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TWO NEW SPECIES OF *SEPIA* (*DORATOSEPION*) (CEPHALOPODA: SEPIIDAE) FROM TAIWAN, BASED ON MORPHOLOGICAL AND MOLECULAR DATA

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ABSTRACT: Two new species of *Sepia* belonging to the *Doratosepion* group, called *Sepia furcata* and *Sepia hirunda*, are described from the waters off Taiwan, based on morphological and molecular evidence. The posterior ends of the fins of both forms extend posteriorly to form long "tails", but there are differences in "tail" length, and the length of the arm 2 between the two species. The two species have different distributions in Taiwan: *S. furcata*, sp. nov. occurs in the northeast and *S. hirunda*, sp. nov. occurs in west and southwest of Taiwan. Analyses of genetic distance using mitochondrial DNA cytochrome *c* oxidase subunit I sequences reveal that the genetic divergence of these two species is much greater than the variation within these two species. Base on morphological and molecular data, these two taxa are considered as two valid species.

INTRODUCTION

Of a total of approximately 112 nominal cuttlefish species of the genus *Sepia*, 41 species belong to the species complex "*Doratosepion*" (Reid 2000). The diagnoses of this group are mainly based on the cuttlebone, which is very elongated, narrow, rose-coloured dorsally, and with two "wings" at the posterior extremity (Roeleveld 1972; Khromov *et al*. 1998).

Around Taiwan, 18 species of Family Sepiidae have been recorded (Lu 1998; Kubodera and Lu 2002), including 5 nominal *Doratosepion* species: *Sepia* (*Doratosepion*) *kobiensis* Hoyle, 1885, *S.* (*D.*) *pardex* Sasaki, 1913, *S.* (*D.*) *tenuipes* Sasaki, 1929, *S.* (*D.*) *longipes* Sasaki, 1913, *S.* (*D.*) *foliopeza* Okutani and Tagawa, 1987 and one undescribed species: *S.* (*D.*) sp. TW1 (Lu 1998).

Sepia (*D.*) sp. TW1 has a pair of elongated "tails" at the posterior end of fins. This is a unique character which differs from that of all of the other *Doratosepion* species. After further sampling and examination in detail, we now find that there are two morphotypes in the original *S.* (*D.*) sp. TW1 of Lu (1998). These two forms are found to be two different new species and are described in this paper. They have different distributions, one occurs in the northeastern waters of Taiwan while the other occurs in the western and southwestern waters of Taiwan.

In this study, we screened morphological characters and genetic markers of these two morphotypes. Mitochondrial cytochrome *c* oxidase subunit I gene (mtCOI) has been used for analyzing the phylogeny of cephalopods (Carlini and Graves 1999) and proved to be suitable for identifying closely related species of *Octopus* (Ho 2001). Furthermore, mtCOI sequence diversity has been used to construct a bar-coding system for animal life (Hebert *et al*. 2003a), it was used to help discriminate between these two species.

MATERIALS AND METHODS

Material examined

Most of the material was collected from fish markets from where a general locality of capture can be ascertained. Other material was collected by fishing boats using bottom trawls. All material studied is listed in the Material examined sections for these two species. Maturity was determined according to Lu and Roper (1979). Institutional acronyms used are:

NMNS National Museum of Natural Sciences, Taichung, Taiwan

MoV Museum Victoria, Melbourne, Australia

NSM National Science Museum, Tokyo, Japan

Other abbreviations are: BTP, bottom trawling program; coll., collected; CR, cruise; FM, fish market; m, meters; ML, mantle length; mm in millimeters; OR3, R/V *Ocean Researcher No. 3*.

Measurements and Description

Measurements, indices and definitions used throughout this paper are modified from Reid (2000) using dorsal mantle length (ML) as a size standard. Table 1 shows the definitions of measurements and counts. Diagrammatic illustrations of measurements and terminology used for key structures are shown in Fig. 1.

Measurements were made either using dial calipers, or an eyepiece micrometer in a stereo microscope. All measurements are expressed in millimeters (mm). The range of values for each character is expressed as: minimum–*mean*–maximum (standard deviation, SD). Values for each sex are given separately. For missing and unknown values, a dash (–) is used in the tables.

Radulae and beaks were dissected from the buccal mass, soaked in a saturated potassium hydroxide solution then cleaned with a sonic cleaner. Suckers and radulae were air dried, mounted, coated with gold and examined in a Hitachi S-3000N scanning electron microscope operated at 15 KV.

Molecular methods

A protocol modified by Chen *et al.* (2000) and Chen and Yu (2000) was used for DNA extraction. A small amount (<10 mg) of muscle tissue was finely chopped in lysis buffer (0.1M Trishydroxymethyl aminomethane [Tris], 100 mM EDTA, PH 8.0), 24 µl 20% sodium dodecyl sulfate [SDS], 2 µl of 20 mg ml^{-1} Proteinase K, and was incubated overnight at 45 °C. The following morning (or whenever tissue was dissolved), DNA was purified by one extraction with saturated NaCl and chloroform, respectively. Isopropanol–precipitated DNA was rinsed (70% ethanol), air dried, and resuspended in 100 µl of sterile deionized and distilled (d.d.) water, and then stored at -20 °C.

The partial mtCOI region was amplified using the metazoan mtCOI primer pair, LCO1490: 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer *et al.* 1994). In brief, a typical 25 µl amplification solution consisted of 25–100 ng genomic DNA and 1.25 unit of Promega *Taq* DNA polymerase in Storage Buffer B. Thermal cycling consisted of 1 cycle at 95 °C (3 min); 35 cycles at 94 °C (1 min), 52 °C (1 min), 72 °C (0.5 min); the final step (72 °C) was prolonged to 10 min for completing the final amplification.

COI PCR products were inserted into a plasmid vector by using the pGEM-T Easy Vector System I (Promega, Madison, WI), and then transformed into the subcloning efficiency DH5α competent cell. The nucleotide sequences were determined by using ABI PRISM BigDye terminator cycle sequencing (ABI PRISM Applied Biosystems, FosterCity, CA). The sequences obtained were submitted to GenBank under the accession numbers listed in Table 2.

The mtCOI sequences were aligned initially using CLUSTAL W 1.7 (Thompson *et al.* 1994), with the orthologous sequences gained from this study and from Genbank (Table 2). These sequences were then edited in order by SEQAPP 1.9 (Gilbert 1994).

The base composition, proportion of substitution and pairwise distance were calculated using PAUP*4.0b10 (Swofford 2002) and MEGA2.1 (Kumar *et al.* 2001). DNA sequences were translated into protein sequences using the invertebrate mitochondrial genetic code of *Drosophila* (Clary and Wolstenholme 1985).

The phylogenetic trees were produced using maximum parsimony (MP), minimum evolution (ME), and maximum likelihood (ML) methods with 1000 bootstrappings.

RESULTS

Species descriptions:

Sepia furcata, sp. nov.
(Figs 2–4; Tables 3)

Table 1. Description of measurements and counts. New definitions are indicated by an asterisk (*). Abbreviations are shown in boldface. Indices (shown in square brackets) are calculated by expressing each measure as a percentage of mantle length or, for cuttlebone characters, cuttlebone length (unless otherwise specified).

Arm Length – **AL**: length of each arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [ALI].
Anterior Mantle to Head length – **AMH**: dorsal length of mantle measured from anterior-most point of mantle to intersection of transverse line joining dorso-lateral mantle margin [AMHI].
Arm Sucker Count – **ASC**: total number of suckers on each arm.
Arm Sucker diameter – **AS**: diameter of largest normal sucker on each arm [ASIn].
Cuttlebone Length – **CbL**: dorsal length of cuttlebone along midline, including spine.
Cuttlebone Width – **CbW**: greatest width of cuttlebone [CbWI].
Club Length – **ClL**: length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [ClLI].
Club Row Count – **ClRC**: number of suckers in transverse rows on tentacular club.
Club Sucker dorsal – **ClSd**: diameter of largest sucker in dorsal-most (closest to swimming keel) longitudinal row [ClSId].
Club Sucker ventral– **ClSv**: diameter of largest sucker in ventral-most (opposite swimming keel) longitudinal row [ClSIv].
Eye Diameter – **ED**: diameter of eye [EDI].
Egg Length – **EgL**: length of egg [EgLI].
Egg Width – **EgW**: width of egg [EgWI].
Free Funnel length – **FFu**: the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [FfuI].
Fin Insertion anterior – **FIa**: anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [FIIa].
Fin Insertion posterior – **FIp**: measured between posterior junction of fin with mantle [FIIa].
Fin Width – **FW**: greatest width of single fin [FWI].
Funnel Length – **FuL**: the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral mid line [FuLI].
Gill Lamellae Count – **GiLC**: number of lamellae on outer demibranch including the terminal lamella.
Gill Length – **GiL**: length of gill [GiLI].
Head Length – **HL**: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [HLI].
Head Width – **HW**: greatest width of head at level of eyes [HWI].
Loculus Length – **LoL**: length of the last loculus (ventral anterior smooth zone of the cuttlebone) [LoLI].
Mantle Length – **ML**: dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle.
Mantle Width – **MW**: greatest straight-line ventral width of mantle [MWI].
Spine Length – **SL**: length of spine [SLI].
Striated Zone Length – **StZ**: length of striated zone of cuttlebone [StZI].
Tail Length * – **TaL**: elongated fin length. Measured from posterior junctions of fin and mantle to end of “tail” [TaLI].
Transverse Row Count – **TrRC**: number of suckers in longitudinal series on tentacular club counted from proximal-most basal suckers (carpus) to distal tip of club.
Ventral Mantle Length – **VML**: length of ventral mantle measured from anterior mantle at ventral midline, to posterior apex of mantle [VMLI].

