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Turonian-Campanian Plagioptychidae (Mollusca: Hippuritoidea) of Gosau-type rudist formations of the Alps (Austria)

By Thomas STEUBER[1]

(With 10 text-figures and 1 plate)

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Abstract

Five species of Plagioptychidae from Turonian - Campanian localities in the Northern Calcareous Alps and the Austroalpine Unit of the Central Alps are described. *Plagioptychus aguilloni* (d'ORBIGNY) is most abundant among the examined specimens. *Mitrocaprina bayani* (DOUVILLÉ), *Plagioptychus haueri* (TELLER), *P. uchauxensis* MENNESSIER, and *P.* aff. *uchauxensis* MENNESSIER are reported from Gosau-type rudist formations of the Alps for the first time. New numerical ages have been derived from strontium-isotope stratigraphy for the localities at Weißenbachalm (88.2 Ma, early Coniacian), Baden-Einöd (85.4 Ma, early Santonian), and Grünbach - Pfarrer Schweighofer (84.8 Ma, middle Santonian). The stratigraphical range of *P. aguilloni* (d'ORBIGNY) is confirmed by the occurrence at nine Coniacian - Santonian localities. Late Santonian shells of this species are significantly larger than Coniacian specimens, while no anagenetic change in the pattern of pallial canals is observed.

Introduction

The Plagioptychidae (Mollusca: Hippuritoidea) have been frequently reported from Gosau-type rudist formations, particularly of the Northern Calcareous Alps. While this reflects the relative abundance of the group, they are frequently referred to in open nomenclature or at the genus level, only. Modern descriptions of sectioned specimens showing the internal characters of both shells are very rare (e.g. SZENTE et al. 1999), and the last comprehensive discussion of the genus *Plagioptychus* MATHERON, 1842, is from MENNESSIER (1957). The present study is based on specimens from the collections of the Naturhistorisches Museum in Vienna, and on material collected by the author. In addition to descriptions of the available specimens, the stratigraphy of occurrences is critically discussed, and new results of strontium-isotope chemostratigraphy are presented for a few localities.

The Plagioptychidae appear first in the Turonian and became extinct in the Maastrichtian. Being relatively rare in Maastrichtian deposits of Europe and the Mediterranean Tethys, endemic species are abundant in the latest Maastrichtian of the Caribbean (STEUBER et al. 2002). Due to the presence of pallial canals in the inner, originally aragonitic layer of the coiled left (upper) valve (LV), the Plagioptychidae were

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[1] Institut für Geologie, Mineralogie und Geophysik, Ruhr-Universität, 44801 Bochum, Germany; e-mail: thomas.steuber@ruhr-uni-bochum.de

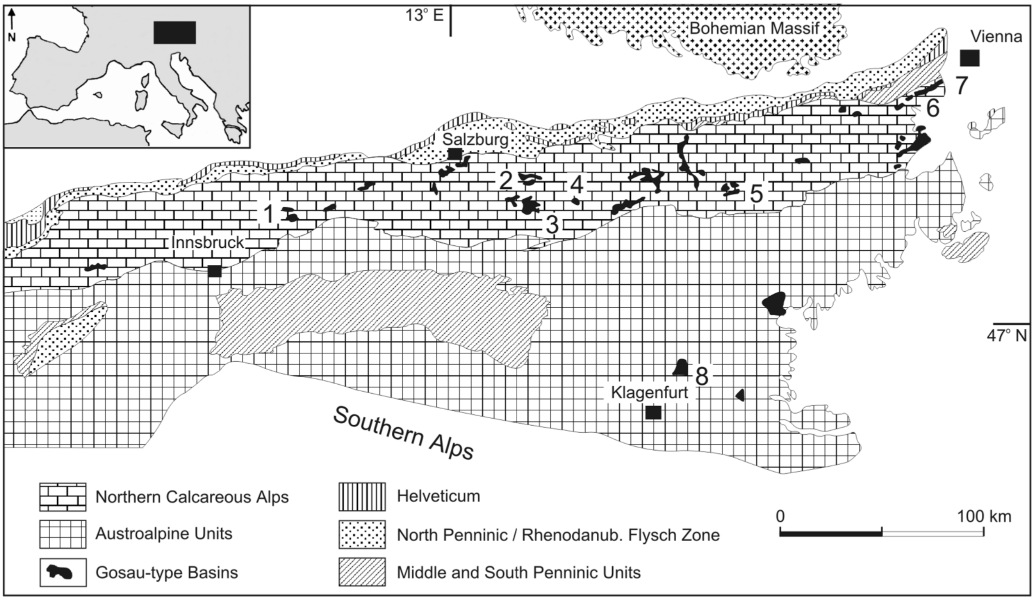

Fig. 1: Locality map of studied rudist formations of the Lower Gosau Subgroup, Northern Calcareous Alps, and of Gosau-type deposits of the Austroalpine Unit (modified after WAGREICH & FAUPL 1994). 1, Brandenberg (Atzlgraben); 2, Wolfgangsee (St. Gilgen, St. Wolfgang); 3, Gosau; 4, Bad Aussee (Weißenbach); 5, Gams; 6, Grünbach (Lupat, 'Pfarrer Schweighofer'); 7, Baden (Einöd); 8, Althofen, Wietersdorf.

originally considered to be related to the Caprinidae. The recognition of the orientation of the posterior myophore in the right (lower) valve (RV) being sub-parallel to the commissural plane led DOUVILLÉ (1888) to separate the group from the caprinids and relate them to the monopleurid rudists. SKELTON (1978) reinstated the conclusions of DOUVILLÉ (1888) and split the Plagioptychidae from the Caprinidae, in which most rudists with pallial canals had again been grouped by DECHASEAUX & PERKINS (1969), ignoring the conclusions of DOUVILLÉ (1988) and MAC GILLAVRY (1937). In addition to differences in the myocardinal organisation, the outer calcitic shell layer is thicker in the LV and much thicker in the RV of the Plagioptychidae when compared to the Caprinidae. In the most recent revision of the genus *Plagioptychus* MATHERON, 1842, MENNESSIER (1957) argued that the external morphology of the right valve (RV) and the position of the cardinal teeth of the left valve (LV) are indicative of common ancestry, and are thus shared in evolutionary lineages of the genus. The pattern of pallial canals in the inner shell layer of the LV is traditionally considered to be diagnostic at the species level.

Localities and Stratigraphy

The stratigraphy of many Gosau-type rudist formations (Fig. 1) has been revised recently (e.g. SUMMESBERGER & KENNEDY 1996, STEUBER 2001), and several occurrences which were previously considered to be of Santonian or Campanian age (KÜHN 1947, 1965) are now known to be of Coniacian or Turonian age. Strontium-isotope stratigraphy (SIS) has shown to be a powerful tool for stratigraphical correlation of rudist formations (STEUBER 2001, 2003a, 2003b; STEUBER et al. 2002) which is frequently difficult due to the absence of stratigraphically useful fossils. The stratigraphy of the localities (Fig. 2) listed below is largely based on previously published data (STEUBER 2001) and complemented by samples analysed for the purpose of the present study (Tab. 1). Details of methods of SIS are given in MCARTHUR (1994), MCARTHUR et al. (2001) and STEUBER (2001).

