

On *Ammonites galliennei* d'Orbigny, 1850

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Ammonites galliennei d'Orbigny, 1850, type species of the genus *Pseudotissotia* Peron, 1897, is redescribed on the basis of the holotype and a topotype series from Poncé, Sarthe, France. The species is smooth and tricarinate in early and middle growth, but acquires broad radial ribs at variable diameters from 70 mm. onwards to maturity. These are accompanied by the appearance of long clavi on the lateral keels and, in strongly ribbed individuals, a nodate siphonal keel, the venter tending to round at the end of the adult body chamber. These previously unrecognised features suggest that *Bauchioceras* Reyment, 1954 should not be separated generically or subgenerically from *Pseudotissotia*, but that *Wrightoceras* Reyment, 1954 should be accorded generic status. It is suggested that the *Pseudotissotiinae* and *Tissotiinae* are homoemorphous in the tendency towards pseudoceratitic sutures and not directly related, the former deriving from *Acanthoceratinae*, the latter from the *Barroisiceratinae* via *Tissotioides* Reyment, 1958.

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Introduction

Although Touraine is the type area of the Turonian stage and has yielded rich ammonite faunas, there is little modern work on either the stratigraphic distribution or taxonomy of the group, other than the recent review by Hancock, Kennedy & Wright (1977). This paper is a contribution to the overall reappraisal of the stratotype and its ammonite fauna, as a contribution to the IGCP/UNESCO 'Mid-Cretaceous Events' project; it deals with the only representative of the important Tethyan subfamily *Pseudotissotiinae* Hyatt, 1903.

In the Touraine region *P. galliennei* is known only from a single locality, Poncé in the Loir Valley. Here it occurs with an associated late mid-Turonian fauna which includes *Collignoniceras woollgari* (Mantell), *Lewesiceras peramplum* (Mantell) and numerous *Romaniceras ornatissimum* (Stoliczka) (= *R. deverioides* (de Grossouvre) and varieties).

Order Ammonitida Hyatt, 1900

Superfamily Acanthocerataceae Hyatt, 1900

Family Acanthoceratidae Hyatt, 1900

Subfamily *Pseudotissotiinae* Hyatt, 1903

Genus *Pseudotissotia* Peron, 1897

Type species: *Ammonites galliennei* d'Orbigny, 1850 by original designation.

Diagnosis: Moderately involute medium-sized ammonites with compressed to depressed whorl section and flattened venters. Early whorls smooth

or with feeble ribs; low broad, wedge-shaped ribs may be developed at maturity. Venter tricarinate-bisulcate. In compressed, feebly ornamented individuals the keels are entire; as inflation increases and ribs appear, the lateral keels develop long clavi corresponding to the terminations of the flank ribs and the siphonal keel may become similarly nodate. At maturity ornament declines and the venter may broaden and become somewhat rounded with a simple, entire aperture.

The suture is relatively simple with low broad feebly denticulate lobes and saddles.

Discussion: *Ammonites galliennei* is a *Prodrome* species; our understanding of it stems from Peron's (1897) description of the species and genus and his illustration of a Poncé specimen (re-illustrated here as Figs. 12—13), erroneously taken as the type by some authors. Reyment (1954, 1955) and Barber (1957) have documented the very wide range of morphological variation shown by the various Nigerian species referred to the genus. Reyment (1954, 1955) recognised two subgenera, *Pseudotissotia* (*Bauchioceras*) Reyment, 1954 (type species *Hoplitoides nigeriensis* Woods, 1911) and *Wrightoceras* Reyment, 1954 (type species *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment, 1954). These have subsequently been treated as subgenera or independent genera. *Bauchioceras nigeriense* is a variable species (Barber 1957); juvenile compressed variants are smooth with entire keels; inflated forms have ribs and nodate keels; all variants

Dimensions:	D	Wb	Wh	Wb:Wh	U
Holotype, MNHP 6776	75,5(100)	28,0(37)	33,2(44)	0,84	11,5(15)
	63,2(100)	24,5(39)	29,0(46)	0,84	~11,0(17)
MNHP, Bourgeois Coll.	88,9(100)	31,8(36)	42,5(48)	0,75	14,8(13)
MNHP, Durand Coll.	132,5(100)	—(—)	57,0(43)	—	30,5(23)
MNHP 1908—36	123,0(100)	36,5(30)	55,0(45)	0,66	29,0(23)
Nantes specimen	110,0(100)	—(—)	49,0(45)	—	22,7(21)
” ” at	96,5(100)	32,0(33)	42,0(44)	0,76	18,5(19)
Rennes no. 1	83,5(100)	33,5(40)	35,5(43)	0,94	19,0(23)
Rennes no. 2	61,5(100)	20,3(33)	30,0(49)	0,68	11,3(18)
Rennes no. 3	51,2(100)	18,7(37)	25,5(50)	0,73	9,0(18)

