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A reconsideration of the palinuroid family Synaxidae (Crustacea, Decapoda), with a new member from the Upper Jurassic of southern Poland

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ABSTRACT

Representatives of the family Synaxidae, commonly referred to as furry lobsters, are rare constituents of modern-day marine communities, while their fossil record suggests that they were more common in the past, in reefal settings during the Late Jurassic across Europe, from where at least three species have been recorded to date. An overview of all known extant and extinct synaxids is presented here and a sixth fossil form is added to the list. The latter constitutes one of the earliest records to date of furry lobsters worldwide and extends the palaeogeographical range of this relatively small group of early palinuroids. It was collected from massive sponge-microbial build-ups (reefal limestones) of middle Oxfordian age (*Gregoryceras transversarium* ammonite Zone) near Kraków, southern Poland, and is here named *Palaeosynaxes montserratae* nov. gen., nov. sp.

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INTRODUCTION

Furry lobsters (or coral lobsters) are small decapod crustaceans that are closely related to slipper lobsters (Scyllaridae) and spiny lobsters (Palinuridae). However, synaxids differ from spiny and slipper lobsters in lacking pronounced supra-orbital horns and in having broad-based, pronounced triangular rostra, while their body is covered in short hairs (hence the name 'furry lobster'), and their antennae are not as enlarged as in scyllarids and palinurids. In modern-day seas, representatives of the family Synaxidae are rare constituents of benthic communities (e.g., Holthuis, 1991), but from the fossil record they were more common in the past, being known in particular from reefal settings of Late Jurassic age across Europe (Bachmayer, 1959 ; Förster, 1973; Fraaije et al., 2020). We herein revise the three taxa recorded to date from such levels, as well as younger forms from the mid-Cretaceous (Garassino and Pasini, 2020) and Upper Eocene (De Angeli and Garassino, 2014), and erect a new genus and species for a form from the Upper Jurassic of southern Poland.

GEOLOGICAL SETTINGS

A road cutting into a small hill near the motorway from Kraków to Katowice, close to the village of Szklary in southern Poland, has been well known for the presence of numerous remains of middle Oxfordian decapod crustaceans (Krobicki, 1994; Krobicki and Müller, 1998a, b; Müller et al., 2000; Garassino and Krobicki, 2002; Krobicki and Zatoń, 2008; Fraaije et al., 2022). Palaeogeographically, the limestones that crop out in a small, abandoned quarry in a forest-lined valley close to Szklary belong to the Late Jurassic sponge megafacies (Matyja and Wierzbowski, 1995) of the peri-Tethyan epicontinental sea across Europe, from Portugal to Romania. Oxfordian-aged sponge bioconstructions predominated within these facies. Sedimentologically, these have been interpreted as cyanobacterial-sponge buildups (bioherms/"reefs") that constructed massive, non-bedded limestones (Figure 1). They are surrounded by micritic, thin-bedded platy-type limestones that primarily formed in inter- and/or peri-bioherm environments (Matyszkiewicz, 1999; Krobicki and Zatoń, 2008; Matyszkiewicz et al., 2012) on a deep-neritic sea floor (Matyja and Wierzbowski, 1995). These limestones are well dated by ammonites (e.g., Matyja and Wierzbowski, 1995), also in the Kraków area in southern Poland (Głowniak, 2006; Matyja and Ziółkowski, 2014) (Figure 2).

ACHELATAN MORPHOLOGY AND CLASSIFICATION

We here follow the classification of achelatan lobsters as based on carapace morphology (e.g., Holthuis, 1991; Martin and Davis, 2001; Lavalli and Spanier, 2010; Schweitzer et al., 2015), in which four families are recognised, namely the Cancrinidae, Palinuridae, Scyllaridae, and Synaxidae. Extant synaxids comprise only two genera: *Palib-*

