Japanese Journal of Ichthyology
Vol. 36, No. 2 1989

魚類学雑誌
36巻2号 1989年

The Brain of *Rhyacichthys aspro* (Rhyacichthyidae, Gobioidei)

Roland Bauchot, Monique Diagne, Jean-Marc Ridet
and Marie-Louise Bauchot

(Received October 20, 1988)

Abstract *Rhyacichthys aspro* has one of the highest encephalization indices of the Gobioidei, at the level of the amphibious *Periophthalmus* (Gobiidae, Oxudercinae). This high encephalization can be explained by its adaptation to the turbulent waters of mountain torrents. The brain morphology is typical of a perciform fish and similar to that of a gobioid except in the form and size of the cerebellum. The quantitative analysis of the brain structures shows a large size of the olfactory centers, a small size of the visual centers (compared to those of other Gobioidei) and a very large size of the cerebellar centers (more than twice the size in other Gobioidei). The brain organization shows that *Rhyacichthys aspro*, although some of its brain structures are typically gobioid (tegmentum, medulla oblongata), is not a generalized gobioid, because of the high degree of its biological adaptation and the correlated large size of its cerebellum.

Rhyacichthys aspro (Kuhl et Van Hasselt, 1837) is a gobioid of the monospecific family Rhyacichthyidae and lives in the tropical hill-streams of the Indo-Australasian archipelago. Miller (1973) gave a good review of every paper published on this species; from its osteological study, he writes: "It is shown to possess primitive features unique among gobioids". More recently, Prince Akihito (1986), after Springer (1983), states: "It is not considered to represent the form closest to the ancestral form of gobiids because it has some specialized characters in addition to its unspecialized characters". We are thankful to Prince Akihito who sent us a specimen of *Rhyacichthys*, allowing us to study its brain in order to try to evaluate the status of this species.

Although Miller wrote, "the biology (of *Rhyacichthys*) is virtually unknown", he reported that fish "lives in fast water, has an extensive lateral-line system, clings to rocks and slips around and under them when disturbed, being difficult to dislodge; it seems to congregate on large bowlders which give it absolutely safe hiding places; it moves from place to place by rapid darts; it has a herbivorous diet of algae from the surfaces of stones". It is unknown, however, if the reproductive habits of this species are typical of freshwater gobioids which make migrations to and from spawning areas. Blanco (1938) suggests that *Rhyacichthys* migrates seaward to spawn, with the fry ascending rivers (P. Miller, pers. comm.).

Material and methods

Our specimen, fixed and preserved in formalin, was 144 mm in standard length, with a body weight of 48.7 g and a fresh brain weight of 90.7 mg. The brain was dissected from the skull and prepared for histological studies. The sections, 10 μm thick, were stained by cresyl violet. From the anterior tip of the olfactory bulb to the beginning of the spinal cord, 50 sections, 0.19 mm distant from each other, were photographed in order to make a quantitative study of the different parts of the brain. On each photograph, each brain subdivision was delimited. From the areas, calculated by weighing, the different volumes were deduced. Although the specimen was not fixed for histological studies, we obtained good pictures of the brain nuclei and tracts.

Results

1. Encephalization. Fig. 1 shows, in double logarithmic coordinates, the position of *Rhyacichthys* in comparison with other Gobioidei (Kassem, 1987; Bauchot et al., 1989) and with other Teleostei (Ridet, 1982). It is remarkable that this species, considered as primitive, lies almost at the top of all gobioids, being surpassed only by some periophthalmines. The aim of this study is to look for explanations of this high level of encephalization. The quantitative analysis of the

