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Fin crawling in flatfishes (Teleostei: Pleuronectiformes)

Flossenkriechen bei Plattfischen

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Summary: In addition to swimming, epibenthic teleost fish can walk or crawl over the bottom. A crawling mode of locomotion in flatfish has gone almost entirely unreported in the scientific literature. Here we describe this 'fin crawling' type of locomotion of flatfish and document its occurrence within the order Pleuronectiformes, suggesting possible steps in its evolution. Flatfish locomotion was filmed for this study by SCUBA-supported video. Internet sources were also searched for films of flatfish locomotion. We have gathered evidence for fin crawling in 52 flatfish species of 8 different families. Crawling flatfish show forwardly-directed, near-sinusoidal waves of dorsal/anal fin movements; the caudal fin is motionless and the axial musculature clearly not involved. 'Contact patches' (i.e. sites where several fin rays simultaneously exert force against the substratum) move backwards along the body as the wave of fin ray movements travels forward and new fin ray tips enter the patches. Fin crawling locomotion apparently evolved early in the phylogeny of the Pleuronectiformes.

Key words: Locomotion; dorsal/anal fins; fin crawling; Pleuronectiformes

Zusammenfassung: Außer zu schwimmen können epibenthische Fische über den Boden laufen oder kriechen. Ein kriechender Fortbewegungstyp von Plattfischen ist bisher in der wissenschaftlichen Literatur nahezu unbeachtet geblieben. Wir beschreiben hier diesen Fortbewegungsmodus „Flossenkriechen" von Plattfischen, dokumentieren seine Verbreitung innerhalb der Ordnung Pleuronectiformes und geben mögliche Evolutionsschritte zu diesem Verhalten an. Die Fortbewegung von Plattfischen wurde während SCUBA-Tauchgängen gefilmt. Filme über die Fortbewegung von Plattfischen wurden im Internet gesucht. Wir haben so Belege für Flossenkriechen bei 52 Plattfischarten aus acht verschiedenen Familien gesammelt. Kriechende Plattfische zeigen vorwärts gerichtete, nahezu sinusförmige Wellen von Bewegungen der Rücken- und Afterflosse; die Schwanzflosse bleibt dabei bewegungslos und die Axialmuskulatur ist nicht an der Bewegung beteiligt. „Kontaktpunkte" (Orte, an denen mehrere Flossenstrahlen gleichzeitig Druck gegen das Substrat ausüben) wandern den Körper entlang nach hinten, während sich die Welle der Flossenstrahlenbewegungen nach vorne bewegt und neue Flossenstrahlen die Kontaktpunkte treffen. Der Bewegungstypus „Flossenkriechen" ist offensichtlich früh in der Evolution der Plattfische entstanden.

Schlüsselwörter: Fortbewegung; Rückenflosse; Afterflosse; Flossenkriechen; Pleuronectiformes

1. Introduction

The swimming locomotion of teleost fish has variously been categorized as anguilliform, carangiform, balistiform, etc. (Breder 1926; Webb 1984; Helfman et al. 2009). Flatfish (Order Pleuronectiformes, containing some 678 species: Nelson 2006) have attracted much study because of their remarkable early development/metamorphosis and adult asymmetry (Schreiber 2006). Although planktonic larval flatfish have swimbladders, these are lost during development. Consequently, adult flatfish are negatively buoyant and primarily epibenthic. For example, the plaice *Pleuronectes platessa* and the long rough dab *Hippoglossoides platessoides* have body densities of 1.05-1.07 g ml^{-1} (c.f. 1.03 g ml^{-1} for sea water) (Davenport & Kjørsvik 1986). Adult flatfish swim actively with a 'pleuronectiform' type of locomotion, undulating the rear part of the body (including the axial fins) using the axial musculature. Undulations start cranially and pass caudally, as in the swimming of many other fish. Some flatfish cover considerable distances by alternately swimming upwards using pleuronectiform swimming and gliding unpowered with a rigid, low-drag body (e.g. Takagi et al. 2010).