Table 2. The materials used in phylogenetic analysis, including species name, Genbank accession number and specimen information.

Species	Genbank access No.	Material examined
Outgroup (Family Sepiolidae)		
Euprymna berryi Sasaki 1929	AF350493 (Zheng *et al*. unpublished)	
Ingroup (Family Sepiidae)		
Sepia aculeata Van Hasselt, 1834	AF350494 (Zheng *et al*. unpublished)	
Sepia furcata-1	AY530207	male NMNS3983-006-01, 42.6mm ML
S. furcata-2	AY530208	male NMNS3983-006-02, 42.5mm ML
S. furcata-3	AY530209	female paratype5 NMST-Mo74887, 54.92mm ML
S. furcata-4	AY530210	female NMNS3983-006-06, 56.3mm ML
Sepia hirunda-1	AY530211	male NMNS3984-008-03, 50.6mm ML
S. hirunda-2	AY530212	male NMNS3984-008-04, 48.9mm ML
S. hirunda-3	AY530213	female NMNS3984-008-07, 56.6mm ML
S. hirunda-4	AY530206	female NMNS3984-008-12, 50.5mm ML

Material examined

Holotype. male (46.1 mm ML), Taiwan, Yi-Lan, 24 56.54′N 122 1.51′E, 115-170 m, 7.v.2001, coll. KS "Li", (NMNS3983-001)

Paratypes. Paratype 1, female (51.0 mm ML), Taiwan, Chin-Shan, 25 17.64′N 121 42.44′E, 100 m, 23.vi.2000, coll. BTP, (NMNS3983-002). Paratype 2, male (53.2 mm ML), same data as for paratype 1, (MoV F91355). Paratype 3, female (48.7 mm ML), Taiwan, Ta-Shi FM, 3.xi.2002, coll. CW 'Ho', (MoV F91356). Paratype 4, male (52.2 mm ML), Taiwan, Chin-Shan, 25 20.69′N 121 39.93′E, 100m, 31.iii.2000, coll. BTP, (NMST-Mo74886). Paratype 5, female (54.9 mm ML), Taiwan, Ta-Shi FM, 15.iii.2002, coll. CC 'Lu', (NMST-Mo74887).

Other material. 2 males (44.6–50.8 mm ML), Taiwan, Ta-Shi FM, 18.iv.1997, coll. CC 'Lu', (NMNS 3983-004). 1 male (47.0 mm ML), collecting data missing (NMNS 3983-005). 1 male (57.0 mm ML), same data as for paratype 1 (NMNS 3983-003). 1 male (42.4 mm ML), Taiwan, Ao-Ti, 25 7.23′N 122 00.55′E, 200 m, 15.xi.2000, coll. BTP, (NMNS 3983-007). 1 male (54.0 mm ML), Taiwan, Chin-Shan, 25 20.95′N 121 39.10′E, 100 m, 23.vi.2000, coll. BTP, (NMNS 3983-008). 7 males (40.4–64.3 mm ML), Taiwan, Ta-Shi FM, 15.iii.2002, coll. CC 'Lu', (NMNS 3983-006). 2 males (39.5–40.6 mm ML) 2 females (44.1–54.7 mm ML), Taiwan, Tan-Shui, 100m, 9.vi.2002, coll. JP "Chen" and PH "Ho", (NMNS 3983-009). 3 males (42.0-50.8 mm ML) 11females (32.8–54.0 mm ML), Taiwan, Ta-Shi FM, 9.i.2003. coll. CC "Lu", (NMNS 3983-010).

Diagnosis

Small to moderate size. Arm formula 2.3=4.1 in both sexes, male arms 2 elongate, twice as long as other arms in mature specimens and with sparse biserial suckers in distal portion; female arms 2 slightly longer than other arms; arms 2 with greater number of suckers than remaining arms of both

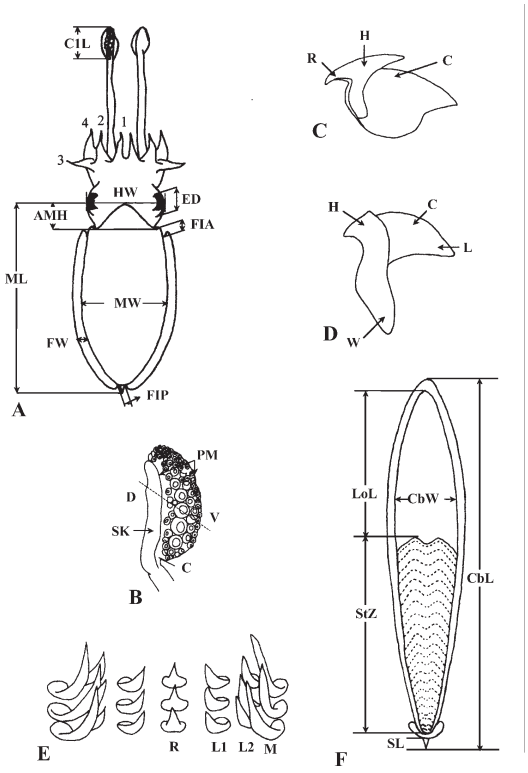

Figure 1. Measurements and terminology: (A) whole animal dorsal view (for abbreviations and definitions see Table 1); (B) tentacular club (C, carpus; D, dorsal; PM, protective membranes; SK, swimming keel; V, ventral). The Club Row Count (ClRC) shown as a hatched line on this figure; (C) upper beak (C, crest; H, hood; R, rostrum); (D) lower beak (C, crest; H, hood; L, lateral wall; W, wing); (E) radula (R, rhachidian teeth; L1, first lateral teeth; L2, second lateral teeth; M, marginal teeth); (F) cuttlebone, ventral view (for abbreviations and definitions see Table 1). [all these figures modified from Reid (2000): fig.1]

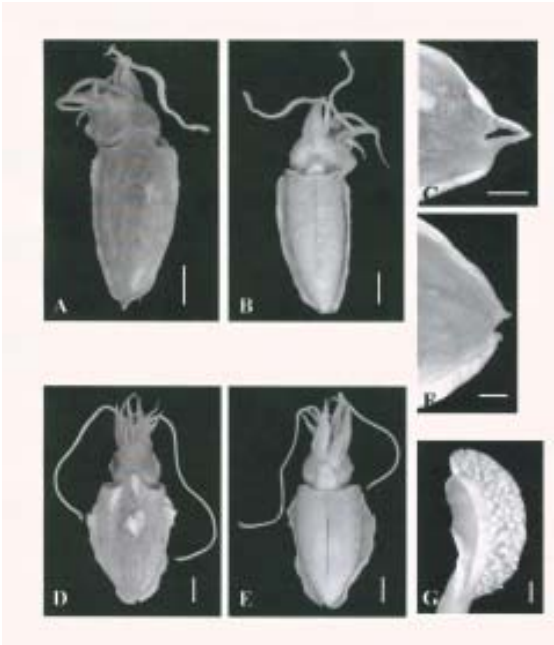

Figure 2. *Sepia furcata*: (A) whole male animal, dorsal view; (B) whole male animal, ventral view; (C) male " tail", dorsal view (A–C holotype, NMNS 3983-001, 46.1 mm ML, A and B scale bar = 1 cm, C scale bar = 5 mm); (D) whole female animal, dorsal view, (E) whole female animal, ventral view, (F) female "tail", dorsal view (D–F paratype 3, MoV F91356, 48.7 mm ML, D and E scale bar = 1 cm, F scale bar = 5 mm); (G) tentacular club, oral view, female paratype 3, MoV F91356, 48.7 mm ML, scale bar = 1 mm.

sexes, over 100 in male and nearly 100 in female. Cuttlebone of female wider than male, anterior striate inverted M-shaped. "Tails" of male about 3 longer than female and male tail length about 10% of mantle length.

Description

Counts and indices for subadult (dev. stage 4) or adult (dev. stage 5) individual specimens are given in Tables 3.

