AMMONITES OF THE GENUS ACANTHOHERAS
FROM THE CENOMANIAN OF ROUEN, FRANCE

by W. J. KENNEDY and J. M. HANCOCK

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 rhomboideus, 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, one of which, A. rhomboideus var. crassum, is new. A. rhomboideus is a widespread species and marks an horizon low in the Middle Cenomanian. Acanthoceras bornei 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 Bronnigart. 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). Jeffries (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. Jouv in 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 indivius and Hébert (1884) even included the beds containing ‘Ammolites’ inflatus and Terrilites bergeri that we should now consider Upper Albion.

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 preservations. 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
(= Metacanthophiles Hyatt 1900)

Type species, Ammonites rhomboideus Bronnigart ex Defrance MS in Cuvier and Bronnigart 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. coronatum' 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 first 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 Grossoùvre (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 prendrais comme type de ce genre _Acanthoceras rhotomenses_.' 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 Grossoùvre (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. 20). In addition there is sometimes a faint longitudinal striation.

_Relations with other genera._ Even as restricted by De Grossoùvre (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. *Montelliceras* Hyatt, 1902: 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 *Montelliceras* by the absence of siphonal tubercles, but this distinction can only be used on juveniles. More distinctive of *Montelliceras* 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 *Montelliceras*, including the type, possess mid-lateral tubercles.

*Calycoceras* Hyatt, 1900: type species *Ammonites particularis* Mantell; Middle to Upper Cenomanian. *Calycoceras* appears to be derived from *Montelliceras* 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 *Montelliceras* 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 *Montelliceras* by strong umbilical bullae, e.g. *Calycoceras* cotteaudi (Collignon), *C. nitidum* (Crick). However, there are some species of *Montelliceras* which also have umbilical bullae in the middle stages, e.g. *Montelliceras* lynense (Spath) (Pervinquière 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* whiteli 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-brownii* (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* Pervinquière (= *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.

*Platianthoceras* Haas, 1964 (= *Paracanthoceras* Haas, 1963, non Furon, 1935); type species *Metacoceras 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 rhoatomagense*. (ii) 'Also the ribs persist into maturity in *A. rhoatomagense*, 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 rhoatomagense* (Brongniart)

The *Acanthoceras rhoatomagense* 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 rhoatomagense* (Brongniart 1822) forma typica

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

1822 Ammonites Rhoatomagensis Brongniart, p. 606, pl. 6, fig. 2.
1867 Ammonites Rhoatomagensis Lamk.; Guéranger pars; pl. 2, figs. 2 and 6 only.
1912 Acanthoceras rhoatomagense DeFrance in Brongniart; Douville, fiche 238.
1956 Acanthoceras clausa Benavides-Claeers, pp. 466-7, pl. 53, figs. 1-4.

Lectotype. Selected by Douville (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 rhoatomagense* Brongniart. 1a, 1b, Side and ventral view of R.8. 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 E. Basse de Mésorval. 4a, 4b, Side and front views of a juvenile, A633F. 5, Original figures of the lectotype by Brongniart in Cuvier and Brongniart, 1822, pl. 6, fig. 2.

Figs. 6a, b. *Acanthoceras rhoatomagense* intermediate between var. subflexuorum 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 rhoatomagense* (Brongniart): from quarry on Chard side of boundary fence, ¾ mile north of Tytherleigh, near Chardstock, Devon; presumably from the Middle Cenomanian basement bed of the Chalk; ventral, front and side views of C 73085.

