**Tanidromites insignis (von Meyer, 1857) (Crustacea: Decapoda: Brachyura) from Late Jurassic non-biohermal facies of the Western Tethys (Pieniny Klippen Belt, Western Carpathians, Slovakia)**

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With 5 figures and 1 table

Abstract: The first decapod crustacean remains from Late Jurassic limestones of the Pieniny Klippen Belt (Western Carpathians, Slovakia) are recorded. The material originates from a Middle Oxfordian ammonite shell bed and comprises a single dorsal carapace of the homolodromioid crab, *Tanidromites insignis*, as well as several fragments of chelipeds of unknown affinity which, however, might belong to primitive brachyurans. Although they usually are considered to be bound to reefal structures, all material studied herein is non-related to biohermal facies and, as such, does not represent a typical occurrence.

Key words: Decapoda, Homolodromioidea, Tanidromitidae, *Tanidromites*, Oxfordian, Pieniny Klippen Belt, Slovakia.

1. Introduction

Ever since its original description (von Meyer 1860), the family Prosopidae has accommodated virtually all brachyuran crustaceans recorded from strata of Late Jurassic age. However, recent revisions (Schweitzer et al. 2007a; Schweitzer & Feldmann 2008a, b, 2009a-c, 2010a-c; Feldmann et al. 2006, 2008) have revealed too wide a range of variation of morphological features of the dorsal carapace for them to be assigned to a single family. The former Prosopidae sensu von Meyer, 1860 has been subdivided into several independent dromiacean families within two distinct superfamilies, the Homolodromioidea Alcock, 1900 and the Glaessneropsioidea Patrulius, 1959. The former contains also the extant Homolodromiidae Alcock, 1900 (Schweitzer & Feldmann 2009a). Jurassic dromiaceans almost exclusively occur as isolated dorsal carapaces, although there are a few reports of specimens preserving appendages (Forster 1985; Garassino et al. 2005; the latter report has been questioned, see below). Such crabs have been demonstrated to range from the Late Pliensbachian to the Recent, across the globe. During the Oxfordian they flourished and were considered to have occupied the microbial-sponge and coralgal megafacies belt from Portugal to southern Poland and Romania (Müller et al. 2000; Feldmann et al. 2006; Schweitzer et al. 2007a, b; Krobicki & Zaton 2008;
However, material described in the present paper differs in stemming from non-biohermal facies; it also represents the first documented occurrence of a Jurassic primitive crab from the Pieniny Klippen Belt and from the Slovakian portion of the Western Carpathians.

2. Geological setting

Our material was collected in a small, disused quarry just below the top of the Štepnická skala Hill (coordinates: N 49°5’45.1”, E 18°17’55.6”), situated SSW of the town of Púchov (western Slovakia) and c. 500 m
Table 1. Summary of all known representatives of the genus *Tanidromites*, with their stratigraphical and geographic distribution (cf. Schweitzer & Feldmann 2009c: table 1.).

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Geographic distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. pustulosa</em> (v. Meyer, 1860)</td>
<td>Tithonian</td>
<td>Czech Republic</td>
</tr>
<tr>
<td><em>T. scheffnerae</em> Schweigert &amp; Kopka, 2011</td>
<td>Late Kimmeridgian</td>
<td>Germany</td>
</tr>
<tr>
<td><em>T. sculpta</em> (Quenstedt, 1857)</td>
<td>Kimeridgian</td>
<td>Germany</td>
</tr>
<tr>
<td><em>T. insignis</em> (v. Meyer, 1857)</td>
<td>Middle Oxfonian – latest</td>
<td>Germany, Switzerland, Poland, Slovakia</td>
</tr>
<tr>
<td><em>T. lithuanicus</em> Schweigert &amp; Kopka, 2011</td>
<td>Middle Callovian</td>
<td>Lithuania</td>
</tr>
<tr>
<td><em>T. montreulense</em> Crönier &amp; Boursicot, 2009</td>
<td>Early Callovian</td>
<td>France</td>
</tr>
<tr>
<td><em>T. richardsoni</em> (Woodward, 1907)</td>
<td>Late Bajocian</td>
<td>England</td>
</tr>
</tbody>
</table>

Notes: *Prosopon lingulatum* v. Meyer, 1858 is considered a younger synonym of *Tanidromites sculpta* (Quenstedt, 1857) (Schweitzer et al. 2010); for more details references are made to Schweitzer & Feldmann (2008a: 141) and Schweigert & Kopka (2011: 229). Schweitzer & Feldmann (2009c) reported the presence of *Tanidromites* sp. also in the Tithonian Ernstbrunn Limestone of Austria. Frantescu (2011) reported a single specimen of *Tanidromites cf. richardsoni* (Woodward, 1907) from the Upper Jurassic (Upper Oxfordian to Early Kimmeridgian) of Romania.