Tab. 1: Analytical results of low-Mg calcite of rudist shells from localities in the Lower Gosau Subgroup (Fig. 1). Numerical ages from HOWARTH & MCARTHUR (1997, version 3:10/99).

Locality Sample no. (NHMW)	^{87}Sr/^{86}Sr	± 2 s.e. (x 10^{-6})	^{87}Sr/^{86}Sr mean	± 2 s.e. (x 10^{-6})	age (Ma)	Sr	Mg	Fe	Mn
						(µg/g)			
Styria: Bad Aussee, Weißenbachalm									
2004z0087/0001-1	0.707337	7				1478	3856	62	16
2004z0087/0001-2	0.707341	7	**0.707339**	12	>87.82 **88.22** <88.61	1557	3936	116	23
Lower Austria: Baden-Einöd									
1933/38-1	0.707435	7				no data			
1933/38-2	0.707431	7				no data			
1933/38-3	0.707429	7	**0.707432**	4	>85.09 **85.38** <85.65	no data			
Lower Austria: Grünbach-Pfarrer Schweighofer									
2004z0078/0003-1	0.707441	7				1394	1517	<20	<20
2004z0078/0003-2	0.707453	7	**0.707447**	12	>84.13 **84.79** <85.39	no data			

Turonian

Salzburg, St. Wolfgang: 89.3 - 89.8 Ma; Late Turonian (SUMMESBERGER & KENNEDY 1996, STEUBER 2001). Recognised species: *Plagioptychus uchauxensis* MENNESSIER.

Styria, Gams, south of Langriedler Hof: Late Turonian or older (SUMMESBERGER & KENNEDY 1996). A numerical age of 89.2 Ma was derived from other rudist-bearing deposits of the Gams area (STEUBER 2001). Recognised species: *Plagioptychus haueri* (TELLER).

Coniacian

Tyrol, Brandenberg, Atzlgraben: 88.9 Ma; earliest Coniacian (STEUBER 2001, see also HERM et al. 1979, SUMMESBERGER & KENNEDY 1996, SANDERS et al. 1997). Recognised species: *Plagioptychus* aff. *uchauxensis* MENNESSIER.

Styria, Bad Aussee, Weißenbachalm: 88.0 Ma; middle Coniacian (STEUBER, 2001; based on a single analysis); two samples from plagioptychids collected for this study gave a mean ^{87}Sr/^{86}Sr value of 0.707339 which indicates a similar numerical age of 88.2 Ma. SZENTE et al. (1999) discussed a late Santonian - early Campanian age, based on traditionally accepted but erroneous ranges of rudist bivalves such as *Vaccinites inaequicostatus* (MÜNSTER in GOLDFUSS) and the misidentification of *Plagioptychus toucasi* MATHERON. Recognised species: *Plagioptychus aguilloni* (d'ORBIGNY).

Styria, Hieflau, Waaggraben: Stratigraphy inferred from specimens of *Plagioptychus aguilloni* (d'ORBIGNY) which are similar to those from Weißenbachalm and the Grünbach region, but smaller than those from Weißenbachalm, and significantly smaller than those from the Grünbach region. Phyletic size increase appears to be a common evolutionary pattern in Cretaceous rudists (SKELTON & MASSE 1998; STEUBER 2003a; see discussion below). Considering the size increase observed in specimens from Weißenbachalm (88.2 Ma) and the "Pfarrer Schweighofer" locality in the Grünbach region (84.8 Ma), an early Coniacian or even Turonian age for the Waaggraben locality is suggested. Waaggraben is the type locality of *Hippurites exaratus* ZITTEL, 1866. The stratigraphy of this species is not well constrained. Recognised species: *P. aguilloni* (d'ORBIGNY).

Santonian

Lower Austria, Baden-Einöd: 85.4 Ma; early Santonian (Tab. 1). KÜHN (1930) concluded on a late Santonian - early Campanian age, the early Campanian being based on the occurrence of *Vaccinites oppeli* (DOUVILLÉ). SIS of samples from a large specimen of *V. oppeli* from this locality (NHMW 1933/38) indicates a well defined early Santonian age. Recognised species: *Plagioptychus aguilloni* (d'ORBIGNY), previously mentioned from this locality by KITTL (1893).

Upper Austria, Gosau region: late Santonian. Numerical ages (STEUBER 2001) from Wegscheidgraben (84.1 Ma) and Nefgraben (83.9; Steuber 2001) are consistent with the well established biostratigraphy of these deposits (SUMMESBERGER 1980; SANDERS et al. 1997). Specimens described here are from Wegscheidgraben, Nefgraben and Brunftloch. Recognised species: *Plagioptychus aguilloni* (d'ORBIGNY).

Lower Austria, Grünbach region, Lupat: 84.0 Ma, late Santonian (STEUBER 2001). Plagioptychids from the locality 'Pfarrer Schweighofer' gave a slightly higher numerical age of 84.8 Ma (middle Santonian, Tab. 1, Fig. 2). Other specimens from the Grünbach region are labelled 'Adrigan Bauer'. Recognised species: *Plagioptychus aguilloni* (d'ORBIGNY).

Middle Campanian

Carinthia, Althofen: Rudist associations known from various localities of the Austroalpine unit in Carinthia (St. Paul/Lavantal, Wietersdorf, Treibach/Althofen) were shown to be very similar after taxonomic revision (STEUBER 2001). Samples from Wietersdorf have ^{87}Sr/^{86}Sr values which indicate the earliest middle Campanian (80.1 Ma; STEUBER, 2001), and a similar age can thus be inferred for the other occurrences known from the region. Recognised species: *Mitrocaprina* bayani (DOUVILLÉ).

Systematic Palaeontology

Only the most important references are given in the synonymy lists. Refer to www.ruhr-uni-bochum.de/sediment/rudinet/intro.htm for a more complete synonymy and references to occurrences. Synonymy lists are annotated with symbols as coded in MATTHEWS (1973). The studied material is kept in the Naturhistorisches Museum, Vienna.

