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Micronautilus n. gen., a new dwarf Bathonian (Middle Jurassic) nautilid from Western France

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ABSTRACT
The new genus *Micronautilus* n. gen. (type species *Micronautilus evolutus* n. gen., n. sp.) is described and assigned to the family Paracenoceratidae Spath, 1927. Known from only two species with a very small shell, this taxon is regarded to represent a natural lineage within the family. As currently known, the occurrence of *Micronautilus* n. gen. is limited to the Bathonian of Western France, extending from the Zigzag Zone to the Retrocostatum Zone. The origin of *Micronautilus* n. gen. is likely to lie in the upper Bajocian group of nautilids assigned to '*Cenoceras' fuscum* (Crick, 1898). Paleoenvironmental data suggest that the dwarfism of this new taxon cannot be interpreted as a consequence of an isolated population or any specific environmental conditions.

KEY WORDS
Cephalopods,
Nautilida,
Jurassic,
Bathonian,
biostratigraphy,
dwarfism,
new genus,
new species.

RÉSUMÉ
Micronautilus *n. gen., un nouveau genre de nautilidé nain dans le Bathonien (Jurassique moyen) du Poitou.*
Un nouveau genre de nautile, *Micronautilus* n. gen. (espèce type *Micronautilus evolutus* n. gen., n. sp.) est décrit et rattaché à la famille des Paracenoceratidae Spath, 1927. Actuellement représenté par deux espèces de très petite taille, ce taxon est considéré comme une lignée bien individualisée au sein de la famille. Dans l'état actuel des connaissances, *Micronautilus* n. gen. semble confiné au Bathonien de l'ouest de la France, depuis la Zone à Zigzag jusqu'à la Zone à Retrocostatum. L'origine de *Micronautilus* n. gen. se trouve probablement au sein du groupe de nautiles du Bajocien supérieur assigné à '*Cenoceras*' *fuscum* (Crick, 1898). Les données paléo-environnementales suggèrent que le nanisme de ce nouveau genre ne peut pas être interprété comme la conséquence d'une population isolée ni de conditions environnementales particulières.

MOTS CLÉS
Céphalopodes,
Nautilida,
Jurassique,
Bathonien,
biostratigraphie,
nanisme,
genre nouveau,
espèces nouvelles.

INTRODUCTION

During more than three decades of investigation of Jurassic strata in Western France (ranging mainly through Aalenian to Oxfordian stages), I collected hundreds of nautilids belonging to several well-known genera including *Cenoceras* (*sensu lato*) Hyatt, 1884, *Digonioceras* Hyatt, 1894 and *Paracenoceras* Spath, 1927. Closer examination of this material has already led to the designation of a new genus, *Pictonautilus* (Branger, 2004) and ongoing studies clearly show that several other new species, especially from the *Pseudaganides* group, are also present. Within the middle-upper Bathonian material, in addition to medium- to large-sized nautilids, it has been possible to recognize a distinct group of small nautilid conchs that exhibit adult shell characteristics. One of these unusual forms represents the smallest Jurassic nautilids yet described and is assigned here to *Micronautilus* n. gen.

MATERIAL AND METHOD

For more than thirty years, I visited many quarries and temporary road work sections throughout the well-known Jurassic strata in Western France. Fossils described in this paper have been collected within an accurate biochronological chart based on ammonites from the Submediterranean Realm (Cariou & Hantzpergue *in* GFEJ 1997). One locality in particular, Buffevent quarry (46°20'28"N, 0°30'21"W), was investigated in close detail (Branger 2009) and provided most of the specimens for this study (Figs 1; 2 below). Other localities are Saint-Maixent-l'École (46°25'37"N, 0°12'28"W); les Hauts-de-Rochefort quarry at Sainte-Éanne (46°23'30"N, 0°07'55"W) (Branger 1989); Trottebuie (46°25'37"N, 0°12'28"W) (Énay *et al*. 2012); Saint-Gelais (46°22'54"N, 0°22'37"W), les Lucs near Échiré (46°21'30"N, 0°25'36"W); Souché (46°19'10"N, 0°25'05"W) and Jard-sur-Mer (46°25'08"N, 1°38'21"W). The measurements of nautilid conchs employed here follow those of Tintant (1984a), namely: shell diameter (D), whorl height (H), whorl width (W) and width of the umbilical area (U). In addition, the depth (P) and the width (L) of the lateral lobe of the suture lines have also been estimated. Different ratio have also been used to compare the fossils: h = H/D; w = W/D; u = U/D.

Some shells have been identified as adults. This assertion is based by comparison with mature modifications seen in shells of recent nautilids already described by Collins & Ward (1987) and summarized by Klug (2004). The most evident feature is the septal crowding at the end of the phragmocone but we can also notice the change in coiling with reduction of relative whorl height accompanied by a more rounded venter.

All the material is from P. Branger's collection and is stored at the Musée Bernard d'Agesci in Niort (France).

Abbreviations

Measurements

D	shell diameter;
H	whorl height;
L	width;
P	depth;
U	width of the umbilical area;
W	whorl width.

Ratio

h	H/D;
u	U/D;
w	W/D.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1795
Subclass NAUTILIA Wade, 1988
Order NAUTILIDA Agassiz, 1847
Superfamily Nautiloidea de Blainville, 1825
Family Paracenoceratidae Spath, 1927

Genus *Micronautilus* n. gen.

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Diagnosis. — Small sized adult nautilids (less than 60 mm in diameter) with a generally compressed shell showing a quite deep and narrow hyponomic sinus. The whorl section may be oval on the phragmocone, becoming subrectangular to subquadrate, depending on the species, rarely depressed at adult stage. The umbilicus is open with an umbilical area up to 20% of shell diameter, boarded by a subvertical wall. Septa are relatively close, mostly on the type-species; sutures always exhibit a shallow lateral lobe (Fig. 3A-C).

Type species. — *Micronautilus evolutus* n. sp. (Figs 1-5; Appendix 1).

Composition of the genus. — *Micronautilus evolutus* n. gen., n. sp. (type) and *Micronautilus minoti* n. gen., n. sp.

Etymology. — The generic name *Micronautilus* refers to the very small diameter of these nautilid shells.

