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Zoogeography of Taiwanese Fishes

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ABSTRACT Three categories (freshwater, amphidromous, and marine fishes) of Taiwanese fishes are analyzed on the basis of zoogeographic elements, *viz*. China element, Indo-China element, Indo-West Pacific element, Indo-Pacific element, North-Pacific element, Japan-Oregon element, and circumtropical element. Freshwater fishes, which include the China and Indo-China elements, are distributed on part of the boundary area between the Palaearctic and Oriental regions of Wallace (1876). Diadromous fishes include the North-Pacific, Indo-China and Indo-West Pacific elements. Taiwanese salmon, a landlocked (initially diadromous) species that became established in Taiwan between 0.5 my B.P. and the early Pleistocene, is recognized as a distinct taxon included within the *Oncorhynchus masou* complex, which comprises here three species and two subspecies, *viz*. *Oncorhynchus masou masou* (Sancheoneo, Songeo, Sakura-masu or Yamame), *O. masou ishikawae* (Satsuki-masu or Amago), *O*. sp. (Biwa-masu), and *O. formosanus* (Taiwanese salmon), based on molecular, morphological and biological studies. Marine fishes are discussed under the following headings, brackish-water fishes (fishes of brackish waters and seas adjacent to continental coastlines, North Pacific and Indo-West Pacific elements; fishes of brackish waters and seas primarily around islands, Indo-West Pacific element), reef fishes (fishes of inshore reefs along continental coastlines from 0 to ca.100 m depth, Indo-West Pacific element; fishes of inshore reefs primarily around islands from 0 to ca.100 m depth, Indo-West Pacific element; fishes of offshore reefs along continental shelf edges from ca.150 to 300 m depth, circumtropical and Indo-Pacific elements; fishes of offshore reefs primarily around islands from ca.150 to 300 m depth, Indo-Pacific element), demersal fishes (fishes on continental shelves shallower than ca.150 m depth, Indo-West Pacific and Japan-Oregon elements; fishes on edges and upper continental slopes from ca.150 m to 500 m depth, Indo-West Pacific, Indo-Pacific, and circumtropical elements; fishes on lower continental slopes to abyssal plains from ca.500 m to 6,000 m depth, circumtropical element and rarely Indo-Pacific element), pelagic fishes (epipelagic fishes from 0 to ca.150 m depth, Indo-West Pacific, Indo-Pacific or circumtropical elements; meso- and bathypelagic fishes from ca.150 to 3,000 m depth, circumtropical element). The distribution of Taiwanese marine fishes are influenced by the Kuroshio Current, low-salinity and low-temperature waters from mainland China, and sea-bottom topography.

Key words : Taiwanese fishes, zoogeographic element, Taiwanese salmon

INTRODUCTION

The fishes of Taiwan were first studied by Jordan and Evermann (1902) and Jordan and Richardson (1909), especially, the freshwater fishes of Taiwan being later reported by Oshima (1919, 1923). Later, J. T. F. Chen (1969) and S.-C. Shen (Shen ed., 1993) published comprehensive studies on Taiwanese fishes; most recently, Shao *et al*. (2008) compiled a list of the marine fishes of southern Taiwan. Zoogeographically, shallow-water marine Taiwanese fishes belong to the Indo-West Pacific region, the deep water meso- and benthopelagic fishes are tropical. On the other hand, freshwater Taiwanese fishes have origins and relatives with both the northern and southern parts of mainland China. The following discussion of zoogeographic characteristics of Taiwanese fishes is based upon their life history/habitat characteristics and zoogeo-

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graphic element.

Freshwater fishes Living in freshwater environments (lakes, ponds, and rivers) throughout life; corresponding to "the primary division of strictly freshwater fishes" sensu Darlington (1957).

Diadromous fishes Migrating between marine and freshwater habitas during life; including anadromous, catadromous, and amphidromous fishes. Anadromous fishes mature in marine environments and move into rivers to spawning. Catadromous fishes mature in freshwater and subsequently move downstream to spawning in the sea. Amphidromous fishes mature and spawn in freshwater, but spend their larval stage in the sea. These categories follow Myers (1949).

Marine fishes Living in marine environments throughout life. Some brackish-water species are included with marine fishes, because of fully marine relatives. Taiwanese marine fishes are here considered based on their habitats; brackish water, reef, demersal, and pelagic.

East Asian freshwater, amphidromous, and marine fishes occupy several zoogeographic areas, those of the former two groups having been considered by Mori (1936b) and Aoyagi (1957), and the latter by Nakabo (2002b). However, such zoogeographic areas overlap as seen in Taiwanese fishes. Accordingly, fishes should be recognized based on their origins in each zoogeographic area. The concept of zoogeographic element was presented by Ekman (1953) and further discussed by Nishimura (1971). Ekman's (1953) zoogeographic elements are set at the specific or familial levels, whereas Nishimura (1971) presented aspects of zoogeographic elements of marine animals only at the specific level. Zoogeographic element are here considered at the generic, familial, or suprafamilial levels. Definitions of Indo-West Pacific and Indo-Pacific regions follow Nakabo ed. (2002).

China element Freshwater species with origins primarily in the China subregion sensu Mori (1936b).

Circumtropical element Marine species with warm water origins worldwide (Nishimura, 1971).

Indo-China element Freshwater and amphidromous species with origins primarily in the Indo-China subregion of Mori (1936b).

Indo-Pacific element Marine species with relatives or origins in the Indo-Pacific.

Indo-West Pacific element Brackish water, marine and amphidromous species with origins mainly in the Indo-West Pacific (Ekman, 1953; Nishimura, 1971).

