

## Observations on the skulls of sturgeons (Acipenseridae): shared similarities of *Pseudoscaphirhynchus kaufmanni* and juvenile specimens of *Acipenser stellatus*

Eric J. Hilton

Geology Department, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, U.S.A. (e-mail: ehilton@fieldmuseum.org)

Received 6 January 2004 Accepted 30 March 2004

**Key words:** stellate sturgeon, large Amu-Dar shovelnose sturgeon, Acipenseriformes, Chondrostei, comparative osteology

### Synopsis

A novel hypothesis uniting *Acipenser stellatus* and *Pseudoscaphirhynchus* as sister groups has recently been proposed based on analysis of DNA sequences. In this paper I compare specimens of *A. stellatus* and *P. kaufmanni*, and show that they share several putatively derived similarities in the structure of their skulls, including: the presence of large spines on the dermal bones of skull; lateral extrascapular bones that enclose the confluence of the posttemporal, supratemporal, and otic sensory canals; elongate dorsal rostral bones; border rostral bones distinct in shape from dorsal rostral bones; greatly enlarged jugal that lacks a median flange; rostral canal bones that loop posteriorly at the anterior commissure of the rostral sensory canals; and the presence of an elongate, flat, and broad posterior ventral rostral bone. These similarities support a close relationship between *A. stellatus* and *Pseudoscaphirhynchus*, but still remain to be critically tested.

### Introduction

The 25 living species of sturgeons (family Acipenseridae) are currently classified in four genera (*Pseudoscaphirhynchus*, *Scaphirhynchus*, *Huso*, and *Acipenser*). Acipenseridae is widely regarded as the sister-group of Polyodontidae, the paddlefishes. These two families, together with two entirely fossil families (†Chondrosteidae and †Peipiaosteidae) comprise the order Acipenseriformes (e.g., Grande & Bemis 1996). Living and fossil sturgeons are restricted to the northern hemisphere. All living species breed in freshwater and many are anadromous. All species of sturgeons are CITES listed and afforded some form of protection in their native ranges. Despite the global endangered or threatened status of sturgeons and their commercial importance, very little is known about their phylogenetic relationships and evolutionary history; see Bemis et al. (1997) and Birstein & Bemis (1997) for recent discussions.

The two genera of shovelnose sturgeons, *Pseudoscaphirhynchus* (three species) and *Scaphirhynchus* (three species), commonly are interpreted as sister-groups (e.g., Findeis 1997) as the subfamily Scaphirhynchinae, although both morphological (e.g., Bailey & Cross 1954) and molecular (e.g., Birstein et al. 2002) evidence does not always support such a grouping. Additionally, the monophyly of *Pseudoscaphirhynchus* is uncertain (e.g., Mayden & Kuhajda 1996). The two species of the genus *Huso* (*H. huso* and *H. dauricus*) were found to form a monophyletic group basal to all other sturgeons by Findeis (1997), although they are often interpreted as sister-group to (e.g., Artukhin 1995, Mayden & Kuhajda 1996) or nested within the genus *Acipenser* (e.g., Birstein et al. 1997, 2002, Birstein & DeSalle 1998). With 17 species, *Acipenser* has the most species of any sturgeon genus. Findeis (1997) was unable to find any morphological synapomorphies for *Acipenser* as currently constructed and most modern

analyses question its monophyly. Mayden & Kuhajda (1996), however, discovered three putative synapomorphies of *Acipenser* (parietal spines in the form of elevated ridges, mouth small and transverse, and a broad branchiostegal connection; see their Figure 9), although not all species of *Acipenser* were studied. There are many lingering questions regarding the phylogenetic interrelationships within the family Acipenseridae.

In contrast to most other modern phylogenetic studies that have tested the monophyly of Scaphirhynchinae, Birstein et al. (2002) did not recover a sister-group relationship between *Scaphirhynchus* and *Pseudoscaphirhynchus* based on their analysis of short sequences from five mitochondrial genes (337 bp 12S, 523 bp 16S, 643 bp NADH5, 410 bp control region, and 526 bp *cyt b*; see also Birstein et al. 1997). Ludwig et al. (2000, 2001) and Fontana et al. (2001) found *Scaphirhynchus* to nest within *Acipenser*, although none of these studies included *Pseudoscaphirhynchus*. Birstein et al. (2002) found a monophyletic *Scaphirhynchus* basal to all other sturgeons and *Pseudoscaphirhynchus* nested within *Acipenser*. Specifically, a sister-group relationship between *A. stellatus* and *Pseudoscaphirhynchus* was recovered with very strong statistical support (e.g., bootstrap value = 100; see their Figures 1 and 2a); this grouping had never been suggested before.

During an ongoing morphological and systematic study of the sturgeons generally, and the genus *Acipenser* in particular (Hilton, Grande & Bemis unpublished data), I discovered several similarities between the skulls of *A. stellatus* and *P. kaufmanni*. In light of the recent findings of Birstein et al. (2002), these observations seem worthy of an original contribution. Both of these species occur within the Ponto-Caspian biogeographic region as defined by Bemis & Kynard (1997). *Acipenser stellatus* Pallas 1771, the stellate sturgeon, is found throughout the Caspian, Azov, Black, and Aegean Seas and their tributary rivers (Shubina et al. 1989), although their range in these rivers has been reduced due to dam building and other human-induced factors (e.g., in the Danube River, Hensel & Holčík 1997). This species may reach over 2 m in total length, although they are more commonly found to be about 1 m in length (Shubina et al. 1989). *Pseudoscaphirhynchus kauffmani* (Bogdanov 1874), the large Amu-Dar shovelnose sturgeon, is

endemic to the Amu-Darya River and its tributaries (Birstein 1997) and has been a victim of the drying of the Aral Sea (Zholdasova 1997). There are two forms of *P. kaufmanni*, a dark colored dwarf form and a light colored normal form (Salnikov et al. 1996); the forms also differ in position of fins (Birstein 1997). The three species of this genus are relatively small sturgeons, with a maximum size of 75 cm in length in *P. kaufmanni* (Berg 1962); this measurement includes the caudal filament, which may be more than one-third the total length (Hilton 2004). The dwarf form of *P. kaufmanni* reaches a maximum length of about 23 cm, excluding the caudal filament (Salnikov et al. 1996).

