

Antaganides n. gen., a new genus
of Middle Jurassic nautiloid,
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with discussion on the phyletic origin
of the family Pseudonautilidae

Patrick BRANGER



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ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

***Antaganides* n. gen., a new genus of Middle Jurassic nautiloid, ancestor of *Pseudaganides* Spath, 1927, with discussion on the phyletic origin of the family Pseudonautilidae**

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Submitted on 15 December 2023 | accepted on 29 February 2024 | published on 3 October 2024

[urn:lsid:zoobank.org:pub:2C97C1BD-2DAA-485A-8AE0-2E3DD501D5F2](https://zoobank.org/pub:2C97C1BD-2DAA-485A-8AE0-2E3DD501D5F2)

Branger P. 2024. — *Antaganides* n. gen., a new genus of Middle Jurassic nautiloid, ancestor of *Pseudaganides* Spath, 1927, with discussion on the phyletic origin of the family Pseudonautilidae. *Geodiversitas* 46 (14): 471–493. <https://doi.org/10.5252/geodiversitas2024v46a14>. <http://geodiversitas.com/46/14>

ABSTRACT

An important collection of nautiloids from the Middle Jurassic of western France has enabled a revised understanding of the origin and evolutionary progression of the genus *Pseudaganides* Spath, 1927, a genus characterised by a particularly sinuous suture line. This study describes and introduces a new genus, *Antaganides* n. gen. at the origin of the family Pseudonautilidae. Progressive deepening of the lateral lobe and appearance of a laterodorsal saddle are the major elements of the evolutionary mode within this family. Of the species described herein, six are new. Three are related to *Antaganides* n. gen.: *A. sauvaleti* n. gen., n. sp., *A. fournieri* n. gen., n. sp. and *A. grulkei* n. gen., n. sp. Three further specimens are related to *Pseudaganides*: *P. aquitanense* n. sp., *P. buffeventi* n. sp. and *P. crechensis*. Results confirm the absence of a relationship with older folded-wall nautiloids such as the genus *Belmonticeras* Rulleau, 2008. The stratigraphical position of *Pseudaganides subbiangulatus* (d'Orbigny, 1850) is questioned and for this species, a case of sexual dimorphism is considered with *P. dimidiatus* (Marchand & Tintant 1971). From a palaeobiogeographic viewpoint, it appears that the *Antaganides* n. gen.-*Pseudaganides* lineage first evolved on the north-western margin of the Tethyan Ocean before migration into the Indo-Malagasy domain at the beginning of the Callovian.

RÉSUMÉ

Antaganides n. gen., un genre nouveau de nautiloïde du Jurassique moyen, ancêtre de *Pseudaganides* Spath, 1927, avec une discussion sur l'origine phylétique de la famille des Pseudonautilidae.

Une importante collecte de nautilites dans les assises du Jurassique Moyen de l'ouest de la France a permis d'établir l'origine et le mode d'évolution du genre *Pseudaganides* Spath, 1927, genre caractérisé par une ligne de suture cloisonnaire particulièrement sinueuse. Cette étude conduit à décrire un genre nouveau, *Antaganides* n. gen. qui serait à l'origine de la famille des Pseudonautilidae. L'approfondissement progressif du lobe latéral et l'apparition d'une selle latéro-dorsale constituent les éléments majeurs du mode évolutif à l'intérieur de ce groupe. Parmi les espèces décrites, six sont nouvelles. Trois se rapportent à *Antaganides* n. gen.: *A. sauvaleti* n. gen., n. sp., *A. fournieri* n. gen., n. sp. et *A. grulkei* n. gen., n. sp. Trois autres sont attribuées à *Pseudaganides*: *P. aquitanense* n. sp., *P. buffeventi* n. sp. et *P. crechensis*. Nos résultats confirment l'absence de parenté avec les nautilites à cloisons plissées plus anciens comme ceux du genre *Belmonticeras* Rulleau, 2008. La position stratigraphique de *Pseudaganides subbiangulatus* (d'Orbigny, 1850) est remise en question et, pour cette espèce, un cas de dimorphisme sexuel est envisagé avec *P. dimidiatus* (Marchand & Tintant 1971). D'un point de vue paléobiogéographique, il apparaît que la lignée *Antaganides* n. gen.-*Pseudaganides* aurait d'abord évolué sur la marge nord-ouest de l'océan téthysien avant de gagner le domaine indo-malagache au début du Callovien.

KEY WORDS

Jurassic,
Bajocian,
Bathonian,
Callovian,
Nautilida,
biostratigraphy,
cephalopods,
evolution,
new combination,
new genus,
new species.

MOTS CLÉS

Jurassique,
Bajocien,
Bathonien,
Callovien,
Nautilida,
biostratigraphie,
céphalopodes,
évolution,
combinaison nouvelle,
genre nouveau,
espèces nouvelles.

INTRODUCTION

Pseudaganides Spath, 1927 constitutes a distinct and easily recognizable genus among Jurassic nautiluses, characterized by its s-shaped, goniatic, suture lines. It is widely represented within Middle and upper Jurassic strata from the Tethyan province, mainly in Europe but also in India (Waagen 1875; Spath 1927; Halder 2000) and Madagascar (personal data). Spath (1927) erected this genus to include also the few Lower and Middle Jurassic species bearing such suture lines. The genus is later included within the family Pseudonautilidae Shimansky & Erlanger, 1955, opinion followed by Kummel (1956). More recently, Rulleau (2008) described *Belmonticeras* Rulleau, 2008 and included Toarcian to Bajocian specimens of larger size that were previously interpreted as the ancestors of *Pseudaganides* (Tintant & Kabamba 1983).

To date, according to this restricted definition, the oldest specimen of *Pseudaganides* was the specimen described and figured by Alcide d'Orbigny (1842: 160, pl. 134, fig. 1-3). This species, *Pseudaganides subbiangulatus*, whose lectotype (MNHN.FR54480) is stored in the Muséum national d'Histoire naturelle in Paris, has been revised by Marchand & Tintant (1971). The specimen is quite large for the genus (136 mm) and shows the typical s-shaped suture lines with deep lateral lobes. This fossil was collected by Mr. Cabannet (d'Orbigny 1850) in the region of Nantua (French Jura) and, until present, is the only known representative of this species. D'Orbigny gave this specimen a Bathonian age and, according to Mangold's opinion, Marchand & Tintant (1971) supposed that it to have come from the *Retrocostatum* Zone of the Upper Bathonian. No other specimen or species of *Pseudaganides* has ever been cited from Bathonian strata since d'Orbigny's publication. In contrast, typical *Pseudaganides* become common within the Callovian (Marchand & Tintant 1971) and overlying Upper Jurassic strata (von Loesch 1914; Marchand & Tintant 1971; Tintant 1984; Tintant *et al.* 2002; Jain *et al.* 2023).

The aim of this paper is to present part of the results of more than four decades of investigations on the Middle Jurassic strata of Western France, from the Aalenian to Callovian. Nautiloids are far less abundant than ammonites but extensive searching has provided the opportunity to collect adequate examples to provide a good overview of this family during this period. Among this fossil assemblage, large specimens belonging to the taxa *Cenoceras s.l.*, *Digonioceras* Hyatt, 1894 and *Ophionautilus* Spath, 1927 dominate (Branger 2004). Beside this, especially within Bathonian levels, smaller forms are present: the first with sharp ventral ridges assigned to a new genus, *Pictonautilus* Branger, 2004, a second, *Micronautilus* Branger, 2023 and a third that presents some morphological similarities with the genus *Pseudaganides*, but without its typically folded suture lines. In this region, the first *Pseudaganides* occurs at the top of the Bathonian and becomes increasingly common within the Callovian. This frequency contrasts with the almost total lack of *Belmonticeras* Rulleau, 2008 within older strata. This situation initiated the search for a hypothetical link between these two genera. Despite an extensive searching within the underlying rocks only a single example and one small *Belmonticeras* was found in the Lower Bajocian (*Laeviuscula* Zone),

but no *Pseudaganides*. The origin of *Pseudaganides* is likely to be found within this group of small nautiloids all of which display similar morphology. They are described herein by the introduction of a new genus and three new species. It is the opportunity to clarify the phyletic relationship between *Pseudaganides* and unravel its phylogeny.

From another perspective, despite extensive searching no specimens of *Pseudaganides subbiangulatus* (d'Orbigny, 1850) from the Upper Bathonian were found. From this level only small specimens with slightly folded septa occur that clearly belong to another *Pseudaganides* species. Early Callovian *Pseudaganides* differs from *Pseudaganides subbiangulatus* and are considered a separate new species.

MATERIAL AND METHODS

This study is based on large collections made by the author employing high-precision biostratigraphical methods over a period in excess of forty years in the Jurassic strata of Western France. Fossils described herein have been collected within an accurate biochronological framework based on ammonites from the Submediterranean Realm (Cariou & Hantzpergue in G.F.E.J. 1997). Quarries and temporary sections throughout the well-known Jurassic outcrops in Western France provided the material for this research (Fig. 1). Buffevent quarry (46°20'28"N, 0°30'21"W; POC0009) in Branger (2009), Trottebuie (46°25'37"N, 0°12'28"W) (Énay *et al.* 2012) and les Hauts-de-Rochefort quarry at Sainte-Éanne (46°23'30"N, 0°07'55"W; NAQ0021) (Branger 1989) were investigated in close detail. Other localities, Niort (46°18'25"N, 0°27'42"W); les Lucs, municipality of Échiré (46°21'30"N, 0°25'37"W); la Crèche (46°21'08"N, 0°17'58"W); Chaban de Chauray (46°21'08"N, 0°17'58"W); Salles (46°23'45"N, 0°06'19"W); A83 highway trench at the Viaduc de l'Égray (46°25'25"N, 0°27'28"W) (Gauthier *et al.* 2002); Aiffres (46°18'07"N, 0°26'07"W); Bougon (46°21'18"N, 0°03'11"W); les Maisons-Blanches, near Limalonges (46°08'15"N, 0°10'28"E); Pamproux (46°23'43"N, 0°3'0"W; POC0015). These localities have been extensively scrutinized in addition to a small number of specimens from la Grève quarry (46°57'19"N, 0°01'38"W) near Saint-Laon, Vienne département, and Montreuil-Bellay (47°06'37"N, 0°06'14"W), Maine-et-Loire département.

MEASUREMENTS AND RATIOS

The measurements of nautilid conchs employed here follow those of Tintant (1984), namely (Fig. 2): shell diameter (D), whorl height (H), whorl width (W) and width of the umbilical area (U). Different ratios have also been used to compare the fossils: $h = H/D$; $w = W/D$; $u = U/D$, E/H . In addition, the depth (P) and the width (L) of the lateral lobe of the suture lines have also been estimated. All these measures are presented graphically (Figs 5-9).

A number of shells have been identified as adults. This assertion is based on a comparison with mature modifications seen in shells of recent nautilids as described by Collins & Ward (1987) and summarized by Klug (2004). The clearest indicator is septal crowding (approximation) at the end of

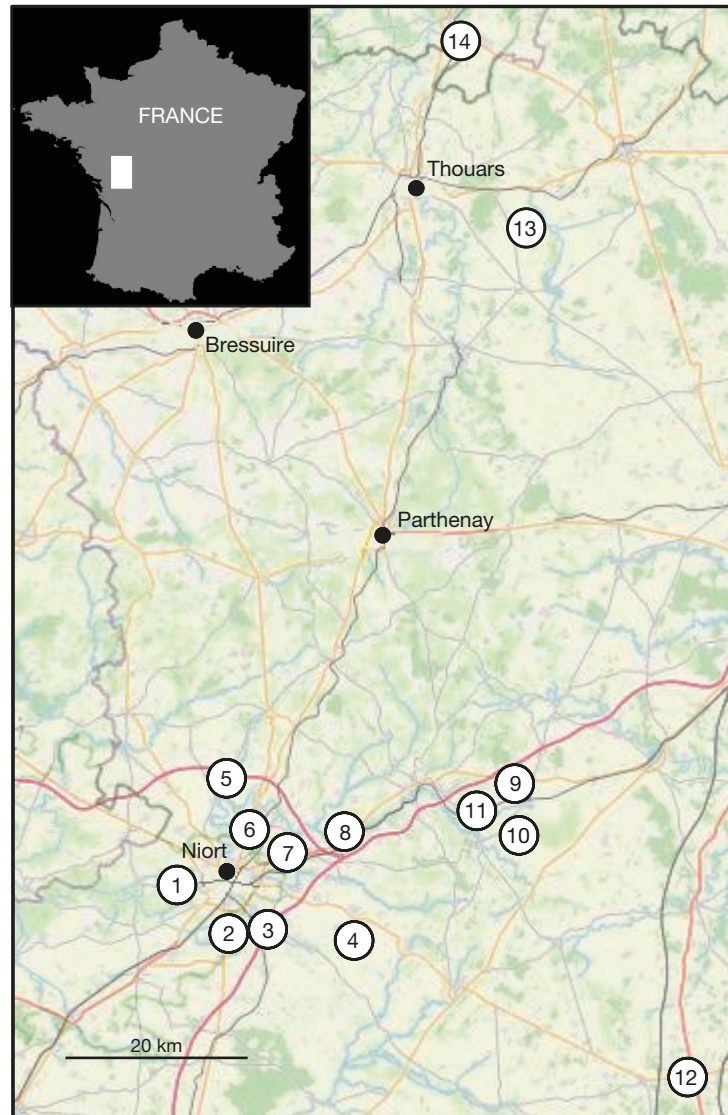


FIG. 1. — Geographical map reporting the position of the localities that provided specimens of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927: 1, Buffevent quarry; 2, Niort; 3, Aiffres; 4, Trotte-buie quarry; 5, A83 highway trench at Viaduc de l'Égray; 6, Les Lucs (Échiré); 7, Chaban-de-Chauray; 8, La Crèche; 9, Salles; 10, Bougon; 11, Les Hauts-de-Rochefort quarry; 12, Les Maisons-Blanches; 13, La Grève quarry near Saint-Laon; 14, Montreuil-Bellay.

the phragmocone and a change in coiling with reduction of relative whorl height accompanied by rounding of the venter.

All specimens from P. Branger's collection are stored at the Musée Bernard d'Agesci in Niort (France) (MBAN).

SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1798

Subclass NAUTILIA Wade, 1988

Order NAUTILIDA Agassiz, 1847

Superfamily NAUTILACEAE de Blainville, 1825

Family PSEUDONAUTILIDAE Shimansky & Erlanger, 1955

Genus *Antaganides* n. gen.

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DIAGNOSIS. — Small sized shells, maximum around 60 mm or less at adult stage, compressed, showing a wide shallow lateral lobe and a shallow ventral lobe. Septa moderately spaced, 8 to 9 chambers are present for half a whorl. Flanks slightly rounded and venter flattens on the body-chamber. Most species possess a closed umbilicus except as juveniles. When visible, the siphuncle is close to the venter.

TYPE SPECIES. — *Antaganides fournieri* n. sp. (Fig. 3C1-C3).

COMPOSITION OF THE GENUS. — Four nominal species are assigned to this new genus, *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb. from the Upper Bajocian, *Niortense* Zone, *Antaganides sauvageti* n. gen., n. sp. from the Lower Bathonian, *Zigzag* Zone, *Antaganides fournieri* n. gen., n. sp. from the Middle Bathonian, *Progracilis* and *Bremeri* Zones and *Antaganides grulkei* n. gen., n. sp. from the same level. None of the new species described here has previously been reported or figured by any author.

ETYMOLOGY. — Genus *Aganides*, the first name given by Spath to the group of *Nautilus kutchensis* Waagen, 1873, later transformed into *Pseudaganides* due to preoccupation of the name, combined with the prefix “ante” meaning “before”.

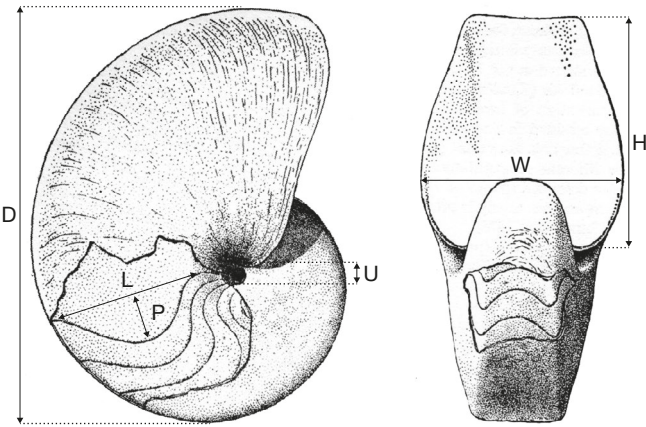


FIG. 2. — Dimensional characteristics measured in this study, drawing from Dzik (1984).

OCCURRENCE. — To date, *Antaganides* n. gen. has been recorded from Upper Bajocian and Bathonian.

REMARKS

Due to its small relative size and compressed shell shape, *Antaganides* n. gen. cannot be mistaken with any other contemporaneous Middle Jurassic nautilids. From the Inferior Oolite Formation, Crick (1898) described two small sized species, *Cenoceras fuscum* (Crick, 1898) and *Cenoceras bradfordensis* (Crick, 1898). These species are also reported from the Upper Bajocian (Chirat 1997). *Cenoceras fuscum* differs by its more robust section, its well-marked angular margins, and a different aperture (see Chirat 1997: pl. 5, figs 4-5) and the umbilicus is more open. *Pictonautilus* Branger, 2004 of Bathonian age has the same characteristics. *Cenoceras bradfordensis* is closer to *Antaganides* n. gen., a little larger and a little older. For this species, Crick (1898) recognized two morphospecies, one with a compressed shell and another with a more inflated section. He considered this difference to be due to sexual dimorphism. *Cenoceras bradfordensis* could be an ancestor of *Antaganides* n. gen. but further studies will clarify if this species should be integrated into the new genus. The closest genus to *Antaganides* n. gen. is represented by *Pseudaganides*, with many morphological similarities: h, w, u, W/H (Figs 5-8). The ratio “h” of the height of the whorl compared with the diameter of the shell (H/D) among the different species of *Antaganides* n. gen. and *Pseudaganides* is about 0.6, and is fairly constant (Fig. 5). The ratio “w” of the width of the whorl compared with the diameter of the shell (W/D) varies from 0.4 to 0.6 within the two genera (Fig. 6). The umbilical width compared with the diameter of the shell ($U/D = “u”$) is always very low, from 0 to 0.1 except for one *Pseudaganides* species (Fig. 7). The individuals of both genera are relatively compressed, W/H varies between 0.7 and 1, sometimes a little less (Fig. 8). The main difference consists in the shape of the septal suture lines which is particularly folded on the whole shell of *Pseudaganides* (Figs 4; 9).

TABLE 1. — Measurements (D, H, W, U, P, L, in mm) for *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N117	54	33	0.6	29	0.53	0	0	0.87	3	18	16
	34	19	0.55	16	0.47	0	0	0.84	—	—	—
2023.PB.N129	52	32	0.61	31	0.59	0	0	0.96	4	15	20
	39	25	0.66	20	0.51	0	0	0.8	—	—	—

Antaganides cf. *erycinus* (Tagliarini, 1901), n. comb.
(Figs 3A1-A3; 13A, B)

Nautilus erycinus Tagliarini, 1901: tav. V, pl. 2-3-4-5.

?*Cenoceras* sp. 1 aff. *bradfordensis* – Chirat 1997: pl. 6, fig. 4a, b.

?*Cenoceras* aff. *bradfordensis* – Chirat 1997: pl. 14, figs 4-5, pl. 15, fig. 1.

MATERIAL EXAMINED. — **France** • 2 specimens; Nouvelle-Aquitaine, Parthenay, Sainte-Ouene, Viaduc de l’Égray; [46°25’25”N, 0°27’28”W]; *Niortense* Zone; level 32; Upper Bajocian; Patrick Branger leg.; MBAN; 2023.PB.N117 (Fig. 3A1-A3), 2023.PB.N130 • 2 specimens; Nouvelle-Aquitaine, Niort; [46°18’25”N, 0°27’42”W]; *Niortense* Zone; Upper Bajocian; Patrick Branger leg.; MBAN; 2023.PB.N129 and 2023.PB.N148 (Fig. 13A, B).

OCCURRENCE. — Upper Bajocian, *Niortense* Zone, *Polygynalis* Subzone.

MEASUREMENTS. — See Table 1.

DESCRIPTION

Small sized nautilus, maximum diameter 55 mm, the diameters of specimens 2023.PB.N117 (Fig. 3A1-A3) and 2023.PB.N130 are 52 and 54 mm respectively. Shell compressed on the last whorl with an oval section except on the body-chamber where the venter flattens. Height rapidly increasing. Juvenile whorls have a subrectangular section with flattened flanks except at the very end of the body-chamber where they are slightly inflated, boarding a closed umbilicus. The aperture is well preserved on 2023.PB.N117 (Fig. 3A1-A3) and is similar to that of *Pseudaganides*. Suture line (Fig. 4A) has wide shallow lateral and ventral lobes. The siphuncle is small in diameter, located on the ventral half of the septa, at about one third of the median height of the whorl. On 2023.PB.N129, the two last septa of the phragmocone are approximated, indicating an adult stage. This specimen has also kept the muscle scar on its left side (Fig. 13A).

REMARKS

The cited specimens are similar to the examples published under the name *Nautilus bradfordensis* (Crick, 1898) by Chirat (1997) from the *Garantiana* and *Parkinsoni* Zones that also belong to Upper Bajocian. The type specimen of *Antaganides erycinus* n. comb. is a little older and occurred within the dark grey limestone formation (calcare grigio scuro) near Erice, Western Sicily, whose age is Lower Dogger according to Tagliarini (1901), equating to the Upper Aalenian and Lower Bajocian.

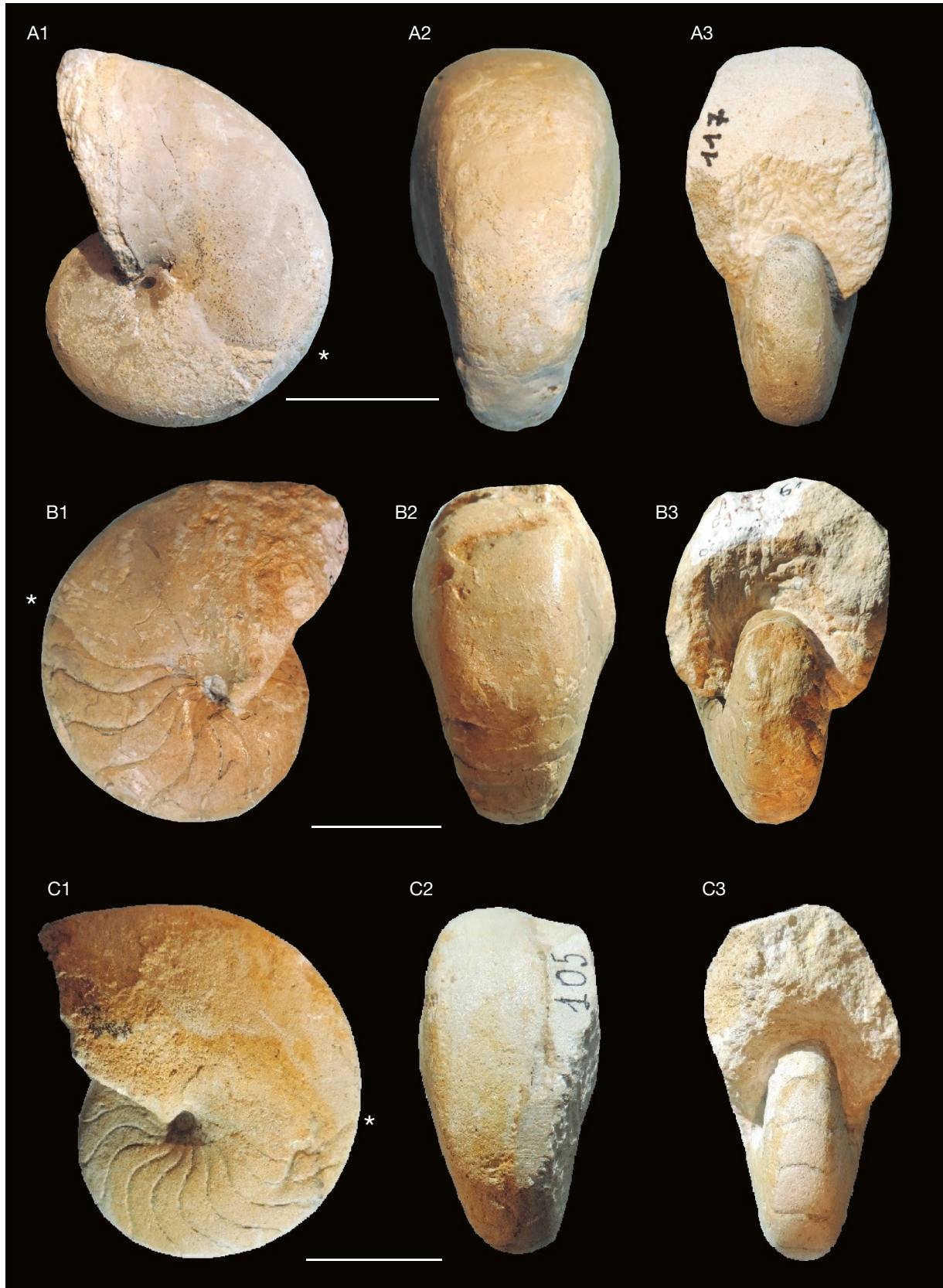


FIG. 3. — **A1-A3**, *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb., specimen 2023.PB.N117, bed 32, viaduc de l'Égray, Upper Bajocian, *Niortense* Zone; **B1-B3**, *Antaganides sauvageti* n. gen., n. sp., holotype (2023.PB.N64), viaduc de l'Égray, Lower Bathonian, *Zigzag* Zone; **C1-C3**, *Antaganides fourmieri* n. gen., n. sp., holotype (2023.PB.N105), adult shell, les Hauts-de-Rochefort quarry, Middle Bathonian, *Progracilis* Zone. *, end of the phragmocone. Scale bars: 2 cm.

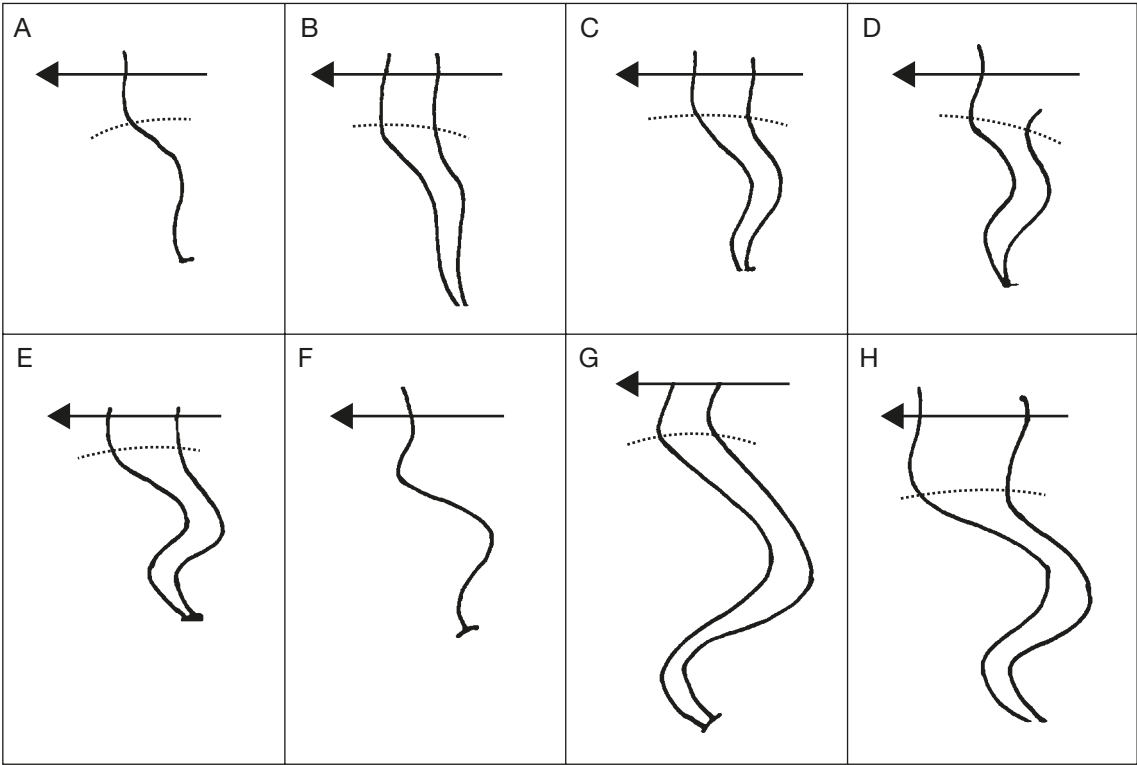


FIG. 4. — Suture lines of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927: **A**, *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb., 2023.PB.N117; **B**, *Antaganides sauvageti* n. gen., n. sp. 2023.PB.N64; **C**, *Antaganides fourmieri* n. gen., n. sp., 2023.PB.N105; **D**, *Pseudaganides aquitanense* n. sp., 2023.PB.N96; **E**, *Pseudaganides buffeventi* n. sp., 2023.PB.N76; **F**, *Pseudaganides crechensis* n. sp., 2023.PB.N107; **G**, *Pseudaganides subbiangulatus* (d'Orbigny, 1850), 2023.PB.N73, Patina Zone; **H**, *Pseudaganides subbiangulatus*, 2023.PB.N112, Anceps Zone.

