New biostratigraphic data on an Upper Hauterivian—Upper Barremian ammonite assemblage from the Dolomites (Southern Alps, Italy)

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ABSTRACT

A biostratigraphic subdivision, based on ammonites, is proposed for the Lower Cretaceous pelagic to hemipelagic succession of the Puez area (Southern Alps, Italy). Abundant ammonites enable recognition of recently established Mediterranean ammonite zones from the upper Hauterivian Balearites balearis Zone (Crioceratites krenkeli Subzone) to the upper Barremian Gerhardtia sartousiana Zone (Gerhardtia sartousiana Subzone). Ammonites are restricted to the lowermost part of the Puez Formation, the Puez Limestone Member (ca. 50 m; marly limestones; Hauterivian–Barremian). Numerous ammonite specimens are documented for the first time from the Southern Alps (e.g., Dolomites). Ammonite abundances are clearly linked to sea-level changes from Late Hauterivian to mid Late Barremian times. Abundance and diversity peaks occur during phases of high sea-level pulses and the corresponding maximum flooding surfaces (P. mortilleti/P. picteti and G. sartousiana zones). The ammonite composition of the Puez Formation sheds light on the Early Cretaceous palaeobiogeography of the Dolomites. It also highlights the palaeoenvironmental evolution of basins and plateaus and provides insights into the faunal composition and distribution within the investigated interval. The intermittent palaeogeographic situation of the Puez locality during the Early Cretaceous serves as a key for understanding Mediterranean ammonite distribution.

1. Introduction

Lower Cretaceous pelagic to hemipelagic sediments cover relatively small, restricted areas in the higher Dolomites (Southern Alps). In the Southern Alps, cephalopod-bearing deposits are mainly recorded in two different facies (Lukeneder, 2010), the calcareous limestones of the Biancone Formation (= Maiolica Formation in the Appenines; see Weissert, 1981) and the more marly Puez Formation (Lukeneder, 2010).

The stratigraphy of the Lower Cretaceous Puez area is based on microfossils, nannofossils and ammonites (Lukeneder and Aspmair, 2006; Lukeneder, 2010), but a detailed ammonite biostratigraphy and zonation was still missing because ammonites have not been collected bed-by-bed over the last 150 years. This paper presents the results of the systematic ammonite sampling at the Puez section and concludes with a detailed ammonite zonation of that locality. The Mediterranean character of the ammonite fauna is comparable to numerous Lower Cretaceous east-central European (Czech Republic, France, Hungary, Slovakia, Spain), eastern Europe (Bulgaria, Romania) and African (Algeria, Morocco) localities.

The main goal of this paper is to present a valid definition of the Lower Cretaceous ammonite zonation within the Dolomites for the Puez Formation. The Hauterivian and Barremian ammonite faunas from the Puez key-section can be correlated with the most recent ammonite standard zonation for the Lower Cretaceous (Reboulet et al., 2009). Future work will involve palaeomagnetic, isotope and geochemical analyses along with a precise biostratigraphy based on macro-, micro- and nannofossils.

2. Geological setting and section studied

The outcrop is situated on the Puez-Odle-Gardenaccia Plateau in the Dolomites (maps Trentino—Alto Adige; South Tyrol; Lukeneder, 2010). The exact position is about 30 km northeast of Bozen (Fig. 1A; E 011°49′15″, N 46°35′30″; Lukeneder, 2010). The grey, green to red succession of the Puez Formation is located on the southern side of the Piz de Puez.

2.1. Geological setting and palaeogeography

The studied sites are outcrops on the Puez-Gardenaccia Plateau (Lukeneder, 2010). They are located within the area of the
Puez-Odle-Geisler natural park in the northern part of the Dolomites. The Dolomites (Permian–Cretaceous) are an internal part of the Southern Alps; they are a northern Italian chain that emerged during the deformation of the passive continental margin of the Adriatic (= Apulian Plate) of the South Alpine–Apennine Block (Dercourt et al., 1993; Fourcade et al., 1993; Bossellini, 1998; Cecca, 1998; Stampfli and Mosar, 1999; Scotese, 2001; Stampfli et al., 2002; Bossellini et al., 2003). This block was limited by the Penninic Ocean (= Alpine Tethys) to the north and the Vardar Ocean to the southeast (Scotese, 2001; Stampfli et al., 2002). The Puez Formation comprises three members from bottom to top: Puez Limestone, Puez Redbed and Puez Marl (Lukeneder, 2010). The succession shows a transition from limestones and marly limestones into a marl–marly limestone alternation in the upper half of the section. A detailed description of the geology and lithostratigraphy is given in Lukeneder (2010). The complex Mediterranean palaeogeography, and the presence of microplates in the Tethyan oceanic corridor between Africa and Europe, was discussed in detail in Lukeneder (2010, 2011). The Trento Plateau extends from the south (around Trento) up to the Puez region and was formerly surrounded by two basins: the Lombardian Basin to the west and the Belluno Basin to the east (Lukeneder, 2010). According to recent investigations by Muttoni et al. (2005), the Lombardian Basin, and thus the adjacent Trento Plateau to the east, were located at approximately 20°N in Valanginian–Hauterivian times and at almost 30°N in the Aptian.

3. Previous work

During the late 19th and early 20th centuries, a rich fauna of cephalopods was collected from Lower Cretaceous sediments from this area by Haug (1887, 1889), Hoernes (1876), Uhlig (1887), Rodighiero (1919) and Pozzi (1993). Additionally, microfacies and ammonites were reported from the “Alpe Puez” by Cita and Pasquaré (1959) and Cita (1965), leading them to assume a Hauterivian–Barremian age for the Puez area. After this period, documented by numerous publications on the ammonite fauna of the Puez and adjacent areas by the latter authors, no further investigations were undertaken at the main locality of Puez. This phase of stagnancy in Lower Cretaceous papers was followed by descriptions of small ammonoid faunas from different localities near the Puez area, e.g., from La Stua by Baccelle and Lucchi-Garavello (1967) and Stöhr (1993, 1994). The latter papers compared the faunas from La Stua with the Puez ammonite faunas from Haug (1887, 1889) and Uhlig (1887). The most recent contributions on the Lower Cretaceous of the Puez area were published during the last decade and focused on stratigraphy (Lukeneder and Aspmair, 2006), palaeoecology (Lukeneder, 2008) and lithostratigraphy (Lukeneder, 2010, 2011).

4. Material

The ammonites originate from the Puez locality (Dolomites; Fig. 1). Bed-by-bed collecting and a systematic-taxonomic study
Fig. 2. Ammonite assemblage from the Puez locality. Phylloceratina, Lytoceratina, Ammonitina within the log (left) and the ammonite zonation indicated. Upper Hauterivian beds shaded in dark grey and Barremian in light grey. Ammonite occurrences and ranges marked by solid black circles. Bold horizontal line, stage boundary; dashed horizontal lines, zonal boundaries; dotted horizontal lines, subzonal boundaries.
provide the basic data for statistical analysis of the investigated ammonite fauna. The material was collected over the last 3 years within the FWF project P20018-N10 and is stored in the South Tyrol Museum of Natural Sciences and the Natural History Museum in Vienna. The preservation of the ammonites is fair (mostly compressed steinkerns without shell) and represents almost the totality of the macrofauna (96%). Some specimens show partly preserved suture lines. During this study, approximately 1209 ammonites, 40 bivalves, 39 brachiopods, and abundant encrusting species (bivalves, corals, serpulids; Lukeneder, 2008) were examined.

The ammonite assemblage consists of 17 families including 44 different Upper Haurerivian—Upper Barremian genera: Phylloceratidae with Phylloceras, Phyllophachyceras, Sowerbyceras; Lytoceratidae with Lytoceras, Eulytoceras, Proetragonitidae; Desmoceratidae with Plesiostipitidus, Barremites, Valderodessa, Abrytusites, ?Pseudohaploceras, Melchiorites; Silesitidae with Silesites; Holcodiscidae with Astieridus, Holcodiscus, Maurellicus; Pulcheliidae with Gerhardtia, Heinzia, Kototeshivilia, Discoideilla; Haploceratidae with Neolissoceras; Crioceratidae with Crioceratites, Pseudothoarumnia, Pararococeratidae; Emericiceratidae with Emericeria, Honnoratia, Partnoceras; Acrioceratidae with Acrioceras, Dissimulites; Anyplogenerata; Ammonitidae with Toxicoceratidae; Audoulceratidae; Heteroceratidae with Moutoniceratidae; Leptothecoceratidae with Karsteniceras, Hamulinites, Sabaudiella; Ptychoceratidae with Ptychoceras; Hamulinitidae, and Hamulina, Anahamulina, Vaseckina, Pychohamulina, Duyeva; Megacrioceratidae with Megaciceras; Macroscaphitidae with Macroscaphites, Costiscus.

