

A REVISION OF *LOLIOLUS* (Cephalopoda; Loliginidae),
INCLUDING *L. NOCTILUCA*, A NEW SPECIES OF SQUID
FROM AUSTRALIAN WATERS

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ABSTRACT: A new species of squid, *Loliolus noctiluca* (Myopsida: Loliginidae) is described and illustrated from Australian waters, the first record of the genus in the region. The genus is revised with complete redescrptions being given for *L. hardwickei* and *L. affinis*. *L. typus* Steenstrup and *L. investigatoris* Goodrich are placed into synonymy with *L. hardwickei*. Natsukari's (1983) synonymy of *Loliolus rhomboidalis* with *Loligo kobienensis* is accepted. *Loliolus steenstrupi* Dall is considered a *nomen dubium*. A key to identification of the valid species of the genus is given. *Loliolus noctiluca* occurs in East Australian coastal waters and estuaries and tolerates salinities as low as 24‰.

During a visit to Australia in 1976, one of us (CFER) first discovered the presence of a species of *Loliolus* in Australian waters in the Sydney Fish Market. Examination of unidentified collections in the Australian Museum, Sydney and the Museum of Victoria, Melbourne confirmed a wide spread distribution of the undescribed species. Many additional specimens subsequently were collected through various field collecting programs. The new species is described and illustrated in this paper.

Loliolus has been an ill-defined genus of loliginid squid considered limited in distribution to the Indian Ocean and eastward into the Indonesian chain. The discovery of a new species in eastern Australian (Pacific Ocean) waters represents a major expansion in the known range both in longitude and latitude. While studying the Australian species it became apparent that a close examination of other nominal species would be necessary in order to make proper comparisons between species. Since most of the original species descriptions are relatively uninformative, especially in view of newly recognized characters, the type specimens were secured and combined with more recently collected material to conduct this revision of the genus.

Loliolus was erected by Steenstrup (1856) to accommodate two new species, *L. typus* and *L. affinis* from the Indian Ocean. Subsequently three additional species have been named: *L. investigatoris* Goodrich, 1896, from the Bay of Bengal; *L. steenstrupi* Dall, 1871, from the Gulf of California; and *L. rhomboidalis* Burgess, 1967, from the Indian Ocean. In this paper *L. steenstrupi* is considered a *nomen dubium* and *L. rhomboidalis*, being placed in synonymy with *Loligo kobienensis* by Natsukari (1983), is removed from the genus *Loliolus*.

MEASUREMENTS AND ABBREVIATIONS

Measurements and indices used throughout this paper are those given in Lu & Tait (1983) and Roper & Voss (1983), using dorsal mantle length (M.L.) as a standard. Fin angle (F.A.) is the angle between the posterior

borders of the fins, this is twice the equivalent measurement used by Roper, Lu & Mangold (1969). Measurements for all specimens are on file in the Department of Invertebrate Zoology, Museum of Victoria. Other abbreviations used include AM—Australian Museum, Sydney; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; IM—Indian Museum, Calcutta; NMV—National Museum of Victoria (now Museum of Victoria); NMNH—National Museum of Natural History, U.S.A. (also USNM—U.S. National Museum, used only for catalogue numbers); MUZD—Melbourne University Zoology Department; QM—Queensland Museum, Brisbane; RSMAS—Rosenstiel School of Marine & Atmospheric Science, Miami; ZMC—Zoological Museum, Copenhagen.

Regression analyses and comparisons between regression lines are according to the method given by Zar (1974).

Family LOLIGINIDAE Steenstrup, 1861

Genus *Loliolus* Steenstrup, 1856

TYPE SPECIES: *Loliolus typus* Steenstrup, 1856 (= *Loligo hardwickei* Gray, 1849)

DIAGNOSIS: Loliginids with heart-shaped fins; the entire length of the left ventral arm in males hectocotylied with no normal suckers on the proximal portion of the arm.

Loliolus noctiluca, sp. nov.

Figs. 1, 2, 3a, b, 4-6; Tables 1, 2, 5, 6; Appendices 1, 2

DIAGNOSIS: Largest mantle sucker rings on club smooth; medial mantle suckers 3-6 times the diameter of marginal mantle suckers. No normal suckers on hectocotylied arm (left IV) of males, suckers modified into conspicuous elongate interconnected papillae with minute apical suckers. A pair of photophores embedded in the posteroventral surface of the ink sac.

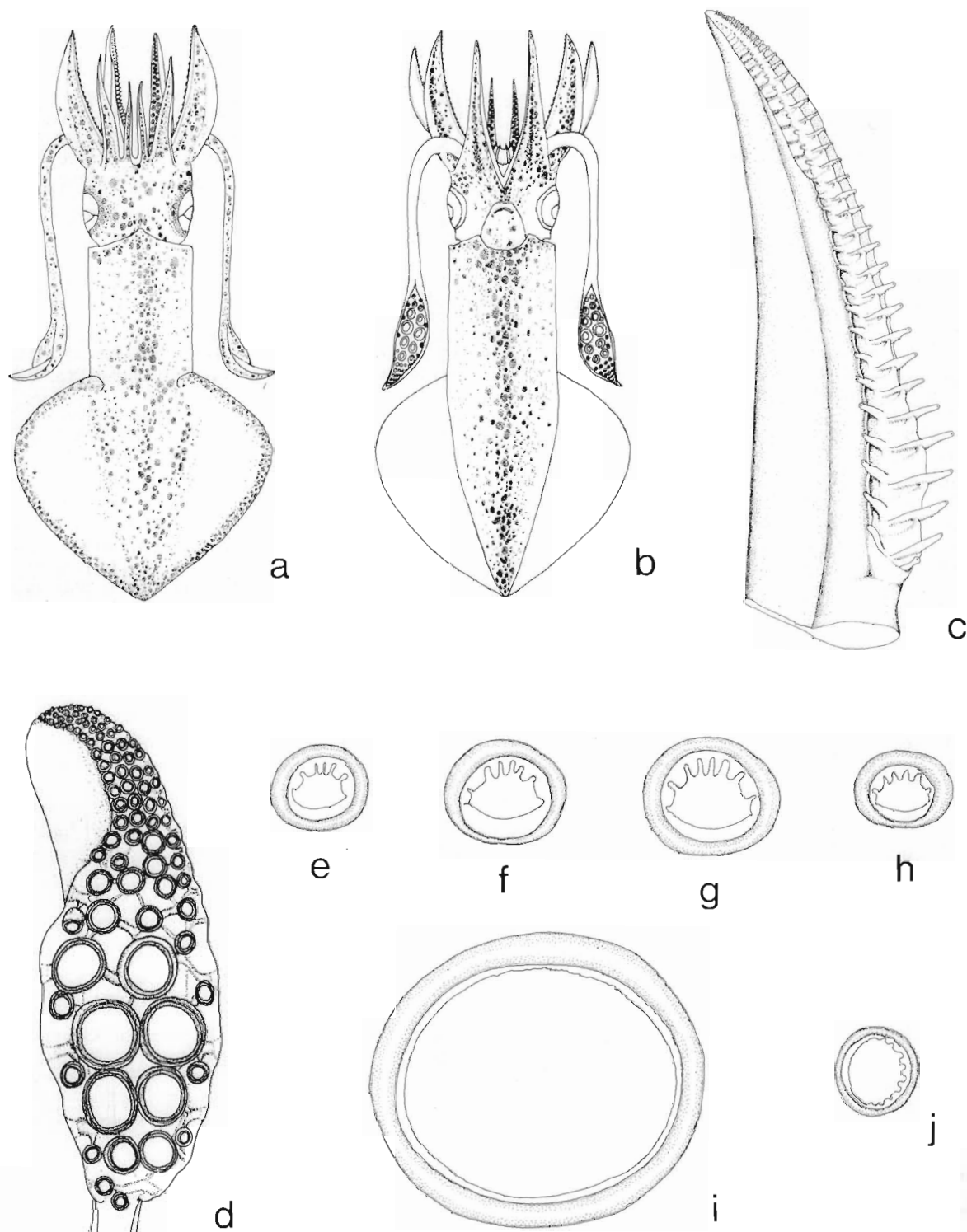


FIG. 1—*Loliolus noctiluca* n. sp. a-b, Holotype NMV F31119, male 59 mm ML. a, dorsal aspect. b, ventral aspect. c, hectocotylus, Paratype NMV F31121, 58 mm ML. d, Left tentacular club of Holotype. e-h, Holotype, largest sucker rings from arms I-IV respectively. i-j, Holotype, club manal sucker rings. i, largest median manal sucker, j, largest marginal manal sucker. (e-j to same scale).

MATERIALS EXAMINED: See APPENDIX 1. Measurements of some additional material (APPENDIX 2) is included in Tables 1 and 2.

DESCRIPTION: *Mantle* cylindrical anteriorly; tapers very gradually posteriorly to a blunt rounded tip; median antero-dorsal lobe rounded, very pronounced; ventrolateral lobes pointed, conspicuous; ventral mantle margin between lobes deeply concave to accommodate large funnel (Fig. 1a, b). *Fins* large, FLI = 51-62, FWI = 55-76; heart shaped, posterior margins straight, continuous around apex of mantle; anterior margins convex with slightly developed lobes; lateral lobes broadly rounded. Fin length and width indices increase with mantle length. Fins of males longer than females at equal mantle length. The gladius is visible through the integument in the anterior two-thirds of the mantle, then submerges below the muscles of the mantle and fins in the posterior one-third of the mantle.

Head broad, short, as wide as mantle, dorso-ventrally flattened. Eyes large (EDI = 11-18), a small pore present between the eye and base of third arm; olfactory apparatus a conspicuous, vertical crest with indentation on posterior side of head. *Funnel* stout, bluntly tapered anteriorly, free in its anterior quarter; funnel and mantle locking cartilage simple, straight groove and ridge, strongly developed. Dorsal funnel organ large;

median limbs very long, broad in posterior half, tapered to a blunt point posteriorly; anterior half of limb narrow; apical papilla simple, subterminal, thumb-like; ventral pads elongate, ovoid, broader anteriorly, medial borders curved, lateral borders nearly straight (Fig. 2a). Funnel valve very well developed, corners rounded, anterior border nearly straight.

Arms short, order III \geq IV, II, I, longer in males than in females, especially Arms I and II. Arm I laterally compressed with a distinct aboral keel for nearly its entire length. Arm II laterally compressed distally, a very low aboral keel present proximally, absent distally. Arm III robust, laterally compressed, a very conspicuous, broad, aboral swimming keel that remains broad well distally. Arm IV trapezoidal in section, very well developed tentacular sheath dorso-laterally, low, angular keel ventro-medially. Protective membranes very broadly developed on all arms except on Arm IV where they are low and weak; trabeculae muscular but do not extend beyond edge of protective membrane on Arms I-III; form scalloped border along membrane of Arm IV. Arm suckers larger in males than females; suckers largest on Arm III and smallest on Arm IV in both sexes (Table 1). *Arm sucker dentition* on chitinous rings of largest suckers on Arms I-III with 4-7 large, truncate teeth in distal half; teeth broad, low laterally,

TABLE 1
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Loliolus noctiluca n.sp.

Measure/ Index	n	MALES			n	FEMALES		
		Mean	S.D. (n - 1)	Range		Mean	S.D. (n - 1)	Range
ML (mm)	25			35-62	12			33-83
MWI	25	28.6	1.6	26-31	12	30.0	3.7	26-37
HLI	25	21.9	2.4	17-28	12	23.8	2.2	20-27
HWI	25	28.3	1.3	24-30	12	27.6	2.8	23-34
EDI	25	15.6	0.8	13-17	12	14.7	2.0	11-18
FLI	25	58.3	2.9	51-62	12	54.6	5.7	40-60
FWI	25	67.4	5.2	55-76	12	65.7	5.6	58-74
FL/FW	25	86.9	4.3	78-97	12	83.3	8.2	67-97
FA(°)	25	103.2	4.5	92-111	12	104.9	3.7	96-112
AL _I I	25	22.9	3.1	16-27	12	19.5	4.8	14-32
AL _{II} I	25	34.2	3.2	25-38	12	28.9	5.2	20-42
AL _{III} I	25	38.7	2.6	34-44	12	37.3	4.2	33-49
AL _{IV} I	25	35.6	2.6	31-41	12	35.8	3.6	30-44
HcAI	23	38.1	2.7	32-44	—	—	—	—
TtLI	25	73.1	10.4	60-106	12	81.2	19.9	55-136
CIL	25	28.9	2.6	25-36	12	31.8	3.6	28-41
AS _I I	25	0.61	0.09	0.5-0.8	12	0.52	0.09	0.4-0.7
AS _{II} I	25	0.79	0.10	0.5-1.0	12	0.66	0.08	0.5-0.8
AS _{III} I	25	0.86	0.10	0.7-1.1	12	0.80	0.09	0.7-0.9
AS _{IV} I	25	0.54	0.08	0.5-0.8	12	0.48	0.08	0.3-0.6
CISI	24	2.25	0.31	1.7-2.8	11	2.58	0.45	2.0-3.4
GWI	22	21.3	1.3	18-23	11	22.7	1.8	20-26
RLI	5	17.4	1.5	15-19	5	18.2	1.9	16-20
RWI	5	4.48	0.44	3.8-4.8	5	4.87	0.33	4.4-5.2
SpL (mm)	17	4.15	0.64	3.2-5.2				
SpLI	17	7.74	0.90	5.6-9.3				
SpRI	17	81.2	3.6	73-87				
SpWI	17	4.36	1.50	3.1-7.8				

