Hunt et al., eds., 2012, Vertebrate Coprolites. New Mexico Museum of Natural History and Science, Bulletin 57.

STOMACH AND GASTROINTESTINAL TRACT CONTENTS IN LATE CENOMANIAN (UPPER CRETACEOUS) TELEOSTS FROM BLACK SHALES OF GERMANY AND ANALYSIS OF FISH MORTALITY AND FOOD CHAINS IN THE UPWELLING-INFLUENCED PRE-NORTH SEA BASIN OF EUROPE

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Abstract—Three fish skeletons of *Anogmius*, *Elopopsis* and *Protostomias* from the black shales of the Cenomanian/Turonian boundary of northern Germany have preserved swallowed fish, and gastrolites (stomach contents) and intestinilites (gastrointestine tract contents). In the *Anogmius* specimen four small fish skeletons, and half digested skeletons, and intestinilites indicate this fish is a predator. In the *Elopopsis* specimen only elongate intestineilites are preserved. In the barbell-luring fish *Protostomias* the gestrolite includes small fish scales, whereas other specimens from Morocco give further evidence of fish predation with swallowed fish. *Clupavus* was the smallest and most common schooling fish of the upwelling- influenced Pre-North Sea Basin of Europe and seems to have been at the base of the fish food chain at the Cenomanian/Turonian boundary. The largest fish predator was *Xiphactinus*, several meters long, which was itself preyed upon by *Isurus*, the largest shark at this time. The fish faunal assemblages and their taphonomy at the Cenomanian/Turonian are different in upwelling deep basin sediments (= black shales), slope facies (= marls), carbonate platform deposits (= platy limestones), and coastal sands (= greensands). In the Pre-North Sea Basin at least four fish biocoenosis types can be distinguished depending on facies, bathymetry, and water temperature within the water column (warm surface, cold bottom currents). Fish mortality was connected to plankton blooming due to upwelling which caused mass mortalities of fish. Planktonic foraminifa indicate that mortality events first affected the oxygen minimium zone (OMZ), then dropped into the upper warm water column, and larger bloomings also reached the lower cold water zones.

INTRODUCTION

Worldwide only a few fish sites are known from the Cenomanian/Turonian boundary. The most famous are known in the Old World and are in Italy (black shales from Sicily: Leonardi, 1965; Comen: Sorbini, 1976), Morocco (black shales: Cavin, 1997, 1999a, b, 2000), Lebanon (platy limestones: Arambourg, 1954), Slovenia (black shales: Cavin et al., 2000) and Croatia (platy limestones: Diedrich et al., 2011; Fig. 1).

The first fish faunas in northern Europe in the Pre-North Sea Basin of Cenomanian and Turonian in age were described from England by Woodward (1902-1912). Many new sites are known from northwestern Germany (Diedrich, 2001) which have produced a moderately diverse and partly unique fish fauna, the ongoing description of which is continued with this paper. The first described remains of fossil fishes from the Cenomanian/Turonian boundary of northwestern Germany were found in the Teutoburger Wald Mountains (Fig. 1) and consist of two skeletons of *Syllaemus* and *Protostomias* from Lengerich (Diedrich, 2001, 2011). This material, together with Middle Turonian fish remains from the coastal greensands of the Münster Basin as well as the Turonian greensand fish fauna from Czech Republic (Fritsch, 1878), provide an overview of the main carbonate facies and ichthyofaunas of the southern Pre-North Sea Basin.

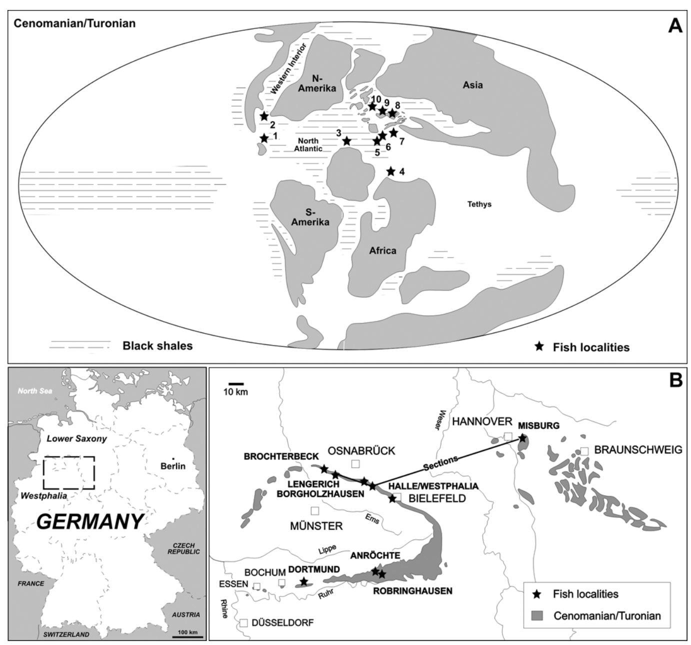

FIGURE 1. **A**, Regions of Cenomanian/Turonian fish-rich localities. **1-2**, USA. **3**, Morocco. **4**, Lebanon. **5-6**, Italy (Comen, Sicily). **7**, Croatia. **8**, Czech Republic. **9**, Germany. **10**, England. **B**, Upper Cenomanian fish sites, including Misburg in northern Germany and outcrops of Cenomanian/Turonian rocks (compiled from Diedrich, 2001; sections see Fig. 2).

MATERIAL AND METHODS

Since 1984, vertebrate fossils have been systematically collected and excavated in northwestern Germany (Fig. 1) from several localities in the Teutoburger Wald including Brochterbeck (Wallmeyer and Söhne quarry, sheet 3712 Tecklenburg, coordinates Longitude3415.00 and Latitude 5788.39), Lengerich (Dyckerhoff GmbH quarry, sheet 3813 Lengerich, coordinates Longitude5783.50 and Latitude 3424.50), Borgholzhausen (Vogt quarry, sheet 3915 Bockhorst, Longitude3451.60 and Latitude 5772.40; and Fahrtmann/Didier quarry, sheet 3815 Dissen, Longitude3452.25 and Latitude 5775.30), Halle, Westphalia (Dieckmann GmbH quarry, sheet 3916 Halle, Westphalia, coordinates Longitude3454.70 and Latitude 5771.80), and Brackwede (escarpment, sheet 3916 Halle, Westphalia, coordinates Longitude3765.65 and Latitude 5763.75), and in Hanover-Misburg (Hanoversche Portlandcementfabrik, old quarry 2, sheet 3625 Lehrte, coordinates Longitude3559.12 and Latitude 5806.32), and Baddeckenstedt (old quarry, sheet 3927 Ringelheim, coordinates Longitude3584.00 and Latitude 5774.00). Other material from the Middle Turonian coastal greensand facies, is mostly from mining or quarrying activities or intermittent outcrops and various sites in Westphalia.

The material described herein (Table 1) is housed in several German collections: **EZM**, Erd Zeit Museum Borgholzhausen; **GPIM**, Geologisch-Paläontologisches Institut und Museum der Westfälischen Wilhelms-Universität Münster; **MVKW**, Museum Villa Kupferhammer Warstein; **NMD**, Naturkundemuseum Dortmund; **RE**, Ruhr Museum Essen; and **WMfNM**, Westfälisches Museum für Naturkunde in Münster.

GEOLOGY AND SEDIMENTOLOGY

In the northern German Hanover region of the southern Lower Saxony Basin, Cenomanian/Turonian sediments are more or less horizontal at the fish localities of Hanover-Misburg and Baddeckenstedt. In the Teutoburger Wald Mountain (northern Münster Basin) the limestones belong to the southern part of a fold belt and consist of Jurassic and Cretaceous sediments that dip at all sites to the north-east at 20-60°. Sediments are completely overturned in the Cenomanian/Turonian boundary outcrops. The Cenomanian/Turonian boundary limestone sequences consists of black shale, gray, greenish and reddish marl in sequence sets (Diedrich, 2001, 2010; Fig. 2). The stratigraphy, microfacies and marine facies of the Cenomanian/Turonian boundary in the Hanover region (Hilbrecht and Hoefs, 1986) and Teutoburger Wald have been discussed extensively (see Diedrich, 2001, 2010). The Cenomanian/Turonian boundary, the so-called Blackcoloured Formation, or Oceanic Anoxic Event 2, in the Teutoburger Wald Mountain region, is subdivided into the Bunte Member, Carbonate Member, Black Shale Member, and Greengrey Marl Member (Fig. 3, Diedrich, 2001, 2010).

The Blackcoloured Formation in northern Germany has been successfully correlated from the most basinward section of Hanover-Misburg, to the Lengerich and Halle, Westphalia outcrops to the submarine swell facies of Baddeckenstedt (Diedrich, 2001). Many macro- and microfossils have been described (Hilbrecht and Hoefs, 1986; Hilbrecht, and Dahmer, 1994; Ernst and Wood, 1995; Diedrich, 2001, 2010) and have been utilized to subdivide the Cenomanian/Turonian boundary in detail (Fig. 2). Marker beds (e.g., fossil-rich beds), event horizons, sequence stratigraphy and isotope stratigraphy, fish assemblages and even giant ammonite accumulations were used for a high resolution stratigraphic analysis (Diedrich, 2001, 2010). Fish remains, including skeletons, described in this paper from the Teutoburger Wald outcrops occur in the *Chondrites* Horizon, *Puzosia* Event I, Black Shale IV (= *N. juddii* Horizon 2), Black Shale V, and *M. mytiloides* Horizon II.

The green sandstone, typical of the southwestern Münster Cretaceous Basin (Fig. 12) were deposited from the Cenomanian to Turonian. The Essen Greensand Formation dates to the Cenomanian, whereas the Bochumer Greensand Member of the Oerlinghausen Formation is Middle-Upper Turonian and the Soest Greensand Member of the Salder-Formation is Upper Turonian in age (Kaever, 1985; Hiss, 1995). At the two fish localities Anröchte and Remkersleben the Soest Greensand Member is exposed.

