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The Nucleus Size and Possible Paedomorphosis of the Pituitary in the Goby, *Rhinogobius flumineus*

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ABSTRACT—This study offers an example of the attempts to correlate the shape of an organ to the nucleus size. The pituitary glands of gobiid teleosts are partly embedded in the hypothalamus in contrast to those of non-gobiid teleosts. The pituitaries of the embryonic smelt, catfish, and guppy are partly embedded in the hypothalamus as in the embryonic and adult goby, *Rhinogobius flumineus*. The nucleus size of cerebellar granular cells, that may represent the genome size, is variable in gobies (16 species studied) as in non-gobiid perciforms (63 species studied). However, the ratio of the nucleus size of cerebellar Purkinje's cells to that of granular cells is consistently low in gobiids compared with non-gobiid perciforms. This ratio is a sort of peramorphic (morphologically advanced) index, and the low value may represent paedomorphosis (juvenile morphology). The gobiid pituitary gland partly embedded in the hypothalamus may be the result of paedomorphosis that could be reflected in the relatively poor increase rate in the size of Purkinje's cells as against the genome size.

INTRODUCTION

The nucleus size and the cell size, which are intimately correlated, are highly variable even within a definite cell type. In a previous paper [15], the author reported the nucleus size of granular cells of the cerebellum in various vertebrates, especially in fishes and amphibians. The nucleus and cell sizes are usually discussed in correlation to the genome size, that is the DNA content in the haploid or diploid nucleus, because the nucleus size is highly proportional to the genome size [2, 3, 4, 8]. The various genome sizes of vertebrates are obviously not related to the numbers of genes, because the body organization of vertebrates is fundamentally the same at least among gnathostomes. Some authors consider non-genic DNA is useless junk, but others regard such DNA has some biological significance by determining nucleus and cell sizes which then influence the life style of the organisms through cell cycle length and cell metabolism [2, 3, 8, 13]. On the other hand, the life style itself could be connected, at least partly, to events in heterochrony, such as peramorphosis and paedomorphosis, that represent relations among size, time (ontogeny), and shape (morphology) [1, 6]. In sum, the nucleus size may be related, though roughly and indirectly, to the shape of organisms and probably also of organs.

The pituitary gland of gobiid teleosts does not hang from the brain, but is partly embedded in the hypothalamus. Thus, it does not represent "the hypophysis cerebri" [9, 14]. The cause of this peculiar shape of the gobiid pituitary is not thus far explained. In this paper, the author attempts to explain this shape in relation to the nucleus size in gobies.

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MATERIALS AND METHODS

The development of the freshwater goby, *Rhinogobius flumineus* (MIZUNO), was studied. The egg masses, which were laid under submerged stones, were collected from the Hio River, Tatatsuki, Osaka. They were maintained in a laboratory aquarium with water temperature around 25°C. The developing embryos were fixed with Bouin's solution at adequate intervals. In this species, the egg capsule and the egg itself are large. The embryos hatch out at a morphologically well developed stage. The hatchling is about 7 to 8 mm in total length. The fixed embryos and hatchlings were embedded in paraffin and were sectioned sagittally. The sections were stained with paraldehyde fuchsin and Masson-Goldner's method and the developmental process of the pituitary region was observed. In addition, the pituitary of the adult goby was observed histologically and the nuclear sizes of the cerebellar granular and Purkinje's cells were measured to the nearest 0.5 μm with an ocular micrometer under oil-immersion condition. See Tsuneki [15] for the reason why cerebellar neurons were chosen for measurement. The pituitary cells themselves are not adequate for measurement, because they are highly active, protein-secreting cells.

For systematic comparison, the pituitary glands of 79 species of adult or subadult perciform teleosts (the order Perciformes) were studied histologically and the nuclear sizes of their cerebellar granular and Purkinje's cells were measured. Among them, 16 species were gobies (the families Eleotrididae and Gobiidae). Only perciforms were studied here, because teleosts as a whole are too diversely radiated [11]. These perciform materials are those used for the study of the saccus vasculosus [17].

