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

魚類学雑誌
36巻2号 1989年

Gross Structure and Dimensions of the Gill in an Air-Breathing Estuarine Goby, *Pseudapocryptes lanceolatus*

Amrendra N. Yadav and B. R. Singh

(Received January 13, 1989)

Abstract The gills of the air-breathing estuarine goby, *Pseudapocryptes lanceolatus*, are reduced owing to the development of a specialized organ of O_2 uptake from air. In the first gill arch, the filaments of the outer hemibranch are reduced to nearly one-half in comparison to those of its inner hemibranch. A smaller number of secondary lamellae per mm (27.6) occurring on one side of the gill filament reduces the gill surface area. A bilogarithmic plot of the gill area and the body weight indicates a curve with two significantly different components, one ($b=0.924$) related to the fish weighing up to 6 g and the other ($b=0.405$) to the fish weighing 8 g and above.

Gill morphometric is a measure to evaluate the potentiality of gas exchange on the surface of the gills in teleosts. Price (1931) recorded a good correlation between the gill surface area and the body weight in a black bass, *Micropterus dolomieu*. The variations in the relationships of the gill area and body weight among many marine teleosts were considered by Gray (1954) to represent different ecological niches occupied by them.

Among the estuarine gobies, Schottle (1931) measured the gill surface area of three species of *Gobius*, two species of *Boleophthalmus* (*B. boddarti*, *B. viridis*) and four species of *Periophthalmus*. The gill surface area of these and other marine fishes, such as *Blennius pholis* (Milton, 1971), *Mnierpes macrocephalus* (Graham, 1973, 1976), *Periophthalmus cantonensis* and *Boleophthalmus chinensis* (Tamura et al., 1976) indicates that both inter- and intraspecific variations occur in the respiratory surface area of gills depending upon their habit and habitat. The morphological parameters of the fish gill system have been well reviewed by Laurent (1982, 1984) and Hughes (1982, 1984a, b).

Information regarding gill dimensions of air-breathing gobies is scanty. Tamura and Moriyama (1976) measured the gill dimensions of two air-breathing gobies, *Periophthalmus cantonensis* and *Boleophthalmus chinensis*. As *Pseudapocryptes lanceolatus* (Bleeker) is known to represent the first stage of structural adaptation to aerial respiration (Das, 1934), it was thought appropriate to examine the structure and dimensions of the gills in the fish.

Materials and methods

Pseudapocryptes lanceolatus (Perciformes, Gobiidae) were obtained from Kakdeep, West Bengal, India. The fish were weighed and fixed in aqueous Bouin's solution in order to examine the gross structure and dimensions of the gills. The gill filaments in the individual arches were dissected out at the interval of every six filament. An average filament length was determined for each section in a particular arch. This was done for all the four gill arches of one side. The total number of gill filaments and the number of secondary lamellae per mm occurring along the length of a filament were counted. The average bilateral surface area of the secondary lamellae taken from the base, middle and tip of the filament was traced on a transparent graph paper with the help of an Ermascope. The gill area was calculated by employing the equation of Muir and Hughes (1969):

$$\text{Gill area} = 2(L/d')bl$$

Where L=total length of filaments; $2/d'$= secondary lamellae on both sides of a gill filament; bl=average bilateral surface area of the secondary lamellae.

Measurements of the gill dimensions were made on 35 specimens of *P. lanceolatus* in a weight range of 1 to 21 g (mean weight, 8.21 g). The data were then reduced to seven average body weights. Various gill parameters (Y) such as the total number of filaments, filament length, number of secondary lamellae/mm, total number of secondary lamellae, average area of the secondary lamellae, total gill area and gill area/g body weight were plotted on a double logarithmic grid against the body weight (W) by employing the equation:

$$\text{Log } Y = \log a + b \log W$$

Where Y=a particular parameter of the gill to be analysed; a=value for a 1 g fish (intercept); W=weight of fish in g; b=regression coefficient (slope).

