Further investigations on fincrawling in flatfishes (Teleostei: Pleuronectiformes): phylogenetic implications

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Further investigations on fincrawling in flatfishes (Teleostei: Pleuronectiformes): phylogenetic implications

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Abstract: Fincrawling is a unique, recognizable behaviour pattern exhibited by many flatfishes (order Pleuronectiformes), whereby the fish uses the fin rays of the dorsal and anal fins to walk over the substratum. The distribution of this behaviour among flatfishes indicates it appeared early in the phylogeny of the Pleuronectiformes. Fincrawling is a common character of the Pleuronectoidei, and a possible synapomorphy of the suborder.

Résumé : *Recherches complémentaires sur l'aptitude à ramper avec les nageoires chez les poissons plats (Teleostei : Pleuronectiformes) : implications phylogénétiques.* Ramper grâce aux nageoires est un comportement unique présent chez de nombreux poissons plats (ordre des Pleuronectiformes), au cours duquel l'animal utilise les rayons de ses nageoires dorsales et anales pour se déplacer sur le substrat. La présence de ce comportement au sein des poissons indique qu'il est apparu tôt dans l'évolution des Pleuronectiformes. Ramper grâce aux nageoires-est un caractère commun aux Pleuronectoidei et une possible synapomorphie du sous-ordre.

Keywords: Fincrawling ● Dorsal fin ● Anal fin ● Flatfish ● Pleuronectiformes

Introduction

Fincrawling is a recognizable behaviour pattern of some flatfishes (order Pleuronectiformes), whereby the fish, instead of swimming, uses the fin rays of the dorsal and anal fins to walk over the bottom (see the numerous videos listed in table 1, e.g. www.youtube.com/watch?v=2Psc0X7W_UQ). Wirtz & Davenport (2018) described this unique behaviour pattern in detail. Fincrawling flatfish show near-sinusoidal waves of dorsal and/or anal fin movements; the caudal fin is motionless. '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 forwards and new fin ray tips enter the patches. 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). Fincrawling flatfish can even turn by dorsal and anal fin waves moving in opposite directions. Fox et al. (2018) independently described the fincrawling mechanism for six species of Pleuronectidae, referring to the contact patches as 'feet'. Wirtz & Davenport (2018) showed that this type of

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locomotion apparently evolved early in the phylogeny of the Pleuronectiformes, either once or several times. Their review lacked observations for several families (Psettodidae, Citharidae, Rhombosoleidae, Achiropsettidae, Poeciliopsettidae). Here we present the results of additional observations and advance a hypothesis concerning the origin of this behaviour pattern.

Materials and Methods

Flatfish locomotion was filmed by SCUBA-supported video near Caniço, Madeira Island (32º38´N-16º49´W) and Tarrafal, the Cape Verde Islands (15º16´N-23º45´W) with Canon Powershot digital cameras. We also searched internet sources (mainly YouTube and FishBase) for films of flatfish locomotion. Finally, we contacted SCUBA divers and the keepers of several public aquaria around the world and asked them to film flatfish locomotion for us. These additional films were deposited in ResearchGate to make all data publicly accessible. Motion Analysis Tools-DX9-Shareware Version 2.7.3 (Ottawa Hospital Rehabilitation Centre, Ottawa, ON, Canada) and the free analytical tool Kinovea (https://www.kinovea.org/) were used to analyse the films. Still images of flatfish in books or on internet sites were used as evidence only when unambiguously showing fincrawling behaviour.

Identified cases of fincrawling were mapped onto the most recent phylogeny of the Pleuronectiformes (Atta et al., 2021). Recent morphological and molecular studies, including evidence from fossils, have provided new insights into the phylogeny of the order Pleuronectiformes (Campbell et al., 2019 & 2020; Chanet et al., 2020; Atta et al., 2021). The tree proposed by Atta et al. (2021) has been chosen here as the most recent one**.** The positions of several groups are different amongst these works, meaning that flatfishes' classification is not yet stable. But the discrepancies between these trees (viz: status of Citharidae and positions of the Achiridae and Samaridae) do not affect the distribution of the fincrawling among these groups.

