

New middle and late Emsian, and early Eifelian rhynchonellide (brachiopod) genera of the family Nucinulidae SARTENAER, 2004

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Abstract

Four new genera are described: *Lapinulus*, type species *L. pila* (SCHNUR, 1851) from the late Emsian in the Grand Duchy of Luxembourg, the SW “Eifelkalkmulden”, and other regions of Germany; *Oligodesmerhynchus*, type species *O. lodanensis* (BURHENNE, 1899) from the late Emsian of the Lahnmulde; *Palinulus*, type species *P. zairensis* n. sp., from the late Emsian of the central Dra plains (Anti-Atlas), Morocco; and *Cuinulus*, type species *C. melanopotamicus* n. sp. from the late Emsian and early Eifelian of the Dinant Basin. Other species of *Cuinulus* n. gen. are described: *C. concavus* n. sp. from the late Emsian and early Eifelian of the “Eifelkalkmulden”; *C. leonensis* n. sp. from the early Eifelian of the Cantabrian Cordillera; *C. assaensis* n. sp. from the early Eifelian of the western Dra plains, and possibly Algeria and Mauritania; *C. eifeliensis* (BIERNAT, 1954) from the late Emsian and early Eifelian of the northern Holy Cross Mountains; *C.? arnaoensis* n. sp. from the late Emsian and early Eifelian of the Cantabrian Cordillera; and *C.? nalykini* (BUBLICHENKO, 1928) from probable late Emsian and early Eifelian age of the SW Altai Mountains.

Key-words: Nucinulidae, rhynchonellids, brachiopods, Emsian, Eifelian, W Europe, N Africa, Altai Mountains.

Résumé

L'auteur fonde quatre nouveaux genres: *Lapinulus*, avec *L. pila* (SCHNUR, 1851) de l'Emsien supérieur du Grand-Duché du Luxembourg, du SW de l'Eifel et d'autres régions d'Allemagne comme espèce-type; *Oligodesmerhynchus*, avec *O. lodanensis* (BURHENNE, 1899) de l'Emsien supérieur de la Lahnmulde comme espèce-type; *Palinulus*, avec *P. zairensis* n. sp. de l'Emsien supérieur des plaines centrales du Dra (Anti-Atlas), Maroc, comme espèce-type; et *Cuinulus*, avec *C. melanopotamicus* n. sp. de l'Emsien supérieur et de l'Eifelian inférieur du Bassin de Dinant comme espèce-type. D'autres espèces du genre *Cuinulus* n. gen. sont décrites: *C. concavus* n. sp. de l'Emsien supérieur et de l'Eifelian inférieur de l'Eifel; *C. leonensis* n. sp. de l'Eifelian inférieur de la Cordillère Cantabrique; *C. assaensis* n. sp. de l'Eifelian inférieur des plaines occidentales du Dra, et peut-être d'Algérie et de Mauritanie; *C. eifeliensis* (BIERNAT, 1954) de l'Emsien supérieur et de l'Eifelian inférieur de la partie septentrionale des Monts Sainte-Croix; *C.? arnaoensis* n. sp. de l'Emsien supérieur et de l'Eifelian inférieur de la Cordillère Cantabrique; et *C.? nalykini* (BUBLICHENKO, 1928) d'âge Emsien supérieur et Eifelian inférieur probable de l'Altai SW.

Mots-clefs: Nucinulidae, Rhynchonellides, Brachiopodes, Emsien, Eifelian, Europe W, Afrique N, Altaï.

Introduction

An improved definition by SARTENAER (2004) of the species proposed by DE VERNEUIL (1850, p. 175) as *Terebratula Orbignyanus* resulted in its exclusion from *Uncinulus* BAYLE, 1878 in which it has generally been included after the establishment of this genus, and its assignment to a new genus. It is now necessary to clarify the generic and specific status of forms unduly mentioned or described and/or figured as *U. orbignyanus* in the literature in various areas of the world (major areas in italic): Algeria, South China, *Dinant Basin* (Belgium and France), France (Armorican Massif, Montagne Noire, The Pyrenees), Germany (Aachen area, Bergisches Land, Dillmulde, *Eifel area*, Harz Mountains, Hunsrück, *Lahnmulde*, *Mosel valley*, *Rhine valley*, Sauerland, Siegerland, Thuringia, Wittgensteiner Mulde), Mauritania (Zemmour), Morocco (Anti-Atlas, Meseta), Poland (Holy Cross Mountains), Portugal, Russia (Kuznetsk Basin, C Urals), Spain (*Cantabrian Cordillera*, Sierra Morena), Spanish Sahara.

The assignment of European, North-African and Asiatic forms to one and the same species and to one and the same genus (*Uncinulus*) has led to an oversimplification and confusion. A European *Uncinulus orbignyanus* [“*orbignyanus*”] Subzone and *U. orbignyanus* [“*orbignyanus*”] Community were even proposed by TERMIER, H. & G. (1960, table, p. 141), LLOPIS LLADÓ (1961, fig. 2), and LECOMTE *et al.* (1998, pp. 191, 194).

SARTENAER (*in* BULTYNCK & MORZADEC, 1979, p. 678; *in* BULTYNCK *et al.*, 1982, p. 33; 1982, p. 131) stated that most of the forms identified as *Uncinulus orbignyanus* (DE VERNEUIL, 1850), *U. lodanensis* (BURHENNE, 1899) and *U. pila* (SCHNUR, 1851) in the literature belonged neither to the genus nor to these species (forms improperly identified as such will be referred to as “*orbignyanus*”, “*lodanensis*” and “*pila*” in the remainder of the text). He suggested that the establishment of new genera was necessary in order to accommodate these species as

originally defined, and consequently, the forms erroneously assigned to them. The establishment of the genus *Nucinulus* SARTENAER, 2004 has been the first step in this direction. Four more new genera are proposed in the present paper.

The present investigation entails the examination under a new light of the alleged transitional forms “*orbignyanus*”-*pila*, “*orbignyanus*”-*subwilsoni*, and “*orbignyanus*”-*lodanensis*. These species have commonly been misinterpreted. Exaggerated weight has been given to some external characters (e.g. the presence or absence and/or distribution of costae bundles, the presence or absence of a median ridge in the sulcus and a median furrow on the fold and their occasional restriction to the posterior part of sulcus and fold) while some others have often been neglected (e.g. size). As will be shown, the definition of the new genera and species proposed in the present paper rests on a combination of various internal and external characters.

Family Nucinulidae SARTENAER, 2004

Remark: The assignment of four new genera (*Cuninulus*, *Oligodesmerhynchus*, *Lapinulus*, and *Palinulus*) to the family Nucinulidae entails some emendations related to the size, the “M”-shaped front, the dental plates, and the cardinal process:

- the type genus (*Nucinulus*) and *Oligodesmerhynchus* are small-sized, but *Palinulus* is small- to medium-sized, *Cuninulus* middle-sized, and *Lapinulus* middle- to large-sized;
- the “M”-shaped front due to the median notch formed by the furrow on the fold, and the corresponding ridge in the sulcus, is distinct in the type genus, *Cuninulus*, and *Oligodesmerhynchus*, attenuated in *Palinulus*, and only sometimes slightly marked in *Lapinulus*;
- clearly detached dental plates are only present in the type genus and *Oligodesmerhynchus*; they are absent in the other genera, but vestigial umbonal cavities are usually observed in transverse serial sections;
- the cardinal process is not always simple; in *Lapinulus* it is more elaborated.

Cuninulus n. gen.

DERIVATIO NOMINIS

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

TYPE SPECIES

C. melanopotamicus n. gen., n. sp.

DIAGNOSTIC FEATURES

Medium-sized. Dorsibiconvex. Contour subpentagonal to subrounded. “M”-shaped central part of front. Width consistently and clearly greater (10 to 30 per cent) than length and thickness. *Paries geniculatus*, *squamatae*, *glottae* present. Long marginal spine-like projections of

costae. 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 (= costae bundle), which, in rare cases, either does not reach the front or is absent, and high fold divided by a median furrow; ridge and furrow clearly marked at front. Greatest thickness of shell at front margin. Wide apical angle. Numerous divided and intercalated costae, flattened and provided with median narrow grooves in the *paries geniculatus*. Occasional presence of costae bundles on the flanks. Variable contour [fan (half open)- to slightly mushroom-shaped; sometimes subrectangular in the apex] of the delthyrial cavity in transverse serial sections. Thick shell. Stout septum. Absence of dental plates (vestigial umbonal cavities sometimes present). Thick undivided hinge plate. Large and robust teeth. Short cardinal process with numerous ridges. Crura rounded in their proximal part in transverse serial sections. Ventral muscle field deeply impressed. Dorsal muscle field only slightly impressed.

SPECIES ASSIGNED TO THE GENUS

Outside the type species, *C. concavus* n. sp. from the Eifel area, *C. leonensis* n. sp. from the Cantabrian Cordillera, *C. assaensis* n. sp. from the Morocco-Algerian borders, *C. eifeliensis* (BIERNAT, 1954) from the Holy Cross Mountains, *C. arnaoensis* n. sp. from the Cantabrian Cordillera, and *C. nalivkini* (BUBLICHENKO, 1928) from the Altai Mountains (only known to the author from the literature), are assigned to the new genus of late Emsian to early Eifelian age. *C. suborbignyanus* (BRICE, 1981) from the Armorican Massif is also assigned to the genus; this species has been fully described by BRICE (1981, pp. 205, 207, 212, 214, figs. 5A,B, p. 206, fig. 7, p. 213, pl. 25, figs. 6a-e, 7a-c, 8a,b, 9a,b, 10, 11 as *Uncinulus suborbignyanus*), and given a late Emsian age.

DESCRIPTION AND COMPARISONS

Transitional forms between “*orbignyanus*” (here assigned to *Cuninulus*) and “*pila*” are discussed under the description of *Lapinulus* n. gen.

Cuninulus n. gen. and *Nucinulus* SARTENAER, 2004 have been confused in the past, because most of their external characters are similar. Therefore, only differences are pointed out here, all other characters being those mentioned by SARTENAER (2004, pp. 82-83) in his description of the genus *Nucinulus*. *Cuninulus* differs from *Nucinulus* by a larger size (almost twice as large); a generally greater shell thickness; higher tongue and fold; a greater width resulting in wider flanks, and a transverse instead of a mostly elongated subpentagonal contour; a width generally clearly greater than length (in *Nucinulus* width is only slightly greater than length, and sometimes even equal to it); an often wider sulcus at front; a generally wider apical angle; longer marginal spine-like projections of the costae; the exceptional absence of a median ridge (= costae bundle) dividing the sulcus and/or its rare disappearance before reaching the front (in *Nucinulus* this ridge is always present and visible

at front); the occasional (rare or common depending on the species) presence of one to three (usually one or two) more or less pronounced costae bundles on each flank of the dorsal valve with, eventually, corresponding bundles on the ventral valve.

Cuninulus and *Nucinulus* have some similar internal features: a thick hinge plate, a well developed and stout septum, and a very short, pad-like cardinal process covering the whole hinge plate and exhibiting numerous ridges. But *Cuninulus* differs by a thicker shell; a fan (half open)-to mushroom-shaped contour of the delthyrial cavity in transverse serial sections (this contour is subrectangular in *Nucinulus*); the absence of dental plates, but vestigial umbonal cavities are sometimes present; larger and more robust teeth; an undivided hinge plate; and different crura (rounded in their proximal part in transverse serial sections in *Cuninulus*, wing-shaped in the same part in *Nucinulus*).

Species included in *Cuninulus* n. gen. have been previously assigned to *Uncinulus* BAYLE, 1878. Similarities and differences between the two genera are on the whole those mentioned between the latter genus and *Nucinulus* SARTENAER, 2004. The following alterations concern chiefly the internal characters. In *Uncinulus* and *Cuninulus* the shell in the apical region is thick, the contour of the delthyrial cavity in transverse serial sections is fan (half open)- to mushroom-shaped, and dental plates are absent (vestigial umbonal cavities are sometimes present). In *Uncinulus* costae bundles are always absent, the cardinal process is stockier, and the central part of the hinge plate extends anteriorly in transverse serial sections as a transverse section of a ship (for comparison see text-fig. 1 in SARTENAER, 2004).

Descriptions of the new species assigned to the genus, including measurements and counting of costae, are based on 50 to 150 specimens.

Cuninulus melanopotamicus n. gen., n. sp.

(Plate 1, Figures 1-10; Text-figure 1)

On the southern border of the Dinant Basin, *C. melanopotamicus* has been identified only as *Uncinulus orbignyanus* (generally) and *U. ladanensis* (sometimes). Therefore, the author does not see the need of a long list of citations.

DERIVATIO NOMINIS

Μελας αινα, αν (Greek, adjective) = black; ποταμός, ου (ο) (Greek, masculine) = river; the name draws attention to the Eau Noire Formation in which the species is particularly abundant.

TYPES, LOCUS TYPICUS AND STRATUM TYPICUM

Holotype, IRScNBa12151 (Pl. 1, figs. 6-10). Specimen figured by SARTENAER (*in* ROBASZYNSKI & DUPUIS, 1983, pl. 2, p. 193, fig. 19 = ventral view, as “*Uncinulus orbignyanus*”). Paratype A, IRScNBa12152 (Pl. 1, figs. 1-5). Chanly near Wellin on the southern border of the Dinant Basin. About 20 m above the base of the Eau Noire Member (Colb) of the Bure Formation (Col-a-c

= lower Couvinian), the member being about 90 m thick in the Chanly section. Collected by J. Godefroid (see GODEFROID, 1968b, p. 29).

Paratype B, IRScNBa12153 (Text-fig. 1). Jemelle, opposite the railroad station, on the southern border of the Dinant Basin. 10 m below the top of the Eau Noire Member. Collected by J. Godefroid (see GODEFROID, 1968b, pp. 72-73, pl. 5).

DESCRIPTION

Remark: In the literature there are only two descriptions of the species from the southern border of the Dinant Basin: a very short one (a very wide sulcus with a median ridge, and a median furrow on the fold) by LE MAÎTRE (1929, p. 62 as *Uncinulus orbignyanus* from Fourmies, France); and MAILLIEUX (1938, pp. 38-39) referring to specimens identified as *U. ladanensis*, but considered in this paper to be within the range of variation of the present species.

Few illustrations of the species exist in the literature: LE MAÎTRE (1929, pl. 3, figs. 12a-c as *U. orbignyanus* = ventral, dorsal, and anterior views of one specimen; 1934, pl. 18, fig. 2 as *U. orbignyanus* = ventral view), MAILLIEUX (1938, figs. 3, 3a-c, p. 39 as *U. ladanensis* = dorsal, ventral, lateral and anterior views of one specimen), and SARTENAER (see above).

The following features are specific: thickness of dorsal valve varying between 58 and 70 per cent of the shell thickness; longitudinal median ridge (= costae bundle) in the sulcus and median furrow on the fold always present; longitudinal median ridge (= costae bundle) of sulcus relatively high, subangular to rounded; numerous costae [median costae: 18 to 30 (most of the values: 24 to 30), 4 to 9 of them being parietal; lateral costae: 16 to 22]; ventral median costae close-set in the anterior half of the unrolled length of the valve and narrower than the lateral costae, parietal costae having an intermediate width; costae bundles on the flanks present in 36 per cent of specimens; length/width ratios: 0.79 to 0.88 (holotype: 0.84); thickness/width ratios: 0.58 to 0.83 (holotype: 0.80); thickness/length ratios: 0.67 to 0.95 (holotype: 0.95); width of sulcus at front: 47 to 72 per cent (most of the values between 54 and 67 per cent) of the shell width; apical angle varying between 115° and 126° (most of the values between 119° and 126°).

