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INTERRELATIONSHIPS OF THE FAMILY PLEURONECTIDAE (PISCES : PLEURONECTIFORMES)

By

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Contents

I. Introduction

The fishes of the family Pleuronectidae, inhabiting the sand-muddy bottom between shallow inshore waters and continental slope, are widely distributed in the

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The present work was submitted as a partial fulfillment of the requirements for Doctor's degree in Fisheries Science at Hokkaido University in 1984.

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world. This family is characterized in having both eyes on the right side of the body, the optic nerve of the left eye always dorsal, the preopercle with a free margin and the fin rays without spines. The Pleuronectidae includes 114 species. While most are marine, some of them enter such fresh waters as rivers, lakes and marshes.

The phylogeny of the pleuronectid fishes has been studied by several investigators (Regan, 1910 ; Norman, 1934 ; Kuronuma, 1938 ; Hubbs, 1945 ; Kim, 1973 ; Li, 1981). These authors, except Kim (1973), discussed the relation only among the subfamilies on the basis of several characters including osteology. Kim (1973) studied the interrelationships of 14 species of the Pleuronectinae (*sensu* Norman, 1934) based on the comparative osteology of the cranium, the urohyal, the vertebrae and the caudal skeleton. Though there are many studies on both internal and external morphology in the present family owing to their morphological peculiarities (e.g. Kyle, 1921 ; Hikita, 1934 ; Chabanaud, 1936 ; Yazudani, 1969 ; Groot, 1971 etc.), most of those studies were fragmentary and did not treat the interrelationships of the pleuronectids.

Under the circumstances, it is necessary to clarify the interrelationships of the pleuronectid fishes on the basis of as many internal and external characters as possible. In order to analyse the interrelationships of the species of the Pleuronectidae, numerical phenetics (Sneath and Sokal, 1973) was adopted as a systematic methodology.

The classification of righteye flounders has been studied by many ichthyologists since the end of the nineteenth century. In 1910, Regan treated the righteye flounders as a single family Pleuronectidae for the first time. Since then, the classification of this group has been discussed mainly at a subfamilial level based on several internal and external characters (Regan, 1929 ; Norman, 1934 ; Berg, 1940 ; Hubbs, 1945 etc.), though some or all the subfamilies were sometimes raised to familial rank (Regan, 1920 ; Jordan, 1923 etc.). Nelson (1976) divided the Pleuronectidae into four subfamilies and the Pleuronectinae into two tribes.

In the present study, all the pleuronectid species are classified into the supraspecific taxa which are newly defined by the ranking on the basis of their phenetic interrelationships.

II. Acknowledgments

I wish to express my sincere gratitude to the late Dr. Takao Igarashi, the former professor of Hokkaido University, for his guidance in the course of the present study and critical reading of the manuscript. Also, I wish to thank Dr. Keikichi Hamada, professor of the same university, for critical reading of the manuscript. I wish to express my thanks to Dr. Seikichi Mishima, professor of the same university, for critical reading of the manuscript. I wish to express the deepest appreciation to Dr. Kunio Amaoka, professor of the same university, for his valuable advice and critical reading of the manuscript.

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III. Materials

The specimens examined for the present study the listed with their catalogued numbers, the numbers of the specimens and the sizes. The abbreviations prefixed to the catalogued numbers indicate the following institutions where those specimens belong :

BMNH : British Museum (Natural History), London
BSKU : Department of Biology, Faculty of Science, Kochi University, Kochi
CAS : California Academy of Science, San Francisco
E, I, IA: Australian Museum, Sydney
FAKU : Faculty of Agriculture, Kyoto University, Kyoto
HUMZ : Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate
IFES : Iwate Fisheries Experimental Station, Kamaishi
LACM : Los Angels County Museum, Los Angels
MCZ : Museum of Comparative Zoology, Cambridge
NMC : National Museum of Canada, Ottawa
RUSI : J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown
SAM : South African Museum, Cape Town
SU : Natural History Museum, Stanford University, now housed at CAS
USNM : U.S. National Museum, Washington D.C.
WAM : Western Australian Museum, Perth
ZMA : Zoölogisk Museum, Universiteit van Amsterdam, Amsterdam

Atheresthes stomias, 21 specimens, 192.3-530.0 mm SL, HUMZ 7473, 22029, 22356, 33697, 34353, 34456, 34463, 34801, 44991, 67168, 67170, 67303, 67305, 67306, 67927, 68045, 68119, 68302, 68495, 68515, 100250.

A. evermanni, 27 specimens, 131.0-239.0 mm SL, HUMZ 21871, 56755, 58322, 58324, 58327-58332, 58355-58337, 58339, 58340, 58343-58347, 59119, 67653, 68049, 79653, 82015, 100279; IFES 655.

Reinhardtius hippoglossoides, 23 specimens, 119.3-291.1 mm SL, HUMZ 53256-53259, 53540, 53541, 53543, 53544, 53934, 53938, 53974, 54502, 55930, 55941, 55953, 55969, 55971, 56197, 56706, 78628, 86256, 88324; IFES 624.

Hippoglossus hippoglossus, one specimen, 668.7 mm SL, HUMZ 87211.

H. stenolepis, 17 specimens, 192.0-294.7 mm SL, HUMZ 54794, 55352, 56714, 56730, 57220-57222, 58544-58547, 83325, 83326, 84355, 85843, 87798, 92531.

Eopsetta exilis, 18 specimens, 128.8-175.0 mm SL, CAS 26480(5); HUMZ 32596, 32601, 32610, 32615, 32617, 32621-32623, 32625, 32628, 80769-80771.

E. jordani, 4 specimens, 63.3-339.4 mm SL, CAS 45961(3); HUMZ 14278.

E. grigorjewi, 24 specimens, 65.0-188.0 mm SL, HUMZ 33799, 51905, 52036, 52528, 52529, 52534, 52537, 52544, 52545, 56981, 57090, 59256, 59262, 59263, 61845-61847, 61982, 61985, 61986, 75373, 77525, 94705; IFES 651.

Verasper variegatus, 14 specimens, 187.3-369.9 mm SL, HUMZ 41558, 51685, 57069, 57150-57155, 57216, 57217, 66209, 100278; IFES 647.

V. moseri, 12 specimens, 185.9-461.2 mm SL, HUMZ 4284, 20258, 51685, 57074, 57148, 57149, 72900, 82050, 100276, 100277; IFES 653, 661.

Psettichthys melanostictus, 10 specimens, 100.0-200.8 mm SL, CAS 34777(2); HUMZ 80760-80762; LACM 3895(2), 31981-10(2), 34277.

Hippoglossoides platessoides platessoides, 5 specimens, 244.0-340.0 mm SL, FAKU 2 uncatalogued specimens; HUMZ 87214; NMC 64-0396(2).

H. p. limandoides, 6 specimens, 214.9-312.5 mm SL, FAKU 2 uncatalogued specimens; HUMZ 87212, 87213, 87221, 87222.

H. elassodon, 21 specimens, 141.6-296.0 mm SL, HUMZ 44994, 55965, 55967, 83324, 84281, 84317, 84394, 84397, 84398, 85174, 85175, 85177, 85178, 85191, 85223, 85333, 85518, 85532, 85554, 86003, 86158.

H. dubius, 26 specimens, 159.0-283.5 mm SL, HUMZ 52983, 52994, 52955, 53146, 53188, 52954, 53250, 53251, 53554, 53556, 53558, 53560, 53563, 53932, 59675, 72627, 75505-75508, 79682, 79683, 93991, 2 uncatalogued specimens; IFES 625.

H. robustus, 21 specimens, 179.4-292.0 mm SL, HUMZ 52914, 52917, 53249, 53552, 53948, 53950, 53965, 54472, 54474, 54480, 54487, 54495, 54503, 55949, 55951, 55954, 55955, 85559, 85560, 85681, 86222.

H. pinetorum, 36 specimens, 127.7-254.0 mm SL, HUMZ 52524, 52526, 52527, 54444, 54446, 56067-56073, 56715, 56716, 58533, 58534, 58536-58541, 59117, 59661-59665, 59667-59670, 99480, 100298-100300.

Acanthopsetta nadeshnyi, 28 specimens, 179.4-302.7 mm SL, HUMZ 52958, 52959, 52963, 52965, 52971, 52972, 52996, 52999, 53024, 53034, 53113, 53121, 53122, 53140-53142, 53144, 53147, 53208, 53210, 53213, 53231, 78635, 78779, 79689, 79697, 87594; IFES 650.

Dexistes rikuzenius, 30 specimens, 94.0-162.0 mm SL, HUMZ 35730, 47456, 48127, 57073, 57167, 57168, 57171, 57173, 57177, 57178, 57180-57183, 57187-57190, 57193, 57194, 59114, 59235, 59279, 59285, 59293, 59319, 62604, 78588, 79807; IFES 641.

Pleuronectes isolepis, 13 specimens, 122.0-235.5 mm SL, CAS 15152(5); HUMZ 21165-21169, 80766-80768.

P. vetulus, 14 specimens, 116.1-373.8 mm SL, CAS 34733(6); HUMZ 7502, 14281, 14282, 34378, 34394, 34462, 34464, 46294.

P. bilineatus, 19 specimens, 145.3-281.0 mm SL, HUMZ 33721, 54039, 54065, 54118, 54119, 54861, 54887, 54893, 54429, 55431, 55433, 55449, 55450, 66331, 81118, 83081, 86200, 83178, 84270.

P. mochigarei, 22 specimens, 125.9-241.4 mm SL, HUMZ 20271, 52881, 53182, 53228, 58562, 58563, 58565-58569, 58571-58576, 80975, 87821, 90721, 90722, 90831.

P. limanda, 3 specimens, 105.0-146.5 mm SL, HUMZ 87829-87831.

P. asper, 28 specimens, 127.5-254.0 mm SL, HUMZ 54600, 54627, 55918, 56719, 58179, 58561, 58564, 58570, 58578, 58579, 58582, 58584, 58587, 58588, 58590, 58592, 58594, 58595, 58597, 58599-58602, 83075, 86029, 86129, 86233, 90714.

P. korigarei, one specimen, 233.0 mm SL, USNM 75669, holotype, radiograph only.

P. sakhalinensis, 26 specimens, 122.2-202.0 mm SL, HUMZ 53566, 54017, 55246, 55247, 55872, 56196, 60437, 60444, 60448, 60458, 60467, 60598, 61604, 61606, 61609, 61616, 61622, 61624, 61638, 61649, 61651, 61656, 61658, 61671, 61674, 61676.

P. ferrugineus, 5 specimens, 238.6-313.0 mm SL, FAKU 2 uncatalogued specimens; HUMZ 87215-87217.

P. punctatissimus, 20 specimens, 125.5-199.0 mm SL, HUMZ 53976, 53977, 54435, 56712, 58527-58529, 58531, 58532, 63576-63578, 80805, 80824, 87614, 96452, 3 uncatalogued specimens; IFES 643.

P. proboscideus, 21 specimens, 164.6-231.0 mm SL, HUMZ 54895, 60332, 76290, 76291, 76293, 76452-76455, 76711, 76713-76715, 76717, 76718, 76790, 82761, 82763, 82770, 82773, 85694.

P. herzensteini, 31 specimens, 115.8-212.0 mm SL, HUMZ 51947, 51959, 52503, 52509, 52514, 52515, 52520, 52523, 52535, 52539, 52541-52543, 52754, 52755, 52758, 52759, 52761, 52762, 52764, 52767, 52768, 52843, 53978, 54439-54442, 90916, 99481; IFES 642.

P. yokohamae, 21 specimens, 99.5-250.0 mm SL, HUMZ 51952, 52027, 52037, 54011, 54440, 56971, 56972, 56983, 56988, 56994, 57114, 57115, 57119, 57132, 59099, 59100, 60260, 61980, 62208, 62209, one uncatalogued specimen.

P. schrenki, 24 specimens, 154.0-293.0 mm SL, HUMZ 4237, 56711, 58646, 59194, 75631, 75632, 75635-75638, 75640, 75646, 75683, 75687, 75690, 75696, 75698-75700, 92329, 96449, 99487, 99491, 99494.

P. americanus, 2 specimens, 279.0-289.0 mm SL, HUMZ 48292, 48305.

P. quadrituberculatus, 15 specimens, 200.0-334.0 mm SL, HUMZ 20070, 54603, 54866, 54869, 54873, 54876, 55194, 55353, 55397, 55398, 55399, 55402, 55404, 76590, 93098.

P. platessa, 3 specimens, 145.2-157.0 mm SL, HUMZ 87823-87825.

P. obscurus, 20 specimens, 141.5-276.0 mm SL, HUMZ 19978, 53986, 59187-59193, 59195, 75540, 75542, 75544, 75551, 75643, 75644, 92002, 99489, 99495, 99497.

P. glacialis, 4 specimens, 139.0-155.8 mm SL, SU 3046(3); USNM one uncatalogued specimen.

P. pinnifasciatus, 26 specimens, 115.2-242.5 mm SL, FAKU 10000-10002; HUMZ 41565, 41569, 43994, 59196-59198, 75555, 75556, 75558-75560, 75653-75655, 75662, 75663, 75666, 75668, 75672, 75674, 75676, 75682, 99488.

P. putnami, 20 specimens, 16.5-194.0 mm SL, NMC 82-0014(2); USNM 68139, 73841, 126828(3), 156093(3), 165255(2), 165256, 165257(5), 165258(2), radiograph only.

Platichthys flesus flesus, 3 specimens, 153.4-198.0 mm SL, HUMZ 87826-87828.

P. stellatus, 24 specimens, 185.0-275.6 mm SL, HUMZ 20252, 52927-52931, 53980-53982, 53984, 55854-55856, 58548-58555, 84451, 87741; IFES 644.

Hypsopsetta guttulata, 11 specimens, 78.2-169.1 mm SL, CAS 11401(3); HUMZ 80763-80765; LACM 6622-4(5).

Pleuronichthys decurrens, 15 specimens, 50.4-164.0 mm SL, CAS 23703(3), 34727(2), 34729(5), 38760(5).

P. cornutus, 30 specimens, 82.8-196.5 mm SL, HUMZ 33603, 33739, 48982, 51873, 52032, 52574, 57089, 57141-57143, 57145, 58804, 59111, 59229, 59260, 60024, 60263, 94712, 100288-100297, one uncatalogued specimen; IFES 649.

P. verticalis, 9 specimens, 75.5-170.0 mm SL, CAS 34728(2), 40718(2); LACM 1623(5).

P. coenosus, 9 specimens, 131.2-199.5 mm SL, CAS 46539(4); LACM 32148-42(5).

P. ritteri, 9 specimens, 51.6-179.6 mm SL, CAS 11403(4); LACM 38089(5).

P. ocellatus, 10 specimens, 56.6-130.2 mm SL, LACM 8824-17(2), 38221-7(3); SU 16837(3), 18965(2).

Glyptocephalus cynoglossus, 2 specimens, 231.0-323.0 mm SL, HUMZ 87218, 87219.

G. stelleri, 31 specimens, 144.5-335.0 mm SL, HUMZ 52878, 53310, 53546, 53548, 53941, 59105, 59671, 59672, 61809, 61811, 61815, 61816, 61818-61820, 61822, 61823, 61825, 61827, 61828, 61831, 61835, 61837, 61839, 78632, 78633, 79686, 95310, 100287, one uncatalogued specimen; IFES 654.

Errex zachirus, 20 specimens, 235.5-484.4 mm SL, HUMZ 30967, 34343, 34344, 34346, 34405, 34473, 34999, 44993, 44997, 45014, 45017, 46227, 55904, 55908, 55911, 55925, 76320, 77085, 78426, 88310.

Kareius bicoloratus, 20 specimens, 122.2-256.7 mm SL, HUMZ 56075-56079, 56986, 56993, 57118, 57120, 59237, 59240, 59248, 67079, 67080, 91869, 94374, 96450, 96707, 100284; IFES 657.

Microstomus kitt, 12 specimens, 196.2-305.0 mm SL, HUMZ 86783-86792, 87223, 87224.

M. achne, 34 specimens, 142.6-327.5 mm SL, HUMZ 19443, 33244, 35248, 45559, 45560, 48304, 52038, 52883-52885, 56733, 57133-57138, 57140, 57199-57202, 57204, 57205, 57207, 57209-57212, 57214, 59321, 75747, 90915, 100281.

M. pacificus, 23 specimens, 237.5-360.2 mm SL, HUMZ 30943, 33789, 44992, 45001, 45002, 45015, 45016, 67108-67110, 67112-67114, 67116, 67233, 67846, 67848, 67909, 68404, 76428, 77310, 84901, 89398.

Tanakius kitaharai, 26 specimens, 123.5-270.7 mm SL, HUMZ 35598, 44020, 56934, 56936, 56938, 56979, 57157, 57160, 57161, 57163, 57165, 59232, 59280, 59282, 59283, 59286-59289, 59292, 59294, 59331, 62603, 63655, 99478; IFES 646.

Embassichthys bathybius, 17 specimens, 279.4-435.1 mm SL, HUMZ 31653, 31658-31660, 31662, 31663, 67383, 68305, 77496, 80780, 80781, 82043, 84234-84236, 85420, 86878.

Clidoderma asperrimum, 15 specimens, 148.1-320.3 mm SL, HUMZ 20243, 34265, 45038, 45416, 46367, 46398, 51684, 55430, 55434, 78055, 78629, 78630, 79652, 80979; IFES 652.

Paralichthodes algoensis, 8 specimens, 91.7-352.5 mm SL, RUSI 7377, 10471, 4 uncatalogued specimens, radiograph only; SAM 15342, 26319.

Poecilopsetta beanii, 5 specimens, 79.8-107.1 mm SL, CAS 49898(3); USNM 2 uncatalogued specimens.

P. colorata, 5 specimens, 70.8-119.3 mm SL, BMNH 1879.5.14.97, holotype, 1927.1.6.62-3, radiograph only; USNM 137392, one uncatalogued specimen, radiograph only.

P. hawaiiensis, 9 specimens, 82-121 mm SL, USNM 51638, holotype, 51690(8), paratypes, radiograph only.

P. praelonga, 2 specimens, 107.6-119.6 mm SL, USNM 138004; one specimen from Dr. Whitehead.

P. plinthus, 31 specimens, 80.8-147.5 mm SL, HUMZ 35804, 35882, 37441, 48094, 51722, 51723, 51875-51878, 51880, 57218, 57219, 58650, 58653, 58654, 58656, 58659, 58660, 58752, 58753, 58755-58758, 58761, 58795, 58799, 79831, 79890, 79934.

P. natalensis, one specimen, 119.5 mm SL, BMNH 1922.3.27.7, holotype, radiograph only.

P. megalepis, one specimen, 99.0 mm SL, USNM 93094, holotype, radiograph only.

P. albomarginata, 5 specimens, 97.5-116.5 mm SL, USNM 93303, holotype, 93304(2), paratypes, radiograph only, 217997(2).

P. albomaculata, 3 specimens, 97.5-109.0 mm SL, BMNH 1939.5.24.1774-6, syntypes, radiograph only.

P. zanzibarensis, 9 specimens, 70.0-100.5 mm SL, BMNH 1939.5.24.1777-84, syntypes, radiograph only.

Nematops microstoma, one specimen, 76 mm SL, BMNH 1879.5.14.91, holotype, radiograph only.

N. grandisquama, 4 specimens, 40.5-69.5 mm, ZMA 112.647(4), syntypes.

N. macrochirus, 17 specimens, 82.0-120.7 mm SL, BMNH 1931.7.23.1, holotype, radiograph only; one specimen from Dr. Nielsen, radiograph only; I. 20435-013(15).

N. chui, one specimen, 66.5 mm SL, USNM 93087, holotype, radiograph only.

Marleyella bicolorata, 5 specimens, 77.5-152.5 mm SL, BMNH 1922.3.27.5, holotype, 1922.3.27.6, paratype, 1939.5.24.1794-6, radiograph only.

M. maldivensis, 2 specimens, 75.0-105.0 mm SL, BMNH 1939.5.24.1797-8, syntypes, radiograph only.

Oncopterus darwinii, 4 specimens, 169.5-220.5 mm SL, MCZ 11397(3), radiograph only ; USNM 86732.

Psammodiscus ocellatus, 5 specimens, 55.0-91.7 mm SL, BMNH Reg. No. 221(4), syntypes, radiograph only ; WAM P. 5530.

Pelotretis flavilatus, 17 specimens, 202.3-287.0 mm SL, FAKU 42288, 42370, 42371, 42377, 42385, 42437, 44532, 44534, 46491, 46492, 47004, 47005, one uncatalogued specimen ; HUMZ 62197-62200.

Azygopus pinnifasciatus pinnifasciatus, 7 specimens, 67-161 mm SL, E. 3600, holotype, IA 3028, 3030-3032, 3587, paratypes, radiograph only ; HUMZ 86624.

Ammotretis rostratus, 9 specimens, 83.5-165.5 mm SL, BMNH 1848.3.18.245, holotype, radiograph only ; I. 17326-006(3), 19883-009(4), radiograph only ; HUMZ 86623.

A. brevipinnis, one specimen, 72.5 mm SL, BMNH 1925.1.26.1, holotype, radiograph only.

A. lituratus, 4 specimens, 59.9-191.0 mm SL, I. 10026, syntype of *A. tudori*, radiograph only ; HUMZ 87306-87308.

A. macrolepis, one specimen, 76.5 mm SL, E. 455, holotype, radiograph only.

A. elongatus, 8 specimens, 99.4-151.0 mm SL, BMNH 1925.1.26.3, radiograph only ; USNM one uncatalogued specimen, radiograph only ; I. 12391, syntype, radiograph only, 13205(2), 13206, 13207(2).

Taratretis derwentensis, 5 specimens, 43.0-68.0 mm SL, I. 20579-001(2), radiograph only ; HUMZ 87303-87305.

Colistium nudipinnis, one specimen, 404.0 mm SL, BMNH 1924.1.7 : 4, radiograph only.

C. guntheri, 2 specimens, 280.0-325.5 mm SL, BMNH 1923.11.5.5, radiograph only, 1924.1.7.3.

Rhombosolea retiaria, one specimen, 238.5 mm SL, BMNH 1886.11.18.76, radiograph only.

R. plebeia, one specimen, 271.0 mm SL, HUNZ 86607.

R. tapirina, 5 specimens, 181.5-209.0 mm SL, HUMZ 86608-86612.

R. leporina, 6 specimens, 104.5-137.0 mm SL, HUMZ 86617-86622.

Peltorhamphus novaezeelandiae, 6 specimens, 118.8-224.8 mm SL, HUMZ 86613-86616 ; 021, 031, from Dr. James.

P. latus, 6 specimens, 51.1-111.1 mm SL, A34, 35, 4 uncatalogued specimens from Dr. James.

P. tenuis, one specimen, 132.4 mm SL, 90 from Dr. James.

Samaris cristatus, 10 specimens, 77.5-143.6 mm SL, BSKU 7820, one uncatalogued specimen, radiograph only ; one specimen from Dr. Kyushin ; S. 252 from Dr. Asano ; HUMZ 80621-80623, 86847, 92804, 92805.

S. macrolepis, one specimen, 33.5 mm SL, BMNH 1888.12.1.32, holotype, radiograph only.

Plagiopsetta glossa, 32 specimens, 52.7-146.0 mm SL, BSKU 2573-2575, 2577-2579, 2581-2585, radiograph only ; FAKU 28130-28132, 28134, 28135 ; HUMZ 36300, 36393, 37129, 48065, 48076, 58700, 79906, 79908-79911, 80548-80552.

Samariscus corallinus, 3 specimens, 68.4-85.7 mm SL, USNM 51596, holotype, 51676(2), paratypes, radiograph only.

S. macrognathus, one specimen, 43.7 mm SL, USNM 93088, holotype, radiograph only.

S. latus, 21 specimens, 75.0-101.4 mm SL, BSKU 7774-7779, radiograph only ; FAKU 18186, 18188, 18192, 26764, 26767, 26768, 28150, 28165, 28167, 28172 ; HUMZ 35745, 35850, 35907, 58674, 58805.

S. longimanus, 8 specimens, 66.6-100.0 mm SL, USNM 137384, 137385(2), 137886(3), 137387, 137388, radiograph only.

S. sunieri, 8 specimens, 53.1-99.0 mm SL, ZMA 109.317(8), syntypes.

S. xenicus, 33 specimens, 38.9-59.3 mm SL, FAKU 11784, 28846-28857, 33150, 33151, 33153, 33154, 33156-33162, paratypes, 35193-35196, 2 uncatalogued specimens ; HUMZ 101738-101740.

S. inornatus, one specimen, 80.3 mm SL, BMNH 1927.1.6.67, paratype, radiograph only.

S. luzonensis, one specimen, 57.1 mm SL, USNM 93089, holotype, radiograph only.

S. asanoi, one specimen, 63.0 mm SL, S. 297, holotype, from Dr. Asano.

S. maculatus, one specimen, 85.6 mm SL, BMNH 1879.5.14.84, holotype, radiograph only.

S. japonicus, one specimen, 89.2 mm SL, HUMZ 48102.

S. huysmani, one specimen, 93.0 mm SL, ZMA 109.325, topotype.

S. fasciatus, one specimen, 53.7 mm SL, USNM 93090, holotype, radiograph only.

S. triocellatus, 5 specimens, 33.0-58.5 mm SL, USNM 141767, holotype, 141768(3), 167246, paratypes, radiograph only.

IV. Methods

The osteological observations were based on entirely stained and dissected specimens. The small specimens were prepared by staining in an alyzarin bath and soaking in a 3-5 per cent potassium hydroxide (KOH) solution to remove the flesh. The method of Dingerkus and Uhler (1977) were also employed for some small specimens. The rare specimens including type series were studied by radiography. The illustrations of the bones were made mainly using a camera lucida attachment on a Wild M-8 dissecting microscope. The osteological terminology in the present study follows Amaoka (1969, 1979), Uyeno (1975) and Matsubara et al. (1979).

For the counts of fin rays and vertebrae radiographs were used.

As discussed in the chapter V, numerical phenetics was adopted as a systematic methodology in the present study and the calculation of similarity and the cluster analysis were performed by HITAC M-200 H of Hokkaido University Computing Center.

V. Systematic methodology

1. APPLICATION OF NUMERICAL PHENETICS

We have three theories of the relationships in modern systematic methodology (Mayr, 1976): evolutionary systematics, cladistics (Hennig, 1966) and phenetics (Sneath and Sokal, 1973). Accordingly, which of those theories is applied to a particular study has become an important problem in systematic studies. In order to select the systematic theory for the present study, the problems on logical consistency, character weighting and phylogenetic speculation are discussed below.

Logical consistency

Repeatability and objectivity in classification are prerequisite in systematic studies (Sneath and Sokal, 1973). As already pointed out by Sawada (1982), evolutionary systematics may not satisfy the prerequisite because of lacking logical consistency of actual analysis. On the other hand, logical consistency is certified in the two alternatives, cladistics and phenetics, though they are based on the different basic assumption of systematic theory.

Character weighting

The character weighting, one of the most important problems in systematics, has frequently been debated in modern methodology. Throughout the controversy on the matter, pheneticists have consistently insisted that each character should be given the equal weight in creating taxonomic groups (Sneath and Sokal, 1973). On the other hand, for almost all the evolutionary systematicists, the question whether each character analysed should be provided with high or low weight must be solved prior to their own phyletic analyses (see Mayr, 1969). This viewpoint has also been followed by several cladists (e.g. Hecht and Edwards, 1977), though the equal weighting with logical ground is supported by some cladists (e.g. Eldredge and Cracraft, 1980). Several criteria have been applied to the character weighting (see

Hecht and Edwards, 1977). As pointed out by Sneath and Sokal (1973), if differential weighting for each character is admitted, exact rules must be given for estimating it. This essential problem in both evolutionary systematics and cladistics (in evolutionary systematics in particular), however, remains unsettled.

The problem on the character weighting was discussed in detail by Sneath and Sokal (1973 : 109-113), and they rightly concluded that the equal weighting was the only practical solution (Løvtrup, 1977).

Phylogenetic speculation

The three theories employed in modern systematic studies generally have the same processes in that the selection of characters and the distinction of character states are required as the first step in their own systematic procedures.

In phenetics, once an overall similarity among taxonomic units was adopted as the systematic premise (or basic assumption) in the classification of the organisms studied, the subsequent processes, the calculation of similarity and the cluster analysis (shown by dendrogram), are performed without any phylogenetic speculation. In both cladistics and evolutionary systematics, the character phylogeny (determining polarity) which is apparently interpreted as phylogenetic speculation must be made for each character before constructing the cladogram and the phylogram. For cladistics in particular, that process is prerequisite to apply the synapomorphy which plays the most important role in its systematic theory. The following three methods, though several criteria have been proposed, have frequently been used : ancestor-descendant relationships, paradromism of Maslin (1952), commonality principle (Kluge and Farris, 1969 ; Lundberg, 1972 ; Hecht and Edwards, 1977 ; Eldredge, 1979 etc.). These three methods are, however, criticized by several investigators (Colless, 1967 ; Lundberg, 1972 ; Wiley, 1981 ; Watrous and Wheeler, 1981 ; Sawada, 1982). After all, the most effective method in determining polarity is the out-group comparison (Schaeffer et al., 1972 ; Ross, 1974 ; Eldredge and Cracraft, 1980 ; Wiley, 1981 ; Watrous and Wheeler, 1981 ; Sawada, 1982). To find out the out-group(s), which is the heart of the method, several ways have been proposed : overall similarity (Kluge and Farris, 1969 ; Lundberg, 1972), *a priori* knowledge (Ross, 1974 ; Eldredge and Cracraft, 1980 ; Wiley, 1981 etc.) and so on. However, the first was criticized by Sawada (1982) because of its inconsistency, while the second was legitimately criticized by Colless (1967). Colless says that the related-group criterion (=out-group comparison) requires an *a priori* knowledge of the higher level phylogeny, so we must ask how that phylogeny was established. Sawada (1982) put forward a new method to detect the most related groups by the unique and unreversed character states of Wilson (1965). To judge whether the character states in question are unique and unreversed or not, he used Wilson's consistency test. Colless (1966), however, criticized Wilson's consistency test on several points.

Despite of the most important phylogenetic speculation in the systematic process, there are no ways to determine the polarity of each character with certainty.

The phylogenetic speculation, if it is made in phenetics, are deduced from the phenogram obtained by the consistent systematic process without any phylogenetic speculation.

Consequently, phenetics is applied as a systematic methodology in the present study.

Phenetics (numerical phenetics by Mayr, 1965) has been extensively discussed in modern systematic theories by Sokal and Sneath (1963) and Sneath and Sokal (1973). In spite of their efforts, this methodology has not been always accepted by systematicists. In fish systematics in particular, there are a few papers using phenetics (some papers in the references in Sneath and Sokal (1973); Cowan, 1972; Okiyama and Ueyanagi, 1978; Campos, 1979; Spain et al., 1980 etc.).

The most fundamental principle embodied in phenetics is that similar organisms are related. The taxanomic units are grouped by numerical methods on the basis of the degree of an overall similarity between them using as many characters as possible. *A priori* all the available characters are of equal weight in creating taxonomic groups. As stated by Sneath and Sokal (1973), to reduce subjective bias and increase objectivity, many characters are used without the previous arbitrary selection or elimination and the explicit methods are provided in processing the data and evaluating the results.

2. PROCEDURES IN THE PRESENT STUDY

This study was carried out in the following sequences:

(1) Collection of comparative morphological data
(2) Selection of unit characters
(3) Distinction of character states and coding
(4) Calculation of similarity between operational taxonomic units
(5) Cluster analysis for forming phenetic groups
(6) Taxonomic ranking

These operational processes are prerequisite to certify repeatability and objectivity in classification. The order of the steps within the procedures cannot be changed without destroying the *rationale* of the classificatory process (Sneath and Sokal, 1973).

Each step is discussed below in detail.

(1) Collection of comparative morphological data

The morphological characters used in the present study are composed of both internal and external characters.

The internal characters comprise mainly the osteological characters from the following parts: jaw apparatus, cranium, orbital bones, suspensorium and opercular apparatus, hyoid arch, branchial apparatus and gill rakers, fins, pectoral girdle, pelvic girdle, urohyal, vertebrae and their accessory bones, caudal skeleton and fin. The character such as presence or absence of the elongation of the intestine is also included in this category.

The external characters are made up of the characters which have been used chiefly in the taxonomic study.

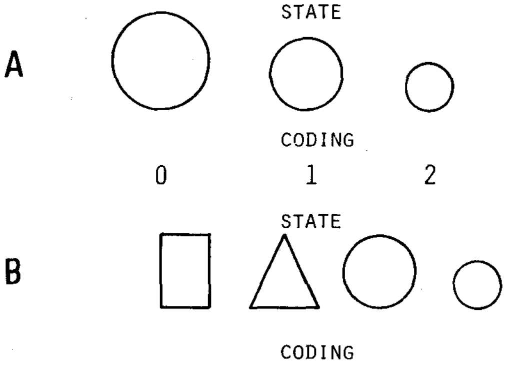
(2) Selection of unit characters

In the present study, the definition of a unit character is nearly in accordance with that of Sneath and Sokal (1973: 74). The unit character is a taxonomic character with two or more states, which cannot be subdivided logically except for subdivision by the method of coding.

As already mentioned, since it is desirable for numerical phenetics to use a large number of characters to increase reliability, as many characters as possible from both outer and inner morphological features are adopted as the unit characters. However, the characters with an intraspecific variation were excluded from the unit characters because it was impossible or very difficult in some cases to determine the character state for each OTU (operational taxonomic unit: species or subspecies in the present study) in question. All the proportional and meristic characters were, thus, not used to elucidate the interrelationships of the pleuronectids.

(3) Distinction of character states and coding

The unit characters used in the present study are composed of three types: two-state characters, quantitative multistate characters and qualitative multistate characters. Two-state characters are represented by many "presence or absence" characters. This type of unit character is most dominant in the present study. In this case, each character state is coded as 0 or 1. Quantitative multistate characters are the multistate characters with more than two character states whose character states can be arranged in a single logical sequence (in order along a one-dimensional axis). Fig. 1A is an example of this type of unit character. In this example, three character states are recognized and coded as 0, 1, 2 in order. Qualitative multistate characters are the multistate characters whose character states cannot be arranged in a single logical sequence. In such a case, the multistate character is operationally converted into several new characters which are composed only of two-state and/or quantitative multistate characters. In this process, the following case may occur:



new character - 1	0	1	1	1
new character - 2	1	0	1	1
new character - 3	1	1	0	0
new character - 4	NC	NC	0	1

Fig. 1. Examples of distinction of character states and coding. A, quantitative multistate character; B, qualitative multistate character. For explanation, see text.

no comparison is possible in the data matrix because characters or character states are absent on the logical ground. In this case, the value of the character state is considered unknown or inapplicable: NC implying "no comparison with the entry" is used in the data matrix (Sneath and Sokal, 1973). This process is exemplified in Fig. 1B. Assume that four character states, that is, square, triangle, large and small circles, are recognized but these character states cannot be arranged in a single logical sequence except for two character states, large and small circles. In such a case, this qualitative multistate character is converted into four new characters as follows: 1) square or not, 2) triangle or not, 3) circle or not, 4) size of circle, large or small. Each character state in these four characters is coded as 0 or 1. However, when the last character, size of circle, is compared, the character state of the OTU with square or triangle is coded as NC.

(4) Calculation of similarity between operational taxonomic units

In this step, the similarity between every OTU is calculated using the general coefficient of similarity of Gower (1971) with a slight modification. The Gower's coefficient for two OTU's **j** and **k** is defined as

$$S_G=\frac{\sum_{i=1}^{n} W_{i\mathbf{jk}}\cdot S_{i\mathbf{jk}}}{\sum_{i=1}^{n} W_{i\mathbf{jk}}} \qquad (0\leqq S_{i\mathbf{jk}}\leqq 1)$$

where $W_{i\mathbf{jk}}$ is a weight for unit character i. The weight $W_{i\mathbf{jk}}$ is set to 1 when a comparison is considered valid for unit character i and to 0 when the value of the state for unit character i is NC for one or both OTU's. For two-state character $S_{i\mathbf{jk}}=1$ for matches and 0 for mismatches. In the present study, according to the recommendation by Sneath and Sokal (1973: 136), negative matches are coded as 1 as well as positive matches, though Gower did not permit the negative matches in both $W_{i\mathbf{jk}}$ and $S_{i\mathbf{jk}}$. For quantitative multistate character, $S_{i\mathbf{jk}}$ is defined as

$$S_{i\mathbf{jk}}=1-\frac{|X_{i\mathbf{j}}-X_{i\mathbf{k}}|}{R_i}$$

where $X_{i\mathbf{j}}$ and $X_{i\mathbf{k}}$ are the values of the character states of OTU's **j** and **k**, and R_i is the range of unit character i in the data matrix analysed.

The modified Gower's coefficient employed in the present study is considered a very useful tool to estimate the similarity between two OTU's based on mixed types of unit characters.

(5) Cluster analysis for forming phenetic groups

Each OTU is grouped by cluster analysis on the basis of the similarity matrix. The selection of a clustering method becomes an important problem in modern numerical phenetics, since a large number of clustering methods have been developed. As stated by Sneath and Sokal (1973), it is reasonably considered that the best fit to the original similarity matrix among the OTU's is a natural concept. Therefore, the degree of the fitness to the original similarity matrix among the OTU's in each clustering method can be regarded as an optimality criterion in selecting a clustering method. In order to measure the degree of the concordance between the dendrograms produced by different clustering methods and the original similarity matrix on which they are based, Sokal and Rohlf (1962) developed the method of

Table 1. Example for new amalgamating method employed in present study forming new cluster (**J, K, L**) comprising three clusters **J, K** and **L** at same time. For explanation, see text.

	J	K	L	M
J		96.25	93.08	89.75
K	96.25		96.25	90.05
L	93.08	96.25		85.33
M	89.75	90.05	85.33	

cophenetic correlations which is the most frequently applied strategy in the numerical taxonomy. It has been found that the unweighted pair-group method using arithmetic averages (UPGMA) with the highest cophenetic correlation coefficient (CPCC) is the most faithful to the original similarity matrix based on several empirical studies (Sokal and Rohlf, 1962; Boyce, 1969; Presh, 1979), and Farris (1969) substantiated it by mathematical proof (Sneath and Sokal, 1973). Consequently, UPGMA was chosen as a clustering method in the present study.

In this calculation, the following situation may occur: the similarity S_{JK} between any two clusters **J** and **K** is equal to S_{KL} but not equal to S_{JL} (Table 1). In such a case, a new cluster comprising three clusters (**J, K, L**) is formed in the computer program employed in the present study, though the choice conventionally is the first link, i.e. **J** and **K** over **K** and **L** in the previous works (Sneath and Sokal, 1973). This amalgamating method is applied to all the possible cases that may occur among more than two clusters.

The result of the cluster analysis is represented by means of a dendrogram called a phenogram, by which the interrelationships of the pleuronectids are depicted.

(6) Taxonomic ranking

In this step, each pleuronectid species is ranked to a supraspecific taxon according to one Sneath and Sokal's (1973) phenetic criterion of ranking that gaps between taxa of equal rank should be as nearly equal as possible. This was done using phenon lines. The line delimiting a given rank must be a straight line drawn across the phenogram at a similarity level and must not bend up and down according to personal and preconceived whims about the rank of the taxa (Sneath and Sokal, 1973). In the present study, to avoid taxonomic confusion, namely to minimize unnecessary taxonomic changes, the degree of the similarity level, at which the phenon lines should be drawn, was determined on the basis of careful consideration of the previous hierarchic ranks in the family.

VI. Comparative morphology

In the present chapter, the following three procedures, (1) collection of comparative morphological data, (2) selection of unit characters, and (3) distinction of character states and coding, are carried out for each morphological region.

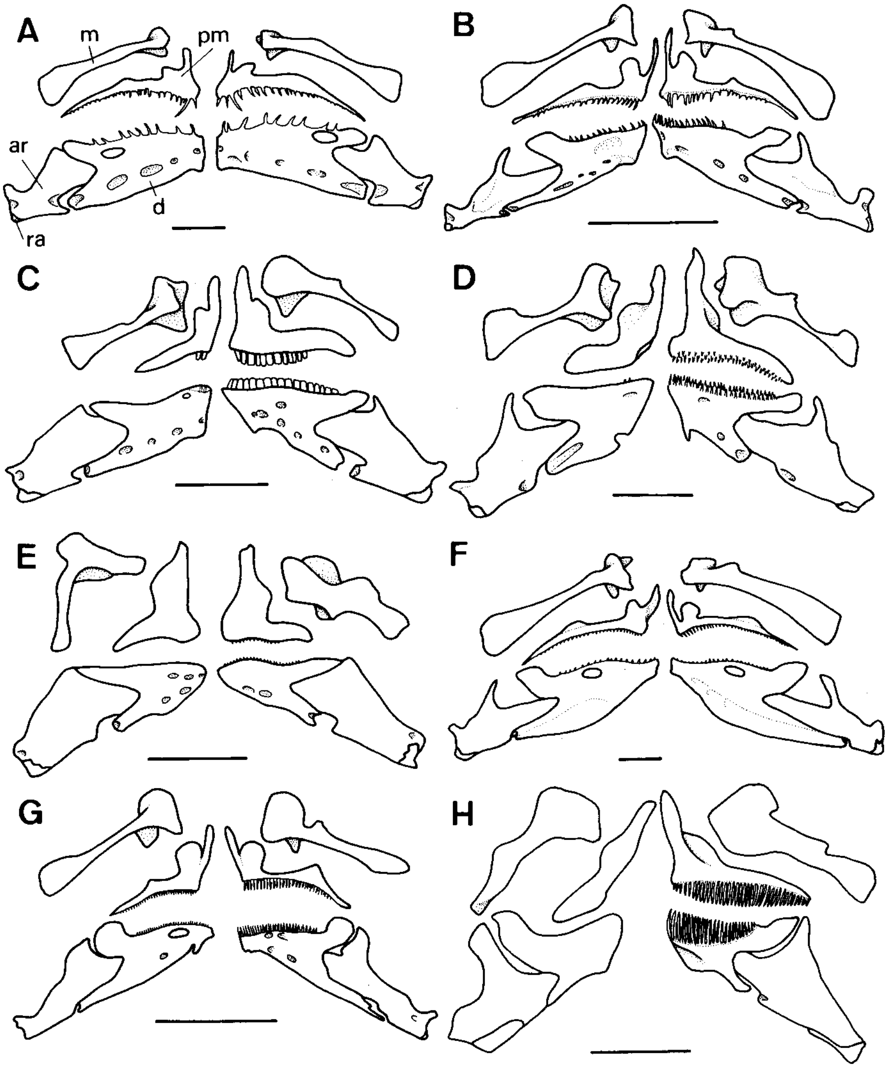


Fig. 2. Lateral aspect of jaw apparatus in eight righteye flounders. A, *Reinhardtius hippoglossoides* ; B, *Eopsetta jordani* ; C, *Pleuronectes obscurus* ; D, *Hypsopsetta guttulata* ; E, *Pleuronichthys cornutus* ; F, *Paralichthodes algoensis* ; G, *Poecilopsetta plinthus* ; H, *Pelotretis flavilatus*. ar, articular ; d, dentary ; m, maxillary ; pm, premaxillary ; ra, retroarticular. Scales indicate 5 mm.

1. JAW APPARATUS

DESCRIPTION The jaws are composed of the upper and lower jaws. The upper jaw comprises premaxillary and maxillary: supramaxillary is absent. The lower jaw consists of dentary, articular and retroarticular.

Based on the degree of the bilateral symmetry on both jaws, the pleuronectid fishes herein studied can be classified into two groups. In the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Psettichthys*, *Hippoglossoides*, *Acanthopsetta* and *Paralichthodes*, and the subfamilies Poecilopsettinae and Samarinae, both jaws are nearly symmetrical (subsymmetrical) (Figs. 2A, B, F, G and 3B). On the other hand, in the remaining pleuronectids examined both jaws are asymmetrical (Figs. 2C-E, H and 3A).

