# On the Circulatory Systems of the Snakeheads Channa maculata and C. argus with Reference to Bimodal Breathing

Atsushi Ishimatsu, Yasuo Itazawa and Tatsusuke Takeda

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Abstract The circulatory systems of Channa maculata and C. argus were studied using the resin injection method. The heart has two aortae separately emerging from the bulbus arteriosus. A part of the blood ejected from the ventricle enters the anterior ventral aorta, and is sent to the 1st and 2nd branchial arches where it releases carbon dioxide into the water. It is then collected in the efferent branchial arteries and is again scattered into the numerous capillaries of the suprabranchial organ where it is fully oxygenated. The oxygenated blood is drained into the anterior cardinal vein and is returned to the heart through the venous system. The other part of the blood enters the posterior ventral aorta and is sent to the 3rd and 4th branchial arches. It passes the gills and goes to the lateral dorsal aortae to be engaged in the systemic circulation. The 4th branchial arch is much reduced. The inner hemibranch of it is composed mainly of clustered loops of shunt vessels whereas the outer hemibranch has a few small filaments. The heart lacks the sino-atrial valves.

Air-breathing fishes show diverse modifications of the circulatory system reflecting their various ways of adaptation to air breathing. They have been one of the most attractive subjects of comparative anatomy and physiology. As for the genus Channa (=Ophicephalus), several studies have been published on the structure of the air-breathing organ (Munshi, 1962; Fukuda, 1971; Hughes and Munshi, 1973) and the circulatory system (Rauther, 1910; Lele, 1932; Wu and Chang, 1947; Das and Saxena, 1956). The latter subject has been only briefly described.

The present study was attempted to reveal detailed features of the circulatory systems of two snakeheads inhabiting Japan, using the resin injection method. The results will be discussed from the viewpoint of comparative anatomy referring to the functional aspects of the system.

#### Material and methods

Three specimens of Channa maculata (Lacepède) ranging from 30 to 40 cm in total length were collected by angling in Hyogo Prefecture and eleven C. argus (Cantor) of the same size

were also collected by angling in Fukuoka Prefecture. Two of *C. maculata* and six of *C. argus* were subjected to resin injection, and one of the former and five of the latter were fixed in 10% formalin to observe the gross structure of the respiratory organs and some histological features.

Fish were anesthetized in quinaldine solution (1:20000) and the abdominal wall of the fish was incised about 2 cm directly above the heart. A small amount (0.1 to 0.2 ml) of heparin solution was injected into the exposed ventricle to prevent coagulation of the blood. After a few minutes, a polyethylene tubing of 2.3 mm in outer diameter was inserted into the bulbus arteriosus from a small opening made on the ventricle and fixed at the border between the bulbus and the ventricle by ligature (Fig. 1). The whole circulatory system was flushed with a physiological saline containing about 1% isoamyl nitrite as the vasodilator until the outflowing saline became colorless. The sinus venosus was cut before flushing to easily expel the blood and flushing saline.

Twenty grams of a resin Mercox CL

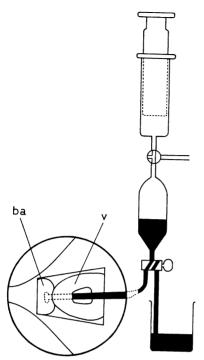


Fig. 1. Diagram to show the apparatus used in resin injection with an enlarged view of the dissected portion of the fish and the fixed tubing (in circle).

(Dainippon Ink Inc.) of red or blue color was quickly mixed with 0.5 g of the solidifying agent. Then this mixture was injected into the circulatory system from the bulbus arteriosus through the polyethylene tubing (Fig. 1). The injection was completed in three to five minutes, because the resin began to solidify about five minutes after mixing with the solidifying agent. The fish were kept for four to five hours wrapped in a wet towel to allow the resin to solidify completely, and then immersed in concentrated hydrochloric acid for 24 hours to dissolve all the tissues leaving a resin mold of the blood vessels. Then the resin mold was rinsed using water to remove dissolved tissues and hydrochloric acid. Some of resin-injected specimens were not immersed in the acid and were kept for investigation of position of blood vessels in the body.

Nomenclature of blood vessels follows Bertin (1958) as far as possible, and some synonyms are shown in parentheses in the list of abbreviations below.