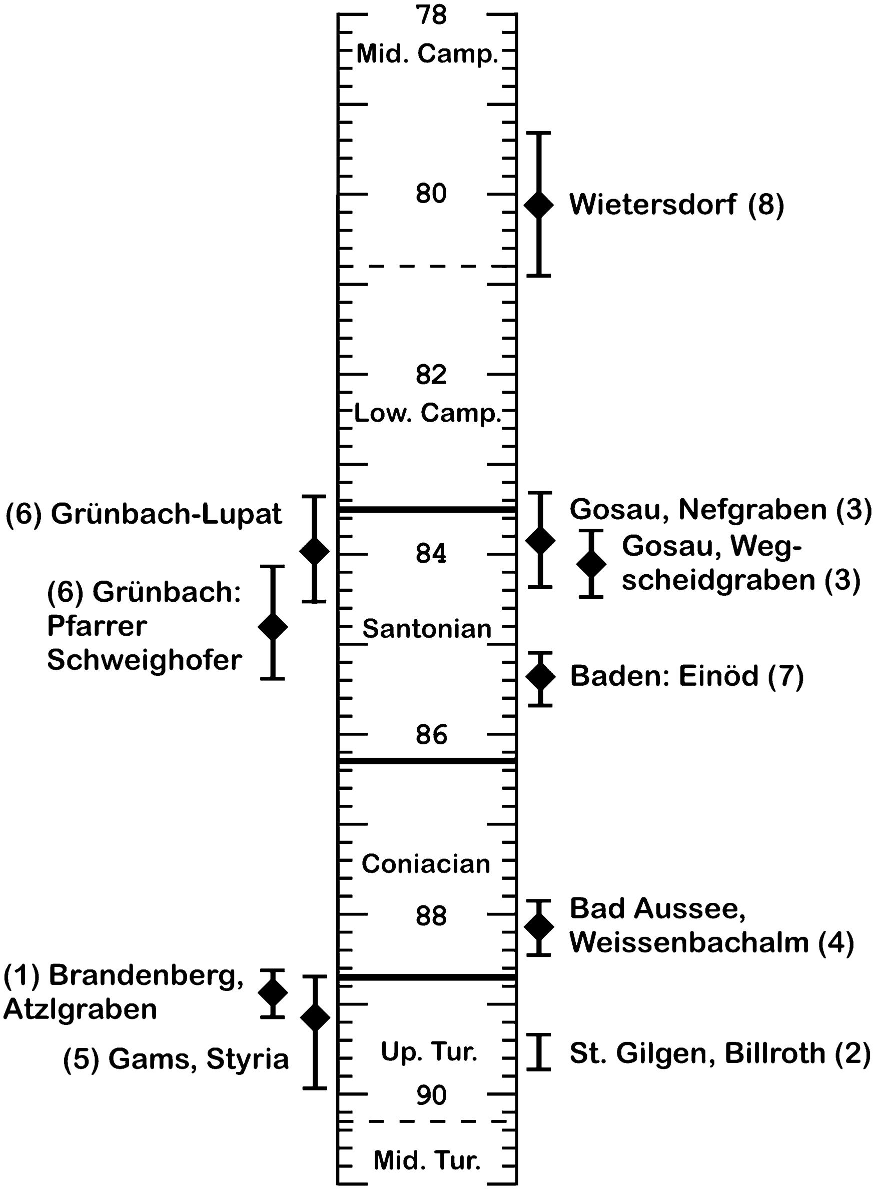

Fig. 2: Numerical ages derived from strontium isotope stratigraphy (Tab. 1) of occurrences of plagioptychids in the Northern Calcareous and Central Alps. Error bars indicate age range due to limits of analytical precision and uncertainty about the seawater Sr-isotope composition (McARTHUR et al., 2001). Time scale of OBRADOVICH (1993). Numbers given with names of localities refer to those indicated on Figure 1.

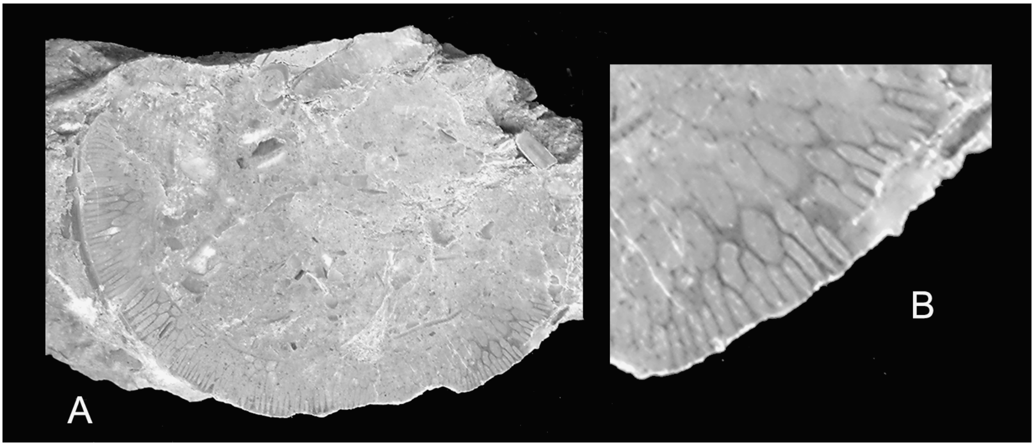

Fig. 3: *Mitrocaprina bayani* (DOUVILLÉ, 1888) from Althofen, NHMW 2004z0083/0001. A, LV in abapical view, x2; B, detail of posterior inner shell wall with pallial canals.

Family Plagioptychidae DOUVILLÉ, 1888

Genus *Mitrocaprina* BOEHM, 1895

***Mitrocaprina bayani* (DOUVILLÉ, 1888)**

Text-Figure 3

* 1888 *Coralliochama Bayani* – DOUVILLÉ: 725, pl. 25, fig. 7, text-fig. 9.
1895 *Mitrocaprina Bayani* DOUVILLÉ – BOEHM: 102.
1937 *Mitrocaprina bayani* (DOUVILLÉ) – MAC GILLAVRY: 164, pl. 7, figs. 3,9.
? 1937 *Mitrocaprina* cf. *bayani* DOUVILLÉ – MAC GILLAVRY: 165, pl. 7, fig. 2.
1950 *Mitrocaprina bayani* DOUVILLÉ – RENGARTEN: 43, pl. 9, fig. 2, text-fig. 18.
1967 *Mitrocaprina bayani* (DOUVILLÉ) – POLŠAK: 50, 168, pl. 17, fig. 2,2a,2b.
1969 *Mitrocaprina polsaki* nov. sp. – ASTRE: 11.
1999 *Mitrocaprina bayani* (DOUVILLÉ) – STEUBER: 46, text-fig. 24.

Material: One LV, labelled '*Caprina Aguilloni* ORB., Kittl coll., Althofen, Kärnten', NHMW 2004z0083/0001.

Description: The dorsal part of the LV is crushed, and the inner shell shows patches of early diagenetic dissolution. The antero-posterior commissural diameter is less than 32 mm. No remnants of cardinal teeth and myophores are preserved. Four rows of polygonal canals are present in the posterior shell, and three rows in the anterior shell. Only a single continuous row of polygonal canals runs along the inner margin of the ventral shell, while a second row is discontinuous. Three rows of sub-polygonal canals in the posterior shell are also seen in an early ontogenetic stage, as the studied section also crosses the apical part of the LV, which is frequently recrystallised in such early growth stages of other specimens. This supports previous observations that there is little ontogenetic change in the pattern of pallial canals of the Plagioptychidae (DOUVILLÉ 1888, STEUBER 1999). The LV from Althofen is slightly larger than the type specimens from the Santonian of Rennes-les-Bains, which have up to three rows of polygonal canals in the anterior shell, but fewer in the posterior part bordering the posterior myophore. Much larger specimens have been described from Paleokastron (Boeotia, Greece). This locality was previously assigned to the Santonian - Lower Campanian, but Sr isotope stratigraphy has revealed a latest Turonian - early Coniacian age (Steuber 2001). A larger specimen with a complex pattern of several rows of polygonal canals similar to the Austrian specimen was figured by Polšak (1967) from the Santonian - Lower Campanian of Croatia. A larger specimen has also been reported from the Santonian of Transcaucasus (Rengarten 1950). *M. bayani* from the Maastrichtian of Cuba (Mac Gillavry 1937) is remarkably similar to the type specimens, and to the LV from Althofen, including the pronounced prosogyrate curvature of the umbo. The disjunct stratigraphical and regional distribution of the species is remarkable. It is reported from the Alps for the first time.

