

AMMONITES OF THE GENUS *ACANTHOCERAS* FROM THE CENOMANIAN OF ROUEN, FRANCE

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ABSTRACT. Although *Acanthoceras* only forms a minority of the ammonites from the Craie de Rouen, the locality is important as being the type locality of *Acanthoceras rhotomagense*, the type species of the genus and the most oft-quoted species. This study shows that almost all the *Acanthoceras* from Rouen can be regarded as one variable species which can be conveniently divided into five varieties, only one of which, *A. rhotomagense* var. *clavatum*, is new. *A. rhotomagense* is a widespread species and marks an horizon low in the Middle Cenomanian. *Acanthoceras basseae* sp. nov., also from Rouen, is a rarity.

WELL-PRESERVED fossils from the chalk at Rouen were described as early as 1822 by Cuvier and Brongniart. Casual references in the literature and labels in museums show that it has been much collected from ever since, but there are few descriptions of the section. The best is still that of Bucaille in Lennier (1880) quoted by Jukes-Browne and Hill (1903, p. 253), but there are also brief descriptions by Dollfus and Fortin (1911) and Follet (1943). Jefferies (1963, fig. 10) showed the position of the fossil-rich horizon in relation to the Plenus Zone. The section given here (fig. 1) is based on our own field notes.

The Cenomanian Chalk of Normandy contains several glauconitic horizons, well shown in the coast sections at St. Jouin and Cap de La Hève. These glauconitic developments are probably reflections of local differential uplift, on top of which sedimentation was relatively slow. Some of these glauconitic developments are accompanied by phosphatisation. It is one such bed at Côte St. Catherine in Rouen which has yielded the many fossils commonly known as the fauna of the Rouen Chalk; strictly, the Craie de Rouen includes all the chalk at Rouen below that with *Inoceramus labiatus* and Hébert (1884) even included the beds containing '*Ammonites*' *inflatus* and *Turrilites bergeri* that we should now consider Upper Albian.

As far as we know from our own field work, there is only one horizon at Rouen itself which contains well-preserved, light-brown, phosphatic internal moulds. All museum specimens used in this study are in a similar preservation, or have traces of phosphatic test, and we have ignored the few specimens labelled 'Rouen' in other preservasions. When we refer to 'the Rouen fauna' we mean that from the fossil-rich bed.

SYSTEMATIC DESCRIPTIONS

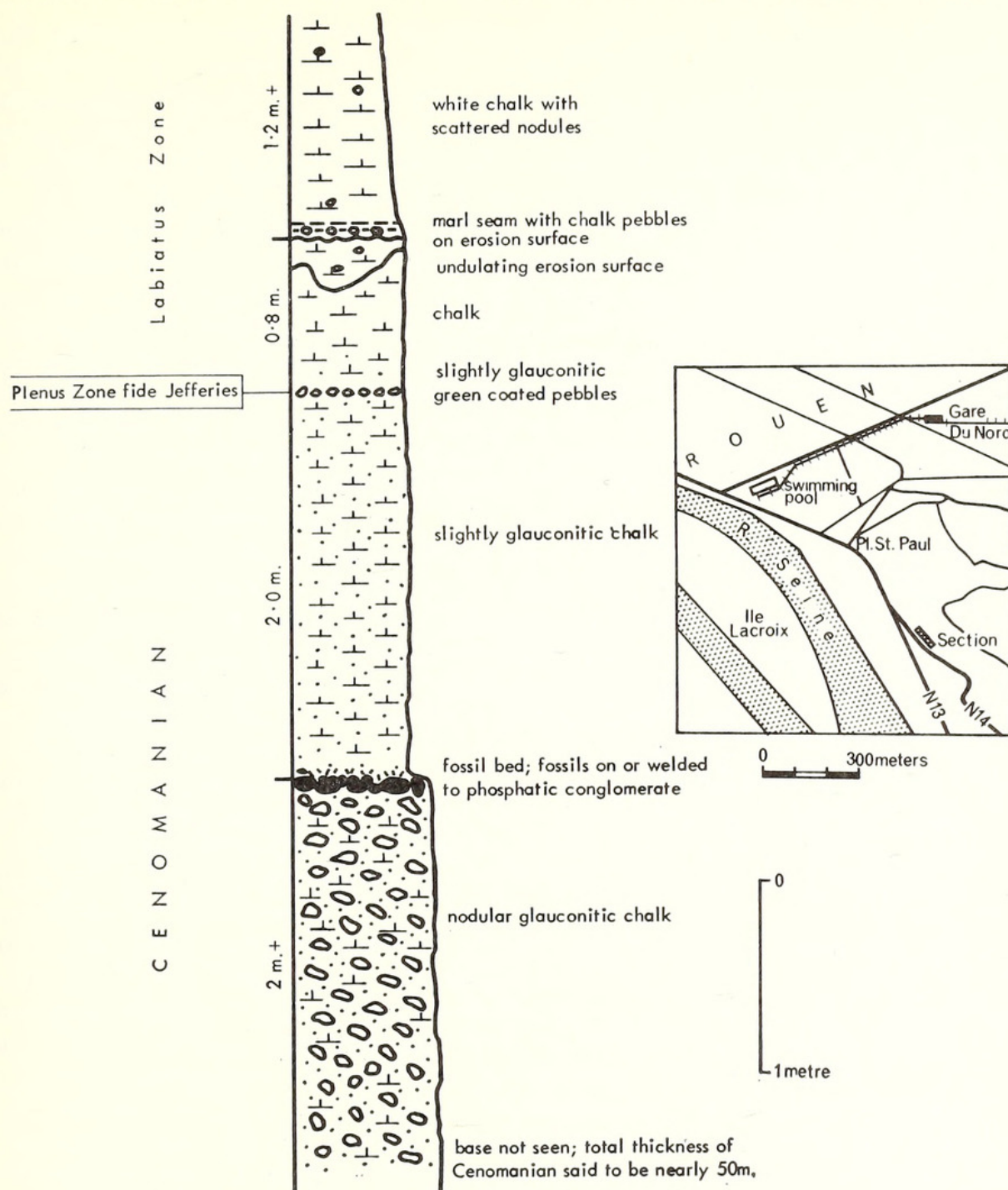
Family ACANTHOCERATIDAE Hyatt 1900

Genus ACANTHOCERAS Neumayr 1875

(= *Metacanthoplites* Hyatt 1900)

Type species. *Ammonites rhotomagensis* Brongniart ex DeFrance MS in Cuvier and Brongniart 1822; designated by De Grossouvre 1894.

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TEXT-FIG. 1. Vertical section showing the stratigraphical position of the fossil-bed of the Craie de Rouen at Côte St. Catherine, Rouen. Sketch-map shows the position of an exposed section.

Generic characters. Decorated ammonites, rather evolute: whorl height normally 6.5–12.5 times as great as the depth of the impressed area, not changing markedly with age but commonly becoming slightly more evolute.

Intercostal whorl section is roughly square sometimes slightly depressed, not changing appreciably during ontogeny. The whorl section through the ribs is markedly angular, commonly on some variant of a square with diagonals cutting the corners; sides may be parallel or diverging slightly towards the umbilicus.

The ribs are strong, generally straight, showing a weak forward projection. Most ribs begin on the umbilical slope, are nearly always strong on the lower part of the sides where they commonly, but by no means invariably, develop a bullate tubercle. Near the top of the side there is a tubercle developed that is the most persistent series in the genus, sometimes developing into great spires; only in one aberrant species, '*A. cornigerum* Crick, are they lost.

Above this upper lateral tubercle is the angular shoulder, on which the ribs show a further forward projection, and nearly terminate at a series of ventro-lateral tubercles, although there is usually a weak connecting rib across the venter between pairs of ventro-lateral tubercles. This connecting rib is sometimes lost in the middle or later stages of ontogeny. The upper lateral and ventro-lateral tubercles may be bullate or clavate or neither. The venter is flat. On the early whorls there is a siphonal tubercle which may persist as strongly as the ventro-lateral tubercles to considerable diameters, but more commonly weakens and disappears before a diameter of 100 mm. is reached.

The above two paragraphs apply to full-length (primary) ribs. In young individuals there are one, or more rarely two, shorter (secondary) ribs intercalated between any two primary ribs. Such ribs begin gently, above the level of the basal lateral tubercles on the primary ribs, and thereafter behave as primary ribs. The persistence of secondary ribs varies greatly from species to species, and in some forms (which might be better classified as *Calycoceras*) lasts throughout the septate stage.

In some species the ribbing weakens slowly during ontogeny, but the very slight amount of change in any features during the ontogeny of the septate portion was even noted by Brongniart (1822).

Acanthoceras is a large genus growing up to a third of a metre or more in diameter. Such large specimens have generally been obtained from the Chalk, and it is not always possible to say from these how much space is occupied by the adult body chamber.

De Grossouvre (1894) in amending and restricting Neumayr's genus, laid stress on the suture line: 'Je réserverai donc le nom générique d'*Acanthoceras* aux formes à lobes et selles large, de forme approximativement rectangulaire, dont le premier lobe latéral présente une fourche terminal nettement accusée, et je prendrai comme type de ce genre *Acanthoceras rhotomagense*.' We would add that the lateral lobe is narrow compared with the first lateral saddle in the middle of which an accessory lobe, nearly half as long as the first lateral lobe, is commonly developed; neither de Grossouvre (1894, fig. 12) nor d'Orbigny (1841, pl. 106, fig. 3) shows this adequately.

All the above description is based on internal moulds, and it should be noted that the shell of *Acanthoceras* is thick (possibly as much as 2 mm. in some large specimens) so that the appearance of an individual with the shell is somewhat different from the mould. On the shell the second-order ribs, for example, begin lower on the sides, and even the first-order ribs are stronger on the umbilical slope than is apparent from the mould. Moreover, the shell possesses decoration not present on the mould: strong striations parallel to the ribbing are common (see Sharpe 1855, pl. 16, fig. 2a). In addition there is sometimes a faint longitudinal striation.

Relations with other genera. Even as restricted by De Grossouvre (1894) *Acanthoceras* at first included many forms which are today separated generically. Indeed, every genus in the family, with the exception of *Mammites* Laube and Bruder, 1886, has been erected

since 1894. Happily, only a few of these newer genera are liable to be confused with *Acanthoceras* s.s.

