

ORIGIN, EVOLUTION AND SYSTEMATICS OF THE CRETACEOUS AMMONITE *SPATHITES*

by W. J. KENNEDY, C. W. WRIGHT, and J. M. HANCOCK

ABSTRACT. *Spathites* Kummel and Decker, 1954, a predominantly early to mid-Turonian genus common in Tethyan regions of both the Old and New Worlds, is a key genus in the early radiation of the Mammitinae (of which the *Metoicoceratinae* and *Fallotitinae* are shown to be synonyms). *Spathitoides* Wiedmann, 1960 is a strict synonym and *Jeanrogericeras* Wiedmann, 1960 (of which *Fallotites* Wiedmann, 1960 is a synonym) no more than subgenerically distinct. The genus evolved from *Metoicoceras*; a succession is demonstrated from *S.* (*Jeanrogericeras*) to *S.* (*Spathites*). *Mammites* is an early offshoot from the former subgenus, whilst the Coniacian *Buchiceras*, previously referred to the Tissotiidae, is a direct descendant of the *S.* (*S.*) *rioensis* Powell to *S.* (*S.*) *chispaensis* Kummel and Decker to *S.* (*S.*) *puercoensis* (Herrick and Johnson) lineage.

LOWER Turonian successions, especially those of Tethyan regions, have yielded great numbers of ammonites with a reduced acanthoceratid ornament, currently referred to *Spathites* and *Spathitoides* of the Vascoceratinae, *Fallotites* of the Fallotitinae, and *Jeanrogericeras* of the Mammitinae. The type specimens of the type species are mostly distinct enough, but it has proved difficult to allocate a number of other species to one or other genus.

This is particularly true where large subsequent collections have shown that the range of intraspecific variation in some forms spans currently accepted generic limits.

Study of the earliest described species of the group, *Ammonites reveliereanus* Courty, 1860, as part of our over-all revision of the ammonite fauna of the Turonian stratotype, provides a basis for the discussion of all the above genera, which are regarded as members of the subfamily Mammitinae, in direct lineal descent from the late Cenomanian *Metoicoceras*.

SYSTEMATIC PALAEOLOGY

Repositories of material. These are indicated as follows: OUM, University Museum, Oxford; MNHP, Muséum d'Histoire Naturelle, Paris; SP, Sorbonne Collection, now housed in the Université Paris VI; FSR, Faculté des Sciences, Rennes; AM, Muséum d'Histoire Naturelle, Angers; CS, Château de Saumur; UT, Texas Memorial Museum, Austin; WW, C. W. Wright coll.

Suture terminology. The suture terminology of Wedekind (1916) (see Kullman and Wiedmann 1970 for a recent review) is followed here: I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Dimensions. All dimensions are given in millimetres, figures in parentheses being the percentage of the total diameter. D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilicus.

Superfamily ACANTHOCERATAEAE Grossouvre, 1894

Family ACANTHOCERATIDAE Grossouvre, 1894

Subfamily MAMMITINAE Hyatt, 1900

(= *Metoicoceratinae* Hyatt, 1903; *Fallotitinae* Wiedmann, 1960)

Discussion. The systematics of the latest Cenomanian and Turonian Acanthoceratidae are in a state of flux, but a classification at subfamily level is emerging that will accord with phylogeny. The earliest Acanthoceratidae known are *Mantelliceras*, subfamily Mantelliceratinae, which are directly descended caenogenetically from species of *Stoliczkaia* (Lyelliceratidae, *Stoliczkaia*) with bituberculate venter on the inner whorls. Mantelliceratinae, characterized by dominant, more or less

sharp ribs, appear to have persisted through the Cenomanian and seem to have produced forms with trituberculate venters. Acanthoceratinae characterized by trituberculate venter and a tendency to coarse rounded ribbing and tuberculation, first appeared early in the Lower Cenomanian, but later than *Mantelliceras*, with *Acompsoceras*, whose origin is uncertain. Its strong ventrolateral and weak siphonal tubercles, the latter normally present on the inner whorls only, suggest that its most probable source lies in Mantelliceratinae, but trituberculate-ventered *Stoliczkaia*, *S. (Lammayella)* Wright and Kennedy, persist into the Lower Cenomanian and it is conceivable that here lies the origin of Acanthoceratinae.

During the mid Cenomanian the subfamily gave rise to the Euomphaloceratinae (Cooper 1978; Kennedy, Wright, and Hancock 1980a), a line which ended with *Romaniceras* in the late Turonian. Both Acanthoceratinae and Euomphaloceratinae are characterized by, amongst other features, a row of siphonal tubercles. Late in the Cenomanian, *Thomelites*, itself probably derived from some siphonally tuberculate member of the Mantelliceratinae, began to lose its siphonal tubercles and gave rise to *Metoicoceras*, in which the venter is bituberculate in all but the early stages of early species such as *M. praecox* Haas and *M. latoventer* Stephenson.

Hyatt (1903, p. 115) erected a family Metoicoceratidae for this genus (and placed it in his superfamily Mantelliceratida), but he had previously (1900, p. 588) established a family Mammitidae (in his superfamily Mammitida) for another stock with bituberculate venters. The two families were reduced to subfamily status within the Acanthoceratidae by Wright and Wright (1951, p. 24). Re-examination of the Lower Turonian acanthoceratids with bituberculate venters suggests an even simpler situation with a lineal phyletic succession *Thomelites* → *Metoicoceras* → *Spathites* (*Jeanrogericeras*) [= *Fallotites*] → *S. (Spathites)* → *Buchiceras* and an offshoot branch *Spathites* (*Jeanrogericeras*) → *Mammites* → *Metasigaloceras*. All these genera are closely related morphologically and we consider that they should all be placed in one subfamily Mammitinae. We maintain Mammitinae within the Acanthoceratidae because there are no sufficiently important distinguishing features present throughout ontogeny to separate it further from the other subfamilies.

Genus SPATHITES Kummel and Decker, 1954
[= *Spathitoides* Wiedmann, 1960]

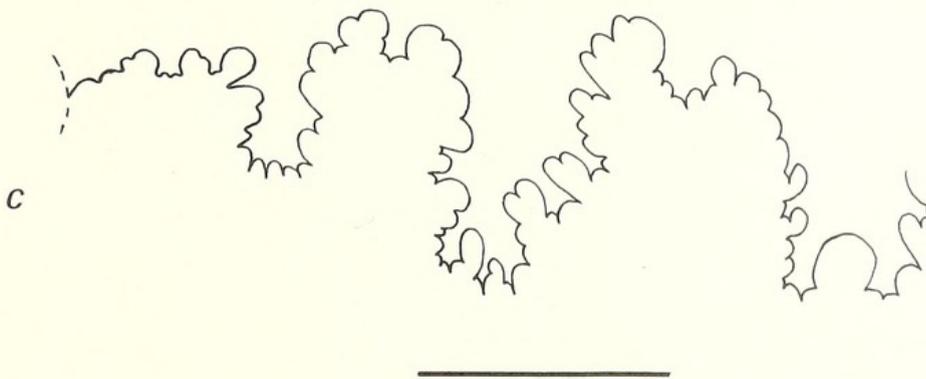
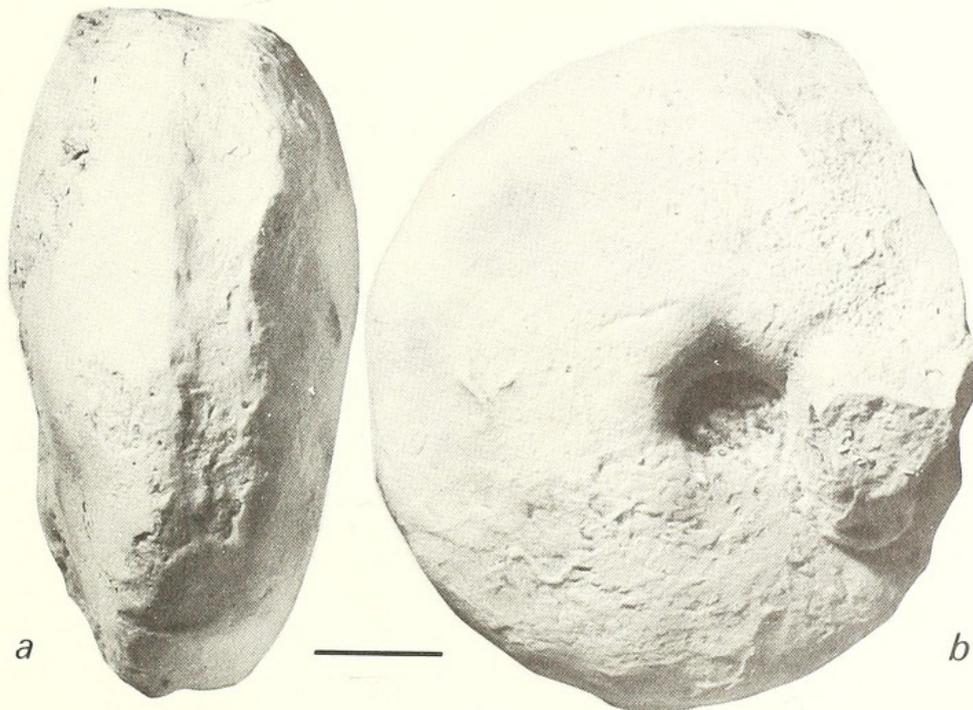
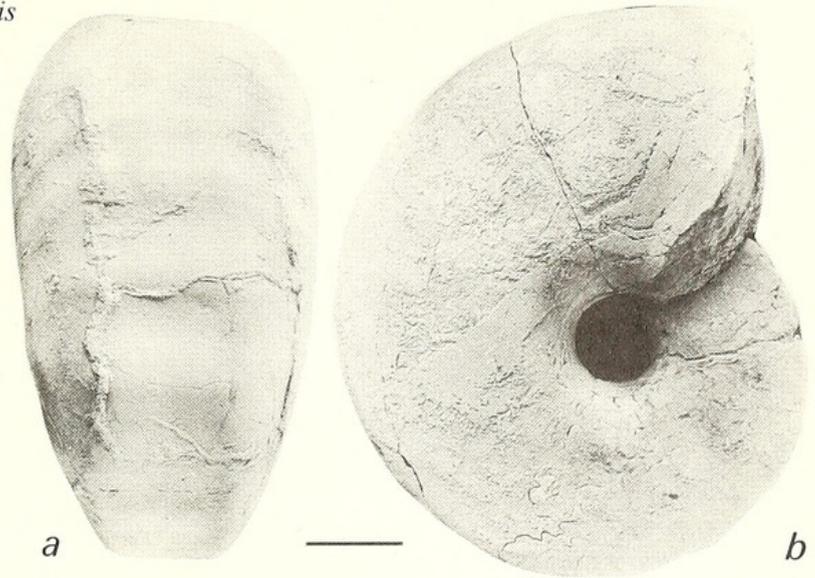
Type species. *Spathites chispaensis* Kummel and Decker, 1954, by original designation.

