Sturgeon rivers: an introduction to acipenseriform biogeography and life history

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Synopsis

We present an overview of the global distribution of all 27 living species of Acipenseriformes in an attempt to understand their biogeographic history and the range of life history patterns displayed by different species. Our biogeographic analysis (based on the most recent phylogenetic analysis including fossil Acipenseriformes) suggests that Acipenseriformes originated in Europe, and that early diversification took place in Asia. Acipenseriformes do not have a common life history; variation within and between species is the rule rather than exception. The few relatively well-known case studies (e.g., Caspian Sea sturgeons, European Atlantic sturgeons in the Gironde system, and shortnose and North American Atlantic sturgeons in rivers of the east coast of America) greatly influence what we think we know about sturgeon biology. Our present level of phylogenetic understanding does not allow us to determine whether anadromy or potamodromy is the plesiomorphic life history pattern for Acipenseriformes. We propose that rivers in which spawning occurs must be the central unit for biogeographic analysis of living Acipenseriformes. After mapping these rivers, we recognized nine biogeographic provinces for acipenseriforms. Some repeated historical patterns emerge from this analysis, but, again, we are limited by our current understanding of phylogenetic relationships within the genus *Acipenser* in particular. Distribution and biogeographic data are central to deciding where to make new efforts to update existing status information for acipenseriform species. We single out a widely ranging and highly variable species, *Acipenser ruthenus*, as particularly intriguing, for it spans three of our nine biogeographic provinces, and apparently has different life history patterns in different river systems. Finally, we note new areas in need of basic research, particularly the need for more detailed descriptions and analyses of life histories of different populations of sturgeons.

Introduction

This paper attempts a new approach to the global biogeography of Acipenseriformes, although we admit from the outset that this is daunting topic be-cause in its most comprehensive form, such an analysis concerns the history of the entire Holarctic region for the last 200 million years. Still, this topic is important because it lies at the interface between basic research on Acipenseriformes and practical

steps needed to plan for sturgeon and paddlefish conservation (e.g. Rochard et al. 1990). Our review has several explicit purposes.

First, although Acipenseriformes has long been regarded as a biogeographically interesting group, the phylogeny necessary to study this question has yet to be assembled. Comprehensive phylogenetic understanding, particularly concerning relationships within the genus *Acipenser*, still eludes us. Complicating factors include high levels of ontogenetic and individual variation, hybridization, and extirpation of many populations within the historic ranges of certain species (Bemis et al. 1997b this volume). Some key intergeneric relationships are equally problematic. Results from karyological and molecular phylogenetic approaches (Birstein & DeSalle 1997) place the two species of *Huso* within *Acipenser* (as sister taxa to *A. ruthenus*) whereas osteological data place *Huso* as the sister taxon of all other sturgeons (Findeis 1997 this volume). Future updating of our interpretations is inevitable as our phylogenetic insight into Acipenseriformes improves.

Second, a detailed understanding of the geographic distribution of acipenseriforms is complicated by the wide ranges historically reported for adults of certain species, so that a more restrictive and useful definition of species ranges is required. We explicitly propose the concept that rivers in which spawning occurs should be the central unit of analysis for interpreting the biogeographic ranges of acipenseriform species (and other groups containing anadromous species). We provide a global summary of these rivers, but given the scope of the question (i.e., identify all rivers in the world in which sturgeons or paddlefish historically spawned) it is certain that more exhaustive analyses will yield additional rivers. It may also be necessary to find more restrictive ways to define our concept of spawning rivers, and perhaps we will succeed in provoking such a response.

Third, Acipenseriformes exhibit a broad array of spawning and feeding migratory patterns, with some species utilizing fresh water exclusively, others fresh water and estuarine environments, while others span the range from fresh water to fully marine environments. Different life history patterns have certainly influenced the biogeography of Acipenseriformes, although at present, we can do little more than catalogue them, because no one understands the genetic bases or adaptive significance of these patterns. An important but still neglected approach to studying the evolution of different life history patterns of acipenseriforms are ideas of Balon (1990 and references therein) that emphasize the importance of altricial or precocial patterns of development. This is likely to prove a productive approach, for size and yolk content differences are known for different species of sturgeons, though they have not yet been correlated with different patterns of life history.

Fourth, we want to introduce the remaining papers in the status part of this collection (Bemis et al. 1997a), which detail aspects of life history and biogeography for many of the extant species of Acipenseriformes. One need that emerges immediately is for more detailed river surveys and life history studies of virtually all species of sturgeons, particularly those from geographically remote regions in Asia and northern North America. These surveys need to be done with the most advanced technologies available, including in particular telemetry of individuals to determine life history patterns (Kynard 1997 this volume) and molecular based identification of populations within and between river systems (Wirgin et al. 1997 this volume).

Basic background

Biogeographic observations

We begin with three general biogeographic observations:

1. With the exception of the Pearl River in China, all spawning rivers used by Acipenseriformes lie entirely within the north temperate zone of Asia, Europe or North America, although individual adults have been taken at sea south of the Tropic of Cancer. All known fossil Acipenseriformes are also from north temperate localities (Grande & Bemis 1991, Jin 1995, Bemis et al. 1996 this volume, Grande & Bemis 1997). The absence of Acipenseriformes from tropical rivers is proba-

bly related to thermal requirements for maturation and early development, which generally need temperatures below 20° C (e.g., Artyukhin 1988, Dettlaff et al. 1993).

2. With the exception of *Acipenser ruthenus*, which lives in both Europe and Asia, no species within Acipenseriformes is known to spawn in rivers on two continents and few species spawn in more than two of the biogeographic provinces that we define below. This situation is unlike that, for example, for salmonids of the North Pacific Ocean, several of which spawn in both North American and Asian rivers (e.g., chum salmon, *Oncorhynchus keta* spawns in rivers along the east and north coast of Asia as well as the west coast of America, Salo 1991). Our interpretation concerning sturgeons and continents is subject to falsification, but all detailed work to date suggests that this pattern will hold true. For instance, *Acipenser medirostris* (west coast of North America) and *A. mikadoi* (Sea of Okhotsk and Sea of Japan) were at various times considered to be conspecific, but recent genetic and molecular data confirm that they are distinct species (Birstein 1993b, Birstein et al. 1997 this volume).

3. Much of the historic work concerning the distribution of different species of sturgeons (e.g., Berg 1948a, 1948b, 1959) predates contemporary concepts of continental drift. More recent accounts (e.g., Berra 1981, Hocutt & Wiley 1986, Bănărescu 1990, 1992, 1995) predate contemporary phylogenetic interpretations of acipenseriforms. If one restricts analysis to †Chondrosteidae, †Peipiaosteidae, Polyodontidae and the tribe Scaphirhynchini, all of which are small groups with intriguing but fairly simple biogeographic distributions (Grande & Bemis 1991, Jin 1995, Bemis et al. 1997b), then historical biogeography is easy to contemplate. The widely ranging genus *Acipenser*, however, imposes many difficult biogeographic questions, which is why it is a focus in our present analysis.

Life history observations

We make seven general observations about acipenseriform life history and spawning biology:

1. Acipenseriformes spawn repeatedly, but most females do not spawn annually. This pattern resembles that for anadromous fishes such as shad (*Alosa*; e.g., Leggett 1976) but is different from that typical for Pacific salmonids (*Oncorhynchus*; see Groot & Margolis 1991).

2. All acipenseriforms spawn in freshwaters of low salt content (0–0.1‰) even though adults of some species may migrate to feed in estuarine or brackish waters (approximately 14 to 27‰, Pearse & Gunter 1957) or seawater (35‰).

