

A Review of the Genus *Oxynotus* (Squaliformes, Oxynotidae)

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Abstract A review of *Oxynotus* showed that the genus is represented by five species: *O. brunien-sis*, *O. caribbaeus*, *O. centrina*, *O. paradoxus*, and *O. japonicus*. The key to species of the genus is given and the geographical distributions of the five species are reported. Examinations of speci-mens of *Oxynotus* collected from the eastern Atlantic and Mediterranean revealed that a problem-atic species *O. shubnikovi* Myagkov, 1986, is concluded to be a junior synonym of *O. centrina* (Linnaeus, 1758).

Key words: Squaloid shark, *Oxynotus*, taxonomy, review.

Introduction

The shark family Oxynotidae is represented by a single genus *Oxynotus*, being distinguished from related families of Squaliformes by its two very large, high, sail-like spiny dorsal fins. The genus *Oxynotus* currently includes five species, *O. centrina* (Linnaeus, 1758), *O. paradoxus* Frade, 1929, and *O. caribbaeus* Cervigon, 1961 from the Atlantic Ocean, *O. brunien-sis* (Ogilby, 1893) from the South Pacific, and *O. japonicus* Yano & Murofushi, 1985 from Japan (Compagno, 1984; Yano & Murofushi, 1985). In addition, one questionable species, *O. shubnikovi* Myagkov, in Gubanov, Kondyurin, & Myagkov, 1986, has been described from Namibia (Compagno, 1999). Bass *et al.* (1976) stated that a species of *Oxynotus* recorded as “*O. centrina*” from Angola, Namibia, and South Africa might not be *O. centrina*, but rather an undescribed species that differs from *O. centrina* in having a much shorter interdorsal space. Myagkov in Gubanov *et al.* (1986) described *O. shubnikovi* as a new species from south-west of the Cunene River mouth, off northern Namibia. Compagno *et al.* (1991) stated that *O. shubnikovi* was provi-

sionally accepted as being distinct from the closely similar species *O. centrina* from the eastern North Atlantic and Mediterranean. However, these species need to be critically compared via the examination of adequate samples to deter-mine if they can be separated with confidence by the morphometric characters that were used by Myagkov in Gubanov *et al.* (1986). The purpose of this paper is to clarify the taxonomic status of *O. shubnikovi* with a brief review of the genus.

Methods

Measurements follow Yano & Murofushi (1985). Vertebral numbers were counted by soft X-ray following the method of Springer and Gar-rick (1964).

Institutional abbreviations are as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadel-phia; BMNH, Natural History Museum, London; FSFL, National Fisheries Research Institute of Far Seas Fisheries (formerly Far Seas Fisheries Laboratory), Shimizu, Japan; HVM, Heda Vil-lage Museum, Heda, Shizuoka, Japan; NSMT, National Science Museum, Tokyo; SAM, South

African Museum, Cape Town, South Africa; TAMBL, Toba Aquarium, Toba, Japan; TMFE, Department of Fisheries, Faculty of Marine Science and Technology, Tokai University, Shimizu, Japan.

Materials Examined

Oxynotus bruniensis. FSFL ED053, female, 711 mm TL (total length), 583 mm PCL (precaudal length, measured from snout tip to upper caudal origin), 34°58.2'S, 151°06.7' E, 381 m depth, bottom trawl, 31 Dec. 1975; FSFL B1797, male, 578 mm TL, 461 mm PCL, 43°05.0'S, 174°55.5'E, 380–470 m depth, bottom trawl, 13 July 1967; FSFL M219, female, 604 mm TL, 485 mm PCL, off New Zealand, bottom trawl, 22 Sept. 1974; TMFE 2795, male, 394 mm TL, 295 mm PCL, 44°39'S, 172°53'E, 476–515 m depth, bottom trawl, 8 Mar. 1983; NSMT-P 42784, male, 594 mm TL, 464 mm PCL, 43°53'S, 178°25'E, 226–237 m depth, bottom trawl, 25 Nov. 1983; NSMT-P 41162, female, 713 mm TL, 567 mm PCL, 49°47'S, 167°38'E, 254 m depth, bottom trawl, 9 Dec. 1984; NSMT-P 42785, 556 mm TL, 434 mm PCL, 43°53'S, 178°25'E, 226–237 m depth, bottom trawl, 25 Nov. 1983; NSMT-P 41163, 557 mm TL, 437 mm PCL, 43°53'S, 178°25'E, 226–237 m depth, bottom trawl, 25 Nov. 1983.

