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VERSITA

On variation in *Schloenbachia varians* (J. Sowerby, 1817) from the Lower Cenomanian of western Kazakhstan

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ABSTRACT:

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An assemblage of 94 specimens of *Schloenbachia varians* (J. Sowerby, 1817) from the Lower Cenomanian *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone of the Besakty section in the Mangyshlak Mountains of western Kazakhstan includes 26 complete adults that range from to 59–174 mm in diameter. No size-related dimorphism was detected in the assemblage, which shows wide, continuous intraspecific variation. This is described in terms of five formae; from robust to gracile these are: *ventriosa*, *varians sensu stricto*, *subtuberculata*, *intermedia*, and *subplana*. The ratio of robust (*ventriosa* + *varians sensu stricto*) to gracile (*subtuberculata* + *intermedia* + *subplana*) individuals is 34% to 66%. The reference specimens of the formae and their synonyms are described and illustrated, and related to the Besakty material. The modification of adult body chamber ornament of all formae is documented, and *Jakeiceras* Cooper and Owen, 2011 is shown to be based on an adult of a passage form between *forma subtuberculata* and *forma intermedia*. The differences between Lower Cenomanian *S. varians*, lower Middle Cenomanian *S. coupei* (Brongniart, 1822), and upper Middle and lower Upper Cenomanian *S. lymensis* Spath, 1926b are described and illustrated.

Key words: Ammonites; *Schloenbachia*; variation; Cenomanian; Cretaceous; Kazakhstan.

'Depressed, thickish, carinated, with a row of large tubercles near the front, and one or two rows of tubercles placed on furcate radiating undulations; inner whorls half concealed; aperture roundish.

No ammonite is more variable than this in the strength of the undulations and proportions of the tubercles, still, however, it may be known by the large tubercles near the front…and two lesser on each radius near the concurrence of it, the inner of which is the smallest, and sometimes obscure, or united to the other.' (James Sowerby, 1817, p. 169).

'This species of ammonite is one of the most proteiform of the whole genus, presenting great variety in the figure, disposition, and number of the tubercles and costae. It is, however , readily distinguished from its associates, by the acute entire keel, and the bifurcating tubercular radii….In a suite of fifty specimens, in which every individual presented some peculiarity, three principal varieties were observed, each passing insensibly into the other' (Gideon Mantell 1822, pp. 115–116).

'*Ammonites varians*, as its name implies, assumes many forms (Daniel Sharpe, 1853, p. 22)'

INTRODUCTION

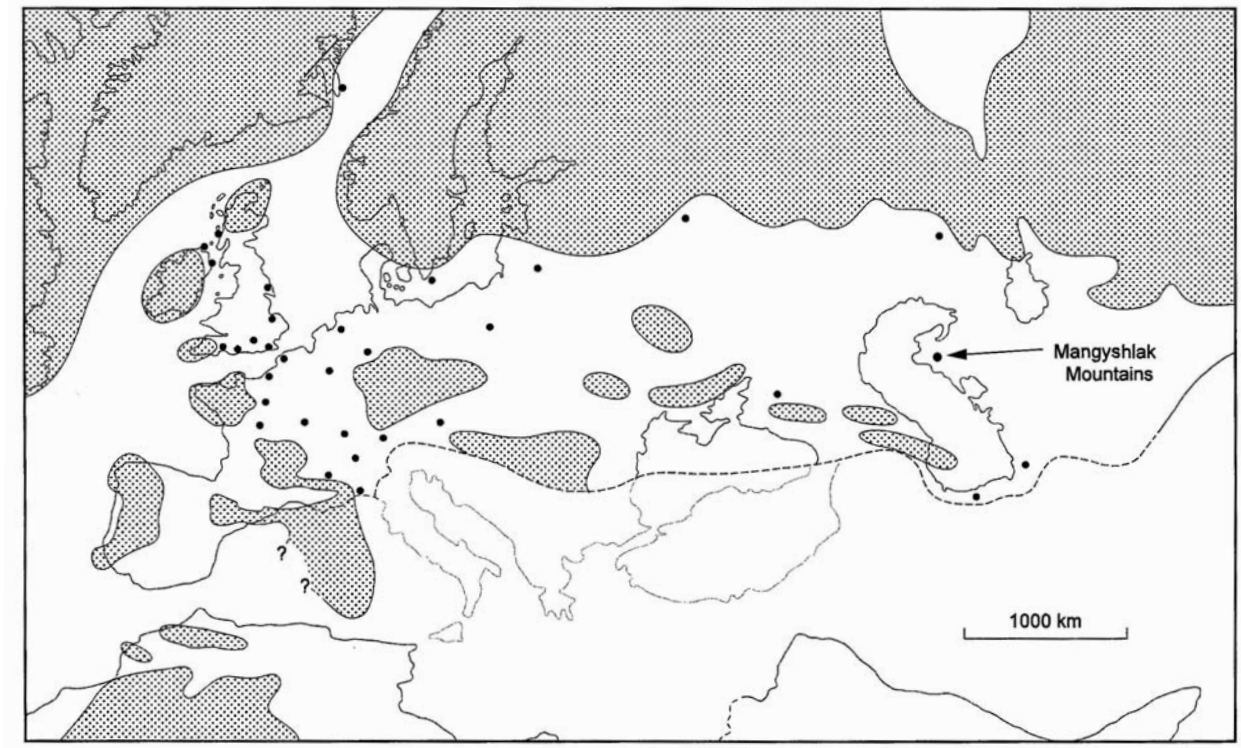
In 1996, Marcinowski, Walaszczyk and Olszewska-Nejbert illustrated as their plate 14 a remarkably preserved *Schloebachia varians* (J. Sowerby, 1817) from bed 30 of the Besakty section in the Mangyshlak Mountains of Western Kazakhstan. The specimen (reillustrated here as Plate 3) is remarkable because it is very well-preserved, an internal mould that shows crowding of septa at the adapertural end of the phragmocone-indicating it to be an adult-and modification of ornament at the greatest preserved diameter, indicating proximity to the adult apertural margin. It had been Ryszard Marcinowski's ambition to describe the rich ammonite faunas collected by the 1992 expedition to the Mangyshlak Mountains, but health and his early death in 2010 prevented this. I was subsequently asked to take on the task and this is the first contribution to this end. I first met Ryszard forty years ago, when he visited the United Kingdom under the auspices (as I recall it) of a British Council exchange programme. T ogether with the late Jake Hancock we visited the Isle of Wight, and, in particular, localities in the Cenomanian Lower Chalk. One of these, at the top of Gore Cliff, at the southernmost extremity of the island, is marked by two levels of glauconitic chalk, the lower the classic Glauconitic Marl of English terminology. At that time, these beds yielded fragments and nuclei of ammonites in an abundance that defeated even the most enthusiastic collector. Of these, more than 99% are fragments of *Schloenbachia*, a dominance, in the early Cenomanian, that extends across the Boreal Realm, from Greenland to Kazakhstan, and Iran north of the Zagros suture Zone (Text-fig. 1). The Besakty assemblage described here shows a similar dominance; almost 90% of the ammonites collected are *Schloenbachia*, and of these, 26 % have complete adult body chambers.

The evolution and variation in *Schloenbachia* is a topic that fascinated both Ryszard, and Jake Hancock. The latter presented his views on the topic at a Palaeontological Society Annual Meeting in the 1960's, and it had long been his intention to submit a Palaeontographical Society Monograph on the genus; it was for his reason that the late C.W. Wright and I omitted *Schloenbachia* from our Palaeontographical Society Monograph *The Ammonoidea of the Lower Chalk* (1984–1996; in progress). I am currently preparing the final part of this monograph, which will include comprehensive synonymies; the present account is a necessary preliminary. Hancock's views on *Schloenbachia* were published (with Ryszard's encouragement) in outline in *Acta Palaeontologica Polonica* in 1979, in an account of the Cenomanian cephalopods from the Glauconitic Limestone southeast of Esfahan, Iran. Hancock's views are the starting point for all subsequent discussions on evolution and variation in *Schloenbachia*. A part of that account is reproduced below. The position of the Besakty section in the Mangyshlak Mountains is shown in text-figs 1 and 11 of Marcinowski *et al.* (1996), the stratigraphic section in their text-fig. 12. The present material comes from bed 30 of the section. Marcinowski *et al*. (1996, p. 31) described this as being 10.8 m in thickness: "Light- and grey-green, poorly cemented fine-grained quartz sandstones with glauconite and muscovite flakes. Throughout the bed occur irregularly shaped, relatively hard, sometimes lightly phosphatised concretions of the limy sandstones, up to 1.5 m in diameter. Although the concretions are dispersed throughout the bed they are most abundant in its middle part. Moreover, they seem to be larger and more regular downward. The common fauna, except numerous serpulid patches from soft sandstones, come exclusively from the sandstone concretions." They illustrated an outcrop as their pl. 9, fig. 2.

The present assemblage of 112 specimens is as follows:

Schloenbachia varians (J. Sowerby, 1817): 94 (84%);
Placenticeras mediasiaticum (Luppov, 1963): 10 (8.9%);
Sharpeiceras laticlavium (Sharpe, 1855): 1(0.9%);
Sharpeiceras schlueteri (Hyatt, 1903): 4 (3.6%);
Mantelliceras cantianum (Spath, 1926a): 1 (0.9%);
Hypoturrilites gravesainus (d'Orbigny, 1841): 1 (0.9%)

Bed 30 is also characterised by abundant large *Inoceramus crippsi* Mantell, 1822. Taken together this ammonite-inoceramid association indicated the *Sharpeiceras schluerteri* Subzone of the Lower Cenomanian *Mantelliceras mantelli* Zone of the standard ammonite zonation of the northwest European succession shown in Text-fig. 2. A striking feature of the subzone is the occurrence of large *Schloenbachia varians* and large *Inoceramus crippsi*, an event recognised at Folkestone in Kent (Gale and Friedrichs 1989), the Boulonnais in the Pas-de-Calais, Aube and Marne in France (Amédro *et al*. 2012), northern and southern Germany (Wilmsen and Niebuhr 2010), and here, 3,800 km to the east in Kazakhstan. At Folkestone, the *schlueteri* Subzone is represented by rhythmically bedded clay rich and clay poor couplets in the Lower Chalk, couplets interpreted by Gale (1995) as representing the 21,000- year precession cycle. On the basis of the records in Gale and Friedrichs (1995), the subzone represents a minimum of 105, 000 years (five couplets, the total range of *S. schlueteri* at Folkestone).



Text-fig. 1. The geographic distribution of *Schloenbachia* during the early Cenomanian

SUBSTAGE	ZONE	SUBZONE
Upper Cenomanian	*Neocardioceras juddii*	
	Metoicoceras geslinianum	
	Calycoceras guerangeri	
Middle Cenomanian	*Acanthoceras jukesbrownei*	
	Acanthoceras rhotomagense	*Turrilites acutus* *Turrilites costatus*
	Cunningtoniceras inerme	
Lower Cenomanian	*Mantelliceras dixoni*	
	Mantelliceras mantelli	*Mantelliceras saxbii* *Sharpeiceras schlueteri* *Neostlingoceras carcitanense*

Text-fig. 2. Standard ammonite zones and subzones of the Old World Boreal Cenomanian

CONVENTIONS

All dimensions are given in millimeters; D = diameter; Wb = whorl breadth; Wh = whorl height; U=umbilicus; ic=intercostal dimension; c=costal dimension. Figures given in parentheses are dimensions expressed as a percentage of the diameter.

The suture terminology is that of Korn *et al*. (2003); E=external lobe; A=adventive lobe (=lateral lobe, L, of Kullman and Wiedmann 1970); U= umbilical lobe.

REPOSITORIES OF SPECIMENS

These are indicated as follows: UW: Museum of the Faculty of Geology of the University of Warsaw; BMNH: The Natural History Museum, London; BGS: British Geological Survey, Nottingham, including the collections of the Geological Museum (GSM); MHNG: Muséum d'Histoire Naturelle, Geneva; MNHP: Muséum National d'Histoire Naturelle, Paris; OUM: Oxford University Museum of Natural History.

SYSTEMATIC PALAEONTOLOGY

Introduction

The following is a direct quotation from Kennedy, Chahida and Djafarian (1979):

"Genus *Schloenbachia* Neumayr, 1875

Type species: *Ammonites varians* J. Sowerby, 1817, p. 169, pl. 176, by the subsequent designation of H. Douvillé, 1890, p. 290.

Diagnosis. - A highly variable group of medium-sized, strongly dimorphic ammonites; involute and compressed to evolute and highly inflated; carinate, the keel being strong to weak. Compressed forms may be smooth and constricted, although most forms bear umbilical and lower lateral tubercles which may or may not be connected by fine striae or ribs to about twice as many ventrolateral clavi. More inflated forms usually have strong umbilical and lower lateral tubercles, each lower lateral tubercle giving rise to a pair of flexuous ribs, with strong ventrolateral clavi at the end of each rib. With increasing inflation the ribbing breaks down into tubercles only; very inflated forms bear huge upper lateral and smaller lower lateral or umbilical tubercles or septate spines.

Discussion. - The diagnosis indicates the wide variation seen in this genus. Most specimens described to date are internal moulds, when the extremes of ornament are rather reduced, for the tubercles of inflated variants commonly represent the bases of septate spines. Some compressed *Schloenbachia* are almost smooth; others develop puzosiid-like constrictions and yet others bear looped hoplitid-like ribs.

This is the commonest genus in the Boreal Cenomanian, and usually outnumbers the remainder of the ammonite fauna at any given level throughout most of the stage. Large collections from this region indicate very clearly that in the Lower and Middle Cenomanian, any collection from a given horizon represents but a single, rather variable species. The majority of named *Schloenbachia* 'species' are thus no more than variants of a limited number of true species.

Hancock (in preparation) has reviewed and revised the nomenclature of *Schloenbachia,* and his suggestions are followed here. In the Lower Cenomanian, a single species, *Schloenbachia varians* (J. Sowerby, 1817) is recognised, and for convenience, a number of intergrading variants may be named, from hypernodose *ventriosa* through *varians*, *tetrammata*, *subtuberculata* and '*subvarians*' to the almost smooth *subplana*. In the Middle Cenomanian, members of the genus are referred to *Schloenbachia coupei* (Brongniart, 1822), and again, a number of intergrading variants may be named, from hypernodose forms through *trituberculata*, *quadrata*, several unnamed forms to *costata*. Unfortunately, the type of *S. coupei* itself lies away from the common range of variants.

In the Upper Cenomanian, the youngest species of the genus are represented by *Schloenbachia lymense* Spath; none of the variants of this species have, however, received names at his time

One of the difficulties introduced by recognition of such wide variation is that differences between individuals at either end of the spectrum of intraspecific variation are far greater than differences between comparable regions of the plexus of variation in successive species. Thus *Schloenbachia varians subplana* and *ventriosa* are far easier to distinguish than the hypernodose variants of the Lower Cenomanian *S. varians* and the Middle Cenomanian *S. coupei*, a phenomenon which has led some workers to believe that Brongniart's *Ammonites coupei* was a synonym of Sowerby's *Ammonites varians*.

Hancock (*in litt*.) has noted, however, a number of evolutionary changes which affect the ornament. The easiest to detect is the change in the strength of the umbilical tubercles, which, in any given morphotype tend to become more and more prominent as one ascends the

Cenomanian stage. But to use this feature to fix an horizon from a *Schloenbachia* one must compare the specimen with others of comparable inflation and at the same stage of ontogeny.

More obvious are shifts in the general population structure. The proportion of inflated individuals decreases higher in the Cenomanian; in the early Cenomanian forms such as *S. varians varians* are a common element of the *Schloenbachia* population; through the Middle Cenomanian they become decidedly uncommon; in the Upper Cenomanian, inflated forms can still be found but are very rare."

Discussion

Since writing this over 30 years ago, there have been a number of contributions of relevance, while a number of details of the above overview require revision: the presence of septate spines is questionable, while only a single variable species is present in the Upper Cenomanian. Descriptions of highly variable *Schloenbachia* collections as single variable species are given by Marcinowski (1983: the Mangyshlak and Tuarkyr regions, western Kazakhstan), Kennedy and Juignet (1984: Sarthe, France), Kaplan, Kennedy, Lehmann and Marcinowski (1998: Westphalia, Germany; see also Hiss, 1982), Seyed-Emami and Aryai (1981, northeast Iran; see also Wilmsen and Mosavinia 2011), Immel and Seyed-Emami (1985, Central Iran), Kennedy, Amédro, Robaszynski and Jagt 2011 (southern Belgium and northern France) and others. Cooper and Owen (2011) provided a comprehensive review of late Albian Hoplitoidea, and greatly expanded the scope of the family Schloenbachiidae, to which Wright (1957, 1996) had previously referred the genus *Schloenbachia* only, dividing it into subfamilies Schloenbachiinae, Pleurohoplitinae, and Dimorphoplitinae. Discussion of their interesting review is largely outside the scope of the present work, but for their introduction of a new genus, *Jakeiceras*, with *Schloenbachia glabra* Spath, 1938, as type species. They provided no diagnosis, but noted that their new genus "differs from *Schloenbachia* in being more compressed and high-whorled, with flat subparallel flanks, strongly prorsiradiate umbilical bullae which become small and pinched on the adult body chamber, with dense subdued sickle-shaped ribs which broaden on the outer flank in *Hyphoplites*-like fashion and small oblique outer ventrolateral clavi; lateral tubercles are lacking (at least on the outer whorl). It differs from weakly-ornamented forms of *Schloenbachia*, e.g. *S. subvarians*, from which it is derived in having subparallel flanks, a broader venter, stronger keel and adult rib pattern like *Hyphoplites*." (Cooper and Owen 2011, p. 303). As will be demonstrated below, the type specimen of the type species, *Schloenbachia glabra* is an adult of a feebly ornamented variant of *Schloenbachia varians*, the supposedly differentiating features being those of the adult body chamber.

Interpretation of *Schloenbachia* species as highly variable is a widespread, if not invariable view. A simple record of a specimen, or a few specimens as *Schloenbachia varians*, or *Schloenbachia coupei*, though valid, has its limitations, as it does not convey an image of the morphology of the specimen(s). Kaplan *et al*. (1988) used *forma* as a non-Linnean term for morphological variants of *Schloenbachia*, and a similar approach is followed here. My understanding of the variation and evolution in *Schloenbachia* has developed over the years on the basis of new publications, and the study of substantial new collections of many hundreds of specimens from southern England, now in the Oxford University Museum of Natural History (Bayliss, Gale, and Huxtable collections), and the Mangyshlak collections housed in the University of Warsaw. On the basis of this and previous accounts, the three species of *Schloenbachia* recognized here are those recognized by Hancock (see above), *varians*, *coupei* and *lymensis*. It is the first of these that is described below.

Within *Schloenbachia varians* (J. Sowerby, 1817), the following formae are recognised, all, it should be noted, based on the nuclei that dominate in so many faunas, especially those in condensed units such as the Glauconitic Marl and Tourtias of the Anglo-Paris Basin. The specimens and images of the predominantly nuclei to which these names were originally applied are shown in Text-figs 3–7. It should be noted that when individuals at the same ontogenetic stage are compared, there is continuous variation, with passage forms between the various formae. Where proportions of formae within assemblages are given, these are based on the assignation of passage forms to the *formae* they most closely resemble. Subjective as this is, it allows the proportion of robust versus gracile variants to be established, a proportion that changes significantly through time (and between onshore and offshore environments according to Wilmsen and Mosavinia 2011).

Forma ventriosa Stieler, 1922 (= *Ammonites coupei* var. *inflata* of Sharpe, 1853, *semenovi* Manija, 1974): bituberculate, with strong conical lateral tubercles, and strong ventrolateral clavi (Text-fig. 3D, E).

Forma varians sensu stricto J. Sowerby, 1817: no clearly differentiated umbilical bullae on phragmocone; lateral tubercles prominent, outer flank ribs reduced, ventrolateral clavi strong (Text-fig. 3A–C).

Forma subtuberculata Sharpe, 1853 (= *sharpei* Semenov, 1899): individuals with umbilical, inner lateral and ventrolateral tubercles , the outer flank ribs strength-

ened, and approaching long, crescentic bullae (Text-figs 3F, G; 7G, H).

Forma intermedia Mantell, 1822 (= *tollotiana* Pictet, 1847, *subvarians* Spath, 1926a, *ecarinata* Spath, 1928, *donovani* Manija, 1974): individuals with well-differentiated ribs and small umbilical and inner lateral bullae, the latter giving rise to pairs of flexuous ribs that link to ventrolateral tubercles (Text-figs 4A–E, I, J; 7E, F).

Forma subplana Mantell, 1822 (= *dorsetensis* Spath, 1926b): individuals with tiny umbilical and inner lateral bullae, and ventrolateral clavi, delicate growth lines, lirae and riblets (Text-figs 5F–H, 6E, D; 7A, B).

