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Recognising variability in the shells of argonauts (Cephalopoda: Argonautidae): the key to resolving the taxonomy of the family

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Abstract

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Argonauts (Cephalopoda: Argonautidae) are a family of pelagic octopuses that are most commonly recognised by the beautiful white shells of females (known as paper nautilus), prized by beachcombers the world over. Taxonomic delineation of the group has historically relied exclusively on features of the shells of females and has resulted in more than 50 species names being coined worldwide. This approach has created considerable confusion in the taxonomy of the family because argonaut shells are not true molluscan shells and display considerable variation in form. This study closely examined a large number of argonaut shells from museum collections throughout the world. Two types of shell formation that had been previously attributed to separate argonaut species were recognised within individual shells. It is proposed here that the different shell forms reflect the effects of ecological or biological factors or events, often manifesting as dramatic changes in shell growth and shape within the development of an individual shell. The resulting combinations of shell formation types clearly explain both the extreme variation observed across large numbers of argonaut shells and the high number of nominal species names coined in the past. Researchers coining new fossil argonaut species based solely on shell characters are advised to proceed with caution. This study supports parallel morphological and molecular research recognising the existence of only four extant argonaut species worldwide: *Argonauta argo*, *A. hians*, *A. nodosus* and *A. nouryi*.

Keywords

paper nautilus, *Argonauta argo*, *Argonauta hians*, *Argonauta nodosus*, *Argonauta nouryi*, Coleoidea, Octopoda, shell morphometrics

Introduction

Argonauts (Cephalopoda: Argonautidae) are a family of pelagic octopuses that inhabit tropical and temperate oceans of the world (fig. 1). Derived from benthic octopus ancestors, argonauts have departed the sea floor to carry out their entire life cycle in the open ocean (Young et al., 1998). Argonauts are most widely recognised by the beautiful white shells of females that are commonly known as paper nautilus and are prized by beachcombers the world over. These shells function as both brood chambers for the females' eggs (Naef, 1923) and hydrostatic structures by which female argonauts are able to attain neutral buoyancy (Finn and Norman, 2010).

Images of argonaut shells have a long history, adorning artefacts dating back to Minoan civilisations (3000–1050 BC; Walters, 1897; Mackeprang, 1938; Hughes-Brock, 1999) and featuring in the earliest conchological works (e.g. Rumphius, 1705; Argenville, 1742; Gualtieri, 1742; Seba, 1758; Martini, 1769). By contrast, the identity of the occupant of the shell (i.e. the argonaut) has remained largely unknown or misinterpreted. For example, in the early 1800s it was widely believed that the octopus commonly found in the argonaut shell was not the rightful owner, but was a parasite having

devoured the original occupant (Sowerby and Sowerby, 1820–1825; Broderip, 1828).

In the absence of knowledge about the animals that created the shells, a taxonomic system that relied completely on shell features arose for the family. Variations in shell shape and appearance formed the basis of new species descriptions, giving rise to 53 species names and 11 subspecies names worldwide (Sweeney and Young, 2004).

At the core of this taxonomic system is the issue that argonaut shells display a considerable degree of variability. This variability has been observed across shells produced by individuals of the same species (Voss and Williamson, 1971) and even between opposing faces of the same shell (Cotton and Godfrey, 1940; Trego, 1992). This variability is likely to be exacerbated by the female argonaut's ability to repair (Power, 1856; Hoyle, 1886; Boletzky, 1983; Trego, 1993) and completely rebuild the shell (Holder, 1909a, 1909b; Alliston, 1983).

Argonaut shells are not true molluscan shells. Unlike the shells of other molluscs (e.g. gastropods), argonaut shells are not produced by the derivatives of the shell field (the mantle epithelium responsible for shell secretion in other molluscs; see Kniprath, 1981). In argonauts, the shell field disappears during embryonic development (Kniprath, 1981). The argonaut



Figure 1. Live female argonaut (*Argonauta argo*) observed swimming close to the ocean surface and holding her white paper nautilus shell that functions as a brood chamber for the female's eggs and as a hydrostatic structure for maintaining neutral buoyancy.

shell is a secondary calcium carbonate structure secreted from webs on the distal ends of the female argonaut's first (dorsal) arm pair.

Female argonauts commence forming shells approximately 12 days after hatching (*A. argo*: Power in Roberts, 1851; Power in Catlow, 1854) at a size of approximately 5–7 mm mantle length (*A. argo*: Jatta, 1896; Naef, 1923; *A. hians*: Nesis, 1977; *A. nouryi*: Finn, 2009). The initial shell is formed without sculpturing (Jatta, 1896). By the time the female argonaut reaches 10 mm mantle length, the shell (which is now 14 mm in length) is fully formed (*A. hians*: Nesis, 1977). The webs on the female's dorsal arms overlap the edge of the shell and add to it as the female grows. Irregularities in the lay of the web along the shell edge is presumed to cause the undulations in the surface of the shell, visible as radiating ridges (or ribs) in fully formed shells (Mitchell et al., 1994).

Once the female argonaut reaches maturity, she lays long strands of eggs that are attached to the internal central axis of the shell. Female argonauts are continuous spawners (Boletzky, 1998; Rocha et al., 2001; Laptikhovsky and Salman, 2003) with asynchronous ovulation and monocyclic spawning (i.e. egg-laying occurring over an extended and continuous spawning period in relation to the animal's life; Rocha et al., 2001). Spawning is thought to extend over several months (Boletzky,

1998) and based on published counts, proposed spawning frequencies and proposed spawning durations, it has been surmised that the potential fecundity of a female *A. argo* could exceed one million eggs (Laptikhovsky and Salman, 2003).

To stabilise argonaut taxonomy, the aim of this study was to examine the inter- and intra-specific variation in argonaut shell shape. Four key species (identified from morphological studies; see Finn, 2013, 2016) and shells at the centre of taxonomic confusion for these species were targeted. These target groups were the *Argonauta nouryi/cornutus* complex, the *A. hians/boettgeri* complex, the *A. nodosus/tuberculatus* complex and *A. argo*. This study supports parallel morphological and molecular research recognising the existence of only four argonaut species worldwide: *A. argo* Linnaeus, 1758; *A. hians* [Lightfoot], 1786; *A. nodosus* [Lightfoot], 1786; and *A. nouryi* Lorois, 1852.

Materials and methods

More than 1500 argonaut shells were examined over the course of this project. Most of the shells examined reside in museum collections within Australia, South Africa, Europe and the United States. Institutions visited include: Australian Museum, Sydney, Australia (AMS); Academy of Natural

Sciences, Philadelphia, USA (ANSP); The Natural History Museum, London, UK (BMNH); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museums Victoria, Melbourne, Australia (NMV); Queensland Museum, Brisbane, Australia (QMB); South African Museum, Cape Town, South Africa (SAM); South Australian Museum, Adelaide, Australia (SAMA); Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH); Tasmanian Museum and Art Gallery, Hobart, Australia (TMAG); National Museum of Natural History, Smithsonian Institution, Washington, USA (USNM); Western Australian Museum, Perth, Australia (WAM). Material loaned from the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM) was examined at NMV.

While all shells examined ultimately helped in the formation of ideas and an understanding of shell shape variation, two large collections were pivotal in enabling argonaut shell variability to be interpreted.

The first lot, is a large collection of beach-cast argonaut shells collected by Andrés Gonzalez-Peralta (*Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, MEXICO*) on the beach at El Mogote, La Paz, Baja California Sur, Mexico, North America, 24° 10' 00" N, 110° 24' 00" W, during the winters of 2000 and 2005. These shells are lodged in the collection of SBMNH with the following registration numbers: 172 *Argonauta* shells collected on 15 January 2000 – SBMNH 345766 (93 shells), SBMNH 345767 (15 shells) and SBMNH 345768 (64 shells); 92 *Argonauta* shells collected on 31 January 2005 – SBMNH 357476 (77 shells) and SBMNH 357475 (15 shells).

The second lot was obtained by chance when researchers on a research expedition off Rowley Shoals, Western Australia left a pelagic trawl net in the water while steaming between two stations: north-east of Mermaid Reef (Stn. 10, 17° 23' S, 118° 52' E) and south-west of Imperieuse Reef (Stn. 11, 16° 53' S, 119° 53' E). This occurred on board the FV *Courageous* on 18–19 August 1983. On recovering the net, researchers P. Berry and N. Sinclair were surprised to find 73 female argonauts with intact shells. Two specimens were lodged in NMV while the remainder were retained by WAM. The collection records of these lots are as follows: 71 female argonauts – WAM S31520; 2 female argonauts – NMV F87104.

Shell terminology and measurements follow Finn (2013). The opening of the shell is termed the *aperture* while the left and right sides of the shell are termed *lateral faces*. An extension of the axial thickening beyond the surface of the lateral face of the shell is termed an *ear*. The lateral faces are adorned with *ribs* radiating from the central axis of the shell towards the *keel*. Ribs may be *smooth* (i.e. continuous) or *tuberculated* (i.e. consisting of raised separate tubercles). The keel is bordered by two opposing rows of *keel tubercles*. The keel surface may be *concave*, *straight* or *convex*. The presence of tubercles on the keel surface is known as *inter-keel tuberculation*. To allow quantitative comparison of a large number of shells, a set of standard measurements was taken. These measurements included: shell length (ShL), maximum length of shell (note that P indicates that the ShL measurement was taken from a scaled digital photograph of the shell, not

directly from the shell); shell weight (ShW), weight (grams) of dry shell; shell breadth (ShB), maximum breadth of the shell; rib count (RC), number of ribs adorning a single lateral face, counted around the keel and aperture edge; ear width (EW), external measurement between lateral tips of opposing ears; aperture length (ApL), internal distance from the axial thickening to the ventral keel surface; aperture width (ApW), internal measurement between two opposing lateral walls at widest point; keel width (KW), external measurement of keel at ventral most position; keel tubercle count (KTC), number of keel tubercles counted around a single face (see fig. 2).

Scatter plots of measurements against ShL were used to assess differences across large numbers of shells. Regression lines were plotted using Microsoft Excel for Mac 2011. Analysis of covariance (ANCOVA) was performed using Systat 13.2 to assess the significance of the difference between the slopes of the regression lines.

Scanning electron microscopy was used to examine shell microstructure and allow accurate measurement of shell thickness. Shell sections were placed in a sonicator bath for short periods (5–10 seconds) to dislodge any debris, allowed to air-dry, then placed onto double-sided carbon tabs (Ted Pella, Redding) and sputter coated with gold. Scanning electron micrographs were taken using a Zeiss EVO 40 XVP (Zeiss, Cambridge) housed at SBMNH.

Where female argonauts could be definitively linked with shells, a set of soft body measurements was taken following Finn (2013). These measurements included: dorsal mantle length (DML), length from posterior tip of mantle to furrow between mantle edge and base of first arms; mantle width (MW), lateral width of mantle at widest point; head width (HW), lateral width of head measured between the opposing eye surfaces; arm length (AL), length of arm from the edge of the mouth to arm tip, measured along the face of the arm using a piece of string (for arms 2–4); funnel length (FL), distance from the anterior tip of the funnel to the posterior medial margin. The relationship between features of female argonauts and their shells were examined using scatter plots and linear regression.

Results

Argonauta nouryi Lorois, 1852; the *A. nouryi/cornutus* complex

In spring each year, small argonauts wash up in large numbers on beaches in the southern Gulf of California (Gonzales-Peralta in Saul and Stadum 2005). These small argonauts are regularly attributed to two species: *A. nouryi* Lorois, 1852 and *A. cornutus* Conrad, 1854¹ (García-Domínguez and Castro-Aguirre 1991; Gonzales-Peralta 2006).

A. nouryi was described by Lorois in 1852. The identification of this species resides solely in features of the shell, which is described as elliptical with numerous fine lateral ribs and weak keel tubercles. Fig. 3 incorporates a

1 A third large form also washes up on southern Gulf of California beaches in spring and is regularly attributed to the species *A. pacificus*, a synonym of *A. argo*; see Finn (2013) for details.

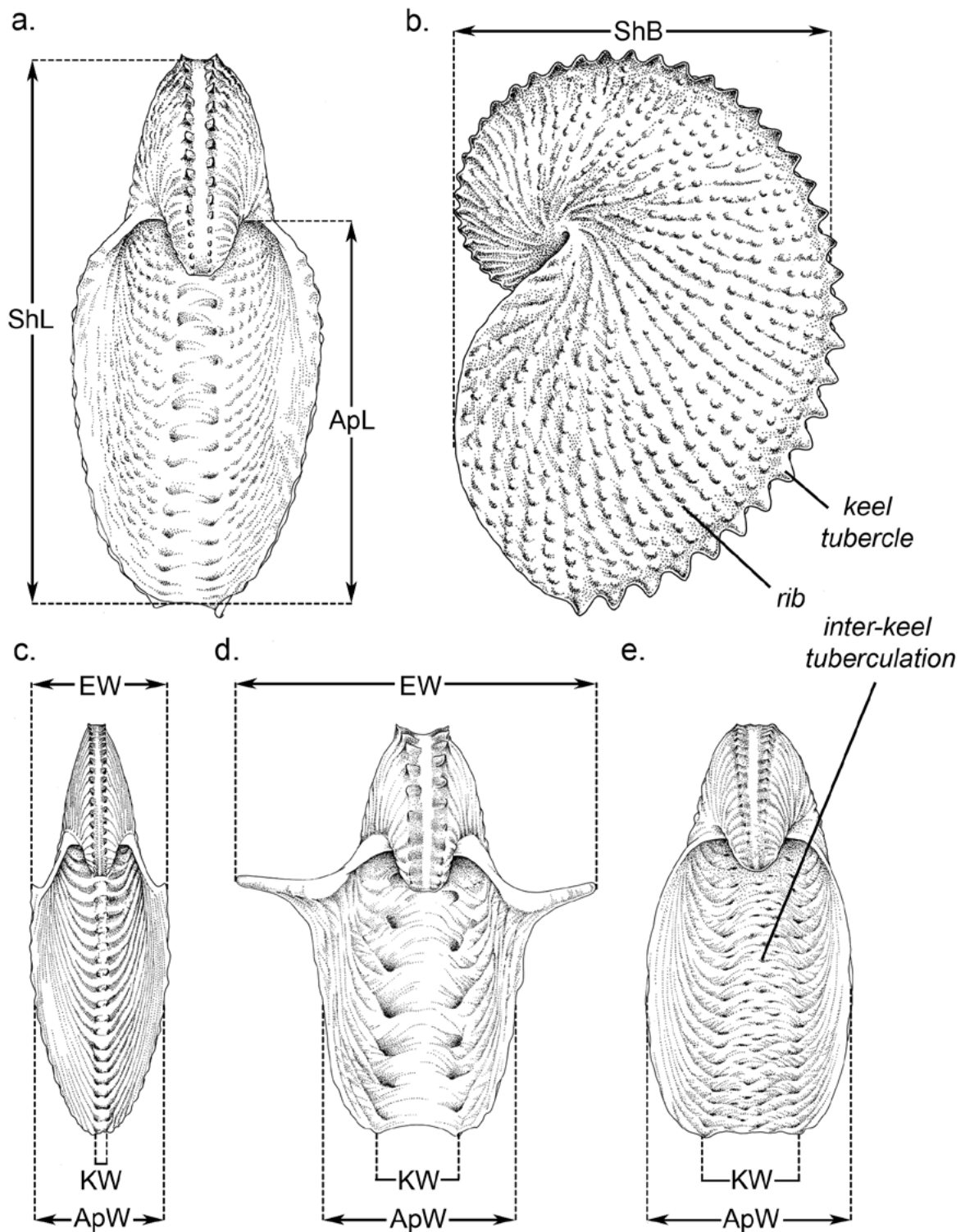


Figure 2. Argonaut shell measurements and terminology, following Finn (2013): a, *Argonauta nodosus* aperture view (NMV F164695); b, *A. nodosus* lateral view (NMV F164695); c, *A. argo* aperture view (WAM S31503); d, *A. nouryi* aperture view (SBMNH 345766, specimen #074); e, *A. nouryi* aperture view (SBMNH 345768, specimen #109). Abbreviations: ApL = aperture length; ApW = aperture width; EW = ear width; KW = keel width; ShB = shell breadth; ShL = shell length. Illustrations: R. Plant.

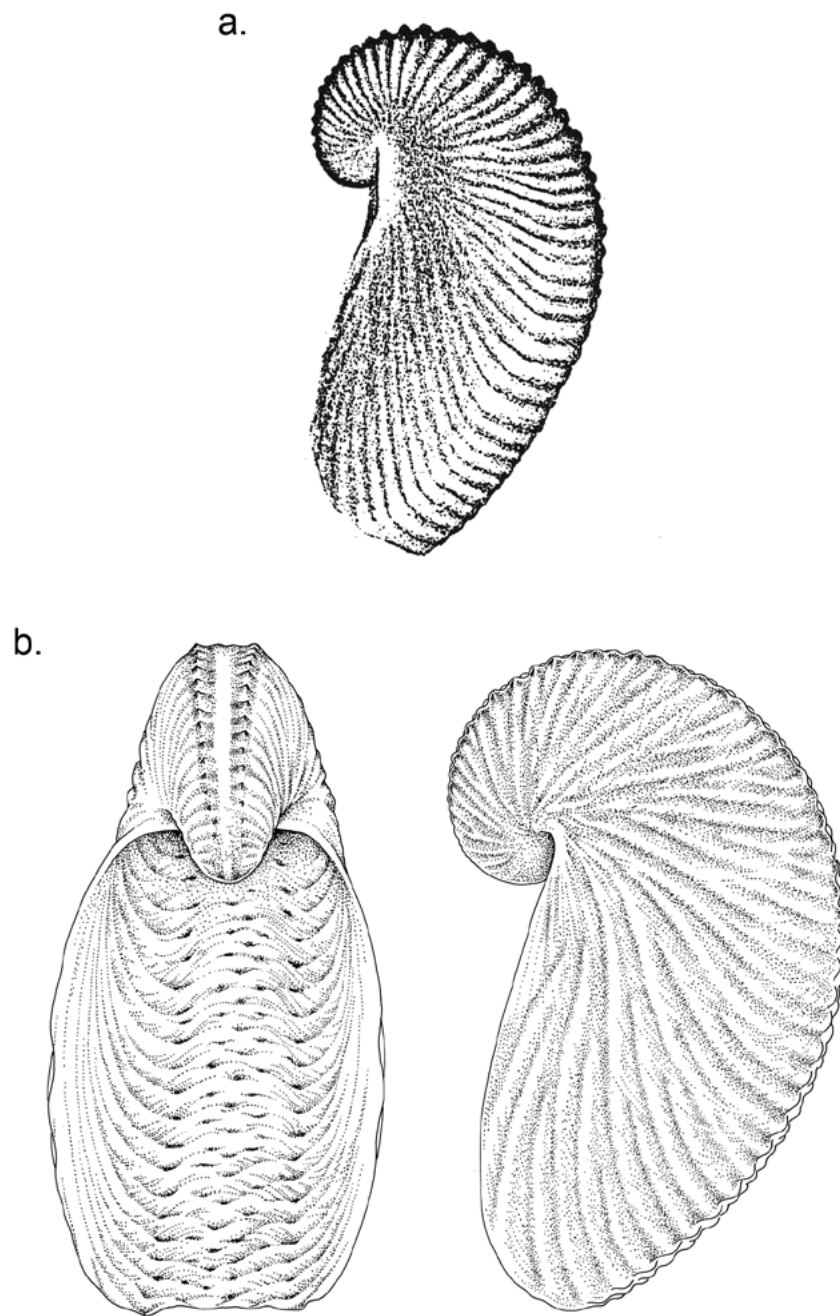


Figure 3. Comparison of a shell from the examined SBMNH lot with an illustration taken from the original description of *Argonauta nouryi* Lorois, 1852: a, reproduction of the illustration from the original description of *A. nouryi* Lorois, 1852, plate 1, fig. 5; b, illustrations of a shell matching the description of *A. nouryi* taken from the examined lot (shell #109, 66.5 mm shell length, SBMNH 345768). Illustration: R. Plant. Scale bar = 1 cm.