Abbreviations for anatomical terms. aba  $1 \sim$ 4. 1st to 4th afferent branchial arteries: acv. anterior cardinal vein; at, atrium; ava, anterior ventral aorta; avv, atrio-ventricular valve; b, branch of eba 2 in C. maculata; ba, bulbus arteriosus; bf, bifurcation of eba 1; br, brain; bua, buccal artery; c, connecting artery between eba 1 and eba 2 in C. argus; ca, cerebral artery; cb, choroid body; cc, common carotid; ccv, common cardinal vein; ce, cut ting edge of eba 1; cma, coeliacomesenteric artery; cn, connecting artery between op and ora in C. maculata; da, dorsal aorta; dar, ductus arteriosus; e, eye region; eba 1~4, 1st to 4th efferent branchial arteries; ec, external carotid; eh, artery from the external branch of eba 2 to hba; efa 1, 2, 1st and 2nd efferent filamental arteries;  $g_{1\sim4}$ , 1st to 4th branchial arches; hba, hypobranchial artery; hmp, hyomandibular process; ia, inter-aortic artery; ica (ic in Fig. 23), internal carotid artery; ioa, infraorbital artery; isv, shunt vessels in inner hemibranch of  $g_4$ ; l, liver; lda, lateral dorsal aorta (=suprabranchial artery in Lele, 1932 and in Das and Saxena, 1956); ma, mandibular artery; n, nasal region; ona, orbitonasal artery (=posterior carotid artery in Lele, 1932 and in Das and Saxena, 1956); onv, orbitonasal vein; op, oval plexus; opa, optic artery; opca, opercular artery; opha, ophthalmic artery; ora, orbital artery (=external carotid in Wu and Chang, 1947 and orbitonasal artery in Lele, 1932 and in Das and Saxena, 1956); osv, shunt vessels in outer hemibranch of  $g_4$ ; p, pulmonary artery; pc, pulmocutaneous artery; pcv, posterior cardinal vein; pt, polyethylene tubing used in resin injection; pva, posterior ventral aorta; sb, suprabranchial artery (=eba 1 and 2); sbo, suprabranchial organ; sca, subclavian artery; sly, semilunar valve; soa, supraorbital artery; sv, sinus venosus; v, ventricle; va, ventral aorta.

#### Results

The injected resin was carried through the entire arterial system and most parts of the venous one (Figs. 2, 3). The circulatory system in the head region is described mainly using *C. maculata* and especially referring to bimodal breathing. The other species, *C.* 

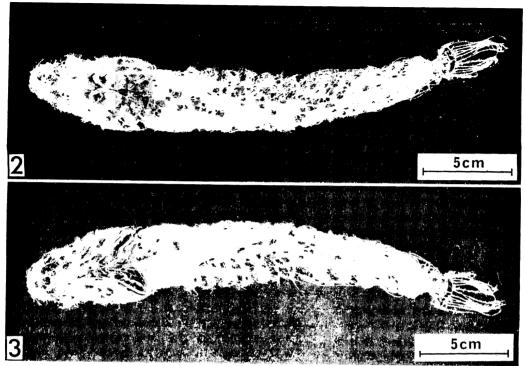


Fig. 2. Dorsal view of a whole preparation of *C. maculata*. Fig. 3. Ventral view of the whole preparation of *C. maculata*.

argus, is referred to when a difference is found between the two species and when the preparation is better in this species.

The overall views of the blood vessels in the head region are presented first (Figs. 4, 5). The suprabranchial organs (sbo), i.e., the air-breathing organs, occupy a fairly large part of the occipital region, extending from the level of the brain (br) to the posterior margin of the operculum. The organ is divided into three chambers by cartilaginous processes, the hyomandibular and the epibranchial of the 1st branchial arch. anterior region of the organs in Fig. 4 seemingly lacks blood vessels, but this is attributable to the incomplete distribution of the resin. The hyomandibular process (hmp) is visible inside the organ in the region devoid of vessels (Fig. 4). The 1st to 3rd branchial arches  $(g_1 \text{ to } g_3)$  are relatively large, bearing many filaments as in ordinary water-breathing teleosts. The condition is, however, quite different in the 4th branchial arch  $(g_4)$  which bears only a small number of short filaments

showing a rudimentary appearance (Fig. 5).