D=diameter, Wb=whorl breadth, Wh=whorl height, U=umbilicus. Figures in parentheses are dimensions expressed as a percentage of the total diameter.

tending to loose ornament at maturity. As is described below, *P. galliennei* shows a similar range of variation, although at different ontogenetic stages, having smooth juveniles and ribbed or smooth middle growth stages, the latter with nodate keels and tending to retain ribs to maturity. So similar are individuals of the two species in middle growth (compare our figures with those in Barber 1957) that but for differences in preservation, they could easily pass for individuals from the populations which yielded the types of the two species. We would therefore conclude from these new observations that separation of *Bauchioceras* and *Pseudotissotia* at the generic or subgeneric level is inappropriate in terms of the scope of genera and subgenera of *Pseudotissotiinae* as currently conceived.

In contrast, *Wrightoceras* merits generic separation. When young, it is variable but typically has feeble ribs, commonly has inflated inner flanks, and a concave, bicarinate venter showing no more than a feeble siphonal ridge in some individuals; when adult the flanks are smooth and the venter tabulate. It is clearly separable from *Pseudotissotia* at all growth stages. *Discovascoceras* Collignon, 1957 should possibly also be treated as a synonym of *Pseudotissotia* for the type specimen of the type species: *Discovascoceras tesselitense* Collignon (1957, pl. 1, figs. 1, 1a) is close to, if a little more evolute than *Pseudotissotia nigeriensis tricarinata* (Reyment) (cf. Barber 1957, p. 47, especially pl. 20, figs. 1a, b).

Occurrence: Early to Middle Turonian. The geographic range includes France, Spain, north and west Africa, the Middle East, Texas, Mexico and Central America. A late Cenomanian species, "*P. inopinata* Kennedy & Bayliss has been described from Devon, England (see below).

Pseudotissotia galliennei (d'Orbigny)

