Internal Anatomy of Catfishes

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Recognizing well the diversity of internal anatomy in catfish, the account here is predominantly directed to two North American species which are far the most studied—*Ictalurus punctatus*, the channel catfish and *Ameiurus nebulosus*, the bullhead—and also the African *Clarias gariepinus*. Some important publications on the subject are, among others, Cleland (1858), Alexander (1965), Grizzle and Rogers (1976; the most complete description, very useful for histology and references), Nawar (1955), Taverne and Aloulou-Triki (1974), and Sinha (1986a).

The coelomic cavities, circulatory system, branchial respiratory system, digestive system, kidneys and urogenital system, spleen, thymus, trunk musculature, endocrine organs and nervous system are briefly discussed, while histology and physiology are almost not considered.

COELOMIC CAVITIES

The peritoneal cavity (Fig. 5.1B) is short and broad in relation to the typical shape of catfishes adapted to benthic life, with a flattened ventral

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face and a triangular section at the posterior end of the head, a round belly and a long anal fin following a rather anterior vent. Even in pelagic families, such as Schilbeidae and Plotosidae, the visceral region retains a similar shape while the tail is lengthened and often curved ventrally.

The pericardial cavity is lodged at the posteroventral end of the branchial basket and shaped as in other teleosts (Fig. 5.1A). It is limited
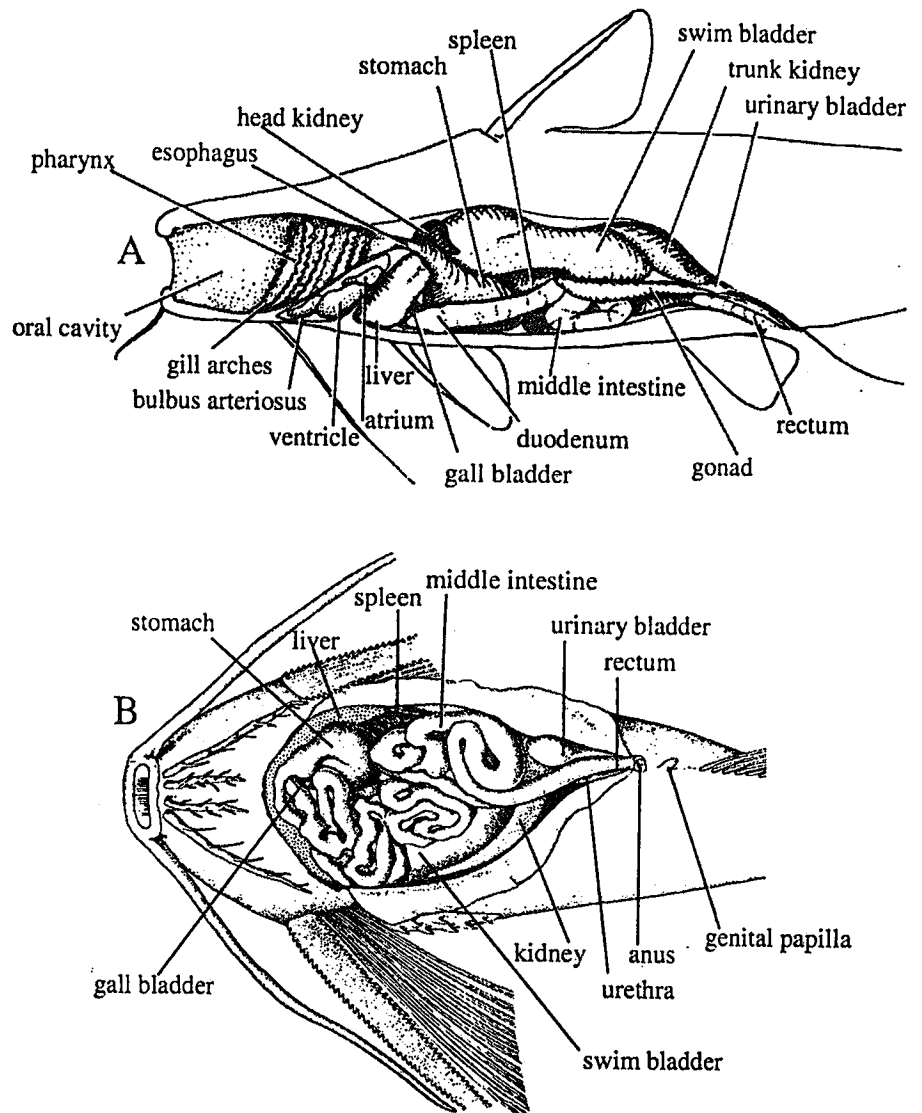

Fig. 5.1. A. *Ictalurus punctatus*. Diagrammatic view of right half of the oropharynx and head and trunk kidneys, urinary bladder and organs in the opened visceral and pericardial cavities (slightly modified, after Grizzle and Rogers, 1976). B. *Synodontis acanthomyas*. Ventral view of situs viscerum (after Taverne and Aloulou-Triki, 1974).

