A new occurrence of sharks in the Menilite Formation (Lower Oligocene) from the Outer (Flysch) Carpathians of Poland

MAŁGORZATA BIEŃKOWSKA-WASILUK^{1,2} AND ANDRZEJ RADWAŃSKI¹

¹Institute of Geology, University of Warsaw, Al. Żwirki i Wigury 93, PL-02-089 Warszawa, Poland. ²Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warszawa, Poland. E-mail: mbienk@twarda.pan.pl

ABSTRACT:

Bieńkowska-Wasiluk, M. and Radwański, A. 2009. A new occurrence of sharks in the Menilite Formation (Lower Oligocene) from the Outer (Flysch) Carpathians of Poland. *Acta Geologica Polonica*, **59** (2), 235–243. Warszawa.

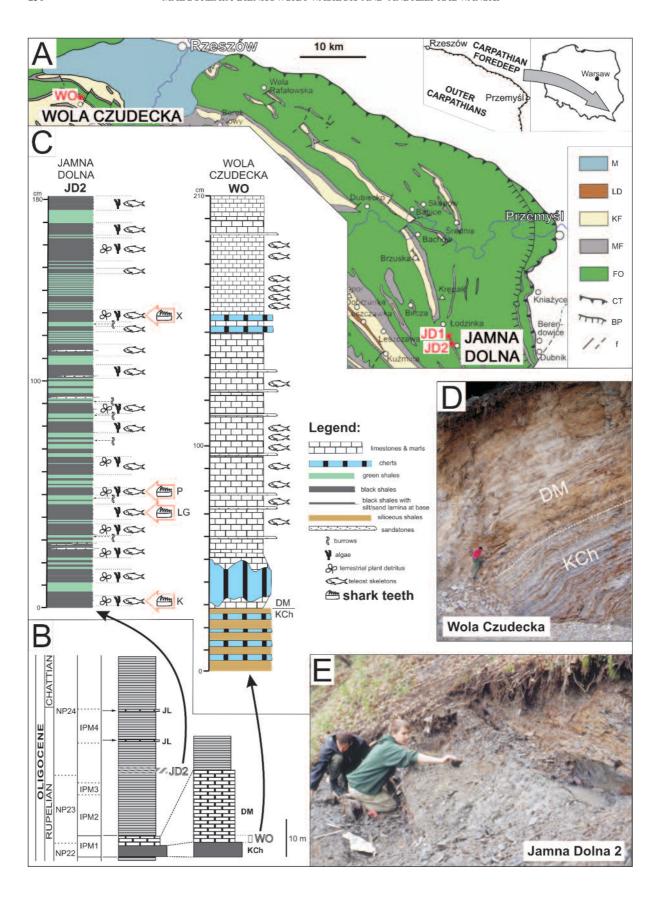
Two newly recognized sections (Jamna Dolna 2 and Wola Czudecka) of the Lower Oligocene Menilite Shales (Menilite Formation) in the Polish Outer (Flysch) Carpathians have recently yielded a small shark assemblage. It comprises teeth of *Heptranchias howelli* (Reed, 1946), not hitherto reported from Europe, as well as the remains of other sharks (teeth of *?Mitsukurina, Alopias*, gillrakers of *Cetorhinus*) all contributing to the fish assemblage of the Carpathian Menilite Formation, which has long been famous mostly for its teleost content. The life environment of the studied sharks and the basin bottom conditions are briefly discussed.

Key words: Hexanchoid sharks; "Notidanus"; Heptranchias; Menilite Shales/Formation; Oligocene; Outer Carpathians; Poland.

INTRODUCTION

The aim of this report is to describe several isolated shark teeth, from the so-called Menilite Shales (Menilite Formation) of Early Oligocene age, from the eastern part of the Outer (Flysch) Carpathians in Poland (see Text-fig. 1A). The Menilite Shales have long been known due to the ubiquity of teleost fish, monographs on which (J.J. Heckel, D. Gorjanović-Kramberger, M. Paucă) have been published since the mid-19th century – see summaries by Jerzmańska (1968), Kotlarczyk *et al.* (2006), and Bieńkowska (2007).

The occurrence of sharks and/or other elasmobranch fish in the Carpathian flysch in Poland is still an extreme rarity. The newly recognized taxa enlarge the list of elasmobranchs known of the Menilite Formation in Poland. Apart from "Notidanus sp.", only the Thresher Shark Alopias (under its historical name 'Alopecias') and gillrakers of the Basking Shark Cetorhinus were previously reported from the main part of this formation (Jerzmańska and Jucha 1963; Jerzmańska and Kotlarczyk 1988; Kotlarczyk et al. 2006, p. 27 and fig. 19 I, J, K). Besides the main part of the Menilite Formation, there is also a single sedimentological report (Dżułyński and Sanders 1962, pl. 11 A; = Dżułyński 1963, pl. 25, fig. 2; and 2001, fig. 21) of a robust tooth (? Alopias sp.) dragged along the bottom to be preserved in the groove cast, from the lower (turbidite) part of the formation.



LOCATION OF THE MATERIAL

The Menilite Formation (sensu Kotlarczyk and Leśniak 1990 and Kotlarczyk *et al.* 2006) is a 100 to over 400 metres-thick unit of the Carpathian flysch sequence. The formation, referred formerly to the Menilite (or Menilitic) Beds (see Jerzmańska and Kotlarczyk 1968), together with the overlying Krosno Formation, constitute the Menilite-Krosno Series (see Jucha 1969, Kotlarczyk *et al.* 2006), which is the youngest lithostratigraphic unit of the Carpathian flysch sequence. The shark remains were found in two sections of the Skole Nappe: Jamna Dolna and Wola Czudecka (see Text-fig. 1A; see Bieńkowska 2007).

