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Pristification: Defining the convergent evolution of saws in sharks and rays (Chondrichthyes, Neoselachii)

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Convergent evolution is the development of analogous structures or bauplans in at least two independent lineages of organisms. Convergence is driven by the occupation of similar ecological niches and by various physical and phylogenetic constraints (McGhee, 2011). Despite the wide recognition of this phenomenon in evolutionary biology, formal terms and definitions for specific examples are rare. The most notable is carcinisation, which refers to the appearances of a crab-like bauplan among crustaceans (Keiler *et al*., 2017). Here the term 'pristification' is proposed for the convergence of saws in sharks and rays. It was coined previously in a preliminary publication (Greenfield, 2021a) but is formally defined for the first time. Not only does it highlight a remarkable convergent structure, but it also serves as a template for future terminology.

Results

Saws and their functions

A saw is an elongated, dorsoventrally-compressed, cartilaginous rostrum with lateral rows of enlarged denticles (Fig. 1). The rostral denticles were formerly thought to have evolved from oral teeth but are now known to be modified dermal denticles (Smith *et al*., 2015; Welten *et al*., 2015). Saws are multifunctional and primarily used for hunting and feeding. They stun or kill prey through rapid, lateral strikes and manipulate it towards the mouth, sometimes by pinning it to the substrate (Wueringer *et al*., 2012a; Nevatte *et al*., 2017; Burke & Williamson, 2021). They are also covered in hundreds of sensory organs, the ampullae of Lorenzini, that detect the electric fields emitted by prey (Wueringer *et al*., 2011, 2012b, 2021). They may be used for defence against predators or conspecifics, but this has

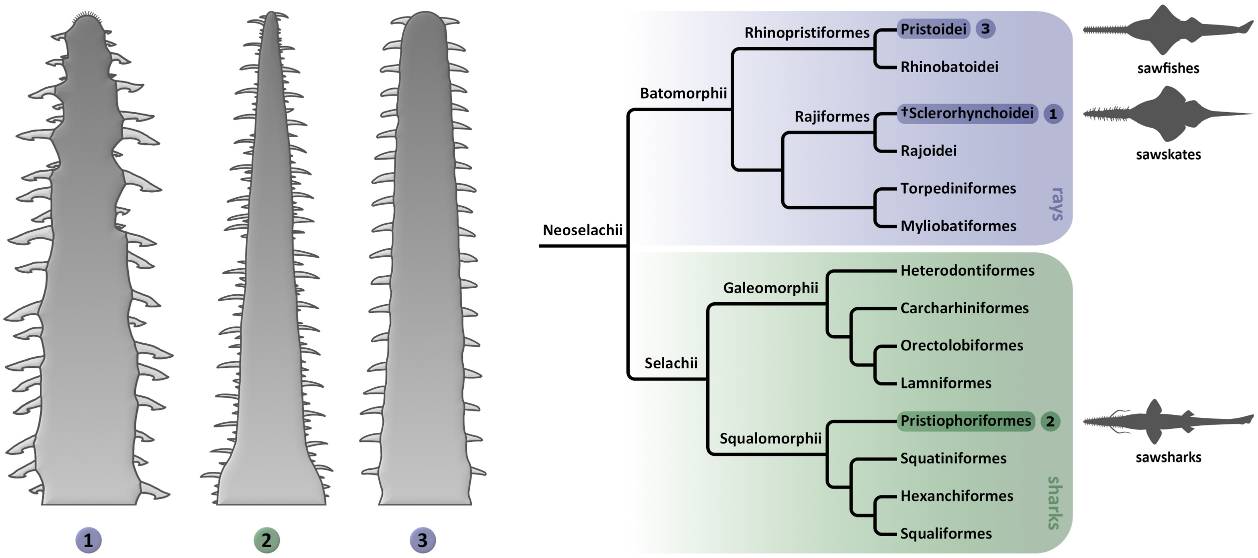

FIGURE 1. The saws (left) and a phylogenetic tree (right) of the three clades of saw-bearing fishes. The numbers represent the order in which the clades appeared in the fossil record and correspond between both sides of the figure. The sawskate (1) is *Onchopristis numida*; its saw and silhouette are the author's own work. The sawshark (2) is *Pristiophorus cirratus*; its saw is redrawn from Lange *et al*. (2015) and its silhouette is redrawn and modified from Compagno (1984). The sawfish (3) is *Pristis pristis*; its saw is redrawn from Lange *et al*. (2015) and its silhouette is redrawn and modified from Ebert & Stehmann (2013). The tree topology is mostly based on Pavan-Kumar *et al*. (2020), with Rajiformes added based on Villalobos-Segura *et al*. (2019).