Japan-Oregon element Marine species with origins in both East Asian seas and Pacific coast of North America (Ekman, 1953; Nishimura, 1971), derived from the North Pacific element.

North Pacific element Anadromous, amphidromous, and brackish water species here with origins primarily in the North Pacific.

1. Freshwater fishes

Wallace (1876) divided the world fauna into the six regions, *viz*. Palaearctic, Neoarctic, Neotropical, Ethiopian, Oriental and Australian regions. In the East Asia, the Palaearctic region borders on the Oriental region, in which Taiwan was included by Wallace (1876). The mammals of Taiwan are allied to Indian or Malayan species, rather than to Chinese species, and the birds are related to those of the Himalayas, South India, the Malay Islands, or Japan, rather than to those of the Chinese Continent (Wallace, 1876, 1880). On the other hand, the freshwater fishes of Taiwan evenly comprise Palaearctic and Oriental species (sensu Wallace, 1976) according to Oshima (1923); the two regions were subsequently referred to the China and Indo-China subregions, respectively by Mori (1936b), and correspond to the East and South China regions sensu Li (1981). Tzeng (1986b) discussed the origins of Taiwanese freshwater fishes in relation to the geological history of Taiwan and the Chinese Continent. These freshwater fishes are here described zoogeographically according to the China and Indo-China elements, with reference to Oshima (1923), Mori (1936b), Li (1981), Kuronuma (1961), Rainboth (1996), and Kottelat (2001). Identifications follow Tzeng (1986a), Tao (2004), and Chen and Chang (2005).

1) China element

The fishes included here are distributed widely in middle China from Guandong Province northward to Liaoning Province, and also in the Korean Peninsula, Taiwan, Kyushu, Shikoku, Honshu, and southern Hokkaido. In Taiwan, such fishes include *Opsariichthys evolans*, *O. pachycephalus*, *Zacco platypus*, *Rhodeus ocellatus ocellatus*, *Tanakia himantegus*, *T. chii*, *Hemibarbus labeo*, *Pseudorasbora parva*, *Squalidus argentatus*, *S. iijimae*, *Microphysogobio brevirostris*, *M. alticorpus*, *Cyprinus carpio*, *Carassius* spp., *Gobiobotia cheni*, *G. intermedia*, *Cobitis sinensis*, *Misgurnus anguillicaudatus*, *Pseudobagrus brevianalis brevianalis*, *P. brevianalis taiwanensis*, *Tachysurus adiposalis*, *Liobagrus formosanus*, *Silurus asotus*, and *Oryzias latipes*.

Ma *et al.* (2006) demonstrated two genetically differentiated morphotypes (L1 and L2) in *Z. platypus*, being distributed only in northern areas within Taiwan. Type L1 is recognized as *Opsariichthys evolans* (Jordan and Evermann, 1902) by Chen and Chang (2005) and Chen *et al*. (2008). Type L2 was most likely introduced to Taiwan from Lake Biwa, Japan, along with *Plecoglossus altivelis altivelis*, about 20 years ago (Chen and Chang, 2005).

2) Indo-China element

The fishes included here are distributed mainly in nor-

thern South East Asia and southern China from Guangxi Province northward to near the Changjiang River, in addition to Hainan Island and Taiwan. In Taiwan, they include *Candidia barbata*, *Pararasbora moltrechti*, *Sinibrama macrops*, *Metzia formosae*, *Chanodichthys erythropterus*, *Culter albumus*, *Hemiculter leucisculus*, *Cultrichthys erythropterus*, *Puntius semifasciolatus*, *P. snyderi*, *Megalobrama amblycephala*, *Distoechodon tumirostris*, *Spinibarbus hollandi*, *Acrossocheilus paradoxus*, *Onychostoma alticorpus*, *O. barbatulum*, *Cirrhinus molitorella*, *Aphyocypris kikuchii*, *Formosania lacustre*, *Crossostoma lacustre*, *Hemimyzon formosanus*, *H. taitungensis*, *Sinogastromyzon puliensis*, *S. nantaiensis*, *Clarias fuscus*, *Monopterus albus*, *Trichogaster trichopterus*, *Macropodus opercularis*, *Anabas testudineus*, *Channa asiatica*, *C. maculata*, *C. striata*, and *Macrognathus aculeatus*.

2. Diadromous fishes

1) North Pacific element

Taiwanese representatives of this element include *Oncorhynchus formosanus* and *Plecoglossus altivelis altivelis*.

***Oncorhynchus formosanus* (Taiwanese salmon):** Recently considered to be a subspecies of *Oncorhyncus masou*, along *O. m. masou* (Sancheoneo, Songeo, Sakura-masu or Yamame), *O. m. ishikawae* (Satsuki-masu or Amago), and *O. m.* subsp. (Biwa-masu) (Kimura, 1990; Hosoya, 2002), the systematic position of Taiwanese salmon is reconsidered here. Based on molecular, morphological and biological studies, Biwa-masu is considered to be a separate species from Sancheoneo (Songeo, Sakura-masu, or Yamame) and Satsuki-masu (Amago), the latter two being recognized as subspecies following molecular studies by Oohara and Okazaki (1996) and McKay *et al*. (1998). Biwa-masu and Satsuki-masu (Amago) are biologically separated from each other in Lake Biwa and its associated streams (Kato, 1978b; Kuwahara and Iguchi, 2007). Taiwanese salmon is also recognized as specifically distinct from Sancheoneo (Songeo, Sakura-masu, or Yamame), Satsuki-masu (Amago), and Biwa-masu following molecular analyses (Numachi *et al*., 1990; Gwo *et al*., 2008). The following specific and subspecific names follow Kimura (1990), the classification of the *Oncorhynchus masou* complex shown here being consistent with Mayr's (1942, 1969) criterion.

