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Beitr. Paläont., **22**:13–21, Wien 1997

Upper Campanian *Belemnitella* from Austria

by

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CHRISTENSEN, W.K., 1997. Upper Campanian *Belemnitella* from Austria. — Beitr. Paläont., **22**:13–21, 1 plate, 1 text-figure, 3 tables, Wien.

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Key words: *Belemnitella*, upper Upper Campanian, Upper Cretaceous, Austria.
Stichworte *Belemnitella*, oberen Obercampan, Oberkreide, Österreich.

Summary

A small fauna of *Belemnitella* from the upper Upper Campanian of Austria is described. It includes *B. hoeferi* (SCHLOENBACH, 1867b) from the Gschliefgraben tectonic window of the northern Ultrahelvetic series and the Gosau Group of the Northern Calcareous Alps, in addition to *B.* cf. *minor* II CHRISTENSEN, 1995 from the Gosau Group. The little known but valid *B. hoeferi* belongs to the *B. mucronata* group and can be distinguished from most species of this group on the basis of the slender guard. *B. hoeferi* evolved probably by allopatric speciation from an initial migrant, which may have invaded the northern European margin of the Tethyan Realm coincidently with the upper Upper Campanian transgression. *B.* cf. *minor* II invaded the Austroalpine realm in the uppermost Upper Campanian, that is slightly later than *B. hoeferi.*

Zusammenfassung

Eine kleine *Belemnitella*-Fauna aus dem oberen Obercampan von Österreich wird beschrieben. Sie umfaßt *B. hoeferi* (SCHLOENBACH, 1867b) aus dem Ultrahelvetikum des tektonischen Fensters vom Gschliefgraben bei Gmunden (Oberösterreich) und aus der Gosau-Gruppe der Nördlichen Kalkalpen sowie *B.* cf. *minor* II CHRISTENSEN, 1995 aus der Gosau-Gruppe der Neuen Welt (Niederösterreich) und des Beckens von Gosau (Oberösterreich). Die wenig bekannte aber gültige Art *B. hoeferi* gehört zur *B. mucronata* Gruppe und kann mit Hilfe des schlankeren Rostrums von den meisten Arten unterschieden werden. *B. hoeferi* entwickelte sich wahrscheinlich durch allopatrische Speziation aus einem Einwanderer, der den nördlichen, europäischen Rand der Tethys im Zuge der Transgression im oberen Obercampan erreicht haben könnte. *B.* cf. *minor* II erreichte das Austroalpin im obersten Obercampam, das ist geringfügig später als *B. hoeferi.*

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1. Introduction

During the Cenomanian, the earliest stage of the Upper Cretaceous, belemnites had a tripartite distribution. The family Belemnitellidae PAVLOW inhabited the North Temperate Realm (= Boreal Realm of authors), the family Dimitobelidae WHITEAVES inhabited the South Temperate realm (= Austral Realm) and the family Belemnopseidae NAEF inhabited the Tethyan Realm. The latter family became extinct in the Middle Cenomanian, and, consequently, a Tethyan Realm cannot be defined on the basis of belemnites during the remaining part of the Upper Cretaceous. It can be recognized, however, on the basis of other fossil groups such as rudistid bivalves, ammonites, echinoids, actaeonellid gastropods and larger foraminifera. The North Temperate Realm includes the North American and North European Provinces (CHRISTENSEN 1975, 1976, 1988b, 1993b, 1997, in press).

After the extinction of the belemnopseids, the belemnitellids migrated intermittently southwards into the European part of the Tethyan Realm. The first invasion took place in the middle Upper Cenomanian, when *Praeactinocamax plenus* (BLAINVILLE, 1825) entered the Vocontian Basin in the Alpes-Maritimes of southeast France coincidently with a rapid rise of sea-level and a cool climatic phase, the so-called Plenus Cold Event (GALE & CHRISTENSEN 1996, CHRISTENSEN, in press). Moreover, lack of competition of the Tethyan belemnopseids may also have been of significance for this southwards migration. Subgenus *Actinocamax (Praeactinocamax)* NAIDIN, 1964, type species *Belemnites plenus* BLAINVILLE, was raised to full generic rank by CHRISTENSEN (1997). Later

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invasions occurred from the Upper Santonian to the Maastrichtian (GALE & CHRISTENSEN 1996, CHRISTENSEN 1997, in press).

