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**Systematic Palaeontology
and Stratigraphic
Distribution of
the Ammonite Faunas of
the French Coniacian**



THE PALAEOLOGICAL ASSOCIATION

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SPECIAL PAPERS IN PALAEOLOGY NO. 31

SYSTEMATIC PALAEOLOGY
AND STRATIGRAPHIC
DISTRIBUTION OF
THE AMMONITE FAUNAS OF
THE FRENCH CONIACIAN

BY

W. J. KENNEDY

with 33 plates and 42 text-figures

THE PALAEOLOGICAL ASSOCIATION
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CONTENTS

INTRODUCTION	1
THE SENONIAN DEFINED	3
RESEARCHES IN AQUITAINE: THE SENONIAN SUBDIVIDED	
Introduction	3
The work of Coquand	3
Arnaud's contribution	4
The work of de Grossouvre	6
Later work	7
Present observations in Aquitaine	8
General	8
Richemont	8
Javrezac	9
Parc François Premier	9
Antignac	9
St. Georges-de-Cubillac	11
St. Christophe	11
Vénérand	12
St. Césaire	12
Carrières de Chancelade	12
St. Cirq	13
Montignac	14
St. Nathalène	15
Carlux	15
Sauveterre-la-Lémace	15
The Ammonite sequence in Aquitaine	15
TOURAINNE: THE CRAIE DE VILLEDIEU	
Introduction	17
Present observations	19
Villedieu-le-Château and environs	19
St. Paterne-Racan	21
St. Fraimbault	23
Cangey	23
THE DIEULEFIT BASIN (DRÔME)	23

THE BEAUSSET BASIN (VAR)	24
Introduction	24
Stratigraphy	25
CONIACIAN AMMONITE ZONATION	25
Introduction	25
Coniacian ammonite zones	25
The Coniacian–Turonian boundary in France	27
Subdivision of the Coniacian	28
The Coniacian–Santonian boundary in France	29
CONVENTIONS	30
SYSTEMATIC PALAEOLOGY	30
Genus <i>Onitshoceras</i> Reyment, 1954	30
<i>O.?</i> <i>ponsianum</i> (de Grossouvre, 1894)	32
Genus <i>Tongoboryceras</i> Houša, 1967	34
<i>T.</i> cf. <i>tongoboryense</i> (Collignon, 1952)	34
<i>T. hancocki</i> sp. nov.	34
Genus <i>Menabonites</i> Houša, 1967	36
<i>M.</i> sp.	36
Genus <i>Pachydiscoides</i> Spath, 1922	37
<i>P. janeti</i> (de Grossouvre, 1894)	37
Genus <i>Placenticeras</i> Meek, 1876	38
<i>P. fritschi</i> de Grossouvre, 1894	38
<i>P. semiornatum</i> (d'Orbigny, 1850)	44
Genus <i>Forresteria</i> Reeside, 1932	45
Subgenus <i>Forresteria</i> Reeside, 1932	45
<i>F. (F.) alluaudi</i> (Boule, Lemoine and Thévenin, 1907)	46
Subgenus <i>Forresteria (Harleites)</i> Reeside, 1932	46
<i>F. (H.) petrocoriensis</i> (Coquand, 1859)	49
<i>F. (H.) nicklesi</i> (de Grossouvre, 1894)	58
Genus <i>Peroniceras</i> de Grossouvre, 1894	62
Subgenus <i>Peroniceras</i> de Grossouvre, 1894	62
<i>P. (P.) tridorsatum</i> (Schlüter, 1867)	62
<i>P. (P.) lepeei</i> (Fallot, 1885)	68
<i>P. (P.)</i> aff. <i>lepeei</i> (Fallot, 1885)	70
<i>P. (P.) subtricarinatum</i> (d'Orbigny, 1850)	71
<i>P. (P.) westphalicum</i> (Von Strombeck, 1859)	71
<i>P. (P.) dravidicum</i> (Kossmat, 1895)	78
<i>P. (P.)</i> sp.	80

CONTENTS

v

Subgenus <i>Zuluiceras</i> Van Hoepen, 1965	80
<i>P. (Z.) bajuvaricum</i> (Redtenbacher, 1873)	80
<i>P. (Z.) isamberti</i> (Fallot, 1885)	86
<i>P. (Z.)</i> sp. nov.	86
Genus <i>Gauthiericeras</i> de Grossouvre, 1894	88
<i>G. margae</i> (Schlüter, 1867)	88
<i>G. nouelianum</i> (d'Orbigny, 1850)	96
<i>G.?</i> <i>boreaui</i> (de Grossouvre, 1894)	102
Genus <i>Protexanites</i> Matsumoto, 1955	104
Subgenus <i>Protexanites</i> (<i>Protexanites</i>) Matsumoto, 1955	104
<i>P. (P.) bourgeoisi</i> (d'Orbigny, 1850)	105
<i>P. (P.) bontanti</i> (de Grossouvre, 1894)	112
Genus <i>Paratexanites</i> Collignon, 1948	114
<i>P. zeilleri</i> (de Grossouvre, 1894)	115
<i>P. serratomarginatus</i> (Redtenbacher, 1873)	117
<i>P. desmondi</i> (de Grossouvre, 1894)	122
Genus <i>Tissotioides</i> Reyment, 1958	122
Subgenus <i>Tissotioides</i> (<i>Tissotioides</i>) Reyment, 1958	122
<i>T. (T.) haplophyllus</i> (Redtenbacher, 1873)	123
Genus <i>Metatissotia</i> Hyatt, 1903	126
<i>M. ewaldi</i> (Von Buch, 1848)	127
<i>M. slizewiczi</i> (Fallot, 1885)	130
<i>M. nodosa</i> Hyatt, 1903	131
<i>M. redtenbacheri</i> (de Grossouvre, 1894)	132
<i>M. desmoulinsi</i> (de Grossouvre, 1894)	132
<i>M.?</i> <i>nanclasi</i> (de Grossouvre, 1894)	133
Genus <i>Phlycticrioceras</i> Spath, 1926	134
<i>P. trinodosus</i> (Geinitz, 1850)	136
Genus <i>Tridenticeras</i> Wiedmann, 1962	137
<i>T.</i> sp.	138
Genus <i>Nostoceras</i> Hyatt, 1894	140
Subgenus <i>Eubostrychoceras</i> Matsumoto, 1967	140
<i>E.</i> sp.	140
Genus <i>Scalarites</i> Wright and Matsumoto, 1954	140
<i>S.</i> sp.	140
Genus <i>Baculites</i> Lamarck, 1799	142
<i>B. incurvatus</i> Dujardin, 1837	143
<i>B. cf. brevicosta</i> Schlüter, 1876	146

Genus <i>Scaphites</i> Parkinson, 1811	146
<i>S. (S.) meslei</i> de Grossouvre, 1894	148
Genus <i>Otoscapites</i> Wright, 1953	150
<i>O. arnaudi</i> (de Grossouvre, 1894)	150
ACKNOWLEDGEMENTS	151
REFERENCES	151

ABSTRACT. Examination of sections in Touraine, the Aquitaine, Dieulefit (Drôme), and Beausset (Var) Basins in France together with a restudy of museum collections provides a basis for the subdivision of the Coniacian stage into a Lower Coniacian *Forresteria* (*Harleites*) *petrocoriensis* Zone, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone, and Upper Coniacian *Gauthiericeras* *margae* Zone below and *Paratexanites* *serrato-marginatus* Zone above. Forty-three ammonite species including one new one, *Tongoboryceras hancocki*, are described, and referred to nineteen genera.

INTRODUCTION

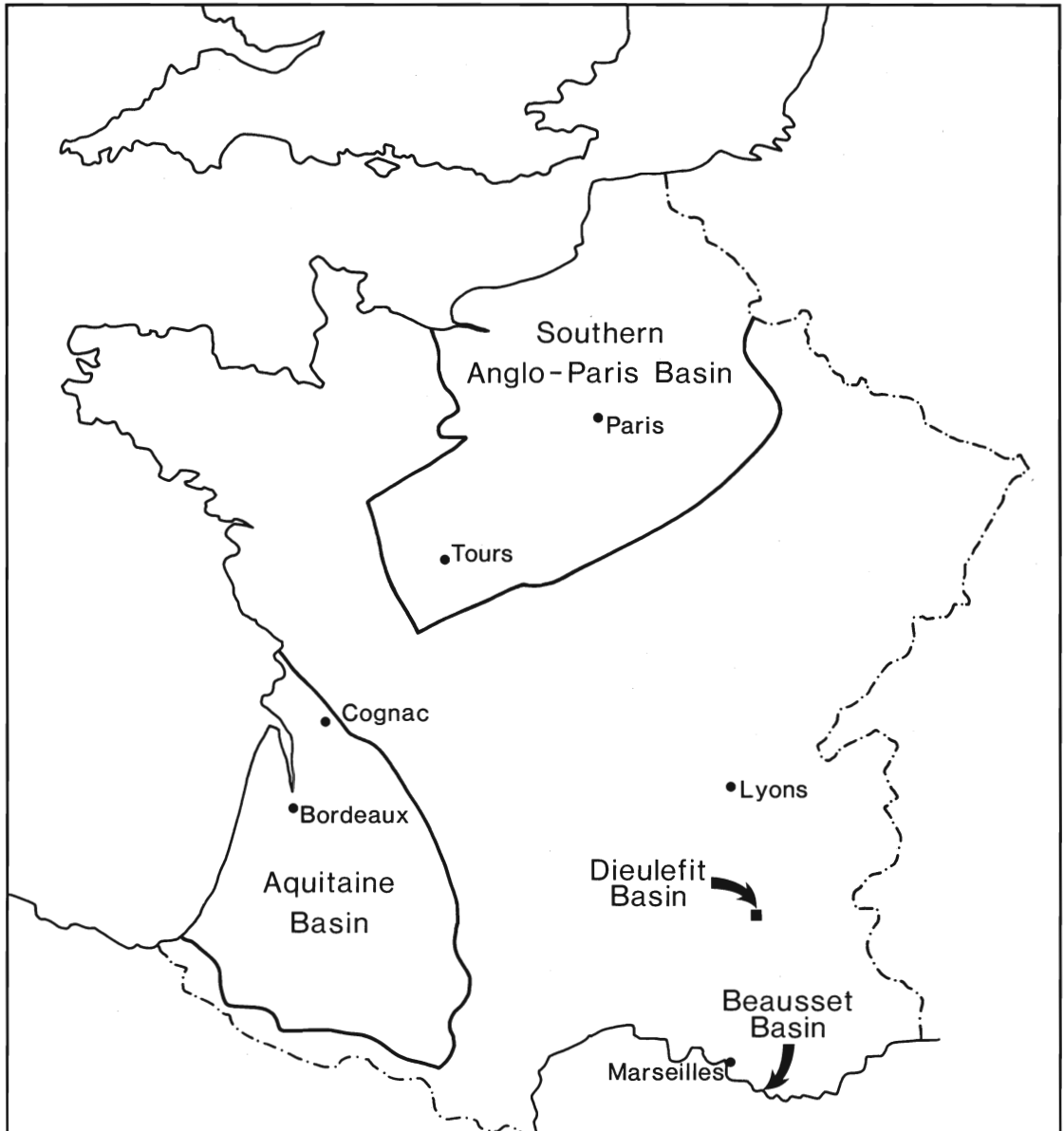
THE étage Coniacien was introduced by Henri Coquand in 1857 as the lowest division of d'Orbigny's étage Senonien, introduced in 1843. It has passed into the literature as a universally applied division of the Upper Cretaceous. The standard zonation of the stage is based on ammonites, and is the twofold division of de Grossouvre (1889, 1901), who recognized a lower *Barroisiceras* [*Barroisia*] *haberfellneri* Zone and an upper *Paratexanites* [*Mortoniceras*] *emscheris* Zone on the evidence of sequences in Aquitaine and Touraine in France. These zones have been universally accepted as standard zones for the Coniacian, and were adopted by the 1959 *Colloque sur le Crétacé Supérieur Française* (Dalbiez 1960), in the *Treatise on Invertebrate Paleontology* (Wright 1957) and by Séronie-Vivien (1972) in her definitive revision of the stratotype, among many others. Yet in 1947 Basse had pointed out that the *B. haberfellneri* of de Grossouvre was based on a misinterpretation of Von Hauer's species, and that the French material all belonged to a distinctive form which she named *Reesideoceras gallicum* Basse, 1947 (a synonym of *Ammonites petrocoriensis* Coquand, 1859), although she nevertheless referred to a 'haberfellneri' Zone in some of her later works. As confirmed below, true *Barroisiceras* does not occur in France; indeed, there is no good evidence that the type species actually occurs in the Coniacian. Similarly the index species of the *P. emscheris* Zone does not occur in France.

Confusion is not limited to nomenclature. Collignon (e.g. 1960) used the *haberfellneri|emscheris* standard in his early works, but developed a threefold zonation in Madagascar, with zones of *Peroniceras dravidicum* (oldest), *Kossmaticeras theobaldianum* with *B. onilahyense*, and *Prionocycloceras guyabanum* with *Gauthiericeras margae* (youngest). In 1979 Collignon *et al.* recognized a sequence of three zones in the Coniacian of the Beausset Basin (Var): *Peroniceras tricarinarium* (oldest), *B. haberfellneri* and *G. margae* (youngest), although the middle zone was not proven by ammonites. Robaszynski *et al.* (1980) recognized a *Peroniceras tridorsatum* Zone at the base of the Coniacian in the Boulonnais (with, however, only eight specimens of the genus *Peroniceras* known from the area (Amedro and Robaszynski 1978)) and French textbooks now cite a standard sequence of *tricarinarium|haberfellneri|margae* Zones. That *B. haberfellneri* does not occur in France has already been noted. In those areas where a faunal sequence can be determined, *Forresteria* (*Reesideoceras*) *petrocoriensis* (Coquand, 1859)—the *B. haberfellneri* of authors—always precedes *Peroniceras* species, and marks the base of the Coniacian in the type area (Kennedy, Wright and Hancock 1983). Yet more recently Matsumoto (in Matsumoto *et al.* 1981) proposed as standard zones for the European Coniacian a sequence of *P. subtricarinarium* Zone (below) and *Protexanites bourgeoisi* Zone (above) on the basis of what could be gleaned from the literature.

These observations suggested that a re-examination of both the taxonomy and stratigraphic distribution of the ammonite faunas of the French Coniacian was essential before any discussion of zonation, correlation, and evolution of the ammonites of this part of the Cretaceous could be attempted. Both aspects of this revision presented considerable problems. There had been no serious work on Coniacian ammonite systematics and stratigraphy in the region since that of de Grossouvre (1894, 1901), based in large part on material collected in the Aquitaine and the southern Paris Basins by Arnaud and other local workers from exposures that have long since disappeared. Between 1971 and 1982 joint field-work with Dr. J. M. Hancock in these and other areas produced sufficient

ammonites to confirm the meticulous records of Arnaud and others. It also yielded lithological samples to compare with museum specimens in order to validate provenance, often a problem with old collections. In 1981 the collections of the Sorbonne, now housed in the Université Pierre et Marie Curie, Paris, finally yielded up much of the material cited and figured by de Grossouvre. It is on all these specimens that this account is based.

It must be stressed that ammonites are generally very rare in the Coniacian of France (and indeed most of north-western Europe), and only five areas, the Aquitaine Basin, a small area in Touraine in the southern Paris Basin, a few square kilometres of outcrop around Dieulefit (Drôme), the Beausset



TEXT-FIG. 1. Principal regions cited in the text.

Basin (Var), and the environs of Rennes-les-Bains in the Corbières (Aude) have yielded ammonites in any numbers (text-fig. 1). Around Villedieu-le-Château (Loir-et-Cher), the most famous Coniacian ammonite locality in France, Jarvis *et al.* (1982) mention no new records of Coniacian ammonites in their revision of the Craie de Villedieu, whilst my own collecting produced only four specimens from this locality, visited at intervals during the last decade. In spite of these difficulties the French succession provides a basis for a zonation of the Coniacian that both clarifies and resolves problems outlined above.

THE SENONIAN DEFINED

When Alcide d'Orbigny divided the Upper Cretaceous into stages, he at first recognized only two, Turonian below and Senonian above (*Paléontologie Française*, II, *Gastéropodes*, 1842–1843, pp. 403 ff.). The definition of these stages was brief, the Senonian being defined as follows: 'Je propose pour l'horizon géologique de la craie blanche le nom de terrain *sénonien*, Sens, l'antique Senones, étant situé précisément au milieu de la craie blanche la mieux caractérisée' and the Turonian thus: 'je propose de désigner à l'avenir l'étage qui m'occupé sous le nom de terrain **TURONIEN** de la ville de Tours (*Turones*), ou de la Touraine (*Turonia*) situées sur ces terrains.' D'Orbigny subsequently recognized that his étage Turonien included two distinct faunas, and referred the lower fauna to an étage Cenomanien, restricting the étage Turonien to the upper. The separation of these two stages is discussed in detail elsewhere (e.g. Wright and Kennedy 1981).

The definition of the étage Senonien was clarified in the *Prodrome* (1850), where d'Orbigny listed 1,552 species from his 'Vingt-Deuxième Étage' including no less than 101 cephalopods. In the *Cours Elementaire* (d'Orbigny 1852, pp. 666–691) the stage is reviewed at length, its limits defined in terms of fauna, the origin of the name discussed, and synonyms and the units referred to it described as well as its geographical distribution. Most significant in the present context is d'Orbigny's citation of the 'Type français sous-marin' as follows: 'Épernay, Meudon, Sens, Vendôme, Tours (tranchée de la route de Paris), Royan, Cognac, Saintes; Maastricht, Cypli' (1852, p. 667).

The Senonian, in a white chalk facies around Sens, has been variably treated by later workers. Most followed d'Orbigny in regarding it as encompassing everything between the Turonian and the Danian, or between the Turonian and Maastrichtian. Coquand (1857 onwards, see below), however, divided the Senonian into Coniacien, Santonien, Campanien, and Dordonien; the last has fallen out of use, yielding to Dumont's Maastrichtian, but the first three are now in widespread usage; the Senonian is becoming obsolete among Upper Cretaceous workers, in much the same way as is the Neocomian among those studying the Lower Cretaceous. De Grossouvre (1901) and Sornay (1957, pp. 318–325) provide useful summaries of early views. The 1:50 000 geological map of Sens (Bouiller *et al.* 1971) and the accompanying memoir show that white chalks mapped as Coniacian and Santonian outcrop close to the town, and similar facies of Turonian to Upper Campanian date outcrop in the environs.

There are few ammonite records from this area; the only Coniacian form recorded is a specimen collected by Lambert at Maillot, 2 km south-east of Sens. De Grossouvre (1901, p. 114) identified it as *Peroniceras moureti* de Grossouvre, 1894 (= *P. tridorsatum* (Schlüter, 1867) herein).

RESEARCHES IN AQUITAINE: THE SENONIAN SUBDIVIDED

INTRODUCTION

Overlapping with and succeeding d'Orbigny's work, d'Archiac (1836, 1843, 1851, 1857) and Coquand (1856 onwards) developed subdivisions of the Upper Cretaceous of the Aquitaine Basin.

The work of Coquand. In 1857 and 1858 Coquand divided d'Orbigny's Senonien into four successive stages: Coniacien, Santonien, Campanien, and Dordonien. The étage Coniacien was defined as follows in 1857 (p. 748):

'B. CRAIE SUPÉRIEURE

Première étage — Coniacien

A. Sables et grès de Richemont (*Ostrea auricularis*, Coquand).

B. Calcaire chloriteux (*O. auricularis*, Coq., *Ammonites polyopsis*, Dujard., *A. Bourgeoisi*, d'Orb., *Terebratula Arnaudi*, Coq., *T. coniaciensis*, Coq., *Rhynchonella Baugasi*, d'Orb., *Sphaerulites Coquandi*, Bayle, *Micraster brevis*, Agass.). Cet étage correspond au sixième horizon de rudistes.'

The succeeding Santonian stage was defined as follows (1857, p. 749):

'Deuxième étage — Santonien

Craie tendre avec silex (*Pleurotomaria santonesa*, d'Orb., *Janira Truelli*, d'Orb., *Spondylus hippuritorum*, d'Orb., *Rhynchonella vespertilio*, d'Orb., *R. intermedia*, Coquand, *Terebratula Nanclasi*, Coq., *Micraster laxoporus*, d'Orb., *Hemiaster stella*, Desor, *Salenia geometrica*, Agass.).'

These names replaced a number system used by Coquand in 1856 (p. 59), with the Coniacian and Santonian together comprising Coquand's Première étage (Table 1). In the text of the earlier work, Coquand mentions localities which, strictly speaking, constitute the stratotypes of the two stages. It should be noted that the grounds of the seminary at Richemont are unequivocally the type section for the base of the Coniacian, and that both general areas and specific localities are given for the other two substages. Van Hinte (1979) is mistaken in taking Javrezac as their type section. In his later works, Coquand gave a series of additional localities, as discussed in detail by Séronie-Vivien (1972).

In his *Synopsis des animaux et des végétaux fossiles observés dans la formation crétacée du sud-ouest de la France* (1859), Coquand lists the faunas of the Coniacian and Santonian stages. Relevant in the present context are records of '*Amonites Nouleti* d'Orb.' [sic] from the Coniacian (presumably an error for *Ammonites nouelianus* d'Orbigny, 1850, a *Gauthiericeras* species) and the following from the Santonian: *Ammonites Bourgeoisi* d'Orbigny (in the absence of specimens one can only infer a texanitid), *Ammonites Orbigny* d'Archiac (unrecognizable), *Ammonites Polyopsis* Dujardin (a *Placenticeras*), *Ammonites santonensis* d'Orbigny (this name is regarded as unavailable under the terms of Opinion 126 of the International Commission on Zoological Nomenclature (1936): see Kennedy and Wright 1979, p. 676; the type specimen is a juvenile *Neoptychites cephalotus* (Courtiller, 1860) of the Turonian), *Ammonites coniaciensis* Coquand (the clear description shows this to be a *Texanites* (*Texanites*); two specimens (Boucheron Collection from La Valette) survive in the collections of the École des Mines (now housed in the collections of the Faculté des Sciences, Lyon) and will be described elsewhere), *Baculites incurvatus* Dujardin and *Scaphites constrictus* d'Orbigny (in the absence of Coquand's material uninterpretable; the correct author is Sowerby; d'Orbigny's material is conspecific with Sowerby's and is a Maastrichtian *Hoploscaphites*).

Arnaud's contributions. Coquand's work was followed by that of Arnaud, who published a long series of papers (1862–1897) dealing with the Cretaceous of the whole of the Aquitaine Basin. He described localities and sections in great detail and had the benefit of studying the railway cuttings of the area soon after their construction, amassing fossil collections that will never be repeated. Arnaud modified Coquand's scheme and introduced a letter system to designate the main lithostratigraphic units in the Cretaceous of Aquitaine, as shown in Table 1. His *Memoire sur le Terrain Crétacé du Sud-Ouest de la France* (1887f) is the most important synthesis, and is remarkable for the detailed tables, some nearly 3 m long, giving precise measurements and faunal lists from sections extending across Aquitaine from the most north-easterly outcrops of the Senonian around Saintes (Charente-Maritime) to the most southerly around Gourdon (Lot) and Fumel (Lot-et-Garonne) (text-fig. 2). Arnaud recognized the lateral facies changes within the sequence, but did not introduce formational names. His initial division was as follows (1877f, p. 3):

'1^{re} série: Coniacien

15. Marnes et grès: *Rhynchonella petrocoriensis*;
16. Calcaires noduleux ou cristallins: *Ammonites tricarinatus*;
17. Calcaire glauconieux à *Rhynchonella baugasi*.

TABLE I

	Coquand 1856 (p. 59)	Coquand 1857c (p. 748)	Arnaud 1878, etc.	De Grossouvre 1889	De Grossouvre 1894, 1901	De Grossouvre 1901	Matsumoto 1981	Kennedy herein
3 ^e sous-étage		2 ^e étage—SANTONNIEN	N ² Santonien supérieur N ¹ Santonien moyen M ² Santonien M ¹ inférieur	Zone à <i>Am. syrtaalis</i> (= <i>polyopsis</i>) (= <i>Ribour</i>)				
2 ^e sous-étage		1 ^e étage—CONIACIEN	L ² Coniacien supérieur L ¹ Coniacien moyen K. Coniacien inférieur	1 ^o à <i>Am. emscheris</i> (= — <i>Bourgeois</i>) Zone à <i>Am. tricarinalis</i>	Coniacien supérieur	Coniacien supérieur Zone à <i>Mortonoceras emscheris</i>	<i>Protexanites bourgeoisii</i>	Upper CON.
1 ^e sous-étage				2 ^o à <i>Am. haberfellneri</i> (= <i>petrocoriensis</i>)	Coniacien inférieur	Coniacien inférieur Zone à <i>Barroisoceras haberfellneri</i>	<i>Peronoceras sabitricarinatum</i>	MIDDLE CON. LOWER CON.
								<i>Paratexanites serratomarginatus</i> <i>Gauthiericeras margae</i> <i>Peronoceras tridorsatum</i> <i>F. (Reesidooceras) petrocoriensis</i>

PREMIERE ETAGE

2^e série: *Santonien*

18. Marnes et grès inférieurs: *Rhynchonella deformis*; *Botriopygus*;
 19. Marnes à *Ostrea vesicularis* et *O. proboscidea*;
 20. Marnes et grès supérieurs: *Sphaerulites Hoenighausi*, *Ostrea acutirostris*;
 21. Calcaire noduleux glauconieux: *Conoclypeus ovum*?

This scheme is modified in the ribbon diagram at the end of Arnaud's memoir, as follows:

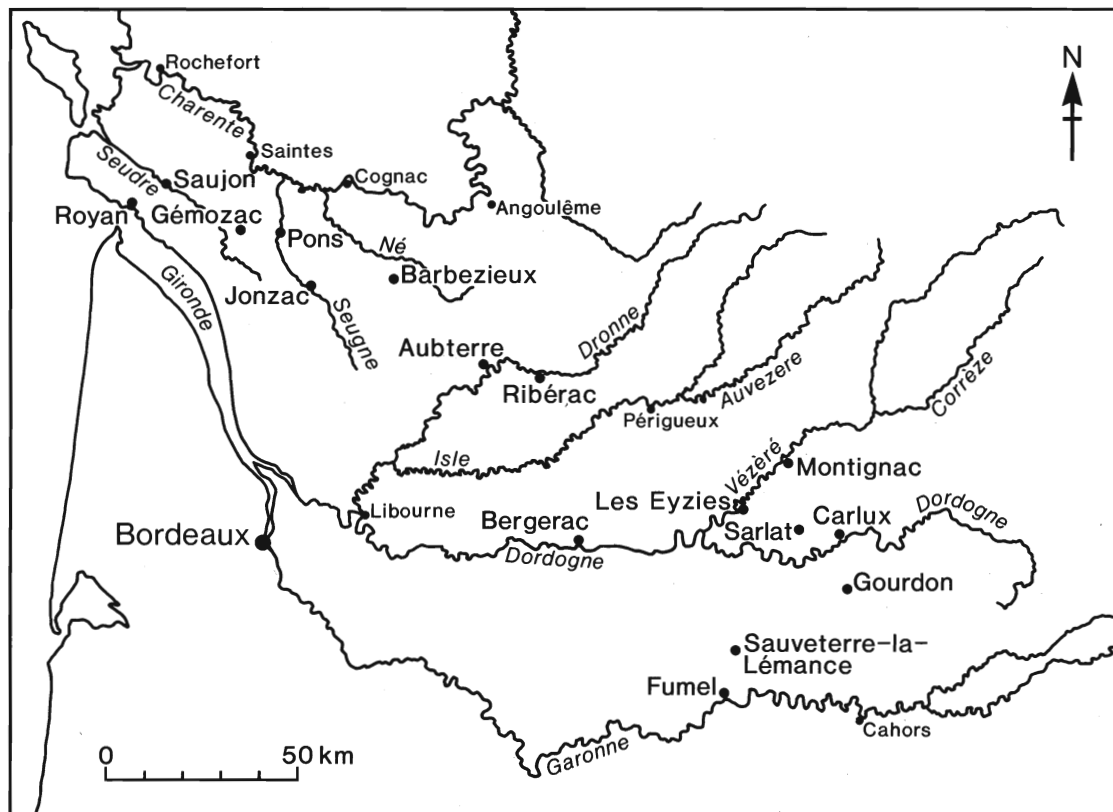
Santonien	N'	Marnes et grès santonien supérieurs. { N ^o Calcaire glauconieux à <i>Conoclypeus ovum</i> N ^b Banc à <i>Ostrea acutirostris</i> N ^a Grès à <i>Sphaerulites Hoenighausi</i>
	N	Marnes à <i>Ostrea vesicularis</i> et <i>O. proboscidea</i>
	M	Marnes et grès santonien inférieurs. <i>Botriopygus Toucasanus</i> : M ^a Pierre de taille de La Trape
Coniacien	L	Calc. à <i>Rhynchonella Baugasi</i> . { L ^b Pierre de taille de Périgueux L ^a Pierre de taille du Sarladais L Calcaire cristallin à <i>Ammonites tricarinatus</i>
	K	Marnes et grès. <i>Ammonites Petrocoriensis</i> , <i>Rhynchonella Petrocoriensis</i>

Arnaud's subsequent papers provide many additional details, but the scheme remains essentially that of the 1877 memoir: the most succinct summary is that of his 1887 correlation of the chalks of northern France with those of Aquitaine:

N ²	Calcaire marneux, gris, à silex: Saintes; — calcaires glauconieux, gris: <i>Conoclypeus ovum</i> : Charmant, Le Bugue; — grès argileux; <i>Ostrea acutirostris</i> : Sarlat, Le Got, Villefranche.	} sup. } } moyen } } inf. }
N ¹	Calcaire marneux; banc à <i>Ostrea vesicularis</i> et <i>O. proboscidea</i> : Granconière, Charmant, Boussitrant; — calcaire à silex; mêmes Ostracées: Le Sout. Villefranche-de-Belvès.	
M ²	Calcaire noduleux: Lavalette, Périgueux; <i>Botriopygus Nanclasi</i> ; — calcaire jaune arénacé, pierre de taille; <i>B. Toucasianus</i> : Miremont. Moulin-Lescot, etc.	
M ¹	Calcaire marneux, gris; <i>Rhynchonella Eudesi</i> ; Saint-Martin-de-Cognac, Périgueux, Miremont; — calcaire rouge compacte: La Trape, Saint-Cernin, Freycinet-le-Gelat. etc.	} sup. } } moyen } } inf. }
L ²	Calcaire arénacé, glauconieux: pierre de taille de Périgueux; <i>Micraster brevis</i> , <i>Rhynchonella Baugasi</i> ; — calcaire rouge compacte: Villefranche (gare), etc.	
L ¹	Calcaire noduleux, glauconieux: Bussac, Cognac, Pons, Périgueux; — calcaire jaune, pierre de taille du Sarladais; Aubas, Miremont, Sarlat, etc.	
K	Grès glauconieux: <i>Rhynchonella Petrocoriensis</i> : Phélippeaux (Jonzac), Cognac, Angoulême; — marnes et calcaires marneux; <i>Ostrea Petrocoriensis</i> : Gourde-de-l'Arche, Montignac, Fumel.	

The value of Arnaud's work is greatly enhanced by the meticulous labelling of his specimens, many of which can be linked to specific citations in his works.

The work of de Grossouvre. De Grossouvre's contribution to our understanding of the Cretaceous system has been a lasting one, and his *Recherches sur la Craie Supérieure* is a far-reaching survey which includes the basis of Upper Cretaceous ammonite zonation and the only comprehensive modern account of post Turonian Upper Cretaceous ammonite faunas of western Europe. The work suffered an unfortunate publication history, as de Grossouvre wryly remarks (1901, pp. v-vii), and the first part (*Stratigraphie Générale*) appeared in 1901, after the second part (*Paléontologie des Ammonites de la Craie supérieure*), which was published in 1894. I have been unable to determine the relative dates of writing of the two parts.



TEXT-FIG. 2. The Aquitaine Basin showing the principal localities mentioned in the text.

In his account of the ammonites, de Grossouvre relied heavily on collections from Aquitaine, especially those made by Arnaud, referring material to the letter divisions recognized by the latter. De Grossouvre recognized three divisions ('Assise') in the Coniacian on the basis of the Aquitaine sequence, although he did not propose them formally as zones. In 1901, following his general discussions, detailed regional account of the Upper Cretaceous of France, and general account of the Upper Cretaceous throughout the world, de Grossouvre proposed a standard zonation, dividing the Coniacian into two zones. In the tables (1901, pp. 830 ff.), the indices are given, *Barroisiceras haberfellneri* for the lower zone, *Mortoniceras emscheris* for the upper. The *haberfellneri* Zone encompassed the lower and middle divisions of his earlier work. As well as providing this zonation in his synthesis, de Grossouvre reviews the sequence in Aquitaine, discussing the Coniacian on pp. 374–375.

Later work. Following publication of de Grossouvre's *Recherches*, the Coniacian of Aquitaine received little attention. There are a number of minor contributions in the explanations of the 1:80000 geological maps of the area (some of which, e.g. Angoulême, Jonzac, were mapped by de Grossouvre and his collaborators) and in the annual notes in the *Bulletin du Service de la Carte Géologique de France* (a full list of these is given by Séronie-Vivien (1972)). On only a minority of the relevant maps is the Coniacian subdivided (in some cases it is not even separated from the Santonian), but the accompanying memoirs essentially follow Arnaud's divisions.

The most significant contribution since de Grossouvre's work is Séronie-Vivien's revision of the Coniacian, Santonian, and Campanian stages in Aquitaine (1956 onwards), with the eventual

publication of her *Contribution à l'étude du Sénonien en Aquitaine Septentrionale* (1972). The emphasis of this work is towards microfacies analysis and microfauna, but 138 sections are listed and a third of these described in detail. Stratigraphic syntheses are given and facies maps provided which in general confirm Arnaud's work. Séronie-Vivien notes a small number of additional ammonites and reviews ammonite occurrences, but the taxonomy is that of de Grossouvre and many of the records discussed are doubtful in the absence of specimens. The same is also unfortunately true of the detailed records in the memoirs accompanying the 1:50000 sheets of the area; *B. haberfellneri* is widely recorded but all cited specimens located are *Forresteria (Harleites) petrocoriensis*.

In spite of these difficulties, these works provide a sound lithostratigraphic framework for the area, although no formal lithostratigraphic nomenclature exists. Terms like Coniacien Inférieur and Supérieur are used by Séronie-Vivien and a Coniacien inférieur, moyen, and supérieur on many of the 1:50000 maps, the divisions corresponding approximately to Arnaud's K and L, and K, L¹ and L² respectively, although not necessarily corresponding exactly from map to map.

Of works subsequent to those given in Séronie-Viviens' bibliography, none relates to the macrofauna, although the microfauna and flora are dealt with in detail by several workers (references in Van Hinte 1979).

PRESENT OBSERVATIONS IN AQUITAINE

General

In the absence of formal lithostratigraphic nomenclature, and because most of the ammonites available are located stratigraphically in terms of Arnaud's nomenclature, this is followed here.

In general, the Coniacian-Turonian boundary is clearly defined across the whole basin. Where the underlying Turonian is a limestone sequence, there is a terminal hardground, often bored, encrusted, and mineralized. Where the top of the Turonian is more argillaceous, there is a discontinuity and erosion surface with only localized hardground development.

The Coniacian sequence is up to 90 m thick in the Périgueux region. The lower part, corresponding to Arnaud's L¹, is a predominantly terrigenous-clastic suite. Séronie-Vivien's lithofacies map (1972, pl. 4) shows sands and sandstones over the north-western half of the area: these are commonly cross-bedded, and correspond to the Sables et Grès de Richemont of Coquand. A narrow transition zone of bioclastic limestones separates these from the glauconitic and marly facies to the south-west—the Marnes de Montignac and Gourde-l'Arch of de Grossouvre (1901).

The upper part of the sequence consists of bioclastic limestones with subsidiary terrigenous elements, massive or nodular, in which Séronie-Vivien (1972, pl. 5) again recognizes three facies belts trending north-north-west to south-south-east. To the north-west the facies is one of bioclastic pelletal calcarenites and calcirudites, in the central belt bioclastic limestones, and in the south-easterly zone sandy bioclastic limestones and calcirudites. This suite of facies corresponds to Arnaud's division L¹. The highest Coniacian, corresponding to Arnaud's L², presents a variety of facies of bioclastic limestones, sometimes glauconitic, generally well cemented, and often rich in oysters.

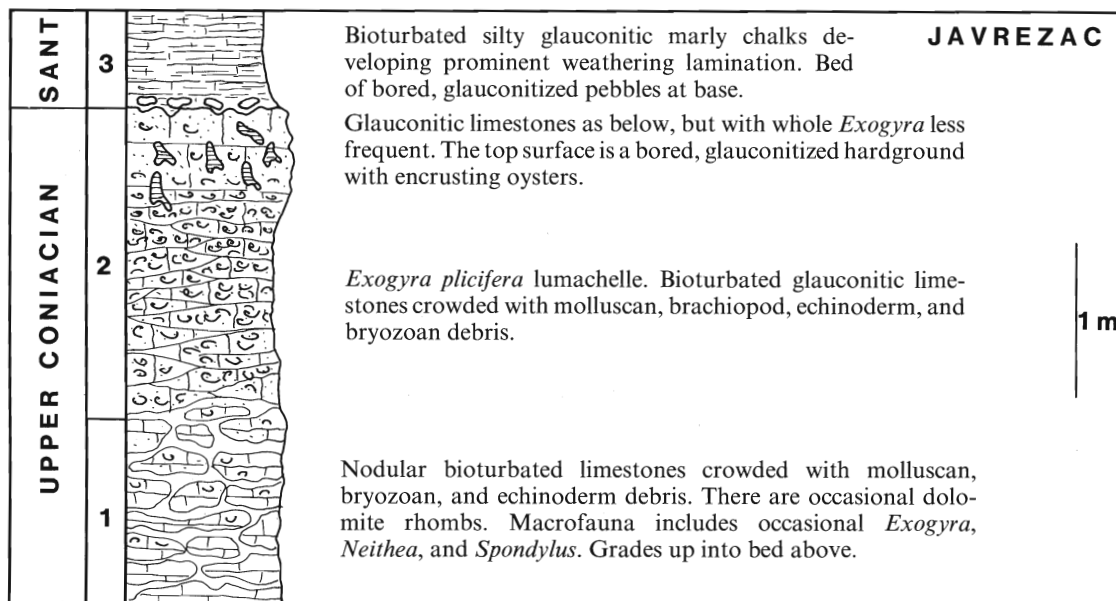
The Coniacian-Santonian boundary is generally marked by a change to bioclastic chalks, sometimes argillaceous and with flints, corresponding to Arnaud's Assize M¹. In the Cognac area, and in particular at Javrezac, a type locality mentioned by Coquand, there is a marked hardground at the top of the Coniacian limestones.

A small number of localities which either yielded ammonites during the present study or provide good evidence of stratigraphic relationships are described below.

Richemont (Charente). Coquand unequivocally cites the grounds of the Seminary at Richemont as the type locality for the base of his étage Coniacien. The Seminary ($x = 390, 1; y = 83, 5$) is now an École Rurale, but the picturesque cliff on the south-west side of the Antenne provides spectacular exposures of albeit rather dirty and alga-covered Turonian rudistid limestones. The gardens in front of the building expose the top of the limestones separated by a marked hardground from 2 to 3 m of planar and trough cross-bedded coarse quartzose glauconitic sandstones with shell debris. The junction is difficult to decipher, as Turonian and Coniacian are welded together. Fresh temporary

outcrops, however, confirmed the top of the Coniacian as a dolomitized hardground cut by large (up to 4 cm diameter) *Thalassinoides* burrows that pipe Coniacian sediment down for at least 70 cm into the top of the Turonian. The Coniacian yields only oysters and bryozoan debris.

Javrezac (Charente). Javrezac was one of the localities mentioned by Coquand for both Coniacian and Santonian stages. The section is in road cuttings on both sides of the D79, 2.5 km west of Cognac and west-north-west of Javrezac in the direction of Saintes ($x = 390, 1; y = 81, 5$). Séronie-Vivien (1972, p. 31, text-fig. 2) gives a measured section, but failed to recognize the extensive cambering that repeats the more prominent beds. See text-fig. 3 for details of the succession.

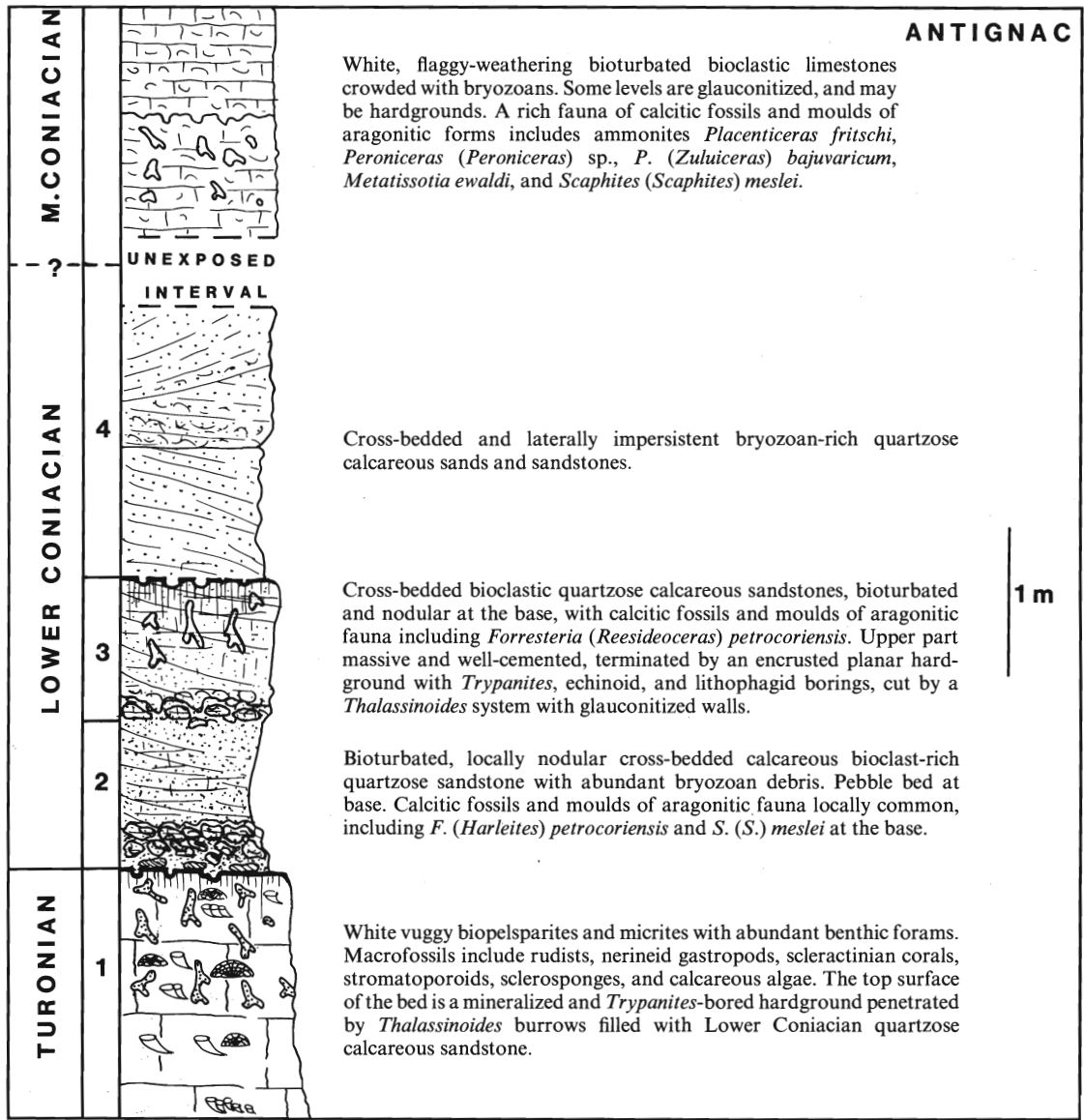


TEXT-FIG. 3. The Coniacian-Santonian succession at Javrezac (Charente).

Parc François Premier, Cognac (Charente)

Coquand mentioned this locality in 1857 and in 1858 ('... escarpment sous le Parc') for both the Sables et Grès de Richemont and the Calcaires Chloriteux. Séronie-Vivien (1972, p. 30, text-fig. 31) took this as her reference section, pointing out that Coquand (1857c, pp. 857-859) at the Réunion extraordinaire de la Société Géologique de France at Angoulême used the locality to demonstrate the separation of the two groups of 'craie inférieur' and 'craie supérieur'. The section is on the west bank of the Charente just east of the road-bridge and below the Parc François Premier and suburbs to the south ($x = 392, 6; y = 81, 5$). Upper Turonian limestones are succeeded by 2-3 m of deeply weathered and decalcified Sables et Grès de Richemont—Assize K of Arnaud—but the nature of the junction is not as clear as at Richemont. These sands are planar and trough cross-bedded, and become progressively more calcareous and burrowed upwards, with a transition to the bioclastic bryozoan rich limestones of Arnaud's L¹. These limestones are dolomitized with hardgrounds at some levels, as well as nodular developments.

Antignac (Charente-Maritime). The hamlet of Antignac is 10 km south-east of Pons and 24 km south-west of Cognac ($x = 381, 0; y = 359, 0$), on the south bank of the Treflé. A small, intermittently worked quarry on the south side of the D150, 300 m west-north-west of the western outskirts of the village, shows the Turonian-Coniacian contact, while a further shallow excavation 300 m further



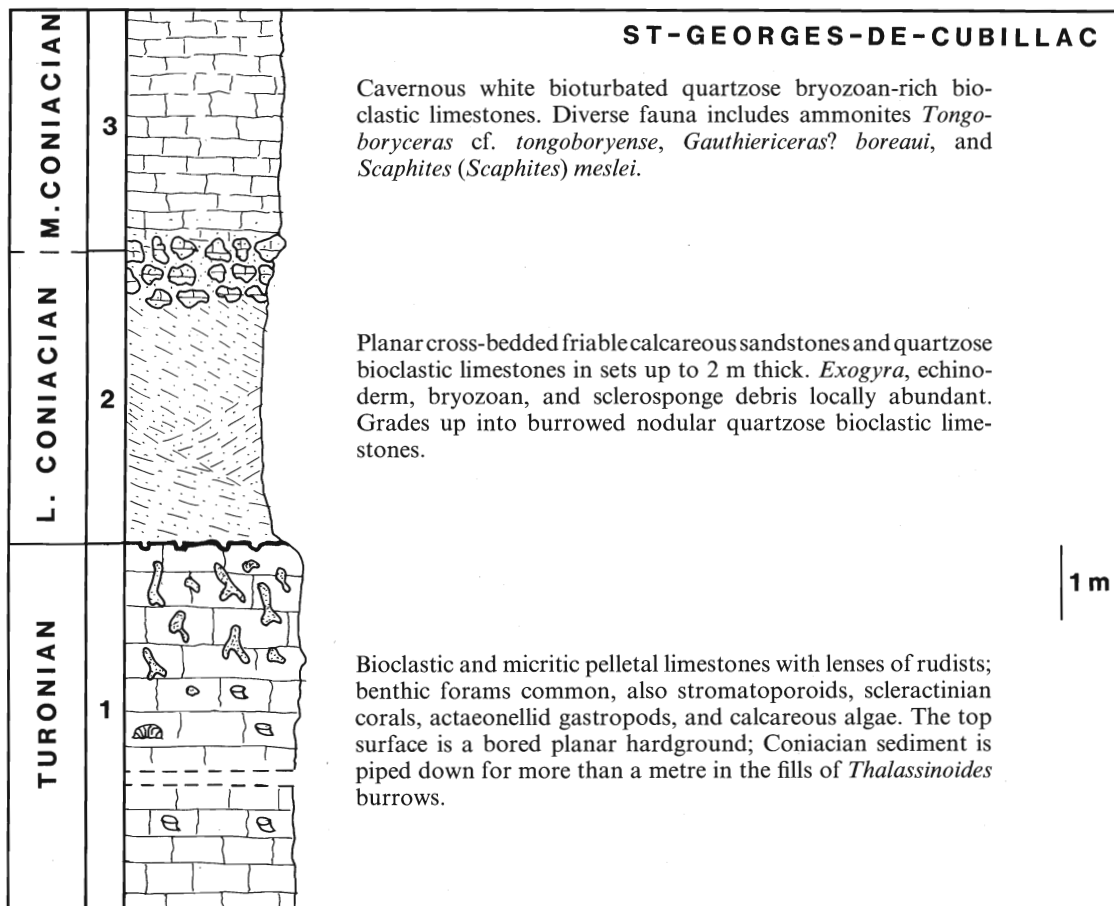
TEXT-FIG. 4. The Turonian-Coniacian succession at Antignac (Charente-Maritime).

west-north-west on the north side of the road exposes Coniacian bioclastic quartzose limestones and calcareous sandstones with a rich molluscan fauna.

The section is shown in text-fig. 4. The Coniacian yields ammonites at two levels in the basal 1.5 m: *Forresteria (Harleites) cf. petrocoriensis* (Coquand, 1859) and *Scaphites (Scaphites) meslei* de Grossouvre, 1894. Collignon (*in* Platel 1975, Carte Géologique de France 1 : 50 000, Jonzac (731)) lists '*Barroisicerias haberfellneri*' and '*Harleites cf. alstadenensis*' (e.g. *F. (H.) petrocoriensis*) from this unit in the area. Above, the 'Coniacien Moyen' yields *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), *Peroniceras (Peroniceras) sp.*, *Metatissotia ewaldi* (Von Buch, 1848), *Placenticerias*

fritschi de Grossouvre, 1894, and *Scaphites (Scaphites) meslei* de Grossouvre, 1894. Collignon (in Platel 1975) records a similar fauna.

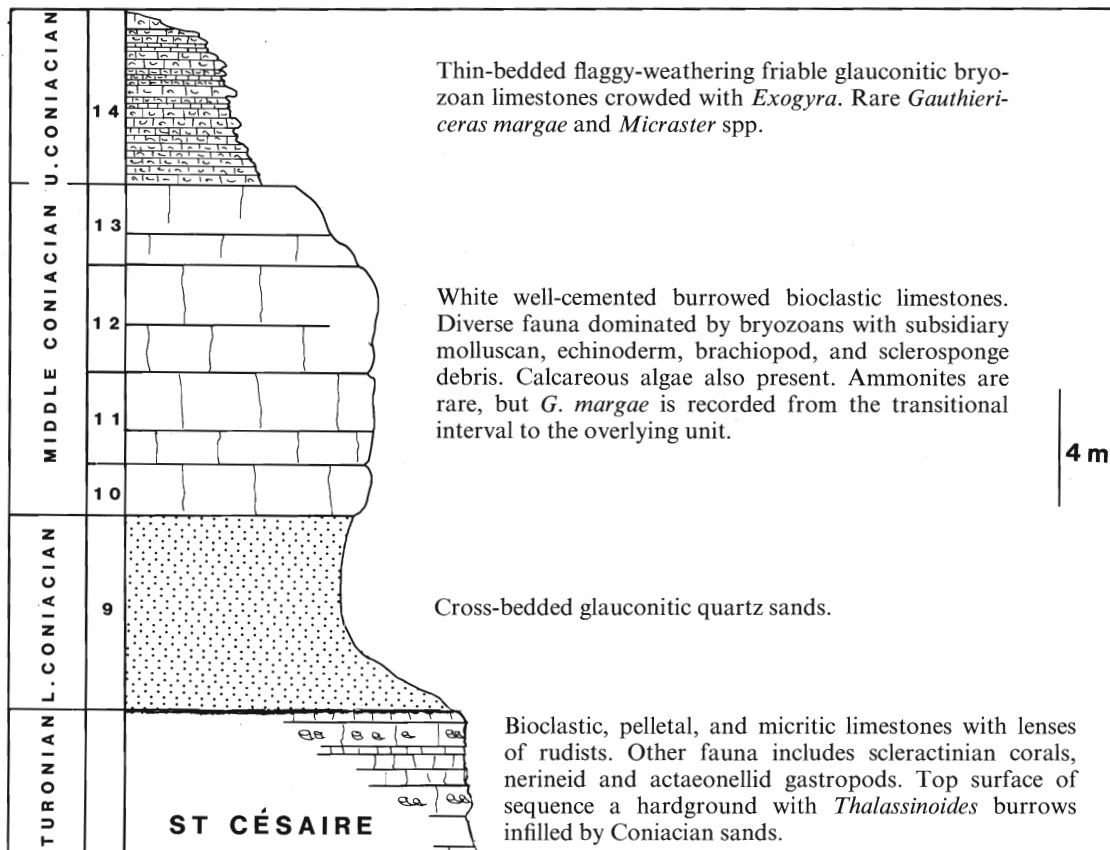
St. Georges-de-Cubillac (Charente-Maritime). The village of St. Georges-de-Cubillac is 10 km south-south-west of Pons. A Turonian to middle Coniacian sequence can be traced in cuttings and wooded quarries on the downthrow side of the north-west to south-east fault in the meander of the Treffé 2 km north-east of the village ($x = 380, 2; y = 359, 3$). Four metres of Turonian limestones with rudists outcrop in the roadcut but the Turonian-Coniacian boundary is not exposed. Three to four metres of Coniacien inférieur—quartzose calcareous sands—are exposed in the wood above, followed by cavernous-weathering hard bioclastic quartzose limestones of the 'Coniacien moyen' with a rich fauna, as at Antignac (text-fig. 5). Ammonites are: *Tongoboryceras cf. tongoboryense* (Collignon, 1952), *Gauthiericeras? boreau* (de Grossouvre, 1894) and *Scaphites (Scaphites) meslei*.



TEXT-FIG. 5. The Turonian-Coniacian succession near St. Georges-de-Cubillac (Charente-Maritime).

St. Christophe (Charente). The sand-pits at St. Christophe are 8 km south-west of Saintes and a few hundred metres east of the hamlet of Les Hillairets ($x = 377, 25; y = 2064, 75$). The Sables et Grès de Richemont (Coniacien Inférieur in the memoir accompanying the Pons Sheet: Platel 1977) are 8 m thick and are succeeded by quartzose bioclastic limestones with *Tissotioides haplophyllus* (Redtenbacher, 1873).

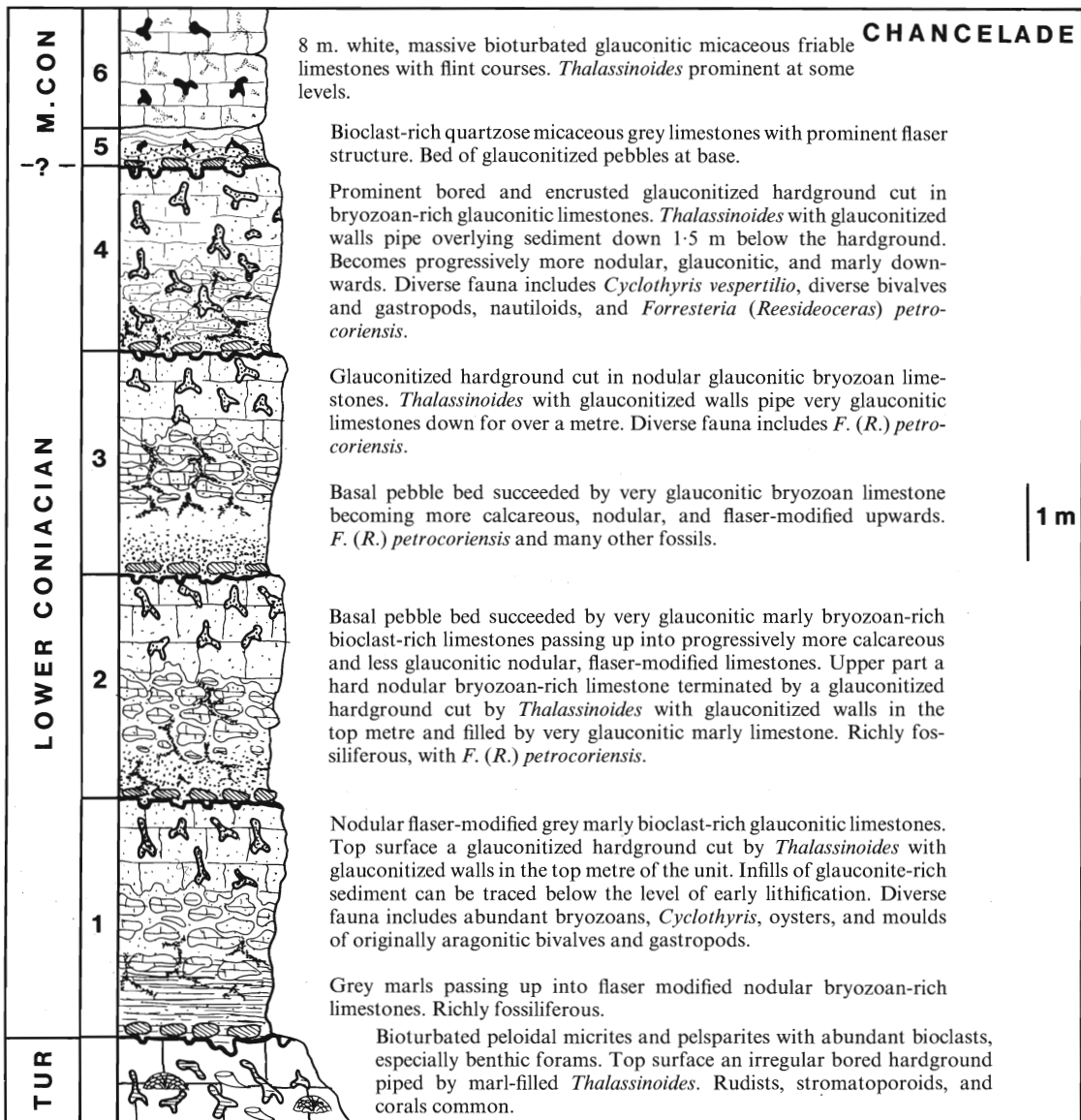
Vénérand (Charente-Maritime). Vénérand is 8 km north-east of Saintes on the N138. Two disused quarries west of the village on the south side of the D129^{E2} show the Turonian–Coniacian boundary (west of the railway at $x = 373, 4, y = 93, 2$) and ‘Coniacien moyen’ (east of the railway at $x = 373, 8, y = 93, 1$). The quarries are shown on the 1:50000 Saintes sheet, and are mentioned by Vigneau (1975). The ‘Coniacien moyen’ at Ecurat, 8 km to the east-south-east yielded *Metatissotia ewaldi* (Von Buch, 1848), *M. slizewiczi* (Fallot, 1885), and *Placenticerus fritschi* de Grossouvre, 1894 to Gillard (1944), who also records ‘*Barroisicerus haberfellneri* et var’ (e.g. *F. (H.) petrocoriensis* (Coquand, 1859)) from the ‘Coniacien inférieur’ north of Saintes.



TEXT-FIG. 6. The Turonian–Coniacian succession at St. Césaire (Charente-Maritime).

St. Césaire (Charente-Maritime). St. Césaire is on the Coran, 10 km east of Saintes, and there are a series of quarries around the village and northwards to St. Bris-des-Bois, noted in a recent publication by Moreau (1980). Text-fig. 6 shows the generalized section from Upper Turonian to Upper Coniacian.

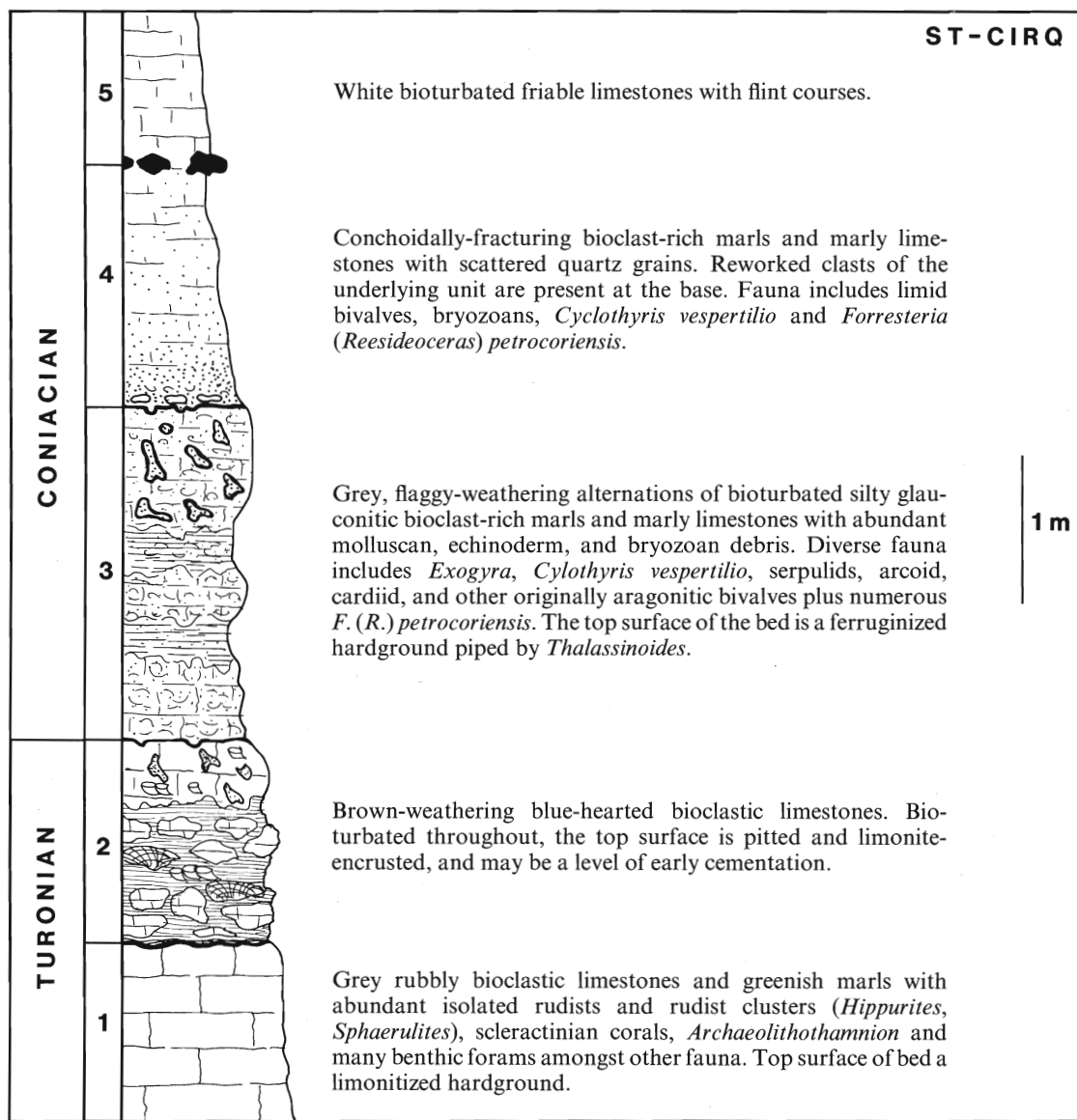
Carrières de Chancelade (Dordogne). The Carrières de Chancelade are on the west side of the Beaurnonne 0.6 km north of Chancelade and due west of Lavaure, some 5 km north-west of Périgueux ($x = 468, 7; y = 3325, 7$). This locality provides a fine succession of Turonian and Coniacian sediments with a series of glauconitized hardgrounds in the lower part of the sequence which yield numerous ammonites. Many occur in a striking preservation with bright-green coatings like that of



TEXT-FIG. 7. The Turonian-Coniacian succession at the Carrières de Chancelade near Périgueux (Dordogne).

many museum specimens in the Arnaud and other collections from Chancelade itself and nearby railway cuttings such as Gourde-de-l'Arche. The present collections are exclusively *F. (H.) petrocoriensis*. See text-fig. 7 for details.

St. Cirq (Dordogne). The railway cutting at St. Cirq has been well known since the work of Arnaud; a recent account is given by Vigneaux (1975, p. 94, text-fig. 51). The cutting lies on the north-west side of the railway below the road bridge south-east of St. Cirq ($x = 492, 2; y = 292, 0$) which itself lies midway between Le Buge and Les Eyzies-de-Tayac. More than 20 m of the Turonian is exposed, and is separated from the succeeding Coniacian by a marked hardground and erosion surface. The



TEXT-FIG. 8. The Turonian-Coniacian succession at St. Cirq (Dordogne).

succeeding glauconitic marls of the 'Coniacien inférieur' yielded abundant *F. (H.) petrocoriensis* at the base (text-fig. 8).

Montignac (Dordogne). Road cuts on the D704 1.8 km east of the centre of Montignac and 2 km south-south-west of Aubas ($x = 508, 5; y = 308, 0$) show the Turonian-Coniacian boundary. The marls of the 'Coniacien inférieur', exposed to 3.5 m, yield many fossils corresponding to the 'Montignac' fauna of Coquand and d'Orbigny. Ammonites are frequent, with *F. (H.) petrocoriensis* in the basal metre. There is a transition up into the succeeding bioclastic limestones of the Coniacien Moyen, visible at the junction with the minor road to Aubas.

St. Nathalène (Dordogne). The hamlet of St. Nathalène lies 6 km north-east of Sarlat-la-Canéda, on the Enea. Lower Coniacian marls with abundant *F. (H.) petrocoriensis* are exposed in small quarries and cuttings east of the minor road to Proissans, 1 km north of St. Nathalène ($x = 517, 0$; $y = 290, 6$). The succeeding middle Coniacian limestones outcrop alongside the road further north.

Carlux (Dordogne). A series of exposures around Carlux some 10 km east of Sarlat-la-Canéda show the full sequence of Turonian resting on Kimmeridgian. The Turonian–Coniacian boundary is exposed in a series of small outcrops north of the D47B towards Carlux. The boundary is a hardground separating quartzose bioclastic sandstones and calcareous marls with *F. (H.) petrocoriensis*.

Sauveterre-la-Lémace (Lot-et-Garonne). A semi-continuous section from Upper Turonian to Santonian is exposed on the road from the village out towards the Château ($x = 342, 6$; $y = 4939, 5$). The Turonian–Coniacian boundary is a hardground, succeeded by Lower Coniacian marls with *F. (H.) petrocoriensis* that pass up into middle Coniacian limestones, as shown in text-fig. 9. A succession of Upper Coniacian to Santonian limestones extends to at least 90 m, but lacks diagnostic macrofauna (see Séronie-Vivien 1972, p. 112, text-fig. 36, 36b for details).

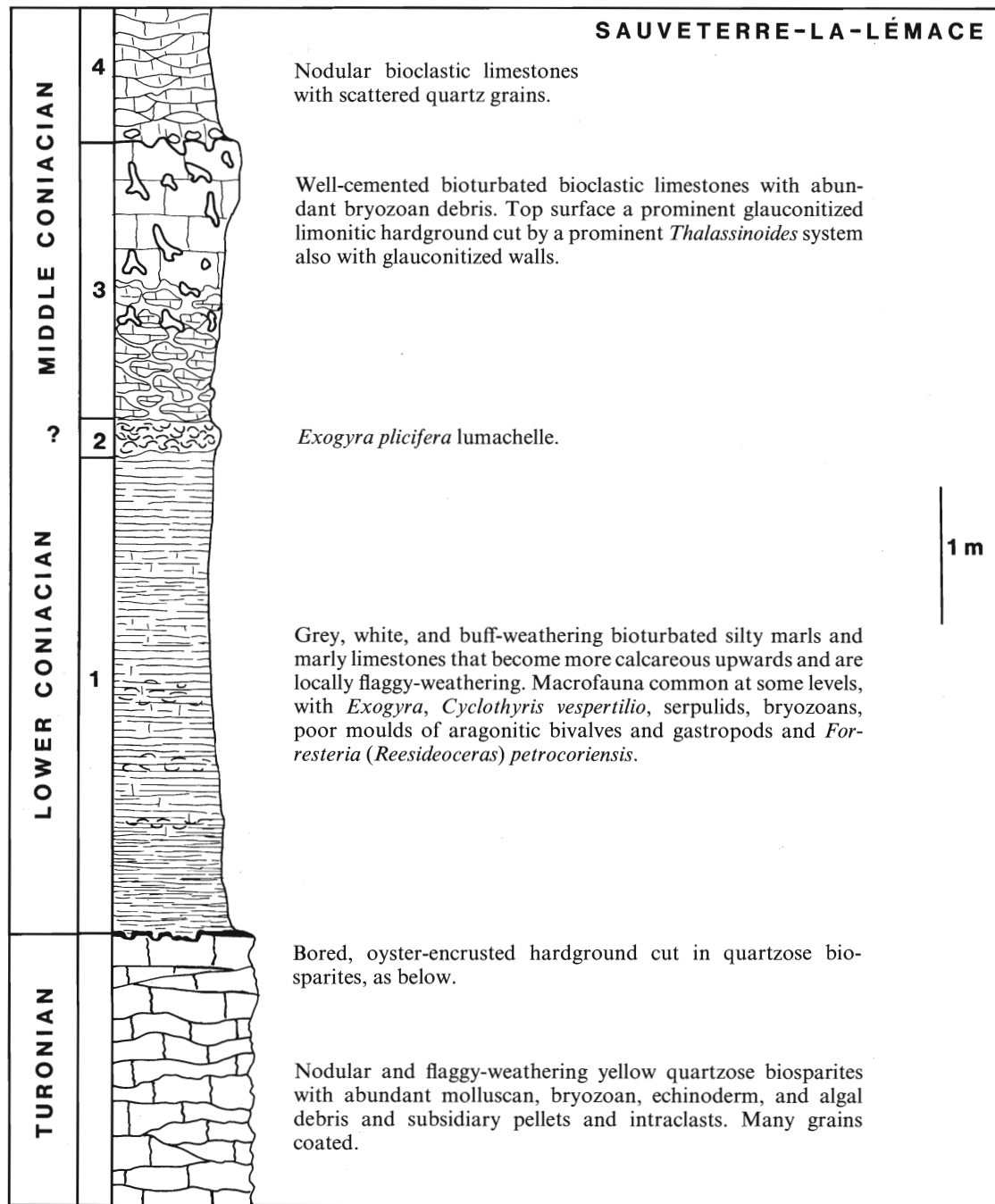
THE AMMONITE SEQUENCE IN AQUITAINE

The sections described above show that from Antignac, 10 km south-east of Pons and 24 km south-south-west of Cognac, south and east into the Dordogne as far as Périgueux and Sarlat-la-Canéda, the lowest Coniacian (Arnaud's L¹) yields *F. (H.) petrocoriensis*, often in numbers. Museum material shows the species to be present at many other localities, especially around Périgueux. To the north-west of Antignac, the facies of the Sables et Grès de Richemont is not conducive to ammonite preservation. There are, however, records of *B. haberfellneri*, by which name *F. (H.) petrocoriensis* is usually known in France, from north of Saintes (Gillard 1944). No other ammonite species occur associated with *F. (H.) petrocoriensis* in our collections apart from a single *Scaphites (Scaphites) meslei* de Grossouvre, 1894, from Antignac. Among more than a hundred museum specimens from the Dordogne, the only associated species are single specimens of *Metatissotia desmoulinsi* (de Grossouvre, 1894), *M. nodosa* Hyatt, 1904, and *M.? nanclasi* (de Grossouvre, 1894).

Species definitely recorded from L¹ are: *Onitshoceras? ponsianum* (de Grossouvre, 1894), *Tongoboryceras* cf. *tongoboryense* (Collignon, 1952), *T. hancocki* sp. nov. (the holotype only), *T. sp.*, *Placenticerias fritschi* de Grossouvre, 1894, *F. (H.) nicklesi* (de Grossouvre, 1894), *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867) *P. (P.) subtricarinatum* (d'Orbigny, 1850), *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), *Gauthiericeras? boreau* (de Grossouvre, 1894), *Tissotia redtenbacheri* (de Grossouvre, 1894), *Metatissotia ewaldi* (Von Buch, 1848), *M. slizewiczi* (de Grossouvre, 1894), *M. nodosa* (Hyatt, 1904), *Tissotioides haplophyllus* (Redtenbacher, 1873), *Scaphites meslei* de Grossouvre, 1894, *Otoscaphtes arnaudi* (de Grossouvre, 1894) and *Baculites incurvatus* Dujardin, 1837.

