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Encephalization in Gobioidei (Teleostei)

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Abstract We have measured the brain and body weight and determined the encephalization index for 180 species of fishes belonging to six families of the suborder Gobioidei. Within the Teleostei, these fishes exhibit a remarkably broad range in the values of their encephalization indices, but most values are in the low to middle range. Within the Gobioidei there is relatively little difference in the degree of encephalization among the different families and subfamilies except the Kraemeriidae and Amblyopinae which have low encephalization indices and the Oxudercinae (including *Periophthalmus*) and Rhyacichthyidae which are highly encephalized. We have shown that the form of the body has an effect on the degree of encephalization. Elongate fishes have low values, probably because of the excessive mass of their body skeleton which raises the body weight relative to the brain size. The environment in which the fishes live is correlated, in general, with their relative brain size. The values of the encephalization index arranged from low to high by habitat are as follows: mud-dwelling fishes, fresh-water fishes, brackish-water fishes, burrowing marine fishes, free-living marine fishes, torrent fishes and amphibious fishes. The low values of the Amblyopinae and Kraemeriidae can be explained in terms of their being both mud-dwelling and elongate.

The teleost suborder Gobioidei includes the Gobiidae, the family with the largest number of species (2,000 or more), and five other families. These fishes are small in general, carnivorous, benthic or bottom-oriented, and many have the pelvic fins joined to form a sucking disc. They differ greatly in morphology, from stout-bodied to very elongate. They differ even more markedly in the variety of habitats they occupy and the ecological adaptations they have acquired for these diverse habitats. They occur in fresh, brackish and salt water. In the sea they are found from the littoral zone to deep water and on a variety of substrata from mud bottoms to rocky surfaces and coral reefs. Many are commensal on sessile invertebrates such as corals, gorgonians and sponges. Some are symbiotic, such as those which share a burrow with alpheid shrimps and those which clean other fishes. In freshwater they occupy a variety of habitats from the calm water of lakes or pools to torrential streams. Most remarkable are amphibious species such as those of the genus *Periophthalmus*, which are most often encountered in mangrove areas.

We became curious whether there would be any differentiation of the brain of gobioid fishes that might be correlated with the plethora of biotopes they occupy. An initial study of a few species (Kassem, 1987; Kassem et al., 1989) was promising and led us to undertake the present broad study of the group.

It has been difficult to obtain material of gobioid fishes from many different habitats for our research, but thanks to the help from numerous specialists on gobies and related fishes, we have been able to assemble the data for this paper. We are thankful also for the information provided by the specialists on the biology of these fishes.

Material and methods

Table 1 gives the list of the 180 species of Gobioidei we have investigated. Specimens have been obtained from our own collecting in the field (French coasts, Réunion, Red Sea (Elat, Israel), Hawaii, Marshall Islands, Australia, New-Caledonia and Southern India), from collections of the Muséum National d'Histoire Naturelle (Paris) and gifts from colleagues. These fishes belong to 99 genera and to 10 different families and subfamilies of the Gobioidei. We adopted the classification of Hoese (1984) which is also shown

Table 1. Brain-body weight relationship in Gobioidei. The figures after each genus name represent the mean encephalization indices. x, ecological group (a, amphibious fish; f, fresh-water fish; s, sea-water fish; b, brackish-water fish; m, mud-living fish; t, torrent-water fish); (n), number of specimens; LT, total length (mm); cc, condition coefficient; Bw, body weight (g); bw, brain weight (mg); i, encephalization index.

	x	n	LT/cc	Bw/bw	i
Rhyacichthyidae					
Rhyacichthys (143)					
R. aspro (Kuhl et Van Hasselt, 1837): Japan	t	(1)	225/16.3	185.8/168.1	143
Eleotrididae					
Bostrychus (70)					
B. sinensis (Lacepède, 1801): West Pacific	b	(4)	140/16.3	44.7/44.7	70
Butis (104)					
B. amboinensis (Bleeker, 1853): Fiji, Japan	b	(4)	136/11.2	28.2/40.6	93
B. butis (Hamilton-Buchanan, 1822): Australia, Japan	b	(4)	145/12.9	39.5/69.2	115
Dormitator (71)					
D. latifrons (Richardson, 1837): Panama	f	(4)	150/16.5	55.8/50.5	71
Eleotris (51)					
E. acanthopoma Bleeker, 1853: Japan	b	(2)	80/15.0	7.67/13.4	51
E. fusca (Bloch et Schneider, 1801): Japan	b	(2)	260/15.7	276/84.0	51
E. melanosoma Bleeker, 1852: Japan, Philippines	b	(7)	170/17.0	83.4/49.4	53
E. oxycephala Temminck et Schlegel, 1845: Japan	f	(2)	210/15.4	142.6/63.6	52
E. sandvicensis Vaillant et Sauvage, 1875: Hawaii	b	(2)	155/15.4	57.4/37.5	50
Erotelis (52)					
E. smaragdus (Val., 1837): West Colombia	b	(4)	200/6.8	54.7/38.8	52
Gobiomorphus (80)					
G. australis (Krefft, 1864): Australia	b	(2)	175/13.8	73.7/57.7	75
G. coxii (Krefft, 1864): Australia	b	(2)	120/13.7	23.6/38.8	84
Gobiomorus (60)					
G. dormitor Lacepède, 1800: Colombia	f	(4)	900/10.3	7508/381	60
Hypseleotris (133)					
H. aurea (Shipway, 1950): Australia	t	(2)	55/8.5	1.41/14.4	154
H. galii (Ogilby, 1898): Australia	f	(2)	55/9.2	1.53/8.86	111
Microphilypnus (105)					
M. sp.: Venezuela	f	(1)	25/9.1	0.143/2.18	105
Mogurnda (126)					
M. mogurnda (Richardson, 1844): Australia	b	(1)	200/26.6	213/160	126
Odontobutis (65)					
O. obscura (Temminck et Schlegel, 1846): Japan	f	(2)	175/20.5	110/65.4	65
Ophieleotris (70)					
O. aporos (Bleeker, 1854): Australia	b	(2)	290/11.3	275/108.4	70
Ophiocara (98)					
O. porocephala (Val., 1837): Japan	f	(4)	340/21.0	824/235	98
Prionobutis (152)					
P. microps (Weber, 1980): Australia	b	(2)	230/11.0	134/152.4	152
Xenisthmidae					
Xenisthmus (105)					
X. polyzonatus (Klunzinger, 1871): Australia	s	(1)	25/11.6	0.18/1.64	63
X. sp.: Rotuma	s	(2)	25/9.4	0.15/3.00	147
Microdesmidae					
Microdesminae					
Gunnellichthys (47)					
G. monostigma Smith, 1958: Japan	s	(1)	90/2.5	1.81/5.50	47
Microdesmus (15)					
M. retropinnis Jordan et Gilbert, 1882: Colombia	s	(2)	110/1.5	1.95/2.74	15

