

# Shell accumulation of the brachiopod *Pygope catulloi* PICTET, 1867 (Lower Valanginian; Northern Calcareous Alps, Upper Austria): Palaeoecological implications

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(With 5 text figures, 1 table and 2 plates)

Manuscript submitted on October 23<sup>rd</sup> 2001,  
the revised manuscript on December 10<sup>th</sup> 2001.

## Abstract

A shell accumulation of the brachiopod *Pygope catulloi* from the upper Steinmühl Formation (Lower Cretaceous; Northern Calcareous Alps, Upper Austria) is recorded for the first time. Extraordinary environmental conditions during the Lower Valanginian led to an accumulation within a single layer. The acme of *Pygope catulloi* within the investigated area seems to coincide with drastic sea-level falls during the Lower Valanginian. The pygopid assemblage most probably inhabited a submarine ridge where bottom currents hindered rapid accumulation of pelagic sediments and the sedimentation rate was very low.

**Key words:** Brachiopods, Lower Cretaceous, Austria, Shell accumulation, Palaeoecology

## Zusammenfassung

Aus der Oberen Steinmühl-Formation (Unterkreide; Nördliche Kalkalpen, Oberösterreich) wird erstmals ein gehäuftes Auftreten von *Pygope catulloi* beschrieben. Besondere Umweltbedingungen während des Unter-Valanginiens führten zu einer Anreicherung innerhalb einer einzelnen Schicht. Die Hauptverbreitung von *Pygope catulloi* scheint im untersuchten Gebiet mit drastischen Meeresspiegel-Rückgängen während des Unter-Valanginiens zusammenzufallen. Die untersuchte Pygopen-Vergesellschaftung lebte wahrscheinlich auf einem submarinen Rücken, auf welchem Bodenströmungen eine schnelle Anhäufung von pelagischen Sedimenten verhinderte und die Sedimentationsrate sehr gering war.

**Schlüsselwörter:** Brachiopoden, Unterkreide, Österreich, Schalenanreicherung, Palökologie

## Introduction

Upper Jurassic to Lower Cretaceous pygopids (order Terebratulida) are one of the most astonishing groups of brachiopods, firstly because of their spectacular external morphology and secondly because of their sensitive indication of environmental changes within the palaeorelief (KÁZMÉR 1998).

Lower Valanginian deposits of Upper Austria yielded large amounts of *Pygope catulloi* (PICTET, 1867). This new occurrence was detected during palaeoecological and sedi-

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mentological studies at an outcrop in the Ternberg Nappe in Upper Austria. Most of the investigated brachiopods display poor preservation, mainly due to tectonic processes. Being characteristic Tethyan organisms, pygopids are valuable index fossils and indicators for palaeobiogeography and palaeobathymetry.

Previous work about pygopids and their preferred palaeohabitat, their palaeogeographic distribution and their living-mode was undertaken for example by SUESS (1867), GEYSSANT (1966), AGER (1967, 1975), MIDDLEMISS (1973, 1984), VÖRÖS (1977, 1980, 1982, 1987), SANDY (1988), KROBICKI (1993) and KÁZMÉR (1990, 1993, 1998). In his paper on pygopid brachiopods, KÁZMÉR (1993) summarized the results of previous investigations of the above-mentioned authors.

### Geography, Location and Geological Setting

According to LUKENEDER (1997, 1998, 1999) the investigated section lies 7 km west of Losenstein, 1 km south of Kienberg in the Losenstein Syncline (Ternberg Nappe, Upper Austria, 800 m, ÖK 1:50000, sheet 69 Großraming) (see text-fig. 1).

The outcrop of the pygopid-layer is situated in the upper part of the KB1 ravine (800 m). The fossiliferous horizon is located on the left, nearly vertical (dipping 040/85), step-like wall of the gorge, exposed over a length of 5 metres and a height of 4 metres. Rich vegetation, steep terrain and the "soft nature" of the marly rocks make the sampling very difficult. The exact position of the investigated beds is fixed by GPS data (N 47°54'33", E 14°21'10") (LUKENEDER 2001, LUKENEDER & HARZHAUSER in press).

The Losenstein Syncline is situated in the southernmost part of the Ternberg Nappe of the Northern Calcareous Alps. Directly to the south follows the Schneeberg Syncline, the Anzenbach Syncline and then the Ebenforst Syncline of the Reichraming Nappe (Northern Calcareous Alps, text-fig. 1). In the Reichraming Nappe, Valanginian deposits have been recorded in two different facies termed the Rossfeld and the Schrambach Formation. The Rossfeld Formation, which accumulated only in the southern part of the nappe, represents a southerly derived synorogenic turbidite sequence. The Schrambach Formation, forming the northern part of the nappe, comprises deep-water limestones with, from the Upper Valanginian upwards, distal turbiditic intercalations.

### Lithology and Lithostratigraphy

The section within the Lower Cretaceous is represented by two formations, from bottom to top (text-fig. 2):

**S t e i n m ü h l** Formation (approx. 20 m): Early Berriasian to late Early Valanginian in age, which consists in the lower part of red ("Ammonitico Rosso" type) and in the upper part of grey ("Maiolica" type) condensed pelagic limestones with rare ammonites, but abundant calpionellids and dinoflagellates. The latter groups allow precise biostratigraphic correlations. In the topmost bed *Pygope catulloi* is abundant.

**S c h r a m b a c h** Formation (approx. 100 m): Late Valanginian to Late Barremian in age, which consists of pale grey limestones intercalated with grey to black calcareous marls (laminated "black shales"), and marls.

