GETTING HOOKED: THE ROLE OF A U-SHAPED BODY CHAMBER IN THE SHELL OF ADULT HETEROMORPH AMMONITES

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ABSTRACT

Cretaceous heteromorph ammonites of the suborder Ancyloceratina had a striking ontogenetic change in their shell shape. Juveniles had virtually all possible types of coiling of their shells, ranging from regular planispiral and orthoconic to torticonic, hamitoconic and gyroconic. The adults uncoiled the last whorl of their shell forming a U-shaped recurved body chamber with the aperture facing upward. Examination of ribbing pattern and its resolution in various parts of the living chamber in 11 species revealed that the ribs were less developed and had some traces of wear on the inner surface of the hooked chamber, being well developed both on the lateral and outer lower parts. This could indicate that the adult animals were semi-loosely hooked (*Ancyloceras*, *Macroscaphites*) or permanently clipped (*Scaphites*, *Hoploscaphites*) onto either horizontal or upwardly angled stipes of non-calcified algal macrophytes or branched animals. Comparison of the adult mode of life with those of modern cephalopods suggested that ammonites of the suborder Ancyloceratina had developed a stationary brooding phase that could have several ecological advantages over free-swimming monomorph ammonites.

INTRODUCTION

Heteromorph ammonites represent a polyphyletic group of ectocochliate cephalopods in which the external shell differs from the 'regular' planispiral shell of monomorph ammonites. These ammonites are known from the late Triassic and the middle Jurassic, but were most abundant in the Cretaceous (Wiedmann, 1969). Among them, ammonites of the suborder Ancyloceratinae were widely distributed in Cretaceous seas with two peaks in abundance during the Early Cretaceous (Valangian-Aptian; Ancyloceratidae, Ptychoceratidae, Heteroceratidae) and Late Cretaceous (Albian-Maastrichtian; Turrilitidae, Scaphitidae, Baculitidae) (Kennedy & Cobban, 1976; Page, 1996; Cecca, 1998). A majority of ammonites belonging to this suborder are characterized by a striking change in their shell shape (and corresponding mode of life) between juvenile and adult (mature) ontogenetic phases (Davies *et al.*, 1996; Tsujita & Westermann, 1998). Juveniles (and possibly immature adults) had a variety of coiling types of their shells, including regular planispiral (*Scaphites*, *Macroscaphites*), torticonic (*Nostoceras*), hamitoconic (*Polyptychoceras*) and gyroconic (*Ancyloceras*) (Klinger, 1980). The extreme rarity of remnants of the soft body in ammonites has given rise to a variety of hypotheses regarding their possible lifestyles in the juvenile stage, from planktonic and semi-planktonic (Ward, 1979; Westermann, 1996) to nekto-benthic and benthic (Vašiček & Wiedmann, 1994), depending on the shape of their shell.

However, at maturity all these animals suddenly changed the coiling pattern of their shell to form the characteristic recurved body chamber, resembling a U-shaped hook with the shell aperture facing upwards (Ward, 1979; Klinger, 1980; Westermann, 1996). The shaft of the hook (i.e. vertical part of the body chamber between the phragmocone and last whorl) was either quite short as in *Scaphites* or long as in the majority of Ancyloceratina (Westermann, 1996; Monks, 2000; Landman *et al.*, 2010a). The formation of the final U-shaped body chamber provides an evolutionary example of the so-called 'terminal-countdown' (T-C) strategy that combines determinate growth with the development of novel form (Seilacher & Gunji, 1993). It has been shown that this type of T-C heteromorphy appeared independently in at least in five non T-C lineages of ammonites during the Cretaceous, suggesting its adaptive nature (Kaplan, 2002). What could be the peculiarities in the adult mode of life that triggered such a radical shift in the growth pattern of the ammonoid shell?

It has generally been accepted that the adults of Ancyloceratina were mainly planktonic (Donovan, 1964; Ward, 1979; Westermann, 1996), with a U-shaped adult living chamber reflecting an adaptation to a pelagic life with limited motility (Batt, 1989). It was suggested that uncoiling of the adult chamber would enhance stability in positioning of the animal in the water column by creating some distance between the phragmocone (acting as a float) and ammonite body in the living chamber (acting as a weight) (Klinger, 1980). Improved hydrostatic stability of the U-shaped Ancyloceratina when compared with that of planispiral ammonites would, however, severely impede their mobility due to the upward position of the shell aperture (Ward, 1979; Klinger, 1980). Possibly, movements of

these heteromorphs were restricted to vertical migrations (Westermann, 1996). To decrease the vulnerability to predation in the water column, some Ancyloceratina were assumed to be associated with algal mats on the bottom (Vašiček & Wiedmann, 1994). A similar association has been suggested between Jurassic spiroceratids and floating algal mats (Dietl, 1978; Westermann, 1996). Alternative hypotheses also exist about the buoyancy of heteromorph ammonites, suggesting that they were benthic animals (Ebel, 1992, 1999).

There is plethora of views on feeding mechanisms in adult Ancyloceratina. The upward position of the shell aperture would obstruct contact with the substrate, preventing bottom feeding. Cecca (1997) hypothesized that the ancyloconic shell was developed both in Protancyloceratinae (early Tithonian radiation) and Crioceratinae (Late Valanginian–Hauterivian radiation) as a response to the appearance of new food resources such as pelagic Foraminifera and Nannoconida. The adult Ancyloceratina were assumed to make extensive foraging vertical migrations from the relatively safe near-bottom habitat to epipelagic waters in the same way as many modern cephalopods (Nesis, 1985). They might capture plankton using long and slender tentacles (Cecca, 1997) or cirri on their umbrella as depicted by Westermann (1996). Nesis (1986) put forward the hypothesis that adult ammonites with an ancyloconic shell built mucous nets and consumed the mucous with captured plankton in analogy with modern gastropods of the family Vermetidae (Barash & Zenziper, 1985; Kappner, Al-Moghrabi & Richter, 2000). Kakabadzé & Sharikadzé (1993) proposed that adult animals with an ancyloconic shell could change their position from vertical to sub-horizontal by regulating the amount of liquid in the phragmocone and thus pick up their prey from the bottom. Monks & Young (1998) suggested that the ammonite body was smaller than the living chamber and so, by changing the body position inside the living chamber, the animals could tilt their U-shaped shell and hunt on the bottom.

The aim of the present study is to examine some morphological features of the adult shell in heteromorph ammonites of the suborder Ancyloceratina in order to reveal possible selective forces that led to development of the uncoiled and recurved U-shaped adult body chambers. Comparative analysis of reproductive strategies in modern cephalopods, together with analysis of possible shelf habitats in the Cretaceous, suggest a new hypothesis for the role of the 'hooked' adult shell.