Rich vascularization in the suprabranchial organs strongly suggests an efficient respiratory function (Figs. 6, 7). The respiratory surface is composed of small patches of congregated blood vessels lined with non-respiratory tissues. Munshi (1962) observed similar structures in *C. punctatus* and *C. striatus* and called them 'respiratory islets'. Capillaries of the islets originate from the 1st and 2nd efferent branchial arteries, of which the former (eba 1) irrigates the antero-dorsal and lateral portions of the suprabranchial organ, and the latter (eba 2) the postero-ventral portion (Figs. 8, 9).

The blood oxygenated at the suprabranchial organ is drained into the anterior cardinal vein (acv) and mixed with the deoxygenated blood from the orbitonasal vein (onv) originating at a more anterior part of the head. The anterior cardinal vein and the posterior cardinal vein (pcv) unite at the posterior end of the organ, to form the common cardinal vein (ccv) which returns the blood to the

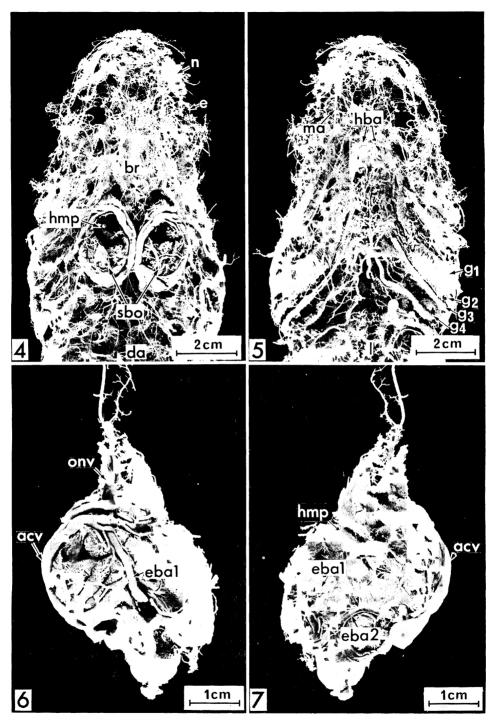


Fig. 4. Dorsal view of the blood vessels in the head region of C. maculata. The suprabranchial organs (sbo) occupy a large part of the occipital region. Fig. 5. Ventral view of the blood vessels in the head region of C. maculata. Reduced 4th branchial arches  $(g_4)$  can be seen. Fig. 6. Dorsal view of the isolated right suprabranchial organ of C. maculata. The gas exchange surface is composed of a large number of respiratory islets. Fig. 7. Ventral view of the isolated right suprabranchial organ of C. maculata.

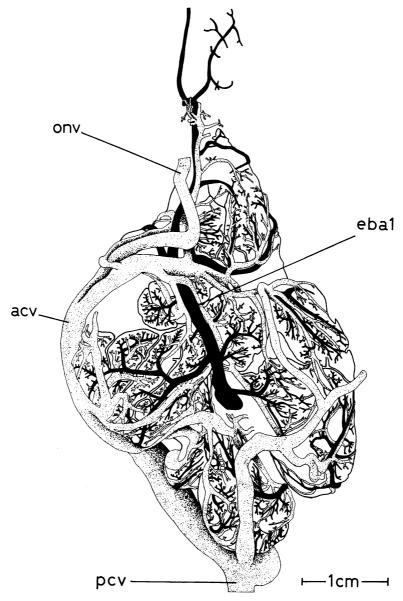


Fig. 8. Illustration to show the dorsal view of the right suprabranchial organ of C. maculata based on Fig. 6. Solid vessels are arteries and dotted ones veins.

sinus venosus.