As will be seen from the descriptions below, the adapertural part of adult phragmocones, and especially adult body chambers, show marked changes in ornament from nuclei.

Schloenbachia glabra Spath, 1926a, p. 81, the type species, by original designation, of *Jakeiceras* Cooper and Owen, 2011, (p. 303) is based on the original of *Ammonites goupilianus* of Sharpe (*non* d'Orbigny), 1856, p. 38, pl. 17, fig. 5. This specimen, BMNH 33550, is the holotype by monotypy, from Hamsey, near Lewes, Sussex, illustrated here as Text-fig. 6B, C, H. It is a composite mould with a distinctive bright ochreous coating. Derived from a well-cemented chalk, and showing no sign of post-mortem crushing, the dimensions are as follows:

D	Wb	Wh	Wb/Wh	U
72.5 (100)	27.0 (37.2)	36.4 (50.2)	0.74	20.2 (27.9)

The position of the last septum cannot be established. The radial fracture is at a diameter of 70.5 mm. Coiling is moderately involute, the umbilicus comprising 27.9% of the diameter, of moderate depth, with a flattened, outward inclined subvertical wall. The umbilical shoulder is narrowly rounded to angular. The whorl section is compressed, with a whorl breadth to height ratio of 0.74, the flanks flattened, subparallel, the ventrolateral shoulders broadly rounded, the venter obtusely fastigiate, with a strong, blunt siphonal keel. On the penultimate whorl, 12–14 small bullae perch on the umbilical shoulder and give rise to narrow, prorsirdiate ribs that link to a small inner lateral tubercle, from which ribs branch in pairs. This style of ornament extends for only a short distance on the outer whorl, and is replaced by crowded minute bullae that give rise to delicate prorsiradiate ribs/riblets that are straight on the inner flank, convex at mid-flank, and concave on the outer flank. They increase by branching and intercalation on the flanks. The ventrolateral region of the adapical half of the outer whorl is damaged, but on the adapertural part a ridge marks the ventrolateral shoulder and bears numerous small clavi that correspond to the termination of the flank ribs. The narrow interspaces, conspicuous on the inner and middle flank effaces on the outer flank and ventrolateral shoulder. The ornament of the penultimate whorl is that of passage forms between formae *subtuberculata* and *intermedia* of comparable size, while the distinctive features that Cooper and Owen based their new genus on are restricted to the adult body chamber. This style of ornament is shown by adults of what are interpreted here as compressed variants *of Schloenbachia varians*, as illustrated in Text-figs 6A and F, and Pl. 7, fig. 6; Pl. 8; Pl. 9, figs 4, 5; Pl. 10, figs 4, 5, and Pl. 13, figs 1–5.

Schloenbachia varians (J. Sowerby, 1817)
(Pls 1–14, Text-figs 3–9)

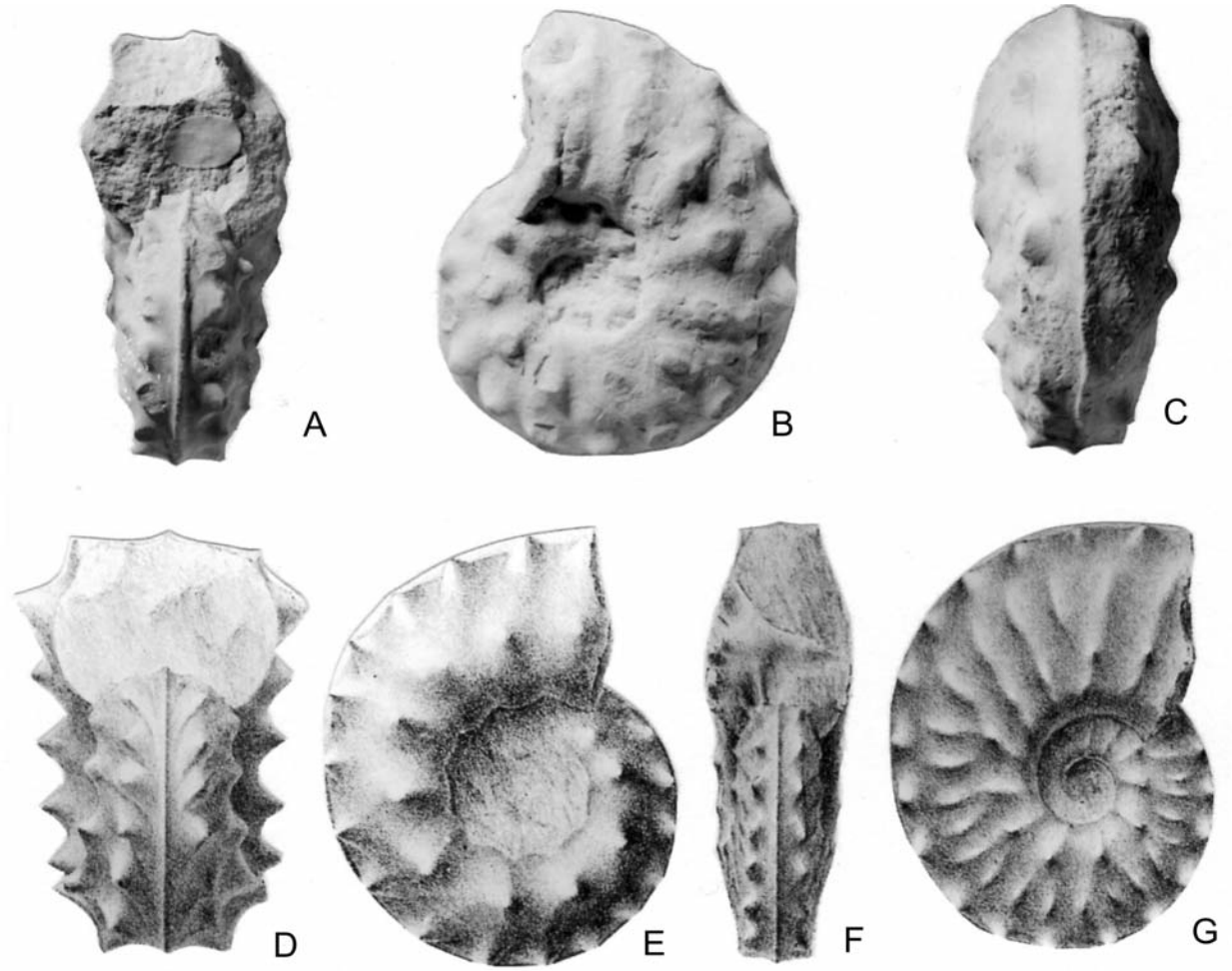
1817. *Ammonites varians* J. Sowerby, p. 169 (*pars*), p. 176 uppermost figure, left-hand figure in lowest row.
1822. *Ammonites varians* var. *subplana* Mantell, p. 116, pl. 21, fig. 2.
1822. *Ammonites varians* var. *intermedia* Mantell, p. 116, pl. 21, figs 5, 7.
1847. *Ammonites tollotianus* Pictet, p. 109, pl. 10, fig. 5.
1853. *Ammonites varians* var. *subtuberculata* Sharpe, p. 22, pl. 8, figs 5, 6 (*non* 8 = *Schloenbachia lymensis* Spath, 1926b)
1853. *Ammonites varians* var. *intermedia* Sharpe, p. 23, pl. 8, fig. 7 (*non* Mantell = *S. subvarians* Spath 1926a).
1853. *Ammonites coupei* var. *inflata* Sharpe, p. 24, pl. 8, fig. 1 (= *S. ventriosa* Stieler, 1922).
1922. *Schloenbachia ventriosa* Stieler, p. 31.
1926a. *Schloenbachia subvarians* Spath, p. 81.
1926a. *Schloenbachia glabra* Spath, p. 81.
1926b. *Schloenbachia subvarians* Spath, p. 430.
1926b. *Schloenbachia subvarians aperta* Spath, p. 430.
1926b. *Schloenbachia subvarians densicostata* Spath, p. 430.
1928. *Schloenbachia ecarinata* Spath, p. 241.
1972. *Schloenbachia varians* (J. Sowerby), and varieties; Hancock, Kennedy and Klaumann, p. 447, pl. 81, figs 3–7.
1974. *Schloenbachia semenovi* Manija, p. 137, pl. 8, fig. 1; text-fig. 30.
1974. *Schloenbachia donovani* Manija, p. 138, pl. 8, fig. 2; text-fig. 31.
1976. *Schloenbachia varians* (J. Sowerby). Juignet and Kennedy, p. 78, pl. 7, figs 4, 5, 6, 8, 9; pl. 8, figs 1–3, 5, 6.
1979. *Schloenbachia varians* (J. Sowerby); Wiedmann and Schneider, p. 664, pl. 1, figs 1–3; pl. 6, figs 1–7; pl. 7, figs 1–6; pl. 8, figs 1, 2; pl. 9, figs 1–4; text-fig. 8a–d.
1981. *Schloenbachia varians varians* (Sowerby); Seyed-Emami and Aryai, p. 28, pl. 8, figs 1–4.

1981. *Schloenbachia varians ventriosa* Stieler; Seyed-Emami and Aryai, p. 29, pl. 8, figs 2, 3.
1981. *Schloenbachia varians subtuberculata* (Sharpe); Seyed-Emami and Aryai, p. 30, pl. 7, figs 6–8.
1981. *Schloenbachia varians subvarians* Spath; Seyed-Emami and Aryai, p. 31, pl. 7, figs 2, 4, 5.
1981. *Schloenbachia varians subplana* (Mantell); Seyed-Emami and Aryai, p. 31, pl. 7, figs 1, 3.
1982. *Schloenbachia varians* (J. Sowerby, 1818); Hiss, p. 192.
1982. *Schloenbachia varians ventriosa* Stieler, 1992; Hiss, p. 195, fig. 8.1, 2.
1982. *Schloenbachia varians varians* (J. Sowerby, 1817); Hiss, p. 195, fig. 8.3–8.5.
1982. *Schloenbachia varians subtuberculata* (Sharpe, 1853); Hiss, p. 195, figs 8.6–8.7.
1982. *Schloenbachia varians costata* (Sharpe, 1853); Hiss, p. 196, figs 8.8–8.10.
1982. *Schloenbachia varians subvarians* Spath, 1926; Hiss, p. 196, figs. 8.11–8.13.
1982. *Schloenbachia varians subplana* (Mantell, 1822); Hiss, p. 196, figs 8.14, 8.15.
1983. *Schloenbachia varians* (Sowerby) (and subspecies); Marcinowski and Radwanski, pl. 6, figs 1–11.
1983. *Schloenbachia varians* (Sowerby, 1817); Marcinowski, p. 168, figs 5–7.
1984. *Schloenbachia varians* (J. Sowerby); Kennedy and Juignet, p. 123, figs 11k, l; 12a–l; 13a–l; 14a-g; 15a–k; 16a–l; 17a–f; 18a, b.
1985. *Schloenbachia varians* (J. Sowerby, 1817); Immel and Seyed-Emami, p. 94.
1985. *Schloenbachia varians subvarians* Spath; Immel and Seyed-Emami, p. 95, pl. 2, fig. 1.
1985. *Schloenbachia varians subtuberculata* (Sharpe, 1857); Immel and Seyed-Emami, p. 95, pl. 2, fig. 2.
1985. *Schloenbachia varians varians* (J. Sowerby, 1818); Immel and Seyed-Emami, p. 95, pl. 2, fig. 3.
1985. *Schloenbachia varians ventriosa* Stieler, 1922; Immel and Seyed-Emami, p. 95, pl. 2, fig. 4.
1985. *Ammonites tollianus* Pictet, 1847; Kennedy, p. 383, text-fig. 1.
1991. *Schloenbachia varians* (J. Sowerby, 1817); Delamette and Kennedy, p. 444, figs 8.18–8.20, 8.23, 8.24, 8.27–8.30, 9.22.
. *Schloenbachia varians* (Sowerby); Thomel, pl. 43, figs 1, 2, 4, 6; pl. 44, figs 1–8; pl. 45, figs 1–9; pl. 46, figs 1–3, 10.
1996. *Schloenbachia varians varians* (J. Sowerby); Marcinowski, Walaszczyk and Nejbert, pl. 14.
1998. *Schloenbachia varians* (J. Sowerby, 1817); Kaplan, Kennedy, Lehmann and Marcinowski, p. 107, pl. 10, fig. 12; pl. 11, fig. 5; pl. 12, figs 1–4, 6, 9-12; pl. 13, figs 3–5, 13, 14; pl. 14, figs 1–21; pl. 15, figs 1–13; pl. 16, figs 1–14 (with additional synonymy).
1999. *Schloenbachia varians* (J. Sowerby, 1817); Gale, Hancock and Kennedy, pl. 1, figs 1, 2, 12–15, 17–20; pl. 2, figs 5, 6, 11, 12.
2008. *Schloenbachia varians* (J. Sowerby, 1817); Kennedy, King and Ward, p. 129, pl. 5, figs 10–12, 14, 15; pl. 6, figs 3, 6–13.
2011. *Schloenbachia varians* (J. Sowerby, 1817); Kennedy, Amédro, Robaszynski and Jagt, p. 218, text-figs 10E, F, S–X, 11L–O, Q–T.
2011. *Schloenbachia varians* (J. Sowerby, 1817); Wilmsen and Mosavinia, p. 174, text-figs 4–6, 7A–E, H.
2011. *Schloenbachia varians* (J. Sowerby); Cooper and Owen, p. 303, text-fig. 6E–F.
2011. *Jakeiceras glabrum* (Spath, 1926); Cooper and Owen, p. 303, text-fig. 6G–H.

TYPE: Lectotype, by the subsequent designation of Spath, 1938, p. 544, is BMNH 43962b, the original of J. Sowerby, 1817, pl. 176, top figure, refigured here as Text-fig. 3A–C. It is from the Lower Chalk of an unknown locality in southern England.

MATERIAL: The present account is based on 94 specimens from bed 30 of the Besakty section in the Mangyshlak Mountains of Western Kazakhstan, referred to the Lower Cenomanian *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone: UWZl/63/0098, 0100, 1255–1259, 1261, 1262,1264–1266, 1268, 1269, 1458 –1466, 1468–1481, 1485–1488, 1604–1614, 1616–1620, 1626–1629, 1631–1632, 16381643, 1646–1650, 1653, 1656, 1657, 1665–1667, 1672–1679, 1690–1692. Most are internal moulds; a few retain areas of recrystallised shell. Many specimens are encrusted by lichens on surfaces that were exposed on the desert floor (Pl. 5, for example).

DESCRIPTION: Of the 94 specimens that form the basis of his account, 26 specimens are complete adults, ranging from 59–174 mm in diameter, a ratio of 1: 2.95, the smallest adult (Pl. 12, Figs 4–6) is thus 33.9% of the diameter of the largest (Pl. 4, Fig. 9; Pl. 5). Of the 94 specimens, 31 retained measurable adult phragmocones, with diameters of 49.4–132 mm, a ratio of 1: 2.67, the smallest adult phragmocone is thus 37.4% of the diameter of the largest. These results are plotted as simple histograms in Text-fig. 8. It is generally assumed that the sexes were separate in ammonites (see discussion in Davis *et al*. 1996), and that the females – macroconchs – were larger than the males – microconchs. In one group of Cretaceous ammonites, the heteromorph Scaphitoidea, the dimorphs differ in the morphology of the adult body chamber, and if this is used to differentiate macro- and microconchs, the smallest females are



Text-fig. 3. *Schloenbachia varians* (J. Sowerby, 1817). A-C – the lectotype, BMNH43962b, the original of J. Sowerby, 1817, pl. 176, top figure. It is from the Lower Chalk of an unknown locality in southern England. D-E – syntype of *Schloenbachia ventriosa* Stieler, 1922: copy of Sharpe, 1853, pl. 8, fig. 1. The specimen is lost; Sharpe records it as from the 'Chloritic Marl of Bonchurch, Isle of Wight'. F, G – the lectotype of *Schloenbachia subtuberculata* (Sharpe, 1853): copy of Sharpe, 1853, pl. 8, fig. 5. The specimen is lost; Sharpe records it as from the 'Chalk with siliceous grains of Chardstock', Devon. All figures are ×1

smaller than the largest males (Cobban 1969): the sexes overlap in size. If this is the general case, then a plot of adult size of an assemblage will not necessarily be bimodal. If the possibility of an original variance in the ratio of sexes in a life assemblage is admitted, or if *post-mortem* processes have modified the original size distribution of the assemblage, then the possibility of separating an assemblage into sexes on the basis of size alone diminishes further (see Davies *et al*. 1996, p. 519). This is the case with the present material, as is clear from Text-fig. 8.

Forma ventriosa

The reference specimen is the original of *Ammonites varians* var. *inflata* Sharpe, 1853, p. 24, pl. 8, fig. 1, the holotype of *Schloenbachia ventriosa* Stieler, 1922 (p. 31) from the 'Chloritic Marl of Bonchurch, Isle of Wight, in the collection of Mr. Saxby' (Sharpe 1853, explanation of pl. 24). The specimen is lost; the original illustration is reproduced here as Text-fig. 3D, E. From the locality details given by Sharpe, the specimen is from the Glauconitic Marl, which yields abundant phosphatised ammonites diagnostic of the *Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone (Text-fig. 2). The specimen shows no trace of sutures, but these are equally omitted from figure 8 on the same plate, the surviving holotype of *Schloenbachia lymensis* Spath, 1926b (Text-fig. 11A, B), in which the sutures are clearly visible; one presumes the omission to be artistic license. The original figure of *ventriosa* represents a specimen 59 mm in diameter, with a depressed reniform whorl section, the intercostal whorl breadth to height ratio 1.22, the costal whorl breadth to height ratio 1.60, with the greatest breadth at the lateral tubercles. The umbilical seam is notched to accommodate the lat-

eral tubercles of the preceding whorl. There are an estimated 12 strong conical to subspinose tubercles on the outer whorl, linked to the umbilical seam by a low, broad rib. Pairs of feeble broad ribs link these tubercles to strong ventrolateral clavi, of which there are an estimated 20–21 on the outer whorl. A progressively narrowing and weakening strongly prorsiradiate rib extending from the ventrolateral clavi towards the strong siphonal keel is shown in the apertural view of the specimen.

The holotype of *Schloenbachia semenovi* Manija, 1974 (p. 137, pl. 8, fig. 1) is the original of *Schloenbachia coupei* Semenov, 1899, pl. 2, fig. 6, *non* Brongniart, reproduced here as Text-fig. 7C, D, from Bichakty (=Besakty), the source of the present material. The species was compared with *Schloenbachia ventriosa*, from which it was differentiated on the basis of fewer (7–8 versus 10–11) lower lateral tubercles, and a smaller umbilicus. In fact, the total number of lateral tubercles on the outer whorl of Semenov's specimen cannot be established because of damage and obscuring matrix; at least 10 are present, and the total number is estimated here at 10–11, whilst the umbilicus is filled by sediment and the width of the umbilicus cannot be established. It is a typical *forma ventriosa*.

Twelve specimens (14% of the total) are assigned to *ventriosa*: UW Z1/0063, 0098, 1261, 1462, 1464, 1470, 1478, 1606, 1607, 1629, 1647, 1649, 1677 (Pl. 1, figs 1–7; Pl. 2).

