

On the oldest Jurassic ammonites of Europe (Northern Calcareous Alps, Austria) and their global significance

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With 16 figures and 2 tables

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Abstract: The earliest ammonite species of Jurassic type, *Psiloceras spelae* GÜEX, was unknown till 1998. This species bridges the long gap between the latest Triassic and the earliest Jurassic ammonoids. It was discovered in North America, then in South America and finally in Europe. The species is proposed as boundary marker for the base of the Jurassic system. It is known in two forms which are regarded as subspecies. The European subspecies is here introduced as *P. spelae tirolicum* n. ssp. This taxon occurs in the Northern Calcareous Alps of Tyrol as the oldest European Jurassic type ammonite. Both subspecies characterize the first Jurassic ammonite biohorizon and are closely related. Their slight differences may be due to biogeographic separation. The preservation admits a complete diagnosis of the new subspecies. Besides psiloceratid characters still phylloceratid characters are present indicating the origin of the psiloceratids.

Additionally, slightly younger psiloceratids are described which were known only from South and North America thus far. They are older than the oldest psiloceratids hitherto known from Europe. All these forms are elements of the first biochronological ammonite unit of the Jurassic, the Tilmanni Chronozone which is situated below the Planorbis Chronozone. It is assumed that during the end-Triassic biotic crisis only those ammonites survived which lived in the open parts of the oceans. A re-population of neritic shelf areas took place from the oceanic realms in line with the gradual Hettangian transgression. This may explain the global similarity of the first Jurassic ammonites and their later biogeographic diversification. A time calculation based on the sedimentation rate of the *P. spelae tirolicum* n. ssp. bearing sections leads to the conclusion that the earlier Triassic-Jurassic ammonite gap of about 250 to 300 ka now can be reduced to approximately 100 ka.

Key words: Ammonitina, *Psiloceras*, Jurassic, Early Hettangian, evolution, palaeobiogeography, biostratigraphy, Northern Calcareous Alps, Karwendel Syncline, Tyrol, Austria.

1. Introduction

The Northern Calcareous Alps of Austria are known since more than 100 years as a major host of Tethyan (i.e. tropical) Hettangian ammonites (e.g. WÄHNER 1882-1898; LANGE 1952; BLIND 1963; KMENT 2000) occurring there in sequence with their presumed

Triassic precursors (MOJSISOVICS 1893; WIEDMANN 1970). The latter are missing in North-western Europe and are reported globally from a few places only (Tibet: YIN et al. 2006; North America: TOZER 1979, 1994; South America: PRINZ 1985; HILLEBRANDT 1994). Until recently the *Psiloceras planorbis* group was held unanimously as representative of the oldest

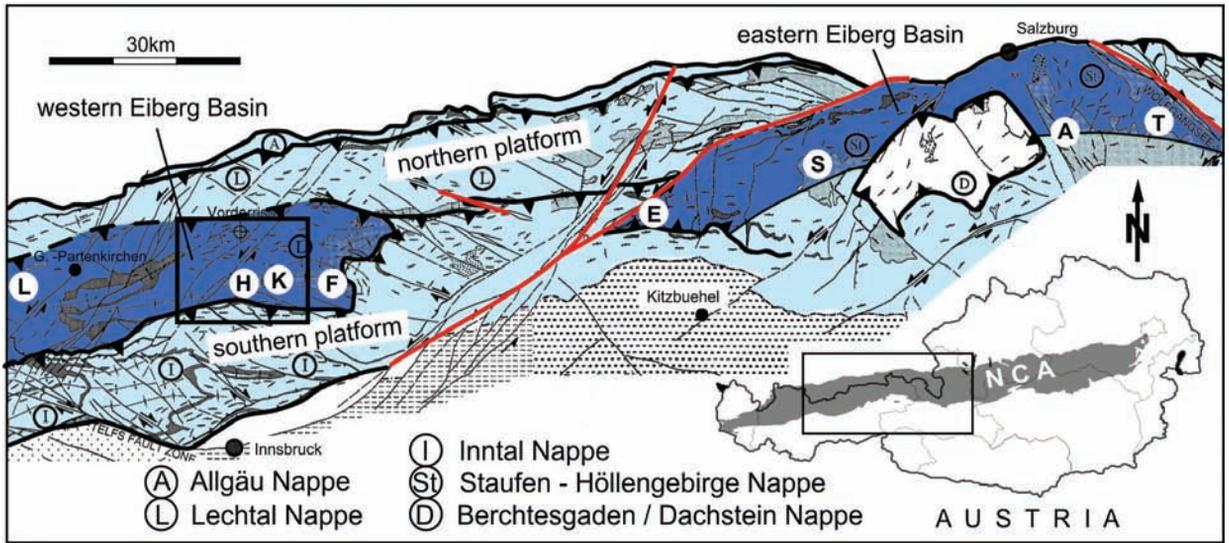


Fig. 1. Present day palaeogeography of the Eiberg Basin within the western NCA on a tectonic base map of LINZER et al. 1995 (T: Tiefengraben and Kendlbachgraben, A: Adnet, S: Steinplatte, E: Eiberg, F: Fonsjoch, K: Kuhjoch, H: Hochaplgraben, L: Lahnenwiesgraben) (box indicate Fig. 2).

Jurassic ammonites in Western Europe (PAGE 2003; BLOOS 2004) and therefore used to define the base of the Jurassic System (WARRINGTON et al. 2008). New investigations in North America (GUEX 1980, 1995; GUEX et al. 1998), however, demonstrate that morphologically different *psiloceratids* appear distinctly earlier than *P. planorbis* and may be missed in the epicontinental sea of North-western Europe due to unfavourable (very shallow marine) environment. *Psiloceras spelae*, described by GUEX et al. (1998) from Nevada, is the oldest representative of these American forms. Here we present a closely related new subspecies of *P. spelae* found in the NCA some metres above the last Triassic *Choristoceras marshi* and 18 m below *Psiloceras calliphyllum*, till now regarded as the oldest Alpine Jurassic species of *Psiloceras* (BLOOS 2004) and as a gross stratigraphical equivalent of *P. planorbis*. In the search for a new internationally agreed definition of the base of the Hettangian stage, the responsible working group and ISJS have recently decided to use the FO of *P. spelae* as the defining marker. Occurrence of *P. spelae* in the Alps (and thus in the Tethys) indicates the global presence of the proposed marker. The new subspecies is further useful for an improved biochronologic subdivision of the Triassic-Jurassic transitional interval

as well as for a more exact time indication of the end-Triassic mass extinction.

2. Geological and stratigraphic setting

The worldwide end-Triassic sea-level fall coinciding with a biotic crisis in most fossil groups (HALLAM & WIGNALL 1997) has an amplitude of at least 100 m in the Northern Calcareous Alps as measured along the palaeoslope of the Steinplatte platform in the Eiberg Basin (KRISTYN et al. 2005). The regression was fast and culminated near the end of the Late Rhaetian, it was followed by a slow long-term sea-level rise that started in the latest Rhaetian, continued through the Hettangian, and exceeded the Rhaetian highstand relatively late in the Late Sinemurian (KRISTYN et al. 2005). Caused by the sea-level fall, the Triassic carbonate platforms emerged. For this reason, a hiatus exists between Triassic and Jurassic sediments in most shallow-water sections of the NCA, and ammonites are rare in the Triassic-Jurassic boundary interval of the adjacent basins.

There are three basins extended east – west and separated by carbonate platforms in the NCA around the Triassic-Jurassic boundary: Allgäu Basin in the north, Eiberg Basin in the middle and Hallstatt/



Fig. 2. Triassic – Jurassic boundary sections in the western Karwendel Syncline (boxes indicate locality maps in Figs. 3-4).

Zlambach Basin in the south. The Allgäu Basin is floored by Rhaetian shallow water limestones attributed to the Restental Member of the Koessen Formation (GOLEBIOWSKI 1990) and starts subsiding to deeper neritic conditions already in the earliest Jurassic. The neighbouring Eiberg Basin (Fig. 1) was a large intraplateform trough in the Rhaetian, which can be traced over 200 km from the Salzkammergut (Austria) in the east to the Lahnenwiesgraben valley (NW Garmisch-Partenkirchen, Bavaria, Germany) in the west. The Hallstatt/Zlambach Basin followed south of the wide Dachstein lagoon connecting the NCA with the Tethys Ocean.

At present continuous Triassic-Jurassic sections are known from the Allgäu and Eiberg but not from the Hallstatt/Zlambach Basin. Rhaetian sediments are strongly faulted and folded in the Zlambach area near Bad Goisern (Salzkammergut, Austria) and are gene-

rally too soft to keep open good exposures. Clayey marls with foraminifers and ostracodes of latest Rhaetian and earliest Hettangian age (? *spelae* horizon) are locally present (HILLEBRANDT & URLICHS 2008) but have not yet yielded determinable ammonites (only a single protoconch). Despite middle to Late Hettangian limestone sequences are continuously exposed, the long-known *P. calliphylum* bearing Early Hettangian (NEUMAYR 1879; RAKUS 1999) occurs only in erratic drift blocks. The *P. spelae tirolicum* n. ssp. level was also not yet found in the Allgäu Basin, which may have been more restricted and/or too shallow in that time interval.

Sedimentation across the Triassic-Jurassic boundary was continuous in the deeper parts of the basins. But in the Allgäu and Eiberg basins an abrupt lithological change from carbonates to marls and clayey sediments indicates a dramatic sedimentary turnover.

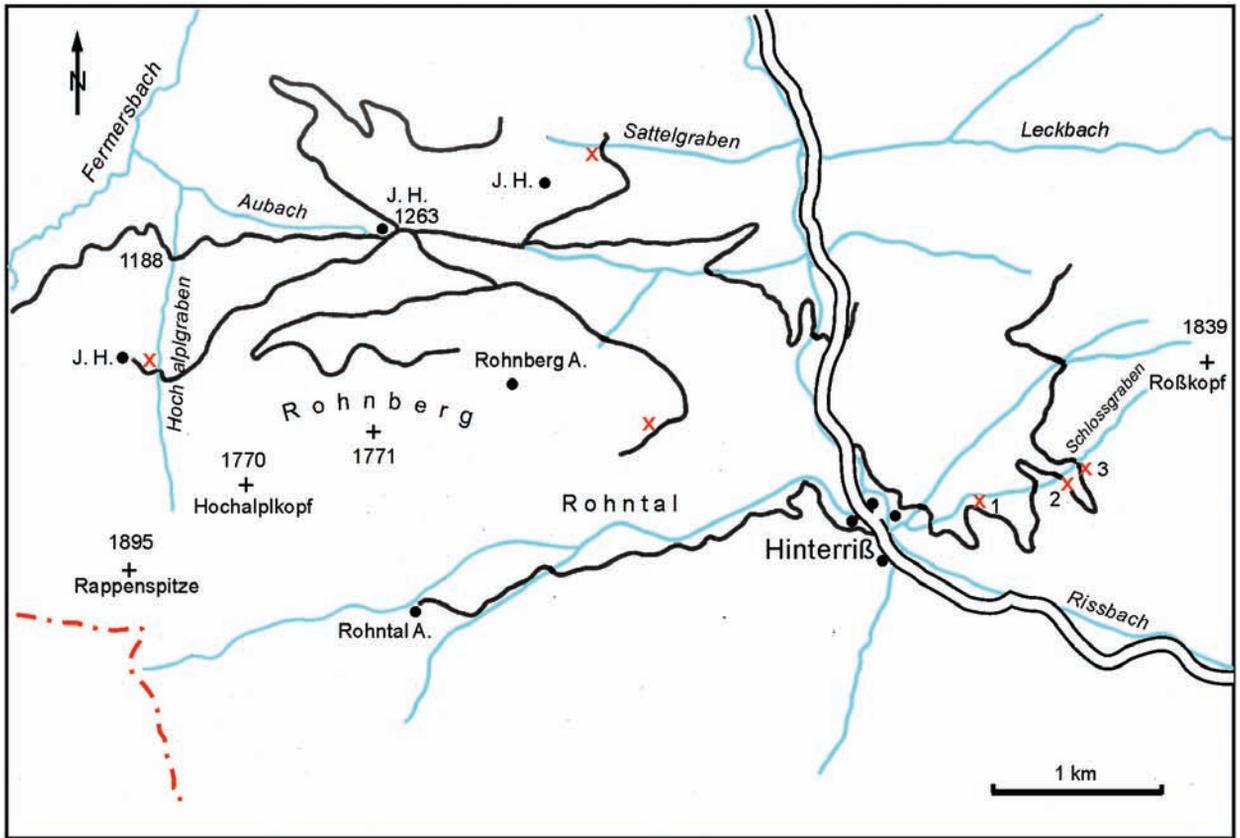


Fig. 3. Map with location of Hochalplgraben and Schlossgraben sections. Red crosses mark localities. For details see text.

In the Eiberg Basin the boundary between the Eiberg and Tiefengraben Mbs. is marked by a platy, black, bituminous layer on top of the uppermost Triassic limestone bed T (HILLEBRANDT et al. 2007, fig. 23a, b). This layer indicates 1) an anoxic event and 2) the peak of the end-Triassic regression (= Top-Koessen event). The lowermost marls of the Tiefengraben Mb. are grey to yellowish (thickness < 50 cm), Grenzmergel s. str., and are followed by the 2-3 m thick Schattwald Beds which are mostly of dark red colour and sometimes laminated. Their type locality is in the Allgäu Mountains (Tannheim valley, Tyrol) in the west and they can be traced at least over 300 km to the Restental (Enns valley, Upper Austria) in the east. The marls are more or less clayey, of low but variable thickness and have been described as poor in macrofossils (TOLLMANN 1976) which has led to speculations about abnormal salinity conditions (BRANDNER 1984: 446). Nevertheless, foraminifera, ostracodes and a newly collected rhynchonellid brachiopod from the red marls as well as pectinid bivalves in the

greyish marl intercalations demonstrate normal marine conditions for most of the Schattwald Beds at least in the Eiberg Basin. The overlying grey and more or less clayey marls of the lower Tiefengraben Mb. contain *P. spelaie tirolicum* n. ssp. as described below. The middle Tiefengraben Mb. is distinguished by silty to arenitic interlayers and the upper one by onset of shelly-rich limestone interbeds.

P. spelaie tirolicum n. ssp. was discovered in the western part of the Karwendel Syncline, a local east-west extended structure, approximately 30 km long, within the Lechtal Nappe of the NCA that belongs to the western part of the Eiberg Basin (Figs. 1-2). Between Mittenwald and Hinterriß its southern limb offers several localities where the *tirolicum* level is exposed, i.e. the Hochalplgraben, Schlossgraben and Kuhjoch sections (Figs. 3-4). The level is located above the Eiberg Mb. (Rhaetian) and below the Lower Jurassic Breitenberg Mb. ("Liasbasiskalk" of ULRICH 1960). Between these two members occur up to 20 m of marly sediments which were formerly called the

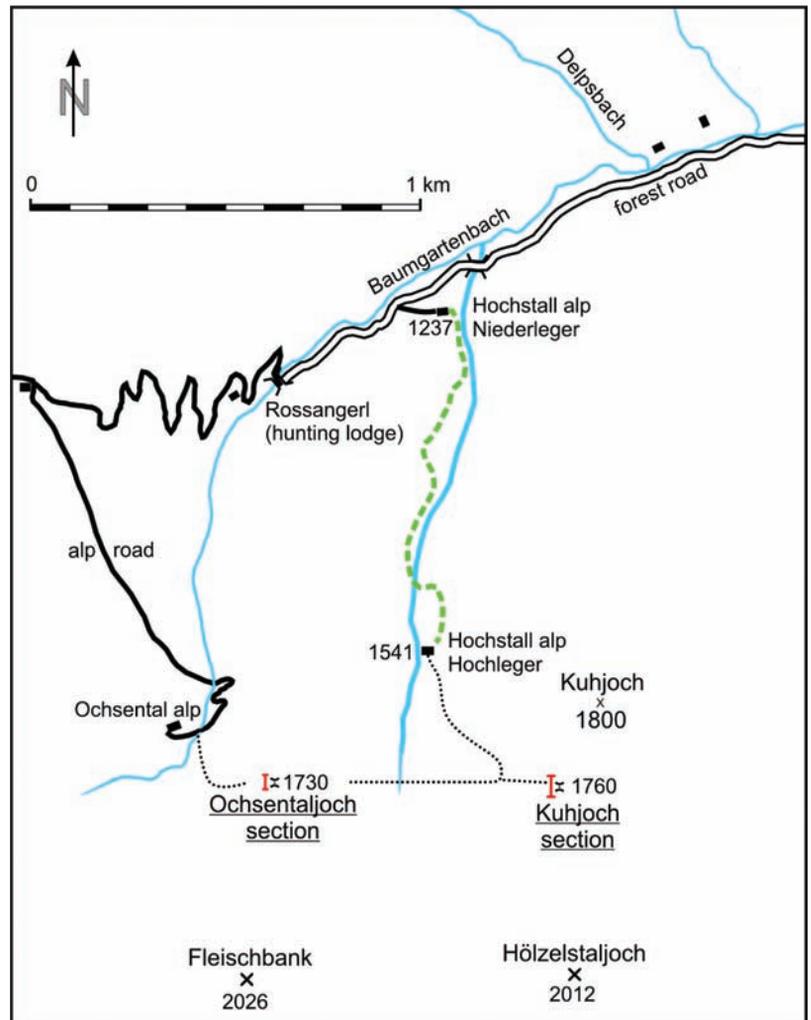


Fig. 4. Map showing the locations of the Kuhjoch and Ochsentaljoch sections.