TAPHONOMY

Selachians are represented by two rare skeletons of *Squalicorax* from the *Chondrites* Horizon of Halle, Westphlia and *Paraorthacodus* sp. from Black Shale III-XVI of Hanover-Misburg (Fig. 9E). The other shark material consists of isolated teeth, dermal denticles and vertebrae (Diedrich, 2001; Table 1). In contrast, the teleosts are represented by many articulated skeletons and skeletal fragments (Table 1). The preservation of selachians and teleosts in the Blackcoloured Formation of northwestern Germany is dependant on the sediment type and the environment (Diedrich, 2001). Fish remains or even skeletons occur in four main facies and taphocoenoses (Table 1). The preservation of vertebrates in

TABLE 1. Shark and fish species from the Blackcoloured Formation (Cenomanian/Turonian boundary) of northwestern Germany (Pre-North Sea Basin).

Species	**Locality**	**Stratigraphy**	**Facies**
Sharks			
Chiloscyllium greenei (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Eostriatolamia (?) *subulata* (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Isurus denticulatus (isolated teeth)	Halle, Westphalia	*Chondrites* Horizon, *C. naviculare* ammonite biozone, *Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Lamna appendiculata (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Lamna arcuata (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Paranomotodon angustidens (isolated teeth)	Halle, Westphalia, Misburg	*Puzosia* Event I, *M. geslinianum, N. judii* ammonite biozones	Marl ramp, black shale anoxic basin facies
Paraorthacodus sp. (skeleton, one tooth)	Hanover-Misburg, Brochterbeck	Black shale III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Protolamna acuta (isolated teeth)	Halle, Westphalia	Black shale II, *C. naviculare* ammonite biozone	Black shale anoxic basin facies
Protolamna sokolovi (isolated teeth)	Halle, Westphalia	Black shale II, *C. naviculare* ammonite biozone	Black shale anoxic basin facies
Pseudocorax primulus (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Pseudoscyliorhinus schwarzhansi (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Pteroscyllium nolfi (isolated teeth)	Halle,/Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Ptychodus decurrens (isolated teeth)	Halle, Westphalia, Lengerich	*Chondrites* Horizon, *C. naviculare* ammonite biozone, *Puzosia* Event I, *M. geslinianum* ammonite biozone Black shale IV, *N. judii* ammonite biozone	Limestone swell, marl ramp, black shale anoxic basin facies
Heterodontus canaliculatus (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Hexanchus microdon (isolated teeth)		*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Scyliorhinus aff. *destombesi* (isolated teeth)	Halle, Westphalia	*Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell facies
Squalicorax falcatus (skeletal fragment, teeth)	Halle, Westphalia	*Chondrites* Horizon, *C. naviculare* ammonite biozone, *Puzosia* Event I, *M. geslinianum* ammonite biozone	Limestone swell, Marl ramp facies
Teleosts			
Anogmius ornatus (one skeleton with consumolite and stomach contents)	Hanover-Misburg	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Aulolepis typus (skeletons)	Halle, Westphalia, Lengerich	Black shale II, and Green marl, *C. naviculare* ammonite biozone, Black shale III, *N. judii* ammonite biozone	Black shale anoxic basin facies, marl ramp facies
Apateodus aff. *striatus* (skeletal remains)	Lengerich	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Belonostomus cinctus (some lower jaws)	Hanover-Misburg	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Cimolichthys lewisiensis (one skeleton)	Halle, Westphalia	Black shale II, *C. naviculare* ammonite biozone	Black shale anoxic basin facies
Clupavus maroccanus (skeletons)	Brochterbeck, Lengerich, Halle, Westphalia, Bielefeld, Baddeckenstedt, Hanover-Misburg	Black shale II, *Chondrites* Horizon, *C. naviculare* ammonite biozone, Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin, marl ramp facies
Cylindracanthus cf. *minor* (skeletons, several cranial rostrae)	Halle, Westphalia	*Chondrites* Horizon, Green marl, *C. naviculare* ammonite biozone	Marl ramp facies
Diplomystus brevissimus (skeletons)	Halle, Westphalia, Hanover-Misburg	*Chondrites* Horizon, *C. naviculare* ammonite biozone, Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin, marl ramp facies
Elopopsis microdon (one skeleton with consumolite)	Hanover-Misburg	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Enchodus venator (a few skeletons, isolated teeth)	Halle, Westphalia, Baddeckenstedt	*C. naviculare* ammonite biozone, Black shales III-XVI, *N. judii* ammonite biozone	Limestone swell, Black shale anoxic basin facies
Ichthyotringa furcata or (?*Rhinellus* cf. *africanus*) (skeletal fragments)	Halle, Westphalia	*Chondrites* Horizon, *C. naviculare* ammonite biozone	Marl ramp facies
Leptotrachelus sp. (skeleton fragment)	Hanover-Misburg	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Pachyrhizodus cf. *subulidens* (one skeleton)	Halle, Westphalia	Green marl, *C. naviculare* ammonite biozone	Marl ramp facies
Palaeobalistum cf. *guttorosum* (skeleton, isolated teeth)	Halle, Westphalia, Borgholzhausen	*Puzosia* Event I, *M. geslinianum* ammonite biozone, Black shales III-XVI, *N. judii* ammonite biozone	Limestone swell, Black shale anoxic basin facies
Protosphyraena sp. (skeleton, pectoral fins)	Halle, Westphalia	*Chondrites* Horizon, Green marl, *C. naviculare* ammonite biozone	Marl ramp facies
Protostomias maroccanus (one skeleton with consumolite)	Lengerich	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Rharbichthys cf. *ferox* (skeletal fragment)	Lengerich	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Syllaemus anglicus (skeletons, scales)	Borgholzhausen, Lengerich, Hanover-Misburg	Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Tsefatia formosa (skeletons)	Halle, Westphalia, Borgholzhausen, Lengerich, Baddeckenstedt	*Chondrites* Horizon, Green marl, *C. naviculare* ammonite biozone, Black shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies
Xiphactinus sp. (skeletal fragment)	Hanover-Misburg	Black Shales III-XVI, *N. judii* ammonite biozone	Black shale anoxic basin facies

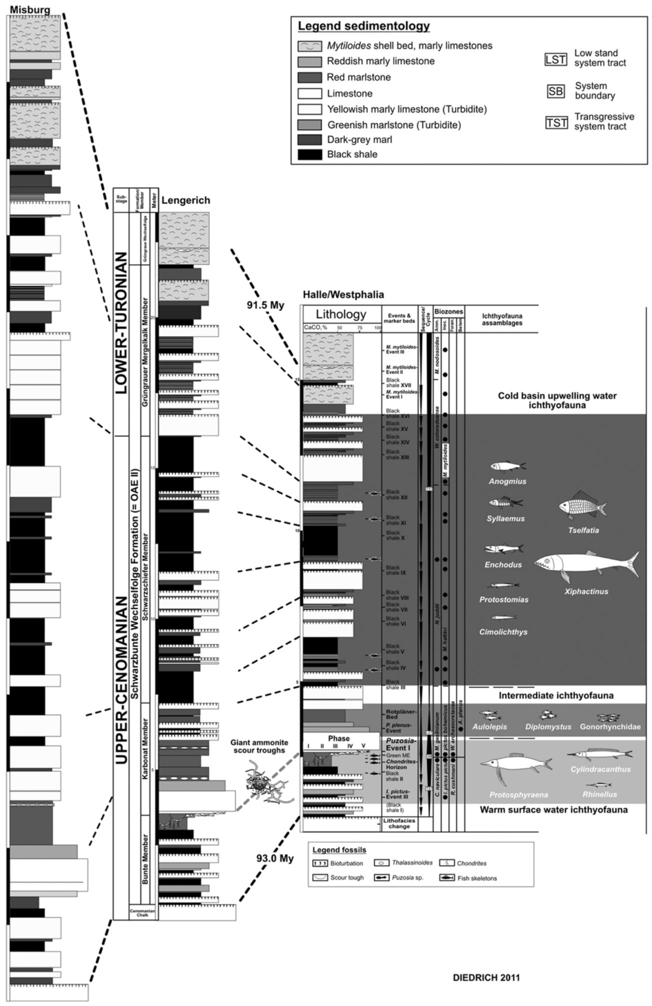

FIGURE 2. Stratigraphy and correlation of the Blackcoloured Formation at Halle, Westphalia (Cenomanian/Turonian boundary, Upper Cretaceous) and ichthyofauna assemblages depending on facies, bathymetry and water temperature (compiled from Diedrich, 2001, 2010 and new data).

the Cenomanian/Turonian boundary section of north-west Germany is as follows:

Black Shales: Articulation of skeletons is common in the black and organic-rich, anoxic, foraminiferal mudstones. The skeletons are found in different layers of the black shales, but mainly at the base of the shales in the mm thinly laminated beds (Fig. 2). There are only a few other fish-rich beds, such as the Black Shale II (*C. naviculare*/*Inoceramus pictus bohemicus* zone) of the early Late Cenomanian, and the Black Shale IV (*N. juddii* bed 1), Black Shale V (*N. juddii* bed 2) and Black Shale X (*N. juddii* bed 3) of the latest Cenomanian (*Neocardioceras juddii*/*Mytiloides hattini* zones; Diedrich, 2001).

Grey Marls: Only the very important teleost-bearing bed, the *Chondrites* Horizon, is composed of grey marls (foraminiferal mudstones: Fig. 2). It is mm- to cm-bedded and at the top of the sequence granular marcasite is present on the surfaces which have a characteristic limonitic orange color after oxidation (Diedrich, 2001). In these strongly bioturbated layers (*Chondrites* and *Zoophycos*) a range of fish preservations are present from nearly completely articulated to completely disarticulated teleosts. The enrichment of fish bones and scales is so great that beds approach being bonebeds.