MATERIAL AND METHODS

Heteromorph ammonites deposited in the collection of the Department of Earth Sciences of the Natural History Museum, London, were used for the present study. Specimens of the following ammonites were examined: *Proustraliceras gigas* (6 specimens), *Macroscaphites yvani* (3 specimens), *Acrioceras tabarelli* (2 specimens), *Heteroceras emerici* (3 specimens), *Ancyloceras matheronianus* (3 specimens), *Audouliceras audouli* (1 specimen), *Scaphites aequalis* (11 specimens), *Hamites (Ptychoceras) chaixianus* (2 specimens) and *Nostoceras (Bostrychoceras) sanctaeluciae* (1 specimen) (identifications follow collection labels). Two specimens of *Audouliceras renauxianum* from Ulianovsk, Russia and *Pseudocrioceras* sp. from Dagestan, Russia from the private collection of Aleksandr Mironenko (Moscow, Russia) were also examined. Additionally, high resolution photographs of heteromorph ammonite shells were examined from several descriptive papers and reviews: American Scaphitidae (Landman *et al.*, 2010a); *Nipponites* spp. (Ward & Westermann, 1977; Okamoto, 1988), *Diplomoceras* spp. (Olivero & Zinsmeister, 1989), *Didymoceras* sp. and *Pravitoceras* sp. (Misaki *et al.*, 2014), *Ainoceras* spp. (Misaki & Ohara, 2011); *Lithancylus* sp. (Mikhailova & Baraboshkin, 2001); and *Heteroceras* spp. (Delanoy, 1997).

The sculpture patterns and rib development were examined on the internal, lateral and outer parts of the phragmocone and living chamber in specimens that were sufficiently well preserved to evaluate the development and possible wear of the ribs. Three degrees of rib development were distinguished. Well developed ribs were similar to those on the external parts of the shell; slightly flattened ribs had smoothed ridges in comparison to those on the external parts, but the rib pattern was clearly visible; and in flattened ribs the ridges were hardly visible. Particular attention was paid to the rib resolution on the internal and external parts of the U-shaped hooked part of the living chamber. The variability of the foramen shape (the hole formed by the uncoiled living chamber and phragmocone in scaphitids, Landman *et al.*, 2010a) or inner part of the recurved living chamber (in other ancyloceratins, especially in *Heteroceras* spp.; Delanoy, 1997) in individuals belonging to the same species were also studied by producing photos and/or superimposing images. The main axis of the foramen or hook relative to the transverse plane of the shell was determined by examination of the left and right sides of the living chamber and recording their relative height (Fig. 1A, B). The shell surface was examined to record locations of scars and traces of possible epizoan fauna.

RESULTS

The rib resolution was different in various parts of the living chamber in almost all ammonites studied. In *Proustraliceras gigas*, ribs showed some flattening, suggesting wear, on the inner surface of the hooked chamber, whereas ribs were well resolved both on the lateral and outer lower parts of the chamber (Fig. 2). In *Macroscaphites yvani*, ribs were well resolved on the inner surface of the vertical shaft, but as in *P. gigas* they were almost untraceable on the inner surface of the hook (Fig. 3C, D). Similar patterns of rib resolution on the inner surface of the vertical shaft and hook were also observed in *Audouliceras audouli* (Fig. 3A, B) and *Ancyloceras matheronianus* (Fig. 4). Despite the same inner diameter of the shell, the ribs were better resolved in the inner part of the phragmocone than in the U-shaped living chamber in *Audouliceras renauxianum* (Fig. 5). In *Scaphites aequalis*, the ribbing was well developed on the adoral part of the phragmocone (upper part of the foramen), but almost indiscernible in the adapical hooked part of the living chamber (i.e. lower part of the foramen). The inner surface of the living chamber of *Hamites chaixianus* had almost indiscernible ribbing, whereas lateral and outer walls of the whorls had well resolved ribs.

Scaphitid ammonites had a wide variability both in size and shape of the foramen enclosed by the U-shaped hook, indicating that the coiling pattern during formation of the hooked living chamber was not as regular as that of the juvenile shell. The size of the foramen of the hooked living chamber varied from a small horizontal slit to a vertical oval (Fig. 1C). The hook curvature also differed, ranging from tight curvature with the shell aperture facing the phragmocone to a more open hook with the aperture facing outwards. In *Heteroceras* spp., the shell shape in adult animals showed strong individual variation both in relative size of the vertical shaft and adapical hooked part, especially in the adoral perimeter of the living chamber (Fig. 6).

