



# After 100 years: a detailed view of an eumalacostracan crustacean from the Upper Jurassic Solnhofen Lagerstätte with raptorial appendages unique to Euarthropoda

PAULA G. PAZINATO , CLÉMENT JAUVION , GÜNTER SCHWEIGERT, JOACHIM T. HAUG  AND CAROLIN HAUG 

## LETHAIA



Pazinato, P. G., Jauvion, C., Schweigert, G., Haug, J. T., & Haug, C. 2020: After 100 years: a detailed view of an eumalacostracan crustacean from the Upper Jurassic Solnhofen Lagerstätte with raptorial appendages unique to Euarthropoda. *Lethaia*, <https://doi.org/10.1111/let.12382>.

The Solnhofen Konservat-Lagerstätte yields a great number of remarkably preserved fossils of eumalacostracan crustaceans that help us understand the early radiation of several groups with modern representatives. One fossil from there, *Francoecaris grimmi* Broili, 1917 is a small shrimp-like crustacean originally described about 100 years ago as a mysidacean crustacean (opossum shrimps and relatives) from latest Kimmeridgian – early Tithonian (Upper Jurassic) of the Solnhofen Lithographic Limestones of Southern Germany. New material with exceptionally preserved specimens, allied with modern imaging techniques (mostly composite fluorescence microscopy), allows us to provide a detailed re-description of this species. The most striking feature of *Francoecaris grimmi* is an extremely elongated thoracopod 7 with its distal elements forming a spiny sub-chela. This character supports a sister group relationship of *Francoecaris grimmi* with Eucopiidae, an ingroup of Lophogastrida, pelagic peracaridans common in marine environments throughout the world. We also discuss other supposed fossil representatives of Lophogastrida, identifying all of them as problematic at best. The structure of the sub-chela in *F. grimmi* indicates an original use in raptorial behaviour. *Francoecaris grimmi* appears to be unique in possessing such a far posterior sub-chelate appendage as a major raptorial structure. In most representatives of Euarthropoda in which sub-chelate appendages occur and are used for food intake, they are usually closer to the mouth. □ *Euarthropoda*, *eumalacostracan crustacean*, *Lophogastrida*, *raptorial*, *Solnhofen Lagerstätte*, *Upper Jurassic*.

Paula G. Pazinato ✉ [paula.pazinato@palaeo-evo-devo.info], Joachim T. Haug [joachim.haug@palaeo-evo-devo.info], Carolin Haug [carolin.haug@palaeo-evo-devo.info], Department of Biology II, LMU Munich, Großhaderner Straße 282152, Planegg-Martinsried, Germany; Clément Jauvion [clement.jauvion@mnhn.fr], Muséum national d'Histoire naturelle, CNRS UMR 7207, CR2P, Centre de Recherche en Paléontologie - Paris, Sorbonne Université, 8 rue Buffon, 75005, Paris, France; Clément Jauvion [clement.jauvion@mnhn.fr], Muséum national d'Histoire naturelle, CNRS UMR 7590, IRD, Institut de Minéralogie, de Physique des Matériaux et de Cosmochimie, IMPMC, Sorbonne Université, 61 rue Buffon, 75005, Paris, France; Günter Schweigert [guenter.schweigert@smns-bw.de], Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1 70191, Stuttgart, Germany; Joachim T. Haug [joachim.haug@palaeo-evo-devo.info], Carolin Haug [carolin.haug@palaeo-evo-devo.info], GeoBio-Center, LMU Munich, Richard-Wagner-Straße 1080333, München, Germany; manuscript received on 5/09/2019; manuscript accepted on 7/02/2020.

Today, malacostracan crustaceans are among the most prominent non-vertebrate components of faunas, especially of the marine environments. A major diversification of the group occurred in the late Palaeozoic and many of the modern lineages have fossil representatives in the Mesozoic (Klomp-maker *et al.* 2013). Our knowledge of the history of malacostracan crustaceans is, in many aspects, very detailed due to the presence of Konservat-Lagerstätten containing fossils with exceptional preservation. Among these are the Upper Jurassic lithographic limestones of Southern Germany, also referred to as Solnhofen Lithographic Limestones in a wide

sense (Barthel 1978; Barthel *et al.* 1990; Arratia *et al.* 2015).