Genus *Plagioptychus* Matheron, 1842

***Plagioptychus aguilloni* (d'Orbigny, 1840)**

Text-Figures 4-7

* 1840 *Caprina Aguilloni* d'Orb. – d'Orbigny: 169.
1842 *Plagioptychus paradoxus* – Matheron: 188, pl. 5, figs. 1-3,6.
1847 *Caprina Partschii* – Hauer: 1, pl. 3.
1850 *Caprina Aguilloni* d'Orb. – d'Orbigny: 184, pl. 538, figs. 1-3,6.
1866 *Caprina Aguilloni* d'Orb. – Zittel: 154, pl. 26, figs. 8-10, pl. 27, figs. 2-8.
? 1866 *Caprina Aguilloni* d'Orb. var. *exogyra* – Zittel: 156, pl. 27, fig. 1.
1888 *Plagioptychus Aguilloni* d'Orb. – Douvillé: 716, pl. 24, figs. 1-2, pl. 25, fig. 1, text-fig. 5.
1893 *Plagioptychus Aiguilloni* [sic] Orb. – Kittl: 380.
? 1900 *Plagioptychus* sp. (cf. *aguilloni* d'Orb.) – Redlich: 665, 675.
1950 *Plagioptychus paradoxus* Matheron – Rengarten: 39, pl. 7, figs. 2-3.
1957 *Plagioptychus paradoxus* Matheron – Mennessier: 849.
1961 *Plagioptychus aguilloni* Orb. – Plöchinger: 371.
1968 *Plagioptychus aguilloni* (d'Orbigny) – Kennedy & Taylor: 328, text-figs. 2-3.
? 1975 *Plagioptychus aguilloni* (d'Orb.) – Czabalay: 447, pl. 6, fig. 4.
1976 *Plagioptychus paradoxus* Matheron – Lupu: 137, pl. 32, fig. 4.
1977 *Plagioptychus aguilloni* (d'Orbigny) – Pons: 56, pl. 4, fig. 4, pl. 5, figs. 1-3.
? 1982 *Plagioptychus aguilloni* (d'Orbigny) – Czabalay: 29, 70, pl. 6, fig. 5.
1988 *Plagioptychus aguilloni* (d'Orbigny) – Yanin: 282, pl. 10, figs. 1-2.
1988 *Plagioptychus paradoxus* Matheron – Yanin: 282, pl. 9, fig. 3.
1993 *Plagioptychus paradoxus* Matheron – Cherchi et al.: 95, text-fig. 2, pl. 6, figs. 2,5.
p 1997 *Plagioptychus aguilloni* d'Orbigny – Höfling: 50, 53, 82, [? pl. 19, fig. 7].
1999 *Plagioptychus aguilloni* d'Orbigny – Sirna & Paris: 46, pl. 2, fig. 5.
1999 *Plagioptychus paradoxus* Matheron – Sirna & Paris: 46, pl. 3, figs.1-2.
? 1999 *Plagioptychus* aff. *paradoxus* Matheron – Szente et al.: 587, pl. 2, figs. 10,12.
1999 *Plagioptychus toucasi* Matheron – Szente et al.: 587, pl. 2, figs. 9,11,13.
2000 *Plagioptychus aguilloni* (d'Orbigny) – Skelton & Smith: 123.

Material: Four LVs and one bivalve specimen from Bad Aussee, Weißenbachalm (NHMW 2004z0087/0001-0004; NHMW 2004z0089/0001); two LVs with fragments of RVs from Gosau, Brunftloch (NHMW 1887/XIII/22; NHMW 2004z0080/0001); one bivalve specimen from Gosau, Nefgraben (NHMW 1884/D/2513), and a LV with fragments of the RV from Wegscheidgraben (NHMW 2004z0080/0003); two LVs from Hieflau, Waaggraben (NHMW 2004z0088/0001-0002); one LV, respectively, from Grünbach, Lupat (NHMW 2004z0078/0001) and Grünbach, Adrigan Bauer (NHMW 2004z0079/0002); three specimens, one of them with both valves preserved, from Grünbach, Pfarrer

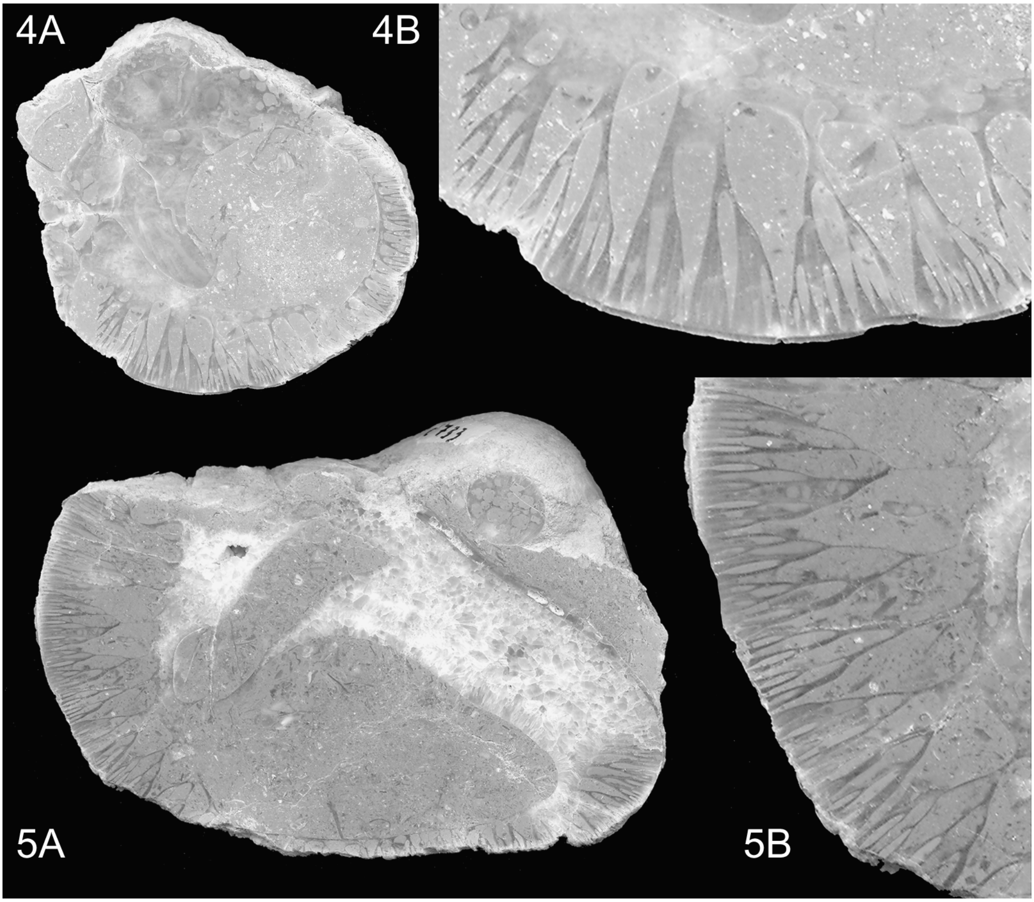

Fig. 4, 5: *Plagioptychus aguilloni* (d'Orbigny, 1840) from (4) Waaggraben near Hieflau, NHMW 2004z0088/0001, (5) Weißenbachalm near Bad Aussee, NHMW 2004z0087/0001. (A) Adapical views of (5A: dorso-ventrally compressed) LV, x1,05. (B) Details of posterior inner shell wall with pallial canals.

