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FISH OTOLITHS FROM THE LATE MAASTRICHTIAN KEMP CLAY (TEXAS, USA) AND THE EARLY DANIAN CLAYTON FORMATION (ARKANSAS, USA) AND AN ASSESSMENT OF EXTINCTION AND SURVIVAL OF TELEOST LINEAGES ACROSS THE K-PG BOUNDARY BASED ON OTOLITHS

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*Abstract***.** Otolith assemblages have rarely been studied across the K-Pg boundary. The late Maastrichtian Kemp Clay of northeastern Texas and the Fox Hills Formation of North Dakota, and the early Danian Clayton Formation of Arkansas therefore offer new insights into how teleost fishes managed across the K-Pg boundary as reconstructed from their otoliths. The Kemp Clay contains 25 species, with 6 new species and 2 in open nomenclature and the Fox Hills Formation contains 4 species including 1 new species. The two otolith associations constitute the Western Interior Seaway (WIS) community. It contains the earliest unambiguous representatives of the Gadiformes (cods and hakes) and the Heterenchelyidae (mud eels). The WIS community differs significantly from other Maastrichtian otolith assemblages previously studied from Mississippi and Maryland, which constitute the Appalachian community, with only 4 shared species (similarity percentage of 7.3%) between both communities. The difference is interpreted to be related to cold-water influence in the WIS community, which may have still been connected to the Arctic Basin, and to the depostional environment (muddy bottom) in the Kemp Clay.

The Kemp Clay is unusually rich in taxa that survived the end-Cretaceous extinction event and are still present in the Danian of the Clayton Formation, or, as the case may be, in the Danian and Selandian of the boreal northern European community known from Denmark. Approximately 54% of all otolith-based teleost species identified from the Maastrichtian WIS community survived the K-Pg boundary event (versus 11-12% in other communities) and 73% of the genera (versus 40-50% in other communities). The early Danian Clayton Formation contains an impoverished inherited association with 14 species, of which 11 are survivors from late Maastrichtian times, 1 species is new, and 2 remain in open nomenclature. This compares to a significantly higher degree of newly evolved species in only slightly younger faunas from the middle to late Danian and Selandian of Europe indicating an initially slow pace of recovery.

The observed differences in survival and the composition of survived and extinct taxa are discussed in the light of the ongoing discussions concerning the consequences and effects that led to the end-Cretaceous extinction event commonly thought to have been caused by a large meteorite impact. In our assessment, an 'impact winter' could have had a major influence on the life cycle of tropical to subtropical fishes while perturbations in the pelagic food web or ocean surface acidification might have had a minor and more selective effect. Overall, teleost fishes were significantly affected by the end-Cretaceous mass extinction, but to a much lesser extent than in many other biota. This study provides more evidence of the importance of Late Cretaceous otolith assemblages in the USA for interpreting teleostean evolution.

The newly described taxa are: *Elopothrissus carsonsloani* n. sp., *Pythonichthys arkansasensis* n. sp., *Congrophichthus transterminus* n. gen., n. sp., *Rhynchoconger brettwoodwardi* n. sp., *Palaeogadus weltoni* n. sp., *Dakotaichthys hogansoni* n. gen., n. sp., and *Ampheristus americanus* n. sp.

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INTRODUCTION

Late Cretaceous strata, primarily those consisting of sands, marls, and clays, in North America have been shown to contain well-preserved, and often abundant, teleostean otoliths (Huddleston & Savoie 1983; Nolf & Stringer 1996; Stringer et al. 2016; Schwarzhans et al. 2018b; Stringer et al. 2020). In spite of the presence and potential for otoliths, investigations and subsequent publications have been very limited. This relatively sparse quantity of previous research amplifies the importance of the detailed investigation of the otoliths from the Kemp Clay. Furthermore, the otolith assemblage from the Kemp Clay provides insight into the evolution of the Late Cretaceous bony fish fauna and affords an opportunity to discern lineage changes in the bony fishes across the K-Pg boundary as well as the effect of the Yucatan bolide impact (Chicxulub structure). This investigation examines the Kemp Clay otoliths in light of recent studies of Late Cretaceous bony fishes in North America (Stringer et al. 2016; Stringer et al. 2018; Schwarzhans et al. 2018b; Stringer et al. 2020). Furthermore, this study includes new analyses based on in situ skeletal otoliths and computed tomography such as Beckett & Friedman (2016) and Schwarzhans et al. (2018a) as well as updated taxonomy based on molecular studies such as those by Santini et al. (2009), Near et al. (2012, 2013), Betancur et al. (2013), and Nelson et al. (2016). The present investigation of the Kemp Clay otoliths also benefits from a greater understanding of the evolution of the bony fishes (Alfaro et al. 2009; Alfaro & Santini 2010; Friedman 2010; Friedman & Sallan 2012; Carnevale & Johnson 2015).

LOCATION OF INVESTIGATED SITES

The Cretaceous otoliths for this investigation were collected from a site on the South Sulphur River, Hunt County, Texas, USA (Fig. 1). The site is located south-southwest of Commerce, Texas, and is 1.2 km west of the intersection of State Highway 24/50 and Farm-to- Market Road 1568 on the south bank of the South Sulphur River. Coordinates for the site are 33.209063, -95.927835.

Several other studies have been conducted in the general vicinity of the South Sulphur River site. Meyer (1974) in his exhaustive study of Late Cretaceous elasmobranchs from the Mississippi and East Texas embayments of the Gulf Coastal Plain collected at a site described as approximately 1.6 km upstream from State Highway 50 (Meyer's site #50 or Commerce site). He described a thin layer of silty-sandy phosphatic clay that weathered reddish-brown that contained typical Maastrichtian fish fossils and identified it as possibly Kemp Clay. Case & Cappetta (1997) reported on a site on the north bank of the South Sulphur River approximately 600 m west of the bridge on State Highway 24 (also known as State Highway 50) and approximately 8 km from the center of the campus of the University of Texas A&M-Commerce (formerly known as the East Texas State Teachers College). They reported collecting in layers of sand and clay of the Kemp Clay. Becker et al. (2006) noted that South Sulphur River sites exposing the Kemp Formation have been intensely collected by both amateurs and professional paleontologists for decades, especially for chondrichthyan remains.

In addition to the Cretaceous otoliths from the South Sulphur River, 67 specimens of the the gadiform *Dakotaichthys hogansoni* n. gen., n. sp. were obtained from the Cretaceous (early-late Maastrichtian) Fox Hills Formation in the southwestern portion of North Dakota, USA (Fig. 1). These specimens were part of the extensive study of the chondrichthyan and osteichthyan remains from the Fox Hills Formation of North Dakota conducted by Hoganson et al. (2019). A detailed map indicating the location of the Fox Hills Formation site is presented in text-fig. 1 in Hoganson et al. (2019). The specimens included in this study came from a north-facing roadcut and adjacent ditch on FAS 2416, approximately 5 km ENE of Burnstad in Logan County, North Dakota, USA.

The Paleocene otoliths included in this study were obtained from two sites in central Arkansas, USA (Fig. 1). The first locality, known as the Interstate-30 (I-30) slide site, is located approximately 6.9 km west of Malvern, Hot Spring County, Arkansas (Fig. 2B; 34.22531, -92.51437). The site is approximately 1.6 km south of the intersection of Highway 48 on the west side of Interstate 30. The second locality, known as the McNeil Creek site, is located in Benton, Saline County, Arkansas (34.571, -92.5921). The site is on McNeil Creek, which is located on the southwest side of Interstate 30 and runs adjacent and roughly parallel to the interstate

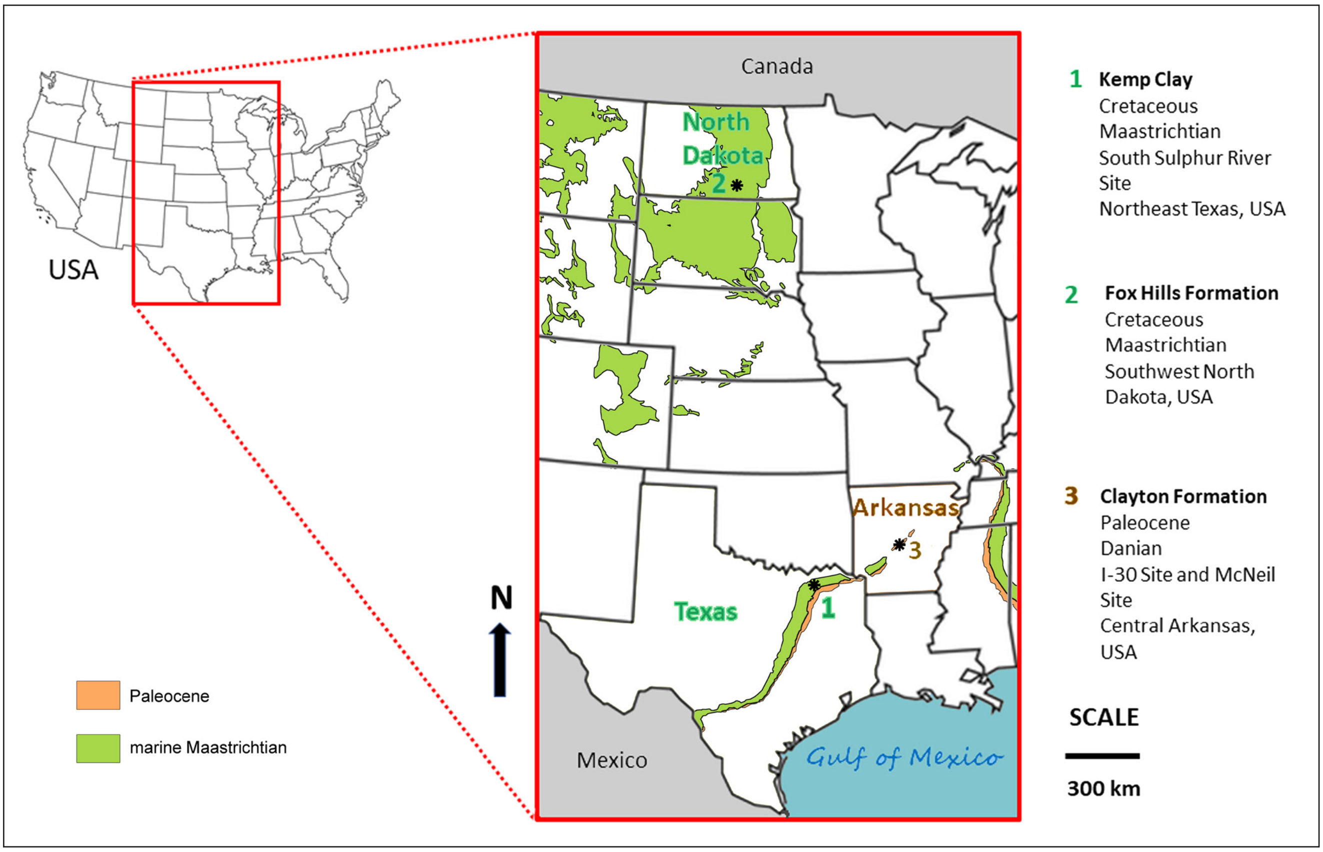


Fig. 1 - Locality map of Maastrichtian sites in Texas and North Dakota and early Danian sites in Arkansas that produced otoliths for this study. Generalized outcrop geology depicting Maastrichtian and Paleocene in the USA based on Reed et al. (2004), Geologic map of North America.

highway. The site is approximately 0.55 km southwest of the intersection of Arkansas Highway 35 (West Carpenter Street) and Interstate 30.

METHODOLOGY AND TERMINOLOGY

A bulk sample was taken along the south bank of the South Sulphur River and in the river bed during a low-water stage. The bulk sample weighed approximately 27 kg originally but was reduced to approximately 9 kg at the site by water screening using a 0.3 mm sieve. This size sieve would retain any identifiable otoliths in the sample. The sample was transported back to the lab, where it was washed again and dried for microscopic examination. The Kemp Clay residue was microscopically examined, and all otoliths that were at least one-half complete were extracted. The residue yielded 1,202 mostly complete teleostean otoliths, which is an average of 44.52 otoliths/kg of sediment. This average is very high compared to other Cretaceous sites. For example, the Woodbury Formation of New Jersey only produced 5.22 otoliths/kg of sample (Stringer et al. 2016), while the Ripley Formation of Mississippi yielded almost the same concentration with 5.34 otoliths/kg of sample (Stringer et al. 2020). An extremely small concentration was reported by Nolf & Dockery (1993) with only 0.08 otoliths/kg of sediment from the Coffee Sand of Mississippi. The height, length, and height/length ratios are known for all of the specimens.

All of the figured otolith specimens from the Kemp Clay and the Clayton Formation have been deposited in the Perot Museum of Nature and Science, Dallas, Texas, USA (DMNH 2020-02-01 to 73). The specimens from the Fox Hills Formation are deposited at the North Dakota Geological Survey, Bismarck, North Dakota, USA (NDGS 5597 to 5611).

The otoliths were photographed by Schwarzhans using a Canon EOS mounted on the phototube of a Wilde M400 photomacroscope. Each of the figured otoliths were taken at regular focus levels for each view remotely controlled from a computer. The individual photographs of each view were stacked using the Helicon Focus software of Helicon Soft. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast or balance or retouch small inconsistences, such as adhered sand grains, incrustations, or pigmentation spots, as far as possible without altering the otolith morphology in any way. Care is taken to photograph the inner and outer faces of the otoliths with the central portion of the respective faces positioned at level in order to avoid distortions that otherwise occur in strongly bent specimens. The same principle is applied for lateral views, in which the otoliths are oriented in an upright position either along the horizontal or vertical axis depending dorsal/ventral and anterior/posterior views respectively. This type of standardized techniques has been shown to be essential for comparison with other research. Fixing otoliths in plasticine has proven to be the most effective method of achieving the desired results.

All of the figured otoliths show right otoliths. In some instances, left otoliths have been mirror imaged to facilitate standardized orientations and comparisons. These otoliths are annotated in the captions as "reversed." Individual specimens are shown from the inner face view, and in some cases, are shown from other views such as the outer face or ventral, dorsal, anterior, or posterior views. The

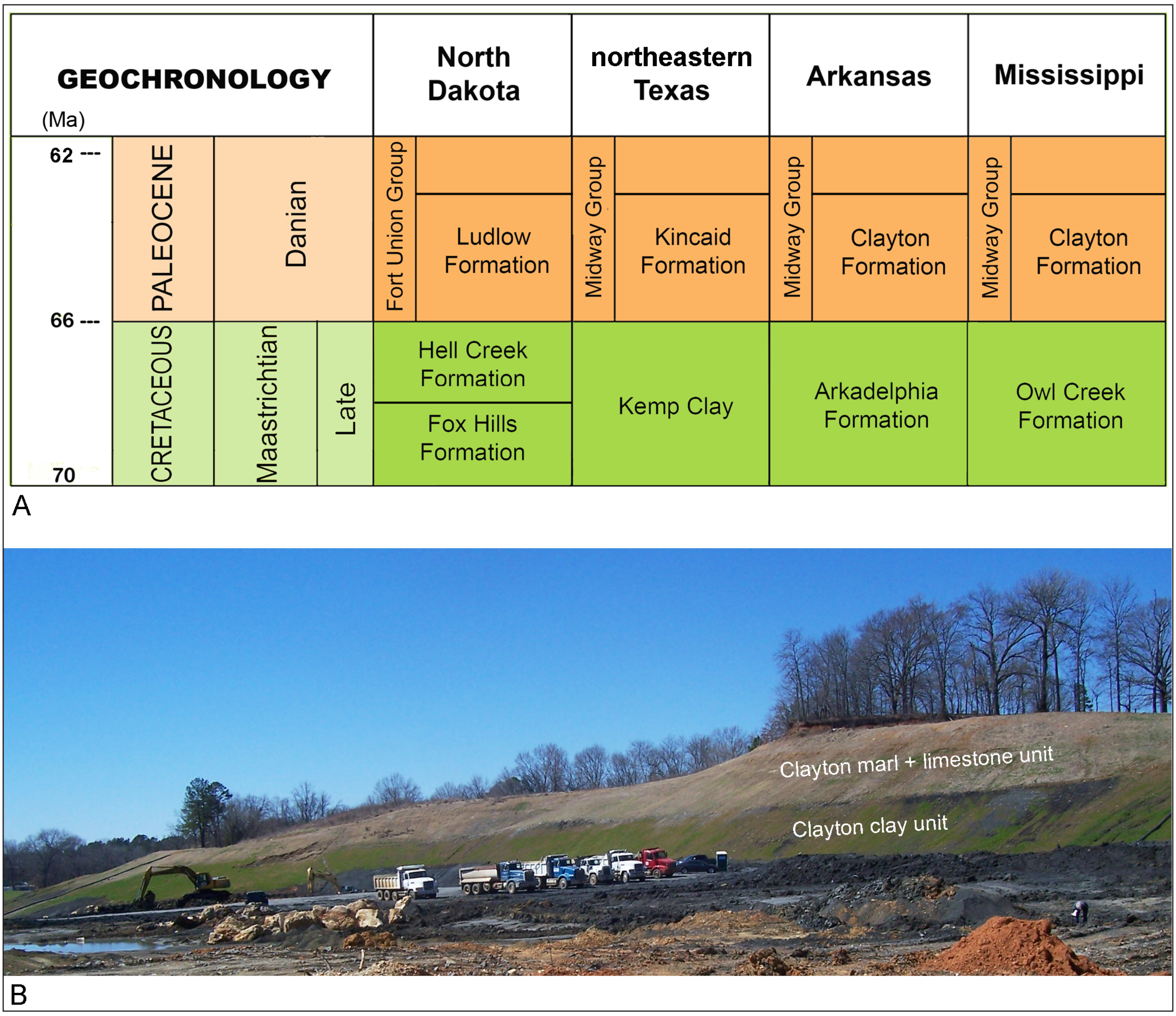


Fig. 2 - A) Generalized stratigraphic correlation of the late Maastrichtian and Danian formations of North Dakota, Texas, Arkansas, and Mississippi. B) Photograph of I-30 landslide near Malvern, Arkansas with the Danian Clayton Formation exposed. The otoliths were collected from near the base of the exposure.

other views are shown without annotation since their orientation can be easily deduced from the figure of the inner face of the otolith.

The morphological terminology of the sagittae otoliths (subsequently referred to as "otolith" or "otoliths") follows Koken (1884) with revisions made by Weiler (1942) and Schwarzhans (1978). Measurements were made using a camera lucida mounted on the microscope or from photographs obtained from the photomacroscope. The following abbreviations are used for expressing ratios: OL = otolith length, OH = otolith height, OT = otolith thickness, CaL = cauda length, CaH = cauda height, CCL = length auf caudal colliculum, CCH = height of caudal colliculum, OsL = ostium length, OsH = ostium height, OCL = length of ostial colliculum, OCH = height of ostial colliculum. The OsL is measured from the anterior tip of the ostium to an inflection point at the ventral margin of the ostium marking its termination, which may differ in cases from the posterior inflection of the dorsal margin of the ostium or the termination of the ostial colliculum. The CaL is measured from the same inflection point at the ventral margin of the sulcus to the termination of the cauda. The measures relating to OsL and CaL were taken when the sulcus margins were better-defined than the margins of the colliculi. Conversely, OCL and CCL were measured when the colliculi margins were clearer than the sulcus margins. Inclination angles were measured with the otolith oriented along its long axis, or in the case of high bodied otoliths along the sulcus axis.

REGIONAL GEOLOGY AND STRATIGRAPHY

The Cretaceous otoliths for this investigation were obtained primarily from the Kemp Clay (Fig. 2A). The Kemp Clay is widely distributed from central Texas to northeastern Texas, which leads to some variation in the lithology along the section. West of Bexar County in central Texas, there are lithological changes, and the Escondido

Formation is recognized rather than the Kemp Clay (Stephenson 1941; Welton & Farish 1993; Case & Cappetta 1997). The Kemp Clay is part of the Navarro Group (Cretaceous, Maastrichtian) and has a long history. The Navarro group was first used as a stratigraphic unit in 1887 and was formally designated as formation in 1901 (Hill 1887, 1901). Later, Navarro was elevated in rank to a group and subdivided into formations (Adkins 1933; Stephenson & Monroe 1937; Stephenson 1941). The Kemp Clay is the youngest formation of the Navarro group and the Cretaceous section as a whole in central Texas (Swanson et al. 1981; Case & Cappetta 1997; Woodward 2003; Clark 2009). The formation is separated from the overlying Paleocene strata by an obvious erosional unconformity and an impactite bearing layer at the base.

The Kemp Clay consists mainly of a dark clay with low calcium carbonate content. Although widely spaced, the Kemp Clay has layers and concretionary masses of gray dense, fine calcareous sandstone. Other descriptions note that the formation is comprised of a gray (weathers to red) clay (little to no silt) and is fairly uniform in composition from base to top. Impact glass is present at the top of the formation at the K-Pg boundary (Chimene & Maddocks 1984; Keller et al. 2007; Clark 2009). Sedimentary structures in the Kemp Clay are very limited and consist primarily of rare laminations (Stephenson 1941; Clark 2009) except for the uppermost part of the formation near the K-Pg boundary and the generally accepted bolide event. In central Texas, well data indicate a thickness of about 110 m for the Kemp Clay, but in other localities, the thickness is only 25 m (Barnes 1970). The differences in thickness appear to be related to the extent of the overlap of the overlying Paleocene strata. The Kemp Clay extends from western Hopkins County in northeastern Texas to Bexar County in central Texas. The outcrop is typically only about 3 km wide, but in southern Hunt County, it widens to almost 18 km, which is the maximum areal extent for the formation. The site for this study is located in this portion of the formation. It should be noted that no Paleogene strata are known from or adjacent to the study area on the South Sulphur River. Except for Cretaceous strata, the only other exposures near the site are Quaternary fluviatile terrace deposits and alluvium according to the Geologic Atlas of Texas, Texarkana sheet, 1:250,000 scale (Barnes 1991). Several studies indicate or suggest that the Kemp Clay is stratigraphically equivalent to the Escondido Formation in west Texas, the Arkadelphia Marl in Arkansas, the Fox Hills Sandstone of the Western Interior, the Severn Formation in Maryland, and the Navesink Formation in New Jersey (Stephenson 1941; Waage 1968; Swanson et al. 1981; Welton & Farish 1993; Baker 1995; Becker et al. 2006; Hoganson et al. 2019).

The fossiliferous nature of the Kemp Clay in Texas has been noted for over 150 years by numerous studies including Shumard (1862), Hill (1887), Adkins (1933), Stephenson (1938), Stephenson (1941), Powell (1965), Barnes (1991), Welton & Farish (1993), Becker (2006), and Clark (2009). The Kemp Clay at the sampled location has been characterized as having a typical late Maastrichtian fossil assemblage (Clark 2009). Powell (1965) noted the presence of abundant Cretaceous foraminifera and ostracods in the Kemp Clay along the South Sulphur River. The section of the South Sulphur River just southwest of Commerce in Hunt County, including the locality of this study, has been known for Cretaceous vertebrates for decades by professionals and amateurs (Welton & Farish 1993; Case & Cappetta 1997). The Kemp Clay locality in this study and adjacent areas along the South Sulphur River are known for their abundant skeletal remains of Cretaceous cartilaginous and bony fishes from the "fish-bed" (Davis & Ball 1991). This bed in the Kemp Clay has yielded thousands of Cretaceous shark and fish remains. In addition, a Late Cretaceous eutherian mammal was reported from this bed by Tokaryk & Case (1987). Besides the various Cretaceous fossils, the only other remains from the South Sulphur River in this area are Pleistocene vertebrates, primarily mammals, from the terrace deposits (Slaughter & Hoover 1963; Davis & Ball 1991). Although younger than the better known fossil localities along the North Sulphur River (McKinzie et al. 2001) 30 km to the north, the South Sulphur River contains similar types of Late Cretaceous vertebrates and invertebrates.

The Paleocene samples and resulting otoliths were collected from two sites (Interstate 30 slide site and the McNeil Creek site) in Arkansas from the Clayton Formation (Fig. 2A; Midway Group, lower Paleocene). The formation is lower Paleocene (Danian) in age and is primarily early to middle P1 Planktonic Foraminiferal Zone (McFarland 2004;

Dockery 1996; Hart 2017). Cicimurri & Ebersole (2015) indicate the age of the Clayton Formation slightly younger in Arkansas (late NP1, NP2, and early – middle NP3). According to Dockery (1996) and Dockery & Thompson (2016), the age of the formation is approximately 61.6 to 65 Ma, which is similar to the age indicated by Cohen et al. (2018). McFarland (1998) and Hart (2017) noted that the Midway Group is not normally divided in Arkansas, but numerous workers have recognized two formations: the Clayton Formation and the overlying Porter Creek Formation. He also noted that the Clayton Formation tends to contain most of the calcareous and sandy lithologies and produces a rich invertebrate fauna with some vertebrates also known (mainly fish and crocodile teeth). McFarland (2004) described the Midway sequence in Arkansas as representing a marginal marine depositional environment.

