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A commensal relationship between alpheid crustaceans and gobiid fish in the middle Miocene of southern Poland (Central Paratethys)

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ABSTRACT:

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Remains of decapod crustaceans of the family Alpheidae Rafinesque, 1815 and bony fish of the family Gobiidae Bonaparte, 1832 co-occur at a number of localities in the Korytnica Basin (Holy Cross Mountains) and in a newly exposed section along a stream near Niskowa (Outer Carpathians), both in southern Poland. These remains (alpheid major right-sided cheliped tips and gobiid otoliths) are interpreted as documenting a commensal partnership that existed in the shallowest zones of the middle Miocene Fore-Carpathian Basin in southern Poland under environmental conditions that must have been comparable to those of the present-day tropical/subtropical Indo-West Pacific and Caribbean.

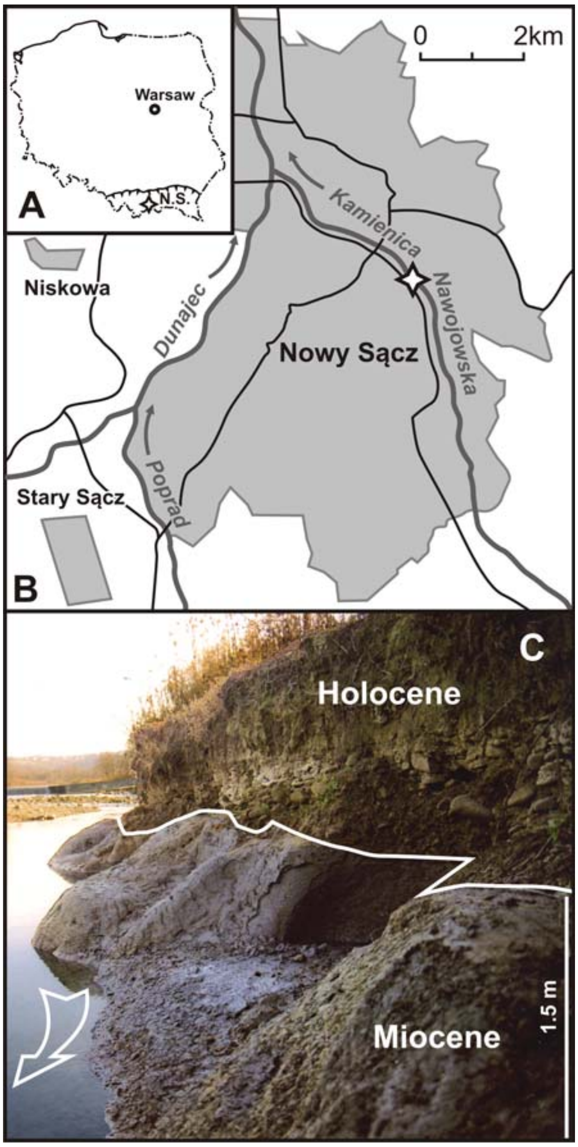
Key words: Alpheid crustaceans; Gobiid fish; middle Miocene; Poland.

INTRODUCTION

The rich and hugely diverse organic life of the middle Miocene epicontinental sea in southern Poland and the Ukraine that has been distinguished as the northern (Fore-Carpathian) part of the so-called Central Paratethys, has been studied for almost two centuries. In addition to the alpha taxonomy of particular animal groups, these studies have focused on palaeobiological and palaeoecological interpretations of selected forms, as well as their diversity and interrelationships (see Bałuk and Radwański 1977; Hoffman 1977; Radwański 1977; Radwańska 1992; Radwański *et al.* 2006, 2012; Wysocka *et al.* 2012, 2016; Zágoršek *et al.* 2012, and references therein).

During screening of fossil assemblages in the last decades, a few tiny (meso- and micro-sized), broad claws have been handpicked; these have remained enigmatic and indeterminate until recently. Such claws are known from two localities (Korytnica in the Holy Cross Mountains and a new section along the Kamienica Nawojowska stream near Niskowa in the Carpathians), from where ubiquitous fish otoliths had been studied previously (Radwańska 1992), the most characteristic amongst them being those of gobiids.

