

The Comparative Morphology of Skate Egg Capsules (Chondrichthyes: Elasmobranchii: Rajiformes)

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Abstract. The egg capsules of 64 skate species of 20 genera, among the 30 genera of the order Rajiformes were examined to determine the interrelationships within the order Rajiformes. As a result, we found that there may be four basic lineages in this order, i.e., *Bathyraja* (Arhynchobatidae), *Amblyraja* (Rajidae), *Dipturus* (Rajidae) and *Rostroraja* (Rajidae). It is also likely that the genus *Amblyraja* forms the subfamily Amblyrajinae and the genus *Rostroraja* the subfamily Rostrorajinae. A new genus *Beringraja* is established for two species (*B. binoculata* (Girard, 1855) and *B. pulchra* (Liu, 1932)), in which egg capsules contain more than one embryo. We propose that the genus *Fenestraja* should be re-allocated to the family Arhynchobatidae and that *Raja clavata* Linnaeus, 1758 should be included in the genus *Malacoraja*.

Key words: Rajiformes, egg-capsule, *Beringraja*, Rajidae, Arhynchobatidae, Anacanthobatidae

Introduction

Rajiformes (skates) are the only order of the batoids to be oviparous (egg laying) (Ishiyama 1958). This order is thus regarded as a natural group. The morphology of the skate egg capsule is species specific, making it possible to identify the species from the egg capsule. So far, the egg capsules of at least 90 species have been described by several authors (Table 1). However, these authors studied egg capsules from some restricted areas and did not treat them on a worldwide scale. It is clear from previous studies that the morphology of skate egg capsules is not only useful for species identification, but also to determine the interrelationship between skate species (Ishiyama, 1958; Ishihara, 1990). This has also been found for the morphology of the egg capsules from the ratfishes, class Holocephali (Dean, 1904, 1906, 1912).

At present, the order Rajiformes is divided into three families containing 30 genera (Compagno, 1999, 2005; Ebert

& Compagno, 2007). However, the number of studies into the interrelationships of skates is not prolific and limited to several authors, McEachran & Compagno (1982), McEachran (1984), McEachran & Miyake (1986) and McEachran & Dunn (1998).

The aims of the present study are: to obtain the morphological characteristics for egg capsules of each skate species, to compare those characteristics within the order Rajiformes and to determine the interrelationships of skates based on egg capsule characteristics. To achieve these aims, it is necessary to examine as many egg capsules from the different species as possible. The Rajiformes consist of 245 valid species (Ebert & Compagno, 2007), which are placed in three families and 30 genera (Compagno, 1999, 2005; Ebert & Compagno, 2007). In the present study, egg capsules of 64 species from 20 genera were examined.

Materials and Methods

Collection

Egg capsules were collected from Japanese bottom trawlers or borrowed from scientific institutions. Species identification of the egg capsule was determined by identifying the pregnant female from which the egg capsule was extracted or by identifying the embryo within the egg capsule already showing species identity. Voucher specimens were obtained from the following organizations along with location, depth and date collected:

Organization (Abbreviation)

Biological Science, Kochi University (BSKU)
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Table 1. List of literature describing skate egg capsules in order of publication date.

Authors	Species
Garman, 1899	<i>Raja badia</i>
Holt, 1899	<i>Raja alba</i>
Dollo, 1904	<i>Raja arctowski</i> , <i>Raja blanda</i> (= <i>R. brachyura</i>), <i>R. circularis</i>
Lo Bianco, 1909	<i>Raja asterias</i>
Waite, 1909	<i>Raja nasuta</i>
Williamson, 1913	<i>Raja batis</i> , <i>R. blanda</i> (= <i>R. brachyura</i>), <i>R. circularis</i> , <i>R. clavata</i> , <i>R. fullonica</i> , <i>R. microocellata</i> , <i>R. maculata</i> (= <i>R. montagui</i>), <i>R. macrorhynchus</i> (= <i>R. nidarosiensis</i>), <i>R. oxyrhynchus</i> , <i>R. radiata</i>
Jensen, 1914	<i>Raja spinicauda</i> , <i>Raja hyperborea</i>
Clark, 1919-1922	<i>Raja spinicauda</i> , <i>R. marginata</i> (= <i>R. alba</i>), <i>R. batis</i> , <i>R. circularis</i> , <i>R. clavata</i> , <i>R. fyllae</i> , <i>R. hyperborea</i> , <i>R. lintea</i> , <i>R. maculata</i> (= <i>R. montagui</i>), <i>R. microocellata</i> , <i>R. naevus</i> , <i>R. nidarosiensis</i> , <i>R. oxyrhynchus</i> , <i>R. radiata</i> , <i>R. undulata</i>
Clark, 1926	
Clark, 1929-1932	
DeLacy & Chapman, 1935	<i>Raja binoculata</i> , <i>R. rhina</i>
Vladykov, 1936	<i>Raja diaphanes</i> , <i>R. erinacea</i> , <i>R. laevis</i> , <i>R. radiata</i> , <i>R. scabrata</i> (= <i>R. radiata</i>)
Breder & Nichols, 1937	<i>Raja eglanteria</i>
Breder & Atz, 1938	<i>Raja eglanteria</i>
Whitley, 1938	? <i>Raja australis</i> , ? <i>R. dentata</i> , ? <i>R. lemprieri</i> , <i>R. nasuta</i> , ? <i>R. nitida</i> , ? <i>Irolita waitii</i>
Ishiyama, 1950	<i>Raja kenoei</i> (= <i>Dipturus kwangtungensis</i>), <i>R. fusca</i> (= <i>Okamejei kenoei</i>), <i>R. garmani</i> (= <i>O. acutispina</i>), <i>R. hollandi</i> (= <i>O. boesemani</i>), <i>R. macrophthalms</i> (= <i>O. meerdervoortii</i>), <i>R. meerdervoortii meerdervoortii</i> (= <i>O. kenoei</i>), <i>R. pulchra</i> , <i>R. parmifera</i> , <i>R. isotrachys</i> (= <i>Bathyrja bergi</i>), <i>R. diplotaenia</i>
Follett, 1952	<i>Raja trachura</i> (= <i>Bathyrja abyssicola</i>)
Bigelow & Schroeder, 1953	<i>Raja erinacea</i>
Andriyashev, 1954	<i>Raja batis</i> , <i>R. hyperborea</i> , <i>R. radiata</i>
Kreff, 1957	<i>Raja spinicauda</i>
Ishiyama, 1958	<i>Breviraja parmifera</i> , <i>B. trachouros</i> , <i>B. tobitukai</i> , <i>Raja acutispina</i> , <i>R. hollandi</i> (= <i>O. boesemani</i>), <i>R. gigas</i> , <i>R. fusca</i> (= <i>O. kenoei</i>), <i>R. porosa meerdervoortii</i> (= <i>O. kenoei</i>), <i>R. porosa tobae</i> (= <i>O. kenoei</i>), <i>R. kenoei</i> (= <i>Dipturus kwangtungensis</i>), <i>R. macrocauda</i> , <i>R. macrophthalma</i> (= <i>O. meerdervoortii</i>), <i>R. pulchra</i> , <i>R. tengu</i> , <i>Rhinoraja kujiensis</i> , <i>Rh. longicauda</i> , <i>Rh. odai</i>
Cox, 1963	<i>Breviraja kincaidi</i> (= <i>Bathyrja interrupta</i>), <i>Raja trachura</i> (= <i>B. abyssicola</i>), <i>Raja stellulata</i> , <i>Raja binoculata</i> , <i>R. inornata</i> , <i>R. rhina</i>
Hitz, 1964	<i>Raja binoculata</i>
Boeseman, 1967	<i>Raja nidarosiensis</i>
Wallace, 1967	<i>Anacanthobatis marmoratus</i> , <i>Raja alba</i> , <i>R. miraletus</i> , <i>R. barnardi</i> (= <i>R. wallacei</i>)
McEachran, 1970	<i>Raja garmani</i>
Hart, 1973	<i>Raja kincaidi</i> , <i>Raja binoculata</i> , <i>R. rhina</i> , <i>R. stellulata</i>
Ishiyama & Ishihara, 1977	<i>Bathyrja maculata</i> , <i>B. caeluronigricans</i> (= <i>B. matsubarae</i>), <i>B. minispinosa</i>
Templeman, 1982	<i>Raja radiata</i>
Lamilla <i>et al.</i> , 1984	<i>Psammobatis lima</i>
Ishihara & Ishiyama, 1985	<i>Bathyrja pseudoisotrachys</i> (= <i>B. bergi</i>), <i>B. interrupta</i>
Ishihara, 1987	<i>Raja boesemani</i> , <i>R. kenoei</i> , <i>R. kwangtungensis</i> , <i>R. meerdervoortii</i>
Bor, 1998	<i>Raja alba</i> , <i>R. batis</i> , <i>R. brachyura</i> , <i>R. circularis</i> , <i>R. clavata</i> , <i>R. fyllae</i> , <i>R. microocellata</i> , <i>R. montagui</i> , <i>R. naevus</i> , <i>R. radiata</i> , <i>R. undulata</i>
Stehmann & Merrett, 2001	<i>Bathyrja richardsoni</i>
Ebert 2005	<i>Bathyrja aleutica</i> , <i>B. interrupta</i> , <i>B. lindbergi</i> , <i>B. maculata</i> , <i>B. minispinosa</i> , <i>B. parmifera</i> , <i>B. taranetzi</i> , <i>B. trachura</i>
Treloar <i>et al.</i> , 2006	<i>Amblyraja cf. hyperborea</i> , <i>Dipturus</i> sp. A, <i>D. sp. B</i> , <i>D. sp. L</i> , <i>D. cerva</i> , <i>D. cf. gudgeri</i> , <i>D. whitleyi</i> , <i>Pavoraja nitida</i>
Ebert & Davis, 2007	<i>Amblyraja badia</i> , <i>Bathyrja abyssicola</i> , <i>B. aleutica</i> , <i>B. kincaidii</i> , <i>B. microtrachys</i> , <i>B. spinosissima</i> , <i>B. trachura</i> , <i>Raja binoculata</i> , <i>R. inornata</i> , <i>R. rhina</i> , <i>R. stellulata</i>