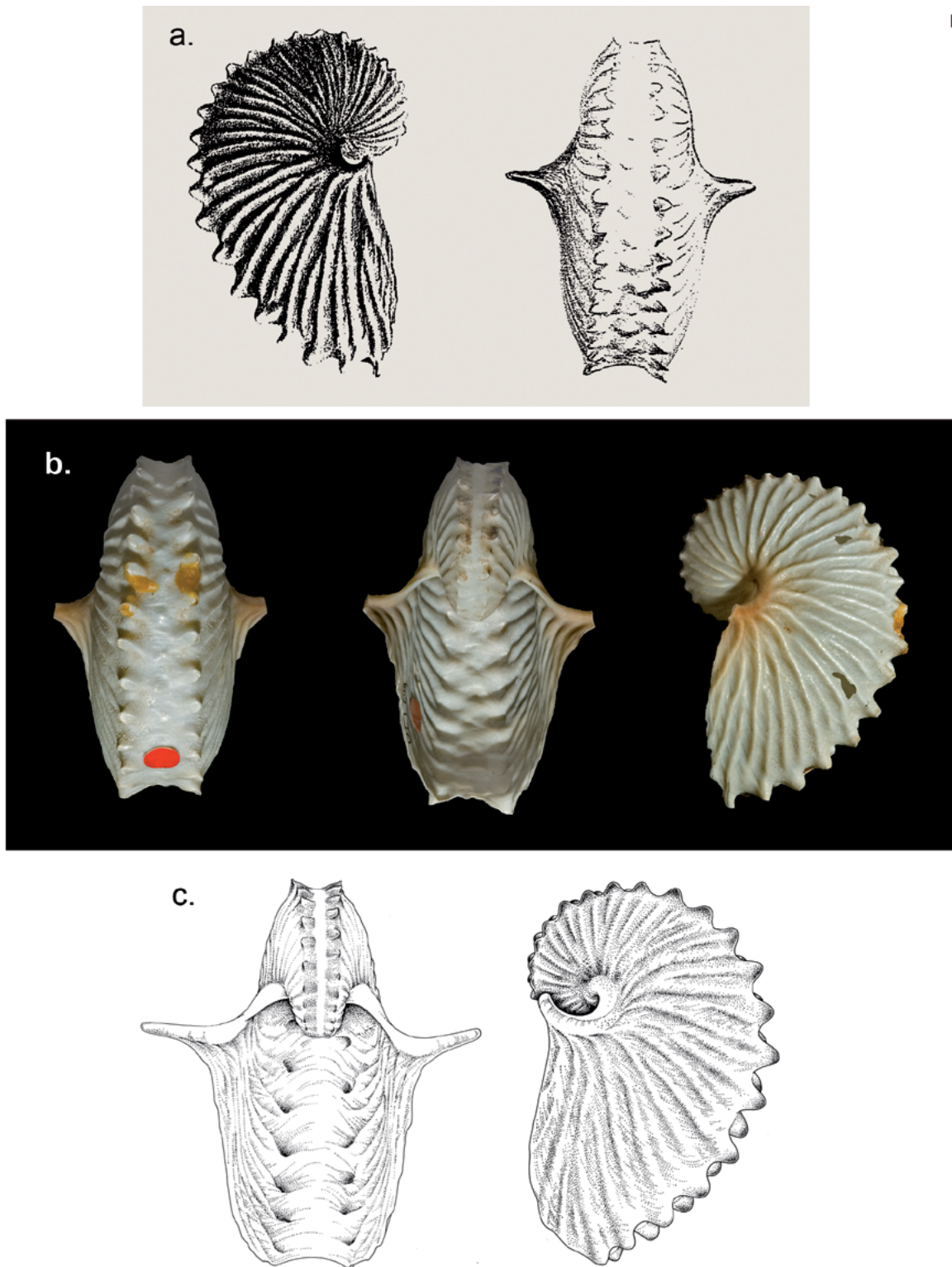


Figure 4. Comparison of a shell from the examined SBMNH lot with the type specimen and illustrations taken from the original description of *Argonauta cornutus* Conrad, 1854: a, reproduced illustration taken from the original description of *A. cornutus* Conrad, 1854, plate 34, fig. 2; b, photographs of the type specimen illustrated in the original description (58.6 mm shell length, ANSP 63496; please note, the original description illustrations mirror the characters of the shell, most likely due to the engraving and printing process of the era); c, illustrations of a shell matching the description of *A. cornutus* taken from the examined lot (shell #74, 65.0 mm shell length, SBMNH 345766). Illustration: R. Plant. Scale bar = 1 cm.

reproduction of the illustration presented by Lorois, 1852 (plate 1, figure 5), and illustrations of a shell from the Gulf of California that is consistent with the original description (shell #109, SBMNH 345768). According to Keen (1971) “the ‘shell’ is more elliptical than that of *A. cornutus*, with only the early part of the coil moderately well tinged with brown along the wide and weak tuberculate keel. The surface is delicately ribbed and has a finely granular texture” (p. 895). Voss (1971) believed that “*Argonauta nouryi* is a distinctive species [...]. The shells are longer than in any other species of *Argonauta*, the ribs are more numerous, there are no distinct tubercles marking the edges of the carinal area; the carina is wide, very convex, and covered by numerous, small, blunt tubercles formed by the crisscrossing of the ribs” (p. 32).

Argonauta cornutus was described by Conrad in 1854. The identification of this species also resides solely in features of the shell, which is described as having a broad keel, large keel tubercles and large ears. Fig. 4 incorporates a reproduction of the illustration presented by Conrad, 1854 (plate 34, figure 2), photographs of the type specimen (ANSP 63496) and illustrations of a shell from the Gulf of California that is consistent with the original description (shell #74, SBMNH 345766). According to Keen (1971), “the surface of the yellowish-white ‘shell’ is finely granular, the spines and part of the spire dark brown, the keel relatively broad, and the two long axial expansions suffused with purplish brown” (p. 894). Voss (1971) summarised that “*Argonauta cornutus* seems best characterised by the few radial ribs, the presence of fine sharp tubercles or papillae over the sides of the shell, the few rather sharp, large carinal tubercles on each side, the convex carinal surface, and the few, large, blunt tubercles on the carinal surface between the two rows of carinal boundary tubercles” (p. 32).

The distributions of these two species are reported to overlap, with *A. cornutus* known from the Gulf of California to Panama and *A. nouryi* being widespread in the equatorial Pacific, ranging from the west coast of Southern California to Peru (Keen 1971).

A mixed lot

As described in the Materials and Methods section above, the 157 shells in the collection at SBMNH were collected on the same beach in Baja California on the same day. These shells had previously been identified as representing both *A. cornutus* and *A. nouryi* and were registered accordingly: SBMNH 345766, *Argonauta cornutus* 93 shells; SBMNH 345768, *Argonauta nouryi*, 64 shells.

Initial examination of the lots indicated that the shells had been attributed to either *A. cornutus* or *A. nouryi* based on the presence or absence of ears – a character historically attributed to only *A. cornutus*. Further examination of the lot revealed that separation of the shells into two distinct groups (i.e. either *A. cornutus* or *A. nouryi*) was not as straightforward as first thought. While some shells within the lot displayed all the characters associated with either *A. cornutus* or *A. nouryi*, the lot also appeared to contain shells with combinations of the attributes of the two shell types. To illustrate this variation, three shells of similar size but varied appearance were selected. Fig. 5 presents photographs of these three shells from multiple perspectives:

- Shell #74 (SBMNH 345766), *cornutus*-type voucher (fig. 5a, i–iv and fig. 4c). Shell morphometrics: ShL 65.0; ShW 4.0; ShB 40.7; RC 45; EW 58.1; ApL 45.9; ApW 28.4; KW 15.6; KTC 27.
- Shell #42 (SBMNH 345766), *intermediate* voucher (fig. 5b, i–iv). Shell morphometrics: ShL 61.2; ShW 3.1; ShB 36.4; RC 47; EW 36.1; ApL 43.1; ApW 30.9; KW 14.0; KTC 32.
- Shell #109 (SBMNH 345768), *nouryi*-type voucher (fig. 5c, i–iv and fig. 3b). Shell morphometrics: ShL 66.5; ShW 2.4; ShB 39.9; RC 54; EW (28.3); ApL 48.8; ApW 32.5; KW 15.8; KTC 54.

While it would be straightforward to attribute shell #74 (fig. 5a) to *A. cornutus* Conrad, 1854, and shell #109 (fig. 5c) to *A. nouryi* Lorois, 1852, placement of shell #42 (fig. 5b) presents problems. While shell #42 possesses the aperture shape of *A. cornutus*, it lacks its protruding ears. While shell #42 possesses the keel tuberculation and reduced ventral keel tubercles of *A. nouryi*, its dorsal keel tubercles are large and pronounced.

To determine whether there was a significant difference between eared and earless shells within the lot, a quantitative approach was undertaken. All intact shells within the lot were individually measured and weighed. All shells were designated as being either eared or earless based on the relative EW and ApW measurements. Because EW is an external measurement (i.e. measured across the extremities of the opposing ears) and ApW is an internal measurement (i.e. measured between the lateral walls of the shell), 1.0 mm was added to the ApW to accommodate for the thickness of the lateral walls of the shell. Shells were classified as follows:

- eared = $EW > ApW + 1.0$ mm (103 shells)
- earless = $EW \leq ApW + 1.0$ mm (35 shells)

Scatter plots were generated to compare eared and earless shells for all measured characters. Characters of primary interest were those previously reported to distinguish *A. cornutus* and *A. nouryi*.

Shell shape. The most universally recognised character of *A. nouryi* is reportedly the elliptical shape of the shell: “The whorls increase in size very rapidly and the last is very elongate. Viewed laterally it is much shallower than is usual in the genus” (Robson, 1932, p. 198). The shells are said to be “more elliptical than that of *A. cornutus*” (Keen, 1971, p. 895) and “longer than in any other species of *Argonauta*” (Voss, 1971a, p. 33).

To investigate variation in shell shape across the lot, ShB was plotted against ShL (fig. 6). Probability plots indicate that both ShB and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ShB the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in shell shape exists between eared and earless shells ($F_{(1,136)} = 5.58, p = 0.02$).

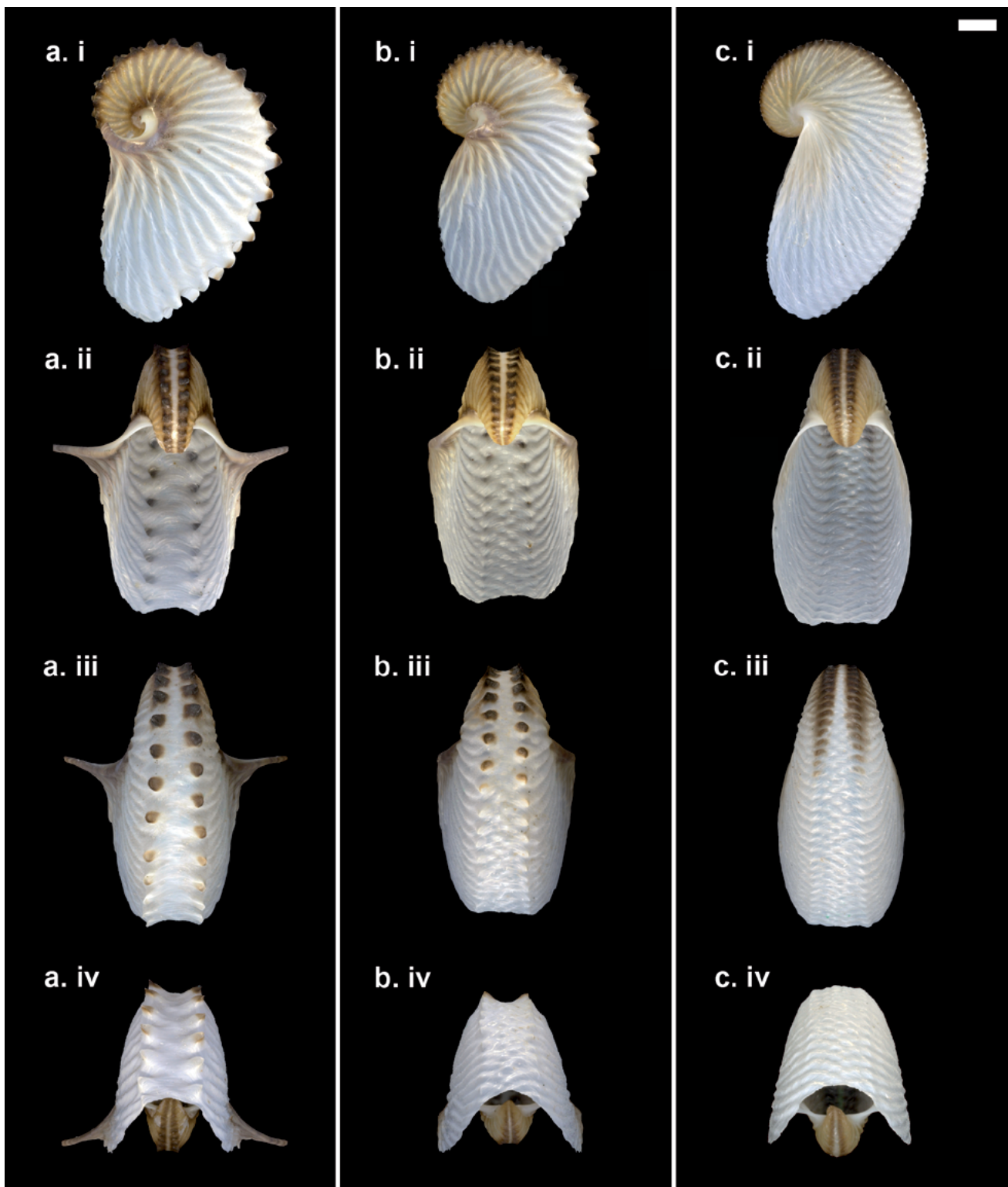


Figure 5. Three similarly sized shells of varied appearance selected from the examined SBMNH lot: a–c, three similarly sized shells of varied appearance selected from the single lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000; a, shell #74 (65.0 mm shell length, SBMNH 345766) assigned the name *cornutus-type voucher*; b, shell #42 (61.2 mm shell length, SBMNH 345766) assigned the name *intermediate voucher*; c, shell #109 (66.5 mm shell length, SBMNH 345768) assigned the name *nouryi-type voucher*; i–iv, multiple perspectives of each shell; i, left lateral view; ii, anterior aperture view; iii, posterior keel view; iv, ventral view. Scale bar = 1 cm.

Rib count. *Argonauta nouryi* shells are reported to have more ribs than *A. cornutus* shells: the ribs in *A. nouryi* are “more numerous” than in other species of *Argonauta*, while *A. cornutus* is reported to have “few radial ribs” (Voss, 1971, p. 32–33).

To investigate variation in the number of ribs per shell across the lot, RC was plotted against ShL (fig. 7). Probability plots indicate that both RC and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear

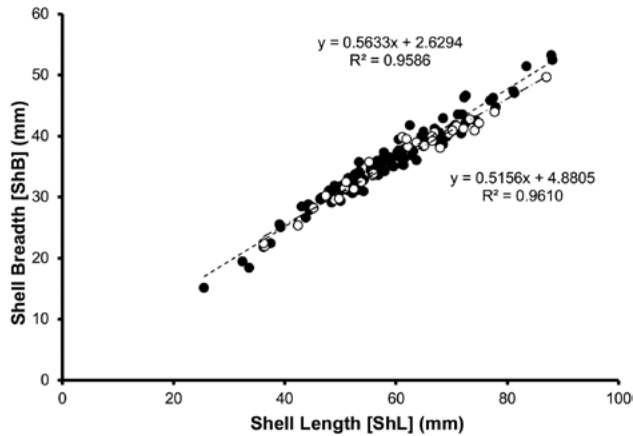


Figure 6. Variation in shell shape across the examined SBMNH lot. Scatter plot of shell breadth (ShB) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

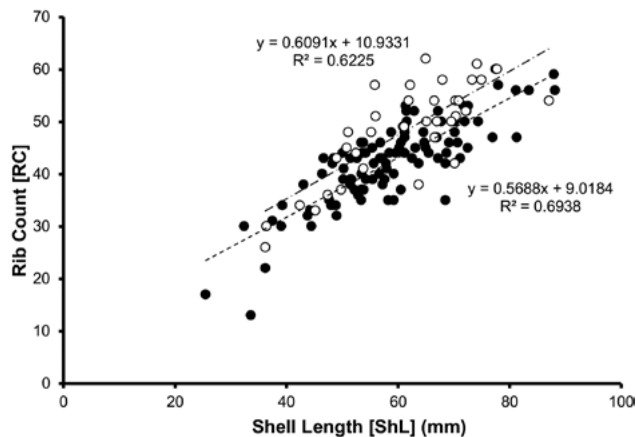


Figure 7. Variation in rib number across the examined SBMNH lot. Scatter plot of rib count (RC) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 3045766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, RC the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the number of ribs per shell does exist between eared and earless shells ($F_{(1, 136)} = 21.2$, $p < 0.001$).

Other features. To investigate the full range of quantifiable shell characters across the lot, scatter plots were similarly generated to investigate KTC, ApL, ApW and KW.

Keel tubercle count. To investigate variation in the number of keel tubercles per shell across the lot, KTC was plotted against ShL (fig. 8). Probability plots indicate that both KTC and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, KTC the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the number of keel tubercles per shell does exist between eared and earless shells ($F_{(1, 136)} = 51.66$, $p < 0.001$).

Aperture length. To investigate variation in the length of the shell apertures across the lot, ApL was plotted against ShL (fig. 9). Probability plots indicate that both ApL and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ApL the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the length of the aperture does exist between eared and earless shells ($F_{(1, 136)} = 18.63$, $p < 0.001$).

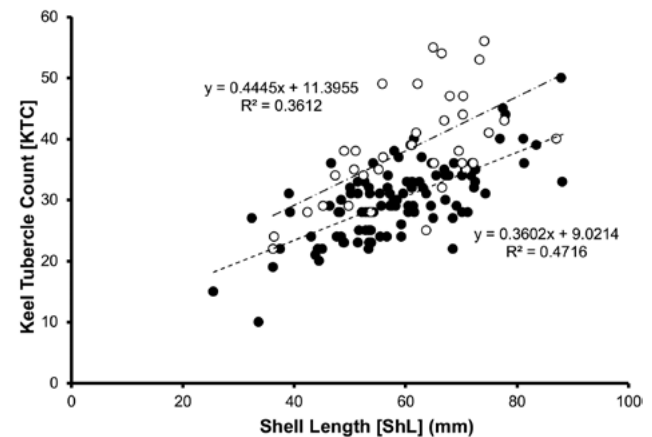


Figure 8. Variation in keel tubercle number across the examined SBMNH lot. Scatter plot of keel tubercle count (KTC) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Aperture width. To investigate variation in the width of the shell apertures across the lot, ApW was plotted against ShL (fig. 10). Probability plots indicate that both ApW and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ApW the

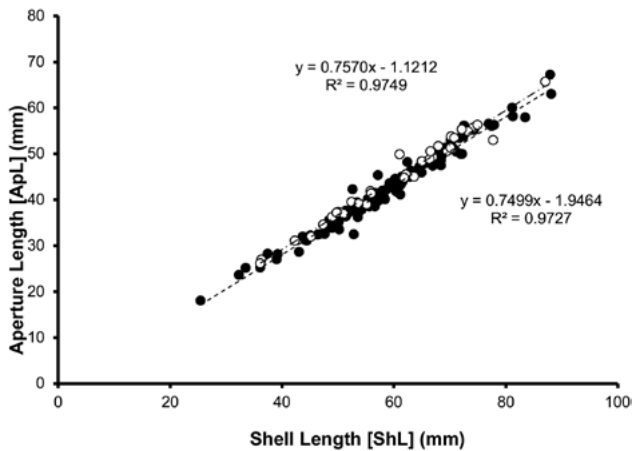


Figure 9. Variation in aperture length across the examined SBMNH lot. Scatter plot of aperture length (ApL) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

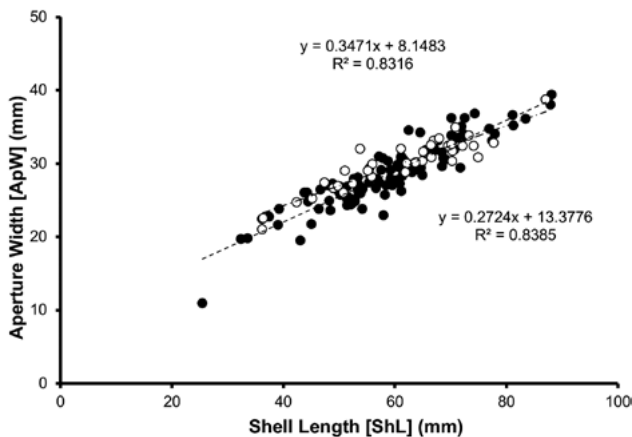


Figure 10. Variation in aperture width across the examined SBMNH lot. Scatter plots of aperture width (ApW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the width of the aperture does exist between eared and earless shells ($F_{(1,136)} = 4.07$, $p = 0.046$).

Keel width. To investigate variation in the width of the shell keels across the lot, KW was plotted against ShL (fig. 11). Probability plots indicate that both KW and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, KW the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are equal and hence a significant difference in the width of the keel does not exist between eared and earless shells ($F_{(1,136)} = 0.87$, $p = 0.353$).

Statistical analysis indicates that significance differences in shell dimensions was associated with the presence or absence of ears. Eared shells have significantly lower RC ($p < 0.001$), lower KTC ($p < 0.001$), shorter ApL ($p < 0.001$), increased ShB (i.e. shortened; $p = 0.02$) and increased ApW ($p = 0.046$). Earless shells have significantly higher RC ($p < 0.001$), higher KTC ($p < 0.001$), longer ApL ($p < 0.001$), reduced ShB (i.e. elongate; $p = 0.02$) and reduced ApW ($p = 0.046$). KW was found to not be significantly different between shell types ($p = 0.353$).

Historically, the features of eared and earless shell types have been considered to represent separate species such that features of eared shells are considered characteristic of *A. cornutus*, while features of earless shells are considered characteristic of *A. nouryi*.

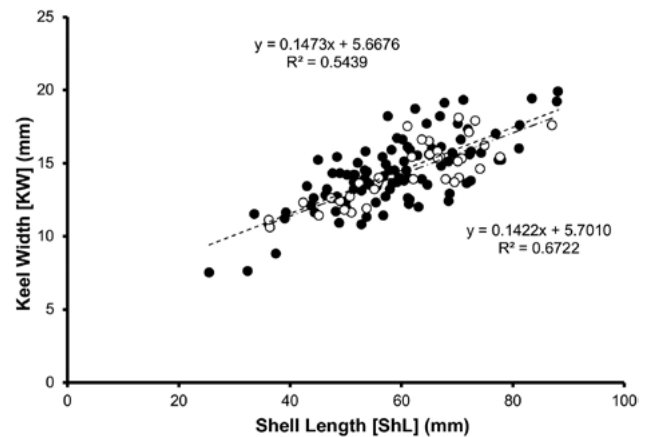


Figure 11. Variation in keel width across the examined SBMNH lot. Scatter plot of keel width (KW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Two types of shell formation

Close examination of individual shells revealed that features considered characteristic of each shell type could occur on a single shell. While individual shells could display features of both eared and earless shell types, the characters did not appear in isolation. Sequential growth sections of the shells appeared to display all the characteristics of one shell type or another. For example, the initial component of the shell (the smallest whorl) may display all the characters historically associated with an *A. cornutus* shell while the latter component (the larger final whorl) may display all the features associated with an *A. nouryi* shell.

The most dramatic examples were shells that appeared to have been repaired over the course of the argonaut's life. Fig. 12 presents photographs of one such shell from lot SBMNH 357476 (52.3 mm ShL). The initial component of the shell clearly displays the features historically attributed to *A. nouryi* (numerous fine ribs, reduced keel tubercles and no apparent ears), while the later component, following the clear repair line, displays a transition to features historically attributed to *A. cornutus* (ribs reduced in number and more pronounced, keel tubercles reduced in number and of larger size, and initiation of ears).