	D	Wb	Wh	Wb:Wh	U
Sharpe 1857, pl. 7, fig. 1, c	59.3 (100)	38.8 (65.4)	24.2 (40.8)	1.60	22.2 (37.4)
ic		29.5	24.2	1.22	
1470 c, at	54.9 (100)	38.3 (69.7)	22.4 (40.8)	1.71	11.8 (21.5)
1261c	82.2 (100)	48.4 (58.9)	39.3 (47.8)	1.23	24.0 (29.2)
ic		39.7	39.3	1.0	
1606 c	89.0 (100)	63.7 (71.5)	34.7 (39.0)	1.84	26.9 (30.2)
ic		48.1	34.7	1.2	
1464c	109.3 (100)	74.2 (68.1)	48.3 (44.3)	1.54	32.6 (29.9)
98 at	136.8 (100)	-	62.4 (45.9)	-	39.6 (29.1)
At.115.4 c	115.4 (100)	62.3 (54.0)	56.1 (48.6)	1.1	33.3 (29.0)
ic		51.5	56.1	0.91	

Specimen 1470 (Pl. 1, figs 1–3) is a phragmocone 66.6 mm in diameter that most closely resembles the reference specimen. It has an intercostal whorl breadth to height ratio of over 1.29, with 12 low, broad, straight radial ribs that arise at the umbilical seam and link to strong conical to subspinose lateral tubercles. These give rise to pairs of low barely perceptible ribs that link to strong ventrolateral clavi, of which there are an estimated 20–21 on the outer whorl. Of other phragmocones, specimen 1647, 67 mm in diameter, has a costal whorl breadth to height ratio of 1.77, 13 lateral tubercles and an estimated 20 ventrolateral clavi. Specimen 1607 has 12 massive lateral tubercles at a diameter of 103 mm. Specimen 1478 is a hypernodose individual 83.5 mm in diameter, with a costal whorl breadth to ratio of 2.1; the intercostal ratio is 1.8 at a diameter of 89.1 mm in specimen 1606 (Pl. 1, Fig. 6), and a minimum of 1.7 in specimen 1464 at a whorl height of 55 mm. Specimen 0098 (Pl. 1, fig. 7; Pl. 2) is a complete adult with a maximum preserved phragmocone diameter of 125 mm, an intercostal whorl breadth to height ratio of 1.1 and a costal whorl breadth to height ratio of 1.33. There are 12 primary ribs on the outer whorl of the phragmocone. They arise at the umbilical seam, and are low, coarse, radial, strengthening across the umbilical shoulder and inner flank, linking to the strong conical-bullate lateral tubercles. These give rise to pairs of concave prorsiradiate ribs, some of which are discontinuous and have the form of long, incipient outer lateral bullae, weakly linked to strong ventrolateral clavi, from which narrowing and effacing ribs sweep forwards across the venter. The body chamber extends for an estimated 240°, but the adapertural part lacks most or all of the flank and ventral region, so that the terminal aperture is not preserved. The umbilicus broadens, and the umbilical wall becomes progressively more outward inclined. Seven primary ribs are preserved. They arise at the umbilical seam, and are initially broad and coarse, but weaken, narrow, and sharpen as size increases. The lateral tubercles change from rounded-conical to sharp narrow bullae, the outer flank ribs develop into sharp bullae, and the adapertural part of the body chamber become trituberculate, with mid- and outer lateral bullae and ventrolateral clavi. Specimen 1480 (Pl. 4, Figs 5, 6) is a small, worn adult, the phragmocone 58 mm in diameter, and incomplete with a maximum preserved diameter of 71 mm, and only a 90° sector of body chamber preserved. There are 12 rounded-feebly bullate lateral tubercles on the outer whorl of the phragmocone, linked to the umbilical seam by a low, effaced rib. Pairs of low, weak ribs link to approximately twice as many ventrolateral clavi. On the body chamber, the ornament modifies markedly. The primary ribs narrow, and the lateral tubercles are transformed into strongly prorsiradiate bullae, giving rise to pairs of narrow ribs that link either singly or in pairs to well-developed ventrolateral clavi; it is transitional to *varians sensu stricto*.

varians sensu stricto

The reference specimen is the lectotype, by the subsequent designation of Spath, 1938, p. 544, BMNH

43962b, the original of the uppermost of the specimens figured on James Sowerby's pl. 176, and illustrated here as Text-fig. 3A–C.

Some may consider Spath's statement to be ambiguous as a lectotype designation, coming as it does in the midst of a confused section of text:

'It is clear, therefore, that what Mantell renamed var. *tuberculata* really represents the true *Amm. varians*; and that a lectotype has to be chosen from among the first four specimens figured by Sowerby. The obvious choice is fig. 1 (upper figure) which is wrongly drawn only in as far as it shows an umbilicus of about 33 per cent rather than 28 per cent.' It is accepted as a valid lectotype designation here. The lectotype is a composite internal mould in hard chalk, with indications of a suture 120° from the adapertural end. The dimensions are as follows:

D	Wb	Wh	Wb/Wh	U
56.6 (100)	~27.0 (~47.7)	26.0 (45.9)	~1.04	15.3 (27.0)

54% of the previous whorl are covered. The umbilicus is of moderate depth, the umbilical wall flattened and subvertical, the umbilical shoulder broadly rounded. The intercostal whorl section is slightly compressed, rounded-trapezoidal, with an obtusely fastigiate venter with a strong siphonal keel. Twelve primary ribs arise at the umbilical seam on the outer whorl, and strengthen across the umbilical wall and shoulder, developing into coarse, straight, feebly prorsiradiate primary ribs that link to strong rounded-conical inner lateral tubercles. These give rise to one or two primary ribs, while occasional ribs intercalate on the outer flank, sweep forwards and link to strong ventrolateral clavi, of which there are an estimated 19–20 ribs on the outer whorl.

Twenty specimens, 21.5% of the total, are referred to *varians sensu stricto*: UW Zl /63/0100, 1254, 1255, 1463, 1264, 1468, 1469, 1474, 1479, 1485, 1488, 1605, 1610, 1614, 1627, 1628, 1631, 1638, 1666, 1672, 1679 (Pl. 3, Figs 1–5; Pl. 4, Figs 1–4, 7–9; Pl. 5). Adult individuals have maximum diameters of 90 to 175 mm.

	D	Wb	Wh	Wb/Wh	U
1679c	55.5 (100)	27.5 (49.5)	25.7 (46.3)	1.1	17.1 (30.8)
1463 ic	77.3 (100)	32.5 (42.0)	35.0 (45.3)	0.93	22.7 (29.4)
1469 c	76.8 (100)	47.7 (62.1)	37.3 (48.6)	1.28	19.7 (25.7)
1489 ic	96.8 (100)	44.9 (46.4)	44.4 (45.9)	1.01	29.3 (30.3)
1605 c	100.5 (100)	52.3 (52.0)	44.4 (44.2)	1.18	28.5 (28.4)
1255 ic	134.8 (100)	50.3 (39.0)	58.8 (43.6)	0.85	35.5 (26.2)

Specimen 1468 (Pl. 3, Fig. 2) most closely resembles the lectotype. It is wholly septate, with a maximum preserved diameter of 73.6 mm. Coiling is moderately evolute, with 36% of the previous whorl covered. The umbilicus is deep, comprising 45% of the diameter, with a convex outward-inclined wall and broadly rounded umbilical shoulder, the intercostal whorl section compressed, with a whorl breadth to height ratio of 0.87, the greatest breadth just outside the umbilical shoulder, the inner flanks convex, the outer flanks converging to an obtusely fastigiate venter with a strong siphonal keel. The costal whorl section is polygonal, with a whorl breadth to height ratio of 1.1, the greatest breadth at the lateral tubercles. Low, broad, blunt primary ribs arise at the umbilical seam, and strengthen across the umbilical wall and inner flank, linking to a strong rounded-conical lateral tubercle, of which there are fourteen on the penultimate whorl. There are seven such tubercles on the fragmentary outer whorl, and nine coarse clavi, perched on the ventrolateral shoulder. The lateral tubercles give rise to a single prorsiradiate rib that links to a ventrolateral clavus. Other clavi are linked to a rib that is strengthened into a bulla-like sector that is only tenuously linked to a lateral tubercle. In other phragmocones of this size, the bullae may give rise to pairs of slender ribs, either singly or in pairs. Ventrolateral clavi may be linked to a bulla by a single rib or by two ribs that link them to successive bullae in zigzag pattern, a morphology transitional to *forma subtuberculata*, well-seen in specimens 1627, 1638, and 1679 (Pl. 4, Figs 1–4). There is every gradation between specimens with few and many ribs on the outer flank. Specimen 1474 is interpreted as the body chamber of a small individual, with a maximum preserved diameter of 97 mm. The ribs are narrower and sharper on the inner flank than on phragmocones, the lateral tubercles changing from rounded-conical to narrow bullae that weaken and efface at the adapertural end. Specimen 1463 (Pl. 3, Figs 1–3) is a further small adult, with a maximum preserved diameter of 92 mm, with a 240° sector of body chamber preserved. On the penultimate whorl, 11–12 low, broad primary ribs arise at the umbilical seam and strengthen across the umbilical wall and shoulder, developing into strong conical inner lateral tubercles. This ornament extends onto the adapical part of the outer whorl, the tubercles giving rise to pairs of low, broad ribs that link to strong oblique ventrolateral clavi. This ornament changes progressively on the adapertural sector of the phragmocone and the body chamber, the ribs weaken, narrow, and sharpen, the lateral tubercles weakening and changing in feeble bullae. On the adapical part of the body chamber, these are linked by single weak, narrow outer flank ribs to progressively weakening ventrolateral clavi. Large phragmocones such as specimens 1488, 1605, 1628 are up to 100 mm in diameter, with 13–14 lateral tubercles, an estimated 20 ventrolateral clavi, and a variable number of ribs on the outer flank. There are two large adults that are referred to *varians sensu*

stricto. Specimen 1255 (Pl. 3, Figs 4, 5) has a maximum preserved diameter of 135 mm, and retains a 240° sector of body chamber. There are 10–11 coarse primary ribs on the outer whorl of the phragmocone, linked to massive conical lateral tubercles. There are seven primary ribs on the body chamber. The adapical three are as on the phragmocone, and link to massive lateral tubercles. The succeeding ribs weaken and narrow, the lateral tubercles modifying progressively into bullae, which weaken markedly on the final ribs. There are ten ventrolateral clavi on the body chamber, linked to the lateral tubercles by a single rib, or linked to a single intercalated rib that strengthens into an outer lateral bulla so that the ribs are trituberculate, with inner and outer lateral and ventrolateral tubercles. The tubercles weaken markedly on the last few ribs. Specimen 0100 (Pl. 4, Fig. 9; Pl. 5) is the largest adult in the assemblage, 175 mm in diameter, and retaining a 240° sector of body chamber. There are 12 primary ribs on the outer whorl of the phragmocone, linking to conical to feebly bullate tubercles, much weaker than those on the previous specimen, while the outer flanks are ornamented by more numerous, weaker ribs, as in smaller specimens described above. The body chamber ornament is weak, with six primary ribs, the lateral tubercles reduced to feeble bullae, the ventrolateral clavi weak, distant, and becoming oblique, rather than parallel to the siphonal keel.

Forma subtuberculata

The reference specimen, now lost, is the original of *Ammonites varians* var. *subtuberculata* of Sharpe, 1853, p. 22, pl. 8, fig. 5, designated as lectotype of *Schloenbachia subtuberculata* by Wright and Wright (1951, p. 34). The original illustrations, reproduced here as Text-fig. 3F, G, show a specimen with the following dimensions:

D	Wb	Wh	Wb/Wh	U
58.4 (100)	19.5 (33.4)	29.8 (51.0)	0.65	16.0 (27.4)

There are 13 primary ribs on the outer whorl. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder without developing a clearly differentiated bulla on all but the final few ribs, where a minute bulla is indicated. The primary ribs are markedly prorsiradiate on the inner flank, and link to a small inner lateral bulla. The outer flank rib pattern is complex. Some of the lateral bullae give rise to a single concave rib; others give rise to a pair of ribs, the adapical of the rib pair weakly to strongly linked to the bulla; there are also single intercalated ribs not linked to a lateral bulla, while some ribs are linked neither to a bulla nor a ventrolateral clavus (as are most of the ribs), and are long, concave incipient bullae in some cases. There are an estimated 22–24 ventrolateral clavi on the outer whorl.

The lectotype (designated by Spath, 1938, p. 545), of *Schloenbachia sharpei* Semenov, 1899 (p. 100, pl. 2, fig. 9, pl. 3, fig. 1) is a large phragmocone from 'Bishakty', the locality of the present material, and in all probability from the same bed. The approximate relative proportions, taken from Semenov's figures (Text-fig. 7G, H) are as follows:

D	Wb	Wh	Wb/Wh	U
100	47	57	0.82	24.0

There are 13 primary ribs on the outer whorl, and perhaps 24 ventrolateral clavi. The primary ribs give rise to narrow prorsiradiate ribs on the inner flank that link to a well-developed inner lateral bulla. The outer flank ribbing is complex; in some cases a pair of ribs arise from a lateral bulla, in other cases a single rib, the ribs linking singly or in pairs at the ventrolateral clavi, while there are short intercalated ribs that link to a ventrolateral clavus, and others that are not attached to either a bulla or clavus.

As discussed above, the holotype of *Schloenbachia glabra* Spath, 1926a (Text-fig. 6B, C, H), the type species of *Jakeiceras* Cooper and Owen, 2011, is no more than an individual close to *forma subtuberculata* with adult body chamber preserved, and corresponds to material described below in which shell is preserved.

Thirty six specimens are referred to this *forma*, 39% of the total in the assemblage, making it the dominant morphotype: UW Zl/63/1256. 1259, 1265, 1266, 1268, 1458, 1459, 1461, 1471, 1472, 1475, 1476, 1478, 1487, 1604, 16099, 1611, 1612, 1616, 1618, 1620, 1632, 1639, 1641, 1642, 1643, 1648, 1650, 1653, 1657, 1667, 1676, 167, 1692 (Pl. 6, Figs 1, 3–5; Pl. 7, Figs 1–4, 7–9; Pl. 8, Figs 1–5; Pl. 9, Figs 4, 5; Pl. 11). The smallest complete adult is 74.4 mm in diameter; the largest is 145 mm in diameter.

	D	Wb	Wh	Wb:Wh	U
1475 c	69.1(100)	22.8 (33.0)	31.6 (45.7)	0.72	17.1 (24.7)
1632 c	78.6 (100)	23.6 (30.0)	33.3 (42.4)	0.79	21.8 (27.7)
1667 c	86.5 (100)	33.5 (38.7)	38.8 (44.9)	0.86	24.8 (28.7)
1471 c	100.4 (100)	26.4 (26.3)	40.1 (39.9)	0.66	29.6 (29.5)
1458 c	127.4 (100)	36.3 (28.5)	54.8 (43.0)	0.66	36.5(28.6)
1259 ic	142.4 (100)	40.6 (28.5)	63.3 (44.5)	0.64	34.8 (24.4)

Specimen 1459 (Pl. 6, Figs 2–4) most closely resembles the illustration of the reference specimen. It is a phragmocone 64.6 mm in diameter. Coiling is moderately involute, with 60% approximately of the previous whorl covered. The umbilicus comprises 25% of the diameter, with a feebly convex outward inclined umbilical

wall, and narrowly rounded umbilical shoulder. The whorl section is compressed, with feebly convex inner, and flattened, convergent outer flanks in intercostal section, with the greatest breadth just outside the umbilical shoulder. The ventrolateral shoulders are broadly rounded, the venter obtusely fastigiate, with a strong siphonal keel. The costal whorl breadth to height ratio is 0.77, the greatest breadth at the inner lateral bulla. Eighteen primary ribs arise at the umbilical seam, sweep forwards and strengthen across the umbilical wall and shoulder. They are narrow, straight and prorsiradiate on the inner flank, and link to a tiny inner lateral bulla. These bullae give rise to a single rib that is clearly linked to the bulla, a second rib, generally adapical to the former, may be weakly linked to the bulla, or may be an intercalatory, the ribs linking singly, looping in pairs, or declining before reaching a small ventrolateral clavus, of which there are an estimated 21–22 on the outer whorl. Some of the outer flank ribs that are only tenuously linked to tubercles may be strengthened into a long weak incipient outer lateral bulla. Other phragmocones have the outer flank ribs even and linking inner lateral and ventrolateral tubercles, sometimes in a distinct looping and zigzag pattern (specimen 1268: Pl. 7, Figs 4, 5) while the primary ribs, strengthening across the umbilical shoulder may give an impression of incipient bullae. Specimen 1471 (Pl. 8, Figs 3–5) is well-preserved internal mould of a complete adult 102 mm in maximum diameter, with a 240° sector of body chamber preserved. There are seventeen primary ribs on the outer whorl of the phragmocone, the inner lateral bullae giving rise to two strongly to weakly linked secondary ribs. On the body chamber, these detach, and the ribbing weakens progressively, with some ribs developing a clear umbilical bulla. On the adapertural part of the body chamber the ribs become markedly prorsiradiate, effacing on the outer flank. The strongly prorsiradiate aperture is slightly flared, and preceded by a broad, shallow constriction. Specimen 1487 (Pl. 8, Figs 1, 2) has a maximum preserved diameter of just over 100 mm, and retains a 240° sector of body chamber, with well-preserved recrystallised shell in places. There are 13–14 coarse primary ribs on the outer whorl of the phragmocone, with incipient umbilical bullae that become distinct on the adapical part of the body chamber, and feeble inner lateral bullae. The ribs, umbilical and inner lateral tubercles efface, followed by the ventral clavi, leaving the surface of the shell ornamented by crowded growth lines, lirae and striae, concave on the umbilical wall, markedly prorsiradiate and falcoid on the flanks, and projecting strongly forwards on the ventrolateral shoulders and venter, exactly as in the holotype of *Schloenbachia glabra* (Text-fig. 6B, C, H). Small, well-developed umbilical and inner lateral tubercles characterise the body chambers of several larger adults, including no. 1657 (Pl. 7, Fig. 7–9), 115 mm in estimated diameter, 1604, 134 mm in diameter (Pl. 6, Figs 1, 7), and 1458 (Pl. 11), 135 mm in diameter.

The largest adult is specimen, no. 1259 (Pl. 9, Figs 4, 5), 144 mm in diameter. The penultimate whorl of the phragmocone bears 16 primary ribs, with strong inner lateral bullae. Body chamber ornament is weak and irregular. There are well-developed small umbilical and inner lateral bullae, borne on progressively weakening and increasingly strongly prorsiradiate primary ribs. Traces of recrystallised shell are present on the outer flank immediately before the aperture, with well-preserved delicate falcoid growth lines.

Forma intermedia

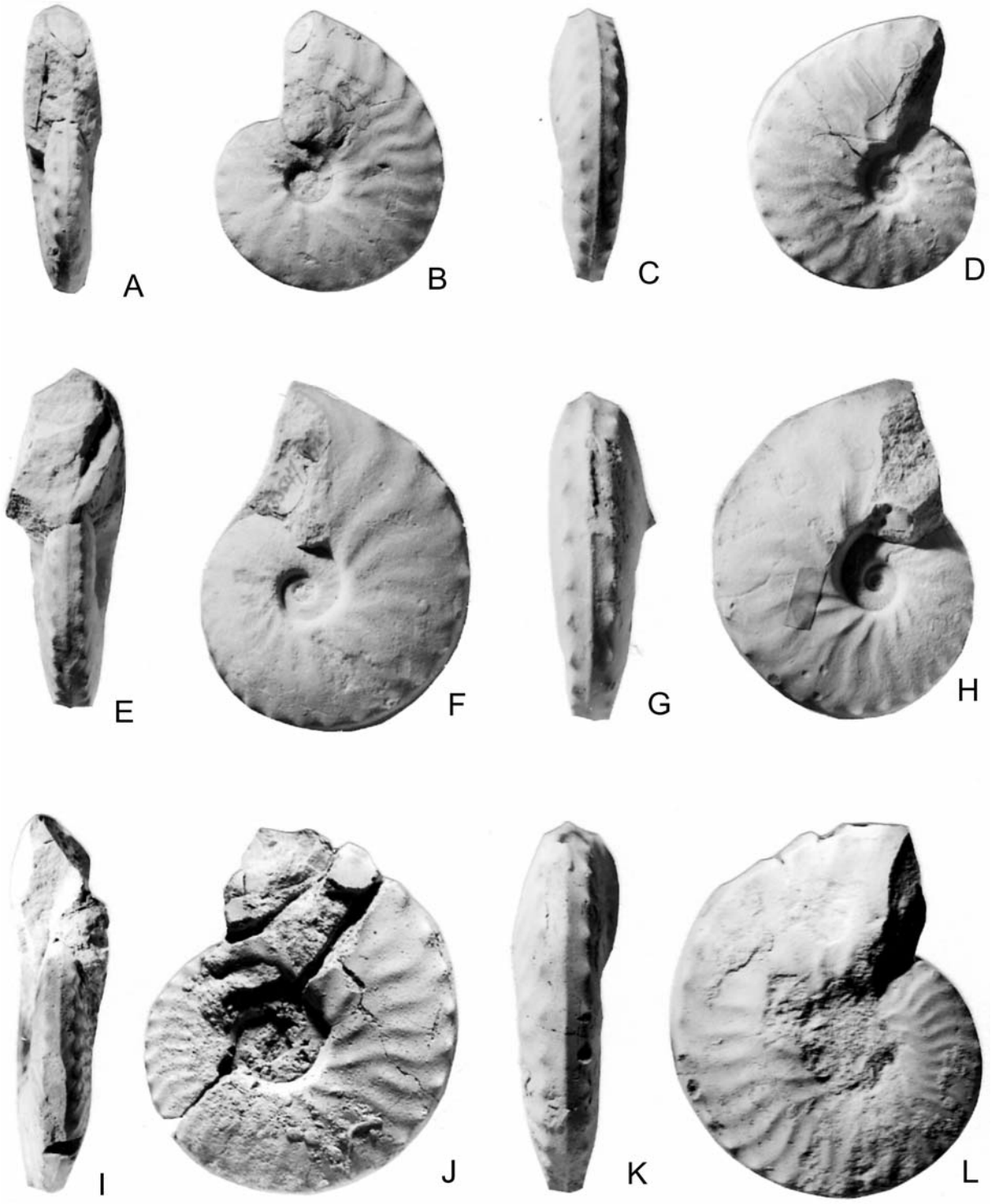
This is the *forma* with the most complex history in terms of the name to apply to its members. Chronological preference is given here, and, accordingly, the reference specimen is BMNH 33547 (Text-fig. 4E–H), the original of *Ammonites varians* var. i*ntermedia* Mantell, 1822, p. 116, pl. 21, fig. 5, designated lectotype of *Schloenbachia intermedia* by Spath, 1938, p. 546, from the Lower Chalk of the Lewes region in Sussex (Mantell records his specimens of *Ammonites varians* from 'Hamsey, Middleham, Stoneham etc').