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 Kanagawa Prefectural Museum of Natural History (KPM)
 Los Angeles County Museum (LACM)
 Museum, Tokyo University of Fisheries (MTUF)
 National Museum, New Zealand (NMNZ)
 National Science Museum, Tokyo (NSMT)
 Royal British Columbia Museum (RBCM)
 Texas A&M University Wildlife Collection (TCWC)
 Virginia Institute of Marine Sciences (VIMS)

Materials Examined

Genus *Bathyrja* 16 species

B. abyssicola (Gilbert, 1896): LACM 3772-1, 105.8 mm capsule length
 × 65.2 mm, capsule width, 32°33' N; 120°05' W, Aug. 8, 1978.

B. aleutica (Gilbert, 1895): KPM-NI 28909, 128.0 × 90.0 mm,
 Same Fish Market, Aomori Prefecture, 1952; MTUF 26070,
 126.0 × 89.0 mm, off Abashiri, Hokkaido, Dec., 1971.

B. bergi Dolganov, 1983: KPM-NI 28912, 118.0 × 85.0 mm,
 off Akita; MTUF 26071, 117.7 × 84.6 mm, off Monbetsu,
 Hokkaido, Dec., 1952.

B. diplotaenia (Ishiyama, 1952): KPM-NI 28908, 110.0 × 76.0
 mm, no data; MTUF 26159, 114.0 × 75.4 mm, off Muroran,
 Hokkaido, Oct. 18, 1948.

B. interrupta (Gill & Townsend, 1897): MTUF 26160, 83.8 ×
 69.0 mm, 58°30' N; 175°10' W, 300 m depth, Oct. 20, 1962.

B. irrassa Hureau & Ozouf-Costaz, 1980: MTUF 24832, 113.8 ×
 73.6 mm, 48°18' S; 70°52' E, Nov. 23, 1977.

- B. maccaini* Springer, 1971: MTUF 26161, 156.6 × 80.0 mm, 62°24' S; 61°01' W, 107–109 m depth, Jan. 27, 1982.
- B. maculata* Ishiyama & Ishihara, 1977: MTUF 26162, 101.9 × 62.8 mm, 61°07' N; 179°10' W, 245 m depth, May 30, 1963.
- B. matsubara* (Ishiyama, 1952): MTUF 26163, 111.4 × 64.8 mm, off Same, Aomori Prefecture, May 23, 1951.
- B. minispinosa* Ishiyama & Ishihara, 1977: MTUF 26164, 75.9 × 55.1 mm, 58°30' N; 175°10' W, 300 m depth, Oct. 20, 1962.
- B. parmifera* (Bean, 1881): KPM-NI 28911, 130.0 × 89.0 mm, Bering Sea, 1962; MTUF 26166, 129.0 × 88.7 mm, Bering Sea, 1962.
- B. shuntovi* Dolganov, 1983: MMNZ 6757, 87.9 × 46.6 mm, 48°15.5' S; 177°48.5' E, 503–512 m depth, Nov. 17, 1975.
- B. smirmovi* (Soldatov & Pavlenko, 1915): KPM-NI 28910, 125.0 × 88.0 mm, no data; MTUF 26167, 124.0 × 87.4 mm, off Tsuiyama, Hyogo Prefecture, Feb. 20, 1966.
- B. trachouros* (Ishiyama, 1958): MTUF 26168, 116.4 × 84.0 mm, off Shiogama, Miyagi Prefecture, May, 1951.
- B. trachura* (Gilbert, 1892): MTUF 26169, 74.6 × 61.1 mm, Gulf of Alaska, Oct., 1987.
- B. violacea* (Suvorov, 1935): MTUF 26170, 67.4 × 85.4 mm, off Abashiri, Hokkaido, Oct. 2–3, 1971.
- Genus *Notoraja* 1 species
- N. tobitukai* (Hiyama, 1940): BSKU 23096, 36.0 × 24.8 mm, 32°53' N; 133°29.1' E, 483 m depth, Nov. 14, 1981.
- Genus *Brochiraja* 1 species
- B. asperula* (Garrick & Paul, 1974): NSMT P42505, 37.3 × 22.0 mm, 48°27' S; 179°03' E, 637–638 m depth, Nov. 14, 1983.
- Genus *Psammobatis* 3 species
- P. rudis* Günther, 1870: ISH 499-178, 56.9 × 34.1 mm, 52°45.7' S; 63°47.9' W, 295 m depth, Aug. 24, 1978.
- P. rutrum* Jordan, 1890: ISH 81-171, 52.2 × 35.4 mm, 49°30' S; 66°30' W, 100 m depth, Jan. 20, 1971.
- P. scobina* (Philippi, 1857): LACM 10438-4, 52.0 × 31.4 mm, 52°35' S; 65°08' W, 128 m depth, Feb. 13, 1964.
- Genus *Rhinoraja* 5 species
- R. kujiensis* (Tanaka, 1916): MTUF 26171, 110.8 × 71.8 mm, off Same, Aomori Prefecture, May, 1951.
- R. longicauda* Ishiyama, 1952: MTUF 26172, 85.0 × 48.0 mm, off Shiogama, Miyagi Prefecture, May 22, 1951.
- R. murrayi* Günther, 1880: MTUF 26165, 59.8 × 33.6 mm, Kerguelen Islands, Jan. 14, 1985.
- R. odai* Ishiyama, 1958: MTUF 26173, 56.8 × 31.5 mm, off Mikomoto-jima, Shizuoka Prefecture., 330–350 m depth, 1952.
- R. taranetzi* Dolganov, 1983: RBCM 989-92, 67.3 × 46.6 mm, Alaska, July 16, 1989.
- Genus *Atlantoraja* 1 species
- A. castelnaui* (Ribero, 1904): ISH 439-178, 103.0 × 80.0 mm, 41°27.5' S; 64°04.5' W, 100 m depth, July 24, 1978.
- Genus *Sympterygia* 1 species
- S. bonapartei* Müller & Henle, 1841: LACM 10438-3, 81.0 × 31.4 mm, 52°35' S; 65°08' W, 128 m depth, Feb. 13, 1964.
- Genus *Amblyraja* 3 species
- A. doellojuradoi* (Pozzi, 1935): ISH 112-171, 86.4 × 56.2 mm, 53°0' S; 64°0' W, 295–300 m depth, Aug. 12, 1971.
- A. georgiana* (Norman, 1938): ISH 315-176B, 116.5 × 80.0 mm, 54°39' S; 34°55' W, 463–497 m depth, Dec. 12, 1967.
- A. radiata* (Donovan, 1808): MTUF 26692, 79.7 × 63.4 mm, 44°02' N; 52°0' W, 91 m depth, May 19, 1949; ISH 210-159, 50.2 × 41.3 mm, 56°45' N; 1°49' E, 95 m depth, Dec. 17, 1959.
- Genus *Dipturus* 7 species
- D. batis* (Linnaeus, 1758): MTUF 26174, 217.1 × 124.7 mm, off Concarneau, 1989.
- D. gigas* (Ishiyama, 1958): KPM-NI 28907, 218.0 × 138.0 mm, South China Sea, 1952; MTUF 26175, 220.0 × 140.0 mm, South China Sea, 1952.
- D. kwangtungensis* (Zhu, 1960): MTUF 26176, 65.0 × 40.0 mm, off Shimonoseki, Yamaguchi Prefecture, 1950.
- D. laevis* (Mitchell, 1817): CAS 64131, 70.8 × 46.2 mm, Shrimp Pass, year unknown.
- D. macrocauda* (Ishiyama, 1955): MTUF 26177, 130.0 × 60.0 mm, off Miya, Aichi Prefecture, March, 1951.
- D. nasutus* (Müller & Henle, 1841): NMNZ 8353, 121.7 × 71.4 mm, 47°11' S; 167°41' E, 29–31 m depth, Feb. 22, 1972.
- D. tengu* (Jordan & Fowler, 1903): MTUF 26682, 85.0 × 55.0 mm, no data.
- Genus *Fenestraja* 1 species
- F. sp.* : TCWC 2196-1, 44.0 × 25.8 mm, off Pascagoula, Mississippi, Oct., 1955
- Genus *Leucoraja* 5 species
- L. erinacea* (Mitchell, 1825): VIMS 01340, 53.0 × 36.0 mm, 42°39' N; 66°10' W, 62 m depth, Nov. 17, 1969.
- L. fullonica* (Linnaeus, 1758): MTUF 26693, 82.0 × 48.0 mm, off Concarneau, March, 1987.
- L. naevus* (Müller & Henle, 1841): MTUF 26694, 61.0 × 34.0 mm, off Concarneau, March, 1987.
- L. ocellata* (Mitchell, 1815): VIMS 01358, 78.0 × 48.0 mm, 43°25.5' N; 60°30' W, July 23, 1970.
- L. wallacei* (Hulley, 1970): RUSI A4802, 73.0 × 42.0 mm, Eastern Cape, South Africa, Sept. 29, 1986.
- Genus *Malacoraja* 1 species
- M. senta* (Garman, 1885): VIMS 01333, 55.0 × 41.9 mm, 42°16' N; 69°27' W, 200 m depth, Dec. 23, 1969.
- Genus *Okamejei* 5 species
- O. acutispina* (Ishiyama, 1958): KPM-NI 28904, 50.0 × 26.0 mm, no data; MTUF 26683, 49.4 × 26.3 mm, off Obama, Shimane Prefecture, 1952.
- O. boesemani* (Ishihara, 1987): KPM-NI 28902, 60.0 × 36.0 mm, East China Sea, 1952; MTUF 26684, 60.6 × 36.7 mm, East China Sea, 1952.
- O. kenojei* (Müller & Henle, 1841): KPM-NI 28903, 48.0 × 29.0 mm, off Choshi, Chiba Prefecture, 1956; MTUF 26685, 47.8 × 29.1 mm, off Choshi, Chiba Prefecture, 1956.
- O. meerdervoortii* (Bleeker, 1860): KPM-NI 28906, 34.0 × 24.0 mm, off Maizuru, Kyoto-fu, 1948; MTUF 26686, 34.7 × 24.8 mm, off Maizuru, Kyoto-fu, 1948.
- O. schmidtii* (Ishiyama, 1958): KPM-NI 28905, 55.0 × 31.0 mm, off Miya, Aichi Prefecture, 1952; MTUF 26687, 56.0 × 30.3