The Jamna Dolna 2 (JD2 in Text-fig. 1B–C) section is an artificial exposure about 2 km south of the former Jamna Dolna exposure (JD1 in Text-fig. 1A; see Jerzmańska and Kotlarczyk 1968). The Wola Czudecka (WO in Text-fig. 1B–C) section was accessible in a local quarry (see Text-fig. 1D), about 1 km northwest of the village of Wola Czudecka.

The Menilite Formation is composed primarily of black or brown siliceous shales (Menilite Shales), intercalated with sandstones, cherts, diatomites, limestones and marls, some of which are referred in the sections studied to separate lithostratigraphic units (see Text-fig. 1B-C): the Kotów Chert Member (KCh), the Dynów Marl Member (DM), and the Jasło Limestones (JL). At Jamna Dolna 2, shark remains occur in a 180 cm-thick interval of black and green shales (see Text-fig. 1E), situated about 15 m above the top of the Dynów Marl Member (see Text-fig. 1B; and Bieńkowska 2007). At Wola Czudecka, they occur primarily (see Text-fig. 1D and Pl. 2, Figs 1-6) in cream-coloured marly laminae separating thin-bedded coccolith marls and limestones. In both exposures, the shark remains are associated with ubiquitous teleost skeletons; at Jamna Dolna 2 they are also associated with algae and terrestrial plant detritus (see Text-fig. 1C; and Bieńkowska 2007).

STRATIGRAPHIC AGE

The age of the fish-bearing sequences of the Menilite Formation investigated is documented by calcareous nannoplankton and referred to the Rupelian Stage of the Early Oligocene (as revised by Professor J. Kotlarczyk in Kotlarczyk *et al.* 2006, p. 10, fig. 2).

PRESERVATION OF THE MATERIAL

Most of the studied material is poorly preserved (see Pl. 1, Figs 1–5), being tightly embedded into the black shale rock matrix, from which it cannot be extracted. By splitting the shale slabs, the teeth crack into pieces firmly adhered to two counterparts that preserve precisely the original shape of the entire tooth. Consequently, for some specimens (Pl. 1, Figs 1a–1b and 3a–3b), the two sides of the split-off shale are illustrated instead of the labial and lingual sides of the tooth.

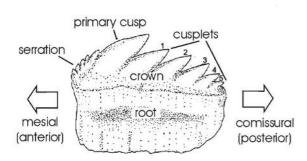
The other shark remains (see Pl. 2, Figs 1–6) are better preserved, but all are firmly adhered to, or more or less deeply embedded in, the parent rock and none of them can be inspected three-dimensionally.

SYSTEMATIC ACCOUNT

Class Chondrichthyes Huxley, 1880 Subclass Elasmobranchii Bonaparte, 1838 Order Hexanchiformes Buen, 1926 Suborder Hexanchoidei Garman, 1913

The terminology of hexanchiform teeth, albeit clearly defined in individual accounts (see Kemp 1978; Ward 1979; Cappetta 1975, 1976, 1987; Adnet 2006), differs in details between particular authors. To avoid any confusion, the terminology used here is shown in Text-fig. 2.

Text-fig. 1. A – Location of Wola Czudecka (WO) and Jamna Dolna (JD1 & JD2) in the Outer Carpathians, SE Poland (see insert); geological map based on Jucha (1969) and Kotlarczyk *et al.* (2006); M – Miocene deposits on the Carpathian nappes, LD – Leszczawka Diatomite, KF – Krosno Formation, MF – Menilite Formation, FO – flysch deposits older than the Menilite Formation, CT – Carpathian overthrust upon Miocene deposits of the Carpathian Foredeep, BP – overthrust of the Skole Nappe upon the Boryslav-Pokuttya Nappe, f – faults; **B** – Position of teeth-bearing sections in the synthetic lithological column of the Menilite Formation in Jamna Dolna and Wola Czudecka area, and stratigraphy of the Menilite Formation, based on Kotlarczyk and Leśniak (1990) and Kotlarczyk *et al.* (2006): NP22-24 – calcareous nannoplankton zones, IPM1-4 – ichthyofaunal zones, JL – Jasło Limestones, KCh – Kotów Chert Member, DM – Dynów Marl Member; C – Studied section at Jamna Dolna 2 (JD2) and lower part of section at Wola Czudecka (WO); K, LG, P, X – tooth-bearing horizons; **D** – Kotów Cherts (KCh) and Dynów Marls (DM) in western part of Wola Czudecka quarry in July 2005; **E** – Exposure of black and green shales at Jamna Dolna 2 during fieldwork in May 2004, to show the scree which yielded some of the specimens studied (see Pl. 1, Figs 1 and 4)



Text-fig. 2. Morphological terms of hexanchiform antero-lateral tooth of the lower jaw, as used in this study (Compiled and/or modified from: Kemp 1978, p. 62: figs 1–4; Ward 1979, p. 112: fig. 1; Cappetta 1987; Adnet 2006)

REMARKS: According to Cappetta's (1987, p. 44) interpretation, adopted in the present paper, the suborder Hexanchoidei Garman, 1913, contains the two basic families, the Hexanchidae and the Heptranchidae, comprising both present-day and fossil forms. The subsequent suggestions (see Long et al. 1993; Herman et al. 1994; Adnet 2006) of the need of familial and intrafamilial reordering of the Hexanchoidei based on a number of new features (e.g. the taxonomic significance of commissural teeth, ontogenetic versus phylogenetic development of the mesial serration, the ontogenetic enlargement of the primary cusp and of the number of cusplets in the lower lateral teeth, and the age of the tooth-bearing fish) are not considered further herein. Although all these attributes are important in the research on present-day hexanchoid sharks, they have practically no importance in the study of isolated fossil teeth, the taxa of which were registered by Cappetta (1987).