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yet to be conclusively demonstrated. Overall, saws are clearly advantageous structures for benthic fishes that target small prey.

Saw-bearing fishes

In crown-group sharks and rays (Neoselachii), saws convergently evolved three times: in sawskates (Sclerorhynchoidei), sawsharks (Pristiophoriformes), and sawfishes (Pristoidei) (Fig. 1). Their saws mainly differ by the attachment and replacement styles of the rostral denticles. They are attached to the edges of the rostrum and replaced when lost in sawskates and sawsharks, while they are embedded in sockets and not replaced in sawfishes (Slaughter & Springer, 1968; Smith *et al*., 2015; Welten *et al*., 2015). Sawskates were the earliest of the saw-bearing fishes to evolve, appearing in the Barremian stage of the Early Cretaceous (Kriwet, 1999; Cuny *et al*., 2015). They were long classified as primitive sawfishes but were first proposed to be a separate group by Cappetta (1974, 1980a). Their close relationship to skates (Rajoidei) was unknown until more recent phylogenetic analyses (Villalobos-Segura *et al*., 2019, 2021a, b). They are still often called sawfishes, but this misnomer should be avoided in favour of the more accurate sawskates (Greenfield, 2021a, b). They were the most diverse of the three clades, comprising over 20 genera, and they went extinct during the Cretaceous-Paleogene mass extinction (Kriwet & Kussius, 2001; Cappetta, 2012).

Sawsharks were the next to evolve, appearing in the Santonian stage of the Late Cretaceous (Cappetta, 1980b). They consist of two extant genera (*Pristiophorus*, *Pliotrema*) and two extinct genera (*Propristiophorus*, *Ikamauius*) (Nevatte & Williamson, 2020). Their closest relatives are angelsharks, cow sharks, and dog sharks (Squalomorphii) (Pavan-Kumar *et al*., 2020). Sawfishes were the latest to evolve, appearing in the Ypresian stage of the early Eocene (Cappetta, 2012). They likewise consist of two extant genera (*Pristis*, *Anoxypristis*) and two extinct genera (*Propristis*, *Mesopristis*) (Farrés & Fierstine, 2009). Their closest relatives are guitarfishes (Rhinobatoidei) (Pavan-Kumar *et al*., 2020). Sawsharks were considered to be sawfishes by some early naturalists, but were first recognised as distinct by Müller & Henle (1837). Unfortunately, the future of saw-bearing fishes is uncertain; for instance, all sawfish species are currently Critically Endangered (IUCN, 2024). Although not endangered, sawsharks nonetheless face several threats as well (Nevatte & Williamson, 2020). Understanding their evolutionary history and the ecological pressures that shaped them is important for their modern conservation.

Pristobenthic ecomorphotype

Compagno (1990) designated the pristobenthic ecomorphotype to refer to saw-bearing fishes. This concept correctly acknowledged their similar niches. However, it also incorrectly implied that they all have an equivalent bauplan. While sawsharks and sawfishes do have comparable bauplans, sawskates are significantly different from the other two clades. Relatively complete specimens of sawskates show that their pectoral and pelvic fins were adjoined, their dorsal fins were reduced, and both placed behind the pelvic fins, and their caudal fin was greatly reduced (Cappetta, 1980a; Kaddumi, 2009). They had a more ray-like body indicative of poorer swimming and a more sedentary lifestyle, contrasting the shark-like bodies of sawsharks and sawfishes which are better suited for active swimming. This suggests that the evolution of the saw occurred separately from the rest of the body. As a result, the pristobenthic ecomorphotype should be restricted to sawsharks and sawfishes. A novel ecomorphotype, 'sclerobenthic', is created here for sawskates.

