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Balsscallichirus Sakai, 2011 (Decapoda: Axiidea: Callianassidae) in the fossil record: systematics and palaeobiogeography

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(With 13 figures and 2 tables)

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Abstract

The fossil record of the ghost shrimp genus *Balsscallichirus* Sakai, 2011 (Crustacea: Decapoda: Callianassidae) is revised. *Barnardcallichirus* Sakai, 2011 and *Tirmizicallichirus* Sakai, 2011 are considered subjective synonyms of *Balsscallichirus*. Based on the examination of extant species it is argued that the morphology of the major cheliped merus, in combination with other hard part morphology characters, is sufficient for assignment of the fossil material into the genus. Main identifying characters are on merus which is keeled along its midline and its lower half is tuberculated; its lower margin possesses broad proximal meral hook continuing into a lobe distally; the entire lower margin is subdivided into numerous irregularly spaced spines. Three species, *Callianassa sismondai* A. Milne-Edwards, 1860, *C. floriana* Glaessner, 1928, and *Podocallichirus laepaensis* Hyžný & Muñiz, 2012, originally described from the Miocene of Italy, Austria and Spain, respectively, are assigned to *Balsscallichirus* herein. *Neocallichirus wellsi* Schweitzer, Feldmann & Gingerich, 2004 from the Upper Eocene of Pakistan is tentatively assigned to that genus as well. Spatial and temporal distribution of the genus indicates that at least since the Oligocene, and possibly even sooner (the Late Eocene), the genus has been restricted to the Western Tethys Region. Later, it migrated also into West Atlantic establishing present day communities.

Key words: Decapoda, Callianassidae, *Callianassa*, *Tirmizicallichirus*, *Podocallichirus*, fossil record, palaeobiogeography

Introduction

Ghost shrimps of the family Callianassidae Dana, 1852 are soft-bodied, usually heterochelous decapods representing major bioturbators of muddy and sandy (sub)marine

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substrates. Their robust fossil record is understudied owing to preservation often considered as taxonomically insufficient. Their remains, however, are present in many assemblages of Mesozoic and most assemblages of Cenozoic decapod crustaceans (Glaessner 1969), and thus, it is believed that detailed taxonomic evaluation of their fossil record can help to understand the evolution of major bioturbators.

The core of the present revision of the fossil record of *Balsscallichirus* Sakai, 2011 is the case study of *Callianassa floriana* Glaessner, 1928, a ghost shrimp originally described from the Miocene of Austria. Thorough re-evaluation of the type collection plus new findings from several different localities of the Oligocene and Miocene of Hungary and Austria allowed determination of intraspecific variation in the cheliped morphology and evaluation of taxonomically important characters present on a major cheliped. Identifying these characters also in *Podocallichirus laepaensis* Hyžný & Muñiz, 2012 from the Late Miocene of Spain and *Callianassa sismondai* A. Milne-Edwards, 1860 from the Middle Miocene of Italy has consequently lead to considering these taxa congeneric. All mentioned fossil taxa exhibits very close morphological affinities to extant species of *Balsscallichirus* Sakai, 2011, *Barnardcallichirus* Sakai, 2011, and *Tirmizicallichirus* Sakai, 2011. The latter two genera are considered synonymous with *Balsscallichirus*, thus, all three discussed fossil species are assigned herein to this genus. Additionally, *Neocallichirus wellsi* Schweitzer, Feldmann & Gingerich, 2004, from the Eocene of Pakistan is tentatively assigned to *Balsscallichirus*; confirmation of the generic assignment, however, must await re-examination of the type material.

This contribution is a part of the systematic revision of the Oligo-Miocene ghost shrimps (Decapoda: Axiidea: Callianassidae) of the Central Paratethys conducted by the author (Hyžný 2011, 2012; Hyžný & Hudáčková 2012; Hyžný & Müller 2010, 2012; Hyžný & Dulai 2014; Hyžný & Gašparič 2014). For correlation between the Central Paratethyan stages and Mediterranean scale a reference is made to Harzhauser *et al.* (2002: fig. 2) and Piller *et al.* (2007: fig. 1).

Study Area

Studied material of Callianassa floriana comes from these localities (Fig. 1):

1) St. Florian (Styrian Basin, Austria) – the type locality of *Callianassa floriana*. Glaessner (1928: p. 170) reported the material as coming from the Helvetian “sandiger Tegel”. The lithology can be correlated with the Florianer Beds (“Beds of St. Florian”), which are characterized by lagoonal deposits (Gross *et al.* 2007). Glaessner (1928) stated age as “Helvetian”, in current terminology comprising both the Karpatian and Lower Badenian deposits. The offshore facies of the Kreuzkrumpel Formation is of the Karpatian age, and the fine clastics exposed at St. Florian and representing marginal sediments, are assigned to the Lower Badenian (Gross *et al.* 2007).

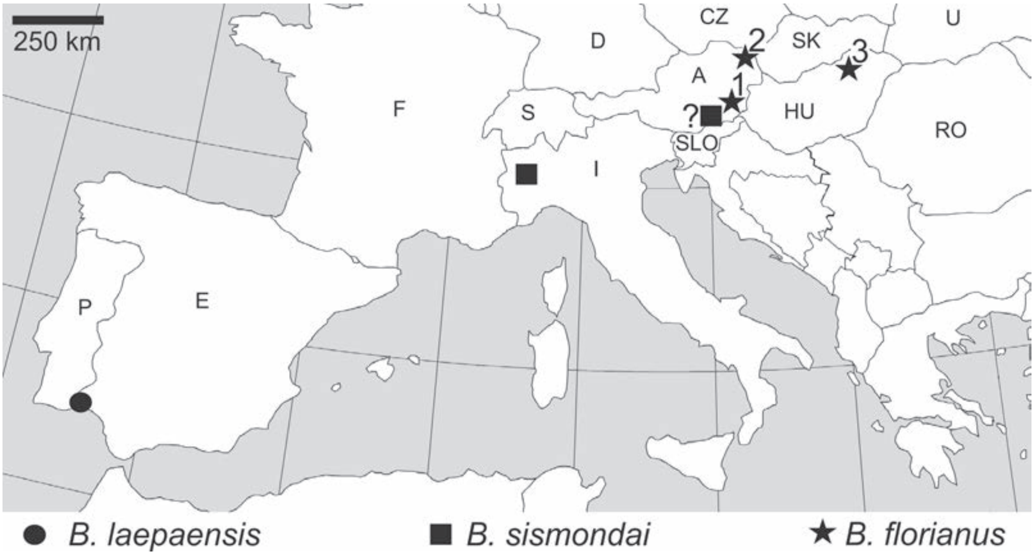

Fig. 1. Outline map of Southern and Central Europe indicating position of the studied areas for respective species. Numbers 1–3 indicate position of the Styrian, Vienna and Great Hungarian basins, respectively.

2) Zehndorf bei Preding (Styrian Basin, Austria) – At the locality Florianer Beds of the lower Badenian age (see above) are exposed.

3) Pöls (Styrian Basin, Austria). At the locality volcanic tuffs described by Kopetzky (1957) are exposed. Two layers of tuff are intercalated within the shallow marine fine clastic lower Badenian Florian Formation containing foraminifers and molluscs (Handler *et al*. 2006).

4) St. Josef (Styrian Basin, Austria). At the locality the same sedimentological settings as at Pöls is exposed.

5) Teiritzberg (Korneuburg Basin, Austria). At the locality the Korneuburg Formation of the Karpatian age represented mainly by grey to yellow marly silt and fine to medium sand is exposed (Harzhauser & Wessely 2003). More details on geological settings and palaeoecology were discussed by Wessely (1998) and Harzhauser (2002). Decapod crustaceans of the Korneuburg Basin were summarized by Müller (1998b).

6) Baden-Sooss (Vienna Basin, Austria). The brickyard of Baden-Sooss is the stratotype of the Middle Miocene regional stage Badenian. The exposed sediments belong to the Baden Formation. The section can be correlated with calcareous nannoplankton Zone NN5 and foraminifera Zone M6 (based on the presence of *Orbulina suturalis*); thus, middle part of the Langhian (Rögl *et al*. 2008) and middle Badenian *sensu* Hohenegger *et al*. (2014).

7) D-318 borehole, Miskolc area (Great Hungarian Plain, Hungary). The studied material comes from the depth 745.7–749.1 m where the Törökbálint Sandstone Formation has been identified. The formation is characterized by alternation of dominantly coarse and fine grained sandstone (Császár 1997). The age is Upper Oligocene (Egerian).