## Materials and methods

I examined alcohol-preserved (a), dry skeletons (ds), and cleared and double stained (c&s) specimens with the aid of Wild dissecting microscopes. I prepared cleared and stained specimens following a protocol modified from Dingerkus & Uhler (1977). I prepared drawings electronically using Adobe Illustrator software, based on digital images (Olympus C-3020 Zoom or a Nikon Cool-Pix 990 camera). I examined the following specimens (SL = standard length, measured from tip of snout to posterior-most keeled lateral scute):

*Acipenser brevirostrum*: FMNH 112209 (1 ds, 740 mm SL); FMNH 112212 (1 ds, 710 mm SL); FMNH 112913 (1 ds, 755 mm SL); MCZ 54167 (1 c&s, 472 mm SL); UMA F10431 (1 ds, 930 mm SL); also UMA specimens listed in Hilton & Bemis (1999) and Hilton (2002).

*Acipenser fulvescens*: FMNH 85157 (1 ds, unknown SL, adult).

*Acipenser medirostris*: CAS Acc. 1956-v:9 (1 ds, unknown SL, large juvenile).

*Acipenser stellatus*: FMNH 63706 (3 a, 112-145 mm SL; 1 c&s, 126 mm SL); MCZ 163644 (1 c&s, unknown SL but head length 58 mm and largest c&s specimen examined); UMMZ 184979 (1 c&s, 190 mm SL); UMMZ 145831 (1 a, 225 mm SL).

*Huso huso*: CAS 211810 (1 c&s, 130 mm SL); FMNH 76855 (1 a, 825 mm SL); MCZ 54269 (1 a, 228 mm SL).

*Pseudoscaphirhynchus kaufmanni*: AMNH 97566 (1 c&s, 175 mm SL); INHS 64426 (1 a, 160 mm SL); MCZ 27653 (1 c&s, partially disarticulated, unknown SL; 165 mm TL without the caudal filament according to Findeis 1993).

*Scaphirhynchus platorhynchus*: FMNH 98286 (1 ds, est. 700 mm SL).

*Scaphirhynchus albus*: UMA F10371 (1 c&s, 139 mm SL).

### Institutional abbreviations

AMNH, American Museum of Natural History, New York NY; CAS, California Academy of Science, San Francisco CA; FMNH, Field Museum of Natural History, Chicago IL; INHS, Illinois Natural History Survey, Champaign IL; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge MA; UMA, University of Massachusetts Museum of Natural History, Amherst MA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor MI.

### Results

#### *Spines of the dermal bones of skull*

Thorn-shaped spines on the skull and pectoral girdle in both *A. stellatus* and *P. kaufmanni* are particularly well developed on the supracleithra, posttemporals, dermopterotics, parietals, frontals, and some of the dorsal rostral bones. In *P. kaufmanni*, the spines on the anterior-most pair of dorsal rostral bones are particularly large (Figure 1). This seems to be a fixed pattern, as I found this pair of elements, each with an enlarged spiny process, in all three specimens of *P. kaufmanni* that I examined, and thus may represent a rare consistency in the pattern of dorsal rostral bones. Berg (1962), however, reported between one and five spines on the tip of the snout in *P. kaufmanni*. Spines are also well developed on the dermal bones of the skull and the supracleithrum in *A. stellatus* (Figure 1), although this may be a function of the ontogenetic stage of these specimens (see Discussion). Kittary (1850: plate 7, Figure 5) illustrated the skull of *A. stellatus* at an apparently more

advanced ontogenetic stage (no length of the specimen was provided), but it is impossible to determine from this drawing if spines are present.

#### *Extrascapular bones*

The median extrascapular bone of sturgeons develops in the midline of the skull around the supratemporal sensory canal. The median extrascapular of *P. kaufmanni* (Figure 1) is relatively narrower and more elongate than that of other sturgeons, although there is much individual variation in the shape of this bone in all species. Of the cleared and stained specimens of *A. stellatus* that I examined, this bone is most completely developed in MCZ 163644, in which it is roughly triangular in shape, and extends forward between the posterior portions of the parietals. In the other available specimens of *A. stellatus* this bone is still little more than a tubular ossification of the supratemporal sensory canal (Figure 1). The median extrascapular of *A. stellatus* is much like that of other species of *Acipenser* in the specimen illustrated by Kittary (1850).

A variable number of lateral extrascapular bones surround the supratemporal sensory canal in *A. stellatus* and *P. kaufmanni* lateral to the median extrascapular, as in other sturgeons (there are often anamestic lateral extrascapulars as well). In the specimens of *A. stellatus* that I examined, the lateral extrascapulars are small tubular ossifications that are only slightly and irregularly expanded (Figure 1); this is likely due to the ontogenetic stage of the specimens. The lateral extrascapulars are more expanded and plate-like in the specimen of *A. stellatus* illustrated by Kittary (1850). In *P. kaufmanni*, these bones are broad elements with an irregular shape (Figure 1). In both *P. kaufmanni* and *A. stellatus*, the lateral-most lateral extrascapular of each side supports the confluence of the posttemporal, supratemporal, and otic sensory canals, so that the otic canal enters the dermopterotic directly from the lateral extrascapular rather than from the posttemporal, which is the pattern in other species of sturgeons.

