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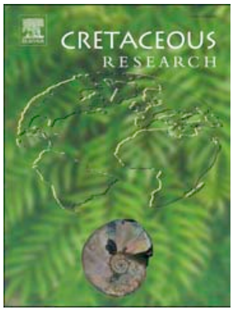

Revision of *Vaccinites loftusi* (Woodward, 1855) (Bivalvia: Hippuritida) and proposal of three new *Vaccinites* species from the Campanian—Maastrichtian of Eurasia

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Revision of *Vaccinites loftusi* (Woodward, 1855) (Bivalvia: Hippuritida) and proposal of three new *Vaccinites* species from the Campanian—Maastrichtian of Eurasia

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A B S T R A C T

The revision of *Vaccinites loftusi* (Woodward) comprised the critical analysis of issued descriptions and figures, together with the study of the type specimens and newly collected material from the type locality in Turkey, and also from western Bulgaria, eastern Serbia, and Spain. Five (three of them new) different although phylogenetically related species are characterized, each one arisen in a different area of the Mediterranean Tethys. Main diagnostic characters considered are size and ontogenetic development of the ligament ridge and secondary pillars, while angular measures of pillar—myo-cardinal arrangement and main infolds setting, although clustered for each species, depict extensive overlap. *Vaccinites alceotarlaoi* sp. nov., from the lower Campanian of Serbia and Spain, appears as the most primitive and the origin of the other species. *Vaccinites pirenaicus* sp. nov., *Vaccinites bilottei* sp. nov., and *Vaccinites loftusi* arose at the late Campanian in Pyrenees, Bulgaria, and Middle East, respectively. *Vaccinites syriaca* Vautrin originated from *V. loftusi* at the early Maastrichtian. The purported origin of the Eurasian multiple-fold hippuritids (*Pironaea* spp) from any of these species, with short secondary pillars not affecting the radial pattern of the canal system of the left valve, is rejected.

Keywords:
Hippuritids taxonomy; Late Cretaceous; Turkey; Bulgaria; Serbia; Spain.

1. Introduction

Woodward (1855) proposed the hippuritid species *Hippurites loftusi*, *H. colliciatus*, *H. corrugatus* and *H. vesiculosus*, based on fossil material collected by W.K. Loftus “from a limestone in the Bákhtíyárí Mountains on the Turco-Persian Frontier”. A note in Loftus (1855, p. 284) emended the fossil locality, “The locality for the Asiatic Hippurites there described should have been Hakim Khan in Turkey in Asia, instead of Bákhtíyárí Mountains”. The fossils are preserved in The Natural History Museum [formerly British Museum (Natural History)], London, UK. With the exception of *H. colliciatus*, the generic ascription of these species has changed in subsequent literature: *loftusi* and *vesiculosus* being attributed to *Vaccinites* Fischer by Toucas (1904) and *corrugatus* to *Pironaea* Meneghini by Douvillé (1894).

Since Milovanović (1960), *V. loftusi* has been considered the origin of Eurasian multiple-fold hippuritids (*Pironaea* spp). Bilotte (1981) proposed the genus *Pseudopironaea*, to include *V. loftusi* as well as other *Vaccinites* species with undulated inner margin of the outer shell layer in the right valve; all these species being considered as *Pseudovaccinites* Sénesse, within the Subfamily Pseudovaccinitidae Bilotte. Bilotte (1985) recognized the non-validity of both genus *Pseudopironaea* and Subfamily Pseudovaccinitidae.

As compiled in Steuber (2002), *Vaccinites loftusi* has been subsequently reported from other areas in Turkey, and also from different localities in Bulgaria, Croatia, Serbia, Spain, and the United Arab Emirates-Oman border region. The main aim of the present paper is the revision of this species based, besides on the available descriptions and figures in literature, on the study of the type specimens and newly collected material from the type locality in Turkey, and also from western Bulgaria, eastern Serbia, and Spain (Fig. 1, Appendix 1).

2. Material and methods

All specimens reported as (or related to) *V. loftusi* in literature are commented and/or described and figured, together with the newly collected material, ordered by geographic areas (Fig. 1): Turkey, Bulgaria, Serbia, Spain, Croatia, UAE-Oman, Syria (section '3. Results'). The key aspects of the shell morphology and evolution of these fossils, and the stratigraphy and palaeogeography of the fossil localities, are discussed (section '4. Discussion'). And finally, the distinction of five different species is proposed (section '5. Systematic palaeontology') and some conclusions are summarized (section '6. Conclusions').

All transverse cross sections are figured in standard orientation, that is, in adapical view and with the dorsal side up, unless indicated. The main criterion for the orientation of hippuritid right valves' transverse cross sections is the axis ATPT (anterior-posterior axis defined by the centres of AT and PT) which is represented horizontal. Thus, dorsal is upwards, ventral is downwards, and anterior and posterior, respectively at left and at right in adapical view. Consequently, as it corresponds to be, P1 and P2 are posterior, or postero-ventral (P2). The hippuritid accessory cavity, known in the ancient literature as anterior accessory cavity, is located above the axis ATPT, thus antero-dorsal. In cross section drawings, the OSL is represented in black, RV's ISL in pale grey, and LV's ISL in dark grey. Acetate peels have been used when drawing the enlarged details of ligament ridges.

The abbreviations of morphological characters and measures considered in the study (Fig. 2) are: *a* = angle defined by the tip of P2 and the centres of P1 and PM; ADC = antero-dorsal cavity; AT = anterior tooth; ATPT = axis defined by the centres of AT and PT; *b* = angle defined by the centres of P1, PM, and PT; *c* = angle defined by the centres of PM, PT, and AT; ISL = inner shell layer; L = ligament ridge; LP1 = portion of shell circumference between L and P1; LP2 = portion of shell circumference between L and P2; LT = angle defined by L and the axis ATPT; LV = left valve; MC = main body cavity; OSL = outer shell layer; P1 = first pillar (formerly S or Sp); P1P2 = portion of shell circumference between P1 and P2; P2 = second pillar (formerly E or Ep); PM = posterior myophore; PT = posterior tooth; RU = ratio between LP2 and the shell circumference; RV = right valve; S = secondary pillars (infolds of the outer shell layer).

The repositories of studied specimens are: MCSN = Museo Civico di Storia Naturale, Trieste, Italy; MGB = Museu de Geologia de Barcelona, Spain;

MGL = Musée de Géologie de Laussane, Swizerland; NHMUK = The Natural History Museum [formerly British Museum (Natural History)], London, UK; PUAB = Paleontological Collections of the Universitat Autònoma de Barcelona, Bellaterra, Spain; UCBL-EM = Collection de l'École nationale supériéure des Mines de Paris, Université Claude Bernard, Lyon I, Villeurbanne, France; US = Sofia University, Bulgaria.

Figured specimens in literature without indication of register number or repository have been identified by their locality and publication reference (Appendix 1).

3. Results

3.1. Turkey

3.1.1. Hekimhan

The type locality of *Vaccinites loftusi* is Hekimhan, Malatya, Turkey. Upper Cretaceous outcrops around Hekimhan "correspond to the transgressive and the following regressive sequence of the Malatya Basin. Rudists are very abundant in the Tohma Reefs of the transgressive sequence, while they are rare in the Zorbehan Formation of the regressive sequence" (Özer et al., 2008). Thus, the type stratigraphic unit of Woodward's hippuritids is considered as being the Tohma Reefs, above the Hekimhan Conglomerates, and is dated as late Campanian by the Sr-isotope values measured on the rudist shells (Schlüter et al., 2008). Material studied was collected at Stops 1-3, during the Pre-Meeting Field Trip (1) (Özer et al., 2008) of the Eight International Congress on Rudists, 2008, Izmir, Turkey.

Woodward (1855, pl. 3, figs. 1-4) figured in engraving three specimens as *Hippurites loftusi*. Figures 1 and 2 are a lateral view of both valves and a detail of a small portion of the left valve, respectively, of a complete specimen with conical right valve, NHMUK PI OR 33901. Figure 3 is the transverse cross section of the right valve of another specimen, also with both valves articulated but with a cylindrical right valve, that was cut nearly 10 mm below the commissure, NHMUK PI OR 33903. Figure 4 is the interior view of a disarticulated left valve with broken off part of the right valve pillars remaining adhered, NHMUK PI OR 33902; the size, form and location of the three main infolds disregards the adscription of this specimen to *V. loftusi*, rather corresponding to a large *V. vesiculosus* Woodward. Skelton and Fenerci-Masse (2008, pl. 6) provided new pictures of Woodward's specimens and considered NHMUK PI OR 33903 as being the holotype "by effective monotypy, as the only unambiguously recognisable specimen illustrated by Woodward".

Drawings of Woodward's (1855, pl. 3, fig. 3) specimen were used in subsequent papers (e.g. Sladić-Trifunović, 1978, text-fig. 1.A1), but no more *V. loftusi* specimens from Hekimhan have been subsequently figured, although citations are abundant: Karacabey (1974) cited the species, together with *Pironaea corrugata* (Woodward), when creating *Joufia capadociensis melitensis*; Karacabey-Öztemür (1981), together with *Pironaea praeslavonica* Milovanović, Sladić and Grubić, when creating *Miseia regularis* and *M. hekimhanensis*; Özer (1988a), together with *Pironaea corrugata*, *Colveraia variabilis* Klinghardt, *Joufia reticulata* Böhm, and *Miseia* sp., in a stratigraphic section; Özer (1988c), together with *Colveraia variabilis*, *Balabania acuticostata* Karacabey-Öztemür, *Miseia hekimhanensis* Karacabey-Öztemür, *Joufia* *reticulata*, and *Pironaea corrugata*, when creating *Branislavia orientalis*; Özer (1992), together with *Vaccinites ultimus* Milovanović, *Pironaea corrugata*, *Pironaea praeslavonica*, *Joufia reticulata*, *Colveraia variabilis*, *Sabinia rtanjica* Pejović, *Miseia hekimhanensis*, *M. osculata* Karacabey-Öztemür, and *Branislavia orientalis* Özer, when creating *Miseia merici* and *M. bilacunosa*; and Özer et al. (2008), together with *Hippurites colliciatus*, *H. lapeirousei* Goldfuss, *Pironaea corrugata*, *Joufia capadociensis* (Cox), and undetermined radiolitids in a road close to Hekimhan, and together with *P. corrugata*, *P. polystyla* (Parona), *Vaccinites ultimus*, *V. vesiculosus*, *Hippurites colliciatus*, *Hippuritella variabilis* (Munier-Chalmas), *H. lapeirousei*, as well as rare *Balabania* and *Joufia*, at Hasar Hill.

3.1.1.1. Woodward's material (Fig. 2, 3)

NHMUK PI OR 33901 is a complete specimen with both valves conjoined. Not sectioned. RV is wide conical and posteriorly curved, LV is low conical with sub-central apex. Heights of valves are 72 and 13.5 mm, respectively. Anterior-posterior diameter measures 63 mm and dorsal-ventral 70 mm. Both valves show rounded ribs; those of the LV are perforated by large (1-2 mm) irregular pores. LP2 is 1/4 of the shell circumference.

NHMUK PI OR 33903 is a specimen with both valves conjoined. LV is low conical (10 mm high) with sub-central apex. RV is nearly cylindrical, with the apical part incomplete (90 mm high), and is transversally sectioned 15 mm below the commissure. Anterior-posterior diameter measures 58 mm and dorsal-ventral 63 mm. Both valves show rounded ribs; those of the LV are perforated by large (1-2 mm) irregular pores. Transverse section of the RV shows: L is long triangular, anteriorly curved; P1 is short rectangular and P2 is longer and slightly pinched at the base; LP1 = P1P2 and LP2 is 1/4 of the shell circumference; AT is larger than PT; PM is located slightly dorsal to ATPT axis; angle LT is 30º, allowing a relatively large ADC; angles *a*, *b*, and *c* are 130º, 90º, and 195º, respectively; infolds at the inner shell margin are wide and short.

3.1.1.2. New material (Figs. 4-6)

Twelve specimens, PUAB 75823, PUAB 75827, PUAB 75830, PUAB 75839, PUAB 75842, PUAB 75845, PUAB 75846, PUAB 75852, PUAB 75864, PUAB 75866, PUAB 75867, PUAB 78592, most of them with conjoined valves. Specimens are conical and vary in size, 47.5 to 87.5 mm in mean diameter, although most do not outnumber 65 mm. The outer surface bears rounded ribs nearly 10 mm wide, limited by narrow furrows in coincidence with the infolds of the OSL. Transverse cross sections close to the commissure show the ligament ridge form is highly variable: wide triangular at its base, may present a uniform triangular or a narrow prolongation, or become lamellar; has a rounded tip in some specimens or a clear or hardly to distinguish truncated tip in other, but serial sections show it is always truncated at early growth stages (juveniles) in all specimens; frequently it is curved anteriorly. P1 is quadrangular to short rectangular. P2 is longer and sometimes more or less pinched. LP1 is comprised between 18º-41º; P1P2, 28º-47º; and LP2, 45º-87º, that is, RU between 0.12 and 0.24 of the valve circumference, lower values corresponding to those specimens having larger size and a lamellar ligament ridge. PM is located slightly dorsal to the ATPT axis. Angles *a*, *b*, *c*, are comprised between 75º-125º, 120º-175º and 170º-205º, respectively. Angle LT is comprised between 14º-60º, thus ADC being relatively large. The inner margin of the outer shell layer is undulated, forming secondary pillars in coincidence with the furrows at the outer surface; these secondary pillars are mostly very short, wider than long, although some slightly longer than wide pillars may also develop in some larger adults with lamellar ligament ridge, thus resembling those of figured specimens attributed to *Pironaea syriaca* Vautrin (e.g. Vautrin, 1933, pl. 4, fig. 1). Serial transverse sections of larger specimens indicate that these characters (lower RU values, a lamellar ligament ridge, and some longer than large secondary pillars) may be justified by their larger size. The number of secondary pillars does not significantly vary along ontogeny.

The LV is low conical with sub-central more or less prominent apex. At the outer surface, prominent ribs, outwards increasing in number as to equal that of the RV ribs, limited by deep furrows, cover the wide canals and are perforated by large irregular pores. Pores look large because of weathering; when (rarely) preserved, a reticule of small polygonal pores may be observed covering each large pore. Oscula are marginal.

3.1.2. Other Turkish areas (Fig. 7A-C)

Only three specimens of *V. loftusi* from other Turkish localities have been figured: Özer (1983, pl. 3, figs. 8, 9) correspond to a specimen from Asmayaylasi, S of Ankara, Tuz Gölü Basin, central Anatolia, shown in oblique-lateral view of both valves (fig. 8) and transverse cross section of right valve (fig. 9), displaying the myo-cardinal elements and a triangular ligament ridge with rounded distal end; Steuber et al. (1998, text-fig. 3D) is a drawing of the transverse cross section of the right valve, without myo-cardinal elements and depicting a truncated ligament ridge, of a specimen from Höbek Tepe, 5 km WSW of Amasya, north-central Anatolia; Özer (2002, pl. 2, fig. 3) is the transverse cross section of a specimen from Sereflikochisar [= Çereflikoçhisar], SE of Ankara, central Anatolia, displaying the myo-cardinal elements, an open triangular ligament ridge with rounded distal end, and an also open P1.

Kaya et al. (1987) cited *V. loftusi*, together with *Hippurites radiosus* DesMoulins, *H. colliciatus*, *Vaccinites ultimus*, *Joufia reticulata*, *Radiolites* sp., and *Biradiolites* sp., from the Hatipler Formation in the area of Yiğilca, NW Turkey. Özer (1988c) cited the species from Maliboğazy, S of Candir, 60 km NE of Ankara, together with *Biradiolites bulgaricus* Pamouktchiev and *Sphaerulites solutus* Pethö when creating *Bournonia anatolica*. Özer (1988a, text-fig. 3) included the species, together with *Pironaea polystyla*, *P. praeslavonica*, *Vaccinites orientalis* Milovanović, *Hippurites cornucopiae* Defrance, *H. heritschi* Pejović and Kühn, *Pseudopolyconites ovalis* Milovanović, *Lapeirousia* gr. *jouanneti* (DesMoulins), and *Sphaerulites solutus* in the stratigraphic section of Asmayaylasi, S Koçhisar and, together with *P. praeslavonica*, *Vaccinites* cf. *sulcatus* (Defrance), and *H. heritschi*, in the stratigraphic section of Yasilyurt. Özer (1992) cited *V. loftusi* from Haymana, S of Ankara, together with *H. cornucopiae*, *H lapeirousei*, *H. heritschi*, *Sauvagesia* sp., *Durania* sp., and *Radiolites* sp., and from Asmayaylasi, together with *H. cornucopiae*, *H. heritschi*, *V. orientalis*, *P. polystyla*, *P. praeslavonica*, and *S. solutus*, when creating *Miseia merici* and *M. bilacunosa*.