Green Marl Bed: This turbidite (Fig. 2) is rich in planktonic foraminifa such as *Hedbergella* and the green color results from early diagenetic glauconite (Diedrich, 2001). There are different styles of preservations of extremely rare teleosts. Completely articulated skeletons (e.g. *Pachyrhizodus*; Fig. 9A) are present in this foraminifera/calcisphere grainstones, but also fragments such as parts of fins or partial articulated skeletons or skulls.

Scour troughs: Scour troughs are only present in the Blackcoloured Formation in the *Puzosia* Event I (Fig. 2). They are the products of the giant ammonite *Puzosis dibleyi* and different facies-adapted "subspecies" whose shells produced scours up to 50 cm deep into the sediment. The macrofauna of the *Puzosia* Event I was trapped in these troughs in the depressions around the ammonites and their body chambers (Diedrich, 2001, 2010). Isolated teeth or vertebra, and fragments of selachians and teleosteans are preserved there in a calcisphere/foraminifal wacke-/packestone limestone. This sediment is the product of a high energy and oxic swell/upper swell slope facies. Several species are known from those scour troughs (Table 1).

Greensands: The greensands (Essen/Soest/Anröchte) are equivalent to the Cenomanian to Turonian (even partly up to the Lower Coniacian) deposits, but of coastal origin, whereas the shallow marine glauconitic sands result from cold water upwelling (Kaever, 1985; Hiss, 1995; Fig. 12). Teleost remains occur, especially in the Middle-Upper Turonian layers, where fish skeletons are known (Fig. 10), whereas only a few isolated shark and fish teeth are found at any stratigraphic levels. These faunas contain more robust fish skeletons with giant forms and strongly scaled species. The exact stratigraphic level of older finds is unclear. It is possible that tempestites might have caused some limited fish layers in the Middle-Upper Turonian (Bochum Greensand Member).

DISCUSSION

Types Of Stomach and Gastrointestinal Contents

The terminology for fish trace fossils related to digestion utilized herein follows the definitions of Hunt and Lucas (2012). By their terminology the fish of the Cenomanian/Turonian of northern Germany have preserved undigested complete fish and gastrolites in the stomach, and intestineilites (colulites) in the gastrointestinal tract.

Anogmius ornatus with Small Fish and Consumulites in its Stomach

A few specimens of *Anogmius ornatus* Woodward 1923 have been described from the Pre-North Sea Basin (Woodward, 1923), and northern Tethys (Leonardi, 1965) and possibly with other species from North America (Stewart, 1899) but here the first fish is described with stomach contents in form of swallowed fish, gastrolites and intestinelites (Figs. 3-4). A nearly complete skeleton from Hanover-Misburg, consists of both part and counterpart slabs. The stomach/gastrointestinal tract contents contain bromalitic material, including at least four small fish skeletons. The *Anogmius* skeleton demonstrates three stages of prey digestion: (a) four freshly swallowed fish with the head directed posteriorly; (b) partly digested prey in which bones and scales are enclosed in a phosphatic bromalitic matrix (gastrolite); and (c) phosphatic bromalitic material (intestinelite) which does not contain scales or bone material. The four fish are partly in anatomical articulation and must have been swallowed just before the death of the predator (Fig. 4). They preserve some anatomical features which indicate that they represent the small and common *Clupavus* (cf. Fig. 7). *Anogmius* apparently swallowed its small prey whole with the head first. Most predatory fish with small or absent dentition simply catch their prey by opening their mouth quickly, creating a suction, and drawing the prey inside (e.g., Randall and Farrel, 1997). Swallowing head first is necessary, especially for larger prey, to keep the sharp fins of the prey from catching in the gullet.

Protostomias maroccanus with Consumulites as Stomach Contents

Protostomias maroccanus Arambourg, 1943 occurs in Tethys and the southern boreal Pre-North Sea Basin (Fig. 1) in zones influenced by

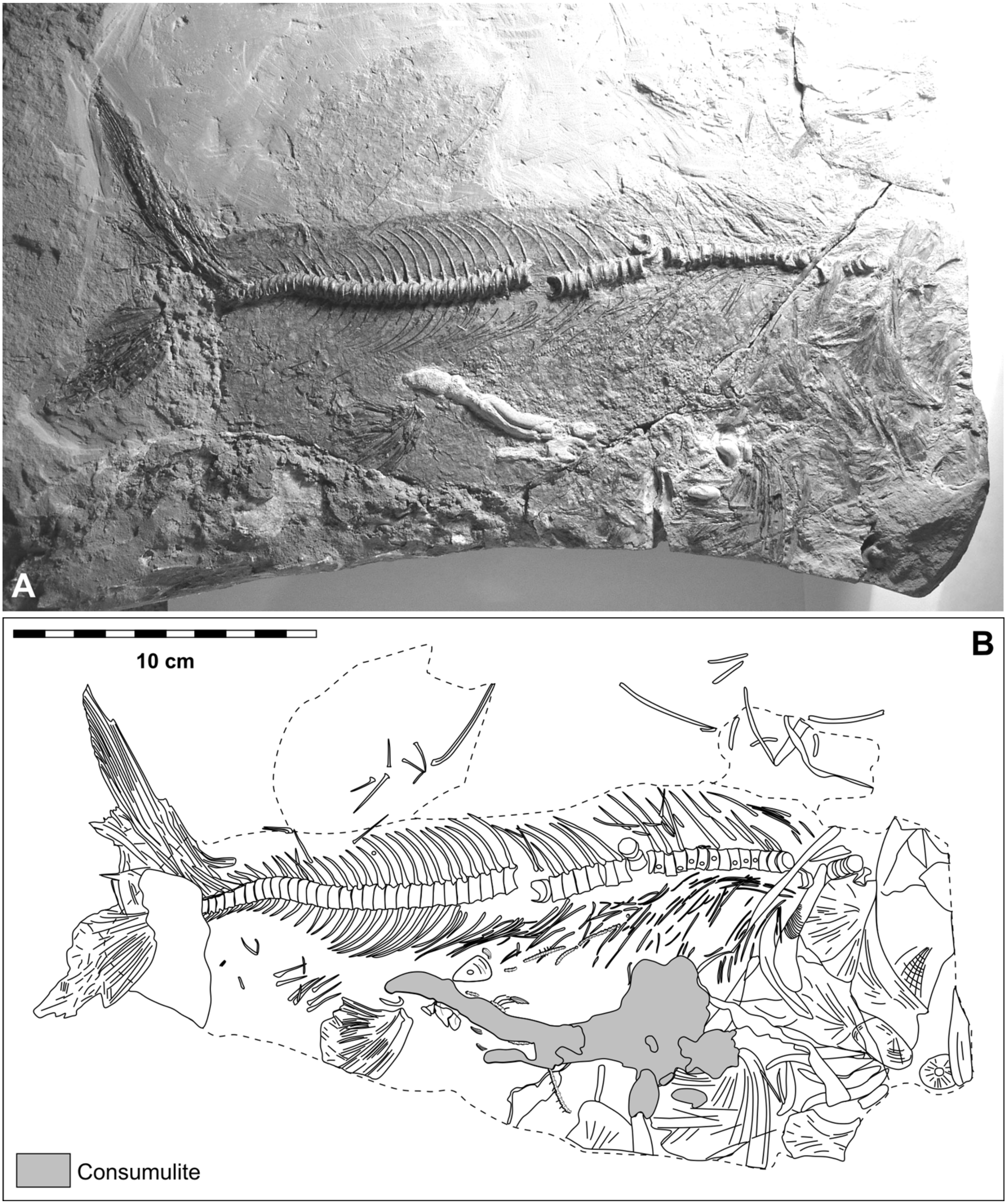

FIGURE 3. **A-B**,The Upper Cenomanian (Upper Cretaceous) teleost fish *Anogmius ornatus* Woodward, 1923 from Hanover-Misburg (Germany) with non-digested fish stomach contents, gastrolites and intestinelite (consumulite) material (for more detail see Fig. 4; RE no. 551.763.310, A 4873). **A**, Photograph. **B**, Interpretive drawing.