Material of *Callianassa sismondai* as reported by Glaessner (1928) comes from the locality at Spielfeld in Styrian Basin, Austria, where Middle Miocene (Badenian) silts and sands of the Kreuzberg Formation are exposed (Hohenegger *et al*. 2009).

Material of *Podocallichirus laepaensis* comes from the Upper Miocene medium- to coarse-grained sands exposed at "Valleforero" section in the Lepe area (Guadalquivir Basin, SW Spain) as discussed in Hyžný & Muñiz (2012).

Material and methods

Extant material comprises *Callianassa masoomi* (*Tirmizicallichirus massomi sensu* Sakai 2011) from Qeshm Island, Persian Gulf (male; NHMW 24990). It was studied using stereomicroscope and photographed under alcohol.

Fossil material consists of three taxa. All material except the holotype of *Callianassa sismondai* A. Milne-Edwards, 1860 was studied firsthand through revision of older collections (*Callianassa floriana*) and re-study of the published material (*Podocallichirus laepaensis*). Preparation of the material was performed with preparatory needles and a fine pneumatic needle. Specimens were photographed either dry and uncoated or coated with ammonium chloride sublimate (for details see captions to respective figures).

Measurements were taken on investigating major chelipeds following the scheme depicted in Fig. 2.

Abbreviations:

Mxp3 – maxilliped 3

P1–5 – pereiopods 1–5

Plp1–5 – pleopods 1–5

Institutional abbreviations:

NHMW – Natural History Museum, Vienna, Austria

UMJGP – Universalmuseum Joanneum (Geology & Palaeontology, Centre of Natural History), Graz, Austria

HNHM – Hungarian Natural History Museum (Palaeontological Department), Budapest, Hungary

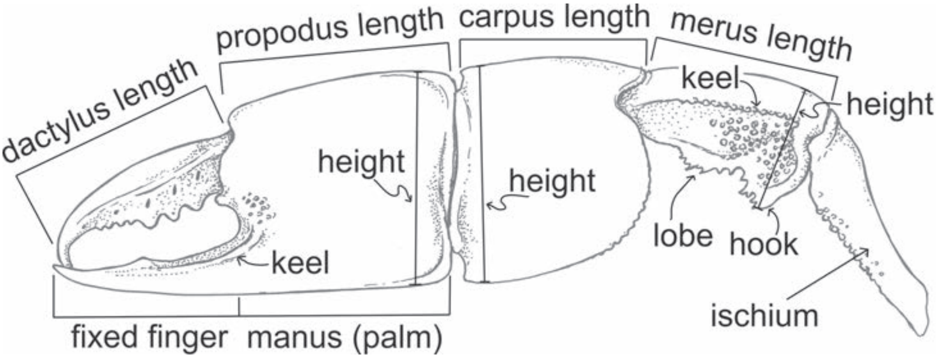

Fig. 2. Sketch of major cheliped of *Balsscallichirus* SAKAI, 2011 indicating important characters and measurements.

MNHN – Natural History Museum, Paris, France

CBG/CD – Center for diffusion and research of biodiversity and geodiversity, City of Lepe, Spain

KGP-MH – Comenius University (Department of Geology and Palaeontology), Bratislava, Slovakia

Systematic palaeontology

Order Decapoda LATREILLE, 1802

Infraorder Axiidea DE SAINT LAURENT, 1979

Family Callianassidae DANA, 1852

Subfamily Callichirinae MANNING & FELDER, 1991

Genus *Balsscallichirus* SAKAI, 2011

= *Barnardcallichirus* SAKAI, 2011
= *Tirmizicallichirus* SAKAI, 2011

Type species: *Callianassa* (*Callichirus*) *balssi* MONOD, 1933, by original designation.

Extant species included: *Balsscallichirus balssi* (MONOD, 1933); *B. gilchristi* (BARNARD, 1947) nov. comb.; *B. guineensis* (DE MAN, 1928); *B. masoomi* (TIRMIZI, 1970) nov. comb.; *B. tenuimanus* (DE SAINT LAURENT & LE LOEUFF, 1979) nov. comb. (see Table 1).

Fossil species included: *Balsscallichirus florianus* (GLAESSNER, 1928) nov. comb.; *B. laepaensis* (HYŽNÝ & MUÑIZ, 2012) nov. comb.; *B. sismondai* (A. MILNE-EDWARDS, 1860) nov. comb.; ?*B. wellsi* (SCHWEITZER, FELDMANN & GINGERICH, 2004) nov. comb. (see Table 1).

Diagnosis: Mxp3 ischium-merus pediform (*sensu* Manning & Felder 1991, with parallel mesial and lateral margins; propodus broadened; dactylus digitiform. P1 (chelipeds) unequal and dissimilar; major merus with distinctly broad meral hook subdivided in numerous spines followed by a spiny lobe or serrated meral margin; lateral surface of merus keeled along midline and strongly tuberculated on the lower half; major carpus broad, rounded proximally; major propodus massive, square or elongated in outline with fixed finger keeled longitudinally; major dactylus armed with teeth on the occlusal surface and hooked tip. Telson subquadrate, wider than long, with low median convexity or almost straight on posterior margin. Uropodal endopod oval; uropodal exopod broadly rounded on lateral margin.

Discussion: Many currently recognised genera within the subfamily Callichirinae have complex taxonomic history. The genus *Callichirus* was introduced by Stimpson (1866) and later it was redefined by Manning & Felder (1986, 1991) resulting in exclusion of several species assigned to the genus since its original description (*e.g.* Le Loeuff & Intès 1974; de Saint Laurent & Le Loeuff 1979). Sakai (1999) grouped some of these taxa under the newly erected genus *Podocallichirus* Sakai, 1999. *Podocallichirus* has a very complex taxonomic history (see Hyžný & Karasawa 2012 and Hyžný & Muñiz 2012 for a review). Basically, there are two different concepts of the genus: 1) original concept given by Sakai (1999) comprising the type species *Callianassa madagassa* Lenz & Richters, 1881 plus six other species; supported by De Grave *et al.* (2009) and Hyžný & Muñiz (2012); and 2) concept of the monotypic genus *Podocallichirus* comprising the type species only; supported by Sakai (2011) and Poore (2014). Recently, Sakai *et al.* (2014) synonymised *Lepidophthalmus socotrensis* Sakai & Apel, 2002 with *C. madagassa*. Both taxa possess similarly shaped minor chela with strongly spinulous upper margin of dactylus and occlusal margins of fingers (Lenz & Richters

Table 1. Synopsis of species of *Balsscallichirus* Sakai, 2011 known to date.
* – assigned to the genus tentatively without examination of the type material.

Taxon (original description)	Stratigraphic range	Occurrence
Callianassa (*Callichirus*) *balssi* Monod, 1933	Recent	East Atlantic Ocean
Callianassa gilchristi Barnard, 1946	Recent	West Indian Ocean
Callianassa (*Callichirus*) *guineensis* De Man, 1928	Recent	East Atlantic Ocean
Callianassa (*Callichirus*) *massoomi* Tirmizi, 1970	Recent	West Indian Ocean
Callichirus tenuimanus de Saint Laurent & Le Loeuff, 1979	Recent	East Atlantic Ocean
Podocallichirus laepaensis Hyžný & Muñiz, 2012	Late Miocene	Spain
Callianassa sismondai A. Milne-Edwards, 1860	?Early–Middle Miocene	Italy, ?Austria
Callianassa floriana Glaessner, 1928	Late Oligocene–Middle Miocene	Austria, Hungary
**Neocallichirus wellsi* Schweitzer, Feldmann & Gingerich, 2004	Late Eocene	Pakistan

1881: figs 20–21; Sakai & Apel 2002: fig. 5d; Sakai *et al*. 2014: figs 6A–B). Clearly, the original concept of *Podocallichirus sensu* Sakai (1999) is unstable and therefore it is abandoned here. In agreement with Sakai (2011) and Poore (2014), *Callianassa madagassa* is considered the only member of *Podocallichirus*.

