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Dimensions of the Gills of an Indian Hill-stream Cyprinid Fish, *Garra lamta*

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Abstract A description of gill structure in a hill-stream fish, *Garra lamta*, is given. Quantitative data of the gills are discussed in relation to their respiratory function. The interbranchial septum is quite long and approaches the condition recorded in *Neoceratodus* and *Latimeria*. Values for the total filament length in relation to body weight of various specimens of *Garra lamta* fall between the regression lines drawn for intermediately active and sluggish fish. Comparatively lower value for gill area per unit body weight (321.4 mm^2/g) for a fish of 4.1 g may be due to the sedentary habit of the fish.

About five species of the cyprinid genus *Garra* inhabit comparatively cold, hyperoxic waters of the hill-streams of India. They have undergone a great variety of adaptive modifications for living in torrential streams (Hora, 1922). Induced by the necessity of living in the swift currents of the streams, the integument of the antero-ventral side of the body has been modified into a specialized disc-shaped structure. The structure imparts a distinct character to the genus *Garra*.

Of five species of *Garra* (*G. gotyla*, *G. mullya*, *G. modestus*, *G. lamta* and *G. jerdoni*) reported, *G. lamta* is commonly found in the waters of the hill-streams of the Chotanagpur division of India. Morphological modifications and behaviour of certain species of *Garra* have been studied by some workers (Hora, 1922; Jones, 1941; Bose et al., 1971). However, no information is available on the respiratory apparatus of these hill-stream fishes.

Paucity of information regarding the respiratory behaviour of these interesting fishes inhabiting hyperoxic waters of the hill-streams has attracted our attention to study the adaptations in the respiratory apparatus of *Garra lamta*. Findings of such a study will throw light on the intricate architecture of the gill sieve of an interesting fish inhabiting swift currents of torrential streams. The data will also be valuable in modelling artificial gills for aquatic exploration by humans.

Materials and methods

Garra lamta belongs to the family Cyprinidae of the order Cypriniformes. The specimens were collected from Jonha Falls (Goutamdhara) near Ranchi, India, which is situated at an altitude of 2128 feet above sea-level. The River Gunga falls down from a height of about 90 feet. A large number of specimens were collected with the help of local fishermen from the side pockets of the main stream by blocking it and mechanically draining out the water. The collection operation was carried out in the month of March when the current of water was comparatively slow. The range of body weight of the fish collected was from 1 to 5.5 g. Five fish were used for each determination.

After taking the fresh weight of the fish, the opercula were removed and the entire fish with gills were immediately fixed and preserved in Bouin's solution and were stored in the refrigerator. The gill area was estimated according to the method described by Hughes and Morgan (1973). All the measurements were made under dissecting binocular microscope with ocular micrometers and an improved variety of camera lucida (ermascope).

For histological studies, gills were fixed in Bouin's and Zenker's fixatives. Six μm thick horizontal sections (with reference to the axis of gill filaments) were stained in haematoxylin and counterstained by eosin. The maximum and minimum distances of water-blood pathways were determined directly from the photomicrographs. The actual thickness of water-blood pathway was determined by dividing the measured thickness by the total magnification. Harmonic mean (t_h) of the diffusion distances

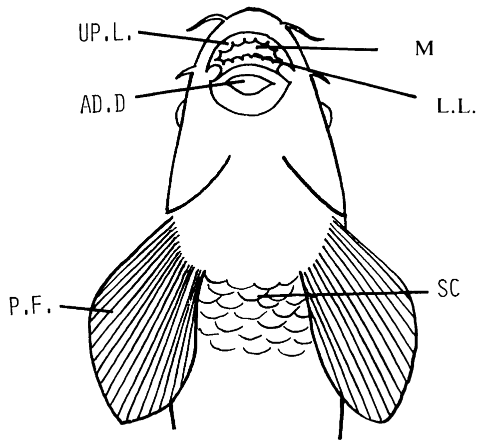

Fig. 1. Ventral view of the fish showing adhesive disc (AD.D), lower lip (L.L.), mouth (M), pectoral fin (P.F.), scales (SC) and upper lip (UP.L.).

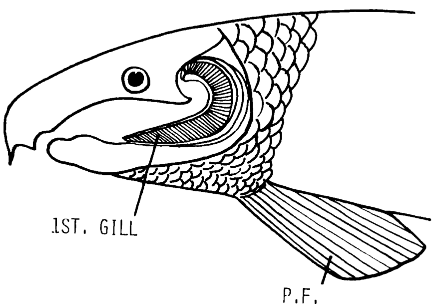

Fig. 2. *Garra lamta* dissected out to show the orientation of the gills in the branchial chamber (left lateral view). Pectoral fin (P.F.) is also shown.

was determined.