“Rhätische Grenzmergel” by FABRICIUS (1960, 1966), the present Tiefengraben Member.

In the last decades in the NCA the T-J boundary was located at lithological breaks, sometimes between the Kössen and Kendlbach fms. but more often at the base of the Calliphyllum Bed (discussion in KUERSCHNER et al. 2007). Now for the T-J boundary a level with *P. spelae* within the basal Tiefengraben Mb. (lower Kendlbach Fm.), a few metres above the Schattwald Beds has been selected in the Eiberg Basin. The Kuhjoch section was proposed as candidate GSSP for the base of the Jurassic by HILLEBRANDT et al. (2007) where *P. spelae* occurs in the lower part of the Tiefengraben Mb., approx. 18 m below the Calliphyllum Bed. Hence it is possible to recognise a sequence from the Late Rhaetian at the

base, containing the last *Choristoceras* (and conodonts), a latest Rhaetian without ammonites (5.8 m thick in the proposed candidate GSSP) and an intermediate earliest Hettangian (approx. 17-18 m thick) overlain by the Calliphyllum Bed of late Early Hettangian age. The presence of Triassic inorganic- and organic-walled microfossils in the lower metres of the Tiefengraben Mb. – including also the reddish Schattwald Beds – until close to the FO of *P. spelae tirolicum* n. ssp. supports the proposed boundary position (HILLEBRANDT & URLICHS 2008). Between *P. spelae tirolicum* n. ssp. and the *Psiloceras calliphyllum* Bed three levels contain ammonites (*Psiloceras*) unknown previously from Europe but suggesting a correlation with North and South America.

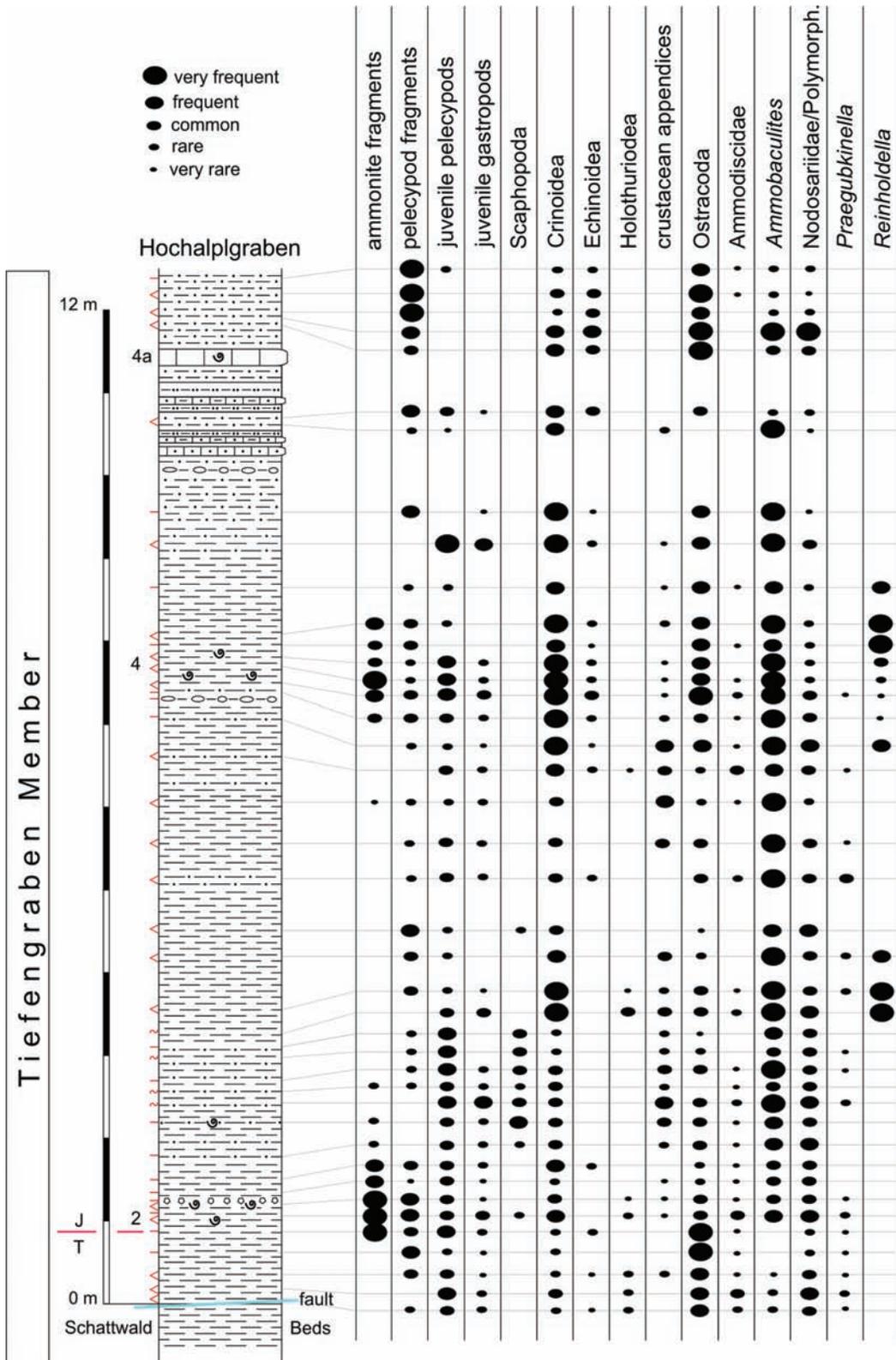


Fig. 5. Hochalplgraben section with distribution of shell fragments of ammonites, bivalves, and microfossils. Level 2: beds with *Psiloceras spelae tirolicum* n. ssp.; level 4: beds with *Psiloceras* cf. *pacificum*; level 4a: limestone bed with *Psiloceras* sp. A. Layer with pentagons = crinoid bed.

3. Descriptions of sections

All described earliest Hettangian ammonites from different sections and levels of the Tiefengraben Mb. have been recorded from the southern flank of the western Karwendel Syncline. A section on the northern flank (close to Tölzer Hütte) potentially may also be fossiliferous in ammonites but has not yet been sufficiently investigated. The horizon with *Praegubkinella turgescens* (an aragonitic foraminifera typical for the beds with *P. spelae tirolicum*) was also found at this site. The sections are introduced from west to east.

3.1. Hochalplgraben

This section is located west of Hinterriß (Gauß-Krüger coordinates $x = 4455.64$, $y = 5260.45 = 47^{\circ}29'02''\text{N}/11^{\circ}31'50''\text{E}$) (Figs. 3-5): The steeply dipping beds of the section are exposed between a waterfall in red Lower Jurassic cherty limestones and ca. 15 m in vertical distance below a forest road that crosses the mountain torrent in 1325 m altitude. It is the place where the bed with *Psiloceras spelae tirolicum* n. ssp. was first discovered by one of us (L.K.). Originally the outcrop on the western bank of the torrent was extended from the last Koessen limestones to the lower clayey marls of the Tiefengraben Mb. It was destroyed in 2005 by a landslide. But a new exposure presenting the *tirolicum* level could be opened by digging. The top of the Schattwald Beds is strongly affected by tectonics at this site. There a fault separates the Schattwald Beds from the overlying greyish, clayey marls of the Tiefengraben Mb. s. str. According to palynological data (BONIS et al., submitted) only a minor part of the Tiefengraben Member is missing by the fault. A tectonically less reduced succession of the basal Tiefengraben Mb. is exposed nearby at a forest road east of the Rohnberg (a mountain 3 km east of Hochalplgraben). The Hochalplgraben section was later enlarged up to the first limestone bed of the upper Tiefengraben Mb., but the transition to the Breitenberg Member is still not visible. Shell fragments of ammonites occur in the residues of many microfossil samples taken from the measured section (Fig. 5). The Hochalplgraben section is the locality with the most frequent and best preserved specimens of the new subspecies.

A detailed study of the *P. spelae tirolicum* beds (Fig. 5, level 2) was carried out in 2007. Most ammonites are preserved with their original aragonitic shell

and embedded parallel to the bedding plane. They are usually flattened by compaction or, more rarely, the phragmocones are preserved by infilling of pyrite. Some crushed specimens are preserved with complete or nearly complete body chamber. The lowest *P. spelae tirolicum* n. ssp. was found 65 cm, the last 160 cm above the faulted base of the Tiefengraben Mb. The *spelae tirolicum* beds have thus a thickness of nearly 1 m and can be divided by a 1 cm thin but distinct layer with crinoid ossicles at the base of their upper third. The majority of the uncrushed phragmocones were found closely (5-15 cm) below the crinoid layer. One more ammonite level was discovered 6.5 m above the *spelae tirolicum* beds in the middle part of the Tiefengraben Mb., just above a layer with calcareous concretions (Fig. 5, level 4). Ammonites are rare and small, and have been determined as *Psiloceras* cf. *pacificum*. 3.5 m higher, a fragment of the outer whorls (with body chamber) of a smooth psiloceratid (*Psiloceras* sp. A) was found in a limestone bed at the top of the section (Fig. 5, level 4a). The basal part of this bed contains an accumulation of shallow neritic bivalves (*Liostrea*, *Modiolus*, *Plagiostoma*, *Agerchlamys*) and rare small rhynchonellids.

3.2. Schlossgraben

This section is located east of Hinterriß ($47^{\circ}28'33''\text{N}/11^{\circ}28'55''\text{E}$) (Fig. 3, localities 1 to 3): A forest road crosses the mountain torrent several times along which three main outcrops exist. The lowest one is located within the torrent (1060 m) (Fig. 3) and exposes the middle part of the Tiefengraben Mb. and the transition to the Breitenberg Mb. The second one is found just south of the torrent at the roadside in 1140 m where a local anticline shows the uppermost metres of the Eiberg Mb. and the lowest Tiefengraben Mb. (up to the Schattwald Beds). There, *Choristoceras marshi* was found at the top of bed T. The third exposure is next to a further passage of the road crossing the Schlossgraben in 1180 m (slope at the roadside). This exposure presents along a 30 m roadcut a more expanded sequence from the upper Eiberg Mb. to the lower Tiefengraben Mb. including the *P. spelae tirolicum* n. ssp. level. The Schattwald Beds are again sheared parallel to the bedding planes but the grey marls above are undisturbed. Most *tirolicum* specimens here are crushed except for one limonitic uncrushed cast (phragmocone and initial body chamber; Fig. 10.5).

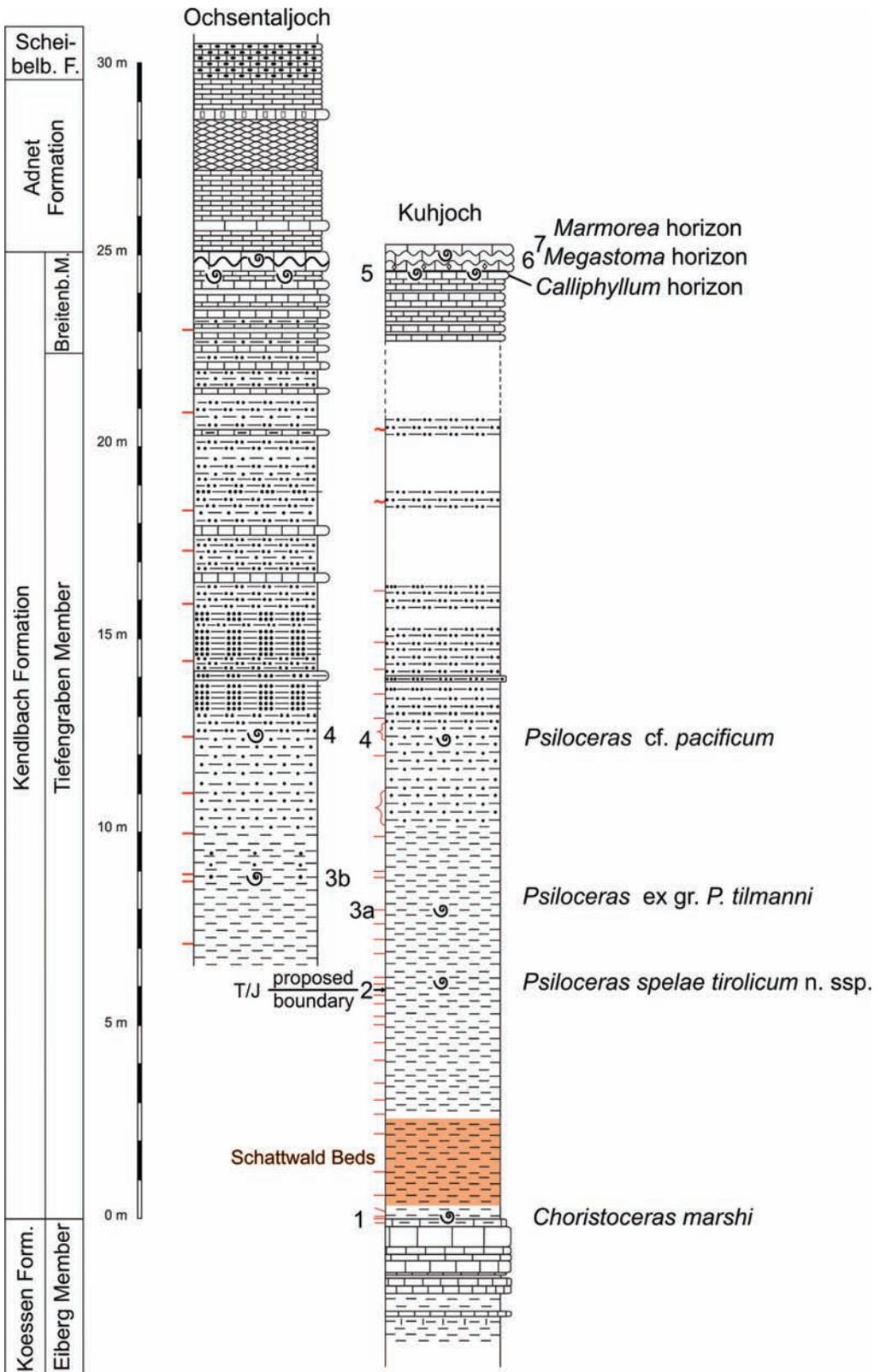


Fig. 6. Ochsentaljoch and Kuhjoch sections with distribution of ammonite beds. Investigated levels are indicated.

3.3. Ochsentaljoch

This locality is situated at a small pass across the mountain ridge between the Ochsental and Hochstall valleys (47°29'0"N/11°31'50"E) (Figs. 4, 6). The section is exposed on the western slope some metres below the pass. It forms a natural outcrop from the Eiberg Mb. to the Lower Jurassic Adnet. and Scheibenberg Fms. The lower part of the Tiefengraben Mb. is faulted. The studied section starts some meters below the first arenitic beds of the middle Tiefengraben Mb. The section contains two ammonite beds: a lower (Fig. 6, bed 3b) (corresponding to level 3a of the Kuhjoch section) with a smooth whorl fragment of an ammonite of the *Psiloceras tilmanni* group and an upper (Fig. 6, bed 4) that contains badly preserved *P. cf. pacificum*.

