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A TAXONOMIC REVISION OF NORTH PACIFIC SWELL SHARKS, GENUS
CEPHALOSCYLLIUM

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jayna Ann Schaaf-Da Silva

December 2007

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ABSTRACT

A TAXONOMIC REVISION OF THE NORTH PACIFIC SWELL SHARKS, GENUS *CEPHALOSCYLLIUM*

by Jayna A. Schaaf-Da Silva

This study is a taxonomic revision of the genus *Cephaloscyllium* (Gill 1862) (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from the western North and the eastern Pacific based on morphometric and meristic data. Concerning the western North Pacific, this study formally places *C. parvum* Inoue & Nakaya 2006 in synonymy with *C. sarawakensis* Yano *et al.* 2005, re-describes *C. umbratile* (Jordan and Fowler 1903) and *C. fasciatum* Chan 1966, and describes two new species from Taiwanese waters. A key to the species of *Cephaloscyllium* is presented for this region. For the eastern Pacific, a re-description of *C. ventriosum* (Garman 1880) is provided based on the Chilean holotype specimen. *Cephaloscyllium uter* (Jordan & Gilbert 1896) is upheld as a junior synonym of the former based on a comparison of the holotype with California specimens. Finally, the zoogeography of the genus is discussed in detail. The hypothesized center of origin of swell sharks is the Indo-West Pacific and distribution patterns can be attributed to dispersal events.

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INTRODUCTION

The swell sharks, genus *Cephaloscyllium*, belong to the family Scyliorhinidae and can be distinguished from other related genera by crests present on the cranium above the eye, a second dorsal fin considerably smaller than the first dorsal fin, and labial furrows rudimentary or absent. The taxonomy of *Cephaloscyllium* has been confusing, mainly due to a lack of detailed descriptions, and in some instances type material. Many species are very similar and this has led to misidentifications in the literature and museum collections. Recently, research expeditions and commercial and artisanal fisheries have revealed new shark species and there has been an effort to describe these new species. Despite such efforts to document undescribed species, little is known about the biology, behavior, and ecological status of this group.

The focus of Chapter 1 is the *Cephaloscyllium* species of the western North Pacific (WNP), including Thailand, Vietnam, Malaysia, the Philippines, China, Taiwan, and Japan. The taxonomic revision presented in Chapter 1 provides re-descriptions of *C. umbratile* and *C. fasciatum* based on the holotype specimens, and a re-examination of two recently described species from Malaysia. Most notably, an additional two species of *Cephaloscyllium* are described from Taiwan.

Chapter 2 involves a systematic study of the *Cephaloscyllium* species of the eastern Pacific. The genus arguably has one representative species in the eastern

Pacific, but the systematic literature is quite confusing. This study marks the first morphometric and meristic analysis comparing the holotype of *C. ventriosum* from Chile with California *Cephaloscyllium* specimens.

The zoogeography of *Cephaloscyllium* is presented in Chapter 3. Current *Cephaloscyllium* distributions are discussed in detail and a hypothesis for the mechanisms driving the zoogeography of this group is discussed. The history of the *Cephaloscyllium* lineage, from a center of origin through a hypothesized sequence of colonization, is proposed based on biological, fossil, and molecular literature.

An overall summary and areas for future study are outlined in the conclusions at the very end of this document.

CHAPTER 1:
A TAXONOMIC REVISION OF THE WESTERN NORTH PACIFIC SWELL
SHARKS, GENUS *CEPHALOSCYLLIUM* GILL, 1862 (CHONDRICHTHYES,
CARCHARHINIFORMES, SCYLORHINIDAE)

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Abstract

The genus *Cephaloscyllium* Gill, 1862 (Chondrichthyes, Carcharhiniformes, Scyliorhinidae) until recently had only two species recognized, *C. isabellum* [= *C. umbratile* (Jordan & Fowler 1903)] and *C. fasciatum* Chan, 1966, from the western North Pacific (WNP), with one dubious species, *C. formosanum*, having been described by Teng (1962). Recently, two additional species were described, *C. sarawakensis* Yano *et al.*, 2005 and *C. parvum* Inoue & Nakaya, 2006 from this region. Here I present a revision of this genus for the WNP, including re-descriptions of *C. umbratile* and *C. fasciatum* based on the holotypes, a re-examination of the two recently described species, and a description of two new species from Taiwan. *Cephaloscyllium umbratile* can be distinguished from its congeners based on maximum size, length of first dorsal fin base, anal-caudal fin space, and dorsal-caudal fin space. I conclude, based on a comparison of *C. parvum* and *C. sarawakensis*, that the former is a junior synonym of the latter species. The two new species can be separated from other WNP species by color pattern, shape of the anterior nasal flap, anal and dorsal fin size, internarial width, and mouth size. Finally, I present a revised dichotomous key to the WNP *Cephaloscyllium* recognizing six contemporary taxa: *C. circulopullum*, *C. fasciatum*, *C. sarawakensis*, *C. umbratile*, *C. sp. nov. 1* and *C. sp. nov. 2*.

Introduction

One of the more enigmatic, albeit poorly studied groups of carcharhiniform sharks are the catsharks (Chondrichthyes: Scyliorhinidae). Currently, the Scyliorhinidae is composed of roughly 16 genera and 151 species, accounting for 13% of all extant cartilaginous fishes (Human *et al.* 2006). The interrelationships of the Scyliorhinidae, the largest family within the order Carcharhiniformes, have long been debated by taxonomists. According to recent molecular phylogenetic investigations, the subfamily Scyliorhininae including the genera *Cephaloscyllium*, *Poroderma*, and *Scyliorhinus* represent a monophyletic, basal group (Iglesias *et al.* 2005; Human *et al.* 2006). These genera, members of the “true” catsharks, have long been considered plesiomorphic for several reasons: they are oviparous as opposed to pseudoplacental, small in size, and possess multicuspid teeth, few and poorly calcified vertebrae, unprotected eyes (lacking a nictitating membrane), flexible lobe-like fins with a reduced second dorsal fin, and an eel-like swimming mode (Springer 1979).

Members of the genus *Cephaloscyllium* Gill, 1862 are also known as swell sharks, their common name being derived from the unique ability to swallow either air or seawater, inflating their stomachs to deter predation. They inhabit continental and oceanic insular waters of the temperate and subtropical Indo-Pacific (Inoue & Nakaya 2006). *Cephaloscyllium* are distinguished from other

genera by a few key characters, including the lack of labial furrows and the presence of supraorbital crests on the chondrocranium (Compagno 1988).

Species of *Cephaloscyllium* are directly and indirectly impacted by commercial, artisanal, and recreational fisheries (Graham *et al.* 1997; Lisney & Kyne 2003). Typically, swell sharks are taken as bycatch, and areas with directed fisheries for this group have sparsely recorded catch information (Francis 2003). The impact of fisheries on *Cephaloscyllium* is not known in many areas; hence it is imperative that adequate descriptions are available to identify individual species.

Taxonomic classification errors in this group have been profuse and stem from confusion in the literature regarding color patterns, and unreliable morphological characters (Inoue & Nakaya 2006). In fact, the morphological conservancy within the group has made it difficult to establish strong characters, and existing keys rely on a combination of often minute characters (Springer 1979). Juvenile specimens have been known to be mistaken for the wrong species (Chan 1966) based on color patterns which tend to vary with growth.

The taxonomy of *Cephaloscyllium* is essentially problematic, partly due to the presence of several undescribed species. Nakaya (1975) reported eight species worldwide, while Springer (1979) recognized only five species in the genus. Compagno (1984) recognized seven valid species, with the possibility of an undescribed species from the western North Pacific (WNP). Last and Stevens (1994) reported seven species from Australian waters alone, five of which are

currently undescribed. Teng (1962) described one dubious species from Taiwan, *C. formosanum* that has since been synonymized as *C. umbratile* (Compagno 1984). In turn, *C. umbratile* has been synonymized with *C. isabellum* by Springer (1979). *Cephaloscyllium sarawakensis* and *C. parvum*, were each independently described by Yano *et al.* (2005) and Inoue and Nakaya (2006), respectively. Indeed, the lack of detailed species descriptions, and in some instances type material, has rendered this revision of the WNP *Cephaloscyllium* long overdue.

Of the 13 currently recognized species in the genus, Compagno *et al.* (2005) reported seven to be formally described, two of which are from the WNP, *C. fasciatum* Chan, 1966 and *C. umbratile* (Jordan & Fowler, 1903). Recently, three more species have been described from this region: *C. circulopullum* Yano *et al.*, 2005, *C. parvum* Inoue & Nakaya, 2006, and *C. sarawakensis* Yano *et al.*, 2005. The WNP is home to at least two more undescribed species; here I describe these two new species from Taiwanese waters.

Materials and Methods

Morphometric measurements follow Compagno (1984, 2001), and Springer (1979) and are listed in Appendix 1. Measurements were taken to the nearest 0.1 mm (except for total length, pre-caudal length, and girth which were measured to the nearest 1 mm) with a metric caliper and/or measuring tape and are presented as a proportion of total length (TL) in Tables 1, 2, and 3. In the species

descriptions, the first measurement presented for each character represents the corresponding holotype; the second measurement(s) given in parentheses represents the range for paratypes, where available. Vertebral counts were determined from x-radiographs. Tooth counts were taken for the upper and lower jaws directly from specimens.

Figures were produced in a variety of ways. Photographs were taken directly from specimens with a digital camera and edited with Adobe Photoshop 8.0. Additional photographs were provided by the corresponding museum or researcher. Maps were created with ArcView 3.1 and further edited with Adobe Photoshop 8.0. Illustrations were completed in pen and ink media and digitally scanned. Tables were created with Microsoft Excel.

Data analyses including all scatter plots were conducted using Microsoft Excel. SPSS was used to produce Principle Component Analyses and for variable selection.

Specimens were either collected by David A. Ebert or loaned by a museum. A list of comparative material is provided at the end of each species section; additional material is listed in Appendix 2 for *C. circulopullum* and *C. isabellum*.

Institutional abbreviations are as follows: British Museum of Natural History (BMNH); California Academy of Sciences (CAS); Museum of Comparative Zoology, Harvard University (MCZ); Kochi University, Japan

(BSKU); National Museum, Kuala Lumpur, Malaysia (IK); National Museum of Natural History (NMNH); National Science Museum, Tokyo, Japan (NSMT); Scripps Institution of Oceanography (SIO); Stanford University (SU: now housed at CAS); Yano *et al.* (2005) catalog number (MSR); DAE designations are David A. Ebert field numbers and corresponding specimens are housed at the museum at Moss Landing Marine Laboratories.

Systematics

Cephaloscyllium Gill, 1862

Scyliorhinus Blainville, 1816: 121.

Cephaloscyllium Gill, 1862: 407, 408.

Type species. *Scyllium laticeps* Duméril, 1853, by original designation.

Diagnosis. Stocky, stout-bodied catshark with very short snout, wide mouth, short tail, and flattened head. Body spindle-shaped, firm and thick-skinned, with well-calcified dermal denticles. Head very depressed and broad, narrowly rounded in lateral view; head short, bluntly pointed in lateral view; snout shape rounded-parabolic in dorsoventral view; nostrils not enlarged, placed ventrally and thus hidden in lateral view; anterior nasal flaps broadly triangular to lobate, lacking barbells, positioned just anterior to mouth or reaching it; nasoral grooves absent; ampullae not greatly enlarged on snout. Eyes cat-like, dorsolateral on head. Mouth broadly arched, very large and wide, with lower symphysis usually behind upper so appears to have a slight overbite

in lateral view, upper teeth exposed in ventral view. The presence of supraorbital crests of the chondrocranium in combination with the lack of upper and lower labial furrows is distinguishing. The first dorsal fin, which is larger than the second, originates posterior to origin of pelvic fins; origin of second dorsal fin over or slightly posterior to anal fin origin; pectoral fins large and somewhat rounded; anal fin moderately large, smaller than pelvic and first dorsal fins, but larger than second dorsal. Caudal fin broad and short, between a fourth and a fifth of the total length in adults. Color varies from beige to brown and sometimes uniform grey background, with darkly pigmented to obscure dorsal saddles numbering 4–9, blotches (sometimes blotches inside saddles as in juvenile *C. sarawakensis*), reticulated dark lines (as in *C. fasciatum*), or numerous blotches of dark brown to crème in addition to the saddles. Possess the ability to inflate the stomach with water or air to give a balloon-like, almost spherical shape to the trunk.

Teeth, similar in both upper and lower jaws, relatively small and numerous. Each tooth with a high central cusp and one or two lateral cusplets on either side. Tooth rows in either upper or lower jaws, 54–85.

Common name. Swell sharks or balloon sharks, refers to the ability to inflate the body by swallowing water or air.

Distribution. Swell sharks inhabit continental and oceanic insular waters of the temperate to sub-tropical Indo-Pacific (Inoue & Nakaya 2006). They range

in depth from the subtidal to the uppermost continental slope (~670 m). In the WNP, swell sharks range from the South China Sea to northern Japan, and as far south as Malaysia (Fig. 1).

FIGURE 1. Map of the western North Pacific, including known species ranges for *C. circulopullum* (pink), *C. fasciatum* (orange), *C. sarawakensis* (green), *C. umbratile* (purple), *C. sp. nov. 1* (red) and *C. sp. nov. 2* (yellow).

Etymology. The generic name derives from the Greek *kephale*, meaning head, and *skylion*, meaning dogfish.

***Cephaloscyllium* sp. nov. 1**
(Figs. 2, 3a, 7a; Table 1)

Type Series and Locality. Holotype, CAS 224876, immature female, 202 mm total length, collected from Tungkang, Taiwan, 22°27.6'N, 120°26.4'E, collected by David A. Ebert on 21 April 1988, in excellent condition.

FIGURE 2. *Cephaloscyllium* sp. nov. 1 holotype (CAS 224876), dorsal view. Photo by D.A. Ebert

Diagnosis. Body comparatively slender, head short. Snout moderately flattened, very short, broadly rounded. Anterior nasal flaps not overlapping mouth posteriorly, narrowly lobate, inner margin with a deep notch. First dorsal fin behind half of pelvic fin base; length from snout tip to first dorsal fin origin 48% TL, mouth width 52.5% HL. First dorsal fin considerably larger than second dorsal fin. Pectoral fins relatively large and broad. Color pattern consists of speckled dorsal saddles, three lateral clusters of spots arranged into rosettes between the paired fins. Dark lateral blotch between paired fins absent. Anal fin relatively large; dorsal fins relatively small.