Diffusing capacity of the gills was estimated with the help of modified Fick equation (Hughes, 1972):

$$\frac{V_{O_2}}{\Delta PO_2}=\frac{K\cdot A}{t_h}=Dt$$

Where, V_{O_2}=oxygen uptake, ΔPO_2=partial pressure of oxygen between water and blood, K=Krogh permeation coefficient (0.00015 ml O_2/min/μm/cm^2/mmHg at 20°C), A=gill area (cm^2), t_h=harmonic mean of diffusion distances (μm) and Dt=diffusing capacity (ml O_2/min/mmHg/kg).

Observations

Physico-chemical characters of waters. The water of Jonha Falls was slighlty acidic having pH 6.1, free carbon dioxide 6 mg/*l* and dissolved oxygen 9.1 mg/*l* at a temperature of 19°C. The bicarbonate alkalinity was rather low (13 ppm).

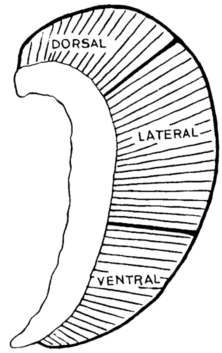

Fig. 3. Diagram of a single gill arch of *G. lamta* showing its subdivision into dorsal, lateral and ventral regions.

Morphology of the fish. The antero-ventral part of the fish bears a disc-shaped structure which is a modification of the lower lip (Bose et al., 1971). The isthmus of the adhesive disc is flat and scaleless and helps the fish to attach itself to the substratum in the hill-streams (Fig. 1). In nature this structure does not hamper the movement of jaws during gill ventilation.

Gross structure of the gills. *Garra lamta* has four pairs of holobranchs. Each gill arch is oriented in such a fashion that its ventral part is more anterior than the dorsal part (Fig. 2). In all the gills filaments are borne by epi- and ceratobranchials only. The second gill arch bears a greater number of filaments than other arches (Table 1). Each hemibranch of all the gills is divisible into dorsal, lateral and ventral regions having an average number of 15, 20 and 20 filaments respectively (Fig. 3). The number of filaments in each of the three regions varies according to the size of the gills which is directly proportional to the weight of the fish. The filaments are swollen at their tips and narrow towards their bases. An interesting feature in the anatomy of the gills of *G. lamta* is the length of the interbranchial septum which extends almost to the tip of the holobranch (Fig. 4). A large interbranchial septum distinguishes the gills of the genus *Garra* from other teleostean gills.

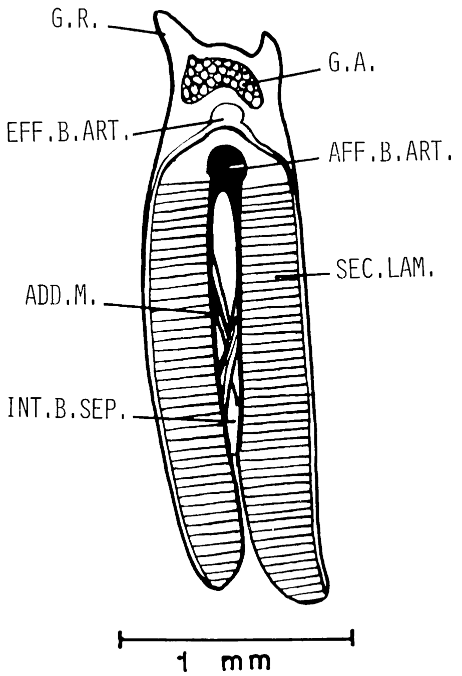

Fig. 4. Horizontal longitudinal section of the gill showing two primary lamellae which bear adductor muscle (ADD.M.), afferent branchial artery (AFF.B. ART.), efferent branchial artery (EFF.B.ART.), gill arch (G.A.), gill raker (G.R.), interbranchial septum (INT.B.SEP) and secondary lamellae (SEC.LAM.).