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by the sternohyoidei muscles, the peritoneo-pericardial septum, pectoral girdle, complex vertebra and lateral membranes.

The swim bladder is an outgrowth of the posterior end of the esophagus lined by a splanchnopleura, with a quasi-virtual coelomic space and a somatopleura; it is located just under the anterior backbone, outside the main peritoneal cavity, so that it could erroneously be considered as extraperitoneal (Grizzle and Rogers, 1976).

The shape, location and size (Fig. 5.1B) of the swim bladder are crucial for equilibrium, whatever the way of life-benthic, semi-benthic or pelagic. That functional constraint probably explains the unusual disposition of the neighbouring viscera: the head and trunk kidneys are completely separated by the swim bladder; the liver is compressed just behind and partially under it (Fig 5.1A, B). Bridge and Haddon (1893) and Hora (1937), on the contrary, proposed that the special needs of the kidneys and liver are responsible for the unusual forms of the swim bladder in the context of the shortened peritoneal cavity.

CIRCULATORY SYSTEM

The circulatory system of most catfishes is similar to that of most teleosts (Fig. 5.2), and namely to that of another otophysan, Cyprinus (Bertin, 1957), with a few particularities in parts which are variable in teleosts.

The heart is usually somewhat assymetrical; for example, in Clarias gariepinus, the sequence of the cavities is slightly curved to the left (Nawar, 1955). The wall of the sinus venosus is devoid of myocardial fibres. That of the bulbus arteriosus is mainly composed of elastic fibres (Grizzle and Rogers, 1976). There is only one row of semilunar valves between the ventricle and bulbus (ibidem); according to Bertin (1957), the muscular ring bearing the valvules represents the reduced conus arteriosus.

The two posterior afferent branchial arteries and the two anterior ones often originate together from the ventral aorta. There is no pseudobranch nor hyoidean hemibranch and the eyes and brain are irrigated by the internal carotids which are the anterior continuation of the dorsal aortic roots (Fig. 5.2). The two posterior branchial efferents meet before joining the aortic roots. Fishes lack a true lymphatic system. A carototid labyrinth of enigmatic function is present in catfishes (Fig. 5.3) (Srivastava and Singh, 1980).

The venous system is generally built similar to that in most other teleosts (Fig. 5.2). There is only one caudal vein, as in Cyprinus, but not
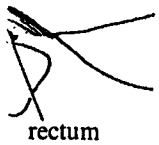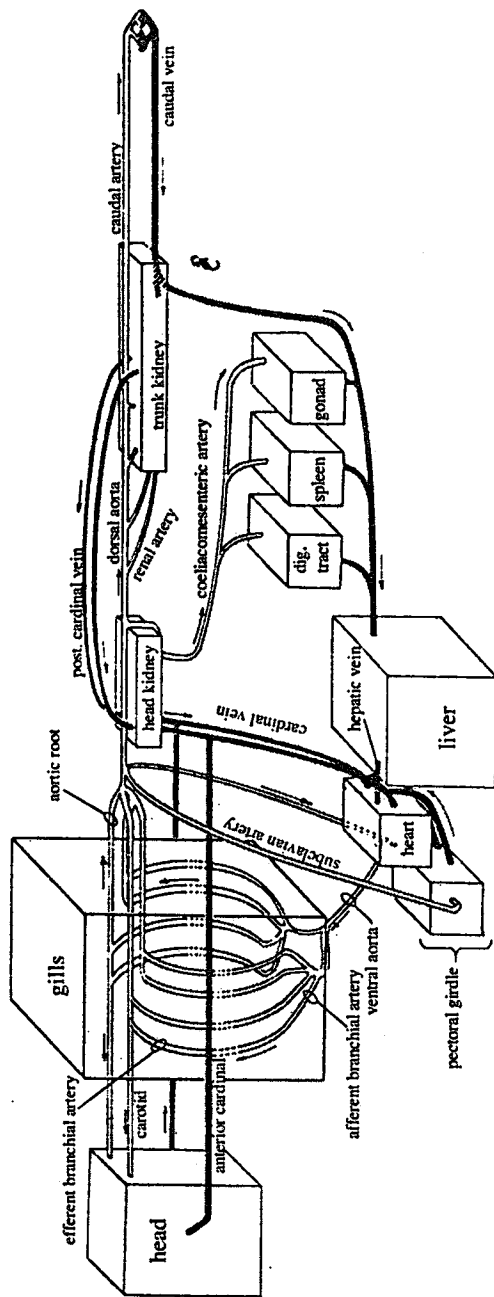
Fig. 5.2 *Ictalurus punctatus*, scheme of major arteries and veins (slightly modified from Grizzle and Rogers, 1976). Notice the posterior cardinal venae joining the head and trunk kidneys. The size of the parallelepipeda is nearly proportional to the importance of blood flow. The part of the branchial arteries in dotted lines represents the capillaries between the afferent and efferent arteries
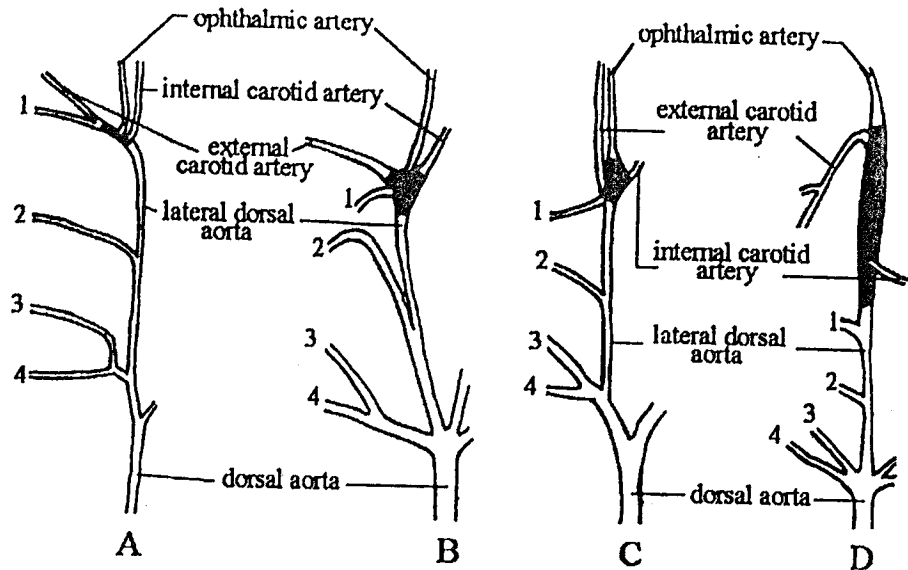
Fig. 5.3 Schematic drawings illustrating the position of the carotid labyrinth (dark zone) with respect to first efferent branchial artery (first, second, third and fourth efferent branchial arteries indicated respectively by the numbers 1, 2, 3 and 4), lateral dorsal aorta, external carotid artery, internal carotid artery and ophthalmic artery in *Clarias batrachus* (A), *Heteropneustes fossilis* (B), *Mystus seenghala* (C) and *Rita rita* (D) (slightly modified from Srivastava and Singh, 1980).