3.2. Bulgaria (Fig. 7D-G)

Douvillé (1897, p. 210, pl. 33, fig. 1, 1a, 1b) described a specimen (MGL 25365) from Gabrovo, SW of Tirnova [= Veliko Tarnovo], central Bulgaria, showing the two valves in lateral view, its well-preserved left valve, and the transverse cross section of its right valve displaying all the myo-cardinal elements. Toucas (1904, text-fig. 127) is a drawing of the transverse cross section of the same specimen, identified as *Hippurites loftusi* and *Vaccinites loftusi*, respectively, in Douvillé's and Toucas' papers.

Pamouktchiev (1963, p. 102, pls. 3-6) described *Vaccinites loftusi* from Yaroslavtzi, Breznik, western Bulgaria, and figured six specimens: a RV transverse cross section (pl. 3, fig. 3) with a long ligament ridge bearing a narrow distal prolongation; a RV transverse cross section and its drawing (pl. 4, fig. 2, text-fig. 2), displaying the myo-cardinal elements; a lateral view of both valves and the RV transverse cross section (pl. 5, figs. 1, 2) with no myo-cardinal elements; two left valves (pl. 6, figs. 1, 2); and a lateral view of both valves and its left valve (pl. 6, figs. 3, 3a). The ligament ridge has a rounded distal end in all figured specimens' transverse sections.

The transverse cross section of specimen US, Cr_2 33 in Pamouktchiev (1963, pl. 4, fig. 2) was reproduced, together with the lateral view of both valves and a detail of the left valve of specimen US, Cr_2 216, in Pamouktchiev (1981a, pl. 86, 1, 1a, pl. 87, fig. 1).

Tzankov (1965) cited *V. loftusi* from Breznik, western Bulgaria, together with *Hippuritella variabilis* and *Vaccinites ultimus*, when creating *Mitrocaprina bulgarica*. Pamouktchiev (1967) cited this species from Yaroslavtzi, Breznik, together with *Vaccinites archiaci* (Douvillé), *Pironaea corrugata*, *P. polystyla slavonica* Hilber, *Radiolites radiosus* d'Orbigny, and *Praeradiolites subtoucasi*

Toucas, among others, when creating several new species of *Biradiolites*. Tchechmedjieva (1967) also cited this species when describing the species of *Plesiocunnolites* Alloiteau (scleractinian corals) from the same locality.

Pamouktchiev (1975b, 1978, 1979, 1981b) cited *V. loftusi* when depicting the phylogeny of genus *Pironaea*, listing the rudists of Bulgaria, discussing on infolds and ontogeny in hippuritids, and depicting the phylogenetic lineages of *V. sulcatus*, respectively. Yanin (1976) cited *V. loftusi* within a stratigraphic distribution of rudists in Bulgaria and Swinburne et al. (1992, text-fig. 2) in the list of the rudist species recorded from the Bulgarian deposits in Pamouktchiev's and Tzankov's papers.

3.2.1. New material from Yaroslavtzi (Fig. 8)

The four specimens at our disposal (MGB 87334 to MGB 87337) have a conical, slightly curved, right valve. The juvenile part has a wide apical angle and numerous wide smooth rounded ribs limited by narrow furrows. The number of ribs increases only slightly in the adult part, but with a distinctive coarse ornamentation caused by pronounced growth increments. Mean diameter is comprised between 67.5 and 82.5 mm and height bigger than 120 mm. Transverse cross sections close below the commissure show L is long triangular, wide at the base, and with a rounded tip; serial sections indicate the tip is also rounded in juveniles. P1 is very short, with a base wider than its length or quadrangular. P2 is longer, sub-rectangular. LP1 is comprised between 30º-43º; P1P2, 40º-47º; and LP2, 77º-88º, that is, RU between 0.21 and 0.24 of the valve circumference. AT section is larger than PT. PM is aligned or slightly dorsal to the ATPT axis and approximately aligned, and equidistant, with the tips of L and P1. Angles *a*, *b*, and *c*, are comprised between 70º-85º, 150º-175º, and 180º-190º, respectively. A quite large antero-dorsal cavity is developed between teeth, L, and the inner margin of the outer shell layer. This last is undulated, forming very short, wider than longer, secondary pillars in coincidence with the furrows at the outer surface. Both the pattern and number of secondary pillars do not show significant differences between successive serial sections, that is, along ontogeny.

The left valve is badly preserved in two of the specimens (MGB 87336 and MGB 87337); it is conical, up to 20 mm high with sub-central apex. Weathering shows the canals, 3-4 mm wide, and where preserved, large irregular polygonal pores; no reticules may be observed. The oscula are marginal.

3.3. Eastern Serbia (Fig. 7H-L)

Vaccinites loftusi has been reported from the localities Bačevica and Vrbovac in eastern Serbia. Milovanović (1932, pls. 4, 5) figured the RV transverse cross section (pl. 5, fig. 1) of a specimen from Bačevica, and three specimens from Vrbovac: the lateral view of both valves and the well-preserved left valve of the first (pl. 4, figs. 1, 2), the transverse cross section of the RV of the second (pl. 5, fig. 2), and the lateral view and transverse cross section of the right valve of the third (pl. 5, figs. 3, 3a). Milovanović (1934b, pl. 1, fig. 2) figured the transverse cross section of another specimen from Bačevica, as *Hippurites (Vaccinites) loftusi* var. *timacensis*, reproduced as *Hippurites loftusi timacensis* by Sladić-Trifunović (1978, text-fig. 1.B1).

Sladić-Trifunović (1980, pl. 4, fig. 4, 4a, 5) figured as *Hippurites loftusi* two specimens from Bačevica: Ba-12, showing the transverse cross section of the right valve and an enlargement of the ligament ridge part, showing it is truncated; and Ba-36, only an enlargement.

The myo-cardinal elements are not displayed in any of the figured right valves transverse cross sections of Bačevica and Vrbovac specimens.

3.3.1. New material from Bačevica and Vrbovac (Fig. 9)

Material collected by A. Tarlao, now in MCSN: eighteen specimens, MCSN 1844 to MCSN 1861 (six amongst them with both valves) from Bačevica and three more, MCSN 1862 to MCSN 1864 from Vrbovac.

The specimens are conical, mean diameter is comprised between 35 and 65 mm, and the highest one, nearly cylindrical at its upper half, is more than 128 mm high. Transverse cross sections close below the commissure show L is triangular, wide and short or long, may present a narrow prolongation at the end and/or be open at the outer margin; serial sections indicate its tip is truncated in adult as well as in juvenile shells. P1 is short rectangular. P2 is longer and may be slightly pinched at the base. PM is located slightly dorsal to the ATPT axis. Angle LT is around 40º-60º, leaving an ADC of moderate size. Angles *a*, *b*, *c* are comprised between 75º-120º, 115º-180º, 180º-205º, respectively; LP1, 34º-51º; P1P2, 36º-50º; L-P2, 72º-99º, that is, 0.19-0.28 of the shell circumference. Secondary pillars are wider than long. Because of weathering, pores are badly preserved in the six available left valves.

The specimens occur together with *Pironaea milovanovici* Kühn.

3.4. Spain

3.4.1. South-eastern Spain (Figs. 7M, N, 10)

Specimens have been found at three outcrops, namely Pilonets, Barranc de la Casella, and Nicolasa Quarry, between the municipalities of Alzira, Tavernes, and Barxeta in southern Valencia province. Corresponding to the lower part of the mapped lithological unit ‘calizas con hippurites’ in IGME (1982) and ‘Level C’ in Pons and Vicens (2002), specimens occur together with *Bournonia* sp., *Darendeella anatolica* Karacabey-Öztemür, *Joufia reticulata* Böhm, *Praeradiolites subtoucasi* Toucas, *Hippurites colliciatus* Woodward, *H. heritschi* Kühn, *H. lamarcki* Bayle, *Pironaea polystyla* (Pirona) *sensu* Douvillé 1894, pars, *P. milovanovici* Kühn, *Vaccinites ultimus* Milovanović, and *Mitrocaprina* sp.

The twenty-nine available specimens, with long cylindrical adult shells, are quite small, 29 to 47.5 mm in mean diameter. Transverse cross sections close below the commissure show L is triangular, wide and short or long, may present a narrow prolongation at the end and/or be open at the outer margin, and truncated at the end; serial sections indicate its tip is also truncated in juveniles. P1 is short rectangular. P2 is longer and may be slightly pinched at the base. PM is located slightly dorsal to the ATPT axis. Angle LT is comprised between 47º-58º, leaving an ADC of small size. Angles *a*, *b*, *c* are comprised between100º-130º, 95º-130º, 190º-220º, respectively; LP1, 37º-55º; P1P2, 31º-55º; L-P2, 77º-103º, that is, 0.21-0.28 of the shell circumference. Secondary pillars are wider than long. In the few specimens preserving its left valve, the outer surface is weathered and details of the pores can’t be observed.

The co-occurring specimens of *Pironaea milovanovici* are also smaller than those from Serbia (Munujos et al., 2016).

Douvillé (1894, pl. 17, fig. 5) figured the transverse section of the right valve of a specimen from Quatretonda, SW of our outcrops, that he named *Pironaea* sp.; Pamouktchiev (1981b) established *Vaccinites espagnicus* based on this figure. The restudy of the specimen (UCBL-EM 15903) (Fig. 7M, N) shows that it is very poorly preserved and with important parts lacking; only with great uncertainty could be related to the specimens described herein.

3.4.2. Pyrenees (south-central and south-eastern) (Figs. 11, 12)

Specimens have been found at different outcrops in the over-thrusting sheets of both the south-central Pyrenees (Serra d'Arquells and Castellonroi, in Serres Marginals unit, and Torallola, in Boixols unit, the southernmost and the northern unit of the three recognized, respectively) and south-eastern Pyrenees (Coll de Pal road, in Cadí unit, the uppermost one of the lower units).

Amongst collected specimens, five come from Serra d'Arquells and two from Castellonroi. Another specimen occurred at Torallola, in the olistostromic Pumanyons Member of the turbiditic Vallcarga Formation, W of Pobla de Segur. Still another was found at Coll de Pal road. Some differences become evident between Pyrenean specimens from different localities, mainly concerning the ligament ridge, but secondary pillars are wider than long in all them.

Specimens from Serra d'Arquells (PUAB 02881, PUAB 59789, PUAB 59902, PUAB 64071, PUAB 64079) have a conical right valve, low conical in juvenile shells becoming nearly cylindrical in adults. Mean diameter ranges between 70 and 90 mm, the largest one being 150 mm high; a juvenile, 35 mm in mean diameter and 30 mm high, was also collected. The outer surface presents wide rounded ribs limited by narrow furrows in the juvenile part of the shell, while a distinctive coarse ornamentation caused by pronounced growth increments characterizes the adult part. Transverse cross sections close below the commissure show L is wide but long, nearly sub-rectangular with pointy tip in larger specimens, with a hardly distinguishable slight truncation in adults although, as seen in serial sections, evidently truncated in juveniles. P1 is sub-rectangular. P2 is longer and more or less pinched at its base. LP1 ranges between 36º-42º; P1P2, 32º-38º; and LP2, 68º-78º, that is 0.19-0.22 of the shell circumference. LT is comprised between 55-72º. AT section is larger than PT. PM is long, very narrow, and located slightly above the ATPT axis; its anterior margin is approximately aligned, and equidistant, with the tips of L and P1. Angles *a*, *b*, and *c*, are comprised between 110º-125º, 120º-140º, and 195º-215º, respectively. A relatively small antero-dorsal cavity is developed between teeth, L, and the inner margin of the outer shell layer. This last is undulated, forming very short, wider than longer, secondary pillars in coincidence with the furrows at the outer surface. The pattern and number of secondary pillars do not show significant differences between successive serial sections, that is, along ontogeny. Two specimens (PUAB 59789 and PUB 64071) preserved the left valve, although manifestly weathered: its outer margin is undulated, in coincidence with the short infolds of the outer shell layer of the right valve, and also with P1 and P2, depicting two marginal oscula; wide radial ribs traversed by large pores indicate the presence of the canals below; no detail of the pores can be observed because of weathering.

One of the specimens from Castellonroi (PUAB 59907) is an incomplete right valve, 82.5 mm in mean diameter and 110 mm high, where the apical part is preserved but the upper one lacks. Thus, it corresponds to the juvenile part of the shell and no myo-cardinal elements can be observed in the transverse cross section. The wide long triangular L presents a lamellar truncated apical prolongation. P2 is curved towards P1 and almost not pinched at its base. The second specimen (PUAB 91005), with both valves, is larger and complete although “faulted” and slightly displaced longitudinally, 88 mm in mean diameter and 126 mm high. L is wide triangular with a hardly distinguishable slight truncation at the tip. P1 is short rectangular. P2 is narrower, longer and curved towards P1. Angles: LP1, 34º; P1P2, 27º; LP2, 61º, that is, 0.17 of the shell circumference. Angle LT measures 43º. LV, where better preserved, shows a mesh of polygonal pores, limited by narrow walls with sharp crests, and centred sub-rounded large orifices (Fig. 12).

The specimen from Torallola (PUAB 59925) grew, attached to a colonial coral, with the right valve 82.5 mm in mean diameter and 100 mm high, following a double geniculation. The left valve is not preserved but the sockets of its myo-cardinal elements, filled with matrix, can be observed in the transverse cross section of the right valve: LP1, 45º; P1P2, 44º; LP2, 89º, that is, 0.25 of the shell circumference. Angle LT measures 40º. The wide long triangular L displays a long lamellar truncated apical prolongation at all growth stages.

The specimen from Coll de Pal road (PUAB 33645) is a large right valve, 110 mm high, with a mean diameter of 90 mm. The upper part is scratched; nevertheless, the myo-cardinal elements are cut in the transverse cross section, being like those of larger specimens in Serra d’Arquells. L is sub-rectangular with pointed tip, with a hardly distinguishable slight truncation at the end. P1 is also rectangular but wider than L. P2 is only slightly pinched at its base.

3.5. Croatia (Fig. 7O, P)

Polšak and Mamužić (1969) reported *V. loftusi* from Hvar and Šćedro islands, Croatia, in rocks attributed to their Rudist Zone VI (upper Campanian-Maastrichtian). Sladić-Trifunović (1980, pl. 4, fig. 1-3) figured as *Hippurites loftusi* two specimens from Pokonji Dol, Hvar Island: Pd-8, shown in external view of both valves and transverse cross section of the right valve; and Pd-3, in transverse cross section of right valve. Any of both displays the myo-cardinal elements, and the long triangular ligament ridges seem to have rounded tip. Pejović and Radoićić (1987) cited *V. loftusi* from the Voščića Formation at Povlja, eastern Brač Island.

3.6. United Arab Emirates-Oman border region (Fig. 7Q)

The three specimens mentioned by Morris and Skelton (1995) from Qarn Murrah (UAE) and Jebel Huwayyah *Loftusia* beds (Oman) "… are very poorly preserved internally." and "… were not enhanced by sectioning" (op. cit., p. 290). No myo-cardinal elements are designed and only a slight undulation appears at the inner margin of the outer shell layer (op. cit. text-fig. 5).