All species (except the type species) treated as *Podocallichirus* by Sakai (1999, 2005) were once again re-assigned to four newly erected genera by Sakai (2011), namely *Balsscallichirus*, *Barnardcallichirus*, *Forestcallichirus* and *Tirmizicallichirus*. All these genera are based largely on male pleopods which are claimed by some authors (Biffar 1971; Felder & Manning 1995; Dworschak 2008, 2011a, b) as changing with maturity. Many other characters are shared by *Balsscallichirus*, *Barnardcallichirus* and *Tirmizicallichirus* (see diagnosis above and compare with diagnoses given by Sakai 2011: pp. 414, 416, 474), including major cheliped merus which is usually consistent with the genus concept based on the soft part morphology (*e.g.* third maxillipeds, pleopods, uropods, telson), as shown by Manning & Felder (1991). Therefore, these three genera are considered synonymous. Based on the alphabetic order, *Balsscallichirus* is chosen to be a valid generic name also for species once treated under *Barnardcallichirus* and *Tirmizicallichirus*. Morphology of major cheliped merus of *Balsscallichirus* as recognized herein is considered unique among callianassid ghost shrimps and it is taken as a main proxy character for the generic assignment.

The major merus is always keeled along its midline and the lower half of the lateral surface is usually tuberculated. Proximal meral hook is very broad (Tirmizi 1970: fig. 2E; Sankolli 1971: fig. 7a–d; Le Loeuff & Intès 1974: figs 12b, 13b; de Saint Laurent & Le Loeuff 1979: fig. 13a, e, g) often continuing into a lobe distally and subdivided in numerous spines (Figs 2–3; Sankolli 1971: fig. 7a–d). As a result, the lower margin is spiny along its entire length.

Major cheliped merus (if preserved) in all fossil taxa presented herein exhibits the same basic morphology as discussed above. Therefore, all these taxa are considered congeneric and assigned to *Balsscallichirus*. The variation in development of a meral hook, lobe and spines is reflected during the ontogenetic growth. Large specimens often have a very high merus with strongly developed spines. The lobe positioned distally from the hook is sometimes less developed, usually in smaller specimens. Exceptions to these general rules, however, can be observed. For details see discussion for respective species.

Similarly shaped major cheliped merus is present also in extant *Paratrypaea bouvieri* (Nobili 1904). It, however, differs from representatives of *Balsscallichirus* in absence of distinct tuberculation on merus, differently shaped dactylus and generally small size of individuals (for details see Dworschak 2012).

An additional note can be made on *Balsscallichirus masoomi* (Fig. 3). Tirmizi (1970) described *Callianassa masoomi* based on three small (total length 22.5, 29 and 30.5 mm) female specimens from Karachi, Pakistan. A year later, Sankolli (1971) described *Callianassa kewalramanii* based on 16 specimens, both males and females (total length 20–46.5 mm) from Bombay and Ratnagiri, India. Sakai (1999) synonymised

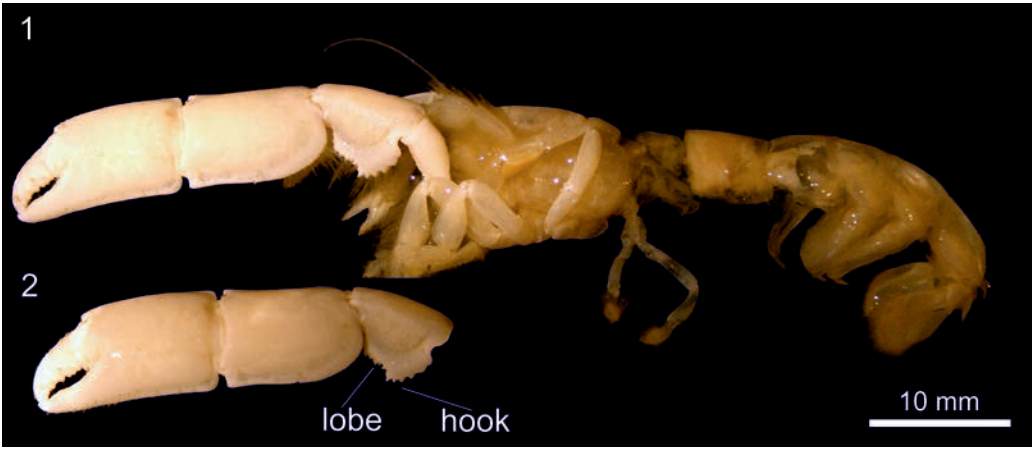

Fig. 3. *Balsscallichirus masoomi* (Tirmizi, 1970) from Qeshm Island, Persian Gulf (NHMW 24990). **1**: animal in lateral aspect with major cheliped in ventro-lateral aspect. **2**: major cheliped in lateral aspect. Specimen was immersed in alcohol prior to photography.

both taxa and re-assigned them to the newly erected genus *Podocallichirus*. He further noted (Sakai 1999: p. 59) that *Podocallichirus masoomi* is "probably identical with *P. gilchristi*". Later, he still maintained *P. masoomi* and *P. gilchristi* as distinct species (Sakai 2005) and in his latest monograph (Sakai 2011) he considered the two species so distinct, that he erected separate genera for them, *Tirmizicallichirus* and *Barnardcallichirus*, respectively. Regarding the major cheliped morphology, *Callianassa masoomi* and *C. gilchristi* are closest to each other from all species treated here under *Balsscallichirus* (see also Hyžný & Muñiz: fig. 4).

Occurrence: Late Eocene; Late Oligocene to Holocene. *Balsscallichirus wellsi* (Schweitzer, Feldmann & Gingerich, 2004) comb. nov. from the Late Eocene of Pakistan is considered the oldest representative of the genus. For other occurrences see Table 1. *Balsscallichirus* is today restricted to the East Atlantic and East Indian oceans (Sakai 2011; Sepahvand & Sari 2010; Sepahvand *et al.* 2013).

Balsscallichirus florianus (Glaessner, 1928) nov. comb.

(Figs 4.1–4.7, 5.1–5.4, 6.1–6.6, 7.1–7.2, 12.1)

1928 *Callianassa floriana* Glaessner, p. 170, pl. 3, fig. 5.
1929 *Callianassa floriana* Glaessner, 1928 – Glaessner, p. 81.
1998a *Callianassa floriana* Glaessner, 1928 – Müller, p. 10.
1998b "*Callianassa*" aff. *sismondai* A. Milne-Edwards, 1860 – Müller, p. 273; pl. 1, figs 1–2.
non 2005 "*Callianassa*" cf. *floriana* Glaessner, 1928 – Polkowsky, p. 24; fig. 14; pl. 2, fig. 1.
2011 "*Callianassa*" *floriana* Glaessner, 1928 – Hyžný, table 2.

Diagnosis: *Balsscallichirus* with major P1 fixed finger keeled; tubercles present on the outer lateral surface of propodus at articulation with dactylus and sometimes also along the keel of the fixed finger; occlusal margin of dactylus armed with three triangular teeth proximally, lateral surface keeled, without pronounced tuberculation.

Measurements: See Table 2.

Type material: St. Florian: holotype consisting of part NHMW 1846/0049/0010 (Fig. 4.4) and counterpart NHMW 1846/0049/0009 (Fig. 4.3), and paratypes NHMW 1846/0049/0003 (Figs 4.1–4.2), 1846/0049/0007 (Fig. 4.7), 1846/0049/0008 (Fig. 4.6), 1846/0049/0011 (Fig. 4.5), 1846/0049/0012 (Fig. 4.9), 1846/0049/0013 (Fig. 4.8).

Other material: St. Florian: NHMW 2014/0404/0001–0002, UMJGP 75662 (Figs 5.1–5.2). Pöls: NHMW 1861/0001/0325a–c (Figs 6.1, 6.3), 2014/0407/0001 (Fig. 6.4), 2014/0407/0002 (Fig. 6.5), 2014/0407/0003 (Fig. 6.6). St. Josef: UMJGP 75416 (Fig. 6.2). Zehndorf bei Preding: UMJGP 61186. Baden Sooss: NHMW 2014/0408/0001.

Table 2. Measurements (in mm) of major cheliped elements of *Balsscallichirus florianus* (Glaessner, 1928) nov. comb. H=max. height; L=max. length.