O. centrina. AMNH 55507, female, 541 mm TL, 424 mm PCL, 36°30'N, 4°33'W (Spain, Mediterranean), 80 m depth, 31 May 1984; ANSP 575, female, 210 mm TL, 152 mm PCL, Italy, Mediterranean; FSFL EG147, female, 545 mm TL, 438 mm PCL, 25°31'N, 15°47'W (Western Sahara), 180 m depth, bottom trawl, 7 Dec. 1974; FSFL M232, female, 440 mm TL, 349 mm PCL, 25°25'N, 15°58'W (Western Sahara), 212 m depth, bottom trawl, 8 Dec. 1974; FSFL ED325, male, 545 mm TL, 439 mm PCL, 10°54'N, 17°04'W (Guinea), 111 m depth, bottom trawl, 6 Jan. 1975; FSFL 247, male, 522 mm TL, 413 mm PCL, 4°42'N, 9°18'W (Liberia), 142 m depth, bottom trawl, 15 Jan. 1975; FSFL L247, male, 522 mm TL, 413 mm PCL, 9°30'S–6°40'S,

12°54'E–11°54'E (off Angola) 34–200 m depth, bottom trawl, 27 July–28 Aug. 1973; SAM 25051, female, 512 mm TL, 402 mm PCL, off Walvis Bay, Namibia, 24 May 1967.

O. japonicus. Holotype: NSMT-P 54576 (formerly HVM 00019), mature male, 540 mm TL, 435 mm PCL, off Heda in Suruga Bay, 225–270 m depth, bottom trawl, 28 Feb. 1982. Other specimens: HVM00036, female, 645 mm TL, 514 mm PCL, off Kunou-san in Suruga Bay, 350 m depth, bottom trawl, 30 Sep. 1984; HVM00044, female, 505 mm TL, 443 mm PCL, off Ukusu in Suruga Bay, 300 m depth, bottom trawl, 22 Jan. 1986; HVM00048, 645 mm TL, 516 mm PCL, female, off Heda in Suruga Bay, 300 m depth, bottom trawl, 3 Mar. 1987; HVM00049, female, 545 mm TL, 422 mm PCL, off Kunou-san in Suruga Bay, 150 m depth, bottom trawl, 25 Mar. 1987; HVM00051, female, 611 mm TL, 501 mm PCL, off Heda in Suruga Bay, 300 m depth, bottom trawl, 14 Apr. 1988; TAMBL (Toba Aquarium) 1559, female, 594 mm TL, 473 mm PCL, 10 miles from Omaezaki, Enshu-nada Sea, bottom trawl, 21 Dec. 1987.

O. paradoxus. FSFL N707, male, 555 mm TL, 436 mm PCL, 25°28.3'N, 16°04.5'W (Western Sahara), 532 m depth, bottom trawl, 7 Jan. 1972; BMNH 1931.4.14.1, female, 508 mm TL, 400 mm PCL, 70 miles WNW of the Jastnets, Ireland.

O. caribbaeus. We used data presented by Cervigon (1961) and Carpenter (1966) for two Caribbean Sea specimens.

Morphometric and Meristic Comparisons of the Species of *Oxynotus*

Morphometrics

The general appearances of *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus* and *O. paradoxus* are shown in Fig. 1. Proportional dimensions in percentage of total length of *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus* and *O. paradoxus* are given in Tables 1 and 2.