Conventions. NHMV Natural History Museum Vienna, NMB South Tyrol Museum of Natural Sciences. All ammonite specimens in Figs. 3, 6 and 8 were coated with ammonium chloride before photographing. The basic classification of Cretaceous Ammonoidea by Wright et al. (1996), Klein (2005); Vermeulen and Klein (2006) and Klein et al. (2007, 2009) has been followed. The detailed ammonite systematics and taxonomy were adopted and correlated with papers by numerous authors cited in Section 5 below.

5. Biostratigraphic ammonite zonation

The ammonite species and resulting ammonite zones indentified herein for the Puez Formation allow a correlation of the Hauerivian and Barremian strata at the Puez locality with the recent standard zonation (Reboulet et al., 2009). The ammonite zonation established by the Cretaceous Ammonite Working Group ("Kilian Group") at the international meeting on Lower Cretaceous ammonite zonation in Vienna (Reboulet et al., 2009) is followed. Earlier zonations by Hoedemaeker (1990), Rawson et al. (1999), Hoedemaeker and Rawson (2000), Hoedemaeker et al. (2003) and Reboulet et al. (2006) have been considered for correlation of former and recent literature zonations. If a particular zonal ammonite is absent the zonal boundary is interpreted by comparison with faunas that characterize the zone elsewhere. The idea of a Pseudothoarumnia mortilleti Subzone (middle subzone within the “Pseudothoarumnia ohmi” Zone) is accepted. P. mortilleti was meant to be a senior synonym of Pseudothoarumnia catulli (Company et al., 2003, 2005, 2008). A scheme is therefore, followed that includes a P. mortilleti Subzone (Figs. 2, 3, 5, 7). The scheme including a P. catulli Subzone as in Reboulet et al. (2009) is not followed because of the contradiction in synonymy mentioned.

The biostratigraphy is compared to sections in Europe (abridged list) from the Northern Calcareous Alps of Austria (Immel, 1978, 1987; Vašíček and Faupl, 1999; Lukeneder, 2003, 2004a), the Ger-ece and Bakony Mountains in Hungary (Janssen and Fözy, 2005; Fözy and Janssen, 2006, 2009), the Balkan Mountains of Bulgaria (Dimitrova, 1967; Mandov, 1976), the Silesian Units within the Western Carpathians and Pieniny Klippen Belt of Czech Republic and Slovakia (Uhlíř, 1883; Vašíček, 1972, 1994, 1996, 2002, 2008; Vašíček et al., 1994, 2004; Vašíček and Michálek, 1999), the Southern Alps of northern Italy and Umbria-Marche Apeninnes of central Italy (Uhlíř, 1883, 1887; Haug, 1887, 1889; Rodigheiro, 1919; Cecca and Pallini, 1994; Cecca et al., 1994a, b; 1995, 1996, 1998; Faraoni et al., 1995, 1996), different districts around the Vocontian Basin of southeast France (Pictet and Lorliol, 1858; Lory and Sayn, 1895; Busnardo et al., 2003). The biostratigraphy is compared with sections in North Africa: Algeria (Vermeulen and Lahondère, 2006) and Morocco (Company et al., 2008).

The biostratigraphic zonation at Puez ranges from the Upper Haurerivian Balearites balearis Zone up to the Upper Barremian Gerhardtia sartousiana Zone (Figs. 2, 3, 7). Not every standard zone or subzone could be detected at the locality using index ammonite species.

5.1. Balearites balearis Zone

The Balearites balearis Zone is divided into the Balearites balearis, Binellliceraceras binelli, Crioceratites krenkeli and Spathicrioceratites setzi subzones (Reboulet et al., 2009): for correlation, see also Company et al. (2002, 2003). The B. balearis Zone is the oldest ammonite zone detected at Puez, where the succession begins within the B. binelli Subzone. The dominance of the family Crioceratidae (e.g., Crioceratites and Pseudothoarumnia) hints at the Upper Haurerivian. The presence of Pararococeratidae radians (Fig. 4H) and Plesiostipitidus strengthens the Upper Hauerivian age for the lowermost parts of the Puez Formation at Puez (Figs. 2—4). Desmoceratidae occur typically with the genera Plesiostipitidus and Abrytusites (Fig. 4U), and Haploceratidae with Neolissoceras subgrasinum. The B. binelli Subzone is not indicated by the index species but occurs with the family Phylloceratidae comprising Phylloceras tethys and Phyllophachyceras winkleri. The B. binelli Subzone is defined here to be located below the C. krenkel Subzone and characterized by the absence of C. krenkel. The C. krenkel Subzone begins with the first appearance of C. krenkel within bed P1/21 (Fig. 3). The abundance of the index ammonite C. krenkel and the co-occurring ammonite assemblage in beds P1/21 up to bed P1/44 hint at the presence of the C. krenkel Subzone. The C. krenkel Subzone is dominated by the index ammonite C. krenkel (Fig. 4A—C) and is accompanied by P. radians, Anahamulina jourdani (Fig. 4M), P. tethys, Phyllophachyceras infundibulum (Fig. 4V), Phylloceras terverii (Fig. 4W), P. winkleri and Plesiostipitidus subdiffilicus (Fig. 4T). As noted by Reboulet et al. (2009), B. binelli and C. krenkel occur only in the uppermost part of the B. balearis Zone, which is characterized by the range of the index species. The uppermost subzone within the B. balearis Zone, the Sp. setzi Subzone, could not be determined so far based on the zonal index ammonite. Its base is tentatively located at the base of bed P1/44 (Figs. 2—4).

Beds within the B. balearis Zone display relatively low numbers of species per bed from one to four. The same numbers are shown in families per bed, with lower numbers in the lower parts increasing to the top of the zone (Fig. 7). The mean number of families in the
B. balearis Zone is five, the maximum is eight within the C. krenkeli Subzone. The minimum is located in the lowermost parts of the zone with one. The evaluation of biodiversity calculated from the ratio between number of species vs. number of individuals per species, the Shannon index, shows a mean value for the B. balearis Zone of 0.84 (min. 0.5, max. 1.8; beds with no specimens excluded). This indicates a low species richness and low evenness in their abundance (Fig. 7).

**Discussion.** Company et al. (2003) reported a more intense ammonite diversification and increased abundance in several ammonite groups for Upper Hauterivian faunas within the zone from the Betic Cordillera compared to the subzones below (e.g., C. balearis and C. binelli subzones). The data provided by Company et al. (2003) broadly correlate with the data presented herein and show that the C. krenkeli Zone is characterized by the occurrence of the index ammonites C. krenkeli, Crioceratites majoricensis, A. journani, N. subgrasianum, P. subdifficilis, A. neumayri, P. guerrianiunum, D. vermeuleni, L. subfimbriatum, P. tethys, P. winkleri and P. infundibulum.

The same faunal compositions were shown by Fözy and Janssen (2006, 2005) within their Crioceratites/Pseudothurmannia assemblages for the B. balearis Zone from the Seresce Mountains in Hungary. The B. balearis Zone embraces, according to these authors, Phylloceras infundibulum (= Phyllocypachysca infundibulum), Phylloceras sp., Lytoceras sp., Plesioposspidiscus spp. and generally Crioceratites sp. accompanied by C. krenkeli. The same condition can be recognized in the more southwestern Bakony Mountains of Hungary (Fözy and Janssen, 2006) with P. tethys, P. infundibulum, P. winkleri, L. subfimbriatum, Neolioscosas gracianum, Abrutysites spp., P. subdifficilis, C. krenkeli, P. radians, Silistes spp. and Discoidella favrei. This assemblage is equivalent to the fauna corresponding to the interval of the B. balearis Zone (C. krenkeli Subzone) and “P. ohmi” Zone at Puez.

Data from Puez correlate with reported Upper Hauterivian assemblages from the Northern Calcareous Alps in Austria comprising P. subdifficilis, P. cf. mortilli, Megacrioceras cf. doublieri, L. subfimbriatum, P. tethys and P. infundibulum (Vašíček and Faupl, 1999). The same situation was shown from the Northern Calcareous Alps by Lukeneder (2003), who established a C. krenkeli-abundance zone similar to the C. krenkeli beds of Puez comprising also abundant species such as C. krenkeli, P. infundibulum and L. subfimbriatum. Vašíček (1999) reported M. doublieri from beds of the Subsasynella sayini or P. ligatus Zone from the Northern Calcareous Alps in Austria, and therefore appearing earlier than at Puez, where it appears in the B. balearis Zone. Delanoy et al. (1987) designated this new genus Megacrioceras (e.g., M. doublieri) for this Upper Hauterivian form of Ptychoceratidae. They assumed a range for the taxon in southeast France from the S. sayni Zone to the P. anglicostata Zone.

Equivalent “Pseudothurmannia” Beds were detected by Vašíček et al. (1994) in Silesian Units of the Western Carpathians, showing the same dominance in Pseudothurmannia. These beds are herein assumed to be equivalent to the B. bealearis and “P. ohmi” Zones (= Euptychoceras borzai and C. binelli Zones in Vašíček et al., 1994).