Description. Proportional dimensions in percentage of total length are shown in Table 1. Head length (HL) measured from snout tip to fifth gill opening 27.4% of PCL. Snout moderately flattened, short, broadly rounded, preorbital length 29.8% HL and 72.0% interorbital width. Pre-pectoral length 18.3% TL. Eye small slit, cat-like, horizontal eye length 18.7% HL. Spiracle small, diameter 27.0% of horizontal eye length. Gill openings very small, vertical length of first gill opening 8.6% HL. Mouth small, labial furrows absent. Mouth width 52.5% HL. Anterior nasal flaps not overlapping mouth posteriorly, with elongate lobe and deep notch on inner margin. Internarial distance 24.0% mouth width. First dorsal fin origin about opposite or behind half of pelvic fin base, length from snout tip to first dorsal origin 48.0% TL; snout tip to second dorsal fin origin 83.5% PCL. First and second dorsal fins small, height of first dorsal fin 40.2% overall length; height of second dorsal fin 36.2% overall length. Second dorsal fin only slightly smaller than first, height of second dorsal fin 71.4% first dorsal fin. Pectoral fins relatively large and broad, anterior margin 62.6% HL, length of base 71.8% anterior margin. Pelvic fin small, overall length 14.4% PCL, base 66.3% overall length. Anal fin larger than dorsal fins, height 4.8% and overall 14.4% PCL. Height of second dorsal fin 71.4% anal fin height, height of first dorsal fin equal to anal fin height. Caudal fin broad, asymmetrical, with subterminal notch, length of dorsal lobe of caudal fin 36.9% PCL, length of ventral lobe 35.2% dorsal lobe.

Body firm and thick-skinned, with well calcified dermal denticles. No ridge of enlarged denticles along dorsal caudal fin margin. Teeth very small, similar in both jaws, 3 cusps. Total vertebral number 120, monospondylous 44, precaudal 74, and pre-caudal diplospondylous 30.

TABLE 1. Morphometric and meristic data for the holotype (HT) specimens for *Cephaloscyllium* **sp. nov. 1** (CAS 224876) and *Cephaloscyllium* **sp. nov. 2** (CAS 224877). TL is the actual measurement in millimeters; all other measurements are expressed as percentage of TL except vertebral and tooth counts. Abbreviations are listed in the Appendix 1.

	C. sp. nov. 1	C. sp. nov. 2		C. sp. nov. 1	C. sp. nov. 2
	HT	HT		HT	HT
	CAS 224876	CAS 224877		CAS 224876	CAS 224877
TL	202	188	P1H	8.9	7.4
PCL	72.3	77.7	P1I	5.4	3.7
PD2	60.4	63.8	P1P	8.4	6.9
PD1	48.0	48.9	D1L	8.7	9.0
IDS	6.9	9.0	D1A	7.9	8.0
DCS	6.4	7.4	D1B	5.9	6.9
PAL	57.4	60.1	D1H	3.4	3.7
PP2	41.1	43.1	D1I	3.0	2.7
PP1	18.3	19.7	D1P	3.0	3.7
SVL	45.0	46.8	P2L	10.4	8.0
PPS	14.9	18.6	P2A	5.4	5.3
PAS	8.4	11.2	P2B	6.9	6.4
PCA	22.3	22.9	P2H	3.5	3.7
ACS	5.9	6.4	P2I	3.0	2.7
INO	8.2	8.0	P2P	6.9	5.3
HDH	7.4	10.1	CLO	--	1.1
HDW	13.9	13.3	CLI	--	3.7
TRH	8.4	12.8	CLB	--	0.5
TRW	12.4	13.3	D2L	6.9	6.9
GIR	35.6	47.9	D2A	5.9	5.6
CPH	3.2	3.7	D2B	5.0	4.3
CPW	2.2	3.2	D2H	2.5	2.1

...continued on the next page

Table 1. (continued)

	HT	HT		HT	HT
HDL	19.8	22.3	D2I	2.2	2.7
PG1	15.3	16.0	D2P	2.0	2.7
PSP	9.9	9.6	ANL	10.4	10.1
POB	5.9	6.4	ANA	6.9	7.4
EYL	3.7	3.2	ANB	7.4	8.0
SPL	1.0	0.5	ANH	3.5	3.2
ESL	1.0	1.1	ANI	3.0	1.6
ING	4.5	4.8	ANP	5.0	3.7
GS1	1.7	1.6	CDM	26.7	25.5
GS2	1.7	1.6	CFW	6.4	6.4
GS3	1.7	1.6	CPV	9.4	10.1
GS4	1.5	1.6	CST	4.5	4.3
GS5	1.5	1.1	CTR	5.4	5.3
POR	5.0	4.3	CTL	6.9	6.4
PRN	2.5	1.6	PDO	11.9	18.1
MOL	4.2	3.7	DAO	3.5	4.3
MOW	10.4	7.4	DAI	0.0	0.0
NOW	3.0	2.7	U tot	60	48
INW	2.5	4.0	L tot	60	52
ANF	1.2	1.6	VERT	120	117
P1L	13.4	11.7	mono	44	46
P1A	12.4	11.7	predip	30	33
P1B	8.9	8.0	caudaldip	46	38

Size and Sexual Maturity. Unknown at present.

Coloration. Background color golden to light brown dorsally; pale ventrally. Small brown specks cover dorsal and lateral surfaces. Seven dorsal H-shaped saddles clearly defined; first in line with the gills, second above pectoral fin insertion, third just before pelvic fin origin, then one at each dorsal fin base, one at caudal fin origin, and dorsal caudal lobe; saddles open, outline brown and variegated, not dark and solid. Dark lateral blotches absent; three rosettes of

small brown speckles present laterally, between the pectoral and pelvic fins.

Rosettes on head, one behind each orbit, one between orbits, one over each gill series, and a few on the snout. Each paired fin has one rosette placed dorsally, larger rosettes on larger fins. Paired rosettes are present laterally above pelvic fin origin, between dorsal fins, caudal peduncle, and lower caudal lobe. It is unknown how or if the color pattern changes into adulthood.

Comparison with Other Species. *Cephaloscyllium* **sp. nov. 1** is distinct from *C. sp. nov. 2* in possessing a lobate anterior nasal flap, and a color pattern of H-shaped dorsal saddles with variegated outlines, and distinctive rosettes. *C. sp. nov. 1* has short anterior nasal flaps, open saddles, but the borders are dark and solid and not H-shaped.

Cephaloscyllium **sp. nov. 1** differs from *C. circulopullum* in lacking a dark lateral blotch between the paired fins, and possessing a lobed anterior nasal flap.

Cephaloscyllium **sp. nov. 1** has a remarkably distinct color pattern from *C. fasciatum*. Although the two species have open dorsal saddles, *C. sp. nov. 1* displays saddle borders that are not dark and solid as in *C. fasciatum*. In contrast, the saddle borders of *C. sp. nov. 1* are variegated and patchy and form an H-shape. Also, this new species has distinctive rosettes and no reticulated lines. The anal fin is slightly larger in the new species. The posterior margin of the anal fin is 6.8% PCL for *C. sp. nov. 1*, but 3.1–4.1% PCL for *C. fasciatum* (Fig. 3).

FIGURE 3. Posterior margin of the anal fin as a proportion of pre-caudal length vs. pre-caudal length for select *Cephaloscyllium* species.

Cephaloscyllium **sp. nov. 1** is different from *C. sarawakensis* based on color pattern, and size and position of the dorsal fins. The new species does not display the distinctive polka-dots and the dark lateral blotch of *C. sarawakensis*.

Overall, the two dorsal fins of *C. sp. nov. 1* are smaller than in other species of swell shark. The first dorsal fin base is relatively short in *C. sp. nov. 1* (Fig. 4). This length is 8.2% PCL in *C. sp. nov. 1*, whereas *C. sarawakensis* has a dorsal fin base between 9.2–12.3% PCL.

FIGURE 4. First dorsal fin base as a proportion of total length vs. total length for select *Cephaloscyllium* species.

The first dorsal fin height is relatively short (Fig. 5) in *C. sp. nov. 1*, at 4.8% PCL.

This measurement is 5.8–7.3% PCL in *C. sarawakensis*. In *C. sp. nov. 1* the first

dorsal fin originates behind the first half of the pelvic fin base. In *C.*

sarawakensis, however, the first dorsal fin originates closer to the pelvic fin origin.

FIGURE 5. First dorsal fin height as a proportion of total length vs. total length for select *Cephaloscyllium* species.

Cephaloscyllium **sp. nov. 1** can be separated from adult *C. umbratile* by color pattern, and morphology of the anterior nasal flap. *Cephaloscyllium umbratile* does not have open saddles, nor are they H-shaped. *Cephaloscyllium umbratile* has a sub-triangular anterior nasal flap shape (Fig. 6); it is not deeply notched.

FIGURE 6. Anterior nasal flaps of a. *Cephaloscyllium* **sp. nov. 1**; b. *Cephaloscyllium* **sp. nov. 2**; c. *Cephaloscyllium fasciatum*; d. *Cephaloscyllium umbratile*; e. *Cephaloscyllium sarawakensis*; f. *Cephaloscyllium circulopullum*. Illustration by J.A. S.-Da Silva.

Remarks. Another good meristic to use for swell shark identification is color pattern. The only caveat is that color pattern of swell sharks tends to change somewhat as the animal grows into an adult. If young similar-sized specimens of *C. sp. nov. 1*, *C. sp. nov. 2*, *C. circulopullum*, *C. fasciatum*, *C. sarawakensis*, and *C. umbratile* are examined side-by-side, it is fairly easy to tell that they are all separate species (Fig. 7). *Cephaloscyllium fasciatum* has an intricate color pattern that stays relatively consistent throughout growth. In contrast, *C. umbratile* and *C. sarawakensis* go through a rather dramatic color change with growth. *Cephaloscyllium umbratile* has a juvenile color pattern that is simple and an adult color pattern that is heavily mottled. *Cephaloscyllium sarawakensis* is just the opposite; the juvenile color pattern is elaborate with polka-dots, whereas the adult pattern lacks the polka-dots. Although the color pattern of adult *C. sp. nov. 1* is presently unknown, the juvenile markings are quite distinct from any other *Cephaloscyllium* species within this region.

Cephaloscyllium fasciatum and the two new species have open dorsal saddles; that is, the background color shows through and the saddle is represented only by a solid or broken outline. *Cephaloscyllium umbratile*, *C. sarawakensis*, and *C. circulopullum* have closed dorsal saddles.

FIGURE 7. Lateral view of the western North Pacific swell sharks; a. *Cephaloscyllium* sp. nov. 1; b. *Cephaloscyllium* sp. nov. 2; c. *Cephaloscyllium fasciatum*; d. *Cephaloscyllium umbratile*; e. *Cephaloscyllium sarawakensis*; f. *Cephaloscyllium circulopullum*. Illustration by J.A. S.-Da Silva.

Distribution. *Cephaloscyllium* **sp. nov. 1** is known only from off the south coast of Taiwan.

Etymology. The species will be named after the Latin *pardus* for leopard, referring to the rosette-type spots along the dorsal and lateral surfaces.

Common Name. Leopard-spotted swell shark

Study Material. 1 specimen—Holotype, CAS 224876, female, 202 mm TL, Tungkang, Taiwan.

Cephaloscyllium* **sp. nov. 2*
(Figs. 8, 3b, 7b, 11b; Table 1)

Type Series and Locality. Holotype, CAS 224877, immature male, 188 mm total length, collected from Su-ao, Taiwan, 24°35.7'N, 121°50.7'E, collected by David A. Ebert on 3 April 1988, in excellent condition.

FIGURE 8. *Cephaloscyllium* **sp. nov. 2** holotype (CAS 224877), lateral view. Photo by D.A. Ebert.

Diagnosis. Body comparatively slender, head short. Snout moderately flattened, very short, broadly rounded. Anterior nasal flaps not overlapping mouth posteriorly, short and triangular; internarial distance long. Mouth small,

width 33.2% HL. First dorsal fin origin in line with pelvic fin insertion; length from snout tip to first dorsal fin origin 48.9% TL. First dorsal fin only slightly larger than second dorsal fin. Pectoral fins relatively large and broad. Color pattern consists of eight angular, open dorsal saddles, four are before the first dorsal fin origin. Lateral blotch present between the paired fins; angular, open, with a dark outline. Anal fin relatively large; dorsal fins relatively small.

Description. Proportional dimensions in percentage of total length are shown in Table 1. Head length measured from snout tip to fifth gill opening 28.7% of PCL. Snout moderately flattened, short, broadly rounded, preorbital length 28.7% HL and 80.0% interorbital width. Pre-pectoral length 19.7% TL. Eye small slit, cat-like, horizontal eye length 14.3% HL. Spiracle small, diameter 15.6% of horizontal eye length. Gill openings very small, vertical length of first gill opening 7.2% HL. Mouth small, labial furrows absent. Mouth width 33.2% HL. Anterior nasal flaps not overlapping mouth posteriorly, with elongate lobe and deep notch on inner margin. Internarial distance 54.1% mouth width. First dorsal fin origin about opposite or behind half of pelvic fin base, length from snout tip to first dorsal origin 48.9% TL; snout tip to second dorsal fin origin 82.1% PCL. First and second dorsal fins small, height of first dorsal fin 41.1% overall length; height of second dorsal fin 30.4% overall length. Second dorsal fin only slightly smaller than first, height of second dorsal fin 56.8% first dorsal fin height. Pectoral fins relatively large and broad, anterior margin 52.5% HL,

length of base 68.4% anterior margin. Pelvic fin small, overall length 10.3% PCL, base 80.0% overall length. Anal fin larger than dorsal fins, height 4.1% and overall 13.0% PCL. Height of second dorsal fin 65.6% anal fin height, height of first dorsal fin about equal to anal fin height. Caudal fin broad, asymmetrical, with subterminal notch, length of dorsal lobe of caudal fin 32.8% PCL, length of ventral lobe 39.6% dorsal lobe.

Body firm and thick-skinned, with well calcified dermal denticles. No ridge of enlarged denticles along dorsal caudal fin margin. Teeth very small, similar in both jaws, 3 cusps. Total vertebral number 117, monospondylous 46, precaudal 79, and pre-caudal diplospondylous 33.

Size and Sexual Maturity. Unknown at present.

