

## Restatement of *Terebratula Orbignyana* DE VERNEUIL, 1850 on the basis of the original collection

by Paul SARTENAER

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### Abstract

Most of the fossils described by DE VERNEUIL (1850) come from Colle near Sabero, Leon. Other fossils come from various localities, some of them far away from Sabero. It is not clear from which locality the only specimen of *Terebratula Orbignyana* figured by DE VERNEUIL comes. Transverse serial sections made in one specimen of DE VERNEUIL's original collection from Aleje near Sabero, and in specimens collected by the author at El Millar show dental plates and other features not observed in serial sections published in the literature. Accordingly, a new family, Nucinulidae, and a new genus, *Nucinulus*, type species *N. orbignyana* of probable late Emsian age, are established.

**Key-words:** Nucinulidae, *Nucinulus*, rhynchonellids, brachiopods, late Emsian, Spain.

### Résumé

La plupart des fossiles décrits par DE VERNEUIL (1850) proviennent de Colle près de Sabero, Léon, les autres de diverses localités, certaines éloignées de Sabero. La provenance du seul spécimen de *Terebratula Orbignyana* figuré par DE VERNEUIL n'est pas établie. Des sections séries transverses exécutées dans un spécimen de la collection originale de DE VERNEUIL provenant d'Aleje près de Sabero et dans des spécimens récoltés par l'auteur à El Millar montrent des plaques dentales et d'autres caractères non observés dans les sections séries publiées dans la littérature. En conséquence sont fondés une nouvelle famille, Nucinulidae et un nouveau genre, *Nucinulus*, avec *N. orbignyana* d'âge emsien supérieur probable comme espèce-type.

**Mots-clefs:** Nucinulidae, *Nucinulus*, Rhynchonellides, Brachiopodes, Emsien supérieur, Espagne.

### Introduction

Most of the fossils described by DE VERNEUIL (1850) from the "remarkable locality" (p. 163) of Sabero come from Colle, a locality referred to by him as "the richest locality of the Sabero district" (p. 164), and more broadly "from

the limestone belt, that stretches from Colle to Aleje" (p. 163). Colle is located 8 km W and Aleje 5 km NE of Sabero in the northeastern part of the Province of Leon in the Cantabrian Cordillera, Spain. Coal and iron have been mined until 15 years ago in the Sabero vale on the left bank of the Esla river in the middle of a coalfield. The remainder of the fossils comes from various localities, some of them far away from Sabero. This is the case of *Terebratula Orbignyana*, which is mentioned by DE VERNEUIL (1850, p. 175) from five localities, only two of them (Alejico and Peña de la Venera) in the proximity of Sabero. The other three localities are: El Millar (41 km W of Sabero in the Bernesga valley, Province of Leon), Arnao (on the Atlantic coast N of Oviedo, Province of Asturias), and Viescas (7 km S of Salas and 45 km from Oviedo, on the main road, N634, from Oviedo to Galicia, in the western part of the Province of Asturias).

The material from Sabero that is often referred to in the literature as the "Sabero fauna" was partly collected by D. Casiano de Prado, who worked for the Palentina Leonesa Company. DE VERNEUIL studied the D. Casiano de Prado material and collected himself at Sabero and other localities.

For a long time the original collection of DE VERNEUIL was considered as lost. In 1977 the writer visited the "Laboratoire de Paléontologie, Université de Paris-Sud, Centre d'Orsay", where the collections from l'"École des Mines" of Paris had been transferred. He was fortunate enough to locate the only specimen figured by DE VERNEUIL (designated as the lectotype in the present paper). Also located were located 13 specimens from Aleje, two specimens from Alejico, two specimens from Viescas Conceja de Salas, and two specimens from Millar, all of them glued (some detached) on cardboard labels that have become almost unreadable with time (spellings are those written with DE VERNEUIL's hand writing).

