The Paleocene cephalopod fauna from pebble point, Victoria (Australia)-fulcrum between two Eras

P D. Ward
University of Adelaide

D Flannery
California Institute of Technology

Emma Flannery
University of Wollongong, enf733@uowmail.edu.au

Timothy F. Flannery
University of Melbourne

The Paleocene cephalopod fauna from pebble point, Victoria (Australia)-fulcrum between two Eras

Abstract

Three species belonging to three genera of early Cenozoic nautilid cephalopods are described from Paleocene aged beds of the Pebble Point and Dilwyn formations, Victoria, Australia: Aturoidea distans Teichert, Eutrephoceras victorianum Teichert, both previously known from these deposits, and Nautilus praepompililus Shimansky, previously unknown from Australia. Here we present new occurrence and paleoecological information about these three taxa based on previously and newly collected specimens from Pebble Point Formation beds, as well as presenting the first paleotemperature analyses for Australian nautiloid cephalopods of any age. We sampled for shell carbonates from the single known specimen of Nautilus praepompililus, as well as from a specimen of Aturoidea distans from the Pebble Point beds. The A. distans samples showed temperature of calcification to have been between 20 and 25°C; and for N. praepompilius the temperatures were between 18 and 21°C. There were too few samples to provide statistical analyses, yet the implication is that these two taxa inhabited different depths during calcification. For comparison, we have sampled shell carbonates from the only known extant site where two different nautilid genera coexist, Manus Island, Papua New Guinea. There, specimens of Nautilus pompilius and Allonautilus scrobiculatus calcified (1984 specimens) at temperatures of 12 to 17°C, conforming to previous measurements in the literature and significantly colder than any of the Paleocene specimens sampled here.

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

The Paleocene cephalopod fauna from Pebble Point, Victoria (Australia) – fulcrum between two Eras

P.D. Ward [1,*], D.T.O. Flannery [2], E.N. Flannery [3] and T.F.F. Flannery [4]

[1] Sprigg Centre for Geobiology, University of Adelaide, South Australia, Australia (ward.biology.uw@gmail.com)
[2] NASA Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California, U.S.A.
[3] Centre for Archaeological Science, University of Wollongong, New South Wales, Australia
[4] Melbourne Sustainable Society Institute, University of Melbourne, Victoria, Australia
* To whom correspondence should be addressed. E-mail: ward.biology.uw@gmail.com

Abstract　　　　Ward, P.D., Flannery, D.T.O., Flannery, E.N. and Flannery, T.F.F. 2016. The Paleocene cephalopod fauna from Pebble Point, Victoria (Australia) – fulcrum between two Eras. *Memoirs of Museum Victoria* 74: 391–402.

Three species belonging to three genera of early Cenozoic nautilid cephalopods are described from Paleocene aged beds of the Pebble Point and Dilwyn formations, Victoria, Australia: *Aturoidea distans* Teichert, *Eutrephoceras victorianum* Teichert, both previously known from these deposits, and *Nautilus praepompilius* Shimansky, previously unknown from Australia. Here we present new occurrence and paleoecological information about these three taxa based on previously and newly collected specimens from Pebble Point Formation beds, as well as presenting the first paleotemperature analyses for Australian nautiloid cephalopods of any age. We sampled for shell carbonates from the single known specimen of *Nautilus praepompilus*, as well as from a specimen of *Aturoidea distans* from the Pebble Point beds. The *A. distans* samples showed temperature of calcification to have been between 20 and 25°C; and for *N. praepompilius* the temperatures were between 18 and 21°C. There were too few samples to provide statistical analyses, yet the implication is that these two taxa inhabited different depths during calcification. For comparison, we have sampled shell carbonates from the only known extant site where two different nautilid genera coexist, Manus Island, Papua New Guinea. There, specimens of *Nautilus pompilius* and *Allonautilus scrobiculatus* calcified (1984 specimens) at temperatures of 12 to 17°C, conforming to previous measurements in the literature and significantly colder than any of the Paleocene specimens sampled here.

Keywords　　　　Mollusca, Nautilidae, Cenozoic, palaeoclimate, fossil, extinction.

Introduction

One of the most striking aspects of the Cretaceous/Paleogene Cretaceous-Paleocene (K/Pg) mass extinction was the complete eradication of the ammonoids, shelled cephalopods that ranged from the Devonian until their very rapid decline to extinction (in fact geologically instantaneous) in this last of the so called "Big Five" mass extinction events. While there have been reports of some ammonite species actually ranging up into the Paleocene (Landman et al., 2014), these reports remain controversial, and even if correct, record only a minute fraction of ammonite biomass that disappeared with the K/Pg boundary event. Yet an enduring mystery remains why the nearly lookalike nautiloid cephalopods crossed the boundary at all. In this short contribution we look at the oldest record of post-K/Pg nautilid cephalopods yet known from Australia. This locality, Pebble Point, Victoria (fig. 1), is well known to the extraordinary Australian scientist, Tom Rich of Museum Victoria, who we honor in this volume.

In the post K/Pg world of the early Cenozoic Era, the surviving dinosaurs recovered and expanded to become the global avifauna; yet never again would they be the largest of land vertebrates or be large land animals or even ecological dominants. Similarly, in the sea, the surviving cephalopods, including the remaining externally shelled cephalopods (the phragmocone-bearing nautilids: Cephalopoda; Nautiloidea; Nautilida), would also evolve new species and body forms. Some, such as the taxon represented by a magnificent new specimen of the nautilid genus *Aturoidea* recently discovered at Pebble Point, Victoria, and described herein, converged onto the ammonoid shell plan of having complex septa rather than the far simpler septal morphologies found in almost all nautiloids that preceded the K/Pg mass extinction. But just as the avian dinosaur survivors of the K/Pg event were eclipsed by terrestrial mammals almost immediately from the Paleocene Epoch onward (with but one period of competitive struggle for the role of dominant terrestrial vertebrates in the Eocene), so too did the shelled cephalopods that survived the K/Pg event see but a short flowering during the Paleocene and Eocene. Kummel (1956) lists six genera but hundreds of
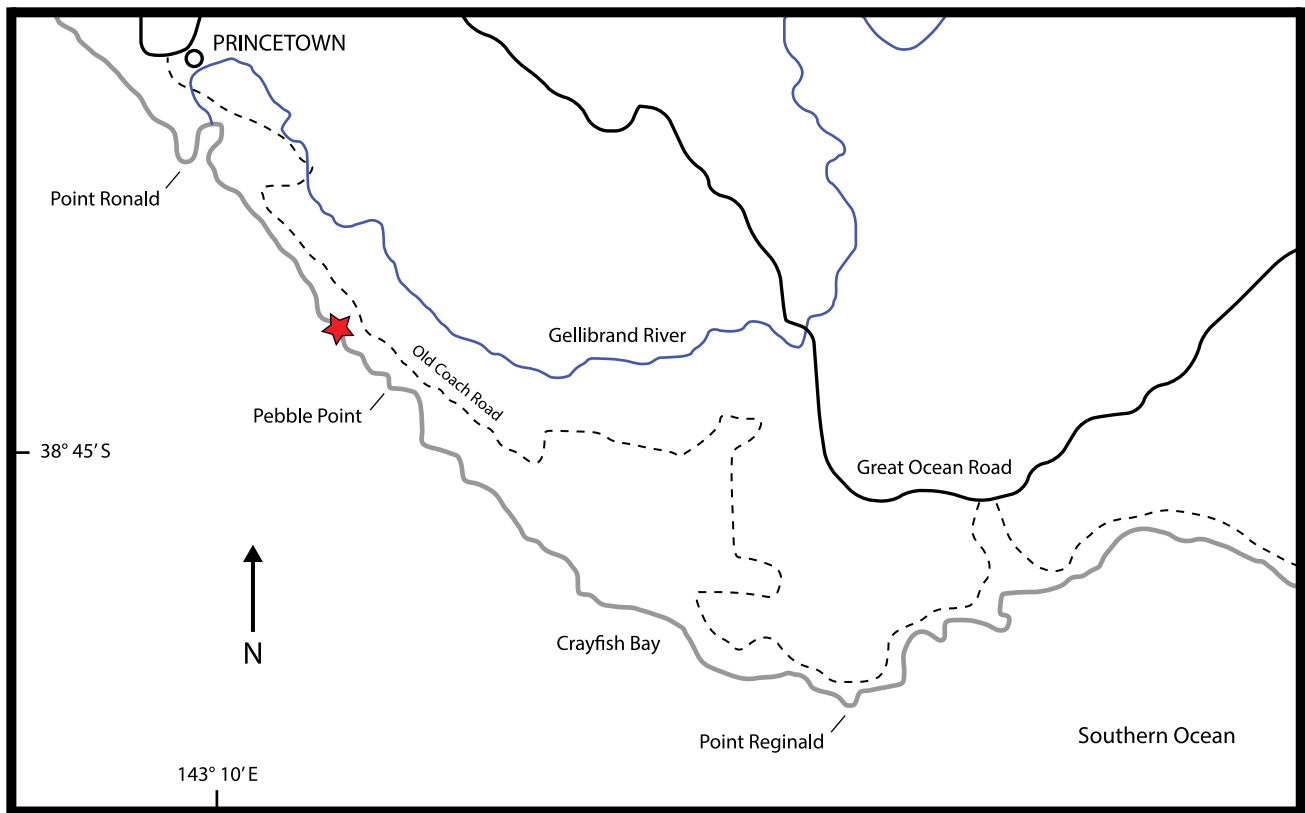
Figure 1. Map showing the location of sampling from Pebble Point Formation outcrop.