Belemnitella mucronata (SCHLOTHEIM, 1813) has been recorded by previous authors from the Upper Campanian at several localities in the northern European part of the Tethyan Realm, including the Aquitaine Basin in southwest France, the Sub-Alpine Chain in southeast France, the Ultrahelvetic and Northern Calcareous Alps of Austria, the Balkans and Turkey. These records are, however, open to discussion, because many authors in the last part of the 19th century and the beginning of the 20th century lumped *B. mucronata*-like specimens, that is species of *Belemnitella* d'ORBIGNY, 1840 as well as *Belemnella* NOWAK, 1913, in *B. mucronata.*

ALI-ZADE (1972) described four species and nine subspecies of *Belemnitella* from the Upper Campanian of Azerbaijan in the Caucasus, including *B. mucronata, B. minor* JELETZKY, 1951, *B. langei* JELETZKY, 1948 and *B. conica* ARKHANGELSKY, 1912.

Upper Campanian taxa of *Belemnitella* were described recently from Romania by NEAGY & GEORGESCU (1991) and Bulgaria by STOYANOVA-VERGILOVA & JOLKICEV (1993). These authors recorded *B. mucronata, B. minor, B. langei, B. najdini* KONGIEL, 1962 and *B. conica*, as well as subspecies of these taxa, all known from the North European Province, in addition to some new, local species. However, the descriptions of the species leave much to be desired, because the internal characters were rarely studied or not studied at all, and the quality of the plates in the article by NEAGU & GEORGESCU is extremely poor.

COMBÉMOREL (1996) described five 'nearly-complete' specimens and about 30 fragments of *Belemnitella* sp. from the 'Craie marneuse' of the Chartreuse in the Sub-Alpine Chain, Savoie, southeast France. He noted that this unit is Late Campanian or Early Maastrichtian in age, 'zone à *G. calcarata*, début de la zone à *G. havanensis*'. However, ROBASZYNSKI & CARON (1995) placed the *G. calcarata* Total Range Zone and the *G. havanensis* Interval and Partial Range Zone in the upper Upper Campanian. They correlated the *G. calcarata* Zone with the upper part of the *Nostoceras (Bostrychoceras) polyplocum* ammonite Zone and the *G. havanensis* Zone with the topmost *N. (B.) polyplocum* Zone and the basal *Didymoceras donezianum* ammonite Zone (Fig. 1). Thus, *B.* sp. from Chartreuse is late Late, but not latest, Campanian in age.

I describe here a small sample of *Belemnitella hoeferi* from the upper Upper Campanian of the Gschliefgraben tectonic window of the northern Ultrahelvetic series in Austria, the geology of which was fully discussed by PREY (1983). In addition, one specimen of *B. hoeferi* and three specimens of *B.* cf. *minor* II CHRISTENSEN, 1995 from the Gosau Group of the Northern Calcareous Alps are also included in this study.

2. Systematic Palaeontology

Family Belemnitellidae PAVLOW, 1914

Genus ***Belemnitella*** d'ORBIGNY, 1840

Type species *Belemnites mucronatus* SCHLOTHEIM, 1813.

Diagnosis Small to very large belemnitellids (length from apex to protoconch up to 80 mm) with a deep alveolus; anterior end of guard completely calcified and prolonged ventrally along ventral fissure in a tongue-like extension; well developed dorso-lateral longitudinal depression and straight double furrows, in additon to single lateral furrows; longitudinal striae may be present; vascular imprints branch off double furrows posteriorly at an angle less than 30 degrees; juvenile guard short and stout; alveolar angle 17 to 24 degrees, Schatzky Distance long, commonly larger than