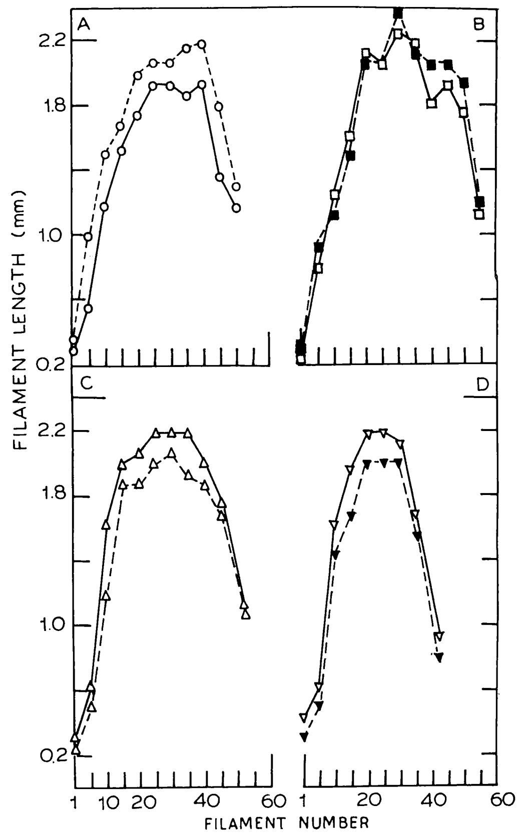

Fig. 5. Plots showing the length of individual gill filaments along the four gill arches. A: 1st arch. B: 2nd arch. C: 3rd arch. D: 4th arch. Measurements for the anterior (——) and posterior (------) hemibranchs are plotted separately.

Dimensions of gill area. Anterior and posterior hemibranchs of each gill showed variation in the length of filaments at different regions of the gill arch (Fig. 5). In the first pair of gill

Table 1. Summary of gill dimensions of *Garra lamta* of 4.1 g body weight.

Parameters	1st pair of gills	2nd pair	3rd pair	4th pair	Total gills
Number of filaments	200	220	208	168	796
Average filament length (mm)	1.54	1.62	1.48	1.45	1.52
Total filament length (mm)	307.90	356.93	307.27	242.96	1210.98
Secondary lamellae/mm (both sides)	69.31	65.20	65.30	64.18	66.06
Total secondary lamellae	21340.61	23270.27	20065.68	15592.40	79999.61
Bilateral surface area of a secondary lamella (mm^2)	0.01513	0.01606	0.01811	0.01679	0.01647
Total gill area (mm^2)	322.88	373.72	313.50	261.84	1317.59
Weight specific gill area (mm^2/g)	78.75	91.15	88.66	63.86	321.36

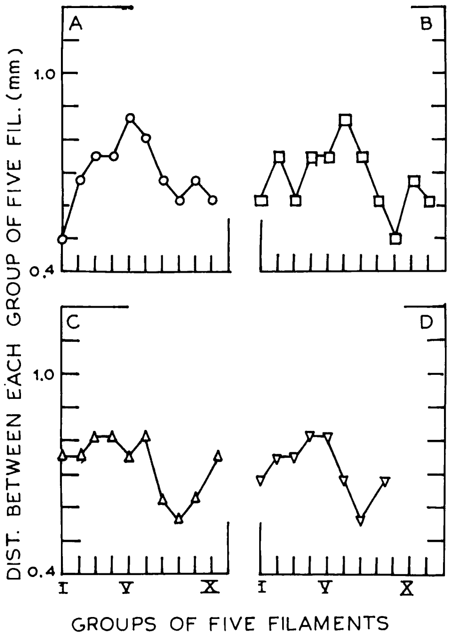

Fig. 6. Plots showing the distance between each group of five filaments on the entire length of anterior hemibranch of the four gill arches. A: 1st arch. B: 2nd arch. C: 3rd arch. D: 4th arch.

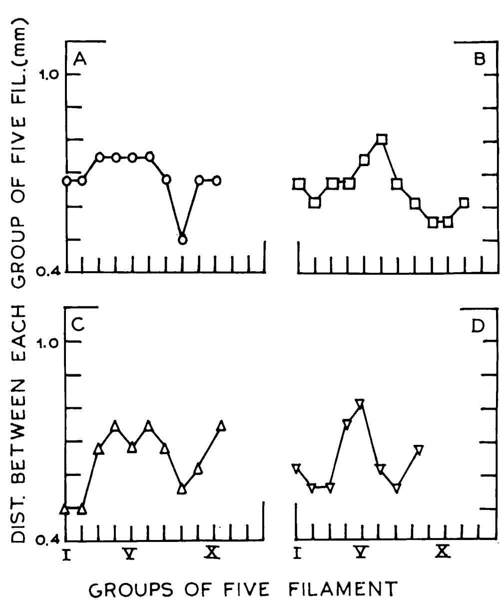

Fig. 7. Plots showing the distance between each group of five filaments on the entire length of posterior hemibranch of the four gill arches. A: 1st arch. B: 2nd arch. C: 3rd arch. D: 4th arch.