Autran (1993) reported faunas from the Upper Hauterivian of the Castellane region (southeast France) by referring to ammonite zonations as H6 (B. bealearis Zone; see Busnardo, 1984) and H7 (P. ohmi Zone). H6 was characterized by the assemblage of P. infundibulum, L. subfimbriatum, Acriceras sp., Plesioposspidiscus spp., Paraspiticeras sp., M. doublieri and P. favrei (= D. favrei).

Upper Hauterivian faunas from the historic Veveyse de Châtel section (“Ultrahelvétique des Préalpes externs”) in Switzerland were reinvestigated by Busnardo et al. (2003). The fauna of the equivalent B. balearis Zone comprises P. tethys, P. infundibulum, P. winkleri, L. subfimbriatum, Lytoceras sp. and Plesioposspidiscus spp. The upper boundary of the comparable B. balearis Zone at Puez could not be attributed to a single bed and is tentatively located within bed P1/47.

Avram (1994) reported two different and specifiable pseudothurmannid assemblages for the South Carpathian region around Svinia. The lower one is with Pseudothurmannia pseudomalbosi from the B. bealearis/P. ohmi Zone boundary, and the upper is characterized by the mixed assemblage of P. anglicostata, P. picteti and P. cf. catulliol (= junior synonym of P. mortilli; see Company et al., 2003, 2008) accompanied by the first Paraspiticeras specimens, making it comparable to the P. picteti Zone at Puez (Figs. 3 and 4). Avram (1994) also noted the presence of the first D. favrei (= Avram’s Psilotissotia favrei) within the first levels above the Pseudothurmannia beds. D. favrei starts at Puez with P. pseudomalbosi within the P. mortilli Zone. The accompanying lytoceratid and phylloceratid faunas are equivalent in both areas, i.e., Svinia and Puez.

5.2. “Pseudothurmannia ohmi” Zone

At the Puez section the “P. ohmi” Zone (= P. anglicostata auct. Zone) could not be determined based on the index ammonite. The lower boundary of the “P. ohmi” Zone at Puez has not yet been fixed to a single bed. It is tentatively located at the base of bed P1/47 (Figs. 2–4). The “P. ohmi” Zone reaches up to bed P1/86 (Figs. 2 and 3). The “P. ohmi” Subzone has so far not been determined using the index ammonite. Its base is tentatively located at bed P1/47 and its upper boundary is assigned to be at the top of the last bed before the overlying Pseudothurmannia mortilli Subzone. This part of the section (i.e., “P. ohmi” Subzone) is characterized by the presence of Pseudothurmannia sp., Karsteniceras sp. and Sabaudiaella simplex (Fig. 4N, O). The P. mortilli Subzone starts with the first appearance of P. mortilli at bed P1/50 (Fig. 4F). This appearance coincides at the Puez locality with the last occurrence of C. krenkeli. P. mortilli typically co-occurs with P. pseudomalbosi from beds P1/50 up to P1/58 (Fig. 4D, E). The P. mortilli Subzone from beds P1/50 to P1/65 comprises a characteristic ammonite association of P. mortilli, P. pseudomalbosi, Honomoratia thiollierei (Fig. 4J, K), Hamulina sp., Anahamulina sp., Hamulinites munieri (Fig. 4P) P. subdifficilis and Plesioposspidiscus sp. The subzone is also marked by the first occurrence of the family Pulchelliidae with D. favrei (Fig. 45), and Discoidella sp. P. tethys, P. infundibulum, L. subfimbriatum, Lytoceras sp., and Lytoceras anisoptychum occur frequently. The P. picteti Subzone starts with its index species P. picteti from bed P1/66 and reaches up to the end of the P. picteti Subzone, thus to the end of the “Ps. ohmi” Zone with bed P1/86. The P. picteti Subzone is characterized by the association of P. picteti (Fig. 4G), Paraspiticeras cf. guerini (Fig. 4L), Paraspiticeras sp., Acriceras tabarelli (Fig. 4I), Sabaudiaella sp., Anahamulina sp., Megacrioceras ex. gr. doublieri (Fig. 4Q), Plesioposspidiscus cf. breskovskii, Plesioposspidiscus sp., Barremites sp., Abrutysites sp., Astieridiscus sp. (Fig. 4R) and N. subgrasianum. Additionally, representatives of the families Phylloceratidae and Lytoceratidae occur with P. tethys (Fig. 4Y), Phylloceras sp., P. infundibulum, L. subfimbriatum, L. anisoptychum (Fig. 4X), and Protetragonites sp. Desmoceratidae occur with the first specimens of Barremites and Abrutysites. Haploceratidae show their last members with N. subgrasianum within the P. picteti Subzone. Bed P1/86 therefore tentatively marks the upper boundary of the Hauterivian faunas within the “Pseudothurmannia ohmi” Zone.
mean number of families in the B. balearis Zone is 8.6, the maximum is twelve within the P. picteti Subzone. The minimum is located in the “P. ohmi” Subzone with six families per subzone. The Shannon index shows a mean value for the “Pseudothurmannia ohmi” Zone of 1.6 (min. 0.6, max. 2.6; beds with no specimens excluded). This indicates a higher species richness (e.g., twice) than is seen in the B. balearis Zone (Fig. 7).

Discussion. The P. ohmi Zone was defined by Hoedemaeker and Leereveld (1995). The P. ohmi Zone with the P. ohmi, P. catulloi or P. mortilleti and P. picteti Subzones are as proposed by Company et al. (2008) and established by Reboulet et al. (2009). P. mortilleti was meant to be a senior synonym of P. catulloi (Company et al., 2003, 2008). Company et al. (2008) established a scheme with a P. mortilleti Zone, which is followed herein (Figs. 2, 3, 5, 7).

Fözy and Janssen (2006, 2009) reported from the “P. ohmi” Zone in the Gergesc Mountains in Hungary similar faunas to those of Puez, dominated by P. infundibulum, Phylloceras sp., Lityoceras sp., Plesiospitidiscus sp., Anahumulina sp., and “P. ohmi”.

Similar to the first appearance of D. favrei at Puez within the P. mortilleti Subzone, Vermeulen (2002) reported first appearances of D. favrei and Psilototissa sp. at Angles (Barremian stratotype; Alpes de Haut-Prevence, southeast France) from the same subzone, and additional occurrences within the P. picteti Subzone.

Equivalent faunas were reported from Upper Hauterivian sections of Río Argos section in southeast Spain by Hoedemaeker (1994). He reported assemblages with P. thrystys, P. winkleri, L. subfimbriatum, N. subsgrasianum, D. favrei, P. mortilleti, “P. catulloi”, P. subdifficilis, C. krenkeli and first appearances of L. densifimbriatum, P. crebrisulcatus, S. vulpes, Paraspiticeras sp. and H. thiollierei (Hoedemaeker’s Emericerceras thiollierei) at the top of Hoedemaeker’s “Pseudothurmannia catulloi” Zone (= top of P. picteti Zone in Reboulet et al., 2009). According to Klein et al. (2007), Honnorrata honnorratiana and H. thiollierei are the same species; hence, H. thiollierei is the senior synonym and has priority. H. thiollierei and Paraspiticeras first occur at Puez within the P. mortilleti Zone.

Upper Hauterivian sequences were reported by Barga et al. (1982) from the Jaén province (Betic Cordillera), comprising similar components to those of Puez with P. mortilleti, A. tabarelli and first appearances of D. favrei (= P. favrei in Barga et al., 1982) within their “P. angulocostata”, which is now in parts equivalent to the “P. ohmi” auct. Zone and the P. mortilleti Zone of Reboulet et al. (2009). C. krenkeli occurs a few metres below this level in their “P. ligatus” Zone, which corresponds to the upper part of the B. balearis Zone (i.e., C. krenkeli Subzone) of Reboulet et al. (2009).

Vasiček (1994) reported D. favrei (= Vasiček’s P. favrei) from the P. angulocostata Zone of the Western Carpathians (Czech Republic and Slovakia), which is equivalent to the more recently established “P. ohmi” Zone (Reboulet et al., 2009). Vasiček’s D. favrei derives most probably from the P. mortilleti Subzone because he gave the exact range of the appearance of his P. mortilleti (= P. catulloi). This agrees with the occurrence at Puez.

Cecca and Pallini (1994) detected several assemblages from the Umbria-Marche Apennines (Central Italy) with co-occurrences of P. mortilleti catulloi and D. favrei (= Cecca and Pallini’s P. favrei). They assumed the fauna to be uppermost Hauterivian (i.e., former P. angulocostata auct. Zone, now P. ohmi auct. Zone and P. mortilleti Subzone; Reboulet et al., 2009). The subspecies name of P. mortilleti catulloi given by Cecca and Pallini (1994) once again shows the confusion within the determination of the members of the Pseudothurmannia group, which is also evident for example in Hoedemaeker (1994), Vermeulen et al. (2002) and Company et al. (2003). Some species determinations made by Cecca and Pallini (1994) seem to be incorrect (see also Vermeulen and Klein, 2006) because M. moutonianum cannot occur with or above Silestes seranonis and Gerhardtia provincialis (= Cecca and Pallini’s Heinizia provincialis). Uppermost Hauterivian faunas from the Maiolica Formation of the Lessini Mountains and Central Apennines (northeastern and central Italy) were reported from Faraoni et al. (1995, 1996). These faunas were regarded as having been deposited within a guide level, the so-called Mediterranean Foroni Level (see also Galeotti, 1995; Baudin et al., 1997) within the “P. ohmi” auct.” Zone (i.e., P. catulloi Subzone = P. mortilleti Subzone). Assemblages include the same members as seen at Puez with P. infundibulum, E. anisoptychum, P. catulloi, P. favrei (= D. favrei), Plesiospitidiscus sp. and E. thiollierei (= H. thiollierei).