The premaxillaries (pm) are L-shaped bones bordering the upper margin of the gape. The premaxillary is generally composed of an ascending process (as), an articular process (ap) and an alveolar process bearing the teeth (Fig. 4A). Both ascending processes are firmly united with each other. On the dorsal surface near the middle part of the bone, there is a postmaxillary process (pp) which is connected with the maxillary by a ligament. In the fishes of the pleuronectine genera *Hypsopsetta* and *Pleuronichthys*, the pleuronectine *Pleuronectes yokohamae*, *P. schrenki*, *Microstomus achne* and *M. pacificus*, and the fishes of all the rhombosoleine genera except *Azygopus*, the premaxillary bears the teeth only on the blind side (Figs. 2D, E, H and 3A), whereas in the other pleuronectid fishes examined the bone bears the teeth on both sides (Figs. 2A-C, F, G and 3B). In *Pleuronectes herzensteini*, *P. yokohamae*, *P. schrenki*, *P. americanus* and *Microstomus kitt*, the intraspecific variations are slightly observed in presence or absence of the premaxillary teeth on the ocular side*.

The maxillaries (m), which are paired, are bar-like in shape and situated on the premaxillaries. The maxillaries do not border the gape. The head of the maxillary (mh) covers the articular process of the premaxillary pedicel(Fig. 4A). The maxillary is expanded posteriorly and connected medially with the outer surface of the posterior end of the premaxillary and the postmaxillary process by a ligament. The maxillary head has three processes. The upper process of the head is a cranial

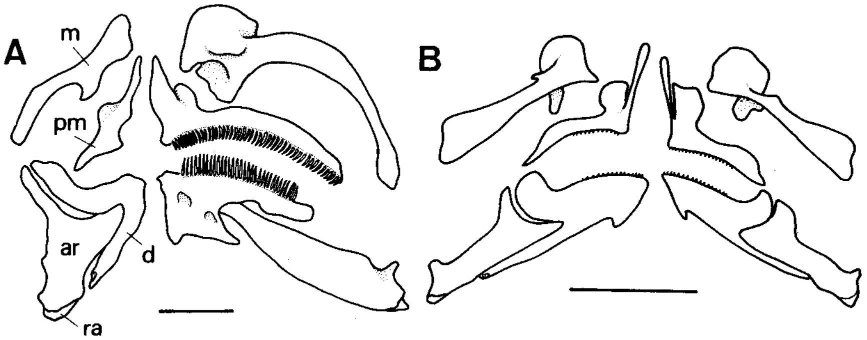


Fig. 3. Lateral aspect of jaw apparatus in two righteye flounders. A, *Peltorhamphus novaezeelandiae* ; B, *Samariscus latus*. Abbreviations as in Fig. 2. Scales indicate 5 mm.

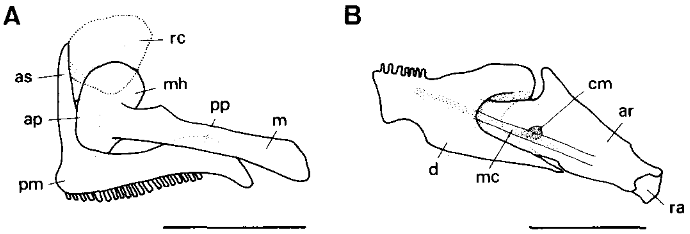


Fig. 4. Lateral aspect of upper jaw (A) and medial aspect of lower jaw (B) in *Pleuronectes herzensteini*. ap, articular process of premaxillary; as, ascending process of premaxillary; cm, coronomeckelian; mc, meckelian cartilage; mh, maxillary head; pp, postmaxillary process of premaxillary; rc, rostral cartilage. Other abbreviations as in Fig. 2. Scales indicate 5 mm.

condyle. The process at the upper end of its anterior part is a maxillary spike. The lower part of the maxillary head is a premaxillary condyle. The premaxillary condyle has the outer and inner processes covering the articular process of the premaxillary. The maxillary is connected with the articular at the small process behind the maxillary head by a ligament.

The dentaries (d) are paired bones which border the lower edge of the gape, and which are firmly united with each other anteromedially. The bones generally bear the teeth on both sides, but in the pleuronectine *Pleuronichthys cornutus*, *P. verticalis*, *Microstomus achne* and *M. pacificus* and the fishes of the rhombosoleine genera *Pelotretis*, *Ammotretis*, *Rhombosolea* and *Peltorhamphus*, the teeth are present only on the blind side (Figs. 2E, H and 3A). But, a specimen has a few teeth on the ocular side in *Pleuronichthys verticalis*, *Microstomus achne* and *M. pacificus* and some specimens have several teeth in *Pleuronectes yokohamae* and *P. schrenki**. The dentary is divided posteriorly by a deep notch into two branches, the upper and lower limbs. The dentary is connected by a ligament with the posterior end of the maxillary at its lateral surface and at the posterior end of the upper limb. The lower limb is perforated by a mandibular sensory canal with several openings. The deep hollow space into which fits the anterior portions of the articular and of the meckelian cartilage occurs between both limbs (Fig. 4B).

Each articular (ar) inserting into the hollow between both limbs of the dentary is articulated to the retroarticular posteroventrally. It is perforated by a sensory canal running from dentary to preopercle. The meckelian cartilage (mc), which is attached to the tendon of the adductor mandibulae, lies on the inner surface of the articular, and its anterior part inserts into the hollow between both limbs of the dentary together with the articular (Fig. 4B). The articular is connected with a small process behind the head of the maxillary by a ligament.

Each retroarticular (ra) is an irregularly shaped bone bordering the posteroventral part of the articular. The retroarticular is articulated to the articular and connected with the anterior margin of the interopercle by a ligament.

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* The data from Norman (1934), Hikita (1934), Fitch (1963), Kato *et al.* (1974), Last (1978), and Okisu and Yusa (1979) are also included.

Table 2. Comparison and coding of character of jaw apparatus in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

Bilateral symmetry on both jaws	Subfamilies and genera
subsymmetrical (0)	Pleuronectinae *Atheresthes, Reinhardtius, Hippoglossus, Eopsetta, Verasper, Psettichthys, Hippoglossoides, Acanthopsetta, Paralichthodes* Poecilopsettinae Samarinae
asymmetrical (1)	Pleuronectinae *Dexistes, Pleuronectes, Platichthys, Hypsopsetta, Pleuronichthys, Glyptocephalus, Errex, Kareius, Microstomus, Tanakius, Embassichthys, Clidoderma* Rhombosoleinae

UNIT CHARACTER The jaws of flatfishes have been studied by several investigators (Traquair, 1865; Kyle, 1921; Norman, 1934; Yazudani, 1969 etc.). They have been discussed mainly in relation to their food and feeding behavior (e.g. Norman, 1934; Yazudani, 1969). In the family Pleuronectidae, a few characters such as the degree of the bilateral symmetry, presence or absence of the teeth of each jaw and others have been used in the classification (see Norman, 1934; Nelson, 1976).

In the present study, the pleuronectid jaws show interspecifc variations in the following characters: 1) the degree of the bilateral symmetry on both jaws, 2) presence or absence of the teeth of the premaxillary on the ocular side, and 3) presence or absence of the teeth of the dentary on the ocular side.

The first character, the degree of the bilateral symmetry on both jaws, clearly has two character states, subsymmetrical and asymmetrical. Accordingly, this is used as a unit character with two states and the character state is coded as 0 for their subsymmetry and as 1 for their asymmetry. As for the second and third characters, presence or absence of the premaxillary and dentary teeth on the ocular side, the intraspecific variations were observed in several species in the present study and also in the previous works as already stated. Thus, these characters were excluded from the analyses.

Consequently, only a single unit character was recognized in this anatomical region (Table 2).

2. CRANIUM

DESCRIPTION The pleuronectid cranium is so asymmetrical that each skeletal component varies in shape and arrangement with the species and the side of the body.

The cranium is divided into the following regions: the rostral, the orbital, the otic, the occipital, the skull roof and the basicranial regions.

The rostral region at the anterior part of the cranium comprises nasal, mesethmoid and prefrontal. The orbital region consists only of pterosphenoid. The otic region at the posterolateral portion of the cranium is composed of sphenotic, prootic, pterotic and epiotic. The occipital region comprises supraoccipital, basioccipital, exoccipital and intercalar. The skull roof is made up of frontal and parietal. The basicranium consists of prevomer and parasphenoid.

The nasals are generally paired cylindrical bones attached to the anterior margins of the prefrontals. The pleuronectids examined here were classified into three groups according to the composition of the nasals. The first group contains the members of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Psettichthys*, *Acanthopsetta*, *Platichthys*, *Hypsopsetta*, *Glyptocephalus*, *Errex*, *Kareius*, *Microstomus*, *Tanakius*, *Clidoderma* and *Paralichthodes*, the pleuronectine *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. mochigarei*, *P. asper*, *P. sakhalinensis*, *P. americanus*, *P. quadrituberculatus*, *P. glacialis* and *P. pinnifasciatus*, *Nematops macrochirus* of the subfamily Poecilopsettinae and all the members of the subfamily Rhombosoleinae examined. The members of this group have a pair of nasals, though the degree of their bilateral symmetry varies with the member (Fig. 5A-J, L, M, O, Q-V). Within these fishes, in the members of *Reinhardtius*, *Paralichthodes* and *Nematops*, they are nearly symmetrical (Fig. 5O, Q). In the members of *Ammotretis*, *Taratretis* and *Peltorhamphus*, the nasal of the blind side has a lateral branch (Fig. 5S, T, V). In the other members of the first group, these bones are asymmetrical in that the bone of the ocular side is larger in size than that of the blind side, though in the members of *Glyptocephalus* and *Errex* the bone of the blind side is larger than that of the ocular side (Fig. 5L). The second group includes the remaining members of the subfamily Pleuronectinae and all the members of the subfamily Samarinae examined. In this group, the bone of the blind side is absent (Fig. 5K, N, W-Y). But, in a specimen of *Pleuronectes limanda*, there is a small nasal of the blind side. In the third group comprising the members of the poecilopsettine genus *Poecilopsetta*, the bone of the ocular side is absent (Fig. 5P).

The mesethmoid (me) is an unpaired bone connected anteriorly with the prevomer. The mesethmoid bears on its dorsal surface a median longitudinal keel together with the prevomer.

The pleuronectid fishes herein studied were classified into seven groups based on the relation among the mesethmoid and the other bones. The first group comprises the members of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hypsopsetta*, *Microstomus*, *Tanakius*, *Clidoderma* and *Paralichthodes* and the rhombosoleine genus *Pelotretis*. The mesethmoid is connected laterally with the prefrontal of the ocular side, posteriorly with the frontal of the ocular side, and posterolaterally with the prefrontal of the blind side. The mesethmoid is in contact with the interorbital process which is the frontal of the blind side extending forward along the inner surface of the interorbital bone (=frontal of the ocular side). The mesethmoid forms the anterior part of the upper orbital cavity (Figs. 6A, B, 8A,

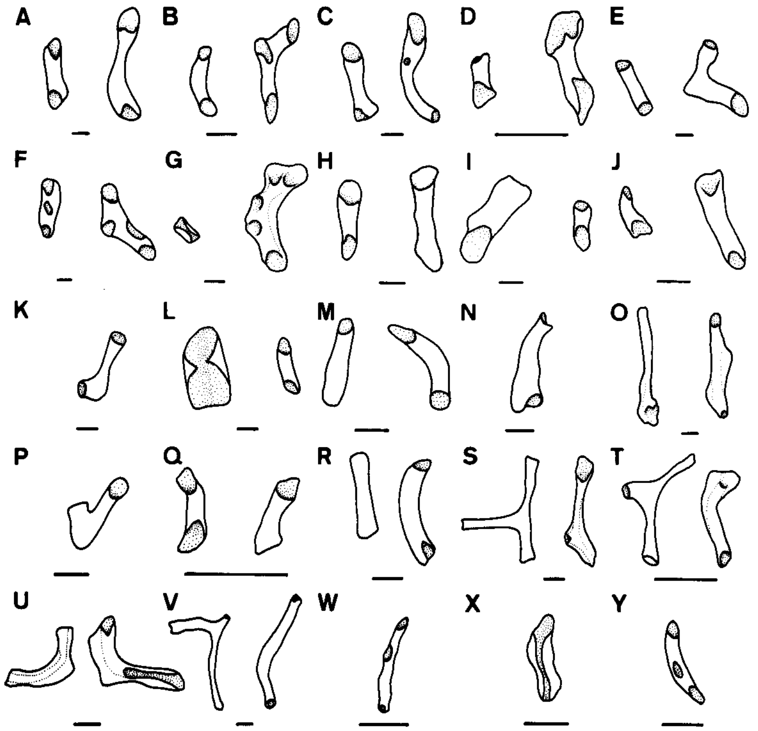

Fig. 5. Dorsal aspect of nasals in 25 righteye flounders. A, *Atheresthes evermanni* ; B, *Hippoglossus stenolepis* ; C, *Eopsetta exilis* ; D, *E. jordani* ; E, *Verasper variegatus* ; F, *Acanthopsetta nadeshnyi* ; G, *Pleuronectes vetulus* ; H, *P. mochigarei* ; I, *Platichthys stellatus* (reversed specimen) ; J, *Hypsopsetta guttulata* ; K, *Pleuronichthys cornutus* ; L, *Glyptocephalus stelleri* ; M, *Microstomus achne* ; N, *Embassichthys bathybius* ; O, *Paralichthodes algoensis* ; P, *Poecilopsetta plinthus* ; Q, *Nematops macrochirus* ; R, *Pelotretis flavilatus* ; S, *Ammotretis rostratus* ; T, *Taratretis derwentensis* ; U, *Rhombosolea leporina* ; V, *Peltorhamphus novaezeelandiae* ; W, *Samaris cristatus* ; X, *Plagiopsetta glossa* ; Y, *Samariscus latus*. Scales indicate 1 mm.

D, 9C, 11A, 12B, 13A and 14A). The second group consists of the fishes of the pleuronectine genera *Psettichthys*, *Hippoglossoides*, *Acanthopsetta*, *Dexistes*, *Pleuronectes*, *Platichthys* and *Kareius*. The relation among the mesethmoid and the other bones is similar to that of the preceding group, but the mesethmoid is not in contact with the interorbital process (Figs. 6C, D, 7, 11B, C and 12A). In the third group represented only by the members of the pleuronectine genus *Pleuronichthys*, the mode of the connection of the mesethmoid with the other bones is similar to that of the first group, but the mesethmoid forms only a part of the anterior wall of the upper orbital cavity (Figs. 8B and 12C). In the fourth group including the members of the pleuronectine genera *Glyptocephalus* and *Embassichthys*, the relation among the mesethmoid and the other bones is similar to that of the second group, but the mesethmoid is in contact posterolaterally with the anterior trace of the interor-

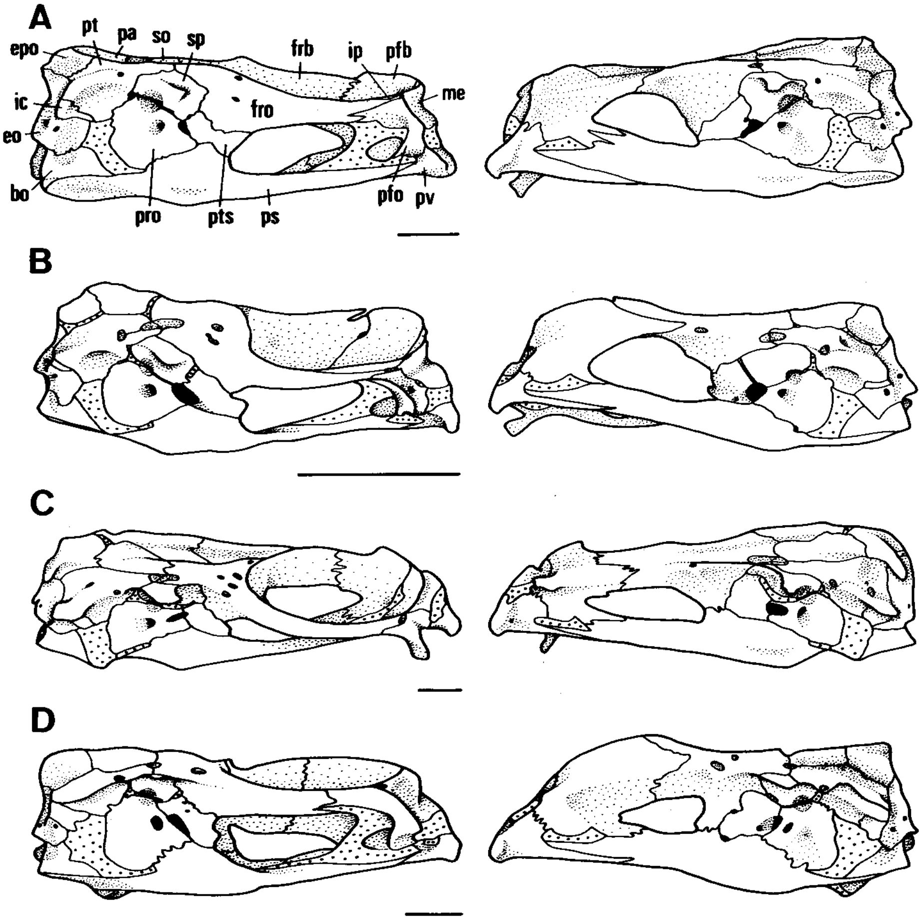

Fig. 6. Lateral aspect of crania in four righteye flounders. A, *Hippoglossus stenolepis* ; B, *Eopsetta jordani* ; C, *Hippoglossoides dubius* ; D, *Acanthopsetta nadeshnyi*. bo, basioccipital ; eo, exoccipital ; epo, epiotic ; frb, frontal of blind side ; fro, frontal of ocular side ; ic, intercalar ; ip, interorbital process ; me, mesethmoid ; pa, parietal ; pfb, prefrontal of blind side ; pfo, prefrontal of ocular side ; pro, prootic ; ps, parasphenoid ; pt, pteroid ; pts, pterosphenoid ; pv, prevomer ; so, supraoccipital ; sp, sphenotic. Left, ocular side ; right, blind side. Scales indicate 5 mm.

bital process (Fig. 8C). The fifth group contains the fishes of the pleuronectine genus *Errex*, all the poecilopsettine genera examined, the rhombosoleine genera *Ammotretis*, *Taratretis* and *Peltorhamphus* and the samarine genus *Samariscus*. In this group, the mode of the connection of the mesethmoid with the other bones is similar to that of the first group, but the mesethmoid does not form the anterior part of the upper orbital cavity because the frontal of the ocular side is connected with the prefrontal of the blind side at the posterior margin of the mesethmoid, or because the cartilage is present between those bones (Figs. 9A, B, D, 10A, D, 13B, C, 14B, C and 15C). In the sixth group containing the members of the rhombosoleine genera *Azygopus* and *Rhombosolea*, the connection of the mesethmoid with the other bones is similar to that of the preceding group, but the mesethmoid is not in contact with the interorbital process (Figs. 10B and 15A). In the seventh group comprising the fishes of the samarine genera *Samaris* and *Plagiopsetta*, the mesethmoid is connected laterally and posteriorly with the prefrontals of both sides and attached posteriorly to the frontal of the ocular side, but it is not in contact with the interorbital process. The mesethmoid does not constitute the anterior portion of the upper orbital cavity (Figs. 10C and 15B).

The prefrontals (pfo and pfb) lying on the sides of the mesethmoid are very asymmetrical paired bones. Each element is generally connected anteriorly with the prevomer, posteriorly with the frontal of the same side and ventrally with the

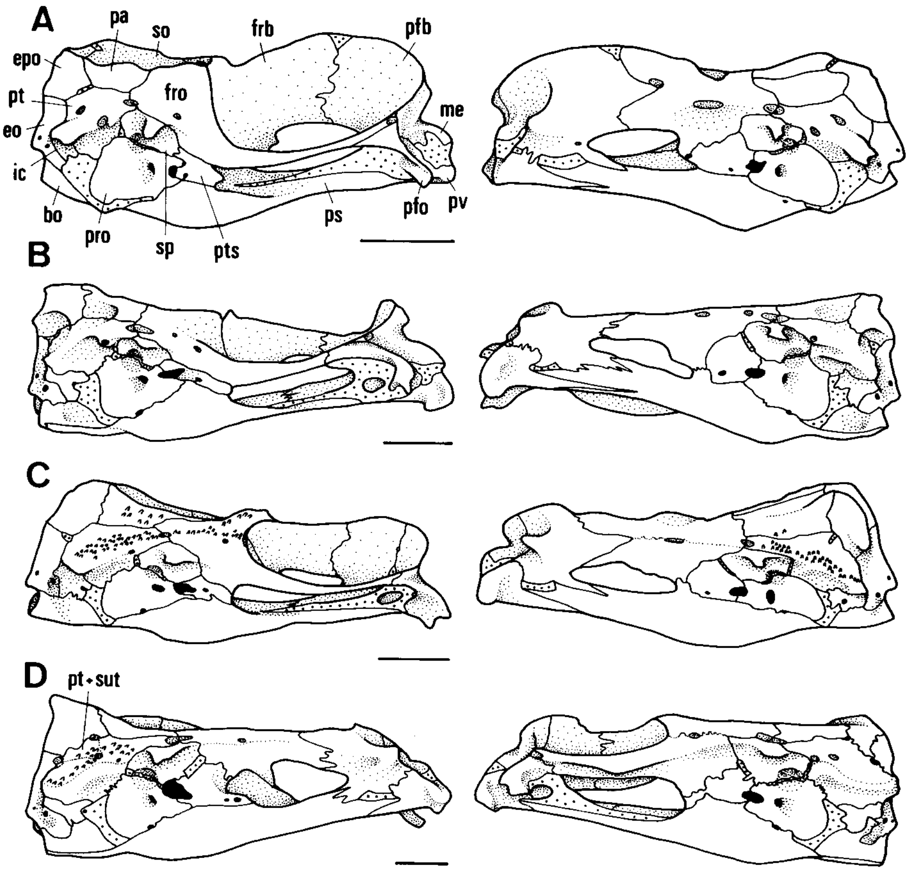

Fig. 7. Lateral aspect of crania in four righteye flounders. A, *Dexistes rikuzenius*; B, *Pleuronectes vetulus*; C, *P. herzensteini*; D, *Platichthys stellatus* (reversed specimen). sut, supratemporal. Other abbreviations as in Fig. 6. Left, ocular side; right, blind side (except D). Scales indicate 5 mm.

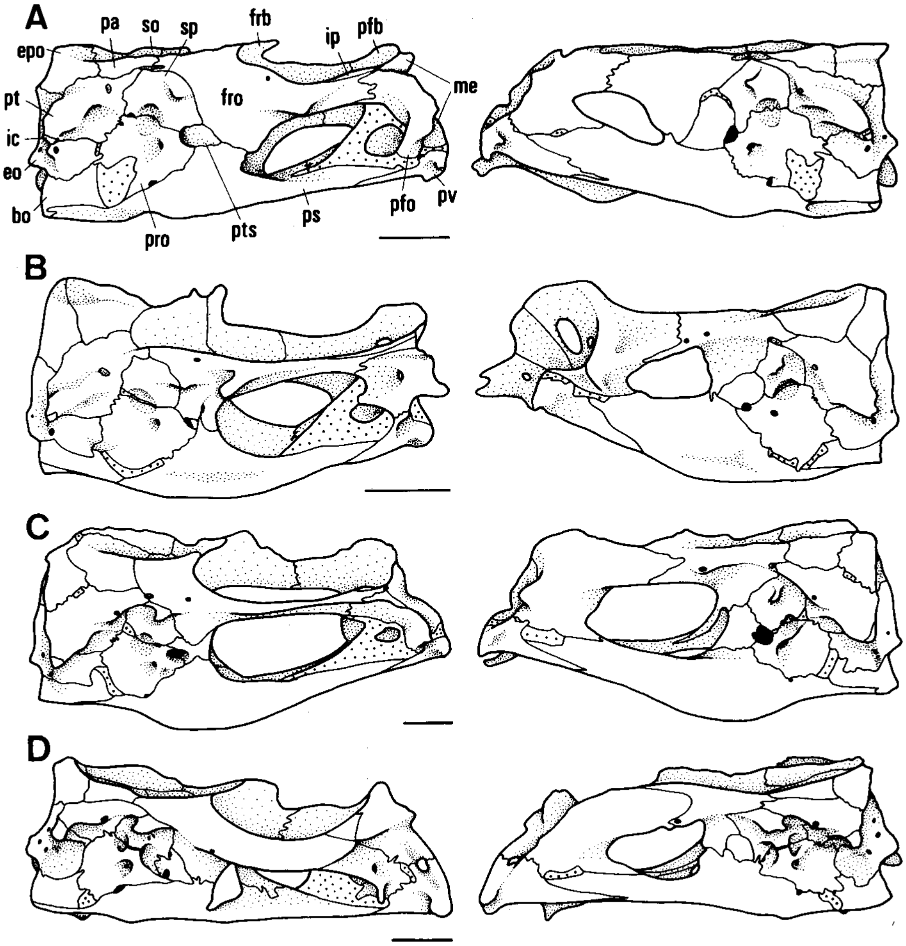

Fig. 8. Lateral aspect of crania in four righteye flounders. A, *Hypsopsetta guttulata* ; B, *Pleuronichthys cornutus* ; C, *Embassichthys bathybius* ; D, *Paralichthodes algoensis*. Abbreviations as in Fig. 6. Left, ocular side ; right, blind side. Scales indicate 5 mm.

parasphenoid (Figs. 6-16). These bones are more or less connected with each other by a cartilagenous component or directly under the anteriormost part of the interorbital bone. The size of the cartilage varies with the species.

On the ocular side, the prefrontal forms the anterior or anterodorsal part of the lower orbital cavity. In the fishes of the subfamilies Poecilopsettinae and Samarinae, the prefrontal is attached to the corresponding element of the blind side behind the mesethmoid (Figs. 13B, C and 15B, C). Among these fishes, in the Poecilopsettinae, the prefrontals are attached to each other on the lower part of the anterior portion of the frontal of the ocular side, but on the upper part of the same portion in the Samarinae. In the other pleuronectids, the prefrontal is separated from that of the blind side by the mesethmoid (Figs. 11, 12, 13A, 14 and 15A). The preorbital is attached to the lateral aspect of the anterior part of the prefrontal.

On the blind side, the prefrontal forms the anterior and anterolateral portions of the upper orbital cavity. The prefrontal is connected anterolaterally with the frontal of the ocular side by a cartilagenous component or directly. In the members

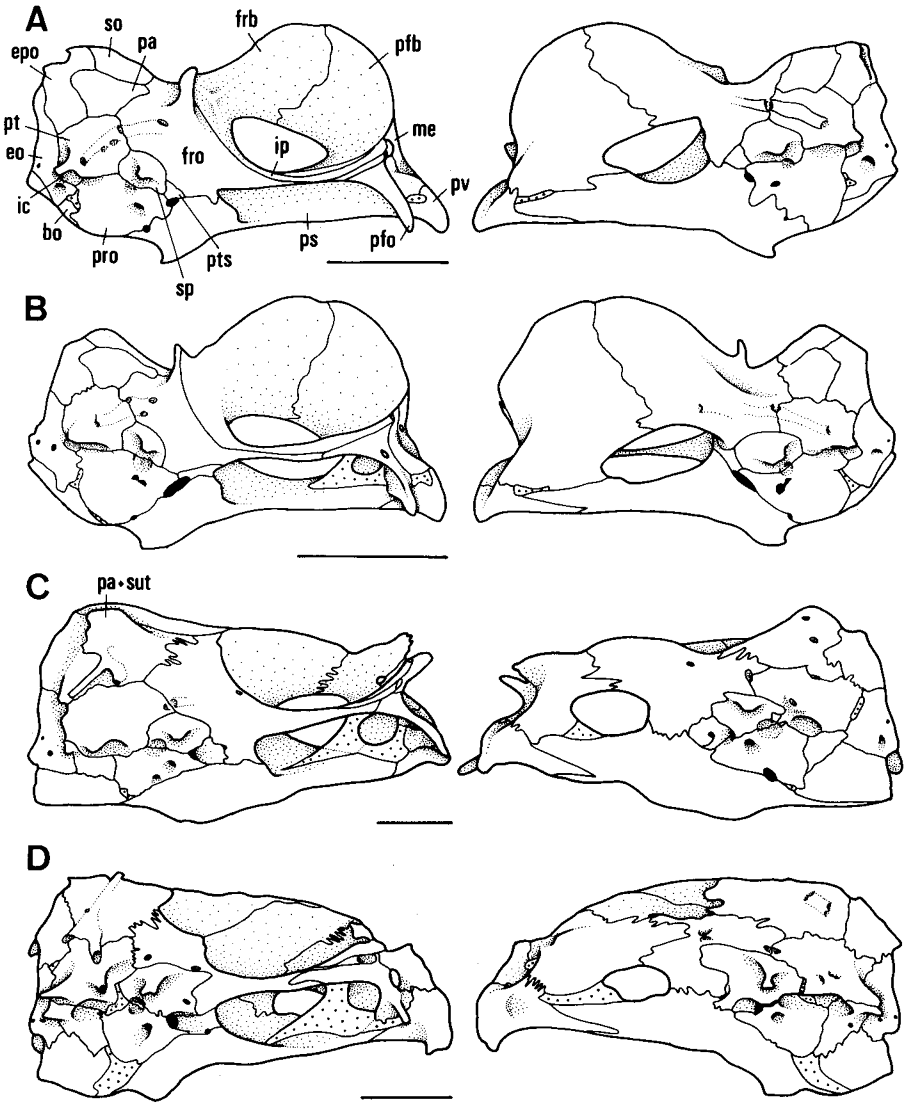

Fig. 9. Lateral aspect of crania in four righteye flounders. A, *Poecilopsetta plinthus*; B, *Nematops macrochirus*; C, *Pelotretis flavilatus*; D, *Ammotretis rostratus*. Abbreviations as in Figs. 6 and 7. Left, ocular side; right, blind side. Scales indicate 5 mm.

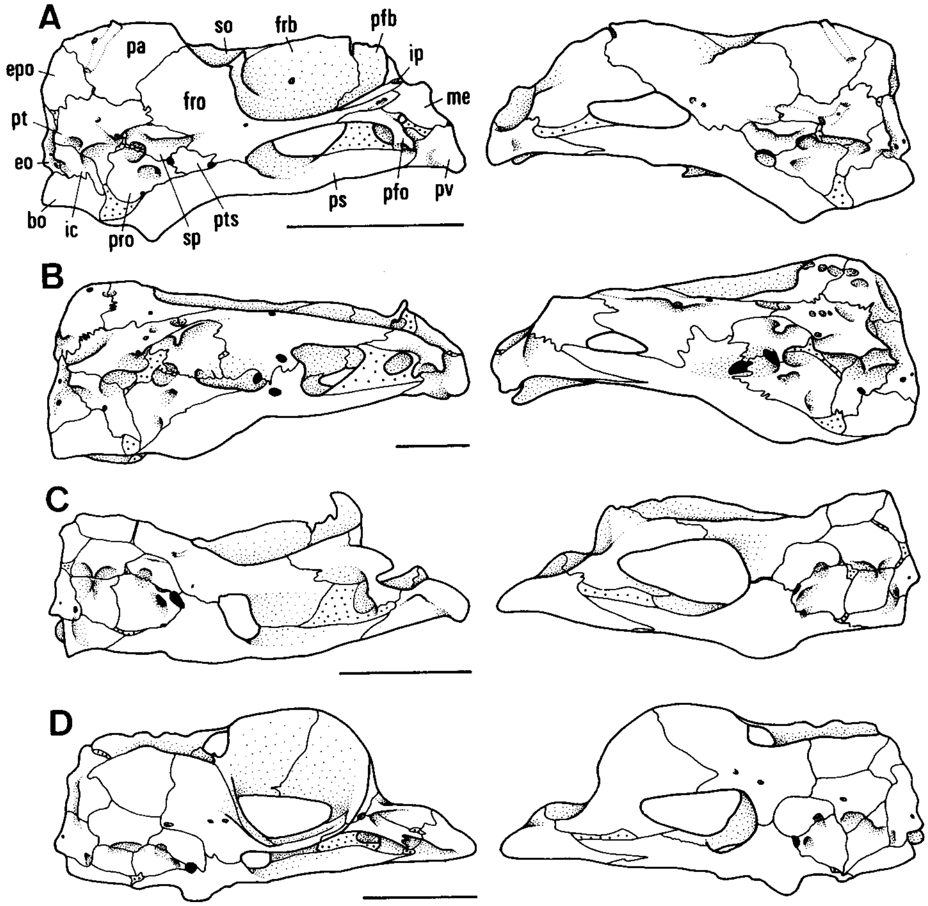

Fig. 10. Lateral aspect of crania in four righteye flounders. A, *Taratretis derwentensis* ; B, *Rhombosolea leporina* ; C, *Samaris cristatus* ; D, *Samariscus latus*. Abbreviations as in Fig. 6. Left, ocular side ; right, blind side. Scales indicate 5 mm.

of the subfamilies Poecilopsettinae and Samarinae, the prefrontal is also attached to that of the opposite side behind the mesethmoid. In the fishes of the subfamily Samarinae, the prefrontal is further attached to the frontal of the ocular side in the middle part of the orbital cavity of the upper eye (Fig. 15B, C). The preorbital is attached to the lateral process of the prefrontal in the fishes of the Pleuronectinae and Rhombosoleinae. In the fishes of the Samarinae, the preorbital is attached to the middle of the anterior part of the prefrontal by a ligament (Fig. 18D).

The pterosphenoids (pts), if present, are usually paired bones forming the anterolateral walls of the cranium. The pterosphenoid is absent on both sides in the fishes of the subfamily Samarinae and the rhombosoleine genus *Azygopus*, and on the blind side in the fishes of the rhombosoleine genera *Rhombosolea* and *Peltorhamphus* (Fig. 10B-D).

On the ocular side, the pleuronectids with the pterosphenoid are basically classified into two groups according to the connection of the pterosphenoid with the other bones of the cranium. The first group comprises the members of the pleuronectine genera except *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, the poecilopsettine members such as *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus* and the rhombosoleine members such as *Ammotretis rostratus*, *A*, *lituratus*, *A. elongatus*, *Rhombosolea plebeia*, *R. tapirina* and *Peltorhamphus novaezeelandiae*. The pterosphenoid is from large to moderate in size and surrounded by the frontal dorsally, by the sphenotic posterodorsally, by the prootic posteroventrally and by the parasphenoid ventrally. The pterosphenoid forms the posterior wall of the orbital cavity of the lower eye (Figs. 6, 7, 8C and 9B, D). The intraspecific variations are found in *Psettichthys melanostictus* and *Nematops macrochirus*. In a specimen of the former species, the pterosphenoid does not form the posterior wall of the orbital cavity because of the connection of the frontal with the parasphenoid at its anterior margin. In a specimen of the latter species, the pterosphenoid is separated from the sphenotic because of the attachment of the frontal to the prootic at its posterior margin. The second group consists of the members of the pleuronectine genera *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, the poecilopsettine members such as *Poecilopsetta praelonga* and *P. plinthus* and the rhombosoleine members such as *Pelotretis flavilatus*, *Taratretis derwentensis*, *Rhombosolea leporina* and *Peltorhamphus latus*. In this group, the pterosphenoid is from rather moderate to small in size. The mode of the connection of the pterosphenoid with the other bones is similar to that of the preceding group, but the pterosphenoid does not form the posterior wall of the orbital cavity because of the attachment of the frontal to the parasphenoid at its anterior margin (Figs. 8A, B, D, 9A, C and 10A, B). There are some variations in the mode of the connection of the pterosphenoid with the other bones in *Pleuronichthys cornutus* and *P. ocellatus*. In a specimen of the former species, the pterosphenoid is separated from the sphenotic because of the attachment of the frontal to the prootic at its posterior margin. In a specimen of the latter species, the pterosphenoid is separated from the frontal by the sphenotic.

On the blind side, the pleuronectids with the pterosphenoid are fundamentally divided into four groups according to the arrangement of the pterosphenoid and its surrounding bones. The first group is composed of all the members of the subfamily Pleuronectinae except *Hippoglossoides platessoides limandoides*, *H. elassodon*, *H. dubius*, *H. robustus*, *Acanthopsetta nadeshnyi*, *Pleuronectes vetulus*, *Hypsopsetta guttulata*, *Pleuronichthys decurrens*, *P. cornutus*, *P. verticalis*, *P. coenosus*, *P. ritteri*, *P. ocellatus* and *Paralichthodes algoensis* and the poecilopsettine members such as *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus*. The pterosphenoid shows the same mode of the connection as seen in the first group on the ocular side (Figs. 6A, B, 7A, C, D, 8C and 9B). But, in a specimen of *Pleuronectes herzensteini*, the same arrangement as that in the second group on the ocular side is observed. The second group comprises the members of the pleuronectine genera *Hippoglossoides* except *H. pinetorum*, *Acanthopsetta*, *Hypsopsetta* and *Pleuronichthys*, a pleuronectine *Pleuronectes vetulus*, the poecilopsettine members such as *Poecilopsetta praelonga* and *P. plinthus*, and the rhombosoleine members such as *Pelotretis flavilatus* and *Ammotretis lituratus*. The relation among the ptero-

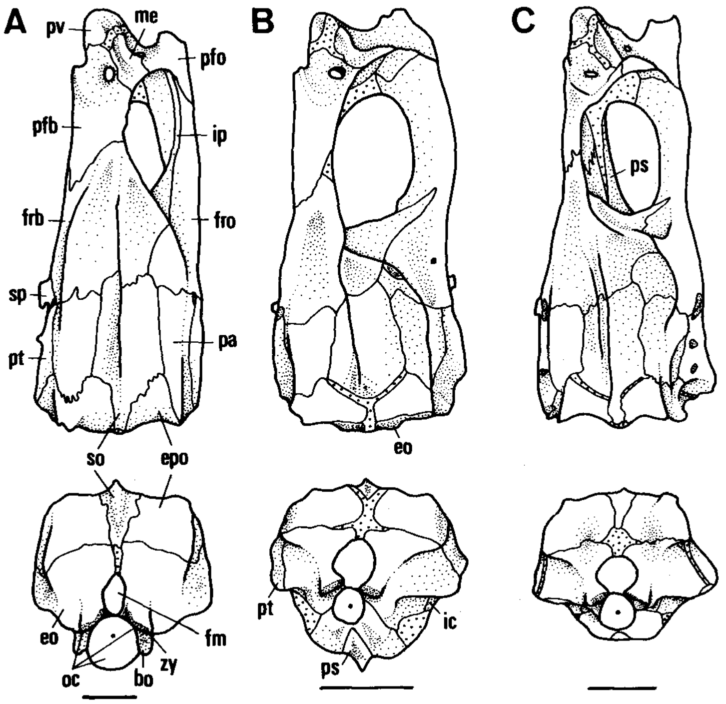

Fig. 11. Dorsal and posterior aspects of crania in three righteye flounders. A, *Verasper variegatus*; B, *Dexistes rikuzenius*; C, *Pleuronectes vetulus*. oc, occipital condyle; zy, zygapophysis of exoccipital. Other abbreviations as in Fig. 6. Scales indicate 5 mm.

sphenoid and the other bones is the same as that in the second group on the ocular side (Figs. 6C, D, 7B, 8A, B and 9A, C). But, in one specimen of each of *Hippoglossoides elassodon* and *H. dubius*, the arrangement of the pterosphenoid and its adjacent bones is the same as that in the first group on the ocular side. In the third group consisting only of *Paralichthodes algoensis*, a member of the Pleuronectinae, the pterosphenoid is bounded by the frontal anterodorsally, by the sphenotic posterodorsally and by the parasphenoid ventrally, and does not form the posterior wall of the orbital cavity (Fig. 8D). In the fourth group comprising the rhombosoleine members such as *Ammotretis rostratus*, *A. elongatus* and *Taratretis derwentensis*, the mode of the connection of the pterosphenoid with the other bones is similar to that in the second group on the ocular side, but the pterosphenoid is separated from the frontal by the sphenotic (Figs. 9D and 10A).

The sphenotics (sp) are paired bones forming the anterior lateral walls of the cranium.

On the ocular side, in the fishes of the rhombosoleine genus *Azygopus* and the subfamily Samarinae, the sphenotic is bounded by the frontal anterodorsally, by the pterotic posterodorsally, by the prootic posteroventrally and by the parasphenoid ventrally (Fig. 10C, D). In the other pleuronectid fishes examined here, the sphenotic is bounded by the pterosphenoid anteriorly, by the frontal anterodorsally, by the pterotic posterodorsally and by the prootic ventrally (Figs. 6-9 and 10A, B). The variations in these arrangement were observed in *Pleuronichthys cornutus*, *P. ocellatus* and *Nematops macrochirus*. In a specimen of the first and third species, the sphenotic was separated from the pterosphenoid because of the connection of the frontal with the prootic at its anterior margin. In a specimen of the second species, the sphenotic was also connected with the parasphenoid anterior to the pterosphenoid.

On the blind side, in the fishes of the rhombosoleine genera *Azygopus*, *Rhombosolea* and *Peltorhamphus* and the Samarinae, the relation among the sphenotic and the other bones is the same as that in the former group on the ocular side (Fig. 10B-D). In a pleuronectine *Paralichthodes algoensis*, the sphenotic is bounded by the frontal anterodorsally, by the pterotic posterodorsally, by the prootic posteroventrally, by the parasphenoid ventrally and by the pterosphenoid anteroventrally (Fig. 8D). In *Ammotretis rostratus*, *A. elongatus* and *Taratretis derwentensis* of the Rhombosoleinae, the sphenotic is bounded by the same bones as those in the

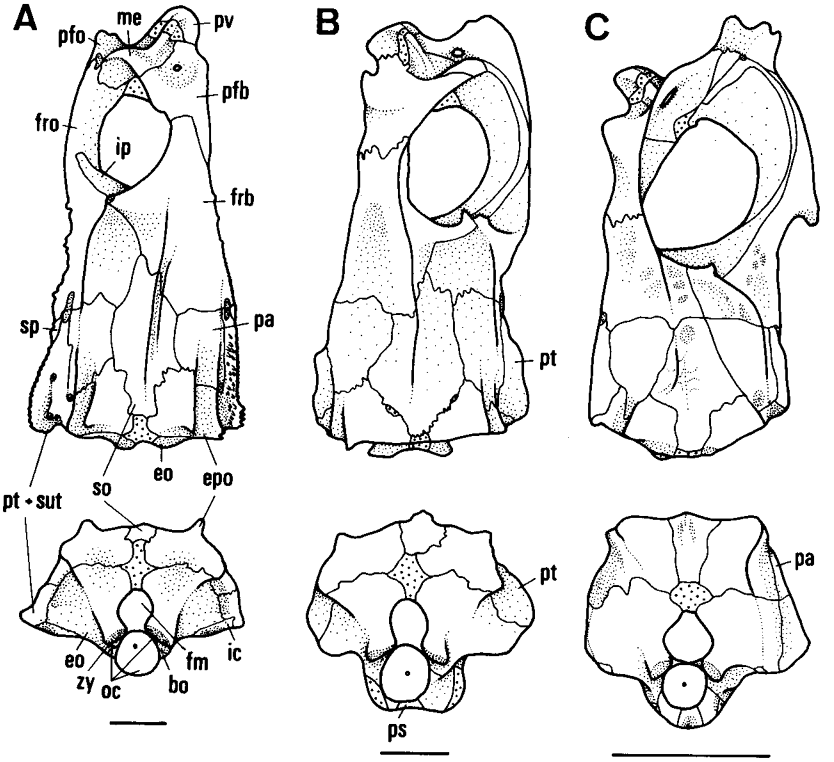

Fig. 12. Dorsal and posterior aspects of crania in three righteye flounders. A, *Platichthys stellatus* (reversed specimen); B, *Hypsopsetta guttulata*; C, *Pleuronichthys cornutus*. Abbreviations as in Figs. 6, 7 and 11. Scales indicate 5 mm.