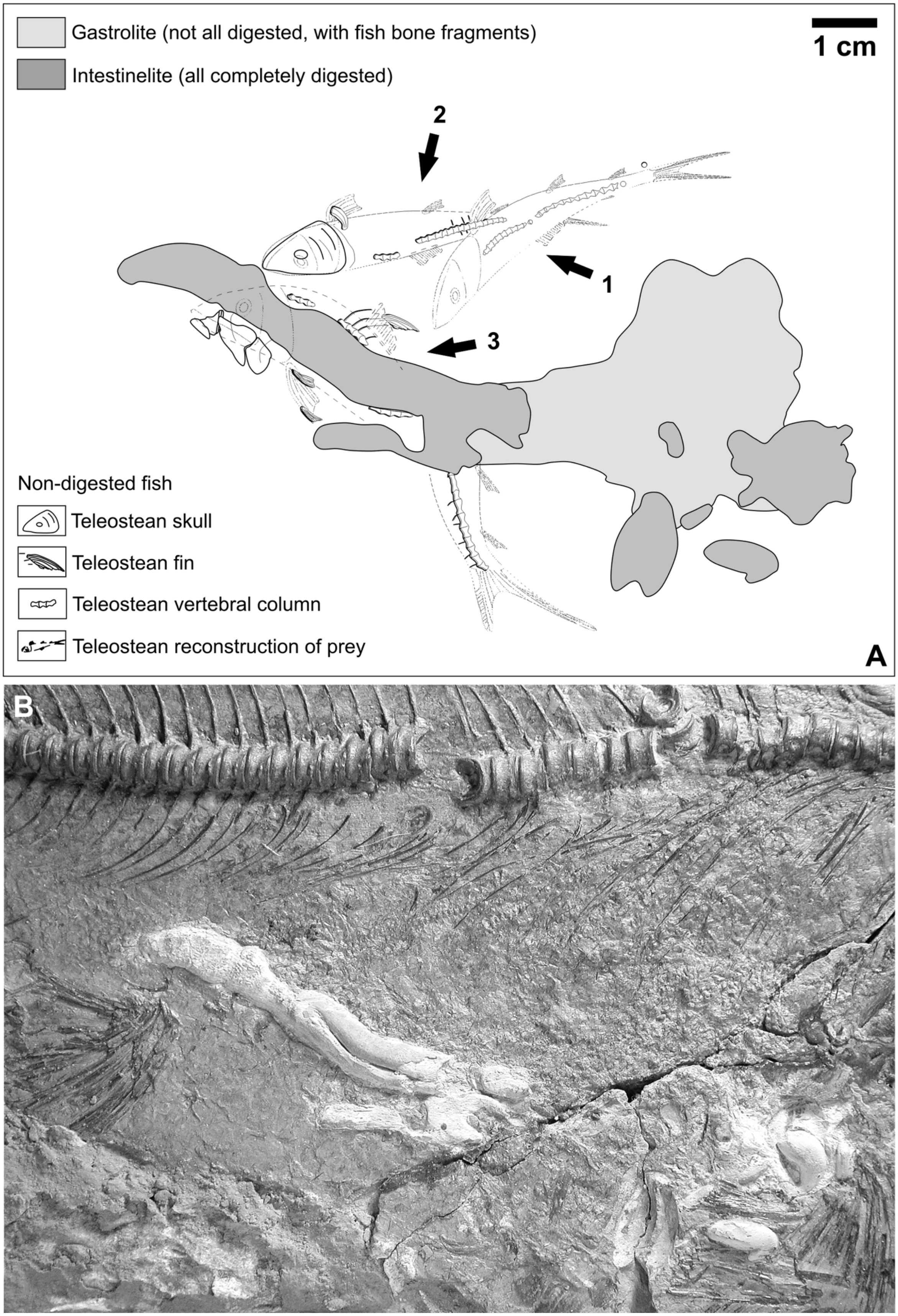

FIGURE 4. **A-B**, *Anogmius ornatus* Woodward, 1923 from the Black shales III-XVII (*N. judii* zone, Blackcoloured Formation, Cenomanian/Turonian boundary) of Hanover-Misburg (Germany) with four small fish (?*Clupavus*) in the stomach, and also other partly digested small fish remains and a large consumulite (RE no. 551.763.310, A 4873). **A**, Interpretive drawing. **B**, Photograph.

upwelling during the Early (Arambourg 1943, 1954) to Late Cenomanian (Sorbini, 1976). It occurs in the ?Lower Cenomanian of Aïn El Kerma and Djebel Tselfat (Taverne, 1991). Due to the lack of index fossils in the Moroccan localities, their exact stratigraphic position is unclear (Arambourg, 1943, 1954) and they could also be of late Cenomanian age. During the latest Cenomanian (*N. juddii*/*M. hattini* subspecies biozone), these fish are rare elements of the ichthyofauna at the localities of Lengerich (Germany), Floresta (Sicily: Leonardi, 1965) and Cinto Euganeo (northern Italy: Sorbini, 1976). Bannikov et al. (1984) described specimens from the Upper Cenomanian of Aksu-Dere (Crimea). All localities are situated in upwelling influenced areas as indicated by the occurrence of black shales during the Oceanic Anoxic Event II (Upper Cenomanian/ Lower Turonian boundary: Fig. 2).

The digested skeleton of prey (small fish) is preserved in the stomach region as demonstrated by small fish scales and beige-colored gastrolitic (phosphatic) material (Fig. 5A-B). Further evidence for the predatory behaviour of *P. maroccanus*, comes from the Lengerich skeleton in which a large bromalite structure is visible in the stomach region (Fig. 5C.3). Scales of a fish are recognizable but they cannot be identified due to advanced digestion. Characteristic bones of these fish were impossible to identify, but numerous scales of small diameter (1-2 mm) belong to a very diminutive fish, maybe to one of the small fish occurring frequently in the black shales of NW Germany, such as *Clupavus*, or a juvenile of a larger fish such as *Ichthyotringa* (Fig. 5C.1).

Judging from comparison of body form with the Recent *Stomias*, *Protostomias* could not have been an active fish hunter. The recent stomiids, like *Stomias*, belong to the ambush predator subguild (Gartner et al., 1997). The mesopelagic *Stomias* has a cranial barbel for luring prey (Randall and Farrel, 1997). *Protostomias* may have had a cranial barbel, but there is no direct fossil evidence. *Stomias* remains virtually motionless with the barbel held outstretched and angled forward (Gartner et al., 1997). *Protostomias* may have used a light organ similar to those of living deep-sea fish for luring prey (Foran, 1991; Gartner et al., 1997). The needle-like teeth of the lower jaws could only have been used to catch and hold prey. Evidence for this hypothesis include two skeletons from Aïn El Kerma (Arambourg, 1954) in which skeletons of other fish were completely preserved in their stomachs. Their last meals were juvenile *Ichthyotringa africanus* (Fig. 5C.1), 6 cm in length, orientated in the stomach of the holotype of *P. maroccanus* with the head directed caudally. The prey of another skeleton of *Paravinciguerria praecursor* Arambourg of 5.5 cm in length was figured by Arambourg (1954, Fig. 5C.2) in an identical position. In both cases, fish obviously were swallowed completely with their head first. This could be a result of the luring prey mode - smaller fishes swam in the direction of the luring barbel situated in front of the mouth of *P. maroccanus* – or the the prey may have been manipulated in the mouth prior to swallowing.

Analysis of the prey of *P. maroccanus* yields insight into its ecology, especially bathymetry. The species is considered to be mesopelagic and the ecology of its victims *Ichthyotringa africanus*, *Paravinciguerra praecursor* and *Clupavus maroccanus* may be relevant. They were not deep-sea fish which poses the question of how and at which water depth *P. maroccanus* caught its prey. *Ichthyotringa africanus* and *Paravinciguerra praecursor* were mesopelagic shoaling fish like *Clupavus maroccanus* but probably did not inhabit the deep sea. Three interpretations are possible:

1. *Protostomias* did not live mesopelagically in the deep sea and rather hunted in the shelf region.

2. *Protostomias* hunted during the night time in shallow-water regions catching juvenile and smaller fish of the upper water column.

3. The last prey could have been an unusual occurrence caught during an upwelling phase which brought *Protostomias* into the shallow shelf (southern Pre-North Sea Basin)

However, it is obvious that *P. maroccanus*, like most fish, did not hunt specific prey. It fed on on at least three different smaller fish species, and that could be an indication of luring prey. A difficult point is to decide whether its prey were typical of its feeding habits, or were the result of unusual circumstances. To verify one of these different hypotheses, more gastrolites from different localities must be recovered.

Elopopsis microdon with Consumolites in the Gastrointestinal Tract

This fish is rarely recorded in Europe (Woodward, 1902-1912; Sorbini, 1976). A single skeleton from Misburg (Fig. 6), from which the caudal part is missing, has three non-connected bromalite bodies, which seem to be from the gastrointestinal tract (intestinelites) rather then stomach contents. These are about 6-8 mm thick and round in cross section, but are incomplete and partially disintegrated. They do not contain any scales or bone fragments of fish and seem to be similar in stage, as in the *Anogmius* specimen (stage c from above – complete digested, phosphatic matrix = intestinelites). The intestinelites are in the posterior of the gastrointestinal tract region starting behind the skull and pectoral fin and ending in the anus area. Similar intestinal casts have been also reported in another elopid fish *Pachyrhizodus* from northern America (Miller, 1957).

OMZ-related Mass Mortalities in Fish Populations, Taphonomy, and Facies Relations

The fish-rich layers contain different species or ichthyo-assemblages and are found within different facies types (Diedrich, 2011; Fig. 2) and different water temperatures. They occur in areas of mixing of warm surface water currents, cold bottom upwelling and Atlantic ocean water mixing in the southern Pre-North Sea Basin, Münster Basin (Diedrich, 2010; Figs. 11-12). The facies related occurrence of fish is a result of the Oxygen Minimum Zone (OMZ) moving within the water column, which changed due to plankton blooming events and temperature changes resulting from upwelling (Fig. 11). This caused red Pläner (= iron-rich marly limestone) on the submarine swell, black shales in the deeper basin areas, and glauconite sands on the coasts (Hiss, 1995; Diedrich, 2001; Fig. 12). A sequence for the mass mortality of planktonic foraminifera has been presented for the Cenomanian/Turonian boundary of the Pre-North Sea Basin (Corfield et al., 1990; Hilbrecht et al., 1992) and nektonic fish mortality can be well correlated to this (Figs. 2, 11).

Initially plankton blooming caused the OMZ to move into the warm surface water column (Fig. 11) and the *Rotalipora*/*Hedbergella* foraminifera died en masse (Corfield et al., 1990; Hilbecht et al., 1992) and accumulated in the Green Marl Bed and Chondrites Horizon marl (ramp facies; Diedrich, 2001; Figs. 11-12). Only the surface water fish (rostrum- bearing predatory forms such as *Cylindracanthus*, *Protosphyraena*, *Rhinellus*/*Ichthyotringa*, and other predators such as *Pachyrhizodus*) were preserved in the Green Marl Bed of the upper ramp facies with complete skeletons present in turbidites.

