



New Albian ammonite faunas from Semelenberg (Alpstein, Switzerland) and their paleoecology

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Abstract

The Alpstein (northeastern Switzerland) has yielded a relatively high diversity of Cretaceous macrofossils. Here, new discoveries of invertebrate fossils from a new locality of the early to late Albian age in Semelenberg (northeastern Alpstein, canton St. Gallen) are documented. In spite of the very small size of these samples and the 1-m-thick, very condensed section, the locality yielded four ammonite species that are here documented for the first time from Switzerland. One of these species is new and *Eoscaphtes kuersteineri* sp. nov. is introduced as new taxon. We also investigated the paleoecology of the middle to late Albian of this region based on the abundant macrofossils. The alpha diversity at Semelenberg is very similar to that of a previously documented fauna from several localities in the northeastern Alpstein region of similar age, which are located 2–10 km west of Semelenberg. A minor discrepancy is rooted in the proportion of benthic organisms, which may indicate slight differences in bathymetry between Semelenberg and the previously studied locality (northeastern Alpstein).

Keywords Ammonoidea · Taxonomy · Paleoecology · Diversity · Albian · Cretaceous · Switzerland

Introduction

In the past few years, a number of studies have improved our understanding of Cretaceous paleoecology in the Alpstein, Switzerland (Sulser et al. 2013; Tajika et al. 2017a, b; Kürsteiner and Klug 2018). These studies documented dynamic paleoecological shifts from the Barremian to the Cenomanian, which were induced by paleoenvironmental changes (e.g., Föllmi and Ouwehand 1987; Föllmi 1989a, b, c; Föllmi et al. 2007). These also revealed that cephalopods is the group of organisms, which are the most diverse and abundant in the Alpstein.

Here we (1) report new discoveries of early to late Albian cephalopod-dominated invertebrate faunas from new outcrops in Semelenberg, (2) analyze the paleoecological structure of the late Albian in Semelenberg and (3)

discuss the faunal diversity of this stratigraphic interval in the Alpstein region in comparison with those of previously studied faunas at different times and localities.

Geological setting, materials and methods

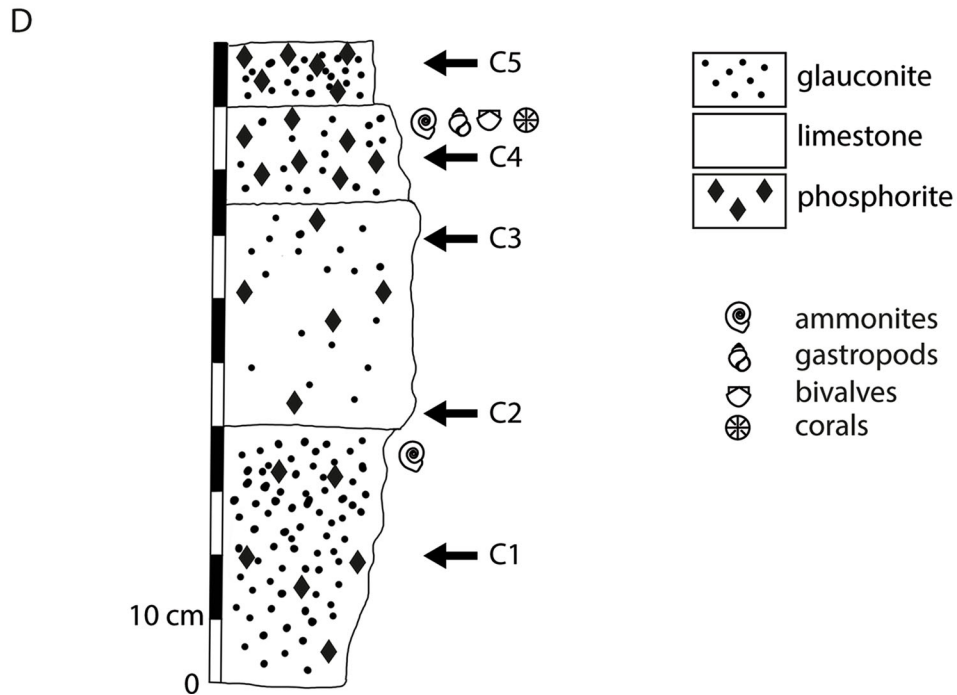
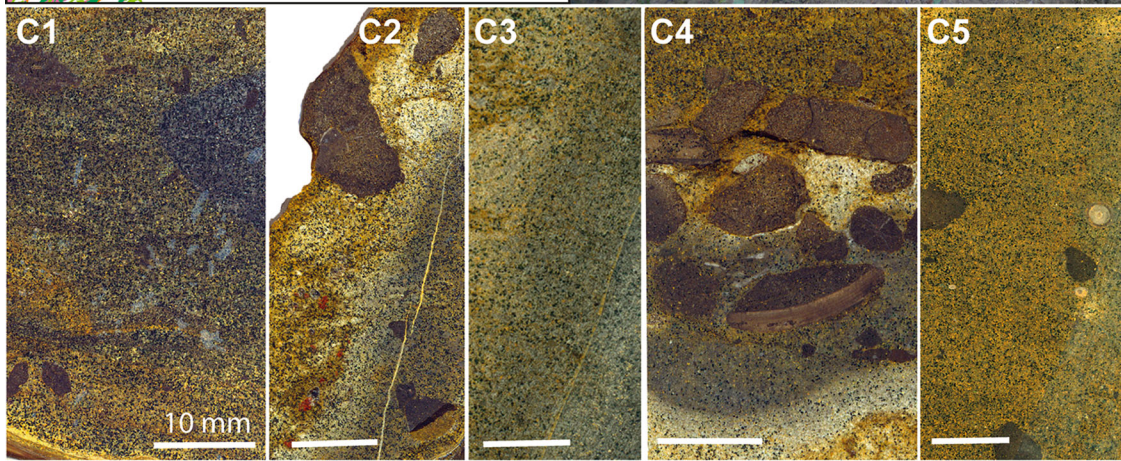
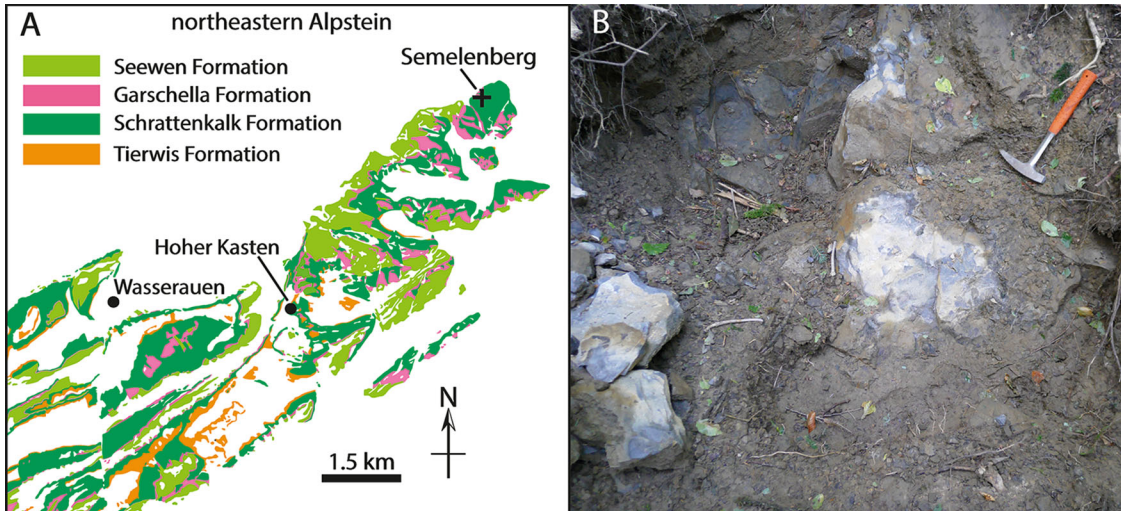
All fossils included in this study were collected by Peter Kürsteiner (St. Gallen) and KT in Semelenberg, Alpstein (canton of St. Gallen, Switzerland; Fig. 1). The Alpstein region is known to expose several fossiliferous sedimentary sequences: Tierwis Formation (uppermost Hauterivian to upper Barremian), Schratenkalk Formation (upper Barremian to middle lower Aptian), Garschella Formation (upper lower Aptian to lowermost Cenomanian; for sedimentological and paleontological details of each sequence, see Tajika et al. 2017a, b). At Semelenberg, only a part of the Garschella Formation is exposed. Most fossils originate from an outcrop named Semelenberg Nord II and some fossils were collected from blocks which were found in the scree (Semelenberg Nord). The blocks collected at Semelenberg Nord yielded ammonites such as *Douvilleiceras* and *Protanisoceras*, which indicate an early Albian age, while the high abundance of *Mortoniceras* and