3.4. Kuhjoch

The proposed candidate GSSP for the T/J boundary is located 750 m east of the Ochsentaljoch at the western slope of the mountain ridge between the Hochstall and Hölzelstal valleys, a few meters below a small mountain pass crossing the crest (47°29'02"N/11°31'50"E) (Figs. 4, 6). Its altitude is 1760 m. An existing outcrop from the Eiberg Mb. up to the silty base of the middle Tiefengraben Mb. was laterally enlarged, and its biostratigraphy was studied in great detail (HILLEBRANDT & URLICHS 2008) as well as its chemostratigraphy and palynology (HILLEBRANDT et al. 2007). The upper part of the Tiefengraben Mb. is covered by grass and natural outcrops continue with the Breitenberg Mb. and the Adnet Fm.

The Kuhjoch section is rich in ammonites and contains altogether seven different levels, one of Rhaetian and six of Hettangian age. Cross sections of *Choristoceras* are common in the limestone beds of the Eiberg Mb. and compressed specimens of *Ch. marshi* were found at the top of bed T (Fig. 6, bed 1). The *spelae* bed (ammonite level 2) starts 5.8 m above (Fig. 6, bed 2) and is approx. 40 cm thick. Specimens are mostly crushed (Fig. 11.4) and limonitic casts are rare (Fig. 10.4, 10.6). The next ammonite level (3a) occurs 1.5 to 1.7 m above top of level (2). In the residue of a washed microfossil sample from this level limonitic casts of the inner whorls and whorl fragments of an ammonite belonging to the *P. tilmanni* group (Fig. 13.1-13.4) were found. Ammonite level (4), located 4 m above level (3a) and 6 m above the *spelae* bed (level 2) has yielded shell fragments and one small, badly preserved specimen of *P. cf. paci-*

ficum. Ammonite level (5) follows 12 m above level (4) and belongs to the Breitenberg Mb. A single limestone bed contains large sized *Psiloceras calliphyl-lum*, *P. costosum* and *P. naumanni*. This level is condensed, containing at least 2 ammonite biohorizons. Ammonites are rare in the next two limestone beds (Fig. 6, levels 6 and 7) but *Alsatites cf. liasicus* and *Alpinoceras haueri* – found and determined by K. KMENT (Bad Tölz) – indicate a Middle and Late Hettangian age.

4. Systematic palaeontology

The described ammonites are from the earliest Hettangian of the western Karwendel Syncline (Northern Calcareous Alps, Tyrol, Austria).

Abbreviations: v = vidi (seen by the author), D = diameter, Wh = whorl height, Ww = whorl width, U = umbilicus; E = external lobe, L = lateral lobe, U = umbilical lobes, I = internal lobes; spec. = specimen with collection number). An arrow marks the end of the phragmocone.

The studied specimens are mostly housed in the collection of the Natural History Museum in Vienna (NHMW) under the depository number NHMW 2009z0034/, sub-numbers 0001 to 0058. In the following, only the sub-numbers are mentioned. SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany. Egressing factor after GYGI (2001).

Superfamily Psiloceratoidea, HYATT 1867

Remarks: Many authors (e.g. WIEDMANN 1970; GUEx 1982, 1987, 1995 etc; RAKUS 1993) supposed a monophyletic origin of the Psiloceratoidea from the Phylloceratoidea, a view also shared by us (Fig. 14). A derivation from the genus *Eopsiloceras* (Fig. 14) is most probable according to sutural similarities. The genus *Rhacophyllites* (Discophyllitidae *sensu* RAKUS 1993) became extinct at the end of the Triassic and the Rhaetian *Tragorhacoceras* (Juraphyllitidae *sensu* RAKUS 1993) is already the first true phylloceratid offshoot.

Family Psiloceratidae HYATT, 1867

Remarks: In HILLEBRANDT (2000a) this family is subdivided in the subfamilies Psiloceratinae HYATT, 1867, Schlotheimiinae SPATH, 1923, Sunrisitinae HILLEBRANDT, 2000, and Alsatitinae SPATH, 1924. The described ammonites belong to the subfamily Psiloceratinae.

Genus *Psiloceras* HYATT, 1867

Type species: *Ammonites planorbis* SOWERBY, 1824.

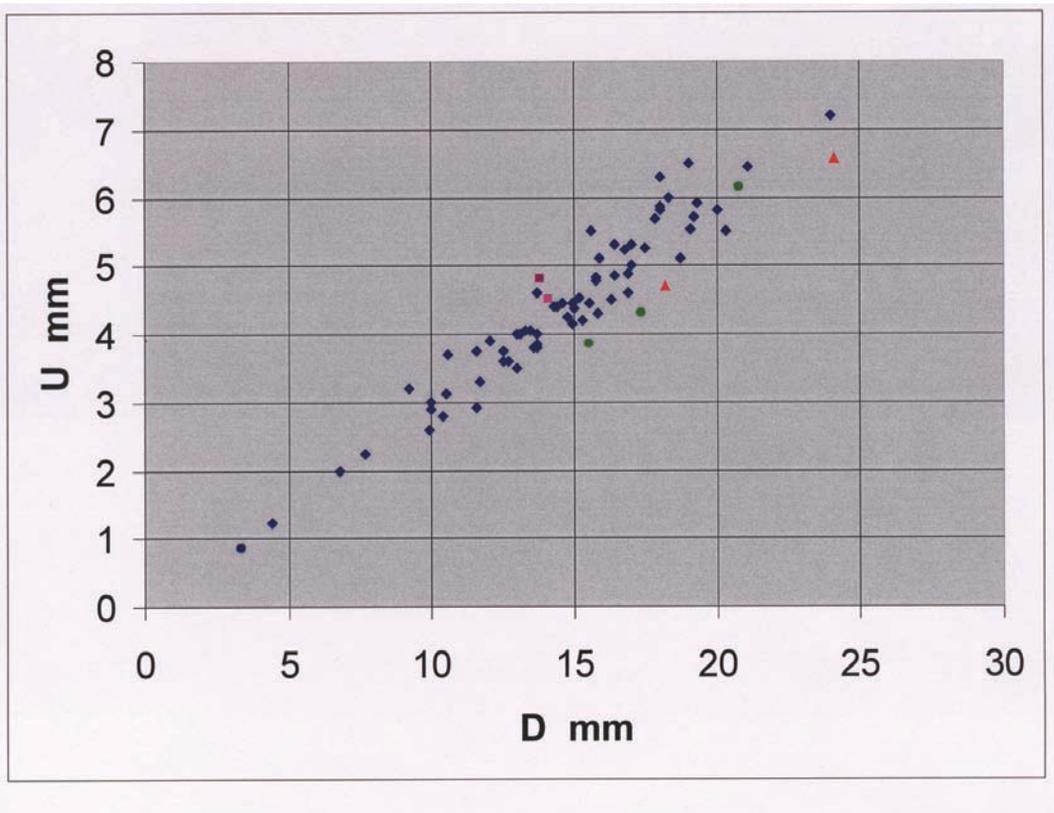


Fig. 7. Diagram with relation of width of umbilicus (U) to diameter (D) of *Psiloceras spelae*.
 Square (violet) = holotype of *P. spelae spelae* (cast);
 square (pink) = holotype of *P. spelae spelae* (thickness of the lacking shell respected);
 triangle (red) = holotype of *P. spelae tirolicum* n. ssp.;
 circle (green) = specimen 13 with egressing body chamber;
 rhomb (blue) = paratypes of *P. spelae tirolicum* n. ssp., all localities.

Fig. 8. 1-11 – *Psiloceras spelae tirolicum* n. ssp.

Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). **1a, b** – Holotype, phragmocone with crushed body chamber, lateral and frontal views (specimen 0001). **2** – Paratype with part of crushed body chamber, lateral view (specimen 0002). **3** – Paratype with phragmocone and crushed body chamber, lateral view (specimen 0003). **4a, b** – Paratype with phragmocone and beginning of the crushed body chamber, lateral and sagittal views (specimen 0004). **5a, b**. Paratype with phragmocone and part of crushed body chamber, lateral and frontal views (specimen 0005). **6, 9** – Paratype, 6. Phragmocone and slightly crushed body chamber, lateral view, 9a, b. Part of Fig. 8.6, opposite side, phragmocone with first part of body chamber, rest of body chamber omitted, lateral and sagittal views (specimen 0006). **7a, b** – Paratype, laterally in part deformed, lateral and ventral views (specimen 0007). **8a, b** – Paratype with phragmocone and part of crushed body chamber, lateral and sagittal/ventral views (specimen 0008). **10a, b** – Paratype with phragmocone and part of crushed body chamber, lateral views (10b = enlarged inner whorls) (specimen 0009). **11a, b** – Paratype of phragmocone and beginning body chamber, lateral and frontal views (specimen 0010).

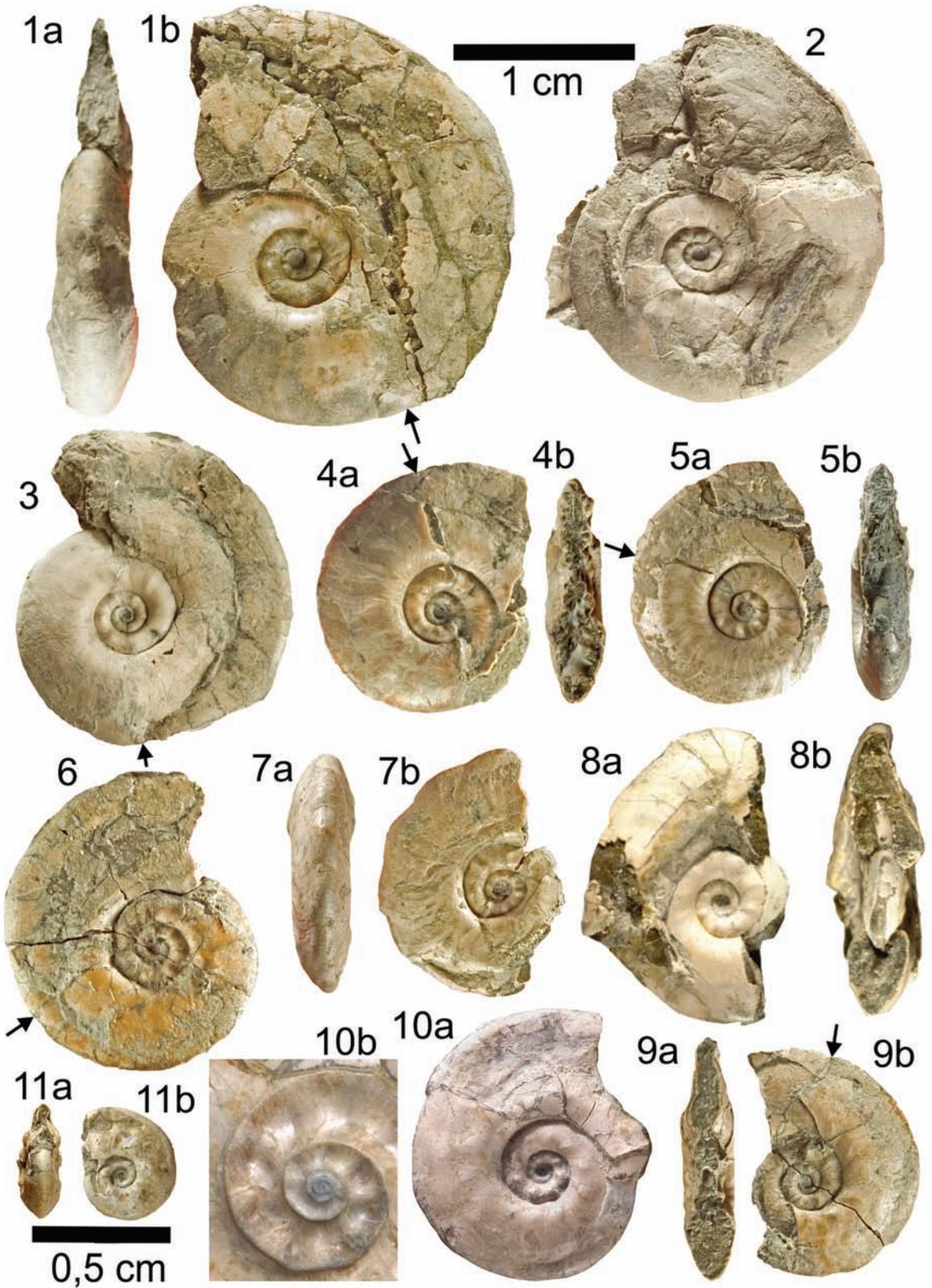


Fig. 8 (Legend see p. 172)

Remarks: Whorl section and suture line of *P. planorbis* are unknown from the type locality and its area (flattened specimens by compaction and with shell). The outer suture line (from the external lobe to the umbilical seam) of uncrushed specimens from Britain and SW Germany were published recently by BLOOS & PAGE (2000). The outer suture line corresponds with that of other species of *Psiloceras*. The suture line can be more or less simplified within the same species. Species with a more elaborated suture line have deeper lobes and the saddles are higher. The saddles are deeper indented and show further subdivisions. Nodes are present on the inner whorls of most species of *Psiloceras* but are not found in the Phylloceratoidea. A more complicated suture line and nodes on the inner whorls are mainly found in species of the Mediterranean Province and partly in those of the East Pacific Realm whereas species with a simplified suture line and smooth inner whorls are dominating in NW Europe. The reasons for these differences are mostly explained by environmental differences. Arguments against this opinion were discussed by BLOOS (2004). At that time the here presented earliest Hettangian *Psiloceras* from the Alps were not yet known. They have already nodes but a simpler suture line than those from the upper part of the Early Hettangian of the Alps. The oldest psiloceratid in the NW European Province, *Psiloceras erugatum* (PHILLIPS) in Great Britain, also offers a simple suture line and is the only species there with nodes (BLOOS & PAGE 2000).

Psiloceras spelae GUEX et al., 1998

Synonyms: See below under *Psiloceras spelae spelae*.

Emended diagnosis: Conch moderately involute. One up to one and a half of the innermost whorls smooth. Succeeding 1.5 whorls with more or less strong nodes on the umbilical edge. The nodes can be elongated towards the flank and retracted to the umbilical edge at the end of the nodose stage. Distinct nodose stage up to an umbilical width of 1.4 to 3.5 mm. 7 to 11 nodes per whorl. Growth lines thickened towards the venter at the end of the body chamber.

Remarks: Two subspecies can be distinguished: The nominotypical subspecies of *Psiloceras spelae* is *Psiloceras*

spelae spelae which was described by GUEX et al. (1998) from the basal Hettangian of the Ferguson Hill section in Nevada (U.S.A.) and was also found in Northern Peru (SCHALTEGGER et al. 2008) in a similar stratigraphic position. The holotype is incompletely preserved. The exact whorl section cannot be recognised; the innermost whorls are not preserved and the suture line is not known. A specimen figured by GUEX (1995, pl. 2, fig. 21) as *Togaticeras togatum* (NEUMAYER) should be restudied because the sculpture of the end of this specimen is similar to *P. spelae*. It shows the typical plicate ribs of the end of the body chamber. The inner whorls are badly preserved and it cannot be excluded that an inner nodose stage exists. The specimen seems to be more involute. An unpublished specimen from Nevada (photograph kindly provided by J. GUEX, Lausanne) (diameter approx. 15 mm) probably shows the typical ribs of the end of the body chamber.

The specimen described from Peru (SCHALTEGGER et al. 2008) is a badly preserved cast which shows the sculptural elements of *P. spelae*.

Both subspecies mainly can be distinguished by the nodular stage. The nominotypical subspecies has more sculptural elements per whorl and they are present up to a larger diameter respectively whorl width.

Psiloceras spelae spelae GUEX et al., 1998

- v 1998 *Psiloceras spelae* sp. n. – GUEX et al., p. 78, pl. 1, fig. 8.
 v 2007 *Psiloceras spelae*. – LUCAS et al., p. 145, fig. 11B.
 cf. 2008 *Psiloceras spelae*. – SCHALTEGGER et al., p. 269, fig. 3c.