species described from beds of those ages. Yet by the Miocene, Kummel recorded but two nautilid genera in the world – and strikingly, *Nautilus* was not one of them, as Kummel proposed that *Nautilus* is the last genus of nautiloid to have evolved, and did not appear until late Pleistocene or recent times (Kummel, 1956; fig. 3).

The importance of the Pebble Point, Australia, fossil fauna is that it provides a link between the pre- and post- K/Pg extinction world, as well as providing an invaluable window into the evolution of the nautilids that developed ammonite-like septa, such as *Aturoidea* and its descendants, which appear to have included *Hercoglossa, Deltoidonautilus*, and in Australia the commonly occurring genus *Aturia* which is found in many global deposits of Eocene through Miocene age. But Pebble Point has also produced the first known fossil of true *Nautilus* from Paleocene strata anywhere in the world. This specimen provides us with a truly important viewpoint about not only the faunal history of Australia, but of the entire concept of living fossils, including their reality as long lived, low diversity clades.

In addition to providing a valuable link in terms of the paleobiogeography of Australia, the Pebble Point fauna represent a taphonomic enigma. As its name implies, the Paleocene strata at Pebble Point are composed of coarse sandstones with interbedded pebbles, indicative of shallow

water. Yet some of the fossils there, including the cephalopods described here, appear to have been transported into these beds from a deeper water habitat, as we show below. In spite of the lithological nature of the formation, which would seemingly preclude the preservation of delicate fossils, not only are truly remarkable specimens present, but also some show little to no post-depositional diagenesis. In this case, the pristine, unaltered and aragonitic shells of the nautilid cephalopods from the Pebble Point and lower Dilwyn Formations have allowed us to make oxygen and carbon isotope analyses of shells from two different nautilid genera, providing the first shell formation temperature for a Paleocene nautilid. It is believed that most mollusks secrete their carbonate shell in equilibrium with seawater in a temperature dependent way. Specifically, if the isotopic ratio of $\delta^{18}O$ of the oxygen in the carbonate structure can be measured, the seawater temperature at which the organism secreted its shell can be calculated, a technique employed successfully for several decades (for summary see Zakharov et al., 2013). It is necessary to make assumptions about the $\delta^{18}O$ of water during the Paleocene, but this is a straightforward calculation based on the isotopic contribution of melting the current ice caps (-1.0‰; Shackleton & Kennett, 1975).

Here, we describe the cephalopod fauna collected to date from the Pebble Point and Dilwyn Formations, and use both
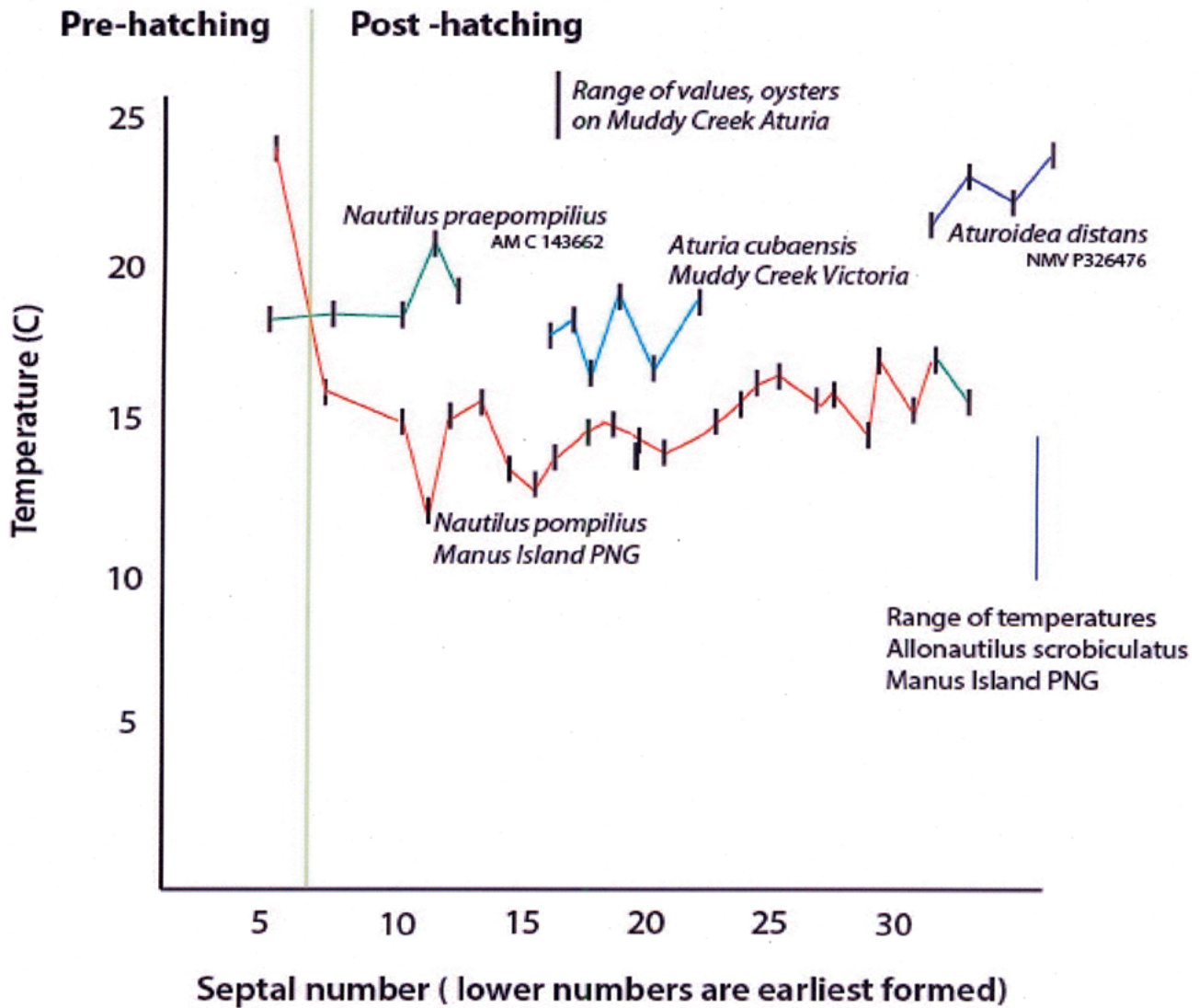
Figure 2. Results of oxygen isotope analyses of shell carbonates. Temperature (°C) is along the Y Axis. The X Axis is septal number, where the first formed septum is 1, and higher numbers pertain to more recently formed septa. PNG= Papua New Guinea.