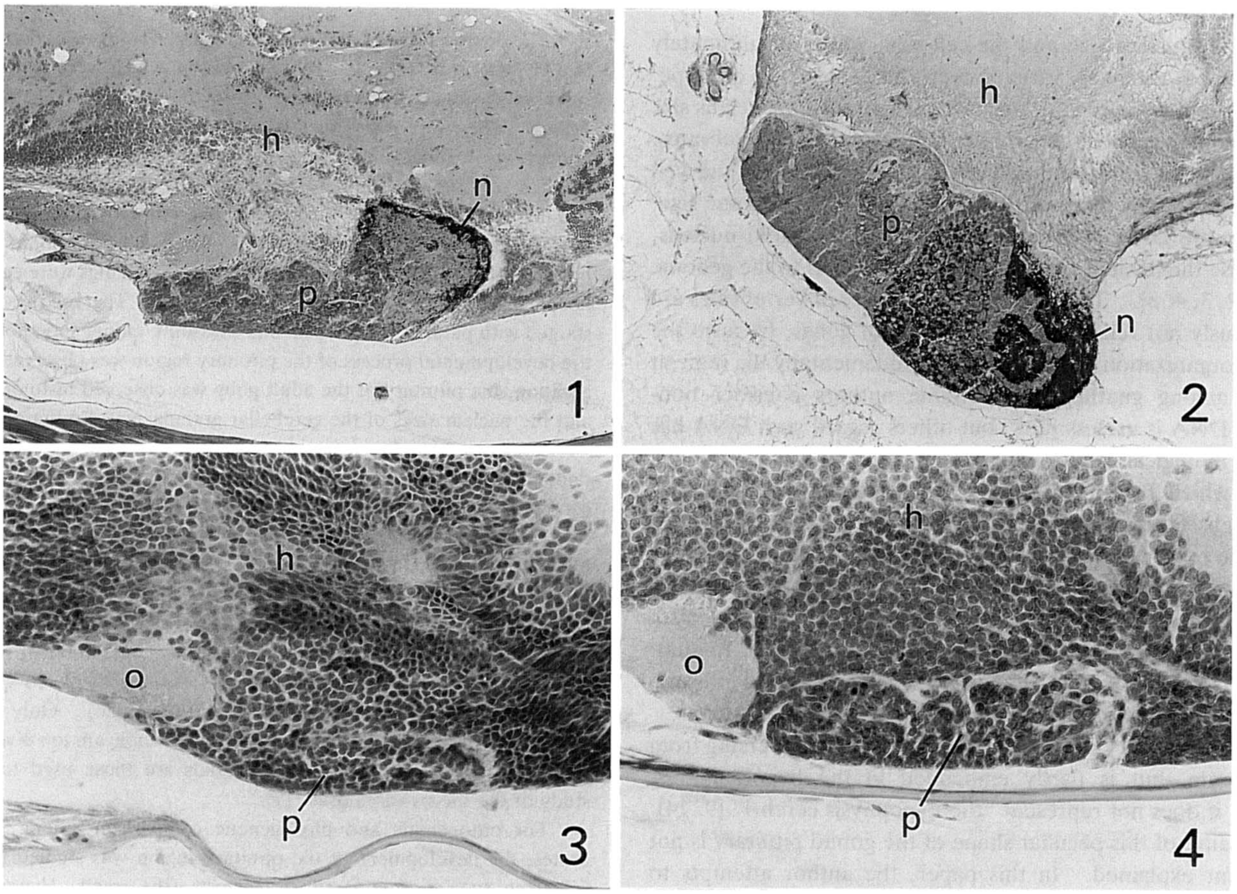
For ontogenetic and phylogenetic comparison among vertebrates, the development of the pituitary region was studied in the following species: non-perciform teleosts (the smelt, *Hypomesus nipponicus*; catfish, *Silurus asotus*; guppy, *Poecilia reticulata*), the lizard, *Takydromus tachydromoides*, chick, and mouse. In addition, developmental changes of the nuclear sizes of granular and Purkinje's cells were recorded in the catfish, lizard, chick, and mouse. In the smelt, guppy, and freshwater goby, *R. flumineus*, the nuclear sizes were measured in the available embryonic and postembryonic stages, but the nuclear sizes did not change distinctly, probably because the numbers of available stages were limited to the earlier stages in the smelt and to the later stages in the guppy and goby. These materials, except for *R. flumineus*, were those used for the study of the development of circumventricular organs [16]. A developmental series of non-gobiid perciforms was not available.