Diagnosis: Ratio between umbilical width and diameter (holotype) without shell 34 % and with shell 32 % (Fig. 7). 11 to 12 sculptural elements (roundish and elongated nodes) per whorl. Elongated nodes persisting up to an umbilical diameter of 3.5 mm. Original whorl section not well known (an original subtriangular whorl section can not be excluded). Suture line, beginning of the nodose stage and innermost whorls not known.

Remarks: Comparison with *Psiloceras spelae tirolicum* n. ssp. see under description (comparisons) of this subspecies.

Fig. 9. 1-12. – *Psiloceras spelae tirolicum* n. ssp.

Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). **1-10** – Paratypes of flattened specimens with at least part of body chamber, lateral views. 1, 2, 4 with plicate ribs at the end of body chamber, 1, 2, 4, 6, 7, 9 with egressing end of body chamber; 1 (specimen 0013), 2 (specimen 0014), 3 (specimen 0015), 4 (specimen 0016), 5 (specimen 0017), 6 (specimen 0018), 7 (specimen 0019), 8 (specimen 0020), 9 (specimen 0021), 10 (specimen 0022). **11, 12** – Paratypes, fragments of end of body chamber with plicate ribs, lateral views, 11 (specimen 0023), 12 (specimen 0024).



Fig. 9 (Legend see p. 174)

Psiloceras spelae tirolicum n. ssp.

Figs. 8.1-8.11; 9.1-9.12; 10.1-10.6, 9, 10; 11.1-11.5

Holotype (specimen 0001) (Fig. 8.1 a, b): Specimen (one side and venter prepared) mostly with shell (part lost by cleaning after taking of photographs). Phragmocone uncrushed and filled with pyrite, half a whorl of body chamber preserved, crushed and filled with clayey marl.

Paratypes: More than 40 specimens, of these 35 specimens measured (Tab. 1), 33 specimens (or fragments) figured.

Diagnosis: Conch moderately involute. Whorl section of phragmocone subtrigonal, largest whorl width at umbilical edge. Umbilical wall steep and umbilical edge rounded. Umbilicus deep. Smooth innermost whorls followed by a stage with 7 to 8 more or less strong sculptural elements (nodes) per whorl. This nodose stage is up to one and a half whorls long corresponding to an umbilical width of 3 mm. Nodes strongest at the umbilical edge; they may be elongated parallel to the sinuous growth lines of the flank. End of body chamber at least sometimes with plicate ribs.

Suture line normally with biphyllid saddles between external and lateral lobes as also between lateral and umbilical lobes.

Etymology: From the occurrence in the Tyrol (= Tirol in German), Austria.

Type locality: Hochalplgraben (4.3 km west of Hinterriß); outcrop in a vertical distance of ca. 15 m below a forest road crossing the torrent at 1320 m above sea level. Topographic map of Bavaria 1:25 000 (sheet 8534 Östliche

Karwendelspitze); x = 4455.64, y = 5260.45). Topographic map of Austria 1:50 000 (sheet 118 Innsbruck) and topographic map of Bavaria 1:50 000 (sheet L 8434 Fall).

Type horizon: Grey, clayey marls with *Praegubkinella turgescens* FUCHS (foraminiferan) of the Tiefengraben Mb., approximately 1.1 m above the boundary with the Schattwald Beds (fault) and 10 to 20 cm below a 1 cm thick crinoid layer.

Material: The new subspecies of *Psiloceras spelae* is presently recorded from three localities (in total more than 100 specimens):

Hochalplgraben (type locality): Here the ammonite beds with the new subspecies are approx. 90 to 95 cm thick. The exact level within these beds is known only for a few specimens. The range of ammonites begins 60 cm below the mentioned crinoid bed and ends about 30-35 cm above it.

a) Uncrushed specimens: In addition to the holotype there were found 11 specimens (diameter 4.4 mm to 20 mm) with uncrushed or only slightly crushed phragmocone and in part with beginning of the crushed body chamber (Fig. 8.1-8.11; 10.1, 10.10).

Specimens whose exact level is known:

Specimen 0003 (Fig. 8.3): found together with the holotype. Specimen 0004 (Fig. 8.4 a, b): immediately below the crinoid bed.

Specimens 0005 and 0007 (Fig. 8.5 a, b, 7): approx. 30 to 35 cm below the crinoid bed.

b) Flattened specimens: 24 specimens could be measured. Most of them are figured (Figs. 9.1-9.10; 10.2, 10.3). Specimen 0030 (Fig. 10.2) was found 60 cm below and specimen 0026 (Fig. 10.3) 30 to 35 cm above the crinoid

Fig. 10.1-10.6, 10.10. *Psiloceras spelae tirolicum* n. ssp.

1-3, 10. Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). 1a, b. Slightly deformed paratype (phragmocone) with nearly smooth inner whorls, lateral and ventral view (specimen 0012). 2 (specimen 0030) and 3 (specimen 0026) paratypes, flattened and with plicate ribs on end of body chamber; 3. Egressing end of body chamber with part of peristome. 10. (= Fig. 8.11) specimen 0010, strongly enlarged to show protoconch and innermost whorls. 10.5, 10.9. Schlossgraben, section at 1180 m, level with *P. spelae tirolicum* n. ssp. (E of Hinterriß) (Figs. 3, 5). 5. Paratype, limonitic cast of phragmocone, approximated suture lines at the end of the phragmocone and crushed body chamber, short continuation of the umbilical seam as groove on the phragmocone, lateral view (specimen 0031). 10.9 Protoconch, oblique lateral view (specimen 0059). 4, 6. Kuhjoch section, level 2 (S of Baumgartenbach valley, Figs. 2, 4, 6). 4. Paratype, limonitic cast of phragmocone and crushed body chamber, lateral view (specimen 0032). 6a, b. Paratype, incomplete phragmocone and fragment of body chamber, lateral and sagittal views (specimen 0033).

Fig. 10.7, 10.8 – Anptychus of *Psiloceras spelae tirolicum* n. ssp. Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). 7. Convex cast of Fig. 8 with remains of carbonized shell. 8. Concave inner side with most of the carbonized, originally organic shell (specimen 0044).

Fig. 10.11-10.14 – *Psiloceras* cf. *pacificum* GUÉX. Hochalplgraben section, level 4 (W of Hinterriß, Figs. 3, 5). 11. Inner whorls, filled up with sediment and laterally deformed, lateral view (specimen 0053), 12a, b. Inner whorls, pyrite-filled, lateral and frontal view (specimen 0052), 13. Filled with pyrite, lateral view (specimen 0050), 14. Specimen filled up with sediment and laterally flattened (specimen 0051).

Fig. 10.15. a, b. *Psiloceras pacificum* GUÉX. New York Canyon (Nevada, U.S.A.), section 1, bed Z7 in GUÉX (1995), Pacificum Zone.

Fig. 10.16. *Togaticeras* cf. *goisernense* RAKUS. Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5), whorl fragment filled with sediment and laterally compressed, lateral view (specimen 0058).

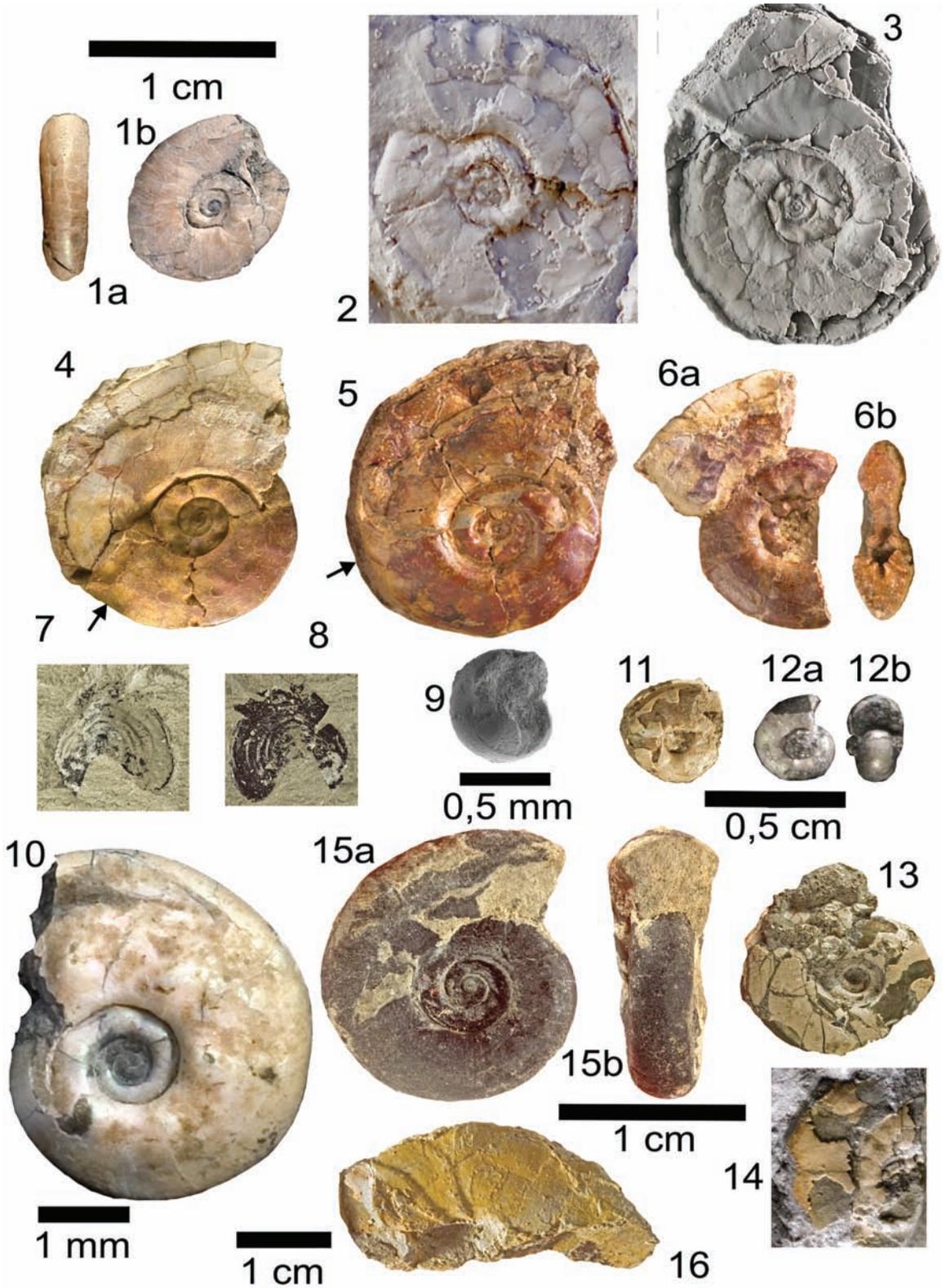


Fig. 10 (Legend see p. 176)

bed. Two whorl fragments (Fig. 9.11, 9.12) and the fragment of an external side of the end of the body chamber are also figured (Fig. 11.5).

- c) More than 50 incomplete and fragmentary specimens.
 d) Corresponding anptychus (shell and cast of the inner side of the shell) (Fig. 10.7, 10.8) (specimen 0044).

Schlossgraben: One limonitic specimen without shell, crushed body chamber half a whorl long (Fig. 10.5) (0031). Limonitic protoconch (Fig. 10.9) (0059). More than 10 moderately to incompletely preserved specimens with shell (not measured and figured).

Kuhjoch: Three limonitic casts of phragmocones, two (Fig. 10.4, 10.6a, b) (specimens 0032 and 0033) with part of the crushed body chamber.

One crushed limonitic cast of a phragmocone.
 8 flattened specimens, at least in part with body chamber (measured) (Fig. 11.4).
 More than 10 flattened, moderately to badly preserved specimens, mostly with shell (not measured and figured).

Measurements: See Table 1 in Appendix.

Description of the holotype: The conch is moderately involute [$U = 27\%$ of D (outer whorl) and 26% (phragmocone)]. The phragmocone has a diameter of 17.6 mm and its whorl height is 7.4 mm. The conch is slightly egressing (egressing factor 1.03) (GYGI 2001) at the end of the probably incomplete body chamber ($Wh = 10.5$ mm). The whorl section of the phragmocone is subtrigonal ($Wh:Wb = 1.56$), the largest width is at the umbilical edge. The umbilical edge is rounded. The umbilical wall is steep and the umbilicus is deep. The last whorl covers nearly half of the whorl height of the preceding whorl.

The protoconch is followed by one and a half whorls which are smooth and serpenticone. The first node appears at an umbilical width of 0.95 mm. This node is weaker than the following ones and is slightly pointed. $6\frac{1}{2}$ nodes are found on the umbilical edge of the first whorl of the nodose stage. Nodes are present up to an umbilical width of 2.3 mm (8 nodes on the last whorl with nodes; altogether 12 nodes). The strongest nodes are found at an umbilical width of 2 mm. The nodes weaken to low, somewhat elongated elevations at the end of the nodose stage. The surface of the last quarter of the last whorl of the phragmocone and the body chamber are smooth. Sinuous growth lines can be seen

in part. Part of the suture line can be recognised at the end of the phragmocone. The saddle between the lateral lobe (L) and the umbilical lobe U_2 is biphylloid.

Description of the subspecies (on basis of more than 40 type specimens):

a) Shape: All specimens are small, not exceeding 25 mm. The variability of the shape is low.

Protoconch: Barrel-shaped protoconchs (e.g. specimen 0059, width 0.4 mm, with part of the first whorl) (Fig. 10.9) were found in the residue of washed samples. In some specimens the protoconch could be prepared (e.g. Figs. 8.10b; 10.10).

Phragmocone: The phragmocone is about 4 whorls long. The diameter of the phragmocone is variable. The maximal diameter (17.5 mm) was found in the holotype, the minimal one (11.5 mm) in specimen 0005 (Fig. 8.5). Approximated suture lines at the end of the phragmocone (diameter 12.7 mm) indicating adult stage are preserved in specimen 0031 (Fig. 10.5). The phragmocone is moderately involute, its average $U\%$ of D is 29 to 30, the extremes are 25 and 35 (Fig. 7).

The whorl section of the innermost whorls is rounded ($Wh:Ww = 0.4$ to 0.75) and becomes subtriangular at a whorl height of 1 mm ($Wh:Ww = 0.8$) (Fig. 12.7, 12.8). The whorl height increases more quickly than the whorl width during ontogeny. This factor can increase to 1.7 (table 1) (holotype 1.56). The maximum width is found at the umbilical edge. The rounded umbilical wall is distinct and steep. The umbilicus is deep. The covering of the preceding whorl by the following whorl is $\sim 60\%$ in the inner whorls and 45 to 57% on the outer whorls of the phragmocone [43.3% in specimen 0009 (Fig. 8.10a), 57.5% in specimen 0003 (Fig. 8.3)].

Body chamber: With exception of a small fragment all body chambers are crushed. The aperture normally is not preserved. The body chamber of specimen 0031 (Fig. 10.5) is longest, more than half a whorl.

One shell fragment was found on a bedding plane representing the ventral end of a body chamber in uncrushed state (Fig. 11.5). Here the venter is broadly rounded and does not show the subtriangular whorl section of the phragmocone.

The end of the body chamber is egressing. The egressing factor of the probably incomplete body chamber of the holotype is 1.03. The highest egressing factor (1.53) is

Fig. 11.1-11.5. *Psiloceras spelae tirolicum* n. ssp.

1-3, 5. Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). All coated with magnesia to show details of sculpture. 1. Spiral rills at beginning of last whorl and weak sculpture of inner whorls, lateral view (specimen 0003). 2. Growth lines and the strong nodes ("Knötchenstadium") of the inner whorls, lateral view (specimen 0005). 3. "Knötchenstadium" and the following stage with stronger growth lines, lateral view (specimen 0009). 5. Fragment of ventral side, end of body chamber with peristome, uncrushed (specimen 0043). 4. Kuhjoch section, level 2 (S of Baumgartenbach valley, Figs. 2, 4, 6), flattened paratype (specimen 0039).

Fig. 11.6. a, b. *Psiloceras* sp. A. Hochalplgraben section, level 4a (W of Hinterriß, Fig. 3, 5), whorl fragment (specimen 0045).