Mantelliceras Hyatt, 1903; type species *Ammonites mantelli* J. Sowerby; Lower Cenomanian. This genus is the ancestor of *Acanthoceras*, but probably by way of *Calycoceras*. Early writers tended to distinguish *Mantelliceras* by the absence of siphonal tubercles, but this distinction can only be used on juveniles. More distinctive of *Mantelliceras* is the persistence of short ribs, the disappearance of lower ventro-lateral tubercles at diameters of 80 mm. or earlier (in rare individuals it may last longer), and the disappearance of all tuberculation on the adult, maturity usually being reached at much smaller sizes than in *Acanthoceras*; moreover, some species of *Mantelliceras*, including the type, possess mid-lateral tubercles.

Calycoceras Hyatt, 1900; type species *Ammonites navicularis* Mantell; Middle to Upper Cenomanian. *Calycoceras* appears to be derived from *Mantelliceras* early in the Middle Cenomanian by the development of a siphonal tubercle, and by increasing the relative strength of the umbilical ribbing or bullae. *Calycoceras* retains the short ribs and ventral ribbing of *Mantelliceras* but develops (in some species) the angular whorl section of *Acanthoceras*, and like *Acanthoceras* often loses the siphonal tubercles long before the ventro-lateral ones. Hence some *Calycoceras* can only be distinguished with certainty from *Mantelliceras* by strong umbilical bullae, e.g. *Calycoceras cottreaui* (Collignon), *C. nitidum* (Crick). However, there are some species of *Mantelliceras* which also have umbilical bullae in the middle stages, e.g. *Mantelliceras lymense* (Spath) (Pervinquier 1907, pl. 16, fig. 16) that Spath (1926) thought was an Upper Cenomanian *Eucalycoceras*. These distinctions still leave forms whose generic attribution is difficult. Thus *Acanthoceras whitei* Matsumoto from southern India, figured by Kossmat (1897, pl. 1, fig. 1), which retains short ribs to a diameter of nearly 100 mm., and whose ribbing does not weaken on the venter, might be better assigned to *Calycoceras*. In *Acanthoceras* gr. *jukes-brownei* (Spath) short ribs are retained to a diameter of more than 300 mm.

Euomphaloceras Spath, 1923; type species *Ammonites euomphalus* Sharpe, 1855; Middle and Upper Cenomanian. *Euomphaloceras* develops from *Acanthoceras* in the Middle Cenomanian by the intercalation of extra ribs or extra tubercles on the venter, e.g. '*Acanthoceras*' *inermis* Pervinquier (= *A. evolutum* Spath). We figure examples of these transitional forms from Rouen (Pl. 92, fig. 4; Pl. 93, fig. 1).

Protacanthoceras Spath, 1923; type species *Ammonites Bunburianus* Sharpe; Middle and Upper Cenomanian. The stratigraphically persistent distinctive feature of this tiny genus, is the triple row of equal-sized clavae, rather closely spaced on the venter. On the adult body chamber of some species these tubercles fuse into smooth chevron-ribs across the venter. The early species (where the genus is diverging from *Acanthoceras*) grade into flat-sided spinose *Acanthoceras*. As has been remarked by Thomel (Porthault *et al.* 1966) *Protacanthoceras* has also been misused for species such as *Eucalycoceras harpax* (Stoliczka) which have strong ribbing on the sides, and grow to a much greater size.

Plesiacanthoceras Haas, 1964 (= *Paracanthoceras* Haas, 1963, non Furon, 1935); type species *Metoicoceras Wyomingensis* Reagan 1924. We agree with Matsumoto and Obata (1966) in regarding this as a synonym of *Acanthoceras*. Haas gave two distinctions: (i) the ventral tubercles 'are, even at an early stage, very inconspicuous and strongly clavate and then assume the aspect of an intermittent keel which soon fades away'. This

could be part of a description of the holotype of *Acanthoceras rhotomagense*. (ii) 'Also the ribs persist into maturity in *A. rhotomagense*, in contrast to the present form.' The abundant European and African material shows that the persistence or disappearance of ribs may be no more than a sub-specific difference. Moreover, in *Acanthoceras wyomingense* (Reagan) itself low, broad ribbing persists at least to a diameter of 220 mm.

Acanthoceras rhotomagense (Brongniart)

The *Acanthoceras rhotomagense* population from Rouen can be divided into 5 morphological varieties as described below. The general features of the population are: *Acanthoceras* with between 15 and 30 ribs per whorl; short ribs are only present in early growth-stages; the siphonal tubercle is lost early in development. Compressed individuals have weak ribs and tubercles, but as the degree of inflation increases, the tuberculation and ribbing become progressively stronger.

Acanthoceras rhotomagense (Brongniart 1822) forma typica

Plate 88, figs. 1–5; Plate 89, fig. 1; text-figs. 2, 6b, 7

- 1822 *Ammonites Rhotomagensis* Brongniart, p. 606, pl. 6, fig. 2.
 ?1867 *Ammonites Rothomagensis* Lamk; Guéranger pars; pl. 2, figs. 2 and 6 only.
 1912 *Acanthoceras rhotomagensis* Defrance in Brongniart; Douvillé, fiche 238.
 1956 *Acanthoceras chasca* Benavides-Cáceres, pp. 466–7, pl. 53, figs. 1–4.

Lectotype. Selected by Douvillé (1912); the specimen figured by Brongniart in Cuvier and Brongniart 1822, pl. 6, fig. 2, now in the Sorbonne, Paris.

Diagnosis. *Acanthoceras* with flat sides, barely depressed to barely compressed whorl sections, and 21–3 ribs per whorl. The short ribs are lost at an early growth-stage (normally by about 40 mm. diameter). There are moderately strong umbilical bullae,

EXPLANATION OF PLATE 88

All figures are of natural size. Specimens are coated with ammonium chloride. All ammonites are from the fossil-bed of the Craie de Rouen.

Figs. 1–5. *Acanthoceras rhotomagense* Brongniart. 1a, 1b, Side and ventral view of R8. 2a, 2b, Ventral and side view of S14. 3a, 3b, 3c, Ventral, front and side views of a plaster-cast of the lectotype in the Sorbonne; cast kindly provided by Mme É. Basse de Ménorval. 4a, 4b, Side and front views of a juvenile, A635f. 5, Original figures of the lectotype by Brongniart in Cuvier and Brongniart, 1822, pl. 6, fig. 2.

Figs. 6a, b. *Acanthoceras rhotomagense* intermediate between var. *subflexuosum* Spath and var. *clavatum* var. nov. Front and side views of S11.

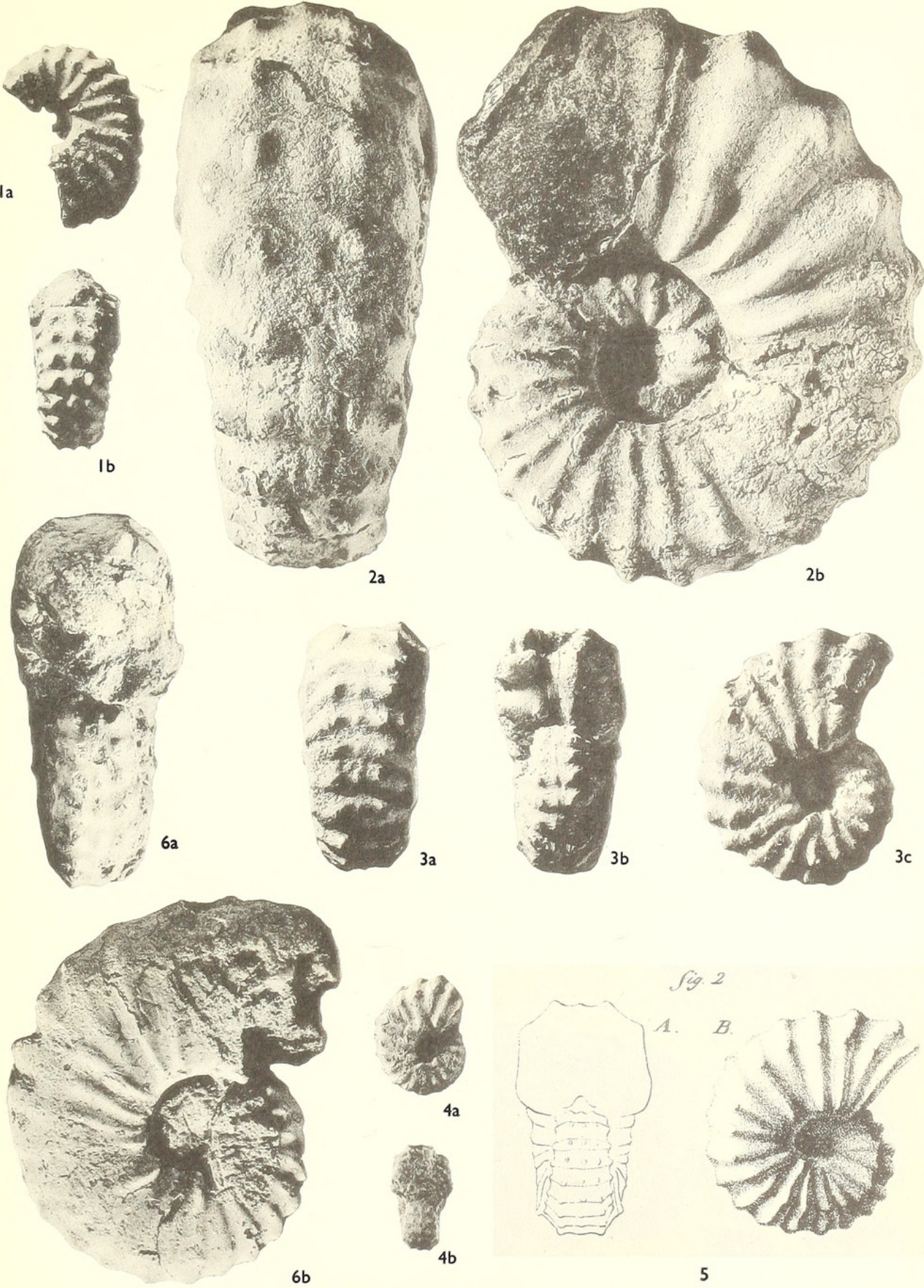
EXPLANATION OF PLATE 89

All figures are of natural size except fig. 3c. Specimens are coated with ammonium chloride.