morphology, the paleontology of attached organisms, and stable isotope geochemistry to reconstruct the cephalopod fauna living offshore of the shallow water Pebble Point fossil beds, and use fossil-based evidence to construct a taphonomic model consistent with the evidence at hand for specimens of the three species that are known: *Aturoidea distans* Teichert, *Nautilus praepompilius* Shimansky, and the third nautilid taxon noted from these beds, *Eutrephoceras victorianum* Teichert, which may also have undergone post-mortal drift, although we as yet have no such evidence.

Geological context

Stratigraphy and material

The Pebble Point Formation is derived from the "Pebble Point Beds" of Baker (1943). Other names used for it include the Pebble Point Grit and the now discarded Bahgallah Formation (Kenley, 1954), which was used later by Ludbrook (1971a, b). The formation is lithologically distinctive. It contains oolites (concretionary) which result in a distinctive appearance in thin section. It was described as rich in foraminifera including

Table 1. Shell measurements of AM C143662, *Nautilus praepompilius*, from the Paleocene Pebble Point Formation.

Diam	H	W	Umb%
21.8	15.5	18.5	1.19
26	18	21.7	1.21
29	21	22	1.05
31.9	21.3	21.9	1.03
33.14	19.52	21.65	1.11
37.8	21.7	21.8	1.00
62.2	36.6	36.3	0.99

miliolines and textuarians by McGowran (1965), but is also rich in other biotic components, including bioclasts from fish, echinoderms, mollusks and ostracods, as well as minerals including glauconite, pyrite, mica, and ferruginised clasts. In having a glauconitic and secondary pyrite component, the formation seems similar to the younger, fossiliferous and glauconitic formations on Maslin Beach, South Australia, which are Eocene in age compared to Paleocene for the Pebble Point Formation. The Pebble Point Formation is relatively thin at approximately 15 m thick, and is conformably overlain by the Dilwyn Formation, a finer clastic unit. The Dilwyn Formation has yielded foraminifera faunas of latest Paleocene to Early Eocene (McGowran, 1965), thus bracketing the Pebble Point Formation as Paleocene in age as the Pebble Point Formation sits with angular unconformity on Cretaceous strata. Further biostratigraphic work on the age of the Pebble Point Formation is reported by McGowran (1970) and McGowran et al. (1971), with a more recent summary in Birch (2003).

Some sedimentologists have characterized the Pebble Point Formation as having been deposited in marginal rather than open marine environments, based on the presence of the foram *Cyclammina*. Yet, the common presence of echinoderms as well as nautilid cephalopods, both intolerant of salinity much higher or lower than open ocean values argues against this, and adds further perplexing mystery to this peculiar faunal and sedimentological unit. While numerous clasts are present, other evidence suggests quiet sedimentation rather than high energy, and the exquisite preservation of some of the enclosed fossils confirms additional evidence for this, as noted by Darragh (1994, 1997).

The Dilwyn Formation has yielded a diverse assemblage of 37 separate invertebrate species (Stilwell, 2003a) from the informally named *"Trochocyathus – Trematrochus* Band" of presumed Paleocene-Eocene age (and thus presumably deposited amid warmer waters than the older Pebble Point Formation). The Pebble Point Formation itself has yielded 46 gastropod, 37 bivalve, 3 scaphopod and 2 cephalopod species, many of which are new and cosmopolitan species (Darragh 1994, 1997). To this list we add the presence of two nautilid species, *Aturoidea distans* and *Eutrephoceras victorianum*, previously noted from there by Darragh (1994, 1997) and the newly noted *Nautilus praepompilius*.

Materials and methods

We record a new specimen of *Aturoidea distans* from the Pebble Point Formation or Lower Dilwyn Formation, north of Pebble Point, collected by the co-authors in early 2014. This specimen is by far the most complete specimen known of this species. The specimen was cleaned using a hammer and chisel and coated with paraloid before being added to the palaeontology collection at the Museum Victoria (NMV P326476).

The following institutional abbreviations are used: NMV P, Museum Victoria palaeontological collections; AM C, Australian Museum mollusk collections; PIN, Moscow Institute of Palaeontology collections.

Isotopic analysis for paleotemperature

Additional specimens from this site are also known. A specimen of *Nautilus praepompilius* Shimansky, was found by chance in the extant *Nautilus* collections of the Australian Museum in Sydney. A second large *Aturoidea* presumed to be from Pebble Point, because of the very distinctive lithology of its body chamber infill, was being used as a doorstop in the Tate Museum of the University of Adelaide. This specimen has yet to be curated into any museum's collection. We also studied other specimens of *Aturoidea distans* from Pebble Point, found in the collections of the Museum Victoria, Melbourne, and a single specimen identified as *Eutrephoceras victorianum* from that same museum.

In addition, to provide a modern counterpoint, we present here new data collected in the same way from modern nautilids, including the first oxygen isotopic data from extant *Allonautilus*. The two shells sampled here were captured from the same trap off Little Ndrova Island, Papua New Guinea, in 1984. These shells are now in the Burke Museum at the University of Washington, but as yet do not have individual specimen numbers. Carbonate temperature analyses have never been done from Papua New Guinea nautilids of modern age. The importance of this site is that both specimens were caught in the same nautilus trap, from 300m depths left overnight in July 1984 off Little Ndrova Island, Papua New Guinea.

Fossil shell carbonate samples from both the single *Nautilus praepompilius* from the Pebble Point Formation, and the specimen of *Aturoidea* from the Pebble Point Formation held in the Tate Museum, University of Adelaide (no registration number), were collected for isotopic analysis of δ^{13}C and δ^{18}O by drilling with a microsampler. Carbonates from the two extant nautilid shells were taken from the septa of bisected specimens with a small set of needle nosed pliers or forceps.