The fragmented teeth, quite often facies-indicative, but unrecognizable at their species and genus (or even family) level, are still reported as "*Notidanus* sp." (e.g., Kotlarczyk *et al.* 2006), which corresponds simply to the 'Hexanchiformes gen. et sp. indet.'.

Family Heptranchidae Barnard, 1925 Genus *Heptranchias* Rafinesque, 1810 *Heptranchias howelli* (Reed, 1946) (Pl. 1, Figs 1-5)

- 1946. *Notidanion howelli*i new species; D. Reed, pp. 1–3, figs 1–4.
- 1978. *Heptranchias howelli*i (Reed, 1946); N.R. Kemp, pp. 71–72; pl. 15, figs 4–7.
- 1987. *Heptranchias howelli*i (Reed, 1946); H. Cappetta, p. 49, fig. 48G.

REMARKS: In the strong accessory denticles (mesial serration) and the more or less depressed first two cusplets, the two well preserved teeth (see Pl. 1, Figs 1a–1b and 2) are close to the holotype of this species established by Reed (1946) upon a single tooth from a beach boulder at the foot of the Eocene cliff at Belmar, New Jersey, U.S.A. The most complete tooth (see Pl. 1, Figs 1a–1b), differs from the holotype in having one cusplet more (six instead of five), which indicates its position in a more distal file of the lower jaw.

The mesial serration in the best preserved specimen (Pl. 1, Figs 1a–1b) has the accessory denticles developed much more strongly than in the Reed's (1946) holotype, to acquire a cockscomb appearance, typical of the Late Cretaceous genus *Notidanodon* Cappetta, 1975, which ranges to the Palaeogene with a single species (see Ward 1979, Hovestadt *et al.* 1983, Cappetta 1987), *Notidanodon loozi* (Vincent, 1876). The genus *Notidanodon* was originally put by Cappetta (1975, 1987) into the family Hexanchidae. This was objected by Maisey and Wolfram (1984, pp. 175–176), who regarded it as a member of the Heptranchidae. In the genus *Heptranchias* of the latter family, accommodated is the species *howelli* of Reed (1946), to which it was assigned ealier by Kemp (1978).

The species *Heptranchias howelli* (Reed, 1946), the only extinct representative of the genus, is noted worldwide, solely outside Europe (see Kemp 1978, p. 71; Cappetta 1987, p. 49) in the Eocene and Oligocene. The only extant species of the genus, *Heptranchias perlo* (Bonnaterre, 1788), is known since the Middle Miocene (Serravallian, Italy; Cigala Fulgosi 1977, pl. 1, figs 1, 6–7, and 10).

The present-day specimens of *H. perlo* have the dentition of the lower jaw (see Cigala Fulgosi 1977, pl. 1, fig. 9d; Kemp 1978, pl. 13, fig. 1; Herman et al. 1987, text-plate, fig. 1) composed of the symphysial plus five antero-lateral files. By analogy, Reed's (1946) holotype is here interpreted as an antero-lateral tooth of the 2nd file of the lower jaw (not the upper jaw, as thought by Reed 1946, p. 1), whereas the completely preserved specimen studied (Pl. 1, Figs 1a-1b) due to its highly pronounced accessory teeth is interpreted as an anterolateral tooth of the 4th rather than the 3rd file, the mesial serration of which is weaker. The posteriorly crushed second specimen, with five cusplets preserved (see Pl. 1, Fig. 2) and the posteriorly more inclined primary cusp and all cusplets, belonged most probably to the 5th file, which is also suggested by its trapezoidal root.

DISCUSSION: Following Adnet's (2006) consideration, we undertake a risk to regard the other hexan-

choid teeth studied (see Pl. 1, Figs 3–5) as conspecific with *Heptranchias howelli* (Reed, 1946). Such a tentative assignment is, obviously, more a guess than precise identification, the more so that any dentition comparable to other extinct species (cf. Vitalis 1942) remains unknown

One specimen (see Pl. 1, Figs 3a–3b), with a mesially damaged root, but with the primary cusp preserved, evidently lacks the mesial serration. The first and second cusplets are inconspicuously smaller than the following ones. On the other hand, a notch behind the primary cusp reminds what has been distinguished (Cappetta 1987, p. 49; Ward 1979) as a separate genus *Weltonia* Ward, 1979.

Another specimen (see Pl. 1, Fig. 4) displays the second cusplet slightly smaller, and the primary cusp almost smooth mesially, just to close those of the genus *Hexanchus* Rafinesque, 1810.

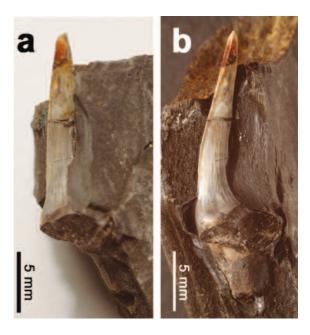
The last two teeth (see Pl. 1, Fig. 5), coming most likely from the same fish specimen, are fragmentary, devoid of the primary cusp broken off. The preserved first and second smaller cusplets are detectable in one specimen (lower left in the photo), but quite inconspicuous in the other (upper in the photo). In these features they both close to those distinguished as the species *Hexanchus agassizi* Cappetta, 1976 (cf. also Ward 1979).

