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On The Morphological Feature of The Gill of Amphibious and Air Breathing Fishes

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Three air-breathers, two amphibious fishes, two sluggish water-breathers and five active or intermediately active water-breathers were compared for the gill structure, and the following results were obtained so far as the used data of these species are concerned.

1) In the ratio of the gill area to body surface area,
air-breathing and amphibious fish < sluggish fish < water-breather.
2) In the total number of filaments,
amphibious fish ≒ sluggish fish < air-breather < water-breather.
3) In the density of secondary lamella,
sluggish fish < air-breather < water-breather.
4) As the ratio of the fourth to the first gill arch, in the length of secondary lamella and the filaments,
air-breather < amphibious fish < water-breather.
5) In the total length of filaments and the area of secondary lamella,
air-breathing and amphibious fish < sluggish fish.
6) There are environmental and respiratory differences among amphibious fishes and air-breathers, and consequently, the differences of gill structure, especially in the fourth gill arch, are indicated.

Introduction

In regard to the feature of the gill of air-breathing fishes, Hughes *et al.* (1973) and Hughes (1974) have reported on *Anabas testudineus* and *Saccobranchus fossilis*. They have dealt mainly with length of filament, area of secondary lamella and fourth gill arch (*Anabas*), but the feature of gill area and the density of secondary lamella are shown also in Gray's "sluggish fishes" (Hughes, 1966).

Since the oxygen uptake by the gill of air-breathers or amphibious fishes in water is only a part in the total differing from that of the sluggish fishes, the former gill structure adapting to the smaller role may approach to that of the latter, when the former activity is intermediate. Nevertheless difference can exist between these similar groups.

We compared the component parameters of gill area among the species of amphibious fishes, air-breathers, water-breathers and sluggish fishes using the data of ours, those of Gray (1954), Hughes *et al.* (1973) and Hughes (1974).

Materials and Methods

Amphibious fishes *Periophthalmus cantonensis* and *Boleophthalmus chinensis* were collected from Ariake Bay, air-breathing *Canna argus* from a river at the suberbs of Nagasaki City and *Anabas testudineus* was obtained from a shop of tropical fishes.

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Table 1. Component parameters measured in gill structure.

Species	*A.testudineus*	*C.argus*	*B.chinensis*	*P.cantonensis*	*A.japonica*	*C.carpio*	*C.auratus*
Number of determinations	5	3	15	11	1	2	12
Average body weight (g)	27.0	671.0	35.2	5.3	10.5	17.2	30.5
Average body length (cm)	8.7	371.0	14.0	7.1	24.2	11.5	9.5
Total gill area (cm^2)	18.2	572.6	33.3	6.6	34.8	71.5	136.9
Gill area/body weight (cm^2/g)	0.67 ±0.22	0.85	0.94 ±0.30	1.24 ±0.44	3.32	4.16	4.49 ±1.64
Gill area/body surface area (cm^2/cm^2)	0.40	0.38	0.56	0.38	1.45	1.74	2.91
Total number of filaments	540	1538	486	306	1024	1250	1560
Average length of filament (mm)	1.15 ±0.25	4.96	4.30 ±0.54	1.25 ±0.25	3.76	3.20	3.59 ±1.28
Length of secondary lamella (mm)(1)	0.367	0.773	0.261	0.191	0.235	0.241	0.313
Height of secondary lamella (mm)(b)	0.095	0.153	0.222	0.161	0.117	0.103	0.109
Number of secondary lamellae/mm on one side of filament (d^{-1})	27.8 ±2.7	12.8 ±1.6	14.2 ±2.0	23.5 ±2.4	23.8 ±2.1	27.6 ±2.3	29.9 ±2.6
Length of secondary lamella × no. of sec. lam./mm (1/d)	10.20	9.89	3.71	4.49	5.59	6.65	9.36
Average length of filament/body length	0.0013	0.0013	0.0031	0.0018	0.0016	0.0028	0.0038
(b/d)	2.64	1.96	3.15	3.78	2.78	2.84	3.26

Table 2. Body weight of the specimens and behavioral activity of each species examined or cited in this study.

