Horned Serpents, Leaf Dogs, and Spoonbill Cats: 500 Years of Paddlefish Ponderings in North America

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he paddlefish, *Polyodon spathula*, is unlike any other fish found in the fresh waters of the northern hemisphere (Fig. 1). Its large size and surfacedwelling habits make it readily observable. Its shark-like appearance and prominent bill, or rostrum, render it instantly recognizable and long-remembered. Small wonder, then, that the paddlefish was discovered and described not once, but repeatedly, by explorers and naturalists, and will probably continue to be described and pondered over well into the 21st century.

Water Demons and Piexe Palla

Undoubtedly, the earliest observations of paddlefish were those by American Indians. Medium to large-sized fish (2-25 kg) were almost certainly encountered by Indians fishing floodplain pools and large lakes. Very large specimens (> 40 kg), which usually occur in the main channel of big rivers or in deep, flooded backwaters, were probably less familiar, especially when viewed at some distance from shore, and may have been interpreted as different creatures. Several tribes in the lower Mississippi Valley (e.g., Quapaws) and Great Lakes Basin (e.g., Hurons) had legends about demons that lived in the water and which were usually seen as evil omens (Meurger and Gagnon, 1988). These monsters were often described as having long, scaleless bodies, large mouths, and a great horn or bone protruding from the forehead. The prevalence of such "horned serpent" myths within the range of paddlefish, and during a time when large individuals would be comparatively common, seems hardly coincidental.

Hernando de Soto has been suggested as the first European to "discover" paddlefish when he crossed the Mississippi River (Carlander, 1954). De Soto himself may or may not have seen paddlefish in the Mississippi, but one of his party, a high-ranking professional soldier, published such a description in 1557 (D. Sheppard, pers. comm.). "A Gentleman from Elvas" wrote of the fishes caught by local Indians using nets in the Wabash River near Terre Haute, Indiana in June 1541 (Clayton et al., 1996). Species included large catfish (probably blue catfish, *Ictalurus furcatus*), suckers (probably buffalo, *Ictiobus* spp.), and a very unusual fish the Portuguese called "piexe palla." This fish had a "snout a cubit in length . . . the tip of its upper lip . . . shaped like a shovel." Appropriately named by the explorers, "piexe palla" means "shovel fish" or "paddle fish."

Two decades after the de Soto expedition, another longsnouted fish was reported by John Sparke the Younger who, in 1564, sailed aboard the *Jesus of Lubeck* under Captain (later Sir) John Hawkins and who kept the ship's register. Sparke was a dutiful reporter and a competent naturalist. He recorded fantastic accounts related to him by early New World settlers (such as unicorns and three-headed serpents), but he himself made conservative observations of fish, reptile, and bird life (Hakluyt, 1810). Near the mouth of a Florida river, he recorded "great fish, some the length of a man and longer, being of bigness according, having a snout much like a sword a yard long." According to zoologist Norman John Berrill, these fish were paddlefish (Berrill, 1952). "Florida" at the time comprised most of the southeastern United States (Williams, 1986) and would certainly have included part of



the geographic range of the paddlefish such as the Mobile Bay drainage. Sparke, however, was writing about observations in the St. Johns River (L. Williams, pers. comm.), an Atlantic drainage far removed from any known records of paddlefish populations in Gulf Slope drainages (Burr, 1981). Paddlefish may have had a more extensive distribution in the 16th century than they do now, but a more likely explanation is that Sparke's fish was a largetooth sawfish (*Pristis pristis*). Largetooth sawfish are marine but occasionally enter freshwater reaches of rivers and are known from the St. Johns (Robins et al., 1986). If it was a sawfish, then it was odd that Sparke failed to mention the teeth on the fish's rostrum. Without additional information, the honor of the first written report of a paddlefish cannot be confidently attributed to John Sparke.

French Explorers Encounter the Spatule

Pierre Esprit Radisson was probably the first well-known European to write about paddlefish. During his Mississippi voyage of 1655-1658, while exploring Lake Winnebago or Green Bay, Wisconsin, Radisson saw "fishes . . . some like the sturgeons [with] a kind of slice at the end of their nose; some *Fig. 1.* Coauthor (SGG) with paddlefish collected from Frasier-Whitehorse Lake, Louisiana. Upper portion of caudal fin is bent toward the camera, making the dorsal lobe appear shorter than it actually is. three fingers broad in the end and two only near their nose; and some eight thumbs long, all marbled of

a blackish color" (Adams, 1961). This record is important, not merely for priority, but because it confirms that paddlefish were native to the Great Lakes prior to the construction of canals in recent times (Rostlund, 1951). It is also interesting for Radisson's approximations of rostral dimensions, which, although imprecise, constitute the first quantitative morphological data published for the species.