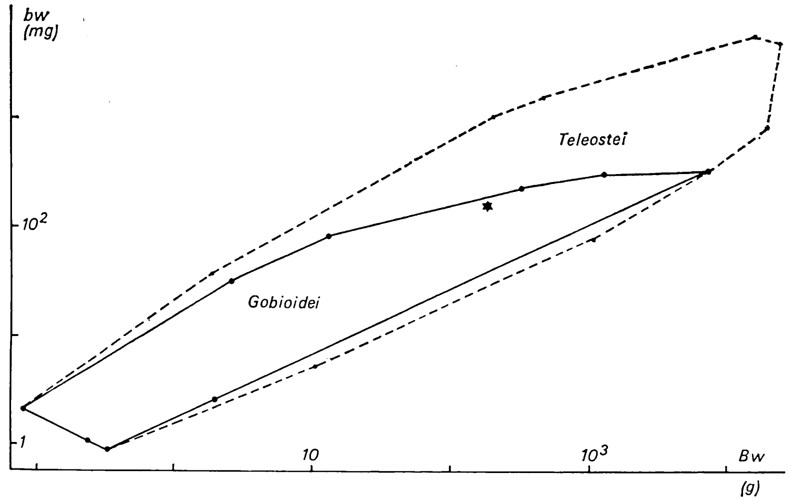

Fig. 1. Position of *Rhyacichthys aspro*, in double logarithmic coordinates, within Gobioidei and Teleostei, for the relation brain weight/body weight.

brain organization will allow us to show precisely which parts of the brain of this species are particularly important.

2. Brain morphology. Fig. 2 gives the general aspect of the brain of *Rhyacichthys* in dorsal, ventral and lateral views. The general morphology is that of an advanced teleost (perciform) with a large-sized telencephalon, showing the beginning of sulci, and a short and elevated form in lateral view. In comparison with other gobioids, the olfactory bulbs are very large, the optic tectum is seemingly small (but the optic tracts and chiasma are very large) and the medulla oblongata is of good size (with a facial lobe dorsally visible). But the most important character is the anomalous size of the cerebellum, far bigger than that of any other gobioid.

From this morphological study we conclude that *Rhyacichthys* probably has a good olfactory sense, a visual sense difficult to assess (large optic tract and chiasma but a tectum of average size), probably numerous external gustatory buds (large facial lobe), and locomotory centers (notably cerebellum) of very large size. This last character is probably related to the ecology of this fish living in the turbid waters of hill-streams.

3. Architecture of the brain. Fig. 3 gives 7 transverse levels of the brain of *Rhyacichthys* at the telencephalic (1), telencephalo-preoptic (2), diencephalo-mesencephalic (3), tecto-hypothalamic (4), valvulo-hypothalamic (5), cerebellar (6) and medullar (7). The main characters are the following:

1) In the telencephalon, the large size of the area dorsolateralis (Fig. 3-1: d.l.), with a visible corticalization, is characteristic of higher Perciformes, but not so well developed as it is in some forms such as *Chaetodon* (Bauchot et al., 1988). Another center of large size is the nucleus dorsoposterior (Fig. 3-2: d.p.) which, following Chanconie and Clairambault (1977), receives afferents from the olfactory bulbs. This large size can be related to the size of the olfactory bulbs and indicates a good level of olfactory perception.

2) The diencephalon is relatively small for a gobioid. The nucleus geniculatus (Fig. 3-3: N.g.) is small and unlaminated, characterizing average vision (a result of adaptation to the turbid waters of hill-streams ?). The nucleus rotundus (Fig. 3-4: C.G.r.), at the limit between thalamus and hypothalamus, has a special aspect, with the nerve cells at the periphery and a central neuropile, characteristic of the Perciformes. The hypothalamus as a whole is large, and particularly the nucleus preopticus, pars magnocellularis (Fig. 3-2: N.po.m.), a character also present in all other gobioids.

3) In the mesencephalon, the tori longitudinales (Fig. 3-4: T.l.) are small and the tectum opticum (Fig. 3-3–5: T.M.), if rather spread, is thin, two characters indicating poorly developed vision. On the contrary the tori semi-circulares (Fig. 3-4,