Species	Body weight (g)	Activity	Used in Fig.	and Table	References
Saccobranchus fossilis	1000	Intermediate	1,2	3	Hughes, 1974
Anabas testudineus	1000	Active	1,2	3	Hughes *et al.*, 1973
Channa argus	671	—	1,2	1,3,4	Present authors
Boleophthalmus chinensis	35.2	Intermediate	1,2	1,3,4	〃 〃
Periophthalmus cantonensis	5.3	Active	1,2	1,3,4	〃 〃
Tautoga onitus	580	Intermediate	1,2	3	Gray, 1954
〃 〃	297	Intermediate	2		Hughes 1966
Stenotomus chrysops	253	Intermediate～Active	1,2		〃 〃
〃 〃		〃 〃		3	Gray 1954
Mugil cephalus	166	Active	1	3	〃 〃
Scomber scombrus	226	Active	1,2	3	Hughes, 1966
Lophius piscatorius	6392	Sluggish	1	3	Gray, 1954
Archosargus probatocephalus	544	Intermediate～Active	2		Hughes, 1966
Opsanus tau	305	Sluggish	2		Hughes & Gray, 1972
Anabas testudineus	27.0	Active		1,4	Present anthors
Anguilla japonica	10.5	Intermediate		1,4	〃 〃
Carassius auratus	30.5	Intermediate～Active		1,4	〃 〃
Cyprinus carpio	17.2	Intermediate		1,4	〃 〃
Sarda sarda	2192	Active		3	Gray, 1954
Brevoortia tyrannus	613	Active		3	〃 〃
Gymnosarda alleterata	5216	Active		3	〃 〃

the others from another shop. The parameters of gill area were measured for several species of amphibious fishes, air-breathers and water-breathers as shown in Table 1. The measurement was carried out during several hours before the blood color faded from the isolated filament.

The gill area was calculated as follows:

Total gill area $= 2(S_1+S_2+S_3+S_4)$,

$S_i = 2N_i\bar{f}_i 2/\bar{d}_i\bar{l}_i\bar{b}_i$

In this formula, S_i…gill area on one gill arch, N_i…number of filaments on one filament series, $\bar{f}_i$…average length of filament, $\bar{d}_i$…average distance between secondary lamellae, $\bar{l}_i$…average length of secondary lamella, and $\bar{b}_i$…average height of secondary lamella.

Then, $2N_i$ means number of filaments on two filament series, $\bar{f}_i 2/\bar{d}_i$ number of secondary lamellae of average length of filament and $\bar{l}_i\bar{b}_i$ average area of secondary lamellae on both sides.

Results

As the calculated values in Table 1 are from specimens of earlier growth stage exept *C. argus,* these values can not be compared directly with each other.

The values for *B. chinensis* and *P. cantonensis* of maximum body weight are presumed from the regression coefficient of the value in body weight of *A. testudineus* and *S. fossilis* by Hughes *et al.* (1973) and Hughes (1974). These presumed values of maximum body weight were calculated from the percentage of the weight of used specimen to their maximum body weight recorded up to this time, assuming that the regression coefficient of *A. testudineus* or *S. fossilis* may applicable to these species. The value of every gill arch is abridged in Table 1. The data of Gray (1954), Hughes (1966), Hughes & Gray (1972), Hughes *et al.* (1973) and Hughes (1974) are cited in Tables 2, 3 and Figs. 1, 2 to compare the data of the largest weight among air-breathers, amphibious fishes, water-breathers and sluggish fishes. These references and their activity are shown in Table 2.

Ratio of gill area to body surface area (Table 3)

The gill areas in five air-breathers, four active or intermediately active water-breathers and one sluggish water-breather were compared as shown in Table 3.

Table 3. Gill area per body weight and per body surface area of each species.