The specimen of *T. Orbignyana* figured by DE VERNEUIL has been refigured by COMTE (1938, pl. 5, figs. 7, 7a-c), who examined DE VERNEUIL's collection at the "École des Mines", in Paris, and stated that the "fossiliferous localities (which are generally noted on the labels

accompanying the specimens) are often located a few kilometres away from the actual localities" (p. 47); he mentions the locality from which the specimen comes from as Sabero. On the label accompanying the specimen the author only found the instructions given by COMTE to the photographer. If Sabero had been written on the original label it would have meant, according to DE VERNEUIL (1850, p. 164), that "species without any other indication than Sabero come from Colle". It is uncertain if COMTE found such a label.

**Superfamily Rhynchonelloidea GRAY, 1848**  
**Nucinulidae n. fam.**

TYPE GENUS

*Nucinulus* n. gen.

DIAGNOSIS

Small-sized. *Paries geniculatus*, *squamae*, *glottae*, and spine-like projections present. Subpentagonal to subrounded contour. Shallow to moderately deep sulcus. Low to moderately high fold. Sulcus, fold and costae starting at the beaks. "M"-shaped front due to a clear median notch formed by a furrow dividing the fold, and to which usually corresponds a ridge in the sulcus. Numerous costae with divisions and intercalations. Clearly detached dental plates. Septum and cardinal process present. Deeply impressed ventral muscle field.

COMPOSITION

*Nucinulus* n. gen. is the sole genus known.

REMARK

The following features, combined, allow the separation of the new family from all known families: the "M"-shaped front; the presence of a *paries geniculatus*, *squamae*, *glottae*, spine-like projections, a septum, a septalium, dental plates, and a simple cardinal process; the high number of costae; sulcus, fold and costae starting at the beaks.

*Nucinulus* n. gen.

DERIVATIO NOMINIS

The name is an arbitrary combination of the reversed first two letters and the last three syllables of *Uncinulus*.

TYPE AND ONLY SPECIES

*Terebratula Orbignyana* DE VERNEUIL, 1850.

DIAGNOSTIC FEATURES

Small-sized. Dorsibiconvex. Contour subpentagonal to subrounded. *Paries geniculatus*, *squamae*, *glottae*, and spine-like projections present. Central part of front slightly to deeply depressed. Commissure generally very slightly grooved. Sulcus, fold and costae beginning at the beaks. Shallow to moderately deep sulcus, divided by a median ridge, and low to moderately high fold, divided by a median furrow; ridge and furrow clearly marked at

front. Greatest thickness of shell at front. Numerous divided and intercalated costae, flattened and provided with median narrow grooves in the *paries geniculatus*. Costae bundles never present. Stout septum. Slender dental plates. Thick, divided hinge plate. Shallow cup-shaped septalium. Short cardinal process with numerous low ridges. Ventral muscle field deeply impressed. Dorsal muscle field only slightly impressed.

DESCRIPTION

Small-sized. Strongly dorsibiconvex. Contour subpentagonal to subrounded in ventral view, subrectangular in anterior view. Quarter-circular to quarter-elliptical profile in lateral view. *Paries geniculatus* (= opposed geniculation of both valves) present. Hinge line short. Front of shell composed of three parts: the lateral parts (flanks) which are abruptly cut by the *paries geniculatus*, and the M-shaped (branches of the "M" are in the shape of sigmas) central part, which is wider than the lateral parts, slightly to deeply depressed, and divided by the median ridge of the sulcus. Central part bordered by a fold on each side in the lower two thirds or three quarters of the shell thickness; these folds are crossed diagonally by the lateral parts of the frontal commissure, which are deeply serrated by the parietal costae. Increased depression on both sides of the median ridge and immediately below the frontal margin, resulting sometimes in two small, but clearly marked pits. Central part of frontal commissure straight with slightly arched borders, taking the exact shape of the median ridge and the depressions on both sides (including pits when present).

Commissure generally very slightly grooved. Cardinal commissure slightly sticking out as a result of the postero-lateral margins of the shell being concave near the commissure. Lateral commissures slightly serrated, passing progressively at a right angle to the frontal commissure. Shallow to moderately deep sulcus and low to moderately high fold beginning at the beaks and passing progressively to the flanks. Greatest thickness of shell located at front margin, the front margin itself located posterior to the most anterior point of the shell, and slightly posterior to the frontal commissure. Well-developed *squamae* and *glottae* present. Well-developed deltidial plates. Costae edges modified into short and slender spine-like projections.