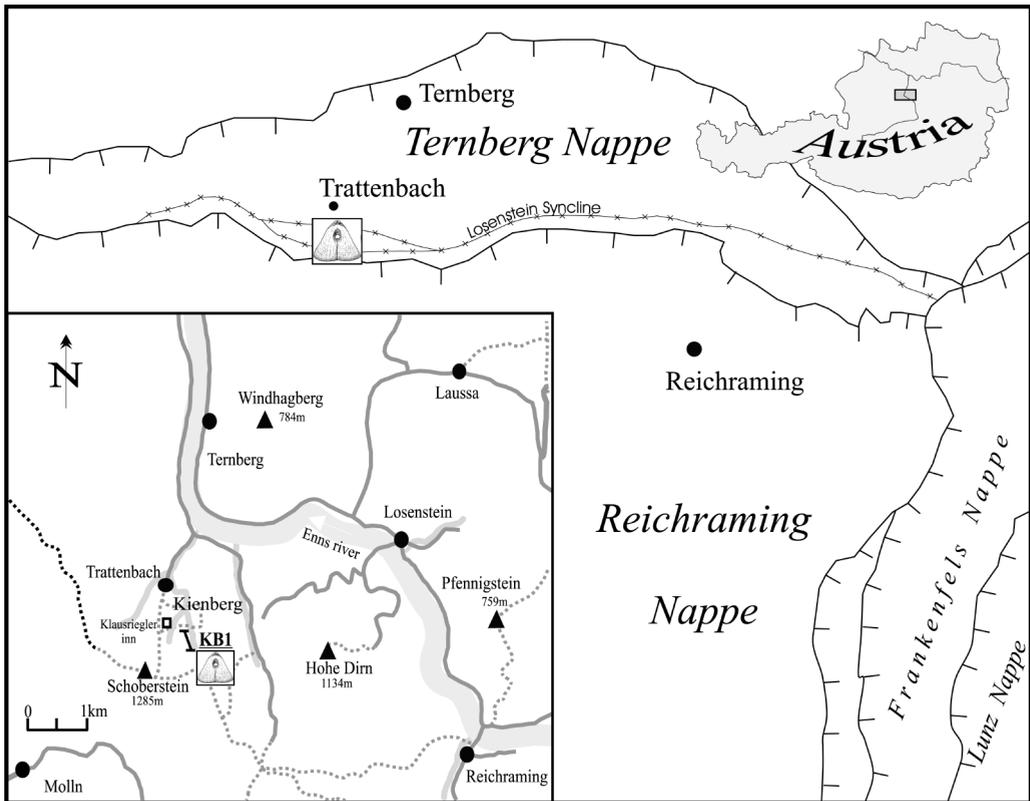


Fig. 1: Position of the investigated section KBI along a ravine (modified after LUKENEDER 1999). The map in the left lower corner shows the geological setting and the geographic position within this region (e.g. Ternberg Nappe, Reichraming Nappe).

The uppermost Lower Valanginian layer of limestones of the Steinmühl Formation is very rich in pygopids and echinids and extremely rich in calpionellids and other fossils (e.g. bivalves, foraminifera and juvenile shark teeth) but is poor in ammonites. The lower part of this formation consists of decimetre to centimetre bedded compact to nodular, red, condensed, pelagic limestones ("Ammonitico Rosso" type), and the upper part consists of decimetre bedded, wavy grey ("Maiolica" type) limestones which are rare in ammonites but contain abundant pygopids. The Steinmühl Formation is directly overlain by the Schrambach Formation (Upper Valanginian), which consists of grey limestones, marly limestones and marls.

The basal Upper Valanginian interval (3 m thick) of the Schrambach Formation consists of a rhythmic marl-limestone alternation. The first few metres of the Schrambach Formation yielded an extraordinarily rich and diverse invertebrate fauna consisting of ammonites, aptychi, belemnites, radiolarians, foraminifera (*Lenticulina*, *Planopsilina*, etc.), ophiurids, echinids, phyllocrinids, bryozoans, brachiopods (*Pygope catulloi* PICTET), ostracods, serpulids and bivalves (inoceramids).

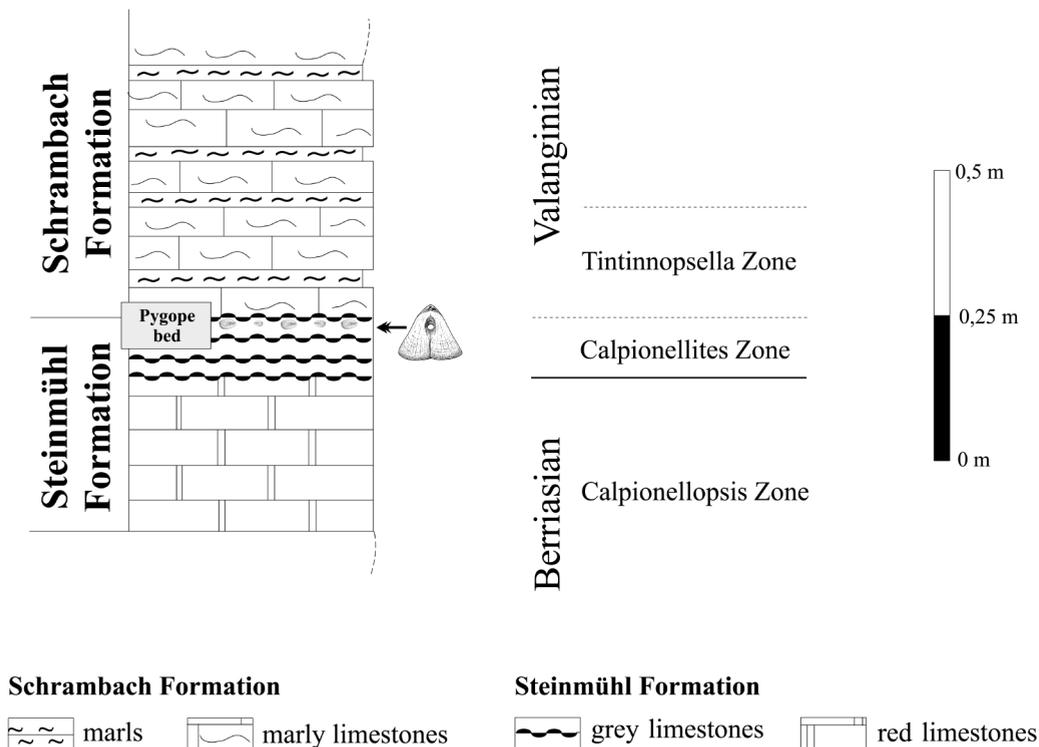


Fig. 2: Detailed stratigraphic column of the Lower Cretaceous strata containing the Lower Valanginian *Pygope catulloi*-bearing bed (*Pygope*-bed) (modified after LUKENEDER 1999).