RESULTS

The pituitary gland of the adult freshwater goby, *R. flumineus*, is shown in Figure 1. As in the other gobies reported previously [9, 14], the pituitary of this species does not hang from the hypothalamus, but is partly embedded in the hypothalamus. Among 16 species of gobies, the pituitary of *Periophthalmus* sp. is only slightly embedded, thus representing the intermediate condition between typical gobies and non-gobiid perciforms (Fig. 2).

The development of the pituitary region of *R. flumineus* is shown in Figures 3 and 4. In embryos and hatchlings, the pituitary is partly embedded in the hypothalamus as in adults. The pituitaries of the embryonic smelt, catfish, and guppy abut widely on the hypothalamus and appear to be embedded slightly in the hypothalamus (Fig. 5). In teleosts, the pituitary develops as a solid cell mass in contrast to the case in selachians and amniotes, in which the pituitary develops as the Rathke's pouch. Figure 6 shows a typical, adult teleost pituitary with a well defined hypophysial stalk.

The nuclear diameters of cerebellar granular cells and Purkinje's cells in 79 species of adult and subadult perciforms are shown in Table 1. Developmental changes of the nuclear sizes in the catfish, lizard, chick, and mouse are shown in Figure 7. From this figure, it is apparent that the nucleus of granular cells hardly changes its size during development. whereas the nucleus of Purkinje's cells increases distinctly in size during development. At this phase of research, the author made a new index, "the PG index", in which the nucleus volume of Purkinje's cells is divided by the nucleus volume of granular cells. The denominator is a sort of standard which may reflect the genome size of the species (see DISCUSSION). PG indexes of the perciforms studied are



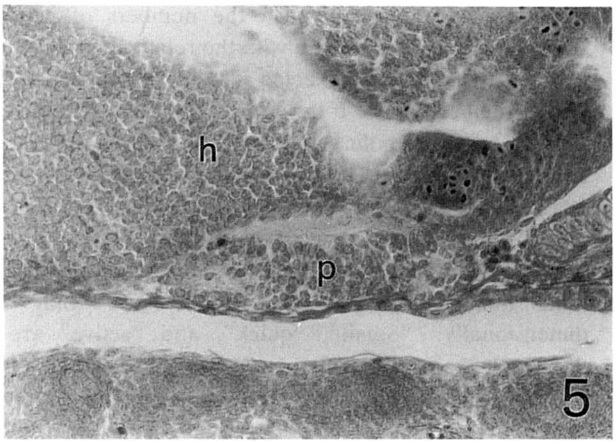
FIGS. 1–6. All photomicrographs are sagittal sections of the pituitary region directed its rostral side to the left. *h*, hypothalamus, *n*, neurohypophysis intensely stained with paraldehyde fuchsin; *o*, optic chiasma; *p*, pituitary.

FIG. 1. An adult of the freshwater goby, *Rhinogobius flumineus*. The pituitary is partly embedded in the hypothalamus. ×85.

FIG. 2. An adult of the mudskipper, *Periophthalmus* sp. The pituitary abuts widely on the hypothalamus. The rostral part is embedded slightly in the hypothalamus and the pituitary stalk is not formed. ×85.

FIG. 3. An embryo of *R. flumineus*. ×340.

FIG. 4. A hatchling of *R. flumineus*. ×340.