Diagnosis. Medium sized, involute ammonites with compressed to depressed whorl sections, trapezoidal when young, but tending to the subquadrate when mature. During early to middle growth there are strong to weak umbilical bullae giving rise to from one to three ribs, with additional shorter, intercalated ribs, each of which bears clavate inner and outer ventrolateral tubercles on either side of a flat or concave venter. When adult, the ornament commonly declines, leaving shells which either have blunt bullae and low ribs bearing low ventral clavi, or are smooth with sharp ventral shoulders with or without low clavi and a concave venter crossed by low, broad ribs corresponding to the clavi.

Suture simple with broad, asymmetrically bifid saddles and narrow lobes, pseudoceratitic in some species.

Discussion. The type species of *Spathites*, *S. chispaensis* Kummel and Decker, 1954 (p. 311, pl. 30, figs. 1, 2; pl. 31, figs. 1–15; text-fig. 1. Text-fig. 1 herein) was originally described on the basis of large collections from the early mid-Turonian Chispa Summit Formation of northern Chihuahua, Mexico, and Chispa Summit, Jeff Davis County, Texas. We have re-examined this material, in the collections of the Texas Memorial Museum, Austin, Texas, and confirm the very wide intraspecific variation described by Kummel and Decker, which is also demonstrated by new material before us (OUM KT. 859, 895, 943, etc.). There is every transition from compressed, feebly ornamented nuclei (Kummel and Decker 1954, pl. 31, figs. 7–9) to depressed ones with strong tubercles and ribs (Kummel and Decker 1954, pl. 31, figs. 10–12). In all forms, however, these decorated inner whorls are followed by a virtually smooth adult stage, where ribbing is restricted to low transverse undulations across the venter (text-fig. 1), corresponding to long low clavi at the shoulder. These adults are close to the holotype of *Neoptychites (Spathitoides) sulcatus* Wiedmann (1960, p. 756, pl. 7, figs. 7, 8, text-figs. 11, 12). This (text-fig. 2) comes from a somewhat lower horizon in the Turonian of northern Spain, and

TEXT-FIG. 1a, b. *Spathites (Spathites) chispaensis* Kummel and Decker. The holotype UT 20811, from the mid-Turonian Ojinaga Formation of the Placer de Guadalupe district, Sabaco (San José de Cochahuatá). Bar scale is 2 cm.



TEXT-FIG. 2a, b, c. The holotype of *Spathitoides sulcatus* Wiedmann, Geol. Pal. Inst. Tübingen Collection no. 1162/4 from the early Turonian south of Pedrosa, Burgos, Spain. Bar scales are 2 cm.

was regarded by Wiedmann as a derivative of *Neoptychites*, characterized by being completely smooth with a trapezoidal whorl section, a narrow umbilicus, and a truncated, concave siphonal region with periodic constrictions. The suture (text-fig. 2) is much subdivided, with the lateral lobe deeper than the external, and asymmetric. The umbilical lobe is short, the incisions on the lobes are sharp, the terminations of the saddles are rounded, and the umbilical saddle is much enlarged. As can be seen from comparing text-fig. 1 and text-fig. 2 the species is identical with the feebly ornamented variants of *S. chispaensis*, the 'constrictions' on the venter noted by Wiedmann corresponding to the interspaces between the ribs on the venter of *S. chispaensis*. The sutures are indeed more incised than those of *S. chispaensis* but no more so than *S. rioensis* Powell (1963, p. 1228, pl. 169, fig. 2; pl. 170, figs. 1-3, 6-7; text-figs. 5j, 6c-e), as can be seen from comparing text-figs. 1b and 8c. We would, therefore, regard *Spathitoides* as a synonym of *Spathites*.

Jeanrogericeras Wiedmann, 1960, is shown, by study at all growth stages of its type species, *Ammonites reveliereanus* Courtiller, 1860, to differ from *Spathites* only in the shape and ornament of the mature last whorl; no more than subgeneric separation is appropriate. Moreover, *Jeanrogericeras*, with its unspecialized last whorl, intermediate between that of *Metioceras* and typical *Spathites*, is clearly more primitive, and, in Europe at least, occurs earlier than *S. (Spathites)*.

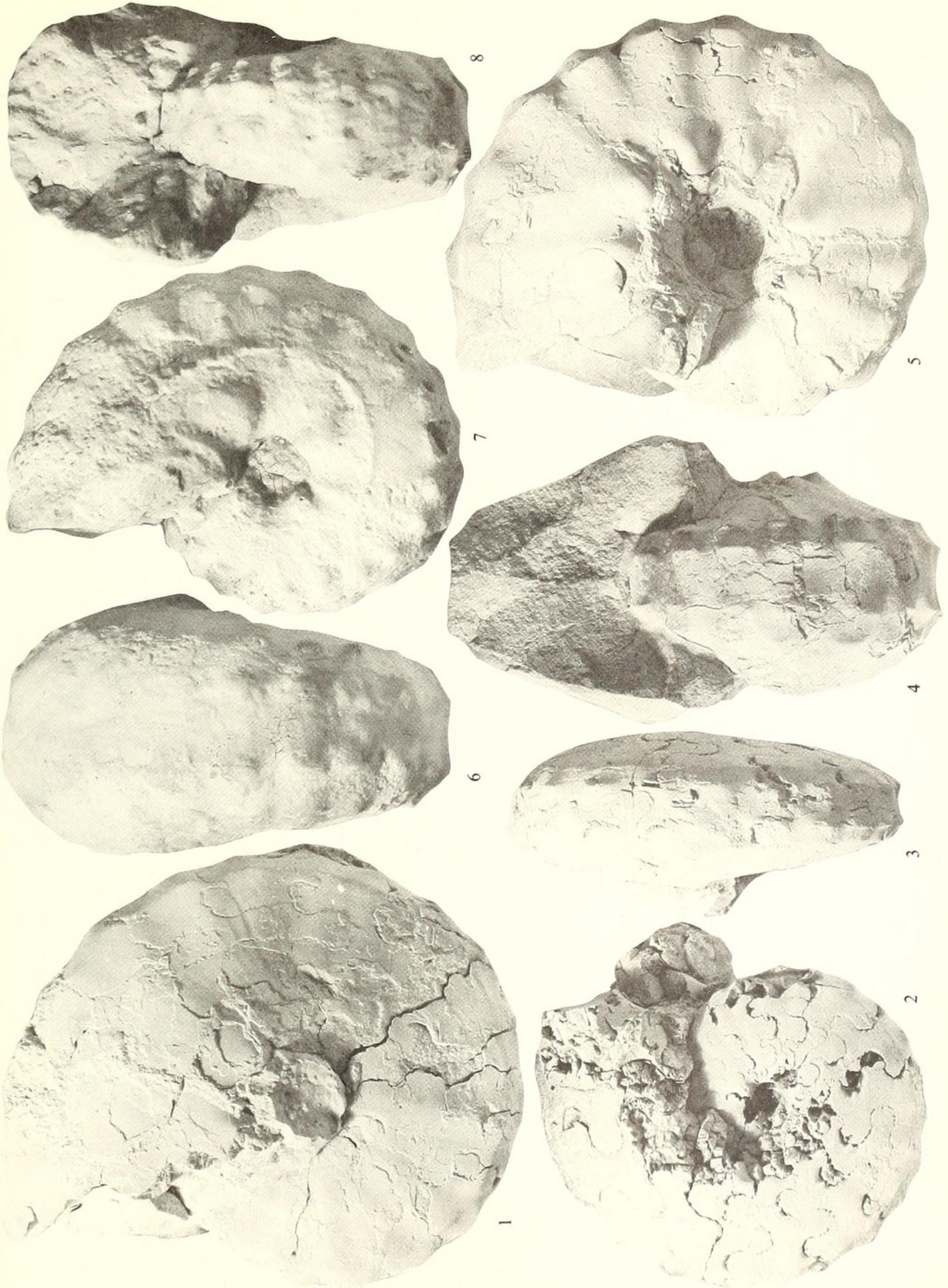
Wiedmann (1960, p. 741) established a genus *Fallotites*, with type species *Vascoceras subconciliatum* Choffat (1898, p. 64), in a new subfamily Fallotitinae. The genus was characterized by inner whorls with subquadrate or trapezoidal section, flat sides and venter and large umbilical tubercles each giving rise to two or three weak ribs, each of which bears weakly clavate inner and outer ventrolateral tubercles; the body chamber loses all ornament except large rounded umbilical tubercles, becomes rounded in section and tends to uncoil. His species of *Fallotites* include both depressed forms and those with a whorl section slightly higher than wide. Moreover, some of his figures show that the body chamber retains very low coarse ribs as well as the umbilical tubercles (Wiedmann 1960, pl. 3, figs. 4-7; pl. 4, figs. 2, 3). The characters of the inner whorl are exactly those of *S. (Jeanrogericeras) reveliereanus* at the corresponding stage (compare Pl. 104, figs. 6-8; Pl. 105, figs. 13-15 with Pl. 105, figs. 1-12), whilst those of the outer whorl are only slightly more extreme than those of some specimens of *reveliereanus* (compare Pl. 106, figs. 4-5 and text-figs. 2 and 5). There is thus a continuum that includes the variable populations of *reveliereanus* and *Fallotites* spp; indeed, Stankievich and Pojarkova (1969) include in *Fallotites* species with much stronger ribbing on the body chamber than occurs in *Jeanrogericeras*. We see no good reason for separating these two taxa and regard *Fallotites* as a synonym of *S. (Jeanrogericeras)*. *Fallotites (Ingridella)* Wiedmann, 1960, includes species with outer whorls that resemble some *Vascoceras*, but they have inner whorls with distinct but subdued inner and outer ventrolateral tubercles, very feeble ribs, and sparse, very large rounded umbilical tubercles that persist to the outer whorl, where other ornament disappears, leaving a depressed rounded whorl section. We would therefore regard *Ingridella* as a further, specialized, subgenus of *Spathites*.

