

HENGESTITES, A NEW GENUS OF GAULT AMMONITES

by RAYMOND CASEY

ABSTRACT. *Hengestites applanatus* gen. et sp. nov., described from the Upper Gault (Lower Cretaceous, Upper Albian) of south-east England, is a primitive member of the Placenticeratidae, a family of ammonites not previously recorded from Britain. It is a characteristic fossil of the *Mortonoceras inflatum* Zone (*Callihoplites auritus* Subzone) but has hitherto escaped notice owing to homöomorphy with *Anahoplites planus* (Mantell). Its occurrence points to a polyphyletic origin for the Placenticeratidae.

DURING the sixteen years that have elapsed since the completion of the late L. F. Spath's 'Monograph of the Ammonoidea of the Gault' (Spath 1923-43) there have been many additions to knowledge of the ammonite fauna of the English Albian. One of the most notable is the genus *Falciferella*, a characteristic ammonite of the Lower Gault whose small size and resemblance to the common *Anahoplites planus* (Mantell) caused its presence to be undetected until as late as 1954 (Casey 1954b). The present paper draws attention to the existence in the Gault of yet another ammonite novelty. This is an Upper Gault form, by no means rare, widely distributed in south-east England, and, like *Falciferella*, is a homöomorph of *Anahoplites planus*. It is described below as *Hengestites applanatus* gen. et sp. nov. and is assigned to the Placenticeratidae, a family of ammonites well known in Cretaceous rocks in many parts of the world, especially North America, though not hitherto recorded from Britain. It is remarkable that specimens of *Hengestites* were long ago collected at Folkestone, Kent, the type locality of the Gault formation, and have lain unrecognized in the cabinets of our museums for nearly a century.

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SYSTEMATIC ACCOUNT

Family PLACENTICERATIDAE Hyatt 1900

Type genus *Placentoceras* Meek 1870, Upper Cretaceous, U.S.A.

The Placenticeratidae have been classified with the heterogeneous group of ammonites known as 'pseudoceratites', i.e. shells in which the septal suture tends to break up into a long series of sub-equal, simplified elements arranged in a gentle curve. Commonly this type of sutural pattern is correlated with an involute lenticular shell having a narrowly truncated or grooved venter, though it is also found in some evolute and inflated forms (e.g. *Stantonoceras* Johnson, *Diplacmoceras* Hyatt). A point of contrast between the Placenticeratidae and typical pseudoceratite families such as the Engonoceratidae and the Sphenodiscidae is that simplification of the individual elements, especially the saddles, is less advanced, both lobes and saddles being minutely frilled or even deeply dissected.

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The family is circum-global in its distribution and is particularly well represented in the U.S.A. Unlike the Engonoceratidae it was not concentrated in the equatorial or 'Tethyan' region and is found in latitudes as far apart as Alaska and Patagonia. Stratigraphically it does not become important until high in the Upper Cretaceous, a single genus only (*Proplacenticerias*) extending down to the Cenomanian. Rare examples of *Hy-pengonoceras warthi* (Kossmat) in the Upper Albian of southern India (Kossmat 1895) and Madagascar (Boule, Lemoine, and Thévenin 1907) are the only occurrences of the Placenticeratidae in the Lower Cretaceous hitherto recorded. After J. P. Smith (1900) and Hyatt (1903), the principal students of the family are Spath (1926), Reeside (1926; 1927), and Wright (1957).

Genus HENGESTITES nov.

(*Hengest*, Saxon chieftain and ancient King of Kent)

Type species. *Hengestites applanatus* gen. et sp. nov., Upper Gault (Upper Albian, *Mortoniceras inflatum* Zone), south-east England.

Generic characters. High-whorled, involute platycone with angular umbilical rim and narrow venter. For a brief period in early youth the sides have faint flexuous riblets that terminate in marginal clavi alternating on opposite sides of the venter. Subsequently the shell becomes quite smooth, the venter sulcate and with carinated edges, later tabulate. Body-chamber unknown. The suture-line has a shallow, squat ventral lobe, a broad bifid or asymmetrically subtrifid principal lobe and a very narrow bifid dorsal lobe. The saddles have a phylloid tendency and are also bifid, and the tops of the auxiliaries are aligned in a gentle forward-facing convexity. A deep, bifid adventitious lobe splits the external saddle into two unequal parts, the ventral part being much the smaller.

