CARDIOCERATID AND KOSMOCERATID AMMONITES FROM THE CALLOVIAN OF YORKSHIRE

by J. H. CALLOMON *and* J. K. WRIGHT

ABSTRACT. New stratigraphic evidence and systematic revision, including the designation of types where necessary, establish unambiguously the definitions and precise ages of a number of classical species of ammonites which, although in part rare in this country, are of great importance in understanding the evolution of the Boreal and Sub-boreal families Cardioceratidae and Kosmoceratidae. They include *Pseudocadoceras boreale* Buckman, 1918, *Chamoussetia funifera* (Phillips, 1829), *Chamoussetia phillipsi* = nom. nov. pro *Ammonites lenticularis* Phillips, 1829, non Young and Bird 1828, *Longaeviceras placenta* (Leckenby, 1859), *Quenstedtoceras flexicostatum* (Phillips, 1829) and *Kosmoceras rowlstonense* (Young and Bird, 1822). Five new specific names are introduced: *Chamoussetia phillipsi* nom. nov., *C. buckmani* and *C. saratovensis* spp. nov., *Pseudocadoceras grewingki whithami* subsp. nov., and *Longaeviceras polonicum* sp. nov.

As with other parts of the Jurassic, Yorkshire is the home of a number of classical species of Callovian ammonites published in the early works of Young and Bird (1822, 1828), Phillips (1829), and Leckenby (1859). Their names have become deeply entrenched in the literature, but not without some confusion. This had commonly two causes: the poverty of the original illustrations with, in many cases, the subsequent loss of the type material; and the lack of precise stratigraphical information on the exact places and levels from which the type material came. Attempts were made to remedy these deficiencies by Buckman (1909–30, 1913), who refigured as many types as he could find and identified as far as possible their horizons; and Howarth (1962), who gave a complete list of the names of Young and Bird's and Phillips' species with a summary in each case of what was known about the types. (The species of Martin Simpson (1843) were also included in Howarth's lists, but as almost all came from the Lias they need not be considered further here.) While these works served positively to identify the type-specimens, the uncertainties attaching in many cases to horizons could not be removed without further stratigraphical fieldwork.

The first modern attempt to classify the Callovian rocks of Yorkshire was made by Buckman (1913), who, however, restricted his efforts largely to a study of the matrices of museum specimens and attempts to relate them to the earlier descriptions of the coastal sections, notably that by Leckenby. Subsequent study of the faunas in the museums, by Spath (1933) and Arkell (1939), made it possible to work out many of the details of the zonal succession present with the aid of those species also known from elsewhere, but there remained a handful which could still not be placed. They are mainly Boreal forms which have assumed a new importance in relation to the more general exploration in recent years of the circum-Arctic Jurassic. An extensive revision of the Callovian stratigraphy of NE Yorkshire by one of us (Wright 1968, 1977, 1978) has provided new evidence, and the purpose of these notes is to clarify the systematic and stratigraphic positions of some of these species, belonging to the genera *Pseudocadoceras*, *Chamoussetia*, *Longaeviceras*, *Quenstedtoceras* and *Kosmoceras*.

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STRATIGRAPHY

The area which has produced by far the most Callovian ammonites in Yorkshire is that around Scarborough, including the famous coastal sections and a few quarries inland, notably those near Hackness. The succession was established by Wright (1968) and is summarized in text-fig. 1, which includes also the standard succession in southern England between Cirencester in Gloucestershire and Dorset for comparison. In Yorkshire much of the confusion in the past arose from the failure to recognize that what appeared to be a monotonous succession of sandstones and chamositic oolites – the Kelloway Rock of early authors, now the Osgodby Formation (Wright 1978) – was divisible into several units, shown by their fossils to be separated by major non-sequences. Careful collecting in recent years indicates that the ammonites in museum collections came predominantly from three levels.

a. Calloviense Zone, Koenigi Subzone: widespread fossiliferous chamositic oolite sandwiched between rather barren sandstones in the Kellaways Rock, labelled β_2 by Wright (1968, p. 372) and particularly well exposed in Cayton Bay.

b Athleta Zone, Proniae Subzone: the lower part of the Hackness Rock from which came most of the material in the classical collections labelled 'Scarborough'. It is particularly fossiliferous at Castle Hill, Scarborough, and at Hackness. Re-excavation of the old quarry there (Wright 1968, p. 391) has now yielded over 130 ammonites.

c. Hackness Rock, Lamberti Zone and Subzone: the top part of the Hackness Rock with a quite distinct fauna. Locally the matrix is also distinct so that material from Gristhorpe Cliffs, for instance, may be recognized easily by the white calcareous rock, the large scattered ooliths, and the black calcitic tests of the fossil shells.

In Wiltshire and Dorset the succession which was pieced together largely from older descriptions and museum collections (Callomon 1955) has been confirmed and greatly amplified by new, temporary exposures and borings around Fairford and Cirencester in Gloucestershire, and Chippenham in Wiltshire, and in a road-cutting for a by-pass at Wincanton in Somerset. The borings were described by Cave and Cox (1975). The faunas of the Koenigi and Calloviense subzones can now be assigned to a succession of eight distinct faunal horizons (Page, 1988), labelled VIII–XV. Full descriptions will be given elsewhere, but a summary has been published (Callomon, Dietl and Page 1989).

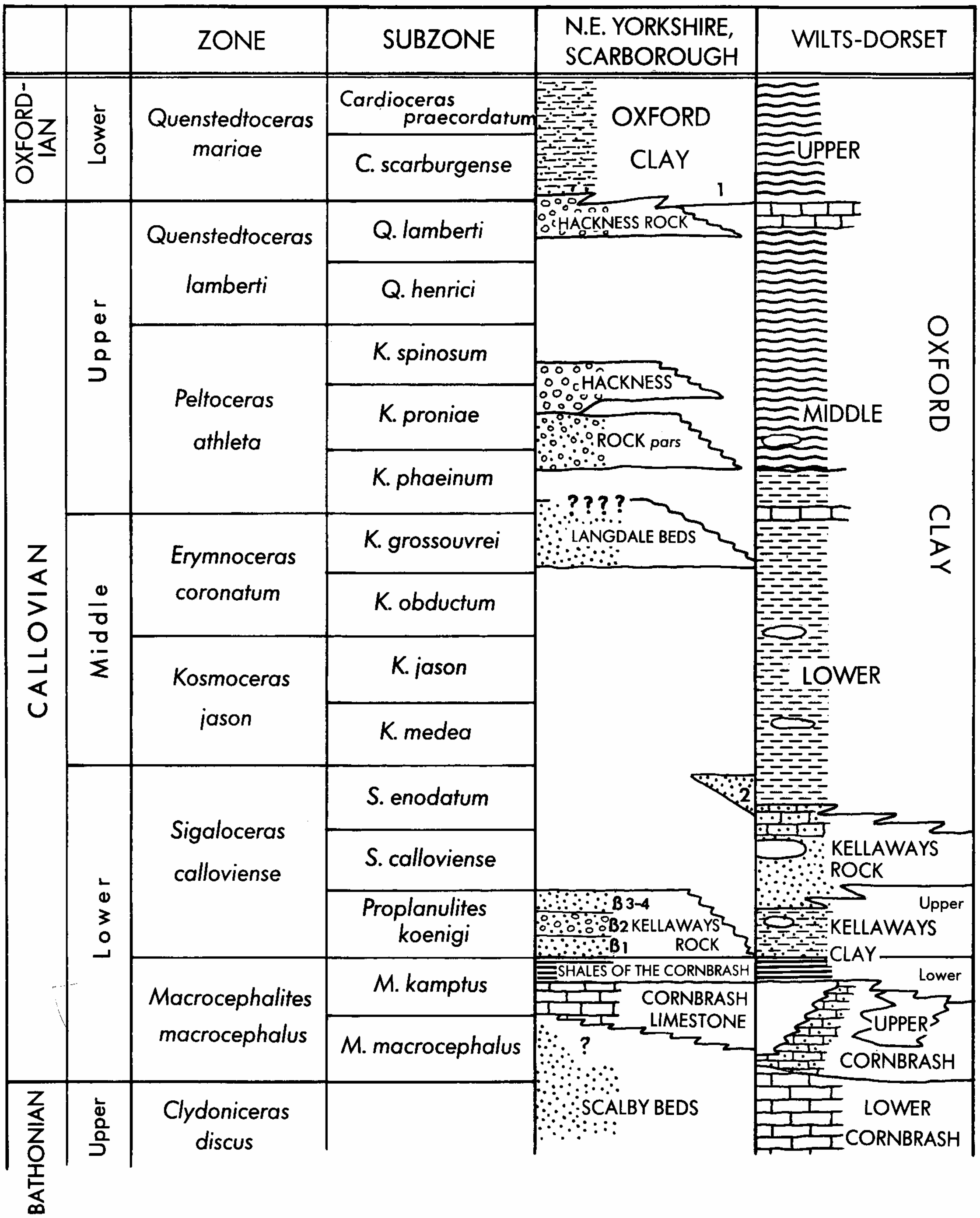
(XVI–XVIII. *Sigaloceras enodatum* (Nikitin): Enodatum Subzone)
XV *Sigaloceras micans* Buckman: *Cadoceras sublaeve* var. *rugosa* Spath, *Proplanulites petrosus* Buckman
XIV *Sigaloceras calloviense* (Sowerby); *Cadoceras sublaeve* (Sowerby), *Proplanulites crassicosta* Buckman
XIII *Kepplerites galilaeii* (Oppel); *Cadoceras tchefkini* Spath non Nikitin
XII *Kepplerites trichophorus* (Buckman)
XI *Cadoceras tolype* Buckman; *Proplanulites ferruginosus* Buckman
X *Kepplerites curtilobus* (Buckman)
IX *Kepplerites gowerianus* (Sowerby); *Cadoceras* sp. *B*, *Proplanulites koenigi* (Sowerby) β
VIII *Kepplerites metorchus* (Buckman); *Cadoceras* sp. *A*, *Proplanulites koenigi* α (s.s.), *P. laevigatus* Buckman, *Macrocephalites lophopleurus* (Buckman)
(I–VII *Macrocephalites* spp.; Macrocephalus Zone)

Even these do not represent anything close to a continuous succession, and there remain many gaps to be filled.

The fauna of the unit β_2 in the Kellaways Rock of the Yorkshire coast characterizes a faunal horizon that probably falls into one of these gaps. It includes the following forms:

Kepplerites (*Gowericeras*) *indigestus* (Buckman, 1922) [M] (pl. 309)

K. (*Toricellites*) cf. *lahuseni* Parona and Bonarelli, 1895 [m], (p. 138) (type *Kosmoceras gowerianum* (Sowerby): Lahusen 1883, pl. 4, fig. 8) (? synonym *Kepplerites distans* Tintant, 1963, p. 182)



TEXT-FIG. 1. Summary of the Callovian stratigraphy of north-east Yorkshire and southern England. (1) Transitional beds with *Quenstedtoceras paucicostatum* Lange. (2) Kellaways Rock extends upwards to include the Enodatum Subzone at its type-locality at South Cave, Humberside. The Scalby Beds are non-marine; their age is not closely determinable.

Cadoceras cf. *tolype* Buckman, 1923 [M] (pl. 406)
C. (*Pseudocadoceras*) *boreale* Buckman, 1918 [m] (described below).
Proplanulites ferruginosus Buckman, 1921 [M] (p. 34; type figured by Clark 1982, pl. 2, fig. 8)
P. rufus Buckman, 1921 [m] (p. 39; Clark 1982, pl. 2, fig. 3)
Chamoussetia phillipsi nom. nov. (described below).

The affinities of this assemblage are closest with that of fauna XI, although whether slightly older or younger cannot at present be determined. The style of ribbing in the *Kepplerites* from this horizon has already some resemblance to that in *Sigaloceras*, but no true representatives of this genus have ever been found in NE Yorkshire. This horizon may be referred to as the *Kepplerites indigestus*/*lahuseni* horizon.

The lower part of the Hackness Rock contains more than one fossil horizon, for it has yielded ammonites not found together in southern England. These include:

Peltoceras athleta (Phillips, 1829)
Kosmoceras gemmatum (Phillips, 1829)
Kosmoceras duncani (J. Sowerby, 1817)
Kosmoceras proniae Teisseyre, 1884
Kosmoceras rowlstonense (Young and Bird, 1822)
Kosmoceras spinosum (J. de C. Sowerby, 1826)
Kosmoceras rimosum (Quenstedt, 1887)

The true *P. athleta*, in which the variocostate modification of the ribbing is extreme and substantially complete already at diameters of 30 mm (see neotype, figured by Spath 1931, pl. 106, fig. 3, pl. 107, fig. 5, designated and refigured by Arkell 1933, p. 610, pl. 37, fig. 6; and topotype figured by Spath 1931, pl. 106, fig. 6*a*, *b*), is virtually unknown in the abundant collections of pyritized material from southern England. These are dominated by forms usually called *P. trifidum* (Quenstedt) (see e.g. Prieser 1937, pl. 2, figs. 7*a*, *b*). *P. athleta* occurs in western France in Horizon XV, Trezeense Subzone of the Athleta Zone in the standard Submediterranean zonation (Cariou 1985, p. 317). It is associated there with numerous *Pseudopeltoceras* and *Binatisphinctes*. These are similarly abundant in the collections from the Hackness Rock of Scarborough (Cox 1988), but whether they occurred together with *P. athleta* there is not known. In contrast, these forms are rare or absent in the *proniae-trifidum* fauna of southern England. It seems probable that the Yorkshire horizon of *P. athleta* is a little older.

Kosmoceras gemmatum (neotype designated and figured by Arkell 1939, p. 189, fig. 4) appears to have been described so far only from Yorkshire where, to judge from the collections, it was relatively common. Its precise horizon remains uncertain, although the forms most closely resembling it found in southern England occur there in the lowest, Phaeinum Subzone of the Athleta Zone.

Kosmoceras duncani was for a long time one of the most widely cited but misidentified species of the Oxford Clay. Its interpretation was stabilized through the designation of a neotype by Arkell (1939, p. 192, pl. 11, figs. 6*a–c*, from St Neots, Cambridgeshire). It is easily recognized by the unusual development of its secondary ribbing, which reunites in bundles of up to five ribs into ventrolateral clavi at the external margin of the shell. Specimens from Scarborough matching the neotype almost exactly are in the Phillips collection in Oxford. In Oxfordshire and Buckinghamshire, the species occurs at a narrow level just below the main horizon yielding *Peltoceras trifidum* and *Kosmoceras proniae*, the index of the middle, Proniae Subzone of the Athleta Zone. The other species of *Kosmoceras* listed above have rather longer ranges but, in the Oxford Clay of southern England, the main occurrences of *K. spinosum*, *rimosum* and *rowlstonense* lie higher than those of *K. proniae*. They are discussed further below.

We have therefore shown in text-fig. 1 the Hackness Rock of the Athleta Zone as spanning two broad horizons: an earlier horizon containing *K. gemmatum*, *K. proniae*, *K. duncani* and *P. athleta*, and a later one dominated by *K. rowlstonense* with *K. rimosum* and *K. spinosum*. It is however not possible at present to separate the two horizons in the field. It seems that reworking under very gentle conditions has condensed the two ammonite faunas into one thin bed of chamosite oolite.

Phosphatic ammonite fragments, sometimes crushed and abraided, are common in the Athleta Zone at Hackness and on the Scarborough coast.

The upper part of the Hackness Rock on the Yorkshire coast seems to lie wholly within the upper, Lamberti Subzone of the Lamberti Zone. *Kosmoceras* has become much less common than in the beds below, amounting to only 10% of the ammonite fauna. It is represented by *K. compressum* (Quenstedt), *K.* cf. *rowlstonense* and *K.* cf. *spinosum* all *sensu* Arkell (1939), in about equal proportions. The Henrici Subzone of the Lamberti Zone and the Spinosum Subzone of the Athleta Zone below, in which the characteristic spinose *Kosmoceras* dominate, appear to be wholly missing (text-fig. 1). The remainder of the fauna of the upper Hackness Rock of Yorkshire is as diverse as that of the English Midlands, as described by Arkell at Woodham (1939), and typical of the Lamberti Subzone. The Cardioceratidae dominate and among these one species from Yorkshire whose interpretation has been uncertain is now redescribed: *Quenstedtoceras flexicostatum* (Phillips, 1829). It is the microconch of *Quenstedtoceras lamberti* (J. Sowerby, 1817).

SYSTEMATIC DESCRIPTIONS

Abbreviations. Numbers refer to specimens in the following collections: BM British Museum (Natural History), London. BGS British Geological Survey, Keyworth. OUM Oxford University Museum. SM Sedgwick Museum, Cambridge. WM Woodend Museum, Scarborough. JKW J. K. Wright collection. JHC J. H. Callonom collection. PFR P. F. Rawson collection. [M], [m] designate macro- and microconch dimorphs respectively; asterisks (*) against items in synonymies or references to figures indicate type specimens.

