AMMONITES POLYOPSIS DUJARDIN, 1837
AND THE CRETACEOUS AMMONITE FAMILY
PLACENTICERATIDAe HYATT, 1900

by W. J. KENNEDY and C. W. WRIGHT

ABSTRACT. Ammonites polyopsis Dujardin, 1837 is referred to the genus Placenticeras Meek, 1876 and shown to have priority over Ammonites ribouianus d'Orbigny, 1850, Placenticeras depressum Hyatt, 1903, P. grossouvrei Hyatt, 1903 (non Semenov, 1899) (renamed P. hyatti Diener, 1925), P. incissum Hyatt, 1903, P. schlueteri Hyatt, 1903, and P. crassatum Hyatt, 1903 amongst others. This plethora of names results from early failure to recognize the strong dimorphism present in the species. Recognition of this dimorphism and the wide intraspecific variation seen in P. polyopsis provides a basis for a review of the Placenticeratidae and its constituent genera, of which revised diagnoses and synonymies are presented. An effect of the nomenclatorial results of the study is that the widely cited P. syrtale Zone should be renamed the P. polyopsis Zone.

The ammonite family Placenticeratidae ranges from the upper Albian to the Maastrichtian. In all probability it was derived from the Hoplitidae via Hengestites Casey, 1960 and Karamaites Sokolov in Casey, 1965. The family is easily recognized by the multiplication of auxiliary and adventive elements in the suture line. At least twenty-four generic names have been established in the family, and a large number of specific names, yet the wide range of variability within taxa has been known for more than 150 years. Placenticeratids have a sporadic occurrence in western Europe but are sufficiently widespread and frequent in the upper Santonian and Campanian to be used as zonal indices in the standard scheme erected by de Grossouvre (1901). Although Hyatt (1903) renamed many of the European Ammonites syrtalis of Schlüter (1871–6) and Placenticeras syrtale of de Grossouvre (1894) only two years after the syrtale Zone was introduced, and made it quite plain that true P. syrtale (a North American lower Campanian species) did not occur in Europe, the syrtale Zone has persisted in the literature, including the Lexique Stratigraphique International (e.g. Sornay 1957) and recent syntheses (e.g. Wright 1957; Basse 1960; Collignon 1960; Pessagno 1969; Séronie-Vivien 1972; Rawson et al. 1978; van Hinte 1979; Wiedmann 1979; Hancock and Kennedy 1981). Summesberger (1979) has used the name Stantonoceras depressum (Hyatt, 1903) for this European form, but has recognized dimorphism.

We describe below the material from Touraine, Aquitaine, and the Corbières in France on which de Grossouvre (1901) based the syrtale Zone, and show that the correct name for the species is P. polyopsis (Dujardin, 1837), of which S. depressum is a synonym. The range of intraspecific variation in P. polyopsis and the marked dimorphism present provides a basis for a survey of all the generic taxa proposed in the family, their diagnoses and synonymies.

SYSTEMATIC PALAEOONTOLOGY

Location of specimens. This is indicated by the following abbreviations: BM(NH), British Museum (Natural History), London; IGS, Institute of Geological Sciences, London; MNHP, Muséum National d'Histoire Naturelle, Paris; SP, Collections of the Sorbonne, now housed in the Université de Paris VI; FSR, Faculté des Sciences, Rennes; EMP, Ecole des Mines, Paris Collections, now housed in the Université Claude-Bernard, Lyon; FSM, Faculté des Sciences, Le Mans, which now houses the collections of the Musée de Tessé, Le Mans.

Dimensions. Dimensions are given in millimetres, in the following order: diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U); c = costal; ic = intercostal. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kulman and Wiedmann 1970) is followed here; I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Family Placenticeratidae Hyatt, 1900
Genus Placenticeras Meek, 1876

Placenticeras polyopsis (Dujardin, 1837)

Plates 86–88; text-figs. 1–4

1837 Ammonites polyopsis Dujardin, p. 232, pl. 17, fig. 12.
1850 Ammonites polyopsis Dujardin; d'Orbigny, p. 212.
1850 Ammonites Ribourianus d'Orbigny, p. 213.
1872 Ammonites syrtales Morton; Schüller, p. 46, pl. 14, figs. 1–10; pl. 15, fig. 5, non figs. 1, 2 (= copy of Morton 1834), 3–4 (= Proplacenticeras pseudoribouryanum (Hyatt, 1903)).

non 1872 Ammonites polyopsis Duj.; Fritsch, p. 35, pl. 5, fig. 3.
1883 Ammonites Ribourianus d'Orbigny; Arnaud, pl. 3.
non 1893 Ammonites polyopsis Duj.; Fritsch, p. 76, text-fig. 56.
1894 Placenticeras syrtales Morton; de Grossouvre (non Morton), p. 128 (pars), pl. 5, fig. 3; pl. 6, figs. 1, 2; pl. 7, fig. 1; pl. 8, fig. 1 (including var. quadratum).