The presence of both shell types on a single shell clearly demonstrates that they represent different types of shell formation, not different argonaut species. This observation is supported by morphological evidence; despite full examination of nine female argonauts with shells (six historically identified as *A. cornutus* and three *A. nouryi*), no morphological characters could be found to separate specimens with different shell types (see Finn, 2013).

The realisation that the two shell morphs represented two shell formation types, not two argonaut species, required that they be defined independent of previous species association:

- Type 1 shell formation (historically attributed to *A. cornutus* shells) – formation of ears, few pronounced ribs, few large keel tubercles, appearance of more pronounced arch in the keel resulting in a tighter final whorl (i.e. increased ShB, reduced ApL).
- Type 2 shell formation (historically attributed to *A. nouryi* shells) – absence of ears, numerous less pronounced ribs, numerous small keel tubercles, appearance of less pronounced arch in the keel resulting in the appearance of a shallower final whorl and elliptical shell (i.e. reduced ShB, increased ApL).

An important character associated with Type 2 shell formation is inter-keel tuberculation (tubercles on the keel surface; see fig. 2e). The appearance of inter-keel tuberculation on the keel of a shell flags a shift to Type 2 shell formation, while a loss of inter-keel tuberculation signifies a shift to Type 1 shell formation.

Based on this realisation, it became clear that this large lot, and all other material examined of these shell morphs, belonged to a single species. Because *A. nouryi* Lorois, 1852, has date priority over *A. cornutus* Conrad, 1854; this study treats *A. nouryi* as the available name. See Finn (2013) for full synonymy.

The key to understanding shell variation

The realisation that individual shells may be composed of combinations of two types of shell formation provided the key to understanding the huge variation in shell shape across the single large collection of argonaut shells from Baja California. Combinations of sequential shell formation could be recognised in all shells and hence their varied appearance could be understood. Shells were recognised within this single lot that display a single type of shell formation plus those with one, two or three transformations between the two shell formation types.

The initial whorl of most of the shells displayed Type 1 formation. Shell #37 displays a single change from Type 1 to Type 2 shell formation (fig. 13). Shell #72 displays a change from Type 1 to Type 2 shell formation and then a change back to Type 1 (fig. 14). Shell #41 displays a change from Type 1 to Type 2 shell formation and then a change back to Type 1 and then to Type 2 (fig. 15). Damage to shells normally results in a conversion to Type 2 shell formation.

In a transition between shell formation types, ears may be formed or subsumed. This is displayed across many shells within the lot. For examples, shell #139 displays subsumed ears as a result of a transition from Type 1 to Type 2 shell formation (fig. 16), while shell #136 displays ear formation, separate from the axis of the shell, as a result of a transition from Type 2 to Type 1 shell formation (fig. 17).

Type material. Available type material for additional species synonymised with *A. nouryi* Lorois, 1852, was also examined for shifts in shell formation type. The holotype of *A. dispar* Conrad, 1854 (54.9 mm ShL, ANSP 129978) displays a single change from Type 2 to Type 1 shell formation (fig. 18). The holotype of *A. expansus* Dall, 1872 (80.2 mm ShL [P], USNM 61368), displays two changes – from Type 1 to Type 2 and then back to Type 1 (fig. 19).

Shell thickness. Preliminary observations suggested that the shell walls of Type 1 formation are thicker than the walls of Type 2 formation. To investigate this phenomenon, a scanning electron microscope was used to examine variation in shell thickness across recognisable shell breaks that corresponded with a switch between shell types (a single damaged shell from lot SBMNH 357476 was sacrificed). Preliminary results indicate a reduction in shell wall thickness between Type 1 and Type 2 formation. Fig. 20 presents two scanning electron micrographs displaying a reduction in thickness across a break signifying transition from Type 1 to Type 2. Shell thickness on the lateral face drops from approximately 220 to 140 μm (fig. 20a), while thickness at the keel drops from approximately 275 to 210 μm in this shell (fig. 20b).

A lack of material that could be fragmented for examination with a scanning electron microscope limited the extent to which this phenomenon could be investigated. The lots housed in the SBMNH collection are too valuable to be considered for this style of destructive investigation.

A reduction in shell wall thickness may be related to producing a larger shell area with less shell material. The resulting thinner walled shell (Type 2) would therefore consist

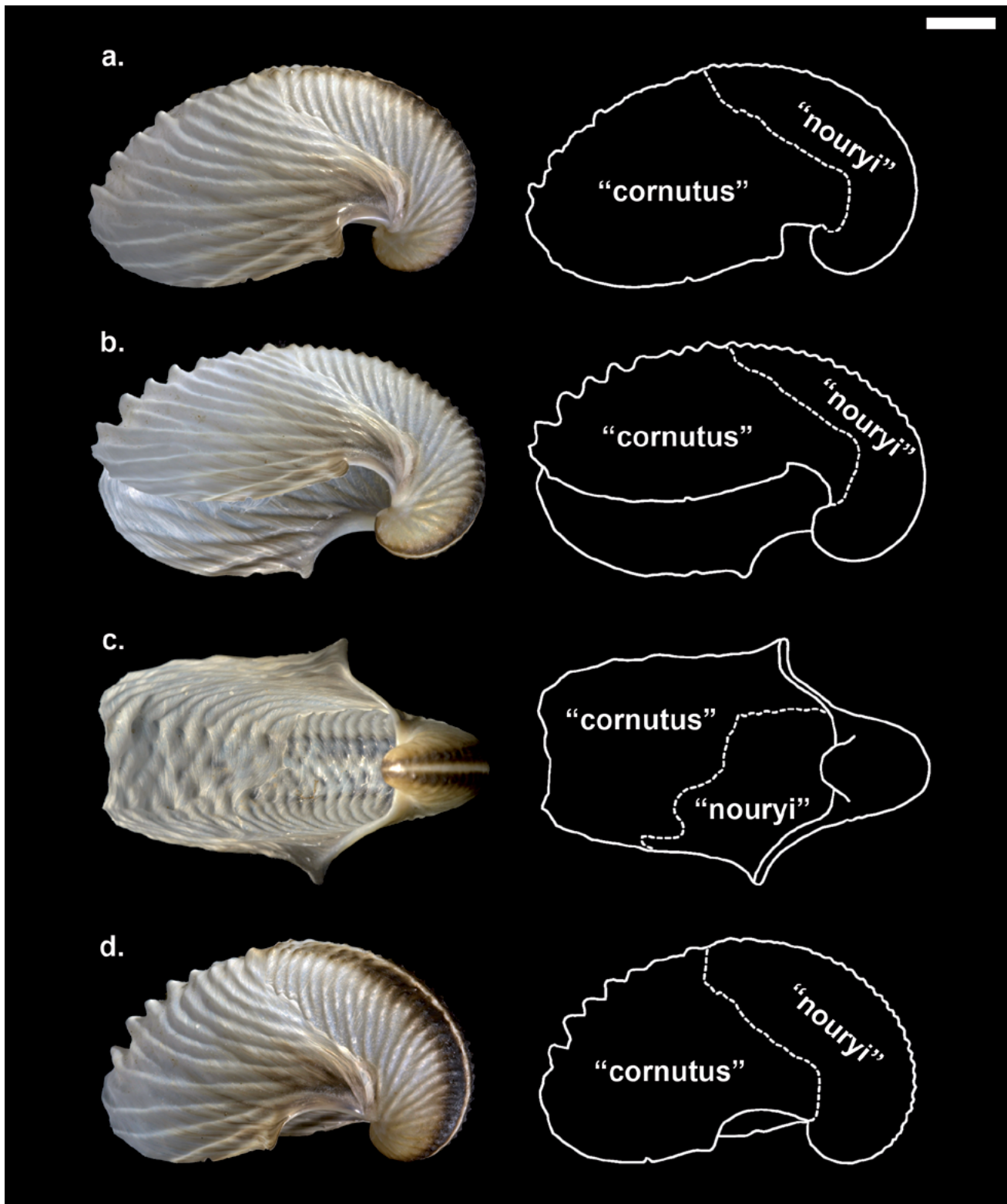


Figure 12. Repaired shell displaying components consistent with *Argonauta nouryi* and *A. cornutus*: a–d, four perspectives of a single shell (52.3 mm shell length, SBMNH 357476) displaying an initial component consistent with *A. nouryi* Lorois, 1854 (“nouryi”) followed by a subsequent component consistent with *A. cornutus* Conrad, 1854 (“cornutus”); a, right lateral view; b, oblique right lateral view; c, anterior aperture view; d, oblique ventral keel view. Dashed line represents repair line separating two visually different components. Scale bar = 1 cm.

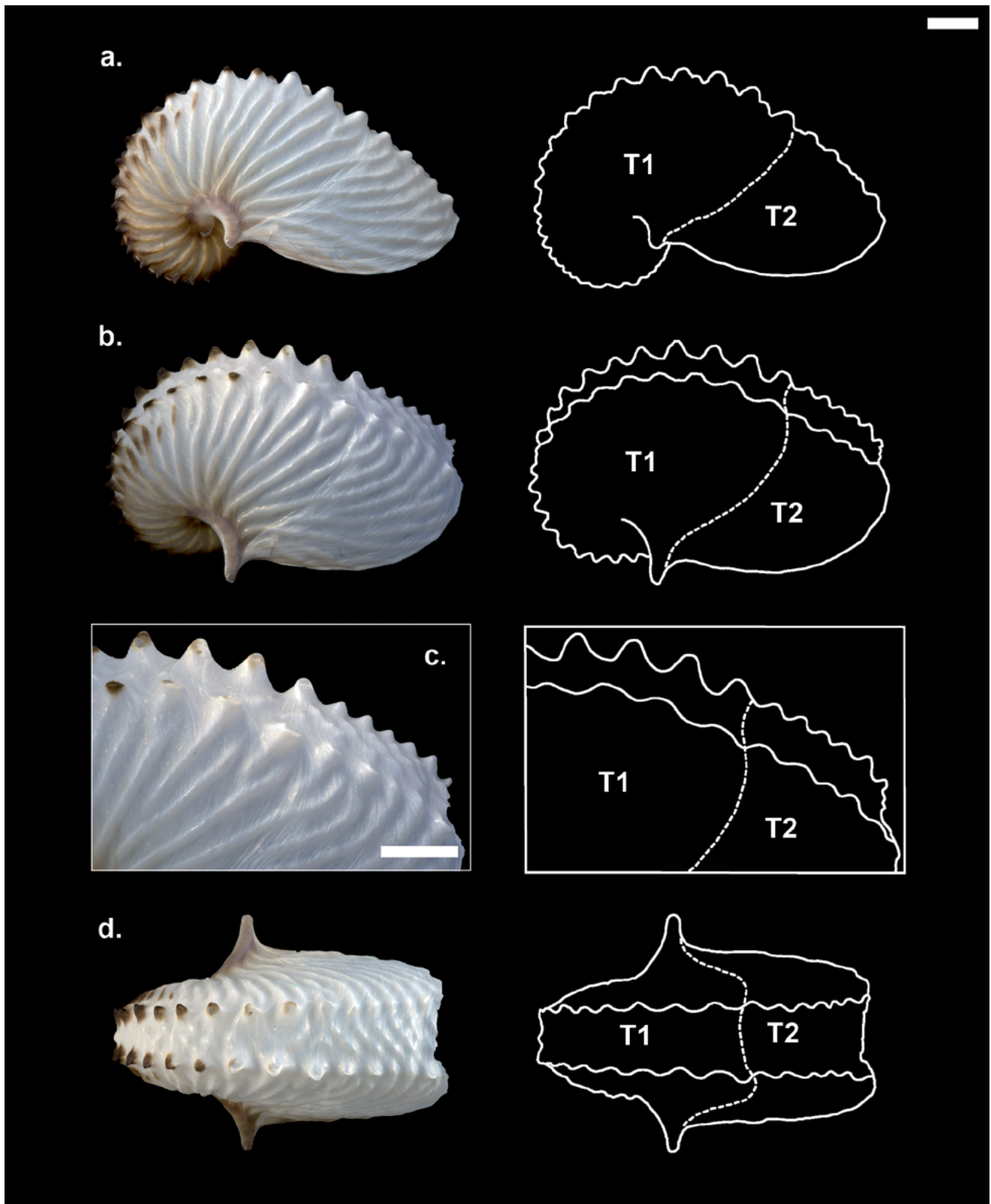


Figure 13. *Argonauta nouryi* shell displaying a single change in shell formation type: a–d, four perspectives of shell #37 (65.5 mm shell length, SBMNH 345766) displaying a single change from Type 1 (T1) to Type 2 (T2) shell formation; a, left lateral view; b, oblique left lateral view; c, close-up oblique left lateral view; d, posterior keel view. Scale bar = 1 cm.

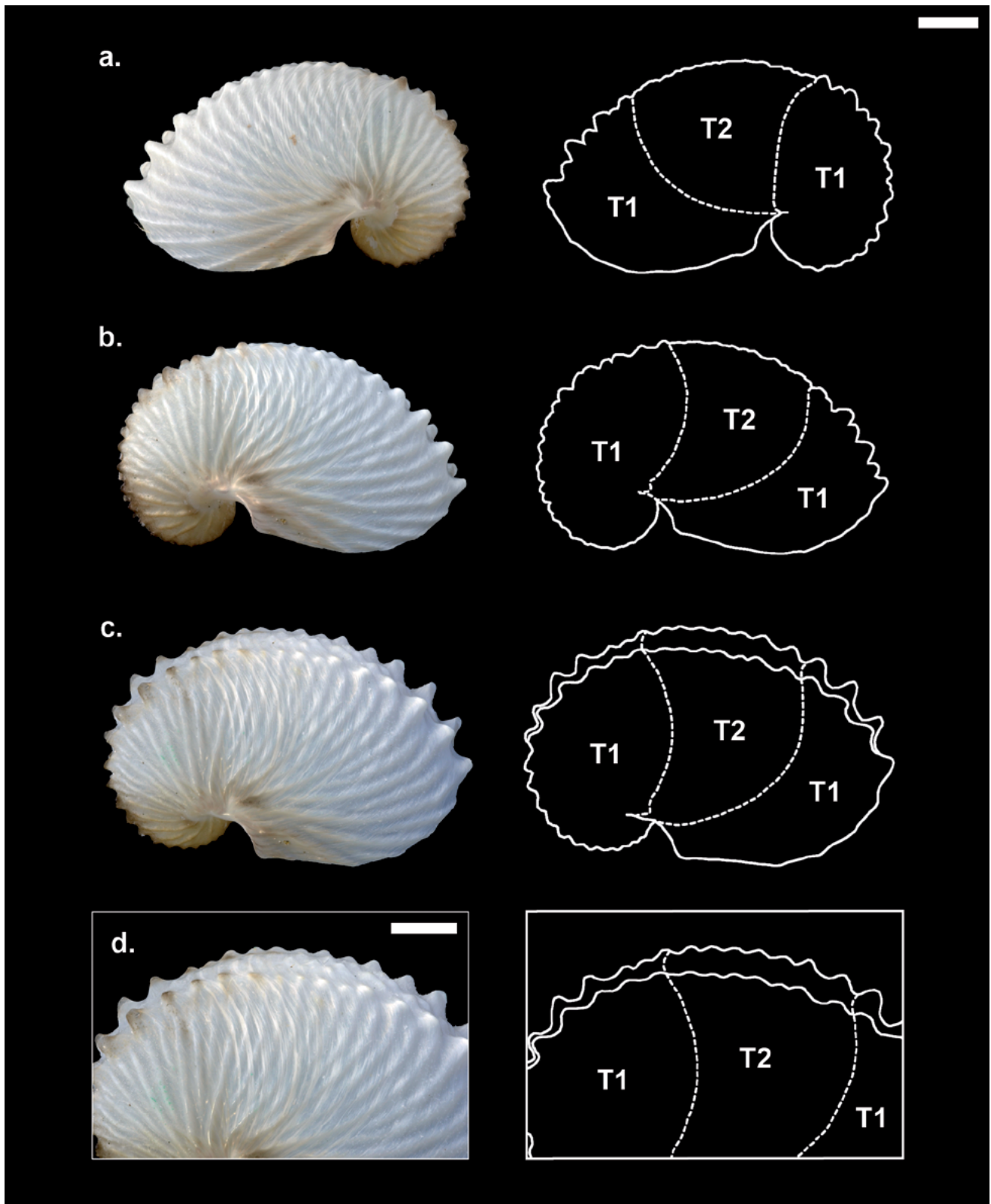


Figure 14. *Argonauta nouryi* shell displaying two changes in shell formation type: a–d, four perspectives of shell #72 (55.4 mm shell length, SBMNH 345766) displaying two changes from Type 1 (T1) to Type 2 (T2) shell formation and back to Type 1; a, right lateral view; b, left lateral view; c, oblique left lateral view; d, close-up oblique left lateral view. Scale bar = 1 cm.

of less calcium carbonate and weigh less than an equivalently sized thicker walled shell (Type 1). The relative weights of the three shells presented in fig. 5 appear to support this theory. The Type 1 shell (*cornutus-type* voucher; 4.0 g) is 1.3 times the weight of the Type 1/Type 2 shell (*intermediate voucher*; 3.1 g) and 1.7 times the weight of the Type 2 shell (*nouryi-type voucher*; 2.4 g), despite the shells having similar ShL. Weight (g) to length (mm) ratios of the three shells were: 1:16 for the Type 1 shell (*cornutus-type* voucher); 1:20 for the Type 1/Type 2 shell (*intermediate voucher*); 1:28 for the Type 2 shell (*nouryi-type voucher*). These ratios suggest that per gram of calcium carbonate, Type 2 shell production results in a shell 1.8 times the length of a Type 1 shell.

To investigate this relationship across the lot, ShW was plotted against ShL with eared and earless shells distinguished (fig. 21). The scatter plot indicates a separation between eared and earless shells based on weight. This difference was analysed statistically to determine significance. Probability plots indicate that both ShW and ShL follow normal distributions. An ANCOVA was used to determine if the

slopes of the regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ShW the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in weight exists between eared and earless shells ($F_{(1, 136)} = 86.7, p < 0.001$).

Argonauta hians [Lightfoot], 1786; the *A. hians/boettgeri* complex

Recognition of shell form transformations in *A. nouryi* provided a new perspective on shell variation in another highly variable group of small argonauts, the *A. hians/boettgeri* complex.

The original description of *A. hians* [Lightfoot], 1786, refers to a single image in Rumphius (1705): plate 18, figure B (fig. 22a), designated as a lectotype by Moolenbeek (2008) in the absence of type material. Shells of *A. hians* can be recognised by smooth lateral ribs and a keel that increases in width with shell growth. Inter-keel tuberculation is absent.

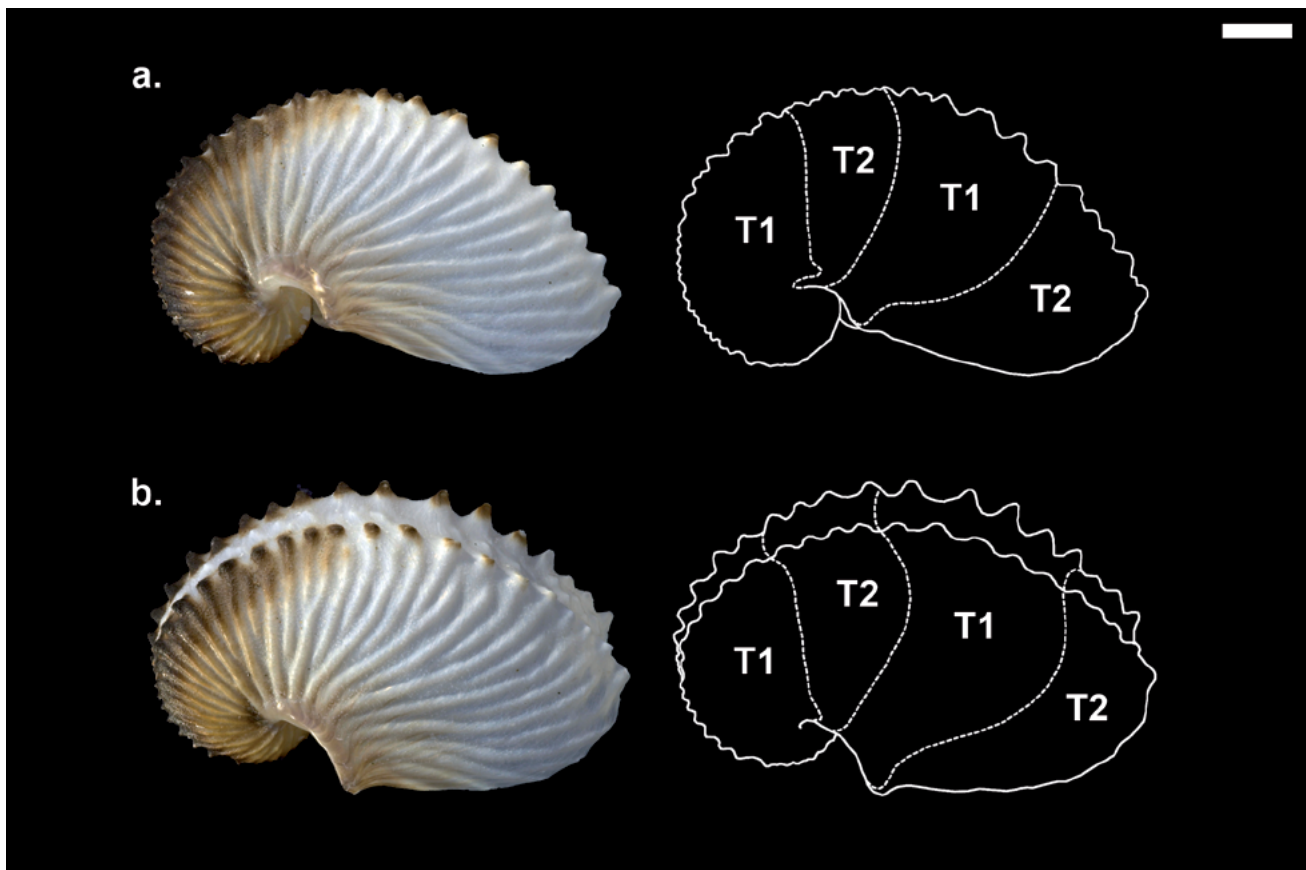


Figure 15. *Argonauta nouryi* shell displaying three changes in shell formation type: a–b, two perspectives of shell #41 (64.7 mm shell length, SBMNH 345766) displaying three changes in shell formation type from Type 1 (T1) to Type 2 (T2) shell formation, back to Type 1 and then to Type 2; a, left lateral view; b, oblique left lateral view. Note that the key to recognising the different shell formation types (challenging in this shell) is to look for reductions in the size of sequential keel tubercles (that would normally increase in size), a change in the relative distance between keel tubercles, a change in the ratio of lateral ribs to keel tubercles, and the appearance or disappearance of inter-keel tuberculation. Scale bar = 1 cm.