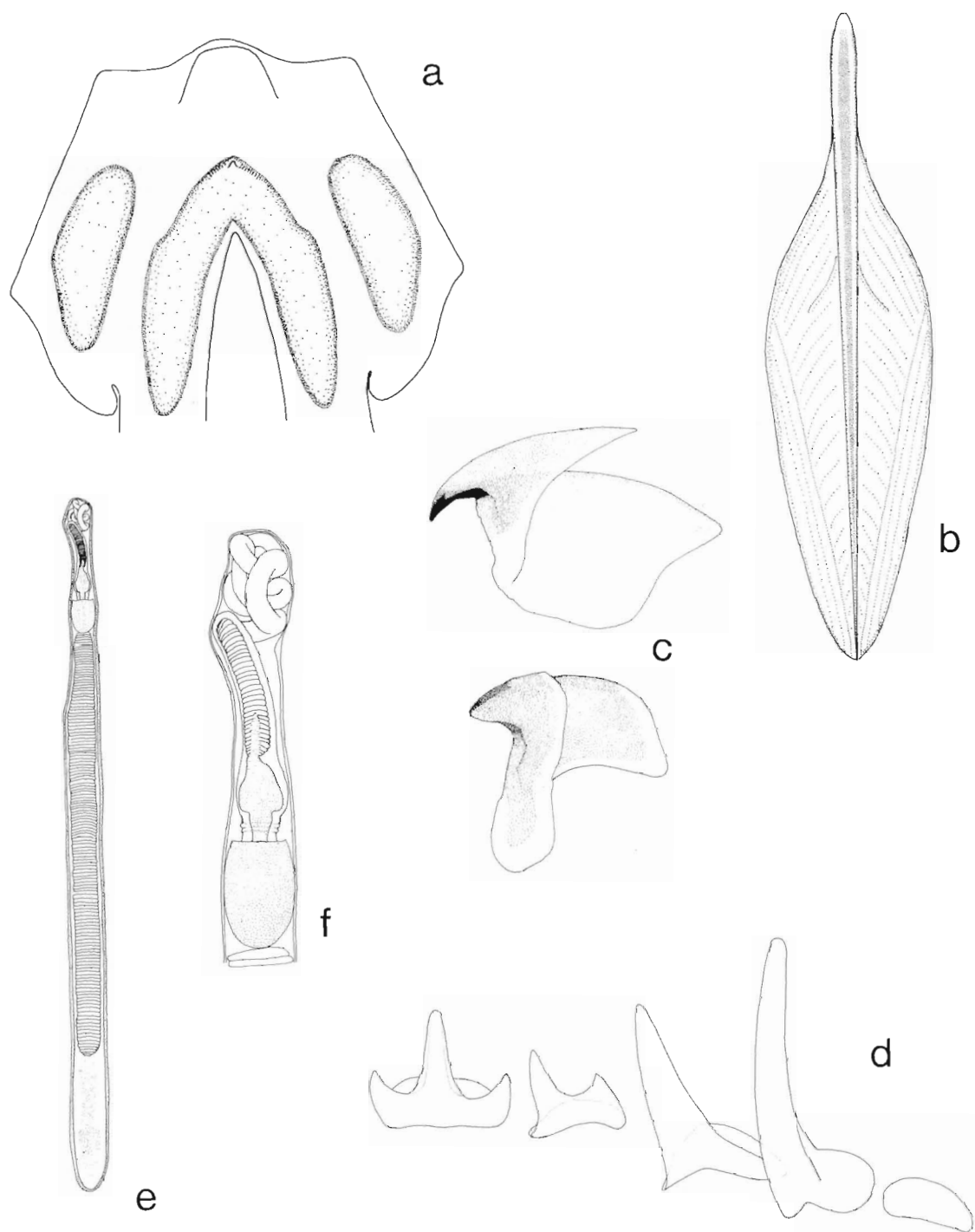


FIG. 2—*Loliolus noctiluca* n. sp. a, Paratype NMV F31122, male, 62 mm ML, funnel organ. b, Paratype NMV F31120, male, 60 mm ML, gladius. c, NMV F31130, female, 60 ML, beaks. d, Paratype NMV F31122, radula. e-f, Paratype NMV F31120. e, spermatophore. f, oral end of spermatophore.

narrow, elongate medially (Fig. 1e,f,g); proximal half a broad, smooth plate. Ring of largest sucker on Arm IV (Fig. 1h) with 3-6 teeth, similar to those on Arms I-III. Distal-most sucker rings with more rounded teeth, generally fewer than those on largest rings. Right ventral arms of males from Queensland and Papua have sucker rings with 3-6 acute, pointed teeth on the distal 31-36 pairs of suckers, with blunt teeth on the remaining proximal 3-9 rows. Females show no corresponding difference.

Left ventral arm of males is *hectocotylised* (Fig. 1c), and is longer, more robust than right ventral arm. All suckers are modified. Armature of ventral row with suckers and stalks modified into long papillae that become shorter and more robust distally; a thick membrane connects the medial bases of the ventral papillae on the proximal two-thirds of the arm and continues to the tip as a low ridge. Suckers of ventral row are small, swollen and fleshy and distally are incorporated into the papillae as slightly swollen tips. Minute, chitinous sucker rings are deeply embedded in the swollen suckers on the proximal portion of the ventral row. Suckers and stalks of dorsal row are modified into shorter and narrower papillae, that distally decrease in length to very small, conical protuberances; dorsal papillae along basal half are fused by a narrow membrane to the medial membrane between the papillae of the ventral row. Suckers of the proximal portion of dorsal row are bulbous with small apertures and the most proximal, at least, possess minute rings. As papillae decrease in size

and become conical, suckers are completely incorporated into the apex of the papillae, and a minute orifice remains to the distal-most papillae. The ventral protective membrane is thicker and wider than that of the right ventral arm; it becomes broader along the distal half of the arm before it tapers to the tip. The dorsal protective membrane originates proximally as a thick, broad, semi-lunar flap with a swollen, convoluted medial surface. A fleshy, convoluted papilla arises from the base of the most proximal sucker stalk. The most proximal section of the ventral protective membrane also is thickened and convoluted. Proximal to the semi-lunar flap, the dorsal protective membrane is thin and narrow with a scalloped border. On the distal third of the arm, the dorsal protective membrane becomes a broadly expanded, thickened flap with a fleshy convoluted medial surface.

Tentacles relatively short, robust; stalks naked and with large, broadly expanded clubs, $CLI = 25-40$ (Fig. 1d). Club suckers tetraserial on manus and dactylus; carpal structures absent; manal suckers in 6-7 rows, large and distinct from dactylus suckers; median 6-8 suckers of manus greatly enlarged (0.8-0.2 mm diameter), 3-6 times the diameter of marginal suckers. Dactyl suckers in 15-18 tetraserial transverse rows, grading to minute distally; no distal circlet of minute dactyl suckers exists. Protective membranes arise at the proximal end of the club and expand rapidly to broad sheaths. The marginal rows of suckers on the manus lie

TABLE 2
COMPARISON OF MORPHOLOGICAL PARAMETERS SHOWING SEXUAL DIMORPHISM IN *Loliolus noctiluca*
Regression data relating to Fig. 5. $y = bx + a$; b = regression coefficient; a = vertical intercept; r = correlation coefficient; p = significance of the regression line; n = sample size; sig. diff. = significant difference between the regression lines of males and females, with respect to slope or elevation.

Ref. Fig. 5	y	:	x	Sex	n	b	a	r	p	sig. diff.
a	HL	:	ML	♂	25	0.181	2.018	0.70	$p < 0.001$	$p < 0.05$ (elev.)
				♀	12	0.199	1.880	0.94	$p < 0.001$	
b	ED	:	ML	♂	25	0.142	0.724	0.91	$p < 0.001$	$p < 0.05$ (slope)
				♀	12	0.088	2.914	0.83	$p < 0.001$	
c	FL	:	ML	♂	25	0.682	-5.109	0.96	$p < 0.001$	$p < 0.005$ (elev.)
				♀	12	0.693	-7.194	0.99	$p < 0.001$	
d	GW	:	ML	♂	22	0.180	1.662	0.87	$p < 0.001$	$p < 0.05$ (slope)
				♀	11	0.251	-1.176	0.97	$p < 0.001$	
e	AL _I	:	ML	♂	25	0.313	-4.340	0.80	$p < 0.001$	$p < 0.05$ (elev.)
				♀	12	0.273	-3.844	0.85	$p < 0.001$	
f	AL _{II}	:	ML	♂	25	0.380	-1.928	0.84	$p < 0.001$	$p < 0.001$ (elev.)
				♀	12	0.369	-3.930	0.90	$p < 0.001$	
g	CL	:	ML	♂	25	0.303	-0.749	0.83	$p < 0.001$	$p < 0.02$ (elev.)
				♀	12	0.291	1.367	0.89	$p < 0.001$	
h	AS _I	:	ML	♂	25	0.0082	-0.1103	0.74	$p < 0.001$	$p < 0.01$ (elev.)
				♀	12	0.0067	-0.0750	0.92	$p < 0.001$	
i	AS _{II}	:	ML	♂	25	0.0094	-0.0808	0.75	$p < 0.001$	$p < 0.002$ (elev.)
				♀	12	0.0076	-0.0520	0.93	$p < 0.001$	
j	CS	:	ML	♂	24	0.0318	-0.4804	0.80	$p < 0.001$	$p < 0.05$ (elev.)
				♀	11	0.0206	-0.2636	0.75	$p < 0.001$	

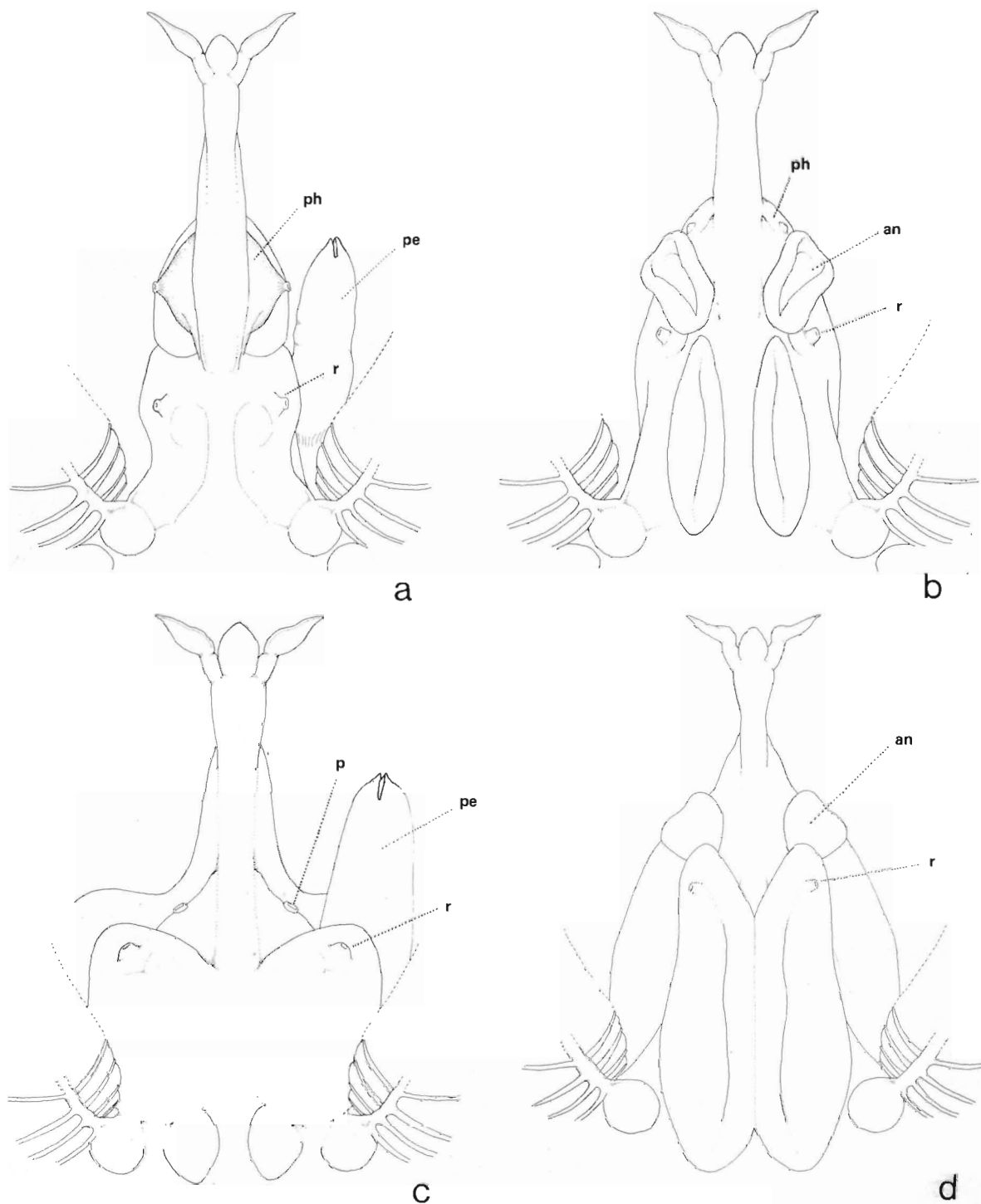


FIG. 3—Ventral views of the visceral mass. a, *Loliolus noctiluca*, male (Paratype, NMV F31121, 58 mm ML). b, *Loliolus noctiluca*, female (Paratype, NMV F31123, 33 mm ML). c, *Loliolus hardwickei*, male (ZMC, 29°18'N, 50°27'E, 49 mm ML). d, *Loliolus hardwickei*, female (ZMC, 29°18'N, 50°27'E, 53 mm ML). Abbreviations: ph, photophore. pe, penis. p, papilla. r, renal opening. an, accessory nidamental gland.

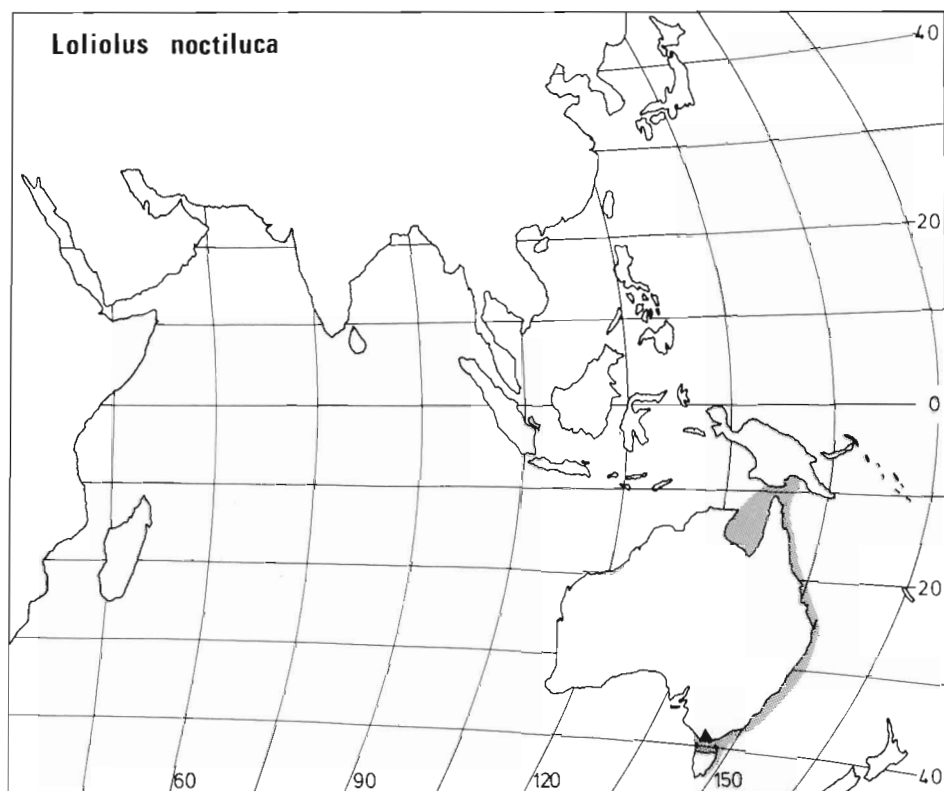


FIG. 4—Distribution of *Loliolus noctiluca* n. sp. Shaded area shows general distribution, solid triangle indicates type locality.