Epibenthic teleost fish have an additional option to move forwards (or even backwards): they can walk or crawl over the bottom. Bottom-walking and crawling have evolved repeatedly in marine and freshwater species (reviewed by Renous et al. 2011). A crawling mode of locomotion in flatfish has gone almost entirely unreported in the scientific literature, except for brief comments (Orcutt 1950; Kruuk 1963; Olla et al. 1969, 1972; Holmes & Gibson 1983; O'Neil & Gibb 2001). It has not been mentioned in recent reviews on fish locomotion (Shadwick & Lauder 2006; Helfman et al. 2009; Domenici & Kapoor 2010), not even when explicitly dealing with epibenthic locomotion (Renous et al. 2011). It is, however, well known to aquarists and SCUBA divers, as evidenced by numerous videos in the public domain (see tab. 1). Holmes & Gibson (1983) called this type of locomotion "shuffle" and "creep". Here we describe the 'fin crawling' type of locomotion of flatfish and document its occurrence within the order Pleuronectiformes, suggesting possible steps in its evolution.

2. Material and methods

Flatfish locomotion was filmed for this study by SCUBA-supported video and still photography near Caniço, Madeira Island (32°38' N, 16°49' W) and Tarrafal, the Cape Verde Islands (15°16' N, 23°45' W) with Canon Powershot digital cameras. Internet sources (mainly YouTube and fishbase) were also searched for films of flatfish locomotion. Still images of flatfish in books or on internet sites were used as evidence only when unambiguously showing fin crawling behaviour (e.g. fig. 1). Full quantitative kinematic analysis of crawling locomotion was not possible as replicated films with fixed cameras were not available. However, Motion Analysis Tools-DX9-Shareware Version .7.3 (Ottawa Hospital Rehabilitation Centre, Ottawa, ON, Canada) was used to analyse short pieces of footage where quantitative data (as well as qualitative information) could be extracted.

Identified cases of fin crawling were plotted onto the most recent key of Pleuronectiformes (Betancur-R. et al. 2013). Probable ancestral states of fin crawling were reconstructed using the rule of parsimony, i.e. minimizing the number of evolutionary transitions.

3. Results

3.1. Basic description of fin crawling locomotion

Crawling flatfish (when moving forwards on relatively smooth, flat sediments) show forwardly-directed, near-sinusoidal waves of dorsal/anal fin movements; the caudal fin is motionless and the axial musculature clearly not involved. Individual dorsal/anal fin rays show extension upwards, outwards and cranially when off the substratum. They are then bent downwards and medially so that their tips contact the substratum. They are next bent against the substratum and medially to dig into the substratum, then retracted caudally until the fin tips leave the substratum (fig. 1). 'Contact patches' (i.e. sites where several fin rays simultaneously exert force against the substratum) move caudally along the body as the wave of fin ray movements travels cranially and new fin ray tips enter the patches. Close-up video or still photography revealed disturbance of the sediment at the contact patches, confirming exchange of forces between fish and substratum (also indicated by the bent fin rays and their tips within the contact patches themselves).

This process is reversed when the fish crawls backwards (i.e. the waves of fin movements are directed caudally, while the positions of contact patches move cranially). When moving in an axial direction (either forwards or backwards) the waves of dorsal and anal fin movement are

Tab. 1: Fincrawling flatfishes.
Tab. 1: Flossenkriechende Plattfische.

