

A NEW SPECIES OF *CISTOPUS* (CEPHALOPODA: OCTOPODIDAE) FROM TAIWAN AND MORPHOLOGY OF MUCOUS POUCHES

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ABSTRACT

Cistopus taiwanicus n. sp. is a medium to large benthic octopus. The primary diagnostic character for the genus *Cistopus* is the possession of eight mucous pouches set in the oral surface of the webs between each of the arm bases. This study describes the morphological characters of *C. taiwanicus* from Taiwanese waters and the histology of the mucous pouches. *Cistopus taiwanicus* can be distinguished from *Cistopus indicus* by enlarged suckers in mature males and lower sucker counts on normal arms and hectocotylized arm. The inner walls of the mucous pouches are composed of columnar epithelial cells and mucus is secreted from the epithelial cells. *Cistopus taiwanicus* shows sexual dimorphism in the openings of the mucous pouches; males possess radial white stripes around the mucous pores and significantly larger pore diameters.

INTRODUCTION

Cistopus indicus (Rapp, 1835 in De Férussac & d'Orbigny, 1834–1848) is a medium- to large-sized octopod. Its local name in China is 'Lai Por' (Cantonese = 'old woman octopus' in English) (Voss & Williamson, 1971; Dong, 1988). It is a benthic species, occurring subtidally to depths of at least 80 m on muddy substrates (Roper, Sweeney & Nauen, 1984; Norman & Sweeney, 1997). It is a common Indo-Malayan octopus, existing in tropical and subtropical coastal waters from southern China, Taiwan, the Philippines, northern Indonesia and west to India (Robson, 1929; Voss, 1963; Voss & Williamson, 1971; Pickford, 1974; Dong, 1978, 1988; Nesis, 1982; Roper, Sweeney & Nauen, 1984; Norman & Hochberg, 1994; Norman & Sweeney, 1997; Lu, 1998; Norman, 1998; Norman & Lu, 2000). *Cistopus indicus* is an important commercial species throughout most of its range, where it is harvested primarily by trawlers (Norman, 1998). Early studies reported landed catches of around 50 tonnes per year in Hong Kong (Voss & Williamson, 1971). It is also an abundant major fisheries species in Singapore and Thailand (Pickford, 1974; Chotiyaputta, 1993).

The genus *Cistopus* was erected by Gray (1849) who defined it as possessing eight small pouches in the web between the bases of each arm. The eight pouches contain mucus, which can be released through a small muscular pore opening to the exterior between the proximal suckers (Norman, 2000). These structures have historically been described as 'water pouches', however they contain mucus rather than water. In this study, the name 'mucous pouches' is proposed. The function of the mucous pouches remains a mystery. Robson (1929) suggested that they might be used to receive spermatophores, while Norman (2000) proposed that they were mucous glands and may be used to help cement the walls of burrows in fine sand or silt. This character is often difficult or even impossible to see in preserved specimens, resulting in the regular misidentification of *Cistopus* (Pickford, 1974; Nesis, 1982).

To date *C. indicus* has been the sole described species in this genus. It was first described as *Octopus indicus* in De Férussac & d'Orbigny (1834–1848) based on a specimen from Celebes (= Sulawesi), Indonesia. Recent studies indicate that more than

one species of *Cistopus* exists (Nateewathana, 1997; Norman & Sweeney, 1997; Norman, 1998, 2000). The presence of the genus *Cistopus* in Taiwanese waters was first recorded by Lu (1998) under the name *C. indicus*. It is common in the fish markets of western Taiwan and traditionally used as food. The aim of this paper is to describe the morphological characters of a new species of *Cistopus* from Taiwan and distinguish it from *C. indicus* and other reported undescribed *Cistopus* species. The mucous pouches of *Cistopus* are examined histologically and described.

MATERIAL AND METHODS

Material examined

Material was obtained from the catches of trawlers working in the coastal waters of Hsinchu County, Miaoli County and Tungkang (Pingtung County), Taiwan. Additional material was collected from fish markets of Wuchi (Taichung County), Makung (Penghu County) and Tungkang. All specimens were transported in plastic bags on ice to the laboratory.

All material is lodged in the National Museum of Natural Sciences, Taichung, Taiwan (NMNS), Museum Victoria, Melbourne, Australia (MV), National Museum of Nature and Sciences, Tokyo, Japan (NSMT), and Research Museum, Research Center for Biodiversity, Academia Sinica, Taipei, Taiwan (ASIZ).

Other abbreviations are: BTP, bottom trawling programme, Academia Sinica; coll., collected by; FM, fish market; ML, dorsal mantle length; MNHN, Muséum National d'Histoire Naturelle, Paris.

Measurements and description

All specimens were examined and measured according to Roper & Voss (1983), Norman, Hochberg & Lu (1997) and Norman & Sweeney (1997). Counts and morphological measurements were made from freshly dead material for observation of the pouch system.

The developmental stage (DevS) was determined according to Lu & Roper (1979). The following measurements were made: total length (TL), total weight (TW), ML, ventral mantle length (VML), mantle width (MW), head length

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(HL), head width (HW), eye length (EL), funnel length (FL), funnel width (FW), the deepest web depth (DWD), the shallowest web depth (SWD), arm length (AL), sucker diameter (SD) and ligula length (LL). Sucker number on normal arms (SNN) and third right arm (SNR3) were counted.

The ventral mantle was cut along by the mantle septum, without cutting the mantle septum, to expose the mantle cavity. The gill number (GN) is the number of gill lamella per demibranch, excluding the terminal lamella. The terminal organ length (TOL) (historically referred to as the penis), spermatophore length (SpL), spermatophore width (SpW), sperm reservoir length (SRL) and spermatophore cord whorls (SpCW) of mature males and egg length (EgL) of mature females were measured. Funnels of live or recently dead specimens were dissected for funnel organ observation. The beaks and radulae were removed from some specimens for examination. The radulae were cleaned, air dried, coated with gold and then examined and photographed using a Hitachi S-3000 N scanning electron microscope. The mucous pouches and pores were stained with methylene blue to maximize contrast for observation and measurement of the pore diameter (PD) and pouch length (PL).

After measurements, all specimens were labelled and fixed in 10% buffered formalin. The fixed specimens were later transferred to 70% ethyl alcohol for permanent storage.

Histological methods

The entire pouch system including the surrounding muscles and connective tissue was dissected from web sectors of fresh specimens that had been collected from the fish market of Tungkang. Samples were fixed in Bouin's fixative, serially sectioned at 5 μ m thickness and then stained differentially with haematoxylin and eosin, periodic acid-Schiff (PAS), alcian blue at pH 1.0, and Gomori's one-step trichrome (modified from Presnell & Schreiber, 1997). A compound microscope (Olympus BX-50) and a digital microscopic camera (Polaroid DMCie) were used to photograph histological slides. The slides are deposited in the National Museum of Natural Sciences, Taiwan.

SYSTEMATIC DESCRIPTIONS

Family Octopodidae d'Orbigny, 1840

Genus *Cistopus* Gray, 1849

Type species: *Octopus indicus* Rapp, 1835 in De Férussac & d'Orbigny, 1834–1848

Diagnosis: Octopods with biserial arm suckers; eight small mucous pouches, each with a small pore, in the oral surface of the webs between the bases of each arm; hectocotylus of mature males with tiny ligula, calamus absent or barely visible.