Occurrence. Highest Cenomanian (Wright and Kennedy, in press) to mid-Turonian of western Europe—England; Touraine, Aquitaine, and Provence in France; Spain, Portugal, Czechoslovakia, the U.S.S.R. (Kirgisia and the Tadzhiksian depression); southern India, north Africa; Texas, New Mexico, and northern Mexico.

EXPLANATION OF PLATE 104

Figs. 1-5. *Spathites (Spathites) puercoensis* (Herrick and Johnson). Specimens are from the mid-Turonian part of the Mancos Shale at USGS Mesozoic Locality D4020 1.1 miles south-west of Ojito Springs, San Ysidro Quadrangle, Sandoval County, New Mexico. USGS Coll., Denver.

Figs. 6-8. *Spathites (Jeanrogericeras) robustus robustus* (Wiedmann). Inner whorls of the holotype Geol. Pal. Inst. Tübingen Collections, Ce 1162/12. Early Turonian of Picofrentes (Soria), Spain.



KENNEDY, WRIGHT and HANCOCK, *Spathites*

Subgenus *Jeanrogericeras* Wiedmann, 1960
 [= *Fallotites* Wiedmann, 1960]

Type species. *Ammonites reveliereanus* Courtiller, 1860, by original designation.

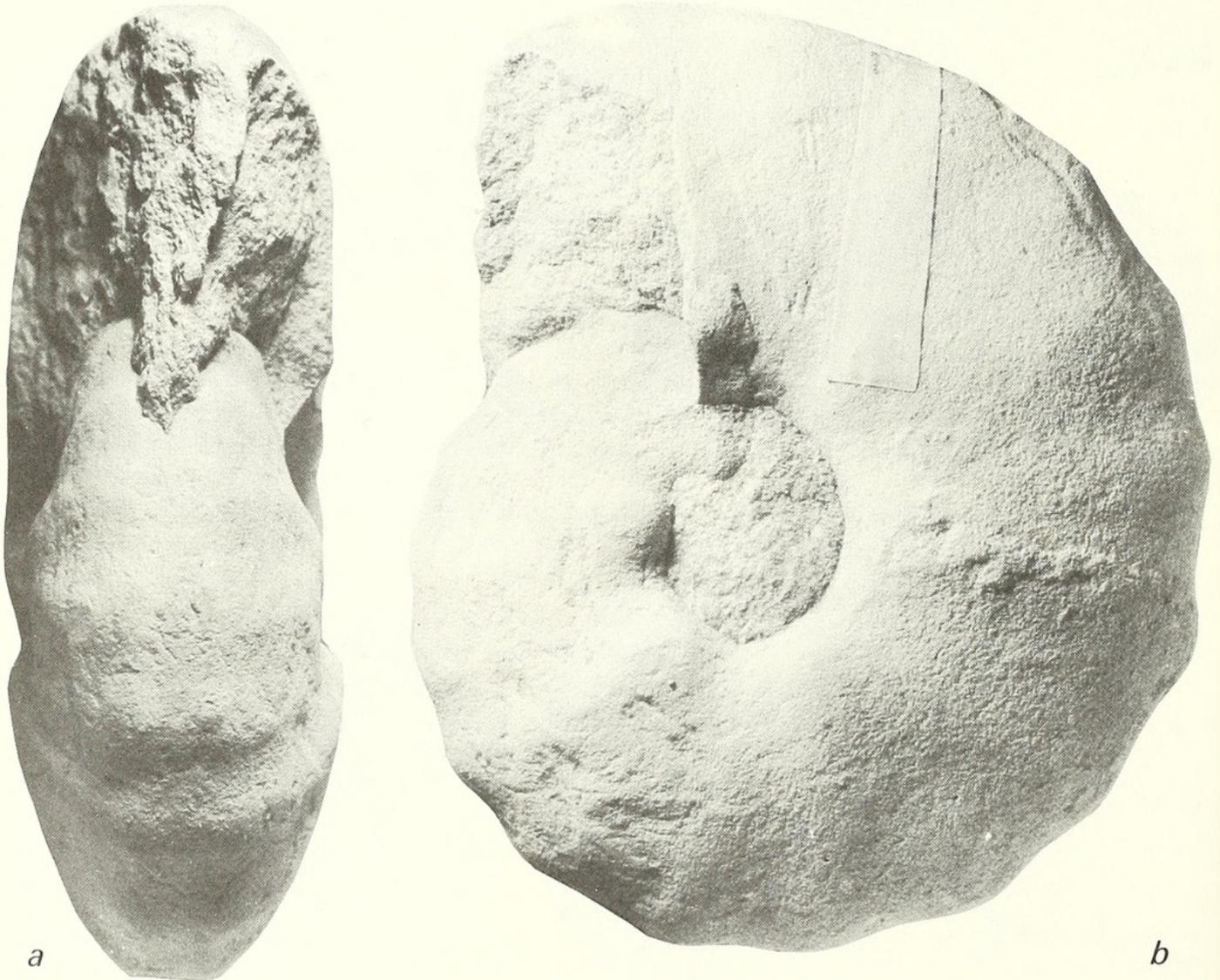
Name of type species. In 1860 Courtiller spelt the name *revelieranus* on p. 249 and *Reveliereanus* in the explanation of plate 2, fig. 5. Where two different spellings of a name appear in the first publication, Art. 32(b) of the *Rules of Zoological Nomenclature* provides that the spelling adopted by the first reviser is to be accepted as the correct original spelling. Courtiller himself was the first reviser and in 1867 consistently spelt the name '*Reveliereanus*'.

Diagnosis. *Spathites* in which the outer whorls retain ribs and tubercles.

Spathites (Jeanrogericeras) reveliereanus (Courtiller)

Plate 105, figs. 1-12; Plate 106, figs. 1-2; text-figs. 3-6

- 1860 *Ammonites revelieranus/Reveliereanus* Courtiller, p. 249, pl. 2, figs. 5-8.
 1867 *Ammonites Reveliereanus* Courtiller; Courtiller, p. 4, pl. 3, figs. 1-4.
 1894 *Mammites Revellieri* (Courtiller); de Grossouvre, p. 28.



TEXT-FIG. 3, a, b. *Spathites (Jeanrogericeras) reveliereanus* (Courtiller). Adult specimen from the mid-Turonian of Loudon, France, in the Sorbonne Collections (ex de Grossouvre Collection).