Lithologies (limestones and marly limestones) were analysed in thin sections and by geochemical analysis. Washed residues were obtained from limestones and marls by dissolution using formic acid, acetic acid and later washing with desogen through sieves of 500  $\mu\text{m}$  to 63  $\mu\text{m}$  mesh. In some cases, ultrasonic treatment was necessary to clean aggregated or encrusted specimens.

The evaluation of the thin sections indicates a change from a calpionellid facies (lower part of the "Ammonitico Rosso" type limestone, calpionellid wackestones), to an echinoid-rich facies (upper part of the Steinmühl Formation, bioclastic wackestones including the *Pygope*-bearing layer). The overlying Schrambach Formation consists of mudstones with rare fossils (e.g. echinoids and foraminifera). The determination of the microfossils was done by Daniela REHÁKOVÁ (Bratislava).

Thin sections from the *Pygope*-bed (text-fig. 2):

Bioclastic wackestone with high amounts of crinoid, bivalve, brachiopod and aptychi fragments. Important calpionellid taxa are *Calpionellites darderi* (COLOM), *Calpionellites major* (COLOM), *Tintinnopsella longa* (COLOM) and *Tintinnopsella carpathica* (MURGEANU & FILIPESCU). Foraminifera are represented by *Lenticulina* sp., *Dentalina* sp., *Gaudryina* sp. and *Textularia* sp. Fragments of calcareous algae – *Pseudocymopolia jurassica* (DRAGASTAN) – and planktonic favusellid forams are observed.

### Systematic Palaeontology

Conventions: The standard dimensions of brachiopods are given in millimetres. The following abbreviations have been used: L = shell length, vl = ventral valve length, dh = dorsal valve length, H = shell height, vh = ventral valve height, dh = dorsal valve height, B = shell width, p = perforation diameter, hl = hole width, h = hole diameter; NHMW Museum of Natural History Vienna. The author follows the classification of MUIR-WOOD (1965) and SULSER (1999).

Order Terebratulida WAAGEN, 1883

Superfamily Terebratulacea GRAY, 1840

Family Pygopidae MUIR-WOOD, 1965

Subfamily Pygopinae DIENI & MIDDLEMISS, 1975

Genus *Pygope* LINK, 1830

Type species: *Terebratula dilatata* CATULLO, 1851. Tithonian, Venetia, Italy.

#### *Pygope catulloi* (PICTET, 1867)

(Plates 1-2)

- 1851 *Terebratula dilatata* (CATULLO) – CATULLO: 75  
 1867 *Pygope catulloi* (PICTET) – PICTET: pl. 32, fig. 2  
 1871 *Terebratula diphya* (BUCH) – QUENSTEDT: pl. 47, fig. 119  
 1965 *Antinomia catulloi* (PICTET) – MUIR-WOOD: H802, fig. 679, 3a-c  
 1966 *Pygope catulloi* (PICTET) – VOGEL: 441, plate 38, fig. 1; pl. 39, fig. 3  
 1969 *Antinomia* cf. *catulloi* (PICTET) – BACHMAYER & KOLLMANN: 82, fig. 95  
 1999 *Pygope catulloi* (PICTET) – SULSER: 158

Material: Seven compressed, damaged, imperfectly preserved specimens: NHMW 2001z0161/0001 - 0007. Two specimens are not damaged at all. All specimens are stored at the Museum of Natural History (NHMW, Vienna, Austria).

Locality: All specimens are from KB1 (SSE Trattenbach).

Description: NHMW 2001z0161/0001 (pl. 1, fig. 1): The smooth, medium-sized, biconvex shell with a median perforation is well preserved. The shell is rounded-triangular in outline. A small, more posteriorly positioned median perforation is visible on the ventral and dorsal valve. The lateral flanks of the shell are flattened. The lateral commissure shows a sigmoidal curvature on the subtriangular-biconvex shell, whereas the anterior commissure is straight. The tube lining is slightly curved upwards from the dorsal to the ventral valve. Growth lines are visible on the anterior side of the ventral valve. In some regions of the internal moulds, slight mantle canal markings are visible. The relatively large (up to 3 mm) pedicle hole is situated at the end of the ventral valve. Further ornamentation features cannot be observed on the internal moulds. Most of the specimens show at least fragmentary preservation of the originally calcitic, relatively thick shell (1.5 mm).