As noted by Company et al. (1994), the transitional interval between uppermost Hauterivian and Lower Barremian strata in southeast Spain is often missing or condensed, depending on the palaeogeographic position during that time. Condensation in deeper environments and concurrent erosion and manifestation of hiatuses were detected in southeast Spain (Company et al., 1994). As they showed in the Sierra del Corque (Capres section CP2; Company et al., 1994), a total loss of sediments from the Upper Hauterivian (B. balearis Zone) up to the Holocodiscus caillaudianus Zone (sea-level rise) occurs. This was interpreted to mirror a sea-level fall during that time. This fits well with the condensed lower Lower Barremian succession at Puez, which needs more detailed sampling. The Kilian Group replaced the H. caillaudianus Zone by the topmost M. moutonianum Zone (Hoedemaeker and Rawson, 2000). A compilation of the faunal data from Company et al. (2003) described typical assemblages for the P. mortilleti Zone, namely the occurrence of P. mortilleti, P. pseudomalbosi, E. thiollierei (= H. thiollierei), Acrioceras meriani, Anhamulina subcylindrica, P. subdifficilis, A. neumayri, P. guerianianum, first D. favrei, L. densifimbriatum, P. thrystys, and P. infundibulum. As they noted, a prominent faunal turnover or renewal takes place within that zone, often referred to as the Mediterranean Foroni Level (Faraoni et al., 1995, 1996; Galeotti, 1995; Baudin et al., 1997, Cecca, 1998; Company et al., 2003). Company et al. (2003) described typical assemblages for the P. picteti Zone, namely the occurrence of P. picteti, E. thiollierei (= H. thiollierei), Acrioceras rankrishnai, Paraspiticeras morloti, A. subcylindrica, Hamulinites munieri, and in the lower parts, the last specimens of P. subdifficilis and A. neumayri, Barremites ssp., first appearances of Silesites sp., P. guerianianum, D. favrei, L. densifimbriatum, first members of P. obliquestrangulatum, P. thrystys, and P. infundibulum. Company et al. (2005) discussed faunal changes linked to the Faraoni Level of the Betic Cordillera. They showed that the ammonite faunal changes (e.g., renewal) from Hauterivian to a more Barremian “face” occurs stepwise during the P. ohmi Subzone/P. mortilleti boundary period, and at the base of the P. picteti Subzone and within the upper part of the P. picteti Subzone, both characterized by diversification and replacement of species. The first step occurs during a second-order peak transgression, and the second at a sea-level highstand. By contrast, the third step is more an “extinction event” marked by extinctions of several species which appeared during the first two steps (Company et al., 2005); this is linked to a major sea-level fall. Company et al. (2005) noted the first step as being characterized by the disappearance of N. subsgrasianum, P. infundibulum and
L. subfimbriatum around the P. ohmi Subzone/P. mortilleti boundary, whereas new forms from Pulchelliidae (D. favrei) and Leptoceratoidea (Hamulinites) occur. At Puez the situation is similar because L. subfimbriatum disappears within the P. mortilleti Subzone, and P. infundibulum disappears within the P. mortilleti Subzone and reappears in the P. picteti Subzone. N. subgrasianum is very rare within the P. mortilleti Subzone, whereas Hamulinites and D. favrei first appear in this Subzone. The second step is somewhat less spectacular (Company et al., 2005), marked by species changes within genera and appearances of closely related forms at the base of the P. picteti Subzone. Examples include P. mortilleti and P. pseudomalbosi replaced by P. picteti, Acrioceras meriani by A. ramkrishnai, and the occurrence of Paraspinoceras morloti. The base of the P. picteti Subzone is characterized by the third step, which ranges more or less up to the Hauterivian/Barremian boundary. Extinctions occur in the Betic Cordillera, for example, in P. picteti, Hamulinites nicklesi, Anhamulina fumisugina, P. morloti, and at Puez in Desmoceratidae, such as A. neumayri in Spain and Abrystusites, P. breskovskii and P. subdificilis. In contrast, members of Holcodiscidae as Taveraidiscus in Spain and Maurelidiscus and Astieridiscus both a Puez, in addition to Silesitidae with Silesites occur within that interval. Desmoceratidae occur with the first “real” Barremites dimbovicorenisi in Spain, and Emericiceratidae occur with the last Paraspinoceras guerinii (= P. guerinianum in Company et al., 2005) in both areas. Lytoceratidae occur with new L. obliquestrangulatum in the P. picteti Subzone. An additional zonation was given by Aguado et al. (2001) for the Betic Cordillera region; this is closely similar to the most recent one by Rebollet et al. (2009). Aguado et al. (2001) characterized the B. balearis Zone by the presence of Anahamulina jourdani and rare first


Fig. 5. Upper Hauterivian–Upper Barremian abundance data of the ammonite families from the Puez locality. Upper Hauterivian beds shaded in dark grey and Barremian in light grey. Note different scales.
Discoidellia. Additionally, numerous specimens of *P. subdifficilis*, *A. neumayri*, *N. subgrasianum*, *L. subfimbriatum*, *P. infundibulum* and *P. winkieli* occur. They used the *P. mortilleti* Zone (= *P. angulicosta* auct. Zone = “P ohmi” Zone; see Reboulet et al., 2009) and decided to record a subzonal with a lower *P. ohmi*, a middle *P. mortilleti* and an upper *P. morloti* Subzone. The *P. mortoli* Subzone is equivalent to the more recent *P. picteti* Subzone (Reboulet et al., 2009).

The *P. mortilleti* Zone of Aguado et al. (2001) is characterized by an assemblage with *P. ohmi*, *N. subgrasianum*, *L. subfimbriatum*, *L. densifimbriatum* and first appearances of *Silesites* and *Barremites*. Additionally, numerous specimens of subzonal index ammonites are *P. mortilleti* in the middle and *P. picteti* in the middle (= *P. mortilleti* Subzone) and subsequently in the upper parts (= *P. picteti* Subzone; Reboulet et al., 2009) of their *P. mortilleti* Zone.

In southeast France the main occurrences of *A. tabarelli* were reported by Thomel et al. (1990) to be Lower Barremian, starting from the basal Barremian. At Puez the occurrence appears to be somewhat earlier within the *P. picteti* Subzone. *A. tabarelli* co-occurs in both areas with *D. favrei*. Clavel et al. (2010) reported similar faunal components from the Upper Hauterivian of southeast France with *P. picteti* and *P. pseudomalbosi*, *Plesiopitidiscus* sp. and *A. neumayri*. Busnardo et al. (2003) reinvestigated and collected numerous faunas from the uppermost Hauterivian from the historic Veveyse de Châtel section in Switzerland. The fauna of the equivalent “P ohmi” auct. Zone (= *P. angulicosta* auct. Zone of Busnardo et al., 2003) Zone comprises *P. tethys*, *P. infundibulum*, *L. subfimbriatum*, *Lytoceras* sp., *Plesiopitidiscus* sp., *P. guerinianum*, the first *Abyrtusites* sp., *Hamulina* sp., *Sabaudiella simplex*, *P. mortilleti* (= *Pararhurmannia* mortilleti after Busnardo et al., 2003), as well as the first *D. favrei* and *H. thiollierei* (= *H. honoratiana* after Busnardo et al. 2003)). The index ammonite *P. angulicosta* co-occurs.

Company et al. (2008) reported uppermost Hauterivian (*P. ohmi* Zone) to Upper Barremian (*G. sartousiana* Zone) faunas from the western High Atlas. They noted that most of the logs are not complete and comprise several hiatuses and condensation phases.