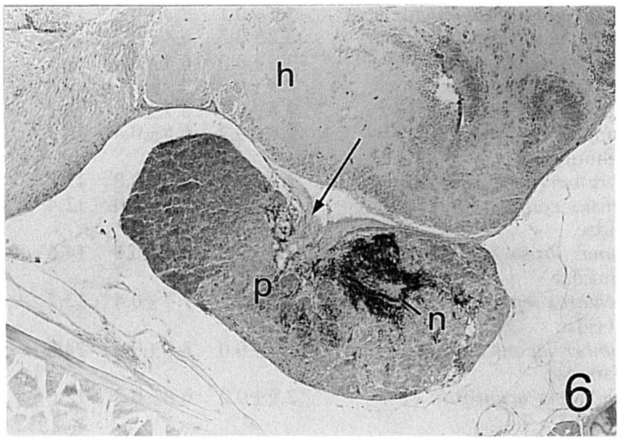


FIG. 5. An embryo of the guppy, *Poecilia reticulata*. The pituitary abuts widely on the hypothalamus and the pituitary stalk is not formed. ×340.

FIG. 6. An adult of *P. reticulata*. The pituitary hangs down from the hypothalamus by the pituitary stalk (arrow). ×85.

TABLE 1. Nucleus diameter of cerebellar granular cells and Purkinje's cells, and PG index in perciform teleosts