non 1895 Placenticeras polyopsis Dujardin; Jahn, p. 130.
1903 Placenticeras depressum Hyatt, p. 237.
1903 Placenticeras grossouvrei Hyatt, p. 237.
1903 Placenticeras incisum Hyatt, p. 238.
1903 Placenticeras schluteri Hyatt, p. 239.
1903 Placenticeras polyopsis (Dujardin); Hyatt, p. 240.
1903 Placenticeras crassatum Hyatt, p. 241.
1916 Placenticeras syrtales Mort. var. guadalope F. Roemer; Stolley, p. 93, pl. 5, fig. 4.
1925 Placenticeras crassatum Hyatt; Diener, p. 185.
1925 Placenticeras depressum Hyatt; Diener, p. 185.
1925 Placenticeras Hyatt Diener, p. 185.
1925 Placenticeras incisum Hyatt; Diener, p. 185.
1925 Placenticeras polyopsis Dujardin; P. J. F. Diener, p. 188.
1925 Placenticeras Schlüteri Hyatt; Diener, p. 189.
1931 Placenticeras syrtales Mort. var. guadalope F. Röm.; Riedel, p. 695.
1931 Placenticeras syrtales Mort. cf. var. milleri V. Hauer; Riedel, p. 696.
1931 Placenticeras syrtales Mort. var. costata Riedel, p. 696, pl. 79, fig. 2.
1937 Placenticeras cf. guadalope F. Roem.; Riedel, p. 217, pl. 16, fig. 3.
1937 Placenticeras radiatum (J. Böhm in sched.); Riedel, p. 219, pl. 16, figs. 1, 2.
1963 Placenticeras cf. hyati Diener; Fabre-Taxy, p. 108, pl. 5, fig. 3.
1963 Stantonoceras guadalope Römer sp.; Fabre-Taxy, p. 109, pl. 3, figs. 5–7.
1963 Stantonoceras cf. ribouri d'Orbigny; Fabre-Taxy, p. 110, pl. 3, figs. 8, 9.
1963 Stantonoceras sancarlostense Hyatt sp. var. collignoni nov. var.; Fabre-Taxy, p. 111, pl. 3, figs. 12, 13.
1963 Stantonoceras sp.; Fabre-Taxy, p. 111.
1978 Stantonoceras depressum (Hyatt); Wiedmann, p. 667, pl. 1, figs. 1, 2; text-figs. 2a, 3a.
1979 Stantonoceras depressum Hyatt; Summesberger, p. 145, pl. 10, figs. 42, 43; pl. 11, figs. 44–47; pl. 12, figs. 48–52; text-figs. 31–37.

Types. Dujardin based this species on two specimens (1837, pl. 17, fig. 12a and b–c; see text-fig. 1). The original of his fig. 12a, a juvenile macroconch, is here designated lectotype. Both specimens are said to be from the 'Craig Tufau', and no locality, other than Tauraine, is given. They have not been traced.

Material. From St.-Patern-Racan, variously labelled 'route' or 'niveau à Spondylus truncatus': FSR, three specimens (plus one unlabelled that is probably from this locality); MNHP B16692; FSM, one unregistered
specimen (ex Quiller Coll.). MNHP B16802 from the Craie de Villedieu of Loir-et-Cher. Several specimens (Gale Coll.) from Bed 22a (Jarvis et al. 1982) of the Craie de Villedieu at La Ribochère, Loir-et-Cher. MNHP unregistered from near Villandréd, Indre-et-Loire. MNHP unregistered from Savonnières (Indre-et-Loire). BM(NH) C26681 and an unregistered specimen in the EMP collections (ex Deshayes Coll.), both from Tours. EMP unregistered (ex Thomas Collection) from Langeais, Indre-et-Loire.

There are numerous specimens from Aquitaine. The Arnaud Collection, now in the Sorbonne Collections housed in the Université de Paris VI, includes the best localized specimens from Arnaud's assize M² at Miremont, Riberaç, Périgueux, Beaulieu (Stiolac, souterrain de Beaulieu); from M¹ to M at Angoumac, Cognac; from M² at Champagnac-de-Belair, St. Léon-sur-Vezère, Versannes, Epagnac, Miremont, Puycat, and Rognac; one specimen is precisely located as from couche 22, route d'Agonac, Périgueux. From N² to N, a specimen of P. cf. polyops (from St. Caprais; from N² at Aurioux, Saintes, a P. cf. polyops. All but one of the specimens figured by de Grossouvre (1894) have not been traced (they are probably in the Université de Paris VI but are not available; a set of casts is in the collections at Rennes and those of the École des Mines, now at Lyons); they are from M² at Beaulieu, and La Valette. A specimen in the EMP collections (ex Boucheron Collection) is also from the last locality. A further specimen in the Collections of the Musée de Gaillac is from Charmant.

There are numerous specimens from the Corbières (Aude), variously labelled Sougraines, environs de Rennes-Bains, Chemin de Creutets, etc., in the MNHP, SP, EMP, FSL, and BM(NH) collections. Stratigraphic data are usually poor, but de Grossouvre (1901, p. 795) notes that it is rare in the lower part of the Santonian but common in the upper part.

<table>
<thead>
<tr>
<th>Dimensions</th>
<th>D</th>
<th>Wb</th>
<th>Wh</th>
<th>Wb:Wh</th>
<th>U</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microconchs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MNHP B16692</td>
<td>72-0 (100)</td>
<td>28-7 (39-9)</td>
<td>30-7 (42-6)</td>
<td>0-94</td>
<td>19-6 (27-2)</td>
</tr>
<tr>
<td>ic</td>
<td>23-4 (32-5)</td>
<td>30-7 (42-6)</td>
<td>0-76</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FSR 1803</td>
<td>79-7 (100)</td>
<td>39-8 (49-9)</td>
<td></td>
<td>16-5 (20-7)</td>
<td></td>
</tr>
<tr>
<td>ic</td>
<td>109-5 (100)</td>
<td>46-3 (42-3)</td>
<td></td>
<td>16-2 (20-6)</td>
<td></td>
</tr>
<tr>
<td>MNHP 'Villandréd'</td>
<td>133-0 (100)</td>
<td>55-4 (41-7)</td>
<td>4-7</td>
<td>31-5 (23-7)</td>
<td></td>
</tr>
<tr>
<td>ic</td>
<td>109-0 (100)</td>
<td>47-0 (43-1)</td>
<td>0-72</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MNHP unreg. at</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ic</td>
<td>140-0 (100)</td>
<td>55-0 (51-6)</td>
<td></td>
<td>20-5 (19-2)</td>
<td></td>
</tr>
<tr>
<td>ic</td>
<td>141-0 (100)</td>
<td>64-0 (45-4)</td>
<td></td>
<td>30-0 (21-3)</td>
<td></td>
</tr>
</tbody>
</table>