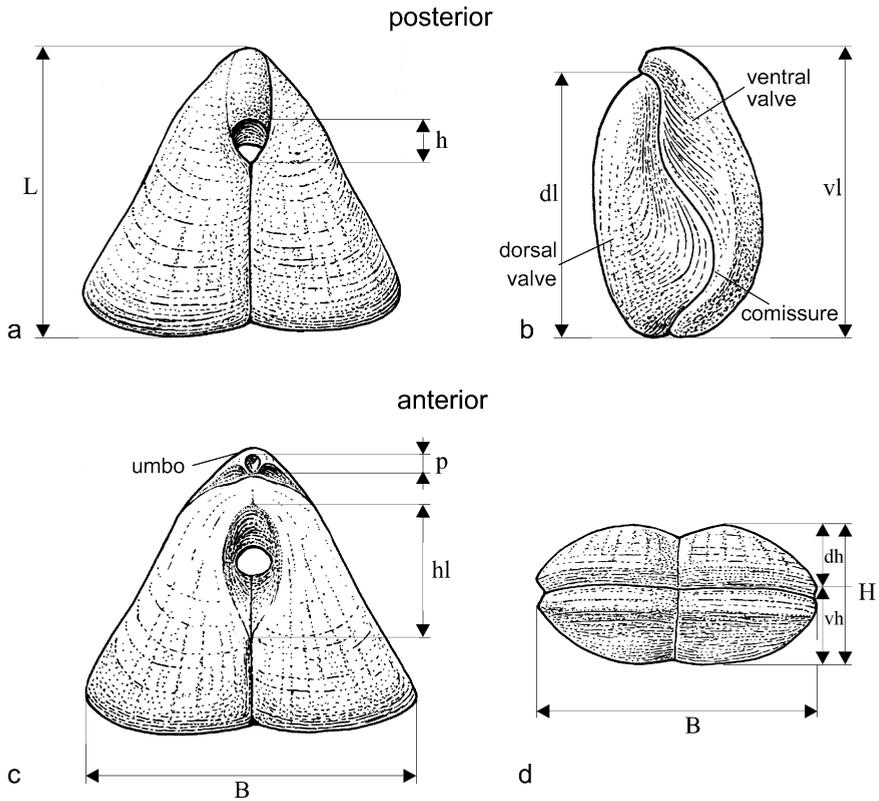


Fig. 3: Dimensions and views of pygopids studied. (a) ventral view, (b) lateral view, (c) dorsal view and (d) anterior view.

**Remarks:** *Pygope catulloi* (PICHET) is clearly distinguished from *Pygope janitor* (PICHET) or *Pygope diphyoides* (d'ORBIGNY) by having flattened lateral edges and a sigmoidal lateral commissure as well as by a more posteriorly orientated and smaller perforation. The Tithonian to Berriasian *Pygope diphya* (BUCH) has curved lateral edges and a lateral commissure, which is almost straight like in most of the other species.

**Measurements:** See table 1 and text-figure 3.

Table. 1. Dimensions of the brachiopods studied (in mm).

	L	vl	dl	H	vh	dh	B	p	hl	h
NHMW 2001z0161/0001	47	47	42	24	14	10	39	2.5	11.5	3
NHMW 2001z0161/0002	49	49	43.5	25.5	15.5	10	58	3	11.05	4.5
NHMW 2001z0161/0003	39	---	39	8.5	---	---	41	---	10	---
NHMW 2001z0161/0004	42	42	40	18	---	---	36	2	8	---
NHMW 2001z0161/0005	39	39	35	24	---	---	32	2	7	2.5
NHMW 2001z0161/0006	37	37	31	22	---	---	---	2	5.5	2
NHMW 2001z0161/0007	36	36	34	22	---	---	32	---	6	---

**O c c u r r e n c e :** *Pygope catulloi* (PICTET) is known from Upper Jurassic (Tithonian) to Lower Cretaceous (Valanginian) sediments of Switzerland, Italy, Hungary, Bulgaria, Poland, Romania and Austria. It experiences its acme during the Lower Tithonian to Lower Berriasian. Many of the Austrian specimens determined as *Pygope diphya* actually belong to *Pygope catulloi*.

**S t r a t i g r a p h y :** The pygopid-bearing section at Trattenbach (KB1) yields the stratigraphically important calpionellid taxa *Tintinopsella* and *Calpionellites*. Due to the occurrence of *Calpionellites darderi* (COLOM), *Calpionellites major* (COLOM), *Tintinopsella longa* (COLOM) and *Tintinopsella carpathica* (MURGEANU & FILIPESCU), the *Pygope*-bearing beds, and with them this part of the Steinmühl Formation, belong to the Calpionellites Zone (Major Subzone) of the uppermost Lower Valanginian (REHÁKOVÁ 2000a, 2000b). This is equivalent with the *Campylotoxus ammonite* Zone (HOEDEMAEKER & RAWSON 2000).

### Preservation Patterns

Calcitic shell structures, such as those in brachiopods, have a better potential for preservation of their original structural pattern and crystal orientation than aragonitic shells have (BANDEL 1990). Shape, structure and composition of fossils are intrinsic variables that relate to the chemical and compactional changes in sediments. To some degree the chronological sequence and interrelationship of diagenetic and tectonic processes can be reconstructed from preservational features.

The case presented in this paper chiefly reflects the varying interplay of shell-filling mechanisms and shell deformation by compaction. Due to hydrodynamic processes (bottom currents), *Pygope catulloi* is found at the investigated section with the ventral (pedicle valve) in contact with the sea-floor. This position contrasts with the living position, where the ventral valve is up. The filling process of closed double-winged shells proceeds through the pedicle hole and geopedal structures, which show grading (fining upward) of the sediment, is visible in most of the investigated specimens (see also NHMW 2001z0161/0007; pl. 2 fig.3).

### Palaeogeography

SANDY (1988) and KÁZMÉR (1993) studied the palaeogeographic distribution patterns of four perforated species of Upper Jurassic-Lower Cretaceous Pygopidae in the Alpine-Carpathian-Balkan region. They suggested that *Pygope catulloi* and *Pygope diphya*, which bear small perforations near their umbos, lived on the southern "margin" (Mediterranean microcontinent: Trento Plateau, Northern Calcareous Alps, Bakony) of the Penninic Ocean. On the other hand, *Pygope janitor* and *Pygites diphyoides*, which bear large, central perforations, inhabited the northern margin (Vocontian Trough, Helvetic Zone) (text-fig. 4). KÁZMÉR suggested that the separation of these two pygopid groups was caused either by a wide Penninic Ocean acting as a barrier or by the adaptation of the forms with smaller perforations to the nutrient-poor environment of the southern margin.