Oncorhynchus masou masou (Brevoort, 1856): Sancheoneo (Songeo, Sakura-masu, or Yamame)

Oncorhynchus masou ishikawae Jordan and McGregor, 1925: Satsuki-masu (Amago)

Oncorhynchus sp.: Biwa-masu

Oncorhynchus formosanus (Jordan and Oshima, 1919): Taiwanese salmon

Oncorhynchus formosanus, originally described by Jordan and Oshima (1919), is landlocked in Taiwan and restricted to six upper streams of the Tachia River, *viz*. Sukairan Stream, Hsueshan Stream, Kiawan Stream, Kaunu Stream, Nan-fu Stream, and Ho-huan Stream (Kano, 1935, 1940). *Oncorhynchus masou masou* is widely distributed along the Sea of Japan coasts (East Sea) of Honshu and Hokkaido, the Korean Peninsula, Maritime Province, and Sakhalin Island, along the Pacific coasts of Hokkaido and Honshu southward to Sagami Bay, and along the Okhotsk coasts of Hokkaido, Sakhalin Island, the Kuril Islands, and southern Kamchatka (Mori, 1935, 1936a; Oshima, 1957; Kiso, 1995). *Oncorhynchus masou ishikawae* is distributed along the Pacific coast of Honshu (between Izu Peninsula and Kii Peninsula), the Pacific coast of Shikoku and the coast of Seto Inland Sea including Osaka Bay (Oshima, 1957). Biwa-masu (*Oncorhynchus* sp.) is endemic to Lake Biwa (Hosoya, 2002).

Oncorhynchus formosanus was initially thought to be a glacial-age relict (Oshima, 1934; Kano, 1935, 1940). Uyeno *et al*. (1975) reported salmonid fossils from the Kusu Basin, Oita Prefecture, Japan, and Uyeno *et al*. (2000), indicating a lepidological similarity of "fossil *Oncorhynchus*" to Biwa-masu (*O*. sp.), recognized the latter as a Lake Biwa relict. Although the "fossil *Oncorhynchus*" has been dated to 0.5～0.4 my B.P. (middle Pleistcene) (Uyeno *et al*., 2000), an interglacial period between the Marine Isotope Stage (MIS) 14 and MIS 12 glacial ages (Gibbard and von Kolfshoten, 2004), the age of *O. formosanus* divergence is uncertain.

The *Oncorhynchus masou* complex is monophyletic according to molecular studies (Murata *et al*., 1998; Gwo *et al*., 2008). Oohara and Okazaki (1996) believed Biwa-masu to be genetically distinct from the more closely related *O. m. masou* and *O. m. ishikawae*, following mitochondrial DNA sequence analysis. And, genetic relationship between *O. m. masou* and *O. m. ishikawae* are recognized again as subspecies from each other based on nuclear and mitochondrial DNA analyses (McKay *et al*., 1998). Notwithstanding, an AFLP analysis by Gwo *et al*. (2008) indicated that within the *Oncorhynchus masou* complex, *O. formosanus* was the most distant, *O. m. masou* being more distant from *O. m. ishikawae* and Biwa-masu (*O*. sp.) than *O. m. ishikawae* was from Biwa-masu (*O*. sp.), a clear conflict with Oohara and Okazaki (1996) and McKay *et al*. (1998). The study by Gwo *et al*. (2008) is considered less reliable here, owing to AFLP analysis often showing genetic similarities among taxa, in addition to Gwo *et al*.'s use of cultivated specimens of *O. m. ishikawae* and Biwa-masu (*O*. sp.).

The meristic counts of the *O. masou* complex, including the "fossil *Oncorhynchus*" are shown in Table 1. *Oncorhynchus formosanus* and the fossil species have ca. 13～14 dorsal-fin and ca.13 anal-fin rays, fewer than Biwa-masu (*O*. sp.), *O. m. masou*, and *O. m. ishikawae*, which have ca.15 dorsal-fin and ca.15 anal-fin rays. Furthermore, *O. formosanus* has ca.61 vertebrae, fewer than the fossil specimen, *O. m. masou*, *O. m. ishikawae*, and

Table 1. Meristic counts of the "fossil *Oncorhynchus*", *O. formosanus*, *O. m. masou*, *O. m. ishikawae* and Biwa-masu (*O.* sp.). Values are expressed as means. Lateral l. sc; lateral line scales

	Dorsal rays	Anal rays	Pelvic rays	Lateral l. sc.	Vertebrae
"fossil *Oncorhynchus*"[*1]	13.3	13.0	9.3	ca.125	63.5
O. formosanus[*2]	13.7	13.3	9.0	123.3	–
O. formosanus[*3]	–	11.4	9.0	121.8	61.8
O. formosanus[*4]	13.8	12.6	–	139.0	61.6
O. formosanus[*5]	14.4	12.6	8.9	129.7	61.9
O. formosanus[*6]	–	13.6	–	–	62.1
O. m. masou[*3]	–	13.2	9.2	121.0	64.9
O. m. masou[*4]	15.4	14.8	–	134.0	64.2
O. m. masou[*5]	15.1	15.4	10.0	129.4	64.8
O. m. ishikawae[*4]	15.4	14.2	–	132.8	64.4
O. m. ishikawae[*5]	14.7	15.0	11.1	139.7	65.6
O. m. ishikawae[*7]	–	–	9.0	–	–
Biwa-masu (*O.* sp.)[*4]	15.4	14.5	–	135.6	64.5
Biwa-masu (*O.* sp.)[*7]	–	–	9.0	–	–

*[1]Uyeno *et al.* (1975); *[2]Teng (1957); *[3]Behnke *et al.* (1962); *[4]Watanabe and Lin (1985); *[5]Jan *et al.* (1990); *[6]Gwo (2009); *[7]Kato (1978b).