Ventral valve (*paries geniculatus* excluded) evenly and slightly convex. Sulcus widening rapidly and wide at front. Greatest width of sulcus measured between the middle points of the curves formed by the lower part of the branches of the "M"; thus, although the sulcus is clearly delimited at front, the term "spurs" cannot be used. Low, rounded and narrow (widening anteriorly) longitudinal median ridge dividing the sulcus into two slightly concave parts, clearly marked at front, and extending to the frontal part of the dorsal valve. Tongue high, subrectangular; upper part slightly to strongly recurved posteriorly and, thus, crest of tongue located posterior to point of maximum length of shell. Crest of tongue located slightly lower than point of maximum

shell thickness. Tongue clearly delimited with the exception of its base that cannot be properly defined on account of the sulcus passing progressively to its tongue along the curved part of the branches of the "M". Beak small, strongly incurved, coming close to the dorsal valve. Short and smooth beak ridges indicating the inversion of curvature near the cardinal commissure. No interarea or exceeding small.

Dorsal umbonal region never extending beyond the ventral umbonal region. Shallow and rounded longitudinal median furrow dividing the fold into two slightly to strongly convex parts, and clearly marked at front.

Numerous low, narrow, fine and rounded costae beginning at the beaks. Lateral costae becoming progressively narrower laterally. Costae flattened and provided with median narrow grooves in the *paries geniculatus*; these grooves correspond to the growth and mobility of the spine-like projections. Separate counts of parietal and median costae have been proven impossible. Primary costa or one of the primary costae of the median ridge of the sulcus almost always stronger than other costae, and remaining stronger even after division(s). Divisions and intercalations are the rule; they occur at variable distances from the beaks. A costa seldom undergoes more than one division. In spite of the divisions and intercalations, costae are regular near the commissure. Furrows very narrow. Costae bundles never present, unless the median ridge of the sulcus is considered as such.

With few exceptions, width is the greatest dimension. Maximum width located anterior to half-length. Wide apical angle.

Moderately thick shell. Contour of delthyrial cavity regular. Slender dental plates. Large and wide umbonal cavities. Teeth stout. Thick, divided hinge plate. Shallow cup-shaped septalium. Well developed stout septum, persisting for about one third of the valve length. Very short pad-like cardinal process, covering the whole hinge plate, with numerous low shark-teeth-like ridges. Outer hinge plates becoming shorter anteriorly and joining the crural bases to form wings inclined towards each other in transverse serial sections. Wings becoming progressively smaller and passing to very slender and short crura. Ventral muscle field deeply impressed, divided by a thin ridge, and surrounded by an acute crest; its width varies between 37 and 50 per cent of the shell width. It is composed of two elongated, longitudinally striated, oval diductor scars extending as far as half the unrolled length of the valve, and enclosing small reniform adductor scars. Impression of the median ridge of the sulcus ending at the base of the diductor scars. Dorsal muscle field only slightly impressed, composed of two elongated oval adductor scars surrounded by an acute crest (not as strong as the crest observed in the ventral valve), and two smaller adductor scars located posteriorly. The two pairs of adductor scars are separated by the strong wedge-shaped part of the septum until the middle of the elongated pair, where the septum thins out and extends as a fine ridge. Width of dorsal muscle field varying around one third of

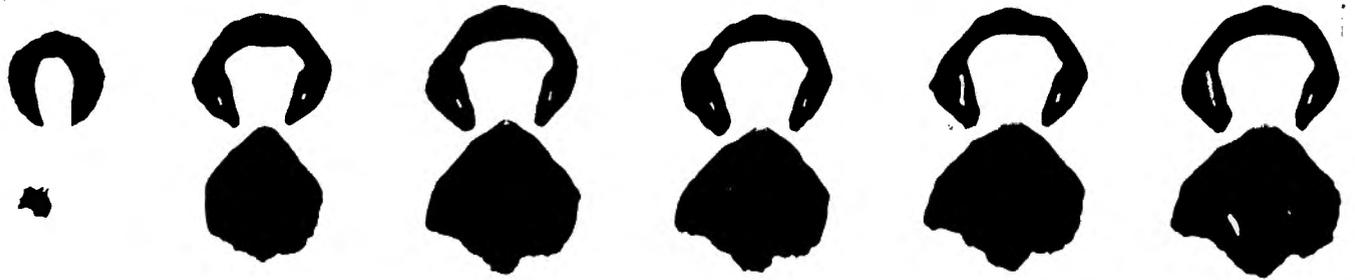
the shell width, and its length around the two-thirds of the unrolled length of the valve.