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They showed that the *P. ohmi* Subzone corresponds to a TST (transgressive system tract) and that the *P. mortilleti* Subzone corresponds to the HST (hightstand system tract) of the sequence Ha6 (the MFS, maximum flooding surface, corresponds to the base of the *P. mortilleti* Subzone = Faraoani Level). The sequence boundary Ha7 is missing in most of the western High Atlas localities owing to hiatuses, and followed immediately by the TST and HST of Ha7 in the upper *T. hugii* Zone. Thus, the HST of Ha6 and LST of Ha7 are absent. The exact sequences at Puez from *T. hugii* to *M. moutonianum* remain unclear, but seem quite similar. In Morocco the top of *T. hugii* and base of *K. nicklesi* were correlated to be the LST of Barr1, but missing. The TST and HST (upper part of *K. nicklesi* Zone and lower part of *N. pulchella* Zone) coincided with a maximum flooding during the Barremian. The uppermost part of *N. pulchella* is interpreted as the LST of Barr2. The *K. compressissima* Zone and the lower-middle part of the *C. darsi* Zone (= *M. moutonianum* Zone) would correspond to the TST and HST of sequence Barr2 and the whole of sequence Barr3. The LST of Ba4 corresponds partly to the lower part of the *T. vandenheckii* Zone, and the TST and maximum flooding surface (MFS) are represented in the *G. sartousiana* Zone. The end of Barremian sedimentation is marked in the western High Atlas by an unsynchronous late Early Barremian to very late Barremian erosive unconformity (see also Hardenbol et al., 1998; Adatte et al., 2005; Arnaud, 2005). According to data from the western High Atlas of Morocco (Company et al., 2008), the *P. ohmi* Zone is characterized by typical faunas with *P. ohmi, P. mortilleti, P. pseudomalbos*, *P. subdificilis*, *A. neumayri* and *Parsipitceras* sp., which broadly correlates with the situation at Puez. By contrast to the situation with *P. picteti*, the *P. picteti* Subzone and the lowermost part of the *T. hugii* Zone are missing in Morocco, marked by a hiatus, and the *P. mortilleti* Subzone is directly overlain by Lower Barremian sediments.

5.3 Taveraidiscus hugii auctorum Zone

The Hauterivian/Barremian boundary could not be determined based on the occurrence of index ammonites, neither could the index ammonite species be detected for the *T. hugii auctorum Zone* or the *Kotetishvilia nicklesi, Nicklesia pulchella* and *Kotetishvilia compressissima* zones (see discussion). The ammonite zonal boundaries are therefore given tentatively (Figs. 2, 3, 6). The base of the Lower Barremian is fixed at the bottom of bed P1/87, which corresponds to the base of the *T. hugii* auct. Zone. It shows first appearances of *Barremites* spp., *Melchiorites* sp., *Silesites* sp., *Holodiscus* sp., *Maurelidiscus* sp., and *Anahumulina* cf. *uhligi*. The upper boundary of the *T. hugii* auct. Zone is located at the top of bed P1/94.

The *T. hugii* auct. Zone, the lowermost Zone of the Lower Barremian, is marked by an increasing number of members of the family Desmoconidae. This family shows first appearances of *Barremites desmoceratae* (Fig. 6). *Barremites psilotaus, Barremites difficilis* (Fig. 6), *Barremites sp., M. cassidoides, and Mechiorteretes* sp. Silesitidae appear with the first Silesites sp. Holcrodiceridae show occurrences of the last *Astieridiscus* sp., whereas real *Holocodiscus* appears and the first appearance of *Maurelidiscus* cf. *kiliani* (Fig. 6K) occurs in bed P1/87. The occurrence of *M. kiliani* (within the *M. kiliani* Zone) was interpreted by Vermeulen (2005a, b, 2009b) to mark the basal Barremian. The *M. kiliani* Zone after Vermeulen (2003; see Vermeulen, 2007b, 2009b) was considered to be an equivalent of the *Taveraidiscus hugii* Zone after Hoedemaeker et al. (2003) and Rehoulet et al. (2009). Emericiceratidae appear with the last *Parasipitceras* sp. Lepptoceratoidae appear with its last *Sabaudiella* simplex. Within the family of Hamulindae the first occurrence of *A. jordani* (last occurrence; Fig. 6F), *Anahumulina* cf. *uhligi* (first appearance; Fig. 6D) and numerous specimens of *Anahumulina* sp. characterize this zone. Representatives of the families Phylloceratidae (*P. tethys, P. infundibulum; Fig. 6U*) and Lytoceratidae (*L. densifimbriatum*) complete the ammonite assemblage of the *T. hugii auct. Zone* at Puez.

Discussion. The *T. hugii auctorum Zone* is subdivided into a *T. hugii* auct. Subzone and an upper *Psilotissotia colombiana* Subzone (Reboulet et al., 2009). Rawson (1996) defined this zone and the first occurrence of *T. hugii* as the base of the Barremian Stage. *P. colombiana* was considered as an index species of the zone (Vermeulen, 1996). A detailed discussion on the zone is given by Company et al. (2008).

Correlatable faunas within the *T. hugii* auct. Zone in the Gerecse Mountains of Hungary show an occurrence of *P. infundibulum, Phylloceras winkleri (= Phyllocyphachyphora winkleri), Phylloceratopsis* sp. *Lytoceras*, *Protetragonites* sp., *Anahumulina* sp., *Hamulina* sp., and typically the pulchellicids *D. favrei*, *T. hugii* and *Taveraidiscus intermedius* (Fözy and Janssen, 2006, 2009).

Lowest Barremian faunas from the Veveyse de Châtel section in Switzerland (Busnardo et al., 2003) comprise faunal equivalents of the Puez *T. hugii* Zone with *P. tethys, P. infundibulum, L. subfimbriatum*; in the lowestmost beds the last *Pezispodicosa* and *Abrytus* specimens occur. *H. thiolierei* shows the last occurrence in the lowermost *T. hugii* beds.

Agudo et al. (1992) described Barremian faunas from the Subbetic domain in the Betic Cordillera. They designated a *Spitinidiscus hugii Zone (= T. hugii Zone after Reboulet et al., 2009).* This zone was defined by a *P. infundibulum, Barremites and Spitidiscus assemblage.*

More recently it was defined again by Agudo et al. (2001) for the
Batic Cordillera region. It was characterized by two subzones in accordance with Rebourlet et al. (2009). The lower *T. hugii* Subzone was characterized by the presence of *Taveraidascus* sp., *Barremites boutini*, *Lytoceras obliquangularatum* ( = *Protetragonites obliquangularatum*), *Hamulina munieri* and the last occurrence of *D. favrei*. The upper *Psilotissotia colombiana* Subzone is characterized by *P. colombiana*, *Holcodiscus*, *L. anisoptychum* and *Anahamulina pavillosa*.

According to data from the High Atlas of Morocco (Company et al., 2008), two significant hiatuses appear at the Hauertivian/Barremian boundary and in the lower part of the *K. nicklesi* Zone. Both were related to third-order sea-level falls by Company et al. (2008), who pointed to similarities with the lowermost Barremian boundary and in the lower part of the *ciorensis* Zone. The upper part of the Barremian is characterized by the presence of *Hamulina munieri* and the last occurrence of *D. favrei*. The upper *Psilotissotia colombiana* Subzone is characterized by *P. colombiana*, *Holcodiscus*, *L. anisoptychum* and *Anahamulina pavillosa*.

5.4. Kotetshivila nicklesi Zone

The *K. nicklesi* Zone extends from the bottom of bed P1/95 up to the top of bed P1/104. The overall situation and assemblage composition is a continuation of the underlying *T. hugii* auct. Zone in that it shows Desmoceratidae with numerous specimens of *Barremites* sp. and *M. cassidoides*. Silesitidae appear with more specimens of *Silesites* sp. *Hamulinites* sp. occur with *Anahamulina* sp. The Phylloceratidae are characterized by the first appearance of *P. ponticuli* and more specimens of *P. infundibulum*. Lytoceratidae first occur as *P. crebrisulcatus* at the top of the zone.

Beds within the *K. nicklesi* Zone display numbers of species per bed from zero to three. Six families occur within the zone with numbers per bed from zero to five, with highest values in the uppermost parts (Fig. 7). The Shannon index shows a mean value for the *K. nicklesi* Zone of 1.3 (min. 0.9, max. 1.6; beds with no specimens excluded). This indicates a somewhat lowered species richness as seen in the uppermost Barremian *T. hugii* auct. Zone (Fig. 7).

Discussion. The base of the *K. nicklesi* Zone is defined by the first occurrence of *N. pulchellia* (Company et al., 2008). In accordance with Hoedemaeker et al. (2003) the *N. pulchella* Horizon was elevated to the rank of a Zone. The *N. pulchella* Zone also replaces the upper part of the *K. nicklesi* Zone (Hoedemaeker and Rawson, 2000).

Comparable to the Puez section, the *N. pulchella* Zone described by Fözy and Janssen (2006, 2009) from the Gerecse Mountains are typical, with *K. nicklesi* (determined as *Subpulchellia nicklesi* in Fözy and Janssen (2006, 2009)) and *N. pulchella*. The assemblage is dominated by the first species, but numerous *Silesites* sp., frequent *Holcodiscus* ssp. and the first occurrences of the genus *Barremites* were reported. The correlatable interval largely lacks ammonites and is not, therefore, yet defined at the Puez locality.