Coloration. Background color medium brown to beige dorsally; pale ventrally. Eight dorsal saddles clearly defined; first behind orbitals, second in line with the gills, third behind pectoral fin insertion, fourth just before pelvic fin origin, then one at each dorsal fin base, one at caudal fin origin, and dorsal caudal lobe; saddles open, outline dark brown and solid. Dark lateral blotches present between paired fins, open and somewhat connected to third saddle. Without polka-dots, rosettes, random speckles, or light-colored spots; spots on snout absent. Angular open blotches present laterally above pectoral fins between second and third dorsal saddles, and spanning gill series. Each paired fin has one angular blotch placed dorsally, larger blotches on larger fins.

Comparison with Other Species. As stated in the above section, *C. sp. nov. 2* differs from *C. sp. nov. 1* in lacking a lobate anterior nasal flap, and possessing a color pattern of dark outlined dorsal saddles.

Cephaloscyllium sp. nov. 2 is separate from *C. circulopullum* in lacking a circular dark lateral blotch between the paired fins, and having a greater internarial distance, and shorter mouth width.

Cephaloscyllium sp. nov. 2 differs from *C. fasciatum* in lacking a lobate anterior nasal flap, having a less-variegated color pattern, and a smaller mouth width. Furthermore, the mouth length is shorter for the new species than *C. fasciatum*; 3.7% TL and 5.1–6.2% TL respectively. In addition, the internarial width is greater in *C. sp. nov. 2*, at 4.0% TL, compared to *C. fasciatum* at 2.0–3.2% TL. *Cephaloscyllium sp. nov. 2* is separate from *C. sarawakensis* in lacking a vertically elongated dark lateral blotch between the paired fins, and having a greater internarial distance. The internarial space of *C. sp. nov. 2* is 4.0% TL; in *C. sarawakensis*, this measurement is 1.9–2.8% TL. In general, *C. sp. nov. 2* has a greater internarial width than other WNP species studied (Fig. 9).

FIGURE 9. Internarial width as a proportion of total length vs. total length for selected *Cephaloscyllium* species.

The mouth width is shorter in this new species, at 7.4% TL, whereas this measurement is consistently greater than 8% TL *C. sarawakensis*. In general, *C. sp. nov. 2* has a shorter mouth width than other WNP species studied and this measurement is very similar for *C. sp. nov. 1* (Fig. 10).

FIGURE 10. Mouth width as a proportion of total length vs. total length for selected *Cephaloscyllium* species.

Cephaloscyllium **sp. nov. 2** differs from adult *C. umbratile* in lacking light colored spots. *Cephaloscyllium umbratile* does not have open saddles, as observed in the new species. Also, *Cephaloscyllium umbratile* has three pre-first dorsal fin saddles, whereas *C. sp. nov. 2* has four pre-first dorsal fin saddles (Fig. 11).

FIGURE 11. Dorsal view of select juvenile swell sharks; a. *Cephaloscyllium sarawakensis* (CAS 224882); b. *Cephaloscyllium* **sp. nov. 2** (CAS 224877); c. *Cephaloscyllium umbratile* (CAS 224880). Photo by D.A. Ebert.

Remarks. Figure 11 shows similar-sized specimens of *C. sp. nov. 2*, *C. sarawakensis*, and *C. umbratile* in dorsal view. In this figure, it is fairly easy to conclude that these three specimens represent distinct species of *Cephaloscyllium*. Although the adult color pattern of *C. sp. nov. 2* is unknown at present, the juvenile markings are unique.

Distribution. *Cephaloscyllium sp. nov. 2* is only known from off the east coast of Taiwan.

Etymology. The species will be named after the Latin *maculata* for spotted, referring to the large dorsal saddles and lateral spots.

Common Name. Spotted swell shark

Study Material. 1 specimen—Holotype, CAS 224877, male, 188 mm TL, Su-ao, Taiwan.

***Cephaloscyllium fasciatum* Chan, 1966**
(Fig. 12, 3c, 7c; Table 2)

Cephaloscyllium fasciatum Chan, 1966: 232, figs. 6 and 7, pl. III; Springer 1979: 39; Compagno 1984: 297; Compagno *et al.* 2005: 216, pl. 36.

Type Series and Locality. Holotype, BMNH 1965.8.11.1, maturing female, 422 mm TL, off Cape Bantagan, Vietnam, 15°55.7'N, 109°18.5'E, in 205–315 m on soft mud bottom, collected on 16 September 1963. Paratypes, BMNH 1965.8.11.2, juvenile male, 246 mm TL; BMNH 1965.8.11.3, juvenile male, 236 mm TL; BMNH 1965.8.11.4, juvenile male, 232 mm TL; BMNH 1965.8.11.5, juvenile female, 224 mm TL; same locality as holotype.

FIGURE 12. *Cephaloscyllium fasciatum* holotype (BMNH 1965.8.11.1), dorsal view. Photo by D.A. Ebert.

Diagnosis. Body comparatively slender, head short, snout moderately flattened, short, broadly rounded in dorsoventral view. Anterior nasal flaps not overlapping mouth posteriorly, narrowly lobate, inner margin with a deep notch. Color pattern of a light grayish-brown ground color with dark brown lines formed into loops, open saddles, reticulations and circles, also some small dark spots on back and sides in adult only. Fins without conspicuous light margins. A dwarf species.

Description. Proportional dimensions in percentage of total length are shown in Table 2. Snout moderately flattened, short, broadly rounded, preorbital length 5.5 (5.7)% of TL. Pre-pectoral length 17.1 (20.1)% TL. Eye small slit, cat-like, horizontal eye length 3.6 (4.9)% TL. Spiracle small; gill openings very small, vertical length of first gill opening 2.1 (1.8)% TL. Mouth small, mouth width 11.8 (10.5)% TL. Anterior nasal flaps not overlapping mouth posteriorly. Internarial distance 22.9 (30.5)% mouth width. First dorsal fin origin behind half of pelvic fin base, length from snout tip to first dorsal origin 53.2 (45.8)% TL; snout tip to second dorsal fin origin 67.6 (60.1)% TL. First and second dorsal fins small, height of first dorsal fin 66.2 (66.6)% length of base; height of second dorsal fin 44.0 (42.8)% length of base. Second dorsal fin much smaller than first, height of second dorsal fin 44.9 (45.7)% first dorsal fin. Pectoral fins relatively large and broad, greatest length 12.0 (12.1)% of TL, length of base 63.3 (63.6)% greatest length. Pelvic fin small, length of base 7.5 (7.3)% TL,

inner margin length 40.0 (42.5)% length of base. Anal fin slightly larger than second dorsal fin, height 37.0 (47.1)% length of base. Height of second dorsal fin 81.5 (65.6)% anal fin height. Caudal fin broad, asymmetrical, with subterminal notch, length of dorsal lobe of caudal fin 23.4 (22.5)% TL, length of ventral lobe 9.8 (10.5)% TL.

Body firm and thick-skinned, with well calcified dermal denticles. Dermal denticles with a broad disc connected at a slant to a four-pointed base. Teeth very small, similar in both jaws, three cusps in adult males, with numerous distinct ridges running from base toward cusp. Holotype with 58 teeth on upper jaw, 56 on lower jaw. Vertebral counts for 421 mm holotype (BMNH 1968.8.11.1): total vertebrae 120, monospondylous 45, diplospondylous 75, caudal 43, and precaudal 77. Vertebral counts for 224 mm paratype (BMNH 1968.8.11.5): total vertebrae 118, monospondylous 45, diplospondylous 73, caudal 40, and precaudal 78.

TABLE 2. Morphometric and meristic data for the holotype (HT) specimen for *Cephaloscyllium umbratile* (SU 12693), including mean and range for the *C. umbratile* specimens available, and *Cephaloscyllium fasciatum* (BMNH 1968.8.11.1), plus the paratype (PT) specimen for *C. fasciatum* (BMNH 1968.8.11.5), and one available specimen (SU 34041). TL is the actual measurement in millimeters; all other measurements are expressed as percentage of TL. Abbreviations as in Table 1.

	<i>C. umbratile</i>	<i>C. umbratile</i>			<i>C. fasciatum</i>	<i>C. fasciatum</i>	<i>C. fasciatum</i>
	HT	Comparative Material			HT	PT	Comparative Material
	SU 12693	(n=18)			BMNH 1968.8.11.1	BMNH 1968.8.11.5	SU 34041
		Mean	Min	Max			
TL	975	360	178	1015	421	224	111
PCL	81.6	76.3	72.0	80.8	78.4	74.1	73.9
PD2	69.9	63.1	59.3	70.0	67.6	60.1	61.8
PD1	56.4	49.0	45.3	56.1	53.2	45.8	49.2
IDS	7.1	7.9	6.6	11.2	7.1	8.0	5.4
DCS	6.8	7.4	6.2	8.5	6.5	9.7	7.9
PP2	50.9	43.5	40.7	48.7	44.6	44.1	45.0
PP1	20.4	19.2	16.9	22.1	17.1	20.1	18.9
SVL	51.3	47.4	44.8	53.4	48.9	43.4	46.0
PPS	21.3	17.7	14.2	20.1	20.7	18.2	19.8
PAS	12.3	9.2	6.9	12.5	8.5	9.2	8.1
PCA	24.8	22.1	19.2	25.3	19.4	19.5	20.2
ACS	7.0	6.2	5.5	6.7	5.3	5.8	7.0
INO	8.7	8.1	7.4	8.8	8.0	8.4	8.8

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Table 2. (continued)

	HT	Comparative Material		HT	PT	CM
HDH	15.4	8.0	6.2	9.8	8.5	10.4
HDW	17.4	13.7	11.1	22.7	12.6	15.0
TRH	12.3	9.8	6.3	13.9	7.4	11.0
TRW	21.5	12.2	7.9	14.6	5.8	6.3
GIR	48.2	37.3	29.8	45.1	31.3	40.5
ABW	19.5	10.7	5.6	14.4	11.2	10.3
TAW	9.7	5.7	4.9	6.1	--	10.8
CPH	2.6	3.4	2.8	4.0	3.3	5.4
CPW	2.8	2.4	2.1	2.7	1.9	3.6
HDL	21.3	20.5	19.0	24.3	20.0	20.7
PG1	15.6	15.8	13.4	18.8	16.5	17.1
PSP	9.5	10.4	9.2	11.4	11.9	10.1
POB	6.1	6.1	5.2	6.8	5.7	5.9
EYL	2.8	3.6	2.9	4.2	4.9	4.5
SPL	0.4	0.6	0.5	0.9	0.5	0.8
ESL	0.7	0.9	0.4	2.1	0.6	1.4
ING	5.8	5.1	4.6	6.0	4.9	5.4
GS1	2.1	2.1	1.6	2.9	1.8	1.8
GS2	2.0	2.0	1.5	2.9	1.5	2.2
GS3	2.0	1.9	1.2	3.0	1.4	1.8
GS4	1.7	1.7	1.1	2.3	1.1	1.5
GS5	1.4	1.4	1.0	1.7	0.8	1.4
POR	4.1	4.4	3.1	6.2	4.6	4.5
PRN	3.5	3.0	1.6	5.1	2.9	3.6
MOL	4.6	5.4	4.6	7.1	6.2	7.0

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Table 2. (continued)

	HT	Comparative Material		HT	PT	CM
MOW	8.6	10.0	7.7	13.3	10.5	10.5
NOW	2.1	2.8	2.2	4.1	2.9	2.8
INW	3.0	2.7	2.4	3.2	3.2	4.5
ANF	0.7	1.1	0.8	1.5	1.6	0.9
P1L	10.8	12.1	10.9	13.9	12.1	12.2
P1A	12.3	12.0	10.9	13.7	12.9	11.7
P1B	7.9	8.1	7.1	10.1	7.7	7.2
P1H	10.5	8.8	6.7	11.5	8.0	9.9
P1I	3.6	4.1	3.3	5.6	5.4	4.5
P1P	10.7	8.1	6.1	10.4	7.3	9.0
D1L	8.9	9.4	4.7	10.7	9.4	10.2
D1A	9.2	9.3	8.3	10.5	9.4	8.6
D1B	6.4	7.1	6.1	7.9	6.9	5.9
D1H	5.0	4.6	3.4	6.3	4.6	5.4
D1I	2.5	2.7	2.1	3.4	3.1	9.9
D1P	5.3	3.8	2.9	5.5	3.3	5.0
P2L	9.2	9.5	7.6	11.1	10.6	10.1
P2A	4.2	5.7	4.3	8.0	7.5	5.4
P2B	6.4	6.9	5.5	8.3	7.3	6.3
P2H	3.6	3.1	2.4	5.1	3.6	3.5
P2I	3.1	2.7	1.5	4.4	3.1	2.7
P2P	6.0	5.5	4.2	7.1	5.1	6.0
CLO	7.3	-0.1	-1.6	1.6	--	--
CLI	10.2	4.2	3.7	5.0	--	--
CLB	1.1	0.9	0.7	1.7	--	--

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Table 2. (continued)

	HT	Comparative Material		HT	PT	CM
D2L	6.7	7.2	6.5	7.8	7.5	8.8
D2A	5.2	5.5	4.6	6.2	5.9	6.3
D2B	4.5	4.9	4.1	5.6	4.9	4.3
D2H	1.9	2.2	1.8	2.9	2.1	3.7
D2I	2.5	2.3	1.7	3.2	3.6	3.8
D2P	2.9	2.5	1.8	3.3	2.5	4.1
ANL	7.8	9.4	8.5	10.2	10.3	11.4
ANA	6.7	7.0	6.0	8.5	8.2	6.8
ANB	5.6	7.3	6.3	8.6	6.8	6.3
ANH	4.5	3.0	2.2	4.0	3.2	3.7
ANI	1.9	2.2	1.6	3.2	2.7	4.1
ANP	3.9	3.9	3.2	5.5	2.7	5.6
CDM	16.7	23.6	21.5	26.6	22.5	damaged
CPV	6.6	10.0	8.5	11.3	10.5	damaged
CST	3.2	4.4	3.3	6.3	4.8	damaged
CTR	5.7	4.9	4.1	5.9	4.8	damaged
CTL	5.8	6.2	4.9	6.7	6.0	damaged
PDO	16.0	13.5	11.7	15.0	13.4	1.8
DAO	1.2	1.0	-1.7	3.3	-1.9	-2.7
DAI	0.5	0.1	-1.3	1.1	0.0	-2.3
U tot	59	--	--	--	56	--
L tot	62	--	--	--	54	--
VERT	--	--	--	--	118	--
mono	--	--	--	--	45	--
precaud	--	--	--	--	78	--
predip	--	--	--	--	33	--
caudaldip	--	--	--	--	40	--

Size and Sexual Maturity. Size at maturity for males 360 mm, and less than 421 mm for females. Maximum size at least 421 mm.