Family/species	Type of evidence	Reference
Achiridae		
Catathyridium jenynsii (Günther, 1862)	film	Simso (2015)
Bothidae		
Arnoglossus bassensis Norman, 1926	film	Finn & Norman (2016)
Arnoglossus laterna (Walbaum, 1792)	photo	Kay & Dipper 2009: 144
Bothus mancus (Broussonet, 1782)	film	Undersea Productions (2016a)
Bothus ocellatus (Agassiz, 1831)	film	Undersea Productions (2016b)
Bothus podas (Delaroche, 1809)	film	Wirtz (2017a)
Bothus pantherinus (Rüppell, 1830)	film	Undersea Productions (2016c)
Cynoglossidae		
Cynoglossus feldmanni (Bleeker, 1854)	film	Schäfer (2016)
Cynoglossus puncticeps (Richardson, 1846)	film	DeLoach (pers. comm. 2017)
Cynoglossus sinusarabici (Chabanaud, 1931)	photo	Dafni (2016)
Paraplagusia japonica (Temminck & Schlegel, 1846)	film	Japan Underwater Films (2016)
Symphurus awarak Robins & Randall, 1965	film	Wilk (2007)
Symphurus insularis Munroe, Brito & Hernández, 2000	film	Wirtz & Dellinger (2017a, b)
Symphurus ommaspilus Böhlke, 1961	film	Wilk (2007)
Paralichthyidae		
Cyclopsetta fimbriata (Goode & Bean, 1885)	film	Wilk (2007)
Paralichthys dentatus (Linnaeus, 1766)	verbal description and drawing	Olla et al. (1972)
Syacium guineensis (Bleeker, 1862)	film	Wirtz (2017c)
Syacium micrurum Ranzani, 1840	film	Wilk (2007)
Syacium papillosum (Linnaeus, 1758)	film	Wilk (2007)
Pleuronectidae		
Platichthys flesus (Linnaeus, 1758)	film	Bidone1967 (2010)
Platichthys stellatus (Pallas, 1787)	verbal description	Orcutt (1950)
Pleuronectes platessa Linnaeus, 1758	verbal description	Holmes & Gibson (1983)
Pleuronichthys sp.	film	Webster (2013)
Pseudopleuronectes americanus (Walbaum, 1792)	verbal description	Olla et al (1969)
Scophthalmidae		
Lepidorhombus whiffiagonis (Walbaum, 1792)	photo	Kay & Dipper (2009:152)
Scophthalmus rhombus (Linnaeus, 1758)	film	Underwater Ireland (2012)
Scophthalmus maximus (Linnaeus, 1758	verbal description	Holmes & Gibson (1983)
Zeugopterus regius (Bonnaterre, 1788)	verbal description	Holmes & Gibson (1983)
Zeugopterus punctatus (Bloch, 1787)	verbal description	Holmes & Gibson (1983)
Samaridae		
Samaris cristatus Gray, 1831	photo	Kuiter & Tonozuka (2004: 400)
Samaris cristatus Gray, 1831	film	Sea Story (2016)
Samariscus triocellatus Woods, 1960	photo	Randall (2016a)