Length from tip of spine to apex of first dorsal

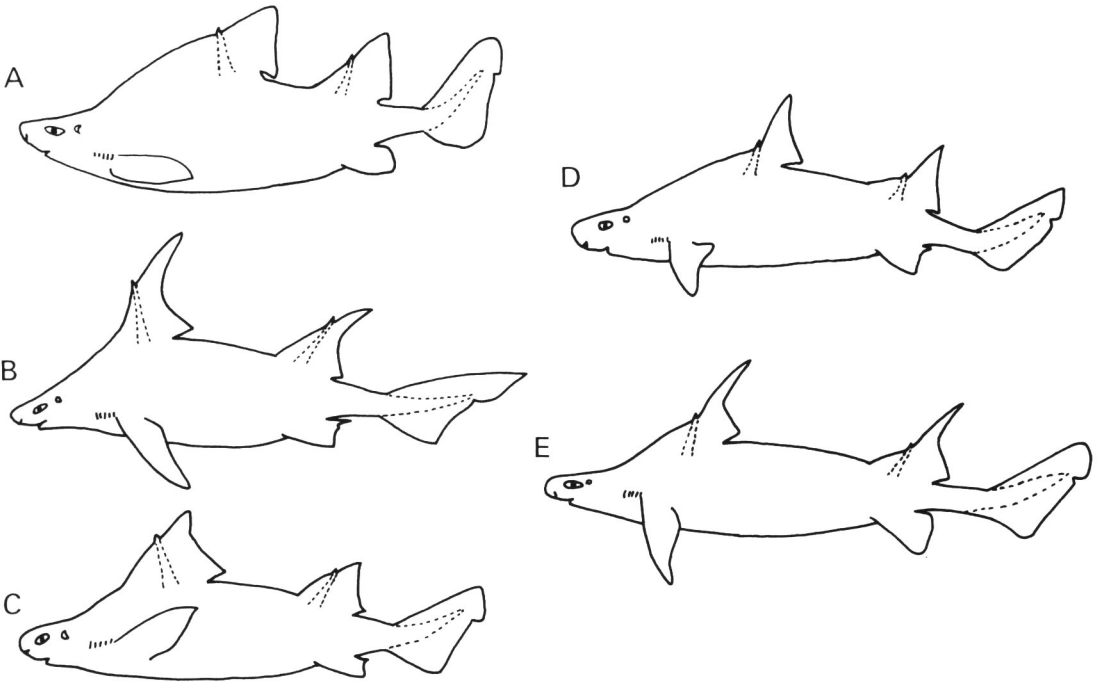


Fig. 1. Lateral views of *Oxynotus bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus*, and *O. paradoxus*. A: *O. bruniensis* (NSMT-P 42785, 556 mm TL, male); B: *O. caribbaeus* (figure from Cervigon, 1961); C: *O. centrina* (FSFL M232, 440 mm TL, female); D: *O. japonicus* (holotype, NSMT-P 54576, 540 mm TL, male); E: *O. paradoxus* (FSFL N707, 555 mm TL, male).

fin (LSA1) is greater than two times vertical height from tip of spine to fin base (VHB1) in *O. japonicus* and *O. paradoxus*, and LSA1 is less than 1.5 times the VHB1 in *O. bruniensis*, *O. caribbaeus*, and *O. centrina* (Fig. 2). Length from tip of spine to apex of second dorsal fin (LSA2) is greater than 1.5 times the vertical height from tip of spine to fin base (VHB2) in *O. japonicus* and *O. paradoxus*, and LSA2 is less than 1.5 times the VHB2 for the three other species (Fig. 3). Interdorsal space (IDS) of *O. bruniensis* is almost equal to or shorter than the length of second dorsal fin base (D2B), IDS of *O. japonicus* is 1.2–1.5 times of D2B, and IDS of *O. caribbaeus*, *O. centrina*, and *O. paradoxus* is longer than 1.5 times the D2B (Fig. 4).