3. The timing of spawning for Acipenseriformes is highly variable, equaling or exceeding the variability found in any other group of fresh water or diadromous fishes. They spawn in all seasons and in highly variable conditions of water flow and temperature.

4. Characteristics of spawning migrations vary greatly among Acipenseriformes in total distance migrated, the distance upstream from salt water, etc. Several evolutionary scenarios and sets of terminology have been proposed to describe these variations in spawning migration pattern (reviewed below).

5. The few studies done to date indicate that the availability of suitable spawning habitat is critical to reproductive success. Spawning sites are characterized by areas with hard substrate of gravel to boulder size rocks containing many crevices. The water velocity near the bottom is typically moderate (Kynard 1997 this volume).

6. Annual spawning success and recruitment is highly unpredictable, and may be zero if river flows are too high during the brief reproductive window of females. High flows, whether caused by natural phenomena or controlled releases by dams, can create high bottom velocities that preclude or greatly reduce spawning success (Kynard 1997 this volume).

7. A particular spawning site is usually used from year to year. Such site fidelity might derive either from the particular characteristics of the site or from homing. Sturgeons are believed to have
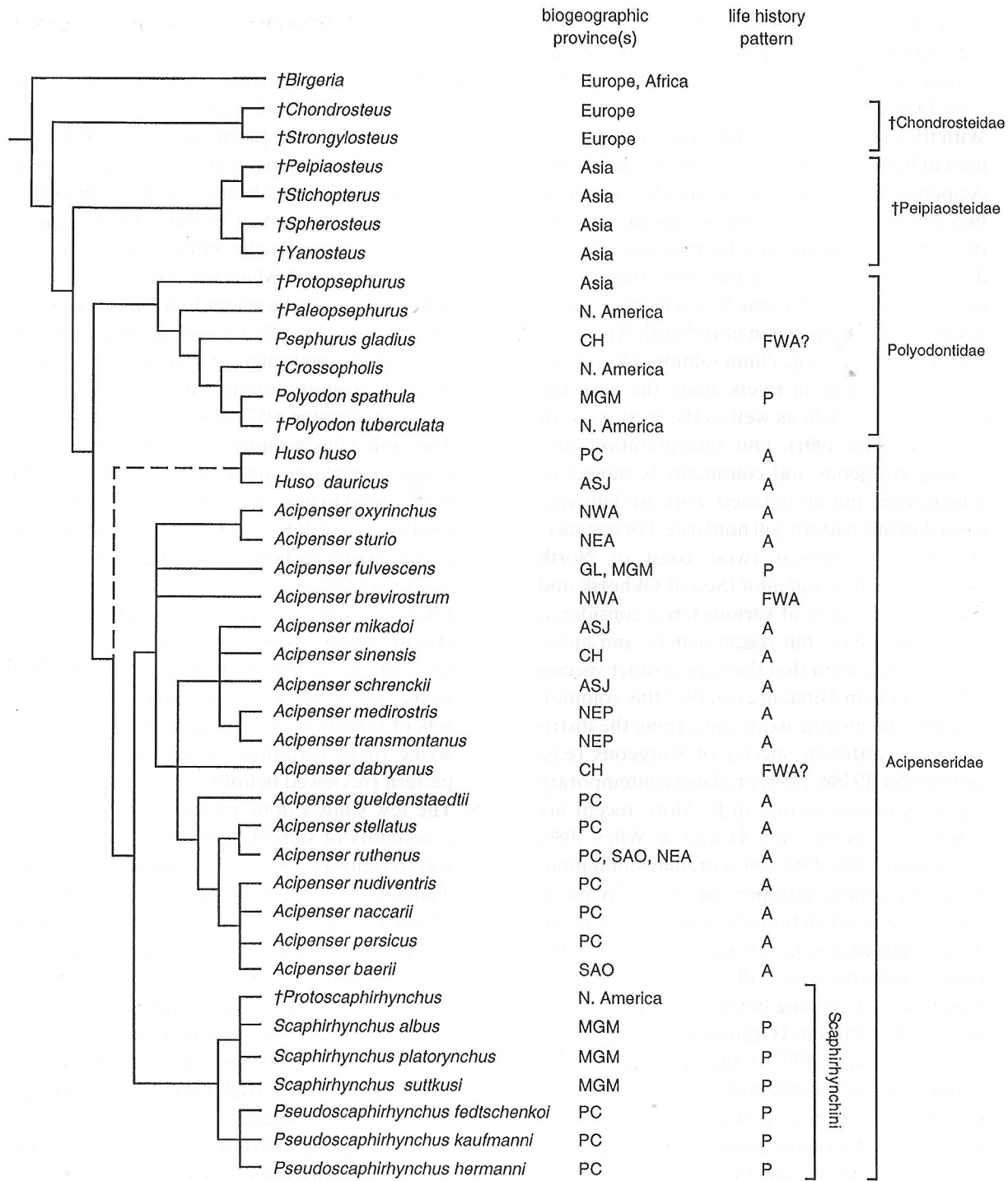
Figure 1. Tree suggesting possible evolutionary relationships among fossil and recent acipenseriforms. See text for explanation and discussion. Biogeographic areas are keyed to the map in Figure 3, and our scheme of provinces is explained in the biogeography section of the text. Fossils are preceded by dagger symbols; continents from which fossils were recovered are indicated. Life history pattern is keyed as follows: A – anadromous; P – potamodromous; FWA – freshwater amphidromous. These terms are defined in the life history section of the text. Data for relationships among acipenserines (*Acipenser* plus *Huso*) based on preliminary analyses by Birstein & DeSalle (1997).

strong homing capabilities, although direct evidence for this is only recently available, and the subject needs additional research (Waldman et al. 1996a,b, Wirgin et al. 1997 this volume). If homing proves to be as important as currently expected, then it might be the proximate explanation for the existence of different morphs or races within species, which is a particularly common pattern in the family Acipenseridae.

Species and evolutionary relationships

Figure 1 presents a tree of the well-preserved fossil and all living species of acipenseriforms. It includes †Birgeria, which was considered to be a closely related outgroup for Acipenseriformes by Bemis et al. (1997b this volume). Next to each extant taxon in Figure 1, we list the biogeographic province(s) in which it occurs and its supposed life history pattern (biogeographic provinces and life history patterns are described further below). For extinct taxa in Figure 1 (indicated with dagger symbols), we identify the continents from which the fossils were recovered. Life history cannot be assessed with certainty in fossils.