Biwa-masu (*O.* sp.), which have ca.63～65 vertebrae. Clearly, the meristic counts of the "fossil *Oncorhyncus*" place it somewhere between *O. formosanus* and the other three present-day taxa in the *O. masou* complex.

Lepidological studies of the *O. masou* complex (Oshima, 1934, 1957; Teng, 1959; Kawashima and Suzuki, 1968; Kato, 1978a, 1981; Kiso, 1995) have shown three significant morphological states, *viz*. scale ridges circular, focus located near scale center (Biwa-masu and the "fossil *Oncorhynchus*"); ridges circular or semicircular, focus located near scale center (*O. formosanus*); ridges semicircular or circular, focus located anterior to scale center (*O. m. masou* and *O. m. ishikawae*). Although young specimens of all taxa have circular scale ridges (Kato, 1978a; Kiso, 1995), the location of the scale focus does not change with growth. On the basis of focus location, therefore, *O. formosanus* is more similar to the "fossil *Oncorhynchus*" and Biwa-masu (*O.* sp.) than to *O. m. masou* and *O. m. ishikawae*.

Oncorhynchus formosanus was initially thought by Oshima (1934) to be similar to *O. m. ishikawae*, although he later (Oshima, 1957) believed it to be closer to *O. m. masou*, a change of opinion based on the presence or absence of red spots on the body (see also Aoki, 1917; Tzeng, 1986b; Gwo, 2008).

The distinctness of *Oncorhynchus formosanus*, both morphologically and genetically, from the other three present-day taxa, and the position of the "fossil *Oncorhynchus*" (Fig. 1) lends to a consideration of divergence time for *O. formosanus*. The genetic distance between Biwa-masu (*O.* sp.) and the *O. masou* two subspecies corresponds to 0.5 my or 1.1～2.0 my, as estimated by two different methods (Oohara and Okazaki, 1996). On the other hand, the "fossil *Oncorhynchus*" existed during

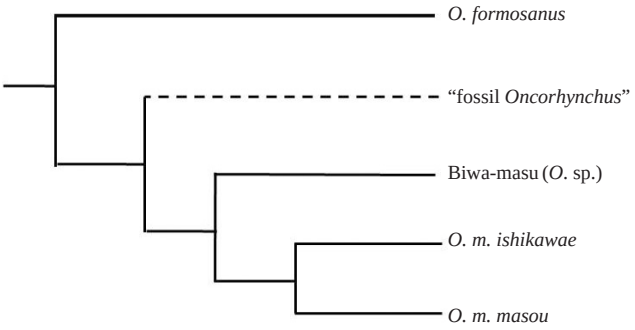

Fig. 1. Hypothetical phylogeny of the *Oncorhynchus masou* complex including "fossil *Oncorhynchus*".

the middle Pleistocene, 0.5～0.4 my B.P. (Uyeno *et al*., 2000). If the "fossil *Oncorhynchus*" is closely related to Biwa-masu (*O.* sp.), as stated by Uyeno *et al*. (2000), the genetic distance between Biwa-masu (*O.* sp.) and the two subspecies of *O. masou* corresponds to ca.0.5 my. Therefore, *O. formosanus* likely separated earlier from other taxa within the *O. masou* complex, including the fossil species. According to Numachi *et al*. (1990), the genetic distance between *O. formosanus* and *O. m. masou* corresponds to 0.1～0.8 my. Accordingly, *O. formosanus* arrived in Taiwan between 0.8 my and 0.5 my B.P., a period during which four glacial ages occurred, *viz*. MIS 14 (0.5 my B.P.), MIS 16 (0.62 my B.P.), MIS 18 (0.71 my B.P.), and MIS 20 (0.79 my B.P.) (Gibbard and van Kolfschoten, 2004). The present difficulty in estimating divergence time from genetic distance may be overcome by furture genetic studies. It is most likely, however, that *O. formosanus* arrived in Taiwan during a glacial age before 0.5 my B.P., because the "fossil *Oncorhynchus*" was present 0.5～0.4 my B.P. Neave's (1958) statement that *Oncorhynchus* diverged from *Salmo* at or near the beginning of the Pleistocene, indicated that *O. formosanus* arrived in Taiwan in the early or middle Pleistocene, which is consistent with the above.

The four recent taxa of the *O. masou* complex apparently achieved their present distribution less than 8500 years B.P. when the Tsushima Strait opened (Oba *et al*., 1991). The distribution of *O. m. masou*, clearly separated from that of *O. m. ishikawae*, in Kyushu, Shikoku, and Honshu (Oshima, 1957), should be interpreted by earlier sea patterns. *Oncorhynchus m. masou* has sea-run forms off the coast of the Sea of Japan (East Sea) and the Pacific coasts of the Tohoku District (Kiso, 1995), and *O. m. ishikawae* has similar forms in Seto Inland Sea and Ise Bay (Kato, 1973a, b, 1975). The distribution of *O. m. masou*, roughly corresponding to the route of the Tsushima Current, and that of *O. m. ishikawae*, roughly corresponding to the route of the Kuroshio Current, are similar to those of two subspecies of the Japanese surfperch *Ditrema temminckii* (Katafuchi and Nakabo, 2007) and those

of two geographic populations of both *Pterogobius elapoides* and *P. zonoleucus* (Akihito *et al*., 2008). Biwamasu is probably relictual in Lake Biwa, because the "fossil *Oncorhynchus*" occurred in Kusu Basin, Oita Prefecture in the middle Pleistocene (Uyeno *et al*., 2000). *Oncorhynchus formosanus* is also relictual in the Tachia River, Taiwan, being well separated genetically from the other three taxa in the *O. masou* complex. A better understanding of the evolutionary history of the *Oncorhynchus masou* complex requires further studies of the molecular genetics, comparative morphology, and biology of the four recent taxa. Furthermore, it remains unclear whether *O. m. ishikawae* in upstream reaches of the rivers flowing into Lake Biwa is native or introduced.