Small to moderate-sized species; ML of males 42.6–*48.1*–53.2 (SD, 4.0, n=7), females 45.7–*50.9*–54.9 (SD, 3.8, n=5). Mantle oblong (Fig. 2A,B,D,E); MWI of males 32.5–*43.3*–52.7 (SD, 7.9, n=7), females 47.3–*50.8*–52.4 (SD, 3.5, n=5); dorsal anterior margin triangular, acute; extending anteriorly to level of one-third of eyes; AMHI of males 7.3–*9.1*–10.0 (SD, 0.9, n=7), females 10.5–*11.7*–14.0 (SD, 1.3, n=5). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 2B,E); VMLI of males 81.5–*85.7*–88.7 (SD, 3.0, n=7), female 78.4–*84.5*–88.9 (SD, 4.3, n=5). Fins widest in posterior third; FWI of males 3.0–*5.8*–9.2 (SD, 2.4, n=7), females 3.0–*7.0*–10.5 (SD, 2.9, n=5); anterior origin posterior to mantle margin; FIIa of males 2.8–*5.0*–6.2 (SD, 1.4, n=7), females 3.4–*6.4*–9.4 (SD, 2.21, n=5); FIIp of males 1.0–*4.1*–8.3 (SD, 2.2, n=7), females 1.0–

Table 3. Measurements (mm), counts and indices of *Sepia furcata*. (A) 7 males; (B) 5 females.

Museum Reg. No.	Holotype NMNS 3983-001	Paratype2 MoV F91355	Paratype4 NMST-Mo74886	NMNS 3983-004-01	NMNS 3983-004-02	NMNS 3983-005	MNNS 3983-006-01
Sex/Dev. stage	M/5	M/5	M/5	M/5	M/5	M/5	M/5
ML	46.14	53.21	52.21	44.55	50.75	47.04	42.62
MWI	32.47	37.08	38.77	50.06	41.00	51.06	52.72
AMHI	9.99	9.10	9.40	8.91	8.97	9.82	7.25
VMLI	87.78	81.47	82.59	88.69	83.59	87.41	88.13
FWI	9.23	4.66	9.12	2.99	4.30	5.04	5.51
FIIa	6.16	2.82	5.92	5.32	5.93	5.68	3.12
FIIp	0.95	4.92	3.05	3.64	3.98	3.91	8.33
TaLI	7.69	13.70	9.60	8.80	8.95	11.14	11.40
FuLI	24.10	26.84	25.03	27.86	25.00	29.66	33.06
FFuI	10.60	10.58	10.86	8.91	8.87	10.37	13.70
HLI	18.66	23.87	20.05	25.61	17.18	27.25	27.50
HWI	31.77	29.13	28.37	35.47	32.30	37.86	39.04
EDI	11.44	8.25	12.72	8.75	7.67	13.27	12.46
ALI1	24.95	35.07	26.99	49.58	32.81	36.88	44.02
ALI2	51.26	93.59	75.48	99.12	81.89	97.68	68.35
ALI3	28.13	47.83	36.26	41.28	42.17	47.53	48.47
ALI4	26.12	31.54	34.50	40.88	43.92	47.83	48.22
ASIn1	0.52	0.71	0.42	0.67	0.47	0.64	0.70
ASIn2	0.48	0.71	0.54	0.76	0.59	0.64	0.75
ASIn3	0.48	0.75	0.44	0.76	0.63	0.85	0.70
ASIn4	0.43	0.79	0.46	0.90	0.63	0.68	0.80
ASC1	69	55	78	78	70	56	82
ASC2	118	109	113	108	124	128	112
ASC3	94	79	100	74	100	93	108
ASC4	101	78	108	119	102	89	90
C1LI	13.07	10.62	12.35	13.06	-	-	14.81
ClRC	4	4	4	4	-	-	4
TrRC	24.00	20.00	24.00	23.00	-	-	25.00
ClSI	0.61	0.56	0.46	0.67	-	-	0.70
ClSdI	0.41	0.30	0.42	0.67	-	-	0.42
ClSvI	0.39	0.38	0.38	0.40	-	-	0.38
GiLC	26.00	20.00	26.00	21.00	26.00	22.00	21.00
GiLI	25.14	17.33	26.22	13.22	33.52	26.98	11.21
CbL	45.66	51.87	51.59	45.25	52.28	50.59	42.63
CbWI	0.18	13.57	14.67	18.61	15.41	18.15	19.94
SL	2.38	3.35	2.81	2.27	3.19	3.10	-
StZI	0.71	73.14	70.73	66.94	73.20	72.77	70.84
LoLI	0.28	23.91	23.74	30.12	23.43	30.95	29.12
LoL/Stz (%)	38.69	32.68	33.57	45.00	32.01	42.54	41.11

Table 3. (Continued)

Museum Reg. No.	Paratype1 NMN S3983-002	Paratype3 MoV F91356	Paratype5 NMST-Mo74887	NMNS 3983-010-03	NMNS 3983-010-09
Sex/Dev. stage	F/5	F/5	F/5	F/5	F/4
ML	51.03	48.73	54.92	53.97	45.68
MWI	48.99	52.43	47.25	49.16	56.20
AMHI	13.97	11.31	10.51	11.78	11.01
VMLI	78.37	87.15	88.87	81.79	86.10
FWI	5.37	10.55	2.99	7.30	8.63
FIIa	3.43	5.50	7.19	9.45	6.37
FIIp	4.23	3.30	5.70	1.00	4.44
TaLI	3.59	2.69	4.06	2.22	3.98
FuLI	32.16	32.46	32.77	29.26	34.81
FFuI	10.09	9.97	14.91	10.88	16.86
HLI	23.26	22.22	27.26	24.83	27.80
HWI	39.68	38.01	38.11	32.81	37.06
EDI	14.31	15.12	13.36	12.66	14.65
ALI1	42.92	31.77	38.55	34.63	45.86
ALI2	54.85	45.48	48.51	48.97	62.72
ALI3	41.17	39.65	38.07	-	49.61
ALI4	34.37	38.23	42.26	40.28	44.90
ASIn1	0.71	0.66	0.73	0.63	0.70
ASIn2	0.71	0.82	0.62	0.59	0.74
ASIn3	0.74	0.82	0.55	0.67	0.79
ASIn4	0.86	0.62	0.58	0.56	0.74
ASC1	65	62	69	56	58
ASC2	105	102	103	90	95
ASC3	94	90	91	-	85
ASC4	105	105	112	72	78
C1LI	14.15	13.65	14.68	-	17.80
ClRC	4	4	4	-	4
TrRC	20	23	20	-	26
ClSI	0.63	0.62	0.73	-	0.88
ClSdI	0.39	0.49	0.58	-	0.66
ClSvI	0.39	0.29	0.44	-	0.44
GiLC	26	27	27	26	26
GiLI	29.90	30.06	25.36	26.66	28.63
EgLI	5.21	13.73	13.07	12.95	-
EgW	2.76	5.73	4.77	5.50	-
CbL	50.71	48.51	54.49	53.51	44.60
CbWI	21.77	22.22	21.21	20.03	24.33
SL	2.27	-	1.73	1.55	1.46
StZI	71.49	28.08	74.75	74.51	65.47
LoLI	28.55	73.41	22.61	21.23	27.42
LoL/Stz (%)	39.94	38.25	30.26	28.49	41.88

3.7–5.7 (SD, 1.8, n=5); fins end with "tail"-like extension posteriorly, tails longer in males (Fig. 2C,F); TaLI of males 7.7–*10.1*–13.7 (SD, 2.0, n=7), females 2.2–*3.3*–4.1 (SD, 0.8, n=5). Funnel of moderate length, robust; FuLI of males 25.0–*27.3*–33.1 (SD, 3.2, n=7), females 29.3–*32.3*–34.8 (SD, 2.0, n=5). Funnel free portion approximately one-third funnel length; FFuI of males 8.9–*10.6*–13.7 (SD, 1.6, n=7), females 10.0–*12.5*–16.9 (SD, 3.1, n=5). Dorsal elements of funnel organ inverted V-shaped with small anterior papilla; ventral elements oval with acute anterior tips (Fig. 3A). Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression, which corresponds to ridge (Fig. 3B). Head slightly slender, narrower than mantle (Fig. 2A,D); HLI of males 17.2–*22.9*–27.5 (SD, 4.2, n=7), females 22.2–*25.1*–27.8 (SD, 2.4, n=5); HWI of males 28.4–*33.4*–39.0 (SD, 4.2, n=7), females 32.8–*37.1*–40.0 (SD, 2.6, n=5). Eyes moderate sized; EDI of males 7.7–*10.7*–13.3 (SD, 2.4, n=7), females 12.7–*14.0*–15.1 (SD, 1.0, n=5); ventral eyelids present.

Male and female arms differ in relative lengths. Arm formula 2.3=4.1 in both sexes. Male arms 2 elongate, AL2I in male 51.3–*81.1*–99.1 (SD, 17.5, n=7), in females (ALI2) 45.5–*52.0*–54.9 (SD, 6.8, n=5). Protective membranes in both sexes narrow. Distal arm tips strongly attenuate in both sexes. Arm suckers in both sexes tetraserial proximally, biserial at distal arm tips with reduced suckers (biserial region covers greater proportion of arms 2 and 3 than arms 1 and 4, particularly arms 2 of males). Suckers normally sized (not greatly enlarged) in both sexes. Sucker counts range from 55–128; arms 2 with higher average counts than other arms; ASC2 in males 108–*116*–128 (SD, 8, n=7), females 90–*99*–105 (SD, 6, n=5).