The stratigraphy of the Interstate 30 Slide site is known in much greater detail than the McNeil site (Phillips et al. 2015; Hart 2017). The Interstate 30 slide site had approximately 440 m of the early Paleocene (Danian) Clayton Formation exposed during remediation conducted because of land sliding toward the interstate highway, with about 7 m of the marl and limestone unit at the top and about 15 m of the clay unit below (see photograph in Fig. 2B). The otoliths have been collected from the base of the exposed section in the Clayton Formation clay unit, which is approximately 25 m above the base of the formation. The Clayton Formation in Arkansas typically has a basal sand (the event sand of the K-Pg bolide impact), a large clay unit (predominantly calcareous marine clays), a marl, and an upper calcarenite limestone (Stone & Sterling 1965). The large clay unit may compose as much as 90% of the formation (Hart 2017). Although the basal sand is not exposed at the Interstate 30 slide site, the other units are exposed (clay unit, marl, and limestone). It should be noted that another site located 200 m east of the Interstate 30 slide site has the Cretaceous Arkadelphia Formation, the basal sand unit (the event sand with reworked Cretaceous foraminifera, impact spherules, and rip-up clasts of the underlying Cretaceous Arkadelphia Formation), and the Clayton exposed (Becker et al. 2006, 2010; Hart 2017). Unfortunately, that site is in a river, and the preservation of the otoliths collected there has been poor thus far. Examination of the various lines of evidence (stratigraphy, sedimentation, and paleontology) indicate that the Interstate 30 slide site is probably late early P1 in age (late NP1 or early NP2).

The McNeil Creek site, which is approximately 30 km northeast of the Interstate 30 slide site, is named for the small creek on which it is found. The areal extent of the early Paleocene Clayton Formation at the McNeil Creek site is only a fraction of that at the Interstate 30 slide site. The exposures of the Clayton Formation along the creek banks are generally less than 1 m. Small (several cm in height) lag deposit lenses are present in the Clayton Formation, which are also found at the Interstate 30 slide site. While the McNeil Creek site can be assigned to the predominantly marine clay unit of the Clayton Formation, it is not possible to ascertain its exact stratigraphic position within the clay unit.

Previous studies

Cretaceous otoliths

Studies of Cretaceous otoliths in North America are summarized and discussed by Stringer, Schwarzhans, Phillips and Lambert (2020), and the reader is directed to that publication for further details. Although the occurrence of Cretaceous otoliths in North America was first mentioned by Wade (1926) from the Coon Creek site in southwest Tennessee, their detailed investigation did not occur until many decades later. Even presently, there are many Cretaceous otolith assemblages that remain unstudied, and many occur in the Late Cretaceous, which is a pivotal time in the evolution of the osteichthyans. Fortunately, the study of Cretaceous otoliths in North America has increased in the past few years with studies of the Eutaw Formation in Alabama (Schwarzhans et al. 2018b), the Woodbury Formation in New Jersey (Stringer et al. 2016), the Tar Hill Formation in North Carolina (Stringer et al. 2018), and the Ripley and Owl Creek formations (Stringer et al. 2020). The investigation of the otoliths of the Kemp Clay have been restricted to three preliminary studies. Stringer (1998a and 1998b) conducted initial studies on the otoliths of the Maastrichtian Kemp Clay, while Woodward (2003) completed an unpublished MS thesis on the Kemp Clay otoliths. Woodward examined over 1000 otoliths and recognized 27 taxa representing 15 families, which indicated a fairly abundant and rather diverse otolith assemblage.

Paleocene otoliths

Investigations of Paleocene otoliths worldwide have lagged greatly behind other Paleogene, Neogene, and Quaternary strata. In fact, there are more studies of Cretaceous otoliths than of Paleocene otoliths in North America (Nolf & Stringer 1996; Schwarzhans 1985b, 2004; Nolf & Dockery 1993). Furthermore, descriptions of Paleocene otolith assemblages have been almost exclusively from Europe. Schwarzhans (2012) noted that of the 109 known Paleocene otolith-based fishes worldwide 91 of them come from the Paleocene of Europe. This statistic emphasizes the importance and significance of this study of the Paleocene otoliths from the Arkansas localities.

Even though Paleocene otoliths have been known for over 100 years in Europe (Koken 1885, 1891a, b; Leriche 1902), scientific investigations have been very limited. Paleocene studies from the middle to late 1900s in Europe included Stinton (1965) and Nolf (1978) with sites from primarily England and Belgium. More recently, Schwarzhans has reported on several European Paleocene sites including Denmark (Schwarzhans 2003), Ukraine (Schwarzhans & Bratishko 2011), and Bavaria and Austria (Schwarzhans 2012).

Although Paleocene otolith investigations have been limited in Europe, studies elsewhere have been even scarcer. Schwarzhans (1985a) described Paleocene otoliths from southern Australia. In North America, studies of Paleocene otoliths are restricted to one investigation in Canada (Schwarzhans 1985b), one in Greenland (Schwarzhans 2004), and one major study in the United States (Nolf & Dockery 1993) with two minor reports of Paleocene otoliths (Frizzell 1965; Cvancara & Hoganson 1993). The Nolf and Dockery (1993) study appears to be based on less than 250 otoliths from the Porters Creek Formation in Alabama. The study does make use of Paleocene otoliths from the Brightseat Formation in the Washington, D.C. vicinity, but no quantitative data are presented. Frizzell (1965) described one taxon of albulid (bonefish) from the Paleocene Porters Creek Formation in Alabama. Cvancara and Hoganson (1993) identified two otolith taxa (a pterothrissid and an ariid) from an extensive examination of the marine vertebrates of the Paleocene Cannonball Formation in North Dakota. Therefore, it is quite apparent that the knowledge of Paleocene fish otoliths and their biostratigraphic ranges in the United States is meager at best. The paucity of Paleocene otolith investigations in the United States certainly points to the significance of the Paleocene otoliths from Arkansas described in this study.

SYSTEMATIC PALEONTOLOGY

Remarks

The identification of fossil otoliths is almost entirely dependent on comparison with extant specimens for systematic allocation, when not calibrated by finds of fossil skeletons with otoliths in situ. The latter is rare and only very recently have otoliths in situ been recorded from Cretaceous fishes (Schwarzhans, Beckett, Schein & Friedman 2018). For these reasons, otolith research in the Late Cretaceous has the dilemma that only a certain percentage of morphotypes can be convincingly attributed to extant groups while many others represent morphologies, which are difficult to relate. Consequently, many generic allocations in the systematic part relate to either fossil, mostly otolith-based genera or extant genera, which are understood as used in a rather broad sense. Some of the well-defined extinct otolith morphologies can not be comfortably allocated with persistent families and even the allocation to orders can be rather vague. This is reflected with an indeterminate familial systematic position. However, in certain other instances, the otolith morphology is so generalized for the family it represents that allocation in a fossil or extant genus is not possible. In these instances, we follow the recommendation made by Janssen (2012) by using ‘the name of the type-genus of the family followed by a question mark, indicating that those species might as well belong to any other known or unknown genus in the particular family.’

The taxa represented by the otoliths in the Kemp Clay, Fox Hills Formation and the Clayton Formation are presented in Table 1 (except Fox Hills Formation) and shown in Figures 3 – 10. The systematic paleontology of the taxa are provided.

Tab. 1 - Taxa represented by otoliths from the Kemp Clay Formation (northeastern Texas, late Maastrichtian) and the Clayton Formation (early Danian, Arkansas). Counts of most common species (> 5 %) in bold and fields in dark grey.

Order / Family / *Species*	**Maastrichtian:** Kemp Clay		**Danian:** Clayton Fm.	
	specimens	percentage	specimens	percentage
Albuliformes				
Albulidae				
Albula cf. *bashiana*	7	0.58	**34**	**8.42**
Pterothrissidae				
Elopothrissus carsonsloani			8	1.98
Pterothrissus conchaeformis	**113**	**9.33**	**47**	**11.63**
Pterothrissus cf. *foreyi*	2	0.17		
Order and family indeterminate				
Genartina sp. 1	3	0.25	8?	1.98
Genartina sp. 2			1	0.25
Anguilliformes				
Anguillidae				
Anguilla? *chickasawae*			8	1.98
Ophichthidae				
Echiophis aff. *semisphaeroides*	2	0.17		
Heterenchelyidae				
Pythonichthys arkansasensis	3	0.25	**82**	**20.30**
Congridae				
Congrophichthus transterminus	3	0.25	25	6.19
Rhynchoconger brettwoodwardi	25	2.06		
Rhynchoconger? *piger*	38	3.14		
Siluriformes				
Ariidae				
Arius? *danicus*	**67**	**5.53**	**107**	**26.49**
Arius? *subtilis*	**195**	**16.10**	**42**	**10.40**
Family indeterminate				
Vorhisia vulpes	**423**	**34.93**		
Aulopiformes				
Paraulopidae				
Paraulopus sp.	4	0.33		
Gadiformes				
Gadidae				
Dakotaichthys hogansoni	16	1.32		
Merlucciidae				
Palaeogadus weltoni	2	0.17		
Family indeterminate				
Archaemacruroides bratishkoi	11	0.91		
Ophidiiformes				
Ophidiidae				
Ampheristus americanus	**130**	**10.73**	13	3.22
Protobythites brzobohatyi	1	0.08		
Bythitidae				
Bidenichthys? *crepidatus*	2	0.17		
Trachichthyiformes				
Trachichthyidae				
Hoplostethus stringeri	52	4.29	7	1.73
Beryciformes				
Berycidae				
Centroberyx apogoniformis	42	3.47	1	0.25
Family indeterminate, type 1				
Eutawichthys choctawae	7	0.58		
Eutawichthys maastrichtiensis	2	0.17		
Family indeterminate, type 2				
Argyroberyx dentatus	1	0.08		
Perciformes				
Serranidae				
Serranus? *caribbaeus*	12	0.99	13	3.22
Totals	**1160**		**404**	

Otolith comparative collections of Recent and fossil specimens were utilized for the identification of the otoliths as well as literature references. The classification scheme follows that of Nelson et al. (2016). Any deviation from this classification is noted.

The following descriptive part is arranged in two distinct parts. The first part contains identifications and descriptions of sagittal otoliths, the ones usually studied in the fossil record. The second part covers utricular (lapilli) otoliths.

SAGITTAL OTOLITHS

Order **Albuliformes** Jordan, 1923
Family Albulidae Bleeker, 1859
Genus *Albula* Scopoli, 1777

Albula* cf. *bashiana (Frizzell, 1965)

Fig. 3 A-D

?1965a *Metalbula bashiana* – Frizzell: pl. 4, fig. 4.
1993 *Albula* cf. *bashiana* (Frizzell, 1965) – Nolf & Dockery: pl. 1, figs. 1-2.

Material: 41 mostly poorly or fragmentary preserved specimens (figured specimens DMNH 2020-02-01 to 02): 7 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 34 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. We follow Nolf & Dockery (1993) in tentatively assigning these otoliths to *Albula bashiana*, which was originally described from the early Eocene and also their rational in placing the species in the extant genus *Albula*. The steeply inclined posterior half of the cauda serves as our main argument in support of Nolf & Dockery's assessment.

Unfortunately, none of the many specimens are well enough preserved for a precise morphological description. Even the few complete specimens show significant indications of erosion. The dorsal rim of the otolith is always abraded to some extend in all specimens and the best specimen from the Kemp Clay (Fig. 3 A-C) shows in addition an eroded midventral rim. We conclude that the specimens described here and by Nolf & Dockery (1993) could possibly represent a different species than *A. bashiana* or the coeval nominal *A. meridiana* (Frizzell, 1965), but better preserved specimens have to be awaited for such assessment. In any case, *A.* cf. *bashiana* represents one of the specimens documented to cross the K-Pg boundary.

Family Pterothrissidae Gill, 1893

Remarks. We follow the arguments of Nolf (2013) and remain keeping the family Pterothrissidae separate from the Albulidae, which is contrary to Nelson et al. (2016).

Genus *Elopothrissus* Schwarzhans, 1981

***Elopothrissus carsonsloani* n. sp.**

Fig. 3 E-J

Etymology: In honor of James Carson Sloan (Benton, Arkansas, USA) a geologist for the State of Arkansas who has been intensely collecting and studying the Clayton Formation.

Holotype: DMNH 2020-02-03 (Fig. 3 E-F), McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Paratypes: 3 specimens, DMNH 2020-02-04 to 06, early Danian, Clayton Formation, Arkansas. 2 specimens same data as holotype, 1 specimen Interstate-30 slide site, west of Malvern, Hot Spring County.

Further specimens: 4 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Diagnosis: Large, very elongate, thin otolith with shallow dorsal rim. OL:OH = 2.3. Anterior and posterior tips of otolith distinctly tapering; long rostrum. Ostium wide, dorsally open; cauda slightly bent along entire course, inclined at about 10° angle. CaL:OsL = 1.35; OsH:CaH = 1.7. Inner face convex; outer face flat to slightly concave.

Description. Large, thin, elongate otoliths up to 13.5 mm length (holotype). OH:OT = 2.7-3.0. Dorsal rim shallow, without prominent angles, highest at about its middle, smooth. Ventral rim more deeply and regularly curved, smooth. Anterior rim with a long, massive, anteriorly tapering rostrum with rounded tip. Posterior rim with slightly dorsally shifted, tapering tip similar to rostrum.

Inner face distinctly convex with strongly supramedian positioned sulcus. Ostium wide, anteriorly and dorsally opened, shallow. Cauda slightly deepened, slightly bent, inclined at an angle of about 10°, terminating moderately close to posterior rim of otolith. Colliculi usually indistinct; caudal colliculum sometimes well marked and then much narrower than cauda. Dorsal depression very narrow, often indiscernible; ventral field smooth, without ventral furrow. Outer face flat to slightly concave, smooth.

Ontogeny. Amongst the available specimens two are large (>13 mm length; Fig. 3 E-G), while the remainder are all very small (<3.5 mm length; Fig. 3 H-J). Only two specimens, the large holotype (Fig. 3 E-F) and the smallest available specimen of 1.5 mm (Fig. 3 J) have a fully preserved rostrum. They are all very elongate, but the degree of the ratio OL:OH considerably increases from the smallest to the largest (1.9 to 2.3), characterized by an elongation of the rostrum, which also finds it expression in a decrease of the ratio CaL:OsL of 1.5 to 1.35. The small specimen shows a mild postdorsal angle and some faint marginal crenulation, which is all missing already with the specimen of 3.1 mm length (Fig. 3 H-I). Like with many other pterothrissids morphological maturity is only reached with specimens larger than 5 mm length, and smaller specimens should not be used for species definition (Schwarzhans 2012).

Discussion. The genus *Elopothrissus* was established for the early Eocene *Pterothrissus protensus* Stinton, 1975, which was placed into synonymy with *Dentex tardinensis* Leriche, 1908, now *Elopothrissus tardinensis* and further contains the Oligocene species *Elopothrissus elongatus* (Weiler, 1942). Numerous small and a single incomplete larger specimen of an unidentified *Elopothrissus* was recorded by Schwarzhans, Huddleston and Takeuchi (2018) from the Santonian of Alabama, documenting that *Elopothrissus* represented an extinct pterothrissid genus extending well across the K-Pg boundary.

Genus *Pterothrissus* Hilgendorf, 1877

Pterothrissus conchaeformis (Koken, 1885)

Fig. 3 K-W

1885 genus inc. sed. *conchaeformis* – Koken: pl. 5, fig. 25.
1930 genus inc. sed. *erhardtvoigti* – Roedel: pl. 1, fig. 14.
2003 *Pteralbula conchaeformis* (Koken, 1885) – Schwarzhans: fig. 7 A-J.
2004 *Pterothrissus conchaeformis* (Koken, 1885) – Schwarzhans: fig. 2 A-D.
2012 *Pteralbula conchaeformis* (Koken, 1885) – Schwarzhans: figs 4-9.
2017 *Pteralbula conchaeformis* (Koken, 1885) – Schwarzhans & Milan: fig. 6 A-D.

Material: 160 specimens, many poorly or fragmentary preserved (figured specimens DMNH 2020-02-07 to 13): 113 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 47 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. *Pterothrissus conchaeformis* has in the past been placed variably in the fossil otolith-based genus *Pteralbula* and the persistent extant genus *Pterothrissus*. The two living species of *Pterothrissus* have recently been separated in two distinct genera: *Pterothrissus gissu* Hilgendorf, 1877 and *Nemoossis belloci* (Cadenat, 1937) by Hidaka et al. (2017). *Pteralbula* has been redefined by Schwarzhans (2018) and as a consequence was reduced to three early Cretaceous species: the type species *Pteralbula cantiana* (Shepherd, 1916), *P. galtina* (Koken, 1891) and *P. todolellana* (Nolf, 2004). The Maastrichtian *Pteralbula foreyi* Schwarzhans, 2010 and *Pteralbula conchaeformis* were both placed in the genus *Pterothrissus* and now represent its earliest unambiguous records.

Pterothrissus conchaeformis belongs to a group of Paleogene and Late Cretaceous species in the genus characterized by a relatively strong curvature of the inner face, a flat to concave outer face (in specimens larger than about 5 mm length) and a marked postdorsal angle, and contains the following species: *Pterothrissus foreyi* (Schwarzhans, 2010) hitherto from the Maastrichtian of Bavaria, *P. conchaeformis* (Koken, 1885) hitherto from the Danian and Selandian of Denmark, Bavaria, and western Greenland, *P. angulatus* Stinton, 1966 from the early Eocene of England and recently from the middle Eocene of New Zealand (Schwarzhans 2019a) and *P. caspianensis* Bratishko, 2013 from the early Oligocene of Kazakhstan. The differentiation of the latter three species depends primarily on the expression of the rather straight dorsal rim and its angle against the sulcus inclination, which is about 20° in *P. angulatus*, about 25° in *P. conchaeformis* and 30-35° in *P. caspianensis*. This results in *P. caspianensis* that dorsal and ventral rims are parallel while in *P. conchaeformis* dorsal and ventral rims run almost but not quite parallel and in *P. angulatus* the posterior part of the otolith is mildly tapering. However, these characters are also subject to considerable variability and ontogenetic effects, as are the ratio OL:OH which ranges between 1.35 and 1.75 in *P. conchaeformis* alone (see Schwarzhans 2003, on specimens from the type-locality). Therefore, the distinction of *P. conchaeformis* and *P. angulatus* at present must be considered as poorly constrained and should be seriously tested, while the identity of *P. caspianensis* appears more secure.

We were unable to comfortably distinguish between *P. angulatus* and *P. conchaeformis* and allocated our specimens from the Maastrichtian Kemp Clay and the early Danian Clayton Formation to the latter, mainly because it has been established for Paleocene records, while *P. angulatus* was used for Eocene specimens. The depicted variations of the dorsal rim and the ratio OL:OH (1.45 to 1.6) (compare Fig. 3 K with 3 T) falls well within the range of variability observed in the species elsewhere and may be enhanced by erosional effects (anterior rim of the specimen figured in Fig. 3 K). At Stevns Klint in Denmark, *P. conchaeformis* has been found right

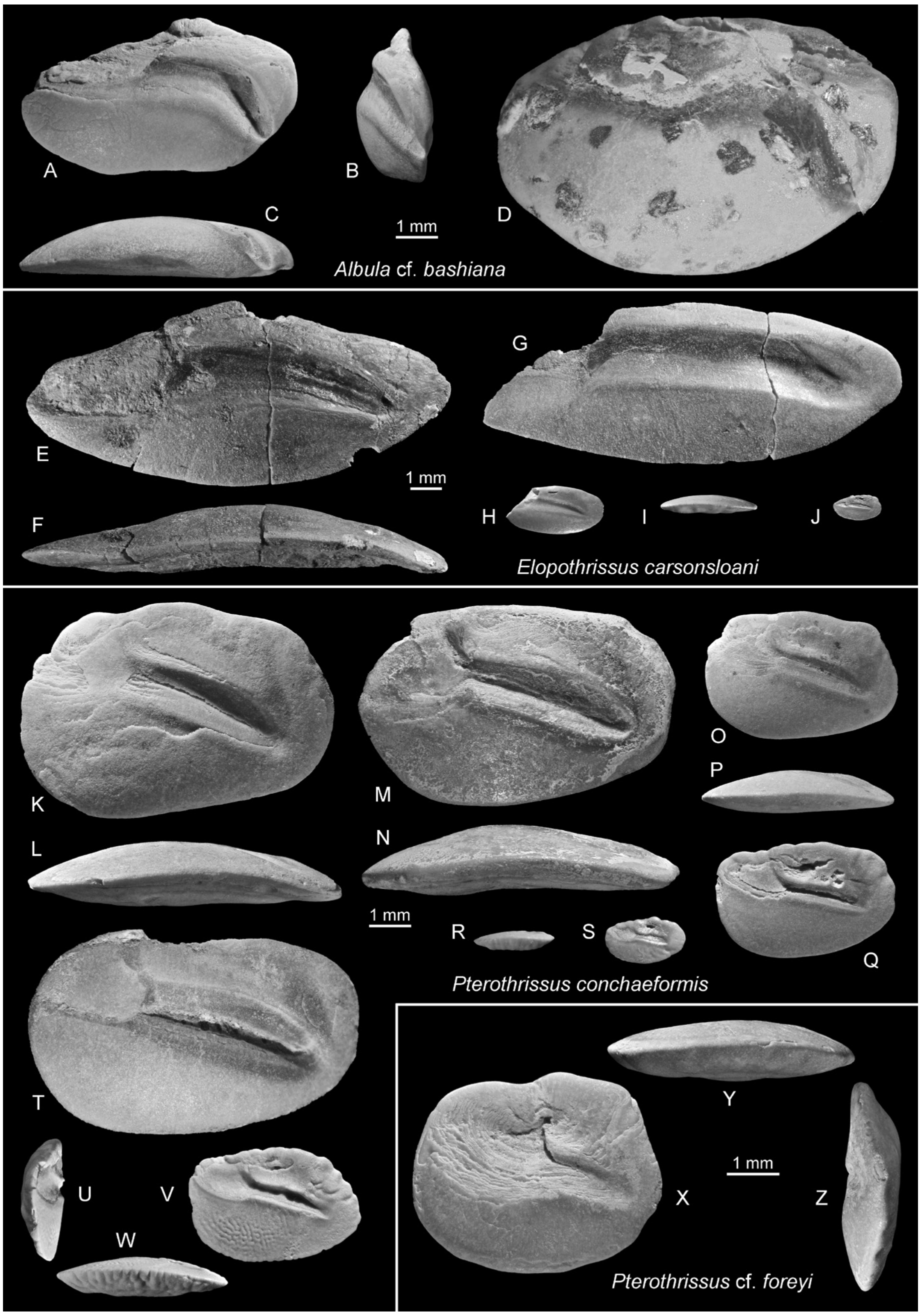


Fig. 3 - A-D) *Albula* cf. *bashiana* (Frizzell, 1965); A-C Kemp Clay, DMNH 2020-02-01 (reversed); D Clayton Formation, DMNH 2020-02-02. E-J) *Elopothrissus carsonsloani* n. sp. Clayton Formation; E-F holotype, DMNH 2020-02-03 (reversed); G-J paratypes, DMNH 2020-02-04 to 06 (G, J reversed). K-W) *Pterothrissus conchaeformis* (Koken, 1885); K-L, O-S, U-W Kemp Clay, DMNH 2020-02-07 to 11 (R-S, U-W reversed); M-N, T Clayton Formation, DMNH 2020-02-12 to 13 (M-N reversed). X-Z) *Pterothrissus* cf. *foreyi* (Schwarzhans, 2010), Kemp Clay, DMNH 2020-02-14.

above the K-Pg event clay (Fiskeler Member). It is thus not surprising that now *P. conchaeformis* is also recorded from the late Maastrichtian Kemp Clay making it another survivor across the K-Pg boundary. A different yet undefined species of *Pterothrissus* has also been recorded from the Maastrichtian of Mississippi (Stringer et al. 2020), which is characterized by a distinctly tapering posterior part of the otolith.

Pterothrissus **cf.** ***foreyi*** (Schwarzhans, 2010)

Fig. 3 X-Z

?2010 *Pteralbula foreyi* – Schwarzhans: figs 4-5.

Material: 2 specimens (figured specimen DMNH 2020-02-14), both eroded on the surface, South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. These specimens depict the characteristic hallmarks of *P. foreyi* hitherto only known from the Maastrichtian of Bavaria, namely the low ratio OL:OH (1.2), the middorsal expansion of the dorsal rim, and the short cauda compared to the ostium (OsL:CaL about 0.7). The preventral angle is more rounded in the Kemp Clay specimen than in the Bavarian ones. This, and the poor preservation have led us to only tentatively assign the Texan specimens to *P. foreyi*.

Order indeterminate
Family indeterminate
Genus *Genartina* Frizzell & Dante, 1965

Remarks. The fossil otolith-based genus *Genartina* ranges from Late Cretaceous (Santonian) to Middle Eocene (Bartonian) and has been placed in a variety of different systematic positions like Osteoglossiformes (Frizzell & Dante 1965), Osmeridae (Nolf 1985), Elopiformes (including Albuliformes) in Schwarzhans (2003, 2012), Harpadontidae (Nolf 2013), Synodontidae (Stringer et al. 2016) or Stomiiformes (Schwarzhans, Huddleston & Takeuchi 2018). Most likely it represents a group of extinct teleost fishes at a higher level than family. We are placing it here as belonging to an indeterminate family and order after Albuliformes reflecting the most common allocation in past literature.

***Genartina* sp. 1**

Fig. 4 A-D

Material: 11 mostly poorly or fragmentary preserved specimens (figured specimens DMNH 2020-02-15 to 16): 3 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 8 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. These are all incomplete but very typical *Genartina* otoliths, which resemble in shape and proportions those of *G. abbatiae* (Stinton, 1965) from the European Paleocene (see Schwarzhans 2003) and early Eocene.