Remarks. The Placenticeratid affinities of *Hengestites* are clearly demonstrable both in shell-form and in sutural characters. Consideration may be given first to the chief points of difference between this ammonite and members of the Hoplitidae, especially *Anahoplites*, with which it has been confused.

1. *Shell-form.* The whorls are more compressed, flatter and more involute than in any described species of *Anahoplites*, and the only other smooth, thinly discoidal Hoplitid that is at all like *Hengestites*, namely *Neosaynella* (Casey 1954a), has a different type of ventral development, the venter being non-sulcate in early youth and acute in maturity. The very narrow, sulcate and bicarinate venter of *Hengestites* is common enough in the Placenticeratidae (see, for example, Hyatt 1903, pl. 36, fig. 3; pl. 43, fig. 8; pl. 46, fig. 2) but cannot be matched in the Hoplitidae. An apparently similar venter, but without sharp edges, seen in some specimens of *Anahoplites planus* (Mantell) (Spath 1925, p. 137, text-fig. 39d) is due to an internal ridge-like thickening of the test in the region of the siphuncle, reproduced as a furrow on internal moulds. In *Hengestites*, which is known only by internal moulds, the ventral sulcus is impressed on the dorsum of the succeeding whorl, proving that it was a corrugation of the test and was not due to differential deposition of shell-substance. *Anahoplites* is further distinguished by the presence of umbilical bullae and of ventral clavi that are lost only in 'gerontic' specimens. Lastly, I know of no Hoplitid in which the sculpture is fully developed at diameters less than 10 mm., though this is not unusual in the Placenticeratidae (compare *P. meeki* Boehm, as described by Reeside 1927, p. 30).

2. *Suture-line*. It is in the characters of the suture-line that *Hengestites* exhibits the widest divergences from the Hoplitidae (text-fig. 2B). The long series of auxiliary saddles with their tops aligned in a gentle curve convex forwards is typical of the Placenticeratidae and is in contrast to the condition seen in *Anahoplites* (text-fig. 2C). In the latter genus, as in all the Hoplitidae, the auxiliaries are fewer in number and are arranged in a straight line descending obliquely backwards to the umbilical seam. A broad, open, strongly asymmetrical first lateral lobe, approaching that of *Hengestites*, occurs in some of the Transcaspian forms of *Anahoplites* and *Epihoplites* figured by Sinzow (1909, pls. 3, 4), but in general this lobe is much narrower necked in the Hoplitinae. So far as I am aware, no Hoplitid possesses a dorsal lobe that is bifid, nor one that is shallower than the adjacent lobe, though this feature of *Hengestites* is met with frequently in the Placenticeratidae. Another Placenticeratid character unknown in the Hoplitidae is the presence in the external saddle of a deep adventitious lobe, in this instance even exceeding the ventral lobe in depth. Small irregularities are sometimes seen in the ventral lobe (Pl. 29, fig. 4) but the marked displacement of this lobe to one side—a consistent peculiarity of *Anahoplites planus* and its allies—is not found in *Hengestites*. Conversely, the ontogenetic change in the principal lobe from bifid to subtrifid, seen in *Hengestites* (text-figs. 1A–C), is alien to the Hoplitidae. In the bifid nature of the principal lobe the immature *Hengestites* shows better agreement with young *Placenticerases*, as illustrated in text-figs. 1A and D.

The Desmoceratid ammonite *Beudanticeras beudanti* (Brongniart), for which *Hengestites* has also been mistaken in a crushed condition, has a rounded venter, a slightly wider umbilicus with blunter rim, and a more complex suture-line of different pattern.