Gill tissues fixed in 2.5% Glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) at 4°C for 24 hours were examined in P 500 scanning electron microscope at the Bose Research Institute, Calcutta.

Results

Gross structure of the gill. *Pseudapocryptes lanceolatus* possesses a well-developed neo-morphic air-breathing organ in addition to four pairs of gills for respiration in water. The air-breathing organ consists of the vascularized epithelium of the suprabranchial chamber, the opercular chamber and the mouth cavity. The suprabranchial chamber is located antero-dorsal to the first gill arch. In the first gill arch, the outer row of gill filaments is reduced in comparison to its inner row (Fig. 1).

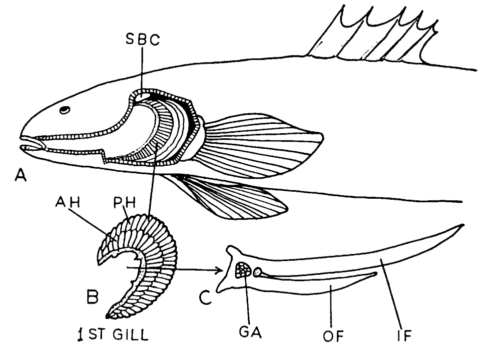

Fig. 1. A: Diagrammatic lateral view of the anterior end of *Pseudapocryptes lanceolatus*, showing the position of the first gill arch and the suprabranchial chamber (SBC). B: 1st gill dissected out from the branchial chamber. AH, anterior hemibranch; PH, posterior hemibranch. C: Transverse section of the first gill. GA, gill arch; IF, inner filament; OF, outer filament.

The gill structure is similar to that of a generalized teleost as described by Hughes and Shelton (1962) and Lagler et al. (1962). The first gill is shorter in comparison to either the second or the third gill. The fourth gill is the shortest in size. The relationship between the filament length and

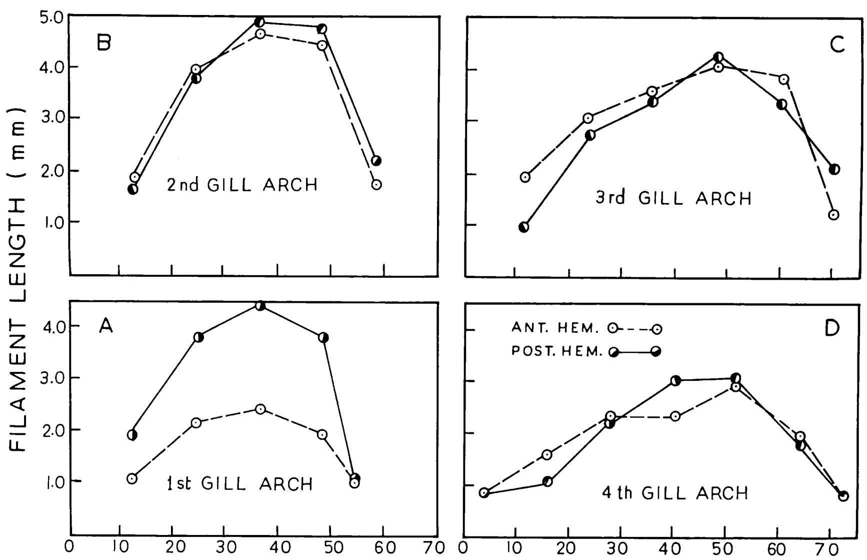

Fig. 2. Length of the filaments plotted against filament numbers. A, 1st gill arch; B, 2nd gill arch; C, 3rd gill arch; D, 4th gill arch. Measurements for the anterior (O---O) and posterior hemibranchs (●—●) are plotted separately.