The lateral dorsal aortae (lda) run forward along the inner wall of the suprabranchial organ, and bifurcate into the orbital (ora) and internal carotid arteries (ica) just above the locus where the anterior ventral aorta (Fig. 19) divides into a pair of the 1st afferent branchial arteries (aba 1) (Fig. 10). The orbital artery curves backward after branching

off the supraorbital (soa) and infraorbital (ioa) arteries (Fig. 14), and then turns forward at the hyomandibular process to continue as the mandibular artery (ma) in the lower jaw (Fig. 11). The opercular artery (opca), arising from the subclavian artery (sca), runs along the posterior margin of the operculum. Capillary networks of the suprabranchial organ, forming respiratory islets, extend over the

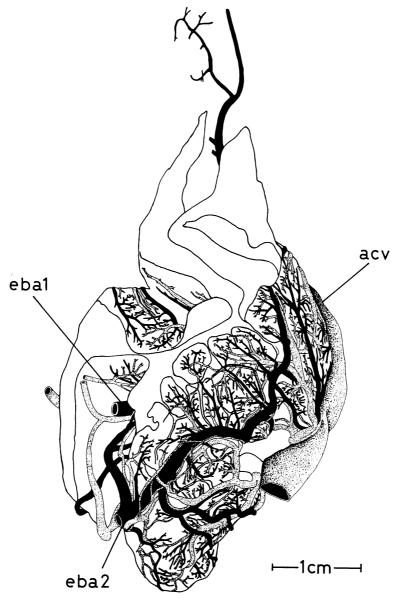


Fig. 9. Illustration to show the ventral view of the right suprabranchial organ of C. maculata based on Fig. 7. Inner side of the organ is left blank.

inner wall of the operculum (Fig. 11).

One of inter-specific differences between C. maculata and C. argus is seen in arrangements of the 1st and 2nd efferent branchial arteries entering the suprabranchial organ (Fig. 12 for C. maculata and Fig. 13 for C. argus). The 2nd efferent branchial artery (eba 2) is not connected with the 1st one (eba 1) in C. maculata, while a branch of the 2nd one,

connecting artery (c), extends to the 1st one to make the connection between them in C. argus (Fig. 13). This connecting artery was also observed in C. argus by Wu and Chang (1947), and described by them as being exceptionally lacking. Such an exceptional lacking of the connecting artery was observed at only the right suprabranchial organ of a single specimen among eleven C. argus

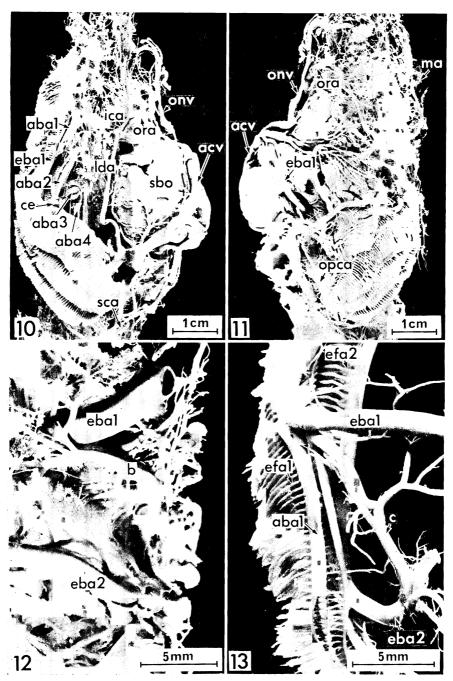


Fig. 10. Left lateral view of the blood vessels in the head region of *C. maculata* with the left suprabranchial organ removed. Fig. 11. Right lateral view of the blood vessels in the head region of *C. maculata*. The suprabranchial organ also occupies a large part of the operculum. Fig. 12. Enlarged ventral view of the left suprabranchial organ of *C. maculata* showing the portion where the 1st and 2nd efferent branchial arteries (eba 1 and 2) enter the organ. Branch of the 2nd efferent branchial artery (b) has no connection with the 1st one. Fig. 13. Enlarged dorsolateral view of the portion of the 1st and 2nd efferent branchial arteries emerging from the left branchial arches of *C. argus*. The connecting artery (c) between them is apparent.

