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Microanatomy of the Paired-Fin Pads of Ostariophysan Fishes (Teleostei: Ostariophysi)

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ABSTRACT Members of the teleost superorder Ostariophysi dominate freshwater habitats on all continents except Antarctica and Australia. Obligate benthic and rheophilic taxa from four different orders of the Ostariophysi (Gonorynchiformes, Cypriniformes, Characiformes, and Siluriformes) frequently exhibit thickened pads of skin along the ventral surface of the anteriormost ray or rays of horizontally orientated paired (pectoral and pelvic) fins. Such paired-fin pads, though convergent, are externally homogenous across ostariophysan groups (particularly nonsiluriform taxa) and have been considered previously to be the result of epidermal modification. Histological examination of the pectoral and/or pelvic fins of 44 species of ostariophysans (including members of the Gonorynchiforms, Cypriniformes, Characiformes, and Siluriformes) revealed a tremendous and previously unrecognized diversity in the cellular arrangement of the skin layers (epidermis and subdermis) contributing to the paired-fin pads. Three types of paired-fin pads (Types 1–3) are identified in nonsiluriform ostariophysan fishes, based on differences in the cellular arrangement of the epidermis and subdermis. The paired-fin pads of siluriforms may or may not exhibit a deep series of ridges and grooves across the surface. Two distinct patterns of unculus producing cells are identified in the epidermis of the paired-fin pads of siluriforms, one of which is characterized by distinct bands of keratinization throughout the epidermis and is described in *Amphilius platychir* (Amphiliidae) for the first time. General histological comparisons between the paired fins of benthic and rheophilic ostariophysan and nonostariophysan percomorph fishes are provided, and the possible function(s) of the paired-fin pads of ostariophysan fish are discussed. J. Morphol. 000:000–000, 2012. © 2012 Wiley Periodicals, Inc.

KEY WORDS: Otophysi; integument; unculi; keratinization; adhesion; rheophily

INTRODUCTION

The superorder Ostariophysi (sensu Rosen and Greenwood, 1970; Fink and Fink, 1981) is a large, morphologically diverse assemblage of primarily freshwater fishes inclusive of milkfishes and their relatives (order Gonorynchiformes), carps, minnows, suckers, and loaches (Cypriniformes), tetras, piranhas and their relatives (Characiformes), catfishes (Siluriformes), and South American knifefishes (Gymnotiformes). Members of this large superorder are found in almost all available freshwater habitats, where they form a dominant proportion of the continental ichthyofaunas. In certain freshwater habitats, for example, in torrential mountain streams, ostariophysans are commonly the only fishes present (Hora, 1930; Pouilly et al., 2006). Survival in such extreme aquatic environments is facilitated by a variety of structural adaptations, the majority of which are proposed to aid in maintaining a benthic position in swift currents (Hora, 1923a,b, 1930; Sheldon, 1937; Chang, 1945; Lundberg and Marsh, 1976; Geerinckx et al., 2011). Though such structural modifications vary greatly across groups, a feature common to most benthic and rheophilic ostariophysans is a thickened layer of skin along the ventral surface of the anteriormost fin rays of the paired fins (Fig. 1). This "thickened skin" has been reported for benthic and rheophilic members of all major ostariophysan groups (excluding Gymnotiformes), including: the gonorynchiform family Kneriidae

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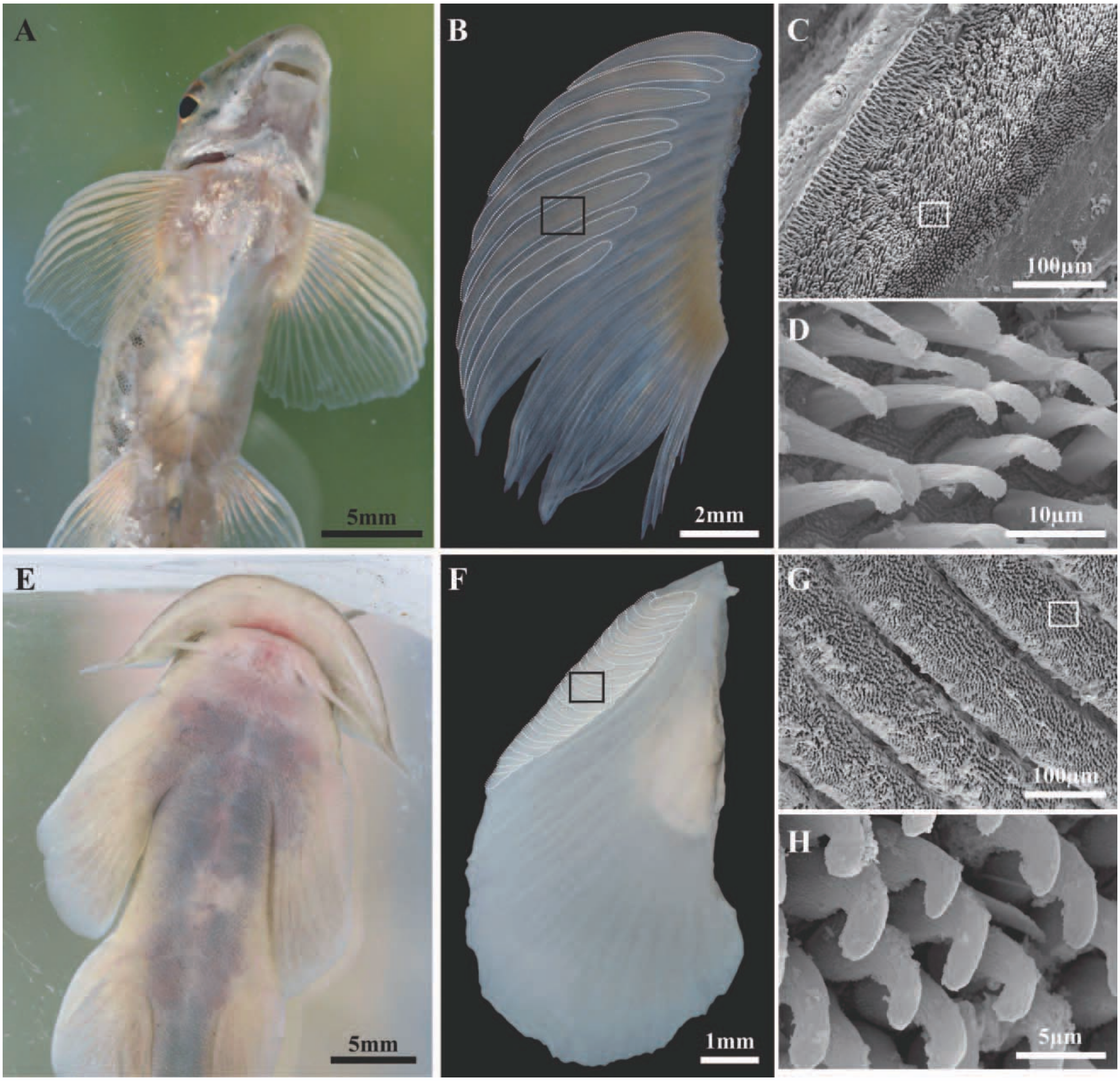

Fig. 1. Overview of the paired-fin pads of ostariophysan fishes. (**A**) *Psilorhynchus nepalensis* (KU 40611), ventral view, fin pads present along ventral surface of six anteriormost pectoral-fin rays and two anteriormost pelvic-fin rays. (**B**) Ventral surface of dissected pectoral fin (right side) of *Psilorhynchus pseudecheneis* (KU 29516), fin pads along ventral surface of eight anteriormost rays highlighted with white dotted line. (**C**) SEM illustrating unculiferous surface of pectoral-fin pad of *P. pseudecheneis* (specimen as in B) from area roughly equivalent to that highlighted by black box in B. (**D**) Close up of area highlighted by white box in C. (**E**) *Myersglanis blythii* (KU 40556), ventral view, illustrating fin pad present along ventral surface of pectoral fin-spine and anteriormost pelvic-fin ray. (**F**) Ventral surface of dissected pectoral fin (right side) of *M. blythii* (KU 40556), fin pad along ventral surface of pectoral-fin spine highlighted with white dotted line. (**G**) SEM illustrating unculiferous surface of pectoral-fin pad of *M. blythii* (specimen as in F) from area roughly equivalent to that highlighted by black box in F. (**H**) Close up of area highlighted by white box in G.

(Roberts, 1982); the cypriniform families Balitoridae (Hora, 1930; Chang, 1945; Kottelat, 1988a,b; Roberts, 1998; Tan, 2006), Catostomidae (Jenkins and Burkhead, 1994), Cyprinidae (Hora, 1930; Roberts, 1990), Gyrinocheilidae (Roberts and Kottelat, 1993), and Psilorhynchidae (Menon and Datta, 1964; Conway and Kottelat, 2007; Conway and Mayden, 2008a,b); the characiform families Crenuchidae (Buckup et al., 2000); and the siluriform families Amphiliidae (Bell-Cross and Jubb, 1973; Roberts, 2003; van Oosterhout et al., 2009), Astroblepidae (Schaefer and Provenzano, 2008), Loricariidae (Schaefer and Provenzano, 2008), and Sisoridae (Das and Nag, 2004).

This thickened skin under the anteriormost paired-fin rays of ostariophysan fishes has been referred to under a variety of names, many of which have functional connotations, including paired-fin skin pads (Schaefer and Provenzano, 2008), adhesive apparatus (Hora, 1922), adhesive surfaces (Doi and Kottelat, 1998), adhesive devices (Das and Nag, 2004), or, more commonly, adhesive pads (Hora, 1930; Chang, 1945; Roberts, 1982; Kottelat, 1988a,b; Conway and Kottelat, 2007, 2010). The external surface morphology of these paired-fin pads has been frequently investigated in ostariophysan fishes using scanning electron microscopy (SEM; Bell-Cross and Jubb, 1973; Roberts, 1982, 1998; Das and Nag, 2004). In most cases, they are covered in a layer of unicellular projections or unculi (Roberts, 1982; Fig. 1C,D,G,H), which are hypothesized to be involved in adhesion (Hora, 1922; Roberts, 1982). The internal anatomy of the paired-fin pads has been investigated less frequently (Hora, 1922; Chang, 1945). Despite the lack of detailed histological examination, there appears to be a general conception that paired-fin pads represent a simple thickening of the epidermis ventral to the anteriormost lepidotrichia of the paired fins (Hora, 1922; Chang, 1945). We used a combination of general histological methods and SEM to investigate the internal morphology of the paired-fin pads of numerous ostariophysan species to test the hypothesis that paired-fin pads represent nothing more than a thickened region of the epidermis.

MATERIALS AND METHODS

Terminology

Terminology for the cellular layers and cell types of the integument generally follows that of Roberts and Bullock (1980). The term alarm substance cell (ASC) is adopted herein (vs. club cell) following Pfeiffer (1960).

Light Microscopy

Entire pectoral and/or pelvic fins were removed from the right side of select preserved specimens. In the case of large specimens, a smaller section of the fin was removed. Dissected fins were rinsed for 1 h in tap water, decalcified (94.38% water, 5.5% HCl, and 0.12% ethylenediaminetetraacetic acid; Electron Microscopy Supplies) for 3 days, rinsed for 1 h in tap water, and dehydrated in a graded series of ethanol (70 and 95%, for 1 h each, 100%, two cycles for 30 min each). Tissues were then cleared in toluene (two cycles for 30 min each) and subsequently embedded in paraffin blocks for sectioning. Transverse sections, 9-μm thick, were cut and affixed to albumenized slides. Slides were examined under a ZEISS SteREO Discovery V20 Stereomicroscope (Carl Zeiss, Jena, Germany) or a Leica DM4500 microscope (Leica Microsystems, Wetzlar, Germany). Representative histological sections were photographed with a ZEISS axiocam MRc5 (Carl Zeiss, Jena, Germany) or a QICAM 12-Bit Mono Fast 1394 Cooled digital camera (QImaging, British Columbia, Canada). The diversity of specimens examined limited our study to partially destructive sampling of museum specimens (see "Materials Examined" section). Due to the lack of knowledge of fixation/preservation methods for much of this material, the histological approach utilized was limited to a relatively general histological examination. Thus, slides were only stained with hematoxylin and eosin (H&E) for histological exploration (following Kiernan, 1990) due to irregularities in staining between different tissue types. Such methods provided sufficient resolution to discern general structural differences/similarities.

SEM

Transverse sections of pectoral fins from selected specimens were rinsed and postfixed for 90 min in 2% osmium tetroxide. Tissues were then rinsed and dehydrated with a graded series of ethanol (70, 85, and 100% EtOH for 1 h each) before critical point drying with a Denton DCP-1 critical point drier (Denton Vacuum, Moorestown, NJ). Once dried, specimens were then placed on aluminum stubs and coated with gold in a Denton Desk IV XLS (Denton Vacuum, Moorestown, NJ) sputter coater. Representative SEM images were photographed with a Philips XL-20 SEM (Philips Electronics N.V., Eindoven, The Netherlands).