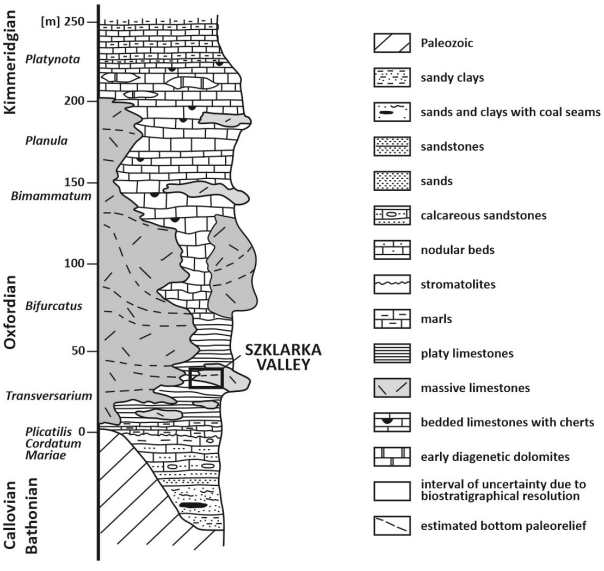

FIGURE 1. Lithostratigraphical column of Oxfordian strata in the Kraków area (southern Poland), with indication of the Szklarka valley locality (modified after Matyszkiewicz, 1996; Matyszkiewicz et al., 2012).

