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Wunderpus photogenicus n. gen. and sp., a new octopus from the shallow waters of the Indo-Malayan Archipelago (Cephalopoda: Octopodidae)

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Abstract

Wunderpus photogenicus n. gen. and n. sp. is a spectacular long-armed species that occurs on soft sediment habitats in shallow waters (typically less than 20 m deep) in Indo-Malayan waters. It is characterized by small eyes on elongate stalks, a long, conical papilla over each eye and a dramatic and fixed color pattern of white bars and spots over a brown-red background. The distribution of the species is centered in the Indo-Malayan Archipelago and extends from Vanuatu to Papua New Guinea, Indonesia and Malaysia, north to the Philippines. Animals typically emerge at dusk and dawn to forage in the twilight, primarily catching small crustaceans and fishes by flaring the arms and webs over patches of sand or coral rubble to trap enclosed (and typically buried) prey. The species also extends its arms into holes to probe for potential prey. The distinctive color pattern of this species is most pronounced when the octopus is disturbed or threatened by real or perceived attackers. It appears to be a warning display and may represent one of two scenarios: either 1) it warns that the octopus is directly toxic or venomous by nature or; 2) it represents impersonations of toxic or venomous creatures with similar color patterns which co-occur in the same habitat. The new genus and species is compared with, and distinguished from, other long-armed octopuses.

Key words: *Wunderpus*, octopus, Octopodidae, Cephalopoda, Indo-Malayan Archipelago, taxonomy

Introduction

In recent years, increased interest in the marine life of the tropical Indo-Malayan Archipelago (particularly Indonesia) has lead to the discovery of a diverse and largely unstudied fauna. The spread of dive resorts and dive boat charters throughout this region, combined with significant improvements in underwater photographic and video technology, has resulted in a flood of images to the outside world of the spectacular life in these waters.

Amongst the images and reports emerging from Indonesia in the mid 1980's was a remarkable long-armed octopus, which quickly received the nickname "Wunderpus" (also referred to as "Wonderpus"). At the same time, collectors in the Philippines and Indonesia started supplying the home and public aquarium trade with occasional live specimens of this octopus.

Despite all the reports and images, specimens required for formal description of this species proved difficult to obtain. Over the past two decades relatively few specimens of this octopus have been preserved and archived in museum collections. This distinctive animal is described here and distinguished from another recently described species of long-armed octopus from the same region with which it frequently has been confused, the "Mimic Octopus" (Norman and Hochberg 2005).

Material and Methods

A total of ten specimens were amassed from diverse sources. Alex Kerstitch kindly donated two specimens; one he collected in Vanuatu, the other was obtained from an unknown locality through commercial aquarium suppliers. Two specimens, collected by B. Bruguier, from unspecified localities in Bali, Indonesia were supplied by Bruno Condé, Director of the Aquarium Tropical, Musée de Zoologie, Université de Nancy, France. An additional mature female, obtained through the commercial aquarium trade, was donated by John Forsythe of the National Research Center for Cephalopods, Galveston, Texas, USA. Most recently three specimens, probably collected in the Philippines, were purchased at an aquarium store in Berkeley, California. They were donated by Dr. Roy Caldwell following study at the University of California, Berkeley. The above eight specimens have been lodged in the Invertebrate Zoology collection of the Santa Barbara Museum of Natural History (SBMNH). Two more specimens were found in the collections of the California Academy of Sciences, San Francisco, California, USA (CASIZ) and the Australian Museum, Sydney, Australia (AMS).

Additional color photographic images, videos, distributional data and behavioral information were kindly supplied by a number of keen amateur and professional underwater photographers and filmmakers. The second

author observed four live individuals *in situ* while diving in northern Sulawesi in 1998 and 1999.

The taxonomic methodology and diagnostic characters used below follow Norman and Sweeney (1997) and Norman *et al.* (1997).

Abbreviations: coll.—collected by; ML—mantle length. Institutions: AMS—Australian Museum, Sydney, Australia; CASIZ—California Academy of Sciences, Invertebrate Zoology, San Francisco, USA; SBMNH—Santa Barbara Museum of Natural History, California, USA; MV–Museum Victoria, Melbourne, Australia.

SYSTEMATICS

Family Octopodidae d'Orbigny, 1840

Genus *Wunderpus* n. gen.

Type Species

Wunderpus photogenicus n. sp.

Diagnosis

Body small; mantle thin-walled, weakly muscular, elongate ovoid to amphora-shaped; mantle aperture wide; funnel organ small, W-shaped, lateral limbs very short; interbrachial water pore system absent; stylets present, short, chitinous (not mineralized); eyes small on elongate stalks; gills with 6–7 (rarely 5) lamellae per demibranch plus terminal lamella; arms long, thin and muscular, >5 times mantle length, dorsal arms shortest, arm formula typically 4=3=2>1; arm autotomy occurs at the level of the 8th to 12th proximal sucker; webs thin and elastic, extend entire length of arms as well-developed ventral margin; suckers biserial, small and widely spaced; suckers normal, functional to tips of all arms other than hectocotylized arm of males; enlarged suckers absent in both sexes; right arm III hectocotylized, very short, less than 1/3 length of opposite arm; copulatory organ with ligula and calamus; ligula size small to moderate (<6% of arm length) with distinct groove; crop with distinct diverticulum; posterior salivary glands larger than buccal mass; intestine relatively short and robust without distinct U-shaped loop; terminal organ (penis) short with simple short diverticulum; spermatophores unarmed; egg size small (chorion capsule of mature ovarian eggs, 2.9–3.6 mm long). Skin largely smooth between erectile primary and secondary papillae; single elongate, conical papilla present medially over each eye (supraocular), tip rounded; body uniformly brown to red color, patch and groove lattice system absent; diagnostic pattern of distinct white bands along arms and white spots and short transverse bars on mantle, head and eye stalks; ocelli absent.

Etymology

Wunderpus: from the German 'wünder' meaning "marvel or wonder".

Remarks

The taxonomy of the family Octopodidae at the generic level is in need of major revision. Over 90% of the 200+ species coined within this family have been placed in the catchall genus *Octopus* Cuvier, 1797 (Hochberg *et al*. 2005; Norman and Hochberg 2005b). A number of taxonomic studies based on morphology have recognized distinct species-complexes within the genus *Octopus* as it currently stands (*e.g*., Robson 1929; Norman 1992a; Norman and Hochberg 1994, 2005b; Norman and Sweeney 1997). Recent molecular studies into the phylogeny of the octopuses of the family Octopodidae (Hudelot 2000; Takumiza *et al*. 2005; Guzik *et al.* 2005; Strugnell *et al.* 2005) have demonstrated that the genus *Octopus* is polyphyletic. Many of the clades proposed in earlier morphological studies are supported by molecular studies. The first step in the review of the generic level taxonomy within the family Octopodidae is to delineate taxa clearly distinct from the genus *Octopus sensu stricto* as represented by the type species of this genus, *O. vulgaris* Cuvier, 1797, and its relatives (a group treated in the literature as the "*O. vulgaris* species-complex", Norman and Sweeney 1997).