Materials Examined

The following specimens, listed alphabetically by family, genus, and species under each order, were examined during the course of this study. The majority of specimens were examined using only light microscopy. Those specimens that were also examined using SEM are indicated with an asterisk. Museum abbreviations: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; AUM, Auburn University Natural History Museum, Auburn; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; CU, Cornell University, Ichthyology Collection; KU, University of Kansas Natural History and Biodiversity Collection, Lawrence; TCWC, Texas Cooperative Wildlife Collection, College Station; UAIC, University of Alabama Ichthyology Collection, Tuscaloosa.

Gonorynchiformes. Chanidae: *Chanos chanos*, AMNH 48715, 2 examined (ex.), 1 pectoral fin sectioned (pect). Kneriidae: *Kneria paucisquamata*, CU 91158, 2 ex, 1 pect.

Cypriniformes. Balitoridae: *Annamia normani*, BMNH uncat., 1 ex., 1 pect.; *Beaufortia* cf. *leveretti*, UAIC 14166.06, 1 ex.; *Gastromyzon borneensis*, BMNH 2001.1.21.58-71, 4 ex.; *Gastromyzon cranbrooki*, UAIC 14288.01, 1 ex.; *Gastromyzon punctulatus*, ANSP 177839, 2 ex.; *Gastromyzon* sp., UAIC 14166.21, 1 ex.; *Homaloptera smithi*, ANSP 56475, 2 ex.; *H.* cf. *smithi*, ANSP 179900, 2 ex.; *Homaloptera stephensoni*, BMNH 2001.1.15.853-872, 10 ex.; *Homaloptera zollingeri*, BMNH 2001.1.15.878-903, 10 ex.; *Pseudogastromyzon fasciatus*, AMNH 11054, 2 ex., 1 pect., 1 pelvic fin sectioned (pel.); *Pseudogastromyzon* sp., UAIC 14180.68, 1 ex.; *Sewellia lineolata*, UAIC 14169.43, 5 ex., 1 pect., 1 pel. Catostomidae: *Cycleptus elongatus*, UAIC 14922.01, 1 ex., 1 pect.; *Cycleptus meridionalis*, UAIC 10765.01, 1 ex., 1 pect. Cyprinidae: *Alburnus alburnus*, AMNH 20536, 1 ex., 1 pect.; *Erimystax dissimilis*, UAIC 12433.11, 1 ex., 1 pect.; *Garra cambodgiensis*, ANSP 178726, 1 ex., 1 pect.; *Garra* sp., KU 40623, 1 ex., 1 pect.*; *Hybopsis amblops*, UAIC 13270.04, 1 ex.; *Labeo longipinnis*, UAIC 14180.55, 1 ex., 1 pect.; *Labeo* sp., CU 92143, 1 ex., 1 pect.; *Phenacobius catostomus*, UAIC 10511.08, 1 ex., 1 pect.; *Rhinichthys atratulus*, UAIC 12432.03, 1 ex.; *Zacco* cf. *platypus*, UAIC 14181.06, 1 ex., 1 pect.; Gyrinocheilidae: *Gyrinocheilus pennocki*, UAIC 14180.51, 1 ex., 1 pect. Psilorhynchidae: *Psilorhynchus balitora*, KU 29191, 1 ex., 1 pect., 1 pel.; *Psilorhynchus pseudecheneis*, KU 29516, 2 ex., 1 pect., 1 pel., 1 pect.*; *Psilorhynchus sucatio*, CAS 50289, 1 ex., 1 pect, 1 pect.*

Characiformes. Crenuchidae: *Characidium fasciatum*, ANSP 159826, 1 ex., 1 pect.; *Characidium zebra*, ANSP 139845, 1 ex., 1 pect.; *Melanocharacidium pectorale*, AUM 40191, 1 ex., 1 pect., 1 pel. Distichodontidae: *Nannocharax faciatus*, BMNH 1981.2.171745-1866, 1 ex., 1 pel.; *Nannocharax parvus*, CU 86332, 1 ex. 1 pect., 1 pel.; *Nannocharax schoutedeni*, AUM 51315, 1 ex. 1 pel.; *Paradistichodus dimidiatus*, BMNH 2006.4.17.79-107, 1 ex. 1 pect. Parodontidae: *Apareiodon orinocensis*, AUM 43666, 1 ex., 1 pect.

Siluriformes. Amphiliidae: *Amphilius platychir*, BMNH 1980.7.24.56-102, 1 ex., 1 pect. Ictaluridae: *Ictalurus furcatus*, TCWC 15705.01, 1 ex., 1 pect.; *Noturus flavus* UAIC 14314.07, 1 ex, 1 pect.; *Noturus eleutherus*, UAIC 14314.08, 1 ex., 1 pect. Mochokidae: *Chiloglanis congicus*, AUM 51304, 1 ex., 1 pect.;

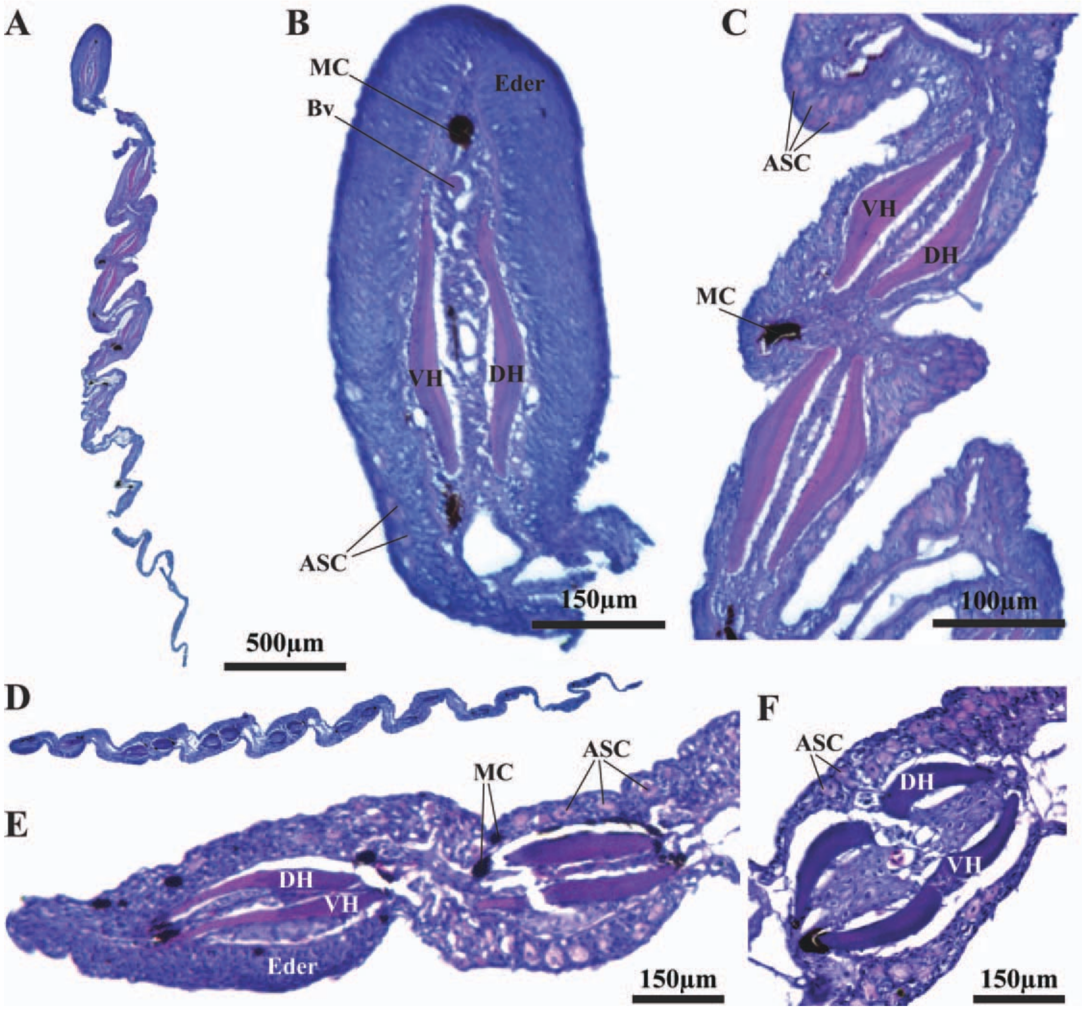

Fig. 2. Transverse sections through the pectoral fins of gonorynchiform fishes *Chanos chanos* (AMNH 48715) and *Kneria paucisquamata* (CU 91158). (**A**) Complete section of pectoral fin of *C. chanos*. (**B**) Anteriormost (uppermost) unbranched pectoral fin ray of *C. chanos*. (**C**) Fifth and sixth branched pectoral-fin rays of *C. chanos*. (**D**) Complete section of the pectoral fin of *K. paucisquamata*. (**E**) Anteriormost unbranched and first branched pectoral-fin rays of *K. paucisquamata*. (**F**) Third branched pectoral-fin ray of *K. paucisquamata*. A and D are illustrated to scale and share a single scale-bar situated between images. ASC, alarm substance cells; Bv, blood vessel; DH, dorsal hemitrichium; Eder, epidermis; MC, melanocyte; VH, ventral hemitrichium.

Chiloglanis sp., CU 93754, 2 ex., 1 pect.; *Euchilichthys royauxi*, CU 91380, 2 ex., 1 pect. Sisoridae: *Glyptothorax lampris*, ANSP 59126, 2 ex. 1 pect.; *Myersglanis blythii*, KU 40556, 2 ex., 1 pect., 1 pect*; *Pseudecheneis* cf. *crassicauda*, KU 40671, 1 ex., 1 pel.

Perciformes. Blenniidae: *Scartella cristata*, TCWC 15699.02, 1 ex., 1 pec., 1 pel. Percidae: *Etheostoma blennius*, AUM 42036, 1 ex., 1 pec., 1 pel.; *Percina kathae*, AUM 49459, 1 ex., 1 pec., 1 pel.; *Romanichthys valsanicola*, BMNH 1960.9.23.25-27, 1 ex., 1 pel.

Scorpaeniformes. Cottidae: *Cottus bairdii*, UAIC 14316.01, 1 ex., 1 pel.

RESULTS

General Anatomy of the Paired Fins of Ostariophysan Fishes

The pectoral and pelvic fins of ostariophysan fishes are composed of a variable number of segmented dermal lepidotrichia that may be unbranched (located anteriorly) or branched (situated posterior to unbranched). Each lepidotrichium is composed of two hemitrichia (also referred to incorrectly as hemitrich halves). In the pectoral fins of "generalized" demersal or pelagic ostariophysans (e.g., *Chanos chanos*), the lepidotrichia are aligned dorsal to ventral and, thus, when the pectoral fins are adpressed to the trunk of the fish, the hemitrichia are arranged lateral and medial to each other. In the pelvic fins of a generalized ostariophysan, the lepidotrichia are aligned cranial to caudal (or slightly oblique to the cranial–caudal axis, depending on the lepidotrichium under examination) when the fin is adpressed to the body, and the hemitrichia are arranged dorsal and ventral to each other. In benthic ostariophysans that live in close association with substrates (e.g., *Psilorhynchus* sp.; Fig. 1A), the pectoral fins are typically aligned more like those of the pelvic fins of generalized teleost fishes; that is, the lepidotrichia are aligned cranial to caudal, forming dorsal and ventral hemitrichia (Fig. 2C). The ventral hemitrichium in such benthic fishes is typically much larger than the dorsal hemitrichium (e.g., Taft, 2011).

The pectoral and pelvic fins of ostariophysan fishes are covered by a layer of epidermis of variable thickness, which may or may not exhibit keratinous structures, including unicellular unculi (Roberts, 1982) and/or multicellular tubercles (Wiley and Collette, 1970). Like other teleosts, the epidermis surrounding the pectoral and pelvic fins of ostariophysan fishes also contains mucocytes, which vary in location between taxa, and modified club cells (Alarm substance cells) that release "schreckstoff" (a potent alarm and immunological substance; von Frisch, 1938, 1941; Chivers et al., 2007) upon rupturing. Deep to the epidermis, the dermis, composed primarily of thin bands of collagen fibers (stratum compactum), is highly reduced around the individual hemitrichia of each lepidotrichium. Melanocytes are typically situated in the outermost layer of the dermis, ventral to the basal lamina. In most taxa, hemitrichia fill the space just deep to the dermis, and the space between each hemitrichium is typically composed of irregularly aligned fibrous connective tissue, lipidocytes, blood vessels, and nervous tissue.

The following sections describe the structural organization of the pectoral and pelvic fins of the numerous ostariophysan taxa that we investigated during the course of this study. Data from the descriptions were also synthesized in Table 1 to allow for easier comparisons.