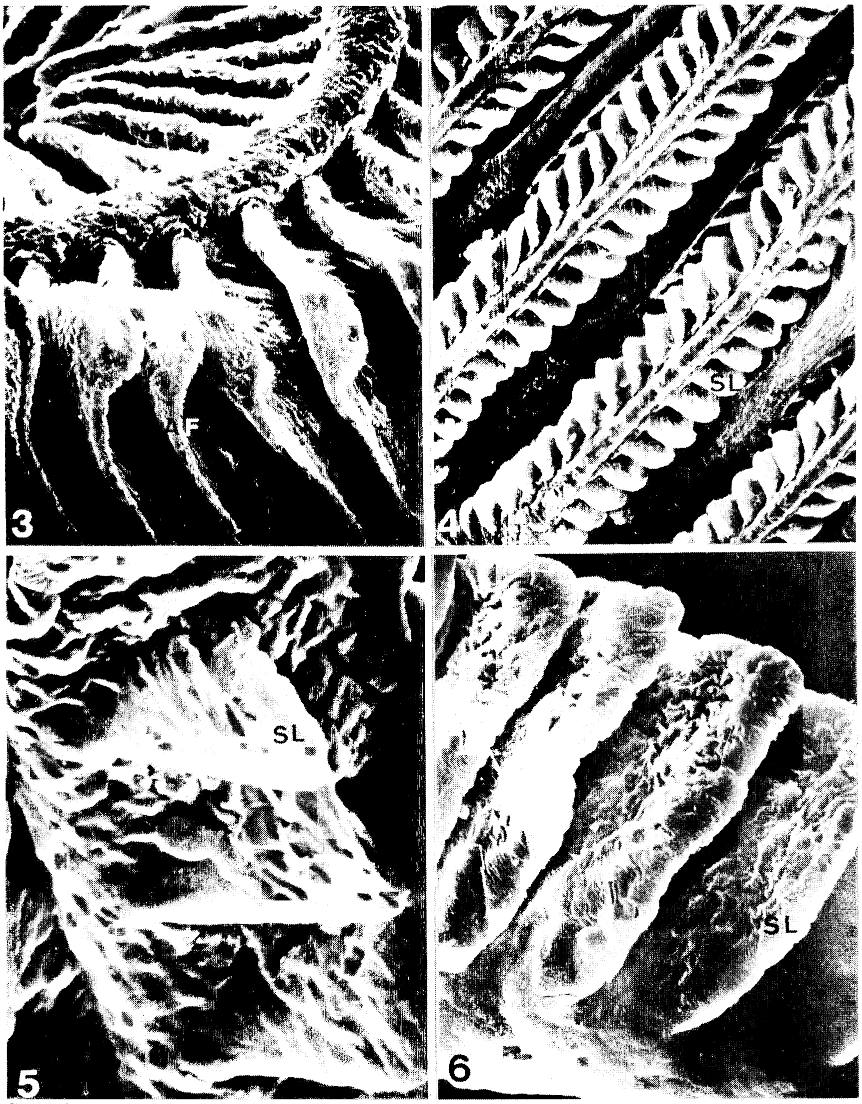

Fig. 3. Scanning electron micrograph (SEM) of the dorsal aspect of the first gill arch showing aberrant gill filaments (AF). ×400.

Fig. 4. SEM of the gill filament from the second gill arch, showing alternate arrangement of the secondary gill lamellae (SL). ×200.

Fig. 5. SEM of the triangular secondary lamellae (SL) from the third gill arch. ×800.

Fig. 6. SEM of the flattened gill lamellae (SL) from the fourth gill arch. ×800.

its number indicates that the filaments in the outer hemibranch of the first gill arch are nearly 45% shorter than those in its inner hemibranch. In the other gill arches, the gill filaments of both the hemibranchs are almost equal in size (Fig. 2).

The average length of the interbranchial septum is 0.46 mm in the first gill arch; 0.39 mm in the second and third gill arches and 0.33 mm in the fourth gill arch. The diameter of the afferent branchial vessel (40 μm) is shorter in comparison to that of the efferent branchial vessel (53.4 μm).