Hectocotylus present, left ventral arm modified; sucker size normal proximally, reduced at distal 1/3 (Fig. 3H); from proximal to distal end of arm, 10 rows of normal suckers, followed by approximately 16 rows of slightly reduced suckers, two dorsal and ventral series displaced laterally; oral surface of modified region fleshy, with transverse ridges and shallow median furrow; protective membrane well developed. Hectocotylised arm not markedly attenuate distally.

Tentacular club small (Fig. 2G); ClLI of males 10.6–*12.8*–14.8 (SD, 1.5, n=5), females 13.6–*15.1*–14.7 (SD, 1.9, n=4). Club crescent-shaped; sucker-bearing face flattened. Club with 4 suckers in transverse rows; 20–26 suckers in longitudinal seriesl, TrRC males 20–*23*–25 (SD, 2, n=5), females 20–*22*–26 (SD, 3, n=4). Suckers differ in size, 4–5 median suckers slightly larger than rest; ClSI males 0.56–*0.6*–0.70 (SD, 0.10, n=5), females 0.62–*0.71*–0.88 (SD, 0.12, n=4); dorsal marginal longitudinal series of suckers larger than ventral; ClSId males 0.30–*0.45*–0.67 (SD, 0.14, n=5), females 0.39–*0.53*–0.66 (SD, 0.11, n=4); ClSIv males 0.38–*0.39*–0.40 (SD, 0.01, n=5), females 0.29–*0.39*–0.44 (SD, 0.07, n=4). Swimming keel of club extends slightly beyond carpus (Fig. 2G). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal membrane longer than ventral membrane, terminate at the extension of posterior end of carpus; dorsal membrane much broader than ventral membrane; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 20–27 lamellae per demibranch; GiLC males 20–*23*–26 (SD, 3, n=7), females 26–*26*–27 (SD, 1, n=5). Gill length: GiLI males 11.2–*21.9*–33.5 (SD, 8.2, n=7), females 25.4–*28.1*–29.9 (SD, 2.1, n=5).

Buccal membrane without suckers. Upper beak (Fig. 3C) rostrum sharply pointed, length approximately equal to width; cutting edge straight; hood low on crest; crest curved, lateral wall elongate to almost same length of crest; wings narrow and short; hood dark brown, lighter on ventral margin, crest only slightly pigmented. Lower beak (Fig. 3D,E) rostrum protrudes only slightly beyond wings, cutting edge curved; hood low on crest; crest straight, no indentation on lateral wall edge; hood and wings width narrow; hood notch shallow (Fig. 3E); wings widely spaced, long; crest wide; rostrum and anterior of wings dark brown, posterior of wings and crest only slightly pigmented. Radula homodont; rhachidian teeth with slight heels, slightly indented basally, slender, triangular, sides straight (Fig. 4I); first lateral teeth similar in length and width to rhachidian teeth, asymmetrical with mesocone slightly displaced towards centre of radula; second

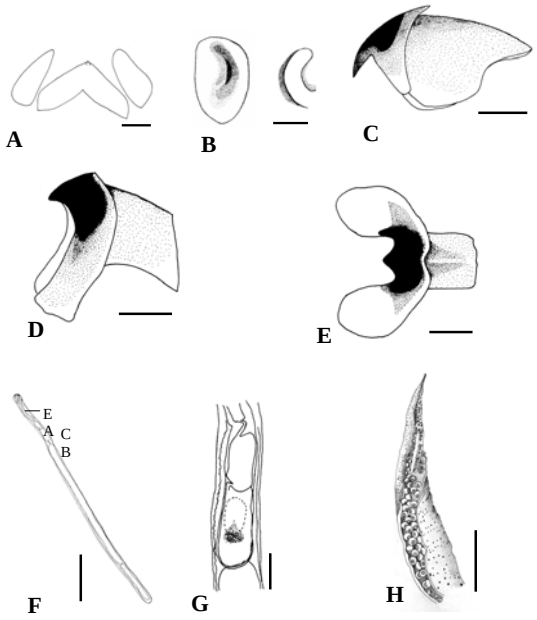

Figure 3. *Sepia furcata*: (A) funnel organ, female paratype 5 NMST-Mo74887, 54.9 mm ML, scale bar = 5mm; (B) funnel-locking cartilage (left), and mantle-locking cartilage (right); (C) upper beak, side view; (D) lower beak, side view; (E) lower beak, ventral view (B–E, female paratype 1 NMNS 3983-002, 51.0 mm ML, scale bar = 2 mm) (F) spermatophore, scale bar = 0.1 mm (CB, cement body; EA, ejaculatory apparatus; SR, sperm reservoir); (G) spermatophore, cement body, scale bar = 0.5 mm (F and G, NMNS 3983-005, 47.0 mm ML).

laterals longer than first, slightly curved on lateral margin; marginal teeth elongate with long tapered and curved mesocone heels rounded.

Spermatophores: cement body bipartite (Fig. 3F,G); aboral end elongate, cylindrical, connects to sperm reservoir via narrow duct; oral end of cement body narrower, cylindrical, approximately same length of, and slightly narrower than aboral end, connects to aboral end via narrow neck; middle tunic commences along aboral part of cement body; ejaculatory apparatus coiled, extends into oral dilation of spermatophore. Smallest male with well developed spermatophores in spermatophoric sac 42.6 mm ML.

Eggs oval; 2.7–*5.9*–7.0 mm long (SD, 2.2, n=4), 1.4–*2.4*–3.0 mm wide (SD, 0.7, n=4). EgLI 5.2–*11.2*–13.7 (SD, 4, n=4), EgWI 2.8–*4.7*–5.7 (SD, 1.3, n=4). Smallest female with well developed eggs in ovaries 48.7 mm ML.

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline lanceolate broadest in anterior third, at anterior end of striated zone; CbL of males 42.6–*48.7*–52.3 (SD, 3.9, n=7), females 44.6–*50.4*–54.5 (SD, 4.0, n=5); CbWI of males 13.6–*16.9*–19.9 (SD, 2.3, n=7), females 20.0–*21.9*–24.3 (SD, 1.6, n=5), females with wider cuttlebones than males, CbW/CbL of males 0.14–*0.17*–0.20 (SD, 0.02, n=7), females 0.20–*0.22*–0.24 (SD, 0.01, n=5); females more convex than males in lateral view (Fig. 4C,G). Bone acuminate, acute at both ends (Fig. 4A,B,E,F); strongly recurved ventrally (Fig. 4C,G). Dorsal surface pinkish (more pronounced posteriorly); evenly convex; calcified medially, thickest posteriorly, slightly granulose with irregular longitudinal ridges (particularly posteriorly). Dorsal median rib distinct anteriorly, indistinct posteriorly, broadens anteriorly; bordered laterally by shallow grooves; lateral ribs present, anterior ribs inverted U-shaped (Fig. 4A,E). Chitin present, wide bands border lateral margins of cuttlebone (covers about half of cuttlebone dorsal surface). Spine present, short; SLI of males 2.3–*2.9*–3.3 (SD, 0.4, n=6), females 1.5–*1.8*–2.3 (SD, 0.3, n=4); curves dorsally. Striated zone convex (Fig. 4B, F); StZI of males 66.9–*71.3*–73.2 (SD, 2.2, n=7), females 65.5–*71.9*–74.7 (SD, 3.8, n=5). Last loculus convex; LoLI of males 23.4–*27.0*–30.1 (SD, 3.2, n=7), females 22.6–*25.6*–28.6 (SD, 3.4, n=5); LoL/StZ(%) of males 32.0–*37.9*–45.0 (SD, 5.2, n=7), females 28.5–*35.8*–41.9 (SD, 6.0, n=5). Sulcus extends entire length of cuttlebone; deep, narrow (widening slightly in anterior part of last loculus); flanked by rounded ribs (in striated zone, lateral sides of rib flat, or concave). Anterior striate inverted M-shape (Fig. 4D,H). Limbs of inner cone extend anteriorly to end of striated zone. Outer cone calcified; narrow throughout; limbs expanded posteriorly forming two short ‘wings’, directed ventrally, forming recurved cup-like structure, chitin around.