Family CARDIOCERATIDAE Siemiradzki, 1891

The evolution of the Cardioceratidae was recently reviewed in some detail (Calloman 1985). Besides the main lineage, leading from Pacific Bajocian *Sphaeroceras* via Bathonian *Arctocephalites*, Callovian *Cadoceras*, Oxfordian *Cardioceras* to Kimmeridgian *Amoeboceras*, there are a number of lesser branches that are still not so well understood. They include three Callovian nominal genera – *Chamoussetia, Pseudocadoceras* and *Longaeviceras* – that include forms which are in part homoeomorphic among themselves and which already mimic morphological features that became dominant only much later, in *Cardioceras* itself. The new collections from Yorkshire remove many previous uncertainties, mainly of precise ages.

Subfamily ARCTOCEPHALITINAE Meledina, 1968
Genus CHAMOUSSETIA Douvillé, 1911

Type species. Ammonites chamousseti d'Orbigny, 1847

Chamoussetia phillipsi nom. nov.

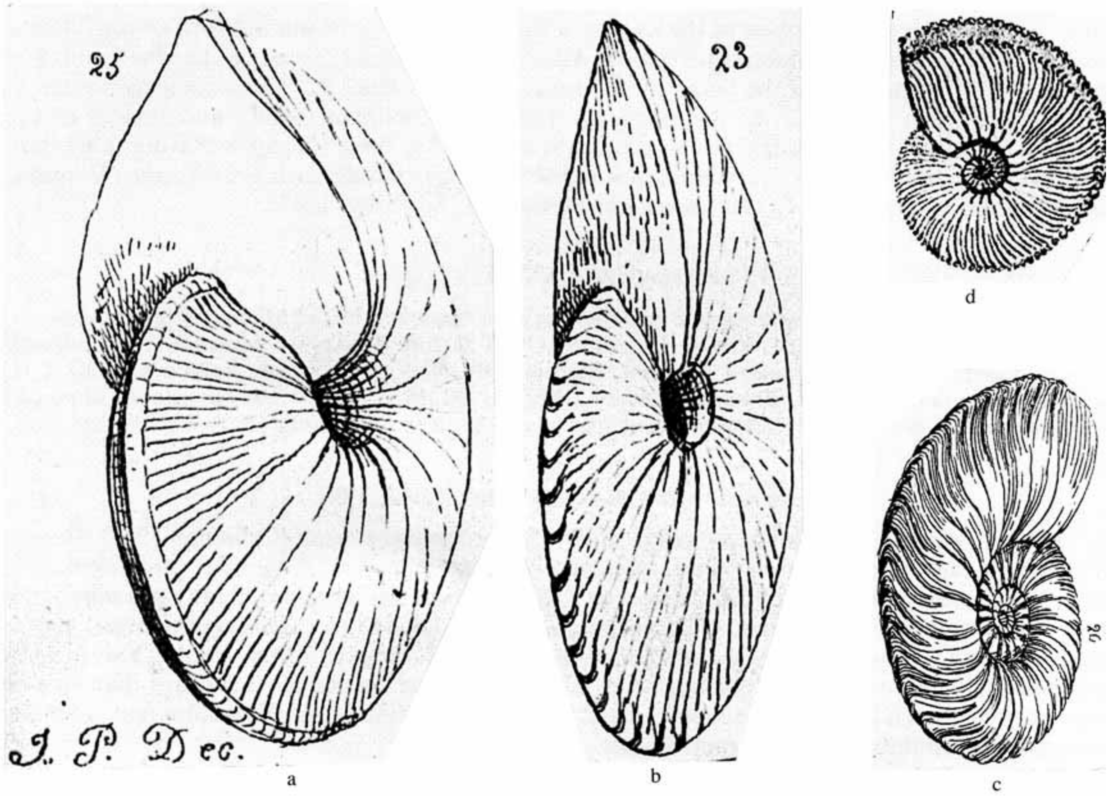
Plate 88, figs. 1–3, plate 89, figs. 1–5; text-fig. 2*a*

*1829 *Ammonites lenticularis* Phillips (non Young and Bird, 1828); p. 131, 142, 164, pl. 6, fig. 25 (refigured unchanged in later editions of 1836 and 1875).
?1875 *Ammonites stuckenbergi* Lahusen; in Stuckenberg, p. 115, pl. 5, figs. 1–3.
1885 *Cardioceras chamousseti* (d'Orbigny); Nikitin, p. 20, pl. 1, figs. 1–4.
?1914 *Phlycticeras hyperbolicum* (Simpson MS – Leckenby); Buckman, pl. 98A, B and text.
1962 *Chamoussetia lenticularis* (Phillips, non Young and Bird): Howarth, p. 125.
non 1828 *Ammonites lenticularis* Young and Bird, p. 269 (holotype figured by Buckman, 1910, pl. 20: an *Amauroceras* from the Middle Lias).
non *1847 *Ammonites chamusseti* d'Orbigny, p. 437, pl. 155, figs. 1, 2 (*recte chamousseti* (art. 31(a), 32(c)(d); cf. Parona and Bonarelli 1895, and Douvillé 1912) (type species of *Chamoussetia*).
non 1887 *Ammonites chamousseti* d'Orbigny; Quenstedt, p. 806, pl. 90, figs. 18, 18p (previously figured in 1857) (= *Chamoussetia* sp. aff. *buckmani*?)

? 1912 *Chamoussetia chamousseti* (d'Orbigny); Douvillé, p. 19, pl. 3(11), figs. 12, 12*a* (nucleus of *buckmani*?)

non 1924 *Chamoussetia lenticularis* (Phillips); Buckman, pl. 462 (= *C. buckmani* sp. nov., holotyp refigured here on pl. 90)

non 1932 *Chamoussetia chamousseti* (d'Orbigny); Corroy, p. 115, pl. 11, figs. 3, 4 (= *C. buckmani*)



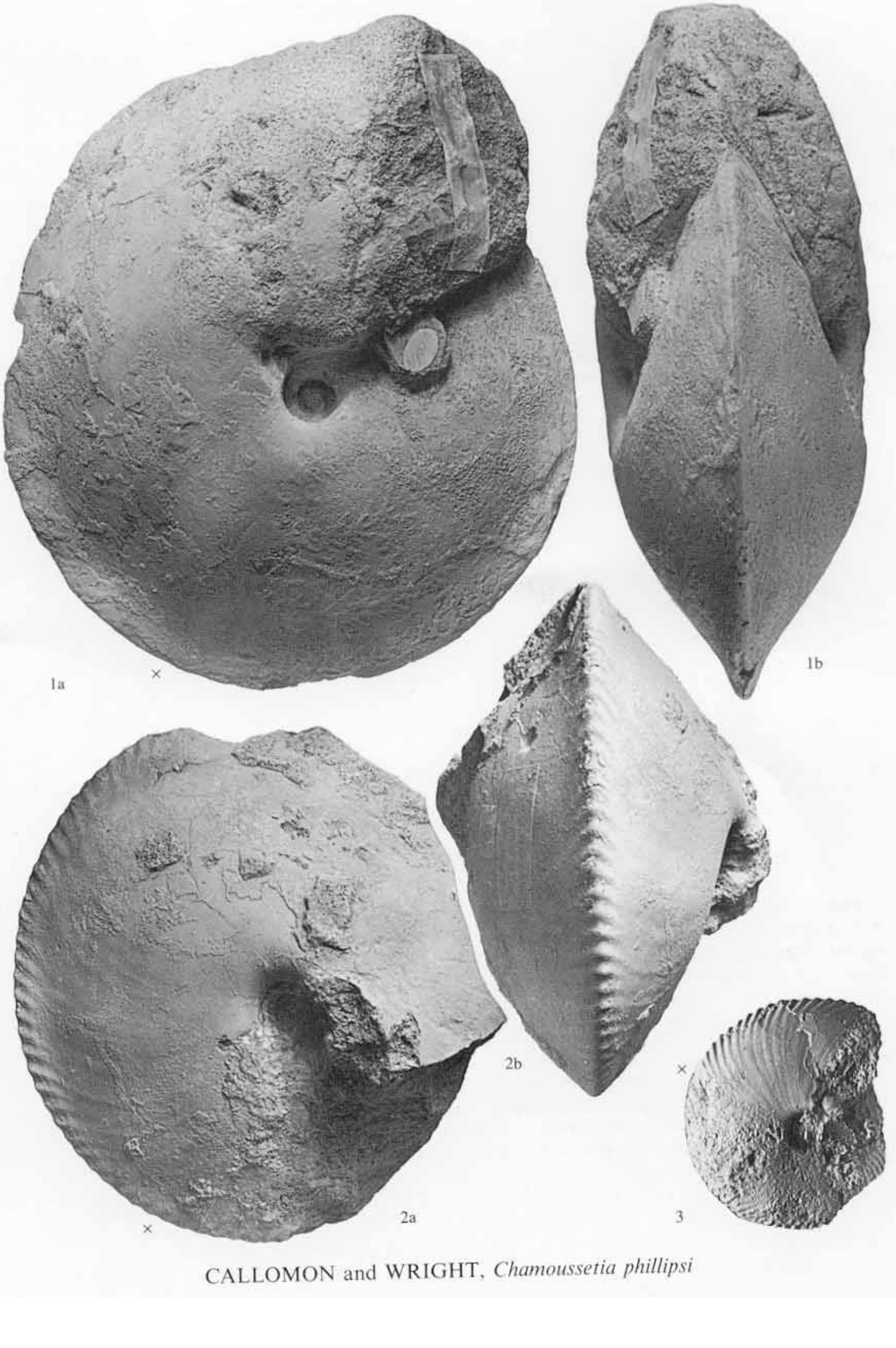
TEXT-FIG. 2. Original figures of Yorkshire species. a, *Ammonites lenticularis* Phillips (1829, pl. 6, fig. 25, draw '×½', here re-enlarged ×2 to natural size) (= *Chamoussetia phillipsi* nom. nov. b, *Ammonites funiferus* Philli (1829, pl. 6, fig. 23, also drawn '×½' and re-enlarged here to natural size) (= *Chamoussetia funifera*). *Ammonites flexicostatus* Phillips (1829, pl. 6, fig. 20, ×1) (= *Quenstedtoceras flexicostatum*). d, *Ammonit rowlstonensis* Young and Bird (1822, pl. 13, fig. 13, ×1) (= *Kosmoceras rowlstonense*).

Nomenclature and neotype. Phillips' species was published in 1829 without formal description s that his intentions must be deduced from his single figure (here reproduced as text-figure 2*a*) an scattered references in the text. The figure, legend and text on p. 142 refer unambiguously to *Chamoussetia* from the Kelloway Rock, i.e. Osgodby Formation, and the species is claimed to b new. On p. 164 it is, however, also cited as from 'ironstone' in the Lias without any reference t

EXPLANATION OF PLATE 88

Figs. 1–3. *Chamoussetia phillipsi* nom. nov. 1*a*, *b*, neotype, [M], adult with half a whorl of bodychamber, B 39516, Bean coll., Scarborough; 2*a*, *b*, [M], mostly bodychamber, SM J47427, Kellaways Rock, Cayto Bay; 3, [m], with a quarter whorl of bodychamber, JKW DC20, ibid. – All Calloviense Zone, Koeni Subzone, *lahuseni* horizon.

A cross marks the position of the last septum at the end of the phragmocone.



CALLOMON and WRIGHT, *Chamoussetia phillipsi*

TABLE 1. Dimensions of *Chamoussetia phillipsi* nom. nov.

	(a) D(max) mm	(b) D(phrag) mm	(c) Bodych. whorl	(d) D: B/D	(e) D(sec − r) mm	(f)
			Macroconchs			
SM J3267 (Buckman pl. 98)	78	(?)	(?)	70: 1·05	< 50	no sutures visible
SM J12206 (Arkell 1948, 398)	160	120	0·50	120: 0·79	< 100	us, some p
SM J12205 (Pl. 89, fig. 1)	90	75	(0·65)	85: 0·79	70	
SM J47428	(90)	75	0·60 +	75: 0·68	75	
SM J12201	110	(?)	(?)	95: 0·60	< 75	no sutures visible
SM J12203	85	(?)	(?)	80: 0·60	< 60	no sutures visible
SM J47427 (Pl. 88, fig. 2)	(95)	(70)	0·75	85: 0·57	> 90	juvenile?
SM J12204	105	80	0·50 +	90: 0·52	100	
SM J12202	90	90	0	80: 0·41	90	
BM 39516 (neotype, Pl. 88, fig. 1)	115	85	0·60	85: 0·40	< 65	us, some p?
BM C.13045 ('Cirencester')	140	100	0·75	100: 0·67	< 100	
			Microconchs			
SM J12180 (Pl. 89, fig. 2)	59	47	0·60	47: 0·48	45	as
SM J12182 (Pl. 89, fig. 5)	41	31	0·60	37: 0·40	30	
JKW DC20 (Pl. 88, fig. 3)	41	37	(0·30 +)	40: (0·40)	30	
PFR M748 (Pl. 89, fig. 4)	49	(35)	0·60	40: 0·37	40	
JKW BC16 (Pl. 89, fig. 3)	(60)	(40)	0·60	48: 0·36	< 40	us, as, p
			Chamoussetia chamousseti (d'Orbigny) [M]			
Holotype (text-fig. 3)	95	77	0·3 +	90: 0·52	95	us, as

(a) Maximum diameter of the preserved shell.

(b) Diameter at the last septum of the phragmocone.

(c) Body-chamber preserved, as fraction of a whorl, estimated to nearest 0·05, or former extent as indicated by traces of the umbilical suture.

(d) Whorl-breadth (thickness) as a fraction of the diameter at the value of the diameter quoted, usually taken near the end of the phragmocone before the onset of the strongly modified part of the adult body-chamber.

(e) Diameter at which the seconary ribbing has totally faded (macroconchs) or has been reduced to vestigial crenulations (microconchs). '<' indicates values less than the diameter at which the venter first becomes visible; '>', greater than the maximum diameter of the preserved shell.

(f) Diagnoses of maturity or otherwise; us, uncoiling of the umbilical seam; as, approximation and simplification of the last septal sutures; p, peristome preserved.

Figures in brackets: estimates where shells are crushed or broken. All specimens from the Scarborough area, except where indicated.

Young and Bird, although elsewhere on this page other species are explicitly ascribed to them. It seems therefore that Phillips was unaware of Young and Bird's previous publication of the name *lenticularis* of which Phillips' is a junior homonym. Whether Phillips' species has subjective junior synonyms whose names could serve instead is a separate question discussed below. To allay confusion the species is however first validly renamed.

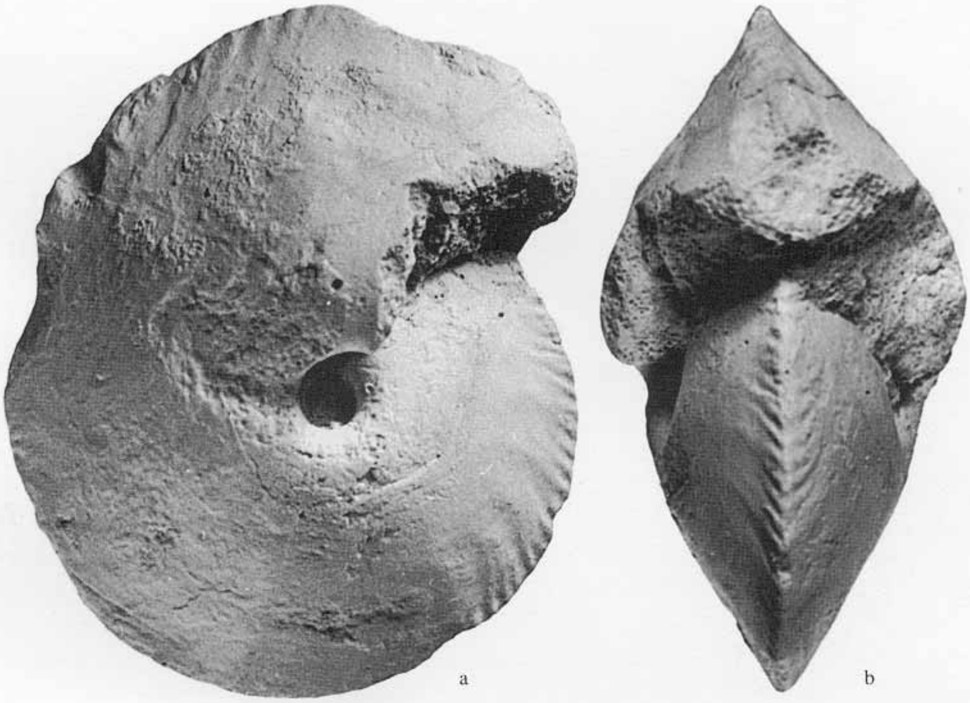
There is no indication of the extent of the type-series, which remains unchanged for the renamed species. No members survive in Phillips' collection in which the figured specimen was still said to be in 1875, and the specimen on Pl. 88, fig. 1 (BM 39516), a macroconch topotype in the Bean collection from Scarborough, is put forward as neotype of the renamed species.