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◀**Fig. 1** Location and geology of Semelenberg. **A** Location of Semelenberg on the geological map (modified after Tajika et al. 2017). **B** Field image of Semelenberg Nord II. **C1–C5** Facies of the four examined layers in Semelenberg Nord II. Scale bars for C1–C5 = 10 mm. **D** Stratigraphic section of Semelenberg Nord II

Hysterocheras combined with rare occurrences of *Mirapelia* and *Hoplites* in Semelenberg Nord II indicate a middle to early late Albian age (faunas ‘Paleoecology 3’ and ‘Paleoecology 4’ in Tajika et al. 2017a: tab. 1, fig. 2). A very low number of possible middle Albian ammonites (*Hoplites mirabiliformis* and *Mirapelia* cf. *buarquianum*) suggest that the fauna mostly contains late Albian faunal elements. The material presented here will be housed in the Naturmuseum St. Gallen with the abbreviation NMSG Coll. PK. In addition, Semelenberg Nord II can be divided into several beds (C1–C5, see Fig. 1). The sedimentary sequence is composed of limestones moderately to very rich in phosphorites and glauconite. The most fossiliferous beds are C4 and the upper part of C3 (Fig. 1), which are moderately glauconitic and very rich in phosphorite.

We examined the paleoecology of the fauna from Semelenberg Nord II (222 specimens) with a focus on the two diversity indices of familial taxonomic richness and ecological disparity. We employed the method introduced by Bush et al. (2007) to calculate the number of ecospace occupied by the fauna as ecological disparity, which was also used in Tajika et al. (2017a). Accordingly, each organism was assigned to an ecological category based on tiering (pelagic, erect, surficial, semi-infaunal, shallow infaunal and deep infaunal), motility level (freely fast, freely slow, facultative-unattached, facultative-attached, non-motile unattached, non-motile attached) and feeding mechanism (suspension, surface deposit, mining grazing, predatory, other; for details of the classification, see table 2 in Tajika et al. 2017a). This combination of different ecological categories (6 for each tiering, motility level and feeding mechanism) yields $6 \times 6 \times 6 (= 216)$ different theoretical ecological types. We compared the number of occupied theoretical ecologies in the fauna with those of Tajika et al. (2017a). To this end, the sample size was standardized using rarefaction analysis with Past 3.15 (Hammer et al. 2001). To detect ecologically dominant taxa in the fauna, the ‘trophic nucleus’-concept was utilized (Neyman 1967; Tajika et al. 2017a). Accordingly, taxa, which constitute 80% of the fauna, were detected. Details of the procedure are given in Tajika et al. (2017a).