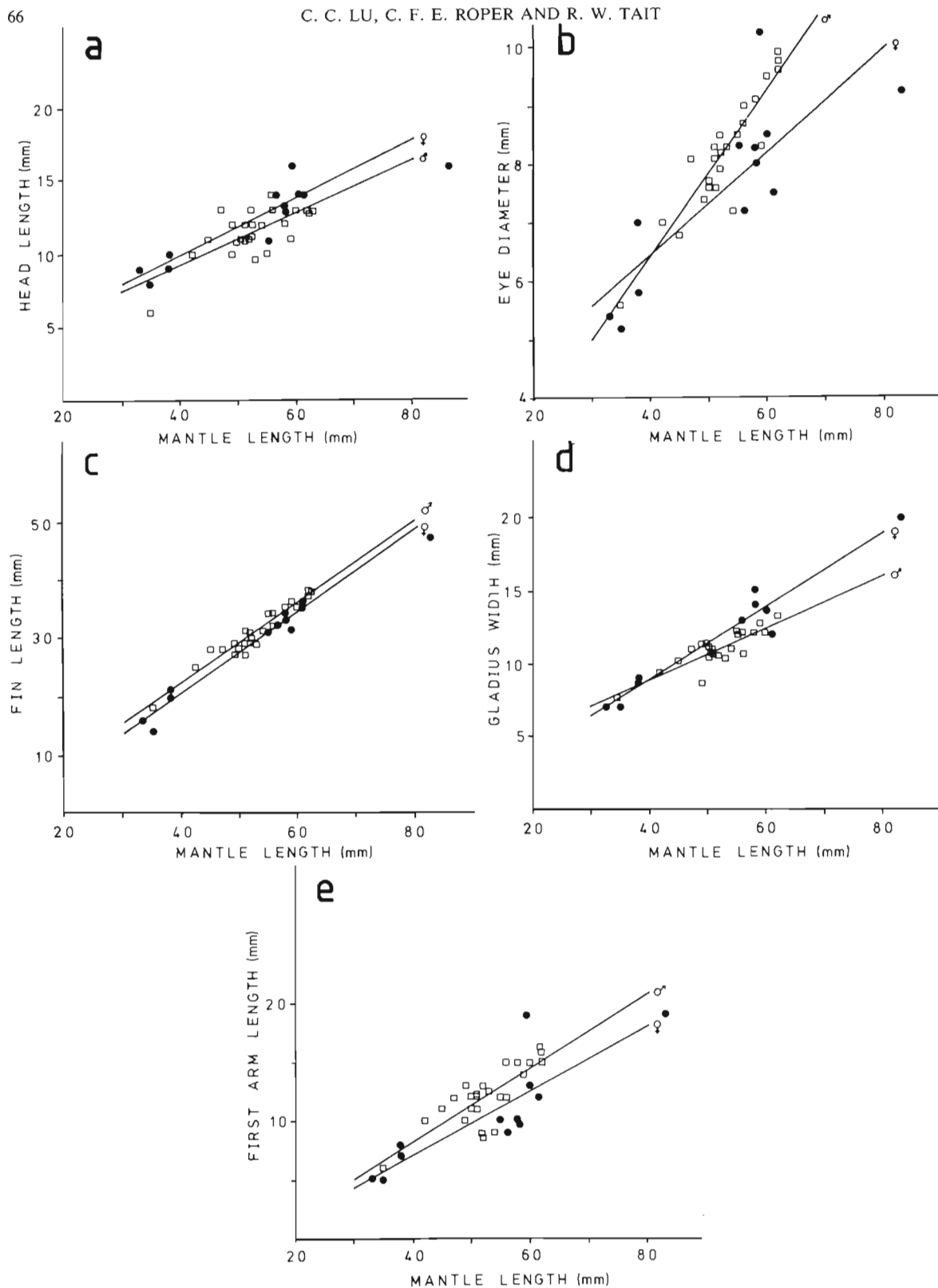
on the expanded protective membrane; sucker stalks arise distally from the broad trabeculae. The protective membranes narrow markedly along the dactylus; the ventral one extends to the tip of the dactylus and the dorsal one terminates along the proximal half of the dactylus. The swimming keel arises on the aboral angle of the club at a point in line with the fourth to fifth row of manal suckers. It expands very rapidly and becomes considerably broader than the oral surface of the dactylus (ratio of 3:2), then terminates abruptly at the tip.

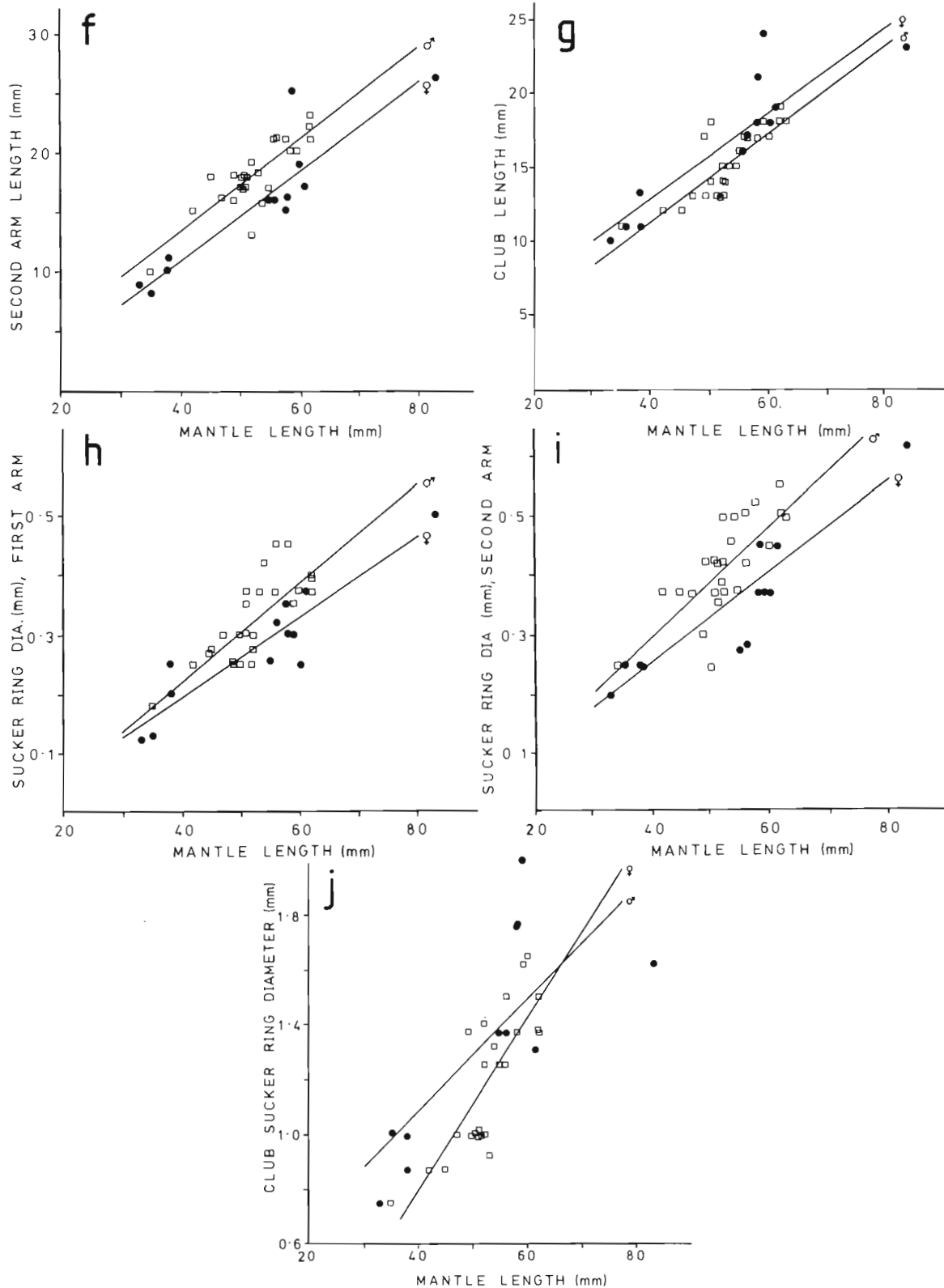
Club sucker dentition (Fig. 1i,j) includes proximal-most suckers with chitinous rings that possess very low, rounded to truncate teeth around entire ring; largest distally, minute proximally. Median manal suckers larger in females than males (see Table 1 and Section on "Sexual dimorphism"). Rings of medial manal suckers with numerous, broad, extremely low (so low that margin appears smooth or finely scalloped), plate-like teeth distally, becoming lower and narrower laterally and barely distinguishable proximally. The outer soft rings with minutely granular sculpture. Lateral manal sucker rings with 10-12 very small, low, truncate to rounded, teeth in the distal half; proximal half to two-thirds smooth. The exterior margin of manal suckers bears numerous, short ribs around entire margin giving pleated appearance. Dactyl sucker rings with 20-30 spaced, small, truncate to rounded teeth around entire margin; longer and narrower distally, grading to shorter

and broader laterally, and minutely emarginate to smooth proximally.

Lappets of *buccal membrane* with 0-6 suckers each, dentition lacking; sucker sizes vary greatly even on individual lappets. Females bear a small buccal seminal receptacle on the convoluted oral surface of the buccal membrane between the ventral lappets. *Gladius* (Fig. 2b) broad (GWI 18-26), slightly more so in females. Vane very thin, strongly curved posteriorly, widest in its anterior third; without thickenings. Free rachis short and narrow (RLI 15-20, RWI 3.8-5.2), median groove rounded, shallow; lateral rods weak.

Upper beak (Fig. 2c) with sharply pointed, long, curved rostrum; width slightly greater than length; rostral margin and tip brown to black, remaining area of rostrum and hood light brown (varies with age and state of preservation). Hood length about three-quarters of crest length; wing length about 1.5-2.0 times rostral length, cutting edge of wing irregular, no notch or prominent tooth present. Crest curved, lateral wall large, pigmented anteriorly, posterior margin with a deep indentation; margins of wing, hood, crest and lateral wall transparent. **Lower beak** (Fig. 2c) with short, pointed rostrum; light yellowish brown except near jaw angle and outer margin of rostrum which are dark reddish brown; cutting edge of rostrum straight, irregularly serrated, rostral width equal or slightly less than rostral length. Hood short, about twice rostral length, wing

FIG. 5—Sexual dimorphism in *Lololus noctiluca* n. sp. For regression formulae



and comparison of lines, refer to Table 2. Open squares—males. Solid dots—females.

length about three times rostral length, cutting edge of wing straight, irregularly serrated; club-shaped darkened area at centre of wing; entire margin of hood and wing transparent. Crest curved, crest length about four times rostral length; lateral wall length about five times rostral length, light brown at centre, transparent around margins. *Radula* (Fig. 2d) with seven transverse rows of teeth; rhachidian tooth slender with sharp curved lateral cusps; first lateral tooth long with a sharp lateral cusp; second lateral tooth straight, without cusps; third lateral tooth straight to slightly curved with broad lateral expansion; marginal plates small, oblong.

Spermatophores (Fig. 2e,f) small (SLI 5.6-9.3); sperm mass comprises 73-87% of length. Aboral part of cement body long, barrel-shaped, oral part flask shaped, connected to aboral part by a short neck. Middle tunic spirally sculptured opposite oral part of cement body, with a single groove around it opposite the neck. Oral dilation of the spermatophore contains several coils of the ejaculatory apparatus. The site for attachment of spermatophores on mature females is on the ventral buccal lappets, adjacent to the buccal seminal receptacle. On females in spawning condition, the spermatophores may be attached to a glandular patch or spermatophore pad on the ventro-lateral surface of the left funnel adductor muscle, adjacent to the opening of the oviduct.

Colour in isopropyl alcohol cream, with large brown to dark maroon chromatophores distributed evenly over mantle, head and aboral surface of arms; chromatophores on dorsal surface of mantle and head usually larger and more concentrated than on ventral surface. A narrow band of very concentrated, small chromatophores borders free dorsal margins of fins; a large semilunar patch devoid (or nearly so) of chromatophores lies medial to the chromatophore band on each fin. A broad band of large, very concentrated chromatophores extend along dorsal midline of fins. The ventral surfaces of fins are devoid of chromatophores. A pair of oval *photophores* (Fig. 3a,b) lie embedded in the postero-ventral surface of the bulbous ink sac, one photophore on each side and slightly dorsal to the intestine that lies ventral to and fused with the ink sac and duct. Each photophore has a short, conical, postero-ventrally directed papilla with a minute, recessed orifice; these lie in line with and anterior to the renal papillae. The major portion of each photophore is a large, swollen, bulb that lies deeply embedded creating a deep pit in the ink sac. A heavy sheath of bronze-coloured, reflective tissue backs the photophores and separates them from the ink sac. No duct or connection appears to exist with the ink sac other than that caused by the membranes that bind the photophores to the sac. The tissue of the photophore is cream-coloured, granular and convoluted. In fully mature females the anterior tips and openings of the swollen nidamental glands lie immediately ventral to the papillae, while the single oviduct and oviducal gland (accessory nidamental gland) opens just postero-dorsal to the papilla on the left side. In general the photophores are remnescent of the type described in *Uroteuthis barischi* (Haneda 1963).

SIZE AT MATURITY: Spermatophores occur in males as small as 40 mm ML and the nidamental glands of females begin enlargement at a similar size. All specimens larger than 50-60 mm ML were completely mature. The largest specimen examined was a female of 83 mm ML and the largest males were 62 mm ML.

Comparison of the two series from northern Port Phillip Bay (NMV F31119-F31122, F31130, F31200, F31211, USNM 813798 and USNM 813974, USNM 813977) taken in October and February respectively, shows no reproductive seasonality (Fig. 6). Animals in both samples matured at similar sizes, although mature females generally were larger than mature males. In the October sample the ratio of males to females was 10.5:1, while in the February sample it was 1.1:1. We have insufficient material to allow an interpretation of these widely variant sex ratios.

HOLOTYPE: 59 mm, mature male; National Museum of Victoria, No. F31119.

TYPE LOCALITY: Northern Port Phillip Bay, Victoria, Australia, 37°53'S, 144°50'E, 9 m. Sandy bottom with scattered patches of sea grass.

DISTRIBUTION: Inshore waters, mainly bays and estuaries, on East and Southeast Australian coasts, including Tasmania (42°56'S) to the Gulf of Papua (7°57'S) and Gulf of Carpentaria (Fig. 4). Taken in bottom trawls and beach seines from 0-46 m.

Loliolus noctiluca is the only member of its genus known in Australian waters. Previously, the easternmost record for the genus was that of *L. investigatoris* from Java (Adam 1954).

