# The biology of extinct and extant sawfish (Batoidea: Sclerorhynchidae and Pristidae)

**Barbara E. Wueringer · Lyle Squire Jr. ·
Shaun P. Collin**

**Abstract** Sclerorhynchids (extinct sawfishes, Batoidea), pristids (extant sawfish, Batoidea) and pristiophorids (sawsharks, Squalomorphi) are the three elasmobranch families that possess an elongated rostrum with lateral teeth. Sclerorhynchids are the extinct sawfishes of the Cretaceous period, which reached maximum total lengths of 100 cm. The morphology of their rostral teeth is highly variable. Pristid sawfish occur circumtropically and can reach maximum total lengths of around 700 cm. All pristid species are globally endangered due to their restricted habitat inshore. Pristiophorid sawsharks are small sharks of maximum total lengths below 150 cm, which occur in depths of 70–900 m. Close examination of the morphology of pectoral fin basals and the internal structure of the rostrum reveals that sclerorhynchids and pristids evolved independently from rhinobatids, whereas pristiophorids are squalomorph sharks. The elongation of the rostrum may be an adaptation for feeding, as all marine vertebrate taxa that possess this structure are said to use it in the context of feeding.

B. E. Wueringer (✉) · S. P. Collin
School of Biomedical Sciences, Sensory Neurobiology Group, The University of Queensland, St. Lucia, QLD 4072, Australia
e-mail: b.wueringer@uq.edu.au

L. Squire Jr.
Cairns Marine, 14 Industrial Avenue, Stratford, QLD 4870, Australia

## Introduction

Within elasmobranchs, three families are known to possess an elongated rostrum bearing lateral teeth: Sclerorhynchids (extinct sawfishes, Batoidea), pristids (extant sawfish, Batoidea) and pristiophorids (sawsharks, Squalomorphi, Table 1; Fig. 1; Cappetta 1987). Here, we review the biology of the two families of saw-bearing batoids and trace the evolution of the elongated rostrum. Pristiophorids will not be treated in detail, as they are sharks and therefore more distantly related to both these sawfish families than they are to each other.

Sclerorhynchid sawfish are an extinct monophyletic batoid taxon, comprising up to 23 genera (although some need confirmation by description of their rostral teeth). Their rostral teeth are attached to the rostrum via connective tissue and, when lost, they are replaced in a conveyor-belt fashion like elasmobranch oral dentition (Schaeffer 1963; Slaughter and Springer 1968; Cappetta 1987). The peduncle of the rostral teeth is expanded (Cappetta 1987). The maximum total length of sclerorhynchids does not exceed 100 cm (Cappetta 1974). Sclerorhynchids are regarded to be benthic sawfish that occupied shallow coastal habitat, but no exact depth ranges are known.

**Table 1** Systematics of saw-bearing elasmobranchs after Cappetta (1987)

| |
| --- |
| Class: Chondrichthyes |
| Subclass: Elasmobranchii Bonaparte 1838 |
| Cohort: Euselachii (Hay 1902) |
| Superorder: Squalomorphii |
|    Order: Pristiophoriphormes |
|       Fam.: Pristiophoridae |
| Superorder: Batomorphii |
|   Order: Rajiformes |
|     Suborder: Sclerorhynchoidei † |
|       Fam.: *Sclerorhynchidae* |
|     Suborder: Pristoidei |
|       Fam.: *Pristidae* |

Taxa that will be presented in depth in the present publication are listed in Italic

Since Cappetta summarized sclerorhynchids in 1987 (Cappetta 1987), the number of described genera has almost doubled, with ten more genera being added to this family.

Pristid sawfish possess rostral teeth that grow continuously from the base and are attached to the rostrum via alveoli (Slaughter and Springer 1968; Compagno and Last 1999). The peduncle is not expanded and the dentine cap is easily worn off (Slaughter and Springer 1968). The maximum total length reported for pristids is around 700 cm (Last and Stevens 1994b). They occur inshore, in freshwater and in marine environments to a maximum depth of 122 m (McEachran and de Cavarlho 2002; Simpfendorfer 2006).

We aim to review pristid species as this family is one of the most problematic elasmobranch families with regards to their systematics (Ishihara et al. 1991b; van Oijen et al. 2007; Wiley et al. 2008). The FAO currently recognizes two species in the Atlantic (*Pristis pristis* and *P. pectinata*) and five species in the Western Central Pacific (*P. pectinata*, *P. clavata*, *P. microdon*, *P. zijsron* and *Anoxypristis cuspidata*; Compagno and Last 1999; McEachran and de Cavarlho 2002). The problems associated with the systematics of sawfish may only be solved with genetic analyses, as some species may be morphologically identical. Historically, species descriptions of pristids based on isolated body parts have caused confusion and often misidentification, i.e. *Pristis zijsron* Bleeker 1851 was described solely on the basis of its rostrum, *Pristis dubius* Bleeker 1852 was described solely on the basis of its caudal fin, and *Pristis leichardti* Whitley 1945 was described only

**Fig. 1** Comparison of the morphology of a sclerorhynchid (**a**), a pristid (**b**) and a pristiophorid (**c**). *Libanopristis hiram* is redrawn after a specimen in the Milano Museo storia naturale. *Pristiophorus cirratus* redrawn after Compagno et al. (2005)



a

*Libanopristis hiram*

b

*Pristis microdon*

c

*Pristiophorus cirratus*
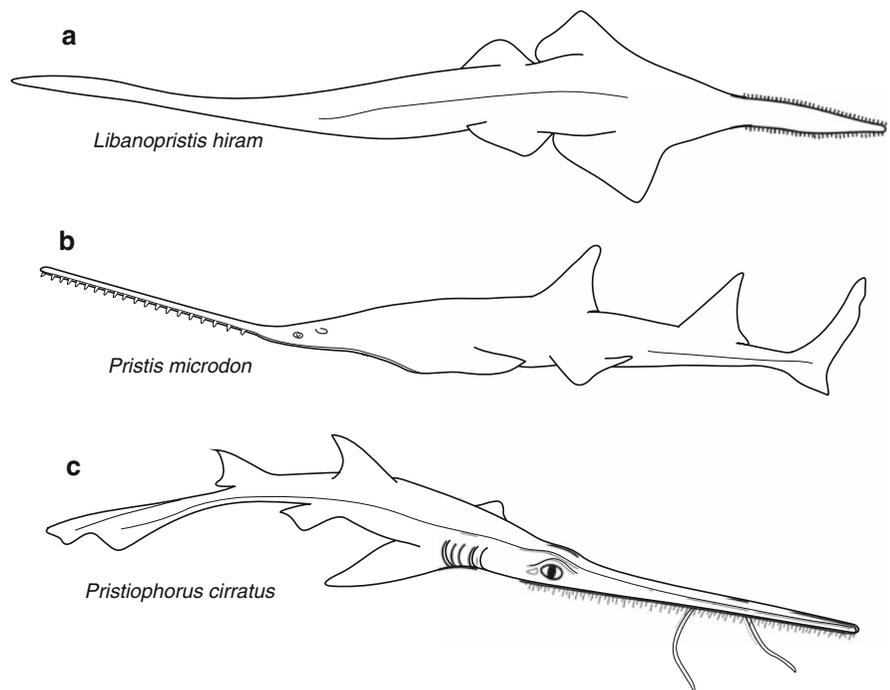
from a single photograph (Thorburn et al. 2003). Interestingly, the cartilaginous lining of a pristid rostral canal was misinterpreted and identified as the echinoderm *Myriosteon higginsi* (Gray 1864) was described (Norman and Fraser 1938).

Pristiophorid sawsharks have laterally positioned gills and numerous, irregularly positioned medium-sized teeth lying between large rostral teeth (Slaughter and Springer 1968; Compagno and Last 1999). The rostral teeth of sawsharks do not grow in length but are replaced periodically after damage or loss (Slaughter and Springer 1968; Compagno and Last 1999). All species of sawshark also possess a pair of long, tape-like barbels situated ventrally on the snout in front of the nostrils (Compagno et al. 2005). The maximum total length for any species of sawshark does not exceed 150 cm (Compagno et al. 2005). Of the nine species of sawshark four occur in the upper layer of the photic zone (i.e. *Pliotrema warreni*, *Pristiophorus cirratus*, *Pristiophorus japonicus*, *Pristiophorus nudipinnis*) down to a depth of several hundred meters. All other species of sawsharks occur between depths of 100–900 m (Compagno et al. 2005).

The present review was undertaken with the aim to compile detailed information about all of the extant species of pristid sawfish and their fossil history, including sclerorhynchids who may have evolved from a common ancestor. This information may shed light on their difficult systematics and provide a concise summary for everyone working with these animals. This review is the first to bring together literature on all recent species of sawfish. Moreover, the evolution of the elongated rostrum will be discussed.

## Phylogeny of saw-bearing batoids (Pristidae and Sclerorhynchidae) with notes on pristiophorids

Chondrichthyes, or cartilaginous fishes, are grouped into Holocephali (chimeras) and Elasmobranchii (sharks, skates and rays). The Neoselachii are an elasmobranch sub-cohort that comprises all modern sharks and rays. They first emerged in the upper Permian, around 250 million yeas ago (Westheide and Rieger 2004). Traditionally, they are divided into two super-orders, the Galea (true sharks) and Squalea

(sharks and rays; Westheide and Rieger 2004). This classification is based on the idea that batoids evolved from squalean sharks (Shirai 1996). The squaleans include, amongst others, the two extant saw-bearing families of elasmobranchs, pristiophorids and pristids (Westheide and Rieger 2004). However, Compagno (1977) divided the Neoselachii into four super-orders, the squalomorph sharks, galeomorph sharks, squatinomorph sharks and batoid rays and suggested that all four super-orders were derived independently.

The analysis of morphological characters alone cannot resolve the position of benthic members of the Neoselachii that possess a dorso-ventrally flattened body (i.e. pristids, rhinobatids, pristiophorids, squatinoids; Maisey et al. 2004). Therefore, Maisey et al. (2004) combined morphological data from Shirai (1996) with a phylogenetic tree based on molecular examination of the RAG-1 gene, a gene that evolves slowly and therefore shows little deviation across taxa. However, this strategy did not resolve, unequivocally, the position of batoids within the neoselachian tree. Molecular data do support the hypothesis that morphological similarities between taxa are a result of adaptations to a benthic lifestyle and therefore can be attributed to convergent evolution (Maisey et al. 2004). This theory is strengthened by the analysis of mitochondrial genes, which suggests that batoids are a sister group to both galean and squalean sharks (Douady et al. 2003). Interestingly, the first appearance of elasmobranch families in the fossil records is remarkably similar to their appearance in the RAG-1 phylogenetic tree, whereas the morphological tree differs from fossil records by 50–80 million years (Maisey et al. 2004).

Within extant batoids, phylogenetic relationships become even more complicated. Both morphological and molecular studies agree that torpediniforms represent a sister group to all other batoids (McEachran et al. 1996; Rocco et al. 2007), but there is currently no consensus on the position of pristids, since analyses have been based on different morphological characters and have yielded different relationships (McEachran et al. 1996). Compagno (1977) places pristiforms as a sister group to rajiforms and mylobatiforms, whereas Nishida (1990) and Maisey (1984) place pristiforms as a sister group to all other batoids. Since molecular studies on elasmobranch systematics rarely include pristids and/or rhinobatids (Douady et al. 2003; Winchell et al. 2004; Rocco

et al. 2007) it may be some time before there is a resolution of their systematic position.