***Plecoglossus altivelis altivelis*:** *Plecoglossus altivelis* is amphidromous, being widely distributed in East Asia, including northern Vietnam, Tonkin Bay northward to the coast of Pohai (China), Taiwan, the Korean Peninsula (western, southern, and eastern districts), the Ryukyu Islands, and Kyushu, Shikoku, Honshu, and Hokkaido (Japan). Initially distributed in the northern area of Taiwan (Tzeng, 1986a), *P. altivelis* became extinct there, but was later introduced into the Tansui River from Lake Biwa stocks (Chen and Chang, 2005). Two subspecies have been recognized, *viz*. *P. a. altivelis* and *P. a. ryukyuensis* (Nishida, 1988). Tao (2004) recognized Taiwanese *P. altivelis* (as *P. a. altivelis*) as being different from *P. a. ryukyuensis* (from Ryukyu Islands), Tzeng (1986a) having earlier described Taiwanese *P. altivelis* as differing in some meristic counts from Japanese *P. altivelis*, *viz*., ca. 10 fewer lateral-line scales, 2 additional scales above the lateral line (TRa, see Nakabo, 2002a), and 2 additional pectoral-fin rays.

The distribution of *Plecoglossus altivelis altivelis* expanded following the opening of the Tsushima Strait 8500 years B.P. However, the initial divergence time of the two subspecies is unknown. It is likely that *P. a. ryukyuensis* was more widely distributed prior to 8500 years B.P.

2) Indo-China element

Rhinogobius species with Indo-West Pacific origins are either amphidromous or landlocked (originally amphidromous). They are widely distributed throughout the Indo-China Peninsula, Hainan Island, Taiwan, Lanyu Islands, mainland China, Cheju Island, the Korean Peninsula, Maritime Province, Ryukyu Islands, Ogasawara Islands, Kyushu, Shikoku, Honshu, southern Hokkaido, and the Philippine Islands (Herre, 1927; Lindberg and Krasyukova, 1975; Chen *et al*., 1998; Akihito *et al*., 2002; Choi *et al*., 2002; Chen and Kottelat, 2003; Wu and Chen, 2008). At least, eight species of *Rhinogobius* are known in Taiwan (Chen *et al*., 2005).

3) Indo-West Pacific element

Rhyacichthys aspro is distributed along the eastern coast of Taiwan (Shao and Chen, 2003). This amphidromous species occurs from Indonesia northward to the Philippine Islands, Taiwan, the southern Ryukyu Islands, and eastward to the Solomon Islands in the West Pacific.

4) Circumtropical element

These fishes, *viz*. *Anguilla japonica*, *A. marmorata*, *Sicyopterus macrostetholepis*, *S. japonicus*, and *Stiphodon elegans*, of circumtropical origins, are distributed primarily along the eastern coast of Taiwan (Tzeng, 1986a; Chen and Fang, 1999; Shao and Chen, 2003). They occur from Indonesia northward to the Philippine Islands, Taiwan, the Ryukyu Islands, the Pacific coasts of Kyushu, Shikoku, and southern Honshu (northward to Boso Peninsula), along the route of the Kuroshio Current. *Anguilla japonica* and *A. marmorata* are catadromous, but *Sicyopterus macrostetholepis*, *S. japonicus*, and *Stiphodon elegans* are amphidromous.

3. Marine fishes

1) Brackish water fishes

(1) Fishes of brackish waters and seas adjacent to continental coastlines

North Pacific element *Salangichthys ariakensis* is distributed along the western coast of Taiwan (Tao, 2004).

Indo-West Pacific element These species occur in northern and western Taiwan (Shao and Chen, 2003), and they (or their relatives) are widespread along the Chinese coasts bordering the East and South China Seas, Yellow Sea coasts of China and Korea, Ariake Bay (Japan), and elsewhere in the Indo-West Pacific. Species include *Ilisha elongata*, *Nematolosa japonica*, *Thryssa hamiltoni*, *T. setirostris*, *Hyporhamphus sajori*, *Lateolabrax* sp. (Tairiku-suzuki), species of Sciaenidae, *Taeniodes cirratus*, and *Boleophthalmus pectinirostris*.

(2) Fishes of brackish waters and seas primarily around islands

Indo-West Pacific element These fishes are distributed along the southern, western, and northern coasts of Taiwan (Shao and Chen, 2003). Together with related taxa they are distributed in Indonesia and northward to the Philippine Islands, Taiwan, the Ryukyu Islands, and the Pacific coasts of Kyushu, Shikoku and Honshu (northward to Boso Peninsula). The Taiwan representatives include *Chanos chanos*, *Ambassis commersoni*, *A. gymnocephalus*, *A. miops*, *Terapon jarbua*, *Rhyncopelatus oxyrhynchus*, *Kuhlia marginata*, *K. mugil*, *Scatophagus argus*, *Liza dussumieri*, *Chelon macrolepis*, *C. subviridis*, *Mugil cephalus*, *Brachyamblyopus anotus*, *Callogobius tanegasimae*, *Awaous melanocephalus*, *Cristatogobius nonatoae*, *Oxyurichthys visayanus*, *Periophthalmus modestus*, *Bostrychus sinensis*, and *Eleotris fusca*.