The direction of the main axis of the foramen in most scaphites is not perpendicular to the transverse plane of the shell, with which it forms an acute angle of about 80–85°. In this case, the upper part of either the left or right lateral side of the hook is noticeably higher than the opposite side (Fig. 1B). In a well preserved specimen of *P. gigas*, one side of the hooked chamber was higher than another (Fig. 2B). In *Acrioceras tabarelli*, the foramen of the hook was also asymmetrical on either side of the shell. Moreover, in this particular specimen (BMNH 46972) transverse planes running through the juvenile shell and adult hooked living
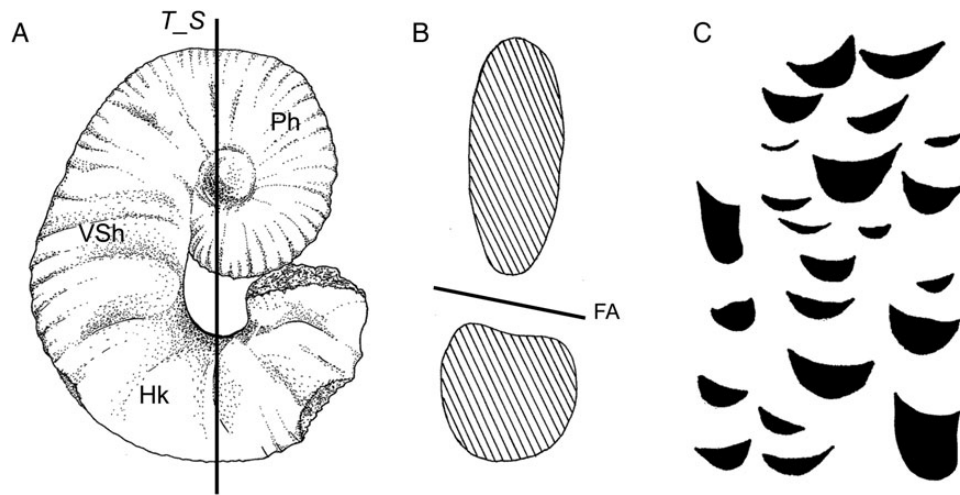
Figure 1. *Scaphites* spp. **A.** General view of the adult shell with phragmocone (Ph), vertical shaft (VSh) and hook (Hk) of the living chamber. **B.** Transverse section through the shell (T_S in **A**), showing angled axis of the foramen of the living chamber (FA). **C.** Variability in shape and size of the foramen enclosed between the phragmocone and the U-shaped living chamber; scaled to same shell size as in **A**.
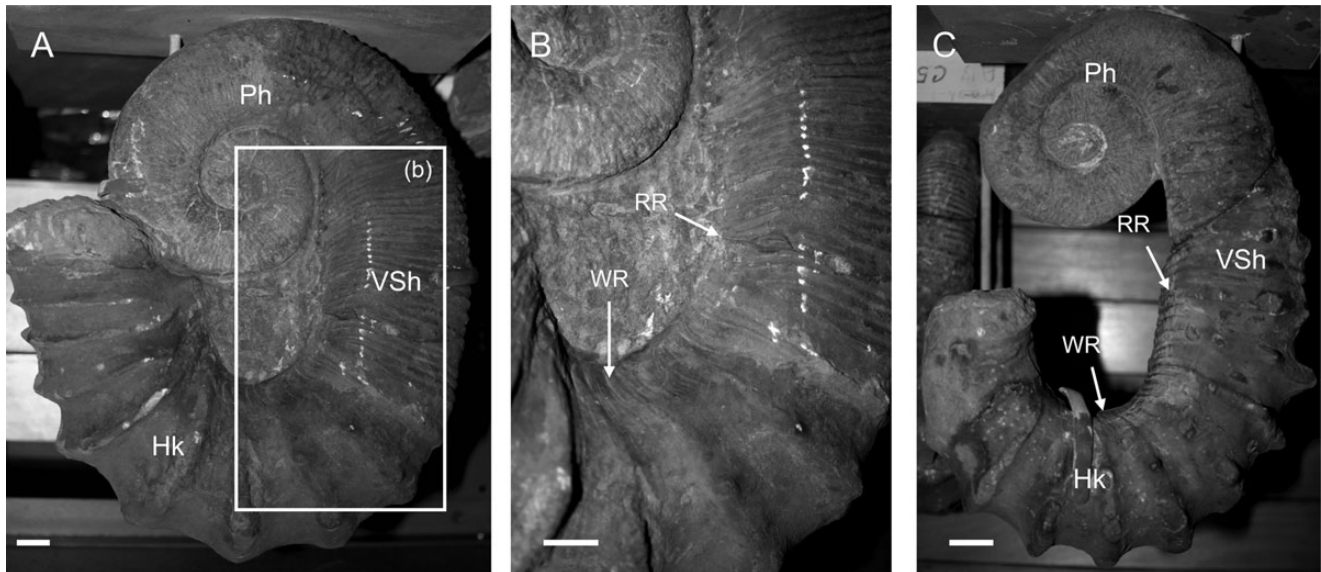

Figure 2. *Proustraliceras gigas*. **A**, **C**. General view. **B**. Inner part of the adult living chamber. Abbreviations: Ph, phragmocone; VSh, vertical shaft; Hk, hooked part of adult living chamber; WR, partially worn ribs in inner part of U-shaped living chamber; RR, resolved ribs on inner part of vertical shaft. Note different shape of foramen enclosed by U-shaped living chamber in the two adult specimens **A** and **C**. Scale bar = 2 cm.

chamber were not parallel. No epizoan traces were observed on any of the ammonites studied.

DISCUSSION

Ornament resolution on the adult shell

Specific patterns of rib formation and possible wear of the shell ribs were revealed in the adult forms of Ancyloceratina ammonites. In specimens examined in the present study as well as observed in the photos taken from literature sources, the internal part of the U-shaped living chamber had ribs that were noticeably less resolved compared with the inner part of the vertical shaft and other parts of the shell. This phenomenon might be explained by peculiarities in shell morphogenesis, when the ornament on the inner surface of the whorl is usually weaker than that of the lateral and outer surfaces. However, the ribs were more resolved on the inner surface of the uncoiled phragmocone in some ammonites (e.g. *Audouliceras renauxianum* and *Acrioceras tabarelli*) than on the inner surface of their U-shaped adult living chamber despite quite similar inner diameters of both parts of the shell, suggesting that the phenomenon is not a simple consequence of constriction by tight coiling. A similar trend in the ornament resolution was also observed on the inner surfaces of the living chamber in *Nipponites* spp. when compared with that of the phragmocone whorls (Ward & Westermann, 1977; Okamoto, 1988). Some other species like *Proustraliceras gigas* had traces of sculptural wear on the internal part of their U-shaped living chamber. If the adult Ancyloceratina were planktonic, living in an unobstructed water column (reviews by Monks, 2000; Landman *et al.*, 2010a), there should be no signs of wear on any part of the shell. The presence of well-resolved
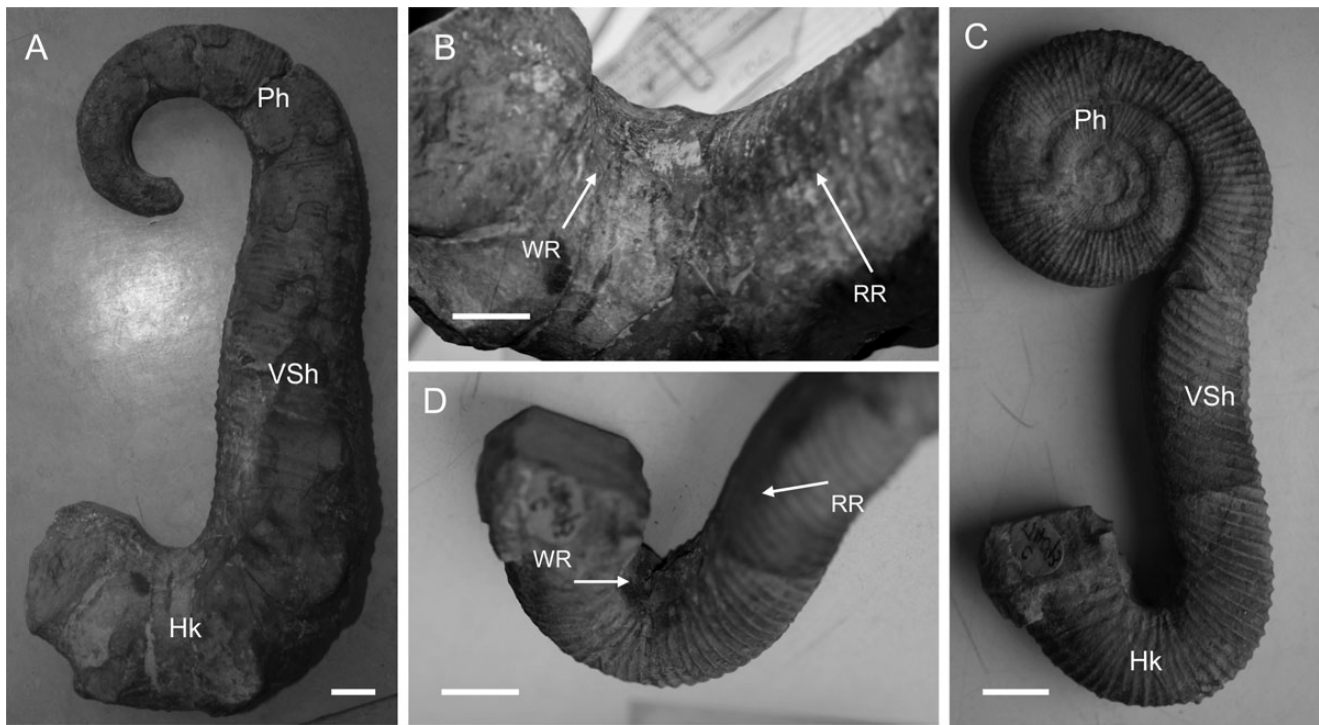
Figure 3. A, B. *Audouliceras audouli*. **C, D.** *Macroscaphites yvani*. General view (**A, C**) and inner part of the adult living chamber (**B, D**). Abbreviations as in Figure 2. Scale bar = 1 cm.