in another cyprinid genus, *Tinca* (Bertin, 1957). Details are to be found in Nawar (1955) and Grizzle and Rogers (1976).

In air-breathing catfish, the branchial arteries are adapted to the circulation of blood in the accessory breathing organs: (1) dendritic organs on the 2nd and 4th branchial arches in suprabranchial cavities (outgrowths of the opercular cavities) and vascularized epithelium of the same cavities in clariids (Munshi, 1961; Hellin and Chardon, 1981; Vandewalle and Chardon, 1991) (Fig. 5.4), long saccate left and right diverticula homologous to the clariids suprabranchial cavities in *Heteropneustes fossilis* (Munshi, 1962), swim bladder in *Mystus gulio* (Natarajan, 1979), partitioned alveolar swim bladder in the less part of the pangasiids (Browman and Kramer, 1985); (2) stomach in trichomycterids (Cala, 1987), astroblepids (Gee, 1976) and loricariids (Carter and Beadle, 1931; Carter, 1935); (3) intestinal mucosa (inhalation through the mouth, expiration by the vent) in for the less some callichthyids (Carter and Beadle, 1931; Kramer and McLure, 1980) and, (4) probably buccal epithelium in aspredinids (Graham, 1997). Notice that in aspredinids, loricariids, astroblepids and callichthyids, air-filled cavities play another