Specimen	Handedness	Merus		Carpus		Propodus		Dactylus
		H	L	H	L	H	L	L
NHMW 1846/0049/0003a	right	-	-	12.4	7.6	12.4	11.5	~11.6
NHMW 1846/0049/0003b	right	-	-	10.6	6.7	10.5	10.4	~9.5
NHMW 1846/0049/0007a	right	-	-	5.3	6.3	5.3	-	-
NHMW 1846/0049/0007b	left	-	-	5.7	-	5.0	5.4	-
NHMW 1846/0049/0008	left	6.7	10.7	11.3	8.6	11.1	11.3	12.1
NHMW 1846/0049/0009–0010	right	6.2	10.4	10.7	7.5	10.4	10.4	10.2
NHMW 1846/0049/0011	right	4.4	8.2	8.7	7.0	8.3	8.8	~7.3
NHMW 1846/0049/0012	right	-	-	6.5	-	6.4	7.4	6.2
NHMW 1846/0049/0013	left	4.4	6.7	7.2	5.7	7.3	7.1	6.4
NHMW 1861/0001/0325a	left	~13.0	17.3	~19.4	~20.1	-	-	-
NHMW 1861/0001/0325b	right	-	-	-	-	20.4	~21.2	-
NHMW 1861/0001/0325c	right	-	-	-	-	20.4	~19.0	-
NHMW 1997/0169/0002	left	10.9	15.1	12	11.5	12.2	14.2	9.3
NHMW 1997/0169/0004	right	-	-	-	-	15.5	13.0	-
NHMW 2014/0404/0001a	left	-	8.5	10.7	7.7	-	-	-
NHMW 2014/0404/0001b	right	4.4	6.7	6.5	7.5	-	6.7	-
NHMW 2014/0404/0002	right	-	-	8.5	8.2	8.5	9.2	9.0
NHMW 2014/0408/0001	right	~4.0	~5.3	5.8	4.0	5.6	5.6	-
HNHM INV 2014.173	left	-	-	6.3	~5.7	6.2	7.2	
HNHM INV 2014.174	left	5.1	~9.6	-	-	-	-	-
NHMW 2014/0407/0001	left	8.2	17.3	15.5	10.3	16.4	-	-
NHMW 2014/0407/0002	right	-	-	-	-	12.4	15.1	-
NHMW 2014/0407/0003	left	-	-	-	-	15.1	~16.0	~15.6

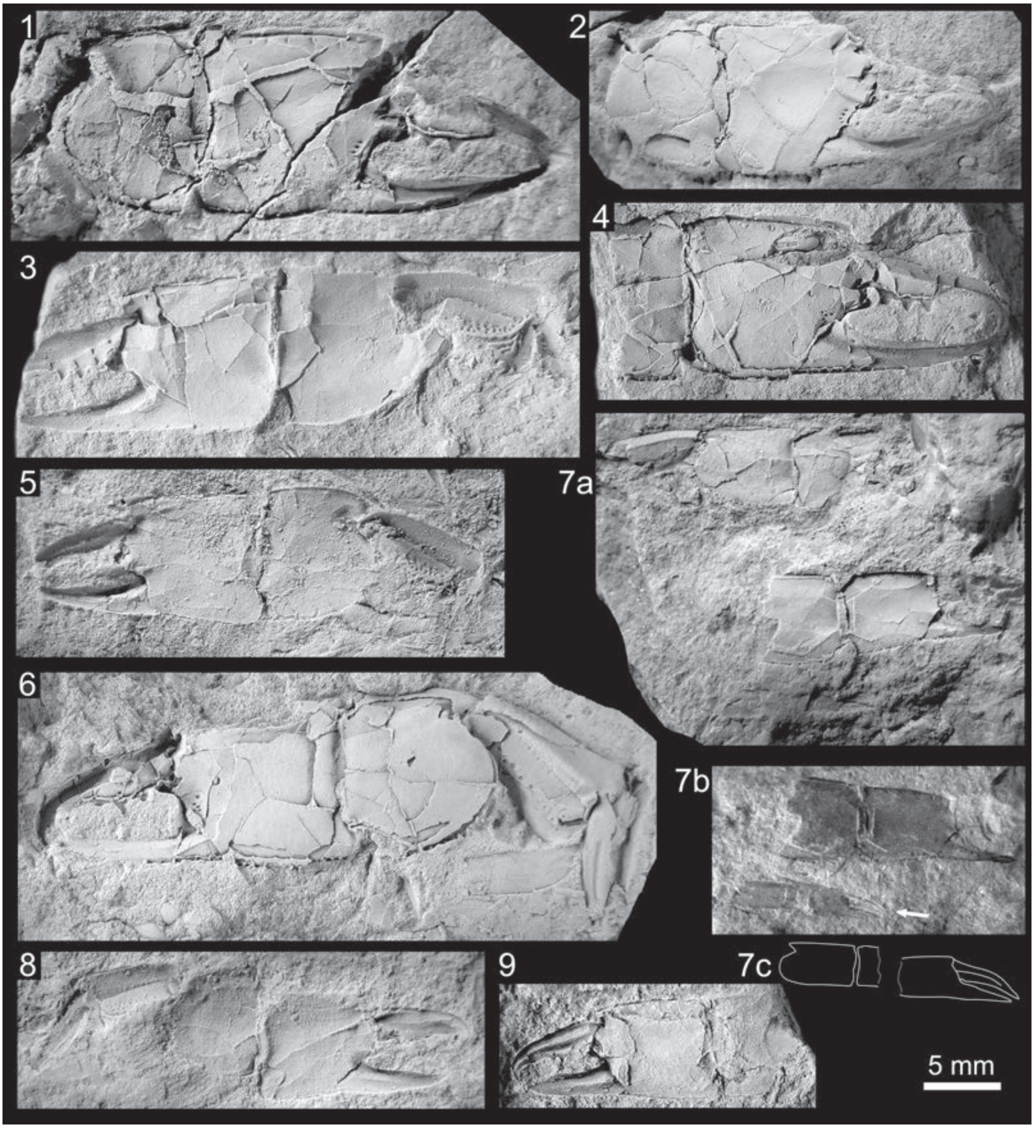

Fig. 4. Type material of *Balsscallichirus florianus* (Glaessner, 1928) nov. comb. from St. Florian, Austria. **1–2**: paratype NHMW 1846/0049/0003. **3**: counterpart of holotype NHMW 1846/0049/0009. **4**: part of holotype NHMW 1846/0049/0010. **5**: paratype NHMW 1846/0049/0011. **6**: paratype NHMW 1846/0049/0008. **7**: paratype 1846/0049/0007. Note minor chela in 7b (arrow) and its interpretative and enlarged drawing in 7c. **8**: NHMW 1846/0049/0013. **9**: NHMW 1846/0049/0012. All specimens represent major chelipeds except minor chela indicated in 7b. All specimens except 7b were coated with ammonium chloride prior the photography. All specimens are to scale.

