PaleoBios 33: 1–6, October 17, 2016

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY

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Cover photo: The Oligocene nautiloid *Aturia angustata* and its lower jaw.

Citation: Goedert, James L. and Steffen Kiel (2016). A lower jaw of the nautiloid *Aturia angustata* (Conrad, 1849) from Oligocene cold seep limestone, Washington State, U.S.A *PaleoBios,* 33. ucmp_*paleobios*_32868

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A lower jaw of the nautiloid *Aturia angustata* (Conrad, 1849) from Oligocene cold seep limestone, Washington State, U.S.A.

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Fossil shells of the extinct nautiloid genus *Aturia* have been found in Cenozoic strata in many parts of the world, and yet there have only been two previous records of fossils of any part of the jaw apparatus of *Aturia*. This suggests that the jaws were only preserved by virtue of special, highly localized conditions. A fossilized lower jaw referable to *Aturia* has been found in western Washington State, USA, associated with two shells of *Aturia angustata* within a piece of limestone that formed as a result of localized hydrocarbon seepage on the deep-sea floor. This is the first report of a nautiloid jaw from Cenozoic strata of western North America, and the first report of any part of the jaw apparatus for *A. angustata*.

Keywords: Oligocene, nautiloid jaw, *Aturia*, Washington State

INTRODUCTION

Fossils of the cephalopod genus *Aturia* Bronn, 1838, have been found in Cenozoic strata around the world, and Chirat (2000) concluded that this is due to shells having been transported by oceanic currents rather than *Aturia* having a worldwide distribution. Others (e.g., Kobayashi 1954, Beu 1973, Lukeneder and Harzhauser 2002) have mentioned the effect oceanic currents might have regarding distribution of *Aturia* shells and those of other nautilids, but what part paleoclimatic conditions might have played, especially with regard to prevailing winds or storm events have only recently been considered (e.g., Grunert et al. 2010, Lukeneder 2015). The oldest fossils of *Aturia* are Paleocene, or possibly latest Cretaceous (Schenck 1931, Miller 1947, Kummel 1956) and *Aturia* ranges up into the latest Miocene (Durham 1940, Beu 1968, Ozawa and Tomida 1996). *Aturia* was also reported from possibly early Pliocene sediments in Chile (Nielsen et al. 2009), but these strata are now considered to be early Miocene based on foraminifers (Finger 2013). In many cases, fossils of *Aturia* are fragmentary, likely the result of damage during post mortem drifting of floating shells (Chirat 2000), after stranding of shells on shorelines (Zinsmeister 1987), and possibly also due to predation by cetaceans and pinnipeds (see Lindberg and Pyenson 2007). Fossils of complete shells of *Aturia* that include the living chamber are, however, not uncommon in some parts of the world (e.g., Moore 1984, 1988, Nielsen et al. 2009, Schlögl et al. 2011).

In spite of the widespread geographic distribution and stratigraphic range of the genus *Aturia*, there have been only two previous reports (Tomida and Tanabe 2004, Schlögl et al. 2011) of the jaw apparatus of *Aturia*. This is not surprising if most fossils of *Aturia* represent shells that have been drifting at sea for long periods of time because the soft parts of the animal would have decomposed and released the jaws long before the shell was deposited. Conversely, in areas that have produced many hundreds of specimens of *Aturia* shells (e.g. western Washington State, see Moore 1984; pers. observations of the authors), that include the living chamber and lack epibionts (thus were not afloat for long before being deposited), the lack of fossils of the jaw apparatus is puzzling and in stark contrast to the deposit recently described by Schlögl et al. (2011) where many hundreds of *Aturia* shells, both juvenile and adult, are associated with jaws. The apparent lack of jaws of *Aturia* may in part reflect a collecting bias, or perhaps they simply are not recognized, but it could also indicate that the jaws of *Aturia* were only fossilized under some special circumstances and/or very localized conditions.