TABLE 2. — Measurements (D, H, W, U, P, L, in mm) for *Antaganides sauvageti* n. gen., n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N64	61	37	0.6	37	0.6	0	0	1	3.5	22	15
	45	28	0.62	26	0.57	0	0	0.92	2	14	14
2023.PB.N93	42	24	0.57	22	0.52	3.5	0.08	0.91	3	19	15
	31	19	0.61	17	0.54	3	0.09	0.89	2.5	14	17
2023.PB.N127	36	23	0.61	22	0.61	2.8	0.07	0.95	—	—	—
2023.PB.N128	27.5	16	0.58	16	0.58	1.5	0.05	1	—	—	—
	21	12	0.57	11.8	0.57	1.4	0.06	1	—	—	—

Antaganides sauvageti n. gen., n. sp.
(Fig. 3B1-B3)

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DIAGNOSIS. — Small nautilus, maximum diameter about 60 mm, shell compressed with an oval section on inner whorls. On the adult body-chamber, the venter flattens. The umbilicus is open on the juvenile but very small. Suture lines with a wide but shallow lateral lobe.

ETYMOLOGY. — After the name of Henri Sauvaget, teacher in Niort, involved in the Museum of Natural History of this town at the beginning of the XXth century and donator of his paleontological collection to this Museum.

TYPE MATERIAL. — **Holotype.** France • 1 specimen; Nouvelle-Aquitaine, Parthenay, Sainte-Ouene, Viaduc de l'Égray; [46°25'25"N, 0°27'28"W]; Zigzag Zone, layer "Banc Pourri"; Lower Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N64 (Fig. 3B1-B3).

OTHER SPECIMENS EXAMINED. — **France** • 1 specimen; Nouvelle-Aquitaine, Aigondigné, Mougou, "Trotte-Buie" (POC0102); [46°25'37"N, 0°12'28"W]; Zigzag Zone, layer "Banc Pourri"; Lower Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N93 • 1 specimen; Nouvelle-Aquitaine, Niort; [46°18'25"N, 0°27'42"W]; Zigzag Zone, layer "Banc Pourri"; Lower Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N127 • 1 specimen; Nouvelle-Aquitaine, Échiré; [46°21'30"N, 0°25'37"W]; Zigzag Zone, layer "Banc Pourri"; Lower Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N128.

TYPE LOCALITY AND STRATUM TYPICUM. — All the specimens come from a layer called regionally "Banc Pourri" that corresponds to the Zigzag Zone of the Lower Bathonian, especially at the Viaduc de l'Égray where the holotype is coming from.

MEASUREMENTS. — See Table 2.

DESCRIPTION
Small shells, around 60 mm in diameter, very involute with a closed or slightly open umbilicus. The type specimen is an adult form displaying approximation of the last two septa. The shell is compressed in the inner whorls and widens on the body-chamber that is always higher than wide. The section of the whorls is trapezoidal and flanks are slightly

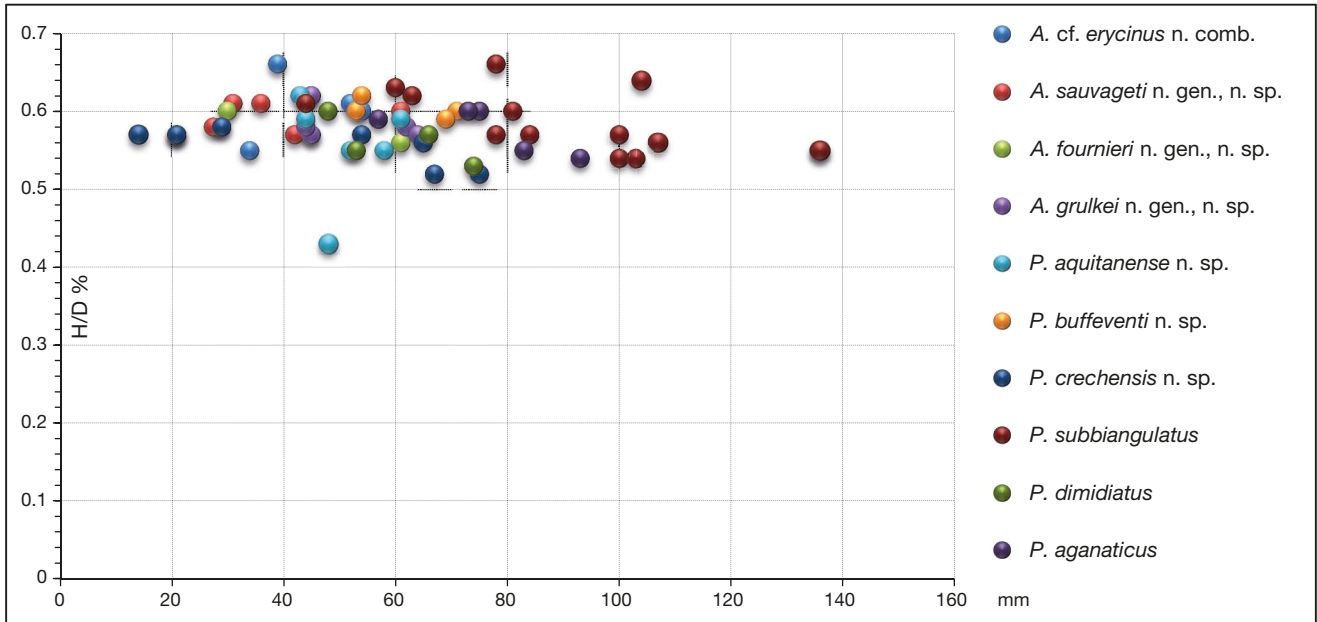


FIG. 5. — Ratio “h” of the height of the whorl compared with the diameter of the shell (H/D) among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927.

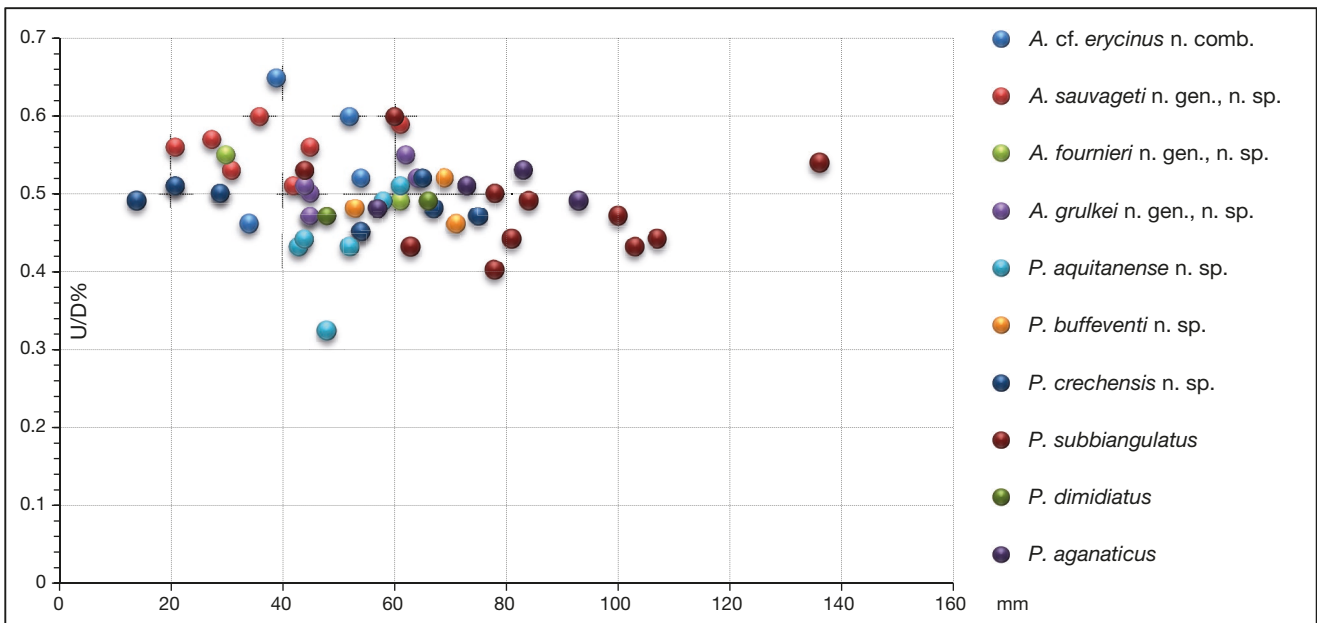


FIG. 6. — Ratio “w” of the width of the whorl compared with the diameter of the shell (W/D) among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927.

rounded. The maximum width is close to the umbilicus, at about $\frac{1}{3}$ of the height of the whorl. Umbilical area is rounded with a perpendicular coiling to the proceeding whorl. The ventral part is limited by rounded shoulders that become more angular but never sharp on the body-chamber. Venter is rounded, flattened on the body-chamber where it can become slightly concave. Suture line (Fig. 4B) shows a wide, shallow lateral lobe and a ventral lobe too.

The aperture is partly broken but the dorsal part seems to be similar to these of *Pseudaganides*.

REMARKS

In Western Europe, Lower Bathonian beds are usually very fossiliferous but no similar species has ever been described. Compared with *Antaganides* cf. *erycinus* n. comb., the shell of *A. sauvageti* n. gen., n. sp. is a little larger and thicker at adult age.

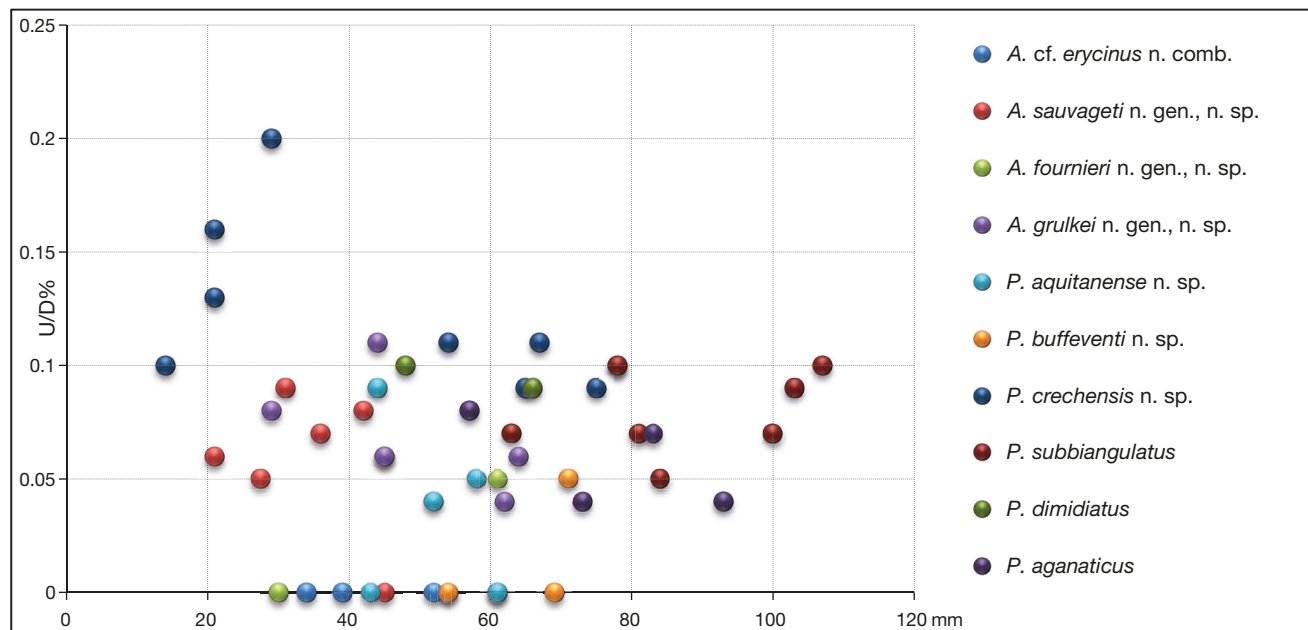


FIG. 7. — Ratio “u” of the umbilical width compared with the diameter of the shell (U/D) among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927.