L² has yielded few ammonites, but Dr. P. Moreau of the Université de Poitiers has precisely localized specimens of all the species present in older collections. These include a giant *Gauthiericeras margae* (Schlüter, 1867) from the Upper Coniacian white glauconitic limestones in the Commune de Chanières in the Vallée de la Coran 9 km east of the centre of Saintes, and a second specimen from a slightly lower level east of the D131 south of La Grélauderie in the commune of St. Bris-de-Bois, 9 km north-east of the centre of Saintes.

From the hamlet of Le Chay, near Saujon (Charente-Maritime), a village that straddles the Coniacian–Santonian boundary, come *Protexanites bourgeoisi* (d'Orbigny, 1850), *P. bontanti* (de Grossouvre, 1894), and *Menabonites* sp. *G. margae* is also known in this area, and all are preserved in distinctive bryozoan-rich limestones.



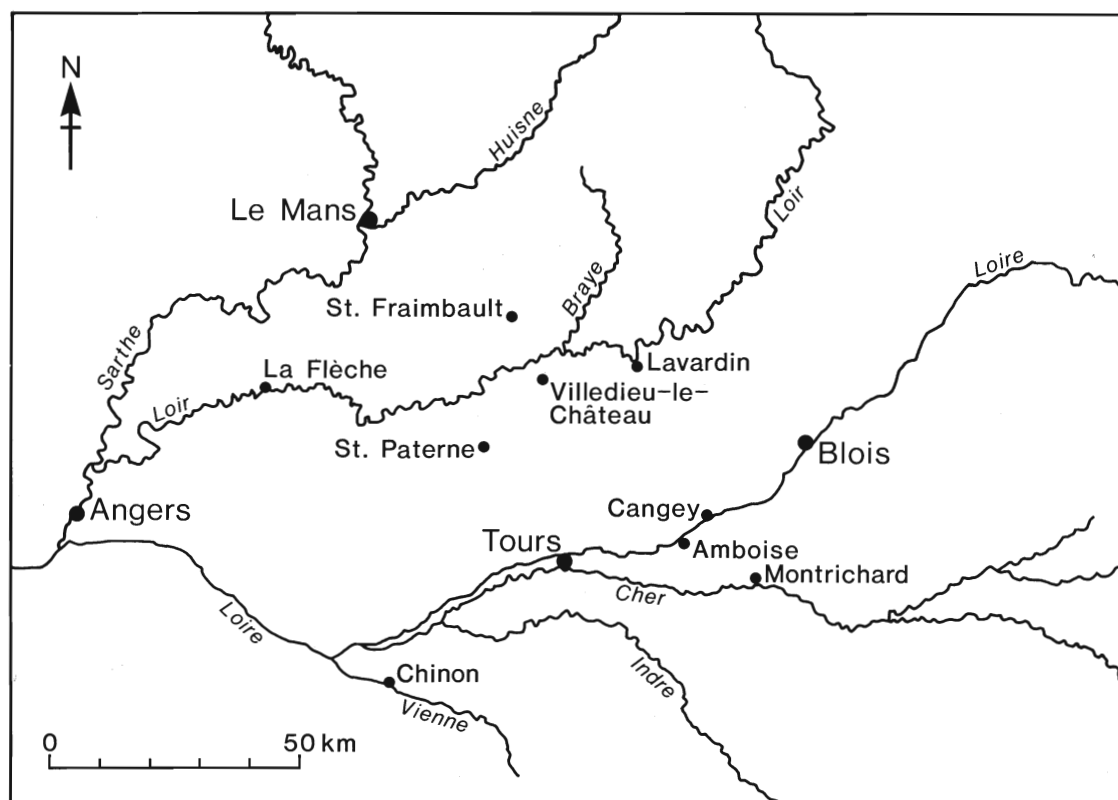
TEXT-FIG. 9. The Turonian-Coniacian sequence at Sauveterre-la-Lémace (Lot-et-Garonne).

TOURAINE: THE CRAIE DE VILLEDIEU

INTRODUCTION


The occurrence of Senonian ammonites in Touraine was well known from the early decades of the last century. d'Orbigny (1850) described a small number of Coniacian species from St. Patern-Racan (Indre-et-Loire), Villedieu-le-Château (Loir-et-Cher) and St. Fraimbault [Frimbault] (Sarthe). Jarvis *et al.* (1982) summarize early controversy over the sequence in what had become known as the Craie de Villedieu. Only with the work of de Grossouvre (1889-1901) did a clearly defined sequence of faunas emerge. De Grossouvre divided the Craie de Villedieu into five zones (A-E) of Coniacian and Santonian age which are in part faunally, in part lithologically defined. This division has been accepted by virtually all subsequent workers and the ammonite occurrences discussed in terms of these zones, which are reproduced in Table 2. De Grossouvre admitted that the fivefold division could only be recognized around Villedieu-le-Château, and that only a threefold division was widely recognizable: 'bancs durs' with ammonites at Villedieu and Cangey, 'marnes glauconieuses à Ostracées', and 'craie assez dure, noduleuse, à texture sableuse, très fossilifère' with *Spondylus truncatus* (1901, pp. 338-350).

Jarvis *et al.* (1982) provided a series of detailed sections around Villedieu-le-Château and designated formal lithostratigraphic divisions, approximately equivalent to de Grossouvre's more widely recognized units, terming the first the Calcaire Dur de La Ribochère Member, the second the Marne Glauconieuse du Château de La Ribochère Member, and the third the Calcarenite à Bryozoaires de La Bouchardière Member. Whether this nomenclature will be adopted by French workers remains to be seen.



TEXT-FIG. 10. Touraine, showing the principal localities mentioned in the text.

TABLE 2

De Grossouvre 1894 (p. 348)		Jarvis, Gale and Clayton (1982, text-fig. 3)			Present work		
Étage	Zone	Formation	Member	Stage	Zone	Substage	
Sénontien	Craie siliceuse à silex de Blois et de Chaumont		----- ?	----- ?	<i>Placenticerus polyopsis</i> (syn. of authors)	UPPER SANTONIAN OF AUTHORS	
	Craie avec silex irréguliers abondants		Calcaire à bryozoaires de La Bouchardière	SANTONIAN			
	Craie noduleuse à texture gréseuse avec quelques silex (zone E)		Craie de Villedieu		----- ?		
	Craie tendre, glauconieuse (zone D)			Marne glauconieuse du Château			
	Lit de Micrasters (zone C)						
	Banc d'Ostracées avec Ammonites à la base (zone B)					CONIACIAN	<i>Paratexanites serratomarginatus</i>
Calcaires durs de Villedieu et de Cangey ayant comme facies latérale des grès siliceux à <i>Actaeonella crassa</i> (zone A)			Calcaire dur de La Ribochère		<i>Gauthierceras margae</i>		
					<i>P. (Peroniceras) tridorsatum</i>		
Turonien	Craie à Bryozoaires avec lit de Lamellibranches et d' <i>O. columba gigas</i> (silex souvent abondants ayant comme facies latéral soit la craie à <i>Terebratulina bourgeoisi</i> soit des sables et grès siliceux)	Tuffeau jaune		TURONIAN	<i>Forresteria (Harleites) petrocoriensis</i>	UPPER TURONIAN	

The lowest hard limestones with Coniacian ammonites have a limited outcrop around Villedieu-le-Château, St. Patern-Racan, and St. Frimbault (text-fig. 10). They occur as far east as Lavardin, but no ammonites are known. To the south, bioclastic limestones in the Loire Valley around Cangey and Limeray east of Tours are partly or wholly equivalent to these limestones and have yielded ammonites.

The succeeding Santonian part of the Craie de Villedieu has a somewhat wider extent. These facies pass northwards and eastwards into chalk facies; to the west and south they are commonly decalcified or represented by terrigenous clastic facies (Alcaydé *in* Megnien 1980).

PRESENT OBSERVATIONS

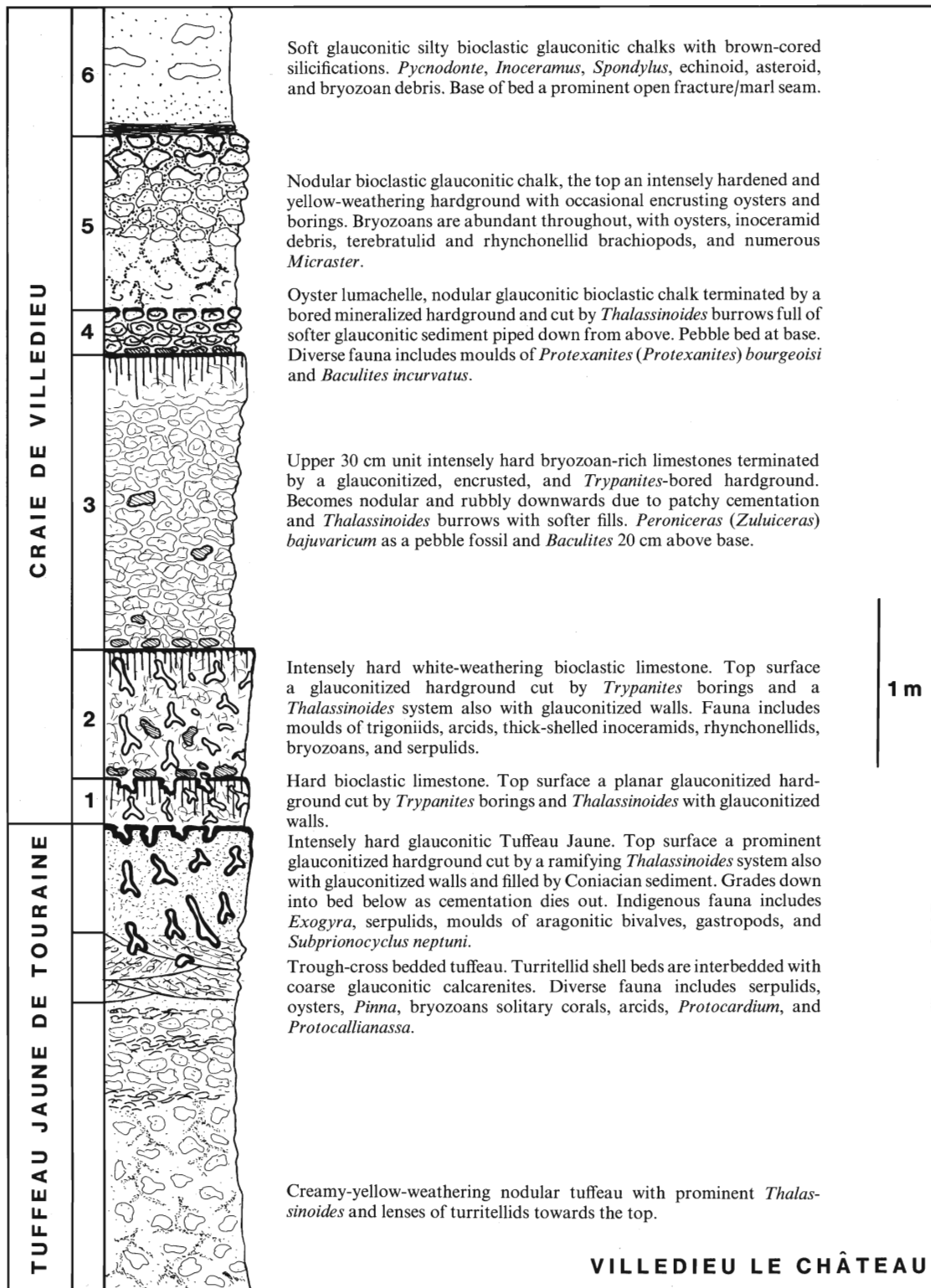
Villedieu-le-Château and environs. The best exposure of the Coniacian parts of the Craie de Villedieu occurs in roadside sections and caves on the northern and western bank of the road from Trehet to Villedieu-le-Château (Loir-et-Cher), in particular opposite the turning to Grouteau ($x = 472$, 4 , $y = 2304$, 1), and is shown in text-fig. 11. The top of the Tuffeau Jaune, a series of glauconitic calcarenites, is exposed to several metres along the section, and the lower, relatively poorly cemented levels are cut by caves and troglodytic dwellings along the road towards Trehet. The roof of these excavations is formed by the lithified top of the formation which is terminated by a prominent planar hardground. This is heavily glauconitized and cut by a ramifying three-dimensional *Thalassinoides* system that extends down for more than a metre into the Tuffeau below. Hardening is intense in the top 65 cm of the Tuffeau Jaune, decreasing downwards below this. There are shell lenses in the top metre, mostly made up of moulds of *Turritella*, with *Rhynchostreon columba* (Lamarck, 1819), *Pinna*, *Granocardium*, *Protocallianassa*, bryozoan debris, *Filograna filosa* (Dujardin, 1837), and, from 47 to 67 cm below the summit, a specimen of *Subprionocyclus neptuni* (Geinitz, 1850) (OUM 17014a-c) which firmly dates the top of the unit as Upper Turonian, *S. neptuni* Zone.

The succeeding Calcaires Durs de La Ribochère (= Unit A of de Grossouvre) form a mural face and are welded to the cemented summit of the Tuffeau Jaune (text-fig. 11). The limestones are 2.5 m thick. They are white to cream-weathering bioturbated bryozoan calcarenites and micrites divided into three beds separated by glauconitized, bored and encrusted hardgrounds. That between Beds 1 and 2 is less conspicuous than that between 2 and 3, and the sequence is terminated by a further strongly mineralized bored and encrusted hardground.

The fills of the burrows in the top of the Tuffeau Jaune record a complex history, with an older, glauconitic fill in the lower parts of some burrows succeeded by essentially glauconite-free calcarenites identical to those of Bed 1 of the Craie de Villedieu above. There are two *F. (H.) petrocoriensis* from Villedieu in the Seunes Collection (Faculté des Sciences, Rennes) preserved in a glauconitic limestone which, if correctly localized, can only come from this early fill and provide a clear date for the base of the Craie de Villedieu.

Above, the Calcaires Durs are obviously condensed, and the two hardgrounds within them may, by analogy with other Upper Cretaceous hardgrounds in western Europe, represent a very long interval of time, or a very short one; there is no way of telling. Ammonites collected *in situ* came from 20 cm above the base of Bed 3, and are *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873) (OUM KZ17022) and *Baculites cf. brevicosta* Schlüter, 1976 (OUM KZ17023), but even the *Peroniceras* shows signs of reworking, and is a pebble fossil. Indeed, bored and encrusted intraclasts occur at several levels in the sequence.

It has proved impossible to place the museum material available into the three divisions recognized in the Calcaires Durs. The source of the material is variably given as 'Carrières de la Ribochère', 'la Ribochère', 'Villedieu' or 'Couture'; most appear to have come from the quarries of La Ribochère, but there are many other outcrops in the area. The revised faunal list is as follows: *Pachydiscoides janeti* (de Grossouvre, 1894), *Onitshoceras? ponsianum* (de Grossouvre, 1894), *Placenticeras fritschi* (de Grossouvre, 1894), *F. (H.) petrocoriensis* (Coquand, 1859), *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867), *P. (P.) westphalicum* (Von Strombeck, 1859), *P. (P.) lepeei* (Fallot, 1885), *P. (P.) dravidicum* (Kossmat, 1895), *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), *Gauthiericeras*



TEXT-FIG. 11. The Turonian-Coniacian sequence between Villedieu-le-Château and Tréhet (Loir-et-Cher).

margae (Schlüter, 1867), *G. nouelianum* (d'Orbigny, 1850), *G.? boreau* (de Grossouvre, 1894), *Paratexanites zeilleri* (de Grossouvre, 1894), *Eubostrychoceras* sp., *Tridenticeras* sp., *Scaphites meslei* de Grossouvre, 1894, and *Baculites* cf. *brevicosta* Schlüter, 1876.

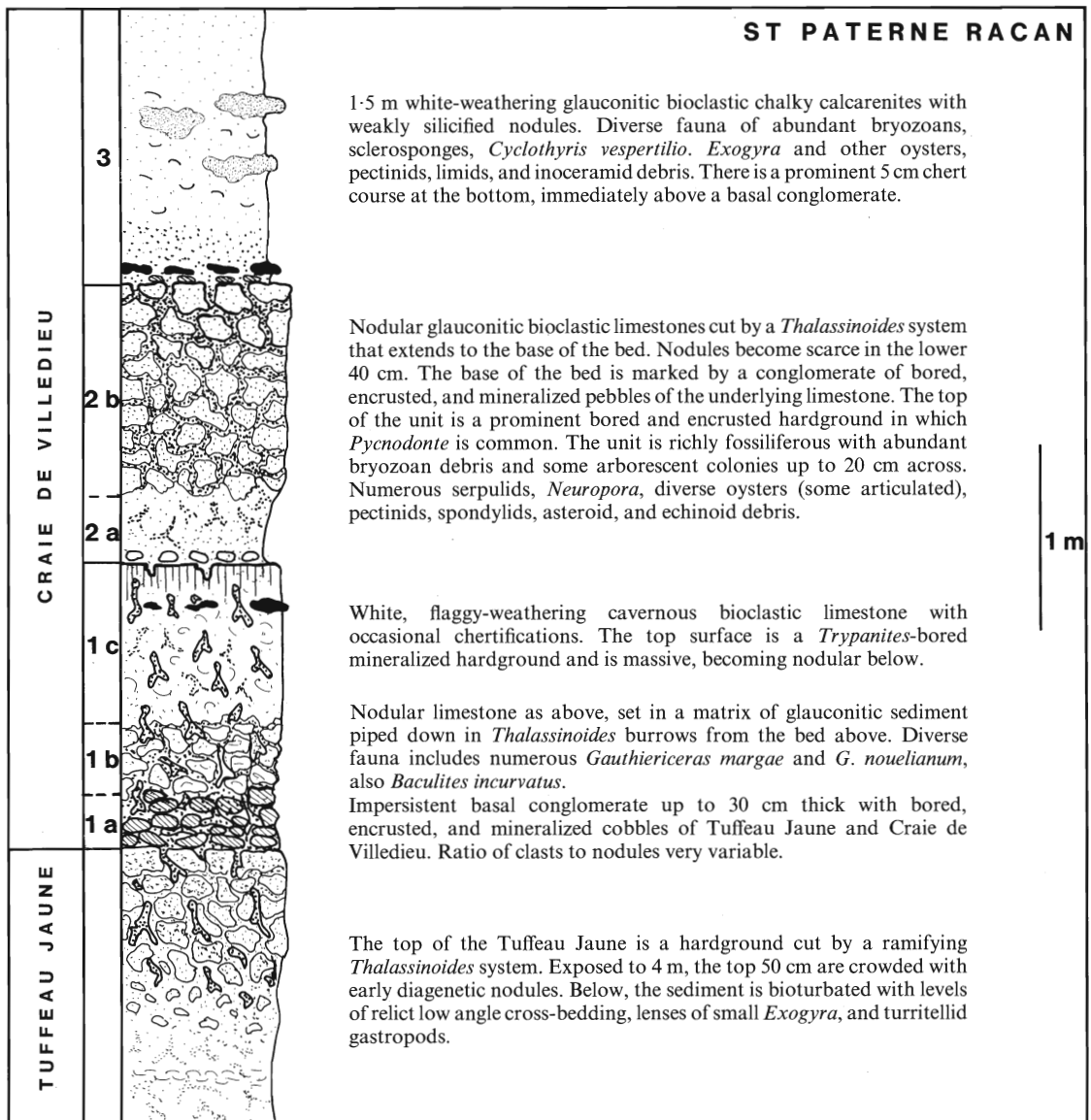
The prominent hardground at the top of the Calcaires Durs de La Ribochère is succeeded by glauconitic bryozoan-rich bioclastic chalks and marls, the Marnes Glauconieuses du Château de La Ribochère of Jarvis *et al.* (1982)—de Grossouvre's zones B and C. The basal unit, Bed 4 of the section shown in text-fig. 11, is a 30-cm bioturbated glauconitic chalk terminated by a bored, mineralized, and encrusted hardground. The bed is crowded with calcitic fossils cemented into hard lumps and perforated by a ramifying three-dimensional *Thalassinoides* system infilled by glauconitic chalk piped down from Bed 5 above. This is de Grossouvre's Bed B, and is a mass of *Ceratostreon proboscideum* (d'Archiac, 1837) and *C. plicifera* (Dujardin, 1837) with many other calcitic fossils and moulds of aragonitic forms. Some of the fossils are reworked pebble fossils. Ammonites from this level are highly distinctive in their preservation and are partially phosphatized in some cases. One side is generally well preserved, sometimes encrusted by bryozoans and serpulids growing on what were moulds at the time of encrustation; the other side is generally not preserved. *Protexanites* cf. *bourgeoisii* (d'Orbigny, 1850) (OUM KZ17078) and *Baculites incurvatus* Dujardin, 1837 (OUM KZ17077) have been collected *in situ* at the base of the bed, resting on the hardground at the top of the Calcaires Durs. Museum material includes numerous *P. bourgeoisii*, *P. bontanti* (de Grossouvre, 1894), *Paratexanites serratomarginatus* (Redtenbacher, 1873), *Phlycticrioceras trinodosus* (Geinitz, 1850), and *Placenticeras semiornatum* (d'Orbigny, 1850).

No other Coniacian ammonites occur in the sequence, and the reader is referred to Jarvis *et al.* (1982) for an account of the rest of the higher units. These authors draw the base of the Santonian on the basis of inoceramid evidence and comparison with the inoceramid sequences in the chalks of the Anglo-Paris Basin and Germany. It is less than clear how this definition of the base of the Santonian relates to the sequences in the Santonian type area and elsewhere in Aquitaine.

St. Paterne-Racan. The Calcaires Durs de La Ribochère can be recognized at a few localities away from the immediate type area (see de Grossouvre 1901; Jarvis *et al.* 1982, in preparation) but only at St. Paterne-Racan (Sarthe), some 20 km south-west of Villedieu-le-Château, can ammonites still be found in numbers. The sections described here occur in the walls and roofs of the caves and troglodytic dwellings of La Vallée de la Roche ($x = 462, 3, y = 290, 3$). The succession is very different from that at Villedieu and is shown in text-fig. 12. The top of the Tuffeau Jaune is a glauconitic calcarenite, exposed to 4 m at the western end of the section. When weathered, the top 50 cm is nodular as a result of early diagenetic cementation. The fauna consists predominantly of fragmentary calcitic fossils including oysters, serpulids, bryozoans, asteroids, echinoids, and *Protocallianassa*. There are occasional composite moulds of arcid bivalves, but no ammonites have been collected.

The upper surface of the Tuffeau is a marked erosion surface with a ramifying *Thalassinoides* system piping the overlying sediment down between nodules. The massive hardground development seen at Villedieu-le-Château is not present. The Calcaires Durs de La Ribochère are represented by Bed 1 of the section, which is 1.6 m thick. The top of this bed is a prominent planar hardground, glauconitized, bored, and encrusted, and penetrated by a ramifying three-dimensional *Thalassinoides* system which extends to the very base of the bed and pipes the glauconitic marly chalk of Bed 2 down to the extent that it forms a matrix to the intraclasts, early cemented nodules, and fossils in Bed 1. This can be divided into three subunits. Bed 1a is a basal conglomerate. This varies laterally over a few hundred metres from a distinct 30 cm boulder bed with intraclasts dominant to a nodular limestone with only scattered intraclasts. Intraclasts are either quartzose glauconitic calcarenites derived from the Tuffeau Jaune or early diagenetic nodules of Craie de Villedieu. The latter are also quartzose glauconitic calcarenites, but the percentage of quartz is lower, the glauconite grains larger, and the carbonate fraction coarser with abundant recognizable bryozoan and *Inoceramus* debris.

Above the basal conglomerate, or resting on top of the Tuffeau Jaune when the former is absent, the remainder of Bed 1 is a nodular limestone below (1b) passing up into a well-cemented massive



TEXT-FIG. 12. The Turonian-Coniacian sequence at St. Patern-Racan (Vallée de la Roche) (Indre-et-Loire).

hardground 80 cm thick. The nodules and hardground are calcarenites with abundant bryozoan, sclerosponge, oyster, *Inoceramus*, and echinoderm debris. There is an extensive fauna of calcitic fossils and moulds of originally aragonitic forms.

Ammonites from Bed 1 are as follows: in the intraclasts of Craie de Villedieu at the base of the bed *Gauthiericeras? boreau*i (de Grossouvre, 1894) (OUM KZ 16590); from 30 to 50 cm above the base of the bed in the nodular unit below the main hardground numerous *G. margae* (Schlüter, 1867) and *G. nouelianum* (d'Orbigny, 1850) with rare *Tridenticeras* and *Baculites*; 30 cm below the top of the bed *Protexanites bourgeoisi* (d'Orbigny, 1850) (A. Gale Collection).

The succeeding glauconitic bioclastic limestones of Beds 2 and 3 of the section shown in text-fig. 12 have not yielded ammonites. They are presumably of Coniacian age, but the distinctive oyster-bed with *Protexanites* and the *Micraster*-rich hardground at Villedieu-le-Château are absent.

St. Frambault. This hamlet (also spelt St. Frimbault) in Sarthe some 11 km north-north-east of Villedieu-le-Château was the source of ammonites in nineteenth-century collections, including several of the syntypes of *Ammonites bourgeoisianus* d'Orbigny, 1850. The 1:80000 geological map shows a crescent of Craie de Villedieu outcropping on the hillside south-east of the village, but there are no useful exposures. Preservation of *Protexanites* indicates the extension of a glauconitic oyster-bed identical to Bed 4 at Villedieu-le-Château, but there is no evidence for the Calcaires Durs de La Ribochère at present.

Cangey. The village of Cangey (Indre-et-Loire) is on the Loire 28 km west-north-west of Tours and 42 km south-east of Villedieu. During the last century Coniacian limestones at the base of the Craie de Villedieu known as the Calcaires de Cangey were worked for building stones in quarries and caves between Cangey and Limeray (de Grossouvre 1894, 1901, p. 338, table 11; Lecointre 1947, p. 73). Most outcrops are now in the walls of troglodytic dwellings and gardens, so that collecting is difficult. The contact between the Tuffeau Jaune and Calcaires de Cangey was not observed during the present study, but both de Grossouvre and Lecointre take it at a bed of *Rhynchostreon columba gigas* that occurs widely in the area. Alcaydé (1968) gives a thickness of 7–10 m for the Calcaires de Cangey; approximately 5 m are visible, and show a series of sequences of burrowed, feebly nodular bioclastic limestones passing up into well-developed nodular hardgrounds and incipient hardgrounds, the tops of which are marked by prominent bedding planes. The limestones are bryozoan–oyster–echinoderm-rich calcarenites with scattered quartz and glauconite; ammonites in museum collections labelled 'Cangey' or 'Limeray' are generally fresh and preserved in an identical matrix, suggesting they came from the old workings. *Peroniceras subtricarinatum* (d'Orbigny, 1850) is the most widely cited species, but museum collections include only *P. (P.) dravidicum* (Kossmat, 1895), *P. (P.)* sp. and *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). De Grossouvre (1894, pl. 4, fig. 6) figured a *Metatissotia* from Cangey, but the specimen has not been traced. In 1889 (p. 497) the same author recorded '*Ammonites Noueli*, d'Orb. (cf. *Bajuvaricus*, Redt.), *A.* sp. nov. and *Ammonites petrocoriensis*, Coq. (1)'. In 1894, however, *A. Noueli* (by then recognized as a synonym of *G. margae*) and '*Barroisia haberfellneri* (of which *petrocoriensis* was taken to be a synonym) were not mentioned from Cangey. Recently, *Forresteria (Harleites)* has been rediscovered here (A. Gale Collection).

The top of the Calcaires de Cangey is a prominent hardground, which correlates with that at the top of the Calcaires Durs de La Ribochère. It is succeeded by a richly fossiliferous calcarenite termed the Banc Glauconieuse à *Cidaridites jouanneti* by Lecointre, equivalent to Bed 4 at Villedieu, while some 2 m above the top of the Calcaires de Cangey, nodular units and hardgrounds in glauconitic bioclastic limestones represent Bed 5 of the Villedieu section. A specimen of *Protexanites bourgeoisi* (d'Orbigny, 1850) from Cangey is in the collections of the École des Mines (now at Lyons).

THE DIEULEFIT BASIN (DRÔME)

Coniacian ammonites were first described from the environs of Dieulefit (Drôme) by Von Buch (1848a, 1848b, 1850) and Thiollière (1849). The chief subsequent accounts are by Fallot (1885), de Grossouvre (1901), and Sornay (1946, 1950). A brief summary in English is given by Moullade in Middlemiss and Moullade (1968) and a detailed map of the eastern part of the area was published on a scale of 1:50000 in 1969. The accompanying memoir (Lorenchet de Montjamont 1970) gives the following succession (loosely translated):

C3, Turonian

C3a 'Grès Rouges'. Glauconitic red, yellow, and grey-greenish coarse sandstones and conglomerates, cross-bedded, with rolled fossils (fish teeth, echinoderm, and bryozoan debris): 50 m.

C3b 'Calcaires Blancs'. White chalky, sometimes glauconitic limestones with cherts: 200–350 m. The fauna is poor, but in the area covered by the Montélimar sheet to the west, it has yielded Upper Turonian ammonites. Moullade (in Middlemiss and Moullade 1968) records *Germariceras* aff. *germari*, *Scaphites geinitzi*, *Lewesiceras peramplum*, and *Pseudotissotia* cf. *nigeriensis*, plus *Inoceramus costellatus*, *I. inconstans*, *I. hercynicus*, *I. cuvieri*. . . . Taken at face value these suggest horizons up to the Upper Turonian *neptuni* Zone.

C3c 'Grès et Sables de Raymonds'. Yellow or white coarse-grained quartzose sandstones with marly intercalations. At the top there is a unit of 15 m of yellow sandstones. Total thickness: 100 m. Macrofaunas are poor, but suggest the Upper Turonian; Porthault (in Lorenchet de Montjamont 1970) suggests that the top may extend into the Coniacian.

C4 Coniacien

'*Grès Verts de Dieulefit, des Rouvières*'. Glauconitic sandstones and limestones with a rich fauna. Total thickness: 30 m.

C5

'*Sables des Vitrouillères — Continental de Dieulefit*'. Yellow and red sands with intercalated lignites and lignitic kaolinic clays. Thickness: 50 m.

It is the Grès Verts de Dieulefit that yield Coniacian ammonites. Fallot (1885, pp. 159f., text-fig. 31) and de Grossouvre (1901, p. 491f.) recognized a detailed faunal succession:

1° Zone inférieure — Grès jaunâtre à *Hemiasper soulieri*.

2° Zone moyenne { (a) Grès vert à *Cardium Latunei*.
(b)

Grès vert à Céphalopodes (*Am. Czörnigi*, etc.)

3° Zone supérieure — Grès jaunâtre à *Trigonia limbata* et Gastéropodes (Fallot 1885, p. 164)

These detailed records show ammonites to be confined to a single narrow interval. Field-work in recent years shows that ammonites are very rare indeed. Some of Fallot's types survive in the collections of the Laboratoire de Géologie at Grenoble, and there are a few specimens in the collections of the Sorbonne (now in the Université Pierre et Marie Curie, Paris), Muséum Nationale d'Histoire Naturelle, École des Mines, and Oxford University Museum.

A revised faunal list is as follows: *Peroniceras (Peroniceras) lepeei* (Fallot, 1885), *P. (P.) tri-dorsatum* (Schlüter, 1867), *P. (P.) westphalicum* (Von Strombeck, 1859), *P. (Zuluiceras) isamberti* (Fallot, 1885), *P. (Z.) bajuvaricum* (Redtenbacher, 1873), *P. (Z.)* sp., *Metatissotia ewaldi* (Von Buch, 1848), *M. slizewiczi* (Fallot, 1885), *Tissotioides haplophyllus* (Redtenbacher, 1873), *Scaphites (Scaphites) meslei* de Grossouvre, 1894, *S. (S.)* sp., and *Scalarites* sp.

The preservation of all of these suggests the Grès vert à Céphalopodes.

A single *P. (P.)* sp. (OUM KZ19351) is from the underlying Grès vert à *Cardium Latunei*.

THE BEAUSSET BASIN (VAR)

INTRODUCTION

Ammonites are generally rare in the Coniacian of Provence. The chief early records are to be found in the works of Toucas, listed at length by Fabre-Taxy (1963).

De Grossouvre (1901, p. 514, table 30) notes only '*Peroniceras bajuvaricum*, *Mortoniceras emscheris* and *M. subtricarinatum*', and only in 1963 with the work of Fabre-Taxy were these records revised, and only one species noted, '*Gauthiericeras*' *bajuvaricum* (Redtenbacher, 1873) (p. 112, pl. 4, fig. 4) from Le Beausset, without precise localization. Thomel (1969, p. 119, pl. F, figs. 1, 2) figured a poor *Peroniceras* (as *P. subtricarinatus* (d'Orbigny)), from Beausset.

The work of Collignon, Crégut, Fabre-Taxy, Philip, and Tronchetti (1979) revealed the Ceyreste area of the Beausset Basin as a critical one for Coniacian ammonite studies; although the material is poorly preserved, a succession of faunas can be demonstrated.

STRATIGRAPHY

The succession (loosely translated from Collignon *et al.* 1979) is as follows:

1. *Calcaires à Rudistes*, at the base. Only the upper part of this unit outcrops in the area and yields *Vaccinites praegiganteus* Toucas, *V. cf. praecorbaricus* Toucas, *V. giganteus* (d'H. Firmas), large *Durania cornupastoris* (des Moulins), and *Biradiolites cf. angulosus* (d'Orbigny). This is dated as Turonian-Coniacian. The sequence is terminated by breccias of limestone and rudist debris capped by a discontinuity surface.

2. *Grès de Sainte Croix et lentille des Camegiers*. These are thinly bedded glauconitic ferruginous sandstones approximately 12 m thick, with an intercalated 3 m lens of limestone breccia with remanié rudists (*V. giganteus*, *Durania* sp.). The poor microfauna is not age-diagnostic.

3. *Marnes de Ceyreste*. Bluish glauconitic marls and marls approximately 50 m thick. The lower part yields numerous ammonites, echinoids, and *Inoceramus cf. waltersdorfensis hannovrensis* (Heinz). The base yielded '*Peroniceras tricarinatum*' (Collignon *et al.* 1979, p. 390, pl. 1, fig. 1) and '*P. moureti* de Grossouvre' (Collignon *et al.* 1979, p. 392, pl. 2, fig. 3) occurs at the top.

A revised faunal list is as follows (based on records in Collignon *et al.* and collections in the Oxford University Museum, nos. KZ16438-16472):

At the base: *P. (P.) subtricarinatum* (d'Orbigny, 1850). In the lower part: *Parapuzosia* sp., *Placenticerias* sp., *Forresteria (Forresteria) cf. alluaudi* (Boule, Lemoine, and Thévenin, 1907), *Peroniceras (Zuluicerias) sp.*, *Scaphites (Scaphites) meslei* de Grossouvre, 1894 and *Otoscaphtes arnaudi* (de Grossouvre, 1894). At the top: *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867).

4. *Grès de Baguier*. Glauconitic sandstones and sandy limestones with bryozoan debris, echinoderms, and rare foraminiferans; approximately 100 m thick.

Gauthiericerias margae (Schlüter, 1867) occurs in the middle of the unit (Collignon *et al.* 1979, p. 390, pl. 2, fig. 4) and *Paratexanites serratomarginatus* (Redtenbacher, 1873) (Collignon *et al.* 1979, p. 391, pl. 2, figs. 1, 2) at the top. The foraminiferal assemblage was regarded as Coniacian by Tronchetti (1971).

5. *Marnes de Saint Cyr*. These yield a Santonian microfauna, but the position of the Coniacian-Santonian boundary has not been determined.

CONIACIAN AMMONITE ZONATION

INTRODUCTION

Coniacian ammonite zones. The above accounts of the stratigraphy of the Aquitaine Basin, the Craie de Villedieu of Touraine, the Dieulefit (Drôme), and Beausset (Var) Basins reveal the great difficulties encountered in developing a sequence of zones for the Coniacian. Ammonites occur in numbers in only a few areas, and new collections to check old records are often lacking, while sequences of assemblages are rarely established in the field. On the basis of data presented above, the following zonation is proposed:

1. *Forresteria (Harleites) petrocoriensis Zone*

The base of the zone is marked by the appearance of the index species. This is the first ammonite to appear in the Aquitaine Basin and it has been collected from several localities during the present study (Antignac (Charente-Maritime), St. Nathalène (Dordogne), St. Cirq (Dordogne), Carrière de Chancelade (Dordogne), Aubas (Dordogne), and Carlux (Dordogne)); it appears within centimetres of the hardground or discontinuity surface between Coniacian sands and marls and Turonian rudistid limestones. Within the type area the appearance of this species thus defines the base of the Coniacian stage. There are few other ammonites found with *F. (H.) petrocoriensis*: a *Scaphites (Scaphites) cf. meslei* from Antignac (Charente-Maritime) and single specimens of three tissotiids are known. These are the holotype of *Metatissotia desmoulinsi* (de Grossouvre, 1894) (p. 62, pl. 2, fig. 6)

(Arnaud Collection), from Gourd-de-l'Arch (but not in the distinctive green-coated preservation), the holotype of *M. nanclasi* (de Grossouvre, 1894) (p. 110, pl. 3, fig. 4) (Arnaud Collection) in the typical green-coated preservation of ammonites from hardgrounds low in the sequence around Périgueux (the precise locality being 'première tranchée de la ligne de Périgueux à Coutras, à la sortie de Périgueux'), and a paratype, now lost, of *M. nodosa* (Hyatt, 1904) (= *Tissotia haplophylla* de Grossouvre *non* Redtenbacher of de Grossouvre 1894, p. 45, pl. 4, fig. 4) (Boreau-Lajanadie Collection) from 'Puymoyen, route de Torsac (Charente) . . . calcaires glauconieux à texture gréseux de l'assise K. de M. Arnaud'.

Reference sections for the *petrocoriensis* Zone (which also show the relationship with the underlying Turonian rudistid limestones and marls) are designated as follows: the lower quarry at Antignac (Charente-Maritime) (p. 9), the Carrières de Chancelade near Périgueux (Dordogne) (p. 13), the railway cutting at St. Cirq, 18 km west-north-west of Sarlat-la-Canéda (Dordogne) (p. 14), the road cut at Aubas (Dordogne), 40 km east-south-east of Périgueux (p. 14), and the exposures at Carlux (Dordogne) (p. 15) and Sauveterre-la-Lémace (Lot-et-Garonne) (p. 15). The presence of the *petrocoriensis* Zone in the Calcaires Durs de La Ribochère of the Villedieu-le-Château area in Touraine is demonstrated by specimens in the collections at Rennes that are believed to be from the earliest glauconitic phase of filling of burrows in the hardground at the top of the Tuffeau Jaune as well as specimens from an imprecise horizon in the succeeding calcarenites.

Records of '*Barroisia*' or *Barroisiceras haberfellneri* from Dieulefit (de Grossouvre 1894, 1901; Sornay 1950; Basse 1960) all appear to be based on the view that *Buchiceras nardini* Fallot, 1885, is a synonym of *Barroisiceras haberfellneri auctorum*, *non* Hauer (e.g. de Grossouvre 1894, p. 59). As shown below, *nardini* is a *Tissotioides*, synonymous with *haplophyllus* Redtenbacher, 1873. There is no unequivocal evidence for the *petrocoriensis* Zone at Dieulefit. *B. haberfellneri* is recorded from the Coniacian of the Corbières by Basse (1939), who, of all authors, is unlikely to have confused Hauer's species and her own *Reesideoceras gallicum* (e.g. *petrocoriensis*). The species is recorded with *Tissotioides*, *Nowakites*, *Parapuzosia*, and *Peroniceras* species from near Soulatge and in isolation near Devois, both in beds regarded as Coniacien Moyen. Basse subsequently (1947) revised her views and suggested the specimens were *R.(?) nicklesi* (de Grossouvre, 1894).

2. *Peroniceras* (*Peroniceras*) *tridorsatum* Zone

The base of the zone is marked by the appearance of diverse *P. (P.)* species. The fauna of this zone is widely recorded in Arnaud's Assise L¹ in Aquitaine and is marked by *P. (P.) tridorsatum* (Schlüter, 1867) and other species with rarer *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). Other ammonites are *Ontishoceras? ponsianum* (de Grossouvre, 1894), *Tongoboryceras hancocki* sp. nov., *T. cf. tongoboryense* (Collignon, 1952), *Placenticeras fritschi* (de Grossouvre, 1894), *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894), *Gauthiericeras? boreau* (de Grossouvre, 1894), *Metatisotia redtenbacheri* (de Grossouvre, 1894), *M. slizewiczi* (de Grossouvre, 1894), *M. ewaldi* (Von Buch, 1848), *M. nodosa* (Hyatt, 1904), *Tissotioides haplophyllus* (Redtenbacher, 1873), *Scaphites (Scaphites) meslei* de Grossouvre, 1894, *Otoscaphtes arnaudi* (de Grossouvre, 1894), and *Baculites* sp.

Sufficient of these ammonites occur together at single localities of Arnaud's to suggest that only one fauna is present, but the evidence from these old collections is not unequivocal. More recent collecting showed *Peroniceras (Peroniceras) sp.*, *P. (Z.) bajuvaricum*, *M. ewaldi*, *Placenticeras fritschi*, and *S. (S.) meslei* occurring side by side at Antignac, but suitable outcrops are now rare in Aquitaine.

Supporting evidence for a *tridorsatum* Zone comes from Dieulefit (Drôme), where the ammonite fauna includes many forms known only from L¹ Aquitaine. Species in common are: *Peroniceras (Peroniceras) tridorsatum*, *P. (Z.) bajuvaricum*, *M. robini*, *T. haplophyllus*, and *S. (S.) meslei*, with as additional elements, *P. (P.) lepeei* (Fallot, 1885), *P. (P.) westphalicum* (Von Strombeck, 1859), *P. (Z.) isamberti* (Fallot, 1885), and *Scalarites* sp.

The association from the Marnes de Ceyreste also suggests that the assemblage represents a single

zonal fauna, with the co-occurrence of *P. (P.) subtricarinarum*, *Parapuzosia (Parapuzosia) sp.*, *Proplacenticerias sp.*, *F. (Foresteria) cf. alluaudi*, *S. meslei*, and *O. arnaudi*.

The situation in Touraine is more complex. The fauna of the Calcaires de Cangey illustrated by de Grossouvre (1894) and described below is comprised of *Peroniceras (Peroniceras) tridorsatum*, *P. (P.) westphalicum*, *P. (Z.) bajuvaricum*, and *Tissotioides haplophyllus*, suggesting the *tridorsatum* Zone, although other species recorded by de Grossouvre (1889), but never mentioned subsequently, indicate that other horizons might be present. The Calcaires Durs de La Ribochère described in detail on p. 19 are obviously condensed and contain elements both older and younger than the *tridorsatum* Zone. The middle part of Bed 3 with remanié *P. (Z.) bajuvaricum* and *Baculites* may correlate with the *tridorsatum* Zone or be younger; the limits of the zone cannot be defined. Species common to the *tridorsatum* zonal assemblage in Aquitaine and elsewhere are *Onitshoceras? ponsianum*, *Placenticerias fritschi*, *Peroniceras (Peroniceras) tridorsatum*, *P. (P.) westphalicum*, *P. (P.) lepeei*, *P. (P.) dravidicum*, *P. (Z.) bajuvaricum*, and *S. meslei*.

Reference sections for the *tridorsatum* Zone are as follows: the upper quarry at Antignac (Charente-Maritime), the ammonite level in the Grès Vert de Dieulefit of Dieulefit (Drôme), and the Marnes de Ceyreste of Ceyreste in the Beausset Basin (Var).

3. *Gauthiericeras margae* Zone

The base of the zone is marked by the appearance of *Gauthiericeras margae* (Schlüter, 1867) and *G. nouelianum* (d'Orbigny, 1850). Also present are *G.? boreau* (de Grossouvre, 1894) which ranges from below, *Tridenticerias sp.*, and *Baculites incurvatus*. *Protexanites bourgeoisi* (d'Orbigny, 1850) first appears in this zone.

The position of the zone is unequivocally demonstrated by specimens of *G. margae* from Assize L² in Aquitaine, especially the careful records of Pierre Moreau, noted above, and the record from the middle part of the Grès de Baguier of the Beausset Basin (Collignon *et al.* 1979). In France, at least, ammonites are common only in Bed 1b of the Calcaires Durs de La Ribochère correlative at St. Paterne-Racan, and this is designated the reference section for the zone.

The presence of *G. margae* in the Calcaires Durs in the Villedieu-le-Château area shows the *margae* Zone to be present in these condensed limestones; it is also noted in the Coniacian of the Corbierès, above beds with a *tridorsatum* Zone fauna.

4. *Paratexanites serratomarginatus* Zone

The base of the zone is marked by the appearance of the index species. Other elements of the assemblage are *Protexanites bourgeoisi* (d'Orbigny, 1850), *P. bontanti* (de Grossouvre, 1894), *Proplacenticerias semiornatum* (d'Orbigny, 1850), *Phlycticrioceras trinodosus* (Geinitz, 1850), and *Baculites incurvatus* Dujardin, 1837.

This is the fauna of Bed 4 of the Craie de Villedieu in Touraine. Its position is indicated by two facts: it occurs above the condensed Calcaires Durs which contain *G. matgae* there, and the index species occurs above *G. margae* in the Beausset Basin. There is no evidence for the zone around Cognac in Aquitaine. Bed 4 of the Craie de Villedieu in the Villedieu-le-Château area is designated as a reference section for the zone.

THE CONIACIAN-TURONIAN BOUNDARY IN FRANCE

In all areas where Turonian ammonites occur close to the boundary they are rare, and none at all are known in Aquitaine. In Touraine a single *Subprionocyclus neptuni* (Geinitz, 1850) from a few tens of centimetres below the top of the Tuffeau Jaune at Villedieu-le-Château indicates the *neptuni* Zone as defined by Kennedy *et al.* (1983) and others. In the Dieulefit area, Middlemiss and Moullade (1968) note *Germariceras* aff. *germari*, *Scaphites geinitzi*, *Lewesiceras peramphum*, and *Pseudotissotia cf. nigeriensis* from the white limestones of the Turonian; these suggest more than one horizon. In the Beausset Basin no Upper Turonian ammonites are known, but Thomel (1969, p. 117, pl. F, fig. 4) has figured a *Subprionocyclus bravaisianus* (d'Orbigny, 1841) (= *S. neptuni* (Geinitz, 1850)) from the

Upper Turonian of Andon (Alpes-Maritimes). These data suggest that the *S. neptuni* Zone extends to the top of the Turonian in France and that no higher fauna between this and the *petrocoriensis* Zone can be recognized.

SUBDIVISIONS OF THE CONIACIAN

When Coquand originally introduced the étage Coniacien (1857*b*, p. 748) it was not divided specifically into substages, although in 1856 he referred to his divisions A and B of the 1857 work as substages. Arnaud referred to his three divisions K, L¹, and L² as Coniacien inférieur, moyen, and supérieur, and a threefold division is also used by de Grossouvre (1894). In 1901, in de Grossouvre's description of the Cretaceous of Aquitaine, three divisions are used although in his synthesis chapter (p. 792) he divides the stage into only an upper and lower. This difference of views persists to the present, and a two or threefold lithostratigraphic division (the latter usually corresponding approximately to Arnaud's divisions) is used on many recent maps; Séronie-Vivien (1972) appears to use both a two- and a threefold division.

Division into substages varies widely in other areas and leads to great confusion, especially where faunal records are concerned, with taxa recorded from the 'Lower' Coniacian of one area and the 'Upper' or 'Middle' of another. Any formal decision will have to be made by the International Commission on Stratigraphy. My own view is that in Aquitaine a threefold division is appropriate, as follows:

Upper Coniacian	}	<i>Paratexanites serratomarginatus</i> Zone
		<i>Gauthiericeras margae</i> Zone
Middle Coniacian		<i>Peroniceras tridorsatum</i> Zone
Lower Coniacian		<i>Forresteria (Reesideoceras) petrocoriensis</i> Zone

These substages are approximately (but not necessarily precisely) equivalent to Arnaud's K, L¹, and L². Table 1 (p. 5) shows the correlation of these subdivisions with those used by previous workers in Aquitaine; it will be used in subsequent accounts.

This table brings out the most important question raised by the present work: why did de Grossouvre recognize a threefold division of the Coniacian in 1889 and 1894, but abandon it for a twofold division in 1901? The answer lies, so far as can be judged, in the table on p. 106 of *Les Ammonites de la Craie Supérieure*, where the fauna of the Coniacien Moyen includes elements of both the Coniacien Inférieur and Coniacien Supérieur, and in particular in the overlapping occurrences of tissotiids, *Barroisiceras 'haberfellneri'* (e.g. *F. (Reesideoceras) petrocoriensis*) and peroniceratids. This is brought out by the lists for the two zones in the 'Classification des Couches Supracrétacées' (1901, p. 792).

The thesis of the present work is that the faunas of de Grossouvre's zones are mixed. This can be demonstrated in two areas where de Grossouvre records what are here regarded as mixed faunas from what he believed to be single horizons.

The first area is Touraine, where around Villedieu-le-Château the 3-m thick Calcaires Durs de La Ribochère yield elements of the *petrocoriensis*, *tridorsatum*, and *margae* Zones, and were placed entirely within de Grossouvre's *haberfellneri* Zone. The detailed description of the Calcaires Durs given on p. 19 and in text-fig. 11 shows the sequence to be condensed and divided into three units separated by marked hardgrounds, with at least some fossils reworked and remanié. Previous workers, including de Grossouvre, did not recognize these facts, which explain how mixed assemblages previously appeared to represent a single faunal association.

The second assemblage that appears to show an overlap of the *petrocoriensis* and *tridorsatum* Zones is the Grès Verts de Dieulefit. According to de Grossouvre and others it includes diverse tissotiids, '*Barroisiceras*' and peroniceratids. De Grossouvre (1894, p. 492) lists: '*Tissotia ewaldi*, de Buch sp., — *robini*, Thiollière sp., — *Slizewiczi* Fallot sp., *Barroisiceras haberfellneri*⁽¹⁾, v. Hauer, sp., *Peroniceras Czornigi*, Redtenb., sp., — *Moureti*, de Grossouvre, — *L'Epeei*, Fallot sp., *Gauthiericeras bajuvaricum* Redtenb., sp. . . . (1) = *Buchiceras nardini* in Fallot.' As already noted,

Buchiceras nardini is a *Tissotioides*, not *Barroisiceras haberfellneri* de Grossouvre (*non* Hauer) (= *F. (H.) petrocoriensis*), and the assemblage is entirely that of the *tridorsatum* Zone.

The co-occurrence of elements of the *margae* and *serratmarginatus* Zones of the present scheme in de Grossouvre's *emscheris* Zone appears to be based on occurrences in Arnaud's L² in Aquitaine. As discussed above (p. 15) ammonites occur so rarely in this unit that it is not possible to place most records in their correct relative positions. *G. margae* and *Paratexanites serratmarginatus* occur nowhere together, so far as is known, and are clearly separated in well-documented sequences in Touraine and Provence. *Protexanites bourgeoisi*, the commonest *serratmarginatus* Zone species does, however, appear in the *margae* Zone.

THE CONIACIAN-SANTONIAN BOUNDARY IN FRANCE

At Javrezac, a locality mentioned by Coquand as a type section for both Coniacian and Santonian stages, the boundary is easily drawn at a hardground between glauconitic limestones of the Coniacian below and marls of the Santonian above (p. 9, text-fig. 3). Defining this boundary using ammonites is much more difficult. The precise position of ammonites within the lower part of the Santonian (Arnaud's assize M¹) is poorly documented, and ammonites are very rare indeed. De Grossouvre (1894) records *Paratexanites* [*Mortoniceras*] *serratmarginatus* (Redtenbacher, 1873) from both the Coniacian and Lower Santonian; in 1901 he decided that the Coniacian specimens all belonged to *P. [M.] emscheris* (Schlüter, 1876) and that *serratmarginatus* was exclusively Santonian. He never illustrated Santonian *serratmarginatus*, and none survive in museum collections that can be attributed to Arnaud's M¹. Indeed, later work has shown that *serratmarginatus* and *emscheris* are not synonyms and that both are from high in the Coniacian (Wiedmann 1979; Kennedy, Klinger and Summesberger 1981). De Grossouvre also indicated that *Protexanites* [*Mortoniceras*] *bourgeoisi* (d'Orbigny, 1850) extended into the lower part of the Santonian (in the table on p. 86) but makes no mention of this in the text. No specimens survive from M¹.

Far more widely recorded is *Texanites texanus* (Roemer, 1852), and this was taken by de Grossouvre as the index of the lower zone of the Santonian. Collignon (1948) correctly interpreted Roemer's species, excluding all European records which he referred to two distinct varieties, *hispanica* and *gallica*, regarded by subsequent workers as either subspecies or separate species. Material from M¹ in Aquitaine (de Grossouvre 1894, p. 80, pl. 16, figs. 2, 4; pl. 17, fig. 1) was referred to the variety *gallica* Collignon, 1948; the two figured syntypes from Aquitaine are actually from M² at Niel-le-Virouil (Charente-Maritime). The only other specimens seen from Aquitaine are two specimens labelled *Ammonites coniaciensis* Coquand, 1859 in the École des Mines Collection (now in the collections of the Faculté des Sciences, Lyons) *ex* Boucheron Collection, from La Valette (Charente), a locality referred to Assize M² by Arnaud, and a specimen in the Sorbonne Collections (now in the Université Pierre et Marie Curie) *ex* Toucas Collection, from M¹, at Rentes, Cognac. This specimen is a crushed *T. (Texanites)* sp. Apart from texanitids, there are poorly preserved *Placenticeras* from M¹ in the Arnaud Collection and records of *Baculites incurvatus* Dujardin, 1837 (e.g. de Grossouvre 1901).

In conclusion, it is not possible to define the position of the base of the Santonian in ammonite terms in Aquitaine with any great confidence. Only from occurrences elsewhere in France, for example Provence (Fabre-Taxy 1963) and the Corbières (Collignon and Bilotte 1983), is it possible to suggest that the appearance of *Texanites sensu stricto* is the best marker for the base of the stage, and even then the name of the zone is uncertain—the fauna may be that of de Grossouvre's *texanus* Zone, but the correct name for the European 'texanus' is unresolved.

It will be noted that there is no ammonite evidence on which to correlate the Aquitaine-Provençal-Corbières sequences with those in Touraine. At Villedieu-le-Château Jarvis *et al.* (1982) place no less than 3.5 m of glauconitic marls and bioclastic chalks in the Coniacian above the bed with the *serratmarginatus* Zone fauna.

CONVENTIONS

Location of specimens. The following abbreviations are used to indicate the repository of specimens mentioned in the text:

BM(NH)	British Museum (Natural History), London.
EMP	École des Mines Collections, formerly in Paris but now in the Université Claude-Bernard, Lyons.
FSL	Faculté des Sciences, Université Claude-Bernard, Lyons.
FSM	Faculté des Sciences, Le Mans.
FSR	Faculté des Sciences, Rennes.
GBA	Geologische Bundesanstalt, Vienna.
LGD	Laboratoire de Géologie, Institut Dolomieu, Grenoble.
LGHPM	Laboratoire de Géologie Historique et de Paléontologie, Marseille.
MNHP	Muséum National d'Histoire Naturelle, Paris.
NHMW	Naturhistorisches Museum, Vienna.
OUM	University Museum, Oxford.
SAS	South African Geological Survey, Pretoria.
SP	Collections of the Sorbonne, now in the Université Pierre et Marie Curie, Paris.

Suture terminology. The system of Wedekind (1916) as reviewed by Kullmann and Wiedmann (1970) is used here. E, external lobe; L, lateral lobe; U, umbilical lobe; I, internal lobe.

Synonymies. Only citations which include illustrations of material or important systematic, stratigraphic, or geographic information are included.

Dimensions. All diameters are given in millimetres. D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. c and ic refer to costal and intercostal dimensions respectively.

SYSTEMATIC PALAEOLOGY

- Order AMMONOIDEA Zittel, 1884
- Suborder AMMONITINA Hyatt, 1889
- Superfamily DESMOCERATACEAE Zittel, 1895
- Family DESMOCERATIDAE Zittel, 1895
- Subfamily DESMOCERATINAE Zittel, 1895
- Genus ONITSHOCERAS Reyment, 1954

Type species. *Onitshoceras matsumotoi* Reyment, 1954, p. 248, pl. 3, figs. 1, 2; pl. 5, fig. 7; text-fig. 1, by original designation.

Diagnosis. Moderately involute, inflated, whorl-section subquadrate. Ribs arise at umbilical shoulder and are of variable strength; all strengthen on ventrolateral shoulders and over venter. Sutures with narrow, deeply incised saddles.

Occurrence. Coniacian of Nigeria and France (?).

EXPLANATION OF PLATE I

Figs. 1-3. *Onitshoceras? ponsianum* (de Grossouvre, 1894). The holotype, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone, Assize L¹ of Arnaud, Pons (Charente-Maritime). SP unregistered (*ex* Arnaud Collection). Figured by de Grossouvre 1894, pl. 25, figs. 1a-b.

Figs. 4-6. *Placenticeras semiornatum* (d'Orbigny, 1850). MNHP 1896-27 (*ex* de Vibraye Collection), Craie de Villedieu, Upper Coniacian *Paratexanites serratomarginatus* Zone, of St. Fraimbault (Sarthe).

All figures $\times 1$.



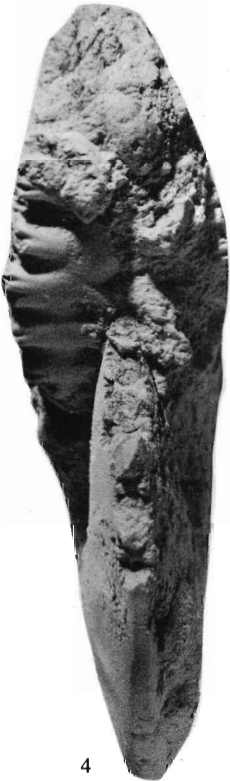
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Onitshoceras? ponsianum (de Grossouvre, 1894)

Plate 1, figs. 1-3; Plate 3, figs. 1-3; text-fig. 14B

1894 *Desmoceras ponsianum* de Grossouvre, p. 167, pl. 25, figs. 1, 5.1954 '*Desmoceras*' *ponsianum* de Grossouvre; Reyment, p. 249.1955 '*Desmoceras*' *ponsianum* de Grossouvre; Reyment, p. 19.

Types. The holotype, by original designation, is the original of de Grossouvre 1894, p. 167, pl. 25, fig. 1, from Assize L¹ of Arnaud near Pons, Charente-Maritime, SP (*ex* Arnaud Collection) (Pl. 1, figs. 1-3). The paratype (de Grossouvre 1894, p. 167, pl. 25, fig. 5) in the MNHP (Pl. 2, figs. 1-3) is from the 'Calcaires durs de la base de la Craie de Villedieu' at La Ribochère, near Villedieu-le-Château, Loir-et-Cher.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	85.5 (100)	36.0 (42.1)	40.3 (47.1)	0.89	17.9 (20.9)
Paratype	77.2 (100)	33.5 (43.4)	36.0 (46.6)	0.93	15.0 (19.4)

Description. The holotype is a fairly well-preserved internal mould. All but a small part of the last whorl is septate. Coiling involute, just over 70% of the previous whorl covered. Umbilicus small (20.9% of the diameter), shallow, with low, rounded, undercut wall on internal mould. Whorl section compressed; whorl breadth to height ratio 0.89, greatest breadth close to umbilical shoulder. Flanks flattened and convergent, ventrolateral shoulders rounded, venter somewhat flattened.

Ornament over most of phragmocone undetectable because surface of mould somewhat corroded. At the beginning of last whorl distant rounded prorsiradiate ribs appear to arise at the umbilical shoulder and strengthen markedly over ventrolateral shoulders and venter. Between these ribs are minor weak and irregular intercalated ribs, only visible on venter. Beginning of body chamber marked by broad, shallow, straight prorsiradiate constriction, followed by marked collar-rib. Most of surface of wholly septate paratype corroded and water-worn; at one point midway round outer whorl a shallow radial or feebly prorsiradiate constriction is visible, preceded by a weak, rounded collar rib. Suture line deeply and intricately subdivided; typically desmoceratid (Pl. 1, fig. 2; Pl. 2, fig. 2; text-fig. 14B).

Discussion. '*D.*' *ponsianum* shows coiling, whorl section, and ribbing that are closely comparable to those of *O. matsumotoi*. Whereas *matsumotoi* has a highly distinctive suture (Reyment 1954, p. 249, text-fig. 1b-c), that of *ponsianum* is typically desmoceratid; there are no constrictions in the former, whereas the latter has a few well-developed constrictions on the body chamber. Thus the two species are readily distinguished but both are very rare and whether *ponsianum* belongs to *Onitshoceras* is uncertain.

Occurrence. The holotype is from Assize L² of Arnaud at Pons (Charente-Maritime). Other ammonites from this division suggest the *tridorsatum* Zone. The paratype, from La Ribochère, cannot be precisely dated and may be from the *petrocoriensis*, *tridorsatum*, or *margae* Zones.

Family PACHYDISCIDAE Spath, 1922

[*nom. transl.* Spath 1923, p. 39 (*ex* Pachydiscinae Spath 1922a, p. 132)]

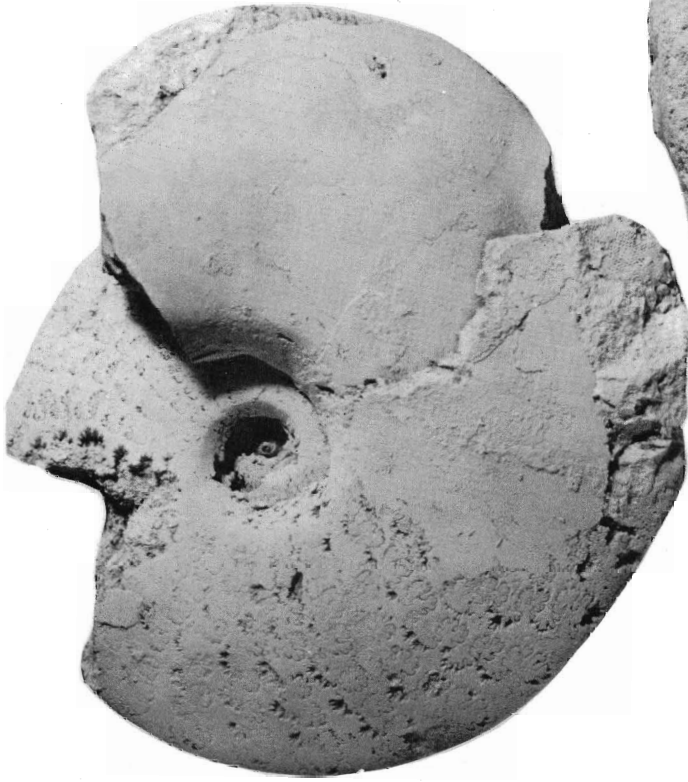
EXPLANATION OF PLATE 2

Fig. 1. *Placenticeras fritschi* de Grossouvre, 1894. FSR unregistered, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).

Figs. 2-4. *Menabonites* sp. Inner whorls of PM 121, Upper Coniacian *Paratexanites serratomarginatus* Zone of La Terragère, Saujon, Charente-Maritime.

Figs. 5-7. *Tongoboryceras hancocki* sp. nov. The holotype, MNHP 17172, Middle-Upper Coniacian of Saujon, Charente-Maritime.

All figures $\times 1$.



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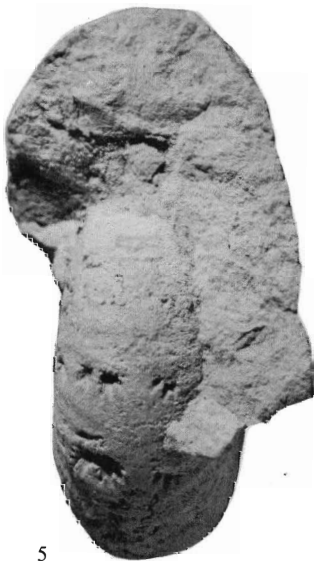
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Genus TONGOBORYCERAS Houša, 1967

Type species. *Lewesiceras tongoboryense* Collignon, 1952, p. 23, pl. 2, fig. 3.

Diagnosis. Moderately involute, inflated, with broadly rounded venter. Inner whorls smooth with strong, distant constrictions forming obtuse angle over venter. Later whorls bear crowded strong flexuous ribs most of which are primaries arising at umbilical shoulder singly or in pairs, with or without umbilical bullae. Suture deeply incised.

Discussion. Houša (1967, p. 42) originally separated *Tongoboryceras* from *Lewesiceras* Spath, 1939, and *Menabonites* Houša, 1967, because of its regularly reniform whorl section, primary and secondary ribs of more or less equal strength, umbilical tubercles that are feeble or absent and absence of ventrolateral tubercles. Wright (1979, p. 316) also pointed out that the genus has a complex suture with long and relatively narrow elements as in *Pseudojacobites* Spath, 1922, is smooth to a much later stage than *Lewesiceras* and has strong constrictions forming a ventral angle rather than a smooth curve.

Occurrence. Upper Turonian to Coniacian, England, France, Austria, Madagascar, and Japan.

Tongoboryceras cf. *tongoboryense* (Collignon, 1952)

1952 *Lewesiceras tongoboryense* Collignon, p. 23, pl. 2, fig. 3.

1955 *Lewesiceras tongoboryense* Collignon, p. 25, pl. 2, fig. 3.

1965 *Lewesiceras tongoboryense* Collignon, p. 33, pl. 428, fig. 1772.

Type. The holotype, by monotypy, is the original of Collignon 1952, pl. 2, fig. 3 (ex Hourcq Collection) from the 'Coniacien Inférieur' of Tongobory, Madagascar (EMP collections).

Material. OUM KZ 19425, from the middle Coniacian *tridorsatum* Zone bioclastic limestones 2 km south-east of St. Georges-de-Cubillac, Charente-Maritime.

Description. Whorl section depressed, reniform, with whorl breadth to height ratio of 1.25, flanks and venter all broadly rounded, with high umbilical wall, undercut on mould. Coiling appears to have been quite involute. Narrow, prorsiradiate flexuous primary ribs arise from umbilical shoulder singly or in pairs, with or without feeble bullae, and accompanied by shorter, intercalated ribs, sweep strongly forwards across ventrolateral shoulder and cross venter with a broad convexity.

Discussion. Coronate depressed whorls distinguish this specimen from *Tongoboryceras hancocki* sp. nov., described below, and suggest comparison with the type species, *T. tongoboryense*.

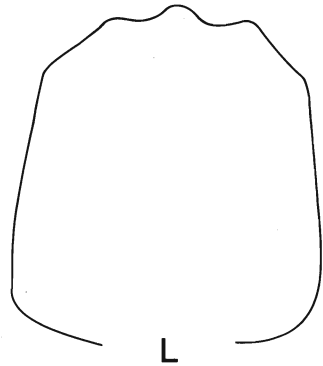
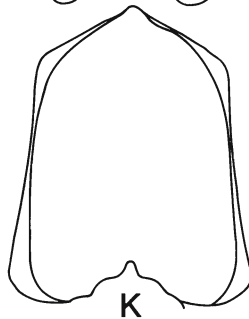
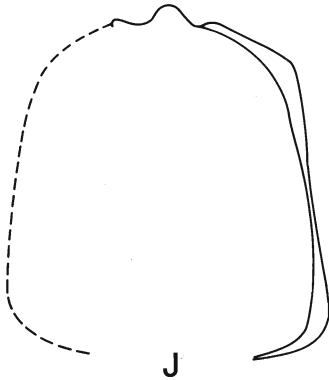
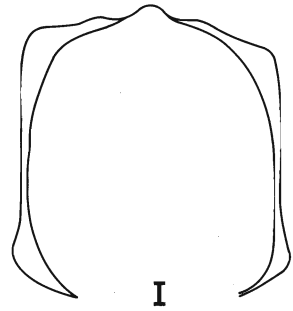
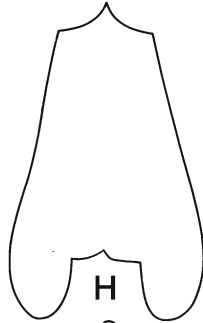
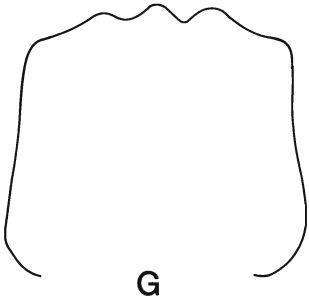
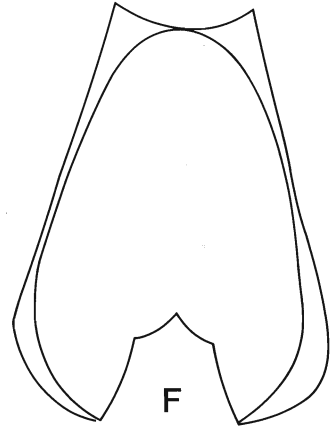
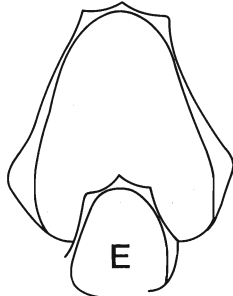
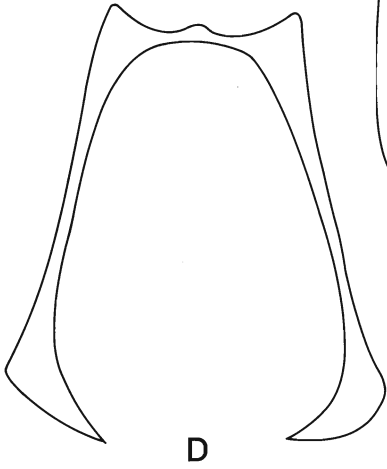
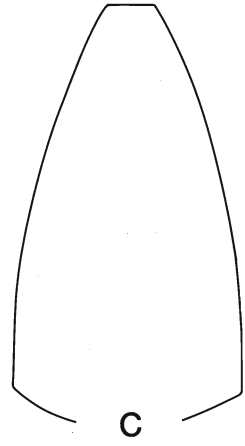
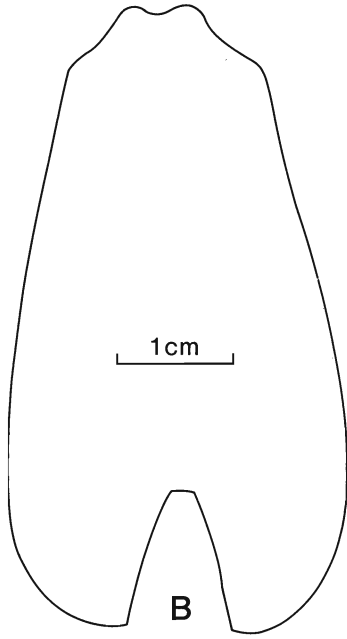
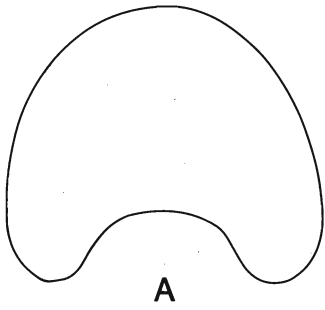
Occurrence. Middle Coniacian *tridorsatum* Zone and correlatives of northern Spain and northern Aquitaine.

Tongoboryceras hancocki sp. nov.

Plate 2, figs. 5-7; text-fig. 13A

Derivation of name. The species is named for Dr. J. M. Hancock of London.