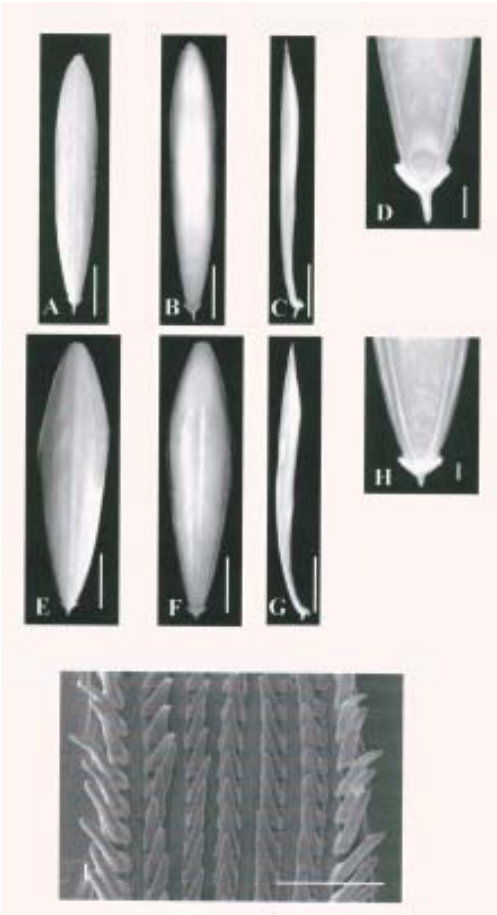

Figure 4. *Sepia furcata*: (A) male cuttlebone, dorsal view; (B) male cuttlebone, ventral view; (C) male cuttlebone, lateral view; (D) posterior end of male cuttlebone, ventral view (A–D, paratype 2 MoV F91357, 53.2 mm ML, A–C scale bar = 1 cm, D Scale bar = 2 mm); (E) female cuttlebone, dorsal view; (F) female cuttlebone, ventral view; (G) female cuttlebone, lateral view; (H) posterior end of male cuttlebone, ventral view (E–H, paratype 1 NMNS 3984-002, 51.0 mm ML, E–G scale bar = 1 cm, H scale bar = 2 mm); (I) radula, female paratype 5 NMST-Mo74887, 54.9 mm ML, scale bar = 300 μm.

Body, head, arms, papillae absent. Colour (alcohol preserved specimens): head pigment present, dark red-brown and denser around eyes; evenly distributed pigment on dorsal side of arms; dorsal mantle pinkish-brown, pigment denser on midline of mantle. Fins pale. Ventral pigment present, denser on borderline of mantle and fins.

Etymology:

The species epithet “furcata” is from Latin, meaning “forked”, and refers to the “shorter tails”.

Sepia hirunda, sp. nov.
(Figs 5–7 ; Tables 4)

Material examined

Holotype. male (53.3 mm ML), Taiwan, An-Ping, 22 50.966′N 120 00.296′E, 120 m, 10.vii.1997, coll. OR3 CR347B, (NMNS 3984-001)

Paratypes. Paratype 1, female (41.1 mm ML), same data as for holotype, (NMNS 3984-002). Paratype 2, males (54.4 mm ML), Taiwan, Tung-Kang, 22 14.099′N 120 29.106′E, 200m, 23.viii.2001, coll. BTP, (MoV F91357). Paratype 3, female (49.4 mm ML), same data as for paratype 2, (MoV F91358). Paratype 4, male (37.6 mm ML), Taiwan, Tung-Kang, 22 16.185′N 120 29.762′E, 100m, 28.i.2001, coll. BTP, (NMST-Mo74888). Paratype 5, female (41.7 mm ML), same data as for paratype 4, (NMST-Mo74888).

Other material. 1 male (49.12 mm ML), Taiwan, Tung-Kang, 24.iii.1997, coll. CC “Lu”, (NMNS 3984-004). 6 males (27.3–46.0 mm ML) 4 females (26.4–41.8 mm ML), same data as for holotype, (NMNS 3984-003). 1 male (47.7 mm ML), same data as for paratype 2, (NMNS 3984-005). 1 male (50.4 mm ML), Taiwan, Feng-Kang, 22 10.328′N 120 31.015′E, 200m, 24.viii.2001. coll. BTP, (NMNS 3984-006). 1 male (47.39 mm ML), Taiwan, Tung-Kang FM, 17.v.2000. coll. CC “Hsu”, (NMNS 3984-007). 1 female (52.98 mm ML), Taiwan, Tung-Kang FM, 9.vi.2000. coll. CC “Hsu”, (NMNS 3984-009). 5 males (41.0–48.0 mm ML) 9 females (24.0–57.9 mm ML), Taiwan, Tung-Kang FM, 21.vi.2002. coll. CW “Ho”, (NMNS 3984-008). 1 male (54.8 mm ML), Taiwan, Tung-Kang FM, 31.viii.2002. coll. CL “Hsu”, (NMNS 3984-010).

Diagnosis

Small to moderate size. Arm formula 4.3>1.2 in both sexes. Arms 4 length over half of mantle length and with more suckers than other arms (from 88 to 130) in both sexes. Cuttlebone of female wider than male, anterior striate inverted M-shaped, deeply incurved

medially. Spine long. "Tails" of male are about 5 longer than female and male tail length about 40% of mantle length.

Description

Counts and indices for individual subadult (dev. stage 4) or adult (dev. stage 5) specimens are given in Table 4.

Small to moderate-sized species; ML of males 37.6–*49.0*–54.4 (SD, 5.5, n=7), females 41.1–*50.5*–57.9 (SD, 6.8, n=7). Mantle oblong (Fig. 5A,B,D,E); females wider than males, MWI of males 36.7–*45.1*–55.3 (SD, 6.6, n=7), females 45.5–*52.8*–58.8 (SD, 5.0, n=7); dorsal anterior margin triangular, acute; extending anteriorly to level of one-third of eyes; AMHI of males 9.4–*12.7*–16.0 (SD, 2.3, n=7), females 10.6–*12.1*–14.4 (SD, 1.2, n=7). Ventral mantle margin emarginate, without distinct lateral angle (Fig. 5B,E); VMLI of males 70.1–*81.7*–89.1 (SD, 6.1, n=7), female 79.8–*84.4*–91.5 (SD, 3.7, n=7). Fins widest in posterior third; FWI of males 3.4–*5.4*–8.6 (SD, 1.9, n=7), females 2.0–*5.0*–9.8 (SD, 2.6, n=7); anterior origin posterior to mantle margin; FIIa of males 2.9–*6.3*–8.7 (SD, 2.4, n=7), females 3.5–*7.1*–9.7 (SD, 2.3, n=7); narrow gap between fins posteriorly; FIIp of males 2.9–*4.0*–4.8 (SD, 0.7, n=7), females 3.6–*6.0*–8.1 (SD, 1.7, n=7); fins end with "tail"-like extension posteriorly, tails in males distinctly longer and more robust than in females, tail elongation of mature males extends to nearly half of mantle length (Fig. 5C,F); TaLI of males 31.2–*42.7*–53.0 (SD, 7.9, n=7), females 4.4–*8.4*–13.3 (SD, 3.3, n=6). Funnel of moderate length, robust; FuLI of males 23.9–*28.0*–32.0 (SD, 3.5, n=7), females 30.8–*32.9*–35.4 (SD, 1.6, n=7). Funnel free portion approximately one-third funnel length; FFuI of males 7.8–*11.1*–15.0 (SD, 1.5, n=7), females 11.0–*13.1*–14.6 (SD, 1.5, n=7). Dorsal elements of funnel organ inverted V-shaped with small anterior papilla; ventral elements oval with acute anterior tips (Fig. 6A). Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge (Fig. 6B). Head slightly slender, narrower than mantle (Fig. 6A,D); HLI of males 14.6–*23.7*–30.6 (SD, 4.8, n=7), females 17.5–*24.9*–29.0 (SD, 4.2, n=7); HWI of males 30.0–*32.8*–36.3 (SD, 2.3, n=7), females 32.9–*35.9*–40.6 (SD, 2.9, n=7). Eyes moderate-sized; EDI of males 10.1–*11.8*–16.5 (SD, 2.3, n=7), females 9.9–*12.0*–13.5 (SD, 1.2, n=7); ventral eyelids present.

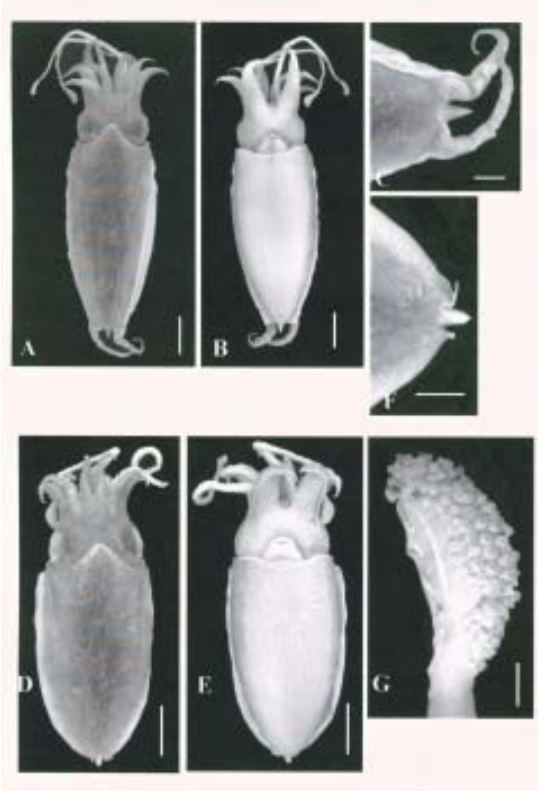

Figure 5. *Sepia hirunda*: (A) whole male animal, dorsal view; (B) whole male animal, ventral view; (C) male " tail", dorsal view (A–C holotype, NMNS 3984-001, 53.3 mm ML, A and B scale bar = 1 cm, C scale bar = 5 mm); (D) whole female animal, dorsal view, (E) whole female animal, ventral view, (F) female "tail", dorsal view; (G) tentacular club, oral view, (D–G paratype 1, NMNS 3984-002, 41.1 mm ML, D and E scale bar = 1 cm, F scale bar = 5 mm, G scale bar = 1 mm.)