Our goal in presenting the tree in Figure 1 is not to present a single preferred hypothesis of relationships among acipenseriform taxa but rather to organize biogeographic and life history information. It should be regarded as a heuristic synthesis of formal phylogenetic analyses presented in this volume (Bemis et al. 1997b, Findeis 1997, Birstein et al. 1997) and elsewhere (Artyukhin 1995, Jin 1995, Grande & Bemis 1996). Some nodes in this tree are corroborated by all contemporary phylogenetic analyses. For example, we are now very confident about the placement of †Chondrosteidae as the sister taxon of all other Acipenseriformes (Grande & Bemis 1996). Both Polyodontidae and Acipenseridae are now considered to be monophyletic families (contrary to the view of Gardiner 1984; see Grande & Bemis 1991), and all available data support our concept of Acipenseroidei, a group containing Polyodontidae and Acipenseridae (see Grande & Bemis 1991, Bemis et al. 1997b for detailed comments on the strength of this node). Rela-
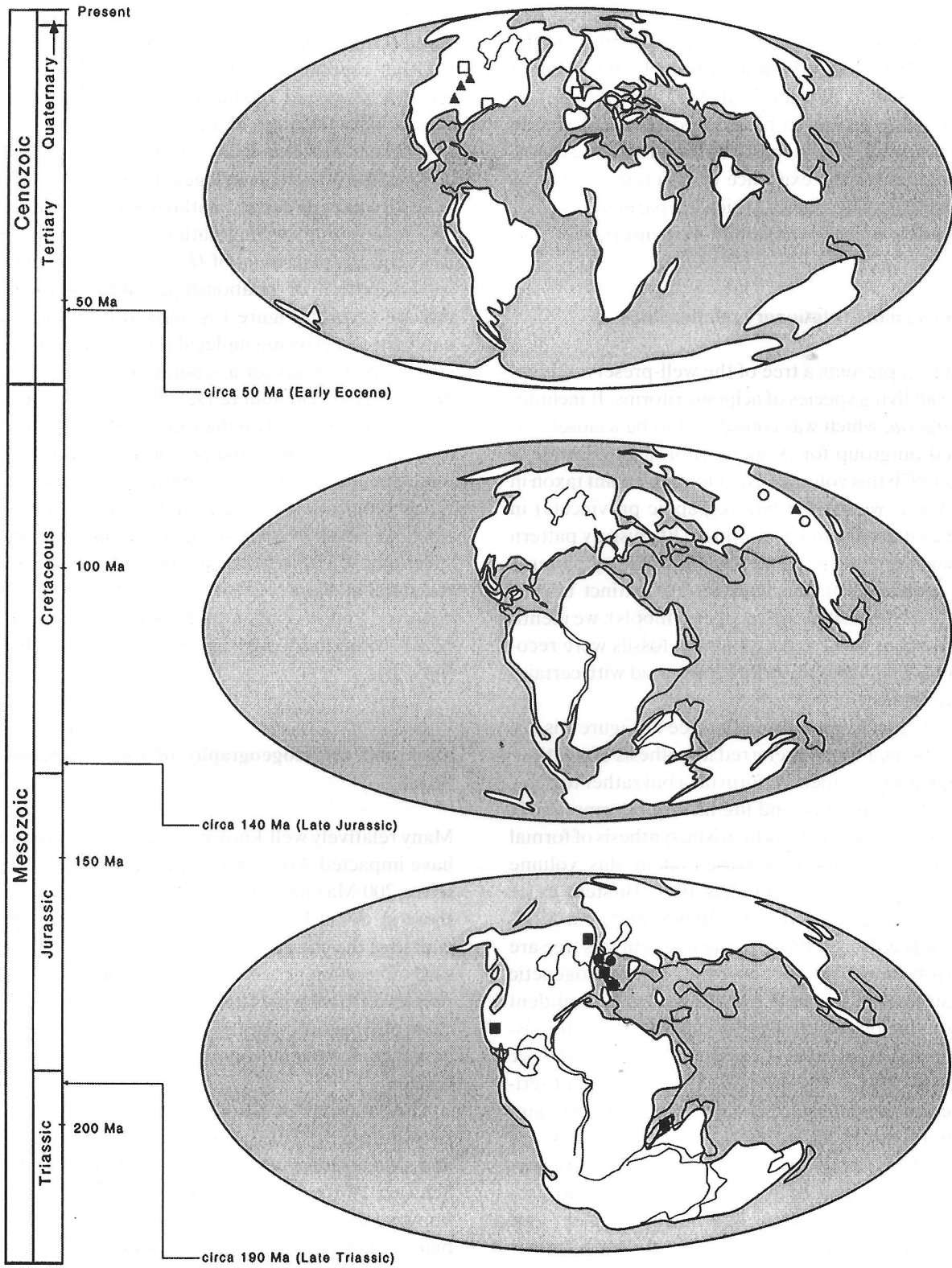
tionships within Polyodontidae also are well understood (Grande & Bemis 1991, Bemis et al. 1997b).

Other aspects of the tree in Figure 1 have been recently proposed on the basis of molecular sequence data (Birstein et al. 1997 this volume) and still others are decidedly controversial. A close comparison of formal phylogenetic hypotheses proposed by various current authors will reveal major differences in branching pattern within Acipenser as well as the placement of Huso. The largely unresolved pattern of relationships within Acipenser that we show in Figure 1 is derived from ongoing analyses of a growing molecular phylogenetic data set that is the basis for a separate formal phylogenetic analysis (Birstein & DeSalle 1997). A special problem is indicated on the tree by the dotted lines leading to Huso huso and H. dauricus. Based on a phylogenetic analysis of osteological and other morphological characters, Findeis (1997 this volume) proposed Huso as the sister taxon of all other species of Acipenseridae, and this is the placement we show in Figure 1. Birstein & DeSalle (1997), however, reported molecular characters that link Huso with Acipenser ruthenus (also see Berg 1948a,b).

Time and the biogeography of fossil acipenseriforms

Many relatively well-known Earth historical factors have impacted Acipenseriformes during their long (circa 200 Ma) history. Our intent is not to review these in detail but to outline the scope and time course of the changes. Divergence times are necessarily uncertain, given the relative paucity of well-preserved fossil taxa. To date, no one has used molecular phylogenetic data to estimate the times of divergence for major lineages within Acipenseriformes.

The outgroup for Acipenseriformes, †Birgeria, is known from the Triassic of Europe, North America and Madagascar (Nielsen 1949, Lehman 1952, Schwarz 1970). Two families of Acipenseriformes known only from fossils (†Chondrosteidae and Peipiaosteidae) are important for understanding the biogeography of the entire order (see discussion of

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Present

Cenozoic

Quaternary

Tertiary

50 Ma

circa 50 Ma (Early Eocene)

100 Ma

Cretaceous

circa 140 Ma (Late Jurassic)

150 Ma

Jurassic

Mesozoic

200 Ma

Triassic

circa 190 Ma (Late Triassic)

←

Figure 2. Paleocoastline maps and the distribution of †Birgeriidae and Acipenseriformes. On the map representing the Late Triassic/ Early Jurassic, the distribution of †*Birgeria* is indicated by solid squares, and the distribution of †Chondrosteidae is indicated by solid circles. On the map representing the Late Jurassic/Early Cretaceous, the distribution of †Peipiaosteidae is indicated by open circles, and the locality for the oldest fossil paddlefish, †*Protopsephurus*, is indicated by a solid triangle. On the map representing the Late Cretaceous/Early Tertiary, the distribution of three additional genera of paddlefishes (†*Paleopsephurus*, †*Crossopholis* and *Polyodon*) in western North America is indicated by solid triangles, and a few localities for fossil species assigned to *Acipenser* are marked with open squares.

the role of fossils in biogeographic studies in Grande 1985). Several fossil Polyodontidae and Acipenseridae are known. With the exception of the Green River paddlefish, †*Crossopholis magnicaudatus*, from the Early Eocene Green River Formation in southwestern Wyoming, the localities in which fossil paddlefishes and sturgeons occur lie within the historic ranges of the extant families. Some additional data about these fossil taxa are summarized in tabular form in Bemis et al. (1997b this volume) and Jin (1995). All well-preserved fossil genera of Acipenseriformes are included in the present study, but because species level distinctions within these genera are often problematic and have

not been the subject of recent comprehensive reviews, generic level distinctions suffice for current purposes.