ribbing and tubercular ornament on the outer surfaces of Ancyloceratina shells with some species even possessing large spines covering external parts of their shells (e.g. *Anisoceras raynaudi*, Klinger, 1980) has been used as one of the main arguments for their planktonic lifestyle (Westermann, 1996; Kaplan, 2002).

Weaker, and in some cases apparently worn, ornament could be a result of existence of some physical obstacle that impacted the development of the ribbing pattern on the inner part of the U-shaped living chamber. It is generally accepted that the life position of the Ancyloceratina was vertical, with the phragmocone uppermost and the living chamber below containing the body (Klinger, 1980; Westermann, 1996). If the animal built its last living chamber around some object (like a branch), negotiating it from underneath, the lifting force of the buoyant phragmocone applied to the place of contact between the shell and branch could impede formation of the ribbing pattern on the inner side of the recurved shell. Furthermore, if the ammonites were semi-loosely hooked (as could have been the case of animals with a widely open hook as in *Ancyloceras* or *Macroscaphites*) or clipped (as in the closed hook of *Scaphites*) on either horizontal or upwardly angled branch-like structures, the inner surface of their living chamber would display some natural wear as a result of friction during movement of the shell along and around the branch.

Variability in adult shell shape

Pelagic animals show relatively narrow intraspecific variability of their body parts. For example, holopelagic heteropod molluscs (e.g. *Atlanta* spp.) are distinguished by morphological and morphometric features of their shell, which show relatively slight variation within each species (Richter & Seapy, 1999). Holopelagic pteropod molluscs (e.g. *Clio pyramidata*) can exhibit spatial shell variation from broadly lanceolate in tropical waters to narrowly pyramidal in polar regions, but within a given area the shell shape is relatively constant (van der Spoel & Dadon,

1999). Little variation is observed in the shape of juvenile shells in Ancyloceratina, unlike that in adult animals (Delanoy, 1997; Landman *et al.*, 2010a). Wide variability in size and inner shape of the U-shaped living chamber in species with a closed or almost closed foramen (e.g. *Scaphites*, Fig. 1C) or with a wide gap between the phragmocone and shell aperture (e.g. *Heteroceras*, Fig. 6) could indicate that these ammonites were clipping or hooking themselves to branches of various thicknesses during formation of the last living chamber.

Symmetry of the adult shell

Shells of juvenile scaphitid ammonites are planispiral and have bilateral symmetry, similar to some other Ancyloceratina ammonites (e.g. *P. gigas*, *Macroscaphites yvani*). The appearance of noticeable asymmetry of the inner part of the living chamber of adult ammonites is difficult to explain by their supposed planktonic lifestyle. However, if the shell was attached to a branch-like structure that was angled upwards, formation of the inner part of the living chamber would follow the obtuse angle of the branch, affecting the symmetry of the inner part of the hooked living chamber.