The specimen is a slightly worn composite internal mould, deformed into an ellipse. The dimensions are:

D	Wb	Wh	Wb/Wh	U
52.6 (100)	15.8 (30.0)	23.6(44.9)	0.67	11.5 (21.9)

Coiling is moderately involute, the umbilicus comprising 21.9% of the diameter, the umbilical wall low, flattened, and outward-inclined, the umbilical shoulder angular to narrowly rounded. The whorl section is compressed, with a whorl breadth to height ratio of 0.67, the inner to middle flanks very feebly convex, subparallel, the outer flanks convergent. The ventrolateral shoulder is angular, the venter obtusely fastigiate, with a strong siphonal keel. The flank ornament is worn. Ten primary ribs arise at the umbilical seam on the adapertural half of the outer whorl. They strengthen across the umbilical shoulder and are narrow and prorsiradiate on the inner flanks. A small inner lateral bulla is preserved on some ribs, the bullae most obvious at the largest preserved diameter. Ribs bifurcate at the inner lateral bullae and additional ribs intercalate at the level of the bullae. The ribs are convex at mid-flank and concave on the outer flank, projecting forwards and linking to small ventrolateral clavi, of which there are an estimated 28 on the outer whorl. There is a marked constriction just

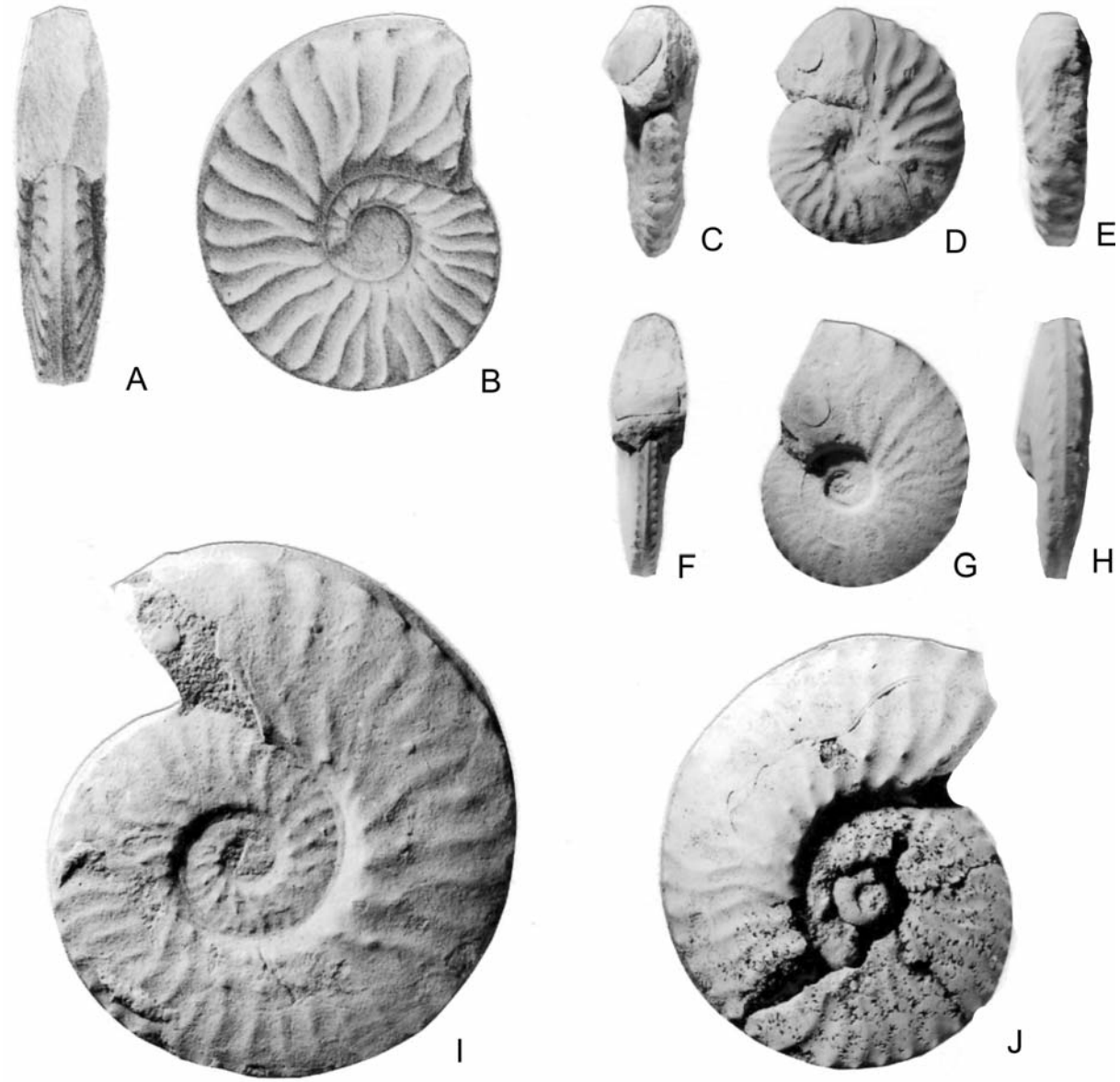
before the flared aperture, and the specimen may be adult. BMNH 5723 (Text-fig. 4A–D) may be the original of Mantell, 1822, p. 115, pl. 21, fig. 7, and thus a paralectotype of *intermedia*. It is a slightly crushed and distorted composite mould 44 mm in diameter, and slightly more strongly ornamented than BMNH 33547.



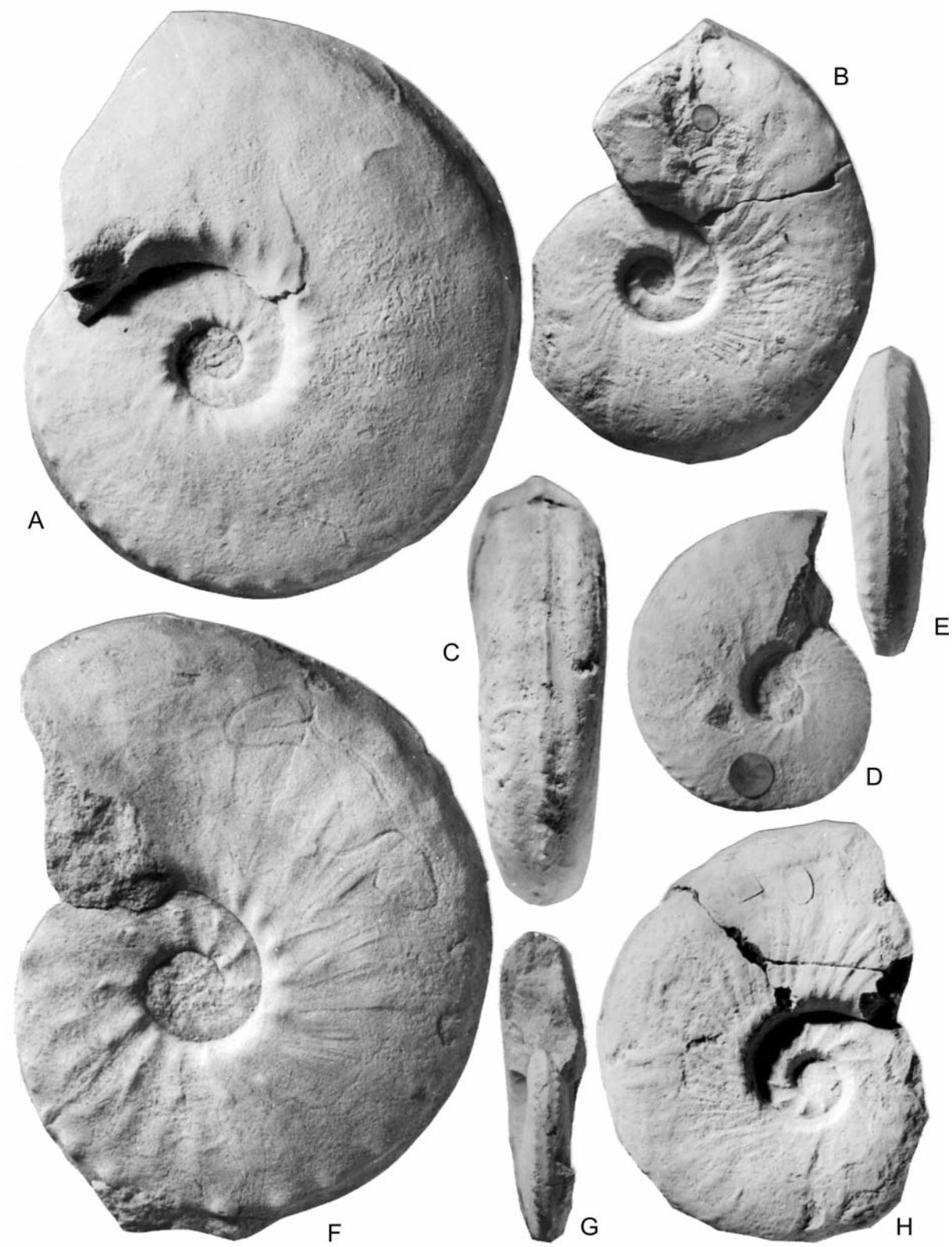
Text-fig. 4. *Schloenbachia varians* (J. Sowerby, 1817). A-D – BMNH 5723, probable original of *Ammonites varians* var *intermedia* of Mantell, 1822, pl. 21, fig. 7, and thus a probable paralectotype of *Schloenbachia intermedia* (Mantell, 1822), from the Lower Chalk of Hamsey, near Lewes, Sussex. E-H – BMNH 33547, the lectotype of *Schloenbachia intermedia* (Mantell, 1822), the original of *Ammonites varians* var, *intermedia* of Mantell, 1822, pl. 21, fig. 5, from the Lower Chalk of Sussex. I-L – MHNG 19442, the holotype of *Ammonites tollotianus* Pictet, 1847, the original of his pl. 10, fig. 5, from the Calcaires de Fiz of Flaine in the Massif de Platé, Haute-Savoie, France. All figures are ×1

There are 12–13 primary ribs on the outer whorl, with tiny bullae perched on the umbilical shoulder, and small but better-developed inner lateral bullae, from which the ribs bifurcate, to give a total of 26–28 ribs bearing small clavi at the ventrolateral shoulder.

This *forma* has generally been referred to *subvarians* Spath, 1926a (p. 81), the holotype of which is the original of Sharpe, 1853, pl. 7 from the 'Chalk with siliceous grains of Chardstock, Devon' but now lost. The original illustration is reproduced here as Text-fig. 5A, B. Spath (1938, p. 546) noted that the figure showed a specimen with an open umbilicus and distinct (instead of effaced) ribbing; the former is a reflection of the specimen being an adult, the latter a reflection of differing preservations: a worn chalk composite mould in the case of Mantell's type, whilst Sharpe's specimen is from a hard limestone. The figure shows a specimen with an estimated 20 ribs at the umbilical shoulder, and over 30 at the ventrolateral shoulder. The dimensions are:



Text-fig. 5. *Schloenbachia varians* (J. Sowerby, 1817). A, B – the holotype of *Schloenbachia subvarians* Spath, 1926a: copy of Sharpe, 1853, pl. 8, fig. 7. The specimen is lost; Sharpe records it as from the 'Chalk with siliceous grains of Chardstock', Devon. C-E – BGS GSM7764, the holotype of *Schloenbachia ecarinata* Spath, 1928, from the Lower Chalk of Ventnor, Isle of Wight. F-H – BMNH 5724, the probable original of *Ammonites varians* var. *subplana* Mantell, 1822, pl. 21, fig. 2, from the Lower Chalk of Ringmer, near Lewes, Sussex, and thus a probable syntype of *Schloenbachia subplana* (Mantell, 1822). I – BMNH 88967, the holotype of *Schloenbachia subvarians aperta* Spath, 1926b, from the Lower Chalk of Pangbourne, Berkshire. J – BGS GSM 32668, the holotype of *Schloenbachia subvarians densicostata* Spath, 1926b, from the Glauconitic Marl of Warminster, Witshire. All figures are ×1



Text-fig. 6. *Schloenbachia varians* (J. Sowerby, 1817). A – BMNH C82614, adult of *forma subplana*, from the Lower Chalk of Hamsey, near Lewes, Sussex. B, C, H – BMNH 33550, the holotype of *Schloenbachia glabra* Spath, 1926a, from the Lower Chalk of Hamsey, near Lewes, Sussex. D, E, G – BMNH 4396d, the original of J. Sowerby, 1817, pl. 176, lower left hand figure, from the Lower Chalk of Ringmer, near Lewes, Sussex. F – BMNH C41454, an adult of a passage form between *forma intermedia* and *forma subtuberculata*, from the Lower Chalk of Pitstone, Buckinghamshire. All figures are ×1

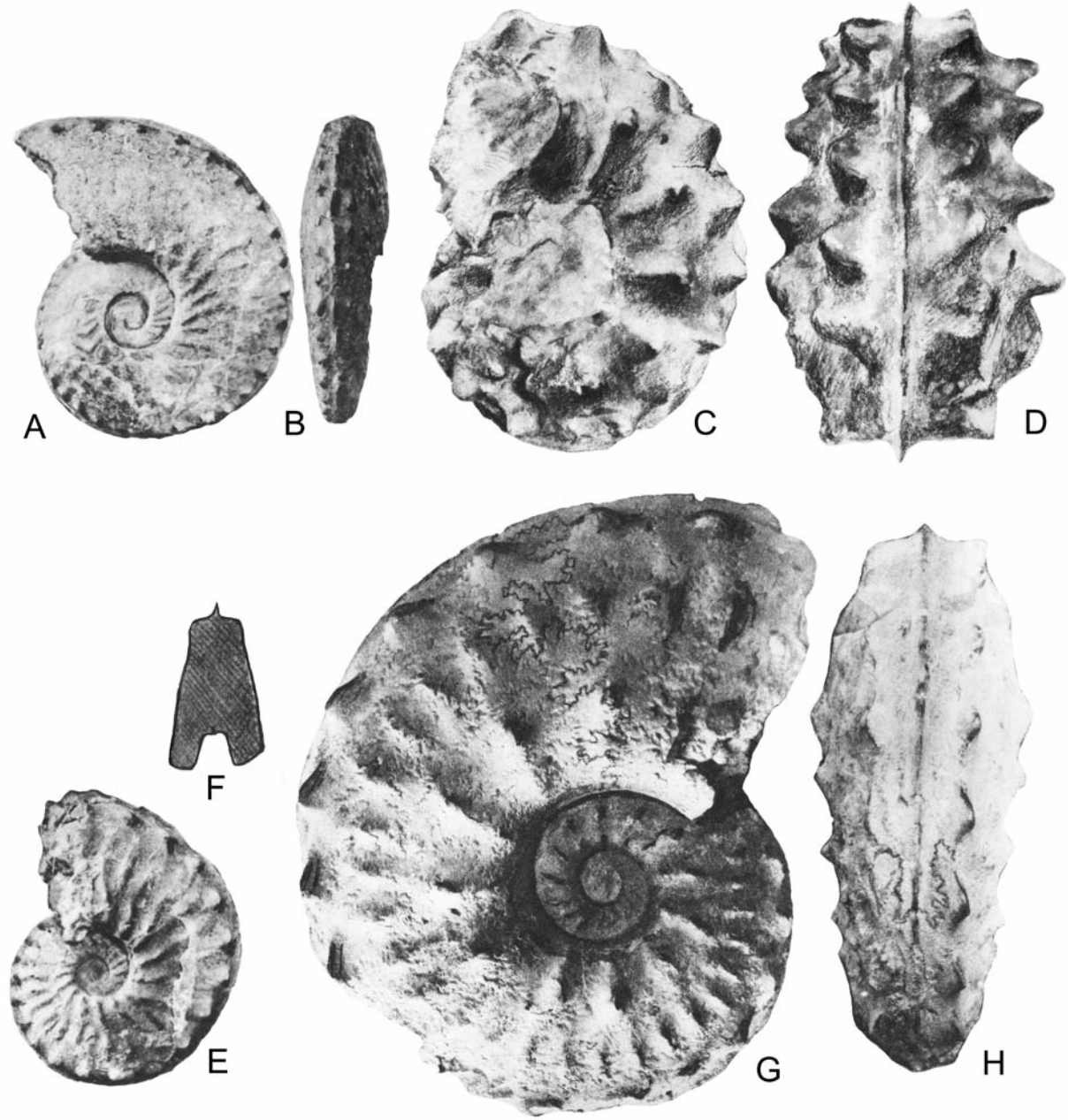
D	Wb	Wh	Wb/Wh	U
55.2 (100)	13.6 (24.6)	24.5 (44.4)	0.56	16.0 (29.0)

Comparable well-preserved specimens from Chardstock (BMNH C77315, C81405), are, from their preservation, from Bed B of the Cenomanian Limestone, and Lower Cenomanian.

The holotype of *Schloenbachia subvarians aperta* Spath, 1926b (p. 430) is BMNH 88967 (Text-fig. 5I) an adult with 24 ribs at the umbilical shoulder and 44 at the ventrolateral shoulder, and a maximum preserved diameter of 83 mm. The dimensions are:

D	Wb	Wh	Wb/Wh	U
81.1 (100)	10.5 (12.8)	31.6 (39.0)	33.2	29.6 (36.5)

The holotype of *Schloenbachia subvarians densicostata* Spath, 1926b (p. 430) is BGS GSM 32668 (Text-fig. 5J), an incomplete small adult 65.4 mm in diameter, with an estimated 40–42 ribs on the outer whorl,



Text-fig. 7. *Schloenbachia varians* (J. Sowerby, 1817). A, B – the holotype of *Schloenbachia dorsetensis* Spath, 1926b, copy of Semenov, 1899, pl. 3, fig. 7. C, D – the holotype of *Schloenbachia semenovi* Manija, 1974, copy of Semenov, 1899, pl. 2, fig. 6. E, F – the holotype of *Schloenbachia donovani* Manija, 1974, copy of Semenov, 1899, pl. 3, fig. 4. G, H – the lectotype of *Schloenbachia sharpei* Semenov, 1899, copy of Semenov, 1899, pl. 2, fig. 9, the originals of all were from 'Bichakty' (= Besakty herein) in the Mangyshlak Mountains of western Kazakhstan, the source of the material described in the present paper. All figures are presumed to be ×1

and umbilical and inner lateral bullae well-developed on the body chamber.

The holotype of *Schloenbachia ecarinata* Spath, 1928, is BGS GSM 7764 (Text-fig. 5 C–E). It is no more than a pathological individual of *forma intermedia* that lacks a keel as a result of non-lethal damage during life, and subsequent repair. It has a maximum preserved diameter of 34.9 mm.

Kennedy (1985, p. 383) revised *Ammonites tollotianus* Pictet, 1847 (p. 109, pl. 10, fig. 5) and showed the holotype to be a *Schloenbachia* corresponding to the present *forma*. It is shown in Text-fig. 4I–L. The specimen has an estimated 17 primary ribs at the umbilical shoulder, and 32–34 at the ventrolateral shoulder. The maximum preserved diameter is 59 mm; at: Text-fig. 5

D	Wb	Wh	Wb/Wh	U
55.3 (100)	13.7 (25)	23.0 (41.6)	0.6	14.9 (26.9)

The holotype of *Schloenbachia donovani* Manija, 1974 (p. 138, pl. 8, fig. 2) is the original of *Schloenbachia varians* Sowerby of Semenov, 1899, p. 102, pl. 3, fig. 4, reproduced here as Text-fig. 7E, F, from Bishakty (=Besakty), the source of the present material. It was compared to *Schloenbachia subtuberculata* by Manija, from which it was differentiated on the basis of its flatter sides and more numerous ribs and tubercles. The figure shows the holotype to have 21 outer flank ribs and tubercles visible on the outer whorl, and an estimated total of 24 approximately. The specimen is interpreted here as a rather typical small specimen of *forma intermedia*, like that illustrated here as Pl. 12, Figs 1–3.

