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ON THE STATUS OF *LINGULA TUMIDULA* REEVE, *L. ADAMSI* DALL, AND *L. SHANTUNGENSIS* HATAI (BRACHIOPODA, INARTICULATA)

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ABSTRACT

Following examination of new material, it is proposed that *Lingula shantungensis* Hatai 1937 be placed in synonymy with *L. adamsi* Dall 1873. The species occurs throughout the western Pacific from the China Sea to Australia, and in the eastern Indian Ocean. *L. tumidula* Reeve 1841 occurs in eastern Australia and the Philippines, but is still known from only a few specimens. It is more closely related to other species of *Lingula*, typified by *L. anatina* Lamarck 1801, than is *L. adamsi*.

Up to 16 extant species of the Inarticulate brachiopod genus *Lingula* have been recognized (Davidson, 1888; Dall, 1920; Thompson, 1927; Hatai, 1940; Hayasaka, 1940). Of these, 13 are quite similar in their external form, which may be characterized by the type species of the genus, *L. anatina* Lamarck. They are elongate-oblong, with slightly convex and subequal valves, which are posteriorly acuminate forming beaks, and have a smooth surface bearing only light concentric lines. They are approximately 2–2.5 times as long as wide. The status of some of these species is currently under debate (Emig, 1977a, 1978, 1979; Emig et al., 1978; Hammond and Kenchington, 1978), but it is certain that several species will be placed in synonymy with *L. anatina*. All these species are Indo-Pacific and are predominantly intertidal (Hammond and Kenchington, 1978; Emig, 1978), with the exception of *L. parva* Smith, a small subtidal species from West Africa (Chuang, 1961; Emig and Le Loeuff, 1978). *L. anatina* is also known from West Africa from a single specimen (Emig, 1977).

Three other species, *L. tumidula* Reeve, *L. adamsi* Dall and *L. shantungensis* Hatai, differ from the other species in their external morphology, in that they have a broad, sculptured, rectangular shell, about 1.5 times as long as wide, with reduced posterior beaks. Davidson (1888) and Hatai (1937) speculated that *L. murphiana* Reeve was related to *L. tumidula* and *L. shantungensis* respectively, since *L. murphiana* is a "large" and "square" species (Johnston and Hirschfeld, 1920), but *L. murphiana* clearly is a species of the *anatina* form (see Hammond and Kenchington, 1978, fig. 2). Hatai (1940) thought that *L. shantungensis* was the "largest of the genus in the present seas." Similar claims have been made on behalf of *L. tumidula* by Davidson (1888) and Johnston and Hirschfeld (1920), the latter authors having seen a specimen with valves 66 mm in length. However, there is a specimen of *L. anatina* from Moreton Bay in the Queensland Museum (Cat. No. G 2304) in which the valves are 66.2 mm long. *L. tumidula* is known from Australia and the Philippines and *L. adamsi* and *L. shantungensis* are recorded only from the China Sea; all three species appear to be predominantly subtidal.

Examination of new material has necessitated a re-evaluation of the status of *L. shantungensis* and a re-description of *L. adamsi* and *L. tumidula*, in which the differences between the species are defined.

Original Descriptions and Type Material

Reeve's original (1841a, b) and subsequent (1859) descriptions of *L. tumidula* from "New Holland" (= Australia; given as Moreton Bay, Australia in the later

publication) mention the subquadrate shape and convexity of the valves, their lightness and horniness, the reduced beaks and umbones and the olive-red burnished color. The dimensions were given as: length 53 mm, width 33 mm (thus, W/L = 0.619). Apparently using the same material, Sowerby (1847) and Davidson (1888) gave slightly different dimensions, resulting in W/L ratios of 0.633 and 0.654 respectively. In addition, Davidson gave the color as "coppery brown or reddish olive, sometimes green near the posterior margin." The figures of all the above authors show the valve surface to be relatively smooth, with concentric growth lines. Sowerby (1847) mentioned the radiating longitudinal striations on the valves, shown in his figures and in those of Davidson (1888). The figures also show the shell to be widest anteriorly, with a mucronate anterior margin. No author commented on the relative convexity of the dorsal and ventral valves, and lateral view figures were not provided. Two specimens from Masbate, Philippines, found in sandy mud at "low water," were described as *L. compressa* by Reeve (1841b), but were later placed in synonymy with *L. tumidula* (Reeve, 1859), thus confirming the opinion of Sowerby (1847).