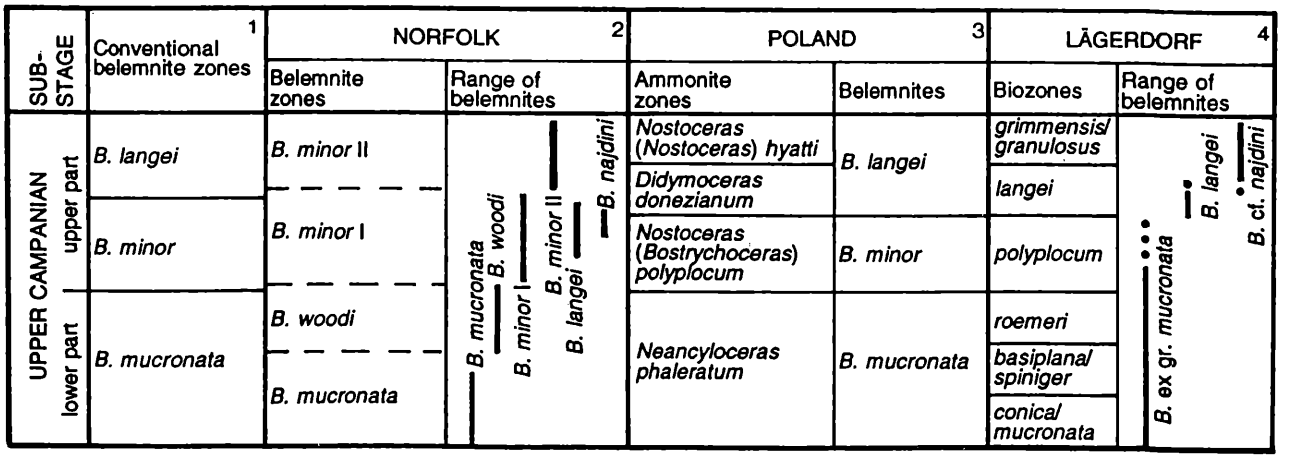

Figure 1. Stratigraphical correlation diagram of the Upper Campanian. Sources: column 1, JELETZKY (1951); column 2, CHRISTENSEN (1995); column 3, BŁASZKIEWICZ (1980); and column 4, SCHULZ et al. (1984). The uppermost Upper Campanian ammonite zone of Poland was originally named the *Nostoceras pozaryskii* Zone by BŁASZKIEWICZ. It was renamed the *N. hyatti* Zone by KENNEDY et al. (1992), because *N. (N.) pozaryskii* of BŁASZKIEWICZ is a junior synonym of *N. (N.) hyatti* STEPHENSON. Vertical axis no to scale.

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4 mm; relationship of length from apex to protoconch and dorso-ventral diameter at protoconch generally isometric.

Discussion The guard is completely calcified only in the genera *Belemnitella* and *Belemnella* of the family Belemnitellidae, and these have, therefore, a true alveolus adorally. However, complete guards of species of these genera are extremely rare, because the most anterior end is usually not preserved due to its fragility. *Belemnitella* includes small to very large species in contrast to the Maastrichtian genus *Belemnella*, which comprises only large and very large species (CHRISTENSEN 1995, 1997).

CHRISTENSEN (1995) introduced a classification of size ranges of species of *Belemnitella* based on the length from the apex to the protoconch (LAP). This is as follows: 1) guard small, LAP less than 55 mm; 2) guard large, LAP between 55 and 65 mm; and 3) guard very large, LAP larger than 65 mm. He also introduced a classification of the relative length based on the Birkelund Index (BI), which is the length from the apex to the protoconch divided by the dorso-ventral diameter at the protoconch. This is as follows: 1) guard stout, mean value of the BI less than 4; 2) guard slender, mean value of the BI 4 to 5; and 3) guard very slender, mean value of the BI larger than 5.

CHRISTENSEN (1995) recognized two groups of *Belemnitella* in the Upper Campanian and Maastrichtian: the *B. mucronata* group and the *B. langei* group. The former includes large to very large species, which are stout to slender, with a small to medium-sized fissure angle and a medium-sized to large Schatzky Distance. Moreover, the bottom of the ventral fissure is usually straight. He placed the following species in this group: *B. mucronata* (essentially uppermost Lower Campanian-lower Upper Campanian); *B. woodi* CHRISTENSEN, 1995 (lower Upper Campanian); *B.* aff. *langei* CHRISTENSEN, 1986 (middle Upper Campanian); *B. minor* I JELETZKY, 1951, *B. pauli* CHRISTENSEN, 1995, *B. langei* sensu SCHULZ, 1978 and *B.* cf. *najdini* sensu SCHULZ, 1978 (all upper Upper Campanian); *B. minor* II CHRISTENSEN, 1995 (uppermost Upper Campanian and lower Lower Maastrichtian); *B. minor* sensu CHRISTENSEN, 1975 and *B. langei* sensu BIRKELUND, 1957 (lowermost Maastrichtian); and *B. junior* NOWAK, 1913 (Upper Maastrichtian), among others. The lower Lower Maastrichtian *B. minor* III of Christensen, 1995 is placed in synonymy with *B. minor* II (see below). *B. pauli* is a transitional form between the *B. mucronata* and *B. langei* group, because it has a large fissure angle and a small Schatzky Distance, but is otherwise very *B. mucronata*-like.

The *B. langei* group includes small, slender to very slender species with a large to very large fissure angle and a small Schatzky Distance. Moreover, the bottom of the ventral fissure is generally irregular. This group includes *B. langei* and *B. najdini* (upper Upper Campanian), as well as *B. pulchra* SCHULZ, 1982 (middle Lower Maastrichtian).

Distribution *Belemnitella* is widely distributed in the North European palaeobiogeographical Province and has also been recorded from the North American Province and northern European part of the Tethyan Realm. It appears at the base of the Santonian and continues to the top of the Maastrichtian (CHRISTENSEN 1997).