Male and female arms similar in relative lengths. Male arms 4 longer than other arms, arm formula 4.3>1.2 in both sexes. ALI4 in males 35.7–*49.4*–61.1 (SD, 8.8, n=7), in females (ALI4) 27.6–*43.9*–57.7 (SD, 11.5, n=6). Protective membranes in both sexes narrow. Distal arm tips strongly attenuate in both sexes. Arm suckers in both sexes tetraserial proximally, biserial at distal arm tips. Suckers normal-sized in both sexes (not greatly

Table 4. Measurements (mm), counts and indices of *Sepia hirunda*. (A) 7 males; (B) 7 females.

Museum Reg. No.	Holotype NMNS 3984-001	Paratype 2 MoV F91357	Paratype 4 NMST-Mo74888	NMNS 3984-005	NMNS 3984-006	NMNS 3984-008-03	NMNS 3984-008-04
Sex/Dev. stage	M/5	M/5	M/5	M/5	M/5	M/5	M/5
ML	53.29	54.39	37.56	47.70	50.39	50.57	48.93
MWI	36.70	44.75	43.96	39.48	43.78	55.35	52.32
AMHI	9.38	10.79	13.53	13.50	16.00	14.38	11.55
VMLI	89.08	83.25	85.78	83.52	70.11	78.41	82.08
FWI	8.61	3.79	6.28	4.99	6.53	3.42	4.09
FIIa	2.95	5.18	8.65	8.07	3.47	7.71	7.87
FIIp	2.93	4.73	4.39	4.00	3.49	3.80	4.76
TaLI	31.17	51.20	34.74	43.90	52.97	42.77	42.49
FuLI	25.78	28.94	24.07	31.64	23.89	32.02	30.00
FFuI	7.77	11.01	15.04	8.57	11.53	12.68	11.02
HLI	14.58	22.19	24.95	23.96	30.60	25.13	24.26
HWI	30.55	33.96	30.03	34.88	32.33	36.31	31.68
EDI	10.62	10.33	16.51	11.66	10.54	13.01	10.06
ALI1	23.49	34.97	30.72	32.35	36.20	51.69	36.13
ALI2	24.62	35.74	36.63	27.61	32.19	41.80	38.71
ALI3	22.29	36.22	34.48	30.96	35.23	48.86	44.29
ALI4	35.75	54.07	49.44	40.36	49.37	61.10	55.47
ASIn1	0.26	0.85	0.80	0.88	0.79	0.71	0.74
ASIn2	0.62	0.77	0.69	0.92	0.79	0.79	0.82
ASIn3	0.60	0.74	0.64	0.92	0.67	1.03	0.69
ASIn4	0.45	0.92	0.75	0.84	0.79	0.79	0.69
ASC1	68	70	55	66	60	75	66
ASC2	76	98	66	78	84	105	98
ASC3	80	102	86	93	62	102	114
ASC4	108	134	88	108	107	138	130
C1LI	10.56	14.41	9.29	-	11.07	13.10	11.69
ClRC	4	4	4	-	4	4	4
TrRC	18	22	19	-	23	21	17
ClSI	0.60	0.74	0.59	-	0.60	0.59	0.53
ClSdI	0.47	0.74	0.43	-	0.40	0.40	0.41
ClSvI	0.32	0.40	0.27	-	0.28	0.44	0.41
GiLC	26	23	24	23	18	25	24
GiLI	21.71	23.37	23.46	26.42	27.60	28.87	22.50
CbL	54.01	54.29	37.90	47.26	46.22	50.55	48.40
CbWI	15.44	17.37	19.68	17.65	16.83	17.22	17.19
SL	-	5.41	4.96	-	35.63	5.60	6.05
StZI	67.28	77.81	61.21	73.98	66.96	60.25	62.01
LoLI	26.27	22.63	31.90	26.23	23.85	27.45	26.71
LoL/Stz (%)	39.05	29.09	52.11	35.45	5.60	45.55	43.08

Table 4. (Continued)

Museum	NMNS	NMNS	NMNS	NMNS	Paratype3 MoV	Paratype5 NMST	Paratype1 NMNS
Reg. No.	3984-008-11	3984-008-08	3984-008-06	3984-008-07	F91358	-Mo74889	3984-002
Sex/Dev. stage	F/5	F/5	F/5	F/5	F/4	F/4	F/4
ML	54.39	52.85	57.88	56.55	49.36	41.68	41.13
MWI	53.17	58.83	57.10	56.30	51.58	47.34	45.49
AMHI	10.61	12.54	14.37	11.87	11.81	12.26	11.14
VMLI	84.43	83.37	79.84	84.05	81.58	86.16	91.49
FWI	7.08	3.58	2.00	3.34	4.58	4.73	9.82
FIIa	7.04	8.33	6.60	5.22	9.66	9.69	3.48
FIIp	4.17	5.66	7.14	5.61	8.12	7.39	3.57
TaLI	13.27	7.91	-	10.61	8.69	5.37	4.45
FuLI	30.76	34.57	32.41	32.31	35.35	31.74	33.16
FFuI	13.61	14.55	14.53	14.09	11.02	12.81	11.01
HLI	29.05	28.72	24.69	22.85	28.32	23.32	17.48
HWI	32.91	40.59	36.52	33.55	34.46	34.38	38.78
EDI	12.58	13.49	12.99	9.94	11.08	12.04	12.21
ALI1	53.58	55.18	41.86	34.85	33.06	39.06	21.69
ALI2	50.78	54.65	46.22	34.52	41.86	38.94	26.50
ALI3	50.73	53.91	-	33.93	38.37	32.41	20.81
ALI4	56.61	57.75	-	40.99	41.41	39.04	27.57
ASIn1	0.92	0.72	0.69	0.74	0.85	0.72	0.63
ASIn2	0.77	0.76	0.40	0.71	0.81	0.58	0.63
ASIn3	0.81	0.79	-	0.88	0.85	0.58	0.58
ASIn4	0.96	0.76	-	0.71	0.85	0.62	0.97
ASC1	85	76	65	67	67	66	63
ASC2	103	99	84	90	97	92	78
ASC3	113	95	-	123	104	100	88
ASC4	137	113	-	127	96	120	113
C1LI	-	-	-	11.76	14.83	13.24	12.08
ClRC	-	-	-	4	4	4	4
TrRC	-	-	-	21	24	20	20
ClSI	-	-	-	0.71	1.01	0.58	0.73
ClSdI	-	-	-	0.46	0.85	0.48	0.49
ClSvI	-	-	-	0.35	0.57	0.48	0.39
GiLC	29	27	27	28	23	25	27
GiLI	24.05	27.59	27.82	23.64	32.19	36.30	31.22
EgLI	5.79	11.03	7.19	6.91	-	-	-
EgW	3.90	5.96	2.59	2.71	-	-	-
CbL	54.19	52.64	57.68	55.92	51.38	40.35	41.27
CbWI	21.49	22.50	20.54	21.80	24.13	24.39	24.55
SL 5.41	5.39	4.63	5.43	-	5.06	67.36	
StZI	55.60	54.06	56.69	60.32	71.17	60.94	56.19
LoLI	32.76	35.16	32.20	29.94	35.31	37.97	37.85
LoL/Stz (%)	58.93	65.03	56.81	49.63	49.62	62.30	4.87

enlarged). Sucker counts range from 55–138; arms 4 with the highest average counts; ASC4 in males 88–*116*–138 (SD, 18, n=7), females 96–*118*–127 (SD, 14, n=6).

Hectocotylus present, left ventral arm modified; sucker size normal proximally, reduced distally, then normal to arm tip (Fig. 6H); from proximal to distal end of arm, 9–10 rows of normal suckers at proximal 1/2, followed by 6–7 rows of markedly reduced suckers, two dorsal and ventral series displaced, suckers on distal 1/4 normal; oral surface of modified region wide, fleshy, with transverse ridges and shallow median furrow; protective membrane well developed. Hectocotylised arm attenuate distally.