The last specimens of *E. thiollierei* occur together with *A. subincuata* and *Silesites vulpes* in the lower parts of the *N. pulchella* Zone at Angles (southeast France; Vermeulen, 2002). The *N. pulchella* Zone is dominated in the western High Atlas of Morocco by the index ammonite *N. pulchella* accompanied by members such as *A. tabarelli*, *Paraspiriceras* sp., *Hamulinites* sp., *Lytoceras* sp. and *P. ponticuli* along with forms such as *D. cf. potieri*, the first specimens of *M. nodosum* and still frequent *T. barremensis*, which is replaced towards the top by *T. suessii* (Company et al., 2008).

5.6. Kotetshivila compressissima Zone

The *K. compressissima* Zone extends from the bottom of bed P1/112 up to the top of bed P1/118. The ammonite assemblage is quite similar to the underlying *N. pulchella* Zone but more numerous in species and specimens. The family Desmoceratidae is represented by *Barremites* sp., *M. cassidoides* and *M. nodosum* sp. and the first specimens of *Valdedorsella cf. uhligi* and *Valdesorsella* sp. *Pulchelliidae* appear with typical *Henizia caicedi* (Fig. 6L, M) and *Kotetshivila* sp. The Acidriceratidae occur with *Dissimilites* sp. The Leptoceratoididae show appearances of *Karstenciura* sp. (Fig. 6S) and are accompanied by the first members of Ptychoceratidae with *Ptychoceras* sp. (Fig. 6G). *Hamulinites* sp. occur with several specimens of *Anahamulina* sp. *Costidiscus nosodosstratium* (Fig. 6H) is the first member of Macroscaphitidae to occur in the uppermost part of the zone. The topmost part of the *K. compressissima* Zone is marked by typical Phylloceratidae with *P. tethys*, *Phylloceras paquieri* and *Phylloceras* sp. in addition to *P. infundibulum* and *Phyllopachyceras eichwaldi*. *L. densifimbriatum* (Fig. 6O), *Lytoceras* sp., the first specimens of *E. phustum* and numerous specimens of *Protetragonites crebrisulcatus* (Fig. 6S) and *Pulchelliidae* are the members of Lytoceratidae (Fig. 2).

Beds within the *K. compressissima* Zone display numbers of species per bed from three to seven. Nine families occur within the zone with numbers per bed from zero to eight, the highest values...
being in the upper half (Fig. 7). The Shannon index shows a mean value for the K. compressissima Zone of 1.6 (min. 0.7, max. 2.3; beds with no specimens excluded). The values indicate a lowering of species richness and a low evenness in their abundance compared to those of the N. pulchella Zone (Fig. 7).

Discussion. The K. compressissima and Moutoniceras moutonianum Zones were established after a proposal by Company et al. (1995) and replaced the top part of the K. nicklesi Zone and the Holcodiscus caillaudianus Zone (Hoedemaeker and Rawson, 2000). After Rebourlet et al. (2009) this zone is divided into the Holcodiscus fallax, Nicklesia didayana, Heinzia communis and Subtorcapella defayae Horizons (Company et al., 1995, 2008; Vermeulen, 2003, 2007a, b; Vermeulen and Klein, 2006).

As noted by Fözy and Janssen (2006, 2009) this zone can be easily recognised in the Gerecse Mountains by the index ammonite K. compressissima (determined as Subphylloceratidae compressissima by Fözy and Janssen (2006, 2009)). Numerous holocidiscids occur throughout the zone, including Holcodiscus gastaldianus, H. nicklesi, H. cf. perezianus and H. fallax. The latter species seems to be restricted to the lower parts and H. caillaudianus to the upper part of the zone (Company et al., 1995; Fözy and Janssen, 2006, 2009). This is reflected in the zonal scheme shown in Rebourlet et al. (2009), where an H. fallax Horizon is noted in the lowermost part of the K. compressissima Zone. After Fözy and Janssen (2006, 2009), Moutoniceras appears within that zone, whereby Moutoniceras nodosum is first representative. Similar to the K. compressissima Zone from Puez, the assemblage from Bersek Quarry shows additional representatives such as Barremites sp., Mechiorites sp. and the first specimens within Leptoceratoididae with Karsteniceras pumilum (Fig. 6D). These are accompanied by numerous Hamulinitidae, including Anahamulina spp.

Delany and Joly (1995) and Joly (2000) reported P. ponticuli (as a typical member of Upper Barremian ammonite assemblages but rare in Lower Barremian) at Puez with the first appearance of P. ponticuli in the K. compressissima Subzone.

Aguado et al. (1992) described Barremian faunas from the Subbetic domain in the Betic Cordillera, characterizing the Subphylloceratidae compressissima Zone (= K. compressissima) by the index ammonite K. compressissima, Subphylloceratidae nicklesi (= K. nicklesi of the recent K. nicklesi Zone; Rebourlet et al., 2009), N. pulchella (index for the recent N. pulchella Zone; Rebourlet et al., 2009), Subphylloceratella brevicostata (K. brevicostata), H. perezianus and H. caillaudianus.

At Angles (southeast France), first K. changarnieri occur in the stratotype in the uppermost K. compressissima Zone in the lower S. defayae Horizon (= S. defayae Subzone after Vermeulen, 2002). Macroscaphites, Costidiscus and E. phestum seem to originate in the K. compressissima Zone at the Puez locality. The K. compressissima Zone is characterized in the western High Atlas of Morocco by a faunal turnover. This begins in the top of the underlying N. pulchella Zone, marked by the new index form K. compressissima and other phyllocerids K. didayana, Heinzia communis and, in upper parts, K. changarnieri. At the base of the zone, holocidiscids show a characteristic diversification (Company et al., 2006, 2008) with H. fallax, H. perezianus, Avramidiscus gastaldianus and, higher in the zone, H. caillaudianus. Anycloceratoidea are present with M. nodosum, Dissimilitites dissimilis and members of “Toxoceras” and Hamulinites.

5.7. Moutoniceras moutonianum Zone

The occurrence of the index ammonite M. moutonianum (bed P1/119) with the co-occurring ammonite assemblage hints at the presence of the M. moutonianum Zone at the Puez section (Figs. 2, 3, 6). The M. moutonianum Zone corresponds to the interval from the bottom of bed P1/119 up to the top of bed P1/137. The family Desmoceratidae is represented by Barremites sp. and M. cassidoides. Among the Silesitidae, real S. vulpes (Fig. 6Q) occur within this zone for the first time. The Acrioceratidae occur once again with D. trinodosum. Heteroceratidae are present at the base of the zone for the first time with the zonal index ammonite M. moutonianum (Fig. 6C). Hamulinitidae occur with several specimens of Anahamulina spp. Phylloceratidae are represented by the last individuals of P. tethys, Phylloceras sp.; moreover, P. infundibulum (Fig. 6T, V), Phyllocypryxa ladinum and Phylloopencvyrs sp. also occur. P. crebrisulcatum and Protegtaronites sp. are the members of Lytoceratidae.

Discussion. The M. moutonianum Zone is defined by the first appearance of its index species and the co-occurrence in upper parts of Toxancylceroceras vandenheckii (Company et al., 1995). This zone replaced (Breboul et al., 2009) the former Corontes darsi Zone sensu Vermeulen (1997, 1998) and the C. darsi Zone sensu Company et al. (2008). The Heinzia sayni Zone of Vermeulen (1997, 1998) is equivalent to the T. vandenheckii Zone. According to the data of Vermeulen (2005a, b), the first occurrence of M. moutonianum coincides with that of C. darsi (Company et al., 2008). Rebourlet et al. (2009) assumed that the M. moutonianum (sensu Company et al., 1995) and C. darsi (sensu Vermeulen, 1997, 1998) zones span the same stratigraphic interval. The M. moutonianum Zone (= Corontes darsi Zone in Company et al., 2008) is subdivided into a C. darsi Horizon and a younger H. caicedi Horizon (Rebourlet, 2009).

Within the Gerecse Mountains, Fözy and Janssen (2006, 2009) noted the presence of the index species M. moutonianum and the genus Heinzia with Heinzia sp. and Heinzia cf. heinzii. It was accompanied by Holcodiscus spp., Hamulinitidae with Anahamulina and Acrioceratidae with Dissimilitites. These authors reported the index ammonite co-occurring with abundant K. changarnieri and K. sauvageau (Subphylloceratella changarnieri and Subphylloceratella sauvageau by Fözy and Janssen (2006, 2009)). Numerous specimens of the genus Heinzia occur, and H. caicedi, when abundant, is typical for that zone. Note that the H. caicedi Horizon in Rebourlet et al. (2009) encompasses the upper half of the M. moutonianum Zone: H. caicedi occurs a few beds lower in the K. compressissima Zone at Puez. The family Desmoceratidae shows mass occurrences of Barremites and Melchiorites in single beds (Fözy and Janssen, 2006, 2009). Macroscaphites cf. binodosus and Costidiscus sp. are present together with Ptychoceras puzosianum within that zone (Fözy and Janssen, 2006, 2009).

Ptychoceros puzosianum occurs somewhat later during the Toxancylceroceras vandenheckii Zone in the Subbetic region (southeast Spain; Company et al., 1995). In contrast, it was found only much higher at Puez in the G. tartousiana Zone. The Acrioceratidae in Spain occur once again with Dissimilitites trinodosum, and Hamulinitidae occur with several species of Anahamulina sp.