Location of epizoans on the shell

The surface of cephalopod shells usually becomes encrusted by epizoans during their life, postmortem drift and final rest on the bottom until buried by sediments (Maeda & Seilacher, 1996). In Recent *Nautilus* spp., various epizoans settle on different parts of the shell, most commonly the umbilical area and both flanks of the shell away from the shell and black area (Landman *et al.*, 2010b). Epizoans do not settle on the areas of possible contact with the bottom and other physical obstacles. For example, positioning of oysters on the ventral part of the shell in *Buchiceras* indicate that this ammonite with a pseudoceratitic suture line was not benthic, but probably floated over the bottom (Seilacher,
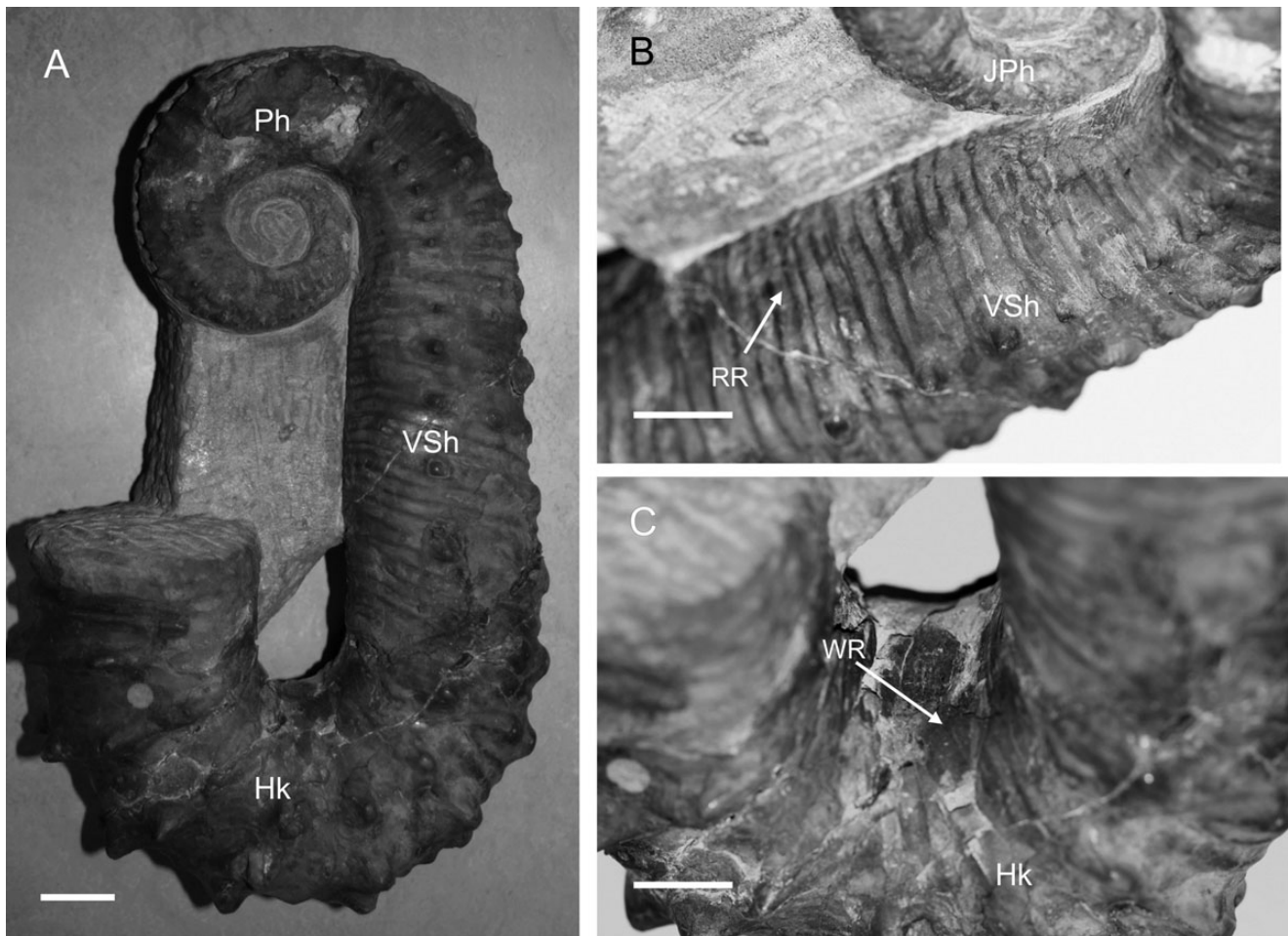
Figure 4. *Ancyloceras matheronianus*. **A.** General view. **B.** Inner part of vertical shaft with resolved ribs (RR). **C.** Inner part of U-shaped adult living chamber with less resolved ribs (WR). Abbreviations as in Figure 2. Scale bar = 1 cm.

1960). Epizoans are rare on heteromorph ammonites (Landman *et al.*, 2010a). However, the shells of *Pravitoceras* sp. and *Didymoceras* sp. were encrusted by sessile commensal anomiid bivalves almost everywhere except the inner part of the hook (Misaki *et al.*, 2014: fig. 8), suggesting that some mechanical obstacle (like a branch going through the hook) prevented epizoan settlement.

A new hypothesis: stationary hooked adult

The patterns in the ornament on different parts of the shell, noticeable asymmetry of the inner part of the living chamber, wide individual variability in shell shape in adults versus juveniles, and distribution of epizoans on the shell surface all combine to question the supposed planktonic lifestyle of adult Ancyloceratina ammonites. It was also unclear why ammonites belonging to several different groups of Ancyloceratina would first develop such an oddly shaped living chamber and then attempt to tilt it in order to expand its hunting range to include bottom-dwelling animals (Kakabadzé & Sharikadzé, 1993; Monks & Young, 1998). In some cases, especially in ammonites with a short recurved living chamber (e.g. *Hoploscaphites brevis*), the shell aperture was reduced in size by constriction and a varix and was also partially obstructed by the phragmocone situated dorsally to it, which would have made it difficult to withdraw the head into the shell (Landman *et al.*, 2010a). With little support for a benthic lifestyle (Ebel, 1992), an alternative hypothesis finds

support in the above features: the shell became uncoiled to develop the final terminal countdown (T-C) stationary stage that was hooked or clipped to a branch-like structure. Effectively, this was the final adult and probably mature phase of their ontogenesis.

What could be the nature of branches to which the ammonites were attached? The pattern and degree of the rib resolution and possible wear would suggest that the shells were hooked onto a hard branch, although probably not a calcified structure that would be expected to cause much stronger wear. Good candidates that possess such branches are brown macroalgae of the order Laminariales, with robust stipes. Some of these algae (e.g. *Macrocystis* sp., *Lessonia* spp.) form modern shallow-water kelp forests with hard, dichotomously branching stipes (especially in *Lessonia*; Cho *et al.*, 2006). Thick stipes and fronds of such macroalgae could provide enough support even for the largest adult heteromorph ammonites such as *Moutoniceras* spp. and *Emericeras* spp., which were nevertheless neutrally or slightly positively buoyant. Their overall shell size could attain 1 m, but the internal diameter of the hooked living chamber was about 5–10 cm (Delanoy *et al.*, 1991), equal to the thickness of modern *Lessonia* stipes.