In *O. centrina*, percentage of interdorsal space to PCL shows negative allometry (Fig. 5). A smaller individual (ANSP 575, 210 mm TL, female, poor condition) has a larger proportional interdorsal space than other larger individuals

(Fig. 5). The proportional interdorsal space of the larger individual from the eastern South Atlantic is almost the same as those of the Mediterranean and eastern North Atlantic specimens (Fig. 5). The proportional interdorsal space of the Walvis Bay (South Atlantic) specimen (550 mm TL) calculated from the illustration of Bass *et al.* (1976) (they suggested it was an undescribed species) is slightly shorter than the proportional interdorsal space of other specimens. However, the interspace between the first dorsal fin and second dorsal spines of the Walvis Bay specimen calculated from the illustration of Bass *et al.* (1976) is 30.1% of PCL and is almost the same as those of other specimens (440–545 mm TL) of *O. centrina* (\bar{x} = 32.3% of PCL, range, 29.1–34.6%) (Table 1).

Meristics

Dental formulae are (12–19)/5–1–5 ($n=5$) in *O. bruniensis*, (9–11)/4–1–4 ($n=5$) in *O.*

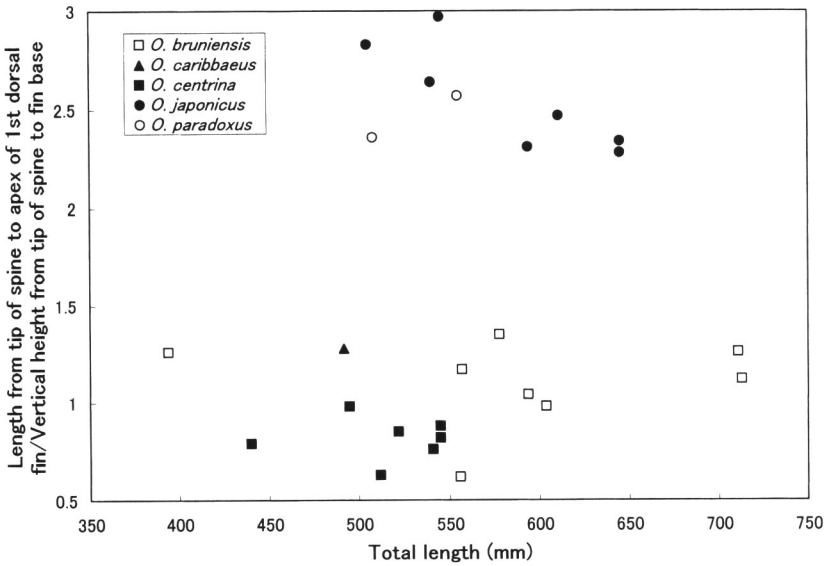


Fig. 2. Relationship between length from tip of spine to apex of first dorsal fin/vertical height from tip of spine to the fin base and total length in *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus*, and *O. paradoxus*. Datum of *O. caribbaeus* is calculated from illustration of holotype by Cervigon (1960).

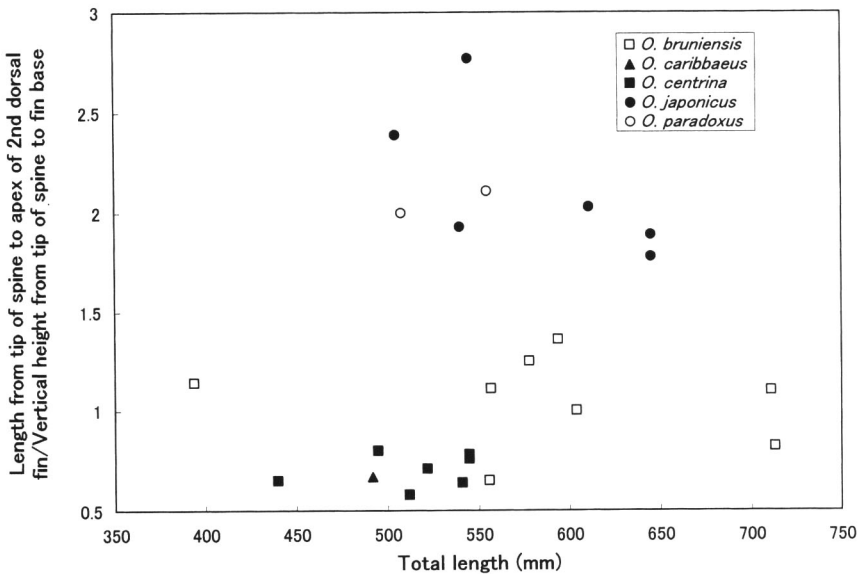


Fig. 3. Relationship between length from tip of spine to apex of second dorsal fin/vertical height from tip of spine to the fin base and total length in *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus*, and *O. paradoxus*. Datum of *O. caribbaeus* is calculated from illustration of holotype by Cervigon (1960).