We report herein a cephalopod jaw found in close proximity to two complete shells of *Aturia* preserved in limestone that formed due to the microbial oxidation of methane at a hydrocarbon seep in the northeastern Pacific Ocean during

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Citation: *PaleoBios,* 33. ucmp_*paleobios*_32868
Permalink: http://escholarship.org/uc/item/9jd5g1rr

Oligocene time.

MATERIALS AND METHODS

A boulder of seep limestone was found loose on a gravel bar (GPS coordinates: 47.2776° N, 123.5220° W) on the Canyon River, Grays Harbor County, Washington State, USA (Fig. 1). It was derived from the Lincoln Creek Formation, and was found in an area where the upper part of the formation of late Oligocene age is exposed (Rau 1966, Prothero and Armentrout 1985). Because only older strata are exposed farther upstream, the boulder is late Oligocene in age at the minimum, but could be as old as latest Eocene. Limestone from hydrocarbon seeps is common in the Lincoln Creek Formation in this area (e.g., Campbell and Bottjer 1993, Peckmann et al. 2002, Kiel 2006, Zwicker et al. 2015) and is easily distinguished, even in the field, from normal concretions. The boulder was approximately 45 cm in width, height, and length and broken up in the field with hand tools in order to extract any macrofossils contained within. It contained a fragment of a solemyid bivalve, an unidentified protobranch bivalve, a scaphandrid gastropod, several foraminifers, and two shells of the nautilid *Aturia angustata* (Conrad, in Dana 1849) and a cephalopod jaw. The fossils are deposited in the Swedish Museum of Natural History, Department of Palaeobiology, Stockholm (SMNH).

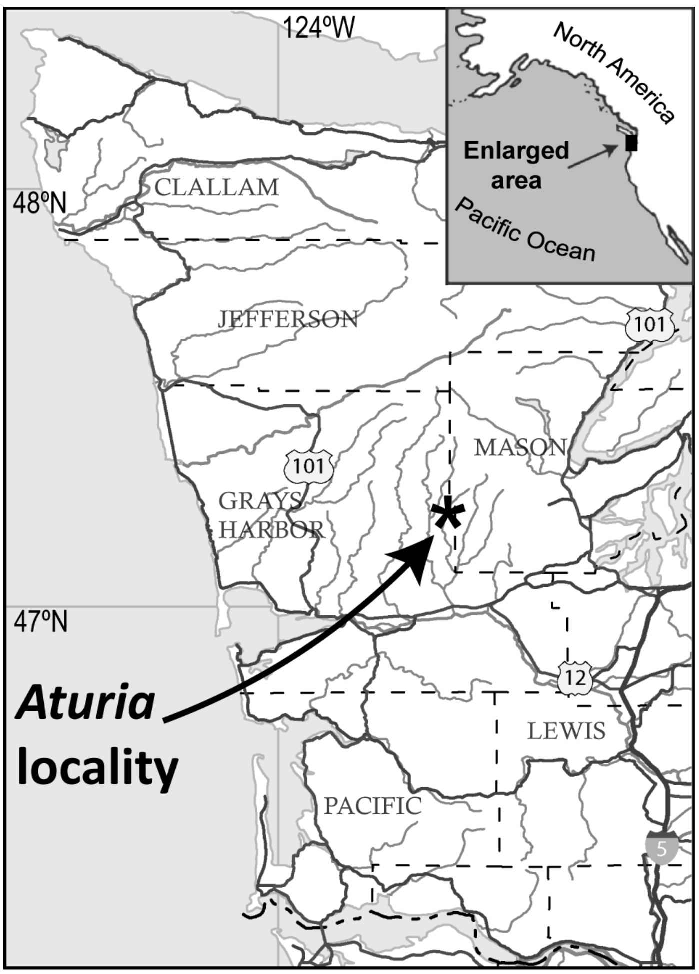

Figure 1. Map showing the *Aturia* locality in Washington State.