Wunderpus n. gen. is distinguished from *Octopus s.s.* by the following characters: eyes small, on elongate stalks (versus moderate to large-sized unstalked eyes); single, elongate, blunt-tipped papilla over each eye (versus two or more smaller supra-ocular papillae); characteristic two-tone color pattern with fixed, relatively limited repertoire (versus highly variable color patterns); skin smooth (versus a "patch and groove" lattice-like sculpture); arm autotomy occurs at a set level at the arm bases (versus no autotomy); male hectocotylised arm short, ~30% of opposite arm length (versus >70%); enlarged suckers absent (versus present on arms of mature males); and funnel organ W-shaped with very short outer limbs, length <40% of medial limbs (versus >80%).

At present we recognize only one species in the new genus. See Discussion below for delineation of *Wunderpus* n. gen. from other long-armed octopuses in the family Octopodidae.

Wunderpus photogenicus n. sp.

Figures 1–6; Table 1

Octopus horridus – Hanlon and Messenger 1996: 72; photo fig. 5.6I [photo: J. Forsythe—collection locality not stated].

Octopus sp. 7.—Gosliner *et al.* 1996: 190; photo 679 [photo: M. Severns—Luzon, Philippines].

Octopus sp. 20.—Norman 2000: 13, 304–305, 315 [photos: A. Kerstitch—Malekula Island, Vanuatu Islands; M.D. Norman and D. Nielsen-Tackett— both North Sulawesi, Indonesia].

"Banded Octopus".—Kerstitch 1989: 375.—Kerstitch 1992: 34–35 [photo: A. Kerstitch—Malekula Island, Vanuatu Islands].

"Poulpe Zébré".—Louisy 1996: 27 [photo: P. Louisy—Bali, Indonesia]

"Ornate Octopus".—Steene 1998: 250 [photo: R. Steene—Lembeh Strait, North Sulawesi, Indonesia].

"Wunderpus".—Norman 2000: 304, 315.—Norman and Reid 2000: 78 [photos: A. Kerstitch—Malekula Island, Vanuatu Islands].—Halstead 2000: 272 [photos: B. Halstead—Madang, Papua New Guinea; Vanuatu Islands].

"Wonderpus".—Norman and Hochberg 2005a: 60 [Table 1].

"Mimic Octopus" (in part).—Butvill 2003: 38–40 [photos: D. Nielsen-Tackett—collection locality not indicated].

TABLE 1. *Wunderpus photogenicus* n. sp. Counts and measurements (mm) of males. Abbreviations: A–E: web sectors starting from dorsal sector; D = damaged; Hc = hectocotylized arm of male (right arm 3); max = maximum depths, lengths or counts per arm pair; + = arm tip missing; ** = all or most arms missing.

Repository	AMS	SBMNH
Catalog number	C304110	345680
Status	Holotype	Paratype
Sex	male	male
Maturity	mature	mature
Total Length	197	149
Total Wet Weight (g)	11.2	7.0
Dorsal Mantle Length	24	20
Ventral Mantle Length	16	14
Mantle Width	12.2	10.8
Head Width	12.8	13.2
Funnel Length	10.0	10.1
Free Funnel Length	5.5	3.0
Funnel Organ Length -lateral limb	1.0	1.3
-medial limb	2.4	3.4
Web Depths (max per pair) A	13	12
B	13	12
C	13	13
D	9	D
E	10	11
Web Depth Formula	C=B=A>E>D	C>A=B>E
Arm Lengths (max per pair) 1	123	110
2	173	122
3	111+	123
Hc	47	38
4	131+	120+
Arm Length Formula	2>1**	3=2>1
Arm Width	4.0	4.0
Sucker Diameter	2.0	1.8
Sucker Counts (max per pair) 1	186	160
2	-	162
3	D	152+
Hc	64	64
4	D	D
Gill Count	5–6	6–7
Ligula Length	1.6	2.0
Calamus Length	0.5	1.0
Terminal Organ Length	4.3	4.1
Diverticulum Length	1.6	1.6
Spermatophore Count	31	24
Spermatophore Length	9.9	10.4
Spermatophore Width	0.4	0.3
Spermatophore Reservoir Length	4.6	5.0
Spermatophore Cord Whorls	32–36	~30
Ejaculatory Apparatus Whorls	~17	-

Type Material

Holotype: male (mature), 24 mm ML; INDONESIA, Bali, specific locality and depth not indicated, coll. Neumann, date unknown, AMS C304110.

Paratypes: 1 female (mature, gravid), 27 mm ML; VANUATU ISLANDS, Malekula Island, 150 m off shore, ~16º15'S, ~167º30'E, on sand bottom under dead coral slabs and rocks, 20 m, coll. A. Kerstitch, M/V *Kalinda*, field no. AK 881124, 24 November 1988, by hand with quinaldine; SBMNH 369471. 1 female (mature, gravid), 36 mm ML; PHILIPPINES, specific locality not indicated, coll. commercial aquarium collector, spring 1986, SBMNH 345682 [*ex* National Resource Center for Cephalopods, Galveston, Texas; maintained in aquarium, died 28 April 1986; photos by John Forsythe of live animals in aquarium]. 1 male (mature), 20 mm ML; INDONESIA, Bali, specific locality and depth not indicated, coll. B. Bruguier, 22 March –18 April 1996; SBMNH 345680 [*ex* Musée de Zoologie, Nancy, France; photos by Patrick Louisy of live animal; DNA voucher]. 1 female (mature, gravid), 35 mm ML; INDONESIA, Bali, additional locality data not available, coll. B. Bruguier, 14 March – 12 April 1996; SBMNH 345681 [*ex* Musée de Zoologie, Nancy, France; photos by Patrick Louisy of live animal; DNA voucher].

Material Examined

Holotype and paratypes (see above). 1 female (submature), 23 mm ML, locality presumed to be the PHILIPPINES (collected by commercial aquarium collectors; locality and depth details not available), purchased in 1986 by Steinhart Aquarium from tropical fish dealer in Brisbane, Australia, CASIZ 081006 [photos by Dustin Chivers of live animal in aquarium]. 1 female (submature), 35 mm ML, purchased in 1985 by Alex Kerstitch from aquarium store in San Francisco, California, SBMNH 345679 [source originally provided as 'Indian Ocean'; videos and color photos by Alex Kerstitch of live animal in aquarium]. 1 male (mature), 20 mm ML, purchased in 2005 by Roy Caldwell from aquarium store (The Octopus's Garden) in Berkeley, California; SBMNH 369187 [maintained in aquarium, died April 2005; DNA voucher]. 1 female (submature) 32 mm ML; purchased in 2005 by Roy Caldwell from aquarium store (The Octopus's Garden) in Berkeley, California; SBMNH 369188 [maintained in aquarium, died April 2005; DNA voucher]. 1 male (mature), 20 mm ML, purchased in 2005 by Roy Caldwell from aquarium store (The Octopus's Garden) in Berkeley, California; SBMNH 369470 [maintained in aquarium, died April 2005; DNA voucher].