The type material is now held by the British Museum (Natural History) (Cat. Nos. ZB 338–ZB 342). Photographs and color notes were provided by that institution as the specimens, now dry and fragile, were not available for examination. Specimen ZB 339, figured by Reeve (1841a), Sowerby (1847) and Davidson (1888), here chosen as the lectotype, clearly shows the diagnostic features. The specimen ZB 338, figured by Reeve (1859) shows evidence of slightly stronger concentric lines on the shell surface. The specimens from Masbate (ZB 341, ZB 342), now labelled "Masbate and Moreton Bay," probably an early curatorial error (Brunton, pers. comm.), are similar except that the latter is not widest anteriorly.

Adams (1863) collected specimens (N = ?) from mud in 7 fm in Tsaulian Harbor, Korean Archipelago, and designated them *L. tumidula*. In 1873, Dall reassigned the material to a new species, *L. adamsi*, but gave no figures, descriptions or reasons. Davidson (1888) endorsed the new taxon, and provided a description which mentions the pronounced sculpture of concentric lines, parallel sides, the nearly straight anterior margin and obtuse posterior margin, the flattened or gently convex profile and the light or brownish yellow coloration. The specimen differed from one figured by Davidson (1871) in that it was widest anteriorly, mucronate, and had a W/L of 0.588, whereas the earlier specimen, which appears to have been from the type material, tapered anteriorly with a straight margin and a W/L of 0.608. The whereabouts of the type material is no longer known. The specimen figured by Davidson (1888) (BM-NH: Cat. No. 12561) was collected near Taiwan, and photographs (Fig. 2e) reveal that the details of the anterior margin appear to have been exaggerated in Davidson's figure. A second specimen, possibly from Taiwan (Cat. No. 21474), is much closer in appearance to the type material, tapering anteriorly with a straight anterior margin, and a W/L of 0.637.

L. shantungensis was described by Hatai (1937) from four specimens from the eastern coast of Shantung, China. They were separated from the two previously described species on the basis of color (blackish-red marginally and dull-light-red in the middle) and qualitative differences in the outline of the shell and its sculpture. The specimens ranged in length from 36.5 mm to 54 mm, and in W/L from 0.555 to 0.628 (W/L = 0.586). The valves were nearly equally convex, with the sides tapering slightly anteriorly, a straight anterior margin, and radiating longitudinal "grooves" on their surfaces. This material is lodged in the collections of the Institute of Geology and Paleontology, Tohoku University, but was not made available for this study. The original description contains adequate photographs.

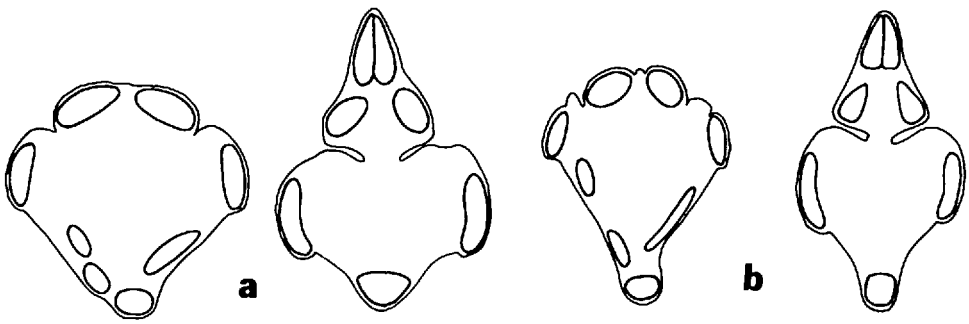

Figure 1. Outline of the body wall and disposition of the musculature of (a) *Lingula adamsi* and (b) *Lingula tumidula*: dorsal view, far left and second from right; ventral view, second from left and far right.