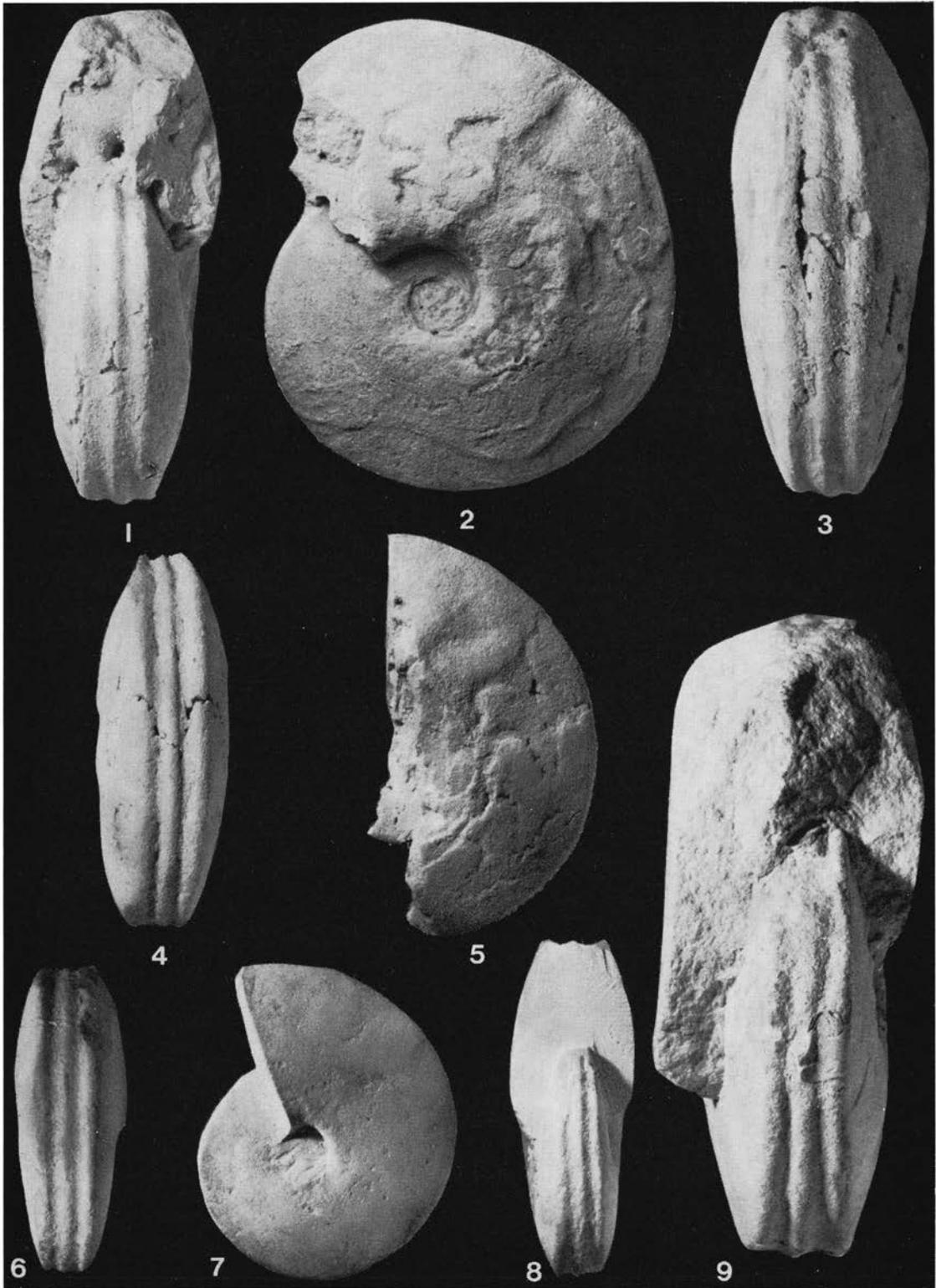
Figs. 1—20, 23—24, 28—30

- 1850 *Ammonites Galliennei* d'Orbigny, p. 190.
 1890 *Tissotia galliennei* (d'Orbigny); Douvillé, p. 531.
 1894 *Tissotia galliennei* (d'Orbigny); de Grossouvre, p. 50.
 1897 *Pseudotissotia galliennei* (d'Orbigny); Peron, p. 28, pl. 2, fig. 3, pl. 3, fig. 1; pl. 17, fig. 2.
 1903 *Pseudotissotia galliennei* (d'Orbigny); Hyatt, p. 36.
 1911 *Pseudotissotia galliennei* (d'Orbigny); Douvillé, p. 303, text-fig. 19.
 1925 *Pseudotissotia galliennei* (d'Orbigny); Diener, p. 226.
 1956 *Pseudotissotia galliennei* (d'Orbigny); Sornay, fiche 39.
 ? 1957 *Pseudotissotia galliennei* (d'Orbigny) var. *inflata* Collignon, p. 15.
 1977 *Pseudotissotia galliennei* (d'Orbigny); Kennedy & Bayliss, pl. 120, figs. 3a—c.
 1977 *Pseudotissotia galliennei* (d'Orbigny); Hancock, Kennedy & Wright, p. 156.