Cistopus taiwanicus new species

(Figs 1–7)

Type material: Holotype NMNS-5255-001, Miaoli, 24°28.74'N 120°34.75'E, 35 m, 3 December 2002, mature male, 135 mm ML, coll. BTP. Eight paratypes NMNS-5255-002, Miaoli, 24°29.21'N 120°34.47'E, 50 m, 6 June 2002, mature female, 125 mm ML, coll. BTP. MV-F109334, Miaoli, 24°31.62'N 120°38.46'E, 25 m, 2 December 2002, mature male, 84.2 mm ML, coll. BTP. MV-F109335, Miaoli, 24°26.31'N 120°31.51'E, 45 m, 2 December 2002, submature female, 110.2 mm ML, coll. BTP. NSMT-Mo75535, Tungkang, 22°16.206'N 120°32.088'E, 75 m, 1 October 2004, mature male, 89 mm ML, coll. BTP. NSMT-Mo75536, same data as for NSMT-Mo75535, submature

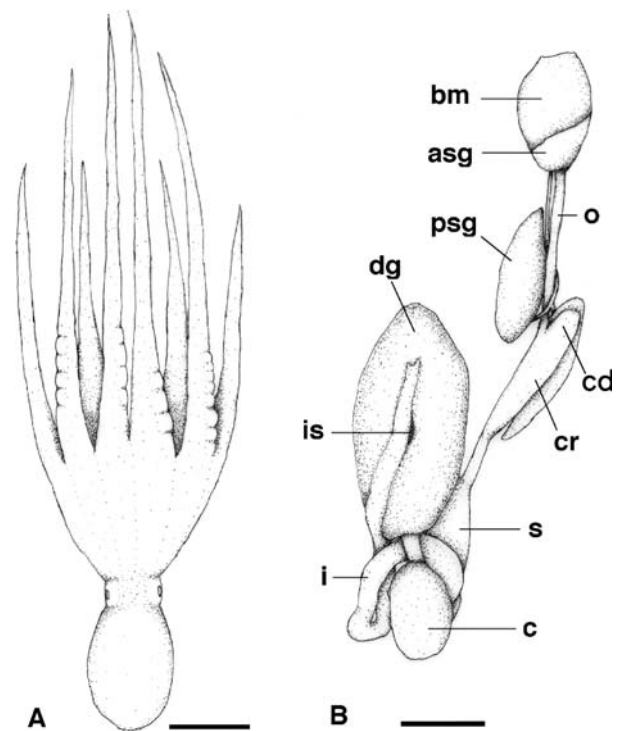


Figure 1. *Cistopus taiwanicus* n. sp. **A.** Dorsal view of whole animal, paratype 6 (ASIZM0001351, male, 96 mm ML), scale bar = 50 mm. **B.** Digestive system, paratype 4 (NSMT-Mo75535, male, 89 mm ML), scale bar = 10 mm. Abbreviations: asg, anterior salivary gland; bm, buccal mass; c, caecum; cd, crop diverticulum; cr, crop; dg, digestive gland; i, intestine; is, ink sac; o, oesophagus; psg, posterior salivary gland; s, stomach.

female, 72 mm ML. ASIZM0001351, Makung FM, Penghu, 2 April 2002, mature male, 96.4 mm ML, coll. CW Ho. ASIZM0001353, Hsinchu, 24°43.06'N 120°25.08'E, 70 m, 5 June 2002, mature female, 141.3 mm ML, coll. BTP. NMNS-5255-006, Miaoli, 24°31.68'N 120°38.64'E, 10 m, 15 June 2004, submature female, 81.5 mm ML, coll. BTP.

Other material examined: NMNS-5255-003, Wuchi FM, Taichung, 18 December 2002, mature male, 116.9 mm ML, coll. WS Chung. NMNS-5255-004, Tungkang FM, Pingtung, 8 December 2002, mature male, 92 mm ML, coll. JX Liao. NMNS-5255-005-1, Tungkang FM, Pingtung, 10 November 2002, mature male, 73 mm ML, coll. JX Liao. NMNS-5255-007, Wuchi FM, Taichung, 29 May 2002, mature female, 119.4 mm ML, coll. JX Liao. NMNS-5255-008, Tungkang FM, Pingtung, 8 December 2002, mature female, 136.3 mm ML, coll. JX Liao. NMNS-5255-009, Wuchi FM, Taichung, 23 June 2007, two mature males, 109 and 98.2 mm ML, coll. JX Liao. NMNS-5255-010-1, Wuchi FM, Taichung, 9 October 2007, mature male, 101 mm ML, coll. JX Liao. NMNS-5255-010-2, Wuchi FM, Taichung, 9 October 2007, submature female, 79.7 mm ML, coll. JX Liao.

Etymology: The specific epithet *taiwanicus* refers to Taiwan, as the only known locality for this species.

Diagnosis: Moderate to large species, ML to around 140 mm. Mucous pouches present in oral surface of webs between arm bases. Arms long, approximately five times ML. Hectocotylized arm with tiny ligula (<0.5% of AL) without calamus. Gills with 9–10 lamellae per demibranch. Sucker counts 131–164 on normal arms, 106–117 on hectocotylized arm of males. Mature males with 2 to 4 enlarged suckers

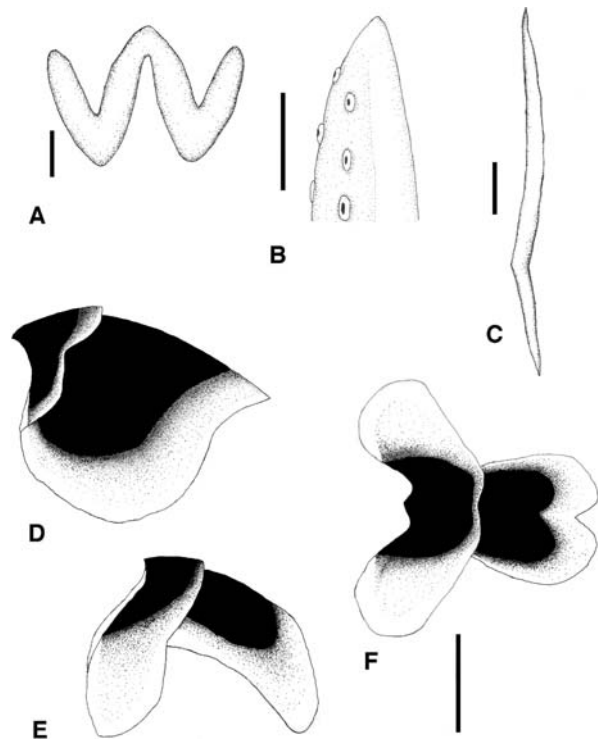


Figure 2. *Cistopus taiwanicus* n. sp. **A, B.** Paratype 6, ASIZM0001351, male, 96 mm ML. **A.** Funnel organ, scale bar = 5 mm. **B.** Distal end of hectocotylized arm, lateral view, scale bar = 2 mm. **C.** Stylet, female, 147.7 mm ML, scale bar = 10 mm. **D–F.** NMNS-5255-007, female, 119 mm ML, scale bar = 5 mm. **D.** Upper beak, lateral view. **E.** Lower beak, lateral view. **F.** Lower beak, ventral view.

(18th–21st) on arms 1 and 2. Mature females with 6,000–8,000 small eggs (5–7 mm). Colour dull grey with iridescent green sheen on lateral mantle in fresh specimens. Skin smooth with few scattered low papillae on dorsal mantle.