Species	Respiration	Gill area/Body weight (cm^2/g)	Gill area/Body surface area (cm^2/cm^2)	Reference
Periophthalmus cantonensis	Amphibious	1.24	0.38	Present authors
Boleophthalmus chinensis		0.94	0.56	〃 〃
Saccobranchus fossilis	Air-breathing	0.32	0.34	Hughes, 1974.
Anabas testudineus		0.39	0.40	Hughes *et al.*, 1973
Channa argus		0.85	0.38	Present authors
Tautoga onitus	Water-breathing	3.92	4.35	Gray, 1954
Stenotomus chrysops		5.06	4.78	〃
Mugil cephalus		9.54	6.54	〃
Scomber scombrus		11.58	8.38	〃
Sarda sarda		5.95	11.55	〃
Brevoortia tyrannus		17.73	18.28	〃
Gymnosarda alleterata		19.39	48.54	〃
Lophius piscatorius	Sluggish	1.96	2.99	〃

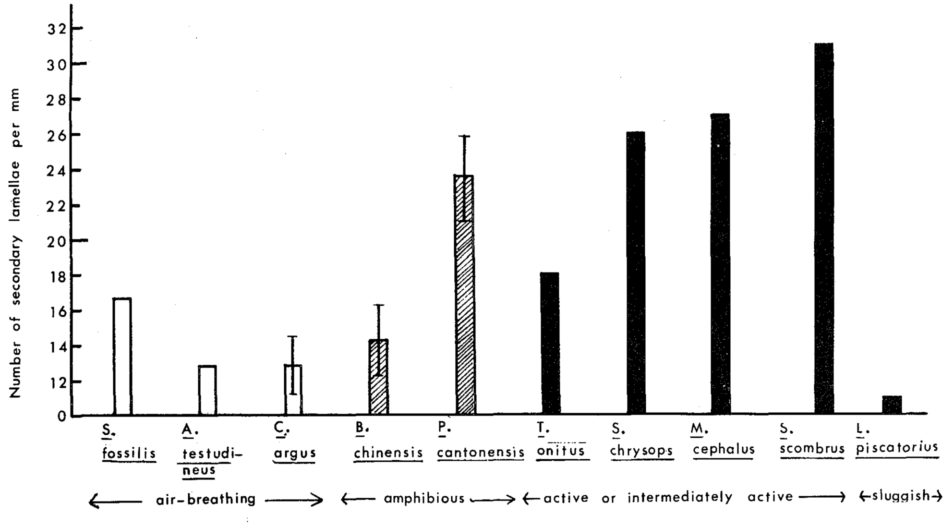

Fig. 1. Number of secondary lamellae per mm on one side of filament of several species.
Vertical lines indicate standard errors. (P=0.05)

The air-breathers and amphibious fishes showed the minimum values of gill area /body surface area lower than 2.0, the water-breathers the highest values of more than 4.0 and the sluggish fish a medium value.

Number of secondary lamellae per mm on one side of filament (Fig. 1)

The species shown in Fig. 1 are the same as those in Table 3. The amphibious *B. chinensis* and the air-breathers showed lower values for the number of secondary lamellae per mm on one side of filament than the water-breathers.