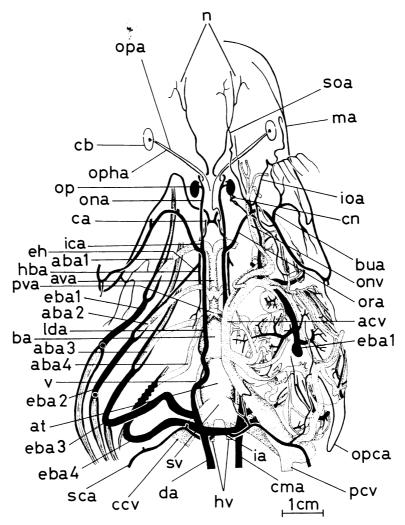


Fig. 14. Illustration to show the dorsal view of the blood vessels in the head region of *C. maculata*. Solid vessels correspond to those carrying the oxygenated blood in the ordinary teleosts, dotted vessels to those carrying the deoxygenated blood.

examined. As for *C. maculata*, no exceptional presence of the connecting artery was observed among three specimens examined, although the result is less convincing because of the small number of specimens.

Of four pairs of efferent branchial arteries, only the 3rd (eba 3) and 4th (eba 4) pairs have a connection with the lateral dorsal aortae (lda), and the 1st (eba 1) and 2nd (eba 2) pairs are distributed only to the suprabranchial organ without connection with the aortae (Figs. 14, 15). This means that the 1st and 2nd pairs of efferent branchial arteries do not

contribute to the systemic circulation. The lateral dorsal aortae run posteriorly parallel to each other without connection between them until they reach the 4th efferent branchial arteries where the aortae are conneted by the inter-aortic artery (ia). This structure is characteristic of the genus *Channa*. The left lateral dorsal aorta continues as the dorsal aorta (da), posteriorly beyond the inter-aortic artery, and the right one continues as the coeliacomesenteric artery (cma) running downward into the abdominal cavity. The subclavian arteries arising from the inter-aortic

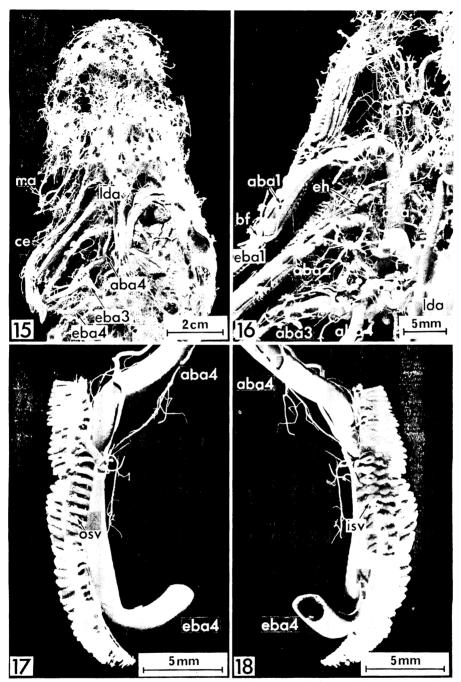


Fig. 15. Dorsal view of the blood vessels in the head region of *C. maculata* with the left suprabranchial organ removed. Fig. 16. Enlarged dorsal view of the afferent branchial system of *C. maculata*. The characteristic arrangement of the 3rd and 4th afferent branchial arteries (aba 3 and 4) is apparent. Bifurcation of the 1st efferent branchial artery (bf) is also visible. Fig. 17. Enlarged lateral view of the isolated 4th branchial arch of *C. argus*. The filaments are much reduced and the shunt vessels (osv) connect the afferent and efferent filamental arteries at the base of the filaments. Fig. 18. Enlarged medial view of the isolated 4th branchial arch of *C. argus*. Clustered shunt vessels (isv) are clearly seen.

artery show a somewhat peculiar course; the right one runs above the coeliaco mesenteric artery while the left one runs under the dorsal aorta and then turns its way upward (Fig. 14). These two arteries branch off numerous arteries and finally exhaust themselves at the brachial region.

At the level of the brain the lateral dorsal aorta is divided into the internal carotid (ica) and orbital (ora) arteries. The internal carotid artery sends off the cerebral artery (ca) which is soon divided into three branches, of which the anteriormost sends off the optic artery (opa) running parallel to the optic nerve. The orbital artery branches off the supraorbital (soa), infraorbital (ioa) and buccal (bua) arteries. The cephalic circle is completed anteriorly by the cerebral artery and posteriorly by the inter-aortic artery between the lateral dorsal aortae (Fig. 14).