role in buoyancy control (Gee, 1976). In clariids, the anterior and posterior dendritic organs are irrigated respectively by the 2nd and 4th afferent branchials and collected by the 2nd and 4th branchial efferents (for more details, see Nawar, 1955; Moussa, 1956). The efferent arteries of the air-breathing organs (Fig. 5.4) open into the dorsal aortic roots (schemas in Graham, 1997, fig. 4.2). In *Heteropneustes*, the saccate organ is fed by a branch of the 4th branchial afferent, just like the respiratory part of the digestive tract of loricariids. In the callichthyids *Hoplosternum littorale* and *Callichthys callichthys*, the blood is normally supplied to the intestine by the coeliac artery (Carter and Beadle, 1931).
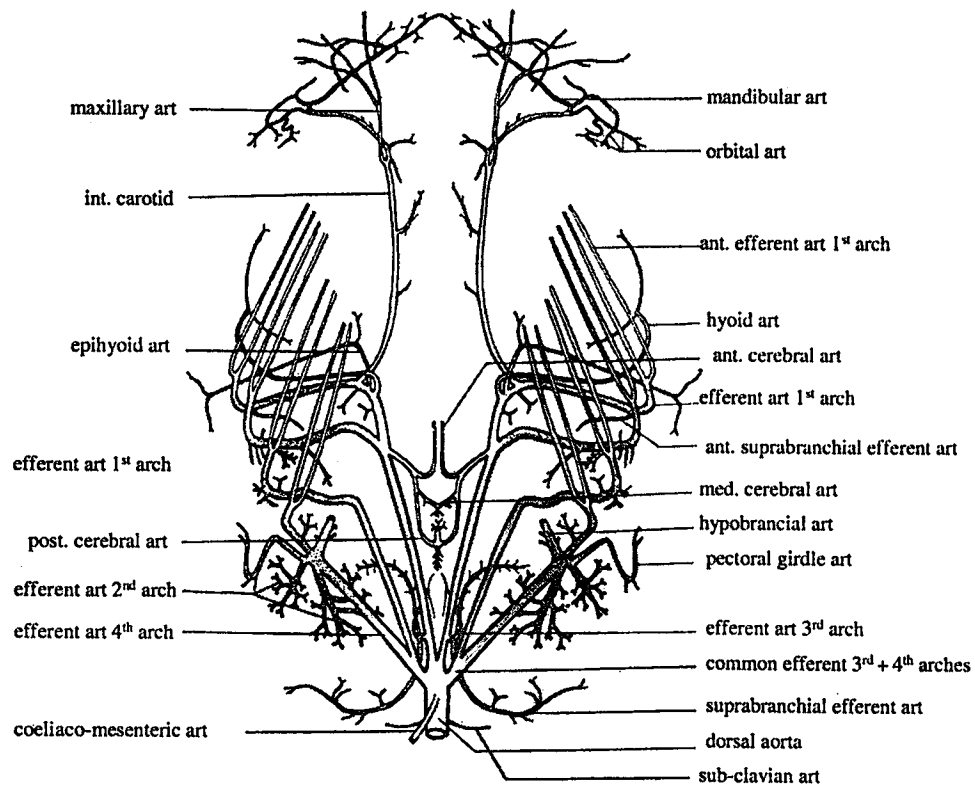

Fig. 5.4   *Clarias gariepinus*, efferent branchial arteries and head arteries (slightly modified from Nawar, 1955). Notice the numerous branches bringing the blood oxygenated in the suprabranchial organ to the last branchial arches. The name of some less important vessels is omitted.

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BRANCHIAL RESPIRATORY SYSTEM

Except in clariids (Fig. 5.4) and heteropneustids (modifications related to air-breathing), the branchial apparatus is classical. In air-breathing catfish, the total respiratory gills area is generally smaller; in clariids, the branchial surface (relative to weight) is smaller in *Clarias* species than in *Pinopterus* species (Graham, 1997).

It is possible, but not experimentally proved, that the gill lamellae perform aerial respiration in clariids (discussion in Graham, 1997: 113).

The branchial respiratory surface is linked to the oxygen content of the waters where the species usually dwell.

The branchial arches bear branchictenies (= gill rakers), whose size and number are related to the diet, as for example in the *Hemisynodontis* and *Brachysynodontis* species figured by Taverne and Aloulou-Triki (1974), in which they form a perfect filter.

DIGESTIVE SYSTEM

The present description is based on the anatomy of ictalurids (description by Grizzle and Rogers, 1974) which are generally omnivorous and opportunistic (Bruslé and Quignard, 2001) like many other catfishes, but various other diets occur in others paralleled by important variations of the digestive tract (Cleland, 1858; Chitray and Saxena, 1962; Taverne and Aloulou-Triki, 1974; Sinha, 1986a).

The mouth is terminal or slightly ventral, depending on the species. It is a broad slit between thick lips. These latter are transformed into a sucker in loricariids and amphiliids (Alexander, 1965).

