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PALAEONTOLOGY

SOME COMPLEX UPPER CRETACEOUS ROTALIID FORAMINIFERA FROM THE NORTHERN BORDER OF THE AQUITAINE BASIN (SW FRANCE). I

BY

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ABSTRACT

The morphology of some complex and ill-known rotaliids of Santonian and Campanian age is described and figured and the phylogenetic relations between these forms are discussed. *Pseudosiderolites vidali* (Douvillé), the most common species, is discussed in connection with its relationship with *Arnaudiella*. The rare occurrence of *Pseudosiderolites* specimens with spines at the top of the Campanian type section is reported. The Campanian species *Arnaudiella grossouvrei* Douvillé derives from *Pseudosiderolites*, from which it differs only by the presence of *Lepidorbitoides*-like lateral chambers between the consecutive whorls of the involute primary spiral chambers. It is not a phylogenetically transitional form between *Pseudosiderolites* and *Orbitoides* or *Lepidorbitoides*. The stratigraphic distribution of *Arnaudiella* necessitates a critical discussion of correlations in the area. Examination of topotype material of *Pokornyellina* ("*Siderina*") *douvillei* (Abrard) from Bernon showed that this form does not differ from *Arnaudiella grossouvrei* and thus is a junior synonym. In strata of Santonian age near Jonzac specimens were found of a trochospirally arranged foraminifer with well developed pillars at the ventral side and orbitoidal lateral chambers at the dorsal side. These are provisionally ascribed to *Sirtina orbitoidiformis* Brönnimann and Wirtz, up to now known only from the Maastrichtian of Iran and Libya. A possible relation with the orbitoidal genus *Clypeorbis* is postulated.

INTRODUCTION

At the Northern border of the Aquitaine basin a number of large and enigmatic rotaliid species occur, which have orbitoidal characters (lateral chambers, ornamentation). These are *Arnaudiella grossouvrei* Douvillé, *Pokornyellina douvillei* (Abrard) (after the concise original description of these forms no additional studies have been published) and a species which is new for the area and which will be ascribed to *Sirtina orbitoidiformis* Brönnimann and Wirtz. The aim of this paper is to describe and figure these forms and to investigate their taxonomic-phylogenetic position, especially the supposed relationships with the orbitoidal foraminifera. To facilitate comparisons this will be preceded by a discussion of the closely related form *Pseudosiderolites vidali* (Douvillé).

It should be noted that in this paper the Dordonian or Maastrichtian of most earlier workers in this area is included in the Campanian (for a discussion of this problem see VAN GORSEL, 1973a).

Pseudosiderolites vidali (Douvillé) 1906

1906 *Siderolites vidali* n.sp. – DOUVILLÉ, p. 598–599, Pl. XVIII–9.
1910 *Siderolites vidali* race *minor* – DOUVILLÉ, p. 54.
1932 *Siderolites heracleae* n.sp. – ARNI, p. 204–219, figs. 2–4, T. VIII–X.
1933 *Siderolites heracleae* var. *pratigoviae* – ARNI, p. 12–14, figs. 5–7, T. I, II–7–8.
1934 *Siderolites vidali* Douvillé – PFENDER, p. 225–235, Pl. XI, 3–5, Pl. XII.
1934 *Siderolites vidali* Douvillé – ANDRUSOV, p. 82–84.
1951 *Siderolites vidali* Douvillé – CUVILLIER and SACAL, Pl. XLV–2, Pl. XLVI.
1953 *Siderolites vidali* Douvillé – PAPP and KÜPPER, p. 351–352, T. 1–6, T. 2.
1955 *Pseudosiderolites vidali* (Douvillé) – SMOUT, p. 206.
1959 *Siderolites vidali* Douvillé – HOFKER, p. 298–301, figs. 139–157.
1962 *Pseudosiderolites vidali* (Douvillé) – KÖHLER, p. 117–119, T. XIV, figs. 1–4.
1963 *Siderolites vidali* Douvillé – HOFKER, p. 109–114, fig. 7.
1966 *Sulcoperculina* aff. *cubensis* (Palmer) – HOTTINGER, p. 296–298, figs. 9a, 10b–e, 11.
1973 *Siderolites vidali* Douvillé – VAN GORSEL, 1973c, Pl. 1–1, Pl. 3–1.

Numerous specimens of this species can usually be found in any sample from the Campanian in the area. On the exterior large pustules can be seen in the central part of the lenticular test; towards the periphery smaller pustules are arranged along the slightly curved sutures of the spiral chambers (Plate I, fig. 1). The involute chambers are planispirally arranged, occasionally slightly trochoid. In the specimens studied the diameter of the protoconch varies between 35 and 100 microns, average about 55 microns (Table I). The second chamber is usually slightly larger. In the first whorl usually 7 chambers can be counted, 11 or 12 in the second and 15 to 18 in the third whorl.

The microspheric generation can only be recognized by its smaller initial chambers. The average diameter of the protoconch of 3 specimens is 18 microns. The diameter of the test is almost equal to that of the megalospheric generation, so the microspheric generation has more whorls ($\pm$ 4) than the megalospheric generation ($\pm$ 3).

After the formation of a chamber its wall is subsequently thickened, especially at the marginal side. This thickened margin or flange is pierced by numerous radial canals (Pl. I, fig. 4). At the lateral sides of the primary chambers a similar thickening is found, though to a much smaller degree and the canals are less distinct.

TABLE I

Average values of measurements and counts on horizontally sectioned megalospheric specimens of *Pseudosiderolites vidali*. Samples Gr 805 and 116 are from the top of the Aubeterre section, Gr 22B and 20 from the base of this section, Gr 71 is from 2 km S of Chalais (oldest French sample) and Gr 842 is from Silberegg, Austria.

Diameters in microns.

Sample number	Number of specimens	Diameter protoconch	Diameter deutero-conch	Nr. of whorls	Number of chambers in whorl: 1	2	3	4
Gr 805	14	65.0	78.2	2.7	7.0	12.1	15.0	
Gr 116	13	66.6	80.0	2.9	7.2	12.6	18.0	
Gr 22B	16	46.1	52.5	3.1	7.0	10.6	16.2	
Gr 20	7	49.7	56.8	3.0	6.7	10.7	16.3	
Gr 71	11	44.9	49.6	3.0	7.3	11.5	17.1	
Total $\bar{X}$	(61)	55.0	64.4	3.0	7.0	11.5	16.7	
Gr 842	10	99.4	113.2	2.8	8.6	15.0	18.0	
Measurements on microspheric specimens:								
Gr 20–9		21	24	$3\frac{1}{2}$	6	9	13	—
Gr 22B–8		14	16	$4\frac{1}{4}$	6	7	9	12
Gr 22B–16		19	19	$4\frac{1}{4}$	7	8	11	18

Apertures have been observed in only one specimen from the top of the Aubeterre section (Pl. I, fig. 5). This specimen shows a basal row of about seven apertures. HOFKER (1963) also describes such a row of basal apertures and states that in the primitive Santonian representatives of *P. vidali* only one basal aperture is found.

STRATIGRAPHIC DISTRIBUTION, EVOLUTION

The earliest representatives of *Pseudosiderolites* in the area have been reported from strata of Santonian age (HOFKER 1959, BARRIER-CHRÉTIEN 1960, SÉRONIE-VIVIEN 1972). These Santonian specimens, as well as specimens from the lower Campanian, are usually very small (less than 1 mm), slightly asymmetric lenticular and the margin is more or less rounded. Such specimens were designated as *Siderolites* sp. by BARRIER-CHRÉTIEN and SÉRONIE-VIVIEN (l.c.), while ANDREIEFF and MARIONNAUD (1973) informally named them *Pseudosiderolites* "*praevidali*". The specimens from the Lower Campanian or Upper Santonian of Northern Spain, described by HOTTINGER (1966) as *Sulcoperculina* aff. *cubensis* are also primitive representatives of *Pseudosiderolites* (HOTTINGER and ROSELL, 1973).

The primitive, small specimens of *Pseudosiderolites* in the Santonian and lower Campanian in Aquitaine show many resemblances with the forms described as *Daviesina minuscula* (Hofker) 1957 and *Daviesina voigti* Hofker 1958 from the boreal Upper Cretaceous (Upper Santonian-Lower Campanian). If the early *Pseudo-*

siderolites specimens, in which the radial canal structure is weakly developed or even absent, turn out to be identical with these forms, they could be designated by the specific name *P. minuscula* (Hofker).

