THE EARLIEST TISSOTIID AMMONITE

by W. J. KENNEDY and O. H. BAYLISS

ABSTRACT. Pseudotissotia (Pseudotissotia) inopinata sp. nov. is described from the Upper Cenomanian phosphatic Calycoceras naviculare/Eucalycoceras pentagonum Zone fauna of Division C of the Cenomanian Limestone of Shapwick Grange, Devon. It is the earliest occurrence of the otherwise exclusively Turonian genus Pseudotissotia Peron, 1897, and the Turonian to Coniacian Family Tissotiidae Hyatt, 1900. The family is otherwise unknown in the Cretaceous of the United Kingdom.

THE ammonite family Tissotiidae Hyatt, 1900, comprises approximately twenty genera with a widespread, largely Mesogean distribution. The group as a whole is characterized by a tendency towards loss of ornament, by the development of an entire, simple keel or keels, involute coiling, and a suture line which commonly shows a tendency towards multiplication of sutural elements and over-all simplification. Tissotia H. Douvillé, 1878, and Buchiceras Hyatt, 1875, are perhaps the best-known genera, and are classic Cretaceous pseudoceratites (e.g. Hyatt 1903), homoemorphous with Triassic ammonoids in their development of entire saddles and denticulate lobes. The group is chiefly known from the Tethyan Realm, especially North and East Africa, the Middle East, Central and South America, Texas and Spain (Bayle 1878; Douvillé 1912; Peron 1897; Hyatt 1903; Reyment 1954a, b, 1955; Barber 1957; Collignon 1958, 1965a; Freund and Raab 1969; Choffat 1898; Benavides-Cáceres 1956; see palaeogeographic maps in Matsumoto 1973a, b). They occur rarely in the U.S. Western Interior (e.g. Cobban and Scott 1972) and are also known from as far south as Madagascar (e.g. Collignon 1965b) and Borneo. In Western Europe the family becomes progressively rarer as one moves northward, the most northerly record hitherto being the occurrence of Pseudotissotia (Pseudotissotia) galliennei (d'Orbigny) in the Turonian of Sarthe and Touraine.

The previously known stratigraphic range of the tissotiids is Turonian to Coniacian. The actual dating of their first appearance in southern areas is difficult to relate to northern European faunal successions, but records by Freund and Raab (1969), Reyment (1955), Barber (1957), Wiedmann (1959), and others suggest it to be some

way up in the Lower Turonian.

So far as evolutionary origins are concerned, Wright in 1952 (p. 221, n. 35) considered the family to be polyphyletic to a minor degree, with their source presumed to be in the Mammitinae. The work of Reyment (1954a, b, 1955) on the rich Nigerian faunas led him (1955, text-fig. 31) to suggest the subgenus *P. (Bauchioceras)* Reyment, 1954 as the rootstock of the group, whilst Barber (1957) suggested that this in turn derived from the vascoceratid *Gombeoceras* Reyment, 1954, during the early Turonian. Subsequently, Collignon (1965a, p. 179) suggested an alternative origin for the group in the vascoceratids, when he demonstrated that the early Turonian genus *Discovascoceras* Collignon, 1958 bore three keels when young, and could equally be regarded as intermediate between the two families.

[Palaeontology, Vol. 20, Part 4, 1977, pp. 901-906, pl. 120.]

It is therefore of great interest to record what appears to be a *P.* (*Pseudotissotia*) from the English Upper Cenomanian, apparently pre-dating the vascoceratids from which certain other tissotids have been claimed, or demonstrated, to be derived, especially as the family has never before been recorded from this country.

SYSTEMATIC DESCRIPTION

Superfamily ACANTHOCERATACEAE Hyatt, 1900 Family TISSOTIIDAE Hyatt, 1900 Subfamily PSEUDOTISSOTIINAE Hyatt, 1903 Genus and Subgenus PSEUDOTISSOTIA Peron, 1897

Type species. Ammonites galliennei d'Orbigny, 1850.

Pseudotissotia inopinata sp. nov.

Plate 120, figs. 1a-d, 2a-c, text-fig. 1

Derivation of name. Latin inopinata—unexpected.

Holotype. Formerly O. H. Bayliss Collection, no. 257; now B.M. (N.H.). No. C80436.

Diagnosis. A Pseudotissotia with a depressed whorl section (breadth to height ratio 1·16), strong umbilical bullae which project into the umbilicus and give rise to broad, subdued, triangulate ribs which efface at mid-flank, and a venter bearing three strong, equal keels.