Nonsiluriform Ostariophysans

Gonorynchiformes. We examined two species of gonorynchiform from two different families, the demersal *Chanos chanos* (Chanidae) and the benthic *Kneria paucisquamata* (Kneriidae). Only *K. paucisquamata* possessed paired-fin pads, which were associated with pectoral rays 1–2 and pelvic ray 1.

In *Chanos chanos*, the ventral epidermis of the pectoral fin is similar in thickness to that of the dorsal surface (~36 μm vs. ~33 μm, respectively; Fig. 2B). The epidermis on both the medial and the lateral surfaces contains ASCs, which stain intensely eosinophilic and contain one or two small centrally located nuclei (Fig. 2B). Mucocytes are rarely observed in the epidermis, but when present, are basophilic, round excretory cells embedded in the superficial layers of the epidermis through which they communicate to the surface via a small pore. The superficial layer of the epidermis is more squamous on the lateral surface of the pectoral fin, whereas, on the medial side the cells are more cuboidal. No keratinization is present in the superficial epithelial cells of the epidermis, and all layers of the epidermis appear basophilic, excluding the outermost layer, which did not stain well (Fig. 2B,C). Deep to the epidermis, the dermis (stratum compactum) consists of one to two layers of collagen fibers (Fig. 2B). The dermis appears to abut the hemitrichia at the ventral and dorsal curvature of the opposing hemitrichia. Irregularly arranged fibroblasts, fibrous connective tissue, blood vessels, and lipidocytes exist between the two hemitrichia. The epidermis between lepidotrichia is thin (Fig. 2C). The pelvic fin of *C. chanos* was not examined histologically.

In *Kneria paucisquamata*, the dermis is reduced to the point that the epidermis appears to abut the outer surface of each hemitrichium (Fig. 2E,F). Melanocytes are found occasionally between hemitrichia and the deep layers of the epidermis (Fig. 2E). Similar tissue exists between hemitrichia as described for *C. chanos* (Fig. 2E,F). The epidermis anteroventral to the two anteriormost rays of the pectoral fin (Fig. 2D) is slightly thicker than the epidermis surrounding the remainder of the fin and represents the paired-fin pads. The superficial layer of epidermis of the anteriormost ray of the paired-fin pad is keratinized, as evidenced by intense eosin staining (Fig. 2E). Several, but not all, of these keratinized cells exhibit unculiferous projections. Unculiferous cells are separated from each other by 3–5 nonunculiferous cells. Both ASCs and mucocytes are common ventrally and dorsally throughout the epidermis except within the portion of the epidermis forming the pads (Fig. 2E,F) and have an identical description as those observed in *C. chanos*. The ASCs are most commonly observed in the epidermis of the skin between lepidotrichia and stain weakly eosinophilic (Fig. 2F). The pelvic fin of *K. paucisquamata* was not examined histologically.

Cypriniformes. We examined 22 species from five families of the Cypriniformes, including Balitoridae, Catostomidae, Cyprinidae, Gyrinocheilidae, and Psilorhynchidae. We first describe the histology of the paired fins of the demersal and semidemersal members of the Cyprinidae (Fig. 3A–C,H–J) and then move on to truly benthic members of Cyprinidae (Fig. 3D–F,K–R) before examining taxa from other families (Fig. 5).

In the demersal species *Alburnus alburnus* (Cyprinidae; Fig. 3H), the epidermis encompassing the entire pectoral fin is extremely thin (around 1–2 cells thick adjacent to lepidotrichia; ~15 μm). Its superficialmost layer exhibits squamous cells but no keratin formation. The dermis is highly reduced to the point where basal layers of the epidermis appear to abut superficial surfaces of the hemitrichia (Fig. 3G). Mucocytes are occasionally observed in the epidermis and are similar in histology to those described in *C. chanos*. Alarm substance cells are similar to those described earlier but

TABLE 1. General features and histological summary of the paired fins of taxa examined

Taxon	Swimming position	Fin-ray pad	No. of fin-rays with pads		Pad type	Ventral/dorsal epidermal thickness	Ventral/dorsal subdermal thickness	Unculi distribution	ASC distribution	Mucocyte distribution
			Pectoral	Pelvic						
Gonorynchiformes										
Chanidae										
Chanos chanos	Demersal	Absent	0	0	–	Same	Same	Absent	Dorsal, ventral, all fin rays	Rare
Kneriidae										
Kneria paucisquamata	Benthic	Present	1–2	1	Type 1	Slightly thicker ventrally (14 μm vs. 10 μm)	Thicker ventrally (20 μm vs. 0 μm)	Ventral surface of fin-ray pads	Widespread, absent from fin-ray pads	Widespread, absent from fin-ray pads
Cypriniformes										
Cyprinidae										
Alburnus alburnus	Demersal	Absent	0	0	–	Same	Same	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Zacco cf. *platypus*	Demersal	Absent	0	0	–	Same	Same	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Erimystax dissimilis	Demersal	Absent	0	0	–	Same	Slightly thicker ventrally (0 μm vs. 10 μm)	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Phenacobius catostomus	Demersal	Absent	0	0	–	Same	Same	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Gobio sp.	Demersal	Absent	0	0	–	Slightly thicker ventrally (24 μm vs. 18 μm)	Same	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Labeo sp.	Benthic	Present	3	1	Type 2	Thicker ventrally (78 μm vs. 71 μm)	Thicker ventrally (70 μm vs. 10 μm)	Ventral surface of fin-ray pads	Common dorsally; ventrally on rays w/o pad only	Dense; dorsal, ventral; all fin rays
Garra cambodgiensis	Benthic	Present	4	1		Thicker ventrally (75 μm vs. 40 μm)	Thicker ventrally (60 μm vs. 10 μm)	Ventral surface of fin-ray pads	Dorsal; all fin rays	Common dorsally; ventrally on rays w/o pad only
Psilorhynchidae sucatio, P. balitora	Benthic	Present	4–6	2	Type 2	Thicker ventrally (36 μm vs. 26 μm in *P. sucatio*)	Thicker ventrally (200 μm vs. 10 μm in *P. sucatio*)	Ventral surface of fin-ray pads	Absent	Present dorsally
Psilorhynchidae pseudecheneis	Benthic	Present	9–10	3	Type 3	Thicker ventrally (80 μm vs. 32 μm)	Thicker ventrally (120 μm vs. 20 μm)	Ventral surface of fin-ray pads	Absent	Present dorsally
Catostomidae										
Cycleptus meridionalis	Benthic	Absent	0	0	–	Thicker ventrally (560 μm vs. 440 μm)	Same	Absent	Aggregated dorsally	Aggregated dorsally
Gyrinocheilidae										
Gyrinocheilus pennocki	Benthic	Present	1	1	Type 1	Thicker ventrally (40 μm vs. 28 μm)	Same	Absent	Common dorsally; ventrally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only
Balitoridae										
Annamia normani	Benthic	Present	8	4	Type 3	Thicker ventrally (70 μm vs. 35 μm)	Thicker dorsally (20 μm vs. 90 μm)	Ventral surface of fin-ray pads	Dorsally between lepidotrichia	Common dorsally; ventrally on rays w/o pad only
Sewellia lineolata, Gastromyzon sp., *Pseudogastromyzon* sp. (2)	Benthic	Present	8–13	6–8	Type 2	Thicker ventrally (30 μm vs. 10 μm in *S. lineolata*)	Thicker ventrally (40 μm vs. 10 μm in *S. lineolata & G. cranbrooki*; 60 μm vs. 40 μm in *P. fasciatus*)	Ventral surface of fin-ray pads	Common dorsally; ventrally on rays w/o pad only	Randomly
Characiformes										
Distichodontidae										
Paradistichodus dimidiatus	Demersal	Absent	0	0	–	Same	Same	Absent	Dorsal, ventral; all fin rays	Occasional; dorsal, ventral; all fin rays
Nannocharax sp. (2)	Benthic	Absent	0	1–2, tips only	–	Same	Same	Absent	Absent	Absent
Crenuchidae										
Characidium sp. (2)	Benthic	Present	2–3	1–2	Type 1	Thicker ventrally (60 μm vs. 20 μm)	Same	Ventral surface of fin-ray pads	Ventral, dorsal; present in pads	Common dorsally; ventrally on rays w/o pad only
Melanocharacidium pectorale	Benthic	Present	3	2	Type 1	Thicker ventrally (60 μm vs. 30 μm)	Thicker dorsally (30 μm vs. 10 μm)	Ventral surface of fin-ray pads	Common dorsally; ventrally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only

TABLE 1. *General features and histological summary of the paired fins of taxa examined*

Taxon	Swimming position	Fin-ray pad	No. of fin-rays with pads		Pad type	Ventral/dorsal epidermal thickness	Ventral/dorsal subdermal thickness	Unculi distribution	ASC distribution	Mucocyte distribution
			Pectoral	Pelvic						
Parodontidae										
Apareiodon orinocensis	Benthic	Present	6	2	Type 3	Thicker ventrally (150 μm vs. 50 μm)	Thicker dorsally (150 μm vs. 20 μm)	Absent	Dorsally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only
Siluriformes										
Ictaluridae										
Ictalurus punctatus	Benthic	Absent	0	0	–	Same	Same	Absent	Dense; dorsal, ventral; all fin rays	Dense; dorsal, ventral; all fin rays
Noturus eleutherus	Benthic	Absent	0	0	–	Same	Same	Absent	Dense; dorsal, ventral; all fin rays	Dense; dorsal, ventral; all fin rays
Sisoridae										
Pseudecheneis cf. crassicauda	Benthic	Present, ridged	1	2	–	Thicker ventrally (180 μm vs. 80 μm)	Thicker ventrally (390 μm vs. 160 μm)	Ventral surface of fin-ray pads	Common dorsally; ventrally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only
Myersglanis blythii	Benthic	Present, ridged	1	1	–	Thicker ventrally (70 μm vs. 50 μm)	Thicker ventrally (260 μm vs. 20 μm)	Ventral surface of fin-ray pads	Common dorsally; ventrally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only
Mochokidae										
Chiloglanis sp. (2)	Benthic	Absent	0	0	–	Same	Same	Absent	Dense; dorsal, ventral; all fin rays	Dense; dorsal, ventral; all fin rays
Euchilichthys royauxi	Benthic	Absent	0	0	–	Same	Same	Absent	Dense; dorsal, ventral; all fin rays	Dense; dorsal, ventral; all fin rays
Amphiliidae										
Amphilius platychir	Benthic	Present	1	1	–	Thicker ventrally (140 μm vs. 110 μm)	Thicker ventrally (290 μm vs. 190 μm)	Ventral surface of rays 1–3	Common dorsally; ventrally on rays w/o pad only	Common dorsally; ventrally on rays w/o pad only

Pad Type, refers to type of pad present (as detailed in text and Fig. 8) in nonsiluriform ostariopysans.

scantly distributed. Unculi are absent. In *Zacco* cf. *platypus* (Cyprinidae; Fig. 3A,H), the pectoral fin is similar to that of *A. alburnus* except that the entire epidermis is thicker in terms of cell number (~7 cell layers thick; ~15 μm).

The pectoral fins of the North American cyprinids *Phenacobius catostomus* and *Erimystax dissimilis* are similar to that of *Zacco* cf. *platypus*, but the epidermis is slightly thicker (~63 μm in *P. catostomus*; 48–63 μm in *E. dissimilis*), and there are Alarm substance cells present in the epidermis between lepidotrichia on both dorsal and ventral surfaces of the fins in both species. In *E. dissimilis* (Fig. 3I), the ventral epidermis is slightly thicker than the dorsal epidermis (~60 μm versus ~48 μm). Taste buds are common features of the superficial layers of the epidermis and are randomly distributed over both dorsal and ventral surfaces along the entire length of the fin in *E. dissimilis* (Fig. 3I).

The histology of the pectoral fin of *Gobio* sp. (Cyprinidae; Fig. 3J) is generally similar to that described for the aforementioned species of cyprinids. The epidermis ventral to the first and second rays is notably thicker (~24 μm) than the epidermis on the dorsal surface (~18 μm). Taste buds are also present but only on the ventral surface of the pectoral fin in this species.

