Decapod crustaceans from the type area of the Helvetian Stage (lower Miocene) in the Bern area, Switzerland

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Abstract

Material collected recently from temporary excavations at the Belpberg near Bern, in the type area of the – now obsolete – Helvetian Stage, allows new data on decapod crustacean faunules from the Upper Marine Molasse of Burdigalian (early Miocene) age to be presented. The comparatively rare and rather poorly preserved, yet fairly diverse, assemblages comprise two thalassinideans (*Pestarella* sp., *Ctenocheles* sp.), an indeterminate paguroid anomuran, as well as three species of brachyuran, *Glebocarcinus helveticus* n. sp., *Portunus* sp. and *Necronectes*? sp. The present material documents fossil representatives of the genera *Pestarella* Ngoc-Ho, 2003 and *Glebocarcinus* Nations, 1975 from Europe for the first time.

Key words: Crustacea, Decapoda, Miocene, Burdigalian, Upper Marine Molasse, Switzerland, new species

Introduction

The Upper Marine Molasse unit at the Belpberg, south of Bern (Switzerland; see Fig. 1), of early Miocene (Burdigalian) age, was laid down in the perialpine Molasse Basin (Pfister & Wegmüller, 1994), in the transitional area between the western Paratethys (Rhône Basin, France) and the central Paratethys in the east. Distinguished within the series of Burdigalian age in the study area, the type area of the Helvetian Stage (now obsolete), are the Sense Beds at the base of the Upper Marine Molasse, the Belpberg Beds and, finally, the Niedermatt Beds (Gruner, 2001) (Fig. 2).

Ever since Ritter (1742), the fossil-rich Belpberg Beds have featured prominently in a number of palaeontological and geological studies. B. Studer (1825), Bachmann (1867) and Kissling (1890) described fossil faunas from the area around Bern and also noted decapod crustacean remains. At the time, Rutsch (1928) presented the most thorough palaeontological and geological study of the Belpberg strata. More recently, bivalve and gastropod faunas from the Belpberg Beds (*sensu stricto*) have been described in detail by Pfister & Wegmüller (1994, 1998, 1999, 2000, 2001, 2007a, b), echinoids by Kroh & Menkveld-Gfeller (2006), bryozoans by Vávra & Pfister (in press) and balanoid cirripedes by Carriol & Menkveld-Gfeller (in press).

As far as decapod crustaceans are concerned, T. Studer (1892, 1896, 1898), Rutsch (1928) and Bachmayer & Rutsch (1962) recorded several species from different localities at the Belpberg. It should be noted that their material came from the fossil-rich sediments in the area

which were referred to as the Belpberg Beds. Initially, these included a wider range of lithostratigraphic units (Rutsch, 1926), but in modern terminology (Rutsch & Schlüchter, 1973), the Belpberg Beds (*sensu stricto*) comprise only the 'Muschelsandstein beds', 'Petrefactenlager' and 'Utzigen Beds' (Fig. 2). The decapod crustacean faunules described below originate from these 'restricted' Belpberg Beds. Gruner (2001) characterised the lithology of the Belpberg Beds *sensu stricto* as a fineto medium-grained sandstone, rich in mica, with intercalated marly layers and/or conglomerates. Rapid facies changes are typical, and the thickness of the Belpberg Beds *sensu stricto* varies between 250 and 300 metres; the unit shows a tendency to decrease in thickness towards the northeast. Interpretations of sedimentary settings by Schoepfer (1989) and Pfister & Wegmüller (1994) suggest deposition within a storminfluenced delta front, ranging into protected shallow-water, prodelta bay environments.

Gruner (2001) dated these beds as middle Burdigalian. For a more detailed discussion on the age of the Belpberg Beds, and on the 'Helvetian Stage', reference is made to Harzhauser *et al.* (2003), while a more general overview of the lithostratigraphy and palaeogeography of the Swiss Molasse was presented by Berger *et al.* (2005a, b).