#### *Bones of the dorsal surface of the snout*

Two series of bones, the dorsal and border rostral bones, cover the snout of sturgeons. The dorsal

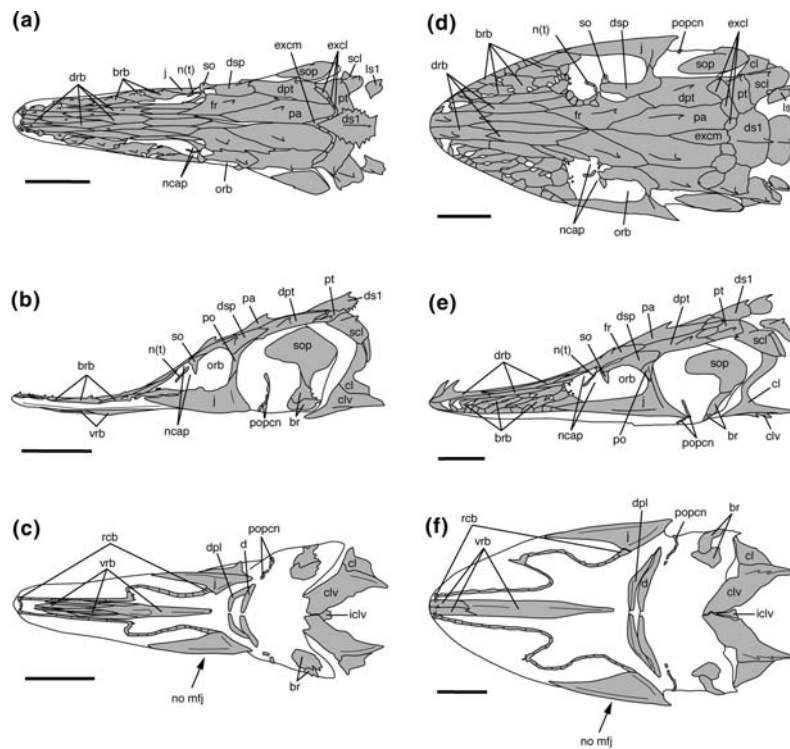


Figure 1. Semi-schematic illustrations of the skulls of *Acipenser stellatus* in (a) dorsal, (b) lateral, and (c) ventral views (based on UMMZ 184979) and *Pseudoscaphirhynchus kaufmanni* in (d) dorsal, (e) lateral, and (f) ventral views (based on AMNH 97566). Note that the jugals of the specimen of *A. stellatus* were displaced slightly medially during preservation of this specimen. Anterior facing left. Scale bars equal 10 mm. Abbreviations: br, branchiostegal; brb, border rostral bones; cl, cleithrum; clv, clavicle; d, dentary; dpl, dermopalatine; dpt, dermopterotic; drb, dorsal rostral bones; ds1, first dorsal scute; dsp, dermosphenotic; excl, lateral extrascapular; excm, median extrascapular; fr, frontal; iclv, interclavicle; j, jugal; ls1, first lateral scute; mfj, median flange of the jugal; ncap, nasal capsule; n(t), tubular nasal bone(s); orb, orbit; pa, parietal; pcl, post-cleithrum; po, postorbital; popcn, ossifications of the preopercular sensory canal; pt, posttemporal; rcb, rostral canal bones; scl, supraclathrum; so, supraorbital; sop, subopercle; vrb, ventral rostral bones.

rostral bones of both *A. stellatus* and *P. kaufmanni* are elongate (Figure 1) relative to those of most other sturgeons (e.g., *A. brevirostrum*, Figure 2), which are typically shorter and broader elements (other exceptions include *H. huso* and *A. ruthenus*, see Discussion). The border rostral bones of most sturgeons are also small irregularly shaped elements that blend into the dorsal rostral series (Figure 2). In both *A. stellatus* and *P. kaufmanni*, however, these bones are quite distinct from the dorsal rostral bones (Figure 1). As in other sturgeons they are irregular in shape, although they tend towards being rectangular (as was noted for *Pseudoscaphirhynchus* by Findeis 1997), and differ noticeably from those of other sturgeons (Figure 2).

#### Shape of jugal

The jugal of sturgeons is the ventral-most ossification of the infraorbital sensory canal, which is continuous with the rostral sensory canal. In most sturgeon species the jugal has horizontal and vertical arms in lateral view (Figure 2b). Also, the horizontal arm does not typically reach the level of the nasal (olfactory) capsule anteriorly (Findeis 1997), although it may lie partially underneath the posterior portion of the nasal capsule (Figure 2). In contrast the anterior portion of the jugal lies completely under the nasal capsule and actually may extend slightly anterior to it in *A. stellatus* and *P. kaufmanni* (Figure 1b and e). In ventral view, there is a pronounced median flange of the jugal in