3.7. Syria (Fig. 7R)

Vautrin (1933) created the species *Vaccinites (Pironaea* Meneghini*) syriaca* based on a large number of specimens from the rudists breccia at Yeyla, 3 km E of Ordou, road Antioquia-Lataquia 30 km S of Antioquia, northern Syria. Description of the stratigraphic section at Yeyla, with its fossil content, provided by Dubertret (1966, p. 317, fig. 23). The author figured the transverse cross section of the right valve of a large specimen (pl. 4, fig. 1) and a detail of the longitudinal section of another one (pl. 5, fig. 3). The former figure was reproduced, erroneously identified as *Vautrinia syriaca*, in Coogan (1969, fig. E243.6b), and redrawn in Pamouktchiev (1981b, text-fig. 1). Vautrin's figured specimens are preserved at UCBL-EM. The type specimen, UCBL-EM 15904, is very large, 130 mm in mean diameter, although the other specimen, UCBL-EM 15905, measures no more than 95 mm; the ligament ridge is long lamellar with rounded tip; RU is 0.15 of the valve circumference; P1 is quadrate and P2 rectangular; most secondary pillars are wider than long, some quadrate, and a few slightly longer than wide.

Vautrin's species has been reported from other areas outside Syria. Özer (1987, pl. 1, fig. 2) figured as *Pironaea syriaca* the transverse section of the right valve of a specimen from Alidami, SE Anatolia. The specimen (Fig. 7S) measures 60 mm in diameter, RU is 0.19 of the valve circumference, and it is not discernible in the picture if the tip of the long ligament ridge is rounded or truncated, nor is it described in the text.

Karacabey-Öztemür and Selçuk (1981) reported Vautrin's species from Hatay, together with *Pironaea corrugata*, *Vautrinia syriaca* and *Sabinia* aff. *klinghardti* when stablishing the new genus *Hatayia* and the new species *Lapeirousella anatolica* and *L. yalazensis*. The species was also cited by Özer et al. (2008), together with *Vautrinia syriaca*, *Vaccinites vesiculosus*, *Caprina* sp., *Pironaea anatolica* Karacabey, *Pseudosabinia klinghardti*, *Dictyoptychus leesi* (Kühn), *D. striatus* Douvillé, *D. euphratica* Karacabey.Öztemür, *D*. sp., and *Paracaprinula syriaca* Piveteau, from Alidami.

Schumann (1999, 2000) reported the presence of Vautrin's species in Saiwan, Oman, and showed some pictures and drawings of it in a poster at the Fifth International Congress on Rudists in Erlangen. In the two transverse sections drawing (Fig. 7T, U), mean diameter is 86.5 and 95 mm and RU 0.17 and 0.20 of the valve circumference; as far as they are represented, the ligament ridge and secondary pillars are similar to those of Vautrin's (1933) type.

With the exception of having a truncated ligament ridge, other characters of several specimens of *Vaccinites loftusi* collected in Hekimhan are like those of Vautrin's species, although they are smaller, as also is Özer's (1987, pl. 1, fig. 2) specimen.

4. Discussion

4.1. Shell morphology and evolution

Generally, in hippuritid phyletic lineages, a truncated ligament ridge is considered more primitive than one with a rounded end. The former is supposed supporting a vestigial ligament while the later indicates its complete absence. The state of this character has been used to discriminate species (e.g. Toucas, 1903, 1904), although associations showing, with different proportion, both states of this character have been reported from the same fossil locality (e.g. Simonpietri, 1999), being considered a single species. It is also assumed that, as in most other rudists, hippuritid phyletic lineages manifestly follow Cope's Rule, tendency for organisms in evolving lineages to increase in size over time, (Simonpietri, 1999; Steuber, 2003).

We observed that *Vaccinites loftusi* specimens from different fossil localities, but also from a single locality, display a wide variability in some of their morphological details (Appendix 1).

We may conclude that all the considered material represents a continuous variation in several characters: shell size, ligament ridge, RU values, and secondary pillars development. Nevertheless, the different assemblages (fossil localities) can be grouped and chronologically ordered considering its degree of evolution, mainly concerning ligament ridge, shell size, and secondary pillars development (Tables 1, 2):

SE Spain and E Serbia specimens appear to be the most primitive, with manifestly truncated ligament ridge in both adult and juvenile shells. Both are relatively small, the former the smallest, and occurring together with *Pironaea milovanovici*, also smaller in the former. Small size could indicate that SE Spain specimens are slightly older than E Serbia ones, but this difference may also be ecological, because the former are long cylindrical occurring in dense thickets and the later are conical occurring isolated. Specimen from Torallola, in south-central Pyrenees, is similar as E Serbia ones.

Specimens from Castellonroi, Serra d'Arquells and Coll de Pal road, in south-central Pyrenees, still have a hardly distinguishable slight truncation of the ligament ridge in adult shells, while it is sometimes rounded in Hekimhan specimens. It is clearly truncated in juvenile shells of both localities. This indicates that Serra d'Arquells, Castellonroi, and Coll de Pal road specimens are slightly more primitive than Hekimhan's ones, and both are more evolved than those from SE Spain, E Serbia, and Torallola in south-central Pyrenees.

The specimens from Hekimhan display an evident diversity in some characters. A lamellar ligament ridge occurs in some adult shells; serial transverse sections, documenting its ontogeny, reveal it changes from wide triangular, to develop a short and later a longer lamellar prolongation, all them with a truncated end, to finally become lamellar with a rounded or hardly to distinguish truncated tip. Simultaneously, lower values of RU are attained and some longer than wide secondary pillars may develop. These last specimens only differ from the type specimen of *P. syriaca* by its smaller size and the not clearly rounded tip of the ligament ridge; thus, *P. syriaca* may be considered more evolved than Hekinham specimens.

Specimens from Yaroslavtzi, W Bulgaria, relatively large, and with rounded tip ligament ridge in both juvenile and adult shells, appear as more evolved. The same may be applied to *P. syriaca*, as already mentioned, although probably following a different, but close, evolutionary line. Both differ in their values of RU and in the development of secondary pillars.

These groups of specimens appear clearly clustered, although with extensive overlap, when plotted for other characters currently used in hippuritid species discrimination, like pillar/myo-cardinal arrangement (indicated by values of *a* and *b* angles) and main infolds setting (indicated by values of mD and RU) (Fig. 13A, B). A survey on serial cross sections of RVs illustrated that RU values decrease with ontogeny.

Specimens from Hekimhan showed that the large irregular pores in the left valve, described in the type specimens of *V. loftusi*, look large because of weathering. In fact, each large pore is covered by a reticule of small polygonal pores, when rarely well-preserved (Fig. 6). Also because of weathering, fine details of the pores have not been observed in the specimens from other localities. Only one specimen from Castellonroi, seems to have a mesh of polygonal pores, limited by narrow walls with sharp crests, and centred sub-rounded large orifices (Fig. 12). Thus, in general, the knowledge of the pores in the left valve is very poor and, consequently, the comparison between the assemblages of the different localities is mainly based on the characters observed in transverse cross-sections of right valves.

Most of the specimens reported in literature from other localities (central and northern Anatolia, Croatia, and UAE) are insufficiently documented to be considered within this discussion.

4.2. Stratigraphy

Not enough precise and comprehensive stratigraphic data are available to unambiguously test this evolution hypothesis. Moreover, different localities may correspond to different biogeographic units where: 1) populations may become isolated; and 2) evolution rate may have not been the same. Co-occurring rudist taxa, taken from literature, are listed in the corresponding outcrop chapter; nevertheless, most citations are relatively old and identifications, as well as their attributed age, need a deep revision. Some of the co-occurring benthic foraminifer citations are relatively recent, although the ranges of the taxa identified are, generally, too wide for our purpose. Strontium isotope stratigraphy data have been published for a few localities, although not particularly from the same rudist horizons treated herein. Following, the most relevant stratigraphic data concerning the studied localities are highlighted and/or discussed and evaluated.

Schlüter et al. (2008) attributed the rudist bearing Tohma Reefs at Yazıhan and Hekimhan (Malatya Basin) to the upper Campanian, based on strontium isotope stratigraphy data. Steuber and Schlüter (2012) reported a mean $^{87}Sr/^{86}Sr$ of 0.707632 for Hekimhan and 0.707642 for Yazıhan, assigning a mean age of ca. 74.00 Ma to both.

Swinburne et al. (1992) reported the presence of the benthic foraminifer *Orbitoides tissoti* (Schlumberger) all along the Yaroslavtzi beds, thus attributing an early Campanian to middle/late Campanian age to them. The occurrence of *Vaccinites loftusi* was reported by the authors at their uppermost part. A value of 0.707625 in $^{87}Sr/^{86}Sr$ analysis was given in this work, indicating an absolute age of ca. 77.1 – 78.7 Ma, when plotted against the general curve for the Late Cretaceous (data from Swinburne, 1990 and Koepnick et al., 1985; McArthur et al. curve was not published until 2001). Schlüter (2008, fig. 4.2) reinterpreted Swinburne's data as corresponding to an age of ca. 73.6 – 75.95 Ma.

Tarlao et al. (2010) described the outcrops around Bačevica and Vrbovac as "a very discontinuous and ill exposed section". They marked the location of the observation points in a detailed map of the area but not being possible to place them on a stratigraphic section. *V. loftusi* specimens are highly abundant at point 9. Considering the benthic foraminifer content in the rudist beds, *Siderolites vidali* Douvillé [=*Pseudosiderolites vidali*] and *Orbitoides tissoti*, the authors included these beds in the Campanian.

Published data on strontium isotope stratigraphy from Nicolasa Quarry (Steuber and Schlüter, 2012) are of doubtful application herein because it is not clear at which rudist horizon the samples were taken. About 180 m of bioclastic limestones with several unconformities and successive different rudist horizons crop out at Nicolasa Quarry section (Pons and Vicens, 2002). The mean $^{87}Sr/^{86}Sr$ of 0.707615 with an age assignation of ca. 75.27 Ma in Steuber and Schlüter (2012) seems to correspond to the uppermost part of the section, as far as it is proposed to indicate the base of their 'Hippuritella lapeirousei Interval Zone'. *H. lapeirousei* first occurrence is at the uppermost part of the section, while the bed with our *Vaccinites* samples is far below (at its base), co-occurring with *Pironaea milovanovici* and *Vaccinites ultimus*. Both species characterize, respectively, the two Steuber and Schlüter's (2012) hippuritid zones immediately below, the 'Pironaea polystyla group' and the 'Vaccinites alpinus' interval zones. The same 0.707615 mean $^{87}Sr/^{86}Sr$ value was used by Steuber (2003) when depicting the evolutionary changes of *Vaccinites* "*alpinus*".

The tectonic structure and Upper Cretaceous sequence stratigraphy of south-central Pyrenees (Berástegui et al., 1993; ECORS, 1988; Simó, 2004) is well understood and consistently accepted. Particularly, the succession of carbonate platforms with rudists is accurately correlated through the over-thrusting sheets. Torallola outcrop, in Boixols unit, is clearly older than the other outcrops, Serra d'Arquells and Castellonroi, in Serres Marginals unit, and Coll de Pal road, in Cadí unit.

Torallola outcrop (Pumanyons olistostrome Member of the turbiditic Vallcarga Formation) is composed of autochthonous deposits (blue clays with interbedded calcareous siltstones) and allochthonous deposits (slumped glauconitic sandstones, marly olistostromes, and para-conglomerates) thus implying their fossil content is older than that in the autochthonous deposits (Rosell et al., 1972). The blue clays contain planktonic foraminifera: *Globotruncana linneiana (*d'Orbigny)*, Globotruncana bulloides* (Vogler)*,* *Globotruncana arca* (Cushman), *Rosita fornicata* (Plummer) [=*Contusotruncana fornicata*], *Globotruncana ventricosa* (White), *Globotruncana rosetta* (Carsey), *Globotruncanita stuartiformis* (Dalbiez) (Gómez-Garrido, 1987), belonging to the upper half of the Globotruncana ventricosa Zone [= Contusotruncana plummerae Zone in Gradstein et al., 2012], with an age ranging between mid-Campanian (79.2 Ma) and early late Campanian (76.1 Ma) (Gradstein et al., 2012). The para-conglomerates contain, together with the rudists and other megafauna, siderolitid foraminifera (Robles, 2014): *Praesiderolites douvillei* Wannier, *Pseudosiderolites vidali* Douvillé, *P.* aff. *vidali*. The former characterizes the lower Campanian, although genus *Pseudosiderolites* may reach the lower upper Campanian. Thus, an early Campanian age seems suitable for the *Vaccinites* from Torallola.

The abundant benthic foraminifers occurring in Serra d'Arquells outcrop is composed of complex agglutinated forms (*Dicyclina schlumbergeri* Munier-Chalmas, *Dictyopsella kiliani* Munier-Chalmas, *Dictyopsella* cf. *cuvillieri*, *Cuneolina* sp.), conical foraminifera (*Abrardia catalaunica* Bilotte, possible *Calveziconus lecalvezae* Caus and Cornella), complex miliolids (*Adrahentina iberica* Bilotte, *Praelacazina fragilis* (Hofker)), meandropsidids (possible *Eofallotia simplex* Hottinger and Caus, *Fascispira*? sp., *Fallotia*? sp.), rotaliids (*Pyrenerotalia longifolia* Boix et al., *Rotalispirella acuta* Consorti et al., and *Rotorbinella* sp.), and orbitoidiforms (*Lepidorbitoides* spp). Based on the literature, the age provided by these taxa varies from mid-late Santonian to late Maastrichtian, a too large stratigraphic range for our purpose; the species of *Lepidorbitoides*, that would provide a narrower range, could not be identified with the random sections available. The stratigraphic position of Serra d'Arquells outcrop is close below the carbonate platform with *Hippurites radiosus*, well characterized in south-central Pyrenees. Strontium isotope stratigraphy was used recently to date the base of this platform (Caus et al., 2015), obtaining a numerical age of ca. 71 Ma. Thus, Serra d'Arquells outcrop should be somewhat older.

The section of Yeyla, type locality of Vautrin's (1933) *Pironaea syriaca*, together with *Vautrinia syriaca* Vautrin and *Hippuritella syriaca* Vautrin, was described by Dubertret (1966) who reported the co-occurrence of the foraminifers *Siderolites calcitrapoides* Lamarck and *Orbitoides antiochena* David and the presence, immediately above, of *Siderolites calcitrapoides* Lamarck, *Omphalocyclus macroporus* (Lamarck), *Orbitoides media* (d'Archiac), and *Orbitoides apiculata* Schlumberger. This last foraminifer association characterizes the Maastrichtian (Özcan, 2007).

4.3. Palaeobiogeography

During Campanian—Maastrichtian, the boundaries of the Mediterranean Tethys were not straight but irregular. Depending on the geodynamic evolution of the plate margins in the Mediterranean region (Philip, 1982) and the global sea-level variation, several shallow marine areas colonised by rudists could easily remain connected to each other, or become more or less isolated from the main part and from other areas, at different time intervals (Fig. 14). These circumstances may have relevant consequences on the isolation of benthic communities, allowing differentiation and subsequent speciation. In fact, several papers focussed lately on Late Cretaceous Mediterranean rudists palaeobiogeography (Philip, 1982, 1985; Pons and Sirna, 1992; Sladić-Trifunović, 2002; Özer et al., 2009).

Centred on the rudists distribution in the Mediterranean Tethys, Philip (1982) distinguished five main palaeobiogeographic units related to the margins of the plates and micro-plates recognized in there: 1) western margins of the European Plate, margins of the Iberian plate, and western margins of the Sardinian Plate; 2) margins of the African Plate; 3) margins of the Adriatic Plate; 4) eastern margins of the European Plate; 5) margins of the Arabian and Turkish cratons. Philip (1985) proposed three sub-provinces of the Mediterranean Province for the Campanian and Maastrichtian: 1) Aquitanian-Pyrenean, with two sub-units 1_1) Aquitanian and 1_2) Pyrenean; 2) South Iberian; and 3) eastern and central Mediterranean, with six subunits, 3_1) North Adriatic, 3_2) Apulia-Apennines, 3_3) Sicily, 3_4) Tunisia, 3_5) Turkey, and 3_6) Bulgaria-Romania. Pons and Sirna (1992) stressed the taxonomic differences between the rudist assemblages of some Mediterranean Tethys areas, related to their occurrence in isolated carbonate platforms or in mixed (carbonate-siliciclastic) platforms. Sladić-Trifunović (2002) distinguished, in what she called Central Tethyan Province, and based in a remarkable increase in number of endemic genera from North to South, four sub-provinces: 1) Carpatian-Balkanid-Pontidian (= NorthernTethyan margin); 2) Transitional; 3) Apulian-Tauridan, intraoceanic; 4) Arabian (= South-eastern Tethyan margin). Özer et al. (2009) distinguished, in Turkey, three Campanian—Maastrichtian main platforms/plate fragments, each with different characteristic rudist and benthic foraminifer associations of varying abundances: Rhodope-Pontide Platform (RPP), Anatolide-Tauride Platform (ATP), and Arabian Platform (AP).