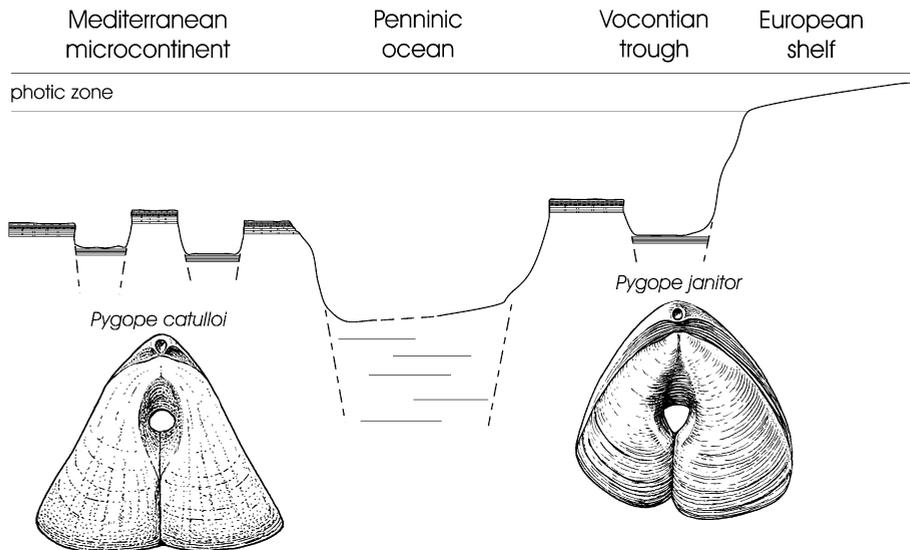


Fig. 4: Hypothetical SE-NW cross-section from the northern to the southern margin of the Tethys (not to scale) with respect to the different occurrences of different pygopid groups. See text for explanation (modified after KÁZMÉR 1993).

### Palaeohabitat

Members of the Pygopidae were well adapted to deep marine conditions where moderate current activity supplied little food to benthic organisms (VOGEL 1966). Some localities, however, yield a pygopid fauna together with shallow marine fossils (e.g. Stramberk, Polen) (KÁZMÉR 1993). Here, the latter fossils were probably redeposited into the deeper marine environment favoured by the pygopids. In more energetic sediments like the crinoidal limestone of the Mühlberg Formation (Northern Calcareous Alps) the specimens are usually disarticulated (author's observations).

AGER (1971) suggested that agitation of the water or the absence of such agitation (shown by the type of sediment) may have been a more important factor in the distribution of Pygopidae than depth. The *catulloi-diphya* pair developed the umbonal perforation at a young stage, which provided a possibility to inhabit environments characterized by harsh conditions (e.g. great depth, little food) and uninhabitable for other species (KÁZMÉR 1993).

Pygopids of the Pienniny Klippen Belt (northern Penninic margin of Polen) are interpreted as opportunistic (*r*-selected) organisms of eurybathic preference whose fossil distribution depends on bathymetrically controlled facies changes (KROBICKI 1993). From the Jaworki-Zaskalskie section (Pienniny Klippen Belt, see KROBICKI 1993) the same lithology change is reported as observed in the KBI section. Red nodular limestones of the Czorsztyn Formation (Kimmeridgian – Tithonian Ammonitico Rosso type) are overlain by greenish and white micritic limestone of the Dursztyn Formation (Berriasian to Valanginian). A common feature of red limestones of this facies was a low or very low

deposition rate. Such conditions prevail over submarine ridges where bottom currents hinder rapid accumulation of pelagic sediments. Abundant occurrences in a monospecific layer are probably the result of the disintegration of local pygopid colonies that had accumulated in patches as more or less monospecific clusters. This is a well known type of distribution in ancient and recent communities (KROBICKI 1993). The abundance, density and diversity of various brachiopod taxa allow an interpretation of their population strategies. The r-selected taxa include organisms which are not restricted to a particular facies and may occupy a wide spectrum of habitats with different environmental conditions.

Extremely opportunistic (r-selected) species (e.g. *Pygope catulloi*) could inhabit all basinal facies. Mass occurrences of pygopids over the intra-oceanic Czorsztyn Ridge, and on its southern slope, were delimited from the north and the south by deep-water troughs in which pelagic limestones of Maiolica facies formed (KROBICKI 1993).

### Sea Level Record

The main goal of this paper is to show the usefulness of pygopid distribution as well as of microfacies (microfossils, lithological changes) as a tool for a more detailed biostratigraphy of carbonate pelagic sequences and for the interpretation of palaeoenvironmental conditions. The thin sections and microfossil material from the KB1 sequence demonstrate that the different lithologies observed around the *Pygope*-bed are consequences of changes of the palaeoceanography and therefore reflect sea-level fluctuations during the Lower Cretaceous, especially within the Berriasian and Valanginian stages (LUKENEDER 2001).

REHÁKOVÁ (2000a) showed that stages of sea-level rises were favourable for dinocyst development. All environmental acme concentrations of cyst taxa were controlled by a sea-level highstand phase. On the other hand, cyst diversity reduction events coincided with sea-level falls. Dinoflagellates were a significant element of the marine phytoplankton during the Jurassic and Cretaceous, when they occurred worldwide in open shelf, slope and basinal environments. Due to favourable conditions for the development of planktonic associations, a rich and structured ecosystem arose in the photic zone of the Tethyan Realm during this time. Apparently not only calpionellids but also calcareous dinoflagellates belonged to the planktonic elements that sensitively recorded a whole complex of environmental changes such as climatic perturbations, nutrient distribution and sea-level fluctuations (REHÁKOVÁ 2000a). As reported by REHÁKOVÁ (2000b) several compositional changes in dinoflagellate and calpionellid assemblages (bioevents) correlate with eustatic sea-level fluctuations in the West-Carpathian (Upper Jurassic-Lower Cretaceous). She described a distinct breccia accumulation, known as the Nozdovice Breccia (Nozdovice Event) at the end of the *Calpionellites* Zone during the Lower Valanginian, characterized by a significant third-order rapid fall in sea-level; this is manifested by changes in the lithology and microfossil content in and around the *Pygope*-bed.

A new, stronger, siliclastic input is represented by the Oravice Event (upper Lower Valanginian), which coincided with a rapid third-order sea-level fall. This abrupt change in environmental conditions totally decimated the calpionellids almost throughout the Tethyan region ("calpionellid crisis") (REHÁKOVÁ 2000b).