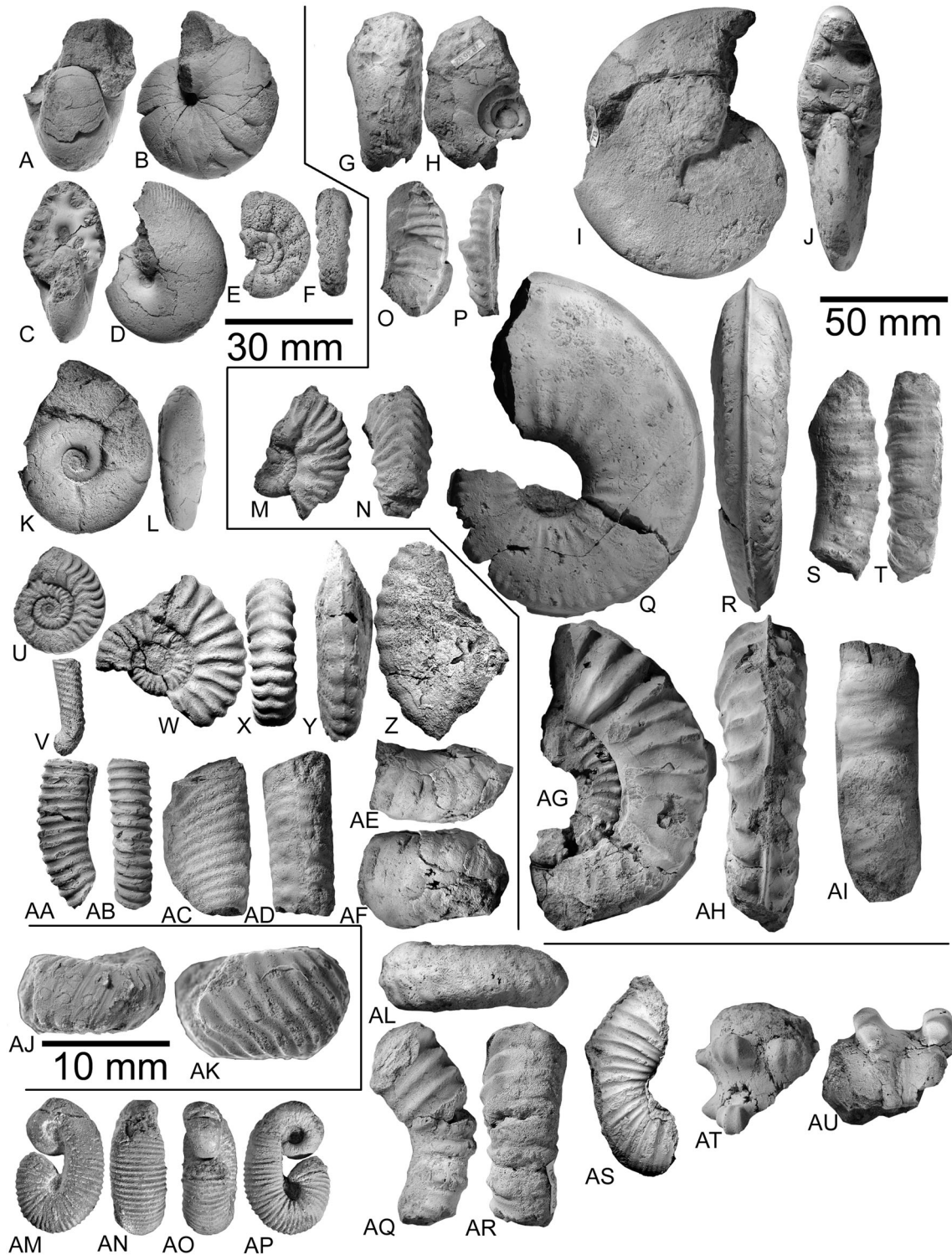
Results

Cephalopod faunas from Semelenberg

Cephalopods collected at Semelenberg I include *Beudanticeras* sp., *Douvilleiceras inaequinodum* (Quenstedt, 1846) and *Protanisoceras cantianum* Spath, 1939, which indicate the early Albian (most likely *Douvilleiceras mammillatum* Zone). At Semelenberg Nord II, we collected the following cephalopods: *Anisoceras armatum* (Sowerby, 1817), *A. perarmatum* (Pictet and Campiche, 1861), *A. pseudelegans* (Pictet and Campiche, 1861), *Beudanticeras* cf. *beudanti* (Brongniart, 1822), *Desmoceras* sp., *Dipoloceras cristatum* (Brongniart, 1822), *Eutrephoceras montmollini* (Pictet and Campiche, 1859), *Hamites virgulatus* (Brongniart, 1822), *H. subvirgulatus* Spath, 1941, *H. cf. intermedius* Sowerby, 1814, *Hoplites mirabiliformis* Spath, 1925, *Hysterocheras* cf. *orbigny* Spath, 1922, *Hyst. varicosum* (Sowerby, 1824), *Idiohamites* cf. *dorsetensis* Spath, 1939, *Kossmatella muhlenbecki* (Fallot, 1885), *Mirapelia* cf. *buarquianum* (White, 1887), *Mortoniceras* sp., *Neophlycticeras blancheti* (Pictet and Campiche, 1859), *Phylloceras (Hypophylloceras) sp.*, *Pseudhellicoceras* cf. *perelegans* Spath, 1937, *Pseud. robertianum robertianum* (d’Orbigny, 1842), *Puzosia (Puzosia) mayoriana* (d’Orbigny, 1841), *Tetragonites* sp. These ammonites indicate an early late Albian age (most likely a mix of *Dipoloceras cristatum* Zone and *Mortoniceras* spp. Zones). Although most of the cephalopods were already documented from the Alpstein (Tajika et al. 2017b; Kürsteiner and Klug 2018), a total of eight species including one new species are here first documented from the Alpstein, to which we give descriptions below. These materials are shown in Fig. 2. Four of these species are documented in Switzerland for the first time: *Hoplites mirabiliformis* Spath, 1925, *Mirapelia* cf. *buarquianum* (White, 1887), *Dipoloceras cristatum* (Brongniart, 1822), *Eoscaprites kuersteineri* sp. nov.

Paleoecology

Taxonomic richness and ecological disparity of the fauna in the late Albian are summarized in Table 1. The results show that the fauna is dominated by normally coiled and heteromorphic ammonites, which represent the ecological category of ‘pelagic, freely fast, predator’. To compare these new results to those of Tajika et al. (2017a), the sample size was rarefied to 70 (Table 1). In addition, the ecological categories of tiering, motility and feeding in the Semelenberg fauna are summarized in Fig. 3. Seven taxa form the trophic nucleus (Table 1).