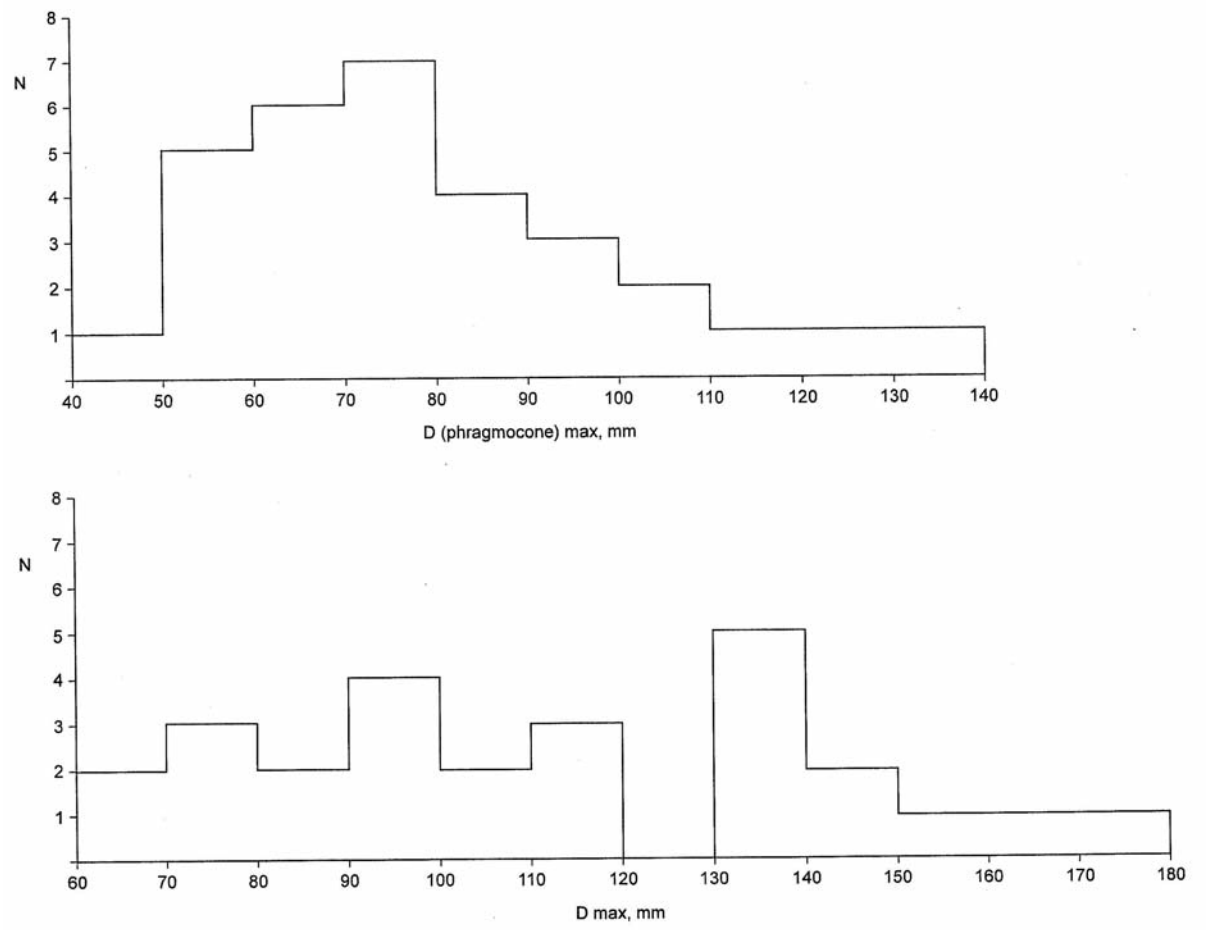
23 specimens are referred to *forma intermedia*, constituting 25% of the total assemblage: UW Zl/63/1256**,** 1258, 1269, 1460, 1465, 1466, 1473, 1477, 1481, 1608, 1613, 1619, 1626, 1640, 1646, 1656, 1658, 1668**,** 1673, 1674, 1675, 1690, 1691 (Pl. 17, Fig. 6; Pl. 9, Figs 1–3; Pl. 10, Figs 1–5; Pl. 12, Figs 1–6). Adult individuals have maximum diameters of from 69.5 to 165 mm.

	D	Wb	Wh	Wb:Wh	U
1640	52.2 (100)	17.1 (32.8)	23.9 (45.8)	0.72	13.9 (26.6)
1675	73.6 (100)	25.1 (34.1)	33.4 (45.4)	0.75	21.5 (29.2)
1465	80.3 (100)	25.0 (31.1)	36.5 (45.5)	0.68	21.0 (26.2)
1477	77.1 (100)	22.6 (29.3)	32.7 (42.4)	0.69	20.6 (26.7)
1608	112.5 (100)	31.5 (28.0)	46.3 (41.2)	0.68	32.1(28.6)
1266	165 (100)	44.4 (26.9)	66.9 (40.5)	0.66	49.5 (30.0)

Specimen 1665 (Pl. 12, Figs 7–9) most closely corresponds to the reference specimen. It is an incomplete small adult with a 180° sector of body chamber preserved. There are nine primary ribs on the adapertural half of the outer whorl of the phragmocone. They arise at the umbilical seam, strengthen and project strongly forwards on the umbilical wall. Tiny bullae perch on the narrowly rounded umbilical shoulder, and give rise to prorsiradiate primary ribs that link to a tiny inner lateral bulla, These bullae give rise to pairs of ribs that flex back and are concave on the outer flank, linking to well-developed ventrolateral clavi. The primary ribs become progressively more prorsiradiate on the body chamber and the umbilical and inner lateral tubercles are eventually lost, the adapertural 90° sector ornamented by strongly prorsiradiate falcoid ribs that become progressively more widely separated, with the wide interspaces deepened into shallow constrictions.

Phragmocones have between 16 and 22 primary ribs, and 28–36 ribs at the ventrolateral shoulder.

Specimen 1466 (Pl. 12, Figs 4–6) is the smallest adult in the assemblage, with a maximum preserved diameter of 69.2 mm. There are 18 narrow straight primary ribs on the inner flanks at a diameter of 56.6 mm, bearing delicate umbilical and inner lateral bullae, from which pairs of concave ribs arise at the beginning of the outer whorl, tending to detach from the bulla as size increases. The ornament changes markedly on the adapertural 90° sector of the body chamber. The umbilical and inner lateral tubercles disappear abruptly, leaving an ornament of falcate ribs of variable strength and spacing, straight and prorsirdiate to mid-flank, then flexing back and concave on the outer flank, with two broad interspaces deepened into shallow but distinct constrictions. Specimen 1608 (Pl. 10, Figs 4, 5) is a larger adult with a maximum preserved diameter of 119 mm and a 200° sector of body chamber preserved. There are 20 primary ribs on the outer whorl of the phragmocone, with typical ribbing and tuberculation. Ornament declines progressively on the body chamber. The adapertural 90° sector of the internal mould is marked by three strong, broad, feebly falcoid constrictions, flanked by feeble collar ribs, with traces of delicate falcoid striae between. The final constriction immediately precedes the adult aperture, which is slightly flared, straight and prosiradiate to mid-flank, and feebly concave on the outer flank, projecting strongly forwards on the ventrolateral shoulder into a damaged ventral rostrum. The outer part of the margin bears a distinctive V-shaped nick, beyond which the margin is reflected inwards. Specimen 1668 is an internal mould of a 180° fragment of body chamber with a maximum preserved whorl height of 55 mm. The umbilical wall inclines markedly outwards at the greatest preserved diameter. Five pairs of small umbilical and inner lateral bullae, borne on widely separated narrow feeble



Text-fig. 8. *Schloenbachia varians* (J. Sowerby, 1817). Histograms plotting: above, maximum diameters of adult phragmocones; below: maximum diameter of complete adults

ribs are present on the adapical 90° sector of the fragment, the lateral bullae giving rise to feeble falcoid ribs separated by wide interspaces, some deepened into incipient constrictions. The adapertural 90° sector of the fragment is near-smooth, with traces of widely separated falcoid ribs, broad and best developed on the outer flank and ventrolateral shoulder.

Forma subplana

The reference specimen is BMNH 5724 (Text-fig. 5F–H), which may be the original of *Ammonites varians* var. *subplana* of Mantell, 1822, p. 115, pl. 21, fig. 1, from the Lower Chalk of Hamsey, near Lewes, Sussex. The dimensions are as follows:

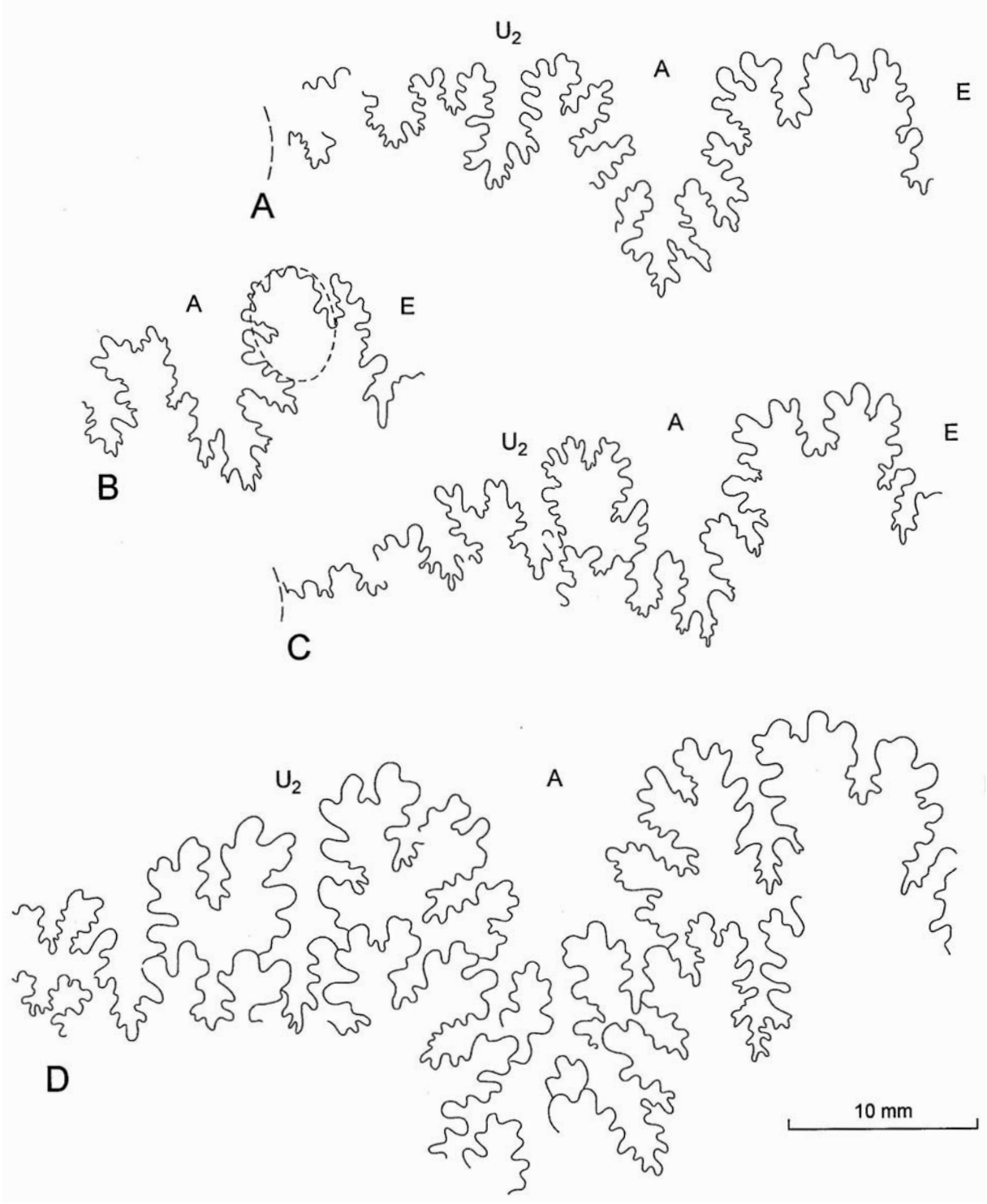
D	Wb	Wh	Wb/Wh	U
37.8 (100)	11.4 (30.2)	19.6 (51.9)	0.58	8.4 (22.2)

It is a somewhat worn, compressed composite internal mould with a whorl breadth to height ratio of 0.58, with a tiny umbilicus that comprises 22.2% of the diameter. Delicate primary ribs arise at the umbilical seam, and strengthen across on the umbilical wall and shoulder. They are very feeble, straight and prorsiradiate on the inner flanks, flex back across the middle of the flanks, increasing by branching and intercalation, sweep forwards and are feebly concave across the outer flank, weakening, and connecting to minute ventrolateral clavi. Tiny umbilical tubercles are preserved in places, and tiny inner lateral tubercles can be distinguished on the adapertural 90° sector of the specimen. A second useful reference specimen is BMNH 43962d, figured by J. Sowerby, 1817, p. 196, pl. 176, left hand lower figure, as *Ammonites varians*, of which it is thus a paralectotype (Text-fig. 6D, E, F).The specimen is a well-preserved if somewhat distorted composite mould, in part body chamber, with the following dimensions:

D	Wb	Wh	Wb/Wh	U
52.6 (100)	14.4 (27.4)	25.7 (48.9)	0.56	11.2 (21.3)

Coiling is moderately involute, the umbilicus com-

prising 21.3% of the diameter, with a low, flattened and outward inclined umbilical wall, the umbilical shoulder sharp. The whorl section is compressed with a whorl breadth to height ratio of 0.56. The inner and middle flanks are subparallel, the outer flanks converging to angular ventrolateral shoulders, the venter fastigiate, with a blunt siphonal keel. Tiny crowded bullae perch on the umbilical shoulder of the adapical part of the outer whorl, and give rise to delicate prorsiradiate ribs, some of which link to tiny inner lateral tubercles. The ribs branch at



Text-fig. 9. *Schloenbachia varians* (J. Sowerby, 1817). External sutures. A – UW/Zl/1481, *varians sensu stricto*. B – UW/Zl/1215, *forma subtuberculata*. C – UW/Zl/1630, *forma intermedia*. D – UW/Zl/1658, *forma intermedia*

these tubercles, and additional ribs intercalate at the level of the tubercles, the ribs flexing back and concave on the outer flank, linking to tiny clavi, borne on the ventrolateral ridge. On the adapertural part of the outer whorl the ribbing strengthens, and is markedly falcoid, and ventrolateral clavi increase in strength. One interspace, 90º from the adapertural end of the specimen is strengthened into a broad shallow constriction.

Ammonites falcato-carinatus Schlüter, 1871 (pl. 3, figs 8, 9) is a *Schloenbachi*a, described by its author as based on a specimen 30 mm in diameter, which is the holotype by monotypy. It was from the Varians Pläner of Kothwelle, near Salzgitter in Lower Saxony. The specimen has delicate falcoid lirae and ventrolateral clavi at which the lirae are shown linking in pairs. It may be a synonym of *forma subplana*, the figure an imperfect restoration, for as Schlüter states, the figure is "die etwas restaurirte Abbildung des einzigen vorliegenden Exemplares" (a restoration of the only available specimen).

The holotype, by monotypy, of *Schloenbachia dorsetensis* Spath, 1926b (pp. 426, 430), is the original of *Schloenbachia subplana* (Mant.) Sharpe of Semenov, 1899, pl. 3, fig. 7, from 'Bishakty'. The original illustration is reproduced here as Text-fig. 7A, B. It falls into the present *forma*, differing in no significant respects from Sowerby's specimen, described above, albeit larger.

Two specimens, UW Zl/ 1262 and 1627, making up 2% of the assemblage, are referred to the *forma*, the latter a passage form between *subplana* and *intermedia*.

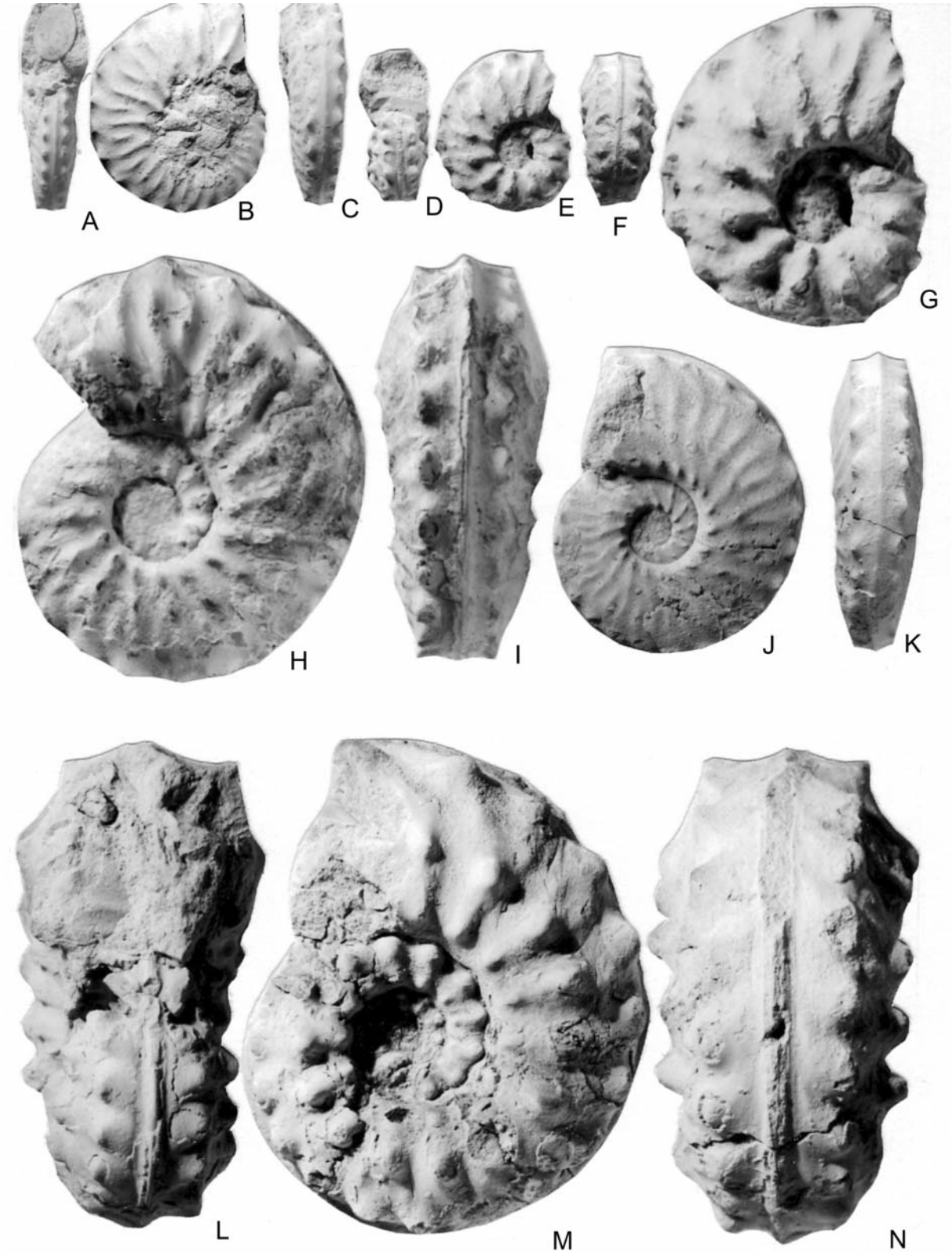
	D	Wb	Wh	Wb;Wh	U
1262ic	104. 3 (100)	-	46.5 (44.6)	-	28.0 (26.8)
		21.8	32.9	0.66	
1617ic	98.5 (100)	28.6 (0.29)	39.7 (40.3)	0.72	28.6 (29.0)

Specimen 1262 (Pl. 13, Figs 3–5) retains recrystallised shell, and is a 180° sector of body chamber, lacking the adapical part. Narrow ribs strengthen across the umbilical wall, and link to small umbilical bullae that in turn give rise to a single rib that links to a tiny inner lateral bulla. These give rise to single narrow prorsirdiate ribs that efface across the flanks, and are accompanied by crowded growth lines and striae on the shell surface that flex back and are feebly flexuous, being very feebly convex across the middle of the flanks. The ventrolateral shoulder is angular, and bears delicate ventrolateral clavi that efface and disappear on the adapertural part of the body chamber.

Specimen 1617 (Pl. 13, Figs 1, 2) is a complete small adult, 98.5 mm in diameter. Coiling appears to have been moderately involute, the umbilicus shallow, although blocked by sediment and mineral overgrowths, with a flattened wall that inclines outwards on the adapertural part of the body chamber. The umbilical shoulder is very narrowly rounded. The whorl section is compressed, with a whorl breadth to height ratio of 0.72, the inner flanks flattened and feebly convergent, the outer flanks convex and converging to quite narrowly rounded ventrolateral shoulders, the venter fastigiate, with a strong siphonal keel. There are twelve primary ribs on the adapertural half whorl of the specimen. They arise at the umbilical seam, strengthen across the umbilical wall, and link to small bullae perched on the umbilical shoulder. These give rise to single narrow primary ribs, slightly prorsirdiate on the adapical end of the phragmocone, but becoming increasingly prosiradiate towards the aperture. The ribs are narrow on the inner flank, and link to a small inner lateral tubercle. At the adapertural end of the phragmocone the lateral bullae give rise to a pair of ribs, and to a single rib on the body chamber. The ribs flex back and are very feeble on the outer flank, where they link to tiny ventrolateral clavi. The ribs become increasingly prorsiradiate towards the adult aperture and efface on the outer flank. Occasional ventrolateral bullae lack an associated flank rib. An interspace close to the aperture is deepened into an incipient constriction.