Species	Granular[1)]	Purkinje[2)]	PG[3)]
Centropomidae			
Chanda sp. (5)*	2.5±0.2	5.8±0.3	12.2
Percichthyidae			
Lateolabrax japonicus (17)	3.0±0.1	7.2±0.6	14.5
Coreoperca kawamebari (8)	3.2±0.2	8.6±0.5	20.0
Serranidae			
Epinephelus septemfasciatus (25)	3.2±0.3	8.2±0.5	16.5
Franzia squamipinnis (13)	2.5±0.0	5.9±0.2	12.8
Centrarchidae			
Micropterus salmoides (19)	3.4±0.2	8.7±0.5	16.5
Lepomis macrochirus (7)	3.0±0.2	7.5±0.5	15.6
Apogonidae			
Sphaeramia nematoptera (9)	2.5±0.1	7.0±0.4	23.3
Sillaginidae			
Sillago japonica (20)	2.9±0.2	8.8±0.9	27.9
Carangidae			
Seriola quinqueradiata (39)	3.6±0.3	10.5±0.5	25.5
Decapterus maruadsi (19)	3.2±0.2	7.9±0.4	15.8
Leiognathidae			
Leiognathus nuchalis (11)	3.2±0.3	8.8±0.6	20.8
Lobotidae			
Datnioides sp. (7)	2.8±0.3	6.7±0.4	14.5
Haemulidae			
Parapristipoma trilineatum (27)	2.8±0.3	9.2±1.0	35.5
Sparidae			
Pagrus major (9)	3.0±0.3	7.3±0.5	14.9
Acanthopagrus schlegeli (25)	2.9±0.2	9.4±0.5	35.9
Monodachtylidae			
Monodachtylus argenteus (5)	2.5±0.2	6.5±0.4	17.2
Toxotidae			
Toxodes jaculator (7)	2.5±0.3	6.5±0.1	18.3
Kyphosidae			
Girella punctata (8)	2.8±0.3	7.0±0.3	15.6
Microcanthus strigatus (19)	2.9±0.2	9.9±0.5	41.9
Scatophagidae			
Scatophagus argus (5)	2.6±0.1	6.1±0.2	13.7
Chaetodontidae			
Chaetodon vagabundus (13)	2.5±0.3	7.1±0.4	22.4
Pomacanthidae			
Centropyge bispinosus (6)	2.5±0.2	7.0±0.3	22.0
Nandidae			
Badis badis (3)	2.6±0.3	5.3±0.4	8.7
Oplegnathidae			
Oplegnathus fasciatus (20)	3.1±0.1	9.4±0.5	28.8
Cichlidae			
Symphysodon aequifasciatus (6)	3.0±0.0	6.9±0.2	11.9
Geophagus steindachneri (10)	3.0±0.1	6.9±0.5	12.8
Pterophyllum scalare (8)	2.9±0.2	6.3±0.3	10.8
Cichlasoma meeki (7)	2.7±0.3	6.8±0.3	15.6
Haplochromis venustus (19)	3.0±0.1	7.9±0.8	19.2
Lamprologus brichardi (10)	2.7±0.3	6.5±0.4	13.6
Hemichromis guttatus (11)	2.7±0.3	6.9±0.3	16.3
Tilapia nilotica (9)	3.1±0.2	7.2±0.3	12.3
Etroplus maculatus (7)	2.9±0.2	7.6±0.4	18.6
Embiotocidae			
Ditrema temmincki (13)	3.6±0.1	8.6±0.7	14.0
Pomacentridae			
Amphiprion clarkii (9)	2.6±0.2	7.0±0.8	19.5
Chrysiptera cyanea (4)	2.4±0.2	6.0±0.2	16.6
Cirrhitidae			
Oxycirrhites typus (14)	2.5±0.3	6.5±0.4	18.3
Mugilidae			
Liza haematocheila (21)	2.7±0.2	7.5±0.3	22.7
Sphyraenidae			
Sphyraena pinguis (29)	3.4±0.2	8.0±0.5	13.6
Labridae			
Pterogonus flagellifera (11)	2.9±0.2	8.0±0.7	20.6
Pseudolabrus japonicus (14)	2.7±0.3	8.2±0.3	27.5
Halichoeres tenuispinnis (12)	2.4±0.2	6.8±0.3	22.2
Halichoeres poecilopterus (18)	2.4±0.2	7.6±0.5	33.1
Stichaeidae			
Dictyosoma burgeri (21)	3.0±0.1	7.5±0.4	16.1
Pholididae			
Enedrias nebulosa (9)	2.6±0.3	5.4±0.5	9.5
Mugiloididae			
Parapercis sexfasciata (17)	2.9±0.2	8.3±0.6	24.3
Blenniidae			
Pictiblennius yatabei (8)	2.9±0.2	6.2±0.3	10.3
Entomacrodus stellifer (10)	2.5±0.4	6.0±0.3	14.3
Callionymidae			
Repomucenus richardsonii (12)	2.8±0.3	6.5±0.6	12.9
Eleotrididae			
Odontobutis obscura (14)	3.6±0.2	8.1±0.4	11.2
Gobiidae			
Favonigobius gymnauchen (7)	3.7±0.3	6.5±0.5	5.7
Rhinogobius brunneus + (6)	2.9±0.2	5.4±0.3	6.6
Rhinogobius brunneus ++ (6)	2.9±0.2	5.6±0.4	7.0
Rhinogobius flumineus (4)	2.7±0.3	5.2±0.3	7.1
Tridentiger obscurus (7)	3.1±0.1	6.3±0.3	8.8
Tridentiger trigonocephalus (4)	2.9±0.2	5.9±0.4	8.2
Glossogobius olivaceus (15)	3.0±0.0	6.0±0.2	8.0
Chaenogobius urotaenia | (6)	2.9±0.2	5.3±0.4	6.4
Chaenogobius urotaenia || (6)	2.9±0.2	5.6±0.5	7.2