With further deepening of the OMZ, fish of the mixed waters were affected, such as *Clupavus*, *Diplomystus*, *Aulolepis*, *Tselfatia* and *Halec*, whose habitat within the water column remains unclear. These fish are found in the *Chondrites* horizon of the dysoxic facies (Fig. 11).

With more massive bloomings, the OMZ reached the lower cold water column which caused the mortality of other planktonic foraminifera (e.g., *Praeglobotruncana*/*Whiteinella*) there (Corfield et al., 1990; Hilbecht et al., 1992) and medium to deeper and cold water fish species accumulated in the black shale facies (Fig. 11) including the teleosts *Syllaemus*, *Cimolichthys*, *Protostomias*, *Elopopsis*, and *Anogmius*, *Xiphactinus* and the shark *Paraorthacodus*.

Fish biocoenoses

Data to reconstruct biocoenoses comes from the taphonomy and facies record of Germany, and comparison to warm surface water fish and species from cold upwellings of Tethys (Mediterannean, northern Africa - lagoon platy limestones; Arambourg, 1954; Diedrich et al., 2011), northern Pre-North Sea Basin limestones (England; Woodward, 1901-

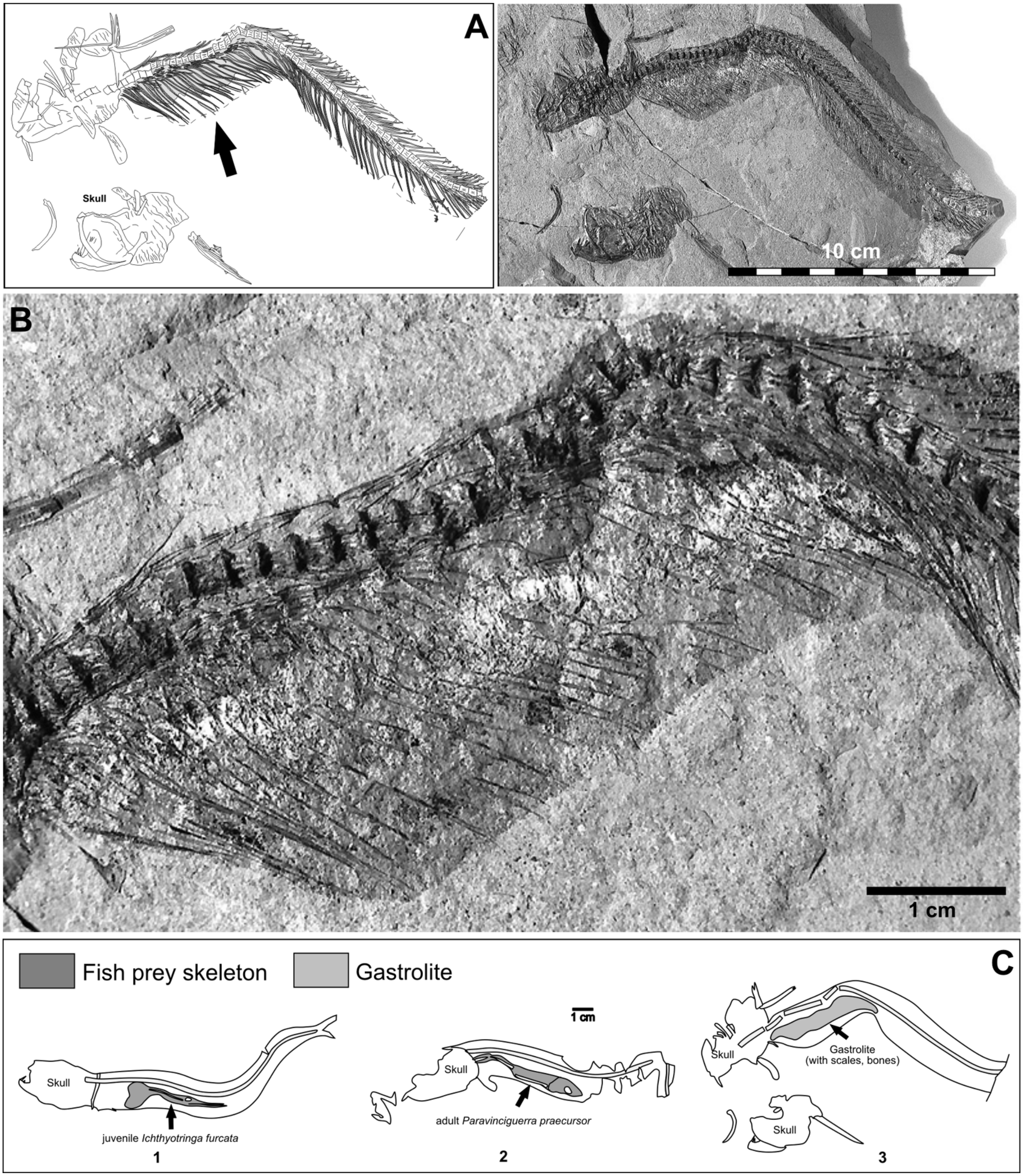

FIGURE 5. **A-B**, *Protostomias maroccanus* Arambourg, 1943 from the Black shales III-XVI (*N. judii* zone, Blackcoloured Formation, Cenomanian/Turonian boundary) of Lengerich (Germany) with gastrolite (GPIM no. 74). **A**, Schematic interpretation. **B**, Photograph. **C**, Schematic comparisons of other *Protostomias* skeletons from Morocco with ingested specimens: **1**, Specimen from Djebel Tselfat with a juvenile holotype skeleton of *Ichthyotringa furcata* (redrawn after Arambourg, 1943). **2**, Specimen from Aïn El Kerma containing an adult *Paravinciguerra praecursor* (redrawn after Arambourg, 1943). **3**, Specimen from Lengerich with digested fish prey.

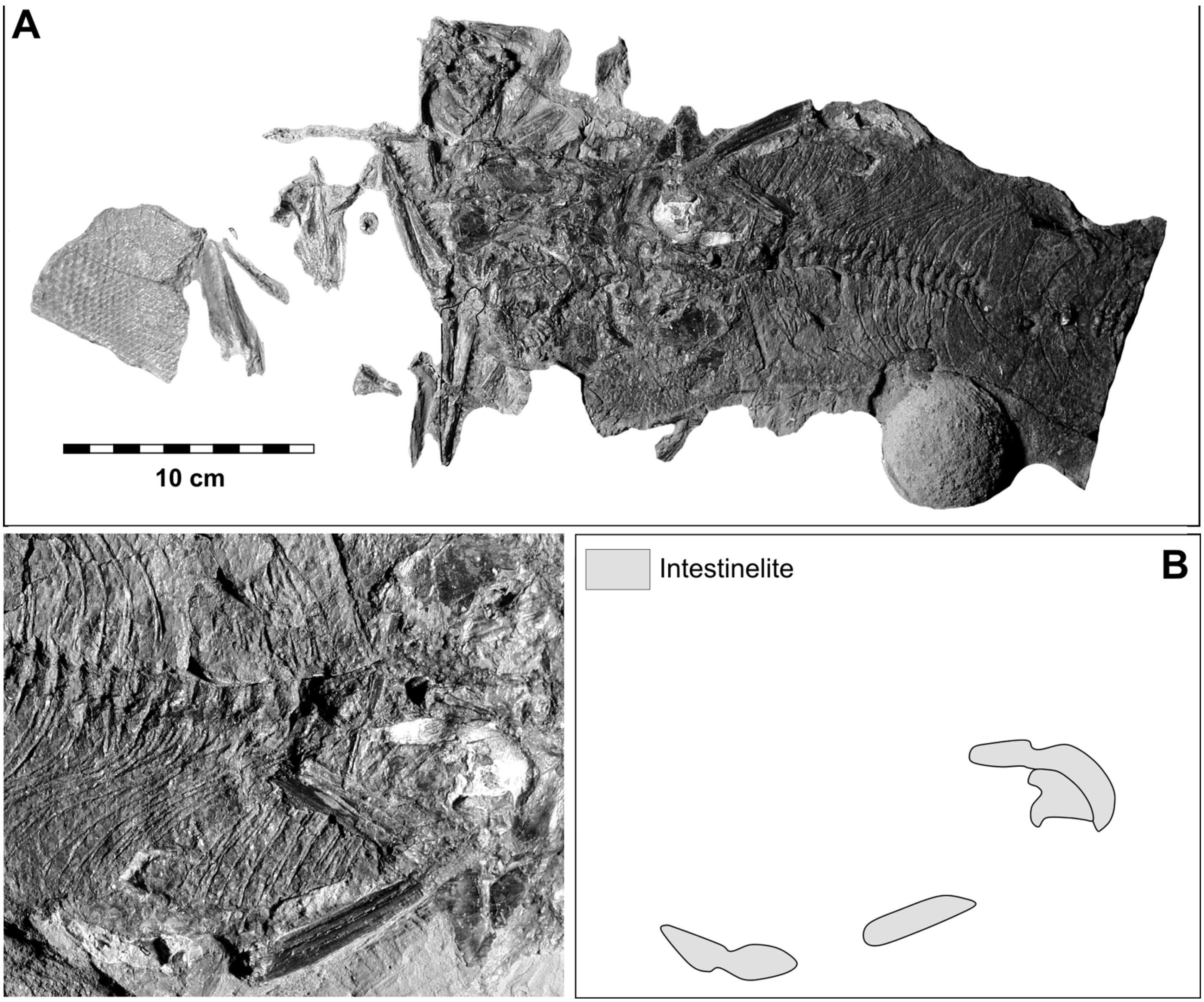

FIGURE 6. **A-B**, *Elopopsis microdon* Heckel, 1856 from the Black shales III-XVI (*N. judii* zone, Blackcoloured Formation, Cenomanian/Turonian boundary) of Misburg (Germany) with intestinelite (RE no. 551.763.310, A-4879/a and 2). **A**, Overview of specimen. **B**, Detail of intestinelite.