SE from the hamlet of Štepnice which forms part of the village of Streženice (Fig. 1B). Strata are in overturned position. Detailed lithostratigraphic and microfacies studies have recently been published by Aubrecht & Jamrichová (2009). The succession is characterised by rapid lateral and vertical changes in bed thickness and sediment composition. It starts with 10 m-thick crinoidal limestones of the Smolegowa Limestone Formation, which are overlain by red nodular, poorly nodular, or non-nodular micritic limestones, locally rich in crinoids, and assigned to the Czorsztyn and/or the Bohunice Limestone formations of Early Bathonian to Early Callovian age. The boundary between the crinoidal and nodular limestones is marked by a hardground with Fe-Mn encrustations. Locally, a several metres-thick set of crinoidal grainstones and packstones with cm-thick lenses rich in brachiopods (Stepnica Formation, Callovian) overlies the red nodular limestones. Middle and Late Oxfordian deposits are represented by ammonite shell beds, followed by micritic limestones with crinoids (*Saccocoma*), probably of Kimeridgian age. Crustacean remains were collected from the middle part of the quarry, from the white to yellowish ammonite shell bed. The associated fauna is sparse; recorded are brachiopods, bivalves and crinoids. Based on ammonites such as *Perispinctes* (*Dichotomosphinctes*) elisabethae de Riaz, 1898 the age of these deposits is Middle Oxfordian, more precisely the Transversarium Zone. Almost identical shell beds were laid down up to the Late Oxfordian Bimammatum Zone; however, only from the Middle Oxfordian portion were crustacean remains collected.

These ammonite shell beds were interpreted by Tomášových & Schloegl (2008) as long-term peaks in ammonite production and not accumulations caused by sediment starvation.

3. Material and methods

The present material comprises a single, near-complete dorsal carapace of *Tanidromites insignis*, three propodi from an unidentified decapod crustacean and exoskeleton fragments apparently of another unidentified crustacean. All specimens originate from a c. 40 cm thick layer of yellowish to pale brown ammonite shell bed around the 32-metre mark in the middle part of the quarry (Fig. 1C).

4. Systematic palaeontology

Institutional abbreviations: Repositories of specimens studied are as follows: SNM-Z – Natural History Museum, Slovak National Museum, Bratislava (Slovakia); MKC – AGH University of Science and Technology, Kraków (Poland).

Remark: The higher classification follows De Grave et al. (2009) and Schweitzer et al. (2010).

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833
Superfamily Homolodromioidea Alcock, 1900
Family Tanidromitidae Schweitzer & Feldmann, 2008a
Genus *Tanidromites* Schweitzer & Feldmann, 2008a

**Type species:** *Prosopon insigne* von Meyer, 1857.

**Included species:** See Table 1.

Species accommodated in the genus *Tanidromites* were formerly placed either in *Prosopon* von Meyer, 1835 or *Coeolopus* Étallon, 1861 (see Schweitzer & Feldmann (2008a, 2010c; Schweigert & Kopfka 2011). Later, with the exception of *Prosopon lingualatum* von Meyer, 1858 (= *Tanidromites sculpta* Quenstedt, 1857; see Schweigert & Kopfka 2011: 229), these were transferred to *Pithonoton* von Meyer, 1842 (compare Beurlen 1928; Glaessner 1929; Wehner 1988). Schweitzer & Feldmann (2008a) erected a separate monotypic family, Tanidromitidae, for *Tanidromites*. Recently another genus, Gabriella Collins, Ross, Genzano & Manzian, 2006, has been assigned to it (Schweitzer & Feldmann 2009c). Lately, several new species of *Tanidromites* were described by Crönier & Boursicot (2009) and Schweigert & Kopfka (2011); for details see Table 1.