The respiratory epithelium of the suprabranchial chamber is formed by abbreviation, shifting and modification of the dorsal gill lamellae of the gill arches during embryogenesis of the fish (Singh et al., 1989). SEM studies of the gills revealed that the dorsal gill lamellae of the first gill arch are more involved in this act as evidenced by the presence of some aberrant gill filaments at its dorsal end (Fig. 3). The gill lamellae are arranged alternatively on either side of a gill filament (Fig. 4). The gill lamellae borne by the third gill arch are almost triangular in outline (Fig. 5). In the fourth gill arch, the gill lamellae are flattened and form blade-like structures (Fig. 6).

Dimensions of the gill. The results on gill dimensions are summarized in Table 1. Expressions relating these to body size are set out in Table 2. In Table 3, the gill area and other parameters of *P. lanceolatus* are compared with those of other fishes.

The gill surface area increases rapidly with an increase in body size. When the fish acquires a body size of nearly 6 g, an abrupt decline in the gill surface area occurs. As soon as the fish attains a body weight of nearly 8 g, the gill area starts increasing steadily but at a slower pace till it acquires the maximum body size.

The slope for the gill area vs. body weight is 0.827, but when the data for the gill area are analysed separately for two different weight groups, the slopes differ considerably. The slope becomes 0.924 for the fish till it acquires a body weight of 6 g, and 0.405 when it attains a body weight of 8 g and above (Fig. 7).

The number of gill lamellae/mm on a gill filament (27.6) is the lowest in comparison to that of other air-breathing fishes except for *Lepisosteus* (Table 3). However, the average bilateral surface area of a gill lamella (0.016 mm^2) is in no way inferior to that of other fishes. Of the three anterior gill arches, the gill area possessed by the first gill arch is reduced. Its slope (0.85) is greater in comparison to others. Although the gill area of the fourth gill arch is the lowest, its slope value (0.84) is almost equal to that of the first gill arch.

Discussion

A gradual decrease in size from the first to the fourth gill arch is a generalized feature among teleosts. *Pseudapocryptes lanceolatus* forms an exception to this generalization because its first gill arch is reduced in size. In this fish, the gill filaments constituting the outer hemibranch of the first gill arch are nearly one-half of that of its inner hemibranch. Das (1934) also pointed out that in this fish nearly two-third reduction in the outer rows of gill filaments occurs in the first gill arch. The reduction in the size of the gill filaments of the first gill arch is due to the fact that the gill lamellae are utilized to form the respiratory epithelium of the suprabranchial chamber for air-breathing purpose (Singh et al., 1989) and the neo-morphic organ for CO_2 elimination at the operculum (Singh et al., in press).

The interbranchial septum has been reported to be nearly one-half of that of the filament length in an intestinal air-breathing fish, *Lepidocephalichthys guntea* (Singh et al., 1981) and two-thirds in *Lepisosteus* (Landolt and Hill, 1975). The interbranchial septum in *P. lanceolatus* is very short and measures nearly one-tenth of the filament length. A shorter interbranchial septum in

Table 1. Gill parameters of *Pseudapocryptes lanceolatus*.