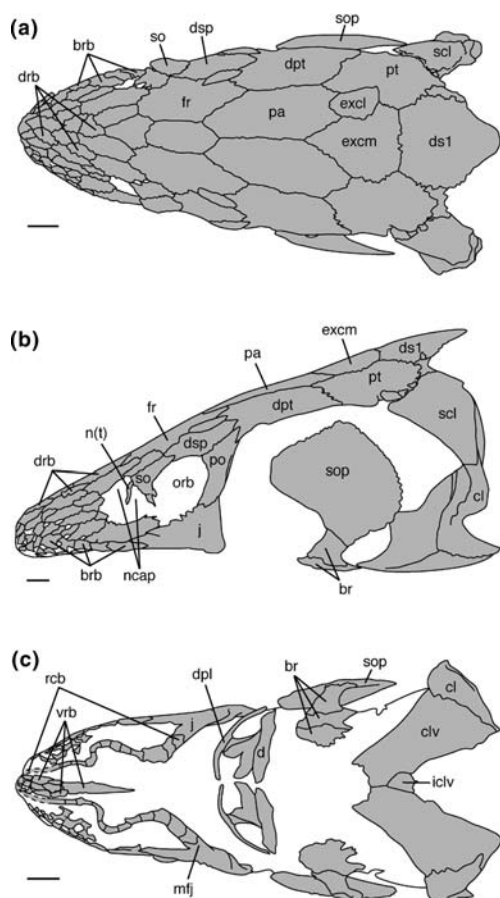


Figure 2. Semi-schematic illustrations of the skull of an adult specimen of *Acipenser brevirostrum* (based on FMNH 112212) shown in (a) dorsal, (b) lateral, and (c) ventral views. Anterior facing left. Scale bars equal 10 mm. Abbreviations as in Figure 1.

most sturgeons (Figure 2c), which carries the infraorbital sensory canal as it enters the bony ossicles of the rostral sensory canal. In contrast, the jugal of *A. stellatus* and *P. kaufmanni* lacks a median flange in ventral view (Figure 1c and f).

#### Rostral canal bones

The rostral canal bones form a series of bony elements surrounding the anterior continuation of the infraorbital sensory canal after it exits the jugal and becomes the so-called rostral sensory canal. Both *A. stellatus* and *P. kaufmanni* have the basic pattern of the rostral canal bones found in other sturgeons (for illustrations and discussion of their

ontogeny in *A. brevirostrum* and *A. oxyrinchus*, see Hilton 2002). Briefly, after exiting the jugal, the rostral canals course anteriorly, looping medially lateral to the barbels. In *Scaphirhynchus*, this portion of the canal loops much further medially before curving lateral to the barbels (personal observation). The canals then again turn and course anteriorly, parallel to the ventral rostral bones. At the tip of the snout, the left and right rostral sensory canals meet in a commissure. Lateral to this commissure there are triradiate lateral commissural bones (Hilton 2002). In both *A. stellatus* and *P. kaufmanni* the sensory canal and its ossifications positioned between the lateral commissural bones loop slightly posteriorly (Figure 1).

#### Ventral rostral bones

The ventral rostral bones of sturgeons form a series of bones in the ventral midline of the snout. The posterior-most ventral rostral bone in both *A. stellatus* (Figure 1c) and *P. kaufmanni* (Figure 1f) is a broad, elongate element that is over half the length of the total length of the series.

#### Discussion

The similarities between the skulls of *A. stellatus* and *P. kaufmanni* described above include several putatively derived traits that seemingly offer morphological evidence in support of Birstein et al.'s (2002) hypothesis of a close relationship between the two. However, I report these observations with some caveats.

All specimens of *A. stellatus* that I examined are juveniles, which may have a substantial effect on interpretation of the observations. For example, the presence of enlarged thorn-shaped spines on the dermal bones in the skull is more wide spread in the family Acipenseridae than considered by Findeis (1997), but this presence is ontogenetically variable. *Huso* also bears spines on the dermal skull roof and supracleithrum similar to those found in *A. stellatus*, *Pseudoscaphirhynchus*, and *Scaphirhynchus* (see below). These are, however, lost during ontogeny in *Huso* (present only as ridges on most bones in the 228 mm SL specimen that I examined). Well-developed spines are

present, particularly on the posterior skull bones (e.g., frontals and parietals), in the 225 mm SL specimen of *A. stellatus* that I examined; the spines on the dorsal rostral bones are smaller at all sizes (Figure 1b). In some species of *Acipenser* spines are never associated with the dermal bones of the skull roof at any stage in ontogeny (e.g., *A. brevirostrum*, personal observation). Adult specimens of *A. stellatus* need to be examined in the future.

On the other hand, it is possible, if not likely, that ontogenetic trajectories and rates will vary between different species of sturgeons, and therefore the adult condition of one taxon may be 'equivalent' to the juvenile condition of another, at least for some characters. During the ontogeny of the skull of sturgeons, the border rostral bones and dorsal rostral bones, which initially develop as two distinct series of elements (Figure 3), become continuous with each other. For example, the dorsal rostral bones are well developed but the border rostral bones are just beginning to develop in the specimen of *Huso* illustrated by Kittary (1850; see Figure 4b), which is presumably a large juvenile or adult (although no length was provided); no border rostral bones are present in specimens up to at least 228 mm SL (personal observation). In contrast, the border rostral bones begin to develop in *A. brevirostrum* by 96 mm SL and become continuous with the dorsal rostral bones as large juveniles between 384 and 472 mm SL (Hilton, Grande & Bemis, unpublished data). Although adult specimens of *A. stellatus* were not available for this study, the border rostral and dorsal rostral bones are in contact with each other in all specimens that I examined. This suggests that the observations made on the available juvenile specimens can be, for some characters at least, compared directly with specimens of other species that are at later stages of ontogeny. Still, in the future it will be important to further evaluate the characteristics described in this paper in adult specimens of *A. stellatus*.