TEXT-FIG. 13. Whorl sections of A, *Tongoboryceras hancocki* sp. nov., MNHP 17172. B, *Placenticerus semiornatum* (d'Orbigny, 1850), MNHP de Vibraye Collection no. 1896-27. C, *Pl. fritschi* de Grossouvre, 1894, FSR La Ribochère. D-F, H, *Forresteria* (*Harleites*) *petrocoriensis* (Coquand, 1859); D, phragmocone of a stout microconch, SP unregistered, ex Toucas Collection, from Aubas; E, phragmocone of a stout microconch, FSR 1905b; F, phragmocone of the original of de Grossouvre 1894, pl. 1, fig. 1, a compressed macroconch, SP unregistered, ex Arnaud Collection; H, body chamber of a microconch, FSR 1905a, taken at the beginning of the body chamber. G, *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867), the holotype of *P. (P.) rousseauxi* de Grossouvre, 1894, pl. 11, fig. 5, SP unregistered, ex Arnaud Collection. I, J, *P. (P.) dravidicum* (Kossmat, 1895), MNHP 1895-9, ex Durand Collection; I, section through phragmocone; J at beginning of body chamber. K, *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), MNHP 1896-27, de Vibraye Collection. L, *P. (P.) tridorsatum* (Schlüter, 1867), the original of *P. moureti* de Grossouvre, 1894, pl. 11, fig. 3, SP, ex Rejaudry Collection.



Holotype. MNHP 17172, from the Middle–Upper Coniacian of Saujon, Charente-Maritime.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
MNHP B17112	78.5 (100)	32.5 (41.4)	29.2 (37.2)	1.1	18.8 (24.0)

Description. The holotype is a well-preserved internal mould in white biosparite. All but a small part of the outer whorl is septate. Coiling involute, about 65% of previous whorl covered. Umbilicus comprises 24% of diameter, of moderate depth, with rounded umbilical wall and shoulder; whorl section depressed, oval, with greatest breadth close to umbilical shoulder; whorl breadth to height ratio 1.1; flanks and venter broadly rounded. Fifteen to seventeen weak umbilical bullae per whorl give rise to one, two, or three primary ribs, with additional long and short secondary ribs, giving a total of almost fifty ribs per whorl. They are low, fairly narrow, straight, and prorsiradiate on the umbilical shoulder but flex back and are feebly concave on mid to outer flank, sweeping forwards over ventrolateral shoulders to cross venter with a broad convexity. Only umbilical part of the body chamber preserved; it shows a coarsening of rather widely spaced umbilical bullae. Some interspaces appear to be slightly deeper than others but these scarcely merit the name of constrictions. Sutures deeply incised, interlocking, typically pachydiscid.

Discussion. *T. hancocki* is easily separated from the type species, *T. tongoboryense* (Collignon, 1952) from the Coniacian of Madagascar, which has a much more depressed reniform whorl section and flexuous ribs. *Lewesiceras westermanni* (Collignon, 1956b) (p. 33, pl. 428, figs. 1775, 1776) is also very depressed and has prominent umbilical bullae and crowded strong ribs. It too is from the Coniacian of Madagascar. *T. rhodanicum* (Roman and Mazeran, 1913) (p. 18, pl. 1, fig. 10; see Wright 1979, p. 316, pl. 6, figs. 1, 7) an Upper Turonian (*Subprionocyclus neptuni* Zone) species known from both England and France has fewer, broader, less flexuous ribs, the primaries with prominent umbilical bullae and strong constrictions that cross the venter with a sharp angulation on the early whorls. As Wright (1979, p. 317) has noted, there is a prolonged early smooth stage in some individuals. *T. donovani* (Collignon, 1965) (p. 11, pl. 380, fig. 1645), from the Upper Turonian of Madagascar, has markedly differentiated primary and secondary ribs; the former number ten per whorl and are associated with feeble constrictions. *Ammonites draschei* Redtenbacher, 1873 (p. 123, pl. 30, fig. 1), referred to *Tongoboryceras* by Houša (1967, p. 42), is a Santonian *Nowakites* (Summesberger 1979, p. 138, pl. 8, figs. 33–36; text-figs. 23–25).

Occurrence. As for type specimen.

GENUS MENABONITES Houša, 1967

Type species. *Pachydiscus anapadensis* Kossmat, 1896, p. 90, pl. 16, fig. 2, by original designation of Houša, 1967, p. 41.

Diagnosis. Moderately evolute with depressed, reniform whorl section. Ornament consists of persistent umbilical bullae giving rise to groups of primary ribs with additional weaker, intercalated ribs. Constrictions with associated ribs present on internal mould. Some species develop ventrolateral tubercles on primary and some secondary ribs.

Discussion. Depressed whorl section throughout ontogeny and persistence of ribbing and tuberculation distinguish the genus from *Lewesiceras* Spath, 1939, and *Tongoboryceras* Houša, 1967, neither of which develop the ventrolateral tubercles of the type and some other species.

Occurrence. Upper Turonian and Coniacian, France, Madagascar, and Southern India.

Menabonites sp.

Plate 2, figs. 2–4

Material. P. Moreau collection no. 121, in the Université de Poitiers, from the Upper Coniacian *serrato-marginatus* Zone of La Terragère, Saujon, Charente-Maritime.

Description. The specimen is wholly septate. Nucleus at a diameter of 48 mm moderately involute with deep conical umbilicus and depressed, reniform whorl section (whorl breadth to height ratio 1.33). Ornament consists of low, feeble, rounded prorsiradiate ribs arising low on flanks or at umbilical shoulder, strengthened across the venter. Periodic weak constrictions are concave and prorsiradiate on flank but cross venter in smooth convex curve. They are preceded by a collar rib strengthened at umbilical shoulder into a feeble bulla and succeeded by weaker rib in some cases. Outer whorl at a diameter of approximately 110 mm rather worn. Coiling more evolute, with whorl breadth to height ratio of 1.4. There are indications that constrictions persist (shown by depressions in umbilical shoulder) and were preceded by strong ribs with weak bullae, with long and short ribs, strongest over venter, between constrictions.

Discussion. The inner whorls of this specimen resemble those of *T. tongoboryense* figured by Collignon in 1965*b* as his pl. 427, fig. 1772, but differ in the form of the constrictions over the venter which cross the siphonal line in a broad sweep rather than projecting in a marked angle.

The strong bullate collar-ribs and persistent constrictions also differentiate the specimen from other *Tongoboryceras*, being close to those of some *Menabonites* (e.g. Collignon 1952, pl. 1, fig. 3; pl. 2, figs. 1, 2), to which genus the specimen is tentatively referred.

Genus PACHYDISCOIDES Spath, 1922

Type species. *Sonneratia janeti* de Grossouvre, 1894, p. 145, pl. 22, fig. 4, by original designation by Spath 1922*a*, p. 124.

Diagnosis. Small, moderately involute with compressed oval to depressed reniform whorl section. Strong umbilical bullae give rise to pairs of strong, coarse, rounded primary ribs which, with accompanying intercalated ribs, pass straight across flanks, strengthening over venter.

Discussion. Small size and strong ornament suggest that *Pachydiscoides* may be a microconch like the tuberculate *Menuites* Spath, 1922, *Teshioites* Matsumoto, 1955, *Urawakites* Matsumoto, 1955, and *Pseudomenuites* Matsumoto, 1955. There is, however, no obvious macroconch genus with which it can be paired, and very few specimens are known, the type species being known from the holotype only. Absence of tubercles separates it from the microconch genera noted above; the only other comparable form is *Tuberodiscoides* Collignon, 1966, from the Santonian of Madagascar. This is very coarsely ribbed and flat-sided with a fastigiate venter and siphonal tubercle.

Occurrence. Coniacian of France. Santonian of Tunisia and Madagascar.

Pachydiscoides janeti (de Grossouvre, 1894)

Plate 13, figs. 1-4

- 1894 *Sonneratia janeti* de Grossouvre, p. 145, pl. 22, fig. 4.
 1907 *Sonneratia janeti* de Grossouvre; Pervinquière, p. 174.
 1921 '*Sonneratia*' *janeti* Grossouvre; Spath, p. 124.
 1952 *Pachydiscoides janeti* Gross; Collignon, p. 27, 86.
 1955 *Pachydiscoides janeti* De Grossouvre; Collignon, p. 29, 79.
 1957 *Pachydiscoides janeti* De Grossouvre; Wright, p. L377, fig. 494, 2*a-b*.

Holotype. By monotypy, the original of de Grossouvre 1894, p. 145, pl. 22, fig. 4, MNHP (unregistered) from the 'Calcaires durs de la partie inférieure de la Craie de Villedieu' of the 'Carrières de la Ribochère, Couture, Loir-et-Cher', ex Le Mesle Collection.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	43.2 (100)	23.5 (54.4)	20.3 (47.0)	1.16	12.8 (30.0)

Description. The holotype is a well-preserved internal mould in well-cemented biosparite. It retains half a whorl of body chamber. Coiling is moderately involute (about half the previous whorl covered) with a deep conical umbilicus. Whorl section depressed and reniform, with greatest breadth at umbilico-lateral tubercle in costal section and close to umbilical shoulder in intercostal section. Fourteen primary ribs per whorl arise as mere striae

on umbilical wall and strengthen into strong, sharp umbilical bullae that are massive on coronate inner whorls and accommodated in notches in umbilical seam of outer whorl. They decrease in strength and migrate outwards to an umbilico-lateral position around the outer whorl, and give rise to pairs of strong, coarse, rounded prorsiradiate ribs. These are accompanied by intercalated ribs that arise at point of bifurcation of primary ribs. They are occasionally linked to bullae by tenuous stria; there are a total of twenty-four ribs per whorl. All ribs sweep slightly forwards and strengthen over ventrolateral shoulders and venter where they are at their greatest strength and have flattened tops. Sutures too poorly preserved for description.

Discussion. The holotype is the only known specimen of this species. *P. pervinquieri* Spath, 1922 (*nom. nov. pro Pachydiscus* nov. sp. of Pervinquière, 1907, p. 174, pl. 7, fig. 11) was compared to *Pachydiscoides janeti* in some detail by Pervinquière. He pointed out that it differed from de Grossouvre's species in being compressed rather than depressed with a much wider umbilicus and rounded umbilical tubercles that are situated on the umbilical shoulder rather than being bullate and displaced outwards to an inner flank position. It is from the Santonian of Djebel Tiouacha, Tunisia.

P. hourcqi Collignon, 1952 (p. 26, pl. 3, figs. 1, 2; see also Collignon 1966, p. 28, pl. 466, figs. 1902-1904) from the Middle Santonian of Madagascar has a less-rounded whorl section, the umbilical tubercles are sited on the umbilical shoulder and are produced into spines, numbering only eight or nine per whorl and giving rise to strong, distant, rather than crowded ribs. *P. hourcqi arcuata* Collignon, 1966 (p. 30, pl. 467, fig. 1907) was differentiated from the type material of the species because of the very wide umbilicus, radially elongated umbilical tubercles and ribs that bifurcate on the outer flank. Its coarse, distant ornament immediately distinguishes it from *P. janeti*. *P. wrighti* Collignon, 1952 (p. 29, pl. 3, figs. 3, 4) is very compressed, coarsely and distantly ribbed, and immediately distinguishable from the present species; it is from the Middle Santonian of Madagascar, as is *P. carinatus* Collignon, 1966 (p. 30, pl. 467, fig. 1908). The latter species is equally distantly and coarsely ribbed, with a compressed triangulate whorl section, with markedly spinate umbilical bullae.

P. hourcqi tuberosa Collignon, 1966 (p. 31, pl. 468, fig. 1909) also from the Santonian of Madagascar, is said to have weak outer lateral tubercles, which would seem to exclude it from *Pachydiscoides* altogether.

Occurrence. As for type species.

Superfamily HOPLITACEAE H. Douvillé, 1890

[*nom. correct.* Wright and Wright, 1951, p. 21 (*pro* Hoplitida Spath, 1922b, p. 95, *nom. transl. ex* Hoplitidae Douvillé, 1890, p. 290)]

Family PLACENTICERATIDAE Hyatt, 1900

[= Hypengonoceratinae Chiplonkar and Ghare, 1976, p. 2; Baghiceratinae Chiplonkar and Ghare, 1976, p. 3]

Genus PLACENTICERAS Meek, 1876

[see Kennedy and Wright 1983, p. 869 for synonymy]

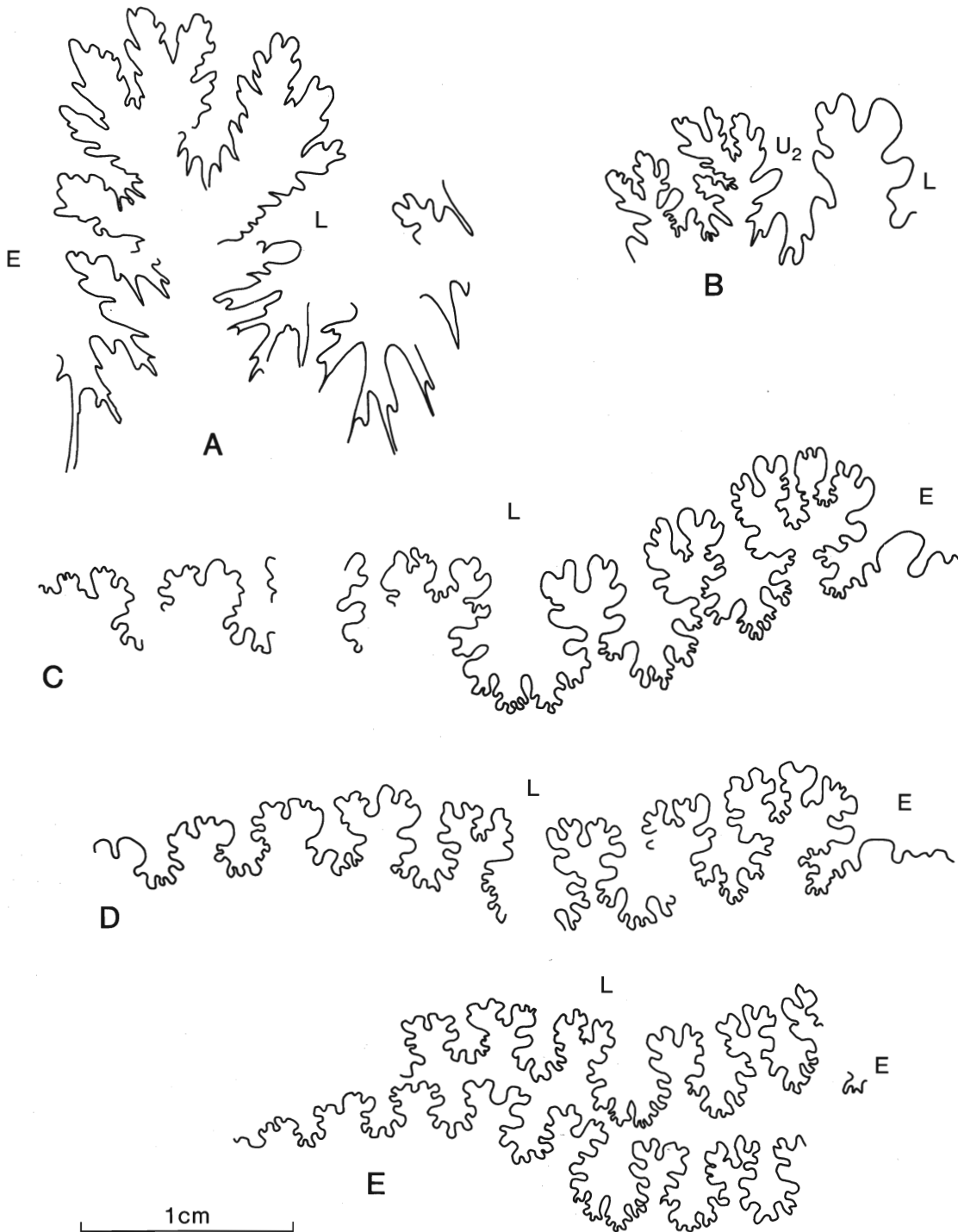
Type species. *Ammonites placenta* DeKay, 1828, p. 278, by original designation by Meek, 1876, p. 462.

Discussion. Kennedy and Wright (1983) have recently provided diagnoses of the genera of Placenticeratidae, and outlined the difficulties encountered in any attempt to subdivide the mainstream stock of the family. Two species only are known from the Coniacian of France, and these are represented by only a few specimens. Observations are correspondingly brief.

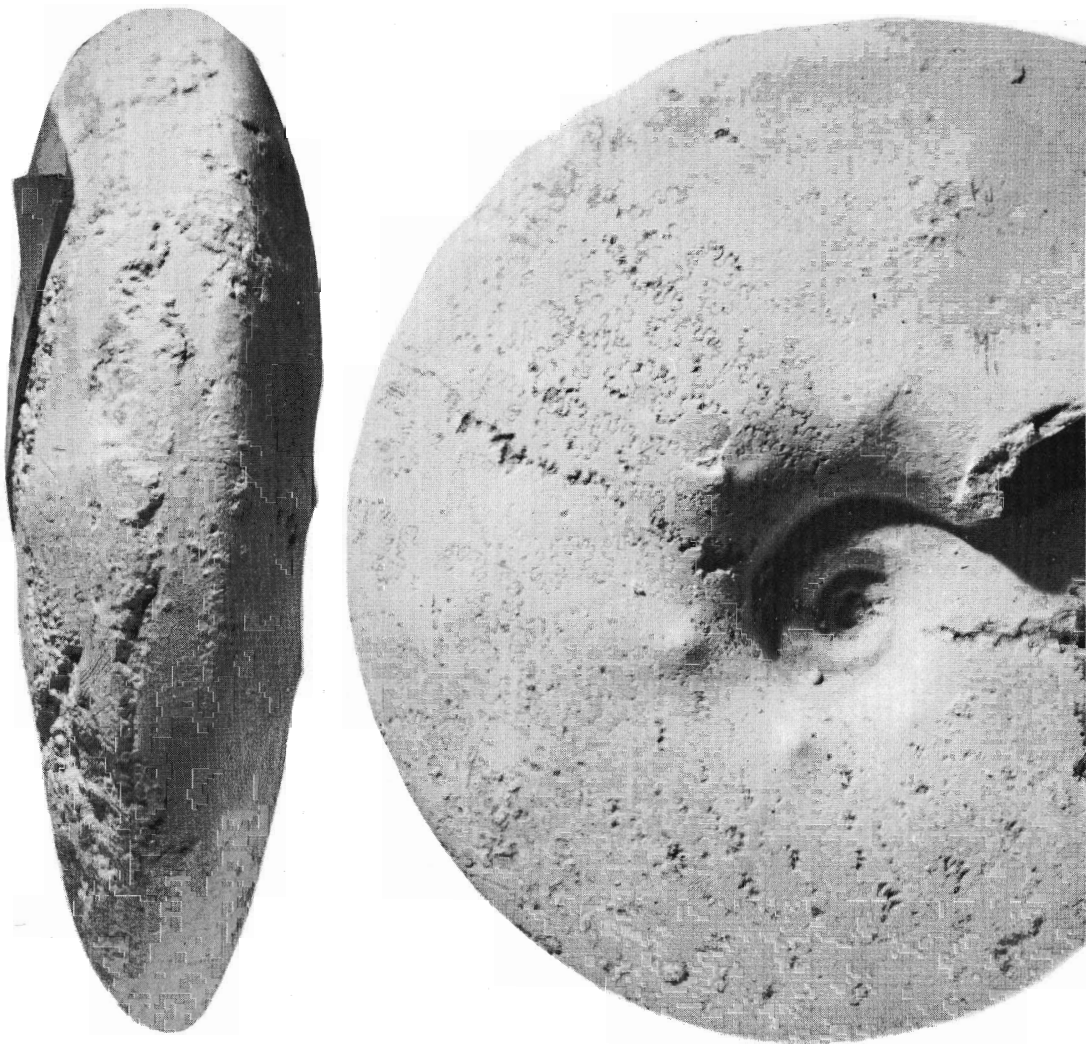
Occurrence. Upper Cenomanian to Maastrichtian. World-wide.

Placenticeras fritschi de Grossouvre, 1894

Plate 2, fig. 1; Plate 3, figs. 4, 5; text-figs. 13c, 14c-e, 15



TEXT-FIG. 14. External sutures of A, *Tongoboryceras hancocki* sp. nov., MNHP 17172. B, *Onitshoceras? ponsianum* (de Grossouvre, 1894), original of de Grossouvre 1894, pl. 25, fig. 5, MNHP unregistered. C-E, *Placenticerus fritschi* de Grossouvre, 1894, FSR La Ribochère.



TEXT-FIG. 15. *Platiceras fritschi* de Grossouvre, 1894. Cast of the missing lectotype (EMP Collections), original of de Grossouvre 1894, pl. 5, fig. 1, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher), $\times 1$.

- ?1843 *Ammonites vibrayanus* d'Orbigny; Geinitz, p. 8, pl. 1, fig. 8.
 ?1849 *Ammonites orbignyanus* Geinitz, p. 114, pl. 4, fig. 1.
 ?1863 *Ammonites orbignyanus* Geinitz; Drescher, p. 330, pl. 8, fig. 1.
 ?1872 *Ammonites orbignyanus* Geinitz; Geinitz, p. 188, pl. 36, fig. 5.
 ?1872 *Ammonites d'orbignyanus* Gein.; Fritsch, p. 36, pl. 10, figs. 4, 5; pl. 11, fig. 2.
 ?1891 *Ammonites orbignyanus* Geinitz; Langenhan and Grundy, p. 9, pl. 2, fig. 8.
 ?1893 *Ammonites (Platiceras) D'Orbignyanus* Gein.; Fritsch, p. 75, fig. 53.
 1894 *Platiceras fritschi* de Grossouvre, p. 124, pl. 5, figs. 1, 2; text-fig. 52.
 ?1897 *Ammonites (Platiceras) D'Orbignyanus* Gein.; Fritsch, p. 36, fig. 18.
 ?1900 *Platiceras orbignyanum* Gein.; Sturm, p. 58, pl. 3, fig. 4.
 ?1913 *Platiceras Orbignyanum* Gein. spec; Scupin, p. 96, pl. 3, fig. 10.

Types. The species is based on three French syntypes: a juvenile (de Grossouvre 1894, p. 127, pl. 5, fig. 2) and a larger specimen (p. 127, pl. 5, fig. 1) from the Calcaires Durs La Ribochère at La Ribochère, Loir-et-Cher, and

a third specimen from Assize L¹, Middle Coniacian, *Peroniceras tridorsatum* Zone of Jonzac, Charente-Maritime. De Grossouvre also refers the originals of *A. d'Orbigny* Geinitz of Fritsch, 1872, p. 36, pl. 10, figs. 4-5; pl. 11, fig. 2, from the Priesener Schichten of Lenešice and the Chlomeker Schichten of Tannenberg, Czechoslovakia, to the species these too ranking as syntypes. Only the Jonzac specimen (SP unregistered) has been traced, but there are casts of the two-figured French specimens in the collections of the EMP and FSR, indicating that the originals are in the SP Collections, although they have not been traced to date. The original of de Grossouvre 1894, pl. 5, fig. 1, is herein designated lectotype of the species.

Material. SP: four of Arnaud's specimens, one from Jonzac, La Boulinerie, three from Saujon (one precisely localized as 'Pompierre', another as La Moulière). All are from Assize L¹, Middle Coniacian, *P. triorsatum* Zone, as is OUM KZ13454 from Antignac (Charente-Maritime). There is also a poor fragment, best identified as *P. cf. fritschi*, from L¹ at Jonzac, La Boulinerie. MNHP: a fragment from the Calcaires Durs de La Ribochère of Villedieu-le-Château, as is a rather better FSR specimen labelled 'La Ribochère, 1904'.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Lectotype (cast)	132.0 (100)	39.0 (29.7)	59.5 (45.1)	0.66	25.8 (19.5)
Paralectotype (de Grossouvre, 1894, pl. 5, fig. 2)	56.0 (100)	— (—)	28.8 (50.4)	0.35	7.9 (14.1)
SP, Arnaud Coll., Saujon, la Pompierre	150.0 (100)	—	67.5 (45.0)	—	29.8 (19.9)
FSR	106.5 (100)	— (—)	45.0 (42.3)	—	17.3 (16.2)

Description. The earliest stages seen are represented by the paralectotype from La Ribochère (de Grossouvre, 1894, pl. 5, fig. 2). The available casts are defective; at a diameter of around 50 mm, coiling is very involute, with about 70% of previous whorl covered; umbilicus small (14% of diameter), shallow, and crater-like with flattened sloping wall, sharp umbilical rim. Whorl section compressed, with whorl breadth to height ratio of approximately 0.35; greatest breadth at umbilical shoulder; inner flanks broadly rounded, outer flanks flattened, converging to narrow venter. Ventrolateral shoulders sharp, with venter sulcate at smallest diameter visible, becoming flattened later. Ornament very weak; ten tiny conical umbilical tubercles per whorl at umbilical shoulder were probably connected by feeble straight riblets or growth striae (preservation is defective) to approximately twice as many concave ribs on outer third of flank which decline before reaching ventrolateral shoulder.

The Saujon specimen (Pl. 3, figs. 3-5) has even more compressed inner whorls linked to an outer whorl that is more compressed and feebly ribbed than the lectotype. On the outer whorl of the latter the umbilical wall is rounded and feebly convex, umbilical shoulder broadly rounded, venter broader, arched, with blunt ventrolateral shoulders. Ornament consists of conical to bullate umbilical tubercles, seven or eight per whorl. They migrate out from the umbilical shoulder on septate part of outer whorl of lectotype, becoming markedly bullate and declining in strength on body chamber of both this and the Saujon specimen. Low, broad prorsiradiate straight ribs sweep across inner and middle flank and strengthen into concave crescentic ribs on outer flank, but decline and disappear before reaching ventrolateral shoulder. There are no ventrolateral clavi. Suture follows typical sagging course, with eight or nine saddles in external part (text-fig. 14C-E).

Discussion. The available specimens are all rather feebly ornamented with only weak umbilical tubercles and crescentic ribs, a morphology seen in variants of many *Placenticeras* species. Several names have been applied to mid-Cretaceous *Placenticeras* from Europe. The earliest of these is *A. polyopsis* Dujardin, 1837, a Santonian species recently revised by Kennedy and Wright (1983). It differs from *P. fritschi* in having strong inner and outer ventrolateral tubercles at a relatively small size (e.g. de Grossouvre 1894, pl. 5, fig. 3) rather than crescentic ribs. Macroconchs and microconchs both have umbilical tubercles that migrate to a mid-lateral position at maturity and are stronger than in *P. fritschi*. Microconchs develop very evolute coiling and a subquadrate whorl section.

The Upper Coniacian. *P. semiornatum* (d'Orbigny, 1850), discussed fully below, is also easily distinguished by the absence of umbilical bullae, crescentic ribs that migrate outwards and turn into rounded or bullate inner ventrolateral tubercles on the body chamber with twice as many outer ventrolateral clavi.

P. orbignyianum (Geinitz, 1849) (p. 114, pl. 4, fig. 1) was based on a juvenile from the Kieslingwalde Sandstein of Silesia. De Grossouvre (1894, p. 126) remarked that 'la figure et description de Geinitz sont insuffisantes pour définir son espèce avec précision', and one can only endorse this view.

P. memoriaschloenbachi Laube and Bruder, 1887, p. 221, pl. 23, fig. 1, is the name given to Upper Cenomanian–Turonian *Placenticeras* in western and central Europe. The original figures show it to have ten small, spirally elongate umbilical tubercles, no crescent ribs on the outer flank, and a very narrow venter with sharp ventrolateral shoulders to a large size. These differences may in part reflect post-mortem crushing of the specimen.

P. kharesmense Lahusen, 1884 (p. 134, pl. 2; pl. 3, fig. 1) (see also Arkhanguelsky, 1916, p. 40, pl. 6, fig. 5; pl. 7, fig. 1) is a further Turonian species, originally described from Turkestan. It differs from the present species most obviously in the development of distinct ventral clavi.

P. kysylcumense Arkhanguelsky, 1916 (p. 45, pl. 7, figs. 4–7) is also from the Turonian of Turkestan, and may well be no more than a robust, strongly ornamented microconch of *kharesmense*. It differs from the material described here in having much stronger umbilical tubercles giving rise to pairs of ribs which develop into lateral tubercles that migrate to an inner ventrolateral position, with twice as many outer ventrolateral clavi also present.

P. pseudorbignyianum Hyatt, 1903 (p. 242 = *A. syrtalis* var. *orbignyana* of Schlüter, 1872, p. 46, pl. 15, figs. 3–5) from Kieslingwalde, Silesia, is based on a distorted juvenile 55 mm in diameter. The figure shows no umbilical bullae, but rounded mid-lateral tubercles on the first half of the outer whorl. The last half is smooth or has feeble ribs (the figure is poor) and no ventral clavi. Unless the figure is wholly inaccurate, the specimen is quite distinct from the present material.

The variable *P. kaffrarium* Etheridge, 1904 (p. 89, pl. 3, fig. 16) was based on a fragment of a rather strongly ornamented form from Umkwelane Hill near Mtubatuba, Zululand, where it occurred with a second essentially smooth species, *P. umkwelanense* Etheridge, 1904 (p. 89, pl. 3, figs. 17–20). Spath (1921, p. 247, pl. 31, fig. 2; p. 300) introduced a third species *P. subkaffrarium*, which he separated from *kaffrarium* on details of ornament. Subsequent work has shown that these forms range through the Lower and Middle Coniacian in Zululand (Kennedy and Klinger 1975), and represent but a single variable species (Klinger and Kennedy 1980, p. 303, fig. 7) which is markedly dimorphic (Klinger and Kennedy in preparation). The compressed, feebly ornamented juveniles of the species (up to 75 mm) are very close to the small paralectotype of *P. fritschi*. Specimens range from entirely smooth (other than growth striae), to those with crescentic ribs on the outer flank and entire sharp ventrolateral shoulders, to those in which a smooth stage is succeeded by one with up to ten tiny umbilical tubercles per whorl in addition. These grade in turn into individuals in which ornament strengthens after an initial virtually smooth stage to give pairs of low falcoid ribs that bear umbilical tubercles, a low lateral bulge or incipient tubercle, and many tiny ventral clavi. This leads eventually to coarsely ribbed specimens which have only eight umbilical tubercles (or even spines) per whorl giving rise to strong ribs, usually in pairs, which develop a massive lateral tubercle giving rise to two or three riblets that terminate in ventral clavi. Larger specimens corresponding in size to the lectotype of *P. fritschi* maintain this range of variation. Coarsely ribbed individuals reach maturity at less than 200 mm diameter, showing a decline in tuberculation on the body chamber, and appear to be microconchs. Other fragments, either smooth or still ribbed, remain septate to whorl heights of over 100 mm, suggesting a minimum adult diameter of 350 mm for presumed macroconchs.

EXPLANATION OF PLATE 3

Figs. 1–3. *Onitshoceras? ponsianum* (de Grossouvre, 1894). MNHP unregistered (ex Bourgeois Collection), paratype, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). Figured by de Grossouvre 1894, pl. 25, figs. 5 a–b.

Figs. 4, 5. *Placenticeras fritschi* de Grossouvre, 1894. SP unregistered (ex Rejaudry Collection), Saujon, La Pompière, Assize L¹ of Arnaud, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridoratum* Zone.

All figures × 1.



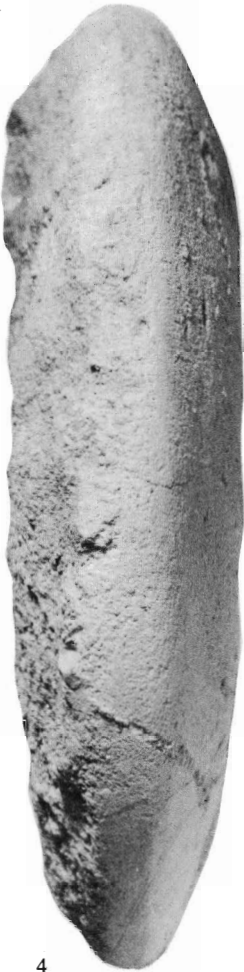
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2



3



4



5

P. kaffrarium and *P. fritschi* are obviously closely allied. If slender, feebly ornamented forms of the former are compared with the latter, they can be separated only on the combination of umbilical tubercles, crescentic ribs and entire ventrolateral shoulders in *fritschi*, whereas *umkwelanense* with umbilical tubercles and ribs always develop ventral clavi. Comparing larger specimens of similar inflation and ornament to the lectotype of *fritschi* it is again possible to find specimens of *umkwelanense* with similar umbilical tubercles and ribs, but these always have ventral clavi on the phragmocone.

A more general difference is the lack of strongly ornamented *Placenticer* associated with *fritschi* in Touraine and Aquitaine, suggesting that the overall range of variation may have differed, or even that *P. fritschi* (and hence *Proplacenticer*) did not show the strong dimorphism of *kaffrarium*. With only one (but not adult) large *P. fritschi* from Touraine and only one from Aquitaine it is impossible to resolve this, but the occurrence of strongly ribbed and tuberculate and feebly ornamented *Placenticer* in contemporary sediments in the Beausset Basin in Provence (*P. (Proplacenticer)* sp. nov. (??) aff. *syrtale* Morton of Collignon *et al.* 1979, p. 389, pl. 2, fig. 5, also OUM K16438, 16439, 16441, 16453) indicates this to be unlikely. The two species are maintained separate until better European material is available.

Of Coniacian material described from Madagascar, *Proplacenticer* aff. *fritschi* de Grossouvre var. *eboroensis* Collignon, 1965b (p. 38, pl. 430, figs. 1780–1781) has ventral clavi and is closer to *Placenticer kaffrarium*. *Proplacenticer satriense* Collignon, 1965b (p. 40, pl. 431, fig. 1782) has rather fewer umbilical tubercles and ventral clavi to a large diameter and more (ten) saddles in the external suture. It is from the Upper Coniacian.

Occurrence. Middle Coniacian, *Peronicer* *tridorsatum* Zone where precisely localized; Jonzac, Saujon, and Antignac (Charente-Maritime), Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). Coniacian of Czechoslovakia.

Placenticer semiornatum (d'Orbigny, 1850)

Plate 1, figs. 4–6; Plate 4, figs. 3–5, 7, 8; text-figs. 13b, 29d

1850 *Ammonites semiornatus* d'Orbigny, p. 212.

1955d *Ammonites (Placenticer) semiornatus* d'Orbigny; Sornay, figs. 1–3.

Types. Two specimens are listed under *A. semiornatus* in the d'Orbigny collection as no. 7179, and the locality is given as Tours. Sornay (1955d) designated the more complete of the two the lectotype.

Material. MNHP ex de Vibraye Collection no. 1896-27 from the Upper Coniacian *P. serratomarginatus* Zone of St. Fraimbault, Sarthe.

Dimensions (mm)	D	Wb	Wh	Wb: Wh	U
Lectotype	84.5 (100)	— (—)	41.2 (48.8)	—	— (—)
Paralectotype	— (—)	21.2 (—)	45.0 (—)	0.47	— (—)
MNHP 1896-27	106.5 (100)	26.0 (24.4)	47.3 (44.4)	0.55	— (—)

Description. The lectotype is a well-preserved internal mould in white biosparite. The last third of a whorl is body chamber. Coiling very involute with small, shallow umbilicus comprising approximately 12% of diameter. Of the preceding whorl 64% is covered; whorl section compressed, lanceolate, with whorl breadth to height ratio of 0.47; greatest breadth low on flanks, umbilical wall low and inclined outwards; the umbilical shoulder sharp, inner flanks gently rounded, outer flanks flattened and convergent. Ventrolateral shoulders sharp; venter narrow and tabulate. Phragmocone with distant low, broad, falcoid concave ribs at smallest diameter visible, extending across outer third of flanks, declining into mere striae that disappear by umbilical and ventrolateral shoulders. As diameter increases inner part of ribs weakens and outer part strengthens into crescentic, prorsiradiate outer lateral bulla on last quarter whorl of phragmocone. On body chamber bulla rotates from prorsiradiate-radial to parallel with venter, becoming in effect an inner ventrolateral clavus, linked to faint, low, broad, flexuous prorsiradiate rib that extends to umbilical shoulder in one direction and a low, broad, prorsiradiate rib that extends to ventrolateral shoulder in other, where feeble outer ventrolateral clavi develop from rib terminations. The wholly septate paralectotype shows the same features of ventrolateral ornament. Lectotype has excentric

umbilical seam, in part accentuated by distortion of phragmocone, and appears to be small adult. In contrast, MNHP 1896-27 is still septate at 105 mm diameter. It shows, however, the same low falcooid distant ribs on early phragmocone and development of ventrolateral tubercles at correspondingly greater diameters, the first clear inner ventrolateral tubercle (as opposed to rib) appearing at a diameter of 85 mm. Suture line follows typical sagging placenticeratid course, with nine saddles in external suture (text-fig. 29D).

Discussion. The small number of specimens of this species known precludes confirmation of the dimorphism suggested by the small size of the possibly mature lectotype and the larger and still wholly septate de Vibraye specimen.

This has been a largely neglected species, although d'Orbigny's original description, albeit brief, is valid (***13. semiornatus**, d'Orb., 1847. Espèce très-aplatie; à tours embrassants, lisses, tronqués sur la carène, et ornés de chaque côté de cette partie de tubercles obliques. Tours, route de Paris' (1850, p. 212)). Schlüter (1871–1876) does not appear to mention it, but de Grossouvre (1894, p. 128) placed it in the synonymy of *P. syrtale* de Grossouvre (*non* Morton) var. *milleri* von Hauer. *A. milleri* von Hauer, 1866 (p. 5, pl. 2, figs. 1, 2) is the type species of *Pseudoplacentieras* Spath, 1926, and the type specimens come from Steinbruch, Styria. They are all very poorly preserved, but have a larger umbilicus than the present species (24% of the diameter), an ornament of dense flexuose growth striae on the flanks, and ventrolateral clavi. There are an estimated nine of these per half whorl, and they are very elongate and lie at an angle of 45° to the venter in the best-preserved specimens, the clavi on opposing flanks corresponding in position and disappearing on the later parts of the body chamber. These features differentiate the species from the present one, although the age of *milleri* is not known. Hyatt (1903), does not mention the species. Sornay (1955d) refers *semiornatum* to *Diplacmoceras* (herein regarded as a synonym of *Placentieras*); it differs from the type species *D. bidorsatum* (Roemer, 1841, p. 88, pl. 13, fig. 5) which has numerous umbilical and inner flank ribs with tiny bullae and distant longer primary ribs terminating in inner ventrolateral clavi. *D. bidorsatum* has no outer ventrolateral tubercles and a narrow sulcate venter, while *D. canaliculatum* Hyatt, 1903 (p. 243) (= *A. bidorsatus* Schlüter, 1872, p. 51, pl. 15, figs. 6–8) has umbilical ribs and bullae on the body chamber, inner ventrolateral tubercles rather like the present form (but no outer ones), and a narrow, sulcate venter throughout.

The inner whorls of some *P. fritschi* and its allies are rather similar to the early stages of *P. semiornatum*, both having falcooid or crescentic outer flank ribs (e.g. de Grossouvre 1894, pl. 5, fig. 2a), but the former has a row of umbilical bullae and does not show the curious transformation of ribs into bullae and then clavi.

Occurrence. Tours (Indre-et-Loire), precise horizon unknown, but probably Santonian. Upper Coniacian *serratmarginatus* Zone, St. Fraimbault (Sarthe).

Superfamily ACANTHOCERATAEAE de Grossouvre, 1894

[*nom. correct.* Wright and Wright 1951, p. 24 (*pro* Acanthoceratida Hyatt 1900, p. 585, *nom. transl. ex* Acanthoceratidae Hyatt 1900, p. 585, *nom. correct. ex* Acanthoceratidés de Grossouvre, 1894)]

Family COLLIGNONICERATIDAE Wright and Wright, 1951

[*nom. subst. pro* Prionotropidae Zittel, 1895, p. 530. *Prionotropis* Meek, 1876, p. 453, *non* Fieber, 1853, p. 127; = *Collignoniceras* Breistroffer, 1947; = Prionocyclusidae Breistroffer, 1947, *ex* *Prionocyclus* Meek, 1876, p. 298, ineligible as family type]

Subfamily BARROISICERATINAE Basse, 1947

[= Diaziceratinae Basse, 1947, p. 159]

Genus and Subgenus FORRESTERIA Reeside, 1932

For synonymy, diagnosis, and discussion see Kennedy, Wright and Klinger 1983.

Forresteria (Forresteria) alluaudi (Boule, Lemoine and Thévenin, 1907)

Plate 8, figs. 4-9

- 1907 *Acanthoceras (Prionotropis) alluaudi* Boule, Lemoine and Thévenin, p. 12, pl. 1, figs. 6, 7; text-fig. 17.
 1979 *Neokanabicerias* sp. aff. *madagascariense* Collignon; Collignon *et al.*, p. 390, pl. 1, figs. 4, 5.
 1983 *Forresteria (Forresteria) alluaudi* (Boule, Lemoine and Thévenin, 1907); Kennedy, Wright and Klinger, p. 267, figs. 5-9, 10a-b, e-f, 11-14, 15a-b, 16-31, 33-34, 35c-e, 40d-e (with synonymy).

Types. Kennedy, Wright and Klinger (1983, p. 268) designated the smaller of the two syntypes, figured by Boule, Lemoine and Thévenin as their pl. 1, fig. 7, lectotype of the species. It is from Mont Carré, Madagascar. The larger paralectotype is pathological.

Material. One specimen only (LGHPM Collections), from Locality 2 of Collignon *et al.* (1979) in the Marnes de Ceyreste, north-east of Ceyreste in the Beausset Basin (Var): Middle Coniacian, *Peroniceras tridorsatum* Zone.

Discussion. This poorly preserved specimen was identified by Collignon *et al.* as *Neokanabicerias madagascariense* Collignon, 1965. Re-examination indicates it to be *F. (F.) alluaudi*. Kennedy, Wright and Klinger (1983) provide extensive illustration and discussion of the variation and ontogeny of this species, and a better preserved Zululand specimen is illustrated here for comparison (Pl. 8, figs. 7-9).

Occurrence. This is a Middle Coniacian species, where accurately dated. The geographic distribution extends from Zululand and Madagascar to Japan, Mexico, the U.S. Western Interior, Colombia (?), Peru, and perhaps Israel. It has not been previously recorded from Europe.

Subgenus FORRESTERIA (HARLEITES) Reeside, 1932

[= *Alstadenites* Reeside, 1932, p. 14; *Reesideoceras* Basse, 1947, p. 132]

Type species. *Reesideoceras gallicum* Basse, 1947, p. 133 (= *Ammonites petrocoriensis* Coquand, 1859, p. 995).

Diagnosis. Variable, early whorls as in *Forresteria sensu lato*. In compressed variants only umbilical bullae, ventrolateral and siphonal tubercles present. In others a strong lateral tubercle develops. Umbilical and lateral tubercles fuse into single umbilical bulla in middle growth, venter changes from fastigiate to sunken between high ventrolateral clavi which decline. End of body chamber smooth or ribbed with flat venter and sometimes loss of clavi.

Discussion. *Harleites* Reeside, 1932 (type species *Barroisiceras haberfellneri* var. *harlêi* de Grossouvre, 1894, p. 56, pl. 2, figs. 2, 8, by original designation) is based on specimens from the Lower

EXPLANATION OF PLATE 4

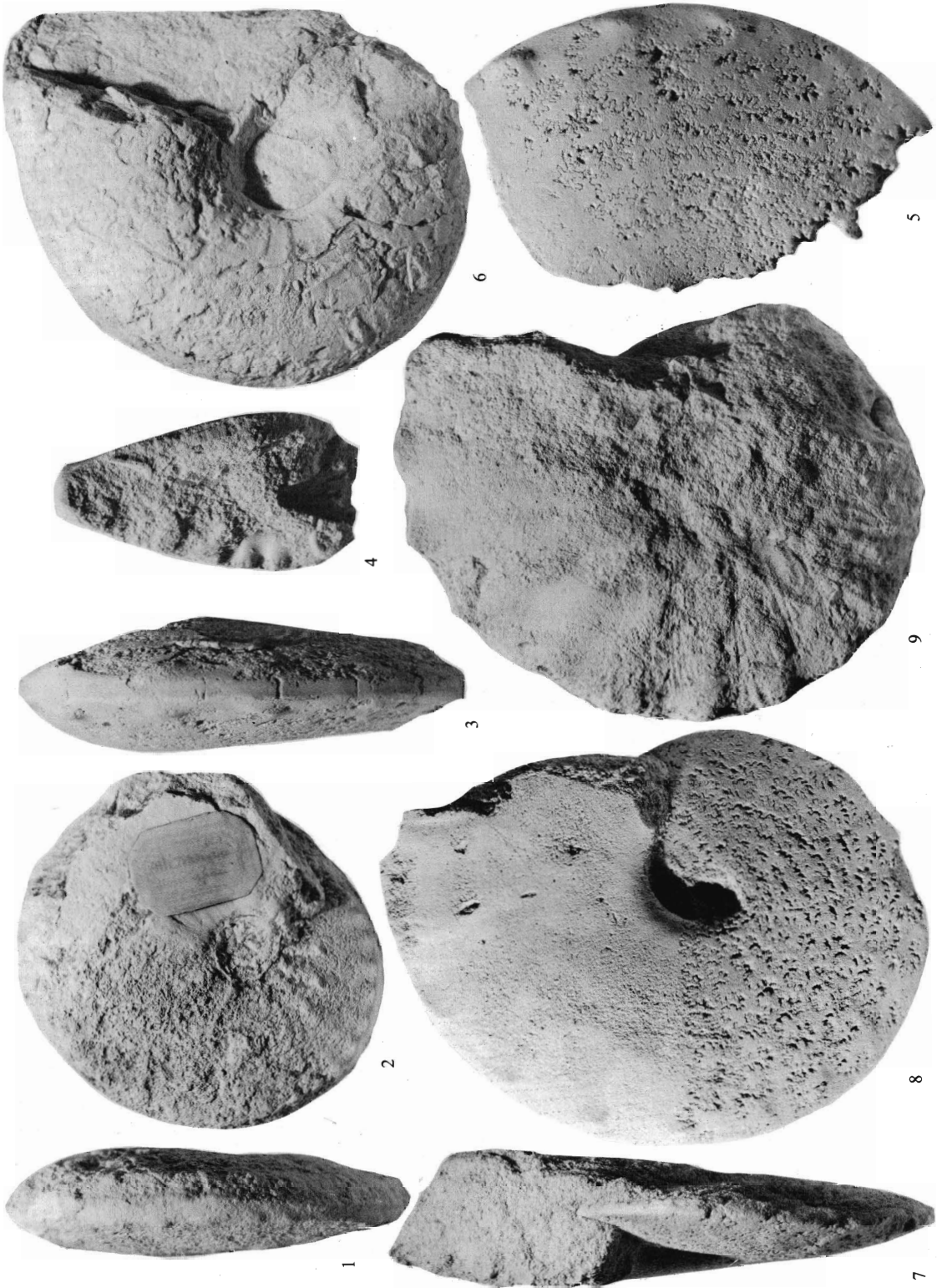
Figs. 1, 2. *Forresteria (Harleites) petrocoriensis* (Coquand, 1859). SP unregistered, Assize K of Arnaud, Lower Coniacian, *F. (H.) petrocoriensis* Zone of Montignac-sur-Vézère (Dordogne). A variant close to *Ammonites alstadenensis* Schlüter, 1876.

Figs. 3-5, 7-8. *Placenticeras semiornatum* (d'Orbigny, 1850). MNHP, d'Orbigny Collection no. 7179. 3-5, paralectotype, 7, 8, the lectotype, both from Tours. Horizon uncertain, but probably Santonian.

Fig. 6. *Onitshoceras? ponsianum* (de Grossouvre, 1894). MNHP unregistered (*ex* Bourgeois Collection), paratype, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). Figured by de Grossouvre 1894, pl. 25, figs. 5a-b.

Fig. 9. *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894). Unfigured paratype, SP unregistered, Assize L¹ of Arnaud, Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone of La Quina, near Lavalette (Charente).

All figures × 1.



Coniacian of the Dordogne, France. It was originally described as a subgenus of *Barroisicerias*, but Basse (1947) noted the presence of a tiny umbilical and inner lateral tubercle on the inner whorls of some of the type material which, taken with the more numerous but feeble ventrolateral and siphonal clavi, led her to treat it as a subgenus of *Forresteria*, a view followed by Wright (1957). Both these authors regarded *Alstadenites* Reeside, 1932 (type species *Ammonites alstadenensis* Schlüter, 1876, p. 151, pl. 40, figs. 13–16 by the subsequent designation of Kennedy, Wright and Klinger 1983, p. 259; lectotype, designated by Kennedy *et al.* op. cit. the original of Schlüter's pl. 40, figs. 13–16) as a synonym, a view followed here (indeed, the type species are synonymous).

Matsumoto (1969, p. 327), however, afforded *Harleites* full generic status (following Parnes 1964, p. 21), on the basis of the more involute shell and weak lateral ornament, with finer, more numerous and more persistent ventrolateral and siphonal tubercles.

Re-examination of de Grossouvre's material shows that the large, almost smooth holotype of *harlei* (de Grossouvre 1894, pl. 2, fig. 2; see Pl. 7, figs. 19–20) shows no trace of tubercles on the earliest part of the outer whorl (in part, perhaps, due to abrasion), but weak umbilical bullae appear on the body chamber (the specimen is septate to a diameter of approximately 60 mm). The same is true of the smaller paratype (de Grossouvre 1894, pl. 2, fig. 8; see Pl. 7, figs. 6–7), but there are specimens such as that figured in de Grossouvre's pl. 2, fig. 7 (see Pl. 7, figs. 10–11) which have an early stage (up to 25 mm) with tiny umbilical and stronger lateral tubercles before the smooth *harlei* stage. These connect, via specimens like de Grossouvre's var. *alstadenensis* (1894, pl. 2, fig. 4; see Pl. 7, figs. 12–13), to the variable but strongly ribbed and tuberculate phragmocones of typical *A. petrocoriensis* Coquand, 1859, p. 995 (= *R. gallicum* Basse, 1947, p. 133), the type species of *Reesideocheras* Basse, 1947. The largest French *Harleites* retain a sharp fastigiate venter with distinct ventral and siphonal clavi to the beginning of the adult body chamber, with renascent umbilical bullae, as noted above. Sadly, the venter of the holotype of *harlei* is damaged, so that the mature venter is not recognizable. The lectotype of *A. alstadenensis* shows, according to Schlüter's figure (pl. 40, fig. 14; see text-fig. 16), persistent ventrolateral clavi with a broadly arched, flattened venter. In the largest known *R. petrocoriensis* (de Grossouvre 1894, pl. 1, fig. 2; see Pl. 6, figs. 10–12), the siphonal clavi are lost at the beginning of the body chamber, and the ventral clavi are raised above a flattened venter, with all tubercles lost on the last quarter whorl.

It is concluded that the types of *Harleites harlei* lie in the same relationship to the type of *R. petrocoriensis*, and other comparably ribbed specimens, as does the holotype of '*H.*' *castellense* to the holotype of *F. (F.) forresteri* (= *alluaudi*) in the U.S., or '*Basseoceras*' *krameri* to *F. (F.) alluaudi* in South Africa, as described by Kennedy, Wright and Klinger 1983. *Reesideocheras* is thus a synonym of *Harleites*, the type species of the latter being *A. petrocoriensis* Coquand, 1859 = *A. alstadenensis* Schlüter, 1876, = *Barroisicerias haberfellneri* de Grossouvre, 1894 (*non* Hauer) (including varieties *harlei* and *alstedenensis* but not *desmoulinsi* de Grossouvre), = *Reesideocheras gallicum* Basse, 1947. *Harleites* (= *Reesideocheras*) is a subgenus of *Forresteria*, distinguished from *F. (Forresteria)* on the basis of smaller adult size, fusion of medio-lateral and umbilical tubercles, and early loss of siphonal clavi leaving a flat or concave venter on the body chamber, on the latter parts of which the ventral clavi may also disappear.

It is uncertain how many of the *Harleites* described by previous authors are referable to the subgenus as interpreted here; Japanese and Madagascan examples may well be no more than compressed and feebly ornamented variants of *F. (Forresteria)*. Because *F. (Forresteria)* and *F. (Harleites)* have very different geographical distributions they cannot be macro- and microconchs, indeed both show dimorphism within the type species of the two subgenera.

F. (Muramotoa) Matsumoto 1969 (type species *F. (M.) yezoensis* Matsumoto, 1969, p. 317, pl. 42, figs. 1–2; text-figs. 8–9, by original designation) is based on three specimens only, from the Coniacian of Hokkaido, Japan. The inner whorls are identical in style and proportions to those of *F. (Forresteria)*, but the ornament is rapidly lost at maturity, leaving a body chamber smooth but for a faintly serrated siphonal ridge. The holotype of the type species is only 75 mm in diameter, and the second Japanese species, *F. (M.) muramotoi* Matsumoto, 1969 (p. 320, pl. 43, fig. 1, text-fig. 11) is equally diminutive. If adult, *F. (M.) yezoensis* and *muramotoi* may represent a specialized micro-

morph offshoot of *F. (Forresteria)*. The fact that no such specimens are known outside Japan suggests them to be micromorph, rather than microconchs.

I cannot agree with Matsumoto (1969) that *Basseoceras* Van Hoepen, 1968 (*non* Collignon, 1965) is a synonym of *Muramotoa*. The type species *Basseoceras krameri* retains ventrolateral and siphonal clavi to a large size, and is simply a feebly ribbed and tuberculate, compressed and involute variant of *F. (F.) alluaudi*.

F. (Harleites) is easily distinguished from genera such as *Barroisiceras* de Grossouvre, 1894 (and subgenera), *Pseudobarroisiceras* Shimizu, 1932 and *Niceforoceras* Basse, 1948, on the basis of the presence of lateral tubercles at some stage of ontogeny. These are strong in some individuals.

Solgerites Reeside, 1932 (= *Piveteauoceras* Basse, 1947) may have lateral tubercles, but the body chamber becomes rounded, with persistent siphonal clavi in some, or strong ventrolateral nodes. It could be related to *F. (Forresteria)* of the *hobsoni* group, but having no good material for study, the position of the genus is unclear to me.

Occurrence. Lower and Middle Coniacian of France, Germany, Czechoslovakia, Colombia, Peru, ?Madagascar, ?Japan, and New Caledonia.

Forresteria (Harleites) petrocoriensis (Coquand, 1859)

Plate 4, figs. 1-2; Plate 5, figs. 1-11; Plate 6, figs. 1-9; Plate 7, figs. 1-20; Plate 9, figs. 1-4; Plate 21, figs. 2, 4; text-figs. 13D-F, H, 16, 18A, B, G

- 1859 *Ammonites petrocoriensis* Coquand, p. 995
 1872 *Ammonites neptuni* Gein.; Fritsch, p. 30 (*pars*), pl. 14, fig. 3a-b.
 1872 *Ammonites dentato-carinatus* Röm; Fritsch, p. 32 (*pars*), pl. 16, figs. 1 (?), 2a-b, ?non 3.
 1876 *Ammonites alstadenensis* Schlüter, p. 151, pl. 40, figs. 13-16.
 non 1885 *Buchiceras nardini* Fallot, p. 241, pl. 3, figs. 3, 4.
 1893 *Ammonites (Acanthoceras) dentatocarinatus* F. Röm.; Fritsch, p. 74, text-fig. 51.
 1894 *Barroisia haberfellneri* de Grossouvre, p. 51 (*pars*), pl. 1, figs. 1-5; pl. 2, figs. 1-5, 7-8 (*non* 6); text-fig. 29 (including vars. *alstadenensis* and *harlei* but not *desmoulinsi*).
 1895 *Acanthoceras dentatocarinatum* Fritsch; Jahn, p. 128.
 1903 *Barroisiceras haueri* Hyatt, p. 105.
 non 1904 *Barroisiceras haberfellneri* F. v. Hauer sp. var. *Alstadenensis* (Schlüter) Grossouvre; Solger, p. 170, pl. 5, fig. 6; text-figs. 56, 57.
 non 1904 *Barroisiceras haberfellneri* F. v. Hauer sp. var. *Harlei* Grossouvre; Solger, p. 172, text-figs. 58-62.
 non 1907 *Schloenbachia (Barroisiceras) haberfellneri* von Hauer var. *Harlei* de Grossouvre; Boule, Lemoine and Thévenin, p. 24, pl. 4, fig. 4.
 1932 *Barroisiceras haberfellneri* (Hauer) s.s.; Reeside, p. 11 (*pars*).
 1932 *Barroisiceras haueri* Hyatt; Reeside, p. 11.
 1932 *Barroisiceras neptuni* (Fritsch and Schlönbach) (not Geinitz); Reeside, p. 12.
 1932 *Barroisiceras dentatocarinatum* (Fritsch and Schlönbach) (not Roemer); Reeside, p. 12.
 1932 *Barroisiceras petrocoriense* (Coquand); Reeside, p. 12.
 non 1932 *Barroisiceras nardini* (Fallot); Reeside, p. 12.
 1932 *Barroisiceras (Alstadenites) alstadenense* (Schlüter); Reeside, p. 12.
 non 1932 *Barroisiceras (Alstadenites) alstadenense* Solger (not Schlüter); Reeside, p. 12.
 1932 *Barroisiceras (Harleites) harlei* Grossouvre; Reeside, p. 13.
 1947 *Reesideoceras gallicum* Basse, p. 133.
 non 1947 *Reesideoceras camerounense* Basse, p. 137.
 1947 *Harleites harlei* de Grossouvre; Basse, p. 139.
 1947 *Harleites alstadenensis* Schlüter; Basse, p. 140.
 1957 *Forresteria (Reesideoceras) gallicum* Basse; Wright, p. L434, fig. 551, 3.
 1957 *Forresteria (Harleites) harlei* (de Grossouvre); Wright, p. L434, fig. 551, 4.
 non 1965b *Harleites harlei* de Grossouvre; Collignon, p. 69, pl. 445, fig. 1821.
 ?non 1969 *Harleites cf. harlei* (de Grossouvre); Matsumoto, p. 328, pl. 43, fig. 2; text-fig. 14.
 ?1981 *Barroisiceras haberfellneri* (Hauer); Gale and Woodroof, p. 558 (*pars*), pl. 1, figs. 1, 2 (not 4).
 1981 *Reesideoceras petrocoriense* (Coquand); Gale and Woodroof, p. 557, pl. 1, fig. 3.

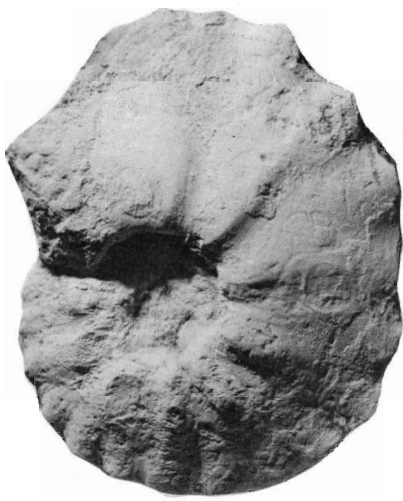
Types. The holotype, by monotypy, of *Ammonites petrocoriensis* Coquand, 1859, was refigured by de Grossouvre in 1894 as his pl. 2, fig. 5, and is preserved in the EMP Collections. It is from Montignac (Dordogne). The holotype of *B. haueri* Hyatt, 1903, p. 105, is in the SP Collections and is the original of de Grossouvre 1894, pl. 2, fig. 1*a-b*. It is from Gourde-de-l'Arche, near Périgueux (Dordogne), as is the holotype of *Barroisia habereffneri* var. *Harlei* de Grossouvre, 1894 (= *H. harlei* auct.) the original of his pl. 2, fig. 2. The lectotype, by subsequent designation by Kennedy, Wright and Klinger 1983, p. 259 of *A. Alstadenensis* Schlüter, 1876, is the original of Schlüter's pl. 40, figs. 13-16, from the 'Emscher-Mergel der Zeche Alstaden, südlich Oberhausen'. It is preserved in the collections of the Paläontologisches Institut, Bonn.

Material. This is the commonest ammonite in the French Coniacian. De Grossouvre (1894, p. 60) mentions more than a hundred specimens in the Arnaud, Boreau-Lajanadie, Desmond, Mouret, and de Grossouvre Collections. Many of these have proved untraceable, but I have seen or collected a comparable number of specimens from this region. Of the specimens figured by de Grossouvre, the originals of pl. 1, figs. 1-4 and pl. 2, figs. 1, 2, 4, 7, and 8 survive in the SP Collections. Most museum material is labelled, or is preserved in a manner indicating that it is from the lower part of Arnaud's Assize K around Périgueux (Dordogne), especially the railway cutting at Gourde-de-l'Arche, the environs of Les Eyzies-de-Tayac and Sarlat-la-Canéda (Dordogne): many specimens in the Sorbonne Collections, e.g. La Brauze, near La Bachellerie (Munier-Chalmas Collection), Aubas, near Montignac and others from St. Cirq, Brantôme, La Tour Blanche, Paulin, and La Quina (Dordogne) (Toucas Collection). Two specimens in the MNHP Collections are from Paulin (Dordogne) and the Sarladais. Specimens in the FSL Collections are labelled Bigond, Montignac, and Le Martinet, near Sauveterre-de-France (Dordogne). Two specimens in the FSR Collections (nos. 1905*a-b*) are labelled 'La Ribochère'; their preservation indicates that they are from the Calcaires Durs de La Ribochère at this locality. Two additional specimens in this collection (*ex* Seunes Collection) are labelled 'Couture', but are preserved in grey, patchily glauconitic limestone. An unlabelled specimen in the FSM (Guéranger Collection) is probably from La Ribochère.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
De Grossouvre, pl. 2, fig. 8	41.5 (100)	9.3 (22.4)	20.7 (49.9)	0.45	6.0 (14.4)
De Grossouvre pl. 1, fig. 4	c	35.0 (100)	14.0 (40.0)	1.0	7.0 (20.0)
" " "	ic		11.4 (32.6)	0.81	
FSR 1905 B		39.8 (100)	— (—)	—	7.5 (18.8)
FSR 1905 A		44.5 (100)	15.0 (33.7)	0.67	9.0 (20.2)
De Grossouvre pl. 1, fig. 1	c	64.0 (100)	22.8 (35.6)	0.76	12.6 (19.7)
" " "	ic		19.5 (30.5)	0.68	
De Grossouvre pl. 2, fig. 1	c	88.0 (100)	— (—)	—	13.2 (15.0)
" " "	ic		— (—)	—	
De Grossouvre pl. 2, fig. 2		63.0 (100)	15.0 (23.8)	0.45	6.7 (10.6)
De Grossouvre pl. 1, fig. 3	c	79.0 (100)	— (—)	—	15.0 (19.0)
" " "	ic		— (—)	—	
De Grossouvre pl. 1, fig. 2		105.5 (100)	36.5 (34.6)	0.65	19.0 (18.0)

EXPLANATION OF PLATE 5

Figs. 1-11. *Forresteria (Harleites) petrocoriensis* (Coquand, 1859). 1, SP unregistered (Arnaud Collection), Assize K of Arnaud, Lower Coniacian, *F. (H.) petrocoriensis* Zone at Gourde-de-l'Arche near Périgueux (Dordogne). 2-4, holotype, EMP Collections from Montignac-sur-Vézère (Dordogne), horizon as above, figured by de Grossouvre 1894, pl. 2, fig. 5. 5-7, SP unregistered (Arnaud Collection), Les Eyzies-de-Tayac (Dordogne), horizon as above. It is the original of de Grossouvre 1894, pl. 1, fig. 1, the holotype of *Barroisiceras haueri* Hyatt, 1903. 8, 9, MNHP unregistered (*ex* de Grossouvre Collection) from Paulin (Dordogne), horizon as above. It is close to *Ammonites alstadenensis* Schlüter, 1876. 10, SP unregistered (*ex* Arnaud Collection), horizon and locality as for fig. 1. The specimen was figured by de Grossouvre 1894, pl. 2, fig. 1. 11, SP unregistered (*ex* Arnaud Collection), details as for fig. 1. The specimen was figured by de Grossouvre 1894, pl. 1, fig. 3. All figures $\times 1$.



1



2



3



4



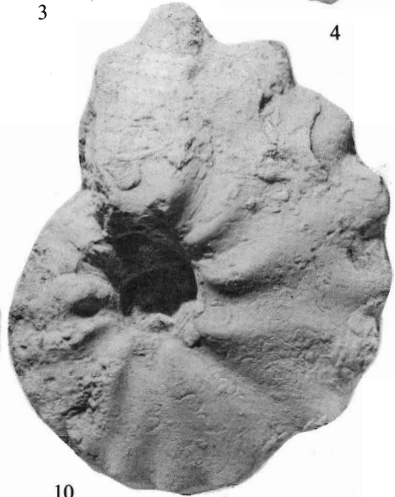
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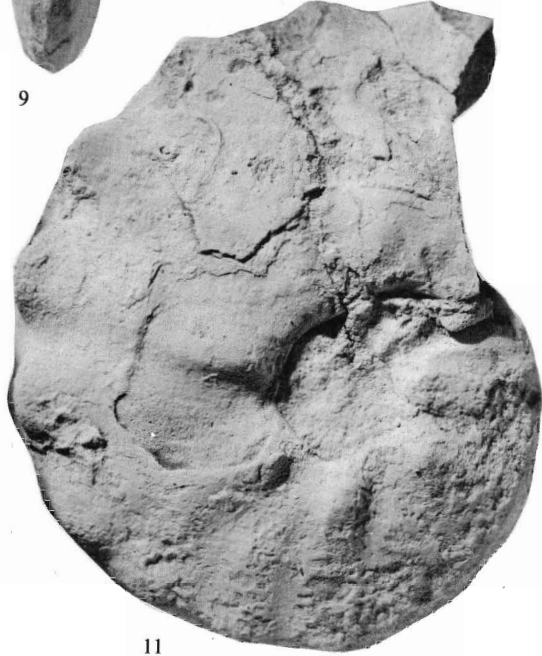
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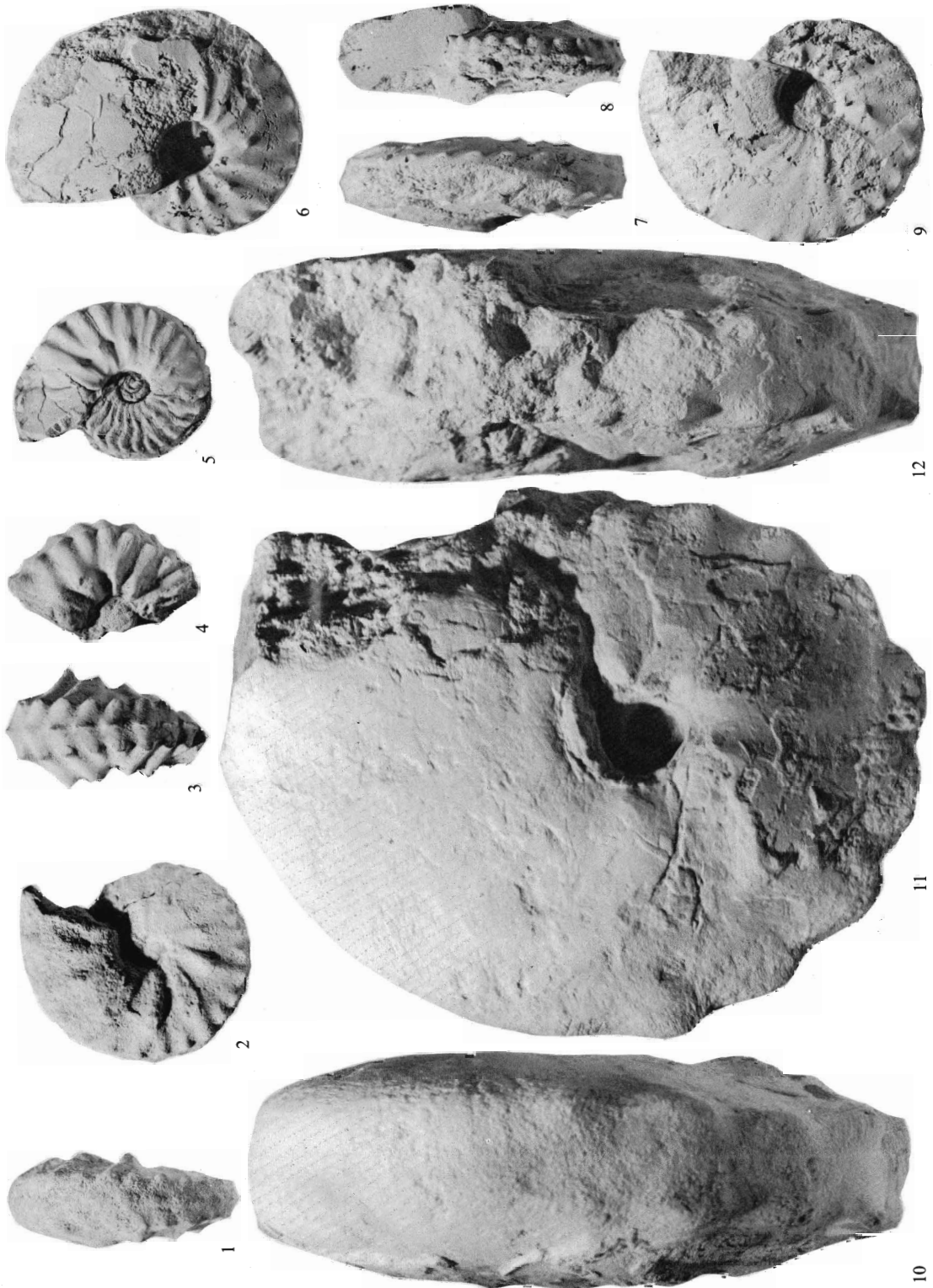
Description. (a) *Microconchs*: early whorls involute, over 75% of previous whorl covered. Umbilicus small, generally around 20% of diameter, of moderate depth. Umbilical wall flattened, umbilical shoulder narrowly rounded, whorl section compressed, with greatest breadth at lateral tubercles (where present) or low on flanks, close to umbilical shoulder. Inner flanks gently rounded, outer flanks flattened and convergent; venter fastigiate. An early feebly ornamented stage with flanks bearing feeble umbilical bullae and numerous ventrolateral and siphonal clavi may persist in the most compressed individuals (e.g. Pl. 7, figs. 6–7, the original of de Grossouvre 1894, pl. 2, fig. 8). Others develop narrow primary ribs with feeble umbilical bullae and stronger lateral tubercles separated by short, weak intercalated ribs, all of which bear delicate ventrolateral clavi with a corresponding row of siphonal clavi (Pl. 7, figs. 10–11, = de Grossouvre 1894, pl. 2, fig. 7). As whorl breadth to height ratio increases, individuals of this type grade into individuals in which ribs and tubercles are well developed with neither dominant (e.g. Pl. 6, figs. 6–9), and eventually to those with strong umbilical bullae and inner laterals that dominate the ribbing (e.g. Pl. 7, figs. 14–15; see also de Grossouvre 1894, pl. 2, fig. 3). As flank ribbing and tuberculation coarsens, so do ventrolateral and siphonal clavi. At a diameter of around 25–35 mm, the lateral tubercle is rapidly absorbed into a persistent umbilical bulla, and flanks are ornamented by low, weak, prorsiradiate ribs that terminate in ventrolateral clavi, siphonal clavi merging into an undulose siphonal ridge. No specimens preserve the adult body chamber complete; estimated adult diameter 50–60 mm. (b) *Macroconchs*: Juveniles show the same ornament as those of microconchs. Beyond a diameter of 35 mm, umbilical and lateral tubercles of strongly ornamented individuals merge into strong, crowded umbilical bullae that number nine or ten per whorl. They give rise to pairs of low, broad, sometimes feebly flexed primary ribs, with occasional intercalated ribs, all of which bear strong, ear-like ventrolateral clavi. The venter is initially fastigiate, but as diameter increases, ventral clavi rise above level of venter, siphonal clavi diminish in prominence and are lost by the end of phragmocone. Mature body chambers show rapid loss of ornament; the last quarter whorl is virtually smooth with broad, feebly concave venter with narrowly rounded shoulders. Suture line simple, relative proportions varying between compressed and inflated individuals. E rather simple; E/L broad and bifid; L narrow, L/U₂ rather broad and plump, U₂ narrow (text-fig. 18A, B, G).