Various morphological characteristics of sclerorhynchid and pristid sawfish and rhinobatid shovelnose rays indicate that both families of sawfish evolved from shovelnose rays (Schaeffer 1963; Cappetta 1974). This contention is strengthened by the fact that rhinobatids appeared first in the fossil record during the Lias stage of the lower Jurassic (Fig. 2; Cappetta 1987). The morphology of the pectoral fin in these three taxa provides a specific insight into their phylogenetic interrelationship: the pectoral basals of pristids morphologically resemble those of rhinobatids, whereas in *Sclerorhynchus atavus* and other sclerorhynchids, all three elements are enlarged, and the pro- and mesoptrygium carry most fin radials (Fig. 3; Cappetta 1974; Kriwet 2004). This, together with the relatively specialized oral teeth found in sclerorhynchids compared to the unspecialized oral teeth of pristids and rhinobatids, lead Cappetta (1974) to conclude that pristids did not evolve from sclerorhynchids, but evolved independently from rhinobatids. If pristids evolved from sclerorhynchids, their basals, which resemble those of rhinobatids, would have been secondarily reduced, which is improbable (Cappetta 1974). Therefore, we suggest that the elongated rostrum bearing lateral teeth evolved independently at least three times within elasmobranchs, e.g. in pristiophorids, sclerorhynchids and pristids.
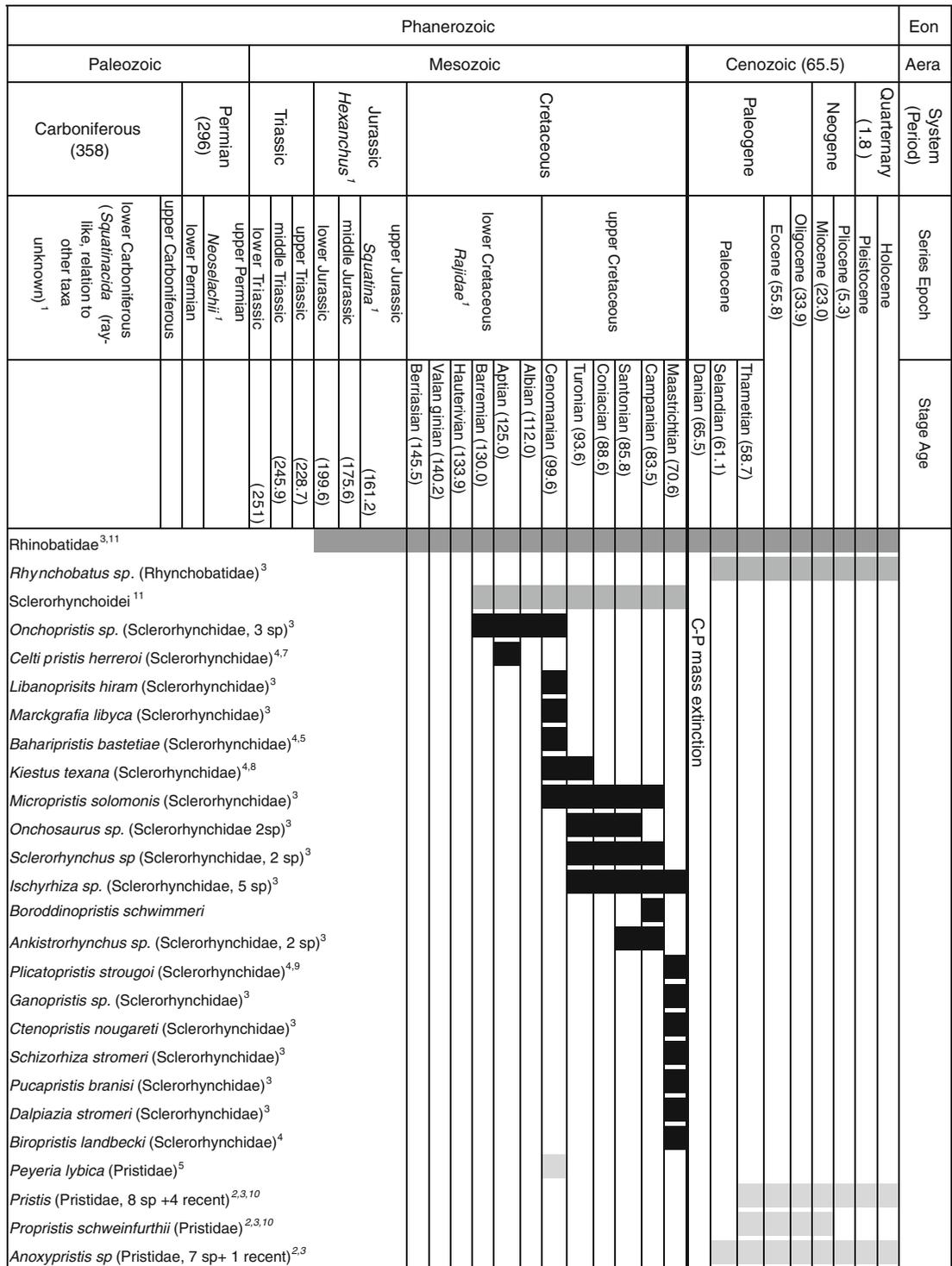
The internal anatomy of the rostrum can also be used to establish the phylogeny of saw-bearing elasmobranchs. Batoid rostra generally possess only one medial canal, which represents the rostral process of the brain cavity (Hoffmann 1912). In pristids, this median canal is filled with loose connective tissue until the distal third of the rostrum, which is filled with hyaline cartilage (Hoffmann 1912). *Pristis* spp. possess one additional canal pair lateral to the medial canal, which contains ophthalmic and buccal nerves and the rostral artery (Fig. 4; Hoffmann 1912). Hoffmann (1912) explains that a second lateral canal pair described in *Pristis* spp. is either the erroneous interpretation of a rostral tooth alveolus or a dried hyaline mass located between two alveoli. However, *Anoxypristis cuspidata* possesses a second paired lateral canal, which contains the canals of ampullae of Lorenzini (which are part of the electroreceptive system) located within both the buccal and ophthalmic groups of ampullae (Fig. 4; Hoffmann 1912). In *Pristis* spp. the ampullary canals are located outside the cartilage and are surrounded by connective tissue (Hoffmann 1912).

In sclerorhynchids and pristiophorids, the rostral cartilage contains only one medial unpaired canal (Fig. 4; Hoffmann 1912; Cappetta 1987; Werner 1989; Kirkland and Aguillon-Martinez 2002). The superficial ophthalmic nerve is located in a paired dorsal groove, whereas the bucco-pharyngeal nerve is located in a paired ventral groove. In sclerorhynchids, these grooves are covered with wood-like cartilage (Cappetta 1987; Werner 1989; Kirkland and Aguillon-Martinez 2002), whereas in pristiophorids they are surrounded by connective tissue (Hoffmann 1912; Kirkland and Aguillon-Martinez 2002). The exposed nerve tracts in the rostrum of sclerorhynchids and pristiophorids may represent a case of convergent evolution (Cappetta 1987; Kirkland and Aguillon-Martinez 2002). However, as sclerorhynchids and pristids are also not directly related but indirectly related through rhinobatids, similarities in their rostra may also be considered convergent (Kirkland and Aguillon-Martinez 2002).

Hoffmann (1912) found the hyaline mass within the medial canal to be short in *Rhinobatus* sp. and therefore concluded that this part should similarly be elongated in pristids. Cross sections of the rostra in two rhinobatids, *Aptychotrema rostrata* and *Rhinobatos typus* (Fig. 4; B. Wueringer, unpublished data) reveal that in *A. rostrata* the ophthalmic and buccal nerves and the rostral artery all run embedded in dense connective tissue alongside the rostral cartilages. In *R. typus*, however, these nerves and the artery run embedded in dense connective tissue outside the cartilage in the posterior portion of the rostrum, but are surrounded by prismatic cartilage in the anterior portion of the rostrum. Based on this evidence, one may suggest two different scenarios as to the evolution of the rostrum, which are not necessarily mutually exclusive:

1. In primitive rhinobatids, rostral nerve tracts run alongside the rostral cartilage, which is similar to the condition in sclerorhynchids. Therefore, it can be concluded that sclerorhynchids evolved from primitive rhinobatids, whereas pristids, whose rostral nerves are encased in rostral cartilage, evolved from advanced rhinobatids,

**Eon:** Phanerozoic

**Aera:** Paleozoic | Mesozoic | Cenozoic (65.5)

**System (Period):** Carboniferous (358) | Permian (296) | Triassic | Hexanchus[1] | Jurassic | Cretaceous | Paleogene | Neogene | Quaternary (1.8)

**Series Epoch:** lower Carboniferous (Squatinacida (ray-like, relation to other taxa unknown)[1] | upper Carboniferous | lower Permian | Neoselachii[1] | upper Permian | lower Triassic | middle Triassic | upper Triassic | lower Jurassic | middle Jurassic | Squatina[1] upper Jurassic | Rajidae[1] lower Cretaceous | upper Cretaceous | Paleocene | Eocene (55.8) | Oligocene (33.9) | Miocene (23.0) | Pliocene (5.3) | Pleistocene | Holocene

**Stage Age (beginning in million years):** (251) | (245.9) | (228.7) | (199.6) | (175.6) | (161.2) | Berriasian (145.5) | Valanginian (140.2) | Hauterivian (133.9) | Barremian (130.0) | Aptian (125.0) | Albian (112.0) | Cenomanian (99.6) | Turonian (93.6) | Coniacian (88.6) | Santonian (85.8) | Campanian (83.5) | Maastrichtian (70.6) | Danian (65.5) | Selandian (61.1) | Thanetian (58.7)

C-P mass extinction

Taxa listed (stratigraphic occurrences):

- Rhinobatidae[3,11]
- Rhynchobatus sp. (Rhynchobatidae)[3]
- Sclerorhynchoidei[11]
- Onchopristis sp. (Sclerorhynchidae, 3 sp)[3]
- Celtipristis herreroi (Sclerorhynchidae)[4,7]
- Libanopristis hiram (Sclerorhynchidae)[3]
- Marckgrafia libyca (Sclerorhynchidae)[3]
- Baharipristis bastetiae (Sclerorhynchidae)[4,5]
- Kiestus texana (Sclerorhynchidae)[4,8]
- Micropristis solomonis (Sclerorhynchidae)[3]
- Onchosaurus sp. (Sclerorhynchidae 2sp)[3]
- Sclerorhynchus sp (Sclerorhynchidae, 2 sp)[3]
- Ischyrhiza sp. (Sclerorhynchidae, 5 sp)[3]
- Boroddinopristis schwimmeri
- Ankistrorhynchus sp. (Sclerorhynchidae, 2 sp)[3]
- Plicatopristis strougoi (Sclerorhynchidae)[4,9]
- Ganopristis sp. (Sclerorhynchidae)[3]
- Ctenopristis nougareti (Sclerorhynchidae)[3]
- Schizorhiza stromeri (Sclerorhynchidae)[3]
- Pucapristis branisi (Sclerorhynchidae)[3]
- Dalpiazia stromeri (Sclerorhynchidae)[3]
- Biropristis landbecki (Sclerorhynchidae)[4]
- Peyeria lybica (Pristidae)[5]
- Pristis (Pristidae, 8 sp +4 recent)[2,3,10]
- Propristis schweinfurthii (Pristidae)[2,3,10]
- Anoxypristis sp (Pristidae, 7 sp+ 1 recent)[2,3]

