AMMONITE ASSEMBLAGE AND AGE OF THE HYDROCARBON SEEP LA ELINA, NEUQUÉN BASIN, ARGENTINA

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Abstract: The ancient hydrocarbon seep deposits at the La Elina Ranch, Neuquén Basin, northern Patagonia, Argentina, are the only Mesozoic seep site in South America yielding metazoan fossils. Apart from benthic mollusc shells and worm tubes, they yielded a number of nektonic ammonoids. Four species of ammonoids were identified: *Hildaitoides retrocostatus*, *Hammatoceras* ex gr. *insigne*, *Calliphylloceras* cf. *nilssoni*, and *Phylloceras* sp. The occurrences of three species (*H.* ex gr. *insigne*, *C.* cf. *nilssoni*, and *Phylloceras* sp.) probably are fortuitous, while *H. retrocostatus* might have actually thrived in, or around the seep, as indicated by numerous well-preserved juveniles, in addition to some adult specimens. The bathymetric estimates indicate a depth not greater than 200 m, while the benthic molluscs, typical of hydrocarbon seeps, indicate a much greater depth. It is hypothesized that the deep-water taxa might have occurred in a shallower setting, owing to rising anoxia and/or strong input of continental waters from the eastern and/or southeastern deltaic system. The ammonite assemblage indicates that the seep at La Elina is (Andean) Middle Toarcian, probably Chilensis Zone, in age.

Key words: Neuquén Basin, hydrocarbon seep, ammonites, Early Jurassic, Toarcian.

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INTRODUCTION

Hydrocarbon seeps are places where hydrocarbons (most commonly methane) discharge from the seabed into the water column. Dissolved methane and sulphate enable the microbially mediated anaerobic oxidation of methane (AOM), which results in the precipitation of methane-derived authigenic carbonates, incorporating ^{12}C-enriched methanogenic carbon around the fluid outlets (Ritger *et al*., 1987; Peckmann and Thiel, 2004). Additionally, the methane and dissolved sulphide, formed during AOM, provide metabolic energy for chemoautotrophic microbes and their chemosymbiotic invertebrate hosts, which frequently form mass accumulations at seeps (Levin, 2005).

Methane-seep environments and associated ecosystems in the modern oceans have been known only since the 1980s (Paull *et al*., 1984), following the earlier (Lonsdale, 1977) discovery of cognate hydrothermal vent ecosystems. Shortly afterwards, palaeontologists identified the fossil analogs of such communities (Gaillard and Rollin, 1986). Since then, the number of hydrocarbon seep sites across the globe and through geological time has grown and currently there are several dozen localities identified (Hryniewicz, 2022).

Modern hydrocarbon seep ecosystems are dominated by polychaetes, in particular siboglinid worms, and molluscs, mostly bivalves and gastropods. Several worms and bivalves host chemosynthesizing bacteria, fueling their nourishment (Dubilier *et al*., 2008). The Cenozoic seep communities are roughly similar to their modern counterparts, especially in the dominance of bathymodiolid and vesicomyid bivalves, both being chemosymbiotic. The situation was different in the Mesozoic, when these two prominent groups of bivalves were not yet present at seeps. Instead, the seeps were dominated by lucinid, solemyid, and modiomorphid bivalves (Amano *et al*., 2022) and abyssochrysoid gastropods (Kaim, 2022). Numerous seeps also were dominated by dimerelloid brachiopods (Kiel *et al*., 2014; Baliński *et al*., 2022), which disappeared from seeps before the mid-Cretaceous.

The fossil record of nektic or nektobenthic organisms at seeps is less obvious. There are numerous examples of shark and skate nurseries of egg capsules, known in recent seeps, and fossil capsules also have been reported from ancient seep deposits (Treude *et al*., 2011; Kiel *et al*., 2013). Ammonoids are extinct animals and therefore absent at post-Cretaceous seeps, but their shells are commonly found in or around Mesozoic seep deposits. Their occurrences at seeps can be fortuitous or deliberate. Ammonoids (and nautilids) cannot swim in deep water because of the risk of implosion (Saunders and Ward, 1987). It is thus obvious that all ammonoid shell occurrences in deep-water seeps have to be accidental as is in the case of gaudryceratid ammonites in Cretaceous hydrothermal vent deposits, with bathymetry interpreted as 2,500–5,000 m (Kaim *et al*., 2021). In other examples, especially in the clearly shallow-water Late Cretaceous seeps of the Western Interior Seaway, USA (Landman *et al*., 2022b), the ammonoids apparently are associated with the seeps (Landman *et al*., 2018, 2022a) and fall into the category of "seep favoured" sensu Sasaki *et al*. (2010). Several other occurrences are less obvious, since bathymetry estimations are not always straightforward or even possible. In some cases, the depth might be not the most important for the composition of seep communities, when other factors influence the local pool of ambient "shallow-water" taxa, e.g., the widespread dysoxia of bottom waters or soupy conditions of the sea bottom.

In the southern Neuquén Basin (Argentina) Toarcian (Early Jurassic), hydrocarbon seep deposits occur at a locality, known as La Elina (Fig. 1), reported by Gómez-Pérez (2001, 2003). The present authors re-visited the La Elina locality and were able to collect fossils from the seep carbonate, including several molluscs and worm tubes. This benthic association (Kaim *et al*., 2015a, b, 2016; AK's own data) indicates deep-water conditions. Here the authors present the detailed composition of the ammonoid fauna in- and around the La Elina seep and briefly discuss its age, provenance, bathymetry and relationship to the seep environment.

STRATIGRAPHIC FRAMEWORK

The studied outcrop including the seep belongs to the Los Molles Fm. The regional stratigraphy was described by Leanza (1990). According to this author, the Los Molles Fm is 1,042 m in thickness and is mainly composed of black shales with subordinate fine sandstones. The age of this formation is Toarcian to Early Bajocian, according to the ammonite content.