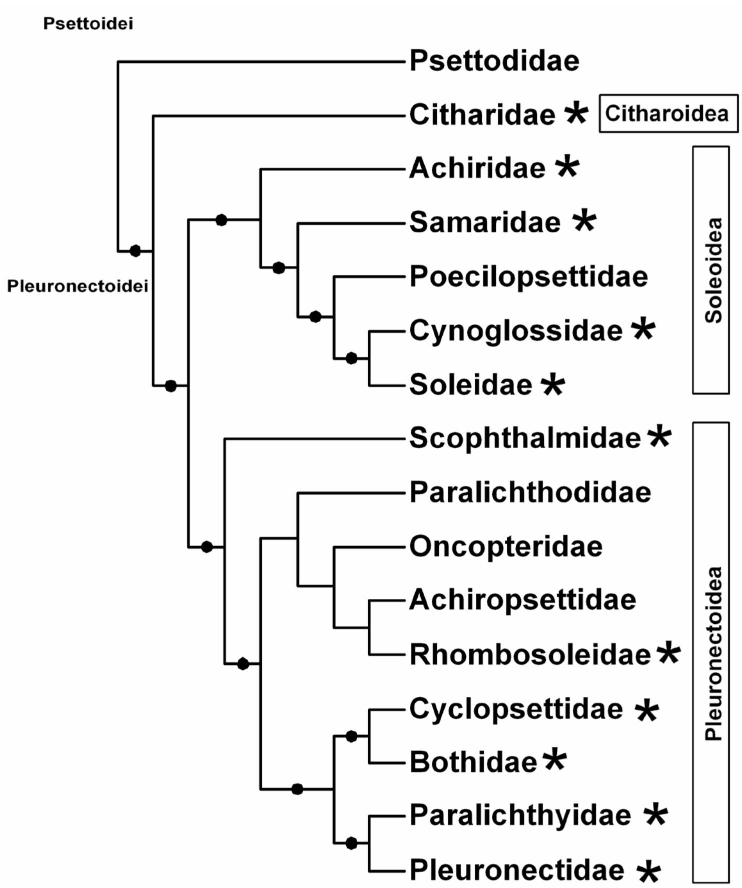

Figure 1. Tree showing the interrelationships of flatfishes and reconstruction of ancestral states of fincrawling. Black star (*) indicates observed presence of fincrawling while black circle (•) indicates ancestral state of fin crawling.

Table 1: Fincrawling flatfishes. List of species, with sources, where fincrawling has been observed.