More exciting is the description of a paddlefish by Father Jacques Marquette, Jesuit missionary and explorer. His memoirs are readily available, in English and original French (Thwaites, 1900), and his encounter with a paddlefish in 1673 is famous and frequently cited (Gowanloch, 1933; Eifert, 1959; McKinley, 1984). Ignoring local Indian legends of water demons, Marquette voyaged down the Wisconsin River and into the Mississippi River where his small boat was struck by monstrous fishes, one of which is described in some detail. It was "a very extraordinary kind of a fish. It resembles the trout, with this difference, that its mouth is larger. Near its nose [nostril?] which is smaller, as are also the eyes - is a large bone shaped like a women's busk, three fingers wide and a cubit long, at the end of which is a disk as wide as one's hand.¹ This frequently causes it to fall backward when it leaps out of the water." The comparison with trout probably alludes to the lack of large, prominent scales, but the fish described is undoubtedly a paddlefish. Like Radisson, his description of the rostrum indicates a substantial expansion near the end, or a spoon-shaped bill.

In 1758, a military engineer named Antoine Simon La Page du Pratz listed fishes found in Louisiana and illustrated three (Gowanloch, 1933). These were the catfish, a gar, and the paddlefish. "Spatule" was the name given by the French to the paddlefish and refers to the shovel- or spatula-shaped snout. La Page du Pratz was probably the first to publish a figure of a paddlefish, but it is a crude illustration demonstrating either a lack of firsthand experience with the species (and fish, in general) or a decidedly odd artistic sensibility. La Page du Pratz's account is significant, though, because it represents an early record of the species from the lower Mississippi Basin. A more detailed description, and realistic illustrations, were published shortly afterwards as European scientists attempted to classify the spatule.

Shark!

Classification of the North American paddlefish was hampered by its resemblance to sharks and a lack of specimens with reliable locality data, which, in turn, resulted in a surprising degree of taxonomic confusion. Although believed to have been monotypic,² the scientific name of the paddlefish in North America changed, and multiplied, several times in the 100 years following its formal scientific description.

The first detailed description and illustration of a paddlefish was by French physician Pierre Jean Etienne Mauduyt de la Varenne in 1774 (McKinley, 1984). He provided two excellent line drawings of a specimen (dorsal and ventral views), morphological description, and measurements of fins and rostrum. He did not propose any name for the species but indicated that the fish is "of the class of cartilaginous fishes, of the genus of sharks," and that Europeans called it the spatule, after the pharmacist's instrument. He also notes that it was abundant in the Mississippi, but further observes that this was a fish "of which few naturalists or travelers have perhaps spoken." Mauduyt de la Varenne's account is of special interest for three reasons: 1) its priority and great detail; 2) the fact that it was largely overlooked until recently; and 3) the small size of the specimen (132 mm), which at the time was rare in museum collections.

The genus of the paddlefish was established 23 years after Mauduyt de la Varenne's description, but in the interim the paddlefish was still regarded as a shark (Jordan, 1917; McKinley, 1984). J. P. Bonaterre in 1788 re-described the paddlefish and named it "chien de mer feuille" or "leaf dog of the ocean," alluding to its similarity with dogfish sharks. Bonaterre was apparently working with no available information on the source of his material or of previous observers; he noted that the country and habits of the fish were unknown. He also failed to provide a Latin- or Greek-based binomial name (genus and species), and was not recognized for the species description under the modern system of taxonomy, which was proposed, promoted, and established by Carl Linnaeus in 1758.

In 1792, Johann Julius Walbaum, who also believed the fish to be a shark, created a formal binomial as the scientific name, Squalus spathula. Squalus was, and is, the genus of dogfish sharks. The species *spathula* refers to the spatula-like rostrum; the difference in spelling (spathula vs. spatula) is believed to be a lapsus calami or error in transcription (N. Douglas, pers. comm.). In 1797, Bernard Germain Etienne de la Ville-sur-Illion, Comte de Lacepede (later "Citoyen" La Cepede), realized that the paddlefish was not a shark, and renamed the fish le Polyodon feuille, which would later be modified to Polyodon folium (Bloch and Schneider, 1801). Polyodon means "many teeth" and probably refers to the numerous and prominent gill-rakers which resemble teeth (Fig. 2); folium is the Latinized form of feuille or "leaf" and refers to the shape of the fish's paddle. The name Polyodon folium would persist in scientific literature for nearly a century (e.g., Mitchill et al., 1827; Wailes, 1854, Bridge, 1897; Allis, 1903) before the current nomenclature of Polyodon spathula would be adopted (e.g., Stockard, 1907). Other names would also be suggested, including Spatularia reticulata in 1804 and Platirostra edentula in 1817 (Jordan et al., 1928). Despite the plethora of names, it was always assumed that there was only a single species of paddlefish, possibly because prior to the mid-19th century only a few specimens, most of intermediate size, had been preserved in

¹ A busk was a long piece of whalebone used to straighten a woman's corset. A cubit was a unit of measure representing the distance from elbow to tip of the middle finger approximating 18 inches (457 mm), 21 inches (533 mm), or more.

² The Chinese paddlefish, *Psephurus gladius*, was largely unknown and not formally described until 1861.



museums, and little was known of paddlefish biology or range (Shaw, 1804; Mitchill et al., 1827).