***Genartina* sp. 2**

Fig. 4 E-F

Material: 1 incomplete specimen (DMNH 2020-02-17) McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. This singular specimen differs from the preceding one in the more elongate shape caused by less steeply curved dorsal and ventral rims, and the considerably deepened, posteriorly widened cauda. The morphological features appear to represent *Genartina* but it does not resemble any *Genartina* species described thus far in the fossil record.

Order **Anguilliformes** Regan, 1909
Family Anguillidae Rafinesque, 1810
Genus indet.

Anguilla*? *chickasawae Schwarzhans & Stringer, 2020

Fig. 4 G-I

1983 Anguilloidei-B – Huddleston & Savoie: fig. 2 C.
2020 *Anguilla*? *chickasawae* – Schwarzhans & Stringer: fig. 5 A-E.

Material: 8 specimens (figured specimens DMNH 2020-02-18 to 19) Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. *Anguilla*? *chickasawae* was originally described from the Maastrichtian of Mississippi and has been diagnosed primarily by a rather elongate shape (ratio OL:OH = 1.5) and a relatively long ostium (CaL:OsL = 1.1-1.4). Outline of otolith and sulcus and otolith proportions of the early Danian specimens depicted here fall well into an expected range of variability (OL:OH = 1.55; CaL:OsL = 1.25-1.35). *Anguilla*? *chickasawae* differs from other Late Cretaceous or Paleogene anguillid otoliths in the relatively long ostium, which in other species is shorter by a factor of 2. We consider *A*? *chickasawae* to represent a fossil genus of the family Anguillidae or a related fossil family of which otoliths are not yet known.

Family Ophichthidae Rafinesque, 1815
Genus *Echiophis* Kaup, 1856

Echiophis* aff. *semisphaeroides (Schwarzhans, 2003)

Fig. 4 J-K

?2003 genus *Anguillidarum semisphaeroides* – Schwarzhans: fig. 9 A-D.

Material: 2 specimens (figured specimen SMNH 2020-02-20) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. *Echiophis semisphaeroides* was originally understood as an anguillid otolith, but a recent figure of the extant *Echiophis brunneus* (Castro-Aguirre & Suárez de los Cobos 1983) in Schwarzhans (2019b) has revealed great similarity in convexity and smoothness of the inner face as well as shape and depth of the sulcus. *Echiophis* is known from three extant species in tropical and subtropical America. Recent ophichthid otoliths show a great diversity and are still poorly known to the extent

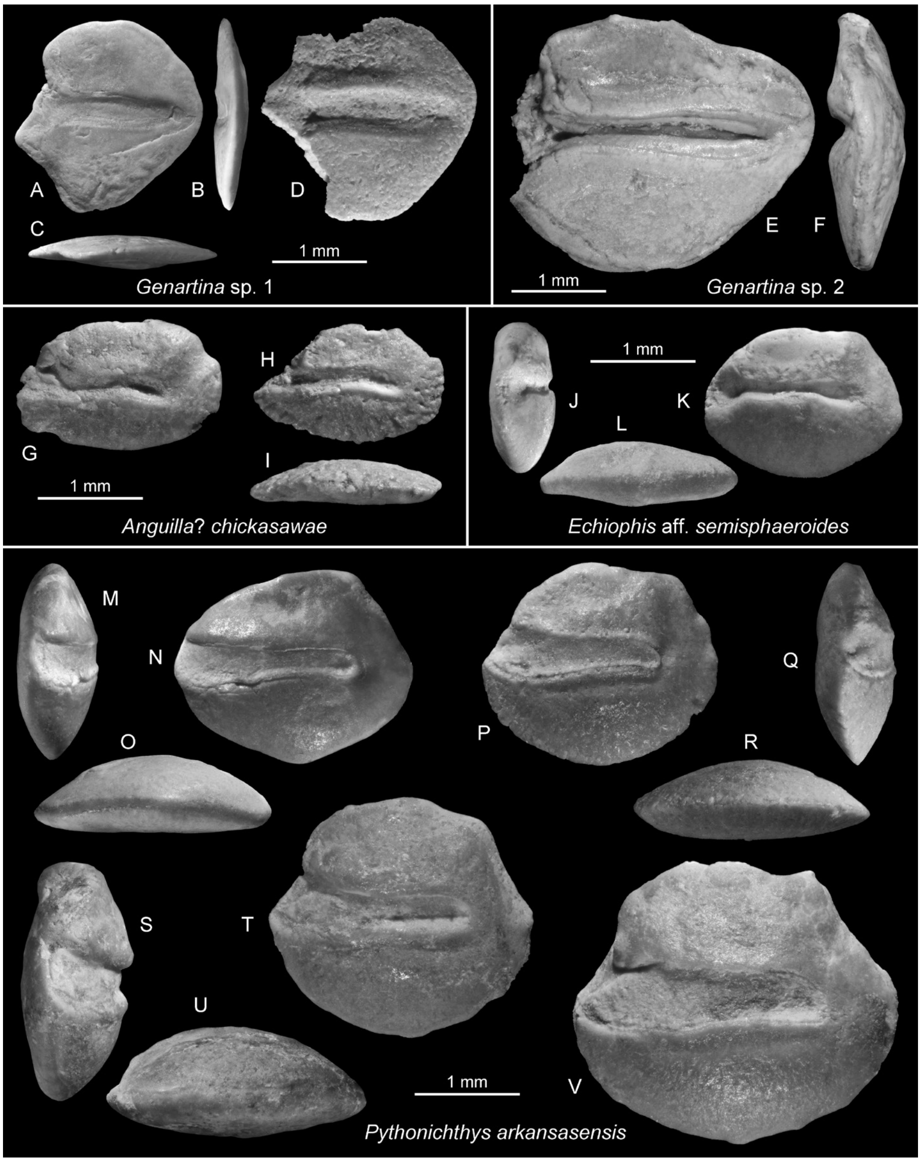


Fig. 4 - A-D) *Genartina* sp. 1; A-C Kemp Clay, DMNH 2020-02-15; D Clayton Formation, DMNH 2020-02-16. E-F) *Genartina* sp. 2, Clayton Formation, DMNH 2020-02-17 (reversed). G-I) *Anguilla? chickasawae* Schwarzhans & Stringer, 2020, Clayton Formation, DMNH 2020-02-18 to 19 (H-I reversed). J-K) *Echiophis* aff. *semisphaeroides* (Schwarzhans, 2003), Kemp Clay, DMNH 2020-02-20 (reversed). M-V) *Pythonichthys arkansasensis* n. sp.; P-R holotype, Clayton Formation, DMNH 2020-02-21 (reversed); M-O paratype, Kemp Clay, DMNH 2020-02-24; S-V paratypes, Clayton Formation, DMNH 2020-02-22 to 23 (V reversed).

that fossil otoliths can rarely be generically allocated with great comfort. In this case, however, the similarity is really significant also in comparison with morphologies known from other anguilliform otoliths.

Echiophis semisphaeroides was originally described from the Selandian of Denmark based on two well preserved specimens by Schwarzhans (2003, as genus *Anguillidarum semisphaeroides*), but allocation to *Echiophis* was made possible after otoliths of the extant *Echiophis brunneus* have become known (Schwarzhans 2019b). Our late Maastrichtian specimens from the Kemp Clay are moderately well preserved and differ slightly from the Paleocene specimens in the cauda being narrower along its anterior half and being slightly widened posteriorly while the cauda does not change width over its course in the Paleocene specimens. This indicates that the Kemp Clay specimens could possibly represent a closely related but distinct species. However, preservation and number of specimens available are not sufficient to presently resolve this, and therefore, we consider it prudent to place the Maastrichtian specimens tentatively in *Echiophis* aff. *semisphaeroides*.

Family Heterenchelyidae Regan, 1912
Genus *Pythonichthys* Poey, 1868

Pythonichthys arkansasensis n. sp.

Fig. 4 M-V

Etymology: Named after the state of Arkansas because of its common occurrence in the early Danian Clayton Formation of Arkansas.

Holotype: DMNH 2020-02-21 (Fig. 4 P-R), McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Paratypes: 4 specimens: 3 specimens (DMNH 2020-02-22 to 23) same data as holotype; 1 specimen (DMNH 2020-02-24) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Further specimens: 80 specimens: 78 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation; 2 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Diagnosis: Almost perfectly round otoliths; OL:OH = 1.1-1.2. Inner face strongly convex, rather smooth with slightly deepened sulcus. OL:SuL = 1.25-1.35. Ostium and cauda about equally long, only very faintly distinguished. Cauda slightly tapering and with very feeble flexed and rounded tip.

Description. Small, nearly round, compact otoliths up to 3 mm length (holotype 2.25 mm). Ventral rim very regularly curved, nearly semicircular, smooth. OH:OT = 2.2-2.5. Dorsal rim less regularly curved, with broadly rounded pre- or postdorsal angles and sometimes slightly undulating. Posterior rim perfectly rounded; anterior tip with very short, blunt rostrum and minute excisura.

Inner face distinctly convex with relatively smooth ventral and dorsal fields without ventral furrow and very feeble and indistinct dorsal depression. Sulcus slightly supramedian, slightly deepened, anteriorly open, posteriorly closed at some distance from posterior rim of otolith. Distinction of ostium and cauda very feeble, sometimes indicated by weak step change in undivided colliculum; ostium and cauda of about equal length. Sulcus slightly widening towards anterior; posteriorly slightly narrowing and very slightly flexed with rounded tip. Posterior half of sulcus often underpinned by broad parallel furrow. Outer face flat and mostly smooth.

Discussion. *Pythonichthys arkansasensis* represents the earliest known otolith-based heterenchelyid and also another species crossing the K-Pg boundary. Several species have been described from the Eocene (see Nolf 2013). There are few useful characters to define heterenchelyid otoliths. Otoliths of *Panturichthys*, the second extant genus in the family, appear to have a shorter sulcus (OL:SuL >1.4, mostly >1.5) and an ostium that does not widen anteriorly while those of *Pythonichthys* have a longer sulcus (OL:SuL <1.4) and tend to have an anteriorly slightly widening sulcus. *Pythonichthys arkansasensis* differs from all extant and fossil heterenchelyid otoliths in the presence of a very feeble flexure of the posterior tip of the sulcus, except possibly for *P. circularis* (Shepherd, 1916) from the Middle Eocene of Europe (see Nolf 2013), which however differs in an even more compressed, round shape (OL:OH <1.1) and the distinctly supramedian position of the sulcus.

The extant members of the Heterenchelyidae, a small family of burrowing eels, are found in the Atlantic and eastern Pacific oceans. The present center of diversity is the Atlantic coast of Africa, where five species are found (Smith et al. 2012). Heterenchelyids are also known for their peculiar habitat living mostly submerged in soft bottom and shallow water. They are known for their head-first burrowing behavior, which requires a specific set of osteological specializations and is regarded as highly derived (Eagderi & Adriaens 2010). Smith et al. (2012) noted that the family was perhaps more diverse and more widespread geographically in the geologic past and that the present representatives are only a remnant of their former diversity. Their abundance in the shallow-water, mud-dominated facies of the Clayton Formation in Arkansas is the highest observed anywhere in the fossil record and indicates that this specialization might already have been achieved as early as the latest Cretaceous/earliest Paleocene.

Family Congridae Kaup, 1856
Genus *Congrophichthus* n. gen.
Type species: *Congrophichthus transterminus* n. sp.

Etymology: A combination of the two generic names *Conger* and *Ophichthus* referring to the morphological similarity of these otoliths.

Diagnosis: A fossil otolith-based genus of the family Congridae with the following combination of characters. Otolith moderately elongate with ventral rim much deeper than dorsal rim and anterior tip sharper than posterior tip. Inner face more strongly convex than outer face. Sulcus moderately deepened, inclined at 5 to 8°, anteriorly reaching very close to anterior rim of otolith, posteriorly terminating distant from posterior rim of otolith; OL:SuL = 1.45-1.55. Ostium widened, short, indistinctly marked against cauda, with faint indication of short, vertically oriented ostial channel as a broad depression rather than a clearly bound feature. Cauda straight, with very slightly flexed tip. Distinct and large dorsal depression; no ventral furrow, but sometimes short vertical furrow at caudal termination.

Discussion. *Congrophichthus* combines characters found in certain congrid, muraenesocid, and ophichthid genera. The sulcus reaching very close to the anterior rim of the otolith is typical for muraenesocid and many ophichthid otoliths. The widened ostium is common in ophichthid otoliths and the indicated dorsal channel, although rather indistinct, is typical for many congrid otoliths. The distinct dorsal depression is found in certain congrid groups

(Schwarzhans 2019b). The outline of the otolith and its general appearance as well as the organization of the sulcus resembles certain Eocene otoliths that are typically associated with muraenesocids, like *Muraenesox cymbium* Stinton, 1966, *M. fissura* (Stinton & Nolf, 1970), and *M. furcatus* Schwarzhans, 2007, but none of these show any indication of an ostial channel and no marked dorsal depression. Because of these two characters, we consider *Congrophichthus* to represent a congrid and regard it as an indication again that not only many extant congrid genera may have originated during the latest Cretaceous or the Paleogene but also that there were several extinct early congrid lineages present at that time (see also Schwarzhans 2019b).

Species. *Congrophichthus* currently is a monospecific genus with *C. transterminus* recorded since late Campanian and across the K-Pg boundary.

Congrophichthus transterminus n. sp.

Fig. 5 M-U

1990 Congridae – Nolf & Dockery: pl. 1, fig. 3.
1993 genus Congridarum sp. – Nolf & Dockery: pl. 1, fig. 4.
1996 Congridae indet. – Nolf & Stringer: pl. 2, fig. 9.

Etymology: From trans (Latin = across) and terminus (Latin = boundary) referring to the occurrence of this species across the K-Pg boundary event.

Holotype: DMNH 2020-02-31 (Fig. 5 P-S), McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Paratypes: 3 specimens: 2 specimens (DMNH 2020-02-32) same data as holotype; 1 specimen (DMNH 2020-02-33) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Further specimens: 24 specimens: 21 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation; 2 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Diagnosis: Same as for genus (monospecific genus).

Description. Moderately elongate otoliths up to 3.5 mm length (holotype). OL:OH = 1.7-1.9; OH:OT = 2.2-2.5. Ventral rim relatively deeply curved with rounded midventral angle. Dorsal rim shallow, with somewhat depressed and rounded predorsal angle above ostial channel, then ascending in more or less straight line to pronounced, rounded postdorsal angle positioned just behind posterior tip of cauda. Anterior tip with relatively pointed, dorsally shifted rostrum at lower margin of ostium. Posterior rim broadly rounded with its tip slightly dorsally shifted, symmetrical to rostrum. All rims smooth; dorsal rim sometimes broadly and irregularly undulating.

Inner face mildly convex with slightly deepened sulcus inclined at about 5-8°. OL:SuL = 1.45-1.55. Ostium reaching very close to anterior rim of otolith, somewhat widened, particularly dorsally with broad and indistinctly bound short vertical ostial channel leading to predorsal angle. Cauda straight or very slightly flexed towards its rounded tip. Colliculum often slightly reduced at caudal tip and ventral region of cauda. Distinct broad and dorsally opening dorsal depression behind ostial channel stretching to about two-thirds of cauda. No ventral furrow, but short vertical furrow sometimes visible leading upwards from caudal termination. Outer face variably convex, usually less than inner face, smooth.

Discussion. The few Maastrichtian specimens are smaller and slightly more elongate than the Danian ones (OL:OH = 1.9 vs 1.7-1.75), but we consider this as an expression of variability. Nolf & Dockery (1990) figured an otolith from the late Campanian Coffee Sand Formation of Mississippi as Congridae indet. which we consider to represent *Congrophichthus transterminus*. A specimen figured by Nolf & Dockery (1993) from the late Danian of Alabama represents the youngest record of the species and shows an intermediate ratio OL:OH of 1.8. Nolf & Dockery (1993) felt that their specimens resembled the Middle Eocene *Conger*? *websteri* Frost, 1933 from England, but specimens of *C.*? *websteri* figured in Schwarzhans (2007) from the Middle Eocene of Germany show now anteriorly widened ostium that terminates further away from the anterior rim of the otolith, a totally straight cauda, and a smaller and much more feeble dorsal depression. *Congrophichthus transterminus* likely represents an early extinct congrid lineage that obviously survived the K-Pg boundary event.

Genus *Rhynchoconger* Jordan & Hubbs, 1925

Rhynchoconger brettwoodwardi n. sp.

Fig. 5 A-E

1993 *Rhynchoconger* sp. – Nolf & Dockery: pl. 1, figs. 7-9.

Etymology: Named in honor of Brett Woodward (Johnson City, Tennessee, USA), a geologist for the State of Tennessee who has studied the Kemp Clay fossils in great detail and initially investigated the specimens described here.

Holotype: DMNH 2020-02-25 (Fig. 5 A-C), South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

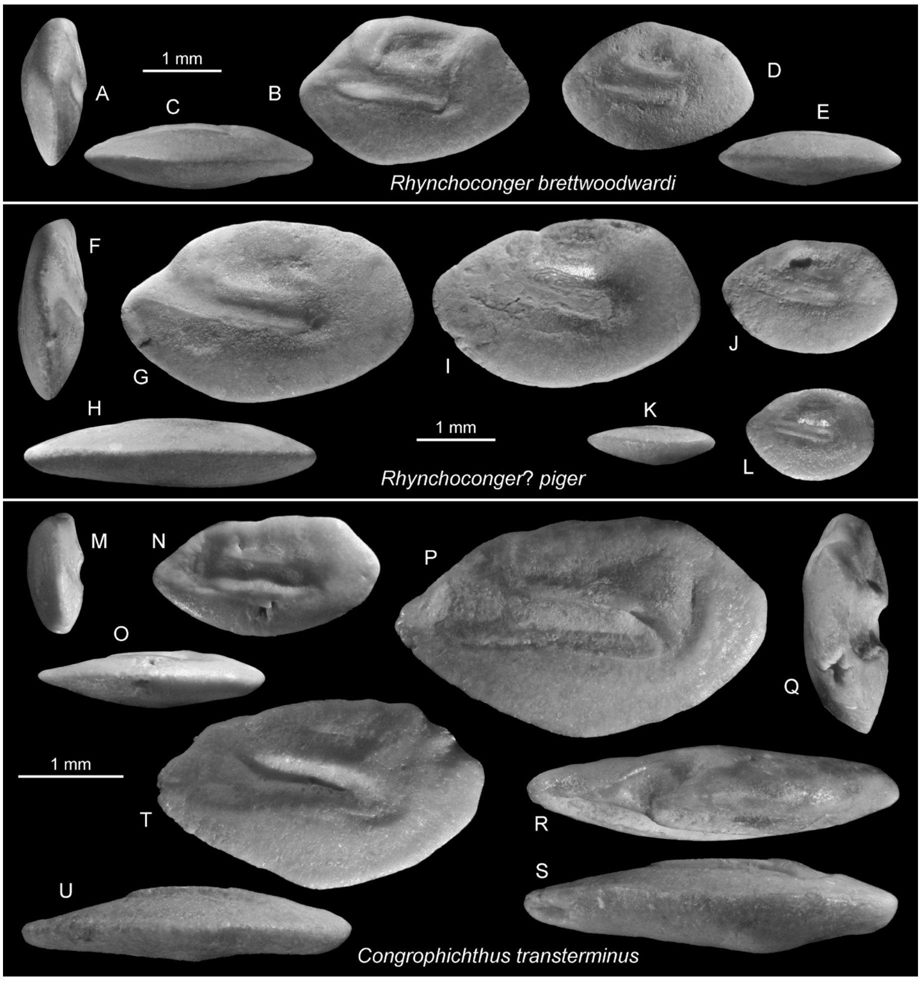


Fig. 5 - A-E) *Rhynchoconger brettwoodwardi* n. sp., Kemp Clay; A-C holotype, DMNH 2020-02-25; D-E paratype, DMNH 2020-02-26 (reversed). F-L) *Rhynchoconger*? *piger* Schwarzhans, 2010, Kemp Clay, DMNH 2020-02 27 to 30 (K-L reversed). M-U) *Congrophichthus transterminus* n. gen., n. sp.; P-S holotype, Clayton Formation, DMNH 2020-02-31 (reversed); M-O paratype, Kemp Clay, DMNH 2020-02-32 (reversed); T-U paratype, Clayton Formation, DMNH 2020-02-33 (reversed).

Paratypes: 3 specimens (DMNH 2020-02-26) same data as holotype.

Further specimens: 21 specimens same data as holotype.

Diagnosis: OL:OH = 1.5-1.6. Dorsal rim with marked pre- and postdorsal angles; predorsal angle distinctly higher. Anterior and posterior tips equally pointed. Sulcus straight, inclined at about 10°, with indistinct, narrow ostial channel. Colliculum well marked, slightly reduced posteriorly; OL:CL = 1.9-2.0. Dorsal depression large, distinct.

Description. Moderately elongate otoliths up to 3 mm length (holotype). OH:OT = 2.2-2.3. Ventral rim regularly curved, deepest anterior of its middle. Dorsal rim with three nearly equally long straight sections, anterior one inclined at about 40-45° up to pronounced, rounded predorsal angle, middle one sliding from predorsal down to rounded postdorsal angle at about 10-15°, posterior one declining from postdorsal angle to posterior tip of otolith at about 50-60°. Anterior and posterior tips moderately pointed; anterior tip positioned higher than posterior tip. All rims smooth.

Inner face distinctly convex with relatively short, slightly deepened sulcus inclined at about 10°. Ostium and cauda not differentiated. Anterior tip of sulcus reaching moderately close to anterior rim of otolith, with faint, thin ostial channel; posteriorly terminating far from posterior tip of otolith. Colliculum undifferentiated, well-marked, slightly reduced posteriorly towards caudal tip; OL:CL = 1.9-2.0. Dorsal depression large, well-marked; ventral field smooth, without ventral furrow. Outer face similarly convex as inner face, smooth.

Discussion. *Rhynchoconger brettwoodwardi* differs from the coeval *R.*? *piger* Schwarzhans, 2010 in the clearly anteriorly closed sulcus, the presence of an ostial channel, and the predorsal angle being distinctly higher than the postdorsal angle. The first two characters and the distinct dorsal depression are typical for *Rhynchoconger* otoliths (see Schwarzhans 2019b). Two further species have been associated with the genus from the European Paleocene: *R. angulosus* (Schwarzhans, 2003) and *R. intercedens* Schwarzhans, 2012. *Rhynchoconger brettwoodwardi* differs from *R. angulosus* in the predorsal angle being much higher than the postdorsal angle (vs. postdorsal angle being more pronounced than predorsal angle) and the anteriorly more distantly terminating sulcus (vs. reaching very close to the anterior rim of the otolith). The specimens of *R. intercedens* differ in the regularly rounded dorsal rim and the much more clearly developed and broad ostial channel. In addition, there are a number of *Rhynchoconger* species described from the Eocene of Europe and New Zealand, which all show a broad and long ostial channel, usually filled with collicular matter and thus represent a more advanced morphology. Nolf & Dockery (1993) also figured specimens identified as *Rhynchoconger* sp. from the late Danian of Alabama that resemble the Kemp Clay specimens in all aspects except that some appear to be exhibiting a somewhat more prolonged posterior tip. We consider these specimens as very likely conspecific and yet another case of survival across the K-Pg boundary.

Rhynchoconger*? *piger Schwarzhans, 2010

Fig. 5 F-L

2010 genus aff. *Rhynchoconger piger* – Schwarzhans: figs. 25-28.

Material: 38 specimens (figured specimens DMNH 2020-02-27 to 30) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. This species was originally only tentatively placed in the genus *Rhynchoconger* and we retain that view mainly because the ostium approaching so closely to the anterior rim of the otolith that sometimes it appears to almost opening to it (Fig. 5 G) and an extremely indistinct or absent ostial channel. What was described as a very broad ostial channel in Schwarzhans (2010) is more likely a dorsal widening or curvature of the ostium. The specimens from the Kemp Clay show a very similar morphology and variability in all aspects as the specimens from Bavaria.

Order **Aulopiformes** Rosen, 1973
Family Paraulopidae Sato & Nakabo, 2002
Genus *Paraulopus* Sato & Nakabo, 2002

***Paraulopus* sp.**

Fig. 6 A-B

Material: 4 specimens (figured specimen DMNH 2020-02-42) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. These are typical *Paraulopus* specimens, but none of them are well enough preserved for specific identification. *Paraulopus* otoliths are common in many late Cretaceous and early Paleogene locations in North America and Europe since Coniacian and possibly Cenomanian (Nolf 2016) but their diagnostic distinction often relies on few and subtle characters, which are easily affected by erosion.

Order **Gadiformes** Goodrich, 1909
Family Merlucciidae Rafinesque, 1815
Genus *Palaeogadus* Rath, 1859

***Palaeogadus weltoni* n. sp.**

Fig. 6 C-E

Etymology: Named in honor of Bruce Welton (Los Angeles) for his contributions to the knowledge of fossil sharks from the Maastrichtian of the USA, and who collected the otoliths from the Kemp Clay described here.

Holotype: DMNH 2020-02-46 (Fig. 5 A-C), South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Diagnosis: OL:OH = 2.1. Dorsal rim higher at obtuse postdorsal angle as predorsal. Collum long. Ostium nearly as long as cauda; CCL:OCL = 1.2. Ventral furrow distinct, more strongly bending upwards anteriorly than posteriorly.