Transverse serial sections from one specimen (paratype B, IRScNBa12153) are shown on Text-figure 1; they are the first sections ever made in specimens of the Dinant Basin.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

At the end of the 19th century the “Grauwacke de Hierges” was divided into a lower and upper level (“niveaux inférieur et supérieur”) that became respectively the “Assise de Hierges” (= Em3 = upper Emsian) and “Assise de Bure” (= Col1 = lower Couvinian) in the beginning of the 20th century. During this period *Cuninulus melanopotamicus* was abundantly mentioned in the upper level (= “Assise de Bure”). The “Assise de Bure”

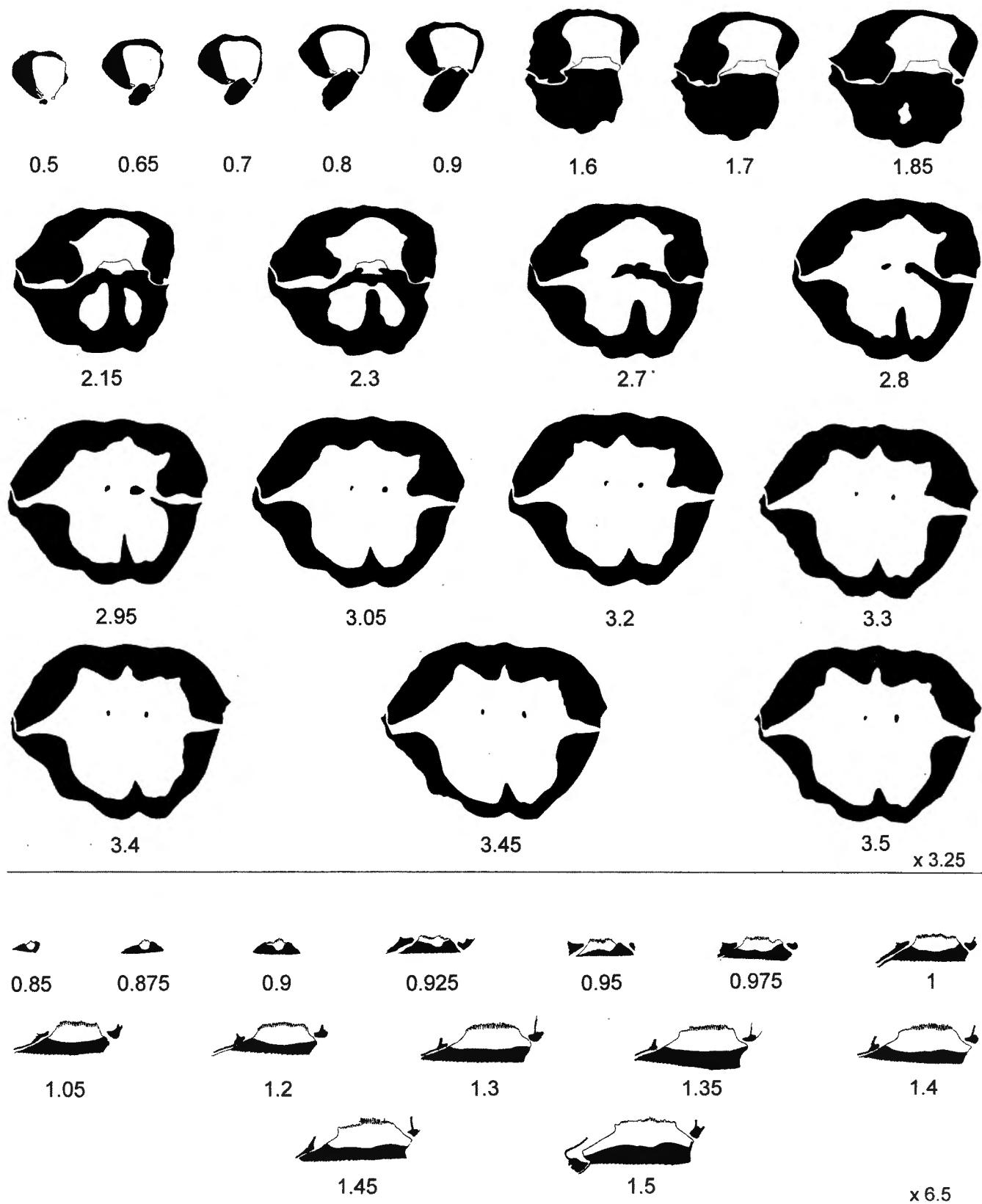


Fig. 1 — *Cuninulus melanopotamicus* n. gen., n. sp. Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Paratype B, IRSNBa12153. Jemelle, opposite the railroad station, southern border of the Dinant Basin. 10 m below the top of the Eau Noire Member (Co1b) of the Bure Formation (Co1a-c = lower Couvinian). Collected by J. Godefroid (see GODEFROID, 1968b, pp. 72-73, pl. 5). Measurements: length = 13.8 mm; width = 14.7 mm; thickness = 10.8 mm.

corresponds to the regional “schistes” or “zone” or “assise à *Spirifer cultrijugatus*” often mentioned in the literature. Further subdivisions of Co1 - Co1a, b, c - were introduced by MAILLIEUX (1912-1938). In present usage the Saint-Joseph (Co1a) and Eau Noire (Co1b-c) formations replace the “Assise de Bure”. *Cuninulus melanopotamicus* is present in the uppermost part of the “Assise de Hierges” (Hierges Formation), in Co1a-c, and in Co2a (Co2 being the “Assise de Couvin” = Couvin Formation); it is particularly abundant in Co1b, disappears in the middle part of Co1c, and reappears in Co2a (one specimen in MAILLIEUX’s collection). The species has been considered a “Leitform” of the *Cultrijugatus*-Schichten in Belgien by KAYSER (1871b, p. 504) or as “belonging to the *Spirifer cultrijugatus* shales” (“propre aux schistes à *S. cultrijugatus*”) by MAILLIEUX (1912, p. 55) or as “a (very) specialized species of the upper part of the “*S. cultrijugatus* zone” or the upper part of the “assise à *S. cultrijugatus*” or of the “assise de Bure (Co1)” by MAILLIEUX (1913a, p. 48; 1913b, foot-note, p. 14, p. 15; 1927, p. 145) or as “a particular species of the *S. cultrijugatus* zone” (“spéciale à la zone à *S. cultrijugatus*”) by LE MAÎTRE (1934, p. 241). Some formal expressions have underlined the presence of the species in Co1, and particularly its abundance in Co1b: “zone à *Rhynchonella Orbignyana*” (GOSSELET, 1888, p. 382); “zone Co1b à *U. orbignyanus*” (LECOMPTÉ, 1960, p. 31; GODEFROID, 1965, p. 82;

1968a, p. 484); “zone à *U. orbignyanus* et *Zdimir hercynicus*” (= middle of the three zones recognized in the “Assise de Bure”) (LECOMPTÉ, 1967, pl. 6, p. 30); “zone à *Uncinulus orbignyanus*” (BULTYNCK, 1970, pp. 24, 28, 29); “*U.*” *orbignyanus* subzone (MAMEDOV & RZHONSNITSKAYA, 1985, table 3, p. 151); “*U.*” *orbignyanus-Zdimir hercynicus*“ zone (RZHONSNITSKAYA, 1986, table 1, pp. 56-57).

In terms of the conodont zonation the species is restricted to the uppermost *Polygnathus serotinus* and *P. patulus* Zones.

The species is restricted to the southern border of the Dinant Basin.

***Cuninulus concavus* n. gen., n. sp.**
(Plate 1, Figures 11-20; Text-figures 3,4)

In the “Eifelkalkmulden”, *C. concavus* has been always identified as *Uncinulus orbignyanus*. Therefore, the author does not see the need of a long list of citations for this one and a half century old species.

DERIVATIO NOMINIS

Concavus, *a*, *um* (Latin, adjective) = undulated; the name draws attention to the undulated topography of the “Eifelkalkmulden”.

Cuninulus leonensis
and *C. ? amaoensis*

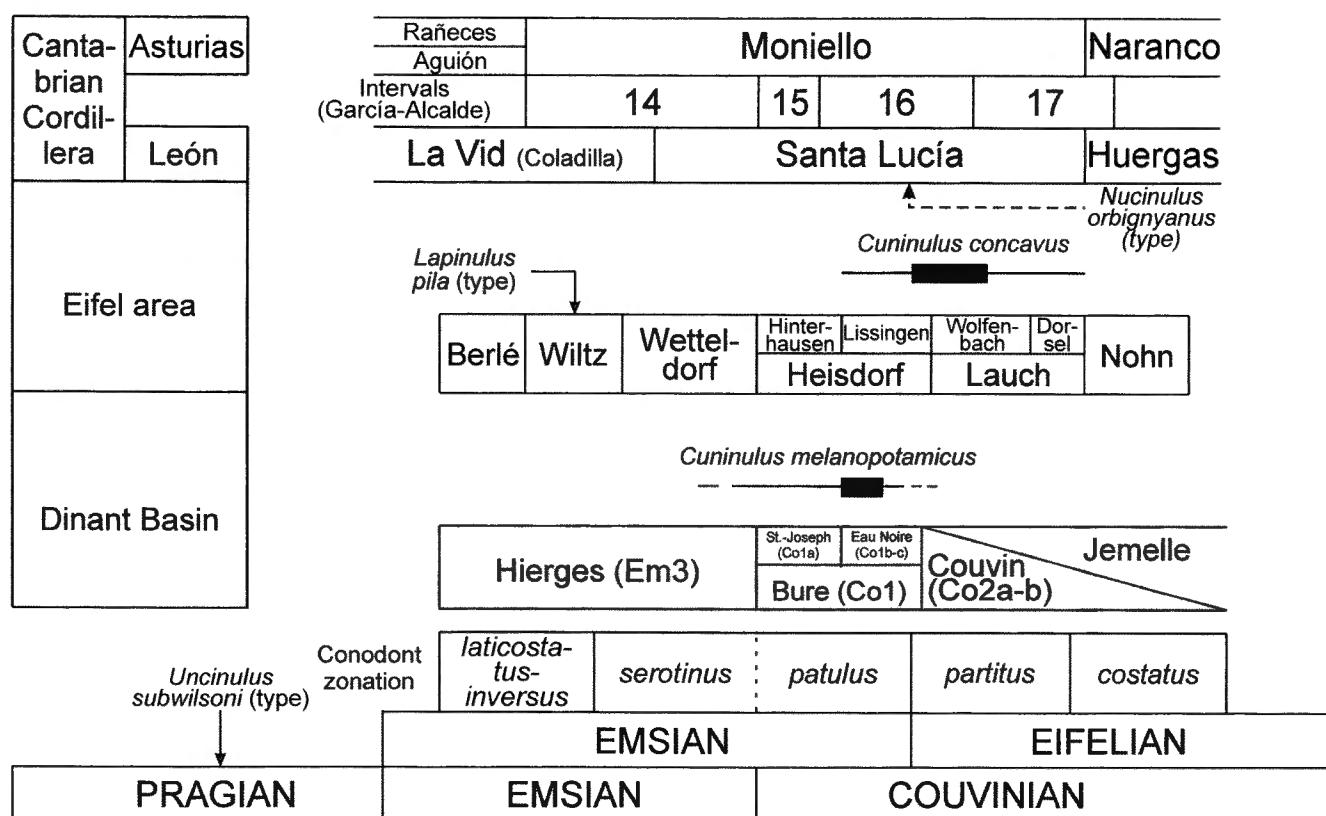


Fig. 2 — Range of some species and type localities of the type species of some genera from the Cantabrian Cordillera, the Eifel area, and the Dinant Basin discussed in the present paper.

TYPES, LOCUS TYPICUS, AND STRATUM TYPICUM

Holotype, IRSNBa12154 (Pl. 1, figs. 11-15). Leudendorf near Uxheim, "Hillesheimer Mulde", "Eifelkalkmulden". Below the bentonite layer Libra I, lower Wolfenbach Member of the Lauch Formation, early Eifelian. Collected by P. Sartenaer, 1974.

Paratype A, IRSNBa12155 (Pl. 1, figs. 16-20). Same locality, member, and collector.

Paratype B, IRSNBa12156 (Text-fig. 3). Western bank of Nohn brook about 500 m SW of Eulenberg, "Hillesheimer Mulde", "Eifelkalkmulden". Wolfenbach Member of the Lauch Formation, early Eifelian. Collected by Sartenaer, P., 1974.

Paratype C, IRSNBa12157 (Text-fig. 4). Same locality, member, and collector.

DESCRIPTION

The species has been described by the following authors: SCHNUR (1853, p. 187 as *Terebratula* conf. *T. Orbignyana*), (1853, pp. 59-60 as *T. Orbignyana*), KAYSER (1871b, pp. 504-505 as *Rhynchonella Orbignyana*), and SCHMIDT [1941, p. 17 as *Uncinulus orbignyanus*; 1942, p. 391 as *U. (U.) orbignyanus*].

The following illustrations of the species exist in the literature: SCHNUR (1853, pl. 26, figs. 2a-f as *Terebratula* conf. *T. Orbignyana* = ventral, dorsal, and anterior views of one specimen, anterior and dorsal view of another specimen, and ventral view of a mould; some of these figures have been duplicated in various popular works), SCHMIDT (1941, pl. 1, figs. 14a-c as *Uncinulus orbignyanus* = dorsal, ventral, and anterior views of one specimen), and WERNER (1980, fig. 17, p. 17 as *U. orbignyanus* = ventral, dorsal, anterior, and posterior views of one specimen). Marginal spine-like projections of costae have been figured by SCHMIDT (1937, figs. 23a,b, p. 36, figs. 24a-c, p. 37).

DIAGNOSTIC FEATURES

C. concavus is an abundant species, which shows little variability as pointed out by KAYSER (1871b, p. 505 as *Rhynchonella Orbignyana*). Thickness of dorsal valve varying between 61 and 70 per cent of the shell thickness; length/width ratios: 0.77 to 0.92 (holotype: 0.77); thickness/width ratios: 0.76 to 0.95 (holotype: 0.76); thickness/length ratios: 0.93 to 1.11 (holotype: 1.05). Apical angle varying between 115° and 128° (most of the values between 118° and 128°).

C. concavus and *C. melanopotamicus* have a similar size. *C. concavus* can be separated from *C. melanopotamicus* by: a generally lower longitudinal median ridge (= costae bundle) in the sulcus and a generally shallower median furrow on the fold; the median ridge in the sulcus only present in 59 per cent of specimens, and when present, disappearing at front in 30 per cent of specimens; median and lateral costae having the same width; the fold rising sometimes abruptly near the frontal margin (it does only occasionally in *C. melanopotamicus*); a lower number of median costae (parietal costae included) (15 to 22 against 18 to 30 in *C. melanopotamicus*); a lower number

of parietal costae (3 to 5 against 4 to 9 in *C. melanopotamicus*); costae bundles on flanks only present in 17 per cent of the specimens (36 per cent in *C. melanopotamicus*); specimens of *C. concavus* often slightly thicker; some specimens of *C. concavus* may reach a slightly greater size than the largest specimens of *C. melanopotamicus*, and have a deeper sulcus and a higher fold.

Transverse serial sections from two specimens (paratypes B, IRSNBa12156 and C, IRSNBa12157) are shown on Text-figures 3 and 4; they are the first sections ever made in specimens from the Eifel area.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

C. concavus was mentioned by SCHNUR (1851, p. 6 as *Terebratula Orbigniana*) in the Eifel area one year after the establishment of *Nucinulus orbignyanus*, and four years before it was for the first time mentioned in the Dinant Basin by DE VERNEUIL (*in Hébert*, 1855, pp. 1174, 1185 as *T. Orbignyana*).

During the second half of the 19th and first half of the 20th century, *C. concavus* was mentioned in the "Grauwacke" and in the "Cultrijugatus-Stufe" ("Cultrijugatus-Schichten", "Cultrijugatus Zone", etc...), which were placed in the Lower or in the Middle Devonian or both; it was considered by KAYSER (1871b, p. 504) as a "Leitform der Cultrijugatus-Schichten", and WEDEKIND (1926, table between p. 200 and 201 as *Uncinulus orbignyanus*) called "Zone des *Spirifer cultrijugatus* und des *Uncinulus orbignyanus*" the uppermost zone of the four zones recognized in the Cultrijugatus-Stufe (= upper half of the "obere Cultrijugatus-Schichten").