A Professor's Plenitude of Paddlefishes

Constantine Samuel Rafinesque, the eccentric naturalist and professor at the University of Transylvania (Kentucky), muddled paddlefish classification with his listing of not one, but four separate species of paddlefish in his classic Ichthyologia Ohiensis, one of the earliest regional fish books (Rafinesque, 1820). He recognized and provided descriptions for Polyodon folium, which he called the western spadefish; Planirostra edentula, the toothless paddlefish; and Proceros spp., the hornfishes. According to Rafinesque, the western spadefish had a large head, toothed jaws, a long gill flap, a "cuneiform" rostrum only as long as its head, and was countershaded with a brown dorsum, and white belly. The toothless paddlefish had a smaller head, no teeth, a "somewhat cuneiform" rostrum longer than its head, and the body was uniformly olive-brown. Polyodon folium and Planirostra edentula are both viewed as archaic synonyms of Polyodon spathula (Jordan, 1923), but Rafinesque's use of the two different binomials may represent

Fig. 2. Paddlefish collected from Frasier-Whitehorse Lake, Louisiana, showing numerous "toothlike" gill rakers. his firsthand knowledge of two different forms or, at least, two very differentlooking specimens.

Rafinesque's reference to paddlefish teeth is open to interpretation. Adult and sub-adult paddlefish are traditionally described as toothless (Mitchill et al., 1827; Beach, 1902), but other sources note that the jaws are "armed with small teeth" (e.g., Norman, 1948). One taxonomic reference describes paddlefish teeth in some detail: double rows in the upper jaw and a single row in the lower jaw of "sharp, curved, and serrated teeth" (Shaw, 1804). Why the apparent confusion on such a basic and presumably obvious morphological feature? Teeth are very prominent in the mouths of newly hatched (yolk-sac) paddlefish larvae (Ballard and Needham, 1964). There are double rows of conical teeth in the upper jaw, and a single row of teeth in the lower jaw, but as paddlefish grow their teeth become relatively smaller and less apparent (Bemis et al, 1997). Teeth are still prominent in specimens 50-100 mm total length (TL), but with further growth replacement becomes less regular and teeth smaller (Grande and Bemis, 1991). Large specimens (> 1500 mm TL) appear toothless,

the teeth either shed or embedded in the jaw. Pointed ridges are found in the jaws of some specimens, however, indicating growth of the jaw bones over the teeth. Rafinesque may have seen or heard of such specimens. We have observed prominent serrations in the jaws of fish up to 500 mm TL, which may represent the "teeth" of this otherwise typically toothless taxon.

The hornfishes were described as "sharks" lacking pectoral and pelvic fins, with a snout protruding in a straight horn, belonging to the genus Proceros (Rafinesque, 1820), later deemed a genus of "mythical" paddlefishes (Jordan, 1923). According to Rafinesque, Proceros maculatus, the spotted hornfish, was iron-gray with white spots and lived in the Mississippi River; P. vittatus had longitudinal stripes and lived in Lake Ontario (Rafinesque, 1820). The spotted hornfish is sketched and named in Rafinesque's infamous Notebook N. 17, which contained descriptions of fishes not personally seen by the professor, but reported to him by other observers (Markle, 1997). Prominent among these observers was John James Audubon, who reported a series of fantastic species to Rafinesque, either as a practical joke or to exact revenge on Rafinesque for the destruction of the ornithologist's violin (Barber, 1980; Gilbert, 1981). Audubon, guilty of fabricating imaginary sturgeons, cannot be blamed for the hornfishes.

The hornfishes were probably atypical specimens, or illustrations, of paddlefish. Descriptions could have been based on mutilated, anomalous, or unusually pigmented specimens. Morphologically anomalous paddlefish are known (Beard, 1878; Rosen and Hales, 1982; Ramos et al., 1994). Coloration varies among individuals, and descriptions of individuals with spots have been published (Mitchill et al., 1827; Alexander, 1914; Coker, 1923). Rafinesque may have appreciated, and exaggerated, natural variation among individuals more so than others, but he may also have seen more specimens, or illustrations of specimens, than had other taxonomists.

If some ichthyologists seemed insufficiently familiar with paddlefish to appreciate such variation, it was nothing compared to that of the average American, who rarely had opportunities to see this species.

Paddlefish and the Public

For many years, curious paddlefish enthusiasts had to be content viewing rare preserved specimens (or parts of specimens), published illustrations, and dioramas. Charles Wilson Peale, in 1784, may have been the first to display a paddlefish to the general public (McKinley, 1984). Peale's

paddlefish was the second exhibit acquired for his museum in Philadelphia that would later become one of the most celebrated natural history collections in North America (Barber, 1980). Jerome V. C. Smith describes a severed rostrum from the collections of the Boston Society of Natural History (Smith, 1833). It was taken from an 18 kg "paddle-nosed sturgeon" speared in 1830 at LeTart's Falls on the Ohio River. In 1878, an artist named David Beard, frustrated "by the absence of any illustration and the very meager descriptions of our most curious native specimens," produced a drawing and detailed description of a paddlefish, 104 cm TL, collected at St. Louis, Missouri (Beard, 1878). Beard's drawing shows a paddlefish with its rostrum angled down towards the river bottom. The left side of the specimen is depicted, possibly for reasons of zoological protocol, but more likely because the right opercular flap of this specimen was abnormally short.