(Table 1, continued)

	x	n	LT/cc	Bw/bw	i
Ptereleotrinae					
Parioglossus (73)					
P. raoi (Herre, 1939): New Guinea, Japan	b	(2)	30/9.2	0.250/2.28	73
Ptereleotris (134)					
P. hanae (Jordan et Starks, 1906): Pacific	s	(2)	125/5.3	10.4/36.2	134
P. microlepis (Bleeker, 1856): Marshall	s	(1)	125/6.3	12.3/39.5	133
Kraemeriidae					
Kraemeria (20)					
K. cunicularia Rofen, 1958: Japan	m	(2)	45/3.8	0.35/0.906	18
K. nudum (Regan, 1908): Red Sea	m	(2)	40/3.9	0.249/1.07	22
Gobiidae					
Oxudercinae (Periophthalminae)					
Boleophthalmus (62)					
B. pectinitrostris (Linnaeus, 1758): Japan	b	(2)	190/6.9	47.2/41.7	62
Oxuderces (97)					
O. dentatus Eydoux et Souleyet, 1848: Malaysia	a	(2)	95/7.7	6.59/21.1	97
Periophthalmus (166)					
P. cantonensis novaeguineensis Eggert, 1935: Australia	a	(2)	85/21.4	13.1/81.3	261
P. koelreuteri africanus Eggert, 1935: Madagascar	a	(1)	125/8.6	16.7/43.8	130
P. koelreuteri koelreuteri (Pallas, 1770): N-Caledonia	a	(1)	150/9.5	32.1/87.2	179
P. papilio Bloch et Schneider, 1801: Africa	a	(2)	165/11.3	50.8/115	185
P. schlosseri australis (Castelnau, 1875): Australia	a	(1)	255/10.1	167.5/166.7	178
P. sobrinus Eggert, 1935: Madagascar	a	(3)	150/14.1	47.5/79.2	136
P. vulgaris Eggert, 1935: New Caledonia	a	(1)	105/7.8	9.03/28.6	120
Scartelaos (154)					
S. histophorus (Val., 1837): Australia	a	(1)	140/5.8	15.9/37.3	126
S. viridis (Hamilton-Buchanan, 1822): Australia	s	(3)	145/7.9	24.1/82.8	182
Amblyopinae (Trypaucheninae)					
Ctenotrypauchen (32)					
C. microcephalus (Bleeker, 1860): Pacific	m	(2)	180/4.4	25.7/18.1	32
Taenioides (49)					
T. cirratus (Blyth, 1860): Japan	m	(2)	300/4.2	114.5/48.3	45
T. limicola Smith, 1964: Japan	m	(2)	65/3.4	0.97/3.85	48
T. rubicundus (Hamilton, 1822): Japan	m	(2)	300/2.5	66.3/35.7	44
Trypauchen (27)					
T. vagina Bloch et Schneider, 1801: India	m	(17)	222/4.4	48.5/22.9	27
Trypauchenichthys (27)					
T. sumatrensis Hardenberg 1931: Malaysia	m	(2)	65/5.6	1.54/3.36	27
Sicydiinae (Tridentigerinae)					
Sicydium (57)					
S. brevifile Ogilvie-Grant, 1884: Ivory Coast	f	(1)	105/12.0	13.8/18.5	53
S. salvini Grant, 1884: Panama	f	(4)	125/13.4	26.1/31.1	60
Sicyopterus (94)					
S. lagocephalus (Pallas, 1774): Péunion	f	(5)	110/11.2	14.9/31.5	92
S. pugnans (Ogilvie-Grant, 1824): Tahiti	f	(4)	72/16.1	6.00/20.7	97
S. taeniurus (Günther, 1877): Tahiti	f	(6)	110/16.4	21.8/37.6	91
Stiphodon (101)					
S. elegans (Steindachner, 1879): Tahiti	f	(5)	50/14.8	1.85/11.25	105
S. stevensoni (Jordan et Seale, 1905): Tahiti	f	(4)	52/12.8	1.80/9.55	96
Tridentiger (108)					
T. obscurus (Temminck et Schlegel, 1845): Japan	s	(6)	85/21.2	13.0/26.9	83
T. trigonocephalus (Gill, 1858): Japan	s	(6)	110/15.4	20.5/52.0	133