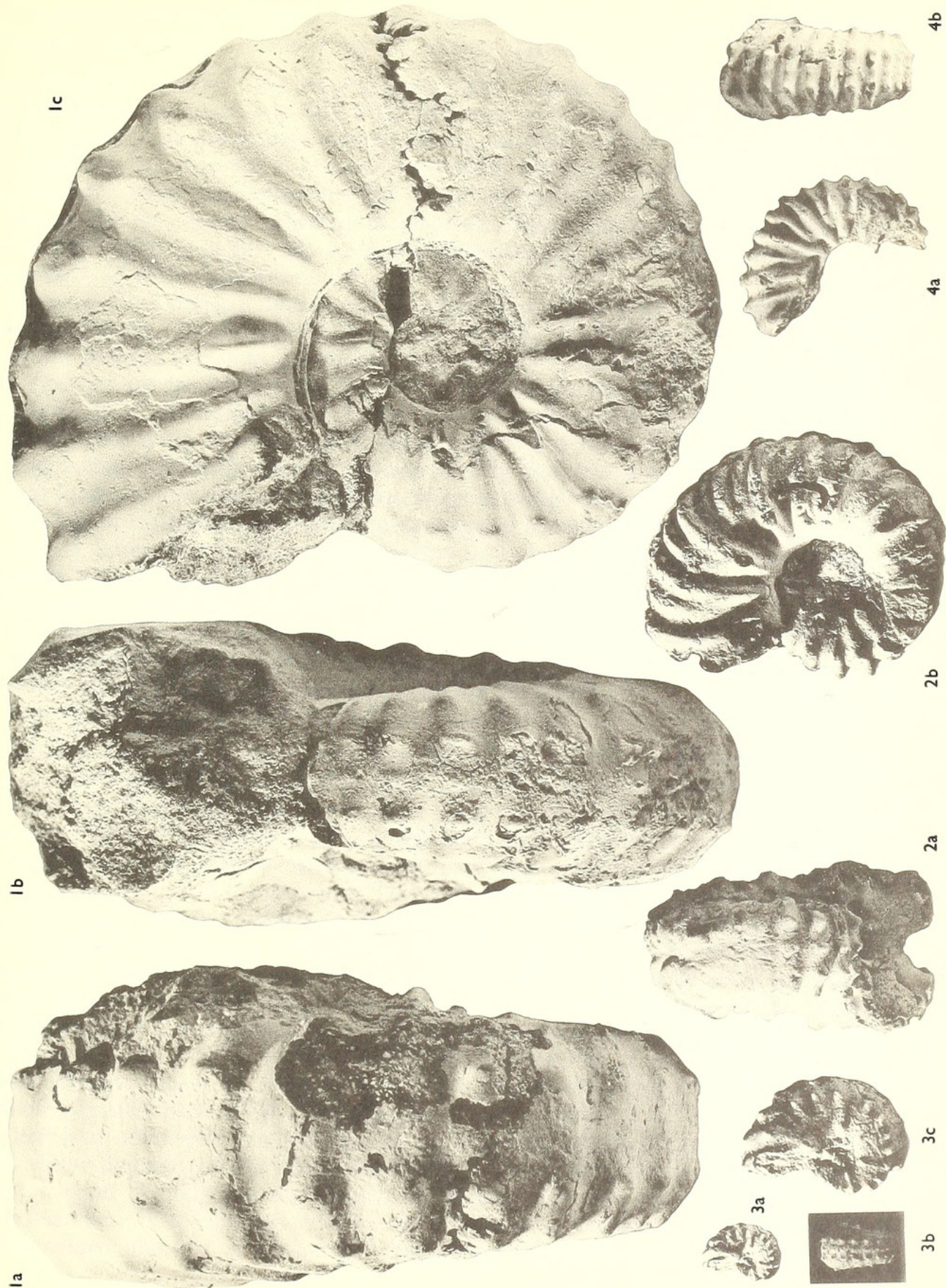
Figs. 1a–c. *Acanthoceras rhotomagense* (Brongniart); from quarry on Chard side of boundary fence, $\frac{1}{2}$ mile north of Tytherleigh, near Chardstock, Devon; presumably from the Middle Cenomanian basement bed of the Chalk; ventral, front and side views of C 73088.

Figs. 2a, b. *Acanthoceras rhotomagense* var. *sussexense* (Mantell); from fossil-bed of the Craie de Rouen; individual showing change from normal to pathological condition; front and side views of C 74797.

Figs. 3a–e. Spinose *Calycoceras* with an *Acanthoceras* nucleus; from fossil-bed of the Craie de Rouen. a, b, Side and ventral views. c, Side view $\times 2$. d, e, Side and ventral views, all of S9.



KENNEDY and HANCOCK, *Acanthoceras* from Rouen



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round to clavate lower ventro-lateral tubercles, clavate upper ventro-lateral and siphonal tubercles. The siphonal tubercles are lost early in ontogeny.

Description of lectotype. The lectotype is a small, wholly septate, phosphatic internal mould. The umbilicus of one side of the specimen is filled by phosphatised sediment.

The specimen is moderately evolute, about two-fifths of the previous whorl being covered. The whorl section is barely depressed; in intercostal section the sides are flat, the shoulders round, and the venter flat. The costal section is polygonal, approximately a square with the corners truncated, the flat sides slightly convergent; the shoulders are flat and the venter is slightly depressed. The umbilicus is small, quite deep, with a round, undercut wall and a round shoulder.

There are 21–2 ribs at a diameter of 38.5 mm., alternating more or less regularly long and short. Each long rib arises at the umbilical seam, strengthens across the umbilical wall and develops an elongate umbilical bulla on the lowest part of the side. On the sides the ribs are moderately strong, becoming increasingly prominent as the diameter increases. They are straight, and slightly narrower than the interspaces. All bear a well-marked lower ventro-lateral tubercle which is slightly bullate. This is connected by a strong, round, forwardly directed rib to a slightly clavate and stronger upper ventro-lateral tubercle. The ribs are slightly depressed between these two tubercles.

The upper ventro-lateral tubercles are connected across the venter by a broad, low, round rib, lower than the upper ventro-lateral tubercles, and bearing a clavate siphonal tubercle. This siphonal tubercle is weaker than the upper ventro-lateral tubercles even at the earliest stage visible (approx. 15 mm.).

The shorter ribs arise gently some way up the sides and become equal to the long ribs at the shoulder and across the venter. Some are tenuously connected to the umbilical tubercles of the long ribs. The last three ribs are all long.

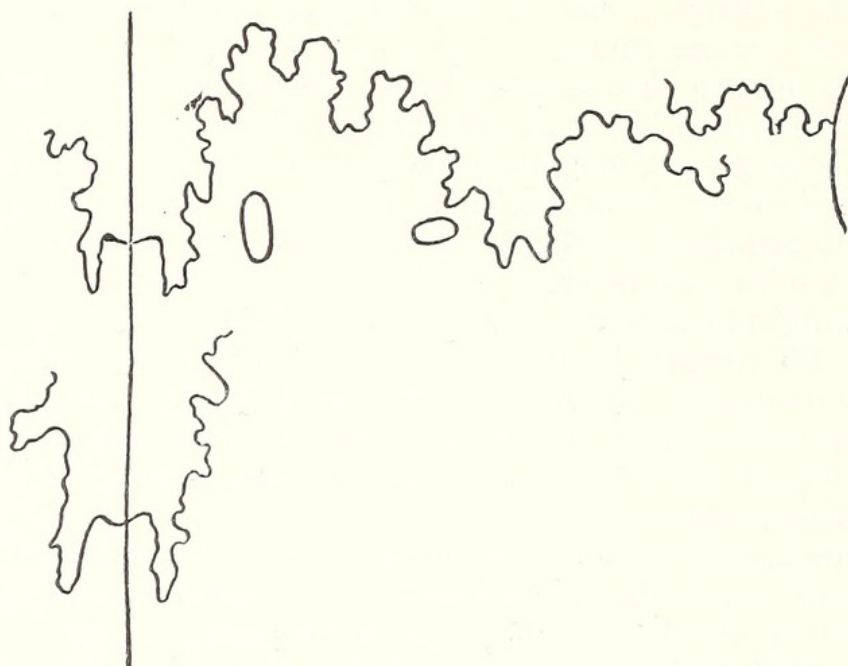
The suture is simple and of normal *Acanthoceras* type.

Discussion. This form is an intermediate between *A. rhotomagense* var. *subflexuosum* and *A. rhotomagense* var. *sussexense*. If it had not been the type form of the genus we should not have felt it necessary to give a name to it; its characters are not sufficiently distinctive for it to be easy to assign a specimen to it. It is not even a common form like *A. rhotomagense* var. *sussexense*: indeed, we have been unable to find anywhere another specimen identical with the lectotype. This is the more disturbing when one recalls that the lectotype is relatively small (less than 40 mm. in diameter) so that the ontogeny may be somewhat different from what we believe. However, we have seen sufficient closely comparable material to be certain that: (i) This is a variety which loses its shorter ribbing at a comparatively early stage: the last three ribs on the type all start at the umbilical edge, but in other specimens short ribs can occur later than this—to diameters of 50–60 mm. (ii) This is not the variety which gives rise to the Mid-Cenomanian *Euomphaloceras*: these all seem to be offshoots of *A. rhotomagense* var. *sussexense* whatever detailed pattern the extra decoration on the venter takes.

There is an adult specimen in the Rouen museum (uncatalogued but labelled 7 on one side) with a diameter of 375 mm., although the aperture is missing and there is only a quarter whorl of body chamber (which has begun to become more evolute). On the body chamber, which begins at 305 mm., the angular whorl shape seen on phragmocones is maintained; the two ventro-lateral tubercles are joined by a rib of about the same

height, whilst pairs of upper ventro-lateral tubercles are set only 27 mm. apart across the ventral depression. On the septate portion the ventro-lateral tubercles are not clavate, and the umbilical bullae are no more than abrupt terminations of the bottom end of the ribs. The ribbing is directed slightly forward.

We figure an adult specimen from England (WJK 2466) which is very close to *A. rhotomagense* although slightly transitional to *A. rhotomagense* var. *clavatum* in that the ventro-lateral tubercles on the late septate portion are clavate (text-figs. 6b, 7). The body chamber occupies two-thirds of the last whorl, and the aperture is simple, with



TEXT-FIG. 2. Suture line of the lectotype of *Acanthoceras rhotomagense* (Brongniart).
After Douvillé 1912; magnification not stated.

a gently sinuous margin. The tubercles weaken on the body chamber, as strong, sharp ribs develop which pass right across the venter. This body chamber decoration is similar in many species of *Acanthoceras*, making it difficult to identify isolated body chambers.

Both Mantell's and Brongniart's works were published in 1822. We have accepted the general view that Brongniart's *Ammonites rhotomagensis* has priority over Mantell's *Ammonites sussexiensis* (see Sharpe 1853-6, p. 34). This view is not invalidated by the fact that Brongniart had already seen Mantell's plates whilst he was writing his own work; and Mrs. Mantell's execrable figures of this species could never have given Brongniart the idea he was describing a closely allied form.