Defining pristification

Pristification is here defined as the convergent evolution of saws. Again, a saw is an elongated, dorsoventrally-compressed, cartilaginous rostrum with lateral rows of enlarged denticles. The word is derived from the Ancient Greek *prístis* ("saw/sawfish") and the Latin *ficatio* ("becoming/making"). Its verb and adjective forms are 'pristify' and 'pristified'. Pristification is strictly the evolution of the structure; as previously discussed, saws are not tied to a specific bauplan even though they are only found in benthic species. It is a type of iso-convergence according to the terminology of McGhee *et al*. (2018), because saws are derived from the same precursor traits. Its definition limits it to cartilaginous fishes (Chondrichthyes), since they are the only group possessing both cartilaginous rostra and denticles (*i.e*., placoid scales). Three pristified clades are currently known, sawskates, sawsharks, and sawfishes, and all are neoselachians. Nevertheless, non-neoselachian chondrichthyans are not necessarily excluded by the definition. It is highly unlikely that new, extant clades of saw-bearing fishes will be discovered, so the fossil record provides the best chance for further examples of pristification.

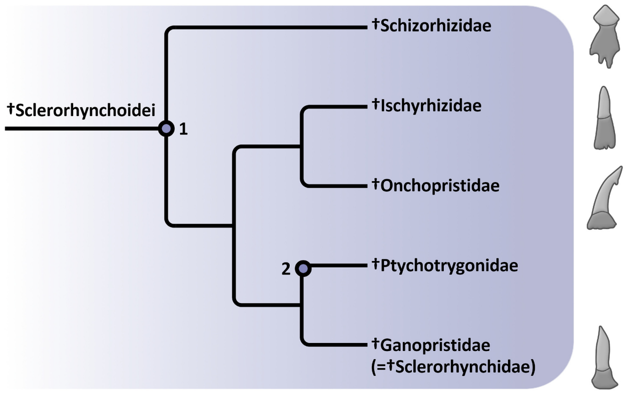

FIGURE 2. A phylogenetic tree of Sclerorhynchoidei showing the evolutionary scenario for depristification and the rostral denticles of the different families. The most recent common ancestor of all sawskates had rostral denticles (1), then ptychotrygonids lost them sometime after diverging from ganopristids (2). The schizorhizid rostral denticle is *Schizorhiza stromeri*, which is redrawn from Cappetta (2012). The ischyrhizid rostral denticle is *Ischyrhiza mira*, which is redrawn from Cappetta (2012). The onchopristid rostral denticle is *Onchopristis numida*, which is redrawn from Stromer (1917). The ganopristid rostral denticle is *Sclerorhynchus* (=*Ganopristis*) *leptodon*, which is redrawn from Arambourg (1940). The tree topology is based on Villalobos-Segura *et al*. (2021b) and the family-level taxonomy is based on Greenfield (2021b).

Defining depristification
'Depristification' is here defined as the secondary loss of one or more components of the saw. It is so far only known to have happened once, in the sawskate family Ptychotrygonidae. Three-dimensional, articulated specimens of ptychotrygonids retain elongated rostra but lack enlarged rostral denticles (Villalobos-Segura *et al*., 2019, 2021a). The other families of sawskates all have rostral denticles, denoting that they were present in the most recent common ancestor and were secondarily lost by ptychotrygonids (Fig. 2). The exact benefits of depristification are unclear due to the uniqueness of this situation, although it might be correlated with increased sensory function of the rostrum.

Conclusions
Pristification is only one of countless sub-phenomena within the broader phenomenon of convergent evolution. Yet, the vast majority are unnamed and undefined despite being studied. Precise terms like pristification are more useful for delineating instances of convergence and for assessing the diversity of structures and bauplans in life. They are also helpful for science communication, mainly for introducing concepts to a lay audience in a concise and accessible form. This should encourage the creation of new terms, with the recommended format being a prefix relating to the convergence concerned plus a suffix of '-ification' or '-isation'. Additionally, the definition of pristification clarifies what saws actually are: they are a structure not confined to any one bauplan, they evolved from the same ancestral characters and are thus iso-convergent evolution, and they are only possible in chondrichthyans. Saws have ecological advantages while still having structural and phylogenetic limitations. Subsequent analyses of living and extinct saw-bearing fishes should take all of this information into account.

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