Description. Like other Cardioceratidae, the genus is strongly if inconspicuously dimorphic. Some dimensions are given in Table I. The same specific name is here used for the whole of a considerable range of morphologies covered by the specimens of both dimorphs thought to come from precisely the same horizon, i.e. treated as a single biospecies. The final diameters of adult shells seem to lie around 100–150 mm (M) and 50 mm (m), with the adult bodychamber occupying about 0·65 of a whorl. The whorl section is markedly lanceolate (Pl. 88, fig. 1 b) in the more compressed macroconchs, less so in the microconchs, but the most remarkable feature is the enormous range of whorl-thicknesses, varying from 40% to over 100% of the whorl-diameters in the macroconchs while fairly constant around only 40% in the microconchs. This is a feature widely characteristic of the Cardioceratidae, from *Arctocephalites* and *Arcticoceras* in the Boreal Bathonian through *Longaeviceras* and *Quenstedtoceras* of the Upper Callovian to *Cardioceras/Goliathiceras* of the Oxfordian (see Callomon 1985). The primary ribbing is fine and dense, fading at about 40 mm. The secondaries are also characteristically fine and dense, remaining as vestigial chevrons on the keel to diameters of between 50–90 mm after which the shells are wholly smooth.

Distribution. Yorkshire: Kellaway Rock, Calloviense Zone, upper Koenigi Subzone, equivalent to about horizon XI of Wiltshire. Gloucestershire: Kellaways Rock in old railway-cutting at South Cerney (BM and BGS Jr 1713). East Greenland: Fossilbjerg Member of Olympen Formation in central Jameson Land. Germany: southern Franconian Alb (Dorn coll. Erlangen). Russia: ?Petchora basin (*Chamoussetia stuckenbergi*); Moscow basin, Kostroma.

Affinities. *C. phillipsi* is closely related to *C. chamousseti* (d'Orbigny), but not identical. The latter was based on a single specimen from the Lower Callovian of Mont-du-Chat, Chanaz, Savoie, in the collection of a M. Itier, reported by Parona and Bonarelli (1895) to be in Belley. The type has recently been rediscovered in the d'Orbigny collection in Paris. Through the courtesy of Drs D. Marchand (Dijon) and H. Gauthier (Paris), we have been able to obtain a cast. It is shown in text-fig. 3. Its principal dimensions are included in Table 1 for comparison. The values agree almost perfectly with those given by d'Orbigny himself. At 90 mm, the relative whorl-height, whorl-breadth and umbilical width are 0·48, 0·52, 0·11 respectively; at 75 mm: 0·52, 0·50, 0·09. About the last third whorl is bodychamber, and the umbilical margin begins to uncoil markedly at the end of the phragmocone. *C. chamousseti* is therefore a relatively small species, like *C. phillipsi*, and its cross-section is similarly lanceolate, but it differs from *C. phillipsi* in the style of the residual ribbing. The secondaries appear to arise by trifurcation and flexuous projection from vestigial primaries at somewhat irregular and indistinct furcation-points high on the whorl-side (text-fig. 3). Nothing like this is to be seen in any of the English specimens of *C. phillipsi* or of the Russian ones illustrated by Nikitin. Where traces of primaries remain (e.g. Pl. 88, fig. 2), they suggest that the furcation-points, if any, lay low on the whorl-side, with both primary and secondary ribs running up the whorl-side with gently projected and uninflected curvature. Whether these pecularities of ornament in the type of *C. chamousseti* are typical of the species or whether they are merely aberrations in one specimen, only new material will be able to tell.

A species very similar to *C. phillipsi*, and possibly identical, is *C. stuckenbergi* (Lahusen, 1875). This was based on some fragmentary material from the Petchora, and when this is redescribed and amplified through new and better-preserved material, *C. phillipsi* may well become a junior synonym. In the meantime however it seems safer and more convenient to retain a separate name for the Yorkshire species.



TEXT-FIG. 3. *Chamoussetia chamousseti* (d'Orbigny), holotype, Mont-du-Chat (Savoie). D'Orbigny coll., Paris, no. 3167-1 (R 2414-1) (= d'Orbigny 1847, pl. 155); photo of plaster-cast, ×1.

Another related but distinct species of *Chamoussetia* includes the forms found fairly commonly in the Kellaways Clay of Wiltshire. The distinguishing features are a larger average adult size, a more compressed and less lanceolate whorl-section, and stronger, coarser secondary ribbing persisting to larger diameters. To record these differences formally, we give this Wiltshire species a new name:

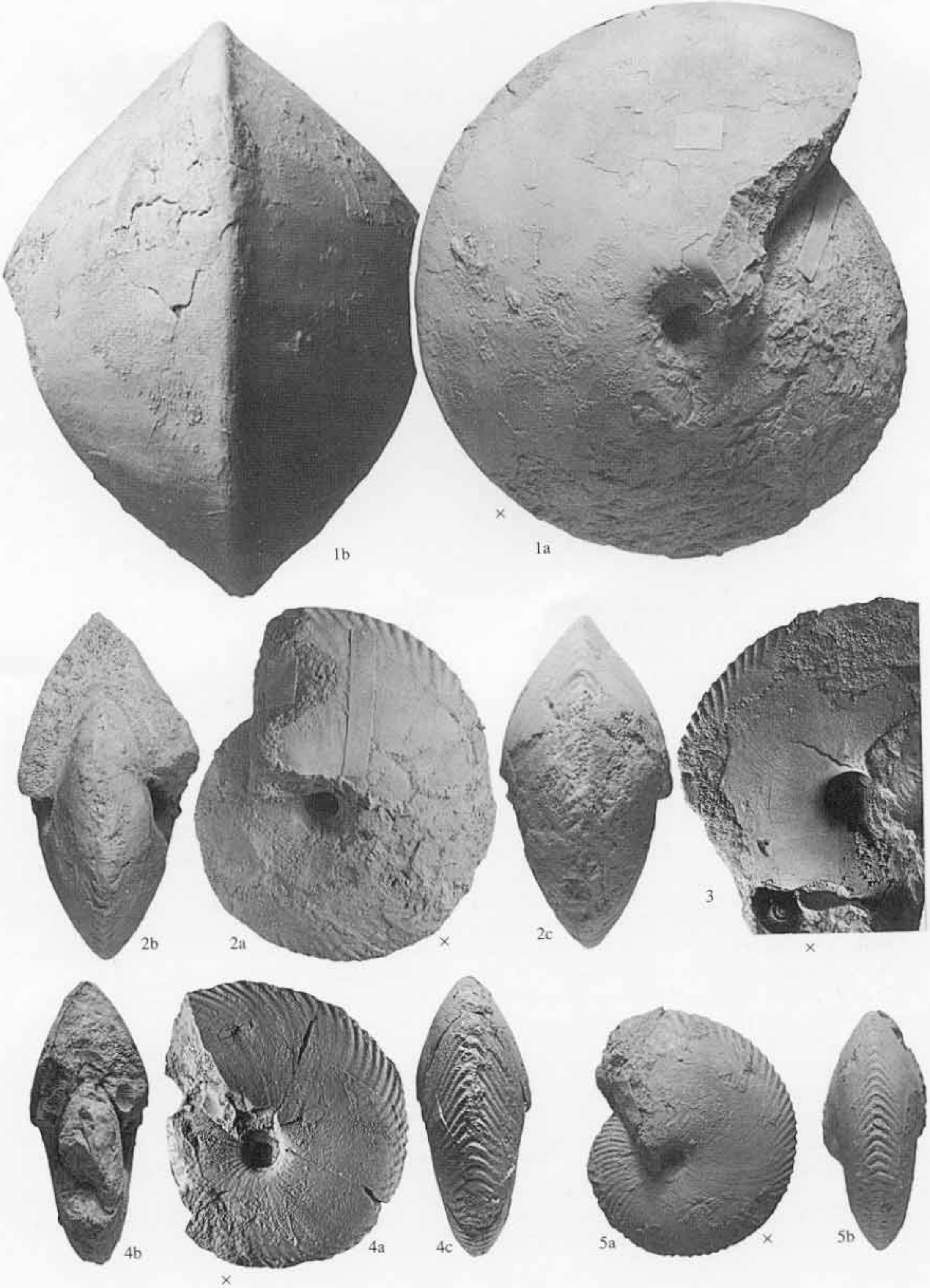
(a) *Chamoussetia buckmani* sp. nov.

Plate 90, plate 91, fig. 2a–c; text-fig. 4a

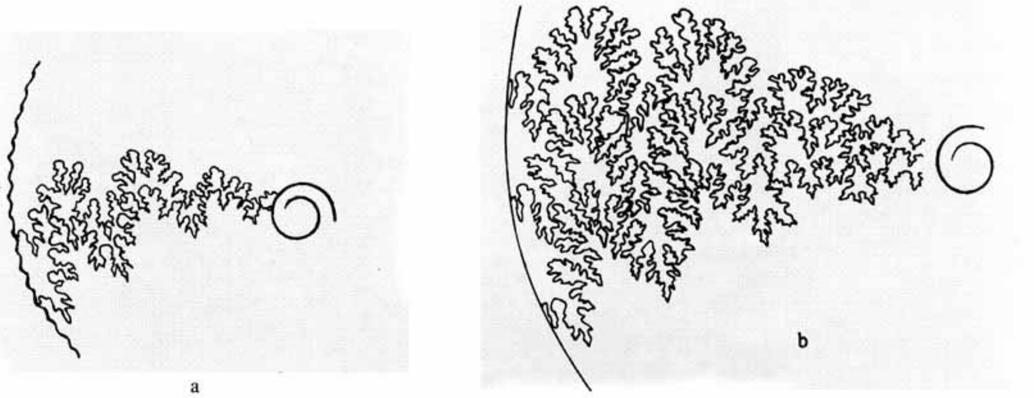
Holotype. The specimen previously figured by Buckman (BGS GSM 30393; 1924, pl. 462). It is refigured here on Pl. 90. Although perhaps not the best-preserved of the available specimens, it is in all respects typical of the species. A paratype showing more of the inner whorls is illustrated on Pl. 91, fig. 2, and a septal suture traced from this specimen is shown in text-fig. 4*a*. Selected dimensions are given in Table 2.

EXPLANATION OF PLATE 89

Figs. 1–5. *Chamoussetia phillipsi* nom. nov. 1*a*, *b*, [M], inflated variant with half a whorl of bodychamber, SM J12205, Leckenby coll., Scarborough; 2*a–c*, [m?], with nearly half a whorl of bodychamber, SM J12180, *ibid.*; 3, [m], with 5/8 whorl of bodychamber, uncoiling umbilical seam and part of the final adult peristome, JKW BC16, Cayton Bay waterworks section, Kellaways Rock, Koenigi Subzone, with imprints of *Kepplerites lahuseni* Parona and Bonarelli [m] in the matrix; 4 *a–c*, [m], complete adult with uncoiling umbilical seam, PFR M748, same horizon as fig. 3; 5*a*, *b* [m], half whorl bodychamber, SM J12182, Scarborough.



CALLOMON and WRIGHT, *Chamoussetia phillipsi*



TEXT-FIG. 4. Septal sutures of *Chamoussetia*. 4a, *Chamoussetia funifera* (Phillips), Upper Callovia Scarborough (WM J157, pl. 93, fig. 2*a*) × 1. 4b, *Chamoussetia buckmani* sp. nov., Lower Callovian, Trowbrid (BM C.80487, pl. 91, fig. 2*a*), × 1.

The age of *C. buckmani* in Wiltshire is early Koenigi Subzone of the Calloviense Zone. The preci level in the succession of faunal horizons summarized in the stratigraphical introduction is still n certain. Direct evidence comes from a recent exposure near Fairford, Gloucestershire, of Kellawa Clay in drainage ditches at the bottom of a gravel-pit (grid-ref. SP 178003; JHC coll. 1987) in whi a bed about 1 m thick yielded eight specimens of *C. buckmani* and only two of *Proplanulites*, o of *Cadoceras* and no *Kepplerites*. This suggests strongly that the species is confined to a narro horizon of its own. Indirect support for this suggestion comes from the compositions of museu collections. By far the largest number of individuals collected at any one locality came from t cuttings at Trowbridge described by Mantell (1850). In contrast, these seemed to have yield relatively little material of the other faunas usually associated with the Kellaways Clay, to jud from Mantell's collection in the British Museum. The figures in Table 2 are taken therefore on from specimens that have come from Trowbridge or from Fairford. At the latter locality, the lev with *C. buckmani* is overlain disconformably by Kellaways Rock with faunas XIII–XV. How b the gap is cannot be determined. The species is represented in the old collections from Cocklebu Hill in Chippenham, which consist mainly of faunas VIII and IX. It occurred in cuttings for a b pass at Wincanton (JHC coll. 1976), whose faunas consisted exclusively of those from horizons VI and IX. The specimen figured by Corroy (see synonymy) came from a famous locality at Poix the Ardennes that yielded a rich and homogenous assemblage also characteristic of about horizo VIII-IX (*Proplanulites* and *Cadoceras* also figured by Corroy 1932; *Kepplerites* by Tintant 1963). A the evidence points therefore to a level somewhere in the range of faunas VIII–IX. *C. phillipsi* younger. As indicated in the stratigraphical introduction, its level in Yorkshire is somewhere clo to that of horizon XI. Occasional specimens in the collections from further south are labelled 'Sou Cerney', near Cirencester. They are preserved in sandstone of the Kellaways Rock and came fro the railway-cutting described by Harker and by Woodward (1895, p. 33). The associated faun indicates horizons not lower than XII and up to perhaps XV. In East Greenland the associate faunas indicate an age also close to that of horizon XII.

EXPLANATION OF PLATE 90

Fig. 1*a–c*. *Chamoussetia buckmani* sp. nov., holotype [M], nearly complete adult; GSM 30393, Kellawa Clay, Trowbridge, Wiltshire, lower Koenigi Subzone.

CALLOMON and WRIGHT, *Chamoussetia buckmani*

TABLE 2. Dimensions of *Chamoussetia buckmani* sp. nov.

	(a) D(max) mm	(b) D(phrag) mm	(c) Bodych. whorl	(d) D: B/D	(e) D(sec-r) mm	(f)
			Macroconchs: Towbridge			
BM 32537	175	125	0·60	125: 0·64	<110	us, as
BM 50447a	165	125	0·50	125: 0·48	100	us, as
GSM 97562	155	115	0·60	125: 0·64	<100	us, as
BM C.89125	150	115	0·50	115: 0·52	90	us, as
BM 37500	140	120	0·30+	125: 0·46	100	us, as
BM 32536	140	105	0·50	110: 0·49	100	us, as
BM 50447b	135	115	0·35+	120: 0·59	90	us, as
BM 50448	(135)	115	0·40+	120: 0·44	100	us, as
GSM 30393 (holotype)	132	105	0·50	100: 0·46	100	us, as
BM C.6637	105	(110)	—	100: 0·44	100	as
BM 50448	105	?	—	100: 0·58	100	wholly sept
BM C.80487 (Pl. 91, fig. 2)	98	?	—	95: 0·40	>95	wholly sept
			Macroconchs: Fairford			
No. 1	140	110	0·60	110: 0·50	90	us, as
2	145	110	0·60	120: 0·50	<100	us, as
3	140	105	0·50	120: 0·51	<100	us
4	(140)	110	0·40	120: 0·50	<100	us
5	(120)	95	0·50	95: 0·42		us
6		100	0·2+	100: 0·60	80	as
7		100	0·4+	100: 0·45	<90	as

Notes: see Table 1. Material from Fairford variably distorted: measurements somewhat approximate.

To complete the list, there are two further species of *Chamoussetia* not so far found outside their type-areas.