Carbonate material was powdered using a Merchantek Micromill for precise sampling of shell material. Two kinds of sampling sites were used, in line with previous studies of ancient cephalopod shells: shell walls and entire septa. Powdered material was analyzed using a Kiel III Carbonate Device attached to a Delta Plus isotope ratio mass spectrometer. Samples (0.020–0.100 mg) were reacted at 70°C with 100% anhydrous phosphoric acid and analyzed interspersed with internal lab calcite standards calibrated to NBS-18 (–23.01‰ VPBD) and NBS-19 (–2.20‰ VPDB) for δ^{18}O and NBS-19
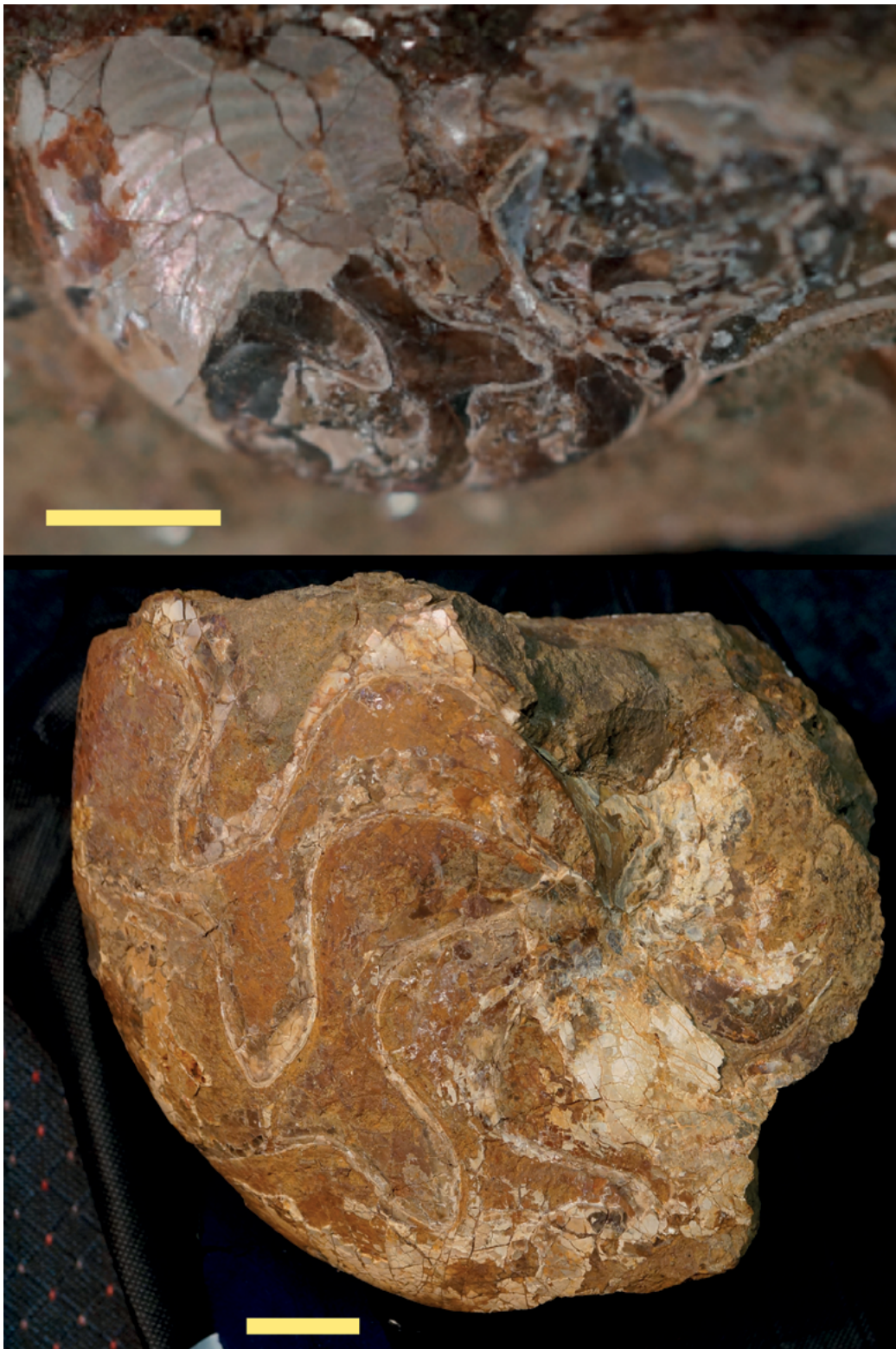
Figure 3. *Aturoidea distans* from Pebble Point, Victoria. Upper: small specimen NMV P 302005, showing the sutural morphology at shell diameter of 30-40 mm. Scale bar = 10 mm. Bottom: large specimen (not curated) in the Tate Museum, University of Adelaide, also from Pebble Point. One of the major differences compared to *Aturia* is the distance between septa. In both small and large (late stage) phragmocones, there is no contact between lobes. Scale bar = 5 mm.
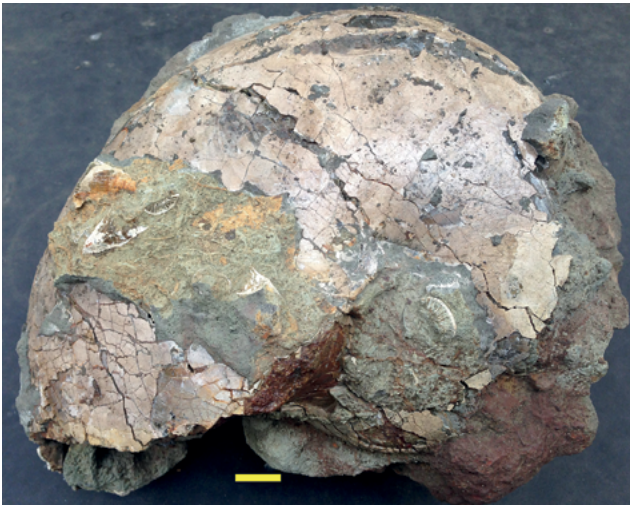
Figure 4. Large *Aturoidea distans* from Pebble Point, NMV P326476. Note also the corals growing on the shell, which could not have grown in this fashion during life of the nautilid. The corals are assumed here to have attached on the shell after the death, transport, and then final resting of the nautilid on a seabed shallower than the nautilid's life and growth habitat. However, these could not have grown in a high sedimentation rate environment. Scale bar = 10 mm.

Figure 5. *Eutrephoceras victorianum*, Pebble Point Formation, NMV P301870. Note the very simple septal suture outlined in black on upper shell. Scale bar = 10 mm.

(+1.95‰ VPBD) and LSVEC (−46.6‰ VPBD) for $\delta^{13}C$ fractionation factors for aragonite and calcite at 70°C. Despite surface confirmation of visibly unaltered material in thick section, the process of drilling into a sample may still entrain adjacent, altered material. The powder aliquot from each sample was thus analyzed for trace element concentrations, including Fe, Mg, Mn, Sr, and Na, using inductively coupled plasma atomic emission spectroscopy (ICP-AES). These data were used to assess diagenesis, both through comparison with published ranges of accepted, unaltered values and through comparison with the $\delta^{18}O$ data. Representative samples of aragonite fossil species common in the section were analyzed using X-Ray Diffraction (XRD) to confirm both primary mineralogy and diagenesis. All analysed samples were confirmed as aragonite with no detectable calcite present.