Schweighofer (NHMW 2004z0078/0002-0004). A large number of unstudied specimens from the latter locality is kept in the collections of the Naturhistorisches Museum, Wien. These are very similar in size and external morphology to the studied specimens and most probably belong to the same species. Two LVs from Baden-Einöd, but with significantly different internal sediments and state of preservation (NHMW 2004z0082/0001-0002).

Remarks on synonymy: There are contrasting opinions and long-lasting discussions about the synonymy of *Plagioptychus aguilloni* (d'Orbigny, 1840) and *P. paradoxus* Matheron, 1842. *P. paradoxus* is listed as type species according to Kutassy (1934), and this is adopted as a subsequent designation by Kutassy (1934) in Dechaseaux & Perkins (1969), which still list the genus among the Caprinidae. Both catalogues ignored Douvillé's (1888) designation of *P. aguilloni* as type species, based on a careful analysis of the synonymy of the then known plagioptychids, concluding that *P. para-*

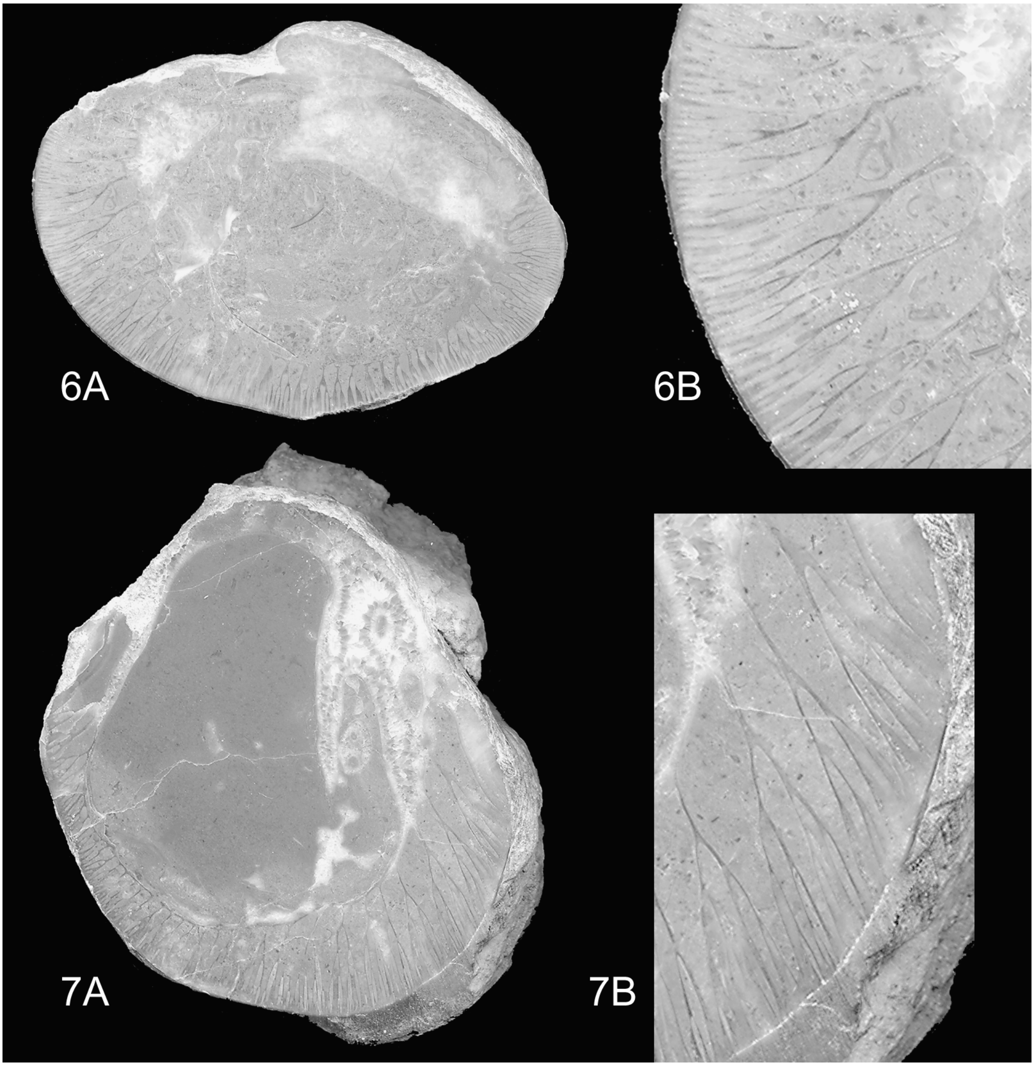

Fig. 6, 7: *Plagioptychus aguilloni* (d'ORBIGNY, 1840) from (6) Lupat, near Grünbach, NHMW 2004z0078/0001, (7) Grünbach, Pfarrer Schweighofer, NHMW 2004z0078/0002. (A) Adapical views of LV, x1,05. (B) Details of posterior inner shell wall with pallial canals.

doxus should be considered as a junior synonym of *P. aguilloni*. Also, DOUVILLÉ (1888) considered that the type series of MATHERON (1842) comprises different species from several localities. MENNESSIER (1957) based his description of a new species, *P. uchauxensis*, on the Turonian specimens from Uchaux included in MATHERON'S type series of *P. paradoxus*, but argued that *P. paradoxus* should be considered as the senior synonym because the type specimens were figured earlier (MATHERON, 1842) than those of *P. aguilloni* (d'ORBIGNY 1850). However, MATHERON'S (1842) figures offer little more detail than the description of d'ORBIGNY (1840). ASTRE & BAUDELOT (1960) did not evaluate