The evolution and intricacies of the "Cultrijugatus-Stufe" concept generated, and still generates, considerable confusion within and outside the Eifel area. Furthermore, the concept would be irrelevant, because it would not shed more light on the stratigraphic position given during this long period to the species here discussed. In the thirties of the 20th century the old terminology progressively gave way to more precise stratigraphic subdivisions ("Heisdorf-", "Lauch-Schichten", etc...), and a consensus was reached by the German geologists on the occurrence of *C. concavus* in the "Heisdorf-" and "Lauch-Schichten" of which it is a "Leitfossil" according to HEIBEL (1969, p. 558), i.e. in terms of the conodont zonation, in the *Polygnathus patulus* and *P. partitus* Zones.

Some problems remain concerning the first and last occurrence of the species. Except a mere mention by RICHTER, R. & E. (1920, p. 27 as *Rhynchonella orbignyanus*), SCHMIDT [1941, table 2, p. 51; 1942, pp. 391, 400, table 1, p. 401, table 2, p. 402 as *Uncinulus (U.) orbignyanus* from the Wetteldorf trench ("Richtschnitt") in the "Prümmer Mulde"] is the only German palaeontologist who mentions "the rather uncommon occurrence ('spärliches Vorkommen') in the Wetteldorf Sandstone of 'slightly impressed moulds' ('wenig ausgeprägte Steinkerne'), 'which in any case are closer to *orbignyanus* than to *pila*'". The author considers that the presence of the species in the Wetteldorf Formation, in which fossils are very often completely absent, rests on a fragile and questionable basis, and must be dismissed. As far as the presence of the species in the lower Upper Emsian ("tieferes Oberkoblenz") as advocated by SCHMIDT (1941, table 2, p. 51; 1942, table 1, p. 401) is concerned, it must be disregarded.

QUIRING (1914, pp. 67-68, 76 as *Rhynchonella orbignyanus* from the "Ahrdorfer Mulde") and PAULUS (1961, p. 30 as *U. orbignyanus* from the "Sötenicher Mulde"), collected the species from beds of questionable age (uppermost "Laucher

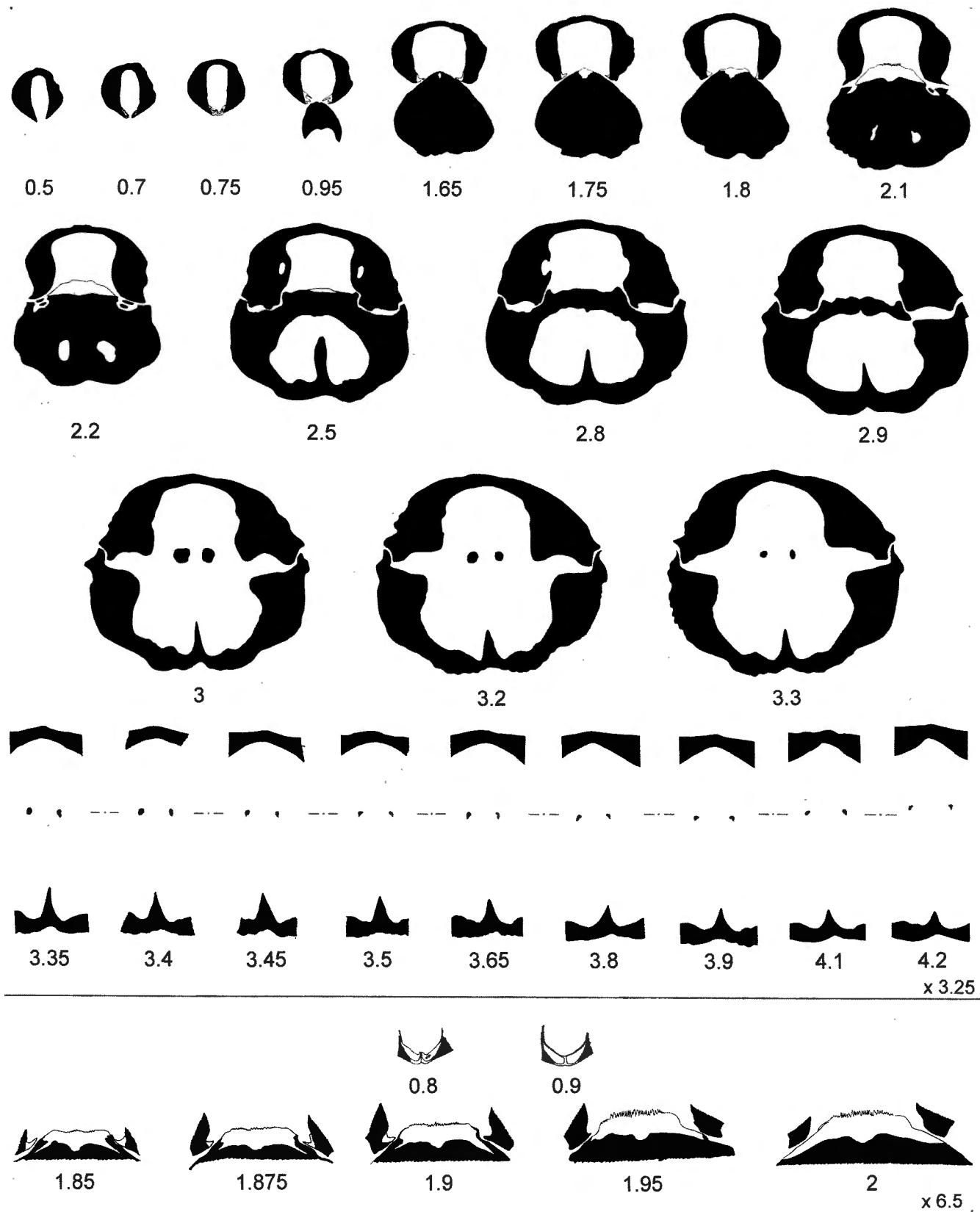


Fig. 3 — *Cuninulus concavus* n. gen., n. sp. Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Paratype B, IRSNBa12156. Western bank of Nohn brook, about 500 m SW of Eulenberg, "Hillesheimer Mulde", "Eifelkalkmulden". Wolfenbach Member of the Lauch Formation, early Eifelian. Collected by P. Sartenaer, 1974. Measurements: length = 15.9 mm; width = 20 mm; thickness = 18.1 mm.

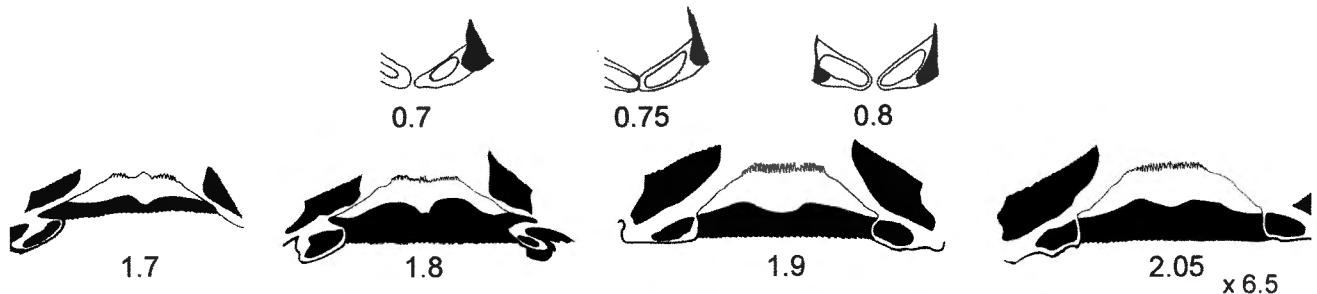
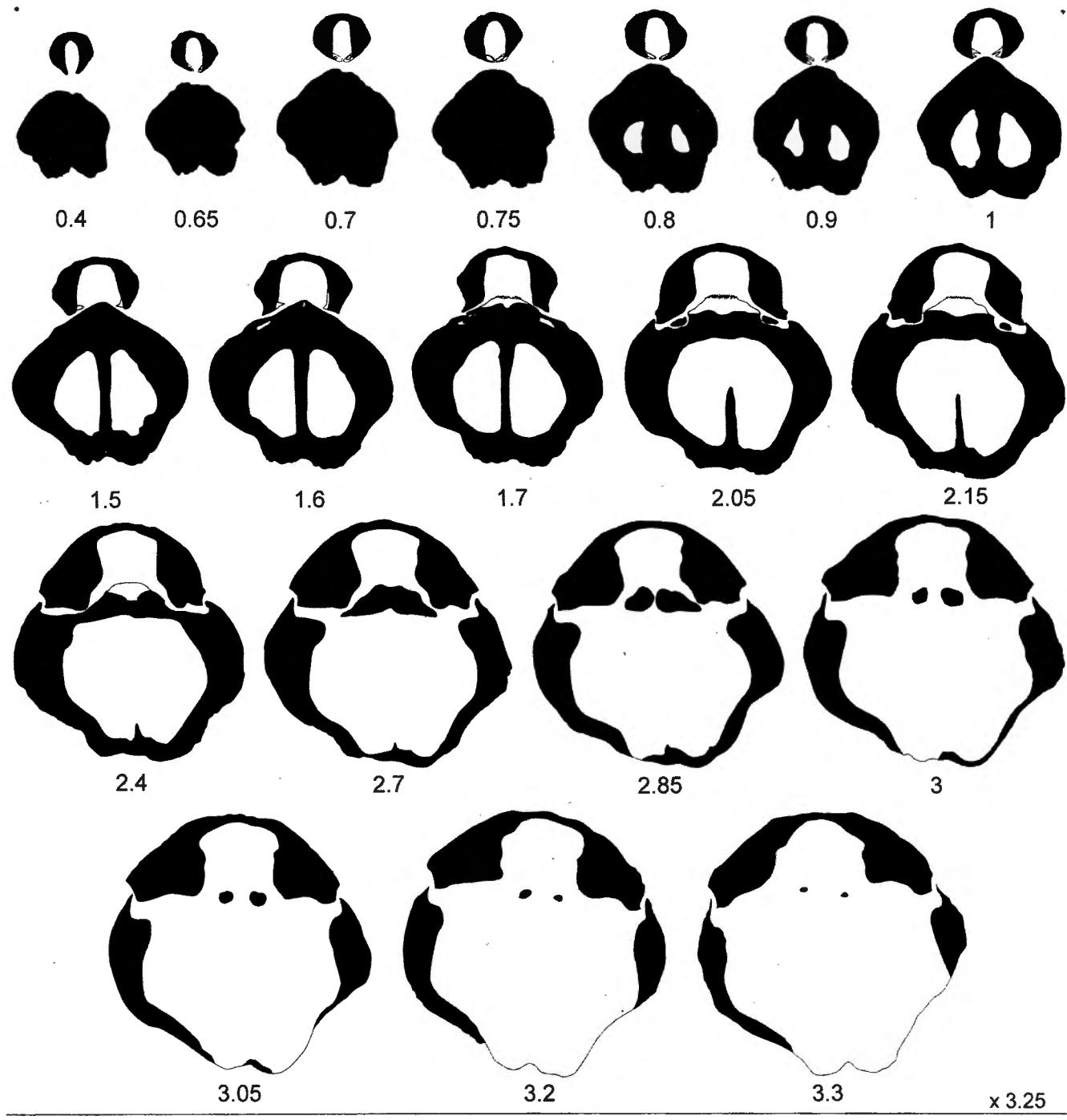


Fig. 4 — *Cuninulus concavus* n. gen., n. sp. Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Paratype C, IRScNBa12157. Western bank of Nohn brook, about 500 m SW of Eulenberge, "Hillesheimer Mulde", "Eifelkalkmulden". Wolfenbach Member of the Lauch Formation, early Eifelian. Collected by P. Sartenaer, 1974. Measurements: length = 15.2 mm; width = 18.7 mm; thickness = 16.7 mm.

Schichten" or lowermost "Untere Nohner Schichten". The doubt raised by QUIRING has been lifted by KRÖMMELBEIN (*in Krömmelbein et al.*, 1955, p. 24) and by HOTZ *et al.* (*in Krömmelbein et al.*, 1955, pp. 56-57), who put these beds in the Dorsel Member (upper member of the Lauch Formation); this should apply also to the "transitional beds" mentioned by PAULUS.

German authors accept that the species does not range above the "Lauch-Schichten", some even stating that the "OCA Fauna" ends at the top of the Lauch Formation that coincides with the top of the "jugleri Event".

If the range of the species in the Heisdorf and Lauch Formations is scrutinized, we must accept that it has never been found in the Hinterhausen Member (= lower member of the Heisdorf Formation) and seldom in the Dorsel Member (= upper member of the Lauch Formation), which is poor in macrofossils.

This leaves us with the following range for the species: Lissingen Member (= upper member of the Heisdorf Formation), in the uppermost part of which a "Massenvorkommen" has only been mentioned in one bed ("Packen" 113) by SCHMIDT [1942, pp. 392, 400, table, p. 402 as *Uncinulus (U.) orbignyanus*] in the Wetteldorf trench; Wolfenbach Member (= lower member of the Lauch Formation) in which "Massenvorkommen" are common; and Dorsel Member.

In terms of the conodont zonation the species is present in the upper half of the *Polygnathus patulus* Zone and in the *P. partitus* Zone. It means that the range of *C. concavus* and *C. melanopotamicus* overlap, the former species being younger on the whole; in particular the acme of *C. concavus* occurs in younger beds.

The species has been mentioned in almost all the "Eifelkalkmulden".

Cuninulus leonensis n. gen., n. sp. (Plate 1, Figures 21-30; Text-figure 5)

DERIVATIO NOMINIS

The name draws attention to the abundance of the species in the northeastern part of the Province of Leon.

TYPES, LOCUS TYPICUS, AND STRATUM TYPICUM

Holotype, GPIT Br.1255/28 (Geologisch-paläontologisches Institut der Universität, Tübingen; Br. = brachiopods) (Pl. 1, figs. 21-25 = pl. 5, figs. 4a-c *in Schumann, 1965 as Uncinulus orbignyanus*). Near Argovejo (Aguasalio Syncline), Province of Leon, Cantabrian Cordillera (see SCHUMANN, 1965, fig. 24). Late Emsian.

Paratype A, GPIT Br.1255/27 (Pl. 1, figs. 26-30 = pl. 5, figs. 3a-c *in Schumann, 1965 as U. orbignyanus*). Same locality and age.

Paratype B, IRSNBa 12158 (Text-fig. 5). Same locality and age. Collected by P. Sartenaer, 1977.

DESCRIPTION

The three species recognized by the author (2004; present paper), *Nucinulus orbignyanus*, *Cuninulus leonensis* n. sp., and *C.? arnaoensis* n. sp., were until now lumped together under a single species. Therefore, descriptions and figures of the literature include or show one or more characters of these three species. Such descriptions were given by DE VERNEUIL (1850, p. 175 as *Terebratula Orbignyana*), BARROIS (1882, p. 265 as *Rhynchonella*

Orbignyana), COMTE (1938, pp. 57-58 as *Uncinulus orbignyanus*), and SCHUMANN (1965, pp. 83-85 as *U. orbignyanus*). Illustrations were given by DE VERNEUIL (1850, pl. 3, figs. 10a-c as *Terebratula Orbignyana* = dorsal, lateral, and anterior views of one specimen supposedly from Sabero; figured again + a ventral view by COMTE, 1938, pl. 5, figs. 7, 7a-c as *Uncinulus Orbignyanus*, and + ventral and posterior views by SARTENAER (2004, fig. 2, p. 85 as *Nucinulus orbignyanus*), BARROIS (1882, pl. 11, figs. 1a,b as *Rhynchonella Orbignyana* = dorsal and anterior views of one specimen from Arnao), SCHUMANN (1965, pl. 5, figs. 1a-c, 2a-c, 3a-c, 4a-c as *Uncinulus orbignyanus* = dorsal, anterior, and lateral views of four specimens + various drawings and photographs of the shell, the cardinal process, marginal spine-like projections, and transverse serial sections from Argovejo), WESTBROEK (1967, pl. 12, fig. 11 as *U. orbignyanus* = lateral view + various drawings and photographs of the shell, the mantle, marginal spine-like projections, *squamae* and *glottae*, and one transverse section).