Forms identical to these ‘enigmatic claws’ have recently been recorded by Kobayashi *et al.* (2008), Karasawa *et al.* (2014), Jagt *et al.* (2015) and Hyžný *et al.* (2017) as being those of representatives of the shrimp family Alpheidae (compare with fig. 3 of Hyžný *et al.* 2017), albeit of indeterminate generic and specific status. Those papers made me reflect on the possible connection of such ‘enigmatic claws’ with gobiid fish, to an extent that is similar to, or identical with, that of the present-day partnership between gobiids and alpheids. Although, for the time being, these alpheid claws cannot be identified to genus or species, it may be suggested that their behaviour was analogous to that of modern pistol (or snapping) shrimps.



Text-fig. 1. Location of the Kamienica Nawojowska section. A – General map of Poland, to locate the region in which the middle Miocene (Badenian) clays are exposed; N.S. – Nowy Sącz; B – Nowy Sącz region with the section marked, after Bitner and Kaim (2004); C – Alpheid/gobiid-bearing middle Miocene (Badenian) clayey sequence in the banks of the Kamienica Nawojowska stream, having been eroded and temporarily exposed during an immense flood in the summer of 2004; photograph by W. Bałuk

PROVENANCE OF THE MATERIAL

At Korytnica (Mt. Łysa site, Korytnica Basin, to the south of the Holy Cross Mountains), alpheid claws have been collected as a 'by product' when sieving samples of the Korytnica Clays from the littoral zone for fish otoliths (see Radwańska 1992, figs 1, 2). At a new locality near Niskowa (Carpathians) (Text-fig. 1A, B), a middle Miocene (Badenian; for a detailed discussion on the age of this locality see Studencka, this volume) clay sequence rests unconformably on a folded Carpathian flysch substrate, having been more or less faulted (see Bałuk 1970; Radwańska 1992, pp. 156, 157, figs 1, 7). During the last three decades, this section has been temporarily exposed along the banks of the Kamienica Nawojowska stream (Text-fig. 1C), a tributary of the Dunajec River. Preliminary accounts of the fossil contents have appeared in recent years (Bitner and Kaim 2004; Szczechura 2006). The material studied has recently been obtained by Professor Wacław Bałuk from washed and sieved clay residues with gastropod assemblages.

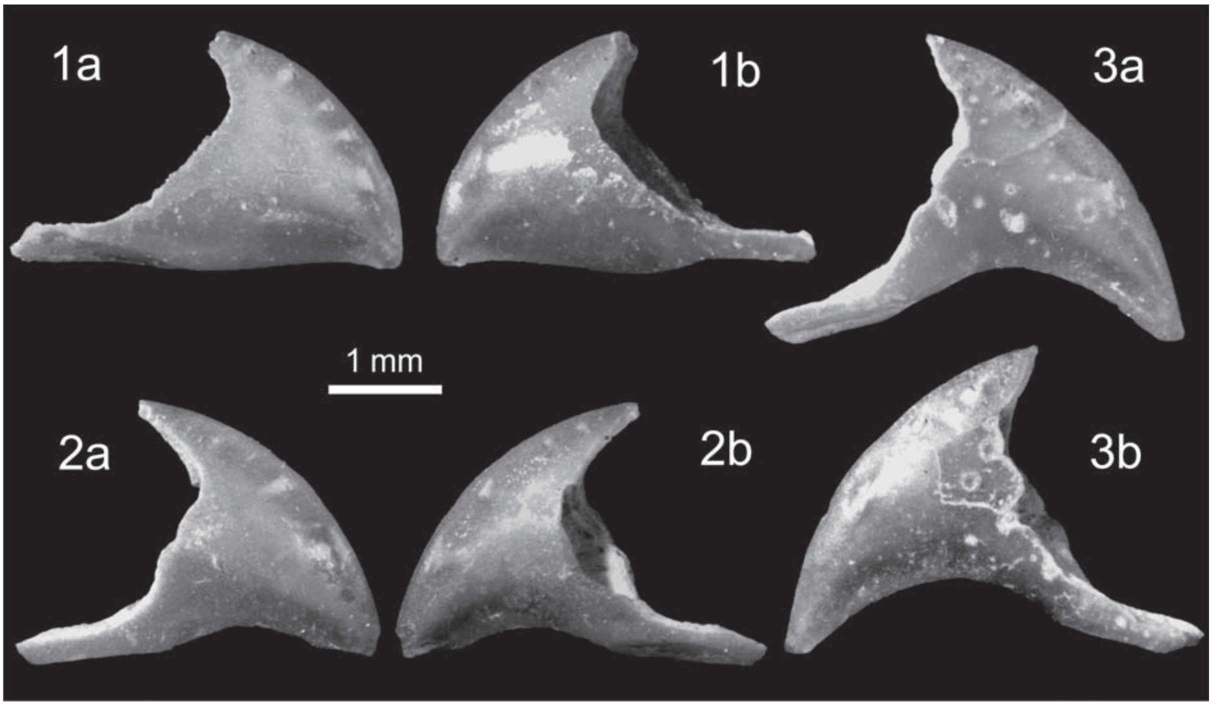
All specimens discussed and illustrated herein are housed in the Stanisław Józef Thugutt Geological Museum of the Faculty of Geology, University of Warsaw and are prefixed with MWG UW ZI/56.