One of the specimens of *P. kaufmanni* that I examined (MCZ 27653) was also used by Findeis (1993, 1997), who reported it to be a small adult male of the dwarf form. It cannot be determined based on recent descriptions (e.g., using coloration, Salnikov et al. 1996) if the other two specimens that I examined (AMNH 97566, INHS 64426) are of the dwarf or normal form, although the skeletal morphology was found to be consis-

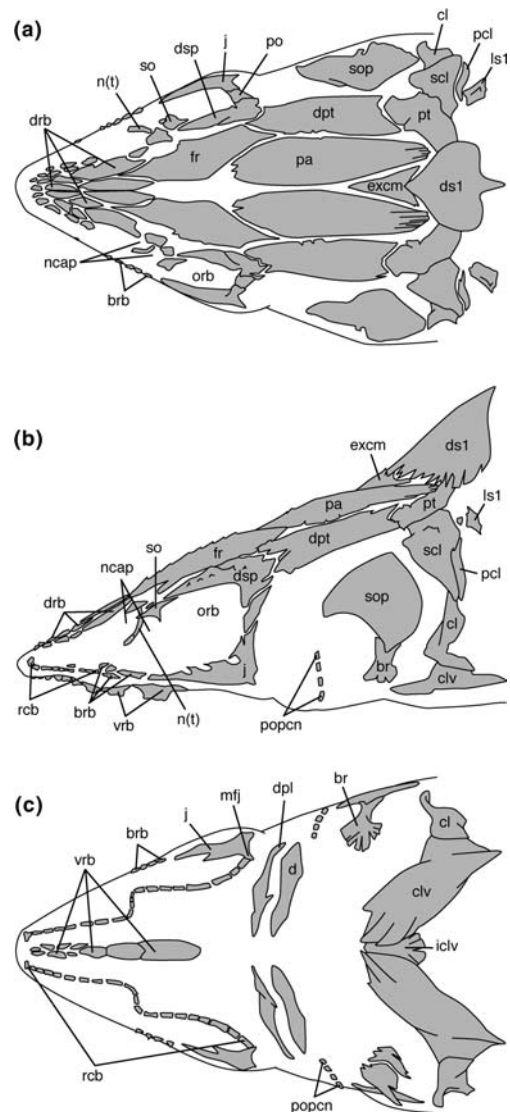


Figure 3. Semi-schematic illustrations of the skull roof of a 75 mm specimen of *Acipenser ruthenus* in (a) dorsal (b) lateral, and (c) ventral views (redrawn and modified from Jollie 1980: Figures 1–3). Anterior facing left. Abbreviations as in Figure 1.

tent between all three specimens. In the future, it will be important to determine if there is any discrete skeletal variation between the dwarf and normal forms. A review of the genus based on external morphology is being made by Mayden & Kuhajda (Kuhajda personal communication 2004).

The skull of *A. stellatus* is remarkable and very distinctive among sturgeons due to its elongate,

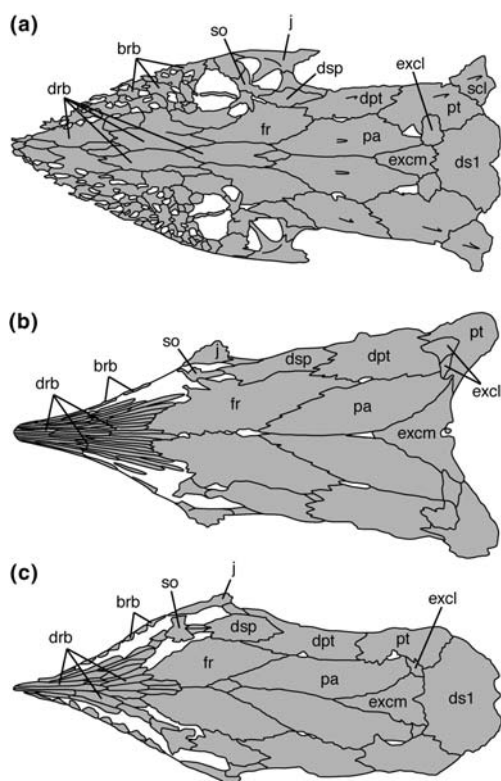


Figure 4. Semi-schematic illustrations of the skull roof of (a) *Scaphirhynchus platorhynchus* (redrawn and modified from Findeis, 1993: Figure 15), (b) *Huso huso* (redrawn and modified from Kittary, 1850: plate 7, Figure 7), and (c) *Acipenser ruthenus* (redrawn and modified from Kittary, 1850: plate 7, Figure 1). Anterior facing left. Abbreviations as in Figure 1.

narrow snout, although there is much variation in snout shape between and within sturgeon species. The elongate snout of *A. stellatus* stands in contrast to the shorter and much broader snout of *P. kaufmanni*. Findeis (1997) used *P. kaufmanni* as an exemplar of the genus. However, there is substantial variation in the head shape within the genus (Berg 1962). For instance, the head of *P. hermanni* is much narrower and more elongate than that of *P. kaufmanni* and there are three distinct forms of *P. fedtschenkoi*: a long rostrum morph that superficially resembles *P. hermanni*; a short rostrum morph that resembles *P. kaufmanni*; and an intermediate form (Berg 1962, see Figures in Birstein 1997). Specimens of *P. hermanni* and *P. fedtschenkoi* were not available for this study and both are critically endangered and very rare in collections (e.g., Birstein & Bemis 1997). How the

shape variation found in *Pseudoscaphirhynchus* correlates to skeletal variation is unknown but will be important for interpreting the similarities that are shared between specimens of *A. stellatus* and *P. kaufmanni*.