- 1896 *Ammonites/Mammites rochebruni* Coquand; Peron, p. 23.
 1902 *Mammites binicostatus* Petrascheck, p. 145, pl. 7, fig. 6a-b; pl. 8, figs. 1a-b, 3a-b.
 1903 *Ammonites Revelieranus* (Courtyiller); Pervinquier, fiche 7, 7a, 7b.
 1907 *Mammites Reveliereanus* Courtyiller; Pervinquier, p. 311.
 1912 *Mammites Revelieri* Courtyiller; de Grossouvre, p. 18.
 1912 *Mammites Reveliereanus* Courtyiller; Roman, p. 12, pl. 1, fig. 1, 1a.
 1928 *Mammites revelierei* Courtyiller; Douvillé, p. 11.
 1935 *Mammites revelierei* Courtyiller; Faraud, p. 18, fig. 3.
 1935 *Mammites revelieranus* Courtyiller; Karrenberg, p. 131, pl. 30, figs. 2-4; pl. 33, figs. 2-3; text-fig. 2 (including vars. *quadrata*, *globosa*, and *lata*).
 1940 *Mammites revelieranus* Courtyiller sp.; Fabre, p. 278, pl. 10, figs. 5-6.
 1960 *Jeanrogericeras revelieranum* (Courtyiller); Wiedmann, p. 740.
 1960 *Jeanrogericeras binicostatum* (Petrascheck); Wiedmann, p. 741, pl. 2, figs. 7-9; text-fig. 5.
 1964 *Jeanrogericeras revelieranum* (Courtyiller); Wiedmann, p. 127.
 1964 *Jeanrogericeras binicostatum* (Petrascheck); Wiedmann, p. 126, figs. 10a-c, 11.
 1967 *Metoicoceras stoliczkai* Sastry and Matsumoto, p. 2, pl. 1, figs. 1a-f.
 1977 *Jeanrogericeras reveliereanum* (Courtyiller); Hancock, Kennedy, and Wright, p. 156.

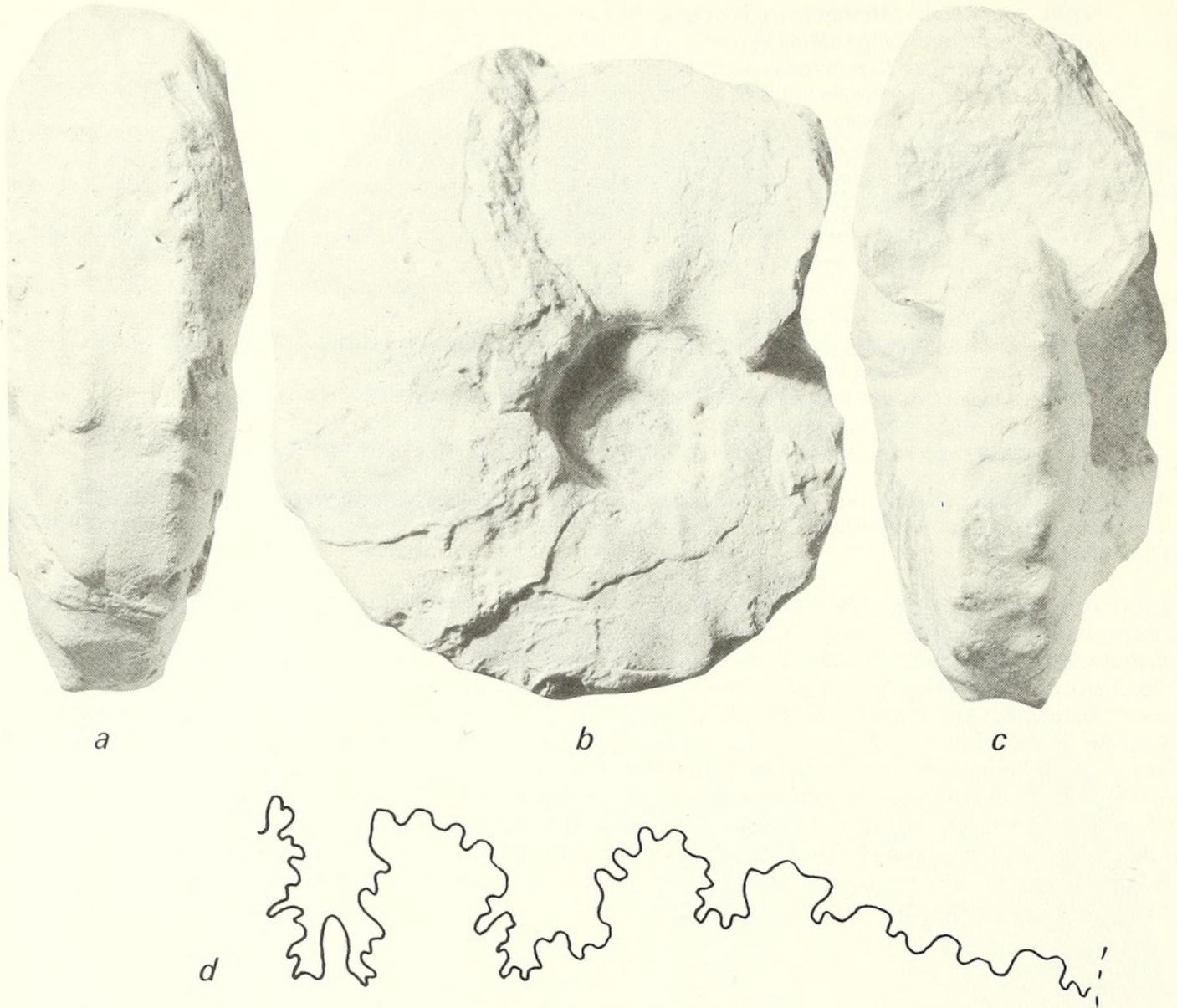
Lectotype. Here designated, the original of Courtyiller 1860, pl. 2, figs. 5-6, refigured by Pervinquier 1903, figs. T1-T2. It was originally in the Museum of the Château de Saumur, but we were unable to locate it with the rest of Courtyiller's types.

Other specimens. The original of Courtyiller 1867, pl. 3, figs. 1-2, survives and is figured here as text-fig. 5; it is probably from the Saumur region. MNHP 6777 (d'Orbigny Collection) from Saumur, one of the syntypes of *A. fleuriausianus* d'Orbigny. A further individual with this number is also a *J. revelieranus*, but is labelled 'Rochefort' on the specimen. MNHP unregistered, from 'Taillebourg, Charente, Ligérien E', bearing an old label '*Ammonites rochebruni* Coquand' (Pl. 106, figs. 1-2). SP, unregistered, de Grossouvre Collection, Loudon (text-fig. 3). OUM KZ767-771 from the St. Cyr-en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay (Pl. 105, figs. 1-12). FSR 1700, from Taillebourg; OUM KZ779-783 from the Calcaire à Céphalopodes, Cimentière Lafarge, east of Route N10, 5 km south-west of Angoulême. Geol. Pal. Inst. Tübingen CE 1162/6, the original of Wiedmann 1960, pl. 2, figs. 7-9, from Ollogoyen, Navarra, Spain. A cast of the holotype of *Metoicoceras stoliczkai* Sastry and Matsumoto, Geological Survey of India Collections no. 18170, from north of Mungilpadi, Perambalur Taluk, Tiruchinapalli (Trichinopoly) district, Madras (text-fig. 4).

Dimensions.

	D	Wb	Wh	Wb:Wh	U
GPIT Ce 1162/6	132.0 (100)	50.0 (380)	61.0 (46)	0.82	24.0 (18)
SP, Loudon	105.5 (100)	37.5 (36)	43.2 (41)	0.87	23.9 (23)
S5	102.5 (100)	43.5 (42)	50 (49)	0.87	18.2 (17.8)
MNHP Taillebourg	95.5 (100)	45.0 (47)	40.0 (42)	1.13	18.2 (19)
GSI. 18170	77.6 (100)	32.2 (41)	38.7 (50)	0.83	17.0 (22)
OUM KZ767	44.0 (100)	19.8 (45)	22.1 (50)	0.89	7.8 (17)
	— (—)	14.8 (—)	16.5 (—)	0.89	— (—)
OUM KZ770	42.8 (100)	26.4 (62)	19.7 (46)	1.34	7.6 (18)
OUM KZ771	32.7 (100)	18.6 (61)	15.7 (48)	1.18	5.3 (16)
OUM KZ768	— (—)	8.0 (—)	12.3 (—)	0.65	— (—)

Description. Juveniles up to 50 mm are very variable. Coiling is involute, with a small umbilicus (usually around 16% of the diameter). Our most compressed individual is OUM KZ768 (Pl. 105, figs. 10-12), with a whorl breadth to height ratio of 0.65. The whorls are high, with the greatest breadth low on the flanks, the inner flanks being gently inflated, the outer flanks flattened, converging to the narrow, tabulate venter. Weak umbilical bullae give rise to pairs of low flexuous ribs, which bear faint inner and well-developed outer ventrolateral clavi on either side of the flattened venter. As inflation increases (Pl. 105, figs. 7-9; text-fig. 5), the whorl section become trapezoidal, with the greatest breadth at the umbilical bullae. In OUM KZ770 (Pl. 105, figs. 4-6), with a whorl breadth to height ratio of 1.18, the umbilicus is deep, with a high subvertical wall and abruptly rounded shoulder, gently swollen inner and convergent outer flanks, and a narrow, flattened venter. There are six or seven strong conical umbilical bullae; these give rise to groups of two or three broad, strong, straight prorsiradiate ribs,