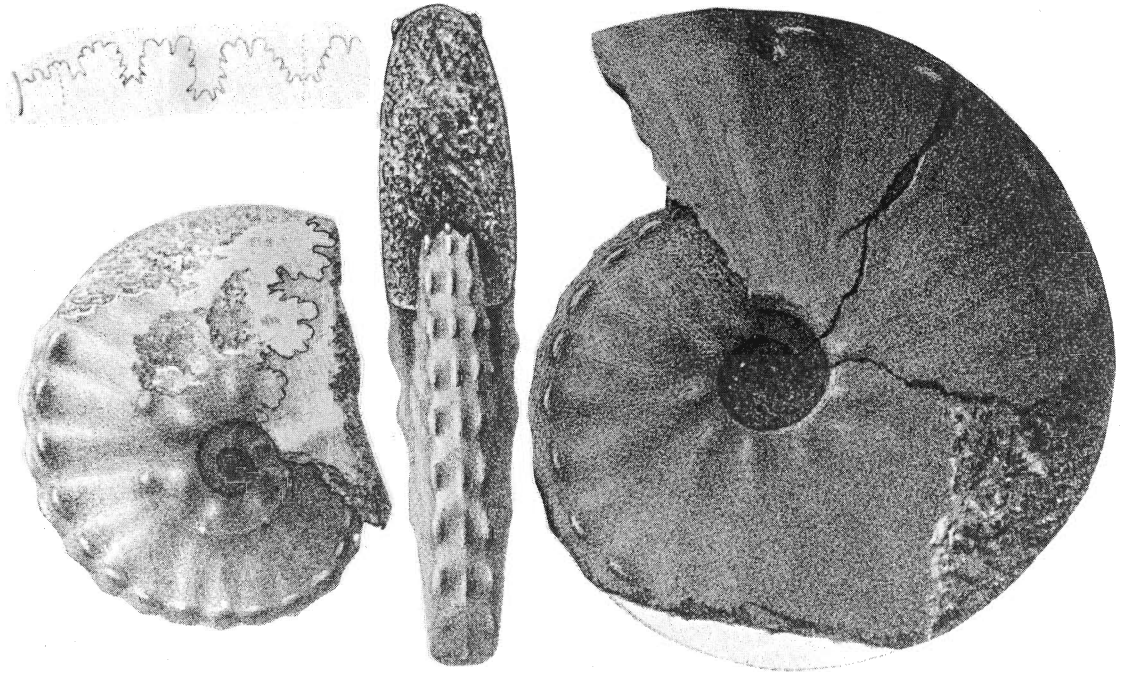
Discussion. Coquand introduced *A. petrocoriensis* in 1859 (p. 995), and although not figured, his description is valid: ‘*A. petrocoriensis*, H. Coq. Coquille légèrement renflée au milieu, de la forme de l’*A. syriacus*, costulée et tuberculeuse; ombilic très étroit; côtes épaisses, plates mal indiquées, partant du pourtour de l’ombilic ou elles commencent par un tubercle très saillant, se bifurquant ou se trifurquant, et s’effaçant pout ainsi dire sur la partie médiane du tour, et se terminant autour de dos par un tubercule très saillant. Dos tranchant, formé par une carène tuberculeuse. Chaque tubercule correspond aux tubercles dorsaux, c’est-à-dire que le dos présente trois séries de tubercles dont les médians tranchants et allongés. Montignac (Dordogne), de la collection de l’École de Mines.’

Von Hauer introduced his *A. haberfellneri* in 1866 (p. 300, pl. 1, figs. 1–4) and it and *A. petrocoriensis* have been confused ever since. Without illustrations it has proved impossible to determine how many passing references to *A. haberfellneri* refer to that species, which is the type species of *Barroisiceras* and has umbilical but no inner lateral tubercles (text-fig. 17), and which refer to *A. petrocoriensis*. *A. geinitzi* of Fritsch (1872, p. 30, *pars*; pl. 14, figs. 3a–b) (*non* Geinitz) and *A. dentatocarinus* Fritsch (1872, p. 32 (*pars*), pl. 16, figs. 1(?), 2a–b) from the Priesener Schichten of Bohemia are *F. (H.) petrocoriensis*, as in all probability are specimens mentioned but not figured by later workers. Jahn’s (1895) specimens of *Acanthoceras dentatocarinum* survive in the collections of the

EXPLANATION OF PLATE 6

Figs. 1–12. *Forresteria (Harleites) petrocoriensis* (Coquand, 1859). 1, 2, SP unregistered (*ex de Grossouvre Collection*), Lower Coniacian *F. (H.) petrocoriensis* Zone, Assize K of Arnaud at Aubas, near Montignac-sur-Vezère (Dordogne). It was figured by de Grossouvre 1894, pl. 1, fig. 4. 3, 4, NHMW 1890. XIII. 185. 5, NHMW 1890. XIII. 184, Priesener Schichten of Priesen, Bohemia, and identified by Jahn as *Ammonites dentatocarinus* Roemer, 1852. 6–9, FSR 1905a, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher), an almost complete microconch. 10–12, SP unregistered (*ex Arnaud Collection*), Gourde-de-l’Arche, near Périgueux (Dordogne), horizon as for fig. 1. It is a complete adult macroconch, and was figured by de Grossouvre 1894, pl. 1, fig. 2. All figures $\times 1$.





TEXT-FIG. 16. *Ammonites alstadenensis* Schlüter, 1876, lectotype, copy of Schlüter's pl. 40, figs. 13-16; the original is from the 'Emscher-Mergel der Zeche Alstaden, Südlich Oberhausen', $\times 1$.

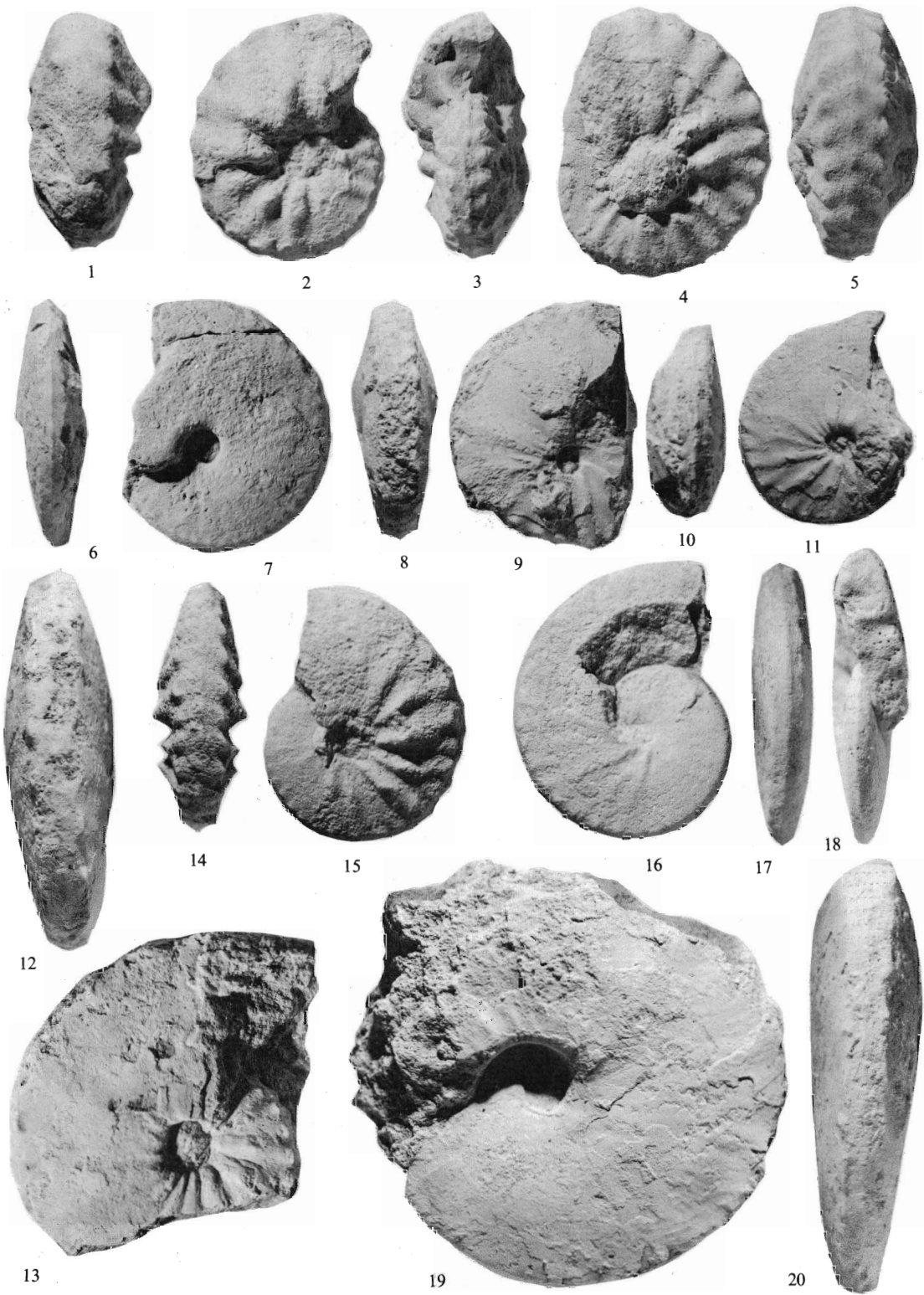
Naturhistorisches Museum, Wien, and confirm the occurrence of the species in this area (see Pl. 6, figs. 3-5; Pl. 9, figs. 1-2).

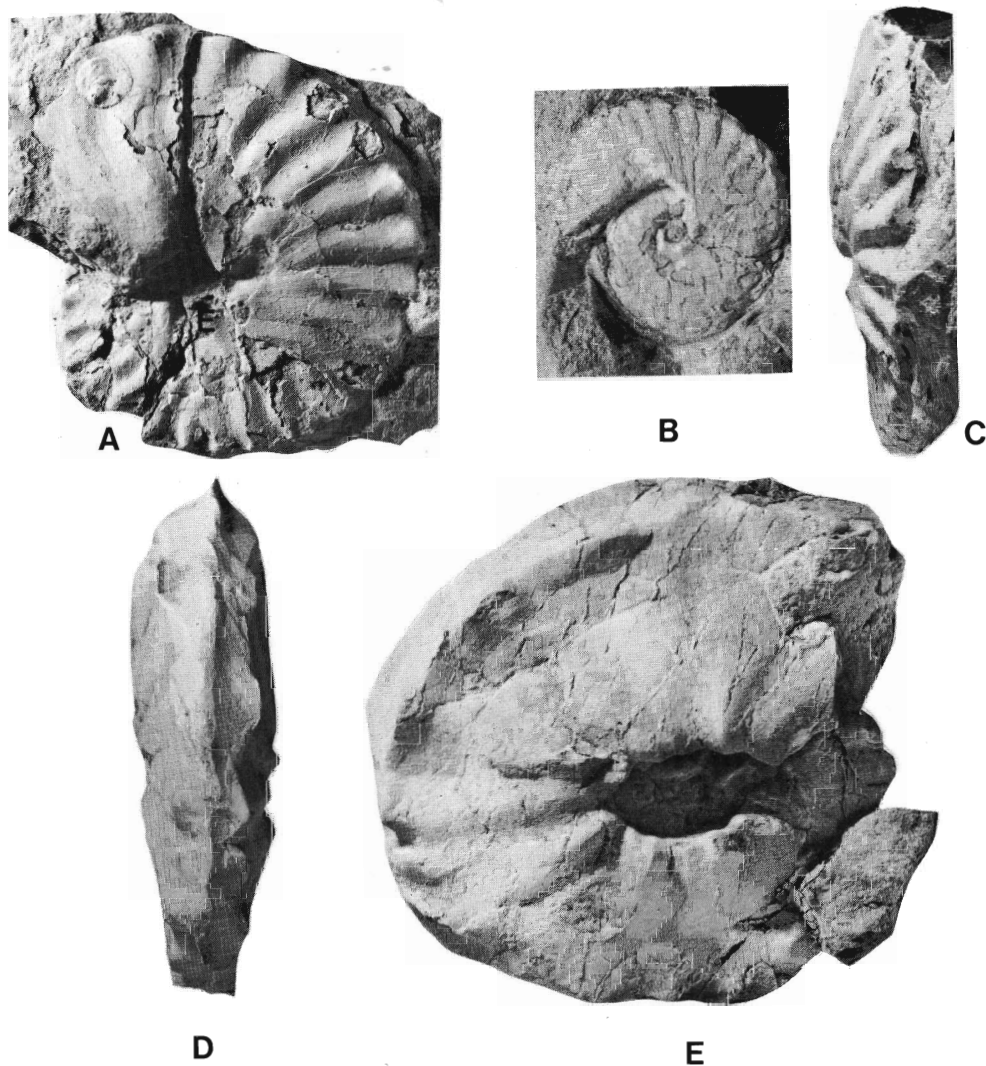
Buchiceras nardini Fallot, 1885 (p. 241, pl. 3, figs. 3-4) was based on specimens from the Grès Vert Sénonien of Dieulefit (Drôme) in the Slizewicz Collection. These have not been traced, but there is a cast of the larger of the two figured specimens in the SP Collections. The original is herein designated lectotype of the species (Pl. 29, figs. 3-4 shows the cast). De Grossouvre (1894, p. 59) believed it to be a synonym of his *Barroisia haberfellneri* (= *F. (H.) petrocoriensis* herein), but Fallot's figure and the cast show umbilical bullae only, a loss of ribs on the outer flank and parts of a suture line with entire saddles. It is certainly not *F. (Harleites)* nor *Barroisiceras*; the suture suggests *Tissotoides haplophyllus* (Redtenbacher, 1873) (see p. 123).

Ammonites alstadenensis Schlüter (1876, p. 151, pl. 40, figs. 13-16) (see text-fig. 16) is a synonym of *F. (H.) petrocoriensis*. As Schlüter states (explanation of pl. 40), his figure 15 is a further view of the

EXPLANATION OF PLATE 7

Figs. 1-20. *Forresteria (Harleites) petrocoriensis* (Coquand, 1859). 1-3; 4, 5, FSR unregistered (Seunes Collection), labelled 'Couture' (Loir-et-Cher) in a glauconitic limestone matrix. 6, 7, SP unregistered (ex Arnaud Collection), Lower Coniacian *F. (H.) petrocoriensis* Zone of Gourde-de-l'Arche near Périgueux (Dordogne), figured by de Grossouvre 1894, pl. 2, fig. 8 as the young of his var. *harléi*. 8, 9, same collection, horizon, and locality as 6, 7. 10, 11, also as 6, 7, figured by de Grossouvre 1894, pl. 2, fig. 7 as intermediate between the varieties *alstadenensis* and *harléi*. 12, 13 also as 6, 7, the specimen figured by de Grossouvre 1894, pl. 2, fig. 4 as var. *alstadenensis* Schlüter, 1867. 14, 15, MNHP unregistered, same horizon as 6, 7, the locality given as 'Sarladais' (Dordogne). 16-18, as 6, 7, at Montignac-sur-Vézère (Dordogne). 19, 20, as 6, 7, the holotype of de Grossouvre's var. *harléi* figured by him in 1894 as pl. 2, fig. 2. All figures $\times 1$.





TEXT-FIG. 17. A-E, *Barroisiceras haberfellneri* (Von Hauer, 1866). A, C, lectotype, original of Von Hauer 1866, pl. 1, figs. 1-2, Gosau Beds of Gams, near Hieflau, Austria; GBA 3464. B, original of Redtenbacher 1873, pl. 23, fig. 2b, GBA 3465, from the same locality. D, E, *Ammonites paeon* Redtenbacher, 1873, lectotype, original of Redtenbacher's pl. 23, figs. 3c-e, from the same locality. All figures $\times 1$.

inner whorls of the specimen shown in his figures 13 and 14; it is so similar to the holotype of *petrocoriensis* (given the different preservation and styles of illustration) and other French specimens to leave no doubt on this point. A label in the drawer containing de Grossouvre's figured specimens and inscribed in his hand reads: '*Ammonites petrocoriensis* Coq. tres voisine sinon identique à *Amm. alstadenensis* (Schl. Lettre du 30.9.1884).' De Grossouvre (1894, p. 51) placed *A. alstadenensis*, *A. paeon* Redtenbacher, 1873, *A. haberfellneri* Hauer, 1866, and *A. petrocoriensis* in synonymy, but used the name *haberfellneri* rather than *petrocoriensis* because 'sa diagnose n'était accompagnée d'aucune figure' (p. 56). This is nomenclatorially invalid, for not only was Coquand's species validly introduced, but *haberfellneri* belongs to a different species and genus, as noted above. De Grossouvre's

view has persisted, however, and the great majority of passing references to *B. haberfellneri* and its eponymous zone are based on his interpretation rather than Hauer's.

De Grossouvre admitted great variation in his *Barroisia haberfellneri* de Grossouvre (*non* Hauer) and named several varieties. Of these, his var. *desmoulinsi* has a continuous keel, simplified sutures, and is a tissotiid, best referred to *Metatissotia* Hyatt, 1903 (= *Dordiella* Reyment, 1958). In contrast, he correctly recognized a continuous variation from compressed, feebly ornamented forms that he named var. *harléi* (p. 56, pl. 2, figs. 7, 8; see Pl. 7, figs. 6–7) to those that were still very compressed but showed a brief stage with ribs, umbilical and lateral tubercles (his var. *alstadenensis* Schlüter, pl. 2, fig. 4; see Pl. 7, figs. 12–13). The two are linked by intermediates (his pl. 2, fig. 7; see Pl. 7, figs. 10, 11), and grade into progressively more strongly ornamented specimens. As described above, microconchs include individuals that are feebly ornamented throughout growth and those that have a strongly ornamented phase at the end of the phragmocone (e.g. Pl. 7, figs. 14, 15), as do macroconchs. The holotype of *petrocoriensis* appears to be an immature microconch, whereas the holotype of var. *harléi* and the lectotype of *alstadenensis* are incomplete macroconchs, as is the holotype of *Barroisiceras haueri* Hyatt, 1903 (= de Grossouvre 1894, pl. 1, fig. 1).

This wide range of intraspecific variation in both micro- and macroconchs together with the different diameters at which changes in ornament take place was taken by subsequent workers to indicate that more than one species was present and de Grossouvre's '*Barroisia*' *haberfellneri* (*non* Hauer) was split into no less than three genera or subgenera (see p. 48). To add to this confusion, feebly ornamented and compressed individuals of *Barroisiceras* and *F.* (*Forresteria*) have been placed in *Harleites* on the basis of whorl form, irrespective of sutures and tuberculation. Only when viewed in the context of the population of which they are a part does this become obvious, as shown by Kennedy, Wright and Klinger (1983) in their account of *F.* (*F.*) *alluaudi* (Boule, Lemoine and Thévenin, 1907).

F. (*H.*) *nicklesi* (de Grossouvre, 1894) (= *Barroisia nicklesi* de Grossouvre, 1894, p. 63, pl. 3, fig. 2) of which *B. sequens* de Grossouvre, 1894 (p. 64, pl. 3, fig. 1) is a probable synonym, and *B. boissellieri* de Grossouvre, 1894 (p. 65, pl. 3, fig. 3) a certain synonym, appears to have rather similar inner whorls to at least some *F.* (*H.*) *petrocoriensis*. In middle growth the two differ strikingly in that the fusion of umbilical and inner lateral tubercles gives a bulla that is displaced out to the inner flank in *nicklesi* rather than perched on the umbilical shoulder. Mature *nicklesi* develop narrow ribs and retain ventrolateral clavi, an ornament quite distinct from the essentially smooth, broad-ventered body chamber termination of *petrocoriensis*.

Basse (1947, p. 133) introduced the name *R. gallicum* citing a range of specimens in her synonymy. She regarded *A. petrocoriensis* Coquand, 1859, which she placed in this synonymy, as invalid, stating on p. 135 that: 'je ne crois pas souhaitable de l'attribuer à l'espèce ici décrite, son accident ne lui permettant pas d'être considéré comme le type d'une espèce.' The type is indeed malformed (Pl. 5, figs. 2–4), but this does not disqualify it as a type, and all the specimens referred with certainty to *gallicum* by Basse are *F.* (*H.*) *petrocoriensis*.

H. (?) *bruggeni* Basse, 1947 (p. 141, = *Barroisiceras haberfellneri* Brüggén (*non* Hauer), p. 730, text-fig. 10) is illustrated by a drawing of the suture line only; from the description it may be a feebly ornamented *F.* (*Forresteria*). *H.* (?) *manasoensis* Basse, 1947 (p. 141, pl. 9, fig. 5) is a smooth barroisiceratid of uncertain affinities, whilst *B. haberfellneri* var. *byzacenicum* Pervinquier (1907, p. 381), referred to *Harleites* by Basse (1947, p. 138), cannot be placed in any genus on the description alone, although it is a barroisiceratid. The *H. harlei* of Collignon (1965b, p. 69, pl. 445, fig. 1821) and Matsumoto (1969, p. 328, pl. 43, fig. 2; text-fig. 14) are compressed *F.* (*Forresteria*).

H. bentori Parnes, 1964 (p. 22, pl. 2, figs. 10, 12; text-figs. 4e, f, h), is a feebly ornamented and compressed *Barroisiceras*, probably no more than a variant of *B. neqarotense* Parnes, 1964 (p. 16, pl. 2, figs. 1–6; pl. 4, fig. 3; text-figs. 4a–c, i, m) as may be the ?*Harleites* sp. of Parnes (1964, p. 23, pl. 3, figs. 1–2).

R. caledonicum Collignon, 1977 (p. 9, pl. 5, fig. 7) is based on a single fragment from a presumed Coniacian horizon in New Caledonia. The ribs are much more delicate than those of *F.* (*H.*) *petrocoriensis*, the whorls subquadrate, the venter broad, and the tubercles very small.

Occurrence. This is the index species of the *F. (H.) petrocoriensis* Zone and occurs widely in Assize K of Arnaud in the Aquitaine Basin, especially in the Dordogne (Les Éyzies-de-Tayac, Sarlat-la-Canéda, and Périgueux areas). It also occurs in the Calcaires Durs de La Ribochère at La Ribochère, Couture, near Villedieu-le-Château (Loir-et-Cher)—de Grossouvre's Zone A, but the specimens are not precisely localized in this unit. The tiny '*Barroisiceras haberfellneri*' of Gale and Woodroof (1981, pl. 1, figs. 1, 2) from Dover, Kent, England, may be a *F. (H.) petrocoriensis*, while the species definitely occurs in north Germany (where it is recorded as *Ammonites/Barroisiceras/Harleites alstadenensis* Schlüter) and in the Priesener Schichten of Bohemia (Czechoslovakia). Because of the confusion of *B. haberfellneri* and *F. (H.) petrocoriensis* it is not clear how many of the widespread records of the former actually refer to specimens of the latter.

Forresteria (Harleites) nicklesi (de Grossouvre, 1894)

Plate 4, fig. 9; Plate 8, figs. 1–3; Plate 9, figs. 7–8, 25–6

- 1894 *Barroisia Nicklesi* A. de Grossouvre, n. sp., p. 63, pl. 3, fig. 2.
 ?1894 *Barroisia sequens* A. de Grossouvre, n. sp., p. 64, pl. 3, fig. 1.
 1894 *Barroisia Boissellieri* A. de Grossouvre, n. sp., p. 65, pl. 3, fig. 3.
 non 1907 *Schloenbachia (Barroisiceras) Haberfellneri* Hauer, var. *Nicklesi* Gross; Boule, Lemoine and Thévenin, p. 25, pl. 4, fig. 2, text-fig. 24.
 non 1920 *Schloenbachia (Barroisiceras) sequens* Grossouv; Taubenhau, p. 35, pl. 9, fig. 3.
 ?1935 *Barroisiceras nicklesi* Gross; Karrenberg, p. 147, pl. 33, fig. 15.
 1939 *Barroisiceras haberfellneri* v. Hauer; Basse, p. 136.
 1947 *Reesideoceras(?) nicklesi* de Gross.; Basse, p. 136.
 ?1978 *Barroisiceras* cf. *B. sequens* (Grossouvre); Wiedmann and Kauffman, pl. 1, 11, fig. 3.
 ?1980b *Barroisiceras* cf. *B. sequens* (Grossouvre); Wiedmann, pl. 11, fig. 3.

Types. The holotype by original designation, of *Barroisia nicklesi* is the original of de Grossouvre 1894, pl. 3, fig. 2, from the 'Calcaires blancs à texture gréseuse et a bryozoaires du coniacien moyen; assize L¹ de M. Arnaud. Toutyfauf, près Angoulême (Charente)'; it is in the SP Collections (*ex* Arnaud Collection). The paratype, from the same level at la Quina, near Lavalette (Charente), is in the same collection. The holotype (by monotypy) of *B. sequens* de Grossouvre (1894, pl. 3, fig. 1) is also from Toutyfauf, and survives in the same collections, as does the holotype (by monotypy) of *B. boissellieri* de Grossouvre (1894, pl. 3, fig. 3) from the 'calcaires blancs grénus de la Quina: assize L¹ de M. Arnaud' (de Grossouvre 1894, p. 65).

Material. Apart from the types, there is a specimen (SP) of identical preservation labelled 'Chez Tardy, Nieuil-le-Virouil, tranchée du Tramway K'. Niel-le-Virouil is in Charente-Maritime, near Jonzac.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Type <i>nicklesi</i>	102.8 (100)	— (—)	46.0 (44.7)	—	27.5 (26.8)
Type <i>boissellieri</i>	115.0 (100)	31.3 (27.2)	44.1 (38.4)	—	35.5 (30.9)
Tardy specimen	111.8 (100)	— (—)	47.2 (42.2)	—	29.3 (26.2)

Description. The holotype of *Barroisiceras nicklesi* is a poorly preserved internal mould. Coiling evolute, approximately 45% of previous whorl covered; umbilicus rather small—26.8% of the diameter, depth moderate;

EXPLANATION OF PLATE 8

Figs. 1–3. *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894). The holotype, SP unregistered (*ex* Arnaud Collection), Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone, Assize L¹ of Arnaud at Toutyfauf near Angoulême (Charente).

Figs. 4–9. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine and Thévenin, 1907). 4–6, LGHPM unregistered, Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone Marnes de Ceyreste near Ceyreste (Var), figured by Collignon *et al.* 1979, pl. 1, figs. 4–5. 7–9, SAS 1438b, Middle Coniacian St. Lucia Formation near Hluhluwle, Zululand, South Africa, illustrated for comparison.

All figures × 1.



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5



6



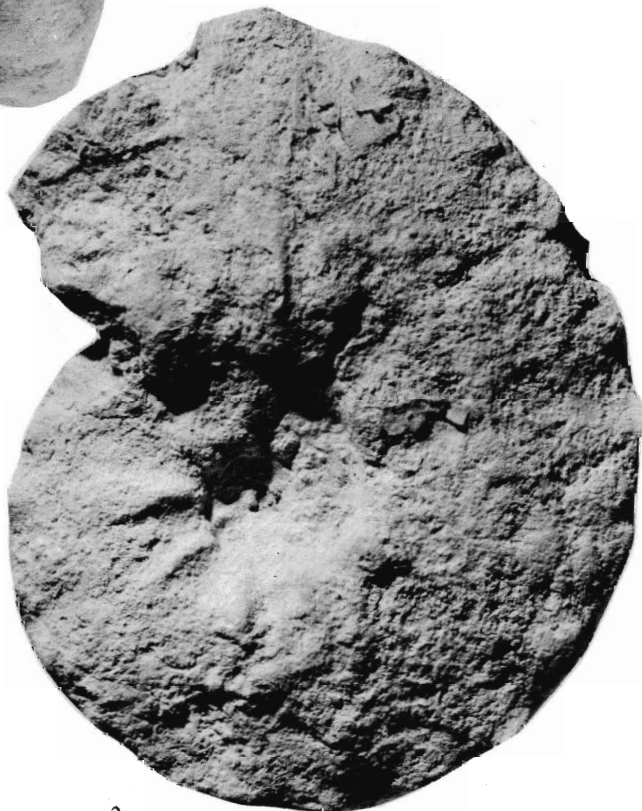
7



8



9



2



3

whorl section compressed, with intercostal whorl breadth to height ratio 0.65 at diameter 80 mm. Greatest breadth is at umbilical bulla and close to umbilical shoulder intercostally. Umbilical shoulder narrowly rounded, inner flanks slightly inflated, outer flanks flattened, converging to narrow obtusely fastigiate venter.

Little is visible of ornament of inner whorls, but there appear to have been a series of rather coarse umbilical bullae linked by a broad strong rib to an inner lateral tubercle. At beginning of outer whorl, these tubercles have fused into a coarse umbilical bulla that increases in strength away from umbilical shoulder to an umbilico-lateral tubercle, of which there are nine on the outer whorl. These give rise to pairs of low, very broad straight prorsiradiate ribs, the adapical one of which is less obviously connected to the bulla than the adapertural. Occasional ribs intercalate or arise singly from weak bullae, to give an estimated total of twenty-two to twenty-four ribs per whorl. All terminate in ear-like ventrolateral clavi. Venter fastigiate, with low siphonal ridge, accentuated between ventrolateral clavi into remnants of a siphonal clavus. Sutures are indecipherable.

The Tardy specimen (Pl. 10, figs. 4-5) shows the bituberculate flanks of the inner whorls much more clearly than the holotype of *nicklesi* and has distinct siphonal clavi at the beginning of the outer whorl. The umbilico-lateral bullae and tubercles are, however, weaker, and decline at the end of the apparently adult body chamber, which bears rather narrow, prorsiradiate, long and short ribs. The sutures are indecipherable.

The holotype of *Barroisia boissellieri* is an adult body chamber and part of the phragmocone. The badly preserved inner whorl shows strong flank ribs with double tubercles. The end of the phragmocone shows their fusion as in the holotype of *B. nicklesi*, followed by a tuberculate early body chamber and final part with narrow ribs and no bullae. Part of an ill-preserved suture is visible; E/L is asymmetrically bifid, L broad, with few but deep, simple incisions.

Discussion. De Grossouvre distinguished *B. nicklesi* and *boissellieri* on details of ornament; they differ only in that *boissellieri* shows modification of ornament associated with maturity whereas *nicklesi* retains the tuberculation of the phragmocone throughout the specimen and presumably lacks part of the body chamber.

The Tardy specimen is more delicately ribbed and tuberculate than the two holotypes, and provides a transition towards the holotype of *B. sequens*, a body chamber fragment which combines the non-bullate primary and secondary ribs of the holotype of *boissellieri* with a more involute coiling and delicate ventrolateral clavi. Without further material it is not, however, possible to confirm *sequens* as a feebly ribbed variant of *nicklesi* although its co-occurrence with *F. (H.) nicklesi* makes this very likely.

It is not possible to determine the affinities of *Schloenbachia (Barroisiceras) sequens* of Taubenhäus (1920, pl. 9, fig. 3); as Basse (1947, p. 137) and Parnes (1964, p. 3) indicate, it is not even generically determinable, whilst the material cited by Karrenberg was not figured. Wiedmann and Kauffman (1978) and Wiedmann (1979) have figured *Barroisiceras* cf. *B. sequens* (de Grossouvre) from near Nidaguila, Burgos, Spain, but the specimen appears to have umbilical bullae only; if correctly identified, this would suggest that *sequens* is not a *F. (Reesideoceras)*.

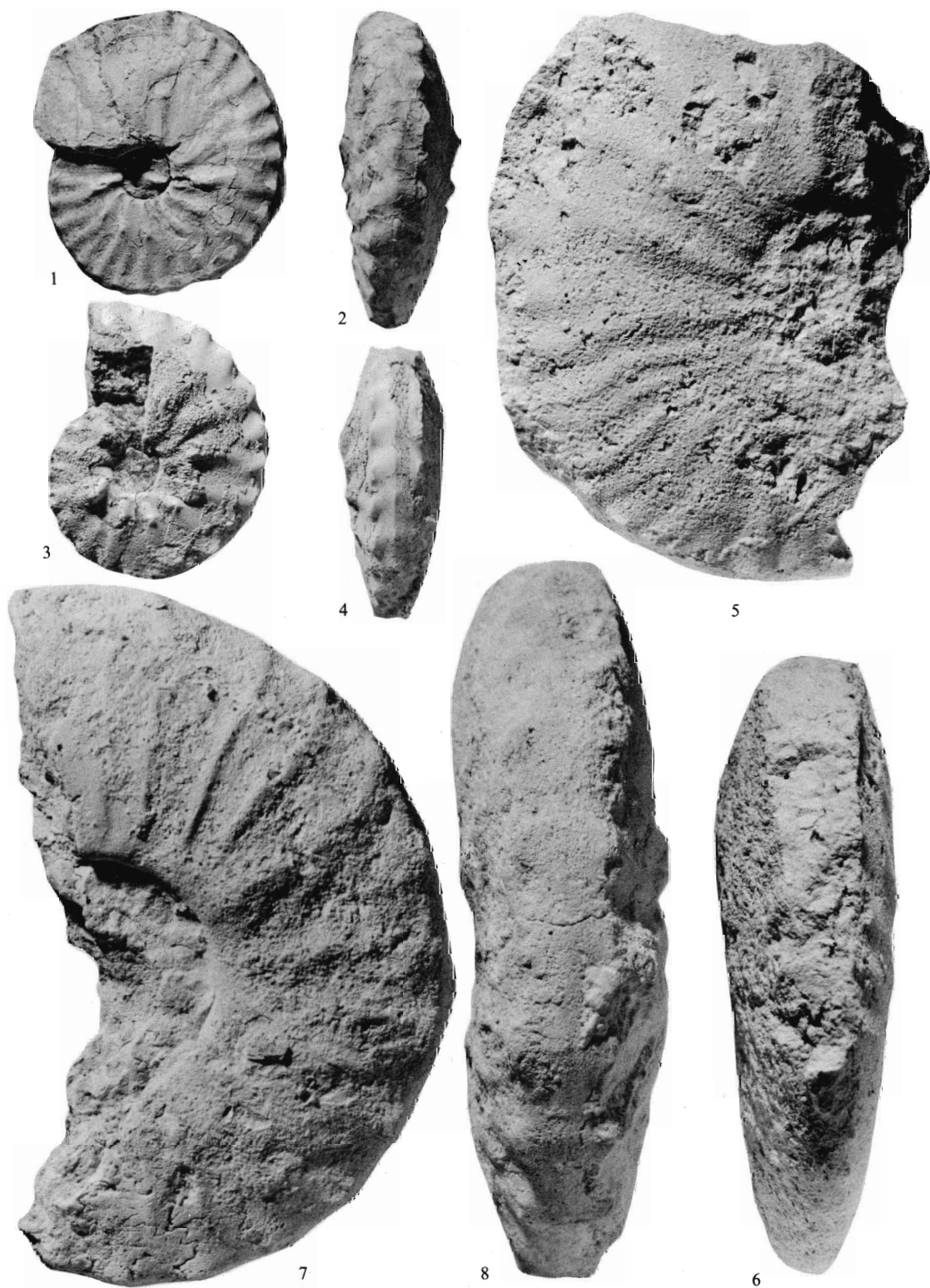
Basse (1947, p. 136) discussed differences between *F. (H.) gallicum* and *F. (H.) nicklesi*, pointing out that the latter is larger, more evolute and shows a rapid development of what she calls 'ornamentation

EXPLANATION OF PLATE 9

Figs. 1-4. *Forresteria (Harleites) petrocariensis* (Coquand, 1859). 1, 2, NHMW 1890. XIII. 182, Priesener Schichten of Priesen, Bohemia. This specimen has been successively labelled both *Ammonites neptuni* and *A. haberfellneri*. 3, 4, FSR 1905b, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).

Figs. 5-8. *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894). 5, 6, SP unregistered (*ex* Arnaud Collection), the holotype of *Barroisia sequens* de Grossouvre, 1894, pl. 3, fig. 1, Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone Assize L¹ of Arnaud at Toutyfauf near Angoulême (Charente). 7, 8, from the same collection and horizon as 5, 6, at La Quina, near Lavalette (Charente), the original of de Grossouvre 1894, pl. 3, fig. 3.

All figures × 1.



KENNEDY, *Forresteria*

sénile'. The inner whorls, so far as these are comparable, appear to have been rather similar. But whereas the fusion of the umbilical and inner lateral tubercles of nuclei leads to a bulla at the umbilical shoulder in *F. (H.) gallicum*, the corresponding fusion in *F. (H.) nicklesi* produces a strong bulla displaced outwards from the shoulder. Whereas mature *F. (H.) nicklesi* develop crowded narrow ribs and retain their ventrolateral clavi, the smooth body chamber of adult *F. (H.) gallicum* is highly distinctive.

F. (H.) camerounensis Basse, 1947 (= *B. haberfellneri* von Hauer var. *alstadenensis* (Schlüter) de Grossouvre of Solger 1904, p. 170, figs. 56, 57; pl. 5, figs. 6a-b) differs from *F. (H.) nicklesi* in its more delicate ribbing and tuberculation but comparison is difficult because of the small size of the lectotype. The paralectotype refigured by Reyment (1958b, pl. 6, fig. 1) is badly preserved, but seems more involute and densicostate.

Occurrence. Assize L¹ of Arnaud at Toutyfaud, near Angoulême, La Quina, near Lavelette (Charente), and Tardy, near Niel-le-Virouil (Charente-Maritime). The record from Spain is uncertain.

Subfamily PERONICERATINAE Hyatt, 1900

[*nom. transl.* Wright 1957, p. L428 (*ex* Peroniceratidae Hyatt, 1900, p. 589) = Gauthiericeratidae Van Hoepen, 1955, p. 367]

Genus and Subgenus PERONICERAS de Grossouvre, 1894

[For synonymy see Klinger and Kennedy 1984, p. 138]

Type species. *Peroniceras moureti* de Grossouvre, 1894, p. 100, pl. 11, fig. 4 (= *A. tridorsatus* Schlüter, 1867, p. 26, pl. 5, fig. 1), by original designation.

For diagnosis and discussion see Klinger and Kennedy 1984, p. 135f.

Occurrence. Middle Coniacian, world-wide. *P. (Peroniceras) [Cobbanoceras] tanakai* Matsumoto, 1965, is questionably dated as approximately Santonian (Matsumoto 1965b, p. 220).

Peroniceras (Peroniceras) tridorsatum (Schlüter, 1867)

Plate 11, figs. 3-6; Plate 12, figs. 1-5; Plate 13, figs. 5-11; Plate 14, figs. 1, 4; text-figs. 13G, L, 18C-E, 19

1867 *Ammonites tridorsatus* Schlüter, 1867, p. 26, pl. 5, fig. 1.

1876 *Ammonites cf. tridorsatus* Schlüter; Schlüter, p. 158, pl. 41, figs. 3-5.

?1885 *Ammonites (Schloenbachia) czörnigi* Redt.; Fallot, p. 229, pl. 1, fig. 1.

1894 *Peroniceras subtricaratum* var. *tridorsatum* Schlüter; de Grossouvre, p. 96, pl. 10, figs. 2, 3; pl. 11, fig. 1.

1894 *Peroniceras moureti* A. de Grossouvre n. sp., p. 100, pl. 11, figs. 3, 4; text-figs. 37, 39.

1894 *Peroniceras rousseauxi* A. de Grossouvre, n. sp., p. 102, pl. 11, fig. 5.

1984 *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867); Klinger and Kennedy, p. 139, figs. 3-15, 16D-E (with full synonymy).

Types. The holotype of the species, from the Coniacian of Westphalia, is lost (Klinger and Kennedy 1984, p. 140). The holotype, by original designation, of *P. moureti* de Grossouvre, 1894, is the original of de Grossouvre's pl. 11, fig. 4, from the 'Calcaires tendres gréseaux de la base de la Craie de Villedieu. Courtiras, près

EXPLANATION OF PLATE 10

Figs. 1-5. *Forresteria (Harleites) nicklesi* (de Grossouvre, 1894). 1-3 SP unregistered (*ex* Arnaud Collection), Middle Coniacian *Peroniceras (Peroniceras) tridorsatum* Zone (?) Gourde-de-l'Arche near Périgueux (Dordogne). 4, 5, from the same collection as above, Middle Coniacian *P. (P.) tridorsatum* Zone, Tranchée du Tramway, Chez Tardy, Niel-le-Virouil (Charente-Maritime). All figures $\times 1$.



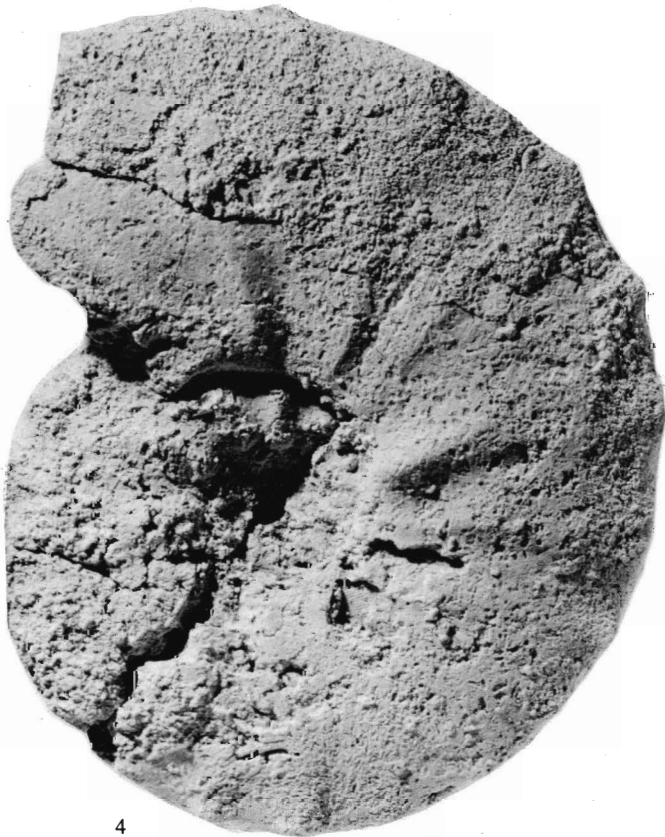
1



2



3



4



5

Vendôme (Loir-et-Cher) (EMP Collections). Paratypes include the specimen figured by de Grossouvre as his pl. 11, fig. 3, which is an unregistered specimen in the SP Collections from assize L¹ of Arnaud at La Boulinerie, near Jonzac (Charente-Maritime), and a specimen from the Coniacian of Lezennes (Nord) in the Musée Gosset at Lille, reg. no. ML7.

The holotype, by monotypy, of *P. rousseauxi* de Grossouvre, 1894, is the original of de Grossouvre, 1894, pl. 11, fig. 5, an unregistered specimen in the SP Collections from Assize L¹ of Arnaud at St. Simon-de-Jonzac (Charente-Maritime).

Material. The original of *P. subtricarinarum* var. *tridorsatum* of de Grossouvre, 1894, pl. 10, fig. 2, an unregistered specimen in the SP Collections (ex Le Mesle Collection) from the Calcaires Durs de La Ribochère, Carrières de La Ribochère, commune de Couture (Loir-et-Cher); the original of de Grossouvre 1894, pl. 11, fig. 1, from Assize L¹ of Arnaud at La Boulinerie, near Jonzac, Charente-Maritime, plus an unfigured fragment of the outer whorl of this specimen (Arnaud Collection) and a further specimen from the same locality and collection labelled '*Peroniceras moureti*----det. de Grossouvre'. Also in the SP Collections is a specimen from Assize L¹ at Les Eyzies (Dordogne). The original of *A. (Schloenbachia) czörnigi* Redtenbacher of Fallot (1885, pl. 1, fig. 1) (now in the Collections at Grenoble), from the Grès Verts de Dieulefit (Drôme), is referred to this species, as are three other specimens from this locality, FSL 14108a-c.

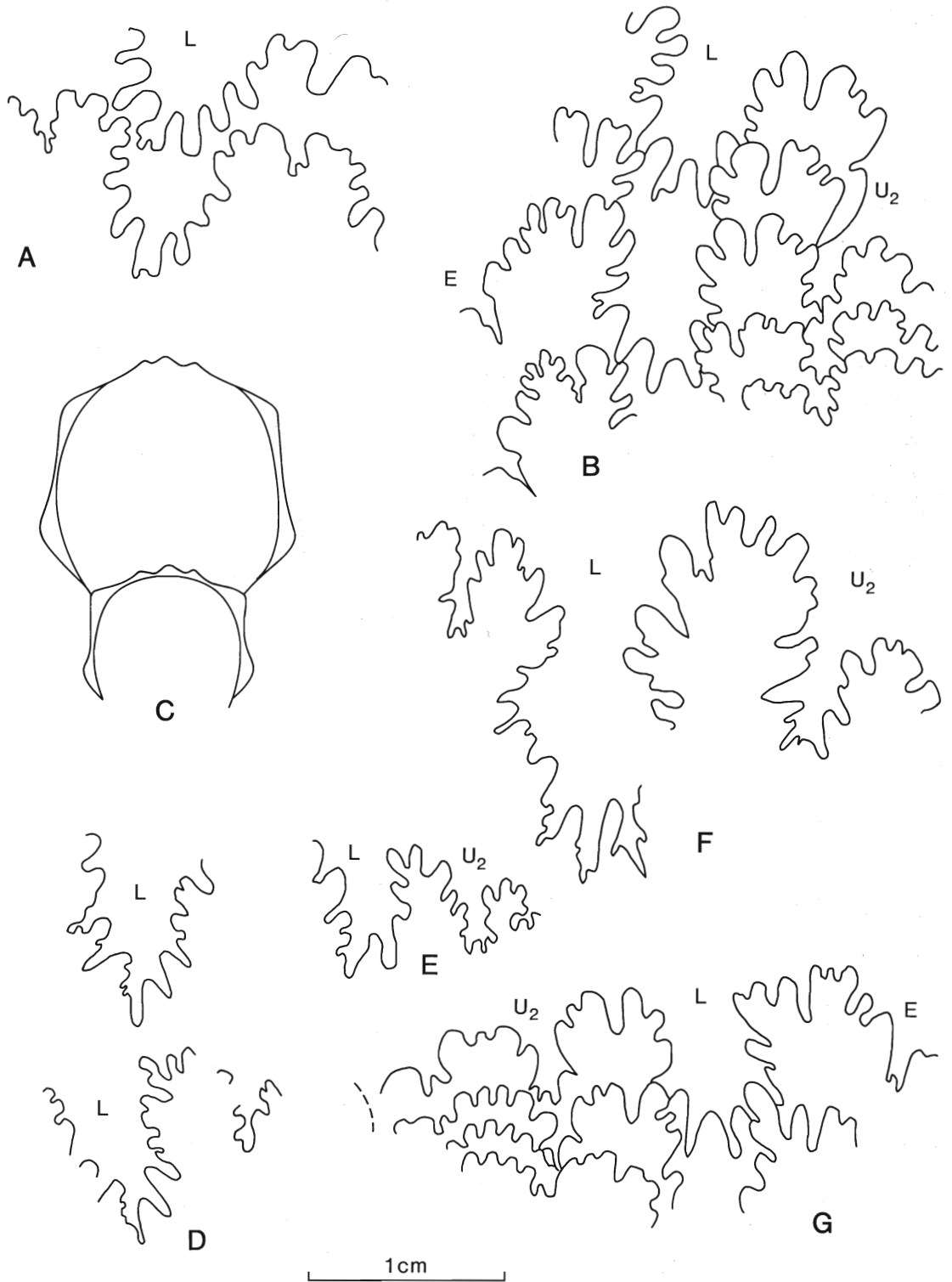
<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype, <i>P. moureti</i>	117.5 (100)	— (—)	31.8 (27.1)	—	60.5 (51.5)
FSL 14108 c	75.5 (100)	23.0 (30.4)	18.5 (24.5)	1.24	42.5 (56.3)

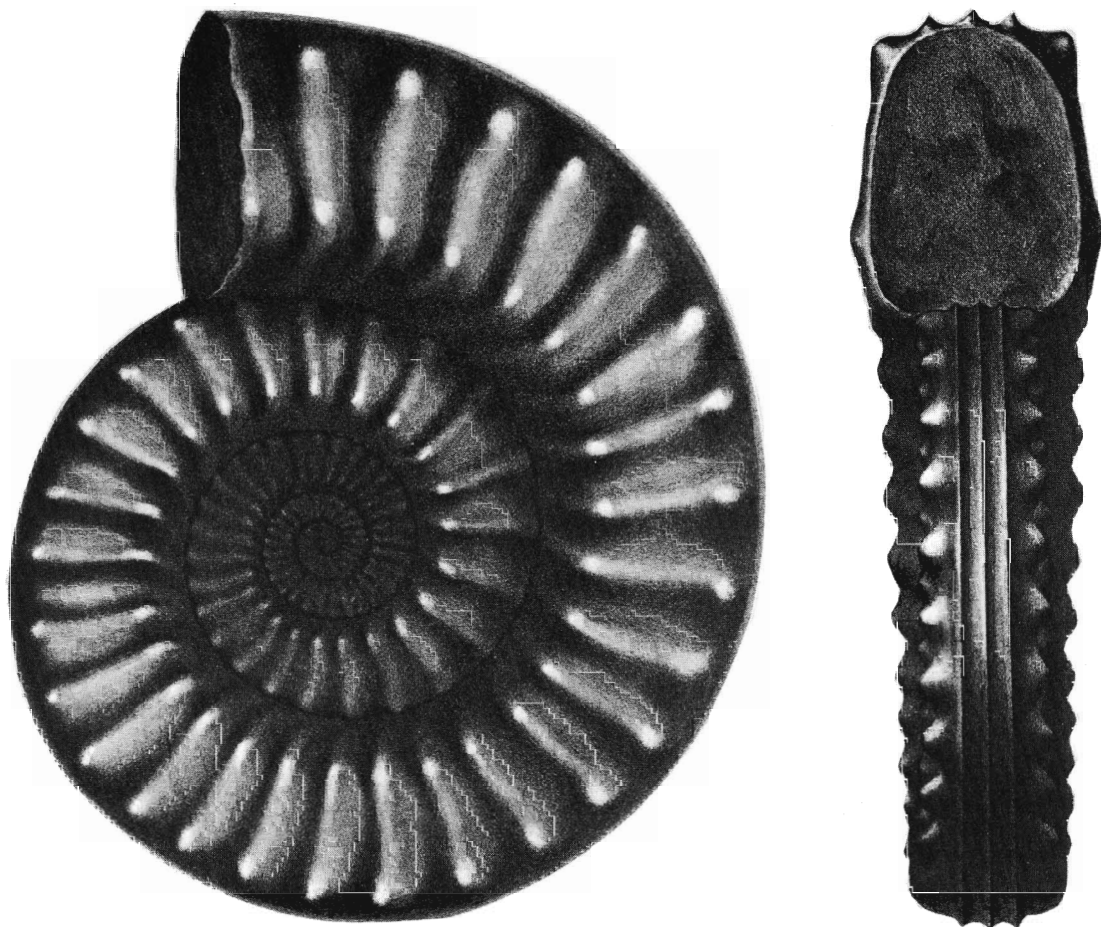
Description. Coiling very evolute, with shallow dorsal impressed zone and U = up to 56%. Whorl section varies from slightly compressed to markedly depressed, with greatest breadth at umbilicolateral bullae; umbilical wall low and flat to concave, umbilical shoulder narrowly rounded, inner flanks swollen and rounded, outer flanks flattened and convergent, ventrolateral shoulders broadly rounded intercostally.

Nuclei bear between twenty-six and thirty-three ribs per whorl at diameters of around 40–60 mm. This increases to eighteen to twenty per half whorl in the largest specimen seen, the holotype of *P. (P.) moureti*, where ribs are all single, long, narrow, crowded, arise at umbilical wall, are prorsiradiate and straight, but may curve forwards to a variable degree to become concave over ventrolateral shoulder; maximum elevation is a little distance out from umbilical shoulder, where they strengthen into bullae. Bullae are weak on compressed individuals and strong on depressed ones. All ribs bear strong, persistent ventral clavi which give rise to a low broad swelling that extends forwards and declines across ventrolateral shoulder. There are three strong keels, the siphonal the most prominent. Suture rather simple (text-fig. 18c-e).

Discussion. De Groussouvre separated *P. moureti* from Schlüter's *A. tridorsatus* (text-fig. 19) on the basis of the more numerous, crowded, and more prorsiradiate ribs of his species. The holotype of *tridorsatus* is lost, however, and Schlüter's illustrations are often highly inaccurate. Examination of the French material listed above shows that there is only one variable species which has strong persistent primary ribs with prominent umbilicolateral bullae. The rib density of nuclei varies from twenty-six to thirty-three at diameters of 40–60 mm, increasing to eighteen to twenty per half whorl in the holotype of *moureti* at a diameter of 120 mm. Ribs also vary from straight and rectiradiate to concave and prorsiradiate, and the whorl section from slightly compressed to relatively depressed. It is concluded from this that *tridorsatum* and *moureti* are no more than variants of a single, distinct species. This is supported by the observation that the outer whorl of the original of de Grossouvre's pl. 11, fig. 1 was identified as *P. moureti* by de Grossouvre although the nucleus was named *P. subtricarinarum* var. *tridorsatum* by him. The conclusion is also confirmed by observations on much larger suites of specimens from South Africa (Klinger and Kennedy 1984).

TEXT-FIG. 18. External sutures and whorl sections. A, B, G, *Forresteria (Harleites) petrocariensis* (Coquand, 1859); A, original of de Grossouvre 1894, pl. 1, fig. 3, SP, ex Arnaud Collection; B, G, original of de Grossouvre 1894, pl. 2, fig. 4, SP ex Arnaud Collection. C-E, *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867); C, D, original of de Grossouvre 1894, pl. 11, fig. 1, SP, ex Arnaud Collection; E, SP unregistered, ex Arnaud Collection. F, *P. (P.) dravidicum* (Kossmat, 1895), MNHP 1895-9, ex Durand Collection.





TEXT-FIG. 19. Original illustrations of *Ammonites tridorsatus* Schlüter, 1867 (pl. 5, fig. 1), $\times 1$. The missing original was from Westphalia.

A further form described from near Jonzac is *P. rousseauxi* de Grossouvre (1894, pl. 11, fig. 5). The holotype, by monotypy, is a fragment of body chamber (Pl. 13, figs. 10–11). De Grossouvre (1894, p. 102) described it as being close to *P. moureti*, but differing in having ribs that were slightly bent (e.g. feebly concave), the ventrolateral tubercles less clavate and more rounded, the whorls depressed, and the umbilicus larger. These differences are slight and are here regarded as no more

EXPLANATION OF PLATE 11

Figs. 1–2. *Peroniceras* (*Peroniceras*) *lepeei* (Fallot, 1885). A cast of the holotype, Middle Coniacian *P.* (*P.*) *tridorsatum* Zone Grès Verts de Dieulefit at Dieulefit (Drôme), LGG unregistered, the original was figured by Fallot 1885, pl. 1, fig. 2.

Figs. 3–6. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). 3, 4, the holotype of *P. moureti* de Grossouvre, 1894, pl. 11, fig. 4, Middle Coniacian *P.* (*P.*) *tridorsatum* Zone part of the Calcaires Durs de La Ribochère of Courtiras, near Vendôme (Loir-et-Cher). 5, 6, cast of *Ammonites* (*Schloenbachia*) *czornigi* Fallot (*non* Redtenbacher), 1885, pl. 1, fig. 1, collection, horizon, and locality as for the originals of figs. 1–2.

All figures $\times 1$.



1



3



4



2



5



6

than those between individuals; the intercostal whorl breadth to height ratio of the holotype of *P. (P.) rousseauxi* is 1.10, the costal ratio 1.19. The juvenile specimen from the Craie de Villedieu figured by de Grossouvre as his pl. 10, fig. 2 is also regarded as a synonym of the present species. There are twenty-eight ribs per whorl, the bullae migrating from the umbilical shoulder to the inner flank from 50 mm diameter onwards, with slightly clavate ventrolateral tubercles (Pl. 14, fig. 4).

Young (1963) suggested that *A. (Schloenbachia) czörnigi* of Fallot, 1885 (p. 229, pl. 1, fig. 1) was a possible synonym of *P. moureti*. A cast of this specimen, which is from Dieulefit (Drôme), is figured here (Pl. 11, figs. 5–6). It is rather worn, but compares well with the inner whorls of the holotype of *P. moureti*, the ventrolateral tubercles being a little less clavate; it is regarded as a probable synonym. Young (1963, p. 73) also suggested that *P. aff. cocchi* Meneghini in Riedel, 1932 (pl. 30, figs. 1, 2), from the Coniacian of Cameroon, might belong to this species; it is a fragment only, however, and cannot be identified with certainty from the figure.

P. (P.) tridorsatum is a close ally of *P. (P.) lepeei* (Fallot, 1885). The two differ chiefly in the absence of umbilical bullae and much more delicate ornament in the latter. It is easily separated from *P. (P.) subtricarinatum* (d'Orbigny, 1850), which has branching and intercalated coarse ribs. *P. (P.) westphalicum* (Von Strombeck, 1859) has coarse ribs that are effaced on the outer flank. *P. (P.) dravidicum* (Kossmat, 1895) has weak lateral keels, ribs branching from umbilical bullae, and a complex suture.

Species described from Zululand by Van Hoepen (1965) are fully discussed by Klinger and Kennedy (1984).

Occurrence. Middle Coniacian, *P. tridorsatum* Zone. In France it is recorded from the chalk facies of the Boulonnais at Lille, Lezennes, and Caffiers, from the Calcaires Durs de La Ribochère at La Ribochère (Loir-et-Cher), Courtiras, near Vendôme (Loir-et-Cher), and it occurs widely in Arnaud's Assize L¹ in Aquitaine, at Dieulefit (Drôme), in the Beausset Basin (Var), the Corbières, and elsewhere. There are widespread records in northern Germany, and the species occurs in northern Spain (Ernst Collection), Italy, Romania, north Africa, Zululand, South Africa, Madagascar, and Texas, U.S.A.

Peroniceras (Peroniceras) lepeei (Fallot, 1885)

Plate 11, figs. 1–2; Plate 12, figs. 10–11; Plate 14, figs. 2–3; text-fig. 20A

1885 *Ammonites (Schloenbachia) L'Epeei* Fallot, p. 231, pl. 1, fig. 2.

1920 *Peroniceras L'Epeei* Fallot; Desio, p. 208, pl. 12, figs. 6, 7; pl. 14, fig. 6.

1925 *Peroniceras L'Epeei* Fallot; Diener, p. 150.

1983 *Peroniceras (Peroniceras) lepeei* (Fallot, 1885); Klinger and Kennedy, p. 153, figs. 16a–c, 17–18.

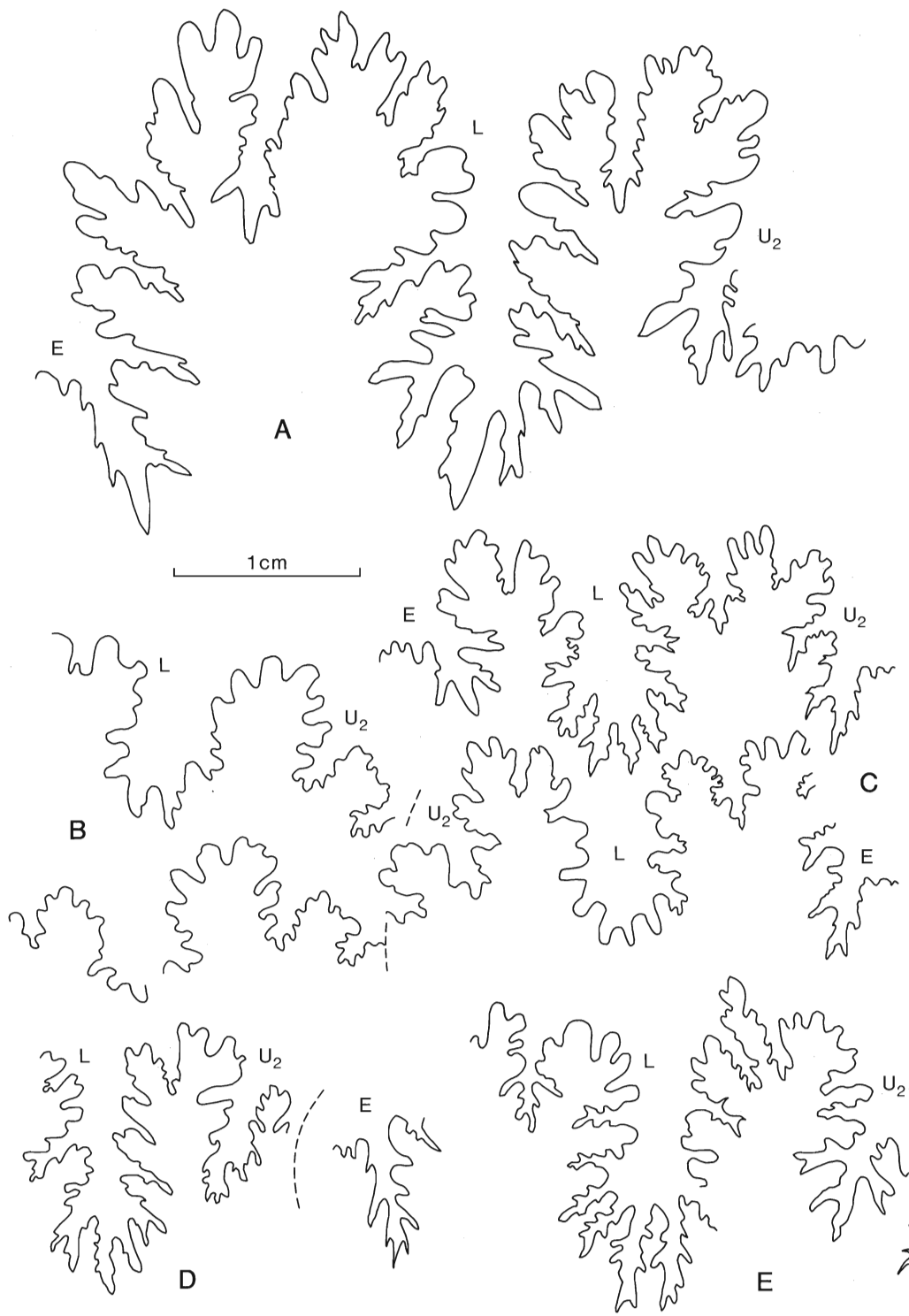
Holotype. By monotypy, the original of Fallot 1885, p. 231, pl. 1, figs. 2, 2a, from the 'Grès vert sénonien' of Dieulefit (Drôme), LGD, *ex* Soulier Collection (Pl. 11, figs. 1–2).

Material. An unregistered specimen in the MNHP (*ex* de Grossouvre Collection), unlocalized, but clearly from the Calcaires Durs de La Ribochère of Sarthe or Touraine, plus two topotypes, SP64-76A and FSL 14. 110.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Holotype	86.3 (100)	18.8 (21.8)	21.8 (25.3)	0.86	36.7 (42.5)
MNHP specimen	74.3 (100)	16.0 (21.5)	20.8 (27.9)	0.77	33.2 (44.6)

Description. Coiling very evolute, umbilicus comprising over 40% of diameter, shallow, with low rounded wall, undercut on mould. Whorl section compressed (whorl breadth to height ratio ranges from 0.77 to 0.86 in specimens studied), with rounded inner and flattened outer flanks, rounded ventrolateral shoulders and broad venter; greatest breadth close to umbilical shoulder. Ornament consists of dense, narrow, crowded primary ribs, eighteen to twenty per half whorl, arising at umbilical seam, strengthening across umbilical wall and shoulder, without developing bullae; narrow and prorsiradiate, feebly concave on inner flank, with weakly clavate oblique ventrolateral tubercle; venter bears three prominent keels of which siphonal is strongest, separated by deep grooves.

The larger Craie de Villedieu specimen shows, at a diameter of 25 mm, a strong siphonal keel and only very weak lateral ones, whilst its outer, still septate whorl shows the ventrolateral tubercles becoming rounded. The



TEXT-FIG. 20. External sutures. A, D, *Peroniceras (Peroniceras) lepeei* (Fallot, 1885), MNHP unregistered. B, C, E, *P. (Zuluiceras) bajuvaricum* (Redtenbacher, 1873); B, MNHP B16690; c, MNHP 1896-27, ex de Vibraye Collection; e, MNHP 1895-9, ex Durand Collection.

suture line of this specimen is shown in text-fig. 20A. E/L is broad and asymmetrically bifid, L deeply incised and L/U₂ large and asymmetrically bifid.

Discussion. This has been a little mentioned species. The immediately distinguishing features are the dense primary ribbing, lack of intercalated ribs and umbilical bullae, rounded or feebly clavate ventrolateral tubercles, and strong siphonal but weak outer keels. These effectively distinguish the species from the *P. (P.) subtricarinarum-dravidicum* group, all of which have strong umbilical bullae in middle and in some cases later growth, giving rise to pairs of ribs, intercalated ribs, and strong ventrolateral clavi. *P. (P.) westphalicum* (Von Strombeck, 1859) (see Schlüter 1867, p. 30, pl. 6, fig. 2) is equally and distantly ribbed with bullae on nuclei and persistent ventrolateral clavi.

There are closer similarities to *P. (P.) tridorsatum*, described above. The two differ in the much denser ribbing of *P. (P.) lepeei*, and the absence of an umbilical bulla. It should be noted, however, that the illustrations of Schlüter (1876, pl. 41, figs. 3–5) show a specimen which has a rib density close to that of *P. (P.) lepeei*, although it retains umbilical bullae and has strongly clavate ventrolateral tubercles.

Occurrence. This is a rare Middle Coniacian, *tridorsatum* Zone species known only from the Coniacian of Dieulefit (Drôme), the Craie de Villedieu of Sarthe or Touraine, and the Coniacian of Italy. To these are added records from the Coniacian of Zululand—divisions II and III of Kennedy and Klinger (1975).

Peroniceras (Peroniceras) aff. lepeei (Fallot, 1885)

Plate 16, figs. 4–5

1894 *Peroniceras Czornigi* Redtenbacher sp. var.; de Grossouvre, p. 103, pl. 11, fig. 2.

Material. An unregistered specimen in the Sorbonne Collections, the original of de Grossouvre 1894, pl. 11, fig. 2, from the 'Grès verdâtres de Dieulefit (Drôme)'.

Description. A crushed composite mould in buff glauconitic sandstone; coiling moderately evolute, umbilicus comprising an estimated 39% of diameter, shallow, with low rounded wall. Whorl section strongly compressed, with whorl breadth to height ratio of approximately 0.74, probably accentuated by crushing. Inner flanks gently inflated, greatest breadth low on flanks, with outer flank feebly concave.

There are an estimated forty-two to forty-four ribs per whorl. Most arise at umbilical shoulder, without developing umbilical bullae. They are accompanied by rare intercalatories. All ribs bear small, markedly clavate ventrolateral tubercles from which a broadened rib extends across ventrolateral shoulder. Venter bears strong siphonal keel separated by strong grooves from slightly weaker lateral keels. Flanks and ventrolateral shoulders decorated by delicate spiral ridges and grooves, especially prominent on last half whorl.

Discussion. De Grossouvre regarded this specimen as a variety of *P. (Zuluiceras) czoernigi* (Redtenbacher, 1873), distinguishing it from the Austrian form on the basis of the distinctive spiral ornament. He also considered Fallot's (1885, p. 229, pl. 1, fig. 2) *A. (Schloenbachia) czörnigi* Redt. to belong to that species, but both of these specimens differ from the lectotype of Redtenbacher's species (Reyment 1958a, pl. 5, fig. 1). The latter is more compressed than Fallot's specimen and has a serrated siphonal keel with weak to obsolete lateral keels, whilst the present specimen is distinguished by a lack of umbilical bullae and three prominent keels, being a *P. (Peroniceras)* rather than *P. (Zuluiceras)*.

De Grossouvre (1894, p. 103) regarded *A. (Schloenbachia) l' Epeei* Fallot (1885, p. 231, pl. 1, fig. 2; see p. 68, Pl. 11, figs. 1–2) as a 'mutation' of *P. czoernigi* (de Grossouvre, *non* Redtenbacher), and indeed, the lack of bullae and dense ribbing suggests that the present specimen is allied to *P. (P.) lepeei*, the only difference being the more involute coiling of the present form. Spiral ridges and striae are widely and variably developed in peroniceratids, in part as a result of preservation (see Klinger and Kennedy 1984).

Peroniceras (Peroniceras) subtricarinatum (d'Orbigny, 1850)

Plate 12, figs. 6-9; text-fig. 21

- 1841 *Ammonites tricarinatus* d'Orbigny, p. 307, pl. 91, figs. 1, 2.
 1850 *Ammonites subtricarinatus* d'Orbigny, p. 212.
 1984 *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850); Klinger and Kennedy, p. 157, figs. 19a-b, d-e, 20-23 (with synonymy).

Types. D'Orbigny (1841, p. 308) referred two specimens to his *A. tricarinatus*, which he subsequently (1850, p. 212) renamed *A. subtricarinatus* because of prior usage of the combination *A. tricarinata* by Poitiez and Michaud (1838). These specimens survive in the d'Orbigny Collection as no. 7183, and are the syntypes of the species. They were re-illustrated by Sornay in 1955. The larger of the two, which served as the basis of d'Orbigny's illustration (1841, pl. 91, figs. 1-2), was designated lectotype by Klinger and Kennedy (1983). D'Orbigny indicated these specimens to be from the 'Grès vert supérieur' in the environs of Sougraine (Aude), and subsequently referred them to his étage Senonien. The preservation of the types indicates that they are indeed from the environs of Sougraine.

Material. Two fragments in the SP (Toucas Collection) from the 'Coniacien Supérieur à *Micraster brevis*, Ravin de Montferrand, Montagne des Cornes', Corbières (Aude) and a further fragment in the Arnaud Collection (same repository) from Assize L¹, Tour de la Roche, St.-Simon-des-Bordes (Charente-Maritime).

Description. The types are composite internal moulds in rusty-weathering brown sandstone. The lectotype is deformed into an ellipse, major diameter 73.5 mm, minor diameter 69.0 mm. The paralectotype is 28.5 mm in diameter. Coiling very evolute, serpenticone, with broad, shallow umbilicus; ventrolateral tubercle of whorl visible in umbilical seam of succeeding one. In the lectotype, the whorl section is quadrate, depressed, with greatest breadth at umbilical bullae; whorl breadth to height ratio 1.20, although this has been increased by distortion. Twenty-four primary ribs on outer whorl arise at umbilical seam and bear strong, prominent umbilical bullae which give rise to strong, broad, distant primary ribs. Probably originally prorsiradiate, they now vary from strongly prorsiradiate and concave to rectiradiate and straight as a result of post-mortem distortion. Most primary ribs arise singly from bullae, but there are occasional pairs of primaries springing from a bulla. Shorter intercalated ribs are inserted between most primaries to give a total of thirty-eight ribs per whorl. All ribs bear a strong clavate ventrolateral tubercle. Venter poorly preserved, with three strong continuous keels, central one strongest, separated by deep grooves; outer keels separated from ventral clavi by shallower groove.

Discussion. This is a very distinctive species, characterized by the very evolute coiling and coarse ornament of ribs arising in pairs from umbilical bullae that persists to a large size. This easily separates it from *P. (P.) tridorsatum* (Schlüter, 1867) and *P. (P.) lepeei* (Fallot, 1885). *P. (P.) dravidicum* (Kossmat, 1895) has delicate ornament, is flat-sided, with weak lateral keels.