A. rhotomagense is distinguished from *A. r.* var. *sussexiense* by the more compressed whorl section, weaker umbilical and lower ventro-lateral tubercles, giving an impression of longer ribs; the siphonal tubercle is also lost earlier.

It is distinguished from *A. r.* var. *subflexuosum* by the stronger tuberculation, more widely spaced ribs, and commonly by the narrower, flat venter.

Acanthoceras adkinsi Stephenson (1953, pp. 200-1, pl. 47, figs. 3, 4) is very close to *A. rhotomagense* differing with certainty only in the maintenance of short ribs to a

diameter of at least 74 mm. The slightly greater whorl compression of *A. adkinsi* cannot itself be regarded as even a subspecific difference.

Acanthoceras stephensoni Adkins (1928, p. 246, pl. 31, figs. 1, 2) which Matsumoto and Obata (1966) say 'is closely allied to the broadly ribbed variety of *A. rhotomagense*', is distinguished by flat, unribbed flanks.

Acanthoceras rhotomagense var. *subflexuosum* Spath 1923

Plate 90, figs. 1-4; text-fig. 8

- 1826 *Ammonites rhotomagensis* DeFrance; J. de C. Sowerby v. 6, p. 25, pl. 515, fig. 1.
- 1867 *Ammonites Rothomagensis* Lamk; Guéranger pars, pl. 2, figs. 1 and 5 only.
- 1923 *Acanthoceras subflexuosum* sp. nov.; Spath, p. 144.
- ?1940 *Acanthoceras* cf. *subflexuosum* Spath; Fabre, p. 233.
- 1951 *Acanthoceras subflexuosum* Spath; Wright and Wright, p. 28.

Holotype. BM 43983a, from the Lower Chalk of Sussex (figured by J. de C. Sowerby 1826, v. 6, pl. 515, upper figure), original designation by Spath 1923, p. 144 n. 3.

Diagnosis. This is a form of *Acanthoceras rhotomagense* with a similar degree of compression to *A. rhotomagense* but with a broader, faintly round, venter. The tuberculation, other than some umbilical bullae, is weaker. The ribbing is slightly denser (typically 25-9 ribs per whorl), and is distinctly, albeit weakly, flexuous.

Description of holotype. The holotype is a small, slightly distorted and abraded, limonite-coated, composite internal mould in grey chalk. Most of the inner whorls and all the ornament of one side have been destroyed. The suture is not visible.

The holotype is moderately evolute, about a quarter of the previous whorl being covered. The whorl section is compressed; in intercostal section the sides are flat and almost parallel, the ventro-lateral shoulders broadly round and the venter flat. The costal section is compressed-polygonal, with the greatest breadth at the umbilical bullae. The umbilicus is small, moderately deep, with a steep umbilical wall and round umbilical shoulder. There are 28 ribs at a diameter of 58 mm., alternating more or less regularly long and short. The long ribs appear to arise at the umbilical seam, strengthen across the umbilical wall, and develop into elongate umbilical bullae just outside the umbilical shoulder. On the sides the ribs are strong, broad, and round, as wide or slightly narrower than the interspaces. The ribs are gently flexed, each passing slightly forwards across the lower part of the sides, and then backwards to a very weak bullate lower ventro-lateral tubercle, then forwards again to a weak clavate upper ventro-lateral tubercle. The venter is rather narrow, with a row of weak clavate siphonal tubercles, connected to the similar upper ventro-lateral tubercles by low, broad, round ribs, separated by narrow interspaces. The shorter intercalated ribs extend across the upper two-thirds of the flank and the venter.

Discussion. This name was introduced by Spath without any description. The holotype is both a juvenile and an extreme variant of this variety, having unusually strong ribs and being unusually compressed, although this latter character may be very slightly exaggerated by crushing.

The ribbing in this variety is weak, but that in *Acanthoceras flexuosum* Crick is even weaker. Moreover, the ribbing on Crick's species has a rather strong forward

TABLE 1. Measurements of *Acanthoceras*: all specimens are from the fossil bed in the Craie de Rouen except the holotype of *A. rhotomagense* var. *subflexuosum*, the lectotypes of *A. r.* var. *sussexiensis* and *A. r.* var. *confusum*, the paralectotype of *A. r.* var. *confusum*, C73088, and WJK 2466.

Collection key: S = Sorbonne; A = École des Mines, Paris; C (or number without prefix) = British Museum (Natural History); GSM = Institute of Geological Sciences, London; CC = J. M. Hancock collection; R or WJK = W. J. Kennedy collection.

Measurements of diameter, whorl height, and whorl width have been made between ribs; equivalent measurements across ribs are obviously greater. When ribbing and tubercles are taken into account, whorl sections often appear more compressed than intercostal measurements of whorl height and whorl width would indicate. a. = approximately.

Specimen	Diameter	Whorl height	Whorl width	Width of umbilicus	Number of ribs on last whorl	Number of primaries	Number of secondaries
<i>Acanthoceras rhotomagense</i> forma typica							
Holotype (Sorbonne)	37.8	17	19.6	8.3	21	11	10
S13	60.5	27	27.8	16.6	19	13	6
S14	87	37.3	39 a.	15.8	22	15	7
S31	85.5	(34.5)	(37.8)	28	18 a.	14 a.	4 a.
S18	39	17.4	20	11	22	10	12
A636	32	16	18 a.	8.5	23	11 a.	12 a.
A646	74.5	32	33 a.	21	22	18 a.	4 a.
R6		24	26				
Rouen Mus. adult	375 a.	132			23	23	0
C73088	109	42.5		36	25	21	4
<i>Acanthoceras rhotomagense</i> intermediate between var. <i>clavatum</i> and <i>rhotomagense</i> s.s.							
S24	52.6	20.7	21.8	15.6	21	13	8
S25	85.6	35.9	36.7	25.3	23	17 a.	6 a.
A645	48.0	20.3	21.5	13.8 a.	22-3 a.	11 a.	11 a.
A649	80.0	32.5	35.9	25.5	17	13	4
A659	62.9	25.7	27 a.	19.8	18	14	4
WJK 2466	270	90	95	100	20	20	0
<i>Acanthoceras rhotomagense</i> var. <i>clavatum</i>							
Holotype							
A660	90.8	36.7	38.3	27.7	22 a.	17 a.	5 a.
S15		35.2	34.5				
S21	60.8	26.6	23.9	15.9	20-1	9-10 a.	
S22		29.6	29.1	19.2	20 a.		
S23	74.3	29.8	29.6	21.7	20 a.		
<i>Acanthoceras rhotomagense</i> var. <i>subflexuosum</i>							
Holotype							
43983a	59.0	26.2	23.0	15.4	28-9	14 a.	14 a.
S3	114.5	45.2	49.5 a.	34.4	27		
S4	107	44.0	48.4	33.4	26	22	4
S10B	14	6.2	7		17-18 a.		
A642	59.4	26.6	28.5	16 a.	29-30	19	10-11
A651	54.7	24.9	26	14.8	27	12-14	13-15
A663	109.6	45.7	46.5	32.9	30	20-2	8-10
C74792	18.4	9.7	9	3.5	19		
<i>Acanthoceras rhotomagense</i> aff. var. <i>sussexiensis-subflexuosum</i>							
A682	80	32.5	41 a.	23.7	27	17	10

Specimen	Diameter	Whorl height	Whorl width	Width of umbilicus	Number of ribs on last whorl	Number of primaries	Number of secondaries
<i>Acanthoceras rhotomagense</i> var. <i>subflexuosum</i> transitional to <i>A. r.</i> var. <i>clavatum</i>							
S11	59.6	25.1	24.3 a.	15.0	24		
<i>Acanthoceras rhotomagense</i> var. <i>sussexiensis</i>							
Lectotype							
BM 5691	145	54.7	62	52.2	23-4	23-4	0
C1030	200	74.8	69.5	72	20	20	0
S1	98.7	36.3	47.5	31.2	24 a.		
S10A	26.5	11.2	13.8	7	17 a.		
S20	60.6	26	29.6	18.7	25	15	10
S26	49	20.6	26.5	15.9	19	16	3
S27	97.6	36	49.8		25		
S28	18.8	8.7	10.7	4.6	18	8	10
S29	26.3	10.4	14.3	7.5 a.	18		
S33	45.2	19.1	23.7	12.6	20 a.	11 a.	9 a.
A635	19.6	8.2	10.5	4.8	17	8	9
A654	92	36.3	43½ a.	36	23	22	1
A655	115	45	58	39.5	25	13-15	10-12
R3		18.6	21.8				
R11		42	50				
CC710	47	19	22.8	14.6	19	14	5
CC711		23.6	26.6				
<i>Acanthoceras rhotomagense</i> aff. var. <i>sussexiensis</i>							
C74799	27	12.7	15	7.7	15	12	3
A644	47	20	23 a.	14.8	15	10 a.	5 a.
A674	36.8	14.9		11.2	16	9	7
<i>Acanthoceras rhotomagense</i> var. <i>confusum</i>							
Lectotype							
Guéranger, pl. 3, fig. 1					20	19 or 20	0 or 1
Paralectotype							
Guéranger, pl. 2, fig. 4	(70) assuming figures	(26.5) × 1		(23)	20	20?	0?
S8	90.5	34	43.5	26.8	18	14 a.	4 a.
S10D	14.2	5.3	7.9	3.2	15	8	7
S17	36	14.3	20.6	10	18 a.	13 a.	5 a.
A635d	20.3	8	12.8 a.	4.9	17	9 a.	7 a.
A637	28.1	12	16.2	7.6	16	12	4
A647	61.4	24	33½ a.	19.3	18	11	7
A653	124	51.5	68 a.	48	18	18	0
C74791	66	28	30	22	21	15	6
Transitions between <i>Acanthoceras rhotomagense</i> var. <i>clavatum</i> and <i>Acanthoceras adkinsi</i>							
S19	60	28.2	26.6	13.7	25	13	12
A650	54.2	24.3		14.0	29	12	17
CC712	51.4	24.5	22 a.	13 a.	29 a.		
<i>Acanthoceras basseae</i>							
Holotype							
S5	70.0	24.8	27.5	16.3	21	14-15	6-7
S16		21.5	24.1				
A684	49.4	21.4 a.	23.5 a.	15.3	18 a.		

sweep, and smaller but sharper lower ventro-lateral tubercles (although the sharpness may well be because the shell is preserved). *A. flexuosum* at the least is a closely allied species.

Acanthoceras adkinsi Stephenson (1953, pl. 47, figs. 3, 4) apparently belongs to the *Acanthoceras rhotomagense* group; it differs from *A. rhotomagense* var. *subflexuosum* in having fewer ribs (23 instead of 25–9); BMNH C74794 from Rouen appears to be an intermediate.