Both sea-level falls, manifested in the Nozdovice and Oravice Events lasting almost the whole Lower Valanginian, are dramatically evident in the KB1 section. The phase of drastic sea-level falls is represented by the Maiolica-like, light grey biomicritic wackestones of the topmost Steinmühl Formation with an abundance of *Pygope catulloi*.

### Palaeoenvironment

The macrofauna of the *Pygope*-bed is dominated by sculpture-moulds of brachiopods, rare ammonites and belemnites (with *Acrothoracica* burrows). The first impression of a rather low-diversity benthic fauna changes radically upon examination of the microfauna. The *Pygope*-bed-sample yielded an unexpectedly well-preserved, condensed and rich microfauna consisting of numerous elements of ophiurids, echinids and crinoids. Furthermore, a large number of ostracods contributes to the autochthonous fauna, while radiolarians and planktonic foraminifera suggest open marine conditions. Partly eroded ammonites with encrusting crinoids on their outer shell surface indicate quiet depositional conditions and low sedimentation rate. They allowed epifauna to settle on primary hardgrounds (text-fig. 5).

Changes of brachiopod spectra thus reflect a complex of changes: (i) changes in pelagic (off-shore) influence; (ii) sedimentological changes relating to the prograding development of fan systems; (iii) eustatic changes in sea level. This change in the brachiopod spectrum shows a development from a deepwater-swell facies, represented by the red limestones of the Steinmühl Formation, to a more deeper-water basin facies reflected by the Schrambach Formation.

The abundant brachiopod *Pygope catulloi* (*Pygope*-bed) reflects a phase of drastic sea-level falls, represented by the Maiolica-like light grey biomicritic wackestones of the topmost Steinmühl Formation, just below the Schrambach Formation. Hydrodynamics or its absence (reflected in the type of the sediment) may have been a more important factor in Pygopidae distribution than sea depth (KÁZMÉR 1993). The *catulloi-diphyia* group (small perforation near the umbos) developed the umbonal perforation at a young stage, which provided an opportunity to inhabit deeper-water environments and facies.

Thus, the occurrence of abundant pygopids and the additional analysis of the micro- and macrofauna support the interpretation of a firm- to hardground palaeoenvironment with an ophiurid-dominated benthic fauna in the upper bathyal or deep sublittoral. Based on the suggested palaeogeographic position of the studied section, any influence of turbiditic redeposition and allochthonous origin of the fauna is definitely excluded.

### Results

- 1) *Pygope catulloi* (PICTET, 1867) is documented for the first time from the Northern Calcareous Alps (precise description and photographs).
- 2) Most specimens of *Pygope diphyia* previously described (from the Northern Calcareous Alps) are actually *Pygope catulloi*.
- 3) A shell accumulation of *Pygope catulloi* (PICTET, 1867) is documented for the first time from the Lower Valanginian of the Losenstein Syncline in Upper Austria.

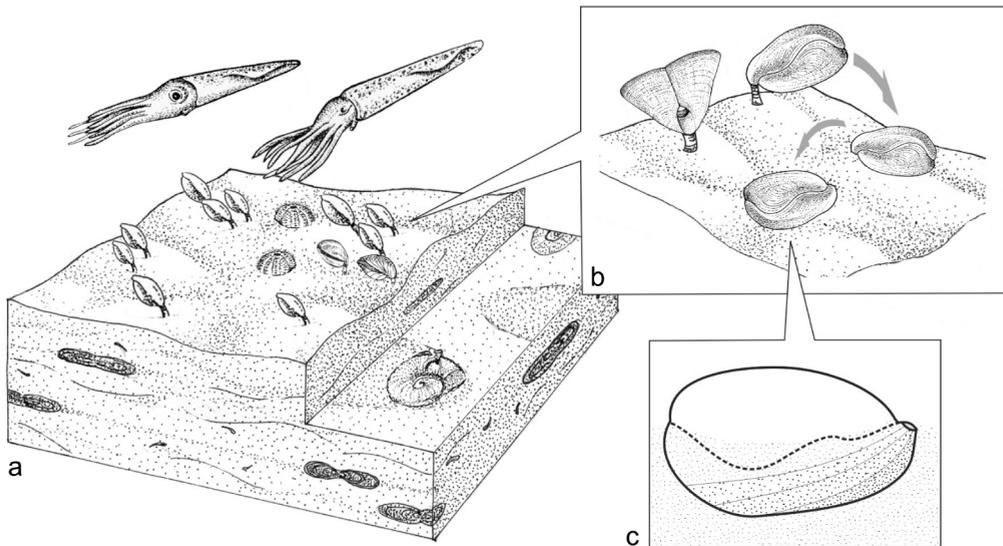


Fig. 5: Sketch showing the preservational history of brachiopod shells in the *Pygope*-bearing beds.

(a) Hypothetical palaeoassociation of the pygopid-bearing layer. Firmground-swell of the deep sublittoral or upper bathyal, settled by clusters of *Pygope catulloi* and regular echinids. Low sedimentation rate allows the encrustation of ammonite shells by crinoids, polychaetes and foraminifera.

(b) After death the articulated valves of *Pygope catulloi* are usually turned in a stable position (bottom currents), with the dorsal valve up; this enabled the gravitational sediment infilling through the foramen (c) (NHMW 2001z0161/0007, pl. 2. fig. 3).

- 4) Six sculpture moulds between 49 and 36 mm in length and 58 to 32 mm in breadth were investigated; 28 further specimens were observed in the field.
- 5) The pygopid shells were deposited during sea-level falls in the Lower Valanginian, which is correlated with the Carpathian Nodrovice- and Oravice-Events during the Lower Valanginian.
- 6) The investigated pygopid assemblage most probably lived on a submarine ridge where bottom currents hindered rapid accumulation of pelagic sediments and where the sedimentation rate was very low.
- 7) Due to hydrodynamic conditions (bottom currents), *Pygope catulloi* is found at the investigated section with the ventral (pedicle valve) in contact with the sea-floor. This position is in contrast to the living position, where the ventral valve is up.
- 8) The shell-filling process of closed double-winged shells proceeds through the pedicle-foramen (also see text-fig. 5 and pl. 2, fig. 3).
- 9) The *Pygope catulloi* occurrence described herein fits well into the hypothesis that the *Pygope catulloi*-*Pygope diphya* pair lived on the southern "margin" of the Penninic Ocean during the Upper Jurassic and Lower Cretaceous.