**Fig. 2** Stratigraphic occurences of rhinobatids and all genera of sclerorhynchid and pristid sawfish. Exponents indicate the following sources: [1]Westheide and Rieger (2004), [2]Bourdon (1999), [3]Cappetta (1987), [4]Suarez and Cappetta (2004), [5]Werner (1989), [6]Case (1987), [7]Kriwet (1999), [8]Cappetta and Case (1999), [9]Cappetta (1991), [10]Kriwet and Benton (2004), [11]Underwood (2006). *Numbers in brackets* indicate the beginning of each period in million years
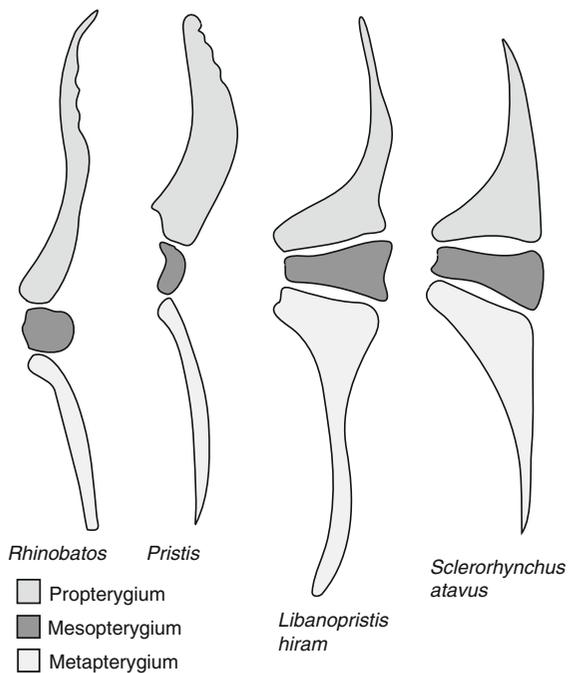
**Fig. 3** Schematic comparison of the pectoral basals of sclerorhynchids, rhinobatids and pristids, redrawn from Cappetta (1974), and Wueringer and Tibbetts (2008)

which show a similar morphology. However, it is unclear if *A. rostrata* represents a primitive rhinobatid and *R. typus* represents an advanced form.

2. Sclerorhynchids evolved a long rostrum by elongation of the basal part of the rostral cartilages. In both species of rhinobatids, the rostral nerves are exposed in the basal part of the rostrum, similar to the situation in sclerorhynchids. This arrangement may explain why sclerorhynchids possess such a strongly tapered rostrum with no marked transition between cephalon and rostrum. Pristids, on the other hand, may have evolved a long rostrum by the elongation of the anterior portion of the rostrum. All nerves are encased in cartilage and there is a clear transition between cephalon and rostrum.

## Feeding behaviour and the elongated rostrum

Throughout the animal kingdom, a handful of aquatic taxa have evolved an elongated rostrum (Table 2).

This adaptation is found in members of the Chondrichthyes, Chondrostei and Teleostomi and its function is assumed to be related to feeding, e.g. the paddlefish, *Polyodon spathula*, possesses a large number of electroreceptors distributed over the dorsal and ventral surfaces of the rostrum, which it uses to search for planktonic prey in the water column (Wilkens and Hofmann 2005). Moreover, juvenile paddlefish under 20 cm in total length, that have not yet developed their filter feeding apparatus, use electroreception to capture individual plankton (Wilkens et al. 2001). It is assumed that all pristid and pristiophorid elasmobranchs use their elongated rostrum for stunning prey and searching through the substrate, but to date this has only been verified in one individual of *P. pectinata* (Breder 1952). Some istiophorids and one species of xiphiid impale their prey with their sword and also use headshakes during prey manipulation (Scott and Tibbo 1968; Shimose et al. 2007).

Speciation can occur when external ecological pressures change and new niches are created. Random mutations can increase the likelihood of some individuals of a population adopting a new niche and adapting successfully to finally reproduce. Initial elongation of the rostrum, and the simultaneous strengthening of the lateral edges by an increase in the size of the dermal denticles could have allowed the ancestors of extant sawfish to manipulate larger but also more agile prey. Further elongation of the rostrum would have expanded their prey selection, enabling them to hunt faster and more agile prey by stunning them with lateral swipes of the rostrum.

Schaeffer (1963) considers the adaptive significance of an elongated rostrum in pristids is for mud grubbing, and believes that the enlargement of dermal denticles and the formation of rostral teeth is a secondary adaptation for slashing prey. However, the rhinobatid *Rhinobatus lentinosus* presses both its rostrum and pectoral fins against the substrate during the final stages of prey manipulation to immobilize prey (Wilga and Motta 1998) and *Pristis microdon* shows similar behaviours, using both the rostral part of the head and the rostrum to pin prey onto the substrate (B. Wueringer, unpublished data). By using the rostrum to immobilize prey, the sawfish has a distinct advantage over the shovelnose ray, as it can use its pectorals more freely to reposition itself over
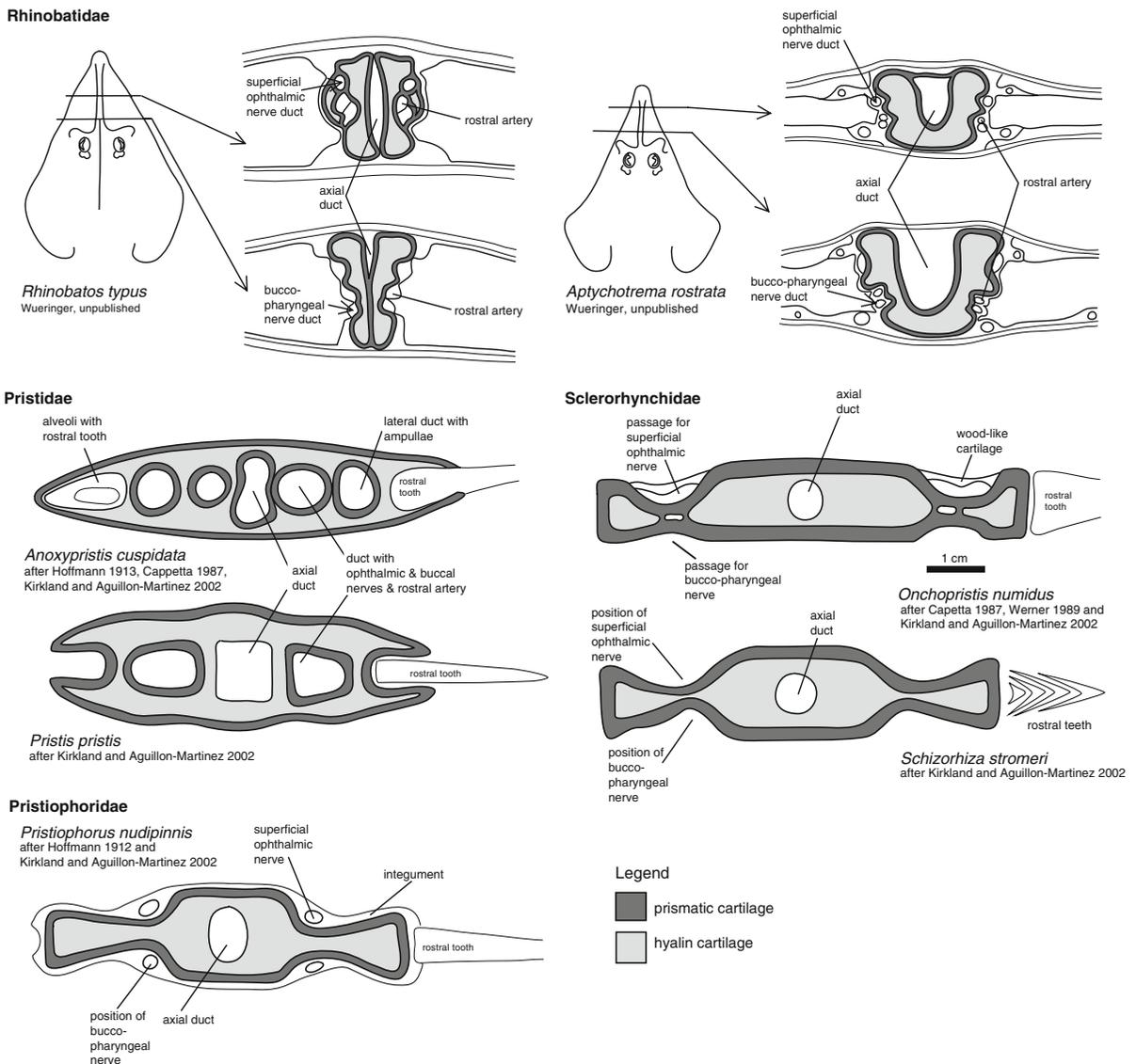
**Fig. 4** Comparison of the internal anatomy of the rostrum of different genera of sclerorhynchids, pristids and rhinobatids. Redrawn from photographs and schematic drawings from Hoffmann (1912), Cappetta (1987), and Kirkland and Aguillon-Martinez (2002)

the prey. Therefore, we believe that the elongated rostrum initially evolved not to aid in mud grubbing, but to aid in prey immobilisation. The morphology of pristid rostral teeth additionally shows a high adaptation for immobilisation of fast prey in the water column. As pristid rostral teeth grow continuously from the base, their weight is minimal. Sclerorhynchids, on the other hand, which replaced their rostral teeth regularly and therefore carried the additional weight of dormant teeth on the rostrum might not

have been well adapted to hunt agile prey in the water column or move their rostrum rapidly.

However, the expansion of the rostrum also allows the simultaneous expansion of sensory sampling by receptors such as the ampullae of Lorenzini of the electroreception system and the neuromasts of the lateral line system along the saw, thereby increasing the electric and hydrodynamic ranges, respectively, in a way similar to what has been described for the cephalofoil in sphyrnid hammerhead sharks (Kajiura

**Table 2** Extant taxa of aquatic vertebrates bearing elongated rostra and an inferior mouth showing their feeding behaviour and habitat

| Family, order | Species | Feeding behaviour | Habitat | Max. TL (cm) |
|---|---|---|---|---|
| Polyodontidae, *Acipenseriformes* | *Polyodon spathula*, Paddlefish | Filter-feeder | Endemic to North America, freshwater | 221 |
| | *Psephurus gladius*, Chinese Paddlefish | Piscivorous predator | Endemic to China, freshwater | 130 |
| Pristiophoridae, *Pristiophoriformes* | 9 Species in 2 genera, *Pliotrema* and *Pristiophorus* | Possibly stun prey with saw, and search in substrate for demersal prey (Schaeffer 1963) | Demersal, marine | 80–150 |
| Istiophoridae, *Perciformes* | 11 Species in 3 genera of billfish | Impale prey and shake head (Shimose et al. 2007) | Marine | 500 |
| Xiphiidae, *Perciformes* | Monospecific, *Xiphias gladius* | Slash at prey, impale it behind head (Scott and Tibbo 1968) | Marine, circumglobal | 450 |
| Pristidae, *Pristiformes* | 4–7 Species of sawfish | Piscivorous, only *Pristis pectinata* known to stun prey with lateral swipes of saw (Breder 1952) | Marine, brackish and freshwater, circumglobal | 700 |

Systematics after Froese and Pauly (2008)

2000; Kajiura and Holland 2002). This notion of sensory optimization is supported by the exceptional density of ampullae of Lorenzini located in the rostrum of extant rhinobatid shovelnose rays such as *A. rostrata* and *R. typus* (Wueringer and Tibbetts 2008), which can be interpreted as an evolutionary stage preceding the expansion of the rostrum. Both sensory systems are used in prey manipulation, which may be especially useful in both murky/turbid environments and low light conditions.