(*b*) *Chamoussetia saratovensis sp. nov.*

1956 *Chamoussetia chamousseti* (d'Orbigny); Kamysheva-Elpatyevskaya *et al.*, p. 47, pl. 19, fig. 57 [M]

1959 *Chamoussetia chamousseti* (d'Orbigny): Kamysheva-Elpatyevskaya *et al.*, p. 148, pl. 11, figs. 5*a*, *b* [M]

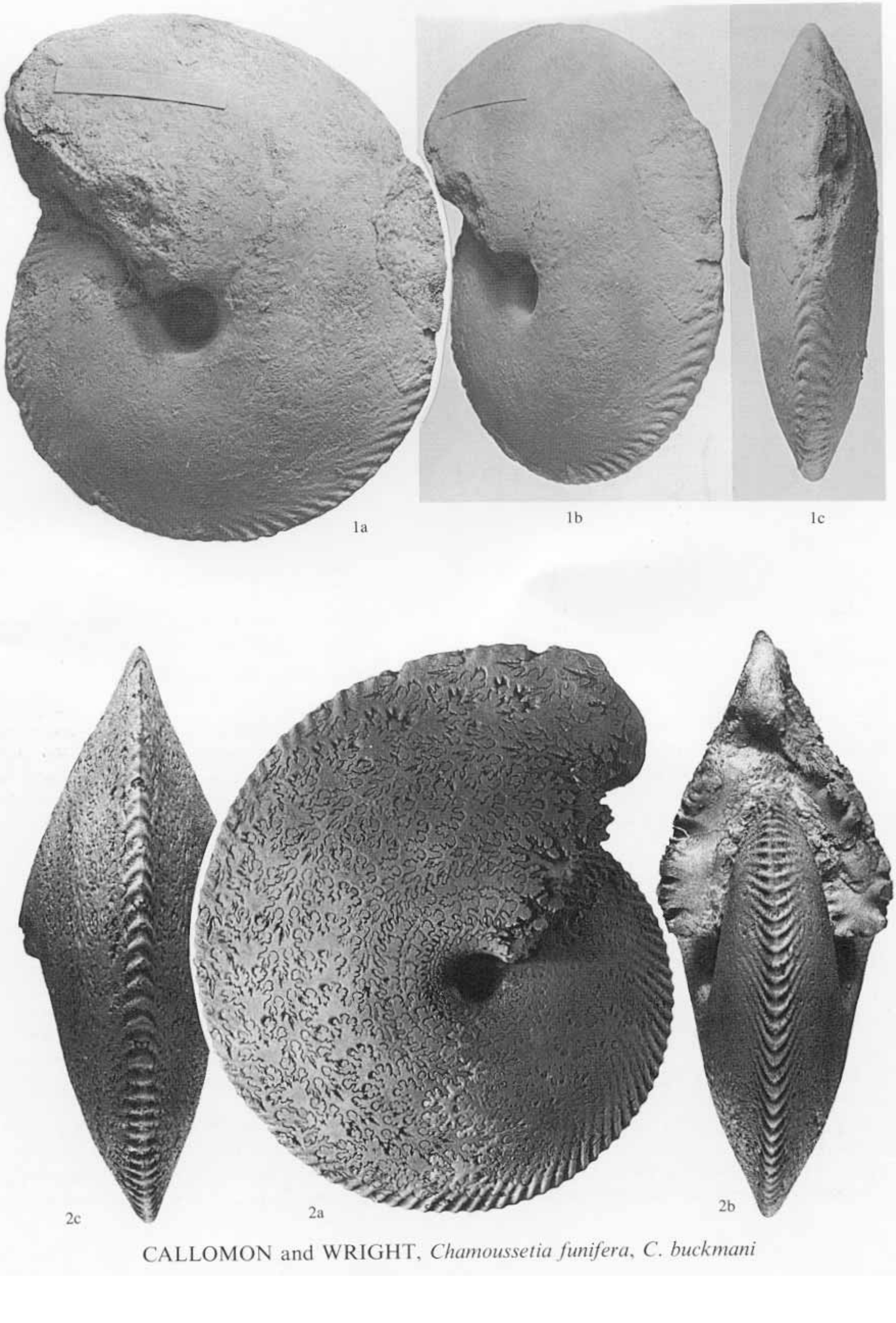
*1965 *Chamoussetia chamousseti* (d'Orbigny); Sazonov, p. 38, pl. 9, fig. 1*a*, *b* (holotype), ?2*a*, *b*, *v*, *g* [M].

All came from a ravine at Malinovy, north of Saratov. They are characterized by very coarse, blunt secondary ribs that persist to large diameters – in the holotype, to 95 mm – on the external margin of a whorl-section that is compressed and acute but does not develop the sharp lanceolate discoidal

EXPLANATION OF PLATE 91

Fig. 1*a–c*. *Chamoussetia funifera* (Phillips), [M], wholly septate phragmocone, SM J12186, Leckenby coll., Scarborough, Athleta Zone.

Fig. 2*a–c*. *Chamoussetia buckmani* sp. nov., [M], wholly septate phragmocone, BM C.80487, Kellaways Clay, Wiltshire (Trowbridge?), Calloviense Zone, Koenigi Subzone.



CALLOMON and WRIGHT, *Chamoussetia funifera*, *C. buckmani*

TABLE 3. Dimensions of *Chamoussetia funifera* (Phillips)

	(a) D(max) mm	(b) D(phrag) mm	(c) Bodych. whorl	(d) D: B/D	(e) D(sec−r) mm	
			Macroconchs			
OUM J30892 (Bletchley)	180	120	0·50	110: 0·28	110	us, p U/D, 0·08
WM J57 (Pl. 93, fig. 2)	110	110	0	100: 0·30	100	wholly sept U/D, 0·08
OUM J16381 (holotype)	105	105	0	100: 0·25	100	wholly sept U/D, 0·08
SM J12185 (Pl. 93, fig. 1)	95	(?)	0	95: 0·26	65	wholly sept U/D, 0·08
SM J12186 (Pl. 91, fig. 1)	86	(?)	0	80: 0·28	70	wholly sept U/D, 0·11
BM 39517 (Pl. 92, fig. 1)	73	(?)	0	70: 0·29	75	c.80 sec. ribs/whorl
			Chamoussetia galdrynus (d'Orbigny)			
Holotype (d'Orbigny pl. 156)	90	(?)	(?)	90: 0·28	90	U/D, 0·06
Douvillé 1912, pl. 3, fig. 6	85	(?)	0	85: 0·28	65	wholly sept
			?Microconch			
SM J12181 (Pl. 92, fig. 2)	(40)	(40)	0+	35: 0·32	40	as, body-ch onset

Notes: see Table 1. U/D: relative umbilical width. *Chamoussetia galdrynus* from Normandy; other specimens from the Scarborough area, except the one from Bletchley.

keel of the other species of *Chamoussetia*. In this respect they resemble more the macroconchs of *Q*. (*Lamberticeras*) of the Upper Callovian, although they differ in having the minute umbilicus of *Chamoussetia*. Their age cannot be given with the same precision as that of English forms, for they are not recorded from detailed sections, and the faunas associated with them continue to present problems of correlation, composed mainly of *Cadoceras elatmae* (Nikitin) and related forms not known from western Europe. Specimens of *Kepplerites* figured from the area and said to have come from the same zone do, however, include the true *K*. (*Gowericeras*) *gowerianum*, and so the age may well be Koenigi Subzone.

(c) *Chamoussetia crobyloides* (Quenstedt, 1887)

1887 *Ammonites lamberti crobyloides* Quenstedt, p. 806, pl. 90, figs. 19, 19p.

The monotypic holotype was a pyritized specimen from clays said to belong to the Brown Jura ζ. This suggests Upper Callovian, very possibly Athleta Zone. Its affinities could therefore be with *C. funifera*, which it resembles in being discoidal, compressed, with minute umbilicus. It differs, however, in having very coarse residual ribbing on the venter.

Ammonites hyperbolicus Leckenby has at times been interpreted as a member of the present group, but there was confusion due to the misidentification of the type (Buckman 1914: see synonymy of *C. phillipsi* above). This specimen was rediscovered and figured by Arkell (1948, p. 397, text-fig. 137) who correctly identified it as a *Goliathiceras* from the Cordatum Zone, and pointed out that the specimen figured by Buckman belonged to an undescribed species of homeomorphic *Chamoussetia*.

Chamoussetia funifera (Phillips, 1829)

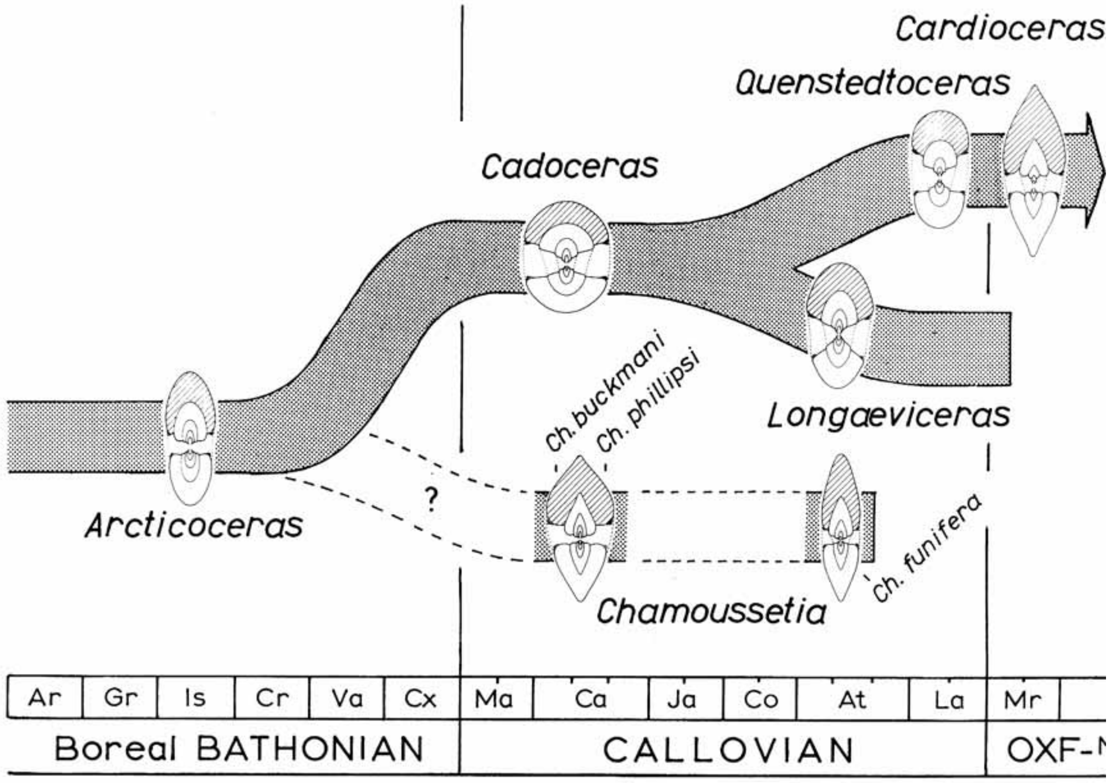
Plate 91, fig. 1, plate 92, plate 93, figs. 1 and 2; text-figs. 2b and 4b

*1829	*Ammonites funiferus* Phillips, p. 142, 175, pl. 6, fig. 23 (refigured unchanged in later editions of 1835 and 1875).
1847	*Ammonites galdrynus* d'Orbigny, p. 438, pl. 156.
1912	*Chamoussetia galdrynus* (d'Orbigny); Douvillé, p. 21, pl. 3(9), figs. 6, 6*a*: text-figs. 16, 17.
1918	*Longaeviceras? funiferum* (Phillips); Buckman, p. xiv.
1962	*Chamoussetia funifera* (Phillips): Howarth, p. 125.

Type. Plate 92, fig. 4 *a–c*; Phillips' collection, OUM J16381, labelled '*Amm. funiferus* Ø, Hackness' in Phillips' handwriting. The original description was confined to a few words (p. 142): 'Ammonites. -13. funiferus. It nearly resembles a. excavatus (Min. Conch. tab. cv). Scarborough, (author's collection)'. There is thus some conflict between the localities given on the label and in the text. Whereas often the place-name 'Scarborough' in old collections can include localities within some distance of the town, Phillips was usually careful to distinguish between it and Hackness. His lists record numerous specimens explicitly from both. In most other respects however Phillips' specimen, which is the only one surviving in his collection, agrees tolerably well with the original figure (reproduced here in text-fig. 2b) which was said to be reduced to half-size. There is no evidence that the type-series contained more than one specimen, and despite some small doubts, therefore, the indications are strongly that the surviving specimen is the holotype. The widely-held belief that Phillips' collection of the material described in his book was lost in 1837 can no longer be upheld (Edmonds 1977).

Description. Measurements are given in Table III. Almost all the available specimens appear to be macroconchs, which are septate to *ca*. 100 mm. Only one specimen is known with complete bodychamber (OUM J30892), but it is too heavily encrusted with concretionary pyrites to be worth figuring. It shows, however, that the adult peristome is ventrally projected into a hood, the keel fading to give a rounded venter as in the presumed ancestral *Arcticoceras*. The whorl-section is compressed and highly arched but not lanceolate as in *C. phillipsi*, the umbilical walls steep but not overhanging. The whorl-thickness is remarkably constant at around 28% of the diameter. The ribbing is fine and dense, fading at around 30 mm and leaving only vestigial secondary chevrons on the keel which fade at between 60–100 mm to leave the shell wholly smooth. In some specimens the ventral chevrons show a slight lateral swelling (Pl. 91, fig. 1*c*, Pl. 92, fig. 4*c*) not seen in Lower Callovian species. Adult sutures are crowded, complex and variable (text-fig. 4*b* and Douvillé's figs. 16, 17), but otherwise typical of Cardioceratidae as a whole and not systematically distinguishable from those of *C. chamousseti*. The only arguably microconch specimen (Pl. 92, fig. 2) seems to consist of the phragmacone just up to the last septum. Its last few sutures appear to be somewhat approximated and simplified, but lacking more abundant material not much can be said about the dimorphism in this species.

Age and distribution. Confusion has arisen in the past because by a coincidence the present species resembles both in form and in preservation the much earlier species *C. phillipsi* from the Kellaways Rock of the same type-area in Yorkshire, neither species having been collected actually in place. It is now clear, however, that *C. funifera* is of Upper Callovian age, its level in Yorkshire being in the lower Hackness Rock, Athleta Zone, Proniae Subzone. This may be seen in the specimen shown in Pl. 93, fig. 2, which has attached to it two fragmentary pieces of characteristic *Kosmoceras* cf. *rowlstonense*. The holotype, if it came from Hackness, also could have come only from the Hackness Rock, for beds lower than Middle Callovian are neither reached in the quarry nor exposed elsewhere in the neighbourhood. The specimen OUM J30892 listed in Table III was found in place at Bletchley, Buckinghamshire, in Middle Oxford Clay (the lower part of bed 21 of Callomon, 1968, p. 282), again in the Proniae Subzone of the Athleta Zone. Douvillé records a total of four known specimens, as *C. galdrynus*, all from Normandy around Dives and apparently found in the Athleta and Lamberti Zones. The holotype of *C. galdrynus* came from the Athleta Zone of Beuseval (Eudes-Deslongchamps



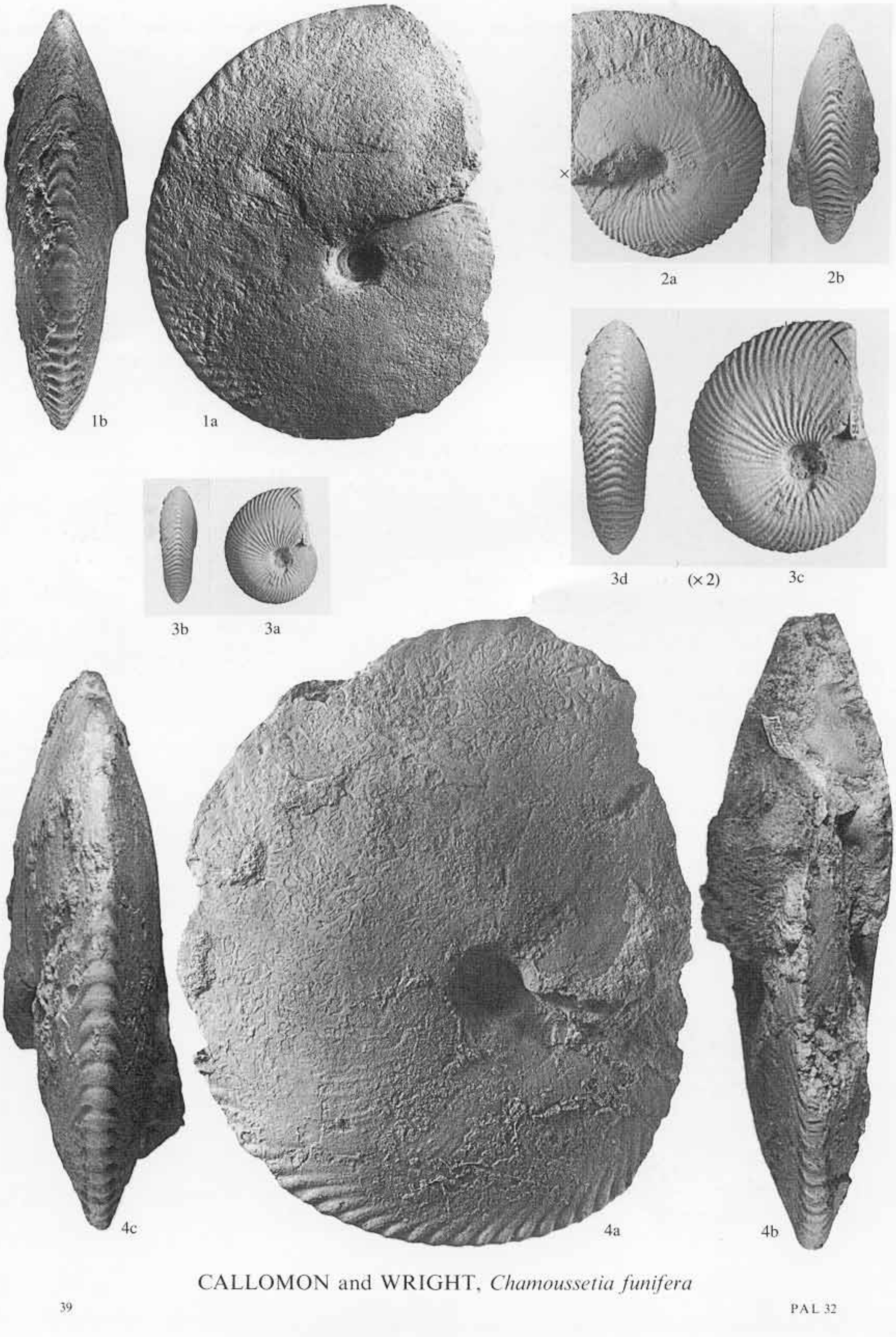
TEXT-FIG. 5. Phylogeny of the Cardioceratidae. Standard zonation of the Boreal Bathonian: Arcticu Greenlandicus, Ishmae, Cranocephaloide, Variabile and Calyx Zones, in ascending order. That of t Callovian and Oxfordian, as in text-fig. 1. Cross-sections drawn from real specimens of *Arcticoceras ishm* (Keyserling), *Cadoceras tolype* Buckman, *Quenstedtoceras ordinarium* (Brown), *Cardioceras scarburgen* (Young and Bird); *Longaeviceras nikitini* (Sokolov): *Chamoussetia buckmani* sp. nov. (Fairford), *Chamousset funifera* (Phillips).

