REVIEW PAPER

Pelvic fins in teleosts: structure, function and evolution

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The pelvic fins of teleosts are paired appendages that are considered to be homologous to the hind limbs of tetrapods. Because they are less important for swimming, their morphology and function can be flexibly modified, and such modifications have probably facilitated the adaptations of teleosts to various environments. Recently, among these modifications, pelvic-fin loss has gained attention in evolutionary developmental biology. Pelvic-fin loss, however, has only been investigated in a few model species, and various biological aspects of pelvic fins in teleosts in general remain poorly understood. This review summarizes the current state of knowledge regarding pelvic fins, such as their structure, function and evolution, to elucidate their contribution to the considerable diversity of teleosts. This information could be invaluable for future investigations into various aspects of pelvic fins, which will provide clues to understanding the evolution, diversity and adaptations of teleosts.

INTRODUCTION

Since their emergence in the middle Devonian (Azuma et al., 2008), teleosts have successfully radiated into various aquatic environments, such as benthic, midwater and surface regions of marine and freshwater systems, and even near-water terrestrial regions. A vast number of extant teleost species (26,840; 49% of all vertebrates) are separated into 40 orders, 448 families and 4278 genera (Nelson, 2006). Teleosts exhibit a diversity of body forms, including various fin designs. Most fishes have two sets of paired fins, the pectoral and pelvic fins, and three median fins, the dorsal, anal and caudal fins. These fins play a dominant role in swimming performance, which can be crucial for survival.
Pectoral and pelvic fins are thought to be homologous with the fore and hind limbs of tetrapods, respectively. Tetrapods evolved from a fish-like ancestor through the lobe-finned fishes, and the evolution of their paired appendages has received considerable attention in evolutionary biology (Shubin et al., 1997, 2006; Ahlberg & Jonanson, 1998; Coates, 2003). This interest is due to the structural and functional difference between tetrapods and ray-finned fishes in their paired appendages, being considered one of the most important differences between the two groups (Coates, 2003; Boisvert, 2005). Recent investigations into the evolutionary, developmental and genetic aspects of pelvic fins have been conducted in only a few teleosts, such as the zebrafish Danio rerio (Hamilton), sticklebacks Gasterosteus aculeatus L. and medaka Oryzias latipes (Temminck & Schlegel) (Grandel & Schulte-Merker, 1998; Sakaguchi et al., 2006; Shapiro et al., 2006), as these fishes were found to be suitable experimental model organisms (Powers, 1989). Investigations of these fish models have contributed greatly to the understanding of various aspects of pelvic appendages in vertebrates (Sordino et al., 1995; Ruvinsky et al., 2000; Sakaguchi et al., 2006). In particular, gasterosteid studies have proven more advantageous than other model species for such studies because independent losses of pelvic fins have been found in multiple lineages, and even with individuals within a species (Nelson, 1971; Bell et al., 1993). Accordingly, gasterosteid studies have illustrated mechanisms of pelvic-fin development, loss and reduction in teleosts (McKinnon & Rundle, 2002; Shapiro et al., 2004; Bell et al., 2007; Cresko et al., 2007). The overall aspects of pelvic appendages in teleosts, however, have not attracted much interest, except for the aforementioned model species. This lack of interest is probably due to teleost pelvic fins appearing to be modest, inconspicuous and functionally unimportant, and teleosts are generally regarded as a lineage outside the mainstream of anthropocentric vertebrate evolution.

In this article, the structural, functional and evolutionary aspects of teleost pelvic appendages are reviewed. Their reductive evolution in particular is highlighted because this has been a recent central topic of interest for pelvic fins. In this review, the ordinal classification of teleosts follows Nelson (2006), and ordinal relationships follow a series of recent molecular studies based on whole mitochondrial genome (mitogenome) sequences (Miya et al., 2001, 2005; Inoue et al., 2003, 2004; Ishiguro et al., 2003; Kawahara et al., 2008; Lavoué et al., 2008) (Fig. 1), which presently provide the most reliable hypotheses on higher teleostean relationships. Orders that appear to be non-monophyletic, based on the mitogenome studies, are indicated by placing quotation marks about the name.

**ADVENT OF PELVIC FINS**

In vertebrates, paired appendages appeared in extinct jawless fishes, the anaspid fishes (Coates, 1994; Janvier, 1996) and the osteostracan fishes (Forey, 1995). Some dispute exists regarding the homology of anaspid paired fins with the pectoral fins of jawed vertebrates (Forey, 1995; Coates & Cohen, 1998). Extant jawless fishes lack paired fins and no traces of pelvic fins were found in extant or extinct jawless fishes (Goodrich, 1986; Forey, 1995; Coates & Cohen, 1998). Pelvic fins first appeared in the most primitive, extinct, jawed fishes, the placoderms (Goujet, 2001), and are usually retained in jawed vertebrates. Therefore, the origin of pelvic fins dates back to at least the appearance of jawed vertebrates, which occurred in the middle Cambrian,
Fig. 1. Phylogenetic relationships among teleostean orders based on a series of molecular phylogenetic analyses that used the whole mitogenome (Miya et al., 2001, 2005; Inoue et al., 2003, 2004; Ishiguro et al., 2003; Kawahara et al., 2008; Lavoué et al., 2008). The pelvic and pectoral fins are shown in red and blue, respectively. Orders that include fishes that have pelvic-fin spines are in boldface. Non-monophyletic orders, based on these molecular studies, are enclosed by quotation marks. The ordinal classification was based on Nelson (2006).
525 million years ago (Blair & Hedges, 2005). Since their emergence, pelvic fins have undergone various changes during the evolutionary history of vertebrates. In tetrapods, they changed drastically into the hind limbs, which are crucial for terrestrial locomotion. In contrast, they have been generally retained for swimming in most teleosts, although they vary in morphology and function and have probably been important for generating the diversity of teleosts.

PELVIC FIN STRUCTURE

The pelvic appendages of teleosts are characterized by distinctive fins, which are mainly composed of slender bony fin rays, a symmetrical pair of pelvic plates (also called pelvises or basipterygia) and a reduced number of radials (Stiassny & Moore, 1992; Coates & Cohen, 1998) (Fig. 2). These plates constitute the pelvic girdle, being bound or sometimes overlapped or sutured to the contralateral one (Stiassny & Moore, 1992) (Fig. 3). The pelvic fins are generally positioned abdominally in the ventral body wall in primitive teleost groups. In derived teleost groups, however, the pelvic fins have become located anteriorly, positioned thoracically or jugularly and are attached to the pectoral girdle, although many exceptions to this condition are known (Greenwood et al., 1966; Rosen, 1982) (Figs 1, 3 and 4).

Teleosts usually have six pelvic-fin muscles, three analogous muscles lying on each side of the pelvis (Winterbottom, 1974b). On the ventral side of the pelvis, the arrector ventralis pelvicus serves the ventrolateral half of the outer fin ray, and two muscles, the abductor superficialis pelvicus and the abductor profundus pelvicus, serve the other fin rays (Fig. 5). On the medial side, the arrector dorsalis pelvicus

![Fig. 2. Ventral views of pelvic girdles; anterior surfaces are located at the top. (a) A teleost (Botia) with fin rays and a splint in the left side removed. (b) A cartilaginous fish (Centroscyllium) with all of the elements on the right side and the fin rays on the left side removed. Radials are shaded. AB, anterior pelvic basal; BP, basipterygium; CB, intermediate segments of clasper base; PB, puboischiadic bar; PL, pelvises; RD, radials; SP, splint; SR, soft rays. Redrawn and modified with permission from Sawada (1982) and Shirai (1992); terminology follows those papers, respectively.](image-url)
serves the dorsolateral half of the outer fin ray, and the adductor superficialis pelvicus and the adductor profundus pelvicus serve the other fin rays (Fig. 5). Infracarinalis anterior is connected to the pelvic girdle and the cleithrum, and the infracarinalis medius is connected to the pelvic girdle and the first anal-fin pterygiophores (Fig. 5). The extensor proprius is often found on the dorsal side of the girdle and serves the innermost fin ray (Winterbottom, 1974b; Stiassny & Moore, 1992) (Fig. 5). Since the function of this muscle is to move the fish downwards, the absence of the extensor proprius might be correlated with a bottom-dwelling habit, or with fishes that lack a mechanism for maintaining neutral buoyancy (Stiassny & Moore, 1992). Pelvic-fin muscles are innervated by motor components of the spinal nerve through the third free vertebra (S3) and one or more posterior spinal nerves in teleosts; in some derived groups, they are also innervated by branches of S2 (Parenti & Song, 1996).