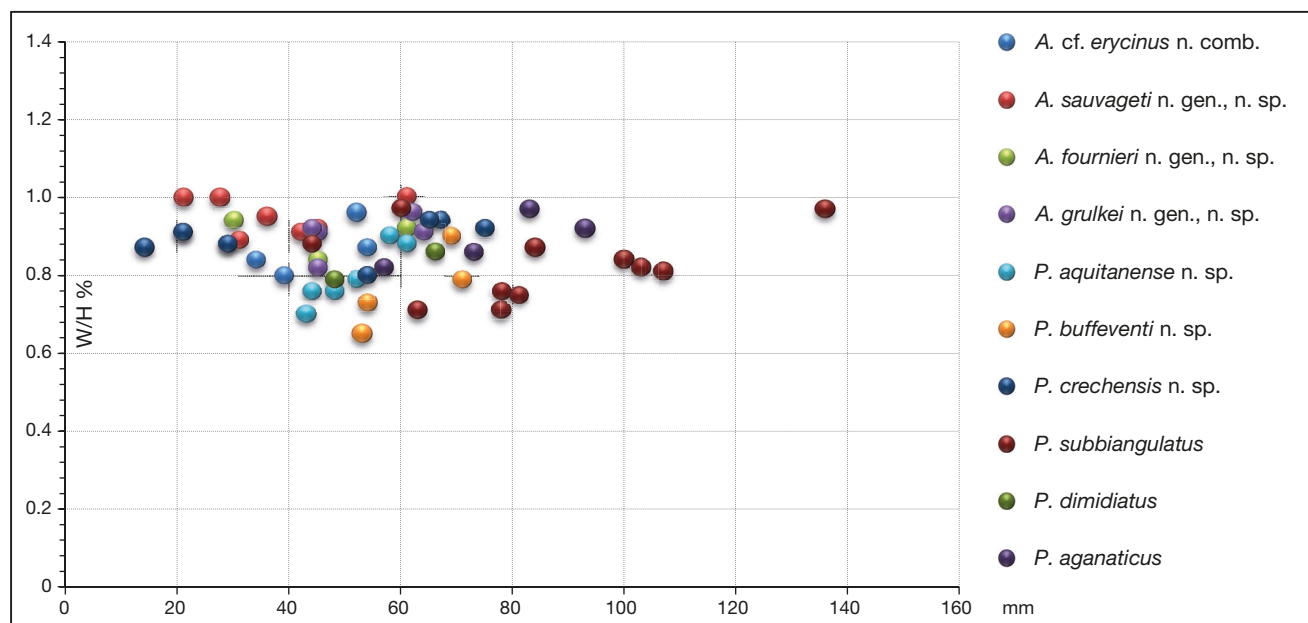


FIG. 8. — Ratio “W/H” of the shell among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927.

Antaganides fournieri n. gen., n. sp.
(Fig. 3C1-C3)

[urn:lsid:zoobank.org:act:48BF9FDC-A9CE-4E62-880D-A58A7C192254](https://zoobank.org/act:48BF9FDC-A9CE-4E62-880D-A58A7C192254)

DIAGNOSIS. — Small sized nautilus, maximum diameter about 60 mm, shell rather compressed on the last whorl with an oval section except on the body-chamber where the venter flattens, sometimes concave. Narrow umbilicus. Suture lines with a wide but shallow lateral lobe.

ETYMOLOGY. — After the name of Alphonse Fournier (1858-1911), surgeon and former preparator at the Museum of Natural History in Niort and, later, at the Faculté des Sciences in Poitiers.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (complete); Nouvelle-Aquitaine, Sainte-Eanne, near la Mothe-Saint-Héray, les Hauts-de-Rochefort quarry (NAQ0021); [46°23'30"N, 0°07'55"W]; Base of *Progracilis* Zone, *Orbigny* Subzone; Middle Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N105 (Fig. 3C1-C3).

OTHER SPECIMEN EXAMINED. — France • 1 specimen (phragmocone); Nouvelle-Aquitaine, La Crèche; [46°21'08"N, 0°17'58"W]; Middle Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N109.

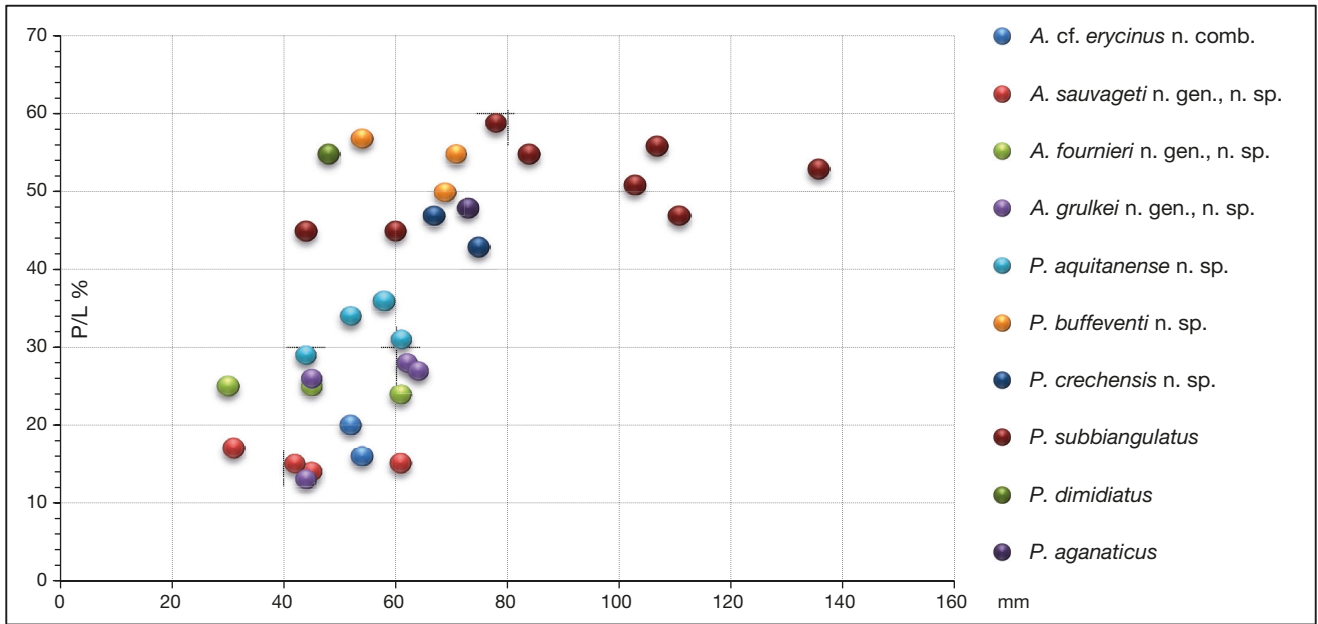


FIG. 9. — Ratio “P/L” of the depth of the width of the lateral lobe compared with its width among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927.

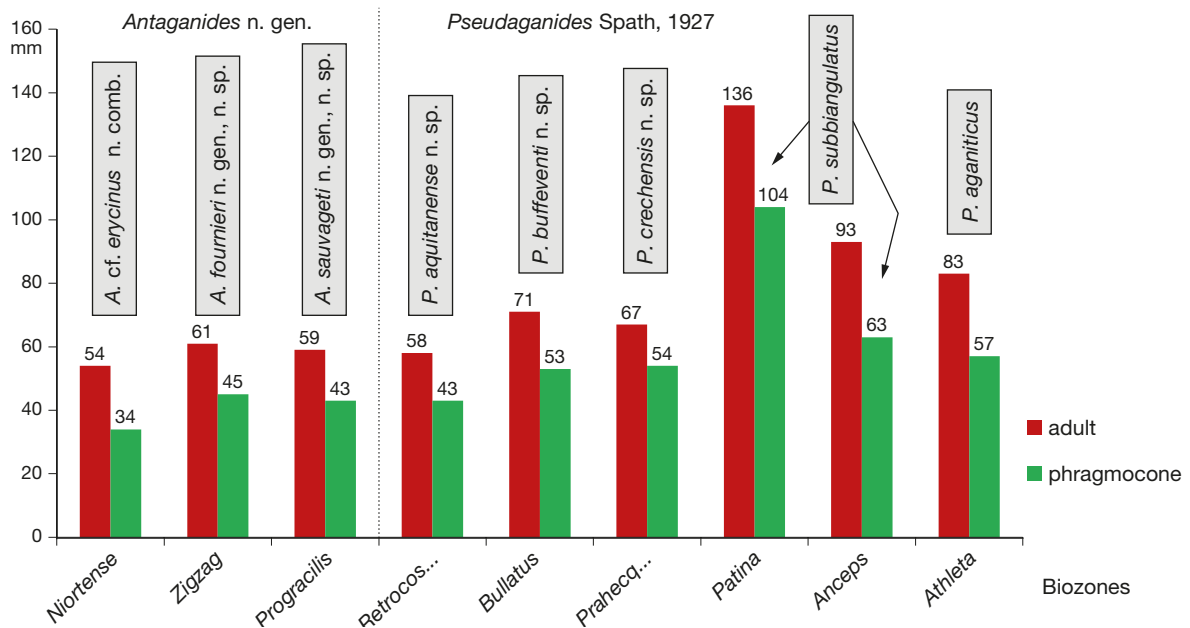


FIG. 10. — Evolution of the size of the adult shell and phragmocone among the different species of *Antaganides* n. gen. and *Pseudaganides* Spath, 1927 for full grown shells.

TYPE LOCALITY AND STRATUM TYPICUM. — *Antaganides fourrieri* n. gen., n. sp. has only been found within the Middle Bathonian of the Submediterranean Realm. The holotype has been found at the base of the *Progracilis* Zone, *Orbigny* Subzone, at les Hauts-de-Rochefort quarry (Sainte-Eanne, France). The species persists until the *Bremeri* Zone, *Fortecostatum* Subzone.

MEASUREMENTS. — See Table 3.

DESCRIPTION

The type specimen is a complete shell, broken on the right side of the body-chamber. The two last septa are slightly

approximated indicating an adult stage. The size of the shell is quite small as for other *Antaganides* n. gen. species, around 60 mm (Fig. 10). The phragmocone is compressed ($W/H = 0.84$) with a subrectangular section. The flanks and the venter are slightly rounded. The body-chamber is more inflated ($W/H = 0.92$) with a maximum width close to the umbilicus at about $\frac{1}{3}$ of the flank. The external part of the shell is rather depressed while the venter is flattening. The umbilical shoulder is rounded whereas the ventral shoulder becomes angular, but never sharp, on the body-chamber. On the first

TABLE 3. — Measurements (D, H, W, U, P, L, in mm) for *Antaganides fournieri* n. gen., n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N105	61	34.5	0.56	32	0.5	3	0.05	0.92	6	25	24
	45	26	0.57	22	0.48	3	0.06	0.84	4	12	25
2023.PB.N109	30	18	0.6	17	0.56	0	0	0.94	4	12	25

quarter of the last whorl, close to the umbilicus, suture line of *Antaganides fournieri* n. gen., n. sp. (Fig. 4C) shows a faint lateral saddle followed by a shallow but well-marked lateral lobe. Close to the umbilicus, last septa are backward projected and do not show any lateral saddle. A shallow ventral lobe is present at any stage.

REMARKS

Antaganides fournieri n. gen., n. sp. size and shape are very similar to *Antaganides sauvageti* n. gen., n. sp. that is a little older. The main difference can be observed on the suture lines, *Antaganides fournieri* n. gen., n. sp. shows a dorsal saddle on the inner whorls and the lateral lobe is deeper than on older *Antaganides* n. gen. species. *Antaganides fournieri* n. gen., n. sp. could also be confused with *Antaganides grulkei* n. gen., n. sp., a nautilus of the same size that seems to be a little more abundant at the same level. By this latter, the shape of the umbilicus shows a gentle slope whereas *Antaganides fournieri* n. gen., n. sp. owns a subvertical umbilical wall.

Antaganides grulkei n. gen., n. sp.
(Fig. 11A, B)

[urn:lsid:zoobank.org:act:6971C0AB-C1CA-44EF-8109-2E5D67A2D8BD](https://zoobank.org/act:6971C0AB-C1CA-44EF-8109-2E5D67A2D8BD)

Nautilus cf. *fuscus* – Lissajous 1923: 48, pl. II, fig. 2-2a.

DIAGNOSIS. — Small sized nautilus, maximum diameter 65 mm, shell rather compressed on the last whorl with an oval section except on the body-chamber where the venter flattens. Umbilicus closed. Suture lines with a wide and shallow lateral lobe.

ETYMOLOGY. — *Antaganides grulkei* n. gen., n. sp. is dedicated to Wolfgang Grulke, Sherborne, United Kingdom, who made a world-wide promotion for nautiloids studies through his magnificent book “*Nautilus, the Beautiful Survivor*” (Grulke 2016). Doing this work, he gave us the opportunity to meet or to discuss with most of the specialists of the world.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (complete); Nouvelle-Aquitaine, Sainte-Éanne, near la Mothe-Saint-Héray, les Hauts-de-Rochefort quarry (NAQ0021); [46°23'30"N, 0°07'55"W]; Base of the *Progracilis* Zone, *Orbigny* Subzone; Middle to Upper Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N97 (Fig. 11A, B).

OTHER SPECIMENS EXAMINED. — **France** • 1 specimen (complete); same data as holotype; 2023.PB.N133 • 1 specimen (complete, body-chambers poorly preserved); Nouvelle-Aquitaine, La Crèche, Champs-Albert; [46°21'08"N, 0°17'58"W]; base of the *Retrocostatum* Zone; Upper Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N134.

TABLE 4. — Measurements (D, H, W, U, P, L, in mm) for *Antaganides grulkei* n. gen., n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N97	62	36.5	0.58	35	0.56	3	0.04	0.96	6	21	28
	45	26	0.57	22	0.48	4	0.06	0.91	–	–	–
2023.PB.N133	64	37	0.57	34	0.53	4	0.06	0.91	6	22	27
	45	28	0.62	23	0.51			0.82	5	19	26
2023.PB.N134	44	25	0.58	23	0.52	5	0.11	0.92	2	15	13
	29	17	0.58	15	0.51	2.5	0.08	0.88	–	–	–

TYPE LOCALITY AND STRATUM TYPICUM. — *Antaganides grulkei* n. gen., n. sp. has been mostly encountered within the Middle Bathonian of the Submediterranean Realm where it appears at the base of the *Progracilis* Zone, *Orbigny* Subzone. The holotype has been found there, in les Hauts-de-Rochefort quarry. It persists until the Upper Bathonian, at the base of the *Retrocostatum* Zone where the youngest specimens have been found. In Burgundy, the nautilus figured as *Nautilus* cf. *fuscus* (Crick, 1898) by Lissajous (1923) also comes from the upper part of the Middle Bathonian, “*Arbustigerum* Zone” (that corresponds to *Morrisi* and *Bremeri* Zones [Mangold *et al.* 2012]).

MEASUREMENTS. — See Table 4.