	Wt. (g)	Length (cm)	Number of filaments	Average length of filament (mm)	Total length of filaments (mm)	Secondary lamellae/ mm on both sides	Total secondary lamellae	Average area of sec. lam. (mm^2)	Total gill area (mm^2)	Gill area/g body wt. (mm^2)
	1.3	7.5	498	1.36	704.0	55.00	38590	0.0163	654.70	503.40
	3.0	8.5	520	1.61	873.9	52.10	42265	0.0331	1538.90	512.86
	4.7	10.2	532	2.11	1143.4	44.09	50184	0.0506	2601.16	553.38
	6.0	11.5	508	2.06	1209.8	41.04	49232	0.0479	2422.00	403.60
	8.0	12.0	508	2.61	1372.7	36.05	49322	0.0924	4558.30	569.60
	13.5	16.0	542	2.85	1604.0	40.80	65419	0.0685	4550.30	336.80
	21.0	16.5	516	2.95	1648.5	40.58	67039	0.0974	6791.26	323.30
Sum.	57.5	83.2	3624	15.55	8556.5	309.66	365054	0.4063	23116.62	3202.94
Av.	8.2	11.8	517.7	2.22	1222.3	44.23	52650	0.0580	3302.37	457.56
SD	6.8	3.7	15.1	0.60	352.7	6.83	10403	0.0298	2109.25	101.99
SE	2.6	1.4	5.7	0.23	133.3	2.58	3932	0.0222	797.23	38.55

the fish would evidently provide a greater movement of the gill filaments.

It is well known that the gill surface area is reduced in fishes that are more dependent on aerial respiration (Schottle, 1931; Dubale, 1951; Carter, 1957; Hughes and Morgan, 1973). The gill area in *P. lanceolatus* is also reduced because it possesses a well-developed air-breathing organ. When the gill area of *P. lanceolatus* is compared with those of other marine air-breathers (Table 3), it is in accord with that of *Boleophthalmus viridis* (Schottle, 1931). However, it is nearly $2^1/2$ times less than that found in *Mnierpes* (Graham, 1973) of similar size. When the gill area of *P. lanceolatus* is compared with that of *Periophthalmus vulgaris* of similar size, the area in the former is nearly $1^1/2$ times larger than in the latter. This testifies that the degree of terrestriality in the present species is less than that of *Periophthalmus vulgaris*.

Usually, the slope of the gill area in relation

Table 2. Regression analysis of the different parameters of the gill in relation to body weight (g).

Body weight (W) vs.	Equation	Correlation coefficient (r)
Total number of filaments	$y=504.19\ W^{0.014}$	0.68
Average length of filaments (mm)	$y=1.24\ W^{0.305}$	0.97
Total length of filaments (mm)	$y=652.82\ W^{0.331}$	0.97
Secondary lamellae/mm on both sides of a filament	$y=55.26\ W^{-0.130}$	0.81
Total number of secondary lamellae	$y=35822.83\ W^{0.130}$	0.94
Average area of secondary lamellae (mm^2)	$y=0.0164\ W^{0.628}$	0.93
Total gill area (mm^2)	$y=607.85\ W^{0.827}$	0.97
Gill area/g body wt. (mm^2)	$y=605.34\ W^{-0.172}$	0.68

Table 3. Comparison of the gill parameters in some air-breathing fishes of both freshwater and marine habitat. * Total gill area for the given length of the fish.

Fish species	Gill area (mm^2)	Slope (b) of gill area	No. of sec. lam./mm on one side of the fil.	Total length of fil. (mm)	Bilateral surface area of sec. lam. (mm^2)	References
A. Fresh water habitat						
Anabas testudineus	278.3	0.615	36.5	516.9	0.015	Hughes et al. (1973)
Saccobranchus fossilis	186.1	0.746	31.6	305.6	0.009	Hughes et al. (1974)
Lepisosteus sp.	394.0	0.738	19.3	—	0.021	Landolt and Hill (1975)
Channa punctata	470.4	0.592	36.0	557.9	0.011	Hakim et al. (1978)
Lepidocephalichthys guntea	493.6	0.744	45.0	264.6	0.020	Singh et al. (1981)
B. Marine habitat						
Blennius pholis	—	0.850	—	—	—	Milton (1971)
Pseudapocryptes lanceolatus	607.8	0.827	27.6	652.8	0.016	Present authors
Boleophthalmus viridis (6.8 cm)	660.0*					Schottle (1931)
Periophthalmus vulgaris (6.7 cm)	470.0*					〃
Periophthalmus vulgaris (8.4 cm)	670.0*					〃
Mnierpes macrocephalus (7.0–8.0 cm)	1540–1680*					Graham (1973)
Pseudapocryptes lanceolatus (7.5 cm)	654.8*					Present authors
Pseudapocryptes lanceolatus (8.5 cm)	1538.0*					〃