**Diagnosis:** Reference is made to Schweitzer & Feldmann (2008a: 137).

*Tanidromites insignis* (von Meyer, 1857)

Figs. 2A-E

*1857 Prosopon insigne* von Meyer, p. 556.

1858 *Prosopon insigne* von Meyer. – von Meyer, p. 61.
1860 *Prosopon insignis* von Meyer. – von Meyer, p. 193, pl. 23, fig. 4.
1925 *Prosopon insignis* von Meyer. – Beurlen, p. 468.
1985 *Pithonoton insignis* (von Meyer). – Collins & Wierzbowski, p. 83, pl. 3, fig. 1 (non pl. 2, figs. 3-4 = *Eodromites acqualitus*).
1985 *Coeolopus etallonii* Collins in Collins & Wierzbowski, p. 81, pl. 2, fig. 1.
1993 *Pithonoton insignis* (von Meyer). – Via & Sequeros, p. 8, text-fig. 2B, pl. 1, fig. 3.
2000 *Pithonoton insignis* (von Meyer). – Müller et al., fig. 17K, L.
2002 *Pithonoton insignis* (von Meyer). – Garassino & Krobicki, fig. 4/3a, b.
2010 *Tanidromites etallonii* (Collins in Collins & Wierzbowski). – Schweitzer et al., p. 61.
2011 *Tanidromites insignis* (von Meyer). – Schweigert & Kopka, p. 227, fig. 6A-E.

**Diagnosis:** Reference is made to Schweitzer & Feldmann (2008a: 138).

**Material:** A single, near-complete internal mould of a dorsal carapace (SNM-Z 36992), with part of the right metabranchial region and most of posterior margin missing. Measurements: maximum length = 7.6 mm; maximum width = 5.3 mm; W/L ratio 0.697.

**Locality and horizon:** The present specimen comes from the ammonite shell beds of the Štepnice Limestone Member (the Bohunice Formation) at Štepnická skala, the age of which is Middle Oxfordian (Transversianum Zone).

**Description:** Carapace longer than wide, widest just posterior to intersection to cervical groove and lateral margin; carapace vaulted longitudinally and transversely; regions smooth, well defined by relatively deep grooves (Fig. 2A).

Rostrum downturned, triangular, with broken tip; aur genest weakly rimmed (Fig. 2D), orbits directed more or less forwards. Lateral margins slightly sinuous, convex from position of outer orbital angle to intersection of cervical groove with lateral margin, convex between intersection of cervical and branchiocardioc grooves with lateral margins, diverging slightly posteriorly to posterolateral corner; intersections of grooves with lateral margins distinctly incised. Posterior margin not well preserved (Fig. 2A, B).

Epigastric regions slightly inflated, positioned at base of rostrum. Mesogastric region well defined, pyriform, widening considerably posteriorly. Metagastric and urogastric regions not visibly separated from each other due to imperfect preservation. Urogastric region defined laterally by arcuate grooves. Cardiac region broad anteriorly, narrowing posteriorly. Hepatic, epibranchial and branchial regions smooth, not differentiated, slightly inflated, well separated from each other by deeply incised cervical and branchiocardioc grooves.

Cervical groove sinuous, weakly concave forwards around base of mesogastric region. Branchiocardiac groove similarly shaped, becoming less deep and concave V-shaped around posterior margins of cardiac region. Both grooves extending onto lateral flanks. Postcervical groove rather shallow, slightly oblique, positioned more-less in the middle between cervical and branchiocardiac grooves.

Ventral surface and appendages not preserved.