In Miocene Molasse strata of Switzerland, decapod crustaceans are comparatively rare. The first to record such from the Upper Marine Molasse was Mayer-Eymar (1872); unfortunately, he failed to provide descriptions and illustrations of this material. New 'Helvetian' taxa named by him are: *Astacus lucernensis, Cancer rietmanni* and *Lupea dubia*. The first two possibly came from the Helvetian proper, in the area between Rotsee and St. Gallen, while the last-named is of unknown provenance, but possibly came from the 'Aargauer Molasse' near St. Gallen. Already two decades later, the whereabouts of these specimens were unknown (T. Studer, 1892); the names have subsequently been considered to be *nomina nuda* by Bachmayer & Rutsch (1962, p. 676) and rightly so. T. Studer erected three new species of crab from the type area of the Helvetian Stage, south of Bern, as follows:

- Dorippe fankhauseri T. Studer, 1892 (p. 6, pl. 1, figs. 1–4), from the 'Petrefactenlager' at Hohburggraben, Belpberg [see also Bachmayer & Rutsch, 1962, pl. 2, fig. 1]; holotype is a carapace (NMBE Ho 1);
- Portunus kisslingi T. Studer, 1892 (p. 8, pl. 1, figs. 5–7), collected *ex situ*, but probably from the 'Petrefactenlager' at Marchbachgraben, Belpberg [see also Bachmayer & Rutsch, 1962, pl. 2, fig. 2]; holotype is a right major cheliped (NMBE Ma 2);
- Atelecyclus tiechei (T. Studer, 1898) (p. 1, pl. 1, figs. 1–6) [= A. tièchi T. Studer, 1896, p. xii, nomen nudum], from the 'Tapeslager' at Marchbachgraben, Belpberg [see also Bachmayer & Rutsch, 1962, pl. 1, fig. 1]; lectotype is a partial carapace (NMBE Ma 1).

More than sixty years later, Bachmayer & Rutsch (1962, p. 678, pl. 3, figs. 1, 2; holotype is a female carapace with major chelipeds preserved,

NMBE Ho 2) described another new species from the Belpberg near Bern, *Macropipus gruneri*, and revised species described by T. Studer. Here we add two specifically indeterminate species of thalassinidean, a single indeterminate paguroid anomuran and three species of crab, one of which is new.

To denote the repositories of specimens illustrated or referred to below, the following abbrevations are used: MNHN, Muséum national d'Histoire naturelle, Paris; NMBE, Naturhistorisches Museum Bern, Bern.

Material studied

In 2003, the Naturhistorisches Museum Bern sent on loan to the senior author, the twenty-five best-preserved decapod crustacean remains (out of c. 100 specimens) collected subsequent to publication of the paper by Bachmayer & Rutsch (1962). The new material was collected from the localities Aarwald, Cheergraben, Chramburgwald and Hohburggraben at the Belpberg near Bern (Fig. 1). The decapod crustaceans from the Burdigalian Upper Marine Molasse at the Belpberg originally were part of the A. Klee and B. Hostettler collections, and some came from excavations executed by NMBE staff at other localities at the Belpberg (Fig. 1). The preservation of these remains is rather poor



Fig. 2. Simplified geological map of the study area, showing the various localities which yielded the decapod crustacean material described herein; 1 – Chramburgwald; 2 – Hohburggraben; 3 – Aarwald; 4 – Cheergraben (modified after Pfister & Wegmüller, 1994; Kellerhals *et al.*, 1999).