Belemnitella hoeferi (SCHLOENBACH, 1867b)

(Plate 1, Figs. 1–11)

1867a *Belemnites Hoeferi* SCHLOENBACH, *nomen nudum*; p. 335
1867b *Belemnites Hoeferi* SCHLOENBACH; p. 589, Pl. 16, figs. 1a–g
1920 *Belemnitella Hoeferi* (SCHLOENBACH); BÜLOW-TRUMMER, p. 190
1983 *Belemnitella mucronata* SCHLOENBACH; PREY, p. 101
1984 *Belemnitella mucronata* (SCHLOTHEIM); KENNEDY & SUMMESBERGER, p. 151
? 1996 *Belemnitella* sp.; COMBÉMOREL, p. 161, Pl. 1, figs. 1–5

Type: Lectotype, here designated, the original of SCHLOENBACH (1867b, Pl. 16, fig. 1), Grünbach near Wiener-Neustadt, inoceramid marls of the Gosau Group, Northern Calcareous Alps. The lectotype and syntypes have not been traced and are apparently lost (H. SUMMESBERGER, personal communication, November 1996).

Measurements of the lectotype: See Table 1. The measurements are taken from the figures of SCHLOENBACH and may thus be defective.

Material Gschliefgraben near Gmunden: 30 specimens, including five 'nearly-complete' specimens, eight alveolar fragments, eleven apical fragments and six fragments of the middle part of the guard. These were collected by Mr H. HÜTTER, Gmunden and Mr U. ROSCHGER, Gmunden.

Grünbach: One specimen, Naturhistorisches Museum Wien (NHMW) 1970/1396/541.

Emended diagnosis Large, slender *Belemnitella* with a large Schatzky Distance, small fissure angle and vascular markings.

Description Guard large and slender, cylindrical or slightly lanceolate in ventral view and high conical in ventral view; guard flattened ventrally over its entire length; apical end acute with a mucro; Birkelund Index from about 4 to 5, with a mean value of 4.4; Schatzky Distance large, fissure angle small, alveolar angle about 20 degrees, and bottom of ventral fissure straight; guard with vascular markings, dorso-lateral depressions and dorso-lateral double furrows, vascular markings extending to apex; pseudogranulation may be present.

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No.	LAP	DVDP	LDP	MLD	SD	FA	AA	BI
				Grünbach				
Lectotype NHMW 1970/1396/541	40	10.5	10.5	10.5	7.5	12	23	3.8
	49*	12.6	13.4	13.4	9.7	22.0	19.0	3.9
				Gschliefgraben				
1	60.3	12.6	11.9	12.6	c.8	–	c.19	4.8
2	57*	11.6	11.6	11.8	–	–	–	4.9
3	57*	12.4	–	–	–	–	–	4.6
4	56.2	12.5	12.9	13.3	8.5	–	20.0	4.5
5	43.5	10.4	–	–	–	–	20.0	4.2
8	–	–	–	–	–	13.0	–	–
22	–	12.4	12.0	–	c.10.5	c.21	–	–
23	–	12.5	13.4	–	–	–	c.22	–

Table 1: Dimensions of the upper Upper Campanian *Belemnitella hoeferi* (SCHLOENBACH, 1867b) from the Gschliefgraben and Grünbach-Neue Welt Basin in Austria. The following abbreviations are used for the characters. LAP = length from apex to protoconch; DVDP = dorso-ventral diameter at protoconch; LDP = lateral diameter at protoconch; MLD = maximum lateral diameter; SD = Schatzky Distance; FA = fissure angle; AA = alveolar angle; BI = Birkelund Index; * = estimated.

Character	$\bar{N}$	$\bar{X}$	SD	CV	OR
LAP	7	51.9	7.8	15.0	43.5–60.3
DVDP	9	11.9	0.9	7.5	10.4–12.6
LDP	7	12.2	1.1	8.9	10.5–13.4
MLD	5	12.3	1.2	9.8	10.5–13.4
SD	5	8.8	1.2	14.0	7.5–10.5
FA	4	17.0	5.2	30.8	12.0–22.0
AA	6	20.5	1.6	8.0	19.0–23.0
BI	7	4.4	0.4	9.8	3.8– 4.9

Table 2: Univariate analysis of the upper Upper Campanian *Belemnitella hoeferi* (SCHLOENBACH, 1967b) from the Gschliefgraben and Grünbach-Neue Welt Basin in Austria. $\bar{N}$ = number of specimens; $\bar{X}$ = mean value; SD = standard deviation; CV = coefficient of variation; OR = observed range. For abbreviations of the characters, see Table 1.

Dimensions: See Table 1.

Biometry Nine specimens from the Gschliefgraben and Grünbach were analyzed biometrically. Only univariate analysis was performed due to the small number of specimens (Table 2).