1890, p. 103). *C. funifera* is thus known only from a very restricted area, between Yorkshire, where it is n uncommon, and northern France where it is very rare.

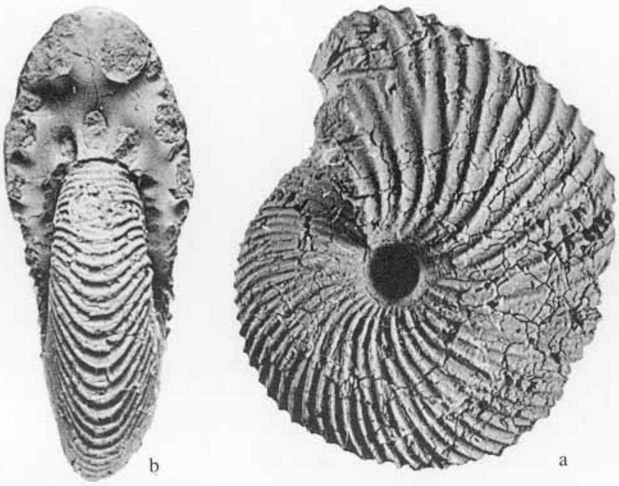
Affinities and phylogeny. The phyletic derivation of the whole genus *Chamoussetia* presents curio problems (see Text-fig. 5). The first tendency in the Cardioceratidae to develop compressed who sections with acute venter may be observed in *Arcticoceras greenlandicus* and *A. ishmae* of t Greenlandicus and Ishmae Zones in the Boreal Middle Bathonian. (For a summary of the bore zonal succession, see Calloman 1985; for examples of *A. ishmae*, see Sokolov 1912, pl. 1, fig. Spath 1932, pl. 15, figs. 1, 7; Calloman 1985, fig. 8H, h; text-fig. 6). These forms have small umbili accentuation of secondary ribs on an acute venter, smooth adult bodychambers and highly variab inflation of the shell just as in *C. phillipsi*, so that they make entirely acceptable ancestors. They a

EXPLANATION OF PLATE 92

Figs. 1–4. *Chamoussetia funifera* (Phillips). 1*a*, *b*, [M], wholly septate, BM 39517, Bean coll., Scarboroug 2*a*, *b*, [m?], bodychamber just commencing, last sutures approximated, SM J12181, Scarborough; 3*a*– wholly septate nucleus, SM J12184, Scarborough (3*c*, *d*, × 2); 4*a*–*c*, presumed holotype, [M], bodychamb just commencing, OUM J16381, Phillips coll., 'Hackness'. All Athleta Zone.



CALLOMON and WRIGHT, *Chamoussetia funifera*



TEXT-FIG. 6. Inner whorls of *Arcticoceras ishmae* (Keyserling), early transient, showing the acutely arched venter and small umbilicus thought to indicate ancestral characters leading to *Chamoussetia*. JHC 2266, lower Ishmae Zone, central Jameson Land, East Greenland; × 1.

classified as members of the subfamily Arctocephalitinae Meledina, 1968. Unfortunately, in the intervening six ammonite zones, between Ishmae and Calloviense Zones, no morphologically intermediate form – 'missing links' – are known from anywhere. On the contrary, there is instead an almost uninterrupted thread leading smoothly from *Arcticoceras* of the Arctocephalitinae to *Cadoceras* of the Cadoceratinae, substantiated by rich material from many places around the shores of the former Boreal Sea, now the Arctic Ocean. If *Chamoussetia* was directly derived from *Arcticoceras*, as still seems likely, where then did its more immediate ancestors evolve, totally hidden from view for such a long time; and why only to burst so suddenly and yet so briefly upon the known world? The only alternative to such a hypothesis would seem to be to derive *Chamoussetia* from some other, later forms which would have to be Cadoceratinae. This could shorten the gap in time but would widen enormously the gap in morphologies to be bridged, again with absolutely no intermediates in sight. It seems preferable therefore at present to follow the first course, and to regard *Chamoussetia* as the last of the Arctocephalitinae.

The problem arises a second time in jumping from *C. phillipsi* of the Lower Callovian, Koenigi Subzone, to *C. funifera* of the Upper Callovian, middle Athleta Zone – a gap of three whole ammonite zones with again no known intermediates (text-fig. 5). Here, however, independent derivation from other sharp-ventered Cadoceratinae presents fewer problems, for possible candidates in early forms of *Longaeviceras* can be traced back into the Middle Callovian.

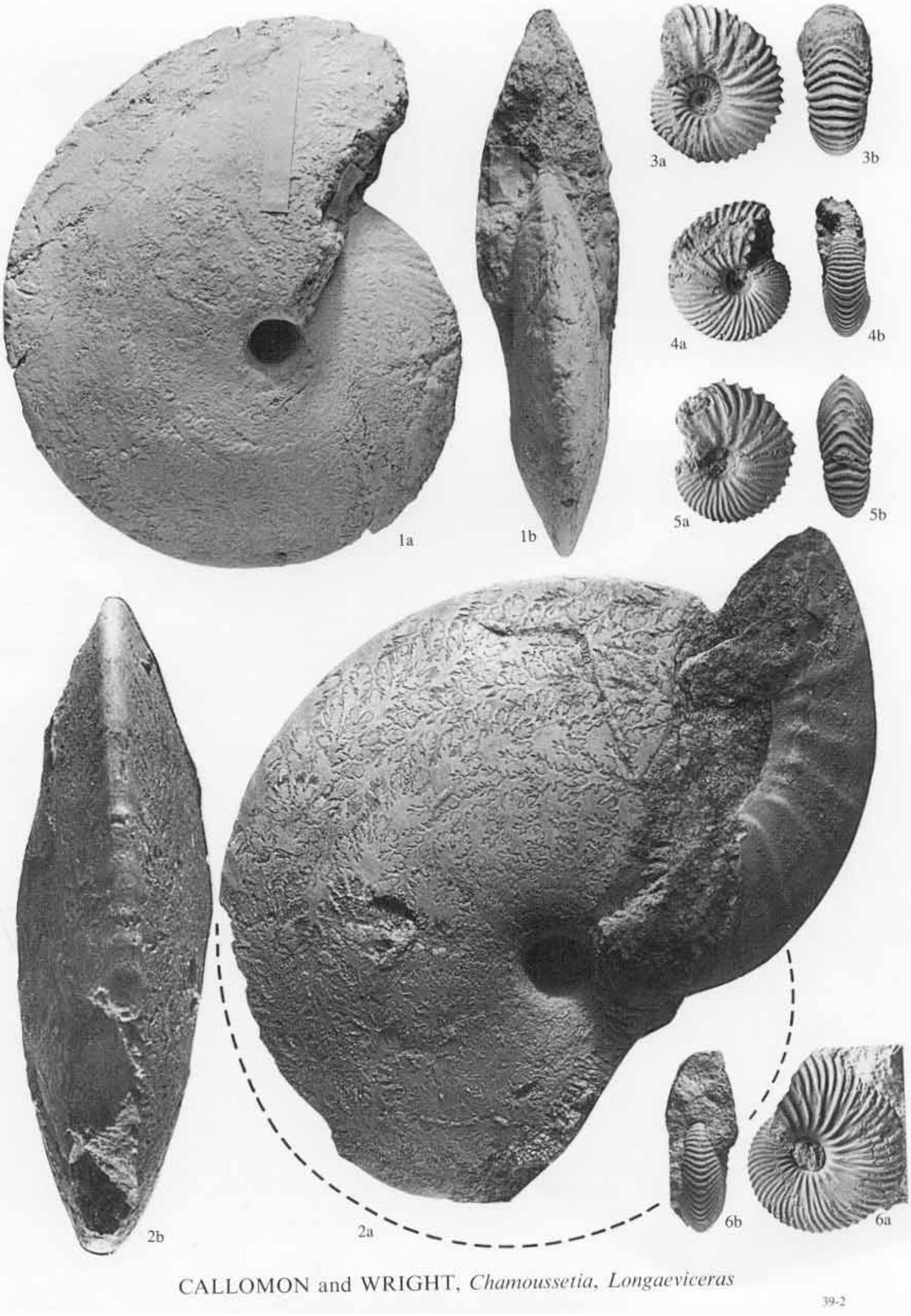
EXPLANATION OF PLATE 93

Figs. 1, 2. *Chamoussetia funifera* (Phillips). 1*a*, *b*, [M], wholly septate, SM J12185, Leckenby coll., Scarborough; 2*a*, *b*, [M], wholly septate, bodychamber just beginning, WM J57, Scarborough. (A bodychamber of *Kosmoceras* cf. *rowlstonense* is attached in the matrix.) Athleta Zone.

Figs. 3 and 5. *Longaeviceras* cf. *schumarowi* (Nikitin). 3*a*, *b*, [m?], wholly septate, SM J4747, Scarborough, Hackness Rock, Athleta Zone, Proniae Subzone; 5*a*, *b*, [m?], wholly septate, JHC 1295, Woodham, Bucks., Oxford Clay, Athleta Zone, Spinosum Subzone.

Fig. 4. *Longaeviceras* cf. *placenta* (Leckenby), wholly septate nucleus, JHC 1296, locality and horizon as fig. 5.

Fig. 6. *Longaeviceras* sp., wholly septate nucleus, OUM J1290, Hackness Rock near Scarborough, probably Gristhorpe, Lamberti Zone.



CALLOMON and WRIGHT, *Chamoussetia*, *Longaeviceras*

Ammonites funiferus has in fact at times been placed in *Longaeviceras* (Buckman, 1918). Howev no *Longaeviceras* has the minute umbilicus of *C. funifera*, and all become more inflated in t mature bodychamber. So here again, it seems preferable to accept a gap in time and to extend t range of *Chamoussetia* from Lower to Upper Callovian. The genus emerges then as a minor b persistent and only slowly evolving element of the Boreal faunas, becoming more and mc restricted geographically, and remaining hidden from the geological record for long periods of tin Such histories may have been not infrequent among the ammonites generally, for the problems cryptogenesis calling for such seemingly improbable solutions are common enough.

Subfamily CADOCERATINAE Hyatt, 1900
Genus PSEUDOCADOCERAS Buckman, 1918

Type species. P. boreale Buckman

Pseudocadoceras boreale Buckman, 1918

Plate 94, figs. 1*, 2–6

cf. 1895 *Quenstedtoceras primigenium* Parona and Bonarelli, p. 93, pl. 2, fig. 4
1918 *Pseudocadoceras boreale* Buckman, p. xiv
*1919 *Pseudocadoceras boreale* Buckman, pl. 121B and legend
non 1965 *Pseudocadoceras boreale* Buckman; Sazonov, p. 3, pl. 6, figs. 7*a*, *b* (M. Callovian).

Description. During a revision of the ammonites of the 'Kelloway Rock' of Yorkshire, Buckman (191 recognized that *Ammonites longaevus* Leckenby was based on a type-series of four syntypes belonging to least two distinct species. Selection of a lectotype of *Longaeviceras longaevum* left three specimens whi became holotype and paratypes of *P. boreale*: all three are figured here on plate 94 (SM J3290-2) together wi three further topotypes. Although no sutures are visible, all six specimens show signs of maturity, either uncoiling of the umbilical suture (Pl. 94, figs. 1–6) or modification of whorl section and ribbing near t peristome (Pl. 94, figs. 2–4, 6). A further crushed adult (JKW CC32, not figured) shows 6/10 whc bodychamber. The adult diameter of the species is therefore quite narrowly defined ($n = 7$: $\bar{d} = 34{\cdot}1$ mm, $= 1{\cdot}95$ mm $= 5{\cdot}7\%$). It is clearly a microconch. The ribbing varies somewhat in density, from 29 ribs (Pl. 9 fig. 1) to 37 ribs (Pl. 94, fig. 3) on the last whorl. The umbilicus is always very narrow. The most characterist feature of the species however is the acute venter on which the secondary ribs inflect sharply, making homoeomorphic with much younger forms of *Longaeviceras* from the Upper Callovian, with which it has times been confused.

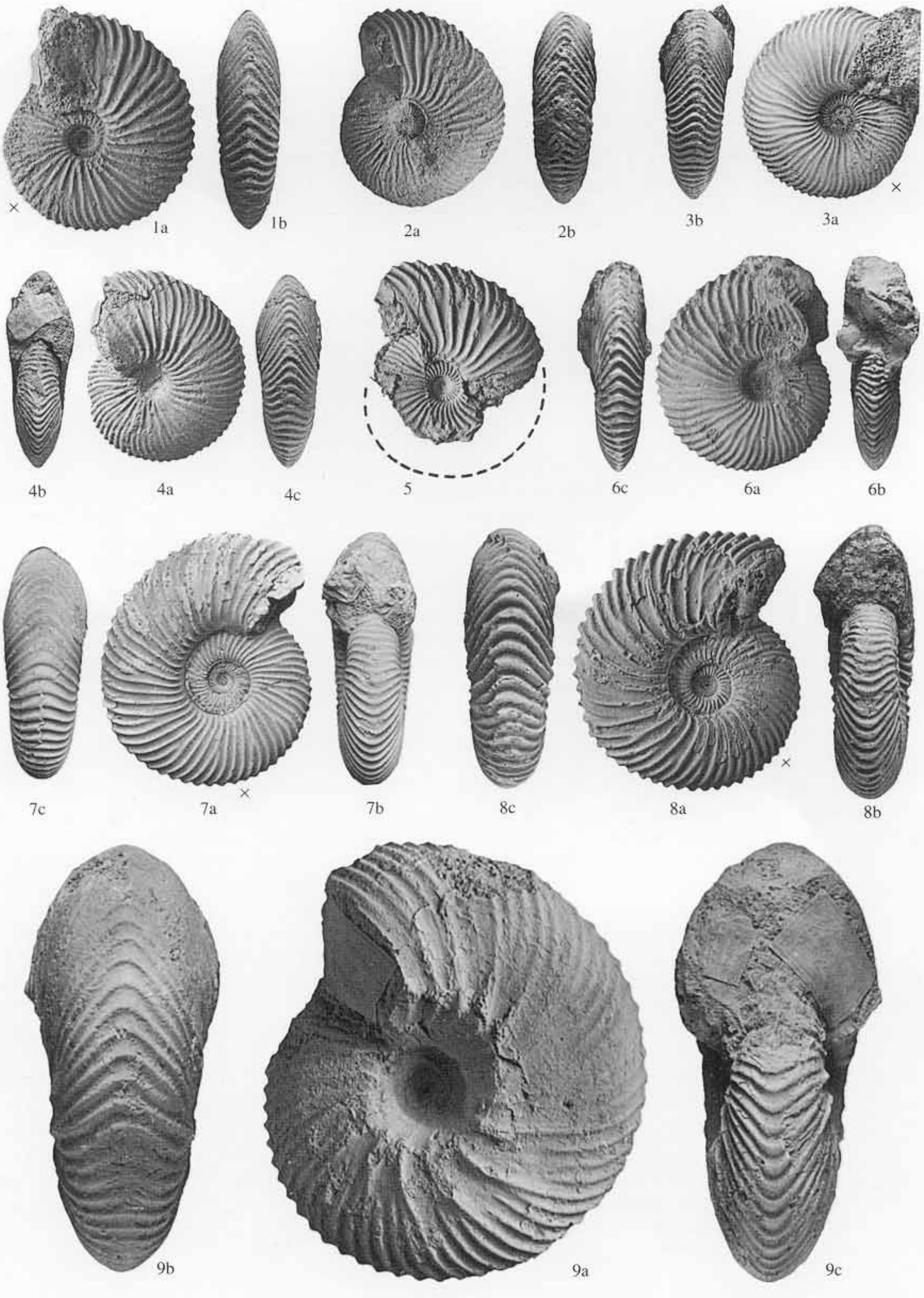
EXPLANATION OF PLATE 94

Figs. 1–6. *Pseudocadoceras boreale* Buckman, [m], all adults with bodychamber. 1*a*, *b*, holotype, SM J329 Leckenby coll., 'Scarborough' (probably Cayton Bay); 2*a*, *b*, paratype, SM J3292, *ibid.*; 3*a*, *b*, chorotyp topotype?, JKW 203, Kellaways Rock, Cayton Bay, loose; 4*a–c*, paratype, SM J3291, 'Scarborough'; chorotype, topotype?, JKW FC2, Kellaways Rock, unit β_2, Cayton Bay, *in situ* below Cayton Cliffs; 6*a*, as 3*a*, *b*, PFR coll. All Calloviense Zone, Koenigi Subzone.