**Remarks:** The species is characterised by its rectangular, strongly vaulted carapace; well-developed, slightly sinuous, almost transverse cervical groove; narrower and well-developed branchiocardiac groove; and well-delineated mesogastric region. Von Meyer (1860) reported the presence of three small tubercles in a triangular arrangement on the cardiac region and a small tubercle in the centre of the urogastric region, a unique feature among all species listed in von Meyer’s table 23. SNM-Z 36992 (Fig. 2A-D) is an internal mould (presumably a moult) of a dorsal carapace without any remains of the original cuticle preserved, which explains why the diagnostic tubercles cannot be seen. Schweitzer & Feldmann (2008a) noted that the mesogastric region equalled about 60 percent of maximum carapace width posteriorly. A quick scan of illustrations in the literature (e.g., Collins & Wierzbowski 1985: pl. 2, figs. 3-4; Wehner 1988: pl. 5, figs. 1-3; Garassino & Krobicki 2002: fig. 4/3a, re-illustrated here as Fig. 2C; Schweigert & Kopka 2011: fig. 6A-F) shows roughly the same configuration of the posterior margin of the mesogastric region and maximum carapace width. Our specimen appears to have a slightly narrower posterior margin of that region, which recalls that of the genus Gabriella (compare Schweitzer & Feldmann 2009c). This can be ascribed both to the mode of preservation (i.e., internal mould; compare with a much better-preserved conspecific specimen from small bioherms in the Dolina Szklarski Valley in southern Poland, Fig. 2E) and intraspecific variation. In all other morphological features, SNM-Z 36992 conforms to the emended description presented by Schweitzer & Feldmann (2008a). It shows a narrow, bilobed rostrum, the point of which is missing.
Collins & Wierzbowski (1985) described the rostrum tip as pointed and noted that it was missing in the specimen illustrated by von Meyer (1860: pl. 23, fig. 4). A photograph of the holotype has recently been published by Schweitzer & Feldmann (2008a: pl. 6, fig. A) and Schweigert & Kopka (2011: fig. 6).

The stratigraphic range of *Tanidromites insignis* is Middle Oxfordian to Latest Kimmeridgian (Collins & Wierzbowski 1985; Schweitzer & Feldmann 2008a; Schweigert & Kopka 2011); records include the Middle Oxfordian of the Kraków area (southern Poland) (Müller et al. 2000; Krobicki & Zaton 2008); and the Late Jurassic of southern Germany (von Meyer 1860; Wehner 1988; Schweitzer & Feldmann 2008a). The youngest record comes from the latest Kimmeridgian (Beckeri Zone, Ulmense Subzone) of southern Germany (Schweigert & Kopka 2011). The type horizon represents slightly spongiolitic limestones of the Early Kimmeridgian age in southern Germany (for details see Schweigert & Kopka 2011: 227; compare Schweitzer & Feldmann 2008a: 139).

Recently Schweigert & Kopka (2011: 227) syno-

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**Fig. 3.** Indeterminate chela sp. 1. A-D – Fragmentary left propodus with a broken fixed finger (SNM-Z 36993) and its interpretive drawing. Scale bar = 1 mm. E – Partial reconstruction of the same specimen (mesial view). F – Frontal view on the same specimen (note the cross section of the fixed finger).
nymized *Coelopus etalloni* Collins in Collins & Wierzbowski, 1985, once considered a distinct species of *Tanidromites* (Schweitzer & Feldmann 2008a: 140), with *T. insignis* (von Meyer, 1857). We concur.

The present specimen extends the geographic distribution of the species to the Western Carpathians.

**Indeterminate decapod crustacean remains:** Isolated fragments of chelipeds, which are not rare at localities where Tithonian limestones are exposed, in particular at Štramberk in the Czech Republic (P. Skupien pers. comm., September 2010) and Ernstbrunn in Austria (A. Kroh pers. comm., October 2010), have never been fully covered in the literature. It comes as no surprise that nearly all papers on Jurassic primitive brachyurans have so far focused solely on dorsal carapace morphology, because the classification of isolated cheliped fragments is fraught with difficulties. To date, but a single undoubted dromiacean dorsal carapace of *Pithonoton elongatum* (von Meyer, 1857) with associated chelae has been recorded (see von Meyer 1860: pl. 23, fig. 16). Schweitzer & Feldmann (2008a: pl. 3, fig. J) have recently published an English translation of von Meyer’s description and reproduced the figure of *P. elongatum* with chelae. In addition, there is one poorly preserved specimen identified as *Pithonoton* sp., from the Late Jurassic of Germany which retains remains of associated appendages (see Garassino et al. 2005). It should be noted, however, that Feldmann et al. (2006: 17) expressed doubts about the generic and familial assignment of that specimen. Two more specimens, representing two forms, both referred to as Prosopidae gen. et spec. indet., retaining the venter together with remains of pereiopods were described by Förster (1985) from Bajocian and Bathonian strata of Switzerland. However, neither of these preserve the dorsal carapace, making their classification a moot point. Several earlier workers (Quenstedt 1857; Étallon 1859; von Meyer 1860) recorded isolated cheliped fragments and referred these to the Prosopidae sensu von Meyer, 1860. Feldmann et al. (2006: 17) considered their association with carapaces as circumstantial and presented a fuller discussion of this issue, to which reference is made. Recently, Crónier & Bourricot (2009) have recorded several fragmentary chelipeds associated with carapaces of altogether three species, thus narrowing the possible affinities should these turn out to belong to one of these three.