Tentacular club small (Fig. 5G); ClLI of males 10.6–*11.7*–14.4 (SD, 1.8, n=6), females 11.8–*13.0*–14.8 (SD, 1.4, n=4). Club crescent-shaped; sucker-bearing face flattened. Club with 4 suckers in transverse rows; 20–24 suckers in longitudinal series, TrRC males 17–*20*–23 (SD, 2, n=6), females 20–*21*–24 (SD, 2, n=4). Suckers differ in size, 4–5 median suckers slightly larger than rest; ClSI males 0.53–*0.61*–0.74 (SD, 0.07, n=6), females 0.58–*0.76*–1.01 (SD, 0.18, n=4 dorsal marginal longitudinal series of suckers larger than ventral series; ClSId males 0.40–*0.47*–0.74 (SD, 0.13, n=6), females 0.46–*0.57*–0.85 (SD, 0.19, n=4); ClSIv males 0.27–*0.35*–0.44 (SD, 0.07, n=6), females 0.35–*0.45*–0.57 (SD, 0.10, n=4). Swimming keel of club extends slightly beyond carpus (Figs. 5G). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal membrane longer than ventral membrane, terminates at the extension of posterior end of carpus; dorsal membrane much broader than ventral membrane; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 18–29 lamellae per demibranch; GiLC males 18–*23*–25 (SD, 3, n=7), females 23–*27*–29 (SD, 2, n=7). Gill length: GiLI males 21.7–*24.8*–28.9 (SD, 2.8, n=7), females 23.6–*29.0*–36.3 (SD, 4.6, n=7).

Buccal membrane without suckers. Upper beak (Fig. 6C) rostrum sharply pointed, length approximately equal to width, cutting edge straight; hood high above crest posteriorly; crest curved, lateral wall elongate to almost same length of crest; wings narrow and short; hood dark brown, lighter on ventral margin, crest only slightly pigmented. Lower beak (Fig. 6D,E) rostrum protrudes only very slightly beyond wings, cutting edge curved; hood low on crest; crest straight; hood and wings width narrow; hood notch deep (Fig. 6E); wings widely spaced, long; crest wide; rostrum and anterior of wings dark brown, posterior of wings and crest only slightly pigmented. Radula homodont; rhachidian teeth with distinct heels, indented basally, slender, triangular, sides straight (Fig. 7I); first lateral teeth shorter than, but similar width to, rhachidian teeth, asymmetrical with mesocone slightly displaced towards centre of radula; second laterals longer than first, distinctly curved on lateral margin; marginal teeth elongate with long tapered and curved mesocone, heels rounded.

Spermatophores: cement body bipartite (Fig. 6F,G); aboral end elongate, cylindrical, connects to sperm reservoir via narrow duct; oral end of cement body narrower, cylindrical, approximately two thirds length of, and slightly narrower than aboral end, connects to aboral end via narrow neck; middle tunic commences along aboral part of cement body; ejaculatory apparatus coiled, extends into oral dilation of spermatophore. Smallest male with well developed spermatophores in spermatophoric sac 37.6 mm ML.

Eggs oval; 3.2–*4.3*–5.8 mm long (SD, 1.1, n=4), 1.5–*2.1*–3.2 mm wide (SD, 0.8, n=4). EgLI 5.8–*7.7*–11.0 (SD, 2.3, n=4), EgWI 2.6–*3.8*–6.0 (SD, 1.6, n=4). Smallest female with well developed eggs in ovaries 52.9 mm ML.

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline lanceolate, broadest in anterior third, at anterior end of striated zone; CbL of males 37.9–*48.4*–54.3 (SD, 5.6, n=7), females 40.4–*50.5*–57.7 (SD, 6.9, n=7); CbWI of males 15.4–*17.3*–19.7 (SD, 1.3, n=7), females 20.5–*22.8*–24.5 (SD, 1.6, n=7), females with wider cuttlebones than males, CbW/CbL of males 0.17–*0.18*–0.20 (SD, 0.01, n=7), females 0.21–*0.23*–0.25 (SD, 0.01, n=7); females more convex than males in lateral view (Fig. 7C,G). Bone acuminate, acute at both ends (Fig. 7A,B,E,F); strongly recurved ventrally (Fig. 7C,G).

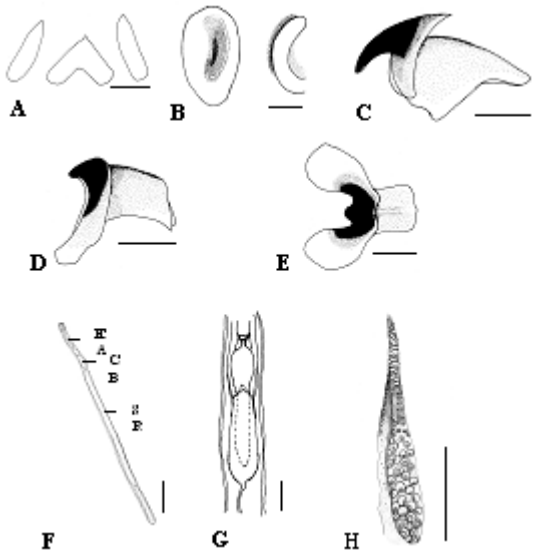

Figure 6. *Sepia hirunda*: (A) funnel organ, male MNMS 3984-006, 50.4 mm ML, scale bar = 5 mm; (B) funnel-locking cartilage (left), and mantle-locking cartilage (right), female MNMS 3984-008-06, 57.9 mm ML, scale bar = 2 mm; (C) upper beak, side view; (D) lower beak, side view; (E) lower beak, ventral view (C–E, male NMNS 3984-008-04, 48.9 mm ML, scale bar = 2 mm) (F) spermatophore, scale bar = 0.1 mm (for abbreviations and definitions see Fig. 3(F)); (G) spermatophore, cement body, scale bar = 0.5 mm (F and G, NMNS 3984-006, 50.4 mm ML)

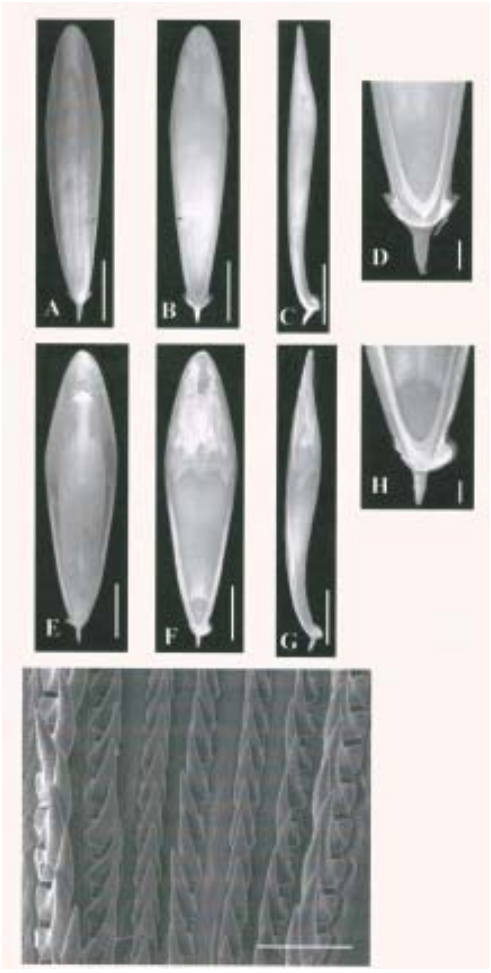

Figure 7. *Sepia hirunda*: (A) male cuttlebone, dorsal view; (B) male cuttlebone, ventral view; (C) male cuttlebone, lateral view; (D) posterior end of male cuttlebone, ventral view (A–D, NMNS 3984-008-03, 50.6 mm ML, A–C scale bar = 1 cm, D scale bar = 2 mm); (E) female cuttlebone, dorsal view; (F) female cuttlebone, ventral view; (G) female cuttlebone, lateral view; (H) posterior end of male cuttlebone, ventral view (E–H, NMNS 3984-008-08, 52.9 mm ML, E–G scale bar = 1 cm, H scale bar = 2 mm); (I) radula, male NMNS 3984-008-07, 56.6 mm ML, scale bar = 300 μm

Dorsal surface pinkish (more pronounced posteriorly); evenly convex; calcified medially, thickest posteriorly, slightly granulose with irregular longitudinal ridges (particularly posteriorly). Dorsal median rib distinct anteriorly, indistinct posteriorly, broadens anteriorly; bordered laterally by shallow grooves; lateral ribs present, anterior ribs inverted U-shaped (Fig. 7B,F). Chitin present, wide bands border lateral margins of cuttlebone (covers about half of cuttlebone dorsal surface). Spine present, long; SLI of males 5.0–*5.5*–6.0 (SD, 0.4, n=5), females 4.6–*5.1*–5.4 (SD, 0.3, n=6); curves dorsally. Striated zone convex (Fig. 7B,F); StZI of males 60.3–*67.0*–77.8 (SD, 6.7, n=7), females 54.1–*59.6*–71.2 (SD, 5.8, n=7). Last loculus convex; LoLI of males 22.6–*26.4*–31.9 (SD, 2.9, n=7), females 29.9–*34.5*–38.0 (SD, 3.0, n=7); LoL/StZ (%) of males 29.1–*40.0*–52.1 (SD, 7.6, n=7), females 49.6–*58.5*–67.4 (SD, 7.0, n=7), females larger than males. Sulcus extends entire length of cuttlebone; deep, narrow widening slightly in anterior part of last loculus; flanked by rounded ribs (in striated zone, lateral sides of rib

flat, or concave). Anterior striate inverted M-shape, deeply incurved medially (Fig. 7D,H). Limbs of inner cone extend anteriorly to end of striated zone; inner cone lateral limbs not separated from outer cone by smooth zones. Outer cone calcified; narrow throughout; limbs expanded posteriorly forming two short "wings", directed ventrally, forming recurved cup-like structure, also chitin around.