In 1910, an American Museum of Natural History expedition conducted by Louis Hussakof collected paddlefish from Moon Lake, Mississippi (Dean, 1923). Paddlefish replicas were cast from molds made in the field and a diorama was later constructed at the museum showing a group of paddlefish entering the seine of a fisherman. A photograph of the exhibit in Natural History magazine suggests that the diorama was impressive. Hussakof, though, did not refer to paddlefish in very impressive terms. At the 40th annual meeting of the American Fisheries Society later that year, in a talk "illustrated with lantern slides," he described paddlefish as feeble, clumsy, and having "absolutely no sport value" (Hussakof, 1910). His conclusions, however, were based on their behavior in the giant winch-operated seines deployed by commercial fishermen from specially designed boats. Large commercial operations had developed, just a decade or so earlier, on the Ohio and Mississippi Rivers to catch paddlefish for their meat, caviar, and oil. Mechanized and highly efficient fishing operations would soon deplete many of these formerly abundant populations (Alexander, 1914; Alexander, 1915).

Repeated attempts by fishery scientists and public aquaria to maintain healthy paddlefish were apparently not successful for many years, the result being that the general public rarely, if ever, saw live paddlefish. Adult and sub-adult fish could be safely transferred to in-lake enclosures for short periods (Alexander, 1915), but most paddlefish transported by specially equipped boat or by rail car rarely survived extended journeys (Coker, 1923). Small specimens were maintained for several years in a small, 5 m deep reservoir in Fairport, Iowa, but lost equilibrium when moved to tanks (Coker, 1923). One paddlefish was maintained at the Lincoln Park Aquarium for nearly a year, but was fed only sporadically and apparently with limited success; it was in "good, though not fat, condition until the accident which caused its death" (Weed, 1925). The New York Aquarium, after a quarter-century of operation, listed the paddlefish in its tour guide but showed no picture and indicated that it "is not adapted to life in captivity," with specimens living but a few days (Townsend, 1929). Years later, the director of the Shedd Aquarium noted that the easily injured rostrum and the difficulty of supplying zooplankton as food made the paddlefish difficult to keep (Chute, 1947). Even today, long-term captivity of paddlefish presents special challenges to aquarium personnel. It is not uncommon to see fish on display at public aquaria that are conspicuously skinnier and more blunt-nosed than their cousins in the wild.

Search for the Smallest Spoonbill

If adult paddlefish were rare curiosities for the general public, young paddlefish were unobtainable "holy grails" for certain biologists. By the beginning of the 20th century, most of the specimens described in print or preserved in museum collections were adults or subadults 500-1500 mm long. Specimens 100-200 mm were unusual, and specimens less than 100 mm were virtually unknown. There was intense scientific interest in finding very small paddlefish so that early anatomical development (e.g., jaw teeth) and life history could be studied, and so that spawning and nursery grounds could be identified.

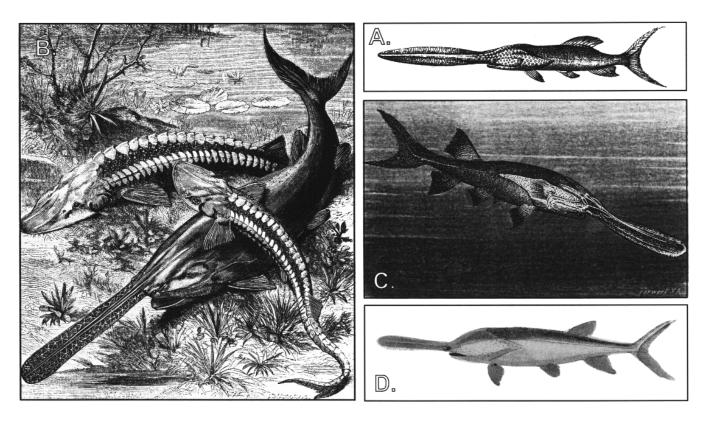
In 1910, following Hussakof's paddlefish talk, Barton Warren Evermann commented that the "queerest thing about the spoonbill is this, that no one has been able to locate the spawning grounds and to find young fry" (Hussakof, 1910). The following year, three papers were published announcing independent discoveries of young-of-year paddlefish. One 74 mm specimen was collected in 1910 from the Mississippi River near St. Louis (Danforth, 1911). It was believed to be the smallest specimen recorded. Famed naturalist Thomas Barbour read the account and reported that there existed in Harvard's Museum of Comparative Zoology additional juvenile specimens, three of which were even smaller: 35-65 mm in length (Barbour, 1911). One was collected in Arkansas, the others near St. Louis, prior to 1860! The specimens were originally in the personal collection of Louis Agassiz and most were well-preserved. Both articles were well-illustrated, but neither described the method of capture or the habitats in which the baby paddlefish were found.

Details on sampling young-of-year, albeit slightly larger, paddlefish were provided by dedicated collector William F. Allen (Allen, 1911). Allen was employed by Edwards Phelps Allis, Jr., an anatomist specializing in primitive fishes, and was commissioned to collect all "ganoids" possible. Before deciding on where to collect, Allen reviewed all available information and selected the confluence of the Ohio and Mississippi Rivers as his sampling site. For one year he seined and set hoop-nets in all habitats and was rewarded with 25 specimens of paddlefish 100-150 mm. All of these, however, were collected on a single date, 1 July 1904, from a tributary slough during a drop in river stage, when water was rapidly receding from the slough. Fish had not been collected there previously, and Allen believed that they migrated during high water the night before or early that same morning. Allen hurriedly preserved the paddlefish (collected during a "violent thunderstorm"), but noted that the bodies of the live paddlefish were almost transparent. He did not observe young paddlefish again until late August and early September, when he seined mud bars and sandbars of the Ohio River at night and early morning.