The oropharyngeal region is divided into the oral cavity and the branchial region (pharynx sensu stricto); its epithelium is much like that of the skin, rich in taste buds, alarm substance cells (more abundant anteriorly) and mucous goblet cells that increase numerically rearward. The epithelium is thickened over the median parurohyal, suggesting a sort of tongue. The epithelium lining the opercular cavity, despite its epidermal origin, is similar, with few sensory receptors and goblet cells. The teeth are small and their shape various (Fig. 5.5): unicuspid, villiform to cardiform, polymorphic in individuals (see also Chitray and Saxena, 1962: fig. 8). They are borne by and incompletely ankylosed (some tooth movement or depression is possible thanks to an unmineralized collagen area at the base) to the premaxillae, dentaries and vomers, and on the left
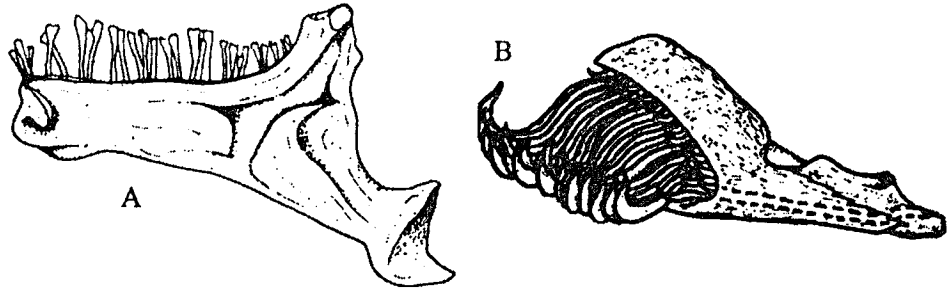
Fig. 5.5 **A.** *Trichomycterus dispar,* mesial view of the right hemimandibula, with spatulate teeth on the dentary. **B.** *Synodontis caudalis,* lateral view of the left mandible with falciform teeth (slightly modified from Taverne and Aloulou-Triki, 1974).
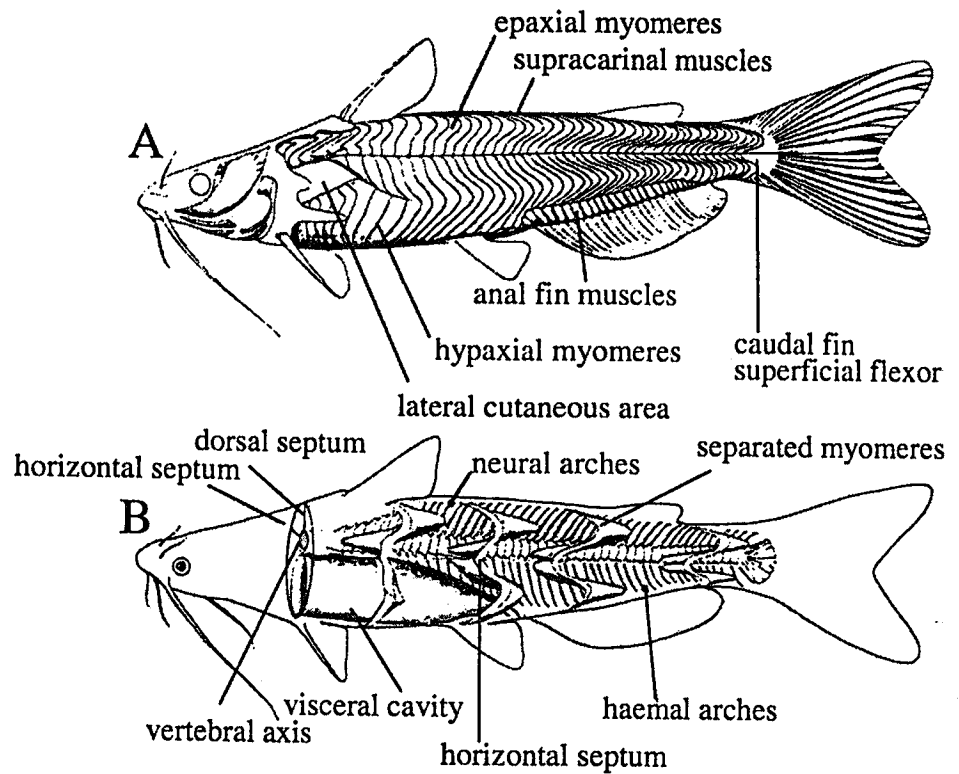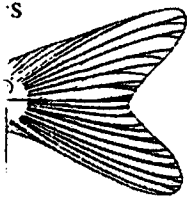

Fig. 5.6 *Ictalurus punctatus* (slightly modified from Grizzle and Rogers, 1976). **A.** Lateral view of segmented musculature of trunk. Notice the lateral cutaneous areas. **B.** Same view with two myomeres dissected.

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and right, upper and lower autogenous pharyngeal bones (Fig. 5.4) (all pharyngobranchial bones, except those of the first branchial arch: schemas in Taverne and Aloulou-Triki, 1974: figs. 7, 42). The epithelium of the branchial region is folded longitudinally. More teeth are found on the vomer (toothed plate) in many families (Chitray and Saxena, 1962; Mo, 1991) and on the maxillae in only two families, diplomystids (Arratia, 1987) and hypsidorids (Grande, 1987). Some genera are edentate, for example *Hypophthalmus* and *Cetopsis*. Vomerine teeth are molar-like in *Plotosus canius* (Sinha, 1986b). The branchial arches bear branchictenies, whose size and number are related to the diet, as for example in the *Hemisynodontis* and *Brachysynodontis* species figured by Taverne and Aloulou-Triki (1974), in which they form a perfect filter.

The pharynx leads to the esophagus through the anterior wall of the peritoneal cavity; the passage is not straightened (Figs. 5.1B, 5.4); it is marked by the apparition of four layers in the wall (tunica mucosa, tela submucosa, muscularis externa and the outer tunica serosa) and deep complicated longitudinal folds allowing expansion during swallowing (Grizzle and Rogers, 1976).

The morphology of the swim bladder (a gut diverticulum) is sophisticated, in relation to its several roles, not only in equilibration, but also in acoustical reception (Clarke et al., 1975; see also chapter on Weberian apparatus; Chardon et al., this volume). The pneumatic duct usually remains present, even in species with a reduced swim bladder, but not in loricariids (Bridge and Haddon, 1893; Chardon, 1968); it originates just before the slight constriction at the limit with the stomach.