**Description.** The species is strongly dimorphic, as demonstrated by Summesberger (1979).

**Microconchs.** The inner whorls up to a diameter of 30-40 mm are compressed, involute, with a small crater-shaped umbilicus (around 15% of the diameter) (Pl. 87, fig. 4). The umbilical wall is flattened and slopes outwards; the umbilical shoulder is abruptly rounded. The whorl section is compressed (whorl breadth to height ratio 0-6 or less), with the greatest breadth close to the umbilical shoulder, the inner flanks rounded, the outer flanks converging to a narrow tabulate venter with sharp ventrolateral shoulders. There are feeble commas-shaped umbilical baulae (six per half whorl in MNHP B16691) which give rise to low, broad prosirradiate ribs that flex back and are feebly concave, that is falcoïd, on the outer flank, and appear to terminate in feeble ventral clavi (the specimens are defective on this point). From around 40 mm the whorls change from compressed with a narrow venter to trapezoidal with a broad, flattened venter and eventually become depressed on the adult body chamber with the greatest breadth at strong umbilical baulae and below mid-flank intercostally. The feeble baulae of the inner whorls strengthen markedly, and migrate out from the umbilical shoulder to first an inner (Pl. 86, fig. 2), and ultimately a mid-flank position (Pl. 87, fig. 6). A low broad rib connects them to the umbilical seam of a large, moderately deep umbilicus, the wall of which merges imperceptibly with the flank. These tubercles are rounded to bulate, strong on the phragmocone and early body chamber of adults, but decline towards the adult aperture to weak, sharp baulae only (Pl. 85, fig. 2).

The umbilical baulae give rise to one or a pair of low, broad, straight, prosirradiate ribs and there are also occasional short intercalated ribs to give a total of nine per half whorl. All ribs bear rounded-clavate inner ventrolateral tubercles that strengthen progressively around the outer whorl. Corresponding to each of these is a
sharp elongate ventrolateral clavus. This initially sits on the sharp ventrolateral shoulder of a rather narrow venter but, as size increases and the venter broadens, the clavus becomes progressively weaker and is eventually reduced to the merest swelling on a blunt angulation between a broad venter and broadly rounded ventrolateral shoulder. The clavi and ribs on opposite flanks vary from slightly offset to alternate in position. The venter is crossed by broadly convex growth lines and striae. The largest observed microconch (Pl. 85, figs. 1–3) has an estimated diameter of 120 mm with just over half a whorl of body chamber, the coiling becoming progressively more evolute towards the aperture.

Macroconchs. The ornament and shell form of nuclei is identical to that of the microconchs described above. The compressed, relatively feebly ornamented or smooth stage persists, however, to a diameter of 60–70 mm (Pl. 86, fig. 4); thereafter an ornament of falcoid ribs with feeble inner and stronger outer ventrolateral clavi is succeeded by an adult whorl which remains compressed but develops initially weak and bullate but subsequently strong and conical umbilicolateral tubercles which migrate to first a mid- and then an outer-flank position. These tubercles are linked to the umbilical shoulder by a low, weak rib, and give rise to a pair of low, broad, straight ribs, each of which bears a clavate inner ventrolateral tubercle. These are initially set at an angle to the line of the venter, but rotate to parallel the venter as size increases. These tubercles are invariably weaker than those of microconchs at the same diameter. Outer ventrolateral clavi are borne on the ventrolateral shoulder, generally offset from or alternating with those on the opposite side of the narrow venter. They persist to the largest diameter seen, a phragmocone 150 mm in diameter (text-fig. 2).

The suture line (text-fig. 3) follows the sagging course typical of the genus. Development of adventive and auxiliary elements gives an adult suture with eight bifid saddles in the external part.

Discussion. This species is surrounded by nomenclatorial confusion because most authors failed to recognize that individuals of the same size with markedly different ornament were dimorphs. The name Ammonites polyopis was validly introduced by Dujardin in 1837, and accompanied by excellent illustrations, reproduced here as text-fig. 1.
In his description (1837, p. 232), Dujardin comments: 'Cet e ammonite varie tellement, que des échantillons isolés pourraient être pris pour des espèces distinctes, si l'on n'observait quelquefois toutes les variations possibles sur les différents points d'un même échantillon.'

The lectotype (Dujardin 1837, pl. 17, fig. 12α; see text-fig. 1c) is a juvenile macroconch, and the paratype (Dujardin 1837, pl. 17, fig. 12b–c; see text-fig. 1α, β) is a microconch. D'Orbigny listed *A. polypus* in the *Prodrome* (1850, p. 212, no. 15), and indicated that there were specimens in his collection. The catalogue records two specimens under no. 7180, from Tours (Indre-et-Loir). One of these specimens survives, and is a fragment of a mature microconch. D'Orbigny also introduced the name *A. semiornatus* in the *Prodrome* (1850, p. 212). The remarks are characteristically brief:

"13. *semiornatus*, d'Orb., 1847. Espèce tres-aplatie; à tours embrassants, lisses, tronqués sur la carène, et ornés de chaque côté de cette partie de tubercules obliques. Tours, route de Paris." This is a perfectly valid indication and two specimens survive in d'Orbigny's collection, under no. 7179. Sornay (1955) has refigured the material, referring it to *Diplaconoceras* (recte *Diplacoceras*) and designating the complete specimen lectotype. Its horizon is unknown, but probably Santonian, a specimen from the Craie de Villedieu of St. Frimbault, Sarthe (MNHP de Vibrate Collection, 1896. 27) in a preservation identical to that of *Protxanites bourgeoisii* (d'Orbigny, 1850) from this locality is of upper Coniacian date. It differs from *Placenteceras polypus* in lacking umbilical tubercles at any stage, and in having low, rursiradiate concave ribs on the outer flank of the early stages that migrate outwards and turn into rounded or bullate inner ventrolateral tubercles that are associated with twice their number of ventral clavi. On the lectotype these rotate progressively around the body chamber to lie parallel with the venter.