THE OTHER SHARKS

Besides the *Heptranchias* teeth, the Menilite Formation also yielded remains of other sharks, either recovered by the present authors or briefly reported in the literature. Some of them are reviewed and discussed herein, especially those that have a bearing on the environmental conditions under which these sharks lived

Order Lamniformes Berg, 1958
Family Odontaspididae Müller and Henle, 1839
? Genus *Mitsukurina* Jordan, 1898
? *Mitsukurina* sp.
(Text-fig. 3)

REMARKS: This lamniform tooth (see Text-fig. 3), as kindly suggested by David P. Ward, should most likely be classified as ?*Mitsukurina* sp. Due to its fine striation on the lingual face (see Text-fig. 3a), and the apparent absence of lateral cusplets, this tooth compares well with those of the Recent species *Mitsukurina owstoni* Jordan 1898. A similar morphology, however, can



Text-fig. 3. ?Mitsukurina sp., isolated tooth from the lower jaw: a – lingual view, b – side view, to expose a part of the root preserved; Menilite Shales at Jamna Dolna 2 (Horizon X, see Text-fig. 1C)

be seen in the Recent genus *Carcharias* Rafinesque, 1810, the Cretaceous genus *Scapanorhynchus* Woodward, 1889, as well as in some species of the Palaeogene genus *Striatolamia* Glikman [Glückman] 1964 (see also Cappetta 1987, Nolf 1988).

Family Alopiidae Bonaparte, 1838 Genus *Alopias* Rafinesque, 1810 *Alopias* sp. (Pl. 2, Figs 1–3)

REMARKS: The Thresher Shark *Alopias*, with its commonest Recent species *Alopias vulpinus* (Bonnaterre, 1788) regarded as its type species (Ward 1978), is an oceanodromous genus which appeared in the Early Eocene (see Antunes 1970; Cappetta 1987, p. 105).

When comparing the tooth reported by Jerzmańska and Jucha (1963, p. 166) and Kotlarczyk *et al.* (2006, fig. 19 I) with the dentition of *Alopias vulpinus* (Bonnaterre, 1788) presented by Nolf (1988, pl. 10, fig. 2), it appears evidently to be from the upper jaw, from about the 5th lateral file. Of several Palaeogene species (see Ward 1978; Cappetta 1987, Nolf 1988, Reinecke *et al.* 2005), this specimen closely resembles *Alopias latidens* (Leriche, 1908) of Nolf (1988, pl. 47, fig. 7), from the Oligocene of Belgium. The possible identity of *A. latidens* and *A.*

vulpinus (Bonnaterre, 1788) was discussed by some authors (see Antunes 1970, pp. 374–375; Antunes and Jonet 1970, pp. 146–149; Ward 1978, p. 25), but was not accepted by Cappetta (1987, pp. 105–106) and Reinecke *et al.* (2005, pp. 37–38).

Our specimens, all firmly adhered to the marly matrix (see Pl. 2, Figs 1–3), closely resemble *Alopias exigua* (Probst, 1879), documented recently by Reinecke *et al.* (2005, pl. 25, figs 1–5) from the Oligocene of northern Germany. From the Belgian specimens illustrated under the same name by Nolf (1988, pl. 47, figs 9–12), they differ in the less slender crown and the more extended root. In view of these differences, they are herein referred to *Alopias* sp.

Family Cetorhinidae Gill, 1862 Genus *Cetorhinus* De Blainville, 1816 Gillrakers *Cetorhinus* sp. [? *C. parvus* Leriche, 1910] (Pl. 2, Figs 4–6)

REMARKS: To understand the finds, it is necessary to point out that the Basking Shark, *Cetorhinus maximus* (Gunnerus, 1765), the only present-day species of the genus and of the family Cetorhinidae Gill, 1862, an oceanic monster growing up to about 12 metres in length (see Budker 1971), is a plankton-feeder. It bears thousands of stiff, bristle-like gillrakers that serve to strain off the plankton from water being passed in enormous quantities from the mouth to the gills. In some reports (see Budker 1971, p. 47), it was noted that the worn rakers are shed, especially in cooler seasons when the density of plankton drops and the sharks retire to the bottom to 'hibernate'. Their vernacular name relates to their habit of lounging ('basking') at the ocean surface.

In the fossil state, the gillrakers of older Tertiary age have usually been reported either as *Cetorhinus* sp. or *Cetorhinus parvus* Leriche (see Jonet 1958, p. 34; Kalabis and Schultz 1974, pp. 185–186; Cappetta 1987, p. 107; Pharisat 1991, p. 24), but those of Pliocene (see Leriche 1908, 1926) and Pleistocene age (see Uyeno and Matsushima 1974) just as *C. maximus* (Gunnerus).

The date of establishment of the species-name *parvus* is not clear (cf. Leriche 1908, 1910, 1926). In Leriche (1908, p. 878) the name *parvus* is evidently a *nomen nudum*, being merely announced there for a future description in the planned monograph of Oligocene fish of Belgium. This monograph appeared in 1910, and this date is claimed to be correct, while the date 1926 cited by Jonet (1958, p. 34)] is an error, since this paper (Leriche 1926, volume for 1922) concerned solely *C. maximus*.