## Use of the elongated rostrum for self-defence

As sclerorhynchids were small benthic rays with unspecialized teeth and a weak tail (for more details see next section), the elongation of the rostrum could have been used for self-defence against larger predators. Extant pristids produce lateral swipes of the rostrum that are presumably used in self-defence (Norman and Fraser 1938; Breder 1952; Martin 2005), although Irvine (1947) and Norman and Fraser (1938) also reported that sawfish use their saw to cut pieces out of large prey. Attacks on whales by sawfish are regarded to be without foundation (Norman and Fraser 1938; Breder 1952), although Indian fishermen believe that sawfish kill dugongs (Lal Mohan 1986; Martin 2005). According to these fishermen, sawfish attack foraging dugongs that get

too close, where the shadow of the dugong appears to trigger the attack (Lal Mohan 1986). Sawfish are generally not considered harmful to humans, unless they are threatened, and apart from early anecdotal evidence of a sawfish cutting a human in two (Norman and Fraser 1938) no other incidences are known. In Australia, at least four species of pristids coexist in habitats with estuarine crocodiles, *Crocodylus porosus*, which might pose a threat. We suspect that adult crocodiles feed on juvenile sawfish but no stomach content data is presently available.

## Description of the fossil record of sclerorhynchids

Sclerorhynchid sawfish are a monophyletic taxon that first occurred at the beginning of the Barremian stage of the lower cretaceous, around 130 million years ago and disappeared during the Maastrichtian at the end of the Cretaceous period, between 70.6 and 83.5 million years ago (Fig. 2; Cappetta 1987; Underwood 2006). They peaked in species diversity during the Maastrichtian (Kriwet and Kussius 2001; Underwood 2006). The transition from the Cretaceous to the Paleogene (formerly 'Triassic') was marked by a mass extinction event that resulted in the loss of $76 \pm 5\%$ of all known species and $84 \pm 5\%$ of all neoselachian species including sclerorhynchids (Kriwet and Benton 2004). Mesozoic occurrences of

sclerorhynchids are questionable and may represent fossils that were included in strata when they were reworked, and not when they were deposited (Kriwet and Benton 2004).

The palaeobiogeographic distribution of sclerorhynchids is circumglobal, and the distribution centre and origin is thought to be located in the Tethys area of middle Europe (Kriwet and Kussius 2001). The remains of four genera are circumglobally distributed, i.e. *Ischyrhiza*, *Onchopristis*, *Onchosaurus* and *Sclerorhynchus*, while most other genera are known to have limited distribution ranges (Kriwet and Kussius 2001). The highest species diversity occurs in Africa, where most monospecific genera have been found (Kriwet and Kussius 2001).

The number of sclerorhynchid genera is unclear, as some genera are only known by their oral teeth, and could belong to either the rhinobatid or sclerorhynchid groups (e.g. *Renpetia* Werner 1989, *Ptychotrygon* Jaeckel 1894). Excluding uncertain genera, 40 species have been described from at least sixteen genera (Kriwet and Kussius 2001) and can be subdivided into three further groups based on the dental histology of their rostral teeth (Cappetta 1987 and see Table 3; Fig. 5). The interrelationships within sclerorhynchids are not yet known, but Kriwet (2004) assumes that forms like *Onchorhynchus*, that possess a thick rostral blade, are less advanced.

Sclerorhynchids reached a maximal total length of 70–100 cm and possessed two dorsal fins positioned more caudal on the tail than in pristids or rhinobatids, which is regarded to be an adaptation to a benthic lifestyle (Cappetta 1974). Moreover, the transition between both the abdomen and the cephalic region and also between the cephalic region and the rostrum is not very pronounced in sclerorhynchids, contrary to the situation in pristids (Cappetta 1974). In some species of sclerorhynchids, the rostral teeth extend anteriorly of the rostrum base, where they slowly transition into dermal denticles (Cappetta 1974).

The oral teeth of sclerorhynchids are arranged in diagonal rows, as in other batoids including rhinobatids and pristids (Kriwet 2004). In general, they are wider than long, with a labial protuberance of the tooth crown well detached from the labial contour (Kriwet 2004). They possess a well-developed occlusal transverse crest that separates a narrow, reduced lingual face from the well-developed labial face (Kriwet 2004). The root extends below the crown in the occlusal view (Kriwet 2004).

Rostral teeth of sclerorhynchids are regularly replaced, contrary to pristid teeth, which grow throughout life (Slaughter and Springer 1968) and are kept short by regular abrasion on the substrate. As sclerorhynchid teeth show only minor signs of wear, Kriwet and Kussius (2001) question the use of the rostrum during foraging, strengthening their argument by suggesting that extant pristids do not use their rostrum during food gathering. However, an ongoing study of pristid foraging behaviour leads us

**Table 3** Sclerorhynchid genera known to date

| Rostral tooth cap with a core of osteodentine | Rostral tooth cap consisting of orthodentine with a pulp cavity | Rostral teeth histology not known |
|---|---|---|
| *Onchosaurus* Gervais 1852 | *Ankistrorhynchus* Casier 1964 | Rostral teeth unknown |
| *Pucapristis* Schaeffer 1963 | *Ctenopristis* Arambourg 1940 | *Biropristis* Suarez and Cappetta 2004 |
| *Schizorhiza* Weiler 1930 | *Dalpiazia* Checchia-Rispoli 1933 | *Celtipristis* Kriwet 1999 |
| | *Ganopristis* Arambourg 1935 | *Kiestus* Cappetta and Case 1999 |
| | *Ischyrhiza* Leidy 1856 | *Renpetia* Werner 1989 |
| | *Libanopristis* Cappetta 1980 | *Ptychotrygon* Jaeckel 1894 |
| | *Marckgrafia* Weiler 1935 | *Ptychotrygonoides* Landemaine 1991 |
| | *Micropristis* Cappetta 1980 | *Archingeayia* Vullo, Cappetta and Neraudeau 2007 |
| | *Onchopristis* Stromer 1917 | Histology not studied |
| | *Sclerorhynchus* Woodward 1917 | *Baharipristis* Werner 1989 |
| | | *Plicatopristis* Cappetta 1991 |
| | | *Borodinopristis* Case 1987 |

Although following Schaeffer (1963), Cappetta (1987) and Kriwet (2004), genera are arranged based on morphological characteristics of their rostral teeth and recently described genera have been added
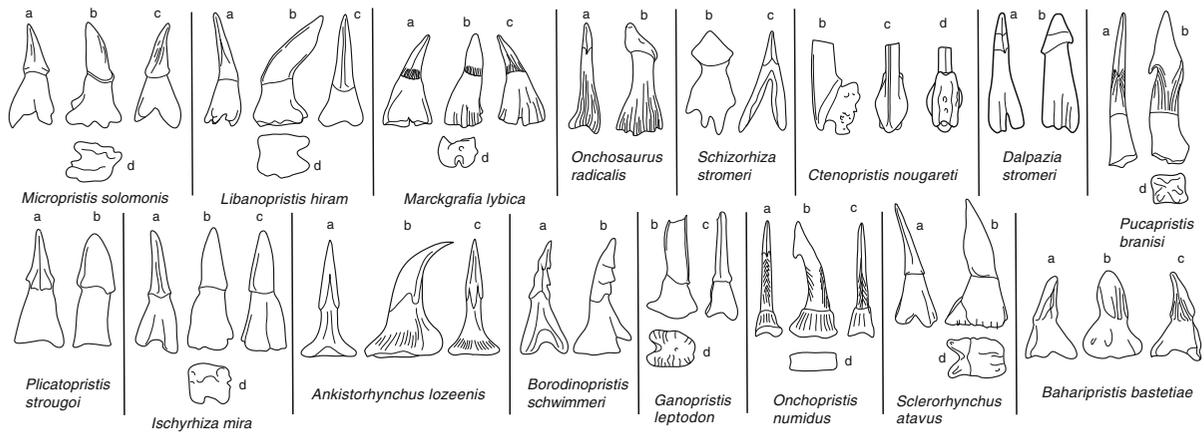
**Fig. 5** The rostral teeth of one representative of each sclerorhynchid genus, where rostral teeth have been described. *a* caudal, *b* lateral, *c* rostral, *d* basal view. Redrawn from photographs and schematic drawings from Schaeffer (1963), Cappetta (1987, 1991), Case (1987), Werner (1989), and Bourdon (1999)

to conclude that at least one pristid, *Pristis microdon*, uses its rostrum during prey manipulation in a variety of behaviours (B. Wueringer, unpublished data). The wide variety of rostral tooth morphology allows us to draw conclusions on the ecology of the respective species.

Interpretations of the habitat and ecology of extinct species are possible by interpreting function from morphology combined with characterisation of the strata that contained the fossils. Kriwet and Kussius (2001) describe the ecological niche occupied by some sclerorhynchid taxa as being similar to the niche presently occupied by pristids, i.e. sluggish bottom dwellers of shallow, coastal habitats (*Libanopristis* and *Sclerorhynchus*) based on their caudally placed dorsal fins and reduced tail. However, *Ischyrhiza*, *Dalpazia* and *Schizorhiza* are interpreted to be more actively moving species (Kriwet and Kussius 2001), based on their wide-ranging distributions. *Ischyrhiza* is also the most successful sclerorhynchid based on its wide distribution (Kriwet and Kussius 2001). Sclerorhynchids are opportunistic in their diet (Kriwet and Benton 2004).

## Description of the fossil record of pristids

Pristids Bonaparte 1838 first appear in the Thametian stage (Kriwet and Benton 2004) of vertebrate evolution and comprise two extinct (*Propristis* Dames 1883 and *Peyeria* Weiler 1935; Cappetta 1987) and two extant genera (*Pristis* Linck 1790 and *Anoxypristis* White and Moy-Thomas 1941). Here, we give brief descriptions of the all genera followed by a synthesis of the literature available on recent species.

### *Peyeria* sp. Weiler 1935

The genus is monospecific. The validity of the assertion that the remains of *Peyeria lybica* Weiler 1935 are those of a pristid has been questioned by Cappetta (1987), who considers the fossil records show a high similarity to batoid thorns. However, Werner (1989) agrees with the identification of the genus after examining the morphological variability of rostral teeth and assigning the oral teeth to this species based on their combined deposits. *Peyeria lybica* occurs during the Cenomanian stage of the upper Cretaceous (Werner 1989), whereas other pristids do not occur until the lower Eocene (see Fig. 2; Cappetta 1987; Werner 1989). Since no pristid remains are known from the 45 million years in between, this species could represent the common ancestor of pristids. It is possible that *Peyeria* diversified by adaptive radiation after the transition from the Cretaceous to the Paleogene, when all sclerorhynchid sawfish were extinct during one of earth's major mass extinction events (Kriwet and Benton 2004). The extinction of sclerorhynchids may have allowed pristids to occupy ecological niches formerly occupied by sclerorhynchids. As proposed

by Schaeffer (1963), the sturdier mode of rostral tooth attachment in pristids could have allowed pristids to replace sclerorhynchids.

The rostral teeth of *P. lybica* are cone-shaped; possess a flattened apex with radial folds and growth rings (see Fig. 6). The basal profile of the rostral teeth is oval to circular (Werner 1989). As in other pristids there is no enameloid cap (Werner 1989). The oral teeth have a smooth crown that is higher than the root (Werner 1989). The labial face is rhombic and convex, whereas the lingual face is divided into three parallel vizors (Werner 1989). The root is low and shifted towards the lingual side, and possesses a rather flat basal canal with a large central foramen (Werner 1989).