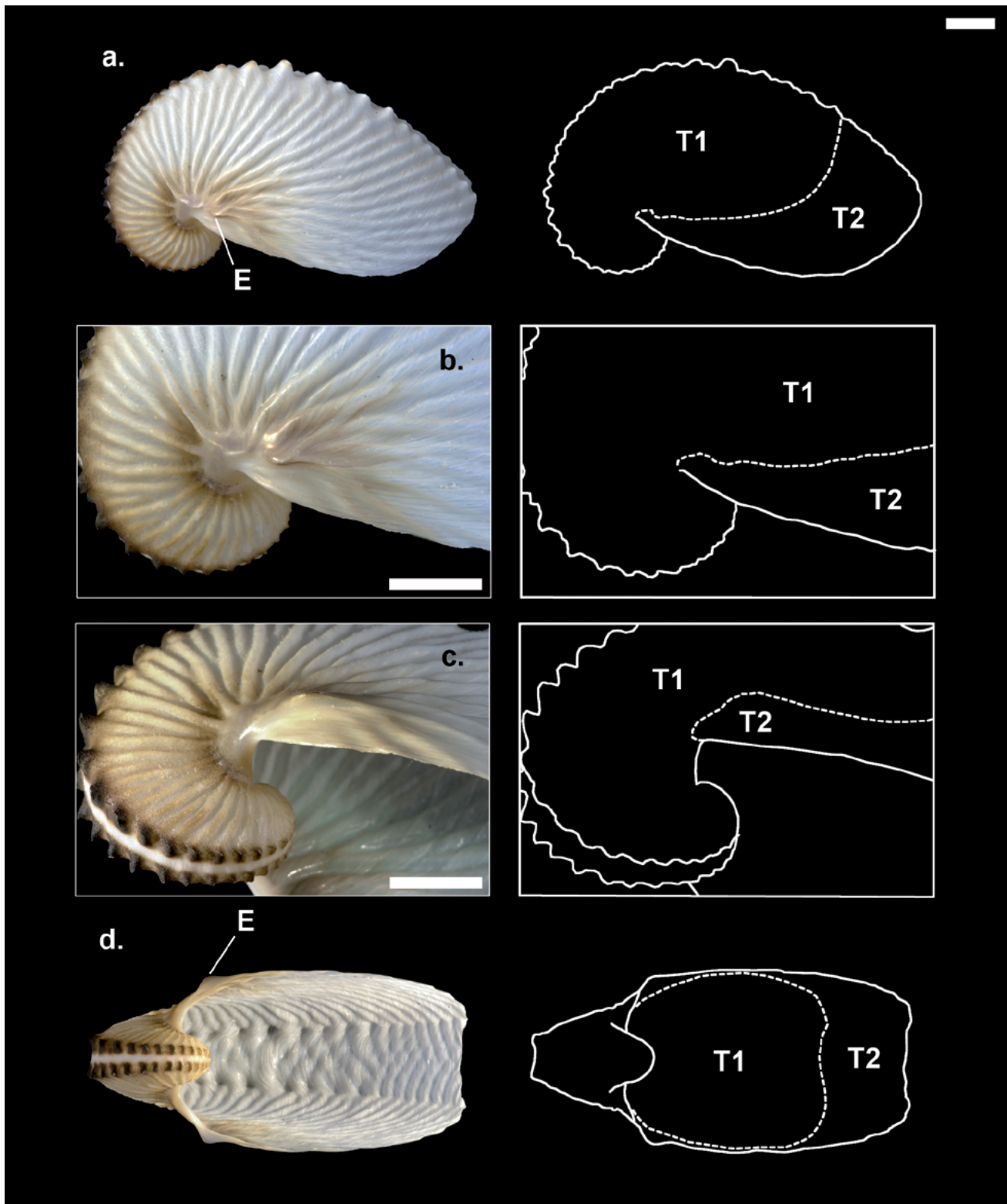


Figure 16. *Argonauta nouryi* shell displaying subsumed ears: a–d, four perspectives of shell #139 (72.2 mm shell length, SBMNH 345768) displaying subsumed ear (E) associated with a shift from Type 1 (T1) to Type 2 (T2) shell formation; a, left lateral view; b, close-up of subsumed ear, left lateral view; c, close-up of subsumed ear, oblique left lateral view; d, anterior aperture view. The shell added to the aperture edge in Type 2 shell formation does not expand the ear, instead subsuming it. The resulting aperture edge is not eared. Scale bars = 1 cm.

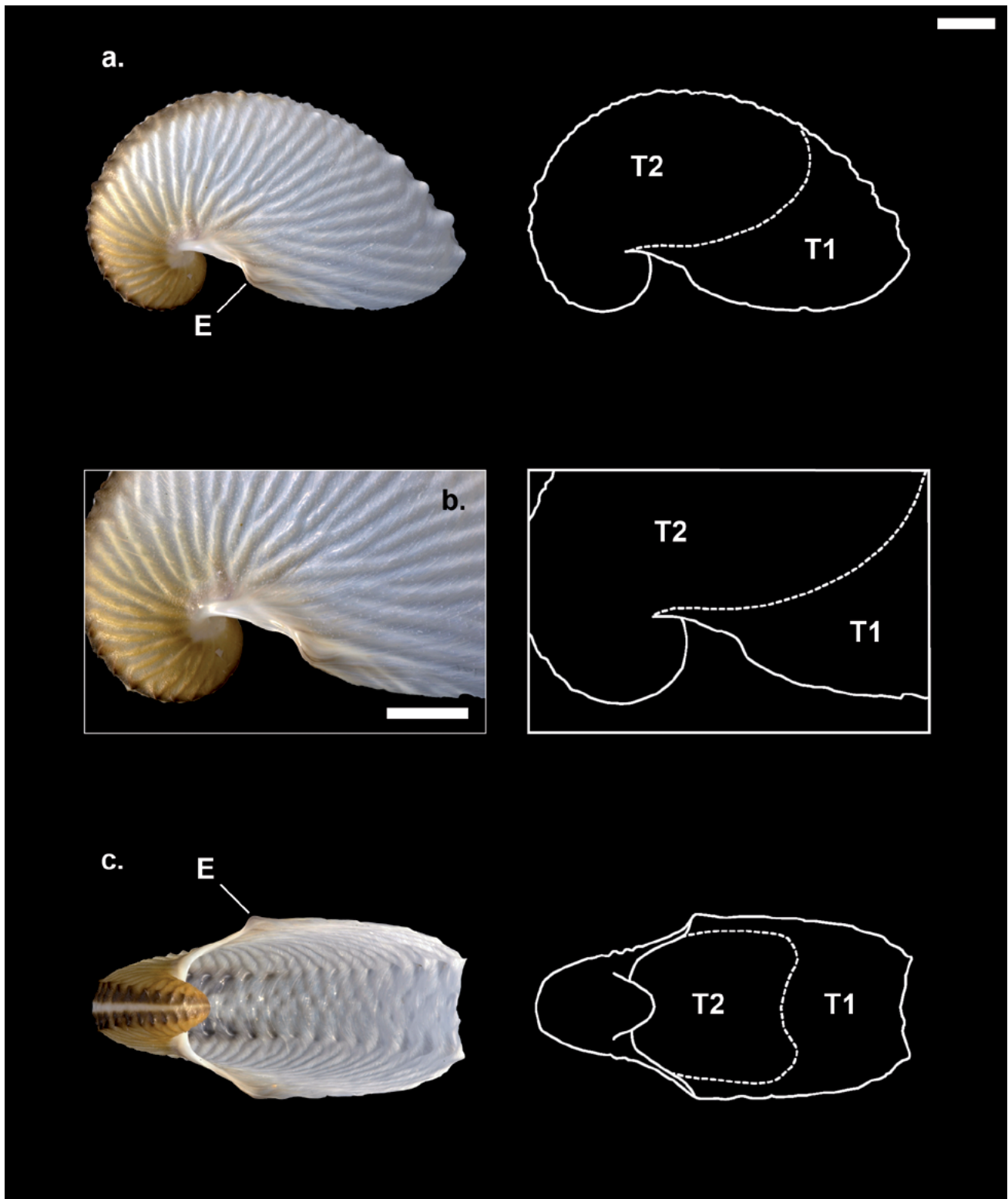


Figure 17. *Argonauta nouryi* shell displaying ear formation: a–c, three perspectives of shell #136 (63.1 mm shell length, SBMNH 345768) displaying ear (E) formation associated with a shift from Type 2 (T2) to Type 1 (T1) shell formation; a, left lateral view; b, close-up of ear, left lateral view; c, anterior aperture view. The shell added to the aperture edge in Type 1 shell formation produces a new ear separate from the axis of the shell. The new ear becomes the widest point on the aperture edge. Scale bars = 1 cm.

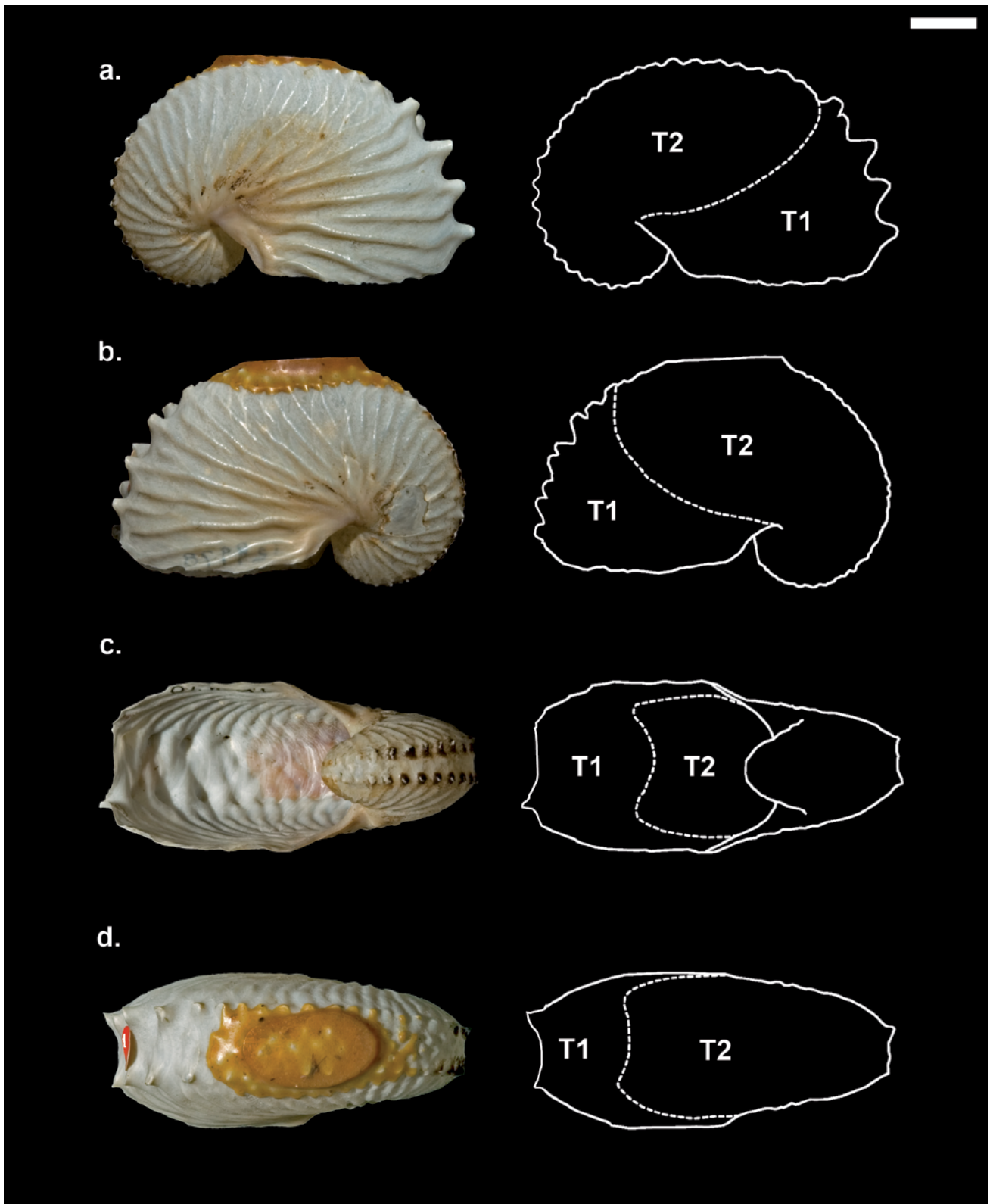


Figure 18. Holotype of *Argonauta dispar* Conrad, 1854 (synonym of *A. nouryi* Lorois, 1852) from the Academy of Natural Sciences, Philadelphia: a–d, four perspectives of *A. dispar* Conrad, 1854 Holotype (54.9 mm shell length, ANSP 129978) displaying a single change from Type 2 (T2) to Type 1 (T1) shell formation; a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

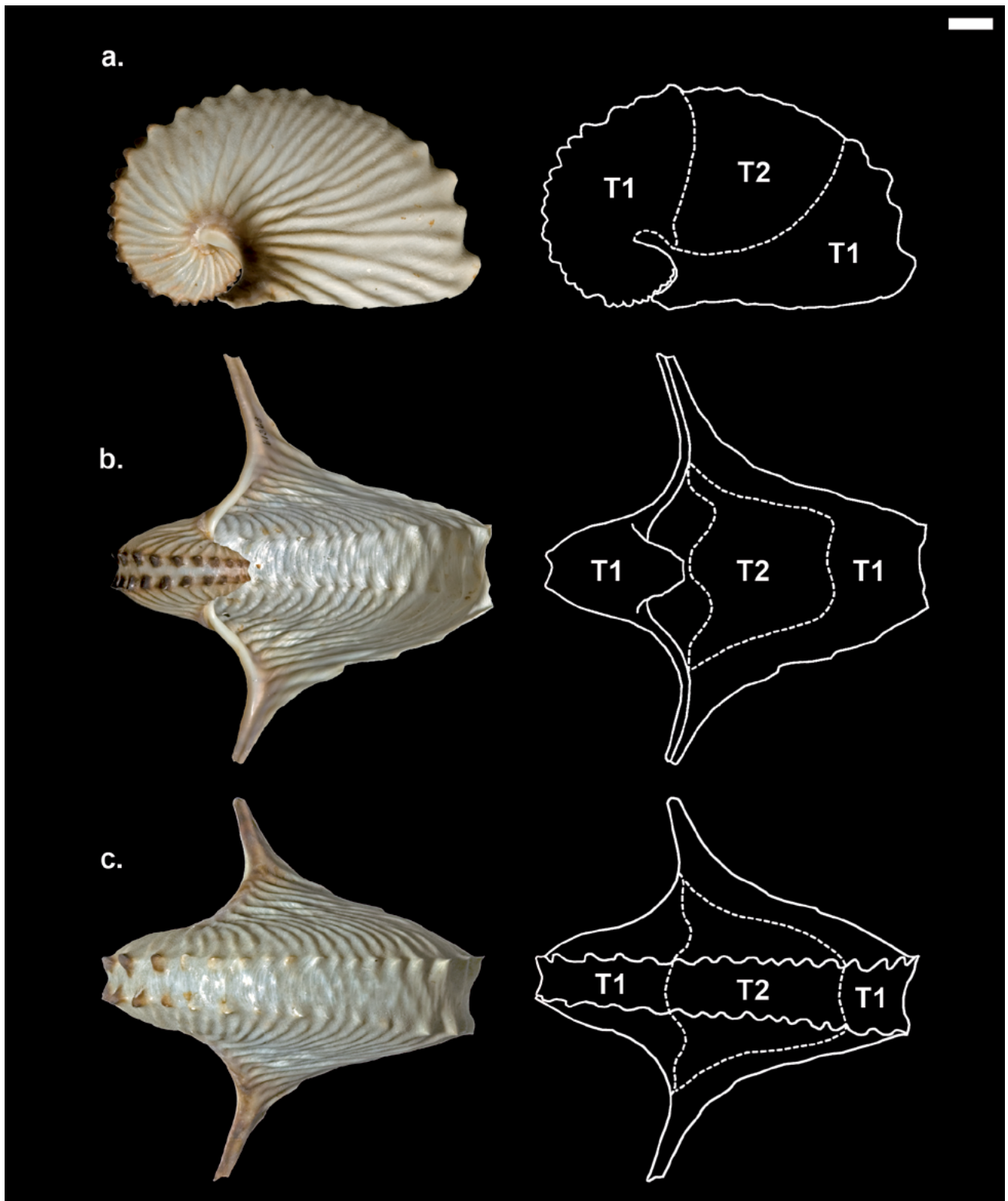


Figure 19. Holotype of *Argonauta expansus* Dall, 1872 (synonym of *A. nouryi* Lorois, 1852) from the National Museum of Natural History (Smithsonian Institution) Washington: a–c, three perspectives of *A. expansus* Dall, 1872 Holotype (80.2 mm shell length [P], USNM 61368) displaying two changes from Type 1 (T1) to Type 2 (T2) shell formation and back to Type 1; a, left lateral view; b, anterior aperture view; c, posterior keel view. Scale bar = 1 cm.

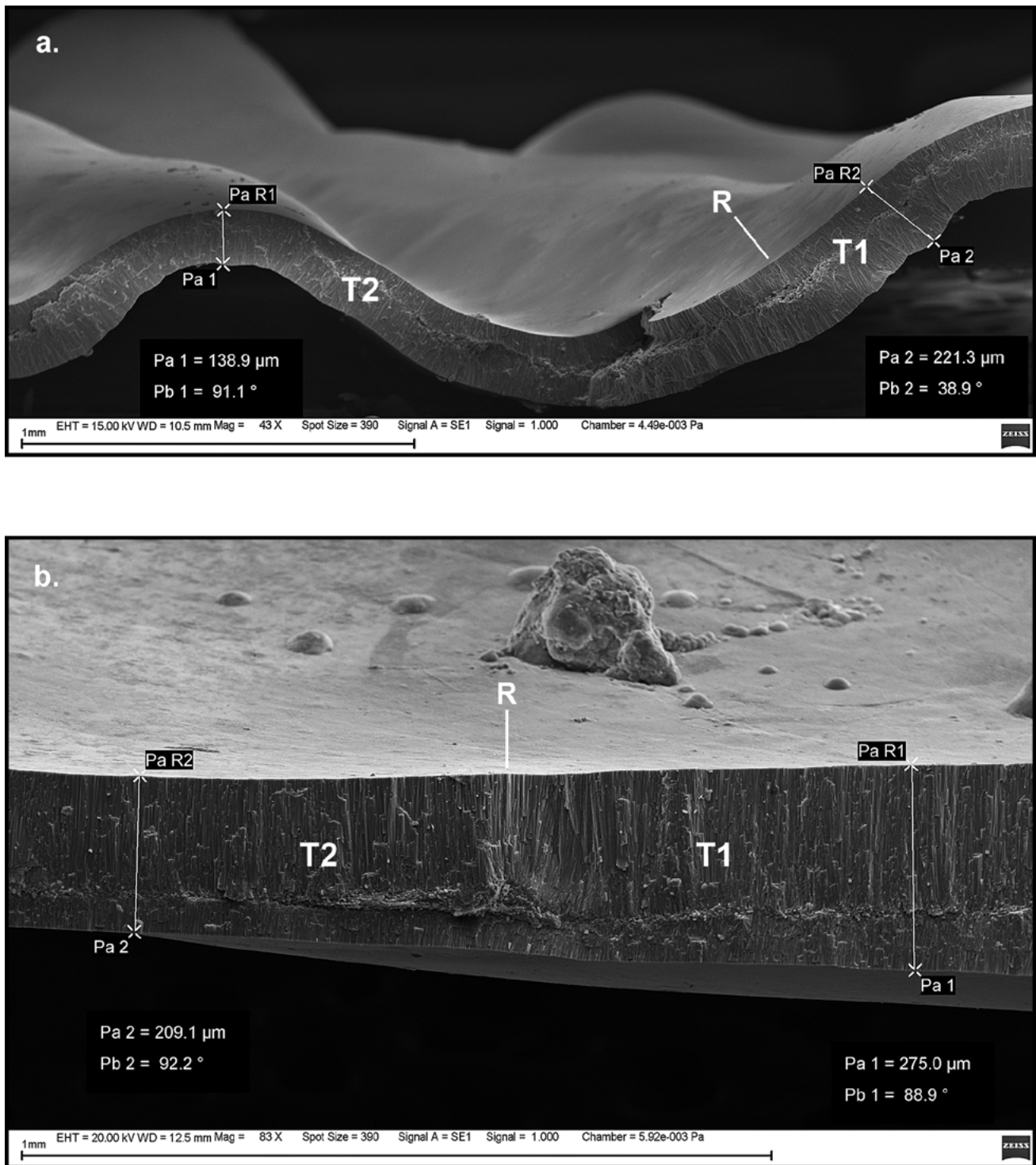


Figure 20. Scanning electron microscope images of *Argonauta nouryi* shell displaying variation in shell thickness: a–b, scanning electron microscope images of shell cross-sections (SBMNH 357476) across shell repairs (R) representing a shift from Type 1 (T1) to Type 2 (T2) shell formation; a, lateral face of shell, inner surface facing up; b, keel, outer surface facing up. Scale bars = 1 mm.