ETYMOLOGY: The specific name *noctiluca* (that shines at night, the moon) refers to the presence of photophores on the ink sac as well as to the semilunar patches devoid of chromatophores on the dorsal surface of the fins.

REMARKS: *Sexual dimorphism.* Although there is no obvious secondary sexual dimorphism in *Loliolus noctiluca*, there are a number of statistically significant morphometric differences between sexes (Fig. 5), statistical comparisons between sexes are given in Table 2. The first and second pairs of arms are longer and their suckers generally larger in males than in females. This is not evident in the third pair of arms, and the fourth pair shows differences only in the diameter of the sucker rings ($p < 0.05$). The club length and diameter of the largest manal sucker rings are greater in females; head length of females also is greater but no difference in head width is apparent. Males have slightly larger fins than females at all sizes.

In all the above, differences between regressions are with respect to elevation only. However, gladius width and eye diameter both show different growth rates between sexes (Fig. 5b, d), which may result in marked dimorphism at larger sizes.

SALINITY TOLERANCE: *Loliolus noctiluca* has been taken in estuarine waters with bottom salinities as low as 24‰ and surface salinities as low as 17.5‰, at temperatures of approximately 11°C (J. Beumer pers.

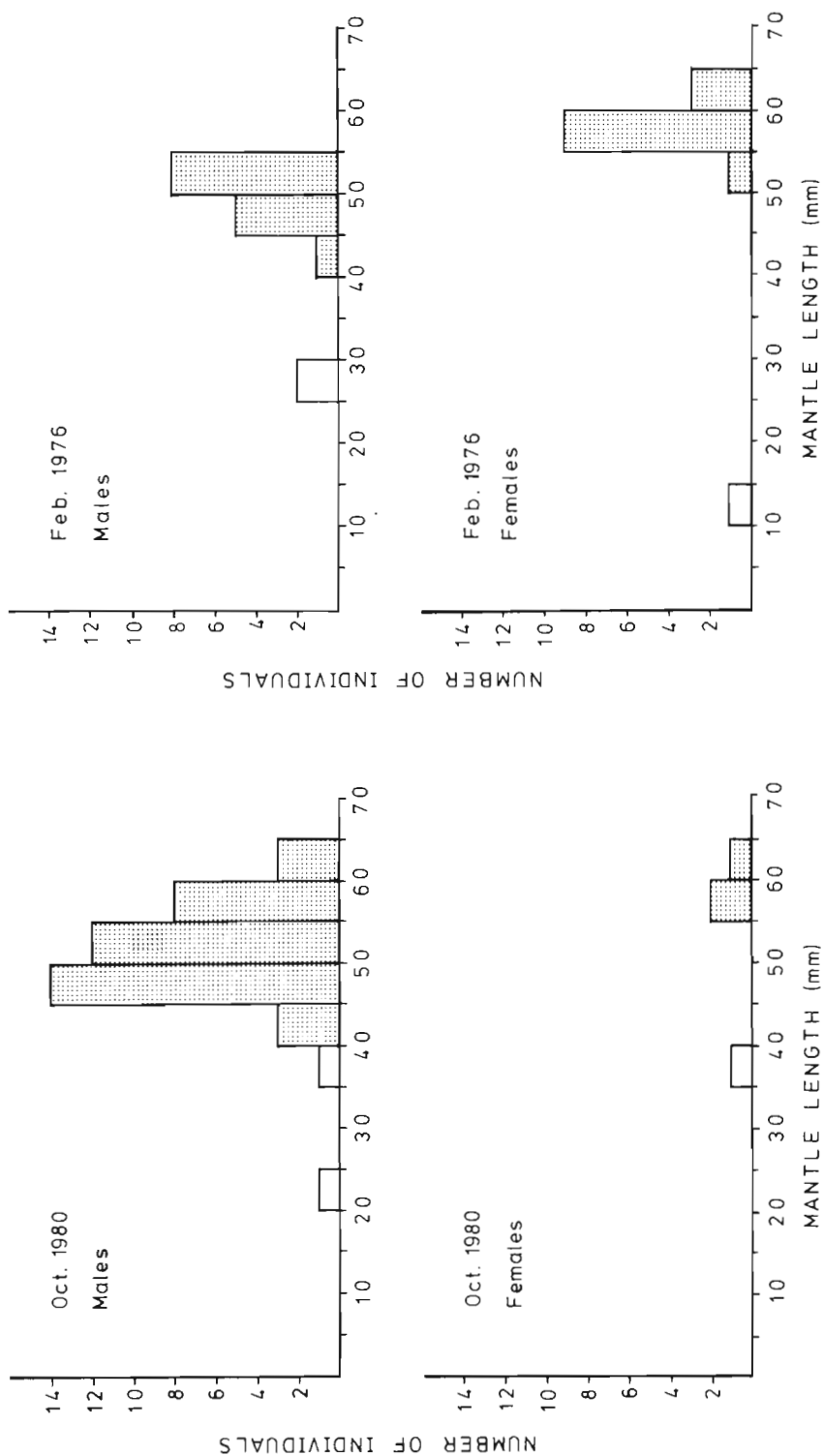


FIG. 6.—Size frequency distributions of two samples of *Loliotus noctiluca* n. sp. from northern Port Phillip Bay, Victoria. October sample, $n = 46$. February sample, $n = 30$. Shaded areas represent sexually mature specimens.

comm). The tolerance of low salinity is unusual for a cephalopod. The only other cephalopod known to withstand less saline waters is *Lolliguncula brevis* from the southeastern United States, where it has been recorded at salinities as low as 17‰ (Dragovich & Kelly 1967, Gunter 1950). *Lolliguncula tydeus* also has been reported from brackish waters, but its exact salinity tolerance is not known (Brakoniecki 1980).

GEOGRAPHIC VARIATION: Two distinct forms of *Loliolus noctiluca* exist on the East Australian coast. Animals from the inshore waters of Bass Strait have blunt or irregular teeth on the suckers of the fourth right arm of males. Males from Queensland to Papua have acute, pointed teeth on the distal 31-36 rows of suckers, with blunt teeth on the proximal 3-9 rows. This difference is not shown in females, nor do any other corresponding morphological differences appear in males. Detailed examination of the spermatophores shows them to be identical between forms. Therefore there is no justification for separate specific or subspecific status for the two forms.

***Loliolus hardwickei* (Gray, 1849)**

Figures 3c,d, 7, 8; Tables 3, 5, 6

Loligo hardwickei Gray, 1849, p. 69; Nesis, 1982, p. 132.

1856 *Loliolus typus* Steenstrup, p. 194, pl. 1, fig. 5, 5'.

1896 *Loliolus investigatoris* Goodrich, p. 8-9, pl. 2, figs. 29-37.

1916 *Loliolus investigatoris*, Massy, p. 222.

1939 *Loliolus investigatoris*, Adam, p. 66, fig. 1.

1954 *Loliolus investigatoris*, Adam, p. 129, figs 2-4.

1968 *Loliolus typus*, Silas, p. 307.

1968 *Loliolus investigatoris*, Silas, p. 307; Nesis, 1982, p. 132, fig. 34a, b, v, g.

MATERIALS EXAMINED: See APPENDIX 3.

DESCRIPTION: *Mantle* (Fig. 7a) stout (MWI 27-53), slightly dorso-ventrally flattened, mantle wall thin, body tapers evenly from about one-third of its length to posterior tip; antero-dorsal lobe conspicuous, rounded; ventro-lateral lobes low, pointed; gladius visible through body wall in mid-dorsal line for almost entire length. *Fins* together heart shaped, occupy 51-71% of mantle length, width greater than length (Table 3); fins continuous around posterior end of body, posterior margins straight, anterior margins convex. *Funnel* small, locking apparatus normal, *valve* terminal, slightly rounded; *dorsal funnel organ* with lateral limbs stout posteriorly, posterior ends rounded, limbs much narrower anteriorly, apex slender, acutely pointed, small blunt apical papilla present; ventral pads ovoid, stout, half to two-thirds of length of dorsal organ. Head and eyes large (Table 3), olfactory crest low, preocular pore present adjacent to base of third arm.

Arm order generally III, IV, II, I (III, II, IV, I in type); Arm I very short, laterally compressed, low aboral keel present for entire length; Arm II slightly compressed distally, low aboral keel present for entire length; Arm III robust, broad, dorso-ventrally compressed, well developed aboral keel present for entire

length, widest at proximal one-third; Arm IV not compressed, trapezoid in section, narrow tentacular sheath present dorsally, low flange present on entire length ventro-medially. Trabeculate protective membranes on Arms I-III well developed, margin generally straight, trabeculae weak, form high points along membrane edges in some specimens; membranes on Arm IV lower than on other arms, trabeculae weak, form high points along edge of membrane. *Suckers* largest at about half arm length, larger in males than in females (Table 3), diminish evenly to become minute at tip. Suckers in ventral rows on Arms II and III of males only similar in size to those in dorsal row but with smaller apertures, giving the ventral suckers a globose appearance; apertures of ventral suckers 0.6-0.9 times diameter of dorsal suckers. *Arm sucker dentition* shows sucker rings of the largest suckers on Arm I with 3-5 large, rounded trapezoidal teeth on distal and lateral margins, proximal plates smooth, low; suckers on Arms II and III in females and dorsal sucker row of males (Fig. 7d) with 3-7 low, square or trapezoidal teeth on distal and lateral margins, proximal plates very low; ventral suckers of Arms II and III in mature males (Fig. 7e) with only 2-4 large trapezoidal teeth on distal and lateral margins, proximal plates higher than those in the dorsal row; Arm IV with 2-5 low, square or trapezoidal teeth similar to those on Arm I.

Left ventral arm of males *hectocotylised* (Fig. 7b), slightly shorter and slimmer than the right ventral arm (Table 3), usually curved orally in preserved specimens. Suckers entirely absent, sucker stalks of ventral row entirely absent or entirely fused with the ventral trabeculate membrane; ventral membrane greatly enlarged and thickened into a fleshy ridge, proximal 2-3 trabeculae further enlarged to twice the height of the rest of the membrane, inclined slightly distally to form a proximal fleshy crest, distal to this crest the membrane diminishes evenly to tip, 2-3 minute normal suckers present at distal tip; trabeculae all broad, nearly joining, fused together for entire length by the thick, fleshy connecting membrane. Dorsal sucker row reduced to minute free papillae, not fused to the protective membranes; papillae opposite the proximo-ventral crest often enlarged, decline evenly to distal tip, 2-3 minute normal suckers at tip; dorsal protective membrane normal, fused at proximal origin to ventral membrane, low, edges may be scalloped for some of its length, declines evenly to distal tip; trabeculae weak. The proximal crest on the ventral membrane, the total lack of suckers and the curve of the arm in preserved specimens combine to give the hectocotylus a sickle-like appearance.

Tentacles short, slender, stalks naked, clubs small, only slightly expanded, CLI 22-38 (Fig. 7c); carpal suckers biserial for first 1-2 rows, other suckers on club arranged tetraserally; dactylus slender, distinct from manus; manal suckers in about 7 rows, median suckers 1.0-1.3 times diameter of marginal suckers; dactylus suckers small, only slightly larger in ventral row, suckers diminish to minute distally. Trabeculate protective membranes arise along proximal portion of carpus; low,

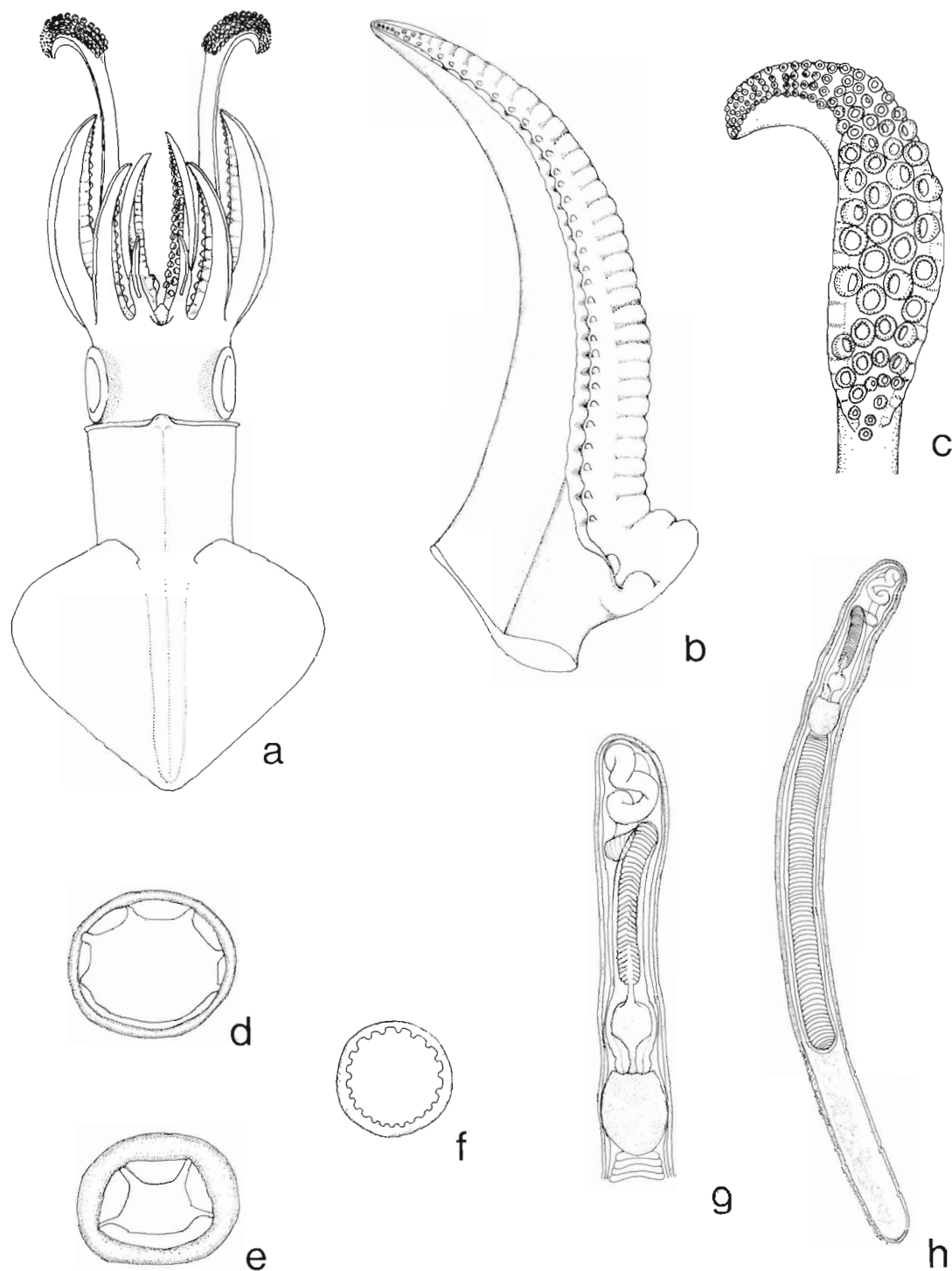


FIG. 7—*Loliolus hardwickei* (Gray), IM $\frac{3646}{7}$, male 33 mm ML. a, dorsal view. b, hectocotylied arm. c, left tentacular club. d, largest sucker ring from dorsal row of the third arm. e, sucker ring from the ventral row in same pair as (d) (d and e to same scale). f, largest club median anal sucker ring. g, oral end of spermatophore. h, spermatophore.