Unfortunately, the fossil record of the brown algae is poor, as they are not calcified and therefore do not fossilize. However, analysis of the associated herbivorous fauna has suggested that kelp-like brown macroalgae originated in the Cretaceous
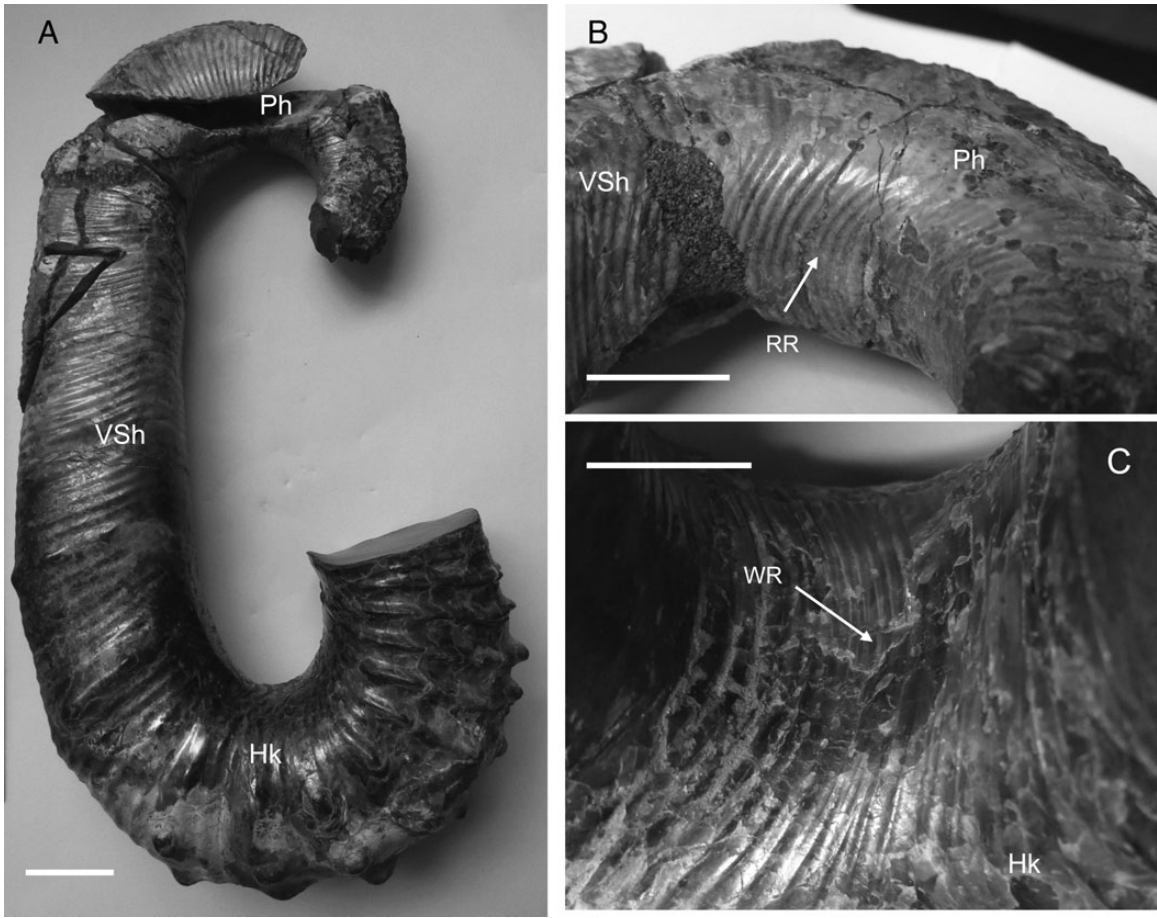
Figure 5. *Audouliceras renauxianum*. **A.** General view. **B.** Inner parts of vertical shaft with resolved ribs (RR). **C.** Inner part of U-shaped adult living chamber with less resolved ribs (WR). Abbreviations as in Figure 2. Scale bar = 1 cm.

Figure 6. Variability in shell shape of adult T-C forms of *Heteroceras* spp. compiled from Delanoy (1997).

(Domning, 1989). Biological, palaeo-oceanographic and geological evidence also suggest that the origin and radiation of kelp belonging to the families Lessoniaceae and Laminariaceae of the order Laminariales happened at least in the Late Cretaceous (Chin, Brown & Heads, 1991). Recent genetic data have pointed to a radiation of brown macroalgae during the Early Cretaceous, with most brown algal orders diversifying in the Late Cretaceous and Paleogene (Silberfeld *et al.*, 2010). Interestingly, these two events of the proposed diversification of brown algae coincide with two peaks in diversity of ancyloceratin ammonites that occurred in the Early and Late Cretaceous (Westermann, 1996). Modern representatives of Laminariales inhabit temperate and cold seas (Raven *et al.*, 2002; Cho *et al.*, 2006). However, it has been argued that macroalgae with fleshy fronds were abundant in Mesozoic warm seas with their abundance subsequently being strongly impacted by the origin and radiation of herbivorous grazing teleost fishes in the late Cretaceous and early Cenozoic (Steneck, 1983). Alternative hypotheses also exist about the possible origin and radiation of kelp in cold seas much later, during the Miocene, based on the occurrence of kelp-associated limpets and herbivorous mammals (Estes & Steinberg, 1988; Vermeij, 2012).

Apart from brown algae, there were other branch-bearing plants (sea grass; Vermeij, 1977) and animals such as hydroid corals, crinoids and erect cylindrical colonies of cheilostome bryozoans (Jablonski, Lidgard & Taylor, 1997) that were abundant in the Late Cretaceous and to which ammonites could potentially have been attached. However, all these branched animals had calcified skeletons that would likely have caused more wear to the moving shell than could be envisaged on a noncalcified macroalgal stipe. Branched corals tend to overgrow the animals attached to their branches, but no traces of such overgrowth are present on the surface of ammonite shells.

Occurrence in thanatocoenoses

The association of adult Ancyloceratina with macroalgae might also explain their specific distribution in ammonite thanatocoenoses. Heteromorph ammonites, especially scaphitids, do exhibit strong facies associations, appearing only in offshore shaley and limy deposits rich in benthic and nektonic faunas (Batt, 1989; Kaplan, 2002; Landman, Cobban & Larson, 2012). They are mainly absent from euxinic bottom sediments where only normally coiled forms and *Baculites* spp. occurred in the upper oxygenated part of the water column (Casey, 1961; Landman *et al.*, 2012). Scaphitids have also been found in beds together with bivalves and some other shallow-water molluscs and remains of drifted plants and amber fragments (Tanabe, 1979), but in general the postmortem transport of adult heteromorphs is curiously restricted compared with that of regular planispiral ammonites. Flotation experiments with recent *Nautilus* shells revealed that small shells became waterlogged faster and drifted much shorter distances than large shells (>20 cm) (Wani *et al.*, 2005). However, juvenile shells of scaphitid ammonites had a wider distribution and occurred en masse in concretions in shallow water (but below the shoreline), with few adult (mainly microconch) shells that often had broken living chambers and no jaws preserved inside the shell (Landman & Waage, 1993). In contrast, adult scaphitids were found in deeper-water concretions located outside shallow-water basins and did not show evidence of any distant postmortem drift (Landman & Waage, 1993, Yahada & Wani, 2013). Moreover, shells of adult scaphitids are usually in a good state of preservation with an intact aperture, often with aptychi inside the living chamber (Tanabe, 1979). This means that they were buried quickly after death without prolonged postmortem drift (Wani, 2007). This fact led to the conclusion (Tanabe, 1979; Yahada & Wani, 2013) that adult scaphitids were not planktonic, contrary to other views summarized by Landman *et al*. (2012).