In the benthic *Labeo* sp. (Cyprinidae: Fig. 3E,K,L), unculiferous paired-fin pads are present on the ventral surface below the four anteriormost pectoral-fin rays (Fig. 3E) and the anteriormost pelvic-fin ray (the latter not examined histologically). The epidermis of the pectoral fin is represented by a thick layer around the entire fin, thickest around the anteriormost rays, decreasing slightly in thickness toward the posterior. The epidermis ventral to the anteriormost rays is only slightly thicker (2–3 cell layers thicker; ~78 μm) than the epidermis dorsal to these rays (~71 μm). The superficial layers of the epidermis directly ventral to the ventral hemitrichium of the three anteriormost rays are keratinized and differentiated into an unculiferous layer (Fig. 3L). The epidermis immediately deep to this unculiferous layer contains only typical epidermal cells. However, in the epidermis where unculi are absent, a dense assemblage of ASCs is present that abut the basal lamina of the epidermis. Mucocytes are also common in the superficial layer of the epidermis dorsal to the lepidotrichia and less common in the epidermis ventral to the lepidotrichia. Taste buds are randomly distributed over the dorsal surface of the pectoral fin and on the ventral surface, but only on those areas of the epidermis lacking unculi. A conspicuous expanded layer of tissue from the subepidermal region is present between the thin dermis and the ventral hemitrichium of the four anteriormost rays (Fig. 3L). This expansion is most pronounced on the three anteriormost rays and is composed of dense, regularly arranged con-

Fig. 3. Transverse sections through the pectoral fins of select cyprinoid cypriniform fishes. (**A**) Complete section of the pectoral fin of *Zacco* cf. *platypus* (UAIC 14181.06). (**B**) Complete section of the pectoral fin of *Gobio* sp. (UAIC 14180.50). (**C**) Complete section of the pectoral fin of *Erimystax dissimilis* (UAIC 12433.11). (**D**) Complete section of the pelvic fin of *Psilorhynchus balitora* (KU 29191). (**E**) Complete section of the pectoral fin of *Labeo* sp. (CU 92143). (**F**) Complete section of the pelvic fin of *Psilorhynchus pseudecheneis* (KU 29516). (**G**) First and second pectoral-fin rays of *Alburnus alburnus* (AMNH 20536). (**H**) First pectoral-fin ray of *Z.* cf. *platypus* (specimen as in A). (**I**) Anteriormost pectoral-fin rays of *E. dissimilis* (specimen as in C). (**J**) Anteriormost pectoral-fin rays of *Gobio* sp. (specimen as in B). (**K**) Anteriormost pectoral-fin rays of *Labeo* sp. (specimen as in E). (**L**) Close up of dashed box in K. (**M**) Fifth branched pectoral-fin ray of *Labeo* sp. (specimen as in E). (**N**) Anteriormost pelvic-fin rays of *P. pseudecheneis* (specimen as in F). (**O**) Close up of dashed box in N. (**P**) Anteriormost pectoral-fin rays of *Psilorhynchus sucatio* (CAS 50289). (**Q**) Close up of dashed box in P. (**R**) Fourth branched pelvic-fin ray of *P. balitora* (specimen as in D). A to F are illustrated to scale and share a single scale-bar. ASC, alarm substance cells; Bv, blood vessel; Der, dermis; DH, dorsal hemitrichium; Eder, epidermis; ImUc, immature unculi; MC, melanocyte; MT, multicellular tubercle; MUc, mature unculi; Sderm, subdermis; TB, taste bud; VH, ventral hemitrichium.

nective tissue. The presence of this dense mass of connective tissue (~63 μm in thickness) pushes the adjacent superficial layer of skin outward, resulting in the grossly observable thickness of the pectoral-fin pads.

In the benthic *Garra cambodgiensis* (Cyprinidae), unculiferous pads are present on the ventral surface of the four anteriormost rays of the pectoral fin and the two anteriormost rays of the pelvic fin (the latter not examined histologically). In this species, the epidermis ventral to the anteriormost rays is almost twice as thick (~75 μm) as the epidermis dorsal to these rays (~40 μm). Alarm substance cells are common only in the dorsal epidermis, abutting the basal lamina. Mucocytes are common in the dorsal epidermis and in the ventral epidermis of those rays lacking paired-fin pads. Taste buds are common in both the dorsal and the ventral epidermis between lepidotrichia. The subepidermal region anteroventral to the ventral hemitrichia of the four anteriormost lepidotrichia is highly vascularized. A dense aggregation of connective tissue, such as that described earlier for *Labeo* sp., is absent from the subepidermal space of this species of *Garra* but was observed in a congener, *Garra* sp. (Fig. 4A,B). The pectoral fin of this latter species exhibits unculiferous pads on the ventral surface of the four anteriormost rays, making them more histologically similar to *Labeo* sp. than to *G. cambodgiensis*. Scanning electron micrographs of transverse sections through the anteriormost pad-bearing pectoral-fin rays revealed that the dense mass of connective tissue located in the subepidermal region anteroventral to the ventral hemitrichia is arranged in loose sheets (Fig. 4B) that are irregularly transversed by capillaries (not pictured). The superficial unculiferous layer of the epidermis of *Garra* sp., consisting of small acuate unculi (~10 μm in height) with slightly recurved tips (Fig. 4C), is easily dislodged. Scanning electron microscopy of areas on the surface of the pectoral-fin pad of *Garra* sp. at which the superficialmost unculiferous layer has been sloughed revealed developing unculi that are roughly cuboid, with tips that are much more blunt than on superficial unculi (Fig. 4D)

In the benthic *Psilorhynchus sucatio* (Psilorhynchidae, Fig. 3P), unculiferous pads are present on the five anteriormost rays of the pectoral fin and the two anteriormost rays of the pelvic fin (the latter was not examined histologically). Unculi are present only on the outermost portions of the pectoral-fin pad (the portion that makes contact with the substrate) and are absent on the sides of the pad. There are no ASCs in the epidermis surrounding the pectoral fin of this species, and mucocytes are present only in the dorsal epidermis. The dorsal epidermis also contains multicellular projections (tubercles) that are keratinized on their surfaces. Taste buds are present on the sides of the paired-fin pads (not photographed). The ventral epidermis is only slightly thicker (~36 μm) than the dorsal epidermis (possibly one or two cells thinner; ~26 μm). The majority of the thickness of the pad is caused by an expansion between the superficial skin layers and the ventral surface of the ventral hemitrichium (Fig. 3Q). This space is compartmentalized by bands of connective tissue stretching between the basal lamina and the ventral surface of the ventral hemitrichium. The tissue inside these compartments is similar in general appearance to undifferentiated mesenchymal cells, along with swirls of fibrous material and fibroblasts. The paired fins of *Psilorhynchus pseudecheneis* (Fig. 3F) and *Psilorhynchus balitora* (Fig. 3D) are identical to that described earlier for *P. sucatio* except that the ventral epidermis contributing to the paired-fin pads in *P. pseudecheneis* (Fig. 3N) is much thicker than the dorsal epidermis (roughly ~80 vs. ~32 μm). In this species, the majority of epidermal cells in the paired-fin pads produce unculi (Fig. 3O). Cells with unculi in various stages of development are found throughout the outermost layers of the epidermis and are present as deep as two to three cell layers distal to the stratum basale. The unculiferous superficial layer has sloughed off the outer surface of the paired-fin pads in several sections and has been replaced by a layer of cells with immature unculi, which are less keratinized than mature unculi and exhibit rounded tips (vs. sharp, slightly recurved tips in mature unculi; Fig. 4F). Thus, the superficial keratinized layer of unculiferous cells forms a single unit band covering the ventral surface of the paired-fin pad (Fig. 4E,F).

In the benthic catostomid *Cycleptus meridionalis* (Fig. 5A,H–J), grossly obvious paired-fin pads are absent, but the epidermis on the ventral surface of the pectoral fin is thicker than that of the dorsal surface (roughly 440 vs. 560 μm, respectively). Alarm substance cells and mucocytes are aggregated in the dorsal epidermis posterior to the anteriormost ray (Fig. 5H,J). Mucocytes are aggregated in invaginations of the dorsal epidermis, forming multicellular gland-like structures (not photographed), with an amucocytic duct leading to the surface of the epidermis. Immediately deep to the epidermis is a thin layer of dermis forming digitate invaginations of the dermis into the basal layer of the epidermis (Fig. 5H). Blood vessels are common in these digitate projections. Deep to the digitate projections, the dermis is composed of dense regular connective tissue with thick collagenous fibers and fibroblasts, which most accurately describe the stratum compactum of the dermis (Fig. 5I). On the ventral side, deep to this layer of dense regular connective tissue, is a layer of mucus connective tissue with sparse fibers and abundant ground substance (Fig. 5I).

In the benthic *Gyrinocheilus pennocki* (Gyrinocheilidae), obvious paired-fin pads are present ventral to the two anteriormost pectoral-fin rays (Fig. 5B) and the anteriormost pelvic-fin ray (the latter

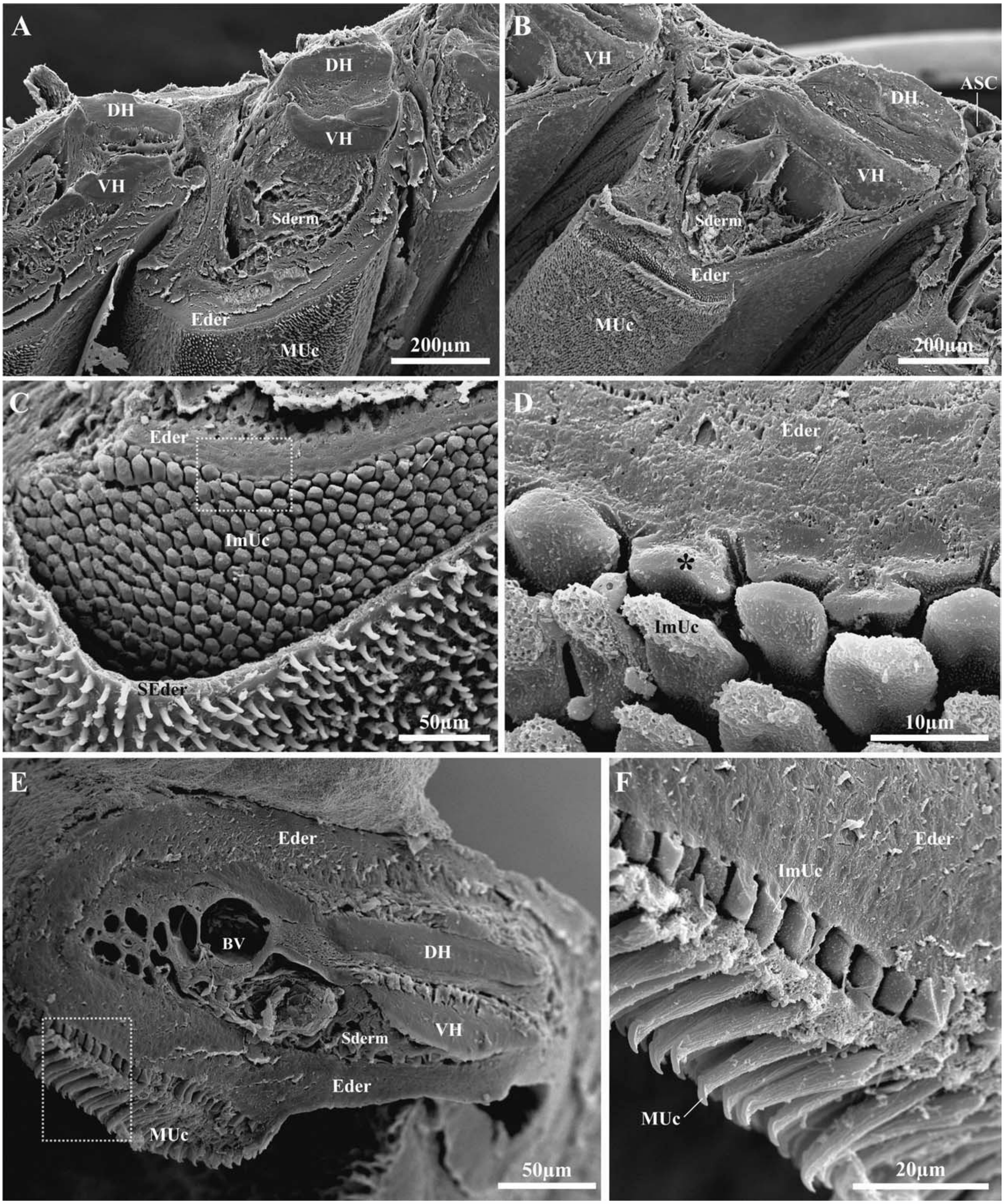

Fig. 4. Scanning electron micrographs of transverse sections through the pectoral fins of *Garra* sp. (KU 40623) and *Psilorhynchus pseudecheneis* (KU 40560). (**A,B**) Anteriormost pectoral-fin rays of *Garra* sp. (**C**) Close up of outermost layers of epidermis below second pectoral-fin ray of *Garra* sp. (**D**) Close up of dashed box in C showing developing unculi; asterisk highlights a single developing unculus. (**E**) Anteriormost pectoral-fin ray of *P. pseudecheneis*. (**F**) Close up of dashed box in E showing mature and developing unculiferous layers. ASC, alarm substance cells; Bv, blood vessel; DH, dorsal hemitrichium; Eder, epidermis; ImUc, developing unculi; MUc, mature unculi; Sderm, subdermis; SEder, sloughed epidermis; VH, ventral hemitrichium.

