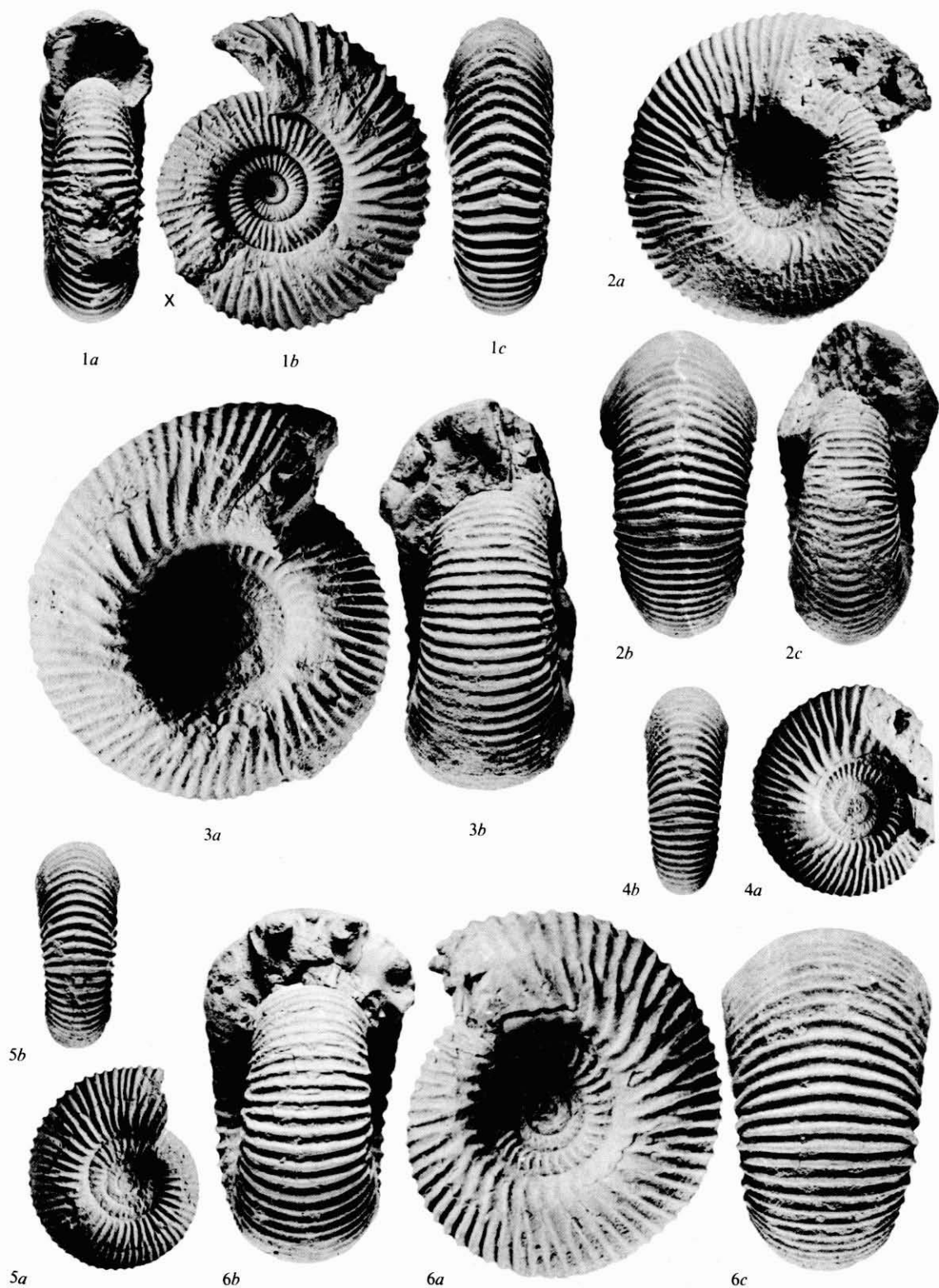
series of highly glauconitic shales. Collected separately, the assemblages are distinguishable, differing slightly in the ranges of variability of the main characters. The youngest of the three has the most evolute variants, with the steepest umbilical walls and sharpest umbilical edges. The three assemblages therefore characterize three successive eudemic faunal horizons in the sense of the previous discussions, and may be labelled α, β, and γ. All the type material came from horizon β. The associated assemblages of *Kepplerites* are also distinguishable. Small collections from other localities could not always be assigned to individual horizons and may in some cases be mixtures from several.