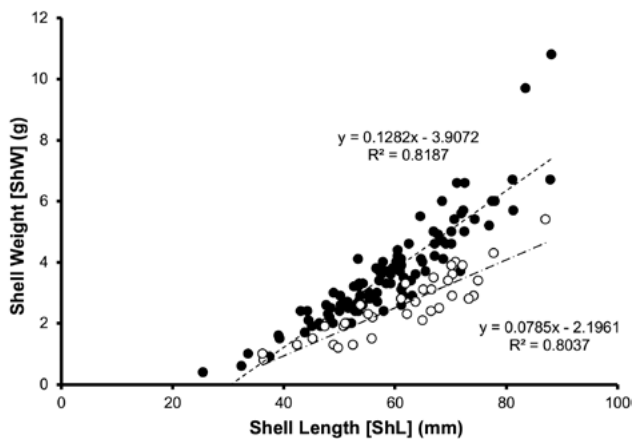


Figure 21. Variation in shell weight across the examined SBMNH lot. Scatter plot of shell weight (ShW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Argonauta hians has long been recognised as displaying considerable variation in shell form. Voss and Williamson (1971) noted that “In the series from Hong Kong the sides of the aperture at the umbilicus range from strongly eared or auriculate with very large few knobs on the keel to specimens with no trace of auriculation and with rather more numerous, smaller knobs” (p. 105). They found that “if the 30 shells are laid out graded from large few knobs and strong auricles to smaller, more numerous knobs and flat sides there is an even gradation with no breaks or sudden changes” (p. 105). They concluded that all shells “belong to the same species” (p. 105).

As part of this study, 274 *A. hians* shells were directly examined in museum and private collections in Australia, United States, Europe, South Africa and Japan. With knowledge gained from examining shells of *A. nouryi*, all shells from all sites were examined for an abrupt change in keel tubercle height or ears that had been formed or subsumed in single shells. Because inter-keel tuberculation is not expressed in argonaut shells other than *A. nouryi*, this character could not be used.

Two shell formation types. Shells of *A. hians* were found to display two clear shell formation types:

- Type 1 shell formation – few pronounced ribs, large prominent keel tubercles, formation of ears.
- Type 2 shell formation – numerous less-pronounced ribs, small and greatly reduced, keel tubercles, absence of ears.

These shell formation types are similar to those expressed in *A. nouryi* except that variation in the arch of the shell was not observed and inter-keel tuberculation was not present.

This variation had been noted by Voss and Williamson (1971) who stated: “The knobs on the keel are very large and

prominent in the first half of the shell and may remain large on the last half or may become considerably smaller” (p. 105).

Two shells are presented as examples:

- A shell from the Philippines (79.6 mm ShL [P], BMNH unreg., “Cuming, i.”) (fig. 23). This shell displays a clear shift from Type 1 to Type 2 shell formation indicated by a reduction in the size and spacing of the keel tubercles, a reduction in the ratio of ribs to keel tubercles from approximately 1.5:1 to 1:1 and ears subsumed.
- A shell from the North West Shelf, Western Australia (53.0 mm ShL, WAM S31510) (fig. 24). This shell displays a shift from Type 1 to Type 2 shell formation. This transition occurred when the shell was at a smaller size and hence the ears are less developed. The resultant aperture shape (fig. 24c) is extremely similar to that observed in Type 2 *A. nouryi* shells; see fig. 5c, ii for comparison.

Variation also occurs between the opposing faces of individual shells, further highlighting the plasticity of shell characters in this species. A single shell is presented here as an example:

- A shell from Madagascar (60.8 mm ShL, NMV F164734, “Madagascar”) displays a large ear on the right side only; the left side is earless (fig. 25).

The *A. hians/boettgeri* complex. Small, earless *A. hians* shells have regularly been attributed to the species *A. boettgeri* Maltzan, 1881 (fig. 22b, c). Smith (1887) outlined the diagnostic characters of *A. boettgeri*: “The distinguishing features of this species are the numerous ribs and tubercles, the total absence of auricular expansions at the sides, its constantly small size, and the fine granulation (a feature not remarked upon by Maltzan), which more or less covers the whole surface, producing a dull non-glossy appearance” (p. 409). Berry (1914) similarly noted that the shell of *A. boettgeri* “seems unique in its small size, compact coil, and the circumstance that the auricular expansion at the sides of the aperture, so frequently developed in other species of the genus, are here notable only for their entire absence” (p. 280). Robson (1932) added “the almost invariable absence of colouring on the carinal knobs” to the distinguishing characters of *A. boettgeri* (p. 197). While Smith (1887) concludes that “the shell of this species must not be confounded with young stages of *A. hians*; the more numerous ribs and tubercles and the rougher granular surface will separate it” (p. 410). Unfortunately, this dichotomy is not so straightforward.

Of the 274 *A. hians* shells examined, 41 can be attributed to *A. boettgeri* based on the above description. While it is possible to select a subset of shells possessing these characteristics, which in isolation appear distinct, examination of the entire range of material quickly dissolves the parameters on which this subset is based. All features mentioned above are variable in *A. hians*: ribs and keel tubercles can be numerous or scarce, pronounced or reduced, consistent across the shell or variable; ears can be present or absent, produced or subsumed, expressed on one side of the shell or both; the shell surface can be granular or smooth, pigmented or white. Two shells, displaying variation across the growth of the shell, are presented as examples:

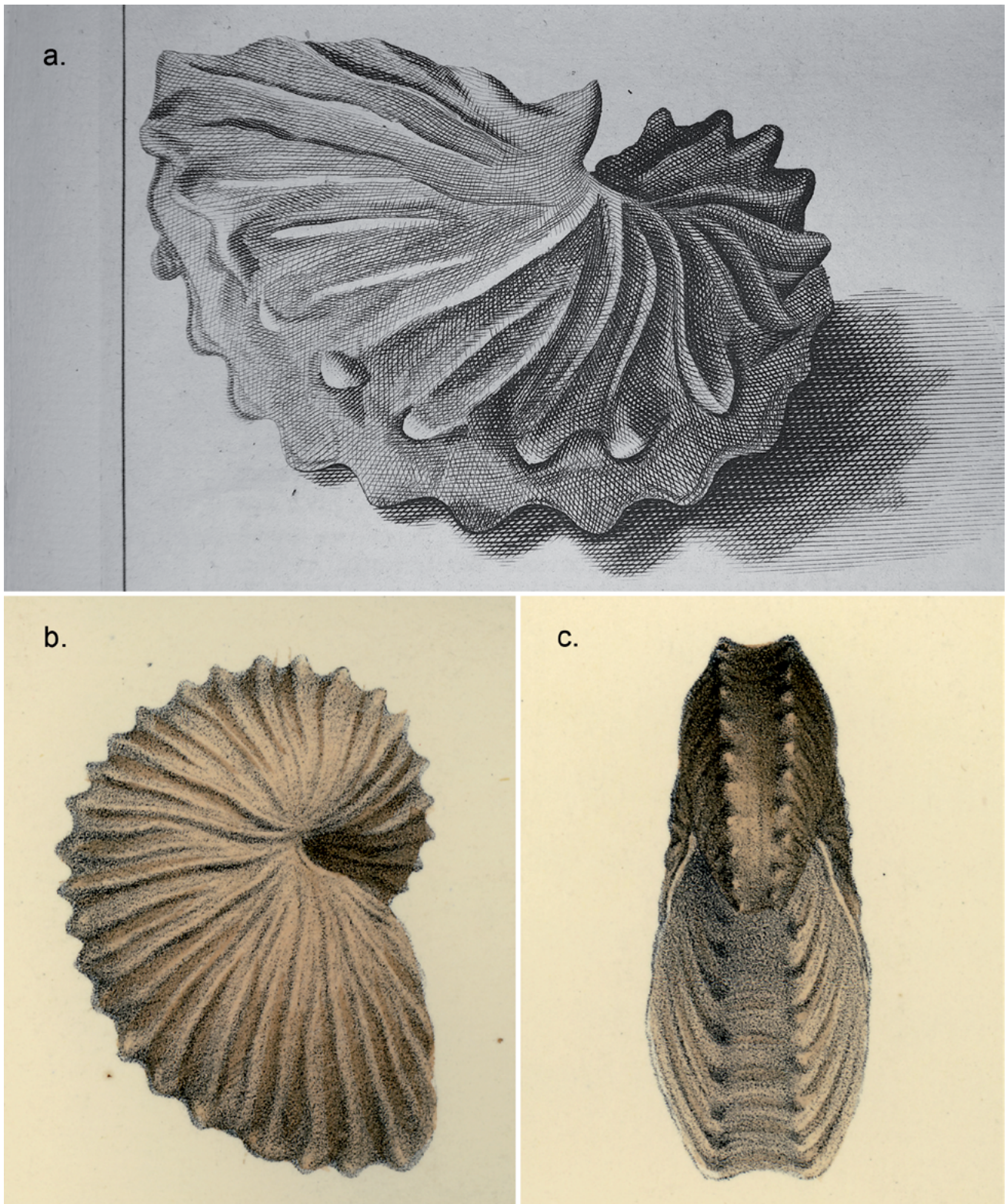


Figure 22. Reproduced illustrations referenced in the descriptions of *Argonauta hians* [Lightfoot], 1786 and *A. boettgeri* Maltzan, 1882: a, illustration of *A. hians* [Lightfoot], 1786, designated as a lectotype by Moolenbeek (2008), Rumphius, 1705: pl. 18, fig. B; b–c, illustrations of *A. boettgeri* Maltzan, 1881, featured in the original publication, Maltzan, 1881: 163, pl. 6 fig. 7; b, right lateral view; c, anterior aperture view.

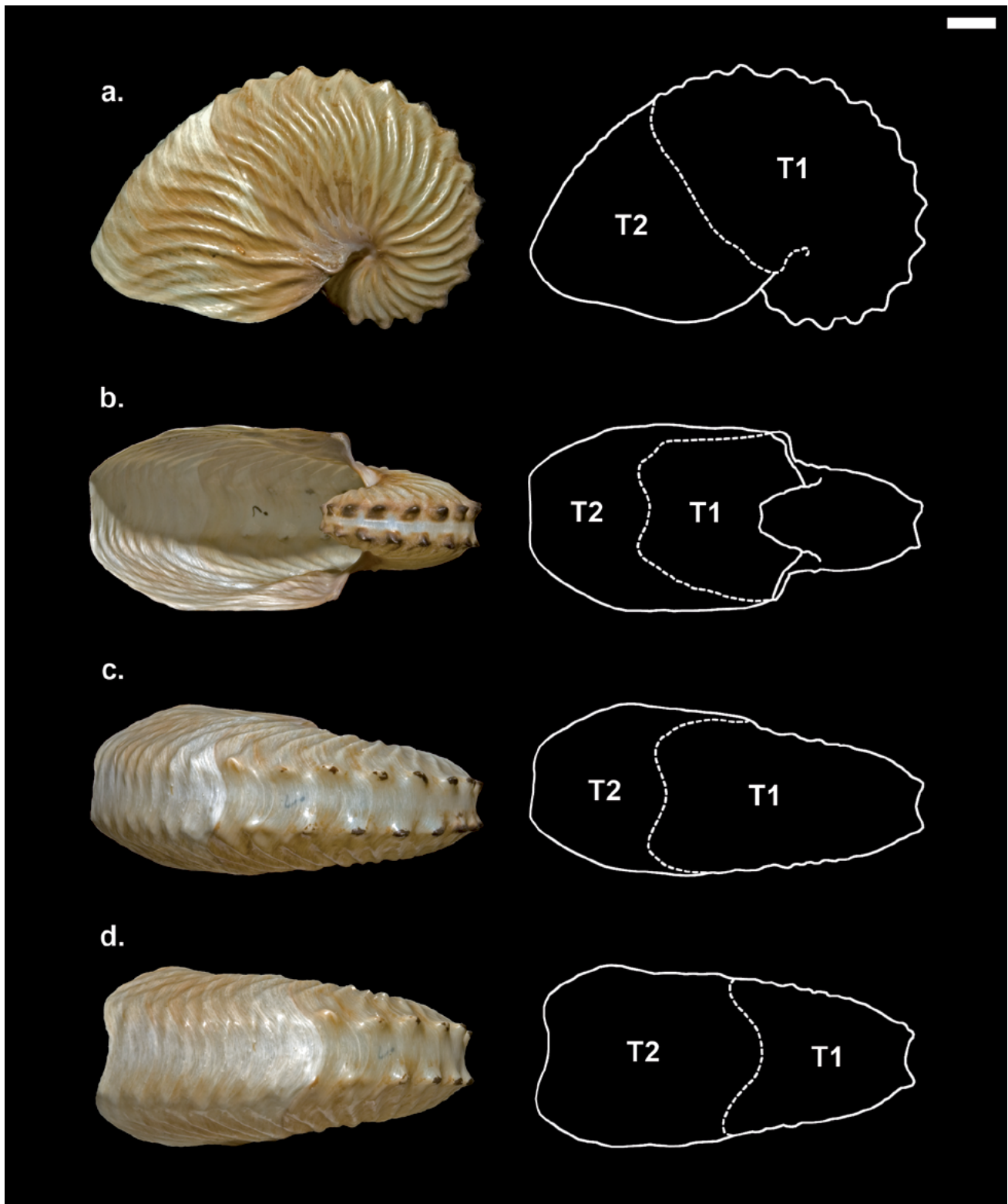


Figure 23. *Argonauta hians* shell from the Philippines: a–d, four perspectives of an *A. hians* shell from the Philippines (79.6 mm shell length [P], BMNH unreg., “Cuming, i.”) displaying a clear shift from Type 1 shell formation (T1) to Type 2 shell formation (T2) indicated by a reduction in the size and spacing of the keel tubercles, a reduction in the ratio of ribs to keel tubercles (from approximately 1.5:1 to 1:1) and subsumed ears; a, right lateral view; b, anterior aperture view; c, posterior keel view; d, ventro-posterior keel view. Scale bar = 1 cm.

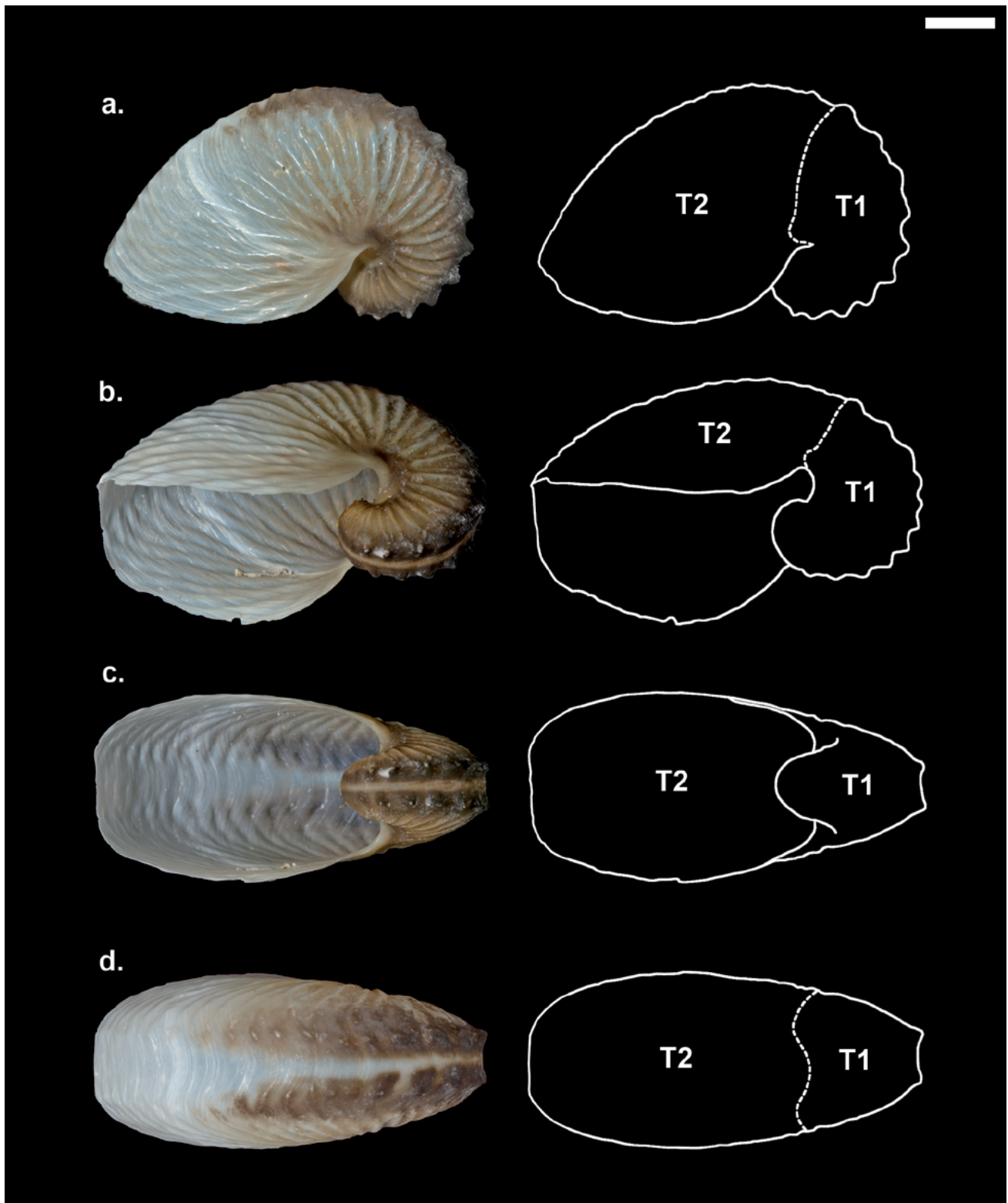


Figure 24. *Argonauta hians* shell from the North West Shelf, Western Australia: a–d, four perspectives of an *A. hians* shell from the North West Shelf, Western Australia (53.0 mm shell length, WAM S31510) displaying a clear shift from Type 1 shell formation (T1) to Type 2 formation (T2) indicated by a reduction in the size and spacing of the keel tubercles and a reduction in the ratio of ribs to keel tubercles (from approximately 1.5:1 to 1:1); a, right lateral view; b, oblique right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

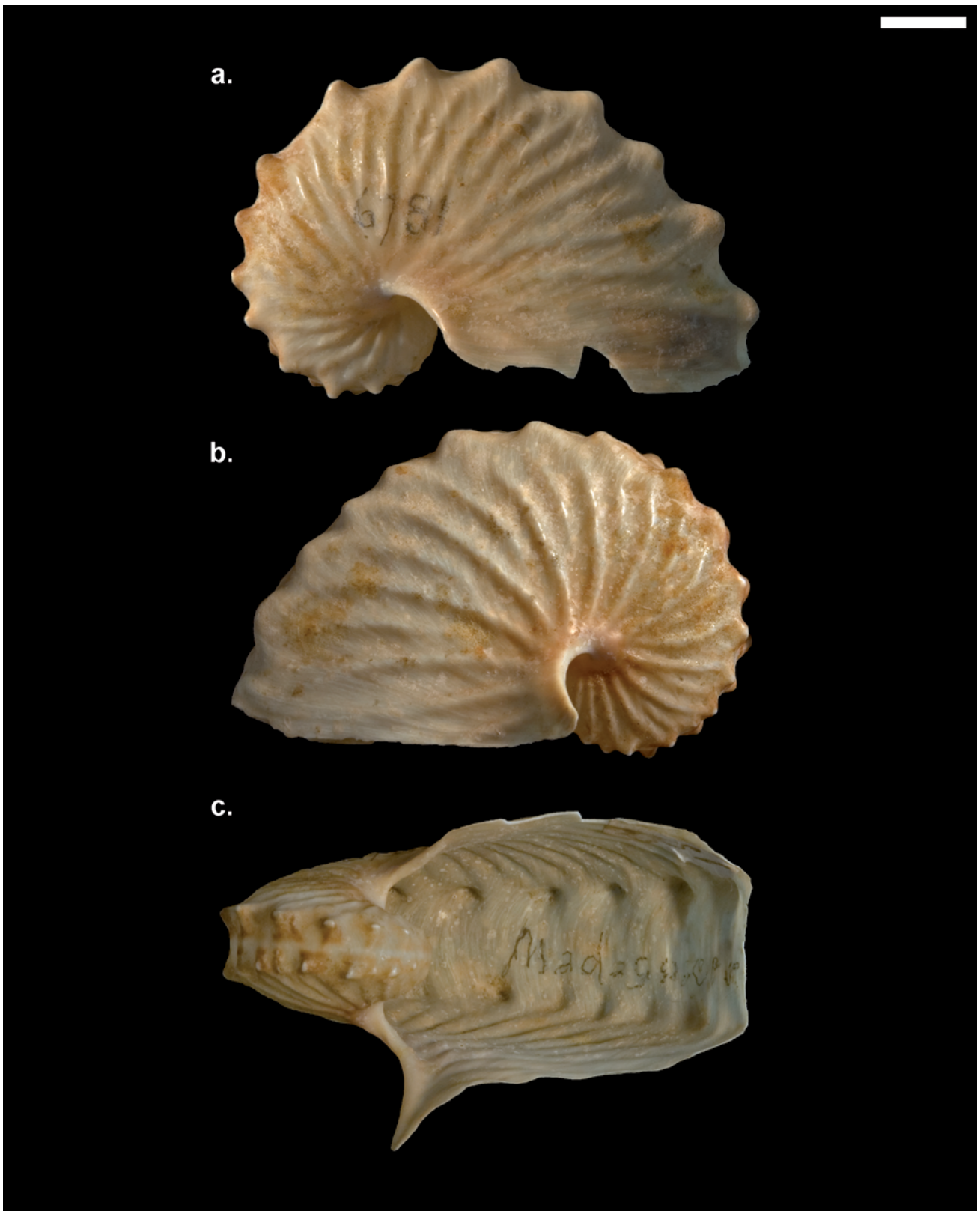


Figure 25. Single eared *Argonauta hians* shell from Madagascar: a–c, three perspectives of a single eared *A. hians* shell from Madagascar (60.8 mm shell length, NMV F164734); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

- A shell from the British Museum (76.1 mm ShL [P], BMNH unreg., locality unknown, “B698, t.”; fig. 26). This shell displays an aperture shape and axial region consistent with the original description of *A. boettgeri* (fig. 22b, c) yet defies the description of *A. boettgeri* by showing signs of possessing ears at an earlier growth stage. While the ears have been subsumed with a shift from Type 1 to Type 2 shell formation, only the keel tubercles on the right side show a reduction in size (fig. 26b); the left keel tubercles have remained large (fig. 26a).
- A shell from Museums Victoria (25.0 mm ShL [P], NMV F164767, locality unknown; fig. 27). This shell would historically have been attributed to *A. boettgeri* due to its small size and distinctive earless aperture. This shell displays a dramatic change in keel tubercle size and spacing associated with a shift from Type 2 to Type 1 shell formation, thus highlighting the plasticity of these characters.