Photographic and/or Video Records Examined

(specimens not captured)

INDONESIA: Lembeh Strait, North Sulawesi, 01º26'N, 125º13'E, 1 mi north of Bitung, 10–15 ft [3–5 m], photos by Bill MacDonald, 03 October 1996; north of Bitung, near Police Pier, on black sand, 9 m, photos by Mark D. Norman, 14 October 1998. Sarena Kecil Island, off south side on sandy slope just above rubble area, 50 ft [15 m],

photos by Denise Nielsen-Tackett, between August and October 1996. Aer Perang (site of fresh water spring), sandy area with scattered rubble, 9 m, photos by Mark D. Norman, 13 October 1998; 35–40 ft [to 12 m], photos by Annie Crawley, 2002. Alor Island, Timor; photos by Roberto Sozzani, date unknown.

NEW GUINEA: Milne Bay, 10º22'S, 150º30'E, 40 ft [~12 m], photos by Fred Bavendam, M/V *Telita*, date unknown; depth unknown, photos by Ron and Valerie Taylor, date unknown. Madang, ~5º00'S, ~145º30'E, depth unknown, photos by Bruce Halstead, date unknown. Irian Jaya, locality details and depth unknown, photos by Robert Sozzani, 2002.

PHILIPPINES: Luzon, Batangas, ~14º00'N, ~121º00'E, depth unknown, photos by Mike Severns, date unknown [= *Octopus* sp. 7 in Gosliner *et al*. 1996]. Anilao, photos by Jeffrey Rosenfield, 2002; photos by Paul Osmond, date unknown.

SOLOMON ISLANDS: Florida Island Group, Gavutu, ~9º00'S, ~160º00'E, depth unknown, photos by Ted DeFeo, 1998.

MALAYSIA: Kapalai, photos by Nils Aukan, date unknown.

VANUATU ISLANDS: Location and depth, photos by Bruce Halstead, date unknown.

Diagnosis

Small-bodied animals (mantle lengths to 36 mm; total lengths to over 230 mm; total weight weight to at least 26 g); elongate, delicate species; eyes small on long stalks, head appears Y-shaped; funnel organ W-shaped with short outer limbs; stylets short, chitinized; gills with 6–7 (rarely 5) lamellae per demibranch plus terminal lamella; arms long (typically 5–7 times mantle length), almost equal in length, dorsal arms slightly shorter (arm formula 4=3=2>1); evidence of arm autotomy present between 8th and 12th proximal sucker; right third arm of males hectocotylized, very short (30% length of opposite arm); copulatory organ small (length 3.4–5.3% of hectocotylized arm length) consists of distinct ligula and calamus; ligula squat, copulatory groove well developed, with single medial row of small raised bumps; calamus distinct; enlarged suckers absent in both sexes. Sucker counts on normal arms range between 160–230; hectocotylized arm with 64 suckers in two available males. Webs thin and retractile, extend along ventral margin to tips of all arms; webs shallow in preserved material (web depths 7.5–11% of longest arm) but capable of considerable expansion in live animal; relative lengths of web sectors variable in preserved material with sector A typically most shallow. Terminal organ in males short and straight with simple diverticulum; spermatophores short (around 50% mantle length), produced in moderate numbers (24 and 31 in storage sac of examined males); spermatophores unarmed; mature ovarian eggs small (chorion capsule length 2.9–3.6 mm). Skin color uniform brown to red; distinct pattern of defined white bands on arms and white spots and stripes on mantle; skin generally smooth, primary papillae present and often conspicuous in white areas on dorsal mantle; patch and groove system absent; single elongate, conical papilla present medially over each eye (supra-ocular), tip bluntly rounded.

Description

The following description is based on detailed examination of two mature males and five females (three submature and two mature). Counts and measurements for this material are presented in Table 1–2. Indices are included in the text: ranges in (parentheses); means in italics. One submature female (34.5 mm ML, SBMNH 345679) is poorly preserved, the body and arms are very soft and stretched. Due to this distortion, data on arm and mantle lengths, and web depths for this specimen are excluded from calculations in the following description.

Small-bodied species (Fig. 1A), mantle lengths to at least 24 mm in mature males, 36 mm in mature females; total lengths to over 230 mm; weights (wet) to at least 26 g. Mantle elongate-ovoid to amphora-shaped (Figs. 1A–C); walls of mantle thinly muscular; mantle width approximately half mantle length (males and females 50.7–*54.7*–63.3%; gravid female with distended mantle 69.8%). Head of moderate width, around half mantle length (males 53.6–*59.8*–66.0%; females 37.4–*44.8*–49.1%; gravid female 27.9%). Head typically wider than mantle in males, narrower than mantle in females due to influence of ovary (head width of males 104.9–*113.6*–122.2% of mantle width; of females 73.7–*79.7*–88.0%; of gravid female 40.0%). Eyes small and stalked, often raised in live animals so head appears Y-shaped. Neck region distinct. Stylets present, short (4.9 mm, 13.9% of mantle length), non-mineralized (Fig. 1D). Pallial aperture of moderate width, approximately 1/2 mantle circumference. Funnel thin walled, moderately long (39.3–*43.4*–50.5% of mantle length); free about half its length (29.7–*46.1*–56.2%). Funnel organ W-shaped (Fig. 1E), located in middle of dorsal funnel; large, medial limbs about 1/3 length of funnel (24.0–*30.7*–37.0%); limbs wide with lateral limbs much shorter than medial limbs (20.0–*36.3*–41.7%).

Webs thin, shallow relative to arm length (deepest 7.5–*9.5*–10.6% of longest arm length); dorsal web typically shortest but formulae variable (see Table 1–2). Web margins well developed on ventro-lateral edge of arms, extend along entire length of all arms; webs frequently flared by live animals during displays (Fig. 4A) or when foraging (Fig. 4D).

Arms long, longest 5–7 times mantle length (5.4–*6.3*–7.2% of mantle length); width moderate (12.3–*16.3*–20.0% of mantle length); arms roughly triangular in cross-section (aboral surface as apex), arm width increases from mouth through proximal quarter of arm length, width uniform in middle quarter, tapers evenly in distal half. Dorsal arms appear shortest in few intact specimens; ventral or lateral arms typically longest (see Table 1–2). Numerous arms missing in several specimens; typically severed between proximal suckers 8–12 suggesting arm autotomy likely occurs (see life history section below for discussion). Suckers biserial; small and widely spaced (Fig. 1F);

infundibulum fleshy with distinct radial cushions; rim scalloped; diameter of suckers small, slightly larger in males (males 8.4–*8.7*–9.0% of mantle length; females 5.3–*6.7*–8.3%). Enlarged suckers absent in both males and females. Sucker counts range between 160–230 on normal arms (male 162–186 in two specimens; female 233 in single specimen where counts were possible). Hectocotylized arm with 64 suckers in both males.