Remarks

On account of its small size and unique shell shape, *Micronautilus* n. gen. cannot be mistaken with any other contemporaneous Jurassic nautilids and its taxonomic validity is unquestionable. At the same stratigraphic level, two other nautilid genera exhibit a compressed shell form: the earliest representatives of *Pseudaganides* Spath, 1927 (Figs 1-3; Appendix 2A) and *Pictonautilus* (Figs 1-3; Appendix 2B). However, both these genera are typically slightly larger than *Micronautilus* n. gen., moreover *Pseudaganides* exhibits a closed umbilicus (U/D = 0). Furthermore, as the suture lines of *Pseudaganides* are much more sinuous than *Micronautilus* n. gen. (Fig. 3E), these two taxa are not considered here to be closely related. *Micronautilus* n. gen. resembles *Pictonautilus* with regard to its shallow, weakly sinuous sutures (Fig. 3D). The angular margins of some *Micronautilus* n. gen. shells are also reminiscent of *Pictonautilus* but the latter exhibits sharp ventral edges. Coeval *Pictonautilus* displays an occluded umbilicus and its inner whorls remain rounded in section. *Pictonautilus clavifer* (Tintant, 1994), of early Bathonian age possesses a relatively stout, small-sized shell and an open umbilicus.

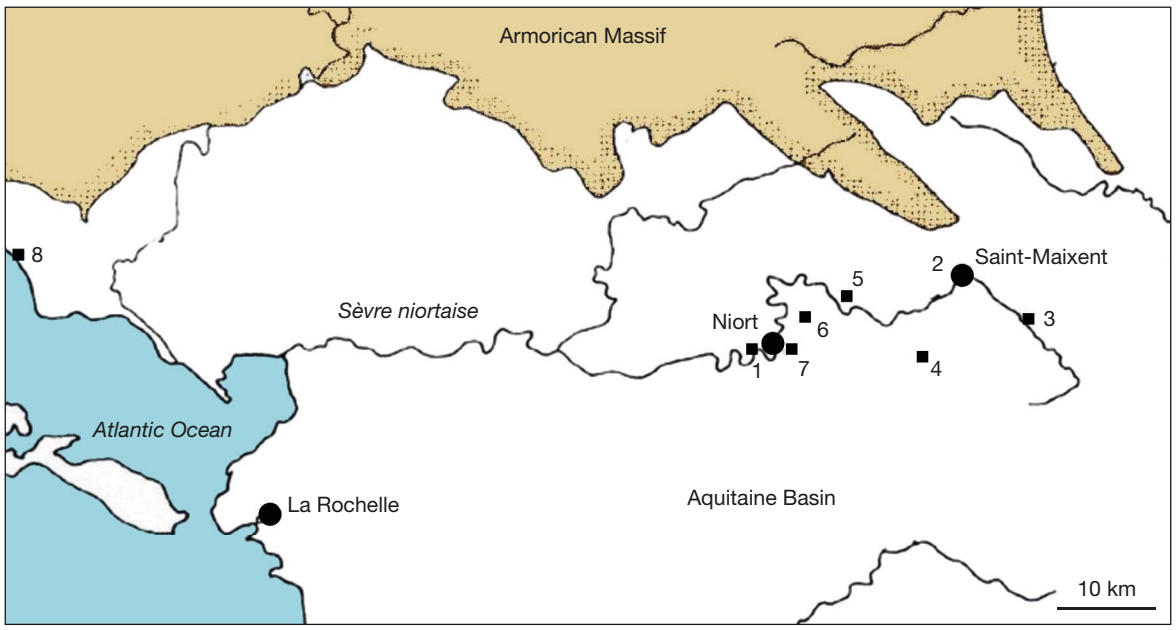

FIG. 1. — Geographical map reporting the position of the localities that provided specimens of *Micronautilus* n. gen. Numbers: **1**, Buffevent; **2**, Saint-Maixent-l'École; **3**, Sainte-Éanne; **4**, Trottebuie; **5**, Saint-Gelais; **6**, les Lucs; **7**, Souché; **8**, Jard-sur-Mer.

TABLE 1. — Measurements in millimetres for the shells of *Micronautilus evolutus* n. gen., n. sp.

No.	D	H	h	W	w	U	u	W/H	P	L	%
2021.BR.N.103	44	22	0.5	20	0.45	8.6	0.19	0.9	–	–	–
(holotype)	42	21	0.5	20	0.47	7.7	0.17	0.95	3	12.5	24
	41	–	–	–	–	7.2	0.16	–	–	–	–
	38	–	–	–	–	6.28	0.16	–	–	–	–
	35	–	–	–	–	5.8	0.16	–	–	–	–
	33	–	–	–	–	5.3	0.14	–	–	–	–
	30	15.5	0.51	13.5	0.45	4.5	0.15	0.87	–	–	–
2021.BR.N.066	39	–	–	–	–	7.3	–	–	–	–	–
	38	19	0.5	18	0.47	6.3	0.19	0.94	2.5	12	20
	30	15	0.5	14	0.46	5.8	0.17	0.93	–	–	–
2021.BR.N.091	38	19	0.5	19	0.5	7.4	0.19	1	3	17	17.6
	31	16	0.51	15	0.48	6	0.19	0.93	–	–	–
2021.BR.N.135	38	18	0.47	17	0.44	5.5	0.14	0.94	1.5	13	11.5
	28	16	0.57	14	0.5	4	0.14	0.87	–	–	–
	27	14	0.51	13	0.49	–	–	0.92	–	–	–
2021.BR.N.136	44	21	0.47	19	0.43	9	0.2	0.9	–	–	–
	39	18	0.46	17.5	0.45	8	0.2	0.97	–	–	–
2021.BR.N.137	28	15	0.53	12	0.42	5	0.18	0.8	–	–	–
2021.BR.N.138	29	15	0.51	14	0.48	4	0.13	0.93	2	10	20
2021.BR.N.139	33	18	0.54	15.5	0.47	4	0.12	0.8	–	–	–

This taxon may be close to an ancestral form of *Micronautilus* n. gen. that originated during Bajocian time through dwarf species like '*Cenoceras' fuscum* (Crick, 1898).

The important intraspecific variation in shell size of modern *Nautilus* Linnaeus, 1758 is well known and, despite of these differences, some of them are considered a single species (Saunders *et al.* 2017; Tajika *et al.* 2018). Nowadays the size variations seem to be linked to the geographical distribution of these animals. The fossils described within the present study are all coming from a restricted area, consequently such an intraspecific diversity is doubtful for this material. Moreover, the features of shells are unlike of coeval species and nowhere in the world any similar species have ever been described.