TABLE 3
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Loliolus hardwickei (GRAY).

Measure/ Index	MALES				FEMALES			
	n	Mean	S.D.(n-1)	Range	n	Mean	S.D.(n-1)	Range
ML(mm)	10			22-52	10			35-69
MWI	10	34.0	5.6	29-46	10	35.2	8.4	27-53
HLI	10	22.0	2.9	18-27	10	24.6	7.1	16-41
HWI	10	36.1	2.9	33-42	10	35.3	3.4	30-41
EDI	10	16.7	1.1	15-19	8	14.7	1.2	13-17
FLI	10	67.5	3.7	59-71	10	68.1	1.8	64-70
FWI	10	79.8	3.7	74-85	10	81.2	6.1	72-90
FL/FW	10	84.0	7.0	72-94	10	85.0	5.0	76-95
FA(°)	10	106.2	8.6	96-124	10	103.0	6.4	94-114
AL _I I	9	23.0	1.7	19-25	10	22.2	1.8	20-26
AL _{II} I	10	40.4	3.2	36-45	10	36.6	3.4	31-43
AL _{III} I	9	52.2	5.5	48-62	10	48.5	4.5	40-58
AL _{IV} I	10	50.3	3.7	46-57	10	46.7	4.1	41-53
HAI	8	46.5	2.3	43-49				
TtLI	10	89.3	23.4	63-147	10	88.1	11.7	73-111
CILI	10	28.8	5.9	22-38	10	29.3	2.8	25-34
AS _I I	10	0.89	0.09	0.8-1.0	10	0.73	0.08	0.6-0.8
AS _{II} I*	10	1.77	0.14	1.6-2.0	10	1.23	0.13	1.0-1.4
AS _{III} I*	10	2.03	0.16	1.9-2.3	10	1.52	0.18	1.3-2.0
AS _{IV} I	10	1.02	0.16	0.8-1.3	10	0.80	0.08	0.7-1.0
CISI	10	1.14	0.21	0.8-1.5	10	1.18	0.28	0.8-1.6
GWl	10	25.6	3.6	23-32	9	26.7	4.7	22-37
RLI	10	18.2	1.2	17-20	10	17.4	2.2	15-22
RWI	10	4.92	0.56	4.0-5.5	10	5.02	0.66	4.0-5.9
SpL(mm)	8	3.02	0.44	2.1-3.5				
SpLI	8	6.57	0.56	6.1-7.7				
SpRI	8	76.1	3.1	71-79				
SpWI	8	3.38	0.61	2.8-4.8				

* suckers from dorsal row of A_{II} and A_{III} of males used.

ventral membrane slightly broader, extends to club tip, dorsal membrane terminates along proximal portion of dactylus. Aboral swimming keel arises about halfway along club, expands distally, terminates abruptly at tip. *Club sucker dentition* on carpal sucker rings with low, square tipped, well spaced teeth on distal margin, reduced on lateral margins and absent or barely discernable on proximal margin; largest suckers on manus with 20-29 very small, blunt triangular or truncate teeth on entire margin (Fig. 7f), lower proximally; proximal teeth not evident in all specimens; marginal anal suckers with 19-28 teeth similar to those of medial suckers, larger on lateral margins. Sucker rings of largest dactylus suckers with square tipped teeth on entire margin, teeth smaller and restricted to distal margins on distal suckers; proximal plates low; suckers at tip without dentition.

Buccal membrane with seven lappets, each bearing 1-6 minute suckers, ventral lappets generally with fewer suckers; each sucker bears 5-6 low semi-lunar teeth on the distal sucker ring margin, proximal plates smooth, low. Females with a large swollen seminal receptacle on the oral surface of the buccal membrane, between the ventral lappets. *Gladius* broad (GWl 22-37), vane very thin, fragile, widest at about half gladius length,

margins strongly curved posteriorly, anterior third of vane tapers sharply in a slightly concave curve to the free rachis; rachis very slender (RLI 15-22, RWI 4.0-5.9), weak, lateral supporting rods very weak, continue to posterior tip.

Upper beak with rostrum sharply pointed, slightly curved, width equal to length; rostral margin brown with dark brown to black tip, remaining area of rostrum and hood light brown. Hood length about 70% of crest length, wing length about 1.5 times the rostral length, cutting edge of wing irregularly serrated, a prominent tooth present at jaw angle. Crest curved, lateral wall large, only lightly pigmented anteriorly, posterior margin with deep indentation, margins of wing, hood, crest and lateral wall transparent. *Lower beak* with rostrum short, pointed, light yellowish brown except margins of rostrum which are dark brown, cutting edge of rostrum straight, irregularly serrated, rostral width approximately equal to rostral length. Hood short, about 1.5 times the rostral length, wing length about twice the rostral length, cutting edge of wing straight, irregularly serrated, a large tooth present at jaw angle. Hood light brownish, wing transparent. Crest curved, crest length about 2.5 times rostral length, lateral wall length about 3.5 times rostral length, very light brown

anteriorly, transparent posteriorly. *Radula* with seven transverse rows of teeth, rhachidian with a sharp slender median tooth, lateral cusps very low, rather blunt; first lateral tooth stout, sharp with a low sharp cusp; second lateral tooth straight, stout, tip slightly rounded; third lateral tooth slender, curved, sharp with a large basal plate; marginal plates very small, irregularly shaped.

Spermatophores (Fig. 7g,h) small (SLI 6.1-7.7), slender, sperm mass comprises 71-79% of total spermatophore length; cement body in two distinct parts, aboral part stout, oval shaped, connected to oral part by a slender neck; oral part short, stout, spirally sculptured, tapers abruptly to junction with the ejaculatory apparatus; middle tunic along cement body neck with one or two closely opposed angular ridges; ejaculatory apparatus tightly coiled, several coils in the slightly dilated oral extremity of the spermatophore.

Colour in isopropyl or ethyl alcohol cream or yellow-cream; body and dorsal surface of fins sparsely covered with large purplish chromatophores, smaller on ventral body surface, dorsal surface of fins with a concentration of small chromatophores at the fin margins, few chromatophores on main fin area, ventral fin surface lacking chromatophores. Dorsal surface of head and aboral surfaces of arms and tentacles with large, sparse chromatophores; dark semi-lunar patches dorsal to each eye; ventral surface of head and funnel without

chromatophores excepting a small patch in the funnel groove. No *photophores* present in this species. A pair of small papillae are located on the integument overlying the postero-ventral surface of the bulbous ink sac, anterior to renal openings, one on either side and slightly dorsal to intestine (Fig. 3c). The location of the papillae is similar to that of the photophores in *Loliolus noctiluca*. However, there is no structure beneath the papillae referable to photophores in *L. hardwickei*. These papillae are absent in females. The accessory nidamental glands are located in their place (Fig. 3d). The function of these papillae is unknown.

SIZE AT MATURITY: Males were observed to have spermatophores in the Needham's sac from about 30 mm ML, enlargement of the nidamental glands in females was not evident until 38-40 mm ML. The largest specimen observed was a female of 69 mm ML, from the Persian Gulf.

SYNTYPES: 1 male, 33 mm ML, 1 female, 49 mm ML, India, British Museum (Natural History), London, No. 1947. 3. 15. 1-2.

DISTRIBUTION: *Loliolus hardwickei* has a wide distribution, from the northern Persian Gulf, the Indian and Burmese coasts and throughout Indonesia (Fig. 8). A single specimen (ZMC) has been recorded from the Chinese coast, opposite Taiwan. This species is found in

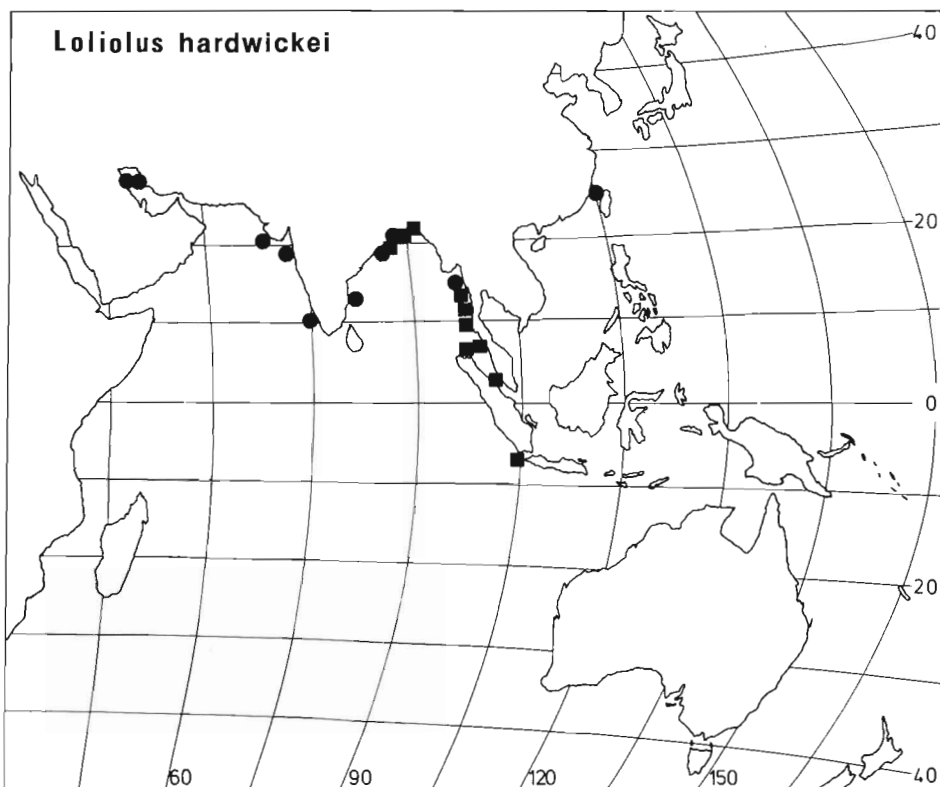


FIG. 8—Distribution records of *Loliolus hardwickei* (Gray). Solid squares represent literature records (see text). Solid dots represent new records. Gray's syntypes from India are not included.

estuaries and shallow coastal waters to a maximum recorded depth of 30 m.

REMARKS: *Loliolus typus* Steenstrup and *L. investigatoris* Goodrich are here synonymised with *L. hardwickei* (Gray), on the basis of a comparison of the type specimens of each. The syntypes of *L. hardwickei*, the holotype of *L. typus* and the syntypes of *L. investigatoris* are in a very good state of preservation and include males with a well developed hectocotylus. The species are considered conspecific primarily by a comparison of the hectocotylus of each, both bearing the proximal crest on the ventral membrane which is unique to this species. The material described as *L. typus* by Grimpe (1932) is referable to *L. affinis*; this is based on Grimpe's excellent illustration of the hectocotylus, matching exactly with that of *L. affinis*.

Massy (1916, p. 222) described a marked sexual dimorphism in this species, with males having longer arms and larger arm suckers. This is shown by the specimens examined but the difference is not so great as Massy appeared to believe. Adam (1939) noted no dimorphism, but in 1954 described the arm suckers of males as being larger in the ventral row. This does not appear to be so, although the ventral suckers may appear larger because of their smaller apertures in a similar sized cup as the dorsal row. Adam (1954) also noted the broader gladius in females. Adam (1954) considered that *Loliolus investigatoris* and *L. affinis* may be synonymous, but without detailing any reasons for this decision. Probably he was misled by Grimpe's (1932) erroneous identification and description of *L. affinis* as *L. typus*. He certainly noted the differences between Grimpe's material and his own.

Nesis (1982, p. 132) regarded *Loliolus investigatoris* Goodrich, 1896, *L. hardwickei* (Gray, 1849), and *L. rhomboidalis* Burgess, 1967, as valid species, and placed *L. typus* Steenstrup, 1856 and provisionally *L. affinis* Steenstrup, 1856 in synonymy with *L. hardwickei*. After examination of all type specimens, we conclude that *L. investigatoris*, *L. typus* and *L. hardwickei* are conspecific and that *L. affinis* is a distinct species. Nesis' provisional inclusion of *L. affinis* as a junior synonym of *L. hardwickei* was probably due to his acceptance of Grimpe's (1932) identification. This is evident by the fact that the figures shown as *L. hardwickei* by Nesis (Fig. 34d, e, e₁) are the figures of Grimpe's *L. typus* (Fig. 1B, 3A, 3B).

***Loliolus affinis* Steenstrup, 1856**

Figs 9, 10; Tables 4, 5, 6

1856 *Loliolus affinis* Steenstrup, p. 194, pl. 1, fig. 6, 6'.

1932 *Loliolus typus*, Grimpe, p. 471-486, figs. 1-3.

1968 *Loliolus affinis*, Silas, p. 307.

1982 *Loliolus hardwickei*, Nesis, fig. 34 d, e, e₁.

MATERIALS EXAMINED: See APPENDIX 4.

DESCRIPTION: Animal small. *Mantle* slightly dorso-ventrally flattened; tapers very gradually posteriorly to a blunt rounded tip; median antero-dorsal lobe rounded, pronounced (Fig. 9a); ventro-lateral lobes pointed, con-

spicuous; ventral mantle margin between lobes deeply concave to accommodate funnel. *Fins* large, FLI=49-64, FWI=57-98; heart shaped, posterior margins straight, continuous around apex of mantle; anterior margins convex with slightly developed lobes; lateral lobes broadly rounded. Fin length and width indices increase with mantle length. The gladius is visible through the integument in the anterior two-thirds of the mantle, then submerges below the muscles of the mantle and fins in the posterior one-third of the mantle. *Head* broad, short, as wide as mantle, dorso-ventrally flattened. Eyes large (EDI=14-29), a small pore present between the eye and base of third arm; olfactory apparatus conspicuous, with an indentation on posterior side of head. *Funnel* stout, bluntly tapered anteriorly, free in its anterior quarter; funnel and mantle locking cartilage simple, straight groove and ridge, strongly developed. Dorsal funnel organ large; lateral limbs very long, broad in posterior half, tapered to a rounded end posteriorly; anterior half of limb narrow with a swollen appearance. Apical papilla simple, thumb-like; ventral pads elongate, ovoid, both medial and lateral borders convexly curved, more so on lateral borders. Funnel valve very well developed, corners rounded, anterior border slightly convex.