The remains of *Peyeria* have been found throughout northeastern Africa (Cappetta 1987; Werner 1989) and in life, members of the genus were thought to occupy an estuary or lagoonal habitat with strong tidal influences (Werner 1989).

### *Propristis* sp. Dames 1883

*Propristis schweinfurthii* Dames 1883 is the only species in this genus and fossil remains are distributed in north and west Africa and north America, where this species occurred from the middle to late Eocene (Cappetta 1987). It is known from a rostrum that is long (2.15 m in length) and slender with parallel edges, where its dorsal and ventral sides of the rostrum are both convex proximally but flat distally (Cappetta 1987). Internally, the rostrum possesses five ducts: a large median duct bordered by two large lateral canals and two small lateral canals (Cappetta 1987). The rostral teeth are dorsoventrally depressed and are as broad as they are high (3 cm), without enameloid and overlap each other to form a continuous cutting edge along the rostrum (Fig. 6; Cappetta 1987). Shallow notches along the lateral edges of the rostrum correspond to rostral teeth insertions (Cappetta 1987). Both the anterior cutting edge and the posterior edge are convex (Cappetta 1987). The oral teeth have not yet been described.

### *Anoxypristis* sp. White and Moy-Thomas 1941

The genus *Anoxypristis* first occurred in the middle Eocene and comprises one extant species (*Anoxypristis*
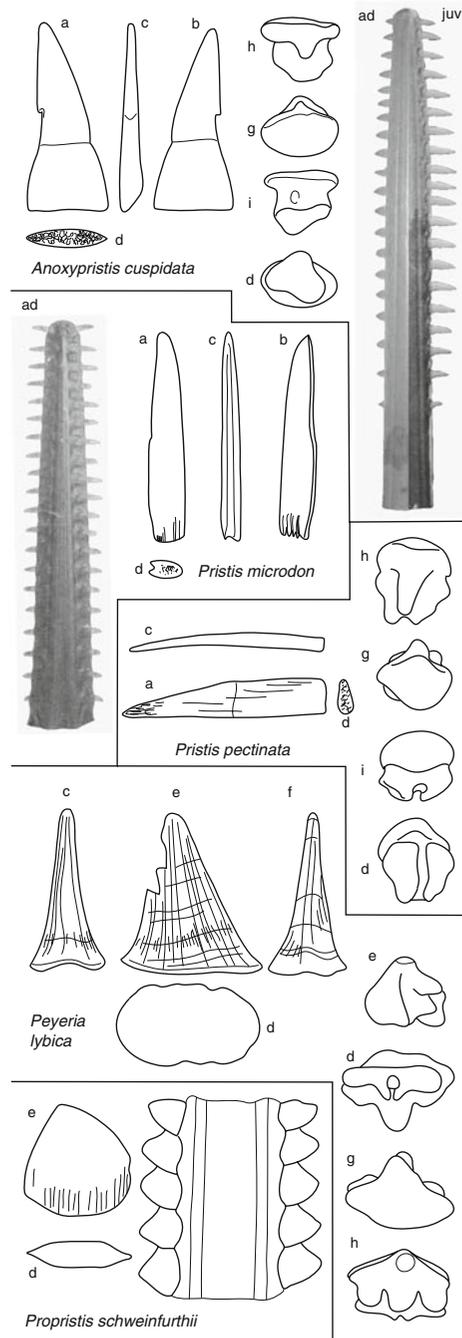


**Fig. 6** Rostral and oral teeth and rostra of extinct and extant pristids. In *Anoxypristis cuspidata*, embryonal rostral teeth with a caudal hook are presented. The rostrum of *A. cuspidata* shows adult (*ad*) teeth on the *left side* and juvenile (*juv*) teeth on the *right side*. Images of rostra show the dorsal view. *a* dorsal, *b* ventral, *c* caudal, *d* basal, *e* lateral, *f* rostral, *g* occlusal, *h* lingual, *i* labial view. Redrawn after Cappetta (1987), Werner (1989) and Herman et al. (1997)

*cuspidata* Latham 1794) and various extinct species, i.e. *P. imhoffi* Leriche 1932, *P. ensidens* Leidy 1877, *P. ferinus* Böhm 1926, *P. mucrodens* White 1926, *P. priemi* Leriche 1932, *P. fajumensis* Stromer 1905, *P. malembeensis* Dartevelle and Casier 1943. Cappetta (1987) places *P. clavata* in the genus *Anoxypristis*, as the internal structure of the rostrum is unknown. However, various morphological characteristics indicate that *P. clavata* belongs to the genus *Pristis*. The distribution of *A. cuspidata* ranges from the Red Sea in the west to the Indo-pacific (Japan) in the east and Australia in the south (Last and Stevens 1994a; Compagno and Last 1999). It occurs in estuaries and inshore regions to depths of 40 m, and may ascend rivers beyond tidal zones (Norman and Fraser 1938; Last and Stevens 1994a; Compagno and Last 1999). It has been reported in salinities from 20 ppt (Taniuchi and Shimizu 1991) to 28 ppt (Thorburn et al. 2003).

*Anoxypristis* is morphologically distinguished from *Pristis* by the complete lack of dermal denticles in neonates (Taniuchi et al. 1991b; Deynat 2005). The first denticles develop at a total length of 65 cm but they remain sparse and irregular throughout all ontogenetic stages (Deynat 2005). Other distinguishing characteristics are that the nostrils of *A. cuspidata* are connected to the side of the head via an incurrent groove (Hussakof 1912; Compagno and Last 1999), it possess a well defined lower caudal lobe (Taniuchi et al. 1991a) and a second caudal keel below the first keel (Compagno and Last 1999). The two dorsal fins are equal in length and height and the first dorsal fin originates dorsally above the middle of the pelvic base (Taniuchi et al. 1991a).

The internal morphology of the rostrum of *Anoxypristis* differs from *Pristis*, as *Anoxypristis* possesses a second pair of lateral canals that does not exist in *Pristis* (Fig. 4; Hoffmann 1912; Cappetta 1987). The rostrum of *A. cuspidata* is flat, long and slender and does not taper markedly (Last and Stevens 1994a; Compagno and Last 1999). The distance between the most basal rostral tooth and the base of the saw is larger than in *Pristis* and seems to increase with age, as it comprises one-sixth of the rostrum in embryos (Hussakof 1912) and one quarter of the rostrum in adults (Last and Stevens 1994b). Rostral teeth are flattened, broad and triangular (see Fig. 6; Taniuchi et al. 1991a; Compagno and Last 1999) with sharp anterior and posterior cutting edges (Cappetta 1987). In embryos, the teeth possess an

enameloid layer and a posterior hook that are worn off in adults (Herman et al. 1997), a characteristic which has led to the invalid description of *Pristis semisagittatus* Shaw 1804. The number of rostral teeth appears to vary between the known studies: 24–28, n = 3 (Hussakof 1912); 27–32 (Miller 1974); 18–22 (Last and Stevens 1994b).

*Anoxypristis cuspidatus* feeds on small teleosts and cuttlefish (Compagno and Last 1999) and has small unspecialized batoid-like oral teeth that differ markedly from *Pristis* (Cappetta 1987; Herman et al. 1997), i.e. they are wider than long with a flattened crown that possesses a weakly arched transverse keel that divides the inner and outer face (Cappetta 1987; Herman et al. 1997). Both faces are convex with a smooth surface, and the inner face bears a prominent uvula (Herman et al. 1997). The root is low with a flat base and does not have a median groove (Herman et al. 1997).

### *Pristis* sp. Linck 1790

*Pristis* first occurred in the Ypresian stage of the Lower Eocene (Cappetta 1987; Kriwet 2005; Cicimurri 2007) but fragmentary specimens indicate that *Pristis* could have occurred during the late Paleocene (Cicimurri 2007). Several extinct species of *Pristis* are known, namely *P. lathami* Galeotti 1837, *P. amblodon* Cope 1869, *P. aquitanicus* Delfortrie 1872, *P. prosulcatus* Stromer 1905, *P. hamatus* White 1926, *P. propinquidens* Casier 1946, *P. atlanticus* Zbyszewsky 1947, *P. brayi* Casier 1949, *P. brevis* Casier 1949, *P. praecursor* Casier 1949, *P. caheni* Dartevelle and Casier 1959, *P. olbrechtsi* Dartevelle and Casier 1959 and *P. pickeringi* Case 1981, with a global distribution in Europe, northern and western Africa, Asia and Antarctica (Cappetta 1987; Kriwet 2005). As fossil remains consist of mainly rostral teeth, species diversity has possibly been exaggerated (Cicimurri 2007). In pristids, the number of rostral teeth is fixed during early development and is therefore considered an important taxonomic characteristic (Thorson 1973; Ishihara et al. 1991a; Taniuchi et al. 1991a; Deynat 2005). All rostral tooth counts given below refer to alveoli per side of the rostrum.

### *Pristis pristis* Linnaeus 1758

*Pristis pristis* is the first species of sawfish ever described, although under this name almost no

information on the species exists. Taniuchi and Shimizu (1991) and McEachran and de Cavarlho (2002) synonymise *P. pristis* with *P. perotteti* Müller and Henle 1841. This attempt may be valid, given that *P. pristis* was described first and only one morphological difference between the two species has been described by one study, i.e. the first dorsal fin of *P. pristis* originates directly above the origin of the pelvis, whereas in *P. perotteti* the first dorsal fin originates anteriorly to the pelvic origin (Ishihara et al. 1991b). Faria and McDavitt (2008), on the other hand, propose the suppression of the species *P. pristis* on the grounds that the species represents a composite that historically has been associated with features from several sawfish species. DNA testing the holotype of *P. pristis* may be the only way to determine for which sawfish species *P. pristis* represents the senior synonym.

### Pristis perotteti Müller and Henle 1841

As mentioned above, this species may be the junior synonym of *Pristis pristis*. Here we present a synthesis of literature of *P. perotteti* under this synonym, in order to maintain the usefulness of this information in case both *P. pristis* and *P. perotteti* are later found to be valid. Thorson (1976) synonymises *P. perotteti* with *P. zephyreus* Jordan and Starks 1895 from the west coast of central America and Thorson (1982) synonymises it with *P. antiquorum* Latham 1794, not realizing that *P. antiquorum* was described first and would therefore be the valid species name. Attempts have been made to synonymise *P. perotteti* with *P. microdon* Latham 1794 (Ishihara et al. 1991b; Compagno and Last 1999), but there is evidence that rostral tooth counts of the two species differ (Ishihara et al. 1991a; Thorburn et al. 2007) and *P. peotteti* is restricted to the Atlantic. Therefore, the synonymy with *P. leichardti* Whitely 1945, as proposed by Taniuchi and Shimizu (1991) also appears invalid, as this species is a junior synonym of *P. microdon* (Taniuchi et al. 1991b; Compagno and Last 1999; Thorburn and Morgan 2005).

The biology of *P. perotteti* in the Lake Nicaragua—Rio San Juan system is well known, mainly through the published works of Thorson (1973, 1974, 1976, 1982), Thorson et al. (1966). The maximum reported total length for this species is 429 cm (Thorson 1982). The rostrum seems to grow more slowly than the body,

since in juveniles it accounts for 30% of the total length (Miller 1995) but in adults it accounts for only 20–22% (Thorson 1982). Females generally have fewer rostral teeth than males (females 14–18, mean 16; males 16–20, mean 18) but numbers overlap (Thorson 1982; Miller 1995). In *P. perotteti* the sub-caudal lobe is always present (Thorson 1982).