Holotype: The catalogue of the d'Orbigny collection lists only one specimen under the name *galliennei*, no. 6776, from Poncé, Sarthe, which is therefore the holotype by monotypy.

Other specimens studied: An unregistered specimen in the Muséum d'Histoire Naturelle, ex Bour-

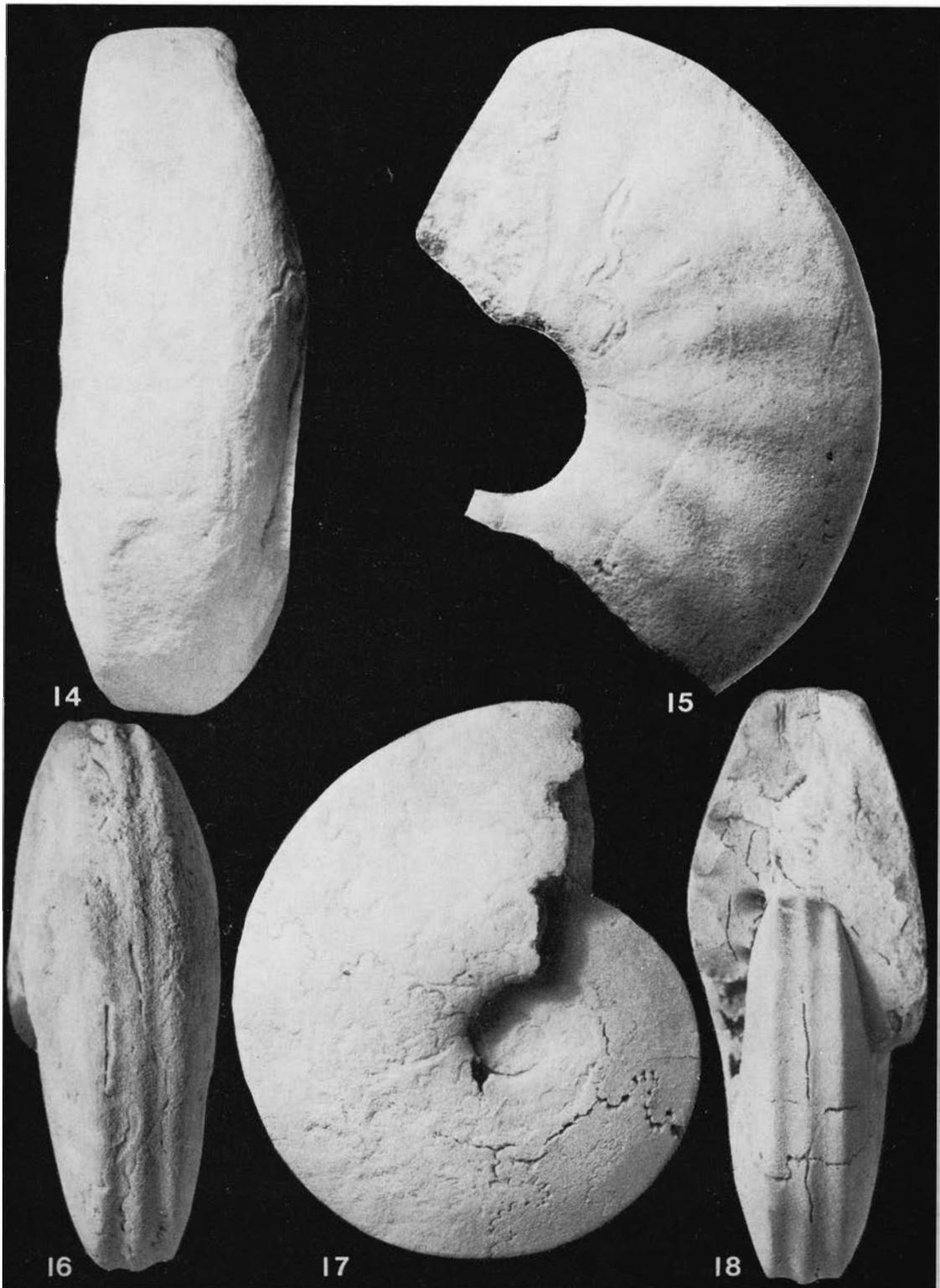
- 1—9. *Pseudotissotia galliennei* (d'Orbigny), from Poncé, Sarthe, France.
 1—3. Muséum & Histoire Naturelle, Paris (MNHP) no. 6776 (d'Orbigny Collection), the holotype by monotype.
 4—5. Faculté des Sciences Rennes (FSR) no. 2; a cast of this specimen is in Paleontologiska Institutionen, Uppsala.
 6—8. FSR no. 3; a cast of this specimen is in Paleontologiska Institutionen, Uppsala.
 9. Apertural view of the Nantes specimen (see also Figs. 23—24); a cast of this specimen is in Paleontologiska Institutionen, Uppsala.