Several exceptional pelvic-fin structures have been reported. It is not uncommon for the two plates of the pelvic girdle to not contact each other, but in the melanostomiid genus _Bathophilus_, the pelvic girdle is widely separated with the pelvic fins placed dorsally (Fink, 1985) [Fig. 6(a)]. In balistoids (triggerfishes and filefishes), the pelvic elements are greatly reduced into an unpaired structure (Matsuura, 1979; Tyler, 1980) [Fig. 6(b)]. Triodontids have a simple pelvis without pelvic fins [Fig. 6(c)], and their pelvis has a suture in the midline (Tyler, 1980). Many fishes probably exhibit sexual dimorphisms in their pelvic fins; some sexual dimorphisms have been reported, usually involving fin length or colouration, such as in the ariid catfishes, cods, darters and tilapias (Schenck & Whiteside, 1977; Barbieri et al., 1992; Oliveira

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Fig. 3. Ventral (top) and lateral (bottom) views of pelvic plates, with associated structures (bottom) in a basal eurypterygian (_Lampanyctus_) (a), an atherinomorph (top: _Teramulus_; bottom: _Rheocles_) (b) and a percomorph (_Morone_) (c). Cartilage and ligament are shown in grey and black, respectively. AP, anterior process; CL, cleithrum; CO, coracoid; EDW, external dorsal wing; EVW, external ventral wing; IW, internal wing; MP, median process; PC, postcleithrum; PCL, postcleithrum ligament; PP, posterior process; R, rib; VW, ventral wing. Redrawn with permission from Stiassny & Moore (1992).
Fig. 4. Diagrammatic representations of pelvic and pectoral-fin positions and pelvic spination in (a) non-eurypterygians (primitive), (b) basal eurypterygians (intermediate) and (c) acanthopterygians (derived). The pelvic and pectoral fins, and pelvic-fin spines are shown in red, blue and green, respectively.

& Almada, 1995; Skjæraasen et al., 2006). More remarkable examples of sexual dimorphisms were reported in the cyprinid *Paedocypris* and the atheriniform phallostethids. In *Paedocypris*, males have enlarged and modified first pelvic-fin rays and associated hypertrophied arrector and abductor muscles, whereas females have a greatly reduced pelvic girdle and muscles (Britz & Conway, 2009). Male phallostethid fishes have an asymmetric priapium modified from the pelvic fins and a part of the shoulder girdle under either side of the head [Fig. 6(d)], whereas females have vestigial or no pelvic fins (Parenti, 1986, 1989).

Pelvic fins are paired appendages, usually exhibiting bilaterally symmetric structures in teleosts. Asymmetric pelvic-fin structures, however, are found in some fishes, especially in many groups of pleuronectiforms. For example, in achirid soles, the right pelvic fin is confluent with the anal fin, and some cynoglossid tonguefishes lack a pelvic fin and girdle on the eyed side (Nelson, 2006). Some gasterosteoid species show reductive trends in their pelvic fins and girdle, even within species, and asymmetric reductions range from the lack of a spine or soft rays on one side (either side) to complete loss (Nelson, 1971; Reimchen, 1980; Bell et al., 1985) (Fig. 7).

The examples given above show that pelvic fins have been subject to various modifications and reductions, even to complete loss. Such modifications include functional changes, that is, they are not used for swimming but for other purposes, such as adhesive sucking disks for grasping, wings for flight and brood pouches. Considering this array of pelvic-fin diversification, the functional diversity of pelvic fins in teleosts will be discussed in the following section.
Fig. 5. Musculature of the pelvic girdle in a hypothetical teleost. Ventral (a) and dorsal (b) views of the pelvic-fin muscles (anterior to the top). Left abductor superficialis pelvicus, adductor superficialis pelvicus, arrector ventralis pelvicus, extensor proprius, infracarinalis anterius and infracarinalis medius removed. ABSP, abductor superficialis pelvicus (red); ABPP, abductor dorsalis pelvicus (orange); ADPP, adductor profundus pelvicus (light blue); ADSP, adductor superficialis pelvicus (blue); ARRDP, arrector dorsalis pelvicus (green); ARRVP, arrector ventralis pelvicus (yellow); EXTP, extensor proprius (purple); ICARA, infracarinalis anterior (light grey); ICARM, infracarinalis medius (dark grey). A tendon is shown in black. Redrawn and modified with permission from Winterbottom (1974).

PELVIC FIN FUNCTION

During swimming, pelvic fins are thought to be held fairly still, acting as static trimming foils rather than dynamic moving structures (Harris, 1937, 1938), while the dominant propulsion is usually generated by the body and caudal-fin (Gosline, 1971; Webb, 1982). Propulsion by the body and caudal fin appears to be a common feature throughout the evolution of fish, and this propulsion system has been retained in almost all groups (Gosline, 1971; Webb, 1982). In contrast, median and paired-fin propulsion is used for slow swimming and during precise manoeuvres (Gosline, 1980). Compared to sharks and rays, bony fishes generally have a swimbladder, which reduces the effort required from fins when moving the body vertically. Additionally, slow swimming using non-caudal propulsion probably occurred in the common ancestor of neopterygians (Webb, 1982). In primitive teleost groups, the pelvic fins are positioned posteriorly on the trunk and are capable of producing depressing and elevating forces, although they are not as functionally important for swimming as in more derived teleost groups, where they are located thoracically (Harris, 1938). Positional transformations of the pelvic fins have given fish the ability to brake and slow down efficiently during swimming, using their pelvic fins in combination with their pectoral fins, which can be likened to a four-wheel braking system (Harris, 1953). Also, fish that have thoracic pelvic fins can efficiently maintain a
Figs. 6. Unusual pelvic fins in teleosts: (a) pelvic-fin on the dorsal side in a melanostomiid Bathophilus; (b) rudimentary and unpaired pelvic complex in a balistoid; (c) pelvis without pelvic fins in Triodon; (d) priapium highly modified from the pelvic fins and a part of the pectoral girdle in a male phallostethid. —, pelvic elements; ---, internal structures. Modified structures of pelvic fins in a phallostethid are shaded.

stationary position in the water by fanning their pelvic and pectoral fins (Harris, 1937, 1938; Gosline, 1971). In deeper-bodied fishes, paired fins are used more for high-speed swimming (Schrank et al., 1999; Webb & Fairchild, 2001). The pelvic fins, however, are considered to be the least important among fish fins because they have been frequently lost during evolution, and the amputation of pelvic fins does not change body motion during swimming (Harris, 1938; Gosline, 1971; Standen, 2008). In the mean time, although only a few studies have examined the pelvic fins of fishes (Lauder & Drucker, 2004), a recent study has suggested that pelvic fins probably play a more complex role in swimming than was previously thought, such as complex three-dimensional motion during slow-speed steady swimming and

Fig. 7. Variation in pelvic skeletal elements in the three-spined stickleback Gasterosteus aculeatus: (a) intact pelvic spines and girdle, (b) asymmetric reduction and (c) complete loss of the pelvic spines. Complete loss of the pelvis is found in some individuals (data not shown). Redrawn with permission from Reimchen (1980).
manoeuvres, moving actively against imposed hydrodynamic loads, and producing powered correction forces during steady swimming and trim correction forces during manoeuvres (Standen, 2008).