Earlier that century, a reward of \$5 offered for a paddlefish less than 150 mm in length went unclaimed (Beach, 1902). In the 1920s, anatomist Allis, wanting even smaller paddlefish, offered a \$1000 reward for any specimen of paddlefish less than 50 mm, a reward that was not claimed and eventually withdrawn (Gilbert, 1981). Smaller specimens of paddlefish would later be discovered, however.

On the morning of 14 May 1932, David Thompson was seining the head of a large island in the Mississippi River near Grand Tower, Illinois, and collected seven specimens of 17-20 mm postlarval paddlefish (Thompson, 1933). These were collected with a 6 m, 4 mm-mesh seine. Collected along with the paddlefish were river prawns (*Macrobrachium* sp.), minnows, sunfishes, and dragonfly nymphs. Comparably sized specimens were again collected by Thompson on 29 May 1944, when he seined the main channel of the Mississippi River at an island sand bar near Cape Girardeau, Missouri (Larimore, 1949). There, water was less than one meter deep, turbid, and 25°C. River stage was high, and substrate was sand with an overlaying layer of muddy ooze. Thompson was again using a 4 mm-mesh seine.

The development of paddlefish is now well documented (Yeager and Wallus, 1990; Bemis and Grande, 1992). But at the time of their collection, Thompson's specimens were considered sensational because they showed how some structures, notably the rostrum, changed in size and shape with the growth of the paddlefish.



How Does a Rostrum Grow?

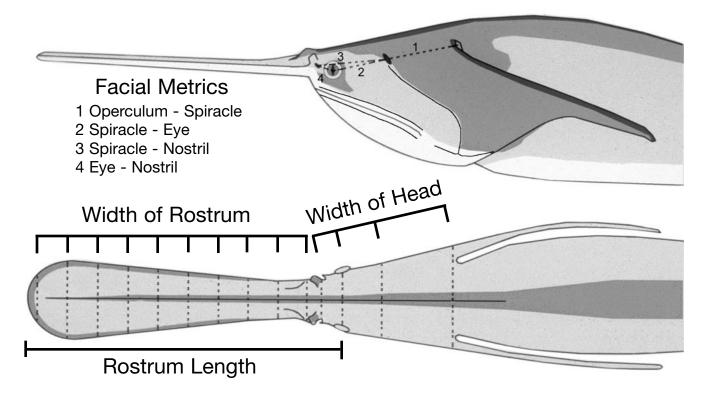
Anecdotal comments indicated that the rostrum did not grow at the same rate as the rest of the paddlefish (e.g., Brehm, 1893). Charles Stockard, who conducted one of the earliest field studies of paddlefish in 1905, provided the first quantitative data to support this hypothesis (Stockard, 1907). Later, David Thompson would use those and other data from preserved paddlefish to describe how the rostrum grows (Thompson, 1933). When paddlefish fry hatch from their egg, the rostrum is very small. It grows rapidly-more rapidly, in fact, than the body (growth of a body part that is disproportionately faster than the growth of the body of an animal is called positive allometric growth). This continues until the paddlefish is approximately 80 mm eye-to-fork length (EFL). Then rostrum growth slows down and keeps pace with growth of the fish (isometric growth). When the fish is larger than 250 mm, rostrum growth becomes slower than that of the fish's body (negative allometric growth).

In subadult and adult paddlefish, the rostrum is absolutely longer in larger fish, but is relatively shorter when expressed as a percentage of body size. How this affects the biology of paddlefish is not known. At one time, the rostrum was believed to be an implement used by the paddlefish to acquire food, either by digging and stirring aquatic invertebrates Fig. 3.
Illustrations of paddlefish from natural history references:
A) Bloch and Schneider, 1801;
B) Wood, 1863; C) Brehm and
Hacke, 1892; D) Cuvier, 1833-1837, reproduced in Aramata, 1990. into the water column or by manipulating aquatic plants for grazing (Mitchill et al., 1827; Beard, 1878; Beach, 1902). The rostrum-as-

utensil hypothesis persisted for decades (Norman, 1948). Doubts were raised nearly a century ago, however, and the theory is given little credibility today (Stockard, 1907; Grande and Bemis, 1991). The rostrum is now believed to function primarily as an electro-sensory organ (Bemis et al., 1997), but it can be injured or lost in turbulent water upon impact with underwater structure (Coker, 1923). Observations of healthy paddlefish that are missing rostra suggest that individuals with shorter (or absent) rostra may function similarly to those with larger, well-developed rostra (Stockard, 1907; Gannon and Howmiller, 1973).

Another, Undescribed Paddlefish in North America?