Description of the cephalopod jaw follows the terminology of Clarke (1962, 1986) as illustrated in Harzhauser (1999).

RESULTS

The two *Aturia angustata* shells are exceptionally well preserved but were slightly damaged while breaking up the hard limestone; the smaller (SMNH Mo182201; Fig. 2A, B) is approximately 33 mm in diameter, the larger one (SMNH Mo182202) is nearly 60 mm in diameter and still embedded in hard limestone. Both *Aturia* shells possess the living chamber and all shell layers are preserved. Only the living chamber of the larger specimen is filled with carbonate, the rest of the shell is filled with calcite and barite. Part of the living chamber of the smaller specimen is broken and crushed inward and these shell fragments have some surficial scratches, possibly from the teeth of scavenging sharks or fish, or from crustaceans. There is no evidence of epibionts on the *Aturia* shells. Within approximately 10 cm of the larger shell (SMNH Mo182202) was a small cephalopod jaw (SMNH Mo182203; Fig. 2C–F).

The fossil cephalopod jaw (SMNH Mo182203) has three-dimensional preservation, with two 'wings' that are positioned at an angle of about 50° to each other; they are gently arched both in the anterior-posterior direction and in the dorsal-ventral direction, have a slightly concave shoulder and are bordered ventrally by a deep gutter that radiates from the anterior rostral tip to each side; the lateral wall is imperfectly preserved and has the posteroventral part missing; the wings are partially covered by a thin black layer that shows fine growth increments; the specimen is approximately 9 mm wide at the posterior end of the 'wings', and just over 10 mm long (from the posterior end of the wings to the tip of the rostrum).

DISCUSSION

Identity

Due to its similarity to the lower jaw of *Nautilus* (e.g., Saunders et al. 1978) and that of a Miocene *Aturia* reported from Japan (Tomida and Tanabe 2004), we consider this specimen to represent the first reported lower jaw of *Aturia angustata*. We regard it to be from the larger of the two shells found in the carbonate boulder because it matches well the expected size of the jaw in relation to shell size, and it was preserved in close proximity to that shell. Although it is much smaller than the three-dimensional cephalopod jaw