According to the recent classification chart for post-Triassic Nautilida (King *et al.* 2016), *Micronautilus* n. gen. would logically be included within the family Paracenoceratidae.

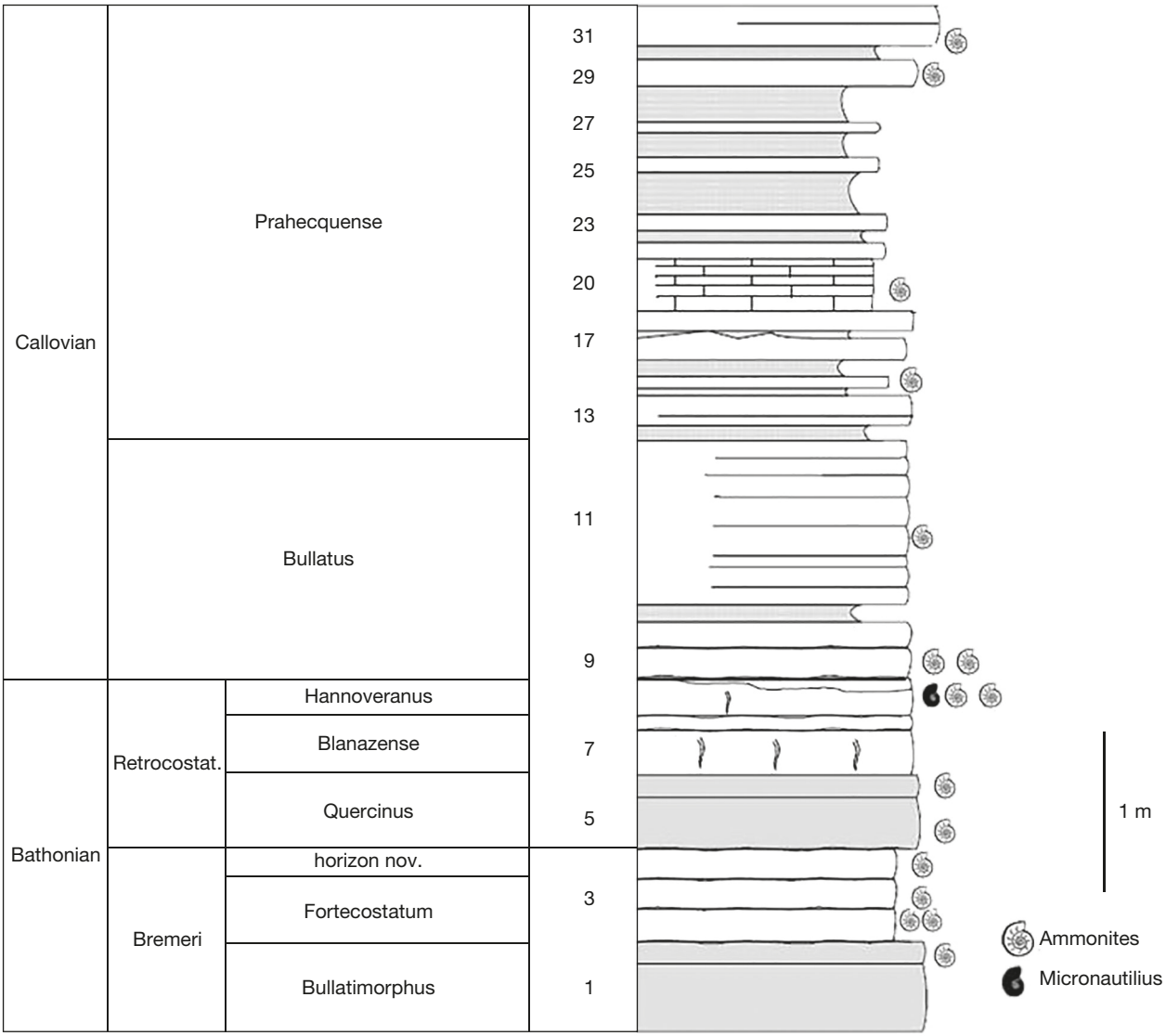

Fig. 2. — Stratigraphic section at Buffevent quarry from Branger (2009).

Occurrence

Micronautilus n. gen. is only currently known from Bathonian limestones in Western France and ranges from the lower Bathonian Zigzag Zone to the upper Bathonian, Retrocostatum Zone.

Micronautilus evolutus n. gen., n. sp.
(Figs 1-5; Appendix 1A-E)

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?*Pictonautilus verciacensis* (Lissajous) – Branger 2004: 143, pl. 1, fig. 3.

Pictonautilus sp.? – Grulke 2016: 141.

Diagnosis. — Small sized nautilid (less than 45 mm in diameter) with a compressed and subrectangular section of the shell. The umbilical area is always open and quite wide, up to 20% of shell diameter. Septa are relatively closely spaced and sutures exhibit a shallow lateral lobe.

Type material. — Holotype N103 from Buffevent quarry, Niort, Deux-Sèvres, France. It is figured in Fig. 1; Appendix 1A.
Eight paratype specimens (figured in Fig. 2; Appendix 1B-E) obtained from several localities (Fig. 1) have also been studied: 2021.BR.N.091, 2021.BR.N.103, 2021.BR.N.136, 2021.BR.N.137, 2021.BR.N.138 are from Buffevent quarry near Niort, 2021.BR.N.139 is from Jard-sur-Mer (Vendée) and 2021.BR.N.066 from Saint-Maixent-l'École.

Type locality and stratum typicum. — *Micronautilus evolutus* n. gen., n. sp. is relatively common at the top of the Calcaire à silex formation (Welsch 1903) of late Bathonian (Retrocostatum Zone) age in Western France, especially in the vicinity of Niort. The taxon has not yet been described from any other area.

Measurements. — see Table 1.

Etymology. — The specific name *evolutus* relates to the relatively wide umbilicus of the shell.