Avram (1994, 2001) defined the ranges of D. dissimilis, D. trinodosum and D. subalternatus within the Romanian Carpathians. He assumed that D. dissimilis was present only in the uppermost lower Barremian, whereas D. trinodosum and D. subalternatus were characteristic for both the uppermost Lower Barremian and lowermost Upper Barremian. The occurrence of D. trinodosum at Puez fits this interpretation. The same situation
was described for southeast France by Ebbo et al. (2000) for a range of *D. trinodosum* starting in the *K. compressissima* Zone and reaching up to the *M. moutonianum* Zone. According to Vermeulen (2007a), species of the genus *Costidiscus* appear from the *T. vandenheckii* Zone and derive from ancestors in the base of the *M. moutonianum* Zone (= *C. darsi* Zone of Vermeulen, 2007a). As noted above, at Puez *Costidiscus nodosostriatum* occurs at the uppermost part of the *K. compressissima* Zone or *K. compressissima/M. moutonianum* boundary interval. Vermeulen (2007a) rejected the idea of *Costidiscus—Macroscaphites* being a sexually dimorphic pair owing to their different stratigraphical range, with *Costidiscus* appearing in the *T. vandenheckii* Zone and *Macroscaphites* in the *K. compressissima* Zone in southern France. The same situation is shown herein and strengthens Vermeulen’s assumption, which contrasts with the remarks made by Avram (1984), Delanyo et al. (1995), Wright et al. (1996) and Delaney et al. (2008). Fözy and Janssen (2006, 2009) reported that both *Macroscaphites* and *Costidiscus* were present in the *M. moutonianum* Zone in the Gercse Mountains of Hungary.

Uhlig (1883) and Vasićek and Wiedmann (1994) noted the typical occurrence of *Karsteniceras pumilium* in the Lower Barremian of the Silesian Unit (Czech Republic), which is in accordance to the specimens found at Puez. Avram (1994) reported a faunal condensation in the lowermost Barremian of the South Carpathian region around Puez. Avram (1994) also reported a faunal condensation in the *T. vandenheckii* Zone and *Macroscaphites* in the *K. compressissima* Zone in southern France. The same situation is shown herein and strengthens Vermeulen’s assumption, which contrasts with the remarks made by Avram (1984), Delanyo et al. (1995), Wright et al. (1996) and Delaney et al. (2008). Fözy and Janssen (2006, 2009) reported that both *Macroscaphites* and *Costidiscus* were present in the *M. moutonianum* Zone in the Gercse Mountains of Hungary.

**Discussion.** The *T. vandenheckii* Zone is marked by the first appearance datum of the index ammonite (= Lower/Upper Barremian boundary; Rawson et al., 1999) and the co-occurrence of *G. sartousiana* in the upper parts (Company et al., 2008; Reboulet et al., 2009). Repeatedly the *T. vandenheckii* Zone is subdivided into the *T. vandenheckii* Subzone and the younger *B. barremense* Subzone. Owing to the absence of the subzonal index ammonites, the *T. vandenheckii* Zone is tentatively subdivided into two equal parts at bed P1/172, which corresponds with the last occurrence of *Heinzia* cf. *sayni* (Fig. 8V). The zone occurs with a typical ammonite fauna comprising members of the family Desmoceratidae, with *Barremites* sp., *Valledorsella* sp., *Cassidinae* and *Mechioceratidae* silesiidae occur with *S. vulpes* (Fig. 85) and *Silesites* sp. throughout the zone. *Holcodiscus* cf. *uhligen* (Fig. 8U) and *Holcodiscus* sp. occur within the Holcodiscidae only in the lower part of the *T. vandenheckii* Zone. Pulchelliidae appear with typical *H. cf. sayni*, *K. changarnieri* (Fig. 8X) in the lower part and additional species of *K. sauvaugaei* in both parts. Emericeratidae occur with *Emer-"icer"* in the upper part of the zone. Ancyloceratidae with *D. trinodosum* (Fig. 8G, H) and *Dissimilites* sp. are frequent in the lower part and are accompanied by the zonal index species *T. vandenheckii* (Fig. 8A, B) and an additional specimen of *Toxanclyloceras* sp. (Fig. 8C) within the family Ancyloceratidae. Within the family Leptoceratoididae, *Karsteniceras* sp. (Fig. 8I) occurs in the lower part of the zone. Hamulinae occur only in the lower part with *Hamulina* cf. *uhligen*, *Hamulina* sp., and with *Pychohamulina* cf. *acuria* (Fig. 8L) in both parts. The lower part shows members of *Duyeina* cf. *kleini* (Fig. 8M) and *Duyeina* sp., whereas the upper part is characterized by the occurrence of the hamuluid member *Vasicekina* cf. *pernai* (Fig. 8K). Macroscaphitidae occur with only one specimen at the base, along with *Costidiscus* sp. Typical members within the Phylloceratidae occur throughout the zone and include *P. ponticul*, *Phylloceras* sp., *P. infundibulum*, *P. eichwaldi*, *Phyllopachyceras* sp. and *Sowerbyceras* ermessi. Lytoceratidae are represented by *L. densifimbriat* and *Lytoceras* sp., *P. crebrisulcatus* and *Protetragonites* sp. throughout the *T. vandenheckii* Zone.

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K. sauvageaui in southern France occur in the M. moutonianum Zone within the H. caicedi Horizon (Vermeulen, 1998), whereas K. changarnieri has its acme in southern France within the K. compressissima Zone and disappears in the Heinizia sayni Zone (uppermost T. vandenheckii Zone of Reboulet et al., 2009).

The same range for K. sauvageaui was reported from Algeria by Vermeulen and Lahondère (2008). At Puez, H. cf. sayni is reported only from the T. vandenheckii Subzone. In Algeria, H. sayni occurs in the upper part of the T. vandenheckii Zone, which is comparable to the H. sayni Zone after Vermeulen (2007a, b). It disappears in the Tethyan region at the base of the B. barremense Subzone (after Vermeulen and Lazarin, 2007). Vermeulen and Lazarin (2007) subdivided the T. vandenheckii Zone into T. vandenheckii, H. sayni and B. barremense subzones. This scheme was redefined by Reboulet et al. (2009) into a T. vandenheckii Subzone and a younger B. barremense Subzone.

Upper Barremian ammonite biohorizons for southeast France were discussed by Bert et al. (2008). The biozone is marked by the strong diversification of the Ancycloceratidae (T oxancylcoceras, Barrancylcoceras) and Acrioceratidae (Dissimulites). The T. vandenheckii Zone after Bert et al. (2008) is characterized by the co-occurrence of Heinizia sayni, Kotethisvila sp., Gassendisceras sp., Barrancylcoceras sp., T. vandenheckii, and Silesitidae. The T. vandenheckii Zone after Bert et al. (2008) included the lower Holodiscus ulighi, the middle H. sayni and the upper B. barremense subzones, and several additional biohorizons were introduced. The lower two subzones are time equivalent to the T. vandenheckii Subzone after Reboulet et al. (2009).

According to Fözy and Janssen (2006, 2009) the T. vandenheckii Zone is the topmost preserved zone at the Bersek Quarry, shown by the presence of the index ammonite and H. sayni. This agrees with the occurrence of H. sayni at Puez within the entire T. vandenheckii Zone. The authors reported the T. vandenheckii Zone by determining T. vandenheckii, H. sayni and an additional fauna comprising Kotetishvila sp. (determined as Subpulchellia in Fözy and Janssen (2006, 2009)), Holodiscus ssp., Dissimulites sp., Anahamulina sp., abundant Melchiorites and Barremites sp., Barremites ex. gr. difficilis and Karstenicera sp. Both the Puez area and the Gerece Mountains show the occurrence of small Leptoceratidae with cyloceras sp., Anahamulina sp., and Ptychoceras cf. acuria (= Anahamulina cf. acuria in Fözy and Janssen (2006, 2009)).

Vasiček (1996) also reported T. vandenheckii from the central Western Carpathians (Butkov, Quarry, Slovakia). From the Silesian of the Czech Republic, Vasiček (1999), Vasiček et al. (2004) reported a typical Upper Barremian assemblage including Macroscaphites binodosus and M. yvani, and C. nodososтратиus within the T. vandenheckii Zone. Vasiček (2008) figured a specimen of K. ex. gr. sauvageaui, described as deriving from the Upper Barremian from the Silesian Unit (Western Carpathians). Patrulius and Avram (2004) described but did not figure an assemblage comprising P. infundibulum and P. ponticuli, P. eichwaldi, P. ladinum, Phyllocycheras sp. and S. eresti. Lytoceratidae are represented by L. densifimbriatum, Lytoceras rarinicum, Lytoceras sp., and E. phystum (Fig. 8D, Z), P. crebrisulcatum and Protexagonites sp. throughout the G. sartousiana Zone.