SCHUMANN stated that the median ridge in the sulcus is always well developed in the Spanish shells while, as a rule, this ridge was only vaguely noticeable in the Eifelian shells. Still he pointed out that "Alle [spanischen] Exemplare stimmen mit denen anderer europäischer Fundpunkte gut überein" [Remark: *Uncinulus orbignyanus* collected and examined by SCHUMANN (1965, pp. 83, 89, fig. 24) all derive from the Aguasalio Syncline, S of Argovejo in the northeastern part of the Province of Leon; the "massenhaft" occurrence of the species 95 km to the NW of Argovejo in the Ensenada of Moniello, NW of Luanco on the Cantabrian coast in the Province of the Asturias is only mentioned].

SCHUMANN expressed his disagreement about the subspecies status, *U. orbignyanus eifeliensis* BIERNAT, 1954, given by BIERNAT (1954, pp. 511-514) to the "Eifler Form". As a matter of fact, BIERNAT does not even mention the German form, and the name *eifeliensis* was given by her with reference to the Eifelian Stage in which the Polish subspecies was found and described.

SCHUMANN also denied any taxonomical value to the following characters which he considered as expressions of a variability due to the strong sensitivity of *U. orbignyanus* to various environments: the length/width ratio varying from one outcrop to the other, more or less strong costae bundles, more or less marked sulcus and fold, the presence or absence of a stronger median costa in the sulcus, and the exclusive presence of small-sized specimens in some beds.

DIAGNOSTIC FEATURES

C. leonensis is an abundant species with a size similar to the one of *C. melanopotamicus* and *C. concavus*. Thickness of dorsal valve varying between 55 and 73 per cent of the shell thickness. Length/width ratios: 0.83 to 1 (holotype: 0.88); thickness/width ratios: 0.68 to 0.85 (holotype: 0.79); thickness/length ratios: 0.76 to 0.93 (holotype: 0.89). Apical angle varying between 105° and 125° (most of the values between 115° and 120°).

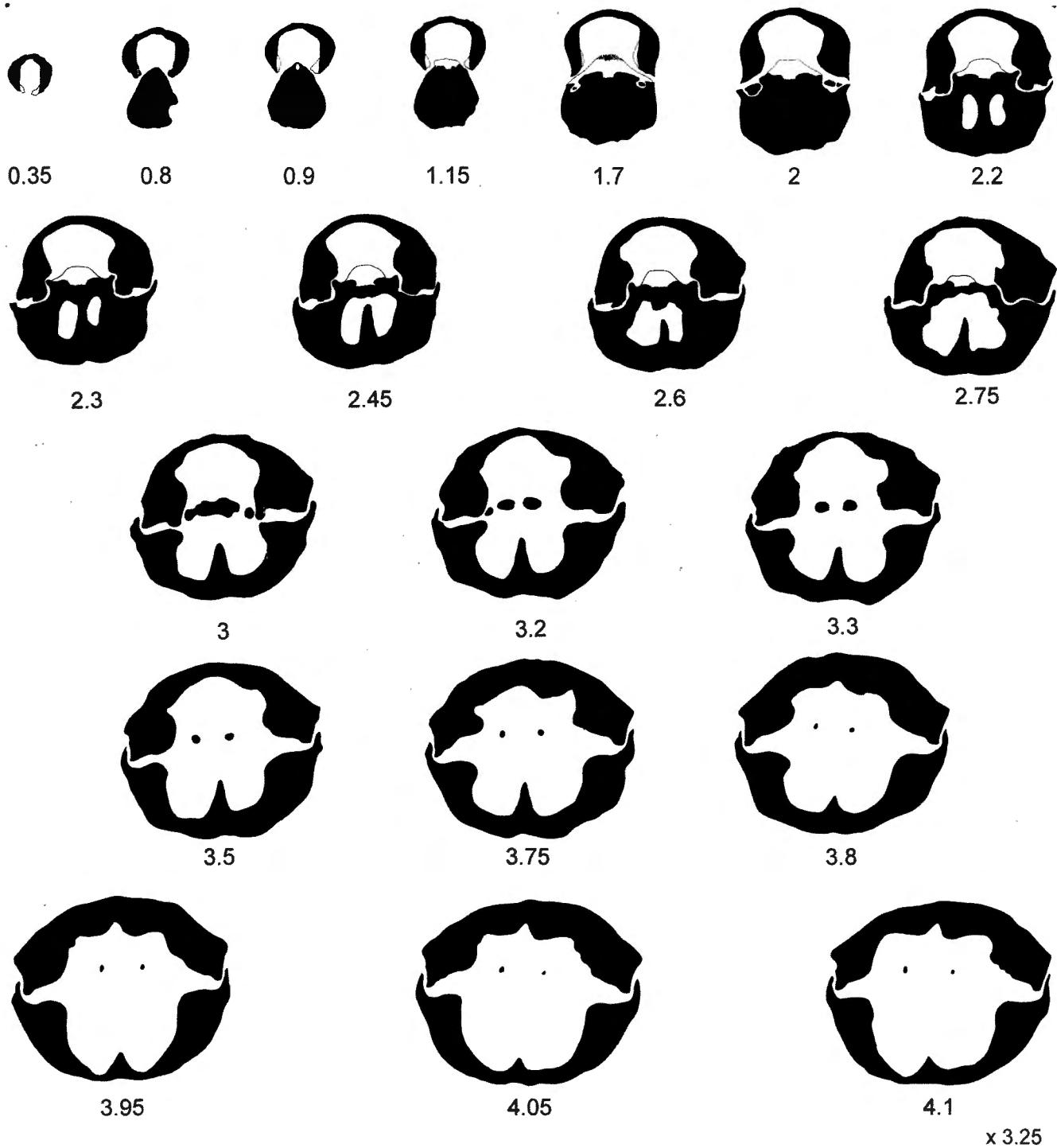


Fig. 5 — *Cuninulus leonensis* n. gen., n. sp. Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Paratype B, IRSNBa12158. Near Argovejo (Aguasalio Syncline), Province of Leon, Cantabrian Cordillera (see SCHUMANN, 1965, fig. 24). Late Emsian. Collected by P.Sartenaer, 1977. Measurements: length = 16.3 mm; width = 17.4 mm; thickness = 13.9 mm.

Median + lateral costae: 20 to 26; parietal costae: 5 to 6; lateral costae: 16 to 27.

C. leonensis differs from *C. melanopotamicus* and *C. concavus* by the absence of costae bundles on the flanks, and by an intermediate number of parietal costae.

C. leonensis, like *C. melanopotamicus*, differs from *C. concavus* by the constant presence of a longitudinal

median ridge (= costae bundle) in the sulcus, and by more pronounced median ridge in the sulcus and median furrow on the fold. Width of median and lateral costae is the same in *C. concavus* and *C. leonensis*, while the ventral median costae in the anterior half of the unrolled length of the valve are close-set and narrower than the lateral costae in *C. melanopotamicus*. The fold on the dorsal

valve of *C. leonensis* never rises abruptly near the frontal margin while it does so occasionally in *C. melanopotamicus* and slightly more often in *C. concavus*. The longitudinal median ridge in the sulcus never disappears at front in *C. melanopotamicus*, but does so in 18 per cent of the specimens in *C. concavus*, and in 10 per cent of the specimens in *C. leonensis*.

Transverse serial sections of one specimen (paratype B, IRSNBa12158) are shown on Text-figure 5; sections from one specimen and sketches have been given by SCHUMANN (1965, fig. 3b, p. 52, figs. 8a,b, p. 60, figs. 9a-d, p. 62, fig. 17, p. 87).

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

C. leonensis comes from the upper part of the Santa Lucía Formation, which stretches out on a distance of about 20 km between Bonar and Argovejo in the northeastern Province of Leon, Argovejo, Aviados, and Vozmediano being the main collecting localities. In terms of the conodont zonation the species is restricted to the *Polygnathus partitus* Zone.

GARCÍA-LÓPEZ & SANZ-LÓPEZ (2002, p. 171) have mentioned the species as "large forms" of *Uncinulus orbignyanus* at the top of the upper member [member IV] of the Santa Lucía Formation).

Cuninulus assaensis n. gen., n. sp.

- v 1964 *Uncinulus ladanensis* (BURHENNE, 1899) - DROT, p. 10, table, p. 94, pp. 150-151, 209;
- v 1965 *Uncinulus ladanensis* - HOLLARD, p. 39;
- v 1967a *Uncinulus ladanensis* (BURH.) - HOLLARD, fig. 7, p. 220;
- v 1967b *Uncinulus ladanensis* - HOLLARD, p. 108;
- v 1974 *Uncinulus ladanensis* (BURHENNE) - HOLLARD, pp. 46-47;
- v 1978 *Uncinulus ladanensis* (BURHENNE) - HOLLARD, pp. 9, 18, table 2, p. 21;
- v 1980 *Uncinulus ladanensis* - BULTYNCK & HOLLARD, fig. 2, pp. 13-14;
- v 1981 *Uncinulus ladanensis* - DROT, p. 56, fig. 9, pp. 57, 58;
- v 1981 *Uncinulus ladanensis* - HOLLARD†, table 1;
- v 1982 *Uncinulus ladanensis* - BULTYNCK & HOLLARD†, table 1, p. 47.

DERIVATIO NOMINIS

The name draws attention to the Assa region in the western Dra plains (Anti-Atlas), Morocco.

HOLOTYPE, LOCUS TYPICUS, AND STRATUM TYPICUM

Specimen of plate 16, figures 5a-c in DROT (1964 as *Uncinulus ladanensis*). N'Kheïla, ESW of Tanzida (sheet Assa), western Dra plains (Anti-Atlas), Morocco (locality As96 of Hollard, H.). Upper part of Yeraïfia Formation (lower Eifelian).

DIAGNOSTIC FEATURES

Thickness of dorsal valve varying between 59 and 76 per cent of the shell thickness. Length/width ratios: 0.72 to 0.93 (holotype: 0.89); thickness/width ratios: 0.65 to 0.78 (holotype: 0.72); thickness/length ratios: 0.76 to 0.95

(holotype: 0.81). Apical angle varying between 116° and 124° (most of the values between 116° and 121°). Median + parietal costae (it is difficult to count them separately): 23 to 43; parietal costae: 5 to 8; lateral costae: 17 to 29.

C. assaensis is distinct from the three species already described by the following characters: a greater number of costae, especially of median costae (parietal costae included); costae bundles on the flanks (2 to 3) present in 50 per cent of specimens; longitudinal median ridge (= costae bundle) in sulcus and median furrow on fold well marked and variable in height and depth respectively as well as in width (when the ridge is high and the furrow deep, they are higher and deeper respectively than in the other species); *squamæ* and *glottæ* particularly developed. Although the size of *C. assaensis* is similar to the one of the three species already described, some specimens may reach a larger size and a greater width. The ventral median costae of *C. assaensis* are close-set in the anterior part of the unrolled length of the valve and narrower than the lateral costae, parietal costae having an intermediate width; in this *C. assaensis* is similar to *C. melanopotamicus*. In *C. assaensis* and in *C. leonensis* the fold never rises abruptly near the frontal margin.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

C. assaensis has been collected in abundance from the upper part of the "Assise de n'Kheïla" (= upper part of Yeraïfia Formation) above the sandstone unit of "Rich IV" in localities of the Provinces of Assa and Tarfaya [n'Kheïla, ESW of Tanzida (As96); SE of Oudate Balra (Tf71); Hassi-Smeira (As257 = As24)] in a restricted region of the western Dra plains (Anti-Atlas). These beds correspond to the *Polygnathus linguiformis linguiformis* β Fauna (later *P. linguiformis pinguis* Fauna), i.e. the lower Eifelian *P. costatus partitus* Zone in terms of the present conodont zonation.

It is highly probable, as suggested by HOLLARD (1967a, fig. 8, p. 222, fig. 14, p. 229, fig. 15, p. 230), that the species is also present on the south flank of the Tindouf Basin (Morocco-Mauritania-Algeria). It is the region where ARDEN & REHRIG (1964, p. 1513, fig. 2, pp. 1516-1517, pp. 1517, 1521, table 1, p. 1522, p. 1523) mentioned a lower Eifelian *Uncinulus* zone (or *U. sandstone*) containing abundant *U. ladanensis*. SOUGY (1964, table 28, p. 374, pp. 389, 390, fig. 66, pp. 435, 436, 437, 439, 444, table 33, pp. 470, 473, table 34, pp. 477, 478, table 36, pl. 36, figs. 6a,b) also collected *U. ladanensis* in the lower Couvinian Tighirt sandstones and siltstones.

Cuninulus eifeliensis (BIERNAT, 1954)

C. eifeliensis, confined to the northern Holy Cross Mountains, was introduced in the literature by SOBOLEV [1901, p. 6, pl. 1, figs. 2, 2a,b as *R. d'Orbigyana*; 1909, p. 147 as *R. Orbignyana* from the Grzegorzowice beds (= *cultrijugatus* beds) at the base of the *Calceola* beds], and first described by BIERNAT (1954, pp. 145, 147, 149, 150, 489, table 1, p. 490, pp. 511-514, 528, 528-529, fig. 12, p. 512, fig. 13, p. 513, pl. 4, figs. 1-5 as *Uncinulus orbignyanus eifeliensis* n. subsp.).

The subspecies is abundant (up to 92 specimens are mentioned, although the description rests on only 17 well

preserved specimens and 15 moulds) in the Lower Eifelian (now late Emsian + lowermost Eifelian) layers 3 to 6 (= lower 105 m) of the Grzegorzowice beds in the Bodzentyn Syncline.

Specimens of the subspecies have been considered by BIERNAT (1954, p. 513) as “intermediate” between “*orbignyanus*” (of which they have the general contour, the dimensions and the large umbo) and “*lodianensis*” (of which they have the costae bundles). As a result DROT (1964, p. 150) and SCHUMANN (1965, pp. 84-85) put the subspecies in the synonymy of “*lodianensis*” and “*orbignyanus*” respectively (see further details under the description of *Oligodesmerynchus* n. gen.). The name given to the subspecies was not the best choice; it applies to the age (Eifelian) given to it by BIERNAT in the Holy Cross Mountains, and in no way to the Eifel area, contrary to SCHUMANN’s (1965, pp. 84-85) interpretation.

The subspecies is here elevated to the species rank.

The following combined features make *Cuninulus eifeliensis* distinct from the other species of the genus: a small to medium size; the constant presence of six costae bundles on each valve (to be added to the median longitudinal ridge in the sulcus, which is also a bundle) and pits, which occur sometimes in other species of *Cuninulus* and in the genus *Nucinulus* (see SARTENAER, 2004, p. 82; present paper); pits are the result of an increased depression on both sides of the median ridge of the sulcus (extending into the frontal part of the dorsal valve) and located below the frontal margin.

Cuninulus? *arnaensis* n. gen., n. sp.

DERIVATIO NOMINIS

The name draws attention to the village of Arnao on the Asturian coast, Cantabrian Cordillera, where the species is abundant. BURHENNE (1899, p. 35) suggested that *Rhynchonella lodianensis* var. *arnaensis* could be an appropriate name for the Arnao species. Although the name is not valid according to the ICZN (Art.12), the author wishes to revive it as *arnaensis* on account of the important place of Arnao in the literature.

HOLOTYPE, LOCUS TYPICUS, AND STRATUM TYPICUM

Holotype = specimen of Plate 11, figs. 1a,b (= dorsal and anterior views) in BARROIS (1882 as *Rhynchonella Orbigniana*). Arnao. Moniello Limestone.

DESCRIPTION AND COMPARISONS

With the exception of the sentence “La ligne cardinale forme un angle de 120°”, the description of BARROIS (1882, p. 265 as *R. Orbigniana*) is the exact copy of the one of DE VERNEUIL (1850, p. 175 as *Terebratula Orbigniana*).