arches the filament lengths of the posterior hemibranch were greater than their counterparts of the anterior hemibranch (Fig. 5A). In the case of the second pair of gills, the filament lengths of both the hemibranchs were more or less equal (Fig. 5B). However, in the case of the third and the fourth pairs of gill arches, the lengths of filaments of the anterior hemibranchs were comparatively greater than the corresponding filaments of the posterior hemibranchs (Fig. 5C, D)

Distance between the two adjacent filaments showed variations at different regions of the anterior and posterior hemibranchs (Figs. 6, 7). The distance between adjacent filaments was minimal at the point where the hemibranchs made a right angle turn to their dorsal regions.

In *Garra lamta* each secondary lamella was wing-shaped, the profile of which was wider at the efferent side than that of its afferent side. The secondary lamellae of the base and middle parts were almost identical as far as their profile and area were concerned. Difference was found in the diameters of afferent and efferent filament arteries. Diameters of these arteries were comparatively greater towards the base of the filaments. The secondary lamellae of the tip regions were comparatively smaller in size and the sections lacked the interbranchial septum (Fig. 8). Secondary lamellae were alternately arranged on the two sides of the gill filaments (Fig. 9). Because of the lesser spacing between the two secondary lamellae, their number per unit area was high (Table 1). In section, each secondary lamella consisted of a series of blood channels separated by characteristic pillar cells (Figs. 9, 10). The harmonic means of twenty-five samples of the water-blood diffusion in the secondary lamellae was 1.75 μm.

Variations in total gill area were observed at different parts of each of the hemibranchs. In all the hemibranchs the gill area was greater in the middle region in comparison to those of ventral and dorsal parts (Fig. 11). The higher gill area obtained in the middle region was obviously due to greater number of total secondary lamellae as a result of greater filament length. Weight specific area was estimated to

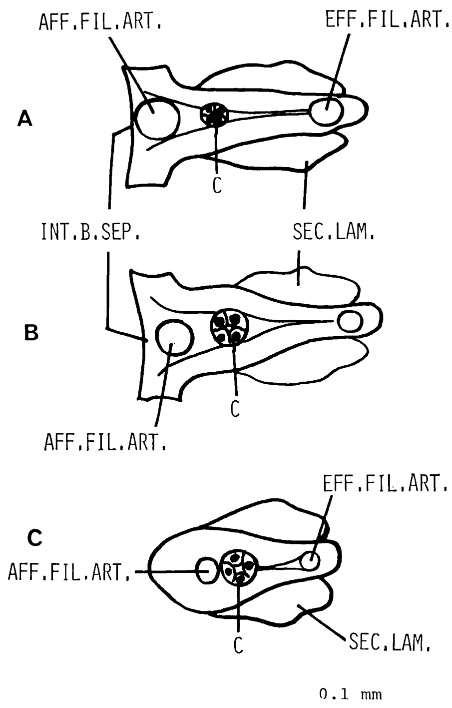

Fig. 8. Cross sections from the base (A), middle (B) and tip (C) of the primary lamella of *G. lamta* showing afferent filamentar artery (AFF.FIL.ART.), cartilage (C) of the gill ray, efferent filamentar artery (EFF.FIL. ART.), interbranchial septum (INT.B. SEP.) and the secondary lamellae (SEC. LAM.).