Figs. 2a, b. *Acanthoceras rhoatomagense* var. sussexiens (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–c. Spinose *Calycoceras* with an *Acanthoceras* nucleus; from fossil-bed of the Craie de Rouen. a, b, Side and ventral views. c, Side view × 2. d, e, Side and ventral views, all of S9.
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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 phosphatized 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 2½-2 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. rhomoginese var. subflexuosum_ and _A. rhomoginenge var. sussexiense_. 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. rhomoginenge var. sussexiense_; 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. rhomoginenge var. sussexiense_ 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. rhotomagensis although slightly transitional to A. rhotomagensis 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

![Diagram](image)

**Text-fig. 2.** Suture line of the lectotype of Acanthoceras rhotomagensis (Brongniart).

After Donville 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 Sharp 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. rhotomagensis* is distinguished from *A. r. var. sussexiensis* 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 adkins* Stephenson (1953, pp. 200–1, pl. 47, figs. 3, 4) is very close to *A. rhotomagensis* 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 stevensoni* 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. rhomagense*, is distinguished by flat, unribbed flanks.

*Acanthoceras rhomagense* var. *subflexuosum* Spath 1923

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

1826 *Ammonites rhomagense* Defrance; J. de C. Sowerby v. 6, p. 25, pl. 515, fig. 1.
1867 *Ammonites Rotomagense* Lamk.; Guérange pars, pl. 2, figs. 1 and 5 only.
1923 *Acanthoceras subflexuosum* sp. nov.; Spath, p. 144.
1940 *Acanthoceras et subflexuosum* Spath; Fabre, p. 223.
1951 *Acanthoceras subflexuosum* Spath; Wright and Wright, p. 28.

_Holotype._ BM 43981a, 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 rhomagense* with a similar degree of compression to *A. rhomagense* but with a broader, faintly round, venter. The tubeculation, 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 less. The costal section is compressed-polygonal, with the greatest breadth on 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 flanks 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. rhombeum* var. *subflexuosum*, the lectotype of *A. r. var. sussexense* and *A. r. var. confusium*, the paralectotype of *A. r. var. confusium*, 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 tuberules are taken into account, whorl sections often appear more compressed than intercostal measurements of whorl height and whorl width would indicate. a. = approximately.

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<th>Whorl width</th>
<th>Width of umbilicus</th>
<th>Number of ribs on last whorl</th>
<th>Number of primaries</th>
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**A. rhombeum** var. *claratum* s.s.

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**A. rhombeum** var. *subflexuosum* s.s.

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**A. rhombeum** var. *sussxense*-*subflexuosum*

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**A. rhombeum** var. *sussxense*-*subflexuosum*

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KENNEDY AND HANCOCK: AMMONITES OF THE GENUS *ACANTHOCERAS* 471

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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 rotomagensis* group; it differs from *A. rotomagensis* var. *subflexuosum* in having fewer ribs (23 instead of 25-9); BMNH C74794 from Rouen appears to be an intermediate.

*Acanthoceras rotomagensis* var. *sussexiens* (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 Rotomagensis* Defrance; Sharpe, pp. 33-4, pl. 16, figs. 1a-c, 3a, b (figs. 2a, b transitional to *A. r. rotomagensis*).

**Explanation of Plate 90**

All figures are of natural size except fig. 29; all specimens are coated with ammonium chloride.

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

Figs. 2a, b. *Acanthoceras rotomagensis* 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 rotomagensis* var. *subflexuosum* Spath; juvenile from the fossil-bed of the Craie de Rouen. a, c. Front and side views. b. Side view x2, of S108.

Figs. 4a, b. *Acanthoceras rotomagensis* 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 rotomagensis* var. *sussexiens* (Mantell); from the Lower Chalk of Haslemere, Sussex. Side and front views of the lectotype, BM 5691.

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

Fig. 3. *Acanthoceras* aff. *rotomagensis* (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 rotomagensis* var. *sussexiens* (Mantell); Side and front views of A654; note slight asymmetry in the position of the siphonal tubercle in this individual.