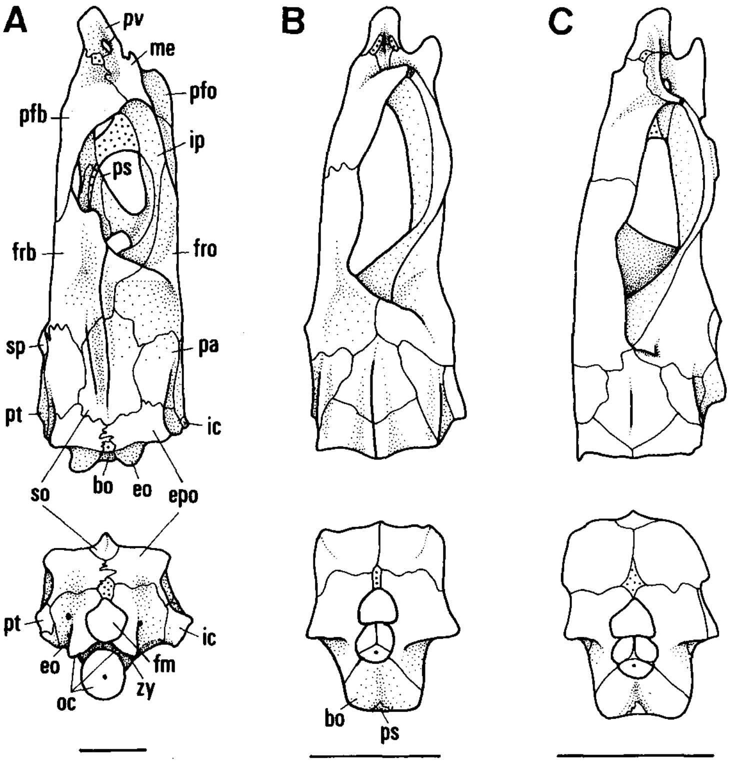

Fig. 13. Dorsal and posterior aspects of crania in three righteye flounders. A, *Paralichthodes algoensis*; B, *Poecilopsetta plinthus*; C, *Nematops macrochirus*. Abbreviations as in Figs. 6 and 11. Scales indicate 5 mm.

preceding species, but it is also bounded by the parasphenoid in front of the pterosphenoid (Figs. 9D and 10A). In the other pleuronectids studied, the arrangement of the sphenotic and its adjacent bones is the same as that in the latter group on the ocular side (Figs. 6, 7, 8A-C and 9A-C).

The prootics (pro) are paired bones forming the midlateral walls of the cranium. The relation of the prootic in regard to the other bones varies with the species and the side of the body.

Regarding the ocular side, the pleuronectids are classifiable into four groups according to the connection of the prootic with the other bones. The first group comprises the members of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Verasper*, *Acanthopsetta*, *Dexistes*, *Microstomus*, *Tanakius* and *Paralichthodes*, the pleuronectine *Eopsetta exilis*, *Hippoglossoides elassodon*, *H. dubius*, *H. robustus*, *H. pinetorum*, *Pleuronectes mochigarei*, *P. asper*, *P. sakhalinensis*, *P. punctatissimus* and *P. obscurus*, and all the members of the subfamily Poecilopsettinae examined. The prootic is surrounded by the parasphenoid, the pterosphenoid, the sphenotic, the pterotic, the intercalar, the exoccipital and the basioccipital (Figs. 6A, C, D, 7A, 8D and 9A, B). But, in a specimen of *Nematops* *macrochirus*, the prootic is also in contact anterodorsally with the frontal. In the pleuronectine members of these fishes except the members of the genera *Microstomus* and *Paralichthodes*, the cartilagenous interspace is usually well developed among the prootic, the pterotic, the intercalar, the exoccipital, the basioccipital and the parasphenoid (Figs. 6A, C, D and 7A). In the members of the pleuronectine genera *Microstomus* and *Paralichthodes* and the Poecilopsettinae, that interspace is small in size (Figs. 8D and 9A, B). The second group consists of the members of the pleuronectine genera *Hypsopsetta*, *Pleuronichthys*, *Embassichthys* and *Clidoderma* and the pleuronectine *Eopsetta jordani* and *E. grigorjewi*. The arrangement of the prootic and the other bones is similar to that in the first group, but the prootic is separated from the intercalar by the pterotic and the exoccipital (Figs. 6B and 8A-C). But, in a specimen of *Pleuronichthys cornutus*, the prootic is also in contact anterodorsally with the frontal. The cartilagenous interspace is large in size in *Eopsetta jordani*, *E. grigorjewi*, *Hypsopsetta guttulata* and *Clidoderma asperrimum* (Figs. 6B and 8A), whereas it is small in size in the members of the genera *Pleuronichthys* and *Embassichthys* (Fig. 8B, C). The third group is composed of

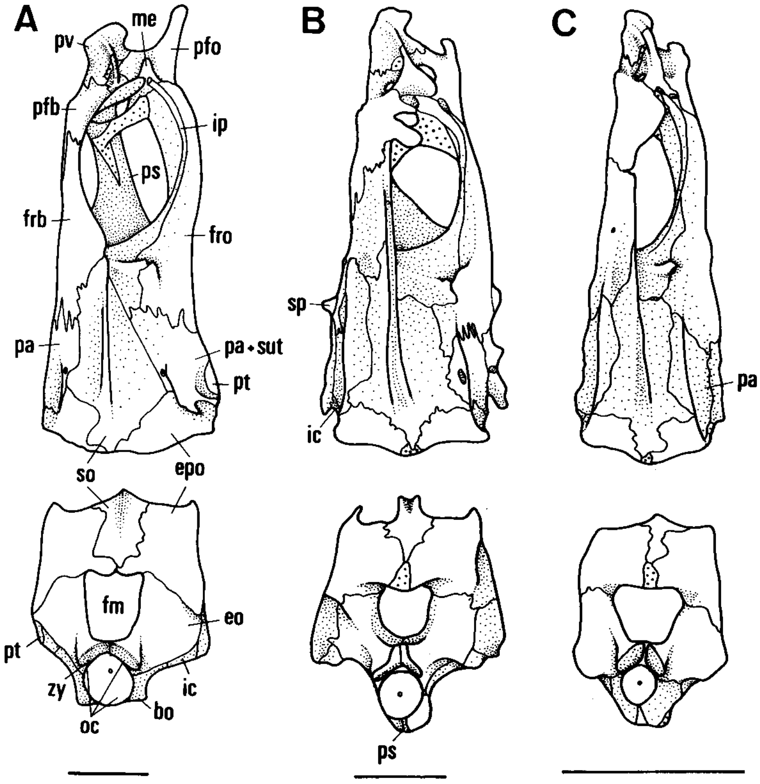

Fig. 14. Dorsal and posterior aspects of crania in three righteye flounders. A, *Pelotretis flavilatus*; B, *Ammotretis rostratus*; C, *Taratretis derwentensis*. Abbreviations as in Figs. 6, 7 and 11. Scales indicate 5 mm.

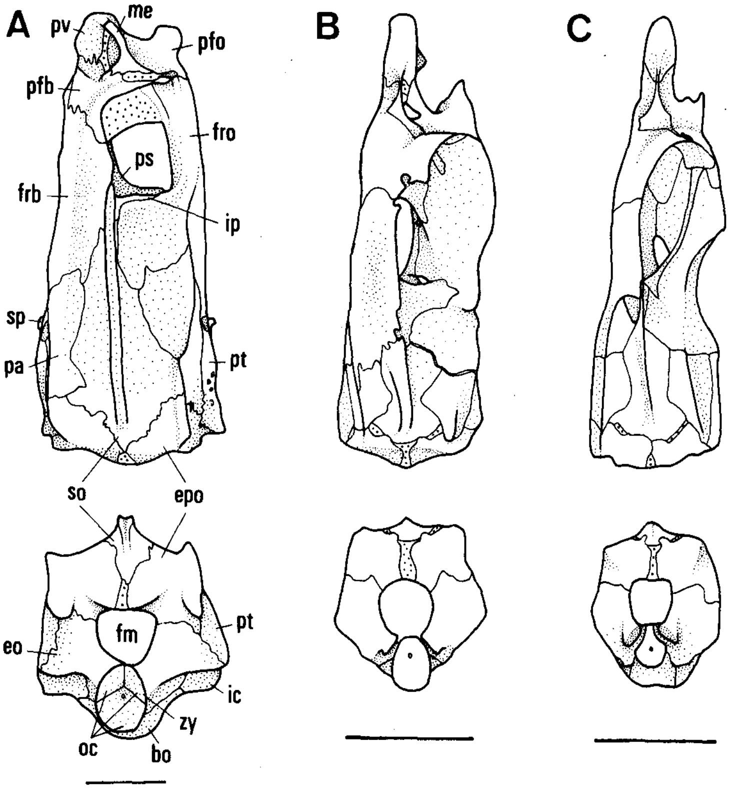

Fig. 15. Dorsal and posterior aspects of crania in three righteye flounders. A, *Rhombosolea leporina* ; B, *Samaris cristatus* ; C, *Samariscus latus*. Abbreviations as in Figs. 6 and 11. Scales indicate 5 mm.

such pleuronectines as *Psettichthys melanostictus*, *Hippoglossoides platessoides limandoides*, *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. limanda*, *P. ferrugineus*, *P. proboscideus*, *P. herzensteini*, *P. yokohamae*, *P. schrenki*, *P. americanus*, *P. quadrituberculatus*, *P. platessa*, *P. glacialis*, *P. pinnifasciatus*, *Platichthys flesus flesus*, *P. P. stellatus*, *Glyptocephalus cynoglossus*, *G. stelleri*, *Errex zachirus* and *Kareius bicoloratus*, and the members of the rhombosoleine genera *Pelotretis*, *Ammotretis*, *Taratretis*, *Rhombosolea* and *Peltorhamphus*. In this group, the relation among the prootic and the other bones is similar to that in the first group, but the prootic is separated from the exoccipital by the intercalar (Figs. 7B-D, 9C, D and 10A, B). Of these members, the cartilagenous interspace, which is surrounded by the prootic, the pterotic, the intercalar, the basioccipital and the parasphenoid, is large in size in *Psettichthys melanostictus*, *Hippoglossoides platessoides limandoides*, *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. limanda*, *P. ferrugineus*, *P. proboscideus*, *P. herzensteini*, *P. yokohamae*, *P. schrenki*, *P. quadrituberculatus*, *P. platessa*, *Platichthys flesus flesus*, *P. stellatus*, *Glyptocephalus cynoglossus*, *G. stelleri* and *Errex zachirus* (Fig. 7B-D), while it is from moderate to small in size in the other members of this

(Figs. 9C, D and 10A, B). The fourth group contains the members of the rhombosoleine genus *Azygopus* and the subfamily Samarinae. In this group, the connection of the prootic with the other bones is similar to that in the preceding group, but the pterosphenoid is absent (Fig. 10C, D). The cartilagenous interspace is small in size among these members.

Regarding the blind side, the pleuronectids are divisible into four groups according to the connection of the prootic with the other bones. The first group includes the same species as those in the first group on the ocular side except *Paralichthodes algoensis.* The mode of the connection of the prootic with the other bones is the same as that in the first group on the ocular side (Figs. 6A, C, D, 7A and 9A, B). The second group contains the same species as those in the second group on the ocular side, and the prootic is connected with the same bones as those in the second group on the ocular side (Figs. 6B and 8A-C). The third group comprises the same fishes as those of the subfamily Pleuronectinae in the third group on the ocular side and the rhombosoleine genera *Pelotretis*, *Ammotretis* and *Taratretis.* The connection of the prootic with the other bones is the same as that in the third group on the ocular side (Figs. 7B-D, 9C, D and 10A). The fourth group consists of the fishes of the pleuronectine genus *Paralichthodes*, the rhombosoleine genera *Azygopus*, *Rhombosolea* and *Peltorhamphus* and the subfamily Samarinae. The mode of the connection of the prootic with the other bones is the same as that in the fourth group on the ocular side, though the pterosphenoid is present in *Paralichthodes algoensis* (Figs. 8D and 10B-D).

The pterotics (pt) are relatively large paired bones forming the dorsolateral walls of the cranium. The pterotic is usually surrounded on both sides by the frontal and the sphenotic anteriorly, by the parietal and the epiotic dorsally, by the exoccipital posteriorly, and by the intercalar and the prootic ventrally (Figs. 6-16).

The epiotics (epo) are paired bones located at the posterodorsal and lateral aspects of the posterior part of the cranium. On the ventral side, the epiotic is connected with the pterotic ventrally and anteriorly and with the parietal anteriorly.

As for the posterior arrangement of the bones, the pleuronectid fishes are classified into five groups according to whether they are connected with each other along the dorsal median line or not, and to the relation between the epiotics and the foramen magnum. In the first group including the fishes of the subfamily Pleuronectinae except *Verasper variegatus* and *Paralichthodes algoensis*, the epiotics are separated from each other along the cranial median line by the posterior part of the supraoccipital, but connected posteriorly with each other by a cartilagenous component. They are connected with the dorsal surfaces of the exoccipitals, but do not form the dorsal margin of the foramen magnum (Figs. 11B, C and 12). In the second group containing only a pleuronectine *Verasper variegatus*, the arrangement of the epiotics and the other bones is similar to that in the preceding group, but these two bones are separated from each other by the posterior part of the supraoccipital (Fig. 11A). The third group is composed of a pleuronectine *Paralichthodes algoensis* and the fishes of the subfamily Poecilopsettinae. The mode of the arrangement of the epiotics and the other bones is similar to that in the first group, but the epiotics are directly connected with each other (Fig. 13). The fourth group comprises the fishes of the subfamily Rhombosoleinae except *Pelotretis flavilatus* and the sub-

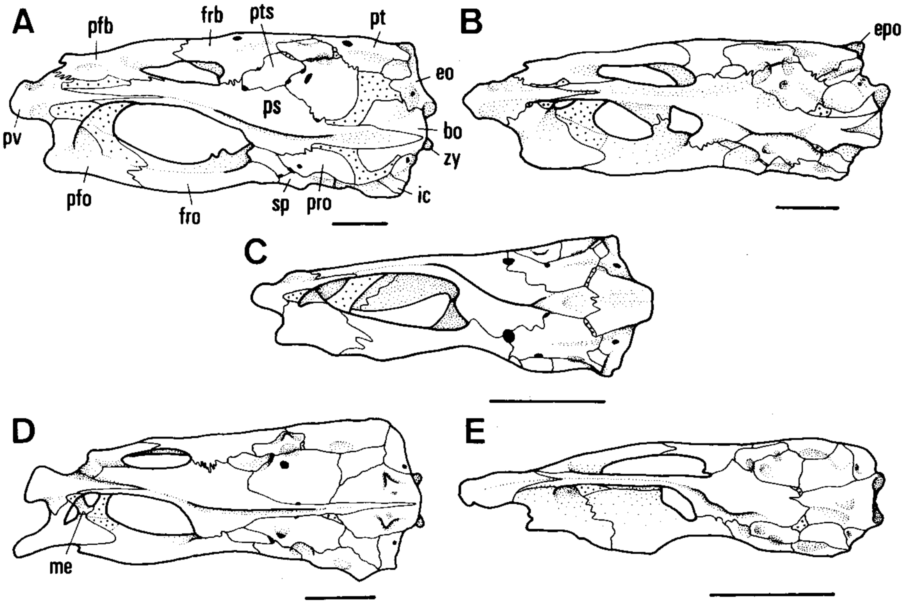

Fig. 16. Ventral aspect of crania in five righteye flounders. A, *Acanthopsetta nadeshnyi*; B, *Paralichthodes algoensis*; C, *Poecilopsetta plinthus*; D, *Pelotretis flavilatus*; E, *Samariscus latus*. Abbreviations as in Figs. 6 and 11. Scales indicate 5 mm.

family Samarinae. In this group, the mode of the arrangement of the epiotics and the other bones is similar to that in the first group, but the epiotics form the dorsal margin of the foramen magnum (Figs. 14B, C and 15). In the fifth group represented only by a rhombosoleine *Pelotretis flavilatus*, the relation of the epiotics and the other bones is similar to that in the preceding group, but both epiotics are directly connected with each other along the median line of the cranium (Fig. 14A).

The supraoccipital (so) is an unpaired bone lying at the middle portion of the posterodorsal part of the cranium. In the pleuronectid fishes examined except *Verasper variegatus*, the supraoccipital is connected with the frontals of both sides anteriorly, with the parietals laterally and with the epiotics posterolaterally (Figs. 11B, C and 12–15), whereas in *Verasper variegatus* it is also narrowly connected with the exoccipitals at its posterior end (Fig. 11A). The supraoccipital forms a keel together with the frontal of the blind side, and is connected with the basal tips of the proximal radials of several anterior dorsal fin rays by a ligament or directly.

The basioccipital (bo) is a single bone lying at the posteriormost ventral portion of the cranium. The basioccipital has a socket-like part forming an occipital condyle (oc) together with the exoccipitals to articulate to the first vertebra. The basioccipital is connected by a pair of Bodelot's ligaments with the inner lateral surfaces of the supracleithra at both lateral surfaces. Anteriorly the cartilagenous interspace is more or less developed.

According to the mode of the connection of the basioccipital with the other bones, the pleuronectid fishes are classified into two groups. The first group comprises the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hippoglossoides* except *H. platessoides limandoides*, *Acanthopsetta*, *Dexistes*, *Hypsopsetta*, *Pleuronichthys*, *Microstomus*, *Tanakius*, *Embassichthys*, *Clidoderma* and *Paralichthodes*, the pleuronectine *Pleuronectes mochigarei*, *P. asper*, *P. sakhalinensis*, *P. punctatissimus* and *P. obscurus* and all the fishes of the subfamily Poecilopsettinae examined. In this group, the basioccipital is connected with the prootic anteriorly, with the exoccipital dorsally and with the parasphenoid ventrally (Figs. 6, 7A, 8, 9A, B and 16A-C). In the second group including the remaining pleuronectids examined, the basioccipital is connected with the prootic anteriorly, with the intercalar and the exoccipital dorsally, and with the parasphenoid ventrally (Figs. 7B-D, 9C, D, 10 and 16D, E).

The posterior portion of the basioccipital forms the floor of the foramen magnum in the fishes of the subfamilies Pleuronectinae except *Paralichthodes algoensis* and Samarinae (Figs. 11, 12 and 15B, C), whereas it does not form the floor in the fishes of the subfamilies Poecilopsettinae and Rhombosoleinae and a pleuronectine *Paralichthodes algoensis* because of the attachment of both exoccipitals (Figs. 13, 14 and 15A).

The exoccipitals (eo) are paired bones constituting the posterolateral and posterior surfaces of the cranium. A pair of zygapophyses (zy) form an occipital condyle together with the basioccipital to articulate to the first vertebra.

The relation among the exoccipital and its adjacent bones varies with the pleuronectids examined. In the pleuronectine *Psettichthys melanostictus*, *Hippoglossoides platessoides limandoides*, *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. limanda*, *P. ferrugineus*, *P. proboscideus*, *P. herzensteini*, *P. yokohamae*, *P. schrenki*, *P. americanus*, *P. quadrituberculatus*, *P. platessa*, *P. glacialis*, *P. pinnifasciatus*, *Platichthys flesus flesus*, *P. stellatus*, *Glyptocephalus cynoglossus*, *G. stelleri*, *Errex zachirus* and *Kareius bicoloratus* and all the members of the subfamilies Rhombosoleinae and Samarinae examined, each exoccipital is connected with the intercalar anteriorly, with the pterotic anterodorsally, with the epiotic posterodorsally and with the basioccipital ventrally, but it is separated from the prootic by the intercalar (Figs. 7B-D, 9C, D and 10). In the remaining members of the subfamily Pleuronectinae and all the members of the subfamily Poecilopsettinae examined, the exoccipital is connected with the prootic anteriorly, with the intercalar and the pterotic anterodorsally, with the epiotic posterodorsally and with the basioccipital ventrally (Figs. 6, 7A, 8 and 9A, B). Within these fishes, in the pleuronectine members except the members of the genera *Hypsopsetta*, *Pleuronichthys*, *Microstomus*, *Embassichthys* and *Paralichthodes*, the cartilagenous interspace is well developed between the exoccipital and the prootic (Figs. 6 and 7A).

In the fishes of the subfamilies Poecilopsettinae and Rhombosoleinae, the zygapophysis on one side is broadly joined to its neighbour on the opposite side (Figs. 13B, C, 14 and 15A). On the contrary, in the fishes of the subfamilies Pleuronectinae and Samarinae, both zygapophyses are separated from each other a little away (Figs. 11, 12, 13A and 15B, C).

In the fishes of the subfamilies Poecilopsettinae and Rhombosoleinae and a pleuronectine *Paralichthodes algoensis*, only the exoccipitals form the floor of the foramen magnum (Figs. 13, 14 and 15A).

The intercalars (ic) are paired bones lying at the posterolateral portions of the cranium. The size and the relation among the intercalar and the other bones vary with the pleuronectids studied here. In this respect, three groups are recognized in the fishes of the Pleuronectidae. The first group includes the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Verasper*, *Hippoglossoides* except *H. platessoides limandoides*, *Acanthopsetta*, *Dexistes*, *Microstomus*, *Tanakius* and *Paralichthodes*, the pleuronectine *Eopsetta exilis*, *Pleuronectes mochigarei*, *P. asper*, *P. sakhalinensis*, *P. punctatissimus* and *P. obscurus*, and the fishes of the subfamily Poecilopsettinae. Of these fishes, in the fishes of the subfamily Poecilopsettinae, the intercalar is small in size (Fig. 9A, B), whereas in the remaining fishes it is moderate in size (Figs. 6A, C, D, 7A and 8D). In this group, the intercalar is bounded by the prootic anteriorly, by the pterotic dorsally, by the exoccipital posteriorly and ventrally, but it is separated from the basioccipital by the exoccipital. Within these fishes, in the fishes of the subfamily Pleuronectinae except the fishes of the genera *Atheresthes*, *Verasper*, *Microstomus* and *Paralichthodes* and *Pleuronectes obscurus*, the cartilagenous interspace is well developed between the intercalar and the prootic (Figs. 6A, C, D and 7A). On the blind side, in a specimen of a pleuronectine *Verasper variegatus*, the intercalar is separated from the prootic because of the connection of the pterotic with the exoccipital at its anterior margin. The second group contains the fishes of the pleuronectine genera *Hypsopsetta*, *Pleuronichthys*, *Embassichthys* and *Clidoderma* and the pleuronectine *Eopsetta jordani* and *E. grigorjewi*. The intercalar is small in size and bounded by the pterotic and the exoccipital, and separated from the prootic and the basioccipital by the exoccipital (Figs. 6B and 8A-C). On the blind side, in a specimen of a pleuronectine *Eopsetta grigorjewi*, the mode of the connection is the same as that in the preceding group. The third group consists of the remaining pleuronectine fishes and the fishes of the subfamilies Rhombosoleinae and Samarinae. The intercalar is moderate in size and bounded by the prootic anteriorly, by the pterotic dorsally, by the exoccipital posteriorly and by the basioccipital ventrally (Figs. 7B-D, 9C, D and 10). Within these fishes, in the following fishes, *Psettichthys melanosticus*, *Hippoglossoides platessoides limandoides*, *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. limanda*, *P. ferrugineus*, *P. proboscideus*, *P. herzensteini*, *P. yokohamae*, *P. schrenki*, *P. quadrituberculatus*, *P. platessa*, *Platichthys flesus flesus*, *P. stellatus*, *Glyptocephalus cynoglossus*, *G. stelleri*, *Errex zachirus* and *Taratretis derwentensis* (in the last species only on the ocular side), the cartilagenous interspace is present between the intercalar and the prootic (Figs. 7B-D and 10A).

The frontals (fro and frb) forming the posterior and dorsal aspects of each orbital cavity are highly asymmetrical paired bones.

On the ocular side, the frontal is connected with the mesethmoid anteriorly or anterolaterally, with the prefrontal of the ocular side anteriorly, and anterolaterally with the prefrontal of the blind side by a cartilagenous component or directly. In the members of the subfamily Samarinae, the frontal is also connected with the prefrontal of the blind side in the middle part of the orbital cavity of the upper eye (Fig. 15B, C). According to the mode of the connection of the frontal posteriorly, the pleuronectids are classified into three groups. The first group includes the members of the subfamily Pleuronectinae except the members of the genera

Hypsopsetta, *Pleuronichthys* and *Paralichthodes*, the members of the subfamily Poecilopsettinae such as *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus*, and the members of the subfamily Rhombosoleinae such as *Ammotretis rostratus*, *A. lituratus*, *A. elongatus*, *Rhombosolea plebeia*, *R. tapirina* and *Peltorhamphus novaezeelandiae*. In this group, the frontal is connected with the frontal of the blind side, the supraoccipital and the parietal posterodorsally, with the pterotic and the sphenotic posteriorly, and with the pterosphenoid posteroventrally, but separated from the parasphenoid by the pterosphenoid (Figs. 6, 7, 8C and 9B, D). The intraspecific variation is observed in *Psettichthys melanosticus* and *Nematops macrochirus*. In a specimen of the former species, the frontal is also connected with the parasphenoid at the anterior margin of the pterosphenoid. In a specimen of the latter species, the frontal is also connected with the prootic at the posterior margin of the pterosphenoid. The second group contains the members of the pleuronectine genera *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, the members of the Poecilopsettinae such as *Poecilopsetta praelonga* and *P. plinthus*, and the members of the Rhombosoleinae such as *Pelotretis flavilatus*, *Taratretis derwentensis*, *Rhombosolea leporina* and *Peltorhamphus latus*. The mode of the connection of the frontal with the other bones is similar to that in the preceding group, but in this group the frontal is also connected with the parasphenoid at the anterior margin of the pterosphenoid (Figs. 8A, B, D, 9A, C and 10A, B). The variations occur in *Pleuronichthys cornutus* and *P. ocellatus*. In a specimen of the former species, the frontal is also connected with the prootic at the posterior margin of the pterosphenoid. In a specimen of the latter species, the frontal is separated from the pterosphenoid because of the attachment of the sphenotic to the parasphenoid at the anterior margin of the pterosphenoid. The third group comprises *Azygopus pinnifasciatus pinnifasciatus*, a member of the subfamily Rhombosoleinae and the members of the subfamily Samarinae. The mode of the connection is similar to that in the preceding group, but the frontal is connected posteriorly and posteroventrally with the pterotic, the sphenotic and the parasphenoid for lack of the pterosphenoid (Fig. 10C, D).

In a pleuronectine *Paralichthodes algoensis* and all the members of the Samarinae examined, the frontal of the ocular side is articulated to the parasphenoid at the interorbital region, narrowly in the former but widely in the latter (Figs. 8D and 10C, D).

On the blind side, the frontal is connected anteriorly with the prefrontal of the blind side in all the pleuronectids examined. On the basis of the posterior connection of the frontal with the other bones, the pleuronectids are divided into four groups. The first group consists of the fishes of the subfamily Pleuronectinae except the fishes of the genera *Acanthopsetta*, *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes* and *Hippoglossoides platessoides limandoides*, *H. elassodon*, *H. dubius*, *H. robustus* and *Pleuronectes vetulus*, and the fishes of the subfamily Poecilopsettinae such as *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus*. The mode of the connection of the frontal with the other bones is the same as that in the first group on the ocular side (Figs. 6A, B, 7A, C, D, 8C and 9B). The intraspecific variation is found in *Pleuronectes herzensteini*. In a specimen of this species, the relation among the frontal and the other bones is the same as that in the second group on the ocular side. The second group is composed of the fishes of the pleuronectine genera

Hippoglossoides except *H. pinetorum*, *Acanthopsetta*, *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, a pleuronectine *Pleuronectes vetulus*, the poecilopsettine *Poecilopsetta praelonga* and *P. plinthus*, and the rhombosoleine *Pelotretis flavilatus* and *Ammotretis lituratus*. The mode of the connection of the frontal with the other bones is the same as that in the second group on the ocular side (Figs. 6C, D, 7B, 8A, B, D and 9A, C). The variations are found in *Hippoglossoides elassodon* and *H. dubius*. In one specimen of each of these species, the relation among the frontal and the other bones is the same as that in the first group on the ocular side. The third group includes the fishes of the rhombosoleine genera *Azygopus*, *Rhombosolea* and *Peltorhamphus* and the subfamily Samarinae. The relation among the frontal and the other bones is the same as that in the third group on the ocular side (Fig. 10 B-D). The fourth group contains the members of the Rhombosoleinae such as *Ammotretis rostratus*, *A. elongatus* and *Taratretis derwentensis*. In this group, the mode of the connection of the frontal with its adjacent bones is similar to that in the second group, but the frontal is separated from the pterosphenoid because of the connection of the sphenotic with the parasphenoid at the anterior margin of the pterosphenoid (Figs. 9D and 10A).

The frontal of the blind side has a bony process called an interorbital process (ip). If it is well developed, it is extended forward along the inner surface of the frontal of the ocular side. In relation to the developmental degree of the interorbital process, the pleuronectid fishes are classified into three groups. The first group contains the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hypsopsetta*, *Pleuronichthys*, *Errex*, *Microstomus*, *Tanakius*, *Clidoderma* and *Paralichthodes*, and all the poecilopsettine genera examined, the rhombosoleine genera *Pelotretis*, *Ammotretis*, *Taratretis* and *Peltorhamphus*, and the samarine genus *Samariscus*. The interorbital process well extends forward along the inner surface of the frontal of the ocular side and is attached anteriorly to the mesethmoid and to the prefrontal of the ocular side or the prefrontals of both sides (Figs. 11A, 12B, C, 13, 14 and 15C). Within these fishes, in *Pleuronichthys* and *Paralichthodes*, the tip of the process is well expanded, though its shape varies with the species (Figs. 12C and 13A). The second group consists of the fishes of the pleuronectine genera *Glyptocephalus* and *Embassichthys*. The middle part of the interorbital process is entirely absent. The anterior remaining part is not tube-like, though the process is tubular in the fishes with the process well extended forward. The third group is composed of the fishes of the pleuronectine genera *Psettichthys*, *Hippoglossoides*, *Acanthopsetta*, *Dexistes*, *Pleuronectes*, *Platichthys* and *Kareius*, the rhombosoleine genera *Azygopus* and *Rhombosolea*, and the samarine genera *Samaris* and *Plagiopsetta*. In this group, the interorbital process is not developed (Figs. 11B, C, 12A and 15A, B).

The frontal of the blind side forms a keel together with the supraoccipital, and is connected with the basal tips of the proximal radials of several anterior dorsal fin rays by a ligament or directly.

The parietals (pa) are paired bones forming the posterodorsal and posterolateral portions of the cranium. The parietal is bounded by the frontal anteriorly, by the supraoccipital dorsally, by the epiotic posteriorly and by the pterotic ventrally. Both parietals are widely separated from each other by the supraoccipital (Figs. 6-

15).

The prevomer (pv) is a single triangle bone lying at the anteriormost portion of the cranium. The prevomer is connected with the mesethmoid dorsally and with each prefrontal dorsolaterally by a cartilagenous component and a suture. The prevomer tapers backward and is attached to the ventral surface of the anterior part of the parasphenoid (Figs. 6-16). The bone is toothless.

The parasphenoid (ps) is a single bone covering the ventral surface of the cranium. In the members of the subfamillies Pleuronectinae and Rhombosoleinae, the posterior tip of the parasphenoid extends to or near the posterior end of the cranium (Fig. 16A, B, D), whereas it does not extend backward in the members of the subfamilies Poecilopsettinae and Samarinae (Fig. 16C, E). The anterior part of the parasphenoid is connected with the prevomer ventrally and with the prefrontals of both sides dorsally.

The mode of the dorsal connection of the posterior part of the parasphenoid with its adjacent bones varies with the species and the side of the body. According to this point, the pleuronectids are divided into three groups on the ocular side, and four groups on the blind side.

On the ocular side, the first group comprises the members of the subfamily Pleuronectinae except the members of the genera *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, the poecilopsettine *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus*, and the rhombosoleine *Ammotretis rostratus*, *A. lituratus*, *A. elongatus*, *Rhombosolea plebeia*, *R. tapirina* and *Peltorhamphus novaezeelandiae.* The parasphenoid is connected posterodorsally with the pterosphenoid, the prootic and the basioccipital (Figs. 6, 7, 8C and 9B, D). The intraspecific variation was observed in *Psettichthys melanostictus.* In one specimen of this species, the parasphenoid is also connected with the frontal. The second group is composed of the members of the pleuronectine genera *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes*, the poecilopsettine *Poecilopsetta praelonga* and *P. plinthus*, and the rhombosoleine *Pelotretis flavilatus*, *Taratretis derwentensis*, *Rhombosolea leporina* and *Peltorhamphus latus.* The parasphenoid is connected posterodorsally with the frontal, the pterosphenoid, the prootic and the basioccipital (Figs. 8A, B, D, 9A, C and 10A, B). The intraspecific variation was found in *Pleuronichthys ocellatus.* In one specimen of the species, the parasphenoid is also connected with the sphenotic at the anterior part of the pterosphenoid. The third group consists of a rhombosoleine *Azygopus pinnifasciatus pinnifasciatus* and the members of the subfamily Samarinae. The parasphenoid is connected posterodorsally with the frontal, the sphenotic, the prootic and the basioccipital (Fig. 10C, D).

On the blind side, the first group includes the members of the subfamily Pleuronectinae except the members of the genera *Acanthopsetta*, *Hypsopsetta*, *Pleuronichthys* and *Paralichthodes* and *Hippoglossoides platessoides limandoides*, *H. elassodon*, *H. dubius*, *H. robustus* and *Pleuronectes vetulus*, and the poecilopsettine *Poecilopsetta beanii*, *P. albomarginata* and *Nematops macrochirus*. The parasphenoid has the same connection with the other bones as that in the first group on the ocular side (Figs. 6A, B, 7A, C, D, 8C and 9B). In one specimen of *Pleuronectes herzensteini*, the mode of the connection of the parasphenoid with the other bones is the same as that in the second group on the ocular side. The second group contains the members of the pleuronectine genera *Hippoglossoides* except *H. pinetorum*, *Acanthopsetta*, *Hypsopsetta* and *Pleuronichthys*, a pleuronectine *Pleuronectes vetulus*, the poecilopsettine *Poecilopsetta praelonga* and *P. plinthus*, and the rhombosoleine *Pelotretis flavilatus* and *Ammotretis lituratus*. The parasphenoid has the same connection with the other bones as that in the second group on the ocular side (Figs. 6C, D, 7B, 8A, B and 9A, C). The variations occur in *Hippoglossoides elassodon* and *H. dubius*. In one specimen of each of these species, the mode of the connection of the parasphenoid with its adjacent bones is the same as that in the first group on the ocular side. In the third group represented by the members of the rhombosoleine genera *Azygopus*, *Rhombosolea* and *Peltorhamphus* and the subfamily Samarinae, the parasphenoid has the same connection with the other bones as that in the third group on the ocular side (Fig. 10B-D). In the fourth group including a pleuronectine *Paralichthodes algoensis* and the rhombosoleine *Ammotretis rostratus*, *A. elongatus* and *Taratretis derwentensis*, the parasphenoid is connected posterodorsally with the frontal, the pterosphenoid, the sphenotic, the prootic and the basioccipital (Figs. 8D, 9D and 10A). The parasphenoid is attached to the sphenotic at the posterior margin of the pterosphenoid in *Paralichthodes algoensis*, but at the anterior margin of that bone in the other three fishes.

In a pleuronectine *Paralichthodes algoensis* and all the members of the Samarinae examined, the parasphenoid is articulated to the frontal of the ocular side at the interorbital region, narrowly in the former but widely in the latter (Figs. 8D and 10C, D).

UNIT CHARACTER The crania of the pleuronectiforms have been studied by many ichthyologists (Cole and Johnstone, 1901; Regan, 1910; Kyle, 1921; Wu, 1932; Norman, 1934; Chabanaud, 1936; Ochiai, 1966; Amaoka, 1969, 1972; Kim, 1973 etc.). Many characters of the cranium such as presence or absence of each element, if each element is present, its shape and developmental degree or the relation among itself and its adjacent ones have been used in the previous phylogenetic studies on flatfishes. They are as follows: presence or absence of the prevomerine teeth, the relation among the supraoccipital, the epiotic and the exoccipital, the relation between both zygapophyses of the exoccipitals, presence or absence of the pterosphenoid, if the bone is present, its size and relation to its adjacent bones, and the relation between itself and the posterior wall of the orbital cavity of the lower eye, the relation among the pterotic, the exoccipital, the basioccipital, the prootic and the intercalar, the relation among the mesethmoid, the prefrontal, the frontal and the pseudomesial bar, the posterior extension of the parasphenoid, and others (see Chabanaud, 1936; Amaoka, 1969; Kim, 1973).

In the present study on the fishes of the family Pleuronectidae, the interspecific variations on the cranial elements were found in the following characters: 1) the composition of the nasals, 2) the relation between the mesethmoid and the anterior part of the upper orbital cavity, 3) the relation between both prefrontals, 4) presence or absence of the attachment of the prefrontal of the blind side to the frontal of the ocular side in the middle part of the orbital cavity of the upper eye, 5) presence or absence of the pterosphenoid on each side, and if the bone is present, its size and relation to its adjacent bones such as the frontal, the sphenotic, the prootic and the parasphenoid, and its relation to the posterior wall of the orbital cavity of the lower eye, 6) the relation between both epiotics, 7) the relation of the epiotics and the foramen magnum, 8) the relation between both zygapophyses of the exoccipitals, 9) the relation of the basioccipital and the floor of the foramen magnum, 10) the size of the intercalar, and its relation to its adjacent bones such as the prootic, the pterotic, the exoccipital and the basioccipital on each side, 11) the size of the cartilagenous interspace on each side, 12) presence or absence of the articulation of the frontal of the ocular side to the parasphenoid at the interorbital region, 13) the developmental degree of the interorbital process, 14) the posterior position of the parasphenoid.

For the first character, the composition of the nasals, three character states may be recognizable : two bones are present, or a single bone is present on the ocular or blind side. However, as shown in the description, there is an intraspecific variation on presence or absence of the bone of the blind side. Therefore, only presence or absence of the nasal of the ocular side is adopted as a unit character because no intraspecific variations were observed in the present study. The character state is coded as 0 for its presence and as 1 for its absence. The second character, the relation between the mesethmoid and the anterior part of the upper orbital cavity, is a unit character with two states. The character state is coded as 0 for the OTU's with the mesethmoid forming the anterior part of the upper orbital cavity, and as 1 for the OTU's with the bone not forming that portion. There are three character states in the third character: both prefrontals are attached to each other on the lower part of the anterior portion of the frontal of the ocular side or on the upper part of the same portion, and these two bones are separated from each other. However, these three character states cannot be arranged in a single logical sequence. Thus, this character is considered a qualitative multistate character and converted into the following three new two-state characters ; (1) presence or absence of the attachment between both prefrontals, (2) the bones are attached to each other on the lower part of the anterior portion of the frontal of the ocular side or not, (3) on the upper part of the same portion or not. In the character (1), the character state is coded as 0 for its presence and as 1 for its absence. In the characters (2) and (3), the character state is coded as 0 for the OTU's with each mode of the attachment between the prefrontals and as 1 for the OTU's with the other mode. When these two characters are compared, the character states of the members whose prefrontals are not attached to each other are coded as NC. The fourth character, presence or absence of the attachment of the prefrontal of the blind side to the frontal of the ocular side in the middle part of the orbital cavity of the upper eye, is used as a unit character with two states. The value of the character state is 0 for its presence and as 1 for its absence. With respect to the fifth character, presence or absence of the pterosphenoid on each side, and if the bone is present, its size and relation to its adjacent bones, and its relation to the posterior wall of the orbital cavity of the lower eye, several character states may be recongnizable. However, as for its size, it is very difficult to recognize several character states. Also, concerning its relation to its adjacent bones, and its relation to the posterior wall of the orbital cavity of the lower eye, there are intraspecific variations as described above. Therefore, these three characters mentioned above cannot be used as unit characters. After all, only

Table 3. Comparison and coding of characters of cranium in 77 righteye flounders. The
Figs. 6-16. NC, no comparison.

Nasal of ocular side	Relation between me and anterior upper orbital cavity	Attachment between both pf	Attachment between pfb and fro in orbital cavity	pts of ocular side	pts of blind side	Relation between both epo	Relation between epo and fm
present (0)	me forms anterior upper orbital cavity (0)	absent (1)	absent (1)	present (0)	present (0)	separated (1)	epo does not form fm (1)
						connected (0)	
	me does not form anterior upper orbital cavity (1)						
absent (1)		present* (0)					
present (0)							
	me forms it (0)	absent (1)					
	me does not form it (1)	present** (0)	present (0)	absent (1)	absent (1)		epo forms dorsal margin of fm (0)
		absest (1)	absent (1)				
				present (0)			
	me forms it (0)				present (0)		
	me does not form it (1)						
					absent (1)		

* on lower part of anterior portion of frontal of ocular side, ** on upper part of same portion.
extend backward.

numerals in the parentheses are the values of the character states. Abbreviations as in

Relation between both zy of eo	Relation between bo and floor of fm	Articulation of fro to ps at interorbital region	ip	ps[†]	Genera and species
separated (1)	bo forms floor of fm (0)	absent (1)	well develop (0)	A (0)	Pleuronectinae *Verasper variegatus*
			middle part absent (1)		Pleuronectinae *Glyptocephalus*, *Embassichthys*
			well develop (0)		Pleuronectinae *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper moseri*, *Hypsopsetta*, *Pleuronichthys*, *Microstomus*, *Tanakius*, *Clidoderma*
			not develop (2)		Pleuronectinae *Psettichthys*, *Hippoglossoides*, *Acanthopsetta*, *Dexistes*, *Pleuronectes*, *Platichthys*, *Kareius*
			well develop (0)		Pleuronectinae *Errex*
joined (0)	NC			B (1)	Poecilopsettinae *Poecilopsetta*
					Poecilopsettinae *Nematops*
separated (1)	bo does not form it (0)	present (0) (narrow)		A (0)	Pleuronectinae *Paralichthodes*
	bo forms floor of fm (0)	present (0) (wide)		B (1)	Samarinae *Samariscus*
			not develop (2)		Samarinae *Samaris*, *Plagiopsetta*
joined (0)	NC	absent (1)		A (0)	Rhombosoleinae *Azygopus*
					Rhombosoleinae *Rhombosolea*
			well develop (0)		Rhombosoleinae *Pelotretis*
					Rhombosoleinae *Ammotretis*, *Taratretis*
					Rhombosoleinae *Peltorhamphus*

[†] A, its posterior tip extends to or near the posterior end of the cranium; B, it does not

presence or absence of the pterosphenoid on each side is adopted as a unit character with two states, because no intraspecific variations were observed as far as its presence or absence is concerned. The character state is coded as 0 for its presence and as 1 for its absence. The sixth character, the relation between both epiotics, is selected as a unit character with two states. The character state is coded as 0 for the OTU's having both epiotics connected with each other and as 1 for the OTU's having the two bones separated from each other. In the seventh character, the relation of the epiotics and the foramen magnum, there are clearly two states without any intraspecific variation: the epiotics forming the dorsal margin of the foramen magnum and secondly not forming the foramen magnum. The character state is coded as 0 for the OTU's with the former state and as 1 for the OTU's with the latter state. The eighth character, the relation between both zygapophyses of the exoccipitals, is used as a unit character with two character states. The character state is coded as 0 for the OTU's with the zygapophyses joined to each other, and as 1 for the OTU's with the zygapophyses separated from each other. The ninth character, the relation of the basioccipital and the floor of the foramen magnum, is adopted as a unit character with two states, since there are no intraspecific variations. The character state is coded as 0 for the OTU's with the basioccipital forming the floor of the foramen magnum and as 1 for the OTU's with the bone not forming the floor. However, in the fishes whose zygapophyses of the exoccipitals are joined to each other, the basioccipital logically cannot form the floor of the foramen magnum. Thus, the character states of the fishes with the junction between both zygapophyses are coded as NC, when this character is compared. In the tenth character, the size of the intercalar is precluded from the unit characters, because it is very difficult to recognize several character states. The relation of the intercalar and its adjacent bones is also precluded from the unit characters because of the intraspecific variations described above. In the eleventh character, the size of the cartilagenous interspace on each side, it is very difficult to determine the character state for each OTU. Thus, this character is also excluded from the unit characters. The twelfth character, presence or absence of the articulation of the frontal of the ocular side to the parasphenoid at the interorbital region, is used as a unit character with two states. The character state is coded as 0 for its presence and as 1 for its absence. Within the OTU's with the articulation mentioned above, there are clearly two states: the width of the articulated portion is narrow or wide. Therefore, the width of the articulated portion is adopted as a unit character with two states. The character state is coded as 0 for the OTU with the frontal of the ocular side narrowly articulated to the parasphenoid, and as 1 for the OTU with the bone widely articulated to the parasphenoid. In this case, the character states of the OTU's whose frontal of the ocular side is not articulated to the parasphenoid at the interorbital region are coded as NC. The thirteenth character, the developmental degree of the interorbital process, is a unit character with three states: the process is well developed, its middle part is absent, and the process is not developed. These three character states can be arranged in a single logical sequence. Therefore, this is a quantitative multistate character and each character state is coded in order as 0, 1, 2 (Table 3). The last character, the posterior position of the parasphenoid, is accepted as a unit character with two states. The character state is coded as 0 for the OTU's with the posterior tip extending to or near the posterior end of the cranium and as 1 for the OTU's with the posterior tip not extending backward.