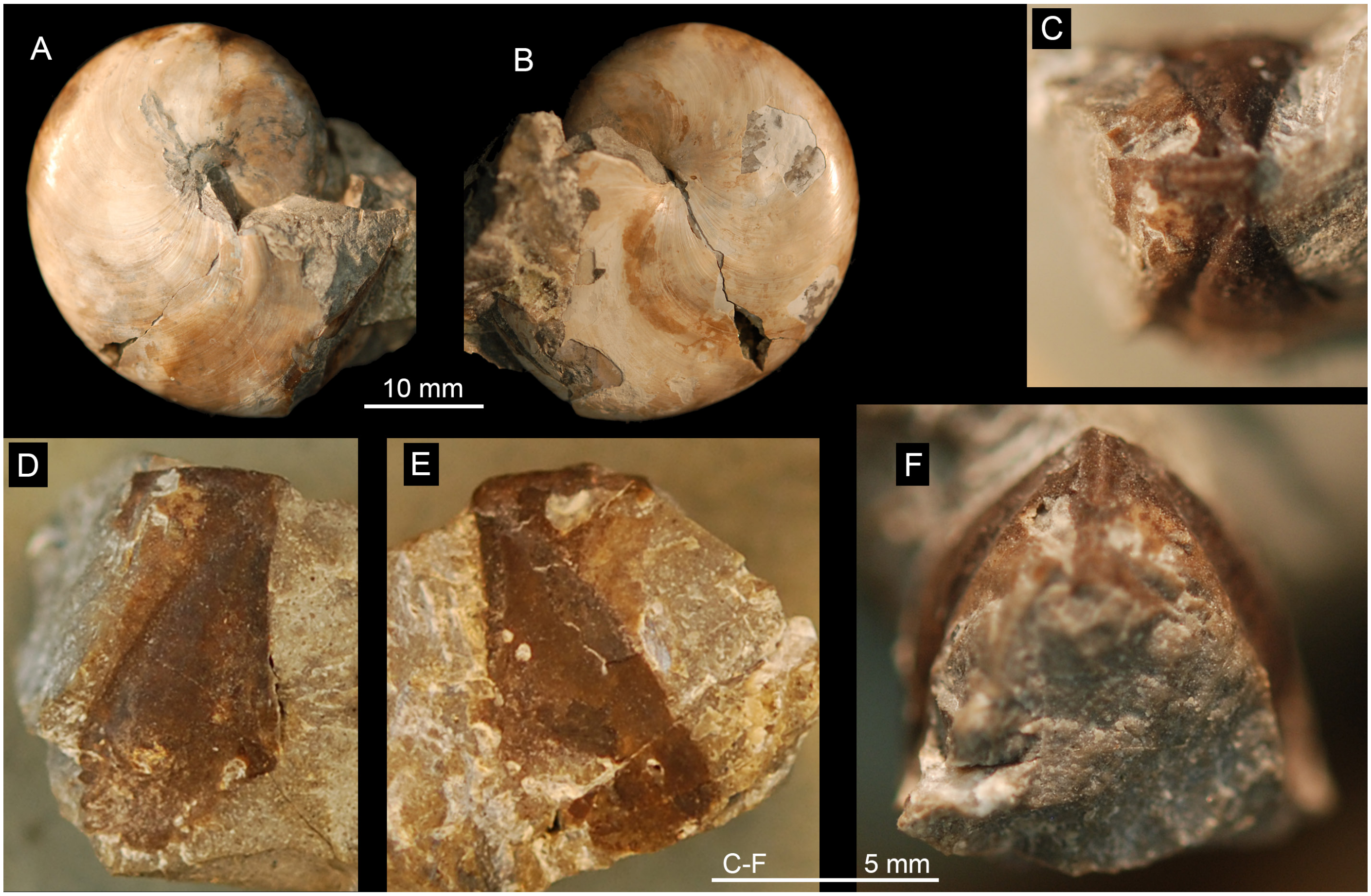

Figure 2. *Aturia angustata* found in Oligocene cold seep limestone from the Lincoln Creek Formation, Washington State, USA. **A, B**. Small shell (SMNH Mo182201). **C−F**. The lower jaw (SMNH Mo182203).

tentatively referred to *A. cubaensis* (Lea, 1841) by Tomida and Tanabe (2004), the jaw from Washington is almost identical in the shape of the wing and the presence of the prominent groove or 'gutter' running along the ventral margin. The specimen from Japan preserved a calcareous tip (Tomida and Tanabe 2004) whereas the specimen from Washington does not. This calcareous tip, or conchorhynch, could be present on the occlusal surface of the Washington jaw and thus not visible because it is embedded in matrix, or it may have become detached from the jaw and/or may have been overlooked when breaking up the seep limestone matrix. The pointed-arch outline of the jaws from Japan and Washington are similar to each other in ventral/dorsal view. Comparisons with the *Aturia* jaws reported by Schlögl et al. (2011) are not possible because they are all two-dimensional, compressed on bedding planes.

Taphonomy and preservation

There are several scenarios that might explain the preservation of two shells and a jaw of *A. angustata* from Washington in a piece of limestone from an Oligocene hydrocarbon seep. It is likely that one of the *Aturia* shells still had part of the body intact when it reached the seafloor, only releasing the jaw during some later stage of decomposition. Another less likely possibility is that the jaw is from another *Aturia* shell that was floating about, and the jaw just happened to land on the seafloor in close proximity to two *Aturia* shells that were already there, or vice versa. The jaws of *Aturia* were apparently preserved only in areas where special conditions prevailed, in this case the localized and rapid precipitation of limestone due to hydrocarbon seepage.