◀ **Fig. 2** Early–late Albian cephalopod fauna of Semelenberg (Alpstein, Switzerland). AQ–AR and AT–AU were collected at Semelenberg Nord and all other specimens come from Semelenberg Nord II. **A**, **B** *Eutrophoceras montmollini* (Pictet and Campiche, 1859); NMSG Coll. PK. 7B.46.06. **C**, **D** *Phylloceras* (*Hypophylloceras*) sp.; NMSG Coll. PK. 7B.46.98. **E**, **F** *Kosmatella muhlenbecki* (Fallot, 1885); NMSG Coll. PK. 7B.46.99. **G**, **H** *Tetragonites* sp.; NMSG Coll. PK. 7B.46.62. **I**, **J** *Beudanticeras* cf. *beudanti* (Brongniart, 1822); NMSG Coll. PK. 7B.46.53. **K**, **L** *Puzosia* (*Puzosia*) *mayoriana* (d’Orbigny, 1841); NMSG Coll. PK. 7B.46.59. **M**, **N** *Hoplites mirabiliformis* Spath, 1925; NMSG Coll. PK. 7B.46.10. **O**, **P** *Dipoloceras cristatum* (Brongniart, 1822); NMSG Coll. PK. 7B.46.15. **Q**, **R**, *Mirapelia buarquianum* (White, 1887); NMSG Coll. PK. 7B.46.28. **S**, **T** *Anisoceras armatum* (Sowerby, 1817); NMSG Coll. PK. 7B.46.30. **U** *Hysterocheras* cf. *carinatum* Spath, 1922; NMSG Coll. PK. 7B.46.19. **V** *Hamites* cf. *intermedius* Sowerby, 1814; NMSG Coll. PK. 7B.46.72. **W**, **X** *Hysterocheras varicosum* (Sowerby, 1824); NMSG Coll. PK. 7B.46.64. **Y**, **Z** *Neophlycticeras blancheti* (Pictet and Campiche, 1859); NMSG Coll. PK. 7B.46.12. **AA**, **AB** *Hamites subvirgulatus* (Spath, 1941); NMSG Coll. PK. 7B.46.80. **AC**, **AD** ?*Idiohamites* sp.; NMSG Coll. PK. 7B.46.7). **AE**, **AF** *Pseudhellicoceras* sp.; NMSG Coll. PK. 7B.46.96. **AG**, **AH** *Mortoniceras* sp.; NMSG Coll. PK. 7B.46.33. **AI** *Anisoceras perarmatum* Pictet and Campiche, 1861; NMSG Coll. PK. 7B.46.34. **AJ** *Pseudhellicoceras robertianum robertianum* (d’Orbigny, 1842); NMSG Coll. PK. 7B.46.88. **AK** *Pseudhellicoceras* cf. *perelegans* Spath, 1937; NMSG Coll. PK. 7B.46.94. **AL** *Turrilitidae* indet, NMSG Coll. PK. 7B.46.43. **AM**, **AP** *Eoscaphtes kuersteineri* sp. nov.; holotype, NMSG Coll. PK. 7B.46.07. **AQ**, **AR** *Protanisoceras cantianum* Spath, 1939; NMSG Coll. PK. 7B.45.05. **AS** *Hamitoides* sp.; NMSG Coll. PK. 7B.46.13. **AT**, **AU**, *Douvilleiceras inaequinodum* (Quenstedt, 1846); NMSG Coll. PK. 7B.45.03

Systematic paleontology

Order Ammonoidea Zittel, 1884.

Suborder Ammonitina Hyatt, 1889.

Superfamily Hoplitioidea Douvillé, 1890.

Family Hoplitidae Douvillé, 1890.

Subfamily Hoplitinae Douvillé, 1890.

Genus *Hoplites* Neymayr, 1875.

Type species *Ammonites dentatus* Sowerby, 1821, p. 3, pl. CCCVIII, fig. 3.

Hoplites mirabiliformis Spath, 1925.

Figure 2m, n.

Synonymy

1925 *Hoplites mirabiliformis* Spath, p. 125, pl. XI, fig. 6a, 6b, text-fig. 31b.

1982 *Hoplites* cf. *mirabiliformis* Colleté et al., pl. 19, fig. 2.

1989c *Hoplites* (*Hoplites*) *mirabiliformis* Föllmi, p. 147, pl. 12, fig. 3a, 3b.

Holotype *Hoplites mirabiliformis* Spath, 1925, p. 125, pl. XI, fig. 6a, b. From Devizes, England, Albian (*Hoplites dentatus* Zone).

Material One fragment (NMSG Coll. PK. 7B.46.10).

Table 1 Familial taxonomic richness and ecological categories of the late Albian fauna of Semelenberg

Paleoecology in Semelenberg Nord II (late Albian)			
Family	Abundance	Ecology	
Brancoceratidae*	49	A	
Desmoceratidae*	43	A	
Hamitidae*	35	A	
Anisoceratidae*	19	A	
Inoceramidae*	18	H	
Turrilitidae*	10	A	
Turbinidae*	9	E	
Tetragonitidae	8	A	
Phylloceratidae	7	A	
Cymatoceratidae	3	B	
Harpagodidae	3	E	
Aporrhaidae	2	E	
Caryophylliidae	2	C	
Trochidae	2	E	
Ampullinidae	1	E	
Belemnopseidae	1	A	
Echinoid indet. 1	1	E	
Echinoid indet. 2	1	E	
Hoplitidae	1	A	
Laqueidae	1	F	
Osteichthyes indet.	1	A	
Pleurotomariidae	1	E	
Ringiculidae	1	E	
Scaphitidae	1	A	
Scaphopod indet.	1	G	
Sponge indet.	1	D	
Tetrarhynchiidae	1	F	

	Familial taxonomic richness	Ecological disparity	Trophic nucleus
Original data ($N = 222$)	28.0	8.0	7
Rarefied data ($N = 70$)	16.4	5.4	NA
‘Paleoecology 4’ in Tajika et al. (2017a)	15.5	5.9	7

Groups in the trophic nucleus are indicated by an asterisk. A, pelagic, freely fast, predators. B, pelagic, freely slow, predators. C, erect, facultative attached, suspension. D, erect, non-motile attached, suspension. E, surficial, freely slow, grazing. F, surficial, non-motile attached suspension. G, semi-infaunal, freely slow, suspension. H, semi-infaunal, facultative-attached suspension. NA, not available. The ecological categories were introduced by Bush et al. (2007)

Description The specimen measures 32 mm in maximal measurable conch diameter. The whorl section is weakly depressed ($ww/wh = 1.09$). There are ten straight to flexuous ribs per quarter whorl, which are interrupted by a