DESCRIPTION

The holotype (2023.PB.N97; Fig. 11A, B) and the specimen 2023.PB.N133 are rather well preserved samples. They only reach a small size, a little more than 6 cm, at the adult stage. 2023.PB.N134 is a young one with a diameter of 42 mm, The shell is always compressed with dorsal sides slightly rounded showing a maximum width at about two third height. Then, the lateral-ventral sides flatten and converge. The ventral part, rounded on the inner whorls, flattens on the body-chamber, boarded by angular but not sharp shoulders. The umbilicus is very small, funnel-shaped. The lateral lobe of the suture line (Figs 4D; 9) is well marked (P/L < 30%) whereas the ventral lobe is very shallow.

REMARKS

Antaganides grulkei n. gen., n. sp. is a very close species to the contemporary *Antaganides fournieri* n. gen., n. sp., comparing size and shape of the shell. In comparison, the umbilicus is funnel-like in one case and deep and boarded by subvertical sides for the other. The lateral lobe of the suture line also shows differences, especially close to the umbilicus where the suture line is more retrosiphonate in *A. fournieri* n. gen., n. sp. than on *A. grulkei* n. gen., n. sp.

Genus *Pseudaganides* Spath, 1927

Pseudaganides Spath, 1927: 22-25.

TYPE SPECIES. — *Nautilus kutchensis* Waagen, 1873, by original designation, from the Callovian of Kutch, India.

COMPOSITION OF THE GENUS. — Six nominal species are assigned to this new genus within Bathonian and Callovian, *Pseudaganides aquitanense* n. sp. from Upper Bathonian, *Retrocostatum* Zone, *Pseudaganides buffeventi* n. sp., Lower Callovian, *Bullatus* Zone, *Pseudaganides crehensis* n. sp., Lower Callovian, *Gracilis* Zone, *Praheccquense*

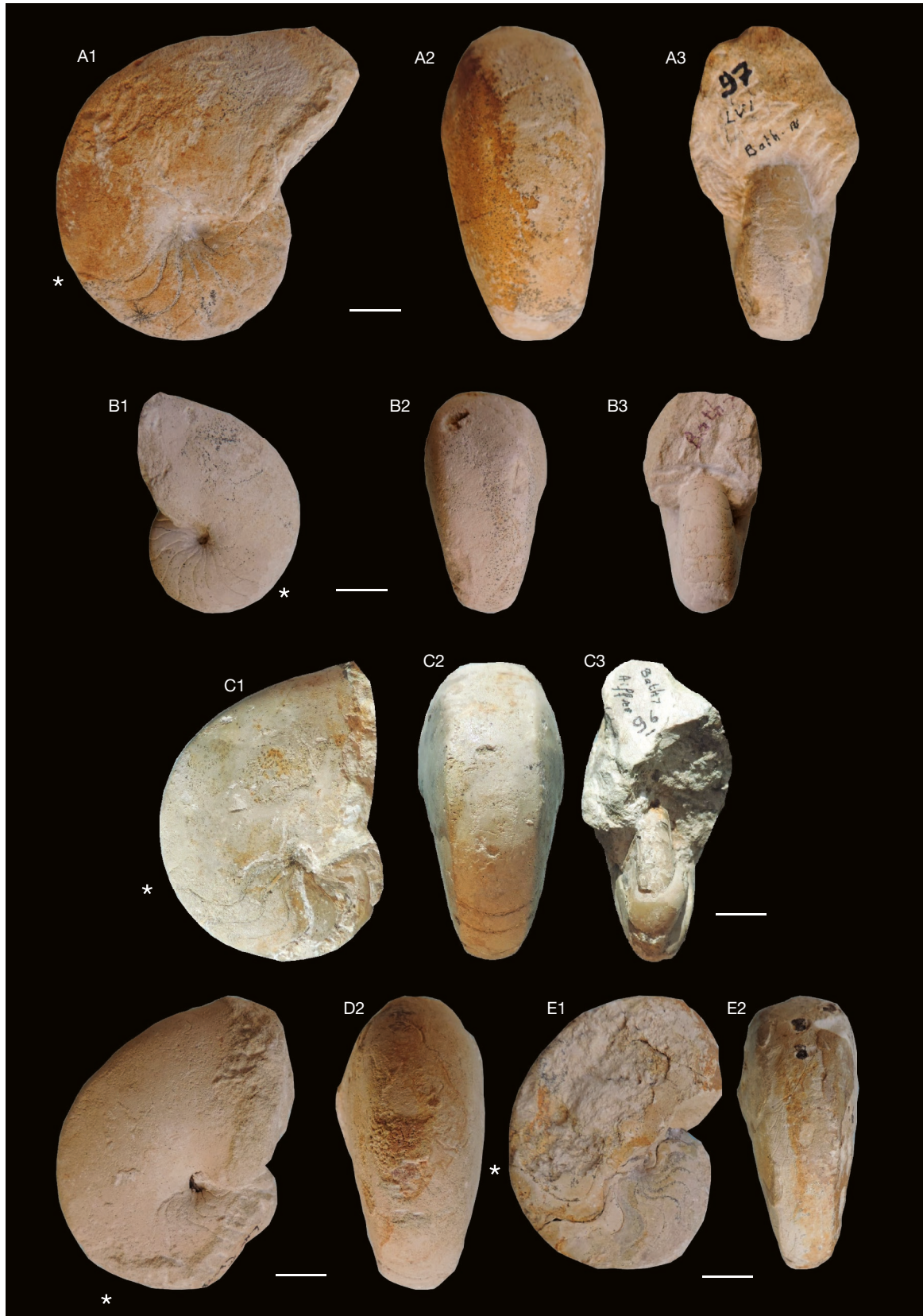


FIG. 11. — **A1-A3**, *Antaganides grulkei* n. gen., n. sp., holotype (2023.PB.N97), adult shell, les Hauts-de-Rochefort quarry, Middle Bathonian, *Progracilis* Zone; **B1-B3**, *Antaganides grulkei* n. gen., n. sp., specimen 2023.PB.N134, Champs-Albert near la Crèche, Upper Bathonian, base of the *Retrocostatum* Zone; **C1-C3**, *Pseudaganides aquitanense* n. sp., holotype (2023.PB.N96), adult shell, Aiffres, Upper Bathonian, *Retrocostatum* Zone; **D1, D2**, *Pseudaganides aquitanense* n. sp., specimen 2023.PB.N106, Champs-Albert near la Crèche, Upper Bathonian, *Retrocostatum* Zone; **E1, E2**, *Pseudaganides aquitanense* n. sp., paratype (2023.PB.N124), bed 8b, Buffevent quarry near Niort, Upper Bathonian, *Retrocostatum* Zone. *, end of the phragmocone. Scale bars: 1 cm.

TABLE 5. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides aquitanense* n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N96	61 43	36 27	0.59 0.62	32 19	0.52 0.44	0 0	0 0	0.88 0.7	6 —	19 —	31 —
2023.PB.N106	58	32	0.55	29	0.5	3	0.05	0.9	7	19	36
2023.PB.N124	52 48	29 21	0.55 0.43	23 16	0.44 0.33	2 0	0.04 —	0.79 0.76	5.5 —	16 —	34 —
2023.PB.N125	44	26	0.59	20	0.45	4	0.09	0.76	5	17	29

Subzone, *Pseudaganides subbiangulatus* and *Pseudaganides dimidiatus* Marchand & Tintant, 1971, from the Lower to Middle Callovian, *Patina* Subzone, *Boginense* Horizon to the *Anceps* Zone, *Bannense* Subzone and *Pseudaganides aganiticus* (Schlotheim, 1820), Upper Callovian to Lower Oxfordian. Many other *Pseudaganides* from the Upper Jurassic (von Loesch 1914) have also to be included within the genus, a revision of this material would be necessary. Based on the angular shape of the ventral lobe, Shimansky & Erlanger (1955) distinguished the genus *Xenocheilus* Shimansky, 1957 that extends from Upper Oxfordian to Lower Cretaceous beds.

CHARACTERIZATION AND REMARKS

Genus *Pseudaganides* is a group including small to Middle sized nautiloids, less than 15 centimeters in diameter, mostly around 10 centimeters or less. Shells are compressed, bearing goniatitic suture lines at all growth stages. These suture lines are characterized by a deep lateral lobe, a dorsal saddle on the entire phragmocone and a ventro-lateral saddle. The ventral lobe is sometimes missing. In most stages of coiling the umbilicus is closed. On the inner whorls, the venter is rounded and flattens, sometimes slightly concave, on the body-chamber. As pointed out by Jeannet (1948: fig. 4) for *P. frickensis*, the opening of the shell is rather particular, lateral borders are quite straight, starting from the umbilicus with a spiny shaped beginning (Figs 13D1; 15C). A deep ventral sinus is always present. The siphuncle is typically close to the venter part of the shell. *Pseudaganides* is known from the top of the Bathonian to the end of the Jurassic from which many new species were described (von Loesch 1914). *P. portlandicus* (Foord & Crick 1890) is atypical, showing an oval and larger shell. It could belong to another genus. All the specimens from the Lower Jurassic to Lower Middle Jurassic with folded suture lines are now gathered within the genus *Belmonticeras* Rulleau, 2008. From a palaeogeographical point of view, *Pseudaganides* seems to be a typical faunal element from the Tethyan realm *sensu* Westerman (2000) and has not yet been reported from the Arabian realm (Tintant 1987). Due to the ventral position of the siphuncle and the strong folding of the septum sutures, it is generally accepted that species of the genus *Pseudaganides* were cephalopods adapted to moderately deepwater environments (Tintant 1987).

Pseudaganides aquitanense n. sp.
(Fig. 11C-E)

[urn:lsid:zoobank.org:act:5A8D33FE-BD65-41CC-BF14-5DE1E26B3B19](https://www.zoobank.org/act:5A8D33FE-BD65-41CC-BF14-5DE1E26B3B19)

DIAGNOSIS. — Small nautilus, maximum diameter 60 mm, shell rather compressed with an oval section except on the body-chamber where the venter flattens. Umbilicus closed. Suture lines with a wide but shallow lateral lobe.

ETYMOLOGY. — From the name of the region Nouvelle Aquitaine where all the specimens of this new species have been collected

TYPE MATERIAL. — **Holotype.** France • 1 specimen (adult); Nouvelle-Aquitaine, Aiffres; [46°18'07"N, 0°26'07"W]; *Retrocostatum* Zone; Upper Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N96 (Fig. 10C).

Paratype. France • 1 specimen; Nouvelle-Aquitaine, Niort, Buffe-vent quarry (POC0009); [46°20'28"N, 0°30'21"W]; *Retrocostatum* Zone; bed 8b; Upper Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N124 (Fig. 11E).

OTHER SPECIMENS EXAMINED. — **France** • 2 specimens; Nouvelle-Aquitaine, La Crèche, Champs-Albert; [46°21'08"N, 0°17'58"W]; *Retrocostatum* Zone; Upper Bathonian; Patrick Branger leg.; MBAN; 2023.PB.N106, 2023.PB.N125.

TYPE LOCALITY AND STRATUM TYPICUM. — Until now, *Pseudaganides aquitanense* n. sp. has only been collected from the Upper Bathonian, *Retrocostatum* Zone, where it seems restricted. The holotype is from Aiffres.

MEASUREMENTS. — See Table 5.

DESCRIPTION

Small *Pseudaganides*, the smallest among Bathonian and Callovian species (Fig. 10), 58 to 61 mm diameter for full grown shells. Inner whorl section is oval, the venter flattens, just slightly rounded before the end of the phragmocone where it is limited by well-marked angulated shoulders that disappear close to the aperture as the shell widens. The umbilicus is closed, boarded by a rounded edge. Maximum width is situated on the dorsal part, close to the umbilicus. Suture line (Fig. 4E) draws a true S, the lateral lobe is wide but not very deep with P/L around 30%. The latero-dorsal saddle is visible for the first time in this lineage on the whole shell. On the holotype (Fig. 11C), the two last septa of the phragmocone are approximated indicating the adult stage.

REMARKS

Pseudaganides aquitanense n. sp. is the only *Pseudaganides* that have been found within Upper Bathonian strata with certainty. Presently, the only cited *Pseudaganides* of this age was *Pseudaganides subbiangulatus*. This Bathonian placement should be now revised because of several major differences with *Pseudaganides aquitanense* n. sp., the size and shape of the suture lines that is more folded on *Pseudaganides subbiangulatus* shells and, above all, because of the age attributed to the *P. subbiangulatus* collected in our study area (see below). *Pseudaganides aquitanense* n. sp. differs mostly from *Antaganides fournieri* n. gen., n. sp. by its suture lines that shows a sigmoidal profile at any growth stage. The sizes of the two species are similar, about 60 millimeters at adult stage. *Antaganides fournieri* n. gen., n. sp. can be interpreted as the probable ancestor of *Pseudaganides aquitanense* n. sp. and *Pseudaganides buffeventi* n. sp. The latter is a larger and younger species with a clearly open umbilicus.

Pseudaganides buffeventi n. sp.
(Fig. 12A, B)

urn:lsid:zoobank.org:act:9238C56A-6889-42C4-AA1B-B9CB9D2E3E41

DIAGNOSIS. — Small nautilus, maximum diameter about 70 mm, shell rather compressed with an oval section except on the body-chamber where the venter flattens, boarded by angular but not sharp shoulders. Umbilicus very narrow. Suture lines with a wide and quite deep lateral lobe.

ETYMOLOGY. — The species is named basing on Buffevent, the name of the locality where the type species has been discovered.

TYPE MATERIAL. — **Holotype.** France • 1 specimen; Nouvelle-Aquitaine, Niort, Buffevent quarry (POC0009); [46°20'28"N, 0°30'21"W]; *Bullatus* Zone; bed 9; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N76 (Fig. 12A).

OTHER SPECIMEN EXAMINED. — France • 1 specimen (adult); Nouvelle-Aquitaine, Salles; [46°23'45"N, 0°06'19"W]; *Bullatus* Zone; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N102 (Fig. 12B).

TYPE LOCALITY AND STRATUM TYPICUM. — Both specimens have been collected at the base of the *Bullatus* Zone, Lower Callovian where it appears to be restricted. The holotype (Fig. 12A) comes from Buffevent quarry.