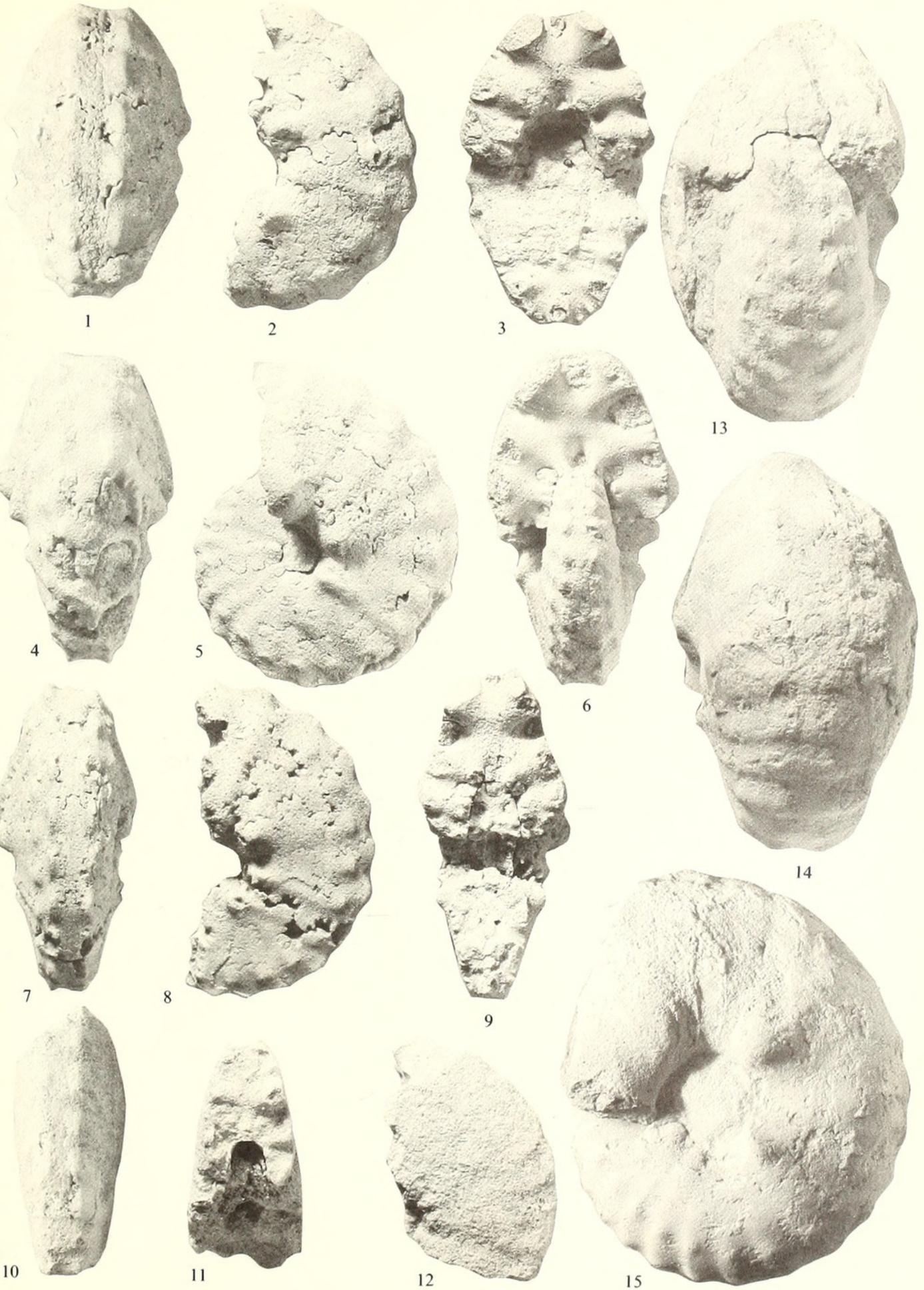


TEXT-FIG. 4a, b, c, d. The holotype of *Metoicoceras stoliczkai* Sastry and Matsumoto, Geological Survey of India Collections no. 18170, from north of Mungilpadi, Perambalur Taluk, Tiruchinapalli district, Madras, India.

with additional intercalated ribs arising below mid-flank to give a total rib-density of 23 or 24 per whorl. Each rib bears a conical to feebly clavate inner and a strong clavate outer ventrolateral tubercle. Rib strength varies even in individuals showing this degree of inflation, as does rib direction, from prorsiradiate to rursiradiate, as in OUM KZ771. The most inflated individuals, including the lectotype, have swollen sides, with a whorl breadth to height ratio of up to 1.4. Here the bullae are coarse, conical, and crowded, 6 to 8 per whorl, giving rise to groups of ribs with inner and outer ventrolateral tubercles as before (Pl. 105, figs. 1-3).

EXPLANATION OF PLATE 105

Figs. 1-12. *Spathites (Jeanrogericeras) reveliereanus* (Courtillet). 1-3, OUM KZ769; 4-6, OUM KZ770; 7-9, OUM KZ767; 10-12, OUM KZ768. All specimens are from the mid-Turonian St. Cyr-en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, France.
Figs. 13-15. *Spathites (Jeanrogericeras) subconciliatus hispanicus* (Wiedmann). OUM Collections, early Turonian of Pedrosa, Burgos, Spain.



KENNEDY, WRIGHT and HANCOCK, *Spathites*

Adult specimens before us show a similar range of whorl inflation from compressed, as in the Loudon example (text-fig. 3), to inflated, as in OUM KZ769. Most individuals, however, have whorl breadth to height ratios of between 0.9 and 1.1. The whorl section is trapezoidal, with the greatest breadth at the umbilical bullae, the flanks convex and the venter narrow and flattened or even sulcate. Five to seven coarse, blunt umbilical bullae each give rise to two or three low, broad, commonly rursiradiate ribs which may bear a trace of an inner ventrolateral tubercle (although this commonly disappears by 70–80 mm diameter), together with long, low, outer ventrolateral clavi, linked by a broad swelling across the flattened to concave venter, giving an undulose lateral profile (Pl. 106, figs. 1, 2) to the shell. Between clavi the ventrolateral shoulders are markedly angular. The last part of the adult body chamber may show a decline in ornament, especially of the ribs and clavi, and may contract (text-fig. 3), so that the coiling becomes scaphitoid and the umbilicus expands to 23% of the diameter.

The sutures are moderately subdivided, with rounded incisions. E/L is massive and asymmetrically bifid; L is deep and narrow; L/U₂ small and bifid, as is U₂ and the first auxiliary element (text-fig. 6).

Discussion. Courtyiller introduced the name *A. reveliereanus* in 1860 with both a description and figure; he illustrated additional material in 1867. Pervinquière (1903) refigured some of these specimens photographically. Coquand had introduced the name *A. rochebruni* in 1858 and de Grossouvre (1894) regarded *rochebruni* as having priority over *reveliereanus*; Peron used this name in 1896 for material from Charente, Touraine, Les Jeannots, and Revest in Provence. Coquand gave no illustrations of *rochebruni* and we have been unable to locate the type specimens in the Collections of the Muséum d'Histoire Naturelle or the School of Mines (now at Lyon) which contains the other ammonite types from this work. Coquand's description could well be of a *Jeanrogericeras*, but significant specific features mentioned by Coquand differentiate it from *reveliereanus*: the presence of 12/13 ventral tubercles per whorl on inner whorls, fewer tubercles on the outer, the umbilical now becoming larger and conical and the ventral tubercles disappearing altogether. Now *J. reveliereanus* has far more ventrolateral tubercles per whorl when young (18–22) and the umbilical bullae tend to weaken with age. It thus seems unlikely, if Coquand's description is accurate, that the two species are the same. *A. rochebruni* might be a *Paramammites* or belong to some other genus. We would therefore continue to use the name *reveliereanus*, at least until the types of *rochebruni* are discovered and illustrated.