mm, off Miya, Aichi Prefecture, 1951.

Genus *Raja* 4 species

R. clavata Linnaeus, 1758: MTUF 26686, 83.0 × 68.6 mm, off Concarneau, 1987.

R. microocellata Montagu, 1818: MTUF 26690, 52.0 × 32.0 mm width, off Rousset, Bretagne, June, 1986.

R. miraletus Linnaeus, 1758: RUSI A4786, 45.5 × 29.0 mm, West Cape, South Africa, Sept. 21, 1986.

R. montagui Fowler, 1980: MTUF 26691, 71.0 × 43.0 mm, off Rousset, Bretagne, June, 1985.

Genus *Rajella* 3 species

R. bigelowi (Stehmann, 1978): TCWC 2720-1, 53.0 × 29.9 mm, 39°04'N; 72°32' W, 778 m depth, Jan. 14, 1974.

R. fuliginea (Bigelow & Schroeder, 1954): TCWC 6443-1, 125.0 × 75.0 mm, 27°35' N; 92°22' W, 768–781 m depth, June 9, 1985.

R. leopardus (von Bonde & Swart, 1923): MTUF 26695, 74.0 × 74.5 mm, 20°27.4' S; 17°53.6' W, 800 m depth, March 24, 1983.

Genus *Rostroraja* 1 species

R. alba (Lacepède, 1803): MTUF 30567, 141.0 × 120.4 mm, False Bay, Cape Town, 1988.

Genus *A sensu* Compagno (1999, 2005) and Ebert & Compagno (2007) 3 species

Raja binoculata Girard, 1855: RBCM 986-60, 228.0 × 194.5 mm, Hecate Strait, June 6, 1969.

Raja pulchra Liu, 1932: MTUF 26681, 145.0 × 70.0 mm, Sea of Japan, 1963.

Raja rhina Jordan & Gilbert, 1880: RBCM 986-61, 103.0 × 69.4 mm, Cherry Point, Feb., 1965.

Genus *B sensu* Compagno (1999, 2005) and Ebert & Compagno (2007) 1 species

Raja eglanteria Bosc, 1802: MTUF 26689, 71.0 × 43.0 mm, Panacea, Gulf of Mexico, May, 1984.

Genus *Anacanthobatis* 1 species

A. ori (Wallace, 1967): MTUF P30568, 36.0 × 19.0 mm, 25°28.3' S; 35°28.7' E, 1,230–1,260 m depth, Nov. 23, 1988.

Genus *Cruriraja* 1 species

C. parcomaculata Smith, 1964: RUSI A3428, 45.0 × 24.4 mm, West Cape, South Africa, 255 m depth, June 27, 1986.

Egg Capsule Morphology

Methods for the measurements of skate egg capsules followed those of Ishiyama and Ishihara (1977). The size of the egg capsule normally correlates with that of the female parent (Ishiyama, 1958), although there are exceptions. In *Amblyraja radiata* (Donovan, 1808), for example, the relative size of the egg capsules differed between the populations of the American and European coasts (Templeman, 1982).

The definitions for the components of the egg capsule were adapted from Bigelow & Schroeder (1953), Ishiyama (1958), Ishiyama (1967) and Ishiyama & Ishihara (1977) (Fig. 1).

The rectangular portion containing the embryo is called the 'main portion'; the ratio between the length and width of the main portion is almost constant. Egg capsules vary in shape from

species to species, from a long rectangular form to an almost square form. The dorsal side of the egg capsule refers to the side that is more concave in shape since it is positioned along the ventral side of the female's body, and thus follows the contour of the cavity. The projections arising from the four corners are called the 'horns'; the length and shape of the horns are important characters to identify a species, but are fragile and easily damaged. The thin portion at each side of the egg capsule is called the 'lateral keel'; the degree of development and thickness of the lateral keels also serve as important characters to identify egg capsules. The thin portions at the anterior and posterior ends of the egg capsules are the 'anterior apron' and 'posterior apron' respectively. The terms "anterior" and "posterior" correspond to the direction in which the egg capsule is positioned inside the oviduct of the mother. When the egg capsule is deposited, the posterior end is determined by examining the shape of the apron and the length of the horns. The posterior horns (if undamaged) are usually longer than the anterior horns and the posterior apron is usually straight or less concave compared with the anterior apron. The degree of development and the thickness of the aprons also serve as identifying characteristics. For example, in a Japanese skate, *Dipturus gigas* (Ishiyama, 1958), the aprons are united with the horns. Any free filaments attached to the lateral keel (sometimes observed in skate egg capsules) are called 'tendrils'. The number of species that have tendrils attached to the lateral keel is restricted. Each horn has an opening, the 'respiratory fissure', to allow seawater to enter for respiration; the location of these fissures on the horns is variable, ranging from the tip to the base. For example, the respiratory fissures are located at the base of the horns in *Bathyraja* species and, on the contrary, they are located at the tip of the horns in *Okamejei* species. The surface of the main portion of the egg capsule is sometimes rough due to the presence of ridges, called 'longitudinal ridges', running lengthways along the capsule. Egg capsules are also covered by thin fibers (also called 'silky fibers'); that can change in density

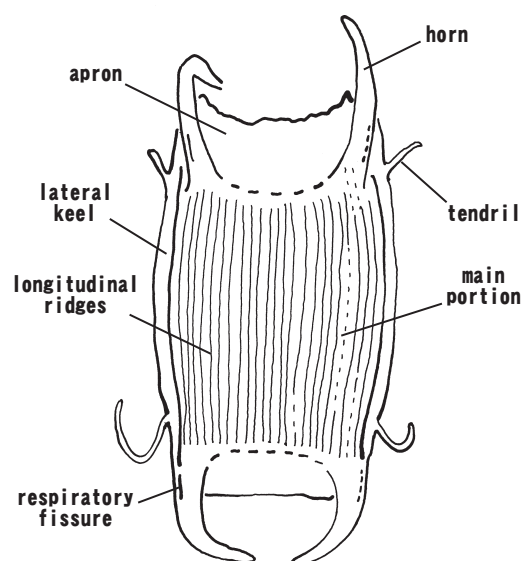


Fig. 1. General shape and structure of a skate egg capsule.

depending on the species. These fibers gradually reduce when the embryo develops and also after the egg capsule has been deposited on the seafloor. It must also be noted that the colour and surface structure of a species' egg capsule can vary between intra-oviductal capsules and capsules that have been retrieved from the seafloor or washed up on the shore.