New Material

Twelve specimens of *Lingula* in the collections of the Queensland Museum, Brisbane, were examined. Eleven were stored in alcohol; the remaining specimen, part of the original material of Johnston and Hirschfeld (1920), was stored dry and had disintegrated. The collections of the Australian Museum, Sydney, yielded a further four wet and five dry specimens. All the material from these two museums was from Australia, except for two specimens from Bougainville, Nuigini. Two lots, consisting of three wet and two dry specimens, respectively, from two different localities in China, were provided by the Smithsonian Institution, Washington, D.C. A single wet specimen from the Philippines was discovered in the collection of the Museum National d'Histoire Naturelle de Paris. All the specimens were measured and details of the shape, color and sculpture were recorded. Many of the dry specimens showed evidence of distortion; where this was deemed significant the ratios of the dimensions were regarded as unreliable, since there is usually a relative decrease in width upon drying. Three specimens from the Queensland Museum (two from lot G 5879 and one from lot G 5659), one from the Smithsonian Institution (from lot 549766), and that from MNHN de Paris (Cat. No. BRA-78.2) were dissected to allow inspection of the internal features, particularly the mantles and muscle arrangements (Figs. 1–3). The valves on two specimens from the Australian Museum were sufficiently flexible to permit the mantles inside to be viewed.

The locality, catalogue details, dimensions, and the width/length and depth/length ratios of each specimen examined are presented in Table 1. The same data for the original material and other material examined from photographs are included where possible.

Discussion

On considering the characteristics of the original material and of the new material examined in this study, two morphological types may be distinguished. The first has a horny, lightly calcified quadrate shell, tapering slightly anteriorly, and a straight anterior margin with rounded corners. The posterior margin is very obtuse, with poorly defined beaks. The sculpture consists of strong concentric ridges, which on closer examination are found to be interspersed with fine lines, and the color typically ranges from yellowish brown to dark reddish brown (Fig. 2a). In profile, the valves are subequal and wedge-shaped (Fig. 2d). In all five specimens dissected, the anterior branches of the *vascula lateralia* (Williams and Rowell, 1965), the mantle sinuses of other authors, are widely separated and nearly parallel, with transverse secondary branches (Fig. 2b). The body cavity is small relative to the mantle cavity, and as a consequence of the broad, obtuse posterior of the shell, is wide and shows a characteristic disposition of the muscles (Fig. 1a). The second morphotype has a relatively smooth, vitreous and more heavily calcified shell, bearing light concentric and radiating lines. The shell is widest anteriorly, with a central rostrum, and has an acuminate posterior margin

Figure 2. *Lingula adamsi*: a, Exterior of a ventral and dorsal valve (Table 1, #36); b, Pattern of branching of ventral mantle sinuses (#36); c, Small specimens (#28 and #30); d, Lateral view (#37); e, Dried specimen, with slightly different anterior margin (#8); f, Neotype (#15).

(Fig. 3a, e). The pattern of branching of the mantle sinuses (Fig. 3c, d) differs from that seen in the first morphotype, while the visceral cavity is not as small relative to the mantle cavity and has a different shape, giving a different disposition of the muscles (Fig. 1b).