Results

Composition of the nautilid fauna

To date, two different nautilid cephalopod genera have been recorded from Pebble Point Formation beds: *Aturoidea distans* (Figures 3 & 4) and *Eutrephoceras victorianum* (Darragh, 1997) (fig. 5). To this list we add a third, *Nautilus* (*ss*), (figs. 6, 7) best attributed to *Nautilus praepompilius* Shimansky (see Shimansky, 1957; Saunders et al., 1996). Biometric results for this *Nautilus* specimen are shown in table 1. Sutures of some these taxa are shown in figure 7.

The species identifications of these three different taxa are problematic for a single reason: as with almost all Post-Triassic nautilid genera and "species", there are (compared to ammonoids) only a small number of morphological characters (Ward, 1984,

1987; Saunders, 1987; Teichert and Matsumoto, 1987; Tintant and Kabamba, 1985). Generally smooth and without ornament, with globular shells and simple septal sutures, the dearth of characters hinders nautilid identification. There is, thus, an abundance of species names for each of these genera throughout their geographic and stratigraphic ranges. We agree with Darragh (1997) that *A. distans* is indistinguishable from *A. brunnschweileri*, described from Paleocene deposits of Western Australia by Glenister *et al.* (1956). Post-Cretaceous nautilid taxonomy has long been a subject of too many species names based on too few characters (Ward, 1987), and while the various genera so adroitly accepted by Miller (1947) and Kummel (1956) more than a half century ago do seem to be well-founded, many of the species included in these genera are not. Kummel (1956) was especially contemptuous of the naming practices in many of the accepted genera, especially *Aturia* and *Cymatoceras*, where every national boundary seemed to be an excuse to erect yet another new species. This has certainly been the practice for some Australian Cretaceous through Miocene nautilids other than the outstanding and careful work of McGowran (1959). Specifically to the work here, the two accepted taxa from Pebble Point, *Aturoidea distans* Teichert (1943) and *Eutrephoceras victorianum* Teichert (1943), could easily be placed in taxa of precedence within these genera. For example *E. victorianum* is virtually identical to *E. hendersoni* from the Cretaceous of Queensland, as well as some of the more inflated *Eutrephoceras*

Figure 6. *Nautilus praepompilius* from Pebble Point, AM C 143662. Scale bar = 10 mm.

Figure 7. Comparative sutures of (1) *Nautilus praepompilius*, (2) *N. pompilius*, and (3) *Aturoidea distans*.

species noted from the Cenozoic of Australia, especially *E. geelongensis* as described by McGowran (1959). More recently, Dzik (1984) and Dzik and Gazdzicki (2001) have tried to unravel the taxonomic identifications of Eocene nautilids, and in fact refer to the Pebble Point Formation nautilid fauna using Teichert's identifications. Dzik (pers comm 2014) however, assures us that he has little confidence in the validity of the Australian names having been species truly distinct from similar looking fossils found elsewhere around the world in the Paleogene. Each of these genera, in fact, could have but a small handful of valid species over the tens of millions of years of their ranges (for *Eutrephoceras*, perhaps 195 million years of geological range, from the Triassic to the end of the Miocene).

Since the period when nomenclature (aiding biostratigraphy) was the only goal of paleontological study, a great deal of information has been added with regard to inter and intra-
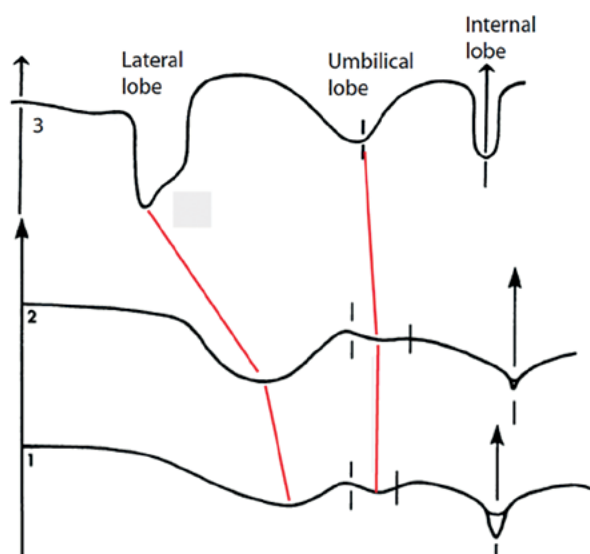
specific variability in the two living nautilid genera, *Nautilus* and *Allonautilus* Ward and Saunders (1997). New DNA work on *Nautilus* (Wray et al., 1995; Bonacum et al., 2010) as well as work conducted by one of the authors here (Vandepas et al., in review) has shown that species of *Nautilus* are, in fact, highly variable, and that rather than the currently "accepted" species *Nautilus pompilius* (the type species), *N. macromphalus, N. stenomphalus*, and *N. belauensis* (with *N. repertus* also accepted in some quarters), there is now good understanding that along the Great Barrier Reef there is a complete morphological mixture of characters that have been used to separate *N. stenomphalus* from *N. pompilius* – and that there is no difference in the COI gene between the morphologically distinct end members of what has been called *N. pompilius* and *N. stenomphalus*. In similar fashion, *N. belauensis* Saunders is now seen as simply a large *N. pompilius*, as is *N. repertus*. If taken to the various so called "species" of *Aturoidea* (and to a great extent *Aturia* as well, although there are distinct differences between Australian specimens of the Eocene *A. clarkei* and the younger A. *cubaensis* and A. *coxi*), some taxon linages would be regarded as a single species. Unlike the case of the two putative *Aturoidea* "species" from Australia, all three of these *Aturia* taxa differ markedly in shell shape and septal morphology, as pointed out to us using actual specimens by Darragh (pers comm 2014). As far as the identifications of the *Aturoidea* and *Eutrephoceras* from Pebble Point go, however, we see no difference between the specimens identified as *Aturoidea brunnschweileri* as identified by Glenister *et al.* (1956) from Western Australia, and *A. distans* from Pebble Point and later specimens of *Eutrephoceras* described by McGowran (1959) The only distinction that can be noted comes from Glenister et al. (1956): "*Aturoidea distans* Teichert from southeastern Australia differs from the Western Australian
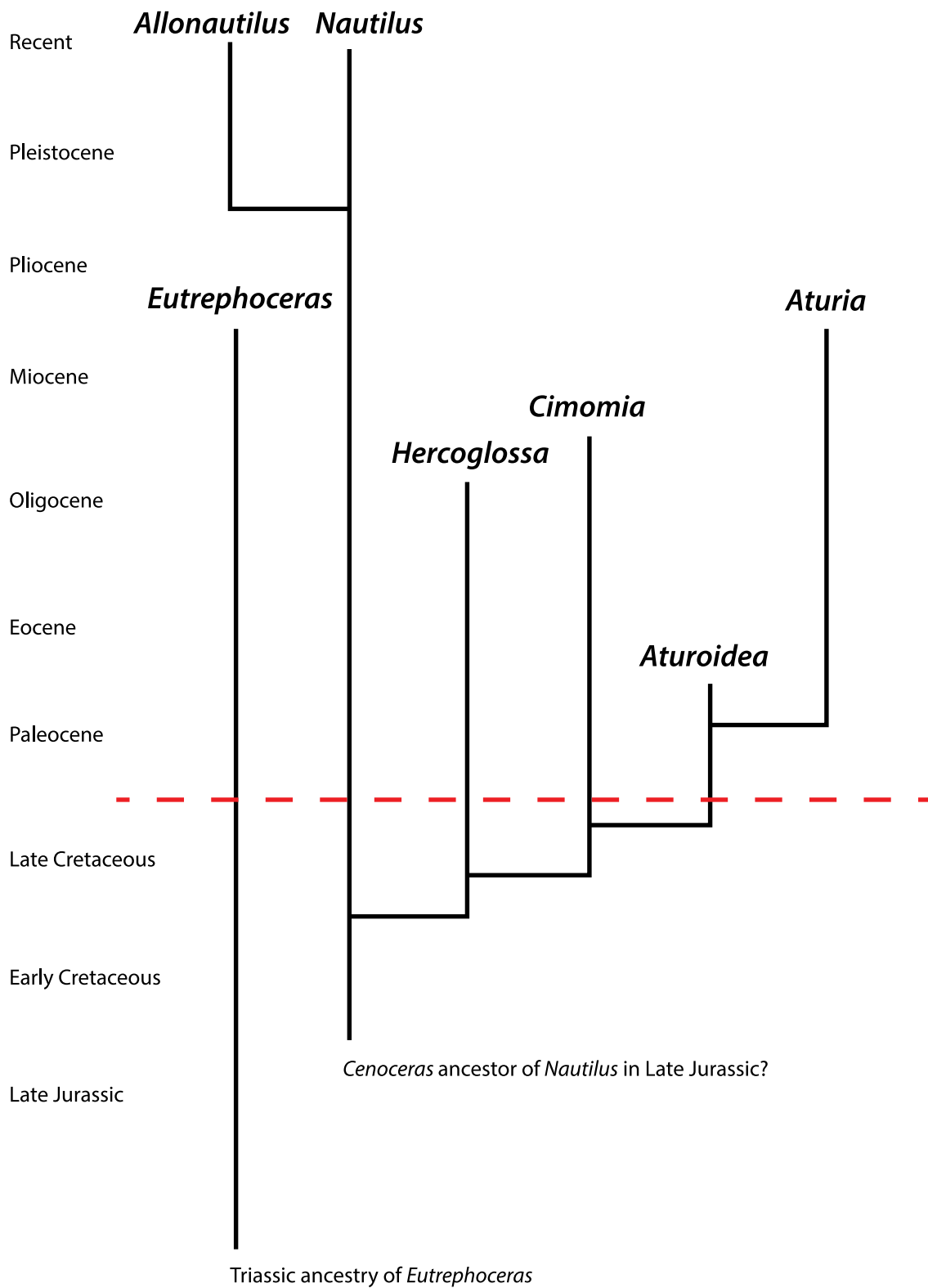
Figure 8. Hypothesized generic level phylogeny of a portion of post-Jurassic nautilids. *Eutrephoceras spp* predate *Nautilus* and were not involved in subsequent generic evolution. *Nautilus* appears in either the Late Jurassic or Early Cretaceous, based on unpublished observations of P. Ward in the British Museum, and gives rise to subsequent genera *Cimomia*, *Hercoglossa*, *Aturoidea*, *Aturia*, and *Deltoidonautilus*. *Nautilus* also gives rise to Allonautilus in either Pliocene or Pleistocene.