Results

Morphological characteristics for the egg capsules of each skate species examined are shown in Table 2. Below are some general characteristics described for each genus.

1. Egg capsules of the genus *Bathyraja* (Fig. 2)

The length of the main portion is about twice its width (long rectangular shape). There are two types of egg capsules in this genus, type B-I (Fig. 2-A) and B-II (Fig. 2-B). In the former type, the surface is rough with well-developed longitudinal ridges and a poorly developed lateral keel. In the latter, the surface is smooth with poorly developed longitudinal ridges and a well developed lateral keel. The base of the horns is tough and depressed in cross section; the posterior horns are longer than the anterior horns, the tips of the anterior and posterior horns are curved and fiber-like respectively. Respiratory fissures are located at the mid-length of the horns. Egg capsules of the majority of the *Bathyraja* species belong to the type B-I, but those of five species; *B. interrupta* (Gill & Townsend, 1897), *B. parmifera* (Bean, 1881), *B. smirnovi* (Soldatov & Lindberg, 1915), *B. trachura* (Gilbert, 1892) and *B. violacea* (Suvorov, 1935) belong to type B-II.

2. Egg capsules of the genus *Brochiraja* (Fig. 3)

The length of the main portion is twice as long as its width (long rectangular shape); its surface is smooth. The posterior horns are long, their length two times the width of the main portion. Cross section of the horns is circular; respiratory fissures are located at mid-length of the horns.

3. Egg capsules of the genus *Notoraja*

The length of the main portion is twice as long as its width (long rectangular shape); its surface is smooth. The posterior horns are long, their length three times the width of the main portion. Cross section of the horns is circular; respiratory fissures are located at mid-length of the horns.

4. Egg capsules of the genus *Psammobatis* (Fig. 4)

The length of the main portion is twice as long as its width (long rectangular shape); its surface is smooth. The posterior horns are fiber-like and long, 1.5 times as long as the width of the main portion; the anterior horns are relatively short; cross section of the horns is circular. Respiratory fissures are present near the tip of the anterior horns and at the base of the posterior horns.

5. Egg capsules of the genus *Rhinoraja* (Fig. 5)

In over-all appearance, the egg capsules of the genus *Rhinoraja* show close similarity to the type B-I of the genus *Bathyraja*; the surface is rough.

6. Egg capsules of the genus *Atlantoraja* (Fig. 6)

The length of the main portion is less than twice as long as its width (rectangular shape); its surface is smooth. The posterior horns are 1.5 times the width of the main portion. Cross section

Table 2. Comparison of egg capsules of 20 groups in the present study. A "+" in the keel column signifies keel present and a "-" signifies keel absent. When the horn is longer than main portion, it is long; if the horn is the same length of main portion, it is moderate; if horn is shorter than main portion, it is short. In the type 2 of *Dipturus* and type 2 of Genus A, apron obscures the horns; the horn shape is listed as "obscure".

Family	Genus	Condition of surface	Shape of horns	Length of post. Horns	Keel	Position of resp. fissures	Types
Arhynchobatidae	<i>Bathyraja</i> type 1	rough	depressed	moderate	-	middle	B-I
	<i>Bathyraja</i> type 2	smooth	depressed	moderate	+	middle	B-II
	<i>Notoraja</i>	smooth	circular	long	-	tip; middle	B-II
	<i>Brochiraja</i>	smooth	circular	long	-	tip; middle	B-II
	<i>Psammobatis</i>	smooth	circular	long	-	near tip; base	B-II
	<i>Rhinoraja</i>	rough	depressed	moderate	-	middle	B-I
	<i>Atlantoraja</i>	smooth	circular	long	+	tip; middle	B-II
	<i>Sympterygia</i>	rough	depressed	short	-	middle	B-I
Anacanthobatidae	<i>Anacanthobatis</i>	smooth	circular	long	-	tip; middle	B-II
	<i>Cruiraja</i>	smooth	circular	long	-	tip; base	B-II
Rajidae	<i>Amblyraja</i>	smooth; rough	circular	moderate	+	near tip; base	A-I
	<i>Dipturus</i> type 1	smooth	circular	moderate	-	tip	D-I
	<i>Dipturus</i> type 2	smooth	obscure	short	+	tip	D-II
	Genus A type 1	smooth	circular	moderate	-	tip	D-I
	Genus A type 2	smooth	obscure	short	+	tip	D-III
	Genus B	smooth	circular	moderate	-	tip	D-I
	<i>Fenestraja</i>	smooth	circular	long	-	tip; base	B-II
	<i>Leucoraja</i>	smooth	circular	long	-	tip; middle	D-I
	<i>Malacoraja</i>	smooth	circular	short	+	tip; near tip	D-I
	<i>Okamejei</i>	smooth	circular	moderate	-	tip	D-I
	<i>Raja</i>	smooth	circular	moderate	-	tip	D-I
	<i>Rajella</i>	smooth	circular	long	-	tip; middle	D-I
	<i>Raja leopardus</i>	smooth	depressed	short	+	middle	D-I
	<i>Rostroraja</i>	rough	depressed	long	+	base	R-I

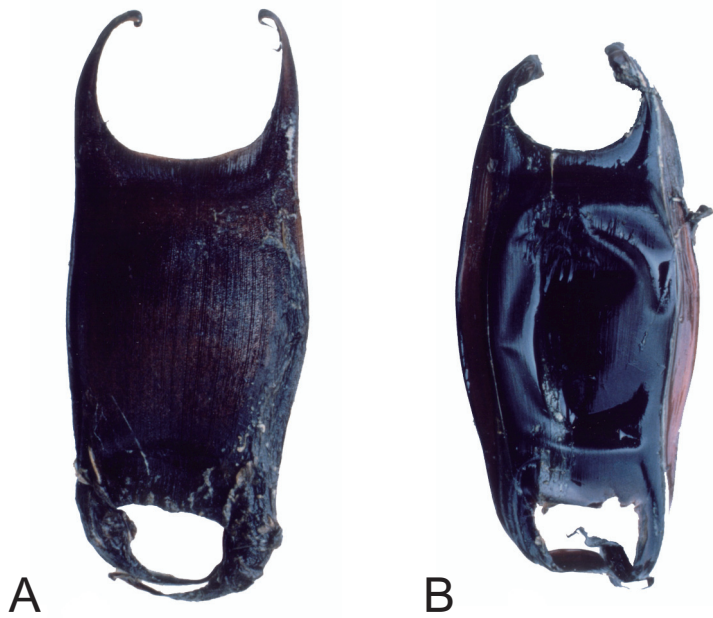


Fig. 2. Egg capsules of the genus *Bathyraja*. A: type B-I, *B. aleutica*, MTUF 26070, 126.0 × 89.0 mm; B: type B-II, *B. smirnovi*, MTUF 26167, 124.0 × 87.4 mm.



Fig. 3. Egg capsule of *Brochiraja asperula*, NSMT P42505, 37.3 × 22.0 mm.



Fig. 4. Egg capsules of the genus *Psammobatis*. A: *P. rudis*, ISH 499-178, 56.9 × 34.1 mm; B: *P. rutrum*, ISH 81-171, 52.2 × 35.4 mm; C: *P. scobina*, LACM 10438-4, 52.0 × 31.4 mm.

of the horns is circular; respiratory fissures are present near the tip of the anterior horns and at the mid-length of the posterior horns.

7. Egg capsules of the genus *Sympterygia* (Fig. 7)

The length of the main portion is more than two times as long as its width (long rectangular shape). The anterior and posterior

horns are almost equal in length. The surface is rough, similar to the type B-I of the genus *Bathyraja*.

8. Egg capsules of the genus *Anacanthobatis* (Fig. 8)

The length of the main portion is more than two times as long as its width (long rectangular shape); its surface is smooth.



Fig. 5. Egg capsules of the genus *Rhinoraja*. A: *R. kujiensis*, MTUF 26171, 110.8 × 71.8 mm ; B: *R. longicauda*, MTUF 26172, 85.0 × 48.0 mm; C: *R. odai*, MTUF 26173, 56.8 × 31.5 mm.



Fig. 6. Egg capsule of *Atlanteraja castelnaui*, ISH 439-178, 103.0 × 80.0 mm.

Fig. 7. Egg capsule of *Sympterygia bonapartei*, LACM 10438-3, 81.0 × 31.4 mm.

Fig. 8. Egg capsule of *Anacanthobatis ori*, MTUF P30568, 36.0 × 19.0 mm.