The stomach is J-shaped; it divides into a thick-walled fundic region and a pyloric one with larger epithelial folds; it is saccate in *Clarias* and *Heterobranchus*. Gastric glands are present only in the pyloric region in which isolated goblet cells are sometimes observed. The muscularis sheet is particularly thick at the level of the pyloric sphincter. The shape and size of the stomach are variable, probably according to the diet (e.g. saccate in *Synodontis acanthomyas*: Taverne and Aloulou-Triki, 1974). Pyloric caeca were observed in the stomach of a *Malapterurus* by Cleland (1858).

The intestine (macroscopic figures of the internal wall are found in Chitray and Saxena, 1962) is longer, straighter than the stomach; its muscular tunica is thinner. The middle intestine appears not very different from the anterior one, except that its lumen is larger. True glands are absent in both. The rectal intestine is separated from the middle one by a thick powerful sphincter, its epithelium rich in goblet cells (Grizzle and Rogers, 1976).

In *Clarias mossambicus*, an omnivorous species feeding on small fish, zooplankton and plant material, protease activity is maximal in the stomach and anterior intestine, and amylase activity rather feeble and restricted to both anterior and posterior intestine (Cockson and Bourne, 1971). Comprehensive information on the alimentary canal and digestion in teleosts is available (Kapoor et al., 1975a)

The intestinal splanchnopleura is rich in lymphatic vessels (Krementz and Chapman, 1975); lymph hearts pumping lymph into veins are described for *Silurus* by Patt and Patt (1969). As mentioned earlier, a true lymphatic system is absent in fishes.

The liver (Fig. 5.1A, B) is large and occupies the space left in the peritoneal cavity under and posterior to the swim bladder. It is divided into anterior, appendicular and posterior lobes, the proportions of which differ among species. The gall bladder (Fig. 5.1A) hangs from the rear of the anterior lobe and opens into the bile duct ending in the duodenal region of the anterior intestine. There is no distinct pancreas in the mesentery.

KIDNEYS AND UROGENITAL SYSTEM

The following description is essentially based on Grizzle and Rogers (1976). The separate left and right head and trunk kidneys fuse on the mid line; the posterior cardinal vein runs from the trunk to the head parts (Fig. 5.1A). The kidneys are extraperitoneal but tend, however, to insinuate between the visceral cavity organs. The head kidney lies just behind the anterior fibrous wall of the visceral cavity.

The head kidney is merely an endocrine and haemopoietic organ; its excretory rudiments degenerate during development. The endocrine tissue is homologous to both the two components of the adrenal gland of mammals: two intermingled kinds of tissues, interrenal and chromaffin, secreting respectively adrenalin and noradrenalin, and controlling carbohydratres and protein metabolism regulation, regeneration and anti-inflammatory reactions.

The trunk kidney, essentially composed of nephrons (few segmental renal tubules undergo multiplication during development) and well-developed glomeruli, is collected by a pair of (opistho) nephric ducts fusing close to the urogenital cloaca. The urinary bladder (Fig. 5.1) opens next to the confluence of the ducts and extends somewhat anteriorly under the trunk kidney.

The gonads of *Ictalurus punctatus* are located posteriorly in the body cavity, just ventral to the trunk kidney and the swim bladder. Short ducts extend from their posterior end to the urogenital cloaca.

The testes consist of numerous digitate projections, more developed in the anterior region rich in seminiferous tubules performing spermatogenesis, contrary to the shorter distinguishable part, the role of which is unclear. Androgen secreting cells could not be located in the testes by Grizzle and Rogers (1976). Similar shape and divisions were described by Meisner et al. (2000: fig. 7) in the auchenipterid *Trachelyopterus lucenai*, an internal inseminator, in which the posterior part of the testes appears as a storage and secretory region for sperm, a sort of seminal vesicle. Other internal inseminators have been observed among auchenipterids and scolopacids (Loir et al., 1989).

Tubular ovaries are enclosed in a fibrous tunica albuginea more developed and rich in smooth muscle fibres in mature glands (Grizzle and Rogers, 1974; with details on histology and oogenesis). The short "oviducts" are genital funnels resulting from folding of the peritoneal wall and opening at the genital pore into the cloacal region.

SPLEEN

The disc-shaped spleen hangs in the mesentery between the fundic stomach and the swim bladder; it is attached to the hepatic portal vein (Grizzle and Rogers, 1976), as in other teleosts (Fig. 5.1A).

THYMUS

The very small thymus lies on the dorsal face of the posterior part of the pharynx.

TRUNK MUSCULATURE

The segmented trunk muscles are disposed in a normal teleostean way, with W-shaped myomeres whose cones become more and more acute posteriorly. Each myomere attaches on several successive vertebral arches (Fig. 5.6A, B).