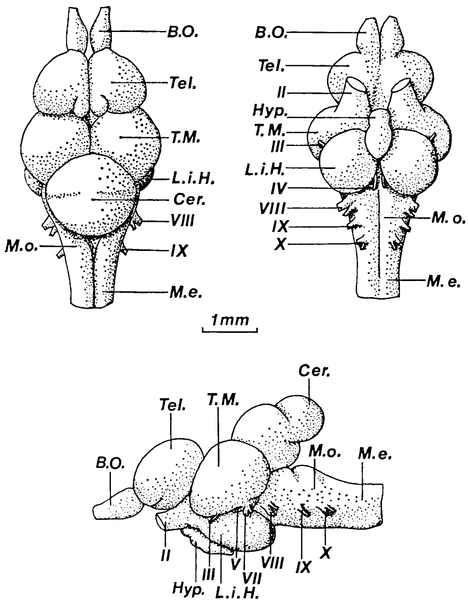

Fig. 2. The external morphology of the brain of *Rhyacichthys aspro*: dorsal view (top left), ventral view (top right) and lateral view (below). Abbreviations for Figs. 2–4: A.a.l., acousticolateral area; A.c., cerebellar auricle; B.O., olfactory bulb; C.C., cerebellar crest; Cer., cerebellum; c.g., granular layer of cerebellum; C.G.h., corpus glomerulosum pars hypothalamica; C.G.r., corpus glomerulosum pars rotunda; c.m., molecular layer of cerebellum; c.P., Purkinje cells layer; d.c., nucleus dorsocentralis; d.d., nucleus dorsodorsalis; d.l., nucleus dorsolateralis; d.m., nucleus dorsomedialis; d.p., nucleus dorsoposterior; Dien., diencephalon; E.g., eminentia granularis; E.t., eminentia thalami; Hyp., hypophysis; I.s., inner segment of dorsal thalamus; L.f., facial lobe; L.i.H., inferior lobe of hypothalamus; M.e., spinal cord; M.O., medulla oblongata; N.c., nucleus corticalis; N.d.l.i., nucleus diffusus lobi inferioris; N.e., nucleus entopeduncularis; N.g., nucleus geniculatus; N.i., nucleus intermedius; N.i.s., nucleus isthmi; N.h.l., nucleus habenularis lateralis; N.h.m., nucleus habenularis medialis; N.l.p., nucleus lateralis profundus; N.l.t., nucleus lateralis tuberis; N.l.v., nucleus lateralis valvulae; N.m., nucleus medialis; N.m.d.VII, dorsal motor nucleus of facial nerve; N.m.v.VII, ventral motor nucleus of facial nerve; N.po., nucleus preopticus; N.po.m., nucleus preopticus pars magnocellularis; N.po.p., nucleus preopticus pars parvocellularis; N.pr., nucleus pretectalis; N.p.t., nucleus posterior tuberis; N.r.t., nucleus ruber tegmenti; N.v.h., nucleus ventricularis hypothalami; N.III, nucleus of common oculomotor nerve; N.IV, nucleus of trochlear nerve; N.V, nucleus of trigeminal nerve; t.c.a., anterior choroid plexus; t.c.4v., choroid plexus of 4th ventricle; Tel., telencephalon; T.l., torus longitudinalis; T.M., tectum mesencephalicum; T.o.l., tractus opticus lateralis; T.o.m., tractus opticus medialis; T.s.c., torus semicircularis; Teg., tegmentum mesencephalicum; V.C., cerebellar valvula; v.d., nucleus ventrodorsalis; v.l., nucleus ventrolateralis; v.m., mesencephalic ventricle; v.t., telencephalic ventricle; v.v., nucleus ventroventralis; 3v., 3rd ventricle; 4v., 4th ventricle; II, tracus opticus; III, common oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, lateral oculomotor nerve; VII, facial nerve; VIII, acousticolateral nerve; IX, glossopharyngeal nerve; X, vagal nerve.

5: T.s.c.), which receive afferent fibres from the acoustico-lateralis system, are very large.

4) The metencephalon comprises a small valvula cerebelli (Fig. 3-5: V.C.), of gadid-type (Banarescu, 1957), considered typical of poor swimmers, and an extremely large cerebellum (Fig. 3-6: Cer.), indicating on the contrary complex locomotory movements. The Purkinje cells are stituated outside the granular layer, another character favouring complex motor activity. There is a neat contradiction between the small size of the valvula cerebelli (notably the size of the reflex lamina), indicative for Banarescu of poor locomotion, and the large size of the cerebellum itself, with the location of the Purkinje cells between the molecular and granular layers, taken by Rossi et al. (1968) as a sign of complex locomotory movements. It would be interesting to study the actual activity of this fish in the field; we think, from this histological study, that it has a high level of motor activity, perhaps related to station-keeping and resisting displacement in fast water currents.