In the absence of any consistent and definable diagnostic shell characters (in combination with a lack of diagnostic morphological characters or distinct distributions; see Finn, 2013), no evidence exists to justify maintaining *A. boettgeri* as a separate species. Consequently *A. boettgeri* Maltzan, 1881, is treated here as a synonym of *A. hians* [Lightfoot], 1786.

Insight from whole animals. As described in the Materials and Methods section above, a single specimen lot of 73 female *A. hians*, most with intact shells, exist in the collections of the

Western Australian Museum and Museums Victoria. On initial examination, it was found that the lot included submature, mature and spawned (i.e. females with eggs attached to the central axis of the shell) individuals. The shells of the spawned females tended to show a shift to Type 2 shell production in the last components of the shells (all other shells were composed entirely of Type 1 shell production). This led to the consideration that shell shape and transformation may be triggered by changes in reproductive stage or condition.

To understand the underlying cause of a change in shell formation type at the point of egg laying, a subset of 33 intact and measurable individuals were selected and fully measured. The subset included submature, mature and spawned individuals, with a size range of 13–27 mm DML and 21–36 mm ShL. Two larger females, also collected over the North West Shelf, were incorporated into the analysis to expand the size range (QM Mo77789: 39.9 mm DML and 51.8 mm ShL; 28.7 mm DML and 38.9 mm ShL).

Changes in shell morphometrics relative to animal size. Shell dimensions were plotted against DML to determine if the size of the shell relative to the size of the female changes between submature, mature and spawned individuals. Scatterplots against DML were generated for ShL, ShB, ApL, ApW, KW and EW. The scatter plots indicate a linear relationship between shell dimensions and animal size, with linear regressions returning coefficient of determination values (i.e. R^2 values) between 0.72 and 0.90 (see Table 1). No discontinuities were observed between the three maturity stages.

Table 1. Linear regression equations for scatter plots of shell dimensions (y) against dorsal mantle length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R^2 values) presented.

y	x	equation	R^2
Shell length (ShL)	Dorsal mantle length (DML)	$y = 1.0936x + 7.9242$	0.8980
Shell breadth (ShB)	Dorsal mantle length (DML)	$y = 0.8705x + 0.6315$	0.8705
Aperture length (ApL)	Dorsal mantle length (DML)	$y = 0.8889x + 3.4049$	0.8882
Aperture width (ApW)	Dorsal mantle length (DML)	$y = 0.3875x + 9.3432$	0.7697
Keel width (KW)	Dorsal mantle length (DML)	$y = 0.1839x + 4.1154$	0.7244
Ear width (EW)	Dorsal mantle length (DML)	$y = 0.3360x + 11.1327$	0.7268

Table 2. Linear regression equations for scatter plots of female argonaut dimensions (y) against dorsal mantle length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R^2 values) presented.

y	x	equation	R^2
Mantle width (MW)	Dorsal mantle length (DML)	$y = 0.4166x + 6.6124$	0.8156
Head width (HW)	Dorsal mantle length (DML)	$y = 0.4594x + 4.5374$	0.8609
Funnel length (FL)	Dorsal mantle length (DML)	$y = 0.4905x + 3.2751$	0.7559
Arm length 2 (AL2)	Dorsal mantle length (DML)	$y = 1.8016x - 1.5714$	0.8773
Arm length 3 (AL3)	Dorsal mantle length (DML)	$y = 1.1550x + 5.5401$	0.8169
Arm length 4 (AL4)	Dorsal mantle length (DML)	$y = 0.8482x + 5.8121$	0.8292

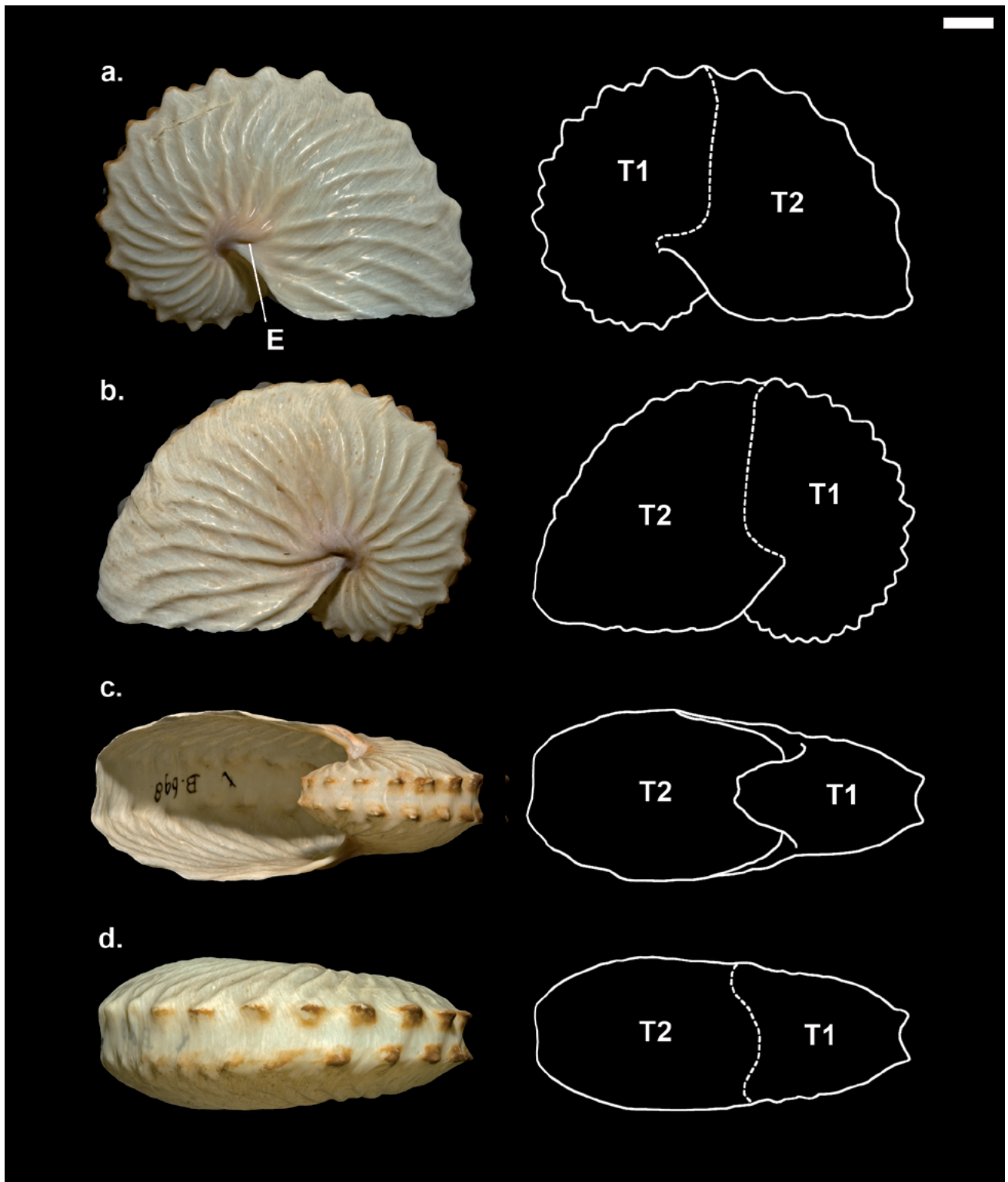


Figure 26. *Argonauta hians* shell from the British Museum: a–d, four perspectives of an *A. hians* shell from the British Museum (76.1 mm shell length [P], BMNH unreg., locality unknown, “B698, t.”) which, while displaying an aperture shape and axial region consistent with the original description of *A. boettgeri* (fig. 22B, C), shows signs of possessing ears (E) at an earlier stage of growth; a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. A shift from Type 1 shell formation (T1) to Type 2 shell formation (T2) is expressed by ears subsumed and a reduction in keel tubercle size on the right side only. Scale bar = 1 cm.

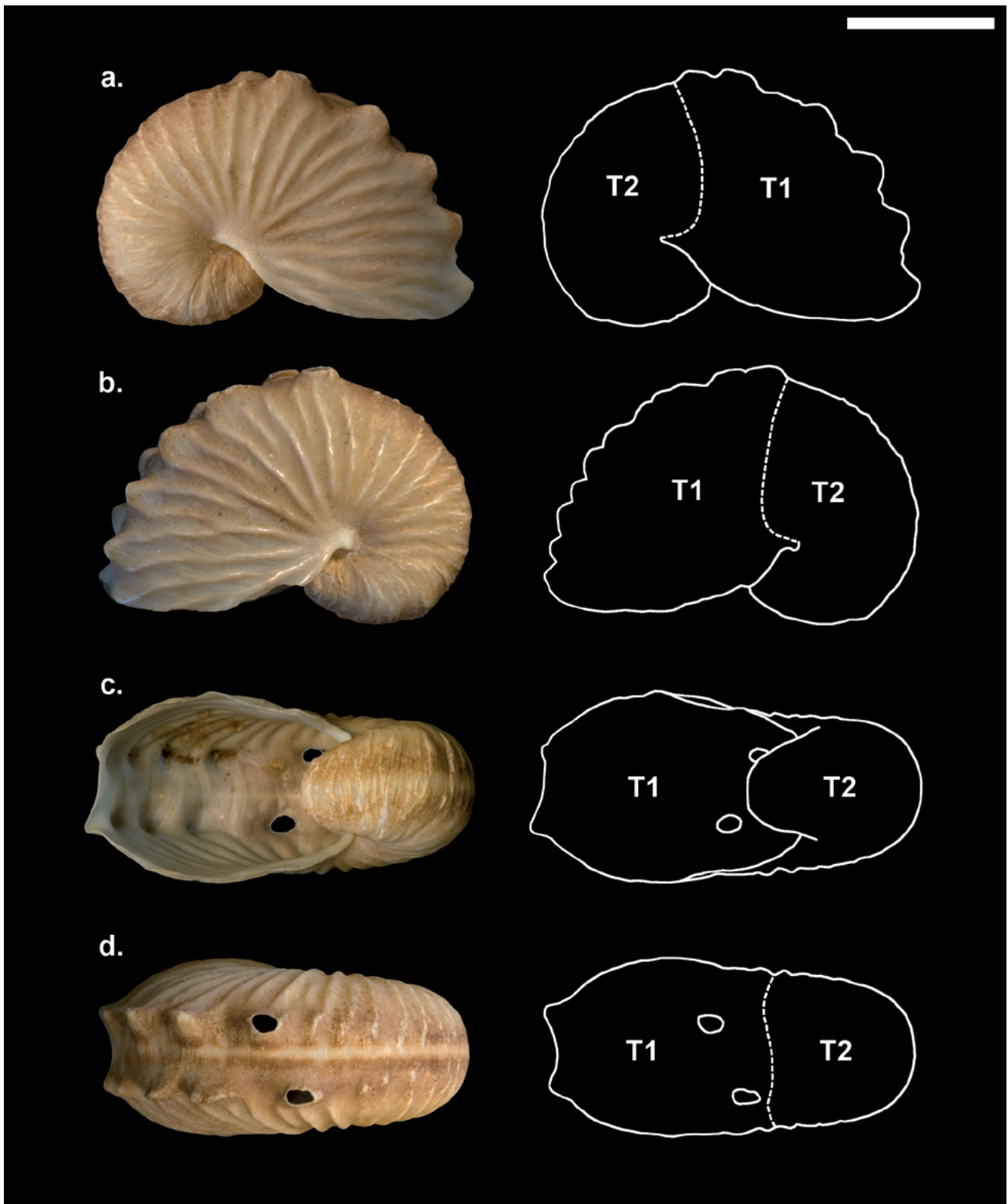


Figure 27. Shell consistent with description of *Argonauta boettgeri* from Museums Victoria: a–d, four perspectives of a shell consistent with *A. boettgeri* (treated here as a synonym of *A. hians* [Lightfoot], 1786) from Museums Victoria (25.0 mm shell length, NMV F164767) displaying an increase in keel tubercle size consistent with a shift from Type 2 shell formation (T2) to Type 1 shell formation (T1); a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

Table 3. Linear regression equations for scatter plots of shell dimensions (y) against shell length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R² values) presented.

y	x	equation	R ²
Shell breadth (ShB)	Shell length (ShL)	$y = 0.7676x - 4.8377$	0.9015
Aperture length (ApL)	Shell length (ShL)	$y = 0.8013x - 2.6968$	0.9613
Aperture width (ApW)	Shell length (ShL)	$y = 0.3369x + 7.0488$	0.7752
Keel width (KW)	Shell length (ShL)	$y = 0.1701x + 2.7255$	0.8254
Ear width (EW)	Shell length (ShL)	$y = 0.2936x + 9.1011$	0.7391

Ontogenetic changes in animal morphology. Dimensions and characters of the female argonauts were plotted against DML to determine if the relative proportions of the female changes between submature, mature and spawned individuals. Scatterplots against DML were generated for MW, HW, FL and AL. The scatter plots indicate a linear relationship between animal dimensions, with linear regressions returning coefficient of determination values (i.e. R² values) between 0.76 and 0.88 (see Table 2). No discontinuities were observed between the three maturity stages.

Ontogenetic changes in shell morphometrics. Shell dimensions and characters were plotted against ShL to determine if relative shell proportions change between submature, mature and spawned females. Scatterplots against ShL were generated for ShB, ApL, ApW, KW and EW. The scatter plots indicate a linear relationship between shell dimensions and characters, with linear regressions returning coefficient of determination values (i.e. R² values) between 0.74 and 0.96 (see Table 3). No discontinuities were observed between the three maturity stages.

The scatter plots provided no evidence of a change in relative shell and animal proportions between submature, mature and spawned individuals. If the examined characters underwent dramatic transformation with changes in state of maturity, it was expected that discontinuities would be observed in the plotted data. It is apparent that the visual change in shell form observed across this lot was not reflected in the relative measurements of the individuals measured.

***Argonauta nodosus* [Lightfoot], 1786; the *A. nodosus/tuberculatus* complex**

The original description of *A. nodosus* [Lightfoot], 1786, refers to a single image in Rumphius (1705): plate 18, figure 1 (fig. 28a), designated as a lectotype by Moolenbeek (2008) in the absence of type material. Shells of *A. nodosus* can be recognised by the presence of lateral ribs composed of separate tubercles.

Two types of *A. nodosus* shells exist in collections: a finer shell with more ribs and small rib tuberculations (fig. 29a), and a coarser shell with fewer ribs and larger rib tuberculations (fig. 29b).

This variation has previously been used as justification for splitting *A. nodosus* into two species. Kirk (1885), in recognising the two forms, generated a new species name for the fine tuberculated and earless form (*A. gracilis*) to separate it from the coarse tuberculated and eared form (known to Kirk, 1885, as *A.*

tuberculata Shaw). Robson (1932) recognised the two shell types as varieties, not separate species, stating: “Though the shell of this species is clearly distinguished from its fellows by the rough tuberculations, there are evidently two well marked varieties – one with very large carinal knobs and coarse sculpture, the other with low knobs and fine sculpture” (p. 200). Dell (1952) called this the “*nodosa-tuberculata* complex”² and described it as follows: “Group 1. The shell is eared laterally and the tuberculations on the ribs are comparatively large – this is what has been called *nodosa*. Group 2. The edge of the lip comes off the previous whorl in an even curve without trace of an ‘ear’. The tuberculations are much finer and more numerous than in Group 1 – *tuberculata*” (p. 54). Dell (1952) considered both forms to belong to a single species.

While both shell varieties are common, individual shells displaying an obvious shift between fine and coarse shell formation are extremely rare. A single shell from Moreton Bay, Queensland (109.1 mm ShL, QM Mo14232) displays a transition from fine shell formation to coarse shell formation at a point of previous damage (fig. 30). While the later component of the shell possesses ears, it is not clear whether the earlier component was eared or earless. No obvious changes were noted in shell thickness, curvature of the keel or relative heights of sequential keel tubercles.

Examination of a large number of *A. nodosus* shells found no examples displaying a marked change in keel tubercle height or ears that had been formed or subsumed. While eared and earless forms exist, transition between the two types appeared more gradual than the sudden transformation documented in smaller species. A shell in the British Museum (109.0 mm ShL [P], BMNH unreg., locality unknown, “B395, e.”) displays an ear on only one side, clearly demonstrating the plasticity of this character in this species (fig. 31).

² Following Finn (2013) it is necessary to correct the original spelling of *A. nodosa* to *A. nodosus*. In accordance with the *International Code of Zoological Nomenclature*, Article 34.2 “the ending of a Latin or latinized adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined [Art. 31.2]; if the gender ending is incorrect it must be changed accordingly (the author and date of the name remain unchanged)” (I.C.Z.N., 1999). As *Argonauta* is masculine “from the final noun *nauta* (a sailor)” (I.C.Z.N., 1999, p. 34) the species-group name must be changed from the feminine *nodosa* (-a feminine) to the masculine *nodosus* (-us masculine).

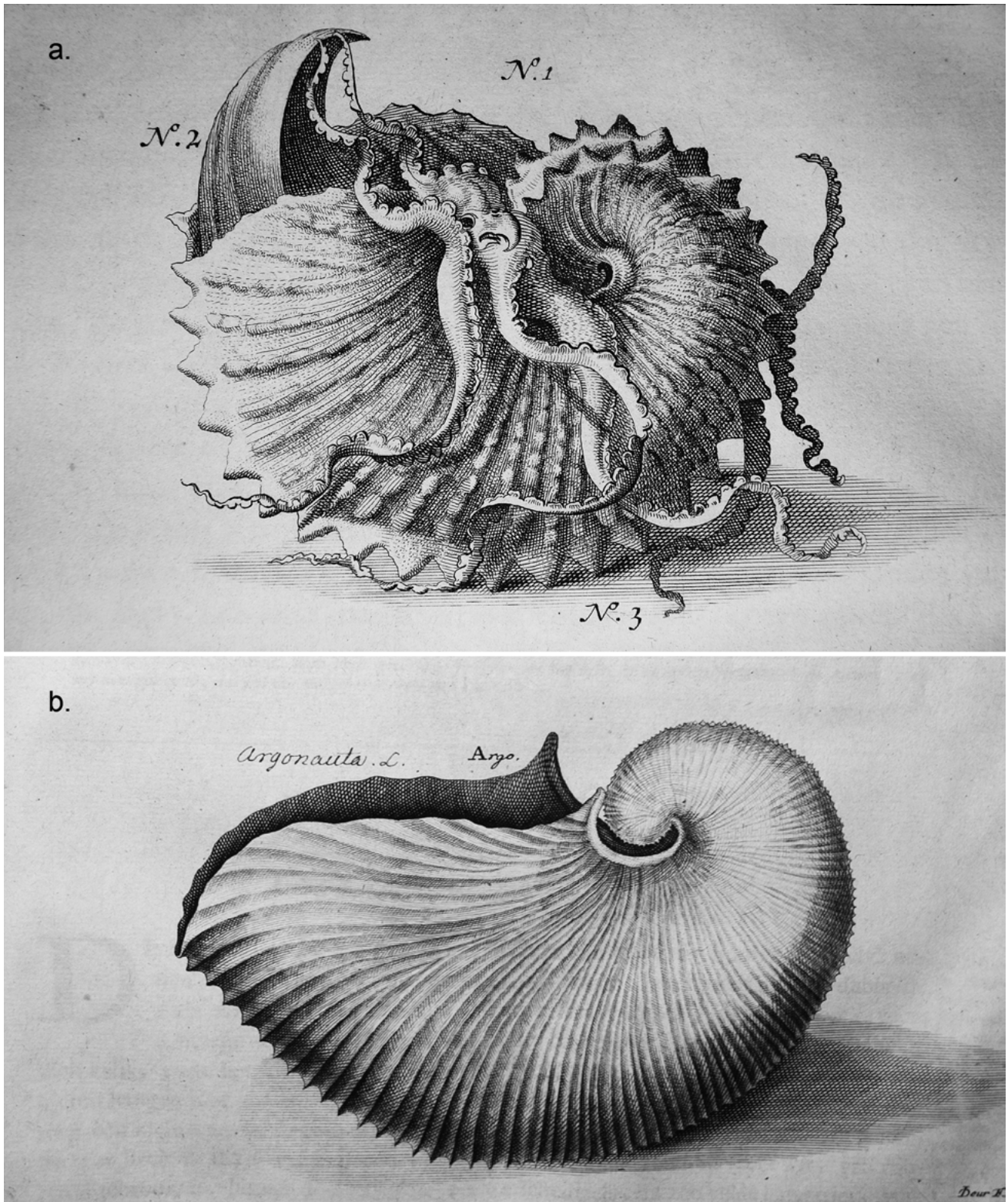


Figure 28. Reproduced illustrations referenced in the descriptions of *Argonauta nodosus* [Lightfoot], 1786 and *A. argo* Linnaeus, 1758: a, illustration of *A. nodosus* [Lightfoot], 1786, designated as a lectotype by Moolenbeek (2008), Rumphius 1705, pl. 18, fig. 1; b, illustration of *A. argo* Linnaeus, 1758, considered a paralectotype following the designation of a lectotype by Moolenbeek (2008), Rumphius 1705, pl. 18, fig. A.