Discussion. G. sartousiana appears in the G. sartousiana Zone and disappears within the G. provincialis Subzone in Algeria (Vermeulen and Lahondère, 2008) and southern France (Vermeulen, 2002). Delanoy (1994, 1997) described typical assemblages from the G. sartousiana Zone from the “Coupe Vergons 2” section (southeast France). The fauna comprises semi-phases with K. sauvageaui (Delanoy’s Psilotsotia sauvageaui) and members of genera such as Macroscaphites, Costidiscus and S. pulchra, P. ponticuli, P. infundibulum and E. phystum. Delanoy (1997) described the same assemblage as typical for the G. sartousiana Zone in southeast France. Upper Barremian ammonite biohorizons for this region were discussed by Bert et al. (2008). They reported the anomalies in
the first occurrence of different sections and therefore had difficulty marking the lower boundary of the *G. sartousiana* Zone. New ammonite biohorizons provided by Bert et al. (2008) were not accepted and transferred to the ammonite zonation scheme for the Mediterranean by the Kilian Group (Reboulet et al., 2009). Bert et al. (2008) summarized the strong diversification in Hemihoplitiidae and the coeval decrease in pulchelliids after the acme of *G. sartousiana*. This acme zone is most probably the last ammonite assemblage determined at Puez. The *G. sartousiana* Zone after Bert et al. (2008) included the lower Camereiceras limentinus, the middle Gerhardtia provincialis and the upper Hemihoplites ferraudianus subzones. Equivalents are the *G. sartousiana*, the *G. provincialis* and the *H. ferraudianus* subzones after Reboulet et al. (2009). The *G. sartousiana* Zone after Bert et al. (2008) is characterized by the co-occurrence of *G. sartousiana*, *G. provincialis*, *C. limentinus*, Hemihoplites spp. and Audouliceras sp. (in upper parts). Hemihoplitiidae with the genera Hemihoplites, Gassendiceras and Pseudoshasticrioceras (see Bert and Delanoy, 2009; Bert et al., 2008) are still missing at the top of the Puez section (log P1), implying the absence of the time equivalent beds from the middle part of the *G. sartousiana* Zone, i.e., the *G. sartousiana/provincialis* boundary upwards. It is difficult to correlate with species determined by Cecca and Pallini (1994; see also Vermoulen and Klein, 2006) because no exact zonation is given and the boundaries are therefore uncertain. Nonetheless, faunas seem to appear with same constituents as those of the Late Barremian time intervals detected at Puez.

Reboulet et al. (2009) divided the *G. sartousiana* Zone into the *G. sartousiana* Subzone, the *G. provincialis* Subzone and the youngest *H. ferraudianus* Subzone. After Bert et al. (2008) the former zone of *H. ferraudianus* was lowered to the rank of a subzone and occupies the upper part of the *G. sartousiana* Zone (Reboulet et al., 2009). Concerning the arguments given by Reboulet et al. (2009), the boundary between the *G. sartousiana* and Imerites giraudi zones is characterized by an important faunal turnover marked by the disappearance of Pulchelliidae and Hemihoplitiidae. Based on the ammonite assemblage and further lithological and microfossil analysis, the upper two ammonite subzones, i.e., the *G. provincialis* and *H. ferraudianus* subzones, are probably missing and a hiatus occurs at this time at the top of log P1 after bed P1/204. Bed P1/204 is directly overlain by Aptian Puez Redbed Member. The situation is marked at the top of bed 204 by an omission horizon, and is accompanied by a remarkable sea-level rise (Adatte et al., 2005; Arnaud, 2005) of the middle Pacheval of the uppermost Puez Limestone Member (lower Puez Formation; Puez/log 1), containing the Melchiorites-Level (beds P1/194–204), which is dominated by the genera Melchiorites and Silesites (Figs. 2, 5, 7). Company et al. (2005) interpreted Barremites, comparable to the morphotype Melchiorites, as being epipelagic nektan and Silesites was described as nektobenthic.

“Faunal turnover”, “mass-occurrence”, and “migrations” have always been considered as being controlled by transgressive and regressive cycles in various Lower Cretaceous ammonite groups (Rawson, 1981; Hoedemaeker, 1980). This phenomenon was described by Bulot (1993) as Opportunity HUFs (Horizons of Faunal Uniformity). Opportunity HUFs were determined to be locally controlled by changing conditions marked by the change in palaeogeographic distribution or of palaeoecological ranges of different ammonite groups. The remarkable assemblage change within the Melchiorites-Level (*G. sartousiana* Zone) reflects a complex of changes in eustasy and in primary bioproducitivity (Lukeneder, 2003, 2004b).

**6. Conclusions**

The macrofauna of the Puez Formation at the Puez section, especially of the Puez Limestone Member, is mainly represented by ammonites. Over 1200 ammonite specimens were collected by bed-by-bed sampling. Aptian and Albian members such as the Puez Redbed Member and the Puez Marl Member are almost barren in ammonites and other macrofossils. The ammonite zonation is based on the most recent standard zonation of the international Kilian Group on Lower Cretaceous ammonites (Reboulet et al., 2009). Several zones and even subzones based on the presence of Mediterranean index ammonites, such as the *C. krenkeli*, *P. mortillette*, *P. pictet*, *M. moutonianum*, *T. vandenheckii* and *G. sartousiana* ammonite zones, were detected. Zones missing in index ammonites are characterized by their typical ammonite associations. The fossiliferous parts of the log begin with the Upper Hauterivian *B. balearis* Zone (*B. binelli* Subzone). The ammonite-rich section ends with a significant hiatus within the lower Upper Barremian *G. sartousiana* Zone (*G. sartousiana* Subzone). This hiatus is marked at the top of bed 204 by an omission horizon, and is directly overlain by the Aptian Puez Redbed Member. The situation is comparable to that of other localities located in southeast Spain and Morocco. The Upper Barremian—Lower Aptian hiatus extends from the middle part of the *G. sartousiana* Zone up to the base of the Aptian, reflecting the absence of at least the topmost part of the *G. sartousiana* Subzone (i.e., *H. ferraudianus* Subzone) and the entire *I. giraudi* Zone.

The ammonite assemblage clearly indicates a Mediterranean character, as reported from numerous comparable Lower Cretaceous localities in east-central European (Czech Republic, France, Hungary, Slovakia, Spain), eastern Europe (Bulgaria, Romania) and African localities (Algeria, Morocco). The fauna is dominated by byphyloceratids (*P. infundibulum*, *P. tethys*), lytoceratids (*Lytoceras, Eulytoceras*, Prototetragonites), desmoceratids (Barremites, Melchiorites, Silesites) and ancyloceratids (*Anachamulina, Crioceratites, Dissimilites, Karsteniceras, Pseudothurmannia, Toxancylcoceras*).
Ammonite abundances are strongly correlated to single intervals of the section. Ammonite-rich beds were detected within the C. krenkeli Zone, the T. vandenheckii Zone and the topmost G. sartousiana Zone. Ammonite peaks occur in bed 66 (n = 60) in the C. krenkeli Zone and in the G. sartousiana Zone in beds 197 (n = 120) and 199 (n = 200). The evaluation of biodiversity calculated by the ratio between number of species vs. number of individuals per species (Shannon index) shows no clear significance throughout the Puez section, although varying from highstand and maximum flooding phases from the Upper Hauterivian with mean values of 1.6 down to (in steps) values of 0.7 in the Lower Barremian M. moutonianum Zone. The Hauterivian is dominated by Pseudothurmannia-Crococeras-Plesiospissidicus, the Barremian by Kotetishvilia-Melchiorites-Sileites. Ammonite abundances are clearly linked to sea-level changes from Late Hauterivian to mid Lower Barremian times. Abundance and diversity peaks occur during phases of high sea-level pulses and the corresponding maximum flooding surfaces (P. mortilleti/P. picteti and G. sartousiana Zone). The Lower Barremian strata at Puez require more sampling for a more detailed zonation. The uppermost Hauterivian to lowermost Barremian strata at Puez require more sampling for a more detailed biostratigraphic scheme for the Puez key-section. More investigations at the stratotype of the Puez Formation will be carried out within the Dolomiti project P20018-N10 (project of the Austrian Science Fund FWF). Additional ammonite collections will be carried out in future to determine the exact position of stage-, zone-, and subzone-boundaries. Analyses will include palaeomagnetic, isotopic and geochemical analyses along with a detailed biostratigraphic based on micro- and nannofossils.

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Oscar Costa (1871–2001) – a remarkable figure

Oskar Costa (1871–2001), a Dutch-Lebanese geologist, made significant contributions to the field of Cretaceous geology, particularly in the study of ammonites. His work was groundbreaking in the understanding of sequence stratigraphy and the biostratigraphy of the Upper Cretaceous in the Mediterranean region. Despite facing numerous challenges, including political and personal hardships, Costa remained committed to his research and dedication to his profession. His legacy continues to inspire researchers and students alike, as evidenced by the dedications and acknowledgments found in the literature.

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