#### COMPARISONS

The genus *Uncinulus* BAYLE, 1878 is still poorly defined. Many species with different external and internal characters have been assigned to it. Therefore, the following comparison between *Uncinulus* and *Nucinulus* n. gen. is a comparison between the type species of these genera: *Uncinulus subwilsoni* (D'ORBIGNY, 1850) and *Nucinulus orbignyanus*.

The genera *Uncinulus* and *Nucinulus* n. gen. have various characters in common, e.g. a *paries geniculatus*; a short hinge line; well developed *squamae* and *glottae*; a very slightly grooved commissure; slightly serrated lateral commissures passing sharply at a right angle to the frontal commissure; a front margin located posterior to the most anterior point of the shell, and slightly posterior to the frontal commissure; costae edges modified into long and slender spine-like projections; a high, subrectangular tongue; a strongly incurved beak coming close to the dorsal valve; no ventral interarea or exceedingly small; short and smooth beak ridges; numerous low and rounded costae beginning at the beaks; divided and intercalated costae; costae bundles never present; stout teeth; a well developed and stout septum.

*Uncinulus* may be easily separated from *Nucinulus* n. gen. by both external and internal characters: a larger size; a globular profile; a slightly convex to vertical front in contrast with the characteristic "M"-shaped front of *N. orbignyanus* described above; the anterior commissure generally arched; an extremely shallow sulcus and an extremely low fold (in the umbonal areas sulcus and fold are inseparable from the flanks); the absence of a longitudinal median ridge in the sulcus and a longitudinal median furrow on the fold; the greatest thickness of shell not located at front margin, but slightly posterior to it; small deltidial plates; a narrow sulcus; a tongue without relief; the crest of tongue located lower; median grooves not always present on the costae in the *paries geniculatus* (they are wide when present); width, length, and thickness close to each other, each of them being alternatively the greatest dimension; the maximum width usually located more posteriorly; a completely different distribution of costae [9 to 11 median + parietal costae in *Uncinulus subwilsoni* against 19 to 29 in *Nucinulus orbignyanus* (0 to 2 parietal costae against about 8 to 12); 20 to 26 lateral costae on each flank in *Uncinulus subwilsoni* against 15 to 23 in *Nucinulus orbignyanus*; less divisions and intercalations]; a very thick shell in the apical region; dental plates absent or vestigial, and thus residual umbonal cavities sometimes present; a stocky cardinal process; short crural bases; different (stout, very short, and strongly curved distally) crura. Transverse serial sections of one specimen of *Uncinulus subwilsoni* coming from La Baconnière (Armorican Massif), about 130 km to the south of the type locality (Néhou, Armorican Massif), are shown on Text-fig. 1.