centrina, (16–19)/(5–6)–1–(5–6) in *O. japonicus*, and 13/5–1–5 (n=1) in *O. paradoxus*. Dental formula of *O. shubnikovii* is 5–0–5/4–1–4 given in the original description by Myagkov in Gubanov

et al. (1986).

Number of turns in the spiral valves is 9 (n=1) in *O. japonicus*, whereas it is 10–11 (n=3) in *O. bruniensis*.

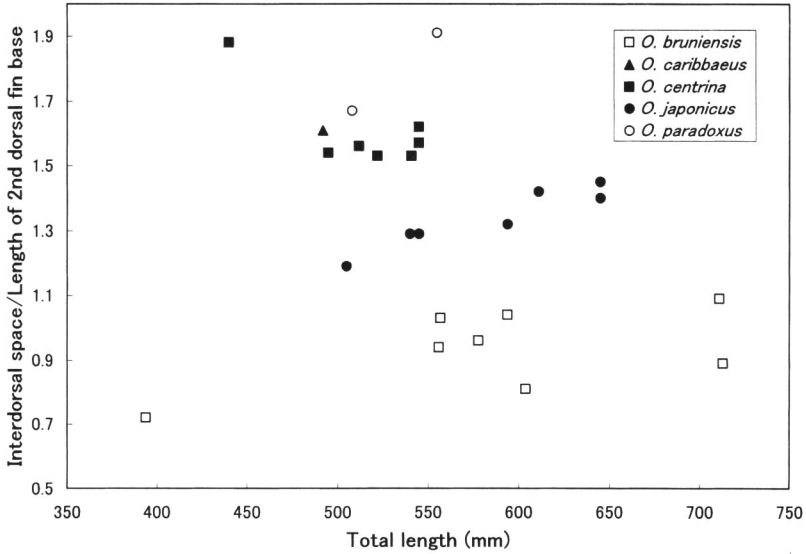


Fig. 4. Relationship between interdorsal space/length base of second dorsal fin and total length in *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. japonicus*, and *O. paradoxus*. Datum of *O. caribbaeus* is taken from measurements of holotype by Cervigon (1960).

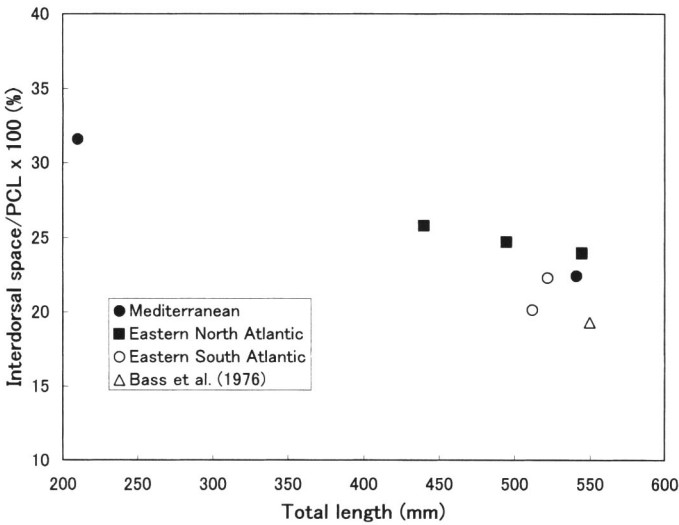


Fig. 5. Relationship between percentage of interdorsal space to precaudal length (PCL) and total length in *Oxynotus centrina* collected from Mediterranean, eastern North Atlantic, and eastern South Atlantic. Datum of *Oxynotus centrina* from Walvis Bay, Namibia is calculated from illustration of Bass *et al.* (1976).