The lithographic limestones of Southern Germany have yielded especially numerous representatives of Decapoda (Oppel 1862; Schweigert & Garassino 2004; Garassino & Schweigert 2006; Schweigert 2011, 2015; Schweigert *et al.* 2016), but also several representatives of Stomatopoda (Haug *et al.* 2009a, 2010). This also includes spectacularly well-preserved larval forms of both groups, only known from very few other localities. Among them are modern-looking larvae of spiny lobster-like crustaceans (Polz 1972, 1973; Haug *et al.* 2011a, 2014a), now extinct larval

types of spiny lobster-like crustaceans (Polz 1996; Haug *et al.* 2009b, 2013; Haug & Haug 2013, 2015, 2016; 2014a), remains of larval clawed lobsters (Haug & Haug 2017), modern-looking types of mantis shrimp larvae (Haug *et al.* 2008, 2015) and now extinct larval forms of mantis shrimps (Haug *et al.* 2009a, 2015). Likewise, representatives of Peracarida are well known from the lithographic limestones of Southern Germany (Polz 1998, 2003, 2004).

Peracarida is mainly represented by fossils of the group Isopoda and their close relatives (Tanaidacea). A peracaridan ingroup that is more challenging concerning the fossil record is Mysidacea, which includes Stygiomysida, Mysida (opossum shrimps) and Lophogastrida. The last two groups have been suggested as being represented in the fossil record (Hessler 1969; Schram 1986; Feldmann *et al.* 2017), yet most of the reported fossils remain problematic. This also accounts for fossils from the lithographic limestones of Southern Germany. Some fossils have been interpreted as representatives of Mysidacea, but all of them remain questionable (Röper 2005).

Mysidaceans are most likely less easily preserved as fossils, as most of them lack the well-calcified shields and tergites that are present in representatives of Decapoda and Isopoda. However, as the lithographic limestones of Southern Germany also preserved so many ‘soft’ larval forms, we should expect the preservation of the weakly calcified mysidaceans as well.

We provide here a re-description of the rather unusual-looking shrimp-like crustacean *Francocaris grimmi* Broili, 1917 from the lithographic limestones of Southern Germany. We discuss its possible identity as a mysidacean, more precisely a lophogastridan, and its implications for lophogastridan evolution and diversification.

## Geological setting

The records of *Francocaris grimmi* come from Solnhofen-type Konservat-Lagerstätten (‘Solnhofener Plattenkalke’ in German) of Franconia, Bavaria, Southern Germany (Fig. 1), a series of laminated limestones that represent deposits of carbonate particles in separated basins of low energy, confined waters at the northern margin of the Tethys Sea (Robin *et al.* 2013; Arratia *et al.* 2015). The fossils originally described by Broili (1917), and most of the new material available used for this study comes from the Konservat-Lagerstätte Zandt, east of Eichstätt in Bavaria. Some additional material is from the latest Kimmeridgian ‘Öchselberg’ limestones, near the small village of Breitenhill, which is a slightly

older deposit than the overlying Zandt Member, according to high-resolution biostratigraphical data based on ammonite assemblages (Schweigert 2007). The most recent discoveries of *Francocaris grimmi* are specimens from the Lower Tithonian Mörsenheim Formation of Daiting. *Francocaris grimmi* has not yet been detected outside the Franconian Jurassic.

## Material and methods

### Material

All available specimens considered to represent the species *Francocaris grimmi* Broili, 1917 were examined. The syntype series of Broili (1917) originally comprised five specimens, of which three are still available: SNSB – BSPG 2 I 17, 1917 I 2 and 1919 I 5 (Fig. 2P, C, L, respectively). The other two specimens are lost. Broili (1917) figured three specimens (his fig. A: SNSB – BSPG 2 I 17, fig. B: SNSB – BSPG 1919 I 5, fig. C: specimen lost). Since the original description, better-preserved material became available and is presented here. The syntype series of Broili (1917) and specimens SNSB – BSPG 1964 XXIII 592, 1982 I 78, 1983 I 153, 1983 I 154, 1984 I, 1986 I, 1986 I 7, 1986 I 8, 1986 I 9 are deposited in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. Specimens GSUB A241 and GSUB A242 are deposited at the Geosciences



Fig. 1. Map of Germany, illustrating the geographical sites of *Francocaris grimmi*. Occurrences of the fossils are marked with full dots.