A second name introduced by d'Orbigny in 1850 (p. 213) was *A. ribourianus*: "49. Ribourianus, d'Orb., 1847. Espèce voisine de l'A. polypus, mais avec le dos carré, et deux rangées latérales de tubercules aigus. France, Villedieu (Loir-et-Cher), M. Bourgeois." The asterisk indicates that d'Orbigny had specimens in his collection, but none is listed in the catalogue. From the description it clearly represents the microconch of *P. polypus*, body chambers of which indeed have a square back and two rows of pointed lateral tubercles.

Schlüter (1872, p. 46) treated *A. polypus* as a junior synonym of *A. syrtalis* Morton, 1834 (p. 40, pl. 16, fig. 4), a view followed by d'Orbigny (1894, p. 128). Both these authors recognized the wide variation in morphology and ontogeny shown by the species, and also placed *A. geinitzii* d'Orbigny, 1850 (p. 213, = *A. vibrayemus* Geinitz (non d'Orbigny), 1843, p. 8, pl. 1, fig. 8), *A. guadaloupae* Roemer, 1852 (p. 32, pl. 2, fig. 1), and *A. milleri* Hauer, 1866 (p. 5, pl. 2, figs. 1, 2) in synonymy.

*A. syrtalis* Morton, 1834, is a lower Campanian species and was revised by Hyatt (1903), Reeside (1927), and Young (1963) while Wolleben (1967) has provided a valuable analysis of populations of this species. Even Hyatt (1903, p. 196) realized the wide variation of the species: 'There is no real line between *P. guadalupae*, sancarlosense and planum, nor between *newberryi* and guadalupae, nor between sancarlosense, syrtale, intercalare and planum, nor between intercalare, stantoni, pseudoplacenta and whitfieldi.' Wolleben (1967) placed all these species in synonymy, as well as *Stantonoceras pseudocostatum* Johnson, 1903 and *P. rotundatum* Johnson, 1903. He recognized, however, a series of chronologically subspecies: *P. syrtale syrtale* (oldest), in which specimens of 'P. syrtale' of previous authors are abundant, *P. syrtale adkinsi* Wolleben, 1967, in which specimens of 'P. pseudosyrtale' of previous authors are abundant, and *P. syrtale rooneyi* Wolleben, 1967, in which specimens of 'P. newberryi' of previous authors are abundant. Nomenclatural problems of this treatment aside, it was unfortunate that Wolleben failed to recognize that this species shows the same type of dimorphism as *P. polypus*, with robust 'Stantonoceras' microconchs and 'Placenteceras' macroconchs.

*P. syrtale* is superficially similar to *P. polypus*, but Hyatt (1903) recognized them as separate, noting that juveniles of the American species lack ribs on the inner whorls and that umbilical bullae remain on the umbilical shoulder, not showing the outwards migration of the French specimens. The sutures are also different, *P. polypus* having eight lobes in the external suture and *P. syrtale* ten or eleven.
TEXT-FIG. 2. Immature macroconch of *Placenticeras polyopsis* (Dujardin, 1837), MNHP B16802, from 'Loir-et-Cher', x 1.

EXPLANATION OF PLATE 85

TEXT-FIG. 3. External suture of *Placenticeras polyopsis* (Dujardin, 1837), based on an unregistered specimen in the Sorbonne Collections (ex Toucas Collection), from near Sougraines, Corbières, Aude.

TEXT-FIG. 4. Whorl sections of *Placenticeras polyopsis* (Dujardin, 1837). a, slender microconch (see Pl. 86, figs. 1–3 for details). b, c, microconch from Couture, MNHP B16805; b is at the beginning of the body chamber, c at the end. d, phragmocone of an immature microconch from near Villandry, MNHP collections. e, phragmocone of macroconch shown in text-fig. 2.

**EXPLANATION OF PLATE 86**

Hyatt (1903) renamed most of Schlüter's (1872) and de Grossoüre's (1894) A. syrtalis and P. syrtale. P. depressum Hyatt, 1903 (p. 237) (=A. syrtalis Schlüter (non Morton), 1872, p. 46 (pars)), pl. 14, figs. 9, 10 only; P. syrtale var. Guadaloupe de Grossoüre (non Roemer) 1894, p. 128, pl. 6, fig. 2 only; pl. 7, fig. 1, lectotype here designated, the original of de Grossoüre 1894, pl. 6, fig. 2) is a microconch P. polyopsis. P. hyatti Diener, 1925 nov. nov. pro P. grossourei Hyatt, 1903 (p. 237) (non Semenov, 1899) = 'Placenticeras syrtale de Grossoüre (pars)', p. 128, pl. 5, fig. 32, p. 16, fig. 1 (no others) was cited erroneously in Hyatt's posthumous work, 'pl. 5, fig. 32, p. 16, fig. 1' not existing in de Grossoüre's work. From the subsequent account, however, it is apparent that the intended citation was 'pl. 5, fig. 3, pl. 6, fig. 1'. The latter is here designated lectotype of the species; it is an adult macroconch. The paralectotype is a juvenile 55 mm in diameter that already has ribs and tubercles at the smallest diameter visible, indicating it to be a juvenile microconch.