Fifteen selected unit characters and coded character states are summarized in Table 3.

3. ORBITAL BONES

DESCRIPTION The orbital bones composed of preorbital and infraorbitals are very asymmetrical in shape and variable in number of elements.

The preorbital (po), if present, is usually larger in size than any of the infraorbitals in most righteye flounders. The preorbital is attached dorsally or posteriorly to the lateral process of the prefrontal and anteriorly to the maxillary head by a ligament.

As for the ocular side, the pleuronectids always have a preorbital, though there are some specific variations in shape (Fig. 17). In the fishes of the pleuronectine genera *Reinhardtius*, *Acanthopsetta* and *Clidoderma* and the rhombosoleine genera *Azygopus*, *Ammotretis*, *Taratretis* and *Peltorhamphus*, a rhombosoleine *Rhombosolea leporina*, and the samarine *Samariscus latus* and *S. xenicus*, the preorbital is penetrated by a sensory canal (Fig. 17B, G, R, S). On the contrary, in the other pleuronectids examined, the preorbital is a simple plate-like bone which is not penetrated by the sensory canal (Fig. 17A, C-F, H-Q, T).

As for the blind side, the fishes of the subfamilies Pleuronectinae, Rhombosoleinae and Samarinae always have a preorbital which is quadangular, ovoidal or simple bar-like in shape (Figs. 18 and 20). The preorbital is usually a thin plate-like bone containing the sensory canal. But, it is simple plate-like in the pleuronectine *Pleuronichthys decurrens* and *P. verticalis*, the rhombosoleine *Pelotretis flavilatus*, *Rhombosolea plebeia*, *R. tapirina*, *Peltorhamphus novaezeelandiae* and *P. latus*, and the samarine *Samaris cristatus*, *Plagiopsetta glossa* and *Samariscus latus* (Fig. 18). However, in a specimen of *Samariscus xenicus* the preorbital consists of two simple bones. On the other hand, the fishes of the subfamily Poecilopsettinae have neither the preorbital nor the infraorbitals.

The infraorbitals (io), if present, are a series of lamina-like bones penetrated by a sensory canal, and usually connected anteriorly with the preorbital and posteriorly with the frontal.

On the ocular side, the pleuronectids can be classified into three groups according to the developmental degree of the infraorbitals. In the first group comprising the fishes of the subfamily Pleuronectinae except *Embassichthys bathybius*, a series of infraorbitals constituted by thin tubular ossifications completely surround the lower margin of the lower eye (Fig. 19A-C). In the second group including the fishes of the pleuronectine genus *Embassichthys* and the rhombosoleine genera *Azygopus*, *Ammotretis*, *Taratretis* and *Peltorhamphus*, there are only one or two tubular bones attached to the posterior part of the ventral edge of the frontal just behind the lower eye (Fig. 19D-F). In the third group consisting of the fishes of the subfamilies Poecilopsettinae and Samarinae and the rhombosoleine genera *Pelotretis* and *Rhombosolea*, the infraorbitals are entirely absent.

On the blind side, in the fishes of the subfamilies Pleuronectinae and Rhombosoleinae, a series of infraorbitals are present (Figs. 18A-C and 20), whereas they

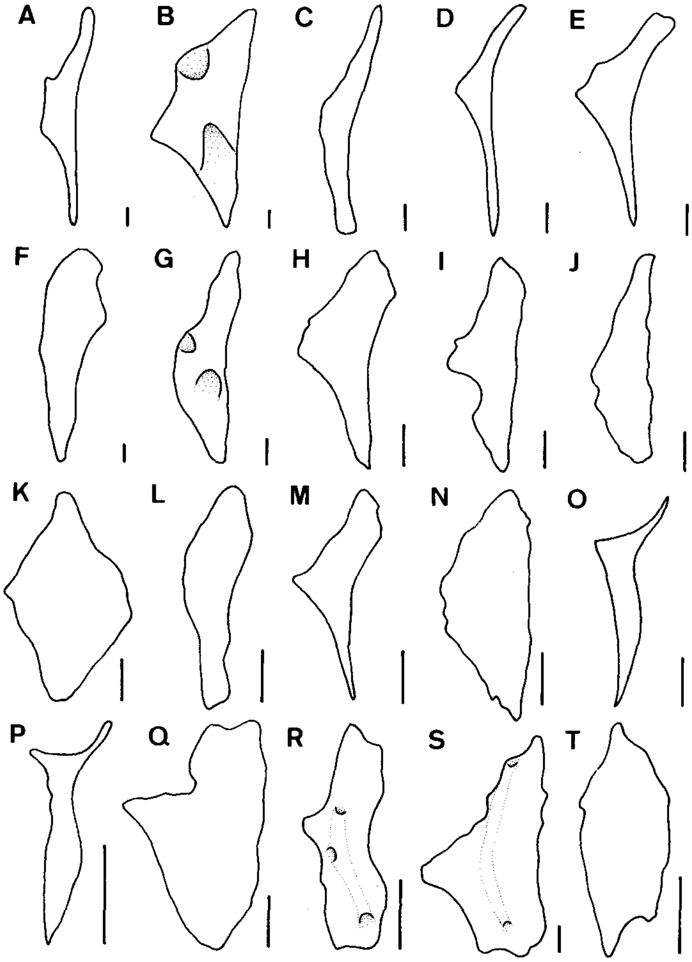

Fig. 17. Lateral aspect of preorbitals on ocular side in 20 righteye flounders. A, *Atheresthes evermanni* ; B, *Reinhardtius hippoglossoides* ; C, *Eopsetta exilis* ; D, *E. jordani* ; E, *Verasper variegatus* ; F, *Hippoglossoides dubius* ; G, *Acanthopsetta nadeshnyi* ; H, *Dexistes rikuzenius* ; I, *Pleuronectes herzensteini* ; J, *P. obscurus* ; K, *Pleuronichthys cornutus* ; L, *Microstomus achne* ; M, *Tanakius kitaharai* ; N, *Paralichthodes algoensis* ; O, *Poecilopsetta plinthus* ; P, *Nematops macrochirus* ; Q, *Pelotretis flavilatus* ; R, *Taratretis derwentensis* ; S, *Peltorhamphus novaezeelandiae* ; T, *Plagiopsetta glossa*. Scales indicate 1 mm.

are completely absent in the fishes of the subfamilies Poecilopsettinae and Samarinae (Fig. 18D). A series of infraorbitals generally run from near the lateral process of the prefrontal to near the anterior end of the frontal almost horizontally along the ventral edge of the prefrontal. But, in the pleuronectine *Pleuronichthys decurrens* and *P. verticalis*, some anterior infraorbitals extend upward beyond the preorbital (Fig. 18A).

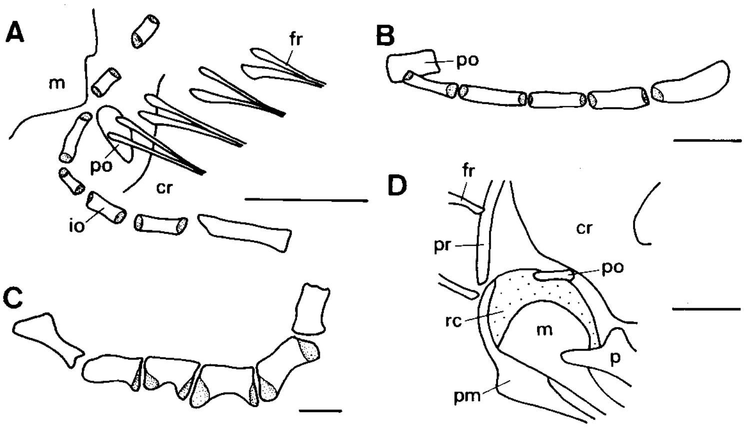

Fig. 18. Lateral aspect of orbital bones on blind side in four righteye flounders. A, *Pleuronichthys verticalis* ; B, *Pelotretis flavilatus* ; C, *Peltorhamphus novaezeelandiae* ; D, *Samariscus latus*. cr, cranium ; fr, dorsal fin ray ; io, infraorbital ; m, maxillary ; p, palatine ; pm, premaxillary ; po, preorbital ; pr, proximal radial of dorsal fin ray ; rc, rostral cartilage. Scales indicate 5 mm.

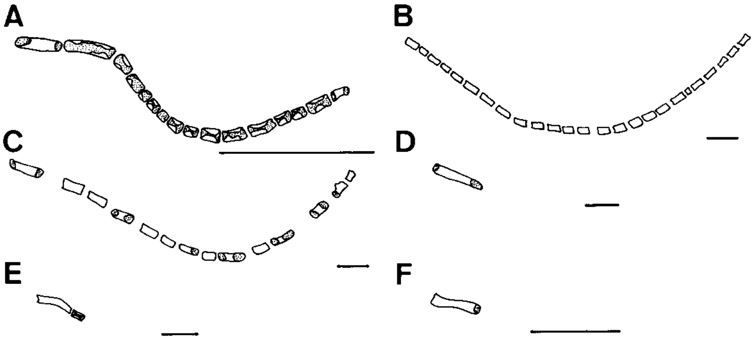

Fig. 19. Lateral aspect of infraorbitals on ocular side in six righteye flounders. A, *Eopsetta jordani* ; B, *Pleuronectes mochigarei* ; C, *P. quadrituberculatus* ; D, *Embassichthys bathybius* ; E, *Ammotretis rostratus* ; F, *Taratretis derwentensis*. Scales indicate 2 mm.

The number of the infraorbitals shows the inter- and intraspecific variations with a range from two in one specimen of each of *Microstomus kitt* and *Paralichthodes algoensis* to twelve in a specimen of *Hippoglossoides elassodon* (Fig. 20 ; Table 4).

UNIT CHARACTER A comparative study on the orbital bones of some families of flatfishes such as Psettodidae, Citharidae, Paralichthyidae and Bothidae, was carried out by Amaoka (1969, 1972). The following characters were used in his phylogenetic study : presence or absence of the preorbital and the infraorbitals on the ocular side, presence or absence of the preorbital on the blind side, and the length

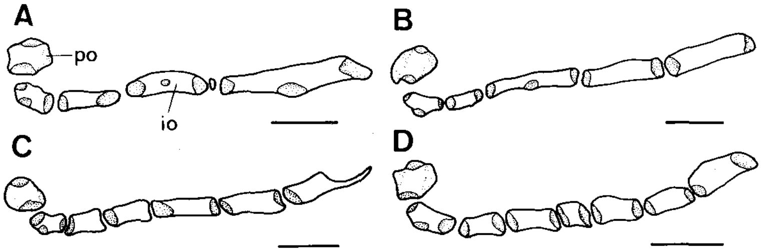

Fig. 20. Variation in orbital bones on blind side in *Dexistes rikuzenius*. A, po+4io (HUMZ 57170); B, po+5io (HUMZ 57166); C, po+6io (HUMZ 57193); D, po+7io (HUMZ 57176). Abbreviations as in Fig. 18. Scales indicate 2 mm.

and number of the infraorbitals on the blind side.

In the present study, it was found that the orbital bones of the pleuronectids show interspecific variabilities in several characters. As for the ocular side, the following characters are recognized: 1) presence or absence of the sensory canal in the preorbital, 2) the developmental degree of the infraorbitals. As for the blind side, the following characters are found: 1) presence or absence of the preorbital, 2) if the preorbital is present, presence or absence of the sensory canal in the bone, 3) the developmental degree of the infraorbitals.

The first character on the ocular side, presence or absence of the sensory canal in the preorbital, is used as a unit character with two character states. The character state is coded as 0 for its presence and as 1 for its absence. The second character on the ocular side, the developmental degree of the infraorbitals, is a quantitative multistate character with three character states: (1) the bones completely surround the lower margin of the lower eye, (2) they consist of one or two bones, (3) they are entirely absent. Each character state is coded in order as 0, 1, 2 (Table 5). The first character on the blind side, presence or absence of the preorbital, is adopted as a unit character. The value of the character state is 0 for its presence and 1 for its absence. The second character on the blind side, presence or absence of the sensory canal in the preorbital, cannot be used as a unit character because of the intraspecific variation. Concerning the third character on the blind side, the developmental degree of the infraorbitals, as described above, the number of the infraorbitals varies with the individual. Therefore, presence or absence of the infraorbitals is taken up as a unit character, since there are no intraspecific variations as far as their presence or absence is concerned. The character state is coded as 0 for its presence and as 1 for its absence.

Four selected unit characters and coded character states are summarized in Table 5.

4. SUSPENSORIUM AND OPERCULAR APPARATUS

DESCRIPTION The suspensorium consists of seven bones, palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic and hyomandibular.

The opercular apparatus is composed of four elements, preopercle, interopercle, opercle and subopercle.

Table 4. Variation in number of infraorbitals on blind side in 68 righteye flounders. The numerals in the parentheses are the numbers of the specimens examined.

Species		Species	
Pleuronectinae		*P. obscurus*	5-6 (6)
Atheresthes stomias	7 (2)	*P. glacialis*	5 (1)
A. evermanni	7-8 (7)	*P. pinnifasciatus*	6-7 (6)
Reinhardtius hippoglossoides	7-8 (8)	*Platichthys flesus flesus*	7 (1)
Hippoglossus hippoglossus	6 (1)	*P. stellatus*	3-7 (6)
H. stenolepis	7-11 (5)	*Hypsopsetta guttulata*	6 (1)
Eopsetta exilis	6 (1)	*Pleuronichthys decurrens*	8-9 (2)
E. jordani	6 (1)	*P. cornutus*	5-6 (5)
E. grigorjewi	4-6 (5)	*P. verticalis*	7-8 (2)
Verasper variegatus	4-5 (5)	*P. coenosus*	5 (1)
V. moseri	5 (2)	*P. ritteri*	5 (1)
Psettichthys melanostictus	8-9 (2)	*P. ocellatus*	5-6 (2)
Hippoglossoides platessoides limandoides	9-10 (2)	*Glyptocephalus cynoglossus*	4 (1)
H. elassodon	9-10 (3)	*G. stelleri*	4 (5)
H. dubius	10-11 (5)	*Errex zachirus*	4 (2)
H. robustus	8-11 (5)	*Kareius bicoloratus*	4-8 (7)
H. pinetorum	7-10 (9)	*Microstomus kitt*	2 (1)
Acanthopsetta nadeshnyi	5-7 (5)	*M. achne*	3-5 (6)
Dexistes rikuzenius	4-7 (6)	*M. pacificus*	6 (3)
Pleuronectes isolepis	5-6 (2)	*Tanakius kitaharai*	5-9 (6)
P. vetulus	8-9 (2)	*Embassichthys bathybius*	3-5 (3)
P. bilineatus	6-8 (4)	*Clidoderma asperrimum*	5-8 (4)
P. mochigarei	8-11 (7)	*Paralichthodes algoensis*	2-3 (2)
P. limanda	6-10 (3)	Rhombosoleinae	
P. asper	6-8 (5)	*Pelotretis flavilatus*	4-5 (5)
P. sakhalinensis	5-9 (5)	*Azygopus pinnifasciatus pinnifasciatus*	4 (1)
P. ferrugineus	5 (1)	*Ammotretis rostratus*	5 (1)
P. punctatissimus	4-8 (5)	*A. lituratus*	7-8 (2)
P. proboscideus	4-7 (3)	*A. elongatus*	5-6 (2)
P. herzensteini	4-7 (7)	*Taratretis derwentensis*	4 (2)
P. yokohamae	3-6 (5)	*Rhombosolea plebeia*	4 (1)
P. schrenki	4-6 (3)	*R. tapirina*	3-4 (2)
P. americanus	4 (1)	*R. leporina*	5-6 (2)
P. quadrituberculatus	6-8 (4)	*Peltorhamphus novaezeelandiae*	5 (2)
P. platessa	7 (1)	*P. latus*	4-5 (6)

Table 5. Comparison and coding of characters of orbital bones in 77 righteye flounders. The numerals in the parentheses are the values of the character states. Abbreviation as in Fig. 18.

Ocular side		Blind side		Genera and species
Sensory canal in preorbital	Infraorbital	Preorbital	Infraorbital	
absent (1)	a series of io (0)	present (0)	present (0)	Pleuronectinae all genera examined except *Reinhardtius*, *Acanthopsetta*, *Embassichthys* and *Clidoderma*
	1 io (1)			Pleuronectinae *Embassichthys*
	absent (2)	absent (1)	absent (1)	Poecilopsettinae *Poecilopsetta*, *Nematops*
		present (0)		Samarinae *Samaris*, *Plagiopsetta*
			present (0)	Rhombosoleinae *Pelotretis*, *Rhombosolea plebeia*, *R. tapirina*
present (0)	a series of io (0)			Pleuronectinae *Reinhardtius*, *Acanthopsetta*, *Clidoderma*
	1 or 2 io (1)			Rhombosoleinae *Azygopus*, *Ammotretis*, *Taratretis*, *Peltorhamphus*
	absent (2)			Rhombosoleinae *Rhombosolea leporina*
			absent (1)	Samarinae *Samariscus*

The palatine (p) forms the anteriormost part of the suspensorium. The palatine is connected dorsally with the prefrontal on the ocular side, anteriorly with the ascending process of the premaxillary by a ligament, and posteriorly with the ectopterygoid and the endopterygoid. The palatine is toothless in all the pleuronectids examined here.

The ectopterygoid (ecp) is boomerang-shaped and connected with the palatine anteriorly, with the endopterygoid dorsally and posteriorly, and with the quadrate ventrally.

The quadrate (q) is a trianglar bone bearing a condyle for the articular at its ventral angle. The medial surface of the posteroventral part of the quadrate has a fossa to house the symplectic. The quadrate is articulated to the ectopterygoid anteriorly and to the preopercle ventrally, and joined to the endopterygoid and the metapterygoid dorsally or posterodorsally.

The symplectic (sy) is rod-like in shape and surrounded by the metapterygoid, the quadrate and the preopercle. Anteriorly, the symplectic is attached to the medial surface of the posteroventral part of the quadrate. Posteriorly, the symplectic is ligamentously connected with the cartilagenous cap of the symplectic process of the hyomandibular by its cartilagenous cap at the posterior end.

The endopterygoid (enp) is a thin translucent bone and subrhomboidal in shape. The endopterygoid is articulated to the palatine at its anteriormost margin and to the ectopterygoid anteriorly, and joined to the metapterygoid and the quadrate posterodorsally or ventrally.

The metapterygoid (mt) is a thin bone surrounded by the endopterygoid, the ectopterygoid, the quadrate, the symplectic and the hyomandibular. The metapter-

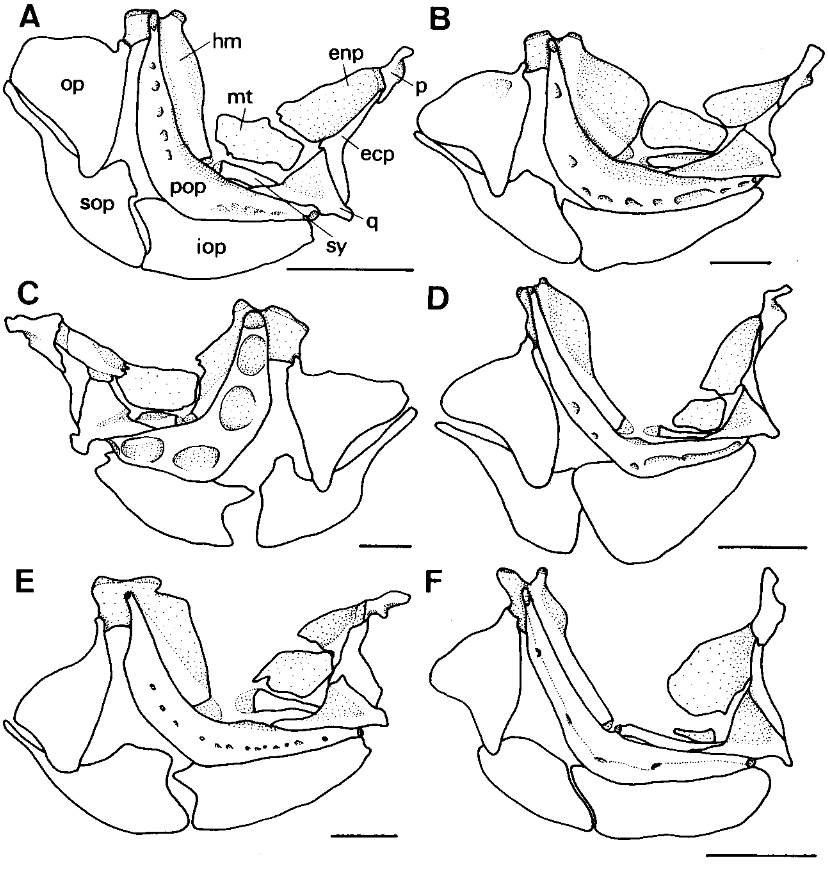

Fig. 21. Lateral aspect of suspensoria and opercular apparatus in six righteye flounders. A, *Eopsetta jordani*; B, *Pleuronectes herzensteini*; C, *Glyptocephalus stelleri* (blind side); D, *Poecilopsetta plinthus*; E, *Rhombosolea leporina*; F, *Samariscus latus*. ecp, ectopterygoid; enp, endopterygoid; hm, hyomandibular; iop, interopercle; mt, metapterygoid; op, opercle; p, palatine; pop, preopercle; q, quadrate; sop, subopercle; sy, symplectic. Scales indicate 5 mm.

ygoid varies in shape and size with the species. Whereas in the fishes of the subfamily Samarinae it is small in size (Fig. 21 F), it is moderate in all the other pleuronectid fishes examined (Fig. 21A-E).

The hyomandibular (hm) is a short flattened bone articulated dorsally to the cranium at the fossa formed by the prootic and the sphenotic and at the facet by the pterotic and the prootic. Posteriorly, the hyomandibular is bordered by the preopercle and posterodorsally articulated to the opercle.

The preopercle (pop) is a falciform bone connected dorsally and anterodorsally with the hyomandibular, anteroventrally with the quadrate, and anteromedially with the symplectic. The preopercle is attached to the interopercle along its ventral margin. Internally, the lateral line canal runs through from dorsal to anterior borders of the bone. Several openings for the canal are found in the bone. In the fishes of the pleuronectine genera *Glyptocephalus* and *Errex*, those openings are large in size on the blind side (Fig. 21C), while they are very small on both sides in the other pleuronectid fishes examined (Fig. 21A, B, D-F).

The interopercle (iop) is a thin translucent bone attached dorsally to the preopercle.

The opercle (op) is a membranous bone located posterior to the preopercle. The opercle is attached to the subopercle along its ventral margin.

The subopercle (sop) is a thin membranous bone attached anteriorly to the interopercle and dorsally to the opercle.

UNIT CHARACTER In the pleuronectiform fishes, the suspensoria and opercular apparatus of some species have been only described by some authors (Traquair, 1865; Cole and Johnstone, 1901; Gregory, 1933; Amaoka, 1969; Frame *et al.*, 1978 etc.).

Though the pleuronectid suspensoria and opercular apparatus show interspecific variations in shape of each element, several distinct character states are not recognizable for most of the variations except in the size of the metapterygoid. Only the metapterygoid has two distinctive character states in size. Therefore, this is adopted as a unit character with two states. The character state is coded as 0 for its moderate size and as 1 for its small size (Table 6).

Table 6. Comparison and coding of character of suspensorium and opercular apparatus in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

Size of metapterygoid	Subfamilies
moderate (0)	Pleuronectinae Poecilopsettinae Rhombosoleinae
small (1)	Samarinae

5. HYOID ARCH

DESCRIPTION The hyoid arch comprises five paired bones, dorsal and ventral hypohyals, ceratohyal, epihyal, interhyal and branchiostegals, and two uniserial bones, basihyal and urohyal. The basihyal and the urohyal are treated elsewhere.

The dorsal hypohyal (dhh) is firmly united with the ventral hypohyal ventrally and with the ceratohyal posteriorly, and ligamentously connected anterodorsally with the posterolateral aspect of the basihyal and the anterolateral aspect of the

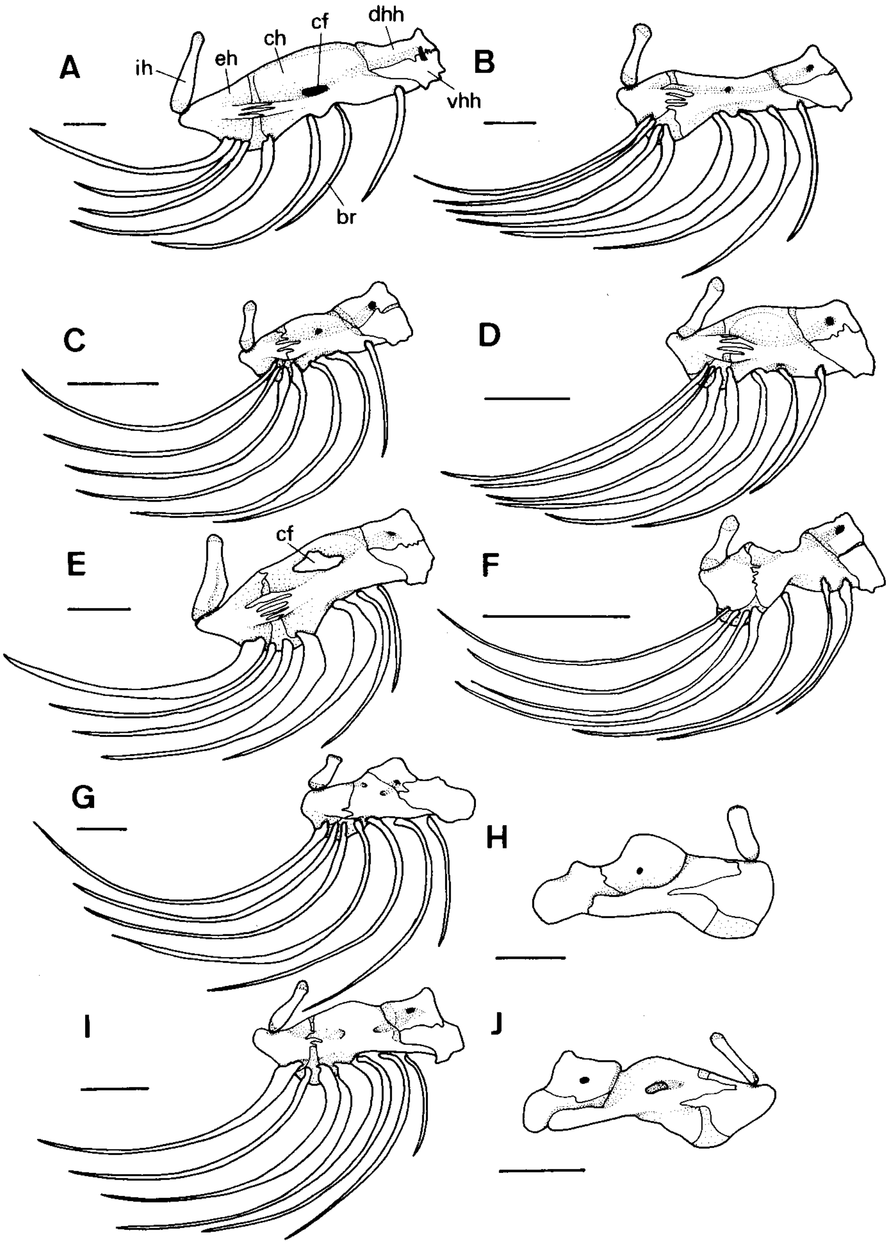

Fig. 22. Lateral aspect of hyoid arches in eight righteye flounders. A, *Atheresthes evermanni* ; B, *Hippoglossoides platessoides limandoides* ; C, *Dexistes rikuzenius* ; D, *Pleuronectes herzensteinii* ; E, *Paralichthodes algoensis* ; F, *Poecilopsetta beanii* ; G (outer side) and H (inner side), *Pelotretis flavilatus* ; I (outer side) and J (inner side), *Peltorhamphus novaezeelandiae*. br, branchiostegal ; cf, ceratohyal foraman ; ch, ceratohyal ; dhh, dorsal hypohyal ; eh, epihyal ; ih, interhyal ; vhh, ventral hypohyal. Scales indicate 5 mm.

first basibranchial. These two dorsal hypohyals are firmly united with each other anteromedially. There is an opening between the dorsal and ventral hypohyals for the hyoidean artery in the pleuronectine *Atheresthes stomias* and *A. evermanni* (Fig. 22A), whereas the opening is in the dorsal one in the other 75 pleuronectids examined (Fig. 22B-J).

The ventral hypohyal (vhh) is firmly united with the dorsal hypohyal dorsally and with the ceratohyal posteriorly. These two ventral hypohyals are firmly united with each other anteromedially.

The ceratohyal (ch) is connected with both hypohyals anteriorly or anterodorsally, and posteriorly with the epihyal by a strongly jagged suture. The ceratohyal is transversed in its outer surface by the groove for the hyoidean artery. In the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hippoglossoides*, *Acanthopsetta*, *Dexistes*, *Clidoderma* and *Paralichthodes* and the rhombosoleine genera *Ammotretis* and *Taratretis*, a foramen is located in the course of the groove, but the hyoidean artery never runs through from outer to inner surfaces of the ceratohyal (Fig. 22A-C, E). Among these species, the foramen is minute in size in *Verasper*, *Hippoglossoides* except *H. robustus*, *Acanthopsetta* and *Dexistes* (Fig. 22B, C), while it is moderate in the other species (Fig. 22A, E). In the members of the rhombosoleine genera *Pelotretis*, *Azygopus*, *Rhombosolea* and *Peltorhamphus* and all the samarine genera examined, the hyoidean artery perforates the middle part of the outer lateral surface of the ceratohyal (Fig. 22G, I). These species except *Pelotretis flavilatus* and *Azygopus pinnifasciatus pinnifasciatus* also have a foramen in its inner lateral surface (Fig. 22J). In the other pleuronectid species studied, there is no foramen or perforation in the outer and inner lateral surfaces of the ceratohyal (Fig. 22D, F).

The epihyal (eh) is connected anteriorly with the ceratohyal by a strongly jagged suture and posterodorsally with the interhyal.

The interhyal (ih) is small rod-like in shape. The interhyal is attached to the symplectic process of the hyomandibular and the symplectic by a cartilage and a ligament. Ventrally, the interhyal fits in a small fossa on the posterodorsal aspect of the epihyal.

The branchiostegals (br) are arched sword-like in shape and increase in length posteriorly. They are attached to the ventral margin of the ceratohyal and the outer lateral surface of the cartilagenous part between the ceratohyal and the epihyal. *Hippoglossoides platessoides limandoides* have eight branchiostegals (Fig. 22B), whereas they are usually seven in all the other pleuronectids examined (Fig. 22A, C-G), and three (four in *Hippoglossoides platessoides limandoides*) are attached to the ceratohyal and four to the cartilagenous part between the ceratohyal and the epihyal (Fig. 22). However, the number of the branchiostegals rarely shows intraspecific variations: six in *Pleuronectes limanda* and *Pelotretis flavilatus* on both sides, eight on the ocular side in *Samariscus xenicus* and on the blind side in *Pleuronichthys decurrens*.

UNIT CHARACTER The hyoid arches of flatfishes have been extensively examined by McAllister (1968), concerning the branchiostegals in particular. In the family Pleuronectidae, according to his study, no characters for the phylogenetic

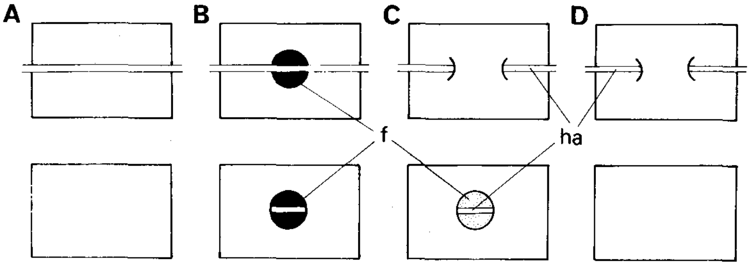

Fig. 23. Schematic diagrams showing several types (character states) of ceratohyals in relation to hyoidean artery in 77 righteye flounders. f, foramen; ha, hyoidean artery. Upper, outer surface; lower, inner surface.

Table 7. Coding in ceratohyal. The character states, A, B, C and D, are the same as those in Fig. 23.

Character state / Unit character	A	B	C	D
(1)	0	1	1	1
(2)	NC	0	1	1
(3)	NC	NC	0	1

work have been found in this part, though the number of the branchiostegals has been used for the taxonomy in the genus *Hippoglossoides* (see Norman, 1934).

The present study indicates that the hyoid arches of the pleuronectid fishes show interspecific variations in the following characters: 1) the position of the opening for the hyoidean artery in the hypohyals, 2) the structure of the ceratohyal in relation to the hyoidean artery, 3) the number of the branchiostegals.

The first character, the position of the opening for the hyoidean artery in the hypohyals, is adopted as a unit character with two states: the opening for the hyoidean artery between both hypohyals and in the dorsal hypohyal. The character state is coded as 0 for the OTU's with the opening between both hypohyals and as 1 for the OTU's with the opening in the dorsal hypohyal. For the second character, the structure of the ceratohyal in relation to the hyoidean artery, four character states are recognizable (Fig. 23). However, it is not directly used as a quantitative multistate character with four character states, since those states cannot be arranged in a single logical sequence. Therefore, it is treated as a qualitative multistate character and turned into three new two-state characters as follows: (1) presence or absence of the ceratohyal foramen or the perforation in the middle part of the outer lateral surface of the ceratohyal, (2) presence or absence of the perforation, (3) presence or absence of the foramen in its inner lateral surface in those fishes with the perforation in its outer lateral surface. The character state in the characters (1) and (2) is coded as 0 for its absence and as 1 for its presence. In the character (2), the character states of the fishes lacking the ceratohyal foramen and the perforation in its outer lateral surface are coded as NC. Concerning the

Table 8. Comparison and coding of characters of hyoid arch in 77 righteye flounders. The numerals in the parentheses are the values of the character states. In the structure of the ceratohyal, the character states, A, B, C and D, are the same as those in Fig. 23. Abbreviations as in Fig. 22. [†] For explanation on coding, see text.

Opening of hh	Structure of ch[†]	Genera
dhh (1)	A	Pleuronectinae *Psettichthys*, *Pleuronectes*, *Platichthys*, *Hypsopsetta*, *Pleuronichthys*, *Glyptocephalus*, *Errex*, *Kareius*, *Microstomus*, *Tanakius*, *Embassichthys* Poecilopsettinae all genera examined
between both hh (0)	B	Pleuronectinae *Atheresthes*
dhh (1)		Pleuronectinae *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hippoglossoides*, *Acanthopsetta*, *Dexistes*, *Clidoderma*, *Paralichthodes* Rhombosoleinae *Ammotretis*, *Taratretis*
	C	Samarinae all genera examined Rhombosoleinae *Rhombosolea*, *Peltorhamphus*
	D	Rhombosoleinae *Pelotretis*, *Azygopus*

character (3), the character state is coded as 0 for its presence and as 1 for its absence. In this case, the character states of the fishes lacking the perforation in its outer lateral surface are coded as NC. The coding for these three characters are summarized in Fig. 23 and Table 7. In the third character, the number of the branchiostegals, there are intraspecific variations in some species as described above. Thus, this character is excluded from the unit characters.

Four selected unit characters and coded character states are summarized in Tables 7 and 8.

6. BRANCHIAL APPARATUS AND GILL RAKERS

DESCRIPTION The branchial apparatus bearing the gills and the gill rakers consists of three unpaired basibranchials, three pairs of hypobranchials, five pairs of ceratobranchials, four pairs of epibranchials and four pairs of pharyngobranchials.

The basibranchial (bb) is composed of three bones and forms the floor of the pharyngeal cavity. These bones are connected ventrally with the dorsal aspect of the urohyal by a fibrous connective membrane. The basibranchials are connected laterally with the hypobranchials.

The first basibranchial is triangular or square in dorsal view and articulated anteriorly to the posterior or ventral aspect of the posterior basihyal. In the pleuronectine *Atheresthes stomias*, *Eopsetta grigorjewi*, *Psettichthys melanosticus*, *Pleuronectes isolepis*, *P. vetulus*, *P. ferrugineus*, *P. punctatissimus*, *Clidoderma asperrimum* and *Paralichthodes algoensis*, there is a wedge-like articulation between the first basibranchial and the following one (Figs. 24B, C, E, F and 25B, C), whereas in the other pleuronectids there is not such an articulation, and it is connected with the second one by a cartilage (Figs. 24A, D, G-I and 25A, D-I). The first basibranchial and the basihyal are articulated ventrally to both hypohyals.

The second basibranchial appears hourglass-shaped in dorsal view. In the pleuronectine *Psettichthys melanosticus*, *Pleuronectes punctatissimus* and *Paralichthodes algoensis*, there is a wedge-like articulation between the second basibranchial and the last one (Figs. 24C and 25C). In the other pleuronectids, it is connected with the last one by a cartilage (Figs. 24A, B, D-I and 25A, B, D-I).

The third basibranchial is rather long. Anteriorly, it is articulated to the second basibranchial and posteriorly to the cartilage lying among the third hypobranchials, the fourth and fifth ceratobranchials.

The hypobranchial (hb) comprises three paired bones and bears the gill rakers on its dorsal surface. The first and second hypobranchials are bar-like bones and the third one is fan-shaped in dorsal view. The first hypobranchial is articulated to the second basibranchial. The second bone is joined to the junction between the second and third basibranchials. The third hypobranchial is loosely connected with the second basibranchial. Posteriorly, the hypobranchials are articulated to the ceratobranchials.

Five pairs of ceratobranchials (cb) are usually found in all the pleuronectids examined here. The first four bones are rod-like in shape and bears the gill rakers on their dorsal surfaces. The first, second and third ceratobranchials are articulated anteriorly to their own hypobranchials and posteriorly to their own epibranchials. The fourth ceratobranchial is attached anteriorly to the cartilage lying behind the third basibranchial and articulated posteriorly to its own epibranchial. The fifth ceratobranchial is elongate, rod-like or triangular in dorsal view. The fifth ceratobranchial is joined anteriorly to the cartilage behind the third basibranchial and posteriorly to the fourth epibranchial by a ligament. The fifth ceratobranchial bears the teeth on its dorsal surface. In *Kareius bicoloratus*, a member of the Pleuronectinae, it is a single triangular bone (Fig. 24I), while a pair of fifth ceratobranchials are present in the other pleuronectids examined (Figs. 24A-H and 25).

Four pairs of epibranchials (eb) are present in all the pleuronectids examined. The epibranchials are short bar-like bones forming the upper limbs of the branchial arches and usually bearing the gill rakers on their dorsal surfaces. The epibranchials are articulated anteriorly to the ceratobranchials and posteriorly with the pharyngobranchials.

In the fishes of the pleuronectine genera *Eopsetta*, *Verasper*, *Hippoglossoides*, *Acanthopsetta*, *Pleuronectes* except *P. limanda*, *P. asper* and *P. sakhalinensis*, *Platichthys*, *Kareius*, *Clidoderma* and *Paralichthodes* and the samarine genus *Samaris*, the upper tip of the first epibranchial is slightly bifurcate or almost simple (Figs. 24B, D-G, I and 25B, C, H). In the other pleuronectids, it is more or less bifurcate (Figs. 24A, C, H and 25A, D-G, I).

In the members of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Eopsetta*

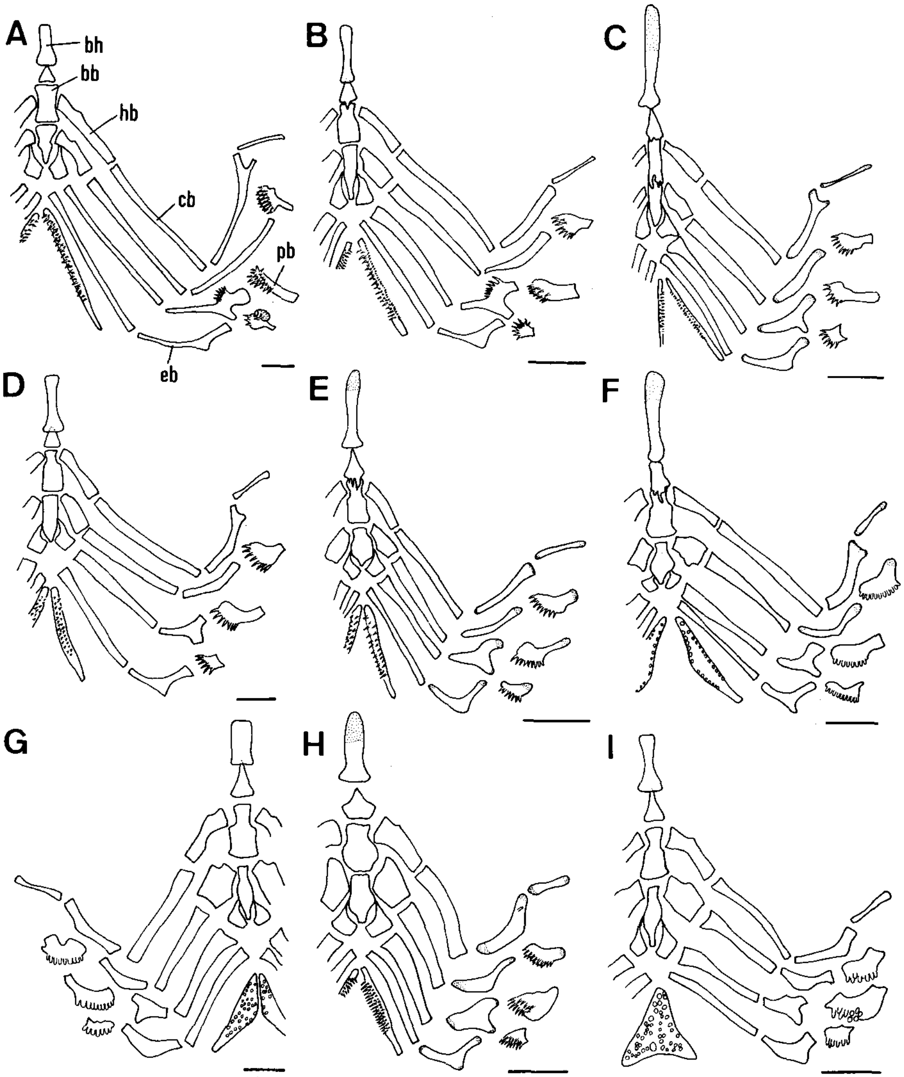

Fig. 24. Dorsal aspect of branchial apparatus on ocular side in nine righteye flounders. A, *Atheresthes evermanni* ; B, *Eopsetta grigorjewi* ; C, *Psettichthys melanostictus* ; D, *Acanthopsetta nadeshnyi* ; E, *Pleuronectes isolepis* ; F, *P. vetulus* ; G, *Platichthys stellatus* (reversed specimen) ; H, *Hypsopsetta guttulata* ; I, *Kareius bicoloratus*. bb, basibranchial ; bh, basihyal ; cb, ceratobranchial ; eb, epibranchial ; hb, hypobranchial ; pb, pharyngobranchial. Scales indicate 5 mm.

and *Verasper*, a pleuronectine *Hippoglossus stenolepis*, and all the samarine members examined, the third epibranchial possesses the teeth on its ventral surface (Figs. 24A, B and 25H, I), whereas in the remaining pleuronectid members the teeth are absent on the third epibranchial (Figs. 24C-I and 25A-G).