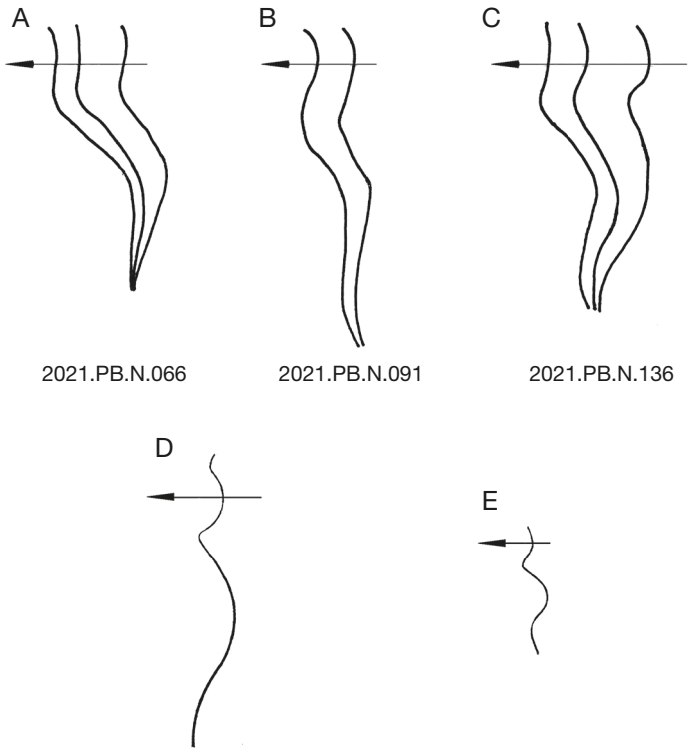

FIG. 3. — Suture lines of *Micronautilus evolutus* n. gen., n. sp. at the end of the phragmocone compared with *Pictonautilus* Branger, 2004 and *Pseudaganides* Spath, 1927: **A**-**C**, *Micronautilus evolutus* n. gen., n. sp.; **D**, *Pictonautilus verciacensis* (Lissajous, 1923), middle Bathonian, Bremeri Zone, Saint-Maixent-l'École (Deux-Sèvres); **E**, *Pseudaganides* n. sp. upper Bathonian, Retrocostatum Zone, Aiffres, Deux-Sèvres.

DESCRIPTION

Micronautilus evolutus n. gen., n. sp. is a very distinctive species characterized by a very small size at adult stage, ranging from 30 mm (estimated diameter) for 2021.BR.N.138 (Fig. 3A-C; Appendix 1C) up to 44 mm in 2021.BR.N.136 (Fig. 5A, B; Appendix 1E). The individuals are relatively evolute for Jurassic nautilids. The umbilicus is widely open since U/D can reach 20% of the diameter on full grown shells. At the very beginning of the embryonic shell, the whorl section is rounded and, until a diameter of about 1 cm is reached, the shell displays reticulate ornamentation. This diameter seems to be approximately the hatching size of the animal according to the weak depression, corresponding to the nepionic constriction, observed on inner whorls of the holotype (2021.BR.N.103). Further adoral, the whorl section becomes sub-rectangular to sub-trapezoidal, compressed with a maximum width located close to the umbilicus. Flanks are flat, sub-parallel, boarded by angular but never sharp ventral edges; the wall of the umbilicus is sub-vertical. The venter is very slightly rounded on the inner whorls and flattens before the beginning of the body chamber, tending to be a little concave on stratigraphically younger specimens. The shell is narrowly camerate, with twelve to thirteen chambers occurring in each half of a whorl when adult. The suture lines are partly hidden on the holotype (2021.BR.N.103) but, on the paratypes, exhibit wide and shallow lateral and ventral lobes (Fig. 3). The hyponomic sinus of the shell is quite deep and narrow. The position of the siphuncle has not been observed.

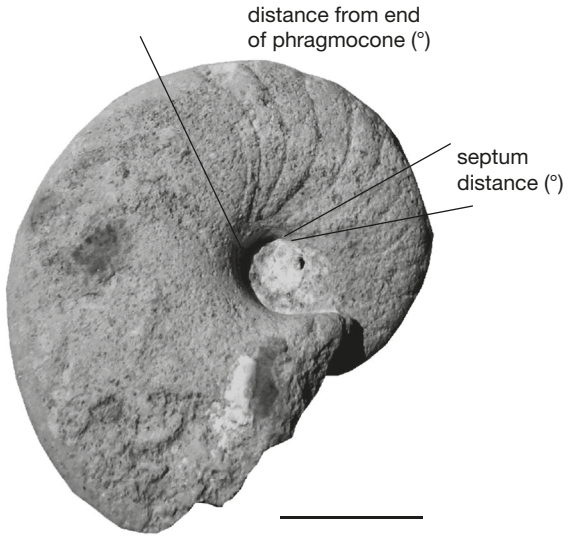

FIG. 4. — Measurement of the septal spacing in the studied *Micronautilus* n. gen. Scale bar: 1 cm.

REMARKS

As discussed above, apart from the two specimens figured under the name of ?*Pictonautilus verciacensis* (Branger, 2004) and *Pictonautilus* sp. (Grulke 2016: 141), *Micronautilus evolutus* n. gen., n. sp. has not previously been illustrated. At the same stratigraphic level, the closest small sized nautilid with a compressed shell belongs to the earliest representatives of *Pseudaganides* (ongoing studies from personal data).