Discussion SCHLOENBACH (1867a, p. 335) established *B. hoeferi nomen nudum* on the basis of one'nearly-complete' specimen and two fragments. SCHLOENBACH (1867b, Pl. 16, fig. 1) described and figured the'nearly-complete' specimen and SCHLOENBACH (1867b) is therefore the author of this species. SCHLOENBACH (1867b) discussed its affinity to *B. mucronata*, but the specimen figured by him as *B. mucronata* (Pl. 16, fig. 2), from Nagoryany (Nagoryany in earlier literature) in Ukraine, belongs to the lower Lower Maastrichtian *Belemnella (Pachybelemnella) inflata* (ARKHANGELSKY, 1912) (cf. CHRISTENSEN 1988a).

The lectotype of *B. hoeferi*, from Grünbach, is characterized by its slender guard, large Schatzky Distance and small fissure angle. NHMW 1970/1396/541 from Grünbach and the specimens from the Gschliefgraben differs in no significant respect from the lectotype, and they are therefore assigned to this valid species. The lectotype is most likely an adolescent specimen.

B. hoeferi belongs to the *B. mucronata* group owing to the size and slenderness of the guard, in addition to the large Schatzky Distance and small fissure angle. However, very few species of the *B. mucronata* group have a mean Birkelund Index of 4.4 or larger, and these are *B.* aff. *langei* from the middle Upper Campanian of Scania (CHRISTENSEN 1986, 1993a) and the Upper Maastrichtian *B. junior* (CHRISTENSEN 1995, Tables 2 and 12). *B. hoeferi* is larger than *B.* aff. *langei* and significantly smaller than *B. junior*. Moreover, *B. hoeferi* differs from *B.* aff. *langei* by its shape of the guard in ventral view. The maximum lateral diameter is situated in the lower third of the guard in *B.* aff. *langei* and in the middle part of the guard in *B. hoeferi*. *B. hoeferi* is markedly slenderer than *B. mucronata* and *B. woodi* and has more prominent vascular markings than *B. woodi*. *B. hoeferi* is smaller and slenderer than *B. minor* I and *B. minor* II and has a smaller Schatzky Distance than *B. minor* II.

B. hoeferi is stouter and has a larger Schatzky Distance, a smaller fissure angle and a larger alveolar angle than *B. langei sensu* Schulz, is slenderer and has a smaller fissure angle than *B. langei sensu* BIRKELUND and *B.* cf. *najdini* sensu SCHULZ, and is smaller and has a smaller fissure angle than *B. minor* sensu CHRISTENSEN.

B. hoeferi is closely similar to *B.* sp. from the Chartreuse (see above) with respect to size, shape and slenderness of the guard, in addition to surface markings. Thus, these taxa may be conspecific, but a specific determination of the specimens from the Chartreuse is not possible, because the internal characters are unknown.

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All growth stages of *B. hoeferi* are present in the sample from the Gschliefgraben, indicating that the species bred there.

Distribution *B. hoeferi* occurs in the the Ultrahelvetic series of the Gschliefgraben area near Gmunden and the Grünbach-Neue Welt Basin of the Northern Calcareous Alps in Austria. In the Gschliefgraben it co-occurs with ammonites, which are of late Late Campanian age, that is probably the *Nostoceras (Bostrychoceras) polyplocum, Didymoceras donezianum* and *Nostoceras (Nostoceras) hyatti* Zones (KENNEDY & SUMMESBERGER, 1984) (Fig. 1). SUMMESBERGER (1997) recorded the ammonite *Pseudokossmaticeras brandti* (REDTENBACHER, 1873) from Grünbach. This ammonite is of late Late, but not latest, Campanian age (HANCOCK & KENNEDY, 1993; KENNEDY & BILOTTE, 1995; WARD & ORR, 1997). The two specimens of *B. hoeferi* from Grünbach are supposed to be of the same age as *P. brandti*.

B. sp. from the Chartreuse in the Subalpine Chain, southeast France, which may be conspecific with *B. hoeferi*, is of late Late, but not latest, Campanian age (see above).

In conclusion, it is inferred that *B. hoeferi* is of late Late, but probably not latest, Campanian age.

Belemnitella minor JELETZKY, 1951

Remarks CHRISTENSEN (1995) recognized three chronological subspecies of *B. minor*, which were considered to form an evolutionary lineage: *B. minor* I JELETZKY from the lower part of the upper Upper Campanian, *B. minor* II CHRISTENSEN, 1995 from the upper part of the upper Upper Campanian, and *B. minor* III CHRISTENSEN, 1995 from the lower Lower Maastrichtian. *B. minor* III was distinguished from *B. minor* II only on the basis of its smaller guard. However, subsequent studies of abundant material of *B. minor* from the lower Lower Maastrichtian Craie Phosphatée de Ciply of the Mons Basin in Belgium have shown that this dissimilarity is incorrect. Therefore, *B. minor* III is placed in synonymy with *B. minor* II (CHRISTENSEN, unpublished).