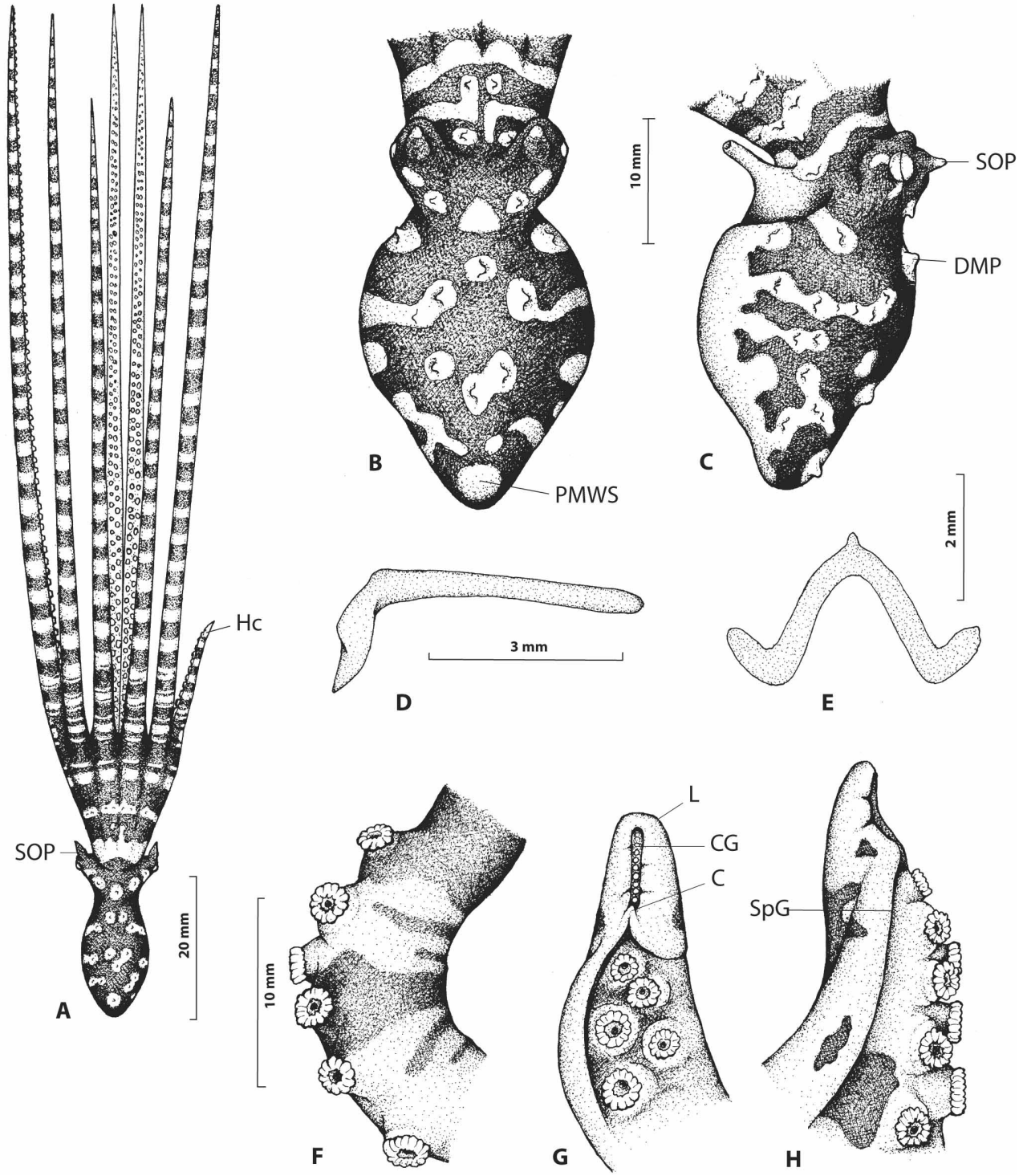

FIGURE 1. *Wunderpus photogenicus* n. sp. **A**. Stylized dorsal view of mature male (paratype, 20 mm ML; SBMNH 345680); **B–C, F**. Details of mature female (paratype, 27 mm ML; SBMNH 369471); **B**. Mantle, dorsal view; **C**. Mantle, left lateral view; **D**. Left stylet (female, 36 mm ML; SBMNH 345682); **E, G–H**. Details from mature male (holotype, 24 mm ML; AMS C304110); **E**. Funnel organ on dorsal surface of funnel; **F**. Arm section showing suckers and color pattern; **G**. Copulatory organ, oral view; **H**. Copulatory organ, left lateral view. Abbreviations: C = calamus; CG = copulatory groove; DMP = dorsal mantle papilla; Hc = hectocotylized arm; L = ligula; PMWS = posterior mantle white spot; SOP = supra-ocular papilla; SpG = spermatophore groove.

Third right arm hectocotylized in males; very short (1.9, 2.0 times mantle length), less than 1/3 length of opposite arm (30.9% in male specimen with intact opposite arm). Copulatory organ (Figs. 1G–H) small (3.4–*4.4*–5.3% of hectocotylized arm length). Ligula squat with well-developed copulatory groove; single medial row of small

raised bumps present in groove; calamus low, small (31.3–*40.7*–50.0% of ligula length). Spermatophore groove well developed and fleshy.

Gills with 6–7 lamellae (rarely 5) per outer demibranch plus terminal lamella.