The studied outcrop (Fig. 1) exposes just a few metres of the lower part of the formation.

SYSTEMATIC PALAEONTOLOGY

The material described is housed in the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala (MOZ-PI).

Suborder Phylloceratina Arkell, 1950
Superfamily Phylloceratoidea Zittel, 1884
Family Phylloceratidae Zittel, 1884
Subfamily Calliphylloceratinae Spath, 1927
Genus *Calliphylloceras* Spath, 1927

Type species: *Phylloceras disputabile* Zittel, 1869; by original designation.

Remarks: Howarth (2020) considers *Calliphylloceras* a junior synonym of *Hypophylloceras* Salfeld, 1924, but apparently only including Upper Tithonian to Cenomanian representatives. Nevertheless, *P. disputabile* is Bathonian–Callovian. Since this classification excludes Lower and Middle Jurassic forms, herein there is a preference to retain *Calliphylloceras* for the pre-Berriasian representatives, and *Hypophylloceras* for those in the younger part of this main lineage of the subfamily (cf. Joly, 2000). The same conclusion, retaining *Calliphylloceras* as a valid genus, was reached by Dietl *et al*. (2021), on the basis of differences in the ornament and septal suture line.

Calliphylloceras cf. *nilssoni* (Hébert, 1866)
Fig. 2A, B

Material: Two incomplete specimens (MOZ-PI-10540/83b-1, 2) from the seep carbonate.

Description: The inner whorls are represented by the smaller specimen. The outer whorl, as shown by the larger specimen, is compressed with a rounded venter, very involute (relative umbilical width U/D = 0.11 at the maximum diameter: D = 35 mm). Both specimens show three slightly sigmoidal constrictions per half whorl in the internal mould, but not reflected in the outer surface.

Remarks: The small umbilicus and the constrictions, only marked on the internal mould, indicate that the specimens belong to *Calliphylloceras*. *C. nilssoni* includes closely comparable Toarcian European specimens (e.g., Joly, 2000, pl. 19, figs 6, 9; Kovács 2011, pl. 2, figs 3, 4). The specimen, figured by Jaworski (1926, pl. 4: 15) as *Phylloceras* aff. *nilsoni* [recte *nilssoni*] (Hébert, 1866), from the Lower Bajocian of Cerro Silla (Mendoza Province) seems indistinguishable from the present ones.

Interestingly, the specimens of the present account also are very similar to Bajocian–Bathonian specimens of *Calliphylloceras achtalense* (Redlich, 1894), as described by Joly (2000, pl. 13, fig. 4) and Joly (2012, pl. 1, fig. 4), and with the lower Aalenian specimens of *C*. aff. *achtalense*, described by Joly *et al*. (2023). Similar specimens from the Lower Bajocian of Paso del Espinacito were described as *C. achtalense* by Joly (2012, pl. 1, figs 4, 5).

Subfamily Phylloceratinae Zittel, 1884
Genus *Phylloceras* Suess, 1865

Type species: *Ammonites heterophyllus* J. Sowerby, 1820; by original designation.