12), coastal greensand facies (Czech Republic; Reuss, 1845-46 ; Geinitz, 1871-75, 1872-75; Fristch, 1878; Bayer, 1909), and black shales of upwelling regions in northern Italy and Morocco (Leonardi, 1965; Sorbini, 1976; Cavin et al., 2000). At least two different fish biocoenoses can be distinguished in the northern German Cenomanian/Turonian boundary section within the water column and possibly an intermediate one contains species of both zones, the warm surface and cold bottom waters. Additionally in the Middle Turonian a third coastal biocoenosis is possibly present, but this is a preliminary conclusion as it is based on sparce material.

Warm surface water fish: These must have periodically or seasonally inhabited medium to cold waters in the water column (Figs. 11-12), and they came from northern Tethys. The best indicators for this hypothesis are similar fish species, such as *Diplomystus brevissimus* (Fig. 8D), which was widespread in Tethys and occurred even in Germany and England (Lebanon, Morocco, Croatia, Italy; Arambourg, 1954; Leonardi, 1965; Sorbini, 1976; Jonet, 1998; Grande, 1982; Cavin et al., 2000; Diedrich et al., 2011). Rostrum-bearing fish such as *Protosphyraena* sp. (Fig. 8I), *Cylindracanthus* cf. *C. minor* (Fig. 8H) and *Rhinellus*/*Ichthyotringa* are very typical of warm surface waters and are found only in the *Chondrites* Horizon and the Green Marl at Hall, Westphalia (Figs. 11-12).

Cold water fish: These occur in upwelling regions and include the "deep sea" fish *Protostomias marocanus* (Fig. 5) which is also found in black shales in Morocco, Italy, Sicily, Russia and Germany (Arambourg, 1954; Leonardi, 1965; Sorbini, 1976; Bannikov et al., 1984). In those cold waters there are also medium-sized *Tselfatia formosa* and *Syllaemus anglicus* (Fig. 9B) which are abundant in non-Tethys warm water of the middle to lower water column and are also found at many black shale upwelling facies sites in Morocco, Italy (black shale facies; Leonardi, 1965; Sorbini, 1976) and even rarely in Libya (platy limestone facies; Arambourg, 1954). Other cold water fish of the pre-North-Sea Basin include *Cimolichthys lewiesiensis* (Fig. 8F) which has only been reported from England (Woodward, 1901-12).

Coastal greensand fish: These fish occur in the upwelling-influenced greensands of the southern Pre-North Sea in the Münsterland Basin around Essen, Dortmund and Anröchte (Kaever, 1985; Fig. 11), and are historically known from many species in the Czech Republic (Reuss, 1845-46; Geinitz, 1871-75, 1872-75; Fristch, 1878; Bayer, 1909). There are rarer remains in Westphalia, where typical fish are *Xiphactinus*

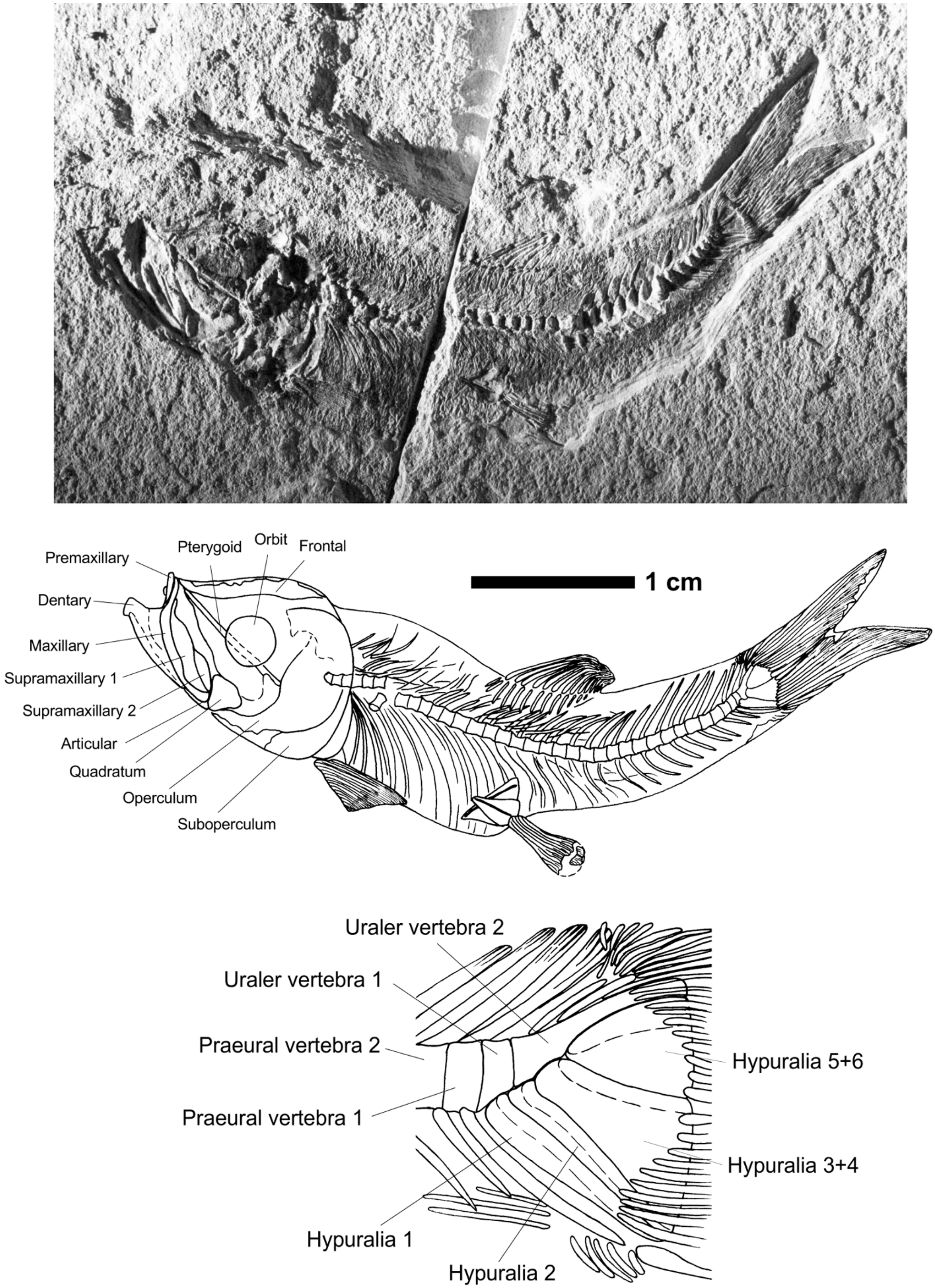

FIGURE 7. *Clupavus maroccanus* Arambourg, 1968 from the Black shale III (*N. judii* zone, Blackcoloured Formation, Cenomanian/Turonian boundary) of Brochterbeck (Germany), the most common small fish (EZC unnumbered).