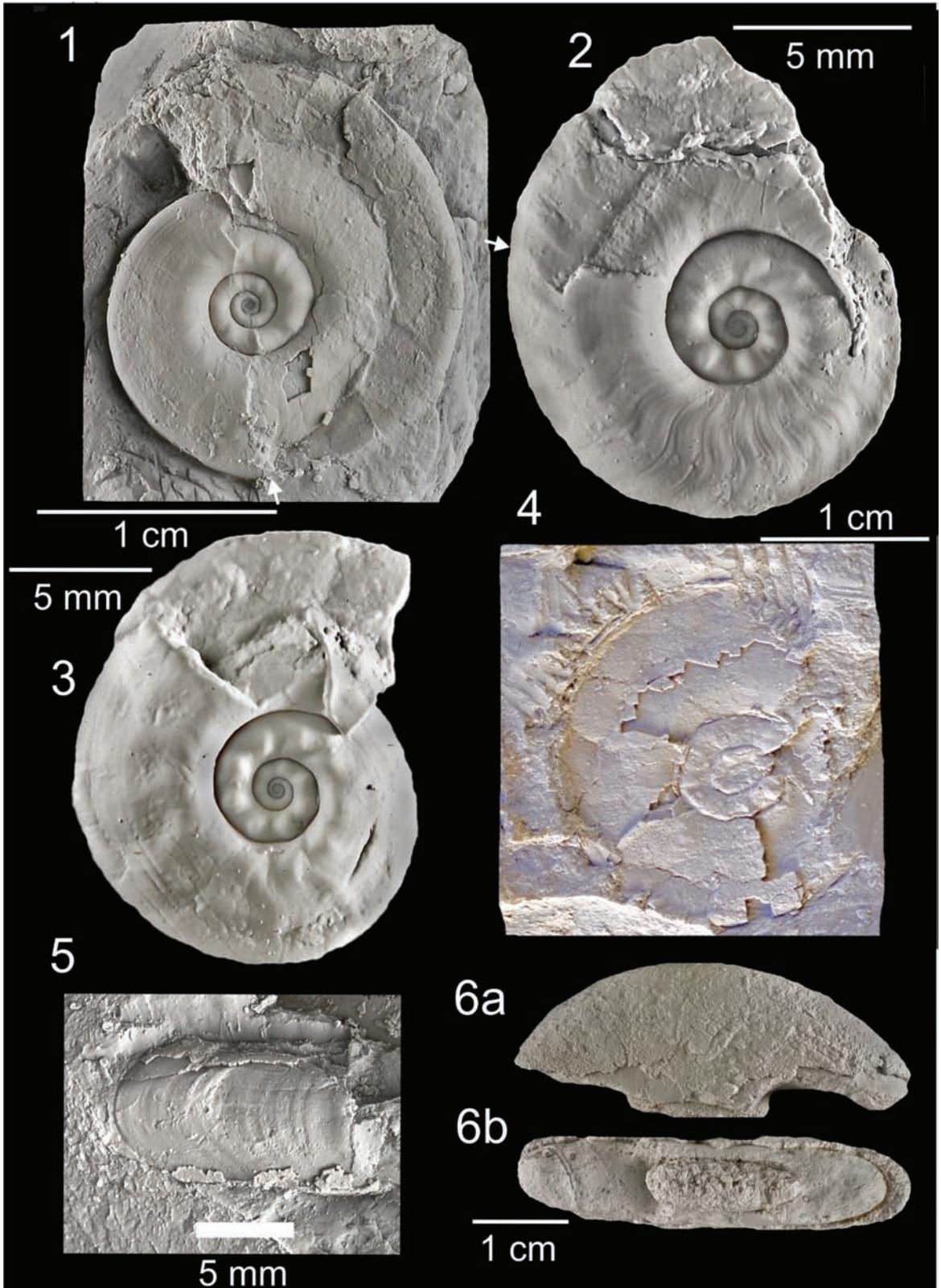


Fig. 11 (Legend see p. 178)

found in specimen 0013 (Fig. 9.1) [1.35 in specimen 0016 (Fig. 9.4), 1.19 in specimen 0019 (Fig. 9.7), 1.11 in specimen 0026 (Fig. 10.3) and 1.07 in specimen 0014 (Fig. 9.2)].

b) Surface and sculpture: The sculpture appears on the shell surface and the cast. Sculptural elements of the shell are not thickened. Part of the shell is smooth or covered by mostly weak growth lines. A further conspicuous and important sculptural element is the presence of the nodes on the inner whorls. The nodes are visible even in badly preserved specimens if the inner whorls are present whereas finer sculptural details are often only observable on uncrushed specimens with preserved shell.

Growth lines: Growth lines are developed in many specimens (best in Fig. 11.2). They are strikingly sinuous. They can be seen mainly on the last part of the phragmocone and on the body chamber. Sometimes they are united to low, broad, indistinct, rib-like elevations (e.g. Fig. 11.2).

Nodes: The nodes are restricted to a nodose stage on the inner whorls. The nodose stage is 1-1½ whorls long. It begins at an umbilical diameter of 0.8-1.0 mm and ends at an umbilical diameter of 1.4 to ca. 2.4 mm. The number of nodes varies from 6.5-7 on the inner whorl of the nodose stage to 7-8 on the outer whorl of this stage. The total of nodes is 7-11. The nodes may vary from weak to strong.

The nodose stage follows the initial smooth stage. The development of nodes at the beginning of the nodose stage can be seen only on specimens with a weak sculpture throughout (Figs. 8.3 = 11.1; 8.11a, b = 10.10; 10.1a, b). It starts at an umbilical width of ca. 1 mm (Fig. 8.3 = 11.1). Some bundled growth lines develop to elongated elevations (6½ on the first whorl with this special sculpture). The highest point of these elevations lies on the umbilical edge and there they sometimes have a sharp edge formed by a strong growth line. After this stage the sculpture disappears gradually and the surface becomes smooth.

Many specimens have strong nodes. The transition from rounded, strong nodes to elongated nodes and low elevations on the umbilical edge in direction of the growth lines is best seen on specimen 0009 (Fig. 8.10 = 11.3).

Specimen 0005 (Fig. 8.5 = 11.2) also has strong nodes (nodose stage only 1 whorl long). The last node is elongated. It follows a nearly smooth stage whose length corresponds to the distance of two nodes. The next sculptural elements on the umbilical edge are bundled growth lines (the first two with a sharp edge).

The transition from the nodes to the more or less strongly developed sculpture of the last part of the phragmocone is formed by weakening nodes which are elongated towards the flanks in direction of the growth lines (Fig. 11.2, 11.3). The nodes and the rib-like elements show some variability in shape and ontogenetic changes.

Sculptural elements on the flank and venter of the phragmocone: Rib-like sculptural elements are found on the flanks of some specimens. They appear after the nodose stage and develop from the bundled and elevated growth lines on the umbilical edge. These wave-like elevations in direction of the growth lines are very low in specimen 0005 (Fig. 8.5

= 11.2), more pronounced in specimen 0009 (Fig. 8.10 = 11.3) and also present on the casts of specimen 0031 (Fig. 10.5), 0032 (Fig. 10.4) and 0033 (Fig. 10.6a, b).

The wave-like sculpture can continue to the venter and is found at specimen 0031 (Fig. 10.5) and the venter (with shell) of specimen 0007 (Fig. 8.7a, b). The distance of this wave-like structure on the venter is 3-4 mm. Specimen 0009 (Fig. 8.10a, b = 11.3) is transitional to specimen 0031.

Rib-like elements of the body chamber: Near the end of the body chamber the mentioned elevations of the growth lines may increase in strength towards the ventral margin and sometimes even cross the venter [specimen 0013 (Fig. 9.1), 0014 (Fig. 9.2), 0016 (Fig. 9.4), 0030 (Fig. 10.2) as also the fragments 0023 (Fig. 9.11) and 0024 (Fig. 9.12)].

Spiral rills: At least in one specimen (specimen 0003, Fig. 11.1) weak spiral rills are developed. They are restricted on the beginning of the last whorl, situated on the ventral half of the flank.

Aperture: In one specimen the lateral part of the aperture is preserved (Fig. 10.3). The peristome is different from the neighbouring rib-like elevations by its differing direction on the flank, by the lack of sinuous bending, by its increased strength, and by its begin at the umbilical seam.

The ventral part of another aperture is visible in Fig. 11.5. There the peristome is not as strong as in Fig. 10.3.

c) Suture line (Fig. 12): The suture line of 4 specimens (one from Hochalplgraben, one from Schlossgraben, two from Kuhjoch) could be drawn. It is possible to present the outer and the inner part of the suture line. The ontogeny of the suture line could be observed in specimen 0033 (Fig. 12.2a-d).

Lobes: At a whorl height of 0.7 mm is found an undivided internal umbilical lobe U_1 and the external lobes U_2 and U_3 . At a whorl height of 1.3 mm two internal umbilical lobes (interpreted as U_1 and U_4) are present. U_4 and U_3 also could be interpreted as suspensive lobes by subdivision of the umbilical lobe between U_2 and U_3 . But in this case U_3 should appear at the umbilical seam and not on the external side. At a whorl height of 4.2 mm a dentition of U_4 and U_3 appears and both lobes also could be interpreted as auxiliary suspensive lobes. The external umbilical lobes are slightly retracted. Specimen 0041 (Fig. 12.3b) shows at a whorl height of 2 mm a similar suture line as specimen 0033 at a whorl height of ca. 1.7 mm. Retracted umbilical lobes are also present in specimen 0041 (Fig. 12.3a), specimen 0008 (Fig. 12.1, 12.5) and specimen 0031 (Fig. 12.6). The U_3 is subdivided in specimen 0008 into additional lobes (? additionally auxiliary suspensive lobes). In general the suture lines are symmetric. Specimen 0032 (Fig. 12.4) offers an asymmetric position of the external lobe.

Saddles: The saddles between E and L as well between L and U_2 are biphyllid in specimen 0033 and specimen 0006 and in part transitional to triphyllid in specimen 0008. Specimen 0046 has a monophyllid appearance.

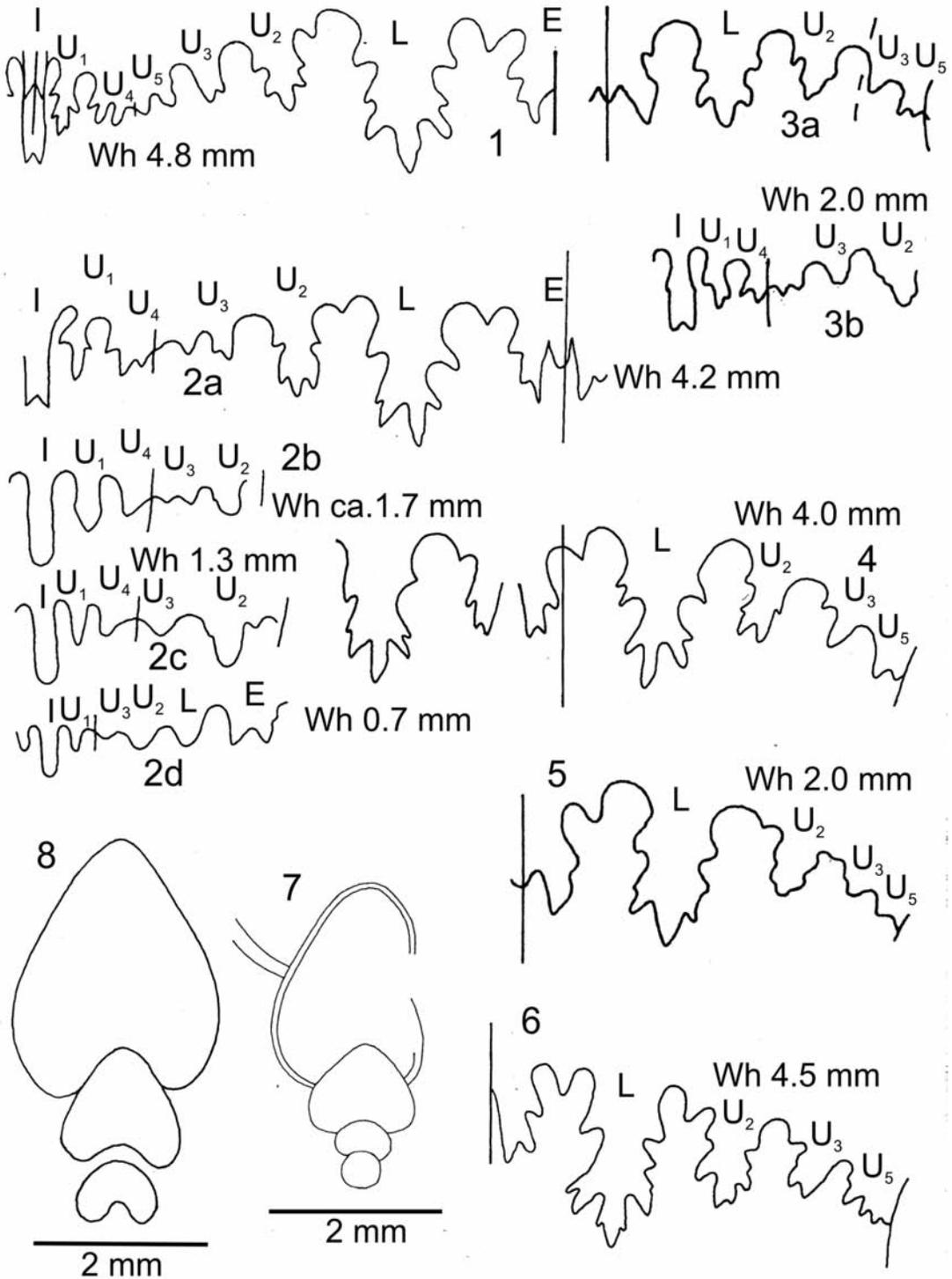


Fig. 12.1-12.8. *Psiloceras spelae tirolicum* n. ssp. Suture lines and whorl sections. 1, 5, 7. Hochalplgraben section, level 2 (W of Hinterriß, Figs. 3, 5). 1, 5. Suture lines (specimen 0008), 7. Whorl section (specimen 0004). 2-4, 8. Kuhjoch section, level 2 (S of Baumgartenbach valley, Figs. 2, 4, 6). 2a-d. Ontogeny of suture line (specimen 0033), 3a, b. Suture line (specimen 0041), 4. Suture line (specimen 0032), 8. Whorl section (specimen 0033). 6. Schlossgraben, section at 1180 m, level with *P. spelae tirolicum* n. ssp. Suture line (specimen 0031).