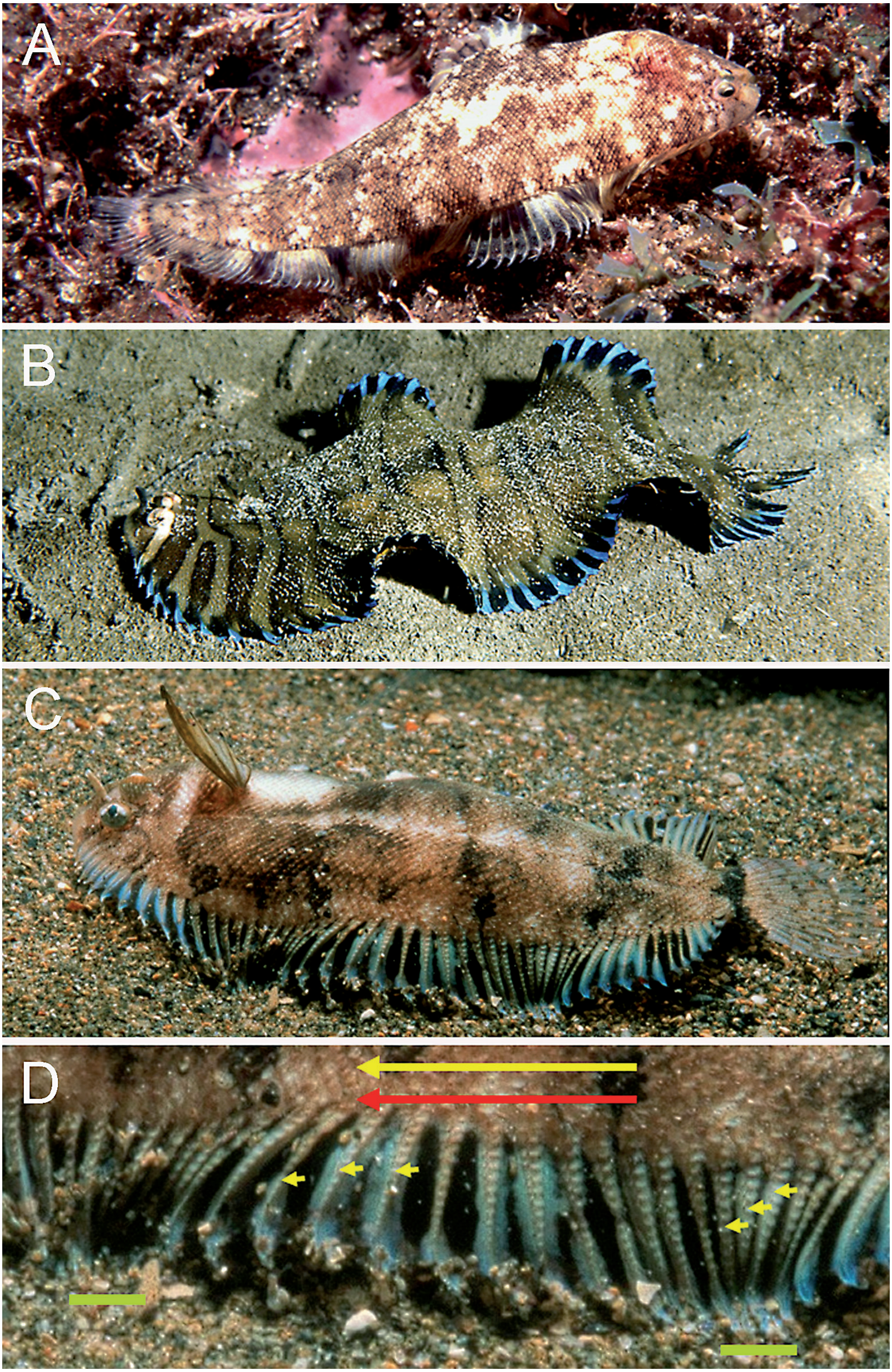
Tab. 1: Continued.
Tab. 1: Fortsetzung.

Family/species	Type of evidence	Reference
Soleidae		
Aesopia cornuta Kaup, 1853	film	Baumeister (2016)
Aseraggodes albidus Randall & Desoutter-Meniger, 2007	photo	Randall (2016b)
Aseraggodes kaianus (Günther, 1880)	verbal description	Kuiter & Tonozuka (2004: 397)
Aseraggodes sp.	film	Japan Underwater Films (2016)
Buglossidium luteum (Risso, 1810)	film	fishbaseyt (2009)
Microchirus ocellatus (Linnaeus, 1758)	film	Wirtz (2017b)
Microchirus variegatus (Donovan, 1808)	photo	Golani et al. (2006: 231)
Monochirus hispidus Rafinesque, 1814	photo	Louisy (2015: 412)
Pardachirus marmoratus (Lacépède, 1802)	film	Roman S. (2012)
Pardachirus pavoninus (Lacépède, 1802)	film	Undersea Productions (2016d)
Phyllichthys punctatus McCulloch, 1916	photo	Kuiter & Tonozuka (2004: 399)
Pseudaesopia japonica (Bleeker, 1860)	film	Japan Underwater Films (2016)
Solea solea (Linnaeus, 1758)	verbal description	Kruuk (1963: 13)
Solea solea (Linnaeus. 1758)	verbal description	Holmes & Gibson (1983)
Solea solea (Linnaeus, 1758)	photo	Irving (1998: 160)
Soleichthys hetorhinos (Bleeker, 1856)	film	shutterstock.com (2016)
Soleichthys "sp. 1"	film	DeLoach (2012)
Soleichthys "sp. 2"	photo	Kuiter & Tonozuka (2004: 397)
Soleichthys "sp. 3"	film	Harding 2017
Synaptura sp.	film	O'Neill & Gibb (2001)
Zebrias fasciatus (Basilewski, 1855)	film	Scubazoo/Science Photo Library (2016)
Zebrias zebrinus (Temminck & Schlegel, 1846)	film	Japan Underwater Films (2013)