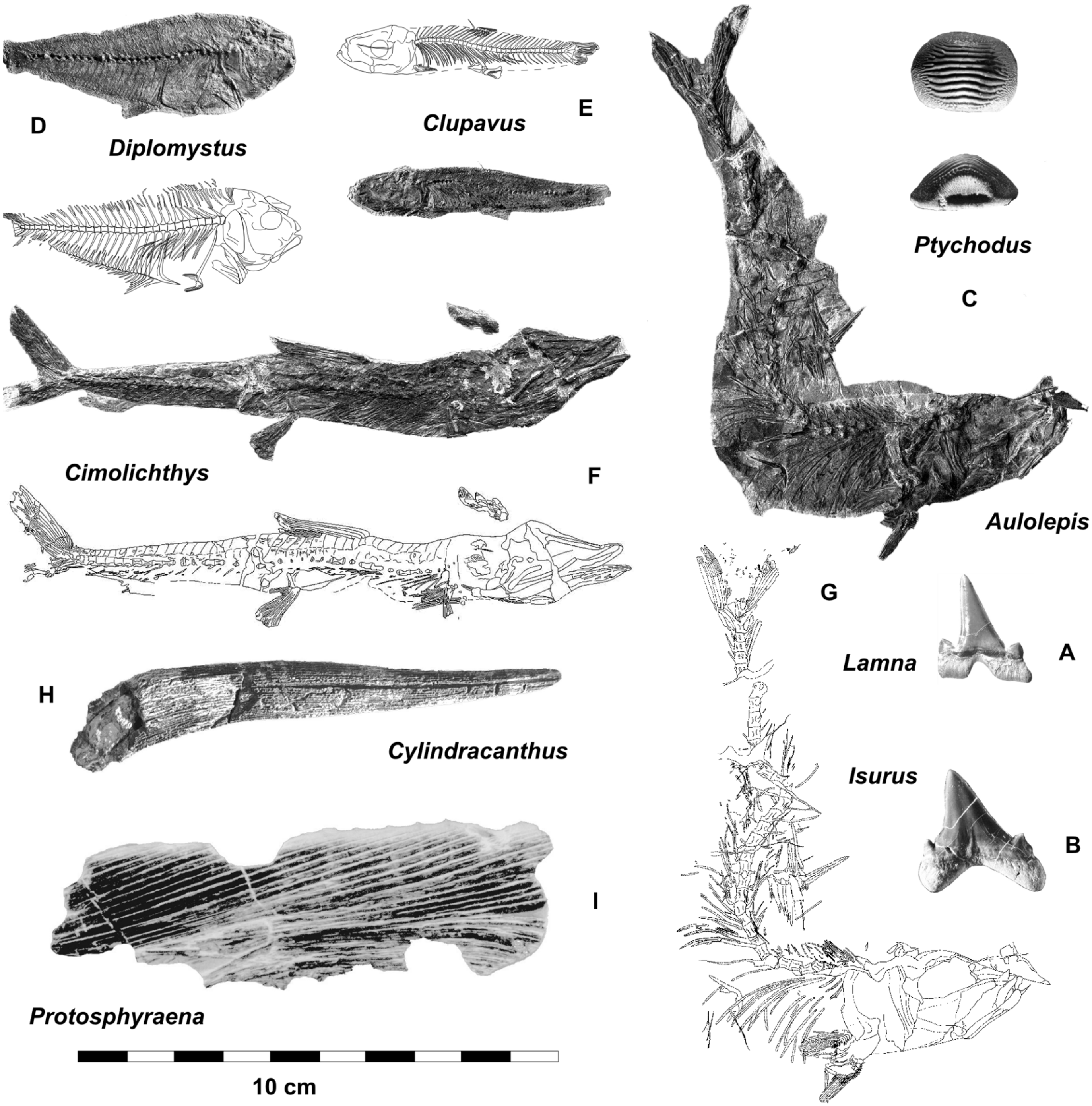

FIGURE 8. Selected shark and fish remains from the Blackcoloured Formation (Cenomanian/Turonian boundary, Upper Cretaceous) of northwestern Germany. **A**, *Lamna appendiculata* from the Puzosia Event I (*M. geslinianum* zone) of Halle, Westphalia (WMfNM no. P.-22020.). **B**, *Isurus denticulatus* from the *Chondrites* Horizon (*C. naviculare* zone) of Halle, Westphalia (EZM Diedrich Hes-1). **C**, *Ptychodus decurrens* from the *Chondrites* Horizon (*C. naviculare* zone) of Halle, Westphalia (EZM Diedrich Hes-2). **D**, *Diplomystus brevissimus* from the Black shale III-XVI (*N. judii* zone,) of Hanover-Misburg (RE no. A551.763.310, A 4866). **E**, *Clupavus maroccanus* from the Black shale III-XVI (*N. judii* zone) of Hanover-Misburg (A551.763.310, A 4870). **F**, *Cimolichthys lewisiensis* from the Black shale II (*C. naviculare* zone) of Halle, Westphalia (WMfNM no. P-20055). **G**, *Aulolepis typus* from the Black shale II (*C. naviculare* zone) of Halle, Westphalia (WMfNM no. WMfNM no. P-20052). **H**, *Cylindracanthus* cf. *C. minor* rostrum from the *Puzosia* Event (*M. geslinianum* zone) of Halle, Westphalia WMfNM, P-23215). **I**, *Protosphyraena* sp. pectoral fin fragment from the Green marl (*C. naviculare* zone) of Halle, Westphalia (WMfNM, P-22036).

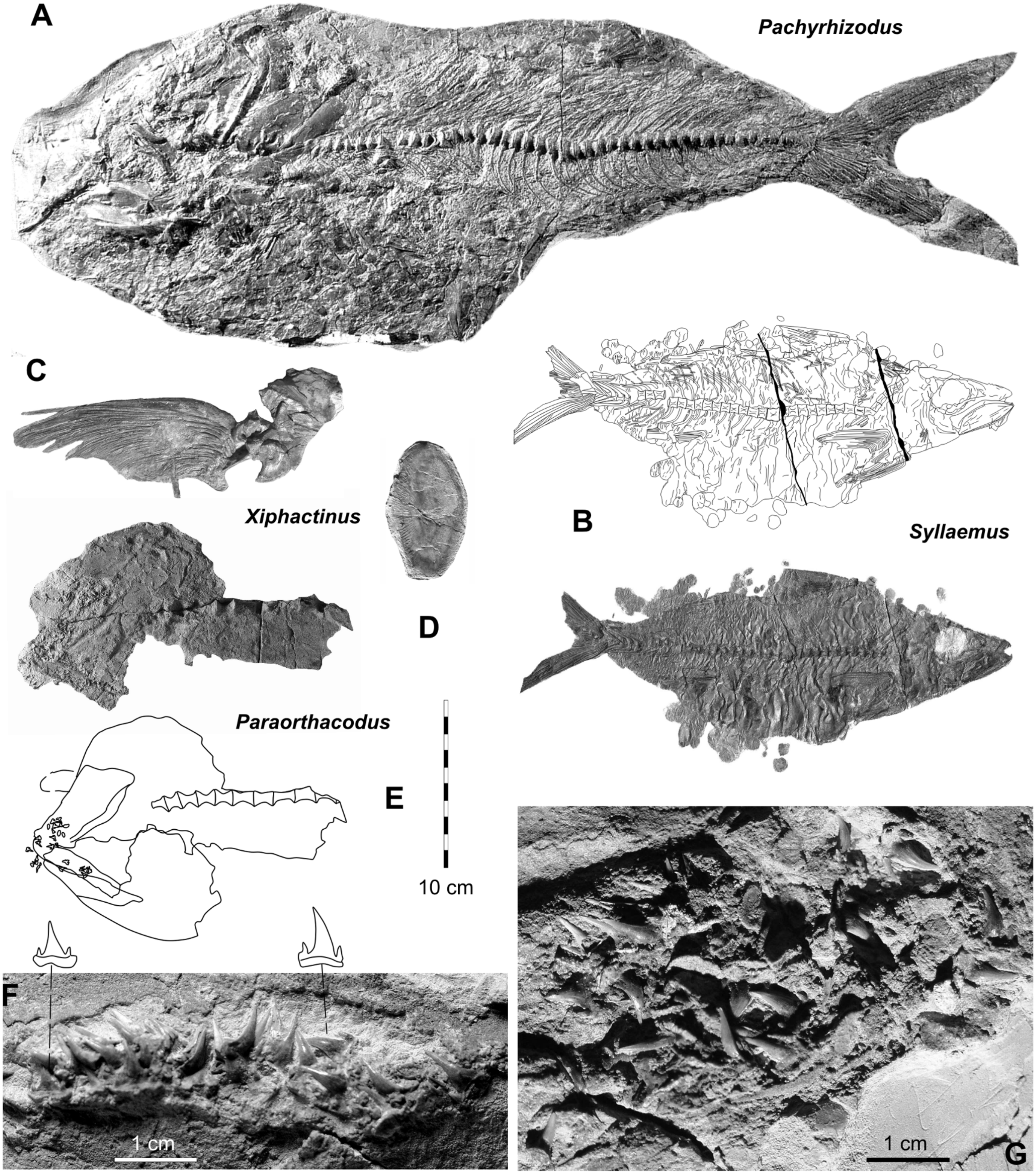

FIGURE 9. Selected shark and fish specimens from the Blackcoloured Formation (Cenomanian/Turonian boundary, Upper Cretaceous) of northwestern Germany. **A**, *Pachyrhizodus* cf. *P. subulidens* skeleton from the Green Marl (*C. naviculare* zone) of Halle, Westphalia (private collection). **B**, *Syllaemus anglicus* skeleton from the Black Shale III (*N. judii* zone), of Lengerich (GPIM collection). **C-D**, *Xiphactinus* sp. pectoral fin and scale from the Black shale III-XVI (*N. judii* zone) of Misburg (RE no. A-1595 and A-1579). **E-G**, *Paraorthacodus* sp. from the Black shale III-XVI (*N. judii* zone) of Misburg (RE collection).