Arms short, order III \geq IV, II, I. Arm I laterally compressed with a distinct aboral keel for nearly its entire length. Arm II laterally compressed distally, a low aboral keel present along entire arm length. Arm III robust, laterally compressed with a very conspicuous, broad, aboral (swimming) keel that remains broad distally. Arm IV trapezoid in section, well developed tentacular sheath dorso-laterally, low angular keel ventro-medially. Protective membranes very broadly developed on all arms except on Arm IV where they are low and weak; trabeculae muscular but do not extend beyond edge of protective membrane on Arms I-III; form scalloped border along membrane of Arm IV. Arm suckers larger in males. Suckers on ventral row of Arms II and III in males larger than those on dorsal row, suckers on Arm III largest, those on Arm I smallest. *Arm sucker dentition* shows chitinous rings of the largest suckers on Arm I with 3-4 truncate teeth on distal margin, proximal margin smooth or irregular. Dorsal row of suckers of Arms II and III in males and both dorsal and ventral rows of suckers in females with 3-7 low, rounded or trapezoidal teeth on distal and lateral margins, proximal plates very low, smooth (Fig. 9d); ventral suckers of Arms II and III of males with 3-5 large, higher trapezoidal teeth on distal and lateral margins, proximal margin smooth and higher than those on dorsal row (Fig. 9e), Arm IV with 3-6 low, truncate or trapezoidal teeth on distal margin, proximal margin smooth. Left ventral arm of males *hectocotyliised* (Fig. 9b) generally equal to or shorter than right ventral arm (only 3 of 10 specimens examined have longer left ventral arm). Tentacular sheath very broad running along entire length of arm. Suckers and sucker stalks in ventral row entirely absent. Ventral protective membrane broad, thickened, becoming narrower toward arm tip;

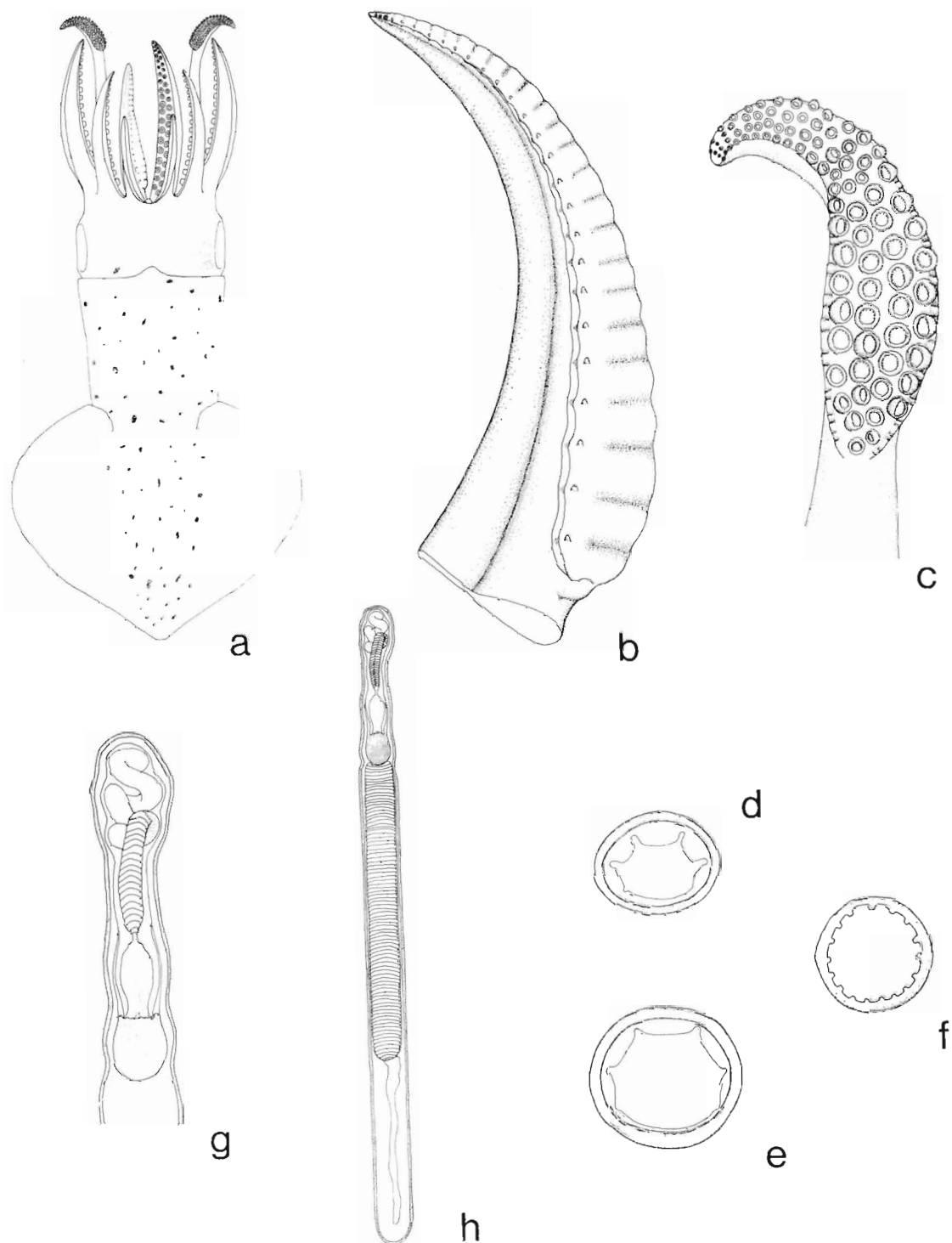


FIG. 9—*Loliolus affinis* Steenstrup. a, ZMC, male 24 mm ML, 12°10'N, 102°27'E, dorsal view. b, ZMC, 26 mm ML, 12°10'N, 102°27'E, hectocotylied arm. c, same specimen as (a), left tentacular club. d-e, CAS 030250, male 25 mm ML. d, largest sucker ring from dorsal row of third arm; e, sucker ring from the ventral row in same pair as (d) (d and e to same scale). f, same specimen as (a), largest club median manal sucker ring. g-h, same specimen as (a). g, oral end of spermatophore. h, spermatophore.

TABLE 4
MEANS, STANDARD DEVIATIONS, AND RANGES OF SELECTED MEASUREMENTS AND INDICES (IN PER CENT) OF
Loliolus affinis STEENSTRUP.

Measure/ Index	MALES				FEMALES			
	n	Mean	S.D.(n-1)	Range	n	Mean	S.D.(n-1)	Range
ML(mm)	10			19-32	5			22-39
MWI	10	39.8	6.4	33-54	5	39.8	3.7	34-44
HLI	10	28.5	9.4	22-47	5	26.7	3.9	22-32
HWI	10	41.6	6.4	35-54	5	39.8	5.4	34-48
EDI	10	20.6	3.5	18-29	5	18.6	2.9	14-22
FLI	10	58.1	4.5	49-64	5	61.4	0.9	60-63
FWI	10	75.7	15.2	57-98	5	77.7	9.0	69-92
FL/FW	10	79.0	13.2	59-95	5	79.7	7.8	68-89
FA(°)	10	110.8	16.1	90-139	5	116.6	18.2	98-132
AL _I I	10	18.7	4.4	12-28	5	16.9	2.5	14-20
AL _{II} I	10	37.2	14.4	23-65	5	29.5	9.0	23-45
AL _{III} I	10	46.6	17.6	32-82	5	41.1	12.8	30-63
AL _{IV} I	9	41.2	13.3	27-69	5	38.5	9.7	32-56
HAI	7	40.9	10.7	33-63				
TtLI	7	59.6	26.8	54-87	5	104.0	58.1	58-200
CLLI	7	19.3	2.5	15-23	5	23.9	4.5	20-29
AS _I I	7	0.76	0.22	0.5-1.0	4	0.62	0.07	0.5-0.7
AS _{II} I	7	1.33	0.54	0.9-2.2	3	0.88	0.08	0.8-0.9
AS _{III} I	7	1.48	0.67	1.0-2.5	3	1.12	0.14	1.0-1.2
AS _{IV} I	7	0.93	0.21	0.6-1.3	3	0.66	0.04	0.6-0.7
CISI	6	0.75	0.11	0.6-0.9	5	0.75	0.17	0.5-0.9
GWI	9	27.0	3.9	24-34	5	31.3	4.3	26-36
RLI	8	22.4	2.9	18-28	5	21.3	2.7	18-24
RWI	9	5.10	1.00	4.3-7.1	4	5.67	1.23	4.4-7.0
SpL(mm)	5			1.7-2.0				
SpLI	5	7.59	0.35	7.3-8.0				
SpRI	5	74.7	1.6	72-76				
SpWI	5	3.35	0.23	3.0-3.6				

trabeculae on ventral row greatly thickened, fused by the broad, fleshy, ventral protective membrane. Dorsal protective membrane thin, very narrow, diminishing distally, disappeared near arm tip. Trabeculae on dorsal row diminished, narrow, incorporated with the protective membrane producing a scalloped margin to the membrane. Suckers on dorsal row absent, diminutive papillae only remaining.

Tentacles relatively short, stalks naked and with small, slightly expanded clubs, CLI = 15-29 (Fig. 9c). Club suckers tetraserial on manus and dactylus; carpal structures absent; manal suckers in 7-9 rows, larger and distinct from dactylus suckers; median suckers of manus slightly larger (1.1-1.3 times) than the diameter of marginal suckers. Dactyl suckers in approximately 15 tetraserial transverse rows, grading to minute distally; no distal circlet of minute dactyl suckers exists. *Protective membranes* arise at the proximal end of the club, low. The protective membranes narrower along the dactylus; the ventral membrane extends to the tip of the dactylus, the dorsal membrane terminates along the proximal part of the dactylus. The swimming keel arises on the aboral angle of the club at about half its length. It expands very rapidly and becomes considerably broader than the oral surface of the dactylus, then terminates abruptly at the tip. *Club sucker dentition* (Fig. 9f) in-

cludes proximal-most suckers with chitinous rings that possess short truncate teeth around entire ring; largest distally, minute proximally. Rings of medial manal suckers with 15-20 small, truncate or blunt, well spaced teeth on entire margin, shorter proximally. The outer soft rings with minutely granular sculpture. Marginal manal sucker rings with 11-18 very small, blunt or truncate teeth, larger on lateral margins, reduced to minute protuberances medially. Dactyl sucker rings with numerous well-spaced, small, truncate to blunt teeth around entire margin.

Lappets of *buccal membrane* with 0-4 minute suckers each. Females bear a small buccal seminal receptacle on the convoluted oral surface of the buccal membrane between the ventral lappets. *Gladius* very broad (GWI 24-36), short, paddle shaped. Vane very thin, strongly curved posteriorly, widest in its anterior third; without thickenings. Free rachis short and wide (RLI 18-28, RWI 4.3-7.1), median groove rounded, shallow; lateral rods weak.

Upper beak with rostrum sharply pointed, long, curved; width equal to length; rostral margin brown with dark brown tip, remaining area of rostrum and hood light brown. Hood length about two-thirds crest length; wing length about twice rostral length, cutting edge of wing irregular, no notch or prominent tooth pre-

sent at jaw angle. Crest curved, lateral wall large, pigmented anteriorly, posterior margin with a deep indentation; posterior margins of wing, hood, crest and lateral wall transparent. *Lower beak* with rostrum short, pointed, light yellowish brown except margins of rostrum which are dark brown; cutting edge of rostrum straight, irregularly serrated, rostral width approximately equal to rostral length. Hood short, about twice rostral length, wing length about three times rostral length, cutting edge of wing straight, irregularly serrated; hood light brown with transparent margin. Wing transparent. Crest curved, crest length about four times rostral length; lateral wall length about five times rostral length, light brown at centre, transparent around margins. *Radula* with seven transverse rows of teeth, rhachidian slender, sharp with low, sharp lateral cusps; first lateral tooth small, sharp, cusp very low, pointed; second lateral tooth straight or slightly curved, sharp, no cusps; third lateral tooth curved, slender, sharp; marginal plates small, approximately equal in length and width.

Spermatophores (Fig. 9g,h) small SLI 7.3-8.0, sperm mass comprises 72-76% of total length; cement body in two distinct parts, aboral part stout, ovoid, connected

to oral part by a slender neck; oral part moderately long, dilated, tapers gradually to junction with the ejaculatory apparatus; middle tunic does not follow contour of the cement body; slight spiral sculpturing along oral end of cement body; ejaculatory apparatus strongly coiled, several coils in the slight dilation at the oral extremity of the spermatophore.

Colour in isopropyl alcohol cream, with brown to dark maroon chromatophores distributed evenly over mantle, head and aboral surface of arms; chromatophores on dorsal surface of mantle and head usually larger and more concentrated than on ventral surface. A broad band of large chromatophores extend along dorsal midline of fins. The ventral surfaces of fins are devoid of chromatophores. No *photophore* is present. Males possess one pair of small papillae on the ink sac, identical to that described for *L. hardwickei*.

SIZE AT MATURITY: Spermatophores are present in males as small as 22 mm ML. The nidamental glands of females began enlargement at a similar size, but no mature female was found in the material studied. The largest male specimen studied is 32 mm ML and the largest female examined is 39 mm ML.

TABLE 5
MEASUREMENTS OF HOLOTYPES AND SYNTYPES OF ALL SPECIES OF *Loliolus* STEENSTRUP 1856.
(Except where otherwise indicated, all measurements are in millimetres.)

	<i>L. hardwickei</i> Syntype	<i>L. hardwickei</i> Syntype	<i>L. typus</i> Holotype	<i>L. affinis</i> Syntype	<i>L. affinis</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. investigatoris</i> Syntype	<i>L. nociluca</i> Holotype
Sex	♂	♀	♀	♂	♀	♂	♀	♀	♂
ML	33	49	27	32	39	22	33	35	59
VML	32	40	23	32	38	19	31	31	54
MW	14	17	13	15	16	10	13	13	17
HL	11	14	9	10	9	5	9	9	11
HW	13	13	14	14	13	9	13	13	17
ED	6	7	7	8	7	4	5	6	8
FL	23	32	17	20	24	13	23	24	36
FW	29	43	22	32	31	17	27	25	43
FA(°)	134	104	127	118	112	124	101	102	108
AL _I	9	12	6	7	7	4	8	7	14
AL _{II}	20	21	17	12	9	8	15	13	20
AL _{III}	23	27	23	18	16	14	20	18	23
AL _{IV}	18	24	16	14	14	12	17	17	22
HcAI	18		16	14		12	15		22
TiL	55	66	44		44	33	29	30	38
CiL	10	21	7		8	8	8	9	18
AS _I	0.4	0.3	0.2			0.2	0.3	0.2	0.4
AS _{II} *	0.7	0.5				0.3	0.6	0.4	0.5
AS _{III} *	0.7	0.6				0.4	0.7	0.5	0.6
AS _{IV}	0.4	0.4	0.3			0.2	0.4	0.2	0.3
CIS	0.3	0.7	0.3		0.2	0.2	0.3	0.3	1.6
SpL							2.1		5.0
NL		10			8.4			6.5	
GW			9		13	7	11	9	13
RL			6.6		7.7	4.5	6.4	6.7	9.4
RW			1.7		2.5	1.2	1.8	2.0	2.3

* suckers from dorsal row of A_{II} and A_{III} of males used.