(Table 1, continued)

	x	n	LT/cc	Bw/bw	i
Gobiinae					
Acanthogobius (83)					
A. flavimanus (Temminck et Schlegel, 1845): Japan	b	(3)	300/10.0	271.0/123.5	83
Acentrogobius (117)					
A. caninus (Val., 1837): Australia	b	(3)	130/22.5	49.3/83.1	127
A. gracilis (Val., 1837): Australia	b	(2)	140/18.4	50.5/75.1	118
A. viridipunctatus (Val., 1837): Thailand	b	(4)	165/13.5	60.7/69.1	107
Amblychaeturichthys (228)					
A. hexanema (Bleeker, 1853): Japan	s	(1)	70/10.0	3.44/30.9	221
A. sciistius (Jordan et Snyder, 1901): Japan	s	(4)	60/12.1	2.63/31.4	254
Amblyeleotris (123)					
A. guttata (Fowler, 1938): New Caledonia	s	(1)	100/12.9	12.9/41.8	132
A. japonica Takagi, 1957: New Caledonia	s	(1)	85/16.2	10.0/37.1	134
A. sp.: Marshall	s	(1)	75/15.4	6.50/28.7	132
A. steinitzi (Klausewitz, 1974): Red Sea	s	(1)	75/10.6	4.45/14.2	97
A. sungami (Klausewitz, 1969): Red Sea	s	(2)	82/13.8	7.62/27.3	120
Amblygobius (144)					
A. albimaculatus (Rüppell, 1830): Red Sea	s	(4)	180/12.6	73.5/83.2	123
A. phalaena (Val., 1837): Pacific Ocean	s	(7)	126/16.2	32.4/93.6	174
A. semicinctus (Bennett, 1833): New Caledonia	s	(2)	126/16.3	32.6/64.8	136
Amoya (101)					
A. chusanensis (Herre, 1940): Australia	s	(2)	72/15.3	5.71/18.9	97
A. moloanus (Herre, 1927): Fiji	b	(2)	80/11.2	5.76/21.4	104
Arenigobius (65)					
A. frenatus Günther, 1861: Australia	b	(6)	100/10.9	10.94/19.9	65
Asterropteryx (104)					
A. semipunctatus Rüppell, 1830: Indo-Pacific	s	(6)	65/18.5	5.08/19.4	104
Awaous (77)					
A. ocellaris (Broussonet, 1782): Tahiti	f	(4)	155/15.5	57.9/55.2	77
Bathygobius (105)					
B. cocosensis (Bleeker, 1854): Australia, S. Africa	s	(8)	120/14.3	24.8/58.8	125
B. cyclopterus (Val., 1837): Red Sea	b	(10)	75/13.5	5.78/23.0	112
B. fuscus (Rüppell, 1830): Japan	s	(6)	85/19.8	12.17/38.4	130
B. kreffti (Steindachner, 1866): Australia	b	(10)	120/14.1	24.4/35.0	84
B. meteori (Klausewitz et Zander, 1967): Red Sea	s	(2)	30/11.7	0.316/2.54	78
B. niger (Smith, 1960): India	s	(2)	66/26.4	7.59/28.6	118
B. soporator (Val., 1837): Ghana	s	(3)	120/14.7	25.4/40.2	91
Brachygobius (107)					
B. sua (Smith, 1931): Thailand	b	(2)	42/31.5	2.34/12.7	107
Caffrogobius (116)					
C. caffer (Günther, 1875): South Africa	b	(7)	180/17.7	103.5/108.5	118
C. multifasciatus Smith, 1959: South Africa	b	(12)	150/14.1	47.7/60.7	106
C. saldanha (Barnard, 1927): South Africa	b	(3)	125/15.8	30.8/64.1	125
Callogobius (62)					
C. sclateri (Steindachner, 1880): N. Caledonia	s	(1)	70/29.1	10.0/18.1	62
Chaenogobius (124)					
C. castaneus (O'Shaughnessy, 1875): Japan	f	(4)	70/13.3	4.55/20.8	121
C. cylindricus Tomiyama, 1936: Japan	b	(2)	48/10.9	1.21/11.5	148
C. heptacanthus (Hilgendorf, 1878): Japan	s	(6)	50/11.3	1.41/13.2	156
C. isaza Tanaka, 1916: Japan	f	(2)	80/14.2	7.26/21.5	93
C. laevis (Steindachner, 1879): Japan	f	(2)	65/13.1	3.60/23.7	162
C. macrognathus (Bleeker, 1860): Japan	b	(4)	32/8.5	0.28/3.66	115