C.? arnadoensis has many characters in common with the species assigned to the genus *Cuninulus*, some specific ones being the longitudinal median ridge (= costae bundle) of variable width and height present in 92 per cent of specimens (97 out of 106), generally [87 per cent of specimens (83 out of 95)] not reaching the anterior commissure and ending at front or sometimes (13 per cent

of specimens) extending into the lower part of the tongue; median + parietal costae: 15 to 24; parietal costae: 2 to 5; lateral costae: 16 to 21; bundles present in 86 per cent of specimens (91 out of 106); apical angle varying between 109° and 121° (most of the values varying between 113° and 116°); length/width ratios: 0.83 to 1.02 (most of the values: 0.86 to 0.97); thickness/width ratios: 0.73 to 0.88 (most of the values: 0.79 to 0.88); thickness/length ratios: 0.84 to 0.92 (most of the values: 0.84 to 0.92).

C.? arnadoensis differs from the other species of *Cuninulus* by a smaller size; a shallow longitudinal median furrow on the fold that is only slightly marked at front, and, in consequence of, an attenuated “M”-shaped central part of front; a generally slightly depressed central part of front [92 per cent of specimens (101 out of 110) are slightly depressed, and the remaining 8 per cent are slightly more depressed]; a very shallow (generally) to shallow sulcus; a lower fold; the width only slightly greater than length; two to three costae bundles generally present on the flanks.

Transverse serial sections made in a few specimens allowed the author to recognize some internal characters of *Cuninulus*: thick shell in the apical region, robust teeth, stout septum, and short cardinal process with numerous ridges. But, although suspected, the presence of dental plates could not be demonstrated, and the shape of crura could not be ascertained.

Therefore, the author does not establish a new genus in spite of the important external differences from *Cuniculus* mentioned above. On the other hand he did not include in the definition of *Cuninulus* some of the characteristic features of *C.? arnadoensis*, notably the small size, that will have to be incorporated in it if further investigations should make the provisional generic assignment more acceptable.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

The large collection made by the author in 1977 in the Cantabrian Cordillera comes from the Moniello Formation in Arnao and Moniello (Province of Asturias), and the upper part of the Santa Lucía Formation in Paradilla (Province of Leon).

Cuninulus? *nalivkini* (BUBLICHENKO, 1928)

C.? nalivkini from the SW Altai Mountains, E Kazakhstan, was described as *Rhynchonella (Uncinulus) Nalivkini* by BUBLICHENKO (1928, table, p. 1206, pp. 1216-1219, 1223, fig. 2, p. 1216, figs. 3a-h, p. 1217, figs. 4, 5a,b, p. 1218; 1974, p. 14, table 2, p. 19, p. 66, pl. 2, figs. 1a,b,v,g).

The species is not rare – BUBLICHENKO mentions 19 specimens – in the Losikha beds (D2co2) of Eifelian age, which BUBLICHENKO correlates with part of the *Cultrijugatus*- and the *Calceola*-Schichten of the Eifel area.

With the exception of citations in beds of Eifelian age from Novaya Zemlya (CHERKESOVA, 1973, p. 324), and Xinjiang Province (China) (HOU, 1962, pp. 55, 57-58, 64, pl. 1, figs. 8, 9a-d) the species is only known from the SW Altai Mountains.

		<u>C. melanopotamicus</u> n. gen., n. sp.	<u>C. concavus</u> n. gen., n. sp.	<u>C. leonensis</u> n. gen., n. sp.	<u>C. assaensis</u> n. gen., n. sp.	<u>C. eifeliensis</u> (BIERNAT, 1954)	<u>C? arnaoensis</u> n. gen., n. sp.	<u>C? nalivkini</u> (BUBLICHENKO, 1928)
Median ridge in sulcus	presence	100%	59%	100%	100%	100%	92%	100% (?)
	reaching front	100%	when present, disappearing at front in 30% of specimens	not reaching front in 10% of specimens	100%	100%	not reaching the anterior commissure in 87% of specimens	restricted to posterior part of ventral valve
Median furrow on fold		100%	100%	100%	100%	100%	100%	100% (?)
Presence of costae bundles on flanks		36%	17%	0%	50%	100%	86%	0 ⁽¹⁾
Number of costae	median + parietal	18-30	15-22	20-26	23-43	~22 ⁽¹⁾	15-24	12 ⁽¹⁾
	parietal	4-9	3-5	5-6	5-8	~4 ⁽¹⁾	2-5	at least 3 ⁽¹⁾
	lateral	16-22	18-22	16-27	17-29	~22 ⁽¹⁾	16-21	at least 12 ⁽¹⁾
		Median costae close-set in the anterior half of the unrolled length of ventral valve		Median costae close-set in the anterior half of the unrolled length of ventral valve				
Apical angle		115-126°	115-128°	105-125°	116-124°	120° ⁽¹⁾	109-121°	120° ⁽¹⁾
Length/width		0.79-0.88 (holotype: 0.84)	0.77-0.92 (holotype: 0.77)	0.83-1 (holotype: 0.88)	0.72-0.93 (holotype: 0.89)	0.69-0.88 (holotype: 0.84)	0.83-1.02 (holotype: 0.90)	0.75-0.81
Thickness/width		0.58-0.83 (holotype: 0.80)	0.76-0.95 (holotype: 0.76)	0.68-0.85 (holotype: 0.79)	0.65-0.78 (holotype: 0.72)	0.54-0.70 (holotype: 0.67)	0.73-0.88 (holotype: 0.73)	0.80-0.93
Thickness/length		0.67-0.95 (holotype: 0.95)	0.93-1.11 (holotype: 1.05)	0.76-0.93 (holotype: 0.89)	0.76-0.95 (holotype: 0.81)	0.70-0.83 (holotype: 0.80)	0.84-0.92 (holotype: 0.84)	0.98-1.24
Width of sulcus at front (% of shell width)		47-72% (holotype: 54%)	65-70% (holotype: 70%)	57-75% (holotype: 58%)	57-78% (holotype: 58%)	56% ⁽¹⁾	51-75% (holotype: 66%)	66% ⁽¹⁾

(1) = on figured specimen

Fig. 6 — Some major external characters of species assigned to *Cuninulus* n.gen.

The generic assignment is questionable because, in the absence of any material at his disposal, the author had to rely on an incomplete original description and on one single figured specimen.

This reservation being made, the following combined features make *C.? nalivkini* distinct from the other species of the genus: a lower number of costae as far as could be judged from the figured specimen (median + parietal costae: about 12; lateral costae: at least 12); the absence of costae bundles on the flanks; a deep sulcus; and the median ridge of the sulcus restricted to the posterior part of the valve. In one of the two sectioned specimens (fig. 4), the vestigial umbonal cavities are more developed than in any specimen of other species of the genus sectioned by the author.

Oligodesmerhynchus n. gen.

DERIVATIO NOMINIS

Ὀλιγός, η, ον (Greek, adjective) = few; δεσμη, ης (ἡ) (Greek, feminine) = bundle; τὸ ρύγχος (Greek, neuter). The name draws attention to the restricted number of costae bundles of the shell.

TYPE AND ONLY SPECIES

Rhynchonella ladanensis BURHENNE, 1899

Lectotype = specimen of Plate 5, figure 8 (= ventral view) in BURHENNE (1899). Lower reaches of the Lahn river (near Leun and Oberbiel). "Leuner Schiefer" ("Tentaculitenschiefer"). Lower Middle Devonian.

The type series of the species described by BURHENNE (1899, pp. 34-35, table, p. 45, pl. 5, figs. 8, 9, 9a,b) is almost exclusively made out of moulds; SOLLE (personal communication) collected specimens with preserved shell, but they were destroyed, together with abundant representatives of the species, during the last world war. The original material is housed in the "Institut für Geologie und Paläontologie, Fahrbereich Geowissenschaften, Philipps-Universität", Marburg. *R. ladanensis* is a small-sized species, the surface of which is composed of few, wide, high, and strongly marked costae bundles separated by deep grooves: two making up the high fold; two bounding the deep sulcus, and one dividing it; one on each flank. Seldom one, exceptionally two weaker bundles are vaguely to be observed on each flank. Sulcus and fold are sharply separated from the flanks. The literature has only remembered the presence of costae bundles, forgetting that the bundles were strong, few, and always present, and that, together with other characters, the small size was part of the definition of the species.

As a consequence, the species has erroneously been mentioned outside the type area *stricto sensu* (Lahnmulde) and the type area *lato sensu* (Lahnmulde, Dillmulde, and Moselmulde) in beds of late Emsian, lower and upper Couvinian, and lower Eifelian age in western Europe [Dinant Basin (Belgium, France), and Germany (Harz)], and in N Africa [NW Algeria (Erg el Djemel, Ougarta, Saoura, Touat, S Tindouf), Mauritania (Zemmour), pre-Saharan Morocco, and NE Spanish Sahara].

The occasional occurrence of costae bundles in variable number and strength (width, height, angularity) in some specimens of "*orbignyanus*" has led some authors either to assign them erroneously to "*lodanensis*" or/and to consider them as transitional forms between "*orbignyanus*" and "*lodanensis*". This character has also been used for separating "*orbignya-*

nus" from "*lodanensis*", an extreme position being the acceptance of the joint occurrence of the two "species".

Transitional or intermediate forms have been mentioned by DAHMER (1925, foot-note 1, p. 38) from the Lahnmulde (type area of *Oligodesmerhynchus ladanensis*), DROT (1964, p. 150; 1981, p. 57) from pre-Saharan Morocco, and SOLLE (1976, p. 182) from the Olkenbacher Mulde. An extreme example of this kind of confusion is *Uncinulus orbignyanus eifeliensis* BIERNAT, 1954, a subspecies from the Holy Cross Mountains to which BIERNAT (1954, p. 511) gave a distinct name, because it showed features both of "*orbignyanus*" and "*lodanensis*", and which DROT (1964, p. 150 as *U. ladanensis*) put into the synonymy of "*lodanensis*", and SCHUMANN (1965, pp. 84-85 as *U. orbignyanus*) into the synonymy of "*orbignyanus*". Another extreme example is the acceptance by CHERKESOVA [1968, p. 121 as *U. orbignianus* Vern. (*U. ladanensis* Burhen.)] of the identity of the two species.

Joint occurrences of "*lodanensis*" and "*orbignyanus*" were mentioned by MAILLIEUX (1938, table, p. 11, pp. 38-39; 1941, p. 9) from the "Assise de Bure" (Cola-c) of the Dinant Basin, LE MAÎTRE (1944, pp. 50-51; 1952, p. 114) from the late Emsian of the Dinant Basin and NW Algeria respectively, GODEFROID (1965, p. 81; 1968b, pp. 12, 30, 43, pl. 9 as *U. cf. ladanensis*, p. 29 as *U. ladanensis*; in LECOMpte, 1973, table 1, p. 155) from the lower Couvinian of the Dinant Basin, DELATTRE, LE MAÎTRE & WATERLOT (1967, p. 218) from the Dinant Basin, HOLLARD (1967a, p. 235) from the W Anti-Atlas, BULTYNCK (1970, p. 21, fig. 4, p. 32, pl. 37) from the late Emsian (Hierges Formation) from the Dinant Basin, and SOLLE (1972, p. 83; 1976, foot-note 8, p. 156) from the Dillmulde and Moselmulde, and Olkenbacher Mulde respectively.

At the same time when Belgian and French authors were associating "*lodanensis*" and "*orbignyanus*", no German palaeontologist did the same in the Eifel area.

Oligodesmerhynchus ladanensis is an abundant (according to the literature) species from the "Leuner Schiefer" (considered as early Middle Devonian age by BURHENNE, 1899, pp. 1-2, 3, 6 as *Rhynchonella ladanensis*) near Leun and Oberbiel in the lower reaches of the Lahn river. The "Leuner Schiefer" ("Tentaculitenschiefer") may be correlated with the "Ballersbacher Kalk" from the Dillmulde, which, in its type locality, is considered as corresponding to the "Heisdorf-Schichten" of late Emsian age. No outcrop of the "Leuner Schiefer" exists any more. When BURHENNE (1899) established *O. ladanensis*, the "Stockhausener Schichten" and the overlying "Leuner Schiefer" were not considered as separate units; therefore, the possibility that the species was collected by him in the "Stockhausener Schichten" cannot be dismissed. SOLLE (1942, pp. 178-179) distinguished the "Leuner Schiefer" from the "Stockhausener Schichten" by its richer calcareous contents [calcareous nodules are present in the "Leuner Schiefer" and not in the "Stockhausener Schichten"], and collected many specimens of the species from the basal part of the "Leuner Schiefer". Specimens of "*orbignyanus*" and "*lodanensis*" were found together by SOLLE (1972, p. 83) in the "Kieselgallen-Schiefer" considered as almost equivalent to the "Stockhausener Schichten" (Upper Kondel Substage). The full range of "*orbignyanus*" in the Lahnmulde, Dillmulde, and Moselmulde area is from the middle late Emsian Laubach Substage (one doubtful specimen) through the latest late Emsian Kondel Substage (rare in the Lower and abundant in the Upper Kondel Substage respectively) to the lowest part of the Eifelian according to SOLLE (1942, p. 213; 1972, fig. 1, p. 69, p. 77; 1976, p. 152). SOLLE (1976) added that "Die Massenvorkommen von *orbignyanus* liegen aber hier ["Kieselgallen-Schiefer" from

the Olkenbacher Mulde] eindeutig tiefer als in Eifel und Ardennen, wo sie das tiefen Mitteldevon kennzeichnen".

The occurrence of "lodianensis" (*Cuinulus assaensis* in the present paper) in younger beds (*Polygnathus linguiformis pinguis* Fauna, i.e. *P. costatus partitus* Zone) than those containing "orbignyanus" (*P. serotinus* Zone) as advocated by HOLLARD (1967a, fig. 7, p. 220, p. 235 as *Uncinulus lodianensis* and *U. orbignyanus*; 1981†, tables 3, 5), BULTYNCK & HOLLARD (1980, fig. 2, pp. 13-14 as *U. lodianensis* and *U. orbignyanus*); and BULTYNCK & HOLLARD† (1982, table 1, p. 47 as *U. lodianensis* and *U. orbignyanus*) is unacceptable, and represents another consequence of wrong identifications.

"lodianensis" occurs in abundance in the southern Province of Tarfaya and in the Dra valley, while "orbignyanus" is extremely rare in the Maïder: one specimen (TM 569) (as *U. orbignyanus* in DROT, 1971, p. 70, pl. 1, figs. 2a-c; 1981, p. 57; HOLLARD, 1974, pp. 20, 47) from the Jbel Issoumour, and one specimen (TM 23) initially (1964) identified as *U. lodianensis* by DROT (1964, p. 150) and HOLLARD (1974, pp. 46, 47) from Jbel Oufatène near by.

DESCRIPTION AND COMPARISONS

Small-sized. Strongly dorsibiconvex. Contour subpentagonal in ventral view, subrectangular in anterior view. *Paries geniculatus* present. Hinge line short. Front of shell composed of three parts: the lateral parts (flanks) which are abruptly cut by the *paries geniculatus*, the "M"-shaped (branches of the "M" are in the shape of sigmas) central part, which is wider than the lateral parts and slightly to deeply depressed. Commissure very slightly grooved. Lateral commissures slightly serrated. Sulcus and fold beginning at the beaks. Greatest thickness of shell located at front margin, the front margin itself located posterior to the most anterior point of shell, and slightly posterior to the anterior commissure. Costae edges modified into short spine-like projections. Ventral valve (*paries geniculatus* excluded) slightly convex. Sulcus widening rapidly and wide at front. Tongue high, subrectangular; upper part of tongue slightly to strongly recurved posteriorly, and thus, crest of tongue located posterior to point of maximum shell length. Crest of tongue slightly lower than point of maximum shell thickness. Tongue clearly delimited, with the exception of its base. Dorsal umbonal region never extending beyond the ventral umbonal region. Wide apical angle. Slender dental plates. Ventral muscle field deeply impressed. Divided hinge plate. Slender septum and septalium. Cardinal process rudimentary.