In the evolution of *Pseudosiderolites* the test becomes larger and the radial canal structure becomes more prominent, which gives rise to the formation of a broad flange around the test. The flange is especially well developed in the outer whorls of larger specimens and often completely subdivides the chambers of the subsequent whorls. At the base of the Aubeterre section (upper Campanian type section) most specimens already possess a distinct flange.

The diameter of the holotype of *Pseudosiderolites vidali* (type locality near Pobla de Segur, N. Spain) is almost 6 mm and at many other localities in Europe specimens with about the same diameter are found (ARNI 1932, 1933, PFENDER 1934, PAPP and KÜPPER 1953, KÖHLER 1962). Curiously at the Northern border of the Aquitaine basin the test diameter seldomly exceeds 2 mm. For this reason DOUVILLÉ (1910) described the specimens from the Charente as *Siderolites vidali* race *minor*. The small specimens from the Aubeterre section are considered to be younger than, for instance, the larger *Pseudosiderolites* specimens from Silberegg, Austria (type locality of *Helicorbitoides longispiralis* (Papp and Küpper); age relationship based on difference in evolutionary stage of the *Helicorbitoides-Lepidorbitoides* lineage). So increase in size of test is either not a uni-directional evolutionary trend or it is an evolutionary trend with environmental influences or else different lineages within *Pseudosiderolites* may be accepted.

In Table I a number of measurements on horizontal sections of *P. vidali* are presented. The samples are arranged in stratigraphic order, Gr 71 being the oldest sample. The two younger samples have larger protoconch and deuteroconch diameters than the three older ones, so there may have been an increase in size of the first chambers during the Campanian. Such an increase is a frequently occurring evolutionary trend in foraminifera, but here the same problem arises as we have with the size of the tests: in the older *Pseudosiderolites* specimens from Silberegg the first

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PLATE I

Fig. 1. Gr 801, 45×. External view of *Pseudosiderolites vidali* from Le Caillaud.

Figs. 2 and 3. Gr 805, 35×. *Pseudosiderolites vidali* from the top of the Aubeterre section, showing formation of spines.

Fig. 4. Gr 22A, 90×. Detail of horizontal section of *P. vidali*, showing radial canals communicating with pores in the wall of the primary chambers.

Fig. 5. Gr 805, top of Aubeterre section, 130×. Detail of partly broken specimen of *P. vidali*, showing a row of basal apertures (arrows). Note imperforate septum and perforate lateral side of the primary chamber wall.

Fig. 6. Gr 376–4, 20×. *Arnaudiella grossouvrei* from Le Caillaud. Note central thickening, porous margin (outlets of radial canals) and narrow involute primary spiral chambers (top left).

PLATE I

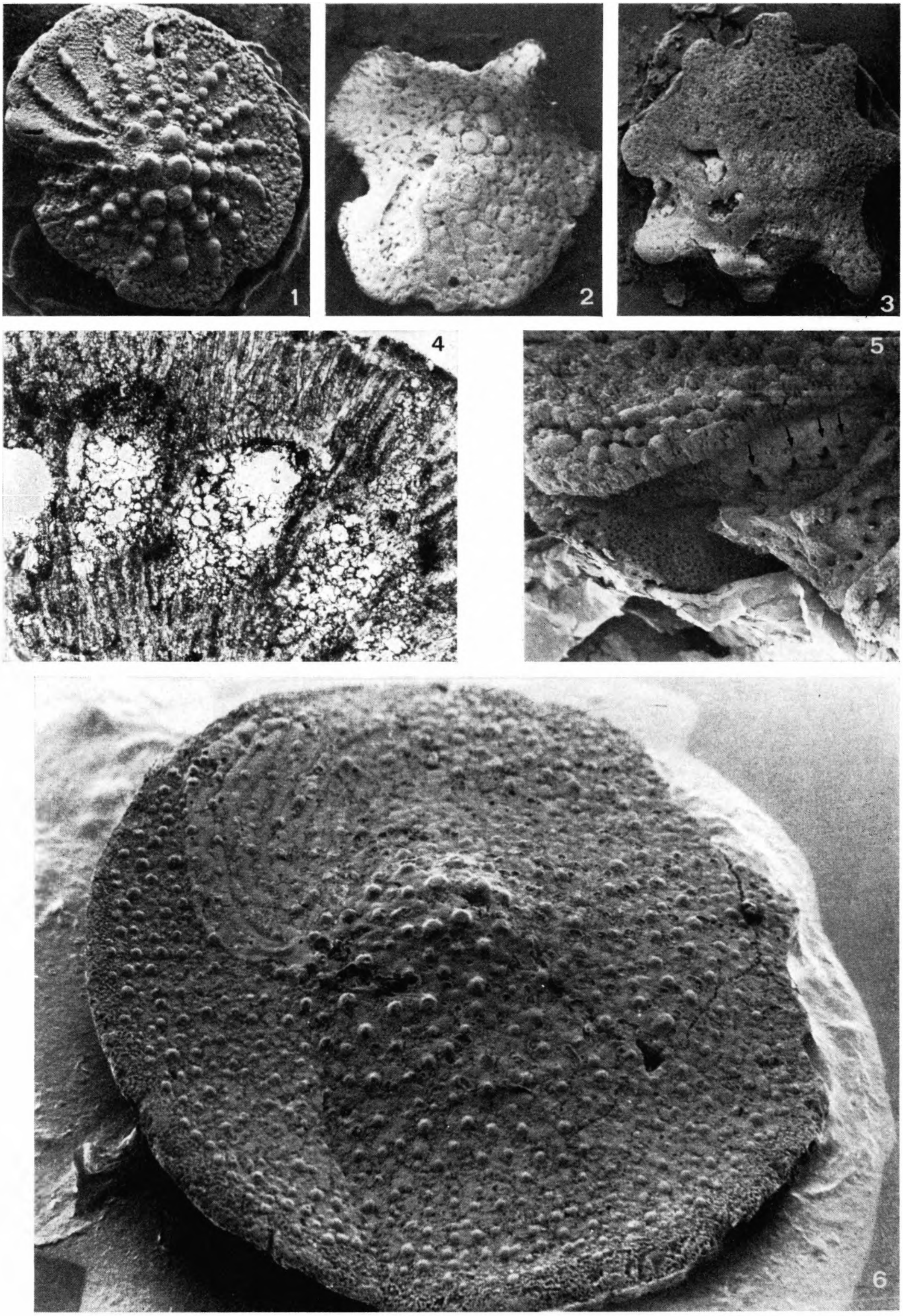
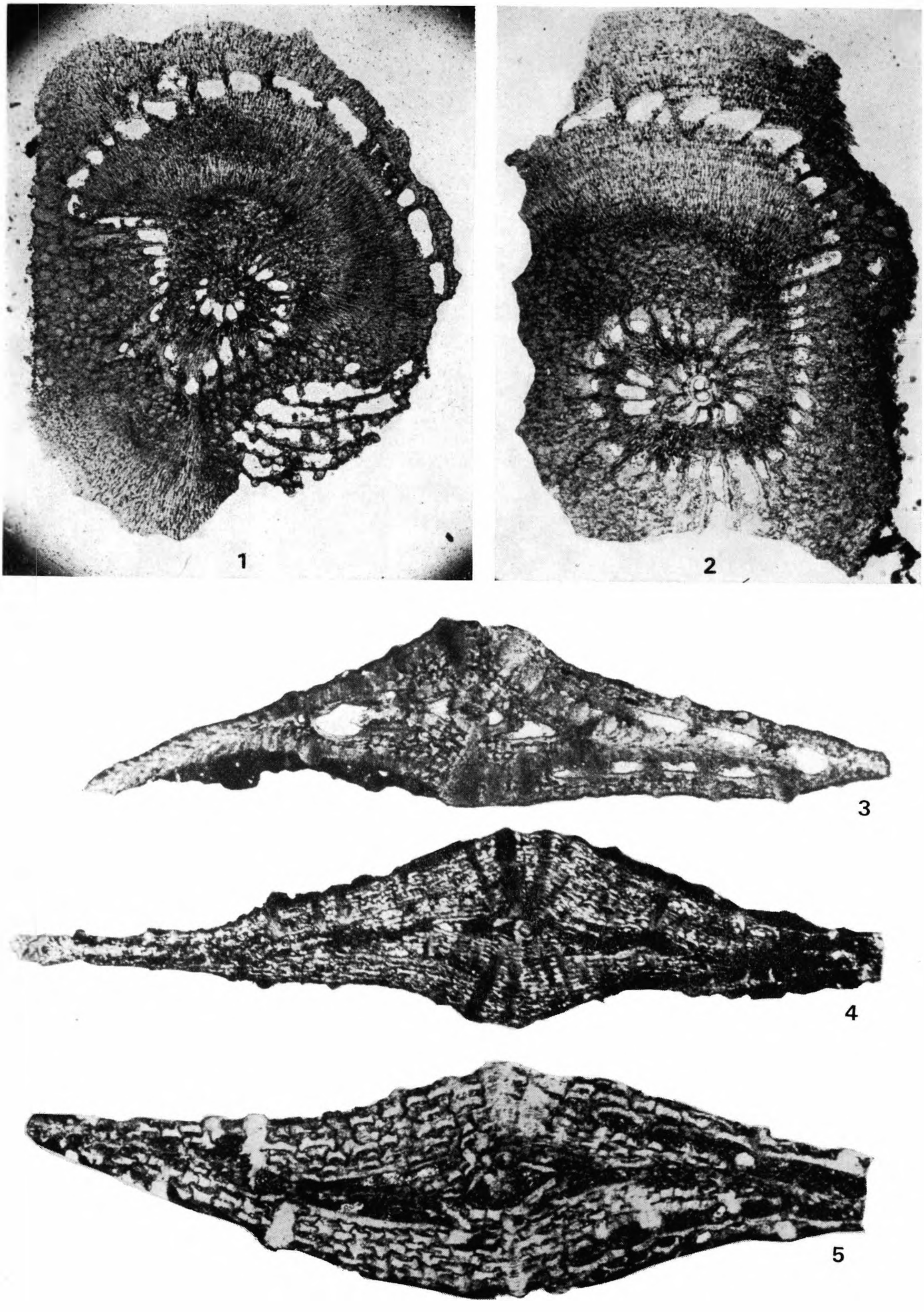