Description: The following description is based on seven mature males and seven females (four mature and three submature). Counts and measurements for these specimens are presented in Table 1.

Medium- to large-sized species, ML to 141 mm and weight to 1226 g in material examined. Mantle elongate, separated from head by a narrow neck region (Fig. 1A). Head narrow (21.8–34.8% ML; 28.2–54.5% MW). Eyes small (6.7–13.5% ML). Funnel of moderate length (26–45.7% ML). Funnel organ W-shaped, length of outer limbs 75–100% of medial limbs, slightly thinner than medial limbs (Fig. 2A). Arms long and stout, 3.8–6.9 times ML, dorsal arms longer than ventral arms (arm formula typically 1.2.3.4). Webs of moderate depth (deepest 14.1–22.5% of longest arm), dorsal web deeper than ventral web (web formula A.B.C.D.E or occasionally B.A.C.D.E). Suckers in 2 rows, medium-sized in females (to 12.1% ML), enlarged suckers (up to 19.8% ML) in mature males on arms 1 and 2 (2–4 in number at 18th–21st proximal suckers; Fig. 4A, B). Third right arm of males hectocotylized. Sucker count 131–164 on normal arms, 106–117 on hectocotylized arms of males. Ligula very small (<1.6 mm, 0.4–0.5% of hectocotylized AL), calamus absent (Figs 2B, 4C). Spermatophore groove conspicuous by its white colour in contrast to the grey-coloured arm. Stylets: thin, clear, nonmineralized rods (Fig. 2C) length around 30% of ML. Gills with 9–10 lamellae per demibranch.

Digestive tract illustrated in Figure 1B. Anterior salivary glands moderate, approximately one-third length of buccal

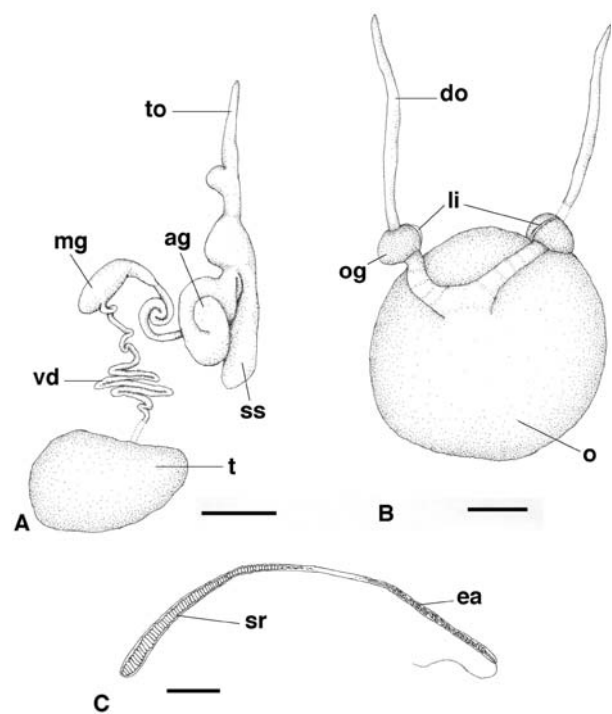


Figure 3. *Cistopus taiwanicus* n. sp. **A, C.** Paratype 4, NSMT-Mo75535, male, 89 mm ML. **B.** Paratype 1, NMNS-5255-002, female, 125 mm ML. **A.** Male reproductive tract, scale bar = 10 mm. **B.** Female reproductive tract, scale bar = 10 mm. **C.** Spermatophore, scale bar = 3 mm. Abbreviations: ag, accessory gland; do, distal oviduct; ea, ejaculatory apparatus; li, ligament wrapping around the oviducal gland; mg, mucilaginous gland; o, ovary; og, oviducal gland; sr, sperm reservoir; ss, spermatophore storage sac; t, testis; to, terminal organ; vd, vas deferens.

mass. Posterior salivary glands well developed, slightly larger than buccal mass. Crop with distinct diverticulum. Caecum with approximately one whorl. Intestine long, with distinct U-shaped loop. Ink sac small. Anal flaps present.

Upper beak (Fig. 2D) with a short hooked rostrum and narrow hood. Lower beak with short rostrum, narrow hood, moderately broad wings and flared lateral walls separated in posterior 20% (Fig. 2E, F). Radula (Fig. 5A, B) with 7 transverse rows of teeth and 2 rows of marginal plates. Rhachidian tooth with 1–2 lateral cusps on each side of median cone. Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over *c.* 3 transverse rows.

Male reproductive tract illustrated in Figure 3A. Terminal organ length variable (10.8–22.7% ML) in mature males, curved with small diverticulum. Vas deferens duct relatively long and coiled. Spermatophores: (Fig. 3C) *c.* 30% of mantle length (length 24–33 mm), narrow (width 0.7–0.9 mm, 2.7–2.9% of SpL); unarmed; abundant (~200–250 in storage sac). Ejaculatory apparatus coiled for approximately one-third of SpL. Sperm reservoir roughly 50% of total SpL, sperm cord spirally wound in 60–78 whorls.

Female reproductive tract illustrated in Figure 3B. Distal oviducts long and thin. Oviducal glands without radiating chambers, wrapped in ligament (Fig. 3B). About 6,000–8,000 small eggs in mature females, EgL about 5–7 mm (3.7–5% ML).

Mucous pouches present within oral surface of webs close to mouth, pores located at level of 3rd or 4th proximal sucker, extend between 2nd and 7th proximal sucker, interbranchial membranes without other anomaly. Mucous pores sexually dimorphic: in males PDs 1–1.8 mm, in females 0.3–0.5 mm,