Collection of the University of Bremen. Specimens SMNS 70520/1, SMNS 70520/2 and SMNS 70520/3 are deposited at the Staatliches Museum für Naturkunde in Stuttgart, all in Germany. From the 16 analysed specimens, two are preserved in ventral orientation (SNSB – BSPG 1964 XXIII 592 and SMNS 70520/1) and the remaining 14 are preserved in lateral orientation. Most of the samples are almost complete specimens; only pieces easily lost after the death of the animal are missing, such as appendages. The impressions most likely represent actual corpses, not exuviae, since the specimens are mostly articulated and there is preservation of internal tissue.

Extant specimens of *Eucopeia grimaldii* used for comparison are from the Zoologische Staatssammlung in Munich, and the specimen of *Eucopeia crassicornis* is from the Muséum national d'Histoire naturelle in Paris.

### Imaging methods

The specimens were documented either with micro- or macro-photography. The microscope used was an inverse fluorescence microscope Keyence BZ-9000, exploiting the auto-fluorescence capacities of the specimens (Haug *et al.* 2008, 2009a, 2011b). To



Fig. 2. Composite auto-fluorescence microscopy images of *Francocaris grimmii* specimens used for this study. All specimens to the same scale and with background removed. A, GSUB A242. B, SMNS 70520/1. C, SNSB – BSPG 1917 I 2. D, SNSB – BSPG 1986 I 7. E, SNSB – BSPG 1986 I 8. F, SNSB – BSPG 1983 I 154. G, SNSB – BSPG 1964 XXIII 592. H, GSUB A241. I, SMNS 70520/3. J, SNSB – BSPG 1986 I. K, SNSB – BSPG 1982 I 78. L, SNSB – BSPG 1919 I 5. M, SNSB – BSPG 1984 I. N, SMNS 70520/2. O, SNSB – BSPG 1986 I 9. P, SNSB – BSPG 2 I 17. Q, SNSB – BSPG 1983 I 153. Images C, G, H, I, O, P and Q were flipped horizontally. Original images can be found at: morphbase.de.



overcome the limited depth of field, stacks of images were recorded with shifting focus. The specimens too large to fit into a single image were documented with several adjacent image details, each with a stack of images. The fossils showed good auto-fluorescence under an excitation wavelength of 543 nm (TRITC, green light). For the extant specimens of *Eucopia grimaldii* Nouvel, 1942, we used white light with phase contrast, the TRITC wavelengths and also an excitation wavelength of 360 nm (DAPI, UV light).

For the extant specimens of *Eucopia crassicornis* Casanova, 1997 and the fossil specimen SMNS 70520/3, we used a Canon EOS Rebel T3i camera equipped with Canon MP-E 65 mm macro lens. Illumination was either provided by a Canon MT24 EX twin flash or two Yongnuo Digital Speedlite YN560 flashlights. Flashes were equipped with polarization filters. A perpendicular oriented filter was placed in front of the lens to achieve cross-polarized light, enhancing contrast and avoiding reflections (Haug et al. 2011c).

To fuse the stack of images, we used Combine ZP (free software). Stitching of the fused images of the fossils was performed in Adobe®Photoshop CS3. For the images of the extant representatives, we used Adobe®Photoshop Elements, using the Photomerge Panorama tool, either with the automatic algorithm or manual stitching (Haug et al. 2011b). Removal of the background and artificial colouring of the images were made using Adobe®Photoshop. The original images with background are deposited in the digital repository MorphDBase. The figures were created using the free software GNU Inkscape.

### Measurements and scatter plot

Once the specimens were documented, we used the images to take morphometrical measurements with ImageJ (public domain). The following measurements were taken from the fossils: (1) body length, from the anterior margin of the shield to the posterior margin of the sixth (last) pleon segment; (2) length of the sixth pleon segment; (3) height of the sixth pleon segment, from the middle of the segment; (4) length of the shield, from the dorso-anterior to the dorso-posterior margin of the shield; and (5) length of the prolongation of the shield, from the dorso-anterior margin of the shield to the rostral furrow (see paragraph ‘*Shield*’ in Results for explanation of the furrow).