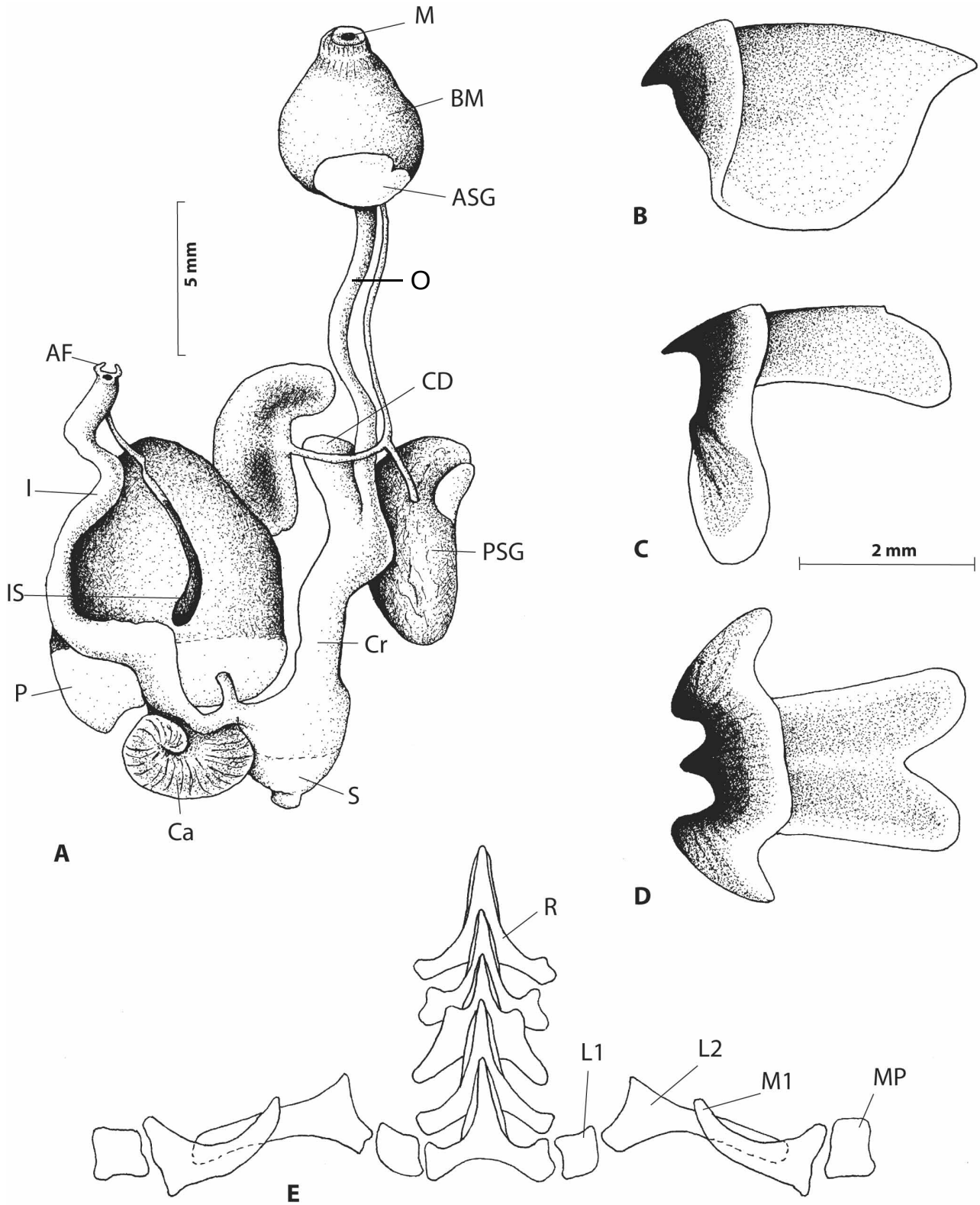

FIGURE 2. *Wunderpus photogenicus* n. sp. **A–E**. Digestive system (paratype, female 27 mm ML; SBMNH 369471); **A**. Entire digestive tract; **B**. Upper beak, left lateral view; **C**. Lower beak, left lateral view; **D**. Lower beak, ventral view; **E**. Radula. Abbreviations: AF = anal flaps; ASG = anterior salivary gland; BM = buccal mass; Ca = caecum; CD = crop diverticulum; Cr = crop; I = intestine; IS = ink sac; L1 = first lateral tooth; L2 = second lateral tooth; M1 = first marginal tooth; MP = marginal plate; O = oesophagus; P = pancreas; PSG = posterior salivary gland; R = rachidian tooth; S = stomach.

Digestive tract (Fig. 2A). Buccal mass large, about 2/3s length of digestive gland. Anterior salivary glands of moderate size, approximately 1/3 length of buccal mass; posterior salivary glands large, as long or longer than buccal

mass. Crop with distinct diverticulum. Stomach bipartite; caecum with single whorl, ducts to digestive gland short and wide. Intestine relatively short, wide; rectum short, muscular; distinct U-shaped loop in intestine absent. Digestive gland approximately ovoid with slight posterior lobes. Pancreatic tissue evident in posterior 20% of digestive gland. Ink sac small, narrow and shallow, only slightly embedded in surface of digestive gland. Anal flaps present, elongate.

Beaks (Figs 2B–D). Upper beak hood relatively small, around 30% of beak length (30.3% in SBMNH 64198); rostrum bluntly hooked, cutting edge rounded; crest slightly rounded. Lower beak, hood and crest rounded; rostrum pointed, cutting edge sharp; lateral walls flared with concave posterior margin (Fig. 2D). Radula (Fig. 2E) with 7 teeth plus 2 marginal plates present per transverse row. Rachidian tooth with very tall mesocone and single lateral cusp on each side in symmetrical arrangement. Lateral cusps migrate from medial to lateral position over 3 rows. First lateral teeth almost square with slight cusp on lateral edge. Second lateral teeth with single distinct cusp at medial end. First marginal teeth tusk-shaped. Marginal plates roughly square.

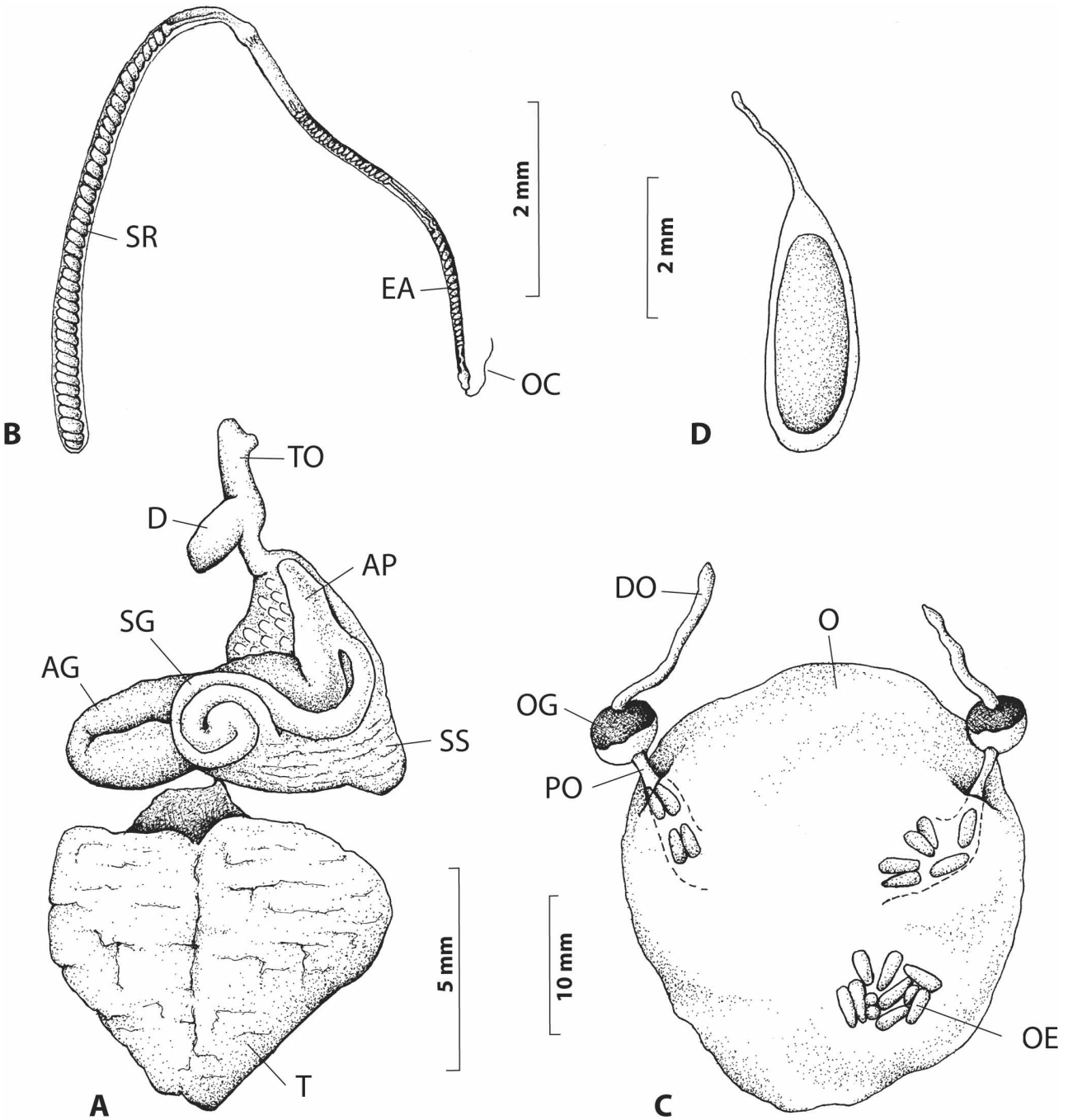

FIGURE 3. *Wunderpus photogenicus* n. sp. **A–B**. Male reproductive system (holotype, 24 mm ML; AMS C304110); **A**. Reproductive tract of mature male, ventral view; **B**. Spermatophore; **C–D**. Female reproductive system (paratype, 36 mm ML; SBMNH 345682); **C**. Reproductive tract of mature female, ventral view; **D**. Mature ovarian egg showing capsule and stalk. Abbreviations: Ap = appendix; AG = accessory gland; D = diverticulum; DO = distal oviduct; EA = ejaculatory apparatus; O = ovary; OC = oral cap thread; OE = ovarian egg; OG = oviducal gland; PO = proximal oviduct; SG = spermatophoric gland; SR = sperm reservoir; SS = spermatophore storage sac; T = testis; TO = terminal organ.