Acanthoceras rhotomagense var. *sussexiensis* (Mantell 1822)

Plate 89, fig. 2; Plate 91, figs. 1–2; Plate 92, figs. 1–2; text-figs. 3, 4, 5, 6a

1822 *Ammonites Sussexiensis* Mantell, pp. 114–15, pl. 20, fig. 2.

1854 *Ammonites Rhotomagensis* DeFrance; Sharpe, pp. 33–4, pl. 16, figs. 1a–c, 3a, b (figs. 2a, b transitional to *A. r. rhotomagense*).

EXPLANATION OF PLATE 90

All figures are of natural size except fig. 3b; all specimens are coated with ammonium chloride.

Figs. 1a–c. *Acanthoceras rhotomagense* var. *subflexuosum* Spath; from Lower Chalk of Lewes, Sussex. Side, front, and ventral views of the holotype 43983a.

Figs. 2a, b. *Acanthoceras rhotomagense* aff. var. *subflexuosum* Spath; unusually inflated juvenile from the fossil-bed of the Craie de Rouen. Front and side views of A635e.

Figs. 3a–c. *Acanthoceras rhotomagense* var. *subflexuosum* Spath; juvenile from the fossil-bed of the Craie de Rouen. a, c, Front and side views. b, Side view $\times 2$, of S10B.

Figs. 4a, b. *Acanthoceras rhotomagense* var. *subflexuosum* Spath; from the fossil-bed of the Craie de Rouen. Side and front views of A663.

EXPLANATION OF PLATE 91

All figures are of natural size. Specimens are coated with ammonium chloride.

Figs. 1a, b. *Acanthoceras rhotomagense* var. *sussexiensis* (Mantell); from the Lower Chalk of Hamsey, Sussex. Side and front views of the lectotype, BM 5691.

Figs. 2a, b. *Acanthoceras rhotomagense* var. *sussexiensis* (Mantell); from the fossil-bed of the Craie de Rouen. Side and front views of A635a.

Fig. 3. *Acanthoceras* aff. *rhotomagense* (Brongniart) transitional to a spinose *Calycoceras*; from the fossil-bed of the Craie de Rouen. Side view of S18 (front view in Pl. 97, fig. 3).

EXPLANATION OF PLATE 92

All figures are of natural size. Specimens are coated with ammonium chloride. All from the fossil-bed of the Craie de Rouen.

Figs. 1a, b. *Acanthoceras rhotomagense* var. *sussexiensis* (Mantell); Side and front views of A654; note slight asymmetry in the position of the siphonal tubercle in this individual.

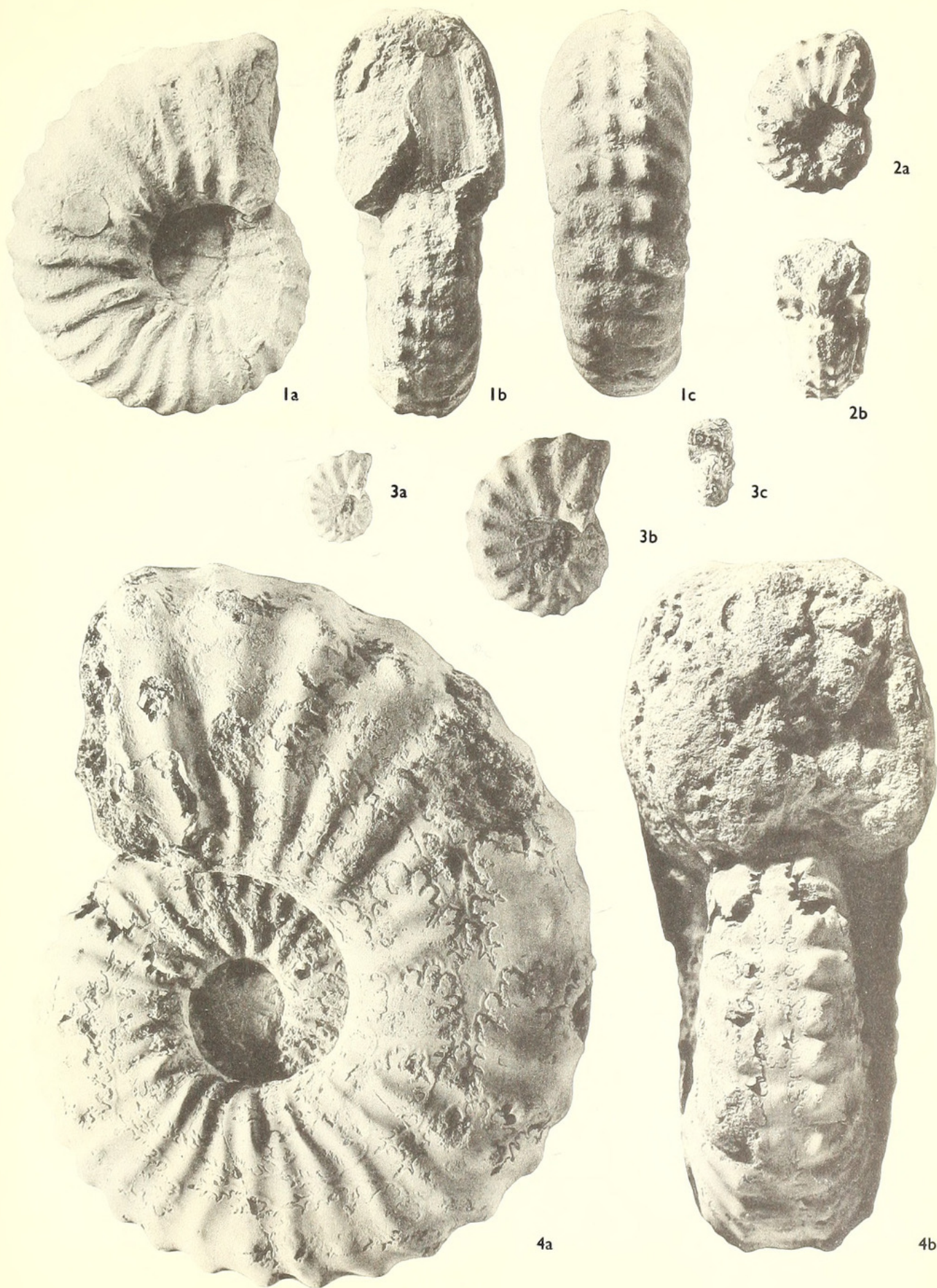
Figs. 2a, b. *Acanthoceras rhotomagense* var. *sussexiensis* (Mantell); Side and front views of a juvenile, S28.

Figs. 3a, b. *Acanthoceras* aff. *rhotomagense* var. *sussexiensis* (Mantell). Ventral and side views of A674; note the narrow venter, relatively compressed whorl, and low rib density.

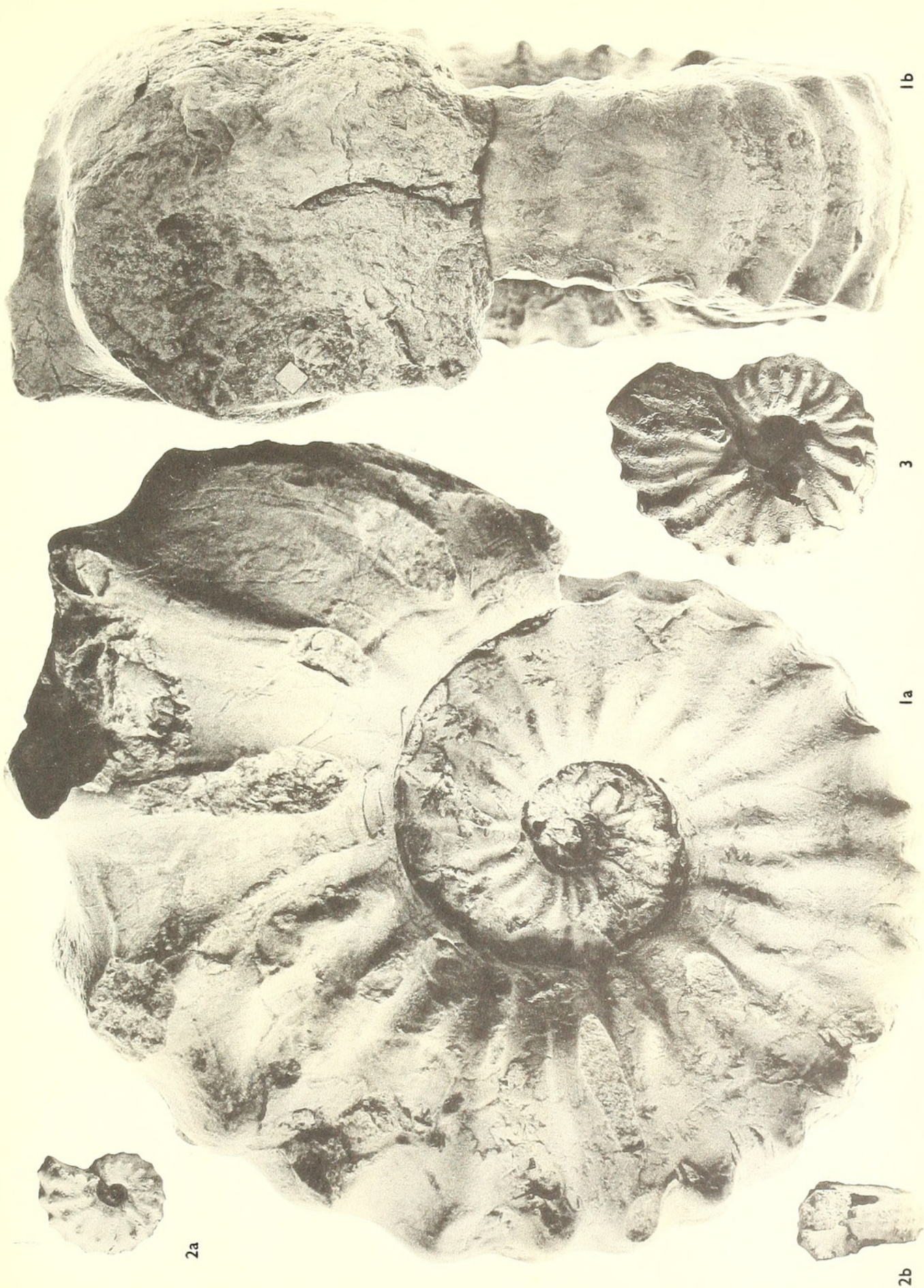
Figs. 4a, b, c. *Euomphaloceras* sp. close to *Acanthoceras rhotomagense* var. *sussexiensis* (Mantell); Front, side, and ventral views of S6; note the rounded whorl-section and the intercalation of extra ventral tubercles.