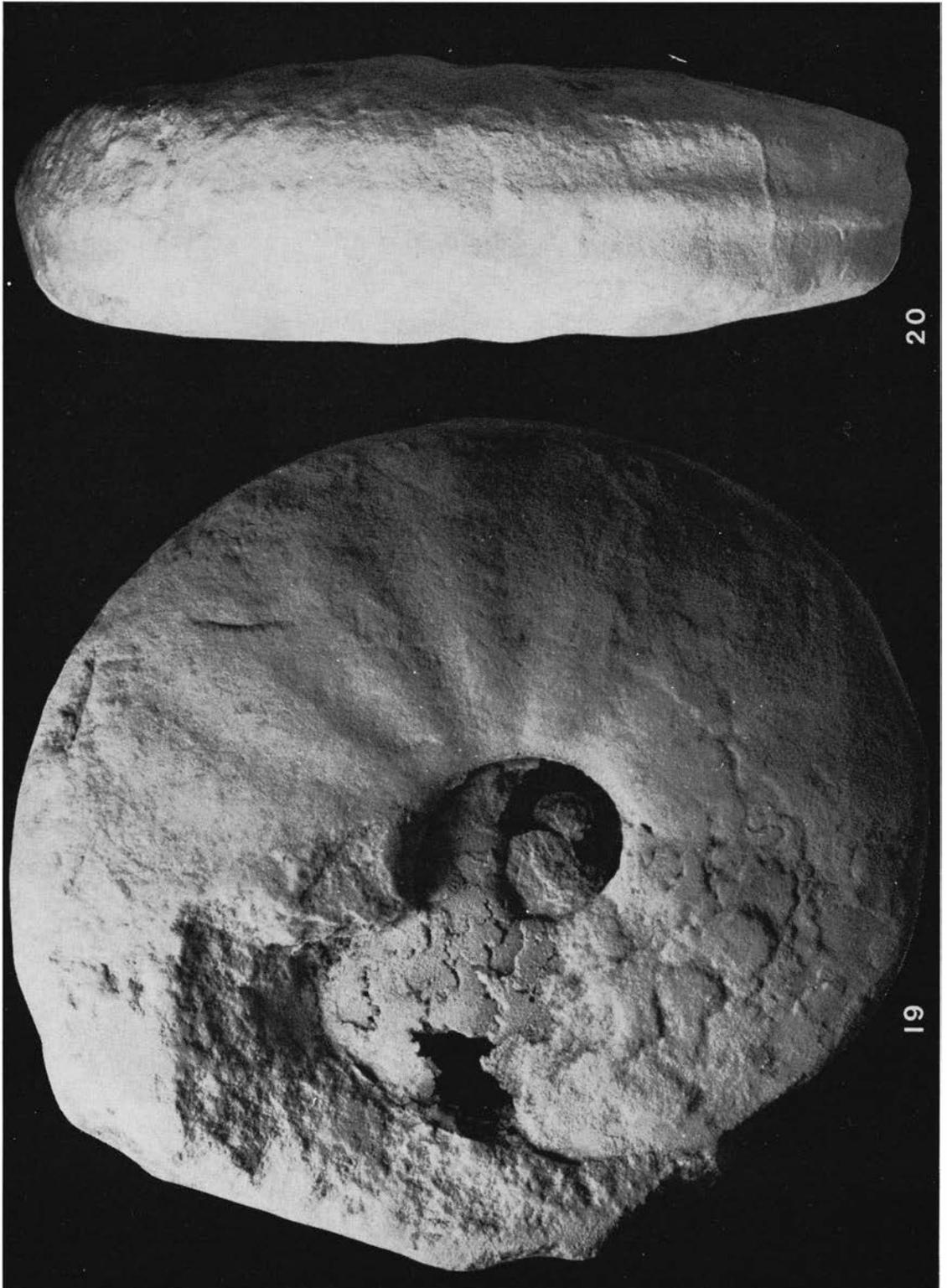
10—13. *Pseudotissotia gallienae* (d'Orbigny).
 10—11. MNHP 6127 (d'Orbigny Collection), the sole specimen of *Ammonites clito* d'Orbigny ms, from Fumel, Lot et Garonne, France.