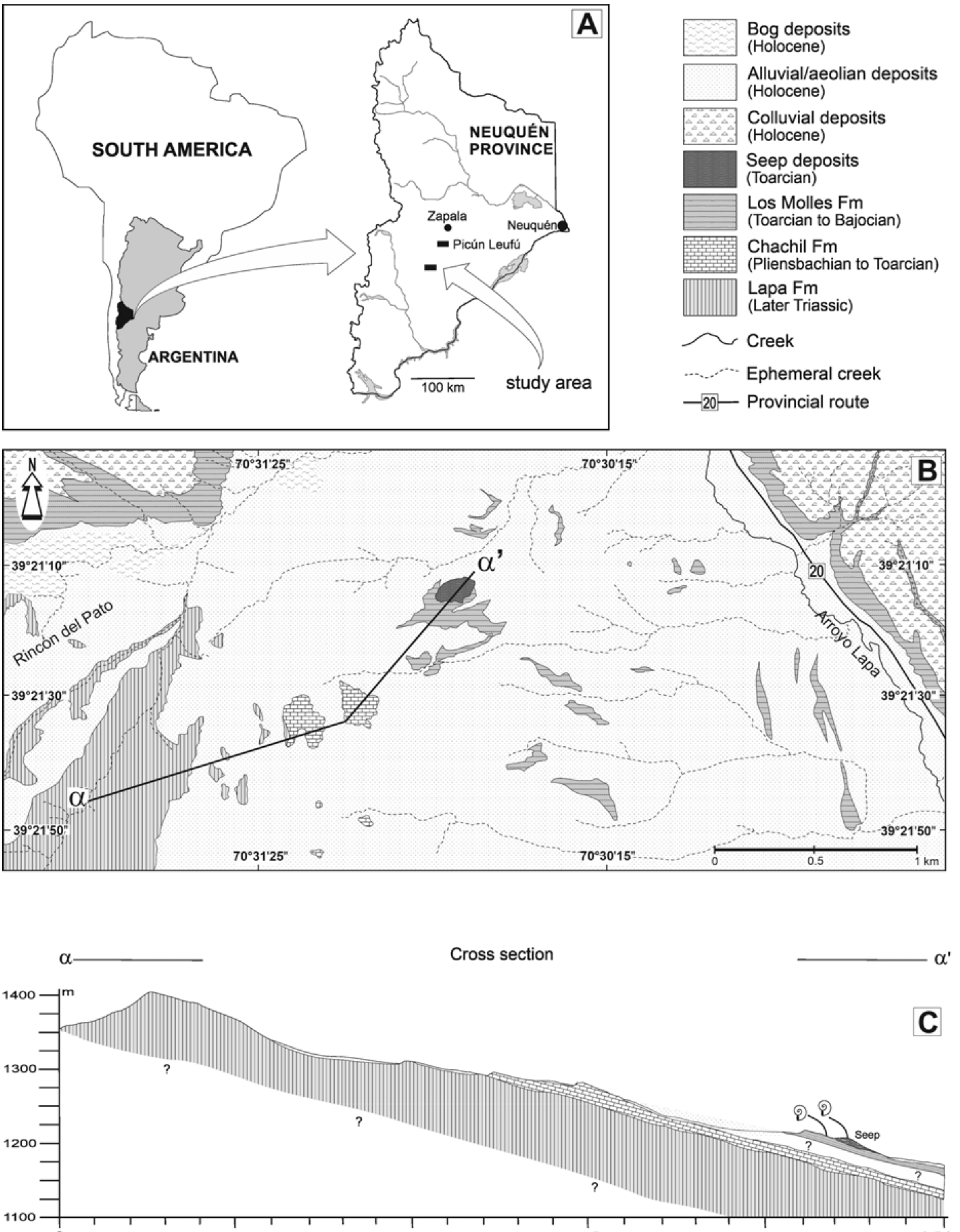

Fig. 1. Location of the studied site. **A**. Location of the study area within Neuquén Province, Argentina. **B**. Geological sketch-map showing the location of the sampled seep. **C**. Cross-section through the seep and adjacent area.

Phylloceras sp.
Figs 2C, 3

Remarks: Fragments of specimens belonging to a species of *Phylloceras* are abundant in the shales surrounding the seep carbonate (Fig. 3) as well as in the seep carbonate itself (Fig. 2C). These occurrences are in the form of fragments of small to very large individuals, indicating that they could correspond to pelagic animals, which died in the deeper waters, west of the study area, and were transported here (further discussed below).

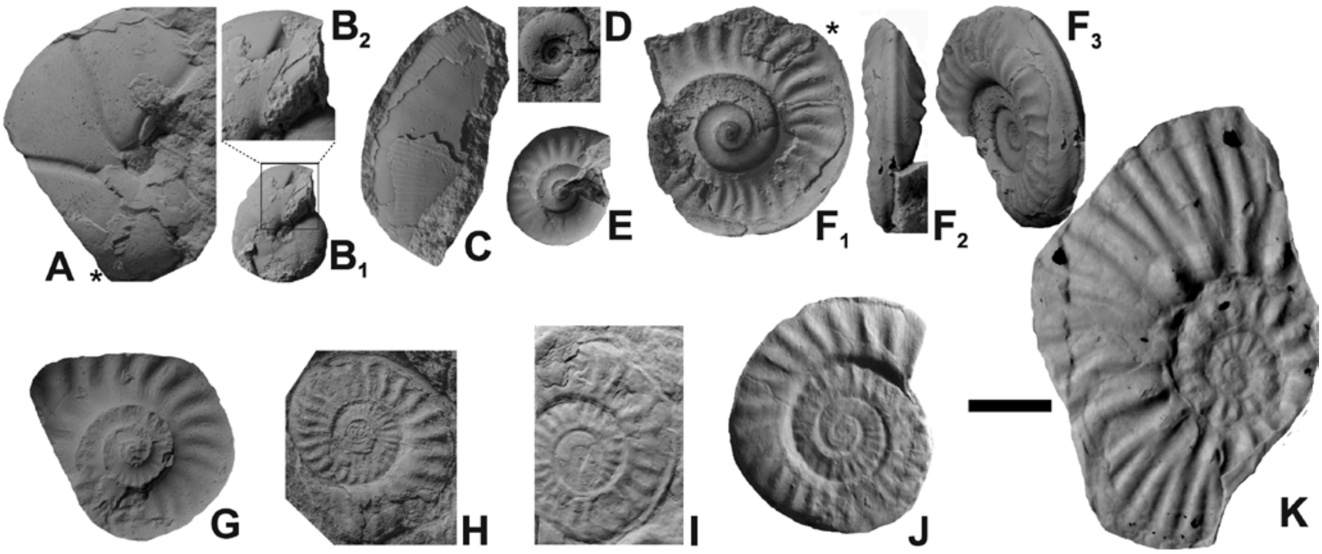

Fig. 2. Ammonites from the seep deposit (A–G) and surrounding shales (H–K), Middle Toarcian, La Elina, Neuquén. **A, B.** *Calliphylloceras* cf. *nilssoni* (Hébert, 1866); A – juvenile? With body chamber (MOZ-PI-10540/83b-1); B – small specimen (MOZ-PI-10540/83b-2), showing the constriction in the internal mould, not reflected in the outer surface of the shell (B_2 double sized). **C.** *Phylloceras* sp., fragmentary specimen (MOZ-PI-10541), showing the thin test with well-defined growth lines. **D–J.** *Hildaitoides retrocostatus* Hillebrandt, 1987; D – inner whorls (MOZ-PI-10540/101); E – juvenile (MOZ-PI-10540/88) showing the onset of the ribbing; F – adult microconch? with body chamber (MOZ-PI-10536) finely preserved, showing the thinness of the test and the keel, well-marked in the internal mould (F_3); G–J – adult microconchs?; G – MOZ-PI-10540/110; H – MOZ-PI-10534/1; I – MOZ-PI-10534/2; J – MOZ-PI-10534/3). **K.** *Hammatoceras* ex gr. *insigne* (Zieten, 1831), plaster cast of an adult? specimen (MOZ-PI-10534/4). Scale bar indicates 10 mm but 20 mm for B_2. The asterisk indicates the last septum.

Suborder Ammonitina Fischer, 1882
Superfamily Hildoceratoidea Hyatt, 1867
Family Hildoceratidae Hyatt, 1867
Subfamily Hildoceratinae Hyatt, 1867
Genus *Hildaitoides* Hillebrandt, 1987

Type species: *Hildaitoides retrocostatus* Hillebrandt, 1987; by original designation.

Hildaitoides retrocostatus Hillebrandt, 1987
Figs 2D–J, 3

Material: More than 30 specimens in flagstones in shales, preserved crushed or as impressions (MOZ-PI-10534/1-3, 10539); four well-preserved specimens from the seep carbonate (MOZ-PI-10536, 10540/88, 101, 110).