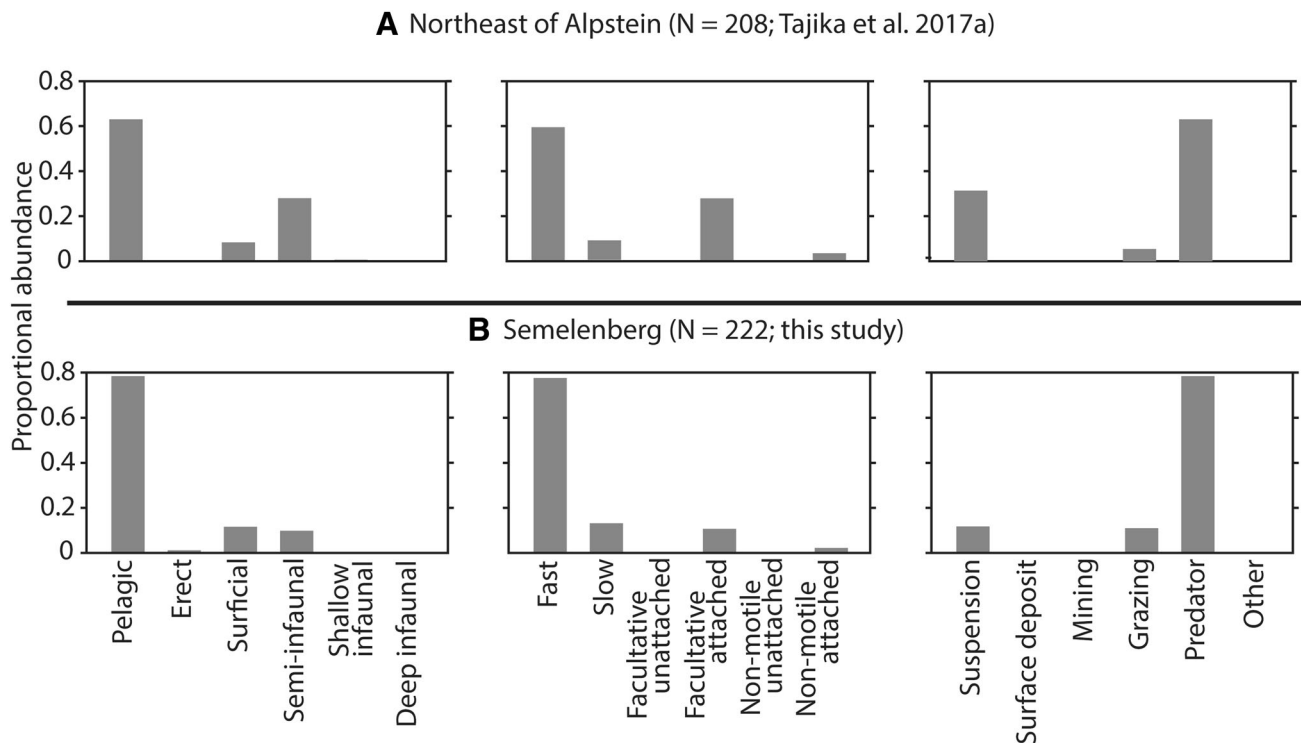


Fig. 3 Proportional abundances of tiering, motility and feeding in the late Albian of the Alpstein. **A** Results from Tajika, Kürsteiner and Klug (2017a). **B** Results of this study

ventral groove. At umbilical tubercles, the primaries split into three ribs, all of which end with moderately strongly developed ventral tubercles.

Discussion The specimen resembles the holotype figured in Spath (1925) in ribbing, tuberculation and whorl section. *H. mirabilis* is similar but the original drawing of the species (Parona and Bonarelli 1897) shows a slightly stronger tuberculation than the present species. Föllmi (1989c) also mentioned that the width of the flank is the highest in the mid flank in *H. mirabilis*. Nevertheless, all the slight differences probably fall within intraspecific variation.

Occurrences Middle Albian (*H. dentatus* Zone). France, England, Austria.

Superfamily Acanthoceratoidea, Grossouvre, 1894.

Family Mojsisovicsiidae Hyatt, 1903.

Subfamily Mojsisovicziinae Hyatt, 1903.

Genus *Mirapelia* Cooper, 1982.

Type species *Ammonites mirapelianus* d'Orbigny, 1850, p. 124.

Mirapelia cf. *buarquianum* (White, 1887).

Figure 2q, r.

Synonymy

1850 *Ammonites mirapelianus* d'Orbigny, 1850, p. 302.

1982 *Oxytropidoceras (Mirapelia) mirapelianum*, Cooper, fig. 14D–14E.

1997 *Oxytropidoceras (Mirapelia) mirapelianum*, Kennedy et al., p. 466, pl. 2, fig. 9; pl. 3, fig. 3, pl. 5, figs. 12–13, pl. 7, fig. 4, pl. 10, fig. 12, pl. 11, fig. 2.

2002 *Oxytropidoceras (Mirapelia) mirapelianum*, Robert, p. 183, pl. 34, figs. 4–5.

2010 *Mirapelia mirapelianum*, Bulot, p. 178.

Lectotype *Ammonites buarquianus* White, 1887, p. 222, pl. 24 (figs. 3–4), pl. 25 (figs. 7–8). From Maroim (Sergipe), Brazil, ?middle Albian.

Material One phragmocone fragment (NMSG Coll. PK. 7B.46.28).

Description The specimen measures 134 mm in maximum conch diameter. It is extremely discoidal ($wh/dm = 0.24$) and subinvolute ($ww/dm = 0.24$). The primary ribs, which are faint probably due to the absence of shell and erosion, are straight to slightly flexuous and moderately distantly spaced (13 ribs per half whorl). The ribs become faint on the outer flank where they split and then end in low tubercles at the ventrolateral edge. A distinct keel is present.

Discussion Our specimen is similar to the lectotype (White 1887) in its rib spacing and high whorl section. But the preservation hampers a more detailed examination of

ribbing, which made the species identification somewhat uncertain.

Occurrences Early middle Albian (most likely *Hoplites dentatus* Zone). Iran, Angola, Texas, Brazil.

Genus *Dipoloceras* Hyatt, 1900.

Type species *Ammonites cristatus* Brongniart, 1822, p. 395, pl. 7, fig. 9.

Dipoloceras cristatum (Brongniart, 1822).

Figure 2o, p.

Synonymy

1822 *Ammonites cristatus* Brongniart, 1822, p. 395, pl. 7, fig. 9.

1928 *Dipoloceras cristatum* var. Scott, p. 114, pl. 16, figs. 3–5, 8–9.

1928 *Dipoloceras fredericksburgense*, Scott, p. 115, pl. 15, figs. 1–5.