The teeth of fossil *Cetorhinus* remained unknown until a report by Landini (1977, p. 111 and pl. 1, figs 18–19), who identified them as *C. maximus* (Gunnerus). Subsequently, Herman (1979) reported a scatter of abundant gillrakers and 201 associated minute teeth in the Pliocene of Belgium. This scatter was referred by him credibly to a single fish specimen, classified as *C.* cf. *maximus*. He also discussed some other finds of Oligocene to Pliocene age and their relationship to the only present-day species (see also a review by Cappetta 1987, p. 107).

A comparable case was subsequently reported by Pharisat (1991) from the Oligocene (Rupelian) of France. Of over 1,300 specimens, many were preserved as bunches of several tens of gillrakers. Such bunches (see Pharisat 1991, fig. 9: bunch of 36 rakers) were certainly pieces of gills with rakers attached, freed when the shark's corpse decomposed. Pharisat (1991), not having been aware of Herman's (1979) report, classified these Oligocene specimens as C. parvus Leriche, 1908, close to the present-day C. maximus (Gunnerus, 1765), albeit he suggested that the few associated isolated teeth belonged to a quite different shark, Physogaleus. Similar occurrences have more recently been noted from coeval (Rupelian) deposits in southern Germany, from the Upper Rhine Graben at Frauenweiler, where isolated and bunched gillrakers are the most common shark remains (see Micklich and Parin 1996, fig. 2), and from the Mainz Basin, where a bunch of 19 gillrakers plus some isolated ones were found (Reinecke et al. 2001, pp. 24-25, pls 36 and 38a-c: classified as C. parvus). Moreover, isolated gillrakers also ascribed to C. parvus were reported from the coeval (Rupelian) Boom Clay Formation in Belgium (Hovestadt and Hovestadt-Euler 1995, pp. 262–263), and from Chattian erratic material from northern Germany (Reinecke et al. 2005, pl. 26, figs 1-4).

Concerning the relationship of *C. parvus* to *C. maximus*, the only discernible differences are in the size of the gillrakers and teeth; those of *C. parvus* being smaller (see Leriche 1908, 1910; Herman 1979). [Hence, a separate genus *Praecetorhinus* was used by some authors (see Reinecke *et al.* 2001, p. 24)]. However, the total length in hunted specimens of *C. maximus* is much smaller than the above-mentioned figure of about 12 m, being slightly over 3 m (see e.g. Uyeno and Matsushima 1974).

Precise data on the morphology and variability of the gillrakers in *C. maximus* are still lacking. When comparing our specimens with *C. parvus*, reported recently by Reinecke *et al.* (2001, 2005), it is evident that they are identical with the Rupelian ones (Rei-

necke *et al.* 2001, pls 36 and 38a–c), but remarkably different from some Chattian ones (see Reinecke *et al.* 2005, pl. 26, figs 2 and 4). Consequently, our specimens are referred in open nomenclature to *Cetorhinus* sp., with the suggestion that they may represent what is known as *C. parvus*.

In the Dynów Marls (see Text-fig. 1C) the isolated gillrakers are common. They are up to 27 mm long, and generally well preserved (see Pl. 2, Figs 4-6). Their occurrence throughout a two metre-thick interval indicates clearly that the Basking Shark was present in the area over a long period. Similarly, common occurrences (65 specimens) of isolated gillrakers referred to Cetorhinus sp. were reported from the Menilite Formation in Poland by Kotlarczyk et al. (2006, p. 27 and fig. 19J) and, earlier, by Jerzmańska and Kotlarczyk (1988, p. 105). From the Menilite Formation in Moravia (Czech Republic), specimens classified as C. parvus, both locally mass-occurring, as well as isolated and dispersed, were reported by Kalabis and Schultz (1974, pp. 185–186 and pl. 1, fig. 1; see also Schultz 1982). The first reports from the Carpathian Menilite Formation were those by Jonet (1947, 1958) from Romania.

THE LIFE HABIT AND ENVIRONMENT

For the Carpathian Menilite Shales environmental data are very limited. Nevertheless, the black shale lithology suggests a pelagic setting with anoxic conditions at, and over the bottom. The abundant teleost ichthyofauna (see Jerzmańska 1968; Kotlarczyk et al. 2006; Bieńkowska 2004, 2007) is dominated by smaller-sized, mostly epi- and mesopelagic species, the majority of which were carnivorous (Bieńkowska 2007). There are spectacular examples of small-sized fish preserved in the intestines of larger, carnivorous fish (see Bieńkowska 2004, pp. 187-188 and fig. 20; Bieńkowska 2007, fig. 40). During the Late Oligocene, there was periodically a significant proportion of epipelagic forms characteristic of Sargassum-like habitats (see Jerzmańska and Kotlarczyk 1975, 1976, 1988, 1991). Consequently, it is reasonable to imagine that the small-sized carnivorous fish and the sharks studied were prowling to hunt above the anoxic chemocline, the limit of which, when accidentally breached, could become a lethal taphonomic and preservational trap for the predators.