(Table 1, continued)

	x	n	LT/cc	Bw/bw	i
C. uchidai (Takagi, 1957): Japan	f	(2)	45/8.8	0.80/7.22	118
C. urotaenia (Hilgendorf, 1878): Japan	f	(6)	100/16.0	16.0/29.3	81
Chasmichthys (152)					
C. gulosus (Guichenot-Sauvage, 1882): Japan	s	(4)	110/15.8	21.2/59.5	152
Chonophorus (44)					
C. lateristriga (Duméril, 1861): Guinea	f	(1)	265/11.2	208/65.3	44
Cryptocentroides (65)					
C. cristatus (Macleay, 1881): Australia	s	(4)	120/11.3	19.5/27.2	65
Ctenogobius (102)					
C. fasciatus Gill, 1883: Barbados	b	(1)	69/10.5	3.43/15.2	102
Deltentosteus (68)					
D. quadrimaculatus (Val., 1837): Red Sea	s	(2)	80/10.9	5.58/14.2	68
Drombus (110)					
D. triangularis (Weber, 1909): Australia	b	(1)	75/19.6	8.26/26.8	110
Eviota (121)					
E. albilineata Jewett et Lachner, 1983: Salomon	s	(2)	32/13.8	0.449/7.27	159
E. monostigma Fourmanoir, 1971: Australia	s	(1)	32/12.8	0.420/3.67	97
E. prasina (Klunzinger, 1871): Salomon	s	(1)	35/14.1	0.604/7.12	134
E. sp.: Marshall	s	(1)	25/22.4	0.350/3.20	95
Exyrias (81)					
E. puntang (Bleeker, 1852): Australia	b	(1)	162/10.4	44.0/50.0	81
Favonigobius (113)					
F. lateralis (Macleay, 1881): Australia	f	(6)	88/9.7	6.63/16.8	85
F. melanobranchus (Fowler, 1934): Australia	b	(4)	83/11.0	6.28/29.4	136
F. reichei (Bleeker, 1853): South Africa	s	(6)	83/12.1	6.90/32.9	143
F. tamarensis (Johnston, 1883): Australia	b	(2)	110/12.5	16.7/28.5	86
Fusigobius (141)					
F. sp.: Red Sea	s	(2)	80/18.5	9.45/36.1	141
Gillichthys (89)					
G. mirabilis Cooper, 1863: West Mexico	s	(5)	210/13.1	121.6/90.2	89
Gladiogobius (96)					
G. ensifer Herre, 1933: New Guinea	b	(4)	55/12.5	2.08/10.7	96
Glossogobius (115)					
G. biocellatus (Val., 1837): Fiji	b	(2)	100/10.9	10.9/27.9	105
G. callidus (Smith, 1937): South Africa	b	(5)	120/10.8	18.7/48.9	123
G. circumspectus (Macleay, 1883): Australia	b	(2)	350/8.8	377/196	116
G. giuris (Hamilton-Buchanan, 1822): Austr., S. Afr.	b	(8)	500/10.2	1278/329.5	113
Gnatholepis (95)					
G. anjerensis (Bleeker, 1850): Hawaii, Red Sea	s	(5)	80/13.9	7.11/21.6	95
Gobiodon (120)					
G. citrinus (Rüppell, 1838): Red Sea	s	(2)	62/22.1	5.27/16.1	98
G. erythrospilus Bleeker, 1875: Marshall	s	(1)	54/21.4	3.38/20.0	131
G. rivulatus (Rüppell, 1830): Salomon	s	(1)	50/27.5	3.44/19.9	130
Gobionellus (93)					
G. oceanicus (Pallas, 1770): Guyana	b	(3)	200/5.5	44.1/56.2	93
Gobiopsis (60)					
G. malekulae (Herre, 1931): Philippines	s	(2)	30/10.0	0.274/2.07	60
Gobiopterus (116)					
G. chuno (Hamilton-Buchanan, 1822): Thailand	f	(5)	27/11.0	0.216/3.04	114
G. semivestitus (Munro, 1949): Australia	s	(1)	27/8.1	0.160/2.60	117
Gobiosoma (64)					
G. paradoxa (Günther, 1861): Panama	s	(3)	40/14.5	0.925/4.72	64
Gobius (140)					

(Table 1, continued)