P. incisum Hyatt, 1903 (p. 238) (=P. syrtale de Grossoüre, 1894, p. 128 (pars), pl. 8, fig. 1 only) is based on a macroconch from a locality M2 of Arnaud at La Valette (Charente) (Rejaudy Collection). It has not been traced (but there are casts in the FSR and EMP collections) and a fine unlocalized specimen in the MNHP collections, illustrated here as Pl. 85, figs. 1–3, serves as a basis for discussion. The dimensions are given above. Ornament consists of umbilical tubercles, of which there are several on the outer whorl. These are weak and markedly bulate at the smallest diameter visible, but strengthen markedly and migrate outwards around the last whorl and are connected to the umbilical seam by a low rib. Very weak pairs of ribs link to strong inner ventrolateral clavi, whilst additional clavi are intercalated to give a total of approximately twenty per whorl. Those on opposing flanks are slightly offset in ventral view, rising high above the narrow venter. At the smallest diameter visible a semicontinuous ridge or angulation marks the junction of venter and ventrolateral shoulder, but this declines on the body chamber where the venter is smooth and concave between persistent ventral clavi. This early decline of outer ventrolateral clavi, and the angulation marking their site which disappears on the body chamber, are features of microconch P. polyopsis, but these are generally depressed and quadrate. At the same diameter, similarly compressed microconchs are still septate and retain discrete outer and inner ventrolateral clavi. The species is interpreted as an unusually compressed microconch of P. polyopsis.

P. schluteri Hyatt, 1903 (p. 239) (= A. syrtalis Schlüter (non Morton), 1872, p. 46 (pars)), pl. 14, figs. 1, 2) was separated by Hyatt on the basis of details of ornament and ontogenetic changes in tuberculation. The specimen shows the same outward migration of umbilical tubercles as P. polyopsis but lacks ribs on the inner flank; it is a clear synonym, and probably a microconch. P. crassatum Hyatt, 1903 (p. 241) (=A. syrtalis Schlüter (non Morton), 1872, p. 46 (pars)), pl. 14, figs. 4–7, fig. 31) was differentiated from P. schluteri by Hyatt because it was more compressed and did not show an outward migration of the umbilical tubercles which disappear and are replaced by low ribs. This is probably no more than a variant of P. polyopsis.

P. pseudorbignyanum Hyatt, 1903 (p. 242) (= A. syrtalis Schlüter (non Morton), 1872, p. 46 (pars)), pl. 15, figs. 3–5 only) is a member of the Coniacian P. orbignyanum (Geinitz, 1850) group which lacks the strong tubercles of the later P. syrtale. Other members are P. frischii de Grossoüre, 1894 (p. 124, pl. 5, figs. 1, 2; text-fig. 52) (the type species of Proplacenticeras Spath, 1926), P. memoriaschloenbachi (Laube and Bruder, 1887) (p. 221, pl. 23, fig. 1), P. kaffairianum (Etheridge, 1904) (p. 89, pl. 3, fig. 16), P. unkwelananensis (Etheridge, 1904) (p. 89, pl. 3, figs. 17–20), and P. subkaffairianum (Spath, 1921).

Explanations of Plate 87

Figs. 1–6. Placenticeras polyopsis (Dujardin, 1837). 1, 2, SP unregistered, juvenile microconch from the Souterrain de Beaulieu on the line from Ribérac to Périgueux, Dordogne; figured by de Grossoüre (1894, pl. 5, fig. 3). 3, 4, MNHP B16691, incomplete microconch showing smooth inner whorls, from the Santonian Craie de Villedieu of Monnat, near Villandry, Indre-et-Loire. 5, 6, MNHP unregistered, incomplete microconch from the Santonian Craie de Villedieu, 2 km west of Villandry, Indre-et-Loire. All ×1.
KENNEDY and WRIGHT, Placenticeras
P. syrtale costata Reidel, 1931 (p. 696, pl. 79, fig. 2) from the Santonian of Ziegeli near Recklinghausen in the Münster Basin is regarded as more than a variant of the present form, as is P. radiatum Riedel, 1937 (p. 219, pl. 16, figs. 1, 2) from the Santonian of Heudeber-Danstedt in the Harz Foreland. However, more and better material of both forms might in future indicate consistent differences justifying subspecific separation.

P. paraplanum Wiedmann, 1978 (p. 666, pl. 1, figs. 3, 4, text-fig. 2a; see also Summesberger 1979, p. 152, pl. 13, figs. 53–57, text-figs. 38, 39) which occurs with P. polyposis in the upper Santonian Gosau Beds of Gosau, Austria. It appears to be separate from P. polyposis on the basis of strongly convex fleuxuous ribs and bullae that remain closer to the umbilical shoulder. Wiedmann compared it to P. planum Hyatt, 1903, which Wolleben (1967) considered no more than a variant of P. syrtale, and it may lie in an analogous position in the spectrum of variation of P. polyposis. One of the specimens referred to the species by Summesberger (1979, pl. 13, figs. 55, 56) shows an outward migration of the umbilicolateral bulla and an early decline of the outer ventrolateral clavi.

P. maherndii Summesberger, 1979 (p. 155, pl. 14, figs. 58–61; pl. 15, figs. 62–66, text-figs. 40–47) is a much better characterized species in which Summesberger was also able to recognize dimorphism. It occurs with P. polyposis in the upper Santonian Gosau Beds of Gosau, Austria. Inner whorls bear falcoid ribs, the macroconch develops weak bullae, and body chambers of both forms bear dense fleuxuous ribs. Distinct as this appears, the material is no more different from the P. polyposis described here than the extremes of P. syrtale discussed by Wolleben (1967) are from each other.