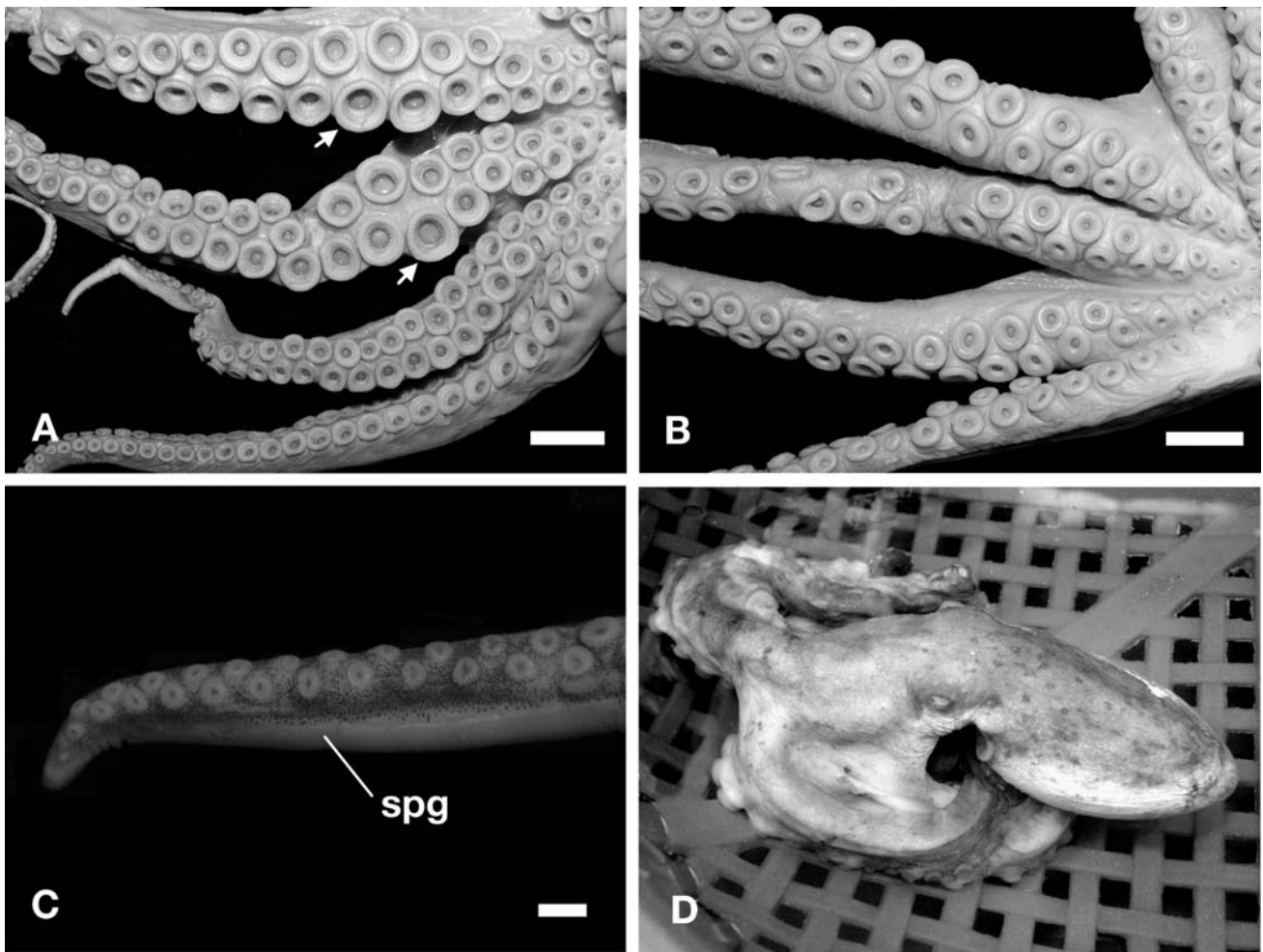


Figure 4. *Cistopus taiwanicus* n. sp. **A, C, D.** NMNS-5255-009, male, 109 mm ML. **A.** Pattern of arm suckers in formalin-fixed specimen, arrows indicate enlarged suckers at first and second right arms, scale bar = 20 mm. **B.** NMNS-5255-007, female, 119 mm ML. Pattern of arm suckers, scale bar = 20 mm. **C.** Distal end of the hectocotylyzed arm, scale bar = 2 mm. **D.** Live animal in Wuchi Fish Market. Abbreviation: spg, spermatophore groove.

sometimes difficult to recognize in females; radial white stripes around rim in males (Figs 5C, 6), white stripes not visible in preserved specimens; stripes absent in females (Fig. 5D). A few specimens possessed conspicuously swollen pouches.

Colour of live specimens dull grey on dorsal surfaces (Fig. 4D), turning dark red-brown when agitated. Lateral and ventral mantle iridescent greenish blue, produced by iridophore layer in skin. Significant stripes or markings absent. Skin smooth with few scattered low papillae on dorsal mantle. Primary papillae absent.

Distribution: Sea off the west coast of Taiwan (from Hsinchu, Miaoli to Pingtung counties) on muddy substrates. Specimens were trawled at depths between 10 and 75 m. The specimens obtained from fish markets were all live in excellent condition, captured near the various fish markets.

Morphology of mucous pouches: *Cistopus* possesses a ring of eight pouches around the mouth between the bases of the arms. These pouches contain mucus that can be released from a small muscular pore. The pouches of males possess radial white stripes around the pore (Fig. 6) that are composed of leucophores, which directly reflect bright white light when fresh material is observed under a dissecting microscope.

The tissues of the mucous pouch are separated from the muscular tissues around the pouch. A duct connects the pouch

to the exterior to release the glandular secretion (Fig. 7A). The inner surface of the pouches is folded and many compact nuclei of the columnar epithelial tissues line the inner wall (Fig. 7B), as is typical for molluscan secretory organs. Several layers of densely packed connective tissues are present, formed by collagen fibres and muscle fibres (shown, respectively, as green and red using Gomori's one-step trichrome) around the folded inner layers. The surface around the opening of mucous pouches is a mosaic of numerous basophilic granules, which extend in some specimens into the inner wall of the duct (Fig. 7C). These basophilic granules are irregular in shape and lack nuclei and cytoplasm.

In the PAS-stained sections, the inner surface of mucous pouch produced a positive PAS reaction (rose to purple-red in colour). The inner wall of the mucous pouch contains secretions reacting positively to alcian blue (pH 1.0) stain. This result indicates that the glandular secretion is a form of acid mucopolysaccharides, a typical ingredient of molluscan mucus.

DISCUSSION

Taxonomic composition of the genus Cistopus

The unique character for the genus *Cistopus* is the presence of the mucous pouches on the oral surface of the web adjacent to