The isolated chelae presented herein were collected from the same layer as the dorsal carapace of *Tanidromites insignis*. Unfortunately, they were not found in direct association with the carapace; consequently, it is not possible to assign them to any decapod group with confidence.

**Indeterminate chela sp. 1**

*Fig. 3A-F*

**Material:** One fragmentary left propodus with a broken fixed finger (SNM-Z 36993). Measurements: maximum length of manus = 3.1 mm (incomplete); maximum height of manus = 2.4 mm.

**Description:** Left propodus with a broken tip of the fixed finger, length exceeding height (height 70 percent of length); more strongly convex on outer than on inner surface. Proximal articulation not well preserved. Outer surface covered with very faint longitudinal ridges composed of tiny tubercles. Fixed finger short, its length 30 percent of that of manus, the outline preserved only as an imprint, which was lost during the preparation. Cross section of fixed finger weakly triangular, occlusal surface flat with no teeth or other armature preserved.
Remarks: SNM-Z 36993 (Fig. 3) is superficially similar to chelae found in Oxfordian sponge bioherms of Dobrogea in Romania, referred to as Indeterminate chela sp. 1 by Feldmann et al. (2006: 17, figs. 3.7-3.9). The general shape of the propodus of form A described by Förster (1985: 50, text-fig. 3) and also that described by Garassino et al. (2005) match those from Romania and Slovakia as well. Our specimen, however, exhibits very faint tuberculated ridges on the outer surface (Fig. 3B). Its preservation as an internal mould with poorly preserved cuticular surface precludes a more detailed comparison.

Indeterminate chela sp. 2
Fig. 4A-C

Material: One fragmentary right propodus (SNM-Z 36994), of which the upper margin is missing. Measurements: maximum length of manus = 5.7 mm; maximum height of manus = 3.5 mm (incomplete).

Description: Fragmentary right propodus with almost complete fixed finger embedded in limestone, length exceeding height, upper margin broken off. Proximal articulation poorly preserved, oblique to long axis of manus. Lower margin straight, slightly concave at articulation with fixed finger. Outer surface covered with up to 5 longitudinal ridges composed of tiny tubercles. Tubercles rounded, close set. Fixed finger relatively long, its length approximately 50 percent that of manus, the tip is broken off; occlusal surface with no apparent armature preserved.

Remarks: This specimen resembles the cheliped fragments described and illustrated by Crónier & Boursicot (2009: 1284, pl. 2, figs. 12-18) from the Early Callovian of NW France. Tubercles on the outer surface of the propodus, however, are set more densely and are more numerous, and the concavity of the lower margin at the base of the fixed finger is stronger in SNM-Z 36994 (Fig. 4). Interestingly, one of the brachyuran species found in association with those chelipeds is Tanidromites montreuilense Crónier & Boursicot, 2009, a congener of T. insignis recorded in the present note. Crónier & Boursicot (2009) compared their chelipeds to those of the extant homolodromioid Dicranodromia A. Milne-Edwards, 1880 suggesting their possible affinities. The association of species of Tanidromites with roughly the same cheliped morphotype reported herein might speak for assignment of indeterminate chela sp. 2 to that genus. However, without any direct evidence, such conclusions might be misleading. Moreover, the insufficient preservation and fragmentary nature of the specimen do not allow further speculations.

Remains of uncertain affinity

Material: several exoskeletal fragments apparently coming from a crustacean (deposited under the collective number SNM-Z 36995). The poor state of preservation and fragmentary nature of these specimens preclude any finer assignment or comparison.

5. Discussion

The material from the Štepnická skala is regarded to be of great significance. Several points are important to consider: first, the material stems from a non-reefal/biothermal facies; secondly, it is of Oxfordian age, when microbial-sponge and coral megafacies were widespread in Europe, but was not collected from such an environment; and thirdly, it comes from the Pieniny Klippen Belt (part of the Western Carpathians) which constituted a palaeogeographically different area during the Late Jurassic than that from which all previously reported primitive Jurassic brachyurans come. The implications are further discussed below.