However, if scaphitid adults were stationary, attached to algal stipes, they should also remain there after death until the time when algal fronds became detached by surge currents and waves during storms. Despite their size, macroalgae are quite vulnerable to breakage. Young plants (to 1 year old) have quite weak attachment to the substrate, while older plants (3–5 years old) can become detached due to deterioration of the holdfast because of sedimentation and grazing, as well as the higher biomass of the plant (Seymour *et al.*, 1989). Stipes might be also be detached from the main stem by the activity of grazing limpets (Santelices *et al.*, 1980). Detached pieces of plants are either transported to areas of accumulation of algal and other organic debris on the bottom (usually at depths of 40–100 m) or become stranded on beaches. Burial in soft algal deposits would keep the quite fragile shells of scaphitids intact, whereas if washed up on the shore any shells attached to the algal stipes would quickly be destroyed. The attachment of adult scaphitid shells to algal stipes obviously would restrict their range of postmortem transport by currents. Relatively quick burial in silt with algal debris on the inner shelf would also prevent postmortem epibiosis, which is indeed extremely rare in heteromorph ammonites (Kaplan, 2002; Landman *et al.*, 2012).

Adult U-shaped phase: a brooding animal?

The small size of ammonitellas (a few millimeters, Landman & Waage, 1993) indicates that heteromorph ammonites had reproductive strategies similar to modern small-egged squid and incirrate octopods that have short, terminal spawning rather than like large-egged nautilus and cirrate octopods that have a prolonged mature phase with continuous laying of large eggs (Nesis, 1985). Some deep-water squid (Onychoteuthidae, Gonatidae) and the majority of small-egged octopods are characterized by brooding of eggs by females. During brooding, the female does not eat, utilizing her body's existing resources to support metabolism. Degeneration of the body muscles during brooding makes the
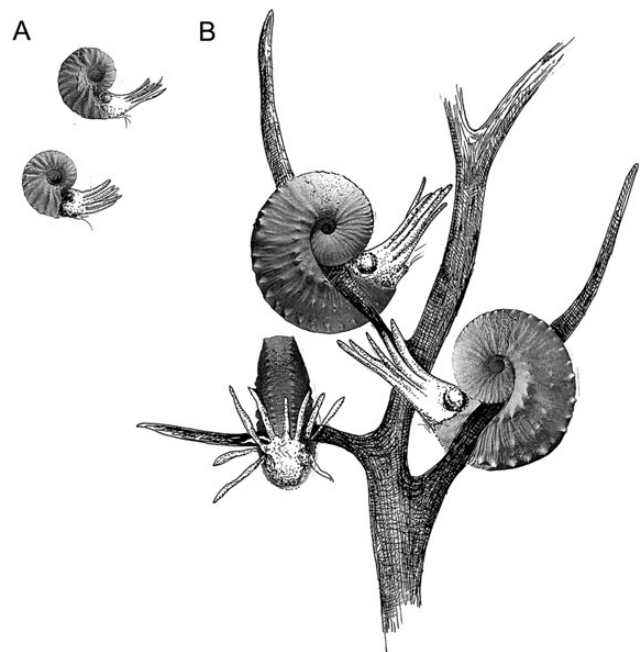

Figure 7. Schematic drawing of possible life cycle in scaphitid ammonites, with planktonic juveniles (**A**) and stationary adults attached to algal stipes (**B**).
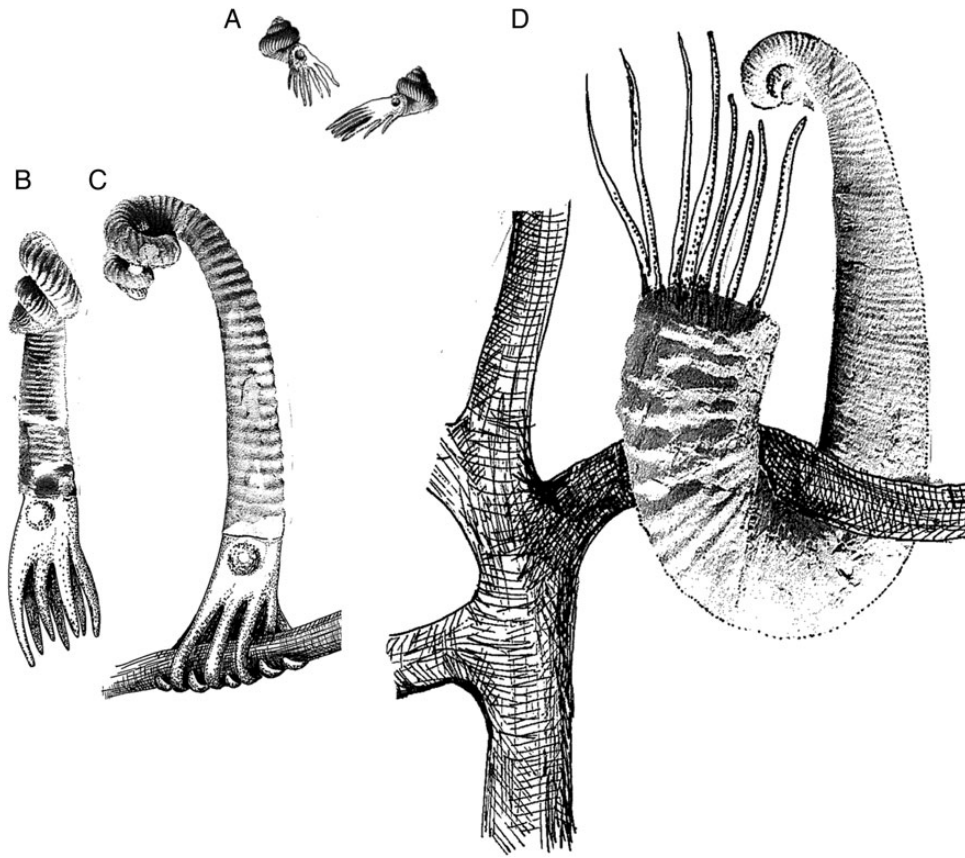
Figure 8. Schematic drawing of possible life cycle in *Heteroceras* spp., with planktonic juveniles (**A**), planktonic or near-bottom subadults (**B**), subadult attached to algal stipe about to start making the final living chamber (**C**) and brooding hooked adult (**D**).

females more vulnerable to predation and therefore they either migrate to ecological refuges (shallow or deep water) or hide in shelters (like octopods). The upward shell aperture of adult heteromorph ammonites could also indicate that the animals did not eat, being attached to an algal stipe when brooding.