The posterior horns are long, about twice the width of the main portion. Cross section of the horns is circular; respiratory fissures are present at the tip of the anterior horns and at the mid-length of the posterior horns; the posterior aprons are well developed.

9. Egg capsules of the genus *Cruriraja* (Fig. 9)

The length of the main portion is more than twice as long as its width (long rectangular shape); its surface is smooth, with poorly developed longitudinal ridges. The posterior horns are long, about two times the width of the main portion; cross section of the horns is circular.

10. Egg capsules of the genus *Amblyraja* (Fig. 10)

The length of the main portion is variable, being less than twice as long as its width (rectangular shape) in *A. radiata* (Donovan, 1808), but it is more than twice as long as its width (long rectangular) in *A. doellojuradoi* (Pozzi, 1935); its surface is rough or smooth. The posterior horns are longer than the anterior horns, but less than 1.5 times the width of main portion; cross section of the horns is circular. Respiratory fissures are present at the tip of the anterior horns and at the base of the posterior horns. The lateral keels are wide, thin and translucent. The morphology of the ten *Amblyraja* species is regarded as conservative with small variation, which is also true of the morphology of the egg capsules of this genus. The egg capsules of the genus are defined as type A-I.

11. Egg capsules of the genus *Dipturus* (Fig. 11)

There are two types of egg capsules in this genus, types D-I and D-II. The type D-I shows close resemblance to the egg capsules from other genera of the family Rajidae. Those of *D. kwangtungensis* (Chu, 1960), *D. macrocaudus* (Ishiyama, 1955) and *D. tenuis* (Jordan & Fowler, 1903) belong to the type D-I (Fig.



Fig. 9. Egg capsule of *Cruriraja parcomaculata*, RUSIA3428, 45.0 × 24.4 mm.



Fig. 10. Egg capsules of the genus *Amblyraja*. A: *A. georgiana*, ISH 315-176, 116.5 × 80.0 mm; B: *A. radiata*, MTUF 26692, 79.7 × 63.4 mm; C: *A. doellojuradoi*, ISH 112-171, 86.4 × 56.2 mm.

11-A). In the type D-II, the aprons and keels are well developed and united with the main portion, the overall appearance is rectangular. Those of *D. batis* (Linnaeus, 1758), *D. gigas* (Ishiyama, 1958) and *D. nasutus* (Müller & Henle, 1841) belong to the type D-II (Fig. 11-B). In both types, the surface is smooth and respiratory fissures are present at the tips of the horns.

12. Egg capsules of the genus A (Fig. 12)

There are two types of egg capsules in the genus A. First, the egg capsule of *Raja rhina* Jordan & Gilbert, 1880 resembles the egg capsules of other genera from the family Rajidae, specifically type D-I of the genus *Dipturus* (Fig. 12-A). Second, the egg capsules of *Raja binoculata* Girard, 1855 (Fig. 12-B) and *R. pulchra* Liu, 1932 (Fig. 12-C) are more specialised; the lateral keels are concave at the mid-length and contain more than one embryo. These egg capsules belong to the type D-III.

13. Egg capsules of the genus B (Fig. 13)

In overall appearance, the egg capsules of the genus B show resemblance to the type D-I of the genus *Dipturus*; the surface is smooth. The lengths of the anterior and posterior horns are the same; cross section of the horns is circular; respiratory fissures are present at the tips of the horns.

14. Egg capsules of the genus *Fenestraja* (Fig. 14)

The length of the main portion is more than twice as long as its width (long rectangular shape); its surface is smooth. The posterior horns are long, more than twice as long as the width of the main portion. Cross section of the horns is circular. Respiratory fissures are present at the tip of the anterior horns and at the base of the posterior horns.

Although the genus belongs to the family Rajidae in the systematics of the order by Compagno (1999, 2005) and Ebert

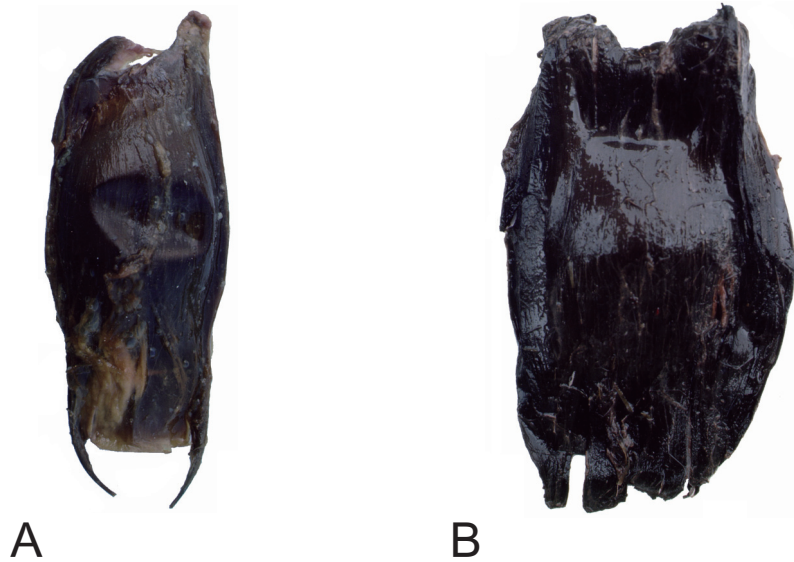


Fig. 11. Egg capsules of the genus *Dipturus*. A: type D-I: *D. macrocauda*, MTUF 26177, 130.0 × 60.0 mm; B: type D-II: *D. gigas*, MTUF 26175, 220.0 × 140.0 mm.

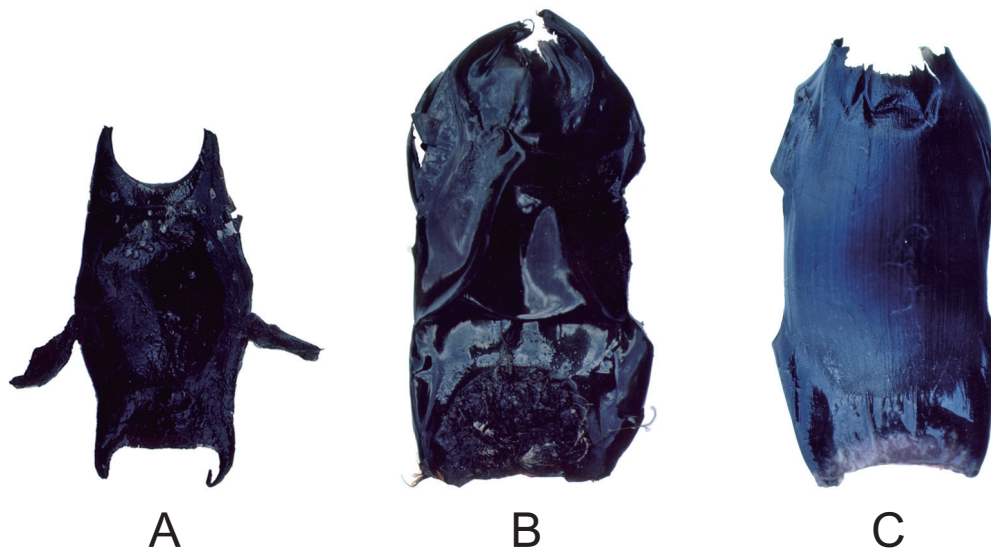


Fig. 12. Egg capsules of the genus A. A: type D-I: *Raja rhina*, RBCM 986-61, 103.0 × 69.4 mm; B and C: type D-III: *R. binoculata*, RBCM 986-60, 228.0 × 194.5 mm and *R. pulchra*, MTUF 26681, 145.0 × 70.0 mm.

& Compagno (2007), the genus should be shifted to the family Arhynchobatidae based on the morphology of the egg capsules, which shows resemblance to the egg capsules of the type II of the genus *Bathyraja*.

15. Egg capsules of the genus *Leucoraja* (Fig. 15)

In overall appearance, the egg capsules of the genus *Leucoraja* show resemblance to the type D-I of the genus *Dipturus*. The surface is smooth; the posterior horns are long, 1.5 times to two times as long as the width of the main portion; cross section of the horns is circular. Respiratory fissures are present at the tips of



Fig. 13. Egg capsules of the genus B. *Raja eglanteria*, MTUF 26689, 71.0 × 43.0 mm.

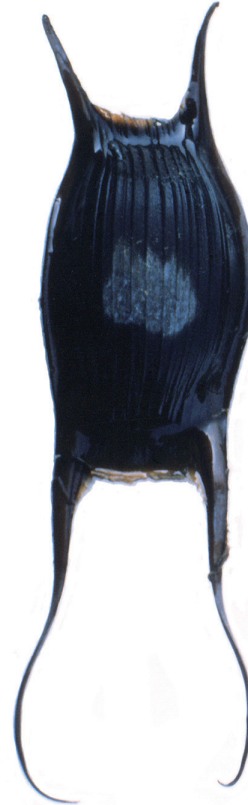


Fig. 14. Egg capsule of *Fenestraja* sp., TCWC 2196-1, 44.0 × 25.8 mm.