An artery (eh) originating from the external branch of the 2nd efferent branchial artery extends to the hypobranchial artery (hba) (Fig. 16). The hypobranchial artery reaches the mandibular artery (ma) where the latter turns forward. The anterior extremity of the 1st efferent branchial artery bifurcates (bf in Fig. 16), and such bifurcation is seen at both anterior and posterior extremities of all the efferent branchial arteries. The characteristic course of the 3rd and 4th afferent branchial arteries (aba 3 and 4) is also seen in the figure. The 4th afferent branchial artery arises anteriorly to the 3rd one from the common root (pva), and runs backward over it. This condition is considered to be a common feature of the circulatory system of the genus Channa, because it was observed also in C. striatus by Das and Saxena (1956) and in C. argus by Wu and Chang (1947).

The most remarkable modification of the branchial arches is seen at the 4th one (Figs. 17, 18). Photographs of *C. argus* are used for explanation, because resin injection was more successful in this species than in *C. maculata* which showed exactly the same features as *C. argus*. The filaments are much reduced and exist mainly in the outer hemibranch. The inner hemibranch is composed of a series of clustered loops of blood vessels (isv) which are considered to be homologous

with filamental vessels in an ordinary hemibranch. The same structure was observed in C. argus by Wu and Chang (1947) and in C. striatus by Munshi (1976). Concerning C. punctatus, Lele (1932) stated that the efferent branchial arteries were directly connected with the afferent ones in the 3rd and 4th branchial arches, but he did not refer to the existence of the clustered loops. In C. striatus, Das and Saxena (1956) observed the same features as C. punctatus and also did not refer to the loops. Diameters of the afferent and efferent filamental arteries of the outer hemibranch become larger at their basal portion where a few shunt vessels (osv) connect the both arteries. This suggests that the clustered loops seen in the inner hemibranch are the more progressed stage of the above-mentioned modification in the outer hemibranch.

Another remarkable feature in both species is the arrangement of the ventral aortae (Fig. 19 for a fixed preparation and Fig. 20 for a resin mold). Two aortae emerge separately from the bulbus arteriosus; the anterior one (ava) supplies blood to the 1st and 2nd branchial arches and the posterior one (pva) is divided, just after emerging from the bulbus, into the 3rd and 4th afferent branchial arteries (see Fig. 16). This feature is very unique among teleosts, and has not been described. Wu and Chang (1947) and Das and Saxena (1956) described that the 3rd and 4th afferent branchial arteries arose f om the basal portion of the ventral aorta, but they did not observe two aortae separately emerging from the bulbus arteriosus. The heart has the atrio-ventricular (avv) and semilunar (ventriculo-bulbar) (slv) valves, but lacks the sino-atrial valves in C. argus. The absence of the sino-atrial valves was confirmed by examination of five specimens. The first two valves were observed also in C. maculata, though the last one was not examined in this species because of poor preparation. No structure to suggest the separation of blood flow was found in the heart of either species.

A branch of the orbitonasal artery (ona) enters an ellipsoid-shaped body which is tentatively called 'oval plexus (op)'. The ophthalmic artery (opha) emerges from the oval plexus and breaks up into numerous

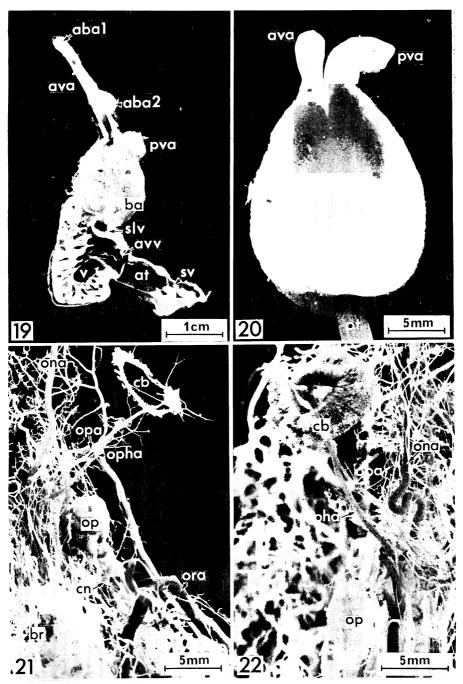


Fig. 19. Median section of the fixed preparation of the heart of *C. argus*. Fig. 20. Median section of resin mold of the bulbus arteriosus of *C. argus*. Two aortae separately emerge from the bulbus. Fig. 21. Enlarged dorsal view of the right orbital region of *C. maculata*. Connecting artery (cn) between the oval plexus (op) and the orbital artery (ora) is apparent. Fig. 22. Enlarged dorsal view of the left orbital region of *C. argus*.