Although many specimens show the sutures, these are often badly corroded. Better preserved examples are shown in Text-fig. 9. E/A is large, broad, and bifid. A is deeply incised and trifid, U2 small and bifid.

DISCUSSION: The Besakty assemblage provides the first large sample of well-preserved *Schloenbachia* with a significant number of adults, and confirms the intraspecific variation of the predominantly juvenile material described by previous authors, as well as documenting the marked changes in ornament of adult body chambers. The material, together with the lectotype and reference specimens reveals *Schloenbachia varians* as a species in which the nuclei of robust individuals: *forma ventriosa* and *varians sensu stricto* have strong lateral tubercles and ventrolateral clavi, with the ribs linking tubercles and clavi weak to near-effaced in the most depressed and strongly ornamented phragmocones, becoming better expressed as tuberculation weakens and whorl section becomes less depressed. Adult body chambers show a decline in tuberculation and the development of narrow ribs that may differentiate into short ribs detached from lateral and ventral tubercles, sometimes strengthened into incipient elongated outer lateral bullae, and thus with a few incipiently to feebly trituberculate ribs. With increasing compression, ribs come to dominate over tubercles; accompanying this change, small umbilical bullae appear, largely restricted



Text-fig. 10. *Schloenbachia coupei* (Brongniart, 1822). A-C – BMNH C82603. D-G – the holotype, the original of Brongniart, 1822, pp. 83, 391, pl. 6, fig. 3, an unregistered specimen in the Sorbonne Collections. H, I – BMNH C75240. J, K – MNHP, unregistered. L-N – MNHP d'Orbigny Collection 6113-2. All specimens are phosphatised individuals from the Middle Cenomanian *Acanthoceras rhotomagense* Zone, *Turrilites costatus* Subzone fauna of the Craie de Rouen of Rouen, Seine-Maritime, France. Figs A-F, H-N are ×1; Fig. G is ×2

to the adult body chamber in *forma subtuberculata*, but extending to the juvenile phragmocone in *forma intermedia* and *forma subplana*. Adult body chambers of these gracile forms show effacement of ribs and flank tubercles, developing an ornament of falcoid growth lines, lirae and striae, with well-developed constrictions preceding the adult aperture and in some cases the adapertural part of the body chamber.

Schloenbachia coupei (Brongniart, 1822) (pp. 83, 391, pl. 6, fig. 3) is based on a single individual, which is thus the holotype by monotypy, from the Craie de Rouen of Rouen, Seine-Maritime, France. The specimen was located in the Sorbonne Collections by the late Dr. H. Gauthier, and is illustrated her as Text-fig. 10D–G. It is a phosphatised juvenile with a maximum preserved diameter of 29.7 mm, retaining phosphatised shell; the position of the last suture cannot be established, but the specimen appears to retain some body chamber. The preservation is that of the Middle Cenomanian *Turrrilites costatus* Subzone of the *Acanthoceras rhotomagense* Zone of the Rouen Fossil Bed of Kennedy and Hancock (1970) of Côte Ste Catherine. The dimensions are:

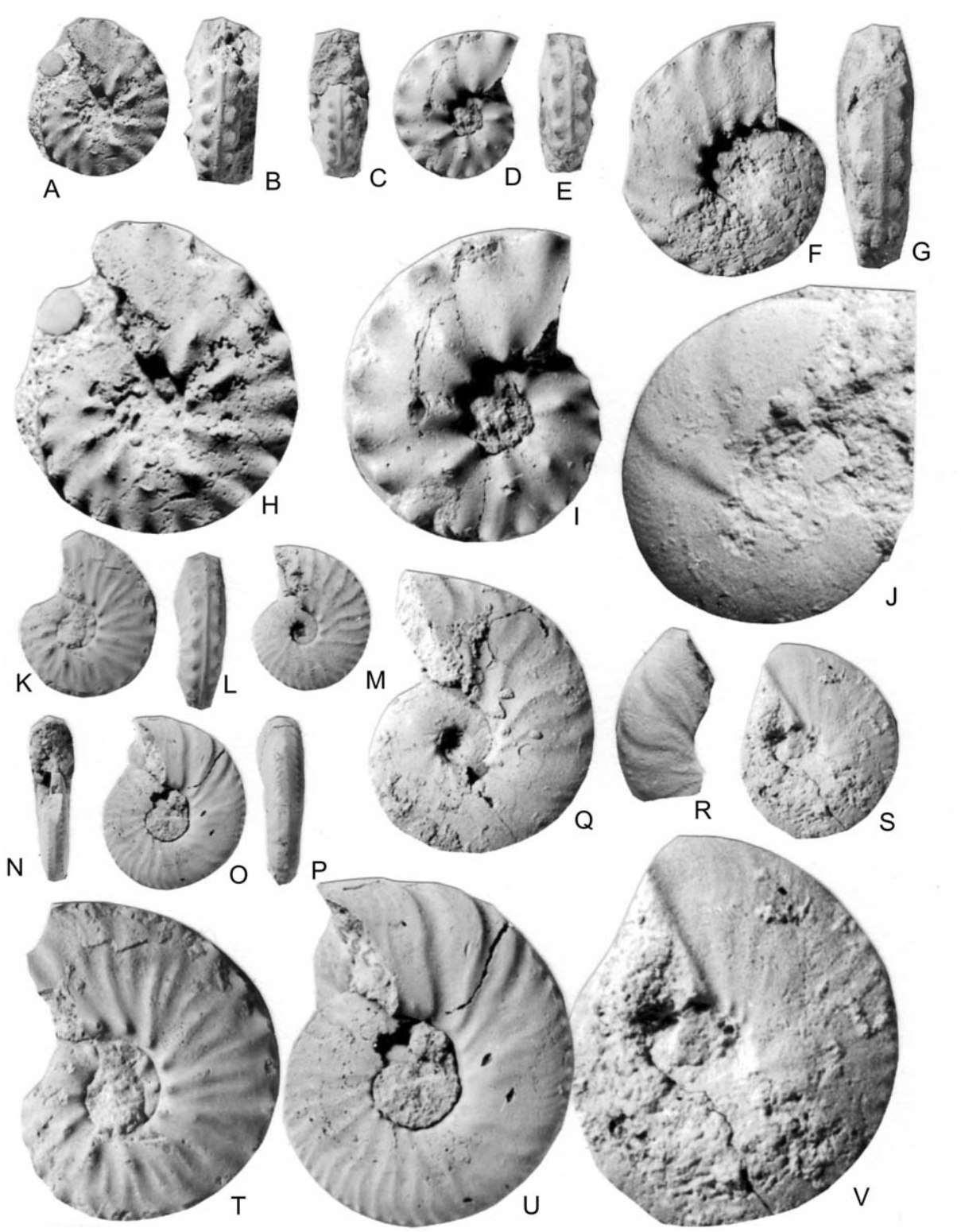
D	Wb	Wh	Wb/Wh	U
29.7c (100)	15.1 51.0)	14.1 (47.5)	1.1	(.0 (30.3)

Coiling is moderately evolute, the umbilicus comprising 30.3% of the diameter, quite deep, with a feebly convex, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The intercostal whorl section is slightly compressed, rounded-trapezoidal with the greatest breadth well below mid-flank, the ventrolateral shoulders broadly rounded, the venter obtusely fastigiate, with a strong siphonal keel. The costal whorl section is slightly depressed, polygonal, the whorl breadth to height ratio 1.1, the greatest breadth at the lateral tubercles. Thirteen low, broad ribs arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, developing into small but clearly differentiated umbilical bullae that give rise to single strong, straight, feebly prorsiradiate primary ribs that link to stronger conical mid-lateral tubercles. These in turn give rise to one or two strongly prorsiradiate secondary ribs. These may link in pairs to a single ventrolateral clavus or each rib of a pair may link to successive clavi, or a single rib may intercalate. There are an estimated 20–22 ventral clavi on the outer whorl of the specimen. This pattern of well-developed umbilical bullae, stronger lateral tubercles and strong ventrolateral clavi, together with well-developed ventrolateral clavi characterises the largest robust topotypes of *coupei*, including specimens such as MNHP (d'Orbigny Collection) 6112-1 and 2, the latter illustrated here as Text-fig. 10L–N. Gracile topotypes of *coupei* are illustrated here as Text-fig. 10A–C, H–K. When compared to similarly gracile forms of *varians*: *forma* s*ubtuberculata* and *forma intermedia*, they differ, like the robust variants, in the presence of umbilical and lateral tubercles throughout ontogeny. The common style of ribbing of *forma intermedia*, with pairs of ribs arising from lateral bullae, each rib linking to single ventrolateral clavus, is replaced by a predominance of individuals in which the ornament is more complex: ribs loop in pairs or zigzag between lateral and ventrolateral tubercles. The largest known topotypes *coupei* have an estimated maximum diameter of around 100 mm, only 57% of that of the largest *varians* in the present assemblage. To summarise, phragmocones of robust individuals of *coupei* have umbilical tubercles throughout ontogeny, as do those ofgracile forms; robust individuals of *varians*: *forma ventriosa*, *forma varians*, and some *forma subtuberculata* lack umbilical bullae on the phramocone, although these may develop on the adult body chamber, and are present throughout ontogeny on some but not all gracile individuals of *forma intermedia*.

The holotype of *Schloenbachia lymensis* Spath, 1926b, is illustrated here as Text-fig. 11A–C, H, together with a series of topotypes. Very few specimens were avaailable to previous workers, but thanks to the persistence of the late Colonel Orval Bayliss of Uplyme, and of John Huxtable of Taunton there are now hundreds of specimens available for study, including many topotypes from near Lyme Regis in Devon. These show *lymensis* to be a diminutive species; the largest known adults are up to 55 mm in diameter, only 32% of the diameter of the largest *varians* in the present collection. Robust forms of *lymensis*, including the holotype (Text-fig. 11A–E, H, I) have strong umbilical bullae and stronger lateral bullae, linked by a very strong primary rib. More compressed individual may have lautiform ribbing (Text-fig. 11, figs K, L, T), or straight prorsiradate ribs on the inner to mid-flanks that broaden on the outermost flankText-fig. 11 F, G). More gracile individuals (Text-fig. 11M, N–P, U) develop crowded flexuous ribs with minute to effaced umbilical bullae and tiny ventral clavi, body chambers developing prominent constrictions at the adult aperture or on much of the body chamber (Text-fig. 11 J, R, S, V). These morphotypes are so far removed from the *varians* population described here that confusion is unlikely.

If stratigraphic distribution is considered:

- Typical *Schloenbachia varians* characterise the Lower Cenomanian *Mantelliceras mantelli* Zone. In the *Mantelliceras dixoni* Zone, gracile vari-



Text-fig. 11. *Schloenbachia lymensis* Spath, 1926b. A, B, H – the holotype, BGS GSM 7765, the original of Sharpe, 1853, pl. 8, fig. 8, from the 'Chalk with siliceous grains near Lyme Regis,' by its preservation and matrix from Bed C of the Cenomanian Limestone, Upper Cenomanian *Calycoceras guerangeri* Zone. C-E, I – OUM K59546. F, G – OUM K59599.J, OUM K47119. K, L, T – OUM K59528. M – OUM K59563. N-P, U – OUM K59562. Q – OUM K57564. R – OUM K59773. S, V – OUM K60547. C-G, I-V, are all from Bed C of the Cenomanian Limestone, Upper Cenomanian *Calycoceras guerangeri* Zone; C-G, I, K-Q, T, U, are from Humble Point, Devon; J, S, V, are from Shapwick Grange, Uplyme, Dorset. R – OUM K47119, from the Upper Cenomanian *Calycoceras guerangeri* Zone fauna of the Chalk Basement Bed at Askerswell, Dorset. Figures A-G, K-P, R, S, are ×1. Figures H, I, J, Q, T-V are ×2

ants dominate, with *forma subtuberculata*, *forma intermedia* and *forma subplana* as in the *mantelli* Zone. Work in progress suggests some inflated individuals may develop umbilical bullae on the phragmocone at the top of the Zone, but this is to be confirmed.

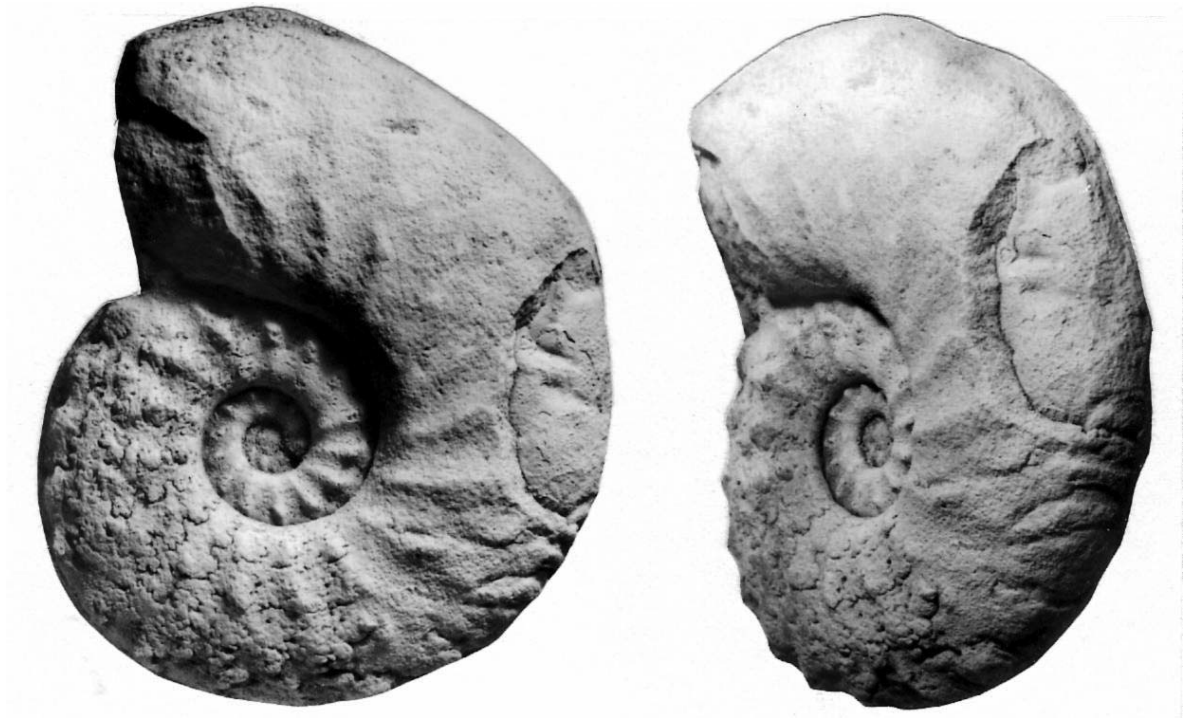
- I have seen no *Schloenbachia* from the Middle Cenomanian *Cunningtoniceras inerme* Zone. *Schloenbachia coupei* characterizes the Middle Cenomanian *Acanthoceras rhotomagense* Zone. *Schloenbachia lymensis* first appears in the Middle Cenomanian *Acanthoceras jukesbrownei* Zone, and has its acme in the lower Upper Cenomanian *Calycoceras guerangeri* Zone.

- The present collection of *Schloenbachia* holds one last specimen of interest. UW Zl/63/1487 (Text-fig. 12) houses the articulated exoskeleton of a small lobster, compared to *Palaeastacus*. The carapace and associated thoracic segments are arranged with the anterior of the specimen directed towards the aperture of the enclosing ammonite's body chamber, the dorsal surface pressed tightly against and following the curve of the venter. The associated appendages, if present, are concealed by matrix.

OCCURRENCE: Lower Cenomanian. The geographic range matches that of the genus (Text-fig. 1), and extends from East Greenland (Donovan 1953, 1954) to the British Isles, Belgium, Germany, Bornholm in the Baltic, Switzerland, Poland, Russia, extending to the coast of the Kara Sea. In France, the genus occurs from the Boulonnais in the north to Northern Aquitaine, and, to the east, extends down the Rhône as far south as the Alpes-Maritimes. There are records from the Mediterranean coast, at Cassis, but these are unfounded (Kennedy 1994). The genus is not known from the western Mediterranean, nor from Spain or points south, as with the well-known North African and Madagascan faunas (the record from Algeria cited by Kennedy and Juignet 1984, p. 123, is based on poorly preserved *Acompsoceras*). To the east, there are records from Ukraine, Crimea, the Mangyshlak Peninsula in western Kazakhstan, the Kopet Dag, Turkmenistan, and Iran north of the Zagros.

Acknowledgements

I am particularly grateful to Professor Irek Walaszczyk for asking me to revise the Mangyshlak ammonites described above. This study builds on the advice of, and discussions with, the late Jake Hancock, Ryszard Marcinowski, and Willy Wright. The technical support of the staff of the Department of Earth Sciences, Oxford, is gratefully acknowledged.



Text-fig. 12. UW Zl/63/1497, a specimen of *Schloenbachia varians* (J. Sowerby, 1817) *forma subtuberculata* with a specimen of the lobster *Palaeastacus* in the body chamber, from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section in the Mangyshlak Mountains, Western Kazakhstan. Figures are ×1

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PLATES 1–13

PLATE 1

Schloenbachia varians (J. Sowerby, 1817) *forma ventriosa*

1-3 – UW Zl/63/1470; **4, 5** – UW Zl/63/1462; **6** – UW Zl/63/1606; **7** – UW Zl/63/0098 (see also Pl. 2)

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

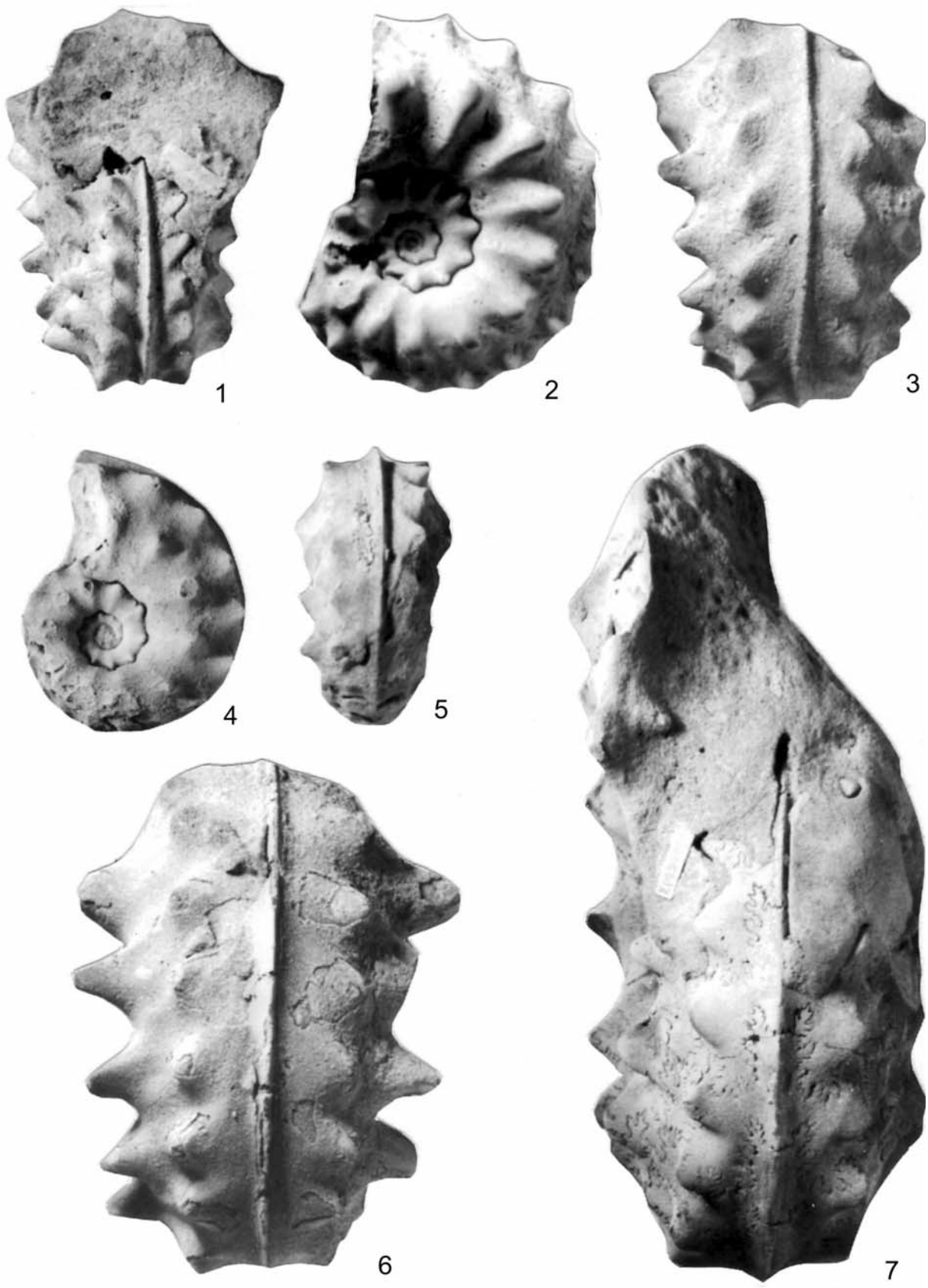

PLATE 2

Schloenbachia varians (J. Sowerby, 1817) *forma ventriosa*; UW Zl/63/0098
(see also Pl. 1, fig. 7)