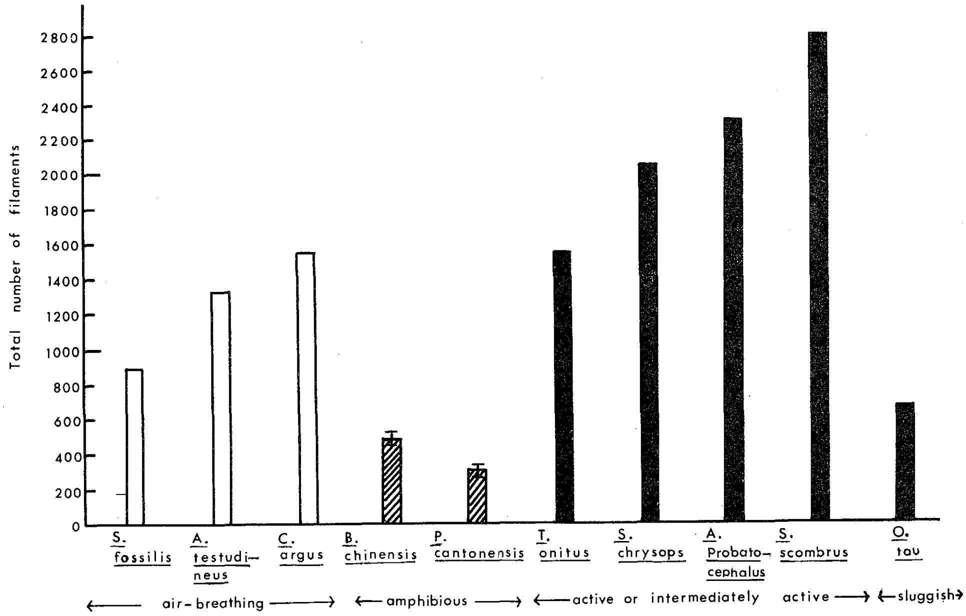

Fig. 2. Total number of filaments of several species.
Vertical lines indicate standard errors. (P=0.05)

The sluggish fish *L. piscatorius* showed the lowest value. The value of *P. cantonensis* was aproximately equal to those of the intermediately active water-breathers.

Total number of filaments (Fig. 2)

The species shown in Fig. 2 are not the same as those in Table 3 and Fig. 1 *Archosargus* and *Opsanus* are replaced instead of *Mugil* and *Lophius*. The total number of filaments of two amphibious fishes showed the minimum value, but, the air-breathing species had the medium values exept *C. argus* which showed the high value as that of *T. onitus*. The value of sluggish fish *O. tau* was near to the amphibious fishes.

Length of secondary lamella, number of secondary lamellae per mm (1/b) and average length of filament/ body length.

In the length of secondary lamella, number of secondary lamellae per mm, the values of the amphibious fishes were low and those of the air-breathers were high. In the average length of filament / body length, the value of *B. chinensis* was high, those of the air-breathers were low.

Fourth gill arch (Table. 4)

The fourth gill arch of the generl water-breather does not differ so much from the other gill arch, but that of the air-breather and amphibious fish are remarkably different or degenerated (Suzuki, 1969; Hughes *et al.*, 1973). Table 4 shows parameters of the length of secondary lamella, length of filament and number of secondary lamellae per mm as the ratio to that of the first gill arch reducing the effect of body weight. In the length of secondary lamella

Table 4. Fourth gill arch/first gill arch (%) of several characters in each species.

Speces	Respiration	No. of filaments	Length of sec. lam. (%)	No. of sec. lam./mm (%)	Length of filament (%)	No. of specimens
Periophthalmus cantonensis	Amphibious	76	76	104	62	11
Boleophthalmus chinensis		126	75	129	62	15
Anabas testudineus	Air-breathing	20	41	119	16	5
Channa argus		40	39	101	42	3
Anguilla japonica	Water-breathing	97	95	101	79	1
Cyprinus carpio		90	89	97	108	2
Carassius auratus		92	95	104	89	12

Table 5. Comparison between air-breathing and sluggish fish of maximum body weight.

Parameter \ Species	*A. testudineus*	*S. fossilis*	*B. chinensis*	*P. cantonensis*	*O. tau*
Body weight (g)	1000	1000	53.0	8.8	1000
Total gill area (cm^2)	389	321.4	50.2−54 5	10.5−11.5	1317
Gill area/body weight (cm^2/g)	0.39	0.32	0.78−0.81	1.03−1.04	1.31
Distance between sec. lam.(mm)	0.078	0.061	0.075	0.047−0.045	0.105
Total filament length (mm)	5230	6172	2500−2960	495−540	8638
Average area of sec. lam.(mm^2)	0.28	0.32	0.08	0.04	0.79
Total number of filaments	1316	880	500−512	315−333	—
Reference	Hughes *et al.*, 1973	Hughes, 1974	Authors	Authors	Hughes & Gray, 1972

The values of *Boleophthalmus* and *Periophthalmus* are presumed dimension from the data in Table 1 by the regression coefficient in body weight of *Anabas-Saccobranchus* by Hughes (1973, 1974).

and that of filament, the values of the air-breathers were low and those of the water-breathers high, and those of the amphibious fishes the medium. In the number of filaments the values of the air-breathers were low, those of the amphibious fishes higher or medium. In the number of secondary lamellae per mm, those of *B. chinensis* and *A. testudineus* were high and the others were not so different.