Cases exist, however, in which pelvic fins are used for different kinds of locomotion, apart from swimming. Some fish groups move as if they walk over aquatic and terrestrial substrata with their pelvic fins (Peters, 1985; Webb, 1996). Walking locomotion on aquatic substrata is fundamentally different from swimming because the fish must maintain contact with the substratum for locomotion (Martinez, 1996). Congiopodids show a primitive walking locomotion involving alternating support between the right pectoral and left pelvic fin, and then the left pectoral and right pelvic fin, in which the movements of the fins are not synchronized (Andriyashev, 1994). As an example of more advanced walking locomotion, frogfishes use their paired pectoral and pelvic fins, which are fleshy and outwardly resemble tetrapod limbs, to traverse the substrate in a manner analogous to the movements of tetrapods, albeit at extremely slow speeds (Pietsch & Grobecker, 1987; Edwards, 1989) [Fig. 8(a)]. The greater part of the propulsive force is created by cyclic movements of the pectoral fins, whereas the pelvic fins create only a minor propulsive force, functioning primarily as a third support point for the body (Pietsch & Grobecker, 1987) [Fig. 8(a)]. In contrast, mudskippers are amphibious fishes that perform terrestrial locomotion, crutching, in which they move forward by swinging their pectoral and pelvic fins in turns (Harris, 1960) [Fig. 8(b)]. During terrestrial locomotion, body mass is transmitted from the pelvic to the pectoral bones, and the pelvic-fin rays are usually modified, becoming short and stiffer to provide support while out of the water (Harris, 1960). The primary propulsive force during walking locomotion, however, often comes from the caudal and pectoral fins; the pelvic fins are only used to lift or raise the body, thereby facilitating walking in some terrestrial or benthic fishes such as blenniids, clindis and searobins (Graham, 1970; Zander, 1972, 1983; Jamon et al., 2007). Furthermore, in climbing perches, the pelvic fins do not contribute significantly to forward propulsion because they do not appear to be involved in terrestrial locomotion (Davenport & Abdulmatin, 1990).

Several families of teleosts can fly, and flight probably developed as a means of escaping from predators (Davenport, 1994). In many of these species (e.g. a freshwater butterflyfish, hatchetfishes, one or two species of halfbeaks and some flyingfishes), only the pectoral fins, and not the pelvic fins, are involved in flight (two-wingers) (Davenport, 1994). Other flyingfishes, however, have hypertrophied both the pelvic and pectoral fins for flight (four-wingers) (Davenport, 1992), and the hypertrophied pelvic fins make it possible to be scaled up to greater body size than two-wingers by having the centres of mass further behind the centre of pressure of the wings (Davenport, 2003). Also, they function as tailplanes or pitching stabilizers and promote autostability at greater body size (Davenport, 1994).

Many cases exist in which the pelvic fins are not used for any kind of locomotion. When the pelvic fins are retained through natural selection, they have probably acquired other functions. For example, in many fishes, the pelvic fins can probably be used to maintain a stationary position when the body is in contact with the substratum for resting or alerting. Ipnopid fishes, which inhabit benthic regions in the deep sea, have greatly elongated pelvic and caudal-fin rays, which allow them to sit above the sea floor (Johnson & Eschmeyer, 1998). The pelvic fins of some fish groups that primarily inhabit shallow fresh water or tidal habitats have been
modified to help the fishes hold still by adhering to hard substrates (Sayer, 2005). Many gobioiids have fused pelvic fins that have become modified into a sucking pad or disc, allowing them to hold position in fast-flowing water, even in hill streams or vertical waterfall beds (Blob et al., 2006; Helfman et al., 2009) (Fig. 9). Such sucking discs or pads, which have been modified from the pelvic fins, have occurred independently in snailfishes, lumpfishes and clingfishes. In lumpfishes, sucking action is initiated by the contraction of a pair of red muscles running between the sucker

Fig. 8. Pelvic and pectoral-fin movements during locomotion in (a) a frogfish and (b) a mudskipper. Time lapse from the top frame is indicated by \( t \) for each frame. Redrawn with permission from Pietsch & Grobecker (1987) and Harris (1960).
skeleton and the hyoid arch, and mucus and several pairs of white muscles running between pelvic fins and girdle help the suction (Davenport & Thorsteinsson, 1990). Some hill-stream ostariophysan fishes, such as some cyprinids, homalopterine and gastromyzontine loaches, and sisorid and loricariid catfishes, have independently evolved sucking pads or adhesive organs, modifying pelvic-fin rays that are located posteriorly on the body. These structures serve as friction devices and facilitate station holding in flowing water, along with other adhesive organs, such as the mouth, the pectoral fins or the ventral surface of the body (Saxena & Chandy, 1966; Roberts, 1982; Sawada, 1982; Das & Nag, 2004; Beamish et al., 2008; Schaefer & Provenzano, 2008). As adaptations to perch habitats in mountain streams, homalopterine loaches and sisorids, Pseudecheneis, have developed enlarged pelvic girdles and well-developed pelvic muscles; in Pseudecheneis, the pelvic girdle reaches the coracoids of the pectoral girdle (Saxena & Chandy, 1966; Sawada, 1982). Additionally, the cyprinids Garra and Psilorhynchus and the sisorids Glyptothorax and Pseudecheneis have independently generated a new muscle, the pars retractor ischii in obliquues inferioris (mesioventralis) (Saxena & Chandy, 1966).

Spination of the pelvic fins, as well as the median fins, is one of the most remarkable features in acanthopterygians, and pelvic-fin spination is considered to serve as a defence measure for the abdomen, which appears to be the most vulnerable area in many fishes (Gosline, 1971). Some groups have developed only an enlarged spine instead of fin rays and membranes in the pelvic fin, which appear to barely produce propulsion (e.g. gasterosteid, triacanthids, triacanthodids and monocentrids). These pelvic-fin spines can often be erected and locked to avoid being depressed by predators (Tyler, 1962; FitzGerald & Wootton, 1986; Moore, 1993). As an example of a more advanced defence, many scorpaenoids (rockfishes, stonefishes, lionfishes and velvetfishes), scats, rabbitfishes and surgeonfishes have developed venom glands that are associated with the pelvic-fin spines, while venom glands are usually accompanied by other spines, such as dorsal (the most common) and anal.

Fig. 9. Lateral views of teleosts having adhesive organs modified from the pelvic fins: (a) a snailfish (Liparis), (b) a clingfish (Aspasma), (c) a goby (Acanthogobius) and (d) a gastromyzontine loach (Gastromyzon). The pelvic-fin elements are shown in red and ventral views of adhesive organs are shown below.
spines, or spines around the head (Halstead, 1971, 1988; Church & Hodgson, 2002; Smith & Wheeler, 2006; Sivan et al., 2007).

Pelvic fins have rarely been modified into organs for reproduction. Male phallostethids have a priapium that is bizarrely modified from pelvic-fin rays and the shoulder girdle. This priapium is an elaborate copulatory organ located under either side of the head [Fig. 6(d)], and, although individuals have vestigial or no pelvic fins, bilateral asymmetry is not exhibited in most females (Parenti, 1986, 1989). The priapium has an external bone, which the male uses to clasp the female during copulation, and a fleshy seminal papilla, which is used to transfer sperm to the female reproductive tract (Grier & Parenti, 1994). In contrast, ghost pipefishes have enlarged pelvic fins and females hold their eggs in a brood pouch formed from fused pelvic fins, unlike syngnathid pipefishes, which have no pelvic fins and in which most of the parental duties are left to the males (Wetzel et al., 1997). The embryos of ghost pipefishes are enclosed in egg envelopes, which are attached to the cotylephores, a female-specific epithelial cellular outgrowth on the inside surface of the pelvic fins found only in brooding females (Wetzel & Wourms, 1995).