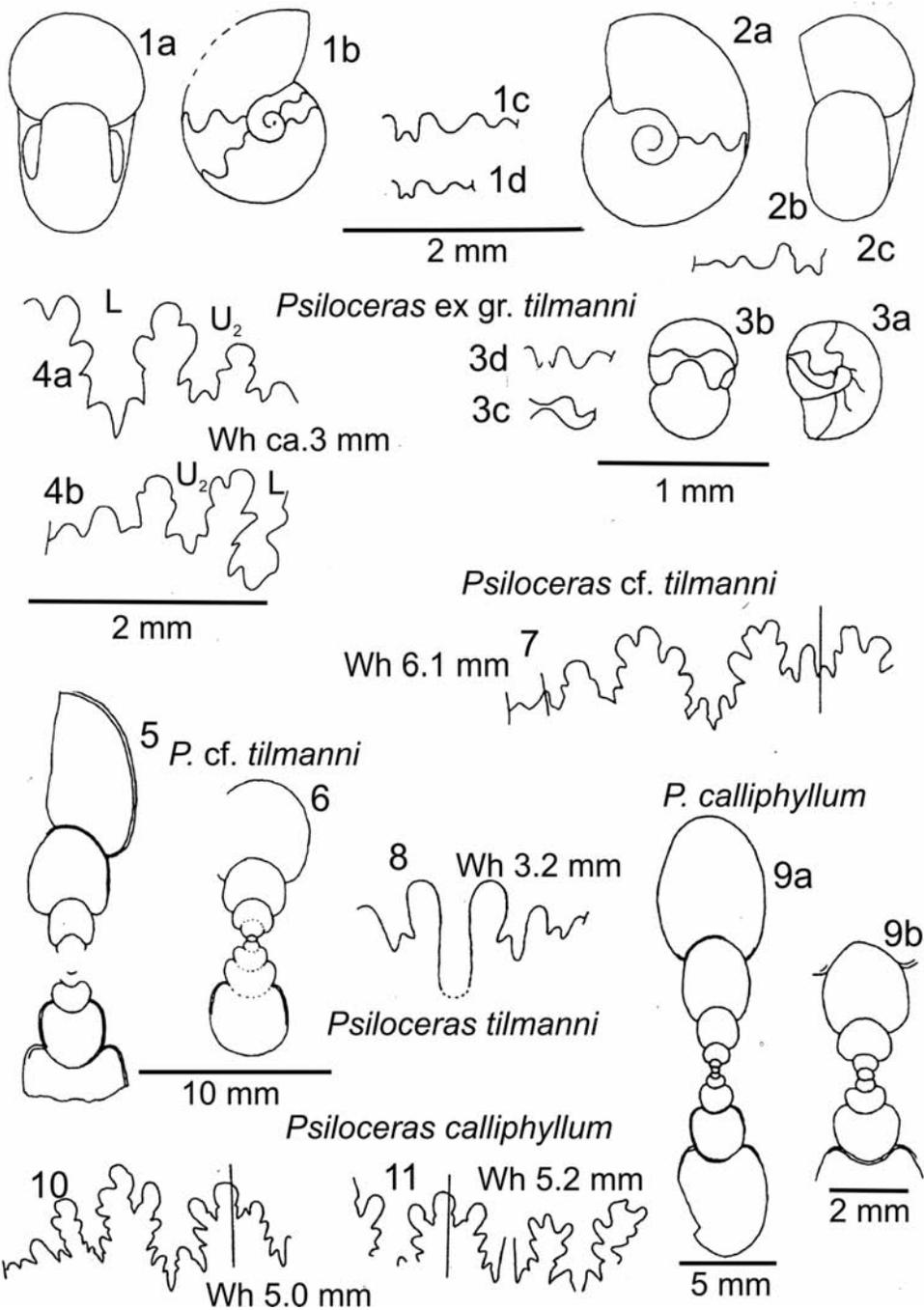


Fig. 13.1-13.4. *Psiloceras ex gr. Psiloceras tilmanni* LANGE. 1a. frontal view, 1b. lateral view, 1c, d. suture lines (specimen 0046); 2a. lateral view, 2b. frontal view, 2c. suture line (specimen 0047); 3. Protoconch, a. oblique lateral view, b. frontal view, c. prosuture and primary suture, d. suture line (specimen 0001-0048); 4a, b. suture lines (specimen 0049).

Fig. 13.5-13.7. *Psiloceras cf. tilmanni* LANGE. Chilingote (Utcubamba valley, N Peru), basal bed with psiloceratids (HILLEBRANDT 2000a, fig. 7). 5, 6. Whorl sections, 5 (sample 900928/1), 6 (sample 900925/10). 7. Suture line (sample 900928/1).

Fig. 13.8. *Psiloceras tilmanni* LANGE. 1.5 km S Tingo (Utcubamba valley, N Peru), internal suture line (TU Berlin HI 900921/5 specimen 3).

Fig. 13.9-13.11. *Psiloceras calliphyllum* (NEUMAYR) (microconch). Baumgartenbach (Pletzboden, W Achensee, Tyrol). 9a, b. Whorl sections, 10, 11. Suture lines (coll. S. SCHÜTZ, TU Berlin; SMNS 67520/1-2).

d) Anaptychus (specimen 0044): Anaptychi of *Psiloceras spelae tirolicum* n. ssp. are rarely preserved. In the *spelae tirolicum* beds of the Hochalplgraben section one isolated specimen has been found (Fig. 10.7, 10.8). It is 6.3 mm long and 6.5 mm wide. The specimen is slightly deformed. Most of the carbonized, originally organic matter is preserved. Small patches of the carbon matter are visible also on the cast of the concave inner side (Fig. 10.7). The sculpture of the anaptychus consists of concentric, wave-like ribs ca. 0.5 mm distant from one another and growth lines ca. 0.05 mm distant from one another. The frontal part of the anaptychus shows an indentation for the beak of the upper jaw. The anaptychi are interpreted as the lower jaws of ammonites. Lower and upper jaws of *Psiloceras* sp. were described by LEHMANN (1970).

Comparisons: The new subspecies has a very similar nodose stage as that of *P. spelae spelae*. The ratio of the umbilical width to the diameter of the holotype of *P. spelae spelae* is near to that of the most evolute specimens of *P. spelae tirolicum* n. ssp. But it must be considered that most specimens of *P. spelae tirolicum* n. ssp. are measured with shell and the holotype of *P. spelae spelae* is preserved as cast (thickness of shell ca. 0.15 mm in *P. spelae tirolicum* n. ssp.) (U% of D without shell 34% and with shell ca. 32%) (Fig. 7). *P. spelae spelae* has more sculptural elements (nodes) per whorl (11 to 12) than *P. spelae tirolicum* n. ssp. (7 to 8) and the sculpture with elongated nodes persists up to an umbilical diameter of 3.5 mm (2.0 to 2.4 mm in *P. spelae tirolicum* n. ssp.). The original whorl section of *P. spelae spelae* is not sufficiently known but an original subtriangular whorl section cannot be excluded. The suture line, the beginning of the nodose stage and the innermost whorls are not known. The differences between both subspecies are thought to be caused by palaeobiogeographic separation and not by different age.

The coiling of *P. tilmanni* LANGE is very variable (HILLEBRANDT 2000a, fig. 40). Small specimens sometimes have a similar umbilical width but the external side of the whorl section is rounded. The growth lines (HILLEBRANDT 2000a, pl. 11, fig. 20b) are less sinuous than in *P. spelae tirolicum* n. ssp. The earliest form of the *P. tilmanni* group (= *P. cf. tilmanni*) described from Chilingote has a steep umbilical wall (HILLEBRANDT 2000a: 98, 180, pl. 11, figs. 1-5) similar to that of *P. spelae tirolicum* n. ssp. Most of these earliest specimens are characterized by a very weak nodose stage. Specimens of *P. tilmanni* s. str. rarely exhibit a coarse nodose stage. 8 to 10 nodes are present. The suture line is characterized by triphyllid saddles next to the lateral lobe (HILLEBRANDT 2000a, fig. 39). A specimen of the earliest *P. tilmanni* (now determined as *P. cf. tilmanni*) has a suture line (Fig. 13.7) with more biphyllid than triphyllid saddles next to the lateral lobe. The inner suture line of *P. tilmanni* (Fig. 13.8) (whorl height 3.2 mm) is similar to that of *P. spelae tirolicum* n. ssp. at a similar whorl height (Fig. 12.1, 12.2a).

The Phylloceratoidea are the source of the Jurassic ammonites (Fig. 14). The Late Triassic genera show similarities with *P. spelae* but no Triassic phylloceratid has an inner nodose stage. *Eopsiloceras planorboides* (GÜMBEL) is

more evolute, especially the inner whorls and the saddles of the suture line next to the lateral lobe are more monophyllid than biphyllid. The umbilical lobes are less retracted. The venter is rounded. A whorl fragment (cf. *Eopsiloceras*) (Fig. 14) of a body chamber with the end of the phragmocone was found in the (? middle) Rhaetian of the Zlambach area. The venter of this specimen is narrowly rounded. The saddles of the suture line next to the lateral lobe are biphyllid. The umbilical lobes are retracted and their number is the same as in *P. spelae tirolicum* at a similar whorl height. *Eopsiloceras germigense* was described by YIN et al. (2007) from the Late Rhaetian Marshi Zone of Tibet. It has a similar suture line with bi- to triphyllid saddles but less retracted umbilical lobes. The growth lines are more sinuous.

Tragorhacoceras (Fig. 14) is more involute than *P. spelae tirolicum* n. ssp. and the whorl section is different. The suture line is similar: biphyllid saddles next to lateral lobe, retracted umbilical lobes and equal number.

The elliptical to subrounded-triangular whorl section of *Rhacophyllites debilis* (HAUER) (RAKUS 1993; WIEDMANN 1970) is more similar to that of *P. spelae tirolicum* n. ssp. than that of other phylloceratids.

The growth lines of all three genera are similar to those of *P. spelae tirolicum* n. ssp. All three phylloceratid genera show similarities but each of them shows also differences of various kind. None of these genera combines all characters found in *P. spelae tirolicum* n. ssp. The greatest similarities are probably with the whorl fragment determined as cf. *Eopsiloceras* (Fig. 14).

Interpretation as microconchs: All specimens of the new subspecies can be interpreted as microconchs on basis of the following characters: small size in adult stage (egression of the body chamber, approximated last suture lines of the phragmocone), short body chamber (hardly more than half a whorl), presence of a conspicuous aperture. A corresponding macroconch is not yet known.

Microconchs of psiloceratids exhibiting similar characters are known from *Psiloceras tilmanni* (HILLEBRANDT 2000a, pl. 11, figs. 15, 17), *Psiloceras calliphyllum* (Fig. 13.9-13.11 and comm. G. BLOOS, not yet published), *Psiloceras sampsoni* (= *pilonotum* QUENSTEDT), named by POMPECKJ (1893), *Psiloceras brevicellatum* (see BLOOS 1999: 18) as well as *Wahneroceras tenerum* and its close relatives.

Variability through time: There cannot be recognised any changes of *P. spelae tirolicum* n. ssp. from base to top of the 90-95 cm thick *spelae tirolicum* bed. Specimen 0030 (Fig. 10.2) was found at the base (60 cm below the crinoid bed) and specimen 0026 (Fig. 10.3) at the top (30 to 35 cm above the crinoid bed). Both specimens have a body chamber which is approximately half a whorl long and the nodose stage is neither especially weak nor especially strong.

Duration of time of the *spelae* biohorizon and the *spelae* beds in the NCA: Based on radiometric data of SCHALTEGGER et al. (2008) the Hettangian has an overall duration of 2 ma. Dividing this amount by 3 zones,

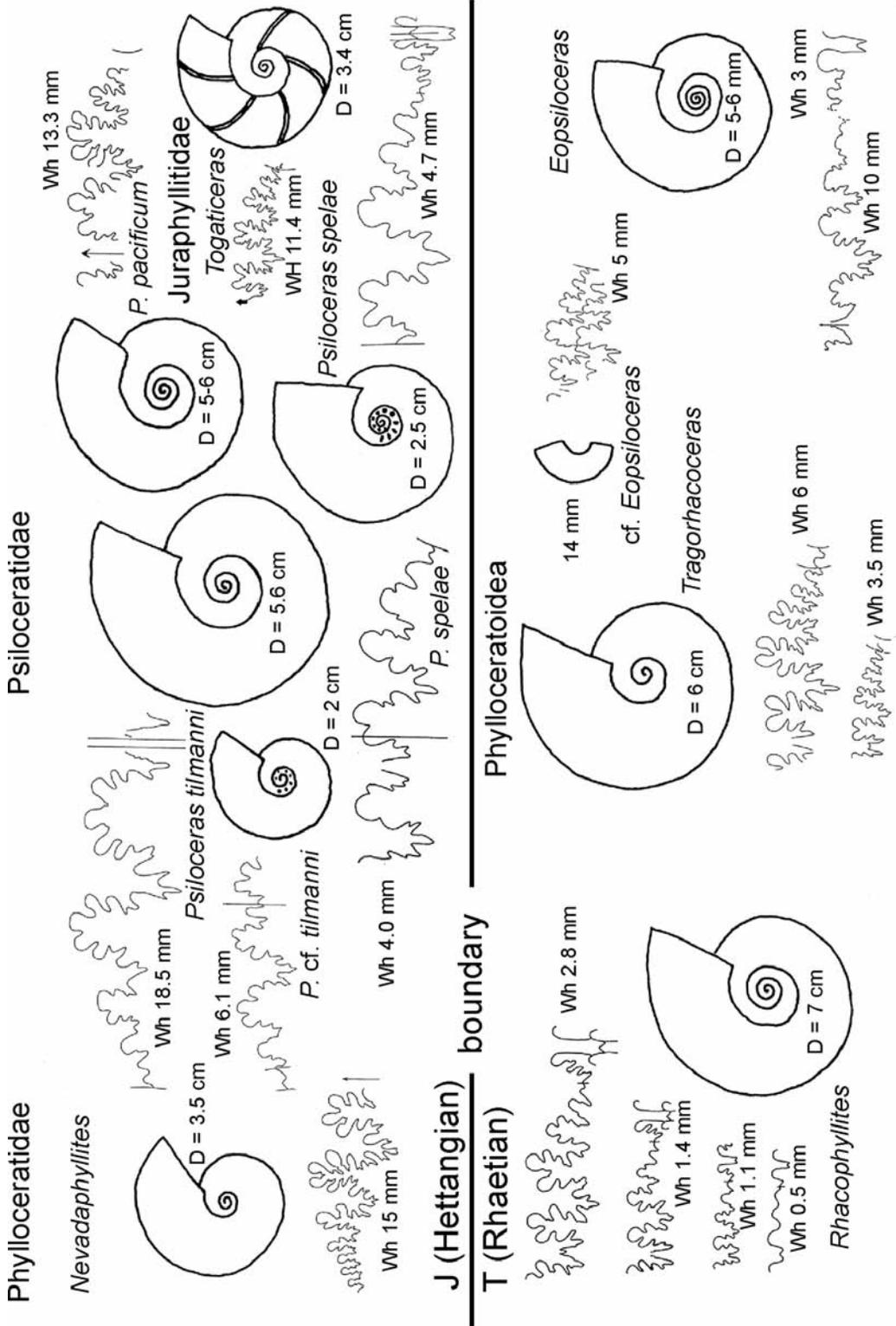


Fig. 14. Evolution of Early Hettangian Ammonitina (Phylloceratidae, Psiloceratidae, Juraphyllitidae) from Late Triassic Phylloceratoidea. Spiral lines of conch and suture lines.

the Planorbis Zone by 3 subzones, and the Tilmanni Subzone by 3 biohorizons there can be calculated a rough time duration of less than 100 ka (approx. 70 ka) for the *spelae* biohorizon. This is certainly an approximation but could come close to its real duration.

The interval with *P. spelae tirolicum* n. ssp. is in the Hochalplgraben 90 to 95 cm thick. The beds from the *spelae* biohorizon to the basis of the *calliphyllum* Bed comprise 17 to 18 m. Following SCHALTEGGER et al. (2008) and the above made calculations, time duration of the Jurassic Tiefengraben Mb. matches 220 ka and time duration of 1 m of sediment 12 to 13 ka.

Based on a cyclostratigraphic survey of Irish and southern England sections A. J. JERAM (Larne, N, Ireland – diagram communicated 2007 to the members of the T/J working group) calculated for the Early Hettangian 550 ka and approx. 200 ka for the period from the *spelae* biohorizons to the basis of the *Neophyllites* biohorizon (equaling base of the *calliphyllum* Bed) giving a similar duration of 11-12 ka per metre of the Tiefengraben Mb. Since both independent calculations are strikingly similar, their results may be a rather realistic approximation.

Age: *Psiloceras spelae tirolicum* n. ssp. is proposed as boundary marker for the base of the first stage of the Jurassic, the Hettangian. Until now this subspecies has been found at three localities in the western Karwendel Syncline. *Psiloceras spelae spelae* from Nevada and *P. spelae* from Northern Peru belong to the same ammonite biohorizon. No further subdivision of the *spelae* Horizon is possible. The two subspecies thus cannot be separated in terms of chronostratigraphy.

P. spelae spelae is found in Nevada (GUEX 1998 et al.) together with a psiloceratid determined as *P. tilmanni* (GUEX et al. 1998). The corresponding specimens are flattened on the bedding plane, and because of the lacking of whorl section, suture line, and umbilical wall an exact determination is not possible. The incompletely preserved specimens probably belong to the *P. tilmanni* group but the assignment to a certain biohorizon is difficult. A species near to *P. tilmanni* (*Psiloceras* ex gr. *P. tilmanni*) was found in the Kuhjoch section 1.5 to 1.7 above the beds with *P. spelae tirolicum* n. ssp. Since ammonites of the tilmanni group are not found in the *spelae* tirolicum bed it cannot be excluded that the age of *P. spelae spelae* is slightly younger than that of *P. spelae tirolicum* n. ssp.