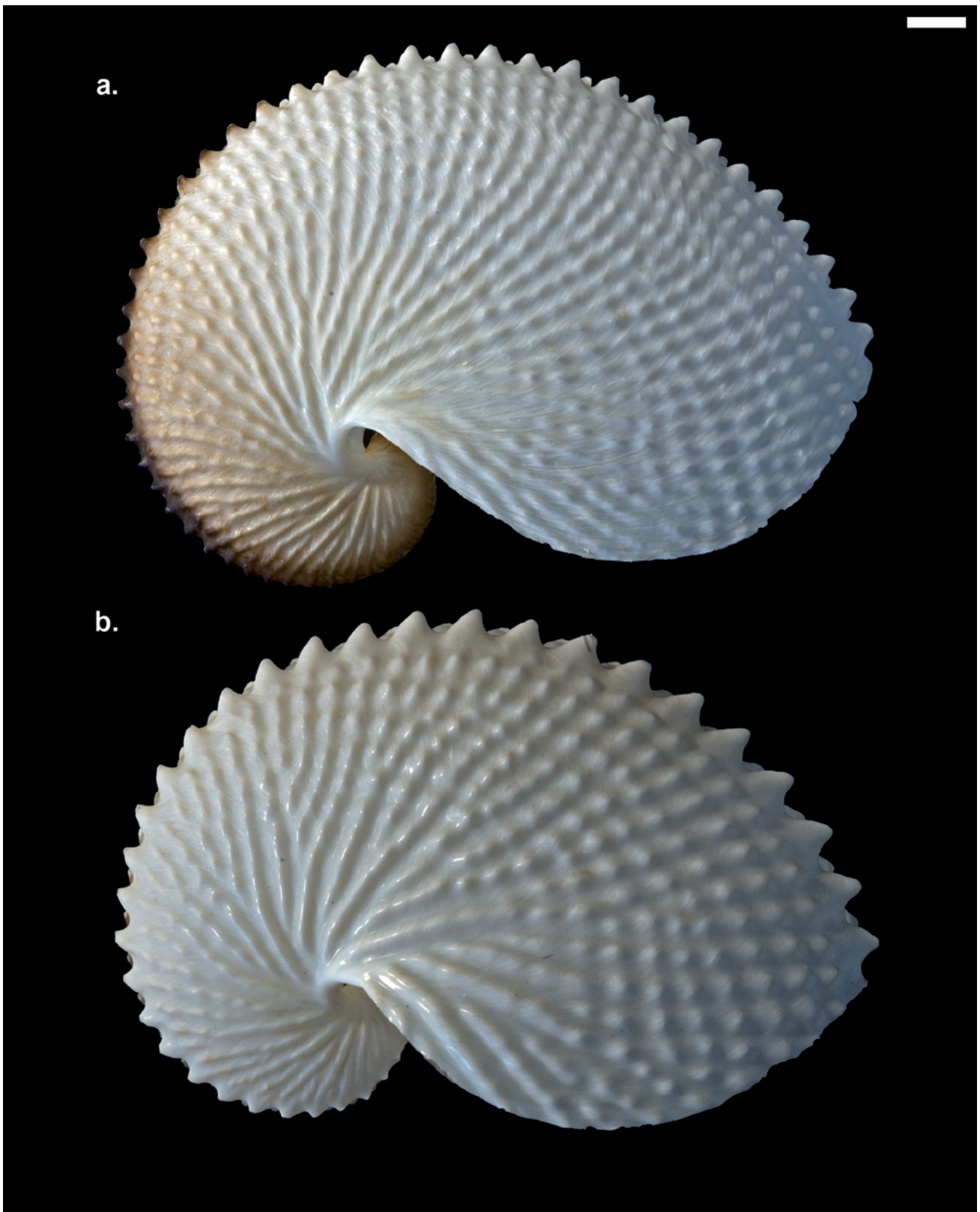


Figure 29. Coarse and fine *Argonauta nodosus* shells: a, fine *A. nodosus* shell from Mayor Is., Bay of Plenty, New Zealand (127.2 mm shell length, NMV F164784); b, Coarse *A. nodosus* shell from the Indo Pacific (127.3 mm shell length, NMV F164774). Scale bar = 1 cm.

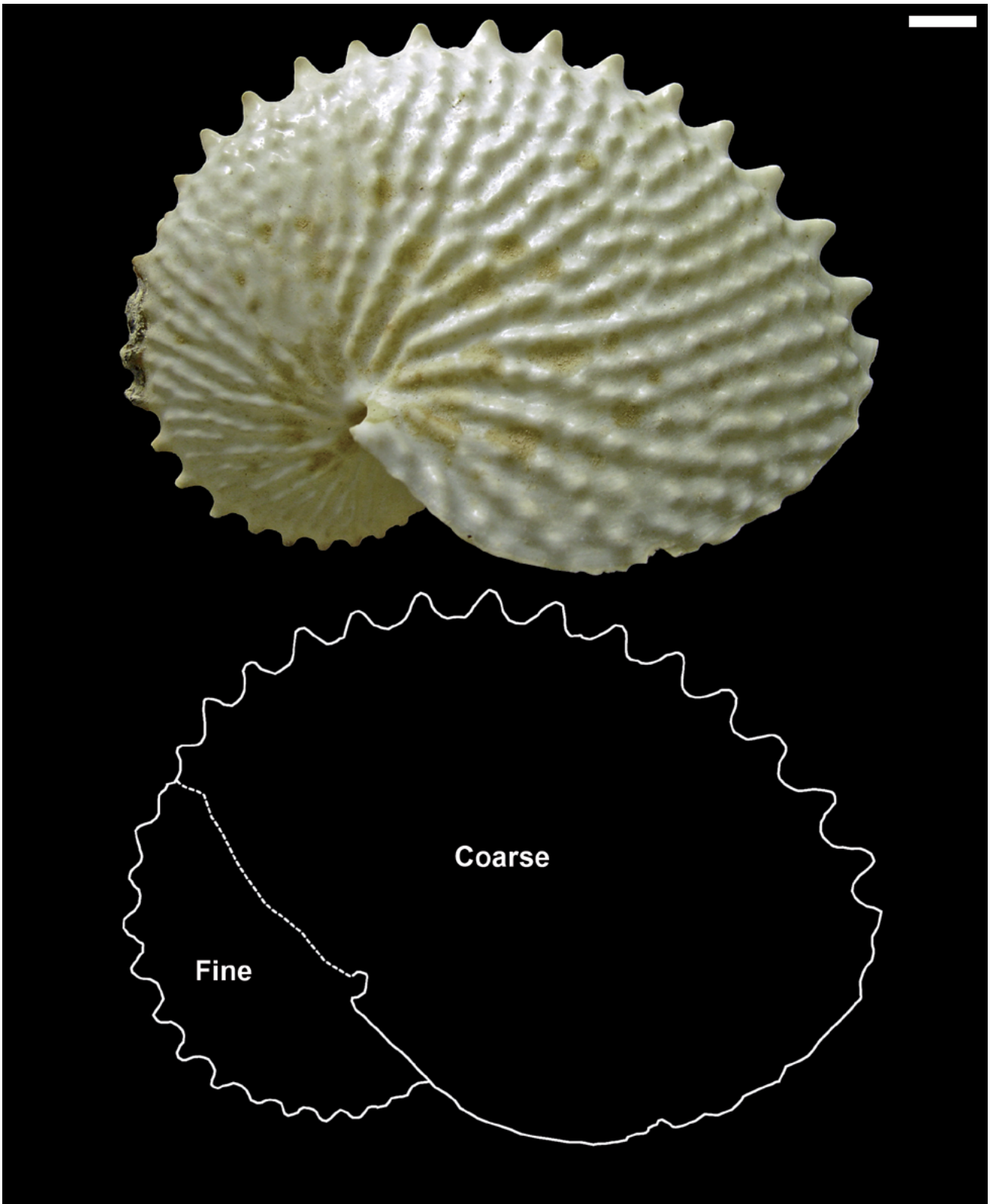


Figure 30. Repaired *Argonauta nodosus* shell from Moreton Bay, Queensland. Left lateral view of repaired *A. nodosus* shell from Moreton Bay, Queensland (109.1 mm shell length, QM Mo14232) showing a transition from fine shell formation (Fine) to coarse shell formation (Coarse) at point of previous damage. Scale bar = 1 cm.

Argonauta argo Linnaeus, 1758

An image referenced in the original description of *A. argo* Linnaeus, 1758, is considered a paralectotype, with designation of a lectotype by Moolenbeek (2008); Rumphius, (1705) plate 18 figure A (fig. 28b). Shells of *A. argo* can be recognised by an extremely narrow keel of consistent width. The keel tubercles are paired and the lateral ribs are continuous (i.e. they are not broken into separate tubercles).

Shells of *A. argo* are extremely consistent in dimensions and sculpturing. The area that has caused the most confusion for naturalists defining the species has been the aperture edge. *A. argo* can display huge variation in the shape of the aperture edge near the axis. Note the variation in the aperture edge of the two shells presented in fig. 32. Unlike ear formation, this variation occurs on the edge of the lateral wall parallel with the longitudinal axis of the shell; it is not a lateral extension. The expression of the lateral ribs can vary slightly from fine to coarse, suggesting the presence of two varieties (fig. 32). Transition between fine and coarse shell formation on a single shell is extremely rare. An illustrated shell from Monterey, California (81.9 mm ShL, USNM 61374) displays a shift from finer to coarser shell formation at the point of earlier damage (fig. 33). Small *A. argo* shells can also display laterally protruding ears. A shell from Venezuela (51.4 mm ShL, USNM 122208) highlights the plasticity of this character, displaying an ear on only the right side (fig. 34). The varied size and shape of the keel tubercles on the opposing sides of this shell demonstrate the range of variability of these structures in this species.

Discussion

Among molluscs, the shells of small argonaut species (in particular, *A. nouryi*) display an unprecedented level of variability. The extreme forms are so different that it initially seems incomprehensible that they could be produced by the same argonaut species. Given this apparent disparity, it is necessary to emphasise that argonaut shells are fundamentally different in nature from the true molluscan shells of non-cephalopod molluscs; they are produced by different structures, for different reasons and have a different construction.

Shell material laid down by females of small argonaut species (*A. nouryi* and *A. hians*) can take one of two distinct morphologies. Firstly, the shell can be heavy and thick walled with prominent sculpture (Type 1 shell formation). The large corrugations of the lateral walls are displayed as distinct robust lateral ribs. The thickened keel is defined by two rows of large and distinct keel tubercles. The axis of the shell projects laterally to form large ears, providing support to the lateral walls. In the second form, the shell can be lightweight and thin walled, with greatly reduced sculpture (Type 2 shell formation). The corrugations of the lateral walls are downgraded to fine lateral ribs. The convex keel is undefined, with the keel tubercles diminished to slight projections of the lateral rib extremities. The axis of the shell is rolled ventrally to join the aperture edge without lateral projection (i.e. earless).

The shell morphology expressed by a growing female argonaut does not follow a predetermined order. Shells of female *A. nouryi* demonstrate that females can switch between

the two shell formation types at least three times during production of a single shell. The initial shell formation type is variable (it can be Type 1 or Type 2), as is the portion of shell laid down before switching to another shell formation type.

It is largely impossible to determine the conditions an argonaut was exposed to at the time that it switched shell formation types. The exception is the response to shell breakage. Individual shells retain evidence of earlier trauma in the form of repairs and irregularities in shell form. *A. nouryi* shells almost invariably display a shift to Type 2 shell formation following major damage. At the time of shell breakage, an argonaut would be exposed and vulnerable. As has been observed for *A. argo*, shell integrity is critical in allowing the argonaut to attain neutral buoyancy, free itself from the sea surface and undertake rapid horizontal locomotion (Finn and Norman, 2010). In the absence of shell-aided buoyancy, the female must remain in the water column by siphon-jetting alone. As such, it would be imperative for a female argonaut to rebuild her shell as quickly as possible following any damage. It is assumed that the shift to thinner walled Type 2 shell formation allows the female to rebuild her shell more rapidly, spreading the available building material (calcium carbonate) over a greater area.

The different morphologies expressed in an individual *A. nouryi* shell are therefore considered to represent periods of varied rate of shell formation. Components of a shell laid down over longer periods are believed to exhibit thicker walls and more prominent sculpture (Type 1), while rapidly produced sections display thinner walls and reduced sculpture (Type 2). The rate at which the female lays down the shell is believed to determine the gross morphology of the shell. Based on this presumption, two hypotheses are raised to explain the variable shell production rate (expressed as the variable shell formation type) evident in undamaged, unrepaired shells:

- Hypothesis 1: *Rate of shell production correlates directly with animal growth.* Three factors are believed to influence octopus growth rate: temperature, nutrition, and maturation or reproduction (see Semmens et al., 2004 for a review). While very little is known about the lives of argonauts, they are known to occur in the open ocean spanning huge geographical distributions. This wide-ranging pelagic existence has the potential to expose them to a mosaic of food availability and water temperatures. Encountering a large school of prey or pocket of warmer water may result in a period of increased growth. Additionally, reproductive investment (i.e. egg production) may slow body growth. This hypothesis suggests that these periods of varied morphological growth of the animal are reflected in the gross morphology of the shell.
- Hypothesis 2: *Rate of shell production influenced by external factors.* The shells of female argonauts, in addition to providing protection and buoyancy, primarily function as a case for external brooding of the female's eggs. Strings of eggs are suspended from the inner core of the shell. This strategy requires that the internal volume of the shell accommodate both the female argonaut and her eggs. This hypothesis proposes that the space constraints associated with commencement of egg

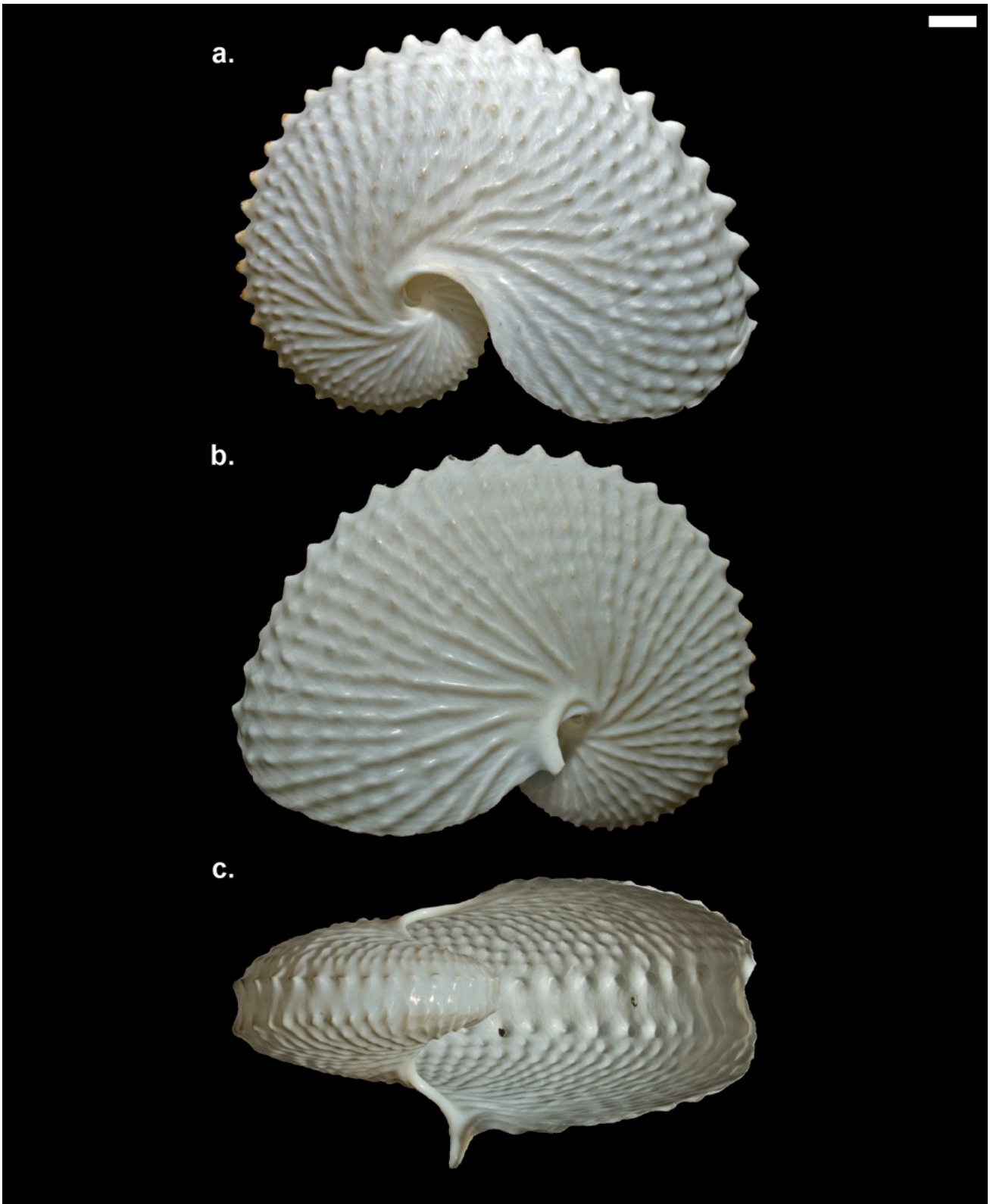


Figure 31. Single eared *Argonauta nodosus* shell from the British Museum: a–c, three perspectives of a single eared *A. nodosus* shell from the British Museum (109.0 mm shell length [P], BMNH unreg., locality unknown, “B395, e.”); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

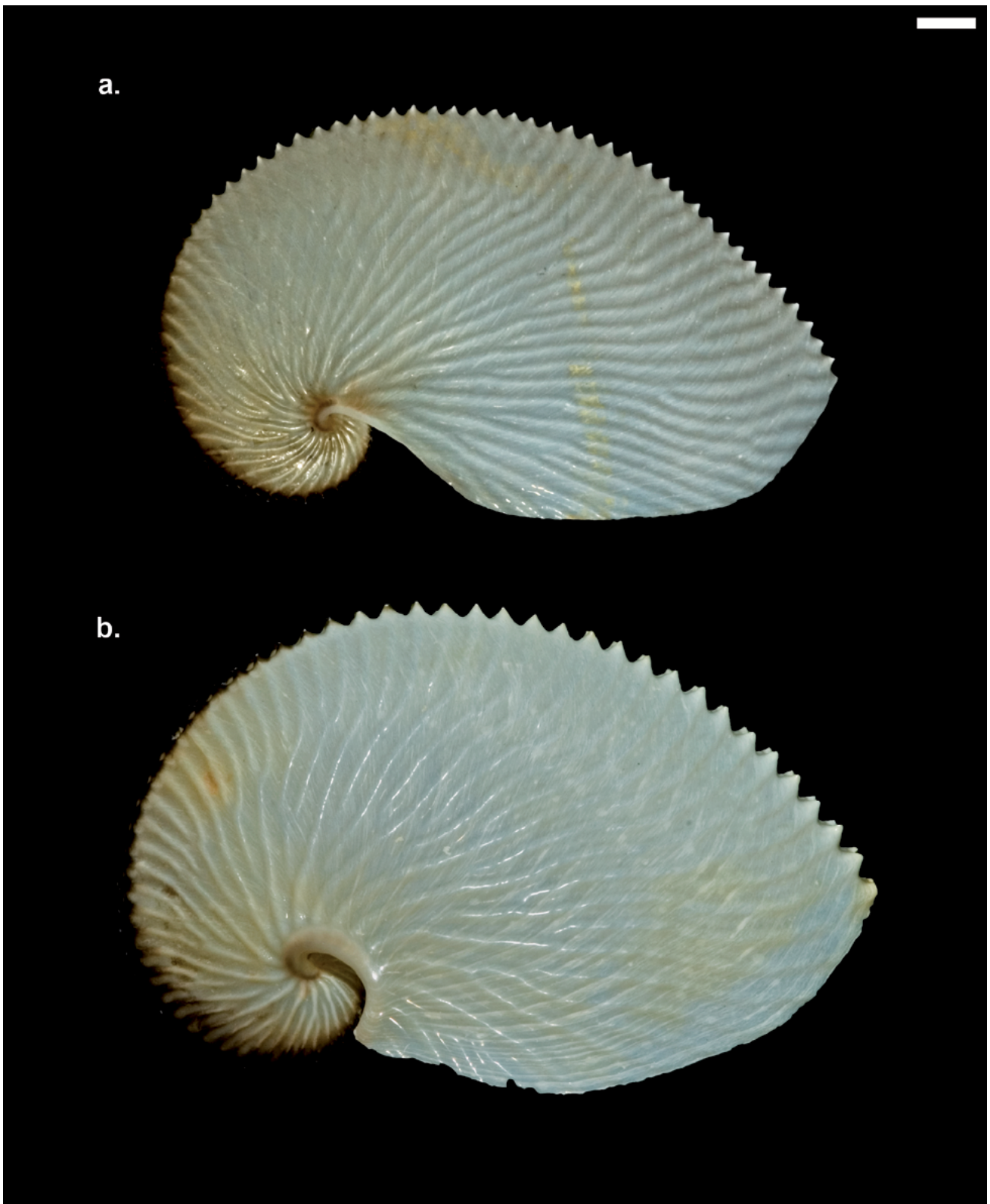


Figure 32. Coarse and fine *Argonauta argo* shells: a–b, shells of *A. argo* displaying different degree of sculpturing and variation in the aperture edge; a, fine *A. argo* shell from off San Clement Island, California (113.3 mm shell length [P], USNM 316580); b, coarse *A. argo* shell from Baja California (128.1 mm shell length [P], ANSP 404279). Scale bar = 1 cm.