The measurements were taken in millimetres and then normalized by dividing each of the values by the respective body length. From the normalized values, two ratios were formed: (1) length of sixth pleon segment/height of sixth pleon segment; and (2)

length of the shield/length of the prolongation of the shield. These two ratios were plotted against each other using LibreOffice (open source), and the plot was redesigned in Inkscape.

## Results

### General body organization

Shrimp-like body, slightly laterally compressed, mostly preserved in lateral aspect; two specimens preserved in dorso-ventral aspect, hence compression probably not strongly expressed (Fig. 2). Body organized presumably into 20 segments, ocular segment plus 19 post-ocular segments, forming three major functionally differentiated body regions: (1) functional head, including the ancestral eucrustacean head and some of the anterior thoracic segments (cephalothorax) dorsally forming the shield; (2) a series of posterior thoracic segments (pereion) with separate tergites for each segment; and (3) six more prominent segments forming the pleon (Fig. 3) and the telson articulated to it.

### Functional head

At least ocular segment and post-ocular segments 1–5 contribute to the head shield (eucrustacean ground pattern condition). Additionally, post-ocular segments 6–9 (thoracic segments 1–4) appear to lack a free dorsal identity (Figs 3K, 4C) and thus are interpreted as contributing to the shield, also being part of the functional head (cephalothorax).

### Shield

In lateral view, outline bottle-shaped; anterior region narrower, elongated, forming a kind of ‘neck’; shield widening towards the posterior end. Two prominent furrows running in anterior–posterior direction (Fig. 3D, E). First furrow extending backwards from antero-lateral margin, reaching to the region where the shield widens. Second one extending from antero-lateral margin backwards, not reaching the middle of the shield. Furrow arrangement in dorsal view not accessible due to orientation. Posterior shield margin almost straight, slightly concave, partly overhanging trunk segments laterally.

### Ventral structures of functional head

Ocular segment recognizable by prominent stalked eye structures (lateral eyes). Eyes extending forward beyond the anterior margin of the shield.