Description. A single, well preserved and highly diagnostic otolith of 3.2 mm length. OH:OT = 2.2. Dorsal rim relatively shallow, slightly depressed anteriorly and higher at the broad, obtuse postdorsal angle, slightly undulating. Anterior tip broadly rounded, inferior, well below lower margin of ostium; posterior tip tapering, rounded, slightly inferior but less ventrally shifted than anterior tip. Ventral rim regularly bent, deepest at anterior portion below ostium, smooth.

Inner face markedly convex along horizontal axis, relatively smooth, with slightly supramedian positioned sulcus. Sulcus homosulcoid, shallow, with cauda being only slightly longer than ostium. Collum long, about 10% of OL, about half the width of widest point of sulcus. Colliculi well marked, slightly deepened, terminating anteriorly and posteriorly far from otolith tips; CCL:OCL = 1.2. Anterior and posterior portions of sulcus outside of colliculi narrowed. Dorsal depression wide, poorly defined. Ventral furrow distinct, marked by color change, not much deepened, running close to ventral rim of otolith, but anteriorly and posteri-

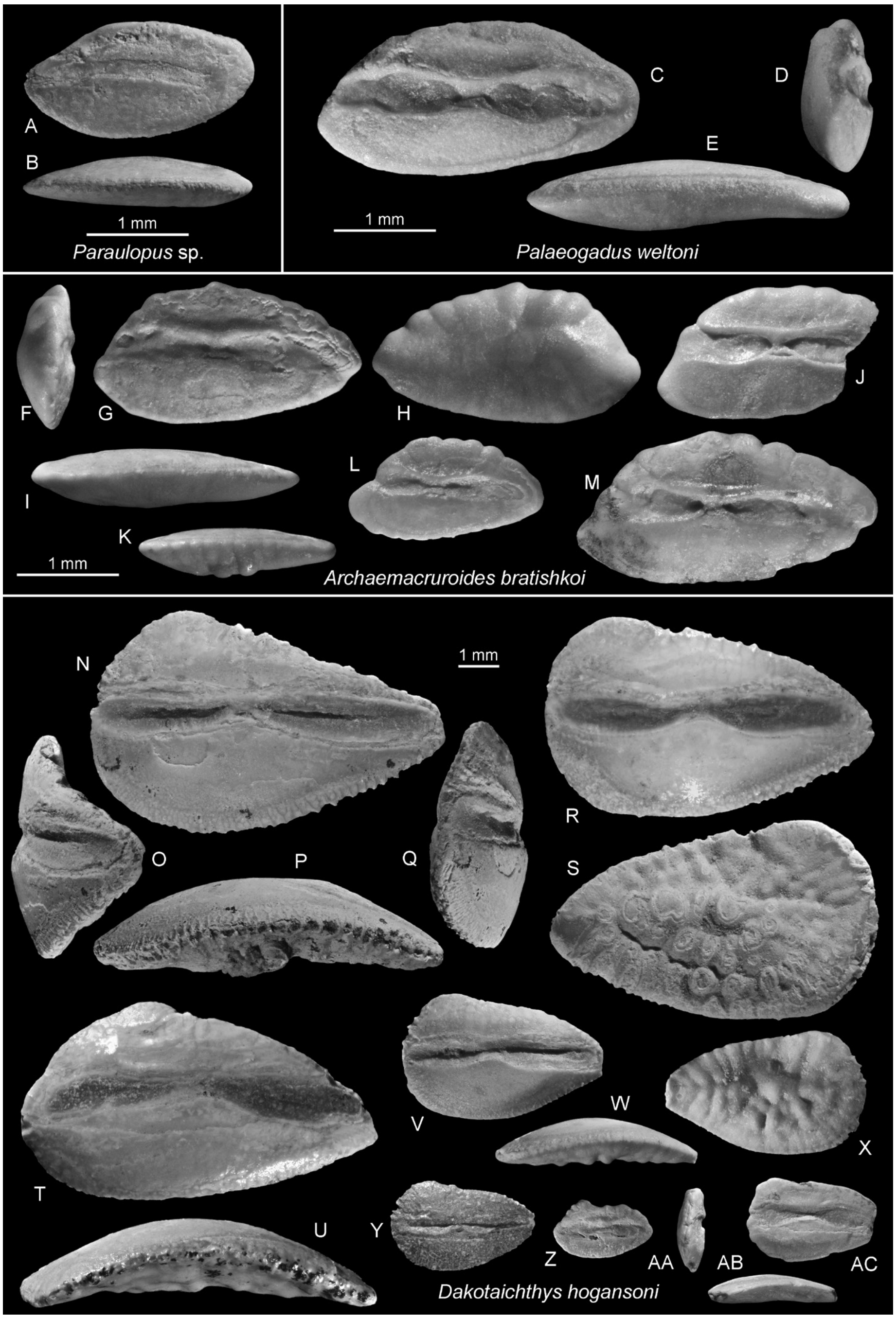


Fig. 6 - A-B) *Paraulopus* sp., Kemp Clay, DMNH 2020-02-42 (reversed). C-E) *Palaeogadus weltoni* n. sp., holotype, Kemp Clay, DMNH 2020-02-46 (reversed). F-M) *Archaemacruroides bratishkoi* (Schwarzhans, 2012), Kemp Clay, DMNH 2020-02-47 to 50. N-AC) *Dakotaichthys hogansoni* n. gen., n. sp.; N-Q holotype, Fox Hills Formation, NDGS 5597 (reversed); R-Y paratypes, Fox Hills Formation, NDGS 5598-5611 (R-S, V-X reversed); Z-AC tentatively assigned specimens, Kemp Clay, DMNH 2020-02-43 to 45.

orly upward bent towards sulcus. Outer face anteriorly slightly convex, posteriorly slightly concave, smooth.

Discussion. *Palaeogadus weltoni* closely resembles *P. sinangulatus* Schwarzhans, 2003 from the Paleocene, Selandian, of Denmark. It differs in the dorsal rim being highest at its postdorsal angle and the predorsal region being depressed (vs. distinct predorsal lobe), and the ventral furrow turning upwards anteriorly and posteriorly (vs. staying close and parallel to the ventral rim of the otolith).

Family Gadidae? Rafinesque, 1810

Genus *Dakotaichthys* n. gen.

Type species: *Dakotaichthys hogansoni* n. sp.

Etymology: Named after the state North Dakota, USA, where most specimens of the type species were found, and referring to the Native American Dakota who reside in this area.

Diagnosis: A fossil otolith-based genus of the family Gadidae with the following combination of characters. Otolith elongate droplet-shaped with rounded anterior tip and tapering, pointed posterior tip. Predorsal region expanded in broad lobe. Inner face distinctly convex in horizontal and vertical direction; outer face flat to slightly concave. Sulcus anteriorly and posteriorly almost reaching rims of otolith (pseudobiostial opening) and distinctly homosulcoid, deepened with central furrow, with ostium and cauda similar in shape and size; cauda slightly longer than ostium, CCL:OCL = 1.1-1.3. Colliculi reaching termination of sulcus, leaving moderately long collum in between. Collum 5-8% of OL, distinctly narrowed, particularly from ventral, with faint ventral pseudocolliculum.

Discussion. *Dakotaichthys* combines characters typical for gadid otoliths, such as *Protocolliolus* with a relatively long collum with a ventral pseudocolliculum and an incised sulcus with a central furrow, and characters typical for macrourid otoliths such as *Coelorhinchus* in respect to the otolith outline and the distinct predorsal lobe. Both genera, the fossil otolith-based *Protocolliolus* and *Coelorhinchus* are known from the middle Paleocene (Selandian) of Denmark. *Dakotaichthys* is considered to represent a gadid because of the sulcus proportions and the sulcus incision as in *Protocolliolus*, but it could alternatively also represent a very early phylogenetic representative of the Macrouridae. In any case, it documents the presence of advanced gadiforms already in the terminal Cretaceous.

Species. *Dakotaichthys* is a monospecific genus with *D. hogansoni* known from the late Maastrichtian of North Dakota and Texas.

Dakotaichthys hogansoni n. sp.

Fig. 6 N-AC

2019 cf. *Bathylagus* sp. – Hoganson, Erickson & Holland: text-figs. 12.59-12.60.

Etymology: Named in honor of John W. Hoganson (Bismarck, North Dakota) in recognition of his many contributions to the paleontology of North Dakota and who also collected and first mentioned these otoliths from the Fox Hills Formation.

Holotype: NDGS 5597 (Fig. 6 N-Q), north facing roadcut and ditch along FAS 2416, 5 km ENE of Burnstad, Logan County, North Dakota, USA, late Maastrichtian, Fox Hills Formation, ?Timber Lake Member.

Paratypes: 16 specimens (NDGS 5598 to 5611) same data as holotype.

Further specimens: 50 specimens same location as type series.

Tentatively assigned specimens: 16 small specimens (DMNH 2020-02-43 to 45) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Diagnosis: See generic diagnosis (monotypic genus).

Description. Large, robust, droplet-shaped otoliths up to about 9 mm length (holotype 8.7 mm). OH:OT = 2.4-2.8. Dorsal rim anteriorly expanded with a broad, irregularly rounded predorsal lobe extending across almost the entire ostium; dorsal rim regularly inclined downwards from highest point of predorsal lobe to tapering, pointed posterior tip. Ventral rim deepest and most strongly curved anteriorly, nearly straight leading up to posterior tip. Anterior rim blunt, broadly rounded; posterior rim tapering, with pointed tip. All rims slightly undulating or crenulated, ventral rim finer and more regular, dorsal rim coarser and more irregular, but marginal ornamentation rarely well preserved.

Inner face strongly convex both in horizontal and vertical direction. Sulcus slightly supramedian positioned, typical homosulcoid and pseudobiostial (i.e., nearly open anteriorly and posteriorly). Cauda slightly longer than ostium; CCL:OCL = 1.1-1.3. Ostial and caudal colliculi well marked, equally high, elongate oval in shape, reaching close to anterior and posterior tips of sulcus respectively, centrally deepened with horizontal furrow. Collum moderately long (5-8% of OL), distinctly narrowed and with faint ventral pseudocolliculum. Dorsal field with poorly defined, long dorsal depression directly above narrow crista superior; its dorsal part showing some faint radial furrows leading from the marginal crenulation. Ventral field smooth except for narrow stretch below ventral furrow which shows multiple faint radial furrows. Outer face flat to slightly concave, intensely ornamented with central field of tubercles and marginal zone with radial furrows.

Discussion. *Dakotaichthys hogansoni* represents typical gadiform otoliths like many that are found in the Cenozoic, even though some ambiguity remains of whether they represent a gadid, as here suggested, or a macrourid (see above). It is the most common otolith-based species in the western region of the Fox Hills Formation of North Dakota, where it occurs, which has been interpreted as estuarine to tidal flat terrain in Hoganson et al. (2019). In the Kemp Clay, it is a rare species and represented only by relatively small specimens (see below). The specimens from North Dakota all show some leaching of the surface and a variable degree of marginal erosion that masks crenulation of the otolith rims in many specimens investigated. Wetting of the otoliths however helped to counter leaching effects and improved the visualization of pertinent morphological features.

The majority of specimens from North Dakota are between 5 and 9 mm length, with a single smaller specimen of 3.5 mm length (Fig. 6 Y). This specimen however is still bigger than the biggest from the Kemp Clay which is about 3.3 mm (reconstructed, posterior tip missing; Fig. 6 AA-AC). We therefore consider the Kemp Clay specimens to stem from juvenile fishes, and in the light of their less than optimal preservation, place them only tentatively in *D. hogansoni* pending the discovery of additional, larger, and better preserved specimens in the future.

Family indeterminate
Genus *Archaemacruroides* Stinton, 1965

Archaemacruroides bratishkoi (Schwarzhans, 2012)

Fig. 6 F-M

2003 Gadiformes spp. – Schwarzhans: fig. 27 A-C (non fig. 27 D-H).
2012 *Palaeogadus*? *bratishkoi* – Schwarzhans: figs. 110-118.

Material: 11 specimens (figured specimens DMNH 2020-02-47 to 50) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. *Archaemacruroides bratishkoi* is a relatively small species with otoliths up to sizes of about 3.5 mm in length. It was originally described from the late Paleocene Thanetian of Bavaria and Austria, but records from the Danian of Faxe in Denmark are here also included in the synonymy. Now, the record from the Kemp Clay extends the stratigraphic range backwards into late Maastrichtian times and again is evidence for a unexpectedly close correlation of the Kemp Clay otolith association with that of the European Paleocene. The species was originally understood as of merlucciid affinities, but is here regarded as a species of the extinct genus *Archaemacruroides* with two species from the European Paleocene - *A. ornatus* Stinton, 1965 and *A. bratishkoi*. The otoliths of this genus are characterized by a relatively flat inner face, a typical gadiform homosulcoid sulcus where the cauda is only slightly longer than the ostium, a long collum, and anteriorly and posteriorly reduced colliculi. The interrelationships of *Archaemacruroides* remains obscure because of its very generalized, plesiomorphic morphology. It is here interpreted to represent a stem gadiform of unresolved familial affinities.

Order **Ophidiiformes** Berg, 1937
Family Ophidiidae Rafinesque, 1810
Genus *Ampheristus* König, 1825

***Ampheristus americanus* n. sp.**

Fig. 7 A-J

Etymology: Named after America indicating its distribution.

Holotype: DMNH 2020-02-51 (Fig. 7 A-C), South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Paratypes: 5 specimens: 4 specimens (DMNH 2020-02-52 to 55) same data as holotype; 1 specimen (DMNH 2020-02-56) Interstate-30 slide site, west of Malvern, Hot Spring County, Arkansas, early Danian, Clayton Formation.

Further specimens: 137 specimens: 125 specimens same data as holotype; 12 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Diagnosis: OL:OH = 1.65-1.95. Ventral rim relatively shallow, deepest anterior of its middle. Dorsal rim flat, with distinct and rounded predorsal angle above anterior tip of ostium and postdorsal angle above posterior tip of cauda; straight and horizontal between both angles. Ostium longer and wider than cauda; cauda slightly flexed, deepened. OsL:CaL = 1.8-2.0; OCH:CCH = 1.8-2.2.

Description. Elongate otoliths up to at least 3.6 mm length (holotype 3.2 mm). OL:OH = 1.65-1.95, increasing with size; OH:OT = 1.9-2.2. Ventral rim regularly curved, deepest anterior of its middle, relatively shallow. Dorsal rim with long, nearly straight and horizontal middle section bound anteriorly by distinct, broadly rounded predorsal angle above anterior tip of ostium and posteriorly by nearly as distinct postdorsal angle above posterior tip of cauda. Anterior rim with blunt rostrum-like tip positioned at about middle axis of otolith. Posterior tip slightly inferior, moderately pointed or angular, not projecting. All rims smooth.

Inner face distinctly convex in horizontal direction, much less so in vertical direction. Sulcus long, very slightly s-shaped, positioned along central axis or slightly supramedian, reaching very close to anterior rim of otolith and terminating at moderate distance from posterior otolith rim. OL:SuL = 1.25-1.3. Ostium shallower than deepened cauda, and about twice as long and twice as wide as cauda. Colliculi well defined and separate. Dorsal sulcus margin slightly concave at collum, ventral sulcus margin with distinct angle at collum. Indistinct dorsal depression above broad crista superior; no or very faint ventral furrow very close to ventral rim of otolith. Outer face convex, somewhat flattening with size, smooth.

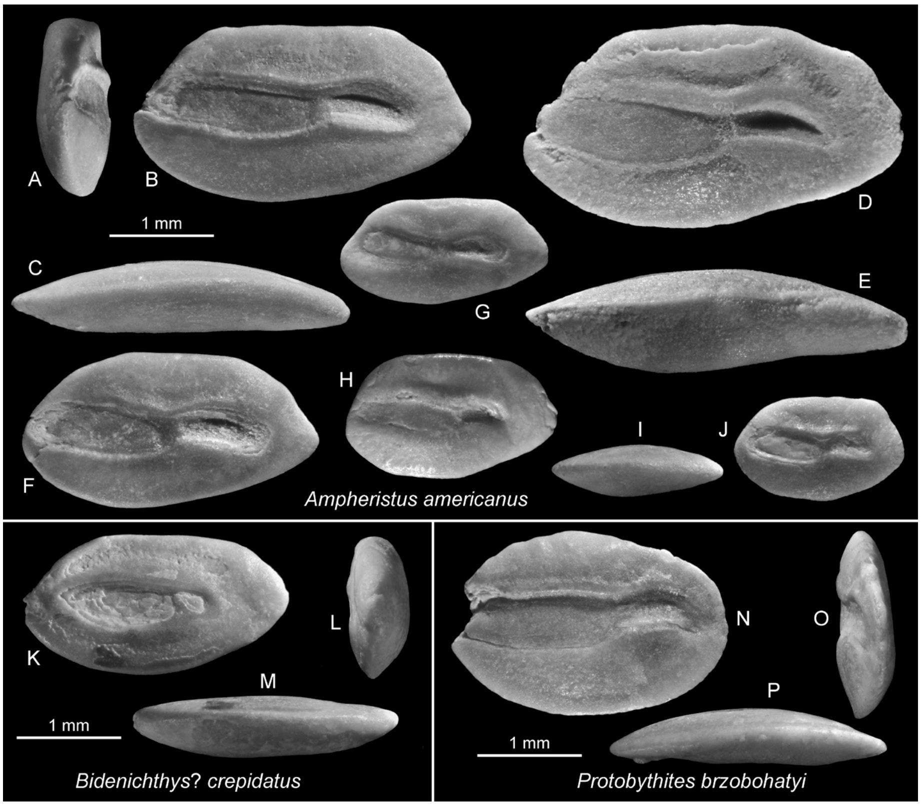


Fig. 7 - A-J) *Ampheristus americanus* n. sp.; A-C holotype, Kemp Clay, DMNH 2020-02-51 (reversed); D-G, I-J paratypes, Kemp Clay, DMNH 2020-02-52 to 55 (F, I-J reversed); H paratype, Clayton Formation, DMNH 2020-02-56. K-M) *Bidenichthys? crepidatus* (Voigt, 1926), Kemp Clay, DMNH 2020-20-57 (reversed). N-P) *Protobythites brzobohatyi* Schwarzhans, 2010, Kemp Clay, DMNH 2020-02-58 (reversed).

Discussion. The relatively long and deepened cauda characterizes this species as a representative of the fossil genus *Ampheristus*, which has been considered to be closely related to the extant *Hoplobrotula* Gill, 1863 (see Schwarzhans 1981). It differs from the European *Ampheristus bavaricus* (Koken, 1891), *A. brevicauda* Schwarzhans, 2010, and *A. traunensis* Schwarzhans, 2010 of the Maastrichtian in the pronounced postdorsal angle. From *A. bavaricus* and *A. traunensis* it further differs in the index OsL:CaL of 1.8-2.0 (vs 1.0-1.6), and from *A. bavaricus* and *A. brevicauda* in the slight flexure of the cauda. More similar is *A. neobavaricus* Schwarzhans, 2012 from the Paleocene of Bavaria with which it shares the general otolith outline and proportions, but differs in the postdorsal angle being more pronounced and the ratio OsL:CaL of 1.8-2.0 (vs 1.5-1.8). In any case, both species are probably closely related and *A. neobavaricus* may in fact have derived from *A. americanus*, which is yet another record of species having survived the K-Pg boundary event. The genus *Ampheristus* is also recorded by several species from Eocene and early Oligocene times, but none of them show any particular resemblance.

Genus *Protobythites* Schwarzhans, 2010

Protobythites brzobohatyi Schwarzhans, 2010

Fig. 7 N-P

2010 *Protobythites brzobohatyi* – Schwarzhans: fig. 91.

Material: 1 slightly anteriorly damaged specimen (DMNH 2020-02-58) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. Otoliths of *Protobythites* are distinguished from *Ampheristus* in the inner face being distinctly convex in horizontal and vertical directions and relatively smooth except for the slightly deepened sulcus, particularly its cauda and the thin appearance with a nearly flat outer face and sharp otolith rims. The dorsal depression is very shallow and a delicate ventral furrow is always present. *Protobythites brzobohatyi* was based on a single well preserved otolith from the Maastrichtian of Bavaria characterized by a wide and long ostium, a short and flexed, narrow cauda (OsL:CaL = 1.9; OCH:CCH = 1.9), a gently curving dorsal rim which is highest anteriorly and a broadly rounded posterior tip. All these characters also distinctly distinguish *P. brzobohatyi* from *Ampheristus bavaricus* despite Nolf (2013) having considered it as an expression of variability. *Protobythites brzobohatyi* now is known from the

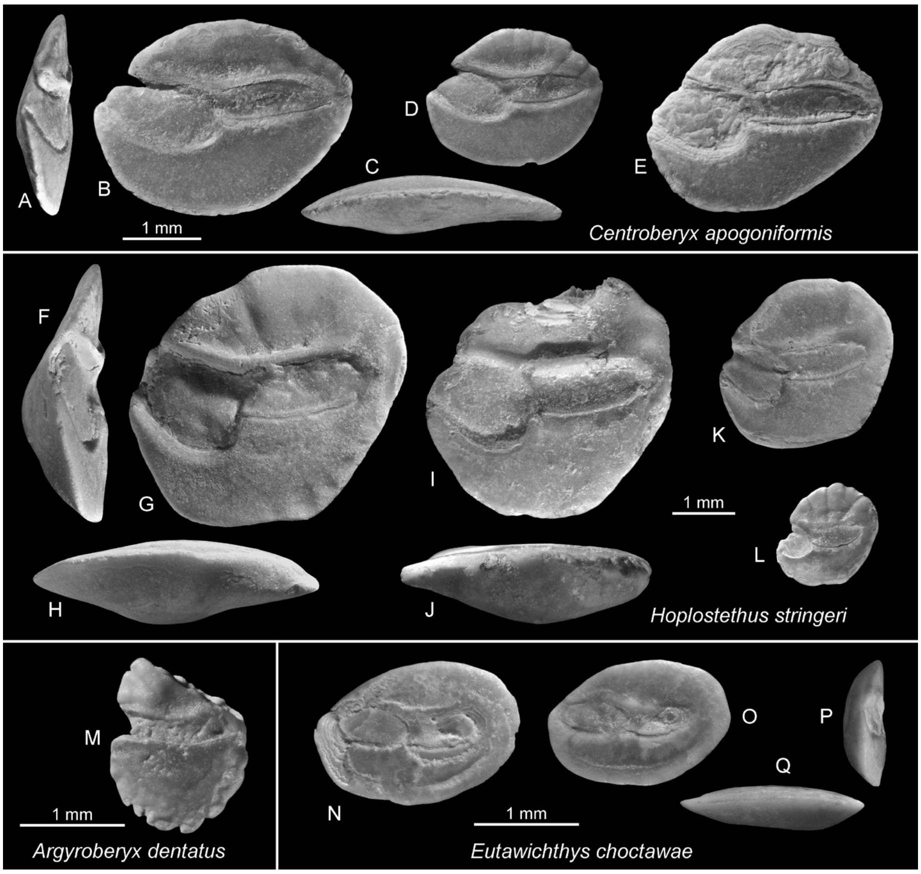


Fig. 8 - A-E) *Centroberyx apogoniformis* Schwarzhans, 2012, Kemp Clay, DMNH 2020-02-63 to 65. F-L) *Hoplostethus stringeri* (Nolf & Dockery, 1993); F-H, K-L Kemp Clay, DMNH 2020-02-59 to 61 (F-H, L reversed); I-J Clayton Formation, DMNH 2020-02-62. M) *Argyroberyx dentatus* (Liebus, 1927), Kemp Clay, DMNH 2020-02-68. N-Q) *Eutawichthys choctawae* Stringer & Schwarzhans, 2020, Kemp Clay, DMNH 2020-02-66 to 67 (reversed).

Maastrichtian of Bavaria and Texas. Nolf & Dockery (1993) figured an otolith from the late Danian of Alabama as *Ampheristus* sp. which resembles *P. brzobohatyi* in the thin appearance, the convex inner face, and the gently curving otolith rims, but differs in the pointed posterior tip and the narrower ostium. It could indicate that the genus *Protobythites* also survived across the K-Pg boundary event into Paleocene times. Another, common species in the Paleocene of Denmark, which was hitherto recorded as *Ophidiidarum seelandicus* Koken, 1885 is here also tentatively placed in *Protobythites* and is characterized by a broadly rounded postdorsal angle, a partly crenulated dorsal rim, and a distinctly pointed posterior tip.

Family Bythitidae
Genus *Bidenichthys* Barnard, 1934

Bidenichthys? crepidatus (Voigt, 1926)

Fig. 7 K-M

1926 *Ot. (Ophidiidarum) crepidatus* – Voigt: pl. 2, figs. 11-13.
?1983 Ophidiidae sp. – Huddleston & Savoie: fig. 3 A.
?1996 Ophidiidae indet. – Nolf & Stringer: pl. 4, fig. 9.
2010 *Bidenichthys crepidatus* (Voigt, 1926) – Schwarzhans: figs. 93-103.