Various uses of pelvic fins to support different kinds of behaviour are reported in many fish groups. For example, the anglerfish Lophius piscatorius L. has been observed using its pelvic fins for digging, creating recesses in the seafloor for concealment. While digging, the pectoral fins simultaneously scoop up sediments, and the anal and caudal fins scrape sediments (Laurenson et al., 2004). In the orange chromide Etpolus maculatus (Bloch), the pelvic fins are used for courtship, spawning and communicating with their young through a flickering behaviour (Cole & Ward, 1969; Baldaccini, 1973; Ostrander & Ward, 1985). Balistoids use their rudimentary and unpaired pelvic complex [Fig. 6(b)] for a vibrating behaviour during aggressive and courtship displays, in which fishes expand their ventral flap (including the pelvic complex) and vibrate their first dorsal spine (Kawase & Nakazono, 1994; Kawase, 1998, 2005). Various kinds of additional fish behaviours that involve pelvic fins have been reported (Arnold, 1969; Rubenstein, 1981; Coyer, 1982; Andrade & Abe, 1997; Gerstner, 2007). Note that the same behaviour, however, is not always equivalent in different situations or in different fish groups (Simpson, 1968; Tricas et al., 2006).

The rockling Ciliata mustela (L.) has solitary chemoreceptor cells on its pelvic fins as well as on its chin barbel, anterior dorsal fin and dorsal trunk skin (Bardach & Atema, 1971). The cells on the pelvic and pectoral fins are particularly sensitive to a wide, feeding-related stimulus spectrum, including animal extracts and amino acids, whereas those on the dorsal fins are particularly sensitive to the body mucus of non-congeners (Peters et al., 1991). Although few studies have reported on sensory functions of pelvic fins, it might be possible that pelvic fins have some kind of sensory function in other teleosts. In this section, various functional acquisitions of teleost pelvic fins are described, but many others likely remain unknown.

PELVIC FIN EVOLUTION

Evolutionary changes in the positions of paired fins and the spination of the pelvic fins are usually considered to correlate with the higher evolutionary relationships of teleosts (Greenwood et al., 1966; Rosen, 1982) (Figs 1, 3 and 4). In primitive
teleosts, the pelvic girdle is generally positioned abdominally and is free-floating in the ventral body musculature, being only loosely attached to the tips of the ribs by myoseptal connective tissue strands (Stiassny & Moore, 1992) [Fig. 3(a)]. In more derived groups, the pelvic fins and girdle have migrated anteriorly to the thoracic or jugular position, with ligamentary attachment to the pectoral girdle (Stiassny & Moore, 1992; Johnson & Patterson, 1993) [Fig. 3(c)]. Most non-eurypterygian fishes exhibit the primitive condition when pelvic fins are present. An osteoglossiform, *Pantodon buchholzi* Peters, however, has pelvic fins that are located under the pectoral fins, similar to the arrangement in derived teleosts (Fig. 4). Basal members of the eurypterygian fishes begin to show anterior migration of the pelvic fins to the subthoracic area, together with dorsal migration of the pectoral fins (Rosen, 1973). Aulopiformes, the basal-most member of the Eurypterygii, includes species in which pelvic fins exhibit anterior migrations (Alepisauroidae and Giganturoidei) and species that do not (Chlorophaulacoidei and Synodontioidei) (Sato & Nakabo, 2002) (Fig. 4). In the mean time, ateleopodiforms, a basal member of the Eurypterygii, have thread-like pelvic fins with a largely cartilaginous girdle in most species (Sasaki *et al.*, 2006), which is located anterior to and below the pectoral-fin base (Fig. 4). All myctophiforms, a group that is more derived than the Aulopiformes and the Ateleopodiformes, have pelvic fins in the abdominal position (Paxton, 1972; Sato & Nakabo, 2002) (Fig. 4). Moreover, the pelvic fins of lampridiforms are usually inserted abdominally or thoracically, with ligamentary connections to the postcleithrum (Stiassny & Moore, 1992), although the connections in radiicephalids are more abdominal (Oelschläger, 1983). Acanthomorpha is the sister group of these two orders; members of this group generally show thoracic or jugular pelvic-fin positions with ligamentary connections to the postcleithrum, and the girdle is usually more elaborated, with bony expansions of the median processes forming an overlapping connection or a suture between the two sides (Stiassny & Moore, 1992) (Figs 1, 3 and 4). Furthermore, the anterior and posterior infracarinalis have no tendinous connections in most acanthomorph fishes (character 1 in Tables I and II) (Johnson & Patterson, 1993). Besides the lack of connections, acanthopterygian fishes are assumed to have developed spination in the pelvic fins and tend to have reduced the number of pelvic-fin soft rays (*e.g.* five soft rays with one spine in ordinary percomorph fishes; character 8 in Tables I and II) (Rosen, 1973; Stiassny & Moore, 1992; Johnson & Patterson, 1993). Non-acanthopterygian fishes, such as siluriforms, notacanthids, polymixiids and zeiforms, have a pair of pelvic-fin spines (or more than one in notacanthids) that are structurally different from those in acanthopterygians (Stiassny & Moore, 1992; Johnson & Patterson, 1993; Nelson, 2006). Johnson & Patterson (1993) suggested that pelvic-fin spines in ‘Stephanoberyciformes’ also differ from those in other acanthopterygians because they have a broadly open symmetrical base that grasps the unmodified cartilaginous margin of the pelvic girdle, as in the zeiforms. Parenti & Song (1996) suggested that the innervation patterns of the pelvic-fin muscles may correlate with phylogenetic positions among teleosts. They thought that the innervation of the pelvic-fin muscles by the motor component of S3 or one or more posterior spinal nerves is plesiomorphic, and that additional innervations by the S2 branches are apomorphic. Despite variation in the ultimate position of the pelvic fins in adults (even thoracic or jugular), non-acanthopterygians consistently have the plesiomorphic condition. Many acanthopterygians have the apomorphic condition,
Table I. List of morphological characters related to the pelvic fins and girdle used for phylogenetic studies. Four characters among the eight of Stiassny & Moore (1992) were listed in Johnson & Patterson (1993) and Wiley et al. (2000). See Fig. 3 for characters on the pelvic girdle.

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<td>1. Infraclinalis muscles joined (0) or separate (1)</td>
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<td>2. Median pelvic process ends in cartilage (0) or ends in bone (1)</td>
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<td>3. Posterior pelvic process ends in cartilage (0) or ends in bone (1)</td>
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<td>4. Pelvic-fin spine absent (0), present with a symmetrical base (1) or present with a complex base (2)</td>
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<td>5. Pelvic radials in a continuous row (0), or either in a discontinuous row or absent (1)</td>
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<td>6. Anteromedial process of pelvic bone absent (0) or present (1)</td>
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<td>7. No ligament from shaft of postcleithrum to posterolateral corner of pelvic girdle (0), ligament present (1) or girdle secondarily displaced posteriorly (2)</td>
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<tr>
<td>8. Pelvic fins with seven or more rays (0), or with six or fewer rays (1)</td>
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<tr>
<td>9. One or more free pelvic radials (0), or no free pelvic radials (1)</td>
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<tr>
<td>10. Pelvic bones loosely attached or overlapping medially (0), with broad median contact (1) or sutured (2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. No discrete anterior pelvic processes (0), anterior pelvic processes present in plane of body wall (1) and anterior pelvic processes present and ventrally displaced (2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. No association of pelvic girdle with the cleithrum or coracoid (0), pelvic girdle directly or ligamentously attached to the cleithrum or coracoid (1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13. No ligamentous association between contralateral pelvic finbases (0), inter-pelvic ligament present (1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14. External ventral and external dorsal wings of unequal size, internal wings not strongly peaked (0), external ventral and external dorsal wings of equal size, internal wings not strongly peaked (1)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Although atherinomorphs, ‘Stephanoberyciformes’, ‘Gasterosteiformes’ and Batracoidiformes have the plesiomorphic condition (Parenti & Song, 1996). Concurrently, the radials of the pelvic fins show a reductive trend among teleosts (Johnson, 1992; Johnson & Patterson, 1993). Three or four autogenous radials are usually found in non-eurypterygian teleosts, but the medial radial is fused to the ventral half of the medial-fin ray in eurypterygian fishes, and the two remaining radials are reduced to being cartilaginous, or are absent, in more derived groups such as the acanthopterygians (characters 5 and 9 in Tables I and II) (Gosline, 1961; Johnson, 1992; Johnson & Patterson, 1993). Johnson & Patterson (1993) proposed that the absence of free pelvic radials is synapomorphic to percomorph fishes (character 9 in Table I and II). Considering the phylogenetic structures in Fig. 1, however, the transformations of all of the characters mentioned in this section from the plesiomorphic to the apomorphic condition, and vice versa, must have occurred during multiple independent events.