We organize our comments on the biogeography of fossil Acipenseriformes around three paleocoastline maps and a time scale (Figure 2; base maps were redrawn and simplified from Smith et al. 1994). The lowest map shows a reconstruction of the continents and their coastlines in the Late Triassic/Early Jurassic, with the localities of the outgroup taxon, †*Birgeria*, plotted in solid squares in Europe, North America and Madagascar. Also plotted on the lowest map (solid circles) are localities for †*Chondrosteus* and †*Strongylosteus*, from the Early
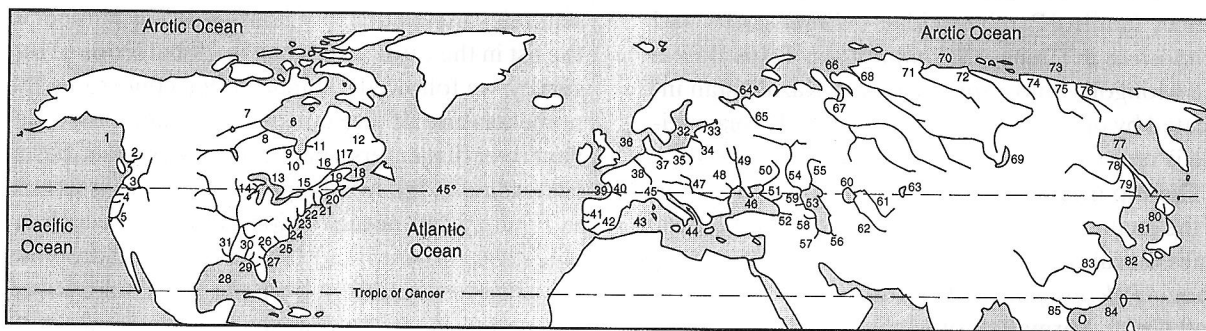

Figure 3. Major rivers, lakes, seas and oceans of the Holarctic relevant to the biogeographic ranges of recent Acipenseriformes. Base map redrawn from Bond (1996: Fig. 30–3); data used to assemble this figure are derived chiefly from secondary sources (Anonymous 1980, Vladykov & Greeley 1963, Scott & Crossman 1973, Hart 1973, Trautman 1981, Lee et al. 1980, Holčík 1989). Key: 1 – Gulf of Alaska; 2 – Fraser R.; 3 – Columbia R.; 4 – Rogue & Klamath R.; 5 – Sacramento R.; 6 – Hudson Bay; 7 – Churchill R.; 8 – Nelson R.; 9 – Albany R.; 10 – Moose R.; 11 – Rupert R.; 12 – Hamilton Inlet; 13 – Great Lakes (Superior, Huron, Michigan, Erie, & Ontario); 14 – L. Winnebago, Fox R., & Menominee R.; 15 – St. Lawrence R.; 16 – Ottawa R.; 17 – St. Maurice R; 18 – Gulf of St. Lawrence; 19 – St. John R.; 20 – Kennebec/ Androscoggin R. & Merrimack R.; 21 – Connecticut R.; 22 – Hudson R.; 23 – Delaware R.; 24 – Chesapeake Bay system (includes Potomac & Susquehanna); 25 – Santee R.; 26 – Savannah R. & Altamaha R.; 27 – St. John's; 28 – Gulf of Mexico; 29 – Suwanee R. & Apalachicola R.; 30 – Alabama R.; 31 – Mississippi R. (includes Missouri, Ohio, & Tennessee rivers); 32 – Baltic Sea; 33 – Neva R., Nara R., & Luga R.; 34 – Wista R.; 35 – Oder R.; 36 – North Sea; 37 – Elbe R.; 38 – Rhine R.; 39 – Bay of Biscay; 40 – Gironde Estuary (Garrone & Dorgonne R.); 41 – Douro R. & Guadiana R.; 42 – Guadalquivir R.; 43 – Mediterranean Sea; 44 – Adriatic Sea; 45 – Po R.; 46 – Black Sea; 47 – Danube R.; 48 – Dnestr R.; 49 – Dniepr R.; 50 – Don R.; 51 – Kuban R.; 52 – Rioni R.; 53 – Caspian Sea; 54 – Volga R.; 55 – Ural R.; 56 – Gorgan R.; 57 – Qezel Owzan R.; 58 – Kura R.; 59 – Terek R.; 60 – Aral Sea; 61 – Syr Darya R.; 62 – Amu Darya R.; 63 – L. Balkash; 64 – White Sea; 65 – Severnaya-Dvina R.; 66 – Kara Sea; 67 – Ob R. (includes Irtysh R.); 68 – Yenesei R.; 69 – L. Baikal; 70 – Laptev Sea; 71 – Khatanga R.; 72 – Lena R.; 73 – East Siberian Sea; 74 – Yana R.; 75 – Indigirka R.; 76 – Kolyma R.; 77 – Sea of Okhotsk; 78 – Amur R.; 79 – Tumnin R.; 80 – Ishikari R.; 81 – Sea of Japan; 82 – East China Sea; 83 – Yangtze R.; 84 – South China Sea; 85 – Pearl R.
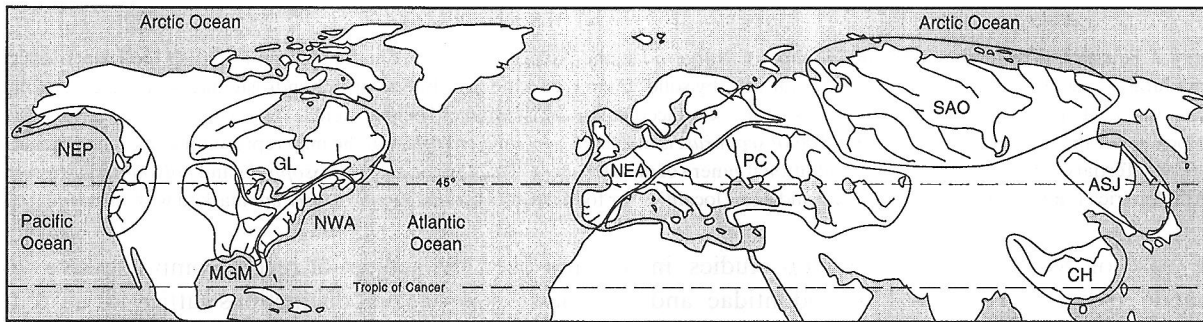
Figure 4. Nine biogeographic provinces for recent Acipenseriformes discussed in text. Also see Table 1. Key: NEP – North Eastern Pacific; GL – Great Lakes, Hudson Bay & St. Lawrence R.; NWA – North Western Atlantic; MGM – Mississippi R. & Gulf of Mexico; NEA – Northeastern Atlantic, including White, Baltic & North seas; PC – Ponto-Caspian Region, including Mediterranean, Aegean, Black, Caspian & Aral seas; SAO – Siberia & Arctic Ocean; ASJ – Amur R., Sea of Okhotsk & Sea of Japan; CH – China.

Jurassic of England and Germany, respectively. These are the diagnosable genera in the family †Chondrosteidae.

The middle map in Figure 2 shows a reconstruction of the continents and coastlines in Late Jurassic/Early Cretaceous times, with the localities plotted for the earliest known paddlefish, *†Protopsephurus* (solid triangle), and all four genera of the extinct family †Peipiaosteidae (*†Peipiaosteus* and *†Yanosteus* in China, *†Stichopterus* in Trans Baikal and Mongolia, and *†Spherosteus* in Kazakhstan indicated by open circles). The range of †Peipiaosteidae is restricted to Asia (Grande & Bemis 1996).