Coloration. Color pattern of a light grayish-brown ground color with dark brown lines formed into loops, open saddles, reticulations and circles, with a few small dark spots on back and sides (juveniles lack spots), underside of head and abdomen lightly spotted, no white or light spots on the body in adults. Number of predorsal saddles 4–5.

Comparison with Other Species. *Cephaloscyllium fasciatum* has a very distinct color pattern that easily distinguish it from other swell sharks, despite the multitude of new species recently described for this genus. We recognize that *C. fasciatum* may or may not have a lateral blotch, but never is the blotch large, dark and solid like that of *C. circulopullum* or *C. sarawakensis*. The small size of *C. fasciatum*, along with the color pattern and lobate anterior nasal flap, can also help to distinguish it from other *Cephaloscyllium*.

Remarks. This re-description of *C. fasciatum* is based on the holotype specimen and one paratype specimen that were loaned from the BMNH. The original description failed to report all morphometric measurements defined in Compagno (2001) and erroneously reported a 188 mm TL female *C. sarawakensis* as *C. umbratile*.

Distribution. *Cephaloscyllium fasciatum* has been verified as occurring in the Western Pacific, specifically Vietnam, China (Hainan Island), Philippines (Luzon) and northwestern Australia (Compagno *et al.* 2005).

Etymology. The species was named after the Latin *fasciata* for banded, referring to the variegated color pattern of open saddles and circles with connecting dark lines.

Common Name. Reticulated swell shark

Study Material. 6 specimens—Type material: Holotype, BMNH 1968.8.11.1, female, 421 mm TL, Cape Bantagan, Vietnam. Paratypes, BMNH 1968.8.11.2, male, 246 mm TL, Cape Bantagan, Vietnam; BMNH 1968.8.11.3, male, 236 mm TL, Cape Bantagan, Vietnam; BMNH 1968.8.11.4, male, 232 mm TL, Cape Bantagan, Vietnam; BMNH 1968.8.11.5, female, 224 mm TL, Cape Bantagan, Vietnam. Comparative material: SU 34041, female, 111 mm TL, Hainan, China Sea.

***Cephaloscyllium umbratile* Jordan and Fowler, 1903**
(Fig. 13, 3d, 7d, 11c; Table 2)

Scyllium laticeps Nystrom, 1887: 49; Ishikawa and Matsuura 1897: 62

Cephaloscyllium umbratile Jordan and Fowler, 1903: 602, fig. 1; Garman 1913: 80; Fowler 1914: 32; Chen 1963: 29, fig. 9; Lindberg and Legeza 1959: 44, fig. 24; Chan, 1966: 229, figs. 4, 5, 7b, 7d, pl. II; Besednov 1969: 27, figs. 9, 10; Michael 1993: 53; Compagno *et al.* 2005: 218, pl. 36.

Scyliorhinus umbratilis Regan, 1908: 459.

Cephaloscyllium formosanum Teng, 1962: 48, fig. 11.

Cephaloscyllium isabellum (in part as western North Pacific “*umbratile*”): Compagno 1984: 298.

Type Series and Locality. Holotype, SU 12693, mature male, 975 mm TL, collected from Nagasaki, Japan, 32°43'N, 129°50'E, collected by M. Yahiro, stuffed skin.

FIGURE 13. *Cephaloscyllium umbratile* holotype (SU 12693). Photo courtesy of the California Academy of Sciences.

Diagnosis. A large-sized species of *Cephaloscyllium*; snout broad and relatively long; mouth broad and strongly arched. First dorsal fin origin behind

half of pelvic fin base; base of first dorsal fin usually less than interdorsal space, especially in larger specimens; anal-caudal space and dorsal-caudal space relatively long, hence caudal peduncle long; color in life is light crème to beige background with brown, dark grey, and/or tan spots ventrally, laterally, and on fins, seven broad tan dorsal saddle bands, three of which are on the head, apparent in juveniles but somewhat mottled to the point of obscurity in adults.

Description. Proportional dimensions in percentage of total length are shown in Table 2. Body fusiform, relatively stout; head long 21.3% TL, depressed, height 0.89 times width. Snout relatively long, preorbital length 28.5% HL and 69.8% interorbital width; snout narrowly rounded in lateral view, width broad, 42.9% HL, horizontal length 1.46 in length of eye.

Eye small slit, cat-like shape, nearer tip of snout than first gill opening; horizontal length 7.61 in head, 2.0 times height. Spiracle very small, circular, close behind eye; maximum diameter 7.0 in eye length. Gill openings large, subequal in size; becoming progressively smaller posteriorly; height of first gill slit 10.0% HL. Mouth broad, strongly arched; half as long as wide, width 1.18 in preoral length; labial furrows absent. Nasals very large, nearer tip of snout than eye, not confluent with mouth; anterior nasal flaps not extending to the mouth; not bell-shaped, only slightly oblique; nostril width about equal to internarial distance.

First dorsal fin large, placed far back on the body, slightly rounded, posterior margin slightly convex, length 8.9% TL; fin origin just posterior to pelvic insertion, insertion of fin well forward of anal fin origin; much larger than second dorsal fin. Length of first dorsal fin 0.75 in second dorsal fin; height of first dorsal fin 0.38 in second dorsal fin. Second dorsal fin relatively small, nearer first dorsal than base of caudal lobe; upright, lobate or convex posterior margin, short free rear tip, fin origin just behind origin of anal fin; interdorsal space 0.96 in length from snout tip to pectoral-fin origin, caudal peduncle relatively long 6.8% TL. Pectorals large, as broad as long, angles rounded. Length of anterior margin 57.7% HL, length of pectoral fin base 64.2% length of anterior margin. Pelvic fin small, overall length 11.3% PCL, length of base 68.9% overall length. Anal fin nearly as large as first dorsal, much larger than second dorsal, overall length 9.6% PCL. Height of second dorsal fin 43.7% anal fin height. Caudal fin large, asymmetrical, broad, longer than head, with subterminal notch; lower lobe much larger in area than upper lobe. Length of ventral lobe of caudal fin 39.3% dorsal lobe.

Body thick-skinned, with well-calcified dermal denticles. Teeth similar in upper and lower jaws; small and numerous, multicuspid in 2–3 series, each with a long median cusp flanked by one lateral cusplet, less than one half the length of median cusp, cusps conical at the apex, striate near the bases. Upper jaw tooth count, 59; lower jaw tooth count, 62. Vertebral counts based on the 250mm

specimen reported in Chan (1966) are as follows: total vertebral number 109, caudal 37, and precaudal 72.

Size and Sexual Maturity. Males mature at about 947–948 mm total length and females 948–1011 mm total length; maximum length at least 1200 mm for males and 1100 mm for females.

Coloration. In life lightly pigmented background color, from crème to light-beige, pale below; dark-grey, tan, and deep brown mottling dorsally and laterally, and on fins. The dorsum and lateral surfaces have no obvious boundaries, the ventral surface with little to no markings. Seven dorsal bands are apparent in younger specimens but seem to fade in adulthood. The first behind eye, second over base of pectoral, next between it and first dorsal where another is, and finally last at second dorsal; on caudal, two broad cross bars, one at base of caudal, the other near its tip. Spotting and mottling is simple in juveniles but intense in adults, possibly obscuring the dorsal saddles.

Comparison with Other Species. *Cephaloscyllium umbratile*, formerly synonymized with *C. isabellum*, is upheld as a valid species based on the combination of key characters. *Cephaloscyllium umbratile* is not a dwarf species of swell shark; hence, differences in size at maturity and maximum size allow it to be distinguished from *C. circulopullum*, *C. fasciatum*, and *C. sarawakensis*.

The color pattern of *C. umbratile* can be used to for field identification; it has seven distinct dorsal bands that are usually deep-brown in life, three of

which are pre-first dorsal fin. However, taxonomy should not be based on these bands alone, as they become obscure in adulthood. We disagree with Yano et al. (2005) concerning the dark lateral blotch in this species. Although adult *C. umbratile* may appear to have a dark lateral blotch between the paired fins, there is no such blotch in younger, smaller specimens. Mottling intensifies as the animal reaches adulthood, but without the dark lateral blotch in young *C. umbratile*, it can be easily distinguished from *C. circulopullum* and *C. sarawakensis*.

A few characters can be used to separate this swell shark from other large-sized species, specifically *C. isabellum*. The first dorsal fin base of *C. umbratile* is relatively short (Fig. 14) in proportion to total length. The length of the first dorsal base of *C. umbratile* remains at a constant proportion to total length compared to *C. isabellum*. *Cephaloscyllium isabellum* has a dorsal fin base that increase slightly with increased total length.

FIGURE 14. First dorsal fin base as a proportion of total length vs. total length for selected *Cephaloscyllium* species.

The anal-caudal fin space of the caudal peduncle tends to be greater in *C. umbratile* than in *C. isabellum* (Fig. 15). In these two specimens, the measurement of the anal-caudal fin space is 5.5–7.0% TL, and 4.3–5.4% TL respectively. The caudal peduncle increases with total length in *C. umbratile*, whereas in *C. isabellum*, it stays proportional to total length.

FIGURE 15. Anal-Caudal fin space as a proportion of total length vs. total length for selected *Cephaloscyllium* species.

The dorsal-caudal fin space of the caudal peduncle is generally greater in *C. umbratile* than in *C. isabellum*; the length ranges from 6.2–8.5% TL (Fig 16). By comparison, the same measurement of *C. isabellum* ranges from 4.3–5.8%.

FIGURE 16. Dorsal-Caudal fin space as a proportion of total length vs. total length for selected *Cephaloscyllium* species.

Remarks. The Japanese Swell shark was originally described from a 975 mm specimen; a stuffed skin that apparently went missing prior to 1979. Springer (1979) synonymized *C. umbratile* with *C. isabellum*, based on the lack of strong morphometric differences. However, in his report he measured only 12 specimens and it is unclear how many were *C. umbratile* and how many were *C. isabellum*. Springer did not view the *C. umbratile* holotype specimen, the only type material catalogued for this species, because it was lost. Springer published morphometric values for three *C. isabellum* specimens, two of which were re-measured for this report; but no data on the *C. umbratile* specimens. Consequently, it is unknown what he meant by “inconclusive morphometric

differences” (Springer 1979). This re-description of *C. umbratile* is based on the holotype specimen that was subsequently found.

Compagno (1984) reported that *C. umbratile* is a synonym of *C. isabellum*, but he suggested three types of this species: a true *C. isabellum* type [= *C. isabellum*], a true *C. umbratile* type [= *C. umbratile*], and a pseudo-*umbratile* type. It has been established that the species Compagno refers to as pseudo-*umbratile* from Hong Kong is actually *C. sarawakensis* (L.J.V. Compagno, pers. comm.)

Distribution. *Cephaloscyllium umbratile* has been verified as occurring in the WNP, specifically Taiwan, Japan, and the China Sea.

Etymology. The species was named after the Latin *umbra* for shaded.

Common Name. Japanese swell shark

Study Material. 19 specimens—Type material: Holotype, SU 12693, male, 975 mm TL, Nagasaki, Japan. Comparative material: CAS 214726, female, 450 mm TL, Tahsi, Taiwan; CAS 224879, female, 266 mm TL, Tahsi, Taiwan; DAE TAI-006, male, 274 mm TL, Tahsi, Taiwan; DAE TAI-173, female, 269 mm TL, Tahsi, Taiwan; DAE TAI-205, female, 178 mm TL, Tahsi, Taiwan; CAS 224881, male, 244 mm TL, Tahsi, Taiwan; DAE 880804-05, female, 262 mm TL, Tahsi, Taiwan; CAS 224880, male, 193 mm TL, Tahsi, Taiwan; DAE 880804-08, male, 235 mm TL, Tahsi, Taiwan; DAE 881104-01, female, 476 mm TL, Tahsi, Taiwan; DAE 881905, male, 521 mm TL, Tahsi, Taiwan, all collected by David A. Ebert, April–May 1988 and May 2005; BSKU 34133, male, 389 mm TL, Okinawa Trough,

Japan; BSKU 34134, male, 371 mm TL, Okinawa Trough, Japan; BSKU 34135, male, 290 mm TL, Okinawa Trough, Japan; BSKU 34136, female, 307 mm TL, Okinawa Trough, Japan; BSKU 34336, male, 365 mm TL, Okinawa Trough, Japan; BSKU uncatalogued CAS 224878, male, 372 mm TL, Tosa Bay, Kochi City, Japan; MCZ 1044, male, 1015 mm TL, Kujiukuri, Japan.

***Cephaloscyllium sarawakensis* Yano, Ahmad, Gambang, Hamid, Razak, and Zainal, 2005**

(Fig. 17, 3e, 7e, 11a; Table 3)

Cephaloscyllium sarawakensis Yano *et al.*, 2005: 147, pl. 92-101.

Cephaloscyllium parvum Inoue and Nakaya, 2006: 77, figs. 1-3, 6a.

Cephaloscyllium umbratile (not Jordan & Fowler 1903): Teng 1962: 45, fig. 10 (Taiwan); Chen 1963: 29, fig 9 (Taiwan); Chan 1966: 229, figs. 5, 7b, 7d, pl. 2 (South China Sea); Bessednov 1969: 27, figs. 9, 10 (Gulf of Tonkin).

Cephaloscyllium sufflans (not Regan 1921): Fourmanoir and Nhu-Nhung 1965: 13, fig. 1 (Vietnam).

Cephaloscyllium formosanum (not Teng 1962): Shen 1984: 2, pl. 2 4-4a, 4-4b (Taiwan).

Cephaloscyllium isabellum (in part as *pseudo-umbratile*): Compagno 1984: 298 (China).

Cephaloscyllium sp.: Compagno 1988: 115 (China); Compagno *et al.* 2005: 222, pl. 36 (China).

Type Series and Locality. Holotype, MSR 201, mature female, 354 mm TL, collected from Tanjong Sirik, Sarawak, Malaysia, 04°48'N 109°56'E to 05°19'N 111°16'E, in 118 and 165 m of water, collected July 2–11, 1998.

FIGURE 17. *Cephaloscyllium sarawakensis* (CAS 224882), lateral view. Photo by D.A. Ebert.