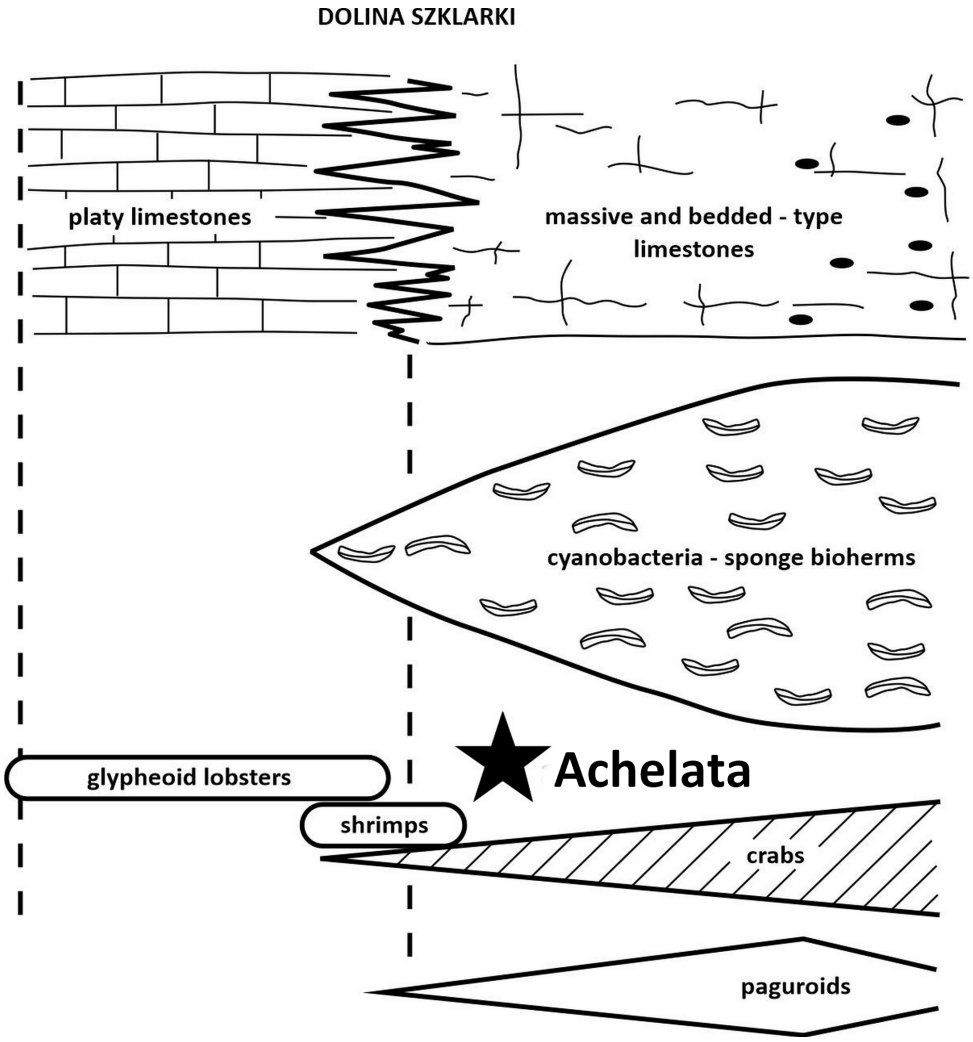

FIGURE 2. Sedimentology, palaeoecology, and presence of decapod crustaceans in the Szklarka valley outcrop (see Figure 1 after Müller et al., 2000; supplemented by Fraaije et al., 2022). The black star denotes the approximate level of provenance of the holotype of *Palaeosynaxes montserratae* nov. gen., nov. sp. (Figure 4).

ythus Davie, 1990 and *Palinurellus* von Martens, 1878. Synaxids are differentiated from palinurids in that they lack pronounced supra-orbital horns. Moreover, they have short antennal flagella, a long and broad triangular anterior part of the carapace (i.e., rostrum to cervical groove), a prominent, broad-based rostrum and a tapered carapace that is not depressed or flattened, but tubular. They also have more robust first pereiopods than most extant achelatans. All these features may be considered ancestral in the evolutionary history of this group of decapod crustaceans. This observation is corroborated by data obtained in a detailed study of the morphology of achelatan larvae carried out by Baisre (1994), who demonstrated that *Palinurellus* was the most basal amongst extant palinuroids.

Within the family Synaxidae (Figure 3), only three extant species have been recorded to date. The first, *Palibythus magnificus* Davie, 1990 (Figure 3C), is known from depths between 220 and 275 metres near western Samoa in the Pacific Ocean. The other two, *Palinurellus gundlachi* von Martens, 1878 (Figure 3A; Caribbean Sea and Atlantic coast of South America) and *P. wienecki* (De Man, 1881) (Figure 3B; Indo-Pacific), both of which inhabit shallow-water reef environments at depths between 9 and 35 metres, occurring deep within holes and crevices, and apparently active only at night, which explains why they have only rarely been collected (Holthuis, 1966, 1991; Davie, 1990; Lavalli and Spanier, 2010; Idreesbabu et al., 2018).