Variations in pelvic-fin and pelvic girdle morphology were incorporated as markers in some large-scale phylogenetic analyses of higher teleosts (Johnson, 1992; Stiassny & Moore, 1992; Johnson & Patterson, 1993; Wiley et al., 2000). Despite
Table II. Character matrix used in analyses of Johnson & Patterson (1993), Wiley et al. (2000) and Stiassny and Moore (1992), with taxa arranged in the phylogenetic structure of Fig. 1. Characters and character states are shown in Table I; non-monophyletic orders, based on molecular studies, are enclosed by quotation marks.

<table>
<thead>
<tr>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 2. 3. 4. 5. 6. 7. 8. 9. 10. 11. 12. 13. 14.</td>
</tr>
<tr>
<td>Eurypterygii</td>
</tr>
<tr>
<td>Aulopiformes 0 0 0 0 0 0 0 0 ? ? ? ?</td>
</tr>
<tr>
<td>Ctenosquamata</td>
</tr>
<tr>
<td>Myctophiformes 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>Lampriformes 1 1 0 0 0/1 0 0 0 1 1 0 1 1 0</td>
</tr>
<tr>
<td>Acanthomorpha</td>
</tr>
<tr>
<td>Paracanthopterygii</td>
</tr>
<tr>
<td>Polymixiiformes 1 1 1 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>Percopsiformes 1 1 1 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>Gadiformes 1 0 0 0 1 0 0 0/1 1 0 ? ? ? ?</td>
</tr>
<tr>
<td>Zeiformes 1 1 1 0/1 1 0 0 0/1 0/1 0/1 0 1 1 0</td>
</tr>
<tr>
<td>Acanthopterygii</td>
</tr>
<tr>
<td>Berycomorpha</td>
</tr>
<tr>
<td>‘Stephanoberyciformes’ 1 0/1 0/1 0/1 1 0/1 1 0/1 0 0 2 1 0 0</td>
</tr>
<tr>
<td>‘Beryciformes’ 1 1 1 2 1 1 1 1 0 0 0/2 2 1 0/1 0</td>
</tr>
<tr>
<td>Percomorpha</td>
</tr>
<tr>
<td>‘Non-Atherinomorpha’ 1 1 1 0/2 1 0/1 2 1 1 1 1 0 0 0</td>
</tr>
<tr>
<td>Atherinomorpha 1 1 1 0/1/2 0/1 0/1 0/1/2/3 0/1 0/1 0/2 2 1 1 1</td>
</tr>
</tbody>
</table>

these efforts, the resulting phylogenies differed somewhat from one another (Fig. 10) as well from those based on molecular markers (Fig. 1). Wiley et al. (2000) added the morphological characters from Johnson & Patterson’s (1993) large-scale phylogenetic analyses into their molecular phylogenetic analysis that used the 12S and 28S rRNA gene sequences. In total, 14 characters that were based solely on pelvic anatomy were used in these studies (Tables I and II; taxa arrangement follows Fig. 1). Although these 14 characters suggested evolutionary trends in pelvic fins and girdles, all characters required parallel changes or reversals when mapped onto the phylogenetic tree, indicating that they do not reflect real phylogeny. Therefore, phylogenetic trees based on these characters show considerable differences from trees constructed from molecular analyses (Fig. 10).

Several examples exist in which molecular phylogenetic results disagree with the evolutionary trends in pelvic fin and pelvic girdle changes. The monophyly and phylogenetic placement of the berycomorph orders ‘Stephanoberyciformes’ and ‘Beryciformes’ are controversial, and their classification was subject to revision (Greenwood et al., 1966; Stiassny & Moore, 1992; Johnson & Patterson, 1993; Moore, 1993; Colgan et al., 2000). Based on anatomy, including the pelvic fins and girdle, ‘Stephanoberyciformes’ show plesiomorphic state characters (e.g. no ligament from the postcleithrum to the pelvic girdle; see Tables I and II); they were therefore placed in a more primitive position (Johnson & Patterson, 1993) (Fig. 10). Conversely beryciform holocentrids were regarded as being closely related to the Percomorpha instead of other ‘Berycomorphes’ (e.g. pelvic girdle halves
Fig. 10. Phylogenetic hypotheses regarding higher teleostean orders based on morphological characters. Phylogenetic trees of (a) Stiassny & Moore (1992) using eight characters of the pelvic fins and girdle and (b) Johnson & Patterson (1993) using 39 characters, including 10 characters related to the pelvic fins and girdle (Tables I and II). ‘Smegmamorpha’ was proposed by Johnson & Patterson (1993) and contains Synbranchiformes, Mugiliformes, ‘Gasterosteiformes’, Atherinomorpha and Elassoma. Classification of teleostean orders follows Nelson (2006). Non-monophyletic orders, based on molecular studies, are enclosed by quotation marks.

sutured with ligamentary association only in holocentrids and percomorphs, character 7 in Tables I and II; Fig. 10) (Stiassny & Moore, 1992). Phylogenetic analysis using whole mitogenome sequences, however, revealed that these two orders were joined together to form the Berycomorpha, with members being nested within each other (Miya et al., 2005) (Fig. 1). Therefore, these character variations occurred independently within the berycomorphs. In the mean time, Atherinomorpha was formerly regarded as a sister group of Percomorpha, and abdominally positioned pelvic fins and the lack of a pelvic spine were found in many species, traits that were considered to be pre-percomorph morphologies (Rosen, 1973) (Figs 1, 3 and 4). In addition, in atherinomorph fishes, the pelvic girdle shows some primitive conditions [e.g. no ligamentary connection to the postcleithrum, but to the second, third, fourth or fifth rib instead, unlike most other acanthopterygians, see Fig. 3(b) and Tables I and II] (Stiassny & Moore, 1992; Parenti, 1993). Recent morphological and molecular studies, however, have revealed that atherinomorphs share some synapomorphies with the percomorphs and should be included among them (Johnson & Patterson, 1993; Miya et al., 2003, 2005; Setiamarga et al., 2008). These facts show that the evolution of the pelvic fins and girdle has not been simple and cannot be explained without reversals or parallel evolution. Therefore, although a few evolutionary trends exist, the pelvic fins are greatly changeable and many characters related to the pelvic fins and girdle seem to have been generated or lost multiple times, independently, throughout the evolution of teleosts.

**REDUCTIVE EVOLUTION**

Among the major fish fins, the pelvic fins are considered to be, functionally, the least important for swimming (Gosline, 1971), and thus they have been subject to various extreme modifications (often for functions other than locomotion), reductions and even complete loss during the evolution of teleosts. Fishes that have lost
Table III. Teleostean families, including fishes lacking pelvic fins. Bold entries indicate a family or an order in which all members lack pelvic fins. The number of families in an order is indicated in parentheses when all families lack pelvic fins; non-monophyletic orders, based on molecular studies, are enclosed by quotation marks.