Material: 2 specimens (figured specimen DMNH 2020-02-57) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. This species has first been described from erratic boulders in northeastern Germany of late Campanian age by Voigt (1926). It apparently became a widespread species during the Maastrichtian and in the Paleocene was replaced by *Bidenichthys*? *midwayensis* (Nolf & Dockery, 1993) in North America and *B.*? *lapierrei* (Nolf, 1978) in Europe. Differences between the species are subtle and few. Otoliths of *B.*? *midwayensis* differ from *B.*? *crepidatus* in being more elongate while those of *B.*? *lapierrei* tend to have a shorter sulcus that also is positioned at near equidistance from the anterior and posterior tips of the otolith (vs approaching anterior tip distinctly closer than posterior tip in *B.*? *crepidatus*).

The allocation of these species to *Bidenichthys* remains tentative. Møller et al. (2016) have argued that this allocation merely represents an association with the most plesiomorphic otolith morphology found in Recent bythitid otoliths and that likely they represent an extinct genus of some stem-group bythitid, but that the otoliths lack sufficient diagnostic character for a proper definition thereof. In this respect, it is of relevance to note that Carnevale & Johnson (2015) described *Pastorius methenyi* from the Campanian/Maastrichtian of Italy based on an articulated skeleton and considered it represented a sister-group to all extant bythitoids. Hence, we are of the opinion that only the discovery of otoliths in situ will eventually resolve the systematic position of these early bythitid otolith-based species.

Order **Trachichthyiformes** Bleeker, 1856
Family Trachichthyidae Bleeker, 1856
Genus *Hoplostethus* Cuvier, 1829

Hoplostethus stringeri (Nolf & Dockery, 1993)

Fig. 8 F-L

1993 "genus Trachichtyidarum" *stringeri* – Nolf & Dockery: pl. 3, figs. 1-5.

Material: 59 specimens (figured specimens DMNH 2020-02-59 to 62): 52 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 7 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, Arkansas, early Danian, Clayton Formation.

Discussion. *Hoplostethus stringeri* has originally been described from the late Danian of Alabama and has now also been found as a common element in the late Maastrichtian of the Kemp Clay. *Hoplostethus stringeri* differs from *H. lacinatus* (Koken, 1885) from the Paleocene of Denmark in the wider, i.e., more deeply ventrally expanded ostium and the blunter rostrum resulting in a less diagonally oriented long axis of the otolith.

Order **Beryciformes** Regan, 1909
Family Berycidae Regan, 1909
Genus *Centroberyx* Gill, 1862

Centroberyx apogoniformis Schwarzhans, 2012

Fig. 8 A-E

2004 *Centroberyx* sp. – Schwarzhans: fig. 10 F-H.
2011 *Centroberyx* sp. – Schwarzhans & Bratishko: fig. 11 G-H.
2012 *Centroberyx apogoniformis* – Schwarzhans: figs. 141-146.

Material: 43 specimens (figured specimens DMNH 2020-02-63 to 65): 42 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 1 fragmentary specimen Interstate-30 slide site, west of Malvern, Hot Spring County, Arkansas, early Danian, Clayton Formation.

Discussion. *Centroberyx apogoniformis* is easily recognized by its relatively elongate shape and the low and regularly curved dorsal rim. It has been regularly recorded from the Paleocene of Europe and now also for the first time from the Late Cretaceous of North America. A single large fragment from the Paleocene Clayton Formation may also represent this species.

Family indet. type 1
Genus *Eutawichthys* Schwarzhans, Huddleston & Takeuchi, 2018

Eutawichthys choctawae Stringer & Schwarzhans, 2020

Fig. 8 N-Q

2020 *Eutawichthys choctawae* – Stringer, Schwarzhans, Phillips & Lambert: fig. 9 U-W.

Material: 7 specimens (figured specimens DMNH 2020-02-66 to 67) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. *Eutawichthys choctawae* was established on a single, large, well-preserved specimen of 9.2 mm length characterized by a lobe at the position of the predorsal angle, an anteriorly closed, straight sulcus with an oval ostium, a nearly flat inner face, and in being oval in outline and relatively elongate (OL:OH = 1.6). The specimens now available from the Kemp Clay are considerably smaller (1.5-2 mm length) and differ from the holotype from the Ripley Formation of Mississippi in the absence of the predorsal lobe, in being less elongate (OL:OH = 1.45), and in the ventral furrow running at some distance from the ventral rim of the otolith. We regard these minor differences as an expression of ontogenetic changes.

Eutawichthys maastrichtiensis (Nolf & Stringer, 1996)

1996 "genus Apogonidarum" *maastrichtiensis* – Nolf & Stringer: pl. 5, figs. 9-10.
2020 *Eutawichthys maastrichtiensis* (Nolf & Stringer, 1996) – Stringer, Schwarzhans, Phillips & Lambert: fig. 9 U-W (see there for further synonymies).

Material: 2 poorly preserved, eroded specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay. See Nolf & Stringer (1996) for a description of the species.

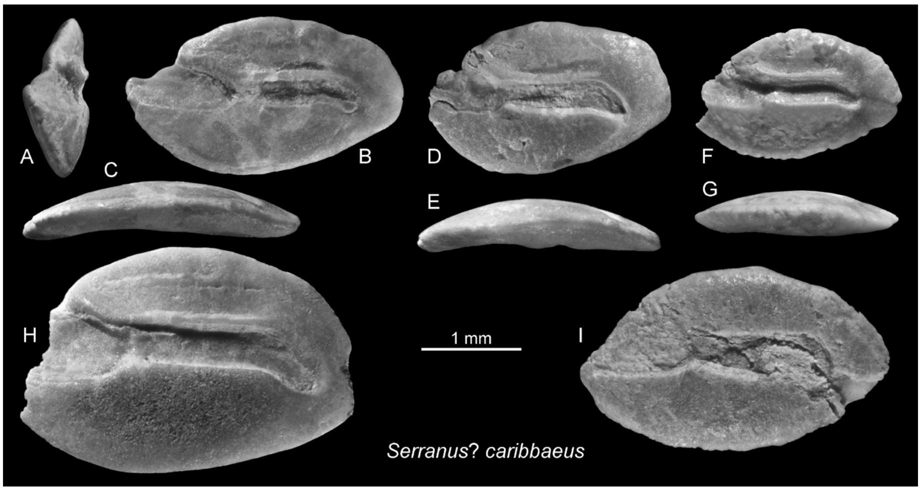


Fig. 9 - A-I) *Serranus*? *caribbaeus* (Nolf & Dockery, 1993); A-C, F-H Kemp Clay, DMNH 2020-02-69 to 71 (F-G reversed); D-E, I Clayton Formation, DMNH 2020-02-72 to 73.

Family indet. type 2
Genus *Argyroberyx* Schwarzhans, 2010

Argyroberyx dentatus (Liebus, 1927)

Fig. 8 M

1927 Ot. (Ganoidarum) *dentatus* – Liebus: pl. 14, figs. 5-6.
1927 Ot. (Ganoidarum) *ovatus* – Liebus: pl. 14, fig. 7.
?1927 Ot. (Berycidatum?) *carinthiacus* – Liebus: textfig. 2.
2010 *Argyroberyx dentatus* (Liebus, 1927) – Schwarzhans: figs. 116-120.
2013 ?*Diretmida dentata* (Liebus, 1927) – Nolf: pl. 162.

Material: 1 incomplete specimen (DMNH 2020-02-68) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. The single available specimen from the Kemp Clay lacks the posterior-dorsal portion. However these otoliths are so distinctive that even such incomplete specimen can be comfortably assigned to *A. dentatus* based on the slightly upward bent cauda and the regularly curved ventral rim, both of which distinguishes *A. dentatus* from *A.*? *dockeryi* (Nolf & Stringer, 1996) as described from the Ripley Formation of Mississippi (Stringer et al. 2020). *Argyroberyx dentatus* was hitherto only recorded from the Late Cretaceous of Europe.

Order **Perciformes** Bleeker, 1859
Family Serranidae Swainson, 1893
Genus indet.

Serranus*? *caribbaeus (Nolf & Dockery, 1993)

Fig. 9 A-I

1993 *Nemipterus caribbaeus* – Nolf & Dockery: pl. 5, figs. 8-13.
2004 genus ?*Sparidarum carribaeus* (Nolf & Dockery, 1993) – Schwarzhans: fig. 14 C-H (species misspelled).

Material: 25 specimens (figured specimens DMNH 2020-02-69 to 73): 12 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 13 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. This species was described by Nolf & Dockery (1993) based on a set of well preserved and adult specimens up to 4.8 mm length from the late Danian of Alabama and placed in the family Nemipteridae. Schwarzhans (2004) placed it in the sister family Sparidae in open generic nomenclature. Here we move it as genus indet. to the Serranidae primarily because the otoliths are more elongate than usually found in Sparidae and Nemipteridae and being more in line with Serranidae. However, the otoliths of most of the basal percomorph families share the principal plesiomorphic organization and are difficult to distinguish even on the family level. Those from the early Paleogene and the latest Cretaceous are even more generalized and hence all allocations must be understood as very tentative until otoliths have been found in situ. Schwarzhans & Bratishko (2011) made the same observation and regarded the low level of morphological diversity as an indication of basal phylogenetic positions within percomorph clades. This view is corroborated by the phylogenetic evaluation of percomorphs by Alfaro et al. (2018) who put the cladogenesis of most percomorph families and lineages in the time interval of the latest Cretaceous and Paleocene.

The specimens obtained from the Kemp Clay and the Clayton Formation are mostly eroded or incompletely preserved except for a few specimens just below 3 mm length (Fig. 9 A-E), which fit well in the variability as depicted by Nolf & Dockery. This extends the occurrence of *Serranus*? *caribbae-*

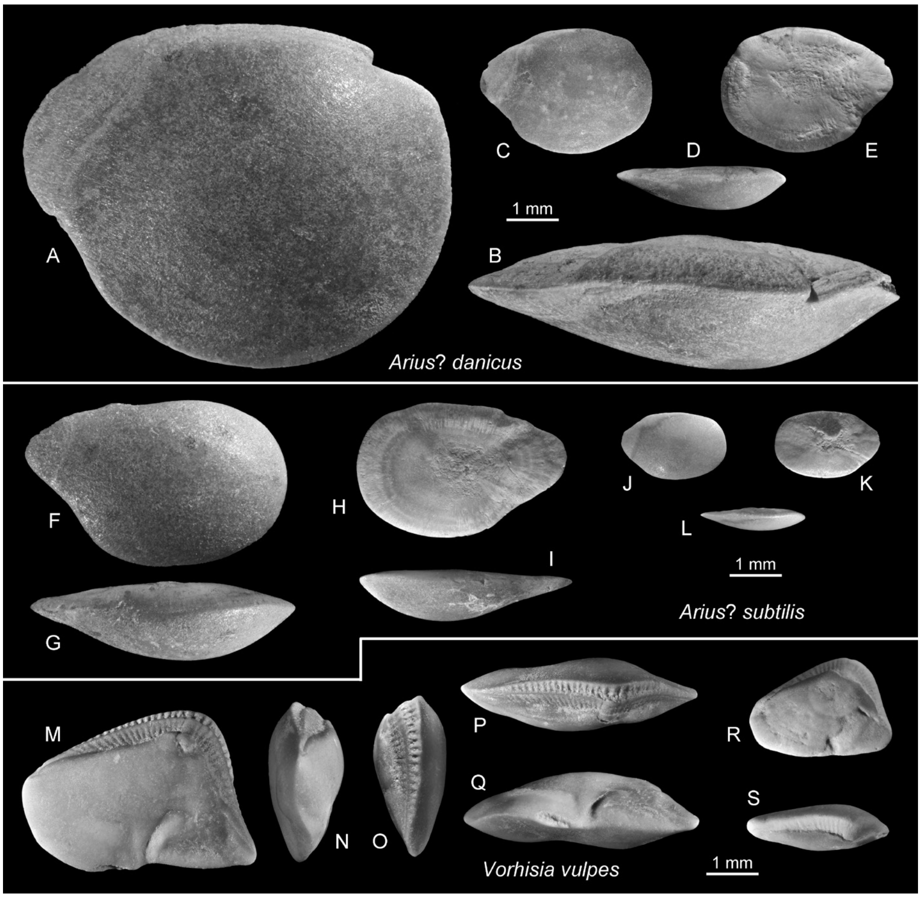


Fig. 10 - A-E) *Arius*? *danicus* Koken, 1891; A-B Clayton Formation, DMNH 2020-02-34; C-E Kemp Clay, DMNH 2020-02-35. F-L) *Arius*? *subtilis* Schwarzhans & Bratishko, 2011; F-G Clayton Formation, DMNH 2020-02-36; H-L Kemp Clay, DMNH 2020-02-37 to 38 (H-I reversed). M-S) *Vorhisia vulpes* Frizzell, 1965, Kemp Clay, DMNH 2020-02-39 to 40 (reversed).

us well beyond the K-Pg boundary into the earliest Selandian. According to Dockery & Thompson (2016) the Matthews Landing Marl Member from which the otoliths were described by Nolf & Dockery (1993) is lower P3, i.e., earliest Selandian.

LAPILLI OTOLITHS

Order **Siluriformes** Cuvier, 1817
Family Ariidae Blleker, 1862
Genus indet.

Arius*? *danicus Koken, 1891

Fig. 10 A-E

1891a *Arius danicus* – Koken: pl. 81, fig. 1.
1930 *Arius rotundus* – Roedel: pl. 1, fig. 17.
2003 *Arius danicus* Koken, 1891 – Schwarzhans: fig. 11 J-K.
2004 *Arius danicus* Koken, 1891 - Schwarzhans: fig. 3 A-F.
2010 *Arius danicus* Koken, 1891 - Schwarzhans: figs. 31-32.
2011 *Arius danicus* Koken, 1891 - Schwarzhans & Bratishko: fig. 4 A-E.
2012 *Arius danicus* Koken, 1891 - Schwarzhans: figs. 48-51.
2018 *Arius danicus* Koken, 1891 – Schwarzhans, Huddleston & Takeuchi: fig. 7 A-H.

Material: 174 specimens (figured specimens DMNH 2020-02-34 to 35): 67 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 107 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. *Arius*? *danicus* is a common, widespread and long ranging species in the Late Cretaceous since Santonian and into Paleocene of North America and Europe. In the light of the many extant ariid genera and the still limited knowledge of their otoliths we consider its generic placement, and that of the subsequent species, as elusive until otoliths in situ have been found.

Arius*? *subtilis Schwarzhans & Bratishko, 2011

Fig. 10 F-L

1926 Otolith – Wade: pl. LXXI, figs 9 – 10.
1983 Ariidae – Huddleston & Savoie: fig. 2, D – E.
1996 Ariidae – Nolf & Stringer: pl. 2, fig. 10
2011 *Arius subtilis* – Schwarzhans & Bratishko: fig. 4, F – H.
2020 *Arius*? *subtilis* Schwarzhans & Bratishko, 2011 – Stringer, Schwarzhans, Phillips, and Lambert: fig. 13 A-E.

Material: 237 specimens (figured specimens DMNH 2020-02-36 to 38): 195 specimens South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay; 42 specimens Interstate-30 slide site, west of Malvern, Hot Spring County, and McNeil Creek, Benton, Saline County, Arkansas, early Danian, Clayton Formation.

Discussion. *Arius*? *subtilis* is as widely distributed as *A.*? *danicus* but does not extend to earlier times than the Maastrichtian. It differs from *A.*? *danicus* in the more elongate shape and small specimens are also relatively thinner. It also does not appear to grow to the large size of *A.*? *danicus*. The specimen of Fig. 10 F-G of 5 mm length is yet the largest recorded, while *A.*? *danicus* can grow to sizes of at least 8 mm length (Fig. 10 A-B).

Family indet.
Genus *Vorhisia* Frizzell, 1965

Vorhisia vulpes Frizzell, 1965

Fig. 10 M-S

1965 *Vorhisia vulpes* – Frizzell: fig. 2.
2020 *Vorhisia vulpes* Frizzell, 1965 – Stringer, Schwarzhans, Phillips & Lambert: fig. 13 F-L (see there for further synonymies).

Material: 423 specimens (figured specimens DMNH 2020-02-39 to 41) South Sulphur River, Hunt County, Texas, USA, late Maastrichtian, Kemp Clay.

Discussion. *Vorhisia vulpes* is commonly understood as an extinct ariid or at least siluriform because of its large size lapillus and some general resemblance with extant ariid lapilli. Its sulcus ('mesial shallow depression' in the terminology of Ohe in Aguilera et al. 2013) however bears some characteristics that are unknown from any other extant lapilli otoliths: the intense, regular and radial or cross-cutting ridge and furrow pattern along its entire course. In some large otoliths (Fig. 10 M-Q) the sulcus shows a continuous longitudinal ridge separating two about equally wide portions which both carry the same cross-cutting ridge and furrow pattern. It is therefore likely that *Vorhisia* represents an extinct family of the Siluriformes or Ostariophysi and it could even relate to an extinct higher taxonomic group, or when considering that certain extant Holostei also have large lapilli could even represent a non-teleost fish.

Vorhisia vulpes is the most common species by far in the Maastrichtian Kemp Clay (nearly 35%) and is also common in many other Maastrichtian formations of North America like the Ripley Formation (Stringer et al. 2020), Severn Formation (Hudleston & Savoie 1983; Nolf & Stringer 1996), Fox Hills Formation (Frizzell 1965b; Carpenter et al. 2003; Hoganson et al. 2019) and the Arkadelphia Formation (unpublished data). Its abundance is highest in the Kemp Clay, Fox Hills Formation, and Arkadelphia Formation. Carpenter et al. (2003) have shown with an analysis of $\delta^{18}O$ and $\delta^{13}C$ mapping across the growth rings that *V. vulpes* spawned in estuarine waters with otoliths of the juveniles exhibiting brackish water signals. This life cycle may explain its abundance in sediments of the Western Interior Sea and other sediments close to the continent and fluvial discharge systems. *Vorhisia vulpes* has not been found outside of North America and specifically not in Europe. *Vorhisia vulpes* is also one of the prominent victims to the K-Pg boundary event in North America that abruptly terminated its occurrence.

Fish otoliths and faunal provinces during the Maastrichtian

Recent years have seen a surge of the knowledgebase of otoliths from Maastrichtian strata. Maastrichtian otolith assemblages have been described from North America from the late Maastrichtian Severn Formation of Maryland (Huddleston & Savoie 1983; Nolf & Stringer 1996), the early Maastrichtian Ripley Formation and late Maastrichtian Owl Creek Formation of Mississippi (Stringer 1991; Nolf & Stringer 1996; Stringer et al. 2020), the Fox Hills Formation of North Dakota (Frizzell 1965; Frizzell & Koenig 1973; Carpenter et al. 2003; Hoganson et al. 2019) and here now from the Kemp Clay of northeastern Texas. North American Maastrichtian locations have thus proven to be particularly rich in otoliths. This contrasts with only one sizeable otolith-based fauna described from the middle Maastrichtian of Bavaria and Austria (Koken 1891b; Liebus 1927; Schwarzhans 2010), in the former Peninnic Ocean, and a few isolated records from the boreal northern-central European sea from the late Maastrichtian of Denmark (Schwarzhans & Milan 2017) and from the late Campanian from an erratic boulder found in Cöthen in northern Germany (Voigt 1926). The otoliths described by Voigt are somewhat obscure, and his work is rarely cited. According to Voigt (1926) the erratic boulder stems from a regressive environment of the "Mucronaten-Senon", i.e., from a late Campanian time, which probably relates to the late Campanian cooling event (LCE) at about 75-76 Ma (Voigt et al.

2012; Linnert et al. 2014, 2018). He speculated the origin of the erratic boulder to be from terrain now submerged in the Baltic Sea to the east of Schonen, the southern province of Sweden. The specimens were housed in the paleontological collection of the University of Hamburg and were destroyed during World War II. The late Voigt recalled that fossils from the type collection were rescued from the burning and later from the smoldering building, but otoliths were not amongst them (personal communication to WS). With the increasing knowledge of late Cretaceous otoliths we can now better assess their identities and value their importance. The following is a brief update of the interpretation of these otoliths: *O.* (?*Arius*) *glaber* Voigt, 1926 is regarded as a junior synonym of *Arius*? *danicus* Koken, 1891. *O.* (*Morrhua*) *anhaltinus* Voigt, 1926 is regarded as a species of the genus *Eutawichthys*, i.e., *E. anhaltinus* (Voigt, 1926) and related to *E. choctawae* and *E. maastrichtiensis*. *O.* (*Morrhua*) sp. represents an unidentifiable and strongly eroded otolith. *O.* (*Gadidarum*) *erraticus* indeed represents a gadiform otolith, the oldest known, possibly of the genus *Dakotaichthys*, but the preservation of the figured specimens is poor and therefore a species cannot be defined. *O.* (*Ophidiidarum*) *crepidatus* Voigt, 1926 has been reviewed as *Bidenichthys*? *crepidatus* by Schwarzhans (2010). *O.* (*Sparidarum*) *teumeri* Voigt, 1926 has been reviewed as *Centroberyx teumeri* and *O.* (*Sparidarum*) *senoniensis* has been regarded as a junior synonym of *Centroberyx teumeri* by Schwarzhans (2010). *O.* (*inc. sed.*) *obliquesulcatus* Voigt, 1926 finally is based on a strongly eroded specimen and cannot be maintained as valid species. No marine Late Cretaceous otoliths are known from outside of North America and Europe (with some freshwater to marginal marine Late Cretaceous otoliths recorded from India by Nolf et al. 2008).

The richest otolith assemblages in terms of valid, non-open nomenclature species are the ones from the Kemp Clay (23 species), the Ripley and Owl Creek formations (27 species), and the Gerhartsreiter Formation near Siegsdorf in Bavaria (33 species). The Severn Formation has yielded 13 species, the late Campanian from Cöthen 5 species, the Fox Hills Formation 4 species, and Denmark 3 species, although 5 more species have been recorded from the basal Danian from the latter region, which may also be considered to have been present in the underlying Maastrichtian as well. Comparing the Kemp Clay assemblage with those of the Ripley, Owl Creek, and Severn formations immediately shows a very low percentage of shared species, i.e., 4 species of a total of 50 species recorded combined in all these formations and locations. Considering a distance of only 600 km between the northeastern Texas Kemp Clay location and the Ripley and Owl Creek locations in Mississippi and considering further that no major geographic obstacles were present at the time of deposition, this is an extremely low semblance, also reflected in a percentage similarity measurement of only 7.3% (see Reitz & Wing 1999 and Stringer et al. 2018 for explanation). The four shared species are *Arius*? *subtilis, Vorhisia vulpes, Eutwaichthys choctawae* and *E. maastrichtiensis* (whereas the unidentified *Paraulopus* from the Kemp Clay may potentially represent a further shared species considering *P. pseudoperca* being recorded from the Ripley and Owl Creek formations). In fact the percentage similarity measurement is lower than between the Mississippi locations and the assemblage described from Bavaria at 8.5% and with 6 shared species, which was across a distance of 3500 to 4000 km even in the Late Cretaceous when North America and Europe were still much closer than they are today and connected by a nearly continuous shelf sea (Fig. 11).