SCHALTEGGER et al. (2008) figured *P. spelae* from a section in Northern Peru near to one described by HILLEBRANDT (2000a, fig. 5a). *P. spelae* was found there 5.4 m above the last *Choristoceras* (*C. crickmayi*) and 13 m below the first *P. tilmanni* (SCHALTEGGER et al. 2008, fig. 2). The first *P. tilmanni* were found by HILLEBRANDT (2000a, fig. 5a) 11.5 m above the last *Choristoceras*. The distance between the last *Choristoceras* and the first *P. tilmanni* is much higher (18.4 m) in the section of SCHALTEGGER et al. (2008, fig. 2). Nevertheless, there is at least 6.5 m between *P. spelae* and *P. tilmanni* and both species are not found together. The sections described by HILLEBRANDT (2000a) and SCHALTEGGER et al. (2008) have the highest sedi-

mentation rate of all known T/J boundary sections with ammonites.

Near the *spelae* horizon also changes in the foraminifera, ostracods, and palynomorphs occur. They may be useful to recognize approximately the base of the Jurassic in sections lacking ammonites.

Psiloceras sp. ex gr. *Psiloceras tilmanni* LANGE, 1925
Fig. 13.1-13.4

Localities:

- Kuhjoch section (Figs. 4, 6): Marls with *Reinholdella* sp. 1.5 to 1.7 m above top of the range of *Psiloceras spelae tirolicum* n. ssp. and *Praegubkinella turgescens* FUCHS.
- Ochsentaljoch section (Figs. 4, 6): Marls with *Reinholdella* sp., sample 1.5 to 1.6 m above first sample of measured section.

Material:

- Kuhjoch: All specimens were found in a sample (061021/8) which was taken for micropaleontological investigations. One fragmented specimen with a diameter of ca. 5 mm (specimen 0049) and 9 small casts (innermost whorls and protoconchs) with a diameter up to 1.7 mm.
- Ochsentaljoch: A whorl fragment (specimen 0057), 1 cm long with a whorl height of at least 1 cm. Mostly without shell.

Description:

- Kuhjoch specimens: The fragmented specimen 0049 is a crushed limonitic cast. The exact whorl section of the involute conch cannot be seen. The umbilical wall is high and rounded. The shell surface is smooth. A clear nodose stage is not visible. The suture line could be drawn of both sides at the end of the whorl fragment at a whorl height of ca. 3 mm. The saddle between E and L is biphyllid and irregularly triphyllid between L and U₂. The umbilical lobes are retracted.

The involute specimen 0046 (Fig. 13.1a-d) has a diameter of 1.6 mm (Wh = 0.75 mm, Ww = 1.1 mm; Wh: Ww = 0.68; U = 0.3 mm, U% of D = 18.8). The whorl section is rounded and wider than high. The external suture line is still very simple (L, U₂, U₃).

The involute specimen 0047 (Fig. 13.2a-c) has a diameter of 1.7 mm (Wh = 0.8 mm, Ww = 1.1 mm, Wh: Ww = 0.73, U = 0.45 mm, U% of D = 26.5). The rounded whorl section is wider than high. The external suture is the same as found in specimen 0046.

Specimen 0048 (Fig. 13.3a-d) is a protoconch with ³/₄ of the first whorl. The barrel shaped protoconch has an angustisellate prosuture and a primary suture with a lateral lobe and an umbilical lobe U₂ at the umbilical seam.

- Ochsentaljoch specimen (specimen 0057): A rounded umbilical edge is present on the inner side of the flank. The outer flank is incomplete and the transition to the venter is missing. The shell surface is smooth.

Remarks and comparisons: The Kuhjoch specimens are too small for an exact determination. The specimens are distinguished from *P. spelae tirolicum* n. ssp. by the whorl

section and the suture line. In *P. spelae tirolicum* n. ssp. the whorl section is already subtriangular at a whorl height of 1 mm whereas in *P. ex gr. P. tilmanni* it is broadly rounded at the same whorl height. The saddles of the suture line of *P. spelae tirolicum* n. ssp. are mostly biphyllid whereas in *P. ex gr. P. tilmanni* they are transitional to triphyllid.

Juvenile specimens of *P. tilmanni* from Peru are very similar. A specimen (900928/2/7) from the basal part of the beds (Chilingote) has a diameter of 3 mm. The nodes are very weak on the last whorl as also in a specimen (900928/2/6) with a diameter of 6 mm. The umbilical width of the inner whorls is similar. Specimens 900928/2/6 and 7 still have a whorl section wider than high as also found in *P. ex gr. P. tilmanni*. The saddles of the suture line (Fig. 13.7) of a specimen from the lowest bed with specimens of the *P. tilmanni* group (*P. cf. tilmanni*) are transitional from biphyllid to triphyllid. An exact determination of the Ochsentaljoch fragment is impossible.

Age: The Kuhjoch sample with *P. ex gr. P. tilmanni* probably corresponds to the lowest part of the *P. tilmanni* horizon in Peru. The fragment from Ochsentaljoch was found slightly higher (ca. 1 m) than the Kuhjoch specimens.

Psiloceras cf. pacificum GUEX, 1980
Fig. 10.11-10.14

- cf. 1980 *Psiloceras pacificum* sp. n. – GUEX, p. 137, pl. 1, fig. 6.
cf. 1995 *Psiloceras pacificum* GUEX. – GUEX, p. 18, pl. 3, figs. 1-16, pl. 4, figs. 1-10, pl. 6, figs. 1, 10; text-figs. 9-10.

Localities:

Hochalplgraben section (Fig. 5): Clayey marls with *Reinholdella* sp. (foraminiferan), 6.2 to 6.6 m above crinoid bed within beds with *Psiloceras spelae tirolicum* n. ssp.
Ochsentaljoch section (Fig. 6): Marls with *Reinholdella* sp., 5.0 to 5.2 m above the first sample of the measured section.
Kuhjoch section (Fig. 6): Marls with *Reinholdella* sp., ca. 6 m above beds with *Psiloceras spelae tirolicum* n. ssp.

Material:

Hochalplgraben: 4 specimens, diameter 3.5 to ca. 12 mm; small, badly preserved specimens and whorl fragments (Wh up to 10 mm; original diameter ca. 30 mm).
Ochsentaljoch: 1 specimen, diameter 11.5 mm.
Kuhjoch: 1 specimen, diameter 3.9 mm.

Measurements: See Table 2 in the Appendix.

Description: All specimens are small or very small, in part uncrushed, but mostly crushed.

Hochalplgraben: Specimens 0050 and 0052 are uncrushed (in part with shell) and pyrite-filled. Specimen 0050 (Fig. 10.13) has a diameter of 10 mm and is moderately involute (U 32% of D). The whorl height increases slowly. At the end of the conch the whorl height is slightly higher than the whorl width. The external side is broadly round, the

umbilical wall steep, the umbilical edge slightly rounded and the umbilicus is deep. The surface of the conch is smooth. Nodes are not visible. The suture line is partly exposed. The saddle between L and U₂ is triphyllid and the umbilical lobes are clearly retracted.

Specimen 0051 (Fig. 10.14) is flattened and only a segment is preserved without the innermost whorls. The original diameter was ca. 12 mm. The whorl height increases more quickly than in specimen 0050. The shell surface is smooth. The inner whorl is not sufficiently preserved to identify nodes.

The umbilicus of the involute and small specimen 0052 (Fig. 10.12a, b) is filled with pyrite. The whorl section is wider than high and broadly rounded. The umbilical wall is steep. Weak nodes (ca. 7 per whorl) are visible near to the umbilical edge.

Specimen 0053 (with shell) (Fig. 10.11) is filled with sediment and laterally deformed. The umbilicus is deep, the umbilical wall steep and on the slightly rounded umbilical edge are found 7 to 8 distinct nodes.

Of specimen 0054 (not figured) the inner side of the shell and its cast are present. The fragment is 15 mm long and the whorl height is 10 mm, part of the crushed venter can be seen. The surface is smooth. The original diameter of the specimen was probably approximately 30 mm.

Ochsentaljoch: Specimen 0055 (not figured) is uncrushed. The shell is broken by compaction into many small fragments. The general shape is comparable with that of specimen 0050 from the Hochalplgraben.

Kuhjoch: The small specimen (specimen 0056; not figured) is filled in part with sediment, the shell is crushed. The involution is similar to that of the small specimen (specimen 0053) from the Hochalplgraben. Weak nodes are visible.

Remarks and comparisons: The small specimens are not sufficiently preserved for an exact determination. Very similar are small specimens of *Psiloceras pacificum* GUEX (Fig. 10.15a, b) from the type locality as also are specimens from Northern Peru which were determined by HILLEBRANDT (2000a, e.g. pl. 13, figs. 21a, 22) as *Psiloceras tilmanni* LANGE.

Age: *P. pacificum* appears in North America (Nevada) in the middle part of the Early Hettangian. Specimens similar to *P. pacificum* are found in South America (Northern Peru) mainly in the upper part of beds with *Psiloceras tilmanni*.

Psiloceras sp. A
Fig. 11.6a, b

Locality: Hochalplgraben section (Fig. 5, level 4a); limestone bed (20 cm thick and with bivalves mainly in the lower part), 10 m above the crinoid layer within beds with *Psiloceras spelae tirolicum* n. ssp.

Material: Whorl fragment (max. length 4.2 cm) (specimen 0045).

Description: The fragment has an outer spiral curvature of a moderately involute specimen with a diameter of at least 5 cm. The fragment consists of an outer whorl (cast with recrystallized shell, probably body chamber) and an incomplete, calcitic inner whorl (probably phragmocone). The flanks of the outer whorl are weakly arched and nearly flat. The venter is highly arched. The umbilical wall is low. The surface of the shell is smooth. The whorl height of the outer whorl is 16.4 mm and the whorl width 10.0 mm ($Wh : Ww = 1.64$).

Remarks and comparisons: The body chamber of the specimen is smooth. Above beds with completely smooth *Psiloceras* and an inner nodular stage species are found with an inner ribbed stage and a smooth body chamber: *P. planocostatum* HILLEBRANDT, *P. primocostatum* HILLEBRANDT, *P. minillaensis* HILLEBRANDT in South America, in part *P. polymorphum* GUÉX in North America and in part the *P. calliphyllum* group in the Northern Calcareous Alps. *Psiloceras erugatum* (PHILLIPS) in Great Britain also is characterized by an inner nodular stage, a more or less strongly and regularly ribbed phragmocone and a body chamber that can be smooth. This species probably descended from a smooth Tethyan forerunner. The most similar species is *Psiloceras minillaensis* found in Northern Chile (HILLEBRANDT 2000a).

The curvature of *Psiloceras* sp. A can be compared with that of a specimen figured by HILLEBRANDT (2000a, pl. 11, fig. 12; U of D 33.3 to 34.5%) as *P. tilmanni* but this specimen has a much wider whorl section. The curvature and the whorl section of *Psiloceras* sp. A is similar to that of *P. primocostatum*. The whorl sections of the more evolute *P. pacificum* and also *P. polymorphum* are much wider. *P. erugatum* and *P. minillaensis* have a similar whorl section but a more evolute conch as also most specimens of the *P. calliphyllum* group which appear at the Ochsentaljoch section 10 m above this limestone bed with bivalves. *Psiloceras* sp. A is probably a species not yet described from elsewhere.

Age: *Psiloceras* sp. A was found in a bed above the beds with *P. cf. pacificum* and below the condensed *calliphyllum* bed. The biostratigraphic position must be in-between, in the middle part of the Early Hettangian.

Superfamily Phylloceratoidea ZITTEL, 1884
Family Juraphyllitidae ARKELL, 1950
Genus *Togaticeras* RAKUS, 1993

Type species: *Phylloceras togatum* NEUMAYR, 1879

Togaticeras cf. *goisernense* RAKUS, 1999
Fig. 10.16

cf. 1999 *Togaticeras goisernense* n. sp. – RAKUS, p. 331, text-fig. 3, pl. 1, fig. 1.

Locality: Hochalplgraben section (Fig. 5); clayey marls with *Psiloceras spelae tirolicum* n. ssp.

Material: Whorl fragment (max. length 23 mm) (specimen 0058).

Description: The whorl fragment is preserved with shell, but the shell is mostly lost and the fragment is filled with sediment (? body chamber). The cast is laterally compressed by compaction. The whorl height is 12 mm, the flanks are flat, the venter is rounded and the umbilical wall is steep low. Two constrictions are visible at the end of the fragment in a distance of 5 mm (middle part of flank). The constrictions are prorsiradiate from the umbilical wall to the middle of the flank. On the ventral part of the flank they bend forward and are crossing the venter forming a short arc. The constrictions consist of a shallow groove and a following low wall. The remaining surface is smooth.

Comparison: The fragment is very similar to *T. goisernense* which was described from the Early or mid-Hettangian of the Zlambach Graben near Bad Goisern, Austria.

Age: Earliest Hettangian, *spelae* horizon.

5. Palaeobiogeography, evolution, and biostratigraphy

The end-Triassic biotic crisis is now thought to be connected with the CAMP volcanism (LUCAS & TANNER 2007; PALFY 2003). This volcanism is regarded as source of high concentration of carbon dioxide in the atmosphere leading to an acidification of the air and subsequently of the ocean (HAUTMANN 2004). The beginning of this volcanism is linked in the NCA to the sudden change from carbonate to terrigenous sedimentation and contemporaneously from an arid to a more humid climate as indicated in the palynological record (KUERSCHNER et al. 2007). The duration of the crisis is still difficult to estimate but hundred thousand years based on calculation of the sedimentation rates may be a good approximation.

A contemporaneous and widespread recorded sea-level fall in the NCA must have been relatively fast (less than 100 ka) and was followed by a very slow sea-level rise during the crisis interval and the Early Hettangian. Ecological conditions were further affected by a spread of dysoxic or even anoxic bottom water to the shelf (HALLAM & WIGNALL 1997) during the maximum of regression. All that may have led to a worldwide disappearance of ammonites from the shelf seas during the crisis when almost all Triassic ammonoid groups of the open sea became extinct except for the Phylloceratina (Fig. 16). A single neritic ammonoid group (Choristoceratidae) survived this crisis in the Panthalassa Ocean and repopulated locally the Early Hettangian shelves of North and South America.

	Zones	Northern Calcareous Alps this paper	NW Europe (Great Britain) PAGE 2003 (modif.)	North America (Nevada) GUEX et al. 2004 (modif.)	South America (Chilingote) HILLEBRANDT 2000b(m.)
Lower Hettangian	Planorbis	P. naumanni	C. johnstoni	C. crassicostatum	P. cf. calliphylloides
		P. costosum + P. calliphyllum	P. plicatulum	-----	P. rectocostatum
		Neophyllites	P. psilonotum	P. polymorphum	P. primocostatum
	Tilmanni	Neophyllites	P. planorbis	-----	P. planocostatum
		P. erugatum	P. pacificum	-----	P. tilmanni
		P. cf. pacificum	P. marcoux + Odog.	P. cf. tilm. + Odog.	P. cf. spelae
		P. ex gr. P. tilmanni	?	P. spelae	
Psiloc. spelae					
Rhaetian	Marshi	Choristoceras marshi	Choristoceras crickmayi	Ch. marshi + Ch. crickmayi	

Fig. 15. Correlation of Early Hettangian ammonite zones, subzones and horizons (grey), broken lines approximated correlation.

The evolution of the first Jurassic ammonites may have been begun in the open seas far from the land areas. From there they immigrated repeatedly to the shelf seas. The immigration began with the pandemic *Psiloceras spelae* followed by the probably also still pandemic *Psiloceras tilmanni*. The immigration reached first the shelves immediately adjacent to the open parts of the Tethys and of the eastern Pacific. In basins more distant from the open sea such as Northwest Europe or the backarc area of Northern Chile the earliest forms of *Psiloceras* are lacking despite of continuous marine conditions as in Great Britain or Ireland (WARRINGTON et al. 2008; SIMMS & JERAM 2007).

A second significant evolutionary step is the splitting of the psiloceratids into regional trends caused by geographical separation (e.g. *Psiloceras planorbis*). In spite of increasing provincialism some faunal exchange can be observed at least between the Northwest European and the Mediterranean Provinces. A very important evolutionary event was the acquisition of a nodose juvenile stage which is not known in phylloceratids. This stage was lost in different species of the epicontinental shelf (e.g. of NW Europe) not connected directly with the open oceans. The trend from smooth forms to those with ribs was a gradually

process and probably occurred in different evolutionary lines. An increase of complication but also a simplification of the suture line can be observed in several groups of species during phylogeny. The whorl width increased during the evolution of *Psiloceras*.