Not all pelagic cephalopods that brood their eggs have terminal spawning and degeneration of muscle tissue during brooding. Some holopelagic octopods belonging to the superfamily Argonautoidea have batch spawning and enormous fecundities (up to 1 million eggs) in order to survive in pelagic waters subject to extensive predation at all trophic levels (Laptikhovsky & Salman, 2003). Most probably, this type of reproductive strategy was also characteristic of pelagic, non-T-C, planispiral ammonites that likely produced small eggs in large numbers (Laptikhovsky *et al.*, 2013).

It seems less likely that the shell in T-C heteromorph ammonite adults acted as a brooding chamber similar to that of the modern pelagic *Argonauta* spp. as Lewy (2002) suggested. More probably, these animals simply kept their fertilized eggs in the oviducts inside their body until hatching (ovoviviparity), as in the recent pelagic octopod *Ocythoe tuberculata* (Laptikhovsky & Salman, 2003; Salman & Akalin, 2012).

Proposed life cycle of T-C heteromorph ammonites

Assuming the final 'stationary' phase of ontogenesis as outlined above, it is possible to speculate on the life cycle of the T-C Ancyloceratina heteromorphs (Figs 7, 8). Judging from the shape of the shell, the juveniles of Ancyloceratina had a wide variety of lifestyles from nektic planispiral *Macroscaphites* and *Pravitoceras*, to active planktonic planispiral *Scaphites*, nekto-benthic torticonic

Nostoceras, gyroconic *Ancyloceras* and *Audouliceras*, benthic hamitoconic *Polyptychoceras* and vermiconic *Nipponites* (Klinger, 1980; Westermann, 1996). Upon maturation, adult ammonites perhaps migrated nearshore and then started to live among macroalgae. As in some modern loliginids (Rasero & Portela, 1998), the start of maturation and the inshore spawning migration might have been triggered by preliminary mating, which could also have triggered the start of uncoiling of the shell in females.

Males would probably not have had a stationary phase as they did not participate in brooding, and therefore could retain the type of their subadult shell until the end of their life, at least in some species. The indirect evidence for this is the presence of both uncoiled and coiled adult stages in *Macroscaphites yvani*. In this species, the uncoiled adults were first suggested to be microconchs (i.e. males, to which the name *M. yvani* was applied) and coiled adults to be macroconchs (i.e. females, named *M. recticostatus = Costidiscus recticostatus*) (Delanoy & Poupon, 1992). According to the new hypothesis presented here, the larger planispiral 'macroconch' *M. recticostatus* should be the male, as in many other teuthid and octopod species where male is the larger sex (Nesis, 1985), and the uncoiled 'microconch' should be the shell of the brooding female.

In other heteromorph ammonites such as scaphites, two dimorphic forms have been observed in the final uncoiled phase, albeit with significant overlap (30%) in sizes and some morphological features. These have also been interpreted as sexual dimorphs, with macroconchs being females and microconchs being males, but no evidence of sex assignation has been presented (Landman *et al*; 2010a; Landman *et al.*, 2012). If microconchs and macroconchs were indeed different sexes, both males and females might have attached themselves in close proximity in the

spawning grounds. Males could have transferred their sexual products to females via either floating spermatophores (as in modern sedentary vermetid gastropods; Scheuwimmer, 1979) or detached hectocotyli as in Argonautoidea (Nesis, 1986). It is quite unlikely that the uncoiled male and female shells became hooked to each other during mating as the foramen of the shell is usually too small or of the wrong shape to accommodate the living chamber of another individual passing through it. More research is needed to confirm that the dimorphism seen in some heteromorph ammonites is indeed of a sexual nature.

During the transitional stage of forming the shaft and hook of the living chamber, the female could still have retained the same mode of life as the juvenile/subadult, or perhaps crawled among the algae to be able to feed (Fig. 8). In either case, the awkward shape of the shell would have impeded the movement of the animal, making it more vulnerable to predation. Probably, this is why these transitional shells are rarely found and almost always have traces of lethal damage near the shell aperture (Landman *et al.*, 2012). Transitional stages in other heteromorphs (such as *Heteroceras* spp.) lived longer and are found more frequently (Delanoy, 1997), most likely having a similar lifestyle to *Baculites* spp. (Jacobs, 1990) (Fig. 8). As soon as the final shape of the shell had been formed and the shell was attached to a stipe, the female had no need to withdraw her head and tentacles within the shell to avoid predation.

CONCLUSION

The new 'sedentary adult' hypothesis suggests that the appearance of the T-C shell morphology in several independent lines of heteromorph ammonites was a possible adaptive response to radiations of algal macrophytes that formed shallow-water kelp forests in the Early and Late Cretaceous. It is likely that the T-C Ancyloceratina ammonites radiated following the adoption of a new reproductive strategy characterized by a sedentary adult female phase in which eggs were brooded while the shell was attached to algal stipes.

Location of the adult brooding ammonite among kelp fronds could have given several ecological advantages to T-C heteromorphs in comparison with planispiral ammonites. First, hiding the shells of adult ammonites among the macroalgal stipes would have concealed them from pelagic predators and also made them less accessible to benthic predators such as crabs. A similar reproductive strategy is utilized by spawning females in some loliginid squid (e.g. *Doryteuthis gahi*) that attach their egg masses to kelp fronds well above the bottom (Arkhipkin, Laptikhovsky & Middleton, 2000). Second, stationary brooding females would have expended less energy for active metabolism than free-floating ones and therefore channelled more resources into reproduction. This is especially important in cases of ovoviviparity when animals spend their internal resources on larval development. Third, as macroalgae are located in warmer and more productive shallow waters nearshore (down to 25–30 m; Raven *et al.*, 2002), the temperature-dependent egg development would have been faster and food resources more abundant for hatchlings and juveniles than in offshore habitats. As they grew, juveniles could have been dispersed further offshore by tidal currents to exploit the resources of the shelf. A similar scheme of inshore-offshore ontogenetic migration is observed in the majority of Recent loliginids (Nesis, 1985). And, fourth, inshore stationary brooding would have kept the adults away from offshore anoxic zones. This also might explain the fact that adult heteromorphs were found away from these anoxic zones (Tsujita & Westermann, 1998; Landman *et al.*, 2012). Owing to the complete extinction of all ammonites at the end of Cretaceous, they did not encounter the later radiation of brown algal kelps that occurred during climate cooling in the Miocene (Estes & Steinberg, 1988).

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