Vertebral numbers in *O. japonicus*, *O. bruniensis*, *O. centrina*, and *O. paradoxus* are compared in Table 2. Precaudal vertebral numbers in *O. centrina* and *O. paradoxus* (i.e., 64–66) are slightly greater than those of *O. japonicus*

and *O. bruniensis* (i.e., 58–64).

The male specimen (555 mm TL) of *O. paradoxus* had well developed claspers with spurs and claws. The male specimens (499–545 mm TL) of *O. centrina* also had hard, calcified claspers with

Table 1. Averages of proportional dimensions as percentage of total length of *Oxynotus bruniensis* (*O.bu*), *O. caribbaeus* (*O.ca*), *O. centrina* (*O.ce*), *O. japonicus* (*O.ja*) and *O. paradoxus* (*O.pa*). Datum of *O. caribbaeus* is taken from measurements by Cervigon (1960) (asterisks) and calculated from illustration of holotype by Cervigon (1960).

Species	<i>O.bu</i>	<i>O.ca</i>	<i>O.ce</i>	<i>O.ja</i>	<i>O.pa</i>
Number of specimens	8	1	8	7	2
Range of total length (mm)	394–713	494	210–545	505–645	508–555
Snout tip to:					
outer nostrils	1.7	2.4	1.5	2.1	1.8
eye	3.8	4.1	3.3	5.2	3.8
spiracle	8.6	8.3	8.6	9.8	9.0
mouth	4.8	4.7	4.8	5.6	5.8
1st gill opening	14.4	14.2	15.4	15.6	14.2
2nd gill opening	15.0	—	13.7	17.2	15.3
3rd gill opening	15.9	15.4	17.7	17.7	16.6
4th gill opening	16.7	—	18.7	19.0	17.7
5th gill opening	17.4	20.6*	19.8	19.5	18.4
pectoral origin	17.6	17.2	19.7	19.8	19.6
pelvic origin	61.8	52.6*	61.7	62.6	60.4
cloaca	65.3	—	65.5	65.4	65.4
1st dorsal origin	15.4	20.1	15.7	20.1	16.6
1st dorsal spine origin	35.5	21.9	30.0	38.7	29.2
2nd dorsal origin	56.1	49.7	57.6	59.3	56.4
2nd dorsal spine origin	63.7	59.2	65.2	66.7	65.2
upper caudal origin	78.9	72.2	78.8	81.0	78.6
lower caudal origin	75.5	68.6	77.2	76.5	75.7
Distance between bases:					
1st and 2nd dorsal	12.7	19.2*	19.7	16.7	21.9
1st and 2nd dorsal spine	19.2	28.4	25.8	22.9	27.1
2nd and caudal	9.9	13.0	10.0	9.6	11.4
pectoral and pelvic	39.3	33.1	37.2	38.1	37.8
pelvic and caudal	9.4	10.1	9.4	8.6	9.9
Distance between origin:					
pectoral and pelvic	44.3	35.5	42.8	43.4	41.8
Nostrils: distance					
between inner corners	1.2	—	1.2	1.1	1.3
Mouth:					
width	5.5	4.0*	5.6	5.5	5.4
Gill opening length:					
1st	0.9	1.2*	1.4	1.1	1.3
2nd	1.0	—	1.7	1.5	1.3
3rd	0.9	—	1.6	1.4	1.3
4th	1.0	—	1.6	1.3	1.1
5th	0.9	1.0*	1.6	1.1	1.1
Spiracle: max. width	1.8	—	3.0	2.4	2.2
Eye:					
horizontal diameter	4.1	3.0	4.5	4.5	4.5
vertical diameter	1.3	1.2	1.5	1.6	1.8
Interorbital width:	8.2	7.1*	9.4	9.7	8.5
1st dorsal fin:					
overall length	31.4	15.4	27.3	25.9	23.2
overall length from spine	11.4	14.2	14.0	9.1	8.6
length base	28.5	15.8*	24.4	21.8	18.9
length base from spine	8.4	9.5	9.7	5.1	4.7
length post. margin	17.0	18.9	15.4	15.2	15.0
height	17.2	20.6*	14.5	16.5	16.2
length from tip of spine to apex of fin	10.5	13.6	8.3	13.3	15.3
vertical height from tip of spine to base	9.7	10.7	10.3	5.2	6.2
spine	0.7	1.8	0.9	0.6	0.5