0.45

1.25

1.5

1.55

1.6

1.65



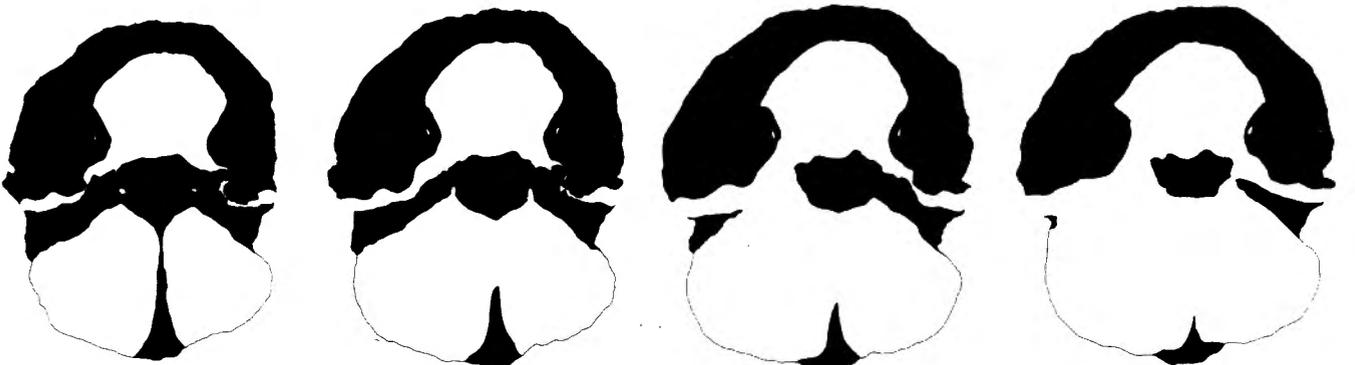
1.85

2.05

2.35

2.5

2.6



3.05

3.2

3.4

3.55



3.8

4.4

5.5

5.6

5.7

5.9

6

x 3.25

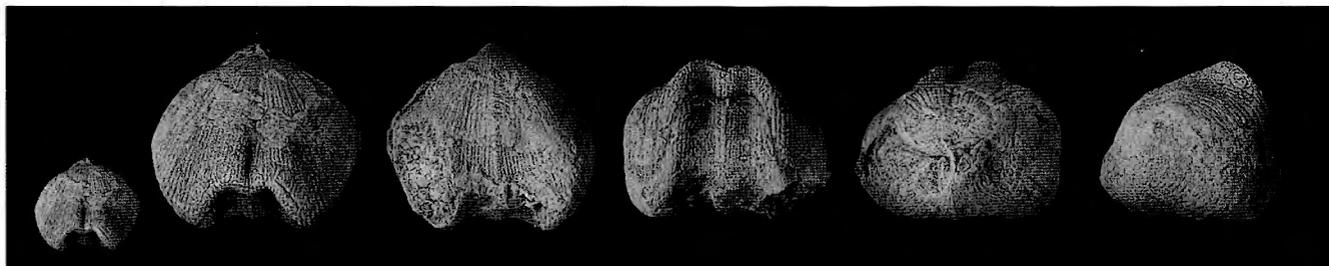


Fig. 2 — *Nucinulus orbignyanus* (DE VERNEUIL, 1850). Lectotype (= pl. 3, figs. 10a-c in DE VERNEUIL, 1850). Near Sabero, Leon. Probably late Emsian. Dorsal (x1 and x2), ventral (x2), anterior (x2), posterior (x2), and lateral (x2) views. Costal formula: 28 median + parietal, 23 lateral costae.

### *Nucinulus orbignyanus* (DE VERNEUIL, 1850)

Figures 2, 3

#### LECTOTYPE

Among the syntypes the only specimen figured by DE VERNEUIL (1850, pl. 3, figs. 10a-c) is here selected as the lectotype. This specimen has been refigured (magnification  $\times 5/4$ ) by COMTE (1938, pl. 5, figs. 7, 7a-c) and by the author (Text-fig. 2).

#### MATERIAL

The description of the species, and thus of the new genus, is based on: 20 specimens of DE VERNEUIL's original collection (see Introduction); and 58 specimens from El Millar collected by the author, in 1977, in the upper part (between 65 and 27 m below the top) of the Santa Lucía Formation. 39 specimens (12 in DE VERNEUIL's collection) are in good state of preservation, 14 (4) satisfactory, and 25 (4) are fragmental.

#### DESCRIPTION

The following description refers only to specific characters in need of further elaboration.