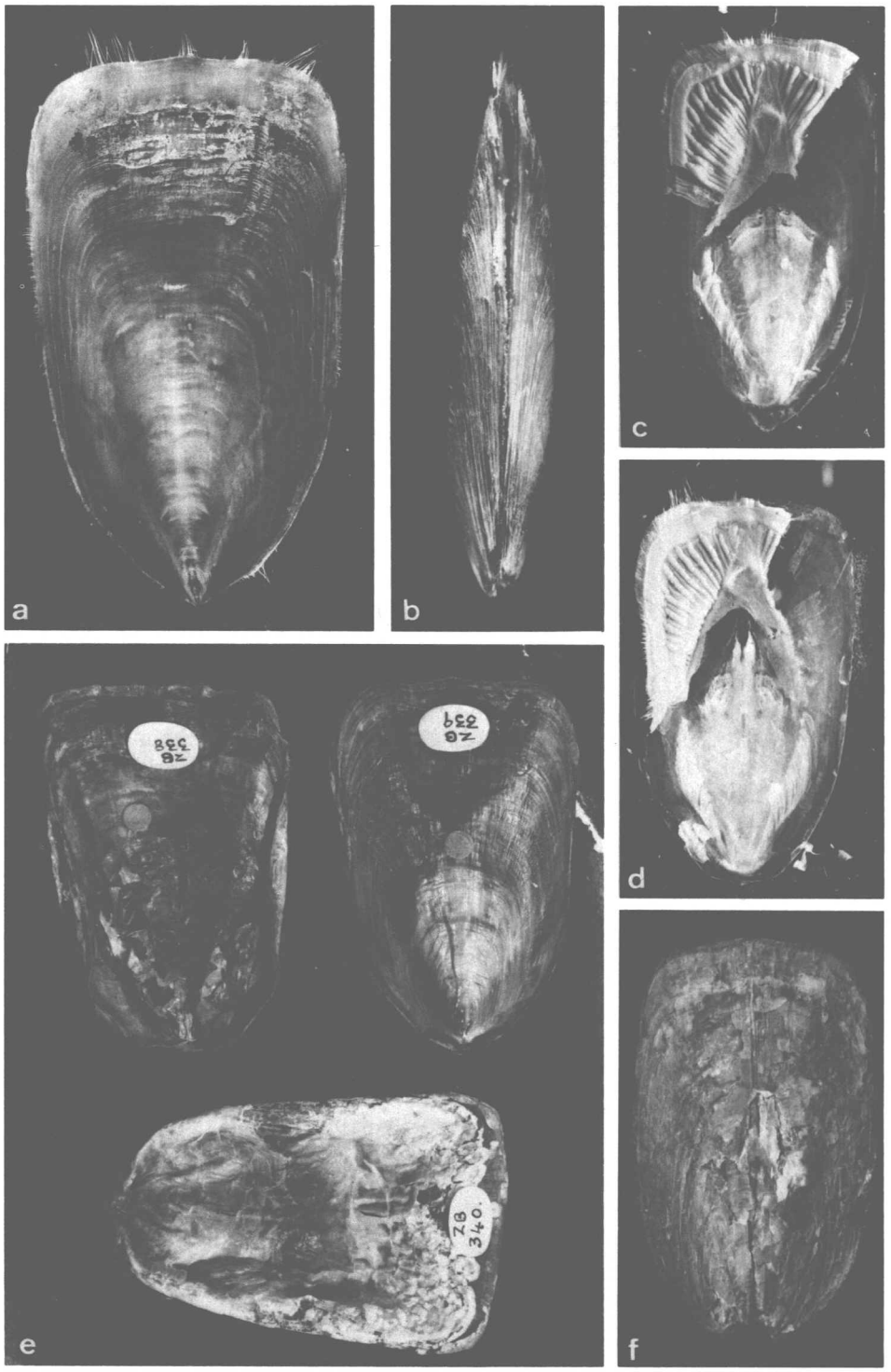

Figure 3. *Lingula tumidula*: a, Exterior of a ventral valve (Table 1, #6); b, Lateral view (#6); c, Internal view of ventral valve and pattern of branching of mantle sinuses (#6); d, Internal view of dorsal valve and mantle sinuses (#6); e, Type specimens (#1–#3); f, Specimen showing different valve shape, tapering anteriorly (#5).

The records which are identified as the first morphotype are #7–#38 listed in Table 1, and include the type material of both *L. adamsi* and *L. shantungensis*. The latter species falls easily within the range of variability observed for the diagnostic characters in the other specimens, so the basis for its separation must be considered trivial. Hatai's mention of "longitudinal grooves" on the valves refers to the siphonal ribs which may be seen to varying degrees on all *Lingula* species. As Dall's name has priority, *L. shantungensis* becomes a junior subjective synonym of *L. adamsi*. There remains an anomaly in the literature regarding *L. adamsi* that requires correction. Dall (1920, p. 264) listed specimens of *L. adamsi* in the collections of the U.S. National Museum, all from localities in southern Japan. Examination of this material, now re-catalogued as USNM 274151, 274152, 274153, shows that it belongs to a species having the *L. anatina* type of morphology. The only similarity with the true *L. adamsi* is the strong burnished red color. Recognition of this error eliminates "conspicuously long setae" (Dall, 1920) as a diagnostic character for *L. adamsi*. The setae were absent from most specimens in this study due to damage, but they may be seen on the specimens in Figure 2c. The Queensland Museum and the Australian Museum material, which had previously been mis-identified as *L. tumidula* because of the type locality of that species (Johnston and Hirschfeld, 1920; Hammond and Kenchington, 1978), is now included in *L. adamsi*, extending the range of this species from the China Seas to Nuigini and Australia as far south as Moreton Bay. The specimen from Broome, Western Australia (C 48315) extends the range into the Indian Ocean for the first time.