The correlation of the Kemp Clay assemblage with that of the Fox Hills Formation is expectedly high, with three of the four species recorded from the Fox Hills Formation also known from the Kemp Clay, and the fourth, *Pollerspoeckia siegsdorfensis* shared with Bavaria. One species is exclusively shared between the Kemp Clay and the Fox Hills Formation, namely *Dakotaichthys hogansoni*, which is the most common species in the latter formation (66% of total specimens). Correlation with the boreal chalk of northern Europe (Denmark) or the late Campanian erratic bolder from northern Germany is strongly restricted because of the low yield of otolith fossils so far from these rocks. However, rich otolith assemblages have been described from the Danian chalk and the Selandian greensand of Denmark (Schwarzhans 2003) and correlation with these faunas is discussed below. In combination with the assemblage observed in the Maastrichtian of Bavaria, there are at least six species shared with the Kemp Clay, i.e., *Pterothrissus conchaeformis, P. foreyi, Rhynchoconger*? *piger, Arius*? *danicus, Protobythites brzobohatyi* and *Bidenichthys*? *crepidatus*. Three of these, namely

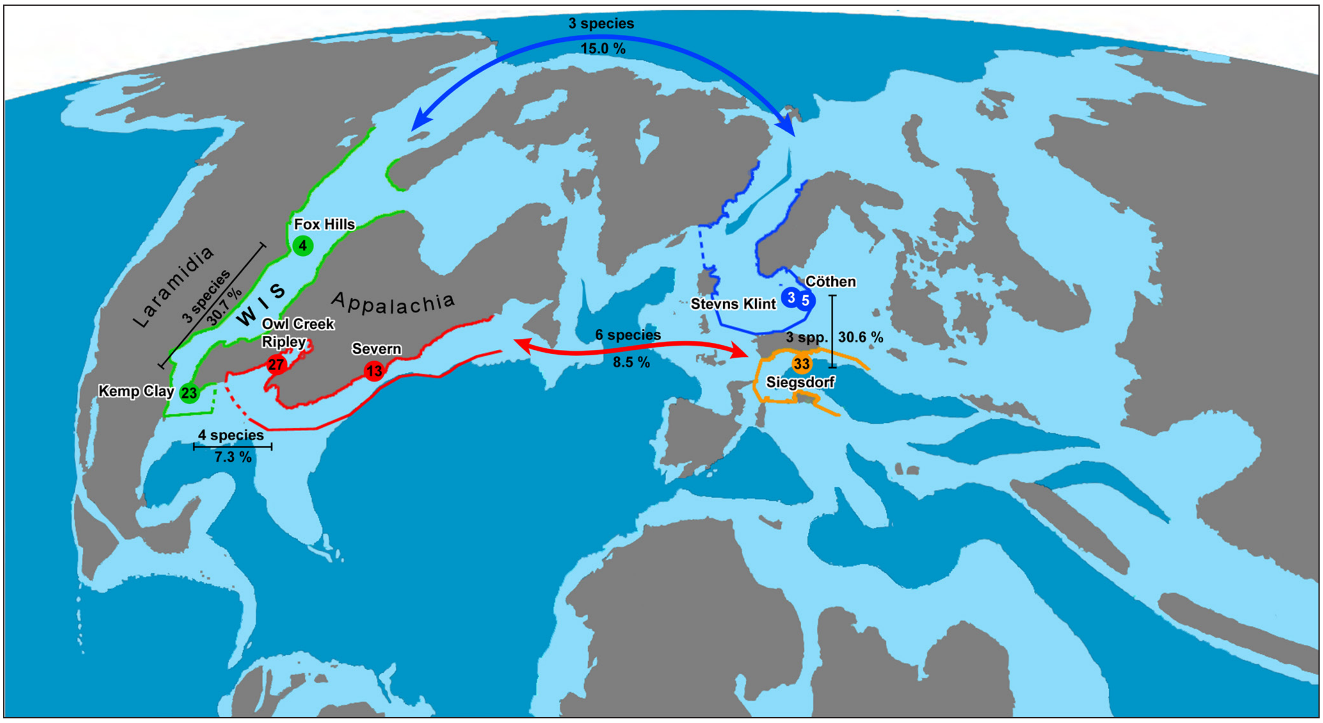
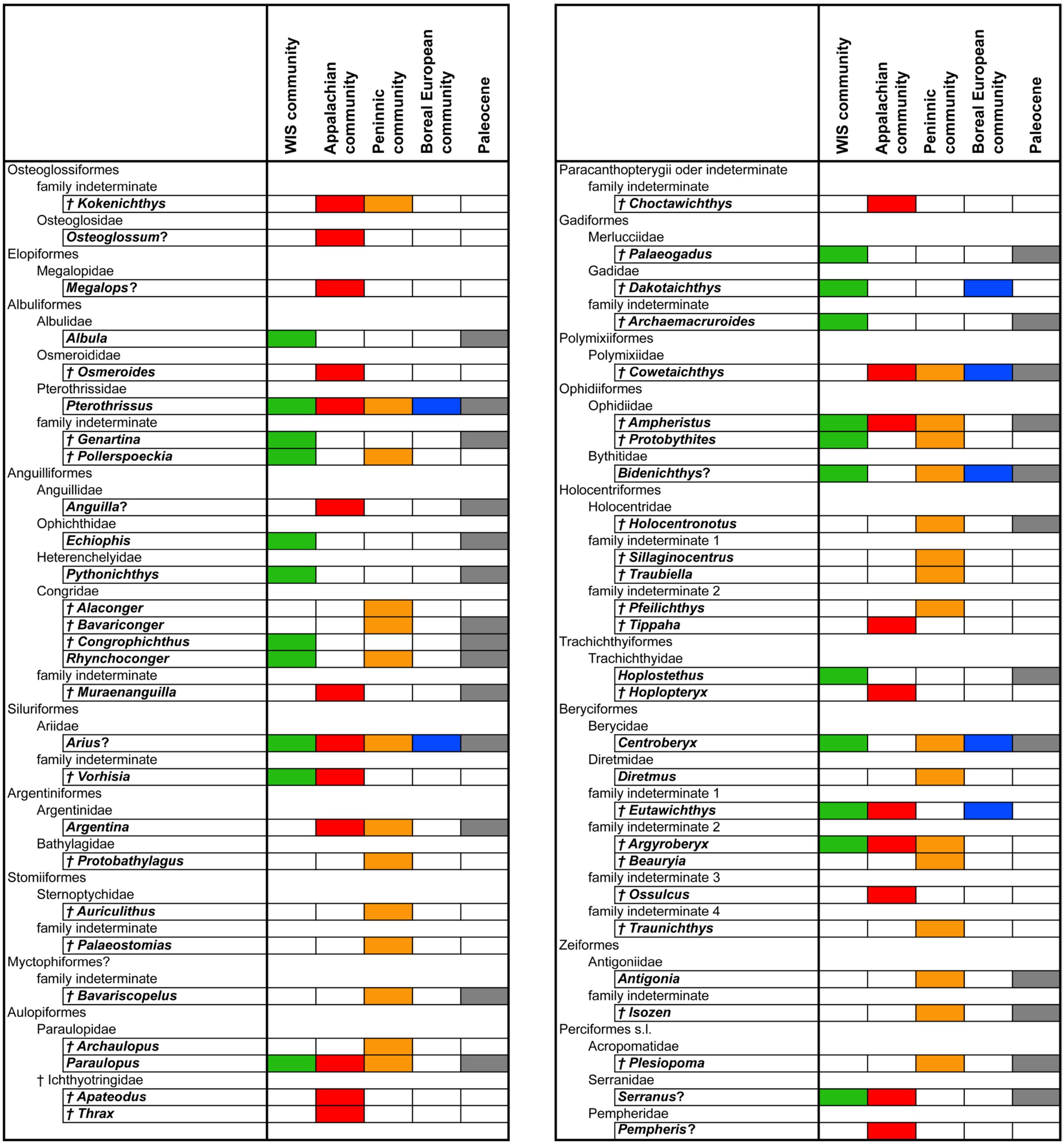


Fig. 11 - Maastrichtian otolith locations, otolith-based faunal communities and exchange. Symbols in North America denote formation names where each symbol may represent more than one location; symbols in Europe represent locations. Count of identified species are shown in symbols. Faunal communities are color coded: green WIS community, red Appalachian community, blue boreal European community, and orange Peninnic community. Inferred faunal movements marked by arrows with faunal correlation marked by bars. Count of shared species and percentage similarities denoted. Paleogeographic map modified from Scotese (2014b).

Pterothrissus conchaeformis, Arius? *danicus* and *Bidenichthys*? *crepidatus* are shared with the late Campanian of northern Germany and/or the basal Danian of Denmark resulting in a comparison index of 15% between the Kemp Clay and the combined northern European communities.

A correlation on the genus level (or lineages) including records in open nomenclature further accentuates four distinct Maastrichtian fish communities as characterized in the following (Fig. 12). The otolith associations from the Ripley, Owl Creek, and Severn formations from Mississippi and Maryland represent a distinct faunal association that we name here the **'Appalachian community'** since it is found along the southern and eastern coast of the former North American land mass Appalachia (Fig. 11). This province is characterized by an abundance of primitive teleosts for instance of the Osteoglossiformes (*Osteoglossum*?, *Kokenichthys*) and *Osmeroides* of the Albuliformes, Siluriformes (*Arius*?, *Vorhisia*), Aulopiformes (*Paraulopus* and extinct ichthyotringids), a variety of highly specialized putative Berycida otolith morphologies like *Tippaha, Eutawichthys,* and *Argyroberyx*, but also *Hoplopteryx* and certain primitive assumed perciforms tentatively associated with the Serranidae and Pempheridae. The Severn otolith association stems from a nearshore, shallow water environment where *Vorhisia vulpes* was particularly common (55%) and also *Eutawichthys* spp. (27%) (Huddleston & Savoie 1983). The Ripley Formation was deposited on the inner to middle shelf with access to deeper water taxa such as *Hoplopteryx* spp. which were by far the dominant fishes (71.4%) (Stringer et al. 2020). The overall composition, however, remains relatively similar. We interpret the Appalachian faunal community as having lived along a relatively wide shelf in a warm, possibly subtropical paleoenvironment of the nascent northwestern Atlantic. The Ripley Formation has been described as shallow to middle shelf sand deposit in Mancini et al. (1996) grading laterally to chalk sequences at greater depth. The overlying mudstone of the Owl Creek Formation and its lateral Prairie Bluff Chalk equivalent (no otoliths known) represent a deepening according to Larina et al. (2016). The Owl Creek Formation at the type location was estimated to have been deposited in 20-30 m water depth (Larina et al. 2016; Stringer et al. 2020).

As already stated above, the Kemp Clay and Fox Hills Formation contain a rather different oto-



	WIS community	Appalachian community	Peninnic community	Boreal European community	Paleocene
Osteoglossiformes					
family indeterminate					
† Kokenichthys		🟥	🟧		
Osteoglosidae					
Osteoglossum?		🟥			
Elopiformes					
Megalopidae					
Megalops?		🟥			
Albuliformes					
Albulidae					
Albula	🟩				⬛
Osmeroididae					
† Osmeroides		🟥			
Pterothrissidae					
Pterothrissus	🟩	🟥	🟧	🟦	⬛
family indeterminate					
† Genartina	🟩				⬛
† Pollerspoeckia	🟩		🟧		
Anguilliformes					
Anguillidae					
Anguilla?		🟥			⬛
Ophichthidae					
Echiophis	🟩				⬛
Heterenchelyidae					
Pythonichthys	🟩				⬛
Congridae					
† Alaconger			🟧		
† Bavariconger			🟧		⬛
† Congrophichthus	🟩				⬛
Rhynchoconger	🟩		🟧		⬛
family indeterminate					
† Muraenanguilla		🟥			⬛
Siluriformes					
Ariidae					
Arius?	🟩	🟥	🟧	🟦	⬛
family indeterminate					
† Vorhisia	🟩	🟥			
Argentiniformes					
Argentinidae					
Argentina		🟥	🟧		⬛
Bathylagidae					
† Protobathylagus			🟧		
Stomiiformes					
Sternoptychidae					
† Auriculithus			🟧		
family indeterminate					
† Palaeostomias			🟧		
Myctophiformes?					
family indeterminate					
† Bavariscopelus			🟧		⬛
Aulopiformes					
Paraulopidae					
† Archaulopus			🟧		
Paraulopus	🟩	🟥	🟧		⬛
† Ichthyotringidae					
† Apateodus		🟥			
† Thrax		🟥			
Paracanthopterygii oder indeterminate					
family indeterminate					
† Choctawichthys		🟥			
Gadiformes					
Merlucciidae					
† Palaeogadus	🟩				⬛
Gadidae					
† Dakotaichthys	🟩			🟦	
family indeterminate					
† Archaemacruroides	🟩				⬛
Polymixiiformes					
Polymixiidae					
† Cowetaichthys		🟥	🟧	🟦	⬛
Ophidiiformes					
Ophidiidae					
† Ampheristus	🟩	🟥	🟧		⬛
† Protobythites	🟩		🟧		
Bythitidae					
Bidenichthys?	🟩		🟧	🟦	⬛
Holocentriformes					
Holocentridae					
† Holocentronotus			🟧		⬛
family indeterminate 1					
† Sillaginocentrus			🟧		
† Traubiella			🟧		
family indeterminate 2					
† Pfeilichthys			🟧		
† Tippaha		🟥			
Trachichthyiformes					
Trachichthyidae					
Hoplostethus	🟩				⬛
† Hoplopteryx		🟥			
Beryciformes					
Berycidae					
Centroberyx	🟩		🟧	🟦	⬛
Diretmidae					
Diretmus			🟧		
family indeterminate 1					
† Eutawichthys	🟩	🟥		🟦	
family indeterminate 2					
† Argyroberyx	🟩	🟥	🟧		
† Beauryia			🟧		
family indeterminate 3					
† Ossulcus		🟥			
family indeterminate 4					
† Traunichthys			🟧		
Zeiformes					
Antigoniidae					
Antigonia			🟧		⬛
family indeterminate					
† Isozen			🟧		⬛
Perciformes s.l.					
Acropomatidae					
† Plesiopoma			🟧		⬛
Serranidae					
Serranus?	🟩	🟥			⬛
Pempheridae					
Pempheris?		🟥			

Fig. 12 - Occurrence of genera per otolith-based faunal communities.

lith association. The most common faunal elements in the Kemp Clay are ariids (21.6%) and the enigmatic siluriform *Vorhisia vulpes* (34.9%), which are all also common in the Appalachian community; and it is furthermore rich in ophidiids (nearly 11%), pterothrissids (9.5%) and a diverse association of anguilliforms containing the earliest records of a putative ophichtid and a heterenchelyid. Another interesting aspect is the occurrence of three species of gadiform otoliths. The Fox Hills Formation shows a much lower diversity (Hoganson et al. 2019), but is remarkable for the dominance of only two species: the ubiquitous *Vorhisia vulpes* and the gadid *Dakotaichthys hogansoni*, which is also present albeit relatively rare in the Kemp Clay. Only 8 of 21 genera found in the Kemp Clay (38%) are also known from the Appalachian community. And only 8 of the 23 genera of the Appalachian community are shared with Peninnic community (35%), which is nearly the same ratio as between the Appalachian community and the Kemp Clay despite the much larger about 6-fold paleo-distance. The Kemp Clay was obviously a mud-rich environment which explained the diversity of anguilliform fishes and has been regarded as estuarine with some freshwater influence (Case & Capepetta 1997), but the presence of ammonites, benthic foraminifera, and rudists (Stephenson 1938) indicate a fully marine environment. The Fox Hills Formation in North Dakota, from which otoliths have been described by Hoganson et al. (2019), likewise is interpreted as an estuarine setting. Both locations are situated along the former Western Interior Seaway (WIS) that linked the Arctic Basin through central North America with the Gulf of Mexico during much of Cretaceous times (Slattery et al. 2015; Hoganson et al. 2019). The Fox Hills Formation in North Dakota was located in the middle portion of the ancient seaway and the Kemp Clay in northeastern Texas at its southernmost peripheries. There has been some debate among geologists for a long time when exactly the WIS closed, whereas the initial closure would be expected either between the two locations here studied for otoliths or to the north of them. Certain studies show the WIS being closed by late Maastrichtian (Roberts & Kirschbaum 1995; Kennedy et al. 1998; Erickson 1999; Crowell 2011), while more recent studies promote that a continuous connection persisted until the very end of the Cretaceous, albeit with possible short-lived interruptions, but sediments were subsequently eroded in some areas (Boyd & Lillegraven 2011; Slattery et al. 2015; Hoganson et al. 2019; DePalma et al. 2019). This latter concept is based on the observation of faunal connectivity of primarily ammonites of the Arctic Basin with Dakotan and Texan locations (Slattery et al. 2015; Hoganson et al. 2019; DePalma et al. 2019). The occurrence of abundant gadids in the Fox Hills Formation of North Dakota and the rare presence of gadiform otoliths in the Kemp Clay indicate indeed that boreal influence might have been a driving element of the faunal associations. Gadiforms, as represented by their unmistakable otoliths, appear to have been cool-water fishes in their origin and despite the lack of data from the Arctic Basin proper, late Cretaceous and early Paleogene gadiform evidence in the boreal province of northern Europe support above assumption. We therefore conclude that the fundamental difference observed between the Kemp Clay otolith association and that from the Ripley and Owl Creek formations is likely caused by two effects: a substantial difference of the environment with a muddy, turbid environment for the Kemp Clay versus a more clear water environment at the other locations (especially the Ripley Formation); and secondly by the influence of cold water entering through the WIS southwards (Hoganson et al. 2019) versus a warm, subtropical temperature in the Appalachian community. We further conclude that the joint occurrence of gadiform otoliths in the Kemp Clay and the Fox Hills Formation of North Dakota links both assemblages despite considerable sedimentological differences and the much impoverished fauna in the Fox Hills Formation. The thus characterized otolith assemblages are interpreted to represent the outliers of a '**WIS community**' (Fig. 11).

The richest Maastrichtian otolith association so far has been described from the Gerhartsreiter Formation near Siegsdorf in Bavaria, located on the periphery of the former Peninnic Ocean (Faupl & Wagreich 2000; Neugebauer et al. 2001; Wagreich & Krenmayr 2005) and is therefore named here the '**Peninnic community**' (Fig. 11). The high diversity of the otolith assemblage in the Gerhartsreiter Formation (Schwarzhans 2010) is probably due to a warm, subtropical climate like that of the southern Appalachian locations, and its position on the shelf but with influence from deep water in the vicinity. At least the presence of, mostly rare, argentiniform, stomiiform, and putative myctophiform otoliths point to influence from further offshore environments provided that those teleost groups were already preferring deeper water. The most common taxa in Bavaria are the enigmatic *Pollerspoeckia* and *Bavariscopelus*, aulopiforms, ophidiiforms, and the putative primitive acropomatid of the fossil genus *Plesiopoma*. The Peninnic community shares with the Appalachian community the diversity of aberrant Berycida otolith morphologies. In the Peninnic community such forms are *Argyroberyx, Beauryia, Traunichthys, Pfeilichthys, Sillaginocentrus* and *Traubiella* many of which have not been found elsewhere. The most common Berycida genus from the Appalachian community - *Eutawichthys* - however is missing. We therefore conclude that the fish fauna of the Late Cretaceous Peninnic community showed some relationship with the northwestern Atlantic

Appalachian community but also contained a large amount of indigenous taxa.

Few otoliths are known from the European boreal chalk sea (Voigt 1926; Schwarzhans & Milan 2017), the '**Boreal European community**' (Fig. 11) (following Schönfeld & Burnett 1991 and Voigt et al. 2010), and therefore little can be concluded for their composition and faunal affinities. However, the late Campanian fauna described by Voigt (1926) is remarkable for the first stratigraphic occurrence of a gadiform otolith, albeit poorly preserved and not identifiable in detail, and therewith supports cold water influence as it certainly appears that the gadiforms were indicative of cold waters even in the Late Cretaceous. Also, a rich otolith association has been observed in the middle Danian of Faxe (Schwarzans 2003) and some of those faunal elements were also observed in the most basal Danian chalk of Stevns Klint (Schwarzhans & Milan 2017). One could presume that at least some of the most basal Danian species identified in Stevns Klint could also be present in the terminal Maastrichtian of the region.

Extinction and survival of teleosts across the K-Pg boundary

Setting the scene: Few events in Earth's history have attracted more interest and scientific research activities than the mass extinction event at the boundary of the Cretaceous to the Paleogene (K-Pg boundary event). The K-Pg boundary (or K-T boundary in older literature) marks the extinction of such iconic animals as non-avian dinosaurs and pterosaurs, and in the sea forms such as ammonites, belemnites, and rudists. However, the extinction event also strongly affected planktonic foraminifers and calcareous nannoplankton, while non-calcareous plankton such as radiolarians, dinoflagellates and diatoms appear to have been much less affected (Hollis 1993; MacLeod et al. 1997). It has been discussed in the literature whether the extinction event was sudden and instantaneous or whether biota underwent some ecological stress leading up to the extinction event (compare e.g., Dodson 1996 and Fastovsky & Sheehan 2005; Stinnesbeck et al. 2012 and Landman et al. 2015; Lamolda et al. 2016). Also, it has been discussed whether certain of the disappearing biota survived the extinction event for a short period of time (Rigby et al. 1987; Landman et al. 2012). There is a growing evidence that the K-Pg extinction event was triggered by the very large Chixculub meteorite impact on the Yucatan Peninsula of Mexico (Smit 1990; Hildebrand et al. 1991; Arenillas et al. 2006; Kring 2007; Schulte et al. 2010, 2011; Penfield 2019). Other roughly time equivalent meteorite impact structures have been located in Boltysh, Ukraine (Jolley et al. 2009) or were interpreted for the Shiva structure off India (Chatterjee 1997; Chatterjee et al. 2006) and have given rise to the idea of quasi periodically recurrent and astrologically caused comet showers hitting Earth at 30 ± 3 Ma intervals (Hut et al. 1987; Rampino & Haggerty 1995; Barash 2011; but see Racki 2012). Other alternative explanations linking the extinction event to large scale Deccan volcanic activities have been discussed as well (Keller et al. 1993, 2012; Keller & Stinnesbeck 1996). An extraterrestrial cause of the K-Pg boundary extinction had been postulated prior to the discovery of the Chixculub crater by Alvarez et al. (1980) based on the observation of an iridium excursion at the boundary between Cretaceous and Paleogene, and has subsequently been proven to be an ubiquitous worldwide marker (Esmeray-Semlet et al. 2016). The global boundary for the base of the Paleogene thus has been defined at the base of the boundary clay which contains the iridium event and ejecta spherules at the stratotype El Kef in Tunisia (Molina et al. 2006, 2009). A sequence of sections across the K-Pg boundary has revealed a sedimentological pattern changing from tens of meters thick mass flow units in very proximal positions to turbidite-induced sediments further away and a centimeter-thick, rust-brown boundary clay with ejecta spherules and the iridium signal in distal positions on a worldwide scale (Schulte et al. 2010). Recent results provided further overwhelming support for the impact scenario from wells drilled on the Chixculub structure (Lowery et al. 2018; Gulick et al. 2019) and the spectacular find of "acipenseriform fishes, densely packed in a deposit (of the Hells Creek Formation at Tanis, Montana, USA) that contain ejecta spherules in their gills and were buried by an inland-directed surge" (DePalma et al. 2019). The impact is thought to have caused an earthquake with moment magnitude of about 11 (Day & Maslin 2005) that in consequence is thought to be responsible for a giant scale mass failure of the North Atlantic margin and the generation of the largest mass-flow deposit on Earth into the Gulf of Mexico (Norris et al. 2000). Super-tsunamis roamed the adjacent shores far inland of the Gulf Coast (Bourgeois et al. 1988; Campbell et al. 2008; Schulte et al. 2011; DePalma et al. 2019) and indications far away along the Tethyan realms (Kobar et al. 2015, 2017) indicate that seismic shock waves and tsunamis may have traveled the mid and low latitudes of the world ocean.

Different concepts have been developed about which effects and mechanisms were triggered by the Chixculub impact and which may have been responsible in the aftermath of the impact for the extinctions on land and in the oceans. For the extinction event in the oceans, model calculations have suggested that soot from wildfires on land, and dust and sulfur aerosols released from anhydrite rocks at the impact site were injected in the atmosphere and partially blocked incoming solar radiation causing darkness for a time (Pope et al. 1994) resulting in a global short-lived "impact winter" (Vellekoop et al. 2014, 2015, 2016; but see MacLeod et al. 2018) or "cosmic winter" (Barash 2011). One theory formulated that photosynthesis was temporarily inhibited causing a collapse of food webs leading to reduction of primary productivity in a "strangelove ocean" (Hsü & McKenzie 1985). The sulfur aerosols released through acid rain are thought to have been responsible for the massive extinction of many planktonic foraminifers and calcareous nannoplankton and therewith could have resulted in the collapse of the biological pump, i.e., the transport of organic matter to the seafloor in a "living ocean" model (d'Hondt et al. 1998; d'Hondt 2005; Esmeray-Senlet et al. 2015; Birch et al. 2016; Vellekoop et al. 2017). Both models were criticized by Alegret et al. (2011), who argued that the low extinction rate observed in the deep sea benthos contradicts a major perturbation of the export productivity and suggested that "surface ocean acidification was the main cause of extinction of calcifying plankton and ammonites" (see also Henehan et al. 2019). Kaiho et al. (2016) suggested that "stratospheric soot was ejected from the oil-rich area by the asteroid impact and was spread globally" resulting in colder climates at mid and high latitudes.

Previous studies about of fish faunas across the K-Pg boundary extinction event. Obviously, not all animal groups in the sea suffered in the same way from the extinction event, whichever cause it may have been (see above). The K-Pg boundary effects on fishes have rarely been investigated. The extinction effects for Chondrichthyes were studied by Noubhani & Cappetta (1997), Kriwet & Benton (2004), and Adolfssen & Ward (2014) with somewhat diverging results ranging from 23 to 57% percent of loss of genera across the K-Pg boundary. Kriwet & Benton (2004) found that open marine apex predators and durophagous demersal forms were most severely affected, while deep-sea forms were apparently little affected. Adolfssen & Ward (2014) in a study of shark teeth across the K-Pg boundary at Stevns Klint in Denmark analyzed a relatively low extinction rate of 23% loss of the genera compared to the two other evaluations. The effects on teleost fishes were analyzed based on skeleton data by Cavin (2001) and Friedman (2009), on otoliths from Kressenberg in Bavaria and Kroisbach in Austria by Schwarzhans (2012), and on teleost denticles by Sibert et al. (2014, 2018) and Sibert & Norris (2015). Cavin and Friedman studied the extinction effects on the family level and found it to have been selective primarily for apex predators of the Ichthyotringoidei, which were replaced in a rapid adaptive radiation by the Scombriformes during the Paleogene. However, these studies suffered from relatively sparse data both from the Maastrichtian and Danian. Sibert et al. and Sibert & Norris l.c. identified a major faunal turnover in the composition of fish denticles from deepwater sediments in the Pacific Ocean across the K-Pg boundary, but the denticles cannot be identified to a suitable taxonomic level for an in depth systematic interpretation. Schwarzhans (2012) noted an extinction loss of 45% of teleost genera recorded by means of otoliths in the Peninnic community and only three species (9%) having survived the K-Pg boundary event in the area. This study, however, is rather localized in nature and has a time gap of about 3.5 mya between the early late Maastrichtian of the Gerhartsreiter Formation and the Danian P1b Biozone from Kressenberg and Kroisbach (Schwarzhans, 2012). The available data and a few new otolith-based data from Denmark were subsequently summarized by Schwarzhans & Milan (2017).