The top map in Figure 2 shows a reconstruction of the continents in Late Cretaceous/Early Tertiary times. Localities are plotted for three fossil paddlefishes: *†Paleopsephurus* from the Late Cretaceous Hell Creek Formation of Montana, *†Polyodon tuberculata* from the Early Paleocene Tullock Formation of Montana and *†Crossopholis* from the Early Eocene Green River Formation in Wyoming. A scaphirhynchine sturgeon, *†Protoscaphirhynchus* occurs in the Late Cretaceous Hell Creek Formation of Montana (and in fact was recovered from the same hadrosaur stomach as was the paddlefish *†Paleopsephurus*). Fossils assigned to the genus *Acipenser* are, for the most part, fragmentary, and have never been comprehensively reviewed or compared with the living species. For establishing the presence of *Acipenser* in North America, we plot in Figure 2 the locality of *†Acipenser albertensis* from the Late Cretaceous of Alberta and other fossil species assigned to *Acipenser* from the Early Eocene of England and Miocene of Virginia.

Biogeography of living acipenseriforms

Figure 3 maps selected major rivers of the world in which acipenseriforms spawn. The rivers, lakes and seas relevant to our analysis are coded by number to the list in the caption. Given the global scope of our survey, we followed a standard rule concerning the nomenclature of streams: we only name the relevant river that enters a particular ocean or sea basin. For example, the Mississippi River (# 31) is named in Figure 3 but not its major tributaries, which include the Missouri and Ohio rivers. Anadromous acipenserids are absent from the Mississippi River, and some acipenseriform species occur only in its upper tributaries (e.g., *Scaphirhynchus albus* lives in far upstream reaches of the Missouri River), but for purposes of our survey, the only river noted is the Mississippi. We also simplified many river systems and omitted many smaller rivers from our diagram.

We also found it convenient to define nine biogeographic provinces with which acipenseriforms are associated (Figure 4). Table 1 lists the provinces and species of acipenseriforms that currently live in each. Although some species occur in more than one province, we defined them for and primarily use them to discuss the biogeography of *Acipenser* and *Huso*. Most provinces are based on drainages feeding into distinct oceanic basins. Discrete geo-

graphic boundaries currently limit emigration of sturgeons from some of these provinces to adjacent provinces (e.g., around the lower one half of Florida there are no suitable spawning rivers). In other cases, the provinces are readily distinguishable based on geological history (e.g., the Mediterranean basin connected to the North Eastern Atlantic through the strait of Gibraltar in the Messinian; see Hsu 1972).

Life history

This section explains the life history patterns scored on the tree in Figure 1. Although some authors comment on evidence for anadromy in fossil acipenseriforms (e.g., Bai 1983), we consider that it is not pos-

sible to make meaningful comparisons based on such speculations. Thus, we restrict the analysis of life history patterns shown in Figure 1 to extant species.

Acipenseriforms migrate for two basic reasons: feeding and reproduction, and we illustrate some possible life history patterns in Figure 5. *Downstream migrations* of sturgeons are always associated with feeding. The interfaces between freshwater and saltwater or between rivers and large lakes can be nutrient rich, with abundant food. The shallow (< 100 m), near-shore continental shelf regions in which some species of sturgeons feed at sea are similarly productive environments. Sturgeons are not known to utilize deep environments while at sea, and do not in general make extensive offshore migrations. *Upstream migrations* are usually associat-

Table 1. Occurrence of species of acipenseriforms in nine biogeographic provinces (mapped in Figure 4).

NEP – North Eastern Pacific	*Acipenser medirostris*
	Acipenser transmontanus
GL – Great Lakes, Hudson Bay & St. Lawrence River	*Acipenser fulvescens*
	Acipenser o. oxyrinchus
NWA – North Western Atlantic	*Acipenser brevirostrum*
	Acipenser o. oxyrinchus
MGM – Mississippi R. & Gulf of Mexico	*Polyodon spathula*
	Acipenser oxyrinchus desotoi
	Scaphirhynchus albus
	Scaphirhynchus platorynchus
	Scaphirhynchus suttkusi
NEA – Northeastern Atlantic, including White, Baltic & North seas	*Acipenser ruthenus*
	Acipenser sturio
PC – Ponto-Caspian Region, including Mediterranean, Aegean, Black, Caspian & Aral seas	*Acipenser gueldenstaedtii*
	Acipenser nudiventris
	Acipenser naccarii
	Acipenser persicus
	Acipenser ruthenus
	Acipenser stellatus
	Acipenser sturio
	Huso huso
	Pseudoscaphirhynchus fedtschenkoi
	Pseudoscaphirhynchus hermanni
	Pseudoscaphirhynchus kaufmanni
SAO – Siberia & Arctic Ocean	*Acipenser baerii*
	Acipenser ruthenus
ASJ – Amur R., Sea of Okhotsk & Sea of Japan	*Acipenser mikadoi*
	Acipenser schrenckii
	Huso dauricus
CH – China	*Acipenser dabryanus*
	Acipenser sinensis
	Psephurus gladius

anadromy

ocean

estuary

juveniles & adults forage in shallow waters (< 100 m depth) for several years after leaving estuary

juveniles may reenter estuary or ascend into fresh water to feed in summer

most juveniles & adults forage in estuary or riverine reaches downstream of spawning site

spawning site (often just below major rapids or other barrier to migration)

observed spawning migration patterns:
    one step
    short two step
    long two step

freshwater amphidromy

ocean

estuary

some juveniles & adults forage in ocean

juveniles & adults forage in riverine reaches downstream of spawning site

spawning site (often just below major rapids or other barrier to migration)

observed spawning migration patterns:
    one step
    short two step

potamodromy

lake

some juveniles & adults forage in lake

juveniles & adults forage in riverine reaches downstream of spawning site

spawning site (often just below major rapids or other barrier to migration)

observed spawning migration patterns:
    one step
    short two step

marine environments
brackish water environments
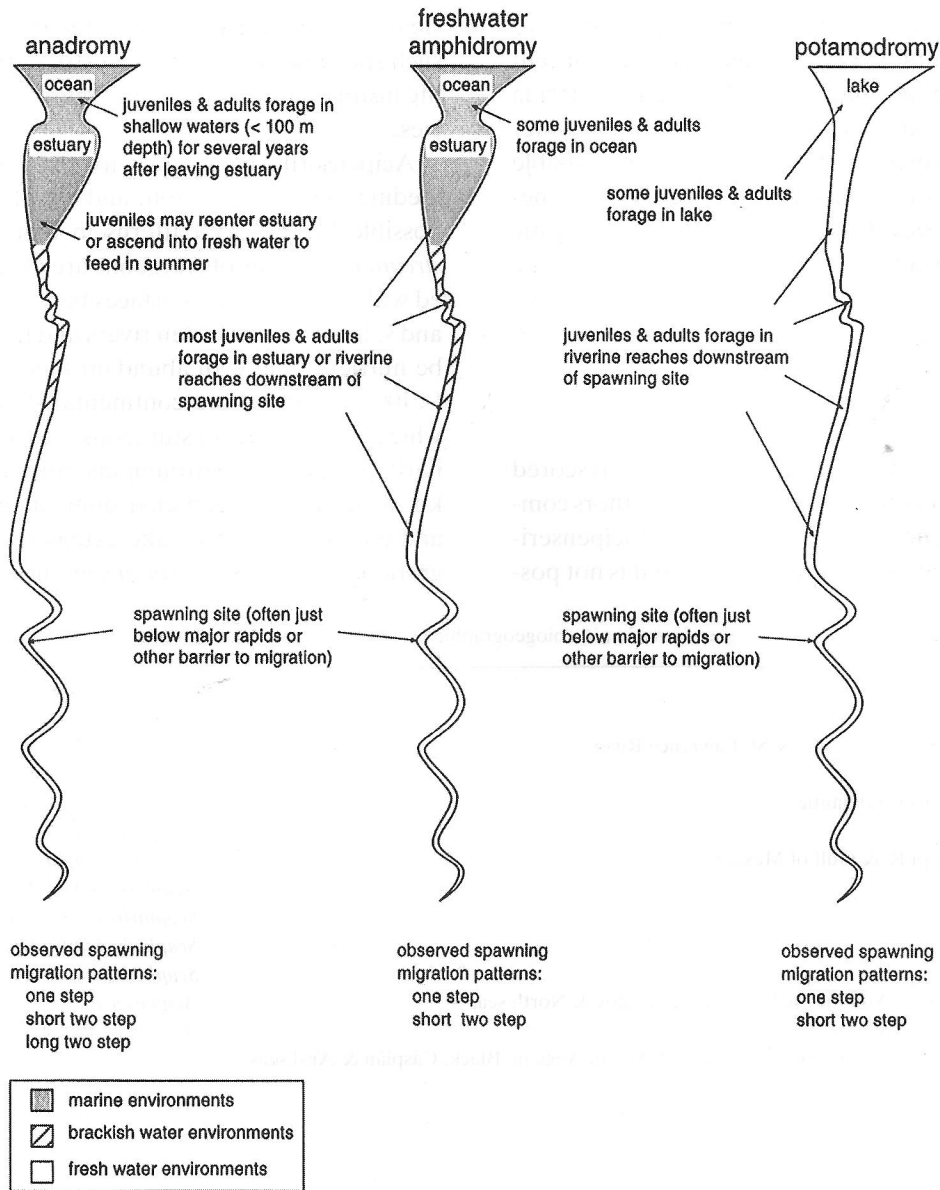fresh water environments