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

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

Figs. 4a, b. *Exomphaloceras* sp. close to *Acanthoceras rotomagensis* var. *sussexiens* (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. *rotomagensis* var. *sussexiens* (Mantell). Side and front views of C74799, parietotype of *Acanthoceras hypococostum* (J. de C. Sowerby); note low rib density combined with relatively narrow venter.
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1861 Ammonites sussexiensis Mantell; Sharpe, p. 34, pl. 15, fig. 1 (= Euconuloceras interne (Pervinquière)).
1863 Ammonites rhotamogonae Brogniart; Pictet pars; pl. 2, figs. 1a–e only.
1878 Acanthoceras rhotamogonae Brogniart; Bayle, pl. 63, figs. 1–3; 14–5.
1903 Acanthoceras sussexiensis; Spence, p. 144 n.
1926a Acanthoceras sectenae Spach, p. 62.
1931 Acanthoceras hippocastanum Spach; Collignon, pl. 4, fig. 1.
1951 Acanthoceras sectenae Spach; Wright and Wright, p. 28.
1951 Acanthoceras sussexiensis (Mantell); Wright and Wright, p. 28.
1963 Acanthoceras natalampiensis 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, 5699) in the Mantell collection labelled Ammonites sussexiensis belong elsewhere.

Diagnosis. Form of Acanthoceras rhotamogonae characterized by a more depressed quadrate whorl section than A. rhotamogonae itself, with strong, dense, rounded, slightly rursiradial instead of prorsiradial 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 limonite coating. Just under half the latter 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, rectiradial in the earlier growth stages, rursiradial in the later stages. Each rib bears a strong, slightly spinose lower ventro-lateral tulecle. 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. rhomagense* var. *confusum* are more common: in these there is increasing spinosity, fewer ribs, and sometimes increasing rib strength.

Being common, *A. rhomagense* var. *sussexiense* has often been figured, usually under other names, particularly *A. rhomagense* (e.g. Wright in Arkell *et al.* 1957, L415, fig. 7) has used the figure of Bayle (1875) 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. sussexiense*; 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. sussexiense* in general style of ornament (Pl. 92, fig. 4; Pl. 93).

*Acanthoceras crassioratum* 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. rhomagense* var. *sussexiense*.

*Acanthoceras aff. rhomagense* var. *sussexiense* (Mantell)

Plate 92, figs. 3, 6

We have seen a number of specimens which have the decoration of *A. rhomagense* var. *sussexiense* but which are markedly more compressed. In this respect they are transitions to *Acanthoceras similans* Spath (Schlüter 1871, pl. 7, fig. 2), 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 rhotomagensis* var. *suscivum* (Mantell). From Bonchurch, near Ventnor, Isle of Wight; horizon unrecorded. Side view of GSM 7756, the holotype of *Acanthoceras vectense* Spath. ×1.
TEXT-FIG. 4. Acanthoceras rhotomagense var. sussexiense (Mantell). Front and ventral view of specimen in fig. 1, the holotype of Acanthoceras rhotomagense Spath. ×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. sussexiens.

_Acanthoceras rhotomagense var. confusum_ (Guéranger 1867)

Plate 94, figs. 1-4; Plate 95, fig. 1

1856 _Ammonites hippocamptus_ Sowerby; Sharpe, pp. 37-8, pl. 17, figs. 4a, b, c; figs. 3a, b represent a form halfway to _A. r. sussexiens._

1853 _Ammonites rhotomagensis_ Bronnillart; Pictet pars, pl. 2, figs. 2a-c and 3 only.

1857 _Ammonites confusus_ Guéranger, pp. 5, 6, pl. 2, fig. 4; pl. 3, fig. 1r; pl. 8, fig. 1.

1897 _Acanthoceras confusum_ Guéranger; Pervièvre, p. 268, pl. 13, figs. 4a, b.

1907 _Acanthoceras quadristum_ 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 Téssé 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. sussexiens_, 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. sussexiens_, from which it is distinguished by the fewer (and sometimes heavier) ribs and a general clumsy appearance.

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**EXPLANATION OF PLATE 93**

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

Figs. 1a, b, 2a, b. _Eosapholoceras_ transitional from _Acanthoceras rhotomagense var. sussexiens_ (Mantell), showing internalation 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 82.