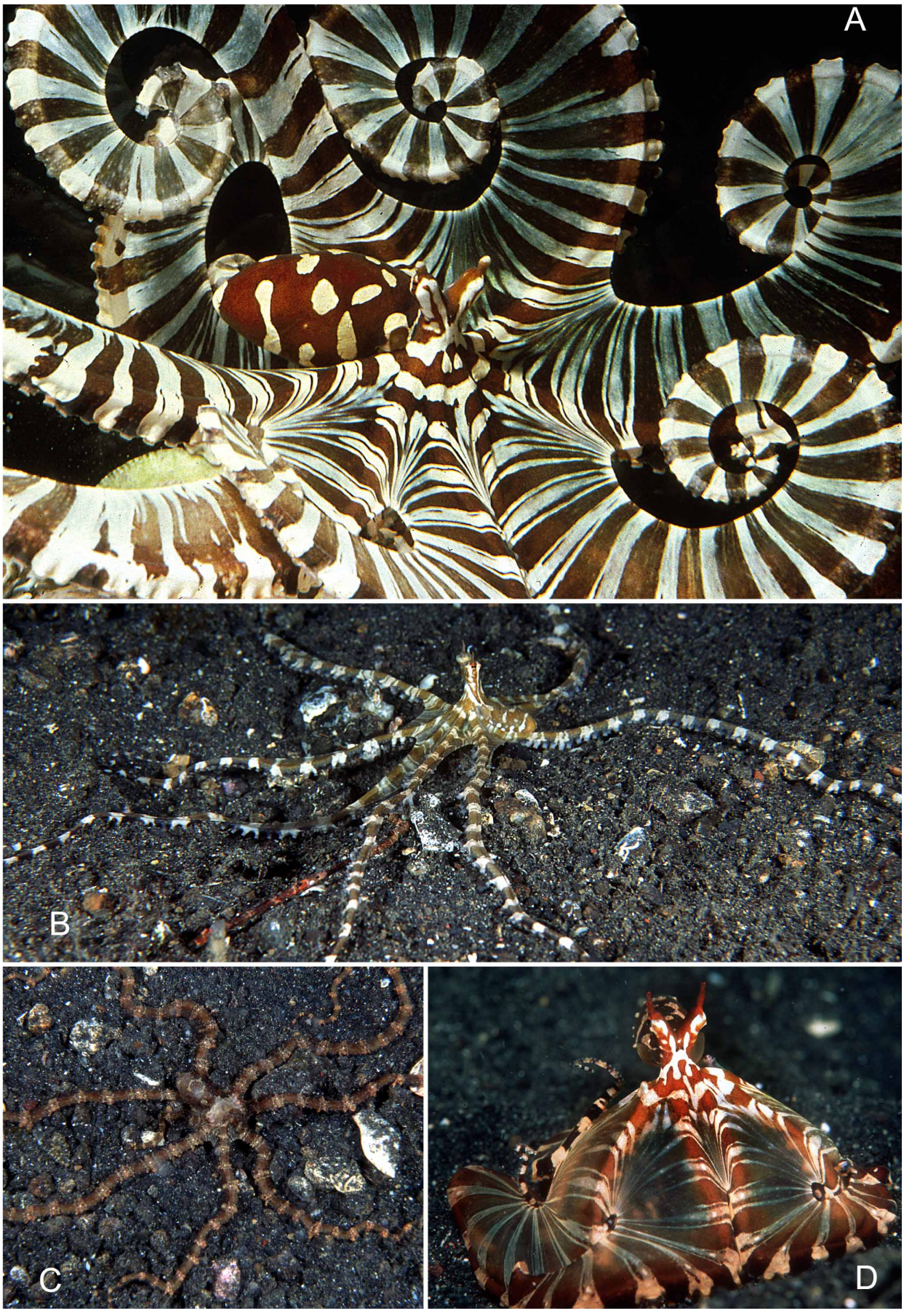

FIGURE 4. *Wunderpus photogenicus* n. sp. Photographs of live animals: **A**. Alarm display of female from Vanuatu; aquarium photograph (27 mm ML, SBMNH 369471; Photo: A. Kerstitch); **B**. Female from Philippines stretched out on substrate; photographed in Steinhart Aquarium (23 mm ML, CASIZ 081006; Photo: D. Chivers); **C**. Foraging animal showing suppressed color pattern; *in situ* photograph, Lembeh Strait, North Sulawesi, Indonesia (Photo: M.D. Norman); **D**. Foraging animal showing flared web of speculative pounce posture; *in situ* photograph, Lembeh Strait, North Sulawesi, Indonesia (Photo: D. Nielsen-Tackett).

FIGURE 5. *Wunderpus photogenicus* n. sp. Photographs of live animals: **A**. Alarm display; *in situ* photograph, Lembeh Strait, North Sulawesi, Indonesia (Photo: M.D. Norman); **B**. Detail of male from Bali showing small stalked eyes; photographed in Nancy Aquarium (20 mm ML, SBMNH 345680; Photo: P. Louisy); **C**. Detail of female possibly from Philippines showing raised papillae on dorsal mantle and head; aquarium photograph (35 mm ML; SBMNH 345681; Photo: A. Kerstitch); **D**. Foraging animal showing regenerating arms (left arms 2 & 3, right arm 2); photographed *in situ* in Lembeh Strait, North Sulawesi, Indonesia (Photo: M.D. Norman); **E**. Male (on right) clasping female in mating posture; photographed *in situ* in Lembeh Strait, North Sulawesi, Indonesia (Photo: D. Nielsen-Tackett).

Male reproductive tract (Fig. 3A). Terminal organ short and robust (18.0–*19.3*–20.5% of mantle length); diverticulum simple single loop (37.2–*38.1*–39.0% of organ length); genital aperture subterminal. Vas deferens duct thin, long. Spermatophoric gland robust with distinct recurved coil. Accessory gland robust, distal end reflexed. Appendix present at junction of spermatophore storage sac and spermatophoric ducts. Spermatophore storage sac broad and short, spermatophores visible through thin sac wall; spermatophores present in moderate numbers (24 and 31 in storage sacs of examined males).