Figure 5. Concepts of anadromy, amphidromy and potamodromy in acipenseriforms. These terms are defined and further explained in the text. Patterns of spawning migrations used by fish employing these different life history patterns are indicated in text below each condition. Once a spawning migrant enters a river, it typically follows one of three spawning migration patterns. These are keyed to the drawing as follows: one step – short or long migration, spawning; short two step – migration, overwintering, short migration, spawning; long two step – migration, overwintering or oversummering (or both), long migration, spawning. See text for additional explanation.

ed with spawning activities, although in many cases, anadromous sturgeons may re-enter estuaries or even freshwater reaches of rivers during summer months to feed and amphidromous sturgeons may move from one riverine or estuarine foraging site to another. Fish with mature gonads that migrate up-stream during the spawning season are commonly referred to as *spawning fish* or *spawners*, regardless of whether they successfully complete spawning. The age at first spawning migration is an important life history parameter for all species of sturgeons, although it is unknown in many cases. *Emigration*

refers to an individual that leaves its river basin and migrates via a sea or lake. Emigrants may return to their natal river to spawn or colonize a new river basin (non-natal emigrants).

Thanks to McDowall (1987, 1988, 1992), other terms necessary to accurately describe migrations of Acipenseriformes have widely accepted definitions, which are:

Diadromous/diadromy – Fishes that migrate between salt water and fresh water (Myers 1949, McDowall 1988, 1992). Many, but not all, acipenseriforms are diadromous.

Anadromous/anadromy – Diadromous fishes that spend most of their lives at sea but return to fresh water to breed (Myers 1949, McDowall 1988, 1992). Most species in the genus *Acipenser* are anadromous, as are both species in the genus *Huso*. Surprisingly limited information is available about the physiological mechanisms that underlie anadromy in acipenseriforms (McEnroe & Cech 1985, 1987)

Amphidromous/amphidromy – Diadromous fishes whose migration from fresh water to the salt water, or vice-versa, is not for the purpose of breeding although it occurs regularly at some point(s) in the life cycle (McDowall 1988, 1992). McDowall (1992) defined two types of amphidromy: freshwater amphidromy, in which spawning is in fresh water and growth occurs during migrations into salt water, and marine amphidromy, in which spawning occurs in salt water and growth occurs during migrations into fresh water. All acipenseriforms spawn in fresh water, so that only freshwater amphidromy is relevant for the group. Only a few cases convincingly document freshwater amphidromy for any species of Acipenseriformes, because this requires detailed knowledge of the movements of individuals which can only be obtained from tagging and recapture or telemetric studies. The best documented of these species is the shortnose sturgeon, *Acipenser brevirostrum* (Bain 1997 this volume, Kynard 1997 this volume).

Potamodromous/potamodromy – Fishes that migrate within a river system to breed and forage (McDowall 1988, 1992). All shovelnose sturgeons (tribe Scaphirhynchini, *Scaphirhynchus* and *Pseudoscaphirhynchus*) are potamodromous. Paddlef-

ishes (Polyodontidae) are potamodromous, for the few reports of *Polyodon* taken at sea seem to represent rare individuals, and all fossil polyodontids are from freshwater deposits (Grande & Bemis 1991, Bemis et al. 1997b this volume). The only possible exception is the Chinese paddlefish, *Psephurus gladius*, which was historically captured near the mouth of the Yangtze River and from the East China Sea, but which now is so rare that its true life history pattern will probably remain unknown. Based on the few data available, we think that it is probably fresh water amphidromous, because juvenile Chinese paddlefish were historically taken in the estuary of the Yangtze River (see Wei et al. 1997 this volume). Some species of *Acipenser*, such as *A. ruthenus*, are commonly considered to be potamodromous, such as the populations in upper reaches of the Danube River described by Hensel & Holčík (1997 this volume). Recent information suggests that *A. ruthenus* may prove to be amphidromous, because juveniles are commonly captured in salt water at the mouth of the Danube River. Other species, such as *A. schrenckii*, may be facultatively potamodromous, with some populations in upper reaches of the Amur River apparently never venturing near the estuary (Krykhtin & Svirskii 1997 this volume). Some authors refer to such populations as *residents*, meaning that the individual fish do not migrate to the sea. Poorly understood are other cases demonstrating the type of facultative potamodromy that occurs when dams obstruct passage of a formerly anadromous or amphidromous species, a condition referred to as *damlocked* (Kynard 1997 this volume). By itself, potamodromy can only provide negative evidence concerning a species' ability to cross large ocean basins.

In those marine coastal rivers that have sturgeons, usually at least two species (and sometimes as many as six) are present. If only two species are present, one is always anadromous, and the other is usually potamodromous (or amphidromous; see comments on the difficulties of detecting amphidromy above). Two clear examples of this are found in the Hudson River, which has *Acipenser oxyrinchus* (anadromous) and *A. brevirostrum* (amphidromous), and the Yangtze River, which has *A. sinensis* (anadromous) and *A. dabryanus* (amphidro-

mous or potamodromous). If only one species is present, it is usually anadromous. The Northeast Atlantic region (Figure 4) has a high frequency of rivers, particularly in western France and the Iberian Peninsula, that have only one anadromous species, *A. sturio*. The absence of a second species in these rivers is not due to anthropogenic effects, but instead reflects the historical situation (Holčík 1989). It is unclear why the pattern that is so common elsewhere is not followed in the northeast Atlantic region.

In Figure 1, most taxa are scored with either an 'A' for anadromy or 'P' for potamodromy; only one species (*A. brevirostrum*) is marked 'FWA' to indicate freshwater amphidromy because without better telemetric and tagging studies, we cannot know how many seemingly freshwater species actually use patterns of freshwater amphidromy. Future work will almost certainly change some of our 'P' scores to 'FWA' scores. In some cases, a species may be potamodromous in one river basin and anadromous in another; in such cases, we scored the species 'A'.