<table>
<thead>
<tr>
<th>Order</th>
<th>Families</th>
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<tbody>
<tr>
<td>Osteoglossiformes</td>
<td>‘Stephanoberyciformes’</td>
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<tr>
<td>Osteoglossidae</td>
<td>Cetominidae</td>
</tr>
<tr>
<td>Notopteridae</td>
<td>Megalomycteridae</td>
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<tr>
<td>Gymnarchidae (15)</td>
<td>Ophidiiformes</td>
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<tr>
<td>Anguilliformes</td>
<td>Beloniformes</td>
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<tr>
<td>Saccopharyngiformes (4)</td>
<td>Belonidae</td>
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<tr>
<td>Clupeiformes</td>
<td>Cyprinodontiformes</td>
</tr>
<tr>
<td>Pristigasteridae</td>
<td>Rivulidae</td>
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<tr>
<td>Siluriformes</td>
<td>Goodeidae</td>
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<tr>
<td>Trichomycteridae</td>
<td>Cyprinodontiformes</td>
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<tr>
<td>Siluridae</td>
<td>‘Hypoptychidae’</td>
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<tr>
<td>Claridae</td>
<td>Gasterosteidae</td>
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<tr>
<td>Schilbeidae</td>
<td>Syngnathidae</td>
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<tr>
<td>Gymnotiformes (5)</td>
<td>Synbranchiformes (3)</td>
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<td>Aulopiformes</td>
<td>Caulophrynidae</td>
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<tr>
<td>Giganturidae</td>
<td>Neoceratidae</td>
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<td>Lampriformes</td>
<td>Melanocetidae</td>
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<td>Lophotidae</td>
<td>Himantolophidae</td>
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<td>Radicephalidae</td>
<td>Diceratiidae</td>
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<tr>
<td>Trachipteridae</td>
<td>Oneirodidae</td>
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<td>Percopsiformes</td>
<td>Thaumatichthyida</td>
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<td>Amblyopsidae</td>
<td>Centrophrynidae</td>
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<tr>
<td>Gadiformes</td>
<td>Ceratidae</td>
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<tr>
<td>Macrouridae</td>
<td>Gigantactinidae</td>
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<td>Linophrynidae</td>
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<td>Atheriniformes</td>
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<td>Phallostethidae</td>
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<td>Ptilichthyida</td>
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<td>Zaprioridae</td>
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<td>Trichiurae</td>
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<td>Xiphiidae</td>
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<td>Stromateidae</td>
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<td>Channidae</td>
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<td></td>
<td>Tetraodontiformes</td>
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<td>Balistidae</td>
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<td></td>
<td>Monacanthidae</td>
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<tr>
<td></td>
<td>Ostraciidae</td>
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<tr>
<td></td>
<td>Triodontidae</td>
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<tr>
<td></td>
<td>Tetraodontidae</td>
</tr>
<tr>
<td></td>
<td>Diodontidae</td>
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<td></td>
<td>Molidae</td>
</tr>
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</table>

Their pelvic fins are found in 100 families in 20 teleostean orders (Table III). In several families, only the pelvis has been retained (e.g. Comepholidae, Cryptacanthidae and Triodontidae). Based on recent phylogenies, single ancestral losses affecting multiple families have been suggested for some groups such as ‘Anguilliformes’ + saccopharyngiforms, ceratoids, synbranchiforms and tetraodontids + diodontids, whereas multiple independent losses within a family have been suggested for other groups such as trichomycterids, gasterosteids and cyprinodontids. Losses are sometimes only found in adults (e.g. giganturids, stomiids, synbranchids and cynoglossids). Losses have occurred independently in various teleostean lineages during at least 80 separate events. As for the other fins, the caudal fin is very rarely lost, with losses having occurred in only a few groups (e.g. molids, notopterids and trichiurids). Dorsal and anal-fin losses are relatively rare, although they sometimes appear to be lost because of confluence with the caudal fin, which has frequently occurred in fishes with eel-like body forms. Compared with the pelvic fins, the pectoral fins have been completely lost far less frequently; the pectoral fins have been lost in only a few groups, including the anguilliform eels, clariids, stomiids, synbranchids and cynoglossids. In general, the pelvic fins are more readily lost or reduced than any of the other major fins.

Two hypotheses can explain the loss of the pelvic fins, the neutral mutation hypothesis (Kimura, 1968) and the adaptation hypothesis (Ayala, 2007).
mutation hypothesis suggests that the pelvic fins are lost because of random mutations in related genes that are involved in pelvic-fin formation; these mutations gradually accumulate in the absence of selective pressure for structure maintenance. In contrast, the adaptation hypothesis suggests that natural selection causes the loss of the pelvic fins because losing them is somehow advantageous. Both hypotheses are plausible, since observations of pelvic finless fishes suggest that maintenance of the pelvic fins was not an advantage for the survival of their respective ancestors. Recent studies on pelvic-fin reduction in selected groups are summarized below.

**CLARIID CATFISHES**

In most vertebrates, including teleosts, elongated bodies are accompanied by the reduction or loss of paired appendages, which is considered an adaptation to burrowing and fossorial behaviours (Gans, 1973, 1975; Withers, 1981; Adriaens et al., 2002). Fishes that show body elongation typically swim by the anguilliform mode (Breder, 1926; Blake, 2004), which involves undulating the body along its full length and using the caudal fin to produce propulsive thrust (Gillis, 1996; Blake, 2004). Body elongation is clearly efficient for extreme anguilliform locomotion because it involves the addition of caudal vertebrae, which do not support ribs that would stress the viscera during undulation (Cabuy et al., 1999). Accordingly, in elongated fishes, the pelvic fins are much less important for swimming and are thus subject to reduction. The pelvic fins also appear to provide little benefit for defence because they can only cover small areas around the pelvic fins within the elongated body.

Clariid catfishes occur in freshwater and terrestrial near-water regions in Africa, Syria, India and South-east Asia (Nelson, 2006), and have features typical of body-elongated vertebrates (i.e. burrowing and fossorial behaviour, anguilliform locomotion and paired-fin reduction). They present a unique example among teleosts in showing a complete series of body forms accompanied by paired-fin reduction at the species level that ranges from a fusiform state, with both paired fins intact, to an anguilliform state lacking all paired appendages (Boulenger, 1908; Pellegrin, 1927; Poll, 1942) (Fig. 11). Among the clariid catfishes, three species, *Channallabes apus* Günther, *Dolichallabes microphthalmus* Poll and *Gymnallabes alvarezi* Roman, show intraspecific variation in pelvic-fin presence or absence (Adriaens et al., 2002). The degree of anguilliformity observed in the clariid catfishes is linked to burrowing and pelvic and pectoral-fin reductions (Adriaens et al., 2002). Anguilliformity was considered to have evolved gradually and unidirectionally within this family (Pellegrin, 1927), but recent phylogenetic studies based on both morphological and molecular markers indicate that anguilliformity has had multiple origins (Teugels & Adriaens, 2003; Agnese & Teugels, 2005; Jansen et al., 2006). Based on nuclear ribosomal RNA (rRNA) gene and spacer sequences, Jansen et al. (2006) showed that anguilliformity has evolved at least four times, and that in each case it arose from a fusiform *Clarias*-like ancestor. Their estimates of divergence times suggest that pelvic finless clariid species diverged from ancestors with pelvic fins between the middle Oligocene and the late Miocene [c. 10–27 million before present (B.P.)].
Fig. 11. The orthogenetic series in clariid catfishes, ranging from a fusiform body with paired fins intact to an anguilliform body with paired fins lost: (a) Heterobranchus longifilis, (b) Dinopterus cunningtoni, (c) Clariallabes melas, (d) Gymnallabes typus and (e) Channallabes apus. Redrawn and modified from Pellegrin (1927).