12—13. MNHP 1008—36, the original of Peron 1896, p. 28, pl. 2, fig. 3, pl. 3, fig. 1, pl. 4, fig. 2, from Poncé, Sarthe.

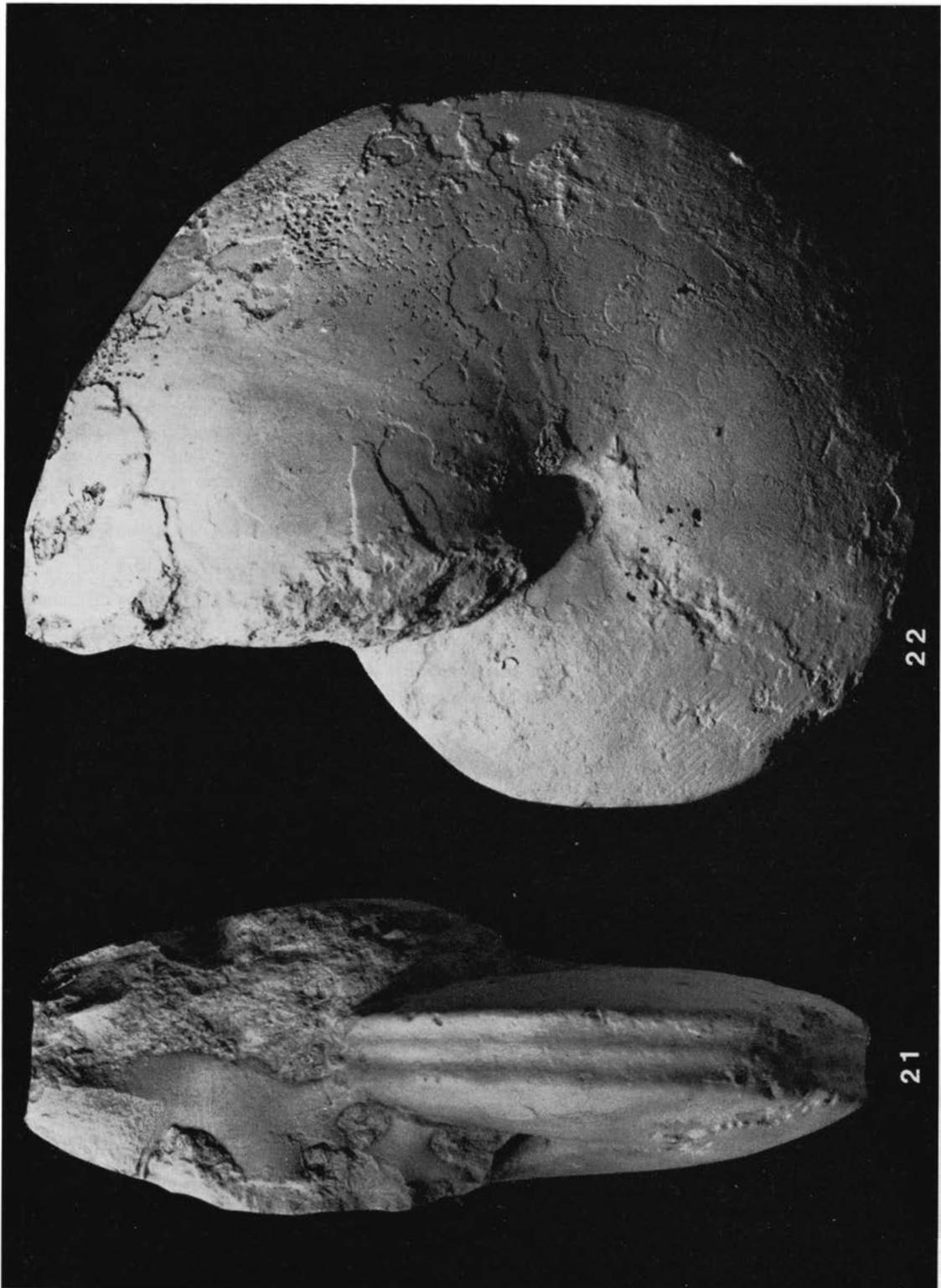


14—18. *Pseudotissotia galliennei* (d'Orbigny) from Poncé, Sarthe.

14—15. MNHP 6791 (d'Orbigny Collection) the only specimen of *Ammonites clytus* d'Orbigny ms.
16—18. MNHP unregistered, ex Bourgeois Collection.



19—20. *Pseudotissotia galliennei* (d'Orbigny), MNHP unregistered, Durand Collection, from Poncé, Sarthe.



21—22. *Pseudotissotia nigeriensis plana* Barber, British Museum (Natural History) (BMNH) C47590 from Gongila, Nigeria.

geois Collection (= Kennedy & Bayliss 1977, pl. 120, figs. 3a—c); MNHP Durand Collection, MNHP 1008—36 (= Peron 1896, p. 28, pl. 2, fig. 3, pl. 3, fig. 1, pl. 4, fig. 2), all from Poncé, Sarthe. MNHP 6791, the holotype of *Ammonites clytus* d'Orbigny ms, from Poncé; MNHP 6127, d'Orbigny Collection, the holotype of *Ammonites clito* d'Orbigny ms, from Fumel (Lot et Garonne).

There are four unregistered specimens in the Sorbonne Collections, one in the Dumas Collection, Muséum d'Histoire Naturelle, Nantes, (no. V40, R.2) and three in the Collections of the Faculté des Sciences, Rennes, all from Poncé.

Description: The smallest specimen available (Figs. 6—8) is 51.2 mm in diameter, and like all the specimens before us is an internal mould. At this diameter, the coiling is very involute with a small deep umbilicus with a subvertical wall and abruptly rounded to subangular shoulder. The whorl section is high and compressed (whorl breadth to height ratio is 0.73 in this specimen) with the greatest breadth low on the flanks, which are swollen towards the umbilicus and converge to the narrow venter. This is flat, with three strong, equal, entire keels (Figs. 6, 8). The flanks are entirely smooth (Fig. 7).

As size increases, this unornamented form persists in most slender individuals, including the holotype (Figs. 1—3) up to at least 90 mm (Figs. 16—18). In more inflated specimens (e.g. Rennes no. 1 and the Nantes individual (Figs. 23—24)), which have whorl breadth to height ratios of 0.94 and 0.76 respectively, ribs appear at a diameter of between 60 and 70 mm. There are perhaps twelve per whorl, arising at the umbilical shoulder as elongate radial bullae which expand and weaken across the middle and outer flank to produce broad, wedge-shaped ribs. Corresponding to these ribs, the lateral keels are crenulated as a reflection of the development of long, low ventral clavi and, in the Nantes example, a corresponding number of low undulations — feeble clavi — are developed on the siphonal keel.

All specimens develop this style of ribbing at maturity, and on the adult body chamber (Figs. 10—11, 14—15, 19—20) the ribs vary from straight and rectiradial to feebly convex and rursiradial (Fig. 15), arising singly or in pairs. All ribbing may be lost at the mature aperture (Fig. 12, 19) and the ventral keels decline, with the venter rounding (Figs. 13, 20). The adult aperture (Fig. 15) is simple, entire and gently sinuous in lateral profile.

The external sutures (Figs. 28—30) consist of a deep and narrow E, broad little incised, bifid

E/L, narrow bifid L, smaller, little incised L/U₂ and U₃ and broad, bifid U₂/U₃.