Table 1. Continued

Species	<i>O.bu</i>	<i>O.ca</i>	<i>O.ce</i>	<i>O.ja</i>	<i>O.pa</i>
Number of specimens	8	1	8	7	2
Range of total length (mm)	394–713	494	210–545	505–645	508–555
2nd dorsal fin:					
overall length	16.9	13.6	15.9	16.2	14.8
overall length from spine	10.6	—	9.3	9.9	8.8
length base	13.6	11.9*	12.0	12.5	12.6
length base from spine	7.3	—	5.5	6.0	4.9
length post. margin	14.0	13.3	10.8	13.9	14.4
height	14.4	16.8*	11.1	14.5	14.6
length from tip of spine to apex of fin	8.7	7.1	6.1	10.9	12.0
vertical height from tip of spine to base	8.4	10.7	8.7	5.4	5.9
spine	0.6	2.4	0.9	0.6	0.4
Pectoral fin:					
length base	5.9	3.0	6.3	5.8	4.9
length ant. margin	15.7	20.1	17.8	17.4	15.0
length distal margin	4.0	5.9	6.3	5.6	7.2
length post. margin	11.8	14.2	11.6	13.1	9.9
Pelvic fin:					
overall length	11.2	8.7*	11.4	11.7	11.4
length base	6.9	5.9	7.1	7.0	6.3
length ant. margin	9.3	8.3	9.8	10.7	9.9
length distal margin	2.3	—	2.6	4.5	1.4
length clasper	9.2	—	11.3	10.2	9.4
Caudal fin:					
length dorsal lobe	22.9	23.7*	21.5	20.8	22.0
length ventral lobe	14.2	12.4	13.7	12.8	12.6
dorsal tip to notch	8.5	10.1	7.7	5.2	6.8
depth notch	3.1	3.6	2.8	2.2	2.7
Trunk at pectoral origin:					
width	14.9	16.6	16.0	16.8	14.4
height	16.9	—	18.0	15.1	14.4

Table 2. Number of vertebrae in *Oxynotus bruniensis*, *O. centrina*, *O. japonicus*, and *O. paradoxus*.

	<i>O. bruniensis</i> (n=4)	<i>O. centrina</i> (n=5)	<i>O. japonicus</i> (n=2)	<i>O. paradoxus</i> (n=1)
Monospondylous	41–45	46–50	44–46	50
Precaudal	58–64	64–66	61–62	64
Caudal	26–29	26–28	26–30	31
Total	84–90	91–94	87–92	95

spurs and claws. In *O. bruniensis*, one specimen (394 mm TL) had soft claspers without sperm in the seminal vesicles and sperm sacs, and the other specimens (556–594 mm TL) had well developed claspers. Two males (556 mm TL and 594 mm TL) had two testes being equal in size and their seminal vesicles and sperm sacs were full of sperm. The male specimen (540 mm TL)

of *O. japonicus* had hard, calcified claspers with spurs and claws.

Discussion

A brief review of *Oxynotus* showed that the genus is represented by five species: *O. bruniensis*, *O. caribbaeus*, *O. centrina*, *O. paradoxus*,

and *O. japonicus*. Bass *et al.* (1976) stated that the *Oxynotus* recorded as *O. centrina* from Angola, Namibia, and South Africa might not be a true *O. centrina* but an undescribed species, that differs from *O. centrina* in having a much shorter interdorsal space. However, our observations show that there are few significant differences among the specimens of *O. centrina* from the Mediterranean Sea, the eastern North Atlantic, and the eastern South Atlantic. In addition, measurements calculated from the illustration of *Oxynotus* in Bass *et al.* (1976) do not show differences from those of the above mentioned specimens. Other key characters of the eastern North and South Atlantic specimens are almost the same as those of the Mediterranean specimens. Therefore, we suggest that the specimens from the eastern North Atlantic and eastern South Atlantic including Namibia are likely to be conspecific.