There are four pairs of pharyngobranchials (pb). The first pharyngobranchial,

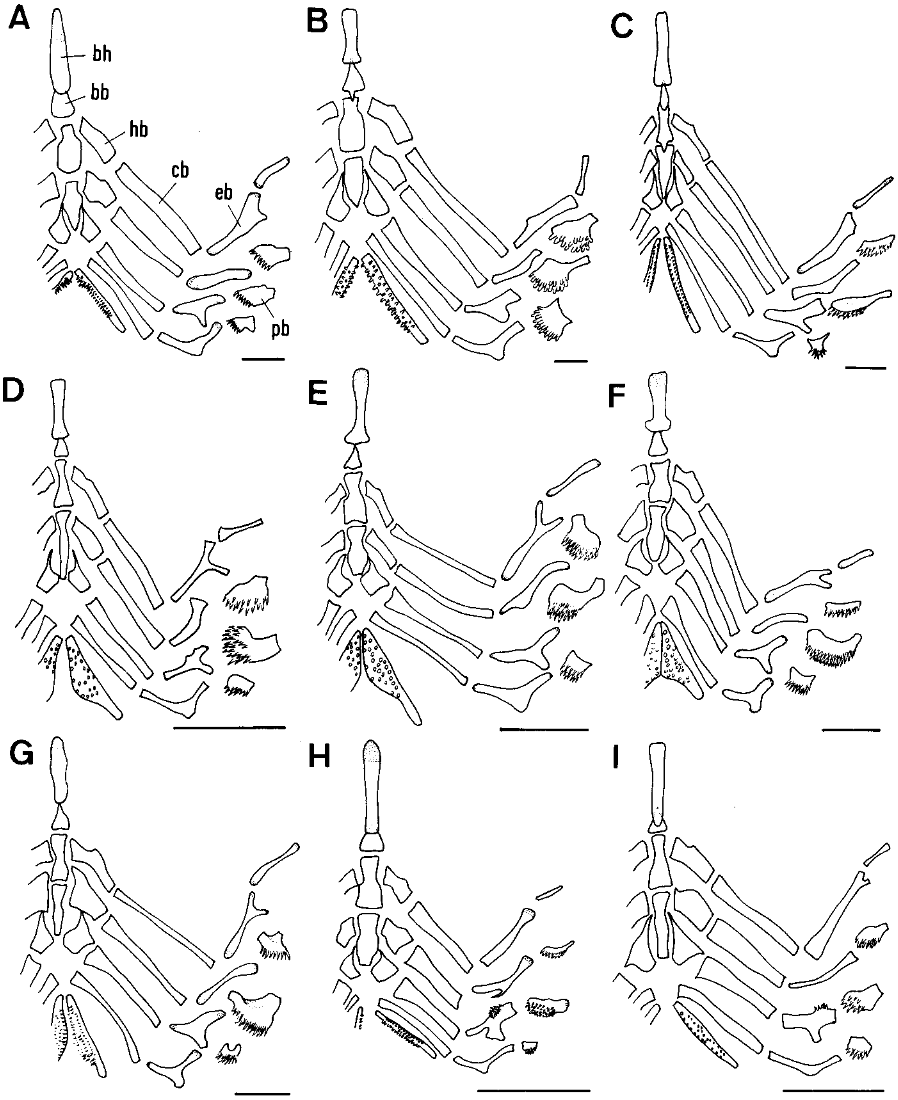

Fig. 25. Dorsal aspect of branchial apparatus on ocular side in nine righteye flounders. A, *Embassichthys bathybius* ; B, *Clidoderma asperrimum* ; C, *Paralichthodes algoensis* ; D, *Poecilopsetta plinthus* ; E, *Azygopus pinnifasciatus pinnifasciatus* ; F, *Rhombosolea leporina* ; G, *Peltorhamphus novaezeelandiae* ; H, *Samaris cristatus* ; I, *Plagiopsetta glossa*. Abbreviations as in Fig. 24. Scales indicate 5 mm.

called a suspensorial pharyngeal, is rod-like and joined anteriorly to the first epibranchial and posteriorly to the ventral surface of the parasphenoid. The second, third and fourth pharyngobranchials bearing the teeth on their ventral surfaces are articulated anteriorly to the second, third and fourth epibranchials respectively.

In dorsal view, the basihyal (bh) is a bar-like bone lying on the anterior tip of the hyoid and branchial arches. Together with the first basibranchial, it is articulated ventrally to the hypohyals.

The branchial arch is composed of an upper limb supported by the epibranchial and a lower limb supported by the hypobranchial and the ceratobranchial. It is generally provided with the gill rakers. In the pleuronectine *Hippoglossus hippoglossus*, *Verasper variegatus* and *V. moseri*, the rhombosoleine *Ammotretis lituratus* and *A. elongatus* and the samarine *Samariscus latus* and *S. xenicus*, the gill rakers

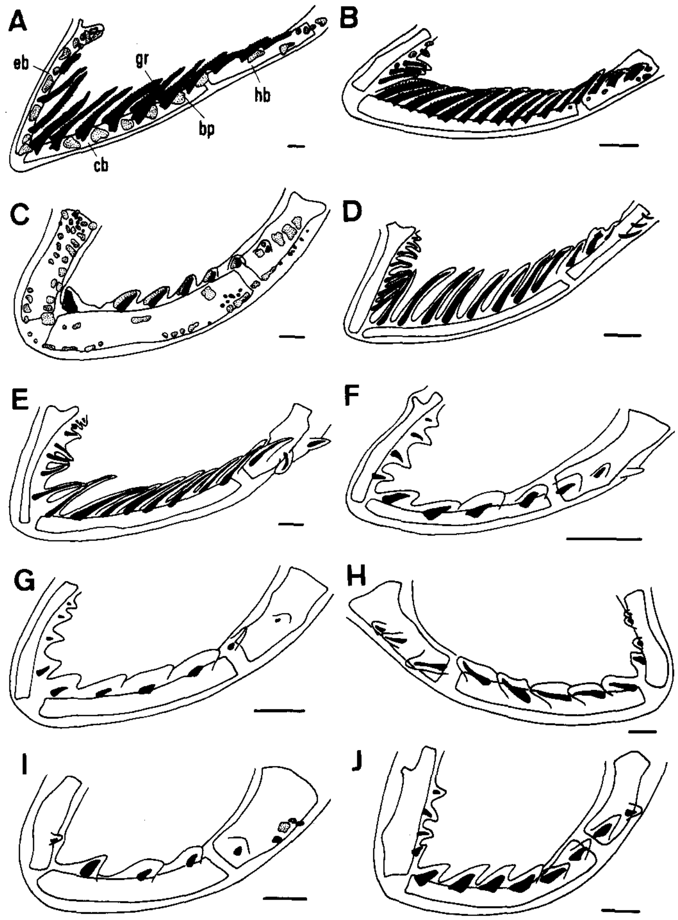

Fig. 26. Lateral aspect of outer side of first gill arches on ocular side in 10 righteye flounders. A, *Atheresthes evermanni* ; B, *Eopsetta grigorjewi* ; C, *Verasper variegatus* ; D, *Psettichthys melanosticus* ; E, *Acanthopsetta nadeshnyi* ; F, *Dexistes rikuzenius* ; G, *Pleuronectes herzensteini* ; H, *Platichthys stellatus* (reversed specimen) ; I, *Hypsopsetta guttulata* ; J, *Glyptocephalus stelleri*. bp, bony plate ; gr, gill raker. Other abbreviations as in Fig. 24. Scales indicate 2 mm.

are usually absent on the upper limb (Figs. 26C and 27J), while they are present in the other pleuronectids (Figs. 26A, B, D-J and 27A-I). But, in some specimens of *Samariscus latus* and *S. xenicus*, there are a few gill rakers on the upper limb.

The pleuronectids are separable into two groups on the basis of the gill raker's spination. In the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta* and *Paralichthodes*, each gill raker possesses the spines on its dorsal surface (Figs. 26A, B and 27C), while in the remaining pleuronectids the spines are absent (Figs. 26C-J and 27A, B, E-J).

The length and shape of the gill rakers vary with the Pleuronectidae. In the

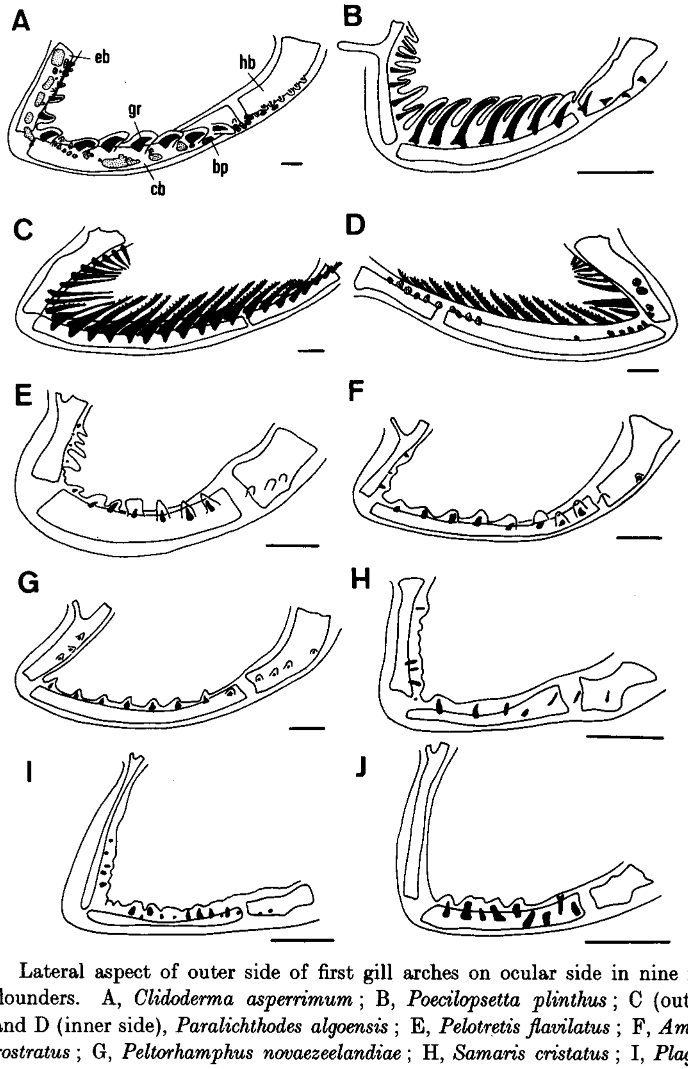

Fig. 27. Lateral aspect of outer side of first gill arches on ocular side in nine righteye flounders. A, *Clidoderma asperrimum* ; B, *Poecilopsetta plinthus* ; C (outer side) and D (inner side), *Paralichthodes algoensis* ; E, *Pelotretis flavilatus* ; F, *Ammotretis rostratus* ; G, *Peltorhamphus novaezeelandiae* ; H, *Samaris cristatus* ; I, *Plagiopsetta glossa* ; J, *Samariscus latus*. Abbreviations as in Figs. 24 and 26. Scales indicate 2 mm.

subfamily Pleuronectinae, the gill rakers vary with the species in length and shape (Figs. 26 and 27A, C). In the subfamily Poecilopsettinae, they are rather elongated (Fig. 27B). In the subfamily Rhombosoleinae, the gill rakers are generally very short (Fig. 27E-G). In the subfamily Samarinae, they are very feeble and small in size (Fig. 27H-J).

Based on the bony plates* (bp) on the branchial arch, the pleuronectids are separable into two groups. In the first group including the fishes of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Hypsopsetta*, *Clidoderma* and *Paralichthodes*, the bony plates are present on the outer and/or inner surfaces of the branchial arch (Figs. 26A-C, I and 27A, D). In the second group containing the remaining pleuronectids examined, they are absent (Figs. 26D-H, J and 27B, E-J).

UNIT CHARACTER The branchial apparatus and the gill rakers of flatfishes have been studied extensively and in detail by Kuronuma (1938) and Amaoka (1969, 1972). In their phylogenetic studies on the pleuronectiforms, they used many characters in this structure such as the shape of each element of branchial apparatus, presence or absence of the gill rakers on the upper limb, presence or absence of the spines on each gill raker, presence or absence of the bony plates on the branchial arch, and others. Also, Groot (1971) discussed the dimensions and form of the gill rakers of many flatfishes in relation to the shape of the alimentary tract, food and feeding behavior.

In the family Pleuronectidae, the interspecific variations were found in the following characters: 1) the relation between both fifth ceratobranchials, 2) the shape of the first epibranchial, 3) presence or absence of the teeth on the third epibranchial, 4) presence or absence of the gill rakers on the upper limb of the branchial arch, 5) presence or absence of the spines on each gill raker, 6) the length and shape of the gill raker, 7) presence or absence of the bony plates on the outer and/or inner surfaces of the branchial arch.

In the first character, the relation between both fifth ceratobranchials, there are two distinctive states: both elements fused with each other in *Kareius* and both separated from each other in all the other pleuronectids examined, without any intraspecific variation. Therefore, this character is employed as a unit character. The value of the character state is 0 for the OTU with both elements separated from each other, and 1 for the OTU having both fused with each other. As for the second character, the shape of the first epibranchial, it is very difficult to recognize several distinct character states as described above. Therefore, it is excluded from the unit characters. The third character, presence or absence of the teeth on the third epibranchial, is regarded as a unit character with two states. The character state is coded as 0 for its presence and as 1 for its absence. The fourth character, presence or absence of the gill rakers on the upper limb of the branchial arch, is not adopted as a unit character because of the intraspecific variation found in the present character as described above. The fifth character, presence or absence of the spines on each gill raker, is used as a unit character, since no intraspecific variation was

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* Amaoka (1969) called them "tubercles".

Table 9. Comparison and coding of characters of branchial apparatus and gill rakers in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

5th cerato-branchials	Teeth on 3rd epibranchial	Spines on gill rakers	Bony plates on outer and /or inner sides of gill arch	Subfamilies, genera and species
separated (1)	absent (1)	present (0)	present (0)	Pleuronectinae *Hippoglossus hippoglossus*, *Paralichthodes*
	present (0)			*Atheresthes*, *Reinhardtius*, *Hippoglossus stenolepis*, *Eopsetta*
		absent (1)		*Verasper*
	absent (1)			*Hypsopsetta*, *Clidoderma*
fused (0)			absent (1)	*Kareius*
separated (1)				other genera examined Poecilopsettinae Rhombosoleinae
	present (0)			Samarinae

observed in any species examined in this regard. The value of the character state is 0 for the OTU's having the gill rakers with spines and 1 for the OTU's having them without spines. For the sixth character, the length and shape of the gill raker, there are various types of gill rakers in the pleuronectids as described above. Therefore, it was impossible to distinguish character states in regard to its length and shape and this character was omitted from the analyses. The seventh character, presence or absence of the bony plates on the outer and/or inner surfaces of the branchial arch, is adopted as a unit character with two character states. The character state is coded as 0 for its presence and as 1 for its absence.

Four selected unit characters and coded character states are summarized in Table 9.

7. FINS

DESCRIPTION In this section, the dorsal, pectoral, pelvic and anal fins are described. The caudal fin is treated elsewhere.

The dorsal fin is a median fin extending along the dorsal edge of the body. This fin is composed of the fin rays supported by the pterygiophores. The fin ray including soft one alone is composed of two segmented and slender rod-like elements united with each other. A pair of elements hold the distal radial between them (Fig. 28).

The fishes of the family Pleuronectidae are classified into two groups according to the position of the origin of the dorsal fin in relation to the dorsomedian line of the head. In the fishes of the pleuronectine genus *Pleuronichthys*, the dorsal fin

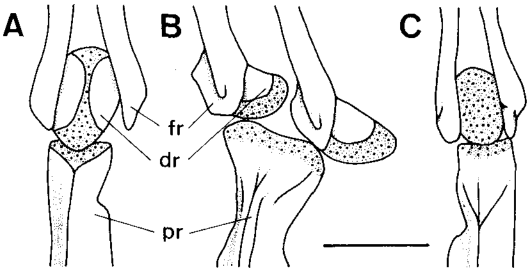

Fig. 28. Anterior (A), lateral (B) and posterior (C) aspects of a dorsal fin ray with its pterygiophore in *Eopsetta grigorjewi*. dr, distal radial; fr, dorsal fin ray; pr, proximal radial. Scale indicates 2 mm.

originates on the blind side (Fig. 29), whereas it originates nearly on the median line of the head in the other fishes of the Pleuronectidae (Fig. 30). In the former group, the dorsal fin also shows some variations in its origin on the blind side. In *Pleuronichthys decurrens*, the dorsal fin originates much lower on the blind side and on a level with the lower corner of the mouth (Fig. 29A), while in the other five species of *Pleuronichthys* it originates on about a level with the snout and well above the lower corner of the mouth (Fig. 29B). The fishes of the Pleuronectidae belonging to the latter group are further subdivided into four groups according to the origin of the dorsal fin. In the first group comprising the fishes of the subfamilies Pleuronectinae and Poecilopsettinae except the pleuronectine genera *Pleuronichthys* and *Paralichthodes*, and the genus *Pelotretis* of the subfamily Rhombosoleinae, the dorsal fin originates above the upper eye (Fig. 30A, C). In the second group including the fishes of the pleuronectine genus *Paralichthodes*, the rhombosoleine genera *Azygopus* and *Taratretis* and all the samarine genera examined, it begins in front of the upper eye (Fig. 30B, D, F, I). In the third group consisting of the fishes of the rhombosoleine genus *Rhombosolea*, the origin of the dorsal fin is near the extremity of the snout which is never hooked (Fig. 30G). In the last group containing the fishes of

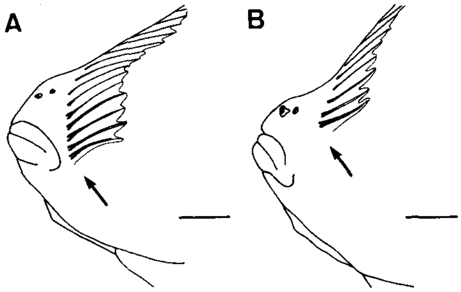

Fig. 29. Diagrams showing origin of dorsal fin on blind side in two species of *Pleuronichthys*. A, *P. decurrens*; B, *P. cornutus*. Arrows indicate its origin of the dorsal fin. Scales indicate 5 mm.

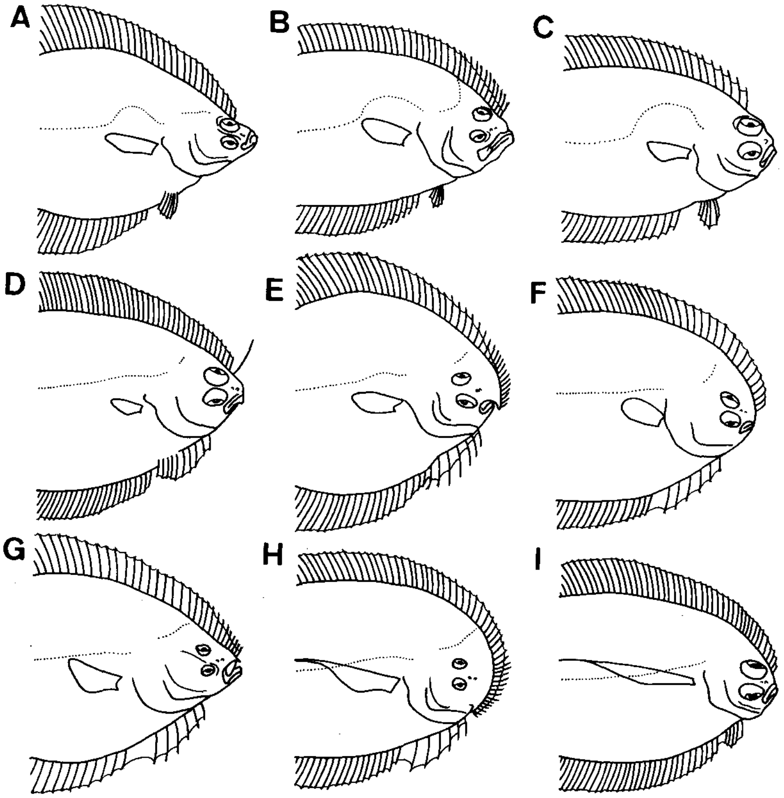

Fig. 30. Schematic diagrams showing origin of dorsal fin in nine righteye flounders. A, *Pleuronectes herzensteini*; B, *Paralichthodes algoensis*; C, *Poecilopsetta plinthus*; D, *Azygopus pinnifasciatus pinnifasciatus*; E, *Ammotretis rostratus*; F, *Taratretis derwentensis*; G, *Rhombosolea leporina*; H, *Peltorhamphus novaezeelandiae*; I, *Samariscus latus*.

the rhombosoleine genera *Ammotretis* and *Peltorhamphus*, the dorsal fin starts at the extremity of the rostral hook (Fig. 30E, H).

Concerning the stoutness of the dorsal fin rays, in the fishes of the pleuronectine genera *Microstomus*, *Embassichthys* and *Clidoderma*, the fin rays are stout, but are not stout in the other pleuronectids examined here.

In the fishes of the pleuronectine genera *Atheresthes*, *Hippoglossus*, *Verasper*, *Hypsopsetta*, *Tanakius*, *Clidoderma* and *Paralichthodes*, the pleuronectine *Eopsetta jordani*, *E. grigorjewi*, *Pleuronectes bilineatus* and *P. mochigarei*, the poecilopsettine *Poecilopsetta plinthus* and *Nematops macrochirus*, and all the rhombosoleine fishes examined, the dorsal fin rays are usually more or less branched. Of these fishes, in *Paralichthodes algoensis* and the fishes of all the rhombosoleine genera except *Azygopus*, all or almost all the rays are branched. In *Verasper variegatus* and *Clidoderma asperrimum*, about the posterior half of the dorsal fin rays are branched. In the other fishes mentioned above, several posterior rays are branched and also a few anterior ones in *Poecilopsetta plinthus* and *Nematops macrochirus*. In the other pleuronectids studied here, the dorsal fin rays are usually unbranched. But, in some specimens of *Pleuronectes ferrugineus*, *Glyptocephalus stelleri* and *Errex zachirus*, several posterior rays are branched.

In some pleuronectid fishes, the anteriormost or several anteior dorsal fin rays are prolonged. In *Azygopus pinnifasciatus pinnifasciatus*, a member of the subfamily Rhombosoleinae, the first ray is long and entirely free (Fig. 30D). In *Psettichthys melanostictus*, a member of the subfamily Pleuronectinae, several anterior rays are a little prolonged and more or less free from membranes. In *Samaris cristatus*, a member of the subfamily Samarinae, anterior 12 or 13 rays are greatly prolonged and filamentous.

In the fishes of the subfamily Pleuronectinae except *Platichthys flesus flesus*, *P. stellatus* and *Kareius bicoloratus* and the rhombosoleine genera *Pelotretis* and *Ammotretis*, scales are distributed along the dorsal fin rays on the ocular side or both sides. The pterygiophore is composed of distal and proximal radials in the family Pleuronectidae. The distal radials (dr) are paired plate-lile bones locating at the anterior portion of its base of the fin ray and united with each other by a cartilage (Fig. 28). The proximal radial (pr) is an unpaired and slender rod-like bone forming the major part of the pterygiophore and inserts between the neural spines of the adjacent vertebrae (Figs. 39-41).

Anteriorly, the relation between the dorsal fin rays and their pterygiophores varies with the pleuronectid fishes studied. In the rhombosoleine *Rhombosolea plebeia* and *R. tapirina*, the anteriormost proximal radial bears one dorsal fin ray (Fig. 31B), while in the other pleuronectid fishes it bears two rays (Fig. 31A, C). But, there are a few intraspecific variations: the anteriormost proximal radial bears one or three fin rays in a few specimens of *Pleuronichthys cornutus* and three in a specimen of *Glyptocephalus stelleri*.

The anal fin is a median fin bordering the ventral edge of the body, and composed of the fin rays supported by the pterygiophores. All the fin rays are soft. The pterygiophore comprises the distal and proximal radials and its structure is similar to that of the dorsal fin ray. In the pleuronectid fishes examined in the present study, the anteriormost proximal radial, which is the largest and stoutest in all the proximal radials, is attached to the anterior margin of the first haemal spine at its upper posterior margin (Figs. 39-41). The stoutness of the fin rays is very

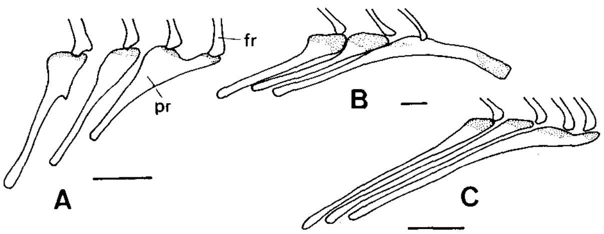

Fig. 31. Lateral aspect of anteriormost portion of dorsal fin with pterygiophores in three righteye flounders. A, *Pleuronectes herzensteini*; B, *Rhombosolea tapirina*; C, *R. leporina*. fr, dorsal fin ray; pr, proximal radial. Scales indicate 2 mm.

similar to that of the dorsal fin rays. Also, presence or absence of the branched rays and the scales along the fin rays is very similar to that in the dorsal fin.

The pectoral fins are usually paired fins located on the anterior part of the body just below the lateral line, and supported by the pectoral girdles. They are composed of soft rays alone. In most pleuronectids examined, the fin rays are usually branched at least at the middle portion of the pectoral fin on the ocular side. In the members of the pleuronectine genera *Hippoglossoides* except *H. pinetorum* and *Embassichthys*, a pleuronectine *Eopsetta exilis*, and all the samarine members examined, the fin rays are usually simple on the ocular side. But, in some specimens of *Embassichthys bathybius*, the middle part of the pectoral fin consists of branched rays on the ocular side.

In the members of the subfamily Samarinae, the pectoral fin is entirely absent on the blind side (Fig. 32F). On the other hand, the other members of the family Pleuronectidae have a pair of pectoral fins, and the fin of the ocular side is generally larger than that of the blind side (Fig. 32A-E).

The pelvic fins are usually paired fins located between the isthmus and the anal fin, and supported by the pelvic girdles.

In the fishes of the rhombosoleine genus *Rhombosolea*, the pelvic fin is entirely absent on the blind side, though the pelvic girdle is equipped (Fig. 32E), while the other pleuronectid members have a pair of pelvic fins (Fig. 32A-D, F). All the fin rays are soft.

The number of the pelvic fin rays ranges from three to thirteen in the pleuronectids. Its number is usually six on both sides in the fishes of the subfamilies

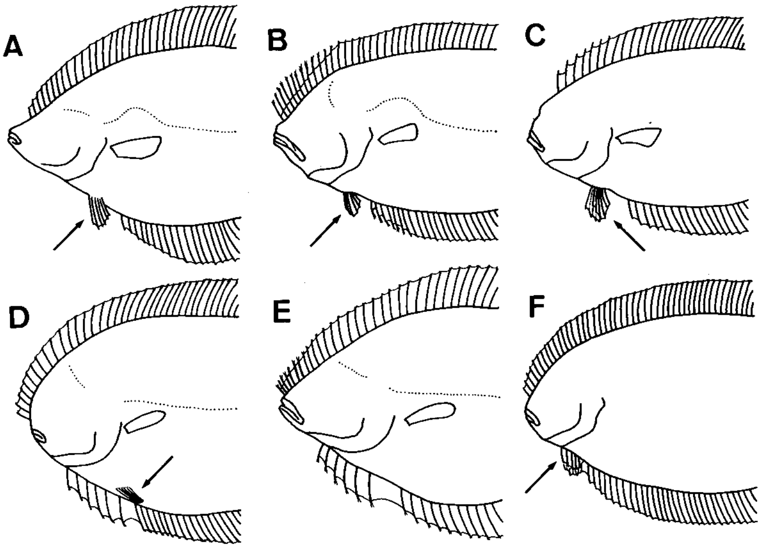

Fig. 32. Schematic diagrams showing pelvic fin on blind side in six righteye flounders. A, *Pleuronectes herzensteini*; B, *Paralichthodes algoensis*; C, *Poecilopsetta plinthus*; D, *Taratretis derwentensis*; E, *Rhombosolea leporina*; F, *Samariscus latus*. Arrows indicate the pelvic fin on the blind side.

Pleuronectinae and Poecilopsettinae except in a pleuronectine *Embassichthys bathybius* which have five. Within the fishes of the subfamily Rhombosoleinae, there are usually six on the ocular side in the fishes of the genera *Taratretis*, *Rhombosolea* and *Peltorhamphus*, seven in *Pelotretis flavilatus* and *Ammotretis rostratus*, ten in *Azygopus pinnifasciatus pinnifasciatus* and *Ammotretis lituratus*, and thirteen in *Ammotretis elongatus*. On the blind side, the count is usually four in *Ammotretis rostratus*, *A. elongatus* and the fishes of the genus *Peltorhamphus*, five in *Azygopus pinnifasciatus pinnifasciatus*, and six in *Pelotretis flavilatus*, *Ammotretis lituratus* and *Taratretis derwentensis*. In the fishes of the subfamily Samarinae, it is usually five on both sides.

The pleuronectid fishes are classified into two groups on the basis of the relation between the pelvic fin of the ocular side and the anal fin. In the fishes of the subfamilies Rhombosoleinae and Samarinae examined except a rhombosoleinae *Azygopus pinnifasciatus pinnifasciatus*, the pelvic fin of the ocular side is united with the anal fin by a fin membrane (Fig. 30E-I), whereas in the other pleuronectid fishes these two fins are separated from each other (Fig. 30A-D).

UNIT CHARACTER The characters in the fins except the caudal fin have been used for the classification of the pleuronectiforms by many investigators (Norman, 1934; Hubbs, 1945; Ochiai,1966; Amaoka, 1969, 1972 etc.). They are as follows: presence or absence of the pectoral and pelvic fins on the blind side, the relation between the pelvic fin of the ocular side and the anal fin, the number of the pelvic fin rays on each side, and others.

In the present study on the family Pleuronectidae, the interspecific variability on the fins was found in the following charactars: 1) the position of the origin of the dorsal fin, 2) the degree of the stoutness of the median fin rays, 3) presence or absence of the branched rays in the median fins, 4) presence or absence of the prolongation of the anterior dorsal fin rays, and if the prolongation is present, its type, 5) presence or absence of the scales along the median fin rays on the ocular side or both sides, 6) the number of the dorsal fin rays borne by the anteriormost proximal radial, 7) presence or absence of the branched rays in the pectoral fin on the ocular side, 8) presence or absence of the pectoral fin on the blind side, 9) presence or absence of the pelvic fin on the blind side, 10) the number of the pelvic fin rays on each side, 11) the relation between the pelvic fin of the ocular side and the anal fin.

In the first character, the position of the origin of the dorsal fin, there are several character states as follows. On the blind side, there are two states: its origin on a level with the snout and on a level with the lower corner of the mouth. On the dorsomedian line of the head, four character states are recognizable: its origin above the upper eye, in front of the upper eye, near the extremity of the snout, and at the extremity of the rostral hook. These six character states mentioned above can not be arranged in order in a single logical sequence. Therefore, this character was treated as a qualitative multistate character and converted into three new characters as follows: (1) the position of the origin of the dorsal fin in relation to the dorsomedian line of the head, (2) the position of the origin of the dorsal fin on the blind side, (3) the position of the origin of the dorsal fin on the dorsomedian line of the head. In the character (1), there are two states: the origin of dorsal fin on the blind side in *Pleuronichthys* and on the dorsomedian line of the head in the other pleuronectids. The character state is coded as O for the OTU's with the former state and as 1 for the OTU's with the latter state. In the character (2), the character state is coded as O for the OTU having the dorsal origin on a level with the snout and as 1 for the OTU having the origin on a level with the lower corner of the mouth. In this case, the character states of the pleuronectids except the fishes of the pleuronectine genus *Pleuronichthys* are coded as NC. In the character (3), there are four character states which can be arranged in a single logical sequence. Therefore, this character is a quantitative multistate character with four character states. Each character state is coded as 0, 1, 2, 3 in order. In this regard, the character states of the fishes of the genus *Pleuronichthys* are coded as NC. The second character, the degree of the stoutness of the median fin rays, is adopted as a unit character with two states. The character state is coded as O for the OTU's with stout fin rays and as 1 for the OTU's without such fin rays. The third character, presence or absence of the branched rays in the median fins, is not used as a unit character because of the intraspecific variation already described in some species. The fourth character, presence or absence of the prolongation of the anterior dorsal fin rays, and if the prolongation is present, its type, is taken up as a unit character. Though there are four character states: *Psettichthys* type prolongation, *Azygopus* type, *Samaris* type and the absence of such a prolongation, these states can not be arranged in a single logical sequence. Therefore, this character was regarded as a qualitative multistate character and divided into the following four characters: (1) presence or absence of the prolongation of the anterior dorsal fin rays, (2) *Psettichthys* type or not, (3) *Azygopus* type or not, and (4) *Samaris* type or not. In the character (1), the character state is coded as O for the OTU's of *Psettichthys*, *Azygopus* and *Samaris* with the prolongation of the anterior dorsal fin rays, and as 1 for the other OTU's. In the characters (2), (3) and (4), the character state is coded as O for the OTU's with each type, and as 1 for the OTU's with another type. When the present three characters are compared, the character states of the species without the prolongation were coded as NC. The fifth character, presence or absence of the scales along the median fin rays on the ocular side or both sides, is adopted as a unit character with two states. The character state is coded as O for its presence and as 1 for its absence. The sixth and seventh characters, the number of the dorsal fin rays borne by the anteriormost proximal radial and presence or absence of the branched rays in the pectoral fin on the ocular side, can not be used as unit characters, because there are intraspecific variations in these characters as described above. The eighth and ninth characters, presence or absence of the pectoral and pelvic fins on the blind side, are unit characters with two states. The character state is coded as O for their presence and as 1 for their absence, respectively. The tenth character, the number of the pelvic fin rays on each side, may be regarded as a unit character with several character states. However, the intraspecific variation has been reported in several species in the previous works. Norman (1934), Hubbs and Wilimovsky (1964), James (1972), Last (1978) reported, for example, the following intraspecific variations: on the ocular side, *Reinhardtius hippoglossoides* (4-7), *Pleuronectes limanda* (5-7), *Pleuronichthys decurrens* (4-7), the fishes of the genus *Microstomus* (5-6), *Azygopus pinnifasciatus pinnifasciatus* (10-11), *Taratretis derwentensis* (5-6); on the

Table 10. Comparison and coding of characters of fins in 77 righteye flounders. The

Origin of dorsal fin		Stoutness of median fin rays	Prolongation of anterior dorsal fin rays	Scales along median fin rays	Pectoral fin of blind side
on blind side (0)	on level with snout (0)	not stout (1)	not prolonged (1)	present (0)	present (0)
	on level with lower corner of mouth (1)				
on dorso-median line of head (1)	above upper eye (0)	stout (0)			
		not stout (1)	prolonged (0)		
			not prolonged (1)	absent (1)	
				present (0)	
	in front of upper eye (1)				
				absent (1)	absent (1)
			prolonged (0)		
					present (0)
			not prolonged (1)		
	above upper eye (0)			present (0)	
	at extremity of rostral hook (3)				
				absent (1)	
	near extremity of snout (2)				

numerals in the parentheses are the values of the character states.

Pelvic fin of blind side	Relation between pelvic fin of ocular side and anal fin	Genera and species
present (0)	separated (1)	Pleuronectinae *Pleuronichthys* except *P. decurrens*
		Pleuronectinae *Pleuronichthys decurrens*
		Pleuronectinae *Microstomus*, *Embassichthys*, *Clidoderma*
		Pleuronectinae *Psettichthys*
		Pleuronectinae *Platichthys*, *Kareius* Poecilopsettinae all genera examined
		Pleuronectinae all genera examined except *Psettichthys*, *Platichthys*, *Pleuronichthys*, *Kareius*, *Microstomus*, *Embassichthys*, *Clidoderma* and *Paralichthodes*
		Pleuronectinae *Paralichthodes*
	united (0)	Samarinae *Plagiopsetta*, *Samariscus*
		Samarinae *Samaris*
	separated (1)	Rhombosoleinae *Azygopus*
	united (0)	Rhombosoleinae *Taratretis*
		Rhombosoleinae *Pelotretis*
		Rhombosoleinae *Ammotretis*
		Rhombosoleinae *Peltorhamphus*
absent (1)		Rhombosoleinae *Rhombosolea*

blind side, *Reinhardtius hippoglossoides* (5-7), the fishes of the genus *Microstomus* (5-6), *Pelotretis flavilatus* (5-6), *Azygopus pinnifasciatus pinnifasciatus* (5-6), *Ammotretis rostratus* (3-6), A. *elongatus* (3-4), *Taratretis derwentensis* (5-6). Therefore, this character was omitted from the analyses. The last character, the relation between the pelvic fin of the ocular side and the anal fin, is accepted as a unit character with two states. The character state is coded as 0 for the OTU's having the pelvic fin of the ocular side united with the anal fin, and as 1 for the OTU's having these two fins separated from each other.

Twelve selected unit characters and coded character states are summarized in Table 10.

8. PECTORAL GIRDLE

DESCRIPTION The pectoral girdle is usually composed of eight paired elements, supratemporal, posttemporal, supracleithrum, scapula, coracoid, actinosts, cleithrum and postcleithrum.

The supratemporals (sut), which are usually tubular, are located on the posterolateral portion of the cranium and form a part of the sensory canal of the head. There are from one to three bones on each side in the family (Figs. 33 and 34).

On the ocular side, in the pleuronectine *Pleuronectes limanda*, *P. proboscideus*, *Platichthys flesus flesus*, *P. stellatus* and *Kareius bicoloratus* and the rhombosoleine *Pelotretis flavilatus* and *Ammotretis rostratus*, the supratemporal is fused with the cranium. Of these fishes, in the latter two species, it is fused with the parietal (Figs. 9C, D and 14A, B), whereas in the other fishes mentioned above it is fused with the pterotic (Figs. 7D and 12A). In the other pleuronectids, the supratemporal(s) is usually never fused with the cranium. But, in a specimen of the pleuronectine *Pleuronectes limanda* and *P. proboscideus* and a rhombosoleine *Pelotretis flavilatus*, it is not fused with the cranium, and in a specimen of a pleuronectine *Pleuronectes ferrugineus* it is fused with the pterotic.

On the blind side, in the pleuronectine *Pleuronectes ferrugineus*, *P. proboscideus*, *Platichthys flesus flesus*, *P. stellatus* and *Kareius bicoloratus*, the supratemporal is fused with the pterotic (Fig. 7D), while in the other species the bone(s) merely lies on the posterolateral portion of the cranium. However, in a specimen of *Pleuronectes ferrugineus* it was not fused with the cranium, and in a specimen of *Pleuronectes limanda* it was fused with the pterotic.

The posttemporal (pot) is located on the uppermost part of the girdle and attached to the epiotic and the exoccipital. It is perforated by the canal connecting with the sensory canal system of the head.

The supracleithrum (scl) is attached dorsally to the inner surface of the posttemporal and ventrally to the outer lateral surface of the cleithrum.

The scapula (sc) is attached anteriorly to the inner surface of the middle part of the cleithrum and connected ventrally with the coracoid by a cartilage. The scapula usually bears the actinosts together with the coracoid dorsally.

In the fishes of the subfamily Samarinae, the scapula is entirely absent on the blind side, whereas it is present on both sides in the other pleuronectids.

The scapular foramen (sf) is surrounded by the scapula or by both the scapula and the cleithrum.

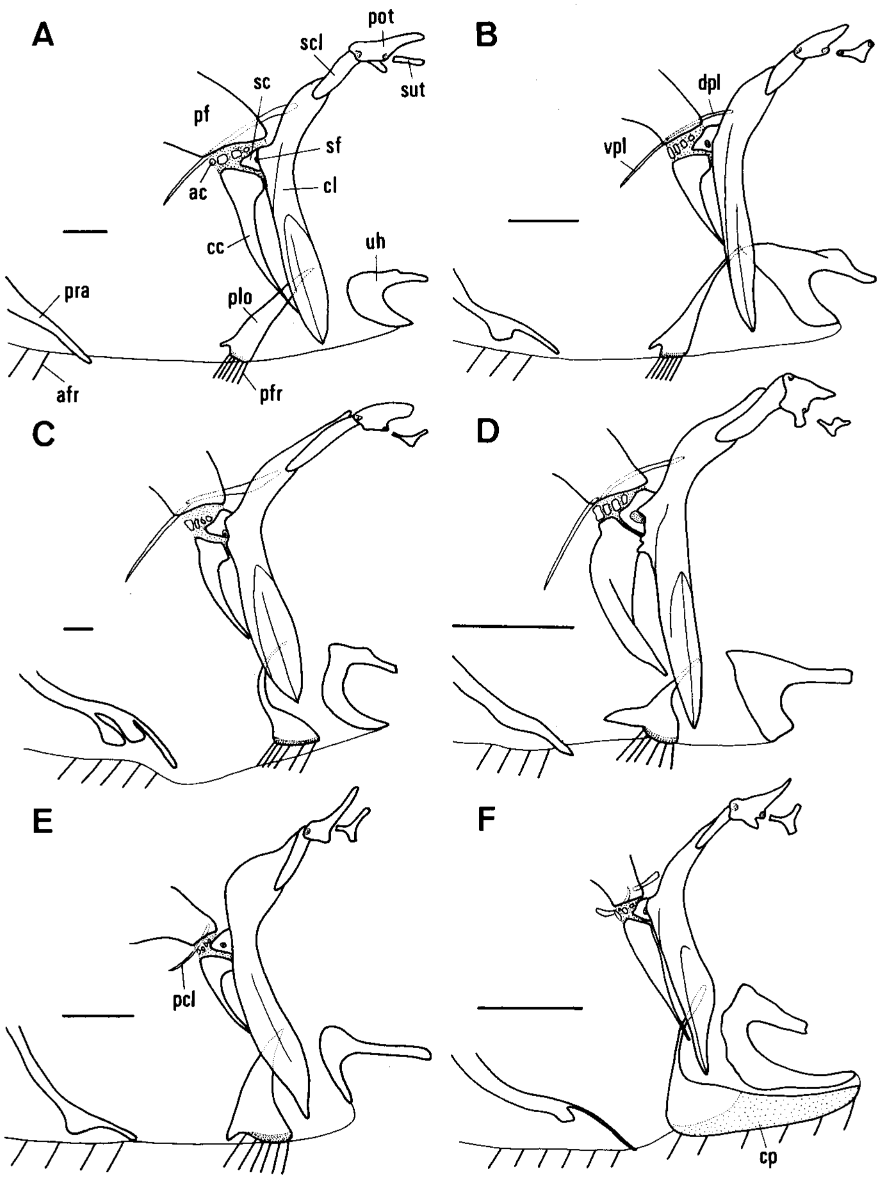

Fig. 33. Lateral aspect of pectoral girdles with their associated bones on ocular side in six righteye flounders. A, *Hippoglossus stenolepis*; B, *Tanakius kitaharai*; C, *Clidoderma asperrimum*; D, *Paralichthodes algoensis*; E, *Poecilopsetta plinthus*; F, *Taratretis derwentensis*. ac, actinost; afr, anal fin ray; cc, coracoid; cl, cleithrum; cp, cartilagenous part of pelvis; dpl, dorsal postcleithrum; pcl, postcleithrum; pf, pectoral fin; pfr, pelvic fin ray; plo, pelvis of ocular side; pot, posttemporal; pra, first proximal radial of anal fin ray; sc, scapula; scl, supracleithrum; sf, scapular foramen; sut, supratemporal; uh, urohyal; vpl, ventral postcleithrum. Scales indicate 5 mm.