Remarks. *Cephaloscyllium parvum* (Yano *et al.* 2005) is considered a junior synonym of *C. sarawakensis* based on morphometric similarities and geographic distribution. It is clear from the distinctive color pattern, including the dark lateral blotches between the paired fins, that *C. parvum* and *C. sarawakensis* are one and the same. Juveniles have the striking color pattern of numerous dark polka-dots which fade upon reaching adulthood (see fig. 17; Inoue and Nakaya, 2006, fig. 3a; Yano *et al.*, 2005, pl. 95; Chan, 1966, fig. 5). I concur with the color pattern change with growth represented in Inoue and Nakaya (2006, fig. 3). I have compared a juvenile female specimen collected by David A. Ebert from Tungkang, Taiwan (CAS 224882) and conclude that this specimen is *C. sarawakensis*. Table 3 gives morphometric and meristic data concerning type material collected by both describing authors, and the juvenile female specimen collected from Taiwan.

TABLE 3. Morphometric and meristic data for the holotype (HT) specimen for *Cephaloscyllium sarawakensis* (MSR201), including mean and range for the *C. umbratile* paratypes (PT) and a juvenile female specimen (CAS 224882), and *Cephaloscyllium parvum* (HUMZ 109126), plus the mean and range for the paratype (PT) specimens for *C. parvum*. TL is the actual measurement in millimeters; all other measurements are expressed as percentage of TL. Abbreviations as in Table 1.

	C. sarawakensis	C. sarawakensis			C. sarawakensis	C. parvum	C. parvum			
	HT	MSR201	PT			Comparative Material CAS 224822	HT HUMZ 109126	PT	(n=4)	
			Mean	Min	Max					Mean
TL	354		361	263	408	161	397	325	166	406
PCL	75.7		75.34	73.8	77.6	70.2	75.7	76.2	71.2	78.0
PD2	63.8		63.34	60.1	64.7	59.0	65.8	63.3	57.9	65.8
PD1	47.2		45.84	44.1	47.8	45.3	49.5	46.1	43.1	47.9
IDS	9.9		9.54	8.7	10.9	8.1	9.1	9.2	8.6	9.7
DCS	8.2		6.88	4.9	8.2	8.1	7.4	7.5	4.9	10.7
PAL	61.6		61.82	59.3	64.1	54.0	62.3	60.2	55.5	63.2
PP2	48.0		46.18	43.6	49.8	41.0	45.1	43.0	40.9	45.0
PP1	18.9		18.82	18.3	19.4	19.3	21.3	18.7	16.6	20.3
SVL	49.2		49.3	44.7	57.2	42.9	--	--	--	--
PPS	19.8		21.64	17.8	24.9	14.3	18.6	18.6	13.3	21.7
PAS	9.6		9.58	7.6	11.2	8.7	12.5	9.3	8.1	10.9
PCA	--		--	--	--	22.4	--	--	--	--
ACS	5.4		6.4	5.6	7.6	6.8	7.0	5.5	4.2	6.6

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Table 3. (continued)

	HT	PT	CM	HT	PT
INO	7.9	7.56	6.7	8.1	7.4
HDH	--	--	--	7.8	7.8
HDW	--	--	--	8.9	5.6
TRH	15.5	10.34	8.7	14.5	13.2
TRW	17.2	14.38	12.2	11.3	--
GIR	--	--	--	15.2	--
ABW	--	--	--	44.7	--
TAW	--	--	--	9.9	--
CPH	--	--	--	6.8	--
CPW	--	--	--	5.0	--
HDL	20.6	20.52	20.2	3.1	--
PG1	15.0	15.68	15.1	21.3	19.6
PSP	10.7	9.98	8.7	16.5	14.0
POB	5.6	6.16	5.5	10.4	8.3
EYL	4.8	4.3	4.2	6.0	5.6
SPL	--	--	--	3.5	3.1
ESL	--	--	--	--	--
ING	--	--	--	--	--
GS1	2.3	1.42	1.1	5.5	5.0
GS2	2.3	1.56	1.1	1.6	1.4
GS3	2.3	1.8	1.4	--	--
GS4	2.5	1.74	1.1	--	--
GS5	0.6	0.72	0.4	--	--
POR	4.8	4.98	4.8	1.1	1.1
PRN	3.4	3.36	2.7	5.7	4.7
				3.7	3.1
				3.3	3.7

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Table 3. (continued)

	HT	PT	CM	HT	PT
MOL	2.3	3.36	2.5	3.1	2.5
MOW	9.6	9.3	8.5	9.2	8.5
NOW	3.4	3.06	2.5	3.3	2.7
INW	--	--	--	2.1	2.0
ANF	--	--	--	1.1	0.8
P1L	--	--	--	--	--
P1A	13.8	12.02	10.6	--	--
P1B	9.0	8.12	6.9	7.8	8.5
P1H	--	--	--	8.6	7.1
P1I	4.5	4.72	3.9	4.3	3.2
P1P	9.6	8.78	7.6	8.5	8.0
D1L	11.9	10.12	8.7	--	--
D1A	--	--	--	--	--
D1B	9.3	7.96	7.5	7.3	7.1
D1H	5.1	5.02	4.6	4.5	4.6
D1I	--	--	--	--	2.2
D1P	5.1	4.66	3.9	--	--
P2L	11.9	10.98	9.1	--	--
P2A	4.8	5.12	4.5	--	--
P2B	7.1	7.6	4.9	6.8	6.6
P2H	--	--	--	--	--
P2I	4.5	3.22	2.5	4.7	3.1
P2P	--	--	--	--	--
CLO	--	7.6	7.6	6.8	1.3
CLI	--	9.2	9.2	11.5	4.2
					10.9

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Table 3. (continued)

	HT	PT	CM	HT	PT
D2L	7.6	7.68	9.6	--	--
D2A	--	--	7.5	--	--
D2B	4.8	4.96	6.2	5.0	4.7
D2H	2.5	2.94	3.1	2.6	2.4
D2I	--	--	3.1	2.5	2.0
D2P	4.2	3.38	4.3	--	--
ANL	9.6	9.42	12.4	--	--
ANA	--	--	9.9	--	--
ANB	6.8	6.22	8.7	7.4	7.2
ANH	3.4	3.64	3.7	3.5	3.2
ANI	--	--	3.1	2.5	2.2
ANP	5.1	4.8	4.3	--	--
CDM	22.0	24.56	26.7	22.5	22.4
CPV	11.9	10.98	11.2	--	--
CST	--	--	4.3	4.4	3.9
CTR	--	--	5.0	5.5	5.2
CTL	--	--	6.2	--	--
PDO	--	--	12.4	--	--
DAO	--	--	2.5	--	--
DAI	--	--	0.0	--	--
VERT	111	--	112	117	109
mono	36	--	42	39	37
precaud	68	--	72	71	68
predip	--	--	30	32	27
caudaldip	--	--	40	46	38

Study Material. *Cephaloscyllium parvum*, 5 specimens—Type material:

Holotype, HUMZ 109126, male, 397 mm TL, Sarawak, Malaysia. Paratypes, HUMZ 170770, male, 166 mm TL, Kaohsiung, southwestern Taiwan; HUMZ 109127, male, 349 mm TL, Sarawak, Malaysia; HUMZ 109125, female, 377 mm TL, Sarawak, Malaysia; HUMZ 109124, female, 406 mm TL, Kaohsiung, southwestern Taiwan. *Cephaloscyllium sarawakensis*, 10 specimens—Type Material: Holotype, IK 0002723, female, 354 mm TL, Tanjong Sirik, Sarawak. Paratypes, IK 0002724, female, 402 mm TL, Tanjong Sirik, Sarawak; NSMT-P 67617, female, 376 mm TL, Tanjong Sirik, Sarawak; MSR 202, female, 408 mm TL, Tanjong Sirik, Sarawak; MSR 204, male, 357 mm TL, Tanjong Sirik, Sarawak; MSR 212, female, 263 mm TL, Tanjong Sirik, Sarawak. Comparative material: MSR 131, male, 327 mm TL, Tanjong Sirik, Sarawak; MSR 189, male, 389 mm TL, Tanjong Sirik, Sarawak; MSR 133, female, 319 mm TL, Tanjong Sirik, Sarawak; CAS 224882, female, 161 mm TL, Tungkang, Taiwan.

Key to the *Cephaloscyllium* Species in the Western North Pacific

- 1a. Lateral blotch between the pectoral and pelvic fins in juveniles absent, intense mottling and white spots in adult color pattern, maximum size greater than 1000 mm TL.....*C. umbratile*
- 1b. Lateral blotch between the pectoral and pelvic fins in juveniles present, no mottling or white spots in adult color pattern, maximum size less than 500 mm TL.....2
- 2a. Lateral blotch dark and prominent throughout growth, dorsal saddles closed, first dorsal origin close to or in-line with pelvic fin origin.....3

- 2b. Lateral blotch, if present, open, dorsal saddles open, first dorsal origin posterior to first half of pelvic fin.....4
- 3a. Dark lateral blotch between pectoral and pelvic fins circular, juvenile coloration relatively plain.....*C. circulopullum*
- 3b. Dark lateral blotch between pectoral and pelvic fins elongate, juvenile coloration consists of polka-dots.....*C. sarawakensis*
- 4a. Anterior nasal flap not deeply notched and elongate/lobate, internarial space about 4% TL, Mouth length <8% TL.....*C. sp. nov. 2*
- 4b. Anterior nasal flap deeply notched and elongate/lobate, internarial space <4% TL, Mouth length >8% TL.....5
- 5a. Rosettes absent in coloration, eight dorsal saddles, four saddles are pre-first dorsal fin, saddles connected by solid dark reticulated lines, saddles not H-shaped, first dorsal fin height >5% PCL, posterior margin of anal fin <5% PCL, posterior margin of anal fin <5% PCL*C. fasciatum*
- 5b. Rosettes present in coloration, seven dorsal saddles, three saddles are pre-first dorsal fin, saddles not connected by dark reticulated lines, saddles H-shaped, first dorsal fin height <5% PCL, posterior margin of anal fin >5% PCL, posterior margin of anal fin >5% PCL.....*C. sp. nov. 1*

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Appendix 1. List of morphometric abbreviations used in tables, based on Compagno (1984, 2001) and Springer (1979).

TL, total length; PCL, precaudal length; PD2, pre-second dorsal fin length; PD1, pre-first dorsal fin length; IDS, interdorsal space; DCS, dorsal-caudal space; PAL, pre-anal length; PP2, pre-pelvic length; PP1, pre-pectoral length; SVL, snout-vent length; PPS, pectoral-pelvic space; PAS, pelvic-anal space; PCA, pelvic-caudal space; ACS, anal-caudal space; INO, interorbital width; HDH, head height; HDW, head width; TRH, trunk height; TRW, trunk width; GIR, girth; ABW, abdomen width; TAW, tail width; CPH, caudal peduncle height; CPW, caudal peduncle width; HDL, head length; PG1, pre-first gill slit length; PSP, pre-spiracular length; POB, pre-orbital length; EYL, eye length; ING, intergill length; GS1–GS5, gill slit height; POR, pre-oral length; PRN, pre-narial length; MOL, mouth length; MOW, mouth width; NOW, nostril width; INW, internarial width; ANF, anterior nasal flap length; P1L, pectoral fin length; P1A, pectoral fin anterior margin length; P1B, pectoral fin base length; P1H, pectoral fin height; P1I, pectoral fin inner margin length; P1P, pectoral fin posterior margin length; D1L, first dorsal fin length; D1A, first dorsal fin anterior margin length; D1B, first dorsal fin base length; D1H, first dorsal fin height; D1I, first dorsal fin inner margin length; D1P, first dorsal fin posterior margin length; P2L, pelvic fin length; P2A, pelvic fin anterior margin length; P2B, pelvic fin base length; P2H, pelvic fin height; P2I, pelvic fin inner margin length; P2P, pelvic fin posterior margin length; CLO, clasper outer length; CLI, clasper inner length; CLB, clasper base length; D2L, second dorsal fin length; D2A, second dorsal fin anterior margin length; D2B, second dorsal fin base length; D2H, second dorsal fin height; D2I, second dorsal fin inner margin length; D2P, second dorsal fin posterior margin length; ANL, anal fin length; ANA, anal fin anterior margin length; ANB, anal fin base length; ANH, anal fin height; ANI, anal fin inner margin length; ANP, anal fin posterior margin length; CDM, dorsal caudal margin length; CPV, pre-ventral caudal margin length; CST, subterminal caudal lobe length; CTR, terminal caudal fin height; CTL, terminal caudal fin lobe length; PDO, pelvic fin midpoint to second dorsal fin origin; DAO, second dorsal fin origin to anal fin origin length; DAI, second dorsal fin insertion to anal fin insertion length; VERT, total vertebral count; mono, monospondylous centra count; predip, precaudal diplospondylous centra count; caudaldip, caudal diplospondylous centra count; U tot, tooth count of upper jaw; L tot, tooth count of lower jaw.

Appendix 2. Additional Material Examined: *Cephaloscyllium circulopullum*,
Cephaloscyllium isabellum.

Cephaloscyllium circulopullum, 2 specimens—Type material: Holotype, IK 0002725, male, 377 mm TL, Tanjong Sirik, Sarawak, Malaysia. Paratype, IK 0002726, male, 378 mm TL, Tanjong Sirik, Sarawak, Malaysia.

Cephaloscyllium isabellum, 8 specimens—Comparative material: USNM 176779, male, 663 mm TL, Auckland, New Zealand; USNM 176795, male, 731 mm TL, Cook Strait, New Zealand; USNM 176801, female, 936 mm TL, Auckland, New Zealand; USNM 320594(1), male, 413 mm TL, South Island, New Zealand; USNM 320594(2), female, 363 mm TL, South Island, New Zealand; USNM 320594(3), female, 395 mm TL, South Island, New Zealand; MCZ 38617, female, 370 mm TL, New South Wales, Australia; MCZ 38621, male, 1050 mm TL, New South Wales, Australia.

CHAPTER 2:

A RE-DESCRIPTION OF THE EASTERN PACIFIC SWELL SHARK,
CEPHALOSCYLLIUM VENTRIOSUM (GARMAN 1880) (CHONDRICHTHYES,
CARCHARHINIFORMES, SCYLORHINIDAE), WITH COMMENTS ON THE
STATUS OF *C. UTER* (JORDAN & GILBERT 1896)

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Abstract

The genus *Cephaloscyllium* Gill 1862 (Chondrichthyes, Carcharhiniformes, Scyliorhinidae), arguably has one representative species in the eastern Pacific, *C. ventriosum* (Garman 1880). While the *C. ventriosum* holotype was collected from central Chile, a dubious species, *C. uter*, (Jordan and Gilbert 1896) was described from California. Garman (1913) classified *C. uter* as a junior synonym of *C. ventriosum*. This study marks the first morphometric and meristic analysis comparing the holotype of *C. ventriosum* from Chile with California *Cephaloscyllium* specimens and presents a revision of the genus for the eastern Pacific. Based on a comparison of morphometric and meristic data from specimens collected from Monterey, California; Santa Catalina Island, California; Santa Barbara, California; Guadalupe Island, Mexico; and Valparaiso, Chile, it is concluded that the California and Chilean *Cephaloscyllium* species represent a single, wide-ranging species, *C. ventriosum*.