Rafinesque's penchant for describing new species and the pronounced allometric growth of the rostrum may have obscured the existence of multiple forms of paddlefish. Natural history illustrations made during the 19th century (Fig. 3), and two common names for the fish used almost



interchangeably, suggest two distinctive morphotypes based on rostral shape. "Paddlefish" implies a long, narrow, straight-sided snout; "spoonbill" suggests a shorter, broader, terminally expanded snout. Additionally, some ichthyologists have made tantalizing references to a second form of paddlefish in North America. George Sprague Myers believed that there were two species of North American paddlefishes, "one not vet described," but unfortunately did not provide a basis for his rationale (Myers, 1949). It is probable that Myers was influenced by an observation Stockard made while doing his fieldwork in the lower Mississippi basin. Stockard believed that there were two distinguishable forms of paddlefish in the population he was studying: a long, narrow-nosed form in the rivers, and a short, broad-nosed form in oxbow lakes (Stockard, 1907). Unfortunately, Stockard published data supporting his observations on negative allometric growth of the paddlefish rostrum but did not provide supporting data for the existence of multiple rostral forms.

While doing stream surveys in the Mississippi delta, we also observed substantial variation in the shapes of paddlefish rostra. Was Stockard correct? To determine the existence of two or more rostral forms, we would need a large number of specimens. In 1993, we were working in the Big Sunflower River in Mississippi and met commercial fisherman William Lancaster, who frequently encountered paddlefish as bycatch *Fig. 4.* Rostral and facial metrics used to describe variation in rostrum size and shape. when fishing for catfish, buffalo, and gar. He agreed to save dead and dying paddlefish for us during his daily net-checks

along a reach of the river that was contiguous with five oxbow lakes. The Mississippi Department of Wildlife, Fisheries, and Parks modified our scientific collecting permit accordingly, and between 1 March 1994 and 28 February 1995, we obtained 118 specimens that were 411 to 1009 mm EFL.

On these specimens, we measured length of the rostrum, breadth at 10 equidistant points along its length, and certain distances between facial features (Fig. 4). Measurements were used to calculate indices that described rostral size and shape: relative length of the rostrum (rostrum length/paddlefish EFL) and anterior expansion of the rostrum or just how spoonlike it was shaped (maximum rostrum breadth/minimum rostrum breadth).

We observed, like others had earlier, that relative rostrum length decreased as size of adult paddlefish increased. Because all of our specimens were from a single location, though, we were able to develop a population-specific relationship between paddlefish and rostrum size and to evaluate variation that occurred within a single population. We found that relative rostrum length (as % EFL) could be estimated from paddlefish size (EFL in millimeters), or vice versa, using this relationship:

Relative Length of Rostrum = $0.716 - (3.61) (10^{-4})$ (Length of Paddlefish)

Paddlefish size, however, only explained 49% of the variation in rostrum length. Statistically, the relationship is "significant," but there is still a substantial amount of variation among individuals that is independent of size. For example, fish that are approximately 600 mm EFL have a predicted rostrum length of 50% EFL, but some of our fish this size had rostra that were considerably shorter (37% EFL) and somewhat longer (57% EFL).

Could our short-nosed specimens be Stockard's oxbowdwelling spoonbill, and long-nosed specimens his riverine paddlefish? There was an easy way to test this: a simple x-y plot of relative rostrum length and rostral expansion (Hoover et al., 2000). If we had Stockard's two morphotypes, then the points would cluster out as long-, straight-nosed forms, and short-, broad-nosed forms. To minimize effects of allometric growth, we selected 30 specimens from a narrow size range (600-650 mm) and plotted anterior expansion of the rostrum against the relative rostrum length. Our results did not indicate two cleanly discrete forms, however. There was one large cloud of points in which the majority of fish had rostra greater than 42% EFL with rostral expansion less than 165% its minimum width. One fish looked a little different, though. It had a rostrum that was 38% EFL and was expanded 175% its minimum width. We concluded that if there was a short-, broadnosed form, then it was substantially less common and not strikingly different from the more common longer, straighternosed paddlefish. Unlike the daring Professor Rafinesque, we were not yet ready to describe a new form of spoonbill.

Acknowledgments

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Literature Cited [and Annotations]

Adams, A. T. (Ed.). 1961. The explorations of Pierre Esprit Radisson: from the original manuscript in the Bodleian Library and the British Museum. Ross

and Haines, Inc., Minneapolis, 258 pp. + lxxxiv.