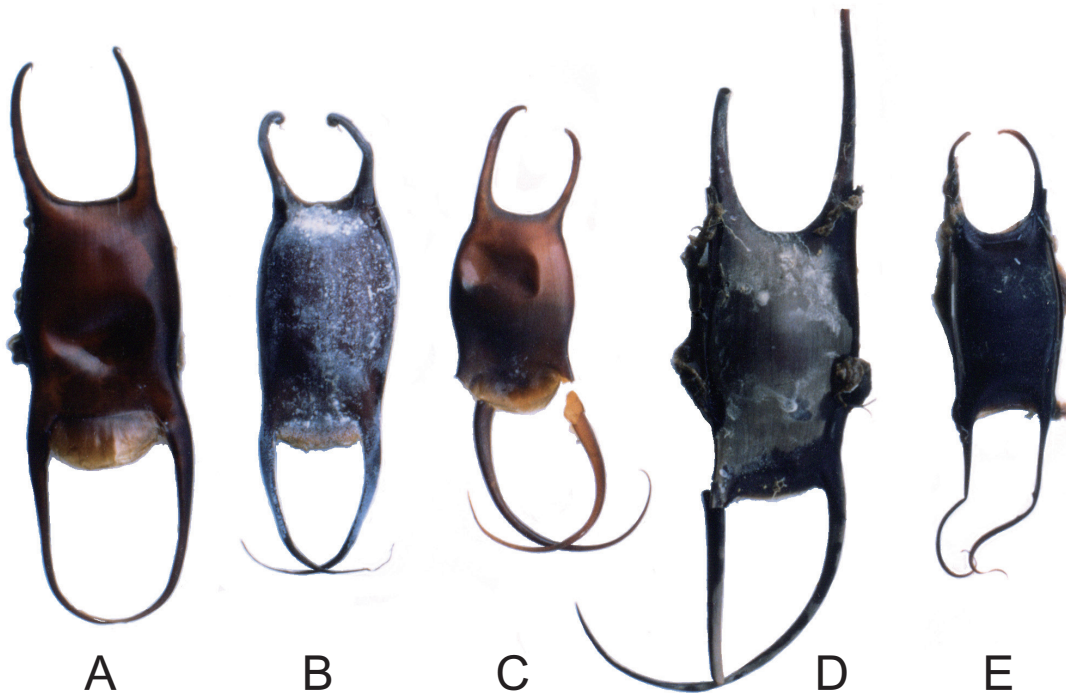


Fig. 15. Egg capsules of the genus *Leucoraja*. A: *L. fullonica*, MTUF 26693, 82.0 × 48.0 mm; B: *L. wallacei*, RUSIA4802, 73.0 × 42.0 mm; C: *L. naevus*, MTUF 26694, 61.0 × 34.0 mm; D: *L. ocellata*, VIMS 01358, 78.0 × 48.0 mm; E: *L. erinacea*, VIMS 01340, 53.0 × 36.0 mm.

the anterior horns and at the mid-length of the posterior horns.

16. Egg capsules of the genus *Malacoraja* (Fig. 16)

In overall appearance, the egg capsules of the genus *Malacoraja* show resemblance to the type D-I of the genus *Dipturus*. The surface is smooth; the horns are short; cross section of the horns is circular. Respiratory fissures are present at the tips of both anterior and posterior horns.

Compagno (1999, 2005) and Ebert & Compagno (2007) moved *Malacoraja fuliginea* (Bigelow & Schroeder, 1954) to the genus *Rajella*. However, based on the morphology of the egg capsules of the species, the species should be left in the genus *Malacoraja*.

17. Egg capsules of the genus *Okamejei* (Fig. 17)

In overall appearance, the egg capsules of the genus *Okamejei* show resemblance to the type D-I of the genus *Dipturus*. The surface is smooth. The lengths of the anterior and posterior horns are the same. Cross section of the horns is circular. Respiratory fissures are present at the tip of each horn. In the egg capsule of *O. kenojei* (Müller & Henle, 1841), tendrils are present on the keel.

18. Egg capsules of the genus *Raja* (Fig. 18)

In overall appearance, the egg capsules of the genus *Raja* show resemblance to the type D-I of the genus *Dipturus*. The surface is smooth; the lengths of the anterior and posterior horns are the same. Cross section of the horns is circular; respiratory fissures are present at the tip of each horn. Tendrils can be present on the keel in some species. The egg capsule of *Raja clavata* Linnaeus, 1758 shows close resemblance to the egg capsules of the genus *Malacoraja*, in which aprons and keels are well developed (Fig. 19).

19. Egg capsules of the genus *Rajella* (Fig. 20)

In overall appearance, the egg capsules of the genus *Rajella*

show resemblance to the type D-I of the genus *Dipturus*. The surface is smooth; the lengths of the anterior and posterior horns are the same. Cross section of the horns is circular; respiratory fissures are present at the tip of the anterior horns and located at the mid-length of the posterior horns.

The egg capsule of *Rajella leopardus* (von Bonde & Swart, 1923) differs not only from the egg capsules of the genus *Rajella*, but also from other genera of the family Rajidae (Fig. 20-A). Lateral keels are well developed with serrated edges; the horns are short and tough; respiratory fissures are present at the mid-length of the horns.

20. Egg capsules of the genus *Rostroraja* (Fig. 21)

The main portion is wide, its length less than 1.5 times its width;



Fig. 16. Egg capsules of *Malacoraja senta*, VIMS 01333, 55.0 × 41.9 mm.



Fig. 17. Egg capsules of the genus *Okamejei*. A: *O. acutispina*, MTUF 26683, 49.4 × 26.3 mm; B: *O. schmidtii*, MTUF 26687, 56.0 × 30.3 mm; C: *O. kenojei*, MTUF 26685, 47.8 × 29.1 mm; D: *O. boesemani*, MTUF 26684, 60.6 × 36.7 mm.

its surface is rough with longitudinal ridges. The horns are tape-like, cross section is depressed; the posterior horns are long, 1.5 times as long as width of main portion. Respiratory fissures are present at the base of each horn; lateral keels are well developed. The egg capsule from this genus is defined as type R-I.

Discussion

In the present study the phylogenetic relationships of skates are determined using the two fundamental steps developed by Hennig (1966). The first step is to determine the basic groups (lineages) of skates based on distributional patterns of skates. The second is to constitute a relationship of and within each

group based on the polarity of the morphology of egg capsule.

World distribution patterns of skates

In the order Rajiformes, more ancient groups such as *Bathyraja* and *Dipturus* are considered to be confined to deep waters and have a worldwide distribution (Hulley, 1972, Stehmann, 1986). Moreover, many *Bathyraja* and *Dipturus* species have a wide depth range from shelf to slope below the depth of 200 m. The distribution pattern of the 30 supraspecific taxa is shown in Table 3. It is evident from this table, that the genus *Amblyraja* also shows a worldwide distribution with the majority of species found in deepwater. Therefore, these three genera (lineages) *Amblyraja*, *Bathyraja* and *Dipturus* should be

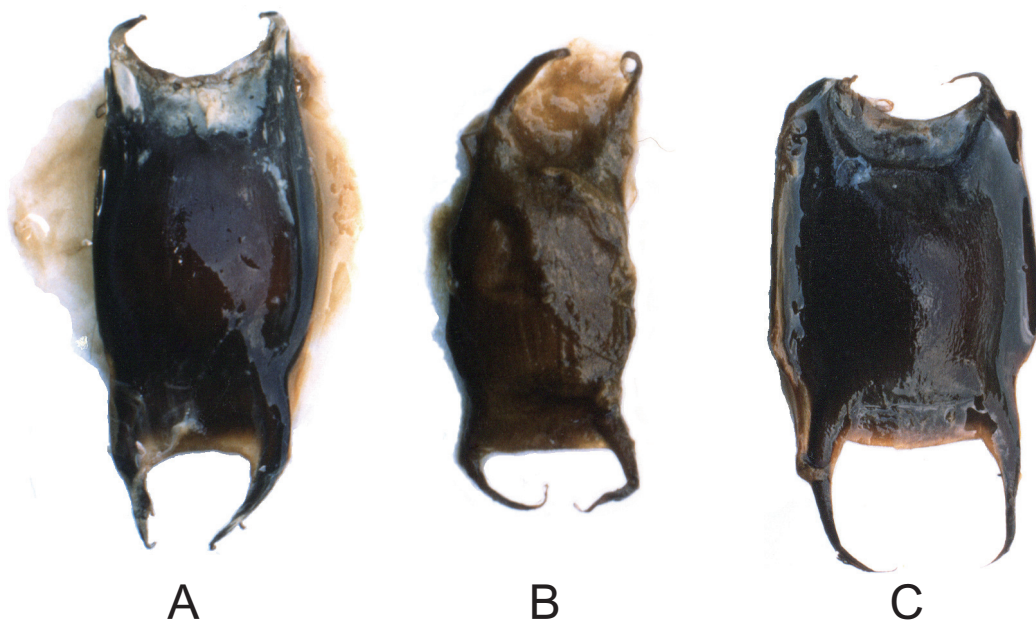


Fig. 18. Egg capsules of the genus *Raja*. A: *R. montagui*, MTUF 26691, 71.0 × 43.0 mm; B: *R. miraletus*, RUSI A4786, 45.5 × 29.0 mm, C: *R. clavata*, MTUF 26686, 83.0 × 68.6 mm.