The specimen is from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

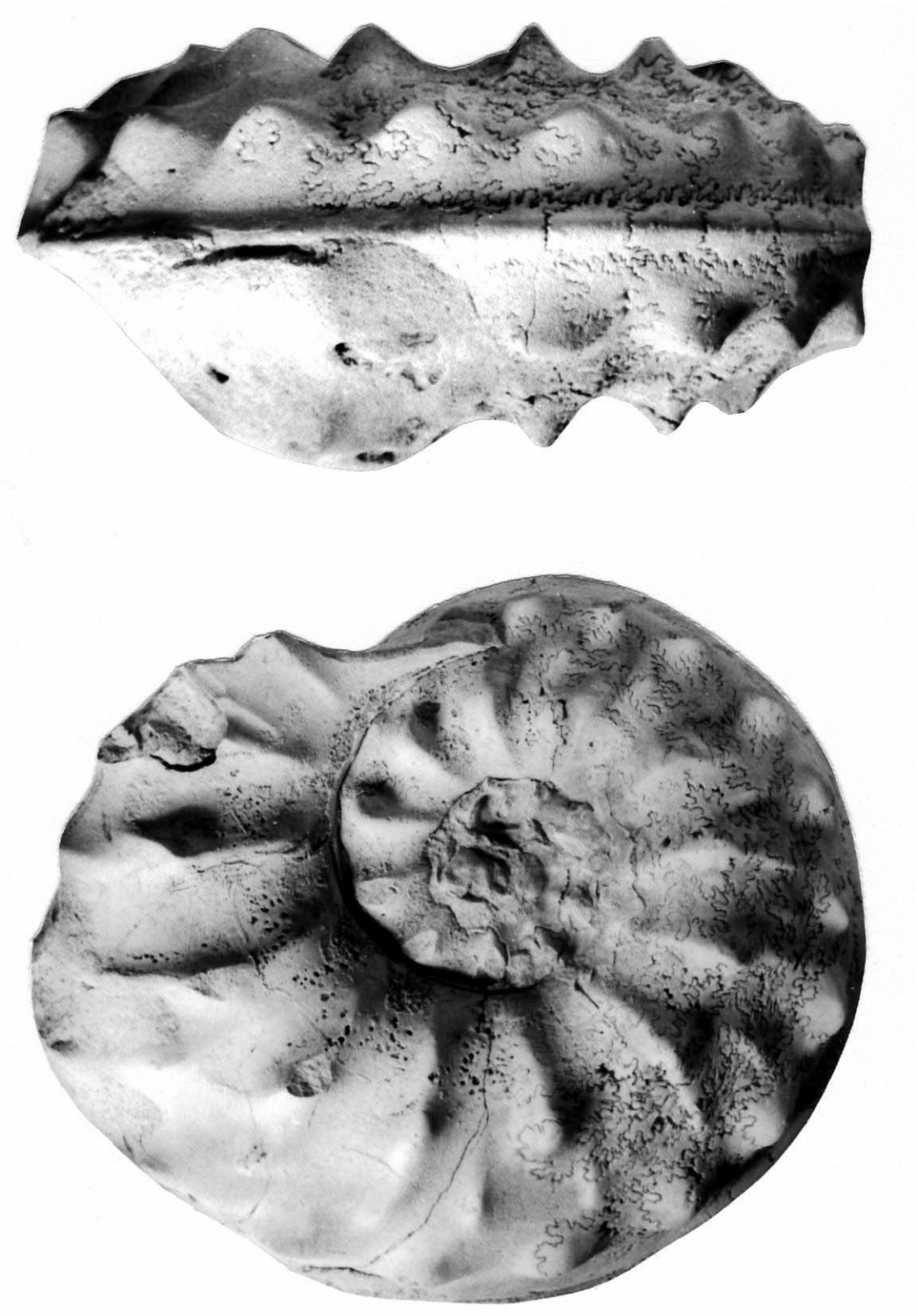

PLATE 3

Schloenbachia varians (J. Sowerby, 1817) *sensu stricto*

1, 3 – UW Zl/63/1463; **2** – UW Zl/63/1468; **4, 5** – UW Zl/63/1255 (with encrusting lichens)

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

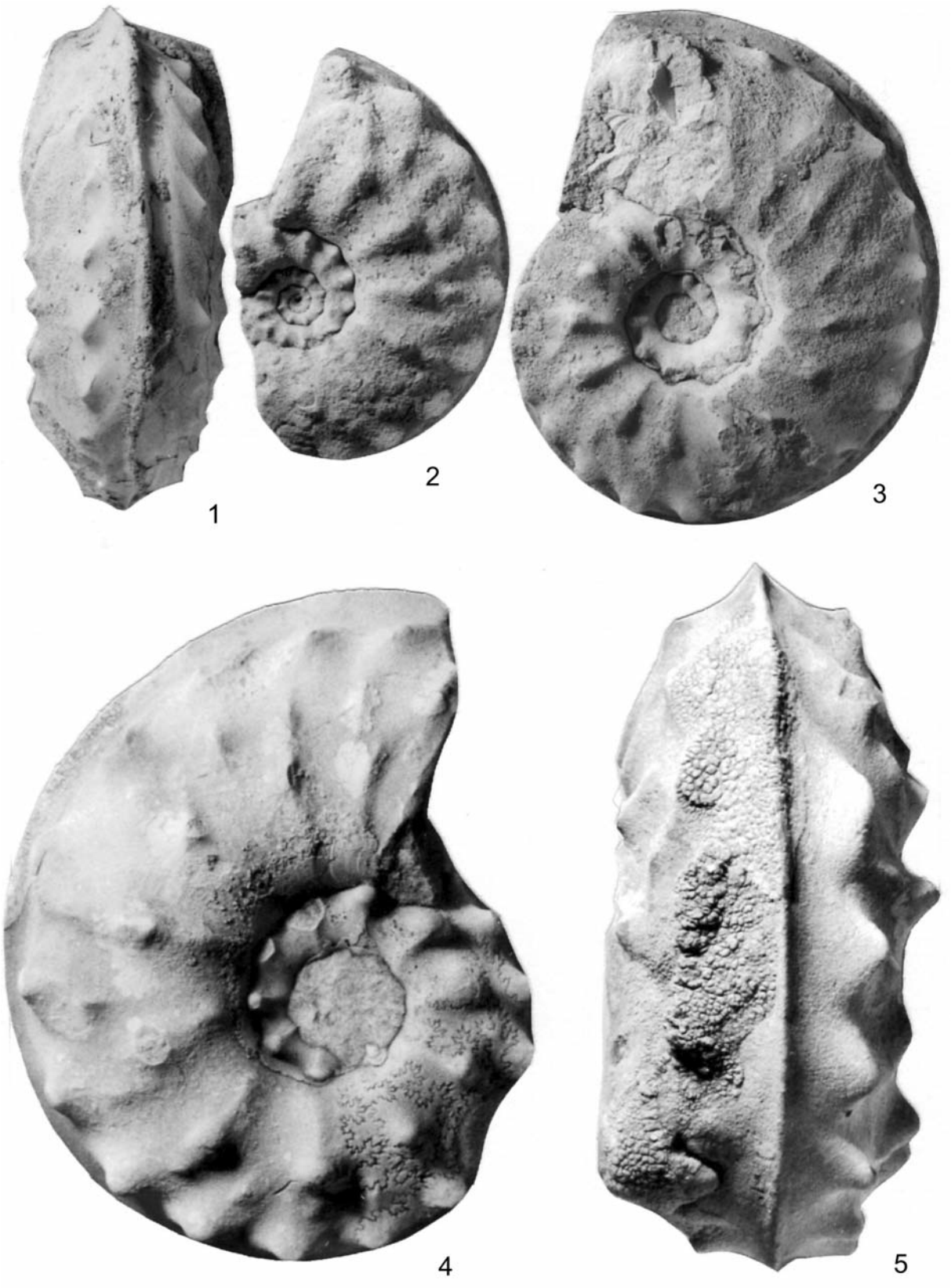

PLATE 4

Schloenbachia varians (J. Sowerby, 1817) *sensu stricto*

1, 2 – UW Zl/63/1626, variant with looped ribbing, transitional to *forma subtuberculata*; **3, 4** – UW Zl/1679; **5, 6** – UW Zl/63/1480, variant transitional to *forma ventriosa*; **7, 8** – UW Zl/63/1465; **9** – UW Zl/63/0100 (see also Pl. 5)

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

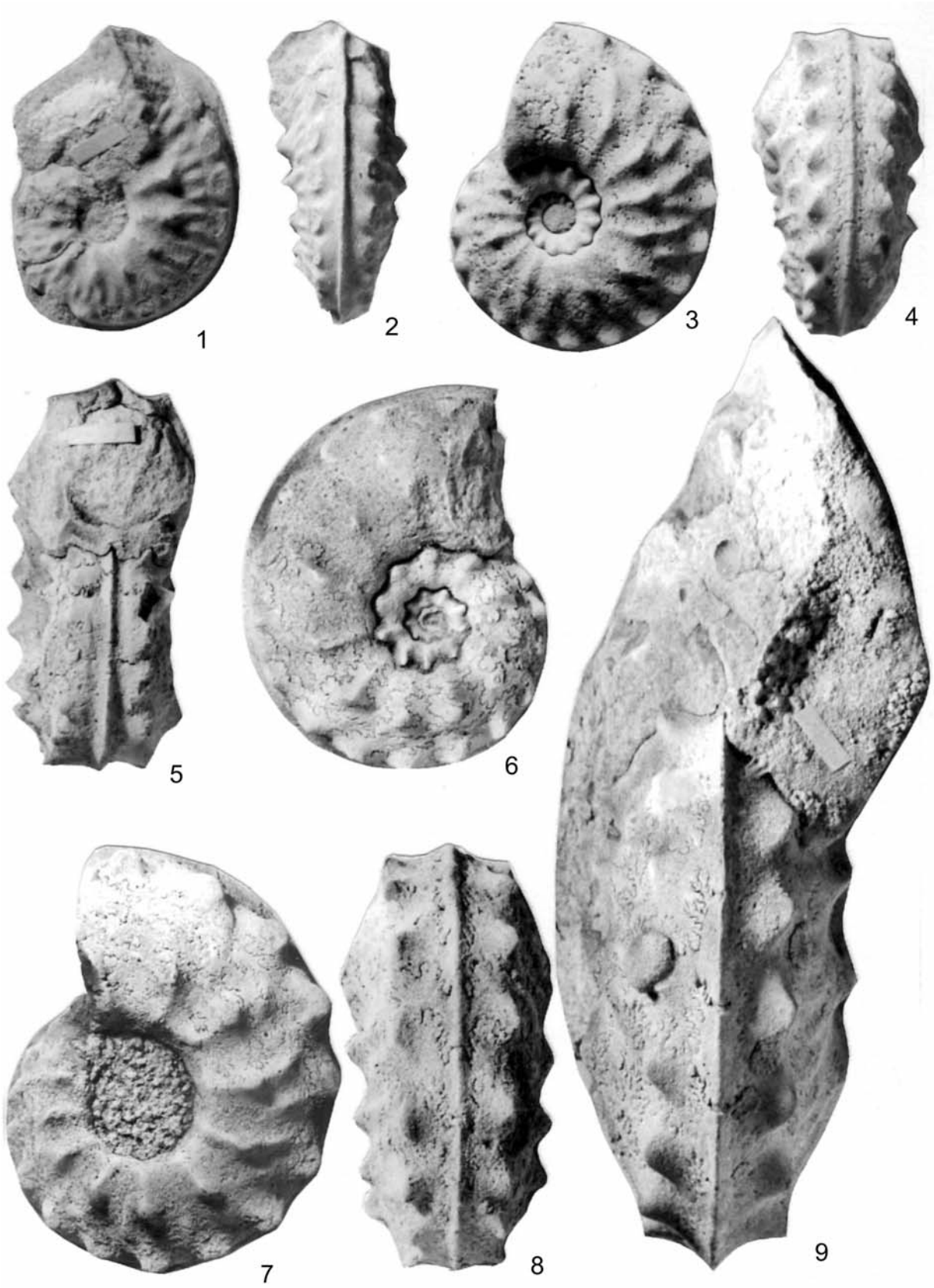

PLATE 5

Schloenbachia varians (J. Sowerby, 1817) *sensu stricto*; UW Zl/63/0100
(with encrusting lichens)

The specimen is from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

PLATE 6

Schloenbachia varians (J. Sowerby, 1817) *forma subtuberculata*

1, 7 – UW Zl/63/1604; **2-4** – UW Zl/63/1481; **5, 6** – UW Zl/63/1476

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

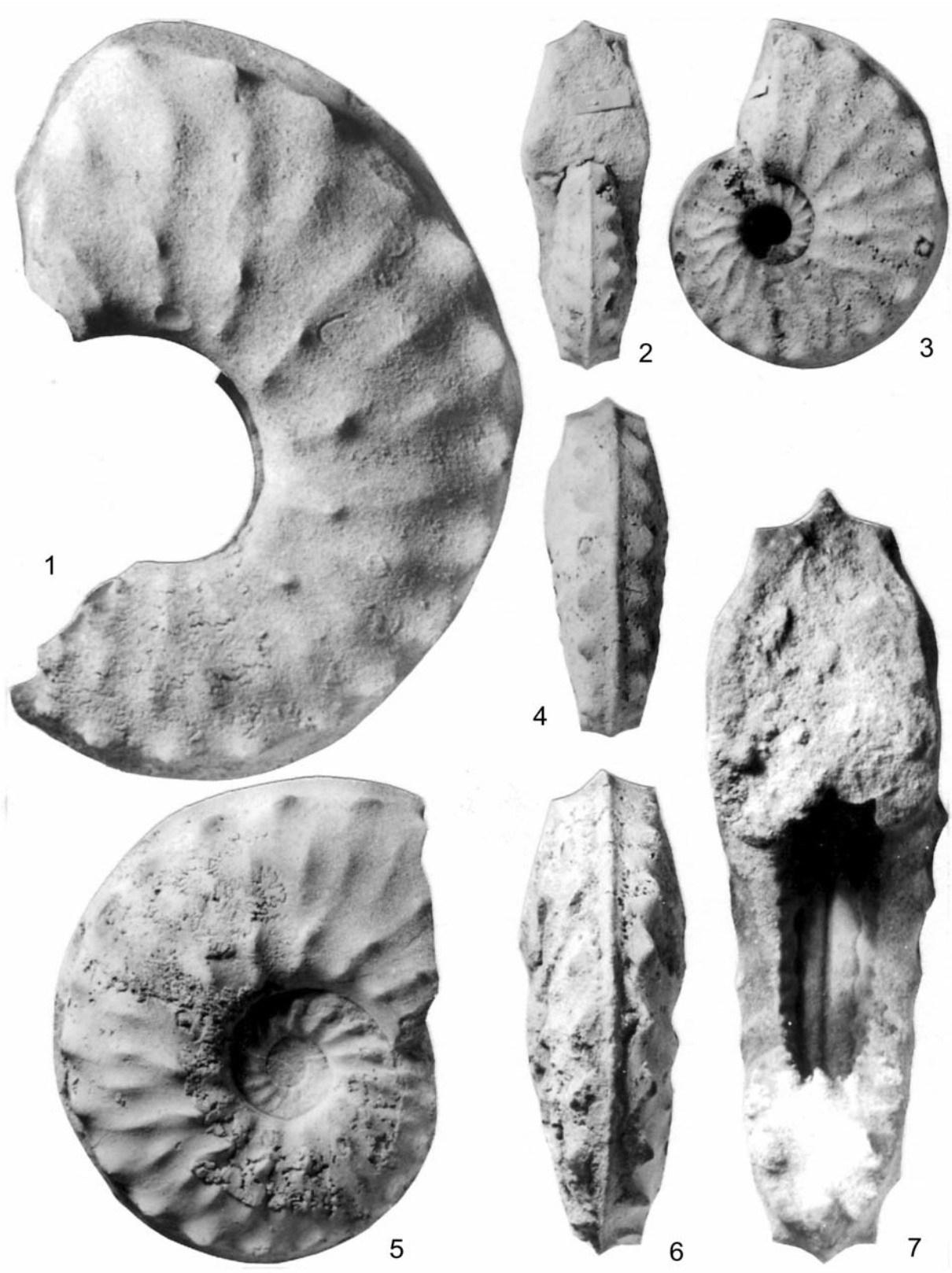

PLATE 7

Schloenbachia varians (J. Sowery, 1817) *forma subtuberculata*

1-3 – UW Zl/63/1642; **4, 5** – UW Zl/63/1268; **6** – UW Zl/63/1617, passage from between *forma intermedia* and *forma subtuberculata*; **7-9** – UW Zl/63/1657

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

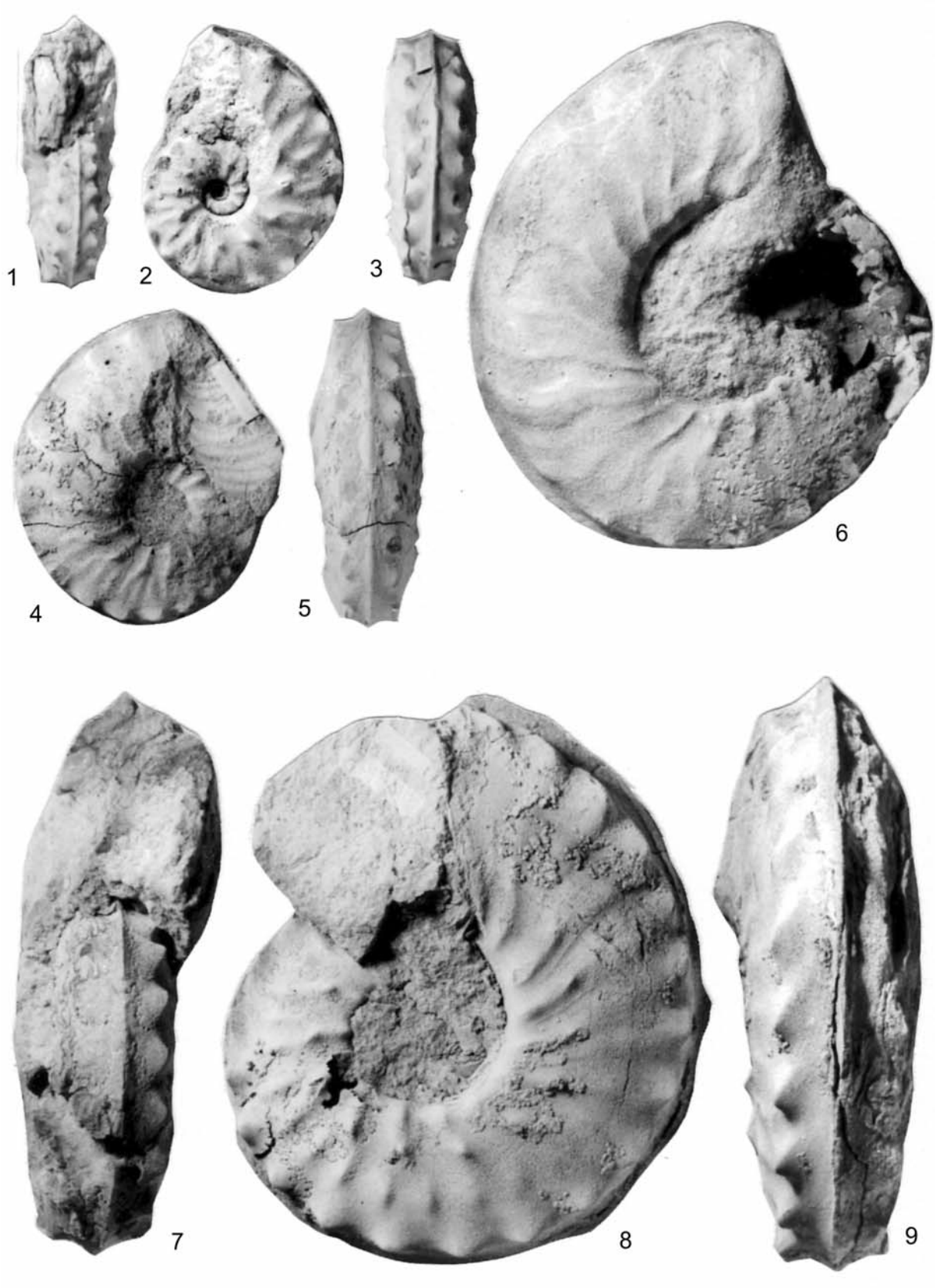

PLATE 8

Schloenbachia subvarians (J. Sowerby, 1817) *forma subtuberculata*

1, 2 – UW Zl/63/1487, a passage form to *varians sensu stricto*; **3-5** – UW Zl/63/1471