Figs. 2a, b. From Noget-le-Horotou (Eure et Loir); horizon unknown but matrix suggests Craie de Théligny (Middle Cenomanian). Ventral and side views of A657; note that the intercalary ribs on the venter carry tubercules of equal strength to those on the primary ribs.

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**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 ventral 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.
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There are many transitions between the two varieties. As with most coarsely ornamented ammonites there is much variation in the detail of the decoration.

As can be seen from the synonymy, and from an examination of museum collections, this variety has been frequently mis-identified as Acanthoceras hippocastanum (J. Sowerby) which is a much younger species of the Naviculare Zone (Upper Cenomanian). It differs from A. rhomomagense var. confusum in (i) being adult at small diameters (perhaps one-fifth of the size of an adult A. r. var. confusum); (ii) being more inflated; (iii) retaining alternately short and long ribs throughout; (iv) retaining strong siphonal tubercles throughout; (v) ribbing between lower and upper ventro-lateral tubercles remaining weak. Of all figures purporting to represent A. hippocastanum, only Sowerby's original can in truth be referred to that species.

Acanthoceras jukes-brownei (Spath) and A. whitei Matsumoto both differ in retaining alternately short and long ribs throughout the septate portion.

Acanthoceras latum Crick (1907, 195, pl. 12, fig. 2, 2a) is a closely allied species with a rapidly expanding whorl section, fewer ribs (about 15 per whorl) which are generally weaker, a much broader venter, and particularly large spinose lower ventro-lateral tubercles. A. quadratum Crick has weaker ribbing than the average individual but is probably synonymous.

Acanthoceras confusum tunetana Pervinquièr (1907, 268–9, pl. 13, figs. 4a, b) is a form with few ribs (17 per whorl) and finger-like horns in the position of the lower ventro-lateral tubercles, but no other tubercles: it is best considered as a separate species.

Acanthoceras sherborni Spath (= Ammonites cenomanensis Sharpe non d'Archiac) is close to A. r. var. confusum; the type is lost. The chief differences of A. sherborni are: (i) slightly fewer ribs (17 at a diameter of 155 mm.—Sharpe's figure is reduced); (ii) greater compression; (iii) the apparent loss of the lower ventro-lateral tubercle giving rise to squarer shoulders. Some of these features could be exaggerated by the imperfect preservation in the Lower Chalk of Dover.

Acanthoceras rhomomagense var. clavatum var. nov.

Plate 96, figs. 2–3; Plate 97, fig. 5

Holotype, A660 in the École des Mines, Paris, from the Craie de Rouen, Ste Catherine, Seine-Maritime, France, here figured as Plate 96, fig. 2.

Diagnosis. A compressed form of Acanthoceras rhomomagense with 21–3 weak ribs per whorl which loses umbilical bulla early in ontogeny; has weak, rounded lower ventro-lateral tubercles, and very large, markedly clavate upper ventro-lateral tubercles on each side of a depressed venter.

Description. The holotype is a well-preserved, wholly septate, phosphatic internal mould, retaining traces of phosphatised shell. It is evolve, about two-fifths of the previous whorl being covered. The whorl section is compressed, with the greatest breadth just below mid-flank. The sides are broadly rounded in intercostal section, with a narrow, high, round venter.

There are an estimated 21 ribs on the outer whorl, nearly all of which extend down to the umbilical edge. They are weak close to the umbilical wall, and strengthen across the
sides, so that they reach a maximum development at mid-flank, although there is much variation in the strength of the early formed part of the rib. The ribs are slightly flexuous, and narrower than the interspaces. Each bears a low, round lower ventro-lateral tubercle which weakens with increasing diameter. This tubercle is connected by a low, forwardly directed rib to a very large clavate upper ventro-lateral tubercle, which becomes more pronounced as the diameter increases. These upper ventro-lateral tubercles form closely spaced pairs across the venter, and rise high above the intervening flat siphonal area. There are traces of a weak, spirally elongate, siphonal swelling.