Belemnitella cf. *minor* II CHRISTENSEN, 1995

(Plate 1, Figs. 12–19)

compare

1989 *Belemnitella* aff. *mucronata* SCHLOTHEIM; CHRISTENSEN [in:] ROBASZYNSKI & CHRISTENSEN, p. 403, Pl. 1, fig. 2

1989 *Belemnitella* aff. *mucronata* (SCHLOTHEIM)/*posterior* KONGIEL; CHRISTENSEN [in:] ROBASZYNSKI & CHRISTENSEN, p. 405, Pl. 1, fig. 6

1995 *Belemnitella minor* II CHRISTENSEN, p. 64, Pl. 7, figs. 3–10; Figs. 20A–D

1995 *Belemnitella minor* III CHRISTENSEN, p. 69, Pl. 8, figs. 1–9

1997 *Belemnitella minor* II CHRISTENSEN; CHRISTENSEN, p. 71, Pl. 2, figs. 3–5

Holotype: By original designation, Natural History Museum, London, BMNH C43553, Whitlingham, Norfolk, Paramoudra$_1$ Chalk (CHRISTENSEN, 1995, Pl. 7, figs. 3–6).

Material: NHMW 1977/1928, lower part of the Nierental Formation, Zwieselberg-Forststraße, about 400 m north of Liesenhütte, Gosau; NHMW 1900/2049/78, Erbstollen at Unterhöflein, Neue Welt; NHMW unregistered, Gadenweith south of Neue Welt, from spoil-heap of a coalmine; all are from the Gosau Group of the Northern Calcareous Alps.

Description: Guard very large and stout; generally subcylindrical in ventral view and high conical in lateral view; guard flattened over its entire length; Schatzky Distance large, fissure angle medium-sized, alveolar angle small, and bottom of ventral fissure generally straight; vascular markings well-developed ventrally and laterally; dorso-lateral depression and dorso-lateral longitudinal double furrows prominent; longitudinal striae and pseudogranulation may be present.

No.	LAP	DVDP	LDP	MLD	SD	FA	AA	BI
NHMW 1900/2049/78								
	46.4	13.7	14.4	14.4	9.5	13.0	19.0	3.4
NHMW 1977/1928								
	50*	16.0	15.6	15.6	8.8	26.5	19.0	3.1

Table 3: Dimensions of the upper Upper Campanian *Belemnitella* cf. *minor* II CHRISTENSEN, 1995 from the Gosau Group of the Northern Calcareous Alps. * = estimated. For abbreviations of the characters, see Table 1.

Dimensions: See Table 3.

Discussion: *B. minor* II is closely similar to *B. mucronata* with respect to slenderness and surface markings, but is distinguished by its larger guard, larger Schatzky Distance and smaller alveolar angle. *B. minor* II differs from *B. minor* I by its stouter guard and larger Schatzky Distance.

The specimens from the Gosau Group have a large Schatzky Distance and a small alveolar angle. Since the material is scanty and the internal characters are known from only two specimens they are referred to as *B.* cf. *minor* II.

Distribution: *B. minor* II occurs in the uppermost Upper Campanian Paramoudra Chalk and the lower Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* Beds of Norfolk (CHRISTENSEN 1995), as well as the uppermost Upper Campanian and lower Lower Maastrichtian of the Mons Basin (CHRISTENSEN, unpublished) and the Maastricht-Aachen-Liège area (KEUTGEN 1996). It may also occur in the Upper Campanian Craie Blanche at Meudon in the Paris Basin.

The Paramoudra Chalk probably equates with the upper part of the *Belemnitella langei* Zone and the overlying *Micraster grimmensis/Cardiaster granulosus* Zone of Lägerdorf, northwest Germany, as well as the

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upper part of the *Didymoceras donezianum* Zone and *Nostoceras hyatti* Zone of central Poland (Fig. 1) (CHRISTENSEN 1995).

The specimens from Austria were not collected together with age diagnostic macrofossils. However, NHMW 1977/1928 came from the lower part of the Nierental Formation, which is of Late Campanian age on foraminiferal evidence (KOLLMANN & SUMMESBERGER, 1982).

In conclusion, *B.* cf. *minor* II occurs probably in the uppermost Upper Campanian in Austria.

3. Palaeobiogeography

The belemnitellids are distributed in the North Temperate Realm, which includes the North European and North American Provinces, in addition to the northern European part of the Tethyan Realm (CHRISTENSEN, 1975, 1976, 1988b, 1993b, 1997, in press). The centre of evolution and dispersal of the belemnitelids lay in the North European Province for the following reason: 1) They are common and all known genera and subgenera occur there. 2) The earliest belemnitellid, *Praeactinocamax primus* (ARKHANGELSKY, 1912), appeared in the Lower Cenomanian, some way above the base of the substage, in this province. 3) The earliest species of the younger genera occurred either only there or appeared earlier there than elsewhere (CHRISTENSEN, 1997, in press).