to the body weight varies from 0.5 to 1.0 in fishes (Hughes, 1972). The slope of the gill area (0.82) in *Pseudapocryptes lanceolatus* is almost similar to those of other fishes, viz. *Blennius pholis* and Gray's "Intermediates". The slops is higher in comparison to that found in *Channa punctata*, *Anabas testudineus*, *Saccobranchus fossilis*, *Lepidocephalichthys guntea* and *Lepisosteus* (Table 3).

The regression line for the gill area versus the body weight shows a two component curve; one related to the fish when it attains a body weight of nearly 6 g and the other when it achieves a body weight of 8 g and above. The two curves differ significantly from one antother ($P<0.05$). The abrupt decline in the gill area in the weight range of 6–8 g coincides with a greater utilization of gill tissue in forming the respiratory epithelium of the suprabranchial chamber for O_2 uptake (Singh et al., 1989) and the neo-morphic organ for CO_2 release at the operculum (Singh et al., in press).

The total length of the gill filaments in *P. lanceolatus* is higher than those of the fresh-water air-breathers. It is nearly two times higher than *Saccobranchus fossilis*, 2.5 times higher than *Lepidocephalichthys guntea* and 1.25 times higher than *Anabas testudineus* (Table 3).

A reduction in the total gill area is caused by the smaller number of secondary lamellae per mm occurring on the gill filaments. Such a device seems to be an adaptation which evades evaporation of water from the gill lamellae and prevents the gills from collapsing in air. The number of the secondary lamellae/mm (27.6) on one side of a gill filament in *P. lanceolatus* is less than that reported for *Anabas testudineus* (Hughes et al., 1973), *Saccobranchus fossilis* (Hughes et al., 1974), *Channa punctata* (Hakim et al., 1978) and *Lepidocephalichthys guntea* (Singh et al., 1981).

The bilateral surface area of the secondary lamellae obtained from regression analysis for a 1 g fish (0.016 mm^2) corresponds to that obtained for *Anabas testudineus* (Hughes et al., 1973). When compared with other air-breathers, it becomes nearly one-fourth smaller than that of *Lepidocephalichthys guntea* and *Lepisosteus* but 1.75 times larger than that of *Saccobranchus fossilis* (Table 3). Although the bilateral surface area of the secondary lamellae is smaller, it does not have a profound effect on the total gill area because the length of the filaments is comparatively larger.

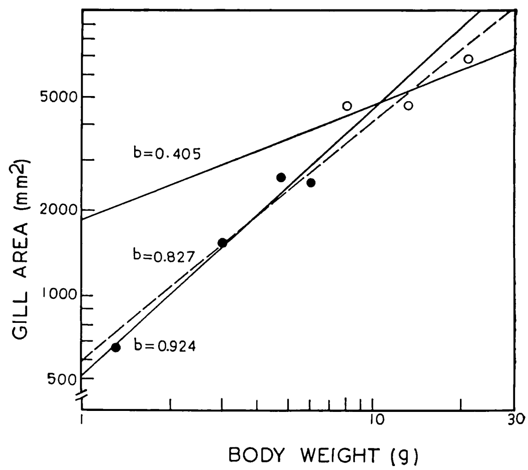

Fig. 7. Gill area plotted against body weight on a log/log co-ordinates, showing three different slopes (*b*). $b=0.924$ for the fish weighing up to 6 g; $b=0.405$ for the fish weighing 8–21 g; $b=0.827$ for the combined data.