The early whorls are poorly visible but show that variation in rib strength was much more marked up to a diameter of about 35 mm., whilst a distinct siphonal tubercle (as strong as the upper ventro-lateral tubercles) was present.

The suture line is well preserved, and is of normal Acanthoceras type (see Pl. 96, fig. 2a).

Discussion. The strong upper ventro-lateral clavae, weak ribs, and compressed section are the distinctive features. We have seen two specimens transitional to A. rhotomagenese. There are also specimens transitional to A. rhotomagenese var. subflexuosum in some of which much of the ribbing is exceptionally weak.

A. rhotomagenese var. clavatum resembles A. wintoni Adkins and the ‘pleisioype’ of

EXPLANATION OF PLATE 95

Both figures are of natural size, and the specimen is coated with ammonium chloride.

Figs. 1a, b. Acanthoceras rhotomagenese var. confusum (Guéranger); from the fossil-bed of the Craie de Rouen. Front and side views of A653; the last suture is at a diameter of approximately 110 mm.

EXPLANATION OF PLATE 96

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

Figs. 1a-c. Acanthoceras intermediate between A. rhotomagenese (Bronniiart) and A. rhotomagenese var. clavatum var. nov. Side, ventral and front views of A659.
Figs. 2a-c. Acanthoceras rhotomagenese var. clavatum var. nov. Side, ventral and front views of the holotype A660.
Fig. 3. Acanthoceras rhotomagenese var. clavatum var. nov. Side view of a paratype S21.

EXPLANATION OF PLATE 97

All figures are of natural size. All specimens are coated with ammonium chloride except fig. 2c. All ammonites are from the fossil-bed of the Craie de Rouen.

Figs. 1a, b. Acanthoceras basseae sp. nov. Side and front views of the holotype S5.
Figs. 2a-c. Acanthoceras aff. basseae sp. nov. Ventral, front and side views of a specimen in the Muséum d'Histoire Naturelle de Rouen. The close spacing of the clavate tubercles on the venter, and the rapid disappearance of these tubercles shown in the ventral view, mean that this ammonite could equally well be referred to Protoanconoceras.
Fig. 3. Acanthoceras aff. rhotomagenese (Bronniiart) transitional to a spinose Calycoeceras. Front view of S18 (side view in Pl. 91, fig. 3).
Figs. 4a, b. Protocanoceras sp. Side and front views of C 74796.
Figs. 5a, b. Acanthoceras basseae sp. nov. Ventral and side views of a paratype A684.
Fig. 6. Acanthoceras rhotomagenese var. clavatum var. nov. Front view of S21 (side view on previous plate).
Figs. 7a, b. Protocanoceras sp. Side and front views of A52.
Figs. 8a, b. Acanthoceras basseae sp. nov. Ventral and side views of a paratype S16.
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Stephenson is even closer (1953, pl. 45, figs. 7, 8; pl. 46, fig. 1). However, in A. rhotomageense var. clavatum there are more ribs, the sipholal tubercle weakens and disappears much earlier, the ribbing on the venter is weaker (it is also weak in Stephenson’s plesiotype), short ribs are absent beyond diameters of 60 mm, (and often do not reach that), and most individuals have flatter sides. Acanthoceras very close to A. winstoni occur in the Chalk basement bed at Snowdon Hill, Chard, Somerset.

There is an allied form (authors’ collections, e.g. cc560) from Snowdon Hill, Chard, in which the lower ventro-lateral tubercles are completely lost, which is homeomorphous with Mantellliceras coudoi except for the lack of short ribs.

_Acanthoceras basseae_ sp. nov.

_Plate 97, figs. 1, 4_

_Holotype._ The unregistered specimen (bearing our label ‘S’) in the collection of the Sorbonne figured as Plate 97, fig. 1, from the Craie de Rouen, St Catherine, Seine-Maritime, France.