Body, head, arm, papillae absent. Colour (alcohol preserved specimens): head pigment present, dark red-brown and denser around eyes; evenly distributed pigment on dorsal side of arms; dorsal mantle pinkish-brown, pigment denser on midline of mantle. Fins pale. Ventral pigment present, denser on borderline of mantle and fin.

Etymology

The species epithet "hirunda" is from Latin "hirundo" for the bird "swallow". A swallow's tail is long and it refers to the long tails of this species.

Molecular phylogenetic analysis:

The 657 bp fragments of the mtCOI were obtained from 8 individuals, 2 males and 2 females each of *Sepia furcata* and *Sepia hirunda* (Table 2). They contain no indels (insertion or deletion), frame-shift or non-synonymous substitution. The empirical base frequencies from these two species: *S. furcata*, adenine (A) 28.27%, cytosine (C) 17.43%, guanine (G) 14.99%, thymine (T) 39.31%; *S. hirunda*, adenine (A) 28.62%, cytosine (C) 16.86%, guanine (G) 14.46%, thymine (T) 40.07%, which were obviously biased to A and T but there are no significance difference between these two species.

The average intraspecific genetic variation of *S. furcata* is 0.30%, and is 0.48% for *S. hirunda*, much smaller than that between *S. furcata* and *S. hirunda*, 3.61% (Table 5). A phylogenetic tree constructed using maximum parsimony methods (Fig. 8) shows *S. furcata* and *S. hirunda* are significant monophyletic groups with high bootstrap value support, while *Euprymna berryi* Sasaki, 1929 is the outgroup. Phylogenetic trees constructed with minimum evolution and maximum likelihood methods also show the same result (data not shown).

DISCUSSION

Although both of these two species have the dominant character, the "tail" and general similarity, there are still some morphological differences between them. Firstly, they have different "tail" lengths. In *Sepia furcata*, the male tail length is about 10% of mantle length and the female tail length shorter than 5% of mantle length, while male tail length is about half of mantle length and the female tail length about 10% of mantle length in *Sepia hirunda*. Secondly, they have a different arm length arrangement. The arms 2 lengths of *S. furcata* males are just a little shorter than the mantle length and twice the length of other arms, while the arms 2 of female are about half of the mantle length, and the other arms are shorter than 40% of mantle length. The longest arms of *S. hirunda* are the arms 4, which are about half of the mantle length in males and 45% in females, respectively. But the difference between the length of arms 4 and the other arms are not so large. In summary, the tail of *S. hirunda* is much longer than that of *S. furcata* in both sexes, and *S. furcata* has obviously elongated arms 2.

From mtCOI sequence data, the genetic divergence of these two species is much greater than the variation within these two species (Table 5) and these two species are each significant monophyletic clades (Fig. 8). Both of these results indicate that these two species are genetically independent. Based on morphological and molecular evidence, we report these two taxa are two valid species and both of them are new to science. It has been reported that mtCOI could be used in species-level diagnoses because of its high rates of sequence change in most animal groups and constraints on intraspecific divergence (Hebert *et al*., 2003b). Our data confirm this result in *Doratosepion* species.

Sexual dimorphism often leads to confusion in determining whether specimens of two sexes are conspecific in *Doratosepion* species (Reid 2000). The same applies to the two species examined in this study. In these two species, the cuttlebones of females are wider than those of males, while the tail lengths and arm lengths of males are greater than females (especially the arms

Table 5. The pairwise mtCOI gene divergence. Upper right is number of nucleotide substitutions; lower left is proportion of distance.

Species	*Euprymna berryi*	*Sepia aculeata*	*Sepia. furcata*-1	*S. furcata*-2	*S. furcata*-3	*S. furcata*-4	*S. hirunda*-1	*S. hirunda*-2	*S. hirunda*-3	*S. hirunda*-4
E. berryi		114	118	117	119	117	114	115	113	113
S. aculeata	17.35		103	103	105	103	102	102	100	100
S. furcata-1	17.96	15.68		1	4	1	24	26	22	23
S. furcata-2	17.81	15.68	0.15		3	0	23	25	21	22
S. furcata-3	18.11	15.98	0.61	0.46		3	26	28	24	25
S. furcata-4	17.81	15.68	0.15	0.00	0.46		23	25	21	22
S. hirunda-1	17.35	15.53	3.65	3.50	3.96	3.50		4	2	3
S. hirunda-2	17.50	15.53	3.96	3.81	4.26	3.81	0.61		4	5
S. hirunda-3	17.20	15.22	3.35	3.20	3.65	3.20	0.30	0.61		1
S. hirunda-4	17.20	15.22	3.50	3.35	3.81	3.35	0.46	0.76	0.15	

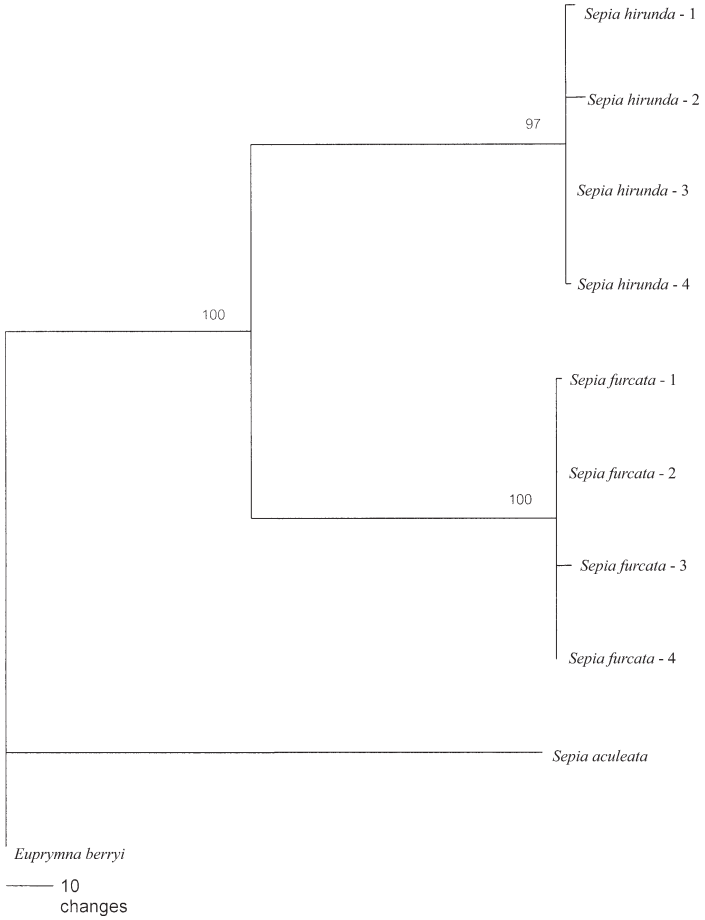

Figure 8. Phylogenetic tree of *Sepia furcata* and *Sepia hirunda* mtCOI sequences using *Euprymna berryi* Sasaki, 1929 as outgroup. Bootstrap support values >50% are indicated beyond nodes. Branches lengths are drown proportional to the number of unambiguous changes. Maximum parsimony tree generated from unweighted data with 1000 bootstrap resampling replications (TL = 666, CI = 0.4399, RI = 0.3502).

2 of *S. furcata*). In this study, we screen the mtCOI sequences of both sexes; the results confirm the identity of both sexes of both species.

The distribution of these two species is also very interesting. Since there have been no records of *S. furcata* and *S. hirunda* outside Taiwanese waters, we consider that they are endemic species of Taiwanese waters. *Sepia furcata* occurs in the northeast while *S. hirunda* occurs in west and southwest of Taiwan; both of these two areas are affected by the same sea current, Kuroshio. The Kuroshio Current is a pelagic water system that runs northward along the east coast of Taiwan year round and enters the Taiwan Strait (the western waters of Taiwan) by passing through the Luzon Strait (the southern waters of Taiwan) in winter (Jan *et al*., 2002). However, the Taiwan Strait, especially the southwestern waters of Taiwan, is also affected by the South China Sea water mass simultaneously (Jan *et al*., 2002). It is hypothesized that *S. furcata* or *S. hirunda* or their ancestral form may have come from tropical waters and followed Kuroshio to enter Taiwanese waters. Speciation then occurred because of the effect of different water masses. To examine this hypothesis, the population genetic structure of *S. furcata* and *S. hirunda* should be analyzed and compared with that of other closely related *Doratosepion* species near Taiwanese waters.

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