It seems that between the disappearance of the last Triassic ammonites and the appearance of the first Jurassic ammonites, in the neritic shelf areas, a global Oceanic super-realm must have existed that unified the otherwise strictly separated Pacific (Panthalassa) and Tethyan realms. Soon this super-realm has been again separated into faunal provinces as the NW European and the Mediterranean provinces (NCA) in the Tethys or the North and South American provinces (sensu WESTERMANN 2000) in the Panthalassa.

If a fossil group is suitable as a global biostratigraphic standard this is highly dependent on the biogeographic distribution of this fossil group and its evolutionary rate. In terms of Jurassic ammonites the

Fig. 16. Correlation of T/J boundary markers from different faunal provinces, time scale according to A. J. JERAM (diagram communicated 2007 to the members of the T/J working group of ISJS).

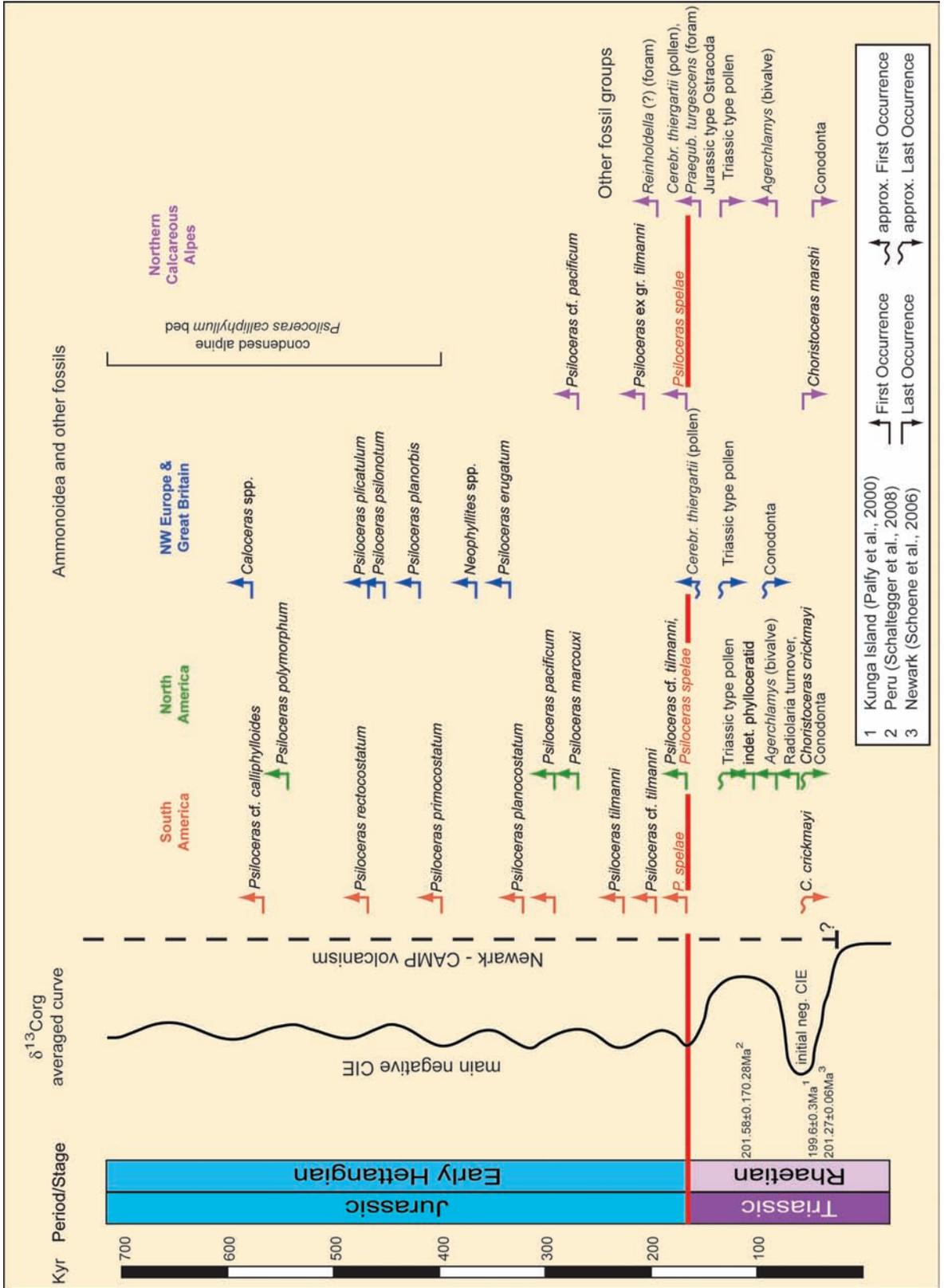


Fig. 16 (Legend see p. 188)

latter is rather fast allowing a biochronology built on chrono- or standard zones divided into subzones and those again into biohorizons. The Planorbis Chronozone was until now the lowest Standard Zone of the Jurassic and formed the base of the Hettangian Stage (OPPEL 1856; DEAN et al. 1961) (Fig. 15). The Planorbis Zone was subdivided in the Planorbis and Johnstoni subzones. The Planorbis Subzone was further divided into 6 biohorizons (PAGE 2003). The lowest biohorizon was characterized by *Psiloceras erugatum*, a species presently only found in Great Britain. WARRINGTON et al. (2008) argued to maintain the former definition of the basis of the Planorbis Chronozone (and, consequently, of the Hettangian Stage and the Jurassic System) by the appearance of the first true *Psiloceras planorbis* (Fig. 15). The latter is, however, an endemic species restricted to NW Europe (mainly Great Britain) whose evolutionary origin is unknown. Since the discovery of ammonite occurrences below *Psiloceras planorbis* in Britain it is an open question if these biohorizons (*Neophyllites* and *P. erugatum*) should be included into the Planorbis Zone or not. If yes, this zone would begin with the appearance of *Psiloceras erugatum*, the earliest known *Psiloceras* in the Northwest European Province.

A long period (ca. 250 000 years) (Fig. 16) exists between the first appearance of *Psiloceras spelae* in the Mediterranean and East Pacific Provinces and the first appearance of *P. planorbis* in Great Britain. This long period includes up to 5 biohorizons (Fig. 15) of which at least the lower three known from South America should not be included into the Planorbis Zone. For the upper two of these three South-American biohorizons a Tilmanni Zone was introduced by HILLEBRANDT (1994, 2000b). For this reason we propose the introduction of a Tilmanni Standard Zone below the Planorbis Standard Zone (Fig. 15). The base of the Tilmanni Standard Zone is defined by the first appearance of *Psiloceras spelae*, represented in the Northern Calcareous Alps by *P. spelae tirolicum* n. ssp. and in North and South America by *P. spelae spelae* GUEX.

The upper boundary of the Tilmanni Zone is defined by the lower boundary of the Planorbis Standard Zone. The lowest position of this boundary could be the first appearance of *Psiloceras erugatum* in Great Britain (PAGE 2003) and the highest position would be the first appearance of *Psiloceras planorbis* in Great Britain (WARRINGTON et al. 2008).

The lowest biohorizon of the Tilmanni Standard Zone is the *spelae* horizon (Figs. 15-16) which is found in the NCA, North America (Nevada) and South America (Northern Peru).

The second biohorizon is characterized in the NCA by a species belonging to the *Psiloceras tilmanni* group s. str. and in South America by the appearance of *Odoghertyceras* and a species related to *P. tilmanni*. *P. cf. tilmanni* is distinguished from *P. tilmanni* s. str. by a relatively high and steep umbilical wall which, in contrary, in *P. tilmanni* s. str. has a low angle.

The second biohorizon of the Tilmanni Standard Zone is difficult to prove in Nevada because between the appearance of *P. spelae* and the next biohorizon (distance more than 7 m) no characteristic ammonites were found. A species described by GUEX et al. (1998) as *Rhacophyllites bloosi* looks similar to *P. cf. tilmanni* with a steep umbilical wall but the whorl section probably is more rounded. This specimen was found ca. 4.8 m above *P. spelae*.

A third biohorizon is found in the NCA which is characterized by *P. cf. pacificum* and can be approximately compared with the beds with *Choristoceras minutum*, *Odoghertyceras deweveri* and *Psiloceras marcouxii* in the sections of the New York Canyon area (Nevada). The lower part of the beds with *P. tilmanni* s. str. in Peru (Fig. 15) can be compared with this horizon. The uppermost part of the Peruvian *tilmanni* Zone (Fig. 15) and most part of the *pacificum* Zone in Nevada cannot be proved with certainty in the NCA thus far. *Psiloceras* sp. A (ca. 3.5 m above *P. cf. pacificum*) may belong to this time span. The best sections in sediments of this time (*tilmanni* and *pacificum* horizons) are in Northern Peru (Chilingote) and Nevada (New York Canyon) and need further study to achieve an exact bed-by-bed correlation.

A detailed subdivision in ammonite horizons of the upper part of the Early Hettangian is possible in Great Britain and in Northern Chile (Fig. 15). In Great Britain and Northern Chile different species appeared at this time which are found only in NW Europe or South America. Fortunately some NW European species also occur in the NCA (BLOOS 2004). But this time span is strongly condensed in the NCA and often more than one ammonite horizon is found in the *calliphyllum* limestone bed which is only 10 to 20 cm thick.

An exact correlation of biohorizons of the upper part of the Early Hettangian (Fig. 15) is much more difficult because the provincialism is stronger pronounced than in the lower part.

The following arguments provide reasons to establish *Psiloceras spelae* as the boundary marker for the base of the Jurassic:

- a) The genus *Psiloceras* characterizes the earliest Jurassic worldwide. *Psiloceras spelae* is the oldest known species of this genus. Therefore it is suitable as boundary marker.
- b) *Psiloceras spelae* occurs globally, represented by *P. spelae spelae* both in North and South America and by *P. spelae tirolicum* n. ssp. in Europe.
- c) Both subspecies can be considered as representatives of the *spelae* biohorizon and enable a global biostratigraphic correlation.
- d) All younger species of the genus *Psiloceras* show a more restricted distribution and admit only a less exact correlation. Only *P. spelae* is distributed globally and therefore is the most suitable species of *Psiloceras* to serve as boundary marker.
- e). *P. spelae tirolicum* n. ssp. is much more frequent in the studied sections and much better preserved as *P. spelae spelae*.
- f). All characters necessary for a complete diagnosis of an ammonite are known from *P. spelae tirolicum* n. ssp. The conch is documented from the protoconch to the peristome from uncrushed specimens. The suture line is completely known in regard of its inner and outer elements and of its ontogeny. The anaptychus is also known.

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Appendix

Table 1. Measurements of *Psiloceras spelae tirolicum* n. ssp. [abbreviations see text (taxonomic description)].

Specimens	D (mm)	Wh (mm)	Ww (mm)	Wh : Ww	U (mm)	U % of D
Hochalplgraben, uncrushed, with shell						
0001	24.1	10.5	-	-	6.57	27.2
(holotype)	18.2	8.6	5.5	1.56	4.7	26.0
0002	20.3	9.1	-	-	5.5	27.0
	15.3	6.25	-	-	4.2	27.5
0003	17.0	6.8	-	-	5.3	31.2
	12.7	5.3	-	-	3.6	28.3
0004	14.4	5.9	3.4	1.7	4.4	30.5
	11.7	4.8	3.0	1.6	3.3	28.0
0005	13.3	5.6	-	-	4.06	30.5
	10.5	4.06	3.3	1.23	3.12	29.8
0006	16.4	6.56	-	-	5.3	32.3
	12.03	5.0	-	-	3.9	32.4
	11.56	4.38	ca. 3.3	ca. 1.39	3.75	32.4
0007	13.44	5.16	3.9	1.32	4.06	30.2
0008	15.78	6.41	-	-	4.84	30.7
	9.91	4.69	3.1	1.51	2.59	26.2
0009	15.16	6.25	-	-	4.53	30.0
	12.5	5.0	ca. 4.0	ca. 1.25	3.75	30.0
0010	4.4	1.9	1.5	1.27	1.23	28.0
	3.35	1.5	1.1	1.36	0.85	25.4
0011	7.7	3.3	ca. 2.0	ca. 1.65	2.25	29.2
Hochalplgraben, crushed, with shell						
0013	20.77	7.38	-	-	6.15	29.6
	17.39	8.0	-	-	4.31	24.78
	15.54	7.08	-	-	3.85	24.75
0014	19.08	7.69	-	-	5.54	29.0
	16.9	7.73	-	-	4.61	27.3
	15.8	6.15	-	-	4.31	28.6
0015	18.0	6.46	-	-	5.85	32.5
0016	16.79	6.15	-	-	5.23	31.2
	15.54	6.37	-	-	4.46	28.7
	14.92	6.3	-	-	4.15	27.8
	13.69	6.0	-	-	3.85	28.1
0017	18.31	7.23	-	-	6.0	32.8
0018	17.85	6.92	-	-	5.69	31.9
	14.92	5.75	-	-	4.46	29.9
0019	14.6	5.75	-	-	4.46	30.5
	13.7	5.85	-	-	3.79	27.6
	11.6	4.77	-	-	2.92	25.2
0020	12.52	5.23	-	-	3.6	28.8
0025	15.79	6.53	-	-	4.79	30.3
0026	16.3	6.65	-	-	4.5	27.6
0028	19.0	7.1	-	-	6.5	34.2
	14.3	5.3	-	-	4.4	30.8
0029	20.0	8.0	-	-	5.8	29.0
	18.7	7.6	-	-	5.1	27.2
0030	15.9	6.1	-	-	ca. 5.1	32.1
	13.6	ca. 5.3	-	-	ca. 3.8	28.8
0042	10.0	4.3	-	-	2.9	29.0

Table 1. Continued

Schlossgraben, uncrushed, without shell						
0031	17.5	8.05	-	-	5.25	30.0
	16.4	7.07	-	-	4.85	29.6
	15.0	6.75	-	-	4.38	29.2
	13.1	5.0	3.0	1.67	4.0	30.5
Kuhjoch, uncrushed, without shell						
0032	16.95	7.88	-	-	4.88	28.8
	14.75	6.75	-	-	4.25	28.8
	13.0	5.38	3.3	1.6	4.0	30.8
0033	15.6	ca. 5.7	-	-	ca. 5.5	ca. 35.2
	10.6	4.0	3.25	1.6	3.7	35.0
Kuhjoch, crushed, in part with shell						
0034	21.1	8.36	-	-	6.44	30.5
	18.0	6.56	-	-	5.82	32.3
0035	24.0	9.5	-	-	7.2	30.0
0036	13.7	5.2	-	-	4.6	33.6
	9.2	4.2	-	-	3.2	34.8
0037	18.0	ca. 6.4	-	-	ca. 6.3	ca. 35.0
	13.7	5.4	-	-	4.0	29.2
Kuhjoch, crushed, with shell						
0038	19.2	7.6	-	-	5.7	29.7
	17.0	6.8	-	-	5.0	29.4
0039	19.3	7.7	-	-	5.9	30.6
0040	10.0	4.6	-	-	3.0	30.0
	6.8	3.2	-	-	2.0	29.4

Table 2. Measurements of *Psiloceras cf. pacificum* [abbreviations see text (taxonomic description)].

Specimens	D (mm)	Wh (mm)	Ww (mm)	Wh : Ww	U (mm)	U % of D
Hochalplgraben						
0050	10.3	4.0	3.6	1.1	3.3	32.0
0051	ca. 12.0	ca. 4.0	-	-	-	-
0052	3.5	1.4	1.9	0.74	1.05	30.0
	2.5	1.0	ca. 1.6	ca. 0.62	ca. 1.0	ca. 40.0
0053	3.8	1.6	-	-	ca. 1.1	ca. 29.0
	3.4	1.25	-	-	1.05	30.9
Ochsentaljoch						
0055	11.5	ca. 4.8	-	-	ca. 3.0	ca. 26.1
Kuhjoch						
0056	ca. 3.9	1.5	-	-	1.15	29.5