In the Outer Carpathian Basin, during deposition of the Dynów Marls, *Cetorhinus* was the most common elasmobranch, as in the Oligocene (Rupelian) sequence at Frauenweiler in the Upper Rhine Graben, Germany (see Micklich and Parin 1996, p. 131). In the Dynów Marls, *Cetorhinus* is associated with *Alopias*, forming a specific, both present-day and ancient, shark assemblage (see Pl. 2, Figs 1–6) typical of the pelagic realm ('epipelagic taxocoen/ichthyocoen' of Litvinov 1989). Such an assemblage is also characteristic of the coeval (Oligocene, Rupelian) deposits of the Mainz Basin in Germany (see Reinecke *et al.* 2001), and of the Boom Clay Formation in Belgium (see Hovestadt and Hovestadt-Euler 1995).

The predatory shark assemblage reported herein, composed of *Heptranchias*, *?Mitsukurina* and *Alopias*, as well as the plankton-feeding *Cetorhinus*, were the true behemoths topping the trophic web in the Menilite environment of the Outer Carpathian Basin in Poland. The record of *Cetorhinus* indicates the presence of ubiquitous nutrient plankton at the surface of the Menilite Sea during Early Oligocene.

Acknowledgements

The contribution was markedly improved thanks to revision by the journal referees, Mr. D.J. Ward and an anonymous reviewer. However, in some parts of the text, the authors alone are responsible for the opinions expressed. Mr. Rafał Nawrot, a student of our Faculty, has generously donated a couple of specimens from his collection to this study.

REFERENCES

Adnet, S. 2006. Biometric analysis of the teeth of fossil and Recent hexanchid sharks and its taxonomic implications. *Acta Palaeontologica Polonica*, **51** (3), 477–488.

Antunes, M.T. 1970. Présence de *Alopias superciliosus* (Lowe) dans les mers du Portugal. Remarques sur les *Alopias* (Selachii) recents and fossiles. *Arquivos do Museu Bocage*, *Série* 2, 2, 363–378.

Antunes, M.T. and Jonet, S. 1970. Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. *Revista da Faculdade de Ciéncias de Lisboa*, *Série 2 (C)*, **16** (1), 119–280.

Bieńkowska, M. 2004. Taphonomy of ichthyofauna from an Oligocene sequence (Tylawa Limestones horizon) of the Outer Carpathians, Poland. *Geological Quarterly*, **48**, 181–192.

Bieńkowska, M. 2007. Tafonomia ichtiofauny oligoceńskiej w Karpatach Zewnętrznych na obszarze Polski. [Taphonomy of the Oligocene ichthyofauna from the Outer Carpathians in Poland]. Unpublished Ph.D. thesis, pp. 1–83; Faculty of Geology, University of Warsaw.

Budker, P. 1971. The Life of Sharks, pp. 1–222. Weidenfeld and Nicolson; London.

- Cappetta, H. 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Géobios*, **9** (5), 551–575.
- Cappetta, H. 1987. Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii. In: H.-P. Schultze (Ed.), Handbook of Paleoichthyology, Vol. **3B**, pp. 1–193. Gustav Fischer Verlag; Stuttgart New York.
- Cigala Fulgosi, F. 1977. Heptranchias perlo (Bonnaterre) (Selachii, Hexanchidae) nel Serravalliano di Visiano (Medesano, Parma, Emilia Occidentale): considerazioni tassonomiche e filogenetiche. Bolletino della Società Paleontologica Italiana, 16, 245–256.
- Dżułyński, S. 1963. Directional structures in flysch. *Studia Geologica Polonica*, **12**, 1–136.
- Dżułyński, S. 2001. Atlas of sedimentary structures from the Polish Flysch Carpathians, pp. 1–132. (Material for 12th Meeting of the Association of European Geological Societes). Institute of Geological Sciences, Jagiellonian University; Cracow.
- Dżułyński, S. and Sanders, J.E. 1962. Current marks on firm mud bottoms. *Transactions of the Connecticut Academy* of Arts and Sciences, 42, 57–96.
- Glikman [Glückman], L.S. 1964. Sharks of the Palaeogene and their stratigraphic significance, pp. 1–229. Nauka; Moskva – Leningrad. [In Russian]
- Herman, J. 1979. Reflexions sur la systématique des Galeoidei et sur les affinités du genre *Cetorhinus* à l'occasion de la découverte d'élements de la denture d'un exemplaire fossile dans les Sables du Kattendijk à Kallo (Pliocène inférieur, Belgique). *Annales de la Société Géologique de Belgique*, **102**, 357–377.
- Herman, J., Hovestadt-Euler, M. and Hovestadt, D.C. 1987. In:
 M. Stehmann (Ed.), Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part A: Selachii, No. 1. Order: Hexanchiformes Family: Hexanchidae. Commissural teeth. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 57, 43–56.
- Herman, J., Hovestadt-Euler, M. and Hovestadt, D.C. 1994. In:
 M. Stehmann (Ed.) [the same title as preceding]. Addendum to Part A, No. 1. Order: Hexanchiformes Family: Hexanchidae. Odontological results supporting the validity of Hexanchus vitulus Springer and Waller, 1969 as the third species of the genus Hexanchus Rafinesque, 1810, and suggesting intrafamilial reordering of the Hexanchidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 64, 147–163.
- Hovestadt, D.C. and Hovestadt-Euler, M. 1995. Additions to the fauna of the Boom Clay Formation of Belgium (Rupelian, Oligocene). *Belgian Geological Survey, Professional Paper*, **278**, pp. 261–282.
- Hovestadt, M., Hovestadt, D. and Smith, R. 1983. A contri-