Anteriorly, the hypaxial and epaxial musculature are separated by the symmetrical lateral bulging of the camera aerea Weberiana of the swim bladder. That area of the bladder lies directly under the skin and as termed the "lateral cutaneous area" (Fig. 5.6), it supposedly plays the role of a tympanum (see: Chardon et al., this volume).
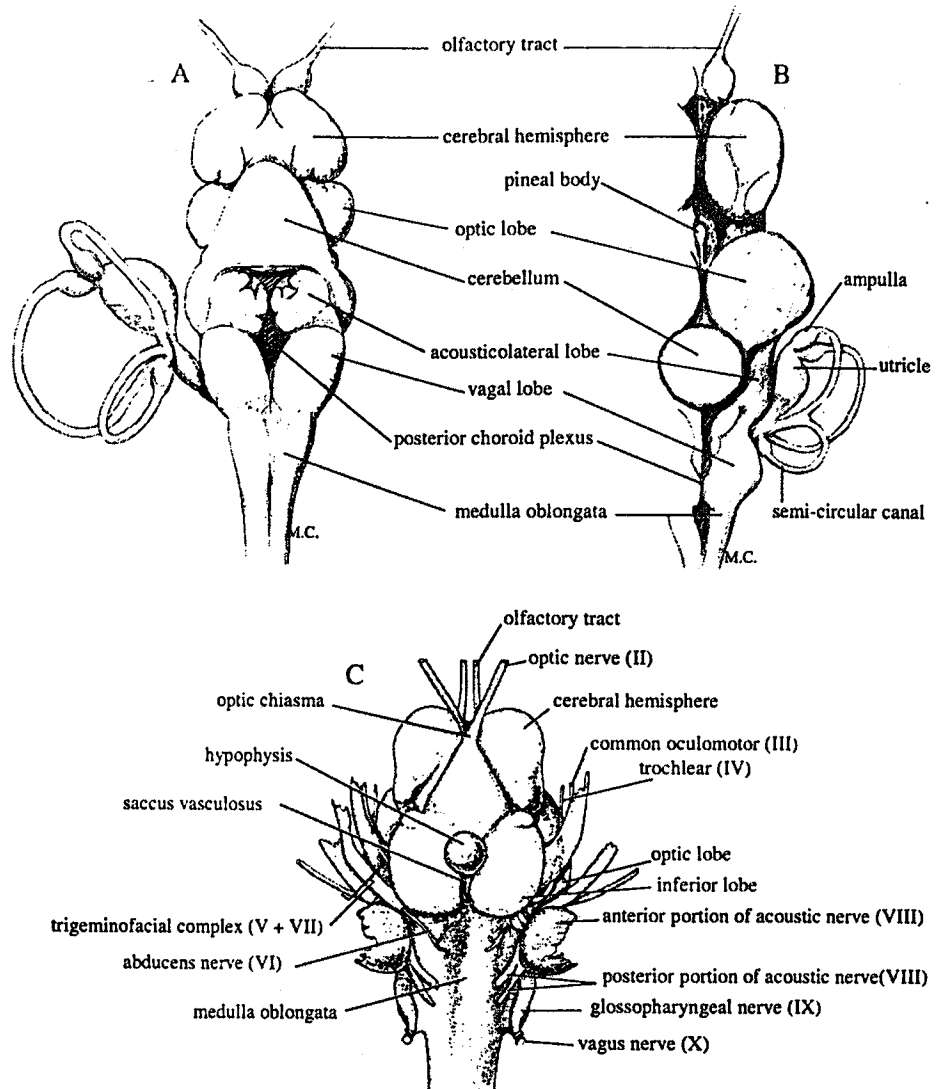
Fig. 5.7 **A.** *Callichthys asper*, dorsal view of brain and left labyrinth. Notice development of the acoustico-lateralis and vagal lobes. **B.** *Corydoras guyanensis.* dorsal view of right half of brain and right labyrinth. Notice the particularly small cerebellum and the relatively large optic lobes. **C.** *Ictalurus punctatus*, ventral view of brain and departure of cranial nerves [slightly modified from Chardon unpublished (A, B) and Grizzle and Rogers, 1976(C)].

ENDOCRINE ORGANS

Besides the interrenal and chromaffin tissues, the hypophysis (Fig. 5.7C), the pineal organ (Fig. 5.7B) described elsewhere, the gonads and the thymus, other endocrine organs are the thyroid, the ultimobranchial

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organs and the caudal neurosecretory system. The thyroid follicles are scattered along the ventral aorta and branchial afferent arteries. The very small paired ultimobranchial organs are situated in the membrane separating the pericardium from the peritoneal cavity. The caudal neurosecretory system consists of neurosecretory cells located in the very posterior spinal cord next to the ependymal canal with their axons extending into the urophysis (a highly vascularized posterior region of the medulla) (Grizzle and Rogers, 1976).

NERVOUS SYSTEM

The brain is fundamentally similar to that of other teleosts. As usual in fish, it does not occupy all the space available in the cavum cranii (Chardon, 1968: fig. 3). This is particulary the case in every species for older fishes whose brain grew with negative allometry. The median parts of the pars superior of the labyrinths are, however, pressed against the brain (Fig. 5.7A).