5. Systematic palaeontology

As a consequence of the differences in key shell morphology characters observed between the studied groups of specimens (‘section 3’) (Table 1), the interpretation of their evolution (‘section 4.1.’), and considering the stratigraphy and palaeogeograpy of the treated fossil localities (‘sections 4.2. and 4.3.’) (Fig. 14), the distinction of five species seems justified. Main discriminant characters are shell size, ligament ridge and its ontogenetic change, and development of secondary pillars (Table 2).

Family: Hippuritidae Gray, 1848

Genus *Vaccinites* Fischer, 1887

Type species. *Hippurites cornuvaccinum* Bronn, 1831, p. 371.

Remarks. Sénesse (1947) proposed to include all hippuritids (previously considered as *Vaccinites*) with reticulate, sub-reticulate or denticulate pores in the genus *Pseudovaccinites*, since the pores of the type species of *Vaccinites* are polygonal. *Pseudovaccinites* Sénesse was synonymised with *Vaccinites* Fischer in Dechaseaux et al. (1969). Bilotte (1981, 1985) retained the use of *Pseudovaccinites* and later (Bilotte, 1992) added, to the type of pores, the ontogenetic reduction or non-reduction of angle α (= LT herein) as criterion to discriminate *Vaccinites* from *Pseudovaccinites*. In the authors’ opinion, at the present state of knowledge, the use of both characters is plenty of difficulties: 1) the classification of pores is still not clear enough and its identification mostly becomes problematic because of weathering; and 2) the ontogenetic change of angle α is hardly observable, and consequently non-evaluable, as far as the myo-cardinal elements are only cut in transverse cross sections of right valves close to the commissure (= adult shell), not in the rest of the valve and definitively neither in its juvenile part. Thus, genus *Vaccinites* is retained here. Nevertheless, we do not consider that the historical genera *Hippurites*, *Hippuritella* and *Vaccinites* are sufficient to express the diversity and phylogenetic relationship among the Hippuritidae, but much more detailed and careful research, not only limited to '*Vaccinites versus Pseudovaccinites*', is still needed before attempting to solve the issue. Other widely accepted hippuritid genera originated later and appear to be derived from the historical ones.

Vaccinites alceotarlaoi sp. nov.

Figures 7H-P, 9A-O, 11A-D

?1894 *Pironaea* sp.; Douvillé, p. 107, pl. 17, fig. 5.

1932 *Vaccinites loftusi* Woodward; Milovanović, pl. 4, fig. 1, 2, pl. 5, fig. 1-3a.

1934 *Hippurites* (*Vaccinites*) *loftusi* Woodward var. *timacensis* Milovanović, pl. 1, fig. 2.

1978 *Hippurites loftusi timacensis* Milovanović; Sladić-Trifunović, text-fig. 1.B1.

1980 *Hippurites loftusi* Woodward; Sladić-Trifunović, pl. 4, fig. 4, 4a, 5.

?1981b *Vaccinites espagnicus* Pamouktchiev, p. 408 (411), text-fig. 1.

2002 *Vaccinites* sp. aff. *loftusi* (Woodward); Pons and Vicens, p. 239, pl. 1, fig. 1b, pl. 2, fig. 1-8, 9a, pl. 4, fig. 5b.

Derivation of name. In homage to Alceo Tarlao, Italian rudistologist, who intensively researched and collected on Serbian rudist bearing rocks.

Holotype. MCSN 1862.

Type locality. Bačevica, E Serbia.

Stratigraphic horizon. Lower? Campanian.

Diagnosis. *Vaccinites* with short, wider than long, secondary pillars; ligament ridge with truncated tip in adult as in juvenile shells.

Description. See sections '3.3.1. New material from Bačevica and Vrbovac', '3.4.1. South-eastern Spain', and '3.4.2. Pyrenees (Torallola)'.

Remarks. *Vaccinites alceotarlaoi* has been reported from: Bačevica and Vrbovac, E Serbia; SE Spain; and Torallola, south-central Pyrenees. It is considered the most primitive and the origin of the other species considered herein. *V. pirenaicus*, *V. bilottei*, and *V. loftusi* are considered derived from *V. alceotarlaoi*, each one developed in a different geographic location, Pyrenees, Bulgaria, and Anatolia, respectively.

Vaccinites pirenaicus sp. nov.

Figures 11E-R, 12A-C

1992a *Vaccinites loftusi* (Woodward); Vicens, p. 142, pl. 8, figs. 7, 8.

1992b *Vaccinites loftusi* (Woodward); Vicens, p. 233, pl. 38, figs. 7, 8.

Derivation of name. From Pyrenees.

Holotype. PUAB 59789.

Type locality. Serra d'Arquells, south-central Pyrenees.

Stratigraphic horizon. Upper Campanian.

Diagnosis. *Vaccinites* with short, wider than long, secondary pillars; ligament ridge wide but long, nearly sub-rectangular with pointy tip in larger specimens, with a hardly distinguishable slight truncation in adults, but clearly truncated in juvenile shells.

Description. See section ‘3.4.2. Pyrenees’ (Serra d’Arquells, Castellonroi, and Coll de Pal road).

Remarks. The species appears as evolved from *V. alceotarlaoi* which has been recognized, besides in E Serbia and SE Spain, in south-central Pyrenees, in an older stratigraphic horizon than that of *V. pirenaicus*. Presumably, *V. pirenaicus* was originated in Pyrenees and has only been recognized, up to now, in south-central Pyrenees: Serra d’Arquells, Castellonroi, and Coll de Pal road in Serra del Cadí.

Vaccinites loftusi (Woodward, 1855)

Figures 2-6, 7A, B, S

1855 *Hippurites Loftusi* Woodward, p. 58, pl. 3, figs. 1-3 [non fig. 4 = *Hippurites vesiculosus* Woodward].

1978 *Hippurites loftusi* Woodward; Sladić-Trifunović, text-fig. 1.A1 [drawing of Woodward’s, 1855, pl. 3, fig. 3].

1983 *Vaccinites loftusi* Woodward; Özer, p. 20, pl. 3, fig. 8, 9.

?1987 *Pironaea syriaca* Vautrin; Özer, pl. 1, fig. 2.

1998 *Vaccinites loftusi* (Woodward); Steuber et al., text-fig.3D

?1999 *Pironaea syriaca* Vautrin; Schumann, p. 59, fig. poster congress.

?2000 *Pironaea* aff. *syriaca*; Schumann, p. 146, text-fig. 5.

2008 “*Hippurites*” *loftusi* Woodward; Skelton and Fenerci-Masse, pl. 6, fig. a-f [new pictures of Woodward’s specimens]

2008 *Vaccinites loftusi* Woodward; Özer et al., p. 7, 8.

?*2008* *Pironaea syriaca* Vautrin; Özer et al., text-fig. 25.

Diagnosis. *Vaccinites* with short, wider than long or quadrate, sometimes with a few slightly longer, secondary pillars; ligament ridge with clearly truncated tip in juvenile shells, but with a hardly distinguishable slight truncation, or even rounded, in adults.

Description. See sections '3.1.1.1. Woodward's material' and '3.1.1.2. New material'.

Remarks. This species seems derived from *V. alceotarlaoi* and is highly variable in some of its characters. Those of some larger specimens remind *V. syriaca*, considered its derived species. The studied material comes from the upper Campanian of Hekimhan, SE Anatolia. Specimens described from other Turkish localities in central and northern Anatolia are recognized as belonging to this species. Citations of *Pironaea syriaca* in southern Anatolia and in Oman, insufficiently described up to now, may also correspond to *V. loftusi*.

Vaccinites bilottei sp. nov.

Figure 7D-G, 8

1897 *Hippurites Loftusi* Woodward; Douvillé, p. 210, pl. 33, figs. 1, 1a, 1b.

1904 *Vaccinites Loftusi* Woodward sp.; Toucas, p. 82, text-fig. 127.

1963 *Vaccinites loftusi* Woodward; Pamouktchiev, p. 102, text-fig. 2, pl. 3, fig. 3, pl. 4, fig. 2, pl. 5, figs. 1, 2, pl. 6, figs. 1-3a.

1981a *Vaccinites loftusi* (Woodward); Pamouktchiev, p. 174, pl. 86, fig. 1, 1a, pl. 87, fig. 1.

Derivation of name. In homage to Michel Bilotte, for his remarkable and continuous work on hippuritids from Pyrenees and elsewhere.

Holotype. MGL 25365, figured in Douvillé (1897, pl. 33, figs. 1, 1a, 1b) and Toucas (1904, text-fig. 127)

Type locality. Gabrowo, SW of Tirnova (= Veliko Tarnovo), central Bulgaria.

Stratigraphic horizon. Upper Campanian.

Diagnosis. *Vaccinites* with short, wider than long, secondary pillars; ligament ridge with rounded tip in adult as in juvenile shells.

Description. See section ‘3.2.1. New material from Yaroslavtzi’.

Remarks. The species has only been recognized, up to now, in western and central Bulgaria.

Vaccinites syriaca Vautrin, 1933

Figure 7R, T, U

1933 *Vaccinites* (*Pironaea* Meneghini) *syriaca* Vautrin, p. , pl. 4, fig. 1, pl. 5, fig. 3.

1969 *Vautrinia syriaca* (Vautrin); Coogan, fig. E243.6b.

?1987 *Pironaea syriaca* Vautrin; Özer, pl. 1, fig. 2. [?= *V. loftusi*]

?1999 *Pironaea syriaca* Vautrin; Schumann, p. 59, fig. poster congress. [?= *V. loftusi*]

?2000 *Pironaea* aff. *syriaca*; Schumann, p. 146, text-fig. 5. [?= *V. loftusi*]

Diagnosis. *Vaccinites* with short and slightly longer secondary pillars; ligament ridge with a clear rounded tip in adult as in juvenile shells.

Description. See section ‘3.6. Syria’.

Remarks. The species is not considered a *Pironaea*, because the short infolds of the outer shell layer do not modify the canal pattern of the left valve, as it is diagnostic for *Pironaea*. Some citations of this species outside Syria may correspond, in fact, to *V. loftusi*. If so, the type material from Syria would be the only recognized occurrence of *V. syriaca*.

6. Conclusions

The hippuritid rudists with short secondary pillars from different localities of the Mediterranean Tethys, reported in literature as (or closely related to) *Vaccinites loftusi* Woodward, although apparently similar, differ each other in important diagnostic characters.

The observed morphological differences between specimens from different localities have been interpreted as due to evolution change and the hippuritid assemblages have been chronologically ordered, although independent stratigraphic data are not sufficiently precise as to unambiguously confirm this age assumption.

A survey on recent Late Cretaceous palaeogeographic reconstructions seems to confirm the relative isolation of some areas from the rest, thus different evolution could have been facilitated.

Consequently, five different species are herein distinguished, three of them new. The species considered and their supposed age and geographic distribution are summarized in Table 2.

All these species appear as closely related, with *V. alceotarlaoi* being the most primitive and the probable origin of the rest. Concerning its origin, Douvillé (1897) included *V. loftusi* in the group of *V. sulcatus* (Defrance), while Toucas (1904) considered to better relate it with the group of *V. moulinsi* (d'Hombres-Firmas) than with *V. sulcatus* one. *Vaccinites archiaci* Munier-Chalmas, a

Campanian Pyrenean species considered as evolved from *V. sulcatus*, with truncated ligament ridge, PM slightly dorsal of ATPT axis, the three main infolds relatively close each other, and the inner margin of the outer shell layer undulated in larger specimens, seems related to the group of species considered herein.

The presence of a reticule of small polygonal pores, covering each large pore of the left valve, is illustrated in well preserved specimens of *V. loftusi* from its type locality. Pores are insufficiently known for the other species.

There is no reason to consider that genus *Pironaea* Meneghini, 1868 evolved from any of the species considered herein. Different species of *Pironaea*, with different development of secondary pillars, co-occur at different localities with *V. alceotarlaoi*, the most primitive species of the group. Secondary pillars should better be considered as convergences.

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FIGURE CAPTIONS

Fig. 1. Location of *Vaccinites loftusi* (Woodward) reported occurrences. 1 = Hekimhan; 2 = northern and central Anatolia; 3 = central and western Bulgaria; 4 = eastern Serbia; 5 = south-eastern Spain; 6 = Pyrenees; 7 = Croatia; 8 = United Arab Emirates-Oman; 9 = Syria.

Fig. 2. Morphological characters and measures considered, indicated on the transverse section of the right valve of NHMUK PI OR 33903, holotype of *Vaccinites loftusi* (Woodward). Abbreviations explained in the text. Scale bar measures 10 mm.

Fig. 3. *Vaccinites loftusi* (Woodward), from Hekimhan, Turkey, new pictures of Woodward's specimens. A-D, NHMUK PI OR 33903, abapical and adapical views of the transverse cross section of the right valve, external surface of the left valve, and detail of the last, respectively. E, NHMUK PI OR 33901, left valve. Scale bars measure 10 mm.

Fig. 4. *Vaccinites loftusi* (Woodward), from Hekimhan, Turkey, transverse sections of right valves with enlarged detail of the ligament ridge. A, B, PUAB 75839. C, D, PUAB 75823. E, F, PUAB 75845. G, H, PUAB 75864. I, PUAB 75866. J, PUAB 75827. K, L, PUAB 75867. Scale bars measure 10 mm.

Fig. 5. *Vaccinites loftusi* (Woodward), from Hekimhan, Turkey, serial transverse sections of right valves with enlarged detail of the ligament ridge. A-J, PUAB 75892. K-N, PUAB 75852. O-V, PUAB 75846. Upper section close to the commissure, distance between successive sections is indicated in mm. Scale bars measure 10 mm.

Fig. 6. *Vaccinites loftusi* (Woodward), from Hekimhan, Turkey, external views of left valves with enlarged detail. A, B, PUAB 75892. C, D, PUAB 75839. E, F, PUAB 75842. G, H, PUAB 75846. Scale bars measure 10 mm.

Fig. 7. Transverse sections of right valves redesigned from figures issued as *Vaccinites loftusi* (Woodward) (A-L, O-Q), *Pironaea* sp. (M, N), and *Pironaea syriaca* Vautrin (R-U). A, Asmayaylasi, S of Ankara, Tuz Gölü Basin, central

Anatolia, Turkey (Özer, 1983, pl. 3, fig. 9). B, Höbek Tepe, 5 km WSW of Amasya, northern Anatolia, Turkey (Steuber et al., 1998, text-fig. 3D). C, Sereflikochisar [Çereflikoçhisar], SE of Ankara, central Anatolia, Turkey (Özer, 2002, pl. 2, fig. 3). D, MGL 25365, Gabrovo, SW of Tirnova (= Veliko Tarnovo), central Bulgaria, (Douvillé, 1897, p. 210, pl. 33, fig. 1a), holotype of *Vaccinites bilottei* n. sp. herein. E-G, Yaroslavtzi, Breznik, western Bulgaria, (Pamouktchiev, 1963, p. 102, pls. 3-6). H, Bačevica, Serbia (Milovanović, 1932, pl. 5, fig. 1). I, J, Vrbovac, Serbia (Milovanović, 1932, pl. 5, figs. 2, 3). K, Bačevica, (Milovanović, 1934b, pl. 1, fig. 2, as var. *timacensis*). L. Bačevica (Ba-12), (Sladić-Trifunović, 1980, pl. 4, fig. 4). M, N, UCBL-EM 15903, Quatretonda, SE Spain (Douvillé, 1894, pl. 17, fig. 5, as *Pironaea* sp.). O, P, Pd-8 and Pd-3, respectively, Pokonji Dol, Hvar Island, Croatia (Sladić-Trifunović, 1980, pl. 4, figs. 2, 3). Q, NHMUK PI LL 41933, Qarn Murrah, UAE (Morris and Skelton, 1995, text-fig. 5). R, (Vautrin, 1933, pl. 4, fig. 1), UCBL-EM 15904, holotype, from the rudists breccia at Yeyla, northern Syria. S, (Özer, 1987, pl. 1, fig. 2) from Alidami, eastern Anatolia, Turkey. T, U, (Schumann, 1999, poster) from Saiwan, Oman. Scale bars measure 10 mm.