- bution to the fish fauna of the Belgian Palaeocene: A review of *Notidanodon loozi* (Vincent 1876). *Tertiary Research*, **5**, 71–79.
- Jerzmańska, A. 1968. Ichthyofaune des couches à ménilite (flysch des Karpathes). *Acta Palaeontologica Polonica*, **13**, 379–488.
- Jerzmańska, A. and Jucha, S. 1963. L'affleurement de la faune de poissons dans les schistes de Jasło à Łubno près de Dynów (Karpathes Polonaises). *Rocznik Polskiego Towarzystwa Geologicznego*, **33**, 159–180.
- Jerzmańska, A. and Kotlarczyk, J. 1968. Ichthyofaunal assemblages in the Menilite Beds of the Carpathians as indicators of sedimentary environment. *Rocznik Polskiego Towarzystwa Geologicznego*, **38**, 39–66.
- Jerzmańska, A. and Kotlarczyk, J. 1975. Fossils of the quasi-Sargasso assemblage in the Menilite Beds of the Skole unit, Polish Carpathian Mountains. Kwartalnik Geologiczny, 19, 875–886.
- Jerzmańska, A. and Kotlarczyk, J. 1976. The beginnings of the *Sargasso* assemblage in the Tethys? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **20**, 297–306.
- Jerzmańska, A. and Kotlarczyk, J. 1988. Podstawy podziału stratygraficznego serii menilitowo-krośnieńskiej Karpat za pomocą ichtiofauny. Przewodnik 59 Zjazdu Polskiego Towarzystwa Geologicznego: Karpaty Przemyskie, pp. 102–107.
- Jerzmańska, A. and Kotlarczyk, J. 1991. Zasięgi pionowe bytowania ichtiofauny nalezionej w serii menilitowo-krośnieńskiej Karpat Rzeszowskich. In: Paleontologia a batymetria; Materiały 14 Konferencji Paleontologów w Karpatach Rzeszowskich, pp. 22–24.
- Jonet, S. 1947. Présence d'un Squale du genre *Cetorhinus* dans l'Oligocène de Roumanie. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, **56**, 17–19.
- Jonet, S. 1958. Contributions à l'étude des schistes disodyliques oligocènes de Roumanie: La faune ichthyologique de Homoraciú, district de Prahova, pp. 1–112. Lisboa
- Jucha, S. 1969. Les schistes de Jasło, leur importance pour la stratigraphie et la sédimentologie de la série ménilitique et des couches de Krosno (Carpathes flyscheuses). *Prace Geologiczne*, **52**, 1–128.
- Kalabis, V. and Schultz, O. 1974. Die Fischfauna der paläogenen Menilitschichten von Speitsch in Mähren, ČSSR. Annalen des Naturhistorischen Museums in Wien, 78, 183–192.
- Kemp, N.R. 1978. Detailed comparisons of the dentitions of extant hexanchid sharks and Tertiary hexanchid teeth from South Australia and Victoria, Australia (Selachii, Hexanchidae). *Memoirs of the Natural Museum of Victoria*, 39, 61–83.
- Kotlarczyk, J. and Leśniak, T. 1990. Lower part of the Menilite Formation and related Futoma Diatomite Member in the

- Skole unit of the Polish Carpathians, pp. 1–74. Akademia Górniczo-Hutnicza; Cracow.
- Kotlarczyk, J., Jerzmańska, A., Świdnicka, E. and Wiszniowska, T. 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene Early Miocene strata of the Polish Outer Carpathian Basin. *Annales Societatis Geologorum Poloniae*, 76, 1–111.
- Leriche, M. 1908. Sur un appareil fanonculaire de *Cetorhinus* trouvé à l'état fossile dans le Pliocène d'Anvers. *Comptes Rendus Hebdomaires des Séances de l'Académie des Sciences de Paris*, **146**, 875–878.
- Leriche, M. 1910. Les Poissons oligocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **5**, 231–363.
- Leriche, M. 1926. Les Poissons néogènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **32** (for 1922), 367–472.
- Litvinov, F.F. 1989. Struktura epipelagicheskogo taksocena Elasmobranchii v Atlanticheskom i Tikhom okeanakh i ee izmeneniya v noveyshee geologicheskoe vremya. Voprosy Ikhtyologii, 29, 973–984.
- Long, D.J., Murphy, M.A. and Rodda, P.U. 1993. A New World occurrence of *Notidanodon lanceolatus* (Chondrichthyes, Hexanchidae) and comments on hexanchid shark evolution. *Journal of Paleontology*, 67, 655-659.
- Maisey, J.G. and Wolfram, K.E. 1984. "Notidanus". In: N. Eldredge and S. Stanley (Eds), Living Fossils, pp. 170-180. Springer Verlag; New York.
- Micklich, N. and Parin, N. 1996. The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): First results and a review. *Publicaciones Especiales*, *Instituto Español de Oceanografia*, **21**, 129–148.
- Nolf, D. 1988. Haaie- en roggetanden uit het Tertiair van Belge, pp. 1–180. Koninklijk Belgisch Instituut voor Natuurwetenschappen; Brussel.
- Pharisat, A. 1991. La paléoichthyofaune du Rupélien marin de Froidefontaine (Territoire de Belfort). *Annales Scien-*