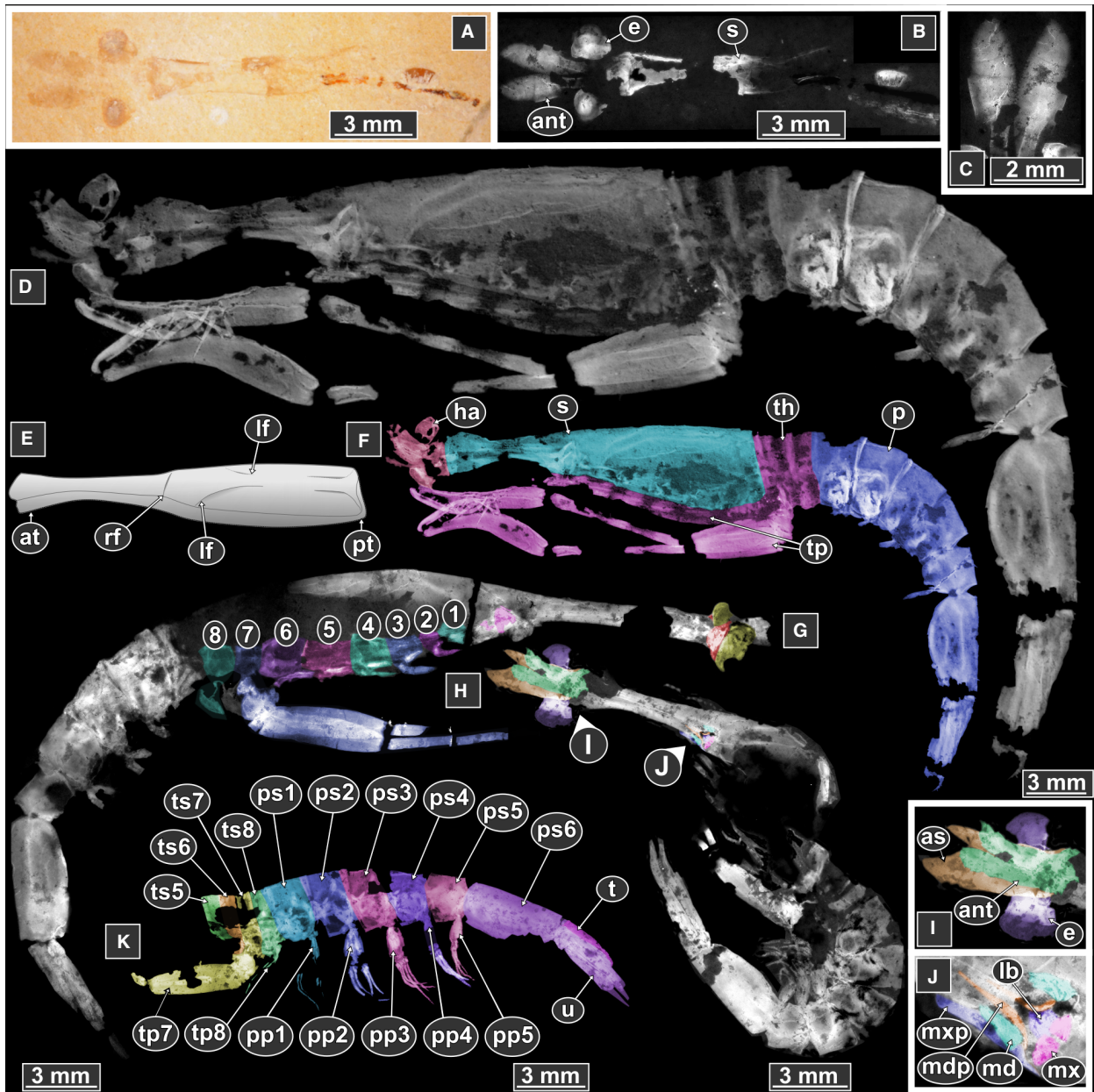


Fig. 3. *Francocaris grimmii*. A, macro-photography image. B–D, F–J, composite auto-fluorescence microscopy images. E, restoration drawing of the shield, based on specimens SNSB – BSPG 1983 I 154 and SMNS 70520/3. ant, antenna; as, antenna scale; at, anterior; e, eye; ha, head appendages; lb, labrum; lf, lateral furrow; md, mandible; mdp, mandibular palp; mf, median furrow; mx, maxilla; mxp, maxilliped; p, pleon; pp1–5, pleopod 1–5; ps1–6, pleon segment 1–6; pt, posterior; rf, rostrum furrow; s, shield; t, telson; th, thorax; ts5–8, thorax segment 5–8; tp(7–8), thoracopods (7–8); u, uropods.

Eye stalk ('ocular peduncle') short, cornea cylindrical and directing outwards (Figs 3G–I, 4A, B). Possible labrum present (Fig. 3J).

Post-ocular segment 1, recognizable by poor remains of appendages, antennulae. Antennula represented by two peduncle elements and two multi-articulated flagella arising from the distal part (Fig. 4A, B).

Post-ocular segment 2, recognizable by appendages, antennae. With proximal element (possible basipod; unclear if coxa is present or not) distally

bearing endopod and exopod (antennal scale; scaphocerite). Endopod proximally with three prominent elements (Fig. 5A). The proximal one (first) is the shortest. Second one is the longest, 3x longer than the first. Third element slightly longer than first (Fig. 5A, B). No remains of flagellum preserved. Exopod (antennal scale) spatulate; longer than the three elements of the endopod combined (Fig. 5A). Transversal furrow at about two-thirds along the proximal–distal axis of the antennal scale