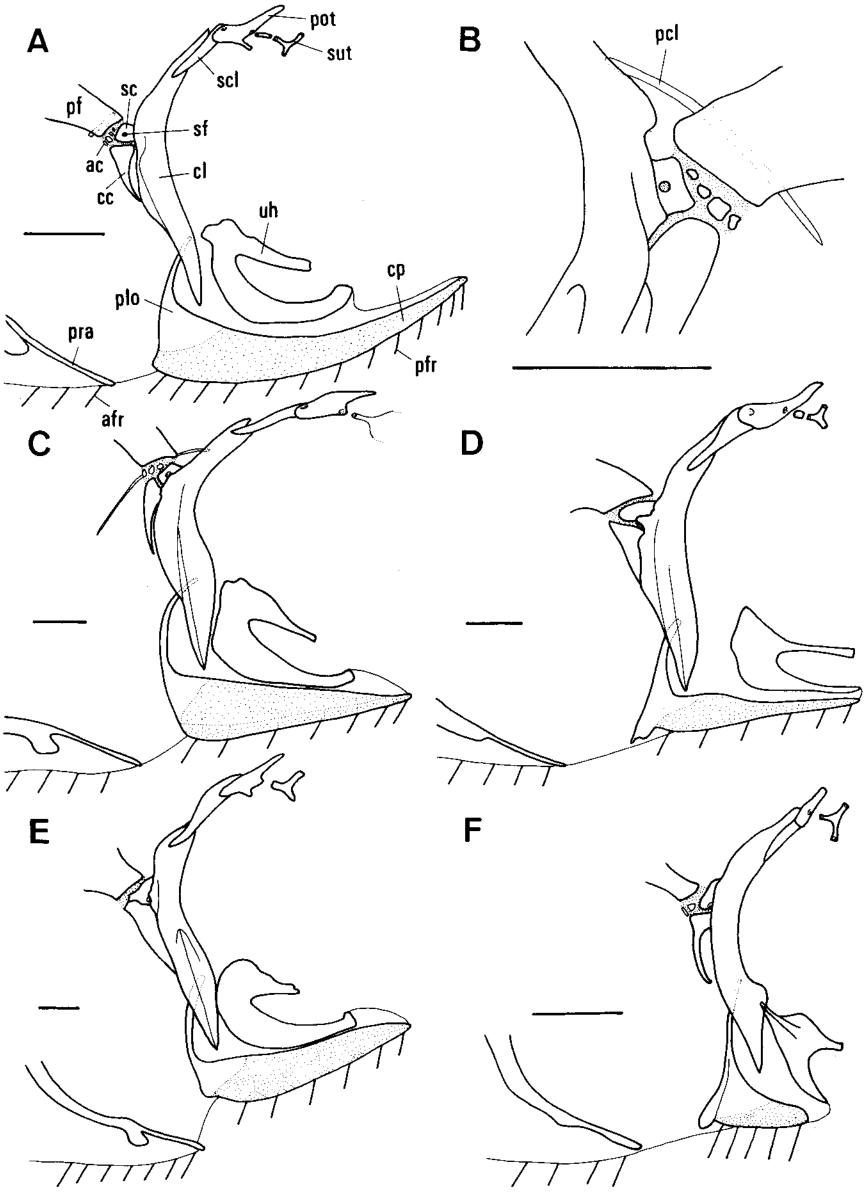

Fig. 34. Lateral aspect of pectoral girdles with their associated bones on ocular side in five righteye flounders. A (ocular side) and B (blind side), *Ammotretis elongatus* ; C, *A. rostratus* ; D, *Rhombosolea leporina* ; E, *Peltorhamphus novaezeelandiae* ; F, *Samariscus latus*. Abbreviations as in Fig. 33. Scales indicate 5 mm.

The coracoid (cc), which usually bears the actinosts together with the scapula, tapers ventrally and at its ventral tip is connected with the inner lateral surface of the lower part of the cleithrum by a ligament. Anteriorly, the coracoid is attached to the cleithrum by a ligament or firmly connected with the cleithrum.

In the fishes of the Samarinae, the coracoid is absent on the blind side, while it is present on both sides in the other pleuronectids.

The actinosts (ac), if present, are small bones bearing the pectoral fin rays together with the scapula. A series of actinosts lie at the cartilagenous part surrounded by the pectoral fin rays, the scapula and the coracoid. They vary in number with the species, the individual and the side of the body (Fig. 35). There are from three to six actinosts with a mode of four on each side in most species (Figs. 33 and 34 A-C, F), though the actinosts are entirely absent on both sides in the fishes of the rhombosoleine genera *Rhombosolea* and *Peltorhamphus* (Fig. 34D, E) and on the blind side in the fishes of the subfamily Samarinae.

The cleithrum (cl) forms the major portion of the the pectoral girdle. It is attached to the inner lateral surface of the supracleithrum at its upper end, and posteromedially to the scapula and the coracoid. Both cleithra are firmly united with each other ventrally and inserted by the dorsal tips of a pair of pelves which are united with each other along their inner margins.

In the rhombosoleine *Peltorhamphus novaezeelandiae* and *P. latus*, the cleithra are attached anteriorly to the posterior aspect of the sciatic part of the urohyal (Fig. 34E). In a pleuronectine *Tanakius kitaharai* and the members of the pleuronectine genera *Glyptocephalus* and *Errex*, the cleithra are slightly inserted by its tip of the cardiac apophysis of the urohyal (Fig. 33B). In the members of the subfamily Samarinae, they are seized by its bifurcated tip of the cardiac apophysis of the urohyal (Fig. 34F). In the other members of the Pleuronectidae examined, the cleithra are separated from the urohyal, but connected with it by a membrane (Figs. 33A, C-F and 34A, C, D). However, in the pleuronectine *Microstomus kitt* and *M.*

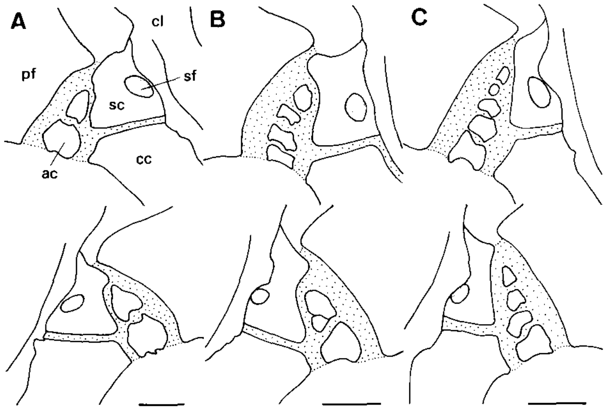

Fig. 35. Variation in number of actinosts on both sides in *Pleuronectes proboscideus*. A, HUMZ 82770 ; B, HUMZ 82773 ; C, HUMZ 82763. Top, ocular side ; bottom, blind side. Abbreviations as in Fig. 33. Scales indicate 2 mm.

pacificus, they are separated from or attached to the urohyal, or slightly inserted by the urohyal.

The postcleithrum (pcl) is usually a slender sword-like bone, and may be present or absent and, if present, the number varies with the Pleuronectidae. In the members of the pleuronectine genera *Atheresthes*, *Reinhardtius*, *Hippoglossus*, *Eopsetta*, *Verasper*, *Dexistes*, *Hypsopsetta*, *Glyptocephalus*, *Errex*, *Microstomus*, *Tanakius*, *Embassichthys*, *Clidoderma* and *Paralichthodes*, a pleuronectine *Pleuronichthys decurrens*, and a rhombosoleine *Taratretis derwentensis*, there are usually two postcleithra, a dorsal postcleithrum (dpl) and a ventral postcleithrum (vpl), which are connected with each other to form a long bar posteroventrally along the abdominal wall (Fig. 33A-D, F). But, a specimen of *Atheresthes* has a single long postcleithrum. The dorsal postcleithrum is attached dorsally to the inner surface of the cleithrum and ventrally to the ventral postcleithrum which is free ventrally in the abdominal wall. Of these fishes, in *Taratretis derwentensis* the postcleithra are smaller than those of any other fish mentioned above (Fig. 33 F). The other members of the subfamily Pleuronectinae and the members of all the poecilopsettine genera and the rhombosoleine genera *Pelotretis*, *Azygopus* and *Ammotretis* (on the blind side in *Ammotretis elongatus*) have usually a slender sword-like postcleithrum (Figs. 33E and 34 B, C). Of these fishes, in the poecilopsettine species and the rhombosoleine *Pelotretis flavilatus* and *Ammotretis lituratus*, the postcleithrum is a short feeble needle-like bone lying in the abdominal wall under the actinosts, the scapula and the coracoid (Fig. 33E), and it is short but rather stout on the ocular side in *Ammotretis elongatus* (Fig. 34A). In the other species mentioned above (on the blind side in *Ammotretis elongatus*), the postcleithrum is a single long bone which is attached dorsally to the cleithrum and ventrally inserts into the abdominal wall (Fig. 34 B, C). But, in a specimen of a pleuronectine *Hippoglossoides elassodon*, there are two postcleithra. In the members of the rhombosoleine genera *Rhombosolea* and *Peltorhamphus* and the subfamily Samarinae, the postcleithrum is entirely absent on both sides (Fig. 34D-F).

UNIT CHARACTER The pectoral girdles of flatfishes have been studied by several workers (Norman, 1934; Ochiai, 1966 etc.). In most cases, presence or absence of each element has been employed in the phylogenetic studies of this group.

In the present study on the pectoral girdles of the Pleuronectidae, the interspecific variation was found in the following characters: 1) the relation between the supratemporal and the cranium, 2) presence or absence of the scapula on the blind side, 3) presence or absence of the coracoid on the blind side, 4) the developmental degree of the actinosts on each side, 5) the relation between the cleithrum and the urohyal, 6) the developmental degree of the postcleithrum.

The fifth character is treated under the urohyal.

The first character, the relation between the supratemporal and the cranium, is not used as a unit character, because there is an intraspecific variation in some species as already described. The second character, presence or absence of the scapula on the blind side, is treated as a unit character with two states, its absence in the Samarinae and its presence in the other pleuronectids. Each state is coded as O for its presence and as 1 for its absence. The third character, presence or

Table 11. Comparison and coding of characters of pectoral girdle in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

Scapula on blind side	Coracoid on blind side	Actinosts		Postcleithrum	Subfamilies and genera
		ocular	blind		
present (0)	present (0)	present (0)	present (0)	present (0)	Pleuronectinae Poecilopsettinae Rhombosoleinae *Pelotretis*, *Azygopus*, *Ammotretis*, *Taratretis*
		absent (1)	absent (1)	absent (1)	Rhombosoleinae *Rhombosolea*, *Peltorhamphus*
absent (1)	absent (1)	present (0)			Samarinae

absence of the coracoid on the blind side, is adopted as a unit character with two states and coded as in the preceding character. Concerning the fourth character, the developmental degree of the actinosts on each side, if the actinosts are present, the number varies with the individual as previously mentioned. However, their presence or absence can be adopted as a unit character since no variations are found on presence or absence of the bones on each side. The character state is coded as 0 for their presence and as 1 for their absence on each side, respectively. In the last character, the developmental degree of the postcleithrum, the number and size of the postcleithra are not treated as unit characters, because there is an intraspecific variation in some species in number, and because it is very difficult to distinguish obvious character states in regard to size. But, presence or absence of the postcleithrum can be adopted as a unit character, since there is no intraspecific variation on both sides as far as its presence or absence is concerned. Thus, the value of each character state is 0 for its presence and 1 for its absence.

Five selected unit characters and coded character states are summarized in Table 11.

9. PELVIC GIRDLE

DESCRIPTION The pelvic girdle supporting the pelvic fin is composed of a pair of pelves.

The pelvis is a thin plate-like bone and equipped with a postpelvic process (pp) at the posteroventral corner in almost all the pleuronectids (Fig. 36). The pelves are firmly united with each other along their inner margins, and the dorsal tips of these bones insert between both cleithra which are firmly united with each other at their lower parts (Figs. 33 and 34).

In the fishes of the subfamily Rhombosoleinae, the pelves are very asymmetrical because of the elongation of the cartilagenous part of the bone of the ocular side (Fig. 36 B), whereas they are nearly symmetrical in the other pleuronectid fishes examined (Fig. 36 A).

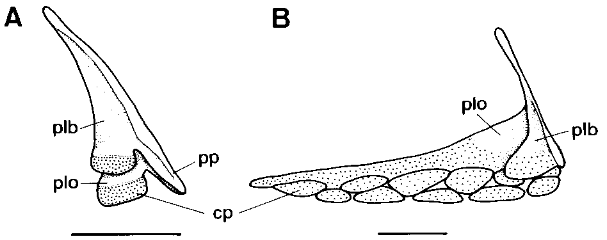

Fig. 36. Lateral aspect of pelves from blind side in two righteye flounders. A, *Pleuronectes herzensteini* ; B, *Pelotretis flavilatus*. cp, cartilagenous part of pelvis ; plb, pelvis of blind side ; plo, pelvis of ocular side ; pp, postpelvic process. Scales indicate 5 mm.

In regard to the position of the anteroventral tip of the pelvis of the ocular side in relation to the cleithrum and the urohyal, the pleuronectid fishes may be classified into four groups. In the fishes of the subfamilies Pleuroenctinae and Poecilopsettinae except a pleuronectine *Clidoderma asperrimum*, the tip of the pelvis is behind the cleithrum (Fig. 33 A, B, D, E). In the fishes of the pleuronectine genus *Clidoderma* and the subfamily Samarinae, the tip extends slightly in advance of the cleithrum (Figs. 33 C and 34 F). In the fishes of the rhombosoleine genera *Pelotretis*, *Azygopus*, *Taratretis* and *Rhombosolea*, the cartilagenous part of the pelvis extends forward and forms the tip of the isthmus together with its tip of the sciatic part of the urohyal (Figs. 33 F and 34 D). In the fishes of the rhombosoleine genera *Ammotretis* and *Peltorhamphus*, the cartilagenous part of the pelvis elongates greatly, extends forward beyond its tip of the sciatic part of the urohyal, and forms its tip of the isthmus by itself (Fig. 34A, C, E).

UNIT CHARACTER The pelvic girdles of the pleuronectiform fishes have been investigated by Norman (1934), Amaoka (1969, 1972) and others. In the family Pleuronectidae, according to Norman (1934), presence or absence of the anterior extension of the pelvic fin (namely pelvis) of the ocular side was regarded as a character for distinguishing the subfamilies.

The present study reveals that the pleuronectid pelvic girdles show interspecific variations in the degree of the bilateral symmetry and the position of the anteroventral tip of the pelvis of the ocular side in relation to the cleithrum and the urohyal.

The former character has apparently two states, asymmetry found in the Rhombosoleinae and subsymmetry in the other pleuronectid fishes. Since this character is a unit character with two states, the character state is coded as O for the OTU's with the subsymmetrical pelves and as 1 for the OTU's with the asymmetrical ones. The latter character has four distinctive character states without any intraspecific variation or intermediate state. Those states are as follows: the anteroventral tip of the pelvis of the ocular side behind the cleithrum, slightly in advance of the cleithrum, beyond the cleithrum and forming the tip of the isthmus together with the urohyal, and beyond the cleithrum and forming the tip of the isthmus by itself. Since those four states can be arranged in order in a single logical

Table 12. Comparison and coding of characters of pelvic girdle in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

Bilateral symmetry	Position of anteroventral tip of pelvis	Subfamilies and genera
subsymmetrical (0)	behind cleithrum (0)	Pleuronectinae all genera examined except *Clidoderma* Poecilopsettinae
	slightly in advance of cleithrum (1)	Pleuronectinae *Clidoderma* Samarinae
asymmetrical (1)	forming isthmus together with urohyal (2)	Rhombosoleinae *Pelotretis*, *Azygopus*, *Taratretis*, *Rhombosolea*
	forming isthmus by itself (3)	Rhombosoleinae *Ammotretis*, *Peltorhamphus*

sequence, this character is regarded as a quantitative multistate character with four character states. Thus, each character state is coded as 0, 1, 2, 3, in order (Table 12).

Two selected unit characters and coded character states are summarized in Table 12.

10. UROHYAL

DESCRIPTION The urohyal is a single flattened bone situated between the hyoid arch and the isthmus. The urohyal is fishhook-like in shape and comprises three parts, main part, sciatic part and cardiac apophysis. The principal part of the urohyal is a thin plate with a pair of ridges along the inner margin.

The main part (mp) is surrounded by a thin membrane, connected anteriorly to the medial parts of the hypohyals by a pair of ligaments and attached dorsally to the ventral aspect of a series of basibranchials by a membrane.

The sciatic part (sp) is connected posteriorly with the cleithrum by a membrane, and its tip extends to the isthmus. In the fishes of the subfamily Rhombosoleinae, this part is attached ventrally to the anteroventral cartilagenous portion of the pelvis of the ocular side by a connective tissue (Figs. 33 F and 34 A, C-E). The lateral surface of this part serves as the point of insertion for the sternohyoid muscles.

The cardiac apophysis (ca) is a projection at the upper posterior part of the urohyal. This projection varies in shape of its tip. In the pleuronectine *Pleuronectes vetulus*, *P. asper*, *P. sakhalinensis*, *P. punctatissimus*, *P. proboscideus*, *Glyptocephalus cynoglossus*, *G. stelleri*, *Errex zachirus*, *Microstomus kitt*, *M. achne* and *M. pacificus*, all the poecilopsettines examined, and the fishes of the rhombosoleine genera *Pelotretis*, *Azygopus*, *Rhombosolea* and *Peltorhamphus*, the cardiac apophysis is thin plate-like (Fig. 37 E, I, L, O). In the pleuronectine *Verasper variegatus*, *V. moseri*, *Pleuronectes bilineatus*, *P. mochigarei*, *P. herzensteini*, *P. schrenki*, *P. quadrituberculatus*, *P. platessa*, *P. obscurus*, *Platichthys flesus flesus*, *P.*

stellatus and *Kareius bicoloratus* and all the samarine members examined, the apophysis is bifurcate at the posterior portion (Fig. 37 C, F, G, P). In the other members of the Pleuronectidae examined, its posterior portion is very slightly or slightly bifurcate (Fig. 37 A, B, D, H, J, K, M, N).

In the rhombosoleine *Peltorhamphus novaezeelandiae* and *P. latus*, the urohyal

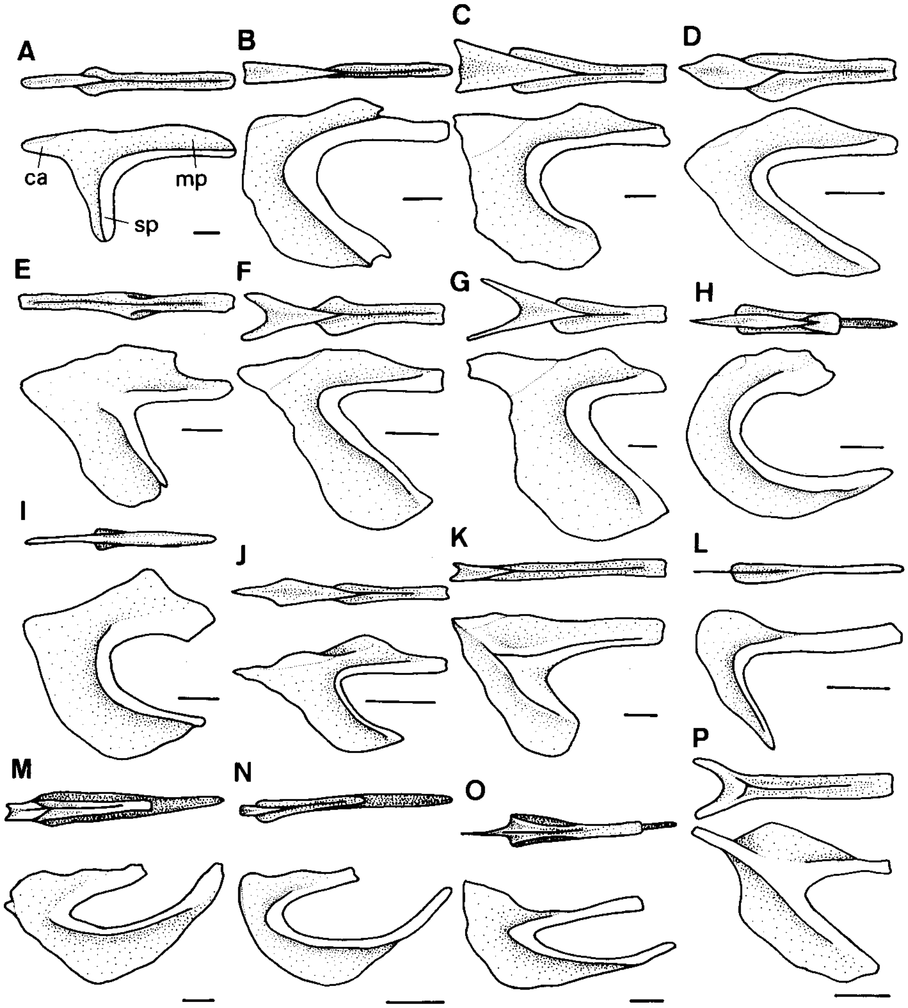

Fig. 37. Dorsal (above) and lateral (below) aspects of urohyals in 16 righteye flounders. A, *Reinhardtius hippoglossoides*; B, *Hippoglossus stenolepis*; C, *Verasper variegatus*; D, *Dexistes rikuzenius*; E, *Pleuronectes vetulus*; F, *P. herzensteini*; G, *P. quadrituberculatus*; H, *Pleuronichthys cornutus*; I, *Microstomus achne*; J, *Tanakius kitaharai*; K, *Paralichthodes algoensis*; L, *Poecilopsetta plinthus*; M, *Ammotretis rostratus*; N, *Taratretis derwentensis*; O, *Rhombosolea leporina*; P, *Plagiopsetta glossa*. ca, cardiac apophysis; mp, main part; sp, sciatic part. Scales indicate 2 mm.

is attached to the anterior parts of the cleithra at the posterior margin of the sciatic part (Fig. 34 E). In a pleuronectine *Tanakius kitaharai* and the members of the pleuronectine genera *Glyptocephalus* and *Errex*, the tip of the cardiac apophysis slightly inserts between both cleithra (Fig. 33 B). In the members of the subfamily Samarinae, the urohyal seizes the cleithra by the bifurcated tip of the cardiac apophysis (Fig. 34 F). In the other members of the family examined, it is usually separated from the cleithra, though the distance between those two bones varies with the species (Figs. 33 A, C-F and 34 A, C, D,). In the pleuronectine *Microstomus kitt* and *M. pacificus*, the urohyal is separated from or attached to the cleithra, or slightly inserts between both cleithra.

UNIT CHARACTER The urohyals of flatfishes have been examined by several authors (Norman, 1934; Hubbs, 1945; Chabanaud, 1954; Ochiai, 1966; Amaoka, 1969, 1972; Kim, 1973 etc.). In this part, the following characters have been studied to elucidate their phylogenetic relationships: the general shape, the shape and developmental degree of the cardiac apophysis, and others (see Amaoka, 1969; Kim, 1973).

The pleuronectid urohyal shows interspecific variations in shape of the cardiac apophysis and the relation between the urohyal and the cleithrum.

For the former character, in some species the urohyal has a cardiac apophysis clearly bifurcated at the posterior portion, while it has a simple one in other species. However, at the same time, several intermediate states are found in several species as stated in the description. Owing to the existence of these intermediate states, it is very difficult to determine the character state in each OTU. Thus, this character was not adopted as a unit character. The latter character, the relation between the urohyal and the cleithrum, showed an intraspecific variation in two species of *Microstomus*. Accordingly, this character was excluded from the unit characters.

In conclusion, no unit characters were selected from the urohyal in the present study.

11. VERTEBRAE AND THEIR ACCESSORY BONES

DESCRIPTION In this part, vertebra, pleural rib, epipleural, epicentrum, epimeral and hypomeral are described.

The vertebrae are divided into two types, abdominal and caudal vertebrae. The abdominal vertebrae are defined as the elements anterior to the vertebra to which the first enlarged proximal radial of the anal fin ray is attached. The remaining elements posterior to the abdominal ones are caudal vertebrae.

Each centrum possesses a neural spine with a neural arch at its base in the subfamily Pleuronectinae (Figs. 38A and 39). In the subfamilies Poecilopsettinae, Rhombosoleinae and Samarinae, the first neural arch is not formed, because two elements of the first neural spine are short (Fig. 38B, C). Each abdominal vertebra except several anterior ones possesses a pair of parapophyses (pp) downwardly directed and usually becoming larger posteriorly (Figs. 39-41). In the fishes of the subfamily Pleuronectinae such as *Atheresthes stomias*, *A. evermanni*, *Eopsetta jordani*, *E. grigorjewi*, *Verasper variegatus*, *Microstomus achne*, *M. pacificus* and *Paralichthodes algoensis*, all the poecilopsettine and rhombosoleine fishes examined,

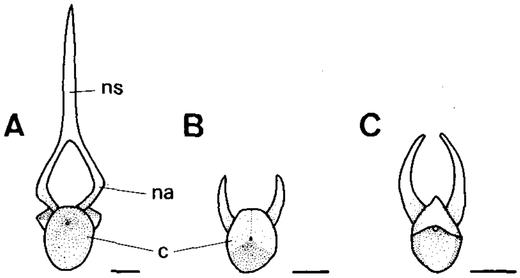

Fig. 38. Anterior aspect of first vertebrae in three righteye flounders. A, *Pleuronectes herzensteini* ; B, *Poecilopsetta plinthus* ; C, *Taratretis derwentensis*. c, centrum ; na, neural arch ; ns, neural spine. Scales indicate 1 mm.

and the fishes of the samarine genera *Plagiopsetta* and *Samariscus*, the posteriormost or several posterior parapophyses usually form haemapophyses (hp) by fusion of two elements (Figs. 40 and 41). Of these fishes, in the fishes of the subfamily Rhomobosoleinae, the posteriormost haemapophysis on the last abdominal vertebra generally extends downward and is attached to the anterior margin of the first proximal radial of the anal fin ray (Fig. 40). But, in a specimen of *Verasper variegatus*, there is no haemapophysis on the abdominal vertebrae. In a specimen of *Pleuronectes yokohamae*, there is a haemapophysis on the last abdominal vertebra.

The caudal vertebra possesses a haemal spine forming a haemal arch at its base (Figs. 39-41).

In some pleuronectid fishes, there are anterior and/or posterior transverse apophyses (ta) at the lateral surface of the centrum. In the fishes of the subfamily

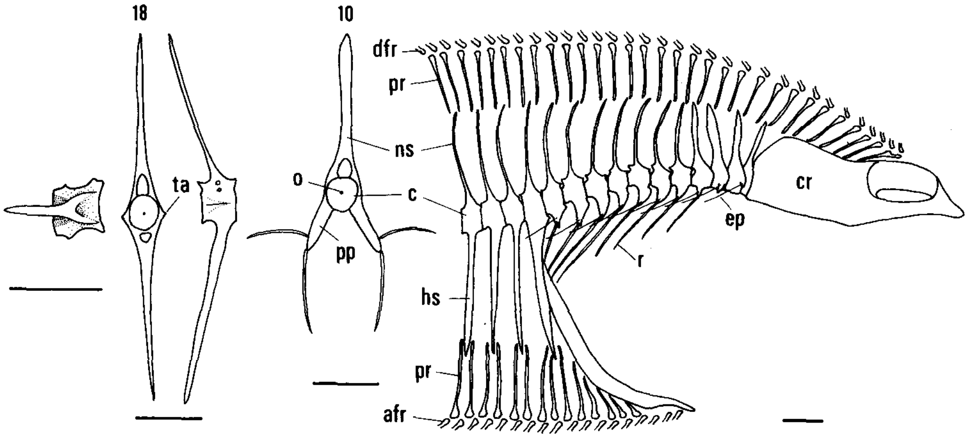

Fig. 39. Lateral, frontal and dorsal aspects of abdominal and anterior caudal vertebrae and their accessory bones in *Pleuronectes herzensteini*. afr, anal fin ray ; c, centrum ; cr, cranium ; dfr, dorsal fin ray ; ep, epipleural ; hs, haemal spine ; ns, neural spine ; o, opening for notochord ; pp, parapophysis ; pr, proximal radial ; r, pleural rib ; ta, transverse apophysis. Scales indicate 5 mm.

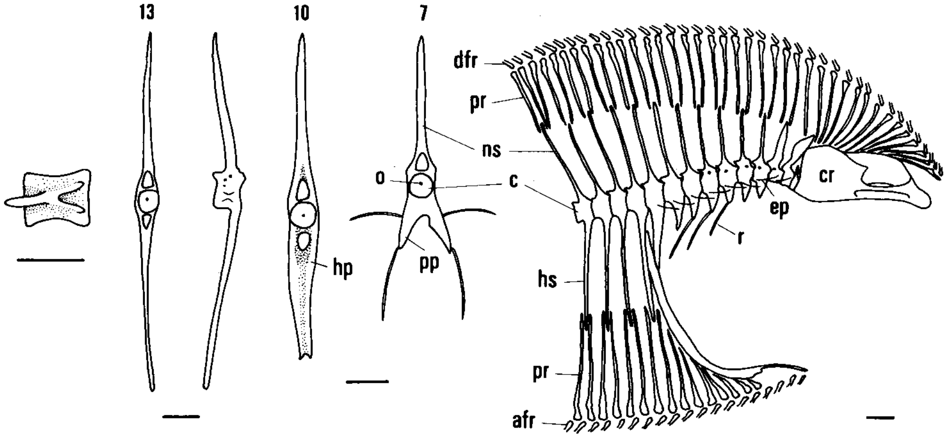

Fig. 40. Lateral, frontal and dorsal aspects of abdominal and anterior caudal vertebrae and their accessory bones in *Taratretis derwentensis*. hp, haemapophysis. Other abbreviations as in Fig. 39. Scales indicate 2 mm.

Pleuronectinae, they are present or absent, and if present, they range from moderate to very small in size (Fig. 39). In the fishes of the subfamilies Poecilopsettinae and Rhombosoleinae, they are absent (Fig. 40). In the fishes of the subfamily Samarinae, they are usually large in size (Fig. 41).

The numbers of the abdominal and caudal vertebrae in the pleuronectid fishes examined are shown in Tables 13-16. The numbers of the abdominal and caudal vertebrae range from 9 to 19 and from 20 to 52 in the subfamily Pleuronectinae (Table 13), from 9 to 11 and from 26 to 33 in the subfamily Poecilopsettinae (Table 14), from 10 to 12 and from 19 to 35 in the subfamily Rhombosoleinae (Table 15), and from 9 to 11 and from 26 to 37 in the subfamily Samarinae (Table 16).

The pleural rib (r) is present in the fishes of the subfamilies Pleuronectinae, Poecilopsettinae and Rhombosoleinae (Figs. 39 and 40), but is absent in the fishes of the subfamily Samarinae (Fig. 41). The pleural rib which is thin rod-like in shape is usually attached near the tip of the parapophysis or the haemapophysis and runs backward and downward between the hypaxial muscle and the peritoneum.

The epipleural (ep) is found in the fishes of the Pleuronectinae, Poecilopsettinae and Rhombosoleinae (Figs. 39 and 40), but is absent in the fishes of the Samarinae (Fig. 41). The epipleural is more slender than the pleural rib and extends horizontally into the horizontal myoseptum between the epaxial and hypaxial muscles. In most pleuronectids examined here, the epipleural is usually found from first or second to last abdominal vertebrae, but in some species it is present on the anterior one or two caudal vertebrae. In the abdominal region, as in the pleural rib, if the parapophysis is absent in the anterior part, the epipleural is directly attached to the lateral aspect of the centrum. If the parapophysis or the haemapophysis is present, the epipleural is attached to the middle part of the lateral surface of this process. In the caudal region, the epipleural, if present, is attached to the lateral surface of the centrum or the anterior transverse apophysis.

The epicentrum (ec), a single thin bone like the epipleural, is present in the

Table 13. Frequency distribution of abdominal and

Species	Abdominal																
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Atheresthes stomias				19	1												
A. evermanni				26													
Reinhardtius hippoglossoides									1	18	4						
Hippoglossus stenolepis								14	3								
Eopsetta exilis				15	1												
E. jordani			4														
E. grigorjewi			20	1													
Verasper variegatus						14											
V. moseri						11											
Psettichthys melanosticus			10														
Hippoglossoides platessoides platessoides					5												
H. p. limandoides					6												
H. elassodon				3	17	1											
H. dubius					26												
H. robustus				2	19												
H. pinetorum		2	32	2													
Acanthopsetta nadeshnyi		1	27														
Dexistes rikuzenius			28	1													
Pleuronectes isolepis	1	12															
P. vetulus			13	1													
P. bilineatus			18	1													
P. mochigarei		1	19														
P. limanda		3															
P. asper	1		26	1													
P. korigarei			1														
P. sakhalinensis	1	19	4														
P. ferrugineus			5														
P. punctatissimus		19	1														5
P. proboscideus		4	17														
P. herzensteini			30														
P. yokohamae		1	19														
P. schrenki			23	2													
P. americanus			2														
P. quadrituberculatus					15												
P. platessa					3												
P. obscurus				19	1												
P. glacialis			2	2													
P. pinnifasciatus				22	3											1	1
P. putnami				16	2											8	4
Platichthys flesus flesus				3											1	2	
P. stellatus			23	1												10	14
Hypsopsetta guttulata				10	1									1	7	3	
Pleuronichthys decurrens					2	12											4
P. cornutus				17	13											19	11
P. verticalis					9										7	2	
P. coenosus					9										1	3	5
P. ritteri				8	1								1	1	6	1	
P. ocellatus				9										2	5	2	
Glyptocephalus cynoglossus				2													
G. stelleri				30	1												
Errex zachirus					19	1											
Kareius bicoloratus			20	1													1
Microstomus kitt			1	11													
M. achne				5	29	1											
M. pacificus				21	2												
Tanakius kitaharai			27														
Embassichthys bathybius					6	11											
Clidoderma asperrimum					1	14											
Paralichthodes algoensis		7										1	6				

caudal vertebral counts in subfamily Pleuronectinae.

Caudal																											Numbers of specimens
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
										1	14	5															20
											1	5	16	4													26
																	1	9	10	3							23
								5	8	4																	17
						4	8	2	2																		16
					1	3																					4
					3	16	2																				21
1	12	1																									14
	11																										11
		2	8																								10
							2	2	1																		5
							2	4																			6
						6	12	3																			21
					2	21	3																				26
					2	17	2																				21
		10	21	5																							36
			3	23	2																						28
			6	19	4																						29
					4	8	1																				13
							9	5																			14
			2	15	2																						19
				18	2																						20
				3																							3
			11	17																							28
					1																						1
			1		13	7	3																				24
				2	3																						5
13	2																										20
	11	9	1																								21
1	17	12																									30
	8	11	1																								20
8	16	1																									25
	2																										2
		3	10	2																							15
				3																							3
8	12																										20
	2	2																									4
14	9																										25
4	2																										18
																											3
																											24
																											11
9	1																										14
																											30
																											9
																											9
																											9
																											9
																				1	1						2
															9	13	9										31
																							1	1	12	6	20
1	14	5																									21
									7	5																	12
								1	7	19	6	2															35
													1	11	10	1											23
											2	14	9	2													27
																					3	8	3	2	1		17
				2	10	3																					15
																											7

Table 14. Frequency distribution of abdominal and caudal vertebral counts in subfamily Poecilopsettinae.

Species	Abdominal			Caudal								Numbers of specimens
	9	10	11	26	27	28	29	30	31	32	33	
Poecilopsetta beanii		5								5		5
P. colorata		4	1			1	4					5
P. hawaiiensis		9					8	1				9
P. praelonga		2						1		1		2
P. plinthus	1	30					1	24	6			31
P. natalensis		1							1			1
P. megalepis		1						1				1
P. albomarginata		5					1	1	3			5
P. albomaculata		3						3				3
P. zanzibarensis		9								1	8	9
Nematops microstoma		1					1					1
N. grandisquama		4		1	3							4
N. macrochirus		16				4	10	2				16
N. chui		1				1						1
Marleyella bicolorata		5		1	4							5
M. maldivensis		2			2							2

fishes of the subfamily Samarinae (Fig. 41), but is absent in the other pleuronectids (Figs. 39 and 40). The epicentrum lying between the epaxial and hypaxial muscles occurs from second to last abdominal vertebrae in *Samaris cristatus*, *Plagiopsetta glossa* and *Samariscus latus*, and in *Samariscus xenicus* it is also present on the first caudal vertebra. The epicentrum is usually attached to the anterior transverse apophysis of the vertebra. In the anterior abdominal vertebrae lacking transverse apophyses, it is directly attached to the lateral surface of the centrum.

The epimeral (em) is present in the fishes of the samarine genera *Samaris* and *Samariscus* (Fig. 41), but is absent in the remaining pleuronectids (Figs. 39 and 40). The epimeral, which extends upward and backward along the dorsal myoseptum, is found from second abdominal vertebra to posterior caudal vertebra. Each anterior epimeral is composed of a single needle-like bone, whereas the remaining ones comprise several thin needle-like bones respectively. In the caudal vertebrae, these bones are connected with one another by a ligament. The epimeral is attached anteriorly to the anterolateral surface of the neural arch and posteriorly to the anterior transverse apophysis by a ligament.

The hypomeral (hm) is present in the fishes of the subfamily Samarinae (Fig. 41), and is absent in the other pleuronectid fishes examined (Figs. 39 and 40). The hypomeral runs downward and backward along the ventral myoseptum. In *Plagiopsetta glossa*, the hypomeral occurring from fourth abdominal vertebra to third caudal vertebra consists of a single element. In *Samaris cristatus*, *Samariscus latus* and *S. xenicus*, the shape and structure are very similar to those of the epimeral.

Table 15. Frequency distribution of abdominal and caudal vertebral counts in subfamily Rhombosoleinae.

Species	Abdominal			Caudal																	Numbers of specimens
	10	11	12	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
Oncopterus darwinii		4		4																	4
Psammodiscus ocellatus	4	1					4	1													5
Pelotretis flavilatus	15	2													1	8	7	1			17
Azygopus pinnifasciatus pinnifasciatus	6	1																	1	6	7
Ammotretis rostratus	9							6	3												9
A. brevipinnis	1						1														1
A. lituratus		3	1							3	1										4
A. macrolepis	1								1												1
A. elongatus	8							1	7												8
Taratretis derwentensis	5							4	1												5
Colistium nudipinnis	1						1														1
C. guntheri	2											2									2
Rhombosolea retiaria	1					1															1
R. plebeia		1			1																1
R. tapirina		5					3	2													5
R. leporina		5	1		5	1															6
Peltorhamphus novaezeelandiae	5												5								5
P. latus	6										1	4	1								6
P. tenuis	1															1					1

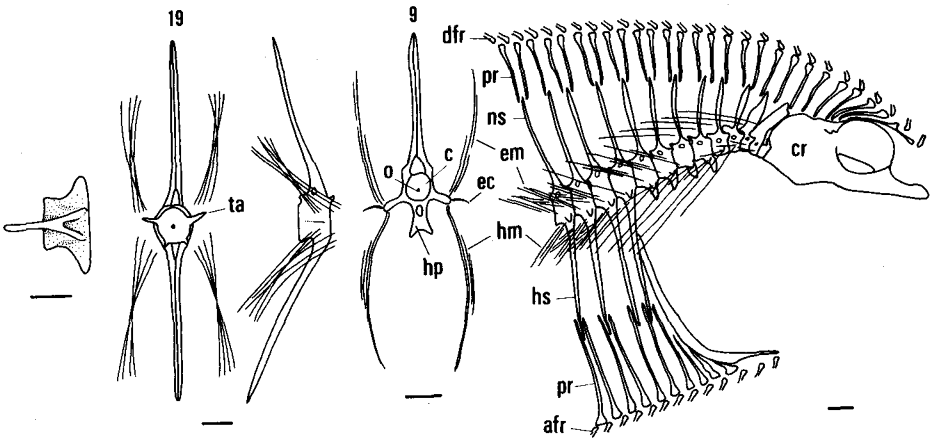

Fig. 41. Lateral, frontal and dorsal aspects of abdominal and anterior caudal vertebrae and their accessory bones in *Samariscus latus*. ec, epicentrum ; em, epimeral ; hm, hypomeral. Other abbreviations as in Figs. 39 and 40. Scales indicate 2 mm.

Table 16. Frequency distribution of abdominal and caudal vertebral counts in subfamily Samarinae.

Species	Abdominal			Caudal												Numbers of specimens
	9	10	11	26	27	28	29	30	31	32	33	34	35	36	37	
Samaris cristatus			10				4	5	1							10
S. macrolepis		1			1											1
Plagiopsetta glossa		32			18	14										32
Samariscus corallinus	3													2	1	3
S. macrognathus	1								1							1
S. latus	21						12	9								21
S. longimanus	8						4	4								8
S. sunieri	8								7	1						8
S. xenicus	9			7	2											9
S. inornatus	1					1										1
S. luzonensis	1					1										1
S. maculatus	1							1								1
S. japonicus		1					1									1
S. huysmani		1					1									1
S. fasciatus		1				1										1
S. triocellatus	5								3	2						5

UNIT CHARACTER Several investigations have been carried out on the vertebrae and their associated bones of the pleuronectiforms (Norman, 1934; Hotta, 1961; Ochiai, 1966; Amaoka, 1969, 1972; Kim, 1973 etc.). In the previous phylogenetic studies, the following characters have been used: presence or absence of the first neural spine, presence or absence of the transverse apophysis, the numbers of the abdominal and caudal vertebrae, presence or absence of the pleural rib and the epipleural, presence or absence of the epicentrum, the epimeral, the hypomeral and others (see Amaoka, 1969).

In the present study, it was found that the vertebrae and their accessory bones of the Pleuronectidae show interspecific variations in the following characters: 1) presence or absence of the first neural arch, 2) presence or absence of the haemapophysis, 3) presence or absence of the transverse apophysis, 4) the numbers of the abdominal and caudal vertebrae, 5) presence or absence of the pleural rib, 6) presence or absence of the epipleural, 7) presence or absence of the epicentrum, 8) presence or absence of the epimeral, 9) presence or absence of the hypomeral.