capillaries in the choroid body (cb) lying between choroid and sclerotic coats of the eyes (Figs. 21, 22). Different appearances of the choroid bodies between the photographs are considered to be due to incomplete distribution of resin in *C. maculata* specimens. The oval plexus is not yet identified, but the connection of the plexus with other blood vessels suggests its homology with the pseudobranch, though histological investigation in the present study revealed a structure different from that in ordinary teleosts.

Another inter-specific difference between the two species was observed in the arrangement of the blood vessels supplying the oval plexus. The oval plexus of *C. maculata* receives blood from two arteries, the orbitonasal artery (ona) and a connecting artery (cn) branching from the orbital artery (ora) (Fig. 21), while the plexus of *C. argus* receives blood only from the former (Fig. 22).

## Discussion

Circulatory systems of vertebrates can be classified into three categories from the viewpoint of the arrangement of systemic and respiratory circulations. In water-breathing fishes, the circulatory systems show a single 'in series' arrangement in which the heart pumps out the blood through the respiratory organs to the systemic circulation. In crocodilian reptiles, birds and mammals, the circulatory systems also show an 'in series' arrangement, but two ventricles share the work of respiratory and systemic perfusions; the left ventricle (high pressure pump) for the systemic perfusion and the right one (low pressure pump) for the respiratory perfusion. In between these two extremes, various types of 'parallel' arrangement can be placed as seen in amphibians, non-crocodilian reptiles and air-breathing fishes. In these animals, the systemic and respiratory circulations are incompletely separated. Consequently, mixing of oxygenated and deoxygenated blood occurs. Among air-breathing fishes, some species such as Clarias and Saccobranchus have air-breathing organs placed between the gills and the systemic circulation so that mixing does not occur. However, many other species have an arrangement in which

the oxygenated blood from the air-breathing organs is sent to the venous system and returned to the heart before it is brought into the systemic circulation (Satchell, 1976).

Both the snakeheads, C. maculata and C. argus, belong to the latter type of arrangement. A part of blood enters the 1st and 2nd branchial arches through the anterior ventral aorta after being ejected from the heart. Then the blood is collected in the efferent branchial arteries and again separated into numerous capillaries of the suprabranchial Ninety percent of carbon dioxide release and 40% of oxygen uptake are carried out in the gills, while 10% of carbon dioxide release and 60% of oxygen uptake depend on the suprabranchial organ in air-saturated water at 25°C (Itazawa and Ishimatsu, unpublished). The lowered level of carbon dioxide in the blood may result in a higher oxygen affinity of the blood and facilitate the oxygen uptake in the suprabranchial organ, though the effect may be slight considering the relatively small Bohr effect generally known in air-breathing fishes. The blood sent to the 3rd and 4th branchial arches through the posterior ventral aorta enters the lateral dorsal aortae to be engaged in the systemic circulation. Oxygen pressure in the blood is considered to be the highest in the anterior cardinal vein which receives the blood oxygenated at the suprabranchial organ, and is lowered in the common cardinal vein and sinus venosus by mixing with the venous blood from the posterior cardinal and hepatic veins, respectively. Satchell (1976) pointed out an advantage of this drainage of the oxygenated blood to the venous system, by stating that 'The lower pressure at the peripheral end of the respiratory capillaries caused by exposing them to the vis a fronte of the central veins, rather than the arterial pressure of the dorsal aorta must lower the average pressure prevailing along their length.' The high level of hemoglobin in the blood of many air-breathing fishes (Munshi and Singh, 1968) may be a countermeasure to the disadvantage due to mixing of oxygenated and deoxygenated blood in this 'parallel' circula-