coordinated so that contact patches are opposite each other on the dorsal and ventral surfaces. However, when manoeuvring, the fish can turn by having dorsal and anal fin waves moving in opposite directions. By this means fish can sometimes turn within their own body length.

There is great variety in numbers of dorsal/anal fin rays amongst flatfish species. Slower crawling flatfish typically have 6 contact patches at any given time; faster crawlers tend to have 4 contact patches (fig. 2). There is also much variation in the relative length of fin

Fig. 1: Examples of flatfish fin crawling. **A** Tonguefish, *Symphurus insularis* (Photo: P. Wirtz). **B** *Aesopia* sp. (Photo: R. Kuiter). **C** Whiskered sole, *Monochirus hispidus* (Photo: P. Louisy). The fish was crawling from right to left of the image. **D** Close-up of contact patches (indicated by green bars) of dorsal fin. Long yellow arrow indicates direction of fish movement; red arrow indicates direction of wave of dorsal fin movement. Note that fin rays in region of contact patches are much closer together (see small yellow arrows) than in regions of the propulsive wave where the rays are elevated above the sediment. Note also that the fin rays within the contact patch are strongly bent against the substratum. The ray tips are spatulate and free of fin membrane.
Abb. 1: Beispiele für Flossenkriechen bei Plattfischen. **A** Hundszunge, *Symphurus insularis* (Foto: P. Wirtz). **B** *Aesopia* sp. (Foto: R. Kuiter). **C** Pelz-Seezunge, *Monochirus hispidus* (Foto: P. Louisy). Der Fisch kroch von rechts nach links. **D** Nahaufnahme der Kontaktpunkte (mit grünen Balken gekennzeichnet) der Rückenflosse. Der lange gelbe Pfeil gibt die Richtung der Bewegung des Fisches an; der rote Pfeil zeigt die Richtung der Wellenbewegung der Rückenflosse. Man beachte, dass die Flossenstrahlen in den Regionen der Kontaktpunkte viel enger zusammen sind (kleine gelbe Pfeile) als in Regionen der Fortbewegungswelle, in denen die Strahlen über das Substrat angehoben sind und, dass die Flossenstrahlen an den Kontaktpunkten stark gegen das Substrat abgebogen sind. Die Spitzen der Flossenstrahlen sind löffelförmig und frei von einer Flossenmembran.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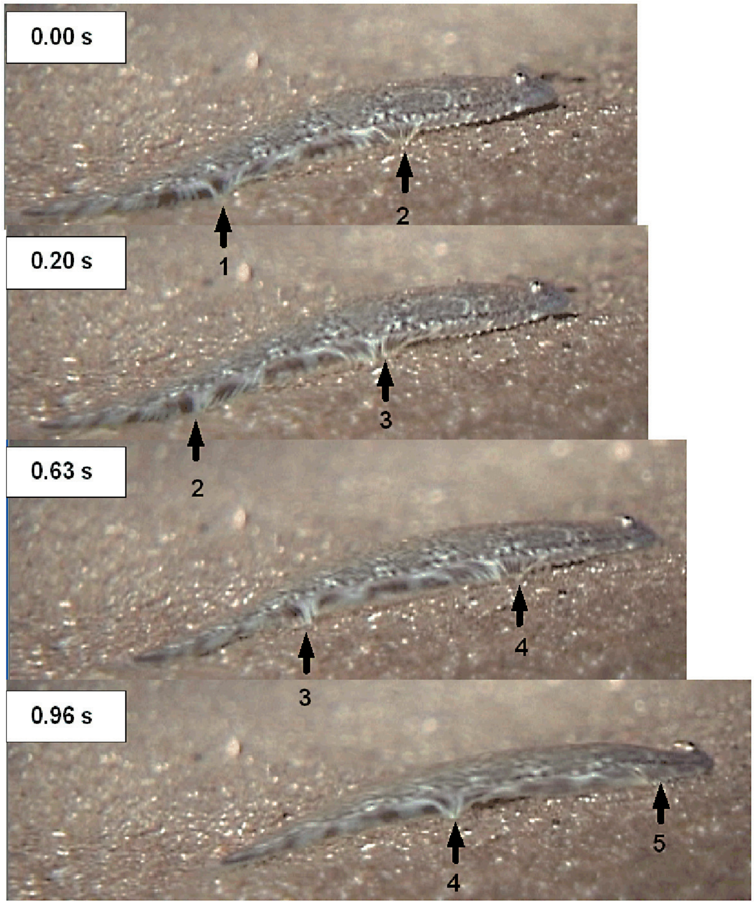