PLATE II



chambers are already much larger than in the youngest Aubeterre sample (average values of 10 horizontal sections from Silberegg: diameter protoconch 99, deuteroconch 113 microns; 8.5 chambers in first whorl, 15 in the second). Fluctuations in size of test and initial chambers are often ascribed to environmental circumstances. Taking into account the geographic distribution of the large *Pseudosiderolites* specimens (Pyrenees, Alps) and the presence of rare large specimens in the Charente, this seems to be the most plausible explanation of the size variations.

In sample Gr 805 (top of Aubeterre section, collected along path from the gate of the castle uphill, uppermost type Campanian or type Dordonian) among several hundreds of *Pseudosiderolites vidali* specimens with a continuous flange a few interesting forms were found: about 8 specimens show one or more indentations in the flange, 3 specimens clearly show one or two spines and in one specimen 8 small spines can be seen (Pl. I, figs. 2 and 3). In these forms the formation of the radial canal structure is concentrated into a limited number of radial directions and a further development will lead to the spinose species *Siderolites calcitrapoides* Lamarck. The derivation of the latter species from *P. vidali* has been postulated earlier by several authors, but transitional populations have never been described. Because of the scarcity of the spinose forms it would be an exaggeration to consider the population from the top of the Campanian type section as transitional between *P. vidali* and *S. calcitrapoides*, but the assumed development towards spinose forms is supported by this find. Real transitional populations can be expected in a level not far above the type Campanian. In the type Maastrichtian only *Siderolites calcitrapoides* is found, so this shift must have taken place somewhere in the time gap between the Campanian and Maastrichtian stratotypes. HOTTINGER and ROSELL (1973) apply the transition *P. vidali* – *S. calcitrapoides* as a criterium to determine the Campanian-Maastrichtian boundary.

PLATE II

Fig. 1. Gr 376–10, Le Caillaud, 14×. Horizontal section of *Arnaudiella grossouvrei*, showing spiral arrangement and well developed flange with radial canals. At the upper part of the picture the flange and the chambers of the outer whorl are sectioned equatorially, on the left and lower right side the lateral sides of the involute primary spiral chambers are sectioned. The knobs on the lower right side are sections through the pillars.

Fig. 2. Gr 376–14, Le Caillaud, 19×. Horizontal section of *Arnaudiella*.

Fig. 3. Gr 84A, S of Chalais, 35×. Vertical section of (primitive) *Arnaudiella grossouvrei*. Note well developed flange with diverging radial canals and lateral chambers occurring only in the umbilical region. At lower right the involute wings of five successive primary spiral chambers are cut.

Fig. 4. Gr 376–1, Le Caillaud, 21×. Vertical section of *Arnaudiella*, showing well developed system of lateral chambers between the V-shaped intersections of the involute whorls.

Fig. 5. Gr 800, Bernon, 40×. Vertical section of topotype of *Pokornyellina douvillei* (Abrard) (=junior synonym of *Arnaudiella grossouvrei*).

For SMOUT (1955) the presence or absence of spines is such a fundamental character that the classifies the species *vidali* and *calcitrapoides* (type species of *Siderolites*) in different families. For this reason the species *vidali* could not be maintained within the genus *Siderolites*, so he created the new genus *Pseudosiderolites* for it. If one accepts the derivation of *S. calcitrapoides* from *S. vidali* one has to reject the classification of Smout in this respect. As the species *vidali* was originally ascribed to *Siderolites* the author would prefer to retain it in this genus. However, supra-specific classification being a matter of subjectivity, in this paper the customary assignment of the species *vidali* to *Pseudosiderolites* is followed.

SÉRONIE-VIVIEN (1972) and ANDREIEFF and MARIONNAUD (1973) mention the occurrence of a different species, *Siderolites denticulatus* Douvillé, in the cliff of Le Caillaud (SE of Talmont, along the Gironde). This form has originally been described from Maastricht and is mainly found in the uppermost part of the Maastrichtian type section. It has a large number of spines, which are interconnected laterally, so that externally the spinose structure is hardly visible. Probably this is a variant of *Siderolites calcitrapoides* (HOFKER 1949, VISSER 1951, VOIGT 1951). In any case it can not be a phylogenetically transitional form between *P. vidali* and *S. calcitrapoides*. The occurrence of *Siderolites denticulatus* in the Campanian of Le Caillaud is therefore highly improbable. Presumably we are dealing here with specimens of *Arnaudiella grossouvrei*, which also occurs in our samples from Le Caillaud (see below), but which is not mentioned by SÉRONIE-VIVIEN and ANDREIEFF and MARIONNAUD (l.c.).

Arnaudiella grossouvrei Douvillé 1906

1926 *Siderina douvillei* n.gen., n.sp. – ABRARD, p. 31–32, fig. 1.
(Not: *Siderina* Dana 1848 (Coelenterata),
Not: *Siderina douvillei* Abrard in HOFKER 1959, p. 301, figs. 155–157)
1951 *Arnaudiella* sp. – CUVILLIER and SACAL, figs. 47–2.
1961 *Pokornyella douvillei* (Abrard) – LOEBLICH and TAPPAN, p. 220.
(Not: *Pokornyella* Oertli 1956 (Ostracoda))
1964 *Pokornyellina douvillei* (Abrard) – LOEBLICH and TAPPAN, p. 618.
1971 *Arnaudiella grossouvrei* Douvillé – GOHARIAN, Pl. 2, figs. 1–2.

This genus was originally described from the Campanian (zone P3 of ARNAUD, 1877, 1878) in the surroundings of Barbezieux and Chalais (department of Charente). Additional studies on this form never appeared and in all text-books the figures of Douvillé have been reproduced.

Arnaudiella can best be characterized as a large *Pseudosiderolites vidali* with a well developed system of *Lepidorbitoides-like* lateral chambers between the consecutive whorls of the involute primary chamber spiral. Externally and in horizontal sections *Arnaudiella* is hardly distinguishable from large specimens of *Pseudosiderolites*, so vertical sections are required to determine whether one is dealing with *Arnaudiella*.