	x	n	LT/cc	Bw/bw	i
G. cobitis Pallas, 1811: France	s	(1)	300/11.9	322/228	146
G. couchi Miller et El-Tawil, 1974: England	s	(2)	150/11.8	39.8/78.5	142
G. niger Linnaeus, 1758: France, Red Sea	s	(6)	150/12.1	40.7/58.1	118
G. paganellus Linnaeus, 1758: France	s	(53)	125/11.0	21.5/65.2	155
Gobiusculus (146)					
G. flavescens (Fabricius, 1779): France	s	(1)	60/11.1	2.40/17.1	146
Heterеleotris (97)					
H. zonata (Fowler, 1934): South Africa	s	(2)	60/12.8	2.77/12.8	97
Istigobius (100)					
I. decoratus (Herre, 1927): Oman, Red Sea	s	(4)	130/13.9	30.5/48.6	98
I. ornatus (Rüppell, 1830): New Caledonia	s	(3)	100/13.0	13.0/24.8	86
I. rigilius (Herre, 1953): Marshall	s	(1)	108/13.3	16.8/45.4	117
Knipowitschia (101)					
K. caucasica (Kawrajsky-Berg, 1916): Roumania	b	(2)	40/11.2	0.715/5.93	101
Lesueurigobius (69)					
L. suerii (Risso, 1810): Red Sea	s	(3)	60/12.1	2.61/9.27	69
Leucopsarion (74)					
L. petersi Hilgendorf, 1880: Japan	f	(8)	55/5.9	0.978/5.49	74
Lophogobius (59)					
L. cyprinoides (Pallas, 1770): East Mexico	b	(4)	100/20.8	20.8/26.0	59
Luciogobius (55)					
L. guttatus Gill, 1859: Japan	b	(2)	55/5.3	0.873/4.00	55
Macrodontogobius (128)					
M. wilburi Herre, 1936: Philippines	s	(4)	55/12.9	2.15/14.2	128
Mauligobius (76)					
M. sp.: Tunisia	s	(4)	150/9.4	31.6/40.0	76
Microgobius (50)					
M. gulosus (Girard, 1858): Florida	b	(2)	75/8.6	3.62/8.72	50
Monishia (75)					
M. ocetica (Norman, 1927): Red Sea	b	(2)	45/13.5	1.23/4.47	58
M. william (Smith, 1947): South Africa	b	(3)	62/18.8	4.47/17.6	91
Mugilogobius (66)					
M. cavifrons (Weber, 1909): Japan	b	(1)	40/17.1	1.10/6.23	73
M. sp.: Philippines	s	(4)	50/12.9	1.61/5.61	59
Nematogobius (97)					
N. ansorgii Boulenger, 1910: Guinea	b	(2)	80/10.2	5.21/21.1	105
N. maindroni (Sauvage, 1880): Ivory Coast	b	(1)	80/10.1	5.18/15.6	88
Oligolepis (72)					
O. sp.: Tahiti	f	(2)	50/12.0	1.50/6.89	72
Oplopomus (140)					
O. oplopomus (Val., 1837): New Guinea	s	(4)	85/13.7	8.41/33.5	140
Oxyurichthys (66)					
O. tentacularis (Val., 1837): Fiji	b	(2)	165/7.2	32.2/36.0	66
Pandaka (149)					
P. lidwilli (McCulloch, 1917): Australia	b	(2)	20/11.1	0.089/2.19	149
Paragobiodon (86)					
P. echinocephalus (Rüppell, 1830): Red Sea	s	(3)	40/32.4	2.07/9.91	86
P. sp.: Philippines	s	(2)	30/31.3	0.845/5.55	85
Pomatoschistus (122)					
P. marmoratus (Risso, 1810): France	b	(2)	65/11.4	3.14/18.3	128
P. microps (Kroyer, 1838): France	s	(3)	65/11.9	3.27/19.7	131
P. minutus (Pallas, 1770): France	s	(5)	100/12.3	12.3/32.0	113
P. pictus (Malm, 1865): England	s	(3)	60/11.8	2.55/13.4	114

(Table 1, continued)

	x	n	LT/cc	Bw/bw	i
Priolepis (57)					
P. cinctus (Regan, 1908): Red Sea	s	(2)	60/12.5	2.70/8.10	57
Proterorhinus (93)					
P. marmoratus (Pallas, 1811): Greece	f	(1)	85/12.3	7.52/21.9	93
Psammogobius (113)					
P. knysnaensis Smith, 1936: South Africa	s	(4)	75/12.0	5.05/20.9	113
Pterogobius (163)					
P. zacalles Jordan et Snyder, 1901: Japan	s	(1)	60/6.0	1.29/13.1	163
Redigobius (85)					
R. bikolanus (Herre, 1927): Australia	f	(2)	49/12.1	1.42/7.37	82
R. dewaali (Weber, 1897): South Africa	b	(4)	42/16.1	1.19/9.32	107
R. macrostoma (Herre, 1931): Australia	f	(4)	50/13.9	1.74/6.04	66
Rhinogobius (63)					
R. flumineus (Mizuno, 1960): Japan	f	(1)	70/13.9	4.75/15.1	73
R. giurinus Rutter, 1897: Japan	f	(1)	100/12.0	12.0/15.6	53
Silhouettea (113)					
S. aegyptia (Chabanaud, 1933): Egypt	s	(5)	50/9.9	1.23/9.09	113
Stenogobius (55)					
S. genivittatus (Val., 1837): Hawaii	b	(5)	165/13.0	58.3/42.1	55
Sufflogobius (83)					
S. bibarbatus (Von Bonde, 1923): South Africa	s	(3)	130/12.3	27.1/39.7	83
Trimma (93)					
T. avidori (Goren, 1978): Red Sea	s	(2)	25/12.5	0.195/1.97	81
T. mendelssohni (Goren, 1978): Red Sea	s	(3)	40/15.9	1.02/5.60	82
T. okinawae Aoyagi, 1940: Loyalty Islands	s	(2)	30/14.7	0.40/3.85	94
T. sp.: Marshall	s	(1)	30/28.7	0.775/6.10	96
T. striata (Herre, 1945): New Guinea	s	(1)	25/14.4	0.225/3.35	110
Valenciennea (103)					
V. puellaris (Tomiyama, 1956): Marshall	s	(2)	140/13.3	36.5/53.4	100
V. sexguttata (Val., 1837): Fiji, Marshall	s	(6)	130/14.2	31.1/53.6	106
Yongeichthys (166)					
Y. nebulosus (Forsskål, 1775): Australia	b	(1)	180/11.7	68.1/118	166

in Table 1.

The geographical origin is given for each species. The more important locations are Japan (37 species), Australia (33), the Pacific Ocean (33), the Red Sea (18), South Africa (12), America (12), the Indian Ocean (11), Europe (11), Africa (10) and New Caledonia (8). The number of specimens for each species is also listed. It varies from one (40 species) to 53 (*Gobius paganellus*), the mean value being 3.30.