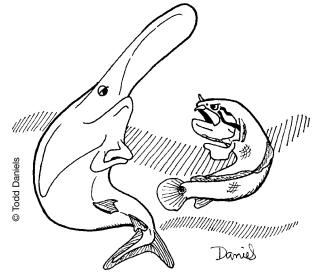
- Alexander, M. L. 1914. The paddle-fish (*Polyodon spathula*). (Commonly called "spoonbill cat.") *Trans. Am. Fish. Soc.* 44: 73-78. [Article provides early documentation of a disappearing population in an intensively fished lake and advocates protective measures for paddlefish.]
- Alexander, M. L. 1915. More about the paddle-fish (*Polyodon spathula*). *Trans. Am. Fish. Soc.* 45: 34-39. [Article describes successful confinement of paddlefish in enclosures and includes notes on the structure of the digestive system.]
- Allen, W. F. 1911. Notes on the breeding season and young of Polyodon spathula. Journal of the Washington Academy of Science 1: 280-282.
- Allis, E. P., Jr. 1903. On certain features of the lateral canals and cranial bones of *Polyodon folium. Zoologische Jahrbucher* 17: 659-679.
- Aramata, H. 1990. Fish of the world: a collection of 19th century paintings. Portland House, New York, 279 pp.
- Ballard, W. W. and R. G. Needham. 1964. Normal embryonic stages of Polyodon spathula (Walbaum). Journal of Morphology 114: 465-478.
- Barber, L. 1980. The heyday of natural history. Doubleday and Company, Garden City, New York, 320 pp. [Book notes Peale's acquisition of a paddlefish and describes in detail the incident involving Rafinesque's destruction of Audubon's violin.]
- Barbour, T. 1911. The smallest Polyodon. Biol. Bull. 21: 207-215.
- Beach, H., Sr. 1902. The paddle fish (*Polyodon spathula*). Bulletin of the Wisconsin Natural History Society. [A fascinating article that speculates freely, and incorrectly, about the feeding and hibernation of paddlefish.]
- Beard, D. C. 1878. The paddle fish of the Mississippi. *Scientific American* 39: 391.
- Bemis, W. E. and L. Grande. 1992. Early development of the actinopterygian head. I. External development and staging of the paddlefish, *Polyodon spathula.Journal of Morphology* 213: 47-83. [Detailed electron microscope photographs and drawings of paddlefish head at more than 20 stages of development.]
- Bemis, W. E., E. K. Findeis, and L. Grande. 1997. An overview of Acipenseriformes. *Env. Biol. Fishes* 48: 25-71.
- Berrill, N. J. 1952. *Journey into Wonder*. Dood, Mead and Company, New York, 338 pp.
- Bloch, M. E. and J. G. Schneider. 1801. Systema ichthyolgiae. Reprint 1967. Verlag Von J. Cramer, Lehre.
- Brehm, A. E. and W. Hacke. 1892. *Die fische*. Brehm's Tierleben, Bibliohraphisches Institut, Leipzig, Germany.
- Bridge, T. W. 1897. On the presence of ribs in Polyodon (Spatularia) folium. Proceedings of the Zoological Society of London XX: 722-724.
- Burr, B. M. 1981. Polyodon spathula (Walbaum). Paddlefish. Pp. 45-46 in D. S. Lee, et al. Atlas of North American Freshwater Fishes, North Carolina State Museum of Natural History, Raleigh, i-x + 854 pp.
- Carlander, H. B. 1954. A history of fish and fishing in the upper Mississippi River. Upper Mississippi River Conservation Committee, Springfield, Il., 96 pp. [This well-researched synopsis covers many species of fishes and bivalves including paddlefish encounters by La Salle in 1682, Captain Jonathan Carver in 1767, and Prince Maximilien of Wied in 1843.]
- Carlson, D. M. and P. S. Bonislawsky. 1981. The paddlefish (*Polyodon spathula*) fisheries of the midwestern United States. *Fisheries* 6: 17-27.
- Chute, W. H. 1947. *Guide to the John G. Shedd Aquarium*. Shedd Aquarium, Chicago, 236 pp.
- Clayton, L. A., J. V. Knight, Jr., and E. C. Moore (Eds.). 1996. The De Soto chronicles: the expedition of Hernando De Soto to North America in 1539-1543. University of Alabama Press, Tuscaloosa, Al.
- Coker, R. E. 1923. Methuselah of the Mississippi. Scientific Monthly 16: 89-103. [Good summary of paddlefish biology.]
- Danforth, C. H. 1911. A 74 mm Polyodon. Biol. Bull. 20: 201-204.