REMARKS ON ALPHEID CLAWS AND OTOLITH TAPHONOMY

The alpheid claws, as well as the gobiid otoliths from the Korytnica Clays and the Kamienica Nawojowska section near Niskowa are represented only by isolated elements; this is a typical state of preservation of these two groups. The elements are very well preserved (Text-figs 2–4), and do not display broken and/or rounded margins and abraded surfaces characteristic of mechanical abrasion due to long transport and/or reworking before final burial. On the contrary, many specimens have a relatively "fresh", glassy surface (Text-figs 2–4). Furthermore, there is no evidence of taphonomic sorting of the material studied. According to the present author, the collected specimens of alpheid claws and gobiid otoliths have an autochthonous character, as has almost the entire assemblage of invertebrate and vertebrate faunal remains recognised in the studied localities (e.g., Bałuk and Radwański 1977; Radwańska 1992).

GENERAL REMARKS ON RECENT ALPHEID/GOBIID COMMENSAL RELATIONSHIPS

To begin with, the genus *Alpheus* Weber, 1795 should be considered. Some of its species, such as *A. djiboutensis* De Man, 1909, *A. heterochaelis* Say, 1818 or *A. bellulus* Miya and Miyake, 1969, burrow at shallow subtidal depths (see Luther 1958; Moore and McCormick 1969, fig. 24/3a, 3b; Karplus 1987,



Text-fig. 2. Middle Miocene (Badenian) alpheid snapping shrimps, movable fingers of 1st right-sided cheliped in outer (1a, 2a, 3a) and inner (1b, 2b, 3b) views, specimens MWG UW/ZI/56/21-23 from Korytnica, Holy Cross Mountains. Photographs by L. Łuszczewska