Fig. 8. *Vaccinites bilottei* n. sp., from Yaroslavtzi, Breznik, western Bulgaria, transverse sections of right valves with enlarged detail of the ligament ridge. A-D, MGB 87334. E, F, MGB 87336. G, H, MGB 87335. I, J, MGB 87337. Upper section close to the commissure, distance between successive sections is indicated in mm. Scale bars measure 10 mm.

Fig. 9. *Vaccinites alceotarlaoi* n. sp., from Bačevica (A-G, J-O) and Vrbovac (H, I), eastern Serbia, transverse sections of right valves with enlarged detail of the ligament ridge. A, B, MCSN 1846. C, MCSN 1853. D, E, MCSN 1849. F, G, MCSN 1847. H, I, MCSN 1862. J, MCSN 1854. K, L, MCSN 1861. M, MCSN 1859. N, MCSN 1855. O, MCSN 1860. Scale bars measure 10 mm.

Fig. 10. *Vaccinites alceotarlaoi* n. sp., from S Valencia province, south-eastern Spain, transverse sections of right valves with enlarged detail of the ligament ridge. A, B, PUAB 41187. C, PUAB 29901. D, PUAB 29727. E, PUAB 41188. F, G, PUAB 29990. H, PUAB 29740. I, PUAB 29983. J, K, PUAB 29891. L, PUAB 29794. M, PUAB 29757. N, PUAB 29755. O, PUAB 29950, two attached specimens. P, Q, PUAB 29919. R, S, PUAB 29844. T, U, PUAB 29978. Scale bars measure 10 mm.

Fig. 11. *Vaccinites alceotarlaoi* n. sp. (A-D) and *Vaccinites pirenaicus* n. sp. (E-R), from southern Pyrenees, northern Spain, transverse sections of right valves with enlarged detail of the ligament ridge. A-D, PUAB 59925 from Torallola. E, PUAB 59907, from Castillonroi. F-K, PUAB 02881 from Serra d'Arquells. L, PUAB 33645, from Coll de Pal road. M-P, PUAB 59789 from Serra d'Arquells. Q, R, PUAB 64071 from Serra d'Arquells. Upper section close to the commissure, distance between successive sections is indicated in mm. Scale bars measure 10 mm.

Fig. 12. *Vaccinites pirenaicus* n. sp., from Castellonroi, south-central Pyrenees. A-C, PUAB 97005, external view of LV and details of the same. Scale bars measure 10 mm.

Fig. 13. A, scatter plot of pillar/myo-cardinal arrangement, as indicated by values of *a* (P2-P1-PM) and *b* (P1-PM-PT) angles on specimens of the considered localities. B, scatter plot of main infolds setting, as indicated by values of mD (mean diameter) and RU (ratio between LP2 and the shell circumference) on specimens of the considered localities.

Fig. 14. Distribution of the recognized species on a simplified part of Camoin et al. (1993) 'Late Maastrichtian Palaeoenvironments' map. Philip's (1985) Mediterranean sub-provinces and/or subunits are indicated: 1_2 = Pyrenean; 2 = South Iberian; 3_1 = North Adriatic; 3_5 = Turkey; and 3_6 = Bulgaria-Romania. Lines linking species in the legend indicate phylogenetic relationship. Maastr. = Maastrichtian; Camp. = Campanian; l. = late; e. = early.

TABLE CAPTIONS

Table 1. Comparison of measure intervals and characters between the different assemblages. Lineal measures in mm. List of abbreviations ordered as from left to right in the Table heading: **mD** = mean diameter; **L adult** = ligament ridge tip in adult shells (R = rounded end; T = truncated end; Rp = rounded prolongation; Tp = truncated prolongation; LR = lamellar with rounded end); **L young** = ligament ridge tip in young shells; **P1** = form of first pillar (Q = quadrate; sR = short rectangular; sR(p) = short rectangular slightly pinched; R = rectangular;

R(p) = rectangular slightly pinched; Rp = rectangular pinched); **P2** = form of second pillar; **S** = form of secondary pillars (A = wide; B = one or more, length>width); **RU** = ratio between LP2 and the shell circumference; **LT** = angle defined by L and the axis ATPT; ***a*** = angle defined by the tip of P2 and the centres of P1 and PM; ***b*** = angle defined by the centres of P1, PM, and PT; ***c*** = angle defined by the centres of PM, PT, and AT.

Table 2. Sequence of main evolutionary changes in the different assemblages, proposal of species attribution, and tentative ages. R = rounded tip; T = truncated tip; (T) = hardly distinguishable slight truncation; **S** = form of secondary pillars (A = wide; B = one or more, length>width).

APPENDIX CAPTION

Appendix 1. List of specimens with characters and measures considered. Lineal measures in mm, angular measures in degrees. List of abbreviations ordered as from left to right in the Table heading: **ap D** = anterior-posterior diameter; **dv D** = dorsal-ventral diameter; **mD** = medium diameter; **h** = high of the shell (> meaning shell incomplete); **LP1** = portion of shell circumference between L and P1; **LP2** = portion of shell circumference between L and P2; **P1P2** = portion of shell circumference between P1 and P2; **RU** = ratio between LP2 and the shell circumference; **LT** = angle defined by L and the axis ATPT; **L** = ligament ridge (R = rounded end; T = truncated end; Rp = rounded prolongation; Tp = truncated prolongation; LR = lamellar with rounded end); **P1** = first pillar; **P2** = second pillar (Q = quadrate; sR = short rectangular; R = rectangular; R(p) = rectangular slightly pinched; Rp = rectangular pinched); **S** =

secondary pillars (A = wide; B = one or more, length>width); ***a*** = angle defined by the tip of P2 and the centres of P1 and PM; ***b*** = angle defined by the centres of P1, PM, and PT; ***c*** = angle defined by the centres of PM, PT, and AT; **Fig.** = reference to figures in this article.

Appendix 1

specimen	source	ap D	dv D	mD	h	LP1	P1P2	LP2	RU	LT	L	P1	P2	S	*a*	*b*	*c*	Fig.
HEKIMHAN																		
NHMUK PI OR 33901	Woodward, 1855, 3.1	70	65	67.5														**3E**
NHMUK PI OR 33903	Woodward, 1855, 3.3	63	58	60.5		40	47	87	0.24	36	R	sR	R(p)	A	130	90	195	**2,3A-D**
PUAB 75823	P-1224, Stop1, N Yazihan	70	60	65	>70	38	34	72	0.20	60	R	sR	R(p)	A	100	130	205	**4CD**
PUAB 75827	P-1224, Stop1, N Yazihan	55	45	50	>49	40	48	88	0.24	42	T?	Q	R	A	100	140	195	**4J**
PUAB 75830	P-1224, Stop1, N Yazihan	65	55	60	>57						Rp	Q	R(p)					
PUAB 75839	P-1224, Stop1, N Yazihan	65	55	60	>56	17	27	44	0.12	14	LR	sR	R(p)	A	85	175	170	**4AB,6CD**
PUAB 75842	P-1226, Stop 3, Hasar Hill	60	50	55	>70						LR	Q	R					**6EF**
PUAB 75845	P-1226, Stop 3, Hasar Hill	65	60	62.5	>82	28	46	74	0.21	37	Rp	R	R(p)	B	75	155	200	**4EF**
PUAB 75846	P-1226, Stop 3, Hasar Hill	65	55	60	>66	34	30	64	0.18	30	R	Q	R	A	105	160	170	**5O-V,6GH**
PUAB 75852	P-1226, Stop 3, Hasar Hill	50	45	47.5	60	31	39	70	0.19	28	R	Q	R	A	125	120	190	**5K-N**
PUAB 75864	P-1226, Stop 3, Hasar Hill	55	45	50	>60	41	31	72	0.20		Tp	R	R	A				**4GH**
PUAB 75866	P-1226, Stop 3, Hasar Hill	55	50	52.5	>68	41	36	77	0.21		R	Q	R	A				**4I**
PUAB 75867	P-1226, Stop 3, Hasar Hill	55	45	50	>74	34	31	65	0.18		T	Rp	R(p)	A				**4KL**
PUAB 75892	P-1226, Stop 3, Hasar Hill	95	80	87.5	92	23	30	53	0.15	22	LR	Q	R(p)	B	105	130	200	**5A-J,6AB**
C, N, NW, TURKEY																		
Asmayaylasi	Özer, 1983, 3.9	60	53	56.5		34	28	62	0.17	17	R	Q	Q	A	90	165	165	**7A**
Amasya	Steuber, 1998, 3D	52	45	48.5		49	38	87	0.24		T	sR	Rp	A				**7B**
Sereflikochisar	Özer, 2002, 2.3	87	81	84		56	39	95	0.26	30	R	R	sR	A	75	160	175	**7C**
BULGARIA																		
Gabrovo (MGL 24365)	Dovillé, 1897; Toucas, 1904	85	80	82.5		31	35	66	0.18	32	R	sR	R	A	78	178	172	**7D**
Yaroslavtzi (US Cr_2 33)	Pamouktchiev, 1963, 4.2	95	85	90		36	47	83	0.23	43	Rp	R(p)	R	A	70	160	180	**7E**
Yaroslavtzi	Pamouktchiev, 1963, 3.3	80	60	70		40	48	88	0.24	?	Rp	sR	R	A	85?	160?	220?	**7F**
Yaroslavtzi	Pamouktchiev, 1963, 5.1	100																
Yaroslavtzi	Pamouktchiev, 1963, 5.2	60	42	51		54	41	95	0.26		R	Q	R(p)	A				**7G**
Yaroslavtzi	Pamouktchiev, 1963, 6.1	95	90	92.5														
Yaroslavtzi	Pamouktchiev, 1963, 6.2	75	60	67.5														
Yaroslavtzi	Pamouktchiev, 1963, 6.3	30	30	30														
Yaroslavtzi (US Cr_2 216)	Pamouktchiev, 1981, 86.1	85																
MGB 87334	Yaroslavtzi	80	70	75	>80	43	45	88	0.24	50	Rp	sR	R	A	85	150	190	**8A-D**
MGB 87335	Yaroslavtzi	85	75	80	>120	41	40	81	0.23	30-40	R	Q	R	A	75	155	185	**8GH**
MGB 87336	Yaroslavtzi	90	75	82.5	>110	38	42	80	0.22	47	Rp	Q	R	A	75	160	185	**8EF**
MGB 87337	Yaroslavtzi	70	65	67.5	>110	30	47	77	0.21	47	R	Q	R	A	70	175	180	**8IJ**
E SERBIA																		

Vrbovac	Milovanović, 1932, 4.1	62	60	61														
Vrbovac	Milovanović, 1932, 5.2	40	40	40		38	34	72	0.20		Tp	R	R(p)	A				**7I**
Vrbovac	Milovanović, 1932, 5.3	45	40	42.5		54	34	88	0.24		Tp	R	R(p)	A				**7J**
Bačevica	Milovanović, 1932, 5.1	60	55	57.5		45	55	100	0.28		R?	R	R	A				**7H**
Bačevica (var. timacensis)	Milovanović, 1934b, 1.2	55	40	47.5		52	37	89	0.25			Q	R	A				**7K**
Bačevica (Ba-12)	Sladić-Trifunović, 1980, 4.4	70	55	62.5							T	Q	R	A				**7L**
Bačevica (Ba-36)	Sladić-Trifunović, 1980, 4.5										T							
MCSN 1844	Bačevica	56	48	52	97	51	40	91	0.25		T	Q	R	A				
MCSN 1845	Bačevica	64	55	59.5	>63	50	41	91	0.25		T	Q	R(p)	A				
MCSN 1846	Bačevica	62	56	59	>88	47	37	84	0.23	45	T	R	Rp	A	105	115	200	**9AB**
MCSN 1847	Bačevica	57	55	56	>55	38	44	82	0.23	45	Tp	Q	R	A	85	155	180	**9FG**
MCSN 1848	Bačevica	37	33	35	>39	50	50	100	0.28		T	Q	R	A				
MCSN 1849	Bačevica	58	55	56.5	>57	40	45	85	0.24	55	T	R	R(p)	A	120	120	195	**9DE**
MCSN 1850	Bačevica	60	51	55.5	>78	41	50	91	0.25		T	sR	R	A				
MCSN 1851	Bačevica	49	43	46	64	38	38	76	0.21		T	sR	Rp	A				
MCSN 1852	Bačevica	54	49	51.5	>89	46	43	89	0.25		T	Q	R	A				
MCSN 1853	Bačevica	45	44	44.5	73	36	47	83	0.23	60	T	Q	R(p)	A	95	130	205	**9C**
MCSN 1854	Bačevica	58	52	55	65					40	Tp	R	R	A	80	145	195	**9J**
MCSN 1855	Bačevica	68	60	64	84	35	39	74	0.21	55	T	R	Rp	A	95	145	200	**9N**
MCSN 1856	Bačevica	49	48	48.5	>34	47	38	85	0.24		T	sR	R(p)	A				
MCSN 1857	Bačevica	48	48	48	>32	44	38	82	0.23		T	sR	R(p)	A				
MCSN 1858	Bačevica	55	46	50.5	>63	45	40	85	0.24		T	Q	R	A				
MCSN 1859	Bačevica	66	60	63	>51	39	37	76	0.21	50	T	R	R(p)	A	75	160	200	**9M**
MCSN 1860	Bačevica	67	58	62.5	85	34	36	70	0.19	50	Tp	R	R	A	80	155	195	**9O**
MCSN 1861	Bačevica	64	52	58	>128	47	41	88	0.24	40	Tp	R	R	A	85	180	180	**9KL**
MCSN 1862	Vrbovac	69	61	65	86	49	45	94	0.26	55	T	R	R(p)	A	115	135	190	**9HI**
MCSN 1863	Vrbovac	54	45	49.5	96	51	44	95	0.26		T	Q	R	A				
MCSN 1864	Vrbovac	50	42	46	>32	49	50	99	0.28		T	R	Rp	A				
SE SPAIN (VALENCIA)																		
PUAB 29727	P-357 Bc. de la Casella	46	48	47	70	43	40	83	0.23		T	R	R(p)	A				**10D**
PUAB 29740	P-357 Bc. de la Casella	42	34	38	>44	45	46	91	0.25	50	T	sR	R(p)	A	100	130	195	**10H**
PUAB 29744	P-357 Bc. de la Casella	37	33	35	>47									A				
PUAB 29754	P-357 Bc. de la Casella	32	26	29	>30									A				
PUAB 29755	P-357 Bc. de la Casella	40	42	41	>56	37	39	76	0.21		T	R	R	A				**10N**
PUAB 29757	P-357 Bc. de la Casella	32	32	32	>23	38	41	79	0.22		T	sR	R	A				**10M**
PUAB 29794	P-357 Bc. de la Casella	38	30	34	>37	55	47	102	0.28		T	R	R(p)	A				**10L**