LOCALITIES

Arnaudiella was found at several localities in the area (see fig. 1):
Charente-Maritime: Gr 376 – SE side of the cliff of Le Caillaud, about

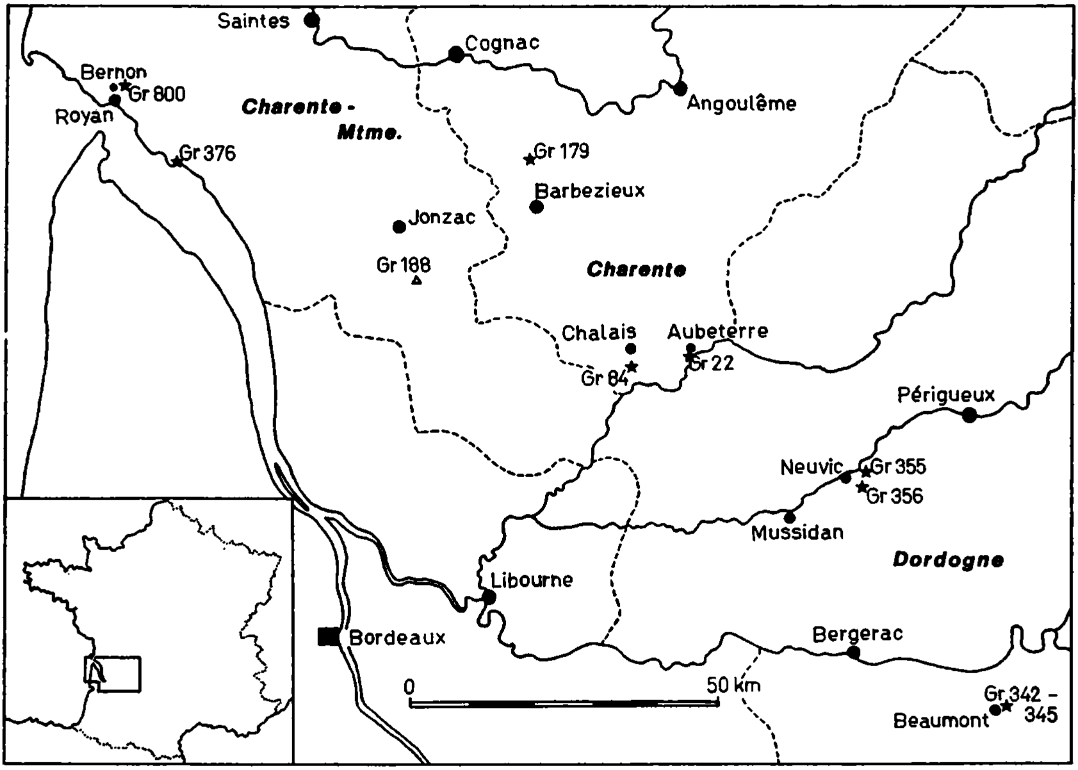


Fig. 1. Map showing localities with *Arnaudiella* (asterisks) and *Sirtina* (Gr 188).

2 m above the base of the cliff, SE of Talmont, along the Gironde; Gr 800 – abandoned quarry about 1 km E of Bernon (N of Royan), at the N side of road V2, which leads from the main road Royan-Roquefort towards the hamlet of Pousseau.

Charente: Gr 20 – base of Aubeterre section, along road D17, S of the gasoline station; Gr 84 – 3 km S of Chalais, along road D464, 250 m W of crossing with road D136 (Chalais-Medillac); Gr 179 – 8 km N of Barbezieux, along road from Barbezieux to Segonzac, at the drive to "Château l'Etoile".

Dordogne: Gr 355 – 2 km SE of St. Léon sur Isle, along a small road leading upward from road N89 to the hamlet of Guillassou; Gr 356 – 2 km SE of Neuvic sur Isle, along road D44 between Linseuil and Théorat, at kilometer stone 19.1; Gr 342–345 – 1 km E of Beaumont, along road D25 (Beaumont-St. Avit Sénieur), between kilometer stones 40.6 and 40.9 (for a description of this section see Séronie-Vivien 1972, coupe 113. *Arnaudiella* was found at different levels within a zone of about ten meters in thickness, which probably agrees with meters 15 to 25 in the column of Séronie-Vivien).

Description

Exterior (Plate I, fig. 6, Plate III, fig. 2) – Large, flat lenticular test with central thickening, which is usually more prominent on one side, and a broad, flattened, occasionally slightly undulating border. The diameter of the test may reach 6 mm, the thickness 1.4 mm, diameter/thickness ratio is generally between 4 and 5.

The surface of the test is occupied by more or less randomly arranged pustules, diminishing in size towards the periphery. In well preserved specimens the curved, involute sutures of the primary spiral chambers can be seen in one quadrant of the test. The sutures of these chambers are often expressed as such, but may also be indicated only by radially directed, curved rows of small pustules. At the margin of the test numerous coarse pores can be observed, which are the outlets of the radial canals.

Interior – The primary chambers are spirally arranged in 2.5 to 4 whorls (Plate II, figs. 1, 2). The diameter of the spherical protoconch varies between 60 and 110 microns, average about 85 microns, the second chamber is usually slightly larger (see Table II). The first whorl usually consists of 8 chambers, which are evolute and often slightly trochospirally arranged. The subsequent chambers become involute and are arranged planispirally. The number of chambers in a whorl increases rapidly in the following whorls: in the second the average number of chambers is 16 (varying between 12 and 22) and in the third about 30 (varying between 22 and 45). The number of chambers in the whorls seems to depend on the size of the first chambers: when this is large there are more chambers in the succeeding whorls.

The chambers of the last whorl are very long and narrow. The spatial shape of these chambers can best be compared with the character V the point of which is situated at the margin of the test and bending backward. Towards the centre of the test these chambers often extend over the previously built part of the test even beyond the imaginary axis of coiling, thus becoming "over-involute".

The septa of the primary chambers are secondarily doubled in the rotaliid manner by the formation of a septal flap. Wide interseptal spaces can often be seen.

Apertures could not be observed in the last chambers of our specimens, possibly because they were too small to be preserved. In horizontal sections often a basal intercameral foramen is observed in the chambers of the first whorl. In the supposed ancestor of *Arnaudiella, Pseudosiderolites vidali*, a row of basal apertures could be observed in the chambers of the outer whorls. It is assumed that such apertures will be present in *Arnaudiella* as well. The curious shape of the chambers of the outer whorls could then be explained by an increase in the number of these apertures.

The marginal side of the primary spiral is extremely thickened with calcareous material, which forms a broad flange around the test and

TABLE II

Measurements and counts on horizontally sectioned specimens of *Arnaudiella grossouvrei* Douvillé. The samples are arranged in supposed stratigraphic succession, Gr 84A being the oldest. Diameters in microns.

Number of specimen	Diameter protoconch	Diameter deuteroconch	Nr. of whorls	Number of chambers in whorl: 1	2	3
Gr 355–3	80	108	$3\frac{1}{2}$	9	16	—
4	109	—	3	9	18	45
5	109	—	$3\frac{1}{4}$	8	16	34
7	93	128	$2\frac{3}{4}$	8	18	—
8	99	124	$3\frac{1}{4}$	7	19	—
11	143	164	$2\frac{1}{2}$	9	—	—
12	88	127	$3\frac{1}{2}$	8	16	—
13	71	101	$3\frac{1}{2}$	7	17	27
14	68	96	$3\frac{3}{4}$	7	17	29
15	102	116	$2\frac{1}{2}$	8	21	—
16	86	93	$3\frac{1}{2}$	8	16	33
17	100	132	$3\frac{1}{4}$	8	22	—
18	83	115	$2\frac{3}{4}$	8	17	—
19	91	96	3	8	20	28
20	70	96	3	8	15	30
21	71	105	$3\frac{1}{2}$	7	17	31
22	110	129	$3\frac{1}{4}$	8	21	—
$\bar{X}$	92.6	115.4	3.2	7.9	17.9	32.1
Gr 376–1	63	74	$3\frac{3}{4}$	8	13	—
3	86	105	3	8	17	—
4	82	—	3	8	—	—
9	75	94	$3\frac{1}{2}$	8	13	—
10	95	101	$3\frac{1}{4}$	8	15	33
12	67	—	$3\frac{1}{2}$	8	14	27
13	67	—	$3\frac{3}{4}$	8	14	—
14	89	119	$2\frac{3}{4}$	8	17	—
15	94	—	$3\frac{1}{4}$	8	15	—
18	65	71	$3\frac{3}{4}$	7	12	24
19	85	113	$3\frac{1}{4}$	8	16	33
21	89	118	3	8	16	—
$\bar{X}$	79.6	99.3	3.3	7.9	14.7	29.3
Gr 342–1	96	113	3	8	16	26
3	93	105	$2\frac{3}{4}$	8	19	—
4	91	116	3	7	—	—
17	88	105	$2\frac{1}{4}$	8	18	—
Gr 343–1	85	115	$3\frac{3}{4}$	8	14	29
Gr 344–1	81	74	$2\frac{3}{4}$	7	16	—
Gr 345–10	87	116	$3\frac{1}{4}$	8	16	30
$\bar{X}$	88.7	100.8	3.0	7.7	16.5	28.3