1931 *Dipoloceras cristatum*, Spath, p. 365, pl. 32, figs. 1–3, pl. 33, fig. 4, pl. 35, figs. 6–8, 10–15, text-figs. 119–121, 122a, 122e, 122f, 122 g, 122 h.

1931 *Dipoloceras fredericksburgense*, Spath p. 371, pl. 34, figs. 8–10, 14, text-figs. 122b, 123.

1941 *Dipoloceras cristatum* Van Hoepen, p. 56, text-figs. 1–2.

1951 *Dipoloceras cristatum*, Collignon, p. 22, pl. 2, figs. 3–4.

1951 *Dipoloceras* sp. aff. *fredericksburgense*, Collignon, p. 26, pl. 4, fig. 1, pl. 6, fig. 1, text-fig. 9.

1963 *Dipoloceras cristatum*, Collignon, p. 146, p. 147, figs. 1291–1292, 1294–1295.

1963 *Dipoloceras* sp. aff. *fredericksburgense*, Collignon, pl. 301, fig. 1301.

1966 *Dipoloceras cristatum cristatum*, Young, p. 130, pl. 15, figs. 1, 4, text-figs. 17c, 20d.

1966 *Dipoloceras cristatum alatum*, Young, p. 131, pl. 31, figs. 4, 5, text-fig. 20a.

1966 *Dipoloceras fredericksburgense*, Young, 1966, p. 130, pl. 32, figs. 1–6, text-figs. 7e, 7 g, 11 g, 17a.

1967 *Dipoloceras cristatum*, Collignon, p. 20, pl. 3, fig. 9.

1975 *Dipoloceras cristatum*, Förster, p. 226, pl. 11, fig. 12, pl. 12, fig. 4, text-fig. 72.

1994 *Dipoloceras cristatum alatum*, Emerson et al., fig. 48.

1994 *Dipoloceras fredericksburgense*, Emerson et al. p. 116.

1999 *Dipoloceras (Dipoloceras) cristatum*, Kennedy et al., p. 1105, figs. 4.9, 5.1–5.11, 6.7–6.12, 7.8, 7.9, 10.5.

Holotype *Ammonites cristatus* Brongniart, 1822, p. 395, pl. 7, fig. 9.

Material One fragment (NMSG Coll. PK. 7B.46.15). Folkestone, England, early late Albian.

Description The whorl fragment measures 54 mm in maximum measurable conch diameter. There is a feebly projected primary rib and nine rather straight secondary ribs. One of the primaries developed a strong node, which is characteristic for this species. Three of the secondary ribs correspond to one primary rib. A keel divides the ribs on the venter. The whorl section and umbilical width are not measurable due to the fragmentary preservation.

Discussion Our specimen appears slightly more compressed than the specimen in the original drawing of Brongniart (1822) while the overall ornamentation and the distinct primary rib are similar.

Occurrences Early late Albian (*Dipoloceras cristatum* Zone). France, England, Poland, Morocco, Tunisia, Zululand, Mozambique, Madagascar, Texas, Suriname, India, Japan.

Family Lyelliceratidae Spath, 1921.

Subfamily Stoliczkaeiinae Breistroffer, 1953.

Remark Cooper (2012) proposed that *Stoliczkaia* Neumayr, 1875 and Stoliczkaeiinae Breistroffer, 1953 be replaced by *Stoliczkaia* and Stoliczkaeiellinae. However, the valid genus name of the Serpentes to which Cooper (2012) referred as the valid “*Stoliczkaia*” is *Stoliczkaia* Jerdon, 1870 (p. 367 in Malkmus et al. 2002). Thus, *Stoliczkaia* Neumayr, 1875 and Stoliczkaeiinae Breistroffer, 1953 are valid.

Genus *Neophlycticeras* Spath, 1922.

Type species *Ammonites brottianus* d’Orbigny, 1841 p. 29, pl. 85, figs. 8–10.

Neophlycticeras blancheti (Pictet and Campiche, 1859). Figure 2y, z.

Synonymy

1859 *Ammonites blancheti* Pictet and Campiche, p. 188, pl. 23, figs. 2–6.

1865 *Ammonites rhamnonotus* Seeley, p. 239, pl. 11, fig. 7.

1875 *Ammonites gardonicus* Hébert and Munier-Chalmas, pl. 4, figs. 1–2.

1931 *Neophlycticeras blancheti* Spath, p. 325, text-fig. 105, pl. 34, figs. 11–13.

1931 *Stoliczkaia rhamnonota* Spath, p. 331, pl. 31. Figs. 4, 7, 9, 12, pl. 32, fig. 8, text-fig. 109.

1968 *Stoliczkaia (Faraudiella) blancheti*, Renz, 1968, p. 46, pl. 5. Fig. 21.

1968 *Stoliczkaia (Faraudiella) gardonicus*, Renz, 1968, p. 46, pl. 5. figs. 17, 18, text-fig. 16a.

1978 *Stoliczkaia (Faraudiella) rhamnonota*, Wright and Kennedy, 1978, p. 396, pl. 36, figs. 5–6.

1981 *Stoliczkaia (Faraudiella) rhamnonota*, Chiriac, 1981, p. 124, pl. 30. fig. 1.

1992 *Stoliczkaia (Faraudiella) blancheti*, Atabekian, p. 202, pl. 113, figs. 1–3, pl. 114, figs. 1–3.

1994 *Neophlycticeras (Neophlycticeras) blancheti*, Wright and Kennedy, p. 563, figs. 2a, 2b, 2c, 2d, 2e, 2f, 2 g, 2 h, 2i, 2j, 2 k, 2 l, 2 m, 6d, 6e, 6f, 7a, 7b, 7c, 7d, 7e, 7f, 7 g, 7 h.

1994 *Neophlycticeras (Neophlycticeras) blancheti*, Kennedy and Delamette, p. 1269, figs. 6.1–6.8, 6.19–6.22, 7.1–7.12, 7.15–7.17, 8.3, 9.1–9.2.

2002 *Neophlycticeras (Neophlycticeras) blancheti*, Amédro, p. 62, pl. 9, figs. 4, 5.

2008 *Neophlycticeras (Neophlycticeras) blancheti*, Kennedy et al., p. 44, pl. 4, fig. 24, pl. 10, figs. 1–2.

Type: Ammonites blancheti Pictet and Campiche, 1859, p. 188, pl. 23, fig. 2. From Sainte-Croix, Switzerland, Albian.