Measurements of fourteen specimens, including the lectotype, are given on Table 1. Maximum width occurs at a point between 53 and 69 per cent (most of the values varying between 57 and 69 per cent) of the shell length anterior to the ventral beak. Thickness of dorsal valve varying between 60 and 74 per cent of the shell thickness. Top of dorsal valve, and thus of shell, occurs at a point between 13 and 28 per cent of the shell length posterior to the point of maximum shell length. Crest of tongue located 12 to 24 per cent lower than point of maximum shell thickness. Width of sulcus at front varying between 48 and 62 per cent (most of the values between 54 and 62 per cent) of the shell width. Apical angle varying between

104° and 118°. 52 to 74 costae (lectotype: 74): 19 to 29 median + parietal costae (lectotype: 28), 15 to 23 lateral costae on each flank (lectotype: 23). 21 ridges on the cardinal process of the sectioned specimen (Text-fig. 3) from DE VERNEUIL's collection coming from Aleje and suitable for such a purpose. Sections were made in specimens from El Millar collected by the author and almost identical externally to the figured specimen of DE VERNEUIL. The specimens show internal features not observed in the sections published in the literature (SCHUMANN, 1965, fig. 17, p. 87), and in those made by the author in alleged representatives of the species from various regions. In particular, dental plates, which are absent in such specimens, are well developed in the specimens from Aleje and El Millar.