Fig. 2: Sequence of dorsal contact patches (arrowed and numbered) in locomotion of tonguefish, *Symphurus insularis*. The fish was filmed at a field rate of 30 fps from the 'side' (actually the dorsal surface). It was moving at about 0.14 body lengths s^{-1}.

Abb. 2: Verlauf der dorsalen Kontaktpunkte (mit Pfeil und Nummer gekennzeichnet) in der Fortbewegung einer Hundszunge, *Symphurus insularis*. Der Fisch wurde mit 30 Bildern pro Sekunde von der Dorsalseite gefilmt. Er bewegte sich mit etwa 0,14 Körperlängen pro Sekunde.

rays, the form of the ray tips, and in the extent of webbing between the rays. This influences the amplitude of the waves of fin movements (compare fig. 1A, 1B). In species with especially long fin rays they are elevated to such a degree that a markedly wave-like outline of the margin of the body results (e.g. fig. 1B).

3.2. Phylogeny of fin crawling

We have gathered evidence for fin crawling in 52 flatfish species of 8 different families (tab. I). The occurrence of fin crawling was plotted onto the most recent key of flatfishes (fig. 3; Betancur-R. et al. 2013). As fin crawling has been recorded in the families Scophthalmidae, Paralichthyidae, Bothidae and Pleuronectidae, the common ancestor of these families was probably already fin crawling. As fin crawling has been observed in the families Samaridae, Cynoglossidae, and Soleidae, it is parsimonious to assume that it also occurs in the family Poecilopsettidae (no evolutionary change necessary), and thus also occurred in the common ancestor

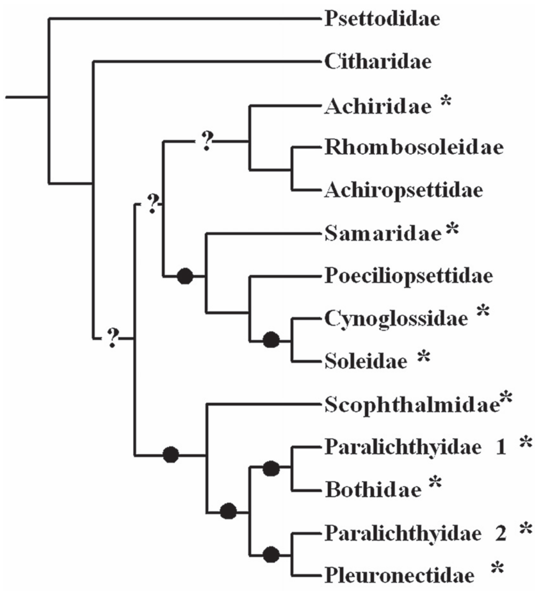

Fig. 3: Phylogeny of flatfishes and reconstruction of ancestral states of "fin crawling". ***** indicates observed presence of fin crawling. • indicates ancestral state of fin crawling. **?** indicates possible ancestral state of fin crawling.