The belemnitellids immigrated intermittently into the North American Province and Tethyan Realm during the Upper Cretaceous. The occurrence of the upper Upper, but probably not uppermost, Campanian *B. hoeferi* in Austria and *B.* sp. in southeast France, in addition to the occurrence of the uppermost Upper Campanian *B.* cf. *minor* II in Austria reflects two of these immigrations into the Tethyan Realm.

The majority of the species occurring in the North American Province are endemic, whilst the species occurring in the Tethyan Realm are conspecific with those from the North European Province, with a few exceptions. *B. hoeferi* has been recorded only from the Tethyan Realm, whilst *B. minor* occurs in the North European Province as well as in the Tethyan Realm.

In passing it can be mentioned that SCHULZ & SCHMID (1983) described *Belemnella (Belemnella) gracilis* (ARKHANGELSKY, 1912) and *Belemnitella pulchra* from the middle Lower Maastrichtian of the northern Ultrahelvetic Buntmergelserie of Bavaria in Germany, and SCHMID & SCHULZ (1979) recorded *B. (B.) gracilis* from the middle Lower Maastrichtian of the Helvetic of Bavaria. *B. (B.) gracilis* is common, whereas only a single specimen of *B. pulchra* has been recorded. As a matter of fact, the specimen of *B. pulchra* is the only specimen of *Belemnitella*, which has been recorded from the Lower Maastrichtian of the Tethyan Realm (CHRISTENSEN, in press).

RAWSON (1993, 1994) showed that sea-level changes were of paramount importance for Lower Cretaceous ammonite biogeography. Rapid sea-level rises triggered migrations of ammonite faunas, and new species evolved occasionally from initial migrants by allopatric speciation. Sea-level falls led to faunal differentiation between adjacent basins and endemism.

HANCOCK (1990, 1993) analyzed the sea-level fluctuations of the British region and North America during the Upper Cretaceous and recorded an upper Upper Campanian peak low in the *Belemnitella langei* Zone *sensu anglico*. This peak is in the middle part of the Beeston Chalk of Norfolk, which equates with the top of the *Nostoceras (Bostrychoceras) polyplocum* Zone of northwest Germany (HANCOCK 1993, CHRISTENSEN 1995).

The upper Upper Campanian transgression may have triggered the migration of a population of *Belemnitella* from the North European European Province into the Tethyan Realm and *B. hoeferi* may have evolved subsequently by allopatric speciation from an initial migrant. *B.* cf. *minor* II invaded the Tethyan Realm in the uppermost Upper Campanian, slightly later than *B. hoeferi*.

To the contrary, SANDERS, KOLLMANN, SUMMESBERGER & WAGREICH (1996) suggested that the mixing of faunal elements from the North Temperate and Tethyan Realms in the Northern Calcareous Alps in Austria may be due to the impingement of cooler oceanic waters or cooler climate. In this context, it is worthy of note that GALE & CHRISTENSEN (1996) showed that the occurrence of *Praeactinocamax plenus* in the Vocontian Basin, southeast France is coincident with a cold temperature event, the Plenus Cold Event, registered by oxygen isotope data from southeast England.

Acknowledgements

Dr. H. SUMMESBERGER, Naturhistorisches Museum Wien placed the belemnite material at my disposal and commented the manuscript. Mr. S.L. JAKOBSEN, Geological Museum, Copenhagen made the photographs. I am very grateful for this help.

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PLATE 1

Figs. 1–11. *Belemnitella hoeferi* (SCHLOENBACH, 1867b) from the upper Upper Campanian of the Gschliefgraben area and Grünbach-Neue Welt Basin in Austria.

- Figs. 1–3. A nearly-complete specimen from the Gschliefgraben with weakly developed vascular markings (no. 2). 1, dorsal view; 2, lateral view; 3, ventral view.
- Figs. 4–6. A nearly-complete specimen from the Gschliefgraben. 4, dorsal view; 5, lateral view; 6, ventral view. It is slightly pathologically or tectonically deformed.
- Fig. 7. Apical fragment in ventral view, showing pseudogranulation, the Gschliefgraben.
- Figs. 8–10. NHMW 1970/1396/541, Grünbach. 8, dorsal view; 9, lateral view; 10, ventral view.
- Fig. 11. Apical fragment in ventral view of the largest specimen from the Gschliefgraben (no. 27).

Figs. 12–19. *Belemnitella* cf. *minor* II CHRISTENSEN, 1995 from the uppermost Upper Campanian, Gosau Group of the Northern Calcareous Alps.