Acanthogobius flavimanus (14)	3.1±0.1	7.4±0.3	14.0
Pterogobius elapoides (8)	3.2±0.3	6.4±0.3	8.0
Pterogobius virgo (15)	3.0±0.0	6.4±0.4	9.5
Luciogobius guttatus (6)	2.9±0.2	5.7±0.3	7.4
Leucopsarion petersi (5)	3.5±0.2	6.1±0.4	5.2
Periophthalmus sp. (10)	2.6±0.2	6.5±0.4	15.3
Acanthuridae			
Zebrasoma veliferum (12)	2.9±0.2	7.0±0.8	13.8
Zanclus cornutus (10)	3.1±0.3	7.1±0.6	12.4
Siganidae			
Siganus fuscescens (19)	2.7±0.3	6.6±0.6	14.6
Trichiuridae			
Trichiurus lepturus (96)	3.2±0.3	7.7±0.4	13.7
Scombridae			
Scomber japonicus (34)	3.0±0.0	8.8±0.8	24.8
Anabantidae			
Ctenopoma acutirostre (10)	2.9±0.2	6.8±0.3	12.6
Belontiidae			
Betta splendens (7)	2.6±0.2	5.6±0.4	9.7
Trichogaster leeri (9)	2.9±0.2	5.8±0.3	7.8
Helostomatidae			
Helostoma temmincki (5)	2.7±0.3	5.6±0.4	8.7
Osphronemidae			
Osphronemus goramy (8)	2.9±0.2	6.8±0.3	12.6
Luciocephalidae			
Luciocephalus pulcher (11)	2.6±0.2	6.0±0.5	12.3
Channidae			
Channa micropeltes (10)	2.9±0.2	7.0±0.3	14.1
Mastacembelidae			
Mastacembelus erythrotaenia (10)	2.8±0.3	5.3±0.3	7.0

1) Nucleus diameter of granular cells (mean, μm±SD)
2) Nucleus diameter of Purkinje's cells (mean, μm±SD)
3) PG index; nucleus volume of Purkinje's cells divided by that of granular cells. The nucleus volume was calculated by assuming the nucleus as a ball.
* The number in parentheses indicates total length (cm) of the individual studied.
+ Black-striped type regarded as a distinct species.
++ Black type regarded as a distinct species.
| Freshwater type regarded as a distinct species.
| | Brackish-water type regarded as a distinct species.

included in Table 1. In the adult smelt, the PG index is 13.7 and in the adult guppy, it is 15.0. In Figure 7, the PG index changes from 3.9 to 16.8 in the catfish, from 2.4 to 7.7 in the lizard, from 1.9 to 12.7 in the chick, from 2.0 to 9.2 in the mouse.

Figure 8 shows the relation between the nuclear volume of granular cells and the PG index in 79 species of perciforms. The circles represent gobies and the solid dots represent non-gobiid perciforms. The arrow is a value of *R. flumineus*. It is apparent that PG indexes of gobies are small compared with those of non-gobiid perciforms.

DISCUSSION

Why is the pituitary of gobies embedded in the hypothalamus? In this paper, the author tries to interpret the pituitary condition of gobies as the result of paedomorphosis. Although the pituitary shape itself may be a trivial matter and this interpretation may be crude, the author here attempts to offer a small example of "a unified biology".

Cavalier-Smith [3] connects a small genome size to *r*-selection and a large genome size to *K*-selection. His arguments may be summaried as follows. Within a monophyletic group in which the numbers of genes are similar, a small genome size with the relatively small amount of non-genic DNA is reflected in a small nuclear size, and thus a small cell size. If the cell is small, it may divide rather quickly. Its metabolic activity may be high, at least latently, because the areas of the nuclear and cell membranes, through which metabolic molecules move, are relatively large compared with the large nucleus and cell. This argument is based on the well known fact that volume decreases three-dimensionally whereas area decreases only two-dimensionally. "Small", "quick", and "active" are fundamental characters favored by *r*-selection [12]. On the contrary, the large genome size, the large nucleus and cell sizes, slow growth rate, and low metabolic activity (dullness) are features favored by *K*-selection. Meanwhile, Gould [6] connects *r*-selection with one of paedomorphic heterochrony (progenesis) and *K*-selection with the other paedomorphic heterochrony (neoteny). *K*-selection is also considered to be related to one of peramorphic heterochrony (hypermorphosis). Progenesis is a truncation of development and is thus related to "small" and "quick". Neoteny causes "young morphology" while hypermorphosis causes "advanced morphology", but both are related to "large" and "slow", though relatively. Thus, Gould's arguments are primarily concerned with shape, which is not dealt with by Cavalier-Smith.