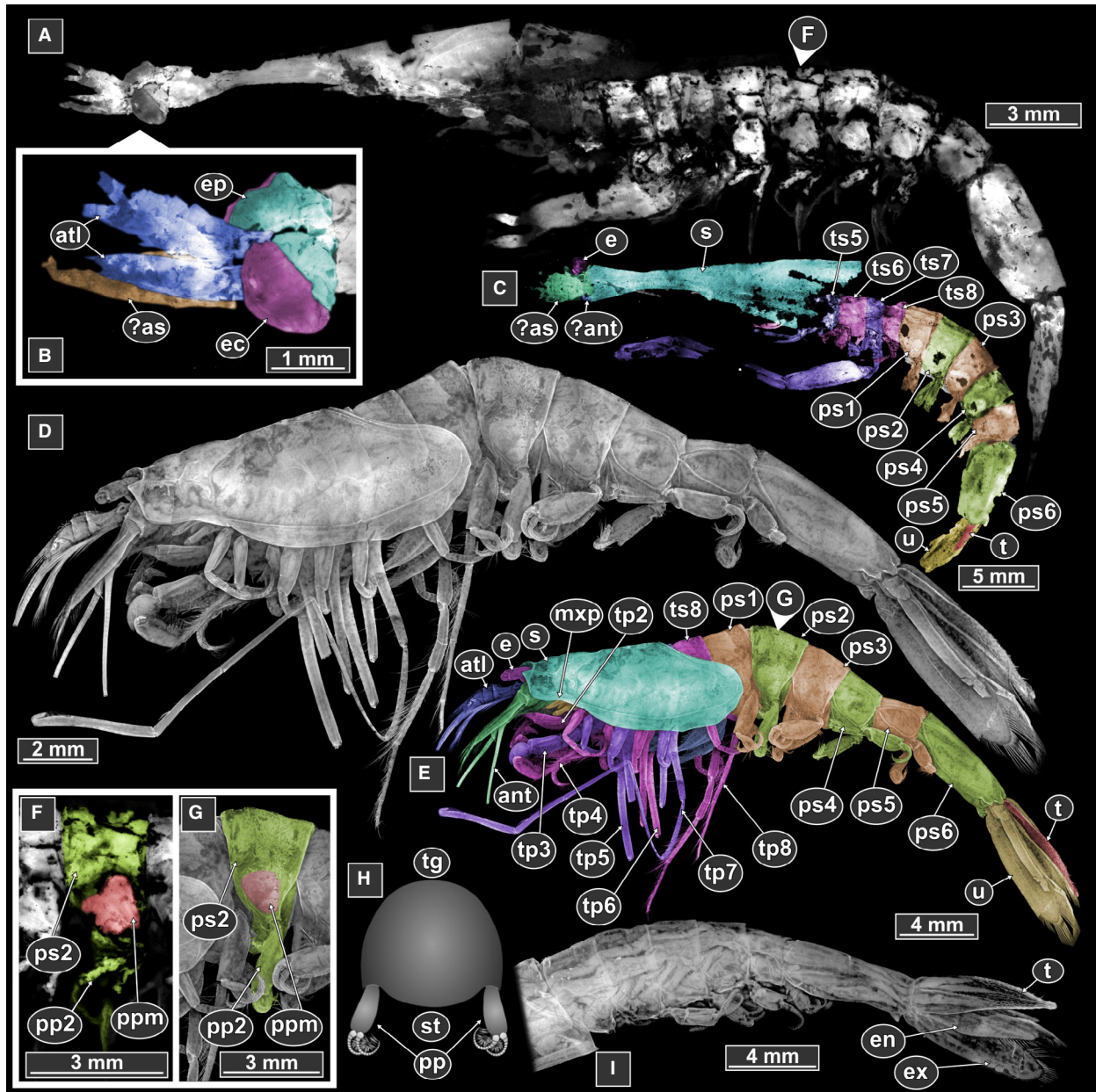


Fig. 4. Comparison of *Francocaris grimmi* and *Eucopeia grimaldii* in lateral view. A–C, F, composite auto-fluorescence microscopy images of *F. grimmi*. D, E, G, I, composite auto-fluorescence microscopy images of *E. grimaldii*. H, schematic drawing of a cross-section of the pleon segments of *E. grimaldii*. ant, antenna; ?ant, possible remains of antenna; ?as, possible remains of antennal scale; atl, antennula; e, eye; ec, eye cornea; en, endopod; ex, exopod; ep, eye peduncle; mxp, maxilliped; oo, oostegites; pp, pleopods; pp2, pleopod 2; ppm, pleopod musculature; ps1–6, pleon segment 1–6; s, shield; st, sternite; t, telson; tg, tergite; tp2–8, thoracopod 2–8; ts5–8, thorax segment 5–8; u, uropods.

(Fig. 5A). Margins of exopod apparently smooth, no setae or spines preserved. Exopod often broken at distal portion, remains of it present in several specimens.