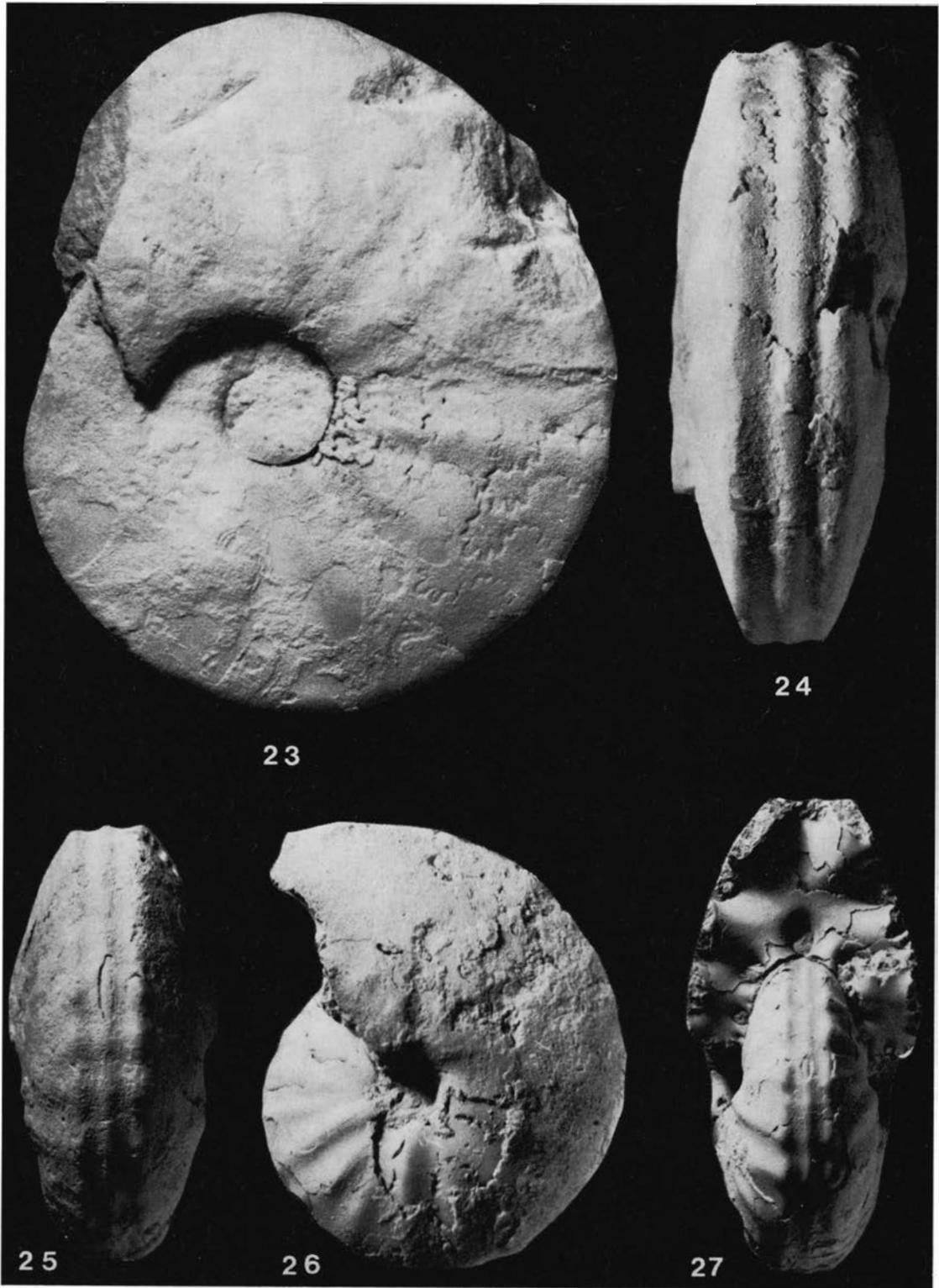
Discussion: *Pseudotissotia galliennei* is a distinctive species, known chiefly from Poncé in Sarthe, with rarer records from Fumel (Lot et Garonne) and elsewhere in Aquitaine. Collignon (1965) has described, but not figured, a variety *inflata* from Tihret (Fezzan); without seeing the specimen we cannot comment on its affinities.