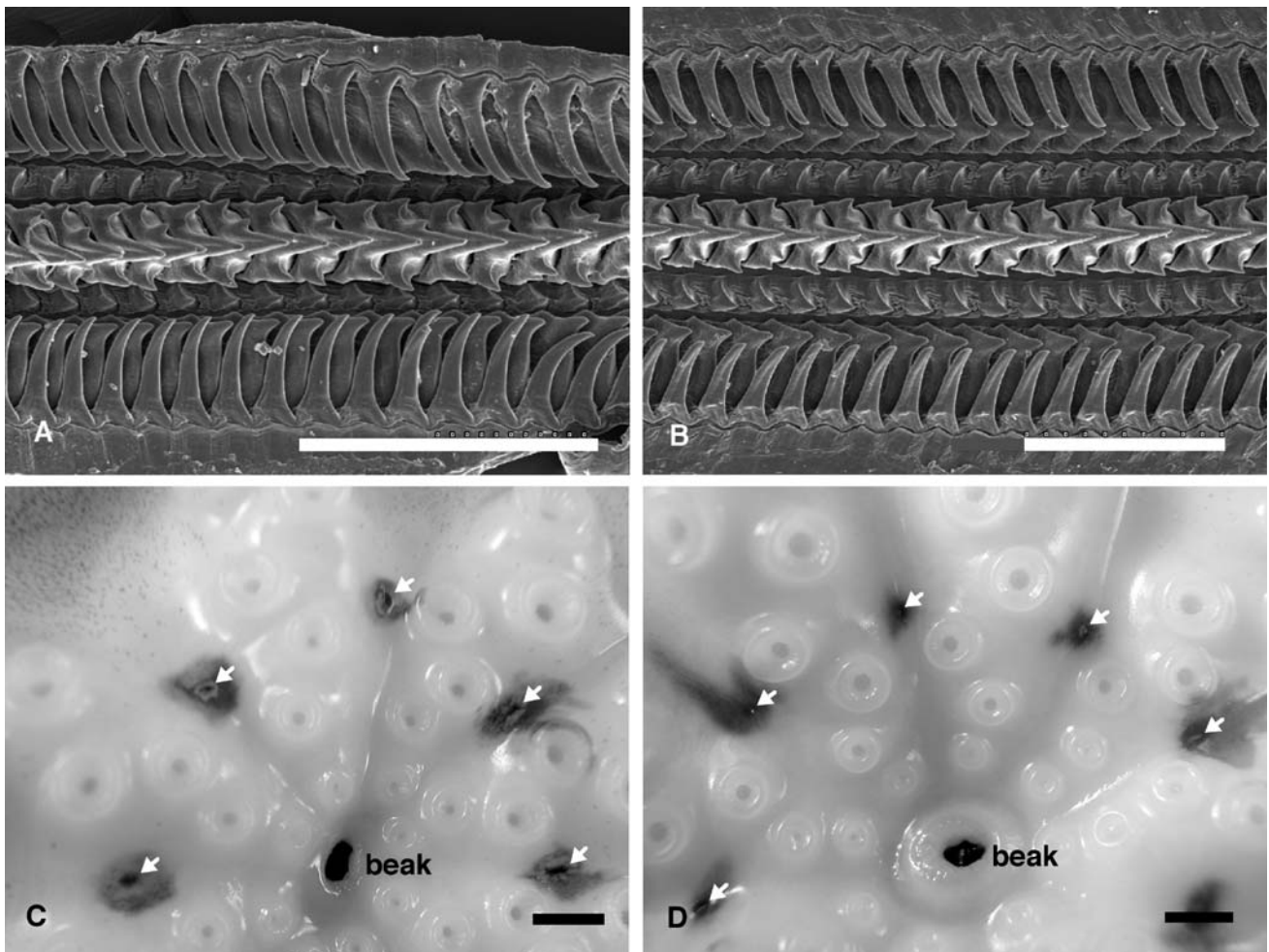


Figure 5. *Cistopus taiwanicus* n. sp. **A, B.** Scanning electron micrographs of radulae, scale bar = 10 mm. **A.** Paratype 6, ASIZM0001351, male, 96 mm ML. **B.** Paratype 1, NMNS-5255-002, female, 125 mm ML. **C, D.** Oral surface of brachial crown of live specimen showing mucous pores, stained with methylene blue for better contrast. Arrows indicate the pores, scale bars = 3 mm. **C.** NMNS-5255-010-1, male, 101 mm ML, pore diameter = 1.4 mm. **D.** NMNS-5255-010-2, female, 80 mm ML, pore diameter = 0.4 mm.

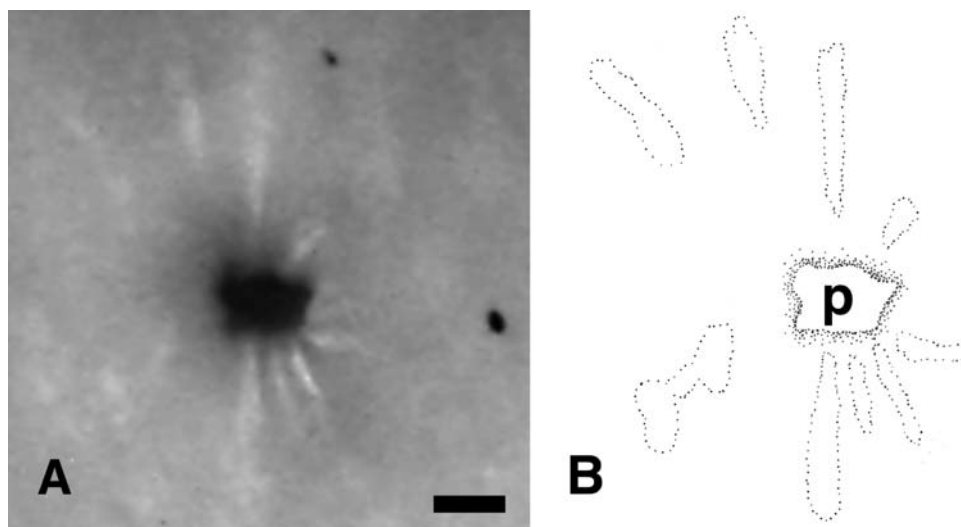


Figure 6. *Cistopus taiwanicus* n. sp. Radial white stripes around the mucous pore, scale bar = 1 mm. NMNS-5255-010-1, male, 101 mm ML, pore diameter = 1.4 mm ML. **A.** Live image. **B.** Drawing of **A.** Abbreviation: p, pore.

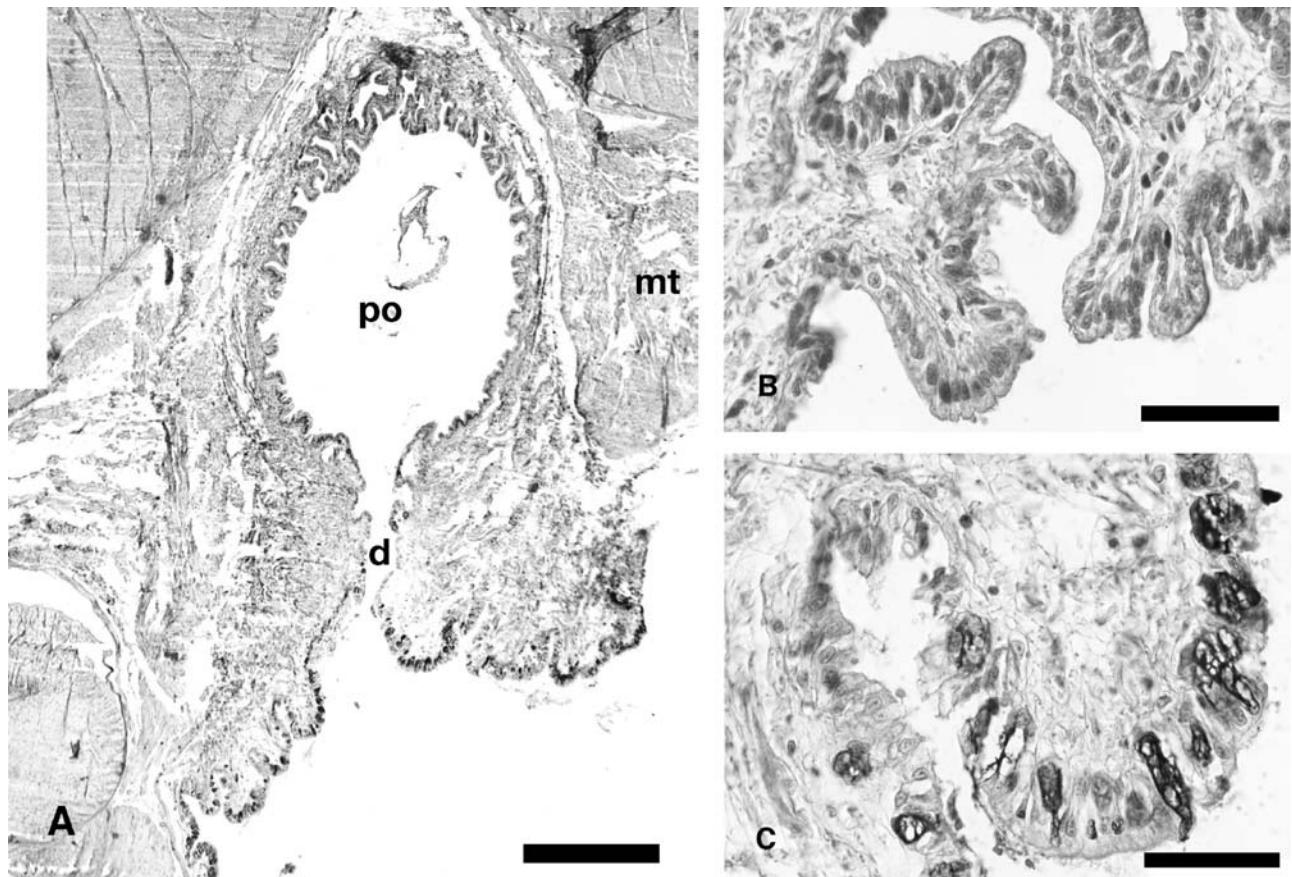


Figure 7. Light micrographs of cross-section of the mucous pouch from *Cistopus taiwanicus* n. sp. (male, 76 mm ML, collected from Tungfang FM). Haematoxylin and eosin staining. **A.** Mucous pouch with folded inner surface and the opening; scale bar = 0.5 mm. **B.** Epithelium on the inner wall of mucous pouch. **C.** Basophilic granules in the surface around the opening of mucous pouch. **B, C.** Scale bar = 0.05 mm. Abbreviations: d, duct; mt, muscular tissues; po, pouch.