Post-ocular segments 3–5, recognizable by possible remains of appendages (mouth parts). Appendages of post-ocular segment 3, mandibles, appear heavily sclerotized proximally (Figs 3H, J, 5A, 6B), with a long and thin distal part (mandibular palp). No

remains of maxillulae preserved. Indications of paired maxillae present.

Post-ocular segment 6, recognizable by proximal elements of an appendage; slightly differing from further posterior appendages, indicating that it might represent a specialized maxilliped (Fig. 3H, J).

Post-ocular segments 7–9, recognizable by proximal elements of rather slim-appearing appendages (Figs 3F, 4C).



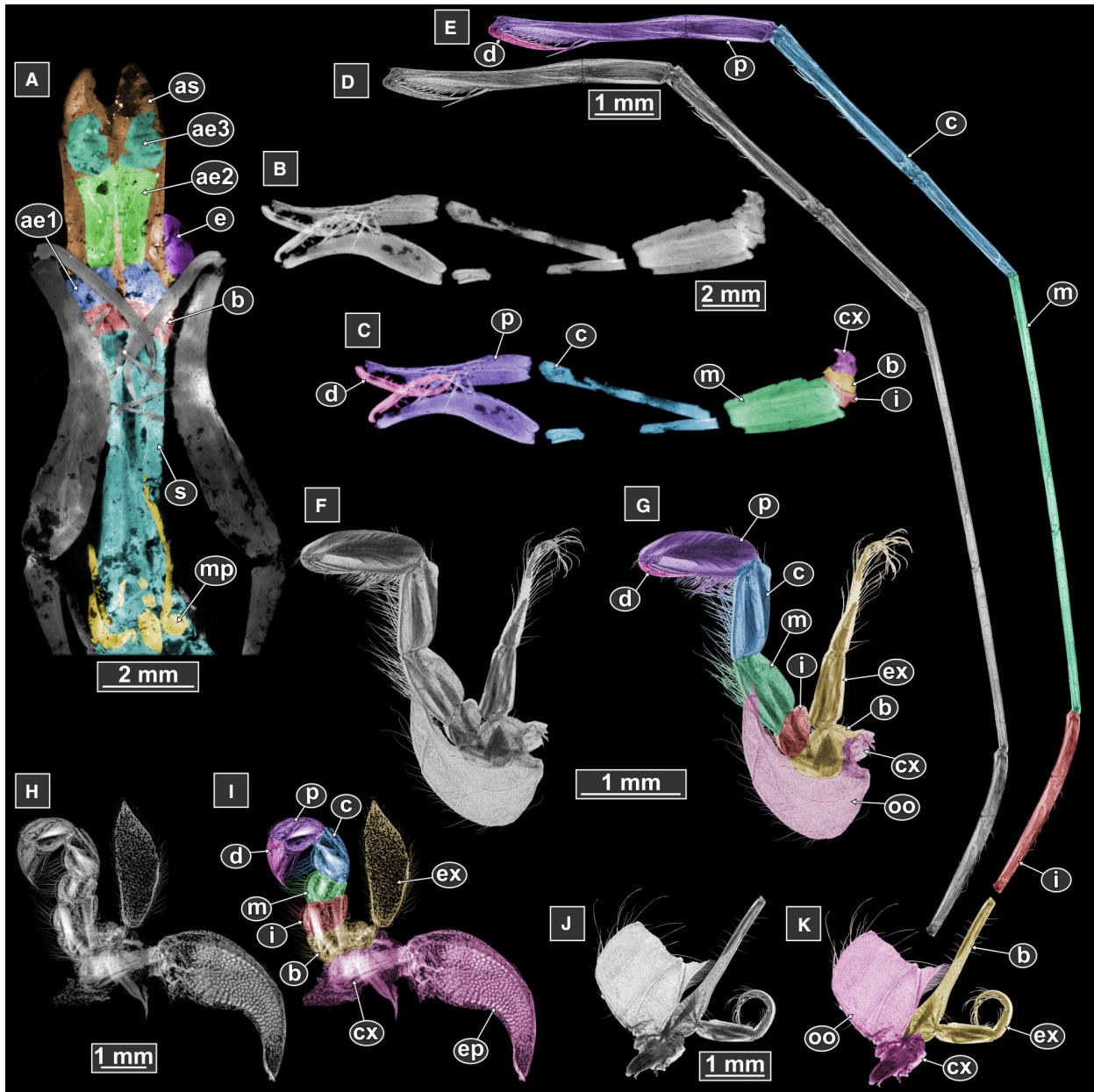


Fig. 5. Comparison of details of *Francocaris grimmii* and *Eucopia grimaldii*. A–C, composite auto-fluorescence images of *F. grimmii*. A, head region in ventral view. B, C, thoracopod 7. D–I, composite bright-field images of *E. grimaldii*. D, E, J, K, thoracopod 7. F, G, thoracopod 4. H, I, thoracopod 1 (maxilliped). ae1–3, antennal element 1–3; as, antennal scale; asf, antennal scale furrow; b, basipod; c, carpus; cx, coxa; d, dactylus; e, eye; ex, exopod; i, ischium; m, merus; mp, mouth parts; oo, oostegites; p, propodus; s, shield.

#### Free thorax segments (thoracic segments 5–8; post-ocular segments 10–13)

Post-ocular segments 10–13, with dorsal sclerotization (tergites). Similar in shape. Posterior margin of each segment overlapping with the anterior margin of the subsequent one (Figs 3K, 4C). Thoracic segment 5 (post-ocular segment 10) partially covered by the shield in lateral view. Posterior half of segment exposed. Thoracic segments 6, 7

and 8 (post-ocular segments 11, 12 and 13) increase gradually in length in anterior–posterior direction.

#### Appendages of free thorax segments

Remains of thoracopods preserved. Biramous (carrying an endopod and exopod). Slender endopods, distally broken off and remains of exopods, with no details due to poor preservation (Fig. 3G, K).