The shape of the pituitary of adult gobies remains as in embryos and hatchlings, and in non-gobiids this shape is retained only in embryonic stages. Therefore, the pituitary partly embedded in the hypothalamus is apparently paedomorphic. Paedomorphosis in this case is not directly related to a small cell size, because the nucleus size of gobiies is not necessarily small among perciforms. Hinegardner and Rosen [7] also reported that the genome size of gobies is moderate among perciforms. Paedomorphosis in this case may be related to the PG index, because this index is consistently low in gobies. Cerebellar granular cells are one of the smallest neurons and Purkinje's cells are one of the largest neurons, but both cells are diploid [5]. The nucleus size of granular cells does not change during development and may directly reflect the genome size. The nucleus of Purkinje's cells increases conspicuously in size during development as shown in Results. The PG index may be a sort of peramorphic index, that is an index of advanced development and shape. As constituting the nervous center of motion coordination, the marked development of Purkinje's cells may also be an indicator of "activeness". Among gobies studied, the mudskipper, *Periophthalmus* sp., shows the largest PG index, and this species is an unusual, semiterrestrial goby with its pituitary only slightly embedded in the hypothalamus. The goby showing the smallest PG index is the ice goby, *Leucopsarion petersi*. This transparent goby is apparently paedomorphic. Incidentally, the largest PG indexes revealed here are among the stripey, *Microcanthus strigatus*, the seabream, *Acanthopagrus schlegeli*, and the grunt, *Parapristipoma trilineatum*. The life style of these perciforms is definitely different from that of gobies, and their

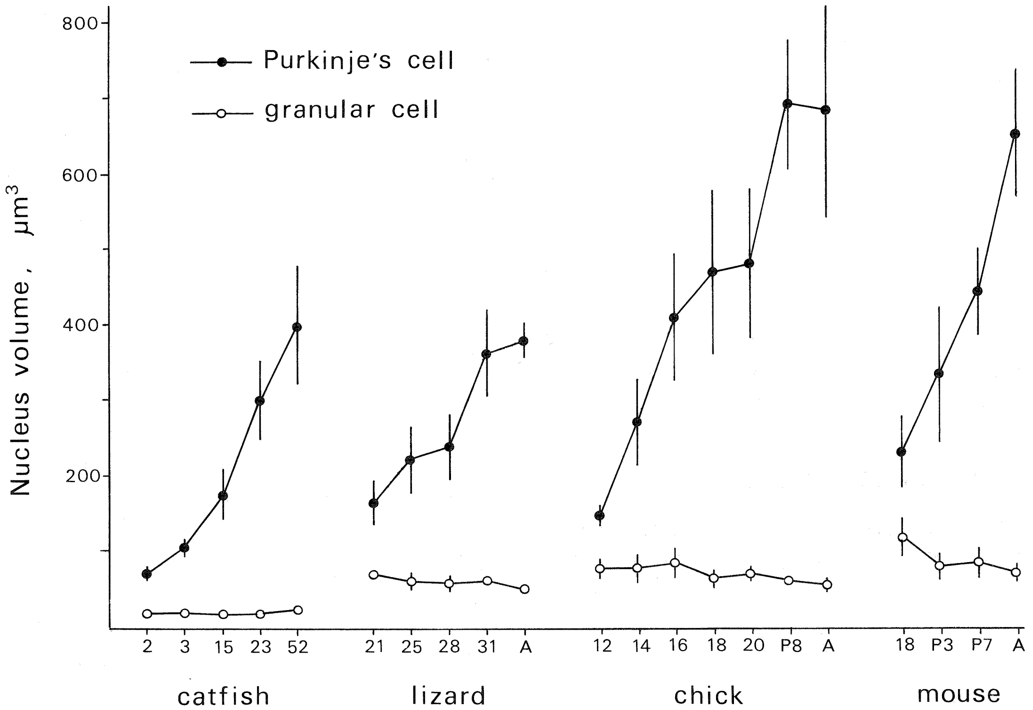


FIG. 7. Changes of nucleus volume of granular cells and Purkinje's cells in the catfish, *Silurus asotus*; lizard, *Takydromus tachydromoides*, chick, and mouse. In the catfish, the numerals of the abscissa indicate total length represented in cm. In the other species, the numerals indicate incubation or gestation days, A indicates adults, and P indicates postnatal days. Bars represent standard deviation in one individual measured.