the mouth. To date only one species has been named for this genus, *Cistopus indicus*. According to Norman & Sweeney (1997), more than one species of *Cistopus* exists. The genuine *C. indicus* (only confirmed distribution from the type locality, Sulawesi in Indonesia, and the Philippines) is characterized by the possession of mucous pouches, an arm formula of 1.2.3.4, a tiny ligula (~0.5% of hectocotylyzed AL), absence of a calamus, 9–10 gill lamellae per demibranch, sucker counts of *c.* 185 on normal arms and *c.* 110–130 on the hectocotylyzed arm and absence of enlarged suckers in both sexes.

The only extant syntype of *Octopus indicus* (MNHN 5-4-1050) was reported to be a female specimen with a mantle length of 78 mm (Lu, Boucher-Rodoni & Tillier, 1995). The specimen was re-examined by one of us (C.-C.L.) in 2004 and was found to be a male with well-developed hectocotylus. This specimen possesses 170–189 suckers on normal arms and 134 suckers on the hectocotylyzed arm, tiny ligula (Fig. 8; 0.9 mm in length, 0.4% of the hectocotylyzed arm), and lacks enlarged suckers (SD up to 8.3 mm, to 10.6% ML). The first species of Norman & Sweeney (1997) possesses 180–200 suckers on normal arms and 116–123 suckers on the hectocotylyzed arm, also with tiny ligula (<1.5 mm in length, 0.5–0.7% of the hectocotylyzed arm), without enlarged suckers (sucker to 13.1% ML in males and 11.0% in females) (Table 2). The two taxa conform in those key characters. We believe that the first species of Norman & Sweeney (1997) belongs to the genuine *C. indicus*, as was identified by them.

To examine the difference in sucker number between *C. indicus* (syntype) and *Cistopus taiwanicus* n. sp. the sucker count

vs AL was plotted following Toll (1988) (Fig. 9). The average sucker counts of normal arms and hectocotylyzed arms of *C. taiwanicus* are separable from those of *C. indicus*. Toll (1988) did not indicate the origin of '*C. indicus*' specimens in his article and his data were therefore not compared with ours.

An undescribed species reported by Norman & Sweeney (1997) can be distinguished from *C. indicus* in that mature males possess 1–2 enlarged suckers on arms 1, 2 and 4, lower sucker counts on the hectocotylyzed arm (60–80) and slightly higher gill lamellae counts (10–11). However, a detailed morphological description and list of material examined was not provided (Norman & Sweeney, 1997).

Nateewathana (1997) reported the genus *Cistopus* from the Andaman Sea, Thailand, and noted that the Andaman Sea material was close in form to this undescribed species, but differed by having a small but distinct calamus, sucker counts on the hectocotylyzed arm (75–124) and fewer gill lamellae (9–10). Nateewathana (1997) provided details of additional characters, including sucker counts of *c.* 102–145 on normal arms, two enlarged suckers (6th–7th) in mature males on arms 1, 2 and 4, a ligula *c.* 1.4% of the hectocotylyzed AL and production of around 100 large eggs (11–15 mm) by mature females.

Cistopus taiwanicus shows many similarities with the genuine *C. indicus* (as described by Norman & Sweeney, 1997), but differs in the presence of enlarged suckers (absence in the extant type and those reported by Norman & Sweeney, 1997) and lower sucker counts on both the normal arms (131–164 *vs* 170–189 in the extant syntype and 180–200 in Norman &

Table 1. Counts and measurements (raw data, measurements in mm) for *Cistopus taiwanicus* n. sp. and *Cistopus indicus* (syntype).