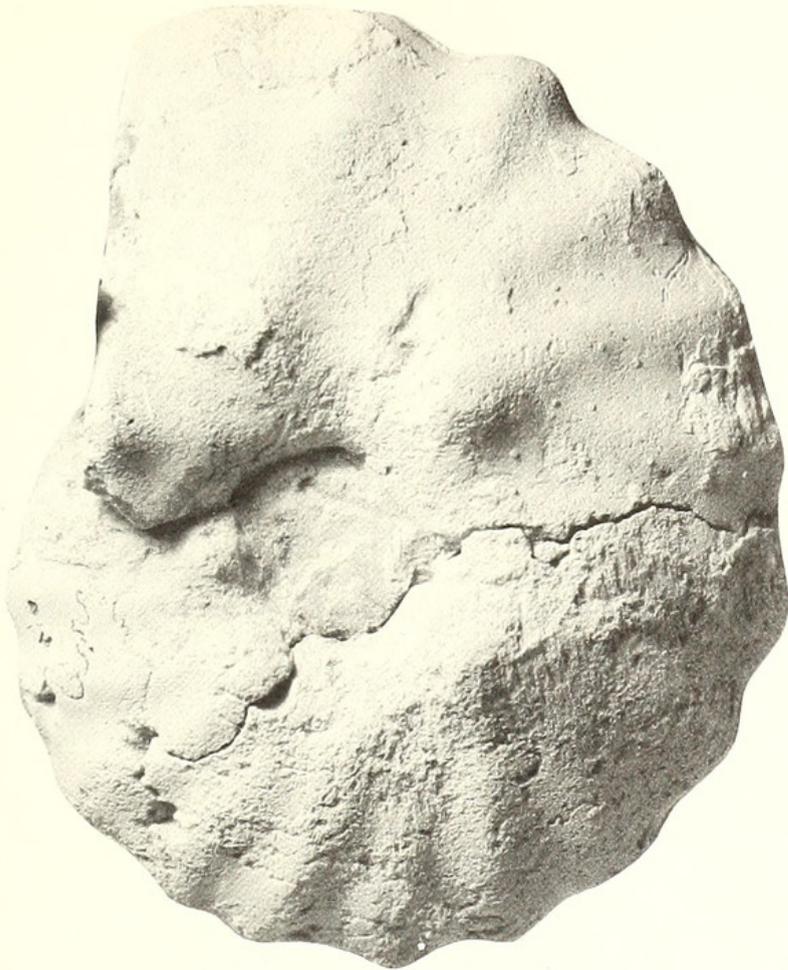
Courtyiller (1860) was clearly aware that individuals of his species varied greatly, describing the 'females' as 'beaucoup plus renflées, surtout vers l'ombilic, que les mâles. Leurs tubercles sont aussi beaucoup plus développés'. Karrenberg (1935, p. 32, text-fig. 2, pl. 30, figs. 2–4; pl. 33, figs. 2–3) discussed this variation at length, naming three forms: (a) Typical form: the whorl section is trapezoidal, with a variable whorl height to whorl breadth ratio. The flanks are rather flat and are clearly differentiated from the flattened venter. The greatest breadth is at the umbilical edge. (b) Var. *quadrata*. The juveniles have the whorl section of the typical form up to a diameter of 30 mm. Later, the flanks become parallel, giving an almost quadrate section. (c) Var. *globosa*. The whorl section is almost circular, with the greatest breadth at approximately mid-flank. It differs from the typical form even when young because of the distinctive section. (d) Var. *lata*. Flanks and venter are evenly rounded, with the whorl section significantly wider than high. The inner whorls show the typical cross-section.

EXPLANATION OF PLATE 106

Figs. 1–2. *Spathites (Jeanrogericeras) reveliereanus* (Courtyiller). Unregistered specimen in the Collections of the Muséum d'Histoire Naturelle, Paris, from Taillienbourg, Charente, France.

Fig. 3. *Spathites (Spathites) puercoensis* (Herrick and Johnson). Ventral view of the specimen illustrated as Plate 104, fig. 1.

Figs. 4–5. *Spathites (Jeanrogericeras) subconciliatus hispanicus* (Wiedmann). OUM Collections, early Turonian of Pedrosa, Burgos, Spain.



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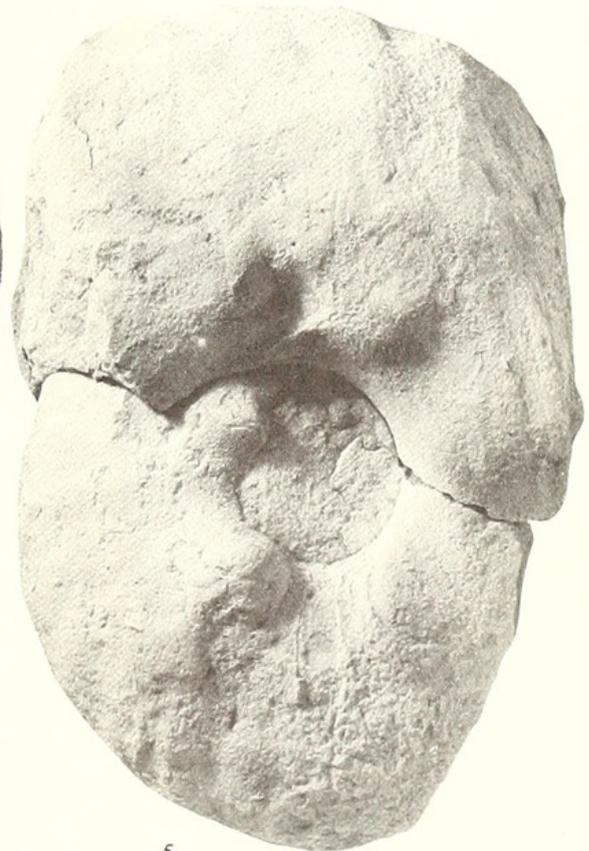
2



3



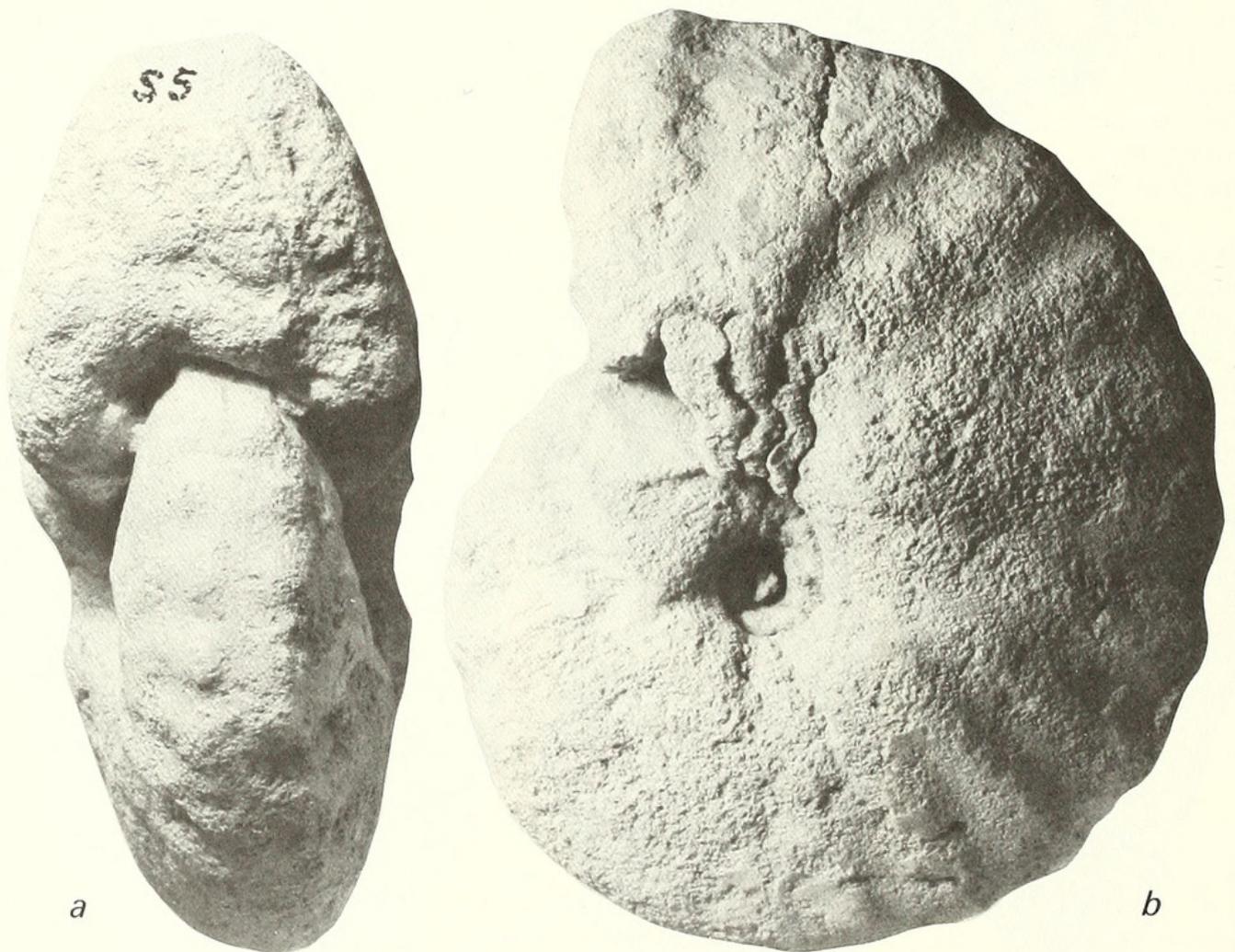
4



5

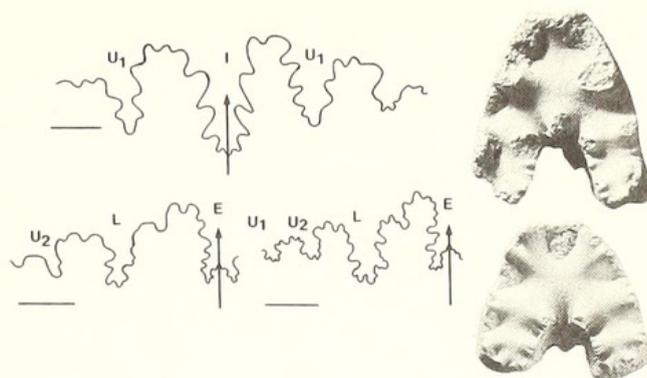
The Touraine material shows even wider variation, as discussed above, the breadth to height ratio ranging from 0·69 to 1·4, with typical covariance of ornament: the compressed individuals have weak bullae, low, flexuous ribs and scarcely detectable inner ventrolateral tubercles; the depressed individuals have massive conical bullae, coarse ribs, and well-differentiated inner and outer ventrolateral tubercles.