Spermatophores (Fig. 3B) short (9.9, 10.4 mm), around 50% of mantle length (41.4–*46.7*–52.0%); narrow without swellings (2.9–*3.5*–4.0% of spermatophore length);

unarmed. Sperm reservoir about 50% spermatophore length (46.5–*47.3*–48.1%); sperm cord coiled in approximately 30–35 coils.

Female reproductive tract (Fig. 3C). Ovary large; proximal oviducts short, about one-half length of distal oviducts; oviducal gland dark in distal half, without evident radiating chambers; distal oviducts slightly swollen; genital aperture subterminal. Ovarian eggs (Fig. 3D) relatively small with short stalks (capsule length 2.9–3.6 mm; 8.2–10.1% of mantle length); 4 follicular folds present. Approximately 2000 mature ovarian eggs present in single gravid female examined. Spawned eggs carried in arms of female (Miske and Kirchhauser 2006).

Colour of live animals (Figs. 4, 5). Body uniformly red dorsally and ventrally; with large, conspicuous white spots and stripes on dorsal, lateral and ventral mantle, head and eyes; large, round white spot present on posterior dorsal tip of mantle; thin white strip extends from posterior ventral eye down stalk onto lateral anterior mantle; conspicuous white bands alternate with red and extend down dorsal and lateral arms from base to tips of arms; each white band complex consists of wide medial band plus narrow band on either side of medial band (Fig. 4C); small round white spot often visible dorsally in center of wide white arm band; elongate papilla over each eye, red with white tip. Dark ocellus on arm base below eyes absent. Ventral mantle and arms light in color; sucker bases yellowish cream. Dorsal mantle and frontal white spot complexes (*sensu* Packard and Sanders 1971) not evident.

Color and patterns of well-preserved specimens similar to those seen in live animals and photographs; body uniformly light red; larger white spots and stripes easily visible on mantle, head and arms; smaller spots and stripes often not observed.

Skin smooth; patch and groove system absent. Conspicuous primary papillae present on dorsal and lateral mantle only in areas where white spots and stripes are present; slight variations in patterns apparent with each individual (Figs. 1B–C, 5C). Single elongate, conical papilla present medially over each eye (supra-ocular), tip bluntly rounded.

Etymology

Specific name in recognition of the considerable photographic interest in this spectacular species in the media in recent years.

Common Name

"Wunderpus".

Distribution

Wunderpus photogenicus n. sp. is known from shallow waters of the tropical Indo-Malayan Archipelago from Indonesia and the Philippines, east to Papua New Guinea, and the Solomon Islands and Vanuatu (Fig. 6). Reports from underwater photographers and data from collected specimens indicate a depth range from 0.5 to at least 20 m.

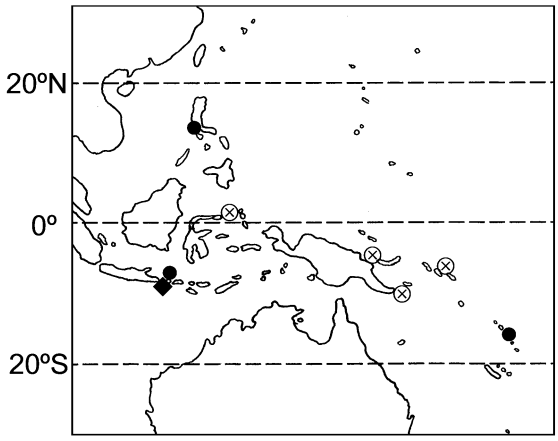

FIGURE 6. *Wunderpus photogenicus* n. sp. Map of distribution of specimens and photographs examined. Symbols: ◆ = holotype; ● = paratypes and additional specimens; ⊗ = photographic records and observations.

Taxonomic remarks

There are a number of other species of long-armed octopuses within the family Octopodidae (see Table 1, Norman and Hochberg 2005a). *Wunderpus photogenicus* n. sp. previously has been confused with a similar Indo-Malayan species that occurs in the same localities and habitat types. The "Mimic Octopus" (*Thaumoctopus mimicus* Norman and Hochberg, 2005) has been described in detail. *W. photogenicus* n. sp. can be clearly distinguished from *T. mimicus* on the basis of the following characters: a) single long supra-ocular papilla over each eye, inflated and blunt-tipped (versus very elongate and finely pointed); b) anterior-ocular papilla on margin of each eye absent (versus present); c) lower number of suckers on hectocotylized arm (64 versus 130–146); e) higher number of suckers on normal arms (to 233 versus to 283); f) shorter arm lengths (5.4–7.2 times mantle length versus 7.4–10.2); g) fewer gill lamellae per demibranch (5–7 versus 9); and h) well-defined color pattern with a large, round white spot on the posterior tip of the mantle (versus less clearly delineated color pattern with a U-shaped white patch) (Figs. 4A, D; Norman and Hochberg 2005a).

Another genus of long-armed octopus from Australia shows some similarities with *Wunderpus photogenicus* n. sp. "The Banded Drop-arm Octopus" (*Ameloctopus litoralis* Norman, 1992) is an intertidal species that also has long thin arms (5–10 times mantle length) with alternating light and dark purple-brown bands along their length. *W. photogenicus* n. sp. can be easily distinguished from *A. litoralis* based on the following characters: a) ink sac and anal flaps present (versus absent); b) webs along the ventral edges of all arms present (versus absent); c) spermatophores narrow (versus inflated or swollen); d) funnel organ well-developed, W-shaped (versus vestigial, consisting only of four small pads); e) terminal organ short, squat with well-developed diverticulum (versus linear in shape, without a diverticulum); and f) distinct white markings on the mantle present (versus absent) (Norman 1992).

Wunderpus photogenicus n. sp. has been reported in the

past under the name *Octopus horridus* d'Orbigny, 1826 (Hanlon and Messenger 1996). *W. photogenicus* n. sp. is easily distinguished from *O. horridus* based on the following characters: a) longer arms (5.4–7.2 times mantle length versus 4.2–4.7); b) shallower webs (7.5–10.6% of arm length versus 15%); c) lower number of suckers on hectocotylized arm (64 versus about 90); d) higher number of suckers on the normal arms (to 233 versus 125–135); e) enlarged suckers in mature males absent (versus present); and f) longer ligula length (3.4–5.3% of hectocotylized arm length versus 1.6–2.0%).

TABLE 2. *Wunderpus photogenicus* n. sp. Counts and measurements (mm) of females. Abbreviations: A–E: web sectors starting from dorsal sector; D = damaged; ind = indistinct; Hc = hectocotylized arm of male; + = arm tip missing; ** = all or most arms missing.