| Museum | NMNS | MV | NSMT | ASIZ | NMNS | NMNS | NMNS | NMNS | MV | NSMT | ASIZ | NMNS | NMNS | NMNS | MNHN |
|-------------|----------|------------|------------|------------|----------|-------------|-------------|------------|------------|------------|------------|------------|----------|-------------|----------|
| Catalog No. | 5255-001 | F109334 | Mo75535 | M0001351 | 5255-003 | 5255-004 | 5255-005-1 | 5255-002 | F109335 | Mo75536 | M0001353 | 5255-006 | 5255-007 | 5255-008 | 5-4-1050 |
| Status | Holotype | Paratype 2 | Paratype 4 | Paratype 6 | – | – | – | Paratype 1 | Paratype 3 | Paratype 5 | Paratype 7 | Paratype 8 | – | – | Syntype |
| Locality | Miaoli | Miaoli | Tungkang | Makung FM | Wuchi FM | Tungkang FM | Tungkang FM | Miaoli | Miaoli | Tungkang | Hsinchu | Miaoli | Wuchi FM | Tungkang FM | Celebes |
| Sex/DevS | M/5 | M/5 | M/5 | M/5 | M/5 | M/5 | M/5 | F/5 | F/4 | F/4 | F/5 | F/4 | F/5 | F/5 | M/5 |
| TL | 870 | 406 | 471 | 564 | 672 | 740 | 407 | 714 | 689 | 396 | 714 | 497 | 594 | 942 | NR |
| TW (g) | 800 | 197 | 343 | 417 | 882 | 426 | 295 | 886 | 514 | 209 | 1030 | 298 | 486 | 1226 | NR |
| ML | 135 | 84 | 89 | 96 | 117 | 92 | 73 | 125 | 110 | 72 | 141 | 82 | 119 | 136 | 78 |
| VML | 104 | 59 | 71 | 67 | 79 | 62 | 51 | 93 | 80 | 55 | 103 | 54 | 79 | 102 | NR |
| MW | 87 | 44 | 65 | 57 | 90 | 63 | 50 | 87 | 85 | 50 | 90 | 57 | 81 | 104 | NR |
| HL | 32 | 24 | 23 | 23 | 36 | 32 | 19 | 36 | 24 | 17 | 38 | 21 | 31 | 42 | NR |
| HW | 43 | 27 | 36 | 29 | 52 | 50 | 31 | 45 | 43 | 27 | 46 | 33 | 37 | 48 | NR |
| EL | 13 | 8 | 12 | 9 | 10 | 11 | 8 | 11 | 9 | 7 | 12 | 7 | 8 | 12 | NR |
| FL | 48 | 34 | 32 | 25 | 46 | 42 | 29 | 36 | 39 | 26 | 47 | 27 | 33 | 49 | NR |
| FW | 23 | 13 | 15 | 13 | 24 | 20 | 13 | 21 | 22 | 14 | 21 | 13 | 16 | 25 | NR |
| DWD | A: 125 | B: 57 | B: 56 | NR | A: 124 | A: 88 | B: 64 | A: 87 | A: 81 | A: 63 | A: 111 | A: 72 | B: 73 | B: 147 | A: 71 |
| SWD | E: 54 | E: 25 | E: 40 | NR | E: 45 | E: 40 | E: 28 | E: 42 | E: 41 | E: 17 | E: 48 | E: 27 | E: 46 | E: 51 | E: 33 |
| AL1 (L/R) | 710/D | D/D | R/D | 403R/D | R/551 | D/631 | R/320D | 570/D | D/D | 291D/348 | D/540 | 394/395 | 449/D | D/819 | 445/455 |
| AL2 (L/R) | 648/656 | D/300R | D/281R | 396/405 | D/549 | R/D | 321/274 | D/560 | 575/498 | 239R/R | R/530 | 389/332 | 344/321R | 716/730 | D/438 |
| AL3 (L/R) | 558/380 | 270/191 | 348/262 | 336D/275 | 381R/313 | R/336 | R/280 | 505/D | 480/R | 336/218R | 534/498 | 311/288 | 341/204R | D/634 | 372/220 |
| AL4 (L/R) | 374R/509 | R/187R | D/323 | 305/315 | 439/R | R/470 | 250D/288 | 462/D | 422/D | R/126R | 363D/398 | 258/260 | 313/309 | 442/D | D/400 |
| SD | 15.7 | 10.5 | 11.8 | 14.7 | 16.9 | 18.2 | 10.8 | 12 | 10.9 | 8.7 | 14.2 | 9.4 | 11.6 | 15.3 | 8.3 |
| LL | 1.6 | 1.0 | 1.3 | 1.5 | 1.4 | 1.6 | 1.5 | – | – | – | – | – | – | – | 0.9 |
| SNN | 164 | 134 | 148 | 137 | 158 | 162 | 149 | 158 | 162 | 161 | 144 | 140 | 131 | 145 | 177 |
| SNR3 | 116H | 106H | 114H | 106H | 112H | 109H | 117H | D | R | 138R | 154 | 144 | R | 144 | 134H |
| GN | 10 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 10 | 10 | 9 | 9 | 9 | 9 | NR |
| TOL | 18.3 | 10.4 | 11.6 | 10.4 | 17.3 | 20.9 | 16.4 | – | – | – | – | – | – | – | NR |
| SpL | NR | 24 | 29 | NR | 33 | 31 | NR | – | – | – | – | – | – | – | NR |
| SpW | NR | 0.7 | 0.8 | NR | 0.9 | 0.9 | NR | – | – | – | – | – | – | – | NR |
| SRL | NR | 12 | 14 | NR | 1.8 | 17 | NR | – | – | – | – | – | – | – | NR |
| SpCW | NR | 60 | 66 | NR | 78 | 75 | NR | – | – | – | – | – | – | – | NR |
| EgL | – | – | – | – | – | – | – | 5 | Submature | Submature | 7 | Submature | 5 | 5 | – |
| PD | NR | 1 | 1.6 | NR | 1.2 | 1.8 | 1 | 0.5 | 0.3 | 0.3 | NR | 0.4 | NR | 0.4 | NR |
| PL | NR | 16.5 | 19.5 | NR | 25 | 26.4 | 15.3 | 10.5 | 11.4 | 9.7 | NR | 9.5 | NR | 20 | NR |

NR, not recorded; D, damaged; R, regenerated; H, hectocotylized arm.

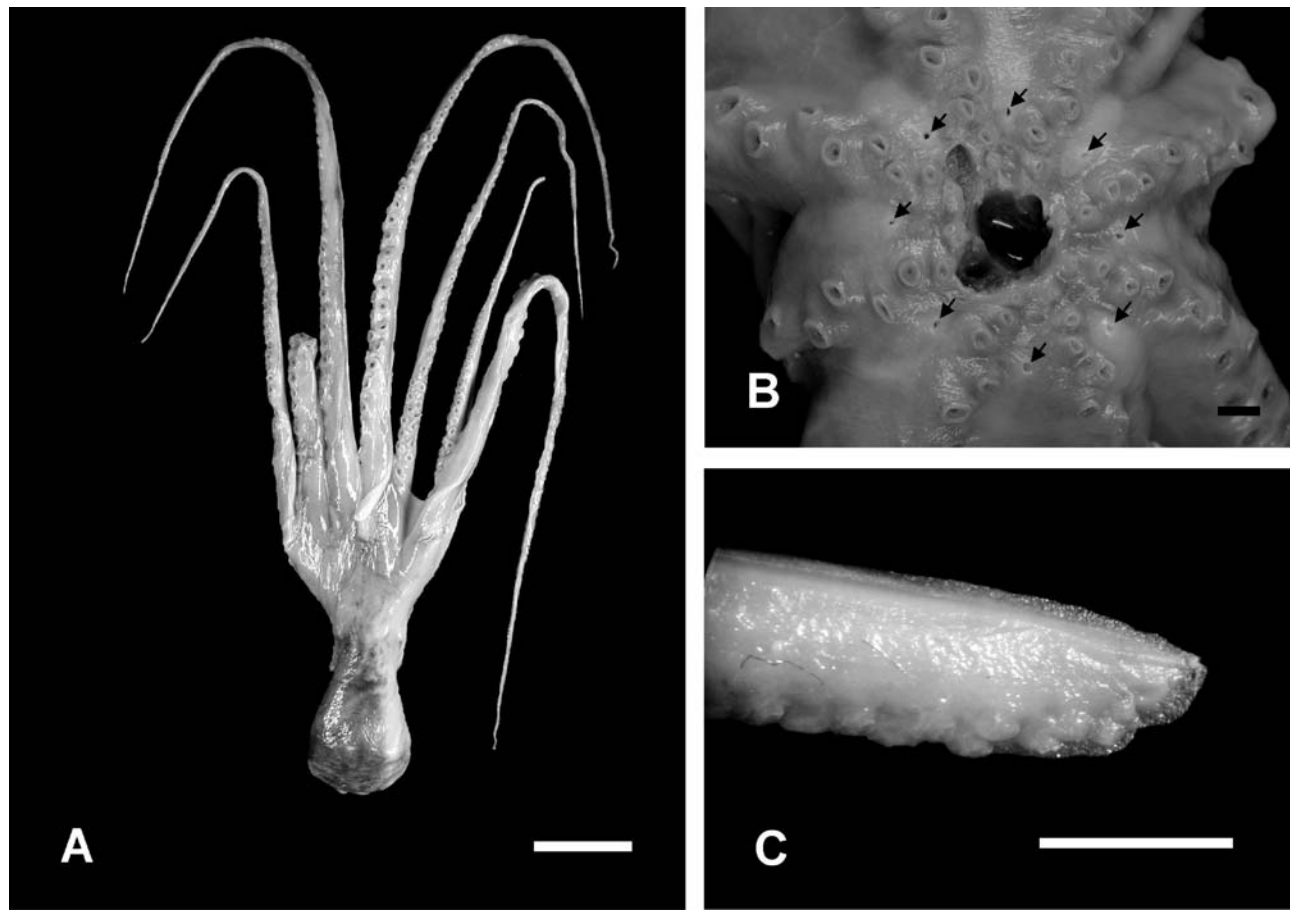


Figure 8. *Cistopus indicus*, syntype, MNHN 5-4-1050, 78 mm ML. **A.** Dorsal view of whole animal, scale bar = 50 mm. **B.** Image of ventral crown for mucous pores, arrows indicate the pores, scale bar = 3 mm. **C.** Distal end of the hectocotylized arm, scale bar = 2 mm.