PUAB 29844	P-368 Pilonets	54	50	52	>40	54	40	94	0.26	58	Tp	Q	R	A	130	115	190	**10RS**
PUAB 29883	P-357 Bc. de la Casella	49			>56													
PUAB 29891	P-357 Bc. de la Casella	50	41	45.5	>49	54	42	96	0.27		T	sR	R	A				**10J**
PUAB 29901	P-365 Bc. de la Casella	36	34	35	72	43	45	88	0.24		Tp	Q	R	A	130	95	220	**10C**
PUAB 29919	P-365 Bc. de la Casella	31	27	29	>34	48	31	79	0.22	47	T	sR	R	A	115	105	190	**10PQ**
PUAB 29950	P-373 Nicolasa Quarry	30									T	Q	sR	A				**10O**
PUAB 29969	P-373 Nicolasa Quarry	37	27	32	>56									A				
PUAB 29970	P-373 Nicolasa Quarry	34	30	32	>44									A				
PUAB 29976	P-373 Nicolasa Quarry	39	33	36	>56									A				
PUAB 29978	P-373 Nicolasa Quarry	47	45	46	>62	47	39	86	0.24	54	Tp	sR	R	A				**10TU**
PUAB 29979	P-373 Nicolasa Quarry	30	34	32	47									A				
PUAB 29983	P-373 Nicolasa Quarry	48	35	41.5	>47						T	sR	R	A				**10I**
PUAB 29985	P-373 Nicolasa Quarry	44	37	40.5	>53									A				
PUAB 29989	P-373 Nicolasa Quarry	42	37	39.5	77									A				
PUAB 29990	P-373 Nicolasa Quarry	56	39	47.5	>60	35	46	81	0.23	50	Tp	sR	R	A	130	105	205	**10FG**
PUAB 41187	P-373 Nicolasa Quarry	36	34	35	>43	52	46	98	0.27	48	T	sR	R	A				**10AB**
PUAB 41188	P-373 Nicolasa Quarry	34	30	32	38	48	55	103	0.29		T	Q	R	A				**10E**
PUAB 41197	P-375 Nicolasa Quarry	69	45	57	>64									A				
PUAB 41213	P-368 Pilonets	38	38	38										A				
PUAB 41215	P-368 Pilonets	50	38											A				
PUAB 41217	P-368 Pilonets	54	45											A				
UCBL-EM 15903	Quatretonda, Douvillé, 1897	53	53	53		40	45	85	0.24		?	sR	R	AB?				**7MN**
PYRENEES																		
PUAB 02881	P-49 Serra d'Arquells	80	80	80	>130	40	38	78	0.22	72	T-R	R	R(p)	A	110	120	215	**11F-K**
PUAB 33645	EV-219 Coll de Pal road	100	80	90	>110	33	30	63	0.18	78	Rp	sR	R	A	120	110	135	**11L**
PUAB 59789	P-49 Serra d'Arquells	95	70	82.5	85	37	32	69	0.19	55	T-Rp	sR	Rp	A	105	140	200	**11M-P**
PUAB 59902	P-49 Serra d'Arquells	80	60	70	75	42	36	78	0.22		Rp							
PUAB 59907	EV-740 Castellonroi	90	75	82.5	110	34	40	74	0.21		T-T	sR	R	A				**11E**
PUAB 59925	EV-650 Torallola	70	60	65	100	45	44	89	0.25	40	Tp	Q	Rp	A	105	125	190	**11A-D**
PUAB 64071	P-49 Serra d'Arquells	100	80	90	150	36	32	68	0.19	58	R	R	Rp	A	125	120	195	**11QR**
PUAB 64079	P-49 Serra d'Arquells	40	30	35	>30						T							
PUAB 97005	EV-744 Castellonroi	97	79	88	126	34	27	61	0.17	43		sR	R(p)	A	113	133	190	**12A-C**
CROATIA																		
Hvar (Pd-8)	Sladić-Trifunović, 1980, 4.2	60	55	57.5		46	32	78	0.22		T	Q	R	A				**7P**
Hvar (Pd-3)	Sladić-Trifunović, 1980, 4.3	80									R?			A				**7O**
UAE (Qarn Murrah)																		

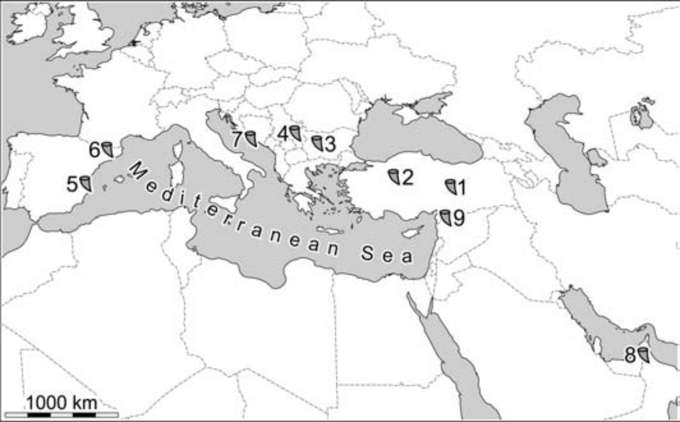
NHMUK PI LL 41933	Morris Skelton, 1995, tf. 5					47	44	91	0.25		L	Q	R	no				**7Q**
(*P. syriaca*)																		
ANATOLIA, E																		
Alidami	Özer, 1986, 1.2	50	50	50		31	37	68	0.19		R	Q	R(p)	B				**7S**
SYRIA																		
UCBL-EM 15904	Yeyla, Vautrin, 1933, 4.1	140	120	130		25	25	50	0.14	30	LR	Q	R	B	100	150	200	**7R**
UCBL-EM 15905	Yeyla, Vautrin, 1933, 5.3			95		23		23		28	LR	Q				155	175	
OMAN																		
Saywan	Schumann, 1999, poster	83	90	86.5		26	36	62	0.17		LR	Rp	Rp	B				**7T**
Saywan	Schumann, 1999, poster	90	100	95		35	37	72	0.20	26	LR	Q	R	B				**7U**

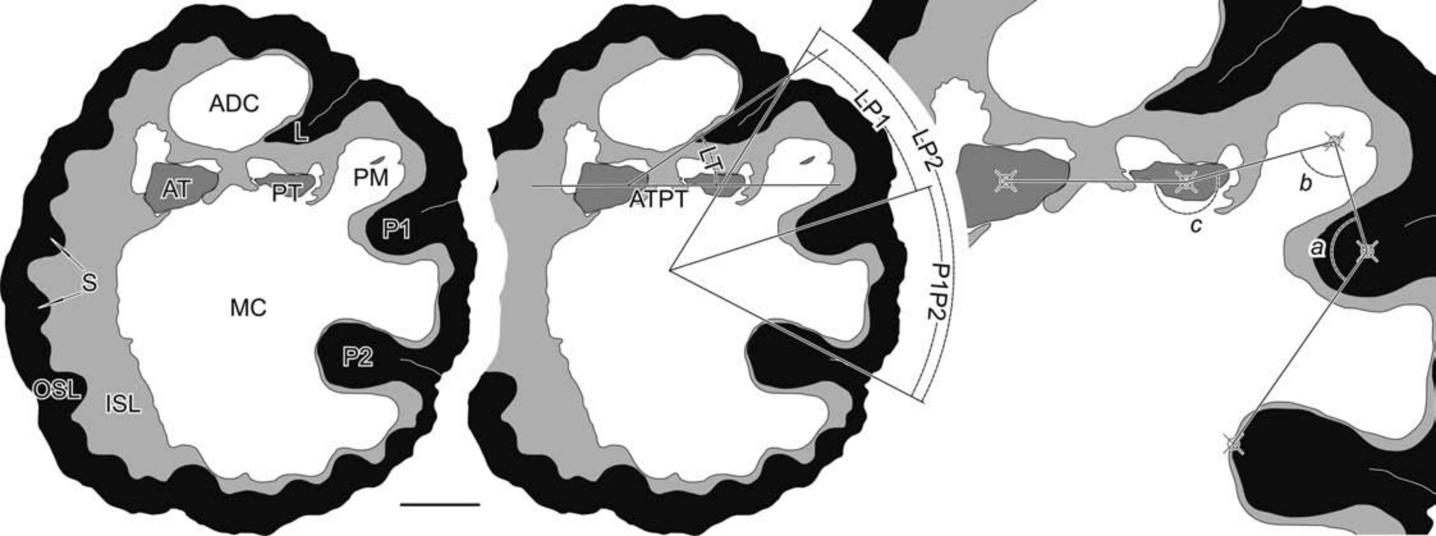
Table 1

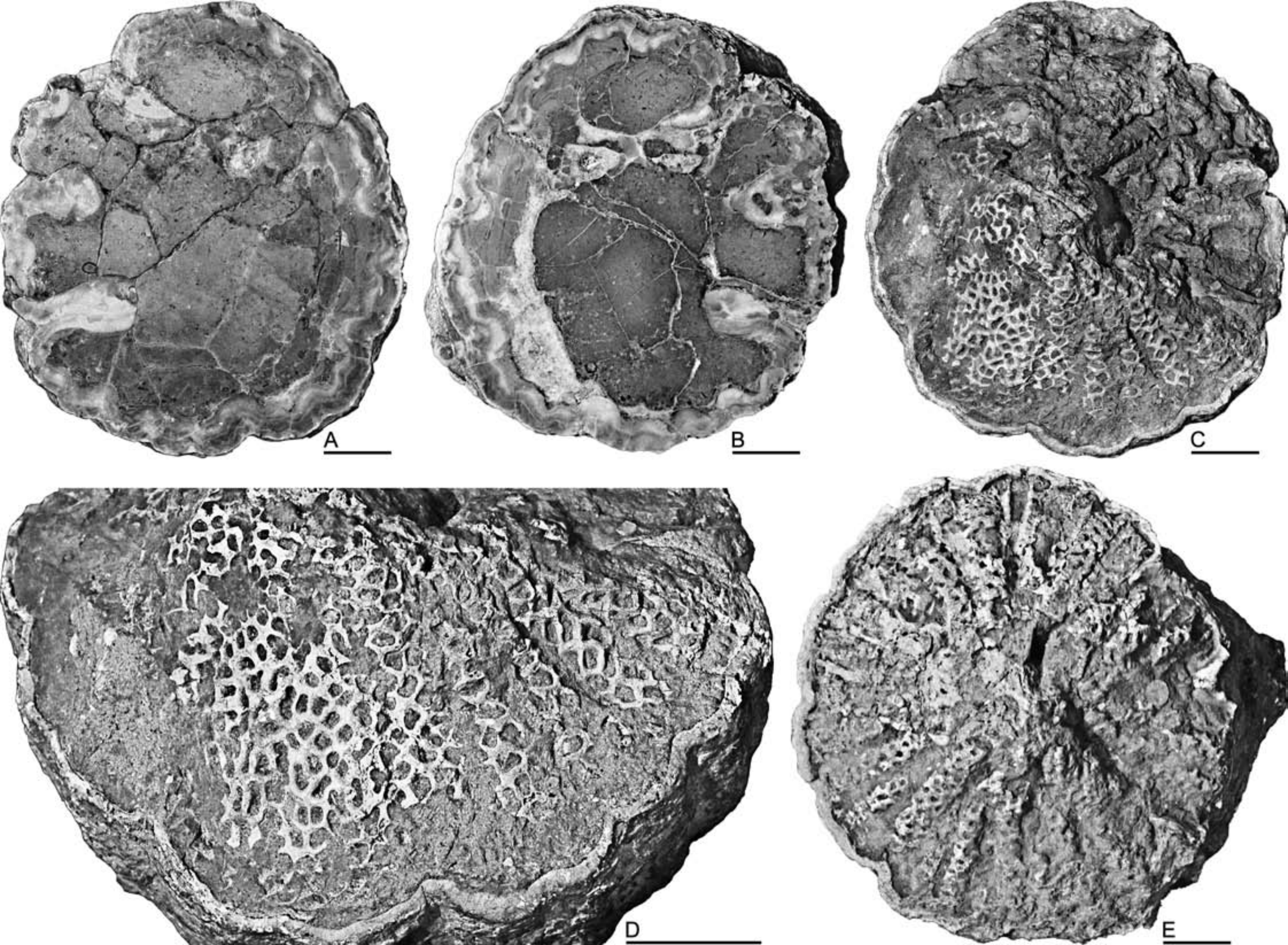
assemblages	**mD**	**L adult**	**L young**	**P1**	**P2**	**S**	**RU**	**LT**	***a***	***b***	***c***
Hekimhan	87.5-50	(T) R	T	Q-sR-R-Rp	R-Rp	B-A	0.24-0.12	60-14	130-100	175-90	205-170
Bulgaria	82.5-67.5	R	R	Q-sR-Rp	R-R(p)	A	0.26-0.18	50-30	85-70	175-150	190-180
E Serbia	62.5-35	T	T	Q-sR-R	R-R(p)-Rp	A	0.28-0.19	60-40	120-75	180-120	205-180
SE Spain	53-29	T	T	Q-sR-R	sR-R-R(p)	A	0.28-0.21	58-47	130-100	130-95	220-190
Pyrenees	90-35	(T)	T	sR	R(p)-Rp	A	0.22-0.17	78-55	125-105	140-110	215-135
Torallola	65	T	T	Q	Rp	A	0.25	40	105	125	190
N Syria	130-95	R	R?	Q	R	B	0.15	30-28	100	150	200