Description: Innermost whorls evolute (U/D = 0.33), smooth, with suboval whorl section. From D = 8–12 mm, appear rursiradiate to curved backwards, wide ribs, which fade into the ventro-lateral shoulder; between 12 and 30 mm in diameter there are 12–13 ribs per half whorl. The umbilicus is relatively wider (U/D = 0.42–0.46); the whorl section is compressed suboval to subrectangular with a fastigate to keeled venter. The largest adult specimen, probably not complete, is about 40 mm in diameter.

Remarks: The adult macroconchs (females) of the species are moderately large, as shown by the holotype with 122 mm diameter, including the body chamber almost complete (Hillebrandt, 1987). The studied specimens are smaller, but many of them are slightly uncoiled in the last part of the last whorl, indicating that they are adults. The largest adult specimen in the present material is only about 40 mm in diameter with its body chamber incomplete, so it could be a microconch (male) or a small macroconch.

Family Hammatoceratidae Buckman, 1887
Genus *Hammatoceras* Hyatt, 1867

Type species: *Ammonites insignis* Zieten, 1831; by subsequent designation of Buckman (1887).

Hammatoceras ex gr. *insigne* (Zieten, 1831)
Fig. 2K

Material: Several fragmentary specimens, mostly seen in the field. One plaster cast (MOZ-PI-10534/4) corresponding to an adult macroconch.

Description: The best specimen is a plaster cast from the shales surrounding the seep. It is moderately involute; the venter is not preserved. Tuberculate on the umbilical shoulder from the inner whorls; in the last whorl, the ribs are coarse, twinned from the umbilical tubercles. Larger but very fragmentary specimens show weakening of the umbilical tubercles in the body chamber.

Remarks and discussion: This combination of morphology and sculpture indicates that the specimens belong to some involute variant of *Hammatoceras insigne.*

Similar, but more evolute specimens from Cerro Puchén (Mendoza Province), were described by Jaworski (1926, pl. 3, figs 2, 3) as *Hammatoceras insigne*. They were assigned by Jaworski (1926, p. 287) to the Jurensis Zone, which is approximately equivalent to the Variabilis Zone (Page, 2003, p. 49). *H. insigne* was cited by Westermann and Riccardi (1972) from a somewhat higher stratigraphic position, in the Tenuicostatum Zone.

Large, incomplete specimens, seen in the field, are comparable to *Phymatoceras* cf. *pseudoerbaense* (Gabilly, 1973), e.g., Hillebrandt (1987, pl. 11, figs 1, 2) from the Middle Toarcian of Río de los Patos (San Juan Province), but the specimens of the present authors are more involute and bear well defined umbilical tubercles.

AGE OF THE SEEP

The ammonite assemblage of the seep and the surrounding shales is composed of the following species:

(1) *Hildaitoides retrocostatus* (moderately abundant as well-preserved juveniles and adult microconchs, in the seep and shales).
(2) *Hammatoceras* ex gr. *insigne* (medium-sized to large, fragmentary specimens in shales).
(3) *Calliphylloceras* cf. *nilssoni* (moderately abundant as small, well-preserved specimens in the seep).
(4) In addition there are abundant fragments, assignable to *Phylloceras*.

H. retrocostatus is known, at present, from the Chilensis Zone of the Andean Middle Toarcian (Hillebrandt, 1987). The genus recently was reported as ranging up to the Lower Aalenian (Parent, 2022). *Hammatoceras* is commonly recorded from the Variabilis Zone and ranges up into the Pseudoradiosa Zone (Gabilly, 1973). The phylloceratid genera are long-ranging ammonites, not useful for time-correlation (Joly, 1976; Howarth, 2020). The Los Molles Formation is known to be Toarcian–Early Bajocian in age (Leanza, 1990). Recent collections in the close locality Morro del Águila (HP, ACG) indicate that the base of the formation is Middle Toarcian. Since the seep belongs to the lower part of the formation, according to the ammonites recorded and the regional stratigraphy, the age of the seep at La Elina can be interpreted as (Andean) Middle Toarcian, probably the Chilensis Zone, time-correlated with the Variabilis Zone of the Tethyan standard chronostratigraphic scale (Hillebrandt, 1987).

PROVENANCE OF THE AMMONITES AND RELATIONSHIP TO THE SEEP ENVIRONMENT

Ammonites in the seep deposits are rather scarce, well-preserved, small hildoceratids (*Hildaitoides*) and phylloceratids (*Phylloceras* and *Calliphylloceras*); gastropods and bivalves are the most diverse and abundant (to be published elsewhere). In contrast, in the surrounding shales ammonites are abundant on fissility planes, as dense concentrations of ammonites (hildoceratids and fragments of large phylloceratids), abundant thin-shelled, nekto-benthic *Bositra*, and rarely other bivalves (Fig. 3).

These concentrations of ammonites with other molluscs could represent bottom accumulations of broken shells, mixed with masses of small ammonites and *Bositra* in a not very deep area, killed by events of rising anoxia and/or the strong input of continental waters from the eastern–southeastern deltaic system.