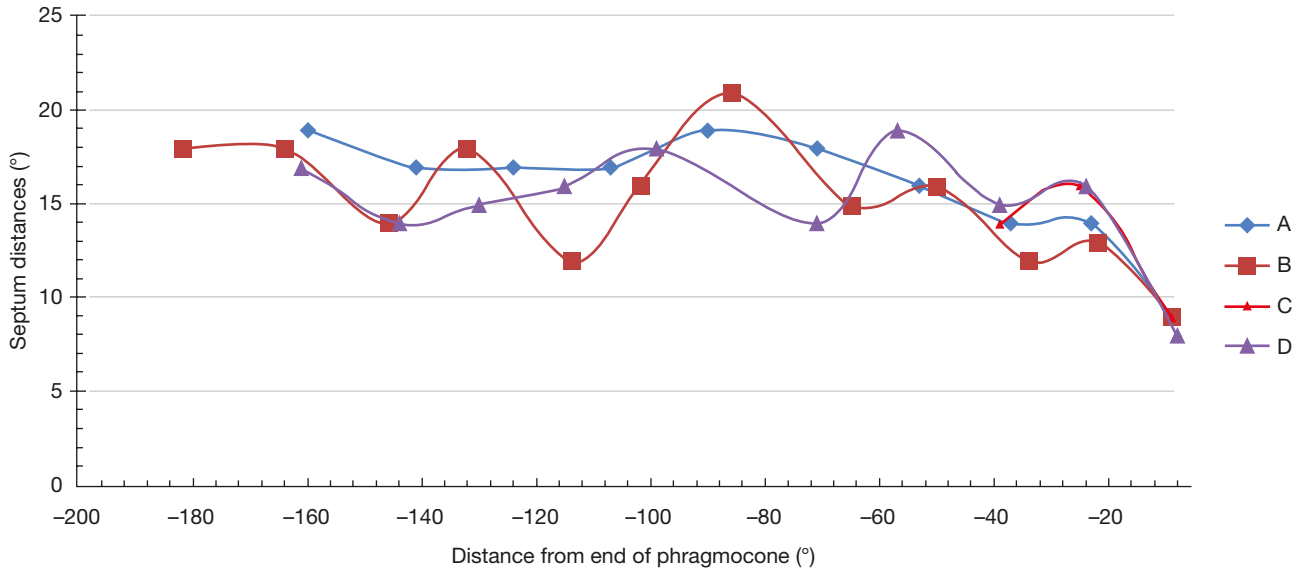

Fig. 5. — Septum distances of *Micronautilus evolutus* n. gen., n. sp.: **A**, 2021.BR.N.066; **B**, 2021.BR.N.091; **C**, 2021.BR.N.136; **D**, 2021.BR.N.138.

This genus is not considered here to be closely related due to its closed umbilicus and suture lines that are much more sinuous than *Micronautilus* n. gen.

Despite of their small size, the specimens of *M. evolutus* n. gen., n. sp. are regarded as mature shells because of two reasons. The first one is related to the crowding of the last septum at the end of the phragmocone. The septal spacing has been measured on four specimens, 2021.BR.N.066, 2021.BR.N.091, 2021.BR.N.136 and 2021.BR.N.138 (Figs 4; 5) according the method used by Kraft *et al.* (2008). As inner whorls are small and hidden by overlapping whorls, they cannot be observed clearly and the measurements have been only done from 180° to 20° before the last septum. All of them show an angular distance that varies from 12 to 20° (Fig. 4). The two last one are approximated like on the modern nautiluses, the angular distance falls under 10°. The second indication of maturity is shown by the increase in the relative umbilical width close to adulthood size when U/D reaches 20% on the largest specimens (Table 1; Fig. 6).

Micronautilus minoti n. gen., n. sp.
(Figs 1-4; 7; Appendices 1F; 3A-D)

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Diagnosis. — Small sized and rather compressed *Micronautilus* n. gen. with a maximum diameter reaching 60 mm. Shell section is oval on inner whorls becoming subrectangular to subquadrate on full grown individuals. Umbilicus is always open. Septa show a broad and shallow lateral lobe and a ventral lobe.

Type material. — All the samples have been collected within the southern part of the Deux-Sèvres department (Fig. 1). Holotype 2021.BR.N.150 is from les Lucs (46°21'27"N, 0°25'31"W), temporary exposure near Échiré, it is figured in Fig. 1; Appendix 3A. Eight paratypes were sampled from various localities. 2021.BR.N.042 (Fig. 4; Appendix 3D), 2021.BR.N.152 (Fig. 2; Appendix 3B) and 2021.BR.N.153 are from the old Trotte-Buie quarry, Mougon commune, 2021.BR.N.095 (Fig. 3A-C; Appendix 3C) was found in Souché (temporary roadworks near Niort), 2021.BR.N.135 (Fig. 6; Appendix 1F) and 2021.BR.N.151 come from les Hauts-de-Rochefort (Sainte-Éanne quarry), 2021.BR.N.155 is from Saint-Gelais.

Type locality and stratum typicum. — Most of the specimens have been collected from the "Banc pourri" (Welsch 1903), a stratigraphic level that extends all along the northern border of the Aquitaine basin. This level has yielded many ammonites, all of them have been reported from the lower Bathonian, Zigzag Zone (Sauvaget 1906; Énay *et al.* 2012). A single example, 2021.BR.N.135, a little younger, middle Bathonian, Progracilis Zone, is assigned to the same species.

Measurements. — See Table 2.

Etymology. — The specific name *minoti* is dedicated to Jean-Michel Minot, an amateur paleontologist who published the first exhaustive monograph on brachiopods from Western France (Minot & Branger 2007) and collected some interesting nautilids.

Description
Small sized nautilus, maximum diameter observed is about 60 mm. The section of the shell is compressed, oval on the phragmocone. It widens on the body chamber where the width can exceed slightly the height (W/H = 1.06 on 2021.BR.N.095), getting rectangular, sometimes quadrate. Venter is rounded on the inner whorls but flattens as the animal becomes adult. The umbilicus is always open (U/D = 0.15) but narrower than on *Micronautilus evolutus* n. gen., n. sp. with an umbilical wall that is subvertical at any stage. The suture line shows a broad and shallow lateral lobe whereas the ventral lobe is faint but clearly visible, at least from a diameter of 15 mm. Each half of a whorl shows nine chambers.

Remark
Micronautilus minoti n. gen., n. sp. has not previously been figured and no former description corresponds to this new species. The shell of *Cenoceras fuscus* (Crick, 1898), upper

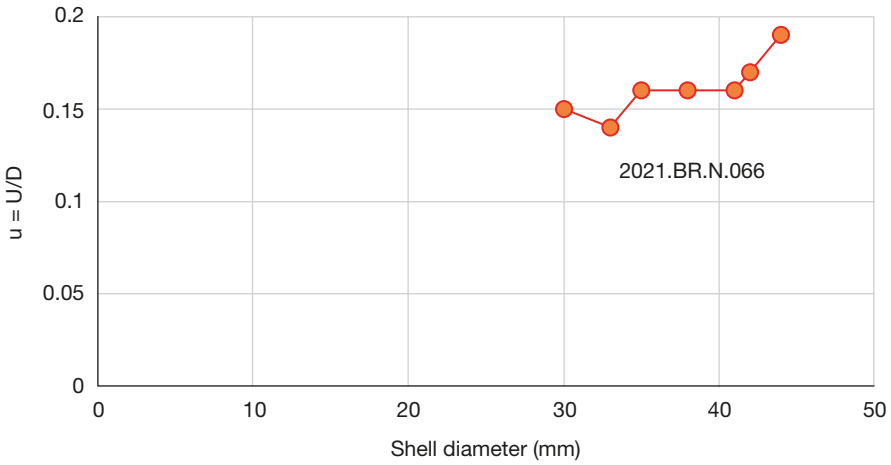

FIG. 6. — Ratio of the width of the umbilicus compared with the size of the shell of *Micronautilus evolutus* n. gen., n. sp. (2021.BR.N.066).