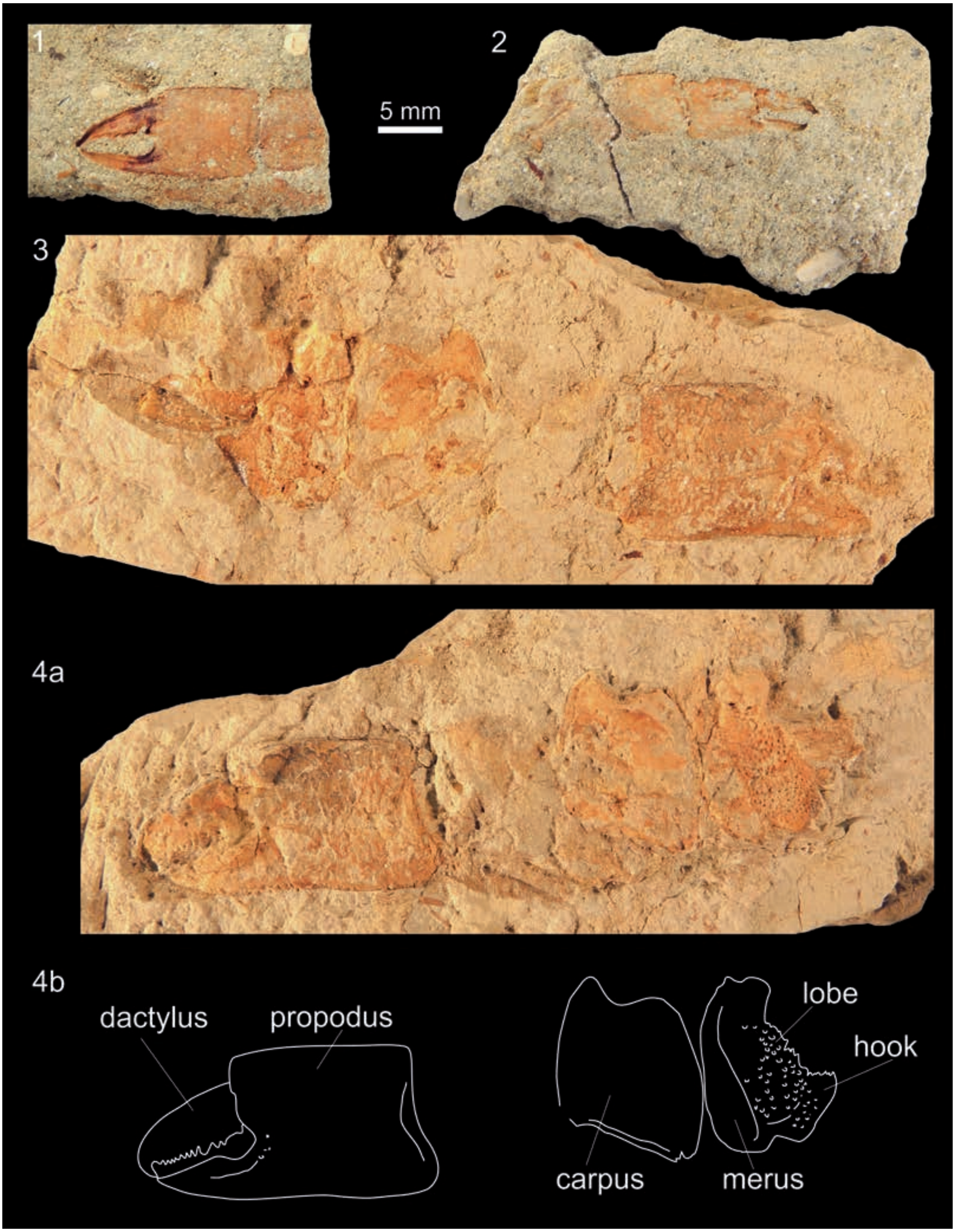

Fig. 5. *Balsscallichirus florianus* (GLAESSNER, 1928) nov. comb. from St. Florian (1–2) and Teiritzberg (3–4), both in Austria. **1–2**: UMJGP 75662. **3–4**: counterpart and part of a major cheliped labelled as NHMW 1997/0169/0002 and 1997/0169/0001, respectively. **4b**: interpretative drawing of 4a. All specimens represent major chelipeds and are to scale.

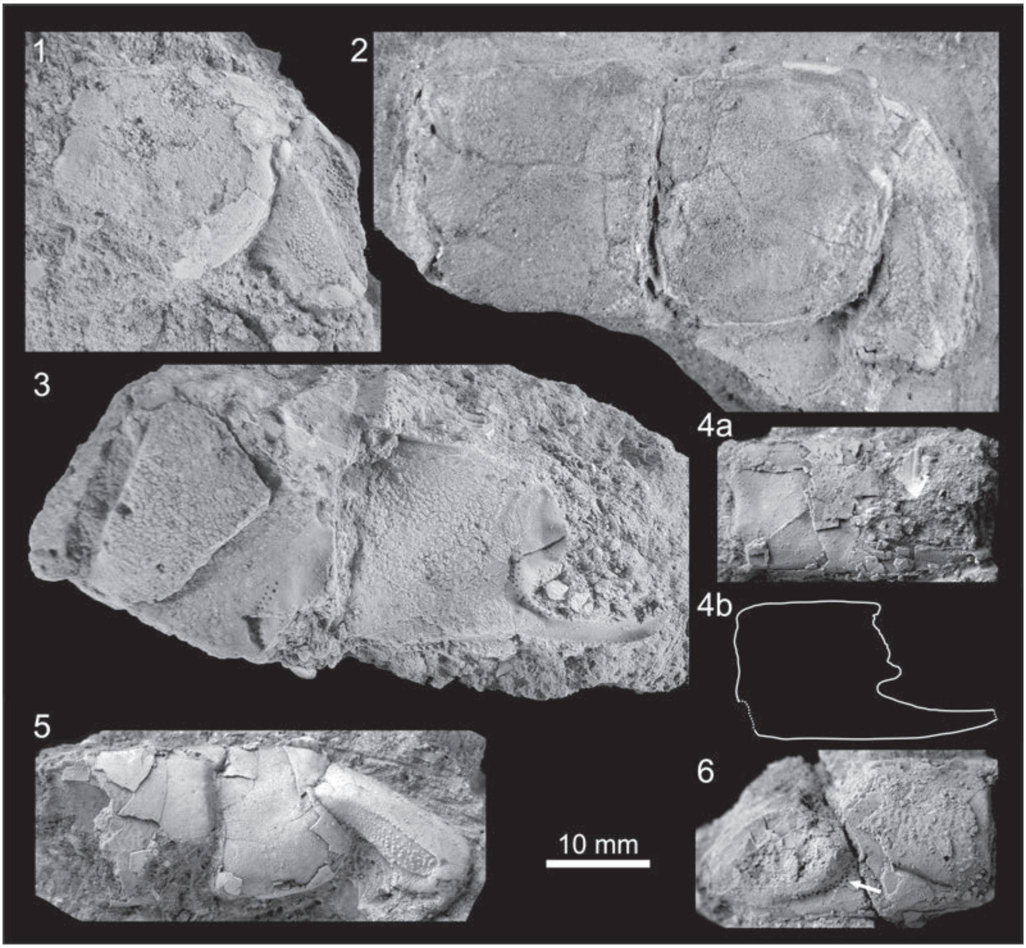

Fig. 6. *Balsscallichirus florianus* (GLAESSNER, 1928) nov. comb. from Pöls (1, 3–6) and St. Josef (2), both in Austria. **1**: NHMW 1861/0001/0325a. **2**: UMJGP 75416. **3**: NHMW 1861/0001/0325b. **4**: NHMW 2014/0407/0002; interpretative drawing is in 4b. **5**: NHMW 2014/0407/0001. **6**: NHMW 2014/0407/0003; arrow indicates tubercles in two rows. All specimens represent remains of major chelae. All specimens were coated with ammonium chloride prior the photography and are to scale.

Teiritzberg: NHMW 1997/0169/0001–0002 (Figs 5.3–5.4), 1997/0169/0003–0004, NMHW 1997/0176/0001. D-318 borehole: HNHM INV 2014.173–175 (Figs 7.1–7.2).

Occurrence: Upper Oligocene (Egerian) of the Great Hungarian Plain, Hungary (herein), Lower Miocene (Karpatian) of the Korneuburg Basin (MÜLLER 1998b) and the Middle Miocene (Badenian) of the Vienna and Styrian basins (GLAESSNER 1928; herein).

Emended description: Major cheliped ischium elongate, lower margin denticulated; merus longer than high, outer surface with distinct keel dividing merus in two parts, lower part densely tuberculated, lower margin of merus denticulated distally, with

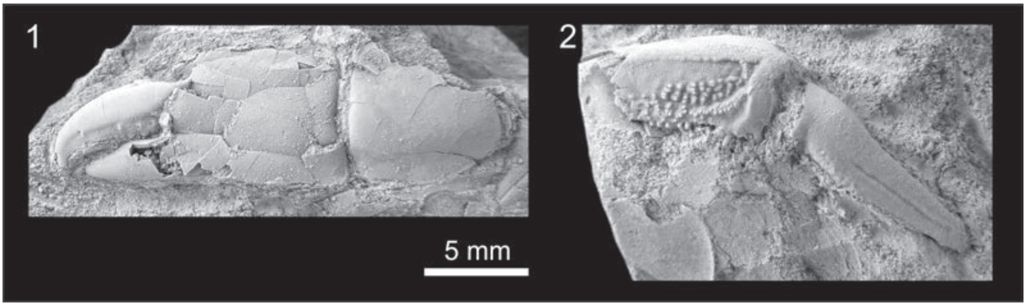

Fig. 7. *Balsscallichirus florianus* (Glaessner, 1928) nov. comb. from D-318 borehole, Hungary. **1**: HNHM INV 2014.173. **2**: HNHM INV 2014.174. Both specimens were coated with ammonium chloride prior the photography and are to scale.

a distinct denticulated lobe proximally; carpus approximately as long as high, lower and distal margins rounded, forming a single edge; propodus square or slightly elongate, upper and lower margins subparallel; fixed finger long and slender, bent upward distally, without armature; dactylus long and slender, with hooked tip, occlusal margin armed with three triangular teeth proximally.

Minor cheliped carpus *c.* two times longer than high, upper and lower margins parallel to each other, proximal margin rounded; propodus slender, longer than high, upper and lower margins parallel to each other; fingers keeled, unarmed.

Variations: The studied material is rich enough to recognize two general types of variations: 1) variations mirroring ontogenetic growth and 2) intraspecific variation.