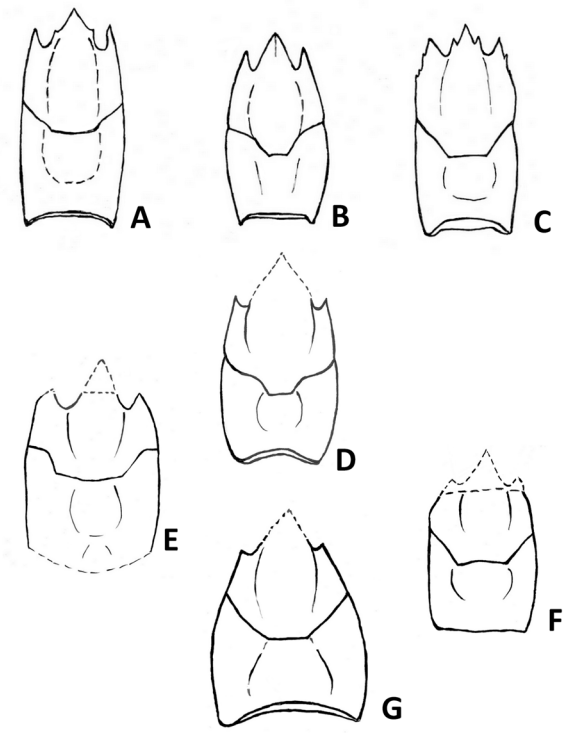

FIGURE 3. Distribution of synaxid achelatans over geological time, from the Late Jurassic to the present day. A, Extant *Palinurellus gundlachi* von Martens, 1878. B, Extant *Palinurellus wienecki* (De Man, 1881). C, Extant *Palibythus magnificus* Davie, 1990. D, Late Eocene *Palinurellus bericus* De Angeli and Garassino, 2014. E, Late Cretaceous (Cenomanian) *Palaeopalinurellus jbeilensis* Garassino and Pasini, 2020. F, Late Jurassic (Tithonian) *Palaeopalinurellus strambergensis* (Bachmayer, 1959). G, Late Jurassic (Oxfordian) *Palaeopalinurellus culocervus* Fraaije, Van Bakel, Jagt, and Brochet, 2020.

Previously, synaxids were interpreted either as sister group to all other achelatans or as an ingroup of the Palinuridae (e.g., Davie, 1990; George, 2006; Palero et al., 2009). In recent years, an increasing number of extinct (Late Jurassic to Late Eocene; Figure 3D-E, G) synaxids have been published (De Angeli and Garassino, 2014; Fraaije et al., 2020; Garassino and Pasini, 2020), demonstrating that furry lobsters were more diverse in late Mesozoic and Paleogene marine ecosystems than they are at the present day.

Palibythus was placed by Davie (1990) in the Palinuridae on account of the presence of a well-developed stridulatory organ. Although *Palinurellus* lacks such an organ, Davie assigned this genus to the Palinuridae as well, interpreting it as a primitive member.

The first extinct species of *Palinurellus*, from the Upper Eocene (Priabonian) of north-east Italy, was recorded by De Angeli and Garassino (2014) as *P. bericus* (Figure 3D). The Late Jurassic genus *Palaeopalinurellus* (Fraaije et al., 2020) differs from *Palinurellus* in the scabrous nature of the ornament of its posterior carapace, the irregular tuberculation of its anterior carapace, and the more angular course of its cervical groove.

Based on a single carapace, Bachmayer (1959, p. 938, pl. 1, fig. 1) recorded a new palinurid, *Palinurus strambergensis* (Figure 3F), from 'grauer Kalk, ob. Malm, Stramberger Schichten' (i.e., Tithonian, Upper Jurassic) at Štramberk (Moravia, Czech Republic). Because of its overall morphology, *Palinurus strambergensis* has recently been transferred to *Palaeopalinurellus* by Fraaije et al. (2020). This species is also known from Kimmeridgian strata in southern Germany (Förster, 1973).

SYSTEMATIC PALAEONTOLOGY

Infraorder ACHELATA Scholtz and Richter, 1995
Superfamily PALINUROIDEA Latreille, 1802
Family SYNAXIDAE Bate, 1881
Genus *Palaeosynaxes* nov.

zoobank.org/F8716888-2DED-4C4A-B199-2CC638D45C6E

Type species. *Palaeosynaxes montserratae* nov. sp.

Etymology. From the Greek *palaios* for 'old', in reference to this being an early member of the family Synaxidae.

Diagnosis. Carapace small, oval, tubular; cervical groove V-shaped centrally; carapace densely covered with coarse, blunt, forwardly directed tubercles, most robust on two postrostral ridges on anterior part.

Palaeosynaxes montserratae nov. gen., nov. sp.
Figure 4

zoobank.org/23EEB842-EF06-4A28-8DE9-D5EDCFA00C5D

Diagnosis. As for genus.

Repository of the type specimen. MAB - Oertijdmuseum, Boxtel, The Netherlands.

Type material. The holotype MAB13942, and sole specimen known to date, is an incomplete carapace with a maximum preserved length of 9.5 mm and a maximum preserved width of 6.0 mm, collected in June 2013 by one of us (À.O.) during a field trip to the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Kraków (Poland).

Etymology. Dedicated to Montserrat Batet, partner of one of us (À.O.), as a token of thanks for her support and understanding.