TABLE 2. — Measurements in millimetres for the shells of *Micronautilus minoti* n. gen., n. sp.

No.	D	H	h	W	w	U	u	W/H
2021.BR.N.042	37	21	0.56	16	0.43	5.4	0.14	0.76
	28.3	16	0.56	13.6	0.48	4	0.14	0.85
2021.BR.N.056	57	29.4	0.51	26	0.45	8	0.14	0.88
	46	25	0.54	26	0.56	4.8	0.1	1.04
	40	23	0.57	19.6	0.49	3	0.07	0.85
2021.BR.N.095	41	22	0.53	23.5	0.57	6.5	0.16	1.06
	31	17	0.54	15.5	0.5	4	0.13	0.91
2021.BR.N.150	45.5	24	0.52	#24	0.52	7.5	0.16	1
	34.5	20	0.57	#16	0.46	3.8	0.19	0.8
2021.BR.N.151	40	22	0.55	#10	0.25	6	0.15	0.5?
	18.4	16	–	#14	–	4	0.21	–
2021.BR.N.152	53	27	0.5	25	0.47	5	0.17	0.92
	30	16	0.53	15	0.5	3.8	0.12	0.93
	25	14	0.56	12.5	0.5	3.7	0.14	0.9
2021.BR.N.153	61	33	0.54	29	0.47	?5	0.08	0.87
2021.BR.N.155	54	28	0.51	27	0.5	9	0.16	0.96
	42	23	0.54	23	0.54	8	0.19	1
	37	19	0.51	17	0.45	6	0.16	0.89

Bajocian, is also rather small but larger than *Micronautilus minoti* n. gen., n. sp. with an open umbilicus. *Micronautilus evolutus* n. gen., n. sp. possesses a smaller, more compressed shell with a relatively wide umbilicus and more crowded septa. Moreover, its stratigraphical occurrence is younger, namely upper Bathonian. The final two septa in the adult shells of both species are typically approximated with an angular distance lower than 10° instead of 12° to 20° for previous ones.

DWARFISM

Dwarfism has been described from several Jurassic nautilids including *Paracenoceras parvulum* Tintant, 1984 and *Paracenoceras dorsoexcavatum* (Parona & Bonarelli, 1895) (Tintant 1984b). The description of the smallest taxon (*P. parvulum*) was based on one complete specimen and two body chambers. According to Tintant, this species was adult with a shell diameter of about 30 mm. According to the plates presented in Tintant's paper, the approximation of the two last septa does not clearly appear. *Paracenoceras parvulum* has only previously been recorded from Burgundy but is now known to occur at the same stratigraphic level (upper Callovian) in Western France (personal data of the author). These small sized specimens are a little larger than those described by Tintant; one example in the author's collection shows feature of an adult specimen at a diameter of 55 mm. Another interesting dwarf species is '*Cenoceras' fuscum* figured in Chirat (1997: pl. 5, fig. 5a-c), whose adult diameter is 48 mm.

Nevertheless, all these nautilids are larger at adult size than *Micronautilus evolutus* n. gen., n. sp. The origin of this unusual dwarfism among nautilids has already been discussed by Tintant (1984b). At the same stratigraphic levels, larger shells,

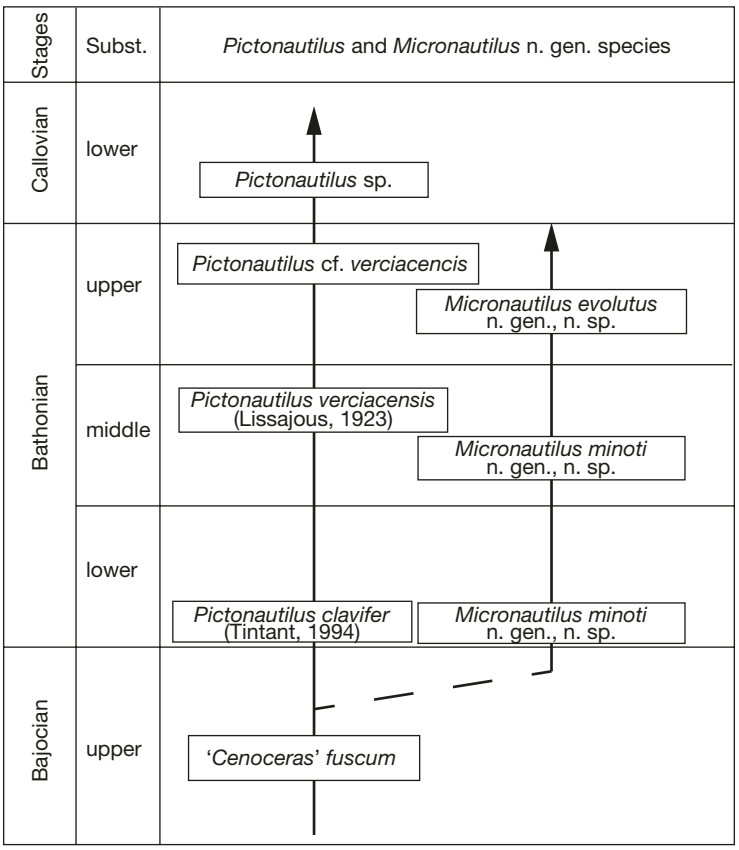

Fig. 7. — Origin and evolution of *Micronautilus* n. gen. and *Pictonautilus* (Branger, 2004) are likely to occur from the *'Cenoceras' fuscum* (Crick, 1898) group at the end of Bajocian.

up to diameter of 300 mm, are mixed with small to dwarf individuals. This is also true for the accompanying ammonite fauna and the benthic elements, bivalves and gastropods, that shows a mixing of larger and smaller individuals. As the limestone layers where the nautilids are preserved have been deposited within an open shelf environment, those populations were not isolated. Consequently, it seems impossible to explain this case of dwarfism as a result of an highly stressed environment, it has to be considered as a specific feature due to the evolution of an original lineage.