Regarding the first type, the tuberculation present on the propodus at the base of the fixed finger is restricted to larger specimens, whereas smaller ones are smooth (Fig. 7.1). Occlusal margin of the dactylus is armed with teeth following certain pattern apparently changing with size. Smaller specimens have teeth nearly uniform in size (Fig. 7.1), but in larger specimens the most proximal teeth tend to be larger (Figs 4.1–4.6) than the distal ones. Development of a notch at the base of the fixed finger also seems to be connected with growth: large propodi have comparatively larger notches (Figs 4.1–4.4, 6.3) than smaller propodi do. Similarly, the fingers are more slender in large specimens (Figs 4.4, 4.6) than in smaller ones. The growth is clearly linear; no allometric tendencies in manus shape have been observed (Fig. 8).

Intraspecific variation concerns number of spines on the lower margin of merus as well as the outline of the meral lobe, which is sometimes poorly developed. As mentioned above, fingers of larger specimens are long and slender, but this is not always so. Sometimes, the fingers can be distinctly short and robust (Figs 5.3–5.4). In such a case the armature of dactylus is more uniform, almost peg-shaped. In some specimens tuberculation is limited to the base of the fixed finger (Figs 4.1–4.2, 4.6), whereas in others the tubercles continue onto the keel of the fixed finger and form two rows (Figs 6.3, 6.6).

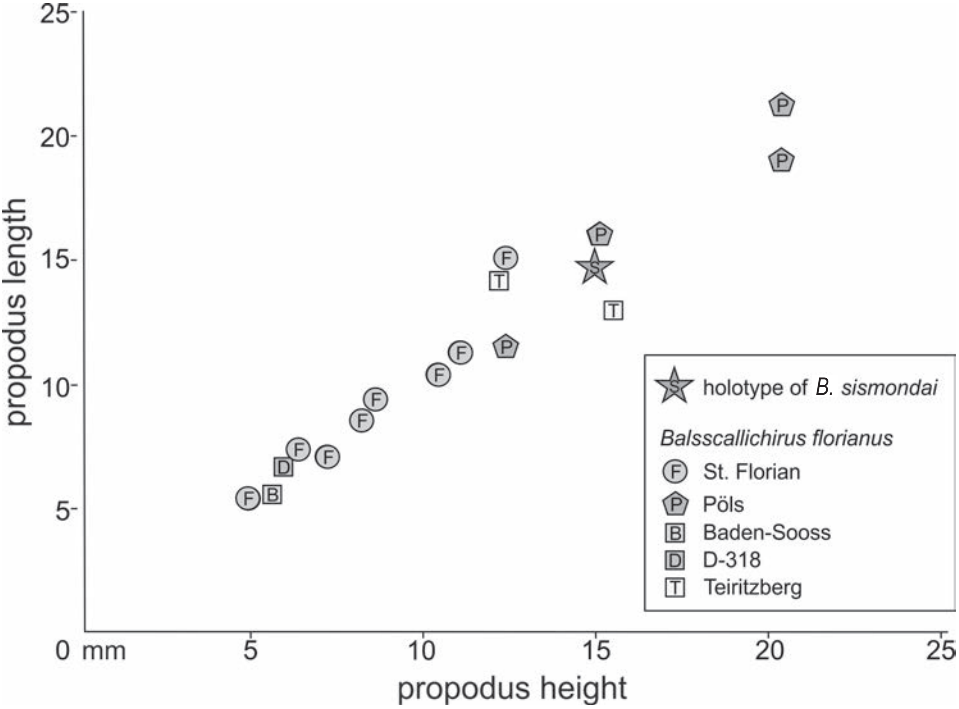

Fig. 8. Length of propodus in relation to its height of *Balsscallichirus florianus* (Glaessner, 1928) nov. comb. from selected localities. Holotype of *Balsscallichirus sismondai* (A. Milne-Edwards, 1860) nov. comb. is indicated for comparison.

Discussion: *Callianassa floriana* Glaessner, 1928 was originally described based on several specimens composed of articulated chelipeds form the Helvetian of St. Florian in Steiermark, Austria (Glaessner 1928). Glaessner (1928: pl. 3, fig. 5) provided rather a simplified figure of the major cheliped consisting of merus, carpus, propodus and dactylus. However, merus in his depiction does not fit the real specimens; it does not show any meral hook, or distinct tuberculation and description does not mention any meral hook either.

When describing *C. floriana*, Glaessner (1928: p. 171) mentioned the presence of a similar form from the locality Pöls (Styrian Basin, Austria), specimens deposited under repository number NHMW 1861/0001/0325 (Figs 6.1, 6.3). Re-examination of the material revealed that it indeed is conspecific with *C. floriana*. Nevertheless, at Pöls at least two different callianassid species occur, the second one being *Glypturus munieri* (Brocchi, 1883) (for details see Hyžný & Müller 2012).

Müller (1998b) reported *Callianassa* aff. *sismondae* from the Karpatian of Teiritzberg (Korneuburg Basin, Austria). This occurrence was based on several rather fragmentary specimens (Figs 5.3–5.4). Based on the dentition of dactylus and morphology of merus, the material is considered as conspecific with *Callianassa floriana*.

Many specimens of *Balsscallichirus florianus* nov. comb. represent articulated chelipeds and although coming from different localities, they are more-less uniformly preserved in fine grained facies (mostly silty clays). This may point either to the substrate preferences of the animals or to a mere consequence of taphonomic bias, because articulated specimens are much rarer in coarser sediment as they usually break into isolated elements (BISHOP & WILLIAMS 2005; compare HYŽNÝ 2012; HYŽNÝ & HUDÁČKOVÁ 2012).

Balsscallichirus laepaensis (HYŽNÝ & MUŇIZ, 2012) nov. comb.

(Figs 9.1–9.3, 12.3)

2012 *Podocallichirus laepaensis* HYŽNÝ & MUŇIZ, p. 621, figs 5, 6, 7.1–7.2.

Emended diagnosis: *Balsscallichirus* with major P1 fixed finger shorter than manus with three rows of tubercles on its occlusal margin, mesial row longest; occlusal margin of dactylus armed with molariform tooth proximally followed with numerous peg-shaped teeth, lateral surface smooth.

Material examined: Type collection consisting of right merus of major cheliped (holotype CBG/CD/001; Fig. 9.3), right propodus (paratype CBG/CD/002; Fig. 9.2), left propodus with articulated dactylus (paratype CBG/CD/003; Fig. 9.1), left propodus (paratype CBG/CD/004), right ischium (paratype CBG/CD/005), left carpus (paratype CBG/CD/006), four right dactyli (paratypes CBG/CD/010, 029, 037, and 038), three left fixed fingers (paratypes CBG/CD/041, 064, and 067) and numerous cheliped elements of fragmentary nature (collective numbers CBG/CD/007–009, CBG/CD/011–028, CBG/CD/030–36, CBG/CD/039–040, CBG/CD/042–063, CBG/CD/065–066, CBG/CD/068–075, CBG/CD/076, KGP-MH LE-001–007 and KGP-MH LE-009–010).

Occurrence: The species is restricted to its type locality at "Valleforero" section in the Quadalquivir Basin (SW Spain). Lepe White Silts exposed here Late Miocene in age (HYŽNÝ & MUŇIZ 2012).

Discussion: Based on the fragmentary material from the Late Miocene of Southeastern Spain, the species was described by HYŽNÝ & MUŇIZ (2012). Its attribution to *Podocallichirus* was made because of close morphological affinities to *C. masoomi*, a member of *Podocallichirus sensu* SAKAI (1999). The authors also noted yet unresolved status of *Podocallichirus* and preliminary generic identification of the material as well (HYŽNÝ & MUŇIZ 2012: p. 621). From the reasons stated above, the original concept of *Podocallichirus* is abandoned herein and *C. masoomi* is considered a member of *Balsscallichirus*. As a logical consequence, *Podocallichirus laepaensis* is transferred to that genus.

Balsscallichirus laepaensis nov. comb. differs from its congeners in the presence of three rows of tubercles on its major cheliped fixed finger. It also has propodus longer than high, although this is rather variable in *B. florianus* nov. comb., and thus, cannot be considered of major taxonomic importance. *B. laepaensis* nov. comb. seems to lack any tuberculation on the outer or inner surface of propodus. This observation can be a matter

Fig. 9. *Balsscallichirus laepaensis* (Hyžný & Muñiz, 2012) nov. comb. from the Guadalquivir Basin, Spain. **1**: paratype CBG/CD/003(major fragmentary propodus articulated with dactylus). **2**: paratype CBG/CD/002 (right propodus). **3**: holotype CBG/CD/001 (right merus). All specimens were coated with ammonium chloride prior the photography and are to scale.

of preservation as only two near-complete propodi with poorly preserved cuticular surfaces are known (Hyžný & Muñiz 2012). Major dactylus of *B. laepaensis* nov. comb. does not possess keels on the lateral and mesial surfaces and in this respect is unique.