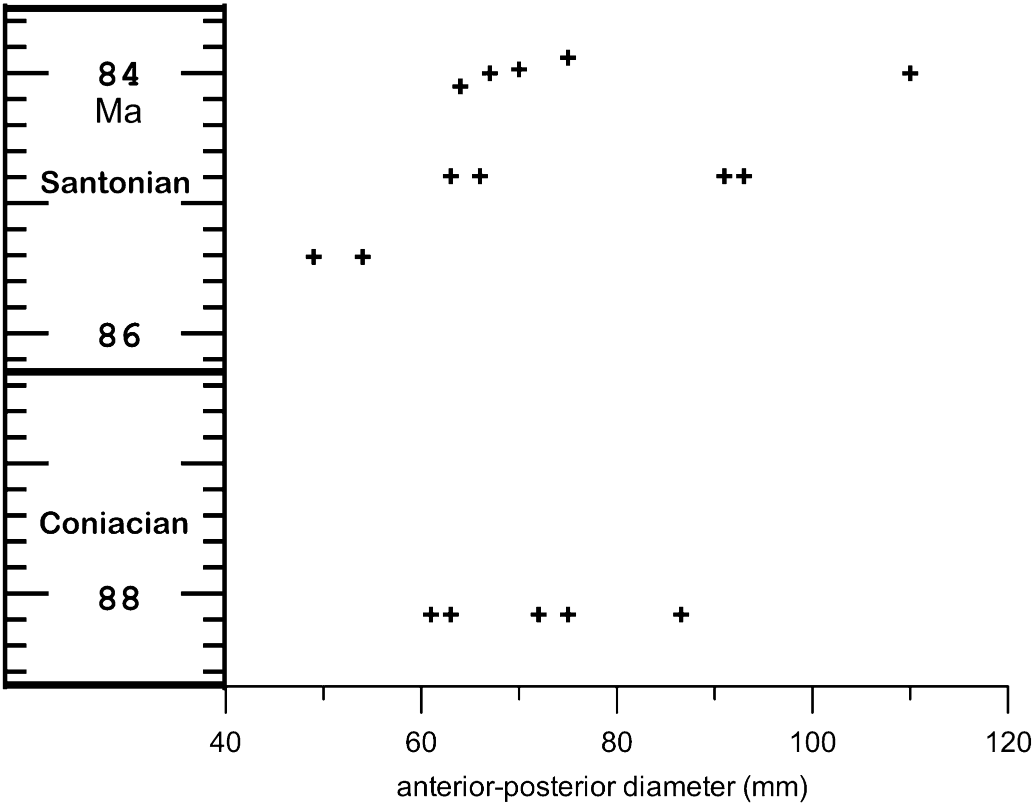

Fig. 8: Anterior-posterior diameter of *Plagioptychus aguilloni* (d'ORBIGNY) as a function of stratigraphical age. Diameter was measured as closely to commissure as possible.

the opinion of Mennessier (1957), left the question open and referred to *'Pl. aguilloni = paradoxus'*. As a result of this confusion, both names are currently in use for this rather common taxon, each name having more than ten records after 1980. Despite this controversial discussion, there is no doubt that both names refer to the same morphospecies, *Plagioptychus aguilloni* (d'ORBIGNY, 1840). This is an available name so that the opinion of DOUVILLÉ (1888) conforms with the ICZN and should be generally followed.

Description: Relatively large shells with commissural diameter of up to 112 mm. One specimen from Nefgraben (NHMW 1884/D/2513), and a large shell from Grünbach, Pfarrer Schweighofer (NHMW 2004z0078/0003), have well preserved gyropleuriform RVs, while conical RVs occur more frequently. This contradicts the classification of MENNESSIER (1957) who separated the 'série sénonienne' of plagioptychids in two groups with conical and gyropleuriform RVs, respectively, and listed *P. paradoxus* (= *P. aguilloni*) among the group with conical RVs. The shape of the RV is obviously related to the habitat and depends on environmental factors such as sedimentation rate, rather than being genetically fixed. ZITTEL (1866) considered *Caprina exogyra* REUSS, 1853 as a variety of *P. aguilloni*, differing by a gyropleuriform RV. This assumption as well as the contrasting proposition of MENNESSIER (1957) that *C. exogyra* is similar to *P. tou-*

casi MATHERON, 1842, are based on external characters and must remain speculative, as long as the internal morphology of the LV of the types of *C. exogyra* has not been described. ZITTEL's (1866) proposition is supported by the specimens of *P. aguilloni* with gyropleuriform RV's described herein.

In most LVs, eight primary pallial canals are seen posterior to the septum which separates the socket of the RV tooth and the adjoining posterior cavity from the main body cavity. A few LVs have nine or 10 primary canals. The separation of the LV posterior tooth and myophore is marked by a restriction of the posterior cavity which is produced by a more or less angular projection of the inner shell wall. In the posterior shell wall, the partitions between pallial canals bifurcate at least three times, but frequently four times. While the branching pattern of pallial canals in the ventral shell wall is related to the thickness of the shell, i.e. there is only a single bifurcation in LVs with a thin shell and two, occasionally three bifurcations in LVs with a thick ventral shell, the branching pattern of the pallial canals in the posterior shell wall is not related to size. Four bifurcations occur in the small specimens from Hieflau, Waaggraben (Fig. 4) and Weißenbachalm (Fig. 5) as well as in the much larger LVs from Grünbach, Pfarrer Schweighofer (Fig. 7). Considering previous observations and those made in shells of *Mitrocaprina bayani* (DOUVILLÉ, 1888; see above) that there is little ontogenetic change in the branching pattern of the pallial canals (DOUVILLÉ 1888, STEUBER 1999), this suggests that size - related morphological change of this character is not a mode of heterochronic evolution in the Plagioptychidae.

There appears to be a tendency of increasing size (commissural diameter) in the studied specimens. The largest shells occur at Santonian localities of the Gosau and Grünbach regions (Fig. 8). The relatively large diameter of one shell from Bad Aussee, Weißenbach (Fig. 5), results from a pronounced dorso-ventral compression and corresponding large anterior - posterior diameter of this particular specimen. The stratigraphy of the locality at Waaggraben near Hieflau is not well constrained (KOLLMANN, written commun.). Shells of *P. aguilloni* from this locality are significantly smaller, and may indicate an early Coniacian or even Turonian age.

Distribution: Turonian of Italy, Austria and East Serbia; Coniacian of West Serbia; Coniacian – Santonian of the Pyrenees, Northern Calcareous Alps (Austria and Germany), Santonian of southern France, West Serbia and Romania; Santonian - Campanian of Italy, the Central Alps and Hungary, Croatia; Coniacian of Azerbaidjan and Armenia. Neither Turonian nor Campanian occurrences of the species are well constrained.

***Plagioptychus haueri* (TELLER, 1877)**

Text-Figure 9

* 1877 *Caprina Haueri* nov. spec. – TELLER: 102, pl. 1, fig. 9, pl. 2, figs. 1-2,5, pl. 3.
1885 *Caprina* (*Plagioptychus*) *Haueri* TELLER – LAUBE: 75.
1887 *Plagioptychus Haueri* TEL. – POČTA: 204.
1957 *Plagioptychus haueri* (TELLER) – MENNESSIER: 841.

Material: A single complete specimen (NHMW 2004z0084/0001), labelled *'Caprina Aiguilloni* [sic] ORB., Südl. v. Langriedler-Hof, Oberkreide: Gosau F., Gams bei Hieflau, Kraus & Kittl coll'.