	Niedermatt Beds		
Upper Marine Molasse (OMM)	(della Valle 1965)		
	Belpberg Beds sensu lato (Rutsch 1926)	Sädel Conglomerate (Rutsch 1928)	
		Belpberg Beds sensu stricto (Rutsch & Schlüchter 1973)	Utzigen Beds (Gerber 1926) with Muschelsandstein (Rutsch 1926) and "Petrefactenlager" (Studer 1825) Upper Muschelsandstein (Gerber 1926) and/or
			Conglomerate with Oysters
		Bütschelbach Conglomerate (Rutsch 1967) and/or Lower Muschelsandstein (Gerber 1926)	
	Sense Beds (Rutsch 1967)		

Fig. 2. Lithostratigraphy of the Upper Marine Molasse in the study area, with pertinent references (modified from Gruner, 2001).

on account of intense 'decalcification', which has left only 'powdery casts' in a silty to sandy matrix. This state of preservation also explains why specific identification is difficult, if not impossible, in particular of thalassinidean and brachyuran taxa.

Systematic palaeontology

Infraorder Thalassinidea Latreille, 1831 Superfamily Callianassoidea Dana, 1852 Family Callianassidae Dana, 1852 Subfamily Callianassinae Dana, 1852

Genus Pestarella Ngoc-Ho, 2003

Type species: Astacus tyrrhenus Petagna, 1792, by original designation.

Pestarella sp.

(Pl. 1, Fig. 1)

Material: A single left propodus, with an incomplete fixed finger (NMBE B9052), from the locality Aarwald (Holzerweg), Belpberg near Bern.

Description: Palm length exceeding width, greatest width 7 mm; length, inclusive of fixed finger, 17 mm; articulation with carpus straight and about 90 degrees, slightly convex longitudinally and more strongly so transversely; upper margin of palm smooth and slightly convex, lower margin smooth, slightly convex proximally and concave distally; a row of very fine granules present at base of dactylus. Dactylus curved, longer than fixed finger, tip more strongly curved; longitudinal groove in upper half of finger, but this could be taphonomically induced. Major portion of fixed finger not preserved, but imprint shows it to have been elongated, triangular, slightly curved; shorter than dactylus, with pronounced grooves centrally on inner and outer sides; no teeth on cutting edges preserved, but halfway, a triangular elevation is seen. *Discussion*: Ngoc-Ho (2003, p. 475) erected the genus *Pestarella* to accommodate five extant callianassine shrimps, three European (Mediterranean) in distribution, one from Senegal and one from South Africa. The European species occur mainly in intertidal to subtidal, muddy bottoms. Our assignment of the Belpberg form to this Recent genus is based on the combination of a convex upper margin, a concave depression on the lower margin halfway the palm and the curvature of the relatively slender fingers. Without better-preserved material, this form cannot be specifically identified and compared in detail with extant taxa.

Family Ctenochelidae Manning & Felder, 1991 Subfamily Ctenochelinae Manning & Felder, 1991 Genus *Ctenocheles* Kishinouye, 1926

Type species: Ctenocheles balssi Kishinouye, 1926, by original designation.

Ctenocheles sp.

(Pl. 2, Fig. 6)

Material: A right cheliped consisting of articulated ischium, merus, carpus and propodus, and a second, incomplete merus (NMBE D3171; leg. T. Pfister), from the locality Hohburggraben, Belpberg near Bern.

Description: Ischium incomplete, transversely oval; merus 25 mm in length, greatest width 7 mm, outer face strongly convex and covered with a longitudinal, more or less regular line of seven pustules bordered by a parallel, scabrous band with setal pits; other merus, incomplete, shows only slightly convex, smooth surface covered with two longitudinal, parallel lines of setal pits; carpus heavily damaged, greatest length 11 mm, greatest width 7 mm; palm very bulbous, smooth, greatest length to base of dactylus 20 mm, greatest width 14

mm; major portions of dactylus and fixed finger missing; base of fixed finger oriented downwards.

Discussion: At first glance, NMBE D3171 would suggest affinities with the nephropoid genera *Oncopareia* Bosquet, 1854 and *Thaumastocheles* Wood-Mason, 1874 (see Tshudy & Babcock, 1997; Chan & de Saint Laurent, 1999; Tshudy & Sorhannus, 2000, 2003). However, the downward orientation of the fixed finger (see Tshudy & Sorhannus, 2000, table 1) favours assignment of the present form to the callianassoid *Ctenocheles*.