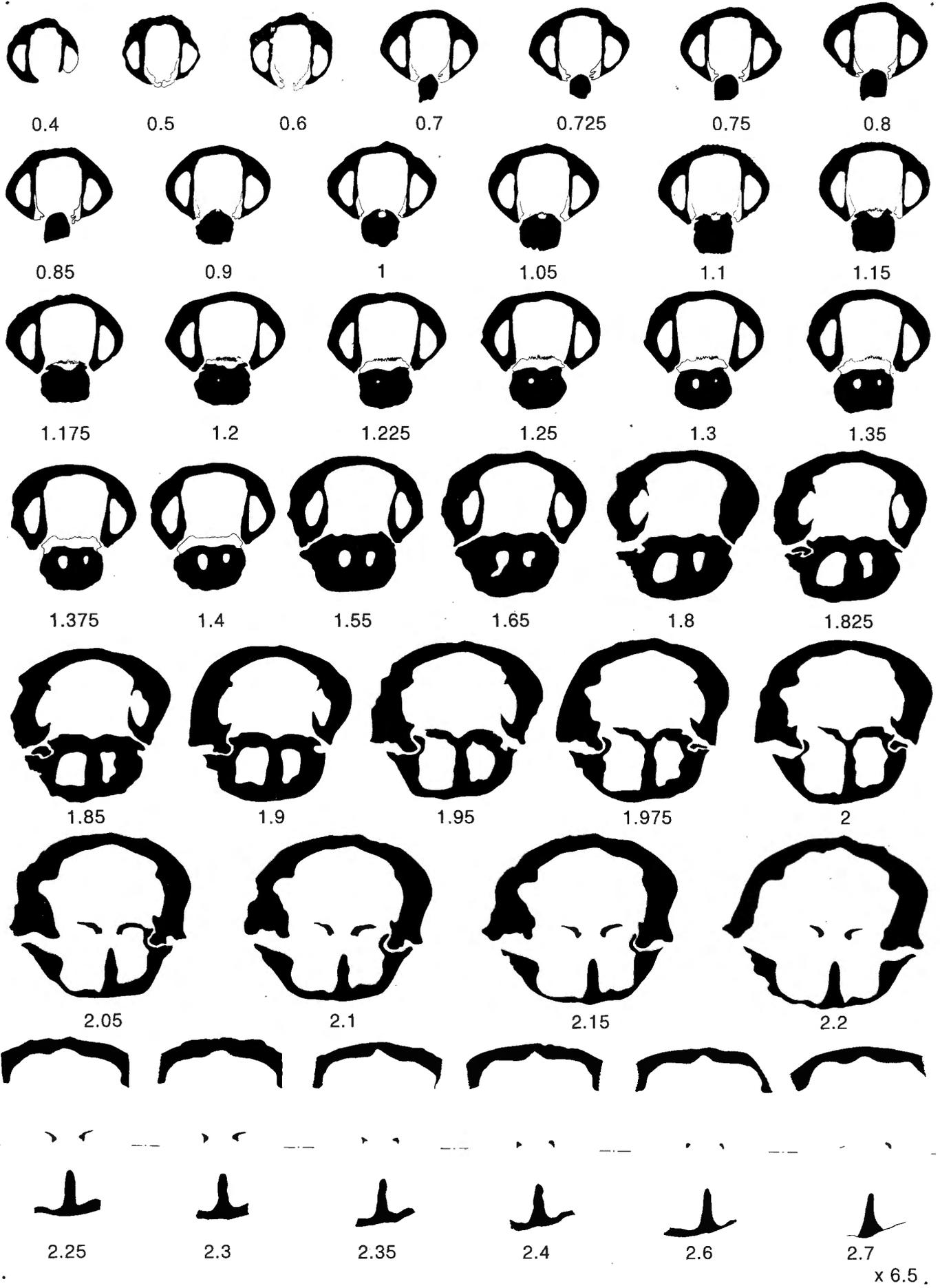
#### STRATIGRAPHIC RANGE

Elements mentioned in the introduction of the present paper suggest that Colle is the type locality of the lectotype of *Nucinulus orbignyanus*. This means, according to ALVAREZ & BRIME (1990, p. 13, fig. 1) and ALVAREZ (1999a, p. 50; 1999b, pp. 55-56) that the "immensa mayoría de los fósiles de Colle, provienen de los niveles calcáreos y margo arcillosos de las capas superiores del Gruppo La Vid", these highest beds (Coladilla Formation) of La Vid Group being of latest Emsian age in this region ("en dicha region"). Nevertheless, these authors do not mention the species in their list of species from this level at this locality for reasons unknown to the author.

It cannot be excluded that the lectotype comes from the upper part of the Santa Lucía Formation, which outcrops also in the Sabero area or from the upper part of latest Emsian-lowermost Eifelian age of the formation at El Millar, one of the localities mentioned by DE VERNEUIL. Specimens from this locality cannot be distinguished externally from the lectotype, and serial transverse sec-



Fig. 1 — *Uncinulus subwilsoni* (D'ORBIGNY, 1850). Camera lucida drawings of transverse serial sections; figures are distances in mm forward of the ventral umbo. La Baconnière, Laval Synclinorium, Armorican Massif. Lower Devonian (nowadays probably middle-upper Pragian). Collected by D.-P. OEHLERT in 1886 (n° 1098), acquired in exchange by the Belgian Royal Institute of Natural Sciences (General inventory number 5348). Measurements: length = 19.4 mm; width = 18.6 mm; thickness = 20 mm.



x 6.5 .

Table 1 — *Nucinulus orbignyana* (DE VERNEUIL, 1850). Measurements (in mm) based on fourteen specimens; figures in parentheses are reasonable estimates on a damaged specimen. Abbreviations used: l = length; w = width; t = thickness; vv = ventral valve; dv = dorsal valve. Column 1 = lectotype; columns 2-5 (IRScNB a12026-a12029), 6 (paralectotype B), 7-9 (IRScNB a12030-a12032), 11 (IRScNB a12033), 12 (paralectotype D) refer to specimens from El Millar; columns 10, 13, 14 refer to paralectotypes C, E, F from Aleje. Column 1 refers to the largest specimen at the author's disposal, columns 12 to 14 to the smallest specimens at hand.

in mm	1	2	3	4	5	6	7	8	9	10	11	12	13	14
l	12.3	12.2	11.9	11.7	11.5	11.5	11.4	11.4	11.1	10.9	10.7	10.5	9.5	9.5
w	13.9	13.8	12.7	12.5	14.1	12.1	11.3	11.8	11.1	12.1	10.6	11.2	10.2	9.8
t	11	11.4	10.4	9.9	11.5	9.5	9.4	9.4	8.8	10	9.3	9.6	8.6	8.2
tvv	3.8	4.2	3.8	(3.5)	4.2	3.8	3.6	3.6	3.4	2.6	3.5	3.1	3.2	2.5
tdv	7.2	7.2	6.6	(6.4)	7.3	5.7	5.8	5.8	5.4	7.4	5.8	6.5	5.4	5.7
l/w	0.88	0.88	0.94	0.94	0.82	0.95	1	0.97	1	0.9	1	0.94	0.93	0.97
t/w	0.79	0.83	0.82	0.79	0.82	0.79	0.83	0.8	0.79	0.83	0.88	0.86	0.84	0.84
t/l	0.89	0.93	0.87	0.85	1	0.83	0.82	0.82	0.79	0.92	0.87	0.91	0.91	0.86
apical angle	118°	109°	115°	114°	115°	114°	113°	107°	104°	115°	106°	105°	110°	104°

tions made in specimens collected by the author at El Millar at about 60 m below the top of the Santa Lucía Formation show internal characters similar to those (Text-fig. 3) of the specimen from Aleje.