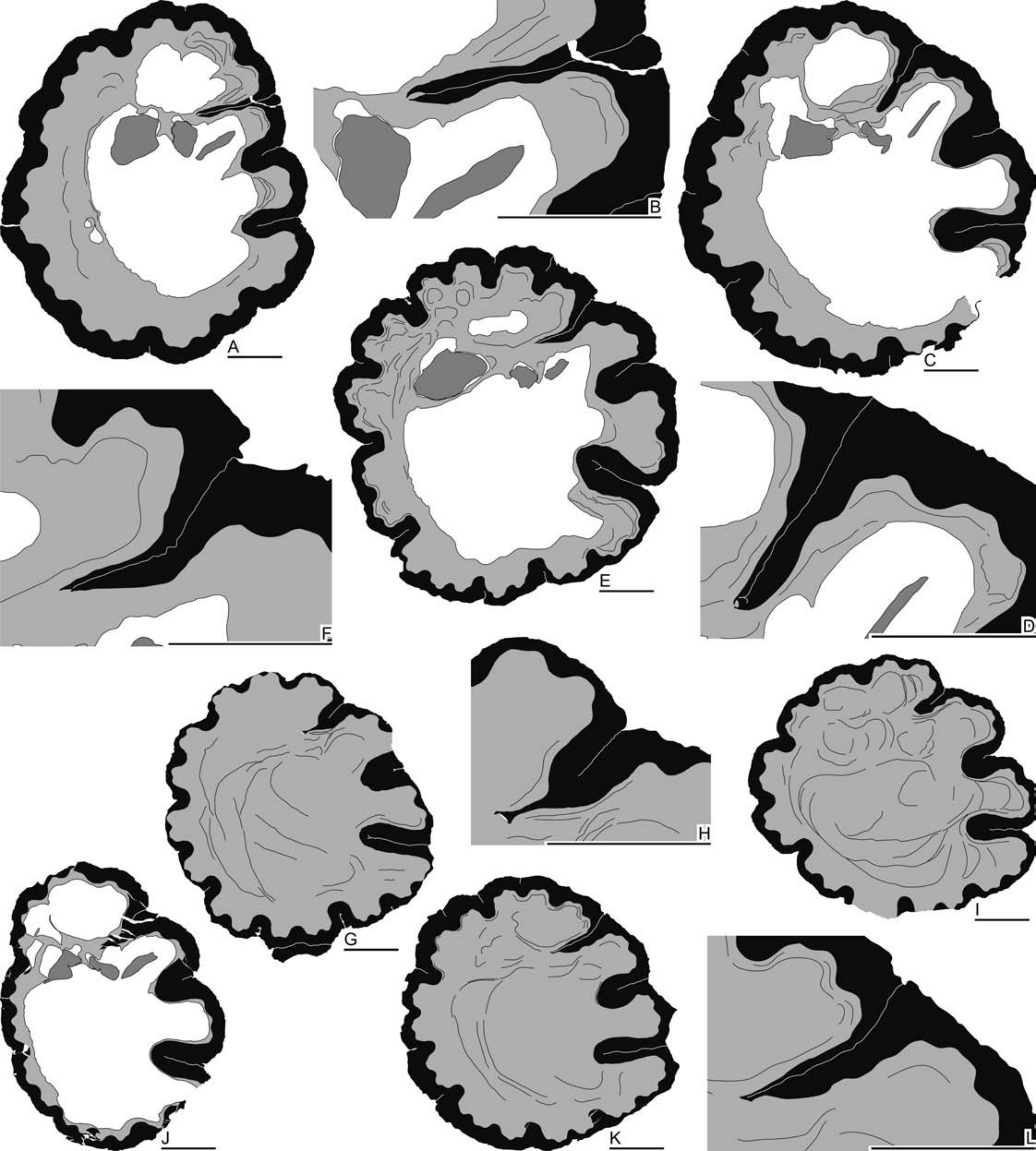
Table 2

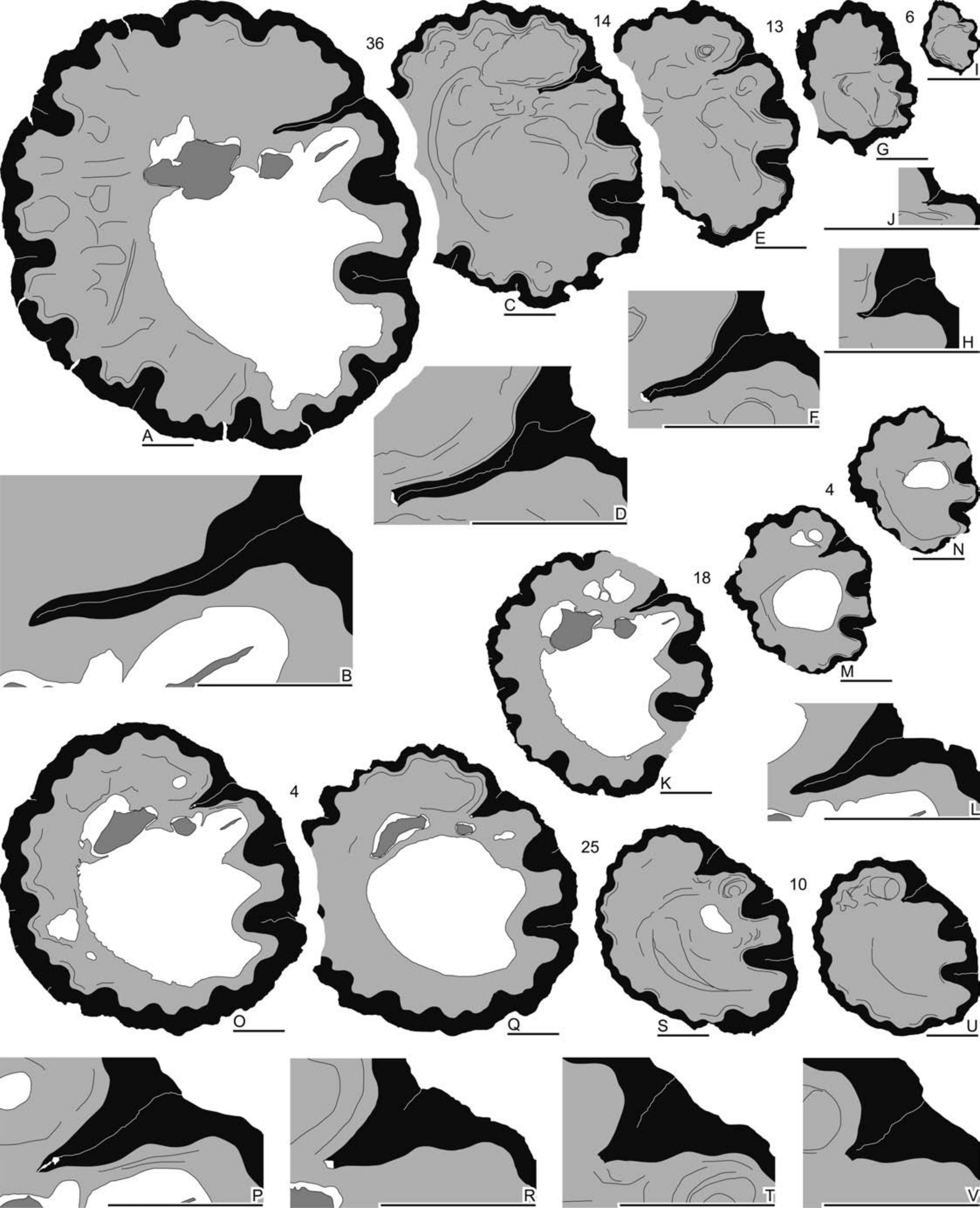
SIZE	LIGAMENT RIDGE TIP ADULT	LIGAMENT RIDGE TIP JUVENILE	S	SE Spain	E Serbia	Torallola	Pyrenees	Hekimhan	Bulgaria	N Syria	SPECIES	AGE
Increasing	R	R	B							**X**	*V. syriacus*	Maastrichtian ?
	R	R	A						**X**		*V. bilottei*	late? late Campanian
	(T) R	T	A-B					**X**			*V. loftusi*	late Campanian
	(T)	T	A				**X**				*V. pirenaicus*	
	T	T	A		**X**	**X**					*V. alceotarlaoi*	early/middle Camp.
	T	T	A	**X**								