The first character, presence or absence of the first neural arch, is used as a unit character with two states. In this case, the character state is coded as 0 for its presence and as 1 for its absence. Regarding the second character, presence or absence of the haemapophysis, the present study reveals that the intraspecific variation occurs in this character in some species. Thus, this character cannot be accepted as a unit character. In regard to the third character, presence or absence

Table 17. Comparison and coding of characters of vertebrae and their accesssory bones of 77 righteye flounders. The numerals in the parentheses are the values of the character states.

First neural arch	Pleural rib	Epipleural	Epicentrum	Epimeral	Hypomeral	Subfamilies and genera
present (0)	present (0)	present (0)	absent (1)	absent (1)	absent (1)	Pleuronectinae
absent (1)						Poecilopsettinae Rhombosoleinae
	absent (1)	absent (1)	present (0)		present (0)	Samarinae *Plagiopsetta*
				present (0)		Samarinae *Samaris*, *Samariscus*

of the transverse apophysis, it is very difficult as noted above to recognize several character states for the OTU's. Therefore, this is excluded from the unit characters here. The fourth character, the numbers of the abdominal and caudal vertebrae, are not used as unit characters, because the intraspecific variation is found in almost all the species. The fifth, sixth, seventh, eighth and ninth characters, presence or absence of the pleural rib, the epipleural, the epicentrum, the epimeral and the hypomeral, are discussed at the same time. In these five characters, no intraspecific variation was found in their presence or absence in all the species examined in the present study. All these five characters can properly be regarded as unit characters. The character state is coded as O for their presence and as 1 for their absence in these unit characters.

Five selected unit characters and each coded character state are summarized in Table 17.

12. CAUDAL SKELETON AND FIN

DESCRIPTION The caudal skeleton supporting the caudal fin is composed of the following bones ; second preural centrum, first preural centrum, hypurals, parhypural, epural, last neural spine and last haemal spine. Stegural and ossicle(s) between the fourth and fifth hypurals are present in some species and/or some specimens of each species.

The caudal fin generally comprises branched and unbranched rays.

The second preural centrum (pc 2) is articulated anteriorly to the third preural centrum and posteriorly to the first preural one. This centrum is fused dorsally with the last neural spine and ventrally with the last haemal spine (Figs. 42 and 43). These spines support one or two rays at both the uppermost and lowermost parts of the fin, respectively.

The first preural centrum (pc 1), which is the terminal vertebra, is articulated anteriorly to the second preural centrum and posteriorly fused or autogenous with

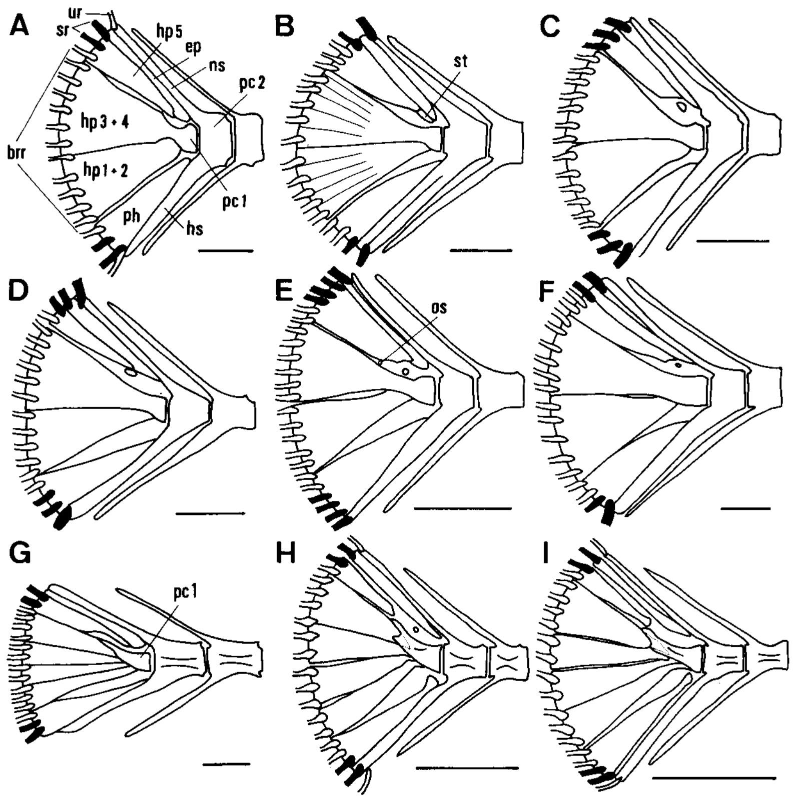

Fig. 42. Lateral aspect of caudal skeletons and fins in nine righteye flounders. A, *Atheresthes evermanni* ; B, *Hippoglossus stenolepis* ; C, *Pleuronectes herzensteini* ; D, *Pleuronichthys cornutus* ; E, *Tanakius kitaharai* ; F, *Clidoderma asperrimum* ; G, *Paralichthodes algoensis* ; H, *Poecilopsetta plinthus* ; I, *Nematops macrochirus*. brr, branched ray ; ep, epural ; hp, hypural ; hs, last haemal spine ; ns, last neural spine ; os, ossicle ; pc 1, first preural centrum ; pc 2, second preural centrum ; ph, parhypural ; sr, segmented ray ; st, stegural ; ur, unsegmented ray. Scales indicate 5 mm.

the hypurals. In the fishes of the subfamily Pleuronectinae except *Paralichthodes algoensis*, the first preural centrum is fused with the third-fourth hypural complex and autogenous with the first-second hypural one (Fig. 42 A–F). In a pleuronectine *Paralichthodes algoensis*, and the fishes of the subfamily Poecilopsettinae and the rhombosoleine genera *Azygopus*, *Ammotretis* and *Taratretis*, the first preural centrum is autogenous with the first, second, third and fourth hypurals (Figs. 42 G-I and 43 B-D). Of these fishes, in the fishes of the Poecilopsettinae, the bone slightly houses the fourth or third and fourth hypurals posterodorsally (Fig. 42 H, I), while it upturns and tapers in the other fishes mentioned above (Figs. 42 G and 43 B-D). In a rhombosoleine *Pelotretis flavilatus*, the first preural centrum is autogenous with the first-second-third-fourth hypural complex (Fig. 43 A). In the fishes of the rhombosoleine genera *Rhombosolea* and *Peltorhamphus*, it is fused with the first-second-

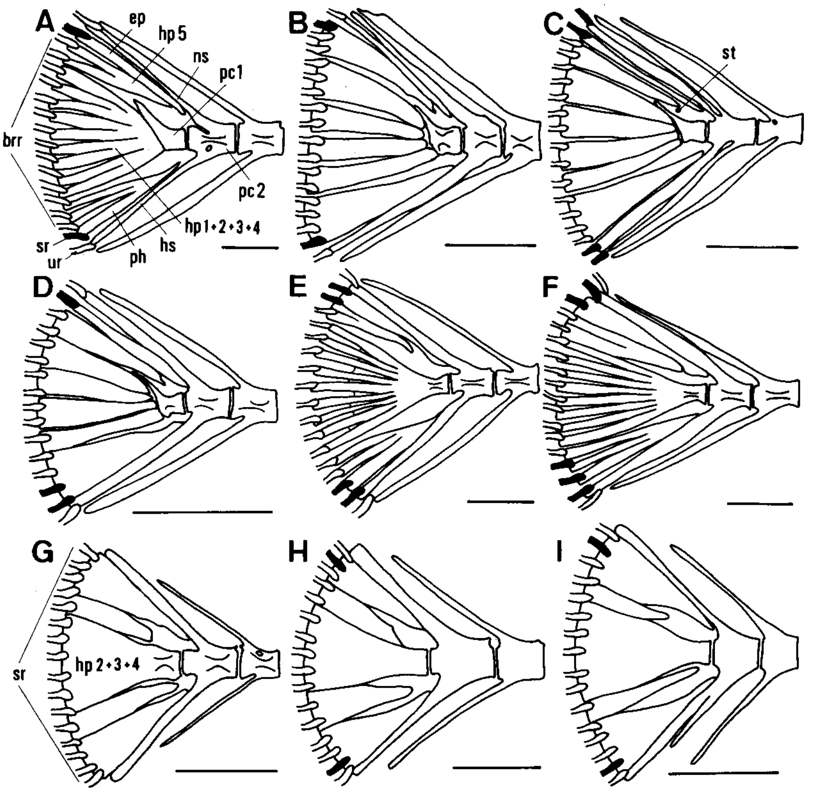

Fig. 43. Lateral aspect of caudal skeletons and fins in nine righteye flounders. A, *Pelotretis flavilatus* ; B, *Azygopus pinnifasciatus pinnifasciatus* ; C, *Ammotretis elongatus* ; D, *Taratretis derwentensis* ; E, *Rhombosolea leporina* ; F, *Peltorhamphus novaezeelandiae* ; G, *Samaris cristatus* ; H, *Plagiopsetta glossa* ; I, *Samariscus latus*. Abbreviations as in Fig. 42. Scales indicate 5 mm.

third-fourth hypural complex (Fig. 43 E, F). In the fishes of the subfamily Samarinae, it is fused with the second-third-fourth hypural plate (Fig. 43 G-I).

The hypurals (hp) are plate-like bones supporting the main part of the caudal fin. The hypurals vary in number with the pleuronectid fishes. In the fishes of the subfamily Pleuronectinae except *Paralichthodes algoensis*, the first and second hypurals, and the third and fourth ones, are fused with each other. The former plate is autogenous, while the latter one is fused with the first preural centrum. The fifth bone, not fused with any other bone, is located between the third-fourth hypural plate and the epural (Fig. 42 A-F). In a pleuronectine *Paralichthodes algoensis* and the fishes of the subfamily Poecilopsettinae, the first, second, third and fourth hypurals are autogenous with the first preural centrum respectively, and the fifth one is between the fourth hypural and the epural (Fig. 42 G-I). In the fishes of the Poecilopsettinae, the fourth or third and fourth hypurals slightly insert into the posterodorsal portion of the first preural centrum (Fig. 42H, I). In the fishes of the genera *Rhombosolea* and *Peltorhamphus* of the subfamily Rhombosoleinae, the first, second, third and fourth bones are fused with one another and also with the first preural centrum. The fifth bone lies between the hypural complex and the epural (Fig. 43 E, F). In *Pelotretis flavilatus* of the subfamily Rhombosoleinae, the composition of the hypurals is similar to that of the preceding group, but it differs from the latter in that the hypural complex (hp 1+2+3+4) is autogenous with the first preural centrum (Fig. 43A). In the fishes of the rhombosoleine genera *Azygopus*, *Ammotretis* and *Taratretis*, the composition of the hypurals is similar to that of a pleuronectine *Paralichthodes algoensis* and the fishes of the Poecilopsettinae (Fig. 43 B-D). In the fishes of the subfamily Samarinae, the second, third and fourth hypurals are fused with one another and further with the first preural centrum. The first and fifth hypurals independently exist respectively (Fig. 43 G-I).

In the members of the genera *Hippoglossus* of the subfamily Pleuronectinae and *Pelotretis*, *Rhombosolea* and *Peltorhamphus* of the subfamily Rhombosoleinae, the large subdivisions are observed in the hypurals from posteriorly to basally, though in *Hippoglossus* the divisions are absent in the fifth hypural (Figs. 42 B and 43 A, E, F).

The parhypural (ph) is a plate-like bone lying between the first hypural and the last haemal spine. In the members of the rhombosoleine genera *Pelotretis*, *Rhom-*

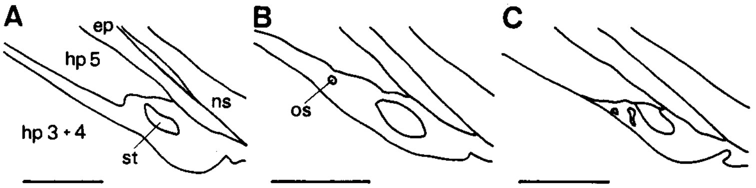

Fig. 44. Variation in stegural and ossicles in *Dexistes rikuzenius*. A, HUMZ 57171; B, HUMZ 57193; C, HUMZ 59235. Abbreviations as in Fig. 42. Scales indicate 2 mm.

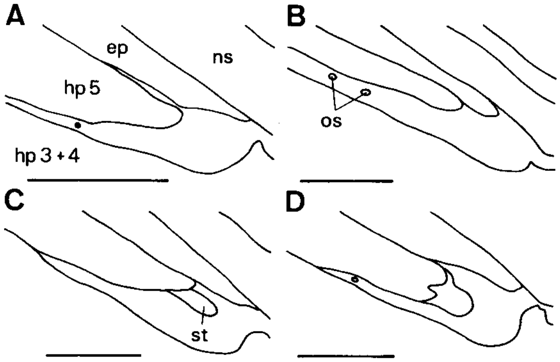

Fig. 45. Variation in stegural and ossicles in *Kareius bicoloratus*. A, HUMZ 57130; B, HUMZ 56986; C, HUMZ 57120; D, HUMZ 56993. Abbreviations as in Fig. 42. Scales indicate 2 mm.

bosolea and *Peltorhamphus*, it is subdivided into a few parts from hind edge to base (Fig. 43 A, E, F).

The epural (ep) supporting from one to three fin rays is located between the last neural spine and the fifth hypural (Figs. 42 and 43).

The last neural spine (ns) and the last haemal spine (hs) are fused basally with the second preural centrum and usually support one fin ray respectively (Figs. 42 and 43).

The stegural (st), which is variable in shape, is located at the space surrounded by the last neural spine, the epural, the fourth and fifth hypurals and the first preural centrum. The stegural, if present, is usually attached to the fifth hypural or both the fifth hypural and the epural (Fig. 42 B, D). In many pleuronectids of which more than one specimen were examined, the intraspecific variation was found in regard to presence or absence of the stegural. The variations in *Dexistes rikuzenius* and *Kareius bicoloratus* of the subfamily Pleuronectinae are shown in Figs. 44 and 45.

In many fishes of the Pleuronectidae, one or two small ossicles (os) are observed between the fourth and fifth hypurals. As in the stegural, their presence or absence and their number varied with many species of which more than one specimen were examined (Figs. 44 and 45).

The caudal fin rays, in the pleuronectid fishes examined except the fishes of the samarine genus *Samaris*, includes branched rays (brr) in the middle portion and unbranched ones at both the uppermost and lowermost parts of the fin base (Figs. 42 and 43 A-F, H, I). In the fishes of the genus *Samaris*, the fin rays are made up of unbranched rays alone (Fig. 43 G).

The total counts of the fin rays range from 16 to 25 in the subfamily Pleuronectinae (Table 18), from 19 to 22 (usually 20 or 22) in the subfamily Poecilopsettinae (Table 19), from 16 to 19 in the subfamily Rhombosoleinae (Table 20), and from 15 to 17 (usually 16) in the subfamily Samarinae (Table 21).

The number of the branched rays is from 10 to 17 in the subfamily Pleuronectinae, from 13 to 15 (usually 14) in the subfamily Poecilopsettinae, from 10 to 14 in the subfamily Rhombosoleinae, and from 11 to 13 (usually 12) in the subfamily Samarinae except *Samaris* (Tables 18-21).

The unbranched rays are divided into two kinds of rays, segmented (sr) and unsegmented rays (ur). An unsegmented ray was found at the upper and lower extremities of the fin base in the fishes of the genus *Atheresthes* of the subfamily Pleuronectinae, the subfamily Poecilopsettinae except *Nematops microstoma**, the subfamily Rhombosoleinae except *Psammodiscus ocellatus**, *Ammotretis elongatus*, *Colistium guntheri* and *Rhombosolea plebeia*, and the subfamily Samarinae except *Samaris cristatus* (Figs. 42 A, H, I and 43 A, B, D-F, H, I; Tables 18-21). Two unsegmented rays are present at the lower extremity in a specimen of *Poecilopsetta zanzibarensis** and at each extremity in *Nematops microstoma** of the Poecilopsettinae. In a few specimens of *Rhombosolea tapirina* and *R. leporina* of the Rhombosoleinae, an unsegmented ray is absent at the upper, lower or both extremities. In the other pleuronectid members examined in the present study including

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* examined only by radiograph.

Table 18. Frequency distribution of numbers of caudal fin rays in subfamily Pleuronectinae. segmented + unsegmented rays, from dorsally to ventrally, and total ray counts.

Species	2+12+2	4+10+3	1+2+12 +1+1	3+11+4	4+11+3	3+12+3	2+13+3	3+13+2	2+14+2
	16	17	17	18	18	18	18	18	18
1. *Atheresthes stomias*									
2. *A. evermanni*			1						
3. *Reinhardtius hippoglossoides*									
4. *Hippoglossus hippoglossus*									
5. *H. stenolepis*									
6. *Eopsetta exilis*									
7. *E. jordani*									
8. *E. grigorjewi*									
9. *Verasper variegatus*									
10. *V. moseri*									
11. *Psettichthys melanostictus*						5	2	2	
12. *Hippoglossoides platessoides platessoides*						4			
13. *H. p. limandoides*						6			
14. *H. elassodon*						21			
15. *H. dubius*				1		19			
16. *H. robustus*						17	1		
17. *H. pinetorum*						31	1	1	
18. *Acanthopsetta nadeshnyi*				1		20	1		
19. *Dexistes rikuzenius*						27	1	2	
20. *Pleuronectes isolepis*						13			
21. *P. vetulus*						12			
22. *P. bilineatus*						17		1	1
23. *P. mochigarei*						15	2	2	2
24. *P. limanda*						3			
25. *P. asper*					1	18		1	3
26. *P. korigarei*						1			
27. *P. sakhalinensis*						20	2		
28. *P. ferrugineus*				1		3			
29. *P. punctatissimus*					1	13	3	2	
30. *P. proboscideus*				4		13			
31. *P. herzensteini*									
32. *P. yokohamae*									
33. *P. schrenki*							2		
34. *P. americanus*									
35. *P. quadrituberculatus*					1	9			2
36. *P. platessa*									
37. *P. obscurus*									
38. *P. glacialis*						4			
39. *P. pinnifasciatus*						11	7	4	1
40. *P. putnami*						8	3		
41. *Platichthys flesus flesus*					1	1	1		
42. *P. stellatus*		1				20	1		2
43. *Hypsopsetta guttulata*									
44. *Pleuronichthys decurrens*									
45. *P. cornutus*									
46. *P. verticalis*									
47. *P. coenosus*									
48. *P. ritteri*									
49. *P. ocellatus*									
50. *Glyptocephalus cynoglossus*									
51. *G. stelleri*									
52. *Errex zachirus*									
53. *Kareius bicoloratus*						18			
54. *Microstomus kitt*									
55. *M. achne*									1
56. *M. pacificus*									
57. *Tanakius kitaharai*									
58. *Embassichthys bathybius*									
59. *Clidoderma asperrimum*									
60. *Paralichthodes algoensis*	4								

Ray formulae are segmented + branched + segmented or unsegmented + segmented + branched +

1+15+2	3+12+4	1+3+12 +2+1	4+12+3	1+2+13 +2+1	3+13+3	2+14+3	3+14+2	2+15+2	5+10+5	4+13+3	3+14+3	3+15+2	2+16+2
18	19	19	19	19	19	19	19	19	20	20	20	20	20
				18									
		1		21									
					1		1	11					
								16					
			1		7								
								4					
						1		19				1	
					1			10					1
							1	8					
					1								
							1						
											1		
					1								
					1								
							1						
					22	1				1	1		
					18	1							
					17	3		2					
								1			1		
					1								
											2		
					16	3		1					
					9	2							
					7		1	2					
	1				19	4	2	1					
					8		1						
					5			2					
			1		4								
					5			2					
								1					
1							1	7				1	
					1								2
									1			1	1
								11					1

Table 18. (continued).

Species	4+12+5	4+13+4	3+14+4	4+14+3	3+15+3	2+16+3	3+16+2	2+17+2	4+13+5	4+14+4	3+15+4
	21	21	21	21	21	21	21	21	22	22	22
1											
2											
3											
4											
5											
6											
7											
8											
9											
10								1			
11											
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39											
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41											
42											
43											
44											
45											
46											
47											
48											
49											
50											2
51		1	1						1	3	5
52									2	5	1
53											
54					1						
55					2	2	7	11			
56				1	7		2				
57										1	3
58	1	1	1	1	2		1	7			
59											
60											

4+15+3	3+16+3	2+17+3	4+14+5	4+15+4	4+16+3	3+17+3	2+19+2	4+16+4	4+17+3	5+16+4	Numbers of specimens
22	22	22	23	23	23	23	23	24	24	25	
											18
											23
											13
											1
											16
											8
											4
											21
											12
											10
											9
											4
											6
											21
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											9
											7
											5
											7
											2
3	3			2	2						21
			1								9
											19
											12
		2				1	2				30
											10
			1	15	1			1	2	1	25
											17
											12
											4

Table 19. Frequency distribution of numbers of caudal fin rays in subfamily Poecilopsettinae. Ray formulae are the same as in Table 18.

Species	1+2+13 +2+1 19	1+2+14 +2+1 20	1+2+14 +2+2 21	1+2+15 +2+1 21	2+2+14 +2+2 22	Numbers of specimens
Poecilopsetta beanii		4				4
P. colorata		3				3
P. hawaiiensis		8				8
P. praelonga		2				2
P. plinthus		30		1		31
P. natalensis		1				1
P. megalepis		1				1
P. albomarginata		5				5
P. albomaculata		3				3
P. zanzibarensis		8	1			9
Nematops microstoma					1	1
N. grandisquama		4				4
N. macrochirus	1	15				16
N. chui		1				1
Marleyella bicolorata		2				2
M. maldivensis		3				3

Table 20. Frequency distribution of numbers of caudal fin rays in

Species	1+1+11 +2+1 16	0+2+12 +2+0 16	1+1+12 +2+1 17	1+2+12 +1+1 17	1+3+10 +3+1 18	1+2+11 +3+1 18	1+2+12 +2+1 18	1+2+12 +3+0 18	0+3+12 +3+0 18
Oncopterus darwinii				2					
Psammodiscus ocellatus		5							
Pelotretis flavilatus									
Azygopus pinnifasciatus pinnifasciatus									
Ammotretis rostratus							8		
A. brevipinnis									
A. lituratus							4		
A. macrolepis									
A. elongatus									
Taratretis derwentensis	1		1				1		
Colistium nudipinnis									
C. guntheri									
Rhombosolea retiaria									
R. plebeia									1
R. tapirina							1		1
R. leporina							5	1	
Peltorhamphus novaezeelandiae					1	2	2		
P. latus					5		1		
P. tenuis							1		

Table 21. Frequency distribution of numbers of caudal fin rays in subfamily Samarinae. Ray formulae are the same as in Table 18.

Species	1+1+11 +1+1 15	1+1+12 +1+1 16	1+1+13 +0+1 16	1+14+1* 16	16** 16	1+1+13 +1+1 17	Numbers of specimens
Samaris cristatus				5	5		10
S. macrolepis				1			1
Plagiopsetta glossa		31	1				32
Samariscus corallinus		3					3
S. macrognathus		1					1
S. latus		17	1				18
S. longimanus		8					8
S. sunieri		7					7
S. xenicus	1	3				1	5
S. inornatus		1					1
S. luzonensis		1					1
S. maculatus		1					1
S. japonicus		1					1
S. huysmani		1					1
S. fasciatus		1					1
S. triocellatus		5					5

* unsegmented + segmented + unsegmented rays.

** all segmented rays.

subfamily Rhombosoleinae. Ray formulae are the same as in Table 18.

1+1+13 +2+1 18	1+2+13 +1+1 18	0+3+13 +2+0 18	0+1+13 +4+0 18	0+2+13 +3+0 18	1+1+14 +1+1 18	0+2+14 +1+1 18	0+2+14 +2+0 18	? 18	1+1+14 +2+1 19	Numbers of specimens
1					1					4
										5
					14					14
3					2					5
1										9
								1		1
										4
								1		1
		1	1				4			6
									1	4
					1					1
				1			1			2
					1					1
										1
1	1					1				5
										6
										5
										6
										1

the radiographic observations for many specimens, there were no unsegmented rays. Some specimens of *Samaris cristatus* of the Samarinae, have one unsegmented ray at each extremity of the fin base.

In the members of the pleuronectine genus *Atheresthes*, the unsegmented ray at the lower extremity of the fin base is fused basally with its adjacent segmented one (Fig. 42 A).

UNIT CHARACTER The caudal skeletons and fins of flatfishes have been discussed in detail by many ichthyologists (Norman, 1934; Ochiai, 1966; Amaoka, 1969, 1972; Kim, 1973 etc.). Many characters in the caudal skeleton and fin have been used in the previous phylogenetic studies on the pleuronectiforms. They are as follows; the relation between the first preural centrum and the hypurals, the number of the hypurals, presence or absence of the stegural, the total number of the caudal fin rays, and others (see Ochiai, 1966; Amaoka, 1969, 1972; Kim, 1973).

In the comparative study of the caudal skeleton and fin of the family Pleuronectidae, the interspecific variability was found in the following characters: 1) the relation between the first preural centrum and the hypurals, 2) the composition of the hypurals, 3) presence or absence of the subdivisions of the hypurals or the hypurals and the parhypural, 4) presence or absence of the stegural, 5) presence or absence of the ossicle(s) between the fourth and fifth hypurals, 6) presence or absence of the branched rays, and if such rays are present, 7) their number, 8) the total number of the fin rays, 9) presence or absence of the unsegmented rays, and if such

Table 22. Comparison and coding of characters of caudal skeleton and fin in 77 righteye flounders. The numerals in the parentheses are the values of the character states. Abbreviations as in Figs. 42. $^{+}$For explanation on coding in these characters, see text.

pcl and hp^{+}	hp^{+}	Subdivisions of hp or hp and ph	Branched rays	Fusion between ray at lower extremity and its adjacent one	Genera
pc 1 fused with hp 3+4	hp 1+2, 3+4, 5	present (0)	present (0)	absent (1)	Pleuronectinae *Hippoglossus*
		absent (1)		present (0)	Pleuronectinae *Atheresthes*
				absent (1)	Pleuronectinae all genera examined except *Atheresthes* *Hippoglossus* and *Paralichthodes*
autogenous	hp 1, 2, 3, 4, 5				Pleuronectinae *Paralichthodes* Poecilopsettinae all genera examined Rhombosoleinae *Azygopus*, *Ammotretis*, *Taratretis*
pcl fused with hp 2+3+4	hp 1, 2+3+4, 5		absent (1)		Samarinae *Samaris*
			present (0)		Samarinae *Plagiopsetta*, *Samariscus*
pc 1 fused with hp 1+2+3+4	hp 1+2+3+4, 5	present (0)			Rhombosoleinae *Rhombosolea*, *Peltorhamphus*
autogenous					Rhombosoleinae *Pelotretis*

rays are present, 10) their number, 11) presence or absence of the fusion between the ray at the lower extremity of the fin base and its adjacent one.

In the first character, the relation between the first preural centrum and the hypurals, there are four character states : the first preural centrum fused with the thrid-fourth, with the second-third-fourth, with the first-second-third-fourth hypural plate, and not fused with the hypurals. However, these states can not be arranged in a single logical sequence. Thus, this character is considered a qualitative multistate character and converted into two characters : (1) presence or absence of the fusion between the first preural centrum and the hypurals, (2) the composition of the hypurals fused with the first preural centrum. In the character (1), the character state is coded as 0 for the OTU's having the first preural centrum not fused with the hypurals, and as 1 for the OTU's having the bone fused with the hypurals. In the character (2), three character states are recognizable as mentioned above. This multistate character is not considered a quantitative multistate character but a qualitative multistate character. Therefore, it is converted into three two-state characters as follows : (1) the first preural centrum fused with the third-fourth hypural plate or not, (2) with the second-third-fourth hypural plate or not, (3) with the first-second-third-fourth hypural plate or not. In these cases, the character state is coded as 0 for the OTU's with each composition of the hypurals and as 1 for the OTU's with another composition of them. When the present three characters are compared, the character states of the species whose hypurals are autogenous with the first preural centrum are coded as NC.

In the second character, the composition of the hypurals, there are four character states as follows : (1) the hypurals separated from one another, (2) the first-second hypural plate, the third-fourth hypural plate, the fifth hypural, (3) the first hypural, the second-third-fourth hypural plate, the fifth hypural, (4) the first-second-third-fourth hypural plate, the fifth hypural. However, these four character states cannot be arranged in a single logical sequence. This qualitative multistate character is divided into four two-state characters as follows : (1) hypurals (1, 2, 3, 4, 5) or not, (2) hypurals (1+2, 3+4, 5) or not, (3) hypurals (1, 2+3+4, 5) or not, (4) hypurals (1+2+3+4, 5) or not. In these cases, possession of each character state is coded as 0, while the lack is coded as 1.

The third character, presence or absence of the subdivisions of the hypurals or the hypurals and the parhypural, is adopted as a unit character with two states, since no intraspecific variation was observed in all the species studied. The character state is coded as 0 for its presence and as 1 for its absence. The fourth and fifth characters, presence or absence of the stegural and the ossicle(s) between the fourth and fifth hypurals, are discussed at the same time. As shown in the description, there is an intraspecific variation in many species. Therefore, these two characters can not be used as unit characters. The sixth character, presence or absence of the branched rays, is accepted as a unit character with two states, since no intraspecific variations were found in all the species examined in the present study including radiography of many specimens. The character state is coded as 0 for the OTU with the branched rays and as 1 for the OTU lacking them. However, the number of the branched rays varies slightly in some species examined here. Thus, the seventh character can not be taken up as a unit character. The eighth character, the total number of the fin rays, is excluded from the unit characters by the same reason as in the preceding character. The ninth and tenth characters, presence or absence of the unsegmented rays, and if such rays are present, their number, vary intraspecifically as described above. Therefore, these two characters can not be regarded as unit characters. The last character, presence or absence of the fusion between the ray at the lower extremity of the fin base and its adjacent one, is used as a unit character, since no intraspecific variation was detected in all the species examined for the present study. Each character state is coded as 0 for the OTU's with such a fusion and as 1 for the OTU's lacking such a fusion.

Eleven selected unit characters and coded character states are summarized in Table 22.

13. OTHERS

In this section, several external and internal characters are treated.

(1) Eyes

In most pleuronectid fishes, the upper eye is usually on the lateral side of the head (Fig. 46B). But, in *Atheresthes stomias*, *Reinhardtius hippoglossoides* and *Hippoglossoides pinetorum* of the subfamily Pleuronectinae, the upper eye is located on the top of the head (Fig. 46A).

In the members of the pleuronectine genera *Atheresthes*, *Acanthopsetta*, *Dexistes*, *Microstomus*, *Tanakius*, *Embassichthys* and *Clidoderma*, a pleuronectine *Eopsetta exilis*, and the members of the rhombosoleine genera *Pelotretis* and *Azygopus* and the samarine genus *Samariscus*, scales are usually found on the surface of each eye (Fig. 47B). In the other pleuronectid members examined, neither eye is scaled (Fig. 47A, C). In *Clidoderma*, scales are replaced by bony tubercles described later.

Within the pleuronectids, only the fish of the genus *Nematops** of the subfamily Poecilopsettinae has a dark membranous orbital tentacle on each eye (Fig. 47C).

(2) Lateral line

The lateral line generally starts at the upper end of the gill opening and crosses the base of the caudal fin onto the fin membrane.

In the fishes of the subfamilies Pleuronectinae and Rhombosoleinae, the lateral line well develops on both sides of the body, whereas in the fishes of the subfamilies Poecilopsettinae and Samarinae that on the blind side is rudimentary and scarcely apparent (Fig. 32C, F).

In most pleuronectid fishes, the supratemporal branch of the lateral line runs upward and forward in the region of the nape (Figs. 30 and 48). However, it is entirely absent in *Embassichthys bathybius* of the Pleuronectinae, all the members of the Poecilopsettinae and the members of *Samariscus* of the Samarinae (Figs. 30C, I and 48). In some pleuronectines with the supratemporal branch such as the members of the genera *Psettichthys*, *Hypsopsetta* and *Pleuronichthys* and *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus* and *P. mochigarei*, the supratemporal branch possesses a posterior branch running just below the dorsal fin (Fig. 48). In the species of the genera *Hypsopsetta* and *Pleuronichthys*, this branch is long and extends beyond the middle of the body, while in the other species it is from moderate to short

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* In *N. chui*, it is only on the lower eye (Fowler, 1934).

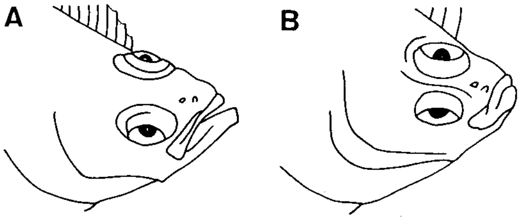

Fig. 46. Diagrams showing position of eyes in two righteye flounders. A, *Hippoglossoides pinetorum* ; B, *Pleuronectes herzensteini*.

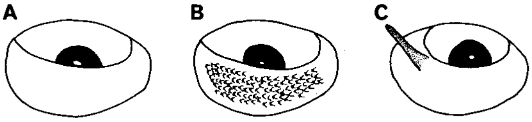

Fig. 47. Diagrams showing several types of eyes in Pleuronectidae. A, normal eye ; B, scaled eye ; C, eye with tentacle.

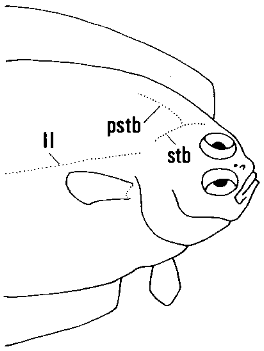

Fig. 48. Diagram showing lateral line of Pleuronectidae. ll, lateral line ; pstb, posterior branch of supratemporal branch ; stb, supratemporal branch.

in length.

(3) Mucous cavities on the blind side of the head

In the members of the pleuronectine genera *Glyptocephalus* and *Errex*, the mucous cavities are well developed on the blind side of the head (Fig. 21C). In the other pleuronectids, they are poorly developed.

(4) Skin

In almost all the pleuronectid fishes, the skin is from moderate to thin in thickness, while in the fishes of the pleuronectine genera *Microstomus*, *Embassichthys* and *Clidoderma* it is thick.

The pleuronectids are usually covered with scales on both sides of the body. However, in *Platichthys*, *Kareius* and *Clidoderma* of the subfamily Pleuronectinae, some or all of the scales transform into bony plates or tubercles on the ocular side or both sides of the body. In *Platichthys*, the body on both sides is covered with a varying number of small bony tubercles and there is nearly always a series of them at the bases of the dorsal and anal fins (Fig. 49A). Embedded scales are present all over or on the hinder part of the body. In *Kareius*, a longitudinal row of more or less contiguous rugose bony plates is between the lateral line and the back, and there is usually a similar row of rather smaller bony plates between the lateral line and the anterior part of the anal fin on the ocular side of the body. An irregular series of small bony plates is located above and below the lateral line respectively (Fig. 49B). Scales are almost absent on both sides at least in adults. In *Clidoderma*, the body

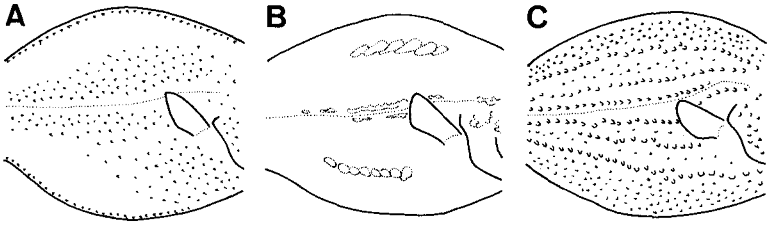

Fig. 49. Diagrams showing bony plates or tubercles on body in three righteye flounders. A, *Platichthys stellatus* ; B, *Kareius bicoloratus* ; C, *Clidoderma asperrimum*.

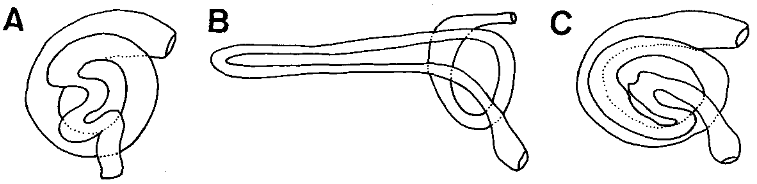

Fig. 50. Diagrams showing alimentary canals in three righteye flounders. A, *Pleuronectes herzensteini* ; B, *Microstomus kitt* ; C, *Poecilopsetta plinthus*.

on the ocular side is covered with close-set and rough bony tubercles, most of which bear small spines, and some of them are arranged in some definite longitudinal rows, but that on the blind side is smooth (Fig. 49C).

(5) Elongation of the intestine

In the members of the pleuronectine genera *Glyptocephalus*, *Errex*, *Microstomus*, *Tanakius* and *Embassichthys*, the second loop of the intestine elongates and extends into a secondary body cavity on the ocular side (Fig. 50B). In the other pleuronectids, the intestine is almost entirely contained inside the body cavity (Fig. 50A, C).

UNIT CHARACTER The characters treated in this section have been used mainly for the classification of flatfishes (see Norman, 1934).

The present study on the above characters mentioned revealed interspecific variations in the following nine characters: 1) the position of the upper eye, 2) presence or absence of the scales on the surface of each eye, 3) presence or absence of a membranous orbital tentacle, 4) the developmental degree of the lateral line on the blind side, 5) the developmental degree of the supratemporal branch of the lateral line, 6) the developmental degree of the mucous cavities on the blind side of the head, 7) the degree of the thickness of the skin, 8) presence or absence of the bony plates or tubercles on the body, 9) presence or absence of the elongation of the intestine.

The first character, the position of the upper eye, is used as a unit character, since two character states, the upper eye on the top of the head and on the lateral side of the head, are recognizable without any intraspecific variation. The character state is coded as 0 for the OTU's with the upper eye on the lateral side of the head and as 1 for the OTU's with the upper eye on the top of the head. The second

Table 23. Comparison and coding of several external and internal characters in 77 righteye flounders. The numerals in the parentheses are the values of the character states.

Scales on each eye	Tentacle on eyes	Position of upper eye	Lateral line of blind side	Supratemporal branch of lateral line	Mucous cavities on blind side of head	Skin	Bony plates or tubercles on body	Intestine	Genera and species
present (0)	absent (1)	lateral of head (0)	developed (0)	present (1)	poorly developed (1)	from moderate to thin (0)	absent (1)	not elongate (1)	Pleuronectinae *Atheresthes evermanni*, *Eopsetta exilis*, *Acanthopsetta*, *Dexistes*
						thick (1)	present (0)		Pleuronectinae *Clidoderma*
				absent (0)			absent (1)	elongate (0)	Pleuronectinae *Embassichthys*
				present (1)					Pleuronectinae *Microstomus*
						from moderate to thin (0)			Pleuronectinae *Tanakius*
absent (1)					well developed (0)				Pleuronectinae *Glyptocephalus*, *Errex*
present (0)		top of head (1)			poorly developed (1)			not elongate (1)	Pleuronectinae *Atheresthes stomias*
absent (1)									Pleuronectinae *Reinhardtius*, *Hippoglossoides pinetorum*
		lateral of head (0)					present (0)		Pleuronectinae *Platichthys*, *Kareius*
							absent (1)		Pleuronectinae *Hippoglossus*, *Eopsetta jordani*, *E. grigorjewi*, *Verasper*, *Hippoglossoides* except *H. pinetorum*, *Pleuronectes* except *P. isolepis*, *P. vetulus*, *P. bilineatus* and *P. mochigarei*, *Paralichthodes*
				present with posterior branch (2)					Pleuronectinae *Psettichthys*, *Pleuronectes isolepis*, *P. vetulus*, *P. bilineatus*, *P. mochigarei*, *Hypsopsetta*, *Pleuronichthys*
			rudimentary and scarcely apparent (1)	absent (0)					Poecilopsettinae *Poecilopsetta*
	present (0)								Poecilopsettinae *Nematops*
present (0)	absent (1)								Samarinae *Samariscus*
absent (1)				present (1)					Samarinae *Samaris*, *Plagiopsetta*
			developed (0)						Rhombosoleinae *Ammotretis*, *Taratretis*, *Rhombosolea*, *Peltorhamphus*
present (0)									Rhombosoleinae *Pelotretis*, *Azygopus*

character, presence or absence of the scales on the surface of each eye, is a unit character with two states. The character state is coded as 0 for its presence and as 1 for its absence. The third character, presence or absence of a membranous orbital tentacle, is adopted as a unit character with two states. The character state is coded as 0 for the OTU with an orbital tentacle and 1 for the OTU without such a tentacle. The fourth character, the developmental degree of the lateral line on the blind side, clearly has two states: the lateral line is developed on the blind side, or it is rudimentary and scarcely apparent. Each character state is coded as 0 for the OTU's with a well-developed lateral line on the blind side and as 1 for the OTU's with a rudimentary and scarcely apparent one. The fifth character, the developmental degree of the supratemporal branch of the lateral line, is used as a unit character. There are three character states which can be arranged in a single logical sequence. Therefore, this character is a quantitative multistate character with three states: the supratemporal branch is absent, it is present, and it is present and also has a posterior branch. In this case, each character state is coded as 0, 1, 2 in order. Concerning the sixth character, the developmental degree of the mucous cavities on the blind side of the head, there are two states: the well-developed state in *Glyptocephalus* and *Errex*, and the poorly developed state in the other pleuronectids examined. Thus, this is accepted as a unit character and each state is coded as 0 for the OTU's of *Glyptocephalus* and *Errex* and as 1 for the other OTU's. The seventh character, the degree of the thickness of the skin, is selected as a unit character with two states. The character state is coded as 0 for the OTU's having from moderate to thin skin and as 1 for the OTU's with thick skin. The eighth character, presence or absence of the bony plates or tubercles on the body, is a unit character with two states. The character state is coded as 0 for the OTU's having the bony plates or tubercles on the body and as 1 for the OTU's lacking such bony plates or tubercles on the body. Incidentally, the following three character states are found within the former OTU's described above: *Platichthys* type, *Kareius* type, *Clidoderma* type. However, these three states cannot be arranged in a single logical sequence. Therefore, this character is interpreted as a qualitative multistate character and turned into three new two-state characters as follows: 1) *Platichthys* type or not, 2) *Kareius* type or not, 3) *Clidoderma* type or not. In these cases, the character state is coded as 0 for the OTU's with each type and as 1 for the OTU's with another type. The character states of the species which have no bony plates or tubercles on the body are coded as NC. The ninth character, presence or absence of the elongation of the intestine, is used as a unit character, since no intraspecific variation was observed in the present study nor in the previous works (Groot, 1971 and others). The character state is coded as 0 for the OTU's having the elongated intestine and as 1 for the OTU's lacking the elongated one.

Twelve selected unit characters and coded character states are summarized in Table 23.

VII. Interrelationships of the fishes of the Pleuronectidae

In the present chapter, procedure (4), (5), (6), calculation of similarity between operational taxonomic units, cluster analysis for forming phenetic groups and

Table 24. List of unit characters with number of character states.