Infraorder Anomura MacLeay, 1838 Superfamily Paguroidea Latreille, 1802

Indeterminate paguroid

(Pl. 1, Fig. 2)

Material: A single incomplete, short (6 mm) finger (NMBE D2818) from the locality Hohbruggraben, Belpberg near Bern.

Description: Dark-coloured, broken-off tip of finger; upper cutting edge with a row of four or five small nodes, increasing in width proximally, and followed by a large node and two adjacent perpendicular ones; remainder of finger not preserved.

Discussion: This tip bears a close resemblance to that of the fixed finger of *Pagurus alatoides* Philippe & Secretan, 1971 (p. 130, fig. 2b) from lower Miocene (Burdigalian) strata of Courennes, Vaucluse (France).

Infraorder Brachyura Linnaeus, 1758 Section Heterotremata Guinot, 1977 Family Cancridae Latreille, 1802 Genus *Glebocarcinus* Nations, 1975

Type species: Cancer oregonensis Rathbun, 1898, by original designation (Nations, 1975, p. 22, as subgenus of *Cancer* Linnaeus, 1758).

Glebocarcinus helveticus n. sp.

(Pl. 1, Fig. 3)

Type: Holotype, and single specimen known, is a near-complete carapace (NMBE D1854) collected by B. Hostettler on 13 June 2002, from the Hohburggraben, Belpberg near Bern; Belpberg Sands (*sensu stricto*), Upper Marine Molasse, Burdigalian (lower Miocene).

Derivation of name: In reference to the country of origin.

Description: Carapace of average size for the genus (greatest width and length 23 and 18 mm, respectively), wider than long, very globose in transverse and oblique sections, highest elevations occupying the protogastric, inner mesobranchial and mesogastric lobes. Carapace with well-defined regions, surface evenly covered with fine granules. Central orbitofrontal area damaged, inner orbital spine twice the size of outer orbital one. Proterogastric, hepatic, inner and outer mesobranchial regions all strongly convex and bearing a central large granule; broad, slightly convex, urogastric region; triangular cardiac region bordered by small triangular metabranchial regions and covered anteriorly with a ridge, interrupted medially. Convex anterolateral margin covered with six flat, triangular and forwardly curved spines. Concave posterolateral margin covered with four rimmed spines, the anteriormost one equal in size to ones on anterolateral margins, other three strongly decreasing in size posteriorly.

Discussion: Two extant species of *Glebocarcinus* are known, both restricted in their distribution to the North Pacific, *G. oregonensis* (Rathbun, 1898) (see Pl. 1, Fig. 4) having been recorded from Alaska to California and *G. amphioetus* (Rathbun, 1898) (see Pl. 1, Fig. 5) from China, Korea, Japan, California and Baja California (Schweitzer & Feldmann, 2000a, p. 235). Morphologically, the new species is closer to *G. oregonensis*.

Other species originally referred to *Cancer (Glebocarcinus)* by Nations (1975, pp. 22, 23), such as *C. (G.) tumifrons* Yokoya, 1933 and *C. (G.) balssi*, have now been transferred to and synonymised with, *Anatolikos* Schweitzer & Feldmann, 2000a and *Platepistoma anaglyptum* (Balss, 1922), respectively. *Cancer allisoni* Nations, 1975 (p. 51, figs. 29, 30/3, 4), known only from middle Miocene–upper Pliocene of Oregon and California, is based on fragmentary chelipeds that cannot be assigned to genus unequivocally.