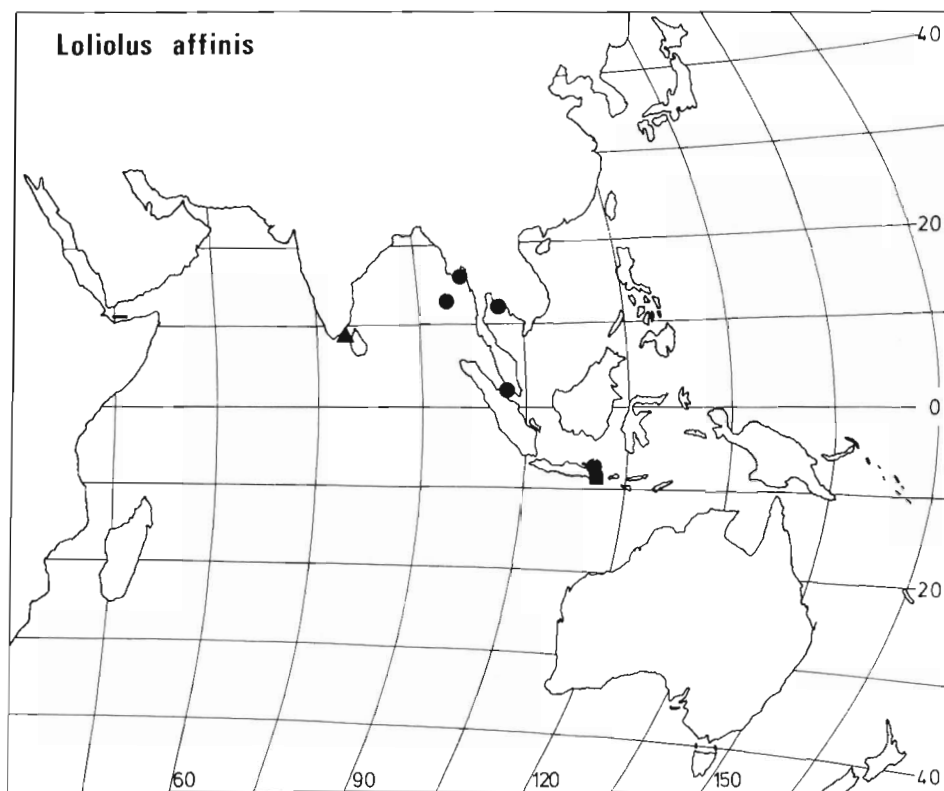


FIG. 10—Distribution records of *Loliolus affinis* Steenstrup. Solid triangle—type locality (approximate). Solid squares—literature records (see text). Solid dots—new records.

SYNTYPES: 1 male, 32 mm ML, 1 female, 39 mm ML, Zoological Museum, University of Copenhagen.

TYPE LOCALITY: "Captured by Governor Christensen on a voyage from the Cape [C. Comorin?] to Tranquebar [India]" (Steenstrup 1857, p. 89). Specimens probably then come from the Gulf of Manaar, Palk Strait region, southern India.

DISTRIBUTION: *Loliolus affinis* is widely distributed in the Bay of Bengal and southeast Asian waters. It has been recorded from southern India (type) and East Java (Grimpe 1932). New records for this species are from the eastern Bay of Bengal, Andaman Islands, southern Malaya, and the Gulf of Thailand (Fig. 10).

SUBMERGENCE OF *Loliolus steenstrupi* AND *Loliolus rhomboidalis*

Loliolus steenstrupi Dall, 1871, based on a single specimen from the Gulf of California, was very inadequately described without illustration or designated type specimen, and Berry (1929, p. 278) claimed it should be "thrown into limbo as unidentifiable". Berry recognized that his *Loliopsis chiroctes* Berry, 1929 possibly could be Dall's *steenstrupi*. This may be so, but Dall's description and the absence of any specimens does not permit it to be placed in synonymy. Thorough searching at NMNH

confirms that no type exists, and indeed, it must be considered a *nomen dubium*.

Loliolus rhomboidalis was described by Burgess (1967) based on specimens collected from the Bay of Bengal and the Andaman Sea. The species is sufficiently different from other congeners that Burgess redefined the genus to accommodate her new species. Natsukari (1983) reported that the original description and illustrations of *Loliolus rhomboidalis* apply very well to *Loligo kobeensis* Hoyle, 1885. Thus, he placed *Loliolus rhomboidalis* in synonymy with *Loligo kobeensis*. During the present study, additional material of *L. rhomboidalis* from the eastern Gulf of Thailand, as well as the holotypes of *Loligo kobeensis* and *Loliolus rhomboidalis* were examined. We agree with Natsukari's conclusion that *rhomboidalis*, being the only species to possess several normal suckers on the proximal portion of the hectocotyliised arm and the only species to have rhomboidal fins, does not belong to the genus *Loliolus*. We accept Natsukari's decision to place *Loliolus rhomboidalis* in synonymy with *Loligo kobeensis*.

COMPARISON OF SPECIES

The genus *Loliolus* was erected by Steenstrup (1856), who separated it from the genera *Loligo* and *Sepioteuthis* on the basis of the hectocotyliised arm

which "throughout its whole length it has not the least trace of a sucker, the surface on which the suckers should be situated being even converted into a compressed, obtusely-toothed edge; we find that all the teeth of this edge are produced from the fused bases of the peduncles of the inner series of acetabula, whilst those of the other row scarcely the smallest trace is left" (Steenstrup 1857, p. 89). Burgess (1967) redefined the genus as having up to seven normal suckers on the proximal portion of the hectocotyliised arm. Following the conclusion reached by Natsukari (1983) and us to synonymise *L. rhomboidalis*, the original definition of the genus as defined by Steenstrup should be retained. The genus *Loliolus* is thus defined as a loliginid squid with heart-shaped fins, with the whole length of the left ventral arm of the male hectocotyliised and with no normal suckers on the proximal portion of the hectocotyliised arm. Of the six nominal species previously placed in the genus *Loliolus*, i.e., *L. hardwickei*, *L. typus*, *L. affinis*, *L. investigatoris*, *L. steenstrupi*, and *L. rhomboidalis*, only *L. hardwickei* and *L. affinis* are recognised as valid. The genus now contains *L. hardwickei* (Gray), *L. affinis* Steenstrup, and *L. noctiluca* n. sp.

Loliolus noctiluca may be readily distinguished from other *Loliolus* by the presence of a pair of luminescent organs, a conspicuously papillated hectocotylus, and large, smooth ringed manal suckers. Each of these features is unique within the genus. The presence of luminescent organs on *L. noctiluca* is of interest. Examination of *L. hardwickei* and *L. affinis* reveals that comparable luminescent organs are lacking in these species. In the males of these species, a pair of papillae with a small orifice is located on the ink sac, anterior to the renal opening, similar to the location of luminescent organs in *L. noctiluca*. However, unlike *L. noctiluca* where the orifice opens into the bean-shaped organ, in the males of other congeners there is no structure beneath this orifice that is referable to a luminescent organ. These papillae with orifice are absent in the females of both species. The accessory nidamental glands are located in the position of the papillae. The function of these papillae is unknown.

The other members of the genus may be distinguished from each other by comparison of the hectocotyliised arms: *L. hardwickei* bears a large proximal crest which is absent in *L. affinis*. Both *L. hardwickei* and *L. affinis* bear modified suckers on Arms II and III of the males. In *L. hardwickei* the suckers on the dorsal row are larger while the reverse is true in *L. affinis*. The tentacular club of *L. hardwickei* and *L. affinis* are similar, being barely expanded and with median and marginal manal suckers of subequal size. The clubs of *L. noctiluca* are greatly expanded and exhibit a large disparity in size between median and marginal manal suckers. A detail comparison of characters separating species of the genus *Loliolus* is found in Table 6.

KEY TO THE SPECIES OF *LOLIOLUS*

1. One pair of luminescent organs present on ink sac,

- rings of large manal suckers smooth, hectocotylus conspicuously papillated *L. noctiluca*
 No luminescent organs on ink sac, large manal sucker rings not smooth, hectocotylus not conspicuously papillated 2
 2. Hectocotyliised arm with a large proximal crest *L. hardwickei*
 No proximal crest present on hectocotyliised arm *L. affinis*

DISCUSSION

The genus *Loliolus*, the third earliest loliginid genus to be erected, appears to be a natural, well-defined group readily distinguishable from other genera in the family Loliginidae. Members of the genus *Loliolus* differ from other loliginid genera in having heart-shaped fins and in having the whole length of the left ventral arm in males hectocotyliised with no normal suckers on the proximal portion of the arm. The fins of other loliginid are rhomboidal except in *Sepioteuthis* which has lateral fins similar to those in *Sepia*. The hectocotylus of all other loliginids affects only the distal portion of the arm with normal suckers retained on the proximal portion of the arm.

Luminescent organs have been described for a number of Indo-West Pacific loliginid squid: *Loligo edulis* (Okada, 1927), *L. chinensis* (Okada, 1927), *Doryteuthis sibogae* (Natsukari, 1976) and *Uroteuthis bartschi* (Haneda, 1963). Luminescent organs have not been reported from loliginids of the eastern Pacific and Atlantic Oceans.

Okada (1927) described the light organs of *L. edulis* as a pair of flat organs on each side of the ink sac and stated that they were the same as those of the Sepiidae both externally and internally. Kishitani (*vide* Haneda 1963) cultivated luminescent bacteria from the ink sac organs of *L. edulis*. A detailed account of observations in living specimens, structure of the light organ, and the culture of luminescent bacteria in *U. bartschi* was presented by Haneda (1963).

The light organs described for *L. noctiluca* appear similar to those described for *Loligo* and *Uroteuthis*, both externally and in gross anatomy. Thus, the light organs in *L. noctiluca* are most likely functioned by symbiotic luminous bacteria, although no luminous activity has been observed. The absence of a functional light organ and, in males, the presence of a papilla in its place in *L. hardwickei* and *L. affinis* are of interest. The fact that light organs do not occur in all members of *Loliolus* is comparable to that in the genus *Loligo* where not all members possess light organs. The presence of one pair of papillae in the males and their absence in the females of two members of *Loliolus* is without parallel in Loliginidae. In a thorough examination of material on hand, which includes specimens of *Loligo japonica*, *L. pealei*, *L. vulgaris*, *Lolliguncula brevis*, *Alloteuthis media*, *A. subulata* and *Doryteuthis plei*, no similar papillae were found.

Boletzky (1971) described a pair of organs of

TABLE 6
COMPARISON OF SELECTED CHARACTERS OF THE THREE SPECIES OF *Loliolus*.

Species	Type Specimens	Size at Maturity and Maximum Size Known	Luminescent Organs	Arm Suckers, A _{III}
<i>L. hardwickei</i> (Gray)	<i>hardwickei</i> : Syntypes, male, 33 mm ML, female, 49 mm ML, India (BMNH)			
= <i>L. typus</i> Steenstrup	<i>typus</i> : Holotype, male, 27 mm ML, locality unknown (ZMC)	Mature: males: 30 mm ML females: 38-40 mm ML	Absent	Suckers of dorsal and ventral rows in males sub- equal in size but those on ventral row with smaller aperture
= <i>L. investigatoris</i> Goodrich	<i>investigatoris</i> : Syntypes, 2 males, 22-33 mm ML; 4 females, 35-47 mm ML, Bay of Bengal (ZMC)	Max. Size: males: 53 mm ML females: 69 mm ML		
<i>L. affinis</i> Steenstrup	Syntypes, male, 32 mm ML; female, 39 mm ML, S.E. Indian Coast (ZMC)	Mature: males: approx. 22 mm ML females: no mature specimen was found Max. Size: males: 32 mm ML females: 39 mm ML	Absent	Suckers on ventral row in males larger than those on dorsal row
<i>L. noctiluca</i> n.sp.	Holotype, male, 59 mm ML, Northern Port Phillip Bay, Victoria Australia (NMV)	Mature: both sexes: 40-50 mm ML Max. Size: males: 62 mm ML females: 83 mm ML	One pair on ink sac	Suckers on dorsal and ventral rows in both sexes similar

unknown function which he called "epirenal bodies" in male *Neorossia caroli*. The position and the superficial appearance of these organs are similar to the above-mentioned papillae in *Loliolus*. We suspect these papillae in the males of *L. hardwickei* and *L. affinis* probably represent vestiges of retrogressive light organs, and in the females, these organs have totally degenerated. However, as stated by Boletzky (1971) on *Neorossia caroli*, the entire complex comprising the papillae, the accessory nidamental glands, and the light organs need to be investigated in order to determine the true nature of these papillae. A detailed study of the light organs in *Loliolus*, whether functional or rudimentary, must wait until adequate material becomes available. Such a study on *L. noctiluca* is being planned.