Regarding the gill area of the individual arches, the surface area possessed by the first gill arch is smaller in comparison to that of the second and third gill arches. The reduction in the gill surface area of the first gill arch in an another air-breathing goby, *Periophthalmus schlosseri* was also recorded by Schottle (1931). She opined that the gill lamellae of the first gill arch were given over entirely to supporting a fold of vascularized epithelium and that the fish had three pairs of functional gill arch. In *Periophthalmus schlosseri* and other gobies, an increase in the amount of vascularized bucco-pharyngeal tissue was found by Schottle (1931) to parallel the decrease in the gill surface area. Todd and Ebeling (1966) also noted that in *Gillichthys*, the gills were short and that the total gill area was smaller in species which breathe air.

Graham (1973) considered that amphibious marine air-breathers are more proficient in aerial release of CO_2 than the fresh-water air-breathers. Hughes (1966) and Thomson (1969) expressed their paradoxical views that the specialization of air-breathing organs on the one hand and the ability to release CO_2 into air on the other were linked with the emergence of terrestrial vertebrates. In *Pseudapocryptes lanceolatus*, the development of the suprabranchial chamber for air-breathing purpose (Singh et al., 1989) and the specialized organ for CO_2 release at the operculum (Singh et al., in press) accounts for a profound reduction in some of the parameters of the gills. This is particularly well documented by the first gill which contributes a greater amount of the gill tissue to the formation of these structures.

Literature cited

Carter, G. S. 1957. Air breathing. Pages 65–79 *in* M. E. Brown, ed. The physiology of fishes. Vol. 1. Academic Press, London.

Das, B. K. 1934. The habits and structure of *Pseudapocryptes lanceolatus*, a fish in the first stages of structural adaptation to aerial respiration. Proc. Roy. Soc. Lond., 115: 422–430.

Dubale, M. S. 1951. A comparative study of the extent of gill-surface in some representative Indian fishes and its bearing on the origin of the air-breathing habit. J. Univ. Bombay, 19: 90–101.

Graham, J. B. 1973. Terrestrial life of the amphibious fish, *Mnierpes macrocephalus*. Mar. Biol., 23: 83–91.

Graham, J. B. 1976. Respiratory adaptations of marine air-breathing fishes. Pages 165–187 *in* G. M. Hughes, ed. Respiration of amphibious vertebrates. Academic Press, London.

Gray, I. E. 1954. Comparative study of the gill area of marine fishes. Biol. Bull., 107: 219–225.

Hakim, A., J. S. D. Munshi and G. M. Hughes. 1978. Morphometrics of the respiratory organs of the Indian green snake-headed fish, *Channa punctata*. J. Zool. (Lond.), 184: 519–543.

Hughes, G. M. 1966. The dimensions of fish gills in relation to their function. J. Exp. Biol., 45: 177–195.

Hughes, G. M. 1972. Morphometrics of fish gill. Respir. Physiol., 14: 1–25.

Hughes, G. M. 1982. An introduction to the study of gills. Pages 1–24 *in* D. F. Houlihan, J. C. Rankin and T. J. Shuttleworth, eds. Gills. Cambridge Univ. Press, London and New York.

Hughes, G. M. 1984a. General anatomy of the gills. Pages 1–72 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. XA. Academic Press, New York.

Hughes, G. M. 1984b. Measurement of gill area in fishes: practices and problems. J. Mar. Biol. Assoc. U. K., 64: 637–655.

Hughes, G. M. and M. Morgan. 1973. The structure of fish gills in relation to their respiratory function. Biol. Rev., 48: 419–475.

Hughes, G. M. and G. Shelton. 1962. Respiratory mechanisms and their nervous control in fish. Adv. Comp. Physiol. Biochem., 1: 275–364.

Hughes, G. M., S. C. Dube and J. S. D. Munshi. 1973. Surface area of the respiratory organs of the climbing perch, *Anabas testudineus* (Pisces: Anabantidae). J. Zool., Lond., 170: 227–243.