Figs. 5a, b. An intermediate between *Calycoceras* and *Acanthoceras*. Side and front views of C74795.

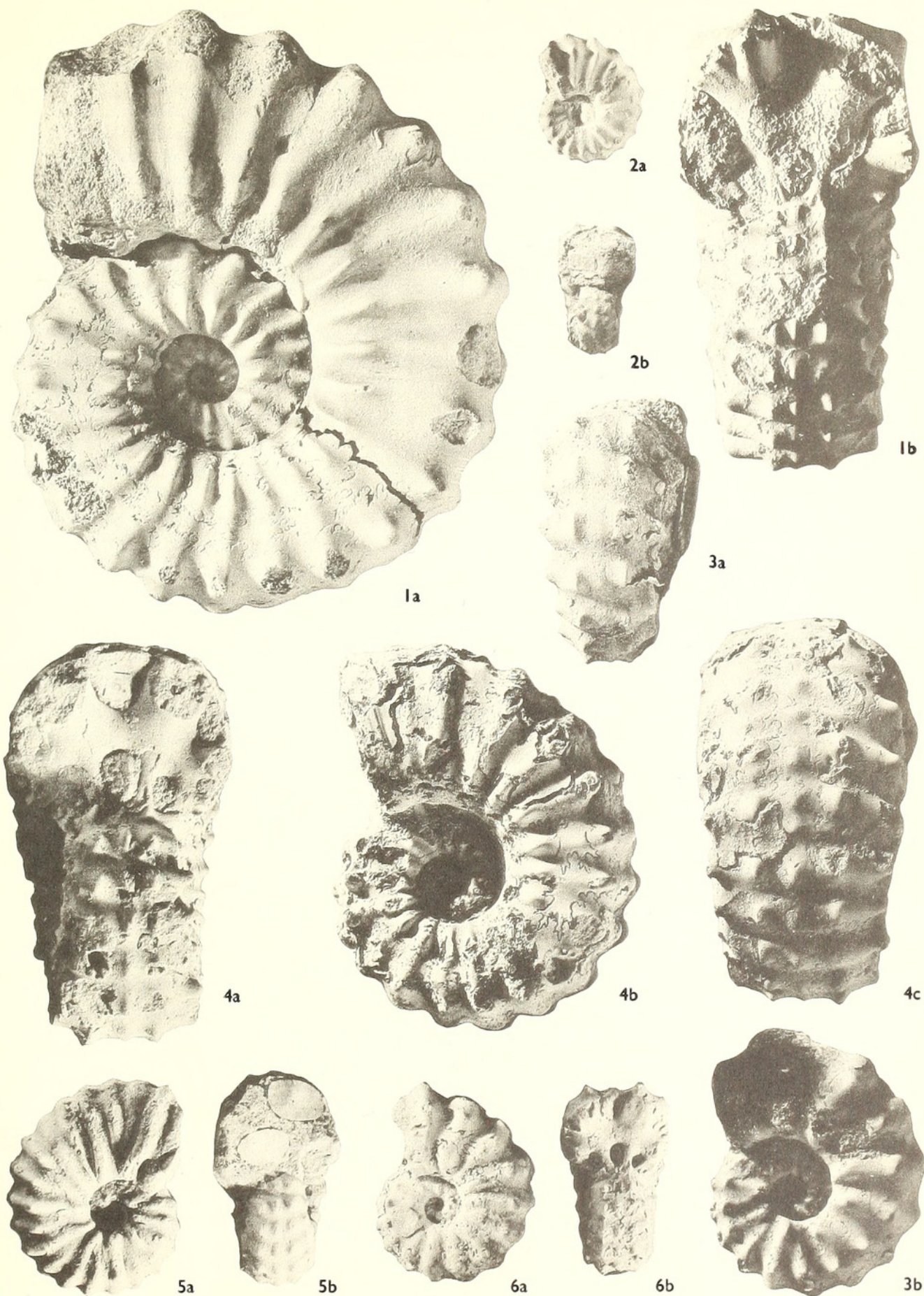
Figs. 6a, b. *Acanthoceras* aff. *rhotomagense* var. *sussexiensis* (Mantell). Side and front views of C74799, paralectotype of *Acanthoceras hippocastanum* (J. de C. Sowerby); note low rib density combined with relatively narrow venter.



KENNEDY and HANCOCK, *Acanthoceras* from Rouen



KENNEDY and HANCOCK, *Acanthoceras* from Rouen



KENNEDY and HANCOCK, *Acanthoceras* from Rouen

- non 1854 *Ammonites Sussexiensis* Mantell; Sharpe, p. 34, pl. 15, fig. 1 (= *Euomphaloceras inermis* (Pervinquière)).
- 1863 *Ammonites rhotomagensis* Brongniart; Pictet pars; pl. 2, figs. 1a-e only.
- 1878 *Acanthoceras rhotomagensis* Brongniart; Bayle, pl. 63, figs. 1-3; ?4-5.
- non 1923 *Acanthoceras sussexiense*; Spath, p. 144 n.
- 1926a *Acanthoceras vectense* Spath, p. 82.
- 1931 *Acanthoceras hippocastanum* Sow; Collignon, pl. 4, fig. 1.
- 1951 *Acanthoceras vectense* Spath; Wright and Wright, p. 28.
- 1951 *Acanthoceras sussexiense* (Mantell); Wright and Wright, p. 28.
- 1963 *Acanthoceras mirialampiense* Wright, p. 606, pl. 84, fig. 3; pl. 85, fig. 1.

Lectotype (here selected). BM 5691 from the Lower Chalk of Hamsey, Sussex, bearing Mantell's original green label, 'xx, 2'. This is possibly the original of Mantell 1822, pl. xx, fig. 2. Two smaller specimens (BM C.73637, 5690) in the Mantell collection labelled *Ammonites sussexiensis* belong elsewhere.

Diagnosis. Form of *Acanthoceras rhotomagensis* characterized by a more depressed quadrate whorl section than *A. rhotomagensis* itself, with strong, dense, rounded, slightly rursiradiate instead of prorsiradiate ribs, all of which are long in the middle and later growth stages. There are strong umbilical bullae and lower and upper ventro-lateral tubercles, the latter two rows fusing in the adult, and a small siphonal tubercle weakening in the middle and later stages.

Description of lectotype. This is a large, very well-preserved if slightly distorted, composite internal mould in grey chalk, with a rusty limonitic coat. Just under half the later whorl is body chamber, where the specimen develops pathological ribbing.

The coiling is evolute, about a fifth or a sixth of the previous whorl being covered. The whorl section is depressed, with the greatest breadth at the umbilical bullae; rounded quadrangular in intercostal section, with flat sides, broadly round shoulders, and a flat venter; costal section trapezoidal-polygonal. The umbilicus is broad and moderately deep, the umbilical wall round and undercut, and the shoulder round. There are 23 ribs per whorl at 77 mm. diameter, 25 at 134 mm., and 24 at 150 mm. The specimen is pathological beyond 130 mm.

All the visible ribs are long; each arises at the umbilical seam, strengthens across the umbilical wall and develops a strong umbilical bulla just outside the umbilical shoulder. The bulla is developed to a varying degree on different ribs, strengthening with increasing diameter. The ribs also become stronger with increasing diameter; they are more or less straight across the whorl sides, broad and round, equal to or slightly wider than the interspaces, subdued at mid-flank, rectiradiate in the earlier growth stages, rursiradiate in the later stages. Each rib bears a strong, slightly spinose lower ventro-lateral tubercle. From this tubercle the ribs project slightly forwards across the shoulder to a clavate upper ventro-lateral tubercle. Upwards of a diameter of 120-30 mm. the two ventro-lateral tubercles increasingly coalesce. The ribs are broad, round, and continuous across the venter, and up to a diameter of 90 mm. there is a weak clavate siphonal tubercle. At greater diameters this tubercle is lost. There is a weak siphonal depression at diameters of 120 mm. upwards.

The last septum is at a diameter of 120 mm., where there is the median siphonal depression on the ribs and the ventro-lateral tubercles have almost coalesced. The type has been damaged in life at the beginning of the secretion of its final body chamber, and as a result has developed irregular ventral ribbing, an irregularity which becomes more

pronounced on later parts of the body chamber. There are thus only four ribs on the last quarter whorl. These ribs are high, distant, and very much narrower than the interspaces, with a strong umbilical bulla and a lower ventro-lateral tubercle now flat and horn-like. There is an upper ventro-lateral tubercle present on the penultimate rib.

Discussion. The lectotype can be matched with the better-preserved material from Rouen, where it is the commonest form. This material shows that the changes during ontogeny are relatively slight (as is usual in *Acanthoceras*), the strong ornament being present from the earliest stages (see Pl. 92, fig. 2). Thus the siphonal tubercle only weakens very slowly, and during most growth stages is as strong as, or only a little weaker than the upper ventro-lateral tubercles, which are themselves weaker than the lower ventro-lateral tubercles.

There is some degree of variation in the density of the ribbing: 22–6 ribs per whorl. There is considerable variation in the persistence of short-ribbing which disappears within the range 37–60 mm. diameter.

With less inflation (sometimes accompanied by weaker decoration) there are transitions to *A. rhotomagense* (e.g. École des Mines A 658). Transitions to *A. rhotomagense* var. *confusum* are more common: in these there is increasing spinosity, fewer ribs, and sometimes increasing rib strength.

Being common, *A. rhotomagense* var. *sussexense* has often been figured, usually under other names, particularly *A. rhotomagense* (e.g. Wright (in Arkell *et al.* 1957, L415, fig. 7) has used the figure of Bayle (1878) to illustrate the type species). *A. vectense* Spath (1926a) is a synonym: the apparent differences arise from the pathology of the lectotype of *A. r.* var. *sussexense*; the holotype of *A. vectense* (GSM 7756) shows well the backward sweep of the ribs in the later stages (text-figs. 3, 4).

Those *Acanthoceras* from Rouen which show any development of *Euomphaloceras*-like multituberculation or rib insertions on the venter, are all close to *A. r.* var. *sussexense* in general style of ornament (Pl. 92, fig. 4; Pl. 93).

Acanthoceras crassiorum Crick (1907, p. 185) differs in having coarser, more widely spaced ribbing, a more compressed whorl section, and more strongly clavate upper ventro-lateral tubercles.

Acanthoceras robustum Crick (1907, p. 189) has weaker, broader, more widely spaced ribs, with all tubercles, except the siphonal series, weaker.