Figs. 7 and 8. *Pseudocadoceras grewingki* (Pompeckj) subsp. *whithami* nov. 7*a–c*, complete adult with fin peristome, JHC 826, Kellaways Rock, Kellaways, Wilts., Calloviense Zone and Subzone; 8*a–c*, holotyp complete adult with final peristome, F. Whitham coll., Kellaways Rock, South Cave, Humbersid Calloviense Zone, Enodatum Subzone.

Fig. 9*a–c*. *Longaeviceras placenta* (Leckenby), [M], topotype, wholly septate, SM J12175, Hackness Roc Scarborough, Athleta Zone.

PLATE 94



CALLOMON and WRIGHT, *Pseudocadoceras*, *Longaeviceras*

Age. Besides distinguishing *L. longaevum* and *P. boreale* morphologically, Buckman assigned them also different horizons, placing the former in the Athleta Zone (Hackness Rock) and the latter in the Koen (Sub)zone (Kellaways Rock s.s.). These assignments were, however, based on a comparison of the matrices museum material, for not a single specimen of either species had been collected *in situ*. This mode of 'arm-ch stratigraphy' having become discredited, the age of *P. boreale* remained uncertain, and because of its sha venter, homoeomorphic with other species of *Longaeviceras*, an Upper Callovian age could not be ruled o Thus later in *Type Ammonites* it appears firmly listed in the *athleta* hemera together with *Longaevicer longaevum* (Davies 1930, table I, p. 28). Most of the material of this rather rare species found subsequen (J. K. Wright and P. F. Rawson collections) was also of uncertain age, being found in fallen blocks on t beach in Cayton Bay. However, three specimens (including plate 94, fig. 5) have now been found *in situ* typical Kellaways Rock of unit β_2 in beach exposures at the foot of Cayton Cliff, Cayton Bay (Wright 196 p. 373 and fig. 9) associated in the same block with *Chamoussetia phillipsi* and *Kepplerites lahuseni*. Buckm was therefore originally correct and the age is no longer in doubt: Lower Callovian, Calloviense Zone, Koeni Subzone, *K. indigestus*/*lahuseni* horizon.

Affinities and nomenclature. There can be little doubt that *P. boreale* is the microconch of son contemporaneous cardioceratid, for it fits the prescription fully in line with a long progression predecessors and successors (see Callomon 1963, pl. I; 1985, fig. 8). As it appears to be the only for occurring at this level (excluding *Chamoussetia*, discussed above), its macroconch companion mu be the *Cadoceras* found with it, *C*. cf. *tolype* Buckman. Although not too common, material is w known. It consists of typical forms of the genus, falling in its range of variability smoothly betwee *C. tolype* Buckman of the Koenigi Subzone, fauna XI, and *C. sublaeve* (Sowerby) of the Callovien Subzone, fauna XIV. One can discern in this sequence a gradual change in the form of the coilin from a rather wide, steep-sided umbilicus of U-shaped profile to a narrower one with more slopir sides and a V-shaped profile. In contrast, the evolution of the microconchs appears to be le continuous, although it has to be remembered that one is here considering rather differe characters. The immediate predecessors of *P. boreale* are little known, for to judge from th collections, the Kellaways Clay of S. England seems to have yielded almost nothing b macroconchs. The successors are however quite common. Two typical examples are figured here f comparison: from the Kellaways Rock of Wiltshire (Pl. 94, fig. 7), Calloviense Zone and Subzon and from the Kellaways Rock of South Cave, Yorkshire (Pl. 94, fig. 8), Enodatum Subzone, faur XVII. Similar but crushed forms occur also in the Medea Subzone of the Jason Zone above. A these later forms resemble most closely *Cadoceras grewingki* Pompeckj (1900, pl. VI, fig. I, lectoty designated by Imlay 1953, p. 94; chorotypes figured by him, especially pl. 49, figs. 5–7), fro Alaska, whose age in terms of the European zonal scheme is, however, not precisely known (s Imlay 1975). For the present purposes, *C. grewingki* is placed here in *Pseudocadoceras*. The Britis specimens may be referred to as *P. grewingki whithami* geogr. subsp. nov. (type, Pl. 94, fig. 8). The is thus between *P. boreale* and *P. grewingki* a marked change from compressed, involute, shar ventered to planulate, evolute, more round-ventered coiling. Later microconchs, in the Middle an Upper Callovian, again develop the sharp-ventered, involute, compressed morphology of *P. boreal P. cuneatum* Sazonov, 1965, *P. boreale* Sazonov 1965 (non Buckman), *P. tsytovitchae* (Parishe 1968), *P. obliteratum* (Kniazev, 1975) partim, *P. parvulum* (Meledina, 1977) partim, *P. filaru* (Meledina, 1977) partim – so much so that they have at times been referred to *Pseudocadocer* although they are almost certainly the microconchs in part of various groups of *Longaevicera* Conversely, the evolute morphology of *P. grewingki* is already found very much earlier, among th microconchs of *Arctocephalites*, *Arcticoceras ishmae* and *Cadoceras variabile* of the Boreal Midd and Upper Bathonian (see Callomon 1985), some of which are quite hard to distinguish fro *P. grewingki*. These earlier forms were incorporated in a new genus *Costacadoceras* by Rawso (1982). It seems, therefore, that from their beginning in the Middle Boreal Bathonian to the top the Upper Callovian, the evolutionary development of these microconchs was very limited and n so much progressive as saltative, changing back and forth between a few basic morphologies an hence producing repetitive homoeomorphs.

This raises acutely the familiar problem of taxonomic nomenclature associated with the recognition of dimorphism, and the question of the stratigraphical range of *Pseudocadoceras*. There are three possible approaches. Firstly, one could retain *Pseudocadoceras* as a separate genus and formally ignore the dimorphism altogether. Then, in view of what has been said above, it is hard to see any alternative to using the name for the whole of the range from Bathonian to Upper Callovian. Secondly, one could incorporate dimorphic status formally at subgeneric level. Then the difficulty arises that forms which by conventional standards differ at specific level at most, are placed in different subgenera not by the criteria of their own morphologies, but according to the morphologies of their supposed macroconchiate partners. Thus, the boundaries which it is relatively easy to draw between *Arcticoceras*, *Cadoceras* and *Longaeviceras* have no equally clear counterparts in the microconchs. Conversely, such boundaries as may occur there, e.g. between *P. boreale* and *P. grewingki*, have no counterparts in the macroconchs, *Cadoceras tolype* and *C. sublaeve*. Finally, one could consistently unite supposed dimorphic pairs under the same specific names. But this presupposes sufficient material at every level to map out in full the variability of biospecies ('populations'), i.e. monographic treatment. And while perhaps desirable theoretically as the ultimate goal, it seems to lie some way off, for the literature reveals at present little general consensus on the nature and extent of biospecies. In the meantime, therefore, different purposes call for different nomenclatural treatments. As the purpose of the present note is primarily to settle the stratigraphic position and morphological characters of a well-defined and distinctive group of forms, it suffices to retain them in *Pseudocadoceras* as nominal genus without further qualification.

Distribution. The geographical distribution of *P. boreale* extended probably over the whole of the N European Boreal/Sub-boreal Province, but so far the only closely comparable form that has been recorded appears to be *P. primigenium* (Parona and Bonarelli) (see synonymy) from Chanaz, Savoie. It may be a senior synonym, but the age of the holotype and only known specimen is uncertain – it could again by M. or U. Callovian – so that pending new, accurately levelled material the name is best left distinct. Similar remarks apply to *P. orbignyi* Maire, 1932 (p. 197), the type of which (*Ammonites leachi* d'Orbigny, 1845, pl. 35, figs. 7–9, non Sowerby) came from the Moscow Basin.

Genus LONGAEVICERAS Buckman, 1918

Type species *Ammonites longaevus* (Bean MS) Leckenby, 1859

After their invasion of Europe from the north in the Lower Callovian, the Cadoceratinae retreated back into the Boreal Province in the Middle Callovian, to be replaced in the Sub-Boreal Province largely by the Kosmoceratidae, before embarking on a second massive southerly invasion in the Lamberti Zone of the Upper Callovan, now as *Quenstedtoceras*. The intermediate forms recording the evolution of *Cadoceras* into *Quenstedtoceras* are therefore relatively poorly known. They include the genus *Longaeviceras*. A systematic study will have to be based on new material from the Arctic, where these forms remained the dominant group. Such material is becoming available (e.g. Bodylevsky 1960; Voronets 1962; Meledina 1977), but fresh problems arise in the stratigraphy: the Sub-boreal forms on which the standard European chronostratigraphy is based are here so rare that the familiar zonal scheme cannot be used in the Arctic Middle-Upper Callovian until closer correlations have been established. Thus, the Coronatum, Athleta and Lamberti Zones are there replaced by broadly equivalent Zones of *Cadoceras* (*Rondiceras*) *milaschevici*, *Longaeviceras keyserlingi* and *Eboraciceras* '*subordinarium*' Meledina (non Buckman).

In Europe these forms are rare but of correspondingly greater interest as they occur in precisely dated successions and hence give the keys to correlation. They are commonest in Yorkshire, which provided some of the earliest named species.

Longaeviceras placenta (Leckenby, 1859)

Plate 94, fig. 9*a–c*

*1859 *Ammonites placenta* (Simpson MS) Leckenby; p. 10, pl. 2, fig. 1
*1920 *Longaeviceras placenta* (Simpson-Leckenby); Buckman, pl. 148 (holotype refigured)
?1957 *Quenstedtoceras principale* Sazonov; p. 119, pl.11, figs. 3, 3*a*, 3*b*. (Saratov)
?1960 *Cadoceras innocenti* Bodylevsky; p. 76, pl. 5, figs. 2*a*, *b* (Olenek, Siberia)
?1977 *Longaeviceras* aff. *nikitini* Sokolov; Meledina, p. 147, pl. 30, fig. 3*a*, *b* (Khatanga, Siberia)

Description. The holotype is a wholly septate macroconch 58 mm in diameter, rather poorly preserved and buried in matrix. Another topotype is therefore figured here. Its dimensions are at diameter 70 mm: whorl-height 46%, whorl-breadth 46%, umbilical width 17% of the diameter, respectively; wholly septate; ribs, 17 primaries, ca. 60 secondaries. In both specimens the umbilicus has gently sloping smooth walls on a V-shaped cross-section but retains throughout growth a sharp upper edge at which the ribbing terminates. Inner whorls are compressed and involute; the adult macroconch bodychamber becomes cadicone, still with sharp umbilical edge, and smooth. The ribbing is projected forward and irregularly variable, with 1–4 secondaries either intercalated between or formed by indistinct bifurcation at mid-flank from more or less widely spaced primaries. The venter is sharply arched, traversed by accentuated chevron-like secondaries. The species is thus morphologically intermediate between ancestral *Cadoceras* and subsequent *Quenstedtoceras*, retaining the characteristic umbilicus and bodychamber of the former but beginning to acquire the irregular differentiated ribbing and tendency towards a keel of the latter, especially *Q*. (*Lamberticeras*), and thence *Cardioceras* itself.

Affinities. There are a number of closely-related species.

(a) *Longaeviceras longaevum* (Bean MS – Leckenby, 1859)

1859 *Ammonites longaevus* Bean MS; Leckenby, p. 11.
*1919 *Longaeviceras longaevum* Bean sp.; Buckman, pl. 121 A

The name was first published by Leckenby but immediately placed by him in synonymy with *Ammonites lamberti* without further description. Nevertheless, subsequent authors have always regarded the name as available, in common with others of Bean's MS names which slipped into print in similarly cursory fashion, and *L. longaevum* has become the type-species of a well-characterized genus, *Longaeviceras*. The type-specimen is also a wholly septate nucleus of a macroconch, but it is too small and poorly-preserved to give much idea of the species. It is slightly more involute and densely-ribbed than *L. placenta* (24 primaries at 50 mm, ca. 65 secondaries), but it seems doubtful whether these differences are more than varietal – they are certainly no greater than those between forms which, at a higher horizon, in the Lamberti Zone, are usually quite happily combined under the same name, *Q. lamberti*. *L. placenta* and *L. longaevum* were published together, but it seems more satisfactory now to follow Leckenby in retaining *L. placenta* even though *L. longaevum* is the generic type species.

(b) *Longaeviceras stenolobum* (Keyserling, 1846)

1846 *Ammonites tchefkini* d'Orbigny var. *stenolobus*; Keyserling, p. 329, pl. 20, fig. 7, pl. 22, figs. 13 and 14.
1881 *Stephanoceras stenolobum* Nikitin; 1881, p. 121, pl. 5, figs. 28 (Petshora), 29–30 (Oka).
1912 *Cadoceras stenolobum* Keyserling; Sokolov, p. 22, 52 (*partim*).
1960 *Cadoceras stenolobum* (Keyserling); Bodylevsky, p. 77, pl. 4, figs. 3*a*, *b*; pl. 10, fig. 1*a*, *b*.
1977 *Eboraciceras stenolobum* (Keyserling); Meledina, p. 116, pl. 19, figs. 2*a*, *b*; pl. 39, fig. 3, pl. 43, fig. 3, pl. 46, fig. 2.

The history of this taxon, involving the oldest available name in the group, is somewhat confused. The name was introduced nominally at infrasubspecific level, but according to current interpretations of the *Rules of Nomenclature* (Art. 45(g)) the designation 'var.' need not be taken to exclude the name from being available at subspecific level. Most subsequent authors have taken it to be available from 1846. An exception was Nikitin (see synonymy) who expressly elevated the taxon to specific rank. The type-series of Keyserling's taxon was indefinite, consisting, to judge from the text, of apparently at least three specimens from various localities on the rivers Syssola and Petshora and their tributaries. All that was figured however were two suture-lines and a plug of matrix from an umbilicus (pl. 20), although it was not stated whether these were all from the same specimen or from several. The taxon was therefore barely interpretable. Nikitin included all of Keyserling's material in his renamed taxon and added at least two more specimens which he figured as well, one from the Petshora and now also one from the area of Elatma, SE of Moscow. No types were designated. Sokolov attempted to rectify this by searching Keyserling's collection at the Mining Institute in St. Petersburg and claimed to have rediscovered 'Keyserling's original', labelled '*Ammonites* n. sp.'. He must therefore have presumed that Keyserling's figures and descriptions were based on a single specimen, which he thought he now had and which he figured (1912, pl. 1, fig. 4, from the Pizhma, a tributary of the Petshora) without, however, formally designating it lectotype. Keyserling's collection was later re-examined by Bodylevsky who came to express doubts about the identity of the specimen figured by Sokolov as 'Keyserling's original': its suture-line does not agree with Keyserling's drawings either in size or in detail, and the label '*Ammonites* n. sp.' was added much later, by Lahusen. Instead he found another fragmentary specimen, 5/8 whorl of a phragmacone originally 120 mm in diameter, whose suture-line agrees closely with Keyserling's drawings and which came from the Syssola, one of the localities expressly recorded by him. Bodylevsky therefore designated this specimen lectotype, and renamed Sokolov's figured specimen *Cadoceras lahuseni* sp. nov. A promised figure and description of the lectotype of *Cadoceras stenolobum* has not so far been published, so that we are restricted to Bodylevsky's text as the only available guide to the interpretation of the species. He continued to include Nikitin's excellent figures, however, and added two more. These are all consistent and show the inner whorls to be much more densely ribbed and less acutely arcuate than those of *L. placenta*, analogous to the way in which subsequently *Quenstedtoceras henrici* differs from *Q. lamberti*. The characteristic umbilical crater also develops rather later during growth. These Russian forms give the impression of being perhaps a little older than the typical forms of *Longaeviceras*, intermediate between the latter and the earlier group of *Cadoceras* (*Rondiceras*) *milaschevici* (Nikitin) of the Coronatum Zone. These become smooth at 60–80 mm diameter, wheres the type of *L. lahuseni* (Bodylevsky) is still strongly and densely ribbed at 120 mm.

(c) *Longaeviceras keyserlingi* (Sokolov, 1912)

*1912	*Cadoceras* (*Quenstedtoceras*) *keyserlingi* Sokolov, p. 25, 53, pl, 2, fig, 2*a*, *b* (lectotype, designated Meledina 1977) (R. Vishera, Petshora)
?1912	*Cadoceras nikitini* Sokolov, p. 24, 53, pl. 1, fig. 3*a–d*, pl. 3, fig. 13 (holotype, monotypy) (R. Adzwa, Petshora)
?1973	*Longaeviceras bodylevskii* Meledina; Kniazev *et al*., p. 656, fig. 1.1 (Anabar, Siberia)
1985	*Longaeviceras nikitini* (Sokolov); Callomon, p. 69, fig. 8P.