New insights into extinction and survival of teleost fishes across the K-Pg boundary. Now, with the new material available from the USA from recently published studies by Hoganson et al. (2019, and reviewed here), Stringer et al. (2020) and contained in this study, the otolith data base has much improved and the recording gap has become much narrowed. The use of otolith data for interpreting the fishes across the K-Pg boundary is not as accurate as the high resolution studies that can be performed with planktonic foraminifers or nannoplankton. However, it gives new insights on how different teleost groups might have managed during the K-Pg boundary event and allows for some speculations about the resilience of those that have survived.

The updated extinction loss of genera and survival level of species of the three main otolith-based teleost communities now known across the K-Pg boundary (Peninnic community, Appalachian community, and WIS community; see above) is summarized as follows.

	Genus Extinction Loss		Species Survival	
	Count	%	Count	%
Peninnic community	15 of 30	50%	4 of 33	12%
Appalachian community	14 of 23	60%	3 of 27	11%
WIS community	6 of 22	27%	13 of 24	54%

From this brief tabulation, it becomes immediately clear that the level of generic extinction levels is rather variable from one area to another, and that it is within the same range as observed in chondrichthyans (see above). Much more surprising is the high level of species survival of the WIS community where more than 50% of the Maastrichtian species identified in the Kemp Clay apparently survived into Danian times (Fig. 13, 14), while for the two other communities the species survival rate is very low averaging at about 11%. One might argue that in the case of the Peninnic community the stratigraphic gap between the Maastrichtian and Danian otolith assemblages is considerably larger (about 3.5 mya) than in the two North American communities (about 1 mya), but we consider that insufficient to explain the observed discrepancies. The situation becomes even more interesting when evaluating where the WIS survivors actually occurred in the Danian and Selandian as the case may be. Nine of the surviving species persisted in the Gulf Coast Paleocene, which was not open northwards to the Arctic Basin at that time (Slattery et al., 2015), but four are only recorded from the northern European boreal community of the Danian and Selandian. Another three species of the WIS community and two additional species kept in open nomenclature (*Genartina* sp. and *Paraulopus* sp.) may be direct predecessors of evolved early Paleocene species meaning that only 7 species of the WIS community definitely went extinct across the K-Pg boundary.

In fact, it appears that the correlation between the otolith associations from the Maastrichtian Kemp Clay to the Danian Clayton Formation of the Gulf Coast is better than that of the Kemp Clay to the coeval Maastrichtian otolith associations of the Appalachian community (11 species versus 4 species) with a percentage similarity measurement of 32.8% (versus 7.3%). Even the correlation of the Kemp Clay otolith association with the boreal European community of the Danian and Selandian is slightly better than that with the Maastrichtian of the Appalachian community with at least 5 shared species. We interpret the observed difference in extinction and survival levels between the Kemp Clay otolith assemblage as compared to the Appalachian or Peninnian communities as an expression of cool-water tolerance that might have been higher in the WIS community than the other two. This would be consistent with the observation by Adolfssen & Ward (2014) about a lower extinction level of chondrichthyans in the boreal European bioprovince than that for instance recorded from Morocco (Noubhani & Cappetta 1997). Such dependence of extinction or survival on temperature levels would align with the concept of an "impact winter" as for instance suggested by Vellekoop et al. (2014, 2015, 2016), because extant teleost fishes are known to have variable degrees of dependency on specific water temperature ranges for survival and spawning (Johannes 1978; O'Connor et al. 2007; Punkhurst & Munday 2011). An "impact winter" could therefore severely perturb and ultimately lead to extinction of fishes in tropical and subtropical environments.

Unlike chondrichthyans, most marine teleosts undergo a pelagic early larval stage or even spawn pelagic eggs. Early marine fish larvae tend to live epipelagic, are visual feeders, and appear to be op-

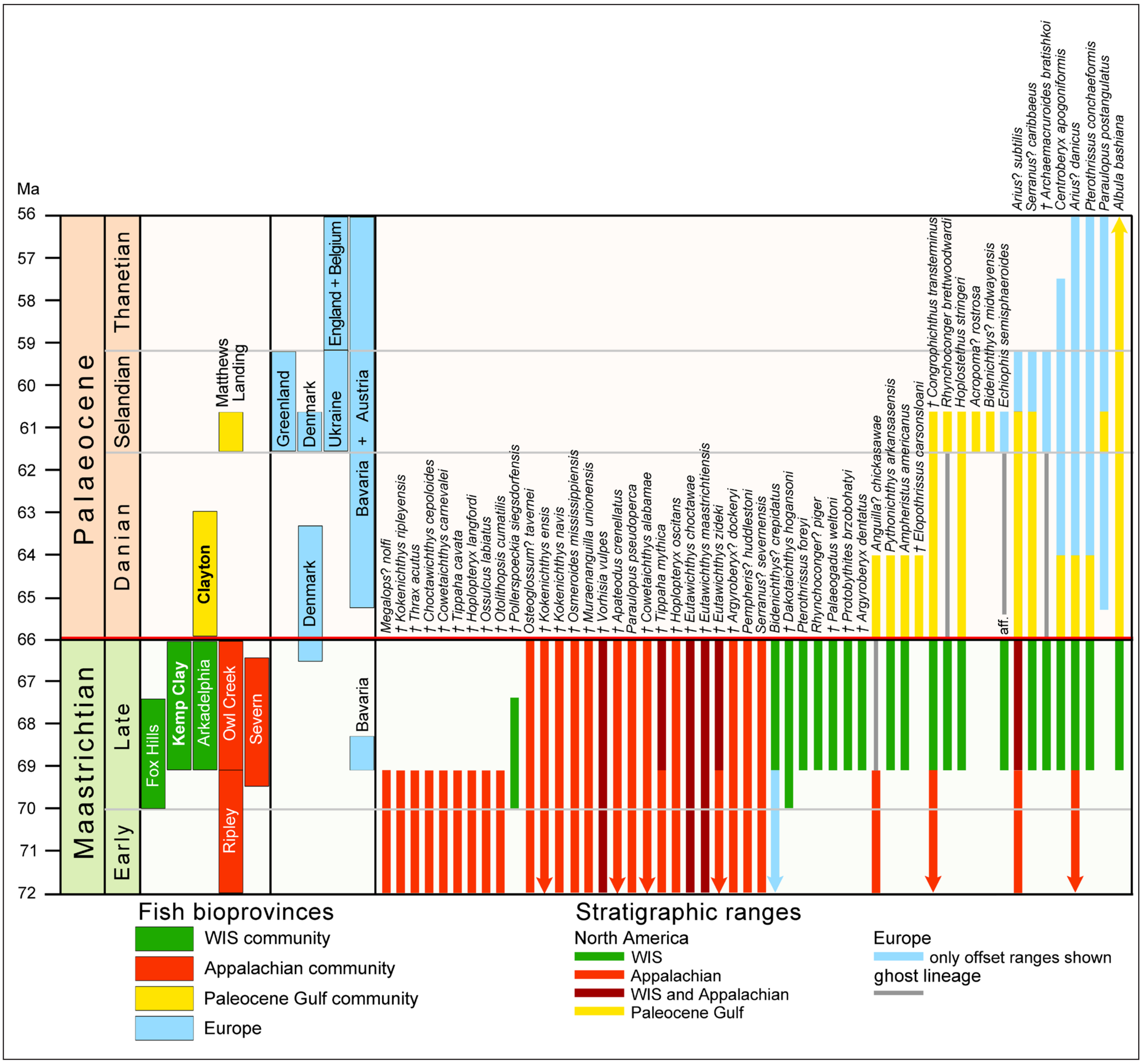


Fig. 13 - Stratigraphic ranges of otolith-based species from the WIS and Appalachian faunal communities in the Maastrichtian and Paleocene communities in the Gulf Coastal Plain and Europe showing extinction and survival of species across the K-Pg boundary event. The stratigraphic position of considered formations (in the USA) and regions (outside USA) depicted on the left.

portunistic to the size of food in relation to the mouth size (Hunter in Lasker 1981; Munk & Nielsen 2005). Small copepod nauplia and other small larvae have been the main food found in stomachs of small fish larvae, and occasionally algae. With growing sizes they may become more food selective, more active in pursuit, and descend into deeper water layers or become demersal (Hunter 1981). Larvae of apex predators are preying on other fish larvae early in their development (Munk & Nielsen 2005). The main driver for the duration of survival of early stage fish larvae until irreversible starvation occurs, seems to primarily depend on egg and yolk sizes and at what size the larvae transform from endogenous to exogenous feeding (Hunt 1981). However the main cause of larval mortality is probably not due to starvation, but it is more likely that larvae are being eaten by predators before reaching the level of irreversible starvation (Monk & Nielsen 2005). Apparently, most marine teleost fish larvae living in the terminal Maastrichtian oceans must have been exposed to acidification effects caused by the Chixculub meteorite impact as postulated in the concept of d'Hondt et al. (1998), d'Hondt (2005) or Alegret et al. (2011). Recent studies of acidification dependency of certain coral reef fishes and their larvae have not revealed a significant direct effect on their vitality (Munday et al. 2011; Punkhurst & Munday 2011). Fossil food dependencies are difficult to evaluate because the source of food during larval development may have been the part of the zooplankton that has no or very little fossil record, e.g., copepods, amphipods and other small crustaceans or algae. Calcareous plankton such as foraminifera or coccoliths may not have played a significant role in the diet of larval fish or at least was relatively easy to substitute. The role of other calcareous planktonic animals such as juvenile ammonites or pteropods, the latter of which seem to have become abundant only after the K-Pg boundary event (Tajika et al. 2017; Peijnenburg et al. 2019) is difficult to assess. The relatively moderate impact of the end-Cretaceous extinction event on teleosts as a whole indicates, however, that the oceanic food web must have been sufficiently resilient to nourish the majority of pelagic larvae of teleost fishes. It may be possible though that certain groups of fishes that became specialized during ontogeny on calcareous plankton, or apex predator (larvae) that were feeding on (juvenile) ammonites became exposed to levels of ecological stress that eventually led to their extinction.

Extinction and survival selectivity. Cavin (2001) singled out families of the basal teleost orders Crossognathiformes and Ichthyodectiformes and the aulopiform suborders Ichthyotringoidei and the Enchodontidae of the Alepisauroidei as victims of the end-Cretaceous extinction event on family level. However he explicitly excluded a number of teleost families that were considered to have already become extinct in the Campanian (e.g., Osmeroididae, Ichthyotringidae, Sardinioididae, Sphenocephalidae) and undefined acanthomorph fishes because of the poor understanding of the systematics of these groups (e.g., Ctenothrissiformes, Dinopterygoidei). Otoliths have revealed an abundance of specialized, advanced morphologies in the terminal Cretaceous that became extinct at the K-Pg boundary and cannot be related to persistent groups or have experienced systematic allocations under dispute. These are: *Kokenichthys* (a putative osteoglossiform), *Vorhisia* (a putative siluriform), *Bavariscopelus* (a putative myctophiform), *Choctawichthys* (a putative paracanthopterygian), *Pfeilichthys, Sillaginocentrus, Tippaha, Traubiella* (putative holocentriforms of two different morphotypes), *Argyroberyx, Beauryia, Eutawichthys, Ossulcus,* and *Traunichthys* (putative beryciforms of four different morphotypes). Unfortunately, calibration of Cretaceous otoliths with in situ finds of articulated skeletons is still at a very low level. Non-invasive micro-CT scanning so far has yielded results for *Osmeroides*, *Apateodus* and *Hoplopteryx*, which convincingly has demonstrated the gain of additional value created by this method (Schwarzhans et al. 2018a). In any case, those enigmatic otolith morphologies listed above indicate that the level of higher systematic extinction at the K-Pg boundary was broader than indicated by Cavin (2001). In addition to the apex predators highlighted by Cavin (2001) and Friedman (2009), it further included a plethora of fishes amongst others of the superorder Berycida, which occupied similar environments during the Late Cretaceous that became the domain of perciform fishes after the K-Pg extinction event.

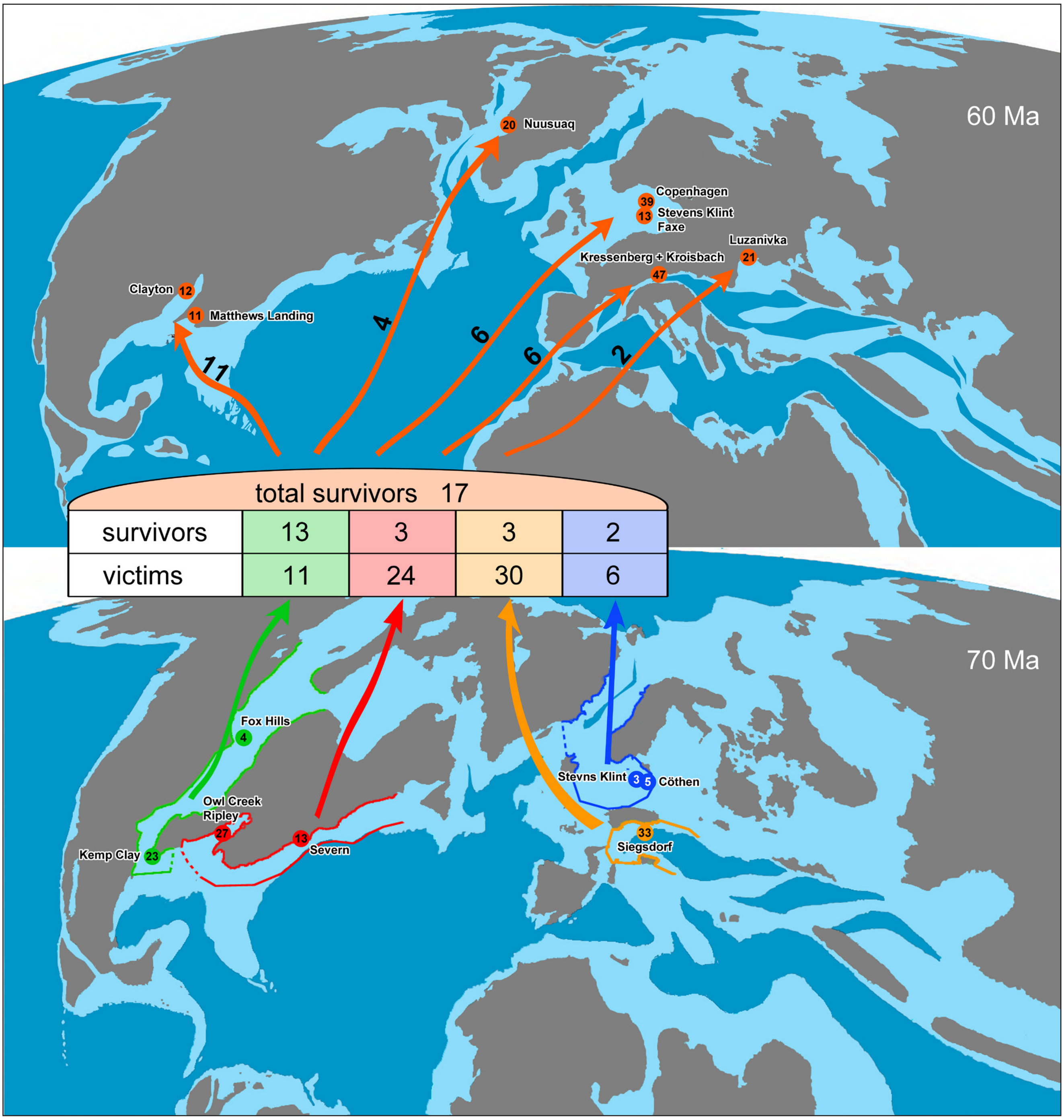
Victims. We suggest that the following groups of teleost fishes might have been particularly vulnerable to ecological stress and risk of extinction:

1. Oceanic apex predators, for example of the Ichthyotringoidei and Enchodontidae both of the Aulopiformes, were probably affected in agreement with the assessments of Cavin (2001) and Friedman (2009). These fishes relied on a particularly long and intact trophic sequence, and failure of one chain link could have generated a devastating effect endangering the end-member of the trophic chain.

2. Fishes with a particularly complex reproduction strategy may have been vulnerable, for instance *Vorhisia vulpes*, and the more so if geographically restricted.

3. Tropical or subtropical neritic fishes that were unable to cope with the effects of a prolonged "impact winter" as might have been the case for many of the Berycida.

4. Fishes living in carbonate platforms or reef environments, which experienced a severe stress during the "impact winter" as well and were generally adapted to retracted and sparse environments during the immediate post- K-Pg event (an exception being e.g., the continuous carbonate Satal Formation in the Sirte Basin of Libya; Barr & Weegar 1972). Such fishes would generally be underrepresented in otoliths due to poor fossilization potential of otoliths in limestone but may contain many



total survivors 17

survivors	13	3	3	2
victims	11	24	30	6

Fig. 14 - Maastrichtian (~70 Ma) and early Paleocene (Danian and Selandian, ~60 Ma) otolith locations, otolith-based faunal communities and exchange. Symbols in North America denote formation names where each symbol may represent more than one location; symbols in Europe represent locations. Count of identified species are shown in symbols. Faunal communities are color coded: Maastrichtian: green WIS community, red Appalachian community, blue boreal European community, light orange Peninnic community; Paleocene dark orange undivided. Arrows in the Maastrichtian field indicate contribution in terms of victims and survivors during the end-Cretaceous extinction. Dark orange arrows in Paleocene field indicate number of survivor species from Maastrichtian in respective region. Note that total number of survivors is smaller than the sum of individual survivors per faunal community because some survivors occurred in more than one faunal community. Paleogeographic map modified from Scotese (2014a, b).

fishes known from articulated skeletons.

Survivors. We suggest that the following groups of teleost fishes might have been in a more favorable position to survive the end-Cretaceous perturbations:

1. Deepwater fishes, since deepwater environments appear to have been generally less affected than shallow water environments (see Kriwet &

Benton 2004). However, there are no confirmed otolith data of deepwater fishes from that time interval.

2. High latitude, cool-water fishes, because they would not have been affected as severely by the "impact winter" and may also have been sheltered more from direct meteorite impact effects such as tsunamis in the Arctic Basin or atmosphere disturbances along the tropics belt. Gadiforms would have particularly benefitted. Judging from their occurrence in the WIS and boreal European communities they were adapted to cool water at that time.

3. Fishes with a preference for muddy bottom conditions like anguilliforms or ophidiiforms or an infaunal life style such as heterenchelyids.

4. Fishes with a large tolerance to temperature and ecological conditions and no specific prey adaptation as may be expected for some lower teleost groups (e.g., albuliforms) or basal perciforms.

Disaster opportunists. Detailed studies have been performed on planktonic faunal events immediately following the meteorite impact (e.g., Alegret et al. 2004; Keller & Pardo 2004; Pardo & Keller 2008). Pardo & Keller (2008) recognized three distinct phases after the impact: an euphotic phytoplankton bloom under early eutrophic conditions, followed by an opportunistic *Guembelitria* bloom, which in turn is followed by low oxygen tolerant heterohelicids before reestablishment of normal conditions and a faunal recovery. This entire phase lasted for slightly over 0.5 mya through the planktonic foraminifera zones P0, Pα and P1a. The otolith record is generally too sparse with too few sampled locations across this short time span for a detailed analysis. However, few otoliths specimens studied from the Pα and P1a intervals of Stevns Klint, Denmark by Schwarzhans & Milan (2017) have revealed *Pterothrissus conchaeformis* to represent by far the most common species in this interval. The extant *Pterothrissus gissu* Hilgendorf, 1877 was found to feed "on a wide variety of prey items consisting of Euphausiacea, Polychaeta, benthic crustaceans, and benthic fishes" according to Fujita et al. (1995). Its Maastrichtian-Paleocene relative therefore may have represented a food generalist at that time as well and thus may have indeed been a true disaster opportunist. Such an explanation would also be consistent with the common occurrence of albulids and pterothrissids in the Clayton Formation of Arkansas as here described, although it probably represents a time already at the beginning of the recovery phase. The most common group in the Clayton Formation are two ariid species, one of which is also recorded throughout the Paleocene of Denmark (Schwarzhans 2003). One extant ariid common in the Gulf of Mexico, *Ariopsis felis,* is highly abundant in the shallow coastal waters and estuaries. It is an opportunistic feeder and scavenger that can utilize different food sources in a variety of habitats (Pattillo et al. 1997). These characteristics would have been ideal for the environmental conditions following the K-Pg extinction event. The most surprising common faunal element in the Clayton Formation is perhaps the heterenchelyid *Pythonichthys arkansasensis*, since heterenchelyid otoliths have never been found as common as here (20%). For example, heterenchelyid otoliths (90 specimens) were recovered from the Yazoo Clay (upper Eocene) in Louisiana, but they only represented 1.62% of the total 5,559 specimens (Nolf and Stringer 2003; table 1). The Heterenchelyidae (mud eels) are as much an infaunal form as it can be with fishes. Eagderi & Adriaens (2010) stated that heterenchelyids spend most of their lives submerged in sediment, and are noted for their head-first burrowing. We therefore postulate that *Pythonichthys arkansasensis* serves as an example of how muddy water tolerant and sediment burrowing fishes thrived in the impact aftermath.

Faunal recovery. Only limited data have previously been recorded from the time interval during the early Paleocene "post-disaster" and recovery phases. The few "post-disaster" data came from the iconic Stevns Klint location in Denmark (Schwarzhans & Milan 2017), and they showed a good consistency of the fish fauna with the subsequent Danian recovery phase and beyond into the Selandian. Now, the Clayton Formation in Arkansas represents the most complete early Danian otolith-based fish fauna known to date, and it allows to analyze the post K-Pg boundary recovery process in more detail. It contains 14 species including species in open nomenclature and 12 identified ones, of which only one is not known from the Maastrichtian (*Elopothrissus carsonsloani*). Of the 11 species of the Clayton Formation shared with the Maastrichtian (Fig. 14) only one is not represented in the Kemp Clay in nearby northeastern Texas (*Anguilla*? *chickasawae*) but this species is known from the Ripley Formation of Mississippi (Stringer et al. 2020). Conversely, 10 of the 23 identified species from the Kemp Clay are also present in the Clayton Formation and further three species from other locations: *Rhynchoconger brettwoodwardi* from the Selandian of Alabama (as *Rhynchoconger* sp. in Nolf & Dockery 1993), and *Echiophis semisphaeroides* and *Archaemacruroides bratishkoi* from Europe. Another two species from the Kemp Clay have putative descendant species in the Paleocene, namely *Palaeogadus weltoni* and *Bidenichthys*? *crepidatus*, but not in the Clayton Formation. The disappearance of some of the faunal elements in the Kemp Clay, most notably of the gadiforms, may be related to other circumstances than the K-Pg boundary extinction event. It is the consensus of geologists that beginning with the Danian the Western Interior Seaway had become permanently closed and the Gulf Coast represented the northern margin of the Gulf of Mexico (Slattery et al. 2015; Hoganson et al. 2019). This development may have eliminated cold water fish species from the Gulf Coast as represented in the Clayton Formation, while they survived in regions under continued boreal influence such as in Denmark (Schwarzhans 2003). However, it should be noted that much less otoliths were recovered from the Clayton Formation than the Kemp Clay and they are also generally less well preserved. Therefore, the data from the Clayton Formation could be biased to some extend as for instance the two unidentifiable species of the genus *Genartina* or *Paraulopus* sp. from the Kemp Clay, indicating that the degree of similarity between both formations and the recovery in the Clayton Formation could have been even larger than currently reflected. In any case, we can conclude that the otolith assemblage retrieved from the early Danian Clayton Formation basically represents an impoverished version of the Maastrichtian assemblage of the Kemp Clay, diminished through the K-Pg extinction event and the disappearance of cool water faunal elements caused by the closure of the Western Interior Seaway. An otolith assemblage described by Nolf & Dockery (1993) from the Selandian of the Matthews Landing Marl Member of Alabama (then considered to be of late Danian age, but see Dockery & Thompson 2016) reveals a great continuity with the Clayton Formation. New incoming species are few: *Paraulopus postangulatus* (Nolf & Dockery, 1993), a descendant of *P. pseudoperca* (Nolf & Dockery, 1990), *Bidenichthys*? *midwayensis* (Nolf & Dockery, 1993), a descendant of *B.*? *crepidatus*, and *Plesiopoma rostrosa* (Nolf & Dockery, 1993; as "genus Apogonidarm" *rostrosus*), which may be related to similar species described from the Maastrichtian and Paleocene of Bavaria and Austria (Schwarzhans 2010, 2012). This indicates that the faunal recovery and evolution of new species from an older stock was slow during the Danian and was still moderate during the Selandian in the Gulf Coast area. Faunal recovery scenarios in the European Paleocene (late Danian and Selandian from Denmark and Bavaria) shows a much larger degree of evolutionary changes versus the Late Cretaceous assemblages (Fig. 14), but can largely be demonstrated to have derived from K-Pg boundary survivors. These are also slightly younger faunas than the one retrieved from the Clayton Formation. They show nevertheless that evolutionary adaptation and radiation began at a relatively low pace during Paleocene since most new species do not markedly differ from their Late Cretaceous predecessors, where known.