Material Two whorl fragments (NMSG Coll. PK. 7B.46.11; 7B.46.12).

Description NMSG Coll. PK. 7B.46.12 is a small fragment, which measures 47 mm in maximum measurable size. The whorl section appears compressed with a rather flat flank, which has a maximum width on the umbilical edge. Ventral tubercles persist. A keel is present, which is composed of flat and keeled nodes.

Discussion Although our specimens are fragmentary, they show the compressed whorl section, the characteristic feeble but relatively dense ribs and constant tuberculation, which are diagnostic characters of *N. blancheti*.

Occurrences Late Albian. France, England, Belgium, Switzerland, Romania, Armenia.

Suborder Ancyloceratina Wiedmann, 1966.

Superfamily Ancyloceratoidea Gill, 1871.

Familij Labeceratidae Spath, 1925.

Genus *Hamitoides* Spath, 1925.

Type species Hamites studerianus Pictet in Pictet and Roux, 1847, p. 137, pl. xv, figs. 1a–c.

Hamitoides sp.

Figure 2AS.

Material A whorl fragment (NMSG Coll. PK. 7B.46.13).

Description The hook-shaped fragment measures 42 mm in maximum measurable diameter. The whorl section appears oval. The specimen is covered with constant fine ribs, which may either be bifurcated or trifurcated around in the middle of the flank or slightly towards the outer part of the flank.

Discussion The fine ribbing is similar to *H. rusticus* and *H. studerianus* but the incomplete preservation of the

specimen hinders more detailed comparisons and thus species assignment.

Occurrences Middle–late Albian (for genus).

Superfamily Turrilitoidea Gill, 1871.

Family Turrilitidae Gill, 1871.

Genus *Pseudhelicoceras* Spath, 1922.

Pseudhelicoceras cf. *perelegans* Spath, 1937.

Figure 2AK.

Synonymy

1937 *Pseudhelicoceras perelegans*, Spath, 1937, p. 531, text-fig. 190g, 190h, 190i, 190j, 190k.

1978 *Pseudhelicoceras perelegans*, Klinger and Kennedy, p. 40.

Type: Pseudhelicoceras perelegans Spath, 1937, p. 531, text-fig. 190g, 190h, 190i.

Material A small fragment (NMSG Coll. PK. 7B.46.94). From Escragnolles, France, middle Albian.

Description The specimen measures 15 mm in maximal measurable conch diameter. The whorl section is broadly rounded with a maximal height of 9 mm. Oblique and fine ribs are equally spaced, each of which bears three rows of tubercles. 8 ribs per quarter whorl are present, which are neither bifurcated nor looped.

Discussion Our specimen resembles the types of *P. elegans*, *P. perelegans* and *P. pseudelegans* in having moderately sized tubercles on every rib but it shows the closest similarity to *P. perelegans* in having closely spaced ribs. However, the two species may fall within one species showing intraspecific and/or ontogenetic morphological.

Occurrences Late Albian. England.

Pseudhelicoceras robertianum robertianum (d'Orbigny, 1842).

Figure 2AJ.

Synonymy

1842 *Turrilites Robertianus*, d'Orbigny, p. 585, pl. 142, figs. 1–6.

1847 *Turrilites Robertianus*, Pictet, p. 399, pl. 15, fig. 7a, 7b, 7c, 7d.

1848 *Turrilites Robertianus*, Quenstedt, p. 302, pl. 22, fig. 5a, 5b.

1854 *Helicoceras Robertianus*, Pictet, p. 713, pl. LVI, fig. 10.

1859 *Turrilites Robertianus*, Chenu, p. 96, text-fig. 422.

1880 *Turrilites Robertsoni*, Wright, p. 244, fig. 144.

1932 *Turrilites (Helicoceras?) Roberti*, Collignon, p. 18, pl. I, fig. 21, 21a, text-fig. 23.

1937 *Pseudhelicoceras robertianum*, Spath, p. 532, pl. LVIII, figs. 34–37, text-figs. 187a, 187b, 187c, 187d, 187e, 189b.

1957 *Turrilites robertianus*, Sornay, fig. 1–8.

1965 *Pseudhelicoceras robertianum*, Clark, p. 38, pl. 8, fig. 5, pl. 9, fig. 5, pl. 10, fig. 1.

1965 *Pseudhelicoceras robertianum*, Clark, p. 38, pl. 8, fig. 8, pl. 9, fig. 4, pl. 10, fig. 5.

1968 *Pseudhelicoceras robertianum*, Wiedmann and Dieni, p. 75, pl. VIII, fig. 12a, 12b, text-fig. 54.

1978 *Anisoceras (Pseudhelicoceras) robertianus*, Scholz, p. 43, pl. 3, fig. 3.

1978 *Pseudhelicoceras robertianum*, Klinger and Kennedy, p. 40, pl. 1, fig. I.

1979 *Anisoceras (Pseudhelicoceras) robertianus*, Scholz, p. 30, pl. 6, figs. 5a, 5b, 5c, 6a, 6b, 7a, 7b, 8, 9a, 9b, 10, 11, text-fig. 9A, 9B, 9C.

1985 *Pseudhelicoceras robertianum*, Atabekian, p. 23, pl. 1, figs. 1–5, pl. II, figs. 1–3.

1987 *Pseudhelicoceras robertianum*, Atabekian, p. 16, pl. I, figs. 1–5, pl. II, figs. 1–3.

1994 *Pseudhelicoceras robertianum*, Emerson et al., p. 291.

2006 *Pseudhelicoceras robertianum*, Gauthier et al., p. 169, pl. 47, figs. 7–10.

2014 *Pseudhelicoceras robertianum*, Mosavinia et al., p. 84, fig. 8D1, 8D2.

Lectotype Turrilites robertianus d'Orbigny, p. 585, pl. 142, figs. 1–6.

Material A small fragment (NMSG Coll. PK. 7B.46.88). From Pertes du Rhône, France, late Albian.

Description The specimen measures 14 mm in maximal measurable conch diameter. The whorl section is broadly rounded with the maximal height of 6.5 mm. Equally spaced main ribs bear four rows of round tubercles. The main ribs are intercalated by two fine secondary ribs.

Discussion Our specimen resembles the type of d'Orbigny (1842) in ribbing and tuberculation.