1.	Jaw apparatus		
	1.	Degree of bilateral symmetry on both jaws	2
2.	Cranium		
	2.	Presence or absence of nasal on ocular side	2
	3.	Relation between mesethmoid and anterior part of upper orbital cavity	2
	4.	Presence or absence of attachment between both prefrontals	2
		Mode of attachment between both prefrontals	
	5.	On lower part of anterior portion of frontal of ocular side	2
	6.	On upper part of same portion	2
	7.	Presence or absence of attachment of prefrontal of blind side to frontal of ocular side in middle part of orbital cavity of upper eye	2
	8.	Presence or absence of pterosphenoid on ocular side	2
	9.	Presence or absence of pterosphenoid on blind side	2
	10.	Relation between both epiotics	2
	11.	Relation of epiotics and foramen magnum	2
	12.	Relation between both zygapophyses of exoccipitals	2
	13.	Relation of basioccipital and floor of foramen magnum	2
	14.	Presence or absence of articulation of frontal of ocular side to parasphenoid at interorbital region	2
	15.	Width of articulated portion between frontal of ocular side and parasphenoid at interorbital region	2
	16.	Developmental degree of interorbital process	2
	17.	Posterior position of parasphenoid	2
3.	Orbital bones		
	18.	Presence or absence of sensory canal of preorbital on ocular side	2
	19.	Developmental degree of infraorbitals on ocular side	3
	20.	Presence or absence of preorbital on blind side	2
	21.	Presence or absence of infraorbitals on blind side	2
4.	Suspensorium and opercular apparatus		
	22.	Size of metapterygoid	2
5.	Hyoid arch		
	23.	Position of opening for hyoidean artery in hypohyals	2
		Structure of ceratohyal in relation to hyoidean artery	
	24.	Presence of absence of ceratohyal foramen or perforation in middle part of its outer lateral surface	2
	25.	Presence or absence of perforation	2
	26.	Presence or absence of foramen on its inner lateral surface in fishes with perforation in its outer lateral surface	2
6.	Branchial apparatus and gill rakers		
	27.	Relation between both fifth ceratobranchials	2
	28.	Presence or absence of teeth on third epibranchial	2
	29.	Presence or absence of spines on each gill raker	2
	30.	Presence or absence of bony plates on outer and/or inner surfaces of branchial arch	2
7.	Fins		
	31.	Position of origin of dorsal fin in relation to dorsomedian line of head	2
	32.	Position of origin of dorsal fin on blind side	2
	33.	Position of origin of dorsal fin on dorsomedian line of head	4
	34.	Degree of stoutness of median fin rays	2
	35.	Presence or absence of prolongation of anterior dorsal fin rays	2
		Type of prolongation	
	36.	*Psettichthys* type	2

Table 24. (continued).

	37.	*Azygopus* type	2
	38.	*Samaris* type	2
	39.	Presence or absence of scales along median fin rays on ocular side or both sides	2
	40.	Presence or absence of pectoral fin on blind side	2
	41.	Presence or absence of pelvic fin on blind side	2
	42.	Relation between pelvic fin of ocular side and anal fin	2
8.	Pectoral girdle		
	43.	Presence or absence of scapula on blind side	2
	44.	Presence or absence of coracoid on blind side	2
	45.	Presence or absence of actinosts on ocular side	2
	46.	Presence or absence of actinosts on blind side	2
	47.	Presence or absence of postcleithrum	2
9.	Pelvic girdle		
	48.	Degree of bilateral symmetry on pelves	2
	49.	Position of anteroventral tip of pelvis of ocular side	4
11.	Vertebrae and their accessory bones		
	50.	Presence or absence of first neural arch	2
	51.	Presence or absence of pleural rib	2
	52.	Presence or absence of epipleural	2
	53.	Presence or absence of epicentrum	2
	54.	Presence or absence of epimeral	2
	55.	Presence or absence of hypomeral	2
12.	Caudal skeleton and fin		
	56.	Relation between first preural centrum and hypurals	2
		Composition of hypurals fused with first preural centrum	
	57.	Hypurals 3+4	2
	58.	Hypurals 2+3+4	2
	59.	Hypurals 1+2+3+4	2
		Composition of hypurals	
	60.	Hypurals 1, 2, 3, 4, 5	2
	61.	Hypurals 1+2, 3+4, 5	2
	62.	Hypurals 1, 2+3+4, 5	2
	63.	Hypurals 1+2+3+4, 5	2
	64.	Presence or absence of subdivisions of hypurals or hypurals and parhypural	2
	65.	Presence or absence of branched rays	2
	66.	Presence or absence of fusion between ray at lower extremity of fin base and its adjacent one	2
13.	Others		
	67.	Presence or absence of scales on surface of each eye	2
	68.	Presence or absence of membranous orbital tentacle	2
	69.	Position of upper eye	2
	70.	Developmental degree of lateral line on blind side	2
	71.	Developmental degree of supratemporal branch of lateral line	3
	72.	Developmental degree of mucous cavities on blind side of head	2
	73.	Degree of thickness of skin	2
	74.	Presence or absence of bony plates or tubercles on body	2
		Its type	
	75.	*Platichthys* type	2
	76.	*Kareius* type	2
	77.	*Clidoderma* type	2
	78.	Presence or absence of elongation of intestine	2

taxonomic ranking, are carried out.

From the preceding sections, 78 unit characters were compiled and are shown in Table 24. The value of the character state for each OTU is shown in Table 25. From the data matrix, the similarity between every OTU was calculated using Gower's coefficient of similarity slightly modified, and each OTU was grouped by cluster analysis, UPGMA in the present study, on the basis of the similarity matrix (CPCC=0.9753). The result of this process is summarized in Fig. 51. Thus, the interrelationships of 77 righteye flounders are depicted by this dendrogram.

Next, taxonomic ranking was carried out. First, each species of the family Pleuronectidae examined here was ranked to genus which is a mandatory supraspecific category for nomenclature (see Wiley, 1981). Determination of the similarity level for a generic phenon line is very important problem in numerical phenetic study. However, it is practically impossible to establish a logical theoretical basis to determine the similarity level for a generic phenon line in a particular group. However, it would seem reasonable to minimize unnecessary taxonomic changes in a widely used classification in order to avoid taxonomic confusion. On this basis, the phenon line for genera may be drawn at a similarity level of 99 or 98 (Fig. 51). If the phenon line is drawn at 99, many current genera would be subdivided and some genera would be united. Therefore, in the present study, the phenon line for genera was drawn at a similarity level of 98, after referring mainly to Norman's (1934) system slightly modified by Hubbs (1945) which is the most frequently quoted in the classification of flatfishes. Nevertheless, Norman's (1934) classification modified by Hubbs (1945) is a little changed by the present ranking as follows.

The species of *Isopsetta*, *Parophrys*, *Lepidopsetta*, *Limanda*, *Pseudopleuronectes*, *Pleuronectes* and *Liopsetta* in Norman's (1934) classification were found to be closely related to one another. Thus, according to the generic ranking, these species are reasonably united in a single genus *Pleuronectes* which is the oldest valid generic name. Similarly, it is concluded that Norman's (1934) *Lyopsetta* and *Eopsetta* should be synonymized and that the species included in both genera should be placed in the genus *Eopsetta*, which has seniority. It is also concluded that the species of *Cleisthenes* should be included in *Hippoglossoides*. *Errex zachirus* which was originally described as *Glyptocephalus zachirus* by Lockington (1879) was included in a new genus *Errex* by Jordan (1919). Later in 1934, this species was included again in *Glyptocephalus* by Norman, though he recognized *Errex* as a subgenus. However, from the present ranking, it is concluded that *Errex* should be retained as a genus. Similarly, it is concluded that *Kareius* treated as a subgenus of *Platichthys* by Norman (1934) should be recognized as a genus.

The category tribe was introduced into this family by Nelson (1976). He established two tribes, Hippoglossini and Pleuronectini, in the subfamily Pleuronectinae of Norman (1934), based on a few characters such as the size and the degree of the bilateral symmetry of the mouth. Examination of 78 characters did not support the erection of these tribes. In the present study, tribes were not introduced into any subfamily.

Because subfamilies have been recognized in the Pleuronectidae for a long time by many investigators, it was considered worth while to evaluate their status.

Table 25. Character state for 78 unit characters in 77 righteye flounders. The number of each unit
Fig. 51.

	OTU	A1	A2	A3	A4	A5	A6	A7	A8	A9	B1	B2	B3	B4	B5	B6	B7	B8	B9	C1
Unit character	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	5	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	6	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	15	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	16	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	18	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	23	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	24	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0
	25	0	0	0	0	0	0	0	0	0	0	NC	0	0	0	0	0	0	0	NC
	26	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	27	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	28	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
	29	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
	30	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
	31	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	32	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	34	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	35	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
	36	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	NC	NC	NC	NC	NC	NC	NC	NC
	37	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC	NC	NC	NC	NC	NC
	38	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC	NC	NC	NC	NC	NC
	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	53	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	55	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	56	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	58	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	59	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	62	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	63	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	64	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	66	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	67	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1
	68	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	69	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	71	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2
	72	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	74	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	75	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	76	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	77	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
	78	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

character is the same as that in Table 24. The symbol of each OTU is the same as that in

C2	C3	C4	C5	C6	C7	C8	C9	D1	D2	D3	D4	D5	D6	D7	D8	D9	E1	E2	E3	E4
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	NC
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 25. (continued).

Unit character

OTU	E5	E6	E7	E8	E9	F1	F2	F3	F4	F5	F6	F7	F8	F9	G1	G2	G3	G4	G5
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
5	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0
6	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1
7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	NC	NC
14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
15	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	NC	NC
16	0	0	0	0	0	0	1	1	0	2	0	0	0	0	1	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
25	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0	NC	NC
26	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
27	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
28	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
29	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
30	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
31	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
32	1	0	0	0	0	0	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
33	NC	NC	NC	NC	NC	NC	0	0	0	0	0	0	0	0	0	0	1	0	0
34	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	1	1	1
35	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
36	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
37	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
38	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
39	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
55	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
56	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NC	NC	NC
58	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	NC	NC	NC
59	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	NC	NC	NC
60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
62	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
63	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
64	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
67	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1
68	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
71	2	2	2	2	2	2	1	1	1	1	1	1	1	1	0	1	1	0	0
72	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
73	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0
74	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1
75	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC	NC	NC	1	NC	NC	NC
76	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	NC	NC	NC	NC	NC	1	NC	NC	NC
77	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC	NC	NC	0	NC	NC	NC
78	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1

G6	G7	G8	G9	H1	H2	H3	H4	H5	H6	H7	H8	H9	I1	I2	I3	I4	I5
0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
0	0	0	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	1	1
1	1	1	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	1	1
0	0	0	0	2	0	0	0	0	2	2	2	0	0	2	2	0	0
1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0
2	2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2
1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
NC	NC	NC	1	1	NC	NC	NC	NC	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
0	0	0	0	1	3	3	3	1	2	2	2	3	3	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1
NC	NC	NC	NC	1	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC
NC	NC	NC	NC	0	NC	NC	NC	NC	NC	NC	NC	NC	NC	1	NC	NC	NC
NC	NC	NC	NC	1	NC	NC	NC	NC	NC	NC	NC	NC	NC	0	NC	NC	NC
1	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0
0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
0	0	0	2	2	3	3	3	2	2	2	2	3	3	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	1	1	1	1	1	0	0	0	0
NC	NC	NC	NC	NC	NC	NC	NC	NC	0	0	0	0	0	1	1	1	1
0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
1	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1
1	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0
1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Subfamilies have been recognized as follows:

(1) Three subfamilies
    Regan (1910)
        Pleuronectinae, Samarinae, Rhombosoleinae
(2) Four subfamilies
    Regan (1929)
        Pleuronectinae, Paralichthodinae, Samarinae, Rhombosoleinae
    Nelson (1976)
        Pleuronectinae, Poecilopsettinae, Samarinae, Rhombosoleinae
(3) Five subfamilies
    Norman (1934), Berg (1940), Hubbs (1945) etc.
        Pleuronectinae, Poecilopsettinae, Paralichthodinae, Samarinae, Rhombosoleinae

It is logical from one point of view that great gaps in similarity should be required to establish subfamilies. Given this point of view, there are only two possible similarity levels for the decision on subfamilial rank. One level is about 60 and the other is about 75 (Fig. 51). If the phenon line is drawn at a similarity level of 60, two subfamilies can be established. One subfamily consists of the species from *Atheresthes stomias* to *Peltorhamphus latus* in Fig. 51. The other subfamily comprises the genera *Samaris, Plagiopsetta* and *Samariscus.* If the phenon line is drawn at a similarity level of 75, four subfamilies are distinguishable. The first subfamily is composed of the species from *Atheresthes stomias* to *Paralichthodes algoensis* in Fig. 51. The second comprises the species from *Poecilopsetta beanii* to *Nematops macrochirus.* The third consists of the species from *Pelotretis flavilatus* to *Peltorhamphus latus.* The fourth is made up of the species from *Samaris cristatus* to *Samariscus xenicus.* Judging from the previous subfamilial classifications mentioned above, it is clear that the subfamilial classification obtained by phenon line 75 requires fewer taxonomic modifications than that by phenon line 60. Consequently, four subfamilies were established according to the phenon line at a similarity level of 75 in the present study: Pleuronectinae, Poecilopsettinae, Rhombosoleinae and Samarinae. Each subfamily is characterized by the following features.

Pleuronectinae: 1) the first neural arch is present.

Poecilopsettinae: 1) both prefrontals are attached to each other on the lower part of the anterior portion of the frontal of the ocular side and 2) the preorbital is absent on the blind side.

Rhombosoleinae: 1) the pelves are very asymmetrical and 2) the anteroventral tip of the pelvis of the ocular side extends forward beyond the cleithrum.

Samarinae: 1) both prefrontals are attached to each other on the upper part of the anterior portion of the frontal of the ocular side, 2) the prefrontal of the blind side is attached to the frontal of the ocular side in the middle part of the orbital cavity of the upper eye, 3) the frontal of the ocular side is widely articulated to the parasphenoid at the interorbital region, 4) the metapterygoid is small in size, 5) the pectoral fin is absent on the blind side, 6) the scapula and the coracoid are absent on the blind side, 7) the pleural rib and the epipleural are absent, 8) the epicentrum and the hypomeral are present, 9) the first preural centrum is fused with

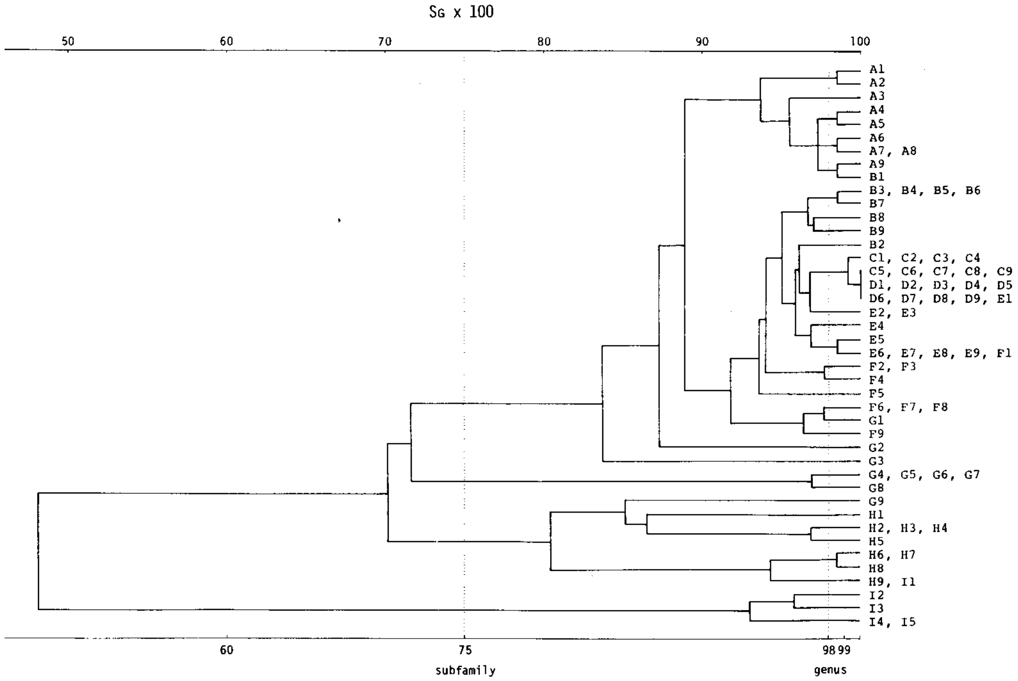

Fig. 51. Interrelationships of 77 righteye flounders. SG, General coefficient of similarity of Gower. A1, *Atheresthes stomias* ; A2, *A. evermanni* ; A3, *Reinhardtius hippoglossoides* ; A4, *Hippoglossus hippoglossus* ; A5, *H. stenolepis* ; A6, *Eopsetta exilis* ; A7, *E. jordani* ; A8, *E. grigorjewi* ; A9, *Verasper variegatus* ; B1, *V. moseri* ; B2, *Psettichthys melanostictus* ; B3, *Hippoglossoides platessoides limandoides* ; B4, *H. elassodon* ; B5, *H. dubius* ; B6, *H. robustus* ; B7, *H. pinetorum* ; B8, *Acanthopsetta nadeshnyi* ; B9, *Dexistes rikuzenius* ; C1, *Pleuronectes isolepis* ; C2, *P. vetulus* ; C3, *P. bilineatus* ; C4, *P. mochigarei* ; C5, *P. limanda* ; C6, *P. asper* ; C7, *P. sakhalinensis* ; C8, *P. ferrugineus* ; C9, *P. punctatissimus* ; D1, *P. proboscideus* ; D2, *P. herzensteini* ; D3, *P. yokohamae* ; D4, *P. schrenki* ; D5, *P. americanus* ; D6, *P. quadrituberculatus* ; D7, *P. platessa* ; D8, *P. obscurus* ; D9, *P. glacialis* ; E1, *P. pinnifasciatus* ; E2, *Platichthys flesus flesus* ; E3, *P. stellatus* ; E4, *Hypsopsetta guttulata* ; E5, *Pleuronichthys decurrens* ; E6, *P. cornutus* ; E7, *P. verticalis* ; E8, *P. coenosus* ; E9, *P. ritteri* ; F1, *P. ocellatus* ; F2, *Glyptocephalus cynoglossus* ; F3, *G. stelleri* ; F4, *Errex zachirus* ; F5, *Kareius bicoloratus* ; F6, *Microstomus kitt* ; F7, *M. achne* ; F8, *M. pacificus* ; F9, *Tanakius kitaharai* ; G1, *Embassichthys bathybius* ; G2, *Clidoderma asperrimum* ; G3, *Paralichthodes algoensis* ; G4, *Poecilopsetta beanii* ; G5, *P. praelonga* ; G6, *P. plinthus* ; G7, *P. albomarginata* ; G8, *Nematops macrochirus* ; G9, *Pelotretis flavilatus* ; H1, *Azygopus pinnifasciatus pinnifasciatus* ; H2, *Ammotretis rostratus* ; H3, *A. lituratus* ; H4, *A. elongatus* ; H5, *Taratretis derwentensis* ; H6, *Rhombosolea plebeia* ; H7, *R. tapirina* ; H8, *R. leporina* ; H9, *Peltorhamphus novaezeelandiae* ; I1, *P. latus* ; I2, *Samaris cristatus* ; I3, *Plagiopsetta glossa* ; I4, *Samariscus latus* ; I5, *S. xenicus*.

the second-third-fourth hypural plate and 10) the composition of the hypurals is hp 1, 2+3+4, 5.

As far as 77 species or subspecies examined here are concerned, the specific arrangement in each subfamily is the same as that in the classification of Norman (1934) modified by Hubbs (1945) except transferring *Paralichthodes algoensis* to the subfamily Pleuronectinae, though several species (even genera) have been added in each subfamily.

Paralichthodes algoensis was first included in the subfamily Samarinae of the Pleuronectidae by Regan (1910), though thereafter it was raised to familial rank by the same author (1920). The subfamily Paralichthodinae in the Pleuronectidae erected by Regan (1929) was retained by Norman (1934) and Hubbs (1945). Nelson (1976), however, placed *Paralichthodes algoensis* in the Samarinae again. Apart from the subfamilial ranking, it was apparently believed to be closely related to the species of the Samarinae. The present study, however, reveals that it is more closely related to the species of the Pleuronectinae than those of any other pleuronectid subfamily. Thus, *Paralichthodes algoensis* is treated as a member of the subfamily Pleuronectinae.

Norman (1934), in his monograph on flatfishes, showed a trichotomous relationship in the Pleuronectidae: Pleuronectinae-Poecilopsettinae stem, Samarinae-Paralichthodinae stem and Rhombosoleinae stem. Judging from the phenogram, it is concluded that the subfamilies Pleuronectinae, Rhombosoleinae and Poecilopsettinae are closely related to one another, and not so much to the subfamily Samarinae.

As a result of the taxonomic ranking mentioned above, the classification of the family is as follows.

Family Pleuronectidae
  Subfamily Pleuronectinae
    Genus *Atheresthes* Jordan and Gilbert, 1880
      A. stomias (Jordan and Gilbert, 1880)
      A. evermanni Jordan and Starks, 1904
    Genus *Reinhardtius* Gill, 1861
      R. hippoglossoides (Walbaum, 1792)
    Genus *Hippoglossus* Cuvier, 1817
      H. hippoglossus (Linnaeus, 1758)
      H. stenolepis Schmidt, 1904
    Genus *Eopsetta* Jordan and Goss in Jordan, 1885
      E. exilis (Jordan and Gilbert, 1880)
      E. jordani (Lockington, 1879)
      E. grigorjewi (Herzenstein, 1890)
    Genus *Verasper* Jordan and Gilbert in Jordan and Evermann, 1898
      V. variegatus (Temminck and Schlegel, 1846)
      V. moseri Jordan and Gilbert in Jordan and Evermann, 1898
    Genus *Psettichthys* Girard, 1854
      P. melanosticus Girard, 1854
    Genus *Hippoglossoides* Gottsche, 1835
      *H. platessoides platessoides** (Fabricius, 1780)
      H. p. limandoides (Bloch, 1787)
      H. elassodon Jordan and Gilbert, 1880
      H. dubius Schmidt, 1904
      H. robustus Gill and Townsend, 1897

- *H. pinetorum* (Jordan and Starks, 1904)

Genus *Acanthopsetta* Schmidt, 1904
- *A. nadeshnyi* Schmidt, 1904

Genus *Dexistes* Jordan and Starks, 1904
- *D. rikuzenius* Jordan and Starks, 1904

Genus *Pleuronectes* Linnaeus, 1758
- *P. isolepis* (Lockington, 1880)
- *P. vetulus* (Girard, 1854)
- *P. bilineatus* (Ayres, 1855)
- *P. mochigarei* (Snyder, 1911)
- *P. limanda* Linnaeus, 1758
- *P. asper* Pallas, 1811
- *P. korigarei** (Hubbs, 1915)
- *P. sakhalinensis* (Hubbs, 1915)
- *P. ferrugineus* (Storer, 1839)
- *P. punctatissimus* (Steindachner, 1879)
- *P. proboscideus* (Gilbert, 1895)
- *P. herzensteini* (Jordan and Snyder, 1901)
- *P. yokohamae* Günther, 1877
- *P. schrenki* (Schmidt, 1904)
- *P. americanus* Walbaum, 1792
- *P. quadrituberculatus* Pallas, 1811
- *P. platessa* Linnaeus, 1758
- *P. obscurus* Herzenstein, 1890
- *P. glacialis* Pallas, 1776
- *P. pinnifasciatus* Kner in Steindachner and Kner, 1870
- *P. putnami** (Gill, 1864)

Genus *Platichthys* Girard, 1854
- *P. flesus flesus* (Linnaeus, 1758)
- *P. f. italicus*** (Günther, 1862)
- *P. f. luscus*** (Pallas, 1811)
- *P. stellatus* (Pallas, 1787)

Genus *Hypsopsetta* Gill, 1862
- *H. guttulata* (Girard, 1856)

Genus *Pleuronichthys* Girard, 1854
- *P. decurrens* Jordan and Gilbert, 1881
- *P. cornutus* (Temminck and Schlegel, 1846)
- *P. verticalis* Jordan and Gilbert, 1880
- *P. coenosus* Girard, 1854
- *P. ritteri* Starks and Morris, 1907
- *P. ocellatus* Starks and Thompson, 1910

Genus *Glyptocephalus* Gottsche, 1835
- *G. cynoglossus* (Linnaeus, 1758)
- *G. stelleri* (Schmidt, 1904)

Genus *Errex* Jordan, 1919
- *E. zachirus* (Lockington, 1879)

Genus *Kareius* Jordan and Snyder, 1900
  K. bicoloratus (Basilewsky, 1855)
Genus *Microstomus* Gottsche, 1835
  M. kitt (Walbaum, 1792)
  M. achne (Jordan and Starks, 1904)
  M. pacificus (Lockington, 1879)
  *M. shuntovi*** Borets, 1983
Genus *Tanakius* Hubbs, 1918
  T. kitaharai (Jordan and Starks, 1904)
Genus *Embassichthys* Jordan and Evermann, 1896
  E. bathybius (Gilbert, 1890)
Genus *Clidoderma* Bleeker, 1862
  C. asperrimum (Temminck and Schlegel, 1846)
Genus *Paralichthodes* Gilchrist, 1902
  P. algoensis Gilchrist, 1902
Subfamily Poecilopsettinae
Genus *Poecilopsetta* Günther, 1880
  P. beanii (Goode, 1881)
  *P. inermis*** (Breder, 1927)
  *P. colorata** Günther, 1880
  *P. hawaiiensis** Gilbert, 1905
  P. praelonga Alcock, 1894
  P. plinthus (Jordan and Starks, 1904)
  *P. natalensis** Norman, 1931
  *P. megalepis** Fowler, 1934
  P. albomarginata Reid, 1934
  *P. albomaculata** Norman, 1939
  *P. zanzibarensis** Norman, 1939
Genus *Nematops* Günther, 1880
  *N. microstoma** Günther, 1880
  *N. grandisquama** Weber and Beaufort, 1929
  N. macrochirus Norman, 1931
  *N. chui** Fowler, 1934
Genus *Marleyella* Fowler, 1925
  *M. bicolorata** (Bonde, 1922)
  *M. maldivensis** Norman, 1939
Subfamily Rhombosoleinae
Genus *Oncopterus* Steindachner, 1875
  *O. darwinii** Steindachner, 1875
Genus *Psammodiscus* Günther, 1862
  *P. ocellatus** Günther, 1862
Genus *Pelotretis* Waite, 1911
  P. flavilatus Waite, 1911
Genus *Azygopus* Norman, 1926
  A. pinnifasciatus pinnifasciatus Norman, 1926
  *A. p. flemingi*** Nielsen, 1961

Genus *Ammotretis* Günther, 1862
- *A. rostratus* Günther, 1862
- *A. brevipinnis** Norman, 1926
- *A. lituratus* (Richardson, 1849)
- *A. macrolepis** McCulloch, 1914
- *A. elongatus* McCulloch, 1914

Genus *Taratretis* Last, 1978
- *T. derwentensis* Last, 1978

Genus *Colistium* Norman, 1926
- *C. nudipinnis** (Waite, 1911)
- *C. guntheri** (Hutton, 1873)

Genus *Rhombosolea* Günther, 1862
- *R. retiaria** Hutton, 1873
- *R. plebeia* (Richardson, 1843)
- *R. tapirina* Günther, 1862
- *R. leporina* Günther, 1862

Genus *Peltorhamphus* Günther, 1862
- *P. novaezeelandiae* Günther, 1862
- *P. latus* James, 1972
- *P. tenuis** James, 1972

Subfamily Samarinae

Genus *Samaris* Gray, 1831
- *S. cristatus* Gray, 1831
- *S. delagoensis*** Bonde, 1925
- *S. macrolepis** Norman, 1927

Genus *Plagiopsetta* Franz, 1910
- *P. glossa* Franz, 1910

Genus *Samariscus* Gilbert, 1905
- *S. corallinus** Gilbert, 1905
- *S. macrognathus** Fowler, 1934
- *S. latus* Matsubara and Takamuki, 1951
- *S. longimanus** Norman, 1927
- *S. sunieri** Weber and Beaufort, 1929
- *S. xenicus* Ochiai and Amaoka, 1962
- *S. inornatus** (Lloyd, 1909)
- *S. luzonensis** Fowler, 1934
- *S. asanoi** Ochiai and Amaoka, 1962
- *S. maculatus** (Günther, 1880)
- *S. japonicus** Kamohara, 1936

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* Though these species or subspecies could not be dissected in the present study, they were assigned to each subfamily and genus judging from certain subfamilial and generic features obtained using radiographs and the previous descriptions (some species or subspecies were observed externally).

** These species or subspecies were assigned to each subfamily and genus using only the previous descriptions, since no specimens and radiographs were available in the present study.

*S. huysmani** Weber, 1913
*S. fasciatus** Fowler, 1934
*S. triocellatus** Woods in Schultz, Woods and Lachner, 1966

VIII. Summary

The present study attempts to clarify the interrelationships of the fishes of the family Pleuronectidae and to classify the species on the basis of these interrelationships. The specimens of 77 species or subspecies of 114 known species collected from nearly all the waters of the world were used for the comparative morphology. The following 12 skeletal parts of each specimen were examined: jaw apparatus, cranium, orbital bones, suspensorium and opercular apparatus, hyoid arch, branchial apparatus and gill rakers, fins, pectoral girdle, pelvic girdle, urohyal, vertebrae and their accessory bones, and caudal skeleton and fin. In addition to skeletons, some external and additional internal characters were examined.

In order to elucidate the interrelationships of the family, numerical phenetics (Sneath and Sokal, 1973) was applied as a systematic methodology. The similarity between every OTU (species or subspecies) was calculated using Gower's coefficient of similarity with a slight modification on 78 morphological characters lacking intraspecific variation. Each OTU was grouped by cluster analysis, UPGMA in the present study, on the basis of the similarity between every OTU. The result of the cluster analysis was represented by means of the dendrogram which showed the interrelationships of the pleuronectids. Then, the species were ranked to supraspecific taxa, genus and subfamily, by selecting a level of phenetic similarity (phenon lines).

Four subfamilies were recognized in the present study.

(1) The subfamily Pleuronectinae is characterized in having the first neural arch. *Paralichthodes algoensis* which has been treated as a member of the Samarinae, or as only a member of the Paralichthodinae or the Paralichthodidae was found to be more closely related to the species of the Pleuronectinae than those of any other subfamily, and was included in this subfamily for the first time. This subfamily contains 63 species or subspecies in 21 genera.

(2) The subfamily Poecilopsettinae is characterized by the following features: both prefrontals are attached to each other on the lower part of the anterior portion of the frontal of the ocular side, and the preorbital is absent on the blind side. This subfamily comprises 17 species in three genera.

(3) The subfamily Rhombosoleinae is characterized by the following features: the pelves are very asymmetrical, and the anteroventral tip of the pelvis of the ocular side extends forward beyond the cleithrum. This subfamily is composed of 20 species or subspecies in nine genera.

(4) The subfamily Samarinae is characterized by the following features: both prefrontals are attached to each other on the upper part of the anterior portion of the frontal of the ocular side, the prefrontal of the blind side is attached to the frontal of the ocular side in the middle part of the orbital cavity of the upper eye, the frontal of the ocular side is widely articulated to the parasphenoid at the interorbital region, the metapterygoid is small in size, the pectoral fin is absent on the blind side ,

the scapula and the coracoid are absent on the blind side, the pleural rib and the epipleural are absent, the epicentrum and the hypomeral are present, the first preural centrum is fused with the second-third-fourth hypural plate, and the composition of the hypurals is hp 1, 2+3+4, 5. This subfamily consists of 18 species in three genera.

IX. Literature cited

Amaoka, K. 1969. Studies on the sinistral flounders found in the waters around Japan. Taxonomy, anatomy and phylogeny. *J. Shimonoseki Univ. Fish.*, **18**(2): 65-340, figs. 1-131.

Amaoka, K. 1972. Osteology and relationships of the citharid fish *Brachypleura novaezeelandiae*. *Japan. J. Ichthyol.*, **19**(4): 263-273, figs. 1-4.

Amaoka, K. 1979. Phylogeny and larval morphology of pleuronectiform fishes (Psettodidae, Citharidae, Paralichthyidae and Bothidae). *Kaiyo Kagaku*, **11**(2): 100-110, figs. 1-12. In Japanese.

Berg, L.S. 1940. Classification of fishes, both recent and fossil. *Trav. Inst. Zool. Acad. Sci. USSR*, **5**(2): 87-345, figs. 1-190. In Russian.

Boyce, A.J. 1969. Mapping diversity: a comparative study of some numerical methods, pp. 1-31. *In* A.J. Cole, ed., *Numerical taxonomy*. Academic Press, London, xv+324 pp.

Campos, H. 1979. Multivariate analysis of the taxonomy of the family Galaxiidae. *Zool. Anz., Jena*, **202**(3/4): 280-288, figs. 1-3.

Chabanaud, P. 1936. Le neurocrane osseux des téléostéens dyssymétriques après la métamorphose. *Ann. Inst. Océanogr.*, **16**: 223-297, figs. 1-112.

Chabanaud, P. 1954. Révision des soleides du genre *Pegusa*. Description d'une espèce inédite. *Bull. Inst. fr. Afr. noire*, **16**, *sér. A*, (1): 245-282, figs. 1-20.

Cole, F.J. and J. Johnstone. 1901. *Pleuronectes*. (The plaice.). *Mem. Liverpool mar. Biol. Comm.*, **8**: i-viii+1-252, figs. 1-5, pls. 1-11.

Colless, D.H. 1966. A note on Wilson's consistency test for phylogenetic hypotheses. *Syst. Zool.*, **15** (4): 358-359.

Colless, D.H. 1967. The phylogenetic fallacy. *Syst. Zool.*, **16**(4): 289-295.

Cowan, I.M. 1972. Comparative morphology of the cottid genus *Myoxocephalus* based on meristic, morphometric, and other anatomical characters. *Can. J. Zool.*, **49**: 1479-1496, figs. 1-57.

Dingerkus, G. and L.D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Tech.*, **52**(4): 229-232, figs. 1-3.

Eldredge, N. 1979. Cladism and common sence, pp. 165-198, figs. 1-9. *In* J. Cracraft, and N. Eldredge, eds., *Phylogenetic analysis and paleontology*. Columbia Univ. Press, New York, 233 pp., 35 figs.

Eldredge, N. and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process*. Columbia Univ. Press, New York, viii+349 pp., 6 figs.

Farris, J.S. 1969. On the cophenetic correlation coefficient. *Syst. Zool.*, **18**(3): 279-285, fig. 1.

Fitch, J.E. 1963. A review of the fishes of the genus *Pleuronichthys*. *Contrib. Sci., Los Angels County Mus.*, (76): 1-33, figs. 1-7.

Fowler, H.W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Proc. Acad. nat. Sci. Philad.*, **85**: 233-367, figs. 1-117.

Frame, D.W., T.J. Andrews and C.F. Cole. 1978. Osteology of the American plaice, *Hippoglossoides platessoides*. *Postilla*, (173): 1-32, figs. 1-13.

Gower, J.C. 1971. A general coefficient of similarity and some of its properties. *Biometrics*, **27**: 857-871.

Gregory, W.K. 1933. Fish skulls. A study of the evolution of natural mechanisms. *Trans. Amer. phil. Soc.*, **23**(2): i-vii+75-481, figs. 1-302.

Groot, S.J. de. 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). *Neth. J. Sea Res.*, **5**(2): 121-196, figs. 1-21.

Hecht, M.K. and J.L. Edwards. 1977. The methodology of phylogenetic inference above the species level, pp. 3-51, figs. 1-6. *In* M.K. Hecht, P.C. Goody and B.M. Hecht, eds., *Major patterns in vertebrate evolution*. Plenum Press, New York, ix+908 pp., 166 figs.

Hennig, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana, xv+263 pp., 69 figs.

Hikita, T. 1934. Flat-fishes found in northern Japan. *Suisan Kenkyu Ihou*, **4**: 187-296, pls. 1-29. In Japanese.

Hotta, H. 1961. *Comparative study of the axial skeleton of Japanese Teleostei*. Nippon Gyogaku Shinkokai, Tokyo, 155+10 pp., 70 pls. In Japanese.

Hubbs, C.L. 1945. Phylogenetic position of the Citharidae, a family of flatfishes. *Misc. Publ. Mus. Zool., Univ. Michigan*, (63): 1-33, fig. 1.

Hubbs, C.L. and N.J. Wilimovsky. 1964. Distribution and synonymy in the Pacific Ocean, and variation, of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum). *J. Fish. Res. Bd. Can.*, **21**(5): 1129-1154, figs. 1-5.

James, G.D. 1972. Revision of the New Zealand flatfish genus *Peltorhamphus* with descriptions of two new species. *Copeia*, **1972**(2): 345-355, figs. 1-7.

Jordan, D.S. 1919. New genera of fishes. *Proc. Acad. nat. Sci. Philad.*, **70**: 341-344.

Jordan, D.S. 1923. A classification of fishes including families and genera as far as known. *Stanford Univ. Publ., Univ. Ser., Biol. Sci.*, **3**(2): 77-243+i-x.

Kato, F., M. Okiyama and M. Tajima. 1974. External morphology and discrimination of two species of flounders belonging to the genus *Limanda* (*L. yokohamae*, and *L. herzensteini*) from the Japan Sea. *Bull. Japan Seas Reg. Fish. Res. Lab.*, (25): 63-87, figs. 1-10. In Japanese.

Kim, Y.U. 1973. Comparative osteology of the right-eye flounders, subfamily Pleuronectinae fishes. *Publ. mar. Lab. Pusan Fish. Coll.*, **6**: 1-38, figs. 1-6. In Korean.

Kluge, A.G. and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.*, **18**(1): 1-32, figs. 1-6.

Kuronuma, K. 1938. *Studies on the heterosomate fishes of Japan*. Ph.D. Thesis, Univ. Michigan, 119 pp., 8 pls. Unpublished.

Kyle, H.M. 1921. The asymmetry, metamorphosis and origin of flat-fishes. *Phil. Trans. R. Soc. London*, (*B*), **211**: 75-129, figs. 1-101, pls. 4-10.

Last, P. 1978. A new genus and species of flounder (F. Pleuronectidae) with notes on other Tasmanian species. *Pap. Proc. R. Soc. Tasm.*, **112**: 21-28, pl. 1.

Li, S. 1981. On the origin, phylogeny and geographical distribution of the flatfishes (Pleuronectiformes). *Trans. Chinese ichthyol. Soc.*, (1): 11-20, figs. 1-3. In Chinese.

Lockington, W.N. 1879. Review of the Pleuronectidae of San Francisco. *Proc. U.S. Natn. Mus.*, **2**: 69-108.

Løvtrup, S. 1977. *The phylogeny of vertebrata*. John Wiley and Sons, New York, xii+330 pp., 5 figs.

Lundberg, J.G. 1972. Wagner networks and ancestors. *Syst. Zool.*, **21**(4): 398-413, figs. 1-5.

Maslin, T.P. 1952. Morphological criteria of phyletic relationships. *Syst. Zool.*, **1**(1): 49-70, figs. 1-19.

Matsubara, K., A. Ochiai and T. Iwai. 1979. *Ichthyology*. Koseishakoseikaku, Tokyo, vii+375 pp., 32 figs. In Japanese.

Mayr, E. 1965. Numerical phenetics and taxonomic theory. *Syst. Zool.*, **14**(1): 73-97, figs. 1-3.

Mayr, E. 1969. *Principles of systematic zoology*. McGraw-Hill, New York, xi+428 pp., 65 figs.

Mayr, E. 1976. Cladistic analysis or cladistic classification?, pp. 433-476, figs. 1-7. *In Evolution and the diversity of life. Selective essays*. Belknap Press of Harvard Univ. Press, Cambridge, ix+721 pp., 11 figs.

McAllister, D.E. 1968. The evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of teleostome fishes, living and fossil. *Natn. Mus. Canada, Bull.*, (211), *Biol. Ser.*, (77): i-xiv+1-239, figs. 1-3, pls. 1-21.

Nelson, J.S. 1976. *Fishes of the world*. John Wiley and Sons, New York, xiii+416 pp., many figs.

Norman, J.R. 1934. *A systematic monograph of the flatfishes (Heterosomata). 1. Psettodidae, Bothidae, Pleuronectidae*. Brit. Mus. nat. Hist., London, viii+459 pp., 317 figs.

Ochiai, A. 1966. Studies on the comparative morphology and ecology of the Japanese soles. *Misaki* *mar. biol. Inst., Kyoto Univ., Spec. Rep.*, (3) : 1-97, figs. 1-39, pls. 1-2. In Japanese.

Okisu, H. and T. Yusa. 1979. Changes of dental numbers with growth in *Limanda yokohamae* (Günther) and discrimination of the species from *L. herzensteini* Jordan et Snyder. *Bull. Tohoku Reg. Fish. Res. Lab.*, (40) : 27-36, figs. 1-8, pl. 1. In Japanese.

Okiyama, M. and S. Ueyanagi. 1978. Interrelationships of scombrid fishes: an aspect from larval morphology. *Bull. Far Seas Fish. Res. Lab.*, (16) : 103-113, figs. 1-3.

Presh, W. 1979. Phenetic analysis of a single data set: Phylogenetic implications. *Syst. Zool.*, **28** (3) : 366-371, figs. 1-2.

Regan, T. 1910. The origin and evolution of the teleostean fishes of the order Heterosomata. *Ann. Mag. nat. Hist.*, (8)**6** : 484-496.

Regan, T. 1920. A revision of the flat-fishes (Heterosomata) of Natal. *Ann. Durban Mus.*, **2** : 205-222, figs. 1-5.

Regan, T. 1929. Fishes, pp. 305-329. *In Encyclopedia Britannica*, 14th ed., IX.

Ross, H.H. 1974. *Biological systematics.* Addison-Wesley Publishing Company, Reading, vi+345 pp., 12 figs.

Sawada, Y. 1982. Phylogeny and zoogeography of the superfamily Cobitoidea (Cyprinoidei, Cypriniformes). *Mem. Fac. Fish. Hokkaido Univ.*, **28**(2) : 65-223, figs. 1-112.

Schaeffer, B., M.K. Hecht and N. Eldredge. 1972. Phylogeny and paleontology. *Evol. Biol.*, **6** : 31-46, figs. 1-2.

Sneath, P.H.A. and R.R. Sokal. 1973. *Numerical taxonomy. The principles and practice of numerical classification.* W.H. Freeman and Company, San Francisco, xv+573 pp., 81 figs.

Sokal, R.R. and F.J. Rohlf. 1962. The comparison of dendrograms by objective methods. *Taxon*, **11** : 33-40.

Sokal, R.R. and P.H.A. Sneath. 1963. *Principles of numerical taxonomy.* W.H. Freeman and Company, San Francisco, xvi+359 pp., 38 figs.

Spain, A.V., C.J. Grant and D.F. Sinclair. 1980. Phenotypic affinities of 11 species of Australian mullet (Pisces: Mugilidae). *Aust. J. mar. Freshwater Res.*, **31** : 69-83, figs. 1-3.

Traquair, M.D. 1865. On the asymmetry of the Pleuronectidae, as elucidated by an examination of the skeleton in the turbot, halibut, and plaice. *Trans. Linn. Soc. London*, **25** : 263-296, pls. 29-32.

Uyeno, T. 1975. Pisces, pp. 176-242, figs. 1-43. *In* T. Shikama, ed., *Paleontology*. 3. Asakura Shoten, Tokyo, iii+527 pp. In Japanese.

Watrous, L.E. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. *Syst. Zool.*, **30**(1) : 1-11, figs. 1-8.

Wiley, E.O. 1981. *Phylogenetics. The theory and practice of phylogenetic systematics.* John Wiley and Sons, New York, xv+439 pp., 11 figs.

Wilson, E.O. 1965. A consistency test for phylogenies based on contemporaneous species. *Syst. Zool.*, **14**(3) : 214-220, figs. 1-3.

Wilson, E.O. 1967. The validity of the "Consistency test" for phylogenetic hypotheses. *Syst. Zool.*, **16**(1) : 104.

Wu, H.-W. 1932. *Contribution à l'étude morphologique, biologique et systématique des poissons hétérosomes (Pisces Heterosomata) de la Chine.* Thèse Univ. Paris, 179 pp., 26 figs.

Yazudani, G.M. 1969. Adaptation in the jaws of flatfish (Pleuronectiformes). *J. Zool., London*, **159** : 181-222, figs. 1-18.