species in that the lateral lobes of its sutures are relatively long, narrow, and pointed." To use such differences to separate two animals of the same age from a contiguous southern ocean on the Australian continent seems surprising, but it certainly was the prevailing means of shelled cephalopod taxonomy throughout the 20th Century.

One of the most significant of the nautilids coming from Pebble Point was collected by Winston Ponder and Tom Darragh several decades ago. It was curated into the collections of the Australian Museum in Sydney but then located among the extant *Nautilus* shells, rather than the paleontological collection, even though it is around 60 million years in age and thus has been seemingly overlooked by those investigating fossil nautilids. It is a true *Nautilus*, and identical to *Nautilus praepompilius* Shimansky, conforming well to the revised description of that taxon by Saunders et al. (1981). It is also very similar to a specimen from the Eocene Hoko River Formation of Washington State by Squires (1988), who was the first North American investigator to break from the then long standing view of American paleontologists that *Nautilus* ss has no fossil record (as also followed by Teichert and Matsumoto, 1987). The specimen illustrated here is, as far as we can discern, the only known *Nautilus* of Paleocene age from anywhere in the world, although the Washington State specimen may in fact be close in age.

Paleotemperature results

Oxygen isotopes as a means of obtaining at least some information about the habitats of ancient chambered cephalopods has been in use for at least 40 years, with its basis coming from studies of *Nautilus* oxygen isotopes, dating back to Eichler and Ristedt (1966). The use of stable isotopes to better understand the life history of fossil cephalopods has become an aggressively researched topic over the last two decades, and for good reason. By sampling through ontogenetic stages, and then comparing obtained results to different taxa from contemporaneous beds, there are now wonderfully delineated studies showing difference in habitat depths in a variety of both ammonite and nautilid taxa both within (i.e., changes in paleotemperatures inferred to have been caused by changes in mean depth of shell formation) and between taxa (where different taxa from the same beds or time intervals are inferred to have formed shell at different mean depths).

As noted above, we sampled several milligrams of shell wall and septa for this study. Each are aggregate in that even using micro-samplers, it is impossible to get a single "day" sample, where the sampled shell material represents the material grown in a single day, and therefore gives some understanding of the mean temperature (and from that, the depth) that the specimen occupied. This problem is far more exacerbated in samples coming from a single septum. It is known that time of chamber formation increases through ontogeny. Whereas some workers proposed that a single *Nautilus* septum could be formed in two weeks (as summary of the many estimates found in Ward, 1987), it is now known that, in *Nautilus* at least, every septum takes far longer to produce. In fact the last several septa might each take six months to calcify, nacre layer by layer (Ward, 1987). Thus such single values are but aggregates of the mean temperature of shell formation for long periods. On the other hand, such information does give good (and the only) information about the temperatures at which the animals lived, and through this, some idea of depth.

While the well-known propensity of *Nautilus* shells to be transported to depositional sites different from their living sites has long and correctly demanded that extreme caution be exercised in any paleoecological studies of ancient chambered cephalopods, there is increasingly a sense that post-mortal drift in ammonites might not have been as universal in nautiluses, and new studies from deep water now show numerous cases of nautilus shells on the bottom in the habitats of the living. For the case here, however, it is apparent that the specimens studied are drift shells, for the following reasons.

First, the sedimentological context of the Pebble Point Formation strongly argues against it being a suitable habitat for living nautilids. Both the clast sizes as well as biological components in the strata are highly indicative of both autochthanous as well as allochthanous components. While it is assumed that many Cretaceous and perhaps early Paleogene nautilids were shallow water in habitat (Dzik & Gazdzicki, 2001), all were certainly living in environments preserved in normal marine strata. The marginal marine conditions assumed for the Pebble Point Formation argues for it being very shallow, perhaps marginal in the sense that it was behind barrier islands, in lagoons, or even estuaries. Modern *Nautilus* shells are found stranded in all such habitats, both inshore from their actual habitats as well as in shallow water deposits sometimes thousands of kilometers from where they lived.