_Diagnosis._ Slightly compressed, evolute, square-whorled, slowly expanding _Acanthoceras_ with 18–22 ribs per whorl.

_Description._ The holotype is a well-preserved phosphatic internal mould, the last third of the outer whorl being body chamber. It is evolute, about a sixth of the previous whorl being covered. The whorl section is slightly compressed, with the greatest breadth at the umbilical bullae. The intercostal section is trapezoidal (the sides diverging towards the umbilicus) with rounded corners. The costal section is similar, but the corners of the trapezium are truncated.

There are 21–22 ribs on the outer whorl, most of which extend down to the umbilical seam. They are weak across the umbilical wall; 12–13 develop a pronounced, transversely elongate umbilical bulla of varying strength at or just outside the umbilical shoulder, five lack the bulla, and four arise just below mid-flank. The ribs pass across the sides with gentle flexure, weakening at mid-flank, and connect to a round lower ventro-lateral tubercle which weakens with age. This is connected by a strong rib to a weakly clavate upper ventro-lateral tubercle, which also weakens with age. A very faint low rib extends across the venter, bearing a low clavate sipholal tubercle which again weakens with age.

The early whorls are well exposed, and show strong umbilical bullae on long ribs which alternate with shorter ribs or ribs which extend to the umbilicus as mere striae. Occasional ribs branch in twos from an umbilical bulla.

The suture line is of normal _Acanthoceras_ type.

_Discussion._ There are no transitions from _A. basseae_ to any of the forms of _A. rhotomageense_ described above, the slowly expanding whorl size giving all specimens a characteristic and immediately recognizable almost serpenticone appearance.

Three other specimens can be accommodated here: an unregistered fragment in the Sorbonne (our number 16); A684 in the École des Mines (Pl. 97, fig. 4), both tootypes; and an English specimen from Eastbourne (ex. J. Parmenter collection no. 7670) from the same horizon as the Rouen fossil bed.

The three complete specimens all have body chambers, whilst the other fragment is small, suggesting that this was a small species.
TEXT-FIG. 7. Side view of the same ammonite figured in text-fig. 66. ×0·57.

TEXT-FIG. 6.  

a, Acanthoceras rhomogeneum var. sussexiense (Mantell). Front view of specimen in text-fig. 5. 
b, Acanthoceras rhomogeneum (Brocchiari) transitional to A. × var. elevatum var. nov. From Band 10 in the 
Lower Chalk at Folkstone — Turritites acutus assemblage-horizon of the Rhomogeneum Zone which is 
slightly higher than the fossil-bed of the Craie de Rouen. Front view of WJK 2466. ×0·66.
TEXT-FIG. 8. Acanthoceras rhomagenese var. subflexuum Spath. From Band 9 of the Lower Chalk at Folkestone, Kent — the *Teudites costatus* assemblage-horizon of the Rhomagenese Zone. Side view of WJK 5138. ×0·85.
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There is also a specimen in the Natural History Museum at Rouen (PL 97, fig. 2) which is transitional between this species and Protacanthoceras in that it shows an early and very rapid loss of all ventral tuberculation whilst retaining ventral ribbing which is becoming chevron-shaped.

There is some superficial resemblance between A. baseae and A. sherborni (the type of which, as already noted, is lost). Sharpe's figure shows that the ribbing is more regular in A. sherborni, and the species is not adult until a much greater size.

GENERAL COMPOSITION OF THE AMMONITE FAUNA

Out of some 90 ammonites that we ourselves have collected at Rouen or were given as a general collection by Dr. R. P. S. Jeffries, more than two-thirds are Sciponoceras gr. baenulae (Mantell), Turrilites costatus Lamarek and transitions to T. acutus Passy, and Schloenbachia coupel (Brongniart) and varieties. The following, in order of abundance by genus, comprise less than a third: Scaphites (chiefly S. obliquus J. Sowerby), Acanthoceras rhotomagensis, Calycoceras gentoni (Brongniart), Hamites (Stomohamites) simplex d'Orbigny, Anisoceras sp., Puzosta sp., Austiceras sp.