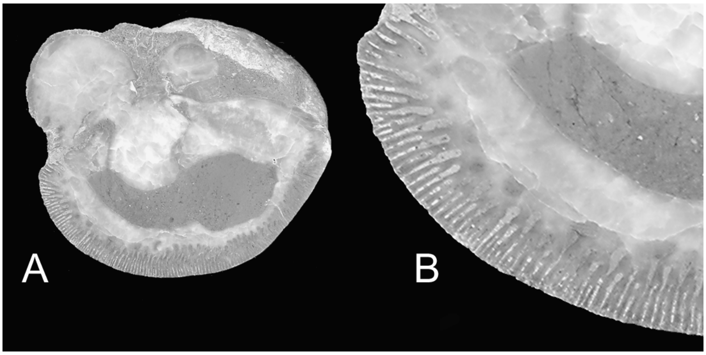

Fig. 9: *Plagioptychus haueri* (Teller, 1877) from Gams, Langriedler Hof, NHMW 2004z0084/0001. (A) adapical view of LV, x1. (B) Detail of posterior inner shell wall with pallial canals.

Description: Commissural diameter is 38 mm. LV globose, externally smooth. RV obliquely conical, with distinct growth lines, apically deformed by having overgrown a flat object. The external form, prominent tooth of RV, the branching pattern of partitions between pallial canals as well as their large number, are similar to the type specimens of Teller (1877). Partitions between pallial canals have one bifurcation along the anterior and ventral shell, and two bifurcations along the posterior shell. The branching pattern is seen clearly only in one of the figured type specimens, and frequently only one of the bifurcated partitions shows a second bifurcation. This occurs more rarely in the specimen from Gams, where two bifurcations are common. The septum which extends from the anterior tooth to the ventral shell wall of the LV is not seen in the described commissural section, but its positions can be inferred from a bulge in the inner shell. Accordingly, this septum demarcates a large posterior cavity, of similar size as the central body cavity.

The species differs from *P. arnaudi* Douvillé by a larger number of pallial canals, and in a more complicated branching pattern of partitions between canals.

Distribution: The species was previously known from the type region, only (Teplice, Czech Republic); Lower Turonian (Peza & Žitt 1999).

Plagioptychus uchauxensis Mennessier, 1957
Text-Figure 10

p 1842 *Plagioptychus paradoxus* – Matheron: 188, pl. 5, figs. 4-5,7.
p 1850 *Caprina Aguilloni* d'Orb. – d'Orbigny: 184, pl. 538, figs. 4-5,7.
1895 *Plagioptychus Arnaudi* Douvillé – Boehm: 138, text-fig. 3a-b.
1920 *Plagioptychus* sp. – Roman & Mazeran: 108, pl. 1, fig. 1,1a, text-fig. 31.
* 1957 *Plagioptychus uchauxensis* nov. sp. – Mennessier: 839, text-figs. 1a,3.
? 1957 *Plagioptychus bellunensis* nov. sp. – Mennessier: 837, text-fig. 2.
? 1965 *Plagioptychus bellunensis* Mennessier – Tzankov: 21, pls. 1,2.

Material: Two specimens (NHMW 2004z0085/0001-0002) from St. Wolfgang, one of them complete, with both valves conjoined. No further details on locality available for these specimens.

Description: Commissural diameter is 77 mm in one and more than 80 mm in the other specimen and thus similar to the type of *P. bellunensis* Mennessier and slightly

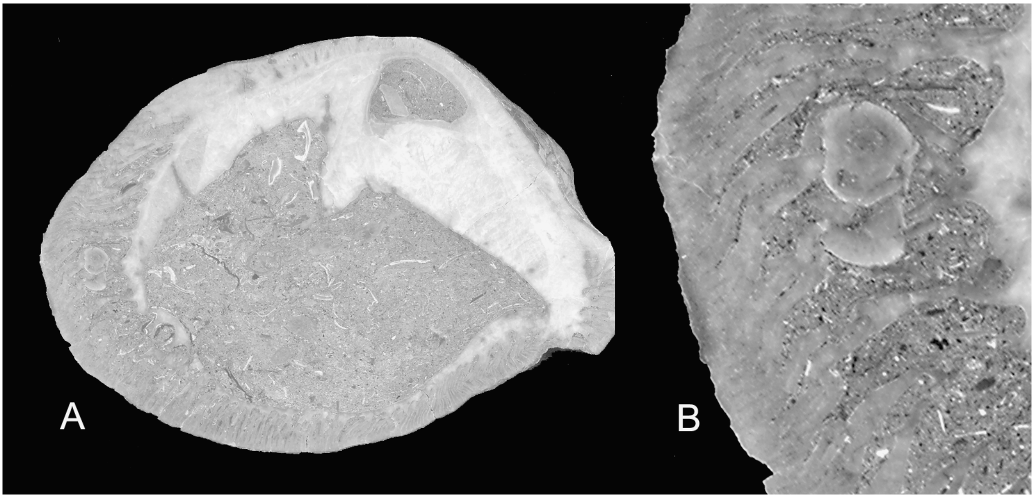

Fig. 10: *Plagioptychus uchauxensis* MENNESSIER, 1957, from St. Wolfgang, NHMW 2004z0085/0001. (A) adapical view of LV, x1,06. (B) Detail of posterior inner shell wall with crushed pallial canals.

larger than the type of *P. uchauxensis* MENNESSIER. The RV is gyropleuriform. The RV tooth is prominent and fills the dorsal half of the posterior cavity. The inner shell wall bearing the pallial canals is completely crushed in one LV, and along the posterior shell in both specimens, but the branching pattern of c. 12 partitions, between primary canals posterior to the inferred position of the septum which separates the posterior cavity from the main body cavity, is still recogniseable (Fig. 10). In the posterior shell wall, most of these partitions bifurcate three times, but the third bifurcation is occasionally present in one of the branches, only.

Remarks: *P. uchauxensis* includes the two specimens from the type series of *P. paradoxus* MATHERON, 1842, which were already considered by DOUVILLÉ (1888) to belong to a different species (MENNESSIER 1957: p. 850). Differences between *P. uchauxensis* and *P. bellunensis* are minor and refer to a slightly more simple branching pattern of the partitions between radial canals in *P. bellunensis*. In *P. uchauxensis*, three bifurcations occur almost generally in the posterior shell while in *P. bellunensis*, a third bifurcation affects frequently only one branch of the partitions. Considering the variability of this character in the samples from Atzlgraben, and in other Plagioptychidae (STEUBER 1999), *P. bellunensis* and *P. uchauxensis* may belong to the same morphospecies. As relatively few specimens are available for a detailed evaluation of the variability of diagnostic characters, the two species are not formally synonymised here. *P. aguilloni* differs from *P. uchauxensis* in having four bifurcations of partitions between canals in the posterior shell wall.

Distribution: Middle Turonian of southern France (Vaucluse; *P. uchauxensis*); Turonian of Bulgaria and the southern Alps (*P. bellunensis*).

***Plagioptychus* aff. *uchauxensis* MENNESSIER, 1957**

Plate 1, Figures 1-5

Material: Six LVs (NHMW 2004z0086/0001-0006) from Atzlgraben, several of them with fragments of the RV.