MEASUREMENTS. — See Table 6.

DESCRIPTION

Small and compressed nautilus, about 70 mm diameter, the section is oval on the inner whorls, becoming rectangular at the adult stage because of the presence of angular but not sharp ventral shoulders on the body-chamber. The umbilicus is not fully closed but very narrow ($u = 0.05$), funnel like, with rounded sides. Flanks are slightly rounded with a maximum width at one third of the height. The venter, rounded at first, flattens from the end of the phragmocone to the aperture. The lateral lobe of the suture line (Figs 3-5) is well marked, ($P/L > 50\%$), more rounded on the second specimen (Fig. 11 b) than on the holotype whereas the dorsal saddle seems to be more angular and narrower by 2023.PB.N102 than on the holotype. The ventral lobe is very shallow on 2023.PB.N102, nonexistent on the holotype. The aperture, well preserved on the type specimen, is typical of *Pseudaganides* with straight lateral borders and a well-marked ventral sinus.

REMARKS

The globose shape of *Pseudaganides buffeventi* n. sp. can be compared with *Pseudaganides subbiangulatus* (d'Orbigny, 1850). The two main differences are the much smaller size for *Pseudaganides buffeventi* n. sp. (Fig. 10) and the width of the umbilicus that is slightly more open on this new species than on d'Orbigny's species (Fig. 8). The suture line (Figs 4; 12) of the two samples recognized as *Pseudaganides buffeventi* n. sp. shows little differences.

Pseudaganides crechensis n. sp.
(Figs 12C1-C3; 13C)

urn:lsid:zoobank.org:act:9DEFECCE-BA77-49A1-BA95-AEAB23E26268

TABLE 6. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides buffeventi* n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N76	69	41	0.59	37	0.53	0	0	0.9	8	16	50
	54	34	0.62	25	0.46	0	0	0.73	11	19	57
2023.PB.N102	71	43	0.6	34	0.47	4	0.056	0.79	11	20	55
	53	32	0.6	26	0.49	—	—	0.65	—	—	—

DIAGNOSIS. — Small nautilus, maximum diameter 75 mm, shell rather compressed with a subrectangular section except on the body-chamber where the sides are a little more rounded. Umbilicus clearly open. Suture lines with a wide and rather deep lateral lobe.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (adult); Nouvelle-Aquitaine, La Crèche, Champs-Albert; [46°21'08"N, 0°17'58"W]; base of the *Gracilis* Zone, *Prahequense* Subzone; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N107 (Fig. 12C1-C3).

OTHER SPECIMENS EXAMINED. — France • 1 specimen (adult); same data as holotype; 2023.PB.N132 • 2 specimens (young shells almost newly hatched); same data as holotype; 2023.PB.N142, 2023.PB.N143 • 1 specimen; Nouvelle-Aquitaine, Niort, Buffevent quarry (POC0009); [46°20'28"N, 0°30'21"W]; base of the *Gracilis* Zone, *Prahequense* Subzone; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N75.

TYPE LOCALITY AND STRATUM TYPICUM. — The holotype of *Pseudaganides crechensis* n. sp. (Fig. 12C1-C3) has been sampled from the base of the *Gracilis* Zone, *Prahequense* Subzone, Lower Callovian, in La Crèche.

MEASUREMENTS. — See Table 7.

ETYMOLOGY. — The species is named based on La Crèche (Deux-Sèvres), the city where four of the five known specimens were collected.

DESCRIPTION

Pseudaganides crechensis n. sp. is a small sized and compressed nautilus, maximum diameter observed is 75 mm on the biggest specimen (2023.PB.N75). The section is oval on the embryonic shell, then subrectangular until the end of the phragmocone where it widens. The body-chamber looks more rectangular at the adult stage because of the presence of angular but not sharp ventral shoulders. Flanks are slightly rounded with a maximum width at one third of the height. At the beginning of the body-chamber, the outer part of the flank is a little depressed. The venter, rounded at first, flattens from the end of the phragmocone to the aperture. The umbilicus is clearly open ($u > 0.10$), funnel like, with rounded sides. The lateral lobe of the suture line (Fig. 4F) is well marked, ($P/L = 0.43$ to 0.47). The ventral lobe is shallow, $P/L = 0.23$ on the type specimen. The two young shells show some ontogenetic elements. The hatching size, indicated by the existence of the nepionic constriction (Landman 1988), corresponds to 1 cm in diameter. At that size the shell shows a cross-hatched ornament of fine growth lines and perpendicular lirae (Fig. 13C). The aperture, very well-preserved on the type specimen (Fig. 12C1-C3), is typical of *Pseudaganides* with straight lateral borders and a well-marked ventral sinus.

TABLE 7. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides crechensis* n. sp.

n°	D	H	h	W	w	U	u	W/H	P	L	%
2023.PB.N75	75	39	0.52	36	0.48	7	0.09	0.92	9	21	43
2023.PB.N107	67	35	0.52	33	0.49	8	0.11	0.94	9	19	47
	54	31	0.57	25	0.46	6	0.11	0.8	—	—	—
2023.PB.N132	65	37	0.56	35	0.53	6	0.09	0.94	—	—	—
2023.PB.N142	29	17	0.58	15	0.51	3.5	0.2	0.88	—	—	—
	21	12	0.57	11	0.52	2	0.16	0.91	—	—	—
2023.PB.N143	21	12	0.57	11	0.52	2.5	0.13	0.91	—	—	—
	14	8	0.57	7	0.5	1.5	0.1	0.87	—	—	—

REMARKS

Pseudaganides crechensis n. sp. presents the same size than *Pseudaganides buffeventi* n. sp. The two species differs mainly from their umbilicus that is open on *Pseudaganides crechensis* n. sp. whereas it is closed on *Pseudaganides buffeventi* n. sp.

Pseudaganides subbiangulatus (d'Orbigny, 1850)
(Figs 13D, E; 14A; 15A1-A3)

Nautilus subbiangulatus d'Orbigny, 1850: 296, n°2.

Nautilus biangulatus d'Orbigny, 1842: 160, pl.134, fig. 1-3.

?*Nautilus textilis* Hébert & Eudes-Deslongchamps, 1860: 5, pl. I, fig. 1a-c.

Pseudaganides subbiangulatus — Marchand & Tintant 1971: 146, pl. IV, 1a, b. — Tintant 1994: 35, pl. 8, fig. 5.

Pseudaganides cf. *aganaticus* — Rulleau 2008: 55, pl. 35, fig. 2a, b.

non *Pseudaganides subbiangulatus* — Courville 2013: 66, pl. 1, fig. 2a, 2b (synonym of *Cenoceras* sp. or *Paracenoceras* sp.)

DIAGNOSIS. — Large sized nautilus for the genus, compressed sub-rectangular section with a flattened venter, becoming concave and boarded by angular margins on the body-chamber. Suture line with a deep lateral lobe followed by a wide lateral saddle.

MATERIAL EXAMINED. — France • 1 specimen (near complete); Nouvelle-Aquitaine, Pamproux (POC0015); [46°23'43"N, 0°3'0"W]; Patina Zone; Patrick Branger leg.; MBAN; 2023.PB.N73 • 1 specimen (near complete); Nouvelle-Aquitaine, Limalonges, les Maisons-Blanches; [46°08'15"N, 0°10'28"E]; Zone ?; Age ?; Patrick Branger leg.; MBAN; 2023.PB.N74 • 1 specimen (near complete); Nouvelle-Aquitaine, Bougon; [46°21'18"N, 0°03'11"W]; Gracilis Zone, Patina Subzone, Boginense Horizon; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N110 (Fig. 13D1-D3) • 1 specimen (near complete); Nouvelle-Aquitaine, Niort; [46°18'25"N, 0°27'42"W]; Anceps Zone, Stuebeli Subzone; Middle Callovian; Patrick Branger leg.; MBAN; 2023.PB.N112 (Fig. 13E1-E3) • 1 specimen (near complete); Nouvelle-Aquitaine, Saint-Laon, la Grève quarry (POC0051); [46°57'19"N, 0°01'38"W]; Anceps Zone; Middle Callovian; Patrick Branger leg.; MBAN; 2023.PB.N144 (Fig. 14A1-A3) • 1 specimen (near complete); Nouvelle-Aquitaine, Chauray, Chaban; [46°21'08"N, 0°17'58"W]; Patrick Branger leg.; MBAN; 2023.PB.N149; • 1 specimen (near complete); Nouvelle-Aquitaine, La Crèche; [46°21'08"N, 0°17'58"W]; Gracilis Zone; Lower Callovian; Patrick Branger leg.; MBAN; 2023.PB.N155 (Fig. 15A1-A3).

MEASUREMENTS. — See Table 8.

DESCRIPTION

The lectotype (MNHN.F.R54480, d'Orbigny collection n°2593 B, stored at the Muséum national d'Histoire naturelle, in Paris) has been revised by Marchand & Tintant (1971: 142, pl. IV, 1a, b). It consists in a large sized specimen (136 mm) for the genus *Pseudaganides*, well preserved, just a little distorted. The body-chamber is not complete. The umbilicus is rather narrow (Fig. 7) with an oblique umbilical wall. Its section is higher than wide, flanks are rounded with a maximum width at about one third of the height. The upper part of the flanks is slightly depressed at the end of the phragmocone and it is separated from the venter by a smooth but well-marked ridge. The flanks of the body-chamber are more rounded. The ventral area is narrow, convex on the phragmocone, slightly concave on the body-chamber. Suture line (Fig. 4G, H) is very sinuous with a wide and deep lateral lobe (P/L = 0.55) and a shallow ventral lobe.

Among our seven specimens, six are a little smaller than the lectotype (measurements from Marchand & Tintant, 1971), the maximum diameter observed is 111 mm, but their shape and septa fit perfectly with the diagnosis of *P. subbiangulatus*. The sample from the collection of the École des Mines figured by Rulleau (2008) also belong to the same species. Only one specimen, 2023.PB.N155 (Fig. 15A1-A3), although distorted, is as large as the lectotype.

REMARKS

Pseudaganides subbiangulatus is the largest *Pseudaganides* species (Fig. 10). When Marchand & Tintant (1971) wrote their revision, they considered that among d'Orbigny's material only one specimen was fitting perfectly to the type. Following his stratigraphical placement, they restricted the species to large specimens of Upper Bathonian age. The samples clearly show that all these former stratigraphic attributions are probably erroneous. Some smaller, below 80 mm, but very similar *Pseudaganides* of Lower and Middle Callovian age were described by Marchand & Tintant (1971: pl. II, fig. 1a-b-c, fig. III, pl. 6) as a new subspecies, *Pseudaganides subbiangulatus* subsp. *dimidiatus*, later named *Pseudaganides dimidiatus* (Tintant 1994). The average size of this new species from Western France and Spain was much smaller than *Pseudaganides subbiangulatus* and is also very different from our specimens, see below.

According to our data and the patterns of the evolution of the genus *Pseudaganides* (see Origin and evolution of the Antaganiides-Pseudaganides group) we assume that the initial stratigraphic placement to the Upper Bathonian by A. d'Orbigny (1842) was erroneous. This fossil was collected by Mr. Cabannet in the neighbourhood of Nantua (French Jura) but, more probably, the lectotype should have been collected within the "alternance calcaréo-marneuse" from the Lower or Middle Callovian described in Nantua's area by Mangold & Énay (2004). *Pseudaganides subbiangulatus* (d'Orbigny, 1850) is now considered as a nautilus of Lower and Middle Callovian age, from the Gracilis Zone, Grossouvrei or Pictava Subzone, to the Anceps Zone, Bannense Subzone.

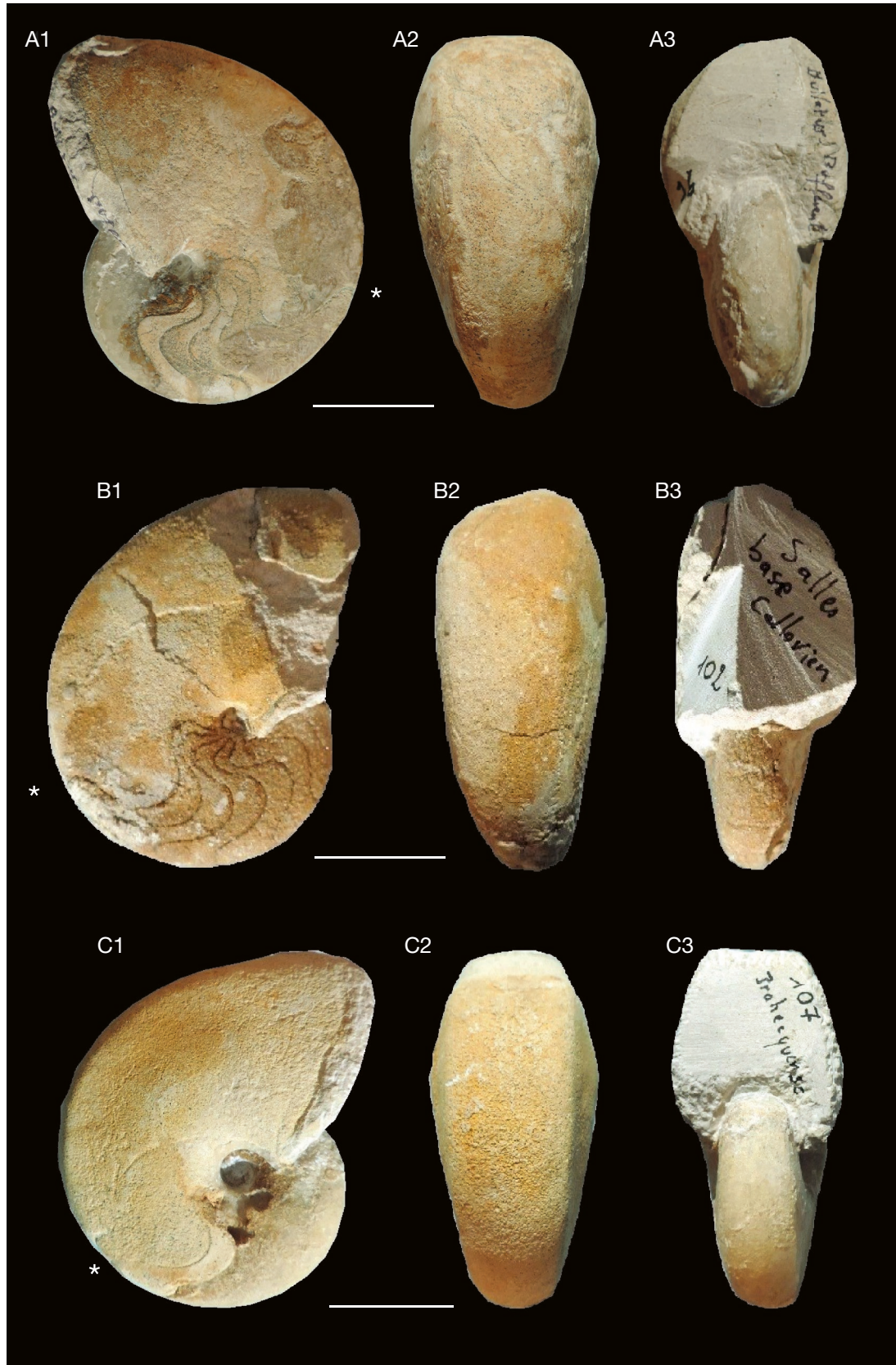


FIG. 12. — **A1-A3**, *Pseudaganides buffeventii* n. sp., holotype (2023.PB.N76), adult shell, bed 9, Buffevent quarry near Niort, Lower Callovian, *Bullatus* Zone; **B1-B3**, *Pseudaganides buffeventii* n. sp., specimen 2023.PB.N102, adult shell, Salles, Lower Callovian, *Bullatus* Zone; **C1-C3**, *Pseudaganides crechensis* n. sp., holotype (2023.PB.N107), Champs-Albert near la Crèche, Lower Callovian, *Gracilis* Zone, *Prahecquense* Subzone. *, end of the phragmocone. Scale bars: 1 cm.