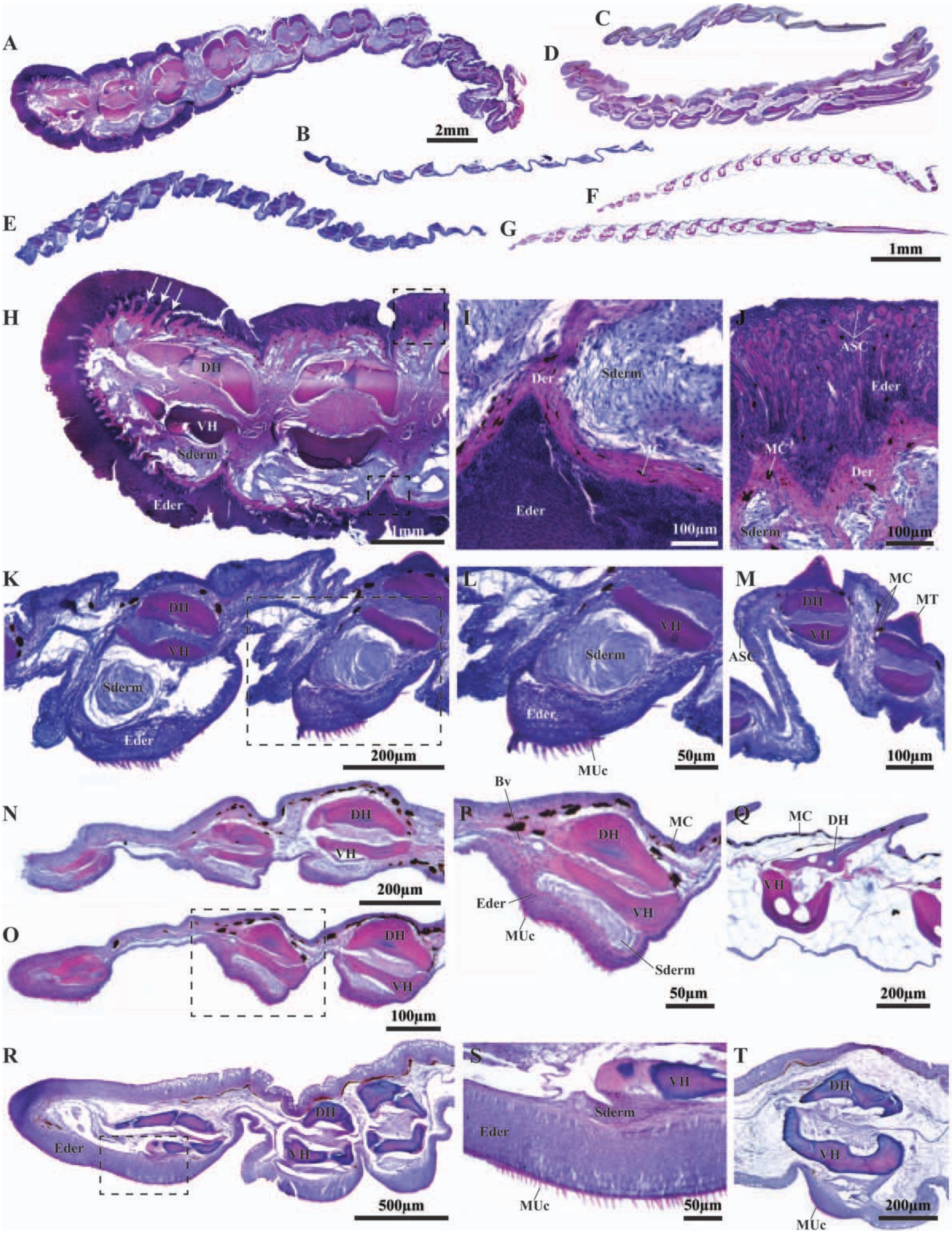

Fig. 5. Transverse sections through the paired fins of select cobitoid cypriniform fishes. (**A**) Complete section of the pectoral fin of *Cycleptus elongatus* (UAIC 14922.01). (**B**) Complete section of the pectoral fin of *Gyrinocheilus pennocki* (UAIC 14180.51). (**C**) Complete section of the pelvic fin of *Pseudogastromyzon fasciatus* (AMNH 11054). (**D**) Complete section of the pectoral fin of *P. fasciatus* (same specimen as in C). (**E**) Complete section of the pectoral fin of *Annamia normani* (BMNH uncat.). (**F**) Complete section of the pelvic fin of *Sewellia lineolata* (UAIC 14169.43). (**G**) Complete section of the pectoral fin of *Sewellia lineolata* (specimen as in F). (**H**) Anteriormost pectoral fin rays of *C. elongatus* (specimen as in A). White arrows point to papillae-like invaginations of dermis. (**I**) Close up of lower dashed box in H. (**J**) Close up of upper dashed box in H. (**K**) Anteriormost pectoral-fin rays of *A. normani* (specimen as in E). (**L**) Close up of dashed box in K. (**M**) Third branched pectoral-fin ray of *A. normani*. (**N**) Anteriormost pectoral-fin rays of *S. lineolata* (specimen as in F). (**O**) Anteriormost pelvic-fin rays of *S. lineolata* (specimen as in F). (**P**) Close up of dashed box in O. (**Q**) Fifth branched pelvic-fin ray of *S. lineolata* (specimen as in F). (**R**) Anteriormost pelvic-fin rays of *P. fasciatus* (specimen as in C). (**S**) Close up of dashed box in R. (**T**) First branched pelvic-fin ray of *P. fasciatus* (specimen as in C). (B)–(G) are illustrated to scale and share a single scale-bar. Scale-bar for A is situated below lower right-hand side of image. ASC, alarm substance cells; Bv, blood vessel; Der, dermis; DH, dorsal hemitrichium; Eder, epidermis; MC, melanocyte; MT, multicellular tubercle; MUc, mature unculi; Sderm, subdermis; VH, ventral hemitrichium.

was not examined histologically). The epidermis of the first pectoral ray is only slightly thicker ventrally than dorsally (∼40 vs. 28 μm). A keratinized epidermis is superficial to the ventral dermis, but no unculi could be detected. Alarm substance cells are present in both the dorsal and the ventral epidermis, but in the ventral epidermis they are absent from the pad of the first ray. Mucocytes are aggregated dorsally and ventrally with a similar distribution to the ASCs. A small pad of connective tissue is present in the subepidermal region of the second ray only, deep to the superficial skin layers and anteroventral to the ventral hemitrichium.

In the benthic *Annamia normani* (Balitoridae), well-developed unculiferous pads are present along the ventral surface of the anteriormost pectoral- (Fig. 5E,K) and pelvic-fin rays. The epidermis contributing to the pectoral-fin pads is at least twice as thick as the dorsal epidermis of the fin (∼70 vs. 35 μm). Alarm substance cells are present only in the dorsal epidermis between lepidotrichia (Fig. 5M). Mucocytes are common dorsally but are absent from the dorsal epidermis of lepidotrichia having pads (present between these lepidotrichia). Deep to the ventral superficial skin layers and ventral to the ventral hemitrichium of those pectoral rays with pads is a large mass of fibrous material, fibroblasts and cells that look like undifferentiated mesenchymal cells (Fig. 5K,L). The fibers of this mass have a swirl-like orientation (Fig. 5L). Keratinized tubercles are common in the ventral and dorsal epidermis immediately adjacent to lepidotrichia (Fig. 5M).

In the benthic dwelling *Sewellia lineolata* (Balitoridae), well-developed unculiferous pads are present along the ventral surface of the anteriormost pectoral- and pelvic-fin rays (Fig. 5F,G). Alarm substance cells are located in the dorsal epidermis between lepidotrichia and in the ventral epidermis posterior to those fin rays bearing pads. Mucocytes are randomly distributed ventrally and dorsally. The epidermis contributing to the paired-fin pads in both fins is slightly thicker than the fins dorsal epidermis (roughly 2–3 cell layers thicker; ∼30 vs. 10 μm). Dense aggregations of connective tissue, composed of cells that look like undifferentiated mesenchymal cells, fibrous material, and fibroblasts, are located between the ventral hemitrichium of those rays associated with paired-fin pads and the superficial skin layers (Fig. 5P). Taste buds are also present, ventrally and dorsally, but are absent from the unculiferous surfaces of the paired-fin pads. Randomly distributed tubercles are common on the dorsal surface of both paired fins. The dorsal hemitrichia of more posteriorly situated pectoral- and pelvic-fin rays exhibit a large process that extends posterodorsally but does not puncture the epidermis (Fig. 5Q). These dorsal hemitrichial processes are much larger in rays of the pelvic fin than in the pectoral fin.

In the benthic *Pseudogastromyzon fasciatus* (Balitoridae; Fig. 5C–D,R–T), well-developed unculiferous pads are present on the anteriormost rays of both paired fins that are similar histologically to those described for *S. lineolata*, except for the following differences. Alarm substance cells are common throughout the epidermis covering the entire dorsal surface of both paired fins (Fig. 5R), as are large keratinized tubercles. Mucocytes are very common in the epidermis dorsally and ventrally between lepidotrichia. Cell layers deep to the keratinized unculiferous superficial layer of the paired-fin pads do not exhibit immature unculi (Fig. 5S), and there is no sign of unculi development (i.e., there does not appear to be a replacement unculiferous layer deep to the superficialmost layer).

Characiformes. We examined 10 species from three families of characiforms: Crenuchidae, Distichodontidae, and Parodontidae.

The paired fins of the demersal distichodontid *Paradistichodus dimidiatus* lack obvious pads. The pectoral fins of this species are histologically similar to those described earlier for *Chanos* and *Alburnus*, differing only in the thickness of the epidermis, which is extremely thin (∼5 μm around the anteriormost ray). In the semidemersal distichodontids, *Nannocharax faciatus*, *N. parvus*, and *N. schoutedeni* the pectoral fins are histologically similar to those of *Paradistichodus*. However, the skin surrounding the entire distal tips of the two anteriormost rays of the pelvic fin is notably thickened compared to that surrounding more proximal portions of these rays or more posterior rays (Fig. 6A). The epidermis of these thickened distal regions, which is surrounded by a well-developed keratinized unculiferous layer, is uniform in thickness around the lepidotrichia (∼80–100 μm around the anteriormost ray in *N. schoutedeni*; Fig. 6K) and almost twice as thick as the epidermis surrounding comparable regions of more posterior rays (∼40 μm around the tip of the first branched pelvic-fin ray of *N. schoutedeni*; Fig. 6L). The dermis surrounding the distal tips of the two anteriormost rays is highly reduced to the point where the basal layers of the epidermis appear to abut the superficial surfaces of the hemitrichia. Alarm substance cells are absent from the epidermis surrounding the distal tips of the two anteriormost pelvic-fin rays but are present in the epidermis surrounding more posterior rays (Fig. 6L). Mucocytes appear to be absent from the pelvic fin in all three species of *Nannocharax* examined.

In species of the benthic *Characidium* (Crenuchidae: *C. fasciatum* and *C. zebra*) that we examined, paired-fin pads are present along the ventral surface of the three anteriormost rays of the pectoral fin and the two anteriormost rays of the pelvic fin. In *C. zebra*, the epidermis ventral to those pectoral-fin rays possessing pads is much thicker than the epidermis dorsal to these rays (∼60 vs. 20–30 μm, respectively). Deep to the epidermis, the dermis is poorly developed and consists of a thin band