Comparison among amphibious fish, air-breather and sluggish fish (Table. 5)

Table 5 shows characters of the gill of *O. tau, A. testudineus* and *S. fossilis* with the body weight of 1000 g, and the amphibious fishes show the presumed values of the largest body weight. As Table 5 shows, the air-breather and the amphibious fish differed from the sluggish fish in the following characters, namely, the gill area/body weight, the distance between secondary lamella, the total filament length and the average area of secondary lamella. These parameters of the air-breathing and the amphibious fishes showed lower values than the sluggish fish. The values of the gill area/body weight were minimum in the air-breather, and those of the average area of secondary lamella were minimum in the amphibious fishes. In the distance between secondary lamella and the total filament lenght, the air-breather or amphibious fish showed lower values than the sluggish fish.

Discussion

On the relation of the gill area, the density of secondary lamella, the length or the number of filaments, the fourth gill arch, the accessory respiratory organs and the oxygen uptake by gill in the air-breather have been reported by Suzuki (1969), Hughes *et al.* (1973) and Hughes (1974).

Differences of the gill among amphibious fish, air-breather, sluggish water-breather and other water-breather.

(Gill area)

The gill area of amphibious gobioids decreases with terrestrial adaptation (Schöttle, 1931), the gill of air-breathers has tendency to degenerate (Carter, 1957). Gill area is proportional to the activity of fish (Hughes, 1966), its smallness indicates sluggish or habitat in high dissolved oxygen (Suzuki, 1969), the regression coefficient of gill area in body weight is small in *A. testudineus* (Hughes, *et al.*, 1973), the gill area of *S. fossilis* is smaller than that of Gray's "sluggish fish" (Hughes, 1974). In this study, the gill area/body surface area of the ampibious fishes are small approaching to the air-breathers. The gills of the amphibious fishes breathe in water and on land, but the amount differs with the habitat (Tamura, *et al.*, 1976). The oxygen uptake by the gill of the amphibious fishes is larger in water than on land (Tamura, *et al.*, 1976), accordingly, the gill structure of these fishes may be mainly related to the respiratory amount in water. It is presumed that the small gill area of the amphibious or the air-breathing fishes are related to the smaller role in the respiration by the gill in water. As shown in Table 3, so far as the data of the used species are concerned, the relation of the gill area/body surface area resulted in the order of

amphibious fish and air-breather < sluggish fish < water-breather.

(Number of secondary lamellae per mm)

The number of secondary lamellae or the density of secondary lamellae is small when the gill area small or the total respiratory water flow is large, and the oxygen consumption is proportional to the constant relating interlamellar distance and 1/2 power of velosity of water flow (Hughes, 1966). The inverse number of the density of secondary lamella of the amphibious fishes is approximately proportional to the oxygen uptake by gill as reported by Kobayashi & Ichikawa (1970) in other fishes.

The number of secondary lamella per mm becomes smaller with growth of fish, and its change is small (Suzuki, 1969). The value of *P. cantonensis* (Fig. 1) is nearly as large as that of the water-breather. Except for *P. cantonensis,* the relation of

sluggish fish < air-breather < water-breather is obtained.

The large oxygen uptake by gill in water of *P. cantonensis* may account for the large value of the species (102ml/kg.hr $= 2.4 \times$ B. chinensis 43ml/kg.hr., Tamura *et al.,* 1976).

(Total number of filaments)

As the total number of filaments increases with growth, the value in relation to body weight is compared. The value of the amphibious fishes are minimum, but the specimens are not largest, and these values will increase more at larger weight. Hughes (1966) has mentioned that the value is large in active water-breather.

(Length of secondary lamella/interlamellar distance, 1/d)

Following the increase of the length of secondary lamella gill area becomes large and the total water flow become smaller (Hughes, 1966), the smaller value of 1/d indicates sluggish or habitat of high dissolved oxygen, and

Time of keeping secondary lamella contact with water $= 2(1/d)^2/k$, that is, 1/d should be larger to take sufficient oxygen by keeping necessary time for contact with water (Suzuki, 1969). Comparing the values of 1/d in Table 1, however, the values are not always small in the air-breather or in the sluggish fish.