S. (Jeanrogericeras) binicostatum (Petrascheck) (1902, p. 145, pl. 7, fig. 6a-b; pl. 8, figs. 1a-b, 3a-b; see also Wiedmann 1960, p. 741, pl. 2, figs. 7-9; text-fig. 5; 1964, p. 126, figs. 10a-c, 11) shows considerable variation, according to Petrascheck's illustrations; Wiedmann (1960, 1964) distinguished it from *S. (J.) reveliereanus* on the basis of the absence of intercalated ribs, eight rather than four umbilical tubercles, sharper ventrolateral shoulders, a more marked, excavated siphonal region, a larger umbilicus and more massive, less asymmetric lobes in the suture line. The lectotype closely matches the individual from Loudon illustrated here as text-fig. 3, whilst sharpness of ventrolateral shoulders appears to be in part a matter of preservation, the Bohemian material being distorted by compaction in our experience. The alleged difference in numbers of umbilical bullae cannot be supported: the small lectotype of *J. reveliereanus* very clearly has at least seven in Pervinquière's figure; other specimens have eight or nine, matching the smaller specimen figured by Petrascheck (1920, pl. 7, fig. 6a-b). Wiedmann's large Spanish specimen (1960, pl. 2, figs. 7-8; 1964, fig. 10a-c) has eight massive bullae, the original of Courtiller (1867, pl. 3, figs. 1-2) has seven. In many specimens before us it is a matter of opinion whether ribs are grouped and attached to bullae or



TEXT-FIG. 5a, b. The surviving Courtiller specimen of *Spathites (Jeanrogericeras) reveliereanus* (Courtiller). CS5, from the Saumur region, Touraine, France.

TEXT-FIG. 6. Suture lines and whorl sections of juvenile *Spathites* (*Jeanrogericeras*) *reveliereanus* (Courty), from OUM KZ767 and 769 from the mid-Turonian St. Cyr en-Bourg Fossil Bed of the Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, France. Bar scale is 1 cm.



intercalated in some cases. None of these criteria seems sufficient to justify specific separation of two taxa.

Metoicoceras stoliczkai Sastry and Matsumoto (1967, p. 2, pl. 1, fig. 1a-f) (text-fig. 4) is also a synonym of *J. reveliereanus*, closely resembling the lectotype of *J. binicostatum*. The suture line is clearly that of a *Jeanrogericeras*, rather than a *Metoicoceras*.

Occurrence. *S. (Jeanrogericeras) reveliereanus* has a restricted range in the mid-Turonian, where it occurs with early *Collignoniceras woollgari* (Mantell), *Kamerunoceras turoniense* (d'Orbigny), and other ammonites in Touraine, and at this and slightly lower levels in Aquitaine, Provence, Spain, and Czechoslovakia. The Indian occurrence is not accurately dated.

MAMMITINE PHYLOGENY

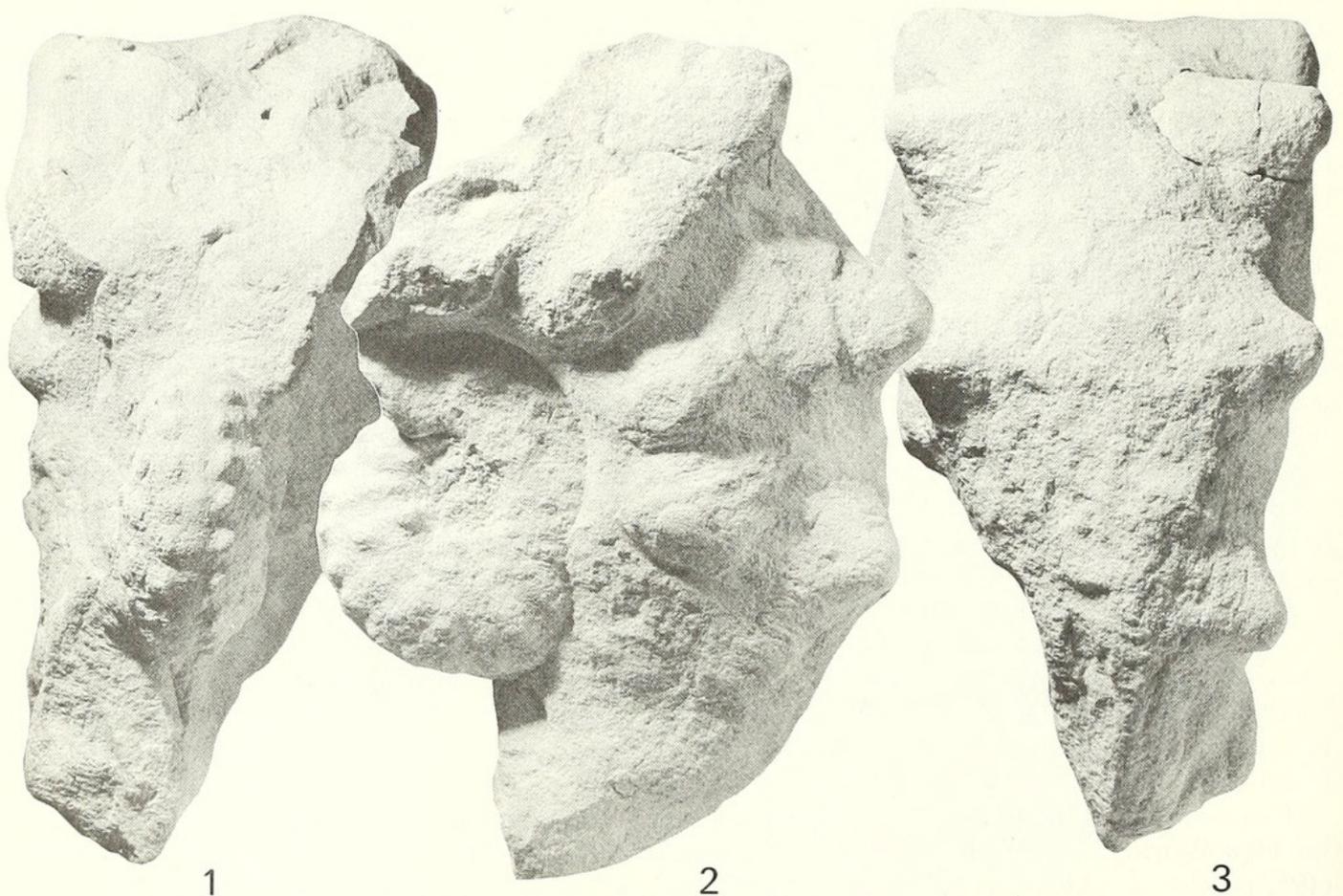
The inferred position of *S. (Spathites)* and *S. (Jeanrogericeras)* in mammitine phylogeny is shown in text-fig. 9. Rather than duplicate existing descriptions we refer the reader to Kennedy, Juignet and Hancock (in press) for an account of the late Cenomanian *Metoicoceras* species and to Kummel and Decker (1954) and Powell (1963) for descriptions of *S. (Spathites)*. More extensive accounts of the late Cenomanian *Thomelites* and Turonian *Mammites* and *Metasigaloceras* will appear elsewhere (Wright and Kennedy, in press).

Thomelites first appears at the base of the Upper Cenomanian, and is represented by an undescribed form from the Chalk Basement Bed of Askerswell, Dorset (Kennedy 1970, p. 644; OUM Collections). By the middle of the Upper Cenomanian, the genus is known from Britain, France, the Middle East, Brazil and elsewhere, and overlaps in time the first *Metoicoceras*, which evolved in the western interior and Texas regions of the United States. As already noted, the earliest species of this genus have a siphonal tubercle when young, but later forms such as *M. defordi* Young (1957), *M. mosbyense* Cobban and *M. muelleri* Cobban (1953), although endemic to this area, show a bituberculate venter throughout. Towards the close of the Cenomanian in the American *S. gracile* Zone *Metoicoceras* spread to the Old World and *M. geslinianum* (d'Orbigny) occurs in England just below the level of the first *S. (Jeanrogericeras)* in Devon, which yields *S. (Jeanrogericeras)* cf. *subconciatus* (Choffat) (Wright's Collection no. 25310). This occurrence can be correlated firmly with Zone III of Wiedmann's Iberian sequence (1960, 1964) which clearly demonstrates the succession with *S. (Jeanrogericeras)* [*Fallotites*] in his Zones III-V and *S. (Spathites)* [*Spathitoides*] occurring only in Zone V. In Europe *S. (Jeanrogericeras)* extends upwards to overlap early *C. woollgari*, *R. (Romaniceras) kallesi* Zàzvòrka, *Neoptychites cephalotus* (Courty), and other species in France and Spain and a somewhat impoverished but contemporaneous assemblage in Czechoslovakia.