Balsscallichirus sismondai **(A. Milne-Edwards, 1860) nov. comb.**

(Figs 10, 12.2)

1846 *Grapsus* sp. – E. Sismonda, p. 69, pl. 3, fig. 7.
1860 *Callianassa Sismondai* A. Milne-Edwards, p. 342; pl. 14, fig. 4.
1895 *Callianassa Sismondae* A. Milne-Edwards, 1860 – Crema, p. 667; figs 4–7.
?1928 *Callianassa Sismondai* A. Milne-Edwards, 1860 – Glaessner, p. 168.
1929 *Callianassa Sismondai* A. Milne-Edwards, 1860 – Glaessner, p. 90.
?1998a *Callianassa* cf. *sismondai* A. Milne-Edwards, 1860 – Müller, p. 10.
non 1998b “*Callianassa*” aff. *sismondai* A. Milne-Edwards, 1860 – Müller, p. 273; pl. 1, figs 1–2.
2006 *Callianassa sismondai* A. Milne-Edwards, 1860 – De Angeli & Garassino, p. 14.
?2011 “*Callianassa*” *sismondai* A. Milne-Edwards, 1860 – Hyžný, table 2.

Emended diagnosis: *Balsscallichirus* with P1 major propodus with tuberculation present on outer (lateral) and inner (mesial) surfaces, close to the base of the fixed finger; dactylus possessing three keels (lateral, medial, mesial) ornamented with tubercles.

Material examined: Right major propodus articulated with dactylus (holotype of *Callianassa sismondai* MNHN.F.B32689; Fig. 10); two fixed fingers and one dactylus from Spielfeld, Austria (NHMW 1860/0005/0008c–e; Figs 11.1–11.3).

Occurrence: The species is known from the ?Early Miocene of Torino, Italy (A. Milne-Edwards 1860; De Angeli & Garassino 2006), possibly also from the Middle Miocene of Austria (Glaessner 1928). A. Milne-Edwards (1860) reported Miocene age of *Callianassa sismondai* without closer indication. Chevalier (1962) studied fossil corals of the Superga Hill at Torino and reported Burdigalian to Aquitanian age for the

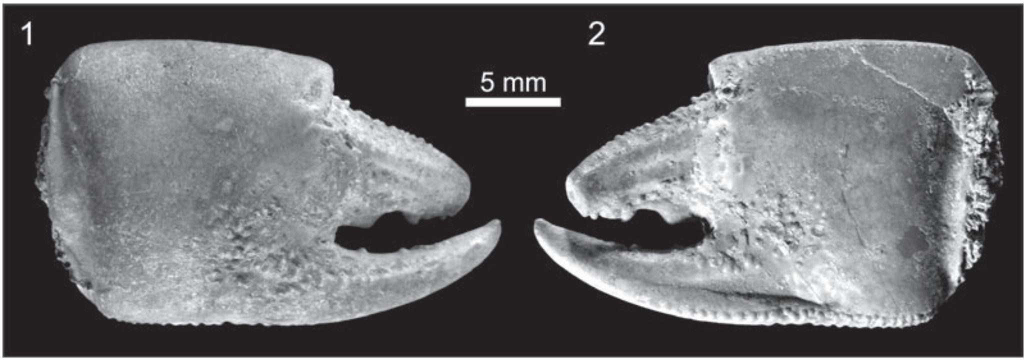

Fig. 10. Holotype of *Balsscallichirus sismondai* (A. MILNE-EDWARDS, 1860) nov. comb. from the Superga Hill, Torino, Italy. **1**: Right major propodus articulated with dactylus (MNHN.F.B32689) in outer lateral view. **2**: the same in inner lateral view.

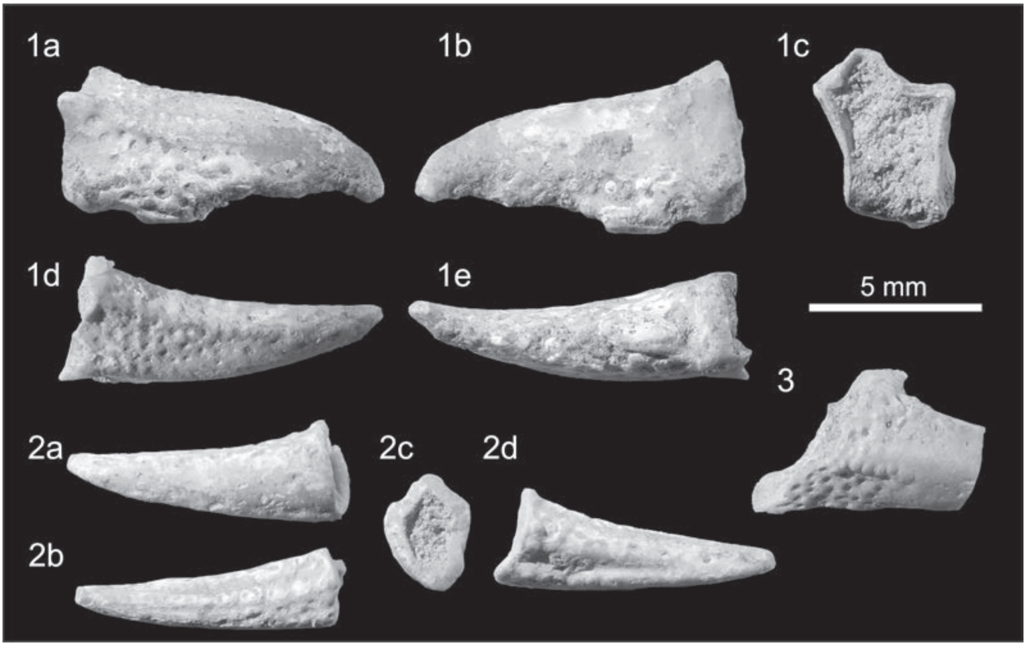

Fig. 11. Isolated fingers of supposed *Balsscallichirus* ?*sismondai* (A. MILNE-EDWARDS, 1860) nov. comb. from Spielfeld, Austria. **1**: dactylus NHMW 1860/0005/0008c in outer lateral view (1a), inner lateral view (1b), cross section at the base (1c), upper view (1d) and occlusal view (1e). **2**: fixed finger NHMW 1860/0005/0008d in inner lateral view (2a), occlusal view (2b), cross section (2c) and outer lateral view (2d). **3**: fragmentary fixed finger NHMW 1860/0005/0008e. All specimens are to scale.

locality. However, since it is not known from which part of the section the holotype of *Callianassa sismondai* comes from, it is difficult to state its age; Early Miocene age is possible.

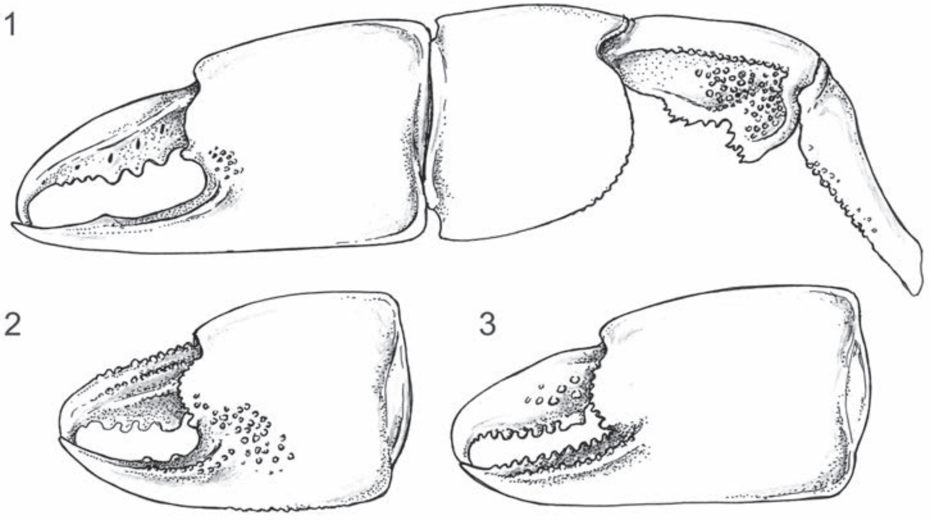

Fig. 12. Reconstruction of major chela of fossil *Balsscallichirus* Sakai, 2011. **1**: *Balsscallichirus florianus* (Glaessner, 1928) nov. comb. **2**: *Balsscallichirus sismondai* (A. Milne-Edwards, 1860) nov. comb. **3**: *Balsscallichirus laepaensis* (Hyžný & Muñiz, 2012) nov. comb.