Introduction

Members of the genus *Cephaloscyllium* Gill 1862, also known as swell sharks, can be separated from other genera in the family Scyliorhinidae by the lack of labial furrows, a second dorsal fin much smaller than the first, and the presence of supraorbital crests on the chondrocranium (Compagno 1988). They possess the unique ability to swallow either air or seawater, inflating their stomachs to deter predation. *Cephaloscyllium* species are occasionally observed by divers, but their cryptic coloration and nocturnal habits make them elusive (Nelson & Johnson 1970). Of the 13 currently recognized species of the genus, only one species is endemic to the eastern Pacific, *Cephaloscyllium ventriosum* (Garman 1880), which ranges from Monterey, California to southern Mexico, and also central Chile (Compagno *et al.* 2005).

Cephaloscyllium ventriosum has a rather complex taxonomic classification history. Originally, *Scyllium ventriosum* was described by Garman in 1880 from one Chilean specimen, which is housed at the Museum of Comparative Zoology at Harvard University. Jordan and Gilbert (1896) later described an eastern North Pacific swell shark, *Catulus uter*, from California. They stated at the end of their brief description that “it is probable that the Californian species is distinct from the Chilean *ventriosu[m]*” but did not explain how it differs from the Chilean form. To complicate matters, the authors did not designate any type specimens for *C. uter*. Garman (1913) synonymized *C. uter* with *Cephaloscyllium*

ventriosum, but recognized the Californian representatives of this genus are somewhat darker in coloration than the Chilean holotype.

Taxonomists, for unknown reasons, were slow in accepting the synonymy of *C. uter* with *C. ventriosum* as proposed by Garman (1913). This is surprising since Garman's influential work achieved universal recognition of the genus *Cephaloscyllium*. Several authors, including Starks (1917), Walford (1935), Roedel and Ripley (1950), among others, considered *C. uter* a valid species, but without explanation. Beebe and Tee-Van (1941) mentioned the Garman synonymy, but commented that the two species are probably distinct due to warmer waters in the south and a lack of southern specimens to verify the synonymy. Kato *et al.* (1967) considered *C. ventriosum* and *C. uter* to be the same species, but did not state why nor reference Garman's synonym. Likewise, Miller and Lea (1972) reported the name for the Californian swell shark as *C. ventriosum*, but with no further explanation. Both Springer (1979) and Eschmeyer *et al.* (1983) upheld the synonymy, as did Compagno (1984). Castro (1983) reported that the southern California coastal *Cephaloscyllium* species is *C. ventriosum*, but suggested an undescribed species inhabits the waters around offshore islands such as Santa Catalina and Guadalupe Island. His reasoning involved the egg case, particularly the tendril morphology, whereby the form occurring around offshore islands has short tendrils while the coastal swell shark egg cases possess long tendrils (Castro 1983). Compagno (1988) reported on the confusion between

C. ventriosum and *C. uter* in the literature, and continued to uphold *C. ventriosum* as the only valid eastern Pacific species, but without explanation or comparison of specimens from these two regions. Ebert (2003), following Kato *et al.* (1967) considered it a single species, but noted that some authors still recognize *C. uter* to be a valid species.

Taxonomic classification has proven difficult for this group because body proportions in individuals of the genus *Cephaloscyllium* in general change ontogenetically during growth (Springer 1979). *Cephaloscyllium* species appear similar, and are consequently distinguished by minor differences and sometimes by locality. Strong key characters are difficult to establish, and earlier keys generally separate species from one another by attributing juvenile characters to some and adult characters to others. Juvenile specimens have been known to be mistaken for completely different species, as in Chan (1966), in which a juvenile *C. sarawakensis* was mistaken for *C. umbratile* (see Chapter 1).

The genus *Cephaloscyllium* is an expanding genus of cat sharks, with 4 species having been described since 1966 and at least 7 new species currently recognized and under study (Last and Stevens 1994, Compagno *et al.* 2005, present study: Chapter 1). To date there has not been a formal comparative analysis between the Chilean holotype and California specimens. Given the rapid increase of new species descriptions within this genus and the poor original descriptions of *C. ventriosum* and *C. uter*, I undertook this study to

examine eastern Pacific *Cephaloscyllium*. Here, I present a detailed description of the holotype, and compare it with California specimens to determine the taxonomic status of both species.

Materials and Methods

Morphometric measurements follow Compagno (1984, 2001) and Springer (1979), and abbreviations are given in Appendix 1. Measurements were taken to the nearest 0.1 mm (except for total length, pre-caudal length, and girth which were measured to the nearest 1 mm) and are presented as a proportion of total length (TL) in Table 1. In the species description, the measurement presented for each character is from the holotype.

Except for the holotype, all the specimens of *C. ventriosum* used in this study were from the eastern North Pacific, including Monterey Bay, Santa Barbara, Santa Catalina Island, and Guadalupe Island. Vertebral counts of the holotype specimen (MCZ 496) were determined from x-radiographs. Tooth counts were taken for the upper and lower jaws directly from specimens. Digital photographs of specimens were processed with Adobe Photoshop 8.0. Table 1 was created with Microsoft Excel.

Institutional abbreviations are as follows: California Academy of Sciences (CAS); Museum of Comparative Zoology, Harvard University (MCZ); National

Museum of Natural History (NMNH); Scripps Institution of Oceanography (SIO); Stanford University (SU: now housed at CAS).

Systematics

Cephaloscyllium ventriosum (Garman, 1880)

(Figure 1, Table 1)

Scyllium ventriosum Garman, 1880: 167.

Catulus uter Jordan & Gilbert in Jordan & Evermann, 1896: 25, pl. 3, fig. 12; Starks 1917: 147, fig. 53.

Scylliorhinus ventriosus Regan, 1908: 458.

Cephaloscyllium ventriosum: Garman 1913: 80, pl. 9, figs. 6–9; White 1937: 117; Kato *et al.* 1967: 24, fig. 36; Nelson and Johnson 1970: 732; Grover 1972b: 191; Miller & Lea 1972: 36–37; Grover 1974: 359, figs. 1–3; Hubbs *et al.* 1979: 4; Springer 1979: 42, figs. 23–25; Castro 1983: 102; Eschmeyer *et al.* 1983: 32–33, pl. 1; Compagno 1984: 303; Compagno 1988: 113, fig. 13.9A; Ferguson & Cailliet 1990: 20–22, 24, 32, 56; Michael 1993: 53; Love 1996: 55; Ebert 2003: 131; Compagno *et al.* 2005: 219, pl. 36; Love *et al.* 2005: 6.

Cephaloscyllium uter: Walford 1935: 28, fig. 26; Jordan *et al.* 1930: 12; Beebe & Tee-Van 1941: 99; Roedel & Ripley 1950: 50, fig. 34; Ripley 1953: 17; Cox 1963: 283, fig. 11.

Type Species and Locality. Holotype, MCZ 496, mature female, 748 mm TL, collected off Valparaiso, Chile (33°5'S, 71°40'W).

Diagnosis. Body comparatively stocky, head short and depressed, greatest height at eyes. Snout moderately flattened, extremely short, broadly rounded in dorsoventral view. Anterior nasal flaps broadly lobate or bell-shaped, overlapping mouth posteriorly. Labial furrows absent. Teeth very small, similar in both jaws. Stomach inflatable, containing air or water. Supraorbital crests present on the chondrocranium. Claspers short and stout. Color pattern includes light spots on body and fins, underside of head and

abdomen spotted; fins without conspicuous light margins (Fig.1). A large species of swell shark.

FIGURE 1. *Cephaloscyllium ventriosum* holotype (MCZ 496), lateral view of head and trunk. Photo courtesy of the Museum of Comparative Zoology, Harvard University (©President and Fellows of Harvard College).

Description. Proportional dimensions in percentage of total length are shown in Table 1. A robust species, large-sized. Head length (HL) measured from snout tip to fifth gill opening 31.3% of PCL. Snout moderately flattened, short, broadly rounded, preorbital length 20.5% HL and 65.0% interorbital width. Pre-pectoral length 19.7% TL. Eye small slit, elongate-oval in shape, cat-like, with dorsal ridge, horizontal eye length 11.8% HL. Spiracle small, near the eye, diameter 26.6% of horizontal eye length. Five gill openings present, small, posterior two over pectoral fin, vertical length of first gill opening 7.9% HL. Mouth wide, greatly arched, labial furrows absent. Mouth width 48.8% HL. Anterior nasal flaps broadly lobate, bell-shaped or subtriangular, overlapping mouth posteriorly. Internarial distance 19.3% mouth width. First dorsal fin origin just posterior to pelvic fin origin, length from snout tip to first dorsal

origin 55.3% TL; snout tip to second dorsal fin origin 85.5% PCL. First and second dorsal fins small, height of first dorsal fin 60.4% overall length; height of second dorsal fin 43.2% overall length. Second dorsal fin smaller than first, height of second dorsal fin 52.5% first dorsal fin. Second dorsal fin smaller than anal fin and opposed to it. Origins of second dorsal fin and anal fin about opposite, or anal fin origin slightly anterior. Insertions of second dorsal fin anal fin in line. Pectoral fins relatively large and broad, anterior margin 20.9% HL, length of base 58.5% anterior margin. Pelvic fin small, overall length 14.1% PCL, base 72.8% overall length. Claspers large in adults, clasper groove unfused between hypopyle and apopyle. Anal fin smaller than first dorsal fin, height 5.4% and overall 11.2% PCL. Height of second dorsal fin 72.7% anal fin height, height of anal fin 72.1% first dorsal fin height. Caudal fin broad, asymmetrical, with subterminal notch, length of dorsal lobe of caudal fin 25.5% PCL, length of ventral lobe 44.4% dorsal lobe.

Body firm and thick-skinned, with well calcified dermal denticles. Dermal denticles on sides of body and over most surfaces erect and needle-shaped, with no lateral expansion of a blade in juveniles; with a stout blade in adults, triangular in shape with a single posterior point, blades nearly parallel to skin surface in ventral surfaces of adults, more erect in dorsal surfaces, ventral denticles smooth without ridges, dorsal denticles with one to several ridges. Newly hatched young possess two rows of enlarged, paddle-shaped denticles

with sharp blades along each side of the mid-dorsal line, from first gill slit to first dorsal fin origin, most likely to aid in emerging from the egg case, shed soon after hatching.

Teeth three to five cusped, in 3–4 series, similar in upper and lower jaws, sexual heterodonty absent. Tooth count: 54/54. Total vertebral number 109, monospondylous 42, precaudal 69, and pre-caudal diplospondylous 27.

TABLE 1. Morphometric and meristic data for the holotype (HT) specimen for *Cephaloscyllium ventriosum* (MCZ 496) and comparative material (n=18). TL is the actual measurement in millimeters; all other measurements are expressed as percentage of TL. Abbreviations are listed in the Appendix 1.

	<i>C. ventriosum</i>	<i>C. ventriosum</i>				<i>C. ventriosum</i>	<i>C. ventriosum</i>		
	HT	Comparative Material (n=18)				HT	Comparative Material (n=18)		
	MCZ 496	Mean	Min	Max		MCZ 496	Mean	Min	Max
TL	792	445	140	830	P1H	11.5	12.0	9.5	16.0
PCL	81.1	77.1	67.4	95.3	P1I	3.9	5.3	4.4	6.5
PD2	69.3	68.7	60.4	83.7	P1P	10.9	10.6	8.0	14.8
PD1	55.3	53.5	45.5	65.2	D1L	10.1	11.2	10.2	13.3
IDS	5.2	7.5	6.0	9.3	D1A	9.7	10.6	9.8	13.6
DCS	5.6	6.1	4.8	9.6	D1B	7.6	8.6	7.4	10.3
PP2	46.0	47.2	35.2	64.6	D1H	6.1	6.4	4.9	7.5
PP1	19.7	20.7	17.3	27.0	D1I	1.6	2.8	2.0	3.6
SVL	49.7	50.9	43.6	62.4	D1P	5.8	5.9	4.4	7.5
PPS	18.4	19.8	15.8	25.9	P2L	11.4	11.8	9.9	14.7
PAS	8.5	11.7	8.5	25.6	P2A	5.3	6.5	5.1	9.9
PCA	19.2	22.4	11.2	30.7	P2B	8.3	8.1	6.0	11.3
ACS	4.7	5.0	4.1	7.4	P2H	3.9	4.5	3.5	6.6
INO	8.0	9.3	8.1	11.8	P2I	2.9	4.0	3.0	6.3
HDH	9.1	9.4	5.7	11.8	P2P	8.3	7.9	5.4	11.0

...continued on the next page

Table 1. (continued)

	HT	CM	HT		CM	HT			
HDW	15.7	16.5	8.9	23.4	CLO	--	3.7	2.3	10.1
ABW	15.4	16.6	9.5	27.4	CLI	--	7.2	5.3	15.6
TRH	9.8	10.3	8.9	11.7	CLB	--	1.1	0.9	2.0
TRW	19.3	15.8	13.9	17.6	D2L	7.4	8.2	6.6	10.4
TAW	5.7	7.5	6.1	11.2	D2A	6.3	7.0	6.0	8.6
GIR	44.8	41.4	0.0	65.0	D2B	5.1	5.8	4.6	7.1
CPH	3.4	3.9	3.3	5.3	D2H	3.2	3.5	2.6	4.0
CPW	2.1	2.6	1.8	3.7	D2I	2.5	2.6	1.6	3.4
HDL	25.4	22.9	19.6	26.6	D2P	3.3	3.3	1.9	4.6
PG1	19.3	16.7	13.8	20.0	ANL	9.1	10.4	9.0	13.0
PSP	9.3	9.6	8.3	11.8	ANA	8.0	9.0	7.5	10.7
POB	5.2	5.5	4.2	7.1	ANB	6.9	8.0	6.6	10.2
EYL	3.0	3.6	2.6	4.6	ANH	4.4	4.5	3.4	5.6
SPL	0.8	0.8	0.5	1.1	ANI	2.3	2.5	2.1	3.3
ESL	1.4	0.9	0.6	1.3	ANP	4.0	4.2	3.0	5.2
ING	7.8	6.9	0.7	8.3	CDM	20.7	24.3	20.9	31.4
GS1	2.0	2.5	1.8	3.3	CFW	6.7	6.9	6.3	8.1
GS2	2.0	2.4	1.5	3.5	CPV	9.2	11.1	9.8	13.1
GS3	2.3	2.3	1.5	3.1	CST	3.0	4.4	2.9	6.1
GS4	1.8	2.0	1.4	3.2	CTR	5.1	5.2	3.7	6.6
GS5	1.4	1.8	1.2	2.9	CTL	5.4	3.3	0.0	6.2
POR	3.2	3.7	2.8	5.0	PDO	12.5	14.0	11.7	17.2
PRN	2.7	2.6	1.8	3.6	DAO	0.0	0.1	-1.9	1.8
MOL	6.6	4.7	3.4	5.8	DAI	1.0	0.6	0.4	0.8
MOW	12.4	12.3	10.6	15.9	U tot	54	55	54	56
NOW	2.0	2.9	2.2	4.4	L tot	54	54	54	54
INW	2.4	2.7	2.4	3.2	VERT	109	--	--	--
ANF	0.8	1.1	0.8	1.6	mono	42	--	--	--
P1L	13.1	14.5	11.9	19.9	Diplo	67	--	--	--
P1A	14.2	15.3	12.9	21.1	predip	27	--	--	--
P1B	8.3	8.9	7.5	11.4	caudal dip	40	--	--	--

Size and Sexual Maturity. Males mature at about 82–85 cm TL, with a maximum recorded size being over 110 cm TL; hatchlings emerge at 13–15 cm TL (Compagno *et al.* 2005).