Occurrence. Middle Coniacian, *P. (P.) tridorsatum* Zone. In France the species occurs in the chalk facies of Emmerin (Nord), in northern Aquitaine, the Beausset Basin (Var), and the Corbières (Aude). Elsewhere, it is recorded widely in north Germany, Switzerland, and Czechoslovakia and is also known from North Africa, Zululand, South Africa, Madagascar, and Mexico.

Peroniceras (Peroniceras) westphalicum (Von Strombeck, 1859)

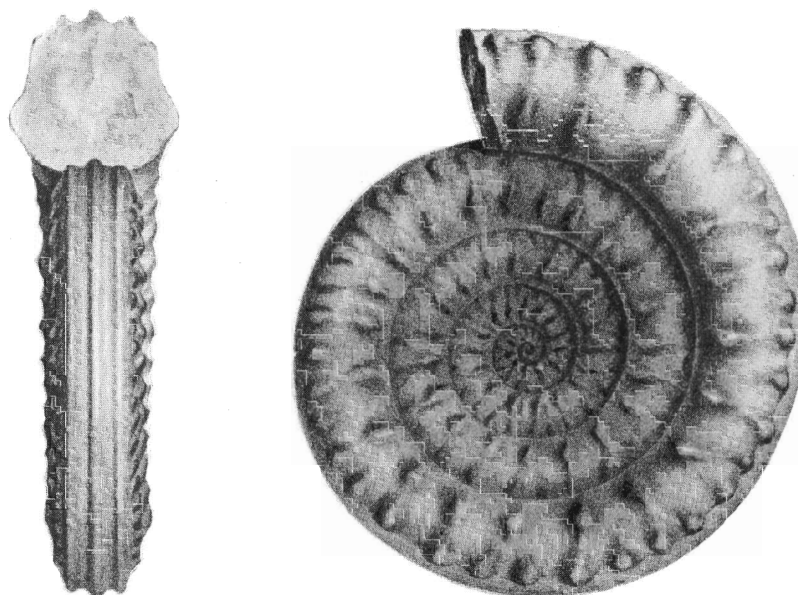
Plate 14, fig. 5; Plate 15, figs. 1-3, 6-7

- 1859 *Ammonites westphalicus* Von Strombeck, p. 56.
 1867 *Ammonites westphalicus* Von Strombeck; Schlüter, p. 30, pl. 6, fig. 2.
 1872 *Ammonites westphalicus* Von Strombeck; Schlüter, p. 45, pl. 13, figs. 5-6.
 1894 *Peroniceras westphalicum* Schlüter sp.; de Grossouvre, p. 98, pl. 12, figs. 1, 4; text-fig. 38.
 1984 *Peroniceras (Peroniceras) westphalicum* (Von Strombeck, 1867); Klinger and Kennedy, p. 164, figs. 24-28 (with synonymy).

Types. Von Strombeck's originals, from the Coniacian of Westphalia, have not been traced.

Material. The original of de Grossouvre 1894, pl. 12, fig. 1, M937/A38.1 (EMP Collections). The locality given is simply 'Touraine', but preservation suggests the Calcaire de Cangey of Cangey (Indre-et-Loire). FSL 14.109 is from the Grès Verts of Dieulefit (Drôme), as is OUM KZ19352, a juvenile here compared to the species.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
FSL 14.109	93.8 (100)	— (—)	28.5 (30.4)	—	45.1 (48.1)
M937/A38.1	93.2 (100)	— (—)	22.8 (24.5)	—	48.6 (52.1)
„ c	85.5 (100)	25.5 (29.8)	21.6 (25.3)	1.18	45.6 (53.3)
„ ic		23.0 (26.9)	21.6 (25.3)	1.06	



TEXT-FIG. 21. Copy of the photographs of *Ammonites tricarinatus* d'Orbigny, 1841 (pl. 91, figs. 1, 2), renamed *subtricarinatus* by d'Orbigny in 1850. The original, from near Sougraine (Aude) is figured as Pl. 12, figs. 7-9. All figures $\times 1$.

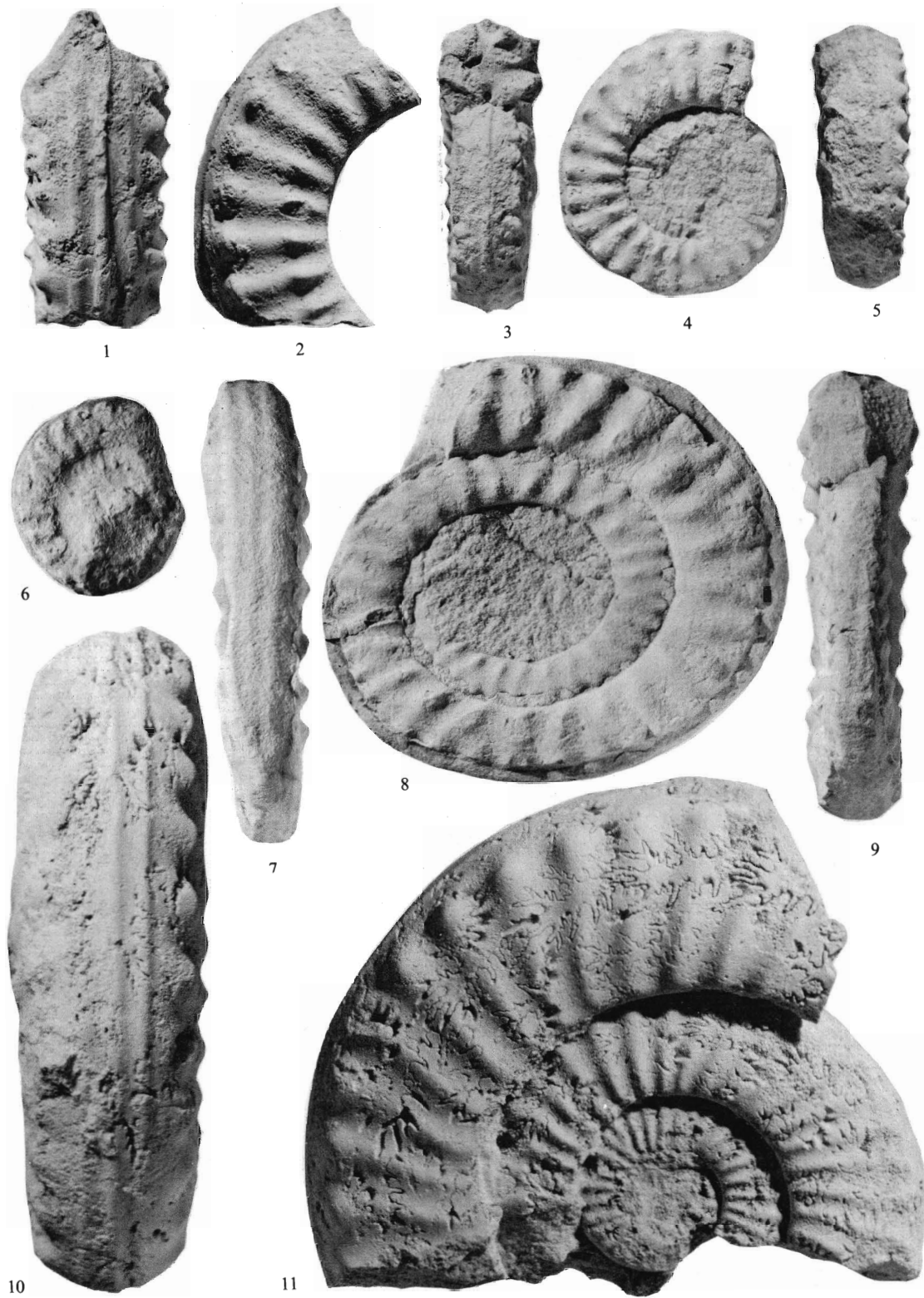
EXPLANATION OF PLATE 12

Figs. 1-5. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). 1, 2, outer whorl and 3-5, nucleus of a specimen from the Middle Coniacian *P. (P.) tridorsatum* Zone, Assize L¹ of Arnaud of La Boulinerie near Jonzac (Charente-Maritime), SP unregistered (*ex* Arnaud Collection). The inner whorls were figured by de Grossouvre 1894, pl. 11, fig. 1 and identified as *P. subtricarinatum* var. *tridorsatum*; the outer (unfigured) whorl was identified by de Grossouvre as *P. moureti*.

Figs. 6-9. *Peroniceras (Peroniceras) subtricarinatum* (d'Orbigny, 1850), MNHP, d'Orbigny Collection no. 7183, from the environs of Sougraine, Corbières (Aude). 6, paralectotype; 7-9, lectotype.

Figs. 10-11. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885). MNHP unregistered and without data, but the preservation indicates the Calcaires Durs de La Ribochère of Touraine.

All figures $\times 1$.



KENNEDY, *Peroniceras*

Description. The two specimens available are rather distinct. In FSL 14.109 coiling is very evolute, umbilicus comprising 52–53% of the diameter, with very shallow impressed dorsal zone. Umbilical wall low, inner flanks rounded, outer flanks flattened, convergent, with broadly rounded ventrolateral shoulders and broad, arched venter. Eighteen strong umbilical bullae, perched on umbilical shoulder, give rise to a low, broad distant rib or ribs, which weaken markedly at mid-flank. There are twenty-five strong ventrolateral clavi on either side of broad venter, which bears strong median keel flanked by grooves and much weaker lateral keels. In M937/A38.1, the whorl section is markedly depressed, twenty bullae correspond to only twenty-two ventral clavi. The suture line, well-exposed in the Dieulefit specimen, is deeply and intricately incised (Pl. 14, fig. 5).

Discussion. Both specimens are juveniles, but a later growth stage is shown by the (untraced) specimen from the Calcaires Durs de La Ribochère of La Ribochère figured by de Grossouvre (1894, pl. 12, fig. 4), where the decline of ribs on the mid-outer flank, strong, ear-like clavi, and decline of umbilical bullae are distinctive.

The species is difficult to interpret, because Von Strombeck's specimens have not been traced. In his description, however, he noted that there were intercalated and bifurcating ribs, giving nineteen or twenty umbilical bullae corresponding to twenty-seven ventral clavi.

Schlüter (1867), to whom the species is generally (but erroneously) attributed, figured a ventral view only (pl. 6, fig. 2) in his first account of the species (the specimen is lost), but gave apparently better illustrations in 1872 (pl. 13, figs. 5, 6) that show the broad, blunt ribs effaced on the mid-outer flank, and the prominent clavi. Matsumoto and Muramoto (1981) have questioned whether or not de Grossouvre's specimens all belong to the same species. The original of his pl. 12, fig. 4 differs from others in having virtually all the ribs single. South African material described by Klinger and Kennedy (1983) is variable in this respect, and all of de Grossouvre's specimens, *P. stefaninii* Venzo, 1936, *P. westphalicum australis* Venzo, 1936, *P. guerini* Collignon, 1965, and probably *P. latum* Matsumoto and Muramoto, 1981, can be regarded as members of a variable *P. (P.) westphalicum*.

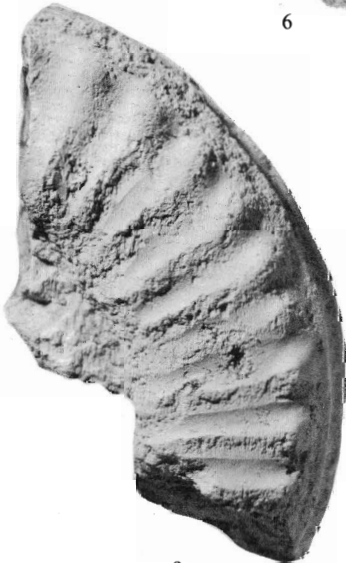
When compared with other species, the decline of bullae, virtual disappearance of ribs on the mid-outer flank, prominent clavi, and branching and intercalation of ribs in *P. (P.) westphalicum* are distinct (see discussion in Klinger and Kennedy 1984).

Occurrence. Middle Coniacian, *P. (P.) tridorsatum* Zone of Dieulefit (Drôme), Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher), Calcaire de Cangey of Cangey (Indre-et-Loire), white chalk of Hallincourt (Nord). Widely recorded in north Germany. Also known from Italy, Zululand, South Africa, Madagascar, possibly Japan, and Texas, U.S.A. Where well dated the species is always Middle Coniacian.

EXPLANATION OF PLATE 13

- Figs. 1–4. *Pachydiscoides janeti* (de Grossouvre, 1894). The holotype, MNHP unregistered, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher), figured by de Grossouvre 1894, pl. 22, fig. 4.
 Figs. 5–11. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867). 5–6, 9, the original of de Grossouvre 1894, pl. 11, fig. 3, a paratype of *P. moureti* de Grossouvre, 1894, Middle Coniacian *P. (P.) tridorsatum* Zone, Assize L¹ of Arnaud of La Boulinerie near Jonzac (Charente-Maritime), SP unregistered (ex Arnaud Collection). 7, 8, from the same horizon, locality, and collection, and also identified by de Grossouvre as *P. moureti*. 10, 11, the holotype of *P. rousseauxi* de Grossouvre, 1894, pl. 11, fig. 5, from the same horizon as the previous specimens at St. Simon-de-Jonzac (Charente-Maritime).

All figures × 1.





TEXT-FIG. 22. *Peroniceras (Peroniceras) dravidicum* (Kossmat, 1895). MNHP 1896-22 (ex de Vibraye Collection), Calcaire de Cangey of Cangey (Indre-et-Loir), scale bar 5 cm.

EXPLANATION OF PLATE 14

Figs. 1, 4. *Peroniceras (Peroniceras) tridorsatum* (Schlüter, 1867), FSL 14.108a, Middle Coniacian *P. (P.) tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme). 4, the original of *P. subtricarinatum* var. *tridorsatum* of de Grossouvre 1894, pl. 10, fig. 2, SP unregistered (ex Le Mesle Collection), Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).

Figs. 2, 3. *Peroniceras (Peroniceras) lepeei* (Fallot, 1885), FSL 14.110, horizon and locality as above.

Fig. 5. *Peroniceras (Peroniceras) westphalicum* (Von Strombeck, 1859), FSL 14.109, horizon and locality as for the originals of Figs. 1-3.

Fig. 6. *Peroniceras (Peroniceras)* sp. FSR unregistered, Calcaire de Cangey of Cangey (Indre-et-Loire).

All figures $\times 1$.



1



2



3



4



5



6

Peroniceras (Peroniceras) dravidicum (Kossmat, 1895)

Plate 15, figs. 4-5; text-figs. 13i, j, 18f, 22

- 1865 *Ammonites sub-tricarinatus* d'Orbigny; Stoliczka, p. 54, pl. 31, fig. 3.
 1895 *Schloenbachia (Peroniceras) dravidica* Kossmat, p. 190, pl. 22, fig. 3.
 1984 *Peroniceras (Peroniceras) dravidicum* Kossmat, 1895; Klinger and Kennedy, p. 170, figs. 29-42 (with full synonymy).

Types. Kossmat (1895, p. 190) referred to the original of Stoliczka (1865, p. 54, pl. 31, fig. 3) from the Trichinopoly Group of Kurribiem, Trichinopoly, southern India and mentioned several other specimens. Matsumoto (1965b, p. 213) has designated the original of Kossmat (1895, pl. 23, fig. 3—the inner whorls of Stoliczka's figured specimen) lectotype of the species.

Material. MNHP 1895-9 (*ex* Durand Collection), from 'Villedieu'; MNHP 1896-22 (*ex* de Vibraye Collection) from the Calcaire de Cangey of Cangey (Indre-et-Loire); SP unregistered (*ex* Toucas Collection) from the Grès Verts de Dieulefit (Drôme).

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
MNHP 1896-27	163.0 (100)	— (—)	40.5 (30.7)	—	84.5 (51.8)

Description. Coiling very evolute, umbilicus comprising over 50% of diameter. Umbilical wall low, notched to accommodate ventrolateral tubercles of succeeding whorl; umbilical shoulder narrowly rounded. Inner flanks rounded, outer flanks flattened and convergent, maximum breadth low on flanks, whorl breadth to height ratio 0.88 (in MNHP 1895-9); ventrolateral shoulders broadly rounded, venter broad and arched. The two specimens show parallel ontogenetic changes but develop what appear to be modifications associated with approaching maturity at rather different sizes (Pl. 15, figs. 4-5; text-fig. 22). On the phragmocone there are eighteen strong umbilical bullae per whorl. These give rise to one or two strong, broad, prorsiradiate ribs, to give a total of twenty-six ribs per whorl. All ribs bear a strong clavate ventrolateral tubercle, housed in notched umbilical wall of succeeding whorl. Venter of innermost whorls poorly preserved; MNHP 1895-9 shows a strong siphonal keel and flanking grooves, with lateral keels poorly developed at a diameter of approximately 50 mm. By a diameter of 65 mm, however, weak lateral keels have developed in this specimen; they strengthen markedly by the beginning of body chamber.

The body chamber of MNHP 1895-9 shows a marked decline in strength of bullae and coarseness of ribs, with most arising singly from the umbilical shoulder. Ventrolateral tubercles are also relatively less prominent and less markedly clavate. Venter distinctly tricarinate, although lateral keels are weak. MNHP 1896-22 has twenty-five to twenty-six umbilical bullae on the outer whorl, but all ribs are single on body chamber to give a total of twenty-eight to thirty. Bullae weaken on body chamber, as do ventrolateral tubercles.

Suture line imperfectly exposed; visible elements deeply incised (text-fig. 18f).

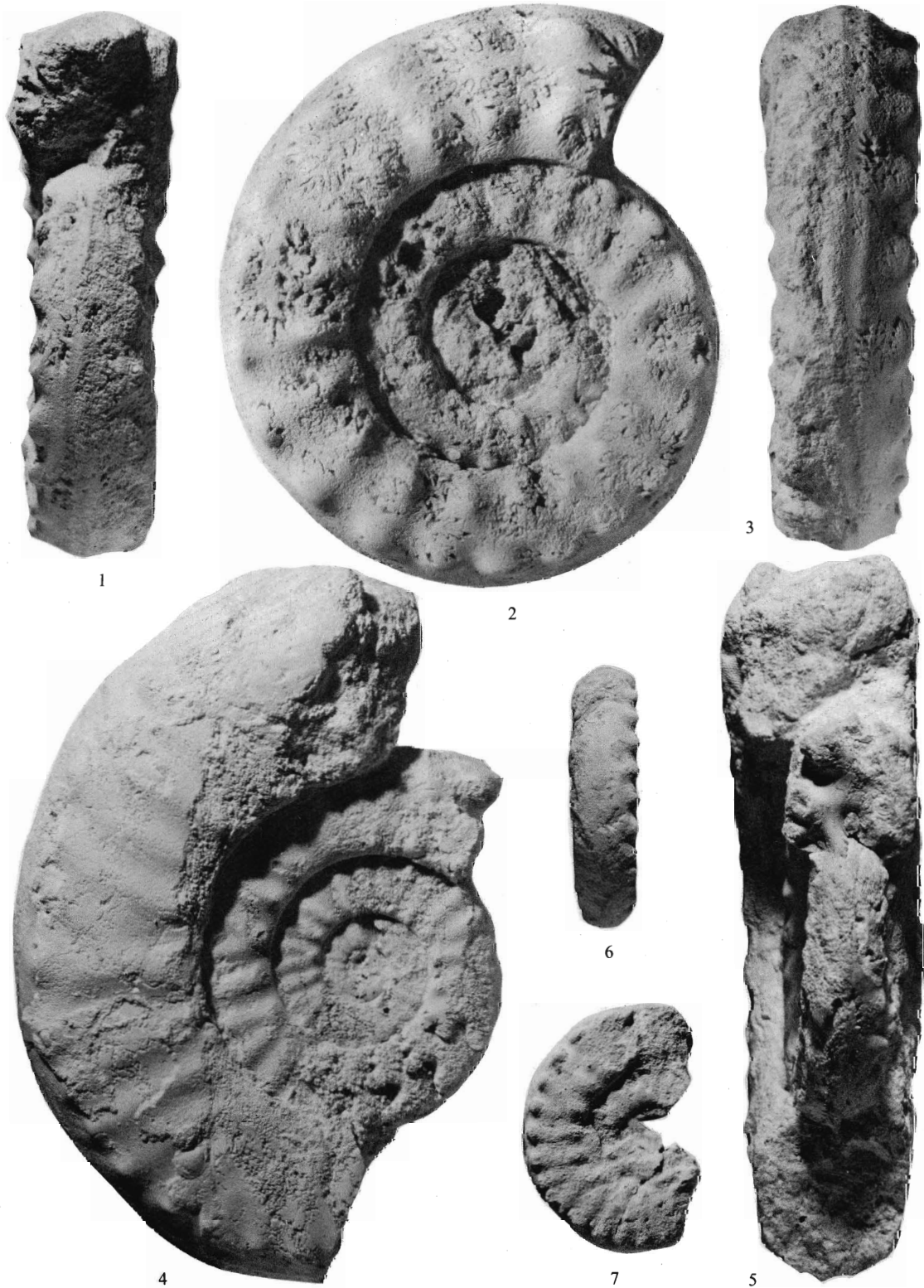
Discussion. The modification of ornament suggests that the two specimens described above are approaching maturity: their different sizes may indicate a size dimorphism like that seen in other Acanthocerataceae. The coarse bifurcating ornament of the inner whorls recalls that of *P. (P.) sub-tricarinatum* (d'Orbigny, 1841) (see p. 70; Pl. 12, figs. 7-9). This, however, is distinctly tricarinate at a stage when the present species is essentially unicarinate, whilst the ventrolateral tubercles are less markedly clavate and the short intercalated ribs prominent. At maturity, *P. (P.) sub-tricarinatum* retains a slowly expanding almost tubular, rounded whorl (see Klinger and Kennedy 1984).

EXPLANATION OF PLATE 15

Figs. 1-3. *Peroniceras (Peroniceras) westphalicum* (Von Strombeck, 1859). EMP Collections, Craie de Villedieu, Touraine. Figured by de Grossouvre 1894, pl. 12, fig. 1.

Figs. 4-7. *Peroniceras (Peroniceras) dravidicum* (Kossmat, 1895). 4, 5, MNHP 1895-9 (*ex* Durand Collection), Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). 6, 7, SP unregistered (*ex* Toucas Collection), Middle Coniacian *P. (P.) tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme).

All figures $\times 1$.



KENNEDY, *Peroniceras*

P. (P.) westphalicum (von Strombeck, 1859) (see p. 71, Pl. 14, fig. 5) is a further species with coarse bifurcating ribs on the inner whorls, but in middle and later growth the umbilical bullae weaken as do the ribs, which fail to reach the ventrolateral clavi in some cases, leaving a smooth zone at mid-flank.

Occurrence. The French specimens are from the lower part of the Craie de Villedieu, the Calcaires Durs de La Ribochère of La Ribochère, Couture, Loir-et-Cher, the Calcaire de Cangey of Cangey, Indre-et-Loire, and the Grès Vert de Dieulefit, Drôme. The type material is from the Coniacian Trichinopoly Group of southern India, and there are records from northern Spain, Italy, north, west, and central Africa, and Madagascar. In Zululand, precisely localized specimens are restricted to divisions II and III of Kennedy and Klinger (1975).

Peroniceras (Peroniceras) sp.

Plate 14, fig. 6

Material. A single unregistered specimen from the Calcaire de Cangey of Cangey (Indre-et-Loire) (FSR Collections).

Remarks. The specimen is very worn, evolute, slowly expanding, with dense broad ribs. It is not specifically determinable but is of interest as a record of a second *P. (Peroniceras)* species from the Calcaire de Cangey.

Subgenus ZULUICERAS Van Hoepen, 1965

[For synonymy see Klinger and Kennedy 1984, p. 180]

Type species. Zuluiceras zulu Van Hoepen, 1965, p. 9, pl. 5, text-figs. 1*g-i*, 2*b*.

For diagnosis and discussion see Klinger and Kennedy 1984, p. 180.

Occurrence. Middle Coniacian, *P. (P.) tridorsatum* Zone of Touraine, Aquitaine, Dieulefit (Drôme), the Corbières (Aude), and Provence in France; Germany, Czechoslovakia, Austria, Italy, Romania, Armenia, Zululand, South Africa, Madagascar, and Japan. Upper Coniacian of Zululand and possibly Japan.

Peroniceras (Zuluiceras) bajuvaricum (Redtenbacher, 1873)

Plate 16, figs. 1-3, 6-11; Plate 17, figs. 1-3; text-figs. 13*K*, 20*B*, C, E, 23, 24, 25

- 1873 *Ammonites bajuvaricum* Redtenbacher, p. 107, pl. 24, fig. 2.
 ?1873 *Ammonites aberlei* Redtenbacher, p. 111, pl. 25, figs. 4*a-c* only.
 ?1873 *Ammonites* spec. indet. Redtenbacher, p. 125, pl. 30, fig. 5.
 1894 *Gauthiericeras bajuvaricum* Redtenbacher; de Grossouvre, p. 88, pl. 9, fig. 1; pl. 12, figs. 2, 3; text-fig. 35.
 1895 *Gauthiericeras bajuvaricum* Redtenbacher; Jahn, p. 136, text-figs. 1, 2.
 non 1907 *Schloenbachia (Gauthiericeras) bajuvarica* Redtenb.; Boule, Lemoine and Thévenin, p. 22, pl. 12, fig. 1.
 ?1913 *Peroniceras westphalicum* d'Orb.; Scupin, p. 94, pl. 4, fig. 8.
 ?1920 *Peroniceras (Gauthiericeras) bajuvaricum* Redtenbacher; Desio, p. 217, pl. 16, figs. 3, 6; pl. 17, fig. 3.
 1936 *Gauthiericeras bajuvaricum* (Redtenbacher) var. *schoenbergensis* Venzo, p. 105, pl. 9, fig. 5; pl. 11, fig. 7.
 1958*a* *Gauthiericeras bajuvaricum* (Redtenbacher); Reyment, p. 43, pl. 11, fig. 1; text-figs. 6, 3*a-b*.
 ?1963 *Gauthiericeras bajuvaricum* Redtenbacher sp.; Fabre-Taxy, p. 112, pl. 4, fig. 4.
 1965*b* *Sornayceras bajuvaricum* (Redtenbacher); Matsumoto, p. 226*f*.
 ?1965*b* *Sornayceras* sp. cf. *S. propoetidum* (Redtenbacher); Matsumoto, p. 233, pl. 39, figs. 2, 3; text-fig. 16.
 1965*b* *Sornayceras omorii* Matsumoto, p. 230, pl. 42, figs. 1, 2; text-figs. 13-15.
 ?1972 *Sornayceras* cf. *bajuvaricum* Redtenbacher, 1873; Atabekian and Akopin, p. 10, pl. 3, figs. 4, 5.
 1984 *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873); Klinger and Kennedy, p. 235, figs. 92*b-c*, 93.

Types. Reymont (1958a, p. 43) designated the original of Redtenbacher 1873, pl. 24, fig. 2a-c lectotype of the species. It is no. 3432 in the Collection of the Geologischen Bundesanstalt, Vienna, and is from the Gosau Beds of Leiner Alpe, Austria. Possible paralectotypes are GBA 1935/01/5 also from Leiner Alpe, and GBA 1935/01/13, from Schmölnauer Alpe, Austria.

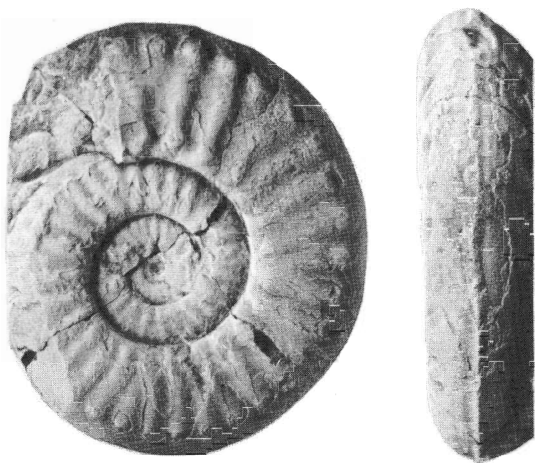
<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wb</i>	<i>U</i>
De Grossouvre 1894, pl. 9, fig. 1	165.1 (100)	44.0 (26.7)	55.2 (33.5)	0.80	62.6 (37.9)
MNHP 7185	125.0 (100)	32.2 (25.8)	45.8 (36.6)	0.70	44.4 (35.5)
MNHP 1895-9, Durand Coll.	105.4 (100)	26.5 (25.1)	32.2 (30.6)	0.82	38.5 (36.5)
OUM KZ17022	86.8 (100)	— (—)	32.8 (37.8)	—	31.1 (35.8)
MNHP 1896-27	68.0 (100)	16.7 (24.6)	22.7 (33.4)	0.74	27.5 (40.4)
MNHP 16805	44.9 (100)	13.5 (30.1)	16.0 (35.6)	0.84	16.0 (35.6)
MNHP B16690	31.7 (100)	9.0 (28.4)	11.4 (36.0)	0.79	12.0 (37.9)

Material. MNHP 7185 (d'Orbigny Coll.), is from 'Villedieu' (= the type of *A. dirce* d'Orbigny m.s.), as is MNHP 16805 and a large FSM specimen (unregistered). MNHP B16806 from 'Carrière de la Ribochère; OUM KZ17022, from 20 cm above the base of Bed 3 of the Calcaires Durs de La Ribochère (= Zone A of de Grossouvre) at the roadside sections between Trehet and Villedieu-le-Château, opposite and E of the turning to Grouteau, Loir-et-Cher; MNHP 1895-9 (ex Durand Collection) labelled '*Am. bourgeoise* Villedieu'; an unregistered MNHP specimen labelled '*A. bajuvaricus*', 'Couture'. The original of de Grossouvre 1894, pl. 9, fig. 1 (MNHP unregistered), from the 'partie inférieure de la Craie de Villedieu, Carrières de la Ribochère, commune de Couture, Loir-et-Cher' (de Grossouvre 1894, p. 90) (ex Le Mesle Collection). Preservation of all specimens shows them to be from the Calcaires Durs de La Ribochère—de Grossouves' Zone A. MNHP 1896.27 (de Vibraye Collection) and MNHP B16690 are both from the Calcaire de Cangey of Cangey (Indre-et-Loire). The preservation of the original of de Grossouvre 1894, pl. 12, fig. 2 (EMP M936/138.1) suggests that it is also from Cangey rather than Villedieu as de Grossouvre stated. An unregistered specimen in the Université de Poitiers is labelled Poncé (Sarthe).

Description. The largest specimen seen is still septate at a diameter of 195 mm, indicating that the species reached a large size. Small and medium-sized specimens (between 30 and 105 mm diameter) are evolute platycones with umbilical diameters ranging between 35 and 40% of diameter. Umbilicus shallow, with low flat wall and narrowly rounded umbilical shoulder; whorl section compressed, with whorl breadth to height ratio 0.74 to 0.84, greatest breadth at umbilical bullae or close to umbilical shoulder intercostally; flanks flattened and convergent, ventrolateral shoulders rounded, venter fastigiate-carinate. Twenty-two to twenty-eight umbilical bullae per whorl give rise to one or two low, broad, straight, prorsiradiate ribs, markedly effaced at mid-flank. Occasional shorter ribs intercalate, to give a total of thirty-four to forty ribs per whorl. All ribs bear bullate or rounded ventrolateral tubercles; a strong, sharp siphonal keel is flanked by broad, shallow grooves, the outer edges of which are sharp but not raised into distinct lateral keels; broad ventrolateral zone between grooves and ventral clavi may be feebly undulose, undulations corresponding to terminations of feeble extensions of ribs on to shoulder. Keel smooth and entire or with shallow depressions extending across venter from interspaces between ventrolateral tubercles to give distinct but weak undulations. MNHP 7185 also shows spiral striations on ventrolateral shoulders.

Largest specimen seen has twenty-two umbilical bullae at diameter 195 mm, but they are much less prominent than on the smaller specimens; ribs are low and weak (in part due to wear), and ventrolateral tubercles low and rounded-bullate, totalling approximately thirty-six per whorl. Venter broad, with blunt siphonal keel and flanking grooves. Suture line moderately intricately incised, with broad bifid E/L, narrow-necked L and large, asymmetrically bifid L/U₂.

Discussion. The lectotype of *A. bajuvaricus* Redtenbacher, 1873 (p. 107, pl. 24, fig. 2) is a damaged, wholly septate internal mould 59 mm in diameter. Coiling is relatively evolute, the umbilicus comprising approximately 33% of the diameter, shallow, with a rounded undercut wall on the mould. The whorl section is compressed (probably accentuated by crushing), with a breadth to height ratio of 0.57, parallel flanks, shoulders rounded in intercostal section and somewhat flattened in costal section. There are twelve to thirteen feeble, crowded umbilical bullae per half whorl, corresponding to twenty-one ribs. The ribs are straight or slightly flexed, radial to feebly prorsiradiate, and arise



TEXT-FIG. 23. *Peroniceras (Zuluiceras) omorii* (Matsumoto, 1965), holotype, Ikushumbets, Ishikari Province, Hokkaido, Japan, Kyushu University Collections no. H5493, $\times 1$. The species is regarded as a synonym of *P. (Z.) bajuvaricum* (Redtenbacher, 1873).

singly or in pairs from the bullae, with some intercalated ribs. The ribs are delicate, narrow close to the umbilicus, but broadening towards the ventrolateral shoulder, where they all bear a small but distinct conical tubercle. From this tubercle a low, broad rib extends over the shoulder. There is a strong siphonal keel, flanked by shallow grooves. The specimen is more compressed and involute than most French specimens, but this is due in part or wholly to distortion. Of other Austrian specimens, GBA 1935/01/13 shows a distinctly serrated keel at similar dimensions to the lectotype, whilst NHMW 1935.III.43, a large fragment tentatively referred to the species, shows an apparently blunter keel at a whorl height of 24 mm.

P. (Z.) aberlei (Redtenbacher, 1873) (p. 111, pl. 25, fig. 4a-e) was based on a series of specimens from the Gosau Beds of Ströbl, Weissenseebach, Austria, preserved in the Francisco-Carolinum Museum, Linz, the Carolina-Augustum Museum, Salzburg, and the Geologische Reichsanstalt, Vienna. Dr. H. Summesberger of the Naturhistorisches Museum, Vienna, has recovered the original of Redtenbacher's fig. 4a-c, which is now in the Oberösterreich Landesmuseum, Linz. It is herein designated lectotype of the species. It is a crushed, distorted mould 59 mm in diameter, and is wholly septate. The coiling is moderately evolute, the umbilicus of moderate breadth with a low wall that is undercut on the mould. There are approximately sixteen well-developed umbilical bullae per whorl, corresponding to twenty-eight ribs. The ribs arise from the bullae either singly or in pairs, and are low, broad, flat, and slightly prorsiradiate. They decline markedly across the middle of the flanks, but strengthen into well-marked, slightly clavate ventrolateral tubercles. From these tubercles low ribs pass across the shoulders, declining rapidly before reaching the grooves on either side of a strong, faintly undulose siphonal keel. The lectotype falls within the range of variation of French specimens referred to *P. (Z.) bajuvaricum*, but it must be admitted that the ill-preserved Austrian juveniles of this

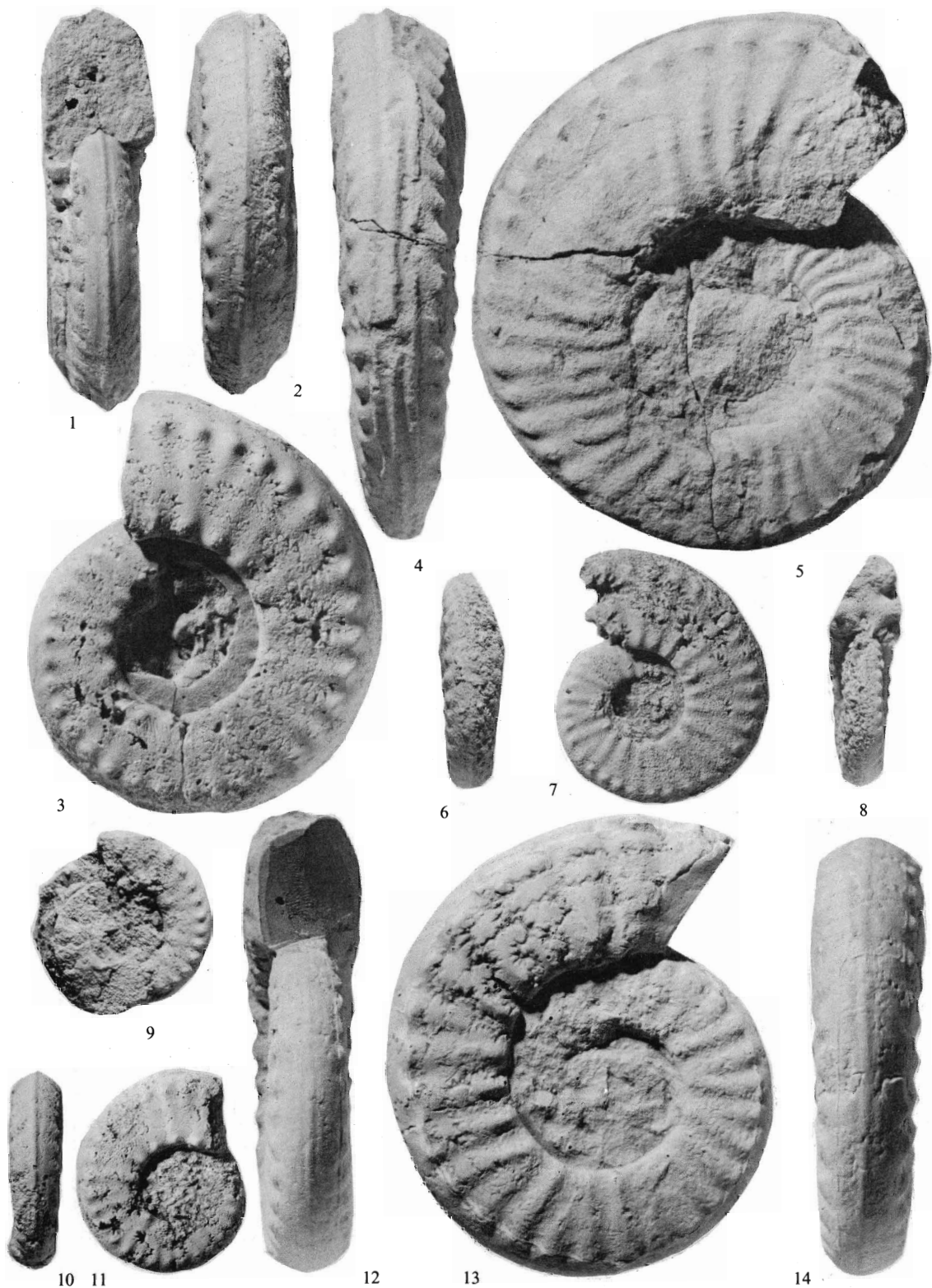
EXPLANATION OF PLATE 16

Figs. 1-3, 6-11. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). 1-3, MNHP 1896-27 (de Vibraye Collection), Calcaire de Cangey of Cangey (Indre-et-Loire). 6-8, MNHP 10805; 9, MNHP B16805, both from the Calcaires Durs de La Ribochère of Couture (Loir-et-Cher). 10, 11, MNHP B16690, same horizon and locality as 1-3.

Figs. 4-5. *Peroniceras (Peroniceras) aff. lepeei* (Fallot, 1885), EMP unregistered, original of de Grossouvre 1894, pl. 11, fig. 2, Grès Verts de Dieulefit of Dieulefit (Drôme).

Figs. 12-14. *Peroniceras (Zuluiceras) isamberti* (Fallot, 1885), casts of the lectotype, the original of Fallot 1885, pl. 2, fig. 1, the original of which is in the LGD Collections and is from the same horizon and locality as the originals of Figs. 4, 5.

All figures $\times 1$.





TEXT-FIG. 24 *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), original of de Grossouvre 1894, pl. 9, fig. 1, MNHP unregistered (ex Le Mesle Collection), Calcaires Durs de La Ribochère of the Carrières de La Ribochère, Couture (Loir-et-Cher), scale bar 5 cm.

subgenus are very unsatisfactory as type specimens of species that grow to diameters of 500 mm and more. *P. (Z.) propoetidum* (Redtenbacher, 1873) (p. 116, pl. 26, fig. 6a-c) is a further Gosau species. The holotype is preserved in the collections of the Geologischen Bundesanstalt, Vienna, and is from the Gosau Beds of Schmölnauer Alpe, near Ströbl, Austria. It is very crushed and distorted, and because of this the proportions cannot be estimated. There are an estimated twenty-four umbilical bullae per whorl, a total of forty-two to forty-four ribs per whorl, and a strong undulose siphonal keel. At the smallest diameter visible these undulations merit description as clavi, but they become much less marked as size increases. The undulations on the siphonal keel and the apparently more involute shell separate this species from the material described here.

P. (Z.) isamberti (Fallot, 1885) (p. 232, pl. 2, fig. 1) is more evolute and slower-expanding than



TEXT-FIG. 25. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873). MNHP, d'Orbigny Collection no. 7185, holotype of *Ammonites dirce* d'Orbigny ms., from 'La Villedieu, Sarthe', $\times 1$.

any of the material referred to the present species, with coarser ribs and ventrolateral tubercles that are markedly clavate. *P. (Z.) omorii* (Matsumoto, 1965b) (p. 230, pl. 42, figs. 1, 2; text-figs. 13–15) (see text-fig. 23) from the Coniacian of Hokkaido, Japan, falls within the limits of *P. (Z.) bajuvaricum* as here interpreted, as may his *Sornayceras* sp. cf. *S. propoetidum* (1965b, p. 233, pl. 39, figs. 2, 3; text-fig. 16). In contrast, *P. (Z.) proteus* (Matsumoto, 1965b, p. 227, pl. 40, fig. 1; pl. 41, fig. 1; text-figs. 11–12), also from Hokkaido is very evolute ($U = 47\%$), slowly expanding, with a whorl breadth to height ratio of 0.88–0.95 and very coarse ribs, far beyond the variation shown by the present material. *P. (Z.) wadae* (Matsumoto, 1971) (p. 142, pl. 24, fig. 1; text-fig. 8) is a much more involute, sparsely, and bluntly ornamented species, also from Japan.

The numerous 'Zuluiceras' and 'Zuluites' described from Zululand by Van Hoepen (1965) are based on large adults that are difficult to compare with the nuclei described from elsewhere. They are discussed at length by Klinger and Kennedy (1984).

Occurrence. The only precisely located French specimen is a pebble fossil from 30 cm above the base of Bed 3 of the Calcaires Durs de La Ribochère of Villedieu-le-Château, high in de Grossouvre's Zone A. The other specimens from this general area are all in a preservation indicating that they are from the Calcaires Durs. The

species is also recorded from the Calcaire de Cangey of Cangey, Indre-et-Loire, and de Grossouvre (1894, p. 81) records it from Assize L¹ of Arnaud, near Cognac (Charente-Maritime). Fabre-Taxy (1963) records it from north of La Cadière (Var); the figure is unrecognizable. The species is recorded from the Coniacian of Italy (Florence) and certainly occurs in the Priesener Schichten of Priesen, Czechoslovakia. The Austrian records are not precisely localized. In Japan representatives of this species are said to be Upper Coniacian. Precisely localized South African (Zululand) specimens are from the Middle Coniacian, Coniacian II-III of Kennedy and Klinger (1975).

Peroniceras (Zuluiceras) isamberti (Fallot, 1885)

Plate 16, figs. 12-14

- 1885 *Ammonites (Schloenbachia) isamberti* Fallot, p. 232, pl. 2, fig. 1.
 1894 *Gauthiericeras bajuvaricum* Redtenbacher sp.; de Grossouvre, p. 88 (*pars*).
 1965 *Sornayceras isamberti* (Fallot); Matsumoto, p. 232.

Types. Fallot (1885, p. 233) describes this species as being very rare, but mentions specimens in the Slizewicz and Soulier Collections. The original of Fallot's (1885) pl. 2, fig. 1 is preserved in the LGD Collections at Grenoble (there is a cast in the SP Collections). It is herein designated lectotype of the species, and is from the 'Grès vert supérieur' of Dieulefit (Drôme); Middle Coniacian, *tridorsatum* Zone.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
Lectotype	74.0 (100)	19.2 (25.9)	22.5 (30.4)	0.85	32.5 (43.9)

Description. Very evolute, umbilicus comprising 43.9% of diameter. Whorls expand slowly; whorl breadth to height ratio 0.85. Umbilical wall low and rounded, whorl sides flattened, subparallel, ventrolateral shoulders broadly rounded, venter fastigiate. Nineteen or twenty well-marked umbilical bullae per whorl give rise to one or two strong, blunt, straight prorsiradiate ribs, the total being thirty-one or thirty-two on the outer whorl. All ribs terminate in strong ventrolateral clavi. Preservation of the venter poor, but a broad smooth zone separates these clavi from shallow grooves on either side of strong siphonal keel. Although wholly septate, mould is too imperfect to show details of suture line.

Discussion. De Grossouvre (1894, p. 88) regarded *A. bajuvaricum* Redtenbacher, 1873 and *A. isamberti* Fallot, 1885 as synonyms, and pointed out that they differ only in the wider umbilicus and coarser, stronger ribbing of the latter. The type of *isamberti* has a whorl breadth to height ratio that falls within the range of specimens attributed to *P. (Z.) bajuvaricum*, and with $U = 43.9\%$ is only a little more widely umbilicate than MNHP 1896-27, where $U = 40.4\%$. Apart from this specimen, U varies from 31.5% to 37.9% in *P. (Z.) bajuvaricum* ($U = 33\%$ in the lectotype). The clavate ventrolateral tubercles are, however, more elongate than those of *bajuvaricum*. Without more material it is impossible to satisfactorily determine whether *isamberti* is a strict synonym of *bajuvaricum*, and it is maintained separate here with some hesitation.

Occurrence. As for types.

Peroniceras (Zuluiceras) sp. nov.

Plate 17, figs. 4-5

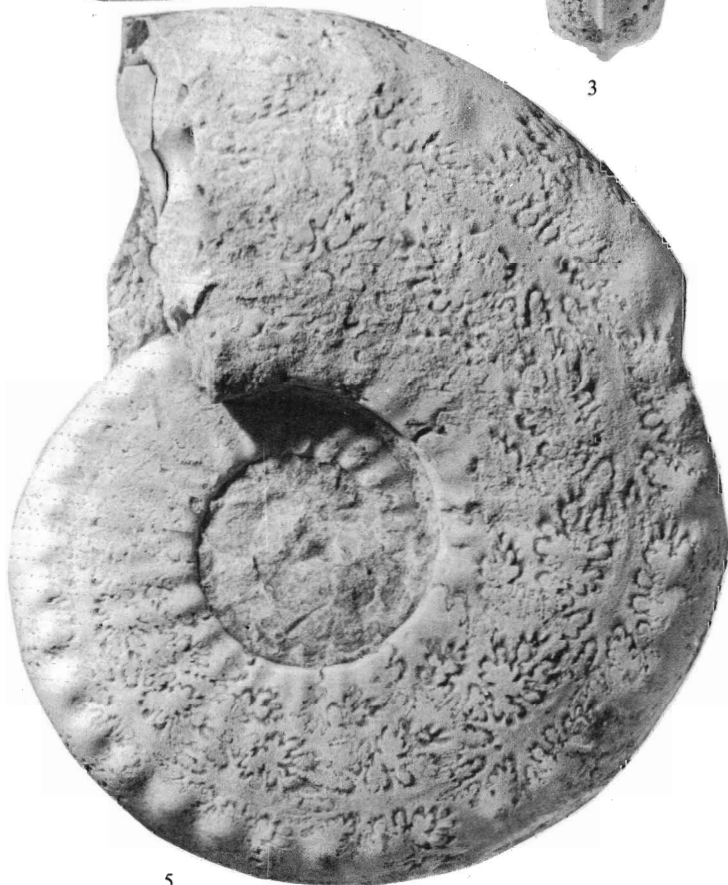
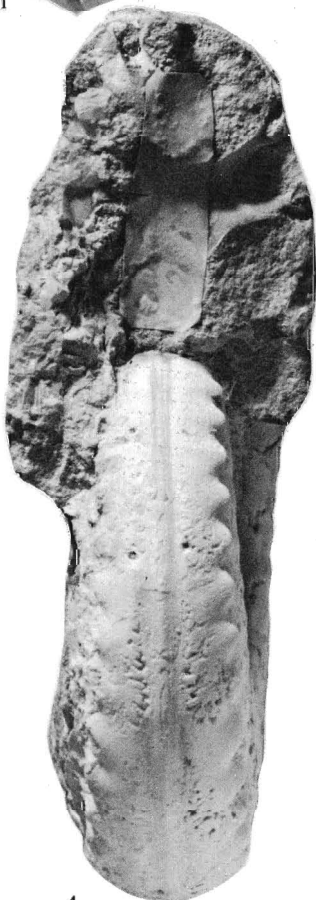
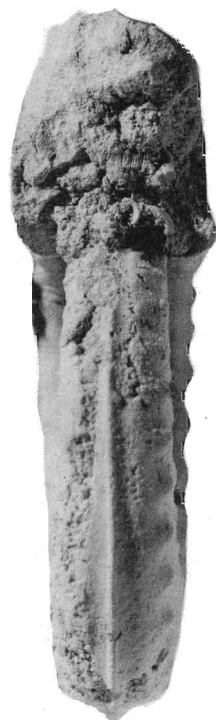
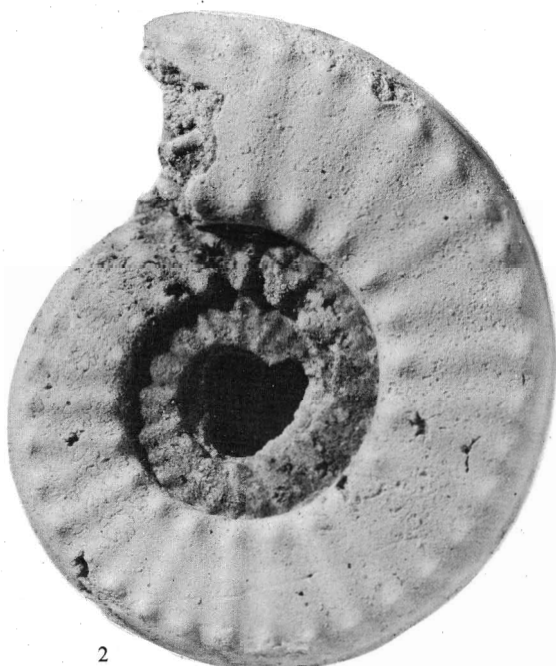
Material. FSL 14.113, from the Middle Coniacian *tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme) (ex Morin Collection).

EXPLANATION OF PLATE 17

Figs. 1-3. *Peroniceras (Zuluiceras) bajuvaricum* (Redtenbacher, 1873), EMP Collections, original of de Grossouvre 1894, pl. 12, fig. 2, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).

Figs. 4-5. *Peroniceras (Zuluiceras) sp. nov.*, FSL 14.113, Middle Coniacian *P. (Peroniceras) tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme).

All figures $\times 1$.



Dimensions (mm)	D	Wb	Wh	Wb:Wh	U
FSL 14.113	135 (100)	39.6 (29.3)	58.0 (43.0)	0.68	42.0 (31)

Description. A wholly septate internal mould. Coiling moderately involute, approximately 45% of previous whorl covered; umbilicus comprises 42% of diameter, of moderate depth, with rounded undercut wall; umbilical shoulder narrowly rounded. Whorl section compressed, whorl breadth to height ratio 0.68; greatest breadth close to umbilical shoulder, sides flattened, convergent, venter broadly fastigiate. Twenty-seven to twenty-eight small bullae at umbilical shoulder give rise to low, broad straight ribs, singly or in pairs; all terminate in conical to feebly clavate ventral tubercles, of which there are thirty-five to thirty-six on the outer whorl. Siphonal keel low, entire, flanked by broad shallow grooves. Suture (Pl. 17, fig. 5) complex, as in other *P. (Zuluiceras)*.

Discussion. This is the best-preserved large French *Zuluiceras*, still septate at a diameter of 135 mm. It most strongly recalls *P. (Z.) bajuvaricum* among the European species, but the expansion rate is significantly higher, with a whorl height of 43% compared to 30–37% in French representatives of Redtenbacher's species, and a consequently smaller umbilicus (U = 31% vs. 35–37% in comparably sized *bajuvaricum*). *P. (Z.) propoetidum* (Redtenbacher, 1873, p. 116, pl. 26, fig. 6) is also similar (with a few more ribs), but the strongly serrated keel of the Austrian form is very different from the smooth and entire keel of the French example.

Of the South African species there is some resemblance to *P. (Z.) rarum* Van Hoepen, 1965 (p. 16, pl. 12, text-fig. 4c) which has, however, a crenulated siphonal keel, and *P. (Z.) modestum* Van Hoepen, 1965 (p. 24, pl. 19, text-fig. 6a–b), which has a rounded whorl section and a serrated siphonal keel.

Genus GAUTHIERICERAS de Grossouvre, 1894

[For synonymy see Klinger and Kennedy 1984, p. 238]

Type species. *A. margae* Schlüter, 1867, p. 29, pl. 5, fig. 2, by original designation by de Grossouvre (1894, p. 87).

Remarks. For a complete diagnosis and discussion of this genus see Klinger and Kennedy 1984, pp. 238–243.

Two definite *Gauthiericeras* species are recorded from France in the following pages: *G. margae* and *G. nouelianum*. The diminutive *Schloenbachia boreau* de Grossouvre, 1894 may also be a *Gauthiericeras*. Of other European species referred to the genus, *G. margae turzoi* Karrenberg, 1935, *G. margae gorda* Karrenberg, 1935, *G. vallei* Ciry, 1940, and *G. vallei gorda* Ciry, 1940, are *Prionocycloceras*.

Occurrence. Upper Coniacian of France, Spain, central Europe, east and west Africa, Madagascar, New Caledonia, Mexico, Colombia, and Peru. If 'S.' *boreau* de Grossouvre, 1894, is accepted, the range is extended to the Middle Coniacian of Touraine and Aquitaine in France.

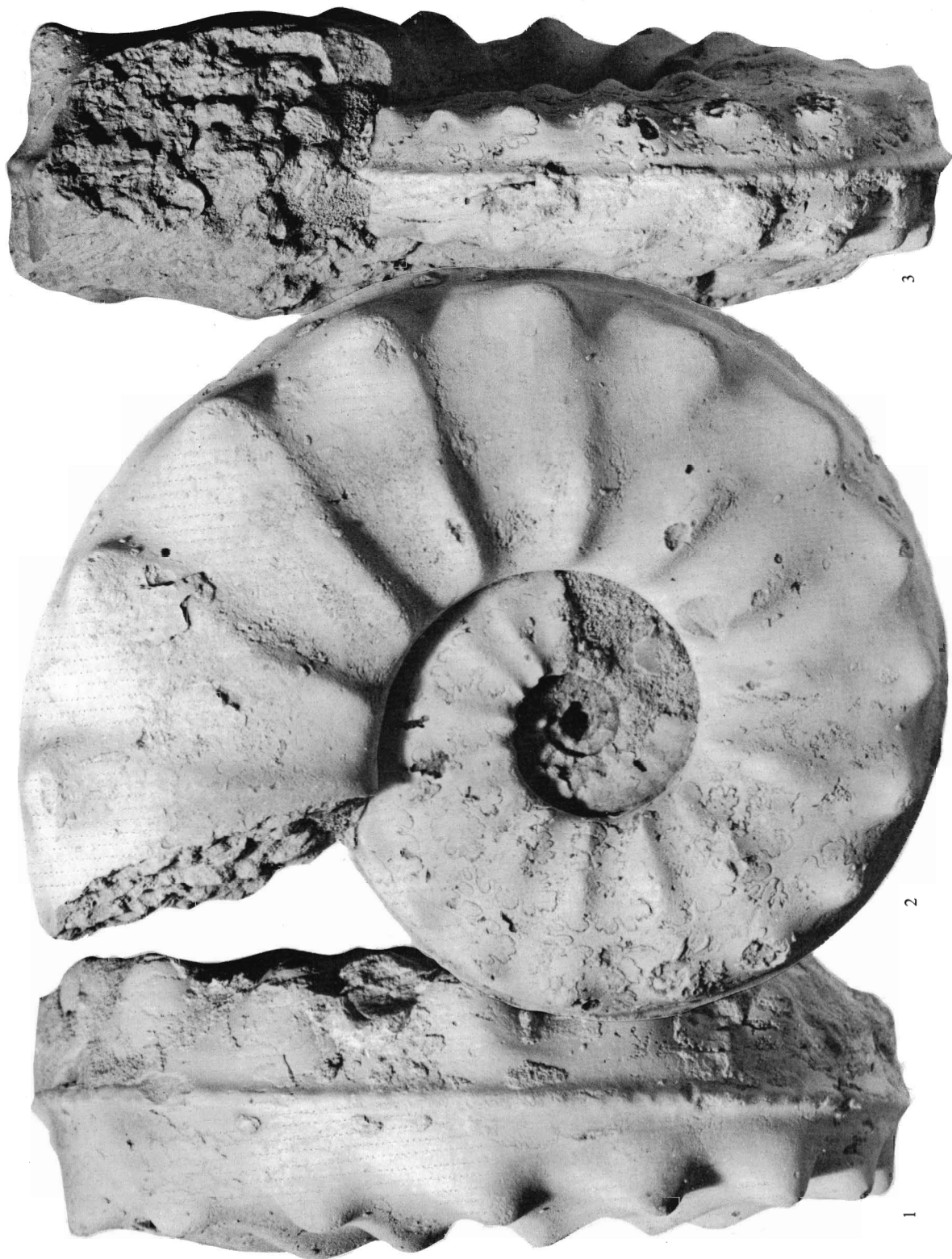
Gauthiericeras margae (Schlüter, 1867)

Plate 18; Plate 20, figs. 3–4, 8–10; Plate 21, figs. 1, 5; Plate 22, figs. 13–17; text-figs. 27, 28, 29A, B, 30A–B, 31

- 1850 *Ammonites nouelianus* d'Orbigny, p. 212 (*pars*).
- 1867 *Ammonites margae* Schlüter, p. 29, pl. 5, fig. 2.
- 1872 *Ammonites margae* Schlüter; Schlüter, p. 43, pl. 12, fig. 4.
- 1873 *Ammonites margae* Schlüter; Redtenbacher, p. 109, pl. 25, fig. 1.
- 1894 *Gauthiericeras margae* Schlüter sp.; de Grossouvre, p. 90, pl. 15, figs. 1, 2; text-fig. 36.
- ?1903 *Gauthiericeras margae* Schlüter; Pervinquier, pp. 112, 123, 129.

EXPLANATION OF PLATE 18

Figs. 1–3. *Gauthiericeras margae* (Schlüter, 1867), FSM unregistered, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). All figures $\times 1$.



KENNEDY, *Gauthiericeras*

- ?1907 *Peroniceras* (*Gauthiericeras*) cf. *margae* Schlüter; Pervinquière, p. 250.
 non 1910 *Gauthiericeras margae* Schlüter n. var. *peruanum* Brügggen, p. 720, pl. 27, fig. 3.
 non 1918 *Schlonbachia* (*Gauthiericeras*) *margae* var. *peruana* Brügggen; Lüthy, p. 41, pl. 1, fig. 2.
 ?1930 *Gauthiericeras Margae* (Schlüter); Lombard, p. 259, pl. 30, fig. 2.
 non 1935 *Gauthiericeras margae* Schlüter var. *turzoii* Karrenberg, p. 148, pl. 32, fig. 15; pl. 33, fig. 16.
 non 1935 *Gauthiericeras margae* Schlüter var. *gorda* Karrenberg, p. 148, pl. 32, figs. 16, 17; pl. 33, fig. 17.
 ?non 1936 *Gauthiericeras margae* (Schlüter); Besairie, p. 203, pl. 24, figs. 17, 18.
 non 1936 *Gauthiericeras margae* (Schlüt.); Venzo, p. 104, pl. 10, fig. 2.
 ?1958a *Gauthiericeras margae* (Schlüter); Reyment, p. 43, pl. 8, fig. 2; text-fig. 5, 2a-b.
 non 1965b *Gauthiericeras margae* Schlüter; Collignon, p. 49, pl. 435, fig. 1798.
 non 1967b *Gauthiericeras margae* Schlüter; Collignon, p. 49, pl. 32, figs. 1, 2.
 1976 *Gauthiericeras margae* Schlüter; Patruilus and Szász, p. 156, pl. 1, fig. 1; text-fig. 1.
 1979 *Gauthiericeras margae* de Grossouvre; Collignon *et al.*, p. 390, pl. 2, fig. 4.

Holotype. By monotypy, the original of Schlüter 1867, p. 29, pl. 5, fig. 2, from the Emscher-Mergel near Herne, Westphalia, no. 25 in the collections of the Geological and Palaeontological Institute of Bonn University. It consists of the mould of the umbilicus and one and a quarter whorls (text-fig. 27).

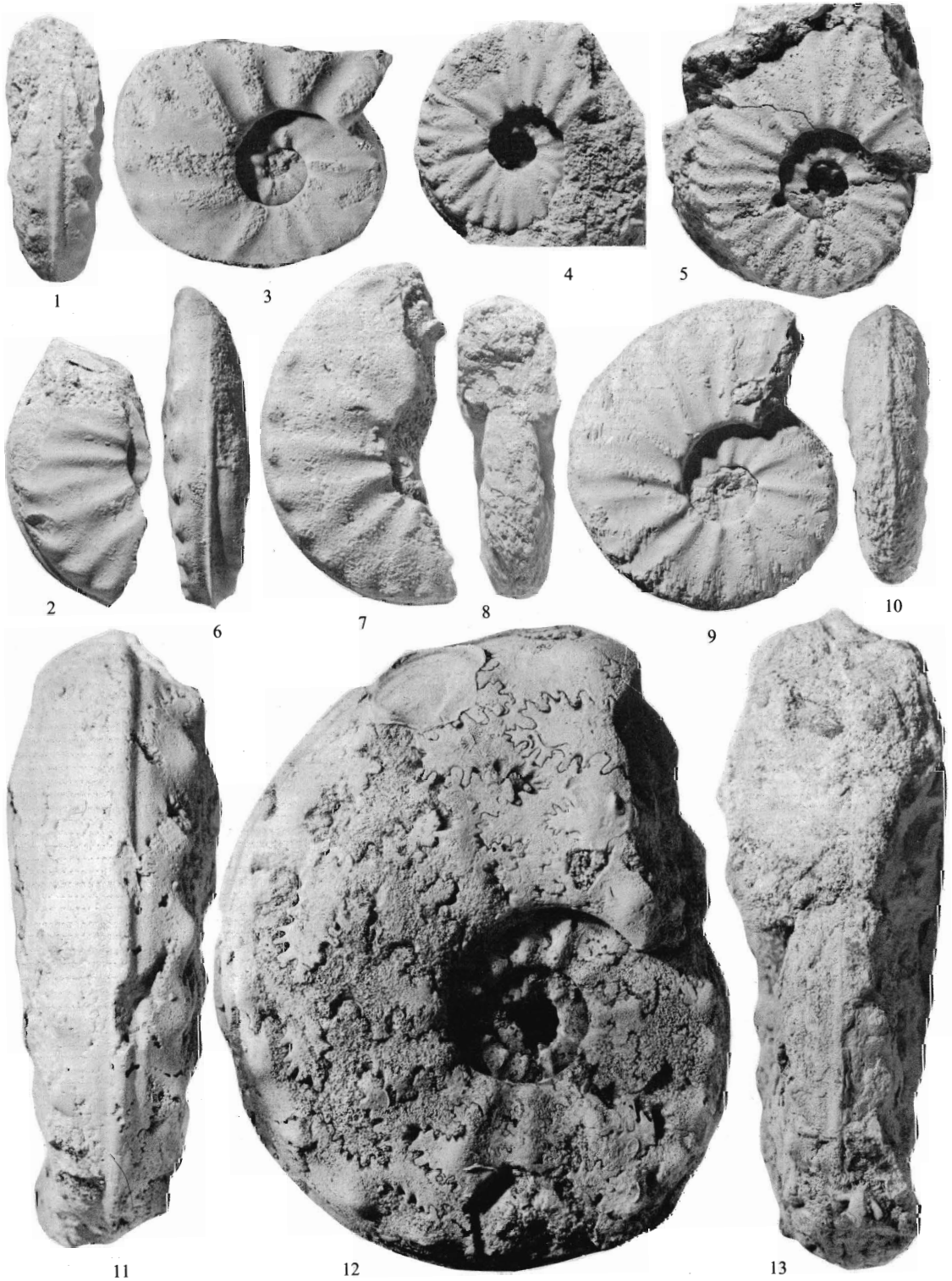
Material. Numerous specimens from 30 to 50 cm above the base of Bed 1 of the Craie de Villedieu at La Vallée de La Roche, south-east of St. Paterne-Racan (Indre-et-Loire) include OUM KZ16609-16612, KZ16614-16618, KZ16620-16623, KZ16625-16633, 16637, 16642, and 16643, and one of the paracotypes of *G. nouelianum* no. 7689 (d'Orbigny Collection, MNHP). Moulds of the two specimens figured by de Grossouvre (1894, pl. 15, figs. 1, 2) from the Calcaires Durs de La Ribochère at La Ribochère, Couture (Loir-et-Cher), are preserved in the EMP Collections, and there is a fine specimen from this locality in the FSM Collections. Specimens from Aquitaine include a specimen from the Upper Coniacian white glauconitic limestones in the Commune de Chanières, Vallée de la Coran, 9.0 km east of the centre of Saintes (Charente-Maritime); one from east of the D131, south of La Grelauderie in the Commune of St. Bris-de-Bois, 1.5 km north-east by east of St. Bris-de-Bois, 9.0 km north-east of the centre of Saintes (both P. Moreau Collection, University of Poitiers); SP unregistered, from Château l'Evêque, Cognac (Charente-Maritime) (identified by de Grossouvre); SP unregistered from Périgueux (Dordogne), from Assize L² of Arnaud; FSR 1411 from Aczema near Aubas (Dordogne); SP unregistered from Saujon (Charente Maritime); and BM(NH) C10788 from Puymoyen (Charente).

<i>Dimensions (mm)</i>		<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
OUM KZ16630	c	160.0 (100)	58.5 (36.6)	— (—)	—	62.0 (38.8)
SP, Saujon	c	130.0 (100)	41.0 (31.5)	44.0 (33.8)	0.93	54.5 (41.9)
"	ic		38.5 (29.6)	44.0 (33.8)	0.88	
OUM KZ16627	c	113.0 (100)	37.3 (33.0)	42.4 (37.5)	0.88	41.5 (36.7)
"	ic		32.5 (28.8)	42.4 (37.5)	0.77	
OUM KZ16631	c	108.5 (100)	43.5 (40.1)	40.5 (37.3)	1.07	40.5 (37.3)
"	ic		34.5 (31.8)	40.5 (37.3)	0.85	
OUM KZ16629	c	101.5 (100)	— (—)	37.2 (36.7)	—	38.7 (38.1)
MHNP 7189	c	78.5 (100)	29.0 (36.9)	28.5 (36.3)	1.02	29.8 (38.0)
OUM KZ16620c	c	57.8 (100)	— (—)	25.0 (43.2)	—	23.0 (40.0)
MNHP Grézac	c	49.0 (100)	— (—)	21.0 (43.2)	—	19.3 (39.9)

Description. Coiling evolute, with broad umbilicus comprising 36.7% to 41.9% of diameter; whorl section varies from compressed to depressed, with greatest breadth at umbilico-lateral bullae and below mid-flank inter-

EXPLANATION OF PLATE 19

Figs. 1-13. *Gauthiericeras nouelianum* (d'Orbigny, 1850). 1, 2, SP unregistered (*ex* Rejaudry Collection), Assize L of Arnaud at Saujon (Charente-Maritime). 3, MNHP B17173, same horizon at Grézac (Charente-Maritime). 4, 5, SP unregistered, same horizon and locality as 1, 2, identified by de Grossouvre as '*Schloenbachia boreau*'. 6, 7, MNHP, d'Orbigny Collection no. 7189a, one of the types of *Ammonites nouelianus*, Upper Coniacian *G. margae* Zone Calcaires Durs de La Ribochère of St. Paterne-Racan (Indre-et-Loire). 8-10, MNHP 17173b, other details as for fig. 3. 11-13, lectotype, MNHP, d'Orbigny Collection no. 7189, same horizon and locality as figs. 6, 7. All figures $\times 1$.



costally. Ornament variable in early and middle growth. At one extreme are weakly ornamented individuals like the Grésac specimen (Pl. 20, figs. 3-4). The sides are rather flat and ornament weak at a diameter of approximately 40 mm. Twelve to fourteen weak but broad umbilical bullae per whorl arise at the umbilical shoulder and extend to mid-flank. They give rise to one or two low, broad ribs that are accompanied by occasional intercalatories to give a total of around twenty-six ribs per whorl, terminating in ventrolateral clavi. At the other extreme are specimens that at the same diameter develop eleven to twelve strong ribs on the umbilical wall but have maximum development of very strong bullae displaced out to an inner flank position, as in the juvenile from St. Paterne (Pl. 20, fig. 8). Others (e.g. OUM KZ16631) have ornament of intermediate strength and density, with a weak bulla at the umbilical shoulder strengthening across the flanks to a maximum elevation close to mid-flank. Ribs arise singly or in pairs from bullae in all these specimens, rib branching pattern resembling a V in weakly ornamented individuals and a Y in strongly ornamented individuals, with shaft of Y made up by the elongate bulla. In some specimens weakly ornamented early stages are followed by a marked increase in strength of bullae and ribs (e.g. MNHP 7189, Pl. 22, figs. 13-15). In others ribbing remains coarse throughout, with intercalated and branching ribs persisting in some specimens to a diameter of 100 mm (Pl. 20, figs. 9, 10) while others have predominantly single ribs from as little as 50 mm (e.g. OUM KZ16631, Pl. 21, fig. 1).



TEXT-FIG. 26. *Gauthiericeras (Ciryella) vascogoticum* Wiedmann, 1960, cast of the holotype, $\times 1$. The original is no. Ce 03 in the Ciry Collection, Université de Dijon, from west of Masa, Burgos, Spain.

In some individuals as size increases ribs arise on the umbilical wall without a bulla on the shoulder, but in an inner flank position (e.g. OUM KZ16631, Pl. 21, fig. 1). In others, an umbilical bulla persists as does an inner to mid-flank strengthening of the rib which may develop into a lateral tubercle. On the few body-chamber fragments of presumed adults the inner part of long umbilico-lateral bullae weakens while inner- or mid-lateral parts persist until they apparently decline towards the aperture. All ribs bear strong ventrolateral tubercles that are clavate to varying degrees in juveniles but become progressively more conical as size increases, especially on body chambers.

In early and middle growth the broad venter bears a strong, blunt, commonly serrated siphonal keel flanked by shallow grooves, the outer edges of which are sometimes strengthened into weak ridges, but never true keels. Large body-chamber fragments show progressive disappearance of lateral grooves and serrations, leaving a fastigiate venter only. Suture line relatively simple, with massive, feebly incised bifid saddles and narrow lobes (text-fig. 30A-B).

Discussion. The material from St. Paterne-Racan is the largest suite of *G. margae* so far described from Europe. It is of interest in showing wide variation in strength of ornament, especially rib strength and position of umbilico-lateral tuberculation. The material gives the impression of being dimorphic, with some specimens showing the loss of intercalated ribs at small diameters and others at a much larger size. Migration and changes in relative development of umbilical and incipient lateral bullae also occur at different rates. There are, however, too few complete specimens to do more than speculate on these lines.