STICKLEBACKS

Sticklebacks provide another example of fishes that show pelvic-fin reductions and losses. Sticklebacks belong to the Gasterosteidae and are distributed in marine, brackish and freshwater regions of the northern hemisphere (Nelson, 2006). Sticklebacks, especially the three-spined stickleback G. aculeatus, the nine-spined stickleback Punigitius pungitius (L.) and the brook stickleback Culaea inconstans (Kirtland), have gained attention and been used in research into pelvic-fin reduction, as well as other adaptive traits (Wootton, 1984; Bell & Foster, 1994; Peichel et al., 2001; Östlund-Nilsson et al., 2007). Populations of some stickleback species also show
various degrees of pelvic-fin reduction (Nelson, 1971; Nelson & Atton, 1971; Bell, 1987) (Fig. 7). Sticklebacks have a pair of strong spines and one or two rudimentary soft rays in the pelvic fin, which apparently produce very little propulsion and function poorly for swimming. In the mean time, pelvic and dorsal spines, and lateral plates comprise important parts of their morphological defence against soft-mouthed, gape-limited predators (Hoogland et al., 1956; Reimchen, 1983). Ancestral marine G. aculeatus usually had a complete pelvic skeleton with bilateral long, stout spines (Reimchen, 1994) [Fig. 7(a)]. In contrast, reductions in the size and number of antipredator structures have occurred to individuals in brackish and freshwater regions (Bell & Foster, 1994). In freshwater individuals, reduction in pelvic structures varies from missing a spine on either fin to the loss of the entire pelvis (Bell, 1987) (Fig. 7). Pelvic-fin reduction is directionally asymmetric (Bell et al., 1985) and is usually accompanied by reduction in the lateral plates and dorsal-fin spines (Giles, 1983; Bell & Foster, 1994; Raeymaekers et al., 2005). Gasterosteus aculeatus has probably undergone multiple, rapid divergences from a uniform anadromous ancestor to freshwater ecotypes following the Pleistocene glacial retreat, c. 10 000–12 000 b.p. (McKinnon & Rundle, 2002; Raeymaekers et al., 2005). Reductions in these traits apparently occurred independently and repeatedly (Cresko et al., 2004; Coyle et al., 2007). Nevertheless, most species in this family do not show remarkable body elongation, and thus in Gasterosteidace body elongation does not correlate with pelvic-fin reduction. Instead, pelvic-fin reductions are thought to have been induced by declines in predation pressure or environmental calcium density, and depending on the specific population, either one or both of these factors have induced reductions (Reimchen, 1980; Reist, 1980; Giles, 1983; Bell et al., 1993; Bourgeois et al., 1994; Ziuganov & Zotin, 1995).

TETRAODONTIFORM FISHES

Clariid catfishes and gasterosteids provide good examples of microevolution in the pelvic fins. In contrast, tetraodontiform fishes were once regarded as demonstrating a macroevolutionary process in the gradual reduction of skeletal elements, including the pelvic fins (Tyler, 1962, 1980; Santini & Tyler, 2003). Tetraodontiforms mainly occur in the marine waters of tropic and temperate regions, but some tetraodontid species have radiated into brackish and freshwater habitats (Dekkers, 1975). Tetraodontiform fishes also show a series of pelvic reductions that ranged from paired structure with spines, soft rays and fin membranes present to the complete loss of all pelvic-fin elements. Triacanthodids and triacanthids, a morphologically primitive group, have pelvic fins with an enlarged spine and reduced or no soft rays. Balistoids, which are regarded as a morphologically intermediate group, have a rudimentary pelvic complex composed of a pelvis, incasing scales and rudimentary rays. Triodontids, tetraodontids, diodontids and molids are considered a morphologically derived group, all of which lack pelvic fins and a pelvic girdle (except for the triodontids that have a pelvis). Several morphological hypotheses exist concerning the familial relationships of the Tetraodontiformes, all of which reflect reductive trends in skeletal elements, including pelvic structures (Breder & Clark, 1947; Winterbottom, 1974a; Leis, 1984; Tyler & Sorbini, 1996) (Fig. 12). Molecular studies, however, have not supported phylogenetic hypotheses based on gradual reductive trends in skeletal elements (Holcroft, 2005; Alfaro et al., 2007; Yamanoue et al., 2010).
According to the whole mitogenome analysis of Yamanoue et al. (2008), the observed reductions in skeletal elements cannot be explained without the occurrence of parallel or reverse evolution, and the above-mentioned primitive, intermediate and derived groups are paraphyletic (Fig. 12). Based on this hypothesis, pelvic-fin reductions occurred at least twice, independently. Among these pelvic finless groups, some pufferfishes (Tetraodontidae) have been observed to exhibit a habit of burrowing into the sand to seek refuge from predation and environmental changes, or to rest (Fujita, 1962; Katayama & Fujita, 1966; Nakajima & Nitta, 2001). None of the members of these groups, however, shows any apparent body elongation. On the contrary, they have rather reduced numbers of vertebrae compared with other perciforms (Tyler, 1980). In contrast diodontids, ostraciids and molids have never been reported as having any burrowing habits. Tetraodontids, diodontids and ostraciids are all rigid-bodied, median and paired-fin swimmers (Wiktorowicz et al., 2007). Their modes of locomotion were once categorized as tetraodontiform, diodontiform and ostraciiform, respectively (Breder, 1926), but they are similar to one another in that, unlike ordinary fishes, the body and caudal fin do not play a dominant role in producing propulsion for swimming. These modes of locomotion represent the extreme opposite of anguilliform locomotion, in which the caudal fin and elongated body are undulated for swimming (Breder, 1926). Instead of the caudal fin, the dorsal, anal and pectoral fins are the principal generators of thrust, especially for slow-speed swimming and manoeuvring (Arreola & Westneat, 1996; Gordon et al., 1996; Hove et al., 2001), and pelvic fins may prove useless in these modes of locomotion. Additionally, these fishes have successfully developed alternative forms of antipredator defence. Diodontids have massive spines on their bodies and effectively protect themselves from predators by inflating their bodies (Wainwright & Turingan, 1997). Similarly, the carapaces of ostraciids can also provide effective protection against predation. Obviously, these alternatives are far more useful than pelvic-fin spine retention.

Balistoids are one of the most diversified groups among the order Tetraodontiformes. They appear in the list of pelvic finless fishes in Table III, but they all have a pelvic complex, which is a vestige of the pelvic fins [Fig. 5(b)]. The pelvic complex is hypothesized to be parsimoniously and unidirectionally reduced in more derived balistoid lineages from an estimation of balistoid phylogeny based on various morphological traits (Matsuura, 1979) (Fig. 13). Molecular phylogenetic analyses based on whole mitogenome data sets, however, have revealed that highly reduced pelvic complexes have multiple origins. Furthermore, optimization of the traits on the resultant tree strongly suggests that pelvic complexes have not only undergone reductions but have also experienced increases in complexity (Yamanoue et al., 2009b) (Fig. 14). Although balistoid pelvic complexes obviously no longer function for propulsion, all balistoids retain at least a vestige of a pelvic complex, and this unique pelvic structure has been retained at least since the divergence between balistids and monacanthids, which occurred c. 118 M b.p. (Yamanoue et al., 2006). This is a surprisingly long period of time compared with the very rapid pelvic-fin reductions that occurred in sticklebacks and clarid catfishes. In this way, the evolution of pelvic structure in balistoids is very different from other fishes that have exhibited reductive trends. This unique pelvic evolution may be linked to a ‘vibrating’ behaviour, a behavioural trait that has been confirmed in all observed balistoids, although it varies among species (Kawase, 1998, 2005). Additionally, the ventral flap in some species exhibits sexual dimorphisms (Kawase, 1998), and this character possibly plays a role in the pelvis.
Fig. 12. Familial relationships of tetraodontiform fishes. (a) A classical hypothesis based on morphology (Tyler & Sorbini, 1996), with state descriptions on the pelvic fins. Morphologically primitive, intermediate and derived groups are shown in red, green and blue, respectively. (b) A recent hypothesis based on whole mitogenome sequences (Yamanoue et al., 2008), with Triacanthodoidei and Tetraodontoidei in grey and purple, respectively.

DEVELOPMENTAL GENETIC MECHANISMS

Investigations examining hybrids between *G. aculeatus* of different phenotypes have provided insights into pelvic-fin development and mechanisms of pelvic-fin reduction (Cole et al., 2003; Cresko et al., 2004; Shapiro et al., 2004, 2006). Genome-wide genetic mapping of hybrids from crosses between different phenotypes has suggested that several chromosome regions control morphological changes in pelvic structure (Peichel et al., 2001). According to other studies, *Pitx1*, a homeobox-containing transcription factor that is critical for hind-limb identity and outgrowth (Logan & Tabin, 1999; Marcil et al., 2003), maps to a chromosomal region that plays a major role in controlling pelvic appendage variation (Shapiro et al., 2004). Although *Pitx1* is indeed involved in the development and variation of the pelvic region, the *Pitx1* protein sequence is highly conserved, regardless of the varied phenotypes (Shapiro et al., 2006). This is because the *Pitx1* protein is a pleiotropic transcription factor that affects the development of multiple tissues; therefore, mutations at the coding region will bring adverse effects during development. Gasterosteids with reduced pelvic fins, however, have lost *Pitx1* expression in the pelvic-fin precursors, but possess an intact *Pitx1* coding region, with no sequence changes relative to populations with fully formed pelvic structures. These observations indicate that mutations in the regulatory *cis*-element of *Pitx1*, which control *Pitx1* expression, in the precursors of the pelvic fins have selectively abolished its expression related to in sexual selection, acting as a constraint on morphological evolution (Gould, 1989; Panhuis et al., 2001; Kokko et al., 2003).
pelvic-fin development, whereas regulatory regions controlling the gene’s expressions elsewhere in the body are not affected (Shapiro et al., 2006).