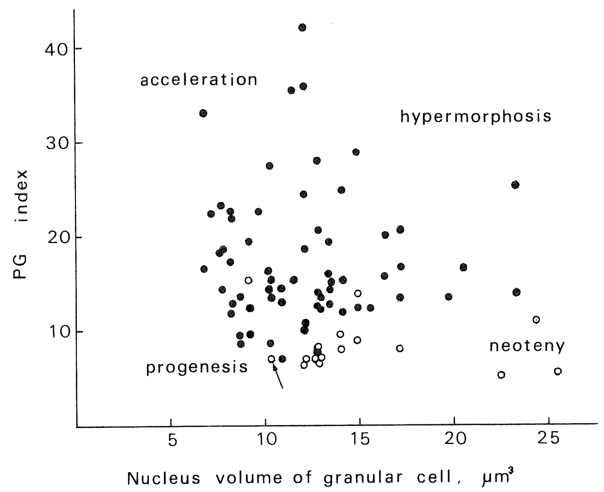


FIG. 8. Relation between nucleus volume of granular cells and the ratio of nucleus volume of Purkinje's cells to that of granular cells in various perciform teleosts. Mean value of one individual was used for representation. Circles indicate gobies. The arrow indicates *R. flumineus*. See the text for four types of heterochrony.

pituitaries are of course provided with a well developed stalk.

Overall biological features of gobies appear to be paedomorphic [10]. Among these features, some may be related to progenesis and *r*-selection. These are early maturation (some gobies are annual), small body size, high speciation rate (the Gobiidae is the largest family among perciforms). The features possibly related to neoteny and *K*-selection are large egg size, small number of eggs (low fecundity), and long embryonic development. In any event, the relatively large head of gobies is apparently paedomorphic.

The author's hypothesis of correlating the four types of heterochrony with genome size and PG index (peramorphic index) is illustrated in Figure 8. A large PG index is related to peramorphosis and a small one to paedomorphosis. The small genome size, roughly represented by the nucleus size of granular cells, is related to acceleration and progenesis, which, at least progenesis, may be the result of *r*-selection, while the large genome size is related to hypermorphosis and neoteny which may be the result of *K*-selection.

Using the data of the nucleus size of the cerebellar granular and Purkinje's cells of 43 species of tetrapods (Tsuneki, unpublished), the author tentatively depicted a figure similar to Figure 8. In this figure, mammals occupy the center, birds occupy the area of acceleration, lizards occupy the area of progenesis, snakes occupy the area of progenesis and neoteny, turtles occupy the area of hypermorphosis (though near to the center of the figure), frogs occupy the area of neoteny, and urodeles occupy the area of extreme neoteny. The upper right-hand corner, the typical hypermorphosis corner, is occupied by few species both in tetrapods (Tsuneki, unpublished) and in perciforms (Fig. 8). Highly peramorphic vertebrates with a large genome size could not be realized.

Some of the difference in nuclear size may be insignificant in terms of adaptation and thus may be neutral. However, apart from the fundamental difference of gene numbers among organisms of fundamentally different body size and organization, the nucleus size in a monophyletic group may frequently have some biological significance not only in terms of *K*-, *r*-selection, but also in terms of heterochrony. This kind of argument may appear to be reliant on "ad hoc" explanations, but these explanations could be united to create a more unified biology. In this biology, genetics (DNA), cytology (nucleus and cell size), embryology (heterochrony), morphology (heterochrony), physiology (metabolic activity), systematics (speciation), and ecology (*K*-, *r*-selection) are all to be assembled.

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