Mediterranean Sea
1
2
3
4
5
6
7
8
9
1000 km


ADC
L
AT
PT
PM
P1
S
MC
P2
OSL
ISL
LP1
LP2
LT
ATPT
P1P2
b
c
a

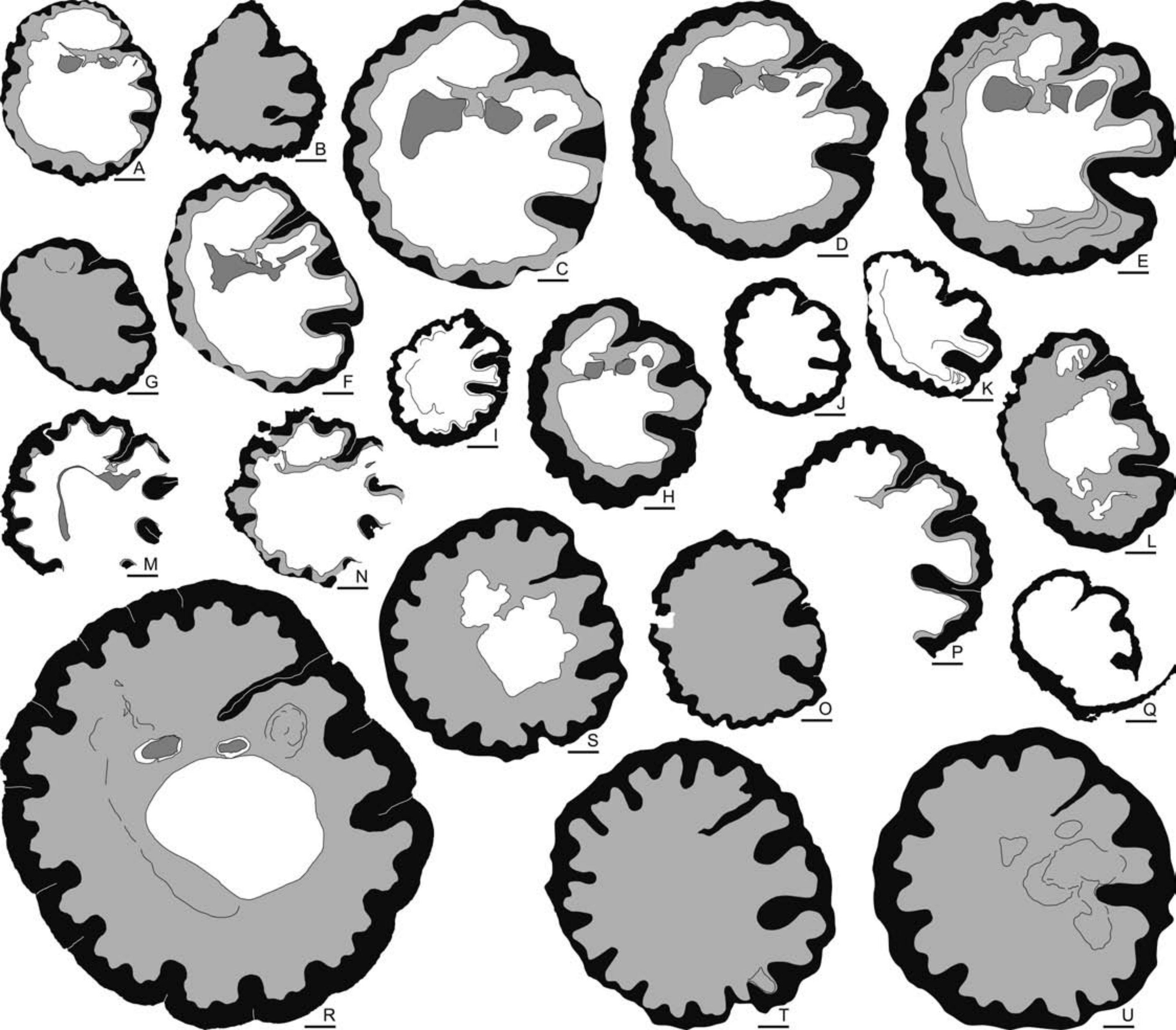

A
B
C
D
E

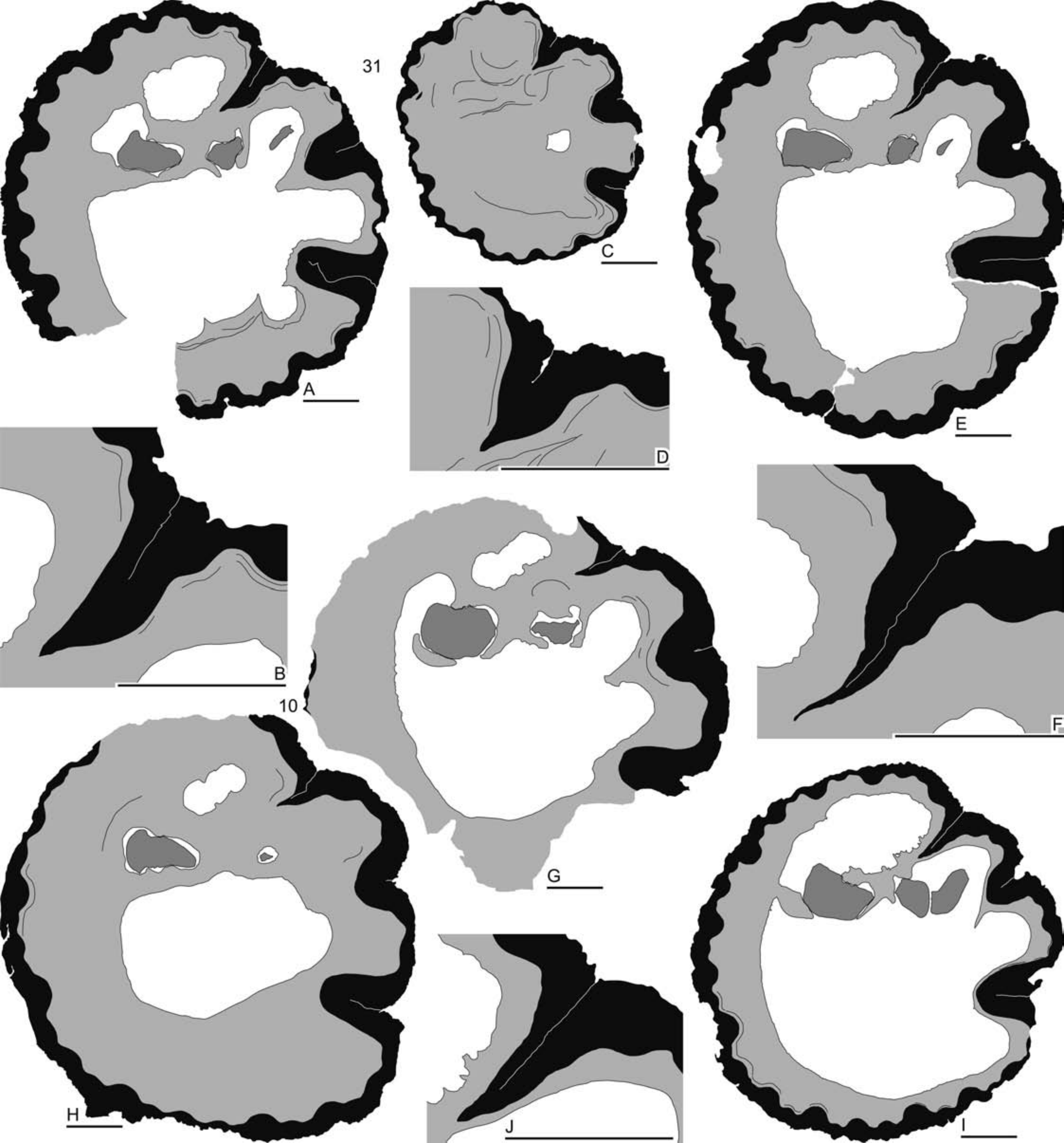

A
B
C
D
E
F
G
H
I
J
K
L

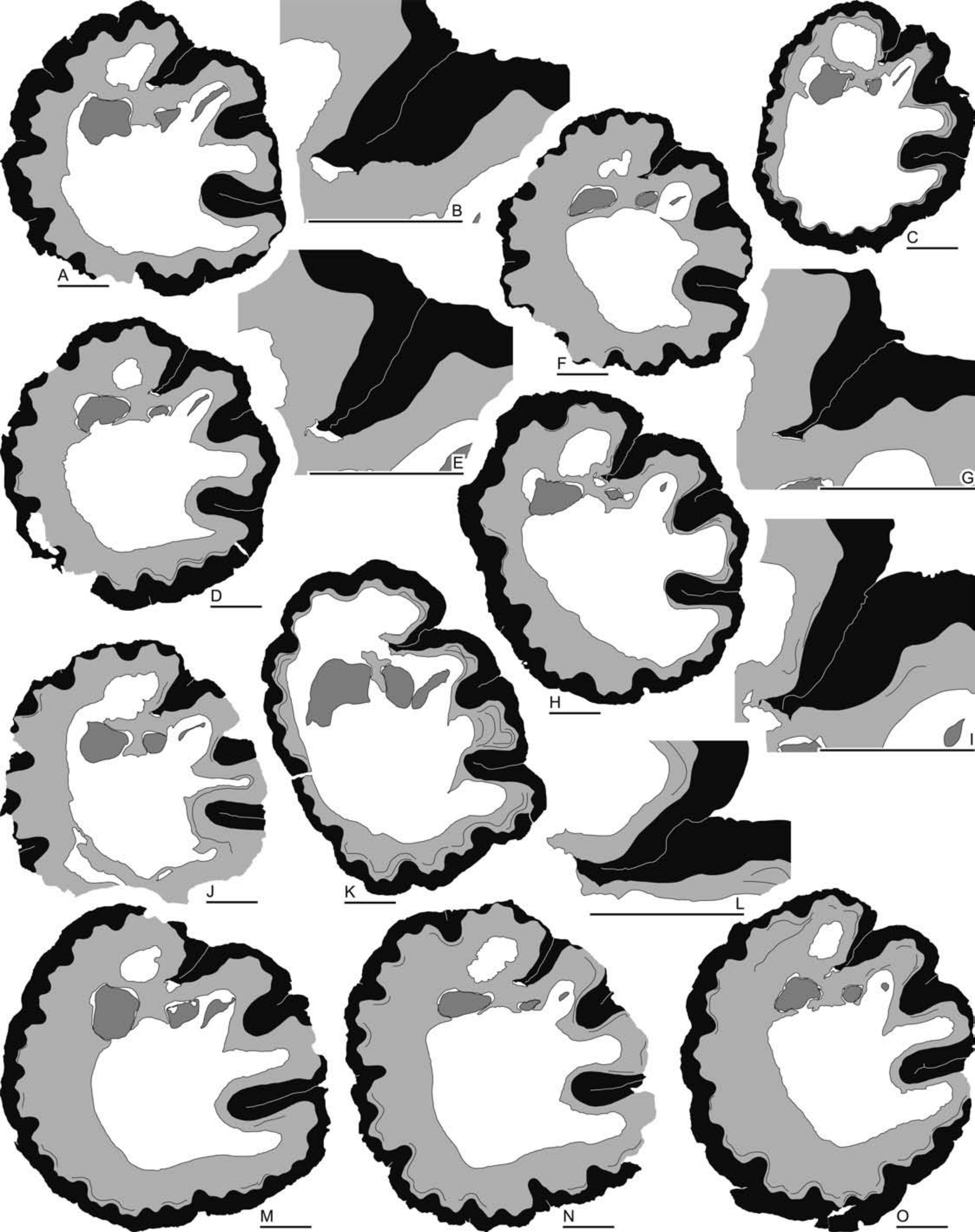


36
14
13
6
A
B
C
D
E
F
G
H
I
J
4
18
K
L
M
N
4
25
10
O
P
Q
R
S
T
U
V


A
B
C
D
E
F
G
H


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U


31
A
B
C
D
E
F
10
G
H
I
J


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O

A
B
C
D
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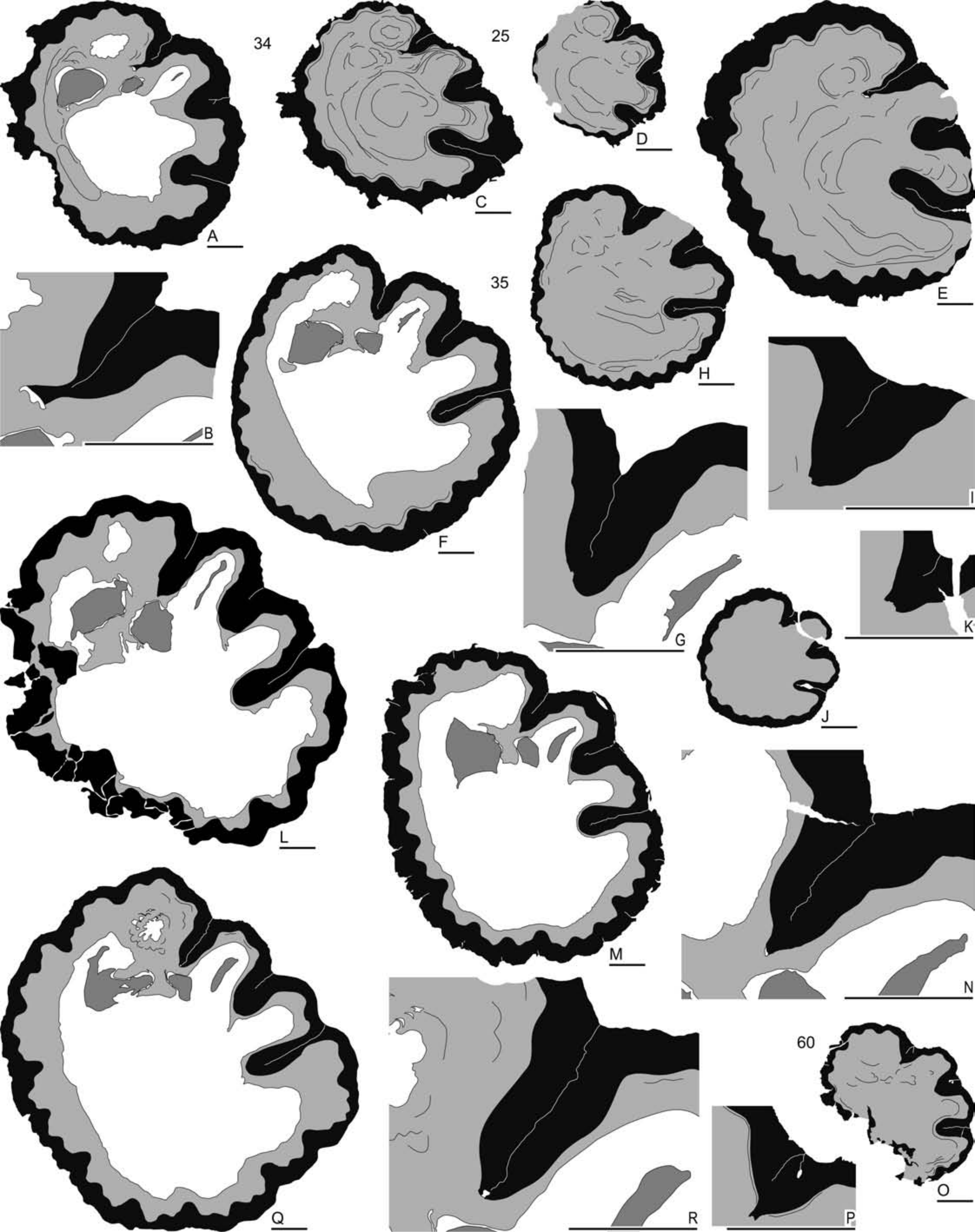
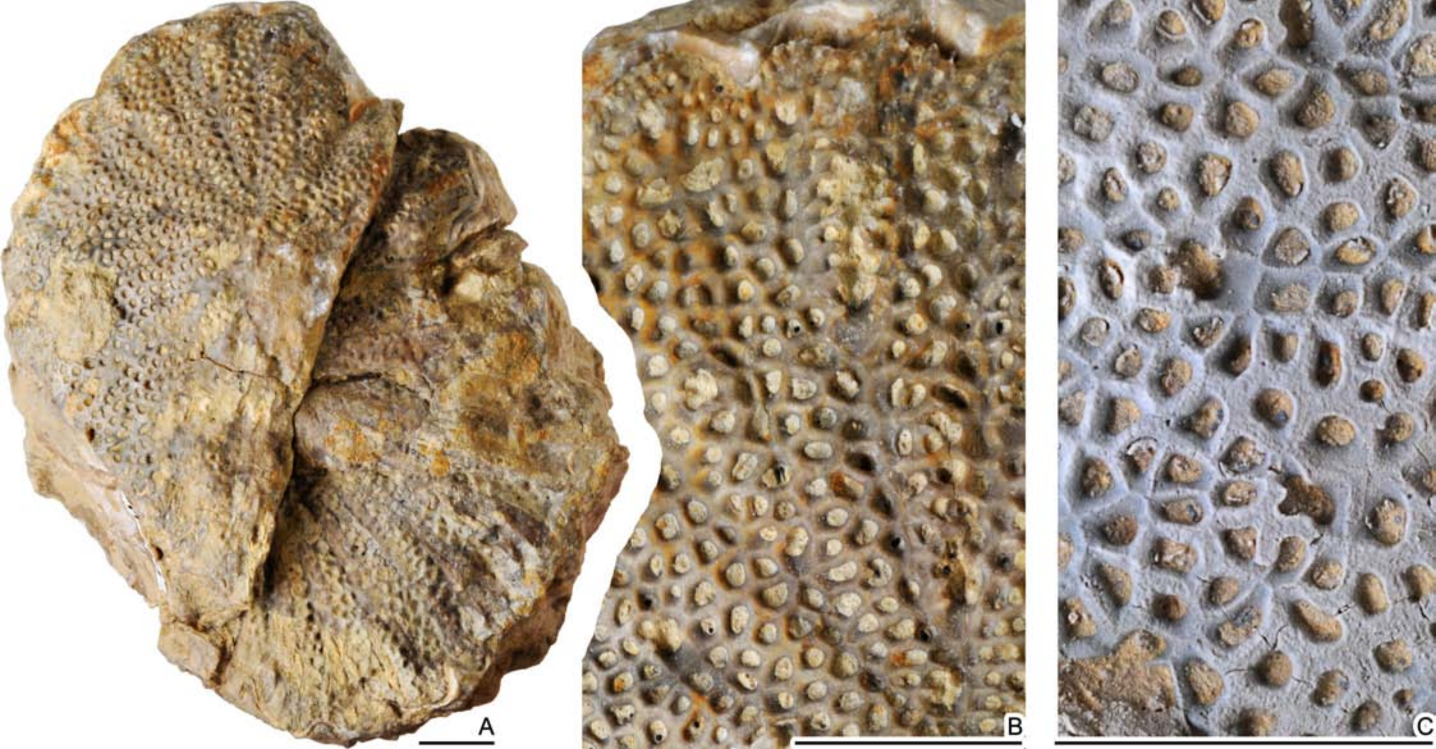
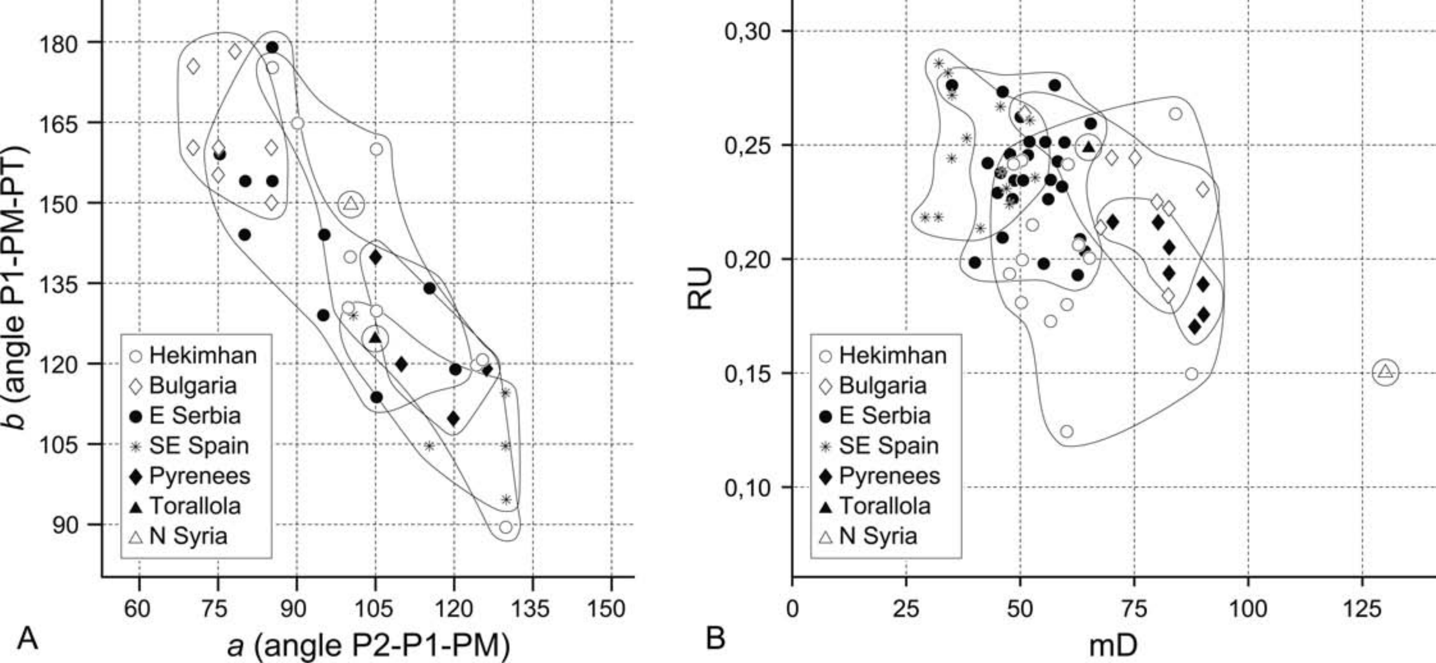
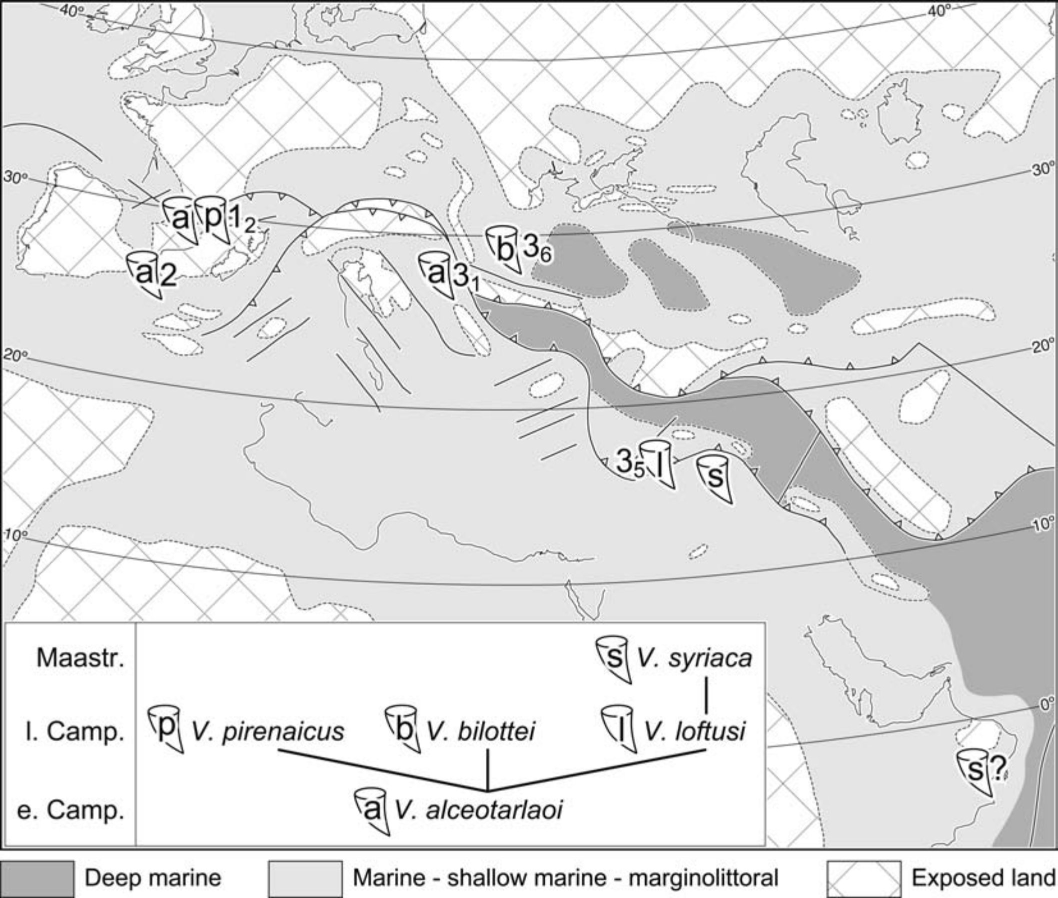
Q
R
S
T
U


34
25
35
60
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R


A
B
C



b (angle P1-PM-PT)
180
165
150
135
120
105
90
60
75
90
105
120
135
150
a (angle P2-P1-PM)
A
Hekimhan
Bulgaria
E Serbia
SE Spain
Pyrenees
Torallola
N Syria
RU
0,30
0,25
0,20
0,15
0,10
0
25
50
75
100
125
mD
B
Hekimhan
Bulgaria
E Serbia
SE Spain
Pyrenees
Torallola
N Syria



40°
40°
30°
30°
20°
20°
10°
10°
0°
a
p
1
2
a
2
b
3
6
a
3
1
3
5
l
s
s?
Maastr.
s V. syriaca
l. Camp.
p V. pirenaicus
b V. bilottei
l V. loftusi
e. Camp.
a V. alceotarlaoi
Deep marine
Marine - shallow marine - marginolittoral
Exposed land

- Hippuritid rudists previously identified as *V. loftusi* in different Mediterranean Tethys areas are different species.
- *V. alceotarlaoi*, *V. bilottei* and *V. pirenaicus* are proposed as new species.
- *V. alceotarlaoi*, from the lower Campanian of E Serbia, SE Spain and Pyrenees originated the other.
- *V. pirenaicus*, *V. bilottei* and *V. loftusi* appear, respectively in Pyrenees, W Bulgaria and Turkey, at late Campanian.
- *V. syriaca* was originated from *V. loftusi* in the Middle East, at early Maastrichtian.
- Any of these species may be considered the origin of genus *Pironae*a.