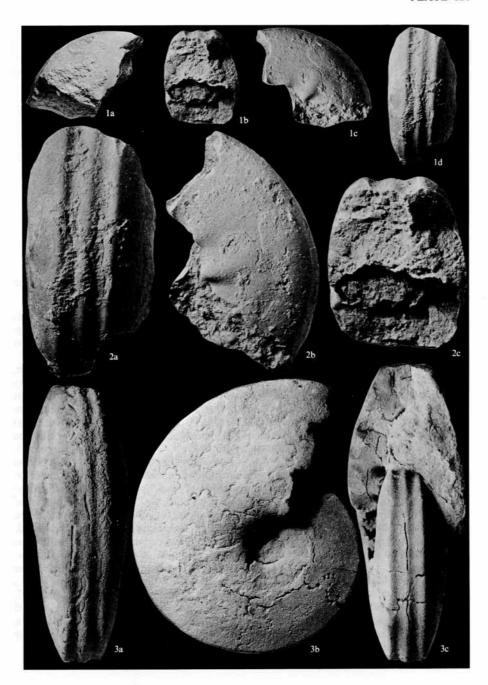
Description. The holotype consists of a phosphatic internal mould of just over one-third of a whorl, is partially septate, and retains a considerable amount of phosphatized shell, which largely obscures the sutures.

The coiling appears to have been quite involute, with a moderately deep umbilicus; the umbilical wall is vertical, with an abruptly rounded shoulder. The whorl section is depressed, with a whorl breadth to height ratio of 1·16; the greatest breadth is at the umbilical bullae. The flanks are flattened and convergent, with rounded ventrolateral shoulders. The venter is broad (approximately 80% of maximum whorl breadth), and bears three distinct, entire, strong keels, the two lateral ones being rather more narrowly rounded than the siphonal. The keels are separated by quite deep, rounded grooves, of somewhat greater breadth.

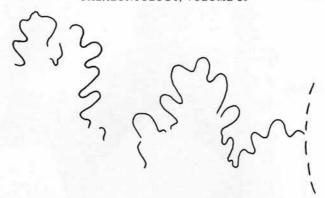
Flank ornament consists of strong, rounded umbilical bullae which project slightly into the umbilicus. From these bullae arise broad, flat, triangulate ribs, which efface completely by mid-flank.

EXPLANATION OF PLATE 120

Figs. 1a-d, 2a-c. Pseudotissotia (Pseudotissotia) inopinata sp. nov. The holotype, Bayliss Collection no. 257, now B.M. (N.H.) no. C80436, a partly septate phosphatic internal mould retaining phosphatized shell. Specimen from the phosphatic Calycoceras naviculare/Eucalycoceras pentagonum Zone fauna of Division C of the Cenomanian Limestone, Shapwick Grange, near Lyme Regis, Dorset. 1a-d, ×1; 2a-c, ×2. Figs. 3a-c. Pseudotissotia (Pseudotissotia) galliennei (d'Orbigny). Specimen from the Turonian Tuffeau of Poncé, Sarthe, France. Muséum d'Histoire Naturelle, Paris, ex Bourgeois Collection, ×1.



KENNEDY and BAYLISS, earliest tissotiid ammonite



TEXT-FIG. 1. Partial suture of the holotype of *Pseudotissotia* (*Pseudotissotia*) inopinata sp. nov. \times 6.

Little of the suture line can be deciphered, but there appears to have been a moderate degree of incision to both lobes and saddles (text-fig. 1).

Discussion. Identification of this fragment as a tissotiid is based upon whorl section, rib-style, and the prominent equal keels. Erection of a new species based on the fragment is justified by the distinctive ornament, and by the great age compared with most other members of the group.

Three subgenera have been distinguished within Pseudotissotia. Of these, P. (Bauchioceras) Reyment, 1954 has crenulate keels, and a siphonal keel which may be very feeble, together with ribs which extend across the whole of the flank at comparable diameters. Species such as P. (B.) nigeriensis (Woods), P. (B.) tricarinata (Reyment) are thus readily distinguishable from P. (P.) inopinata. P. (Wrightoceras) Reyment, 1954 has compressed outer whorls which lack a siphonal keel, whilst the umbilical region may be inflated. Species such as P. (Wrightoceras) wallsi (Reyment), P. (W.) mirabilis (Pervinquière), P. (W.) munieri (Pervinquière), P. (W.) llareni Karrenberg, and P. (W.) gagnieri Faraud may be distinguished from the present form by these criteria. When compared with typical P. (Pseudotissotia), a specimen of the type species of which is figured for comparison (Pl. 120, fig. 3a-c), the attribution of our specimen to the restricted subgenus is quite clear, for it has three distinct, entire keels. When compared with P. (P.) galliennei, P. (P.) inopinata is depressed and broad, rather than high-whorled and compressed, whilst all specimens of P. (P.) galliennei we have seen completely lack umbilical bullae and ribs at comparable diameters; the long, low, fold-like ribs of the adult instead appear at much larger diameters, as in Peron's specimen (Peron 1897, p. 28, pl. 2, fig. 3; pl. 3, fig. 1). The suture of *P.* (*P.*) *inopinata* is, in addition, more divided than that of *P.* (*P.*) *galliennei*. Collignon (1957, p. 15) has described, but not figured, a var. inflata of P. (P.) galliennei, based on a rather worn specimen from the Turonian of Tinhret (Fezzan). It has a breadth: height ratio of 0.83, substantially less than the present species, but further comparison is difficult in the absence of illustrations of Collignon's variety.