Coloration. Color pattern of yellow-brown background, with variegated nearly round dark brown blotches, 10 brown dorsal saddles, numerous light spots on body and fins, underside of head and abdomen spotted; fins without conspicuous light margins. Color is somewhat lighter in fresh specimens. Hatchlings have a similar pattern, but are lighter in color. In larger, mature sharks dorsal saddles become obscure and mottling intensifies.

Biology. These sharks are usually found among rocks and kelp in shallow areas (20–40 m), but they have been taken from depths of 500 m as well as over sandy areas (Grover 1972b, Love 1996). Nocturnal and generally solitary, they feed at night by ambushing prey in the lie-and-wait fashion (Nelson & Johnson 1970).

Cephaloscyllium ventriosum are oviparous, producing two egg cases per clutch. Cox (1963) described the egg case as large, unridged (i.e. not laminated), rectangular with thick tendrils; from 90–125 mm in length and 28–55 mm in width. Anterior end with short, thick horns tapered to points extending as coiled tendrils, anterior horns bend acutely towards each other, often touching. Posterior end blunt, horns short, terminating into thick coiled filaments; thin margin between posterior horns deeply crescent-shaped. Anterior end slightly constricted, tapers gradually toward posterior end, neck of egg case constricted. Tendrils either long (80–200 cm) or short (2 cm). Freshly laid case transparent, light greenish-tan; holds a single egg seen through the case. Exposure to

seawater somewhat darkens the case but it remains translucent (Cox 1963). Eggs hatch in 7.5–10 months depending on water temperature (Ebert 2003) and are apparently preyed upon by carnivorous snails (Grover 1972a). Populations living near the mainland produce eggs with long tendrils, while those living around Santa Catalina Island have short tendrils (Grover 1972b, Castro 1983, Love 1996).

This species is of no interest to fisheries. It is occasionally caught by divers and sportfishers, and often found in lobster and crab traps, but probably not utilized (Compagno 1984, Ebert 2003). According to some reports, swell shark meat is mildly toxic (Roedel & Ripley 1950, Love 1996).

Comparison with *C. uter*. Important morphometric characters used to separate other species of *Cephaloscyllium* fail to separate *C. ventriosum* from *C. uter* (Table 1). The first dorsal fin base of *C. ventriosum* ranges from 7.4–10.3% TL in the 16 specimens examined. The Chilean holotype has a first dorsal fin base of 7.6% TL, which falls within this range. The first dorsal fin height of *C. ventriosum* ranges from 4.9–7.5% TL in the California specimens, and 6.1% TL in the Chilean holotype, again falling within the range. The length of the caudal peduncle, measured by the dorsal-caudal space and the anal-caudal space, also fails to separate the northern and southern forms (Table 1). Characters such as mouth width and internarial width do not uphold *C. uter* as valid either. The shape of

the anterior nasal flap is very similar for both eastern North and eastern South Pacific specimens (Fig. 2).

FIGURE 2. Ventral view of the head, including morphology of the anterior nasal flaps of *Cephaloscyllium ventriosum* (MCZ 1230) collected from Santa Barbara, California (left), and *C. ventriosum* holotype (MCZ 496) collected from central Chile (right). Photo by J.A. S.-Da Silva.

The color pattern of heavy mottling and 10 dorsal saddles is comparable for all of the eastern Pacific specimens studied. There is a somewhat darker coloration in the Chilean holotype, but this could be due to different preservation methods.

Both California and Chilean forms are of the large-size variety; the maximum size is about double that of a dwarf *Cephaloscyllium* species. Ebert (2003) reports *C. ventriosum* to have a total vertebral count of 109–112; the holotype has 109. Ebert (2003) reports *C. ventriosum* to have tooth counts of 55–

69/46–85; the holotype has 54/54. Springer (1979) reports the spiral valve count as 10–11, but the holotype specimen could not be dissected to confirm. No other key characters were identified that would distinguish *C. ventriosum* from *C. uter*.

Concerning many measurements, there was more variation among the different California specimens than between any California specimen and the Chilean holotype. For example, two specimens collected off Santa Barbara show great variation in the size and shape of the pectoral fin (Fig. 3), more so than if either is compared to the Chilean holotype. Given the lack of characters to distinguish California and Chilean *Cephaloscyllium*, I conclude that only a single valid species, *C. ventriosum*, occurs in the eastern Pacific. *Cephaloscyllium uter* is therefore designated a junior synonym of *C. ventriosum*.

FIGURE 3. Pectoral fins of *C. ventriosum* (MCZ 877, left), and *C. ventriosum* (MCZ 1230, right), both collected from Santa Barbara, California. Photo by J.A. S.-Da Silva.

Distribution. Eastern Pacific: Central California (Monterey Bay) to Gulf of California and southern Mexico; central Chile (Compagno *et al.* 2005), but more abundant south of Point Conception, California (Love 1996) (Fig. 4). Since other species such as *C. fasciatum* (Compagno *et al.* 2005) display an amphitropical geographic pattern (see chapter 3), it is likely that *C. ventriosum* does as well, as there are no records of this species occurring from Central America to northern Chile.

FIGURE 4. Map of *Cephaloscyllium ventriosum* distribution in the Pacific Ocean (1=Monterey, CA; 2=Santa Barbara, California; 3=Avalon Harbor, Santa Catalina Island, California; Guadalupe Island, Baja California, Mexico; 5=Valparaiso, Chile).

Etymology. From the Latin *ventriosus*, meaning swell, refers to the common name and the ability to inflate the stomach.

Common Name. Swell shark.

Study Material. 19 specimens—Holotype, MCZ 496, female, 792 mm, Valparaiso, Chile; SU 18493 (2), male and female, 389 and 544 mm TL, Santa Barbara, California; SU 19090, male, 409 mm TL, Avalon Harbor, Santa Catalina Island, California; SU 17778, male, 146 mm TL, Monterey, California; CAS 40675, male, 261 mm TL, Santa Barbara, California; MCZ 877, female, 819 mm TL, Santa Barbara, California; MCZ 1230, female, 830 mm TL, Santa Barbara, California; SIO 51-230, female, 423 mm TL, Santa Catalina Island, California; SIO 65-72, male, 694 mm TL, Guadalupe Island, Mexico; SIO 65-68, female, 788 mm TL, Guadalupe Island, Mexico; SIO 60-28 (3), 2 males and a female, 168 mm TL, 140 mm TL, and 495 mm TL, Guadalupe Island, Mexico; SIO 84-261 (3), 2 females and a male, 217 mm TL, 293 mm TL, and 279 mm TL, Santa Barbara, California; SIO 57-62 (2), male and female, 410 mm TL and 381 mm TL, Santa Catalina Island, California.

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Appendix 1. List of morphometric abbreviations used in tables, based on Compagno (1984, 2001) and Springer (1979).

TL, total length; PCL, precaudal length; PD2, pre-second dorsal fin length; PD1, pre-first dorsal fin length; IDS, interdorsal space; DCS, dorsal-caudal space; PAL, pre-anal length; PP2, pre-pelvic length; PP1, pre-pectoral length; SVL, snout-vent length; PPS, pectoral-pelvic space; PAS, pelvic-anal space; PCA, pelvic-caudal space; ACS, anal-caudal space; INO, interorbital width; HDH, head height; HDW, head width; TRH, trunk height; TRW, trunk width; GIR, girth; ABW, abdomen width; TAW, tail width; CPH, caudal peduncle height; CPW, caudal peduncle width; HDL, head length; PG1, pre-first gill slit length; PSP, pre-spiracular length; POB, pre-orbital length; EYL, eye length; ING, intergill length; GS1–GS5, gill slit height; POR, pre-oral length; PRN, pre-narial length; MOL, mouth length; MOW, mouth width; NOW, nostril width; INW, internarial width; ANF, anterior nasal flap length; P1L, pectoral fin length; P1A, pectoral fin anterior margin length; P1B, pectoral fin base length; P1H, pectoral fin height; P1I, pectoral fin inner margin length; P1P, pectoral fin posterior margin length; D1L, first dorsal fin length; D1A, first dorsal fin anterior margin length; D1B, first dorsal fin base length; D1H, first dorsal fin height; D1I, first dorsal fin inner margin length; D1P, first dorsal fin posterior margin length; P2L, pelvic fin length; P2A, pelvic fin anterior margin length; P2B, pelvic fin base length; P2H, pelvic fin height; P2I, pelvic fin inner margin length; P2P, pelvic fin posterior margin length; CLO, clasper outer length; CLI, clasper inner length; CLB, clasper base length; D2L, second dorsal fin length; D2A, second dorsal fin anterior margin length; D2B, second dorsal fin base length; D2H, second dorsal fin height; D2I, second dorsal fin inner margin length; D2P, second dorsal fin posterior margin length; ANL, anal fin length; ANA, anal fin anterior margin length; ANB, anal fin base length; ANH, anal fin height; ANI, anal fin inner margin length; ANP, anal fin posterior margin length; CDM, dorsal caudal margin length; CPV, pre-ventral caudal margin length; CST, subterminal caudal lobe length; CTR, terminal caudal fin height; CTL, terminal caudal fin lobe length; PDO, pelvic fin midpoint to second dorsal fin origin; DAO, second dorsal fin origin to anal fin origin length; DAI, second dorsal fin insertion to anal fin insertion length; VERT, total vertebral count; mono, monospondylous centra count; predip, precaudal diplospondylous centra count; caudaldip, caudal diplospondylous centra count; U tot, tooth count of upper jaw; L tot, tooth count of lower jaw.

CHAPTER 3:
THE ZOOGEOGRAPHY OF THE GENUS *CEPHALOSCYLLIUM*

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Abstract

Sharks of the genus *Cephaloscyllium* Gill 1862 have a highly ordered amphitropical geographic pattern in the Indian and Pacific Oceans. Members of the genus *Cephaloscyllium*, also known as swell sharks, display patterns of species diversity and endemism that are similar to other shallow marine benthic groups. In this chapter, I discuss the geographic ranges of the 16 valid species of swell shark, outline the history of their lineage, and propose a mechanism for radiation from a point of evolutionary origin in the Indo-West Pacific. Swell sharks exhibit a disjunct distribution that can be attributed to diffusion and quantum dispersal, whereas vicariant events are probably not responsible for their current distribution patterns. However, relictual and vicariant situations cannot be ruled out without conclusive fossil and/or genetic information, but at present time the dispersal hypothesis is the most parsimonious.

Introduction

Sharks of the genus *Cephaloscyllium* Gill 1862 are widely distributed in subtropical and warm-temperate waters, and range from inshore kelp beds to the uppermost continental slopes, to a depth of roughly 670 m. One aspect about their biology that is both remarkable and mysterious is their zoogeographic pattern. The members of this genus occur from 20–45° latitude north and south, a range termed amphitropical.

A map of the global geographic ranges of *Cephaloscyllium* (Fig 1) triggers many questions. In particular, what specific mechanisms have driven the biogeography of this genus to the patterns observed in nature today? Diffuse (i.e., slow, small-scale), as well as quantum (i.e. large-scale), dispersal events are probably the major mechanism influencing the disjunct distribution of these sharks. However, a relictual situation and/or vicariant events may have also played a role. Past marine zoogeographic studies, future genetic analysis, and present-day speculation will hopefully provide some insight to how and why these organisms are distributed in such an intriguing way.

Figure 1. Map of global *Cephaloscyllium* distribution by species.

The Players

For proper discussion, it is helpful to know the players involved; that is, the species and their respective ranges. Compagno *et al.* (2005) reported seven nominal species and six species yet to be described, for a total of 13 species. I recognize 12 of these plus four additional species, two recently described from Malaysia (Yano *et al.* 2005) and two new species from Taiwan (present study: Chapter 1).

The genus can be separated into two sub-groups based on size. The dwarf swell sharks seem to be prominent in the Indo-West Pacific (IWP) and parts of northern Australia, and include: *C. circulopullum* Yano *et al.* 2005, *C. fasciatum* Chan 1966, *C. silasi* (Talwar 1974), *C. sarawakensis* Yano *et al.* 2005, and probably *C. sp. nov. 1*, and *C. sp. nov. 2*. The large-sized group includes: *C. sufflans* (Regan 1921), *C. umbratile* Jordan and Fowler 1903, *C. isabellum* (Bonnaterre 1788), *C. laticeps* (Duméril 1853), and *C. ventriosum* (Garman 1880), among other undescribed species.

Swell sharks occur in four regions of the world: the Indian Ocean, the western North Pacific (WNP), the eastern Pacific, and Australia/New Zealand. *Cephaloscyllium isabellum* is a rather well-known species and occurs in New Zealand waters. *Cephaloscyllium laticeps*, and *C. sp. A–E* are found in proximity to the Australian continent. The southwestern coast of India is home to *C. silasi*, and *C. sufflans* is endemic to southwestern Africa. *Cephaloscyllium umbratile*, *C.*

fasciatum, *C. sp. nov. 1*, *C. sp. nov. 2*, *C. sarawakensis*, and *C. circulopullum* overlap in areas of the WNP, specifically Taiwan (Inoue & Nakaya 2006, Yano *et al.* 2005, present study: Chapter 1). The eastern Pacific swell shark is *C. ventriosum*; its large range extends from California to southern Mexico, and Chile (Compagno *et al.* 2005).