TABLE II (*continued*)

Number of specimen	Diameter protoconch	Diameter deuteroconch	Nr. of whorls	Number of chambers in whorl: 1	2	3
Gr 179–1	100	121	$2\frac{3}{4}$	8	15	—
22	86	90	$3\frac{1}{4}$	8	17	33
23	93	132	$3\frac{1}{4}$	8	15	30
24	77	81	$3\frac{1}{2}$	7	13	22
25	74	92	$3\frac{1}{2}$	8	16	33
26	67	—	$2\frac{3}{4}$	7	17	—
27	69	86	$3\frac{1}{4}$	7	15	—
28	79	111	$3\frac{1}{2}$	7	13	28
29	94	118	$2\frac{3}{4}$	8	15	—
$\bar{X}$	82.1	103.9	3.2	7.6	15.1	29.2
Gr 84A–1	80	101	$2\frac{3}{4}$	8	15	—
2	62	77	$3\frac{1}{2}$	7	14	28
3	86	90	$3\frac{1}{4}$	8	16	32
4	71	80	$3\frac{1}{2}$	7	15	26
5	61	76	$3\frac{1}{2}$	7	12	27
6	79	91	3	—	17	—
7	63	85	3	8	14	30
$\bar{X}$	71.6	85.6	3.1	7.5	14.7	28.6
Total $\bar{X}$	84.5	104.4	3.2	7.8	16.0	29.9

almost or completely subdivides the chambers of the subsequent whorl. This flange is often undulating and is pierced by numerous radial canals with a diameter of about 10 microns. The flange is thickest in the outer whorls. A similar structure with radial canals, although usually less well developed, is found in *Pseudosiderolites* and in *Pellatispira*. In vertical sections the radial canals can be seen to diverge in lateral direction (Plate II, fig. 3). At the external side of the flange the canals are open and debouch into the exterior or into the lumen of the chambers of the next whorl. At the internal side some canals are obviously linked with the interseptal spaces. Most canals, however, seem to be connected with the lumen of the previous spiral chambers by small pores in the walls of these chambers, in the way as figured by HOFKER (1959, fig. 144) for *Pseudosiderolites vidali* (see also Plate I, fig. 4).

At the lateral sides of the primary spiral chambers secondary chambers are formed, which do not differ from the lateral chambers of *Lepidorbitoides*. The lateral chambers are in turn enclosed by the subsequent whorl of the involute primary spiral, so a real orbitoidal pattern (equatorial layer flanked by lateral layers) is not reached in *Arnaudiella*. In specimens from samples Gr 84 (S of Chalais) and Gr 179 (N of Barbezieux) only a small number of lateral chambers is found and these only in the umbilical region

(Plate III, fig. 3). In most other specimens many more of these chambers are formed, which, remarkably, also occur at the lateral sides of the flange with its radial canals (Plate II, figs. 4, 5).

The system of lateral chambers is crossed by textural-inflational pillars, which appear as rounded pustules at the surface of the test. The largest pillars are found in the umbilical region, where they usually continue from the initial chambers up to the surface. Towards the margin we see smaller pillars, which originate along the sutures of the primary spiral chambers and which usually end when they are enclosed by the subsequent whorl of the involute spiral. In horizontal sections, in which the primary chambers of the outer whorls are cut slightly off-centre, isolated calcareous knobs can often be seen, which are sections through these pillars (Plate II, fig. 1).

It should be noted that it has not been possible to distinguish *Arnaudiella* from *Pseudosiderolites* when only a horizontal section is available. Comparison of tables I and II suggests that the initial chambers of *Arnaudiella* are significantly larger and that it has more chambers in its whorls than *Pseudosiderolites*. However, the data of *Pseudosiderolites* from Austria (Silberegg) and an extremely large specimen from the surroundings of Chalais are more like those of *Arnaudiella*. The small values of *Pseudosiderolites* in this area may therefore be mainly determined by environmental circumstances. Further regional investigations are required.

SOME COMPLEX UPPER CRETACEOUS ROTALIID FORAMINIFERA FROM THE NORTHERN BORDER OF THE AQUITAINE BASIN (SW FRANCE). II

BY

J. T. VAN GORSEL

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ORIGIN, EVOLUTION, TAXONOMIC POSITION

As stated above *Arnaudiella* is simply a large *Pseudosiderolites* with lateral chambers between the consecutive whorls. A derivation of *Arnaudiella* from *Pseudosiderolites* has already been suggested by Douvillé in the type description and has since been accepted by several later authors (ABRARD 1940, DROOGER 1960). Both forms occur in the same area and at the same time, so it can hardly be doubted that lateral chambers were acquired in a part of the *Pseudosiderolites* population, thus leading to *Arnaudiella*.

Between specimens of different samples we see distinct differences in the number of lateral chambers between the consecutive whorls. The relative stratigraphic position of the samples is not known, but it seems logical to suppose that samples in which a well developed system of lateral chambers is found are more advanced, so younger, than the samples with a small number of these chambers. On this criterion samples Gr 355 (Isle valley) and Gr 376 (Le Caillaud) would be younger than samples Gr 84 (S of Chalais) and Gr 179 (N of Barbezieux). The specimens from the Beaumont section occupy an intermediate position.

A side-effect of the formation of a large number of lateral chambers is the obscuring of the internal spiral structure. In the supposedly more advanced specimens a larger part of the test is covered with randomly arranged pustules.

It should be stressed that the extra-spiral secondary chambers are not just "vacuoles, resembling lateral chamberlets" as has been stated by several authors, but real lateral chambers, identical with those of *Lepidorbitoides*. This orbitoid character led DOUVILLÉ (1906) and ABRARD (1940) to the assumption that *Arnaudiella* might be a transitional form between *Pseudosiderolites vidali* and *Orbitoides*, which appears in abundance at a slightly higher level (zone Q of Arnaud) in the Charentes. However, the first representatives of the *Orbitoides* lineage (*Monolepidorbis*) appear already at a lower level (Upper Santonian or lowermost Campanian) and the heterohelicid character of the microspheric center of *Orbitoides* prohibits a derivation from a spirally arranged foraminifer (although, curiously, this is still doubted by NEUMANN, 1972).

Arnaudiella as a transitional form between *Pseudosiderolites* and *Lepidorbitoides* is a less improbable supposition. The most primitive member of the *Lepidorbitoides* lineage, *Helicorbitoides voigti*, also shows a planispiral arrangement of the primary chambers and has a peripheral structure with radial canals, so a derivation of this form from *Pseudosiderolites vidali* has been suggested (VAN GORSEL, 1973c). One might suggest that *Arnaudiella* evolved into *Helicorbitoides* by the introduction of secondary equatorial chambers. However, compared with the impressive system of lateral chambers in advanced specimens of *Arnaudiella*, the lateral chambers of *Helicorbitoides voigti* are relatively weakly developed. So with regard to the presence of secondary equatorial chambers *Helicorbitoides voigti* would be a more advanced form, whereas with regard to the development of lateral chambers it is more primitive than *Arnaudiella*. Also on stratigraphic grounds the derivation of the *Helicorbitoides-Lepidorbitoides* lineage from *Pseudosiderolites* via *Arnaudiella* is improbable, although it can not be rejected. At the base of the Aubeterre section only a few meters of sediment occur between our samples Gr 20 with rare *Arnaudiella* and Gr 22 with *Lepidorbitoides* and there are no indications for breaks or condensed sedimentation. This *Lepidorbitoides* shows a predominantly biserial arrangement of the initial chambers (VAN GORSEL, 1973b), which is not the most primitive stage of the *Lepidorbitoides* lineage. If it derives from *Arnaudiella* the initial evolution of this lineage must have been extremely rapid, as the successive stages *Helicorbitoides voigti*, *H. longispiralis* and *Lepidorbitoides pembergeri* are missing. It is assumed that *Arnaudiella* and *Helicorbitoides* represent two different lineages, which both originated from *Pseudosiderolites vidali* at about the same time, but in different areas. Both genera acquired lateral chambers, but in *Arnaudiella* no secondary equatorial chambers are formed and the primary spiral becomes strongly involute (caused by increase in the number of basal apertures?); in *Helicorbitoides* on the other hand secondary equatorial chambers are formed (caused by the acquisition of retrovert apertures) and the primary chamber spiral is shortened in *Lepidorbitoides*.