Among the Placenticeratidae *Hengestites* finds its nearest morphological parallel in the group of *Placenticerases meeki* Boehm, well illustrated by Hyatt (1903, pl. 45, figs. 3–16; pl. 66; as *P. whitfieldi*) from occurrences in the Upper Cretaceous Montana Group of South Dakota and Nebraska, and by Boule, Lemoine, and Thévenin (1907, pl. 12, figs. 5, 5a) from beds of about the same age in Diego-Saurez, Madagascar. Usually, however, both *Placenticerases* and *Proplacenticerases* have umbilical tubercles and other ornament which persist to a relatively late stage of growth. Also, in these two genera, as in *Hypengonoceras* and *Pseudoplacenticerases*, multiplication and equalization of the sutural elements is so far advanced that the identity of the primitive lateral lobe is lost in the mature shell. *Hengestites*, with clearly identifiable principal lobe, thus compares more closely with the genera *Metaplacenticerases* Spath and *Hoplitoplacenticerases*

EXPLANATION OF PLATE 29

All figures are natural size unless otherwise indicated.

Figs. 1–4. *Hengestites applanatus* gen. et sp. nov. 1, Holotype (Sedgwick Museum B 81598), Upper Gault, *inflatum* Zone, *auritus* Subzone (horizon inferred), Folkestone, Kent. Rev. T. Wiltshire Coll. 2, 2a–b. Fragmentary pyritic nucleus showing sculptured stage of the young, enlarged $\times 2$ in figs. 2a, b, Upper Gault, *inflatum* Zone, *auritus* Subzone, Aylesford Brick and Tile Works, Aylesford, Kent. R. A. Milbourne Coll. 3, 3a. Portion of phosphorite nucleus showing the ventral sulcus of the adolescent, Upper Gault (not *in situ*), Aston Clinton, near Aylesbury, Bucks. C. W. and E. V. Wright Coll. 7075. 4. Part of external suture-line at 160 mm. diameter, from venter to middle of first lateral lobe. Upper Gault, condensed *auritus-aequatoriale* Subzones, cutting for by-pass road in Horish Wood, two-thirds of a mile north-east of the Chiltern Hundreds Inn, north-east of Maidstone, Kent. Geological Survey Museum Ca 7250.

Spath, both of high horizon in the Upper Cretaceous and quite different in sculpture from the present genus. A unique feature of *Hengestites* that serves as a ready means of separation from all other genera of the Placenticeratidae is the dwarfing of the ventral portion of the external saddle.

Hengestites applanatus gen. et sp. nov.

Plate 29, figs. 1-4; text-figs. 1A-C, 2A-B

- 1875 *Ammonites splendens*, Sow., grooved var.; De Rance (in Topley), p. 436 (pars).
 1882 *Ammonites splendens?*; Norman, table facing p. 440.
 1887 *Ammonites splendens* (?); Norman, p. 77.
 1900 *Ammonites splendens*, Sow.; Jukes-Browne, pp. 141, 256, 458 (pars).
 1923 *Beudanticeras beudanti* (Brong.); Spath, p. 76 (pars).
 1939 *Anahoplites planus* (Mant.) (sulcate form); Wright and Wright, p. 116.
 1947 *Anahoplites planus* (Mant.) (sulcate form); Wright, p. 188.

Holotype. Sedgwick Museum No. B 81598, Upper Gault (Bed XI), Folkestone, Kent (Rev. T. Wiltshire Coll.).

Description. Shell compressed, strongly involute; whorl-section high and lanceolate, widest near the umbilical margin, the sides subparallel below, converging more rapidly above to a narrowly truncated venter. The narrow umbilicus is limited by a flat, subvertical wall, angular at the rim.

At the earliest observed diameter (7-10 mm.) the ammonite is ornamented by very faint primary riblets, numbering four to one-third of a volution, which commence at the umbilical margin and lean slightly forwards to traverse the flattened sides in a feeble S-bend. Secondary riblets take origin from near mid-flank and are intercalated among the primaries singly or in pairs. Every riblet ends at the peripheral margin in a compressed, hoplitoid clavus directed forwards and inwards at an angle of 30° to the smooth siphonal line, the alternation of the clavi of opposite sides giving the suggestion of a zigzag pattern on the venter.