Low number of strongly marked and wide costae bundles [2/1 median bundles; 1/2 lateral bundles (rarely 2/3, exceptionally 3/4)] in the type species]. Primary costa of the major bundles (external lateral bundles, when present, are too weak to be considered) beginning at the beak, widening anteriorly, undergoing divisions at variable distances from the beak in the anterior two thirds of its length, and giving rise to secondary costae. Secondary costae becoming regular anteriorly, and aligning at front with the intercalated costae present in the wide furrows separating the costae bundles; they are flattened and arranged in a regular alignment on the *paries geniculatus* and on the tongue. These characters are clearly to be seen

on BURHENNE's (1899, figs. 8, 9, 9a,b) figures. The secondary and intercalated costae are in moderate number (median: 6 to 8, exceptionally 9; parietal: 1 or 2 on each flank of sulcus and fold; lateral: 8 to 11 in the type species), low, wide, rounded, and restricted to the anterior two thirds of the shell.

The small size, the plication made out of few clearly marked (wide and high) costae bundles and (wide and deep) furrows, the longitudinal median ridge (= costae bundle) disappearing at front, and the wide apical angle make it easy to identify the genus.

The state of preservation of specimens of the type series, the lack of any mention of internal characters by BURHENNE (1899), the disappearance of previously existing outcrops, and the absence of any collection of the species (outside the type series) in German scientific institutions and universities are important impedimenta in the way to a clear understanding of *Oligodesmerhynchus lodianensis*. These unfavourable circumstances have generated a lot of confusion in the past. The author is quite aware of shortcomings in the description of the species. Some characters need confirmation, some others need fuller information, especially the internal characters that could only be observed, sometimes guessed, on moulds. In spite of this, and taking notice of outstanding and distinct external features of the species, the author considers the establishment of a new genus useful and justified.

Oligodesmerhynchus n. gen. differs from *Nucinulus* by a smaller size (representatives of *Oligodesmerhynchus lodianensis* generally do not reach the size of the smallest specimens of *Nucinulus orbignyanus*), a considerably lower number of costae; the presence of lateral costae bundles; a consistently subpentagonal contour; the absence of pits on both sides of the median ridge (= costae bundle) of the sulcus immediately below the frontal margin; a cardinal commissure sharply sticking out; lateral commissures passing abruptly at right angle (forming spurs) to the frontal commissure; a deeper sulcus and a higher fold clearly separated from the flanks; shorter spine-like projections of the costae edges; the postero-lateral margins of both valves stretching outwards, and, as a consequence, a wider apical angle; and a rudimentary cardinal process.

Lapinulus n. gen.

DERIVATIO NOMINIS

The name is an arbitrary combination of the reversed syllables of the name (*pila*) of the type species, and the last two syllables of *Uncinulus*.

TYPE SPECIES

Terebratula pila SCHNUR, 1851

Remark: *pila*, ae (Latin, feminine = column, pillar) is a substantive, and must be used as a noun standing in apposition as reminded by SOLLE (1936, p. 207) and DROT (1964, p. 14).

MAUZ (1935, p. 79) designated as lectotype the specimen figured by SCHNUR (1853, pl. 26, fig. 1d); figures 1d-f are

ventral, lateral and posterior views of a specimen probably coming from Daleiden. Arguing that the specimen (pl. 26, figs. 1a-c) had not been located in SCHNUR's original collection, SCHMIDT (1941, p. 17, pl. 4, fig. 68) selected another lectotype (not figured) from the same collection. The first designation is the only valid one, and SCHMIDT's substitute is a paralectotype. Both decisions were not the wisest, because the lectotype is an internal mould. The species is indeed mostly preserved as internal moulds, but designation of the only well preserved specimen figured by SCHNUR (1853, pl. 26, figs. 1a-c) would have been better. Even if this specimen seems to be misplaced or lost, it would have been possible to restore its full value by matching it with specimens from the type area with preserved shell such as two specimens (SMF XVII-169d-1,2) available in the "Senckenberg Forschungsinstitut", Frankfurt; these specimens were collected by R. Richter in 1907 from the Wiltz-Schichten of Prüm ("Prümmer Mulde"), above the railroad bridge. More such specimens are present in various collections, e.g. the one mentioned by KAYSER (1871a, p. 316) in the type area: "reiches Material der sogenannten *pila* aus der Grauwacke, z. Th. mit erhaltener Kalkschale". DAHMER (1915, pp. 176, 178, 231) mentioned also specimens with "aussergewöhnlich gute Erhaltung", and "Schalenexemplare" in the Dillmulde. Unfortunately these collections could not be located in German scientific institutions. Still, a collection of 30 specimens of the species, 10 of them with partly or completely preserved shell was located by the author in 1973 in the "Paläontologisches Institut" of the "Museum für Naturkunde der Humboldt-Universität zu Berlin"; they were collected by STEININGER and by HENN (1906 and 1914) in Daleiden ("Prümmer Mulde").

Outside the type region (SW "Eifelkalkmulden" area), where it is abundant in beds of late Emsian age, *Lapinulus pila* has been mentioned in: other parts of Germany [Dillmulde (abundant), Harz, Hunsrück, Kellerwald (abundant), Lahnmulde, Moselle valley (abundant), Rhine valley (abundant), Taunus (abundant)]; adjoining countries [Belgium and France (southern border of the Dinant Basin), France (Armorican Massif, Montagne Noire, Pyrenees), Grand Duchy of Luxembourg]; southern Europe [Portugal, Spain (Cantabrian Cordillera (abundant), Iberian Chain, Pyrenees, Sierra Morena)]; central Europe (Bohemia); North Africa [Algeria, Mali, Morocco (Anti-Atlas, central Morocco)]; Russia (Armenia, Volga-Urals region).

The first descriptions of *Terebratula pila* from the type area by SCHNUR (1851, p. 6; 1853, pp. 186-187, pl. 26, figs. 1a-f), and STEININGER (1853, p. 62) contain most of the characteristic external features of the species.

It is highly probable that many mentions of the species from beds of late Emsian age in regions not far away from the type area (Aachen region, Dillmulde, Lahnmulde, Moselle valley, Rhine valley, Taunus, Dinant Basin) refer correctly to *Lapinulus pila* or to closely allied forms.

Other late Emsian citations cannot be accepted at their face value and must be investigated, e.g. the late Emsian form from the "la Lézais" trench ("Ménez-Bélair" Synclinorium, Armorican Massif) described by BRICE (1981, pp. 202-203, figs. 4A,B, p. 204, pl. 24, fig. 4, pl. 25, figs. 12-14, 15a,b, 16a-c, 17a,b as *Uninulus pila*). A first step in the right direction has been made by BRICE (1981), who established *U. suborbignyanus* BRICE, 1981 from the late Emsian of the same trench. This species, of which the synonymy is not discussed here, does not belong to *Uncinulus*, but to *Cuinulus* n. gen. (see above). The presence of the species in the late Emsian of the Armorican Massif has been confirmed by LARDEUX & MORZADEC (1979,

p. 14), MORZADEC *et al.* (1981, p. 11, fig. 4, p. 12, pp. 13, 15, fig. 5, p. 14), and MORZADEC (1983, p. 276). The species has also been mentioned in Spain: from the middle and late Emsian of the Sierra Morena (Central-Iberian Zone) (PARDO ALONSO & GARCÍA-ALCALDE, 1984a, p. 475; 1984b, p. 83, fig. 3, p. 85; 1996, fig. 3, p. 75 as *Uncinulus* gr. *suborbignyanus*; PARDO ALONSO & GARCÍA-ALCALDE, 1994, fig. 2, p. 155 as *U. cf. suborbignyanus*; PARDO ALONSO *in* GARCÍA-ALCALDE *et al.*, 2000, fig. 4, p. 138); from the early, middle, and late (generally) Emsian of the Asturo-Leonian Domain (Cantabrian Cordillera) as *U. suborbignyanus* (GARCÍA-ALCALDE *in* TRUYÓLS *et al.*, 1990, fig. 1, p. 14), as " "*U. suborbignyanus*" (GARCÍA-ALCALDE, 1992, fig. 4, p. 59, p. 60; 1994, fig. 2, p. 78; *in* TRUYÓLS-MASSONI & GARCÍA-ALCALDE, 1994, fig. 2, p. 223, 234; *in* GARCÍA-ALCALDE & TRUYÓLS-MASSONI, 1994, fig. 2, p. 87, p. 88; GARCÍA-ALCALDE, 1995, fig. 6, p. 21; 1996, fig. 2, p. 60; 1998, p. 244; and GARCÍA-LÓPEZ & SANZ-LÓPEZ, 2002, p. 132), and as " "*U.*" *suborbignyanus* (GARCÍA-ALCALDE *et al.*, 1998, p. 2). Some of these identifications are substitutes for the middle Emsian *U. aff. orbignyanus* of SCHUMANN (1965, pp. 49, 64, 84, 85, fig. 24).

Other mentions deserve to be carefully pondered, in particular those from beds of early Emsian, or assumed early Emsian age, such as those from: the middle Rhine valley (Hunsrück, Taunus), where "Pilabänke" or "pila-Bänke" have often been pointed at (e.g. FUCHS, 1899, 1907; NÖRING, 1939; DAHMER, 1952; ANDERLE, 1967; MITTMAYER, 1978; THEWS, 1996); the Argovejo area in northeastern Province of Leon (SCHUMANN, 1965, fig. 1b, p. 47, pp. 48, 49, p. 51, fig. 3d, p. 52, pp. 60, 64, 67, fig. 15, p. 76, pp. 82-83, 84, 86, 99, fig. 24, pl. 4, figs. 6a-c, 7a,b).

Outside some of the identifications mentioned above, which may be proven incorrect, many more exist as can be suspected from the middle Pragian to lower Givetian (chiefly Emsian and Eifelian) range given to the species in the literature.

Lapinulus pila has been originally described from the "Grauwacke" or the "Spiriferen-Sandstein" of the Eifel area [Daleiden (especially), Waxweiler, Daun, Oberstadtfeld, and Prüm], and considered as a "Leitform" of the "Spiriferen-Sandstein" by KAYSER (1878, p. 153); the species is mostly preserved as internal moulds and casts. In spite of its abundance mentioned in the literature, the figures by SCHNUR (1853, pl. 26, figs. 1a-f) and SCHMIDT (1941, pl. 4, fig. 68), reproduced in various publications, and those by WOLLERT (1986, figs. 46a-c, p. 54) are the only ones illustrating the species in the type area.

It is commonly mentioned in the literature from the "Obere Koblenzschichten" or the late Emsian. In present terminology the range of the species is (from base to top): "Berlé-Schichten", "Wiltz-Schichten" (type area), "Wetteldorf-Schichten", and possibly the base of the "Heisdorf-Schichten", i.e., in terms of the conodont zonation: the *Polygnathus laticostatus*/ *P. inversus* and *P. serotinus* Zones, and possibly the base of the *P. patulus* Zone.

DIAGNOSTIC FEATURES

Medium-large-sized. Generally subglobular. Strongly dorsibiconvex. Contour subpentagonal to subrounded. *Paries geniculatus*, *squamæ*, *glottæ*, and spine-like projections present. Lateral and anterior commissures slightly grooved. Well developed deltidial plates. Sulcus, fold and costae beginning at the beaks or almost. Shallow to moderately deep sulcus and low to moderately high fold only exceptionally divided by a median swelling and

a median furrow respectively. High, subrectangular tongue. Numerous fine divided and intercalated costae, flattened and provided with median narrow grooves in the *paries geniculatus*. Costae bundles never present. Greatest thickness of shell at front margin. Wide apical angle. Dental plates present. Vestigial umbonal cavities sometimes present. Divided hinge plate. Shallow triangular septalium. Short wedge-shaped septum. Short cardinal process with numerous ridges. Ventral muscle field strongly impressed, with variable width and length.

SPECIES ASSIGNED TO THE GENUS

Outside the type species, some specimens described by DROT (1964, pp. 147–148 *pro parte*, pl. 16, figs. 12a-c, 13 as *Uncinulus pila*) from the Anti-Atlas (Morocco) are assigned to the genus; they are discussed below under the Stratigraphic position and geographic location of *Palinulus zairensis* n. gen., n. sp.

DESCRIPTION

Medium-large-sized. Generally subglobular. Subpentagonal to subrounded in ventral and dorsal views. Rounded cardinal angles. Strongly dorsibiconvex. Ventral umbonal region with slight or almost no relief. Flanks of ventral valve (*paries geniculatus* excluded) slightly convex to flat. Dorsal umbonal region vertical and thus not extending beyond the ventral umbonal region. Anterior commissure generally arched. *Paries geniculatus*, *squamatae*, *glostae*, and marginal spine-like projections (resulting from the modification of the costae edges) present. Lateral and anterior commissures slightly grooved, with a very low zigzag deflection. Lateral commissure passing progressively at a right angle to the anterior commissure. Well developed delthyrial plates. Sulcus and fold beginning at the beaks or almost. No spurs bordering the sulcus at front. Sulcus shallow to moderately deep, wide, clearly separated from the flanks although passing to them in a hog's-back way. Bottom of sulcus flat to slightly concave.

Median longitudinal swelling starting almost from the beak commonly absent in the sulcus; when present it is only slightly (low, flat-rounded, wide) pronounced, usually restricted to about half the unrolled length of the ventral valve, but extending sometimes further anteriorly (see pl. 26, fig. 1a in SCHNUR, 1853), and disappears before reaching the front (Remark: it is not clear if the median crest usually observed on internal moulds anterior to the ventral muscle field is a mould of the median swelling). Sulcus passing progressively to a moderately high, subrectangular (with arched top), and clearly delineated tongue. Upper part of tongue slightly recurved posteriorly, the curvature increasing and extending into the frontal part of the dorsal valve in making the tongue look higher, and considerably shifting the frontal margin posteriorly. Top of tongue located posterior to point of maximum shell length and much lower than point of maximum shell thickness. Beak strongly incurved. Long interarea. Fold low to moderately high, more or less clearly separated from the flanks. Top of fold slightly to strongly convex. Median longitudinal furrow starting

almost from the beak rarely present; when present it is only slightly (shallow, wide) pronounced and restricted to the posterior part of the fold (see pl. 26, fig. 1b in SCHNUR, 1853) [Remark: the “Rinne” or “Riss” observed by SCHNUR (1851, p. 6; 1853, p. 186) on internal moulds of the type species is due to the septum]. Numerous (in the type species: 18 to 25 median, 5 to 7 being parietal on each flank of sulcus and fold; 20 to 28 lateral on each flank), narrow, low and rounded costae, starting at the beaks or almost, and regular in the anterior part of shell. Divisions and intercalations occur at variable distances from the beaks.

Costae bundles never present. Costae flattened (usually slightly) on geniculated wall (*paries geniculatus*), and provided with narrow median grooves. Furrows narrow. Length, width and thickness only slightly different [l/w : 0.86 to 0.98 (most of the values: 0.90 to 0.96); t/w : 0.68 to 0.97 (most of the values: 0.84 to 0.97); t/l : 0.87 to 1.07 in subglobular specimens of the type species]. Wide apical angle (115° to 120° in the type species). Greatest thickness of shell at front margin.

Shell thick in the apical region. Contour of the large delthyrial cavity successively longitudinally subrectangular, transversely rectangular and wide, and mushroom-shaped in transverse serial sections. Dental plates present, but generally obliterated by secondary filling of the umbonal cavities. They are best observed on internal moulds. Teeth massive and wide. In transverse serial sections made in three adult specimens of the type species, only one (Fig. 7, sections 7,8) showed a small area of one umbonal cavity filled with sediment; in other specimens a vague contour suggesting the presence of an umbonal cavity is filled with secondary substance, of which only scattered parts may be considered as callosity. Very short cardinal process, with up to 35 lamellae in the type species. In transverse serial sections it opens like a flower bud with few lamellae and immediately expands into two wide unsupported wings that will only later on be covered with lamellae. When the number of lamellae decreases the middle part of the cardinal process becomes narrower and the cardinal process forms a characteristic mount evolving into a mushroom shape. Shape of lamellae variable, chiefly finger- or/and clothes-peg-shaped; lamellae are almost not discernible at the base of the wings, where they are densely applied against each other.

Robust crural bases contrasting with very short and slender crura, which are rounded in their proximal part in transverse serial sections. Divided hinge plate. Shallow triangular septalium. Deeply impressed, very wide (42 to 63 per cent of shell width) and very long (43 to 58 per cent of the unrolled length of the valve) ventral muscle field. Figs. 1c,e on plate 26 in SCHNUR (1853) show the pedicle capsule and the small adductor scars surrounded by the large diductor impressions. Slightly impressed, narrow (30 to 43 per cent of shell width) and long (51 to 72 per cent of the unrolled length of the valve) dorsal muscle field. Fig. 3 on plate 2 in SANDBERGER (1855) shows the two pairs of adductors separated by the strong septum.