STRATIGRAPHIC DISTRIBUTION, AGE

From the cliffs along the Gironde to the valley of the river Isle *Arnaudiella* is invariably found in the so-called P3 zone of Arnaud, below the appearance of large numbers of *Orbitoides*. In the section near Beaumont, Dordogne, however, *Arnaudiella* was found associated with *Orbitoides*. ARNAUD (1877) proposed to use the first appearance of *Orbitoides media* as a criterion to determine the Campanian-Dordonian (later Campanian-Maastrichtian) boundary in this area (it should be noted that most students of orbitoidal foraminifera would assign the earliest "Dordonian sensu Arnaud" *Orbitoides* to the species *tissoti* Schlumberger). Recently several papers appeared, stating that the "Maestrichtien" in the area should be ascribed to the Campanian (VAN HINTE 1965 a.o., GOHARIAN 1971, VAN GORSEL 1973a), but SÉRONIE-VIVIEN (1972) still retains the view of Arnaud and attributes all strata with *Orbitoides* to the Maastrichtian. In any case if, in Northern Aquitaine, the appearance of *Orbitoides* would be a reliable time marker, the *Arnaudiella* specimens from the Beaumont section should be younger than, for instance, those from Le Caillaud. However, if one accepts increase in the number of lateral chambers as an evolutionary trend in *Arnaudiella*, the specimens from Beaumont would rather be the older (lateral chambers mainly in the umbilical region). Reworking might be considered, but it seems more reasonable to assume that the first appearance of *Orbitoides* in this area is determined by environmental circumstances and should not be used as a time marker. The facies of the upper Senonian in the SE Dordogne (hard dolomitic bioclastic limestones with organisms usually found in or near reefs) differs considerably from that of the Charentes (softer marly chalk with abundant oysters). So correlations between these regions based on ecologically influenced appearances or associations of certain forms will be useless. In this case only comparison of the evolutionary stages of genera occurring in both parts of the area will give reliable results.

A preliminary study of *Orbitoides* reveals that *Orbitoides* from the *Arnaudiella* bearing zone near Beaumont (samples Gr 342–345) shows intermediate characters between the oldest *Orbitoides* from the Aubeterre section (Gr 22, collected S of the petrol station along road D17) and the more primitive *Orbitoides* (*Monolepidorbis*) *douvillei*, which occurs in lowermost Campanian or Upper Santonian strata near Belvès (for a detailed description see VAN HINTE 1968). Both from Beaumont and from the base of the Aubeterre section 16 measurable horizontal sections are available. Evolutionary trends in *Orbitoides* are increase in the number of epi-auxiliary chambers (almost invariably 4, no significant change in samples studied), increase in size of the embryon (as expressed by $L_i + l_i$, see VAN HINTE 1966, 1968; average in Belvès is 382, in Beaumont 406 and in Aubeterre 460 microns) and increase in the number of lateral chambers (lateral chambers in Beaumont less well developed than in Aubeterre). So the evolutionary stages of both *Arnaudiella* and *Orbitoides* suggest that the lowermost samples with *Orbitoides* in the section of Beaumont should be correlated with a zone below the first appearance of *Orbitoides* in the Charentes.

Summarizing we may state that:

– apart from the incorrect use of the name Maastrichtian by several authors (all "Maestrichtien" in this area should probably be ascribed to the Upper Campanian and no true Maastrichtian is considered to be present), the method to determine its lower boundary by the first appearance of *Orbitoides* is unreliable and influenced by environmental differences. Accordingly the correlations of ARNAUD (1877) and SÉRONIE-VIVIEN (1972) should be revised.

– *Arnaudiella* is restricted to a narrow zone, which probably agrees with the lower part of the Upper Campanian of the boreal classification.

GEOGRAPHIC DISTRIBUTION

Arnaudiella occurs all over the Northern border of the Aquitaine basin. In our collection we have two specimens of *Arnaudiella* from Orboreac in Eastern Serbia, Jugoslavia (kindly donated by Mrs. M. Sladić-Trifunović). Vertical sections of *Arnaudiella* have been figured by CUVILLIER and SACAL (1951, Pl. XLVII) from the southern part of the Aquitaine basin. From other areas it has been reported rarely and never figured adequately: ROUX and DOUVILLÉ (1910) mention the occurrence of *Arnaudiella* in Tunisia, SIGAL (1952) in Algeria and SOUQUET (1967) in the Spanish Pyrenees.

REMARKS ON *POKORNYELLINA (=SIDERINA) DOUVILLEI* (ABRARD) 1926

In the type description of *Siderina douvillei* Abrard from Charente-Maritime only the exterior and a horizontal section have been described. The animal was characterized as a large *Pseudosiderolites*-like foraminifer, in which the pattern of ornamentation did not reveal the internal spiral arrangement (small, randomly distributed pustules as in *Lepidorbitoides*).

DOUVILLÉ (1928, p. 94) states that *Siderina* Abrard would be a *Pseudosiderolites* without pustules. After HOFKER (1959, p. 301) *Siderina douvillei* is a junior synonym of *Pseudosiderolites vidali*, but ALLARD et al. (1959, p. 616) refer this form to *Arnaudiella douvillei* (Abrard).

LOEBLICH and TAPPAN (1961) noticed that the name *Siderina* has been used earlier for a scleractinian coral (DANA, 1846) and proposed the genus name *Pokornyella* for the species described by Abrard. However, this turned out to be the name of an ostracod genus (OERTLI, 1956), so in LOEBLICH and TAPPAN (1964) it was changed into *Pokornyellina*. They state that "the original illustrations and description of *Siderina* Abrard suggest that it may be congeneric with *Arnaudiella* or *Pseudosiderolites*". Indeed the horizontal section as drawn in the type description shows a well developed marginal radial canal structure and great similarity to the horizontal section of a (microspheric?) *Arnaudiella* or a large *Pseudosiderolites*. Frequently the internal spiral structure is also hard to see on the exterior of adult specimens of both latter genera, especially in specimens which are slightly weathered or not well cleaned, or in which the ornamentation is weakly developed. Photographs in the type description of *Arnaudiella grossouvrei*, for instance, do not reflect the primary chambers

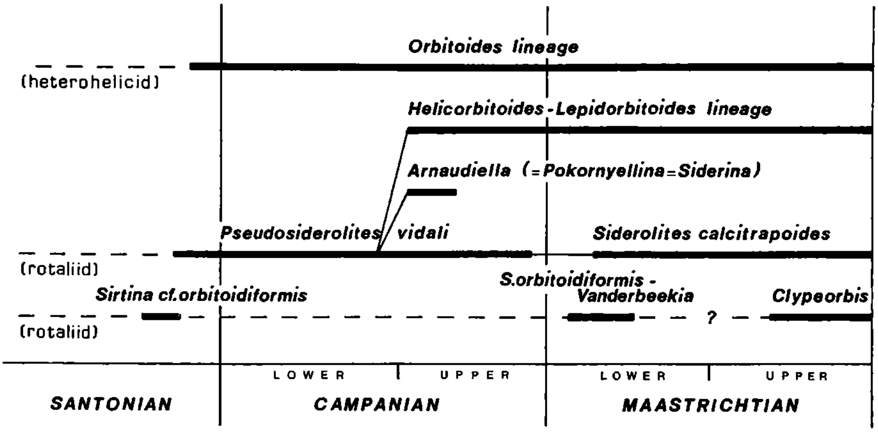

Fig. 2. Stratigraphic distribution and supposed phylogenetic relationships of forms discussed in this paper.

or any arrangement of pustules along the sutures of these chambers (see DOUVILLÉ 1906, Pl. XVIII, figs. 10–15). So there are no significant differences in exterior or horizontal section between *Siderina* Abrard and either *Arnaudiella* or *Pseudosiderolites*. The occurrence of these genera in the same area at about the same level would make it probable that *Siderina douvillei* Abrard is identical with either *Arnaudiella grossouvrei* Douvillé or *Pseudosiderolites vidali* (Douvillé), depending on the presence or absence of lateral chambers. However, both latter species have been mentioned by Abrard in the type description of *Siderina douvillei*. Moreover the new species was erected with the assistance of Douvillé, the original author of the other two. Accordingly, it was felt to be necessary to collect topotype material of *Siderina douvillei*. The type locality is an abandoned quarry, about 1 km E of Bernon (near Royan, Charente-Maritime, see chapter "Localities", sample Gr 800). The quarry is still well accessible today and a few large specimens of the enigmatic genus were found in

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PLATE III

Fig. 1. Gr 84A, S of Chalais, 25×. External view of *Arnaudiella grossouvrei*. Right below the last primary spiral chamber is visible.