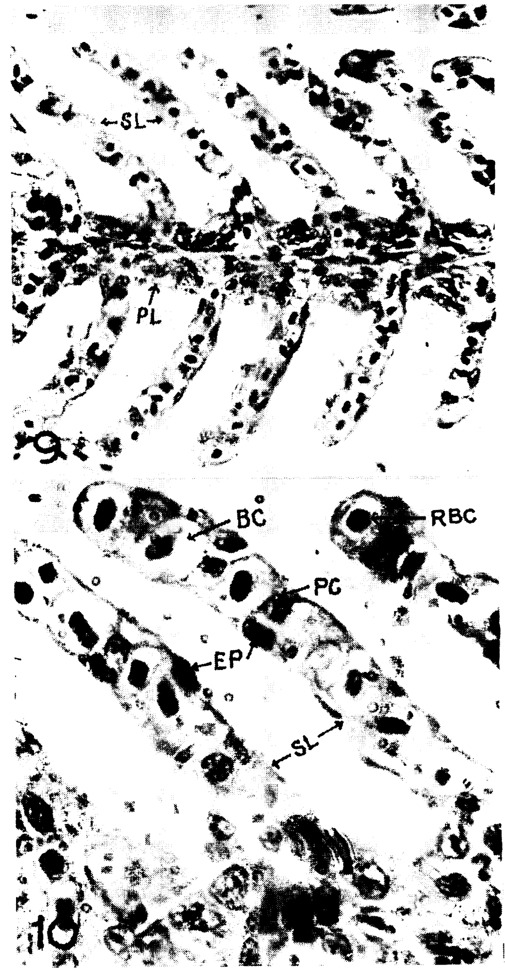

Fig. 9. A part of the horizontal section of the gill showing the alternate arrangement of the secondary lamellae (SL) on the two sides of the primary lamella (PL). ×400.

Fig. 10. Oil immersion photomicrograph of the horizontal section of the gill showing blood channels (BC), epithelium (EP), pillar cell (PC) and red blood corpuscles (RBC). ×1000.

be 321.36 mm^2/g. The second gill arch showed a higher weight specific gill area in comparison to other gill arches (Table 1).

Diffusing capacity. The diffusing capacity (ml O_2/min/mmHg/kg) varied from 0.0547 to 0.0781 among four gill arches and for combined gill arches it was 0.2759 (Table 2).

When these fishes were transferred to the stagnant waters of the plains (average $DO_2=7$ mg/l, temperature=30°C and pH=7.2 in the month of March) they died within a short period. However, these fishes can be transported for a short distance in big earthen pots containing cold water from the stream.

Discussion

Superficially, the gills of *Garra lamta* appear to be similar to those of typical bony fish but detailed studies reveal that they differ from the general pattern in some features. In teleostean fishes the interbranchial septum is reduced but in *G. lamta* it is large and extends almost up to the tip of the filaments. Such an arrangement is closer to the situation found in primitive fishes like *Neoceratodus* and *Latimeria* (Hughes, 1976). It seems improbable that this similarity has an evolutionary significance. We do not

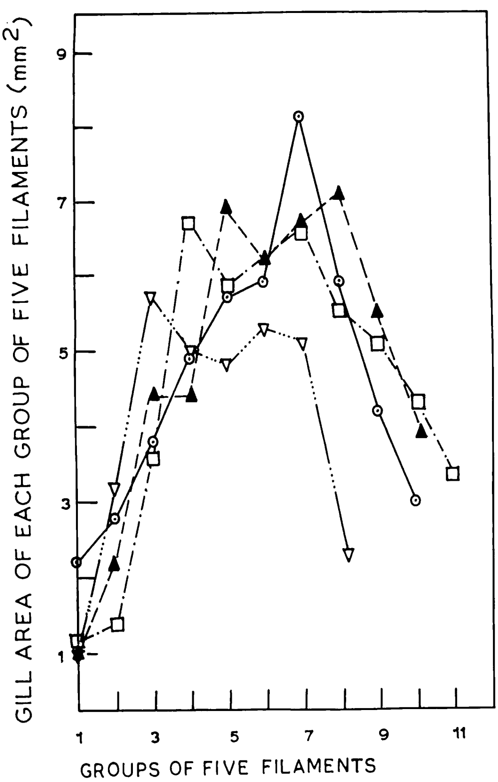

Fig. 11. Plot showing the gill area of each group of filaments at various aspects of the posterior hemibranch of the four gill arches. ⊙, 1st arch; □, 2nd arch; ▲, 3rd arch; ▽, 4th arch.

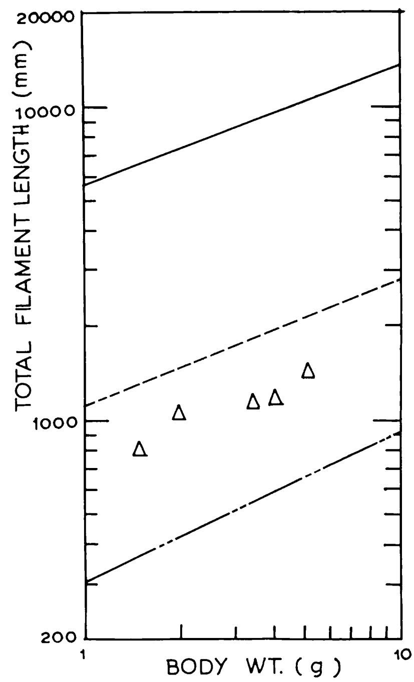

Fig. 12. Log-log plots of total filament length against body weight. The five points for *G. lamta* (△) fall below the line drawn for "Grays intermediate" species (---). The corresponding lines for tunas (—) and toad fish (——·——) are also given.