5) The medulla oblongata is remarkable for the large size of both the facial lobe (Fig. 3-7: L.f.), which receives afferent fibres from skin and lip gustatory buds, and of the area acoustico-lateralis (Fig. 3-7: A.a.l.), which receives fibres from both auditory and tactile acousticolateral system.

A quantitative analysis of the main brain structures provides a better view of the general organization of the brain of *Rhyacichthys aspro*.

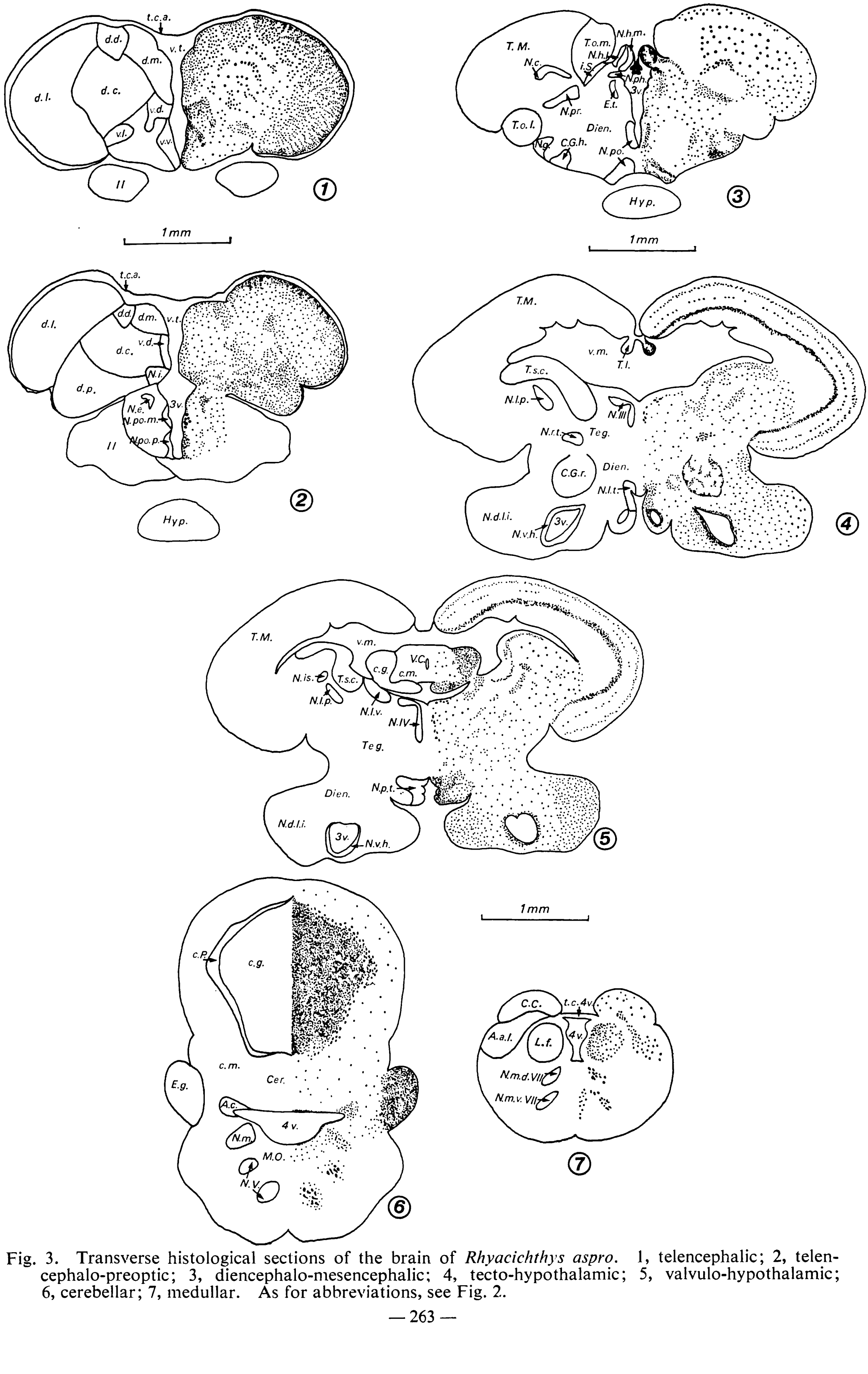

Fig. 3. Transverse histological sections of the brain of *Rhyacichthys aspro*. 1, telencephalic; 2, telencephalo-preoptic; 3, diencephalo-mesencephalic; 4, tecto-hypothalamic; 5, valvulo-hypothalamic; 6, cerebellar; 7, medullar. As for abbreviations, see Fig. 2.

4. Quantitative analysis. Table 1 gives the fresh volumes and their percentage, by reference to the total volume of the brain, of the following subdivisions: olfactory bulbs (B.O.), telencephalon (Tel.), diencephalon (Dien.), tectum mesencephali (T.M.), tori longitudinales (T.l.), tegmentum (Teg.), valvula cerebelli (V.C.), cerebellum (Cer.) and medulla oblongata (M.O.). A graphic representation of this table is given in figure 4 in which the areas of the different structures are proportional to their volumes. The percentages can be compared to the corresponding mean values obtained by the study of 14 species of gobioids (Kassem et al., 1989).

The main characteristics of the brain of *Rhyacichthys aspro* are the following:

1) The olfactory bulbs are very large for a perciform, more than twice the mean value for other gobioids and more than the value of any gobioid species (in the 17 other gobioid species studied (Kassem et al., 1989) the percentages vary from 0.09 to 0.77). The olfactory sense is thus important in this species.

2) Telencephalon sensu stricto (without olfactory bulbs) and diencephalon are relatively small in comparison with the mean values of gobioids. The percentage of the telencephalon lies within the variability of gobioids (12.4 to 20.0%) while that of the diencephalon is very low, lower than in any other Gobioidei studied (18.1 to 31.6%).