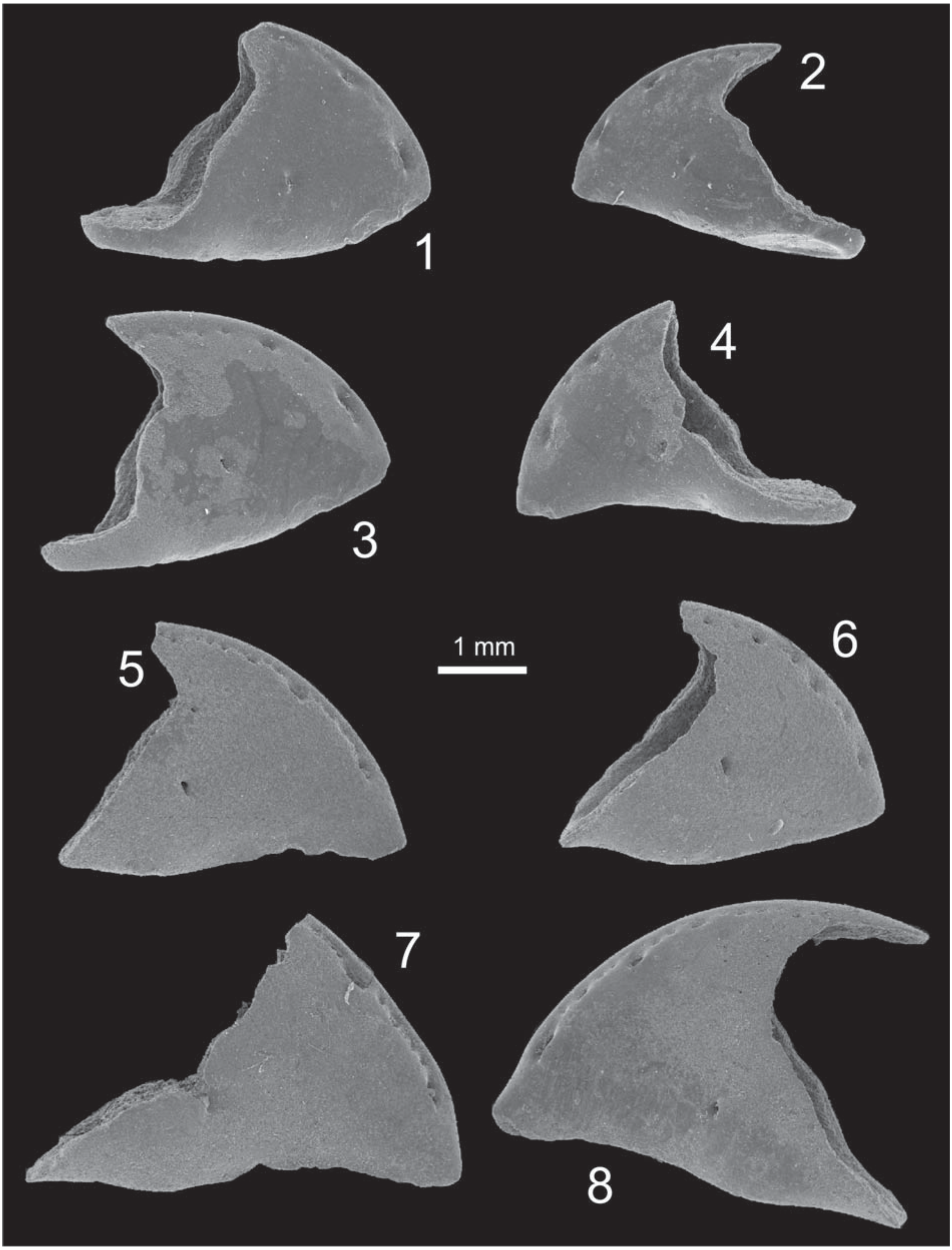
fig. 5, respectively), contrary to those that preferentially produce burrow systems intertidally, such as *A. californiensis* Holmes, 1900, the famous pistol shrimp of the tidal flats of California (see Moore and McCormick 1969, fig. 38/4a, 4b). The captivating popular names of extant species refer to the loud snapping noise that cheliped claws make, associated with a violent squirt in the direction of an adversary or item of prey.

Irrespective of a detailed taxonomic assessment, these 'enigmatic claws' (Text-figs 2 and 3) are interpreted as the tips of cheliped palms, either of fixed fingers, or movable ones, or both. It is suggested that these were more heavily calcified than the proximal parts of chelipeds that are invariably missing from the material studied.

The peculiar requirements of some extant alpheids and their intriguing partnerships with gobiid fish have occasionally been studied, both in the field and in the laboratory (aquaria). The first remarkable report was that by Luther (1958), who studied the behaviour of *A. djiboutensis* in the Red Sea, and documented the near-obligatory partnership of that species with a gobiid that takes care of the burrow they inhabit together. Moreover, as the shrimp is almost blind, the fish guides it outside the burrow, warns it in case of danger so that it can flee into the burrow and disappear. What was more unexpected was the fact that this commensal pair, when reared in an aquarium by Luther (1958), proceeded in the same way. The gobiid led the alpheid and they moved together along the walls of the aquarium, even if there was no possibility of producing a burrow.