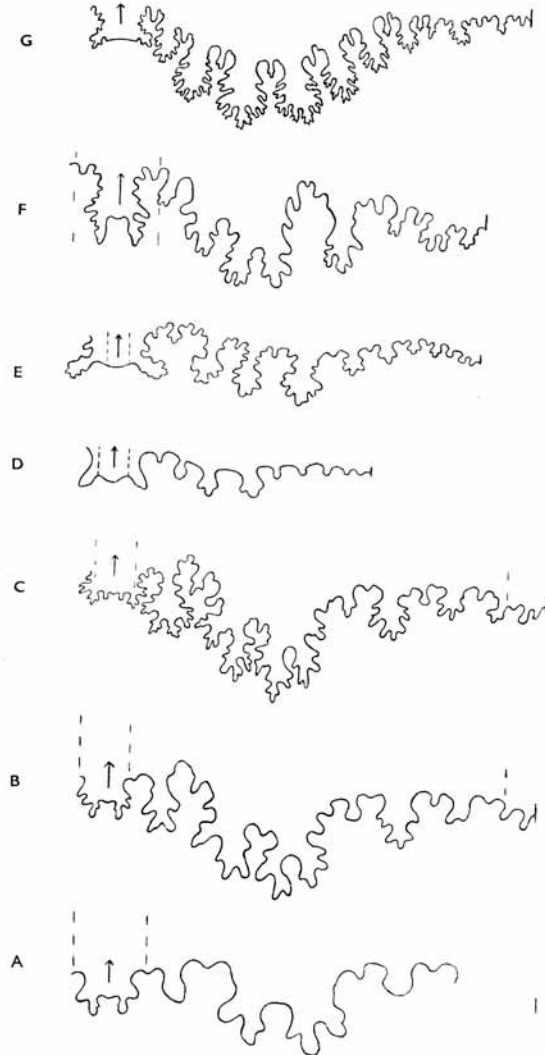
With subsequent growth the sculpture degenerates, the whorls become increasingly compressed, flat-sided and involute, the venter increasingly narrow. Already at 15 mm. diameter the riblets have almost disappeared and the clavi are reduced to gentle waves along the edges of a sulcate venter; at 20 mm. diameter the shell is smooth to the naked eye, the ventral edges sharp and entire. After about 45 mm. diameter the ventral sulcus is lost, the venter then becoming tabulate, though maintaining well-angulated margins until at least 160 mm. diameter.

The sutural characters have been outlined in the foregoing description and discussion of the genus.

Measurements

	<i>Diameter</i>	<i>Whorl-height</i>	<i>Whorl-thickness</i>	<i>Umbilicus</i>
Holotype	163	89 (0.54)	?	18.5 (0.12)
R. A. Milbourne Coll. 1752	c. 40	23	10	?
	18	9.5 (0.53)	5 (0.28)	2.7 (0.15)

(Dimensions are in mm. Figures in parentheses are dimensions expressed as fractions of the diameter.)