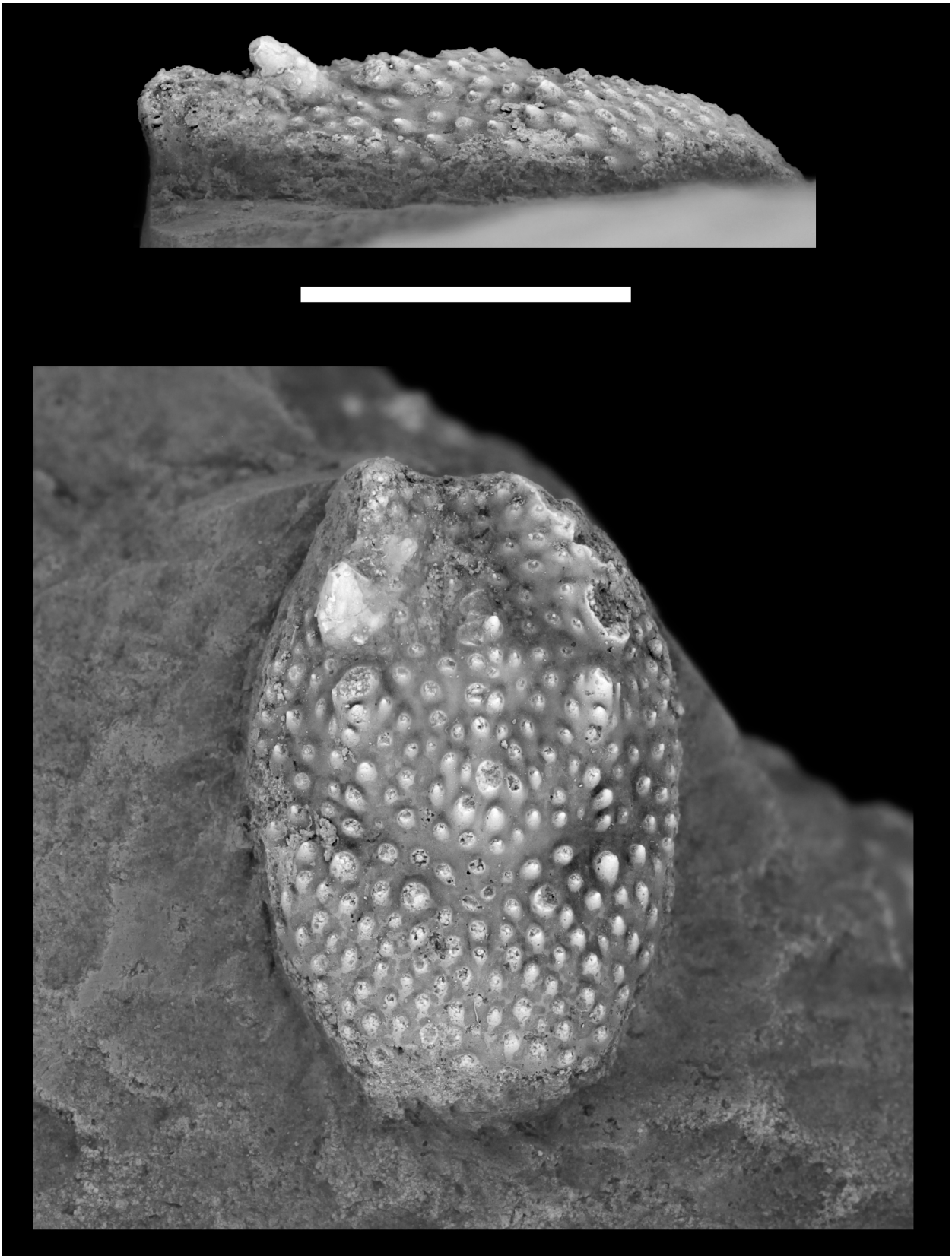

FIGURE 4. *Palaeosynaxes montserratae* nov. gen., nov. sp., holotype (MAB k3781), in left lateral and dorsal views, scale bar equals 5 mm.

Locality and stratigraphy. A road cutting on a small hill close to the village of Szklary, southern Poland, exposing upper middle Oxfordian (*Gregoryceras transversarium* ammonite Zone) reefal strata (Figures 1, 2).