As is the case in teleosts in general (Kotrschal et al., 1998), the brain proportions seem to closely reflect catfish life style: usually life in shallow dark or muddy freshwaters, search for food (carnivorous, insectivorous, omnivorous, scavengers and other diets) with the gustatory and tactile barbels (Alexander, 1965), importance of audition (Weberian apparatus) and lateral line senses, and of electroreception (Bodznik, 1989). Despite a particularly dramatic variation in the proportions of the different nervous centers related to the wide variety of specializations (Fig. 5.7A, B) (important differences, even between two species of the same genus), the description of the brain of the channel catfish by Grizzle and Rogers (1976; including photographs and annotated transverse histological sections) fits for most catfishes (Fig. 5.7). It is supplemented by observations (including a few misinterpretations of the myelencephalic lobes) on representative species of numerous families by Chardon (1968) and unpublished obsevations of the same author.

Physiological roles are briefly given solely to indicate the size or surface-function relationship. Situation and size of the main brain centers is given in Tong and Finger (1983), Finger and Tong (1984) and New et al. (1998).

The olfactory lobes of the telencephalon are large and external swellings that suppose a complex functional specialization. The olfactory bulbs are adjacent to the nares and connected to the lobes by long
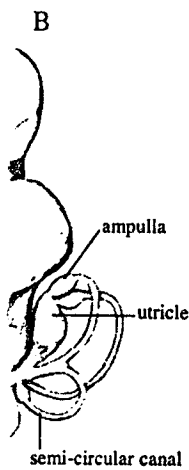
olfactory tracts. They consist in for the less two areas specialized in receiving sensory inputs of for the less two different classes of intermingled olfactory cells, one of which could detect foreign substances from circulation (Morita and Finger, 1998). The telencephalon also plays non-olfactory roles, such as indirect reception and integration of acoustico-laterales inputs, which explain its large size (Finger, 1980).

The pineal body (most often hidden under the anterior reflection of the cerebellum, Fig. 5.7A, B) contains mostly endocrine cells and few (photosensitive) sensory ones. The pituitary gland and the saccus vasculosus are rather small relative to most teleosts.

The most conspicuous specializations in catfish brain concern the development of large bulges along the dorsal somato- and viscero-sensory columns of neurons of the brain stem (Fig. 5.7).

The optic tectum receives most afferent fibres from the retinae (Northcutt and Wullimann, 1988); its two lobes are smaller than in diurnal teleosts. The optic lobes are still more dramatically reduced in blind cave catfishes, such as the ictalurids *Trogloglanis pattersoni* and *Satan eurystomus* described by Langecker and Longley (1993). A comparison of the brains of the Loricarioids *Astroblepus pholeter* (cave dwelling) and *A. grixalvii* (epigean) however shows that the optic lobes are almost equally developed in both species; the telencephalon on the other hand, is bigger in the epigean species (Chardon, 1968).

The cerebellum is large and, contrary to many other teleosts, is reflected forward and extends over the median part of the optic lobes (Fig. 5.7A), perhaps due to flattening of the anterior part of the head. It receives input from the acoustico-laterales nuclei (in the big latero-dorsal acoustico-laterales lobes) (Bleckmann and Bullock, 1989) of the medulla oblongata and from the labyrinths and lateral line directly. The cerebellum is also linked to electrosensitivity (Knudsen, 1977; Bleckmann and Bullock, 1989). A small tectum opticum associated with a large cerebellum is unexpected because of the close anatomo-functional relationship between those two centres; in several cyprinids investigated by Kotrschal (1991), the size of the two centres correlated. The well-developed (Grizzle and Rogers, 1976, Fig. 113) valvula cerebelli, possibly asssociated with taste, strongly projects rostrally into the mesencephalic ventricle. The cerebellum is particularly small in many loricarioids (Chardon, 1968).

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(connections and electrosensitive role observed by Knudsen, 1977; Bodznick, 1989), trigemino-facialis and vagal lobes (Kapoor et al., 1975b) (Fig. 5.7). The vagal lobes are particularly related to taste and the electrosensory lateral line and electrosensory lateral line (Tong and Finger, 1983). Their increase in surface probably represents a mapping similar to that in cyprinids (Finger, 1989). In benthic fishes, chemical (olfactory) perception is supplemented by taste buds which are in fact chemosensory and tactile (Kotrschal, 1991). Gustatory tracts in the brain were described for ictalurids by Herrick (1901).

Cranial nerves are classically distributed (Fig. 5.8) and the trigeminal is externally fused with the facialis on exiting the brain; the branches innervating the barbels and also the lateral line are particularly developed. (Reichel, 1927; Grizzle and Rogers, 1976; Davenport and Caprio, 1982; pers. obs. on *Synodontis, Clarias* and *Arius*). An independant terminal nerve was not observed.

The reader is referred to Nilsson and Holmgren (1993) and Donald (1998) for various aspects of the autonomic nervous system; specific information on the relationship between the coeliac ganglia and spinal and cranial nerves in *Ictalurus punctatus*) can be obtained from Goehler and Finger (1996: fig. 2).

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