The second morphotype includes the type material of *L. tumidula* and the specimen from MNHN Paris, which is henceforth referred to *L. tumidula*. This species differs externally from the *anatina*-like species only in its relative width and the faint radiating sculpture, and internally the pattern of the mantle sinuses and the disposition of the muscles is much alike. It seems probable that *L. tumidula* is more closely related to the other species of *Lingula* than is *L. adamsi*. *L. tumidula* remains known only from Moreton Bay and the Philippines, but undoubtedly occurs in regions between.

There is some variability within each species, which does not, however, impede their recognition. The convexity of *L. adamsi* varies considerably (Table 1), and the thickness of the valves differs such that in some specimens they are translucent and may be flexed, while in others they are thick, rigid and opaque. The anterior margin of small specimens may be concave (Fig. 2c), and in a few specimens there is a faint suggestion of a median rostrum (Fig. 2e). Several of the Australian Museum specimens have an area of darker color anteriorly, which may have once been green. *L. tumidula* is not invariably widest anteriorly, as specimen ZB 342 shows (Fig. 3f). The distinctions drawn between the species concerning the mantle sinus patterns, the shape of the body cavity and the disposition of the muscles are based on few specimens of *L. adamsi* and only one of *L. tumidula*, although for the latter species impressions remaining on the interior of dry valves are consistent with the interpretation of the body cavity and muscles. Schaeffer (1926) stated that the mantles of specimens from Santuao, China, which may be identified from her photographs as *L. adamsi*, did not differ from those of *L. anatina*, which in turn are similar to those of *L. tumidula* (Emig, Hammond, unpublished data). She did not figure the mantle sinuses, rendering this impasse unresolvable. The morphology of the deltidia, which has been suggested by Emig (1977c) as a criterion for the definition of other *Lingula* species, is not considered here because there are insufficient specimens, and the dry material could not be used due to distortion.

Table 1. Locality, museum holding information, dimensions (in millimeters), and ratios (from original measurements or figures, except those in brackets, which are based on recent photographs) for all known specimens of *Lingula tumidula* and *L. adamsi*. BM = British Museum (Natural History); MP = Museum National d'Histoire Naturelle de Paris; TU = Tohoku University; SI = Smithsonian Institution; AM = Australian Museum; QM = Queensland Museum. (a) indicates lectotypes, (b) neotypes, (c) hypotypes.