Soon after this study, it appeared that the alpheid/gobiid commensalism was very common in the Red Sea (Karplus 1987 and references therein) and across the entire Indo-West Pacific, with records by Macnae and Kalk (1962) from Mozambique, by Palmer (1963) from the Persian Gulf and by Farrow (1971) from the Aldabra Atoll in the Indian Ocean. As a result, we now know that alpheids, in sexual pairs, are associated with a gobiid that can even assist enlarging the common burrow. The frequency of alpheid burrows inhabited by a gobiid amounts to 75% (Farrow 1971, p. 486).

Commensal associations between gobiid fishes and various other invertebrates are well known. Many gobies inhabit burrows in sand or mud with the ghost shrimp *Callianassa* Leach, 1814 and were the subject of classical studies by MacGinite and MacGinite (1949). Some of the goby species are also known to be closely associated with sponges and are regarded



Text-fig. 3. Middle Miocene (Badenian) alpheid snapping shrimps; moveable fingers of major right-sided cheliped; 1-4 – Specimens MWG UW/ZI/56/1-4 from Korytnica, Holy Cross Mountains; 5-8 – Specimens MWG UW/ZI/56/5-8 from the Kamienica Nawojowska section near Niskowa, Carpathians as sponge inhabitants (e.g., Colin 2002; Randall and Lobel 2009). Some of them live among corals where the goby benefits from the protection and habitat in the corals (e.g., Herler 2007; Herler *et al.* 2012).

All these mentioned partnerships may have occurred in the habitat studied in the present work, except that there is no evidence of the presence of sponges. Different corals have been noted, but many of them are small, solitary specimens (Roniewcz and Stolarski 1991).

It is of interest, although beyond the scope of the present note, that some other members of the family Alpheidae display an even more peculiar mode of life and behavioural style. For instance, amongst the tiny representatives of the genus *Synalpheus* Spence Bate, 1888, their populations occur in two distinct castes, i.e., queen and soldiers, whose organization recalls that of bees or termites. Such shrimps occur in their hundreds in the internal canals of some Caribbean sponges (see Duffy and Macdonald 1999; Duffy 2002).

ALPHEID/GOBIID ASSEMBLAGE AND ITS ENVIRONMENT

The aim of the present paper is to show that the environmental parameters of the sea water (depth, salinity, temperature, character of the bottom) in the middle Miocene (Badenian) Fore-Carpathian Basin), as well as the life requirements of both alpheids and gobiids compare well with those of the present-day Pacific. Under such conditions, the alpheid/gobiid commensal behaviour has been around for at least 15 million years, and maybe even longer (Hoedemakers and Van Hinsbergh 2013; Hyžný *et al.* 2017).

Palaeoenvironmental conditions during the middle Miocene at Korytnica and the Kamienica Nawojowska section near Niskowa, the two localities studied, have been recognised as identical with those required by modern alpheids (e.g., Kim and Abele 1988; Herler *et al.* 2012), in reflecting deposition at shallow sublittoral depths, just beneath the Lower Water Level (LWL), along the rocky shores that typified the Holy Cross coast (see Radwański 1969; Bałuk and Radwański 1977; Radwańska and Radwański 1984; Radwańska 1992, pp. 147–149).