Repository		SBMNH	SBMNH	SBMNH	SBMNH	CASIZ
Catalog number		345682	345681	369471	345679	81006
Status		Paratype	Paratype	Paratype	-	-
Sex		female	female	female	female	female
Maturity		gravid	mature	submature	submature	submature
Total Length		234	128	D	distorted	D
Total Wet Weight (g)		26.5	20.9	7.6*	21.6	6.8*
Dorsal Mantle Length		36	35	27	35	23
Ventral Mantle Length		~29	D	20	23	11
Mantle Width		25.0	17.9	17	18	12
Head Width		10.0	13.2	13.1	14.6	11.0
Funnel Length		14.3	14.2	10.5	15.5	10.8
Free Funnel Length		5.2	6.9	5.9	8.3	5.5
Funnel Organ Length -lateral limb		1.6	1.5	1.4	ind	0.8
-medial limb		4.4	3.7	3.4	ind	4.0
Web Depths (maximum per pair)	A	D	12	10	9	10
	B	D	15	12	16	11
	C	D	18	16	20	10
	D	16	20	12	18	12
	E	12	19	12	15	11
Web Depth Formula		D>E	D>E=C>B>A	C>B>E=D>A	C>D>B=E>A	D>B=E>C=A
Arm Lengths (max per pair)	1	D	155	D	187+	D
	2	175+	155+	D	249	D
	3	190+	191	D	195+	D
	4	D	176	D	205	140+
Arm Length Formula		D	3>4>1	D	2>4**	D
Arm Width		4.4	4.9	4.4	distorted	4.2
Sucker Diameter		1.9	2.1	1.9	1.6	1.9
Sucker Counts (max per pair)	1	D	D	D	D	D
	2	176+	D	D	D	D
	3	182+	D	D	D	D
	4	D	233	D	D	120+
Gill Count		7	7	6	7	7
Egg Length (chorion capsule)		3.6	2.9	1.6 submat.	-	-
Egg Width		1.2	0.9	0.7 submat.	-	-
Egg Number		~2000	-	-	-	-

Life history and behavior

Little is known of the life history and behavior of this distinctive octopus. It has primarily been encountered on soft sediment substrates where it occupies the burrows of other animals or may dig its own burrow. Individuals were found to occupy the same burrow for periods of at least three weeks. This species appears to have a crepuscular activity pattern, emerging to forage during half-light periods at dusk (about 1600 hrs) and dawn. Reports of day activity from photographers and film crews were determined to be observations of another long-armed species, the "Mimic Octopus" (see Norman and Hochberg 2005a).

Two foraging methods have been observed for this species:

- Speculative "probing" of individual arms down burrows in the mud. When prey are encountered they are seized and withdrawn using suckers on the distal tips of the arms.
- Speculative "web-casting", where the octopus arches its narrow arms over an area of sand or mud forming an umbrella-like empty frame. The thin, semi-transparent webs are then rapidly extended to fill in the umbrella and enclose any small fishes or crustaceans contained within the area of the "cast" (Fig. 4D). Arm tips are used to flush buried prey into the waiting web and suckers.

The diet appears to consist of small fishes and crabs (e.g. *Calappa* spp.) that co-occur in sand, mud and rubble substrates. The second author observed one octopus consuming a crab with a carapace as large as the mantle of the octopus, which prevented the octopus from retracting back into its lair while feeding. Captive animals have been observed to be day active and readily fed on shrimps and pieces of fish meat (A. Kerstitch and R. Caldwell, pers. comm.).

As mentioned above, several of the specimens examined were missing numerous arms, typically severed around the level of the 8th to 12th proximal sucker. Regeneration had commenced from some stumps. One wild animal encountered by the second author possessed three arms regenerating from the base (Fig. 5D). This species thus appears to be capable of arm autotomy (severing an arm at a set cleavage plane near the base), as has been documented in other long-armed octopuses (Norman 1992b). Such behavior provides a wriggling decoy or food offering to attackers, while the animal escapes to regenerate the lost limb.

Predators are unknown, although they are likely preyed upon by flounders and scorpion fishes. One individual octopus rapidly fled from threats by an aggressive mantis shrimp (stomatopod), which was resident within the octopus's home range. This reaction suggests that the shrimp may be a direct competitor, a potential predator, or both.

The third author observed mating in *Wunderpus photogenicus* n. sp. in the wild. The male mounts the female and inserts the short hectocotylized arm (~30% of length of opposite arm) into the mantle of the female (Fig. 5E). This contrasts with the more typical distance or remote mating and insemination behavior observed in other octopus species which possess a long hectocotylized arm (*e.g.* Young 1962; Norman and Finn 2001).

Mature ovarian eggs reach a capsule length of at least 3.6 mm long (approximately 10% of mantle length). Egg size relative to mantle length has been used in other octopus species to successfully predict hatchling behavior. Egg size predicts planktonic hatchlings (see Miske and Kirchhauser 2006).

Certain postures and behavioural displays observed in *Wunderpus photogenicus* n. sp. have been proposed to represent mimicry of other animals. The display shown in Figure 4A has been suggested to be impersonation of scorpaenid lionfishes (*Pterois* spp.), which possess long poisonous spines advertised by similar banded markings (Kerstitch 1989). *W. photogenicus* n. sp. also has been observed to sit with six arms down a burrow while two opposite arms are undulated to produce the appearance of another poisonous animal, a banded sea snake (*Laticauda* sp.; Nielsen-Tackett and Tackett 2000).

Wunderpus photogenicus n. sp. is primarily active at dusk and dawn on soft sediment substrates, which offer little cover or refuge from fishes and other predators. The dramatic color pattern of *W. photogenicus* n. sp. may have evolved as a defensive strategy against these predators through one of two scenarios. Color patterns and potential mimicry behavior may have evolved to impersonate other species, specifically banded poisonous animals such as lion fishes or sea snakes. An alternative explanation is that this species is itself poisonous and is advertising its toxicity in a similar fashion to species of the deadly blue-ringed or blue-lined octopuses (*Hapalochlaena* spp.) of Australia and Asia. Brilliant iridescent blue markings (rings or lines) on these animals warn potential attackers of the high toxicity of their saliva. Toxicology of the salivary glands and other tissues of *W. photogenicus* n. sp. may provide further insights into the significance of the dramatic color pattern of this species.

Discussion

Wunderpus photogenicus n. sp. joins a growing list of species of small octopuses with long arms that live on soft sediment and/or in intertidal habitats around the world. The majority of these taxa exhibit arm autotomy at a set plane near the arm base. These taxa include *Abdopus* species of the Indo-West Pacific (Norman and Finn, 2001); *Amelocto-pus litoralis* Norman, 1992 of northern Australia; *Macro-tritopus defillipi* (Verany, 1851) of the Atlantic Ocean and Mediterranean Sea (and the potentially related '*Octopus*' sp. 17 in Norman, 2000); *Thaumoctopus mimicus* Norman and Hochberg, 2005 of the Indo-West Pacific (and the potentially related '*Octopus*' sp. 18 in Norman, 2000) and a number of unplaced species including '*Octopus*' *mutilans* Taki, 1942 of Japan (Tsuchiya *et al*. 2002), '*Octopus*' *harpedon* Norman, 2001 from northern Australia and '*Octopus*' sp. B Voss and Williamson, 1972 found in Hong Kong.

Generic placement of most of the latter species awaits their thorough morphological description. The single largest impediment to this process is access to well-preserved material. Many of these species are best known from live animal photographs, however little or no voucher material has been collected. Because of the rarity of these animals and the remote locations in which many live, problems occur with collecting permits and access to appropriate expertise and preservation techniques. The limited material that is available, including that of the new species described herein, comes primarily from the marine aquarium trade.

The octopod fauna of Indonesia and elsewhere in the Indo-Malayan Archipelago still remains largely unstudied.

At least 50 undescribed species have been recognized by the authors throughout the region. The group is in need of extensive revision and sources of well-preserved voucher specimens need to be developed.

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