As shown in this paper, museum collections also contain Acanthoceras transitional to Euomphaloceras and Protacanthoceras.

We have seen in the Rouen museum: Forbesiceras including F. largilliertianum (d'Orbigny), Acompsoceras, and several rarities we could not identify at sight (possibly Gaudryceratinae). Follet 1943 (quoted in Sornay (1959)) records a number of other forms of which the following are stratigraphically significant: Calycoceras natualare (Mantell), Mantelliceras cf. tuberculatus (Mantell), Hypholites falcatus (Mantell). These may be misidentifications, or are not from the Rouen fossil bed (some museum specimens labelled 'Rouen' are undoubtedly from another bed), or represent remanié material such as occurs in other chalk basement beds.

AGE OF THE FAUNA

As early as 1858 Saemann recognized a "niveau à Ammonites rotomagensis" in the middle part of the Cenomanian of Le Mans. This effectively Middle Cenomanian dating of the Rouen fauna is in complete agreement with the list by one of us (Hancock 1959) of the ammonites from the Sables at Grès du Mans à Scaphites equatilis et Turrilites costatus.

Detailed collecting from southern England by one of us (Kennedy 1969) has provided some subdivisions of the Middle Cenomanian. The Rouen fossil bed corresponds to an horizon in the lower part of the Middle Cenomanian characterized by Acanthoceras rhotomagensis, Turrilites costatus common and T. acutus uncommon, Sciponoceras abundant (and in south-east England abundant Orbirhychina gr. melitellina) called the T. costatus faunal horizon (Table 2).

Superposition in the Lower Chalk of south-east England, shows that within a metre above the horizon of the T. costatus assemblage occurs a T. acutus assemblage which is to be found in a better preservation in the Chalk basement bed at Snowdon Hill, Chard, in Somerset. In this younger fauna Turrilites acutus is common and T. costatus rare, Calycoceras is more common and includes spinose species of the group of C. newbouldi spinosum (Kossmat), and Sciponoceras is normally rare.
It is of interest to compare the *Acanthoceras* of the two faunas. Many of the individuals in the *T. aequalis* assemblage cannot at present be distinguished from some forms in the earlier *T. costatus* assemblage, e.g. *A. rhomagnense*, *A. r. var. sussexiense* and *A. r. var. confusum*, but the assemblage as a whole is different; in particular the *T. aequalis* assemblage includes species we have not seen from Rouen, including: *A. flexuosum* Crick, *A. deciduam* Hyatt? (although the type is said to be from Rouen), *A. aff. wintoni* Adkins, *A. aff. sherborni* Spath.

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<tr>
<th>Zone</th>
<th>Faunal Horizons</th>
<th>beds mentioned in paper</th>
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<tbody>
<tr>
<td><em>Actinoceras planus</em></td>
<td>Metalloceras gaudianum</td>
<td></td>
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<tr>
<td></td>
<td>Metalloceras gaudianum</td>
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<tr>
<td><em>Calycoceras excavatum</em></td>
<td>(clear subdivisions not yet recognised in north-west Europe; for south-east France, see Thonel in Parkes et al 1963)</td>
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<tr>
<td><em>Acanthoceras rhomagnense</em></td>
<td><em>Acanthoceras</em> (kunze-brounii)</td>
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<tr>
<td><em>Turrilites eurhais</em></td>
<td>chalk base of bed, Snowdon Hill.</td>
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<tr>
<td><em>Turrilites costatus</em></td>
<td>fossil bed, Chalk of Rouen, &quot;Zone à Parag lanceolata&quot;</td>
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<tr>
<td><em>Mantelliceras manteii</em></td>
<td><em>Mantelliceras</em> (koell)</td>
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<td><em>Hypoturrilites</em> (casabianca)</td>
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supported by the occurrence of *Turrilites* aff. *acutus* (= *T. deeringi* Stephenson) in the same fauna.