Fig. 2. Gr 20, base of Aubeterre section, 35×. External view of *Pseudosiderolites vidali* with well developed flange, consisting of radially arranged calcareous elements and canals.

Figs. 3 and 4. Gr 188, S of Jonzac, 40×. Ventral side of specimens of *Sirtina* cf. *orbitoidiformis*, showing tightly packed pustules in the centre and more or less straight radial ridges in the marginal zone, corresponding with the sutures of the spiral chambers.

Figs. 5 and 6. Gr 188, 40×. Dorsal side of specimens of *Sirtina* cf. *orbitoidiformis*. The presence of lateral chambers at this side of the test obscures the internal spiral arrangement.

PLATE III

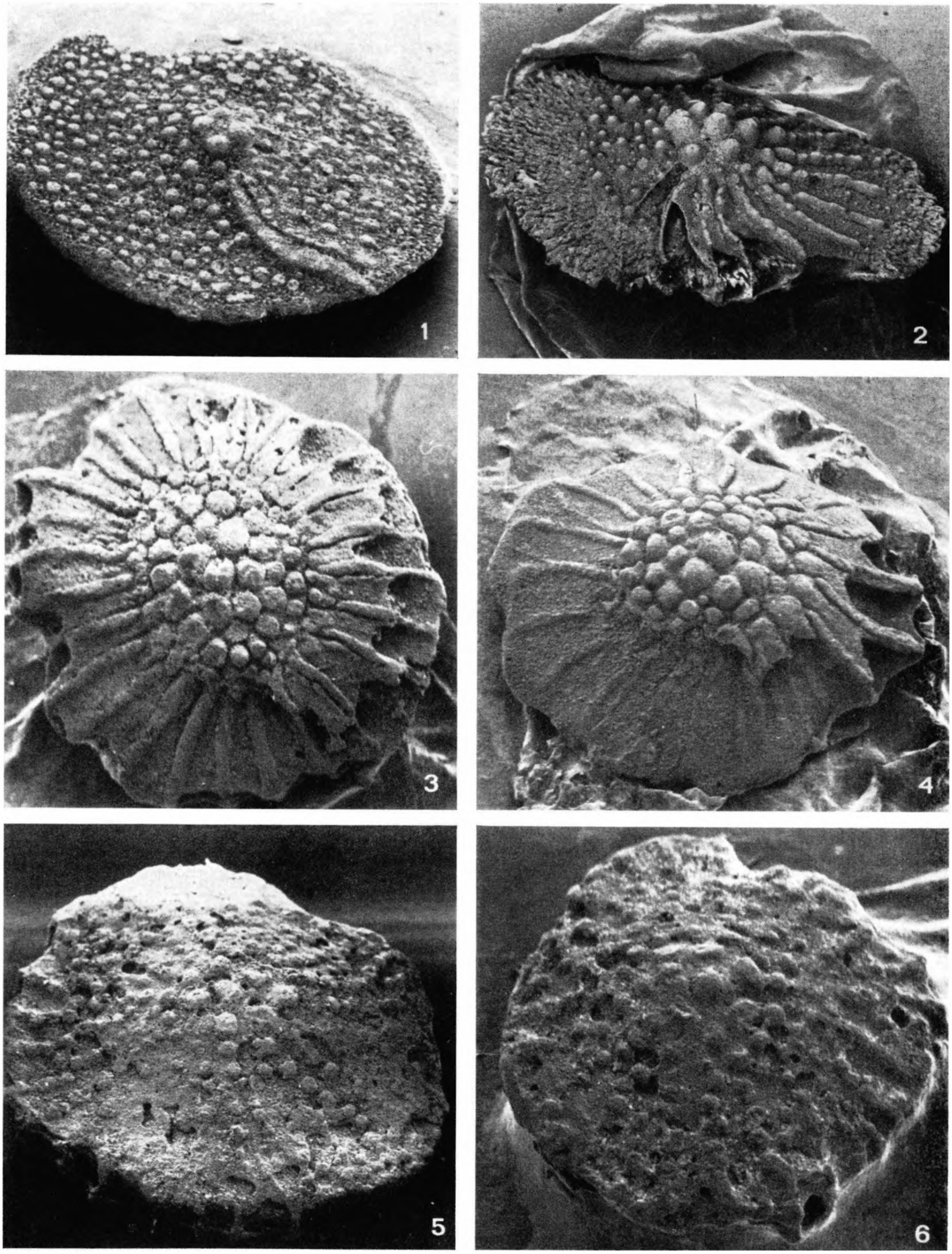
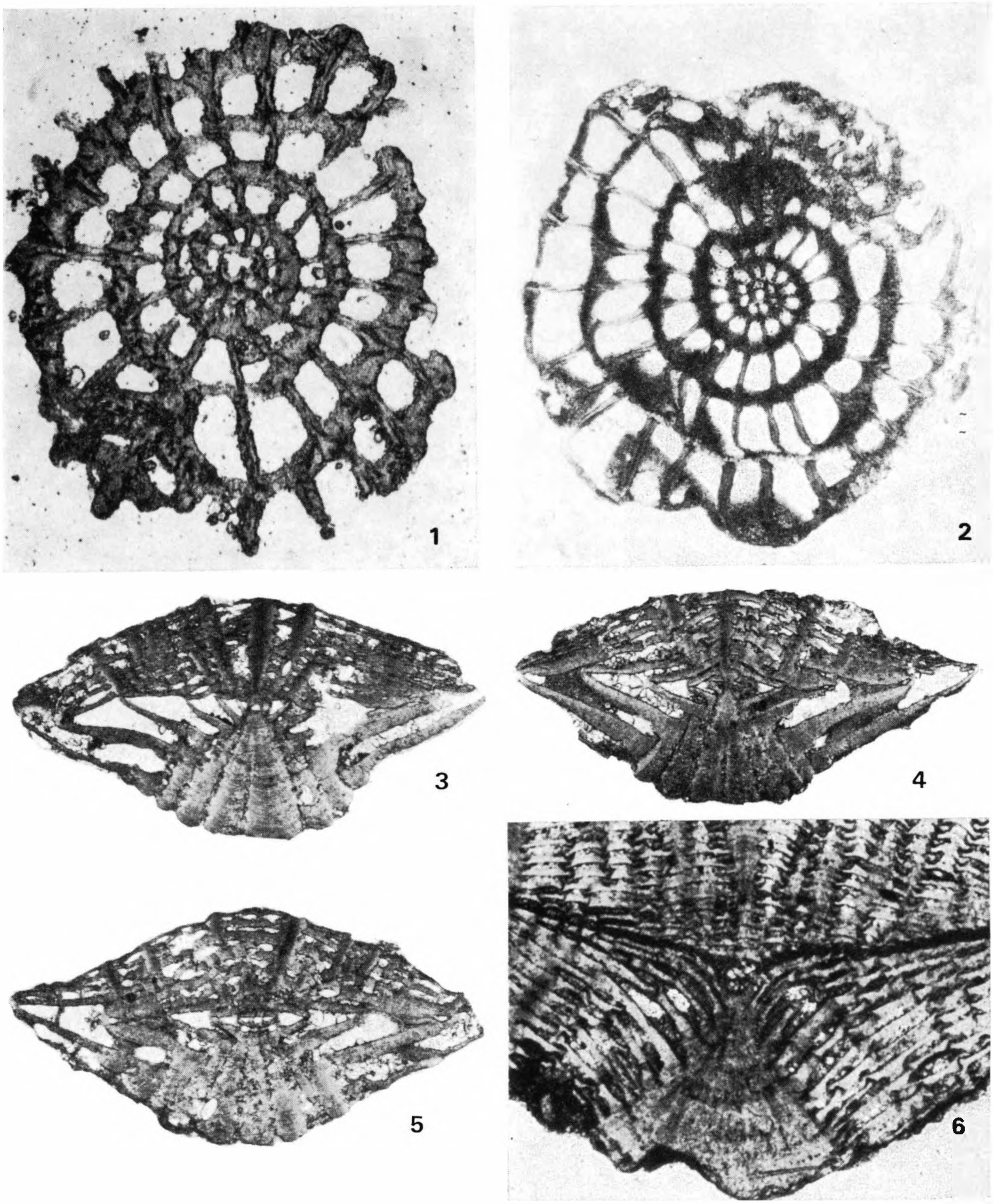