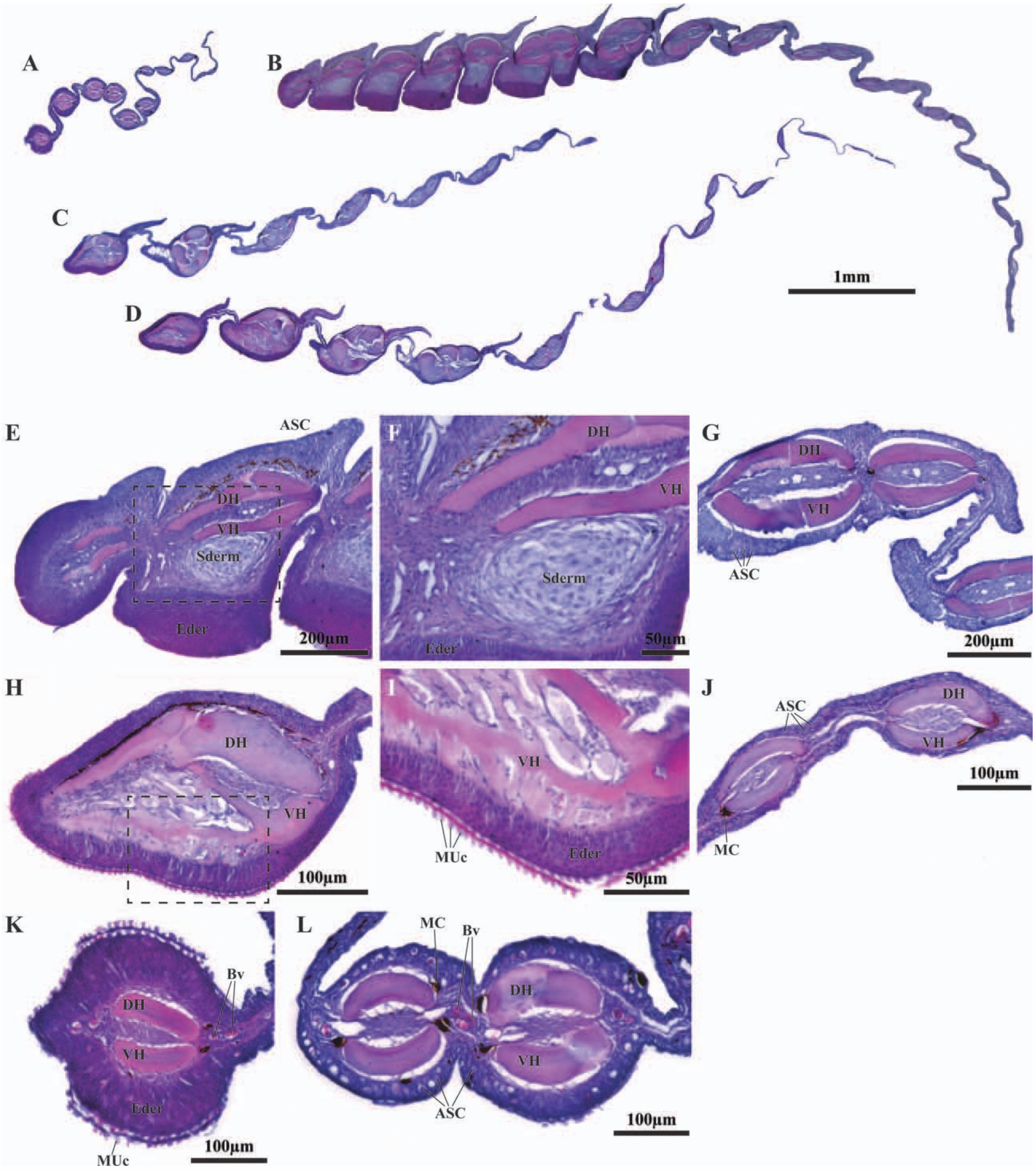

Fig. 6. Transverse sections through the paired fins of select characiform fishes. (**A**) Complete section of the pelvic fin of *Nannocharax schoutedeni* (AUM 51315). (**B**) Complete section of the pectoral fin of *Apareiodon orinocensis* (AUM 43666). (**C**) Complete section of the pelvic fin of *Melanocharacidium pectorale* (AUM 40191). (**D**) Complete section of the pectoral fin of *M. pectorale* (specimen as in C). (**E**) Anteriormost pectoral-fin rays of *A. orinocensis* (specimen as in B). (**F**) Close up of upper dashed box in E. (**G**) Fourth and fifth branched pectoral-fin rays of *A. orinocensis* (specimen as in B). (**H**) Anteriormost pectoral-fin rays of *M. pectorale* (specimen as in C). (**I**) Close up of dashed box in H. (**J**) Fifth and sixth branched pectoral-fin rays of *M. pectorale* (specimen as in C). (**K**) Anteriormost pelvic-fin ray of *N. schoutedeni* (specimen as in A). (**L**) First branched pelvic-fin ray of *N. schoutedeni* (specimen as in A). (A)–(D) are illustrated to scale and share a single scale-bar. ASC, alarm substance cells; Bv, blood vessel; DH, dorsal hemitrichium; Eder, epidermis; MC, melanocyte; MUc, mature unculi; Sderm, subdermis; VH, ventral hemitrichium.

of connective tissue around lepidotrichia. The dermis in certain areas (e.g., dorsal to the dorsal hemitrichium of the anteriormost ray) is reduced to the point that the epidermis appears to abut the outer surface of the hemitrichium. The superficial layer of the epidermis is keratinized ventral to the anteriormost ray and contains an approximately equal number of unculiferous and nonunculiferous cells. Mucocytes are randomly distributed throughout the epidermis of the paired fins except for keratinized regions around the paired-fin pads.

In the benthic *Melanocharacidium pectorale* (Crenuchidae), well-developed unculiferous paired-fin pads are present along the ventral surface of the three anteriormost pectoral-fin rays and the anteriormost pelvic-fin ray (Fig. 6C,D). The epidermis ventral to those rays having paired-fin pads is notably thicker than the epidermis dorsal to these rays in both the pectoral and the pelvic fins (~60 vs. 30 μm and ~30 vs. 20 μm, respectively). In both paired fins, the dermis is reduced to the point that the epidermis appears to abut the outer surface of each hemitrichium (Fig. 6I,J). The superficial layer of the epidermis is keratinized in both paired fins and at least one layer of immature unculi can be identified deep to the outermost layer of mature unculi under the anteriormost ray of the pectoral fin (Fig. 6I). Alarm substance cells are absent from the epidermis contributing to the paired-fin pads but are distributed throughout the remainder of the epidermis surrounding the paired fins, particularly between lepidotrichia (Fig. 6J).

In the benthic *Apareiodon orinocensis* (Parodontidae), paired-fin pads are present along the ventral surface of the six anteriormost pectoral-fin rays (Fig. 6B) and the two anteriormost pelvic-fin rays. The epidermis ventral to those pectoral-fin rays possessing pads is greatly thickened compared to the epidermis dorsal to those rays (~150 vs. 50 μm) and is keratinized, with keratinization obvious deep into the epidermal layers (Fig. 6E). Unculi are completely absent from the paired fins. Deep to the ventral superficial skin layers and anteroventral to the ventral hemitrichium of those pectoral-fin rays with pads, exists a large mass of fibrous material, fibroblasts and cells that appear to be undifferentiated mesenchymal cells (Fig. 6F). Alarm substance cells are completely absent from the epidermis of the four anteriormost rays (both dorsally and ventrally; Fig. 6E) and are present only in the epidermis dorsal to more posterior rays (Fig. 6G).

Siluriform Ostariophysans

Siluriformes. We examined 10 species of catfishes, representing four families: Amphiliidae, Ictaluridae, Mochokidae, and Sisoridae. We first describe the histology of the paired fins of the ictalurids, which we consider to represent the "plesiomorphic" paired-fin bauplan for catfishes, before moving on to describe the more "derived" paired fins of other families.

In the semidemersal *Ictalurus punctatus*, no obvious paired-fin pads are present (Fig. 7A,G) and the epidermis of both the dorsal and ventral surfaces of the paired fins are roughly equal in thickness (110 vs. 130 μm). As is common in catfishes (Arratia and Huaquin, 1995; Arratia, 2003) an extraordinarily high density of ASCs is present in the epidermis. However, ASCs appear to be restricted to deep layers of the epidermis (Fig. 7G,H). Superficial to the ASCs, mucocytes occur in high densities. Deep to the superficial skin layers and in the osseus groove running along the anterior edge of the spinous lepidotrichium a large mass of highly vascularized connective tissue resides (Fig. 7G). In contrast, immediately below the superficial skin layers and the anterodorsal and anteroventral surface of the groove running along the center of the spinous lepidotrichium resides aggregates of secretory cells that stain intensely eosinophilic (Fig. 7G). These secretory cells most likely represent the venom producing cells of the venom gland that commonly runs along the anterior edge of the spinous pectoral-fin ray in catfishes (Halstead et al., 1953; Wright, 2009). The subepidermal space surrounding the lepidotrichia posterior to the first consists of a thin layer of collagenous fibers and vascular canals (Fig. 7I) and is similar to that described for *Chanos chanos*, *Zacco* cf. *platypus*, and *Alburnus alburnus* earlier. The superficial layer of the epidermis ventral to the spinous lepidotrichium is weakly keratinized, and unculi are completely absent. Taste buds are randomly distributed along the superficial surface of the entire pectoral fin. The histology of the pectoral fin of *Noturus flavus* and *N. eleutherus* is largely identical to that described for *I. punctatus*. The pectoral fins of the three species of mochokid examined (Fig. 7B,D) were also very similar histologically to those of the ictalurids.

In the benthic *Pseudecheneis* cf. *crassicauda* (Sisoridae), a large pad, transversed with ridges, is present ventral to the anteriormost lepidotrichium in both paired fins (Fig. 7F,M). The histology of the pectoral fin was not examined, and the following description focuses only on the pelvic fin. The histology of the pelvic fin posterior to the anteriormost lepidotrichium (Fig. 7O) is similar to that described earlier for *I. punctatus*. The subepidermal region between the superficial skin layers and the ventral surface of the anteriormost ray, however, is highly thickened compared to the same region dorsal to the ray (Fig. 7M). This thickened region contains a network of small blood vessels and one large blood vessel immediately ventral to the ray. The epidermis dorsal to the posterodorsalmost portion of the anteriormost lepidotrichium is identical to that surrounding the remaining lepidotrichia. The epidermis covering the anteriormost portion of the anteriormost lepidotrichium, however, is highly keratinized with numerous unculiferous projections that are continuous around the leading edge of the fin (Fig. 7M). No ASCs or mucocytes are present in this portion of the epidermis. Ventral to the anteriormost lepidotrichium,

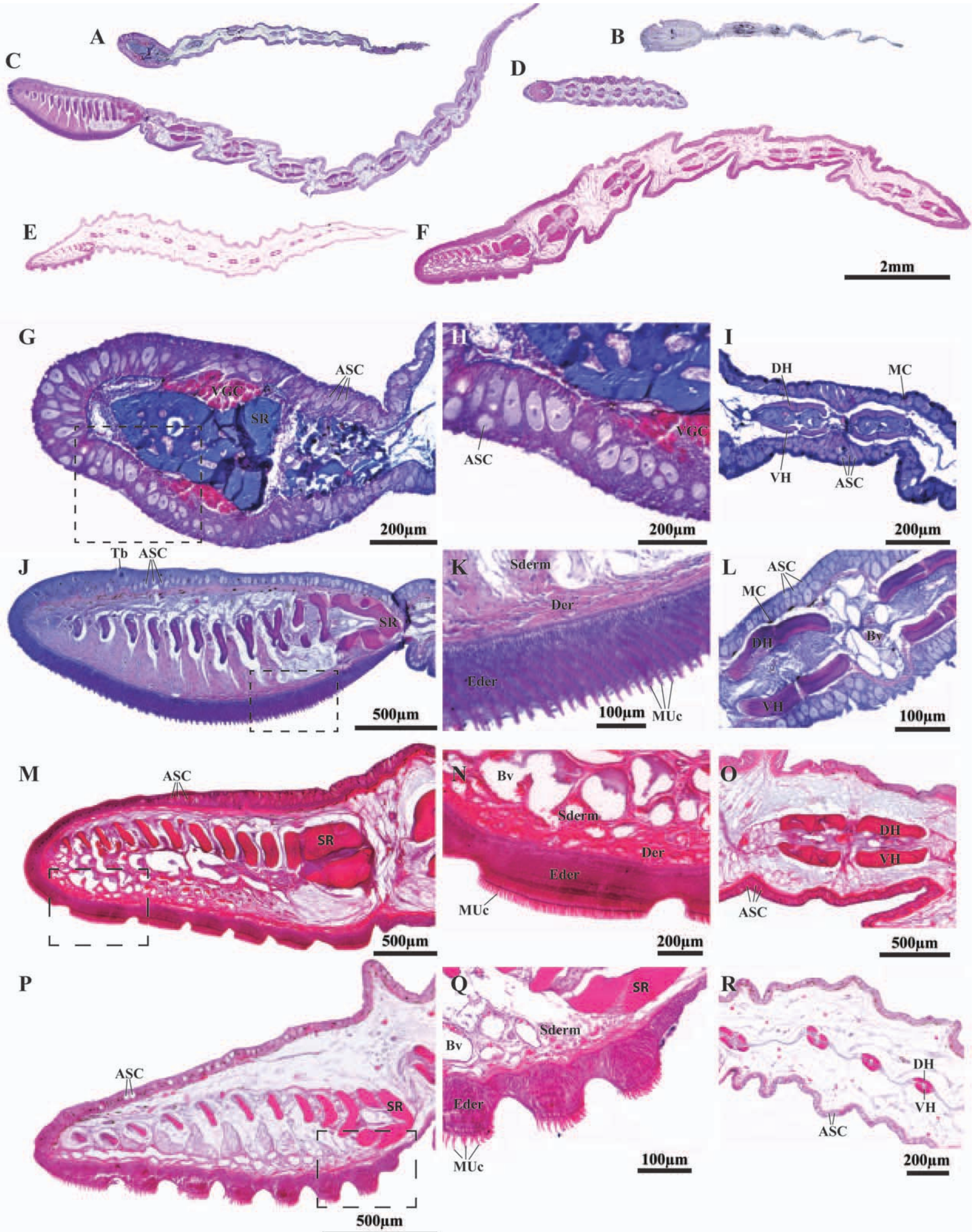

Fig. 7. Transverse sections through the paired fins of select siluriform fishes. (**A**) Complete section of the pectoral fin of *Ictalurus punctatus* (TCWC 15705.01). (**B**) Complete section of the pectoral fin of *Euchilichthys royauxi* (CU 91380). (**C**) Complete section of the pectoral fin of *Amphilius platychir* (BMNH 1980.7.24.56-102). (**D**) Complete section of the pectoral fin of *Chiloglanis congicus* (AUM 51304). (**E**) Complete section of the pectoral fin of *Myersglanis blythii* (KU 40556). (**F**) Complete section of the pelvic fin of *Pseudecheneis* cf. *crassicauda* (KU 40671). (**G**) Spinous (anteriormost) pectoral-fin ray of *I. punctatus* (specimen as in A). (**H**) Close up of dashed box in G. (**I**) Fourth branched pectoral-fin ray of *I. punctatus* (specimen as in A). (**J**) Spinous (anteriormost) pectoral-fin ray of *A. platychir* (specimen as in C). (**K**) Close up of dashed box in J. (**L**) Fourth branched pectoral-fin ray of *A. platychir* (specimen as in C). (**M**) Anteriormost pelvic-fin ray of *P.* cf. *crassicauda* (specimen as in F). (**N**) Close up of dashed box in M. (**O**) Third branched pelvic-fin ray of *P.* cf. *crassicauda* (specimen as in F). (**P**) Spinous (anteriormost) pectoral-fin ray of *M. blythii* (specimen as in E). (**Q**) Close up of dashed box in P. (**R**) Third to fourth branched pectoral-fin rays of *M. blythii* (specimen as in E). (A)–(F) are illustrated to scale and share a single scale-bar. ASC, alarm substance cells; Bv, blood vessel; Der, dermis; DH, dorsal hemitrichium; Eder, epidermis; MC, melanocyte; MUc, mature unculi; Sderm, subdermis; SR, spinous ray; VGC, venom-gland cells; VH, ventral hemitrichium.