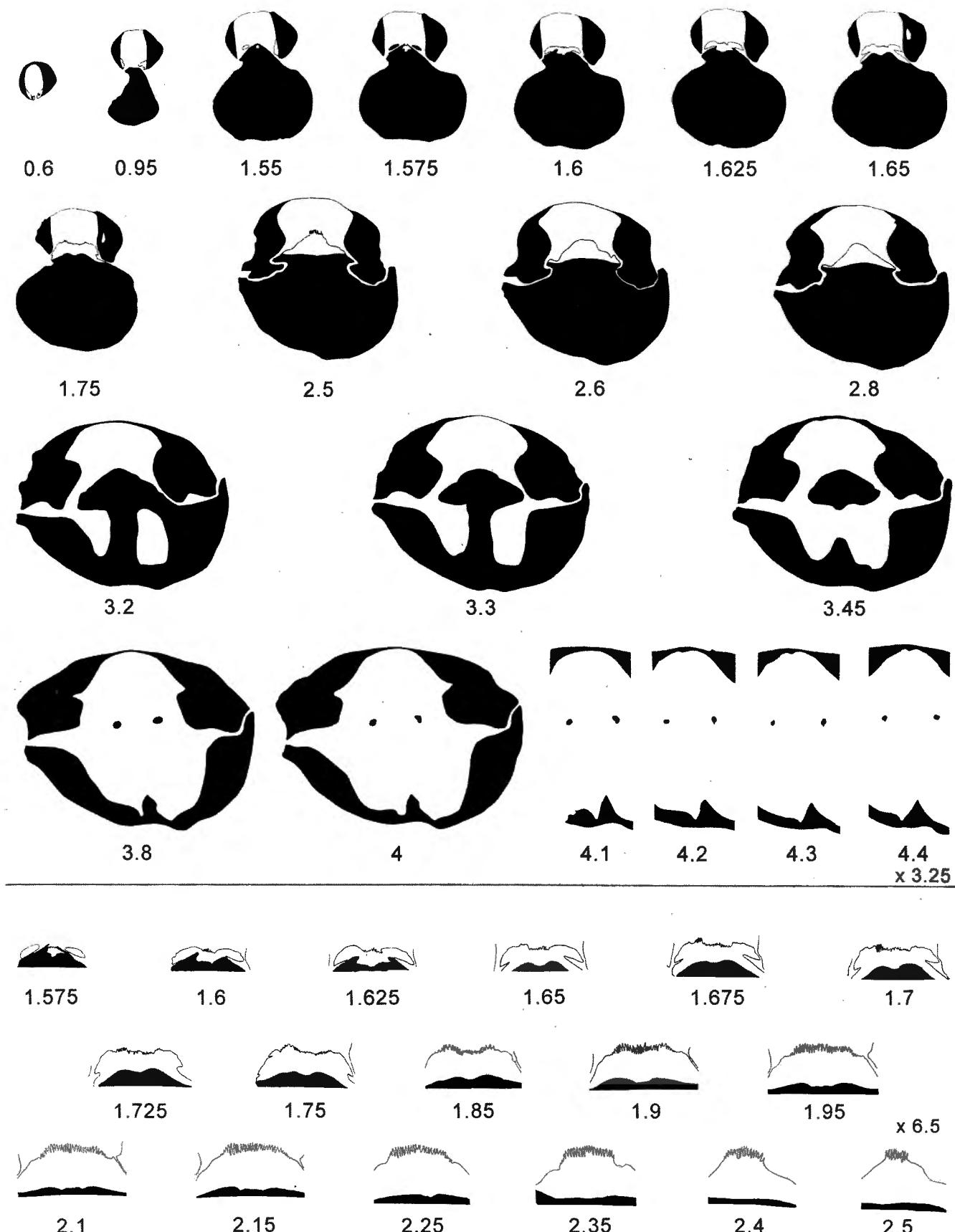


Fig. 7 — *Lapinulus pila* (SCHNUR, 1851). Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Topotype, MB.B.1229.1 ("Museum für Naturkunde der Humboldt-Universität zu Berlin"). Daleiden, "Prümer Mulde", "Eifelkalkmulde", "Wiltz Schichten". Collected by J. Steininger. Measurements: length = 19.8 mm; width = 20.8 mm; thickness = 14.3 mm.

COMPARISONS

Most forms assigned in the literature to the type species of *Lapinulus* n. gen. and *Nucinulus* are alleged to "pila" and "orbignyanus". Therefore comparisons between the two species apply to these alleged forms. Exceptionally such a comparison applies to *Lapinulus pila* and an alleged "orbignyanus", e.g. SCHNUR (1851, p. 6; 1853, p. 187) compared *L pila* (as *Terebratula pila*) to "orbignyanus" (as *T. Orbigniana* and *T. conf. Orbignyana* respectively) (here *Cuninulus concavus*); KAYSER (1871a, pp. 315, 316-317), probably influenced by SCHNUR (1853, p. 187), who estimated that *T. conf. Orbignyana* from the Eifel area was possibly a mere variety of *T. pila* from the same area, considered *pila* a synonym of "orbignyanus" (here *Cuninulus concavus*), and so did SCHULZ (1883, table, p. 167 (as *R. pila* and *R. Orbignyana*), but KAYSER (1871b, pp. 505, 506) changed his mind about this alleged identity.

The numerous expressions used in the literature to designate forms supposed to revolve round "orbignyanus" and "pila" or to link the two species together imply the existence of "typical" or "true" "orbignyanus" [SCHNUR, 1853, p. 187 as *Terebratula Orbignyana* from the Cantabrian Cordillera; LE MAÎTRE, 1934, p. 63 as *Uncinulus orbignyanus* from the Ancestris Basin (Armorican Massif) (it is interesting to note that the "typical forms" of *Uncinulus orbignyanus* cited by this author were put by BRICE, 1981, p. 205 into the synonymy e.p. of *U. suborbignyanus*, BRICE, 1981); SCHMIDT, 1942, p. 391; SCHUMANN, 1965, p. 85 as *U. orbignyanus* from the "cultrigatus-Stufe" of Asturias; ARBIZU *et al.*, 1979, pp. 110, 113 as *U. orbignyanus* from Moniello on the Asturian coast; DROT, 1981, p. 57 as *U. orbignyanus* from the pre-Sahara Morocco; HOLLARD *et al.*, 1982, p. 24], and "typical" or "true" "pila" (DREVERMANN, 1902, p. 103; DAHMER, 1915, p. 231, 1925, footnote 1, p. 39; SCHMIDT, 1942, p. 399).

Such forms are part of either an "orbignyanus" group (KAYSER, 1871b, pp. 504, 505 as "Formenreihe"; OEHLENT, 1889, p. 783 as *Wilsonia Orbignyana* group; GORTANI, 1911, pp. 188, 189 as group and subgroup; DROT, 1964, p. 150; SOLLE, 1976, p. 117; GARCÍA-ALCALDE *et al.*, 1979, fig. 6; Document submitted to the International Subcommission on Devonian Stratigraphy (SDS) by the Federal Republic of Germany on September 29, 1979 in Siguenza, Spain, foot-note 2, p. 3; ARBIZU *et al.*, 1979, fig. 4, p. 108; STRUVE, 1982, pp. 406, 427; HENN, 1985, p. 71; GARCÍA-ALCALDE, 1992, p. 61, 1994, p. 77, 1996, p. 65; BITAM *et al.*, 1996, p. 98) or a "pila" group (MAILLIEUX, 1936, p. 87; MASSA *et al.*, 1965, p. 160; BRICE & DROT in BRICE *et al.*, 1984, pp. 447, 450; GALLE *et al.*, 1994, p. 414; GARCÍA-ALCALDE, 1997, p. 243, 1998, p. 243. GARCÍA-LÓPEZ & SANZ-LÓPEZ, 2002, fig. 3, p. 170) or a "pila"- "orbignyanus" group (DAHMER, 1932, p. 107 as "Formenkreis"; SCHUMANN, 1965, p. 49 as *U. orbignyanus-U. aff. orbignyanus-U. pila* group; MORZADEC in PLUSQUELLEC & SEMENOFF-TIAN-CHANSKY, 1972, fig. 2, p. 413; BULTYNCK & MORZADEC, 1979, p. 678).

The imbroglio started very soon after the establishment of *Terebratula Orbignyana* DE VERNEUIL, 1850 (now *Nucinulus orbignyanus*) when SCHNUR (1853, p. 187 as *Terebratula conf. T. Orbignyana* from the Eifel area; in 1851, p. 6 he considered the Eifelian form identical to the Spanish species) stated that the species could possibly be "a mere variety" ("vielleicht eine blosse Varietät") of *T. pila*, and DE VERNEUIL & BARRANDE (1855, p. 1006) mentioned that various varieties ("plusieurs variétés") of *Terebratula pila* from the same area "seem almost to form a transition" ("semblent presque former un passage") to *T. Orbignyana*.

Since then varieties, intermediate forms ("Mittelformen"), transition forms ("Übergänge", "Übergangsformen"), modifications ("Abänderungen"), aff., cf., and expressions such as "tendency towards, and "closely related", flourished in various countries and regions [Algeria, Armorican Massif, Cantabrian Cordillera, Dinant Basin, Germany (Eifel area, Harz, Lahnmulde), Mali, and Portugal]: KAYSER, 1871b, pp. 503, 505, 506, 507, 516, 1878, pp. 153, 239, pl. 26, figs. 13, 13a-c; BARROIS, 1882, p. 372; SCHULZ, 1883, pp. 162-163; GÜRICH, 1909, p. 144; DAHMER, 1925, foot-note 2, p. 38, p. 39; LE MAÎTRE, 1929, p. 62, pl. 3, figs. 10, 11, 1934, p. 63, 1944, pp. 50-51, 1952, pp. 114, 115; SCHMIDT, 1937, figs. 23a,b, p. 36, 1941, pp. 16, 18, 1942, p. 391; COMTE, 1938, p. 57, 1959, pp. 172, 177, 253, 289; RENAUD, 1942, p. 109; KRÖMMELBEIN in KRÖMMELBEIN *et al.*, 1955, pp. 22, 23, 24; DROT, 1964, p. 47, 148; FUCHS, 1965, p. 333; SCHUMANN, 1965, pp. 49, 64, 84, 85, fig. 24; PERDIGÃO, 1967, p. 38; HEIBEL, 1969, table 4, p. 562, fig. 6, p. 564; MORZADEC in PLUSQUELLEC & SEMENOFF-TIAN-CHANSKY, 1972, p. 414; MITTMAYER, 1974, table 2, p. 75, p. 77; BULTYNCK & MORZADEC, 1979, p. 676; BRICE, 1981, pp. 207, 214; STRUVE & WERNER, 1981, fig. 6, p. 26, fig. 7, p. 27, fig. 8, p. 29, fig. 9, p. 30, 1982, fig. 6, p. 45, fig. 8, p. 48; SARTENAER in BULTYNCK *et al.*, 1982, p. 33; GARCÍA-ALCALDE, 1994, fig. 2, p. 78; and GARCÍA-LÓPEZ & SANZ-LÓPEZ, 2002, fig. 6, p. 135, p. 146.

"Orbignyanus" and "pila" have also been incorporated in evolutionary processes by: COMTE, 1938, pp. 57, 85, 1959, p. 253, table, p. 301, pp. 308, 318; SCHUMANN, 1965, p. 64; PERDIGÃO, 1967, pp. 38, 46, 1973, p. 43; MITTMAYER, 1974, p. 77; and BRICE, 1981, p. 207.

The following comparison between *Lapinulus* n. gen. and *Nucinulus* SARTENAER, 2004 relies only on the original collection of DE VERNEUIL.

Lapinulus n. gen. and *Nucinulus* exhibit many similarities: a strongly dorsibiconvex aspect; a subpentagonal to subrounded contour (although the subpentagonal contour is commonly more elongated in *Nucinulus*); well developed deltoidal plates; the presence of *paries geniculatus*, *squamae*, *glottae*, and marginal spine-like projections; lateral and anterior commissures slightly grooved; sulcus, fold, and costae beginning at the beaks; a shallow to moderately deep and wide sulcus; a subrectangular tongue; the greatest thickness of shell at front margin; numerous, low, rounded, divided and intercalated costae; costae flattened on *paries geniculatus*; the absence of costae bundles on the flanks; narrow furrows; the aspect of the ventral and dorsal muscle fields; a stout and short septum; the presence of a divided hinge plate and dental plates.

Nucinulus can be separated from *Lapinulus* by many characters, e.g. a considerably smaller size; a never subglobular aspect; a straight anterior commissure (in its central part); flanks of sulcus more abrupt, and, in consequence of, more sharply angular (spur-like) borders of sulcus at front; a clear "M"-shaped central part of front; the curvature of the upper part of tongue not extending into the frontal part of the dorsal valve; a higher tongue and fold; the crest of tongue located only slightly lower than point of maximum shell thickness (this crest is located much lower in *Lapinulus*); a longitudinal median ridge (= costae bundle) dividing the sulcus always present, clearly marked at front, and extending into the frontal part of the dorsal valve; a longitudinal median furrow always present and clearly marked at front; a thinner shell in the apical region; a subrectangular contour of the delthyrial cavity; large and wide umbonal cavities; the presence of a septalium; less massive

teeth; less robust crural bases; crura of different shape; and a pad-like cardinal process.

Main differences between *Lapinulus pila* and *Cuininulus concavus* have been given by KAYSER (1871b, p. 506 as *Rhynchonella pila* and *R. Orbignyana*) and SCHMIDT (1941, p. 18 as *Uncinulus pila* and *U. orbignyanus*), both authors accepting the existence of transitional forms.

With the exception of what refers to the costae bundles, the dental plates, and the hinge plate, the similarities between *Lapinulus* and *Cuininulus* are the same as those mentioned between *Lapinulus* and *Nucinulus*. Further similarities are: a thick shell in the apical region; the presence of vestigial umbonal cavities; robust and wide teeth; robust crural bases; and rounded crura in their proximal part in transverse serial sections.

Lapinulus differs from *Cuininulus* by a larger size; the absence of costae bundles on the flanks; a subglobular aspect; an arched frontal commissure; the flanks of the sulcus less abrupt, and, in consequence of, less sharply angular borders of the sulcus at front; a less characterized "M"-shaped central part of front; the curvature of the upper part of tongue extending into the frontal part of the dorsal valve; lower tongue and fold; the crest of tongue located much lower; the longitudinal median ridge of the sulcus and the longitudinal median furrow of the fold usually absent, and when present, restricted to the posterior part of the shell; a different contour of the delthyrial cavity; a divided hinge plate; and, a more elaborate cardinal process.

Uncinulus and *Lapinulus* exhibit some similar features: a medium-large size; a short hinge line; well developed *paries geniculatus*, *squamae*, *glottae*, and marginal spine-like projections; the lateral and anterior commissures slightly grooved with a very low zigzag deflection; a generally arched anterior commissure; no "spurs" whatever at front; a subrectangular and clearly delineated tongue with arched crest; crest of tongue lower than the highest point of shell; a strongly incurved ventral beak; the top of fold slightly convex; numerous, low, rounded, divided and intercalated costae starting at the beaks; a wide apical angle; a very thick shell in the apical region; stout teeth, crural bases and septum; a divided hinge plate; very short crura; a deeply impressed, long and wide ventral muscle field; and a slightly impressed and narrow dorsal muscle field.