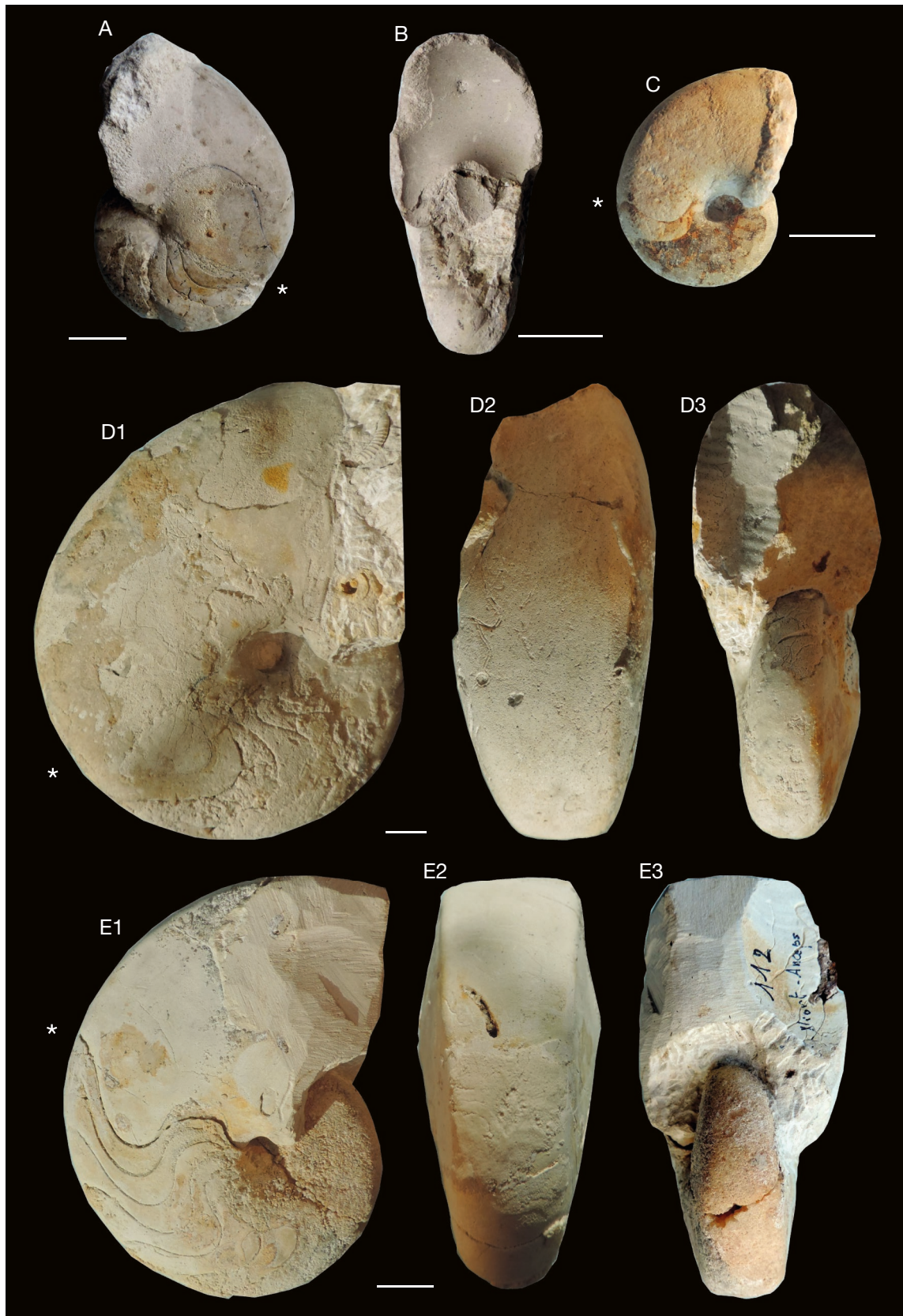


FIG. 13. — **A**, *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb., specimen 2023.PB.N129, with its preserved muscle scar, Niort, Upper Bajocian, *Niortense* Zone; **B**, *Antaganides* cf. *erycinus* (Tagliarini, 1901), n. comb., specimen 2023.PB.N148, with its siphuncle, viaduc de l'Égray, Upper Bajocian, *Niortense* Zone; **C**, *Pseudaganides crechensis* n. sp., specimen 2023.PB.N143, newly hatched shell showing its reticulate ornamentation on the phragmocon; **D1-D3**, *Pseudaganides subbiangulatus* (d'Orbigny, 1850), specimen 2023.PB.N110, full grown shell with its well preserved aperture, Bougon, Lower Callovian, *Gracilis* Zone, *Patina* Subzone, *Boginense* Horizon; **E1-E3**, *Pseudaganides subbiangulatus*, specimen 2023.PB.N112, Niort, Middle Callovian, *Anceps* Zone, *Stuebeli* Subzone. *, end of the phragmocone. Scale bars: 1 cm.

Pseudaganides dimidiatus Marchand & Tintant, 1971
(Fig. 14B1-B3)

Pseudaganides subbiangulatus subsp. *dimidiatus* Marchand & Tintant, 1971: 150, pl. II, fig. 1a-c, fig. III, pl. 6.

Nautilus subbiangulatus – Couffon 1919: pl. XVII, figs 7a-7b.

Pseudaganides dimidiatus – Tintant 1994: 36.

DIAGNOSIS. — Small sized nautilus, less than 80 mm, with a compressed and high section. Flat sides becoming slightly rounded on the body-chamber with a flat, sometime concave, venter.

MATERIAL EXAMINED. — France • 1 specimen (complete); Nouvelle-Aquitaine, Saint-Laon, la Grève quarry (POC0051); [46°57'19"N, 0°01'38"W]; *Gracilis* Zone, *Patina* Subzone to *Anceps* Zone; Lower to Middle Callovian; Patrick Branger leg.; MBAN; 2023.PB.N126 (Fig. 14B1-B3).

MEASUREMENTS. — See Table 9.

DISTRIBUTION. — *P. dimidiatus* is known from Lower Callovian, *Gracilis* Zone, *Patina* Subzone, to Middle Callovian, *Anceps* Zone.

DESCRIPTION

According to Marchand & Tintant (1971), these are small sized individuals, less than 80 mm in diameter, with a compressed and high section. Flanks are flat, becoming slightly rounded on the body-chamber. Suture line with a wide lateral saddle, not as deep as the external one.

REMARKS

As pointed by Marchand & Tintant (1971), *P. dimidiatus* differs from *P. subbiangulatus* in several ways. Besides its smaller size, the existence of quite sharp ridges at an earlier stage proves that it is a different species. All the other characteristics of the shell are the same. According to these authors, the age of the two species were different. New *in-situ* collecting demonstrates that this point of view is probably erroneous. Those authors also assumed that, in the collections, *P. dimidiatus* was rather common beside the total lack of any other sample of *P. subbiangulatus*. This study does not confirm this opinion since, at the same level, we collected more *P. subbiangulatus* than *P. dimidiatus*. Therefore, another explanation which could be considered would be a possible sexual dimorphism. This phenomenon has been described by several 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. Consequently, we suggest that *P. dimidiatus*, the smallest shell, could be the presumed female and *P. subbiangulatus*, the largest, could be the male of a single species.

Pseudaganides aganiticus (Schlotheim, 1820)
(Fig. 14C1-C3)

Nautilites aganiticus Schlotheim, 1820: 63. — von Loesch 1914: pl. XV (VI), fig. 1a-b.

TABLE 8. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides subbiangulatus* (d'Orbigny, 1850).

n°	D	H	h	W	w	U	u	W/H	P	L	%
MNHN.F. R54480 (type)	136 100	75 54	0.55 0.54	54 45	0.40 0.45	9.5 —	0.07 —	0.73 0.83	— —	— —	— —
2023.PB.N73	107 78	60 45	0.56 0.57	49 32	0.45 0.41	11 8	0.1 0.1	0.81 0.71	18 —	32 —	56 —
2023.PB.N74	60 44	38 27	0.63 0.61	37 24	0.61 0.54	— —	— —	0.97 0.88	9 10	20 22	45 45
2023.PB.N110	103 78	56 52	0.54 0.66	46 40	0.44 0.51	10 8	0.097 0.1	0.82 0.76	14 13	27 22	51 59
2023.PB.N112	84 63	48 39	0.57 0.62	42 28	0.5 0.44	6 5	0.05 0.07	0.87 0.71	— —	— —	— —
2023.PB.N144	111 84	63 50	— —	54 40	— —	7 6	— —	— —	17 11	36 20	47 55
2023.PB.N149	100 81	57 49	0.57 0.6	48 37	0.48 0.45	7 6	0.07 0.074	0.84 0.75	— —	— —	— —
2023.PB.N155	136 104	76 67	0.55 0.64	74 —	0.55 —	9 —	0.06 0.07	0.97 —	16 —	30 —	53 —

Pseudaganides aganiticus – Marchand & Tintant 1971: 146, pl. IV, fig. 1a-b. — Jain *et al.* 2023: 17, fig. 14A-H.

DIAGNOSIS. — Small shells, maximum diameter about 90 mm. The umbilicus is quite small, the section is higher than wide with flat sides converging toward a narrow and rounded venter on the phragmocone. This venter flattens on the body-chamber, becoming rarely concave. Most of the time it is boarded by angular ventrolateral shoulders. Suture line with a wide and deep dissymmetric lateral lobe, lateral saddle narrow and quite short, shallow, and rounded ventral lobe.

MATERIAL EXAMINED. — France • 1 specimen (complete); Pays de la Loire, Montreuil-Bellay; [47°06'37"N, 0°06'14"W]; top of the *Anceps* Zone; Middle Callovian; Patrick Branger leg.; MBAN; 2023.PB.N111 (Fig. 14C1-C3).

MEASUREMENTS. — See Table 10.

DISTRIBUTION. — The oldest sample that can be attributed to this taxon has been taken from the top of the *Anceps* Zone, Middle Callovian. It is a common species within Upper Callovian and Lower Oxfordian (Marchand & Tintant 1971; Jain *et al.* 2023).

DESCRIPTION AND REMARKS

As the investigations were mainly focused on Jurassic strata from southern Deux-Sèvres, the collection is lacking in Upper Callovian examples. Nevertheless, the few *Pseudaganides* from these beds clearly belong to *P. aganiticus* (Schlotheim). This species has been revised by Marchand & Tintant (1971) and no further comment is needed. It differs from *P. subbiangulatus* in three major points, a more rounded section on the flanks, a smaller size (Fig. 10) and a rather closed umbilicus (Fig. 7).



FIG. 14. — **A1-A3**, *Pseudaganides subbiangulatus* (d'Orbigny, 1850), specimen 2023.PB.N144, la Grève quarry near Saint-Laon, Middle Callovian, *Anceps* Zone; **B1-B3**, *Pseudaganides dimidiatus* Marchand & Tintant, 1971, specimen 2023.PB.N126, la Grève quarry, Middle Callovian, *Anceps* Zone; **C1-C3**, *Pseudaganides aganiticus* (Schlotheim, 1820), specimen 2023.PB.N111, Montreuil-Bellay (Maine-et-Loire), Upper Callovian, *Athleta* Zone, *Trezeense* Subzone. *, end of the phragmocone. Scale bars: 1 cm.