The location on the body of a female loliginid squid where spermatophores are affixed during copulation is generally considered to be of taxonomic value. Steenstrup (1881, p. 242), on the genus *Lolliguncula* and its type species, *L. brevis*, pointed out the fact that the females received spermatophores on the inner wall of the mantle, near the left gills. In 1887 (Volsøe *et al.* 1962, p. 203) Steenstrup re-affirmed the "difference in the mode of placing of the spermatophores" between

Loligo and *Lolliguncula*. For the genus *Loligo*, Steenstrup (1856, p. 110) reported that the spermatophores were attached to the lips (i.e., buccal membrane) of the female. Steenstrup's statement on the difference of the mode of attachment of spermatophores between *Loligo* and *Lolliguncula* was followed by Naef (1912, pp. 743-744). This seemingly clear-cut difference was later found to be over-simplified. Drew (1911, pp. 327-328) reported that in *Loligo pealei*, spermatophores were found to be attached either on the seminal receptacle, located on the buccal membrane, or on the left side of the inner mantle wall. McGowan (1954) and Fields (1965) reported a similar situation in *Loligo opalescens*. Attachment of spermatophores on the inner mantle wall of the females is, therefore, not restricted to the members of *Lolliguncula*. Examination of material on hand of *Lolliguncula* confirms the absence of a buccal seminal receptacle on *L. brevis* and the spermatophores are attached on the inner mantle wall near the left gill. On the other hand, in all three gravid female specimens of *L. mercatoris*, a buccal seminal receptacle, a structure that has not been described to date, is clearly present. The presence of the seminal receptacle on the buccal membrane of the females of all three species of

Arm Sucker Dentition, A _{III}	Club	Club Manal Suckers	Dentition of Largest Manal Suckers	Hectocotylus
Dorsal row in males and both dorsal and ventral rows in females with 3-7 low square teeth distally; ventral row in males with 2-4 large, trapezoidal teeth distally	Small, CILI = 22-38%, slightly expanded	Small, CISI = 0.8-1.6%, medial suckers 1.0-1.3 times the size of marginal suckers	20-29 small, well spaced truncate or rounded teeth on entire margin	Ventral protective membrane enlarged, thickened, fleshy, raised into tall crest proximally. Dorsal suckers reduced to minute papillae, dorsal protective membrane normal
Dorsal row in males and both dorsal and ventral rows in females with 3-7 low, rounded or trapezoidal teeth on distal and lateral margin, ventral row in males with 3-5 large, trapezoidal teeth distally	Small, CILI = 15-29%, slightly expanded	Small, CISI = 0.5-0.9%, medial suckers 1.1-1.3 times the size of marginal suckers	15-20 small, truncate or blunt, well spaced teeth on entire margin	Ventral protective membrane enlarged, thick, fleshy, no proximal crest. Dorsal suckers reduced to minute papillae, dorsal protective membrane thin, narrow, diminishes distally
4-7 large, truncate or round teeth in distal half, proximal margin smooth	Large, CILI = 25-41%, greatly expanded	Large, CISI = 1.7-3.4%, medial suckers 3-6 times the size of marginal suckers	Smooth	Dorsal and ventral rows with enlarged papillae, larger ventrally. Ventral papillae only partially fused to ventral protective membrane

Loliolus and the discovery of the "spermatophore pad" on the left funnel adductor muscle of some individuals of *L. noctiluca* again demonstrates the need for a critical investigation to delineate the genera in the family Loliginidae.

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APPENDIX 1
MATERIALS EXAMINED: *Loliolus noctiluca*

Sex	ML (mm)	Reg. No.	Location		Date	Depth (m)	Collector
Holotype							
M	59	NMV F31119	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
Paratypes							
M	53	USNM 813977	37°51'S,	144°56'E	10-ii-76	6	CFE Roper
M	60	NMV F31120	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	58	NMV F31121	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	62	NMV F31122	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
M	52	USNM 813798	37°53'S,	144°56'E	29-x-80	9	FRV "Sarda"
F	33	NMV F31123	38°21'S,	145°13'E	9-iv-75	—	M.U.Z.D.
F	58	NMV F31124	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
F	56	USNM 813799	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
M	52	QM M010577	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
F	58	QM M010578	27°15'S,	153°15'E	26-iii-81	—	"Rejoice"
M	54	AM C129497	08°45'S,	146°25'E	7-vi-61	—	DAS Fisheries
F	61	AM C129497	08°45'S,	146°25'E	7-vi-61	—	DAS Fisheries

APPENDIX 2
OTHER MATERIAL OF *Loliolus noctiluca* EXAMINED

No.	Sex	ML (mm)	Reg. No.	Location		Date	Depth (m)	Collector
1	M	55	NMV F31191	38°21'S,	145°13'E	3-ix-1974	—	M.U.Z.D.
1	M	52	NMV F31190	38°21'S,	145°13'E	8-vi-1974	—	M.U.Z.D.
1	M	49	NMV F31204	38°21'S,	145°13'E	7-vi-1974	—	M.U.Z.D.
1	F	55	NMV F31204	38°21'S,	145°13'E	7-vi-1974	—	M.U.Z.D.
1	M	35	NMV F31203	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
2	F	35-38	NMV F31203	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	F	59	NMV F31192	38°36'S,	146°55'E	21-vii-1979	—	J. Beumer
13	M	42-62	NMV F31130	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
2	F	38-60	NMV F31130	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
1	F	83	AM C126821	34°00'S,	151°13'E	14-x-1974	5	V. Wadley
1	M	44	NMV F31205	Gippsland Lakes, Victoria		—	—	B. Rigby
1	F	35	NMV F31208	38°37'S,	145°32'E	17-i-1980	46	"Mary Kain"
1	M	50	NMV F31194	Gippsland Lakes, Victoria		—	—	J. Beumer
2	F	41-54	NMV F31199	38°36'S,	146°55'E	11-xii-1979	—	J. Beumer
1	M	46	NMV F31197	Gippsland Lakes, Victoria		—	—	J. Beumer
1	M	43	NMV F31198	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	F	33	NMV F31198	38°21'S,	145°13'E	9-iv-1975	—	M.U.Z.D.
1	M	50	NMV F31209	38°36'S,	146°55'E	21-vii-1979	—	J. Beumer
1	F	47	NMV F31195	38°36'S,	146°55'E	13-xii-1979	—	J. Beumer
1	F	65	NMV F31202	38°36'S,	146°55'E	13-xii-1979	—	J. Beumer
1	F	61	NMV F31206	37°52'S,	148°02'E	10-viii-1979	—	J. Beumer
1	M	61	NMV F31625	37°53'S,	147°49'E	6-viii-1979	3-5	D. Hobday
1	F	59	NMV F31625	37°53'S,	147°49'E	6-viii-1979	3-5	D. Hobday
1	F	75	NMV F31627	37°59'S,	147°44'E	5-viii-1979	3-5	D. Hobday
2	M	32-43	NMV F31630	Lake Victoria, Victoria		4-viii-1981	3-5	D. Hobday
1	F	27	NMV F31630	Lake Victoria, Victoria		4-viii-1981	3-5	D. Hobday
5	M	21-53	NMV F31200	37°53'S,	144°56'E	29-x-1980	10	FRV "Sarda"
1	M	54	NMV F31201	38°05'S,	145°07'E	—	—	G. Carruthers
1	F	42	NMV F31201	38°05'S,	145°07'E	—	—	G. Carruthers
2	M	60-60	NMV F31632	27°40'S,	153°29'E	6-xi-1981	32	"Iron Summer"
1	F	69	NMV F31632	27°40'S,	153°29'E	6-xi-1981	32	"Iron Summer"
4	M	43-48	NMV F31207	Moreton Bay, Qld.		26-iii-1981	—	"Rejoice"
4	F	36-55	NMV F31207	Moreton Bay, Qld.		26-iii-1981	—	"Rejoice"
42	M	20-60	NMV F31211	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"
4	F	37-62	NMV F31211	37°53'S,	144°56'E	29-x-1980	9	FRV "Sarda"

APPENDIX 2 continued
OTHER MATERIAL OF *Loliolus noctiluca* EXAMINED

No.	Sex	ML (mm)	Reg. No.	Location	Date	Depth (m)	Collector
3	F	52-65	NMV F31193	Botany Bay, NSW	3-ii-1981	—	G. Cuthbert
1	M	44	NMV F31196	Moreton Bay, Qld.	27-ii-1981	11-16	M. Potter
5	F	52-70	NMV F31196	Moreton Bay, Qld.	27-ii-1981	11-16	M. Potter
4	M	49-56	NMV F31210	16°43'S, 145°40'E	7-v-1981	6	"Southern Ocean"
6	F	44-70	NMV F31210	16°43'S, 145°40'E	7-v-1981	6	"Southern Ocean"
1	M	23	NMV F31629	27°36'S, 153°19'E	—	—	V. Wadley
1	M	15	NMV F31681	Moreton Bay, Qld.	—	—	CSIRO
3	F	49-73	NMV F31626	Moreton Bay, Qld.	22-vii-1981	—	"Alwayne"
2	M	39-39	NMV F31634	42°55'S, 147°35'E	—-v-1979	—	S. Bell
2	F	45-52	NMV F31634	42°55'S, 147°35'E	—-v-1979	—	S. Bell
5	M	26-36	NMV F31637	Storm Bay, Tas.	27-iv-1977	—	"Panghana"
6	F	28-39	NMV F31637	Storm Bay, Tas.	27-iv-1977	—	"Panghana"
5	M	33-42	NMV F31635	42°56'S, 147°25'E	23-vi-1976	—	Tas. Fish. Dev. Auth.
1	M	33	NMV F31633	33°49'S, 152°17'E	9-ix-1981	9-15	FRV "Kapala"
1	F	66	NMV F31636	37°53'S, 147°52'E	—-vi-1979	—	Vic. Fish.
1	M	61	NMV F31638	37°52'S, 144°56'E	—-v-1876	—	D. Kershaw
2	F	35-54	NMV F31639	37°51'S, 144°54'E	2-ii-1947	—	H. Morrison
2	F	41-47	NMV F31640	37°52'S, 144°56'E	—-xii-1878	—	—
1	F	74	NMV F31641	Gippsland Lakes, Vic.	—-v-1939	—	T. Yates
1	F	42	NMV F31642	Locality unknown	—	—	—
1	F	43	NMV F31643	37°55'S, 144°59'E	—-v-1878	—	—
1	F	39	NMV F31644	37°55'S, 144°59'E	—-vii-1866	—	—
1	M	48	NMV F31645	Sandridge, Vic.?	—-xii-1872	—	—
1	F	61	NMV F31645	Sandridge, Vic.?	—-xii-1872	—	—
1	M	34	NMV F31646	Locality unknown	—	—	—
1	M	45	AM C102666	33°51'S, 151°10'E	16-iii-1972	8	H. Recher & J. Paxton
1	F	48	AM C102666	33°51'S, 151°10'E	16-iii-1972	8	H. Recher & J. Paxton
1	M	42	AM C126820	Sydney Fish Market	—-v-1977	—	—
3	M	39-44	AM C102661	34°00'S, 151°13'E	18-iii-1975	3	V. Wadley
2	F	59-72	AM C102662	34°00'S, 151°13'E	21-xi-1974	5	V. Wadley
2	M	33-54	AM C131855	34°00'S, 151°14'E	26-8-i-1971	—	NSW Fish.
2	F	42-43	AM C131855	34°00'S, 151°14'E	26-8-i-1971	—	NSW Fish.
2	F	55-61	AM C36839	Port Jackson, NSW	—	—	—
1	M	42	AM C131851	Lake Macquarie, NSW	—-v-1953	—	—
1	F	52	AM C131851	Lake Macquarie, NSW	—-v-1953	—	—
1	F	61	AM C56308	23°52'S, 151°20'E	—-vi-1930	—	W. Bedsor
1	M	41	AM C126818	23°52'S, 151°12'E	—-iii-1977	—	P. Saenger
2	F	50-52	AM C131852	17°24'S, 140°07'E	1963-1964	—	CSIRO
3	M	31-55	AM C126829	17°24'S, 140°08'E	—-xii-1976	7	CSIRO
3	F	35-45	AM C126829	17°24'S, 140°08'E	—-xii-1976	7	CSIRO
1	F	50	AM C131850	17°24'S, 140°46'E	—-xii-1963	—	CSIRO
4	M	48-52	AM C131846	16°23'S, 141°10'E	20-vi-1964	4.5	CSIRO
3	F	47-62	AM C131846	16°23'S, 141°10'E	20-vi-1964	4.5	CSIRO
1	F	41	AM C126825	17°25'S, 140°43'E	—-xii-1976	3.5	CSIRO
1	F	45	AM C119565	8°47'S, 146°33'E	7-vi-1961	—	DAS Fisheries
1	M	50	AM C127910	7°57'S, 145°46'E	4-iv-1955	—	DAS Fisheries
3	F	56-64	AM C127910	7°57'S, 145°46'E	4-iv-1955	—	DAS Fisheries
1	M	45	AM C127905	8°51'S, 146°36'E	22-v-1969	—	DAS Fisheries
15	M	25-54	USNM 813974	37°51'S, 144°56'E	10-ii-1976	6	CFE Roper
14	F	14-68	USNM 813974	37°51'S, 144°56'E	10-ii-1976	6	CFE Roper

APPENDIX 3
MATERIALS EXAMINED: *Loliolus hardwickei*

No.	Sex	ML (mm)	Source & Reg. No.	Location	Date	Depth (m)	Collector
<i>Syntypes</i>							
1	♂	33	BMNH	India	1836	—	General Hardwicke
1	♂	49	1947.3.15.1-2	India			
<i>Other material</i>							
1	♂	27†	Z.M.C.	Unknown	—	—	—
1	♂	22*	IM 44A = $\frac{3645}{7}$	21°39'N, 88°39'E	—	—	HMS "Investigator"
1	♂	33**	IM 45A = $\frac{3646}{7}$	21°39'N, 88°39'E	—	—	HMS "Investigator"
1	♀	35*	IM 47A = $\frac{7783}{6}$	15°13'N, 97°47'E	—	—	HMS "Investigator"?
1	♀	39	IM $\frac{423}{1}$	19°23'N, 85°09'E	—	14-17	HMS "Investigator"?
1	♀	45	IM $\frac{424}{1}$	13°05'N, 80°20'E	—	—	HMS "Investigator"?
1	♀	47	IM $\frac{425}{1}$	13°05'N, 80°20'E	—	—	HMS "Investigator"?
4	♂	35-40	Z.M.C.	29°57'N, 49°08'E	4-III-1938	10	G. Thorson
2	♀	56-65					
4	♂	45-52	Z.M.C.	29°18'N, 50°27'E	4-III-1937	20-24	G. Thorson
4	♀	49-69					
1	♂	40	CAS 030251	11°17'N, 75°47'E	13-I-1941	—	A.W.C. Herre
6	♂	27-35	UMML 1789	21°23'N, 69°46'E	16-XI-1963	18	R.V. 'Anton Bruun'
2	♀	38-40		21°24'N, 69°44'E			
1	♀	38	Z.M.C.	25°11'N, 119°28'E	10-IV-1897		Schönau
2	♀	36-38	Z.M.C.	18°48'N, 72°37'E	12-V-1964	20-30	Jørgen Nielsen

† Holotype of *L. typus* Steenstrup 1856.* Syntypes of *L. investigatoris* Goodrich, 1896.** Illustrated syntype of *L. investigatoris*.

APPENDIX 4
MATERIALS EXAMINED: *Loliolus affinis*

No.	Sex	ML (mm)	Source & Reg. No.	Location	Date	Collector
<i>Syntypes</i>						
1	♂	32	Z.M.C.	Gulf of Manaar		Gov.
1	♀	39		Palk Strait		Christensen
				Region, India		
<i>Other material</i>						
4	♂	19-26	Z.M.C.	12°10'N, 102°27'E	30-XII-1899	Th.
1	♀	29		Coast of Ban Lem Ngop (Thailand)		Mortensen
2	♂	21-25	CAS 030250	Andaman Islands	1940	Herre Expedition
1	♀	27	Z.M.C.	16 km from Rangoon Hbr, Burma	18-XI-1863	Hansiu and Thalbitzen
1	♀	22	Z.M.C.	South Malacca		Poul Fogh
22	♂	10-27	Z.M.C.	Surabaya	1870	Andrea
9	♀	10-26				