Secondly, the presence of solitary corals living on the newly collected *Aturoidea distans* from Pebble Point (fig. 4) is strongly indicative that the specimen had drifted after death and then was eventually buried, but only after having been sitting on a shallow sea bottom long enough for corals to have grown on the specimen. No living *Nautilus* has ever been seen with such large epifauna (Ward, 1987); the weight alone of such epizoans would have compromised neutral buoyancy.

The stable isotope results from four nautilid taxa presented here (fossil *Aturoidea distans, Aturia cubaensis* and *Nautilus praepompilius), and* recent *Allonautilus scrobiculatus and Nautilus pompilius* from a specimen caught in the same trap as the *A. scrobiculatus* at Manus Island, Papua New Guinea) are shown in figure 2 and table S1. From these results it is clear that both extant nautilids grew the carbonate examined here at far lower temperatures than for both of the Pebble Point cephalopods, and somewhat lower than the Miocene *Aturia cubaensis* examined. Modern nautilids inhabit depths of 200 to 300 m in almost all cases, and the temperatures derived here match closely the known depths off Little Ndrova Island at such depths (see Ward, 1987 for comparison of depths and stable isotopes in extant *Nautilus*).

The much warmer temperatures from the fossil taxa examined here can be interpreted in several ways. For the two recent nautilids, temperature depth profiles indicated that both animals sampled lived in water temperatures consistently around 16–20ºC, which in 1984 corresponded to depths of around 200 to 300 m. There is no significant difference in their isotopes. Temperatures derived from fossils considered

autochthanous (such as the corals growing on Pebble Point examples) show quite different temperature levels. In this case the warmer temperatures strongly suggest a more shallow depth of carbonate formation.

While the isotopic values of the recent as compared to older, Pebble Point specimens can be compared, the quite different ice volume of the immediate post Cretaceous world requires an adjustment of approximately minus one per mil. Even accounting for the fact the Pebble Point site was deposited at much higher latitudes than its present position, and water temperatures would have been warmer than now, it is difficult to imagine that the 20–25°C temperatures recorded by the carbonate of Pebble Point taxa could have been formed in anything more than 100 m water depth, and perhaps far shallower. For instance, even though the modern day Philippine Islands has nearly 30°C water temperatures at the surface, at only 100 m those temperatures drop to near 12°C. The Pebble Point nautilids thus seemed to have lived in fairly shallow shelf, but surely more offshore than the shallow, probably wave affected, environments where the Pebble Point Formation was deposited. Whether those habitats were just offshore of the Pebble Point depositional center, or were farther away, cannot be determined.

Finally, we also used oxygen isotope measurements on a specimen of *Aturia cubaensis* from Muddy Creek, Victoria, (NMV P325999). This specimen, figured below, was encrusted with fossil oysters, which surely grew on the shell post death. Oxygen isotopic values for shell carbonate from this specimen averaged 15–18°C, whereas the oysters have values of 25°C. Like the specimen of *A. distans* with epifaunal corals, we interpret this specimen as having lived in colder water but post death floated into warmer, shallower water and was deposited on the bottom, where the oysters grew. They are found on only one side of the specimen, strengthening this interpretation.

Concluding Remarks

Pebble Point Formation deposits to date have received important paleontological attention, including the fundamental work of Darragh (1994, 1997) and Stilwell (2003a, b). They are the oldest known Cenozoic deposits confirmed as Paleocene in age in Australia (although Paleocene strata from Western Australia have been reported as well, as by Glenister et al., 1956) so are of great importance from evolutionary, biogeographic, and sedimentological perspectives. Because of the exquisite preservation of original, unaltered shell material in some specimens, this site can provide new information in regards to paleoecological conditions in the aftermath of the great, Cretaceous/Paleogene mass extinction and provide a link to the better studied Paleogene deposits of the Antarctic Peninsula. We hope that the difficulty of access and study of these beds, which to date have perhaps limited the amount of research conducted here, will be overcome to continue study at one of the most scenic as well as scientifically interesting of all Australian coastlines.

Any work on isotopes requires numerous specimens, and the Pebble Point beds can and will yield new specimens for study. Similarly, it is not only possible but easily accomplished to compare the Cretaceous to modern nautilid cephalopods

from Australia to better understand their evolution. For instance, there is an increase in complexity from *Nautilus praepompilius*, of some 60 million years ago, to *Nautilus* of today. Yet just as clearly the sutures of *Aturoidea* show homologous structures, while other shell characters clearly indicate that *Aturoidea* is a descendent of true *Nautilus,* arising in the late Cretaceous or Paleocene, but dying off far before *Nautilus*, which is still extant. The new model of *Nautilus* evolution is shown in figure 8. This is a hypothesis only. But it is novel, and is supported by both the homologies we observe (the progressive complication of the lateral lobes; the progressive dorsalward movement of the siphuncle; the progressive elaboration of the septal necks) as well as the times of first and last appearance.

Systematic Paleontology

The descriptions and diagnoses of *Eutrephoceras victorianum* and *Aturoidea distans* are well done and nothing here can add useful information. However we do believe that the specimen of *Nautilus praepompilius* should be so described.

ORDER NAUTILIDA

FAMILY NAUTILIDAE

GENUS *NAUTILUS* LAMARCK

Nautilus praepompilius Shimansky

1957. *Nautilus praepompilius.* Shimansky, p. 1

1981. *Nautilus praepompilius.* Saunders *et al*, p.609, figs. 1–4

Types. Holotype; Moscow Institute of Palaeontology (PIN) 1264/1. Syntype PIN 1264/0

Material. A single specimen, Australian Museum, C 143662.

Dimensions. See table 1.

Description. This specimen conforms well to the specimen figured by Saunders et al., 1981 in terms of suture and whorl dimensions. *Nautilus praepompilius* is slightly less inflated than *Nautilus pompilius* and *N. macromphalus*, and its suture shows slightly less complexity as a consequence.

Acknowledgements

References

Baker, G. 1943. Features of a Victorian limestone coastline. Journal of Geology, 51, 359–386.

Bonacum, J., Landman, N. H., Mapes, R. H., White, M. M., White, A. J., & Irlam, J. 2010. Evolutionary radiation of present-day *Nautilus* and *Allonautilus*. American Malacological Bulletin, 29, 77-93.

Birch, W. 2003. Geology of Victoria. Geological Society of Australia. Series: Special Publication, Geological Society of Australia, 23.

Darragh, T. A. 1994. Paleocene bivalves from the Pebble Point Formation, Victoria, Australia. Proceedings of the Royal Society of Victoria, 106, 71–103.

Darragh, T. A. 1997. Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Palaeocene Pebble Point Formation, Victoria, Australia. Proceedings of the Royal Society of Victoria, 109, 57–108.

Dzik, J. 1984. Phylogeny of the Nautiloidea. Acta paleont. Polonica, 45, 1-219.

Dzik, J. & Gazdzicki, A. 2001. The Eocene expansion of nautilids to high latitudes. Paleogeography, Paleoclimatology, Paleoecology, 172, 297-312.

Eichler, R., & Ristedt, H. 1966. Isotopic evidence on the early life history of *Nautilus pompilius* (Linné). Science, 153, 734-736.

Glenister, B. F., Miller, A. K., & Furnish, W. M., 1956, Upper Cretaceous and Early Tertiary nautiloids from Western Australia: Journal of Paleontology, 30, 492-503.