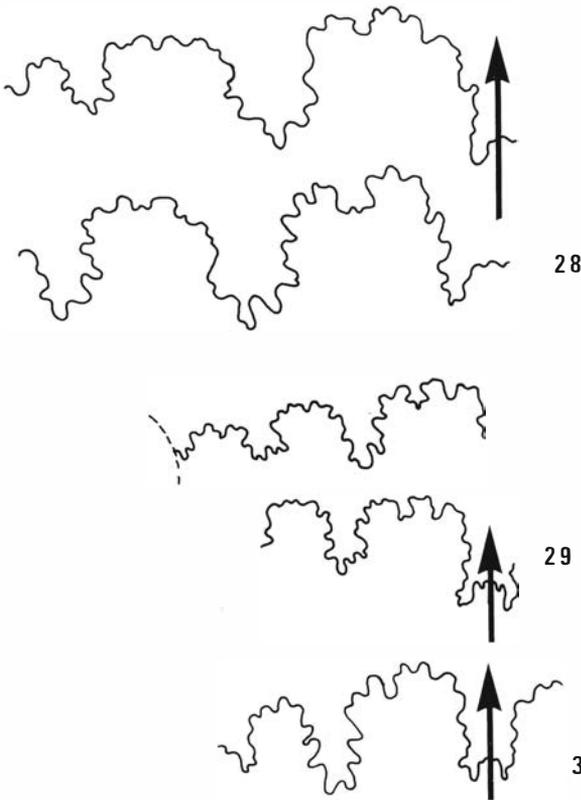
The Cenomanian "*Pseudotissotia*" *inopinata* Kennedy & Bayliss (1977, p. A02, pl. 120, figs. 1a—d, 2a—c) is depressed, rather than compressed and high-whorled, and has relatively strong umbilical bullae and flank ribs already at a whorl height of only 22 mm. *Pseudotissotia adkinsi* Kummel and Decker (Kummel and Decker 1954, p. 316, pl. 32, fig. 6, pl. 33, fig. 3, text-figs. 7—8) differs from *P. galliennei* in lacking flank ornament when adult and being more evolute, as in other forms referred to "*Discovascoceras*". *Pseudotissotia nigeriensis* (Woods) (Woods 1911, p. 284, pl. 23, fig. 3); see also Reyment (1955, p. 71, pl. 15, fig. 2; pl. 22, fig. 3); Barber (1957, pp. 4—51, pls. 20—23) in all its variants can be distinguished in general by having weakly to strongly ribbed and tuberculate inner whorls, followed by an entirely smooth adult body whorl (see Figs. 21—22, 25—26 herein, compared to Figs. 1—8, 19—20). The compressed forms with smooth inner whorls however, *Pseudotissotia nigeriensis plana* Barber (Barber 1957, p. 49, pl. 20, figs. 2a—b; pl. 21, figs. 2a—b; pl. 22, figs. 5, 6a—b; pl. 23, figs. 1a—b; pl. 34, figs. 2, 8—10) may as juveniles be indistinguishable from *P. galliennei*, even though populations of the species are distinct; they tend, however to be more involute. *P. nigeriensis tabulata* Barber (Barber 1957, p. 51, pl. 21, figs. 1a—b, pl. 34, figs. 1, 11) is a similarly smooth form, but as its name suggests, has a tabulate venter, rather than three keels. Both these smooth forms may be easily distinguished from *P. galliennei* when adult as they lack all trace of ribbing (Figs. 21—22).

Pseudotissotia gabonensis Lombard (Lombard 1930, p. 289, pl. 29, figs. 1a—c) has the same proportions as *P. galliennei* but differs in its weaker flank ornament and sutural details. Both of

23—24. *Pseudotissotia galliennei* (d'Orbigny), the Nantes specimen, from Poncé, Sarthe; a cast is in the collections of Paleontologiska Institutionen, Uppsala.

25—27. *Pseudotissotia nigeriensis nigeriensis* (Woods). BMNH C47604, from Gongila, Nigeria.





28—30. External sutures of *Pseudotissotia galliennei* (d'Orbigny). 28 — the Nantes specimen; 29 — Rennes no. 1; 30 — Rennes no. 2. All $\times 1.5$.

these features may subsequently prove not to be of specific significance.

Occurrence: *P. galliennei* characterises a high position in the mid-Turonian, associated with *Collignonicerias woollgari* and *Romanicerias ornatissimum*. In general terms, this is a level below that of the well known English Chalk Rock faunas and above that of the Nigerian *P. nigeriensis* fauna. The geographic distribution is limited to Poncé, Sarthe, Fumel (Lot et Garonne) and elsewhere in Aquitaine, France, and possibly Fezzan, in North Africa, if Collignon's variety *inflata* proves to be conspecific.

Evolutionary Considerations

Nigerian faunas described in detail by Reyment (1955) and Barber (1957) show very clearly that *Pseudotissotia nigeriensis* succeeds, and indeed

arose from, *Gombeoceras* Reyment (1954). The latter, in our view, is sufficiently far in evolutionary terms from its ancestors in Acanthoceratidae, whatever they are, to be regarded as the earliest member of the Pseudotissotiinae. Thus the position of "*Pseudotissotia inopinata* Kennedy and Bayliss (Kennedy and Bayliss 1977, p. 902, pl. 120, figs. 1a—d, 2a—c, text-fig. 1) become even more problematic. Morphologically, the holotype, and only known specimen, is a *Pseudotissotia*, close to the type species although depressed, with stronger bullae and more deeply incised sutural elements. It is, however, only a fragment of a whorl and it comes from a much lower horizon, in the Upper Cenomanian, below the *Sciponoceras gracile* horizon and well below *Gombeoceras*, which in England first appears in the lowest Turonian. It thus pre-dates the clear ancestors of *Pseudotissotia nigeriensis*. Either it is a homoeomorphous development from some earlier acanthoceratid (and would then require a new generic name) or the origins of the Pseudotissotiinae are more complex than outlined above. Without further material of this cryptic form no further comment is possible at present.

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A contribution to
Project MID-CRETACEOUS EVENTS



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