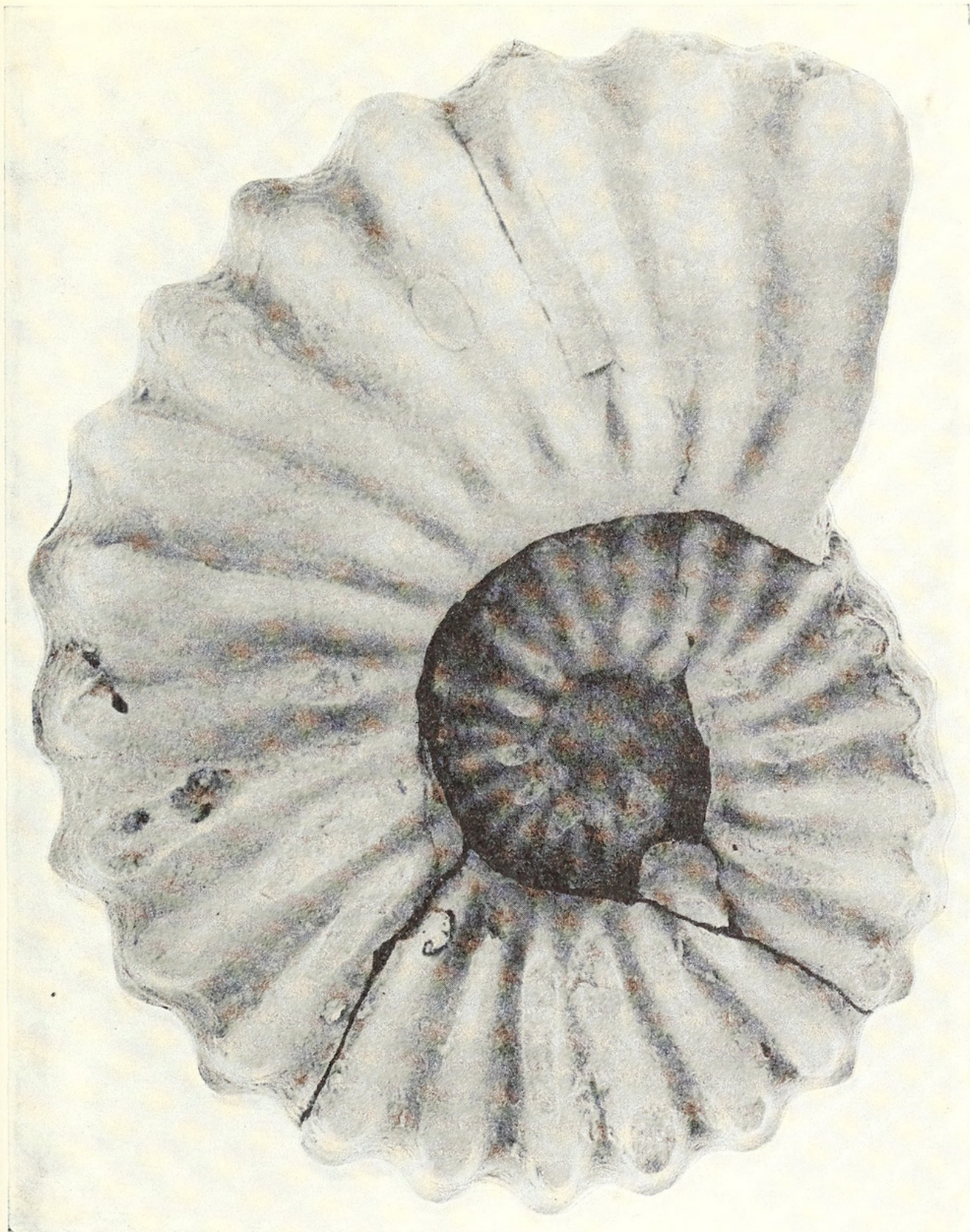
Acanthoceras quadratum Crick (1907, p. 192, pl. 13, fig. 2) has only 21 ribs at a diameter of 108 mm. compared with 25 in the lectotype of *A. rhotomagense* var. *sussexense*.

Acanthoceras aff. *rhotomagense* var. *sussexense* (Mantell)

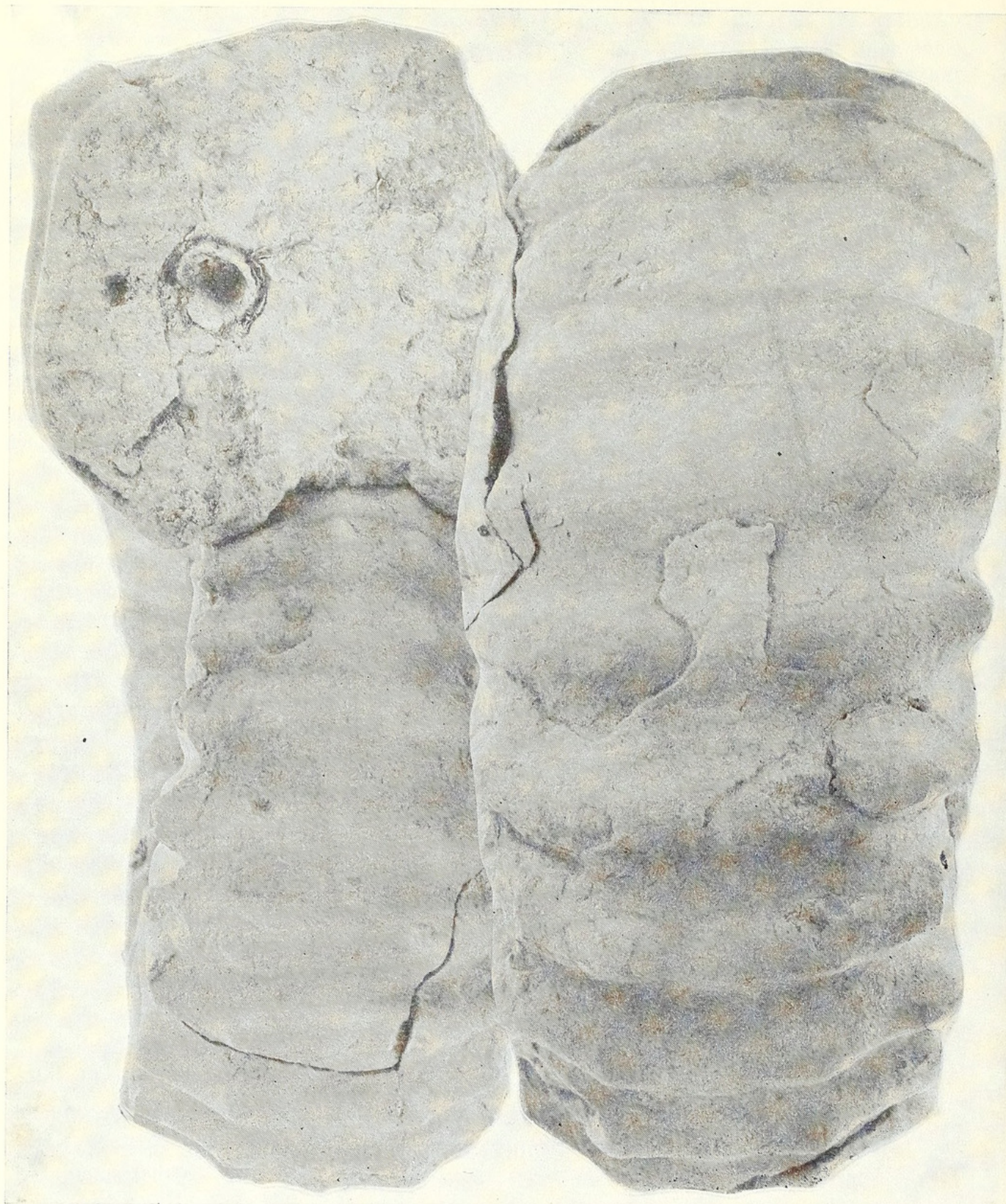
Plate 92, figs. 3, 6

We have seen a number of specimens which have the decoration of *A. rhotomagense* var. *sussexense* but which are markedly more compressed. In this respect they are transitions to *Acanthoceras simulans* Spath (Schlüter 1871, pl. 7, fig. 3), although that species has multiple siphonal tuberculation.

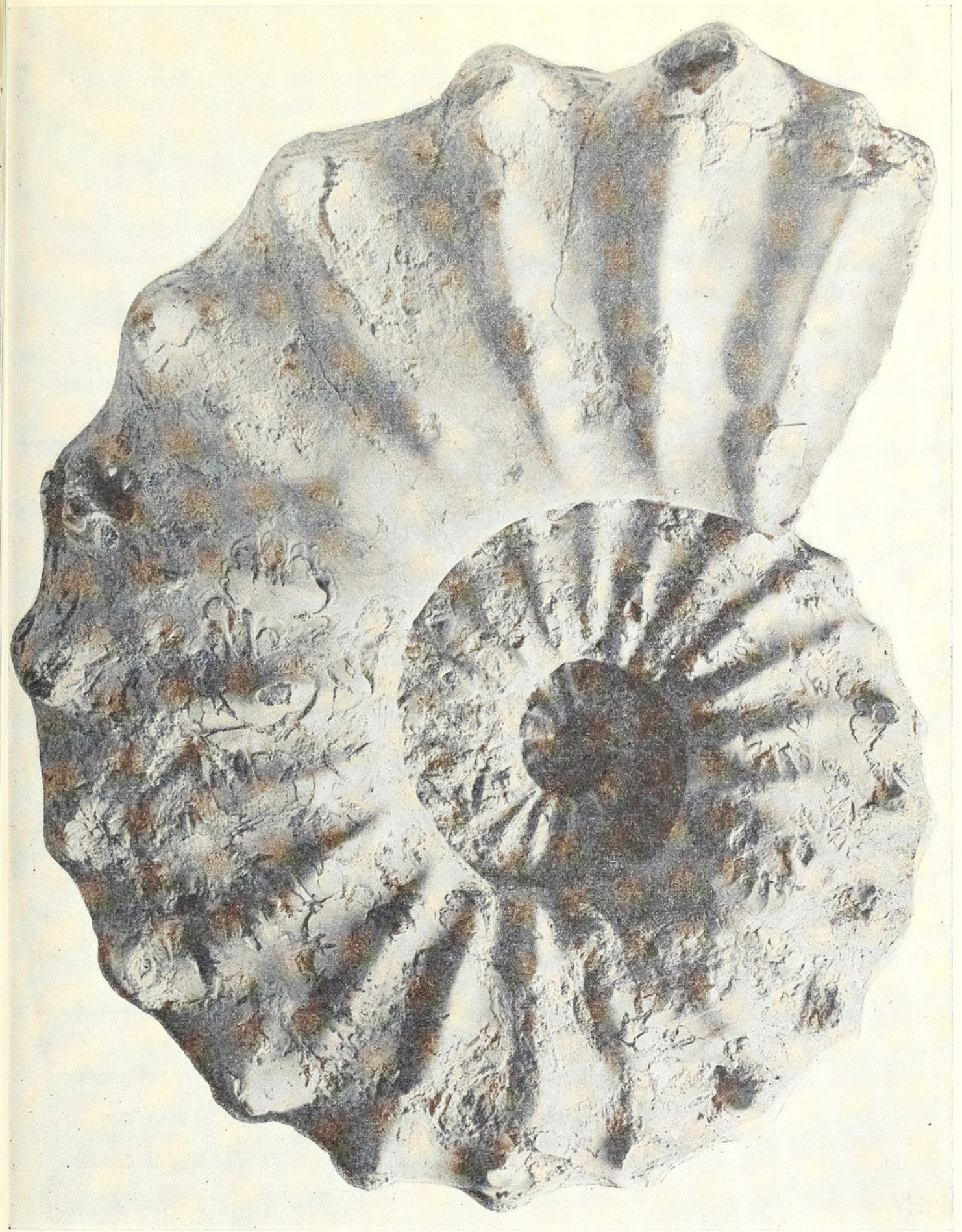
Acanthoceras hippocastanum (J. de C. Sowerby) (lectotype, herein designated, is the original specimen figured by Sowerby (1829, pl. 514, fig. 2, GSM 37667)) was based upon