Family/species	**type of evidence**	**Reference**
Psettodidae	**no data**	
Citharidae		
Citharus linguatola (Linnaeus, 1758)	film	Munaretto (2015a)
Citharus linguatola (Linnaeus, 1758)	film	Munaretto (2015b)
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 regius (Bonnaterre, 1788)	film	Mescachlin (2014)
Zeugopterus regius (Bonnaterre, 1788)	film	Naylor (2016)
Zeugopterus punctatus (Bloch, 1787)	verbal description	Holmes & Gibson (1983)
Zeugopterus punctatus (Bloch, 1787)	film	Tyburski (2017)
Zeugopterus punctatus (Bloch, 1787)	film	Naylor (2017)
Paralichthyidae		
Ancylopsetta cycloidea Tyler, 1959	film	VideotecaFaunaPR (2012)
Paralichthys adspersus (Steindachner, 1867)	film	Book Publisher International (2020)
Paralichthys californicus (Ayres, 1859)	film	Marti & Wirtz (2021c)
Paralichthys dentatus (Linnaeus, 1766)	verbal description and drawing	Olla et al. (1972)
Paralichthys lethostigma Jordan & Gilbert, 1884	film	gcrlweb (2013)
Paralichthys olivaceus (Temminck & Schlegel, 1846)	film	Tsujita (2015)
Pleuronectidae		
Eopsetta grigorjewi (Herzenstein, 1890)	film	Tsujita (2015b)
Isopsetta isolepis (Lockington, 1880)	verbal description	Fox et al 2018
Lepidopsetta bilineata (Ayres, 1855)	verbal description	Fox et al 2018
Lyopsetta exilis (Jordan & Gilbert, 1880)	verbal description	Fox et al 2018
Parophrys vetulus Girard, 1854	verbal description	Fox et al 2018
Platichthys flesus (Linnaeus, 1758)	film	Bidone1967 (2010)
Platichthys stellatus (Pallas, 1787)	verbal description	Orcutt (1950), Fox et al (2018)
Pleuronectes platessa Linnaeus, 1758	verbal descrip-tion	Holmes & Gibson (1983)
Pleuronectes platessa Linnaeus, 1758	film	Naylor (2019)
Pleuronichthys sp.	film	Webster (2013)
Pleuronichthys coenosus Girard, 1854	film	Marti & Wirtz (2021b)
Psettichthys melanostictus Girard, 1854	verbal description	Fox et al (2018)
Pseudopleuronectes americanus (Walbaum, 1792)	verbal description	Olla et al (1969)
Cyclopsettidae		
Citharichthys stigmaeus Jordan & Gilbert, 1882	film	Vantuna Research Group (2013)
Citharichthys stigmaeus Jordan & Gilbert, 1882	film	Marti & Wirtz (2021d)
Cyclopsetta fimbriata (Goode & Bean, 1885)	film	Wilk (2007)
Syacium guineensis (Bleeker, 1862)	film	Wirtz (2017)
Syacium micrurum Ranzani, 1840	film	Wilk (2007)
Syacium papillosum (Linnaeus, 1758)	film	Wilk (2007)

Table 1. Following.

Family/species	type of evidence	Reference
Bothidae		
Arnoglossus bassensis Norman, 1926	film	Finn & Norman (2016)
Arnoglossus laterna (Walbaum, 1792)	photo	Kay & Dipper (2009: 144)
Asterorhombus intermedius (Bleeker, 1865)	film	DiveIndia Andamans (2019)
Bothus lunatus (Linnaeus, 1758)	photo and verbal description	Ivan Sazima (pers. comm to PW)
Bothus mancus (Broussonet, 1782)	film	Undersea Productions (2016a)
Bothus mancus (Broussonet, 1782)	film	Van Geen (2015)
Bothus ocellatus (Agassiz, 1831)	film	Undersea Productions (2016b)
Bothus pantherinus (Rüppell, 1830)	film	Undersea Productions (2016c)
Bothus podas (Delaroche, 1809)	film	Wirtz (2017a)
Achiropsettidae	**no data**	
Rhombosoleidae		
Pelotretis flavilatus Waite, 1911	film	Miller (2021)
Peltorhamphus novaezeelandiae Günther 1862	film by Karl War	Warr & Wirtz (2021a)
Rhombosolea retiaria Hutton, 1874	verbal description	Karl Warr (pers.comm to PW)
Rhombosolea leporina Günther, 1862	verbal description	Karl Warr (pers.comm to PW)
Oncopteridae	**no data**	
Paralichthodidae	**no data**	
Achiridae		
Achirus achirus (Linnaeus, 1758)	film	MrCitzen (2011)
Achirus novoae Cervigón, 1982	film	Hertzman (2019)
Achirus sp.	film	Dimoski (2017)
Catathyridium jenynsii (Günther, 1862)	film	Simso (2015)
Hypoclinemus mentalis (Günther, 1862)	film	Muh-Kuh (2016)
Trinectes maculatus (Bloch & Schneider, 1801)	film	Odum (2018)
Trinectes paulistanus (Miranda Ribeiro, 1915)	verbal description	Ivan Sazima (pers comm to PW)
Cynoglossidae		
Cynoglossus feldmanni (Bleeker, 1854)	film	Schäfer (2016)
Cynoglossus sinusarabici (Chabanaud, 1931)	photo	Dafni (2016)
Paraplagusia japonica (Temminck and Schlegel, 1846)	film	Japan Underwater Films (2016)
Paraplagusia japonica (Temminck and Schlegel, 1846)	film	https://www.youtube.com/channel/UCdfyG8oi-yECVsVY_T_TOEQ
Symphurus awarak Robins & Randall, 1965	film	Wilk (2007)
Symphurus insularis Munroe, Brito & Hernández, 2000	film	Wirtz & Dellinger (2017)
Symphurus ommaspilus Böhlke, 1961	film	Wilk (2007)
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 lenisquamis Randall, 2005	film	Harasti (2020)
Aseraggodes sp.	film	Japan Underwater Films (2016)
Brachirus harmandi (Sauvage 1878)	film	Roestad (2009)