The dorsal surface of the snout of sturgeons is armored by a mosaic of anamestic bones (i.e., space-filling bones that form independent of the lateral line system, see Hilton & Bemis 1999 for discussion). Findeis (1993, 1997) recognized two distinct series of bones on the dorsal surface of the snout: (1) dorsal rostral bones, covering much of the dorsal surface of the snout; and (2) border rostral bones, which are positioned along the posterolateral margins of the snout. Dorsal rostral bones appear earlier in ontogeny than border rostral bones (Findeis 1993; also personal observation) and initially form in the midline of the snout (Figure 3). Although Findeis (1993, 1997) used an ontogenetic criterion to distinguish between the two series, he noted that the fields of ampullary organs on the lateral surfaces of the snout also demarcated their boundary. In *Scaphirhynchus* and *Pseudoscaphirhynchus*, Findeis (1997: character 40) recognized a third series of rostral bones, the so-called ampullary bones, that form around the ampullary organs (see his Figure 18); these develop at the same time as the more posterior border rostral bones (Findeis 1997: 107). However, in adult specimens of *Acipenser* the dorsal rostral bones and border rostral bones are continuous, with bony plates found throughout the field of ampullary organs (Figure 2). This suggests that either: (1) ‘ampullary bones’ are present in *Acipenser* as well; or, and more likely, (2) there is little, if any, reason to distinguish ‘ampullary bones’ from border rostral bones. I therefore recognize two distinct series of bones (the dorsal rostral bones and the border rostral bones, including the ampullary bones of Findeis 1993, 1997), with the acknowledgement that the boundary between the two may become blurred in the adult skull.

Findeis (1997) reported border rostral bones as absent in *Huso*, although this is likely due to the early ontogenetic stage of his specimens (e.g., the small cleared and stained specimen that I examined looks exactly like Findeis’ figured specimen). Kittary (1850) illustrated a specimen of *H. huso* and showed bony elements on the lateral edges of

the snout, which presumably are border rostral bones (Figure 4b). I observed traces of border rostral bones in the thickened skin of the snout on an 825 mm SL alcohol specimen (FMNH 76855), although this needs to be confirmed on additional dry skeletal or cleared and stained material.

The dorsal rostral bones of most sturgeons are short, irregularly shaped blocky elements (Figure 2), while those of *A. stellatus* and *P. kaufmanni* are more elongate (Figure 1). *H. huso* and *A. ruthenus* also have elongate dorsal rostral bones (Figure 4b and c), even more so than either *A. stellatus* or *P. kaufmanni*. The dorsal rostral bones of the specimen of *A. ruthenus* illustrated by Jollie (1980) are not as elongate as those depicted in other illustrations of this taxon (cf., Figures 3 and 4c). Elongate dorsal rostral bones are also found in polyodontids (e.g., Grande & Bemis 1991: Figures 6 and 7 for *Polyodon*; Grande et al. 2002: Figures 7 and 8 for †*Protopsephurus*; labeled as a, b, and c bones).

The heavily ornamented dermal bones of the skull roof, pectoral girdle, and the scutes of most adult sturgeons are relatively flat or slightly keeled bones. Findeis (1997: character 41) considered the presence of spines on the dermal bones of the skull and the supracleithrum to be a synapomorphy of *Scaphirhynchus* and *Pseudoscaphirhynchus*. However, during the juvenile stages of ontogeny in many species of sturgeons (including species of *Acipenser* and *Huso*, personal observation), these elements support sharp, spiny processes that are lost later in ontogeny. In some taxa spines may persist on the scutes of larger juvenile specimens (e.g., *A. medirostris*, personal observation). Cranial spines persist in adults of *Scaphirhynchus* as small, very sharp processes on the dorsal rostral bones, parietals, posttemporals, and supracleithra (Figure 4a; see also Mayden & Kuhajda 1996 and Findeis 1997). In adults of some species of *Pseudoscaphirhynchus* (Figure 1) there are large thorn-shaped spines, termed 'spikes' by Findeis (1997: character 55). There is significant taxonomic variation in the spines on the dermal skull bones in the genus *Pseudoscaphirhynchus* (Berg 1962). For example, spines are only variably present in *P. hermanni* and are completely lacking in *P. fedtschenkoi*. Both ontogenetic and taxonomic variation of these spines needs to be taken into account in future morphological and systematic analyses.

In most sturgeons, the confluence of the posttemporal, supratemporal, and otic sensory canals is in the posttemporal bone. Findeis (1997: character 56) considered the condition of having these sensory canals meeting in the lateral extrascapulars to be a synapomorphy of *Pseudoscaphirhynchus*. The presence of this condition also in *A. stellatus* therefore suggests a close relationship between these taxa. This character should be checked on more specimens of *A. stellatus* and in a broader sample of taxa.

The presence of an enlarged jugal that completely undercuts the nasal capsule and lacks a median flange was considered to be a synapomorphy of *Pseudoscaphirhynchus* by Findeis (1997: character 57). The presence of a very similarly shaped jugal in *A. stellatus* as well suggests a close relationship between the two taxa.

In most sturgeons that I examined, the rostral canal bones between the lateral commissural bones follow the tip of the snout (e.g. *A. brevirostrum* and *A. oxyrinchus*, Hilton 2002; *S. albus*, personal observation). In contrast, in *A. stellatus*, *P. kaufmanni* (Figure 1), and *H. huso* (personal observation) these bones loop slightly posteriorly. This character needs to be checked on a wider survey of taxa.