The different ecological adaptations of these gobioid fishes are also given in Table 1. We have distinguished the following milieus: mud-living fishes (8 species), marine fishes (76), brackish-water fishes (56), amphibious fishes (8), fresh-water fishes (30) and torrent fishes (2).

The degree of lengthening of the body is given by the coefficient of condition (Bauchot and Bauchot, 1978), i.e. the value $c=Bw/L^3$. (Bw= body weight, L=total length). This coefficient is low (2 or less) in very elongated gobioids, high (30 or more) in stout-bodied species; the mean value is 12.9.

The index of encephalization (Bauchot and Stephan, 1964; Bauchot et al., 1979) is calculated from the brain-body weight relationship. Its value $i=100\,k/k^\circ$, in which k is given by the formula:

$$\log bw = -0.03\,(\log Bw)^2 + 0.73\,(\log Bw) + \log k$$

and k° is the corresponding value on the quadratic curve. In this calculation, a species on the curve has an index of 100. A highly encephalized species has an index greater than 100 and a poorly encephalized species an index less than 100. The indices in gobioids vary from 15 (*Microdesmus*

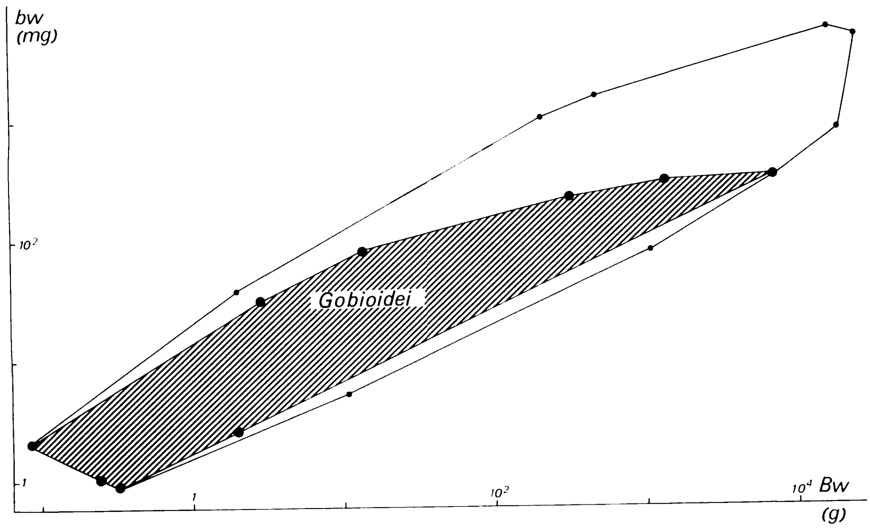

Fig. 1. Brain-body weight relationship in double logarithmic coordinates. Place of the envelope-polygone of Gobioidei relative to that of the whole teleosts (Bw: body weight, bw: brain weight).

retropinnis) to 261 (*Periophthalmus cantonensis*). In Table 1, the body weight is given in grams, the brain weight in mg.

Results

1. The intraspecific variability of indices. A relatively large number of species are represented by only one or two specimens. With so few specimens it is difficult to know in what measure the index calculated is characteristic of the species. To have an understanding of the intraspecific variability of the encephalization indices, we studied the two species representated by a large number of specimens: 53 in *Gobius paganellus* (Gobiinae) and 17 in *Trypauchen vagina* (Amblyopinae).

In the first species, the value of the encephalization index is 154.7+/−22.7, in the second 27.5+/−3.0. The standard deviation in percentage of the mean is 14.7% in the first species, 10.9% in the second. We can then consider that the index of encephalization of a species is precise at 15%. For example, the most poorly encephalized species, *Microdesmus retropinnis*, has an index of $13<i<17$, the most highly encephalized species, *Periophthalmus cantonensis*, an index of $222<i<300$. In the same way, if we compare two species of the same genus, with very different indices, for example *Bathygobius fuscus* ($i=130$) and *B. meteori* ($i=78$), the actual indices can be, for the first: $130-20=110$, and for the second: $78+12=90$. It is then necessary to keep in mind that the indices given in Table 1 have to be corrected following the formula: $0.85i<i<1.15i$.

2. The position of the Gobioidei within the Teleostei. Fig. 1 gives, in double logarithmic coordinates, the envelope-polygone of the 180 species of gobioid fishes, and that of more than 1,000 species of teleosts we collected in the last 14 years. Three conclusions can be made:

1) Gobioidei have body weights ranging from the smallest known fishes (*Pandaka lidwilli*: 0.089 g, a Gobiinae from Australia) to *Gobiomorus dormitor* (7,508 g), an Eleotrididae from Colombia, and occupy the inferior part of the body weight amplitude of the teleosts.

2) The amplitude of the brain weight in the Gobioidei is very large, almost equal to that of all teleosts with body weights inferior to 10 g. Among the larger species, the Gobioidei occupy the lower part of the Teleost polygon; only some eels have a lower encephalization index than these gobioids.