TEXT-FIG. 3. *Acanthoceras rhotomagense* var. *sussexiense* (Mantell). From Bonchurch, near Ventnor, Isle of Wight; horizon unrecorded. Side view of GSM 7756, the holotype of *Acanthoceras vectense* Spath. $\times 1$.



TEXT-FIG. 4. *Acanthoceras rhotomagense* var. *sussexense* (Mantell). Front and ventral view of specimen in fig. 3, the holotype of *Acanthoceras vectense* Spath. $\times 1$.



TEXT-FIG. 5. *Acanthoceras rhotomagense* var. *sussexiense* (Mantell). From the fossil-bed of the Craie de Rouen. Side view of C1030; $\times 1$.

two specimens; the paralectotype (C74799) figured in Plate 92, fig. 6, is from Rouen, and is better referred to as *A. aff. rhotomagense* var. *sussexense*.

Acanthoceras rhotomagense var. *confusum* (Guéranger 1867)

Plate 94, figs. 1–4; Plate 95, fig. 1

- 1856 *Ammonites hippocastanum* Sowerby; Sharpe, pp. 37–8, pl. 17, figs. 4a, b, c; figs. 3a, b represent a form halfway to *A. r. sussexense*.
 1863 *Ammonites rhotomagensis* Brongniart; Pictet pars, pl. 2, figs. 2a–c and 3 only.
 1867 *Ammonites confusus* Guéranger, pp. 5, 6, pl. 2, fig. 4; pl. 3, fig. 1; pl. 8, fig. 1.
 non 1907 *Acanthoceras confusum* Guéranger; Pervinquier, p. 268, pl. 13, figs. 4a, b.
 ?1907 *Acanthoceras quadratum* Crick, p. 192; pl. 13, fig. 2.

Lectotype. The lectotype, herein designated, is the specimen figured by Guéranger (1867) in plate 3, fig. 1 and plate 8, fig. 1, from Guéranger's 'Zone à *Perna lanceolata*' in the lower part of the Middle Cenomanian of the Sarthe. We have been unable to find this specimen in the Musée de Tessé at Le Mans, and it is probably lost. Guéranger did not provide a scale for his plates but the magnification of plate 3 is almost certainly in the range 0.3–0.4. The paralectotype specimen figured in plate 2, fig. 4, is also probably lost. We reproduce Guéranger's figures in Plate 94.

Diagnosis and description. This is a form of *Acanthoceras rhotomagense* which is more depressed, and more strongly tuberculate than *A. rhotomagense* var. *sussexense*, and which has only 19–21 ribs per whorl. The lectotype is an adult with the last 2–3 ribs of the body chamber distinctly approximated and all tuberculation lost.

Discussion. This variety represents a continuation of the trend towards coarser ribbing and stronger ornament seen in *A. rhotomagense* var. *sussexense*, from which it is distinguished by the fewer (and sometimes heavier) ribs and a general clumsy appearance.

EXPLANATION OF PLATE 93

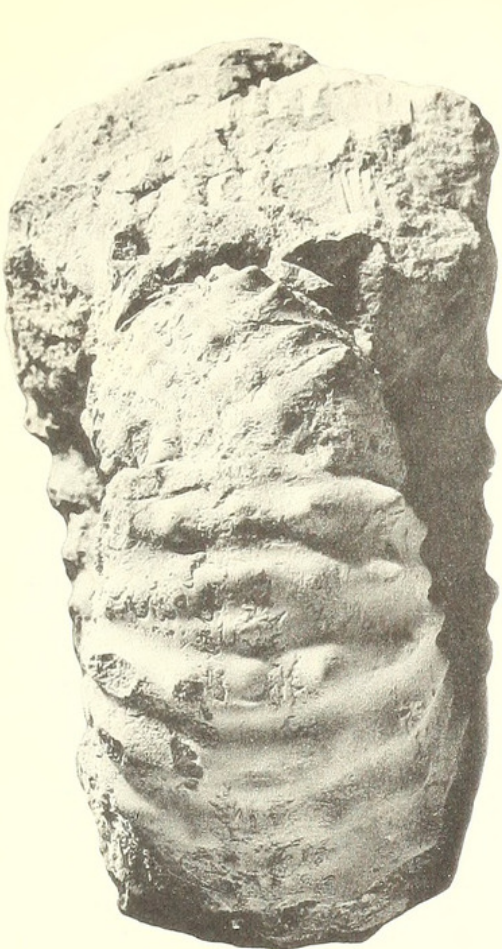
All figures are of natural size; both specimens are coated with ammonium chloride.

- Figs. 1a, b, 2a, b. *Euomphaloceras* transitional from *Acanthoceras rhotomagense* var. *sussexense* (Mantell), showing intercalation of extra ribs on the relatively rounded venter.
 Figs. 1a, b. From the fossil-bed of the Craie de Rouen; front and side views of S2.
 Figs. 2a, b. From Nogent-le-Rotrou (Eure et Loir); horizon unknown but matrix suggests Craie de Théligny (Middle Cenomanian). Ventral and side views of A657; note that the intercalatory ribs on the venter carry tubercles of equal strength to those on the primary ribs.

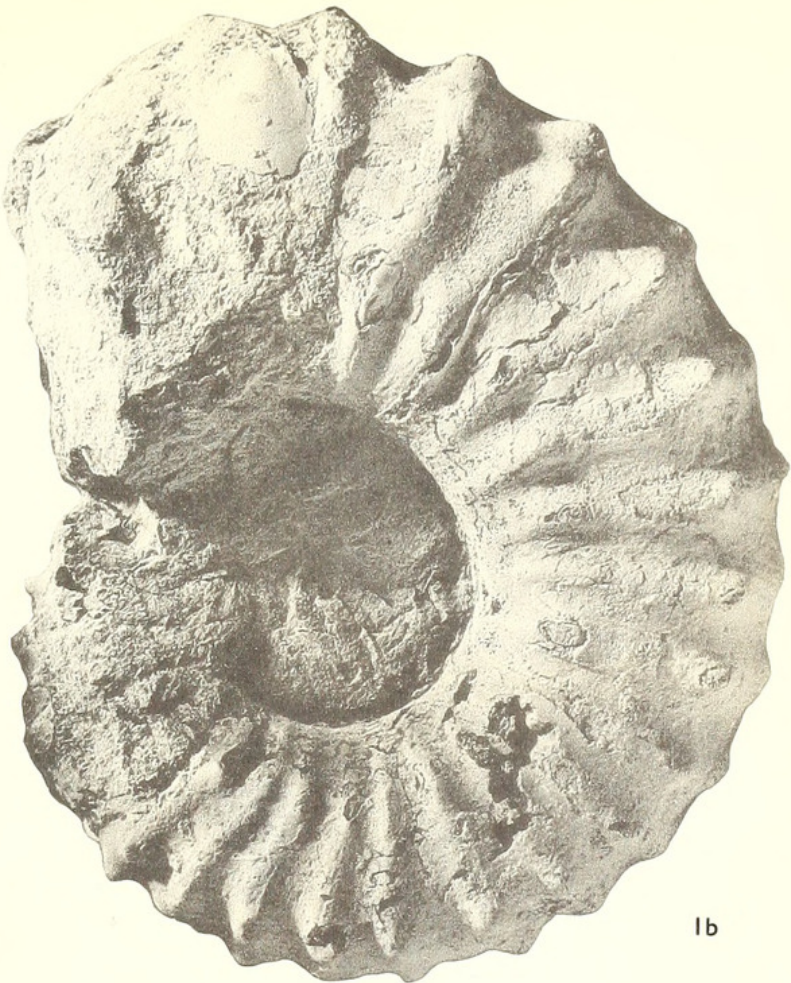
EXPLANATION OF PLATE 94

All figures except 1 and 2 are of natural size. Specimens except those in figs. 1 and 2 are coated with ammonium chloride.

- Figs. 1 and 2. *Acanthoceras rhotomagense* var. *confusum* (Guéranger); from the upper part of the Sands with *Perna lanceolata* (lower part of Middle Cenomanian) in the Sarthe.
 Fig. 1. Lectotype; copy of Guéranger 1867, pl. 3; upper figure; reduction unknown.
 Fig. 2. Paralectotype; copy of Guéranger 1867, pl. 2, fig. 4; magnification unknown but possibly natural size.
 Figs. 3a–e. *Acanthoceras rhotomagense* var. *confusum* (Guéranger); from the fossil-bed of the Craie de Rouen. Various views of different growth stages of the same juvenile, S10D.
 Figs. 4a, b. *Acanthoceras rhotomagense* var. *confusum* (Guéranger); from the fossil-bed of the Craie de Rouen. Side and front views of A647.
 Figs. 5a, b. *Acanthoceras* transitional between *rhotomagense* var. *clavatum* var. nov. and *adkinsi* Stephenson; from the fossil-bed of the Craie de Rouen. Side and ventral views of A650.



1a



1b



2a



2b



Kennedy, W. J. and Hancock, J M. 1970. "Ammonites of the genus *Acanthoceras* from the Cenomanian of Rouen, France." *Palaeontology* 13, 462–490.

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