#	Locality	Museum	Cat. No.	Length	Width	Depth	W/L	D/L
			Lingula tumidula					
	Australia							
1	Moreton Bay	BM	ZB 338	53.0	35.5	—	.694 (.670)	—
2a	Moreton Bay	BM	ZB 339	53.0	33.0	—	.619 (.661)	—
3	Moreton Bay	BM	ZB 340	(55.0)	(38.0)	—	(.685)	—
	Philippines							
4	Masbate	BM	ZB 341	—	—	—	(.674)	—
5	Masbate	BM	ZB 342	45.7	27.9	—	.611 (.602)	—
6c	Philippines	MP	BRA.78.2	52.0	30.0	—	.577	—
			Lingula adamsi					
7	*Korea*	—	—	—	—	—	.608	—
8	*Taiwan*	BM	B12561	36.0	21.2	—	.588	—
9	*Taiwan* (?)	BM	B21474	(32.5)	(21.0)	—	(.646)	—
	China							
10	Shantung	TU	61311	54.0	30.0	13.0	.555	.240
11	Shantung	TU	61311	39.0	24.5	9.0	.628	.230
12	Shantung	TU	61311	38.5	22.0	8.5	.571	.221
13	Shantung	TU	61311	36.5	21.5	8.5	.589	.233
14	Foochow	SI	549766	40.9	24.8	10.9	.606	.267
15b	Foochow	SI	549766	38.7	23.0	11.8	.594	.303
16	Foochow	SI	549766	29.5	17.0	—	.576	—
17	Gulf of Chihli	SI	359345	46.0	25.0	—	.543	—
18	Gulf of Chihli	SI	359345	41.7	22.9	—	.549	—
	Nuigini							
19	Bougainville	AM	C109911	59.1	35.0	17.1	.592	.289
20	Bougainville	AM	C109911	35.5	24.6	11.0	.693	.310
	Australia							
21	Torres Strait	AM	C87688	51.2	34.7	—	.678	—
22	Torres Strait	AM	C87688	53.6	36.2	—	.675	—
23	Gulf of Carpentaria	AM	C104475	52.0	36.0	—	.692	—
24	Gulf of Carpentaria	AM	C74856	48.0	28.0	—	.583	—
25	Gulf of Carpentaria	AM	C107295	55.0	32.0	—	.582	—
26	Coburg Peninsula	AM	C84715	60.0	38.5	—	.642	—
27	Broome	AM	C48315	59.1	35.6	—	.603	—
28c	Moreton Bay	QM	G5659	18.3	11.8	4.1	.645	.224
29	Moreton Bay	QM	G5659	17.7	11.1	3.9	.627	.220
30c	Moreton Bay	QM	G5659	13.6	9.0	2.8	.662	.206
31	Moreton Bay	QM	G11684	57.6	39.5	19.5	.686	.339
32	Moreton Bay	QM	G11685	16.0	10.5	3.5	.656	.219
33	Moreton Bay	QM	G11686	35.2	23.5	8.4	.668	.239
34	Moreton Bay	QM	G11686	11.2	6.9	2.4	.616	.214
35	Yeppoon	QM	G5486	50.7	33.5	14.2	.661	.280
36c	Bowen	QM	G5879	52.9	36.1	14.4	.682	.272
37c	Bowen	QM	G5879	52.6	36.7	14.7	.698	.279
38	Bowen	QM	G5879	50.3	33.2	14.1	.660	.280

Morphometric analysis, using only wet material and original descriptions of *L. adamsi,* reveals two trends. Specimens from the China Sea have a mean W/L of 0.596, which is significantly different from that of the Australian specimens ($\overline{W/L} = 0.662$) ($t_{21} = 6.61^{***}$), suggesting geographical differences. Of the wet specimens from Australia, seven were greater than 50 mm in length, while five were less than 20 mm long. The mean W/L (0.641) and D/L (0.217) of the smaller specimens are both significantly different from the mean W/L (0.677) and (0.290) of the larger specimens ($t_{10} = 4.18^{**}$ and $t_8 = 5.09^{***}$ respectively). These data indicate that the Australian representatives of the species tend to become relatively wider and more convex with growth. However, these apparent trends must be treated with caution. It is not known if *L. adamsi* shows the same variability in growth as *L. anatina,* in which different samples from the same population may show positive or negative allometry or isometric growth of W with respect to L (Chuang, 1962; Hammond and Kenchington, 1978), but it is probable that these interpretations are subject to the same limitations. Large samples of *L. adamsi* are not readily available to resolve the problem. The depth at which samples were taken is not available for all the records, but where it is, the specimens have been collected only subtidally. Interpreting the sampling program of Stephenson, Williams and Cook (1974) in concert with the number of specimens lodged by them in the Queensland Museum, it appears that maximum densities of 30 m^{-2} may occur in Moreton Bay, and that the species is very patchily distributed. This compares unfavorably with densities of up to 864 m^2 recorded intertidally for *L. anatina* (Kenchington and Hammond, 1978). Schaeffer (1926) reported on a collection of 195 specimens of *L. adamsi* from Santuao, China, but no ecological details were given.

Neither Adams' (1863) original description nor any subsequent work mentioned the whereabouts of the type material of *L. adamsi.* It is not in the British Museum (Natural History) or the Smithsonian Institution collections, and, contrary to the suggestion of Hatai (1940), it is not lodged in the Philadelphia Academy of Natural Sciences. Since the type material appears to have been lost, it is necessary that a neotype be designated. For this we propose a specimen from the Smithsonian Institution lot USNM 549766 (Fig. 2f and Table 1), which has the pedicle intact. This specimen was collected in the China Sea, near to where *L. adamsi* originally was found. All the figured Australian specimens (Fig. 2a–d) are to be considered hypotypes.

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