3) The general slope of the polygon of the Gobioidei (about 0.62) is a little inferior to that of all the teleosts (almost exactly 2/3 (Ridet, 1982)), which means that the larger species are less encephalized than the smaller ones. One possible explanation for this is that larger species

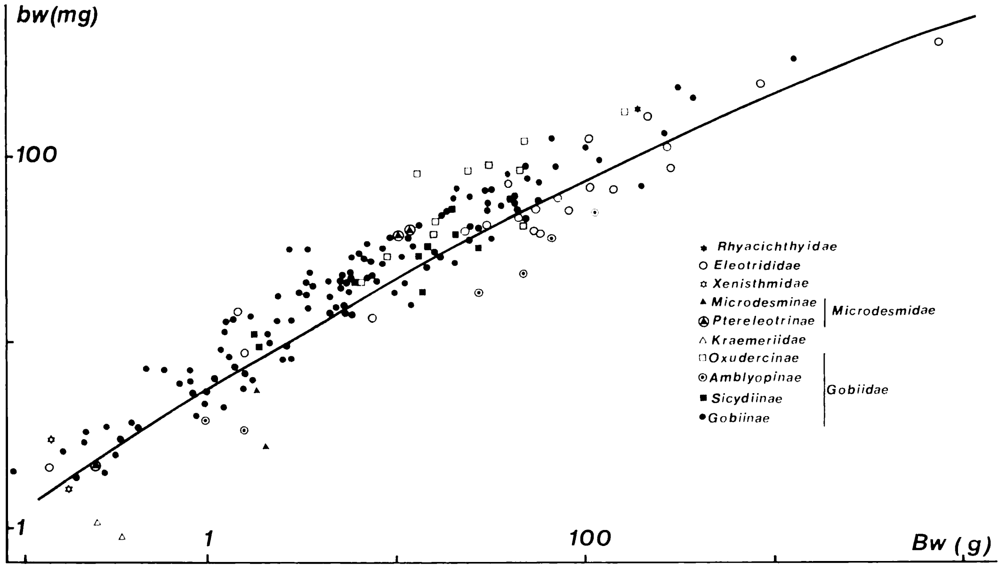

Fig. 2. Brain-body weight relationship in double logarithmic coordinates. The different species are identified following their belonging to the different families and subfamilies (Bw: body weight, bw: brain weight).

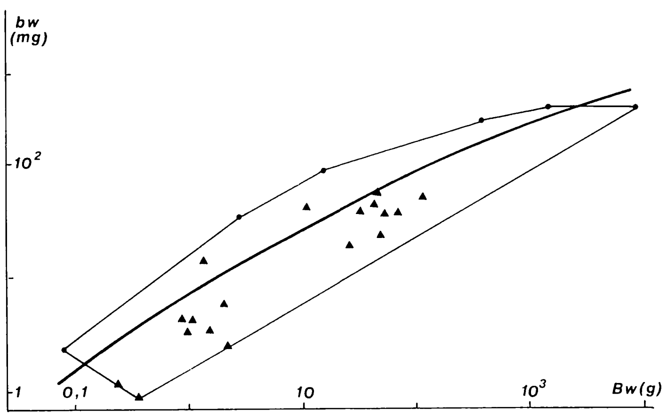

Fig. 3. Brain-body weight relationship in double logarithmic coordinates. The species with an elongated body (condition coefficient inferior or equal to 7) are figured; almost all lie in the inferior part of the polygone (Bw: body weight, bw: brain weight).

could be less apt to be preyed upon than smaller ones (Bauchot and Bauchot, 1985).

3. Repartition of the species of Gobioidei relative to taxinomy. Fig. 2 gives, in double logarithmic coordinates, the brain-body weight relationship of the Gobioidei. The different families and subfamilies are identified. It is clear that the Microdesminae (but not the other microdesmid subfamily Ptereleotrinae, which lies much higher), Kraemeriidae and Amblyopinae (=Trypauchеninae) are poorly encephalized. Those in the low to middle category are the Eleotrididae, Sicydiinae and Xenisthmidae (we need more species and specimens of this family to get more reliable results—see Springer, 1983). Most of the species of Gobiinae have middle to high values of encephalization indices. The most highly encephalized species belong to the Oxudercinae (=Periophthalminae) and the Rhyacichthyidae. This last family is represented in our material by

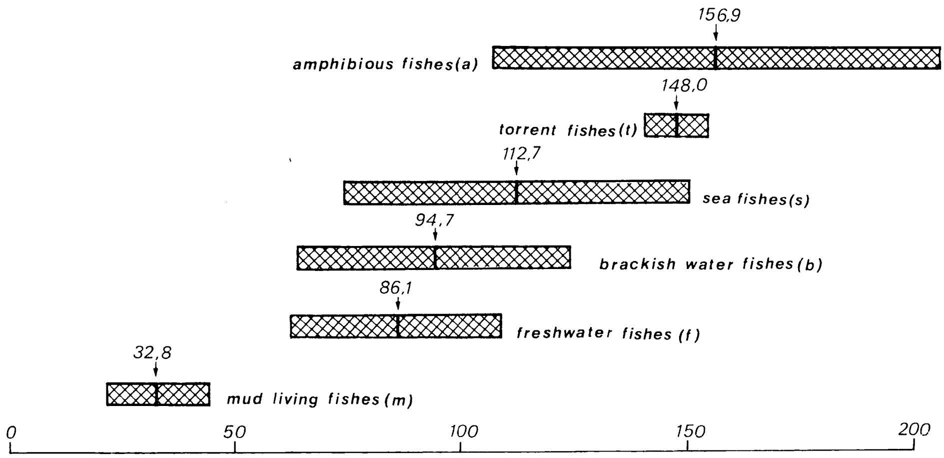

Fig. 4. Mean value and variation amplitude of encephalization indices following different ecological milieus.

only one specimen of the species *Rhyacichthys aspro*, which is the generous gift from Crown Prince Akihito of Japan. We will make a special study of this species, as it was considered by some ichthyologists to be very primitive within Gobioidei (Miller, 1973; Springer, 1983).