Now that *Nucinulus orbignyana* has been redescribed, it will be the task of local geologists to solve the problem of its precise stratigraphic range in the type area and in other localities

## Conclusions

As a result of the rejection of DE VERNEUIL's species from the genus *Uncinulus*, and its assignment to *Nucinulus* n. gen., attention should be devoted to the following problems: (1) the systematic position to be given to forms identified as *orbignyana* in various countries, including Spain; (2) the clear definition of *Uncinulus subwilsoni*,

the type species of *Uncinulus*, which has sometimes been considered as identical to *U. pila* (SCHNUR 1851); (3) the merits of the transitional or intermediate forms (*orbignyana-pila*, *orbignyana-lodanensis* BURHENNE 1899) often advocated in the literature; and (4) a clear definition of these species. These problems extend beyond the scope of the present paper, and will be dealt with in a forthcoming publication.

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Fig. 3 — *Nucinulus orbignyana* (DE VERNEUIL, 1850). Camera lucida drawings of transverse serial sections; figures are distances in mm forward of the ventral umbo. Paralectotype A. Measurements: length = 17 mm; width = 11.9 mm; thickness = 7.8 mm.

## References

- ALVAREZ, F., 1999a. *Colle*, notas sobre un yacimiento clásico en el Devónico Cantábrico (NO de España). In: RÁBANO, I. (ed), Actas, XV Jornadas de Paleontología, 1. *Colección Temas Geológico-Mineros*, 26: 48-53. Madrid.
- ALVAREZ, F., 1999b. El registro paleontológico de Colle (Sabero, NE de León, España). In: RÁBANO, I. (ed), Actas, XV Jornadas de Paleontología, 1. *Colección Temas Geológico-Mineros*, 26: 54-59. Madrid.
- ALVAREZ, F. & BRIME, C., 1990. Reencuentro con los "fósiles de Sabero". Comunicaciones de la reunión de tafonomía y fosilización, Madrid, 20-22 Septiembre de 1990: 13-22.
- BAYLE, E., 1878. Explication de la carte géologique de la France, 4 (1), Fossiles principaux des terrains de la France, Atlas: 79 pls.
- BURHENNE, H., 1899. Beitrag zur Kenntniss der Fauna der Tentaculitenschiefer im Lahnggebiet mit besonderer Berücksichtigung der Schiefer von Leun unweit Braunfels. *Abhandlungen der Preussischen Geologischen Landesanstalt zu Berlin*, 29: 56 pp.
- COMTE, P., 1938. Brachiopodes dévoniens des gisements de Ferroñes (Asturies) et de Sabero (Léon). *Annales de Paléontologie*, 27 (1-3): 41-88.
- ORBIGNY (D'), A., 1850. Prodrôme de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques, 1: I-LX, 1-394. Paris.
- SCHNUR, J., 1851. Die Brachiopoden aus dem Uebergangsgebirge der Eifel. Programm der vereinigten höhern Bürger- u. Provinzial-Gewerbeschule zu Trier, Schuljahr 1850/51: 2-16. Trier.
- SCHUMANN, D., 1965. Rhynchonelloidea aus dem Devon des Kantabrischen Gebirges (Nordspanien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 123 (1): 41-104.
- VERNEUIL (DE) É., 1850. Note sur les fossiles dévoniens du district de Sabero (Léon). *Bulletin de la Société géologique de France*, 7: 155-186.

Paul SARTENAER  
Département de Paléontologie  
Section des Invertébrés Fossiles  
Institut royal des Sciences naturelles de Belgique  
rue Vautier 29, B-1000 Brussels, Belgium  
e-mail: Paul.Sartenaer@naturalsciences.be

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