Occurrence. The holotype and only known specimen of *Pseudotissotia inopinata* is from Division C of the Cenomanian Limestone exposed in the large chalk pit at Shapwick Grange Farm, Devon, near Lyme Regis, Dorset (National Grid Reference SY 313918).

Age. The sequence at Shapwick Grange is closely similar to that on the Devon Coast described by Kennedy (1970, p. 657; text-fig. 15) who also summarizes previous work. Large collections from the succession have enabled us to place the present specimen and associated material precisely in sequence. Division B of the Cenomanian Limestone at Shapwick has yielded scarce Acanthoceras of Middle Cenomanian age. This unit is terminated by a phosphatic veneer, and overlain by the glauconitic chalk of Division C; from the base of this comes a rich phosphatic fauna including, in addition to P. (P.) inopinata, the following ammonites in similar preservation (O. H. Bayliss Collection): abundant Schloenbachia lymense Spath. Calycoceras spp., including C. (C.) naviculare (Mantell), C. (C.) guerangeri (Spath), C. (Lotzeites) aberrans (Kossmat), Eucalycoceras pentagonum (Jukes-Browne), E. rowei (Spath), Protacanthoceras including P. compressum (Jukes-Browne) and P. bunburianum (Sharpe), Thomelites spp., including T. aff. sornayi (Thomel), Forbesiceras spp., Hamites cf. simplex (d'Orbigny) and abundant Scaphites equalis J. Sowerby. This is an Upper Cenomanian, C. naviculare/E. pentagonum Zone fauna.

Occurring somewhat higher in Division C is an essentially indigenous fauna preserved as glauconite-coated moulds. This includes Sciponoceras gracile (Shumard), C. naviculare, Allocrioceras annulatum (Shumard), Pseudocalycoceras dentonense (Moreman), and Metoicoceras geslinianum (d'Orbigny) (= M. gourdoni de Grossouvre). This fauna indicates the latest Cenomanian S. gracile Zone (for a discussion of zonal nomenclature see Kennedy and Juignet 1976, and Rawson et al. in press).

DISCUSSION

The recognition of a Pseudotissotia in the English Cenomanian would seem to confirm Wright's (1952) suggestion that the Tissotiidae are polyphyletic, for Bauchioceras appears to be a quite definite derivative of the early Turonian vascoceratid Gombeoceras, as Reyment (1955) and Barber (1957) demonstrated, whilst Collignon's Discovascoceras is a further contender as a vascoceratid ancestor for other tissotids. The origin of P. inopinata remains a problem. The morphologically closest contemporary ammonites appear to be amongst the Acanthoceratinae. Certain compressed Acompsoceras from the Lower to Middle Cenomanian develop a low siphonal keel and sharp ventral shoulders which are sometimes tuberculate, e.g. Acompsoceras essendiense (Schlüter) and A. renevieri (Sharpe) (Kennedy 1971, p. 67 et seg., pl. 30, pl. 31, fig. 2). These forms may also bear umbilical bullae and ribs, which die out on the flank. Mr. C. W. Wright has also drawn our attention to certain compressed, feebly ornamented variants of Acanthoceras rhotomagense (Brongniart) which show similar flank ornament and develop an incipient siphonal keel; we would suggest, therefore that, within the Cenomanian acanthoceratid radiation, these forms were a possible source for P. (P.) inopinata.

Acknowledgements. We thank Dr. J. M. Hancock and Mr. M. R. Cooper for useful discussions, and Mr. C. W. Wright for advice, and for critically reviewing the manuscript of this article.

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W. J. KENNEDY

Department of Geology and Mineralogy Parks Road Oxford

> O. H. BAYLISS Spring House Uplyme Dorset

Typescript received 12 May 1976 Revised typescript received 19 July 1976