- 10) The *Pygope* accumulation, partly eroded ammonites with crinoidal epifaunas, belemnites with *Acrothoracica* burrows, as well as the perhaps small biostratigraphical gap in the calpionellid subzonation between the Steinmühl- and the Schrambach Formations show a sedimentation stop (omission) during the pygopid accumulation. This favoured the building of a firm- to hardground, which allowed the pygopids and other epifaunal elements to settle on the sea- floor.
- 11) The associated calpionellid fauna indicates an Early Valanginian (Calpionellites Zone; Major Subzone) age of the *Pygopid catulloi*-bearing bed.

### Acknowledgements

Thanks are due to the Austrian Science Fund (FWF) for financial support (project P13641-Geo.). My sincere thanks are extended to Dr. Herbert SUMMESBERGER (Vienna), Prof. Dr. Leopold KRYSZYN (Vienna) and Dr. Mathias HARZHAUSER (Vienna) for their valuable and constructive comments. Dr. Miklós KÁZMÉR (Budapest), Dr. Ortwin SCHULTZ (Vienna) and Dr. Heinz A. KOLLMANN (Vienna) are gratefully acknowledged for their careful reviewing of the paper. Sincere thanks also goes to Dr. Daniela REHÁKOVÁ (Bratislava) and Dr. Daniela BOOROVA (Bratislava) for determinations of thin sections. Dr. Mathias HARZHAUSER kindly helped me with some of the drawings, and the photographs were done by Alice SCHUMACHER (Vienna).

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### Plate 1

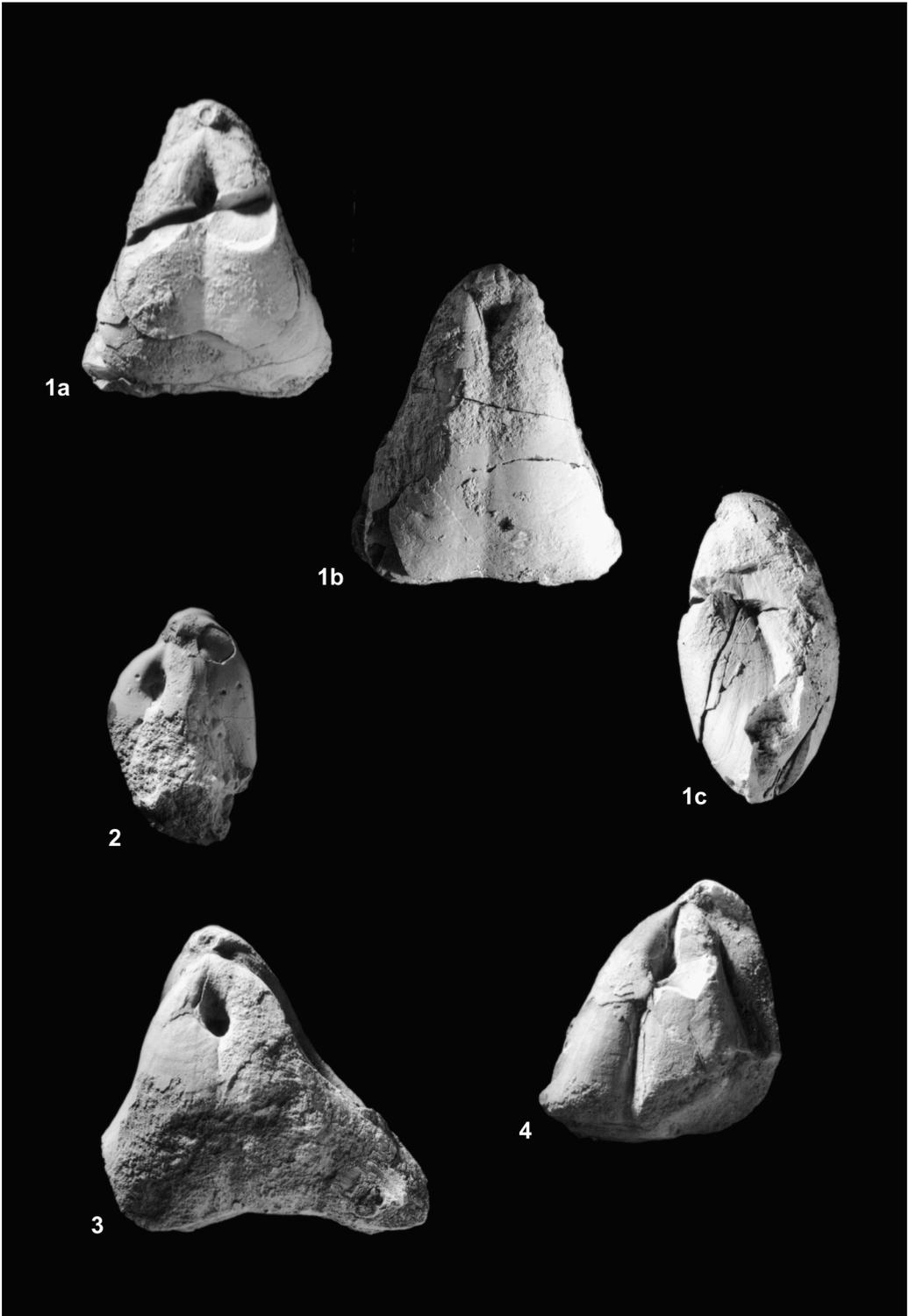
**Fig. 1:** Typical *Pygope catulloi* (Pictet, 1867). –  
(a) dorsal view, (b) ventral view, (c) lateral view  
NHMW 2001z0161/0001, x 1.