This association can in turn be related to the first well-documented occurrences of *S. (Spathites)* in the New World, where the early *C. woollgari* Zone fauna of northern Mexico documented by Powell (1963) yields *S. (Spathites) rioensis* in association with *C. woollgari* (= *Selwynoceras mexicanum* (Böse) of Powell), *Kamerunoceras isovokyense* (Collignon), *Neoptychites xetiformis* Pervinquièrè and *Mammites depressus* Powell. Our present state of knowledge suggests that this occurrence is a little below that of the Touraine assemblages. Above this a sequence can be traced through *Spathites*

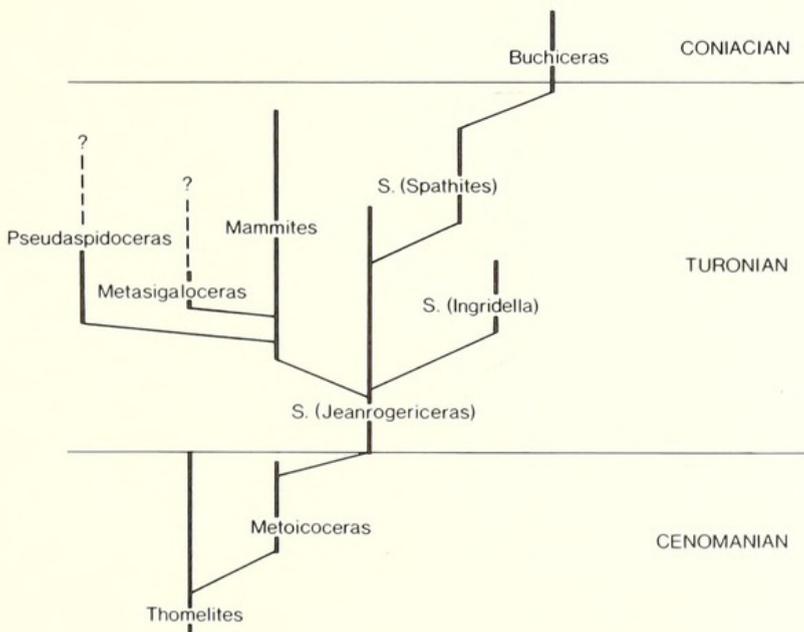
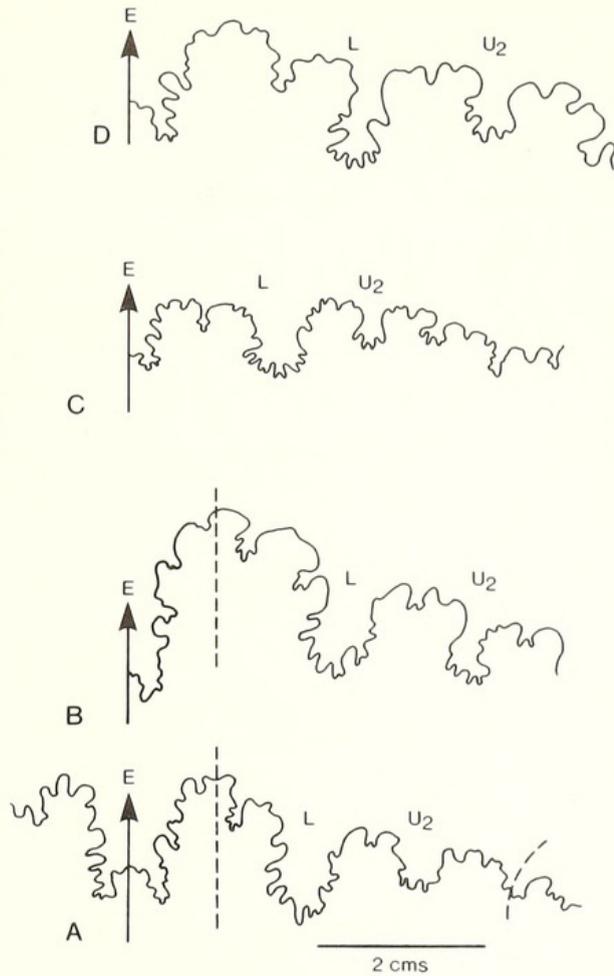
(*S.*) *chispaensis* Kummel and Decker (which occurs with *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka)) at a higher level in the *woollgari* Zone to *S.* (*S.*) *puercoensis* Herrick and Johnson (1900), which occurs in the succeeding North American *Prionocyclus hyatti* Zone. Detailed discussion of these American species is beyond the scope of this contribution, but we note that all species show as wide a range of intraspecific variation as is shown by *S.* (*J.*) *reveliereanum*, as can be seen from Pl. 104, figs. 1–5; Pl. 106, fig. 3.

Of especial interest is the progressive change in sutural complexity in the *rioensis* → *chispaensis* → *puercoensis* lineage, shown here in text-fig. 8. This reduction in incisions and trend towards a pseudoceratitic form provides a clue to the evolutionary origin of the Coniacian *Buchiceras* Hyatt, 1875, currently classed as a tissotiid. In our view, sutural pattern, gross shell form, and ornament all point to *Buchiceras* as the last member of the Mammitinae. Its evolute quadrate whorls with ribs branching from umbilical bullae and terminating in ventral tubercles are mammitine and distinct from Tissotiidae with siphonal keel or row of tubercles, which we now regard as an offshoot of the Barroisiceratinae via *Tissotioides*. This view is confirmed by a most important specimen, now housed at the U.S. Geological Survey at Denver, collected from the *Prionocyclus hyatti* Zone of Bells, Grayson County, Texas, by the late James Conlin of Fort Worth. This has a more compressed body chamber than typical *S.* (*Spathites*) but still shows a slight facet representing the outer flank between the two rows of ventrolateral tubercles; its suture is identical with that of *Buchiceras* and it is clearly intermediate between *S.* (*S.*) *chispaensis* and *B. bilobatum*. We would also argue that the early, robust *S.* (*Jeanrogericeras*) of the *subconciliatus/quadratus* group (e.g. Pl. 104, figs. 6–8) are the origin of *Mammites*. The early whorls of these species and early forms of *Mammites* occurring immediately above them in southern England are identical in their general plan of decoration (text-fig. 7);



TEXT-FIG. 7. 1–3. *Mammites* sp. WW 19898, from the lower part of the *Inoceramus labiatus* Zone of White Cliff, Seaton, Devon. The outer whorls are those of a true *Mammites*, the inner strongly reminiscent of *Spathites* (*Jeanrogericeras*), $\times 0.56$.

TEXT-FIG. 8. Progressive modification of sutures in the *Spathites* (*Spathites*) to *Buchiceras* sequence: A: *Spathites rioensis* Powell, OUM KT1244, low *Collignoniceras woollgari* Zone, Cannonball Hill, Chihuahua, northern Mexico. B: *S. chispaensis* Kummel and Decker, OUM KT943 high *C. woollgari* Zone, Chispa Summit, Texas. C: *S. puercoensis* (Herrick and Johnson), USGS 15947-20, *Prionocyclus hyatti* Zone, USGS Mesozoic locality D4020, 1.1 miles south-west of Ojito Springs, San Ysidro Quadrangle, Sandoval County, New Mexico (kindly supplied by W. A. Cobban). D: *Buchiceras bilobatum* Hyatt, Coniacian of Otusco, Peru. Copy of Brüggén 1910, fig. 9D. A and C are from middle-aged specimens; B and D from adults. Bar scale is 2 cm.



TEXT-FIG. 9. Inferred phylogeny of *Buchiceras*, *Spathites*, and other early Mammitinae.

Mammites has developed by an increase in size and strengthening rather than weakening of ornament during ontogeny.

These last observations fully confirm our initial observations on the relationships of this array of early Turonian acanthoceratids with quadrate or trapezoidal whorls, umbilical and inner and outer ventrolateral tubercles, and simple ribs: they are a homogeneous close-knit group. Refinements in correlation between England, France, Spain, Portugal, and the United States permit the construction of a detailed phylogeny and show this group to be monophyletic rather than heterochronous homoeomorphs.

Acknowledgements. We thank J. Sornay (Muséum d'Histoire Naturelle, Paris), D. Pajaud (Université Paris VI), J. Louail (Rennes), M. Maury (Angers), and our other French colleagues for their help on the revision of the stratotype Turonian. Professor T. Matsumoto (Kyushu), C. Duerdon and K. Young (Austin), D. Reaser (Arlington, Texas), W. A. Cobban and J. D. Powell (Denver), E. G. Kauffman and N. F. Sohl (Washington) assisted with work on U.S. faunas. M. R. Cooper (Salisbury, Zimbabwe), and J. Wiedmann (Tübingen) provided additional help and discussion. Dr. S. C. Hook of the New Mexico Bureau of Mines and Mineral Resources, Socorro, New Mexico, kindly gave us specimens of *Spathites puercoensis* for study.

The technical assistance of the staff of the Geological Collections, University Museum, Oxford, is acknowledged, as is financial assistance from the Natural Environment Research Council, Wolfson College, Oxford, the Lindemann Trust, and the Royal Society.

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Typescript submitted 1 September 1979

Revised typescript submitted 20 November 1979



Kennedy, W. J., Wright, C. W., and Hancock, J M. 1980. "Origin, evolution and systematics of the Cretaceous ammonoid *Spathites*." *Palaeontology* 23, 821–837.

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