Occurrence. The species is confined to the Santonian. In Touraine it occurs widely in the Craie de Villedieu, well-localized specimens coming from de Grossouvre’s (1901) Zone E, the niveau à Spondylus truncatus of previous authors. Jarvis et al. (1982) have shown that the species occurs in the remanié lag at the top of a hardground (Thurtell’s). Of other specimens suggests a similar occurrence. The only associated fauna of stratigraphic significance is Baculites incurvatus Dujardin, 1837. In Aquitaine the species is widespread, as indicated under the list of specimens studied, and Arnaud (1877) cited it from many other localities (see also Sérénio-Vivien 1972). The stratigraphic range spans all of Arnaud’s divisions of the Santonian (M1, M2, N1, N2), and this is confirmed by records in Toucas (1883), de Grossouvre (1894, 1901), and Sérénio-Vivien (1972). The last author recorded it from only 5 m above the base of the Santonian in a temporary trench at l’Amblardice, Montmoreau (p. 78), and low in the Santonian at Castelfadère and Mater (pp. 89, 144). Indeed, most of Arnaud’s specimens are from his divisions M1 and M2—that is to say, the lower Santonian Texanites texanus Zone of de Grossouvre.

In the Corsichires the reliable records are still those of de Grossouvre (1894, 1901), who recorded it as rare in the lower part of the sequence (his texanus Zone) but common above (the ‘banc à Lima marccensis’ and the ‘marnes intercalées entre les deux principaux bancs de rudistes’). This is what Bilotte et al. (1971) referred to as the ‘Série de la Montagne des Cornes’. The species occurs at many localities in the Beausset Basin (Var) (de Grossouvre 1894, 1901; Fabre-Taxy 1963). Fabre-Taxy assumed all the occurrences to be in the upper Santonian.

In Austria the species is abundant in the Gosau and Piesting areas (Wiedmann 1978; Summesberger, 1980). The Gosau records are in the 20 m thick ‘sandkalkband’ at the top of the Santonian. This species occurs widely in the Germanies, and Mr. C. J. Wood has kindly analysed the best-documented occurrences. At Deitersmann’s brick-pit at Rapen, near Recklinghausen, the Recklinghausen Marl yielded P. polyposis associated with Boehmoceras krekelieri (Wegner, 1905) and B. loescheri (Riedel, 1931) and other species. The species suggest the upper Santonian on the basis of Summesberger’s records and the occurrence of Boehmoceras in Arnaud’s Assizes M2 and N2 in Aquitaine. The Recklinghausen occurrences are associated with Marsupites, indicating the M. testudinarius Zone of the north-west European White Chalk facies. Böhm (1915) recorded P. schleiereri Hyatt, 1903 (e.g. P. polyposis) associated with B. krekelieri and other ammonites in the M. testudinarius Zone at Ahau. Riedel (1937) recorded what are here interpreted as P. polyposis from the Salzberg Marl of the Quellenburg–Salzberg region; the associated inoceramid evidence indicates the high Microaster corangium Zone of the White Chalk facies. He recorded from Heudeber-Danstedt what he believed to be different species, P. radiatum and P. intercalare, herein regarded as P. polyposis, associated with a fauna indicating a higher horizon than that at Salzberg.

The more general records of Wiedmann (1979) appear to be based chiefly on Schlüter’s early records; they
suggest *P. polyoptis* is confined to the upper part of the Santonian; indeed, Wiedmann uses the term *syrtaile Zone* in de Grosseuvre’s sense.

These data suggest that *P. polyoptis* ranges from just above the base of the Santonian in Aquitaine to the highest of Arnaud’s divisions (from M3 to N1). Most of the surviving specimens are labelled M1, but there are so few that this may not reflect real abundance. In the Corbières the species occurs both low and high in the Santonian but is commonest above. The same appears to be true in Provence and in Germany and Austria. The Touraine records are stratigraphically isolated and cannot be referred to either upper or lower Santonian with any confidence at this time. The absence of diagnostic elements of the high Santonian crinoid zones of the White Chalk facies (Jarvis et al. 1982) suggest it is lower Santonian, however, as that term is used in the chalk sequences.

Dr. W. A. Cobban (pers. comm., 1982) tells us that he believes fragments of *Placenticeras* from the Tombigbee Sand Member of the Eutaw Formation of Alabama can be referred to the present species; the unit is assigned to the Santonian on other evidence.

**DISCUSSION**

*Stratigraphic consequences.* The upper Santonian *P. syrtaile Zone* of de Grosseuvre and authors should be renamed the *P. polyoptis Zone*. The index species, however, has a range that extends into the lower Santonian.

*Systematic consequences.* The recognition of wide intraspecific variation and dimorphism in *P. polyoptis* leads to a critical review of the systematics of the Placenticeratidae.

The family appears to have evolved rapidly in the upper Albian from *Metaclavites* Casey, 1965 (Hoplitinae) by increase in whorl height and associated development of extra elements in the suture. Almost all members of the family up to the Maastrichtian show at some stage of ontogeny the alternating ventrolateral claví that characterize their hoplitine ancestors.

In the upper Albian there are three genera whose interrelationships are not yet clear. *Hengestites* Casey, 1960, known only from England, has a juvenile stage with feeble flexuous ribs ending in fine ventrolateral claví. The shell then becomes smooth with sharp-edged, sulcate, later tabulate, venter; the suture is not far removed from that of Hoplitinae but shows major subdivision of saddle E/L. *Hypongonoceras* Spath, 1922, known from Spain, Madagascar, Zululand, southern India, and perhaps Japan, has low falcoid ribs and ventrolateral claví to a late stage, together with a suture characterized by many subequal pincer-like saddles. The third genus, for which *Karamaiites* Sokolov in Casey (1965, p. 461) is the earliest of seven names which we regard as synonymous, ranges from upper Albian to Cenomanian and is known from France, Crimea, and Central Asia. It has flat sides on the early whorls which become convex later, and ventrolateral tubercles which persist to a variable extent. The suture is also variable but the 4th lateral lobe is generally smaller than the 5th.