- Dean, B. 1923. The Department of Fishes, American Museum. *Natural History* 23 (6): 606-616.
- Dillard, J. G., L. K.Graham, and T. R. Russell. 1986. *The paddlefish: status, management, and propagation*. North Central Division, American Fisheries Society. Special Publication No. 7. Columbia, Mo., 159 pp.
- Eifert, V. S. 1959. *River world: wildlife of the Mississippi*. Dodd, Mead, and Company, New York, 271 pp.
- Gannon, J. E. and R. P. Howmiller. 1973. Ecological notes on paddlefish (Polyodon spathula) with short rostrums. Michigan Academician 6: 217-222.
- Gilbert, B. 1981. End of a long journey for spoonbill cat. Audubon 83: 66-71. Gowanloch, J. N. 1933. Fishes and fishing in Louisiana. Bulletin No. 23,
- Louisiana Department of Conservation, New Orleans, La., 638 pp. Grande, L. and W. E. Bemis. 1991. Osteology and phylogenetic relationships
- of fossils and recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. *Journal of Vertebrate Paleontology* Vol. 11, Supplement to No. 1: 1-121.
- Hakluyt, R. 1810. The voyage made by M. Iohn Hawkins Esquire, and afterward knight, Captain of the Iesus of Lubek, one of her Maiesties shippes, and General of the Salomon, and other two barkes going in his company, to the coast of Guinea, and the Indes of Noua Hispania, begun in An. Dom. 1564. Collection of the Early Voyages, Travels, and Discoveries of the English Nation Vol. III: pp. 594-618. Evans, Mackinlay, and Priestely, London. [Sparke's written observations of fishes are frustratingly brief for native fish enthusiasts with one exception: a detailed account of the behavior and interactions between flying fishes and bonitos.]
- Hoover, J. J., S. G. George, and K. J.Killgore. 2000. Rostrum size of paddlefish (*Polyodon spathula*) (Acipenseriformes: Polyodontidae) from the Mississippi delta. *Copeia* 2000: 288-290.
- Hussakof, L. 1910. The spoonbill fishery of the lower Mississippi. Trans. Am. Fish. Soc. 40: 245-248. [Plate depicts special boat designed for seining adult paddlefish and a typical catch being processed for roe.]
- Jordan, D. S. 1917. The genera of fishes. Rpt. 1963. Stanford University Press, Stanford, 576 pp.
- Jordan, D. S. 1923. A classification of fishes. Rpt. 1963. Stanford University Press, Stanford, 243 pp.
- Jordan, D. S., B. W. Evermann, and H. W. Clark. 1928. Checklist of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rpt. 1930. U.S. Government Printing Office, Washington, D.C., 670 pp.
- Larimore, R. W. 1949. Changes in the cranial nerves of the paddlefish, *Polyodon spathula*, accompanying development of the rostrum. *Copeia* 1949: 204-212.
- Markle, D. F. 1997. Audubon's hoax: Ohio River fishes described by Rafinesque. Archives of Natural History 24: 439-447. [A fascinating analysis of one of the most celebrated stories in ichthyology.]
- McKinley, D. 1984. History of a neglected account of the paddlefish, *Polyodon spathula. Copeia* 1984: 201-204.
- Meurger, M. and C. Gagnon. 1988. *Lake monster traditions: a cross-cultural analysis*. Fortean Tomes, London, 320 pp. [Book combines anthropology, folklore, popular culture, and biology to examine accounts of lake and river monsters; of particular interest to native fish enthusiasts are the roles attributed to eels, gars, pikes, and sturgeons in cryptozoology.]
- Mitchill, S. L., S. P. Hildreth, and J. W. Clemens. 1827. Notice of the spoonbill sturgeon or paddle fish, of the Ohio, (*Polyodon feuille* of Lacepede). *American Journal of Science and Arts* 12: 201-205. [Three letters describing and illustrating paddlefish.]
- Myers, G. S. 1949. Salt-tolerance of fresh-water fish groups in relation to zoogcographical problems. *Bigdragen tot de Dierkunde* 28: 315-322.

Norman, J. R. 1948. A history of fishes. A. A. Wyn, Inc., New York, 463 pp. Rafinesque, C. S. 1820. Ichthyologia Ohiensis, or natural history of the fishes

inhabiting the Ohio River and its tributary streams preceded by a physical description of the Ohio and its branches. Rpt. 1970. Arno Press, 90 pp.

- Ramos, K. T., C. S. Berkhouse, and J. N. Fries. 1994. Apparent sunburn of juvenile paddlefish. *Prog. Fish.-Cult.* 56: 214-216. [Article demonstrates how sunburn can cause rostral deformities in paddlefish.]
- Robins, C. R., G. C. Ray, and J. Douglass. 1986. A field guide to the Atlantic Coast fishes. Peterson Field Guide Series. Houghton Mifflin Company, Boston, 354 pp.
- Rosen, R. A. and D. C. Hales. 1982. Occurrence of a blind paddlefish, *Polyodon spathula. Copeia* 1982: 212-214. [Blind paddlefish was also melanistic.]
- Rostlund, E. 1951. Three early historical reports of North American freshwater fishes. *Copeia* 1951: 295-296.
- Shaw, G. 1804. Spatularia spatularia. Pp. 362-364. In: General zoology, or systematic natural history. Vol. V. G. Kearsley, London.
- Smith, J. V. C. 1833. Natural history of the fishes of Massachusetts, embracing a practical essay on angling. Rpt. 1970. Freshet Press, New York, 400 pp.
- Stockard, C. R. 1907. Observations on the natural history of Polyodon spathula. American Naturalist 41: 753-766.
- Thompson, D. H. 1933. The finding of very young *Polyodon. Copeia* 1933: 31-33.
- Thwaites, R. G. (Ed.) 1900. Voyages of Marquette by Jacques Marquette. Vol. LIX. In: *The Jesuit relations and allied documents: travels and explorations of the Jesuit missionaries in New France 1610-1791*. The Burrows Brothers Company, Cleveland. [1966 reprint available through University Microfilms, Ann Arbor.]
- Townsend, C. H. 1929. Guide to the New York Aquarium. New York Zoological Society, New York, 170 pp.
- Wailes, B. L. C. 1854. Report on the agriculture and geology of Mississippi embracing a sketch of the social and natural history of the state. E. Barksdale, State Printer, Jackson, Ms., 371 pp.
- Weed, A. C. 1925. Feeding the paddlefish. Copeia 146: 67-68.
- Williams, L. W. 1986. Boldly onward. Precision Publishing, Charlotte Harbor, Fl., 192 pp.
- Wood, J. G. 1863. The illustrated natural history. Routledge and Sons, London.
- Yeager, B. L. and R. Wallus. 1990. Polyodontidae. Pp. 47-56. In: R. Wallus, T. P. Simon, and B. L. Yeager. *Reproductive biology and early life history of fishes in the Ohio River drainage. Vol. I. Acipenseridae through Esocidae.* Tennessee Valley Authority, Chattanooga, Tn. [Good drawings and detailed survey of literature on reproduction and development.]



"It's not how long it is. It's how you use it!"