The fossil record of nektic or nektobenthic organisms at seeps is meagre. There are some examples of shark and skate capsules, reported from ancient seep deposits (Treude *et al*., 2011; Kiel *et al*., 2013) as well some shark teeth (e.g., Landman *et al*., 2022a and references therein). The most common, however – at least in the Mesozoic seeps – are cephalopods. Ammonoids, a group of shelled cephalopods, which gradually became extinct during the K–Pg transition, and therefore are absent from post-Cretaceous seeps, are relatively common in or around Mesozoic seep deposits. The occurrences of ammonoid shells at seeps can be fortuitous or deliberate. Ammonoids (and nautilids) cannot swim in deep water because of the risk of implosion (Saunders and Ward, 1987). It is obvious then that all ammonoid shell occurrences in deep-water seeps have to be accidental, as in the case of gaudryceratid ammonite in Cretaceous hydrothermal vent deposits with bathymetry interpreted as 2,500–5,000 m (Kaim *et al*., 2021). In other examples, especially in the clearly shallow-water Late Cretaceous seeps of the Western Interior Seaway, USA (Landman *et al*., 2022b), the ammonoids apparently were associated with the seeps (Landman *et al*., 2018, 2022a) and fall into the category of "seep favoured" sensu Sasaki *et al*. (2010). Ammonoids from the Western Interior Seaway seeps display offsets in $\delta^{13}C$ towards lower values, indicating that indeed they thrived close to the seeps. Low $\delta^{13}C$ values (down to - 30) in ammonoid shells also are observed from the seep-bearing Lopez de Bertodano Formation, on Seymour Island (Ivany and Artruc, 2016), and the overall offsets of $\delta^{13}C$ between ammonites and benthic molluscs in this formation are reported by Tobin and Ward (2015). This, according to Landman *et al*. (2022b) indicates that the ammonites lived in close proximity to methane seeps. Landman *et al*. (2022b) also argue that the high proportion of juveniles in seep-associated ammonoid assemblages may indicate that they lived next to the seep, perhaps using the ubiquity of food to form a nursery, similar to the ones of sharks and skates, as already suggested by Bourseau (1977). Another example of such ubiquity of juvenile ammonoids is a seep, reported by Smrzka *et al*. (2017) from the Turonian of Morocco.

Several other ammonoid occurrences in seep carbonates are less obvious, since bathymetry estimations are not always straightforward or even possible. In some cases, the depth might be not the most important controlling factor for the composition of seep communities, when some other factors influence the local pool of ambient "shallow-water" taxa, e.g., widespread dysoxia of bottom waters, soupy conditions of the sea bottom or other non-typical features of the shallow seep or vent setting (Miura *et al*., 1997; Vedenin *et al*., 2020; Watanabe *et al*., 2021).

The ammonoids at La Elina are represented by four species, two phylloceratids and two hildoceratoids. Apart from two incompletely preserved *Calliphylloceras* cf. *nilssoni*, the

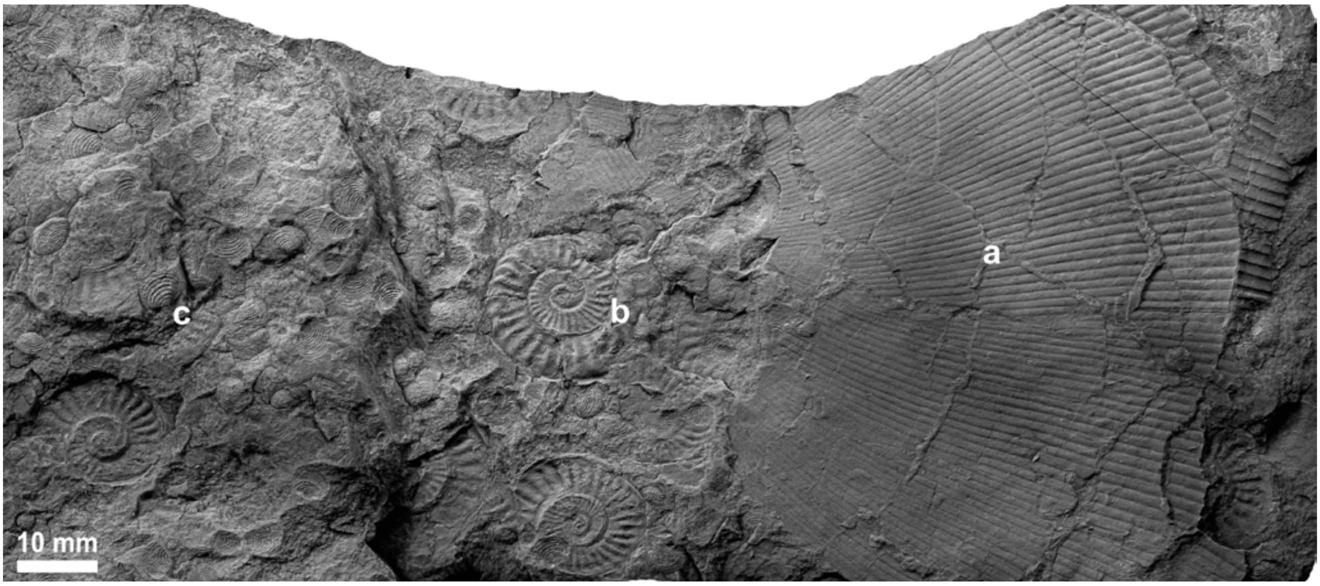

Fig. 3. Block (MOZ-PI-10540/83b-5) of the shales surrounding the deposits of the seep. a – *Phylloceras* sp., b – *Hildaitoides retrocostatus* Hillebrandt, 1987, c – *Bositra*.

phylloceratids are preserved as fragments of *Phylloceras* sp. Phylloceratids display an involute suboxycone shell shape, commonly considered to be characteristic for pelagic to necto-pelagic ammonoids, according to Westermann (1996; see also Lukeneder, 2015), and most likely inhabiting depths of 200–400 m. The palaeotemperature estimates from similarly shaped Cretaceous phylloceratids indicate temperatures characteristic for the range of 100–250 m (Moriya *et al.*, 2003; Lukeneder, 2015). Additionally, Doghuzhaeva *et al.* (2010) noted that phylloceratids could resist relatively high hydrostatic pressure and thus, inhabit deeper waters, thanks to conchs with a small siphuncle diameter and long septal necks.

Hildaitoides retrocostatus is relatively common in the shales around the seep and also is found in the seep carbonate; many specimens are juveniles. The serpenticonic shell shape of *H. retrocostatus* is usually considered to be typical for planktic drifters Westermann (1996). However, Ritterbush *et al.* (2014) argue that shell shape alone is insufficient to corroborate such a hypothesis. For the hildoceratids in the Posidonia Shales, less than 60 m has been estimated (Hewitt, 1996; Westermann, 1996; Lukeneder, 2015).