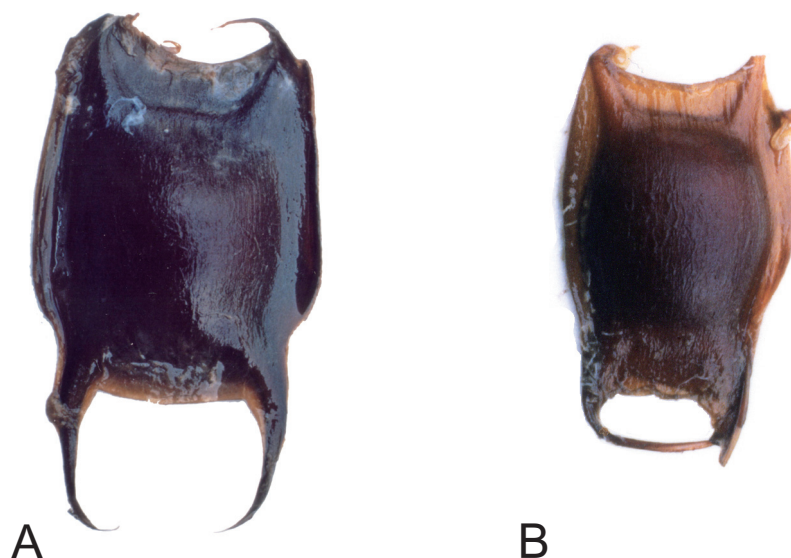


Fig. 19. Comparison between egg capsules of *R. clavata* (A), MTUF 26686 and *M. senta* (B), VIMS 01333.



A



B

Fig. 20. Egg capsules of the genus *Rajella*. A: *R. leopardus*, MTUF 26695, 74.0 × 74.5 mm; B: *R. bigelowi*, TCWC 2720-1, 53.0 × 29.9 mm.



Fig. 21. Egg capsules of *Rostroraja alba*, MTUF 30567, 141.0 × 120.4 mm.

Table 3. Distributional patterns of the 30 genera of skates around the world.

Family	Genus	Atlantic Ocean					Pacific Ocean					Indian Ocean		Polar Oceans	
		E.N. Atlantic	E.S. Atlantic	W.N. Atlantic	W.S. Atlantic	Argentina	Chile	E.S. Pacific	Australia & New Zealand	E.N. Pacific	W.N. Pacific	Indian Ocean	South Africa	Arctic Ocean	Antarctic Ocean
Arhynchobatidae	<i>Arhynchobatis</i>								●						
	<i>Bathyraja</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	<i>Irolita</i>								●						
	<i>Notoraja</i>										●	●			
	<i>Brochiraja</i>								●						
	<i>Pavoraja</i>								●						
	<i>Psammobatis</i>				●	●	●								
	<i>Pseudoraja</i>			●											
	<i>Rhinoraja</i>										●				
	<i>Rioraja</i>				●	●									
	<i>Atlantoraja</i>				●	●									
	<i>Sympterygia</i>				●	●	●								
Anacanthobatidae	<i>Anacanthobatis</i>			●							●	●	●		
	<i>Cruriraja</i>			●	●								●		
Rajidae	<i>Amblyraja</i>	●	●	●	●	●	●	●	●	●	●	●	●	●	●
	<i>Breviraja</i>			●	●										
	<i>Dactylobatus</i>			●											
	<i>Dipturus and Zearaja</i>	●	●	●	●	●	●	●	●		●	●	●	●	
	<i>Fenestraraja</i>			●				●							
	<i>Gurgesiella</i>				●	●	●	●							
	<i>Leucoraja</i>	●	●	●					●				●		
	<i>Malacoraja</i>	●	●	●	●								●		
	<i>Neoraja</i>	●	●	●									●		
	<i>Okamejei</i>								●		●	●	●		
	<i>Raja</i>	●	●	●								●	●		
	<i>Rajella</i>	●	●	●	●				●			●	●		
	<i>Rostroraja</i>	●	●									●	●		
	Genus A									●	●				
	Genus B			●						●					
	Genus C								●						

considered as three basic groups. The egg capsules of these three genera are thus considered to be three basic types.

The species of these three genera are distributed in waters deeper than 200 m and are adapted to the cold waters of high latitudes. The genera *Amblyraja* and *Bathyrāja* are also found in both Arctic and Antarctic seas (Stehmann 1986; Templeman 1982).

Commonality principle adopted for morphology of egg capsules to determine polarity

According to the distributional patterns of the skates in the world, the genera *Amblyraja*, *Bathyrāja* and *Dipturus* might be considered as three basic groups; skate genera can therefore be grouped based on the egg capsule morphology of these three genera. Furthermore, the egg capsule characteristics within each group can be considered more basic or primitive based on the commonality principle (see Table 2).

Grouping of skates based on the morphology of egg capsules

As shown in the previous paragraphs, the morphology of skate egg capsules might have derived from three basic generic types; *Bathyrāja* type (B-I and B-II), *Amblyraja* type (A-I), and *Dipturus* type (D-I, D-II and D-III). Additionally, the genus *Rostroraja* type (R-I) in the *Dipturus* type is considered to be an independent type since its egg capsules possess unique characters, i.e., rough surface, long and depressed horns, developed lateral keels and basic location of respiratory fissures. Thus, based on egg capsule morphology, these four genera are considered to be basic types in the order Rajiformes.

Trend of evolution

Evolutionary trends might be present in the following ways (see tables 2 and 4).

Surface: from rough to smooth

Posterior horns: from short to long, with their cross section from depressed to circular

Aprons and lateral keels: from poorly developed to well developed

Location of respiratory fissures: from base to tip

Interrelationships of skates based on the egg capsules

The interrelationships of skates based on the morphology of their egg capsules are shown in Figure 22.

1. A-I type (the genus *Amblyraja*)

The egg capsules of the genus *Amblyraja* show the following characteristics. Lateral keels are thin and well developed; length of horns is moderate (the same length as the main portion). Therefore, the genus *Amblyraja* might be in one independent lineage.

2. R-I type (the genus *Rostroraja*)

The egg capsules of the genus *Rostroraja* show the following characteristics. Surface rough; horns tape like, posterior horns extremely long; respiratory fissure present at the base of horns; lateral keel well developed. Therefore, the genus *Rostroraja* might be in one independent lineage parallel to the genera *Amblyraja*, *Bathyrāja* and *Dipturus*.

3. B-I and B-II types (the genus *Bathyrāja* and other related genera)

The egg capsules of the majority of *Bathyrāja* species, the

genus *Rhinoraja* and the genus *Sympterygia* show the following characteristics. Surface rough; length of horns moderate (the same length as the main portion); respiratory fissures present at the mid-length of horns. Therefore, the genera *Bathyrāja*, *Rhinoraja* and *Sympterygia* might be one independent lineage with the egg capsules of B-I type. The genera *Atlantoraja* and *Psammobatis*, which possess egg capsules of B-II type, might have derived from a group in *Bathyrāja*. Furthermore, the egg capsules of the genera *Anacanthobatis*, *Atlantoraja*, *Cruriraja*, *Fenestraja*, *Brochiraja* and *Notoraja* might have derived from the egg capsules of B-II type.

The genus *Fenestraja* should be placed in the family Arhynchobatidae rather than the family Rajidae, because the genus possesses egg capsules of the B-II type. The family Anacanthobatidae, consisting of the genera *Anacanthobatis* and *Cruriraja*, might be more closely related to the family Arhynchobatidae than to the family Rajidae.

4. D-I, D-II and D-III types (the genus *Dipturus* and other related genera)

The egg capsules of the majority of *Dipturus* species show the following characteristics. Surface smooth; length of horns moderate (the same length as the main portion); respiratory fissures present at the tip of horns. Therefore, the genera *Dipturus*, *Leucoraja*, *Malacoraja*, *Raja*, *Rajella*, *Okamejei*, part of genus A and genus B might be one independent lineage.