The tectum mesencephali and tori longitudinales are also small in *Rhyacichthys*, compared to the mean value for gobioids (17.13 compared to 24.7 for the tectum itself; 0.19 compared to 0.27 for the tori). With the exception of *Trypauchen vagina* which is almost totally blind, these values are also just beneath the lowest value for gobioids.

4) In comparison with teleosts in general, the tegmentum is large, but, as shown by Kassem et al. (1989), this seems to be a feature common to all Gobioidei. Within this suborder, the tegmentum is, then, fully normal (8.29 compared to the mean 8.1, varying from 6.3 to 11.1%).

5) The valvula cerebelli is feeble in *Rhyacichthys* but not far from the values for other gobioids (0.67 compared to the mean 0.83, and varying from 0.21 to 1.49).

6) The cerebellum, even more than the olfactory bulb, is the structure that distinguishes *Rhyacichthys*. Its value (21.39%) is more than three times that of the mean of other gobioids (7.0) and more than twice that of the gobioids with the best-developed cerebellum (with variations from 4.3 to 10.6%).

7) The medulla oblongata is normal, just a little higher than the mean (19.5 compared to 18.5), and far from the extremes (13.8 and 27.1%).

From this limited quantitative analysis, it is possible to discuss the different specializations of the brain of *Rhyacichthys aspro* more precisely.

Discussion

The general morphology and the quantitative organization of the brain of *Rhyacichthys* are typical of a perciform fish, especially the large size of the telencephalon, which is also a general feature of the Gobioidei (Kassem et al., 1989) as well as of higher teleosts (Ridet, 1982). On the contrary, the diencephalon is relatively small, a feature different from that of perciforms in general and of Gobioidei in particular. This small size of the diencephalic structures could be related to the small size of the visual centers, such as the tectum mesencephali. In *Rhyacichthys*, as in other Gobioidei, the tegmentum mesencephali

Table 1. Fresh volumes, percentages of total brain volumes and comparison with gobiid mean values for different brain subdivisions of *Rhyacichthys aspro*.