the epidermis is marked by a series of transverse ridges that cross the surface of the pad (Fig. 7N). The epidermis contributing to the ridges is very thick compared to the epidermis of the intervening grooves (~180 vs. 80 μm). The superficial epidermis of each ridge is heavily keratinized and exhibits a well-developed layer of unculi (Fig. 7N). Deep to this superficial unculliferous layer are three layers of unculliferous cells in different stages of development. The epidermis of each "furrow" between the ridges is highly squamous, and there is no evidence of keratinization. The benthic *Myersglanis blythii* (Sisoridae; Fig. 1E–H) possesses heavily ridged paired-fin pads, grossly similar to those of *Pseudecheneis* cf. *crassicauda*. The histology of the pectoral-fin pad of this species (Fig. 7E,P,Q) is very similar to that described earlier for the pelvic fin of *P.* cf. *crassicauda*.

In the benthic *Amphilius platychir* a large pad is present on the ventral surface of the anteriormost ray of both paired fins. The histology of only the pectoral fin was examined (Fig. 7C). The epidermis along the dorsal surface of the pectoral fin is similar to that described earlier for *I. punctatus*. The epidermis ventral to the highly modified anteriormost lepidotrichium is notably thicker than the epidermis dorsal to this ray (~140 vs. 110 μm) and is similar in general appearance to that of *P.* cf. *crassicauda* and *M. blythii*, except that pronounced transverse ridges are absent. Unculi are present in the outer layer of the epidermis forming the pad (Fig. 7J,K) and in the outer layer of the epidermis ventral to the next most anterior two rays. Unculiferous epidermal cells are separated from each other by a single layer of nonunculiferous cells. This presence/absence pattern of unculiferous cells throughout the epidermis ventral to the anteriormost ray is highly regular and occurs along the entire surface of the pectoral-fin pad. Deep to the unculliferous superficial cell layer are four layers of unculliferous cells in different stages of development. Like the superficialmost unculliferous cells, the developing unculliferous cells are separated from each other by a layer of nonunculiferous cells in the deeper layers of epidermis, forming a striated pattern of keratinization throughout the outer layer of the epidermis, from the deep epidermis to the superficial layer.

DISCUSSION

Paired-fin Pads of Nonsiluriform Ostariophysan Fishes

Our histological investigation of the paired fins of demersal and benthic ostariophysan fishes documents a striking, and previously unrecognized, diversity in cell layers (both epidermal and subepidermal) involved in the apparent convergent evolution and development of externally homogenous paired-fin pads commonly associated with rheophilic habits globally. Our findings contrast with the historical concept that such pads are formed only by a thickening of the epidermis ventral to the rays that bear them (Chang, 1945). Though this is certainly the case for a number of the taxa that we examined (e.g., *Kneria paucisquamata*, *Garra cambodgiensis*, *Characidium* spp., and *Melanocharacidium pectorale*), in many cypriniform taxa (e.g., *Labeo* sp., *Garra* sp., *Psilorhynchus sucatio, P. balitora*, *Gyrinocheilus pennocki*, and all members of the Balitoridae examined) the epidermis ventral to the anteriormost rays of the paired fins is equal in thickness or only marginally thicker than that situated dorsal to these rays. In these latter taxa, a dense mass of undifferentiated loose or dense connective tissue is situated in the dermis, deep to the epidermis and ventral to the ventral hemitrichium. This subepidermal structure appears to displace the overlying epidermal layer, causing the skin below the ray to appear thickened externally. Interestingly, the cypriniforms *Annamia normani* and *Psilorhynchus pseudecheneis* and the characiform *Apareiodon orinocensis* exhibit paired-fin pads that represent a combination of epidermal and subepidermal modification, including a greatly thickened epidermis (which may be up to three times as thick as the epidermis covering the dorsal surface of the paired fins; Figs. 3N, 5K, and 6E) combined with a dense mass of subepidermal connective tissue between the epidermis and the ventral surface of the ventral hemitrichium. When present, the subepidermal mass of connective tissue is situated along the anteroventral edge of the ventral hemitrichium, with the posteroventral edge either abutting the basal layers of the epidermis or separated from this layer by thin strands of connective tissue (as exemplified by *Labeo* sp.; Fig. 3K). Light microscopy indicates that the mass of connective tissue is similar in appearance to undifferentiated mesenchymal tissue, but histochemistry on these structures is necessary to confirm their exact composition. In most cases, the fibers contributing to the mass are tightly packed together with little space apparent between adjacent fibers (e.g., as exemplified by *Labeo* sp. [Fig. 3K] or *Apareiodon orinocensis* [Fig. 6E,F]). In *Psilorhynchus sucatio*, the fibers of the mass appear loosely connected, with large spaces between adjacent fibers (Fig. 3P,Q). Examination of multiple transverse sections for particular species suggests that the structure is homogeneous along the length of the ray (i.e., from proximal to distal), differing only in terms of circumference (decreasing distally as the ray tapers toward its tip). Scanning electron micrographs of this structure in *Garra* sp. and *Psilorhynchus pseudecheneis* provided no additional insight into its cellular composition (Fig. 4) and further investigation with transmission electron microscopy (TEM) is warranted.

Based on the arrangement of the integumental layers ventral to the anteriormost paired-fin rays of the nonsiluriform ostariophysan fishes that we

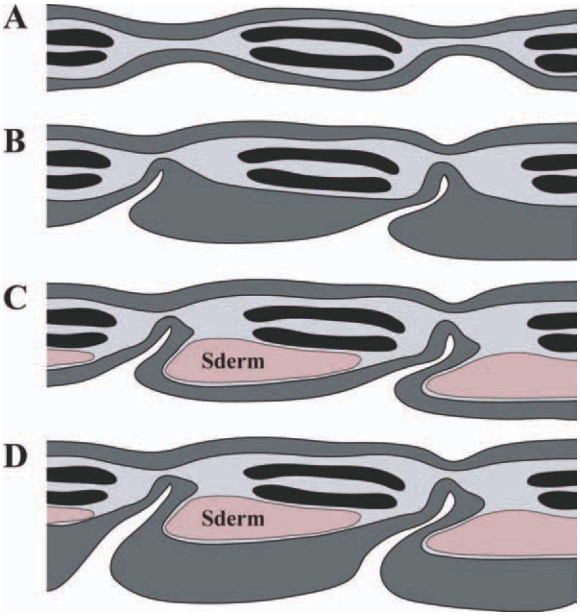

Fig. 8. Schematic showing composition of paired-fin pads in nonsiluriform ostariophysan fishes. (**A**) Paired-fin pads absent, epidermis of similar thickness and composition around entire fin. (**B**) Type 1 paired-fin pads, formed entirely by epidermis, which is markedly thicker and usually with different cellular composition on ventral surface of fin compared to epidermis of dorsal surface of fin. (**C**) Type 2 paired-fin pads, formed by modification of dermis and subdermis (subderm); epidermis of paired-fin pad typically of similar thickness or only slightly thicker, but usually with different cellular composition, to epidermis of dorsal surface of fin. (**D**) Type 3 paired-fin pads, as in Type 2 pads but epidermis of pad greatly thickened. Black, bone; dark gray, epidermis; light gray, dermis; and light red, subdermis. Abbreviation: Sderm, subdermis.

have examined, three distinct types of paired-fin pads (1–3) can be identified (Fig. 8). Type 1 (Fig. 8B) pads are formed by a thickening of the epidermis with no contribution from the subepidermal layers. Type 2 (Fig. 8C) pads are formed by the presence of a large mass of subdermal connective tissue situated ventral to the ray that displaces the overlaying epidermis (the latter similar in thickness or only slightly thicker than the epidermis along the dorsal surface of fin). Type 3 (Fig. 8D) pads are similar to Type 2 pads with the addition of a greatly thickened epidermis.

Within the set of taxa that we have examined, Type 3 pads were least common, followed equally by Type 2 and 1 pads. Within the Characiformes, Type 1 pads appear to be restricted to members of the Characidiinae (sensu Buckup, 1993, 1998) and Type 3 to members of the Parodontidae. Type 2 pads were not present in the benthic and rheophilic characiform taxa that we examined. Within Cypriniformes, Type 1 pads were present only within a single member of the Cyprinidae (*G. cambodgiensis*), Type 2 pads were widespread (identified in members of four out of the five families examined), and Type 3 pads were found only in a single member each of the Psilorhynchidae (*P. pseudecheneis*) and Balitoridae (*A. normani*). *Kneria paucisquamata*, the only benthic and rheophilic member of the Gonorynchiformes that we examined, exhibited Type 1 pads.

Paired-Fin Pads of Catfishes

We examined the paired-fin pads of taxa representing two of the four siluriform families from which they have been reported previously in the literature, including members of the Sisoridae and Amphiliidae. We were unable to investigate the internal anatomy of the well-developed odontode bearing pelvic-fin pad present in members of the Astroblepidae or the loricariid (Loricariidae) genus *Lithogenes* (Schaefer and Provenzano, 2008) due to the scarcity of these taxa in museum collections. As in nonsiluriform ostariophysan fishes, the epidermis contributing to the paired-fin pads of the sisorids and amphiliid examined is histologically very different from the epidermis surrounding the remainder of the fins, being heavily keratinized and stratified (with unculi producing cells), and completely devoid of ASCs (Fig. 7M,N,P,Q). The epidermis surrounding the remainder of the paired fins in these taxa, including the dorsal surface of the anteriormost ray, is densely populated with ASCs (Fig. 7O,R), and is similar in this regard to the pectoral-fin epidermis of ictalurids (Fig. 7G,I) and mochokids, which lack paired-fin pads. The deeper skin layers contributing to the paired-fin pads of the different siluriform taxa examined are generally similar, consisting of a thin, but dense, layer of dermis tightly associated with the inner surface of the basal lamina of the epidermis, and a greatly expanded subdermis composed of connective tissue irregularly interspaced with vascular tissue. The arrangement of the connective tissue of the subdermis is reminiscent of the subdermal mass of connective tissue present in Type 2 and 3 paired-fin pads of nonsiluriform ostariophysan fishes described earlier. Compared to a "typical" catfish (e.g., *Ictalurus punctatus*; Fig. 7G), the arrangement of the deep skin layers of the pectoral fin ventral to the anteriormost ray in *Amphilius platychir* (Fig. 7J) and *Myersglanis blythii* (Fig. 7P) are strikingly different. Many of the differences seem related to the gestalt of the anteriormost ray, which is spinous and hypertrophied in typical catfishes versus pectinate in sisorids and amphiliids (Hora, 1922, 1930), and the absence of the venom gland (which has been secondarily lost in sisorids and amphiliids; Wright, 2009). The anteriormost ray of the pelvic fin is similarly pectinate in *Pseudecheneis* cf. *crassicauda* (Fig. 7M).