It is generally accepted that the first step

toward double circulation depends on the provision of a separate pathway for oxygenated blood to the heart avoiding mixture with deoxygenated blood (Carter and Beadle, 1931; Foxon, 1955). Foxon (1955) regarded the aortae by which the oxygenated and deoxygenated blood separately leave the heart as one of the common features of double circulation. He also pointed out that even hearts showing no anatomical division may have some degree of physiological separation of the blood. In this respect, the hearts of C. maculata and C. argus draw particular interest. They have two separate aortae, one for the systemic circulation and the other for the respiratory circulation, while the venous system shows no anatomical division. The absence of the sino-atrial valves seems to be a very interesting subject because it is said that the valves play an important role in ventricular filling in other teleosts (Johansen, 1971). These two anatomical features of the hearts of C. argus (and probably of C. maculata), which are shared by higher vertebrates, seem to suggest a ground plan in the evolution of the circulatory system in transition from the single circulation of water-breathers to the double circulation of air-breathers.

In Fig. 23 the aortic arches of C. maculata and C. argus (B) are compared with those of the ordinary water-breathing teleosts (A), Protopterus (C) and urodele amphibians (D). In most vertebrates, six pairs of large vessels connecting the ventral and dorsal aortae appear in the embryonic development. Roman numerals in the figure show those aortic arches and their homologies. In the ordinary water-breathing teleosts (A), the last four pairs of aortic arches remain and each pair shows the same structure, having capillary networks of secondary lamellae. In this type of the arrangement, the systemic circulation receives the blood of lowered pressure caused by the large vascular resistance of the gills. This is the typical arrangement of a single 'in series' circulation. But in C. maculata and C. argus (B), there appears a differentiation of aortic arches. Aortic arches III and IV (the 1st and 2nd branchial arches) have no connection with the lateral dorsal aortae and enter the suprabranchial organ with blood

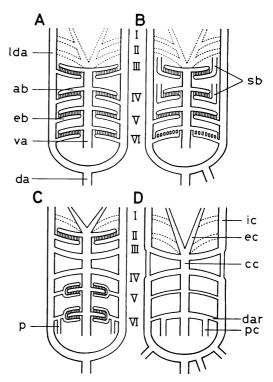


Fig. 23. Comparison of aortic arches among four vertebrates. A: Ordinary water-breathing teleost. B: Snakehead. C: *Protopterus*.
D: Urodele amphibian. (C and D are based on Fig. 315 in Romer, 1970).

of lowered pressure by passing through the gills. Aortic arches V and VI (the 3rd and 4th branchial arches) contribute mainly to the systemic circulation and make only a slight contribution to gas exchange. The gill filaments and secondary lamellae in the aortic arch VI are much reduced and diminish the vascular resistance to blood flow. This ensures a high perfusion pressure in the systemic circulation. As for other species of the genus Channa, both the afferent and efferent branchial arteries of aortic arches III and IV are distributed to the suprabranchial organ in C. punctatus (Lele, 1932). The same situation was observed in C. striatus by Das and Saxena (1956), while Rauther (1910) did not observe the distribution of the afferent branchial arteries to the organ in that species. In Protopterus (C), the aortic arches III and IV have no interruption and connect directly the ventral and dorsal aortae. The pulmonary circulation derives from the aortic arch VI. A similar situation is seen in urodele amphibians (D), although they lack completely the filamental capillary network. These conditions suggest that lungfishes and amphibians have a phylogenetically close relation, and that air-breathing in snakeheads is a way of adaptation different from than that of lungfishes and probably of ancestral terrestrial vertebrates.

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(Department of Fisheries, Faculty of Agriculture, Kyushu University, Hakozaki, Higashi-ku, Fukuoka 812, Japan)

## タイワンドジョウおよびカムルチーの頭部血管系の観 窓

#### 石松 惇•板沢靖男•竹田達右

なお第1・第2出鰓動脈が上鰓器官に入る部分において、カムルチーでは第2出鰓動脈の分枝が第1出鰓動脈と連絡しているのに対し、タイワンドジョウではこの分枝が第1出鰓動脈に達していない。また眼窩鼻動脈側方に卵円形血管叢が存在するが、カムルチーでは眼窩鼻動脈の分枝のみがこれに血液を送っているのに対し、タイワンドジョウではこのほかに眼窩動脈の分枝もこれと連絡している。

(812 福岡市東区箱崎 九州大学農学部水産学科)