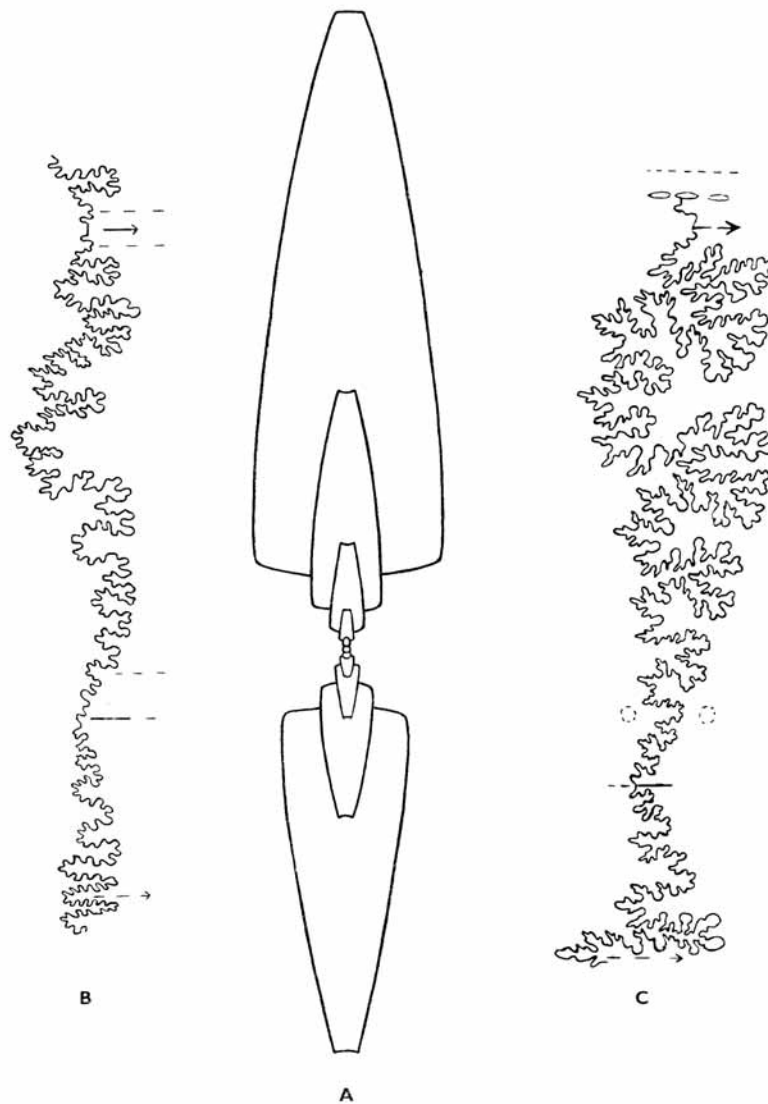
TEXT-FIG. 1. External suture-lines of Placenticeratidae. A, B, C, *Hengestites applanatus* gen. et sp. nov. at 8, 16, and 40 mm. diameter (R. A. Milbourne Coll. 1752). D, E, *Placenticerus meeki* Boehm at 10 and 25 mm. diameter (Upper Cretaceous, Wyoming. After Reeside 1926). F, *Metaplacenticerus californicum* (Anderson) at 50 mm. diameter (Upper Cretaceous, California. After Reeside 1926, reversed). G, *Hypenoceras warthi* (Kossmat) at about 140 mm. diameter (Lower Cretaceous, S. India. After Kossmat 1895).

Remarks. The above description is based on a large series of specimens drawn from a wide area of south-east England. All the zonally authenticated material was obtained from the *auritus* Subzone of the *inflatum* Zone, corresponding to the main mass of Bed XI of the Gault of Folkestone. This is not one of the best horizons in the English Albian for well-preserved macrofossils and the majority of specimens are crushed or fragmentary. None shows the test or the body-chamber, though large unsutured portions of a smooth and compressed ammonite found in the Upper Albian of Ventnor, Isle of Wight, may prove to be the final stage of *Hengestites*. The holotype is the only complete disk examined; it carries no documentation as to horizon within the Gault but is embedded in a large block of pale-grey marly clay with rusty partings—a type of lithology exclusive to Beds XI and XIII of the Gault. This fact, taken in conjunction with the mode of preservation of the fossil—putty-coloured phosphate with a dark-grey, slightly greenish-tinted surface film—indicates Bed XI as the source of the specimen.

Like *Uhligella derancei* (Casey 1949), *Hengestites applanatus* is only a modern re-discovery and was known to early collectors of the Folkestone Gault under another name. De Rance, who wrote the first systematic account of the Gault at Folkestone (1868) knew the species as a 'grooved variety of *Ammonites splendens*' and on his authority it is recorded as such from Bed XI in Topley's *Geology of the Weald*, published in 1875. The identity of De Rance's ammonite with the present species is confirmed by a specimen in the Geological Survey Museum (G.S.M. 97136), acquired from him in 1868. A similar record from Bed VIII of the Gault refers to immature *Euhoplites* of the group of *E. subcrenatus* Spath (e.g. G.S.M. 97135). The holotype was presented to the Woodwardian (now Sedgwick) Museum by the Reverend Thomas Wiltshire (born 1826, died 1902), who for many years spent holidays fossil-collecting at Folkestone (Woodward 1903). Crushed examples of *H. applanatus* collected by L. F. Spath and S. W. Hester from 6 feet above the base of Bed XI at Folkestone are also in the Geological Survey Museum (G.S.M. RE 4022-3). They were recorded by Spath (1923, p. 76) as *Beudanticeras beudanti* (Brongniart).