understand the reason. Such an arrangement of the interbranchial septum may be an adaptation in the gill structure of hill-stream fishes to suit an entirely different ecological condition. However, detailed investigations are warranted in

Table 2. Diffusing capacity (ml O_2/min/mm Hg/kg) for the tissue barrier of the different gills of *Garra lamta*

Organs	Respiratory surface (mm^2/g)	Diffusion distance (μm)	Diffusing capacity $Dt\frac{K \cdot A}{t}$
1st pair of gills	78.75	1.75	0.0675
2nd pair of gills	91.15	1.75	0.0781
3rd pair of gills	88.66	1.75	0.0756
4th pair of gills	63.86	1.75	0.0547
Total gills	321.36	1.75	0.2759

this regard. The number of secondary lamellae per mm of the gill filament of *G. lamta* is quite high (66) in comparison to other hill-stream fishes, *Cobitis taenia* (45.5) and *Noemacheilus barbatulus* (36.4) of approximately the same body weight (Robotham, 1978). Moreover, the weight specific gill area of *G. lamta* (321.36 mm^2/g) is nearer to the value reported for *N. barbatulus* (249.8 mm^2/g). However, *G. lamta* possesses a gill area approximately five times greater than the values reported for the air-breathing climbing perch, *Anabas testudineus*, 64 mm^2/g (Hughes et al., 1973) and the catfish, *Heteropneustes fossilis*, 74 mm^2/g (Hughes et al., 1974). Variations in the relative filament lengths of the two hemibranchs throughout the entire length of the arch may be related to the formation of a complete gill sieve and for the accommodation of four gill arches within the branchial space. The former possibility seems to be improbable because a large interbranchial septum may hinder the formation of a complete sieve between the buccal and opercular cavities. Because of an incomplete gill sieve it is expected that a large quantity of water may pass the branchial apparatus without coming into intimate contact with the secondary lamellae. Swiftly moving waters of the streams ease the problem of ventilation in *G. lamta*. The gills of these fishes are so adapted that they are able to extract adequate oxygen from continuously flowing cold waters for their total metabolic activities. The value (338.6 mm^2/g) reported for the weight specific gill area of the rainbow trout (Jager and Dekkers, 1975) is close to the value (321.4 mm^2/g) obtained for the same weight group of *Garra lamta*. Higher temperature (30°C) and low dissolved oxygen (7 mg/l) in the ambient waters of the plains and weak buccal pressure and opercular suction pumps of *G. lamta* seem to be the possible causes of asphyxiation and death of these fishes even in the presence of a more effective gill area. However, rainbow trout and the carps withstand these adverse ecological conditions of the plains by pumping greater volumes of water through the gill sieve with the help of powerful ventilatory pumps.

Values for the total filament length of various specimens of *Garra lamta* lie between the regression lines drawn for intermediate (*Balistes capriscus*) and sluggish (*Opsanus tau*) fishes (Fig. 12). Gill area per unit body weight also falls below the value of "Grays intermediate". Comparatively lower values for total filament length and gill area in this hill-stream fish may be due to its sedentary habit. In nature *G. lamta* remains attached to rocks of the torrential streams by its adhesive disc and swift moving waters of the stream irrigate its gill sieve. Higher diffusing capacity of the second pair of gills indicates their dominant role in oxygen uptake in comparison to other gill arches (Table 2).

Acknowledgments

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コイ科の渓流魚 *Garra lamta* の鰓の形態計測

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高地の奔流に住む魚，*Garra lamta* の鰓構造が述べてある．この魚の鰓についての定量的データが呼吸機能との関連において論議される．鰓隔膜は非常に長く，*Neoceratodus* および *Latimeria* で記録されている状態に近似している．*Garra lamta* の種々の標本における，体重に対する全鰓弁長の値は，中程度の活動性の魚と遅鈍な魚についてそれぞれ引かれた回帰直線の間にあった．単位体重当りの鰓面積の比較的低い値 (321.4 mm^2/g) は，この魚の定着性の習性によるのかも知れない．