Brain structure	Fresh volume (mm^3)	Volume %	Gobiid mean value
Olfactory bulbs	0.425	1.02	0.42
Telencephalon	6.261	15.06	16.6
Diencephalon	6.955	16.73	23.9
Tectum mesencephali	7.121	17.13	24.4
Tori longitudinales	0.079	0.19	0.25
Tegmentum	3.444	8.29	8.1
Valvula cerebelli	0.278	0.67	0.83
Cerebellum	8.892	21.39	7.0
Medulla oblongata	8.112	19.52	18.5

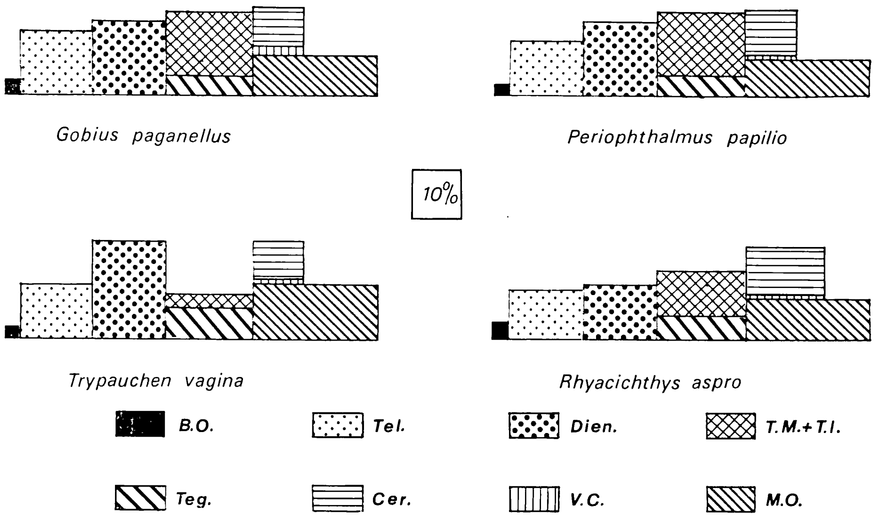

Fig. 4. Quantitative organization of the brain of *Rhyacichthys aspro* compared to that of *Gobius paganellus*, *Periophthalmus papilio* and *Trypauchen vagina*. The areas of the different structures are proportional to the fresh volumes. As for abbreviations, see Fig. 2.

and medulla oblongata are very developed in comparison with other perciforms. In teleosts in general, this large size was considered to be a feature of sedentary species (Ridet, 1982). This explanation cannot be accepted for *Rhyacichthys*, which lives in fast, hill-stream waters. It is likely that the large size of the medulla oblongata is related to the huge size of the cerebellum in this species.

The nervous structures linked with sensory organs seem to be equally developed, with some particularities nevertheless: olfactory and gustatory centers are larger than in other gobioids, and this can be related to the feeding habits (screaping of algae from stones). The large size of the olfactory centers is difficult to explain in fast waters unless this fish spends much of its time under rocks where the waters are relatively still. The visual centers are relatively small (but far from the reduction shown by gobioids like *Trypauchen*) and may be related to the herbivory of *Rhyacichthys*, which has different demands from those of a predatory way of life. The nervous centers linked with the lateral-line system are, on the contrary, somewhat larger than in typical gobioids and are probably related to the problems of locomotion in fast water and migrations to and from spawning places more than they are related to special auditory capabilities.

The only center extremely developed in this species (and which explains, in part, the large size of the brain) is the cerebellum. Is the cerebellum also developed in other torrenticolous Gobioidei? This does not seem to be the case with *Hypseleotris aurea*, the cerebellum of which is as small as in other gobioids. However, if we consider the species of *Sicydium* and *Sicyopterus*, which also live in hill streams, spawn in fresh waters and have tiny larvae that are washed downstream to grow in estuaries or the sea and then ascend rivers prior to maturation, it is clear that they have cerebellar structures far more developed than typical gobioids, but not as much as in *Rhyacichthys*. This difference in relative size of the cerebellum may be the result of greater specialization of *Rhyacichthys* for life in fast waters, or of the larger body size of this species. Ridet (1982) has shown that, considering two species adapted to particular locomotory habits, the cerebellum has a relatively larger volume in the bigger species.