2) Reef fishes

(1) Fishes of inshore reefs along continental coastlines from 0 to ca.100 m depth

Indo-West Pacific element The Taiwanese fishes of this element occur along the southern, western and north-

ern coasts (Shao and Chen, 2003), but can be divided into two groups according to their geographic distribution relative to the Japanese Archipelago and Korean Peninsula.

These fishes, more adapted to temperate regions, are distributed mainly off the Sea of Japan coast (East Sea) of Niigata Prefecture southward to northern and western Kyushu, the Pacific coast of Sendai Bay southward to southern Kyushu, the Seto Inland Sea, Tsushima Islands, Cheju Island and the southern coast of the Korean Peninsula, and the coast of southern mainland China from Taiwan-Fujian southward to Tonkin Bay (Fig. 2-C of Nakabo, 2002b). This overall area closely approximates the "Japan Region" of Briggs (1974). The Taiwan examples include *Myliobatis tobijei*, *Conger japonicus*, *Pterois lunulata*, *Sebastiscus marmoratus*, *Epinephelus akaara*, *E. awoara*, *Apogon kiensis*, *A. semilineatus*, *Parapristipoma trilineatum*, *Hapalogenys mucronatus*, *H. kishinouyei*, *Sparus sarba*, *Acanthopagrus schlegelii*, *Chaetodon modestus*, *Goniistius zonatus*, *G. quadricornis*, *G. zebra*, *Chromis notata*, *Oplegnathus fasciatus*, *Girella punctata*, *Pseudolabrus sieboldi*, *Choerodon azurio*, *Sphyraena pinguis*, *S. japonica*, *Petroscirtes breviceps*, and *Siganus fuscescens*.

The second group occurs along the Pacific coast of southern Japan from Boso Peninsula southward to southern Kyushu, and the coast of southern mainland China from Taiwan-Fujian southward to Tonkin Bay (Fig. 2-D of Nakabo, 2000b). The Taiwan examples include *Narke japonica*, *Scorpaenopsis cirrosa*, *Lutjanus ophuysenii*, *Seriola dumerili*, *Pseudocaranx dentex*, *Decapterus maruadsi*, *D. muroadsi*, *Leiognathus* spp., *Gazza* spp., *Gerres* spp., *Upeneus tragula*, *Parupeneus chrysopleuron*, *Pempheris* spp., *Oplegnathus punctatus*, *Girella leonina*, *Pseudolabrus eoethinus*, *Calotomus japonicus*, *Prionurus scalprum*, *Sphyraena obtusata*, and *Ostracion immaculatus*. Among them, *Seriola dumerili*, *Pseudocaranx dentex*, *Upeneus tragula*, *Parupeneus chrysopleuron*, *Pempheris* spp., and *Sphyraena obtusata* are widely distributed in the Indo-West Pacific and subtropical Atlantic.

The species of *Girella*, *Pseudolabrus* and *Oplegnathus* have related species in the temperate waters of Australia and New Zealand, indicating antiequatorial distributions.

(2) Fishes of inshore reefs primarily around islands from 0 to ca.100 m depth

Indo-West Pacific element These fishes inhabit coral reefs and are distributed mainly along the southern and northeastern coasts of Taiwan, and the coasts of Lanyu and Penghu Islands (Shao and Chen, 2003; Chen, 2003). They and their relatives are distributed in the Philippine Islands, Ryukyu and Ogasawara Islands in Japan, and widely in the tropical Indo-West Pacific. These fishes in Taiwan include species of Lamnidae, Myliobatidae, Muraenidae, Holocentridae, Serranidae, Apogonidae, Lutjanidae, Lethrinidae, Haemulidae, Pomacentridae, Chaetodontidae, Pomacanthidae, Labridae, Scaridae, *Neosynchiropus*, *Pterosynchiropus*, Gobiidae, Acanthuridae, Siganidae and Balistidae.

(3) Fishes of offshore reefs along continental shelf edges from ca.150 to 300 m depth

These fishes inhabit offshore reefs and occur mainly along the southern, eastern and northeastern coasts of Taiwan (Shao *et al*., 2008; Shao, 2009). They and their relatives are distributed along the Pacific coast of Hoshu (northward to Boso Peninsula) and the Izu Islands (Japan), and are widely distributed in the tropical Indo-Pacific and western Atlantic, or circumtropical seas. These fishes in Taiwan include *Centroberyx rubricaudus*, *Ruvettus pretiosus*, and *Lepidocybium flavobrunneum* (circumtropical element), and *Malakichthys* spp., *Neoscombrops katayamai*, *Cookeolus japonicus*, *Pristigenys* spp. (Indo-Pacific element).

(4) Fishes of offshore reefs primarily around islands from ca.100 to 300 m depth

Indo-Pacific element These fishes inhabit offshore reefs and occur mainly along the southern, eastern and northeastern coasts of Taiwan (Shao *et al*., 2008; Shao, 2009). They and their relatives are distributed in the Philippine Islands, the Ryukyu and Ogasawara Islands (Japan), and widely distributed in the tropical Indo-Pacific and tropical western Atlantic. These fishes in Taiwan include species of *Plectoranthias* spp., specis of Etelinae.