There is now little doubt that many of the old records of *Ammonites splendens* J. Sowerby from the Upper Albian of other localities, usually assumed to refer to *Anahoplites planus* (Mantell) or some other smooth Hoplitid, belong in part to *Hengestites* (e.g. the Potterne Rock and the Malmstone of Devizes, recorded by Jukes-Browne 1900, p. 256). This is certainly the case with the Upper Greensand occurrences at Ventnor, Isle of Wight, cited by Norman (1882; 1887), where, as at Folkestone, *Hengestites* is associated with *Mortoniceras inflatum* (J. Sowerby) and *Callihoplites auritus* (J. Sowerby) (Norman Collection, formerly in the Museum of the Ventnor and Bonchurch Literary and Scientific Institution).

The immature specimen illustrated in Pl. 29, figs. 3, 3a, is the original of the Wright brothers' (1939) record of *Anahoplites planus* (Mant.), sulcate form, from the Upper Gault of Aston Clinton, Buckinghamshire. This was considered to have originated in Bed IX (*Hysterocheras orbigny* Subzone) but was not obtained *in situ*. It is a well-preserved fragment with clear but interlocking sutures. Other specimens of the present species in the Wrights' collection comprise two large septate fragments from the Upper Albian of Punfield, Dorset, also cited as a sulcate form of *A. planus* (Wright 1947, p. 188). The horizon of these specimens is now believed to fall within the *auritus* Subzone (C. W. Wright, private communication).



TEXT-FIG. 2. A, B, *Hengestites applanatus* gen. et sp. nov., reconstructed whorl-section, natural size, and complete suture-line at about 90 mm. diameter. The latter is composite, being based on specimens G.S.M. Ca 7256, 7258 and Zn 7101. C, *Anahoplites planus* (Mantell), Upper Gault, Shenley Hill, Beds., complete suture-line at about 60 mm. diameter (after Spath 1925, reversed). Note the asymmetry of the ventral lobe in relation to the siphonal line and to the tubercles on the peripheral margin.

Conditions at Folkestone are no longer favourable for collecting from the higher beds of the Gault, but the species has been obtained in recent years by Mr. R. A. Milbourne from exposures of the *auritus* Subzone in the old Gault workings of the Aylesford Brick and Tile Company at Aylesford, Kent. A pyritic internal mould in his collection shows very clearly the sculptured phase of the young and some of the early stages of sutural development and is figured in Pl. 29, figs. 2, 2*a-b*, and text-fig. 1A-C. A further ten specimens were collected by Geological Survey officers from cuttings made for a new road in Horish Wood, on the north-east side of Maidstone, Kent (G.S.M. Ca 7250, 7256-8, 7881-5; Zn 7101). They are part of a large suite of remanié fossils found in a condensed 'Cambridge Greensand' facies of the *auritus* and *aequatoriale* Subzones. The most complete specimen (Ca 7250) is one-third of a plate-like disk of about 160 mm. diameter, sutured throughout; the whorl is 85 mm. high, the venter scarcely 4 mm. wide; allowing for the missing body-chamber the ammonite must have measured at least 240 mm. diameter. Other fragments belonged to disks of 300 mm. or more. Although dwarfed by the prodigious Placenticeratid of 780 mm. diameter described from the Navarro Group of Texas (Stephenson 1941, p. 432), *Hengestites* was none the less a giant among the ammonoidea of the Gault.