Kenley, P. R. 1954. The occurrence of Cretaceous sediments in southwestern Victoria. Proceedings of the Royal Society of Victoria, 66, 1–16.

Kummel, B. 1956. Post-Triassic nautiloid genera. Bulletin of the Museum of Comparative Zoology, 114, 324-493.

Landman, N., Jagt, J., Jagt Yazykova, E., Machalski, M. & Yacobucci, M. 2014. Ammonite extinction and nautiloid survival at the end Cretaceous. Geology, 42, 707-710.

Ludbrook, N. H. 1971a. Large gastropods of the families Diastomatidae and Cerithiidae (Mollusca: Gastropoda) in southern Australia. Transactions of the Royal Society of South Australia, 95, 29–42.

Ludbrook, N. H. 1971b. Stratigraphy and correlation of marine sediments in the western part of the Gambier Embayment. In Wopfner H. & Douglas, J. G. eds. The Otway Basin of Southeastern Australia, pp. 47–66. Special Bulletin, Geological Surveys of South Australia and Victoria.

Mcgowran, B. 1959. Tertiary nautiloids (Eutrephoceras and Cimomia) from South Australia. Journal of Paleontology, 33, 435-448.

Mcgowran, B. 1965. Two Palaeocene foraminiferal faunas from the Wangerrip Group, Pebble Point coastal section, western Victoria. Proceedings of the Royal Society of Victoria, 79, 9–74.

Mcgowran, B. 1970. Late Paleocene in the Otway Basin; biostratigraphy and age of key microfaunas. Transactions of the Royal Society of South Australia, 94, 1–14.

Mcgowran, B., LINDSAY, J. M. & HARRIS, W. K. 1971. Attempted reconciliation of Tertiary biostratigraphic systems. In Wopfner H. & Douglas J. G. eds. The Otway Basin of Southeastern Australia, 273–281. Special Bulletin, Geological Surveys of South Australia and Victoria.

Miller, A. K. 1947. Tertiary nautiloids of the Americas. Geological Society of America Memoir, 223, 1-234.

Saunders, W. B. 1981. The species of *Nautilus* and their distribution. The Veliger 24, 8-17.

Saunders, W. B. 1987. The species of *Nautilus*. 35-52. In Saunders, W. B. & Landman, N. H. (eds.), *Nautilus* the Biology and Paleobiology of a Living Fossil. Plenum Press, New York and London.

Saunders, W., SHIMANSKY, V., & AMITROV, O. 1996. Clarification of *Nautilus praepompilius* from the Upper Eocene of Kazakistan. Journal of Paleontology, 70, 609- 611.

Shackleton, N. J. & Kennett, J. P. 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP Sites 277, 279, and 281. Initial reports of the deep sea drilling project, 29, 743-755.

Shimansky, V. N. 1957. Noviy predstaveli otryada Nautilida v SSSr. (New members of the order Nautilida in the USSR). Paleontologie Institut Materialy Osnovam Paleontologie, 1, 35-41.

Stilwell, J. D. 2003a. Macropaleontology of the *Trochocyathu*s – *Trematrochus* band (Paleocene Eocene Boundary) Dilwyn Formation, Otway Basin, Victoria. Alcheringa, 27, 245- 275.

Stilwell, J. D. 2003b. Patterns of biodiversity and faunal rebound following the K–T boundary extinction event in Austral Palaeocene molluscan faunas. Palaeogeography, Palaeoclimatology, Palaeoecology, 195, 319-356.

Squires, R. 1988. Cephalopods from the late Eocene Hoko River Formation, northwestern Washington. Journal of Paleontology, 62, 551-562.

Teichert, C. 1943. Eocene nautiloids from Victoria: Proceedings of the Royal Society Victoria, new series, 55, 257-264.

Teichert, C. & Matsumoto, T. 1987. The ancestry of the genus *Nautilus*. In Saunders, W. B. & N. H. Landman (eds.), *Nautilus* the Biology and Paleobiology of a Living Fossil, pp. 25-32. Plenum Press, New York and London.

Tintant H., & Kabamba, M. 1985. The role of the environment in the Nautilacea. In Bayer, U. and A. Seilacher, eds. Sedimentary and evolutionary cycles. Springer Verlag, 58-65.

Vandepas, L., Dooley, F., Barord G.j., Swalla, B. &Ward, P. 2014. The phylogeography of *Nautilus pompilius:* new Pacific sampling suggests Philippine Islands origin. *Molecular Phylogenetics and Evolution* (In-Review).

Ward, P. D. 1987. Natural History of *Nautilus*. Allen and Unwin, London, pp. 267.

Ward, P. & Saunders, W. 1997. A new genus of living nautiloid cephalopod and its bearing on phylogenetic hypotheses of the Nautilida. Journal of Paleontology, 71. 1054-1064.

Wray, C. G., Landman, N. H., Saunders, W. B., & Bonacum, J. 1995. Genetic divergence and geographic diversification in Nautilus. Paleobiology, 220-228.

Zakharov, Y. D., Baraboshkin, E. Y., Weissert, H., Micailova, I. A., Smyshlyaeva, O. P., & Safronov, P. P. 2013. Late Barremian–early Aptian climate of the northern middle latitudes: Stable isotope evidence from bivalve and cephalopod molluscs of the Russian Platform. Cretaceous Research, 44, 183-201.

Table S1. Stable isotope values obtained from nautilid shells.

Sample name / septum number	$\delta^{16}O$	$\delta^{13}C$
Allonautilus scrobiculatus (Papua New Guinea)		
1		
2		
3		
4	-0.03	
5	-0.01	
6		
7	0.05	
8		
9	1.25	
10	1.21	
11		
12	1.66	
13		
14	1.61	
15		
16	1.23	
17		
18	1.53	
19		
20	1.28	
21		
22	1.5	
23		
24	1.46	
25		
26		
27		
28	1.38	
29		
30	1.27	
31	0.58	
32	1.01	
33	0.87	
Nautilus pompilius (Papua New Guinea)		
1		
2		
3		
4		
5		
6	-1.03	
7	0.85	
8		
9		
10		
11	1.06	

Sample name / septum number	$\delta^{16}O$	$\delta^{13}C$
12	1.75	
13	1.09	
14	0.97	
15	1.4	
16	1.6	
17	1.38	
18	1.18	
19	1.08	
20	1.18	
21	1.27	
22		
23	1.14	
24	0.99	
25	0.79	
26	0.68	
27	0.89	
28	0.88	
29	1.15	
30	0.56	
31	0.9	
32	0.56	
33	0.88	
Aturia cubaensis NMV P 325999 Muddy Creek		
PW76	0.51	-0.49
PW77	-0.05	2.58
PW82	0.5	0.42
PW83	0.95	
Aturiacxlam	-0.05	-3.75
auriawall	1.09	2.01
clamonAt	-0.7	1.77
Aturia H=22	1.24	
Aturia H=25	1.26	
Aturia H=28		1.06
Paleocene *Aturoidea distans* NMV P326476 Pebble Point		
	1.23	2.19
	1.19	-0.8
	1.22	0.94
	0.77	0.26
	1.06	1.48
Paleocene *Nautilus praepompilius* AM C143662 Pebble Point		
	0.23	
	0.19	
	0.22	
	-0.78	
	0.06	