Description. Carapace small, oval, tubular, convex in transverse section; base of rostrum broad, tuberculate and concave; cervical groove V-shaped centrally, obscure laterally; carapace densely covered with coarse, blunt, forwardly directed tubercles, most robust on two postrostral ridges on anterior part; another less pronounced ridge of tubercles extending centrally on mesogastric with double circular tubercle arrangement forming a figure 8 on mesogastric area; cervical groove forming wide V in central third of carapace and extending obliquely (*c*. 45 degrees) toward anterolateral border; posterior part of carapace densely covered with coarse, blunt, forwardly directed tubercles, largest around cervical groove; maximum length of preserved posterior part about 35 per cent of total preserved carapace length.

Remarks. The type of ornament, general shape of the anterior carapace and length of the posterior portion, rules out assignment to the families Palinuridae, Cancrinidae, or Scyllaridae and places the present Late Jurassic taxon in the Synaxidae. The two postrostral ridges of larger tubercles on the anterior carapace of *Palaeosynaxes* nov. gen. could be taken as a prelude of the postfrontal horns of members of the Palinuridae. These two rows of forwardly directed tubercles and the subcircular tubercular arrangements on the central gastric area make *Palaeosynaxes* nov. gen. easily differentiated from all other known synaxids.

The Middle Triassic *Yunnanopalinura schrami* Feldmann, Schweitzer, and Zhang in Feldmann, et al., 2012 shows some similarities to synaxids according to Feldmann et al. (2012), but a more detailed comparison is impossible because the Chinese taxon is based on two specimens in which preservation of parts of the cephalothorax is too poor (Fraaije et al., 2020).

DISCUSSION

With recent additions of extinct achelatans, the evolutionary history of the group may be interpreted in greater detail. Combined palaeontological data and morphological observations on extant larvae (Baisre, 1994) demonstrate the Synaxidae to be the most basal group within the Achelata. Palero et al. (2009, p. 153) noted that, 'Under the traditional classification scheme, the presence of a stridulating organ in *Palybithus* and absence in *Palinurellus* would imply that either this specialized structure appeared twice (once in the Synaxidae lineage and again in the Stridentes) or that it disappeared twice (once in the Synaxidae lineage and again in the Silentes)'. We opine that the stridulating organ appeared only once, namely in the Synaxidae, and that this family comprises the precursors of the family Palinuridae. Based on the data from Haug et al. (2009), and herein, we propose an evolutionary scenario of the Achelata as illustrated in Figure 5.

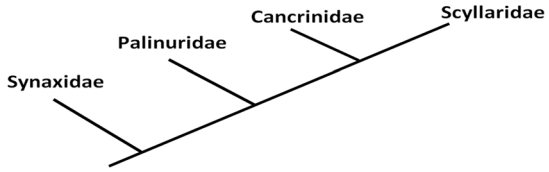

FIGURE 5. Palinuroid evolutionary scenario proposed herein, combining data from Holthuis (1991), Haug et al. (2009), and present observations of *Palaeosynaxes montserratae* nov. gen., nov. sp.

CONCLUSIONS

Palaeosynaxes montserratae nov. gen., nov. sp., from massive sponge-microbial buildups of middle Oxfordian age near Kraków (southern Poland), adds to the diversity of extinct synaxid achelatans. Type of ornament, general shape of the anterior carapace and length of the posterior portion, as well as the presence of two postrostral ridges of larger tubercles on the anterior carapace allow this taxon to be differentiated from all other extinct and modern synaxids of Late Jurassic to Holocene age. It constitutes one of the earliest records to date of furry lobsters worldwide and extends the palaeogeographical range of this relatively small group of early palinuroids. With more carapaces of extinct forms being recovered, described, and formally named, the phylogenetic history of the achelatans, so far based mainly on extant material, may be assessed more accurately, like recent developments for the anomuran superfamily Paguroidea (Fraaije et al., 2022b).

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