Description: Commissural diameter of the largest specimen is 47 mm, they are thus smaller than the types of *P. uchauxensis* and *P. bellunensis*, and of *P. bellunensis* reported by TZANKOV (1965). The inner shell layers of all specimens, including the myocardinal elements, are not well preserved due to recrystallisation, early diagenetic dissolution and subsequent infilling with sediment. The pallial canals are more or less well preserved in the posterior shell walls, while ventral and anterior parts are largely dissolved or recrystallised. In the posterior shell wall, partitions of canals bifurcate up to three times, have a third bifurcation only in one branch, or bifurcate twice. In three of the six LVs, several subpolygonal canals are developed in the posterior part of the shell (Pl. 1, Figs 4-5), but without forming a continuous row. These specimens are thus transitional to *Mitrocaprina*.

Conclusions

Five species of Plagioptychidae have been recognised from localities ranging from the Upper Turonian to the Lower Campanian. *Plagioptychus aguilloni* (d'ORBIGNY) is the single most abundant species among the material studied. It ranges from the Coniacian to the Upper Santonian. With the exception of *P.* aff. *uchauxensis* MENNESSIER from Atzlgraben, the records of *P. haueri* (TELLER) and *Mitrocaprina bayani* (DOUVILLÉ) are based on single specimens, and that of *P. uchauxensis* MENNESSIER on two specimens, only. The wide distribution of plagioptychids in the Gosau-type rudist formations of the Northern Calcareous and Central Alps suggests that further collections will yield records of additional species. The classification of the Plagioptychidae based on the external morphology of the RV (MENNESSIER) could not be confirmed, as both gyropleuriform and conical RVs are reported from *P. aguilloni*. The morphology of the RV depends on the individual life history and on parameters such as rates of shells growth and ambient sedimentation, and is not genetically fixed.

There are no safe records yet of *Plagioptychus arnaudi* DOUVILLÉ, 1888 and *P. toucasi* MATHERON, 1842 from Alpine Gosau-type rudist formations. This is remarkable because both species have numerous records in the Turonian - Santonian of regions both in the West (Spain, France) and the East (Dinarids, Romania, Asia).

Due to the much improved biostratigraphical and chemostratigraphical precision achieved recently, it is now evident that the stratigraphical succession of rudist formations of the Alps is rather continuous from the Turonian to the Early Campanian (SANDERS et al. 1997; STEUBER 2001), and is not restricted to a few correlative horizons, as believed earlier (KÜHN 1965). There is thus a large potential to evaluate evolutionary patterns in rudist bivalves, and particularly in the Plagioptychidae. Phyletic size increase appears to occur in *P. aguilloni*, but the number of studied specimens is still much too low for a meaningful evaluation of this mode of evolution. Obviously, there is no anagenetic change in the evolution of pallial canals in this species.

Although four of the five recognised species of Plagioptychidae are reported here from the Alps for the first time, the distribution of the group in the region is certainly still not well known, considering their abundance and the relatively small number of specimens studied.

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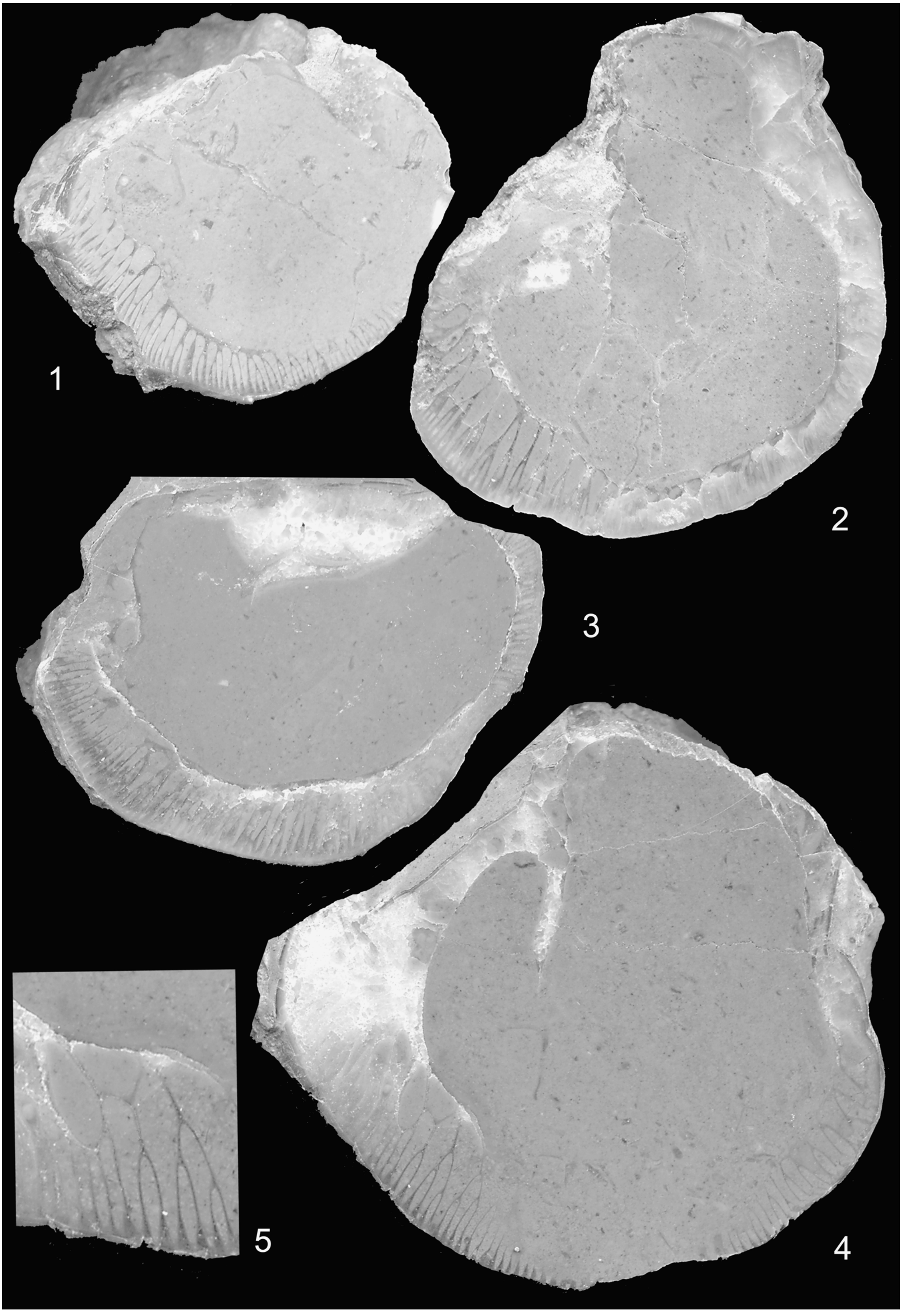
Plate 1

Figures 1-5: Transverse sections of LVs of ***Plagioptychus* aff. *uchauxensis* MENNESSIER, 1957**, from Atzlgraben, all in adapical view; Figures 1-4, x 2,13. 1, NHMW 2004z0086/0002; 2, NHMW 2004z0086/0003; 3, NHMW 2004z0086/0001; 4, NHMW 2004z0086/0004; 5, detail of pallial canals in posterior shell wall of LV shown in Fig. 4; note two sub-polygonal canals at inner margin of inner shell layer.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