Sweeney, 1997) and the hectocotylized arms (106–117 *vs* 137 in the extant syntype and 116–123 in Norman & Sweeney, 1997) (Table 2). The material examined by Norman and Sweeney (1997) is smaller than the specimens in this study (ML to 86 mm *vs* ML to 141 mm), and the sucker index (to 13.1% ML in males; to 11% ML in females) is smaller than the specimens in this study (to 19.8% in males; to 12.1% in females). The range of sucker counts on hectocotylized arms slightly overlap, but there are significant differences in sucker counts on the normal arms. We therefore consider *C. taiwanicus* to be distinct from the genuine *C. indicus*.

The Andaman Sea *Cistopus* sp. reported by Natewathana (1997) differs from *C. taiwanicus* in the production of large-type eggs (11–15 *vs* 5–7 mm), presence of calamus (*vs* absence) and a longer ligula in males (~1.4% *vs* ~0.5% of AL) (Table 2). During a workshop on octopod systematics at the Cephalopod International Advisory Council (CIAC) meeting in Phuket in 2003, *Cistopus* specimens from Phuket (adjacent Andaman Sea) were available for examination. These available preserved specimens in PMBC (Phuket Marine Biological Center) possess very inconspicuous mucous pores and small eggs. More than one species of *Cistopus* may occur in the Phuket region, potentially accounting for the wide range of sucker counts on hectocotylized arm (75–124) reported by Natewathana (1997). The true identities of these specimens require further study.

Pickford (1974) examined many *Cistopus* specimens from Singapore, and Robson (1929) examined limited material from India and China. Both authors found that male material from these locations possess abruptly enlarged suckers on the first and second arms, the same as specimens of this study.

Pickford (1974) also indicated that the eggs of her specimens are small (4–5 mm in length). Von Boletzky (1987) suggested that small-egg species (eggs <10% ML) produced free-swimming planktonic young and that this merobenthic strategy results in wider geographic distributions for such species (Von Boletzky, 1997). It is possible that *C. taiwanicus* of Taiwanese waters has a much broader distribution (potentially as far as India). Additional material and thorough morphological descriptions are required to resolve the status of Chinese and Indian material.

Morphology and the function of the mucous pouches

This study is the first to report on the histological structure of the mucous pouches of *Cistopus*, as well as the first record of sexual dimorphism in pore structure.

The mucus produced by members of this genus appears to be released by columnar epithelial cells in the inner wall of the mucous pouches (Fig. 7B). Numerous folds in the inner surface of the pouches significantly increase the surface area of the inner cavities (Fig. 7A). It appears that the *Cistopus* can control the muscle fibres that surround the pouches to contract the pouches and release the mucus. There is no distinctive musculature such as a sphincter among the sections available. According to the PAS and alcian blue staining, those secretions on the inner wall of the pouches are acid mucopolysaccharides. There are many basophilic granules in the surface around the openings and ducts of the mucous pouches (Fig. 7C). Their function remains unknown.

Table 2. Comparison of member species in the genus *Cistopus*.

| Species | <i>Cistopus taiwanicus</i> n. sp. | <i>Cistopus indicus</i> | <i>Cistopus</i> sp. | <i>Cistopus</i> sp. |
|--------------------------------------|--------------------------------------------|------------------------------|-------------------------|--------------------------------------|
| References | This study | Syntype, male, MNHN 5-4-1050 | Norman & Sweeney (1997) | Nateawathana (1997) |
| Locality | Taiwan | Celebes, Indonesia | Philippines | Andaman Sea |
| Gill number | 9–10 | 9 | 9–10 | 9–10 |
| Enlarged sucker (M) | 18th–21st on arms 1 and 2 | Absent | Absent | 6th–7th on arms 1, 2 and 4 |
| Sucker number on normal arms | 131–164 | 170–189 | 180–200 | 102–145 |
| Sucker number on third right arm (M) | 106–117 | 134 | 116–123 | 75–124 |
| Ligula (% of AL) | 0.4–0.5 | 0.4 | 0.5–0.7 | 1.4 |
| Calamus | Absent | Absent | Absent | Present, small |
| Egg type | 6,000–8,000 small eggs (egg length 5–7 mm) | Potentially large | Unknown | 100 large eggs (egg length 11–15 mm) |

M, males.

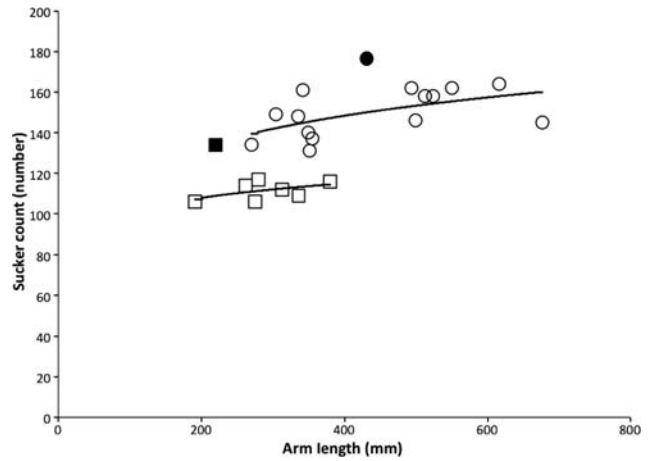


Figure 9. Sucker count vs arm length plot (filled circle, average normal unmodified arms of *Cistopus indicus*, syntype; open circle, average normal arms of *Cistopus taiwanicus* n. sp.; filled square, hectocotylized arm of *C. indicus*, syntype; open square, hectocotylized arm of *C. taiwanicus* n. sp.). Trend line of normal arm: $y = 22.198\text{Ln}(x) + 15.299$; $R^2 = 0.319$. Trend line of hectocotylized arm: $y = 10.507\text{Ln}(x) + 52.028$; $R^2 = 0.2565$.

Previous authors have speculated on the function of the mucous pouches in *Cistopus*. Robson (1929) suggested that the pouches could be used by the female to receive and store spermatophores. However, no specimens have been found with spermatophores or sperm within these pouches (Norman & Sweeney, 1997). Norman (2000) suggested that these glands are used to produce mucus to line burrows within sand or silt, as occurs in *Octopus karna* of southern Australia.

Males of *C. taiwanicus* have significantly larger PDs (1–1.8 mm) than do females (0.3–0.5 mm) (Fig. 5C, D; Table 1). The radial white stripes around the mucous pores in males (Fig. 6; absent in females) reflect bright white light and appear to be caused by epidermal leucophores. Leucophore and iridophores produce structural colours through selective reflection, and these cells are found in the dermis of the skin, ink sacs and photophores of most cephalopods (Cloney & Brocco, 1983). The function of the mucous pouch white stripes is unknown. The mucous pores can be difficult to detect in some material, especially in poorly preserved and contracted specimens, a condition also referred to by Voss (1963) and Pickford (1974).

One possible hypothesis is that the larger mucous pouches of males may be used to build nests (mucous caverns) to attract females. However, much more histological work using a series of specimens at different DevSs and wild observations of the behaviour of *C. taiwanicus* are necessary to shed more light on this fascinating animal and its unusual morphological character.

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