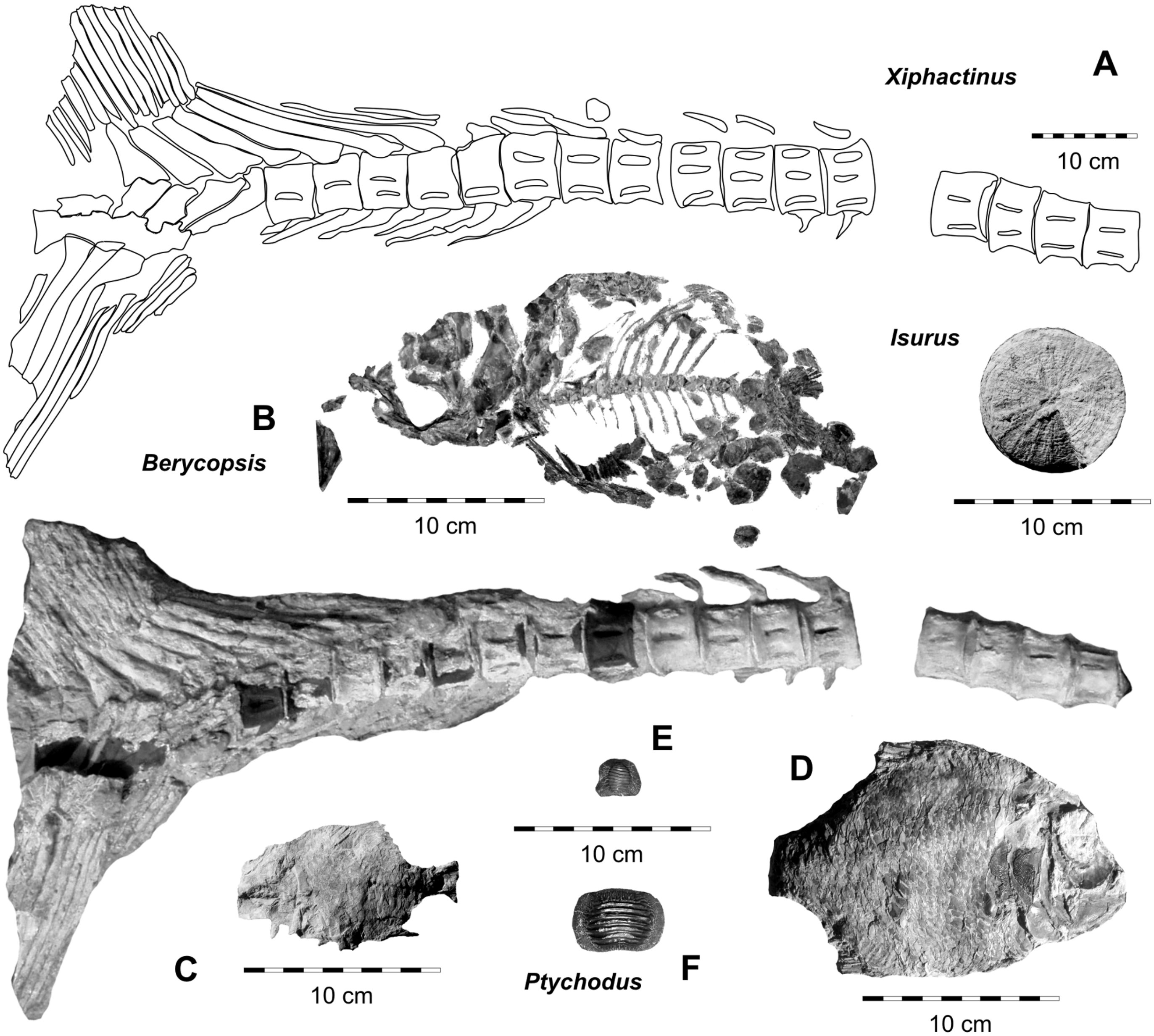

FIGURE 10. Selected shark and fish remains from the Soest Greensand Member (Upper Turonian, Upper Cretaceous) of NW Germany. **A**, *Xiphactinus mantelli*, caudal part, (Newton, 1877) from Anröchte (GPIM no. A1D.6). **B**, *Berycopsis major* skeleton from Dortmund, University metro station (NMD without no.). **C**, *Berycopsis major* skeleton from Zeche Alter Hellweg Unna (RE no. A551.763.310, A 0342/2). **D**, *Berycopsis major* skeleton of Zeche Alter Hellweg Unna (RE no. A551.763.310, A-0342/1). **E**, *Ptychodus mammillaris* tooth from Robringhausen (MVKW Anr-2). **F**, *Ptychodus mammillaris* tooth from Robringhausen (MVKW Anr-1). **G**, *Isurus denticulatus* vertebrae of Zeche Alter Hellweg Unna (RE no. A551.763.310, A 1552).

(Fig. 10A) and more abundant skeletons of *Berycopsis* (Fig. 10B).

Fish food chain

The most abundant small fish in the Cenomanian-Turonian boundary interval of Germany are *Clupavus maroccanus* (Fig. 7), which is mainly found in the black shales, but also in the *Chondrites* Horizon and even in green marl facies, which all are non-warm surface water deposits of the upwelling-influenced sediments (Diedrich, 2010). Their abundance is reminiscent of small shoal fish (cf. Recent sardine) and *Clupavus* fish which also were well spread within Tethys (Taverne, 1977) and were at the base of the food chain (Figs. 7, 11, 12). Other medium-sized predators, *Anogmius*, *Elopopsis* and *Protostomias*, which also all occur in the black shales and upwelling-influenced sediments, and possibly even others such as *Enchodus*, seem to have fed mainly on *Clupavus* (Fig. 12). The medium-sized predatory fish species must have been hunted in the lower water column by the larger forms, such as *Xiphactinus* which was widespread during the Cretaceous in the northern hemisphere (e.g. Reuss, 1845-46; Stewart, 1898; Woodward, 1913; Stovall, 1932; Bardack, 1965), and by surface predators with sword-fish-like elongated rostrae such as *Protosphyraena* and *Cylindracanthus* (Fig. 12). The role of the sharks and their exact diet remains unclear because of a lack of skeletons with gastrolites, but for sure the largest sharks like *Isurus* played an important role in the upper fish food chain. A gastrolite in an *Isurus* skeleton (Campanian in age) from North America has remains of *Xiphactinus* (Shimada, 1997). Small *Paraorthacodus* was possibly also a small fish hunter, and *Ptychodus* may have even been a non-fish bottom feeder, but no specimens have been found with stomach contents yet (Fig. 12).

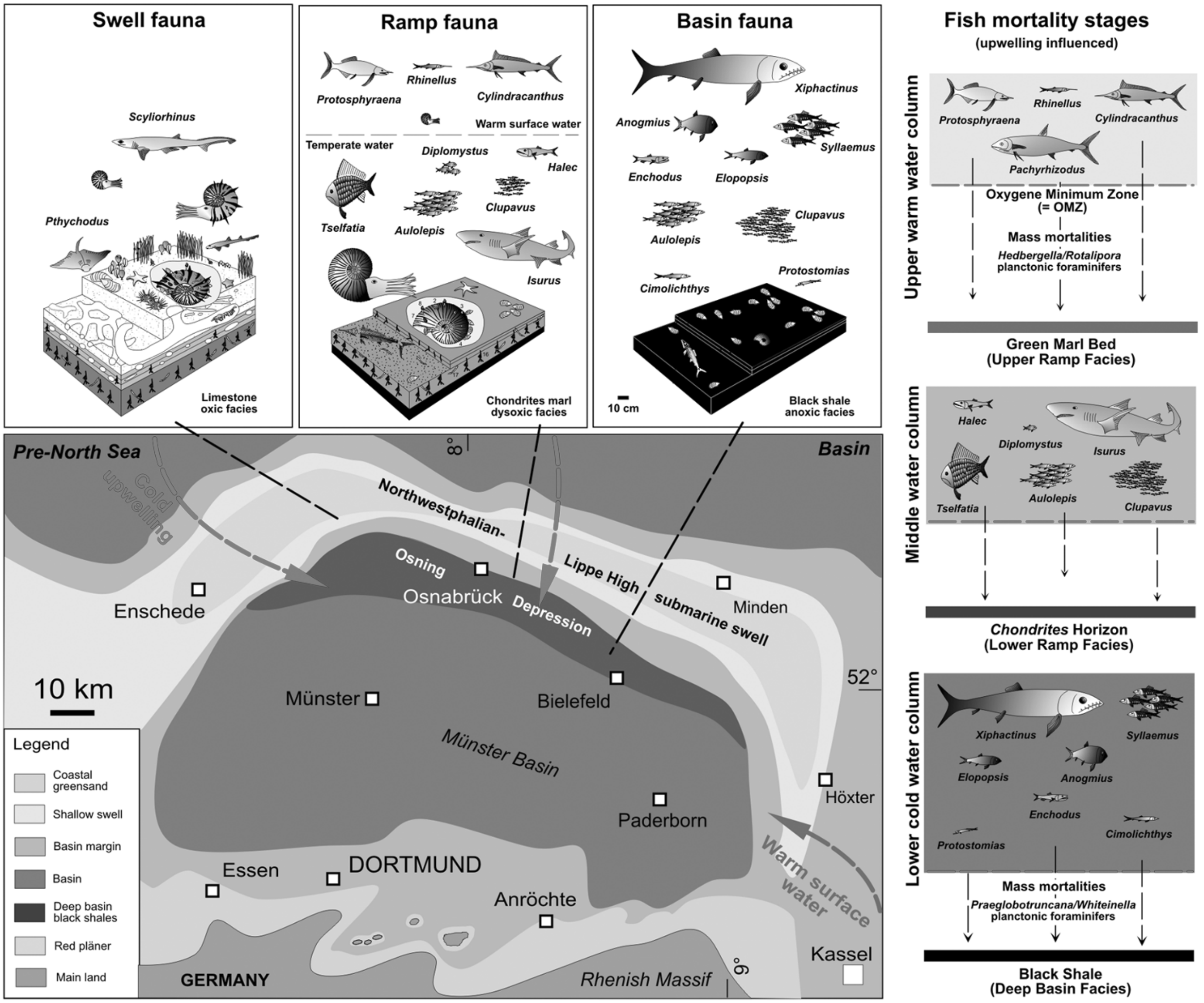

FIGURE 11. Cenomanian/Turonian boundary paleobiogeography, bathymetry, palaeocurrents, facies, ichthyofauna mortality, biocoenoses and fish food chains in the southern Pre-North Sea Basin (Münster Basin) of Central Europe (map after Kaever, 1985, Diedrich, 2001).

CONCLUSIONS

The Cenomanian-Turonian Blackcoloured Formation of northwestern Germany contains fish layers in different facies types and sediment types including marls, black shales and carbonates. Three main biocoenoses types can be reconstructed based on taphonomy and facies-related fish assemblages. The fish fauna of the upwelling cold bottom water (black shale facies) consists of *Syllaemus*, *Aulolepis* and *Clupavus* which seem to have been present in shoals. *Protostomias*, *Elopopsis*, *Anogmius* and *Enchodus* and *Cimolochthys* are cold water related forms. In this facies three medium-sized predator fish skeletons of *Anogmius*, *Protostomias* and *Elopopsis* were found with gastrolites which indicate they were hunters of small *Clupavus*. Other fish which are found in the middle water column are *Tselfatia*, *Diplomystus*, *Halec*. The mixed fish fauna of the Green Marl bed and *Chondrites* Horizon marls contain other warm surface water fish such those with prominent as mainly rostra: *Rhinellus*/*Ichthyotringa*, *Protosphyraena*, *Cylindracanthus*, but also other large predators and *Pachycormus*. The smaller swell fauna, containing small and medium-sized bottom dwelling sharks (*Scyliorhinus*, *Ptychodus decurrens*), is represented only by isolated teeth, and bones which mainly accumulated in giant ammonite scour troughs, and are limited also by taphonomic conditions (skeletons destroyed in swell facies). The younger-aged Middle Turonian fish faunas of the Münster Bay have different fish assemblages with *Xiphactinus* and *Isurus* as top predators, and abundant skeletons of *Berycopsis*, whereas isolated teeth are typically from the bottom dwelling shark *Ptychodus mamillaris*.

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