HENGESTITES AND THE SYSTEMATIC POSITION OF THE PLACENTICERATIDAE

The origin and systematic position of the Placenticeratidae are matters of debate. No unequivocal evidence of ancestry is provided by the form of the shell, and the septal sutures, as in most pseudoceratites, have undergone such profound modification that attempts to homologize the component elements with those of normal ammonites are frankly speculative. Douvillé (1890, pp. 288-91) assigned *Placenticeras* and *Stantonoceras* to the Hoplitidae on the basis of supposed similarities of the early sutures to those of *Anahoplites* ('*Hoplites*') *splendens* (J. Sowerby) and *Cleoniceras* ('*Sonneratia*') *quercifolium* (d'Orbigny), an opinion accepted by Grossouvre (1894, p. 123), Pervinquière (1907, p. 197), and others. The same conclusion as to relationship with the Hoplitidae was reached by Smith (1900) from a study of the immature stages of forms now identified as *Metaplacenticeras pacificum* (Smith) and *M. californicum* (Anderson), though he differed from Douvillé in his interpretation of the origin of the elements of the adult suture-line. Hyatt (1903, p. 192), on the other hand, investigated the young stages of *Placenticeras meeki* Boehm (= *P. whitfieldi* Hyatt) and concluded that at no stage in its development is the genus truly comparable with *Hoplites*. Concerning *Metaplacenticeras*, Matsumoto's recent observations on the ontogeny of *M. subtilistriatum* (Jimbo) (Matsumoto 1953) have led him to the belief that this genus was probably derived directly from the Phylloceratidae rather than from the Hoplitidae. This view accords better with the stratigraphical data, since *Metaplacenticeras* is not a Cenomanian ammonite as thought by Smith, but is of Campanian age and thus far removed in time from the Albian-Cenomanian Hoplitidae.

A connexion between the Placenticeratidae and the earlier pseudoceratites, the Engonoceratidae, is an hypothesis favoured at one time by Spath (1930, p. 390) and this is the view taken in the *Treatise on invertebrate paleontology* (Wright 1957, pp. L 109, 390),

wherein the Placenticeratidae are shown as the lineal descendants of the Engonoceratidae. This phylogeny was supported by consideration of the Upper Albian genus *Hypengonoceras*, at that time the only Lower Cretaceous Placenticeratid known. With its simple, pincer-like endings to the saddles, *Hypengonoceras* shows great resemblance to the Engonoceratids *Knemiceras* and *Parengonoceras* of Lower and Middle Albian age, though it exhibits the more complete fragmentation of the external saddle characteristic of the Placenticeratidae. Derivation of *Hypengonoceras* from *Parengonoceras* or some allied member of the Engonoceratidae seems probable; nothing is known, however, to bridge the gap between *Hypengonoceras* and the rather diverse forms that comprise the Upper Cretaceous Placenticeratidae.

The phylogenetic scheme is complicated by the introduction of *Hengestites*, for this is a cryptogenetic genus, appearing suddenly in the Upper Albian without evidence of ancestry. Unlike *Hypengonoceras*, its sutural characters are opposed to the idea of descent from the Engonoceratidae, and for reasons given above an origin in the Hoplitinae seems almost equally improbable. Since the boreal developments of the Hoplitidae that tended towards pseudoceratitism (e.g. *Gastrolites* McLearn, *Styracoceras* Hyatt) are also very distinct and there is no apparent link with the Lyelliceratidae, a family which sometimes mimicked the Hoplitid venter (Casey 1957, p. 34), the question of the ancestral source of *Hengestites* must be left open.

The discovery of *Hengestites* makes it difficult to conceive of the Placenticeratidae as a monophyletic group springing from the Engonoceratidae via *Hypengonoceras*. The more or less simultaneous appearance in widely separated geographical provinces of these two ammonites—one on the borders of the Indian Ocean, the other in south-east England—each bearing the hall-marks of the Placenticeratidae yet apparently of dissimilar origins, suggests that the family is polyphyletic. It is probable that both *Hypengonoceras* and *Hengestites* are forerunners rather than direct ancestors of the Upper Cretaceous Placenticeratidae.

The origin of the Engonoceratidae has also never been settled. Wright (1957) includes both the Engonoceratidae and the Placenticeratidae in a broad superfamily Hoplitaceae, though Luppov and Mikhailov (1958) unite them with the Sphenodiscidae in a separate unit, the 'Engonocerataceae'. In view of the uncertainty regarding the stem to which the Engonoceratidae and the Placenticeratidae attach themselves some such grouping seems desirable, though the Sphenodiscidae, of Acanthoceratacean affinities, must be excluded. It seems generally to have been overlooked, however, that the name Placenticerataceae (proposed as Placenticeratida) of Hyatt (1900, p. 584) is available for this group and takes priority over 'Engonocerataceae', put forward by Basse (1952, p. 658).