Another explanation which could be evoked would be a possible sexual dimorphism. This phenomenon has been proved by many authors in modern *Nautilus*. Willey (1902) was the first biologist who noticed that males are larger and have a broader aperture than females. More recent studies (Saunders & Spinosa 1978; Saunders *et al.* 2017) lead to the same conclusions. In comparison, the differences between *Micronautilus* n. gen. and other Bathonian nautiluses are disproportionate and cannot be the result of any sexual dimorphism.

ORIGIN AND EVOLUTION

As discussed above, dwarf nautiluses were already present during Bajocian times (Chirat 1997). *Micronautilus* n. gen. could have evolved from these forms through species like '*Cenoceras' fuscum*. All these shells show similarities: small and compressed whorl section, subrectangular section whose venter is boarded by angular wedges. One lineage (Fig. 7) would be constituted by the following species: '*Cenoceras*' *fuscum*, upper Bajocian, *Pictonautilus clavifer* (Tintant), lower Bathonian, *Pictonautilus verciacensis* (Lissajous), middle and upper Bathonian, and *Pictonautilus* sp. (lower Callovian). In the proposed phylogeny, *Micronautilus* n. gen. could have evolved from '*Cenoceras' fuscum* at the very end of the Bajocian and would have disappeared before the beginning of the Callovian stage without any descendants.

CONCLUSIONS

Micronautilus n. gen. represents a newly described phyletic lineage within the family Paracenoceratidae. The shell of this new genus is characterized by its dwarfism, its rather wide umbilical area and a sub-rectangular to sub-quadrate cross section of the conch. The species *Micronautilus evolutus* n. gen., n. sp. represents the smallest Jurassic nautilid described to date and its adult diameter could be reached at 30 mm and never exceeds 44 mm. As currently known, the stratigraphical range of *Micronautilus* n. gen. is restricted to the Bathonian stage of Western France, it extends from the Zigzag Zone to the Retrocostatum Zone. The origin of *Micronautilus* n. gen. is likely to occur in the '*Cenoceras' fuscum* (Crick, 1898) group of nautilids of late Bajocian age. No descendant has been

recorded from Callovian or younger beds. Since the samples have been found associated with larger shells of nautilids as well as ammonites, the dwarfism of this new group cannot be interpreted as the consequence of an isolated population or adaptation to any special environment.

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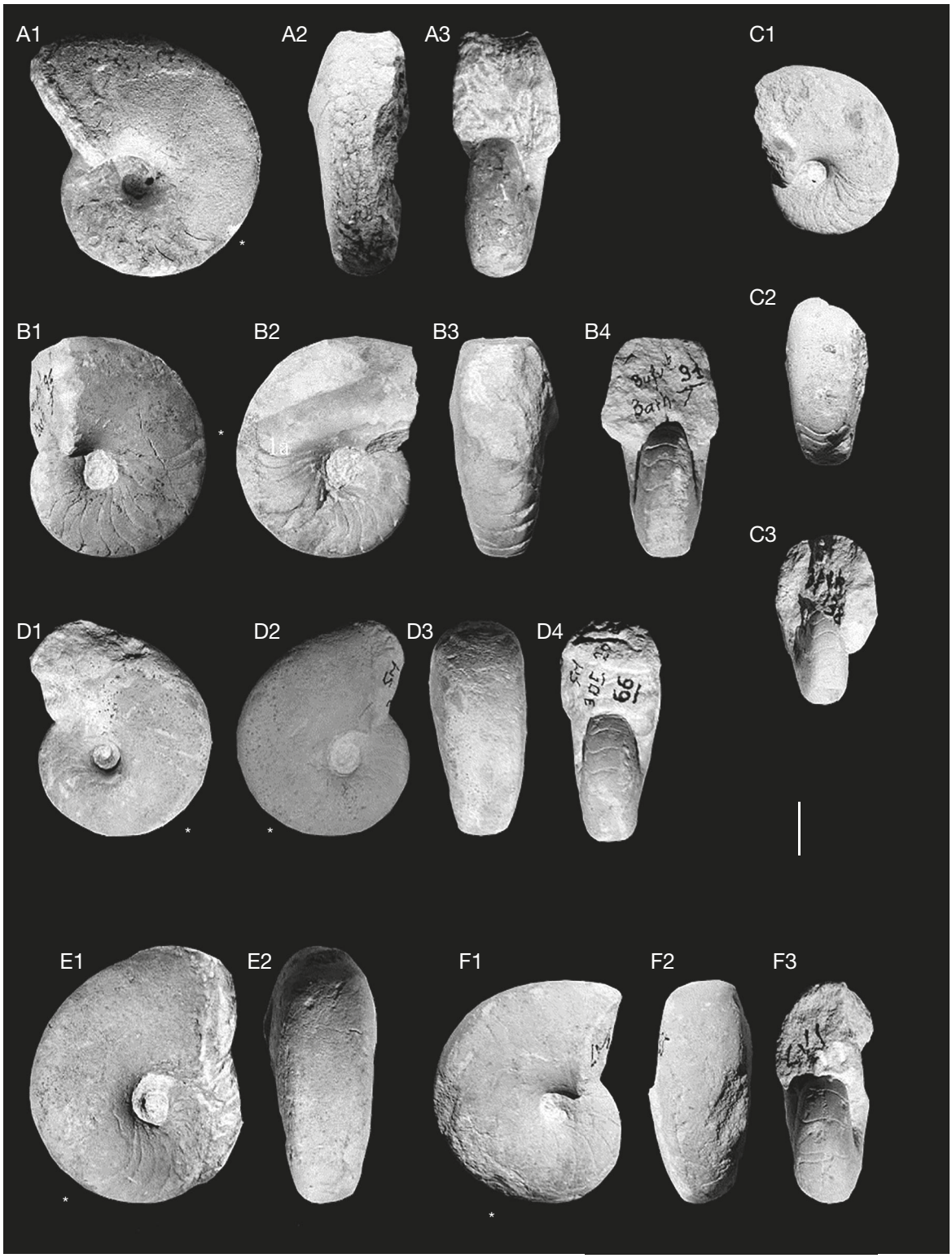
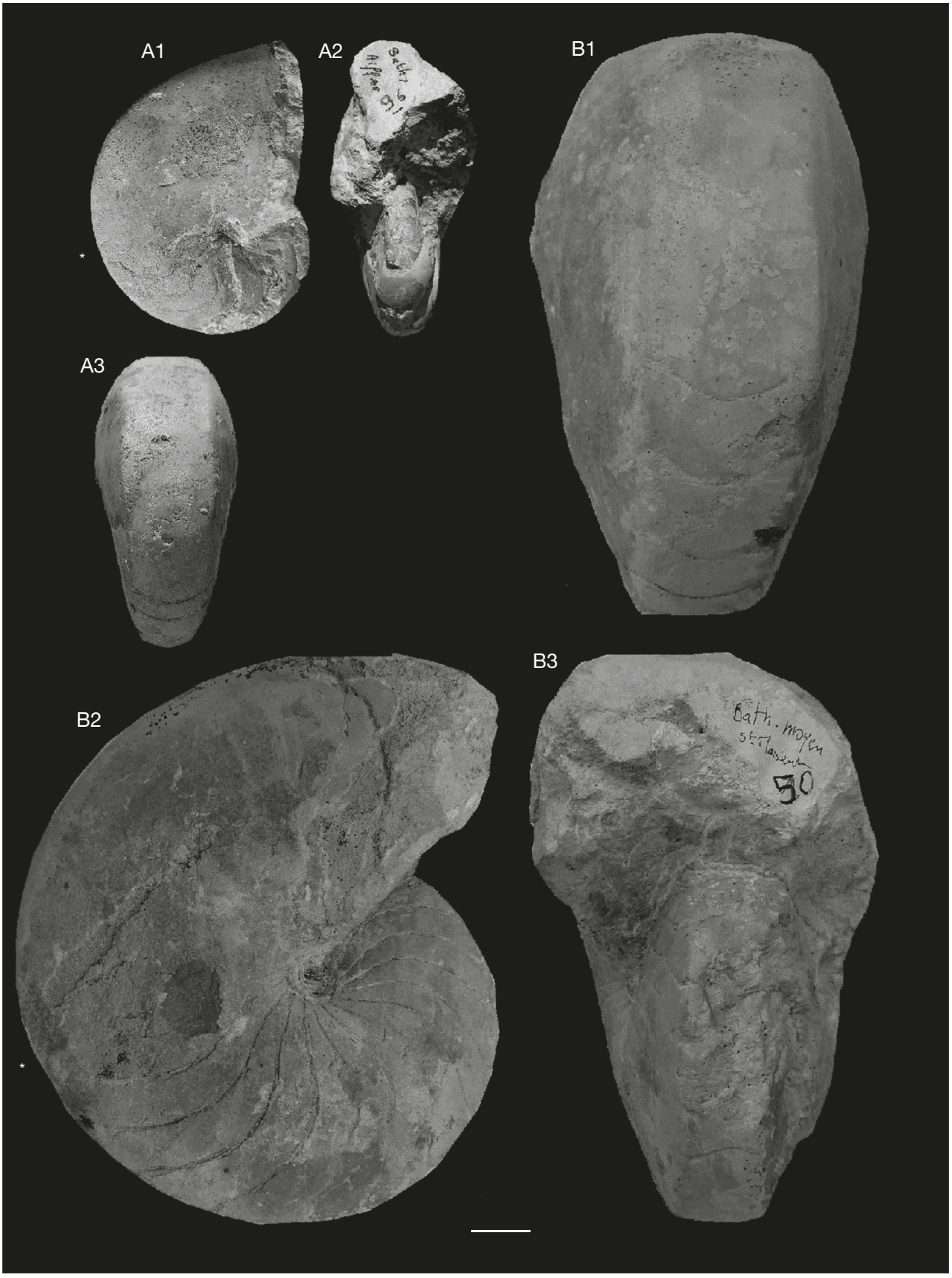
APPENDICES