The series of ventral rostral bones in sturgeons is variable in number, size, and arrangement of individual elements. Findeis (1997: character 30) concluded that the presence of a pair of elements in a posterior position within the series (present in polyodontids and *Huso*) was plesiomorphic for Acipenseridae and that a single median posterior element was a synapomorphy of *Acipenser* + *Scaphirhynchinae*. In the cleared and stained specimen of *H. huso* that I examined, there is a single posterior ventral rostral bone, suggesting that this character is polymorphic in this species. The condition in the basal polyodontid †*Protopsephurus* is unclear, although one specimen illustrated by Grande et al. (2002: Figure 8) appears to have a pair of elements in this position; new specimens, however, are needed to clarify the condition in this taxon.

The condition of having the posterior most ventral rostral bone about two-thirds of the length of the series was considered to be a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus* by Findeis (1997: character 42). Findeis (1997: 108)

acknowledged that this is a subjective character, but noted that ‘in *Acipenser* they are not as dominantly elongate and are thin.’ In several specimens of *A. brevirostrum* that I examined (Figure 2), however, the posterior-most ventral rostral bone is also the dominant element of the series, with the more anterior bones collectively comprising less than half of the length of the series. In *Huso* and most species of *Acipenser*, the posterior-most ventral rostral bone is narrow and strongly keeled (e.g., Hilton 2002: Figure 1b), although it can also be a relatively small, blocky element (Figure 3c). *Acipenser stellatus* has the combination of an elongate posterior ventral rostral bone that is broad and flat (Figure 1), which is similar to the condition found in *Scaphirhynchus* (personal observation) and *Pseudoscaphirhynchus* (Figure 1f).

### Conclusions

Findeis’ (1993, 1997) research resulted in many advances in our knowledge of the comparative osteology and systematic relationships of sturgeons, and stands as the most extensive and critical survey of morphological characters for this group to date. With such a broad scale work, however, there undoubtedly will be errors of omission (e.g., taxon sampling). Many of the characteristics that I discovered in *A. stellatus*, as discussed above, were considered to be synapomorphies of the genus *Pseudoscaphirhynchus* by Findeis (1997). In future morphological analyses of the phylogenetic systematics of sturgeons it will be important to reconsider these characters in light of the observed similarities (some putatively derived) in the skulls of *P. kaufmanni* and *A. stellatus*, which appear to support a close relationship between these two species. In addition, the phylogenetic analysis that originally suggested this relationship (Birstein et al. 2002) was based on relatively short molecular sequences. This data set must be added to and reanalyzed to further test the robustness of this taxonomic grouping.

Molecular and morphological data are often held as competing sources of data for systematic analyses, and comparisons of results are often coined in an ‘us versus them’ framework. This is unfortunate as there is much to both and com-

parisons should be instead discussed as having a reciprocal relationship. As shown by this example from the skulls of these two sturgeon species, novel sister-group hypotheses based on molecular data can serve as a useful impetus to reexamine anatomical features to see if there is morphological support for such hypotheses. It also shows that there is much still to be learned from morphology. Morphology generally, and mistakenly, has been held to be phylogenetically uninformative at low levels of phylogeny (i.e., within a genus), particularly in morphologically conservative groups such as sturgeons. However, there is great systematic potential to the detailed anatomical study of specimens of all taxa of a group, but this will only be discovered with a renewed, active, and continued study of comparative anatomy.

### Acknowledgements

For loan of and permission to prepare specimens in their care and help with specimens, I thank: Scott Schaeffer, Barbara Brown, and Radford Arrindell (AMNH, Ichthyology); Bill Eschmeyer and Dave Catania (CAS); Mark Westneat, Mary Anne Rogers, and Phil Willink (FMNH); Larry Page (formerly INHS); Karel Liem, Karsten Hartel, and Chris Kenaley (MCZ – Fishes); William E. Bemis (UMA); Gerald Smith, William Fink, and Douglas Nelson (UMMZ). I thank William E. Bemis, Lance Grande, and two anonymous reviewers for their helpful comments on earlier versions of the manuscript. This research has been funded by the National Science Foundation (NSF) DEB-0128929 (to Hilton, Grande & Bemis).

### References

- Artyukhin, E.N. 1995. On biogeography and relationships within the genus *Acipenser*. *Sturgeon Quart.* 2: 6–8.
- Bailey, R.M. & F.B. Cross. 1954. River sturgeons of the American genus *Scaphirhynchus*: characters, distribution, and synonymy. *Pap. Michigan Acad. Sci.* 39: 169–208.
- Bemis, W.E., E. K. Findeis & L. Grande. 1997. An overview of Acipenseriformes. *Environ. Biol. Fish.* 48: 25–72.
- Bemis, W.E. & B. Kynard. 1997. Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Environ. Biol. Fish.* 48: 167–184.