*Karamaiites* begins the mainstream of the family which continues with slow elaboration of ornament and suture until the Maastrichtian. Marked dimorphism can be demonstrated whenever large collections of upper Cretaceous specimens are examined. We have insufficient Albian material to pronounce on dimorphism, but in the upper Cenomanian *Proplacenticeras* from Texas it is obviously present, the macro- and microconchs differing in size, but little else. By the upper Turonian the Madagascan faunas show an association of large forms that are said to be smooth when adult, except for minute umbilical tubercles (*Proplacenticeras memoriaschloenbachii* var. *ambloenensis* Collignon, 1965a, p. 14, pl. 381, fig. 1646; pl. 382, figs. 1647–8), and smaller forms with stronger umbilical bullae and weaker clavate mid-lateral to inner ventrolateral and outer ventrolateral tubercles (*Parastationonoceras murphi* Collignon, 1965a, p. 17, pl. 382, fig. 1649); these we take to be macro- and microconchs respectively. The same type of dimorphism may also be present in the so-called ‘Middle’ Turonian of Madagascar (see Collignon 1965a, pl. 383), with *Parastationonoceras* besarrei (Collignon, 1936) as microconch, and in the Coniacian with *Proplacenticeras fritschii eberonii* Collignon, 1965b (p. 38, pl. 430, figs. 1780–1781) as macroconch and *P. kalfrarium* (Etheridge, 1904) as microconch (the nomenclature of Coniacian *Proplacenticeras* is as confused as that of the Santonian species of *Placenticeras* and is not entered into here).

The dimorphism shown by the European *Placenticeras polyoptis* is described above. Suture line apart, macroconch *Placenticeras* and *Proplacenticeras* are very similar, differing only in the degree
of retention of strong ornament and outward migration of umbilical bullae and mid-lateral clavi. The microconchs become more evolute and are sometimes quadrate in whorl section, with persistent ornament. The same is true of the Campanian Placenticeras syrtale group, as documented, but not recognized, by Wolleben (1967).

Two stocks separated from Placenticeras in the Santonian that in our view clearly deserve generic separation. Metaclavites Spath, 1926, is characterized by dense strong flexuous ribbing and no tubercles. We have not seen enough material to recognize dimorphism. Hoplitoplacenticeras Paulcke, 1906, is relatively evolute with a more or less rectangular whorl section and strong ribs and tubercles and lacks a smooth stage. Preliminary observations on material from Zululand (South Africa) indicate dimorphism.

Given the wide range of variation of ornament and progressive increase in numbers of sutural elements, it is difficult to decide on any split in generic classification of the mainstream forms. It would be attractive to refer the whole of the mainstream of the family to one genus, Placenticeras, with Karamaites, Proplacenticeras, and Placenticeras sensu stricto as successive subgenera for those who can find significance in minor sutural differences. It is in our view practicable in the present state of knowledge to distinguish Karamaites, generically or subgenerically, for early forms in which definite dimorphism is not yet demonstrated. Proplacenticeras, however, is tied to its type species, Placenticeras frischi Gressouvre, and study of the type material shows that it is either conspecific with or very closely allied to contemporary material from Zululand (Klinger and Kennedy 1980, p. 305) that covers a morphological range almost as wide as that of Santonian Placenticeras. The progressive increase in the number of auxiliary elements in the suture does not, we believe, allow any sensible division; if reliance were placed on this character a distinct genus or subgenus would logically have to be based on each increase of one new auxiliary lobe in the adult suture. The outward migration in strongly ornamented forms of umbilical tubercles to a mid-lateral position and of mid-lateral tubercles to an inner ventrolateral position is equally continuous. Our conclusion is that we should for the present at least maintain Karamaites for mainstream forms that show no strong differentiation of dimorphs and group in Placenticeras those upper Cenomanian, Turonian, and later species, including the type species of Proplacenticeras, that have strongly differentiated microconchs. If Karamaites is subsequently found to have strongly differentiated microconchs, it should be reduced to a synonym of Placenticeras. We would thus set out the classification of the family as follows (see also text-fig. 5):

![Text-fig. 5. Phylogeny of the Placenticeratidae.](image-url)
Family **Placenticeratidae** Hyatt, 1900, p. 585
(= Hypenoniceratidae Chiponkar and Ghare, 1976, p. 2; Baghioceratinae Chiponkar and Ghare, 1976, p. 3)

*Diagnosis.* Moderate-sized to large; inner whorls at least generally involute, compressed, with narrow flat or grooved venter and little or no ornament; outer whorls similar in macroconchs; microconchs of some genera become evolute and more or less inflated with strong ornament. Suture with adventive and auxiliary elements; the external saddle and first lateral lobe become very wide and develop a number of more or less equal new elements; saddles and lobes may be short and more or less rounded, or long, narrow-necked, and much frilled. Of Albian genera, while *Hypenoniceras* in some respects resembles *Engononiceratidae*, *Hengestites* and *Karamaites* are clearly derived from *Hoplitidae*.

*Occurrence.* Upper Albian to Maastrichtian.

**Genus Hengestites** Casey, 1960, p. 201

*Type species.* *Hengestites planatus* Casey, 1960, p. 201, by original designation.