Jurassic dromiaceans from non-biothermal facies: Concerning the presence of Jurassic dromiaceans in non-reef/biothermal facies, they are known predominately from the Lower and Middle Jurassic; an overview was presented by Krolicki & Zaton (2008: table 1). However, most remains of primitive brachyurans of the Jurassic age appear bound to organic facies, their greatest abundance during the Late Jurassic being correlated with the expansion of sponge and coral reefs along the northern margin of Tethys in Europe (see Wehner 1988; Via & Sequeiros 1993; Müller et al. 2000; Feldmann et al. 2006; Schweitzer et al. 2007a, b; Krolicki & Zaton 2008; Franteescu 2011). So far only a few occurrences of Late Jurassic brachyurans were reported as coming from non-reef/biothermal facies (Garassino et al. 2005; Karasawa & Kato 2007; Kato et al. 2010). They deserve more attention here, as we do not consider them to represent unambiguous occupants of non-reef/biothermal palaeoenvironments.

Although Garassino et al. (2005) recorded several primitive crabs, i.e., Pithonoton marginatum, Goniodromites cf. serratus Beurlen, 1929 and Pithonoton sp. (compare Feldmann et al. 2006: 17) from the Late Jurassic (Kimmeridgian/Tithonian boundary beds) Solnhofen-type lithographic limestones of southern Germany, these originate from limestones quarried at Pfalzpaint and Breitenhill which were deposited close to coral reefs (see Garassino et al. 2005: fig. 1). Specimens most likely represent exuviae that were transported to their final place of burial (G. Schweigert pers. comm., February 2011). Brachyuran remains in Solnhofen-type limestones are otherwise extremely rare (Schweigert 2007: 87; Schweigert 2011: 132).

Lately several Late Jurassic primitive crabs have been described from Japan, beyond Tethys: Goniodromites hirotai Karasawa & Kato, 2007; Goniodromites sakawense Karasawa & Kato, 2007; Pi-
**Tanidromites insignis** (von Meyer, 1857) (Crustacea: Decapoda: Brachyura)

thonoton iyonofutanajima Karasawa & Kato, 2007, *Planoprosopon* sp. (originally described as *Nodoprosopon* sp.) (Karasawa & Kato 2007) and *Planoprosopon kashimaensis* Kato, Takahashi & Taira, 2010 (Kato et al. 2010). All these species were collected from clastic rocks, i.e., the first four from shales of the Middle Tithonian age (Yatsuji Formation) and the last-named from fine- to medium-grained calcareous sandstones of the Late Kimmeridgian-Early Tithonian age (uppermost Tatenosawa Formation). These occurrences, however, cannot be undisputedly considered as remains of inhabitants of non-reefal environment.

Fauna from the Tatenosawa Fm. was collected directly below the Koike Limestone Member which contains also biothermal limestones (Sato & Takei 2008; KakiZaki & Kano 2009). In this case, the onset of biothermal facies, although controlled by occurrences of some ammonites, is not stratigraphically precise because both A3 and A4 ammonite faunas of Sato & Takei (2008) contain Late Kimmeridgian and Early Tithonian ammonites. The A3 fauna was collected from the uppermost Tatenosawa Sandstone Member, and the A4 fauna stems from the base of the Koike Limestone Member. Contrary to the statement of the authors, the Tithonian genus *Virgatosphinctes* Uhlíř, 1910 occurs in both intervals and not only in
the A4 fauna (see SATO & TAKETANI 2008: 368 for the lists of ammonites occurring in A3 and A4 faunas). We presume that the facies boundary between Koike Lm. Mb. and underlying Tatenosawa Sandstone Mb., from which topmost layers decapod fauna has been collected (KATO et al. 2010), may not be necessarily isochronous in the whole area (KIYAMA & IRYU 1998; SATO & TAKETANI 2008; KATO pers. comm., May 2011) and some lateral shift between the facies cannot be completely ruled out (compare KIYAMA & IRYU 1998: fig. 3).