In conclusion, our study of the brain organization of *Rhyacichthys* shows that this species possesses a combination of generalized and specialized gobioid features. Weakly specialized features include the larger olfactory, gustatory or acousticolateral centers and the smaller visual centers. The extremely specialized features mainly include the cerebellum. Our study supports the conclusion of Prince Akihito (1986) that *Rhyacichthys* is highly specialized, but it is important to note that it does not falsify the hypothesis of Springer (1983, abstract) that this species is the sister-group of all other gobioids.

Acknowledgments

We are indebted to Crown Prince Akihito who sent us the material and to V. G. Springer and T. Roberts for critical reading of the manuscript.

Literature cited

Akihito, Prince. 1986. Some morphological characters considered to be important in gobiid phylogeny. Pages 631-639 *in* Indo-Pacific fish biology. Proc. of the 2nd International Conference on Indo-Pacific Fishes. The Ichthyological Soc. of Japan, Tokyo.

Banarescu, P. 1957. Vergleichende Anatomie und Bedeutung der Valvula cerebelli der Knochenfische. Rev. Roum. Biol., 2: 255–276.

Bauchot, R., J.-M. Ridet and M.-L. Bauchot. 1989. The brain organization of butterflyfishes. Env. Biol. Fishes, 25: 205–219.

Bauchot, M.-L., J.-M. Ridet, M. Diagne and R. Bauchot. 1989. Encephalization in Gobioidei (Teleostei). Japan. J. Ichthyol., 36: 63–74.

Blanco, G. J. 1938. The fisheries of northeastern Luzon and the Babuyan and Batanes islands. Philipp. J. Sci., 66: 501–521.

Chanconie, M. and P. Clairambault. 1977. Les projections olfactives secondaires d'un Téléostéen, *Pollachius pollachius*. C. R. Acad. Sci. Paris Sér. D, 284: 1537–1540.

Kassem, M. 1987. Anatomie comparée de l'encéphale et des organes des sens chez les poissons Téléostéens du sous-ordre des Gobioidei. Thèse Doctorat Univ. Paris 7, 91 pp.

Kassem, M., J.-M. Ridet and R. Bauchot. 1989. Analyse volumétrique des principales subdivisions encéphaliques chez les Gobioidei (Téléostéens Perciformes). J. Hirnf., 30: 59–67.

Miller, P. J. 1973. The osteology and adaptative features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. J. Zool., 171: 397–434.

Ridet, J.-M. 1982. Analyse quantitative de l'encéphale des Téléostéens: caractères évolutifs et adaptatifs de l'encéphalisation. Thèse Doctorat ès-Sciences Paris, 265 pp.

Rossi, A., E. Capanna and M. G. Tamino. 1968. Prime osservazioni sulla citoarchitettonia cerebellare nei Teleostei. Mem. R. Accad. Lincei., 45: 1–10.

Springer, V. G. 1983. *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. Smiths. Contr. Zool., 390: 1–40.

(RB, MD and JMR: Laboratoire d'Anatomie Comparée, Université PARIS 7, 2 Place Jussieu, 75251 Paris Cedex 05, France; MLB: Laboratoire d'Ichthyologie générale et appliquée, Muséum National d'Histoire Naturelle, 57 rue Cuvier, 75231 Paris Cedex 05, France)

ツバサハゼ（ツバサハゼ科，ハゼ亜目）の脳

Roland Bauchot•Monique Diagne•
Jean-Marc Ridet•Marie-Louise Bauchot

ツバサハゼはハゼ亜目魚類の中では水陸両生性のトビハゼ類 *Periophthalmus* と同等に最も高い大脳化指数を示すものの一つである．この高い大脳化は山の急流に順応したためだと説明できる．ツバサハゼの脳形態はスズキ目の典型であり，小脳の形態と大きさを除けばハゼ亜目の他の種に似ている．脳構造の量的分析では嗅覚中枢は大きい．他のハゼ亜目のものに較べて視覚中枢は小さく，小脳は2倍以上大きい．ツバサハゼの中脳被蓋と延髄の脳構成はハゼ亜目の典型を示すが，脳全体は一般的なハゼ亜目の構成ではない．それは生息環境への高度な生物学的順応により小脳がそれに対応した大きさを示すからである．