Discussion: Sismonda (1846) reported and figured one specimen of supposed *Grapsus* sp. from Torino. Based on this specimen, A. Milne-Edwards (1860) described *Callianassa sismondai*. More specimens were later reported by Sismonda (1861) and Crema (1895), the repository of the material is, however, unknown and thus, considered lost. Crema (1895: fig. 4) figured one specimen showing entire chela including carpus, merus and ischium. Details, however, are not discernible. General outline of merus seems to match with *Balsscallichirus* as discussed above; however, considering the age of the publication, the possibility of imperfect depiction cannot be ruled out.

Glaessner (1928) reported three isolated or/and fragmented fingers from the Middle Miocene (Badenian) of Spielfeld, Austria (Figs 11.1–11.3). He attributed them to *C. sismondai*, noting that they fully conform to the figures and description given by Crema (1895). As noted above, it is difficult to judge the quality of figures by Crema (1895), especially as the original material is lost (De Angeli & Garassino 2006: p. 14). Moreover, it is questionable, whether fingers alone suffice for species identification. The original material of Glaessner (1928) is here depicted for the first time and is compared to the type material of *C. sismondai*. Although, there are similarities in the nature of preserved tubercles with the type specimen, the occurrence awaits confirmation in the future when more complete material is recovered.

The holotype of *Callianassa sismondai* (Fig. 10) shows close affinities to *B. florianus* nov. comb., specifically both species share general shape of propodus and armature of dactylus (Figs 12.1–12.2). Both species are considered congeneric. *Balsscallichirus sismondai* nov. comb. differs in possessing rather extensive tuberculation on both lateral surfaces of major propodus close to the base of the fixed finger and articulation with dactylus. In *B. florianus* nov. comb., the tuberculation area is restricted to only few tubercles at the notch between fingers (at the base of the fixed finger close to articulation with dactylus). Taxonomic significance of tuberculation in ghost shrimps, specifically in *Glypturus* STIMPSON, 1866, has been currently extensively discussed by HYŽNÝ & MÜLLER (2012), HYŽNÝ *et al*. (2013) and KLOMPMAKER *et al*. (2015) and considered to be taxonomically important on the species level.

Palaeobiogeography

In the geological past, distribution of fossil *Balsscallichirus* seems to be restricted to the Western Tethys Region (Fig. 13). *Balsscallichirus florianus* nov. comb. is restricted to Oligo-Miocene of the former Central Paratethys Sea which spread across the Central and Eastern Europe (HARZHAUSER & PILLER (2007). *Balsscallichirus sismondai* nov. comb. has been reported from the ?Early Miocene of Italy (A. MILNE-EDWARDS 1860; CREMA 1895), thus, it inhabited Proto-Mediterranean and most probably entered also Paratethys as documented by the questionable occurrence from the Styrian Basin (GLAESSNER 1928). *Balsscallichirus laepaensis* nov. comb. from the Late Miocene of Spain further documents the presence of the genus in the Proto-Mediterranean. Based on the material of *B. florianus* nov. comb. from the Oligocene of Hungary, the genus appears to originate in the Paratethys, however, based on postulated faunal immigrations from the Proto-Mediterranean to the Paratethys (KROH & HARZHAUSER 1999; HARZHAUSER *et al*. 2003; MANDIC 2004; MOISSETTE *et al*. 2006) it is reasonable to assume that the same scenario applies also for decapod crustaceans. For instance, both the Karpatian and Early Badenian mollusc faunas are typical migrational faunas coinciding with a marked transgressive event from the Mediterranean area into the Central Paratethys (HARZHAUSER *et al*. 2003). Thus, although not directly confirmed by the fossils, it seems likely that *Balsscallichirus* originated prior the biogeographic differentiation of the Western Tethys Region during the Oligocene or even sooner. This hypothesis may be supported by the ghost shrimp occurrence from the Late Eocene of Pakistan; SCHWEITZER *et al*. (2004) reported *Neocallichirus wellsi* SCHWEITZER, FELDMANN & GINGERICH, 2004 from the Priabonian of the Sulaiman Range in Balochistan. The figured material (SCHWEITZER *et al*. 2004: figs 4A–F) resembles *Balsscallichirus florianus* nov. comb. in several aspects. Propodus and carpus of both taxa have similar outline. The lower margin of merus of *N. wellsi* has hook and lobe armed with denticles. The outline of the merus is rather elongate, approaching the specimen of *B. florianus* nov. comb. in Fig. 6.5. The outer lateral surface of the merus of *N. wellsi* is, however, not preserved, only the inner surface is known. Similarly, dactylus is preserved only as its proximal portion, its ending and armature of occlusal surface is unknown. Knowing these details would be helpful for comparison of *N. wellsi* with *Balsscallichirus* spp. *Neocallichirus* SAKAI, 1988 is often used as a catch-all taxon for the fossil callichirine ghost shrimps and indeed, *N. wellsi* differs markedly from *Neocallichirus horneri* SAKAI, 1988, the

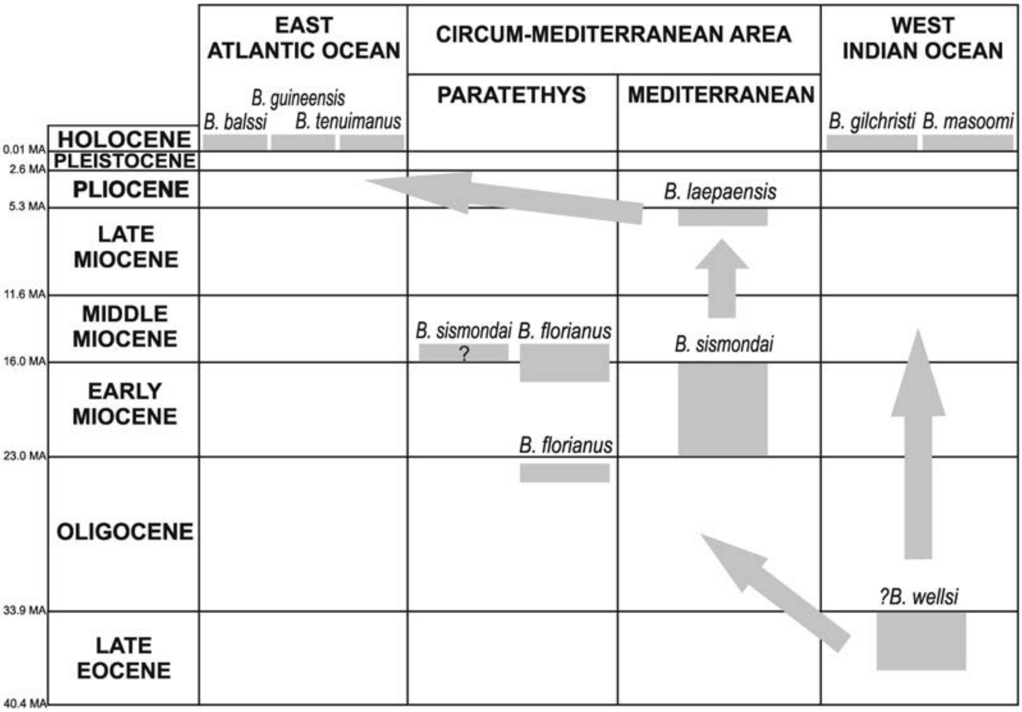

Fig. 13. Tentative biogeographical evolution of *Balsscallichirus* SAKAI, 2011.

type species of *Neocallichirus*. Therefore, *N. wellsi* is here tentatively assigned to *Balsscallichirus*. Re-examination of the material of *N. wellsi* is needed to confirm or reject its generic assignment. If, however, confirmed its attribution to *Balsscallichirus*, it would constitute the oldest known record of the genus having major impact on palaeobiogeographical implications.

Today, *Balsscallichirus* is restricted to West Indian and East Atlantic oceans, suggesting migration from the circum-Mediterranean area into the East Atlantic (Fig. 13).

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