Abb. 3: Stammbaum der Plattfische und Rekonstruktion des ursprünglichen Zustandes von „Flossenkriechen". ***** bedeutet, dass Flossenkriechen in dieser Familie beobachtet wurde. • bedeutet, dass der Vorfahre dieser Famlien bereits mit den Flossen kroch. **?** bedeutet, dass der Vorfahre dieser Famlien möglicherweise bereits mit den Flossen kroch.

of these four families. Currently it cannot be concluded with any certainty that the common ancestor of all the families from Achiridae to Pleuronectidae was already fin crawling but it appears likely. A fin crawling type of locomotion apparently evolved early in the phylogeny of the Pleuronectiformes, either once or several times.

4. Discussion

4.1. Fin crawl mechanism

Flatfish are unique in using the fin ray tips of the dorsal and anal fins in combination for epibenthic locomotion. All other epibenthic fish either use their pectoral and/or ventral fins for walking or crawling, or move by alternating the attachment of the pelvic disc and oral sucking disk in 'inchworm' fashion (Renous et al. 2011). This apparently basal flatfish trait is a consequence of a) the lateral compression of the flatfish body, combined with eye migration that results in the medial dorsal/anal fins being functionally 'lateral', and b) the expansion of the lengthwise extent of the dorsal and anal fins to occupy most of the ventral and dorsal surfaces (except the head and tail). Each fin ray is controlled by three pairs of antagonistic muscles (formally erectors, depressors, and inclinators) that allow the ray to rotate elliptically so that its tip follows (during forwards crawling) a forward, upward and outwardly directed path ('recovery stroke') above the substratum, followed by a descent to contact the substratum, a medially directed path that bends the tip against/into the substratum ('propulsive stroke'), followed by an outward, backward rise to repeat the sequence. The metachronal sequence of ray movements, along almost the entire fish length, produces a smooth, supportive locomotion similar to that of mechanised tracked vehicles. This description deviates from the brief analysis of O'Neil &

Gibb (2001), which indicated that the flatfish *Synaptura salinarum* used fixed points on the dorsal and anal fins to 'step' over the substratum. Interestingly, the coordination of dorsal and anal fin action exhibited by crawling flatfish is a rare example of such coordination in unpaired propulsive structures. The only previously-reported example is that of the propulsive dorsal and anal fins of the oceanic sunfish *Mola mola* (Watanabe & Sato 2008).

Fin crawling is essentially a slow form of locomotion that permits inconspicuous movement and manoeuvring on the sea bed. To put the slowness in perspective, the specimen of *Symphurus insularis* shown in figure 3 was crawling quickly at about 0.14 body lengths s^{-1}. This fish later c-started (swimming acceleration described by Weihs 1972) and left the field of view between one field and the next (speed >2.3 body lengths s^{-1}).

Fin crawling is likely to be energetically inexpensive, not only because of its slowness, but also because the body of the fish is essentially held rigid (promoting low drag) and very close to the substratum. Movement close to the substratum in flatfish has been predicted to reduce energy costs by the phenomenon of ground effect (Videler 1993). In addition, it provides greater manoeuvrability, allowing backwards movement and tight turns.

4.2. Evolution of fin crawling

Currently it cannot be concluded with any certainty that the common ancestor of all the families from Achiridae to Pleuronectidae (fig. 3) was already fin crawling, but it appears likely. A fin crawling type of locomotion apparently evolved early in the phylogeny of the Pleuronectiformes, either once or several times. The five families currently without evidence for this type of behaviour (Psettodidae, Citharidae, Rhombosoleidae, Achiropsettidae, Poeciliopsettidae) require investigation.

A film available on the internet (Underwater Ireland 2012) shows what could be an early stage in the evolution of fin crawling; turbot (*Scophthalmus rhombus*) move all dorsal and anal fin rays downwards and rearwards, in parallel, when starting to swim forwards.

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