Age. The Keppleritids from the Apertum Zone include *K. traillensis* Donovan, 1953, and closely resemble *K. keppleri* (Oppel), typical variants of which occur in the lowest brachiopod biozone of the English Upper Cornbrash, the *siddingtonensis* zone of Douglas and Arkell. This makes the *K. keppleri* horizon the lowest in the Macrocephalus Zone and Subzone, and hence the Callovian Stage by definition (cf. Callomon 1964). The Bathonian–Callovian boundary in the Boreal Realm has therefore been drawn at the base of the Apertum Zone as being the closest correlation possible. The similarity between *C. apertum* and *C. frearsi* lends support to such a correlation, for the latter, as redefined by the neotype, also occurs in beds with *Macrocephalites* in the Elatmae Zone, well below the Calloviense Zone. The main element of the faunas of the Elatmae Zone, *C. elatmae* itself, in turn has close matches in *C. quenstedti* Spath in the 'Hauptbank' of the Macrocephalenoolith in Swabia, referred to previously, and immediately overlying the horizon of *K. keppleri*. An age of *C. apertum* close to the base of the Callovian seems assured, therefore; but it could still just be Upper Bathonian.

Cadoceras nordenskjoeldi sp. nov.

Plate 1, fig. 4; Plate 4, figs. 1–6

1904   *Olcostephanus* Neumayr (?*Simbirskites*, Pavlow and Lamplugh) nov. sp.; Madsen, p. 195, pl. 10, fig. 2.

Material. Holotype [M] (Pl. 1, fig. 4) (MGUH 16581 *ex* GGU 185619) and paratype [M] (Pl. 4, fig. 3) (MGUH 16582 *ex* JHC2311), from the south-west slopes of Fossilbjerget, sections 43, bed 20, and 44, bed 11 respectively. Madsen's specimen almost certainly came from here also. Allotype [m] (Pl. 4, fig. 6) (MGUH 16585 *ex* JHC3560), west slope of Fossilbjerget, section 44, bed 11. In addition, another twenty or so other specimens, more or less fragmentary, from the same area and from the north-east slopes of Olympen, section 59. All the material is crushed.

Etymology. Named after Otto Nordenskjoeld who, as a member of Hartz's Danish East Greenland Expedition of 1900, collected and brought back the specimen described by Madsen. The exact place and horizon are, however, not known precisely and it is therefore preferable to choose as type an accurately localized specimen.

Description. Microconchs and inner whorls of macroconchs indistinguishable up to about 40 mm: evolute, densely ribbed as in many other early *Cadoceras*. Macroconchs develop coarsely and irregularly ribbed evolute outer whorls. Exact degree of inflation cannot be measured in the crushed material, but never large and cannot have exceeded 50% of the diameter even in most inflated variants. Maximum diameter 130–150 mm.

Comparisons. The characteristic features of the species are the evolute coiling and dense ribbing on the inner whorls changing to very coarse, strong ribbing on the outer whorls. The only comparable figures in the literature are of some specimens from northern Siberia: *C. (Catacadoceras) laptievi* Bodylevsky (1960, pls. 1, 2, figs. 1 [M]; Meledina 1977, pl. 38, fig. 1, pl. 39, fig. 2 [M], pl. 8, fig. 4, pl. 15, fig. 3 [?m]); and *C. (Streptocadoceras)* aff. *kialagvikense* Imlay: Meledina (1977, pl. 24, fig. 2,

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EXPLANATION OF PLATE 4

Figs. 1–5. *Cadoceras nordenskjoeldi* sp. nov. 1, adult [M] (MGUH 16583), point 880 m, north-east of Olympen, top, Nordenskjoeldi Zone, horizon α. 2, small, possibly prematurely adult [M] with final peristome and constriction (MGUH 16584), section 44, bed 11, slopes west of Fossilbjerg; same horizon. 3, paratype [M] (MGUH 16582), near section 44 but higher, Nordenskjoeldi Zone, horizon β. 4–6, body-chamber fragments and complete but crushed adult [m] (MGUH 18585, 18586a, b), same locality and level as fig. 2, horizon α.