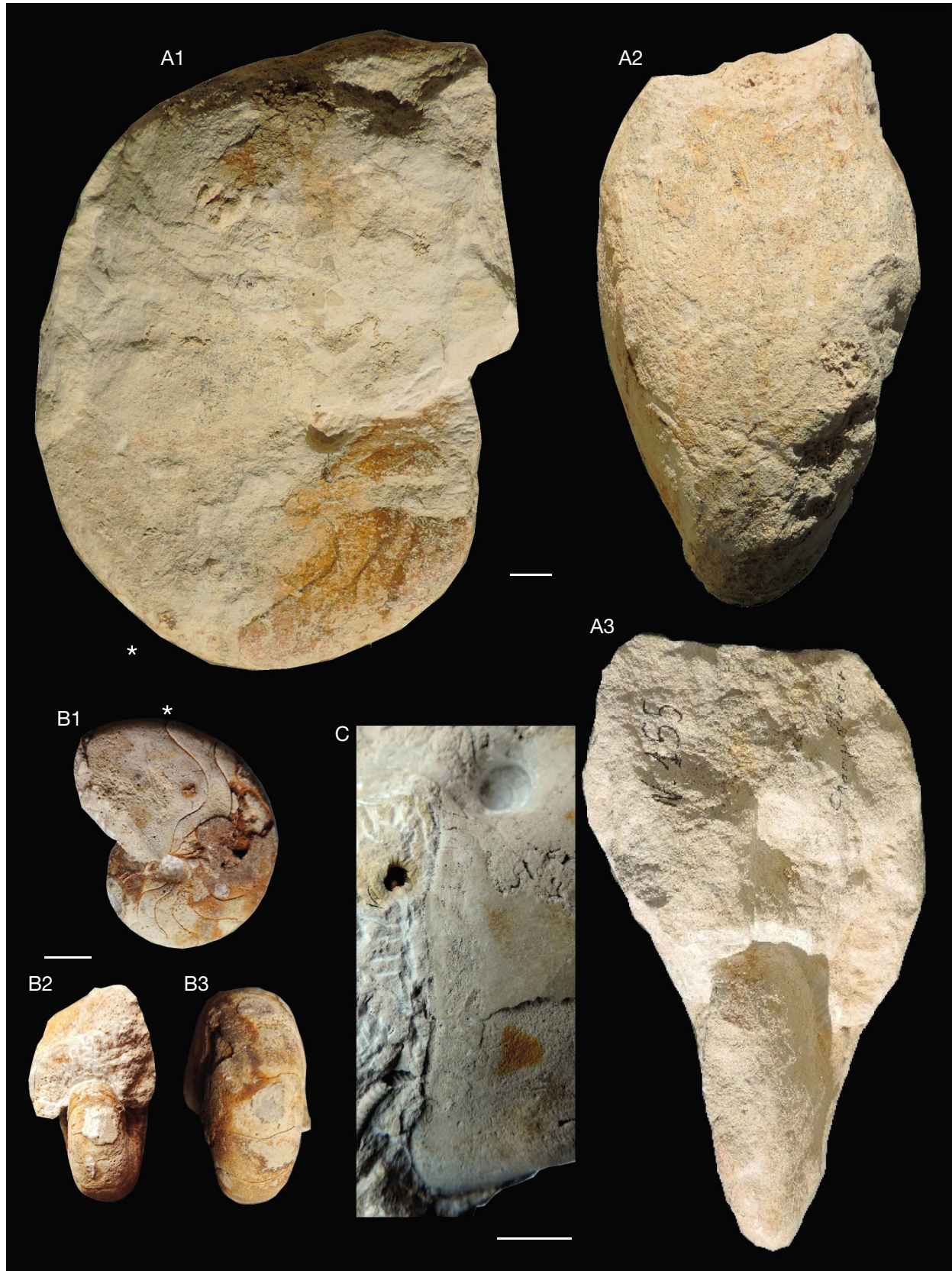


FIG. 15. — **A1-A3**, *Pseudaganides subbiangulatus* (d'Orbigny, 1850), specimen 2023.PB.N155, la Crèche, Lower Callovian, *Gracilis* Zone; **B1-B3**, *Belmonticeras subsinuatum* (d'Orbigny, 1850), specimen 2023.PB.N150, Chauray, Lower Bajocian, *Laeviuscula* Zone; **C**, *Pseudaganides subbiangulatus*, specimen 2023.PB.N110, detail of the well preserved and particular aperture, Bougon, Lower Callovian, *Gracilis* Zone, *Patina* Subzone, *Boginense* Horizon. *, end of the phragmocone. Scale bars: 1 cm.

TABLE 9. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides dimidiatus* Marchand & Tintant, 1971.

n°	D	H	h	W	w	U	u	W/H	P	L	%
UBGD.000920	74	39	0.53	32	0.43	6	0.08	0.82	–	–	–
(Type)	53	29	0.55	21	0.395			0.73	–	–	–
2023.PB.N126	66	38	0.57	33	0.5	6	0.09	0.86	–	–	–
	48	29	0.6	23	0.48	5	0.1	0.79	10	18	55

FROM *ANTAGANIDES* N. GEN. TO *PSEUDAGANIDES*,
THE ORIGIN OF PSEUDONAUTILIDAE

ORIGIN AND EVOLUTION OF THE
ANTAGANIDES-PSEUDAGANIDES GROUP

The stratigraphical succession of the ten described species clarifies the evolutionary lineage of the *Antaganides* n. gen.-*Pseudaganides* group (Fig. 16). This evolution can be summarized by three aspects: the shape of the suture line, the size of the shell and the width of the umbilicus.

The main characteristic of the *Pseudaganides* is the sigmoid aspect of the suture line due to the development of the dorsal saddle and lateral lobe. From *A. cf. erycinus* n. comb. to *A.ournieri* n. gen., n. sp., the lateral lobe deepens progressively from about 15% to 28% (Figs 4; 9). On *Antaganides* n. gen. shell, the dorsal saddle appears for the first time in the inner whorls of *A.ournieri* n. gen., n. sp. that can therefore be considered as the ancestor of all *Pseudaganides*. As *Pseudaganides* is well represented within open shelf margins, ammonite rich facies, we can summarize that the evolution of the shape of the suture line into a more complex aspect could correspond to an adaptation to deepening marine environments.

Another major feature of the evolution for the *Antaganides* n. gen.-*Pseudaganides* lineage is the modification of the size of the shell through time (Fig. 10). All the *Antaganides* n. gen. species are characterized by a small sized shell, around 60 mm in diameter. The first *Pseudaganides*, *P.aquitane* n. sp. possesses the same size shell. From Lower to Middle Callovian, the size of the shell increases continuously from 70 mm, *P.buffeventi* n. sp., to 75 mm for *P.crechensis* n. sp. and, finally, 110 to 135 mm for *P.subbiangulatus*. From Middle to late Callovian, the following species, *P.aganiticus* (Schlotheim) reduces its size, from more than 90 mm to 83 mm.

The modification of the umbilical width constitutes the third evolutionary element. Whereas the umbilicus of all *Antaganides* n. gen. and of the first *Pseudaganides* is almost closed at any growth stage (Fig. 7), never exceeding 5% of the shell diameter, the umbilical area is clearly open on *P.crechensis* n. sp. and *P.subbiangulatus* whose umbilicus widens to a diameter of more of 10%, reaching sometime 20% of the embryonic shell diameter.

The present study demonstrates clearly that the origin of this group has not to be located within Aalenian species as asserted by Marchand & Tintant (1971), nor among forms like *Cenoceras blakei* (Jeannet, 1951) as suggested by Dzik (1984). In that way, Rulleau (2008) was correct when dis-

TABLE 10. — Measurements (D, H, W, U, P, L, in mm) for *Pseudaganides aganiticus* (Schlotheim, 1820).

n°	D	H	h	W	w	U	u	W/H	P	L	%
Type	75	45	0.60	38.5	0.51	7	0.09	0.85	–	–	–
2023.PB.N111	83	46	0.55	45	0.54	6	0.07	0.97	–	–	–
	57	34	0.59	28	0.49	5	0.08	0.82	–	–	–
2023.PB.N147	93	51	0.54	47	0.5	4	0.04	0.92	–	–	–
	73	44	0.6	38	0.52	3.5	0.04	0.86	15	31	48

tinguishing the genus *Belmonticeras*. Near the base of Bajocian, *Laeviuscula* zone (unpublished personal collection), the nautiloid population is already diverse with a number of quite small species. Further studies would surely clarify the true origin of this lineage.

TAXONOMIC CONSEQUENCES

When Kummel (1956) published his work, “Post-Triassic Nautiloid Genera”, and later the “Treatise” (Kummel *et al.* 1964), he assumed that all post-Triassic nautiloids arose from one single species, *Cenoceras trechmanni* from the Carnian of New-Zealand. This opinion was accepted by most of the specialists such as Tintant & Kabamba (1983), Dzik (1984) and Teichert & Matsumoto (1987) although Shimansky (1957) had proposed two roots: Triassic Syringonaulitidae for most younger nautiluses and Clydonautilidae for Pseudonautilidae. More recently, as a conclusion on his work on Liassic and Middle Jurassic material, Chirat (1997) asserted that several genera could have crossed the Trias-Jurassic boundary giving rise to five lineages. King *et al.* (2016) reduced this last possibility to three. This work does not resolve these questions but shows that the phylogeny of Jurassic nautiloids is still in need of further investigations to reach a satisfactory classification. From this point of view, King *et al.* (2016) classified, at least provisionally, that *Belmonticeras* within Clydonautilidae. *Antaganides* n. gen. would be the first Pseudonautilidae of the lineage, followed by *Pseudaganides*, *Xenocheilus*, *Pseudonautilus* and *Aulaconautilus*. The taxonomical rank of *Paracymatoceras*, a ribbed form, contemporary of *Pseudaganides*, is questionable due to the larger size of the shell and its different aperture morphology (Tintant 1971 and personal data from unpublished new specimens of *P.mondegoense* Tintant, 1971). It may represent a last offshoot of *Belmonticeras*.

CONCLUSION

The succession of the different species within the *Antaganides* n. gen.-*Pseudaganides* group indicates a progressive modification of the shell, based mainly on a gradual increase in the folding of the septa probably due to an adaptation to deeper water environments. To a lesser degree, the increase of its size and the width of the umbilicus constitute other morphological elements of its evolution. Therefore, from Upper Bajocian to Upper Callovian, we can distinguish ten different morphospecies from which six are new. From this study, the

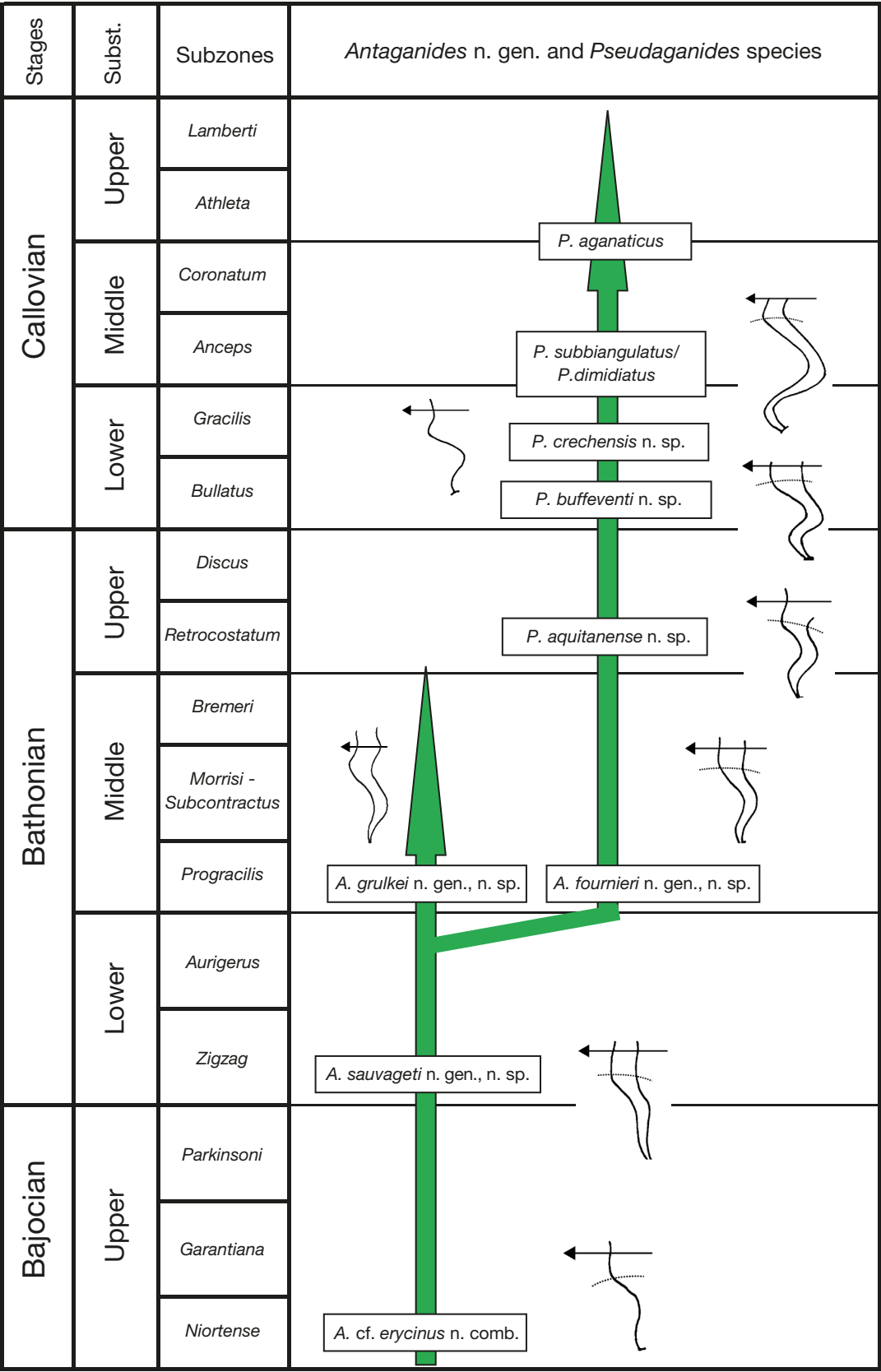


FIG. 16. — Evolution of the *Antaganides* n. gen.-*Pseudaganides* Spath, 1927 group from Upper Bajocian to Upper Callovian.

stratigraphical position of *P. subbiangulatus* is considered. It is reported to be of Upper Bathonian age however a Lower Callovian age would fit better with the evolution trend of the group. The data also confirm the opinion of Branger (2004) that Nautiloids can be a rather precise tool to date Middle Jurassic strata with species whose range rarely exceeds a sub-stage, sometimes no more than an ammonite biozone.

In conclusion, from a palaeobiogeographical point of view, this study confirms that, throughout the Bajocian and Bathonian, this group would have evolved on the western part of the northern margin of the Tethys Ocean before migrating into the Kutch Sea in India (Halder 2000).

Acknowledgements

The author warmly thanks Robert B. Chandler (NHM London, UK) for improving the English text. He is also thankful for helpful comments of Prof. Horacio Parent, (Universidad Nacional de Rosario, Argentina) and of an anonymous reviewer. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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Submitted on 15 December 2023;
accepted on 29 February 2024;
published on 3 October 2024.