This is a group of closely-related forms. Whether they are really separable specifically among themselves, or whether they are merely variants of a single species, remains to be determined when more plentiful material is available. They differ consistently from *L. placenta* in having sharper venters, particularly on the inner whorls, and secondary ribs that rise higher on the whorl side, close to the venter, rather than at mid-flank. Forms like them are occasionally found in the middle Athleta Zone of the Oxford Clay of England (Peterborough, old collections) so that their age is close to that of *L. placenta*

(d) Microconchs

Microconchs of *Longaeviceras* are well known. They include the following group which is most probably the complement of *L. placenta-kerserlingi* etc., although closer pairing is so far not possible.

1913	*Cadoceras* (*Quenstedtoceras*) *mariae* d'Orbigny; Sokolov, pl. 2, fig. 1 (Novaya Zemlya)
1915	*Quenstedtoceras maxsei* Krenkel, p. 227, pl. 22, fig. 15 (Popilany, Lithuania)

1924 *Quenstedtoceras holtedahli* Salfeld and Frebold; p. 4, pl. 1, figs. 3, 3*a* (lectotype, designated here), 4 (Novaya Zemlya)
1957 *Quenstedtoceras cupressum* Sazonov; p. 122, pl. 12, figs. 3, 3*a* (R. Oka)
1960 *Quenstedtoceras novosemelicum* Bodylevsky; p. 80, pl. 7, fig. 2 (lectotype, designated here) (Olenek, Siberia) (*non* pl.10, figs. 4, 5; *non* 1949, *nom. nud.*)
?1965 *Novocadoceras suraense* Sazonov; p. 34, pl. 6, figs. 6*a*, *b* (Elatma)
1985 *Longaeviceras nikitini* (Sokolov); Callomon, p. 69, fig. 8p.

Fragments of forms like these have been found in the Hackness Rock of the Scarborough area (Wright 1968, p. 392, bed 4, recorded as *Pseudocadoceras boreale*). Although the generic name *Novocadoceras* was based on but a single specimen, the holotype of *N. suraense* from Elatma, it could well serve as a subgenus of *Longaeviceras* if one wishes to incorporate the dimorphism in the formal taxonomy at this level.

Age. Although none of the well-preserved Yorkshire material has been found *in situ*, there can be little doubt that it all came from the lower, highly fossiliferous chamositic part of the Hackness Rock (Wright 1968, p. 385, bed 3; p. 392, beds 2–4). This is supported by well-preserved specimens known from the Oxford Clay of the Midlands: Bletchley, bed 21 (Callomon 1968, p. 282; JHC coll. 1975); Oxford, Summertown brickpit (OUM and BGS, recorded as *Ammonites macrocephalus* by Woodward, 1895, p. 43); and Northam brickpit, Eye Green, Peterborough (Brinkmann 1929, p. 33; BM). All these are in the middle Athleta Zone, Proniae Subzone – the only part of the Callovian clays of the Midlands to yield abundant large pyritized ammonites, mostly *Kosmoceras* and *Peltoceras*.

Longaeviceras does however range higher up. Occasionally, nuclei are found in the upper Athleta Zone, Spinosum Subzone, and two are shown here in Pl. 93, figs. 4, 5, from Woodham (Arkell 1939, beds D–E; Callomon 1968, p. 288, again recorded in part as *Pseudocadoceras boreale*). Yet another, shown in Pl. 93, fig. 6, came from the Hackness Rock in a piece of such distinctive matrix – white silty limestone with dispersed very large ooliths – that it can be confidently ascribed to the Lamberti Zone around Gristhorpe Cliff, east of the Red Cliff fault (Wright 1968, p. 391). It is matched exactly by that of a fine collection of Lamberti Zone ammonites in the Sedgwick Museum, Cambridge. A specimen of *L. holtedahli* Salfeld and Frebold (m) was collected in place in the Dunans Clay Member [Oxford Clay] in Staffin Bay, Skye by Dr D. Marchand (Dijon). It occurred in bed 6 of Sykes and Callomon (1979, p. 879), 10 cm above the base, in indubitable Lamberti Zone, with *Q. (Eboraciceras) grande* Arkell.

These late forms invite comparison with a whole new range of forms recently described from Siberia by Kniazev (1975) and Meledina (1977), variously ascribed to *Quenstedtoceras nikitinianum* Lahusen [a *Cardioceras* from the upper Mariae Zone] (Kniazev, pl. 2, figs. 4, 8, 9) or *Eboraciceras subordinarium* Buckman and spp. aff. (Meledina); and a local speciality of small forms described as *Quenstedtoceras* (*Soaniceras*): *Q.* (*S.*) *angustatum* (type species, holotype a small [M], *Q.* (*S.*) *parvulum* [m], to which should probably be added '*Scarburgiceras*' *obliteratum* Kniazev (pl. 3, figs. 2–6 [m]). They are said to come from the 'zone of *Eboraciceras subordinarium*', presumed to be Upper Callovian, and the 'zone of *Cardioceras obliteratum*', said to be Lower Oxfordian. All these forms seem still to be much closer to *Longaeviceras* than to *Quenstedtoceras*, however, for the '*Eboraciceras*' retain the characteristic umbilicus with sloping walls and sharp edge not found in the true

EXPLANATION OF PLATE 95

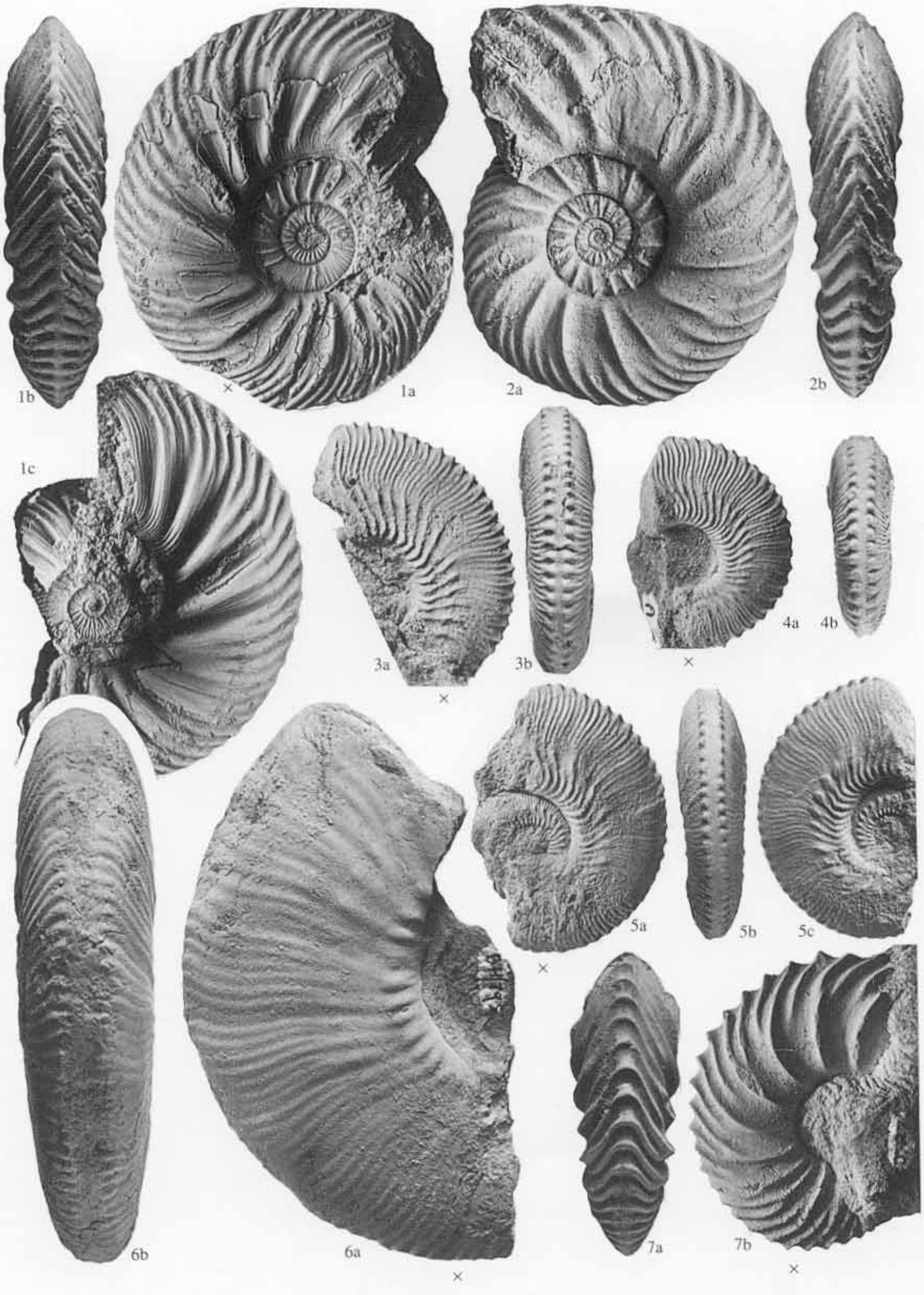
Fig. 1. *Quenstedtoceras flexicostatum* (Phillips). 1*c*, obverse of 1*a*, showing the final adult peristome with striate modification of the ribbing. [m], lectotype, Phillips coll., OUM J16380, Hackness or Scarborough, Lamberti Zone and Subzone.

Fig. 2*a*, *b*. *Quenstedtoceras lamberti* (J. Sowerby), [M], wholly septate phragmocone, topotype, Tidmoor Point, near Weymouth, JHC 93.

Figs. 3–5. *Kosmoceras rimosum* (Quenstedt), adults with bodychamber, [m] *partim* of *K. rowlstonense*. 3*a–c*, JKW BH89; 4*a*, *b*, variant transitional to *K. duncani*, with triplicate looping of secondary ribs at ventrolateral clavi on the inner whorls, JKW A22; 5*a–c*, JKW BH60. Hackness Rock, Hackness quarry, bed 4, Athleta Zone, Proniae Subzone.

Fig. 6*a*, *b*. *Kosmoceras rowlstonense* (Young and Bird), [M], JKW BH79, locality and horizon as figs. 3–5.

Fig. 7*a*, *b*. *Longaeviceras polonicum* sp. nov., [m], adult with half a whorl of bodychamber, WM J22, Scarborough, Hackness Rock, Athleta Zone.



CALLOMON and WRIGHT, *Quenstedtoceras*, *Kosmoceras*, *Longaeviceras* forms of this genus from the Lamberti Zone; and a slighly earlier age, perhaps Spinosum Subzone of t Athleta Zone seems more likely.

The youngest true *Longaeviceras* known so far came from the Scarburgense Subzone of the Mariae Zone the Isle of Skye: *L. staffinense* Sykes (1975, p. 72, pl. 1, figs. 1, 3).

Longaeviceras polonicum sp. nov.

Plate 95, fig. 7, cf. plate 93, figs. 3 and 5

*1952 *Cadoceras nikitinianum* (Lahusen); Makowski, p. 26, pl. 3, fig. 1, 1*a* (holotype), pl. 6, figs. 1, 3 (Łukow, Poland)

aff. 1960 *Longaeviceras novosemelicum* Bodylevsky; pl. 10, figs. 4*a*, *b*, 5*a*, *b* (Novaya Zemlya and Olene Siberia)

Description. All the specimens from Poland cited above are complete adult microconchs. They devel extremely coarse ribbing on the bodychamber in which the somewhat irregular primaries and secondaries a strongly differentiated, giving them their striking appearance. The venter is rounded on the inner whorls b then becomes sharp, the reverse of the order usually found in the Cardioceratidae. It does not, however, fo a keel, and the ribbing crosses the venter with if anything some accentuation, unlike that found *Quenstedtoceras*: the difference may be well seen by comparing Makowski's pl. 6, fig. 3*b* with his pl. 7, fig. 1 The specimen from the Hackness Rock figured here (pl. 95, fig. 7) is a little more compressed than the Poli material but otherwise matches it perfectly. It is in an old museum collection (labelled *Am. flexicostatum* var but another, more poorly preserved (JWK coll. A12) came from Hackness, bed 4.

Affinities. The earliest named species of this group is *L. schumarowi* (Nikitin, 1884) (pp. 68, 143, 3, fig. 16), said to come from the beds with *Cadoceras milaschevici*, i.e. probably late Midd Callovian or early Upper Callovian. The figured specimen (lectotype, designated here) is howev only 35 mm in diameter and shown as wholly septate, so that it is not clear whether it it is a micr or a macroconch. It is also much more inflated: 57% compared with 35–42% cited by Makows for the Polish forms, and 38% at 40–50 mm in the Yorkshire specimen; and the venter remai correspondingly rounded at all stages visible. Such inflated forms also occur in Yorkshire: a septa nucleus is shown here in pl. 93, fig. 3, with a whorl-thickness of 49% at 27 mm. Whether there in fact a complete gradation between *L. holtedahli* (see above, microconchs of *Longaeviceras*) a *L. schumarowi* remains to be seen, but Makowski's illustrations suggest they are distinct.

The macroconchs remain to be positively identified. A likely candidate is another specim figured by Makowski as *Cadoceras schumarowi* (pl. 5, figs. 10, 10*a*, 10*b*) 68 mm in diameter said be 'complete'; but it is difficult to tell whether it is adult. Its whorl-thickness at 70 mm is abo 50%. An inflated but badly crushed specimen from bed 4 of Hackness Quarry (JKW coll. BH is septate to about 80 mm, followed by a little bodychamber, and still quite strongly ribbe *L. fournieri* (Gérard and Contaut 1936) (p. 47, pl. 14, figs. 2, 2*a*) may also be of this group.

The forms now called *L. polonicum* were previously included by Sykes (1975, p. 72) *L. staffinense* from the Oxfordian, whose outer whorls they certainly strongly resemble. The inn whorls of *L. staffinense* are, however, more rectiradiately ribbed, without the strong curved forwa projection which usually characterizes Callovian forms of *Longaeviceras*.

Age. The Polish material all came from concretions in a large glacially transported mass of clay at Łukow, a hence no precise stratigraphy is available. Something may, however, be learned from the associations in t concretions, which show that by far the greatest proportion came from a single well-defined horizon in t lower Lamberti Zone, Henrici Subzone, equivalent to beds H1–3 at Dives, Normandy, and bed D(2) Woodham (Callomon 1968, p. 288) – the true *Q. lamberti* and its allies are absent. Material in the museu shows that these concretions are packed with *Quenstedtoceras* and *Kosmoceras*, any other forms being ve rare. In contrast, the only imprints of other ammonites in the matrix attached to the *Longaeviceras* figured fro Łukow appear also to be of *Longaeviceras*. This suggests that these, in turn, all came from concretions of different age. The Yorkshire material came from the Proniae Subzone of the middle Athleta Zone. Some the nuclei from Woodham that look as if they belong to this group (see Pl. 93, figs. 5*a*, *b*) came from the upp Athleta Zone, Spinosum Subzone.

Genus QUENSTEDTOCERAS Hyatt, 1877

Type species *Ammonites leachi* (J. Sowerby, 1819)

Quenstedtoceras flexicostatum (Phillips, 1829)

Plate 95, fig. 1a–c; text-fig. 2c

*1829	*Ammonites flexicostatus* Phillips; p. 142, 175, pl. 6, fig. 20 (unchanged in later editions)
1912	*Quenstedtoceras lamberti* (Sowerby); Douvillé, pl. 4(10), fig. 49 (Dives, Normandy, bed H4)
1922	*Bourkelamberticeras intermissum* Buckman; pl. 339 (Dorset, Weymouth)
1939	*Quenstedtoceras lamberti* (J. Sowerby) partim; Arkell, p. 171.
1939	*Quenstedtoceras gallicum* Arkell, p. 172 (pro Douvillé 1912 cited above)
1947	*Quenstedtoceras lamberti* (J. Sowerby); Arkell, pl. 2, fig. 11 only.

Type. The legend of Phillips' 'lost collection' having been finally laid to rest (Edmonds 1977), there is no reason to reject material in Phillips' collection at Oxford in the search for survivors of the type-series of his species. In the absence of any indication to the contrary, the number of specimens in the type-series must be regarded as indefinite, and no type has ever been designated although the sole figure of a specimen stated to be in his collection (Phillips 1875, p. 327) was inevitably the basis of all subsequent discussions. There are several specimens in Phillips' collection labelled '*A. flexicostatus*' of which the one that most closely resembles the figure by far and which is labelled in his own handwriting is now designated lectotype and figured here (OUM J16380; pl. 95, fig. 1). As can be seen by comparison, the original figure (reproduced here as text-fig. 2c) was not unsuccessful, the main difference lying in the density of secondary ribs on the last half-whorl, which is rather higher in the type specimen than shown in Phillips' figure.