The discussion outlined above shows that out of the four species, only *H. retrocostatus* might be considered as a possible inhabitant of the seep, as the most common species, represented by numerous juveniles. However, this would require a relatively shallow-water setting for the seep at La Elina. The contradiction between the depth estimate from ammonoids and that from seep molluscs (hokkaidoconchids, neomphalids, paskentanids) might have resulted from mass mortality events, caused by rising anoxia and/or the strong input of continental waters from the eastern and/or southeastern deltaic system (see Arregui *et al.*, 2011). Unfortunately, the mollusc shells at La Elina are invariably recrystallized, preventing isotope studies.

CONCLUSIONS

In the southern Neuquén Basin, at the locality La Elina, interesting hydrocarbon seep deposits occur. The most common fossils in the seep carbonates are mollusc shells and worm tubes.

The ammonoids recorded are *Hildaitoides retrocostatus*, *Hammatoceras* ex. gr. *insigne*, *Calliphylloceras* cf. *nilssoni*, and *Phylloceras* sp. This association indicates that the seep at La Elina is (Andean) Middle Toarcian, probably Chilensis Zone, in age.

The composition, mode of occurrence and abundance of fossils (mainly the ammonites), the lithology, and the regional geology indicate mass mortality events by rising anoxia and/or the strong input of continental waters from an eastern deltaic system. The ammonites themselves indicate a relatively shallow-water environment of 100–200 m in depth. Out of the four species, only *H. retrocostatus* might be suspected as having been an inhabitant of the seep. However, this would require that the shallow-water character of the seep be obscured by environmental conditions, allowing a deep-water benthic seep fauna to thrive in shallower waters.

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REFERENCES

Amano, K., Kiel, S., Hryniewicz, K. & Jenkins, R. G., 2022. Bivalvia in ancient hydrocarbon seeps. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps*. *Topics in Geobiology*, 53: 267–321.

Arkell, W. J., 1950. A classification of the Jurassic ammonites. *Journal of Palaeontology*, 24: 354–364.

Arregui, C., Carbone, O. & Martínez, R., 2011. El Grupo Cuyo (Jurásico Temprano-Medio) en la Cuenca Neuquina. In: Leanza, H. A., Arregui, C., Carbone, O., Danieli, J. C. & Vallés, J. M. (eds), *Eología y recursos naturales de la provincia del Neuquén. Relatorio del 18 Congreso Geológico Argentino*, *Neuquén, 2011.* Asociación Geológica Argentina, Buenos Aires, pp. 77–89.

Baliński, A., Bitner, M. A. & Jakubowicz, M., 2022. Brachiopods at hydrocarbon seeps. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps*. *Topics in Geobiology*, 53: 223–251.

Bourseau, J.-P., 1977. L'Oxfordien moyen à nodules des «Terres noires» de Beauvoisin (Drôme) (*Ammonitina* de la zone à Plicatilis, paléontologie et biostratigraphie; milieu de sédimentation et genèse des nodules carbonatés). *Nouvelles archives du Muséum d'histoire naturelle de Lyon*, 15: 3–25.

Buckman, S. S., 1887. A monograph of the Inferior Oolite ammonites of the British Islands, part 1. *Monograph of the Palaeontographical Society. London*, pp. 1–24.

Dietl, G., Mönnig, E. & Schweigert, G., 2021. The ammonites of the *keppleri* Horizon (basal Callovian, Middle Jurassic) of Albstadt-Pfeffingen (Swabian Alb, Germany) – biostratigraphy and correlation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 302: 1–33.

Doguzhaeva, L. A., Bengtson, S. & Mutvei, H., 2010. Structural and morphological indicators of mode of life in the Aptian lytoceratid ammonoid *Eogaudryceras*. In: Tanabe, K., Shigeta, Y., Sasaki, T. & Hirano, H. (eds), *Cephalopods Present and Past*. Tokai University Press, Tokyo, pp. 123–130.

Dubilier, N., Bergin, C. & Lott, C., 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology*, 6: 725–740.

Fischer, P., 1882. *Manuel de conchyliologie et de paléontologie conchyliologique*. Savy, Paris, 1369 pp.

Gabilly, J., 1973. *Le Toarcien du Poitou*. Unpublished PhD Thesis, Universite de Poitiers, 456 pp.

Gaillard, C. & Rolin, Y., 1986. Paléobiocenoses susceptibles d'être liées à des sources sous-marines en milieu sédimentaire. L'exemple des Terres Noires (SE France) et des tepee buttes de la Pierre Shale Formation (Colorado, USA). *Comptes Rendus de l'Académie des Sciences*, *Série II*, 303: 1503–1508.

Gómez-Pérez, I., 2001. Estromatolitos de aguas profundas en la Formación Los Molles (Neuquén, Argentina): ¿chimeneas de metano en el fondo marino jurásico? *Revista de la Asociación Argentina de Sedimentología,* 8: 1–14.

Gómez-Pérez, I., 2003. An Early Jurassic deep-water stromatolitic bioherm related to possible methane seepage (Los Molles Formation, Neuquén, Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 201: 21–49.

Hébert, E., 1866. Observations sur les calcaires à Terebratula diphya du Dauphiné, et en particulier sur les fossiles des calcaires de la Porte de France (Grenoble). *Bulletin de la Societé géologique de France*, *ser. 2*, 23: 521–532.

Hewitt, R. A., 1996. Architecture and strength of the ammonoid shell. In: Landman, N. H., Tanabe, K. & Davis, R. A. (eds), *Ammonoid Paleobiology. Topics in Geobiology*, 13: 297–339.