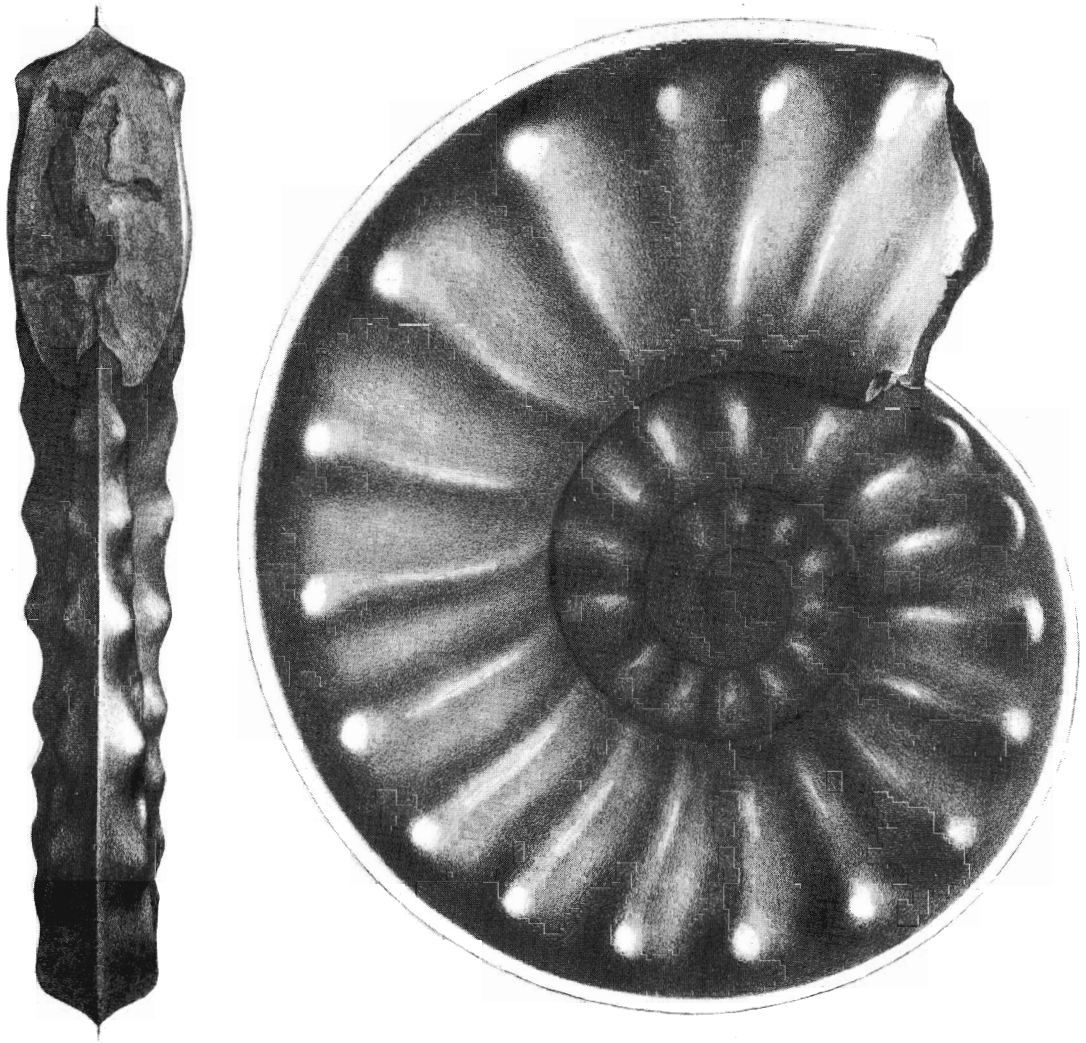
The holotype of *A. margae* is a crushed specimen from the 'Emscher-Mergel', and Schlüter's figure is idealized. The inner whorls are preserved in part as an umbilical mould, and show coarse ribs and bullae, rather like OUM KZ16629 (Pl. 20, figs. 9, 10). The specimen is too poor to show if all the ribs are simple, whether they sometimes arise in pairs, or whether or not there are intercalated ribs. The remaining one and a quarter whorls of the holotype are preserved as a composite mould (text-fig. 28) with the last three-quarters of a whorl body chamber. Because of crushing it is impossible accurately to determine original proportions, but the maximum diameter is approximately 250 mm, with $U = 41\%$. There are approximately eighteen ribs per whorl, all primaries, arising at the umbilical wall, weak at the umbilical shoulder, but markedly strengthened around mid-flank and terminating in a strong ventrolateral clavus. This umbilico-lateral ornament strongly recalls that of the largest specimens from St. Paterne-Racan, and there is little doubt that they represent the same species. The holotype also shows the sutures, and these too match French material.

When Schlüter revised this species in 1872 (p. 43, pl. 12, fig. 4) he figured only a suture line, and this agrees closely with that of both the holotype and the present material.

Redtenbacher (1873, pl. 25, fig. 1) figured a juvenile from the Gosau Beds of Glaneck, Austria, and there are several other specimens available from this locality. They show the same branching and intercalation of coarse ribs with umbilical bullae that differentiate into umbilical and inner lateral bullae ($U = 39\% - 41\%$). The whorl breadth to height ratio is 0.85-0.94 (costal), and only the absence of serrations on the ventral keel, which is a variable feature in French material (and may also reflect differing preservations), is of note. An adult of this species in the collections of the Naturhistorisches Museum Wien (no. 1943 (3) I.1) is shown in text-fig. 31; it has nineteen primary ribs on the outer whorl, and these vary from recti- to rursiradate, exactly as in the crushed holotype.

De Grossouvre's specimens (1894, pl. 15, figs. 1, 2; text-fig. 36) are from the Calcaires Durs de La Ribochère at the base of the Craie de Villedieu at La Ribochère Quarry. They have been generally taken as the typical form of the genus (e.g. Roman 1938; Wright 1957) and match well with the St. Paterne-Racan specimens. The smaller of the two (pl. 15, fig. 2) has umbilical and mid-lateral bullae strongly differentiated, and some of the short intercalated ribs branch from the mid-lateral tubercle.

G. margae peruanum Brügggen, 1910 (p. 720, pl. 27, fig. 3, = *F. (F.) bassae* Benavides-Cáceres, 1956, p. 477, pl. 58, fig. 5) is easily interpreted from the fine figure in Lüthy (1918, p. 41, pl. 1, fig. 2), and is a *F. (Forresteria)*.



TEXT-FIG. 27. Original illustrations of *Ammonites margae* Schlüter, 1867 (pl. 5, fig. 2), $\times 1$. A cast of the original, from Herne, Westphalia, is shown in text-fig. 28.

G. margae turzoi Karrenberg, 1935 (p. 148, pl. 32, fig. 15; pl. 33, fig. 16), *G. margae gorda* Karrenberg, 1935 (p. 148, pl. 32, figs. 16, 17; pl. 33, fig. 17) and *G. vallei* Ciry, 1940 are variants of a single species of *Prionocycloceras*, *P. turzoi*. The species differs from *G. margae* in being smaller, with massive, involute rectangular whorls and umbilical bullae projecting into the umbilicus and numbering only seven to eight per whorl. The ribs are coarser and never develop umbilical and lateral tubercles while the ventrolateral tubercles become horn-like and are housed in deep grooves in the umbilical seam of the succeeding whorl. They extend as ribs across the venter to the weak siphonal keel. *P. turzoi* co-occurs with *G. margae* at Terradillos de Sedano, Burgos, Spain.

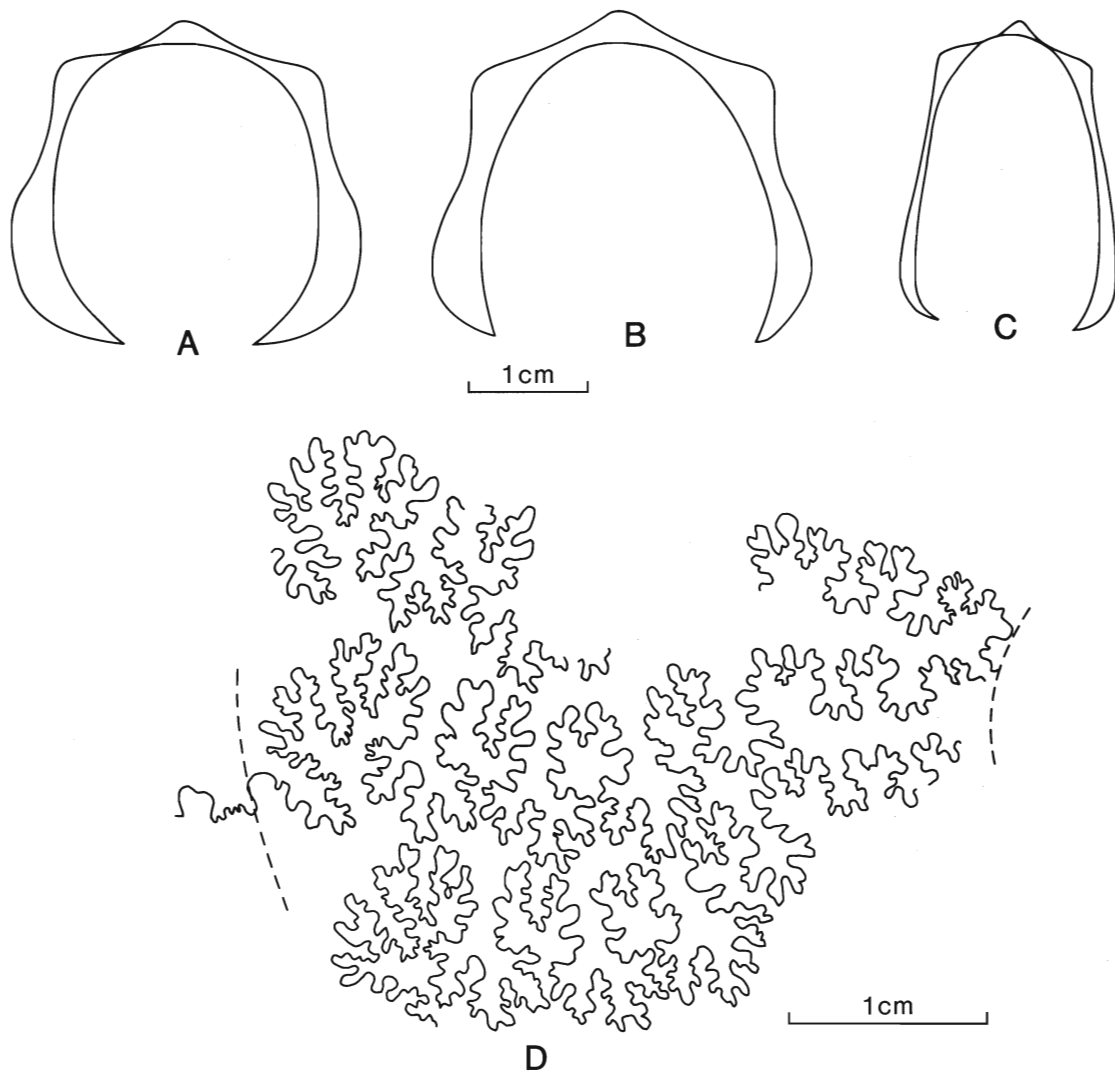
The *G. margae* from Zululand described by Venzo (1936, p. 104, pl. 10, fig. 2) belongs to the group of *G. obesum* Van Hoepen, 1955, which differs from *G. margae* in having simple ribs and not developing a lateral bulla (see Klinger and Kennedy 1983 for a full account of the group).



TEXT-FIG. 28. *Gauthiericeras margae* (Schlüter, 1867), cast of the holotype, Herne, Westphalia, no. 25 in the Collections of the Geologisches und Paläontologisches Institut, Bonn, $\times 0.67$.

Of other species *G. nouelianum* (d'Orbigny, 1850), described below, co-occurs with *G. margae* but is much more involute, compressed, and high whorled with crowded feeble ribs. *G.?* *boreau*i (de Grossouvre, 1894, p. 111, pl. 7, fig. 3) is a diminutive compressed, involute, densely, and flexuously ribbed species that lacks ventrolateral tubercles. *G. roquei* Peron, 1897 (p. 52, pl. 8, fig. 1; pl. 9, figs. 1-2; pl. 17, fig. 6) from the Coniacian of Algeria is a very large form based on a specimen 230 mm in diameter and a fragment. Coiling is very evolute ($U = 44\%$) and according to Peron there are only ten coarse, distant ribs per whorl, which distinguishes it from the material described here. *G. hoepeni* Collignon, 1965*b*, (p. 48, pl. 434, fig. 1796) appears to be a *F. (Forresteria)*.

Occurrence. Upper Coniacian *G. margae* Zone when well localized. Stratigraphic information with most French specimens is imprecise, but there are records from the Calcaires Durs de La Ribochère of Touraine, many



TEXT-FIG. 29. External suture or whorl sections. A, B, *Gauthiericeras margae* (Schlüter, 1867); A, OUM KZ16631b; B, OUM KZ16631a. C, *G. nouelianum* (d'Orbigny, 1850), OUM KZ16644. D, *Placenticerias semiornatum* (d'Orbigny, 1850), MNHP 1896-27.

records from Aquitaine, and a specimen from the Beausset Basin (Var.). It occurs widely in East and West Germany and Austria, Spain, Romania, possibly North Africa, and elsewhere.

Gauthiericeras nouelianum (d'Orbigny, 1850)

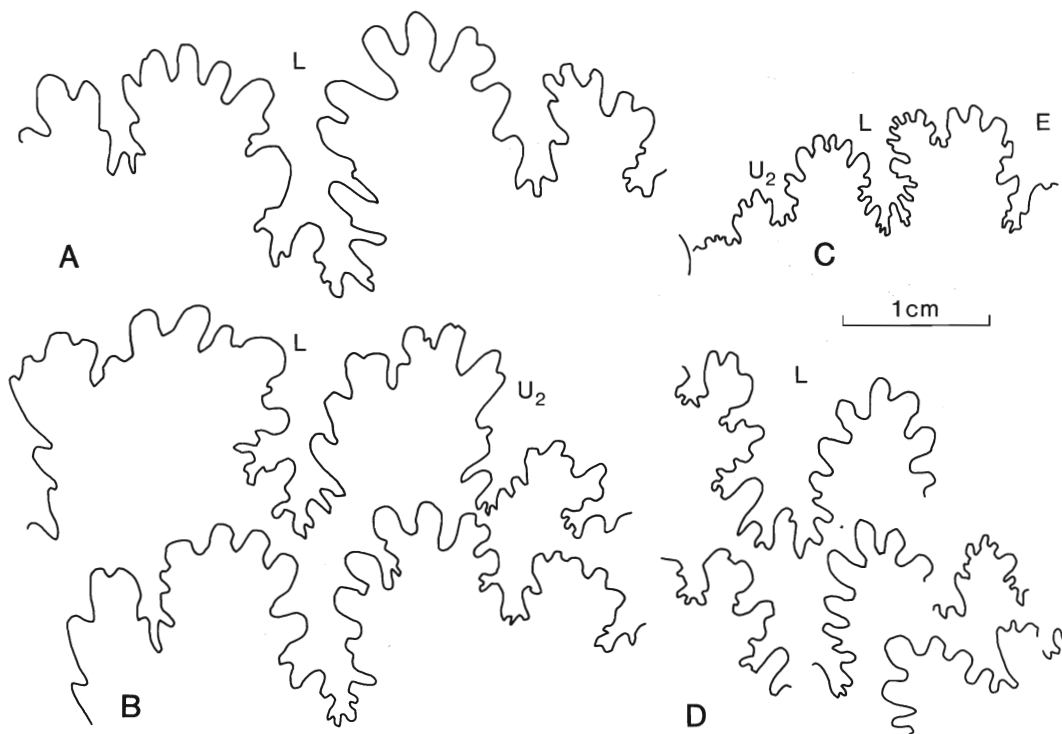
Plate 19, figs. 1-13; Plate 20, figs. 1-7; Plate 22, figs. 18-19; text-figs. 29c, 30c, D

- 1850 *Ammonites nouelianus* d'Orbigny, p. 212 (*pars*).
 non 1903 *Schloenbachia noueli* d'Orb; Fritel, p. 276, pl. 24, fig. 2.
 1955c *Ammonites (Gauthiericeras) nouelianus* d'Orbigny; Sornay, figs. 1, 2.
 ?1967 *Gauthiericeras faure-muretae* Collignon, p. 50, pl. 28, fig. 10.

Types. D'Orbigny introduced the name *nouelianus* in 1850, mentioning specimens from St. Paterne (Indre-et-Loire). The catalogue of the d'Orbigny collections lists the following:

7189	TT	<i>A. Nouelianus</i> d'Orb	St. Paterne	Indre-et-Loire	3
		<i>a</i> id	Junior	id	2
		<i>b</i> id	St. Frambault	Sarthe	1
		<i>c</i> id	St. Christophe	Indre-et-Loire	1

Of specimens labelled 7189, Sornay (1955c) has designated one lectotype (refigured here as Pl. 19, figs. 11–13) and identified a second as *G. margae* (Pl. 22, figs. 13–15); the third is missing. One specimen numbered 7189a is a juvenile of the species (Pl. 19, figs. 6–7); the second is a Cenomanian *Schloenbachia*. The specimen numbered 7189b is lost, whilst 7189c is a *Gauthiericeras*. The preservation of the lectotype matches that of recently collected specimens from Bed 1 of the Craie de Villedieu of St. Paterne-Racan.



TEXT-FIG. 30. External sutures. A, B, *Gauthiericeras margae* (Schlüter, 1867), SP unregistered, from Saujon, ex Arnaud Collection. C, D, *G. nouelianum* (d'Orbigny, 1850); C, OUM KZ16644; D, FSR unregistered, from St. Paterne-Racan.

Material. The following topotypes—FSR, three unregistered specimens: OUM KZ16624, 16638, 16644–16647, all from 30 to 50 cm above the base of Bed 1 of the Craie de Villedieu; SP, unregistered (ex Rejaudry and Pesme Collections) from Assize L of Arnaud at Saujon (Charente-Maritime); two specimens identified by de Gros-souvre as *S. boreau* from the same locality; MNHP unlocalized, in a similar preservation. FSM unregistered from the Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).



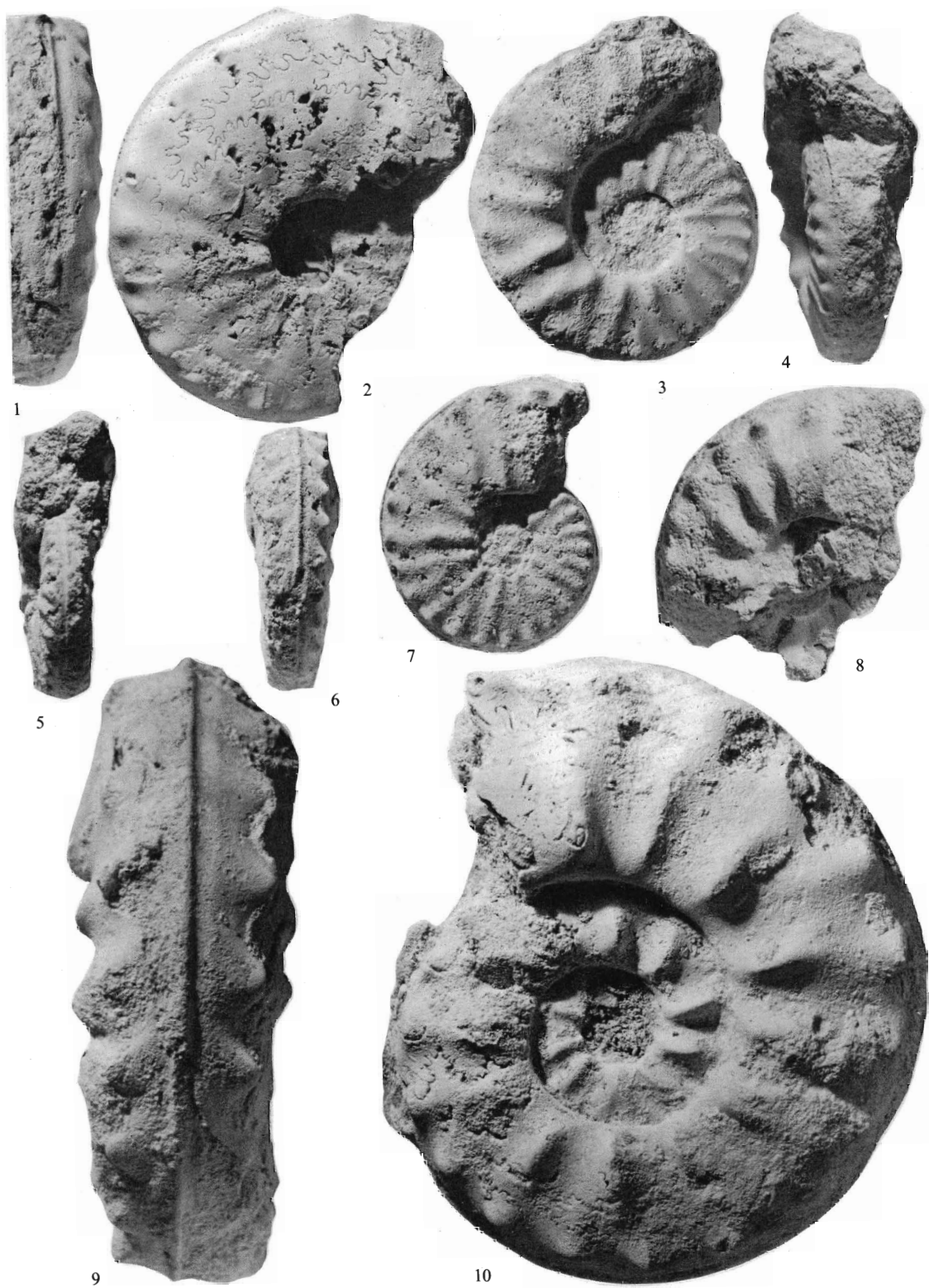
TEXT-FIG. 31. *Gauthiericeras margae* (Schlüter, 1867). NHMW, Gosau Beds of Glaneck, Austria, scale bar 5 cm.

EXPLANATION OF PLATE 20

Figs. 1, 2, 5-7. *Gauthiericeras nouelianum* (d'Orbigny, 1850). 1, 2, FSR unregistered; 5-7, OUM KZ16636a, 30-50 cm above the base of the Upper Coniacian Calcaires Durs de La Ribochère of St. Patern-Racan (Indre-et-Loire).

Figs. 3, 4, 8-10. *Gauthiericeras margae* (Schlüter, 1867). 3, 4, MNHP unregistered, Grézac (Charente-Maritime). 8, OUM 16623; 9, 10 OUM KZ16629, both from the same horizon and locality as figs. 5-7.

All figures $\times 1$.



Dimensions (mm)		D	Wb	Wh	Wb: Wh	U
Lectotype MNHP 7189	c	98.8 (100)	— (—)	42.5 (43)	—	27.2 (27.5)
OUM KZ16645	c	— (—)	24.5 (—)	33.5	0.73	— (—)
OUM KZ16644	c	65.8 (100)	23.8 (36.2)	27.5 (41.8)	0.87	16.8 (25.5)
FSR St. Paterne	c	60.0 (100)	— (—)	26.2 (43.7)	—	12.5 (20.8)
OUM KZ16636	c	43.2 (100)	— (—)	17.6 (40.7)	—	12.0 (27.7)
OUM KZ16646	c	35.5 (100)	10.5 (29.6)	15.5 (43.7)	0.67	— (—)

Description. Relatively involute, with approximately 45% of previous whorl covered; umbilicus shallow, comprises 20–27% of diameter with rounded umbilical wall on moulds; umbilical shoulder narrowly rounded; whorl section compressed, with whorl breadth to height ratios varying from 0.67 to 0.87; greatest breadth close to mid-flank both costally and intercostally, except where particularly strong umbilical bullae are developed. Inner flanks feebly inflated, outer flanks flattened and convergent, venter fastigate to carinate. Twelve umbilical bullae per whorl in specimens up to 75 mm in diameter commonly extend to mid-flank and give rise to pairs of low, broad, straight prorsiradiate ribs projected forwards on the outer flank where they are accompanied by shorter intercalated ribs to give a total of twenty-four to twenty-five ribs per whorl. All ribs bear prominent ventrolateral clavi. Strong, high, entire or feebly and irregularly serrate siphonal keel flanked by shallow grooves, outer edges of which are sometimes accentuated into a weak ridge, but not a well-defined keel. In the lectotype there are twelve long umbilical bullae that extend to mid-flank, where they are strengthened into an incipient tubercle. Occasional ribs branch in pairs at this point, others are simple and there are also intercalated ribs, giving a total of twenty-two ribs per whorl. Suture simple, with narrow E, broad asymmetrically bifid E/L, narrow L, and broad L/U₂ (text-fig. 30c, d).

Discussion. *A. nouelianus* was introduced by d'Orbigny in 1850 with a brief, but adequate description.

Sornay (1955c) was the first to use the name in recent times, and he correctly referred the species to *Gauthiericeras* and distinguished it from *G. margae* by its greater involution and higher and narrower whorls. He also commented that it was not impossible that more material would show that there was a passage to *G. margae*. More than thirty *Gauthiericeras* collected from St. Paterne-Racan fall into two distinct groups. Nine have umbilical diameters of between 20.8 and 27.7%, a compressed whorl (whorl breadth to height ratio is between 0.67 and 0.87), and are closely and feebly ribbed. The others are much more evolute, with umbilical diameters of between 36.7 and 41.9% and quadrate whorls with costal whorl breadth to height ratios of 0.88 and 1.07. The ribbing is coarser than in the first group, with between twelve and fourteen umbilical bullae per whorl. These differences allow the separation of the first group, *G. nouelianum*, from typical *G. margae* and they are retained here as separate species, although it must be admitted that the range of variation encompassed by the two groups is no larger than that shown within populations of other Acanthocerataceae. If further material shows that there is a gradation between the two groups, *nouelianum* d'Orbigny, 1850 has priority over *margae* Schlüter, 1867.

The *G. margae* of Collignon, 1967 (p. 49, pl. 32, figs. 1, 2) is relatively involute ($U = 27\text{--}28\%$) like *G. nouelianum*, but the ribbing is coarse, with predominantly primaries and no indication of lateral tubercles. *G. faure-muretae* Collignon, 1967 (p. 50, pl. 28, fig. 10) has a similarly compressed whorl, so far as can be judged from the crushed holotype ($U = 31\%$). There are twenty predominantly long ribs which Collignon describes as arising at the umbilical seam with a strong umbilical tubercle. This

EXPLANATION OF PLATE 21

Figs. 1, 5. *Gauthiericeras margae* (Schlüter, 1867). 1, OUM KZ16631a, Upper Coniacian *G. margae* Zone, 30–50 cm above the base of the Calcaires Durs de La Ribochère at St. Paterne-Racan (Indre-et-Loire). 5, SP unregistered, Saujon (Charente-Maritime).

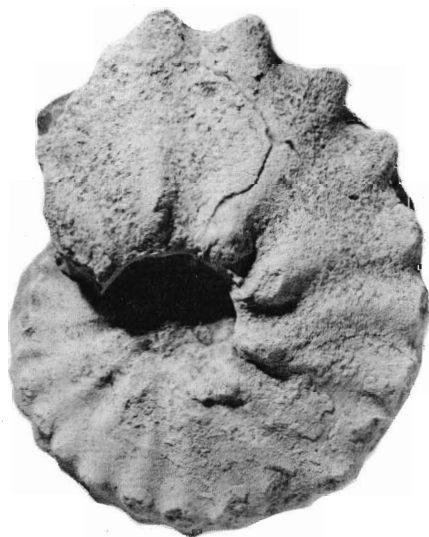
Fig. 3. *Gauthiericeras? boreau* (de Grossouvre, 1894), OUM KZ16648, same horizon and locality as fig. 1.

Figs. 2, 4. *Forresteria (Harleites) petrocoriensis* (Coquand, 1859), SP unregistered, Lower Coniacian, *F. (H.) petrocoriensis* Zone of La Bachellerie (Dordogne).

All figures $\times 1$.



1



2



4



5

appears, from the illustration, to correspond to the condition in *G. nouelianum*, and the two may be synonyms.

G. ?boreau (de Grossouvre, 1894) (p. 111, pl. 7, fig. 3; see below, Pl. 22, figs. 1–12) is feebly and flexuously ribbed, and lacks ventrolateral tubercles. There are specimens with about thirty ribs to a whorl with tubercles that appear to be intermediate between the two forms. Other species, discussed under *G. margae*, are more evolute with less compressed whorls and generally coarse ornament.

Occurrence. Upper Coniacian *G. margae* Zone, Bed 1 of the Craie de Villedieu at St. Patern-Racan (Indre-et-Loire), Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher), and assize L of Arnaud at Saujon (Charente-Maritime) and possibly Morocco.

Gauthiericeras? boreau (de Grossouvre, 1894)

Plate 21, fig. 3; Plate 22, figs. 1–12; text-fig. 39D–E)

1894 *Schloenbachia boreau* de Grossouvre, p. 111, pl. 7, fig. 3.

1921 '*Schloenbachia*' *boreau* Grossouvre; Spath, p. 240.

1970b *Schloenbachia boreau* de Grossouvre; Matsumoto, p. 309.

Holotype. By monotypy, the original of de Grossouvre 1894, pl. 7, fig. 3, a specimen in the Arnaud Collection from his Assize L¹ near Cognac (Charente). This specimen has not been traced in the collections of the Sorbonne where other Arnaud specimens figured by de Grossouvre are preserved.

Material. OUM KZ16590 from a hiatus concretion in the lower 30 cm of Bed 1 of the Craie de Villedieu at La Vallée de La Roche, south-east of St. Patern-Racan, Sarthe, France; OUM KZ16648 from the base of Bed 1b at the same locality, and unregistered specimens in the FSR and FSM Collections; Upper Coniacian *G. margae* Zone. Three unregistered specimens in the SP Collections (*ex* Arnaud Collection), identified as *S. boreau* by de Grossouvre are from Assize L¹ at Saujon (Charente-Maritime). FSL 14114 is from Aezeme, near Aubas (Dordogne).

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
SP, Saujon	40.3 (100)	— (—)	18.5 (45.9)	—	9.0 (22.3)

Description. Involute with small, shallow umbilicus (22% of the diameter); umbilical wall low and rounded, umbilical edge narrowly rounded; whorl section compressed, whorl breadth to height ratio of approximately 0.5. Flanks flattened, subparallel; ventrolateral shoulders broadly rounded. Venter relatively broad, with sharp, high, continuous keel flanked by very shallow grooves. Approximately six umbilical bullae per whorl give rise to low, prorsiradiate primary ribs, either singly or in pairs. Up to three long and short intercalatories, the former arising close to the umbilicus, the latter high on the flank or on the shoulder, are inserted between primaries. Ribs are straight to the mid-flank, but flex and are falcoid on the outer flank, strengthening on ventrolateral shoulder and sweeping strongly forwards before terminating at the edge of shallow ventral grooves. Sutures very simple (text-fig. 39D–E), with broad, little incised elements.

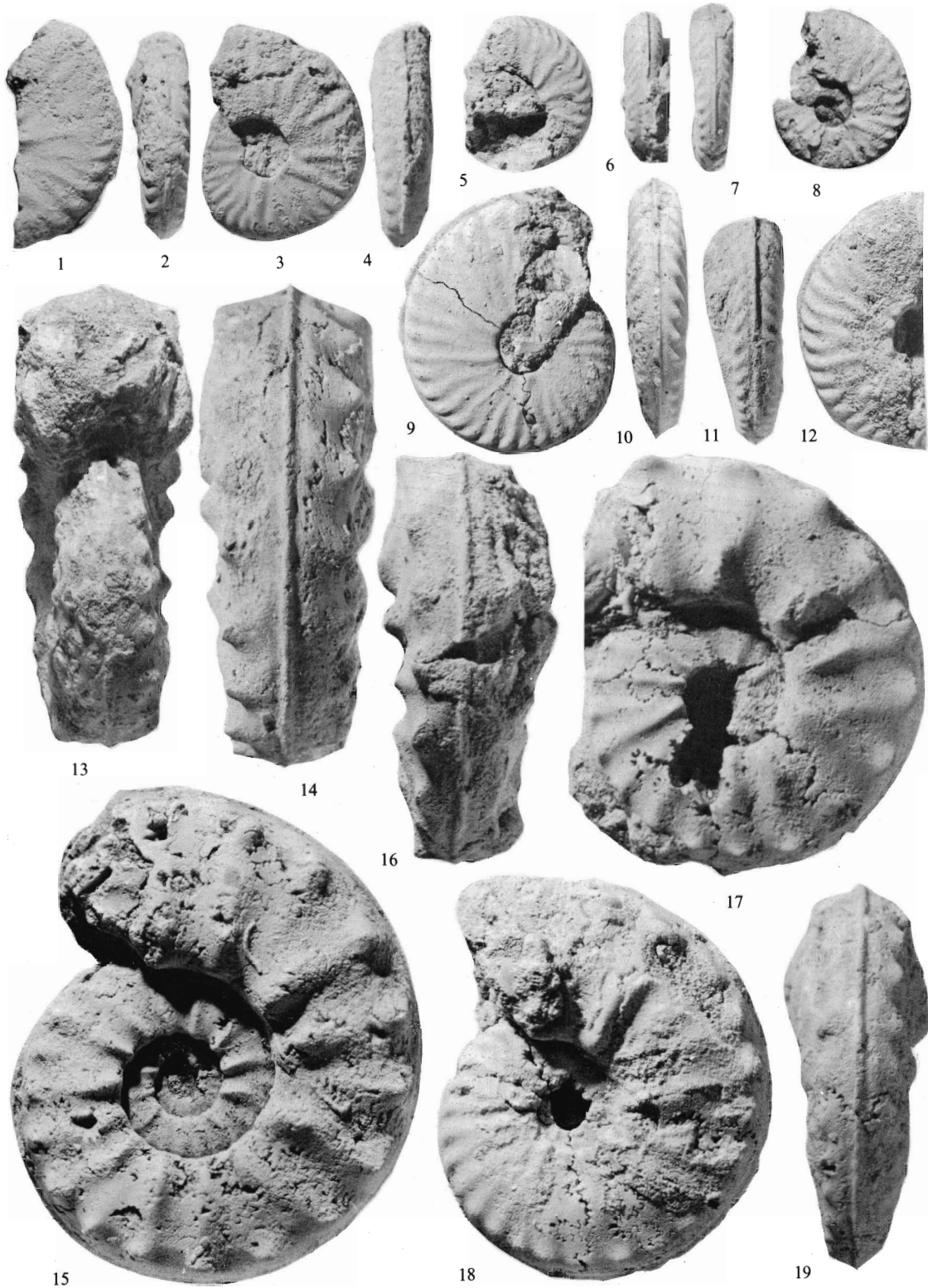
EXPLANATION OF PLATE 22

Figs. 1–12. *Gauthiericeras? boreau* (de Grossouvre, 1894). 1, 2, 5–10, SP unregistered, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone of Saujon (Charente-Maritime). 3, 4, MNHP unregistered, without data but probably also from Saujon. 11, 12, FSR unregistered, Upper Coniacian *G. margae* Zone of St. Patern-Racan (Indre-et-Loire).

Figs. 13–17. *Gauthiericeras margae* (Schlüter, 1867). 13–15, one of the types of *Ammonites nouelianus* d'Orbigny, MNHP, d'Orbigny Collection no. 7189, horizon and locality as for figs. 11, 12. 16, 17, OUM KZ16620, details as for figs. 11, 12.

Figs. 18, 19. *Gauthiericeras nouelianum* (d'Orbigny, 1850), OUM KZ16644, horizon and locality as for figs. 11, 12.

All figures $\times 1$.



Discussion. The Saujon specimen (Pl. 22, figs. 9–10) is adult, with approximated sutures and a phragmocone diameter of 27 mm and total diameter of just over 40 mm. The holotype, in contrast, is almost 60 mm in diameter and may not be complete, suggesting that the species is dimorphic. Although all the specimens are small and have no ventrolateral tubercles, they show close affinities to the inner whorls of *G. nouelianum* (e.g. Pl. 19, figs. 4, 5). Although this species, as interpreted here, is a stouter, larger form with coarser ribs, ventrolateral tubercles, and a typical *Gauthiericeras* suture, there are sufficient similarities to suggest that *nouelianum* and *boreaui* may be congeneric, the latter perhaps representing a dwarf offshoot analogous to *Protacanthoceras* Spath, 1923 (Wright and Kennedy 1980).

Occurrence. Upper Coniacian *G. margae* Zone of St. Patern-Racan (Indre-et-Loire). Middle Coniacian *Peroniceras tridorsatum* Zone of Cognac (Charente), Saujon and St. Georges-de-Cubillac (Charente-Maritime).

Subfamily TEXANITINAE Collignon, 1948

[*nom. transl.* Wright 1957, p. L429, *ex* Texanitinae Collignon, 1948, p. 54 (9)]

Genus PROTEXANITES Matsumoto, 1955

Type species. *A. bourgeoisanus* d'Orbigny, 1850, p. 212 by original designation by Matsumoto (1955, p. 38).

Diagnosis. Medium-sized to large, moderately involute to evolute with compressed rectangular to depressed whorl section. Primary ribs arise singly or in pairs from weak to strong umbilical bullae in early growth stages and may be accompanied by shorter, intercalated ribs, all of which bear submarginal and external clavi. In later growth stages and on mature body chamber of type species, umbilical tubercle migrates outwards to inner flank position and new bulla develops at umbilical shoulder. In others, weak inner lateral tubercle may be present from early stage. Siphonal keel entire or undulating. Suture simple, with broad saddles and narrow lobes.

Occurrence. Upper (and perhaps Middle) Coniacian and Lower Santonian. The geographic range is widest in the Upper Coniacian: France, Czechoslovakia, Austria, Italy, Romania, Spain, North Africa, Zululand, Madagascar, Japan, Venezuela, Colombia, Peru, and California, Texas and U.S. Western Interior.

Subgenus PROTEXANITES (PROTEXANITES) Matsumoto, 1955

Type species. *A. bourgeoisanus* d'Orbigny, 1850, p. 212 by original designation by Matsumoto (1955, p. 38).

Diagnosis. With umbilical, marginal, and external tubercles in early growth, umbilical migrating to inner flank at maturity with development of new umbilical tubercle.

Discussion. Matsumoto (1970a) recognized three subgenera within *Protexanites*. *Anatexanites* Matsumoto, 1970a (p. 239, type species, by original designation, *Mortonicerias fukazawi* Yabe and Shimizu, 1925, p. 130, pl. 30, fig. 1; pl. 31, figs. 1, 2, 6, 7 (*non* 3); pl. 33, figs. 1, 2) is a Santonian subgenus; species other than the type that can be referred to the subgenus are *P. (A.) nomii* (Yabe and Shimizu, 1925), *P. (A.) monchicourti* (Pervinquière, 1907), and *P. (A.) reymenti* Matsumoto, 1970. In the type species, the ribs are initially trituberculate, with umbilical, submarginal, and external nodes, the lateral tubercle, which characterizes the subgenus, appearing at around 27 mm diameter. This contrasts with the condition in *P. (P.) bourgeoisi*, where the lateral tubercle develops by outward migration of the umbilical tubercle accompanied by the appearance of a new umbilical tubercle at maturity only. Evolution from *P. (Protexanites)* to *P. (Anatexanites)* thus involved progressively earlier acquisition of adult features of ancestral *P. (Protexanites)* by descendant *P. (Anatexanites)*.

P. (Miotexanites) Matsumoto, 1970 (type species, by original designation, *P. (M.) minimus* Matsumoto, 1970a, p. 246, pl. 33, figs. 1–3; text-fig. 8) is imprecisely dated within the range Upper Coniacian to Lower Santonian, and is characterized by small size, weak ribs, and no ventrolateral tubercles except on the outer whorl.

Of other texanitid taxa, *P.* (*Protexanites*) most closely resembles *Paratexanites* Collignon, 1948, p. 45 (102), type species, by original designation, *Mortonicerias zeilleri* de Grossouvre, 1894, p. 67, pl. 14, fig. 1. This genus has submarginal, marginal, and external tubercles. These are clearly separated in the type species, but in some *Paratexanites serratomarginatus* (Redtenbacher, 1873) (see p. 117), the pair of tubercles are close together on a single larger protuberance.

Occurrence. *Protexanites* (*Protexanites*) is mostly known from the Upper Coniacian with a distribution as for the genus (above). There are records from the Middle Coniacian of France, Zululand, and possibly Spain, and from the Lower Santonian. All well localized specimens discussed here are Upper Coniacian.

Protexanites bourgeoisi (d'Orbigny, 1850)

Plate 23, figs. 1-4, 7-9; Plate 24, figs. 1-8; Plate 26, figs. 4-5; text-figs. 32, 33, 34, 35A-E, 36B, C, E, F

1850 *Ammonites bourgeoisianus* d'Orbigny, p. 212.

?1872 *Ammonites texanus* Roemer; Fritsch, p. 28, pl. 6, fig. 5.



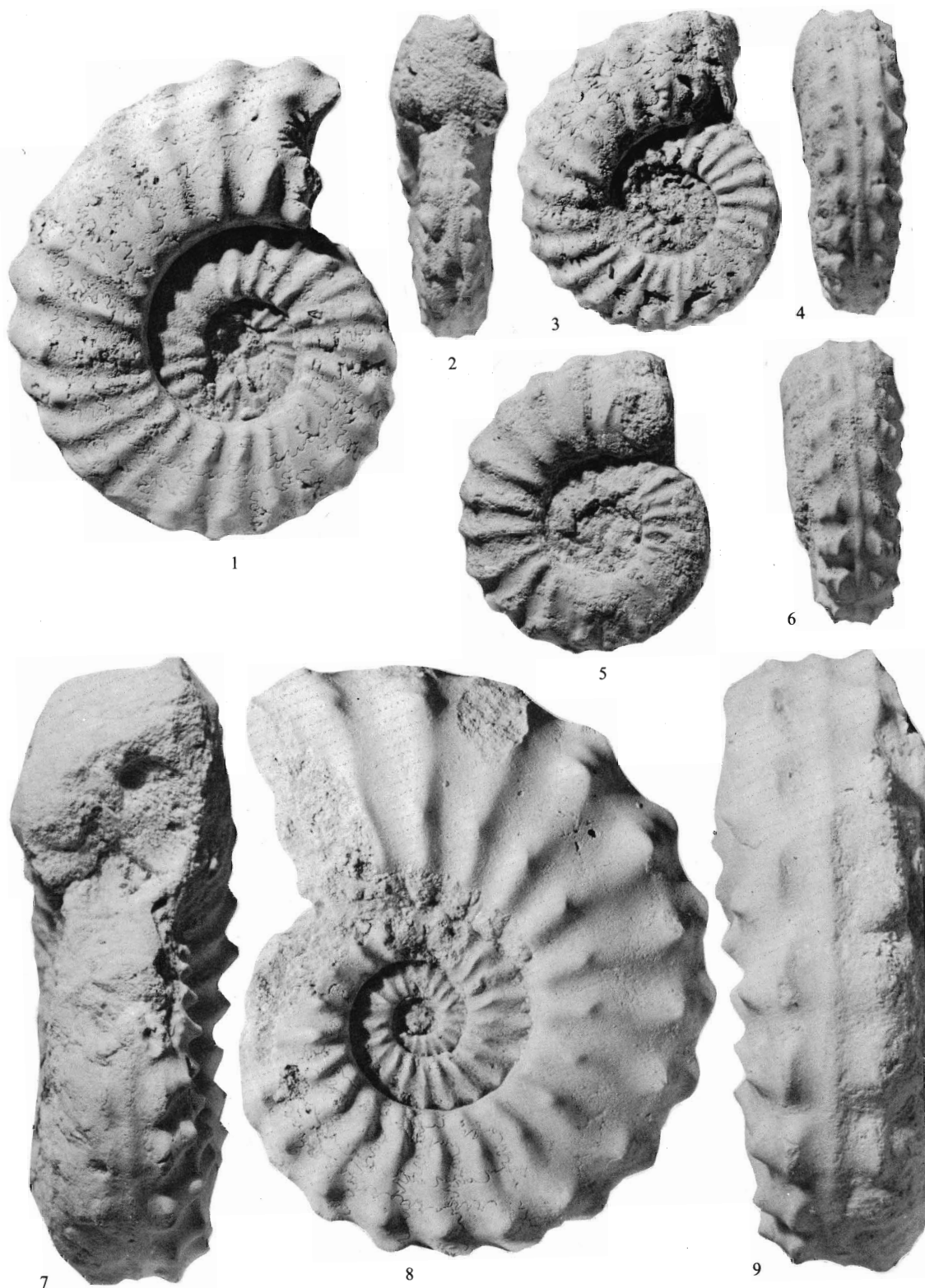
TEXT-FIG. 32. *Protexanites bourgeoisi* (d'Orbigny, 1850). Lectotype, MNHP, d'Orbigny Collection no. 7181a, Craie de Villedieu of St. Fraimbault (Sarthe), $\times 1$.



TEXT-FIG. 33. *Protexanites bourgeoisi* (d'Orbigny, 1850). Adult macroconch with part of the body chamber, Musée d'Angers, unregistered, Craie de Villedieu of Touraine, $\times 0.85$. Compare with the adult microconch in Pl. 23, figs. 7-9.

EXPLANATION OF PLATE 23

Figs. 1-4, 7-9. *Protexanites (Protexanites) bourgeoisi* (d'Orbigny, 1850). 1, EMP Collections, the original of de Grossouvre 1894, pl. 14, fig. 5. 2-4, SP unregistered (*ex* Le Mesle Collection). 7-9, MNHP unregistered. All Upper Coniacian *Paratexanites serratomarginatus* Zone, Bed 4 of the Craie de Villedieu (de Grossouvre's Couche à *Ostrea auricularis*) of the Carrières de La Ribochère (Loir-et-Cher).
Figs. 5, 6. *Paratexanites serratomarginatus* (Redtenbacher, 1873), FSR 2834a, horizon and locality as above. All figures $\times 1$.



KENNEDY, *Protexanites*, *Paratexanites*

- 1876 *Mortoniceras shoshonense* Meek, p. 449, pl. 6, figs. 3a, c, 6b.
 1894 *Mortoniceras bourgeoisi* d'Orbigny sp. emend A. de Grossouvre; de Grossouvre, p. 73, pl. 13, fig. 2; pl. 14, figs. 2-5; text-fig. 32.
 1894 *Mortoniceras shoshonense* Meek; Stanton, pp. 179, 180, pl. 43, figs. 1, 2.
 ?1897 *Mortoniceras bourgeoisi* d'Orbigny emend. de Grossouvre; Peron, p. 51.
 1898 *Mortoniceras shoshonense* Meek; Logan, p. 471, pl. 103, figs. 1, 2.
 non 1904 *Schloenbachia Bourgeoisi* d'Orb. emend. Gross. var. nova *americana* Lasswitz, p. 252, pl. 20, fig. 1.
 ?1907 *Mortoniceras bourgeoisanum* d'Orbigny em. de Grossouvre; Pervinquière, p. 243.
 1927 *Mortoniceras shoshonense* Meek; Reeside, p. 9, pl. 6, figs. 16-23; pl. 7, figs. 1-11; pl. 8, figs. 1-4, 5-15 (var. *crassum*).
 non 1949 *Texanites* sp. aff. *T. bourgeoisi* d'Orbigny; Rivera, p. 29, pl. 26 (= *T. cf. planatus* (Lasswitz); see Matsumoto 1970, p. 234).
 1964 *Protexanites shoshonensis* (Meek); Cobban, p. L15, pl. 4, fig. 4.
 1966b *Ammonites bourgeoisi* (d'Orbigny); Matsumoto, p. 201 f. (*pars*); text-figs. 1-5; pl. 26, fig. 1.
 1970a *Protexanites (Protexanites) bourgeoisi* (d'Orbigny); Matsumoto, pp. 228, 234, 238, 240.
 1970a *Protexanites shoshonensis* (Meek); Matsumoto, p. 234 f.
 1980 *Protexanites (Protexanites) bourgeoisi* (d'Orbigny, 1850); Klingler and Kennedy, pp. 8 f.

Types. D'Orbigny introduced this species briefly but it is, nevertheless, valid. The catalogue of the d'Orbigny collection lists the following:

7181	TT	<i>A. bourgeoisanus</i>	Villedieu	Loir et Cher	1
		a id	St. Fraimbault	Sarthe	5

All of these specimens survive, and Matsumoto (1966b, p. 202) has designated the largest of the St. Fraimbault specimens MNHP 7181a 1 lectotype of the species. The others are referred to as MNHP 7181a 2-5, following Matsumoto. The Villedieu specimen is referred to *Paratexanites serratomarginatus* (Redtenbacher, 1873). The preservation of the types indicates that they are from the couche à *Ostrea auricularis* of the Craie de Villedieu, Zone B of de Grossouvre (1901), Upper Coniacian, *P. serratomarginatus* Zone.

Material. There are numerous specimens from Zone B of the Craie de Villedieu in museum collections, including the following: OUM KZ17078, from the base of Bed 4 between Villedieu-le-Château and Trehet, FSR 2833, 2836, and 889a, MNHP unregistered (3), 1895-9 (Durand Coll.), 1896-27 (de Vibraye Coll.), SP (= de Grossouvre 1894, pl. 14, fig. 5), EMP (twelve specimens), FSM (two specimens), all from the environs of Villedieu-le-Château (Loir-et-Cher); EMP unregistered from Cangey (Indre-et-Loire), no. 113 in the P. Moreau Collection from Le Chay, Saujon (Charente-Maritime), SP unregistered from L¹⁻², Saujon, Le Fort (Charente-Maritime), EMP, La Valette (Charente-Maritime), SP, two unregistered specimens from the Marnes à *Micraster* of the Ravin de Montferrand, Montange des Cornes, Corbières (Aude). BM(NH) C37090 is inferred to be from Bed B of the Craie de Villedieu near Villedieu-le-Château, but BM(NH) C7389, labelled 'St. Georges-de-Didonne' (Charente-Maritime), is mislocalized. A specimen in the Gale Collection is from 20 to 30 cm below the top of the Calcaires Durs at St. Patern-Racan (Indre-et-Loire).

<i>Dimensions (mm)</i>		<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>	<i>Ribs</i>
MNHP (unregistered)	c	51.9 (100)	18.7 (36.0)	17.5 (33.7)	1.07	21.1 (40.7)	24
"	ic		14.9 (28.7)	15.5 (29.9)	0.96		
MNHP, Durand Coll.	c	55.0 (100)	19.2 (34.9)	20.0 (36.4)	0.96	19.0 (34.5)	24
1895-9							
FSR 2836	c	58.2 (100)	34.0 (58.4)	20.0 (34.4)	1.7	26.6 (45.7)	17
"	ic		19.0 (32.6)	18.1 (31.1)	1.05		
MNHP 1896-27	c	68.0 (100)	25.0 (36.8)	24.5 (36.0)	1.02	27.0 (39.7)	20
(de Vibraye Coll.)	ic		20.0 (29.4)	22.3 (32.8)	0.90		
SP, de Grossouvre	c	74.0 (100)	— (—)	25.6 (34.6)	—	31.5 (42.6)	25
pl. 14, fig. 5	ic		— (—)	23.3 (31.5)	—		
MNHP (unregistered)	c	81.5 (100)	28.8 (35.3)	26.2 (32.1)	1.1	35.3 (43.3)	21
"	ic		25.6 (31.4)	23.7 (29.1)	1.08		
FSR 2833	c	81.0 (100)	24.6 (30.3)	28.0 (34.6)	0.88	34.3 (42.3)	—
"	ic		22.0 (27.2)	27.0 (33.3)	0.82		

MNHP 7181a 2	c	111.3 (100)	36.0 (32.3)	40.0 (35.9)	0.90	41.5 (37.3)	22-23
"	ic		? (—)	39.0 (35.0)			
MNHP 7181a 3	c	113.8 (100)	46.0 (40.4)	37.0 (32.5)	1.24	48.7 (42.8)	22
"	ic		39.8 (35.0)	34.8 (30.6)	1.14		
Lectotype MNHP 7181a 1	c	119.0 (100)	46.2 (38.8)	46.0 (38.7)	1.0	52.4 (44.0)	—

Description. Early developmental stages are shown by paralectotype MNHP 7181a 5. At a diameter of 9 mm this inflated and coarsely ribbed specimen has only twelve primary ribs per whorl, all of which bear prominent umbilical bullae, massive conical ventrolateral tubercles, and a strong siphonal keel flanked by deep grooves, the outer edges of which bear irregular swellings. By 18 mm diameter (the next stage at which development is visible) whorl section is quadrate, depressed, with greatest breadth at umbilical bullae. Fourteen strong umbilical bullae per whorl give rise to strong, broad, coarse, straight, prorsiradiate ribs which terminate in strong pointed, clavate marginal tubercles. These are linked by a broad rib to strong high, clavate external tubercles, separated by a depression (no longer a distinct groove) from a lower rounded siphonal keel.

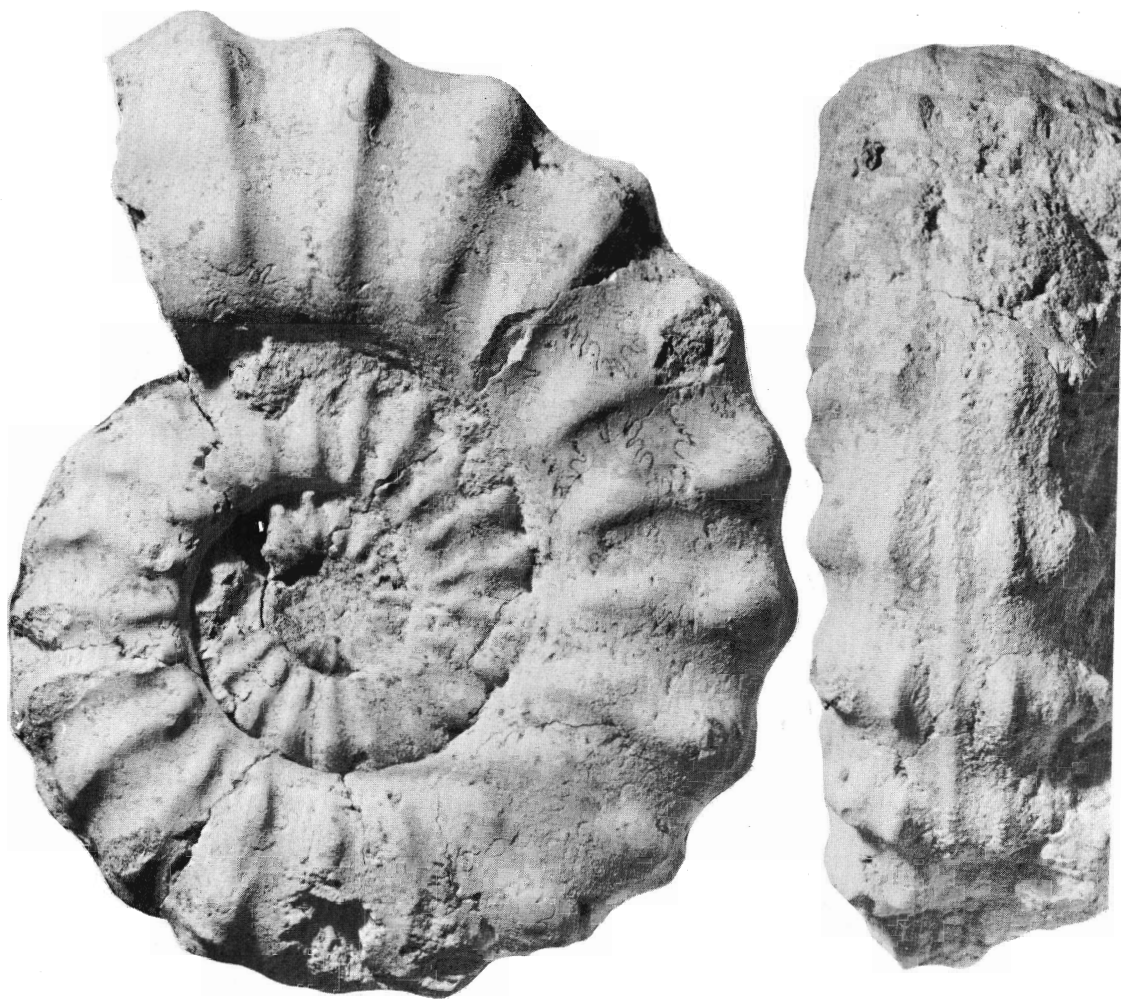
This specimen can be matched in other coarsely and distantly ribbed individuals with septate diameters of up to 75 mm, at which point some show approximated sutures. Coiling is very evolute, with umbilical diameter between 39.0 and 45.7%, the umbilicus of moderate depth with rounded wall and shoulder. The intercostal whorl section is depressed, quadrate to polygonal, with whorl breadth to height ratio of up to 1.14, greatest breadth at or close to mid-flank and costal whorl breadth to height ratio up to 1.7, greatest breadth at bullae. Ornament consists of seventeen to twenty ribs per whorl. These arise from strong, sometimes sub-spinate umbilical bullae, and are distant, strong, rounded, straight, and prorsiradiate, weakening slightly at mid-flank. All bear strong conical to feebly clavate submarginal tubercles linked by a broad rib to strong external clavi. A low swelling extends across a broad depression to either side of a low, rounded, undulose siphonal keel, the undulations corresponding in position to the external clavi. These specimens commonly show an outwards migration of umbilical bullae on their outer whorls, and in some body chambers develop a feeble umbilical bulla, becoming quadrituberculate.

These specimens may be contrasted with much larger specimens, including the lectotype. These vary from compressed to depressed, and in consequence the umbilicus comprises as little as 34% of diameter. There are twenty to twenty-six ribs per whorl, the ribs more numerous and weaker in the more compressed individuals. This same covariance of features extends to the strength and development of the tubercles, as can be seen in the plates. Whereas small specimens described above show an outwards migration of the umbilical bullae from as little as 50 mm onwards, the second group of specimens retain bullae at the umbilical shoulder up to 100 mm, as shown by de Grossouvre's magnificent example (1894, pl. 13, fig. 2). The largest known individuals (nearly 150 mm in diameter) show the same outward migration and appearance of a new bulla as the smaller forms (text-fig. 33). This difference in timing of outward migration of the bulla and appearance of a fourth row of tubercles is taken to indicate the onset of maturity, and this is supported by the approximation of sutures in some examples. The small adults are taken to be microconchs; the larger ones macroconchs. At the largest observed diameters some macroconchs show an incipient division of the submarginal tubercle into a submarginal horn and marginal clavus.

Many specimens show the suture lines (text-fig. 35A-E) which are relatively simple, with a narrow E, broad, bifid E/L, narrow L, and a rather small L/U₂.

Discussion. *Protexanites bourgeosi* is a distinctive species. Of other *Protexanites* described from Europe, *P. bontanti* (de Grossouvre, 1894) (p. 77, pl. 17, figs. 2-3) is more involute (U = 32.3% in the lectotype), with about 30% of the previous whorl concealed. The whorl breadth to height ratio is only 0.8. Weak bullae give rise to flexuous rather than straight ribs with many intercalatories to give a total of thirty-four to thirty-six ribs per whorl with very weak ventrolateral tubercles. Subspecies *shimizui* Matsumoto, 1970a, is equally distinctive.

P. strozzi (Desio, 1920, p. 204, pl. 12, fig. 8), from the presumed Coniacian near Florence, is based on an ill-preserved juvenile only. The whorls are slowly expanding with flexuous ribs that in some cases arise in pairs with some intercalatories and feeble to incipient umbilical bullae. *A. eugnamtus* (Redtenbacher, 1873, p. 117, pl. 27, fig. 1), from the Gosau Beds of Austria, was referred to *Protexanites* by Reymont (1958a) and Klinger and Kennedy (1980b), but has a venter that is in places bicarinate, in places tricarinate, with only umbilical and marginal tubercles. It is perhaps a *Reginaites* Reymont, 1957.

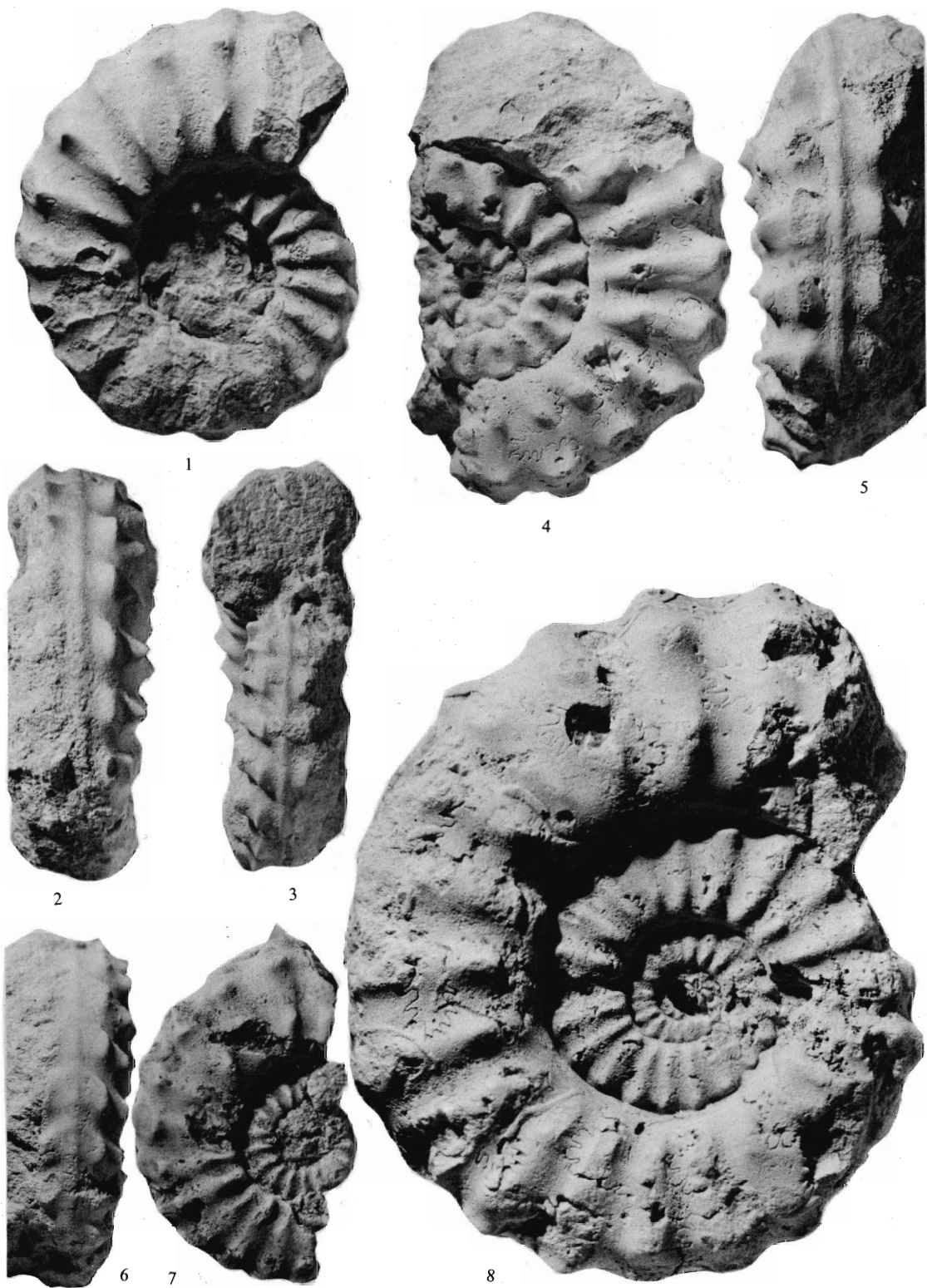


TEXT-FIG. 34. *Protexanites bourgeoisi* (d'Orbigny, 1850). Specimen from the Gale Collection from 20 to 30 cm below the top of the Calcaires Durs de La Ribochère at St. Patern-Racan (Indre-et-Loire), scale bar 5 cm.

EXPLANATION OF PLATE 24

Figs. 1-8. *Protexanites* (*Protexanites*) *bourgeoisi* (d'Orbigny, 1850). 1-3, MNHP 1896.27 (de Vibraye Collection), Upper Coniacian *Paratexanites serratmarginatus* Zone, Bed 4 of the Craie de Villedieu (de Grossouvre's Couche à *Ostrea auricularis*) of the Carrières de La Ribochère (Loir-et-Cher). 4, 5, paralectotype, MNHP d'Orbigny Collection no. 7181a; 8, a further paralectotype, 7181a, both from the same horizon as above at St. Fraimbault (Sarthe). 6, 7, MNHP B16805, from the same horizon at Couture (Loir-et-Cher).

All figures $\times 1$.



P. canaensis (Gerhardt, 1897) (p. 73, pl. 1, fig. 2) from the (presumed) Coniacian of Venezuela is very similar to the present form, but with delicate, rather weak ribs, weak tubercles, and external clavi linked into semi-continuous keels with, at an advanced stage, two external clavi corresponding to one marginal. The variety *obliquecostata* (Gerhardt 1897, p. 76, text-fig. 2a) has rather distinctive feeble marginal clavi.

P. shoshonense (Meek, 1876) (p. 449, pl. 6, figs. 3a, c, 6b) from the Coniacian of Wyoming, has been reillustrated by Reeside (1927, p. 9, pl. 6, figs. 16–23; pl. 7, figs. 1–11; pl. 8, figs. 1–4, 5–15 (var. *crassum*)). It is so close to *P. bourgeoisi* that they are regarded as synonymous. Both show the same early ontogenetic development of ornament, and an outwards migration of the umbilical bulla during late ontogeny with the appearance of new, feeble umbilical bulla in a mature quadrituberculate stage. The American populations appear to lack the slender, densely ribbed individuals that occur in Europe, but this is regarded as a difference of populations rather than species.

P. peroni Matsumoto, 1970a (p. 230, = *Peroniceras czörnigi* Peron (*non* Redtenbacher), 1897, p. 53, pl. 11, figs. 7–8) from the Senonian of Djebel Aures, Algeria, is based on a crushed specimen which may be within the limits of the present species.

Occurrence. Upper Coniacian, *Paratexanites serratomarginatus* Zone, Zone B of the Craie de Villedieu—Bed 4 at La Ribochère, Couture (Loir-et-Cher) and its correlative at Cangey (Indre-et-Loire) and St. Fraimbault (Sarthe). De Grossouvre (1894, p. 76) records it from Langeais, Chenonceaux, and at other localities in Indre-et-Loire. It also occurs in Aquitaine—at Saujon, Le Chay, and Le Fort (Charente-Maritime), in assize L^{1–2} of Arnaud, and is recorded elsewhere (see de Grossouvre 1901), and in the Corbières (de Grossouvre 1894, p. 75). It also occurs in the Gosau Beds of Austria, in northern Spain, Algeria, Tunisia, and Wyoming, Colorado and New Mexico (Cobban, pers. comm. 1983), U.S.A. (sub *Protexanites shoshonense*).

Protexanites bontanti (de Grossouvre, 1894)

Plate 25, figs. 1–4; text-fig. 36A

1894 *Mortoniceras bontanti* de Grossouvre, p. 77, pl. 17, fig. 2, text-fig. 23.

1939 *Mortoniceras bontanti* de Gross; Basse, p. 48, text-fig. 5a–b.

1955 *Protexanites bontanti* (de Grossouvre); Matsumoto, p. 38.

1970a *Protexanites (Protexanites) bontanti* (de Grossouvre); Matsumoto, p. 235, text-fig. 5.

1970a *Protexanites (Protexanites) bontanti shimizui* Matsumoto, p. 237, pl. 31, figs. 1, 2; text-fig. 6.

1980 *Protexanites (Protexanites) bontanti* (de Grossouvre); Klingler and Kennedy, pp. 8, 12, 13.

Holotype. By original designation, the original of de Grossouvre 1894, p. 77, pl. 17, fig. 2, an unregistered specimen in the MNHP Collections, from the 'Couche à *Ostrea auricularis* de la partie moyenne de la craie de Villedieu, Carrières de la Ribochère, commune de Couture (Loir-et-Cher)' (de Grossouvre 1894, p. 79). This corresponds to de Grossouvre's (1901) Zone B and Bed 4 of the present account: Upper Coniacian, *Paratexanites serratomarginatus* Zone.

Material. The paratype figured by de Grossouvre (1894, pl. 17, fig. 3) from the same horizon and locality as the holotype has not been traced. There is, however, a cast (EMP Collections). No. 112 in the collection of Dr. P. Moreau of the Université de Poitiers is from the Upper Coniacian of Le Chay, Saujon (Charente-Maritime).

EXPLANATION OF PLATE 25

Figs. 1–4. *Protexanites (Protexanites) bontanti* (de Grossouvre, 1894). 1–3, holotype, MNHP unregistered (*ex* Bourgeois Collection), Upper Coniacian *Paratexanites serratomarginatus* Zone, Bed 4 of the Craie de Villedieu (the Couche à *Ostrea auricularis* of de Grossouvre), Carrières de La Ribochère (Loir-et-Cher). 4, PM 112, Upper Coniacian *P. serratomarginatus* Zone of Le Chay, near Saujon (Charente-Maritime).

Fig. 5. *Protexanites (Protexanites)* aff. *bontanti* (de Grossouvre, 1894), cast (EMP Collections) of the missing original of de Grossouvre 1894, pl. 17, fig. 3, from the same horizon and locality as figs. 1–3.

All figures $\times 1$.



1



2



3



4



5

Dimensions (mm)	D	Wb	Wh	Wb: Wh	U
Holotype	91.5 (100)	— (—)	36.3 (39.7)	—	29.6 (32.3)
Moreau Coll. 112	114.5 (100)	— (—)	41.8 (36.5)	—	47.0 (41.0)

Description. The holotype is a wholly septate internal mould. Evolute, about 30% of previous whorl covered. Umbilicus of moderate width and shallow, with low, rounded umbilical wall, distinctly undercut on mould. Whorl section compressed, with estimated whorl breadth to height ratio of 0.8; greatest breadth close to umbilical shoulder. Inner flanks flattened and subparallel; outer flanks converge with flattened, fastigiate venter.

Seventeen strong ribs arise at umbilical seam, strengthen into comma-shaped bullae on umbilical shoulder and project into umbilicus. These give rise to low, broad primary ribs; usually one is distinctly linked to the bulla with a second linked tenuously by a mere stria, and sometimes a third. Ribs are crowded, flexuous, prorsiradiate. They pass straight across inner flank, are feebly convex at mid-flank, flexing slightly backwards across outer flank and then straightening across ventrolateral shoulder, broadening into a spatulate termination. Shorter ribs intercalate at mid-flank or below, and strengthen rapidly across outer flank and shoulder to match primaries and give a total of thirty-four to thirty-six ribs per whorl. All ribs bear weak but persistent inner and strong outer ventrolateral clavi, separated by a smooth zone from a broad rounded, undulose siphonal keel, the undulations on which are offset from the outer ventrolateral clavi. Suture line simple, with broad, asymmetrically bifid E/L, narrow L, and small bifid L/U₂.

Discussion. Involute coiling, compressed high whorls, dense flexuous ribs, and weak tubercles easily distinguish *Protexanites bontanti* from nearly all other species referred to the genus and its subgenera. Matsumoto (1970b, p. 237, pl. 31, figs. 1–2; text-fig. 6; see also Matsumoto 1971, p. 146, pl. 23, fig. 4; text-fig. 10) has introduced the subspecies *P. bontanti shimizui* for examples from the Santonian of Hokkaido, Japan, and Saghalien, U.S.S.R. These have a continuous ventral keel without undulations that is as high as the ventral clavi rather than being lower and undulose. They also differ in sutural details. Age apart, the two indeed seem to be no more than subspecifically different.

More difficult to interpret is the paratype of *P. bontanti* figured by de Grossouvre (pl. 17, fig. 3). It is a small adult, and develops an inner lateral tubercle on the body chamber. It is perhaps best referred to as *P. aff. bontanti* until it is established whether or not this is a general feature of adults of the species (Pl. 25, fig. 5).

Occurrence. Upper Coniacian *Paratexanites serratmarginatus* Zone, Bed 4 of the Craie de Villedieu of La Ribochère, Loire-et-Cher and Saujon, Charente-Maritime. Basse (1939) records the species from north of Bugarach, Corbières (Aude). Subspecies *shimizui* is from the Santonian of Hokkaido, Japan, and Saghalien, U.S.S.R.