Fourth gill arch

C. argus is markedly degenerated in the second series of filaments of the fourth gill arch (Suzuki, 1969), and general water-breathers have the same fourth gill arch as the other gill arch (Kobayashi & Ichikawa, 1970). *Anabas testudineus* hardly has the secondary lamellae on the fourth gill arch (Hughes, *et al.,* 1973). As Table 4 shows, the fourth gill arch of amphidious or air-breathing fishes remarkably differ mutually and from the water-breathers, that is, the length of secondary lamella and filament are smaller in the air-breather and the amphibious fish than in the water-breather.

Consequently, the change of the fourth gill arch may be one of the features of air-breathers and the amphibious fishes.

Comparison among air-breather or amphibious fish and sluggish fish

The air-breather and amphibious fish have some characters of approached values, namely the gill area and the total length of filaments as shown above, yet, there are difference in the presence of accessory respiratory organs or secondary cutaneous respiration. Since Hughes has pointed out the great correlation coefficient of these component parameters between gill area and body weight or growth, we have compared the specimens of stages of growth as large as possible for this study. The air-breathers and the amphibious fishes show smaller gill area/body surface area and the area of secondary lamella, smaller total filament length and interlamellar distance than the sluggish fish (Table. 5).

Cause of special features in the gill of amphibious and air-breathing fish

As mentioned above, the air-breathers and the amphibious fishes show several differences in gill structure mutually and the both group from the water-breathers and also from the sluggish fishes. These special features of the air-breathers and the amphibious fishes originate in the accessory or secondary respiratory organs. The air-breathers take oxygen by gill and also by these organs in water. Consequently, even though the total diffusion capacity is large like *A. testudineus* (0.2967), that by gill

(0.0142) is very small (4.8% of total) (Hughes *et al.,* 1973). The structure of the fish gill is presumed to be related to the diffusion capacity of the gill in water. The total oxygen uptake of active fish *P. cantonensis* in water was 196 ml/kg.hr (20℃), but the amount taken by gill was 52% of total (Tamura *et al.,* 1967). Accordingly, the gill area of this species becomes naturally smaller than that of the active water-breathers. However, the amount of oxygen uptake by gill in air-breathers and amphibious fishes differ remarkably, and in addition, since they have environmental difference among species, *B. chinensis,* for example, may be presumed to differ from the other air-breathers in the number of filaments of the fourth gill arch and *P. cantonensis* in the density of secondary lamella.

As to the maintenance of the sensitive delicate gill lamella in air, it may be kept by means of the prevention of the mutual contact with adjacent secondary lamellae, or by means of the stronger stoutness of secondary lamella larger than the water-breathers. From the former, it is presumed that

(1) interlamellar distance(d) > height of secondary lamella (b).

(2) distance between secondary lamella on adjacent filaments is large.

but (1) is not true as shown in Tables 1, 5.

From the latter. it is also considered that

(3) breadth of secondary lamella is large.

(4) area of secondary lamella is small when the breadth is same as that of the water-breathers.

Among the above presumptions, (2) and (3) are unknown, but (4) is possible.

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両生魚と空気呼吸魚の鰓の形態的特性について

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両生魚類又は空気呼吸魚類の鰓の形態的特性を知るために，空気呼吸魚3種，両生魚2種，水中呼吸魚5種と不活潑（水中呼吸）魚2種について，鰓面積の媒介変数を比較した。

(1) 単位体表面積当りの鰓面積に於ては，両生魚と空気呼吸魚＜不活潑魚＜水中呼吸魚

(2) 全鰓弁長に於ては，両生魚≒不活潑魚＜空気呼吸魚＜水中呼吸魚

(3) 鰓弁片密度に於ては，不活潑魚＜空気呼吸魚＜水中呼吸魚

(4) 第4鰓弓上の鰓弁片長・鰓弁長と第1鰓弓上の各々との比に於ては，空気呼吸魚＜両生魚＜水中呼吸魚

(5) 全鰓弁長と鰓弁片の面積に於ては，両生魚と空気呼吸魚＜不活潑魚

(6) 空気呼吸魚の各種間にも環境や呼吸上の相違点があるから，その結果として，鰓構造の相違，特に第4鰓弓上の相違点が空気呼吸魚と両生魚の間に認められる。