*Pristis perotteti* is euryhaline and has been found in the Amazon River 750 km upstream (Thorson 1974). This species can potentially spend its whole life cycle in freshwater and may only enter saltwater to reach other rivers (Thorson 1974, 1982). In Lake Nicaragua, females reach sexual maturity at a total length of 3 m (2.4–3 m in males) and produce litters of 1–13 neonates (Thorson 1976). Sawfish are born at a total length of 73–80 cm (Thorson 1976, 1982) and grow 35–40 cm in the first year, 12 cm in the tenth year and thereafter 4–5 cm per year (Thorson 1982). Copulation has been observed in the lake and the gestation period is 4.5 months (Thorson 1982).

The commercial depletion of *P. perotteti* in the Lake Nicaragua—Rio San Juan system is also well documented. Thorson (1982) estimated this sawfish population from 1966 to 1970 to be the largest in the world. From 1970 to 1975, when commercial exploitation began, as many as 60,000–100,000 sawfish were caught with unselective gear (Thorson 1976). This estimate did not include small companies working in the area (Thorson 1976). Some companies only took fins and juveniles were generally discharged whole (Thorson 1976). Thorson (1976) stated, "Action to protect the sawfish is overdue if not already too late". However, until 1995, the only managed effort to protect freshwater elasmobranchs in Nicaragua was during the Sandinista government, which put a moratorium on sawfish fisheries (Compagno and Cook 1995). During a survey in Lake Nicaragua in 1992 not a single sawfish or bull shark *Carcharhinus leucas* were caught (Taniuchi 1992). In January 2006, Nicaragua finally banned freshwater fishing for sawfish and bull sharks.

### Pristis microdon Latham 1794

Various authors have synonymised *Pristis microdon* with *P. perotteti* although tooth counts of *P. microdon* from Australia and Papua New Guinea exceed those of *P. perotteti* (Ishihara et al. 1991a; Thorburn et al. 2007). Published rostral tooth counts vary, but the

primary literature that does not pool *P. microdon* with *P. perotteti* provides tooth counts within the limits provided by Latham (18–24, Latham 1794), i.e. females 17–21, *n* = 62, mean = 19 (Ishihara et al. 1991a; Thorburn and Morgan 2005; Thorburn et al. 2007), whereas Taniuchi et al. (1991b) present counts of 17–19 rostral teeth in females (*n* = 5). However, there are more differences in tooth counts in males, i.e. 20–22, *n* = 4 (Taniuchi et al. 1991b); 19–23, *n* = 24, mean = 20.9 (Ishihara et al. 1991a); 17–21, *n* = 25, mean = 21 (Thorburn and Morgan 2005; Thorburn et al. 2007). Sexual dimorphism in rostral tooth counts is also reflected in different rostrum lengths between sexes (Thorburn and Morgan 2005; Thorburn et al. 2007).

Other morphological characteristics of *P. microdon* are centered around the fins and the shape of the teeth and saw. The pectoral fins have a broad base and straight posterior and anterior margins (Taniuchi et al. 1991b; Last and Stevens 1994b; Compagno and Last 1999). The origin of the first dorsal fin is well anterior to the origin of the pelvic fin (Compagno and Last 1999; Thorburn and Morgan 2005). A lower caudal lobe is always present (Ishihara et al. 1991b; Taniuchi et al. 1991b; Last and Stevens 1994b; Compagno and Last 1999). The last rostral tooth is positioned just anterior to the base of the saw and the saw tapers slightly and is broad and stout (Fig. 6; Compagno and Last 1999). *Pristis microdon* can be easily distinguished from *P. clavata*, which occurs in the same habitat, as the former possesses a groove along the whole length of the posterior edge of the rostral teeth, whereas in the latter, the groove does not reach the base of the tooth (Thorburn et al. 2007).

*Pristis microdon* is distributed in the tropical Indo-west Pacific from South Africa to Southeast Asia and northern Australia (Last and Stevens 1994b; Compagno and Last 1999; Chidlow 2007; Thorburn et al. 2007). Chidlow (2007) proposes that its range should be extended to south western Australia based on one adult specimen. Within its distribution range, *P. microdon* occurs inshore and in rivers and lakes far beyond tidal reaches (Compagno and Cook 1995; Compagno and Last 1999; Thorburn et al. 2003). Taniuchi and Shimizu (1991) assumed that juveniles remain in salinities around 0–1 ppt, whereas adults move into salinities of 20–25 ppt. However, recent reports indicate that adult sawfish occur in the marine environment in salinities of 31 ppt (Thorburn et al.

2004; Thorburn and Morgan 2005; Thorburn et al. 2007) and only use freshwater as nurseries for the first 5 years (Mizue and Hara 1991; Thorburn et al. 2007). Australian juvenile *P. microdon* feed mainly on *Macrobrachium* sp. and *Arius graeffei* (Peverell 2006; Chidlow 2007; Thorburn et al. 2007).

Information on the growth and life history of *P. microdon* is often pooled with information on other species, depending on which synonyms the respective authors consider valid. Therefore, we will only include primary literature from the Indo-Pacific that explicitly refers to *P. microdon*. Juveniles are born at a total length of 80–90 cm (Thorburn et al. 2007). Reports on sexually mature specimens are rare, but males under a total length of 2.3 m and females under a total length of 2.7 m are immature (Thorburn and Morgan 2005; Thorburn et al. 2007). The long maintained assumptions that Australian *P. microdon* attain a maximum total length well below 3 m (Last and Stevens 1994b; Thorburn et al. 2003) and are stenohaline (Taniuchi and Shimizu 1991; Last and Stevens 1994b) may have lead to the mis-identification of large adults caught in marine environments.

### Pristis pectinata Latham 1794

*Pristis pectinata* is distributed circumtropically, in the western Atlantic from North Carolina to North Argentina (McEachran and de Cavarlho 2002), and also found in the Mediterranean, Asia and Australia (Simpfendorfer 2006). However, the description of individuals found in northern Australia is based on unconfirmed photographs and needs verification (Last and Stevens 1994b; Thorburn et al. 2003). Populations of *P. pectinata* within the USA have declined to below 5% (Wiley et al. 2008) and the largest remaining population is located in south and southwest Florida (Simpfendorfer et al. 2008). This decline is attributed to the fact that *P. pectinata* was long regarded as a problem damaging nets and was subsequently hooked and harpooned (Compagno and Last 1999). In the late 1800s large numbers of sawfish were reported in the Gulf of Mexico and seasonal migrations from Florida state waters were known to occur as far as the waters off New York coastline (Simpfendorfer 2006).

Within its distribution range, *P. pectinata* occupies shallow estuaries to coastal and shelf areas to a depth of 122 m (McEachran and de Cavarlho 2002;

Simpfendorfer 2006; Simpfendorfer et al. 2008). It does not occur as far inland as *P. perotteti* (Thorson 1974, 1982). Juveniles use extremely shallow banks to avoid predation by bull sharks, *Carcharhinus leucas* (Simpfendorfer and Wiley 2003; Thorburn et al. 2003). Neonates are born at a total length of 61 cm (Last and Stevens 1994b; Compagno and Last 1999; McEachran and de Cavarlho 2002; Clark et al. 2003; Simpfendorfer 2006; Simpfendorfer et al. 2008), which has been confirmed in captive born specimens (Clark et al. 2003). Growth rates in this species are amongst the highest reported for elasmo-branchs with juveniles doubling in size in the first year and therefore the age at maturity of this species might be lower than previously thought (Simpfendorfer et al. 2008). Females reach sexual maturity around a total length of 360 cm and produce litters of 15–20 neonates (Simpfendorfer 2000, 2006; Simpfendorfer et al. 2008). Males mature at a total length of 2.7 m (Simpfendorfer 2006; Simpfendorfer et al. 2008). Maximum reported total lengths range between 5.5 m (Compagno and Last 1999; McEachran and de Cavarlho 2002) and 7.6 m (Last and Stevens 1994b; Simpfendorfer 2006).

The rostral teeth of *P. pectinata* are slender with a posterior cutting edge and a groove extending along the whole posterior margin (see Fig. 6; Herman et al. 1997; Simpfendorfer 2006). Herman et al. (1997) report a sexual dimorphism in rostral tooth shape since male teeth are broader than female teeth. Rostral tooth counts reported by various authors vary from 21 to 34 teeth, with all variations containing 25–29 teeth (Wiley et al. 2008). A recent study from Florida found 22–29 teeth per side in 51 specimens with no significant sexual differences (Wiley et al. 2008), confirming an earlier study by Thorson (1973) who also reported no sexual dimorphism (females 26–28 teeth, $n = 3$; males 25–29 teeth, $n = 3$). Wiley et al. (2008) give possible explanations for the differences in rostral tooth counts in other studies: (1) Historic and recent misidentification of specimens caused by taxonomic uncertainty, (2) Inconsistent methodology as some authors count the actual teeth, whereas others count the alveoli, which represent the number of teeth correctly even if a tooth is missing. Some authors also count tooth pairs even though there are differences in tooth counts on both sides, (3) In dried museum specimens, the rostrum could have been cut before the base, (4) Geographic variation.

The pectoral fins of *P. pectinata* have a broad base and a straight hind margin (Last and Stevens 1994b; Compagno and Last 1999). Thorson (1976) reports a distinct sub-caudal lobe but other authors disagree (Last and Stevens 1994b; Compagno and Last 1999). The first dorsal fin originates above (Ishihara et al. 1991b; Last and Stevens 1994b; Compagno and Last 1999) or slightly anterior to the pelvic origin (Last and Stevens 1994b; Compagno and Last 1999).

*Pristis pectinata* feeds on benthic invertebrates, crustaceans and teleosts (Compagno and Last 1999; McEachran and de Cavarlho 2002) and has unspe-cialized batoid teeth with a flattened crown that is divided into an inner and outer face by a strongly arched transverse keel (Herman et al. 1997). The outer crown base overhangs the root-crown junction and the root is divided into two lobes by a central median groove (Herman et al. 1997).

### *Pristis zijsron* Bleeker 1851

Bleeker originally described *Pristis zijsron* and *Pristis dubius* based on a rostrum and a caudal fin, respectively. However, *P. dubius* has been identified as the junior synonym of *P. zijsron* (van Oijen et al. 2007) and *P. zijsron* has been synonymised with *P. clavata*, although morphological differences indi-cate the latter relationship to be invalid (Ishihara et al. 1991b).

*Pristis zijsron* is distributed in tropical waters of Southeast Asia and Australia, and is possibly found from the Red Sea to South Africa (Compagno and Last 1999), where it occurs in freshwater and inshore to depths of 30 m (Peverell and Pillans 2004). A specimen that was tracked for 27 h off the coast of Queensland spent the whole time in waters less than 1 m depth (Peverell and Pillans 2004).

The holotype of *P. zijsron* possesses 26 rostral teeth on each side of the saw. Compagno and Last (1999) report 23–34 teeth per side, whereas Last and Stevens (1994b) report "24–28 (25–34)" teeth per side but do not specify the meaning of the second value. The space between the most basal teeth equals 2–7 times the space between the most rostral teeth (Last and Stevens 1994b; Compagno and Last 1999). The rostrum is long and slender with almost parallel sides (Last and Stevens 1994b; Compagno and Last 1999). This species does not possess a defined lower caudal lobe (Compagno and Last 1999) and the first

dorsal fin originates posterior to the pelvic origin (Ishihara et al. 1991b; Last and Stevens 1994b; Compagno and Last 1999).