Appendix 1. — *Micronautilus evolutus* n. gen., n. sp.: **A**, holotype 2021.BR.N.103, Buffevent quarry, bed 8, upper Bathonian, Retrocostatum Zone, Hannoveranus horizon; **B**, paratype 2021.BR.N.091, Buffevent quarry, top of bed 8, upper Bathonian, Retrocostatum Zone, Hannoveranus horizon; **C**, paratype 2021.BR.N.138, Buffevent quarry, bed 8, upper Bathonian, Retrocostatum Zone, Hannoveranus horizon. The smallest adult with approximated septas; **D**, paratype 2021.BR.N.066, Saint-Maixent-l'École, upper Bathonian, base of the Retrocostatum Zone; **E**, paratype 2021.BR.N.136, Buffevent quarry, bed 3, middle Bathonian, Bremeri Zone, Fortecostatum horizon; **F**, *Micronautilus minoti* n. gen., n. sp. paratype 2021.BR.N.135, les Hauts-de-Rochefort (Sainte-Éanne quarry), middle Bathonian, Progracilis Zone, Orbignyi horizon. An asterisk (*) marks the beginning of the body chamber. Scale bar: 1 cm.



Appendix 2. — *Pseudaganides* Spath, 1927 and *Pictonautilus* Branger, 2004 from Bathonian beds: **A**, 2021.BR.N.096, *Pseudaganides* sp. upper Bathonian, Retrocostatum Zone, Aiffres, Deux-Sèvres, adult specimen, D = 61 mm; H = 36 mm (h = 0.59); W = 32 mm (w = 0.52); O = 0; W/H = 0.88; **B**, 2021.BR.N.050, *Pictonautilus verciacensis* (Lissajous, 1923), middle Bathonian, Bremeri Zone, Saint-Maixent-l'École (Deux-Sèvres), sub-adult specimen, D = 110 mm; H = 58 mm (h = 0.52); W = 64 mm (w = 0.58); U = 7 mm (u = 0.06); W/H = 1.10. An asterisk (*) marks the beginning of the body chamber. Scale bar: 1 cm.



Appendix 3. — *Micronautilus minoti* n. gen., n. sp.: **A**, holotype 2021.BR.N.150, Les Lucs, municipality of Echiré, temporary exposure, lower Bathonian, Zigzag Zone; **B**, paratype 2021.BR.N.152, Trottebuie quarry, municipality of Mougon, bed 8, lower Bathonian, Zigzag Zone; **C**, paratype 2021.BR.N.095, Souché, municipality of Niort, temporary roadworks, lower Bathonian, Zigzag Zone; **D**, paratype 2021.BR.N.042, Trottebuie quarry, bed 8, lower Bathonian, Zigzag Zone. An asterisk (*) marks the beginning of the body chamber. Scale bar: 1 cm.