Karasawa (1990, pp. 7–11, pl. 1, figs. 4, 7, 10, 13, 14) recorded two new species, *Cancer* (*Glebocarcinus*) *itoigawai* and *C*. (*G.*) *kaedei*, both from the lower Miocene Yamanouchi Member, Akeyo Formation in Gifu Prefecture, Japan. The latter was later transferred to the genus *Platepistoma* Rathbun, 1906 by Karasawa (1993, p. 49, pl. 9, figs. 4–6), while the same author added *C*. (*G.*) *amphioetus* from the upper Pliocene Dainichi Sand, Kakegawa Group. Subsequently, Karasawa (1997, p. 45, pl. 11, fig. 2) showed this record of *G. amphioetus* to be based on a single movable finger from the Pliocene of Japan, which could not substantiate the fossil record of this extant species. Schweitzer & Feldmann (2000a, p. 229) transferred the species *itoigawai* to their new genus, *Anatolikos*. Those authors postulated an origination of *Glebocarcinus* in the North Pacific Ocean and subsequent dispersal in that general area; the genus apparently was never speciose.

Moths (2005, p. 87, fig. 10) illustrated a specimen from Burdigalian strata in northern Germany, questionably assigned to *Tasadia carniolica* (Bittner, 1884) (see also Janssen & Müller, 1984). The length-width dimensions and general carapace morphology of this specimen resemble *Glebocarcinus* as here understood.

Superfamily Portunoidea Rafinesque, 1815 Family Portunidae Rafinesque, 1815 Subfamily Portuninae Rafinesque, 1815

Genus Portunus Weber, 1795

Type species: Cancer pelagicus Linnaeus, 1758, by subsequent designation of Rathbun (1926).

Portunus sp.

(Pl. 2, Figs. 2-5)

Material: Three specimens (NMBE D3173 [Cheergraben, Belpberg, 0.15 m above 'Tapeslager'], NMBE B4761 and B4767 [part and

counterpart of a single specimen; Cheergraben, Belpberg, 'Tapeslager'] and NMBE A5542 [same provenance]).

Description: Small-sized hexagonal carapace, slightly wider than long (length/width ratio about 0.85), greatest width at last anterolateral spines. Front broken, width approximately equal to that of orbit; orbits wide and directed forwards. Carapace regions well defined, convex anterolateral margin covered with several small spines and very large, laterally directed last anterolateral spines, situated below mid-length. Long and narrow mesogastric process; protogastric region inflated; epibranchial region forming arcuate ridge from largest anterolateral spine to mesogastric. Mesobranchial and metabranchial regions not differentiated; branchial region inflated and covered with granules. Cardiac region slightly inflated, with longitudinal, central depression. Posterolateral margin straight, interrupted by very large, concave depression for joint with last swimming leg. Very broad, straight and slightly rimmed posterior margin. Chelipeds with elongated merus; carpus short, chela keeled, fingers long. Sternal plate flat, oval; sutures straight, directed centrally and well defined; sternite 4 with distinct medial depression. Male abdomen triangular.

Discussion: The rather poor state of preservation of these specimens precludes definite specific assignment. Overall, they show similarities to both Portunus and Portunites Bell, 1858. The former is characterised by a carapace which is much wider than long, has about eight spiniform, anterolateral teeth, a long epibranchial spine, a straight and wide (i.e., wider than the front) posterior margin and a flattened dorsal surface. The merus of the cheliped typically is very long and much wider than the carapace, the carpus not touching the anterolateral margins, and the hand is keeled and fingers are long. Portunites has a carapace which is slightly wider than long, the anterolateral margin having four or five saw-like teeth, the last (epibranchial) tooth being not enlarged, the posterior margin weakly concave and of the same width as the front, and the dorsal surface areolated. The branchial region has a longitudinal ridge, usually with tubercles on either side (Schweitzer & Feldmann, 2000b, p. 637). The merus of the cheliped is not much elongated, the carpus in contact with the anterolateral margin, while the hand is smooth and the fingers are rather short.