### Pristis clavata Garman 1906

*Pristis clavata* Garman 1906 probably has the most limited distribution of all sawfish as it is confined to tropical waters of Australia and Papua New Guinea (Taniuchi and Shimizu 1991; Last and Stevens 1994b; Compagno and Last 1999; Thorburn et al. 2003). It occurs inshore and in estuaries (Thorburn et al. 2003) and ventures into freshwater. In a recent study only one specimen was caught in freshwater (9.1 ppt), whereas all other specimens were caught in saltwater (41.1 ppt, Thorburn et al. 2003). Previous assumptions of a maximum total length of 2.5 m (Last and Stevens 1994b; Compagno and Last 1999) have likely been disproved by Thorburn et al. (2003), who have not found a single sexually mature specimen below a total length of 2.33 m.

*Pristis clavata* does not possess a defined lower caudal lobe (Ishihara et al. 1991b; Compagno and Last 1999) and its pectoral fins have a broad base and a straight hind margin (Last and Stevens 1994b; Compagno and Last 1999). The origin of the first dorsal fin is slightly posterior to the pelvic origin (Ishihara et al. 1991b; Last and Stevens 1994b; Compagno and Last 1999) and the second dorsal fin is smaller than the first one (Ishihara et al. 1991b).

The rostral teeth are flat and elongated and possess a groove along the posterior edge of the tooth that does not reach the base (Thorburn et al. 2007). Tooth counts vary between authors: 18–22 (Last and Stevens 1994b; Compagno and Last 1999); females 20–22, $n = 5$ and males 19–23, $n = 5$ (Ishihara et al. 1991b). It is unclear whether the space between the last teeth equals the space between the first teeth (Last and Stevens 1994b) or is twice as big (Compagno and Last 1999). The rostrum comprises 19.0–21.1% of the total length (Ishihara et al. 1991b) but the same authors also report previously published values of 22.1–25.8%.

### Conservation status of pristids

Sawfish share several characteristics with other elasmobranchs that make them vulnerable to human exploitation including low fecundity, sexual maturity late in life, long life, long gestation periods and the potential for intermittent breeding (Compagno and Cook 1995; Martin 2005), resulting in a slow intrinsic rate of population increase (Martin 2005). Their restricted habitats of freshwater and inshore coastal areas increase their vulnerability to human exploitation as these habitats overlap with the favourite habitat of humans (Compagno and Cook 1995; Martin 2005).

Due to the unique morphology of the rostrum, sawfish are often caught as by-catch in commercial gillnet and trawl fisheries (Cavanagh et al. 2003; Peverell 2006). Sawfish rostra are sold worldwide as trophies, and their presence in the curio trade was already noted to be large in 1938 (Norman and Fraser 1938). Globally, sawfish are important in cultural mythology, but particularly in tribal societies of Central America, West Africa, Papua New Guinea and Australia (McDavitt 1996). Prices on the Internet average US$119 per rostrum, with prices as high as US$1,242 (Anonymous 2006). The rostra are also important in Chinese traditional medicine and up to 1,500 are sold per year in one of the five most important Brazilian markets (Charvet-Almeida 2002; Martin 2005). In 2004, Ebay provided one of the most important market places for rostra sold world wide (McDavitt and Charvet-Almeida 2004) but this trade has been banned in 2006 (Anonymous 2006).

Since 2003, all seven species of sawfish are globally listed as endangered, with one species (*P. pristis*) being globally listed as critically endangered based on criteria of the IUCN Red List (Cavanagh et al. 2003). The same year *P. pectinata* was protected under the United States Endangered Species Act. Since June 2007 Pristidae are listed on CITES Appendix I, except for *P. microdon* which is listed on Appendix II. Both *P. microdon* and *P. zijsron* are also protected under the EPBC Act 1999 (Australian Environment Protection and Biodiversity Conservation Act) in Australian Commonwealth waters, which incorporate marine waters extending three nautical miles. However, their protection in near shore waters or rivers in Australia is left to state legislation (Thorburn and Morgan 2005).

Northern Australia has been identified as one of the only remaining geographical regions in the world, where sufficiently large populations of four to five species of sawfish occur (Thorburn and Morgan 2005; Peverell 2006), but there is still a negative

interaction between all species and inshore and offshore set net fisheries (Peverell 2006). Therefore, all size classes of sawfish are vulnerable to fishing and are regularly taken as by-catch (Peverell 2006).

## Conclusion and future directions

Published literature on pristiophorid sawsharks is scarce. It appears that this family is known mainly through interactions with deep-sea fisheries, but it is unclear if any aspect of their ethology, i.e. the use of the rostrum, is known from first hand observations. The use of the elongated rostrum needs to be studied in extant species of sawfish in order to shed light on its function and evolution. Moreover, genetic work is needed to verify the number of extant species of pristids. Even though the fossil record of pristids and sclerorhynchids is appreciable, further information is still needed to verify the number of extant species and assess the assignment of oral and rostral teeth in extinct species.

## References

Anonymous (2006) EBay bans the sale of endangered sawfish. Via MSNBC http://msnbc.com/id/11007937. Accessed on Jan 24, 2006

Bourdon J (1999) The life and times of long dead sharks. www.elasmo.com. Accessed on July 02, 2008

Breder CM (1952) On the utility of the saw of the sawfish. Copeia 2:90–91. doi:10.2307/1438539

Cappetta H (1974) Sclerorhynchidae nov. fam., pristidae et pristiophoridae: un exemple de parallelisme chez les selachiens. C R Acad Sci Paris Ser D 278:225–228

Cappetta H (1987) Chondrichthyes II. Mesozoic and cenozoic elasmobranchii. In: Schultze H-P, Kuhn O (eds) Handbook of paleoichthyology. Verlag Dr. Friedrich Pfeil, München, p 193

Cappetta H (1991) Decouverte de nouvelles faunes de selaciens (Neoselachii) dans les phosphates maastrichtiens de la Mer Rouge, Egypte. Munchner Geowissenschaftliche Abh Part A 19:17–56

Cappetta H, Case GR (1999) Additions aux faunes de selaciens du Cretace du Texas (Albien superieur-Campanien). Palaeo Ichthyol 9:5–111

Case GR (1987) *Borodinopristis schwimmeri*, a new ganopristine sawfish from the upper Blufftown formation (Campanian) of the upper Cretaceous of Georgia. Bull N J Acad Sci 32:25–33

Cavanagh RD, Kyne PM, Fowler SL, Musick JA, Bennett MB (2003) The conservation status of Australasian chondrichthyans. Report of the IUCN Shark Spcialist Group. Australia and Oceania Regional Red List workshop. The University of Queensland, School of Biomedical Sciences, Brisbane, Australia, 170 pp

Charvet-Almeida P (2002) Sawfish trade in the north of Brazil. IUCN Shark Spec Group Shark News 14:9

Chidlow JA (2007) First record of the freshwater sawfish, *Pristis microdon*, from southwestern Australian waters. Rec W Aust Mus 23:307–308

Cicimurri DJ (2007) A partial rostrum of the sawfish *Pristis lathami* Galeotti, 1837, from the Eocene of South Carolina. J Paleontol 81:597–601. doi:10.1666/05086.1

Clark S, Violetta G, Henningsen A, Reischuck V, Pete M, Keyon J (2003) Growth in captive smalltooth sawfish, *Pristis pectinata*. American Elasmobranch Society 19th annual meeting, Manaus, Brazil

Compagno LJV (1977) Phylogenetic relationships of living sharks and rays. Am Zool 17:303–322

Compagno LJV, Cook SF (1995) The exploitation and conservation of freshwater elasmobranchs: status of taxa and prospects for the future. J Aquaricult Aquat Sci 7:62–90

Compagno LJV, Last PR (1999) Order Pristiformes. In: Carpenter KE, Niem VH (eds) The living marine resources of the western central Pacific Vol 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophyroidae). FAO, Rome, pp 1397–2068

Compagno L, Dando M, Fowler S (2005) Sharks of the world. Princeton University Press, Princeton

Deynat PP (2005) New data on the systematics and interrelationships of sawfishes (Elasmobranchii, Batoidea, Pristiformes). J Fish Biol 66:1447–1458. doi:10.1111/j.0022-1112.2005.00695.x

Douady CJ, Dosay M, Shivji MS, Stanhope MJ (2003) Molecular phylogenetic evidence refuting the hypothesis of Batoidea (rays and skates) as derived sharks. Mol Phylogen Evol 26:215–221. doi:10.1016/S1055-7903(02)00333-0

Faria V, McDavitt M (2008) The status of *Pristis pristis* (Chondrichthyes, Pristiformes) reconsidered. American Elasmobranch Society 24th annual meeting, Montreal, Canada

Froese R, Pauly D (2008) FishBase version (02/2008). http://www.fishbase.org. Accessed July 15, 2008

Gray JE (1864) Notice of a portion of a new form of animal (*Myriosteon higginsii*), probably indicating a new group of echinodermata. Proc Zool Soc Lond (pt 2):163–166

Herman J, Hovestadt-Euler M, Hovestadt DC, Stehmann M (1997) Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of chondrichthyan fishes. Part B: Batomorphii No. 2: Order Rajiformes—Suborder: Pristoidei—Family: Pristidae—Genera: Anoxypristis and Pristis. No. 3: Suborder Rajoidei—Superfamily Rhinobatoidea—Families: Rhinidae—Genera: Rhina and Rhynchobatus and Rhinobatidae—Genera: Aptychotrema, Platyrhina,

Platyrhinoidis, Rhinobatos, Trygonorrhina, Zanobatus and Zapteryx. Bull Inst R Sci Nat Belg Biol 67:107–162

Hoffmann L (1912) Zur Kenntnis des Neurocraniums der Pristiden und Pristiophoriden. Zool Jahrb 33:239–360

Hussakof L (1912) Note on an embryo of Pristis cuspidatus. Bull Am Mus Nat Hist 31:327–330

Irvine FR (1947) The fishes and fisheries of the Gold coast. Crown Agents for the Colonies for the Government of the Gold Coast, London, 352 pp

Ishihara H, Taniuchi T, Shimizu M (1991a) Sexual dimorphism in number of rostral teeth in the sawfish, Pristis microdon, collected from Australia and Papua New Guinea. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 83–89 (Nature and culture no. 3)

Ishihara H, Taniuchi T, Mitsuhiko S, Last PR (1991b) Record of Pristis clavata Garman from the Pentecost River, Western Australia, with brief notes on its osmoregulation and comments on the systematics of Pristidae. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 43–53 (Nature and culture no. 3)

Kajiura SM (2000) Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. Environ Biol Fishes 61:125–133. doi:10.1023/A:1011028312787

Kajiura SM, Holland KN (2002) Electroreception in juvenile scalloped hammerhead and sandbar sharks. J Exp Biol 205:3609–3621

Kirkland JI, Aguillon-Martinez MC (2002) Schizorhiza: a unique sawfish paradigm from Difunta Group, Coahuila, Mexico. Rev Mex Cienc Geologicas 19:16–24

Kriwet J (1999) Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). Palaeo Ichthyol 9:113–142

Kriwet J (2004) The systematic position of the Cretaceous sclerorhynchid sawfishes (Elasmobranchii, Pristiorajea). In: Arratia G, Tintori A (eds) Mesozoic fishes 3 systematics, paleoenvironments and biodiversity. Proceedings of the international meeting Serpiano, 2001. Verlag Dr Friedrich Pfeil, München, pp 57–74