Occurrences Late Albian. France, England, Germany, Switzerland, Austria, Hungary, Turkmenistan, Iran, Madagascar, Texas.

Superfamily Scaphitaceae Gill, 1871.

Family Sacphitidae Gill, 1871.

Subfamily Scaphitinae Gill, 1871.

Genus *Eoscaphtes* Breistroffer, 1947.

Eoscaphtes kuersteineri sp. nov.

Figure 2AM–AP.

Holotype Complete adult specimen NMSG Coll. PK. 7B.46.07.

Stratum typicum Condensed horizon of middle–late Albian.

Type locality Semelenberg, northern Alpstein, St. Gallen, Switzerland.

Derivatio nominis Honoring Peter Kürsteiner (St. Gallen), who discovered the holotype and found many of the specimens described here. He also invested a lot of time into the investigation of the paleontology and the mineralogy of the Alpstein massif.

Diagnosis *Eoscaphtes* with coarse ribbing and hook-shaped body chamber, which is tightly coiled to the extent that the terminal aperture almost reaches the phragmocone.

Description The mature specimen measures 32 mm in maximal diameter. The juvenile whorls are normally coiled. The phragmocone is sub-evolute ($uw/dm = 0.33$) and thinly pachyconic ($ww/dm = 0.69$). The end of normal coiling is reached near the end of the phragmocone. The body chamber forms the characteristic hook with a nearly straight portion, which is markedly inflated, and with a strongly recurved terminal part. The dorsal edge of the terminal aperture almost reaches the shaft, thus enclosing a drop-shaped secondary umbilical opening. The recurved terminal part of the last whorl is much narrower than the bulging shaft. The whorl section of the body chamber is weakly to moderately depressed ($ww/wh = 1.5$). The ribbing is fine on the phragmocone and becomes rather coarse on the body chamber (approximately 27 ribs). On the hook, the ribs are simple and straight on the shaft and recurvate, curved and bifurcating on the recurved part. A distinct constriction follows directly behind the terminal aperture.

Discussion The present species is morphologically the closest to *E. subcircularis* in having a similar umbilical width in the phragmocone. Although the holotype in Spath (1937) appears crushed, the hypotypes show this similarity. The hypotypes of *H. subcircularis* differ from the present species in having shorter body chambers than our specimen and in having a finer ribbing on the body chamber (MHNG Wi 'Sc'/2: 28 ribs; MGL 12342 Coll. Campiche: 32 ribs). In addition, the body chamber of the present species is more tightly recurved than in the other species. The aperture almost reaches back to the phragmocone. *E. tenuicostatus* differs from the present species in having a larger proportion of phragmocone in relation to the maximum diameter, a less conspicuous ribbing and a more openly coiled body chamber. *E. chardensis* has a more tightly coiled phragmocone. *E. circularis* has a much wider umbilical width of the phragmocone. The types of *E. circularis* lack the body chamber and thus we only know that it is not tightly coiled.

Occurrences As in the holotype.

Discussion

We calculated the two diversity indices for the Albian Semelenberg fauna. Given the high abundance of *Beudanticeras* cf. *beudanti*, *Mortoniceras* sp. and *Hysterocheras* sp., we assume that the age of the fauna is more or less comparable to that of the early late Albian fauna ‘Paleoecology 4’ (northeastern Alpstein) in Tajika et al. (2017a). When the compositions of each fauna are compared, they are similar in terms of the dominance of pelagic and predatory organisms such as normally coiled (Desmoceratidae, Brancoceratidae) and heteromorphic (Hamitidae and Anisoceratidae) ammonites (Fig. 3), while the relative abundance of benthic organisms such as Inoceramidae is much higher in the northeastern Alpstein (‘Paleoecology 4’ in Tajika et al. 2017a). Furthermore, the trophic nucleus (ecologically important groups) in the Semelenberg fauna holds a much lower proportion of benthic organisms (Inoceramidae, Turbinidae; 15%) than in that of NE Alpstein (Inoceramidae; 32%). This higher abundance of benthic organisms (Fig. 3) may be rooted in a slightly shallower water depth in the northeastern Alpstein (Tajika et al. 2017a) than in Semelenberg (this study) which is located slightly farther east in the Alpstein. As discussed by Tajika et al. (2017a), the fact that there is an eastward deepening gradient in the Alpstein may have led to a differentiation in bathymetry between the two localities, although they are reasonably close. Nevertheless, the bathymetrical difference was not large enough to yield two different ecological structures, given that the occupied ecologies in both faunas are almost identical.

In addition, the diversity indices of the two faunas appear to show quite a high similarity (Table 1). When both sample sizes are rarefied to 70, the diversity indices have a similar value (familial taxonomic richness around 16; ecological disparity slightly less than 6). As discussed above, both faunas are dominated by pelagic predators, indicating that the water was sufficiently deep for pelagic animals to thrive. In the context of paleoecological changes from the Barremian to the Cenomanian that were demonstrated by Tajika et al. (2017a), the moderately diverse fauna of Semelenberg in the (middle to) late Albian appears to be consistent, thus confirming the results of Tajika et al. (2017a). That is, the taxonomic richness in the Alpstein between the early Barremian and early Cenomanian was relatively persistent, whereas the ecological disparity rather fluctuated. As discussed before, there were slight differences in faunal composition between the different localities of the area with more or less the same age. Analyses of additional assemblages of other outcrops will help to better reconstruct the paleoenvironment and paleocommunities as well as their changes through time.

Conclusions

1. We document here eight ammonite species including the new species *Eoscaphtes kuersteineri* sp. nov. from Semelenberg, northeastern Alpstein. Four of those species are recorded from Switzerland for the first time.
2. Our paleoecological analysis revealed that the fauna was dominated by pelagic and predatory organisms (mostly ammonites), followed by some epibenthic organisms with suspension and grazing feeding strategies. Familial taxonomic richness is 28 and ecological disparity is 8 in the Semelenberg fauna (Semelenberg Nord II: most likely late Albian).
3. When the diversity of the Semelenberg fauna has been compared with previous studies, it appears that the taxonomic richness and ecological disparity in Semelenberg and other localities in the northeastern Alpstein (Tajika et al. 2017a) of more or less the same age are similarly high. This confirms the pattern of paleoecological changes from the Barremian to the Cenomanian proposed in Tajika et al. (2017a).

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