Externally, the most conspicuous feature of the paired-fin pads in members of the Sisoridae is a prominent series of unculiferous ridges and deep grooves that transverse the surface of the pad (Hora, 1923a; Figs. 1F,G and 7E,F). Within the Sisoridae, a similar series of ridges and grooves is also present on the surface of the so-called "adhesive organ" located on the ventral midline between the bases of the pectoral fins (Saxena, 1961; Sinha et al., 1990; Singh and Agarwal, 1991) and may also be present along the ventral surface of the flattened mandibular barbels in some taxa (e.g., *Oreoglanis*; Ng, 2004; Vidthayanon et al., 2009). The epidermis contributing to the ridges of both the "adhesive organ" and the paired-fin pads of those taxa that have been studied to date is tightly packed with unculi producing cells (Hora, 1923a; Wu and Liu, 1940; Bhatia, 1950; Das and Nag, 2005; Fig. 7M,N,P,Q), which are arranged in a series of regular horizontal layers (or tiers; Das and Nag, 2005) with the cells of each layer uniformly exhibiting unculi at an identical stage of development (earlier stages located deeper than more advanced stages). A similar arrangement of unculi producing cells is found in the paired-fin pads of the cypriniforms *Psilorhynchus pseudecheneis* (Figs. 3Q and 4F) and *Garra* sp. (Fig. 4C,D) but were not obvious in the paired-fin pads of other nonsiluriform taxa examined. As reported previously for other sisorid taxa (Hora, 1923a; Bhatia, 1950), unculi producing cells are absent from the epidermis lining the deep grooves between ridges in the pectoral-fin pad of *Myersglanis blythii* and the pelvic-fin pad of *Pseudecheneis* cf. *crassicauda*.

Recently, Das and Nag (2005) conducted the first ultrastructural and immunohistochemical study of unculi development, focusing on the unculi producing cells in the epidermis of the "adhesive organ" of *Pseudecheneis sulcata*, but not those of the pelvic-fin pad. Using transmission electron microscopy, they elegantly documented the stages in the development of a single unculus (referred to as a spine), highlighting the role of tonofilament aggregation in unculus formation. Despite this recent advance in our understanding of unculi formation, the process of unculi replacement is still unclear. Das and Nag (2005: 236) suggest that damaged mature unculi in the "adhesive organ" of *P. sulcata* are replaced by immature unculi located in the layer below, which upon exposure to the surface "assume maturity by the clumping of tonofilaments and thickening of the plasma membrane." Though this is likely the case, it is unclear whether this process of unculi replacement occurs individually (i.e., immature unculus replaces mature unculus) or on a larger scale (i.e., in sheets as the superficial unculiferous layer of the epidermis is sloughed). We consider the later to be more likely in the unculiferous paired-fin pads of sisorids and other nonsiluriform taxa, given that mechanical damage to the pads frequently results in peeling of the entire superficialmost layer, exposing the underlying layer of immature unculi (e.g., see Fig. 4C). Interestingly, though the paired-fin pads of *Amphilius platychir* are also unculiferous, the arrangement of the unculi producing cells in the epidermis of the pectoral-fin pad of this species is markedly different from that of other ostariophysan taxa in which this character has been investigated (summarized earlier). Instead of being arranged in distinct horizontal layers throughout the superficial layers of the epidermis, unculi producing cells in *Amphilius platychir* are arranged in distinct vertical bands (each a single cell thick), separated from adjacent bands by a single nonunculiferous cell, forming a very regular striated pattern of keratinization throughout the superficial epidermal layers of the pad (Fig. 7K). Based simply on the distribution of unculi producing and nonunculi producing cells, it is likely that unculi are replaced on an individual basis in the pectoral-fin pad of *Amphilius platychir*. Keratinization of the epidermis, though widespread in terrestrial vertebrates, is generally considered to be uncommon among ray-finned fishes (Mittal and Banerjee, 1980; Roberts and Bullock, 1980; Das and Nag, 2008) but appears to be particularly widespread in members of the Ostariophyi (Wiley and Collette, 1970; Mittal and Whitear, 1979; Roberts, 1982; Pinky et al., 2004). When present, keratinous structures are typically restricted to the outer layers of the epidermis. In *Amphilius platychir*, bands of keratinization represented by unculi formation extend deep into the epidermal layer of the pectoral-fin pad. This pattern of keratinization is (to the best of our knowledge) unique among fishes, and possibly also vertebrates. Additional members of the Amphiliidae should be investigated to assess whether this unique feature of the pectoral-fin epidermis represents an autapomorphy for *A. platychir* or is more widespread among amphiliid catfishes.

Comparison with Nonostariophysan Fishes

Several groups of percomorph fishes (sensu Patterson and Johnson, 1993) exclusively inhabit the benthic region of rivers and streams, including (but by no means restricted too) members of the scorpeaniform family Cottidae (e.g., *Cottus*; Freyhof et al., 2005) and members of the perciform family Percidae (e.g., *Romanichthys*, *Zingel*, and darters of the tribe Etheostomatinae; Collette, 1965; Song et al., 1998; Kottelat and Freyhof, 2007). Many of these benthic and rheophilic percomorph taxa exhibit thickened skin around the rays of the fins that are in contact with the substrate, including the anterior rays of the anal fin, the outer rays of the pelvic ray, and the "lowermost" rays of the vertically orientated pectoral fin. Small benthic percomorph fishes living in turbulent intertidal habitats frequently exhibit similar modifications (e.g., members of the Blenniidae; Brandstätter et al., 1990).

We sectioned the paired fins of a small number of benthic and rheophilic percomorphs (*Etheostoma blennius*, *Percina kathae, Romanichthys valsanicola*, and *Cottus bairdii*) and an intertidal percomorph (*Scartella cristata*) to order to make general comparisons between the paired-fin pads of ostariophysans and the thickened skin surrounding the rays of nonostariophysan fishes. As in the ostariophysan fishes, skin thickening around the rays of the paired fins is achieved in very different ways in different percomorph taxa. In the pelvic fins of the percids (Fig. 9C,E,F,K,L) a greatly thickened and homogeneous epidermis, composed of small squamous cells, gives the skin surrounding the rays an external appearance of being thickened, with little contribution from layers deep to the epidermis. In the pelvic fins of the cottid (*C. bairdii*; Fig. 9D,J–M) and blenny (*S. cristata*; Fig. 9B,H–I), the epidermis is relatively thin, composed of only a few cell layers and is bordered ventrally by a similarly thin dermis. Deep to the dermis, the subdermal space is greatly expanded and filled with large amounts of connective tissue creating a large gap between the surface of the hemitrichia and the dermis (Fig. 9J,H). The histology of the lowermost pectoral-fin rays of *S. cristata* ("hook-field" rays sensu Brandstätter et al., 1990; Fig. 9G) is similar to that of the pelvic fin, but differs markedly from that of rays situated more dorsally ("fin-field" rays sensu Brandstätter et al., 1990), both in terms of cellular composition of the epidermis and the subdermis (Brandstätter et al., 1990). In these latter percomorph taxa, the external thickening of the skin surrounding the paired-fin rays is achieved solely by expansion of the deep skin layers and not via modification of the epidermis, and they are similar in this regard to the Type 2 paired-fin pads of nonsiluriform otophysans. The large subdermal mass of connective tissue associated with the pelvic and "hook-field" pectoral-fin rays of *S. cristata*, (a structure described previously by Brandstätter et al. (1990) and referred to as a lepidotrichial chord) and the pelvic-fin rays of *C. bairdii* appear to have an identical cellular composition (viewed using light microscopy) to the subdermal mass of connective tissue present in members of the Cypriniformes and Characiformes, differing only in terms of fiber arrangement, density, and extent. Again, further investigation with TEM is warranted.

Evolution and Function of Paired-Fin Pads in Ostariophysan Fishes

Based on the limited number of taxa that we have examined it would be premature to make explicit inferences about the evolution of paired-fin pads across the Ostariophysi, other than to state that they are clearly homoplastic, evolving separately in each of the four orders of ostariophysan fishes that contain benthic and rheophilic taxa (the Gonorynchiformes, Cypriniformes, Characiformes, and Siluriformes). Within the Characiformes paired-fin pads appear to have evolved at least twice, once within the Crenuchidae (likely at the level of the strictly benthic or hypobenthic subfamily Characidiinae [sensu Buckup, 1993, 1998] as opposed to the more demersal sister taxon Crenuchinae) and once within the Parodontidae. The number of independent evolutionary origins of paired-fin pads is less clear within the Cypriniformes and Siluriformes, the relationships of which are in a state of flux and currently under intense scrutiny (e.g., Sullivan et al., 2006; Lundberg et al., 2007; Conway et al., 2010). On the other hand, the paired-fin pads of gonorynchiform fishes (Anotophysi) are restricted to members of the genera *Kneria* and *Parakneria* (KWC pers. obs.) and are most likely (and most parsimoniously) the result of a single evolutionary event, given that these two knerriid genera are hypothesized to be sister groups (Grande, 1994; Johnson and Patterson, 1997; Lavoué et al., 2005; Britz and Moritz, 2007).

Given the apparently widespread, convergent evolution of paired-fin pads in lineages of benthic and rheophilic fishes across the Ostariophysi it is tempting to speculate that they represent adaptations related to some aspect of benthic life in swift currents. Several Indian authors have dogmatically accepted (following Hora, 1922, 1923a,b, 1930) that the unculiferous paired-fin pads of South Asian cypriniforms (specifically members of the Balitoridae and Cyprinidae) and sisorid catfishes function as "adhesive devices", or represent the border of a larger "adhesive apparatus" formed largely by components of the mouthparts and chest region (Bhatia, 1950; Saxena and Chandy, 1966; Singh and Agarwal, 1993; Das and Nag, 2004, 2005). Adhesion between fish and substrate is hypothesized to be the result of strong friction, achieved via the interlocking of unculi with substrate irregularities, aided by an intense downward hydrodynamic force as water flows over the dorsal surface of the enlarged paired fins (Hora, 1923a,b). Undoubtedly, several of the benthic and rheophilic ostariophysan taxa that possess paired-fin pads are capable of adhering very strongly to the substrate (e.g., certain members of the Balitoridae; Wickler, 1971). This adhesive capability, however, is not expressed to the same degree by all benthic and rheophilic ostariophysan taxa that possess paired-fin pads.

An alternative but nonexclusive functional hypothesis for the ridged, unculliferous surface on the ventral "adhesive apparatus" of sisorid catfishes has been proposed by Wu and Liu (1940).

Fig. 9. Transverse sections through the paired fins of select benthic acanthomorph fishes. (**A**) Complete section of the pectoral fin of *Scartella cristata* (TCWC 15699.02). (**B**) Complete section of the pelvic fin of *S. cristata* (specimen as in A). (**C**) Complete section of the pelvic fin of *Romanichthys valsanicola* (BMNH 1960.9.23.25-27). (**D**) Complete section of the pelvic fin of *Cottus bairdii* (UAIC 14316.01). (**E**) Complete section of the pectoral fin of *Percina kathae* (AUM 49459). (**F**) Complete section of the pelvic fin of *P. kathae* (specimen as in E). (**G**) Second lowest pectoral-fin ray of *S. cristata* (specimen as in A). (**H**) First soft pelvic-fin ray of *S. cristata* (specimen as in A). (**I**) Close up of dashed box in H. (**J**) First soft pelvic-fin ray of *C. bairdii* (specimen as in D). (**K**) Anteriormost (spinous and soft) pelvic-fin rays of *R. valsanicola* (specimen as in C). Asterisk indicates spinous ray. (**L**) Spinous (anteriormost) pelvic-fin ray of *P. kathae* (specimen as in E). (**M**) Close up of dashed box in J. (**N**) Close up of dashed box in K. Arrows point to papillae-like invaginations of dermis. (**O**) Close up of dashed box in L. A–F are illustrated to scale and share a single scale-bar. Bv, blood vessel; Derm, DH, dorsal hemitrichium; Eder, epidermis; MC, melanocyte; Sderm, subdermis; SEder, sloughed epidermis; SR, spinous ray; VH, ventral hemitrichium.

These authors have suggested that the thickened and unculliferous epidermis of the ridged “adhesive apparatus” (which is histologically identical to that of the paired-fin pads; Hora, 1923a; Bhatia, 1950; Das and Nag, 2005) are more likely to provide mechanical protection against abrasion from the substrate than facilitate adhesion to it (Wu and Liu, 1940: 73–74). The high concentration of unculi producing cells in the epidermis of the paired-fin pads (particularly in the ridged paired-fin pads of sisorid catfishes and the Type 3 pads of nonsiluriform otophysans) suggests that this region of the integument is capable of rapid replacement, which may be necessary if damage to the outer surface of pads is commonplace, as is likely the case in such turbulent environments as the interstices between rocks in swift riffles or between boulders in torrential mountain streams.

The function(s) of the paired-fin pads of ostariophysan fishes will likely remain speculative until appropriate experimental studies, designed to test alternative functional hypotheses are conducted. Detailed investigations into the functional properties of unculi at a microscopic level, such as those conducted on the setae present on the feet of geckos (e.g., Autumn et al., 2000; Autumn and Peattie, 2002), may prove to be particularly illuminating in this regard. Until functional data are available, we advise against the use of any terminology that implies function (e.g., adhesive pad or adhesive surfaces) and recommend the use of the simple, and more functionally neutral term “pad,” adopted herein, for the thickened skin along the ventral surface of the paired fins of ostariophysan fishes.

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