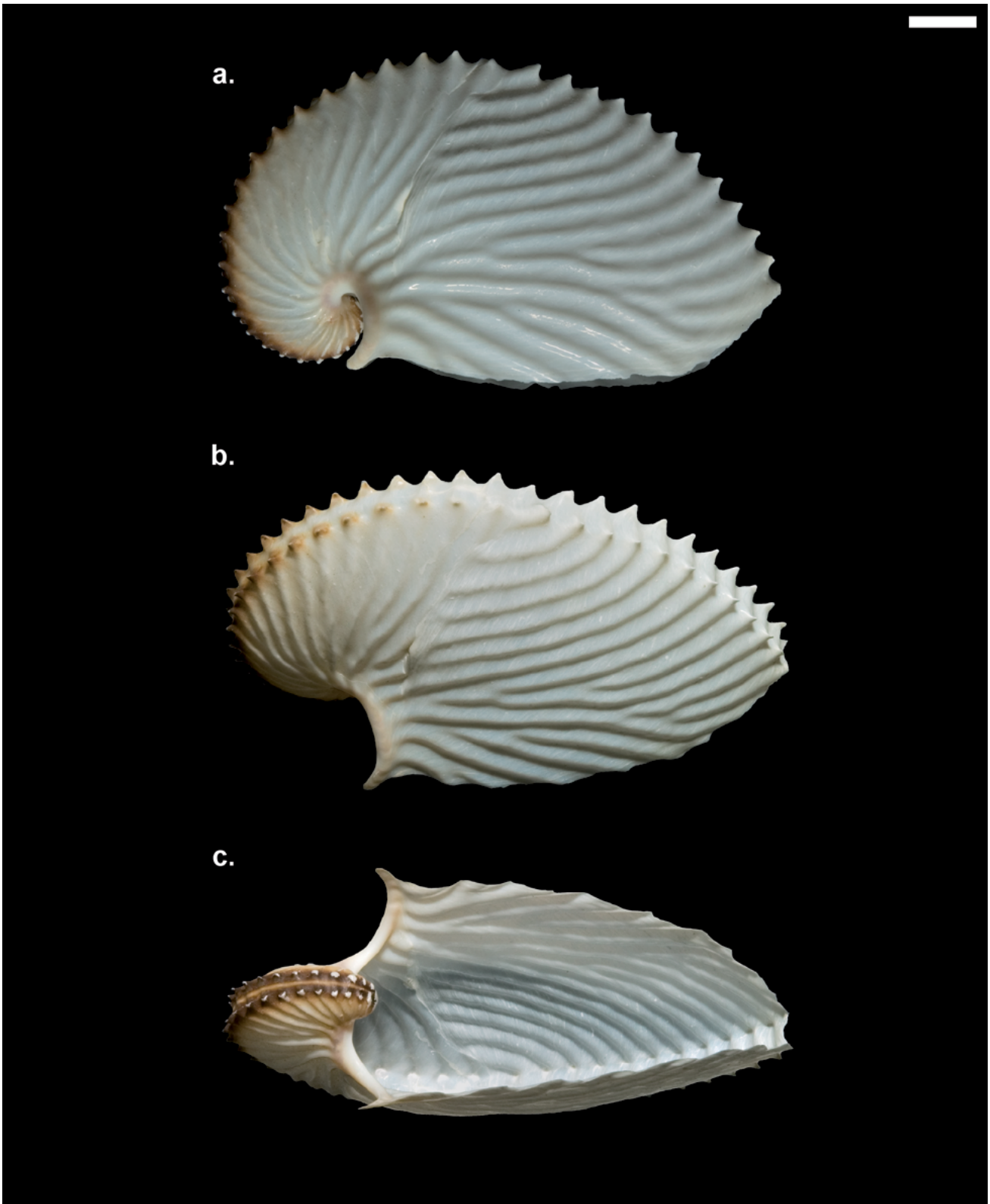


Figure 33. Repaired *Argonauta argo* shell from Monterey, California. Repaired *A. argo* shell from Monterey, California (81.9 mm shell length, USNM 61374): a, left lateral view; b, oblique left lateral view; c, oblique anterior aperture view. Note change in direction of lateral ribs along repair line. Scale bar = 1 cm.

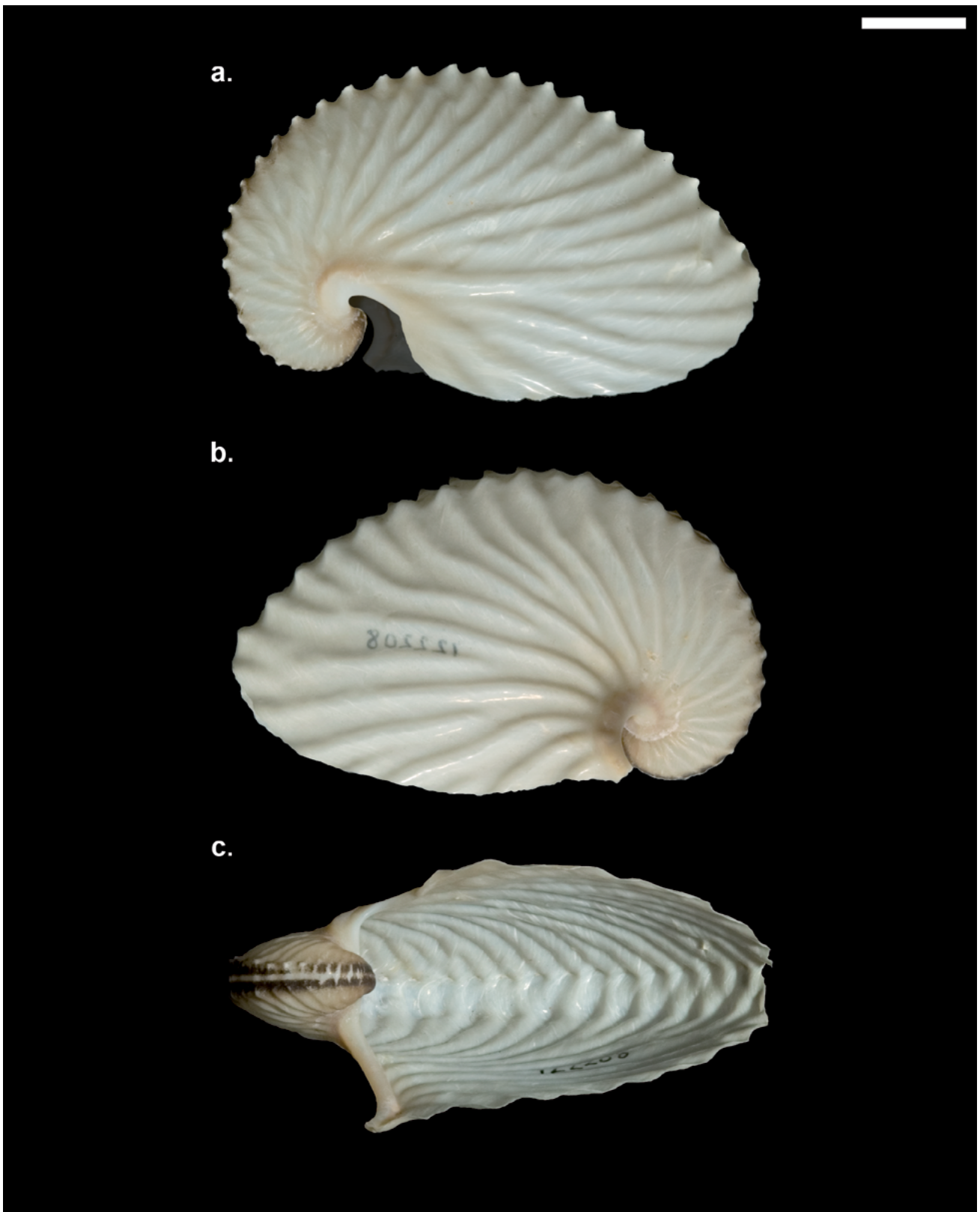


Figure 34. Single eared *Argonauta argo* shell from Venezuela, South America: a–c, three perspectives of a single eared *A. argo* shell from Venezuela (51.4 mm shell length, USNM 122208); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

spawning triggers an increase in shell production rate. The gross morphology of the shell therefore displays intermittent periods of volume constraints as a result of intermittent spawning or brooding events.

To gain insights into the relationships between features of the argonaut shell and its female occupant, focus was directed at *A. hians*. The large single lot of female *A. hians* (with accompanying shells) from Western Australia includes three classes: submature, mature (unspawned) and spawned individuals. Examination of the lot revealed that all spawned individuals (i.e. all individuals with eggs deposited within their shells) displayed a shift from Type 1 to Type 2 shell formation. No converse arrangements were observed. Based on this qualitative observation, this large sample appeared to support Hypothesis 2; the presence of spawned eggs within the shell causing a space constraint and thus triggering a shift to more expansive thin-walled shell production. Hypothesis 1 would predict slower body growth of the argonaut associated with increased reproductive investment in egg production. This would predict slower shell production and hence a shift to Type 1 formation. This was not observed. Quantitative analysis of argonauts in this lot did not provide further insight. A full range of characters of both the animals and shells were measured. Features of the shell, the female and the shell relative to the female were compared, plotted and analysed with linear regression. In all instances, scatter plots indicated linear relationships between animal and shell dimensions, with linear regressions returning high coefficients of determination values (i.e. R^2 values) with no discontinuities observed between submature, mature and spawned individuals.

Examination of shells of larger species (*A. nodosus* and *A. argo*) revealed that they are not subject to the extreme variability in shell form identified in the smaller argonaut species. While both large species display two distinct morphologies (coarse and fine forms), the two shell types are never expressed as alternations on individual shells. Rare examples of extremely damaged shells can display a shift from fine to coarse morphology, but a reversion (i.e. from coarse to fine) was never observed. Because the two shell types do not vary in shell wall thickness or amount of material used, the variation between the two shell types appears fundamentally different from that observed in smaller species. One possible explanation is that the coarser shells of larger species represent reformed shells produced by large individuals (i.e. new shells constructed to replace lost or damaged shells), while the finer shells represent the original shells that are produced as the animals grow.

In the absence of captive rearing studies and sequential collections of the same argonaut species from the same location, it is not possible to conclusively support either hypothesis. Based on limited observational evidence, it is the author's opinion that the variation observed in the shells of small argonaut species is the result of space constraints (i.e. Hypothesis 2) and independent of argonaut growth. The prime circumstantial evidence comes firstly from gross differences in shell occupation between large and small species, and secondly from the dramatic transformation or reversion boundaries on the shells of small species.

Gross differences in shell occupation. At commencement of egg laying, the shells of females of small argonaut species possess an extremely small amount of available space for egg storage. Fig. 35a shows a preserved female *A. nouryi* that had already commenced egg laying with a DML of 15.2 mm (SBMNH 64369). As can be seen from the image, the space at the top of the shell where the eggs are to be stored is extremely small. The shell has barely formed through 90 degrees. Storage of egg-strings within this shell will have a significant impact on the space available for this small female within the shell. Fig. 35b shows a female *A. hians* with a DML of 28.7 mm (QM Mo77789). Yellow eggs are clearly visible and occupy almost half of the shell volume. While the shell has developed through almost a complete rotation, the volume occupied by the eggs significantly displaces the female. With the posterior tip of the mantle firmly against the egg mass, the female is still only partially within her shell. Note the distance of the eye from the edge of the shell aperture. In the absence of eggs, female argonauts typically retract well into their shells with their eyes at the boundary of the lateral walls. Fig. 36a presents a photograph of a live female *A. hians* photographed in an aquarium (after Sukhsangchan and Nabhitabhata, 2007). With a large volume of eggs in the initial whorl of the shell, the female can only partially retract within. The aperture edge of the shell sits posteriorly to the mantle edge and a considerable distance from the female's eye.

Displacement of the female from the shell would provide a strong stimulus for rapid shell deposition, resulting in the extended flange-like form of Type 2 shells. Subsequent interruptions to egg production (or hatching) could explain a return to full occupancy of the shell and Type 1 shell formation, as demonstrated in *A. nouryi*.

The apparent space constraint observed in smaller species is not evident in larger species. Females of *A. nodosus*, observed live, appear uninfluenced by large volumes of eggs held within their shells. Fig. 36b presents a photograph of a live female *A. nodosus*. This female is positioned well within her shell; note the proximity of the female's eye to the edge of the shell aperture. Although not apparent from this photograph, the female is carrying a huge volume of eggs. Fig. 36c presents the egg strings revealed on removal of the female from her shell.

It is possible that the increased size of the shell of larger species at the commencement of egg laying enables egg and female accommodation. The shells of female *A. nodosus* are considerably more developed than those of smaller species when spawning commences; five females with ShL ranging from 54.6 to 62.1 mm (and DML ranging from 31.1 to 38.5 mm) were found to still be immature (see Finn, 2013, for details).

Immediacy of transformations and reversions. Additional qualitative support comes from the abrupt nature of shell transformations and reversions. Shells of female *A. nouryi* display obvious precise boundaries between shell formation types. It is the author's opinion that the distinct boundaries between shell formation types indicates that the causal stimulus acts instantaneously on the female. It is felt that spawning of eggs would have an immediate effect, requiring the female to abruptly change the way the shell material is laid

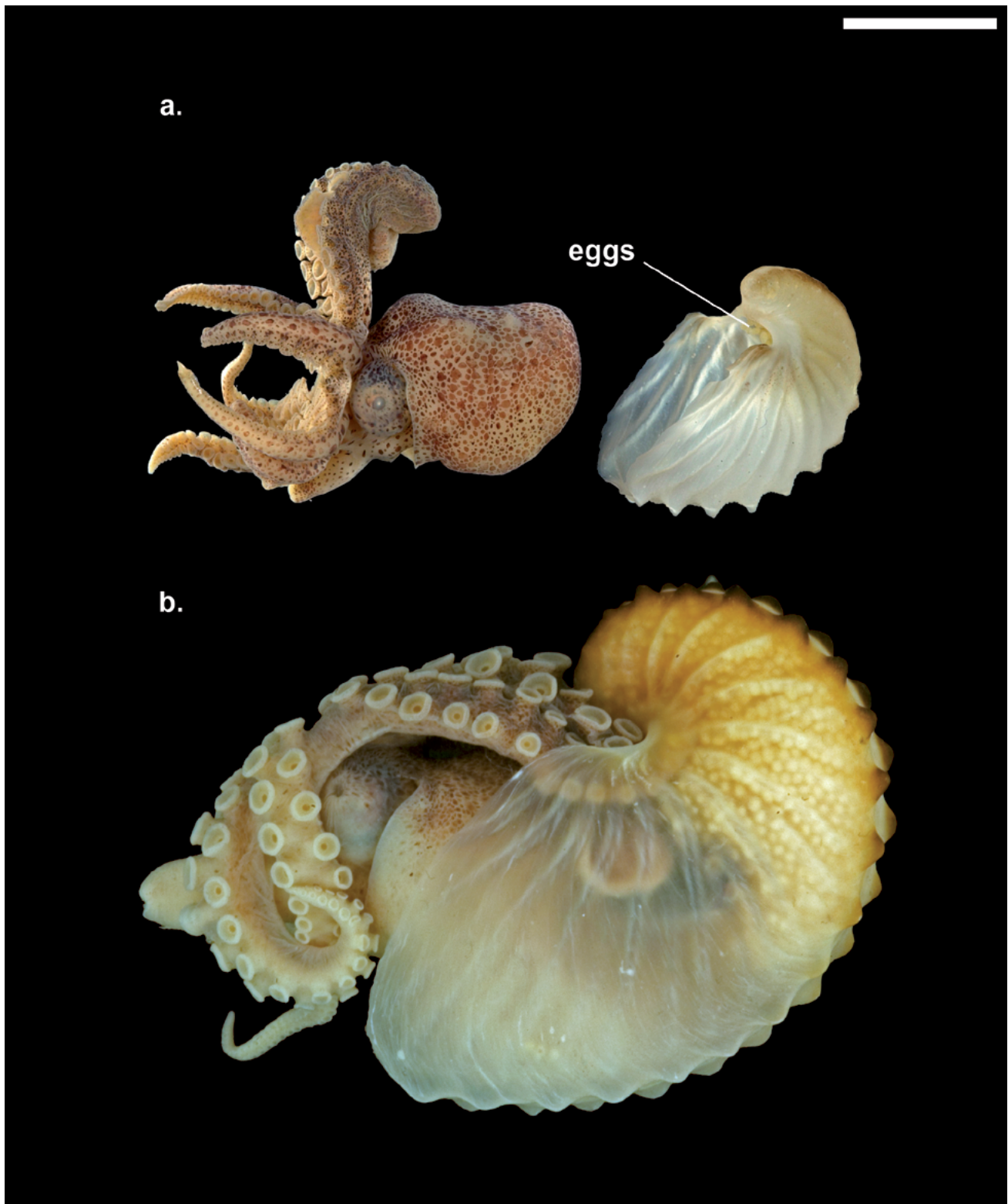


Figure 35. Preserved female *Argonauta nouryi* and *A. hians* with spawned eggs: a, preserved female *A. nouryi* from the Pacific Ocean (15.2 mm dorsal mantle length, 18.4 mm shell length, SBMNH 64369) with spawned eggs attached to the axis of the shell; b, preserved female *A. hians* from the North West Shelf, Western Australia (28.7 mm dorsal mantle length, 38.9 mm shell length, QM Mo77789) with yellow eggs visible in dorsal component of shell. Scale bar = 1 cm.

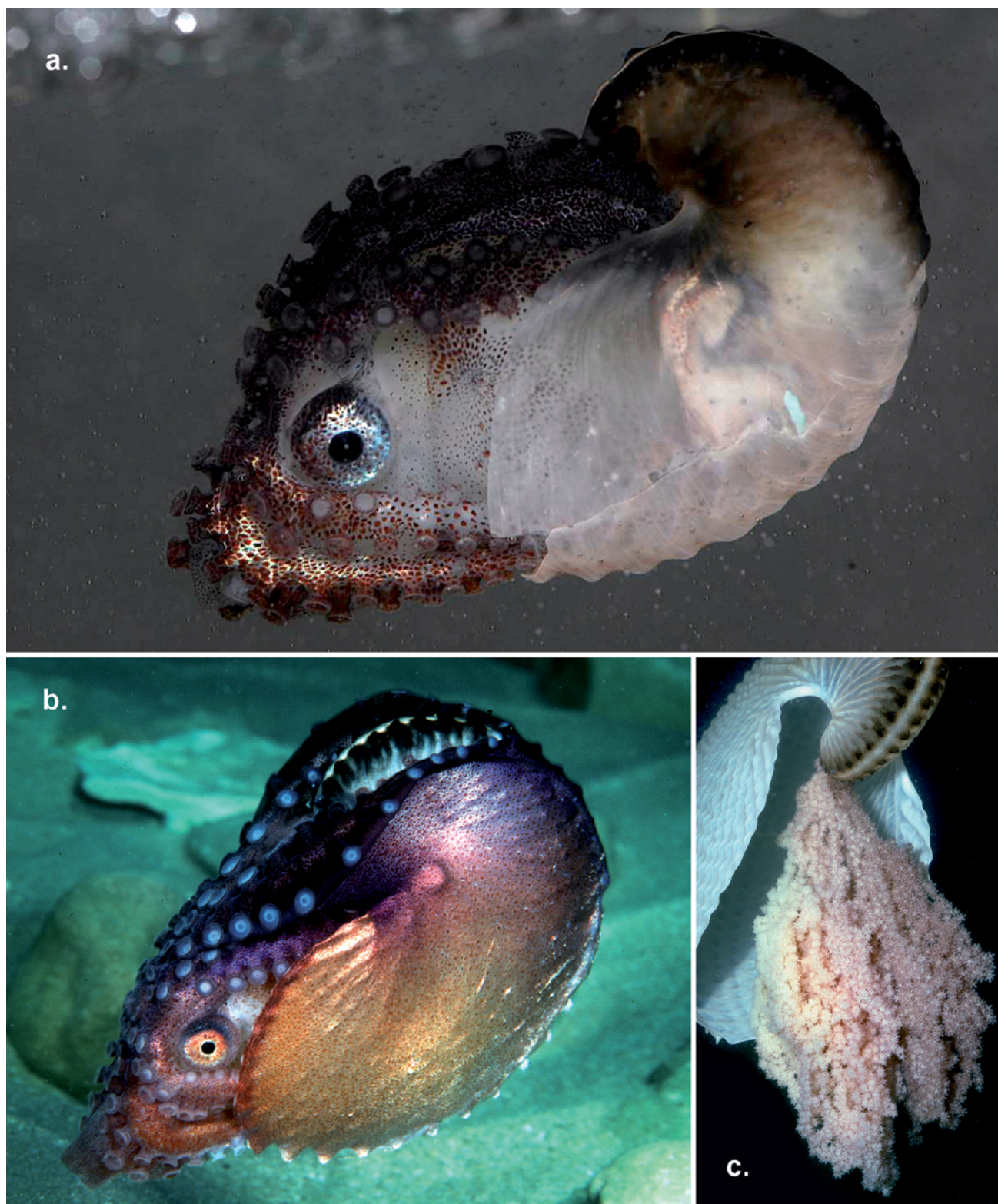


Figure 36. Images of live female argonauts, *Argonauta hians* and *A. nodosus*, demonstrating the effect of spawned eggs on the position of the females relative to their shells: a, live female *A. hians* from Andaman Sea, Thailand, photographed in an aquarium (photo: J. Nabhitabhata, after Sukhsangchan and Nabhitabhata 2007); b–c, *A. nodosus* Phillip Bay, Victoria, Australia (photos: R. Kuitert); b, live female argonaut photographed in the wild; c, eggs of same specimen, shown with argonaut removed from shell.

down to accommodate the increased volume. If a change in the growth rate was responsible for the transformation between shell formation types, it is believed that the transition would be more gradual and the boundaries in the shell less pronounced.

Argonaut nomenclature and the fossil record.

Misinterpretation of intra-specific shell variation has hindered the resolution of extant argonaut systematics. Historic generation of species names based on individual malformed shells, and shells of different formation types, has created confusion and complication. Fortunately, this practice has largely ceased. The last major erection of new species names occurred in 1914 when Monterosato proposed three new species names and one variety based on four shells of *A. argo* (Monterosato 1914). Interpretation of the fossil record, however, appears to be mirroring the historic approach applied to extant argonauts. Variation in shell characters is continuing to be used to designate new fossil argonaut species (Stadum and Saul, 2000), and many have been erected based on single fossilised shells (e.g. Martill and Barker, 2006). Saul and Stadum (2005) reviewed the current situation stating: “ten fossil argonaut species have been placed into four genera based on the absence or presence of keels and the degree of sculpture” (p. 520). If the situation is at all similar to that of extant argonauts, great caution should be undertaken when erecting fossil argonaut species based solely on shell characters.

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