3) Demersal fishes

(1) Fishes of sandy-muddy bottoms on continental shelves shallower than ca.150 m depth

These fishes are distributed off the southern, western, and northern coasts of Taiwan (Shao and Chen, 2003). Together with their relatives, they are distributed off the Sea of Japan (East Sea) coast from southern Hokkaido, the Pacific coast from Miyagi Prefecture southward to the East China Sea, the Yellow Sea and off the coast of mainland China through Taiwan Strait southward to Tonkin Bay (Fig. 3C of Nakabo, 2002b), and include Indo-West Pacific and Japan-Oregon elements. The name of the latter element was given by Nishimura (1971).

Indo-West Pacific element These fishes, some of which are endemic to East Asian waters at the specific level, include *Mustelus* spp., *Dipturus* spp., *Okamejei* spp., *Dasyatis akajei*, *Conger* spp., *Saurida* spp., *Sirembo imberbis*, *Hoplobrotula armata*, *Lophimus setigerus*, *Erisphex pottii*, *Inimicus japonicus*, *Lepidotrigla* spp., *Nemipterus* spp., *Pagrus major*, *Branchiostegus* spp., *Sillago* spp., *Upeneus* spp., *Cepola schlegeli*, *Uranoscopus* spp., *Repomucenus* spp., *Amblychaeturichthys* spp., *Trichiurus japonicus*, *Psettodes erumei*, species of Paralichthyidae, *Engyprosopon* spp., and *Cynoglossus* spp.. A number of the above species are widely distributed in the Indo-West Pacific.

Japan-Oregon element East Asian species of *Pleuron-*

ichthys are *P. cornutus* and *P. japonicus*, the former being found in the Taiwan Strait and the latter from near northern Taiwan, and in the East China Sea (Suzuki *et al*., 2009). Relatives of these two species are distributed along the Pacific coast of North America.

(2) Fishes of edges and upper continental slopes from ca.150 to 500 m depth

These fishes in Taiwan include the Indo-West Pacific, Indo-Pacific, or circumtropical elements, and occur mainly off the eastern coast, although some occur off both the eastern and southern coasts (Shao *et al*., 2008). They are also distributed off the Pacific coast of southern Japan, in the Okinawa Trough, and off southern Taiwan, the Chinese coast facing the South China Sea, and the Pacific and South China Sea coasts of the Philippines. Taiwan representatives include *Dysomma anguillare*, *D. rugosa*, *Glossanodon semifasciatus*, *Ateleopus japonicus*, *Aulopus formosanus*, *Chlorophthalmus acutifrons*, *C. nigromarginatus*, species of Neoscopelidae, *Polymixia* spp. *Coelorinchus* spp., *Glyptophidium* spp., *Helicolenus hilgendorfi*, *Pterygotrigla* spp., species of Peristediidae, *Bembras japonica*, *Parabembras curta*, species of Hoplichthyidae, *Synagrops* spp., *Chelidoperca* spp., *Chrionema* spp., *Bembrops* spp., species of Champsodontidae, *Bathycallionymus* spp., *Foetorepus* spp., species of Gempylidae, *Chascanopsetta* spp., *Arnoglossus* spp., and *Laeops* spp.

(3) Fishes of lower continental slopes to abyssal plains from ca.500 to 6,000 m depth

Such fishes in Taiwan represent circumtropical (mostly) and Indo-Pacific elements, being distributed off the eastern (mostly) and southern coasts (Shao *et al*., 2008; Shao, 2009), in addition to Boso Peninsula southward to southern Kyushu, the Okinawa Trough, Kyushu-Palau Ridge, and the western and eastern Philippines. In Taiwan, they include species of Myxinidae, Etmopteridae, Dalatiidae and Halosauridae, *Synaphobranchus* spp., species of Ipnopidae, *Bathygadus* spp., *Hymenocephalus* spp., *Ventrifossa* spp., *Nezumia* spp., *Acanthonus armatus*, *Xyelacyba myersi*, *Dicrolene* spp., *Bassozetus* spp., *Monomitopus kumae*, and *Halieutopsis* spp.

4) Pelagic fishes

(1) Fishes of epipelagic zones from 0 to ca.150 m depth

Both temperate and tropical species are distributed off the northern, western and southern coasts of Taiwan, or around the entire coast line (Shao and Chen, 2003; Shao *et al*., 2008). Temperate species have origins in the Indo-West Pacific, Indo-Pacific or circumtropical elements, and are distributed from southern Hokkaido southward to the East China and Yellow Seas, and the Chinese coast facing the South China Sea. Examples include *Engraulis japonicus*, *Hypoatherina valenciennei*, *Tylosurus acus melanotus*, *Trachurus japonicus*, *Decapterus maruadsi*, *Sphyraena pinguis*, and *Scomber japonicus*.

The tropical species are included in the circumtropical element, being distributed worldwide, or having worldwide tropical relatives. Taiwan representatives are distributed off the southern, eastern and northern coasts (Shao and Chen, 2003; Shao *et al*., 2008), occurring also off the Pacific coast off Miyagi Prefecture southward to northern and western Kyushu, Ryukyu Islands, and South China Sea. They include *Rhincodon typus*, *Galeocerdo cuvier*, *Prionace glauca*, *Carcharhinus obscurus*, *Sphyrna* spp., *Scomberoides* spp., many species of Clupeidae, most species of Exocetidae, Belontidae and Scombridae.