Patterns of spawning migrations

Within acipenseriforms, variations in the pattern of spawning migration are found at the species, population, and individual levels. The genetic basis of spawning migration characteristics is well established for salmoniforms, for which extensive selection experiments have been done (also see papers in Groot & Margolis 1991). Virtually nothing is known about the heritability of spawning migration characteristics of acipenseriforms, but we expect a similar genetic basis to that known for salmonids. The existence of different spawning migration patterns in sturgeons has been discussed by many authors, including Berg (1934, 1959), Artyukhin (1988) and Kynard (1997 this volume). Berg (1934) introduced the terms *vernal* and *winter* races to describe groups of anadromous fishes migrating into rivers for spawning in the same year (vernal races) or next year (winter races). These terms stimulated a long discussion in the Russian literature concerning Eurasian sturgeons (reviewed by Barannikova 1957,

Gerbilskiy 1957, Kazansky 1962, Artyukhin 1988). Some of the terms and discussions are contradictory and difficult to follow, particularly because it is not always possible to link migration times, spawning sites and specific migrants. Also, the terminology does not easily translate to conditions in North American rivers, many of which are shorter, smaller coastal streams than are the major rivers of the Black and Caspian Sea basins for which the terminology was originally developed. The simplified scheme summarized in the box in Figure 5 draws primarily from Kynard (1997) and Gerbilskiy (1957). It classifies spawning migrations as having one or two steps, with a variable length of time between the actual migration and the time of spawning. This scheme can be readily used to describe either anadromous, amphidromous or potamodromous acipenseriforms and individual variation within populations.

One step spawning migrations are those in which fish move directly upstream to the spawning site, spawn, and return downstream. Depending on the bioenergetic reserves of the fish, the migration may be short or long, and occur in winter or spring. This is usually thought to be the most common pattern for living acipenseriforms, although the few data available (mostly catch records) are conflicting. It corresponds to Gerbilskiy's (1957) migrant type I, in which the oocytes have reached their final size and spermatogensis is finished by the time migration starts. Fat deposits in connective tissue and muscles are depleted, and the stomach and digestive tract are empty and inactive indicating that feeding stopped some time before migration. Such migrants typically use spawning sites in the lower or middle reaches of rivers.

Short two step spawning migrations involve upstream migration, usually in the fall, followed by overwintering near the spawning site, followed by a very short migration to spawn the following spring. This pattern enables fish to use bioenergetic reserves gained during summer foraging for their initial long upstream migration. This corresponds roughly to Gerbilskiy's (1957) migrant type II, in which late stages of oogenesis are in progress, and the oocytes are still embedded in fatty tissue. Spermatogenesis is in the 'first wave' of divisions. There

is abundant fat in connective tissue and dorsal muscles, and the hepatocytes are large because of lipid inclusions. Food remains in the stomach and digestive tract indicate that feeding took place just prior to the start of migration. These fish typically spawn in middle to upstream reaches of many rivers, such as the Volga, Ural, Danube, Hudson or Connecticut.

Long two step spawning migrations refer to fish that make an initial upstream migration, followed either by overwintering, oversummering, or both, then followed by a long upstream migration to the spawning site. Fish with this pattern may be in fresh water without feeding for 12 to 15 months, which effectively precludes this option for small to medium sized species because they lack sufficient bioenergetic capacities. Only very large species, such as *Huso huso* and *Acipenser sinensis* seem likely candidates for this pattern. This corresponds more or less to Gerbilskiy's (1957) migrant type III, which is characterized by late stages of oogenesis, and intermediate levels of fat in the ovary, connective tissues, and muscles at the start of migration. This type of migration is characteristic of some individuals of large species in the longest rivers, such as the Danube, Volga, Amur or Yangtze. The only place in North America where this pattern may have been present is the Columbia River, where very large white sturgeon, *A. transmontanus*, historically spawned in headwaters.

Explanations that have been offered concerning the adaptive significance of different spawning migratory patterns include river length, river gradient, temperature at the spawning site, and bioenergetics. For example, Artyukhin (1988) concluded that spawning in the spring is characteristic of most species of sturgeons in the Ponto-Caspian region that inhabit lowland rivers, whereas spawning during the summer is associated with rivers having a higher gradient. Kynard (1997 this volume) proposed a bioenergetic explanation of migratory patterns. As noted above, spawning migratory patterns can be variable within species or populations, and before conclusions are reached, it seems necessary to develop better understanding of sturgeon life histories. Factors such as spawning site fidelity and behavior between successive spawnings need to be broadly investigated across acipenseriforms, as well as the genetic bases of supposedly different stocks of the same species in particular river systems (Wirgin et al. 1997 this volume). Until then, it is safest to regard the three patterns of spawning migration as descriptive tools, rather than interpretive explanations for particular migration patterns, and we have not attempted to score the migratory patterns of species in Figure 1.

Discussion

Several events in Holarctic history stand out as influencing the contemporary distribution of sturgeons and paddlefishes. A complete review is far beyond our scope, so we note only a few highlights.

Place of origin of acipenseriforms and their early diversification

Some have asserted (e.g., Yakovlev 1977) that Acipenseriformes originated in northeastern Asia in the Triassic. This argument, however, cannot be based on either the earliest known occurrence of fossils or the greatest current diversity of taxa but must instead be consistent with the ranges of outgroup taxa (Nelson & Platnick 1981). Based on available phylogenetic and biogeographic evidence (Figure 1), the most plausible place and time of origin for Acipenseriformes is the Triassic of western Europe, for this is consistent with the range of †*Birgeria* (Europe, North America, and Madagascar) as well as with the range of †Chondrosteidae, which is interpreted by Grande & Bemis (1996) to be the sister taxon of all other Acipenseriformes (Figure 2). The localities of Late Jurassic/Early Cretaceous members of Peipiaosteidae in Central and Eastern Asia suggest (but do not provide definitive evidence for) early diversification of Acipenseriformes in central Asia. If true, this seems consistent with the greatest current species diversity of Acipenseridae in the Ponto-Caspian region and the relatively much later appearance of the group (Late Cretaceous) in North America (Figure 2). We

should expect to find new acipenseriform fossils in Mesozoic deposits across Europe and Asia.

Were early acipenseriforms potamodromous or anadromous?

McDowall (1993) considered that sturgeons (and by extension, acipenseriforms in general) are unlikely to have had a recent marine ancestry, a conclusion that all fossil data and contemporary phylogenetic analyses support. This does not answer, however, whether anadromy originated within Acipenseriformes or was a plesiomorphic feature of the group. Unfortunately, we can only speculate about the answer, because we can never hope to understand much about the life history of †Birgeriidae, †Chondrosteidae or †Peipiaosteidae, and more distant outgroups are not helpful (Bemis et al. 1997b this volume). From the analysis in Figure 1, either potamodromy or anadromy could be the ancestral condition, because each condition appears twice on the tree (potamodromy in most or all species of Polyodontidae and Scaphirhynchini; anadromy in *Huso* and most species of *Acipenser*). If *Huso* is eventually nested within *Acipenser* (e.g., Birstein et al. 1997), then perhaps anadromy will emerge as a derived character of some clade that includes *Acipenser* and *Huso*. This would be very interesting, because anadromy seems likely to be linked to the great diversity within *Acipenser*.

Comments on biogeography of extant species

The Ponto-Caspian region currently has the greatest species diversity of Acipenseridae. Some sturgeons of the Ponto-Caspian region have striking morphological distinctions from all other species, such as the very elongate rostrum found in adult stellate sturgeon, *Acipenser stellatus*. There are some intriguing links of this Ponto-Caspian region both to the North Eastern Atlantic (*A. sturio*) and to the Amur River district (*Huso huso* and *H. dauricus*). One of the most intriguing links of the Ponto-Caspian region is to the Mississippi-Gulf of Mexico region in North America indicated by the scaphir-

hynchine sturgeons. All six extant species of *Scaphirhynchus* and *Pseudoscaphirhynchus* are considered to be potamodromous, and we know that Scaphirhynchini was present in North America in the Late Cretaceous (Figure 2). (A comparably intriguing and old link dating from at least the Late Cretaceous occurs between China and the Mississippi-Gulf of Mexico region as indicated by Polyodontidae; Grande & Bemis 1991.)