PLATE 4

CALLOMON, Evolution of the Cardioceratidae
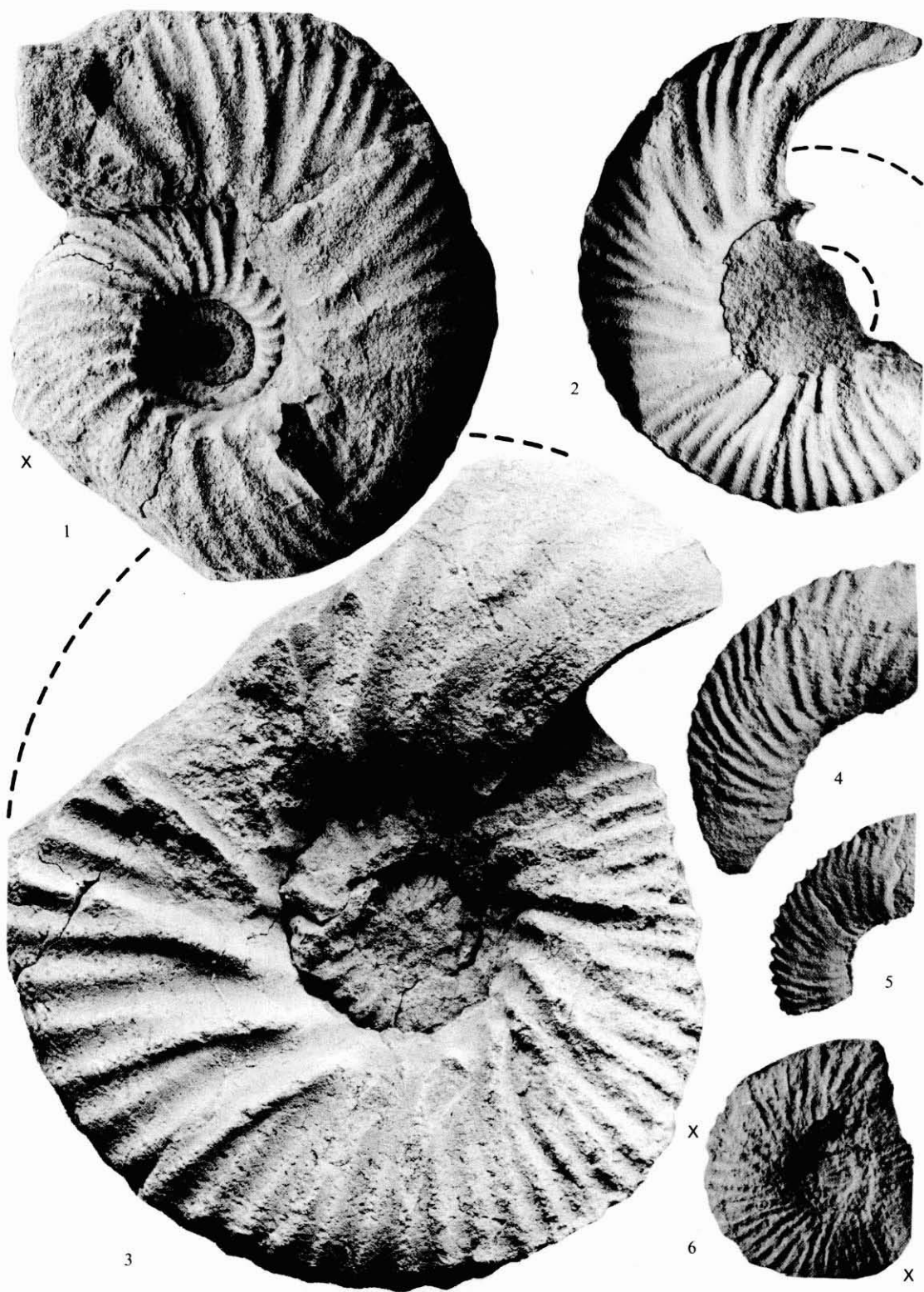
pl. 25, fig. 1 [M]), all from Olenek Bay. They differ in being consistently more inflated and less ser-penticone than the Greenland forms, however, and the only independent indication of their age appears to be their stratigraphical position (Meledina 1977, p. 187) in some 17 m of shales with concretions, between *A. kochi* below and *C. emelianzevi* indicating the Calloviense Zone above. The possibility cannot be ruled out, therefore, that their age is still Upper Bathonian, for in Greenland other forms also not unlike them, resembling *C. subcatostoma* Voronets and *C. ventroplanum* Voronets (1962) from the lower Lena, occur in the Variabile Zone.

Distribution. Known so far only from Jameson Land around the western slopes of Fossilbjerget and north-eastern slopes of Olympen. Beds of the same age are, however, much more widespread in the region. The failure to find ammonites derives almost certainly merely from the lack of concretionary induration of the otherwise soft, micaceous and now deeply weathered shales. Absence from outside East Greenland seems significant, how-ever, and *C. nordenskjoeldi* appears to be a genuinely local endemic species.

Age and associations. *C. nordenskjoeldi* occurs principally at two levels, in concretionary fine-grained sandstones *c.* 6 and 11 m above the glauconitic sandstones of the Apertum Zone. These beds are followed by minor changes of facies and probably mark breaks in sedimentation. The ammonites in them are abundant, typical of eudemic assemblages, but invariably crushed. The two assemblages are once again distinguishable morphologically, and may be labelled α and β. The earlier forms in α are slightly smaller than those in β and their ribbing is not as coarse. The types [M] are from level β. Both assemblages are accompanied by occasional specimens of typical *C. (Paracadoceras)*, rather small, inflated, and smooth, and *Kepplerites* sp. They are succeeded in higher beds by *Cadoceras* s.s. of the Calloviense Zone. Their age must therefore be equivalent to the lower Macrocephalus Zone of Europe.

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J. H. CALLOMON

Department of Chemistry
University College London
20 Gordon Street
London WC1H 0AJ

T. BURKELUND

Institute of Historical Geology
Østervoldgade 10
Copenhagen 1350K
Denmark