History of Lineages

To understand species distributions, it is important to know the history of lineages. When first tackling a biogeographic question, it is helpful to start with the history. Historical biogeography is the study of the development of lineages and biotas including their origin, dispersal, and extinction. According to fossil evidence, the first sharks appeared in the oceans 400 to 350 million years ago (Ferguson & Cailliet 1990). Most of the extant shark species evolved during the Jurassic period. The fossil record is unfortunately lacking for scyliorhinids; and what specimens are available are represented by dermal denticles and/or dentition (Springer 1979, Ferguson & Cailliet 1990). The earliest fossils tentatively assigned to the Scyliorhinidae (Glikman 1964; Springer 1979) appear in the Upper Jurassic, about 161-145 million years ago (mya). At this time in the Earth's history, the southern continent, Gondwana, started to break apart due to continental drift, and the Tethys Sea closed (Fig. 2). Global climate was warm

with no evidence of glaciation, a perfect setting for warm-temperate shark speciation.

FIGURE 2. Illustration of the Earth and placement of continents 150 million years ago.
Illustration by J.A. S.-Da Silva.

Morphometric and genetic studies give reason to believe that *Cephaloscyllium* is a plesiomorphic group within the cat shark family (Nakaya 1975). Recent studies using nuclear coding and mitochondrial ribosomal genes have clarified many of the taxonomic relationships within the scyliorhinids. Indeed, swell sharks are an ancient clade, and represent a basal branch of the Order Carcharhiniformes (Iglesias *et al.* 2005, Human *et al.* 2006). Martin (1990) presented data showing the extremely slow divergence time of shark DNA. So,

not only are swell sharks an old group, but they have changed relatively little compared to other shark groups in the last 100 million years.

Discussion

A Hypothesis for Swell Shark Distribution

Swellsharks probably evolved in the IWP/Northern Australian waters and radiated outwards via dispersal mechanisms. Around 175 mya New Guinea and the west coast of Australia were situated at 30° South (ITC 2000). This area of the world has been argued as a hot spot for evolution (Briggs 1999a, 1999b, 2000). The IWP, specifically the East Indies, has the highest species richness globally, and also a high number of endemics (Briggs 1992, McCosker *et al.* 2004). The largest numbers of swell shark species inhabit IWP waters, and this could be a clue to their evolutionary origin. Briggs (1992) argued that the center of origin represents a “hot spot” and can be recognized by the presence of younger, hence more specialized forms of a clade, surrounded by more generalized forms on the periphery. Thus, new species evolve at the center and radiate outwards in concentric circles. This paradigm was first put forth by Matthew in 1915 (Matthew 1915). Although members of the swell shark genus are very similar, there is a trend toward more intricate color patterns, anterior nasal flap shapes, and dwarf forms in the IWP—these forms are likely the most derived.

Another trend observed by Briggs (2000) is that the ages of genera seem to increase with an increase in latitude. It has been suggested that this pattern reflects a historical process of physiological adaptation to cooler latitudes by forms that were once tropical, but whether *Cephaloscyllium* members were originally tropical is unknown. Following this line of reasoning, Chinese and then Japanese swell sharks should be progressively older than the group of swell sharks at the center of origin. The old forms migrate away from the center of origin, and new forms are continually “pumped out.” Future genetic testing may help determine whether this pattern is observed in swell sharks.

The “outliers,” species that are widely separated from other conspecifics, can only be described by dispersal, extinction, and shifting of areas. The distributions of *C. sufflans* and *C. ventriosum* are probably not controlled by factors of vicariance. According to Reif and Saure (1987), sharks such as *Oxynotus* and *Pristiophorus*, which display an “outlier” distribution, are probably distributed that way because of dispersal events.

The biology and natural history of swell sharks can also give us clues to how their current distributions came to be. If the zoogeographic pattern seen in swell sharks is due to dispersal, would one expect them to be adept or poor dispersers? All members of the genus are relatively small sharks with lobed fins, broad tails, and posteriorly-placed dorsal fins, which indicates they are slow swimmers capable of limited swimming dispersal (Springer 1979, Compagno

1988). The anguilliform swimming pattern they display is considered to be plesiomorphic compared to other shark families (Weber 1990). The snout is short in *Cephaloscyllium*, indicating a primitive electroreception sense (Martin 1990). The exotic and cryptic color patterns suggest a relatively shallow-water habitat for a majority of the species in this genus. Individual sharks probably have a relatively small home range.

The well-known species of swell sharks appear able to reproduce year-round (Taniuchi 1988) and lay egg-cases that hatch after 7-10 months (Compagno *et al.* 2005). Adult migration is likely the key mode of dispersal, but long-range dispersal via egg case flotation may also be effective. If swell sharks depend kelp species to anchor their egg cases (Grover 1972), it makes sense that they display overlapping ranges with large brown kelps like *Macrocystis*, which also has an amphitropical distribution.

The zoogeographic pattern observed for swell sharks can be described as a “stepping-stone” model due to their limited dispersal capabilities. An ancient relative of *Cephaloscyllium laticeps* could have dispersed west to the tip of Africa and established a population. There have been reports of swell sharks inhabiting both the Gulf of Aden, and the Andaman Sea, but their systematic status is unknown at this time (Compagno *et al.* 2005). Biogeographic studies have shown that the generalized movement pattern of dispersal is from the IWP west to the eastern coast of Africa and ultimately the Atlantic (Soler-Gijon & Lopez-Martinez

1998). Such feats seem unrealistic for a small shark, but it is important to recall that in the past these areas were much closer geographically due to continental drift. *Cephaloscyllium silasi* is a dwarf form, and so probably evolved and dispersed relatively recently. The bracket of geologic time when swell shark dispersal occurred is highly debatable.

Similar to the Indian Ocean swell sharks, the WNP species probably crossed the equator from Australia. The dispersal to the WNP most likely occurred before the dispersal west to India because there are more species found in the WNP. The dominant, and arguably more generalized, species in this region is *C. umbratile*. The plethora of dwarf forms in the WNP probably evolved most recently, and have dispersed only a short ways away since. The dwarf species which have dispersed the farthest include *C. silasi* in India, and *C. fasciatum*, and *C. sp. D* in northern Australia. Crossing the equator may have been a difficult feat and perhaps happened via egg-case dispersal or tropical submergence.

It is unknown why *Cephaloscyllium* species do not occur in the tropics. Perhaps their original distribution included the tropics, but their range has shrunk at the equator due to biological interactions or climate change. Swell sharks are relatively hardy, and except for a few species with narrow ranges in heavily trawled areas, their populations have remained stable (Graham *et al.* 1997; Compagno *et al.* 2005). Predation does not seem to be a factor influencing

their distribution. The swell shark diet of small fish and cephalopods, which overlaps with the diets of other elasmobranchs, indicates resource competition may be a factor that influences their lack of occurrence in tropical regions.

The last step in dispersal was to the new world. *Cephaloscyllium ventriosum* is similar to both *C. isabellum* and *C. umbratile* in size and color pattern. It could have arrived first to California from Japan, in which case its closest relative would be the Japanese swell shark. Many marine organisms have made the jump from the western to eastern Pacific (Pequeno & Lamilla 2000, McCosker *et al.* 2004). Although not totally unidirectional, the trend is for dispersal to occur from east to west across the Eastern Pacific Barrier. Giant kelp made this move, and *C. ventriosum*, using kelp as a site for egg-case attachment, might have dispersed to the new world along with it. It is also possible that *C. ventriosum* arrived from Australia on the Antarctic Circumpolar Current and became established in Chile. Future genetic analysis is recommended to help put this debate to rest.

Sympatric Speciation

The last of the four inhabited regions to be discussed is Australia/New Zealand *Cephaloscyllium isabellum*, *C. laticeps*, and the many large-sized undescribed Australian species are probably very closely related. Most likely, the dwarf species are the derived forms. The sporadic data available show that

niche partitioning by depth and substrate type is observed for the Australian swell sharks (Compagno *et al.* 2005), but there is also some overlap of species' ranges near the peripheries. The best theory to explain this pattern is sympatric (i.e. competitive) speciation. Briggs (1999) reports that among the fishes, sibling patterns suggest that sympatric speciation is common. He also noted that new fish species may be dispersing from the IWP in a relatively frequent manner. *Cephaloscyllium* is plesiomorphic and slow to evolve and may have taken millions of years to diverge through sympatric speciation, a pattern commonly observed in fishes (Briggs 1990).

An Alternative Hypothesis

A "good" dispersal model often times has an equally "good" vicariance model. By looking at the location of continents around 175 mya, South America, Africa, and Antarctica were joined in the southern hemisphere. There is a small triangular-shaped sea at the junction of all four continents and it is tempting to hypothesize that swell sharks originated at this location. Not only would this hypothesis explain the eastern Pacific species, South African species, and Indian species due to vicariance, it is easy to imagine dispersal eastward as seaways eventually connected the IWP. According to this hypothesis, when swell sharks evolved in the IWP, they radiated into the many species observed there today.

This hypothesis should be rejected for a few valid reasons. The aforementioned seaway rested at about 60° S latitude, an environment too cold for swell sharks to inhabit. There are no swell sharks inhabiting the coast of Madagascar or the eastern coast of South America today; there was no imaginable barrier to harbor dispersal to these areas at that time, although extinction events may have occurred. We can also use the three “outlier” species to reject this hypothesis. If indeed these three isolated species represent “relict” distributions, why does *C. ventriosum* have the largest species range? If *C. ventriosum* is a relict, the two populations should have diverged by now. However, the northern and southern populations are the same species (Present study, Chapter 2), indicating a relatively recent arrival to the new world. Furthermore, if *C. ventriosum* speciated this early on in geographic time, why has it not speciated since, in over 150 million years? For these reasons, the vicariance hypothesis should be rejected.

Vicariance hypotheses have been rejected by a number of marine biogeography studies. Stepien *et al.* (1996) found that amphitropic pelagic species such as hake have distributions explained by dispersal rather than vicariant events. Reif and Saure (1987) concluded that although vicariance may have played a role in shark speciation, direct evidence has been “overprinted” by dispersal and other factors. Indeed, it is easy to misinterpret a relict distribution pattern as simply long-distance dispersal when there is a lack of fossil and

genetic evidence. Reif and Saure (1987) reported that a genus of shark, *Heterodontus*, with a disjunct distribution was only identified as relict because of strong fossil evidence. Australian skates were shown to have distributions explained primarily by dispersal (Last & Yearsley 2002). Perhaps the discovery of additional shark fossils, or further genetic analysis of the genus *Cephaloscyllium* will help nullify vicariance as a hypothesis for their disjunct distributions.

Conclusion

Extant sharks such as *Cephaloscyllium* have a highly ordered geographic pattern. Swell sharks display patterns of species diversity and endemism in the IWP that are similar to other shallow marine benthic groups. It is concluded that the genus of swell sharks exhibit a disjunct distribution that can be attributed to diffusion and quantum dispersal, and that vicariant events are unlikely responsible for the current distributions patterns. Relictual and vicariant situations cannot be ruled out without conclusive fossil and/or genetic information, however, at present time the dispersal hypothesis is the most parsimonious. The non-random distribution seen today supports the theory that these sharks are not opportunistic dispersalists; their small home ranges and integration into communities provide support for this hypothesis. They likely evolved in the IWP, and spread out in concentric circles to Africa, Australia, the Orient, and ultimately the Americas. The dwarf forms are likely the derived

forms, as they are concentrated at the center of origin. Future genetic testing, will hopefully clarify the interrelatedness of swell shark species.

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CONCLUSION

Swell sharks, genus *Cephaloscyllium*, are quite remarkable sharks mainly because of their ability to suck water or air into their stomachs, making them look like balloons. Unfortunately, much of the existing systematic literature is confusing and incomplete, and their zoogeographic pattern is rather baffling.

The systematics of this group has been especially problematic in the WNP, where there is a high degree of endemism and new species are frequently reported. The current revision of the genus for the WNP is long overdue and includes two re-descriptions, one synonymy, and a description of two new species from Taiwan. *Cephaloscyllium umbratile* is upheld as a valid member of the genus and can be distinguished from its congeners based on maximum size, length of first dorsal fin base, anal-caudal fin space, and dorsal-caudal fin space. *Cephaloscyllium parvum*, however, is not a valid species and is classified as a junior synonym of *C. sarawakensis*. The two new species can be separated from other WNP species by color pattern, shape of the anterior nasal flap, anal and dorsal fin size, internarial width, and mouth size.

Although there is only one species in the eastern Pacific, the taxonomy of *Cephaloscyllium* in this region has proven perplexing, mainly due to inconsistencies in the literature and a lack of comparative material south of Baja California, Mexico. This systematic study marks the first morphometric and

meristic analysis comparing the holotype of *C. ventriosum* from Chile with California *Cephaloscyllium* specimens. It is concluded that the California and Chilean *Cephaloscyllium* species represent a single, wide-ranging species based on a comparison of material collected from Monterey, California to Guadalupe Island, Mexico; and Valparaiso, Chile.

Cephaloscyllium have a highly ordered amphitropic geographic pattern. Based on current molecular, life history, and fossil data, it is concluded that swell sharks likely evolved in the IWP, and dispersed slowly to Africa, Australia, the Orient, and ultimately the Americas. In addition, the genus exhibits a disjunct distribution that can be attributed to dispersal events; vicariant events are probably not responsible for current distributions patterns.

Swell shark research has come a long way in recent years; however, more studies need to be done. Molecular phylogenetics and traditional systematics are examples of crucial areas in need of further research. Currently, there have been no molecular studies completed to explain the interrelatedness of this genus. Only recently have researchers become confident that the subfamily Scyliorhininae represents a monophyletic, basal group.

Large-scale traditional systematic studies must be continued as new species are being reported relatively frequently from isolated areas of the world. Currently, a revision of the *Cephaloscyllium* of Australia and New Zealand is being finalized, and there are at least two new species yet to be described from

Indonesia. Collection expeditions need to be conducted in geographic areas where swell shark data is lacking. Type material is difficult to obtain, sometimes even lost, and many key specimens are worn from age and improper handling. In addition, known species ranges require validation. Finally, museum collections need to be updated with correct scientific names, an arduous task especially for some of the frequently-changing names of *Cephaloscyllium* species. Hopefully, future investigations will incorporate the work presented here and focus on the aforementioned areas of research to broaden our knowledge of this group.