The Ponto-Caspian region has been very unstable over the last 150 million years, the period in which we suppose Acipenseridae has diversified. Some indication about the magnitude of the Earth historical changes in the Ponto-Caspian region is apparent in the diagrammatic maps in Figure 2, which represent only a small window on this part of the world (see Smith et al. 1994 for additional geographical and geological detail). The changes include major sea level variation, conversions of large bodies of water such as the Black Sea from freshwater lakes to marine environments, merging of island arcs with the southern continental borders of Europe and Asia, and major shifts in drainage patterns as mountain building occurred. The Black Sea has repeatedly been connected and disconnected with the Caspian and Aral seas. It is tempting to link the current diversity of acipenserids in this region to its extremely complex history.

Around the Pacific rim, we defined three biogeographic regions (NEP, ASJ, and CH, Figure 2) that together have six species of *Acipenser*. Based on the available phylogenetic interpretation (Figure 1), the five anadromous species (*A. transmontanus*, *A. medirostris*, *A. mikadoi*, *A. schrenckii* and *A. sinensis*) appear to form a monophyletic group. *Acipenser dabryanus*, a potamodromous and potentially amphidromous species believed to be restricted to the Yangtze River, lies outside the group of species from around the Pacific rim (see Wei et al. 1997 this volume and Zhuang et al. 1997 this volume for discussion of the ranges of sturgeons in China). One point concerning sturgeons of the Pacific rim is that we are unaware of any spawning in rivers north of the Fraser River, British Columbia. The explanation for this pattern in the Pacific is unknown, although other taxa of acipenserids, such as *A. fulves-*

cens in North America and *A. baerii* in Siberia, spawn in rivers at higher latitudes.

Some biogeographic patterns may be related to continental movements, such as the sister group relationship between *Acipenser sturio* in Europe and *A. oxyrinchus* in North America. These two species are anatomically similar and were long considered to be conspecific (Vladykov & Greeley 1963). They also share molecular sequence similarities (Birstein et al. 1997 this volume). Although these species live on opposite sides of the North Atlantic Ocean, and are presumably blocked from most interbreeding, we suspect that the separation between these taxa is actually much younger than the North Atlantic Ocean.

Species of acipenseriforms directly impacted by Pleistocene glaciation presumably include boreal taxa such as *A. baerii* (Ruban 1997, this volume). This species occurs in many of the northward flowing rivers of Siberia (SAO region, Figure 4). Although the extent of glaciation in Siberia during the last glacial maximum (18 000 years bp) was not as extensive as one might suppose (Starkel 1991), *A. baerii* was certainly prevented from entering the Arctic Ocean. The location of its glacial refugia is uncertain. In North America, the lake sturgeon, *A. fulvescens*, may have occupied both Mississippian and Missourian refugia during glaciation, and recolonized its range in the northern United States and Canada by dispersal (Ferguson & Duckworth 1997, this volume).

Clearly, much is yet to be learned about biogeography and life history of Acipenseriformes. Synthesis should be the goal, particularly as new data on the status of poorly known populations become more available.

Acknowledgements

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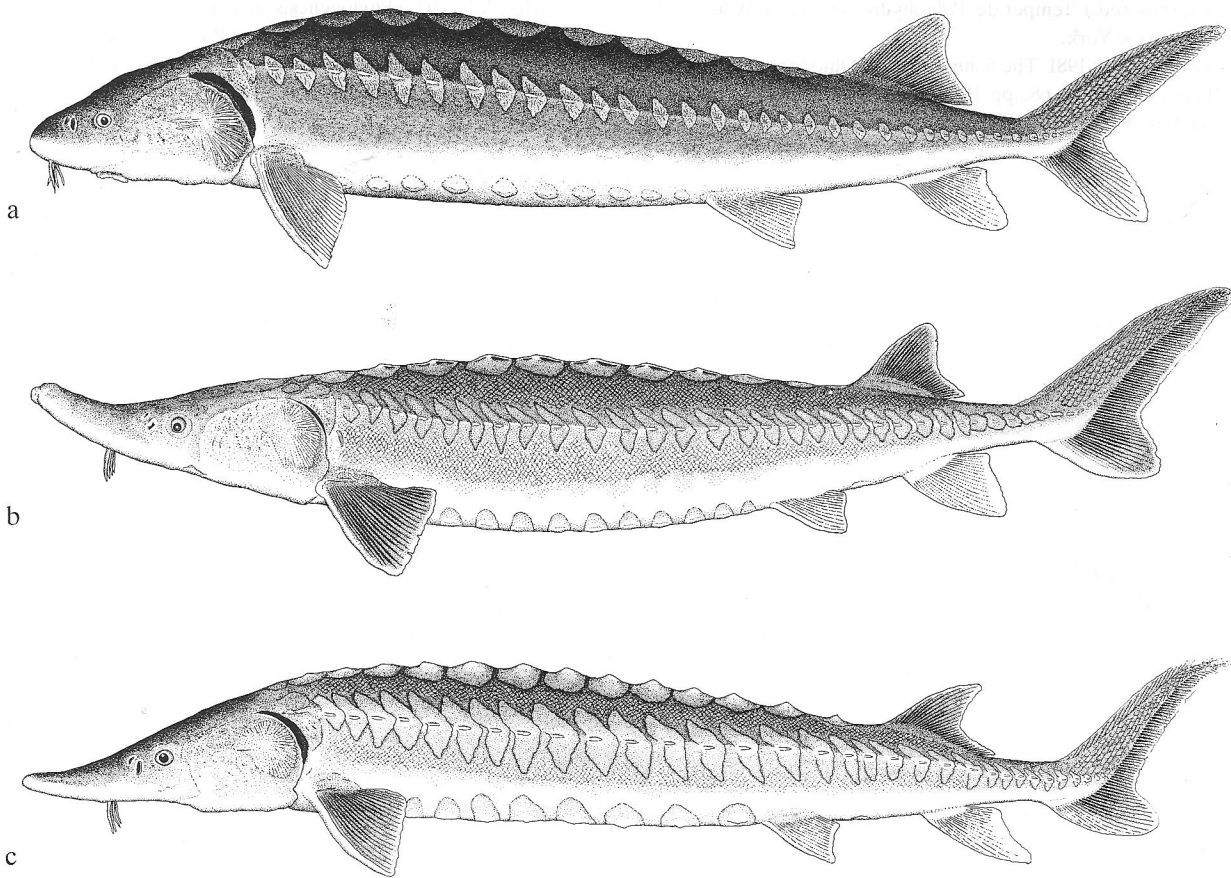
Sturgeons of the western and eastern Atlantic: a – the shortnose sturgeon, *Acipenser brevirostrum* 143 cm TL from the outlet of Washademoak Lake, St. Johns River, New Brunswick, Canada, caught 2.1.1975 (ROM cat # 34310); b – American Atlantic sturgeon, *A. oxyrinchus* 150 cm TL from St. Lawrence River, Kamouraska, Quebec, now residing alive in the Montreal Biodome (hence the typical damage to the tip of the rostrum); c – European Atlantic sturgeon, *A. sturio* 107 cm TL from the Black Sea stock at the 'Grigore Antipa' Natural History Museum, Bucharest. Originals by Paul Vecsei, 1996.