PLATE IV



the basal layers. The large tests (up to 6 mm) show the central thickening and a limited number of small pustules. Unlike the description of Abrard the sutures of the narrow, involute last chambers are visible. An axial section shows a well developed system of lateral chambers between the involute whorls of the primary spiral (Plate II, fig. 5). We are undoubtedly dealing here with representatives of *Arnaudiella grossouvrei*, so *Siderina* Abrard (later changed into *Pokornyellina* Loeblich and Tappan) is a younger synonym of *Arnaudiella* Douvillé. There is no need to designate the specimens from Bernon as *Arnaudiella douvillei* (Abrard), as was done by ALLARD *et al.* (1959), so the species *douvillei* Abrard is considered to be a junior synonym of *A. grossouvrei* Douvillé.

Sirtina cf. *orbitoidiformis* Brönnimann and Wirtz 1962

1962 *Sirtina orbitoidiformis* n.gen., n.sp. – BRÖNNIMANN and WIRTZ, p. 520–526, figs. 1–6.

About 9 km SE of Jonzac and 3 km W of Leoville (Charente-Maritime) a grab sample (Gr 188) was taken from a small outcrop in the NW corner of the intersection of roads D134 and D253E. The rock is a greyish, glauconite bearing limestone with partly silicified sponges. On the geological map (Carte Géol. France 1 : 80 000, nr. 171 Jonzac, 2nd. ed., 1964) these strata are ascribed to the Santonian. A large number of tests of a remarkable rotaliid foraminifer with a diameter up to 2 mm were found in this sample. The test is trochospirally arranged with tightly packed pillars at the umbilical side, comparable with many other rotaliid genera, but at the dorsal side it has a well developed system of *Lepidorbitoides*-like lateral chambers. These specimens, which to my knowledge have never been reported from this area before, are almost identical with forms from the Lower Maastrichtian of Iran and Libya, described as *Sirtina orbitoidiformis* by BRÖNNIMANN and WIRTZ (1962). Our French specimens will provisionally be ascribed to this species.

DESCRIPTION

Exterior – Asymmetrical, rotund lenticular test with an acute margin. The diameter varies between 1.2 and 2.0 mm, thickness between .55 and .9 mm, diameter/thickness ratio between 2.0 and 2.3. The ventral and

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PLATE IV

Figs. 1 and 2. Gr 188–hor. 3 (50×) and Gr 188–hor. 28 (35×). Horizontal sections of *Sirtina* cf. *orbitoidiformis*.

Figs. 3, 4 and 5. Gr 188–14, 5 and 13 (all 35×). Vertical sections of *Sirtina* cf. *orbitoidiformis*, showing a dense system of pillars at the umbilical side of the spiral and lateral chambers traversed by smaller pillars at the other side.

Fig. 6. Gr 813B, 80×. Vertical section of *Clypeorbis mamillata* from Dumes, SW France.

TABLE III

Measurements and counts on horizontal sections of *Sirtina* cf. *orbitoidiformis* from Leoville. Diameter protoconch in microns.

Number of specimen	Diameter protoconch	Nr. of whorls	Number of chambers in whorl: 1	2	3	4	5
Gr 188–3	43	5	7	11	14	18	22
4	41	5¼	7	12	—	—	—
8	47	5½	8	12	—	—	—
9	43	3¾	8	13	15	—	—
12	38	4½	7	12	15	18	—
13	39	5¼	8	12	17	—	—
18	51	4	7	—	—	—	—
25	42	5	7	12	16	—	—
28	38	5½	7	12	17	20	25
31	44	4½	7	13	—	—	—
$\bar{X}$	42.5	4.8	7.3	12.1	15.7	18.7	23.5

dorsal side of the test differ considerably. The central part of the ventral or umbilical side is thickened and is occupied by a large number of tightly packed pillars, the thickest ones in the centre, diameter of a pillar up to .18 mm. (Plate III, figs. 3, 4). The peripheral part of this side lacks the pustules; instead a large number of almost straight radial ridges can be seen, which ridges correspond with the sutures of the primary spiral chambers. The dorsal side is usually less convex and the position of the primary spiral chambers is less well marked (Plate III, figs. 5, 6). Pustules, which are smaller than those at the ventral side of the test, are present all over the dorsal side. In the central part these pustules are more or less randomly distributed, towards the periphery they are usually arranged in a radial direction along the sutures of the primary chambers. As in none of the specimens the last chamber has been preserved, the aperture could not be studied. Intercameral connections have not been observed either, neither in partly damaged specimens, nor in thin sections.

Horizontal section – Spherical protoconch, internal diameter between 35 and 45 microns, and deuteroconch with approximately equal diameter are followed by four to six whorls of primary chambers (Plate IV, figs. 1, 2, Table III). The septa are almost straight and doubled in the rotaliid manner. The first whorl usually consists of 7 to 8 chambers, the second of 11 to 13, the third of 14 to 17 and in the fourth whorl about 18 chambers can be counted. Due to the trochospiral arrangement it is hardly possible to obtain horizontal sections which cross both the first chamber and the outer margin of all subsequent whorls. Some horizontal sections through the umbilical plug show a spiral arrangement of the umbilical pillars, which suggests that a pillar is formed at the umbilical end of each spiral chamber. A marginal structure of radial canals, like in *Pseudosiderolites* and *Arnaudiella*, is lacking.

Vertical section – The distinguishing characteristics of *Sirtina* can best be seen in a vertical section (Plate IV, figs. 3–5). The primary chambers are involute, more involute at the ventral side than at the dorsal side. They are trochospirally arranged, but in some specimens only weakly so, thus approaching a planispiral arrangement. The margin of the spiral chambers is usually sharp, occasionally slightly rounded. The umbilical plug is composed of tightly packed textural-inflational pillars, between which no vertical canals have been observed. At the dorsal side of the primary spiral a well developed system of lateral chambers occurs, traversed by pillars, similar with the lateral layers of *Lepidorbitoides*.

Remarks

Apart from the many similarities with the type specimens of *Sirtina orbitoidiformis* there are also a few minor morphologic differences. First the tests of the French forms are larger (2 mm against 1.5 mm). Secondly in the type specimens the distinct asymmetry of the test is only found in the young specimens; in the adult stage these tend to become symmetrical, whereas in the French specimens the external asymmetry is maintained even in the largest specimens. This suggests that our French specimens may be more primitive than those from Iran and Libya. The stratigraphic distribution (Santonian versus Lower Maastrichtian) agrees with this.

The ancestor of *Sirtina* is not known, but it must have been some form resembling *Rotalia*, in which orbitoidal lateral chambers were acquired.

After the type description of *Sirtina*, Brönnimann and Wirtz describe another new form from the Lower Maastrichtian, *Vanderbeekia trochoidea*. It shows many resemblances with *Sirtina*, but it forms a distinct equatorial layer, which makes it more orbitoid-like. *Vanderbeekia* is supposed to be a more advanced form of *Sirtina*. It may be pointed out that the Upper Maastrichtian orbitoidal foraminifer *Clypeorbis* Douvillé shows a similar asymmetry of the two lateral layers on either side of a thin equatorial layer (Plate IV, fig. 6). The initial chambers of *Clypeorbis* are also trochospirally arranged and a prominent central calcareous mass is formed at the ventral side only. So it is suggested that *Sirtina*, *Vanderbeekia* and *Clypeorbis* are successive stages of one phylogenetic lineage.

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