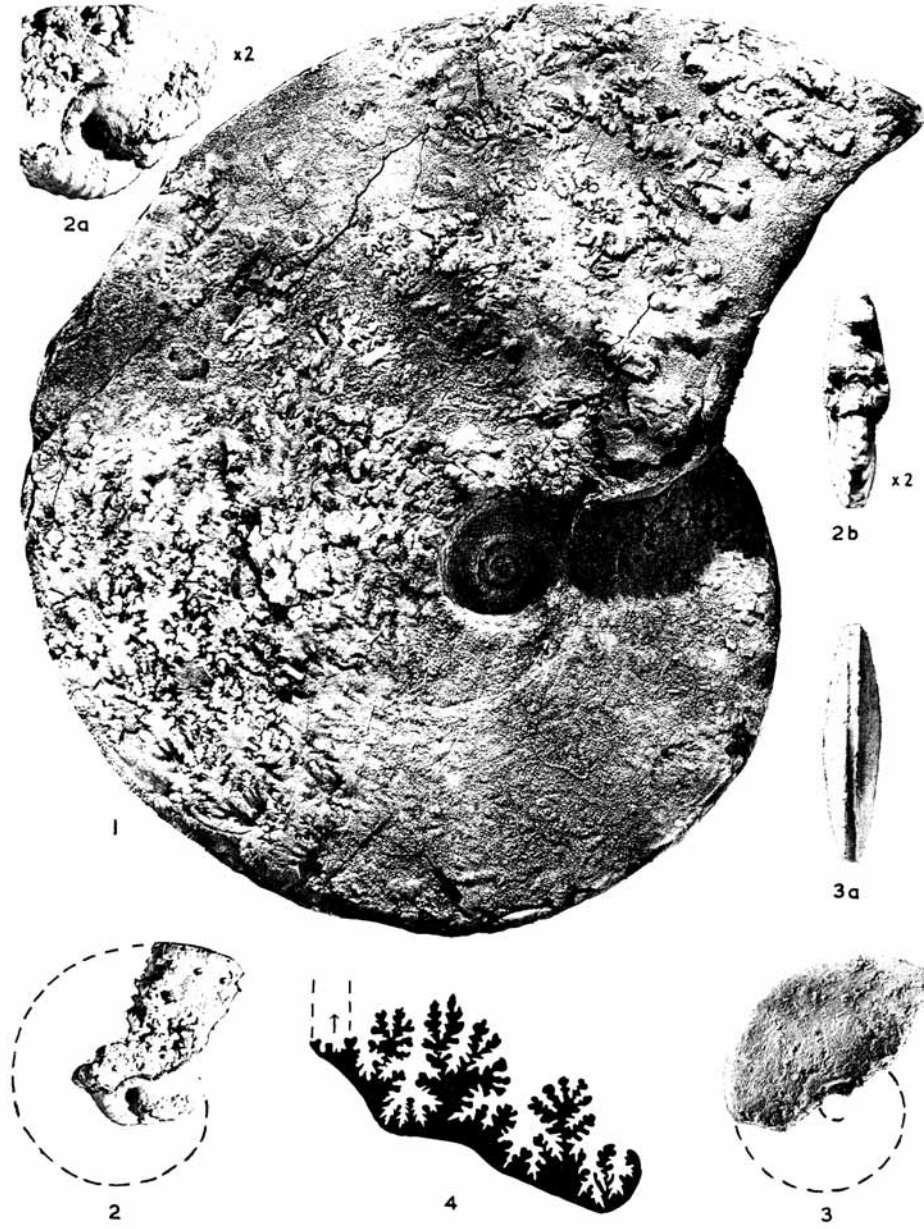
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R. CASEY
Geological Survey and Museum,
London, S.W. 7.

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CASEY, *Hengstites*.