EVOLUTIONARY SIGNIFICANCE AND THE ORIGIN OF SELECTED MODERN TELEOST GROUPS

The Late Cretaceous is known to represent an important period in the evolution of modern teleosts (Arratia & Chorn 1998; Cavin 2008; Carnevale & Johnson 2015; Alfaro et al. 2018). Modern molecular phylogenies are gaining increasing importance for phylogenetic reconstructions of teleosts (e.g., Betancur-R. et al. 2013). Varying molecular clock models are applied to estimate diversion times of major phylogenetic dichotomies but often suffer from the absence of calibration points from paleontological findings either because of lack of data or because of ambiguous or disputed systematic interpretation of fossil finds. Because of their abundance, otoliths can potentially contribute significantly in identifying or narrowing of time intervals for phylogenetic calibrations. However, otolith interpretations also suffer from a number of shortcomings (Schwarzhans 2018 and Schwarzhans et al. 2018), the most important being that their interpretation largely depends on correlation with otoliths from extant fishes which of course loses accuracy in deep time and can be misled by unrecognized homoplasies. In the following, we evaluate the Kemp Clay otolith association in respect to its evolutionary significance and in respect

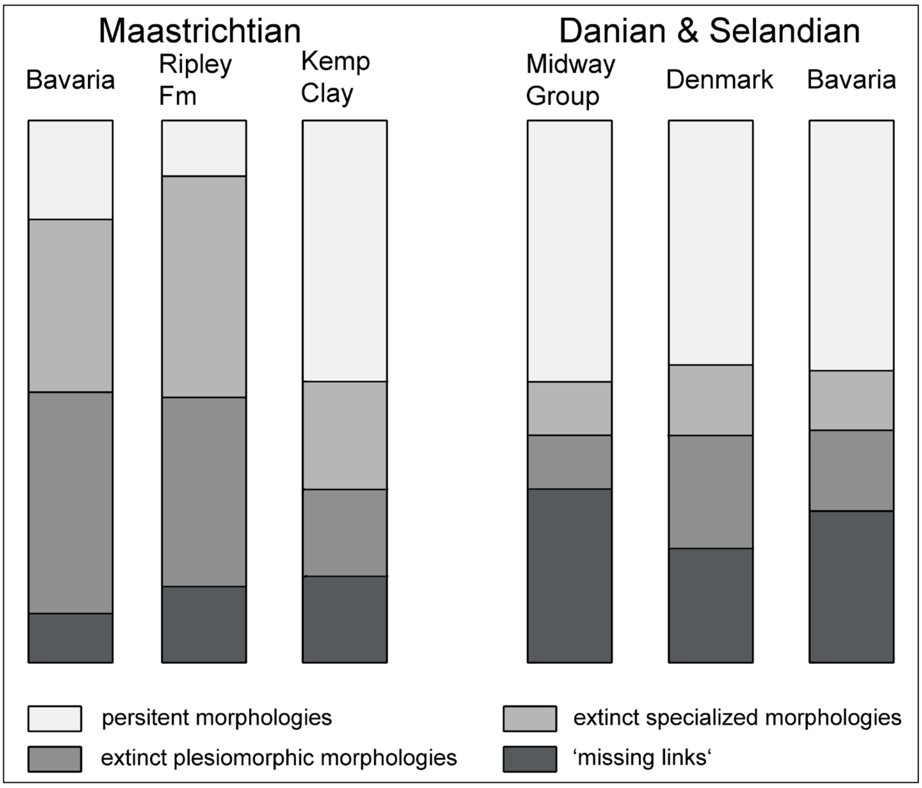


Fig. 15 - Comparison of key faunal communities from the Maastrichtian and the Danian and Selandian in terms of evolutionary categories. 'Midway Group' includes faunas from early Danian Clayton Formation and early Selandian Matthews Landing Marl Member.

to their potential of time calibrations for phylogenies of 'modern teleosts'. In this context we also critically discuss certain previous otolith interpretations where in dispute.

Evolutionary categorization. Schwarzhans (1996, 2012) proposed a scheme for the classification of Late Cretaceous and Paleogene otolith morphologies in evolutionary categories designed to aid phylogenetic interpretations of fossil otolith data. The evolutionary categories are the following (Fig. 15).

Category 1 contains morphologically not significantly altered persistent forms. In the Kemp Clay they are a large group containing 12 species (48%) of the genera *Albula, Pterothrissus, Echiophis, Pythonichthys, Rhynchoconger, Arius*?, *Paraulopus, Hoplostethus,* and *Centroberyx*.

Category 2 contains extinct specialized morphologies without apparent affinities to extant taxa. In the Kemp Clay this category is represented by 5 species (20%) of the genera *Genartina, Vorhisia, Eutawichthys,* and *Argyroberyx*.

Category 3 contains extinct plesiomorphic morphologies which are usually well attributable to living families. In the Kemp Clay this category is represented by 4 species (16%) species of the genera *Congrophichthus, Palaeogadus, Ampheristus,* and *Protobythites*.

Category 4 contains plesiomorphic morphologies that are considered to be placed near to major dichotomies in the phylogeny of modern teleost groups and could informally be termed 'missing links'. In the Kemp Clay we count in this category 4 species (16%) of the genera *Dakotaichthys, Archaemacruroides, Bidenichthys*?, and *Serranus*?.

When comparing the percentages of the four categories with those calculated for the Maastrichtian of Siegsdorf, Bavaria and the Ripley Formation of Mississippi (Fig. 15), it becomes immediately clear that the Kemp Clay association differs from the two other fundamentally in the unusual high percentage of category 1 persistent morphologies and low percentages of category 2 and 3 extinct morphologies and thus reflects again the relatively low extinction rate in the Kemp Clay as described above. In this respect the Kemp Clay fauna resembles much closer the early Paleocene ones from Denmark and the Midway Group (Clayton Formation and Matthews Landing Marl Member, as reinterpreted from Nolf & Dockery 1993) (Fig. 15). The early Paleocene associations differ from the Kemp Clay association in still less extinct specialized morphologies, which reflects the effect of the end-Cretaceous mass-extinction, and the higher degree of in the 'missing link' category, which reflects the onset of phylogenetic radiation after the end-Cretaceous extinction event (Fig. 15).

On the origin of selected modern teleosts. In the following, we present and discuss early otolith records of the Anguilliformes, Gadiformes, Ophidiiformes, and Perciformes s.l. based on data from the Kemp Clay, which provide for new insights or confirm earlier assessments.

Anguilliformes. Anguilliforms are an old group of teleosts, which have been identified by several finds of articulated skeletons in the Late Cretaceous since Cenomanian (Belouze et al. 2003a and 2003b) and by otoliths (Schwarzhans et al. 2018b) since the Santonian Eutaw Formation (84-85 Ma according to Mancini et al. 2005), but otolith morphologies that can be linked to modern forms appeared first during late Campanian: *Congrophichthus transterminus* (as Congridae indet. in Nolf & Dockery 1990) from the Coffee Sand Formation of Mississippi (79-80 Ma according to Mancini et al. 2005). Other congrid otoliths, sometimes tentatively attributable to extant genera like *Rhynchoconger* but more commonly representing extinct lineages regularly occur since middle Maastrichtian (69 Ma). Obviously, congrids already showed some morphological diversity in the Maastrichtian (see Schwarzhans 2019b for further discussion). Some putative anguillid otoliths are identified as well, but their characteristics are less clear. The recognition of *Echiophis semisphaeroides* at least since Paleocene but possibly already in the late Maastrichtian represents the earliest ophichthid record. The finds of many otoliths of a typical and unequivocal heterenchelyid (*Pythonichthys arkansasensis*) from the Kemp Clay and the Danian Clayton Formation is the oldest record of this highly specialized family (68-69 Ma). In conclusion, it appears that many extant anguilliform families, and in a few instances possibly even genera have an early origin dating back to at least Maastrichtian times suggesting that principal anguilliform diversity is well established prior to the K-Pg boundary event. Unfortunately, it is unclear how this observation may line up with the many extinct anguilliform families known from articulated skeletons from the Eocene (Patterson 1993a), but there are also certain anguilliform otolith morphologies which do not correlate with extant groups such as *Muraenanguilla* (72-40 Ma) (see Schwarzhans 2019a, 2019b; Stringer et al. 2020). The 'first unambiguous occurrence date' (meaning the earliest occurrence here recognized, but being aware that earlier occurrences are likely to be found in the future) of the Congridae thus is 79 Ma and that of the Heterenchelyidae 68 Ma (Fig. 16).

Gadiformes. In an article termed "A review of early gadiform evolution and diversification", Kriwet & Hecht (2008) summarized the then known occurrence and distribution of fossil gadiforms. They mentioned a diverse representation of gadiform otoliths since Paleocene times from the North Sea Basin and reported on the earliest skeletal record of a macrourid from the Eocene of Antarctica. In this study, Kriwet & Hecht concluded that gadiforms may have originated in the shallow water of the temperate and boreal oceans, and gadoids in the North Atlantic and macrouroids in the South Atlantic. The assumption of a shallow water origin of macrourids was later supported by many finds of unequivocal macrourid otoliths in the early Eocene of Antarctica, which also contained definitive gadoid otoliths, which are now absent from the southern hemisphere (Schwarzhans et al. 2016). This study showed that while gadiforms indeed lived in cool-water regions, their distribution and divergence in the Paleogene had already progressed significantly and no clear distinction between a gadoid northern hemisphere and macrouroid southern hemisphere birth could be recognized. However, all these studies did not make use of a somewhat cryptic and seemingly doubtful record of gadid otoliths described by Voigt (1926) from a late Campanian erratic bolder from northern Germany (about 75-76 Ma deduced from Voigt et al. 2012). Now, with the record of three gadiform otolith-based species from the late Maastrichtian of the Kemp Clay and one of them also in the Fox Hills Formation of North Dakota (68-70 Ma), the Campanian records appear in a new light. Voigt's gadid otolith records are too poorly preserved for a generic let alone specific identification, but one of them (Ot. *Gadidarum erraticus* Voigt, 1926) really does seem to represent a gadiform otolith. The Maastrichtian records described here already indicate a certain degree of morphological diversification. They include a merlucciid representative of the genus *Paleaeogadus*, a putative stem-gadiform of unknown interrelationship (*Archaemacruroides*) and *Dakotaichthys*, which has an otolith morphology almost like an ideal candidate between a gadid and a macrourid form. *Dakotaichthys hogansoni* is the most common species identified by otoliths from a very shallow, estuarine environment in the Western Interior Seaway of North Dakota (see Hoganson et al. 2019). The new finds of gadiform otoliths from the Kemp Clay and the Fox

Hills Formation are all morphologically relatively generalized and thus may indicate that the gadiform origin may not reach back in time much beyond late Campanian. It further supports a boreal northern hemisphere origin of the group, possibly in the Arctic Basin. It must be noted that certain Cenomanian to Campanian skeleton finds of the extinct family Sphenocephalidae (Sphenocephaliformes) have been interpreted as representing the sister-group to all Paracanthopterygii except Polymixiiformes (see Nelson et al. 2016). In this context, it is interesting to further note that the enigmatic otoliths of *Choctawichthys* Schwarzhans & Stringer, 2020 (in Stringer et al. 2020) have recently been interpreted as representing a basal paracanthopterygian of unknown relationships. In conclusion, gadiform otoliths are unambiguously recognizable in the fossil record by their homosulcoid and pseudobiostial sulcus pattern (see Schwarzhans 1978 for explanation of terms). In our assessment, the Gadiformes are of earlier origin than often assumed and had achieved a basal diversification in the Late Cretaceous just before the K-Pg boundary event, their 'first unambiguous occurrence date' being 75 Ma. They obviously survived the end-Cretaceous mass extinction well, experienced a phase of diversification both morphologically and geographically during early Paleogene, and are considered a group that benefitted particularly well from the global cooling at the turn of the Eocene to Oligocene (Fig. 16).

Ophidiiformes. The discrepancy between the common record of fossil ophidiiform otoliths and rarity of articulated ophidiiform skeletons has long been recognized (Nolf 1980; Schwarzhans 1981). It has been interpreted as an effect related to the shallow marine, well-oxygenated muddy to sandy bottom environment preferred by Paleogene ophidiiforms that would enhance fossilization of their otoliths but would be rather detrimental for the fossilization potential as articulated and hence identifiable skeletons (Møller et al. 2016). It appears that certain ophidiiforms only started to migrate to the deep water during the late Eocene/early Oligocene transformation from a halothermal to a thermohaline circulation in the world oceans (Schwarzhans 2019a). The ophidiiform otolith record is well established in the Late Cretaceous, e.g., the Maastrichtian from Bavaria and Austria, the late Campanian and Maastrichtian of the boreal European bioprovince, and now also from the Maastrichtian of the Kemp Clay in Texas. Carnevale & Johnson (2015) recorded the first articulated ophidiiform skeleton from the Campanian to Maastrichtian of northern Italy (*Pastorius methenyi*), and placed it as the sister-group to all bythitoids. Ophidiiform otoliths are relatively easy to recognize, but their often somewhat reduced morphology and apparent multiple homoplasies (Schwarzhans 1981) renders generic definitions often problematical. The known otolith records from the Late Cretaceous certainly represent the two main groups, i.e., Ophidioidei and Bythitoidei. The ophidioid otoliths often show more morphological diversity than those of the bythitoids and their Cretaceous representatives are placed in the fossil genera *Ampheristus* (one of the few skeleton-based genera that have been found with otoliths in situ) and *Protobythites*. The 'first unambiguous occurrence date' of the Ophidiidae is 69 Ma in the early late Maastrichtian of Siegsdorf, Bavaria. The bythitoid representatives, which reach back into the late Campanian are provisionally placed in *Bidenichthys*? ('first unambiguous occurrence date' at 75 Ma), a genus that bears one of the most plesiomorphic otolith morphologies in the extant representatives of the group. Møller et al. (2016) have argued that such identification merely reflects a catch-all allocation because of lack of sufficient characteristics to define a fossil otolith-based genus and should therefore be seen as a placeholder until more data, preferably otolith in situ, have become available. The earliest unambiguous dinematichthyid has been described from the terminal Maastrichtian of Denmark (Schwarzhans & Milan 2017) at about 66.5 Ma. Dinematichthyid otoliths are already highly diverse in the Danian of Denmark indicating that they might have been of earlier origin than currently perceived. In conclusion, the Late Cretaceous otoliths of the Ophidiiformes exhibit a relatively large diversity (Fig. 16). As a group, the Ophidiiformes survived the K-Pg boundary event well and were one of the most successful groups in the shallow warm seas during Paleogene before their decline and migration into deep water at the turn of the Eocene to Oligocene (Nolf 1980; Nolf & Stringer 2003; Schwarzhans 2019a).

Perciformes s.l. Few groups have seen so many changes in recent phylogenetic studies than the former Perciformes as pooled in Nelson (2006). Concepts and grouping is still in a dynamic phase and since most past otolith-based literature has used the traditional concept of the Perciformes sensu

Nelson, 2006 we discuss our interpretation here on that basis too. Cretaceous perciform otoliths have been the subject of dispute for some time where Nolf & Dockery (1990), Nolf & Stringer (1996) and Nolf (2016) described multiple occurrences and lineages mostly of the Percoidei from Late Cretaceous sediments reaching back into Cenomanian times (Nolf 2016), whereas Schwarzhans (2010, 2012), Schwarzhans et al. (2018b) and Stringer et al. (2019) adopted a much more restrictive view of which forms of Cretaceous otoliths might represent perciforms. In an overview of the early fossil record of acanthomorphs, Patterson (1993) commented in respect to the correlation of skeleton and otolith data that in his opinion "the only outstanding difference is in Cretaceous percoids, where there are no skeletal records and rather diverse otolith records." The situation has changed in the meantime where several skeletal records from the Late Cretaceous have been recovered that show that perciform fishes were indeed present and that their abundance and morphological diversity might have been underestimated because of fossilization bias (Carnevale & Johnson 2015). There is also no doubt that perciform otoliths are present in the Late Cretaceous, but the underlying problem is of a different nature. Many derived perciform groups have highly diagnostic otolith features, but such forms have not been found in the Cretaceous. Otoliths of the Percoidei instead often exhibit a generalized heterosulcoid pattern, which can be quite similar to patterns found in other teleosts, which may not be related and which appear to have had a long history, for instance of the Holocentriformes, Polymixiiformes, Scorpaenoidei, and even certain Aulopiformes. Therefore, Cretaceous records of perciform otoliths require more detailed analysis for recognition unlike gadiform or ophidiiform otoliths which have more unique otolith patterns. In many instances, calibration with otoliths in situ will be the only method to resolve some of the persisting conundrums. For example, discovery of an otolith in situ in the derived, extinct aulopiform *Apateodus* has allowed linkage with isolated otoliths previously thought to potentially represent gempylids (Schwarzans et al. 2018a). Several Cretaceous otolith morphologies that have been considered as possible perciform representatives have alternatively been interpreted as extinct beryciforms or holocentriforms (Schwarzhans 2010; Stringer et al. 2020). We regard past records of apogonid, caproid, moronid, pomacanthid, gempylid, or centrolophid otoliths from the Cretaceous as not sufficiently substantiated and recommend not to use those records for calibration purposes in phylogenetic assessments. However, there are also many records of very generalized 'percoid' otolith morphologies, in the Maastrichtian at least, that appear to be plausible and could represent the families Acropomatidae, Serranidae, and Pempheridae (Nolf & Stringer 1996; Schwarzhans 2010; Stringer et al. 2020). Such forms gain importance and abundance during the early Paleocene, but largely remain very generalized morphologically. Also, Nolf et al. (2008) described a number of unambiguous percoid otoliths from late Maastrichtian freshwater to marginal marine Deccan intertrappean deposits of India. An explosive radiation and morphological diversification (of otoliths) seems to have occurred only after the Paleocene-Eocene Thermal Maximum (PETM) leading to the dominance of this group in the present day (Schwarzhans 2012). The earliest perciforms as based on otoliths would be Serranidae s.l. and Pempheridae s.l. from the Ripley Formation (72 Ma) and Acropomatidae from the early late Maastrichtian of Siegsdorf, Bavaria (69 Ma), but due to the prevailing uncertainties in recognizing and allocating of Late Cretaceous perciform otoliths, we have refrained from proposing those occurrences as stratigraphic calibration points ('first unambiguous occurrence dates') (Fig. 16).

CONCLUSIONS AND OUTLOOK

Late Cretaceous otoliths have been relatively poorly known for a long period of time in otolith research until the publications of Nolf & Dockery (1990), Nolf & Stringer (1996) and Schwarzhans (2010). In recent years there has been a surge in studies about Late Cretaceous otoliths, primarily from the USA (Stringer et al. 2016, 2018, 2020; Schwarzhans et al. 2018b; Hoganson et al. 2019). The description of the otoliths from the Late Maastrichtian of the Kemp Clay in northeastern Texas and from the early Danian of the Clayton Formation in Arkansas now represents a further study in this sequence. As the body of such research increases, it becomes clear that the terminal Cretaceous fish fauna as reconstructed from their otoliths was very diverse both regionally and morphologically right up to the end-Cretaceous mass extinction event. For

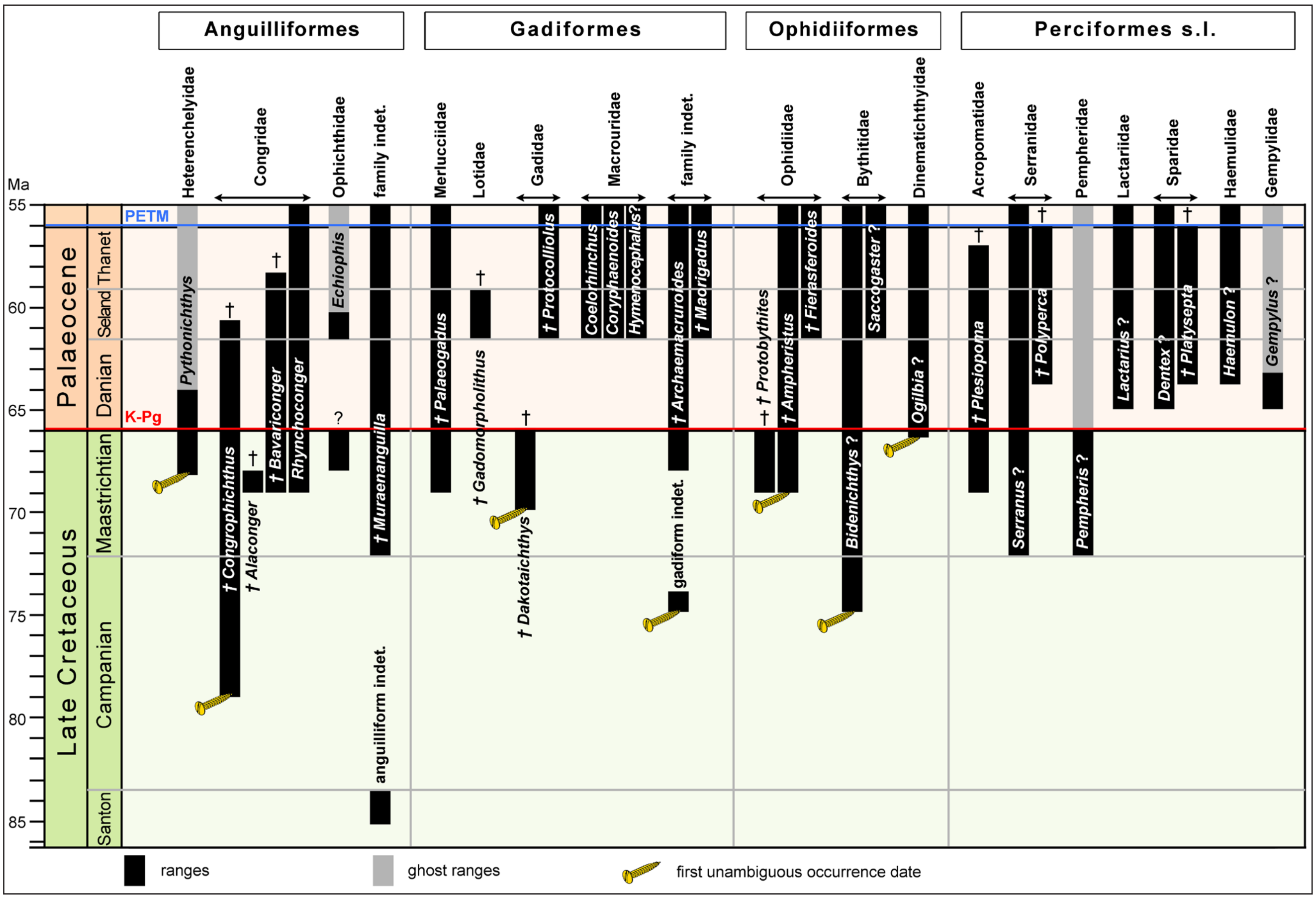


Fig. 16 - Early otolith-based records of the Anguilliformes, Gadiformes, Ophidiiformes, Perciformes s.l. (sensu Nelson 2006) and their managing across the K-Pg boundary or occurrence after the K-Pg boundary. Specific deemed important first unambiguous occurrences are marked.

the first time we are now able to identify faunal elements of teleosts adapted to specific environments, which varied rapidly and drastically across short distances. The otoliths recovered from the early Danian Clayton Formation puts us in the position to further evaluate the recovery fauna after the K-Pg extinction event and analyze its nature and compare it to pre K-Pg extinction event faunas. The main results and new insights from this study are the following.

1. Four different otolith-based faunal communities are identified in the North Atlantic of the Maastrichtian time; they are from west to east: Western Interior Seaway (WIS) community, which is based on the material of this study, Appalachian community, boreal European community and Peninnic community.

2. The adjacent WIS and Appalachian communities show substantial faunal differences with a percentage similarity measurements of less than 10%. The WIS and boreal European community contain putative cool-water faunal elements, and their percentage similarity is 15%.

3. The WIS community contains three gadiform species, representing amongst the first confirmed record of this order in the Cretaceous, and therewith firmly establishes the origin of gadiforms prior to the K-Pg boundary. A re-evaluation of the poorly known boreal European community also reveals the presence of gadiform otoliths. Gadiforms are thus thought to have originated in the boreal northern hemisphere based on present knowledge.

4. Correlation across the K-Pg boundary extinction event with the Clayton Formation reveals that the early Danian fish fauna is a survivors fauna. The WIS community of the Kemp Clay is a prime source for survivors with 54% of the species and 73% of the genera having survived the extinction event (vs 10% of the species and 40 to 50% of the genera of the Appalachian and Peninnic communities).

5. An analysis of the K-Pg boundary extinction and survival confirms that teleosts were gener-

ally less affected than many other marine biota and likely suffered primarily from the postulated "impact winter" after the Chixculub meteor impact.

6. Recovery during Paleocene shows a slow pace of new incoming taxa through evolution. Pterothrissid might have been post-disaster opportunists. Ophidiiforms and perciforms in the warm seas and gadiforms in the cool-water habitats may have been the early radiating survivor groups during the recovery phase.

The Late Cretaceous and the K-Pg boundary extinction are important periods and events for the evolution of teleosts. Otoliths can substantially contribute to a better understanding of teleosts during that period because of their abundance in space and time. However, our understanding of otoliths from pre-Cenozoic times is still significantly hampered by shortcomings in the correlation with otoliths found in situ, which we deem essential to unravel the nature of so many of the observed morphologies that putatively stem from extinct groups. We would hope that future research will guide to more studies of fossil fishes with otoliths in situ. Micro CT-scanning has proven to be a suitable non-invasive method that can routinely be pursued. Until such correlations have been achieved more widely, we promote a conservative approach in aligning pre-Cenozoic otolith morphologies to extant groups of teleosts. Also, we hope that many colleagues will watch out for otoliths in Cretaceous sediments in other regions, particularly outside of North America and Europe. We believe that valuable, additional insight can be gained regarding the evolution of teleost fishes through fossil otolith research in all prospective time intervals and regions of the Earth.

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