- Berg, L.S. 1948. Freshwater Fishes of the U.S.S.R. and Adjacent Countries, Vol. 1, 4th edition, improved and augmented. Izdatel'stvo Akademii Nauk SSSR, Moscow, Russia. 466 pp. (in Russian, an English translation was published as Berg 1962).
- Berg, L.S. 1962. Freshwater Fishes of the U.S.S.R. and Adjacent Countries, Vol. 1, 4th edition, improved and augmented. Israel Program for Scientific Translations, Jerusalem, Israel. 505 pp. (an English translation of Berg (1948), published for the National Science Foundation, Washington, D.C.).
- Birstein, V.J. 1997. Threatened fishes of the world: *Pseudoscaphirhynchus* spp. (Acipenseridae). *Environ. Biol. Fish.* 48: 381–383.
- Birstein, V.J. & W.E. Bemis. 1997. How many species are there within the genus *Acipenser*? *Environ. Biol. Fish.* 48: 157–163.
- Birstein, V.J. & R. DeSalle. 1998. Molecular phylogeny of Acipenserinae. *Mol. Phylogenet. Evol.* 9: 141–155.
- Birstein, V.J., R. Hanner & R. DeSalle. 1997. Phylogeny of the Acipenseriformes: cytogenetic and molecular approaches. *Environ. Biol. Fish.* 48: 127–156.
- Birstein, V.J., P. Doukakis & R. DeSalle. 2002. Molecular phylogeny of Acipenseridae: nonmonophyly of Scaphirhynchinae. *Copeia* 2002: 287–301.
- Bogdanov, M. 1874. A report on a newly discovered acipenserid fish at the meeting of Zoological Section. *Trudy Sankt-Peterburgskogo Obshchestva Ispytatelei Prirody* 5: 48. (in Russian).
- Dingerkus, G. & L.D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *J. Stain Technol.* 52: 229–232.
- Findeis, E.K. 1993. Skeletal anatomy of the North American shovelnose sturgeon *Scaphirhynchus platyrhynchus* (Rafinesque, 1820) with comparisons to other Acipenseriformes. Ph.D. Thesis, University of Massachusetts, Amherst. 444 pp.
- Findeis, E.K. 1997. Osteology and phylogenetic relationships of recent sturgeons. *Environ. Biol. Fish.* 48: 73–126.
- Fontana, F., J. Tagliavini & L. Congiu. 2001. Sturgeon genetics and cytogenetics: recent advancements and perspectives. *Genetica* 111: 359–373.
- Grande, L. & W.E. Bemis. 1991. Osteology and phylogenetic relationships of fossil and Recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. *Society of Vertebrate Paleontology Memoir* 1: 1–121. (supplement to *J. Vertebr. Paleontol.* 11).
- Grande, L. & W.E. Bemis. 1996. Interrelationships of Acipenseriformes, with comments on 'Chondrostei.' pp. 85–115. *In: M.L.J. Stiassny, L.R. Parenti & G.D. Johnson (eds.) Interrelationships of Fishes*, Academic Press, San Diego, California, U.S.A.
- Grande, L., F. Jin, Y. Yabumoto & W.E. Bemis. 2002. †*Protopsephurus liui*, a well-preserved primitive paddlefish (Acipenseriformes: Polyodontidae) from the Early Cretaceous of China. *J. Vertebr. Paleontol.* 22: 209–237.
- Hensel, K. & J. Holčík. 1997. Past and current status of sturgeons in the upper and middle Danube River. *Environ. Biol. Fish.* 48: 185–200.
- Hilton, E.J. 2002. Observations on rostral canal bones of two species of *Acipenser* (Actinopterygii, Acipenseriformes). *Copeia* 2002: 213–219.
- Hilton, E.J. 2004. The caudal skeleton of Acipenseriformes (Actinopterygii: Chondrostei): recent advances and new observations. *In: G. Arratia, M.V.H. Wilson & R. Cloutier (eds.) Recent Advances in the Origin and Early Radiation of Vertebrates*, Verlag Dr. Pfeil, Munich, Germany. (in press)
- Hilton, E.J. & W.E. Bemis. 1999. Skeletal variation in shortnose sturgeon (*Acipenser brevirostrum*) from the Connecticut River: implications for comparative osteological studies of fossil and living fishes. pp. 69–94. *In: G. Arratia & H.-P. Schultze (eds.) Mesozoic Fishes 2 – Systematics and Fossil Record*, Verlag Dr. Pfeil, Munich, Germany.
- Jollie, M. 1980. Development of head and pectoral girdle skeleton and scales in *Acipenser*. *Copeia* 1980: 226–249.
- Kittary, M. 1850. Recherches anatomique sur les poissons du genre *Acipenser*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 23: 389–445.
- Ludwig, A., B. May, L. Debus, I. Jenneckens II. 2000. Heteroplasmy in the mtDNA control region of sturgeon (*Acipenser*, *Huso* and *Scaphirhynchus*). *Genetics* 156: 1933–1947.
- Ludwig, A., N.M. Belfiore, C. Pitra, V. Svirsky & I. Jenneckens II. 2001. Genome duplication events and functional reduction of ploidy levels in sturgeon (*Acipenser*, *Huso* and *Scaphirhynchus*). *Genetics* 158: 1203–1215.
- Mayden, R.L. & B.R. Kuhajda. 1996. Systematics, taxonomy, and conservation status of the endangered Alabama sturgeon, *Scaphirhynchus suttkusi* Williams and Clemmer (Actinopterygii, Acipenseridae). *Copeia* 1996: 241–273.
- Pallas, P.S. 1771. *Zoographia Rossa-Asiatica, sistens omnium animalium in extenso imperio Rossico et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones anatomem atque iconed plurimorum*, III. Petropoli.
- Salnikov, V.B., V.J. Birstein & R.L. Mayden. 1996. The contemporary status of the two Amu Darya River shovelnose sturgeons, *Pseudoscaphirhynchus kaufmanni* and *P. hermanni*. *Sturgeon Quart.* 4: 10–14.
- Shubina, T.N., A.A. Popova & V.P. Vasil'ev. 1989. *Acipenser stellatus* Pallas, 1771. pp. 395–443. *In: J. Holčík (ed.) The Freshwater Fishes of Europe. Vol. 1, Part II. General Introduction to Fishes, Acipenseriformes*, AULA-Verlag, Wiesbaden, Germany.
- Zholdasova, I. 1997. Sturgeons and the Aral Sea ecological catastrophe. *Environ. Biol. Fish.* 48: 373–380.