Table 1 End.

Family/species	**type of evidence**	**Reference**
Brachirus panoides (Bleeker, 1851)	ilm	Paddock Farm (2012)
Brachirus panoides (Bleeker, 1851)	film	Nhi (2015)
Brachirus siamensis (Sauvage 1878)	film	wwwrochenat (2011)
Buglossidium luteum (Risso, 1810)	film	fishbaseyt (2009)
Liachirus melanospilos (Bleeker, 1854)	film	Marti & Wirtz (2021a)
Microchirus ocellatus Linnaeus, 1758	film	Wirtz (2017)
Microchirus variegatus (Donovan, 1808)	photo	Golani et al. (2006: 231)
Monochirus hispidus Rafinesque, 1814	photo	Louisy (2015: 412)
Monochirus hispidus Rafinesque, 1814	film	Gil & Wirtz (2021a)
Pardachirus marmoratus (Lacèpede, 1802)	film	Roman S. (2012)
Pardachirus marmoratus (Lacèpede, 1802)	film	Kasmani (2018)
Pardachirus pavoninus (Lacèpede, 1802)	film	Undersea Productions (2016d)
Pegusa lascaris (Risso, 1810*)*	film	Gil & Wirtz (2021b)
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)
Solea solea (Linnaeus, 1758)	film	WKNaturkart (2013)
Soleichthys dori Randall & Munroe, 2008	film	Popov (2017)
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)
Soleichthys microcephalus (Günther, 1862)	photo	Kuiter & Kuiter (2018: 333)
Synaptura sp.	film	O'Neill & Gibb (2001)
Zebrias scalaris Gomon, 1987	photo	Scubazoo/ Science Photo Library (2016)
Zebrias zebrinus (Temminck & Schlegel, 1846)	film	Kuiter & Kuiter (2018: 333)
Poecilopsettidae	**no data**	
Samaridae		
Samaris cristatus Gray, 1831	photo	Kuiter & Tonozuka (2004: 400)
Samaris cristatus Gray, 1831	film	Sea Story (2016)
Samaris cristatus Gray, 1831	film	liquidguru (2011)
Samariscus triocellatus Woods, 1960	photo	Randall, 2016a
Samariscus triocellatus Woods, 1960	film	Giwdul (2019)

Having accumulated more than 100 records of fincrawling in flatfish species, we can now attempt to reconstruct the origin of this behaviour pattern, by plotting its distribution onto the phylogenetic tree of the order. Probable ancestral states of fincrawling were then reconstructed using the rule of parsimony, i.e. minimizing the number of evolutionary transitions.