The fauna from the north end of False Bay in Zululand, described by Crick (1907), is slightly enigmatic. Apart from species not known elsewhere, much of the fauna correlates with the *Turrilites acutus* assemblage, but *A. quadratum* Crick is probably synonymous with *A. r. confusum* and *A. latum* Crick is close. It is at least possible that several horizons are represented.

**CONCLUSIONS**

An examination of *Acanthoceras* populations from the Middle Cenomanian Craie Chloritée of Rouen shows that most individuals belong to a single species, *Acanthoceras rhotoagense*. This species is highly variable: some individuals are compressed, with weak ribs and tubercles, others are inflated, expanding rapidly, and bearing coarse ribs and tubercles. Five names are useful to describe the population, as shown in text-fig. 9.

In accommodating almost the whole range of *Acanthoceras* from Rouen into five varieties, we have been influenced not only by numerous transitional specimens between varieties, but by the existence of individuals which combine characters of apparently disparate varieties. Thus, whilst *A. r. var. sussexense* apparently grades naturally into *A. r. var. confusum*, a specimen such as BMNH C74791 combines the general decoration of *A. r. var. confusum* with a rib count and a whorl compression of *A. rhotoagense*. Such anomalous forms are sufficiently common to highlight the danger of creating new species of *Acanthoceras* on the basis of single specimens. This variation is comparable to that seen in many Cretaceous ammonites we have examined. Thus there is no doubt that many *Calyoceras*, *Mantelllicerias*, and *Schloenbacchia* assemblages, at present divided into many ‘species’, represent but a single population.

It is also clear that *Acanthoceras* populations from successively higher horizons can be recognized elsewhere. Thus the faunas from Snowdon Hill, Chard (Somerset), are from a slightly higher horizon, and show a slightly different population structure. It is possible to collect individual specimens from this locality which fall within the range of the Rouen material, although the populations differ. These sort of observations make detailed synonymies difficult, because individual specimens from unknown horizons elsewhere in the world may hardly bear separation from the forms named here, although the populations whence they are derived may have a structure quite different from the Rouen assemblage. This seems to be one of the greatest difficulties of ammonite systematics. *Acanthoceras* as described by Crick (1907), Stephenson (1950), and Wright (1963) are particularly difficult to place in this respect.

We should regard the following *Acanthoceras* as being of the *rhotoagense* group:


These are characterized by: (i) early loss of short ribs so that all the ribs are the same length on middle and late growth stages; (ii) loss of the siphonal tubercle during growth; (iii) flat sides. They characterize the early part of the Middle Cenomanian.

This group of ammonites has an almost world-wide distribution in the Middle Cenomanian. It certainly occurs in north-west Europe, South Africa, Madagascar,
TEXT-FIG. 9. Diagrammatic relation between varieties of Acanthoceras found in the Craie de Rouen with percentages of the different forms based on the identification of 162 specimens, mainly in museum collections. Percentages set half-way between two names represent intermediate forms.

Australia, Peru, and Texas. It is apparently absent in the western interior of the United States where its place is possibly occupied by A. amphiholium Morrow and its relatives; Matsumoto and Obata (1966) suggest that A. hazzardi of Texas is probably conspecific with A. amphiholium.

Acanthoceras such as A. jukes-brownei and A. whitei retain alternately long and short ribs to large diameters, and in our experience characterize the upper part of the Middle Cenomanian.

Acanthoceras hippocastanum is an Upper Cenomanian form as discussed on p. 479.

When Acanthoceras from Britain are fully described there seems little doubt that a far more rational taxonomy will prevail, whilst international correlation of the divisions of the Middle Cenomanian will be possible.

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Abbreviations. See explanation of table 1.

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