The egg capsules of D-II type might have derived from the egg capsules of D-I type, in which lateral keels and aprons are well developed to form an almost rectangular egg capsule (Fig. 23). In parallel the egg capsules of the type D-III were derived from the type D-I, containing more than one embryo (Fig. 23). Egg capsules of the D-III type are not only unique among the family Rajidae, but among the order Rajiformes. Therefore, a new genus should be proposed for *Raja binoculata* and *R. pulchra*.

The egg capsules of the genus *Malacoraja* show similarity to the egg capsules of the D-I type, except for well developed keels. Therefore, the egg capsules of the genus *Malacoraja* might have derived from the egg capsules of the type D-I.

The egg capsules of the genera *Rajella* and *Leucoraja* show similarity to the egg capsules of the D-I type by having a smooth surface and circular cross section of the horns. Those egg capsules might have derived from the egg capsules of the D-I type.

The egg capsule of *Rajella leopardus* shows unique characteristics of serrated edges of keels and short horns. Perhaps it might be better to establish a separate genus for this species.

Table 4. Evolutionary trends in skate egg capsules.

Characters	Primitive	Advanced
Surface	rough	smooth
Posterior horns	short	long
Shape of horn section	depressed	circular
Lateral keel	absent	developed
Apron	absent	developed
Respiratory fissure	base of horns	tip of horns

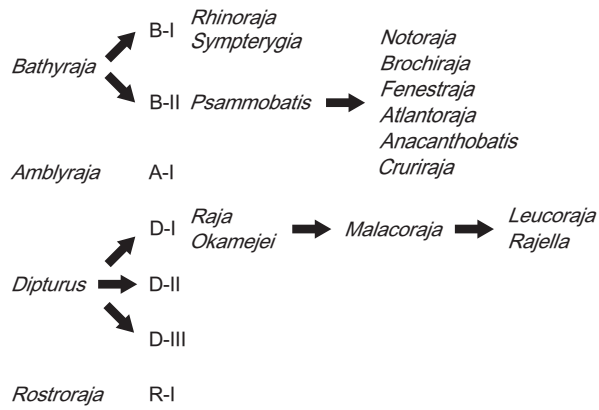


Fig. 22. The interrelationships of skates based on the morphology of the egg capsule.

**Systematics of skates based on their egg capsules,
modified from Compagno (1999, 2005)
and Ebert & Compagno (2007)**

The systematics of skates is proposed here according to the present results for 20 genera; the present systematics do not considerably affect those presented in the former studies.

Order Rajiformes

Family Arhynchobatidae

Genus *Bathyrāja*

Genus *Brochiraja*

Genus *Notoraja*

Genus *Fenestṛaja*

Genus *Psammobatis*

Genus *Rhinoṛaja*

Genus *Atlantoraja*

Genus *Sympterygia*

Family Anacanthobatidae

Genus *Anacanthobatis*

Genus *Cruriraja*

Family Rajidae

Subfamily Amblyrajinae

Genus *Amblyrāja*

Subfamily Rostrorajinae

Genus *Rostroraja*

Subfamily Rajinae

Genus *Dipturus*

Genus *Leucoraja*

Genus *Malacoraja*

Genus *Okamejei*

Genus *Raja*

Genus *Rajella*

Genus *Beringrāja* gen. nov.

Genus A

Genus B

Establishment of a new genus *Beringrāja*

According to the common unique characters found in the egg capsules of *Raja bonoculata* Girard and *Raja pulchra* Liu (Hitz,

1964; unpublished data, Ishihara) in addition to unique shared clasper characters as spoon-shaped distal tip of accessory terminal 1 (Ishiyama, 1967), we propose a new genus *Beringrāja* for the two species.

***Beringrāja* gen. nov. Ishihara, Treloar, Bor,**

Senou & Jeong

Type species: *Raja binoculata* Girard, 1855

Other species in the genus: *Beringrāja pulchra* (Liu, 1932)

Diagnosis. Egg-capsule keels are well developed, with middle part concave. Egg capsule with more than one embryo. Distal tip of the accessory terminal 1 clasper cartilage is spoon shaped, so the clasper component sentinel is widely expanded.

Remarks. The number of embryos in the egg capsule is according to Hitz (1964) for *B. binoculata* and to unpublished data by Ishihara for *B. pulchra*.

Morphology of accessory terminal 1 clasper cartilage according to clasper specimen, KPM-NI 29469 for *B. binoculata* and to Ishiyama (1967: page 35, Figure 7, E, F, H) for *B. pulchra*.

Etymology. The origin of the two species of the genus is thought to be in the Bering Sea since the two species are distributed allopatrically on both sides of the Bering Sea. Therefore, the prefix “*Bering*” is added to the scientific name “*rāja*”.

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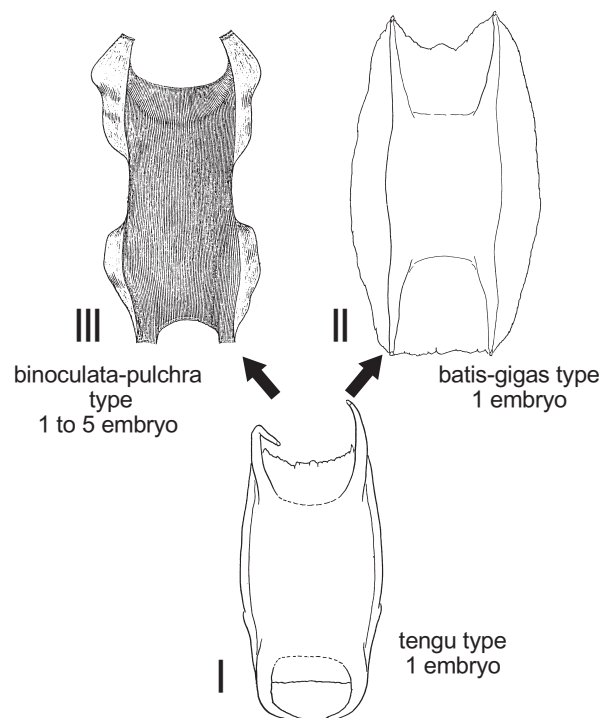


Fig. 23. Possible evolutionary trends in the three types of egg capsules of the family Rajidae, genera *Dipturus* and genus A.

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摘 要

Ishihara, H., M. Treloar, P. H. F. Bor, H. Senou & C. H. Jeong, 2012. The comparative morphology of skate egg capsules (Chondrichthyes: Elasmobranchii: Rajiformes). *Bull. Kanagawa prefect. Mus. (Nat. Sci.)*, (41): 9-25. (石原 元・Michelle Treloar・Peter H. F. Bor・瀬能 宏・鄭 忠勲, 2012. ガンギエイ目エイ類の卵殻の比較形態学的研究. 神奈川県立博物館研究報告 (自然科学), (41): 9-25.)

ガンギエイ目(軟骨魚綱板鰐亜綱)の目内の系統類縁関係を検討する目的で、20属64種のガンギエイ目エイ類の卵殻の形態を比較した。卵殻の形態に本目内30属の地球上の分布パターンの分析を加えて、本目内には以下の4系統の存在が推定された: 1) *Bathyrāja*; 2) *Amblyrāja*; 3) *Dipturus*; 4) *Rostrorāja*。 *Bathyrāja* を原型とする系統は、*Rhinorāja* および *Sympterygia* からなるグループ(B-I)へ特化する系統と、*Psammobatis* から、*Notorāja*、*Brochirāja*、*Fenestrāja*、*Atlantorāja*、*Anacanthobatis* および *Crurirāja* の6群からなるグループへと特化する系統(B-II)に2分される。*Dipturus* を原型とする系統は3分岐(D-I、D-IIおよびD-III)し、そのうちの1系統(D-I)は *Raja* および *Okamejei* からなるグループから、*Malacorāja* を経て *Leucorāja* および *Rajella* からなるグループへと特化する。卵殻の形態から推定された系統を考慮して既存の分類体系を再構築した結果、ガンギエイ目は *Arhynchobatidae* (*Bathyrāja* や *Notorāja* など8属)、*Anacanthobatidae* (*Anacanthobatis* および *Crurirāja* の2属) および *Rajidae* (*Amblyrajinae* の *Amblyrāja*、*Rostrorajinae* の *Rostrorāja*、*Rajinae* の *Dipturus* など3亜科11属)の3科3亜科21属に分類するのが妥当であると判断された。*Rajinae* に含まれる属には、新属 *Beringrāja* (タイプ種: *Raja binoculata* Girard, 1855; *B. binoculata* とメガネカスベ *B. pulchra* (Liu, 1932)の2種から構成され、卵殻に2個以上の胚を持つことを主な特徴とする)と、それぞれ学名未確定の2単系属 (Genus A および Genus B)が含まれる。卵殻の形態から、*Fenestrāja* は *Arhynchobatidae* に、*Raja clavata* Linnaeus, 1758 は *Malacorāja* にそれぞれ帰属させるべきと判断された。

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