Results

We have gathered 104 records of fincrawling behaviour for 85 flatfish species from 48 different genera belonging to eleven recognized flatfish families. These are listed in table 1. In ten of the eleven families, at least two species from two different genera are documented to show fincrawling behaviour. Fincrawling behaviour has been observed in Citharidae, Scophthalmidae, Paralichthyidae, Pleuronectidae, Cyclopsettidae, Bothidae, Rhombosoleidae, Samaridae, Achiridae, Cynoglossidae and Soleidae. Fincrawling behaviour is shown by both dextral and sinistral flatfish species (e.g. Soleidae and Scophthalmidae respectively). Observations of this behaviour pattern are lacking for species belonging to the following families Achiropsettidae, Oncopteridae, Paralichthodidae, Poecilopsettidae and fincrawling could not be observed in films showing members of the family Psettodidae swimming.

The current phylogenetic tree of the Pleuronectiformes (Atta et al., 2021) recognizes 16 different families (Fig. 1). Fincrawling has been recorded in the families Achiridae, Samaridae, Cynoglossidae and Soleidae; it is therefore parsimonious to assume that it also occurred in the common ancestor of these families, including the family Poecilopsettidae. Similarly (compare Fig. 1), it can be argued that the common ancestor of all families from Scophthalmidae to Pleuronectidae was most likely already fincrawling. Thus, the origin of the behaviour pattern fincrawling can be traced back to the base of all flatfish families from Citharidae to Pleuronectidae, i.e. the most recent common ancestor of the suborder Pleuronectoidei.

By mapping the presence of a *recessus orbitalis* (an organ that allows flatfishes to protrude their eyes above the substratum whilst buried; Campbell et al., 2020) onto the flatfish tree, Chanet et al. (2020) have shown that this character is restricted to and a probable synapomorphy of the suborder Pleuronectoidei. Thus, the distribution patterns of the morphological character '*recessus orbitalis*' and the behavioural character 'fincrawling' are congruent.

Discussion

In 1941, Konrad Lorenz showed that behaviour patterns, just like morphological structures, can be used to construct phylogenetic trees. Conversely, by plotting the presence of a behaviour pattern onto an existing phylogeny, the time of its probable origin can be elucidated (e.g. Johnson, 2000; Kitaura et al., 2006; Horka et al., 2018). Our phylogenetic analysis indicates that fincrawling behaviour appeared early in the phylogeny of the Pleuronectiformes. It is a common character of the Pleuronectoidei. If Psettodidae also use fincrawling, this behavior pattern would be a putative synapomorphy of the order Pleuronectiformes. If it could be shown that Psettodidae do not use fincrawling, this behavior pattern would be a synapomorpohy of the suborder Pleuronectoidei. There are films on the internet showing the locomotion of flatfishes belonging to the family Psettodidae (e.g. Mama Dive Amed, 2018; RemsProd, 2021; see Electronic references). Fincrawling behaviour cannot be seen in them. Nevertheless, adult Psettodidae are heavy animals and are unlikely to use fincrawling for locomotion. It could be interesting to look for observations of young or juvenile psettodids to detect eventual fincrawling.

Fincrawling is probably an energetically inexpensive type of locomotion, 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. It also provides greater manoeuvrability than swimming, allowing backwards movement and tight turns.

Fincrawling behaviour is obviously linked to the characteristics of the median fin musculature and its innervation. A detailed analysis of the neuro-muscular anatomy of flatfish median-fin rays, in particular a comparison of the Pleuronectoidei with the Psettoidei, is not yet available but would be desirable. Cunningham (1890: Pl XIL) illustrated, but not in detail, the muscular anatomy of the median-fin rays in *Solea solea* (Linnaeus, 1758) (Soleidae). Hoshino (2001a & b) described median-fin ray characters in citharid species, but this study was limited to the caudal region. Some juvenile flatfishes resemble toxic flatworms in colour pattern (Kuiter, 1991; Randall, 2005). When they are fincrawling, this resemblance is much enhanced. Thus, fincrawling behaviour could have been a "preadaptation" permitting mimicry of flatworms.

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Data accessibility: The films made particularly for this project were deposited in the ResearchGate page of the first author:
https://www.researchgate.net/profile/Peter-Wirtz .

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