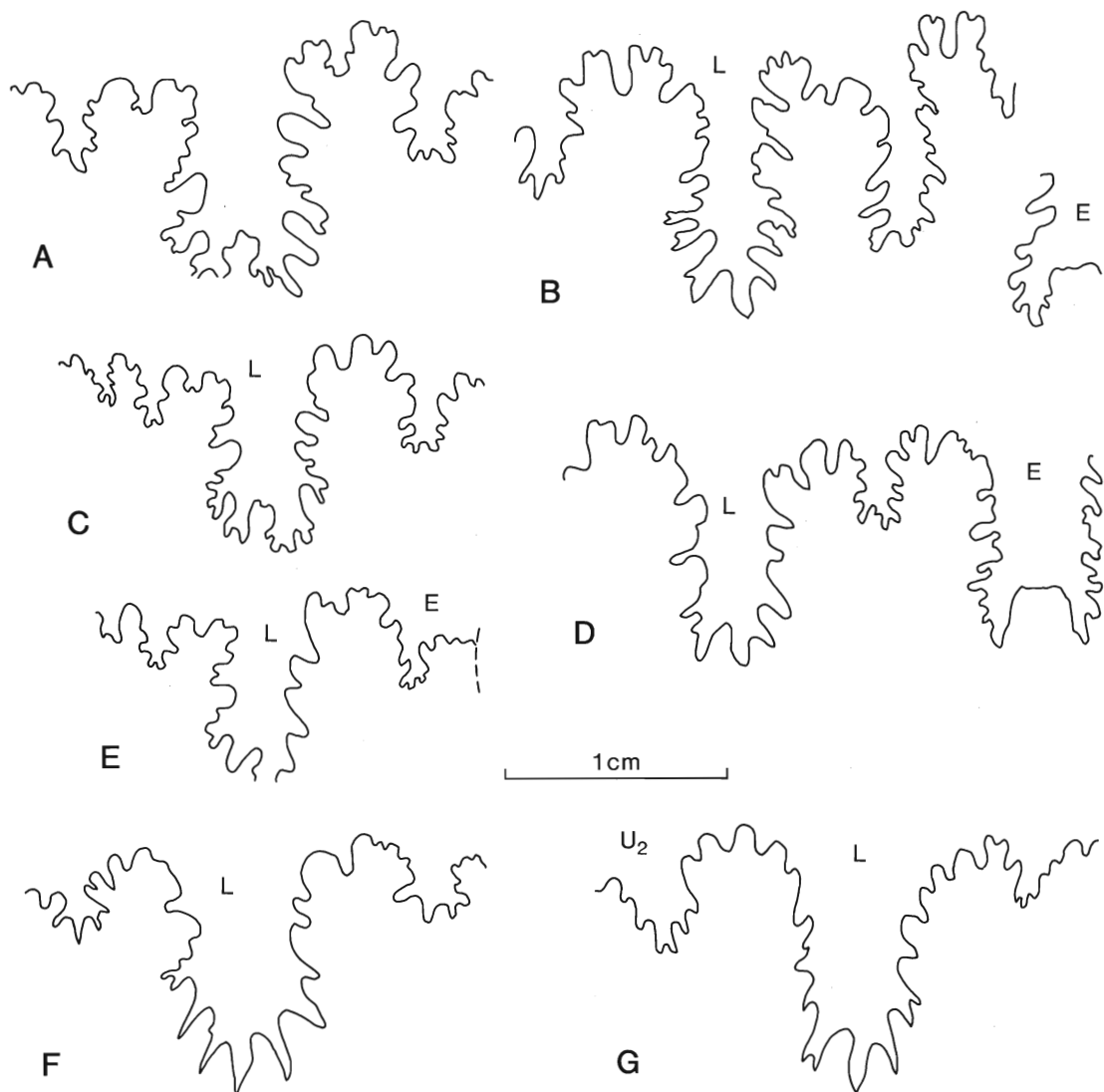
Genus PARATEXANITES Collignon, 1948

[= *Parabevahites* Collignon, 1948, p. 63 (18)]

Type species. *Mortoniceras zeileri* de Grossouvre, 1894, p. 67, pl. 14, fig. 1, by original designation by Collignon, 1948, p. 45 (102).

Diagnosis. Medium-sized to large, evolute, with quadrate whorl section. Umbilical bullae give rise to strong, predominantly single, straight or flexuous ribs with pairs of ribs and intercalated ribs sometimes present on inner whorls, where there are umbilical bullae, marginal and submarginal tubercles close together or on a single protuberance and external tubercles. On outer whorls marginal and submarginal tubercles may become widely separated and the umbilical tubercle migrates out to an inner flank position. The siphonal keel is entire or undulose.

Discussion. Collignon (1948) originally proposed *Paratexanites* as an independent genus and *Parabevahites* (type species *A. serratmarginatus* Redtenbacher, 1873) as a subgenus of *Bevahites* Collignon, 1948. Both Wright (1957) and Matsumoto (1970b) regarded *Parabevahites* as a subgenus of *Paratexanites*. Klinger and Kennedy (1980) pointed out that the chief difference lay in the approximated marginal and submarginal tubercles of the type species of *Parabevahites* and the wide separation of these tubercles in the type species of *Paratexanites*, and regarded them as strictly synonymous, a view followed here.



TEXT-FIG. 35. External sutures. A-E, *Protexanites* (*Protexanites*) *bourgeoisi* (d'Orbigny, 1850); A, C, E, original of de Grossouvre 1894, pl. 14, fig. 4, SP unregistered ex Le Mesle Collection; B, paralectotype, MNHP, d'Orbigny Collection, no 7181a 5; D, MNHP 1895-9, ex Durand Collection. F, G, *Paratexanites serratomarginatus* (Redtenbacher, 1873); F, EMP A.1.83; G, FSR 'A'.

Occurrence. Upper Coniacian and Lower and Middle Santonian. The distribution extends from France to Spain, Germany, Austria, Tunisia, Zululand, Madagascar, Japan, and Texas, U.S.A.

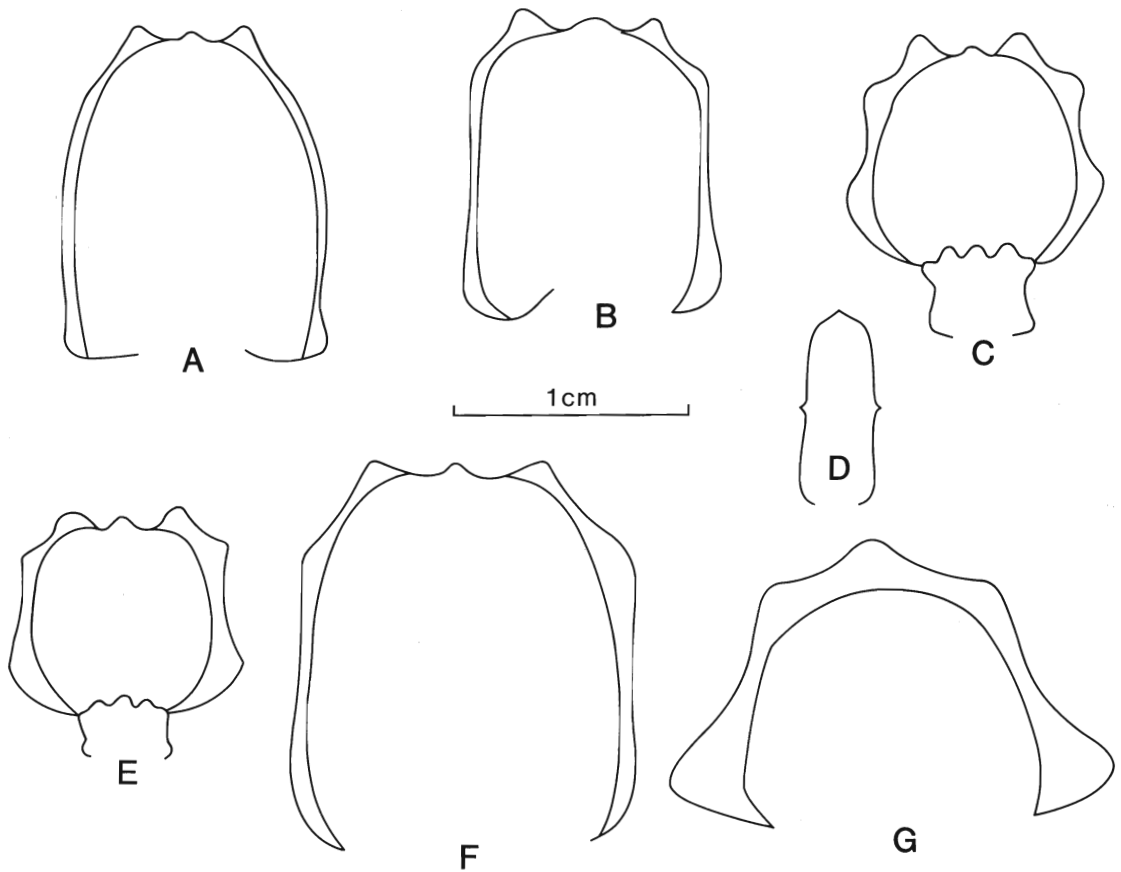
Paratexanites zeilleri (de Grossouvre, 1894)

Text-fig. 37

1894 *Mortonicerias zeilleri* A de Grossouvre sp., p. 67 (*pars*), pl. 14, fig. 1.

1896 *Mortonicerias Micheli* Mariani, p. 53, pl. 8, fig. 1.

1970a *Mortonicerias zeilleri* de Grossouvre; Matsumoto, p. 248.



TEXT-FIG. 36. Whorl sections. A, *Protexanites (Protexanites) bontanti* (de Grossouvre, 1894), holotype, original of de Grossouvre 1894, pl. 17, fig. 2, MNHP unregistered. B, C, E, F, *P. (P.) bourgeoisi* (d'Orbigny, 1850); B, paralectotype, MNHP, d'Orbigny Collection, no. 7181a 3; C, paralectotype, same collection no. 7181a 2; E, paralectotype, same collection no. 7181a 4; F, paralectotype, same collection no. 7181a 5. D, *Metatissotia? nanclasi* (de Grossouvre, 1894), original of de Grossouvre 1894, pl. 3, fig. 4, SP unregistered, ex Arnaud Collection. G, *M. desmoulinsi* (de Grossouvre, 1894), original of de Grossouvre 1894, pl. 2, fig. 6, SP unregistered, ex Arnaud Collection.

Type. The lectotype, by subsequent designation by Matsumoto 1970a, p. 249, is the original of de Grossouvre 1894, p. 67 (*pars*), pl. 14, fig. 1. The specimen has not been traced, but may be in those parts of the SP Collections that are not at present accessible to study. There are casts in the EMP and FSR Collections.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
Lectotype c	137.0 (100)	43.0 (31.4)	41.0 (30.0)	1.05	64.3 (46.9)
„ ic	—	38.8 (28.3)	39.0 (28.4)	0.99	—

Description (based on a cast). Very evolute with broad umbilicus of moderate depth ($U = 46.9\%$); umbilical wall flattened and inclined outwards, umbilical shoulder broadly rounded. Whorl section slightly depressed, with greatest breadth at umbilical bullae and low on flanks intercostally. Inner flanks moderately inflated, outer flanks rounded and convergent, ventrolateral shoulders broadly rounded, venter broad, flattened. Twenty-eight to twenty-nine primary ribs per whorl arise on umbilical wall and strengthen into prominent umbilical bullae that perch on umbilical shoulder on inner whorls but migrate outwards to an umbilicolateral position on outer whorl. Bullae give rise to strong, distant, feebly rursiradial straight ribs, all of which bear a rather weak bullate

submarginal tubercle, stronger, clavate marginal tubercle, and yet stronger clavate external tubercle. These are linked across the venter by a low, undulose siphonal keel.

Discussion. *P. zeilleri* was originally based on two specimens, the lectotype from the Calcaires Durs de La Ribochère at the base of the Craie de Villedieu, and the paralectotype from Hernes, Westphalia, figured by Schlüter (1867, pl. 6, fig. 1). Matsumoto (1970a, p. 248) has subsequently indicated that the latter is, in his view, a crushed *Texanites*. *P. zeilleri* is easily distinguished from *P. serratomarginatus* (Redtenbacher, 1873) (p. 110, pl. 25, fig. 2a-d) by the wide separation of submarginal and marginal tubercles. Differences from the various Japanese species are given by Matsumoto (1970a, p. 249f.). Among the diverse South African *Paratexanites* the closest comparisons are with *P. umkwelanense* (Crick, 1907) (see Klinger and Kennedy 1980, p. 30, figs. 17-20A, 21-30) which has a narrower umbilicus (34.9-44.3% of diameter) and less prominent umbilical tubercles. The two are closely allied, however.

Occurrence. The lectotype comes from the condensed Calcaires Durs de La Ribochère of La Ribochère and cannot be dated precisely.

Paratexanites serratomarginatus (Redtenbacher, 1873)

Plate 23, figs. 5-6; Plate 26, figs. 1-3; Plate 27, figs. 1-7; text-fig. 35F, G

- 1850 *Ammonites bourgeoisanus* d'Orbigny, p. 212 (*pars*).
 1873 *Ammonites serrato-marginatus* Redtenbacher, p. 110, pl. 25, fig. 2a-d.
 1894 *Mortonicerus serrato-marginatum* Redtenbacher; de Grossouvre, p. 69, pl. 16, fig. 1.
 1966 *Protexanites bourgeoisi* (d'Orbigny); Matsumoto, p. 202f. (*pars*); text-fig. 6 only.
 1973 *Parabevahites* cf. *serratomarginatus* (Redtenbacher); Kerckhove and Thieuloy, p. 55, pl. 1, figs. 2-4.
 1979 *Parabevahites serratomarginatus* (Redtenbacher); Collignon *et al.* p. 392, pl. 2, figs. 1, 2.
 1981 *Paratexanites serratomarginatus* (Redtenbacher, 1873); Kennedy, Summesberger and Klinger, p. 117, figs. 1-7 (with synonymy).
 ?1982 *Paratexanites serratomarginatus* (Redtenbacher, 1873); Immel, Klinger and Wiedmann, p. 23, pl. 8, fig. 6.

Types. Redtenbacher based this species on seven syntypes from the Coniacian Gosau Beds of Glanegg, Austria. No. 6381, the original of Redtenbacher 1873, pl. 25, fig. 2a-b preserved in the collections of the Haus der Natur, Salzburg, Austria, has been designated lectotype by Kennedy, Summesberger and Klinger (1981, p. 117). The other paralectotypes are either in this collection or the collections of the Oberösterreichisches Landesmuseum, Linz, Austria (see Kennedy *et al.* 1981 for details).

The holotype, by monotypy, of *P. (Parabevahites) serratomarginatus grossouvrei* Matsumoto, 1970, is the original of de Grossouvre 1894, pl. 16, fig. 1, a specimen in the de Grossouvre Collection from the 'Couche à *Ostrea auricularis* de la partie moyenne de la craie de Villedieu. Carrières de la Ribochère, commune de Couture (Loir-et-Cher)' (de Grossouvre 1894, p. 73).

Material. SP, unregistered (Le Mesle Collection), EMP 1005-7791 (Laville Collection), FSR 'A' (Seunes Collection), FSR 2834-5, all from the couche à *Ostrea auricularis* (de Grossouvre's (1901) Zone B and Bed 4 of the present account) of the Craie de Villedieu at La Ribochère, Couture (Loir-et-Cher). Two unregistered specimens (SP unregistered) are from Grézac (Charente-Maritime); SP (unregistered) is from Assize L, Pons (Charente-Maritime). All Upper Coniacian, *P. serratomarginatus* Zone.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
FSR 2834	58.5 (100)	— (—)	21.0 (35.9)	—	23.0 (39.3)
FSR 'A'	72.3 (100)	— (—)	24.5 (34.0)	—	29.8 (41.2)

Description and Discussion. Kennedy, Summesberger and Klinger (1981, p. 117, figs. 1-4) have redescribed and illustrated the type material and other Austrian specimens. The French material is in general larger than the types, and shows a wide range of variation. The two specimens agreeing most closely with the lectotype are FSR 'A' and the larger specimen from Grézac. Coiling is very evolute ($U = 29.8\%$), the low, flattened umbilical wall abutting against the submarginal tubercles. The umbilical shoulder is narrowly rounded, whorl section compressed (estimated whorl breadth to height ratio 0.9), greatest width at umbilical bulla or close to umbilical

shoulder intercostally. The flanks are flattened, converging slightly to narrowly rounded ventrolateral shoulders and broad, flattened venter. Twenty-one strong umbilical bullae per whorl give rise to single ribs, or rarely pairs of strong straight to feebly flexuous prorsiradiate ribs, with occasional intercalated ribs arising low on flank to give a total of twenty-six ribs per whorl.

From the smallest diameter visible there is a broad swelling at the termination of all ribs, bearing weak marginal and submarginal clavi spaced close together and a stronger external clavus at a somewhat greater separation. A deep interspace separates external clavi from a lower, rounded undulose siphonal keel, undulations corresponding to position of clavi and interspaces. The larger Grézac specimen has rather more flexuous, crowded ribs, and in this respect is closer to the lectotype (Kennedy, Summesberger and Klinger 1981, figs. 1A-C, 2I, 3B). One of the paralectotypes of *A. bourgeoisianus* d'Orbigny, 1850 (MNHP 7181) although worn, continues this style of ribbing to a diameter of 90 mm, with clearly separated marginal, submarginal, and external tubercles visible where well preserved. Matsumoto (1966b, p. 204, text-fig. 6) referred this specimen to *Protexanites bourgeoisi*. It provides a link to the very large specimen from Villedieu illustrated by de Grossouvre (1894, pl. 16, fig. 1) which continues the same style of ornament to a diameter of 130 mm. Matsumoto (1970a, p. 263) named this specimen *Paratexanites serratomarginatus grossouvrei*, separating it from the nominate form because it had 'stronger and more rounded inner ventrolateral tubercles which are approximated with the outer ones, forming double ventrolateral major protuberances . . . the ventral keel shows weak undulations which correspond in number to the radial ribs, but in the Alpine species the keel is continuous, and not undulated'. As Kennedy, Summesberger and Klinger (1981) were able to demonstrate when re-examining the types, some have an undulating keel while the form and positioning of the tubercles is variable to the extent that *grossouvrei* cannot be maintained.

Accompanying the typical form of the species as described above is an evolute distantly ribbed form, represented by the smaller Grézac specimen, FSR 2834 and 2835. There are only twenty-two, as opposed to twenty-six ribs per whorl, whilst the umbilical bullae are stronger and migrate outwards from the umbilical shoulder to an inner lateral position on the body chamber, a new bulla appearing in their place at a diameter of only 35-40 mm. The submarginal tubercle is also stronger, and conical rather than bullate. The two larger specimens of this form are both adults, and by analogy with *Protexanites bourgeoisi*, are interpreted as microconchs. The other wholly septate specimens, in which the umbilical bulla remains at the umbilical shoulder to a diameter of more than 100 mm, are interpreted as macroconchs.

The suture line is simple (text-fig. 35F, G), with a little-incised broad, bifid E/L and narrow L.

Parabevahites serrato-marginatus of Collignon (1966, p. 76, pl. 486, figs. 1962-1963) is excluded from this species. It has a mid-lateral tubercle from a very early stage in ontogeny, is of Middle Santonian date, and appears to be a *Plesiotexanites* species, as does his *Parabevahites* cf. *serratomarginatus* (1966, p. 80, pl. 488, figs. 1967-1969).

De Grossouvre (1894, p. 69) included *A. texanus* Schlüter, 1872 (p. 41, pl. 12, figs. 1-3), from Stoppenberg, Westphalia, Germany, in the present species. Matsumoto (1970a, p. 249, text-fig. 20) has designated the original of these figures the holotype of *Paratexanites rex* Matsumoto, 1970, and included the original of one of Schlüter's (1867, p. 32 (*pars*), pl. 6, fig. 3) *A. texanus* in his species, the correct name of which is *P. desmondi* de Grossouvre, 1894 (see p. 122). The very distant, broad ribs with rounded, conical submarginal tubercles are distinctive. *P. emscheris* (Schlüter, 1876) (p. 155, pl. 42, figs. 8-10) from the Emscher-Mergel of Alstaden, Germany, was also placed in the synonymy of *P. serratomarginatus* by de Grossouvre, but most subsequent authors have not accepted this. The most useful discussion of Schlüter's species is that of Matsumoto (1970a, p. 249), who designated the original of Schlüter (1876, pl. 42, figs. 8-10) lectotype of the species. It is a body chamber only, and comparison with *P. serratomarginatus* is difficult because of the great differences in size. The ribbing is very distant indeed, with a very small inner lateral tubercle and feeble siphonal keel.

P. zeilleri (de Grossouvre, 1894) (p. 67, pl. 14, fig. 1) is from a lower horizon in the Craie de Villedieu of La Ribochère. The lectotype is the only French specimen that can be referred to the species and it differs from

EXPLANATION OF PLATE 26

Figs. 1-3. *Paratexanites serratomarginatus* (Redtenbacher, 1873). 1, FSR 'A'; 2, 3, FSR 2834, both Upper Coniacian *P. serratomarginatus* Zone fauna of Bed 4 of the Craie de Villedieu of La Ribochère (Loir-et-Cher) (*ex* Seunes Collection).

Figs. 4, 5. *Protexanites bourgeoisi* (d'Orbigny, 1850), paralectotype, MNHP 7181a (d'Orbigny Collection), same horizon and locality as figs. 1-3.

All figures $\times 1$.



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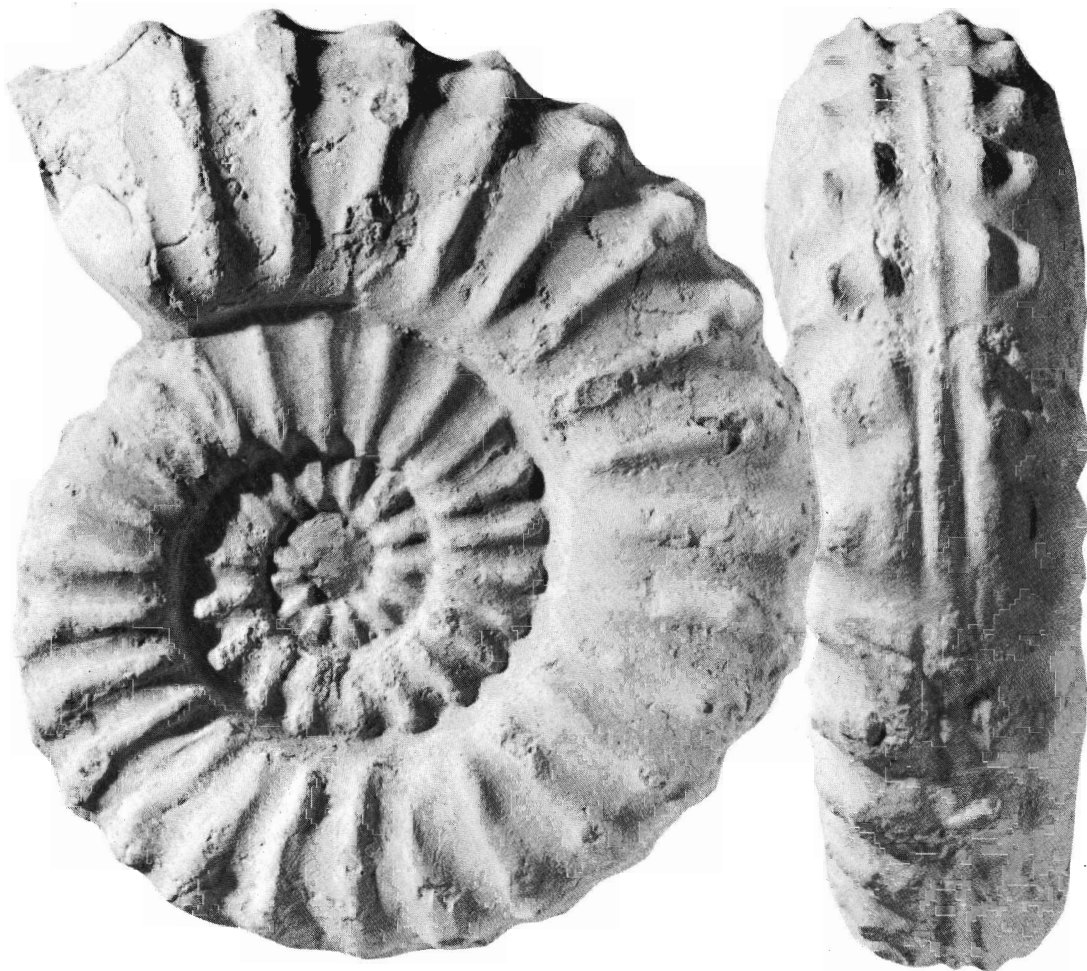


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P. serratomarginatus most obviously in having the submarginal and marginal tubercles widely spaced rather than approximated. *P. collignoni* (Fabre-Taxy, 1963) (p. 117, pl. 3, fig. 11) is based on a poorly preserved and indifferently figured fragment from the Santonian of the Beausset Basin (Var). It is said to differ from the present form in details of the umbilical tubercles, but is unrecognizable.

Differences between the present species and the various Japanese and African forms are clear from the discussions of Matsumoto (1970a) and Klinger and Kennedy (1980).

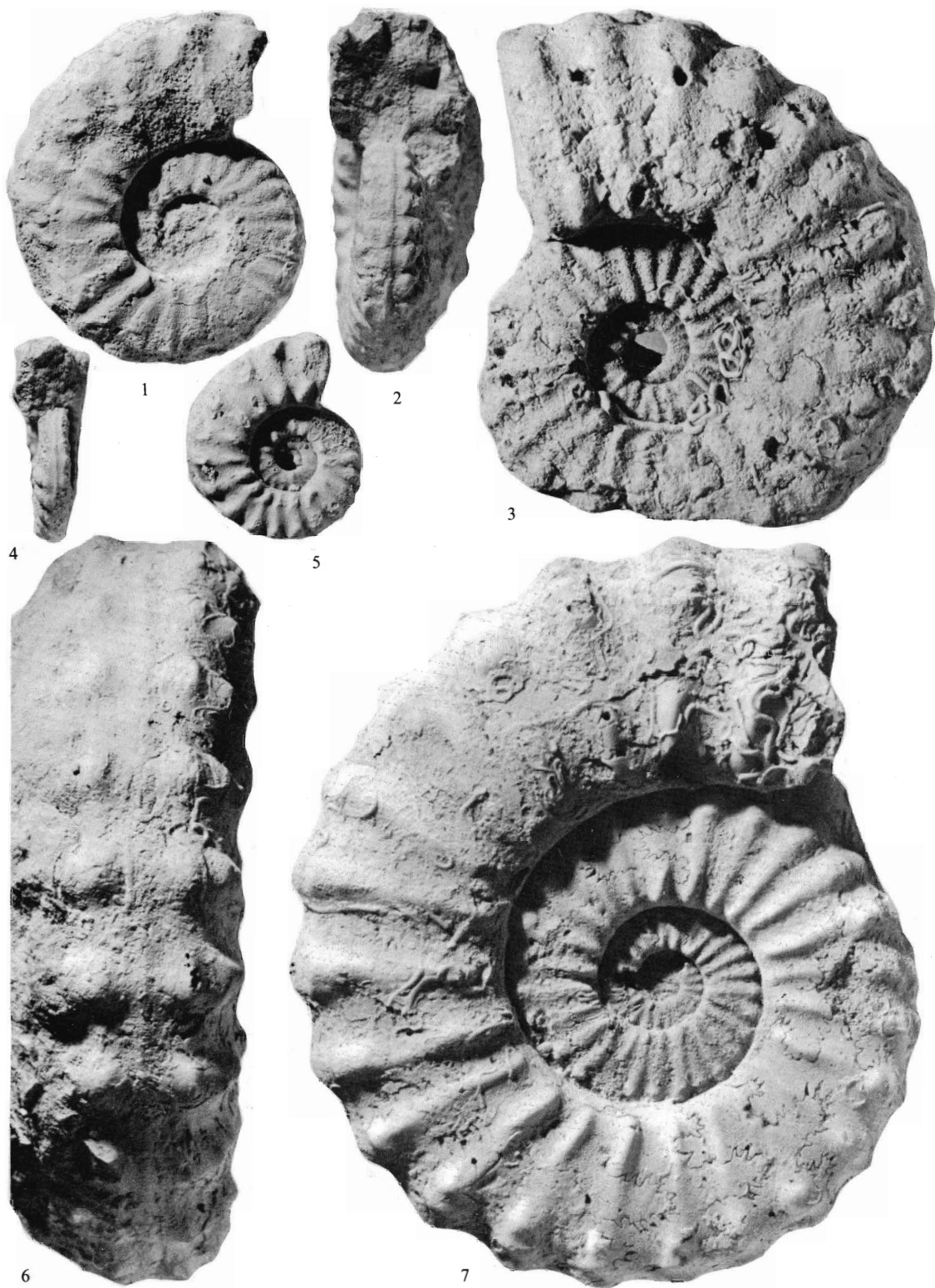
Occurrence. Where precisely located this is an Upper Coniacian species, as is the case with occurrences in Zone B (Bed 4 herein) of the Craie de Villedieu. It occupies a high position in the Coniacian of Aquitaine. Apart from



TEXT-FIG. 37. *Paratexanites zeileri* (de Grossouvre, 1894), cast of the missing lectotype, EMP Collections, $\times 1$. The original was from the Calcaires Durs de La Ribochère of the Carrière de La Ribochère, Couture (Loir-et-Cher).

EXPLANATION OF PLATE 27

Figs. 1-7. *Paratexanites serratomarginatus* (Redtenbacher, 1873). 1, 2, 4, 5, unregistered MNHP specimens, Grézac (Charente-Maritime). 3, FSR unregistered (Seunes Collection), Bed 4 of the Craie de Villedieu at La Ribochère (Loir-et-Cher). 6, 7, EMP A.1.83 (*ex* Le Mesle Collection), same horizon and locality as fig. 3. All figures $\times 1$.



KENNEDY, *Paratexanites*

specimens from Grézac (Charente-Maritime) noted above, de Grossouvre records this distinctive species from Charente, the Dordogne, and the Corbières (Basse (1939) and Collignon (1948) confirm this, the latter citing specimens in the Toucas Collection from the Ravin de Monteferrand, Montagne des Cornes, the former recording a specimen from north of Bugarach) and the Beausset Basin. Collignon *et al.* (1979) have confirmed the Beausset record and placed the species high in the Coniacian. Kerckhove and Thieuloy (1973) record it from near Castellane (Alpes-de-Haute-Provence). There is no evidence from the present study to support the extension of this species into the Santonian, although de Grossouvre (1904, p. 72) records it from Arnaud's niveau M¹, associated with '*Placenticerus syrtale* and *Mortoniceras texanum*' in Aquitaine. Elsewhere, the species is known from the Coniacian of Austria and Japan, and a closely allied form occurs in the Upper Coniacian of Zululand, South Africa.

Paratexanites desmondi (de Grossouvre, 1894)

- 1867 *Ammonites texanus* Rom.; Schlüter, p. 32, pl. 6, fig. 3 only.
 1872 *Ammonites texanus* Rom.; Schlüter, p. 41 (*pars*), pl. 12, figs. 1-3.
 1876 *Ammonites emscheris* Schlüter, p. 155 (*pars*).
 1894 *Mortoniceras desmondi* A. de Grossouvre, n. sp., p. 79.
 1970a *Mortoniceras desmondi* de Grossouvre; Matsumoto, p. 251.
 1970a *Paratexanites* (*Paratexanites*) *rex* Matsumoto, p. 249, text-figs. 9, 10.
 1980 *Paratexanites desmondi* (de Grossouvre); Klinger and Kennedy, pp. 14, 15.
 1980 *Paratexanites rex* Matsumoto; Klinger and Kennedy, p. 15.

Types. The lectotype of *P. desmondi* is the original of Schlüter 1867, pl. 6, fig. 3 only from the glauconitic marls of Stoppenberg, Germany, by the subsequent designation of Diener (1925, p. 146). It is preserved in the collections of the University of Bonn (no. 26a). The paralectotype from the Coniacian-Santonian boundary of Les Bobinnets near Aulas (Dordogne) (Desmond Collection) is lost. The holotype of *P. rex* Matsumoto, 1970 is no. 42 in the collections of the University of Bonn, and is from the glauconitic marls of Stoppenberg, Germany.

Discussion. De Grossouvre based *M. desmondi* on a specimen from Aquitaine, which he did not illustrate, and on Schlüter's figure. Because Matsumoto (1970a) overlooked Diener's (1925) lectotype designation, *desmondi*, based on the poor Schlüter fragment which Matsumoto referred to *P. cf. rex* Matsumoto, 1970 (p. 251, text-fig. 10) unfortunately has priority over *P. rex*, based on much better type material. The French specimen, as described by de Grossouvre, appears to be a different species altogether as Matsumoto (1970a, p. 251) and Klinger and Kennedy (1980, p. 15) have noted. In the absence of this specimen, which requires a new name, further comment is pointless.

Family TISSOTIIDAE Hyatt, 1900
 Genus TISSOTIODES Reymont, 1958

Type species. *A. haplophyllus* Redtenbacher, 1873, p. 100, pl. 23, fig. 1, by original designation by Reymont 1958a, p. 48.

Diagnosis. Small to medium-sized, involute, whorl section compressed to depressed, trapezoidal with fastigiate-carinate venter. Strong conical to bullate umbilical tubercles give rise to low, broad, weak ribs that may efface on flanks. Strong ventral clavi twice as numerous as umbilical bullae. Venter sharp with siphonal keel strengthened into clavi opposite ventral clavi. Ornament may persist to maturity, or decline to give a smoothing outer whorl with umbilical tubercles only. Marginal saddle asymmetrically bifid, other saddles entire; lobes denticulate. Dimorphism reflected only in size differences between adults.

Occurrence. Middle Coniacian, France, northern Spain, Austria.

Subgenus TISSOTIODES (TISSOTIODES) Reymont, 1958

Type species. *A. haplophyllus* Redtenbacher, 1873, p. 100, pl. 23, fig. 1, by original designation by Reymont 1958a, p. 48.

Diagnosis. *Tissotioides* in which ornament persists to maturity.

Discussion. Nuclei of *T. (Tissotioides)* are virtually indistinguishable from *Barroisiceras* de Grossouvre, 1894, apart from the sutural differences. The genus presumably arose from the *Reesideites-Barroisiceras* lineage by saltatory evolution of the suture, as postulated by Kennedy, Cooper and Wright (1979). Body chambers differ: whereas *Barroisiceras* may lose ornament (e.g. Basse 1947, pl. 13, fig. 1) it persists in the present form.

Wiedmann introduced the subgenus *Reymentoceras* Wiedmann, 1960, type species *T. (Reymentoceras) hispanicum*, 1960 (p. 760, pl. 8, figs. 5–8; text-fig. 15), for a species in which ornament is mostly lost at an early stage, leaving an adult growth stage with umbilical tubercles only, smooth flanks, and venter. It appears later than *T. (Tissotioides)* and is only doubtfully separable. *T. (Tissotioides)* differs from the other genera of *Tissotiidae* in its strongly crenulate siphonal keel; all others have an entire keel or keels.

Occurrence. As for genus.

Tissotioides (Tissotioides) haplophyllus (Redtenbacher, 1873)

Plate 28, figs. 2, 3; Plate 29, figs. 3–4; text-fig. 38A–C

- 1873 *Ammonites haplophyllus* Redtenbacher, p. 100, pl. 23, fig. 1.
 1885 *Buchiceras nardini* Fallot, p. 241, pl. 3, figs. 3, 4.
 1894 *Tissotia haplophylla* Redtenbacher sp.; de Grossouvre, p. 42 (*pars*), pl. 4, fig. 5 only (*non* figs. 3, 4; text-fig. 4, = *Metatissotia nodosa* Hyatt, 1903).
 1937 *Tissotia haplophylla* Redtenbacher; Senesse, p. 35, pl. 10, fig. 1; pl. 11, figs. 1, 2.
 1940 *Tissotia haplophylla* Redtenbacher var. *Crassa* Ciry, pl. 6, fig. 1.
 1958a *Tissotioides haplophyllus* (Redtenbacher); Reyment, p. 48, pl. 3, fig. 1; text-fig. 2, 1.
 1978 *Tissotioides haplophyllus* (Redtenbacher); Wiedmann and Kauffman, pl. 11, fig. 4.
 1980 *Tissotioides haplophyllus* (Redtenbacher); Wiedmann, p. 199, pl. 11, fig. 4.

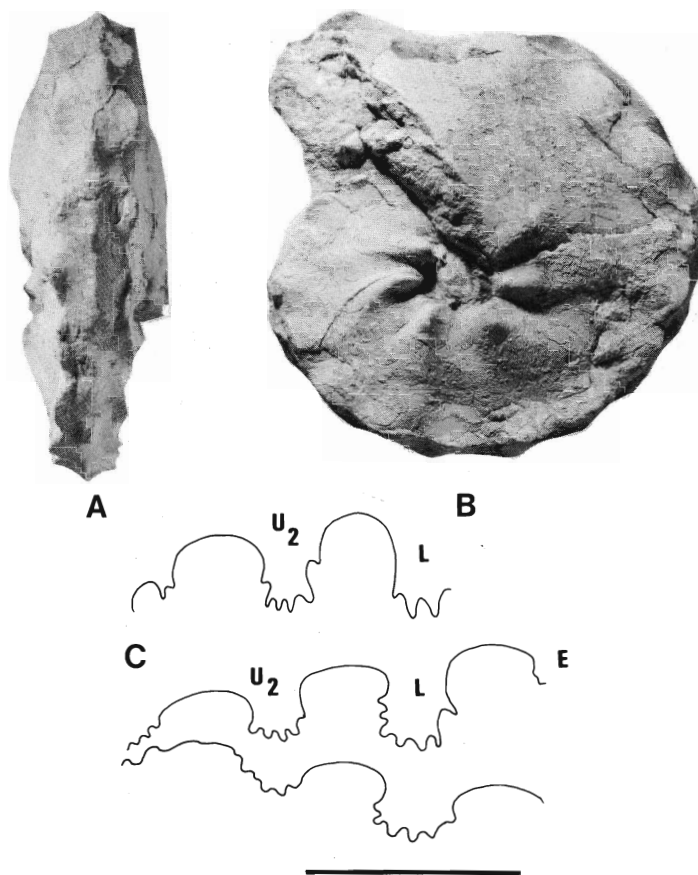
Type. The holotype, by monotypy, is the original of Redtenbacher 1873, pl. 23, fig. 1, from the Coniacian Gosau Beds of Schmölner Alpe, near Ströbl, Austria, in the collection of the Geologischen Bundesanstalt Vienna, no. 1873/01/7, 3442.

Material. In addition to the holotype, two additional Austrian specimens in the Geologischen Bundesanstalt, Vienna, no. 1976/03/2, MC 75/158, from Seitengraben, Weissenbachtal, near Ströbl, and a doubtful juvenile, no. 1935/01/02, from Schmölner Alpe, near Ströbl, mentioned by Brinkmann 1935, p. 3. French specimens are the original of de Grossouvre 1894, pl. 4, fig. 5, from Assise L¹ of Arnaud in the environs of Pons (Charente-Maritime) (SP, *ex* Rejaudry Collection), OUM KZ13293 from the Middle Coniacian *tridorsatum* Zone of St. Christophe (Charente) and OUM KZ19393 from the same horizon at La Pompierre, Jonzac (Charente-Maritime). A cast of the lectotype of *Buchiceras nardini* Fallot, 1885 (herein designated the original of Fallot's pl. 3, fig. 3) from the 'Grès vert Sénonien of Dieulefit' is preserved in the SP Collections. Numerous specimens from the Lower Coniacian *T. haplophyllus* Zone of Terradillos de Sedano (Burgos), Spain, including OUM KZ154–185 were also studied.

Dimensions (mm)		<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
Holotype at	c	54.0 (100)	17.6 (32.6)	27.3 (50.6)	0.65	7.2 (13.3)
Grossouvre 1894,	c	86.0 (100)	36.6 (42.6)	40.5 (47.1)	0.90	16.5 (19.2)
pl. 4, fig. 5	ic		28.4 (33.0)	38.5 (44.8)	0.74	
Lectotype of	c	54.3 (100)	19.0 (35.0)	26.5 (48.8)	0.72	8.5 (15.7)
' <i>Buchiceras</i> ' <i>nardini</i>	ic		18.0 (33.0)	25.5 (47.0)	0.71	

Description. Moderately involute, whorl section compressed with greatest breadth low on flanks intercostally and at umbilical bullae costally. Inner flanks broadly rounded, outer flanks flattened, convergent. Venter fastigiate-carinate, giving a modified trapezoidal section. Ornament consists of seven to nine strong umbilical bullae per whorl. These give rise to pairs of low, broad, straight prorsiradiate ribs which, together with occasional intercalated ribs, link to strong ventral clavi, linked by a broad, low swelling to strong siphonal clavi on low siphonal keel. Suture as for genus.

Discussion. The holotype of *A. haplophyllus* (text-fig. 38) is distorted, and the dimensions given above bear little relationship to its original proportions. There are seven spinose umbilical tubercles and eighteen ribs on the outer whorl. *B. nardini* Fallot, 1885 (Pl. 29, figs. 3–4) was regarded as a synonym of '*Barroisia*' *haberfellneri* by de Grossouvre (1894, p. 59), and indeed true *haberfellneri*



TEXT-FIG. 38. *Tisstotoides haplophyllus* (Redtenbacher, 1873). A, B, holotype, GBA 1873/01/7/3442, $\times 1$. C, external suture. The original is from the Gosau Beds of Schmölnauer Alpe near Ströbl Weissenbach, Austria. Bar scale 1 cm.

EXPLANATION OF PLATE 28

Fig. 1. *Metatissotia redtenbacheri* (de Grossouvre, 1894), holotype, SP unregistered (*ex* Arnaud Collection), Middle Coniacian *Peroniceras tridorsatum* Zone, Assize L¹, tunnel de Laugier, near Les Eyzies-de-Tayac (Dordogne).

Figs. 2, 3. *Tisstotoides haplophyllus* (Redtenbacher, 1873), SP unregistered (*ex* Rejaudry Collection), Middle Coniacian *Peroniceras tridorsatum* Zone fauna of Assize L¹ of Arnaud near Pons (Charente-Maritime), figured by de Grossouvre 1894, pl. 4, fig. 5.

Figs. 4, 5. *Metatissotia ewaldi* (Von Buch, 1848), MNHP unregistered, Middle Coniacian *Peroniceras tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme).

All figures $\times 1$.



1



2



3

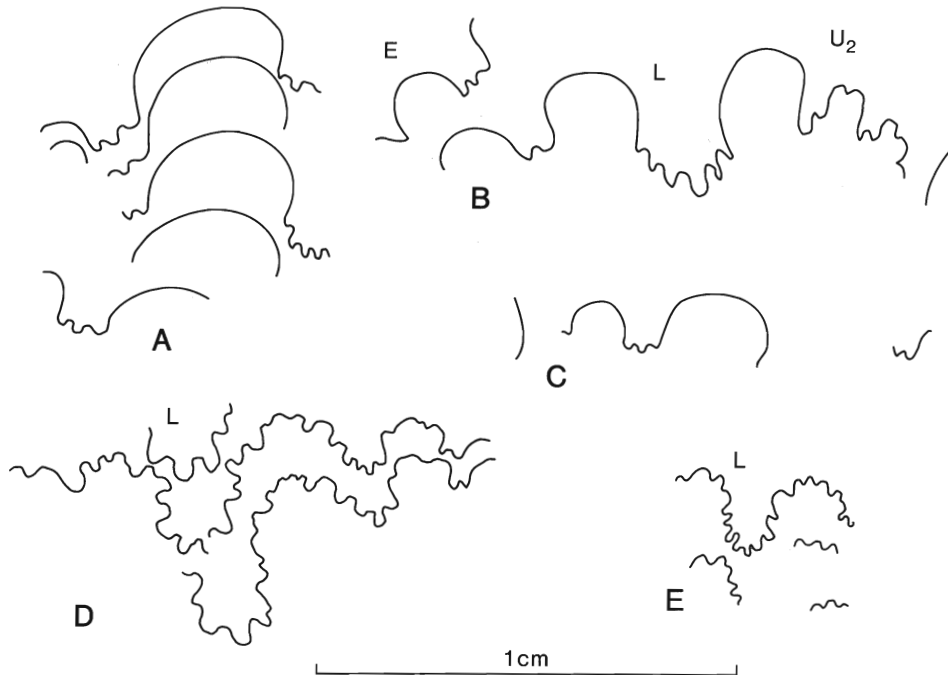


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(e.g. text-fig. 17) is a homoeomorph. The two differ in that the saddles of *Tissotioides* are entire, rather than denticulate, and the lectotype of *nardini* shows an entire lobe in Fallot's figure and on the cast of the specimen. Fallot differentiated his species from *haplophyllus* on the basis of the less elongate tubercles and the more continuous, less tuberculate keel and narrower lobes, but these are slight differences, in part compounded by differences in preservation. The two species are undoubtedly conspecific.



TEXT-FIG. 39. External sutures. A-C, *Metatissotia slizewiczi* Fallot, 1885; A, C, original of de Grossouvre 1894, pl. 7, fig. 2; B, original of de Grossouvre 1894, text-fig. 26; both are SP unregistered from Pons, ex Arnaud Collection. D, E, *Gauthiericeras? boreauui* (de Grossouvre, 1894); D, SP unregistered, Saujon, ex Arnaud Collection; E, SP unregistered, ex Peron Collection.

T. haplophyllus var. *crassa* Ciry, 1940 (lectotype, herein designated, the original of Ciry 1940, pl. 6, fig. 1) from the Coniacian of Terradillos de Sedano, Burgos, Spain, is simply a coarsely ribbed variant of this species, as is shown by new collections from the type locality.

Occurrence. Where well localized, this species is confined to the Middle Coniacian *P. tridorsatum* Zone. In France it is known from St. Christophe, Saujon, and the environs of Pons, from Dieulefit and the Corbières. It is also recorded from the Calcaires Durs de La Ribochère, but the specimen has not been traced; other records given by de Grossouvre refer to *Metatissotia nodosa* Hyatt, 1903. The species also occurs in Austria and northern Spain.

Genus METATISSOTIA Hyatt, 1903
[= *Dordiella* Reyment, 1958b, p. 59]

Type species. *A.ourneli* Bayle in Fournel 1849, p. 360, pl. 17, figs. 1-5, by subsequent designation of Roman 1938, p. 479.

Diagnosis. Small to medium-sized, involute, compressed to depressed. Umbilical tubercles give rise to one or two straight or flexuous primary ribs which, with intercalated ribs, bear ventral clavi. Venter bluntly fastigate to acute and keeled. Ribs decline on outer whorls although tubercles may persist.

Discussion. *Dordiella* Reyment, 1958 (type species *D. bakundu* Reyment, 1958b, p. 60, pl. 1, fig. 2; pl. 4, fig. 2; pl. 7, fig. 2; text-fig. 1, by original designation by Reyment 1958b, p. 59) differs from *Metatissotia* only in its slightly incised second lateral saddle and is regarded as a synonym. *Tissotia* (*Tissotia*) H. Douvillé, 1890, maintains a subquadrate whorl section and is tricarinate at maturity. *T. (Subtissotia)* Hyatt, 1903, is globular when young with a low siphonal keel and ventrolateral tubercles close to the keel. The outer whorls are smooth with a rounded venter. *Heterotissotia* Peron, 1897, has a tricarinate venter.

Occurrence. Chiefly Middle Coniacian. Many occurrences in Tethyan regions are poorly dated within the stage. The genus may extend to the Lower Santonian. The geographic distribution includes France, north and west Africa, Borneo, and Peru.

Metatissotia ewaldi (Von Buch, 1848)

Plate 28, figs. 4–5; Plate 29, figs. 9–11; Plate 30, figs. 1–2, 5–6, 8, 9, 12; Plate 32, figs. 1–3; text-fig. 40B, E

- 1848a *Ammonites ewaldi* Von Buch, p. 221, pl. 1, fig. 4.
 1848b/1850 *Ammonites ewaldi* Von Buch; Von Buch, p. 26, pl. 6, figs. 6, 7; pl. 7, fig. 4.
 1848b/1850 *Ammonites robini* Thiollière; Von Buch, p. 28, pl. 6, fig. 5.
 1849 *Ammonites Robini* Thiollière, p. 744, pl. 1.
 1873 *Ammonites* cfr. *Ewaldi* Von Buch; Redtenbacher, p. 98, pl. 22, fig. 5.
 1885 *Buchicheras ewaldi* de Buch; Fallot, p. 237, pl. 3, figs. 1, 2.
 1894 *Tissotia robini* Thiollière sp. emend. A. de Grossouvre; de Grossouvre, p. 37, pl. 4, figs. 1, 2.
 1894 *Tissotia ewaldi* L. de Buch sp.; de Grossouvre, p. 40, pl. 4, fig. 6; pl. 9, fig. 5.
 1937 *Tissotia robini* Thiollière; Senesse, p. 35, pl. 10, fig. 2; pl. 11, fig. 3.
 1958a *Tissotia ewaldi* (von Buch); Reyment, p. 36, pl. 1, figs. 1–3; pl. 2, fig. 1; pl. 8, fig. 3; text-figs. 1, 1–5; 2, 2.
 1973 *Tissotia* cf. *ewaldi* (de Buch); Kerckhove and Thieuloy, p. 53, text-fig. 1.

Types. The types of both *T. ewaldi* and *T. robini* have not been traced. The material was from Dieulefit (Drôme).

Material. SP: the original of Fallot's 1885, pl. 3, fig. 1 (= de Grossouvre 1894, pl. 4, fig. 1), a cast of Fallot's pl. 3, fig. 2, and a specimen of Hébert's (all unregistered), from Dieulefit (Drôme); the original of de Grossouvre 1894, pl. 4, fig. 2, from Assize L¹ of Arnaud at Pons (Charente-Maritime); a specimen from Assize L¹ at Jonzac (Charente-Maritime); and one from Assize L¹ at Toutyfaud (Charente-Maritime), all SP Collections; OUM KZ13460 from Antignac (Charente-Maritime). All Middle Coniacian, *Peroniceras tridorsatum* Zone. Amongst Austrian specimens are nos. 1873/01/6/3139a (the original of Redtenbacher 1873, pl. 22, fig. 5c–d), 1873/01/6/3139b (ibid. fig. 5g, i), 1873/01/6/3439, (ibid. fig. 5e), 1873/01/6/3433 (Reyment 1958a, pl. 1, fig. 1a–b) in the collections of the Geologischen Bundesanstalt, Vienna, and from the Gosau Beds of Schmölnauer Alpe. Spanish material studied includes OUM KZ186–200, 14001–14005 from the *Tissotioides haplophyllus* Zone of Terradillos de Sedano, Burgos, Spain.

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
de Grossouvre 1894, pl. 4, fig. 2	58·0 (100)	— (—)	29·2 (50·3)	—	5·0 (8·6)
de Grossouvre 1894, pl. 4, fig. 1	87·8 (100)	23·0 (26·2)	45·5 (51·8)	—	9·1 (10·4)

Description. Very involute, umbilicus tiny (up to 10% of diameter) with rounded wall and shoulder. Inner flanks rounded, outer flanks flattened, convergent; venter fastigate. Juveniles ornamented by variable but generally weak umbilical bullae which give rise to narrow prorsiradiate ribs. These branch low on flank into pairs of broader low ribs which, together with shorter intercalated ribs, flex forwards and are convex at mid-flank. They bend back and are concave on outer flank before sweeping forwards to terminate in feeble to well-marked ventrolateral clavi. This ornament varies greatly in strength between individuals. The line of the clavi is marked by a distinct facet so that the very narrow angle of the projected flanks is replaced by a less acute, fastigate

venter. Ornament declines with maturity; in some individuals (e.g. Pl. 32, figs. 1–3) clavi decline and venter broadens and rounds at as little as 50 mm diameter; in the magnificent Dieulefit specimen (Pl. 29, figs. 9–11) ribs are weak already at this diameter but clavi persist to around 70 mm beyond which they decline leaving only a sharp siphonal keel and flanking ridges marking facet at change in whorl profile. E/L is broad and bifid with outer part smaller and varying from entire to subdivided, inner part larger and entire. L is narrow, deep with small incisions, and there are three additional entire saddles separated by narrower, feebly denticulate lobes.

Discussion. Fallot (1885, p. 237) provides a lucid account of the early history of this species, and the deficiencies of Von Buch's (1848*a*) initial introduction of the name *A. ewaldi*, which he, Von Buch, subsequently (1848*b*/1850) regarded as a separate species from *A. robini*. Fallot regarded *ewaldi* and *robini* as the same species, pointing out that apparent differences in ornament are due to the types being of different size, those of *robini* being an adult and those of *ewaldi* being juveniles. De Grossouvre (1894, p. 31) repeated Fallot's statement, and the views of Bayle (1849), but separated the two and he remarked that 'Cette espèce, telle que je l'interprète . . . ressemble à peu près complètement à *T. Robini*: elle en diffère par la forme de la selle ventrale, subdivisée par un lobule en deux parties inégales, dont l'externe est la plus petite; cette subdivision externe est entière, a contour arrondi, tandis que dans *T. Robini* elle est découpée et légèrement bilobée' (1894, p. 40). Subsequent workers (e.g. Hyatt 1903; Diener 1925; Reymont 1958*a*; Wiedmann 1960, 1964) have maintained the two separate on this detail, although the 'species' always occur together. Study of the Austrian material illustrated by Redtenbacher shows, however, that there are individuals that show a slightly incised outer part of E/L, and for this reason *ewaldi* and *robini* are regarded as synonyms. The loss of ornament at greatly different sizes in the two well-preserved French specimens suggests that the species is dimorphic.

M. robini is easily distinguished from *M. nodosa* (Hyatt, 1903) (p. 47; see p. 131, Pl. 29, figs. 7, 8) which is stouter, with stronger, more flexuous ribs. *M. slizewiczi* (Fallot, 1885) (p. 240, pl. 2, fig. 2; see p. 130, Pl. 29, figs. 1–2; text-fig. 39A–C) has persistent umbilical bullae and ventral clavi and is stouter, with an obtusely rather than acutely fastigiate venter. It must be admitted that differences of this sort could well be within the limits of variation of a single species, but the lack of the more strongly ornamented specimens with typical *M. ewaldi* in Austria or Spain supports the view maintained here that they are best regarded as separate species. *M. redtenbacheri* (de Grossouvre, 1894) (p. 42, text-fig. 23; see p. 132, Pl. 28, fig. 1; text-fig. 40A) is a smooth oxycone with a quite distinctive suture line and without a faceted venter.

Occurrence. Middle Coniacian, *P. tridorsatum* Zone and correlatives in Aquitaine (Pons, Jonzac, Toutyfaux, Antignac), Dieulefit (Drôme), Brendon, Les Henri (Var), Soulatge (Corbières), northern Spain, and Austria.

EXPLANATION OF PLATE 29

Figs. 1, 2. *Metatissotia slizewiczi* (Fallot, 1885), SP unregistered (ex Arnaud Collection), original of de Grossouvre 1894, text-fig. 26, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone of Pons (Charente-Maritime).

Figs. 3, 4. *Tissotioides haplophyllus* (Redtenbacher, 1873), cast of the lectotype of *Buchiceras nardini* Fallot, 1885, pl. 3, fig. 3, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme).

Figs. 5, 6. *Metatissotia? nanclasi* (de Grossouvre, 1894), holotype, SP unregistered (ex Arnaud Collection), Lower Coniacian *Forresteria* (*Harleites*) *petrocoriensis* Zone, Assize K of Arnaud, on the railway line from Périgueux to Coutras just outside Périgueux (Dordogne).

Figs. 7, 8. *Metatissotia nodosa* Hyatt, 1903, lectotype, SP unregistered (ex Rejaudry Collection), Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Assize L¹ of Arnaud at St. Hilaire-de-Jonzac (Charente-Maritime), figured by de Grossouvre 1894, pl. 4, fig. 3.

Figs. 9–11. *Metatissotia ewaldi* (Von Buch, 1848), SP unregistered (ex Hébert Collection), Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme), figured by Fallot 1885, pl. 3, fig. 1 and de Grossouvre 1894, pl. 4, fig. 1.

All figures × 1.



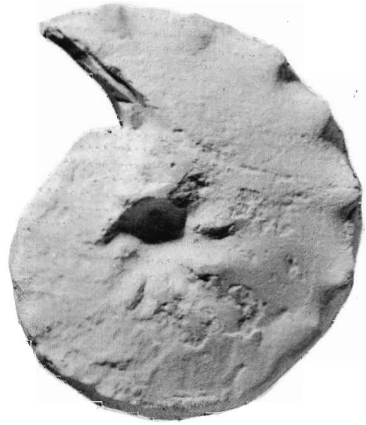
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2



3



4



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6



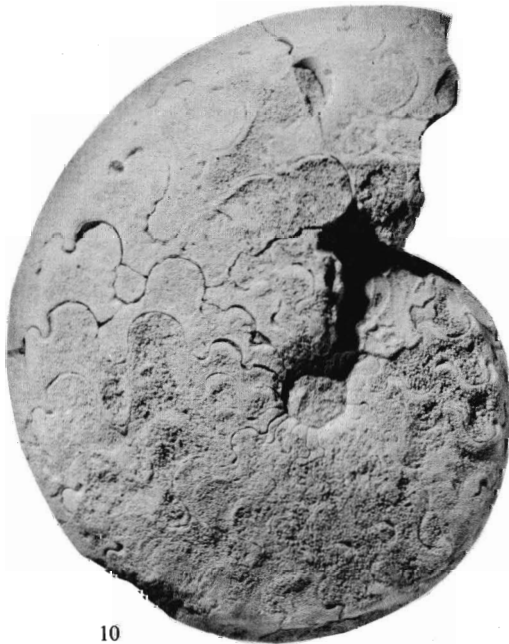
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10



11

Metatissotia slizewiczi (Fallot, 1885)

Plate 29, figs. 1-2; Plate 30, figs. 3-4; text-fig. 39A-C

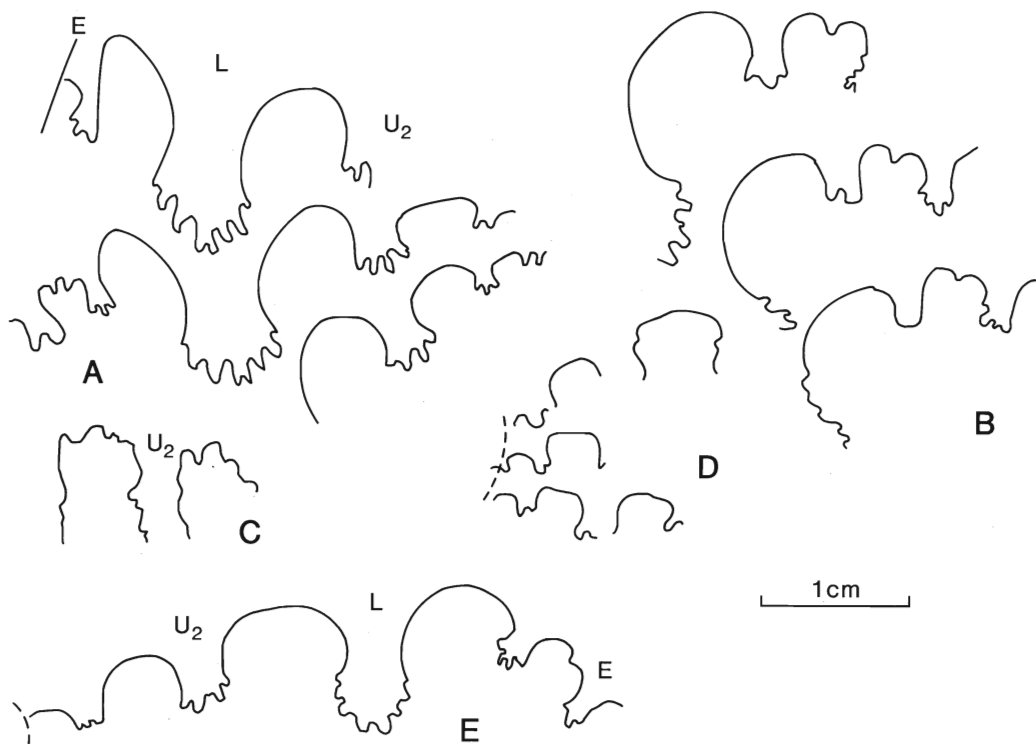
1885 *Buchiceras Slizewiczi* Fallot, p. 240, pl. 2, fig. 2.1894 *Tissotia slizewiczi* Fallot sp.; de Grossouvre, p. 46, pl. 7, fig. 2; text-figs. 25-27.1903 *Metatissotia slizewiczi* (Fallot); Hyatt, p. 49.

Holotype. By monotypy, the original of Fallot 1885, p. 240, pl. 2, fig. 2. This specimen has not been traced, but there is a rather poor cast in the SP collections. The original was from Dieulefit (Drôme).

Material. The original of de Grossouvre's (1894) pl. 7, fig. 2, and his fig. 26, both unregistered specimens from Assize L¹ of Arnaud at Pons (Charente-Maritime) are in the Sorbonne.

Dimensions (mm)	D	Wb	Wh	Wb:Wh	U
Holotype at	98.5 (100)	— (—)	56.0 (56.9)	—	?7.0 (7.1)
de Grossouvre 1894,	90.0 (100)	29.1 (32.3)	49.1 (54.6)	0.59	78.5 (9.4)
Text-fig. 26 at	49.5 (100)	— (—)	25.0 (50.5)	—	5.0 (10.1)
de Grossouvre 1894,	42.6 (100)	10.2 (23.9)	22.0 (51.6)	0.46	4.9 (11.5)
pl. 7, fig. 2.					

Description. There are only three specimens of this species available and they fall into two quite different forms, tentatively interpreted as macroconch and microconch.



TEXT-FIG. 40. External sutures. A, *Metatissotia redtenbacheri* (de Grossouvre, 1894), text-fig. 23, SP unregistered, ex Arnaud Collection. B, E, *M. ewaldi* (Von Buch, 1848); B, three E/L saddles; E, complete suture, original of de Grossouvre 1894, pl. 4, fig. 1, SP unregistered. C, *M. desmoulinsi* (de Grossouvre, 1894), partial corroded suture of the holotype, original of de Grossouvre 1894, pl. 2, fig. 6, SP unregistered, ex Arnaud Collection. D, *M.? nanclasi* (de Grossouvre, 1894), holotype, original of de Grossouvre 1894, pl. 3, fig. 4, SP unregistered, ex Arnaud Collection.

Macroconch (?): The early developmental stages are represented by the Pons specimen, a rather corroded, wholly septate internal mould. Involute, umbilicus deep, comprising 10% of the diameter; wall and shoulder rounded. Whorls compressed (estimated whorl breadth to height ratio 0.88 costally, 0.56 intercostally), greatest breadth at umbilical bulla or close to umbilical shoulder intercostally. Six umbilical bullae on outer whorl, very weak at smallest diameter visible, strengthening progressively to massive node at largest diameter preserved; markedly prorsiradiate, they pass into low, broad ribs that decline across flanks, dividing into two low, broad secondaries which, together with occasional short intercalated ribs (rib total is twelve per half whorl) strengthen markedly with increasing diameter and bear progressively strengthening rounded to clavate ventrolateral tubercles. Venter obtusely fastigate, with rounded siphonal region. The much larger wholly septate holotype has five or six strong umbilical bullae that give rise to low, broad, prorsiradiate ribs either singly or in pairs at smallest diameter visible, but these too decline as size increases. All ribs bear blunt rounded to feebly clavate ventrolateral tubercles that persist. The venter is acutely fastigate. E/L is broad and asymmetrically bifid, the outer half with minor subdivisions, the inner half entire in Fallot's (1885, pl. 2, fig. 2) figure. L is broad and has minor incisions, as do the other saddles. L/U_2 is the same size or larger than the inner, entire half of E/L.

Microconch (?): This is represented by the original of de Grossouvre 1894, pl. 7, fig. 2. Coiling involute, with small, shallow umbilicus ($U = 11.5\%$); umbilical wall low and rounded. Whorl section compressed, with whorl breadth to height ratio of 0.46, greatest breadth low on flanks, with relatively broad, obtusely fastigate venter. Six markedly prorsiradiate weak umbilical bullae per whorl pass into low ribs that decline on outer flank of phragmocone, the only other ornament being ventral clavi on either side of the fastigate venter. On the body chamber, umbilicus and inner flank are damaged but there are low, weak concave ribs preserved on the outer flank which terminate in low, broad ventral clavi. Suture incompletely exposed, with very broad L/U_2 (text-fig. 39A, C).

Discussion. Fallot (1885, p. 240) distinguished his species from *B. ewaldi* on the basis of the very distinctive ornament. De Grossouvre (1894, p. 47) stressed the sutural peculiarities of the species ('Ce qui distingue cette espèce c'est le dessin de ses cloisons . . . le lobe latéral supérieur est plus large que la première selle latérale et plus large aussi que la subdivision adjacente de la selle latérale supérieure. En même temps, la subdivision externe de la selle externe est elle-même profondément bilobée'). The suture line is the most obvious basis for treating the small Pons specimen figured by de Grossouvre (pl. 7, fig. 2) as conspecific, but it is not a juvenile as de Grossouvre stated. The last few sutures are crowded and the body chamber is contracted, the umbilical seam egressing outwards quite markedly. The earliest stages visible on the larger, wholly septate, presumably juvenile macroconch Pons specimen show that at a whorl height of 10 mm the umbilical bullae and ventral clavi are only a little stronger than those of the presumed microconch. The venters show a distinct facet and the bullae are markedly prorsiradiate in both. The microconch thus omits the stage of acquisition of strong ornament that develops so strikingly in the macroconch, and only at diameters of an estimated 25–30 mm or less are the presumed dimorphs closely similar. The size difference between the dimorphs is striking: phragmocone diameters of the microconch and the still not adult, wholly septate, holotype are in the ratio of 1:3.6.

M. slizewiczi is easily distinguished from the other Tissotiidae known from France. *M. ewaldi* (Von Buch, 1848) is weakly ornamented, without persistent tubercles, more compressed, with a different suture (see p. 127, Pl. 29, figs. 9–10; text-fig. 40B, E), *M. redtenbacheri* is a virtually smooth, very compressed oxycone with a distinctive suture (see p. 132, Pl. 28, fig. 1; text-fig. 40A), while *Tissotioides haplophyllus* (Redtenbacher, 1873) (p. 123, Pl. 28, figs. 2–3; text-fig. 38) has a row of siphonal clavi rather than an entire keel as the distinguishing feature.

Occurrence. Middle Coniacian *P. tridorsatum* Zone of Dieulefit (Drôme) and Pons (Charente-Maritime).

Metatissotia nodosa Hyatt, 1903

Plate 29, figs. 7–8

1894 *Tissotia haplophylla* Redtenbacher sp.; de Grossouvre, p. 42 (*pars*), pl. 4, figs. 3, 4 (*non* 5).

1903 *Metatissotia nodosa* Hyatt, p. 47.

Types. Hyatt based this species on the originals of de Grossouvre's pl. 4, figs. 3, 4. The original of fig. 3, an unregistered specimen in the SP collections is herein designated lectotype of the species. It is from Assize L¹ of

Arnaud at St. Hilaire-de-Jonzac (Charente-Maritime) (*ex* Rejaudry Collection). The paralectotype has not been traced. It was from 'Puymoyen, route de Torsac (Charente) collection Boreau-Lajanadie, dans les calcaires glauconieux à texture gréseuse de l'assise K de M. Arnaud' (de Grossouvre 1894, p. 45).

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
Lectotype c	42.5 (100)	12.2 (28.7)	21.2 (49.9)	0.58	6.0 (14.1)

Description. The lectotype is a well-preserved internal mould in white biosparite. Just under two-thirds of the outer whorl is body chamber. Very involute, with small umbilicus (14.1% of the diameter); umbilical wall low, narrowly rounded, whorl section compressed (whorl breadth to height ratio 0.58) with greatest breadth at umbilical bulla; inner flanks rounded; outer flanks flattened, converging to fastigate venter. Nine strong umbilical bullae give rise to one, or less commonly, two low, broad primary ribs. These have an abrupt adapical and gently sloping adapertural face that merges with the flank, and are straight and prorsiradiate on inner flank, convex at mid-flank, and flexed backwards to ventrolateral shoulder. Short intercalated ribs arise as mere striae below mid-flank, but strengthen and broaden to match primary ribs on outer flank. All ribs terminate in ventral clavi, the ribs resembling bent spatulae. Ventral keel entire, with slight undulations. Suture incompletely exposed; simple E, asymmetrically bifid E/L, the inner part of which is entire, broad little incised L, broad entire L/U₂, and auxiliary saddles on umbilical lobe.

Discussion. Hyatt differentiated his species from *Tissotioides haplophyllus* because 'the costae are well developed at an age where these are absent in true *haplophylla*. . . . The keel at the same age is entire, whereas in *haplophylla* there is a row of tubercles. The differences in ventral ornament are the most satisfactory criterion for separating the two.'

Occurrence. Lower Coniacian, *F. (H.) petrocoriensis* Zone of Torsac (Charente). Middle Coniacian *P. tridorsatum* Zone of St. Hilaire-de-Jonzac (Charente-Maritime).

Metatissotia redtenbacheri (de Grossouvre, 1894)

Plate 28, fig. 1; text-fig. 40A

1894 *Tissotia redtenbacheri* de Grossouvre, p. 42, text-fig. 23.

1937 *Tissotia redtenbacheri* de Grossouvre; Senesse, p. 35, pl. 11, fig. 4.

Holotype. The holotype, by monotypy, is the original of de Grossouvre 1894, p. 42, text-fig. 23. It is from Assise L¹ of Arnaud, 'tunnel de Laugerie, près les Eyzies (Dordogne) sur la ligne de Périgueux à Agen' (de Grossouvre 1894, p. 42) (SP, *ex* Arnaud Collection).

Description. The holotype is an almost completely septate internal mould in creamy-white bioclastic limestone. The maximum diameter is 76.5 mm. Oxycone, ornamented by low, irregular flexuous folds and depressions that are markedly prorsiradiate and straight to mid-flank, where they flex backwards and are markedly concave on outer flank, sweeping forwards to acute venter, the overall pattern resembling a sickle. Suture line highly distinctive, with small, entire ventral saddle, narrow prongs to E, asymmetric E/L in which the inner element is entire, narrow little-divided, entire L/U₂, and auxiliary saddles, separated by narrow little-incised lobes.

Discussion. The oxycone shell and unique suture line of *M. redtenbacheri* are so distinctive that confusion with other species is unlikely.

Occurrence. Middle Coniacian, *P. tridorsatum* Zone, Assise L¹ of Arnaud, tunnel de Laugerie, near Les Eyzies-de-Tayac (Dordogne). Also recorded from Soulatge, Corbierès (Aude) (Senesse 1937).

Metatissotia desmoulinsi (de Grossouvre, 1894)

Plate 30, figs. 7, 10, 11; text-figs. 36G, 40C

1894 *Barroisia Haberfellneri* var. *desmoulinsi* de Grossouvre, p. 56, pl. 2, fig. 6.

1903 *Barroisicerias desmoulinsi* Grossouvre; Hyatt, p. 105.

non 1904 *Barroisicerias Desmoulinsi* A. de Grossouvre; Solger, p. 167, text-figs. 53, 54.

non 1904 *Barroisicerias* cf. *Desmoulinsi* A. de Grossouvre; Solger, p. 168, text-fig. 55.

- 1947 *Barroisiceras haberfellneri* var. *desmoulinsi* de Grossouvre; Basse, p. 134.
 1958b *Dordiella desmoulinsi* (de Grossouvre); Reyment, p. 60.
 1970b *Hourcquia* (?) *desmoulinsi* (de Grossouvre); Matsumoto, p. 314.