(2) Fishes of meso- and bathypelagic zones from ca.150 to 3,000 m depth

The deep-sea pelagic fishes are included in the circumtropical element, having worldwide relatives or origins. They are distributed off the eastern and southern coasts of Taiwan (Shao *et al*., 2008), in the Pacific off central Honshu southward, including the Okinawa Trough, and in the South China Sea. Species included are *Squaliolus* spp., species of Nemichthyidae, Alepocephalidae, Gonostomatidae, Sternoptychidae, Astronesthidae, Melanostomiidae, Malacosteidae, Idiacanthidae, Alepisauridae, Paralepididae, Evermannellidae and Scopelarchidae, species of *Bolinichthys*, *Taaninichthys*, *Notolychnus*, *Benthosema*, *Hygophum*, *Myctophum*, *Nannobrachium*, *Lampanyctus* and *Diaphus*.

4. Remarks

The freshwater fishes included in the China element and *Rhinogobius* in Taiwan show a zoogeographic relationship to the China subregion of Mori (1936b), the Korean Peninsula and the southwestern Japan region of Aoyagi (1957). Although it is not clear when the zoogeographic relationships of the freshwater fishes in East Asia became established, the mid-Pleistocene fossil fish fauna of Kusu Basin, Oita Prefecture, is similar to the fish fauna of the China element in East Asian freshwater habitats. The fossil fauna of Kusu Basin includes "Xenocypridinae, gen. et sp. indet", *Xenocypris* sp., *Plagiognathops* sp., *Cyprinus* sp., *Carassius* sp., *Hemibarbus* sp., *Zacco* cf. *Z. temminckii*, *Acheilognathus* sp., "fossil species similar to Biwa-masu", *Rhinogobius brunneus*, *R. giurinus*, *Rhinogobius* sp. dated at 0.5～0.4 my B.P. (Yabumoto, 1987; Nakajima *et al*., 1988; Uyeno *et al*., 2000). Except for three fossil species of Xenocypridinae, relatives of the other fossil species now inhabit East Asian freshwaters, especially the southwestern Japan region sensu Aoyagi (1957), the Korean Peninsula (Kim *et al*., 2005) and Taiwan (Shen ed., 1993). During the mid-Pleistocene (0.5～0.4 my years B.P.), Taiwan marginally shared freshwater areas with the Korean Peninsula and southwestern Japan. In addition, such freshwater areas may have had a marine influence, the fauna including anadromous *Oncorhynchus* and amphidromous *Rhinogobius*. Some freshwater fishes of the China element in Taiwan

have been studied phylogenetically together with species from China, Korea, and Japan (see Ma *et al*., 2006; Chen, Wu, and Hsu, 2008; Chen *et al*., 2008).

The distributions of Taiwanese marine fishes are influenced by the Kuroshio Current and low-salinity and low-temperature waters from mainland China, plus sea-bottom topography. Shao and Chen (2003) showed zoogeographic areas for the coastal fishes of Taiwan, *viz*. northern, western (including Penghu Islands), northeastern, eastern (including Lanyu Islands), and southern areas. However, Penghu and Lanyu Islands are here recognized separately from the above areas.

Fishes of brackish waters and seas adjacent to continental coastlines, North Pacific and Indo-West Pacific elements, are influenced by low-salinity waters from mainland China in the northern and western areas. Fishes of brackish waters and seas primarily around islands, Indo-West Pacific element, are influenced to a small extent by the Kuroshio Current in the southern area.

Fishes of inshore reefs along continental coastlines are influenced by low-temperature waters from mainland China in the southern, western and northern areas, and the Penghu Islands. On the other hand, fishes of inshore reefs primarily around islands are influenced by the Kuroshio Current in the southern and northeastern areas, Lanyu Islands, although some occur at the Penghu Islands. The southern area and Lanyu Islands are close to the Philippine Islands, and the northeastern area to the Ryukyu Islands. Fishes of offshore reefs both along continental edges and primarily around islands are influenced by the Kuroshio Current in the southern and northeastern areas.

Demersal fishes, occurring in waters shallower than ca.150 m depth, representing the Indo-West Pacific and Japan-Oregon elements, are distributed on the continental shelves of the southern, western and northern areas. On the other hand, demersal fishes from ca.150 m to 500 m depth, being included in the Indo-West Pacific, Indo-Pacific, or circumtropical elements, are distributed on the upper continental slopes of the eastern and southern areas. Those from ca.500 to 6,000 m depth, being mostly circumtropical, are distributed on the lower continental slopes to abyssal plains in the eastern and southern areas.

Temperate and tropical pelagic fishes occurring in 0 to ca.150 m depth, representing the Indo-West Pacific, Indo-Pacific or circumtropical elements, differ from each other in the distribution around Taiwan. The temperate pelagic fishes are influenced by low-temperature waters from mainland China, whereas the tropical pelagic fishes are effected by high-temperature waters in the Pacific Ocean, being similar to conditions in the Sea of Japan (East Sea) and along the Pacific coasts of southern Japan. The deep-sea fishes of the meso- and bathypelagic zones, being circumtropical, are found mainly in the deep waters off eastern Taiwan and in the Pacific Ocean, although some also occur off southern Taiwan and in the South China Sea.

Kano (1941) extended the Neo-Wallace Line of Meril (1923) from Bashi Strait to between Taiwan Island and the Lanyu Islands and listed some diadromous, brackish-water and marine fishes distributed in both the Lanyu Islands and Philippine Islands. However, the Neo-Wallace Line cannot be applied to the fishes listed by Kano (1941) because they are found at both the Lanyu Islands and Taiwan Island. As well, Neo-Wallace Line was the extended Wallace Line (Wallace, 1860, 1863; Huxley, 1868), being from the southern Philippine Islands northward to Bashi Strait along the western coast by Merill (1923) on the basis of his study of the Philippie's flora.

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