Uncinulus is distinct in its globular shape; a usually smaller width and greater thickness; a thicker ventral valve; a slightly convex to vertical front without a "M"-shaped central part; a ventral umbonal region with strong relief; ventral flanks (*paries geniculatus* excluded) strongly convex; the lateral commissure passing sharply at right angle to the anterior commissure; small deltoidal plates; the greatest thickness of shell not located at front margin, but slightly posterior to it; an extremely shallow sulcus and an extremely low fold (sometimes almost wanting) almost blending with flanks, only separable from the flanks in about the anterior two thirds of shell; the bottom of sulcus flat to slightly convex; the absence of a median ridge in the sulcus and a median furrow on the fold; a generally moderately high and vertical tongue without relief (almost blending with the *paries geniculatus*); a narrower sulcus at front; the upper part of tongue rarely slightly recurved posteriorly; the crest of tongue often located very low; the dorsal umbonal region sometimes extending beyond the ventral umbonal region; a completely different costation pattern (wider costae, a moderate number of median costae, fewer parietal costae, less divisions and intercalations located in the posterior half, and even third, of shell, costae only slightly or almost not flattened in the *paries geniculatus*); width, length, and thickness close to each other, each of them being alternatively the greatest dimension (thick-

ness is more often the greatest dimension); a generally slightly smaller apical angle; dental plates absent; vestigial umbonal cavities; crura oval in their proximal part and strongly recurved ventrally at their distal end; the fan (half open)-to mushroom-shaped delthyrial cavity in transverse serial sections; and a very short and stocky (not stretched out laterally) cardinal process; a wider and longer ventral muscle field.

Palinulus n. gen.

DERIVATIO NOMINIS

The name is an arbitrary combination of the reversed first letters of *Lapinulus*.

TYPE SPECIES

Palinulus zairensis n. gen., n. sp.

DIAGNOSTIC FEATURES

See COMPARISONS

DESCRIPTION

Small- to medium-sized. Strongly dorsibiconvex. Contour subrounded to transversely or longitudinally subpentagonal. Ventral umbonal region with slight or almost no relief.

Posterior part of ventral valve slightly to strongly convex. Ventral flanks (*paries geniculatus* excluded) slightly convex to almost flat. Dorsal umbonal region vertical, and thus not extending beyond the ventral umbonal region. Central part of front not "M"-shaped or, sometimes, slightly. *Paries geniculatus*, *squamae*, *glottae*, and marginal spine-like projections present. Lateral commissures passing progressively at right angle to the anterior commissure. Lateral and anterior commissures strongly grooved, with a low zigzag deflection. Anterior commissure straight, rarely slightly arched. Sulcus and fold starting imperceptibly at some (generally small) distance from the beaks. No spurs bordering the sulcus at front. Greatest thickness of shell always at front margin. Shallow to moderately deep sulcus. Sulcus wide at front, and clearly separated from the flanks although passing to them in a hog's-back way. Bottom of sulcus flat to slightly concave. Tongue moderately high to high, subrectangular, clearly delineated, and with straight top. Top of tongue located only slightly below the frontal margin. Upper part of tongue slightly recurved posteriorly. Beak strongly incurved. Fold very low to low, not clearly separated from the flanks. Top of fold straight (generally) to slightly convex. A slight, very shallow, longitudinal median depression of variable width, starting at a small distance from the beak, generally present on the fold, and very slightly or not marked at the frontal margin. There is rarely a corresponding median swelling in the sulcus starting also at a small distance from the beak, but in one out of five specimens there is a low and narrow median swelling (i.e. one or two costae slightly higher than the others) at front that may sometimes extend into the base of the tongue. Costae numerous, close-set, narrow, low, rounded, starting at the beaks or almost, and regular in the anterior part of the shell. Divisions and

intercalations occurring at variable distances from the beaks. Costae bundles never present. Costae flattened on *paries geniculatus* with median grooves. Very narrow furrows. Length and width only slightly different. Wide apical angle. Very thick shell in apical region. Dental plates absent, but vestigial umbonal cavities usually present. Contour of delthyrial cavity longitudinally rectangular, then mushroom-shaped in transverse serial sections. Teeth massive and wide. Divided hinge plate. Thick septum. Robust crural bases. Crura oval in their proximal part in transverse serial sections. Very short crura. Cardinal process with numerous lamellae. Deeply impressed ventral muscle field. Slightly impressed dorsal muscle field.

SPECIES ASSIGNED TO THE GENUS

In addition to the type species described by DROT (1964, pp. 147-148 *pro parte*, pl. 16, figs. 6a-c, 7a-c, 11, fig. 64, p. 149 as *Uncinulus pila*) and by the author, the three following forms are assigned to the genus: *U. pila* described by LE MAÎTRE (1944, pp. 5, 7, table, p. 18, pp. 49-51) from the Coblençian of Haci-Remlia (Tafilelt, Morocco); *U. pila* described by SCHUMANN (1965, pp. 82-83, pl. 4, figs. 6a-c, 7a,b, fig. 15, p. 76) from the early Emsian of Argovejo (Aguasalio Syncline), Province of Leon, Cantabrian Cordillera; and *U. pila* described by BRICE (1981, pp. 202-203, pl. 24, fig. 4, pl. 25, figs. 12-14, 15a,b, 16a-c, 17a,b, figs. 4A,B, p. 204) from the late Emsian of "la Lézais en Gahard (Ille-et-Villaine)" trench, Ménez-Belair Synclinorium, Armorican Massif). The final specific assignment of these forms is not examined here.

COMPARISONS

Palinulus differs from *Lapinulus* by a smaller size; a straight, rarely arched, anterior commissure; sulcus and fold starting imperceptibly at some distance from the beaks; a generally higher tongue with straight top; the top of tongue located only slightly below the frontal margin; a generally lower fold not clearly separated from the flanks posteriorly; the top of fold straight (generally) to slightly convex; a slight longitudinal median depression starting at a small distance from the beak generally present on the fold, very slightly marked or not at front; a corresponding longitudinal median swelling in the sulcus starting from the beak rarely present; a very low and narrow median swelling often present at front and extending sometimes into the base of the tongue; length and width only slightly different, but noticeably greater than thickness; crura oval in their proximal part in transverse serial sections; a longer ventral muscle field.

Palinulus zairensis n. gen., n. sp.

DERIVATIO NOMINIS

The name draws attention to the area around Zaïr in the Dra plains (Anti-Atlas), Morocco, where the species is abundant.

TYPES, LOCUS TYPICUS, AND STRATUM TYPICUM

Holotype = specimen of Plate 16, figures 7a-c in DROT (1964 as *Uncinulus pila*). W of Zaïr (x: 448, y: 294),

eastern Dra plains (Anti-Atlas), Morocco (locality Cd D8 of Hollard, H.). Upper part of the "Assise d'El-Ansar" (= lower part of Khebchia Formation), late Emsian.

Paratype = specimen of Plate 16, figures 6a-c in DROT (1964 as *U. pila*). Rich SE of Jbel Hamsaïlikh, Dra plains (Anti-Atlas), Morocco (locality i868 of Jacquemont, P. = locality AT83 of Hollard, H.). Same formation and age.

DESCRIPTION

This refers only to specific characters in need of further elaboration.

Width of sulcus varying between 54 and 71 per cent of shell width. A slight longitudinal median depression on the fold present in 86 per cent of specimens (68 out of 79) with a corresponding median swelling in the sulcus in 11 per cent of specimens (15 out of 138). A longitudinal median swelling present in the sulcus in 27 per cent of specimens (37 out of 138); this swelling extends sometimes into the base of the tongue. Median + parietal costae: 18 to 33 (most of the values: 18 to 26); parietal costae: 3 to 7; lateral costae: 19 to 25. Length/width ratios: 0.90 to 1.04 (most of the values: 0.96 to 1.04); thickness/width ratios: 0.59 to 0.84 (most of the values: 0.67 to 0.84); thickness/length ratios: 0.58 to 0.91 (most of the values: 0.70 to 0.88). Apical angle varying between 111° and 121°. Width of ventral muscle field: 50 to 60 per cent of shell width; length of ventral muscle field: 62 to 65 per cent of unrolled length of valve. Width of dorsal muscle field: 32 to 43 per cent of shell width; length of dorsal muscle field: 44 to 63 per cent of unrolled length of valve. Number of lamellae in the cardinal process: 30 to 40.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCATION

Palinulus zairensis has been collected abundantly from the "Assise d'El-Ansar" (= lower part of Khebchia Formation) in a restricted area in the central Dra plains stretching out on about 80 km from Megsen-Medersam to the W to Zaïr to the E [Megsen-Medersam (AT94); Rich SE of Jbel Hamsaïlikh (AT79, AT80, AT81, i867 = AT78, i869); El-Ansar (AT17); and W of Zaïr (Cd D8, Cd D17)]. These beds correspond to the *Polygnathus laticostatus/inversus* Zone and the lower part of the *P. serotinus* Zone in terms of the conodont zonation. Further West (about 130 km W of the Zaïr area, and about 30 km W of Megsen-Medersam) DROT (1964, pl. 16, figs. 12a-c, 13 as *Uncinulus pila*) figured two specimens from two localities [Sekkine-Diab (Ta13) and El-Ayoun (Ta38)] in the Tata area (Anti-Atlas), Morocco. These two specimens, as well as 45 more specimens (DROT, p. 147, only mentions a few moulds from Ta13 and 6 specimens from Ta38) examined by the author in Hollard's collection, represent a larger form than the one described above. DROT (1964, pp. 147-148 *pro parte*) expressed some reluctance to separate the two forms. These specimens, which are not only present in the localities Ta13 and Ta18, but also in the localities AT17, AT81, and AT94, are assigned to the genus *Lapinulus* by the author.

Localities mentioned above are indicated on the maps published by DROT (1964, fig. 90, p. 224, fig. 91, p. 228).

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Explanation of Plate 1

- Figs. 1-5 — *Cuininulus melanopotamicus* n. gen., n. sp. Paratype A, IRSNBa12152. Chanly near Wellin, southern border of the Dinant Basin. About 20 m above the base of the Eau Noire Member (Co1b) of the Bure Formation (Co1a-c = lower Couvinian). Collected by J. Godefroid (see GODEFROID, 1968b, p. 29). Ventral, dorsal, anterior, posterior, and lateral views (x 1.18). Median costae: 15; parietal costae: 6 on each side; lateral costae: 20.
- Figs. 6-10 — *Cuininulus melanopotamicus*, n. gen., n. sp. Holotype, IRSNBa12151 [= pl. 2, p. 193, fig. 19 (= ventral view) in SARTENAER (in ROBASZYNSKI & DUPUIS, 1983 as “*Uncinulus orbignyanus*”)]. Same locality, member and collector. Ventral, dorsal, anterior, posterior, and lateral views (x 1.16). Median costae: 12; parietal costae: 4 on each side; lateral costae: 18.
- Figs. 11-15 — *Cuininulus concavus* n. gen., n. sp. Holotype, IRSNBa12154. Leudersdorf near Uxheim, “Hillesheimer Mulde”, “Eifelkalkmulden”. Below the bentonite layer Libra I, lower Wolfenbach Member of the Lauch Formation, early Eifelian. Collected by P. Sartenaer, 1974. Ventral, dorsal, anterior, posterior, and lateral views (x 1.13). Median costae: 9; parietal costae: 5 on each side; lateral costae: 19.
- Figs. 16-20 — *Cuininulus concavus* n. gen., n. sp. Paratype A, IRSNBa12155. Same locality, member, and collector. Ventral, dorsal, anterior, posterior, and lateral views (x 1.19). Median costae: 9; parietal costae: 5 on each side; lateral costae: 19.
- Figs. 21-25 — *Cuininulus leonensis* n. gen., n. sp. Holotype, GPIT Br.1255/28 (Geologisch-paläontologisches Institut der Universität, Tübingen; Br. = brachiopods) (= pl. 5, figs. 4a-c in SCHUMANN, 1965 as *Uncinulus orbignyanus*). Near Argovejo (Aguasalio Sycline), Province of Leon, Cantabrian Cordillera (see SCHUMANN, 1965, fig. 24). Late Emsian. Collected by D. Schumann. Ventral, dorsal, anterior, posterior, and lateral views (x 1.11). Median costae: 14; parietal costae: 6 on each side; lateral costae: 27.
- Figs. 26-30 — *Cuininulus leonensis* n. gen., n. sp. Paratype A, GPTI Br. 1255/27 (= pl. 5, figs. 3a-c in SCHUMANN, 1965 as *Uncinulus orbignyanus*). Same locality, age, and collector. Ventral, dorsal, anterior, posterior, and lateral views (x 1.18). Median costae: 11; parietal costae: 5 on each side; lateral costae: 19.

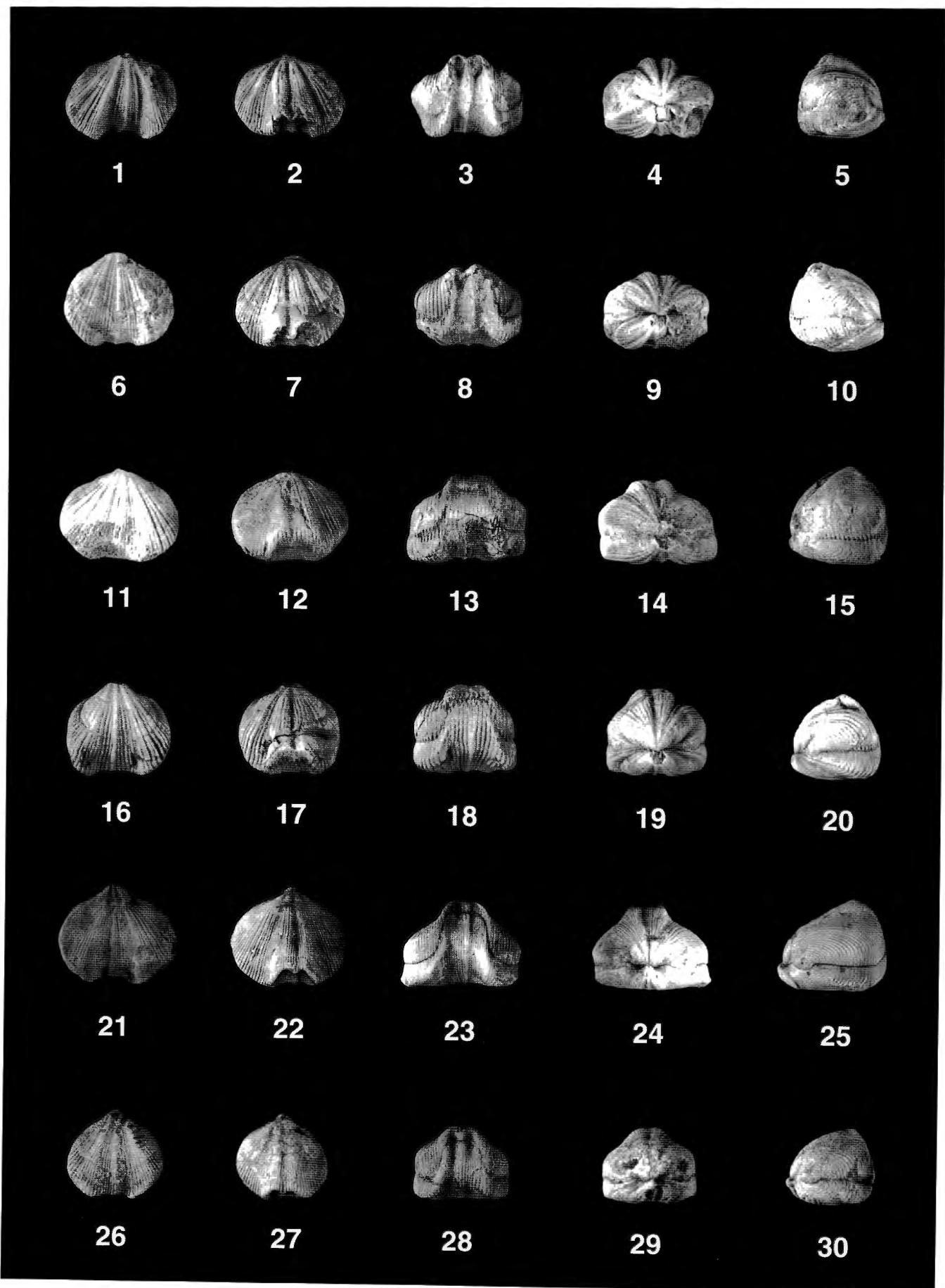


PLATE 1