Hillebrandt, A., 1987. Liassic ammonite zones of South America and correlations with other provinces. With description of new general of ammonites. In: Volkheimer, W. (ed.), *Bioestratigrafía de los sistemas regionals del Jurásico y Cretácico de América del Sur*. Comité Sudamericano del Jurásico y Cretácico, Mendoza, pp. 111–157.

Howarth, M. K., 2020. Systematic descriptions of the Jurassic and Cretaceous Phylloceratoidea, Boreophylloceratoidea, and Aequiloboidea. *Treatise Online*, 128: 1–37. https://doi.org/10.17161/to.vi.13358

Hryniewicz, K., 2022. Ancient hydrocarbon seeps of the World. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps*. *Topics in Geobiology,* 53: 571–647.

Hyatt, A., 1867. The fossil Cephalopoda of the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology,* 5: 71–102.

Ivany, L. C. & Artruc, E. G., 2016. Isotope ecology of a giant heteromorph ammonite from Antarctica. *Geological Society of America, Abstracts with Programs*, 48: 145–144.

Jaworski, E., 1926. La fauna del Lias y Dogger de la Cordillera Argentina en la parte meridional de la Provincia de Mendoza. *Actas de la Academia Nacional de Ciencias de la República Argentina*, 9: 136–317.

Joly, B., 1976. Les Phylloceratidae malgaches au Jurassique. Généralités sur quelques Phylloceratidae et quelques Juraphyllitidae. *Documents des Laboratoires de Géologie de la Faculte des Sciences de Lyon*, 67: 1–471.

Joly, B., 2000. Les Juraphyllitidae, Phylloceratidae, Neophylloceratidae (Phyllocerataceae, Phylloceratina, Ammonoidea) de France au Jurassique et au Crétacé. *Geobios*, *Mémoire*, 23 & *Mémoire de la Societé géologique de France*, *n.s.*, 174: 1–202.

Joly, B., 2012. Les Phylloceratina et Lytoceratina (Ammonoidea) du Bajocien inférieur du Paso del Espinacito (Argentine). Étude paléontologique et implications paléógéographiques. *Bulletin de la Societé géologique de France*, 183: 251–265.

Joly, B., Parent, H. & Garrido, A. C., 2023. Aalenian phylloceratid ammonites from Picún Leufú, Neuquén Basin, Argentina. *Revue de Paléobiologie*, 42: 143–148.

Kaim, A., 2022. A review of gastropods at ancient hydrocarbon seeps. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps*. *Topics in Geobiology*, 53: 323–374.

Kaim, A, Jenkins, R. G., Parent, H., Garrido, A., Hryniewicz, K. & Moriya, K., 2015a. Early Jurassic seep from Argentina displays faunal composition of modern aspect. In: *Jahrestagung der Paläontologischen Gesellschaft*, *ZfB Schiffweiler-Reden*, *14–16 September 2015*, *Abstract volume*, pp. 14–16.

Kaim, A., Jenkins, R. G., Parent, H., Garrido, A. & Moriya, K., 2015b. The earliest mollusc dominated seep fauna from the Early Jurassic of Argentina. *Geophysical Research Abstracts,* 17: EGU 2015–13280.

Kaim, A., Jenkins, R. G., Hryniewicz, K., Parent, H. & Garrido, A., 2016. Early Mesozoic seeps and the advent of modern seep faunas. In: *Book of Abstracts*, *1st International Workshop* *on Ancient Hydrocarbon Seep and Cognate Communities, 13–17 June 2016*, *Warsaw*, *Poland*. Institute of Paleobiology, Polish Academy of Sciences, Warsaw, p. 20.

Kaim, A., Little, C. T. S., Kennedy, W. J., Mears, E. M. & Anderson, L. M., 2021. Late Cretaceous hydrothermal vent communities from the Troodos Ophiolite, Cyprus: Systematics and evolutionary significance. *Papers in Palaeontology*, 7: 1927–1947.

Kiel, S., Glodny, J., Birgel, D., Bulot, L. G., Campbell, K. A., Gaillard, C., Graziano, R., Kaim, A., Lazar, I., Sandy, M. R. & Peckmann, J., 2014. The paleoecology, habitats, and stratigraphic range of the enigmatic Cretaceous brachiopod *Peregrinella*. *PloS ONE*, 9: e109260.

Kiel, S., Peckmann, J. & Simon, K., 2013. Catshark egg capsules from a late Eocene deep-water methane-seep deposit in western Washington State, USA. *Acta Palaeontologica Polonica*, 58: 77–84.

Kovács, Z., 2011. Lower Toarcian Ammonitida fauna and biostratigraphy of the Gerecse Mountains (Hungary). *Fragmenta Palaeontologica Hungarica*, 29: 1–48.

Landman, N. H., Cochran, J. K., Brezina, J., Larson, N. L., Garb, M. P., Meehan, K. C. & Myers, C., 2022a. Methane seeps in the Late Cretaceous Western Interior Seaway. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps. Topics in Geobiology*, 53: 425–477.

Landman, N. H., Jicha, B. R., Cochran, J. K., Garb, M. P., Brophy, S. K., Larson, N. L. & Brezina, J., 2018. 40Ar/39Ar date of a bentonite associated with a methane seep deposit in the upper Campanian Baculites compressus Zone, Pierre Shale, South Dakota. *Cretaceous Research*, 90: 90–96.

Landman, N. H., Larson, N. L., Cochran, J. K., Brezina, J. & Garb, M. P., 2022b. Ammonites as inhabitants of ancient hydrocarbon seeps. In: Kaim, A., Cochran, J. K. & Landman, N. H. (eds), *Ancient Hydrocarbon Seeps*. *Topics in Geobiology*, 53: 375–406.

Leanza, H. A., 1990. Estratigrafía del Paleozoico y Mesozoico anterior a los movimientos Intermálmicos en la Comarca del Cerro Chachil, Provincia del Neuquén. *Revista de la Asociación Geológica Argentina*, 45: 272–299.

Levin, L. A., 2005. Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. *Oceanography and Marine Biology Annual Review*, 43: 1–46.