Types. In introducing the variety *desmoulinsi* de Grossouvre makes reference to the specimen illustrated by him as pl. 2, fig. 6 and the specimen figured by Fritsch (1872, pl. 16, fig. 3) as *Ammonites dentatocarinatus* Roemer. The latter appears to be a *Harleites petrocoriensis* (Coquand); the original of de Grossouvre's pl. 2, fig. 6 from the Lower Coniacian *F. (H.) petrocoriensis* Zone, Assize K of Arnaud at Gourde-de-l'Arche (Dordogne), is in the SP Collections, and is herein designated lectotype of the species (Pl. 30, figs. 7, 10, 11).

Description. The lectotype is the only known specimen. It is a worn and distorted composite mould in grey marly limestone. Approximately one-third of the outer whorl is body chamber. Moderately involute, with small, deep umbilicus (approximately 21% of the diameter). Umbilical wall flattened, sloping outwards; umbilical shoulder broadly rounded; whorl section depressed, with greatest breadth at umbilical shoulder (or just outside) intercostally and at strong umbilical bullae costally. Costal whorl breadth to height ratio 1.38; intercostal ratio 1.15. Flanks flattened and convergent, with broad, fastigiate-carinate venter. Six to seven massive umbilical tubercles per whorl give rise to pairs of low, broad, straight prorsiradiate ribs. Occasional low broad intercalatories are inserted low on flanks. All ribs bear strong ventrolateral tubercles, bullate on flank but expanding at their outer termination into a clavus. A broad, low rib extends to the siphonal keel which, although worn, is entire, broad, and blunt. Sutures imperfectly exposed (text-fig. 40c). Only part of E and broad proportions of L/U₂, U₂, and first auxiliary visible.

Discussion. De Grossouvre introduced the name *desmoulinsi* for the strongly ornamented varieties of his *Barroisia haberfellneri*, that is to say *F. (H.) petrocoriensis*. The specimen he referred to as a transition to his *haberfellneri* (= *petrocoriensis*) (de Grossouvre 1894, pl. 2, fig. 1) is reillustrated here as Pl. 5, fig. 10; it is a rather typical strongly ornamented *H. petrocoriensis*. The specimen figured by Fritsch (1872, pl. 16, fig. 3) that de Grossouvre referred to *desmoulinsi* (also figured by Fritsch 1893, p. 74, text-fig. 51b) is from the Priesener Schichten of Lenešic, Czechoslovakia. It shows an umbilical and lateral tubercle at the smallest diameter, and also appears to be a *H. petrocoriensis*.

Most authors have considered this form to be a *Barroisiceras* or *Reesideoceras* (e.g. *Harleites*). Basse (1947, p. 134) presumed that the tubercle here described as umbilical had developed by fusion of a lateral and umbilical tubercle presumed to be present on the (invisible) inner whorls, and believed that the 'keel' was smooth and entire due to abrasion, as suggested by de Grossouvre. There is no evidence for the former conclusion, and the latter is not the case. Reyment (1958b, p. 60) erected the genus *Dordiella* (= *Metatissotia* herein) for Solger's *B. desmoulinsi* and reillustrated the holotype (pl. 1, fig. 2; pl. 4, fig. 2; pl. 7, fig. 2; text-fig. 1a-d), suggesting that de Grossouvre's *desmoulinsi* was also a *Dordiella*. Latterly Matsumoto (1970b, p. 310) has suggested that the species is a *Hourcquia* of the Vasoceratidae. What little of the suture can be recovered from the holotype of *desmoulinsi* suggests that it was rather simple, and on this basis it is referred to *Metatissotia* (= *Dordiella*) (see text-fig. 40c). Slight additional support for this view is the fact that all well-dated *Hourcquia* are Upper Turonian.

M. desmoulinsi differs from *M. bakundu* (Reyment 1958b, p. 60, pl. 1, fig. 2; pl. 4, fig. 2; pl. 7, fig. 2; text-fig. 1a-d) in being more depressed and inflated with fewer, larger umbilical bullae and stronger ribs and ventrolateral tubercles.

Occurrence. The lectotype was collected by Arnaud, and is said by de Grossouvre to come from the Calcaires glauconieux—Arnaud's Unit K of Gourde de l'Arche, near Périgueux, Dordogne. Unlike most specimens from this general area it is neither green-coated (this may be due to weathering) nor is the matrix glauconitic. It is, however, presumed to be from the Lower Coniacian *F. (H.) petrocoriensis* Zone.

Metatissotia? nanclasi (de Grossouvre, 1894)

Plate 29, figs. 7-8; text-fig. 40D

- 1894 *Schlönbachia Nanclasi* de Grossouvre, p. 110, pl. 3, fig. 4.

Holotype. By monotypy, the original of de Grossouvre 1894, p. 110, pl. 3, fig. 4, from the Lower Coniacian

F. (H.) petrocoriensis Zone, Assize K of Arnaud, 'première tranchée de la ligne de Périgueux à Coutras, à la sortie de Périgueux (Dordogne)' (SP Collections).

<i>Dimensions (mm)</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>
Holotype	38.5 (100)	— (—)	18.0 (46.8)	—	5.3 (13.8)

Description. The holotype is a green-coated internal mould—the typical preservation of ammonites from the Lower Coniacian hardgrounds of the Périgueux area. Very involute, with small umbilicus (13.8% of diameter). Whorl section compressed (estimated whorl breadth to height ratio 0.59); greatest breadth at lateral bulla or close to umbilical shoulder intercostally. Flanks high, flattened, and subparallel, with broadly rounded shoulders; venter abraded; where well preserved, fastigate with delicate siphonal ridge. Five to six primary ribs on the last half whorl, arising at umbilical shoulder without clear bullae. They are broad, low, straight, and prorsiradiate. All develop a small sharp mid-lateral bulla from which arise a pair of ribs, the adapertural one strongly connected to the bulla, the adapical one only weakly so. These secondary ribs flex distinctly backwards over the outer flank to curve forwards on the ventrolateral shoulder. There all terminate in an oblique ventrolateral clavus that gives rise to a broad, low, prorsiradiate rib that merges with the venter before reaching the siphonal ridge. Suture line incompletely exposed (text-fig. 40D); shows only a series of entire saddles.

Discussion. The weak umbilical ornament, lateral bullae, and ventrolateral tubercles suggest affinities with *Forresteria*, the decline of siphonal ornament suggesting a genuinely diminutive adult referable to *F. (Muramotoa)* Matsumoto, 1969. However, the simple, entire elements of the suture line (so far as it is visible) are utterly distinct from those of this subgenus, and indeed the Barroisiceratinae in general. Instead they recall the Tissotiidae. Of these, the ornament most closely resembles that of *Metatissotia* Hyatt, 1903, although here there are only umbilical bullae that may migrate out to an inner lateral position, while species reach a large size. '*Schloenbachia*' *nanclasi* thus probably represents an unnamed dwarf offshoot of Tissotiidae, but with only one specimen and an incomplete knowledge of the sutures further speculation is fruitless. The species is therefore referred to as *M.? nanclasi*.

Occurrence. As for type.

Suborder ANCYLOCERATINA Wiedmann, 1960
Superfamily TURRILITACEAE Gill, 1851
Family ANISOCERATIDAE Hyatt, 1900

[= Algeritidae Spath, 1925, p. 190; Phlycticrioceratidae Spath, 1926, p. 80]

Genus PHLYCTICRIOCERAS Spath, 1926

Type species. *Ancyloceras* (?) *douvillei* de Grossouvre, 1894, p. 254, pl. 35, fig. 8 = *Hamites trinodosus* Geinitz, 1850, p. 18, pl. 3, fig. 4.

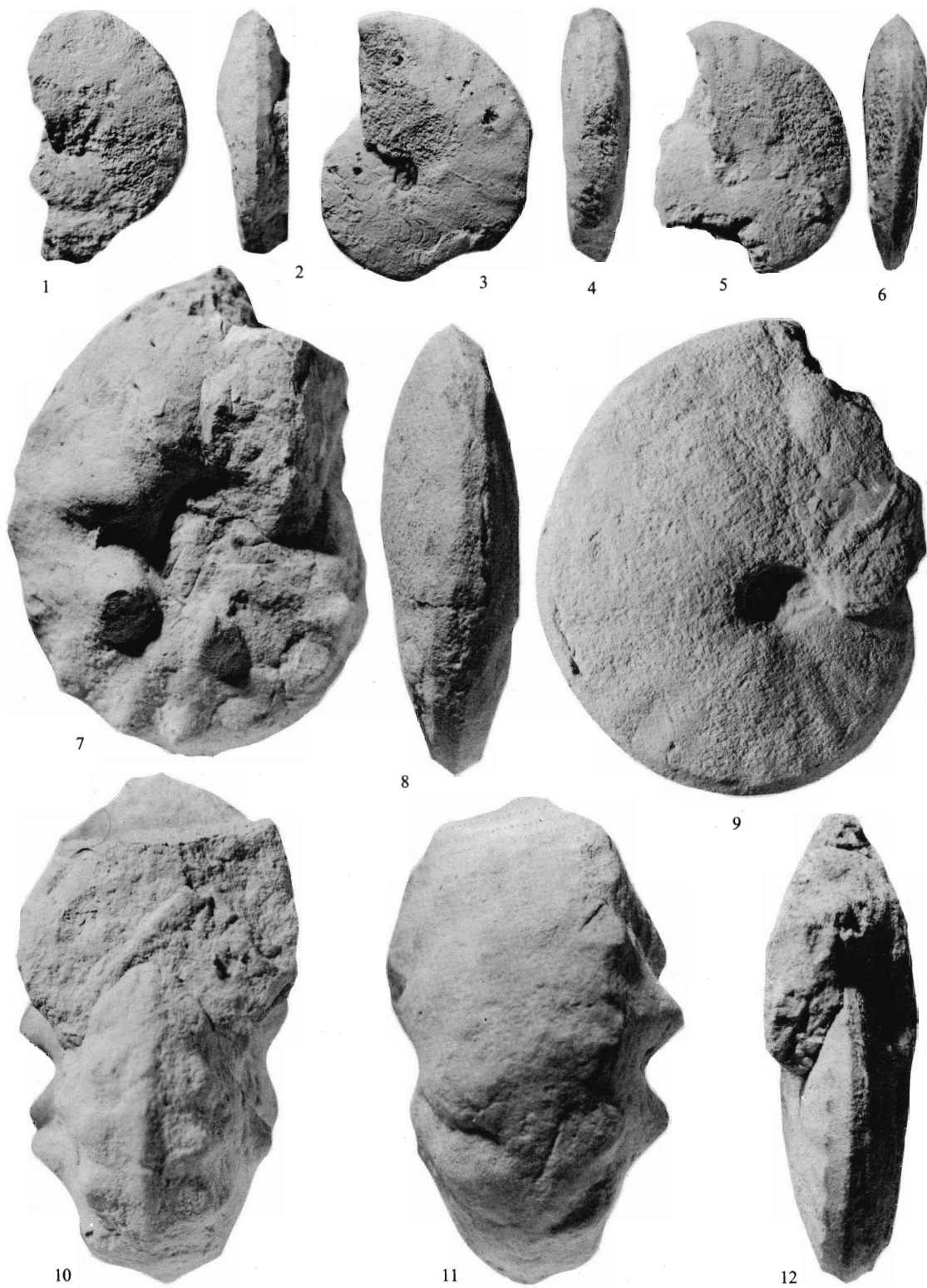
EXPLANATION OF PLATE 30

Figs. 1, 2, 5, 6, 8, 9, 12. *Metatissotia ewaldi* (Von Buch, 1848). 1, 2, 5, 6, SP unregistered, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Assize L¹ of Arnaud of Jonzac (Charente-Maritime). 8, 9, 12, MNHP d'Orbigny Collection no. 7184, original of *Ammonites doris* d'Orbigny m.s., Coniacian of Fumel (Lot-et-Garonne).

Figs. 3, 4. *Metatissotia slizewiczi* (Fallot, 1885), SP unregistered (*ex* Arnaud Collection), Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Assize L¹ of Arnaud of Pons (Charente-Maritime).

Figs. 7, 10, 11. *Metatissotia desmoulinsi* (de Grossouvre, 1894), holotype, SP unregistered (*ex* Arnaud Collection), Lower Coniacian *Forresteria* (*Harleites*) *petrocoriensis* Zone Assize K of Arnaud of Gour-de-l'Arche near Périgueux (Dordogne).

All figures × 1.



Diagnosis. Coiling poorly known; apparently planispiral, with small curved fragments and both curved and straight larger fragments. Whorl section compressed, tear-shaped. Ribs strong, straight recti- to rursiradiate with strong ventrolateral and siphonal tubercles, the latter forming a serrated keel. Periodic constrictions are flanked by slightly flared collar-ribs.

Discussion. Spath (1926, p. 80) introduced this genus briefly: 'The Coniacian *Phlyctioceras* gen. nov. (genotype *A. douvillei* Grossouvre, loc. cit., 1893, p. 254, pl. xxxv, fig. 8), with a median crest, is sufficiently distinct to be placed in a separate family: Phlyctioceratidae nov.' Reeside (1927, p. 3) and Wright (1957, p. L220) provided diagnoses, and Clark (1963, 1965) a discussion of the group.

The presence of a row of siphonal tubercles accompanying the ventrolateral distinguishes *Phlyctioceras* from *Allocrioceras* Spath, 1926 (p. 80) (type species by original designation *Crioceras ellipticum* Woods, 1896, p. 84 (*non* Mantell), renamed *A. woodsi* Spath, 1939, p. 598, = *Hamites angustus* J. de C. Sowerby 1850, p. 346, pl. 29, fig. 12) an Upper Cenomanian to Coniacian genus from which it may have evolved by acquiring the siphonal row of tubercles. Some *Allocrioceras* already have constrictions and associated flared ribs in the Upper Cenomanian *Metoicoceras geslinianum* Zone (e.g. an undescribed form from Texas) and they are also shown by Upper Turonian species such as *A. strangulatum* Wright, 1979 (p. 291, pl. 1, figs. 12–14; pl. 2, fig. 1).

Prophlyctioceras Clark, 1965, p. 33 (type species *H. tanima* Adkins and Winton, 1920, p. 41, pl. 6, figs. 1–2; text-fig. 4) from the Upper Albian of Texas was regarded by Clark as ancestral to *Phlyctioceras*. The type species is known from a few curved fragments only; whorl section varies from rounded to compressed, and is ornamented by coarse primary ribs with irregular fine secondary ribs on and between them. There are large ventrolateral and a siphonal tubercle linked by looped secondary ribs. The material is very similar to contemporaneous *Anisoceras* species and may well be no more than pathological and malformed specimens of the latter. The ornament of primary and secondary ribs easily distinguishes it from *Phlyctioceras* and they do not appear to be closely related. Wiedmann and Dieni (1968, p. 73, pl. 8, fig. 3; text-fig. 53) referred a single fragment to a new species, *Prophlyctioceras ventrinodosum*. This lacks the fine secondaries of the type species.

Phlyctioceras clarki Collignon, 1966 (p. 83, pl. 489, fig. 1972) from the Upper Santonian of Madagascar is an inflated species with dense, fine ribs, no constrictions, and a 'siphonal' tubercle displaced well to one side of the venter of the unique holotype; it appears to be a pathological diplomoceratid or polyptychoceratid.

Smedaliceras Young, 1963, p. 47 (type species *S. durhami* Young, 1963, p. 47, pl. 6, figs. 2, 3, 10–16; text-fig. 7a–e, p) from the Lower Campanian of Texas is a diplomoceratid which has siphonal tubercles. It differs from *Phlyctioceras* in having a circular cross-section and lateral bullae and a siphonal tubercle on every fifth to seventh rib, but not necessarily the same rib. Only six fragments are known.

Boehmoceras Riedel, 1931, p. 690 (type species *Ancyloceras krekekeri* Wegner, 1905, p. 210, pl. 8, fig. 2, by the subsequent designation of Wright 1957, p. L220) from the Upper Santonian of north Germany and Austria was included with a query in the Phlyctioceratidae by Wright (1957) and Summesberger (1979). The coiling is loosely criocone, the whorls expanding rapidly in height. There are blunt low primary ribs that divide into small secondaries on the venter, which has a rounded, serrated 'keel'. It is without doubt a recoiled baculitid, with only a superficial resemblance to *Phlyctioceras*. Its origin lies in the nodose *Baculites* of the Coniacian–Santonian.

Occurrence. Coniacian of France, Germany, Mexico, and Texas, New Mexico, Montana, Utah, Colorado, and Wyoming (Cobban pers. comm. 1983), U.S.A.; also reported from the Campanian of Texas.

Phlyctioceras trinodosus (Geinitz, 1850)

Plate 32, figs. 4, 11; text-fig. 42E

?1847 *Hamites triseriatus* Römiger, p. 659.

1850 *Hamites trinodosus* Geinitz, p. 18, pl. 3, fig. 4.

- 1872 *Hamites* cf. *angustus* Dixon; Schlüter, p. 106, pl. 32, figs. 6, 7.
 1894 *Ancycloceras douvillei* de Grossouvre, p. 254, pl. 35, fig. 8.
 1900 *Hamites trinodosus* Geinitz; Stürm, p. 63.
 1926 *Phlycticioceras douvillei* de Grossouvre; Spath, p. 80.
 1927 *Phlycticioceras oregonense* Reeside, p. 3, pl. 1, figs. 5–18.
 1936 *Phlycticioceras douvillei* de Grossouvre; Renz, p. 10, pl. 1, fig. 3.
 1936 *Phlycticioceras oregonense* Reeside; Renz, p. 11.
 1957 *Phlycticioceras douvillei* (de Grossouvre); Wright, p. L220, text-fig. 247, 1.
 1963 *Phlycticioceras douvillei* (de Grossouvre); Clark, p. 430 (*pars*), pl. 52, figs. 3, 4, ?6, 7, 8; *non* figs. 1, 2, 5.
 1963 *Phlycticioceras* sp. cfr. *P. douvillei* Grossouvre, 1894; Young, p. 45 (*pars*), *non* pl. 4, figs. 2, 3; pl. 11, fig. 2; text-fig. 7f, h.

Types. The holotype of *H. trinodosus* Geinitz, 1850 is the original of his pl. 3, fig. 4, from Kieslingswalde. The present whereabouts of this specimen is unknown. The lectotype of *A. (?) douvillei*, herein designated, is the original of de Grossouvre 1894, pl. 35, fig. 8, from the 'Couches à *O. auricularis* de la partie moyenne de la Craie de Villedieu. Carrières de la Ribochère, commune de Couture (Loir-et-Cher)' (de Grossouvre 1894, p. 255). De Grossouvre also mentions two other specimens in his own and the Le Mesle Collection from the same horizon and locality, but none has been traced.

Material. An unregistered specimen in the FSR Collections from the Upper Coniacian *Paratexanites serratomarginatus* Zone fauna of the Craie de Villedieu of La Ribochère (Loir-et-Cher).

Description. The French material consists entirely of flat, curved fragments. Whorl section compressed with greatest breadth close to broadly rounded dorsum. Flanks flattened and convergent; venter acute costally, rounded in intercostal section. Ornament of low, rounded convex rursiradiate ribs, weak across dorsum; rib index six to seven. All bear a prominent ventrolateral clavus, from which rib extends backwards to a sharp siphonal clavus, ribs linking tubercles being stronger than on flank. There are periodic distant constrictions; in the lectotype of *Phlycticioceras douvillei* there are ten ribs between constrictions, adapical and adapertural sides of the constriction being marked by strengthened collar-ribs which also have ventrolateral and siphonal tubercles. E is broad and shallow, E/L deeply incised and asymmetrically bifid, L deeply incised and symmetrically bifid, and L/U asymmetrically bifid to subtrifid (text-fig. 40E).

Discussion. This species presents nomenclatural problems. The first name that may refer to this form is the Bohemian *H. triseriatus* Römiger (1847, p. 659): 'Hamites triseriatus interim, wegen dreier Knoten-Reihen, deren eine auf der Mittel-Linie des Rückens gelegen est.' This is a valid indication, but the material has never been illustrated, and it is best treated as a *nomen dubium* at present. Geinitz's (1850, p. 18, pl. 3, fig. 4) *H. trinodosus* is recognizable, and the name is used here. The far better characterized *P. douvillei* (de Grossouvre, 1894) is a junior synonym. *P. oregonense* Reeside 1927 (p. 3, pl. 1, figs. 5–18) from the Cody Shale of Wyoming (*Scaphites ventricosus* Zone) is conspecific with the European species; the differentiating features given by Reeside—lesser compression, more widely spaced constrictions—are not significant. Less certain are the affinities of material from Texas described by Young (1963) and Clark (1963), as these are in part Campanian in age. None of them shows constrictions, and it seems more likely that they represent an independent homoeomorphous diplomoceratid or polyptychoceratid lineage.

Occurrence. Upper Coniacian, *Paratexanites serratomarginatus* fauna Zone of the Craie de Villedieu (e.g. de Grossouvre's Zone B) at La Ribochère (Loir-et-Cher). Undifferentiated Coniacian of Germany, northern Mexico, and Texas, U.S.A.; Coniacian *S. ventricosus* Zone of Colorado, Wyoming, U.S.A.

Family NOSTOCERATIDAE Hyatt, 1894

[= Jouaniceratidae Wright, 1952, p. 218; Bostrychoceratinae Spath, 1953, p. 16; Emperoceratinae Spath, 1953, p. 17; Hyphantoceratinae Spath, 1953, p. 16]

Genus TRIDENTICERAS Wiedmann, 1962

Type species. *Turrilites tridens* Schlüter, 1876, p. 136, pl. 35, fig. 9; pl. 36, fig. 1; by original designation.

Diagnosis. Turricone, ornamented by strong, flared ribs with three rows of tubercles, the lower two close together, and with non-tuberculate finer ribs between.

Discussion. Schlüter figured only one specimen of his *T. tridens*, but Wiedmann (1962, p. 193, pl. 11, figs. 3, 7) has illustrated two views of a Spanish specimen agreeing closely with the original. To this can be added a specimen from the Coniacian of Terradillos de Sedano, Burgos, Spain, in the Oxford University Museum Collections (no. KZ14152) and two specimens from the Coniacian of Zûazû, Navarra, Spain, kindly loaned by Dr. G. Ernst of Braunschweig (casts are OUM KZ19173-19174). These show convincingly that, rather than being a survivor of the Turrilitidae which are otherwise restricted to the Albian and Cenomanian, *Tridenticeras* is a recoiled nostoceratid. It is suggested that the origin of the genus lies in *Hyphantoceras* Hyatt, 1900 or an allied genus. Turonian species of *Hyphantoceras* have a loosely and irregularly coiled spire and a recurved body chamber. Ornament of the spire consists of flared ribs with up to four rows of tubercles, with finer, non-tuberculate ribs between. Evolution simply involved recoiling, a trend widely shown by other heteromorphs.

Wiedmann also referred *Turrilites peramplus* Lasswitz (1904, p. 14, pl. 14, fig. 1) to the genus, while it is here suggested that *T. varians* Schlüter, 1876 (p. 137, pl. 35, figs. 11-13; pl. 36, figs. 2-5) is a further representative. This species has early whorls ornamented by fine, non-tuberculate ribs and periodic stronger trituberculate ribs, and a body whorl with flared, feebly tuberculate ribs and weaker non-tuberculate ribs between. This change in ornament matches that shown on adult *H. reussianum* (d'Orbigny, 1850), while the disparate sizes of the two adult specimens of *Tridenticeras varians* illustrated by Schlüter indicate dimorphism in the genus.

Occurrence. Coniacian of Germany, France, northern Spain, and Texas, U.S.A.

Tridenticeras sp.

Plate 32, figs. 13-14

Material. OUM KZ16634 from Bed 1b of the Craie de Villedieu at La Vallée de la Roche, south-east of St. Patern-Racan, Indre-et-Loire, France. Upper Coniacian, *Gauthiericeras margae* Zone.

Description. The specimen is a body-chamber fragment with a maximum whorl height of 26 mm. Coiling is turricone, with a circular cross-section. Ornament consists of narrow, distant flared oblique ribs which bear three small but distant tubercles on the exposed whorl face. There are faint, weak non-tuberculate riblets between the flares in some cases.

EXPLANATION OF PLATE 31

Figs. 1-19. *Scaphites* (*Scaphites*) *meslei* de Grossouvre, 1894. 1, 2, 5, macroconch body chamber, SP unregistered, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone fauna of Assize L¹ of Arnaud at Pons (Charente-Maritime). 3, 4, macroconch body chamber from the same collection and horizon at La Boulinerie near Jonzac (Charente-Maritime). 6, juvenile, SP unregistered, Middle Coniacian *P.* (*P.*) *tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme). 7, 8, juvenile from the same collection, horizon, and locality as figs. 3, 4. 9, 10, microconch from the same collection, horizon, and locality as the preceding. 11, 12, body chamber of a macroconch (?) from the same collection and horizon as figs. 3, 4 at Pont de la Roche, St. Simon-des-Bordes. 13, microconch, SP unregistered (*ex* Pesme Collection), from the same horizon as 3, 4, at Jonzac (Charente-Maritime). 14, holotype of *Scaphites compressus* d'Orbigny, 1842, MNHP d'Orbigny Collection no. 7139, from the environs of Soulage (Aude). 15-17, microconch, FSR unregistered, from the Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher). 18, 19, microconch (?) body chamber from the same collection, horizon, and locality as fig. 13.

Figs. 20-24. *Otoscapites arnaudi* (de Grossouvre, 1894). 20-22, lectotype, SP (*ex* Rejaudry Collection), Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone fauna of Assize L¹ of Arnaud at St. Simon-de-Jonzac (Charente-Maritime). 23, 24, MNHP R1233a-b, from 'Charente-Inferieure'.

All figures × 1.



Genus NOSTOCERAS Hyatt, 1894

Type species. Nostoceras stantoni Hyatt, 1894, p. 569, by original designation.

Subgenus EUBOSTRYCHOCERAS Matsumoto, 1967

Type species. Eubostrychoceras indopacificum Matsumoto, 1967, p. 333, pl. 18, fig. 1, by original designation.

Eubostrychoceras sp.

Plate 32, figs. 5-6

Material. An unregistered specimen in the collections of the Faculté des Sciences, Rennes, from an unspecified horizon in the Calcaires Durs de La Ribochère at La Ribochère, Couture (Loir-et-Cher).

Description. The specimen is a helicoid body-chamber fragment only, with a maximum preserved whorl height of 20 mm. Ornament consists of strong, rounded, crowded ribs. These arise in pairs on the upper whorl face and are feebly convex and prorsiradiate across the outer whorl face. The last preserved rib is markedly flared and follows a constriction.

Discussion. Although poorly preserved, this fragment is of some interest as the first record of *Eubostrychoceras* from the French Coniacian.

Subfamily DIPLOMOCERATINAE Spath, 1926

[= Proavitoceratinae Spath, 1953, p. 17; Scalaritinae Ward, 1976, p. 455]

Genus SCALARITES Wright and Matsumoto, 1954

Type species. Helicoceras scalare Yabe, 1904, p. 9, pl. 3, fig. 2 only; by original designation.

Scalarites sp.

Plate 32, figs. 7-10

Material. SP 64-78a-b, from the Grès vert de Dieulefit of Dieulefit (Drôme). Middle Coniacian, *Peroniceras tridorsatum* Zone.

EXPLANATION OF PLATE 32

Figs. 1-3. *Metatissotia ewaldi* (Von Buch, 1848), SP unregistered (*ex* Arnaud Collection), Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone of Pons (Charente-Maritime).

Figs. 4, 11. *Phlycticrioceras trinodosus* (Geinitz, 1850). 4, FSR unregistered, Upper Coniacian *Paratexanites serratomarginatus* Zone of Bed 4 of the Craie de Villedieu (de Grossouvre's Couche à *Ostrea auricularis*) of La Ribochère (Loir-et-Cher). 11, cast (EMP collections) of the missing holotype figured by de Grossouvre 1894, pl. 35, fig. 8, from the same horizon and locality as fig. 4.

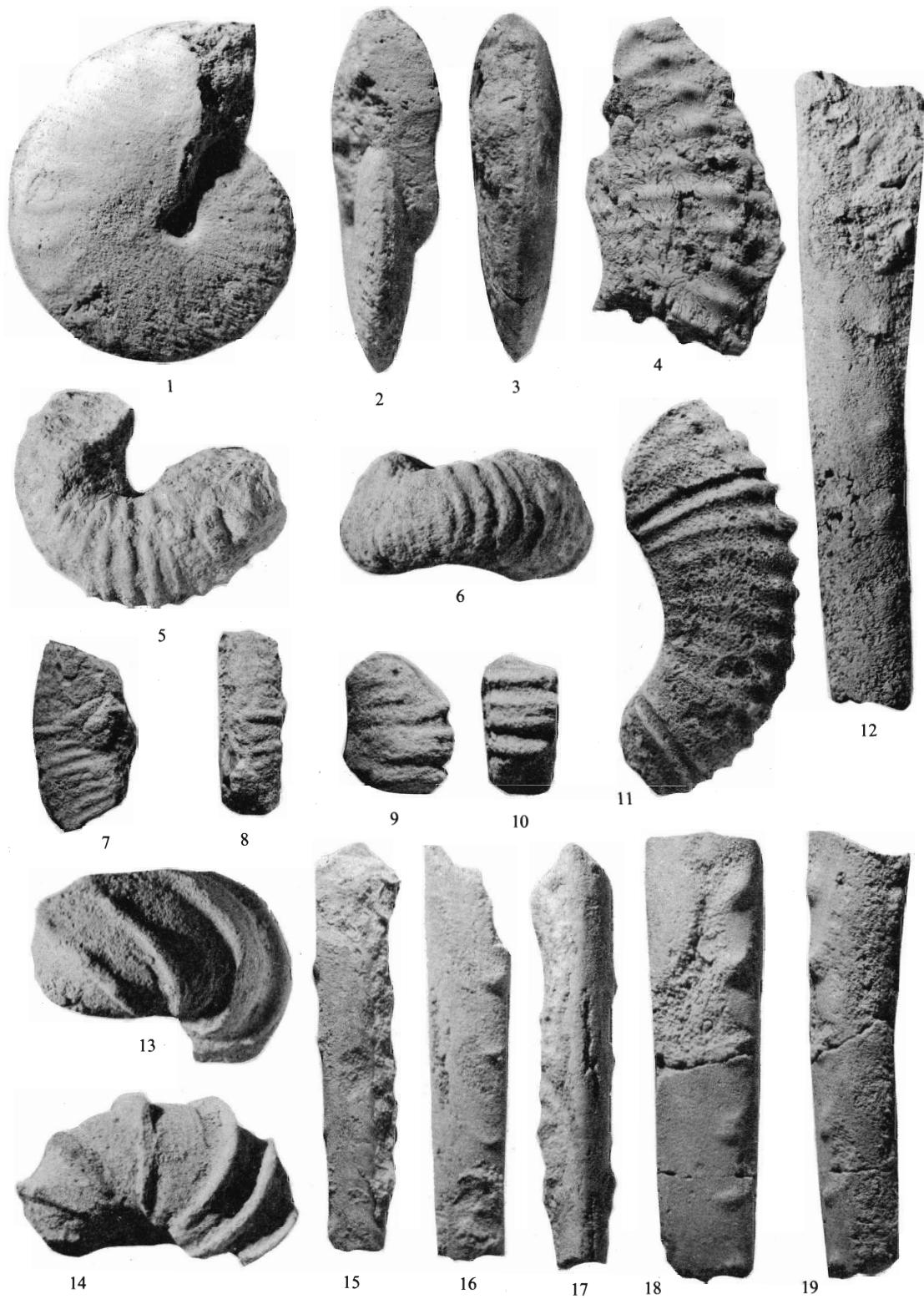
Figs. 5, 6. *Nostoceras* (*Eubostrychoceras*) sp., FSR unregistered, Calcaires Durs de La Ribochère of La Ribochère (Loir-et-Cher).

Figs. 7-10. *Scalarites* sp. SP64-78, Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Grès Verts de Dieulefit of Dieulefit (Drôme).

Figs. 12, 15-19. *Baculites incurvatus* Dujardin, 1837. 12, SP unregistered from the Middle Coniacian *Peroniceras* (*Peroniceras*) *tridorsatum* Zone Assize L¹ of Arnaud at Saujon (Charente-Maritime). 15-17, OUM KZ16639; 18, 19 OUM KZ16641, both Upper Coniacian *Gauthiericeras margae* Zone 30-50 cm above the base of the Calcaires Durs de La Ribochère at St. Patern-Racan (Indre-et-Loire).

Figs. 13, 14. *Tridenticeras* sp., OUM KZ16634, same horizon and locality as figs. 15-19.

All figures × 1.



Description and Discussion. These two short fragments of heteromorph have a compressed oval whorl section and are ornamented by crowded straight, prorsiradiate ribs, the better preserved one showing a distinctive flared rib. These features indicate that they are *Scalarites* (see Matsumoto 1977 for illustrations of a range of species), a genus not previously recorded from the Coniacian in France, although the Upper Turonian *Hamites gracilis* d'Orbigny (1842, p. 488, pl. 120, figs. 10–12; Roman and Mazeran 1913, p. 10, pl. 4, fig. 5; Sornay 1955*b*, text-figs. 1, 5) from Uchaux, Vaucluse, is also a representative of the genus (see Wright 1979, p. 324).

Family BACULITIDAE Gill, 1871

[= Eubaculitinae Brunnschweiler, 1966, p. 24]

Genus BACULITES Lamarck, 1799

[= *Homaloceratites* Hupsch, 1768, p. 110 (*non binom.*); *Euhomaloceras* Spath, 1926, p. 80]

Type species. *Baculites vertebralis* Lamarck, 1799, p. 80, by subsequent designation by Meek, 1876, p. 391.

Diagnosis. Shell straight or slightly curved when adult; up to 2 m long; dimorphic. Ornament variable, from growth striae that pass straight across the dorsum and are concave on the dorsolateral region sweeping forwards on the dorsoventral region to crescentic ribs that are strongest on the dorsolateral area to strong dorsolateral tubercles. Tubercles and ribs may be separated by weaker riblets. Aperture with long dorsal rostrum. Sutures variable, usually only moderately incised.

Discussion. *Baculites* evolved from *Sciponoceras* Hyatt, 1894, by loss of constrictions. There is a succession of species from Turonian to Maastrichtian in which ornament varies from growth lines to ribs to tubercles, both within and between species, although the Turonian representatives have ribs or growth striae only. The genus *Euhomaloceras* Spath, 1926, has *B. incurvatus* Dujardin, 1837 (p. 232, pl. 17, fig. 13) as type species. It was introduced by Spath in characteristically abbreviated form:

‘... the new genus *Euhomaloceras* gen. nov. is proposed for Meek’s group b (“Invertebr. Cret. and Tert. Fossils”: *U.S. Geol. Survey Territ.*, vol. ix, 1876, p. 392) with *B. incurvatus* Dujardin (in d’Orbigny, *Pal. Franc., Terr. Cret.*, vol. 1, 1842, p. 564, pl. cxxxix fig. 8) as genotype. . . .’

Meek’s group b was defined as follows:

‘?b. Shell straight posteriorly, but with the non-septate part gently arcuate; aperture a little oblique; appendage of siphonal side of lip arching slightly with the general curvature of the non-septate part, but not curving over the aperture.—(*B. incurvatus* Dujardin).’

So far as one can judge, the curvature of the body chamber, well illustrated by both Dujardin (1837, p. 232, pl. 17, fig. 13) and d’Orbigny (1842, p. 564, pl. 139, figs. 8–10), was the criterion used by Spath to distinguish the genus from *Baculites*. Only Wright (1957, p. L218) provided a full diagnosis: ‘Body chamber gently curved with distinct rounded siphonal and laterodorsal tubercles.’ There are, however, no siphonal tubercles in this species; the whorl section given by d’Orbigny is exaggerated, and is not shown by any of his specimens.

Curvature of the body chamber is not a very satisfactory criterion for generic separation, because curvature develops in a range of baculitids. Stephenson (1952, pl. 1) figured a *B. claviformis* Stephenson, 1952, 1700 mm long that shows marked curvature. Matsumoto (1959, p. 136, pl. 31, fig. 5) illustrated a specimen of *B. rex* Anderson, 1958 that is as distinctly curved as *incurvatus*, while remarking that both straight and curved specimens were known. Cobban (1977, p. 459, figs. 2–4) described a curved species (*B. reduncus* Cobban, 1977) from the endemic *Baculites* lineage of the U.S. Western Interior. Specimens of *B. vertebralis* itself may have slightly curved body chambers, so that this criterion alone is insufficient for generic separation, and even ancestral *Sciponoceras* may be curved at the end of the adult body chamber (Wright 1979, pl. 1, fig. 3). *Baculites* and *Euhomaloceras* are here regarded as synonyms.

Occurrence. Turonian to Maastrichtian, world-wide.

Baculites incurvatus Dujardin, 1837

Plate 32, figs. 12, 15–19; Plate 33, figs. 1–22; text-figs. 41, 42 F–M

- 1837 *Baculites incurvatus* Dujardin, p. 232, pl. 17, fig. 13.
 1842 *Baculites incurvatus* Dujardin; d'Orbigny, p. 564, pl. 139, figs. 8–10.
 1842 *Baculites tuberculata* d'Orbigny, p. 565.
 non 1887 *Baculites incurvatus* Dujardin; Holzapfel, p. 64, pl. 4, figs. 5, 6; pl. 5, fig. 10.
 1891 *Baculites incurvatus* Dujardin; Langenhan and Grundey, p. 9, pl. 2, figs. 4–7.
 ?1900 *Baculites incurvatus* Dujardin; Stürm, p. 62, pl. 4, fig. 1.
 1905 *Baculites incurvatus* Dujardin; Wegner, p. 206.
 1908 *Baculites incurvatus* Dujardin; Schmidt, p. 246.
 1961 *Baculites incurvatus* Dujardin; Gerth, p. 121, pl. 24, fig. 6; text-fig. 1.
 1982 *Baculites incurvatus* Dujardin; Immel, Klinger and Wiedmann, p. 27, pl. 11, figs. 5–7 (with additional synonymy).

Types. Dujardin based this species on a series of fragments. The largest, MNHP, no. R1025a, was designated lectotype by Immel, Klinger and Wiedmann 1982, p. 27; the paralectotypes are R1025b–e. The horizon is simply given as 'Craie Tufau'.

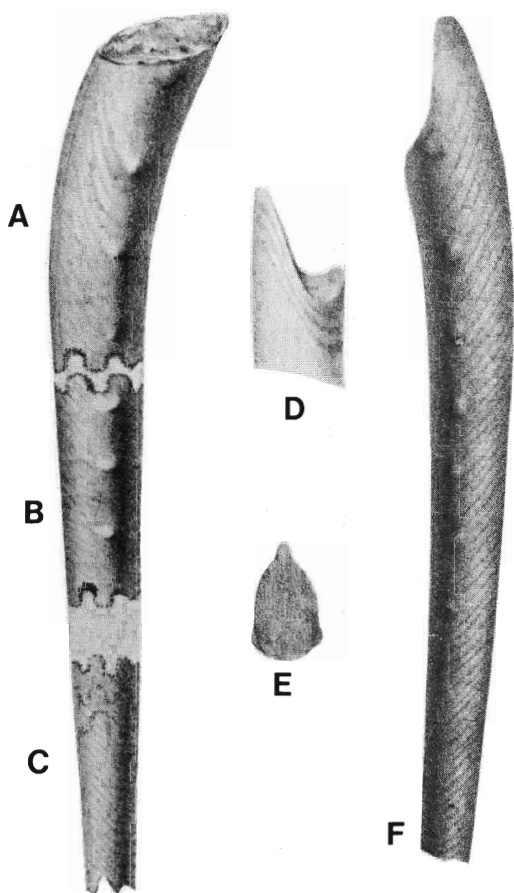
Material. Two specimens labelled 'Tours' in the d'Orbigny Collection, no. 7208; FSR XTS 341—four specimens, FSM—6 specimens, also from Tours, some labelled niveau à *S. truncatus*, Pont de la Roche. OUM KZ16639–16641, KZ16643, from 30–50 cm above the base of Bed 1 of the Craie de Villedieu at la Vallée de la Roche, south-east of St. Paterne-Racan, Indre-et-Loire, and OUM KZ17077 from Bed 4 of the Craie de Villedieu (= Zone B of de Grossouvre 1904), roadside sections between Trehet and Villedieu-le-Château, opposite and east of the turning to 'Grouteau', Loir-et-Cher. There are three unregistered specimens in the Arnaud Collection (SP), from Assize L¹ at Saujon (Charente-Maritime).

<i>Dimensions (mm)</i>		<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>
Lectotype, MNHP R1025a	c	10.8	12.3	0.88
" "	ic	8.5	12.3	0.69
" "	c	11.8	15.2	0.78
" "	ic	10.1	15.2	0.66
Paralectotype, MNHP R1025b	c	8.5	12.3	0.69
" "	ic	7.8	12.3	0.63
MNHP R1044 (d'Orb. Coll. 7208a)	c	14.5	18.0	0.81
" "	ic	12.1	18.0	0.67

Description. Small, maximum observed whorl height 22.5 mm; slowly expanding, phragmocone straight, apertural end of adult body chamber gently curved. Whorl section compressed, intercostal whorl breadth to height ratio varying from 0.67 to 0.63. Dorsum broad and flattened, dorsolateral region broadly rounded, greatest breadth low on flanks which converge to narrowly rounded venter. Sparse conical to comma-shaped dorsolateral bullae, separated by a distance equal to or slightly greater than whorl height at mid-point between tubercles. These give rise to a low, delicate, strongly prorsiradiate straight rib that sweeps forwards across flank accompanied by numerous weak to strong non-bullate ribs and striae, all of which weaken at mid-flank before strengthening on ventrolateral region. All strengthen markedly over venter, which they cross in an acute convex peak, in some cases strengthened into a ventral scale-like projection. In general ventral rib corresponding to bullate flank ribs is stronger than others, so that ventral profile is irregular (Pl. 33, fig. 18). Strength and shape of tubercles and ribs varies greatly from specimen to specimen, from almost ribless (Pl. 32, figs. 15–17) to strongly decorated (Pl. 33, figs. 6–18). One specimen (Pl. 33, figs. 12–14) has doubled tubercles and a shallow lateral groove, but this may be pathological.

Body chamber curvature is shown by lectotype and large Villedieu specimen (Pl. 33, figs. 4–9) at such disparate whorl heights (15.5 mm and 22.5 mm) as to suggest the species is dimorphic. None of the specimens shows the aperture. Suture line (text-fig. 42F–H) simple, with blocky bifid elements.

Discussion. Dujardin's figures, reproduced here as text-fig. 41A–D, are extremely accurate. In contrast, d'Orbigny's illustration (pl. 139, figs. 8–10; see text-fig. 41E–F) bears little relationship to his specimens; the ribbing is even rather than irregular, and the sulci on either side of the venter in the illustration are shown by none of the specimens. In his account of this species, d'Orbigny considered



TEXT-FIG. 41. *Baculites incurvatus* Dujardin, 1837. A-D, copies of Dujardin's original figures (1837, pl. 17, figs. 13a-d): A, is the lectotype, see Pl. 28, figs. 4-6, 15, 19-22 for photographs of the originals. E, F, copies of d'Orbigny's figures (1842, pl. 139, figs. 8-9), see Pl. 28, figs. 1-3 for photographs of the original. All figures $\times 1$.

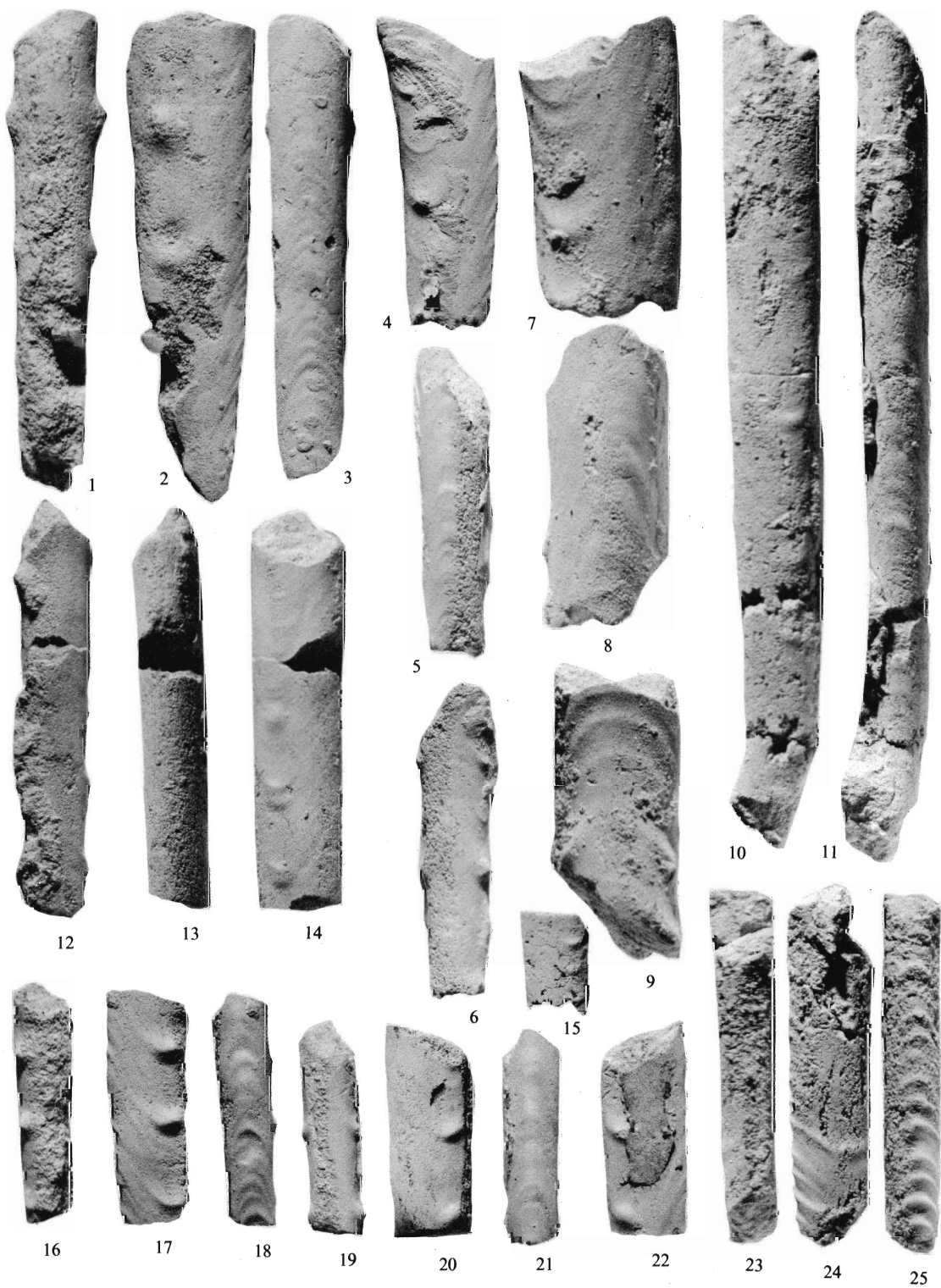
that the curvature of the adult body chamber of Dujardin's material might be a malformation, and suggested that it might better be called *B. tuberculata*; this is thus a synonym of *incurvatus*. *B. incurvatus* differs from *B. brevicosta* Schlüter, 1876, the other European Coniacian species, in having dorsolateral bullae rather than crescentic ribs, whilst Schlüter's species has distinctive ventral riblets.

Occurrence. The species first appears in the Middle Coniacian *P. tridorsatum* Zone in Touraine and Aquitaine, occurs in the Upper Coniacian *G. margae* and *Paratexanites serratomarginatus* Zones in Touraine, and in the Santonian of Touraine, Aquitaine, the Germanies, Czechoslovakia, and Austria.

EXPLANATION OF PLATE 33

Figs. 1-22. *Baculites incurvatus* Dujardin, 1837. 1-3, 16-18, MNHP R1044a, b, d'Orbigny Collection 7208, original of d'Orbigny 1842, pl. 139, figs. 8-10 (see text-fig. 41E-F) from 'Tours'. 4-6, lectotype, MNHP R1025a; 19-22, paralectotype, MNHP R1052b; 15, paralectotype, R1025c, all probably used by Dujardin in the preparation of his pl. 17, fig. 13 (reproduced here as text-fig. 41A-D), the locality is simply given as Touraine. 7-9, OUM KZ17077, Upper Coniacian *Paratexanites serratomarginatus* Zone fauna of Bed 4 of the Craie de Villedieu (de Grossouvre's Couche à *Ostrea auricularis*) between Villedieu-le-Château and Tréhet (Loir-et-Cher). 10, 11, OUM KZ1664; 12-14, OUM KZ16643, Upper Coniacian *Gauthiericeras margae* Zone 30-50 cm above the Calcaires Durs de La Ribochère of St. Patern-Racan (Indre-et-Loire).

Figs. 23-25. *Baculites* cf. *brevicosta* Schlüter, 1876, OUM KZ17023, same horizon and locality as figs. 10, 11. All figures $\times 1$.



Baculites cf. brevicosta Schlüter, 1876

Plate 33, figs. 23–25

Compare:

- 1876 *Baculites brevicosta* Schlüter, p. 141, pl. 39, figs. 9, 10.
 non 1885 *Baculites brevicosta* Schlüter; Moberg, p. 37, pl. 4, figs. 5, 6.
 1905 *Baculites brevicosta* Schlüter; Wegner, p. 207.
 non 1921 *Baculites cf. brevicosta* Schlüter; Spath, p. 261, pl. 24, fig. 5.
 1931 *Baculites cf. brevicosta* Schlüter; Collignon, p. 34, pl. 5, fig. 1; pl. 11, fig. 13.
 1959 *Baculites brevicosta* Schlüter; Matsumoto, pp. 117, 121, 128.

Types. Schlüter based this species on two specimens. The original of his pl. 39, figs. 9–10 is herein designated lectotype. It is from the Emscher-Mergel (Coniacian) of Horst, Westphalia.

Material. OUM KZ17023 from Bed 3 of the Calcaires Durs de La Ribochère between Trehet and Villedieu-le-Château (Loir-et-Cher). Middle or Upper Coniacian.

Description. The specimen is a body chamber fragment only, with a maximum whorl height of 12 mm. The shell expands very slowly. Whorl section compressed with broadly rounded dorsum and dorsolateral region, convergent ventrolateral region, and narrowly rounded venter. Distant primary ribs weak on dorsum, but strengthen on dorsolateral area into concave crescents, sweep forwards and are slightly concave on ventrolateral region, and strengthen markedly over narrow venter. There are two or three intercalated ribs between primaries; these arise as mere striae on flanks, but are as strong as primaries on venter. There are also faint sub-parallel growth striae.

Discussion. Trigonal whorl section, crescentic primaries on the dorsolateral region and strong primary and intercalated ribs are features common to the present specimen and Schlüter's type. They differ in that the type has three primary ribs in a distance equal to the whorl height while there are only two in the French specimen. This is probably within the limits of intraspecific variation, by comparison with other nodose *Baculites*, but as there are so few specimens, this cannot be confirmed.

Occurrence. Coniacian of Westphalia and Touraine, precise horizon unknown. Other records are doubtful.

Superfamily SCAPHITACEAE Gill, 1871

[nom. transl. Wright and Wright 1951, p. 13, ex Scaphitidae Gill, p. 3]

Family SCAPHITIDAE Gill, 1871

Subfamily SCAPHITINAE Gill, 1871

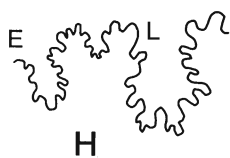
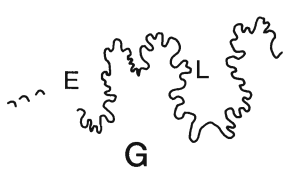
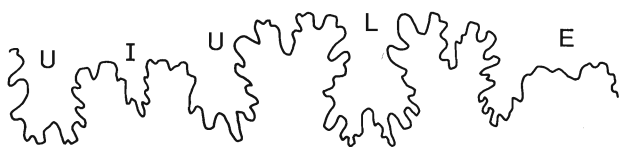
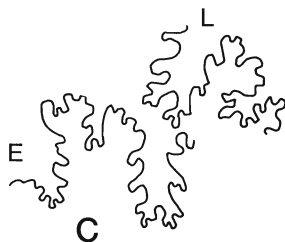
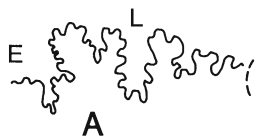
[nom. transl. Wright 1953, p. 473, ex Scaphitidae Gill, p. 3]

Genus SCAPHITES Parkinson, 1811

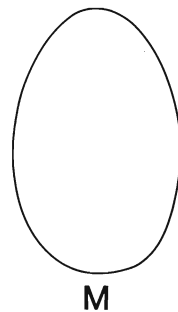
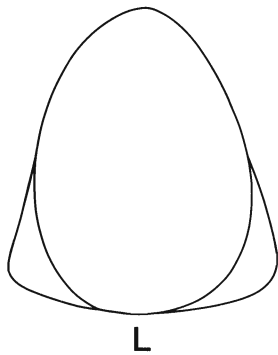
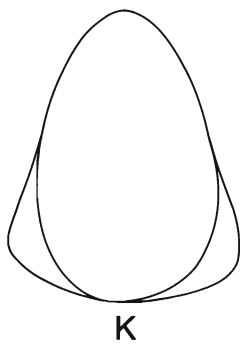
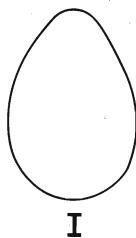
[= *Anascaphites* Hyatt, 1900, p. 572; *Jahnmites* Hyatt, 1900, p. 572; *Yezoites* Yabe, 1910, p. 167; *Holoscaphites* Nowak, 1911, p. 564]

Type species. *Scaphites equalis* J. Sowerby, 1813, p. 53, pl. 18, figs. 1–3. By subsequent designation by Meek 1876, p. 413.

TEXT-FIG. 42. External sutures or whorl sections. A, B, *Otoscaphtes arnaudi* (de Grossouvre, 1894), original of de Grossouvre 1894, pl. 32, fig. 8, SP unregistered, ex Rejaudry Collection. C, D, *Scaphites (Scaphites) meslei* de Grossouvre, 1894, SP unregistered, from Jonzac. E, *Phlyctiocioceras trinodosus* (Geinitz, 1850), FSR unregistered. F–M, *Baculites incurvatus* Dujardin, 1837; F, G, H, OUM KZ16640; I, paralectotype, MNHP R1025d; J, paralectotype, R1025e; K, paralectotype, R1025b; L, MNHP R1044b, ex d'Orbigny Collection 7208; M, paralectotype, R1025c.



1cm



Scaphites (Scaphites) meslei de Grossouvre, 1894

Plate 31, figs. 1-19; text-fig. 42C, D

- ?1842 *Scaphites compressus* d'Orbigny, p. 517, pl. 128, figs. 4, 5 (*non* Roemer, 1841).
 1850 *Scaphites compressus* d'Orbigny, p. 214 (*pars*)
 ?1850 *Scaphites Geinitzii* d'Orbigny, p. 214 (*pars*).
 ?1872 *Scaphites* sp. Schlüter, p. 76, pl. 23, figs. 23-25.
 1872 *Scaphites Geinitzii* d'Orb. var. *binodosus* Röm., Fritsch, p. 42, pl. 14, fig. 13.
 1894 *Scaphites meslei* de Grossouvre, p. 239, pl. 32, figs. 4, 7.
 1894 *Scaphites lamberti* de Grossouvre, p. 241, pl. 32, figs. 1, 5.
 1894 *Scaphites potieri* de Grossouvre, p. 242, pl. 22, fig. 3.
 1895 *Scaphites* cf. *geinitzi* var. *lamberti* de Grossouvre; Jahn, p. 131, pl. 8, figs. 1, 2, 6.
 ?1899 *Scaphites* cf. *meslei* de Grossouvre; Simionescu, p. 258.
 1907 *Scaphites lamberti* de Grossouvre; Boule, Lemoine and Thevénin, p. 31, pl. 6, figs. 7, 8.
 1911 *Scaphites lamberti* de Grossouvre; Nowak, p. 565.
 1916 *Scaphites lamberti* de Grossouvre; Nowak, p. 66.
 1916 *Scaphites arnaudi* de Grossouvre; Nowak, p. 66.
 1934 *Scaphites lamberti* Gross; Andert, p. 402, pl. 19, fig. 4.
 1936 *Scaphites meslei* de Gross.; Venzo, p. 110, pl. 10, fig. 6.
 1952 *Scaphites sagensis* Cobban, p. 30, pl. 10, figs. 7-10.
 ?1955a *Scaphites compressus* d'Orbigny; Sornay, figs. 1-3.
non 1956 *Scaphites* cf. *meslei* Gross., Gerth, p. 433, text-fig. 1.
 1958a *Scaphites* aff. *lamberti* de Grossouvre; Reyment, p. 33, pl. 6, fig. 1.
 1962 *S. (Scaphites) compressus* d'Orbigny; Wiedmann, p. 214, pl. 12, fig. 4.
 1965b *Scaphites meslei* de Gross var. *masiaposensis* Collignon, p. 16, pl. 420, fig. 1739.
 1965b *Scaphites arnaudiformis* Collignon, p. 17, pl. 420, fig. 1743.
 1979 *Scaphites lamberti* de Grossouvre; Wright, p. 304.
 1979 *Scaphites lamberti doylei* Wright, p. 304, pl. 3, fig. 13.
 1979 *Scaphites meslei* de Grossouvre; Collignon *et al.*, p. 388, pl. 1, fig. 2.
 1979 *Scaphites potieri* de Grossouvre; Collignon *et al.*, p. 389, pl. 1, fig. 3.
 1979 *Scaphites* cf. *arnaudi* de Grossouvre; Collignon *et al.*, p. 389.

Types. *S. meslei* is based on four syntypes, one in de Grossouvre's Collection from the 'Calcaires durs de la partie inférieur de la craie de Villedieu; carrières de la Ribochère, commune de Couture (Loir-et-Cher)', figured by him in 1894 as pl. 32, fig. 4 and one (loc. cit., pl. 32, fig. 7) from the same horizon at Lavardin (Loir-et-Cher), which is herein designated lectotype of the species. Two further paralectotypes are in the Rejaudry Collection and are from 'l'assise L¹ de M. Arnaud. Environs de Jonzac (Charente-Maritime)'. None of these specimens has been traced. *S. lamberti* de Grossouvre, 1894 (p. 241, pl. 32, figs. 1, 5) is based on four syntypes, two in the le Mesle Collection from the 'Calcaires durs de la partie inférieur de la Craie de Villedieu; carrières de la Ribochère, commune de Couture (Loir-et-Cher) were figured by de Grossouvre, and the original of his pl. 32, fig. 1, is herein designated lectotype. Two other specimens in the Rejaudry Collection are from 'assise L¹' in the environs of Jonzac (Charente-Maritime). None of these specimens has been traced. *S. potieri* is based on a single specimen only, which is the holotype of monotypy. It was from the 'calcaires durs de la base de la craie de Villedieu, carrières de la Ribochère, commune de Couture (Loir-et-Cher)' and in the collections of the Musée d'Angers. It too has not been traced. The holotype, by monotypy, of *S. compressus* d'Orbigny, 1842 (p. 517, pl. 128, figs. 4, 5) is no. 7139 in the d'Orbigny Collections housed in the MNHP. It is from the environs of Soulage (Aude). The holotype, by monotypy, of *S. lamberti doylei* Wright, 1979 (p. 304, pl. 3, fig. 13) is BM(NH) C79486, and is from the Upper Turonian Chalk Rock (*Subprionocyclus neptuni* Zone) of Hitch Wood, near Hitchin, Herts.

Material. One specimen from the Craie de Villedieu, Calcaires Durs de La Ribochère of La Ribochère (FSR, unregistered). SP Collections: six unregistered specimens from Assize K-L of la Boulinerie, Jonzac (Charente-Maritime); two unregistered specimens from Saujon (Charente-Maritime), probably from Assize K (Pesme Collection); three unregistered specimens from Assize L¹ at Pont de La Roche, St. Simon de Bordes (Charente-Maritime); one specimen labelled 'Coniacien moyen L¹ Pons' (Charente-Maritime); an unregistered cast and a doubtful nucleus labelled 'Dieulefit'. OUM KZ19426 is from the *tridorsatum* Zone 2 km east-north-east of St. Georges de Cubillac (Charente-Maritime). Numerous specimens from the Marnes de Ceyreste of the Beausset Basin (Var) include OUM KZ16438, 16446, 16448-16472. A series of specimens from the Priesener Schichten of

Priesen, Czechoslovakia, including the originals of Jahn's (1895) *Scaphites geinitzi* var. *binodosus* were also available for study (Naturhistorisches Museum Vienna collections).

Description. The French material is all in the form of internal moulds, mostly of body chambers, and shows marked size dimorphism. Coiling of spire involute; umbilicus small (around 16% of the diameter). Whorl section varies from compressed to depressed, with flattened flanks and broadly rounded venter. Ornament consists of numerous narrow prorsiradiate primary ribs, straight to feebly convex across inner flank, but flexed markedly backwards around mid-flank. Many branch low on flank or arise in groups at umbilical shoulder. At smallest diameters visible ribs bifurcate or trifurcate at beginning of ventrolateral shoulder and, accompanied by shorter intercalated ribs, loop across venter without any marked change in strength. At variable points on outer whorl of spire a bulla develops at point of branching, and strengthens progressively. It is least obvious in compressed individuals and most conspicuous in depressed ones.

On body chamber shaft prorsiradiate, distant ribs arise from weak to strong umbilical bullae and strengthen into weak to strong ventrolateral tubercles. Where these are conical or bullate rib is narrow; where they are clavate rib is broad. Ventrolateral tubercles give rise to two or three strong secondary ribs that loop across venter between tubercles, accompanied by short intercalated ribs.

Shaft generally swollen and inflated in dorsal region immediately prior to final hook, which is contracted. Umbilical bullae decline towards aperture, as do ventrolateral tubercles. The aperture is preceded by a strong deep constriction and slightly flared.

Microconchs are adult at lengths of as little as 30 mm. Macroconchs are generally much more massive broad shells and are only known as body chambers more than twice the size of those of microconchs.

Suture line poorly exposed in material studied; E/L is broad and asymmetrically bifid, L narrow and bifid, the elements only moderately subdivided.

Discussion. De Grossouvre (1894) erected three names for Coniacian *Scaphites* from the Craie de Villedieu and Aquitaine. Two of these, *S. meslei* de Grossouvre (1894, p. 239, pl. 32, figs. 4, 7) and *S. lamberti* de Grossouvre (1894, p. 241, pl. 32, figs. 1, 5) he considered to be very close to each other, the difference being that the ventrolateral tubercles of the shaft and hook of the body chamber were rounded in *lamberti* and clavate in *meslei*. Most of the specimens available show either rounded or clavate ventrolateral tubercles, but there is variation in the degree of elongation and roundness of tubercles and some individuals have bullate tubercles in this position. This is not a very convincing criterion for specific separation, especially given the range of intraspecific variation shown by *Scaphites* species, and the two are regarded as synonyms. De Grossouvre separated his third species, *S. potieri* (1894, p. 242, pl. 22, fig. 3) on the basis of its compressed whorls, effaced ribs on the flank of the shaft of the body chamber, and the presence of only two umbilical bullae. Again, this is regarded as intraspecific variation and the holotype is no more than a compressed microconch. Wiedmann (1962, p. 214) revived the name *S. compressus* d'Orbigny, 1842 for this species. D'Orbigny's specimen was refigured by Sornay (1955a) who considered it a valid species, having priority over *S. potieri* de Grossouvre, 1894. The holotype of d'Orbigny's *compressus* is a compressed microconch (Pl. 31, fig. 14). *S. compressus* d'Orbigny, 1842 is, however, a primary homonym of *S. compressus* Roemer, 1842 (p. 19, pl. 15, fig. 1) and is not available. It also seems highly probable that *S. geinitzii* d'Orbigny, 1850 (p. 214) in part referred to the present species, because d'Orbigny cited it from Villedieu. The catalogue of the d'Orbigny collection lists only specimens from Strehlen in Westphalia and Dresden in Silesia, and Wright (1979, p. 299) has designated one of the Strehlen specimens lectotype in accordance with current usage.

S. meslei is the Coniacian representative of a predominantly European *Scaphites* lineage that can be traced back to the Cenomanian *S. equalis* J. Sowerby, 1813 and has *S. geinitzii* d'Orbigny, 1850 as the most important middle to late Turonian species. The most obvious differentiating feature between *meslei* and these forms is the presence of ventrolateral tubercles on the spire and umbilical bullae on the body chamber. This alone suffices to separate it from all the forms of *geinitzii* described by Wright (1979, pp. 298–302). Some *geinitzii* develop strong flank ribs on the shaft, and this is also a feature of *S. kieslingwaldensis* Langenhan and Grundey, 1891 (Wright 1979, p. 303, pl. 3, figs. 10–12), but neither have ventrolateral tubercles on the spire—nor does *S. diana* Wright, 1979 (p. 304, pl. 3, figs. 14–16).

Wright (1979, p. 304, pl. 3, fig. 13) has introduced the subspecies *S. lamberti doylei* Wright, 1979,

for an apparent transitional form between *S. kieslingwaldensis* and *S. lamberti sensu stricto*. It lacks tubercles on the spire, but is already developing feeble umbilical bullae.

S. arnaudiformis Collignon, 1965*b* (p. 17, pl. 420, fig. 1473) from the Coniacian 'Kossmaticeras theobaldi et Barroisiceras onilahyense' Zone of Beantaly, Madagascar, is based on a septate spire only, and has ribbing and ventrolateral tubercles. Collignon separated it from *S. arnaudi* on the basis of its more rounded form, regular, convex ribs, and the very large diameter of the spire. It appears to be a juvenile macroconch of the present species. *S. meslei* var. *masiaposensis* Collignon, 1965*b* (p. 16, pl. 420, fig. 1739) from the *Peroniceras dravidicum* Zone of Masiaposa, Madagascar, has no standing under the *Rules*; it does not appear separable from *S. meslei* as herein interpreted. *S. manasoensis* Collignon, 1965*b* (p. 16, pl. 420, fig. 1740), a further Madagascan species, lacks tubercles on the spire.

Occurrence. French specimens that can be well dated come from the middle of the Coniacian, but the species ranges into the Upper Turonian elsewhere. The geographic range includes southern England, Villedieu (Loir-et-Cher), many localities in northern Aquitaine, especially Charente-Maritime, Dieulefit (Drôme), Bugarach in the Corbières (Aude) (Basse 1939), and the Beausset Basin (Var). The species also occurs in England, northern Spain, Germany, Czechoslovakia, Austria, Romania (?), Madagascar, Zululand (South Africa), and Wyoming, Colorado, and Texas, U.S.A. (Cobban pers. comm. 1983).

Subfamily OTOSCAPHITINAE Wright, 1953

Genus OTOSCAPHITES Wright, 1953

Type species. *Ammonites? bladenensis* Schlüter, 1871, p. 30, pl. 10, figs. 5, 6, by original designation by Wright (1953, p. 475).

Otoscaphtes arnaudi (de Grossouvre, 1894)

Plate 31, figs. 20–24; text-fig. 42A–B

- 1873 *Scaphites* sp. indet. cfr. *auritus* Schlüter; Redtenbacher, p. 130, pl. 30, fig. 11.
- 1894 *Scaphites Arnaudi* de Grossouvre, p. 242, pl. 32, fig. 8.
- 1908 *Scaphites arnaudi* de Grossouvre; Schmidt, p. 244.
- 1916 *Hoploscaphtes arnaudi* de Grossouvre; Nowak, p. 66.
- non 1960 *Scaphites arnaudi* Grossouvre; Wiedmann, p. 722.
- non 1962 *S. (Scaphites)* n. sp. (?) aff. *arnaudi* de Grossouvre; Wiedmann, p. 216, pl. 10, fig. 10; text-fig. 54.
- non 1964 *Scaphites* aff. *arnaudi* Grossouvre; Wiedmann, p. 116.

Types. De Grossouvre (1894, p. 243) based this species on two specimens. The original of his pl. 32, fig. 8 (SP, *ex* Rejaudry Collection) from 'assize L¹' of St. Simon-de-Jonzac (Charente-Maritime) is herein designated lectotype of the species. The paralectotype, from the same horizon at Miremont (Charente-Maritime), in the Arnaud Collection, has not been traced.

Material. Two fragments, MNHP R1233a–b, labelled 'Charente-Inférieur', SP, two specimens from Assize L¹, La Boulinerie, Jonzac (Charente-Maritime).

Description. The lectotype is an adult microconch with body chamber and lappeted aperture preserved. The spire is 22.5 mm in diameter, involute, with small, shallow umbilicus (22% of diameter); compressed whorl section, with whorl breadth to height ratio of 0.57, inner flanks rounded, outer flanks flattened and venter rounded. Seven to eight distant primary ribs per half whorl arise at umbilical seam and are feebly concave and prorsiradiate on inner flank, but flex markedly backwards and are strongly convex at mid-flank, where they branch into bunches of two or three finer secondaries. These are accompanied by shorter intercalated ribs that extend to inner flank as mere striae but are as strong as secondaries on outer flank, where all ribs are markedly concave, projecting forwards, and strengthening over ventrolateral shoulder and crossing venter with a shallow convexity.

This style of ribbing extends on to initial part of body chamber, with primary ribs becoming increasingly prorsiradiate. Venter of the holotype shows two zones, one at beginning of compressed body chamber, other at beginning of final hook, where ribs are very fine and crowded. On final part of hook, however, primary ribs project strongly forwards with marked lateral geniculation, biplicate, and coarsen over outer flank and venter.

Aperture is preceded by very strong rib and broad constriction; aperture itself constricted and flared, with large lateral lappet (incomplete due to damage). External suture simple, with broad, asymmetrically bifid E/L and narrow L.

Discussion. *Otoscaphtes arnaudi* is a very distinctive species, the highly flexuous ribs that are rather similar on spire and hook, and the lack of tubercles distinguishing it from most other forms, as does the large size. *O. bladenensis* (Schlüter, 1871) (p. 30, pl. 10, figs. 5, 6; see Wright 1979, p. 305, pl. 3, figs. 19, 20) is small and evolute with a much less compressed whorl, less flexuous ribs and weak ornament on the body chamber. It is an Upper Turonian form. *O. fritschi* (de Grossouvre, 1894) (p. 243, = *S. auritus* Fritsch, non Schlüter, 1872, p. 44, pl. 13, fig. 14 being the lectotype by the subsequent designation of Wright 1979, p. 306) is much smaller and finely ribbed, the ribs not showing the striking flexuosity of *O. arnaudi*. *O. reidi* Wright, 1979 (p. 307, pl. 3, figs. 17, 18; pl. 7, fig. 8) has a less compressed whorl section and long, narrow body chamber and is ornamented by weak irregularly branching ribs that are very feeble on the body chamber. Of Japanese species, *O. puerculus* (Jimbo, 1894) (p. 37, pl. 5, fig. 4; see Tanabe 1977, p. 401, pl. 62, figs. 1–9; pl. 64, figs. 1–5) is more evolute, less compressed, with a narrow body chamber, and quite different ornament.

S. (Scaphites) n. sp. (?) aff. arnaudi de Grossouvre of Wiedmann (1962, p. 216, pl. 10, fig. 10; text-fig. 54) is based on a small, involute phragmocone only and does not show the ornament typical of de Grossouvre's species. *S. arnaudiformis* Collignon, 1965*b* (p. 17, pl. 420, fig. 1743) appears to be a *Scaphites sensu stricto*. It is based on a phragmocone only, from the Coniacian of Madagascar.

Occurrence. The species is reliably known only from the Coniacian of Charente-Maritime in France. The stratigraphic data given by de Grossouvre indicate it to be from some way above the base of the stage. The Austrian material (Redtenbacher 1873, pl. 30, fig. 11) cannot be precisely dated.

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