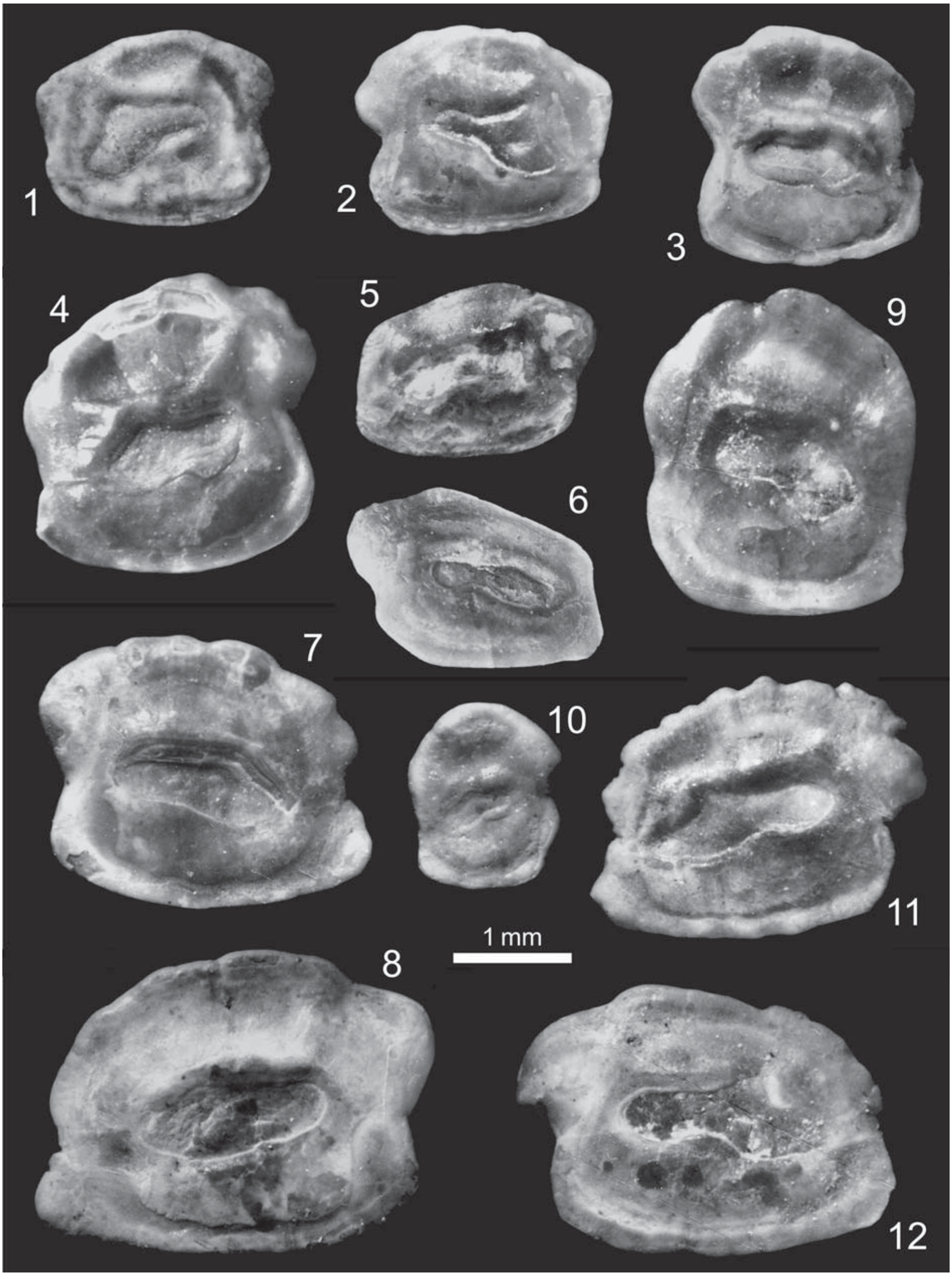
At Niskowa, similar depositional depths are indicated by the extremely rich and diversified organic assemblage as a whole (see Bałuk 1970; Radwańska 1992). Of special interest, both at Niskowa and the new section along Kamienica Nawojowska, is the occurrence of dasycladacean green algae of the acicularid group that are common in the richest samples (Bałuk 1970, p. 109; Małecki 1970; Szczechura 2006).

As far as the frequency of gobiids in the Korytnica Basin is concerned, this has been recorded as extremely high. In the entire fish assemblage based on otoliths of >16,300 specimens (representing 105 species in 47 families), gobiids account for as much as 56% of specimens collected. With the exception of the genera *Deltenosteus* Gill, 1863 and *Gobius* Linnaeus, 1758, these otoliths can only be identified at family rank (Radwańska 1992, pp. 283–293, 311).