Hughes, G. M., B. R. Singh, G. Guha, S. C. Dube and J. S. D. Munshi. 1974. Respiratory surface areas of an air-breathing siluroid fish, *Saccobranchus* (*Heteropneustes*) *fossilis*, in relation to body size. J. Zool., Lond., 172: 215–232.

Lagler, K. F., J. E. Bardach, R. R. Miller and D. M. Passino. 1962. Ichthyology. John Wiley & Sons, New York, 506 pp.

Landolt, J. C. and L. G. Hill. 1975. Observations of the gross structure and dimensions of the gills of three species of gars (Lepisosteidae). Copeia, 1975(3): 470–475.

Laurent, P. 1982. Structure of vertebrate gills. Pages 25–43 *in* D. F. Houlihan, J. C. Rankin and T. J. Shuttleworth, eds. Gills. Cambridge Univ. Press, London and New York.

Laurent, P. 1984. Gill internal morphology. Pages 73–183 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. XA. Academic Press, New York.

Milton, P. 1971. Oxygen consumption and osmoregulation in the shanny, *Blennius pholis*. J. Mar. Biol. Assoc. U. K., 51: 347–265.

Muir, B. S. and G. M. Hughes. 1969. Gill dimension for three species of tunny. J. Exp. Biol., 51: 271–285.

Price, J. W. 1931. Growth and gill development in the small-mouthed black bass, *Micropterus dolomieu* Lacepède. Contr. Stone Lab. Ohio Univ., 4: 1–46.

Schottle, E. 1931. Morphologie und Physiologie der Atmung bei wassers-schlamn-und landlebenden Gobiiformes. Z. Wiss. Zool., 140: 1–113.

Singh, B. R., A. N. Yadav, J. Ojha and J. S. D. Munshi. 1981. Gross structure and dimensions of the gills of an intestinal air-breathing fish (*Lepidocephalichthys guntea*). Copeia, 1981(1): 224–229.

Shingh, B. R., A. P. Mishra, M. S. Prasad and I. Singh. 1989. Development of neo-morphic air-breathing organs in three genera of estuarine gobies. Gegenbaurs Morph. Jb., 135: 529–539.

Singh, B. R., A. N. Yadav, M. S. Prasad and A. P. Mishra. In press. Neo-morphic organ for CO_2 elimination in air-breathing teleosts. Arch. Biol.

Tamura, O. and T. Moriyama. 1976. On the morphological feature of the gill of amphibious and air breathing fishes. Bull. Fac. Fish., Nagasaki Univ., (41): 1–8.

Tamura, O., H. Morii and M. Yuzuriha. 1976. Respiration of the amphibious fishes, *Periophthalmus cantonensis* and *Boleophthalmus chinensis* in water and on land. J. Exp. Biol., 65: 97–107.

Thomson, K. S. 1969. The biology of lobe-finned fishes. Biol. Rev., 44: 91–154.

Todd, E. S. and A. W. Ebeling. 1966. Aerial respiration in the long jaw mudsucker, *Gillichthys mirabilis* (Teleostei, Gobiidae). Biol. Bull., 130: 265–288.

(Department of Zoology, Bihar University, Muzaffarpur-842001, Bihar, India)

河口域に生息する空気呼吸ハゼ *Pseudapocryptes lanceolatus* の鰓の構造と計測値

Amrendra N. Yadav・B. R. Singh

河口域に生息する空気呼吸ハゼ *Pseudapocryptes lanceolatus* の鰓は，O_2 摂取のために特化した器官の発達によって退縮している．第一鰓弓においては，外側の半鰓は内側の半鰓に比べて鰓弁の長さが約 1/2 に退縮している．鰓弁の片側に生ずる二次鰓弁の数は少ない (27.6 枚/mm)．鰓面積と体重を両対数グラフにプロットすると，傾きに統計的有意差のある 2 本の直線が得られ，その傾きは体重 6 g までの魚については 0.924，体重 8 g 以上の魚については 0.405 であった．