Decapod fauna from the Yatsuji Fm. comes from the carbonate-fine siliciclastic unit comprising also reef facies (Torinosu Limestone; see KANO & JIU 1988; SHIRASHI & KANO 2004). One of the authors of the case study (KARASAWA & KATO 2007) confirmed the presence of close reefal facies as well as the possible transport of dromiacean carapaces from this facies to siliciclastic deposits from which the fauna has been collected (KARASAWA pers. comm., March 2011). The preservation of both discussed assemblages indicates at least a short transport (compare KARASAWA & KATO 2007: figs. 1-7; KATO et al. 2010: text-fig. 6).

Tanidromites insignis from the Pieniny Klippen Belt noted here comes from ammonite shell beds and we consider it to be autochthonous or parautochthonous. The fact that it was preserved at all suggests transport over only a short distance. Oxfordian strata at the locality studied belong to the shallower development of the so-called Czorsztyn Succession which was laid down on a former pelagic carbonate platform, the Czorsztyn Ridge (Fig. 5); it represents the shallowest depositional environment within the Pieniny Klippen Basin at that time (BIRKENMAJER 1977; TOMAŠOVYCH & SCHLOGL 2008; see also AUBRECHT et al. 2002; AUBRECHT & JAMRICOVÁ 2009). No reefal/biothermal facies are known from the entire Upper Jurassic in this area (BIRKENMAJER 1977). Within adjacent basins (Magura Basin in the northwest and the Pieniny Basin in the southeast), deposition of deep-sea radiolarites occurred (BIRKENMAJER 1977; WIDZ 1992; MIŠÍK 1999).

Upper Jurassic occurrences of non-reefal/biothermal brachyurans are known from the entire Upper Jurassic in this area (BIRKENMAJER 1977). Within adjacent basins (Magura Basin in the northwest and the Pieniny Basin in the southeast), deposition of deep-sea radiolarites occurred (BIRKENMAJER 1977; WIDZ 1992; MIŠÍK 1999).

Upper Jurassic occurrences of non-reefal/biothermal brachyurans (GARASSINO et al. 2005; KARASAWA & KATO 1997; KATO et al. 2010) discussed above are questionable at best; moreover, they are distinctly younger (i.e. of Kimmeridgian or Tithonian age) than the Middle Oxfordian material presented herein.

**Palaeoecology of dromiaceans during the Oxfordian**: Tethyan sponge and coral reefs were widespread mostly during the Oxfordian, when they abound in the so-called microbial-sponge and coral megafacies. Later, during the Tithonian/Berriasian, mass-occurrences of dromiacean crabs are widely reported, in particular from the so-called Štamberk- and Ernstrbrunn-type coral-bearing limestones (for an overview of the distribution of both facies types see MÜLLER et al. 2000 and KROBICKI & ZATOŃ 2008; see also UNGUREANU & BARBU 2004).

During the Oxfordian, coral reefs were rather rare, contrary to microbial-sponge builds and dispersed on the carbonate platform of the northerly margin of the Tethys. Several occurrences of Oxfordian coral limestones with known primitive brachyuran remains are those of the Stránska skála outcrop near Brno in the Moravian part of the Czech Republic (OPPENHEIMER 1928; ELIAŠ & ELIAŠOVÁ 1984) and in Central Dobrogea of Romania (FELDMANN et al. 2006; SCHWEITZER et al. 2007a, b; FRÂNTESCU 2011), and coral/ microbial reefs of the northern Paris Basin (BERTLING & INSALACO 1998).

Contrary to all previously reported Oxfordian primitive brachyurans, the material described here comes from non-reefal/biohermal facies, which is rather unusual but not completely unexpected as it seems that the family Tanidromitidae was a eurytopic taxon. As far as the ecological preference of the genus Tanidromites is concerned, SCHWEITZER & FELDMANN (2008a) already noted that it probably tolerated low oxygen levels (bedded limestone environments, sponge-algal reefs). Its ecological preferences obviously were relatively broad, because it is known from several markedly different facies types. The oldest representatives of the genus, *T. richardsoni* (WOODWARD, 1907) from the Late Bajocian of England, *T. montreuilense* from the Early Callovian of France, and *T. lithuanicus* SCHWEITZER & KOPPKA, 2011 from the Middle Callovian of Lithuania, are all from shallow-water iron-oolithic limestones or red-brown sandstones with iron-oolithic calcareous sandstone intercalations (WOODWARD 1907; CRÔNIER & BOURSICOT 2009; SCHWEITZER & KOPPKA 2011). To date, *T. insignis* has been collected mostly from Oxfordian Peri-Tethyan sponge megafacies limestones, although the holotype comes from the Lower Kimmeridgian slightly spongiolithic limestones (SCHWEITZER & KOPPKA 2011: 227). Here presented material of *T. insignis* is the first report of the species from facies completely different from all previous occurrences (Fig. 5) and, thus, it is remarkable.