- Figs. 12–15. NHMW 1900/2049/78, Erbstollen at Unterhöflein, Neue Welt. 12, view of the split anterior end showing internal characters; 13, dorsal view; 14, lateral view; 15, ventral view.
- Figs. 16–18. NHMW 1977/1928, lower part of Nierental Formation, Zwieselberg-Forststraße, about 400 m north of Liesenhütte, Gosau. 16, dorsal view; 17, lateral view; 18, ventral view.
- Fig. 19. NHMW unregistered, Gadenweith south of Neue Welt; ventral view. The specimen is tectonically deformed.

All specimens are coated with ammonium chloride, and are natural size.

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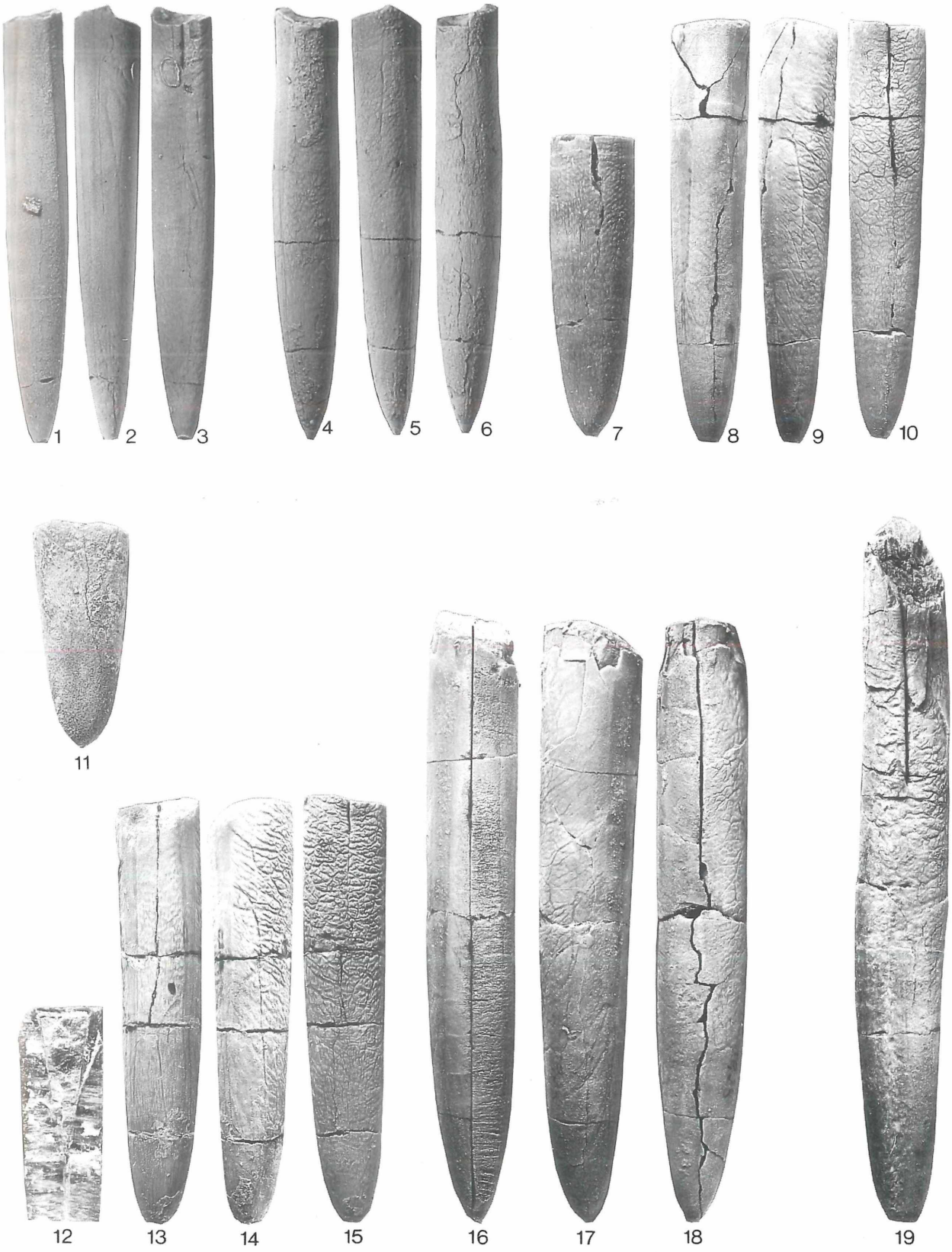
PLATE 1



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Zeitschrift/Journal: Beiträge zur Paläontologie

Jahr/Year: 1997

Band/Volume: 22

Autor(en)/Author(s): Christensen Walter Kegel

Artikel/Article: Upper Campanian Belemnitella from Austria 13-21