- tifiques de l'Université Franche-Comté Besançon, Géologie, **4**, 13–97.
- Reed, M.D. 1946. A new species of fossil shark from New Jersey. *Notulae Naturae of the Academy of Natural Sciences of Philadelphia*, **172**, 1–3.
- Reinecke, T., Stapf, H. and Raisch, M. 2001. Die Selachier und Chimären des Unteren Meeressandes und Schleichsandes im Mainzer Becken (Alzey- und Stadecken-Formation, Rupelium, Unteres Oligozän). *Palaeontos*, 1, 1–73.
- Reinecke, T., Moths, H., Grant, A. and Breitkreutz, H. 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oberes Oligozän). *Palaeontos*, **8**, 1–135.
- Reinecke, T., von der Hocht, F. and Gürs, K. 2008. Die Elasmobranchier des Vierlandiums, Unteres Miozän, im Nordwestdeutshen Becken aus Bohrungen und glaziofluviatilen Geröllen ("Holsteiner Gestein") der Vierlande-Feinsande (Holstein) und der Kakert-Schichten (Niederrhein). *Palaeontos*, 14, 1–54.
- Schultz, O. 1982. Die Fischzähne aus dem Mittel-Oligozän von Nikolčice und Umgebung (Mähren, ČSSR). *Acta Musei Moraviae*, **67**, 51–55.
- Uyeno, T. & Matsushima, Y. 1974. Early Pleistocene remains of Basking Shark, Hammerhead Shark, and others found in Yokohama, Japan. Bulletin of the Kanagawa Prefecture Museum, 7, 57–66.
- Vitalis, I. 1942. Die Zähne der rezenten *Notidanus*-Arten und des fossilen *Notidanus primigenius* Ag., mit besonderer Rücksicht auf die miozänen *Notidanus*-Zähne von Mátraszöllös. *Geologica Hungarica*, *Series Palaeontologica*, **18**, 1-40.
- Ward, D.J. 1978. Additions to the fish fauna of the English Palaeogene; 1. Two new species of *Alopias* (Thresher Shark) from the English Eocene. *Tertiary Research*, **2**, 23–28.
- Ward, D.J. 1979. Additions to the fish fauna of the English Palaeogene; 3. A review of the Hexanchid sharks with a description of four new species. *Tertiary Research*, **2** (3), 111-129.

Manuscript submitted: 15th February 2008 Revised version accepted: 15th March 2009

PLATE 1

Isolated teeth of *Heptranchias howelli* (Reed, 1946) from the Menilite Shales at Jamna Dolna 2 (Lower Oligocene; Outer Carpathians, Poland)

- **1a-1b** Tooth, from the scree (see Text-fig. 1E): two counterparts, to highlight the cockscomb-like mesial serration; Specimen No. JD2.2
 - 2 Tooth, from Horizon P (see Text-fig. 1C); Specimen, crushed posteriorly, No. JD2 P 1
- **3a-3b** Tooth, from Horizon LG (see Text-fig. 1C): two counterparts, to highlight the primary notch; Specimen No. JD2.LG.35
 - 4 Tooth from the scree (see Text-fig. 1E); Specimen No. JD2.1
 - **5** Two teeth, supposedly of the same fish specimen, from Horizon K (see Textfig. 1C); in the background matrix, a skeleton of the pipefish (syngnathid); Specimens No. JD2.K.156 (above) and JD2.K.157 (below)

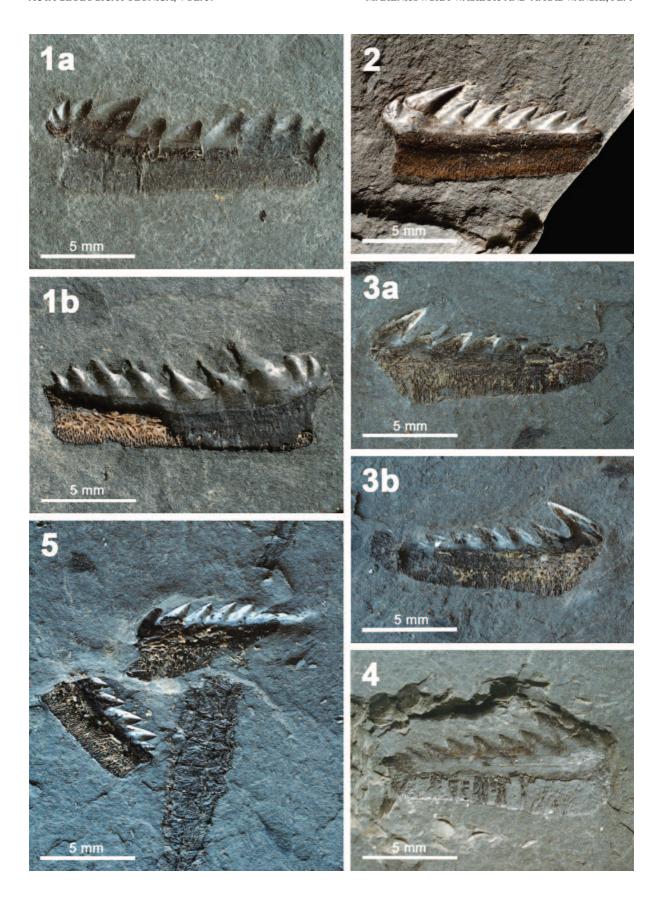


PLATE 2

Shark remains from the Dynów Marls at Wola Czudecka (Lower Oligocene; Outer Carpathians, Poland)

- 1-3 Isolated teeth of the lower jaw of the Thresher Shark, *Alopias* sp.; all in labial view (the lingual side having been firmly adhered to the marly matrix); Specimens No. WO.78-WO.80
- **4-6** Isolated gillrakers of the Basking Shark, *Cetorhinus* sp., preserved on the top surface of marly beds; Specimens No. WO.81-WO.83