Hydrocarbon or 'cold' seeps are highly localized environments where carbonate forms as a result of the microbial oxidation of methane (e. g. Boetius et al. 2000, Peckmann and Thiel 2004). At many ancient cold seep sites found in western Washington State this carbonate precipitation was rapid enough to entomb articulated chitons (Squires and Goedert 1995), delicate sponges (Rigby and Goedert 1996) and preserve microscopic features of mollusk shells (Kiel 2006).

A seep site in Italy even preserved bacterial mats (Peckmann et al. 2004). At one Eocene seep site in Washington the egg cases of catsharks are well preserved and abundant (Treude et al. 2011, Kiel et al. 2013) along with sponges, worm tubes, and abundant mollusks. Pteropod shells dissolve rapidly in deep water (Hodgkinson et al. 1992) and will be preserved in deep-water sediments only under special conditions. Recently, the pteropod *Heliconoides nitens* (Lea, 1833) was reported (Goedert et al. 2013) from the Pacific Basin for the first time, preserved only in a cold-seep deposit but not in deep-water strata surrounding the seep deposit. The pteropods were preserved within and by carbonate that was locally and rapidly precipitated at a seep site. We propose that the same special and localized conditions at an Oligocene seep site in the Lincoln Creek Formation favored the preservation of the *Aturia* jaw described here.

Origin of *Aturia angustata* shells

The presence of a shell with the living chamber intact and an associated jaw, combined with a lack of epibionts, argues against the shell having drifted far after the death of the animal. We therefore conclude that some nautilids, specifically *A. angustata*, actually inhabited the northeastern Pacific Ocean during the Oligocene certainly, and probably inhabited that area from late Eocene to early middle Miocene time, as indicated by the fossil record (e.g., Miller 1947, Moore 1984, 1988). It is inconceivable that these shells might drift here due to prevailing winds and/or ocean currents and still have the living chambers intact, and improbable that any of them would still have soft parts containing the jaws or beaks after drifting any great distance. Nielsen et al. (2009) also called into question the drifting hypothesis in a study of *Aturia* from Cenozoic localities in Chile, pointing out that most of the specimens had all shell layers present and lacked epibionts and microborings. A number of different species of *Aturia* have been proposed (e.g., Miller 1947), and if these are valid species then the idea of a 'cosmopolitan' distribution *sensu* Chirat (2000) is misleading because some species apparently had limited geographic ranges and may represent a diversity of habitats.

Nautiloids at seeps

Fossils of *Aturia* have been found in seep deposits in Italy (Taviani 2001) and listed previously (Peckmann et al. 2002) from an Oligocene seep deposit in the Lincoln Creek Formation on the Satsop River, Washington State. Olsson (1931) reported *Aturia* in molluscan assemblages collected from his '*Pleurophopsis* zone' in the possibly Oligocene Heath Shales and also the Lomitos Cherts in northern Peru, localities that Kiel and Peckmann (2007) confirmed were seep deposits. Kiel and Hansen (2015) reported a 'nautiloid' from a presumably Oligocene seep deposit in Colombia. The perhaps oldest record of a post-Palaeozoic nautiloid from a seep deposit is *Aturoidea* cf. *mathewsonii* (Gabb, 1864) from the Late Cretaceous (Campanian-Maastrichtian) Sada Limestone site in southern Japan (Nobuhara et al. 2008, Tsujino and Iwata 2009). Nautiloids are highly mobile animals, so we regard these occurrences to likely represent shells that sank to the seafloor and fortuitously landed in areas where methane seepage was active with concomitant carbonate formation.

ACKNOWLEGEMENTS

We thank Green Diamond Resource Company (Northwest Timberlands Division), Shelton, Washington, for continuing to allow access to their land for palaeontological research. We are extremely grateful to Senior Editor D.M. Erwin, and S. Nielsen, A. Lukeneder, and an anonymous reviewer for their constructive comments.

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