Kriwet J (2005) Additions to the Eocene selachian fauna of Antarctica with comments on antarctic selachian diversity. J Vertebr Paleontol 25:1–7. doi:10.1671/0272-4634(2005)025[0001:ATTESF]2.0.CO;2

Kriwet J, Benton MJ (2004) Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. Palaeogeogr Palaeoclimatol Palaeoecol 214:181–194

Kriwet J, Kussius K (2001) Paleobiology and paleobiogeography of sclerorhynchid sawfishes (Chondrichtyes, Batomorphii). Rev Esp Paleontol No Extraordinario: 35–46

Lal Mohan LL (1986) Can a sawfish (Pristis sp.) kill a dugong? Sirenews No. 6 (Oct 2006)

Last PR, Stevens JD (1994a) Sharks and rays of Australia. CSIRO Division of Fisheries, Melbourne, 600 pp

Last PR, Stevens JD (1994b) Family Pristidae. Sawfishes. In: Last PR, Stevens JD (eds) Sharks and rays of Australia. CSIRO, Melbourne, pp 360–367

Latham J (1794) An essay on the various species of sawfish. Trans Linn Soc Lond 2:273–282

Maisey JG (1984) Higher elasmobranch phylogeny and biostratigraphy. Zool J Linn Soc 82:33–54. doi:10.1111/j.1096-3642.1984.tb00534.x

Maisey JG, Naylor GJP, Ward D (2004) Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. In: Arratia G, Tintori A (eds) Mesozoic fishes 3 systematics, paleoenvironments and biodiversity. Proceedings of the international meeting Serpiano, 2001. Verlag Dr Friedrich Pfeil, München, pp 17–56

Martin RA (2005) Conservation of freshwater and euryhaline elasmobranchs: a review. J Mar Biol Assoc U K 85:1049–1073. doi:10.1017/S0025315405012105

McDavitt MT (1996) The cultural and economic significance of sawfishes (Family Pristidae). IUCS Shark Spec Group Shark News 8:10–11

McDavitt MT, Charvet-Almeida P (2004) Quantifying trade in sawfish rostra: two examples. IUCS Shark Spec Group Shark News 16:10–11

McEachran JD, de Cavarlho MR (2002) Batoid fishes. In: Carpenter KE (ed) The living marine resources of the western central Atlantic Vol 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. FAO, Rome, pp 1–600

McEachran JD, Dunn KA, Miyake T (1996) Interrelationships of the batoid fishes (Chondrichthyes: Batoidea). In: Stiassney M, Parenti L, Johnson D (eds) Interrelationships of fishes. New York Academic Press, New York, pp 63–83

Miller WA (1974) Observations on the developing rostrum and rostral teeth of sawfish: Pristis perotteti and P. cuspidatus. Copeia 2:311–318. doi:10.2307/1442525

Miller WA (1995) Rostral and dental development in sawfish (Pristis perotteti). J Aquaricult Aquat Sci 7:98–107

Mizue K, Hara M (1991) The rectal gland of freshwater sawfish, Pristis microdon, and the bull shark, Carcharhinus leucas, collected from the Daly and Sepik River. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 63–69 (Nature and culture no. 3)

Nishida K (1990) Phylogeny of the suborder Mylobatoidei. Mem Fac Fish Hokkaido Univ 37:1–108

Norman JR, Fraser FC (1938) Saw-fishes. In: Norman JR, Fraser FC (eds) Giant fishes, whales and dolphins. W.W. Norton, New York, pp 60–63

Peverell SC (2006) Distribution of sawfishes (Pristidae) in the Queensland Gulf of Carpenteria, Australia, with notes on sawfish ecology. Environ Biol Fishes 73:391–402. doi:10.1007/s10641-005-1599-8

Peverell SC, Pillans R (2004) Determining feasibility of acoustic tag attachment and documenting short-term movements in Pristis zijsron Bleeker, 1851. Report for the National Oceans Office. National Oceans Office (18 pp)

Rocco L, Liguori I, Costagliola D, Morescalchi MA, Tinti F, Stingo V (2007) Molecular and karyological aspects of Batoidea (Chondrichthyes, Elasmobranchi) phylogeny. Gene 389:80–86. doi:10.1016/j.gene.2006.09.024

Schaeffer B (1963) Cretaceaous fishes from Bolovia, with comments on pristid evolution. Am Mus Novit 2159:1–20

Scott WB, Tibbo SN (1968) Food and feeding habits of swordfish, *Xiphias gladius*, in the Western North Atlantic. J Fish Res Board Can 25:903–919

Shimose T, Yokawa K, Saito H, Tachihara K (2007) Evidence for use of the bill by blue marlin, *Makaira nigricans*, during feeding. Ichthyol Res 54:420–422. doi:10.1007/s10228-007-0419-x

Shirai S (1996) Phylogenetic interrelationships of Neoselachians (Chondrichthyes: Euselachii). In: Stiassney M, Parenti L, Johnson D (eds) Interrelationships of fishes. New York Academic Press, New York, pp 9–34

Simpfendorfer CA (2000) Predicting population recovery rates for western Atlantic sawfishes using demographic analyses. Environ Biol Fishes 58:371–377. doi:10.1023/A:1007675111597

Simpfendorfer CA (2006) Threatened fishes of the world: *Pristis pectinata* Latham, 1794 (Pristidae). Environ Biol Fishes 73:20. doi:10.1007/s10641-004-4174-9

Simpfendorfer CA, Wiley TR (2003) Nursery areas of the smalltooth sawfish in southwestern Florida: implications for conservation. American Elasmobranch Society 19th annual meeting, Manaus, Brazil

Simpfendorfer CA, Poulakis GR, O'Donnell PM, Wiley TR (2008) Growth rates of juvenile smalltooth sawfish *Pristis pectinata* Latham in the western Atlantic. J Fish Biol 72:711–723. doi:10.1111/j.1095-8649.2007.01764.x

Slaughter BH, Springer S (1968) Replacement of rostral teeth in sawfishes and sawsharks. Copeia 3:499–506. doi:10.2307/1442018

Suarez ME, Cappetta H (2004) Sclerorhynchid teeth (Neoselachii, Sclerorhynchidae) from the late Cretaceous of the Quiriquina formation, central Chile. Rev Geol Chile 31:89–103

Taniuchi T (1992) Report on preliminary investigations of freshwater elasmobranchs in Mexico and Central America. Rep Jpn Soc Elasmobranch Stud 29:33–49

Taniuchi T, Shimizu M (1991) Elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 3–10 (Nature and culture no. 3)

Taniuchi T, Kan TT, Tanaka S, Otake T (1991a) Collection and measurement data and diagnostic characters of elasmobranchs collected from three river systems in Papua New Guinea. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 27–41 (Nature and culture no. 3)

Taniuchi T, Shimizu M, Sano M, Baba O (1991b) Descriptions of freshwater elasmobranchs collected from three rivers in Northern Australia. In: Shimizu M, Taniuchi T (eds) Studies on elasmobranchs collected from seven river systems in Northern Australia and Papua New Guinea. Univ Mus Univ Tokyo, Tokyo, pp 11–26 (Nature and culture no. 3)

Thorburn DC, Morgan DL (2005) Threatened fishes of the world: *Pristis microdon* Latham 1794 (Pristidae). Environ Biol Fishes 72:465–466. doi:10.1007/s10641-004-6922-2

Thorburn DC, Peverell SC, Stevens JD, Last PR, Rowland AJ (2003) Status of freshwater and estuarine elasmobranchs in northern Australia. Australian Department of Environment and Heritage, Canberra, 76 pp

Thorburn D, Morgan D, Gill H, Johnson M, Wallace Smith H, Vigilante T, Gorring A, Croft I, Fenton J (2004) Biology and cultural significance of the freshwater sawfish (*Pristis microdon*) in the Fitzroy river Kimberley, Western Australia, Threatened Species Network, 57 pp

Thorburn DC, Morgan DL, Rowland AJ, Gill HS (2007) Freshwater sawfish Pristis microdon Latham, 1794 (Chondrichthyes: Pristidae) in the Kimberley region of Western Australia. Zootaxa 1471:27–41

Thorson TB (1973) Sexual dimorphism in number of rostral teeth of the sawfish, *Pristis perotteti* (Mueller & Henle, 1841). Trans Am Fish Soc 102:612–614. doi:10.1577/1548-8659(1973)102<612:SDINOR>2.0.CO;2

Thorson TB (1974) Occurence of the sawfish, *Pristis perotteti*, in the Amazon River with notes on *P. pectinata*. Copeia 2:560–564. doi:10.2307/1442561

Thorson TB (1976) Observations on the reproduction of the sawfish, *Pristis perotteti*, in Lake Nicaragua, with recommendations for its conservation. In: Thorson TB (ed) Investigations of the ichthyofauna of Nicaraguan lakes. Univeristy Nebraska-Lincoln, Lincoln, pp 641–650

Thorson TB (1982) Life history implications of a tagging study of the largetooth sawfish, *Pristis perotteti*, in the Lake Nicaragua-Rio San Juan system. Environ Biol Fishes 7:207–228. doi:10.1007/BF00002497

Thorson TB, Cowan CM, Watson DE (1966) Sharks and sawfish in the lake Izabal-Rio Dulce system, Guatemala. Copeia 3:620–622. doi:10.2307/1441111

Underwood CJ (2006) Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. Paleobiology 32:215–235. doi:10.1666/04069.1

van Oijen MJP, Faria VV, McDavitt MT (2007) The curious holotype of *Pristis dubius* Bleeker, 1852 and the unravelling of Bleeker's sawfish taxonomy. Raffles Bull Zool 14:37–49

Werner C (1989) Die Elasmobranchier Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. Verlag Dr. Friedrich Pfeil, München, 112 pp

Westheide W, Rieger R (2004) Spezielle Zoologie. Teil 2: Wirbel-oder Schädeltiere. Spektrum Akademischer Verlag Gustav Fischer, Heidelberg, 712 pp

Wiley TR, Simpfendorfer CA, Faria VV, McDavitt MT (2008) Range, sexual dimorphism and bilateral asymmetry of rostral tooth counts in the smalltooth sawfish *Pristis pectinata* Latham (Chondrichthyes: Pristidae) of the southeastern United States. Zootaxa 1810:51–59

Wilga CD, Motta PJ (1998) Feeding mechanism of the Atlantic guitarfish *Rhinobatos lengtinosus*: modulation of kinematic and motor activity. J Exp Biol 210:3167–3184

Wilkens L, Hofmann M (2005) Behavior of animals with passive, low-frequency electrosensory systems. In: Bullock T, Hopkins C, Popper A, Fay R (eds) Electroreception. Springer, New York, pp 229–263

Wilkens LA, Wettring B, Wagner E, Wojtenek W, Russel D (2001) Prey detection in selective plankton feeding by the

paddlefish: is the electric sense sufficient? J Exp Biol 204:1381–1389

Winchell CJ, Martin AP, Mallatt J (2004) Phylogeny of elasmobranchs based on LSU and SSU ribosomal RNA genes. Mol Phylogen Evol 31:214–224. doi:10.1016/j.ympev.2003.07.010

Wueringer BE, Tibbetts IR (2008) Comparison of the lateral line and ampullary system of two species of shovelnose ray. Rev Fish Biol Fish 18:47–64. doi:10.1007/s11160-007-9063-9