In the material studied, the carapace width does not appears to exceed the length. The anterolateral margin is too poorly preserved to allow clear observations, but the epibranchial spine is clearly produced, the dorsal surface of the carapace flattened, lacking branchial ridges or tubercles, and the posterior margin broad (Pl. 2, Fig. 5). The merus of the cheliped is long, the hand keeled, and the fingers straight and long (Pl. 2, Fig. 2). For this reason, we prefer placement in *Portunus*.

While *Portunites* appears to be confined to strata of Eocene age (Schweitzer & Feldmann, 2000b, p. 638), members of the genus *Portunus* were widely distributed and abundant in Miocene strata in central and southern Europe.

Genus Necronectes A. Milne-Edwards, 1881

Type species: Necronectes vidalianus A. Milne-Edwards, 1881, by original designation.

Necronectes? sp.

(Pl. 2, Fig. 1)

Material: A single, incomplete chela (NMBE D2814), from the locality Cheergraben, Belpberg near Bern.

Description: Preserved is the inner aspect of a portion of a right chela; fixed finger straight, triangular, curved and uniformly covered by flattened granules; inner side with two parallel grooves; cutting edge not visible; darker-coloured tip curving upwards; dactylus more slender than fixed finger, with flattened granules and two parallel grooves; distal half of cutting edge with four to five small nodes, proximal half with two large nodes; cutting edge and tip of darker colour, the latter curving downwards.

Discussion: In curvature and ornament, these fingers differ significantly from those of *Macropipus kisslingi* (Studer, 1892), and in view of size, curvature and ornament they cannot be assigned to *Portunus* sp. in the same faunules (see Pl. 2, Fig. 2).

Conclusions

In their revision of the decapod crustacean fauna of the Upper Marine Molasse at the Belpberg, Bachmayer & Rutsch (1962) listed four species, *Dorippe fankhauseri* (T. Studer, 1892), *Atelecyclus tiechei* (T. Studer, 1898), *Macropipus kisslingi* (T. Studer, 1892) and *M. gruneri* Bachmayer & Rutsch, 1962. Of these, only *D. fankhauseri* and *M. gruneri* are based on more or less complete carapaces, while the generic placement of '*Atelecyclus' tiechei* and '*Macropipus' kisslingi* is far from clear, the former being based on an incomplete venter and the latter only on a propodus with dactylus, which, in our view, would seem to have cancroid affinities.

In the Belpberg faunules, portunids predominate, and their cooccurrence with callianassoids, paguroids, dorippids and ?atelecyclids is strongly reminiscent of other Miocene faunas in Europe, such as the ones described from the Plateau des Courennes (Philippe & Secretan, 1971) and Pignan (Artal & Gilles, 2007) both in southeast France, and the Fore-Carpathian Depression of southern Poland (Förster, 1979a, b).

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Plate 1

Early Miocene (Burdigalian) decapod crustacean taxa from the type area of the Helvetian Stage, Belpberg near Bern, Switzerland. Scale bars represent 10 mm (figs 1, 3) and 5 mm (fig. 2).

- 1. Pestarella sp., NMBE B9052.
- 2. indeterminate paguroid, NMBE D2818.
- 3. Glebocarcinus helveticus n. sp., holotype, NMBE D1854.
- 4. Glebocarcinus oregonensis (Rathbun, 1898) (male specimen), Recent, north Pacific, MNHN B6356.
- 5. Glebocarcinus amphioetus (Rathbun, 1898) (male specimen), Recent, north Pacific, MNHN B20849.



Plate 2

Early Miocene (Burdigalian) decapod crustaceans from the type area of the Helvetian Stage, Belpberg near Bern, Switzerland. Scale bars represent 10 mm.

- 1. Necronectes? sp., NMBE D2814.
- 2-5. Portunus sp., NMBE B4767 (Fig. 2 = counterpart of Fig. 5), NMBE A5542 (Fig. 3); NMBE D3173) (Fig. 4) and NMBE D4761 (Fig. 5 = counterpart of Fig. 2).
- 6. Ctenocheles sp., NMBE D3171.

Miocene decapods from Switzerland