**Palaeobiogeographical implications**: The *Tanidromites* specimen noted herein constitutes the first oc-
currence of the Upper Jurassic dromiacean beyond the Northern margin of the strictly Tethys Ocean Realm. Localities with all reported occurrences of *T. insignis* are summarized in Fig. 5. As noted above, in basins adjacent to the Czorsztyn Ridge deep-sea radiolarites occurred. For this reason, and despite the fact that the connection between the Peri-Tethys and Tethys oceans was fully marine at the time (GOLONKA et al. 2006), the discovery of a member of the Tanidromitidae is surprising considering the place (and also time of occurrence as discussed above). Such deep-marine settings could have acted as physiographic barriers against easy migration of marine faunas, thus limiting their dispersion, especially in non-reefal/biothermal palaeoenvironments. This is even more remarkable because this species represents an accessory element in crustacean assemblages recorded from Oxfordian strata of the Peri-Tethys basins. At the abandoned Zakrzówek quarry (Kraków city area, southern Poland) *T. insignis* accounts for 13.6 percent of all crab remains, and in the Franconian Alb (Biburg area, southern Germany) for only 0.8 percent (see MÜLLER et al. 2000; and WEHN 1988, respectively).

**6. Conclusions**

The material presented herein allows the following conclusions to be drawn. First, the *Tanidromites insignis* specimen, despite its Oxfordian age, is not bound to the microbial-sponge or coral megafacies; moreover, it seems to be the only reported occurrence of an Upper Jurassic dromiacean undoubtly coming from non-reefal/biothermal deposits. Secondly, it broadens the presumed ecological preferences of the species and supports the thesis of the Tanidromitidae as a eurytopic taxon. It therefore seems that primitive brachyurans regarded in the past as a homogeneous group (e.g. GLAESNER 1969) but now revealed to be of a polyphyletic nature (see above), were heterogeneous, at least in part, also ecologically. They most likely represent a mixture of more or less distinct groups ranging from taxa tightly bound to reefal environments to those with a wider ecological tolerance. Thirdly, the *Tanidromites* specimen is the first documented occurrence of its kind in the Pieniny Klippen Belt and from the area of the Western Carpathians as well. The paucity of Jurassic decapod crustaceans in the Pieniny Klippen Belt can be explained as follows. First of all, occurrences of biothermal facies are very limited in this area, being known virtually only from the Early Bajocian (SCHLÖGL et al. 2006). Most late Middle and Late Jurassic facies reflect condensed sedimentation and are simply not conductive to preservation of delicate cuticular structures. Additionally, virtually no attention was paid to small crustacean fossils in this area until very recently. More finds may be expected, because another locality exposing Jurassic strata in the Pieniny Klippen Belt with crustacean remains is known to the authors (see HYŽNY & SCHLÖGL 2009: 62). In general, more extensive sampling is needed in order to obtain relevant material. A good collecting method for such small pieces was described by MÜLLER (1984: 35); it was successfully applied also by MÜLLER & COLLINS (1991). More future research on decapod crustaceans of the Pieniny Klippen Belt is desirable.

**Acknowledgements**

We thank RENÉ H.B. FRAAJJE (Oertijdmuseum De Groene Poort, Boxtel, the Netherlands) for assistance during field work, RODNEY M. FELDMANN and CARRIE E. SCHWEITZER (Kent State University, Ohio, USA) for providing items of literature, and JOHN W.M. JAGT (Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands) for correcting English of the draft. Thanks also to reviews of GÜNTER SCHWEIGERT (Staatliches Museum für Naturkunde, Stuttgart, Germany) and CARRIE E. SCHWEITZER. We would like to express a special thank to the latter reviewer for her constructive criticism and further suggestions. This research was funded by APVV 0248-07 (MH & JS), APVV 0280-07 (MH & JS) and AGH grant 11.11.140.447 (MK).

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