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

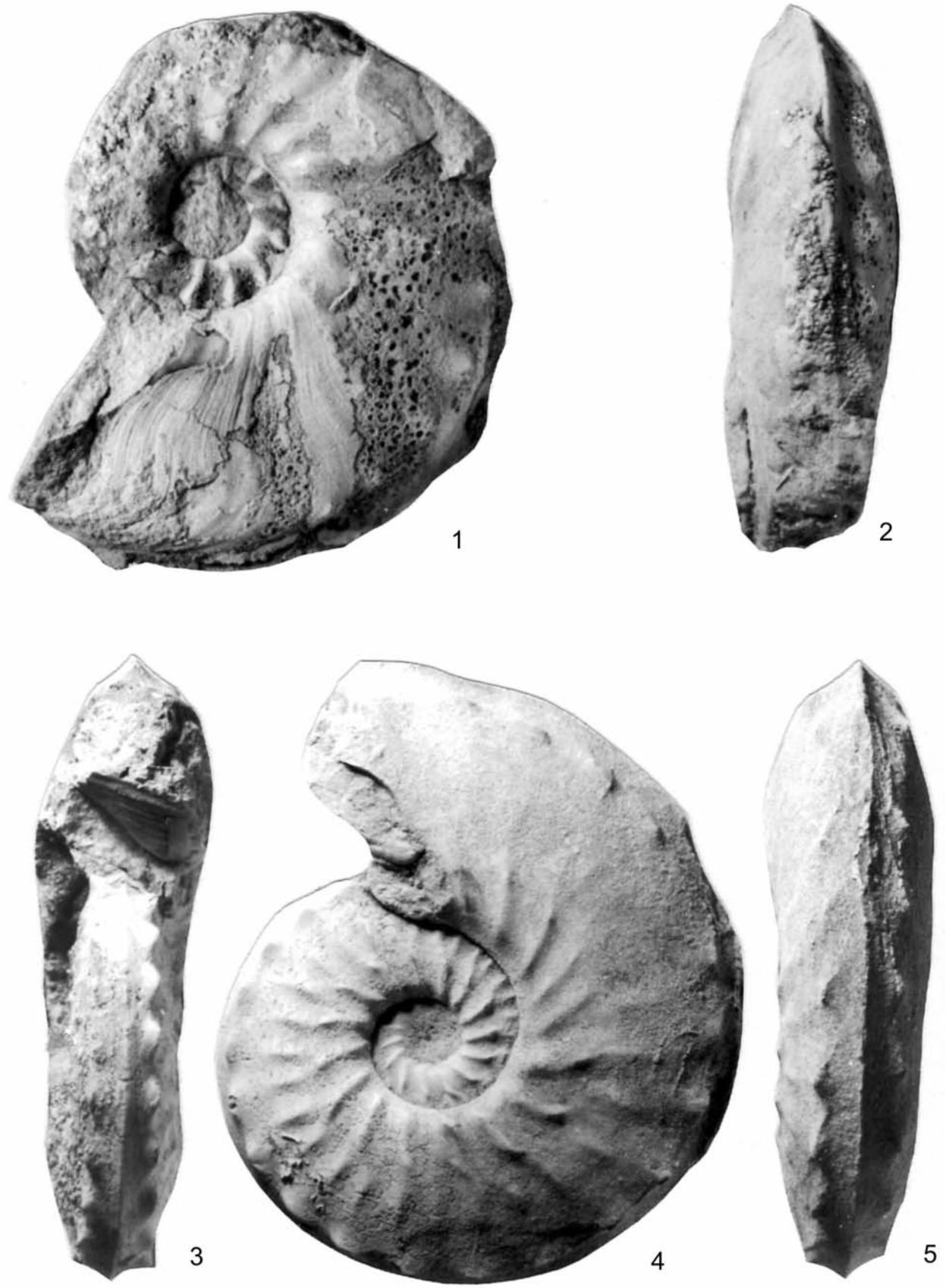

PLATE 9

Schloenbachia varians (J. Sowerby, 1817)

1-3 – UW Zl/63/1477: *forma intermedia*; 4, 5 – UW Zl/63/1259: *forma subtuberculata*
All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

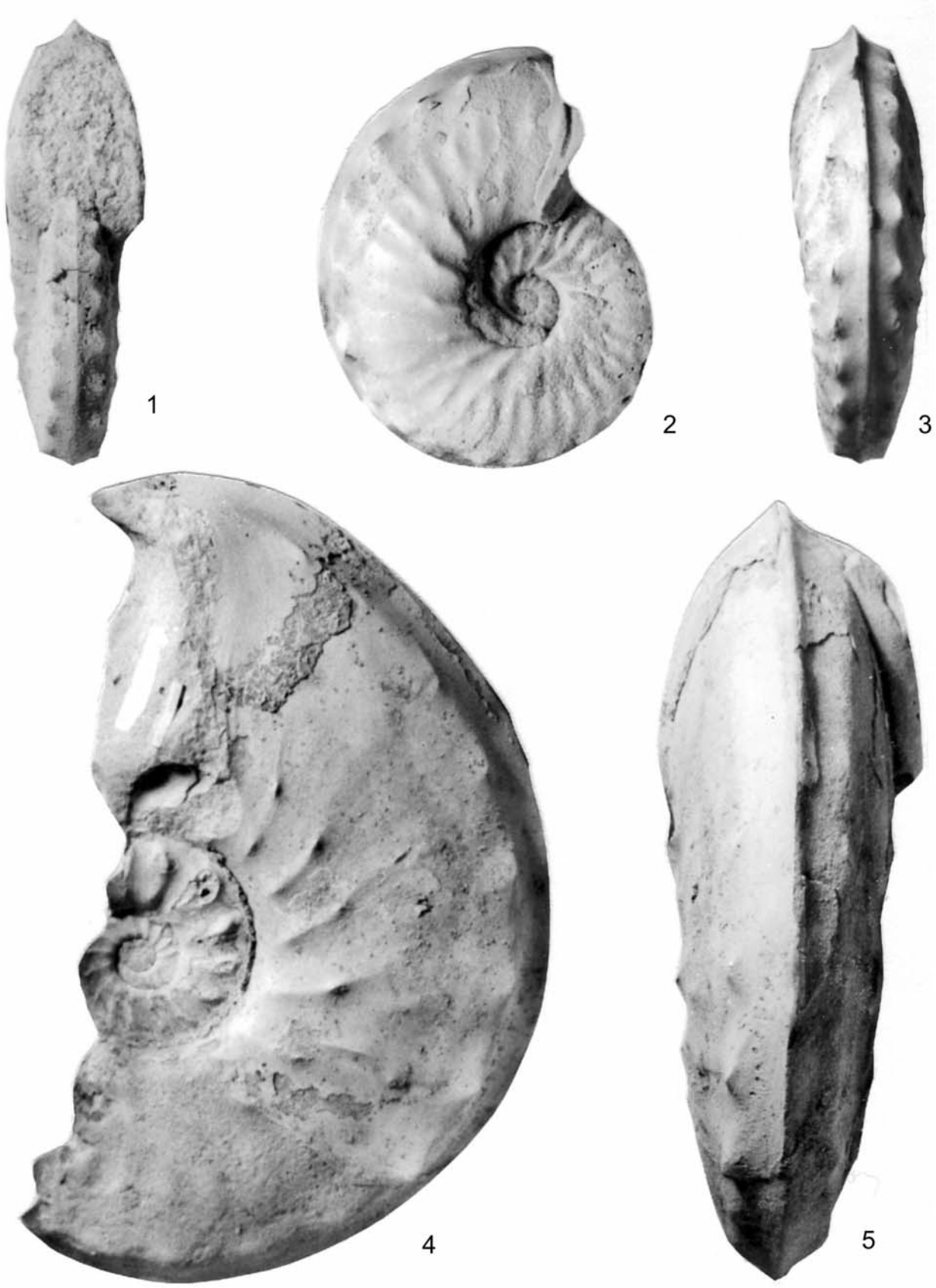

PLATE 10

Schloenbachia varians (J. Sowerby, 1817) *forma intermedia*

1-3 – UW Zl/63/1465; **4, 5** – UW Zl/63/1608

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

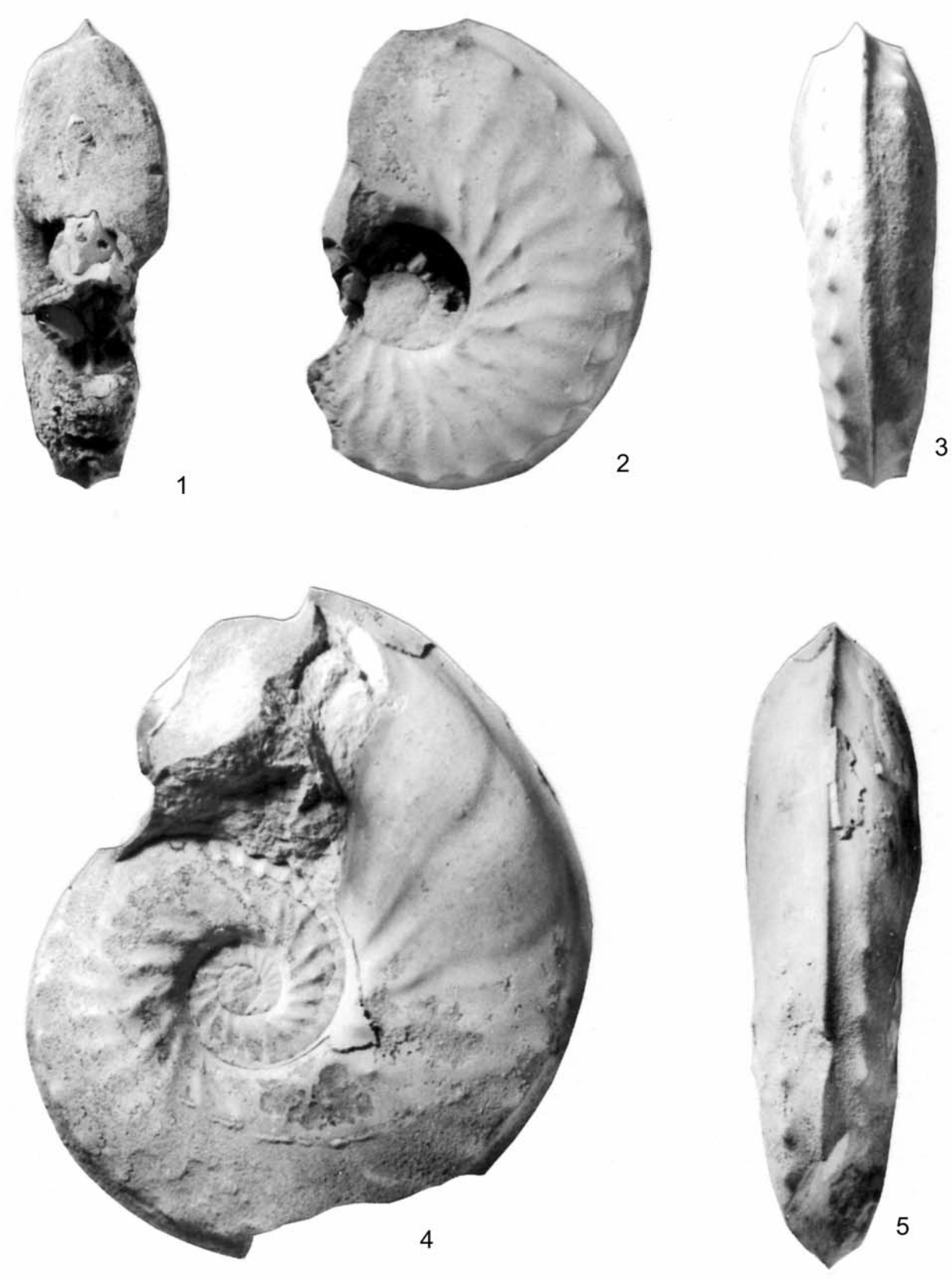

PLATE 11

Schloenbachia varians (J. Sowerby, 1817) *forma subtuberculata*; UW Zl/63/1458

The specimen is from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

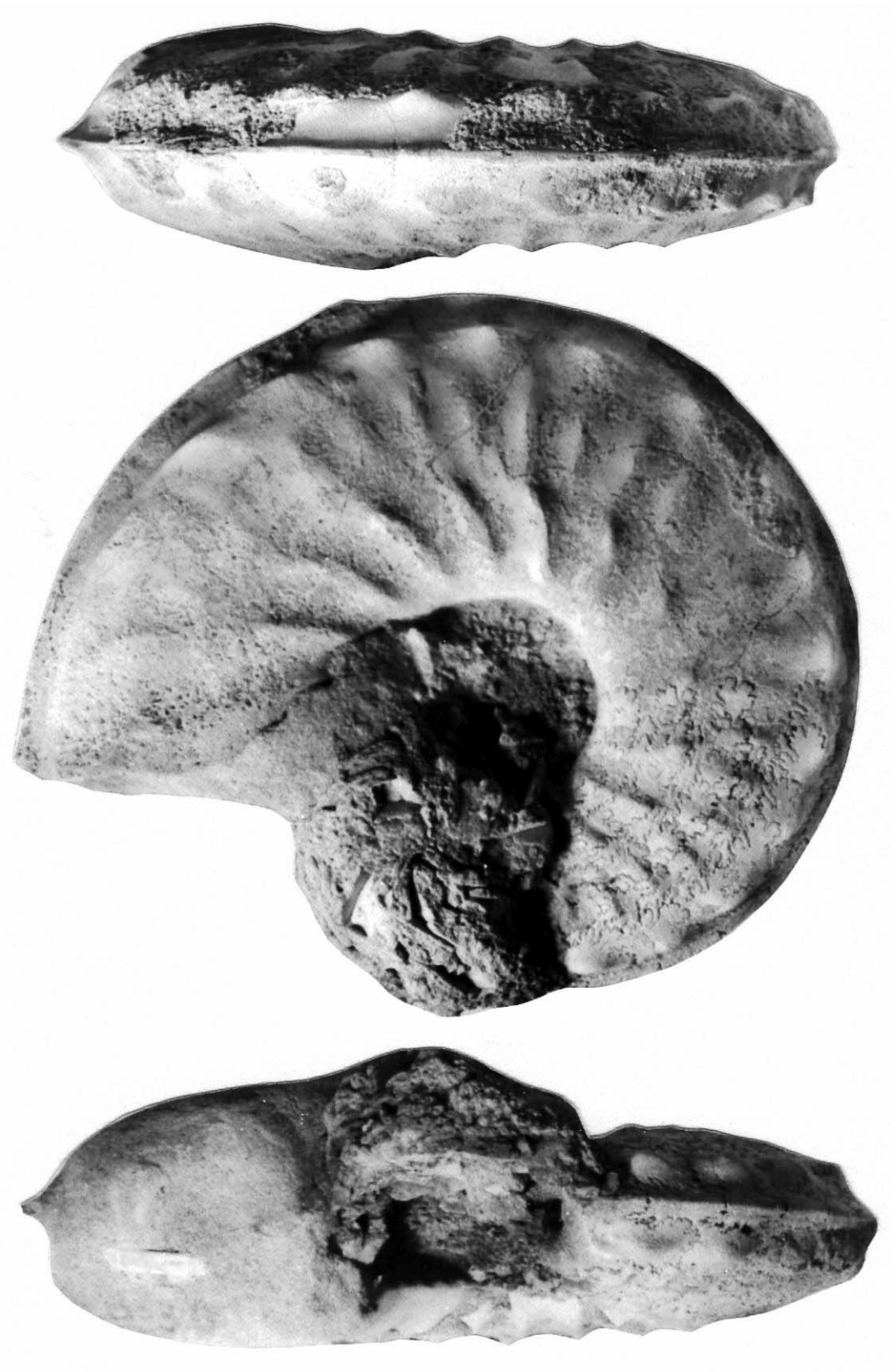

PLATE 12

Schloenbachia varians (J. Sowerby, 1817) *forma intermedia*

1-3 – UW Zl/1473; **4-6** – UW Zl/1466; **7-9** – UW Zl/1665

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1

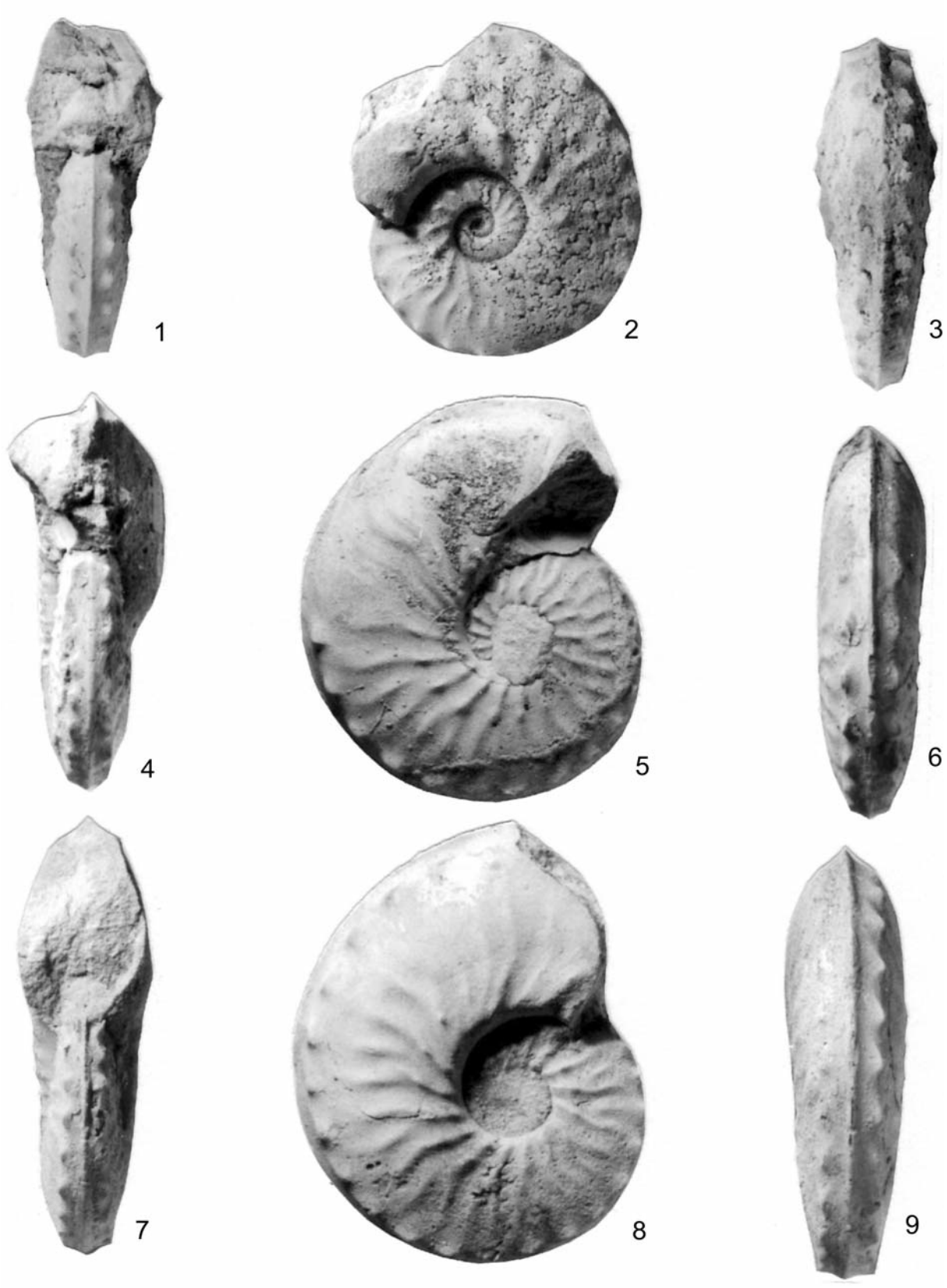

PLATE 13

Schloenbachia varians (J. Sowerby, 1817)

1, 2 – UW Zl/63/1617, passage form between *forma intermedia* and *forma subplana*;
3-5 – UW Zl/63/1262: *forma subplana*

All specimens are from the Lower Cenomanian *Mantelliceras mantelli* Zone, *Sharpeiceras schlueteri* Subzone of bed 30 of the Besakty section, Mangyshlak Mountains, western Kazakhstan.

All figures are ×1