**Fig. 2:** Compressed specimen of *Pygope catulloi* (Pictet, 1867). – dorsal view  
NHMW 2001z0161/0006, x 1.

**Fig. 3:** Flattened and deformed specimen of *Pygope catulloi* (Pictet, 1867). – dorsal view  
NHMW 2001z0161/0002, x 1.

**Fig. 4:** *Pygope catulloi* (Pictet, 1867) valves displaced against each other. – dorsal view  
NHMW 2001z0161/0004, x 1.

All specimens were collected at KB1, which is situated SSE of Trattenbach,  
7 km W of Losenstein, Upper Austria.



## Plate 2

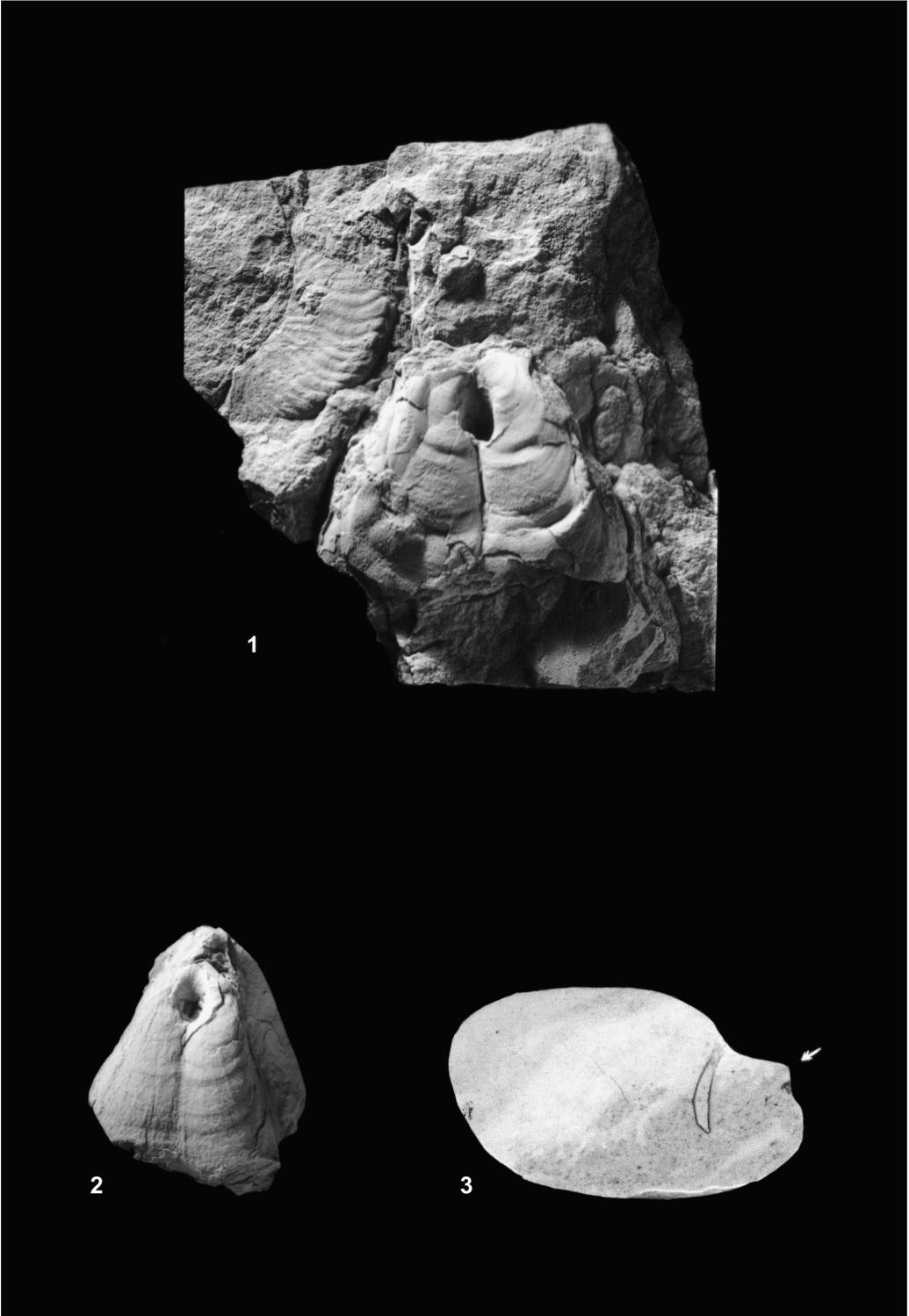
**Fig. 1:** Typical *Pygope catulloi* (Pictet, 1867). –  
(a) dorsal view, (b) ventral view, (c) lateral view  
NHMW 2001z0161/0001, x 1.

**Fig. 1:** Extremely flattened and deformed specimen of *Pygope catulloi* (Pictet, 1867)  
in association with the ammonite *Neocomites* sp. – dorsal view  
NHMW 2001z0161/0003, x 1.

**Fig. 2:** Detailed structure of an internal mould of *Pygope catulloi* (Pictet, 1867). –  
dorsal view  
NHMW 2001z0161/0005, x 1.

**Fig. 3:** Filling structures in a cross-section of *Pygope catulloi* (Pictet, 1867). –  
cut through perforations and polished specimen (with tube lining perforation;  
black tube), position of the pedicle hole marked with white arrow, note fining  
upward of the filling sediment  
NHMW 2001z0161/0007, x 2.

All specimens were collected at KB1, which is situated SSE of Trattenbach,  
7 km W of Losenstein, Upper Austria.



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Jahr/Year: 2002

Band/Volume: [103A](#)

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Artikel/Article: [Shell accumulation of the brachiopod \*Pygope catulloi\* Pictet, 1867 \(Lower Valanginian; Northern Calcareous Alps, Upper Austria\): Palaeoecological implications 143-159](#)