Description and discussion. The uncertainties of interpretation arising from poor illustration hitherto make much of past classification of the species now of little interest. There is not much to add to the discussion by Arkell (1939), who followed Douvillé (1912) in putting *flexicostatum* in synonymy with *lamberti*. Other authors continue to regard them distinct, however, as did Phillips himself, and in Poland they are even used as indices of two separate and successive Zones (Rózycki 1953 and others subsequently, e.g. Dayczak-Calikowska and Kopik in Sokołowski 1976, p. 166). The purpose of this note therefore is not necessarily to revive Phillips' name but to make quite clear to what it refers.

The type of *Q. flexicostatum* is a complete adult microconch with half a whorl of bodychamber. The diameter is 68 mm, septate to 50 mm, and the dimensions are: at 60 mm, whorl-height 39%, whorl-breadth 28%, umbilical width 32% of the diameter, respectively. The only surviving syntype of *Q. lamberti* was unfortunately designated 'type' by Douvillé (1912, p. 59) who refigured it. It is a nucleus 21 mm in diameter, quite uninterpretable in itself (BM 43588), and past authors have invariably based their discussions on topotypes resembling Sowerby's larger figures. They are common enough and come from the same level in the Oxford Clay at Weymouth, almost exclusively from the exposure on the beach at Tidmoor Point. The ones that have been figured are all macroconchs (Buckman 1920, pl. 154, 1925, pl. 154A; Arkell 1933, pl. 37, fig. 3; Arkell 1947, pl. 2, fig. 10; Arkell 1956, pl. 38, fig. 6). Another topotype of *Q. lamberti* is now figured here (Pl. 95, fig. 2), alongside the type of *flexicostatum*: it is also from Tidmoor Point and wholly septate with no approximation of the last sutures. A closer match of a dimorphic pair could hardly be wished for. The ages are identical; that part of the Hackness Rock belonging to the Lamberti Zone contains in abundance the same complete range of variants found in the clays of Tidmoor Point.

The systematic choice is therefore quite clear: if macro- and microconchs are to be united under the same specific name, *Q. flexicostatum* is a junior synonym of *Q. lamberti*. If the dimorphs are to be distinguished nominally at specific or subgeneric level, *flexicostatum* is the oldest available name for the microconch of *lamberti*. There are then two further available specific names of microconchs, given in the synonymy: *Q. intermissum* (from Weymouth) and *Q. gallicum* (from Normandy). These were originally introduced or used as morphospecies to distinguish small differences of morphology within the *lamberti* group (Arkell 1939, p. 172), before the existence of dimorphism was realized – hence the reference to the type of *Q. intermissum* as a juvenile. Both types have again precisely the same ages as *Q. lamberti*, and fall well within the range of what the large collections from Tidmoor Point show to be but a single rather variable biospecies. The types of *Q. flexicostatum* and *Q. intermissum* represent about the extremes in the range of sizes found (septate to 50 and 37 mm, respectively), with the specimen figured by Arkell in 1947 (see synonymy) about in the middle (43 mm). *Q. gallicum* is near the extreme in the range of evoluteness.

Age. Upper Callovian, Lamberti Zone and Subzone, as *Q. lamberti.*

Family KOSMOCERATIDAE Haug, 1887
Genus KOSMOCERAS Waagen, 1869

Type species *Ammonites ornatus rotundus* Quenstedt, 1846 subsequently designated by Buckman 1921, p. 54

Kosmoceras rowlstonense (Young and Bird, 1822)

Plate 95, fig. 6, plate 96, figs. 1–4; text-fig. 2*d*

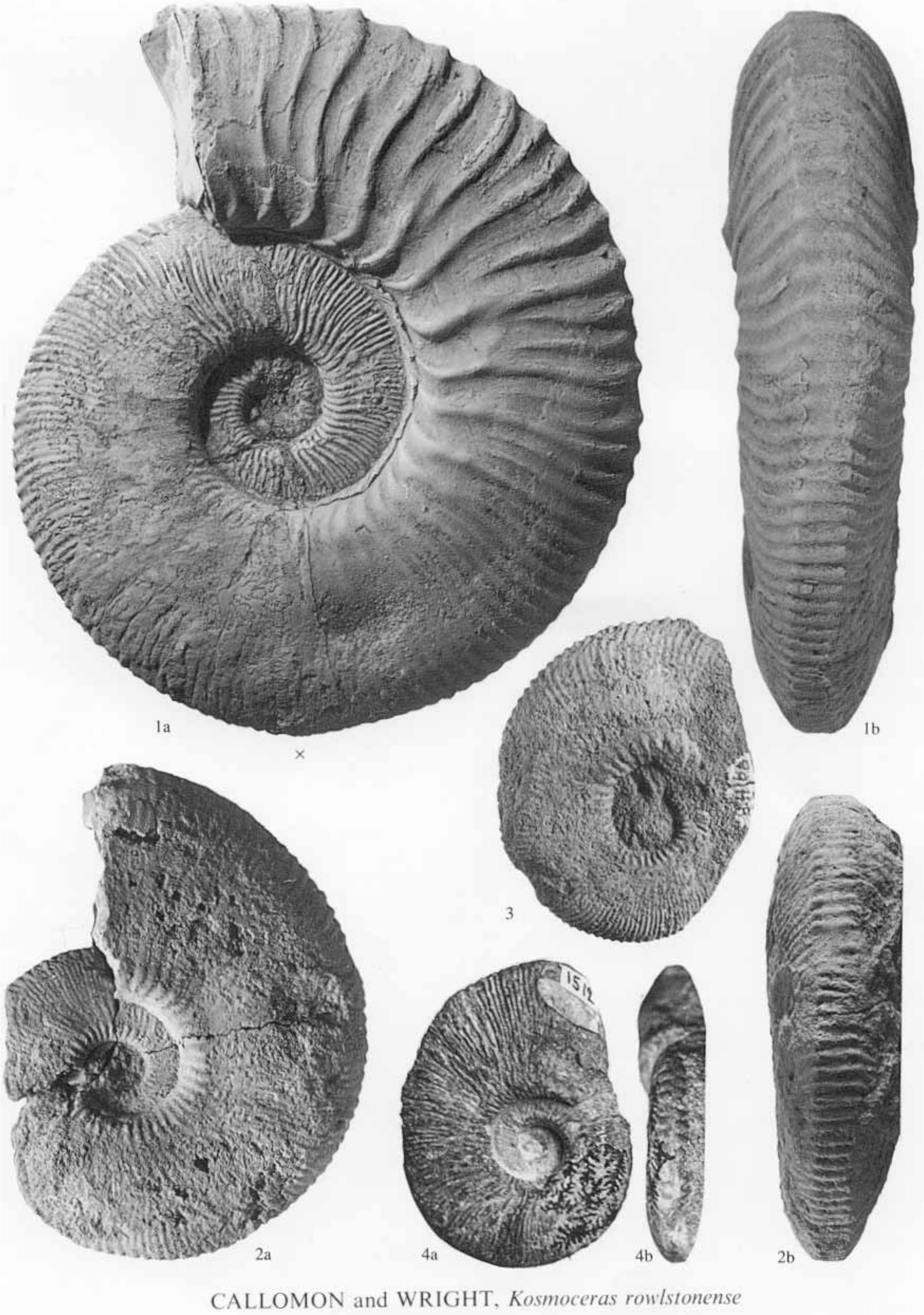
*1822 *Ammonites rowlstonensis* Young and Bird; p. 253, pl. 13, fig. 10
1828 *Ammonites rowlstonensis* Young and Bird; p. 269, pl. 13, fig. 10 (redrawn)
*1923 *Lobokosmokeras rowlstonense* (Young and Bird); Buckman, pl. 437
cf. 1926 *Kuklokosmokeras kuklikum* Buckman; pl. 626A, B
cf. 1939 *Kosmoceras (Zugokosmokeras) rowlstonense* (Young and Bird); Arkell, p. 192 (non p. 185).

History and type. The interpretation of this species has come under a cloud. It was described by Young (1822, p. 253) as follows: 'No. 10, Pl. xiii is a rare and beautiful little flat shell from the calcareous sandstone of Rowlston Scar. It has on the back a double crenulated or serrated keel, or rather, a double row of minute knobs, with a narrow space in between, rather depressed. The knobs are at the ends of its curved ribs, which are numerous towards the back, but fewer and more prominent towards the inner side of the whorl. The aperture approaches to ovate. Sowerby's *A. calloviense* and *duncani* resemble this shell, but as they both differ from it, we name it *A. rowlstonensis.*' The specimen was drawn by Bird, and his figure is reproduced here as text-figure 2*d*. The description was essentially unchanged in 1828 (p. 269), except for the extra information that the species is 'so rare that we have seen only another specimen', and the last sentence which now reads 'It so nearly resembles Sowerby's *A. gulielmi* that we may take it as a variety of the same species'. What was thought to be Young and Bird's specimen in the Whitby Museum (no. 1512) was figured as holotype by Buckman in 1923.

The problem is that the alleged holotype belongs to a well-known species from the Athleta Zone, whereas at Roulston Scar, in the Hambleton Hills at the most southwesterly outcrop of the Jurassic overlooking the Vale of York, some 50 km W of Scarborough, no Middle–Upper Callovian is preserved, only Oxfordian Lower Calcareous Grit (Cordatum Zone) – to which Young's 'calcareous sandstone' usually referred – resting directly on Kellaways Rock. The level of the latter is here probably Koenigi Subzone as elsewhere, although ammonites are too rare at this locality to establish this directly (Wright 1978). The preservation of the supposed holotype, moreover, is without doubt in the familiar chamositic oolite of the Hackness Rock of Scarborough. Although Hackness Rock reappears 4 km N of Roulston, it does so as a flaggy non-oolitic marl: no chamositic oolite is known west of Hackness. There are also differences between Young's description and the supposed

EXPLANATION OF PLATE 96

Figs. 1–4. *Kosmoceras rowlstonense* (Young and Bird) [M]. 1*a*, *b*, ?topotype, BM 39540, Scarborough; 2*a*, *b*, wholly septate, JKW A21, Hackness quarry, bed 4; 3, wholly septate, JKW BH68, same locality; 4*a*, *b*, neotype, figured by Buckman (1923, pl. 437) as 'holotype', probably found as a beach-pebble near Scarborough, Whitby Mus. 1512. All Hackness Rock, Athleta Zone, Proniae Subzone.



CALLOMON and WRIGHT, *Kosmoceras rowlstonense* holotype too substantial to be ignored. Thus, the absolutely characteristic feature of the Upper Callovian f(is the fusion of secondary ribs at the external, ventro-lateral tubercles ('bundling', or looping) of which tl is no sign in Bird's figure nor mention in Young's account: yet elsewhere, in Upper Liassic *Peronoceras*, sim looping is both commented on and correctly drawn. Instead, Bird's drawing shows 52 minute simple tuber on the last half whorl where the Whitby specimen has only 30.

There are, thus, serious discrepancies between Young and Bird's figures and description, which consistent among themselves, and the supposed holotype. Similar contradictions have arisen in other cas see for instance the lengthy discussion of *Ammonites redcarensis* by Buckman (1926, pp. 11–13). It seems q certain on the available evidence, therefore, that the specimen in Whitby figured by Buckman is neither holotype nor, if the type-series consisted already in 1822 of the two specimens mentioned in 1828, a synty We must conclude that Young and Bird's original descriptions were based on some other specimen now l Even so, it is not clear what it might have been. If truly from Roulston, it could conceivably have bee *Kepplerites* microconch, although then highly atypical. Conversely, figure and description do most clo resemble (Middle Callovian) *Kosmoceras gulielmi* (Sowerby) as the authors themselves stated in 1828, but tl it was most unlikely to have come from Roulston. Certainly, nothing like it seems to have been found th since. The name *rowlstonense* has however since come to be widely used in the literature, interpreted in te of Buckman's figure, and to stabilize the nomenclature of this well-known species the specimen from Hackness Rock of Castle Hill, Scarborough (Whitby Museum 1512) is now designated neotype. It is refigu here on Plate 96, fig. 4.

Description and age. The type is a macroconch and the characteristic features are the moderately invol compressed whorl-section and dense ribbing on inner and middle whorls, commencing at the umbilical mar with slight forward twist, rising straight up the whorlside without any lateral nodes or tubercles, and divid into sheaves of 2–4 very fine secondaries. These reunite in pairs at the ventrolateral tubercles on the in whorls, but later lead each to a single tubercle. As in most *Kosmoceras*, the adult bodychamber is hig variable. In some specimens it becomes almost smooth; in others, the dense ribbing persists to the ((*K. kuklikum*, *K. deficiens*) and in yet others it suddenly regains strong, coarse 'gerontic' ribbing reminisc of ancestors in the Middle Callovian (*K. obductum posterior* Brinkmann), as in the fine topotype illustrated Plate 96, fig. 1.

The inner whorls are also variable. Some forms tend to develop a spiral smooth band low on the whorlsi near the umbilical edge, reminiscent of *K. proniae* (Teisseyre, 1884), but without the double row of late tubercles so characteristic of this species; and in others the secondaries on the inner whorls may fuse externa into groups of 3–4, a feature characteristics of *K. duncani* (J. Sowerby, 1817) (neotype, also from Yorksh figured by Arkell 1939, pl. 11, fig. 6).

The microconchs fully cover the same range of morphologies. Should it be desired to name them as separ morphospecies also, the best available name for the forms most closely resembling *K. rowlstonense* appear be *K. rimosum* (Quenstedt 1887, p. 716, pl. 83, fig. 15 – holotype), and some specimens from Hackness shown here in Plate 95, figs. 3–5.

The age of *K. rowlstonense* is Athleta Zone, either the upper part of the Proniae Subzone or the lower p of the Spinosum Subzone, for it seems to be slightly younger than the main fauna of the Proniae Subz known throughout southern England (Callomon, 1968: Calvert, bed 13 *b*; Bletchley, bed 21, recently w exposed in a temporary section at Milton Keynes with abundant pyritized ammonites). *K. kuklikum* a *K. deficiens* came similarly from slightly higher levels in the old brickpits of north Oxford. At Woodhan occurs in the lower Spinosum Clays (bed E, JHC coll., and possibly bed D, recorded by Arkell, 1939).

SUMMARY AND CONCLUSIONS

The following species are described or discussed:

Chamoussetia philipsi nom. nov. pro *Am. lenticularis* Phillips, 1829, non Young and Bird 1828
? = — *stuckenbergi* (Lahusen, 1875)
= — *chamousseti* (D'Orbigny, 1847)
— *buckmani* sp. nov.
— *saratovense* sp. nov.
— *cryboloides* (Quenstedt, 1887)
— *funifera* (Phillips, 1829)
= — *galdrynus* (D'Orbigny, 1847)

	Pseudocadoceras boreale Buckman, 1918	820
? =	— *primigenium* (Parona and Bonarelli, 1895)	
	— *grewingki whithami* subsp. nov.	822
	— *orbignyi* Maire, 1932	823
	Longaeviceras placenta (Leckenby, 1859)	824
	— *longaevum* (Bean MS–Leckenby, 1859)	824
	— *stenolobum* (Keyserling, 1846)	824
	— *keyserlingi* (Sokolov, 1912)	825
? =	— *nikitini* (Sokolov, 1912)	
	— *polonicum* sp. nov.	828
	— *schumarowi* (Nikitin, 1884)	828
	Quenstedtoceras flexicostatum (Phillips, 1829)	829
=	— *lamberti* (J. Sowerby, 1817) (m)	
=	— *intermissum* (Buckman, 1922)	
=	— *gallicum* Arkell, 1939	
	Kosmoceras rowlstonense (Young and Bird 1822)	830
	— *duncani* (J. Sowerby, 1817)	832
	— *proniae* Teisseyre, 1884	832
	— *rimosum* (Quenstedt, 1887)	832

Chamoussetia phillipsi, *C. buckmani*, *C. chamousseti* (Lower Callovian) and *C. funifera* (Upper Callovian) are so similar to each other and so distinct from contemporaneous Cadoceratinae that a separate parallel and slow-evolving derivation from Bathonian *Arcticoceras* seems to be indicated, making this the first group of Cardioceratidae to have developed a keel independently. *Pseudocadoceras boreale* also has a sharper venter, although not a keel proper, and its age is now known to be Lower Callovian, making this apparently the second attempt at evolving a carinate whorl-section. It is not simply related to Upper Callovian *Longaeviceras*, in which the third attempt may be seen, leading to *Quenstedtoceras* and hence *Cardioceras* itself; but here again the evolution is not so much one of replacement as of branching, *Longaeviceras* persisting independently side by side with *Quenstedtoceras* through the Upper Callovian into the basal Oxfordian.

These examples show how, in ammonites, a new character such as the distinctive keel of *Cardioceras* may evolve repeatedly before becoming phyletically stable. A succession of forms sharing a common character may reflect repeated partial homoeomorphies rather than direct lineal descent. To resolve such homoeomorphies can require very detailed stratigraphical time-resolution, such as that made possible by the revision in recent years of the stratigraphy of the Yorkshire Callovian.

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