Pelvic-fin reduction in the G. aculeatus exhibits directional asymmetry; specifically, a tendency exists for any remaining pelvic rudiments to be larger on the left than on the right side (Bell et al., 1985; Cole et al., 2003; Shapiro et al., 2004) (Fig. 7). This left-biased pelvic asymmetry, which is a signature of Pitx1–mediated pelvic reduction, is also found in the Pungitius pungitius and even in distantly related vertebrate lineages such as manatees and mice. These multiple lines of evidence suggest that changes in Pitx1 may represent a key mechanism of pelvic-fin reduction (Shapiro et al., 2006). The homeobox gene Pitx2 is also expressed laterally on the left side in mice, and its laterality is thought to induce asymmetry during hind-limb formation (Marcil et al., 2003). Pitx2 is a member of the Nodal signalling pathway, which is highly conserved and regulates asymmetrical development in vertebrates (Palmer, 2004; Raya & Izpisúa Belmonte, 2006). Studies have suggested that the abolishment of Pitx1 expression related to pelvic-fin reduction or loss might unmask...
the asymmetrical expression of Pitx2 (or other functionally related genes) and cause the left-biased asymmetry found in pelvic structures (Shapiro et al., 2006; Bell et al., 2007). Pitx2 expression, however, was not observed during pelvis development in gasterosteids individuals lacking pelvic spines or in specimens with intact spines (Cole et al., 2003). This suggests that other laterality genes, which are involved in
the left–right patterning of the animal body and probably work upstream of Pitx2, such as Lefty2 and Nodal, might be involved in asymmetric pelvic-fin development in Gasterosteidae (Bell et al., 2007). Also, G. aculeatus populations that show a right bias or no bias in the size of the pelvic vestiges suggest that other genetic mechanisms for asymmetric reduction exist (Bell et al., 2007).

An alternative mechanism for pelvic-fin loss was proposed based on the examination of early development in the fugu, Takifugu rubripes (Temminck & Schlegel) (Tanaka et al., 2005). They demonstrated that limb-bud outgrowth and initiation failed to occur in the fugu during development, and Hoxd9a expression in the pelvic region was undetected during T. rubripes embryonic development, whereas it was expressed abundantly in pectoral fin-bud mesoderm at early stages of fugu embryos and in the pelvic region of the G. aculeatus with pelvic spines. Thus, it was concluded that pelvis loss was associated with altered expression of Hoxd9a, which is a marker for pelvic-fin position in the G. aculeatus. It is, however, not yet known whether the mutational event affecting the regulation of Hoxd9a expression in the pelvic region of T. rubripes occurred in the cis-regulatory element of Hoxd9a, or in a factor operating upstream of the gene. Further studies are still needed to identify the cause of Hoxd9a expression alternation. Although the genetic mechanism of pelvic-fin loss found in gasterosteids was once believed to be shared among various pelvic finless and hind-limbless vertebrates, this result clearly indicated that the mechanism observed in T. rubripes differs from the mechanism documented in gasterosteoids. Accordingly, various mechanisms for pelvic-fin reduction likely exist in teleosts.

CONCLUSIONS AND PERSPECTIVE

This review has only cursorily examined various studies regarding pelvic fins. In general, the main function of fish fins is thought to be to produce propulsive thrust for swimming. The pelvic fins, however, usually play a much smaller role in propulsion compared with other fins in most teleosts. Because the pelvic fins are not crucially important for propulsion, greater flexibility for pelvic-fin modification probably exists through evolutionary processes. Although the pelvic fins exhibit some evolutionary trends through the history of teleosts, many morphological and functional changes have undoubtedly occurred independently multiple times because of their potential evolutionary flexibility. This flexible nature can lead to erroneous conclusions regarding teleostean phylogeny if the pelvic fins are weighted heavily during morphology-based phylogenetic analyses.

Reductions and losses are the most remarkable phenomenon among the structural modifications that have occurred in the pelvic fins. The independent pelvic-fin reductions or losses that have occurred in many teleost lineages are particularly noteworthy, and compared with similar occurrences in other fins, their frequency is overwhelming. Intensive studies of pelvic-fin loss in Gasterosteidea have helped explain the process and mechanism of pelvic-fin reduction in teleosts, but this mechanism probably varies among groups and even among conspecific populations (Adriaens et al., 2002; Tanaka et al., 2005; Bell et al., 2007; Yamanoue et al., 2009b). In this review, several examples of fish groups that have shown pelvic-fin reductions were used. Future studies of these groups promise to broaden the understanding of this phenomenon that has only been studied in Gasterosteidae. Clariid catfishes are a favourable model.
system for pelvic reduction because they have undergone a more typical process of pelvic-fin reduction, being comparable with body elongation. *Clarias gariepinus* (Burchell) and several other clariids are widely cultured for food (Hecht et al., 1996), and they have been well examined in culture-related aspects of biology (Ponzoni & Nguyen, 2008). Phenotypic variation in pelvic fins among close relatives will facilitate genetic analyses by producing hybrids from crosses between different phenotypes. Pelvic-fin-reduced and pelvic-finless clariids, such as some species of *Bathyclarias* and *Gymnallabes typus* Günther, are being tested for their aquaculture potential (Teugels & Gourène, 1998), and they will provide prospective models if breeding and rearing techniques for these species under laboratory conditions are developed.

Another useful model system for studying pelvic-fin modification is the tetraodontiform fishes because they exhibit great diversity in their pelvic fins as well as other morphological characters (Santini & Stellwag, 2002). The difficulty of finding representative models to cover the range of phenotypic variation observed in pelvic appendages, however, appears to be a drawback for this type of research. The *T. rubripes* provides an excellent model for genomic studies (Brenner et al., 1993; Aparicio et al., 2002; Yamanoue et al., 2009a), and the *T. rubripes* has recently gained popularity for use as an evo-devo model because some experimental tools that are needed for dissecting their developmental aspects are available. Furthermore, being an aquaculture species, fertilized *T. rubripes* eggs are relatively easy to obtain (Amores et al., 2004; Saha et al., 2005; Tanaka et al., 2005; Tümpe et al., 2006). Besides the fugu, balistoids, *Stephanolepis cirrhifer* (Temminck & Schlegel) and *Thamnaconus modestus* Günther, are prospective candidates for experimental use because breeding and rearing technology for aquaculture has been largely developed (Matsuura, 2007; Mizuno et al., 2007). They have unpaired pelvic complexes, which exhibit a very unique evolution, and thus examinations of their pelvic complexes will provide new perspectives for the genetic and developmental mechanisms of pelvic fins.

Teleosts have successfully radiated into various habitats, producing vast numbers of species that exhibit great diversity. The flexible nature of the pelvic fins has probably been important for the successful adaptations of teleosts to various environments. Investigations of teleost pelvic fins, using fishes with various morphological aspects, will provide clues for understanding the evolution, diversity and adaptations of teleosts. Despite this, in many studies, the pelvic fins of most teleosts are only used for taxonomic comparisons. To obtain a comprehensive understanding of pelvic-fin biology and evolution in teleosts, considerably more research is necessary that uses multiple model systems with multidisciplinary approaches. Insights and information from such studies will contribute to the understanding of the successful radiation and diversity of teleosts.

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