Myagkov in Gubanov *et al.* (1986) described *O. shubnikovi* as a new species from south-west of the Cunene River mouth, northern Namibia. The original illustration of *O. shubnikovi* (fig. 59 in Gubanov *et al.*, 1986) is similar to specimens of *Oxynotus centrina*. The type locality of *O. shubnikovi* is same as that of specimens of *Oxynotus centrina* examined by Bass *et al.* (1976). The synonym list of Myagkov in Gubanov *et al.* (1986) includes *Oxynotus* sp. of Bass *et al.* (1976). Compagno *et al.* (1991) stated that *O. shubnikovi* was provisionally accepted as being distinct from the closely similar species *O. centrina* in the eastern North Atlantic and Mediterranean, but cautioned that these species need to be critically compared by using adequate samples to determine if they can be consistently separated by morphometric characters. However, the specimen of Bass *et al.* (1976) and our Namibia and Angola specimens are not clearly different from *O. centrina*, and Compagno *et al.* (1991) also suggested that *O. shubnikovi* was closely similar to *O. centrina*. Thus, we reach to a conclusion that *O. shubnikovi* should be recognized to be a junior synonym of *O. centrina*.

We conclude that five species should be recog-

nized in the genus *Oxynotus*: *O. japonicus*, endemic to Japan, known from Suruga Bay and Enshu-nada Sea, *O. bruniensis* from off New Zealand and Australia (Garrick, 1960; Compagno, 1984; Yano, 1990), *O. caribbaeus* from the Caribbean Sea off Venezuela (Cervigon, 1961; Carpenter, 1966; Compagno, 1984), *O. centrina* from the Mediterranean, eastern North Atlantic, tropical east Atlantic from Angola through Namibia to the west coast of South Africa (Bigelow & Schroeder, 1957; Bass *et al.*, 1976; Cadenat & Blache, 1981; Compagno, 1984; Lloris, 1986), and *O. paradoxus* from the eastern North Atlantic (Frade, 1929; Cadenat & Blache, 1981; Compagno, 1984).

Key to Species of *Oxynotus*

- 1a. Spine of first dorsal fin sloping slightly forward; length from tip of first dorsal spine to apex of first dorsal fin less than 1.5 times of vertical height from tip of spine to fin base; length from tip of second dorsal spine to apex of second dorsal fin less than 1.5 times of vertical height from tip of spine to fin base2
- 1b. Spine of first dorsal fin sloping slightly backward; length from tip of first dorsal spine to apex of first dorsal fin greater than 2 times of vertical height from tip of spine to fin base; length from tip of second dorsal spine to apex of second dorsal fin greater than 1.5 times of vertical height from tip of spine to fin base.....4
- 2a. Interdorsal space less than or about equal to length of second dorsal fin base
...*O. bruniensis* (New Zealand and Australia)
- 2b. Interdorsal space longer than length of second dorsal fin base.....3
- 3a. Length from tip of first dorsal spine to apex of first dorsal fin longer than height from tip of spine to fin base; precaudal length (PCL) greater than 3 times of length from snout tip to first dorsal spine; spiracle small, almost circular*O. caribbaeus* (Caribbean Sea)
- 3b. Length from tip of first dorsal spine to apex

- of first dorsal fin shorter than or about equal to height from tip of spine to fin base; pre-caudal length less than 2.9 times of length from snout tip to first dorsal spine; spiracle large, vertically elongated
*O. centrina*
 (Mediterranean, eastern North Atlantic, tropical east Atlantic, and eastern South Atlantic)
- 4a. Second dorsal-fin base 1.7–1.9 in interdorsal space; length from snout tip to first dorsal spine 2.5–2.7 in precaudal length; spiracle almost circular
*O. paradoxus* (eastern North Atlantic)
- 4b. Second dorsal-fin base 1.2–1.5 in interdorsal space; length from snout tip to first dorsal spine 2.0–2.2 in precaudal length; spiracle oval*O. japonicus* (Japan)

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