Lonsdale, P., 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research*, 24: 857–863.

Lukeneder, A., 2015. Ammonoid habitats and life history. In: Klug, C., Korn, D., De Baets, K., Kruta, I. & Mapes, R. H. (eds), *Ammonoid Paleobiology: From Anatomy to Ecology*. *Topics in Geobiology*, 43: 689–791.

Miura, T., Tsukahara, J. & Hashimoto, J., 1997. *Lamellibrachia satsuma*, a new species of vestimentiferan worms (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan. *Proceedings of the Biological Society of Washington*, 110: 447–456.

Moriya, K., Nishi, H., Kawahata, H., Tanabe, K. & Takayanagi, Y., 2003. Demersal habitat of Late Cretaceous ammonoids: evidence from oxygen isotopes for the Campanian (Late Cretaceous) northwestern Pacific thermal structure. *Geology,* 31: 167–170.

Page, K. N., 2003. The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland*, 1: 23–59.

Parent, H., 2022. Aalenian (Jurassic) to Berriasian (Cretaceous) chronostratigraphic zonation and guide ammonites of the Central Andes (Argentina, Chile, Peru). *Volumina Jurassica*, 20: 1–46.

Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P., Golubic, S., Hook, J. E., Sikes, E. & Curray, J., 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science,* 226: 965–967.

Peckmann, J. & Thiel, V., 2004. Carbon cycling at ancient methane-seeps. *Chemical Geology*, 205: 443–467.

Redlich, K. A., 1894. Der Jura der Umgebung von Alt-Achtala, ein Beitrag zur Kenntnis des Jura der Kaukasus-Länder. *Beiträge zur Paläontologie und Geologie der Österreich-Ungarns und des Orients*, 9: 55–81.

Ritger, S., Carson, B. & Suess, E., 1987. Methane-derived authigenic carbonates formed by subduction-induced porewater expulsion along the Oregon/Washington margin. *Geological Society of America Bulletin*, 98: 147–156.

Ritterbush, K. A., Hoffmann, R., Lukeneder, A. & De Baets, K., 2014. Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. *Journal of Zoology*, 292: 229–241.

Salfeld, H., 1924. *Die Bedeutung der Konservativstämme für die Stammesentwicklung der Ammonoideen*. Max Weg, Leipzig, 16 pp.

Sasaki, T., Warén, A., Kano, Y., Okutani, T., Fujikura, K. & Kiel, S., 2010. Gastropods from recent hot vents and cold seeps: systematics, diversity and life strategies. In: Kiel, S. (ed.), *The Vent and Seep Biota*. *Topics in Geobiology*, 33: 169–254.

Saunders, W. B. & Ward, P. D., 1987. Ecology, distribution, and population characteristics of *Nautilus*. In: Saunders, W. B. & Landman, N. H. (eds), *Nautilus*: *the Biology and Paleobiology of a Living Fossil*. Plenum, New York, pp. 137–162.

Smrzka, D., Zwicker, J., Kolonic, S., Birgel, D., Little, C. T. S., Marzouk, A. M., Chellai, E. H., Wagner, T. & Peckmann, J., 2017. Methane seepage in a Cretaceous greenhouse world recorded by an unusual carbonate deposit from the Tarfaya Basin, Morocco. *The Depositional Record*, 3: 4–37.

Sowerby, J., 1820. *The Mineral Conchology of Great Britain*, *Vol. 3, Parts 45–47*. Meredith, London, pp. 99–126.

Spath, L. F., 1927–1933. Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). *Memoirs of the Geological Survey of India, Palaeontologia Indica*, *n.s*., 9: 1–945.

Suess, E., 1865. Über Ammoniten. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften*, 52: 71–89.

Tobin, T. S. & Ward, P. D., 2015. Carbon isotope ($\delta^{13}C$) differences between Late Cretaceous ammonites and benthic mollusks from Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 428: 50–57.

Treude, T., Kiel, S., Link, P., Peckmann, J. & Goedert, J. L., 2011. Elasmobranch egg capsules associated with modern and ancient cold seeps: a nursery for marine deep-water predators. *Marine Ecology Progress Series*, 437: 175–181.

Vedenin, A. A., Kokarev, V. N., Chikina, M. V., Basin, A. B., Galkin, S. V. & Gebruk, A. V., 2020. Fauna associated with shallow-water methane seeps in the Laptev Sea. *PeerJ*, 8: e9018.

Watanabe, H. K., Senokuchi, R., Nomaki, H., Kitahashi, T., Uyeno, D. & Shimanaga, M., 2021. Distribution and genetic divergence of deep-sea hydrothermal vent copepods (Dirivultidae: Siphonostomatoida: Copepoda) in the Northwestern Pacific. *Zoological Science*, 38: 223–230.

Westermann, G. E. G., 1996. Ammonoid life and habitat. In: Landman, N. H., Tanabe, K. & Davis, R. A. (eds), *Ammonoid Paleobiology*. *Topics in Geobiology*, 13: 607–707.

Westermann, G. E. G. & Riccardi, A. C., 1972. Middle Jurassic ammonoid fauna and biochronology of the Argentine-Chilean Andes. Part I: Hildocerataceae. *Palaeontographica*, A140: 1–116.

Zieten, C. H., von, 1830–1833. *Die Versteinerungen Württembergs*. Privately published, Stuttgart, i–viii + p. 1–16, pls. 1–12 (1830); p. 17–32, pls. 13–24 (1831); p. 33–64, pls. 25–48 (1832); p. 65–102, pls. 49–72 (1833).

Zittel, K. A. v., 1869. Bemerkungen über *Phylloceras tatricum* Pusch sp. und einige andere *Phylloceras*-Arten. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 19: 59–68.

Zittel, K. A. v., 1884. Cephalopoda. In: *Handbuch der Paläontologie*, *Vol. 1, Number 2*. Oldenbourg. München & Leipzig, pp. 329–522.