It seems then that the evolutionary level of the species of Gobioidei is related to the degree of encephalization. We need to verify whether or not the encephalization level is correlated with body form or biological adaptations.

4. Influence of body form. We have previously shown (Bauchot and Bauchot, 1985, 1986) that elongate teleosts have low encephalization indices, compared to near relatives which are more stout-bodied. This may be due either to a lower brain weight or a higher body weight. In favour of the first hypothesis is the fact that fishes which swim by undulating movements have smaller nervous centers than those with more elaborated movements. The second hypothesis deals with the fact that an elongate body has an overweight of poorly innervated organs, such as the axial skeleton, fin rays and even the digestive tract.

In order to test the second hypothesis, we calculated the condition coefficient for each species. Fig. 3 gives the location, inside the polygon of Gobioidei, of the species with a coefficient lower than or equal to 7. Of the 18 species with an elongate body, 16 lie in the inferior part of the polygon. We may then say that an elongate body can explain, at least in part, a lower encephalization index.

5. Influence of ecological and biological adaptations. The biology of very few gobioid species is well known. In view of our limited knowledge of these fishes, the best criterion is the milieu of each species. Fig. 4 gives the mean value and amplitude of the indices corresponding to each of the different habitats. The progression goes from mud-living fishes (32.8) through freshwater (86.1), brackish-water (94.7) and sea fishes (112.7) to torrent (148.0) and amphibious fishes (156.9).

The explanations for these differences are probably multiple. From the mud environment to sea, the threat of predation increases and the fishes need to be more cautious; another progression from the first milieu to the last is that of different sense organs. Olfactory centers (Ridet and Bauchot, 1982, 1984) are predominant in mud-living fishes and fishes living in small bodies of water (fresh and brackish waters). Vision or auditory-lateral line centers are increasingly important in fishes living in water of high volumes (some brackish areas and the open sea) where olfaction must be complemented by other senses. A third explanation is to be found in the volumes of cerebellum—gobioids living in torrents have locomotory problems greater than other fishes. This could explain in part the high encephalization level of Rhyacichthyidae (cf. Bauchot and Bauchot, 1979). And finally, the amphibious mode of life of the Oxudercinae, with locomotion, respiratory and sense organs able to cope with two very different milieus, probably needs more complex nervous centers than fishes adapted to a single habitat.

Discussion

We have shown the influence on encephalization indices of three factors: taxinomic level, form of the body and ecological adaptations. Some of these influences, however, may combine, so it may be difficult to determine the more important criterion. For example, most Oxudercinae (=Periophthalminae) are amphibious (*Periophthalmus* and *Scartelaos*) and are highly encephalized. How can we know if this high encephalization is mostly due to this special biological adaptation? Another Oxudercinae (*Boleophthalmus*) lives in brackish waters and is poorly encephalized. The ecological adaptation then seems to be a valuable factor in this case.

Another example is that of the form of the body. Microdesminae, Kraemeriidae and Amblyopinae (=Trypaucheninae) are poorly encephalized, but they are also among the most elongate of the gobioids. Is the degree of encephalization correlated with body form or are the two characters evolved independently? Within the Gobiinae, some of the lower indices belong to elongate fishes, like *Leucopsarion*, *Luciogobius* and *Oxyurichthys*. Unfortunately, these species are also brackish- or fresh-water fishes, so that it is difficult to attribute their low encephalization to their body form or to their milieu. Nevertheless, it seems probable that the body form, with the overweight of poorly innervated organs, is a factor contributing to the low encephalization of the Microdesminae, Kraemeriidae and Amblyopinae, but not the main one, as the other subfamily of the Microdesmidae, the Ptereleotrinae, has both an elongate body and an index superior to the mean. If we remember that the Amblyopinae are mud-living fishes, we find in this adaptation, which involves blindness in some of the species and the reduction of all visual centers, another explanation of the regression of the brain volumes.

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ハゼ亜目の脳における大脳化

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ハゼ亜目に属する6科180種の大脳化指数を，脳重と体重測定によって決定した．真骨魚類全体から見ると，これらハゼ類では大脳化指数が顕著な幅広い変動を示したが，多くの数値は低値から中間値の範囲内にあった．ハゼ亜目の中で，大脳化指数の低い Kraemeriidae と Amblyopinae，および大脳化指数の高い Oxudercinae (トビハゼ科を含む) と Rhyacichthyidae を除くと，科や亜科が異なっても大脳化の程度の差は比較的少ない．魚体の形状が大脳化の程度に影響を与える事が明らかになった．即ち，細長い魚の指数は低い．脳重に較べて体重を増加させる胴の骨格が多いことに原因しているのであろう．一般に，魚の住んでいる環境は相対的な脳の大きさに相関している．生息場所に従って，指数の低いものから高いものの順に並べると，泥生魚，淡水魚，汽水魚，埋没性海産魚，自由遊泳海産魚，急流魚，水陸両生魚の順になる．Amblyopinae と Kraemeriidae の指数が低いのは泥生魚であり，また魚体が細長いためであると説明できる．