*Diagnosis.* Large, high-whorled, involute with angular umbilical rim and narrow venter. Early whorls have faint flexuous riblets ending in alternating ventrolateral clavi. Later shell is smooth, the venter sulcate with carinate edges, then tabulate. Suture with shallow ventral lobe, a broad bifid or asymetrically trifid first lateral lobe, bifid and subphylloid saddles; a deep adventitious lobe divides the external saddle unequally, the ventral part being much smaller.

*Occurrence.* Upper Albian; England.

**Genus Hypenoniceras** Spath, 1922, p. 112

*Type species.* *Placenticeras warshi* Kosmat, 1895, p. 92, by original designation.

*Diagnosis.* With sloping flat sides and narrow flat venter; sparse low falcioid ribs end in alternating ventrolateral clavi. Suture with large pincer-like bifid foliules.

*Occurrence.* Upper Albian; Spain, Madagascar, Southern India, ?Japan.

**Genus Karamaites** Sokolov in Casey, 1965, p. 461.


*Type species.* *Placenticeras grossouvrei* Semenov, 1899, p. 97, by original designation.

*Diagnosis.* Sides flat at first, then inflated and convex; weak sinuous to falcioid ribs may be present on early whorls, with little ornament except for prominent alternate ventrolateral clavi which persist to body chamber. Suture with 4th lateral lobe generally smaller than 5th. So far as is known, dimorphs are not strongly differentiated.

*Occurrence.* Upper Albian to Cenomanian; France, Central Asia.

**Genus Placenticeras** Meek, 1876, p. 462

*Synonyms.* Placenticeras Meek, 1871, p. 429, nom. obl.; *Diplacenticeras* Hyatt, 1900, p. 585; *Diplacenticeras* Hyatt, 1903, p. 242; *Stantonoceratites* Johnson, 1903, p. 208; *Proplacenticeras* Spath, 1926, p. 79; *Pseudoplacenticeras* Spath, 1926, p. 79; *Anaplatenticeras* Ilyin, 1959a, p. 201; *Gissarites* Ilyin, 1959b, p. 727; *Parasiantonoceras* Collignon, 1965a, p. 17; *Asiantonoceras* Ilyin, 1975, p. 172; *Baghiseras* Chiponkar and Ghare, 1976, p. 3; *Malwicaseras* Chiponkar and Ghare, 1976, p. 4; *Placentoscaphites* Chiponkar and Ghare, 1977, p. 68; *Sancarlostia* Chiponkar and Ghare, 1978, p. 79.
Type species. *Ammonites placenta* DeKay, 1828, p. 278, by subsequent designation by Meeck, 1876, p. 462.

*Diagnosis*. Distinguished from *Karamaites* by progressive increase in number of elements in the suture line, by development of strongly differentiated microconchs, and by progressive outward migration of umbilical tubercles to mid-lateral and mid-lateral to inner ventrolateral positions. Extreme forms are smooth, involute discs with narrow tabulate venters on the one hand and on the other forms with evolute, square-sectioned outer whorls with strong ribs and lateral and ventrolateral tubercles.

*Occurrence*. Upper Cenomanian to Maastrichtian; world-wide.

**Genus Metaplacenticeras** Spath, 1926, p. 79


Type species. *Placenticeras pacificum* J. P. Smith, 1900, p. 187, by original designation of Spath, 1926, p. 79.

*Diagnosis*. Compressed and flat-sided; with rather strong falcoid or falcate ribs; venter distinctly triradiate, at least in middle growth. Line of suture follows that of ribs.

*Occurrence*. Santonian, Campanian; Japan, California.

**Genus Hoplitoplacenticeras** Paulcke, 1906, p. 183 (ICZN name no. 1348)

*Synonym. Dechenoceras* Kayser, 1924, p. 175.

Type species. *Hoplitites-Placenticeras plastica* Paulcke, 1906, p. 186; ICZN Opinion 554, 1959; name no. 1629.

*Diagnosis*. Rather evolute, whorl section compressed or trapezoidal, venter flat; with prominent variable coarse rounded or dense fine ribs, nearly straight, with inner and outer ventrolateral tubercles, of which outer may be large and clavate; ribs cross venter transversely and may have trace of siphonal tubercle.

*Occurrence*. Campanian–Maastrichtian; France, Germany, West Africa, Egypt, Zululand (South Africa), India, British Columbia, Texas, Wyoming, Patagonia.

**Acknowledgements**. We thank Messrs. D. Pajaud, J. Sornay, J. Louail, G. Marie, P. Moreau, A. Prieur, R. Busnardo, and D. Phillips for allowing us to study material in their care. We gratefully acknowledge the technical assistance of the Geological Collections, Oxford University Museum, Oxford, and financial support from NERC and Wolfson College, Oxford.

**REFERENCES**


KENNEDY AND WRIGHT: PLACENTICERATID AMMONITES 871

ILYIN, V. D. 1959a. Stratigraphy of the Upper Cretaceous deposits of West Uzbekistan and adjacent regions of Turkmenia. Dokl. Trud. VINGLI, 181–222, 8 pls. [In Russian.]


Morton, S. G. 1834. Synopsis of the organic remains of the Cretaceous groups of the United States. Illustrated by nineteen plates, to which is added an appendix containing a tabular view of the Tertiary fossils discovered in America. Key and Biddle, Philadelphia, 88 pp., 18 pls.


— 1937. Die Salzbergemergel und ihre Äquivalente in Westfalen. Ibid. 58, 207–229, pl. 16.


KENNEDY AND WRIGHT: PLACENTICERATID AMMONITES


W. J. KENNEDY
C. W. WRIGHT
Geological Collections
University Museum
Parks Road, Oxford OX1 3PW
and
Wolfson College, Oxford OX2 6UP

Typescript received 19 November 1982