At Niskowa, the preservationally biased otolith assemblage reveals an even greater predominance of gobiids (92% of a total of 1,578 specimens). Their small otoliths are well preserved and assignable to six species (Radwańska 1992, pp. 318, 319). In the newly collected samples gobiid otoliths constitute the majority, nearly to the exclusion of other forms.

It should be noted that the alpheid/gobiid partnership is not the only one in the rich fish assemblage at Korytnica. Representatives of the family Carapidae Jordan and Fowler, 1902, that live in the intestines of holothurians, occur rarely. Holothurian sclerites are especially common in carapid-bearing samples (see Radwańska 1992, pp. 202–208, 311, 315). The most notable is *Carapus* cf. *caninus* (Günther, 1862), a close relative of the present-day species from the New Guinea offshore, but not noted previously from the fossil record (see Radwańska 1992, pp. 203, 204, figs 54, 55).

In addition, it is of note to stress that the suggested burrows inhabited by the alpheid/gobiid commensal partners, must have been distinctly simpler than those of modern intertidal specimens. Those are typically multi-tiered, as is illustrated by those of *Alpheus floridanus* Kingsley, 1878 from Florida and the Bahamas (see Shinn 1968, pl. 109) or *A. heterochaelis* from the coast of Georgia, USA (see Howard and Frey 1975, pl. 10). In the middle Miocene (Badenian) sequence of the Fore-Carpathian Basin, such intertidal networks of alpheid burrows have so far been recorded only from the Ukraine, i.e., carbonate buildups of the Medobory Biohermal Complex (see Radwański *et al.* 2006, pp. 96, 97, figs 4–6). The older sequences in Poland that have yielded inter- to subtidal networks of alpheid burrows are those of some Upper Jurassic (lower Kimmeridgian) bahamites in the Holy Cross Mountains. In that area, they commonly served as cryptic refuges for living echinoderms, mostly comatulid crinoids, or as taphonomic traps of their corpses (see Radwańska 2005, 2014).



Text-fig. 4. Middle Miocene (Badenian) representatives of the family Gobiidae; 1-8 – Specimens MWG UW/ZI/56/9-16 from Korytnica, Holy Cross Mountains; 9-12 – Specimens MWG UW/ZI/56/17-20 from the Kamienica Nawojowska section near Niskowa, Carpathians

CONCLUSIONS

The common co-occurrence of cheliped remains of alpheid snapping shrimps and otoliths of gobiid fishes in some samples from Korytnica and the Kamienica Nawojowska section near Niskowa, suggests a commensal relationship that is comparable to the modern one in all aspects (burrow construction, guarding and assistance). In addition, the new finds allow the reconstruction of a middle Miocene seascape that matches the present-day, inter- to subtidal or lagoonal zones of the Indo-West Pacific and Caribbean (compare Luther 1958; Shinn 1968; Farrow 1971; Howard and Frey 1978; Förster 1979; Karasawa *et al*. 2014). Such a scenario, in particular with regard to the depth and climatic conditions of the Indo-West Pacific, supplements previous interpretations on the basis of various invertebrates and some fishes (see Bałuk and Radwański 1977; Förster 1979; Radwańska and Radwański 1984; Radwańska 1992; Radwański *et al.* 2006; Wysocka *et al.* 2012, 2016; Zágoršek *et al.* 2012).

The commensal behaviour of alpheid snapping shrimps gobiid fishes, of significance for evolutionary palaeobiology (see Boucot 1990) and panglobal in the tropics today, has been around for at least 15 million years, since middle Miocene time, if not even longer.

Acknowledgements

I would like to offer most cordial thanks to Prof. Dr W. Bałuk, who kindly donated the collected claws specimens from the Kamienica Nawojowska section for investigation, and to Dr. John W.M. Jagt for profitable discussion, particularly on the systematic position of the alpheid material. Thanks to Dr. Marcin Górka for processing Text-fig. 1.

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