Thoracopod 7 entirely preserved, including the distal region (Fig. 5B, C). Extremely elongated, directed forwards. With seven elements, coxa, basipod, five endopod elements. No remains of exopod preserved. Coxa and basipod short. Ischium (endopod element 1) slightly shorter than basipod. Barrel-shaped merus (endopod element 2), middle portion almost twice the width of proximal and distal edges, widest of the elements. Slender and long carpus (endopod element 3), about twice the length of merus. Propodus (endopod element 4) slightly shorter than carpus. Proximal edge wide. Middle portion wider than distal edge. Distal edge slender. Curved backwards. Long spines at the mid-portion of the element. Dactylus (endopod element 5) slender, claw-shaped. About half the length of the propodus. Lateral edge smooth. Median edge armed with spines. Directed inwards, closing against the median edge of the propodus. Distal elements forming a jackknife-like sub-chela (Figs 5B, C, 6A, B).

### *Pleon*

Six segments and a telson. Each segment overlapping the subsequent one, with exception of pleon segments 5 and 6. All segments decreasing slightly in height. Pleon segments 1–5 slightly decreasing in length. Pleon segment 6 is the longest, about 2× longer than the previous one (Figs 4C, 6A, B). Elliptical structure on lateral face of pleon segments 1–5 (Fig. 4F), lacking in some specimens (Fig. 4C).

Pleon curved ventrally towards the thorax. Preservation varies from completely outstretched (Fig. 2G, Q) to angled from 50° to 90° in respect to the thorax (respectively, Fig. 2A, I).

### *Pleon appendages*

Pleopods 1–5 of similar length and shape, with proximal basipod, distally carrying two rami, endopod and exopod. Basipod longer than wide. Endopod and exopod long, slender and multi-annulated (Fig. 3K).

Pleopod 6, uropod, with proximal basipod, distally carrying two rami, endopod and exopod (Fig. 6A, B). Details difficult to determine due to poor preservation. Exopod longer than endopod, flat, scale-like. Posterior portion of the exopod appears to be multi-annulated.

### *Telson*

Telson about 70% the length of pleon segment 6; shorter than uropods. Margins apparently smooth and narrowing towards the posterior portion (Figs 3K, 6A, B).

### *Growth*

The measurements point to different size classes in the data set (Suppl S1). This variation in size indicates different ontogenetic stages. When we plot the normalized ratio of length of pleon segment 6/height of pleon segment 6 versus the normalized ratio of length of shield/length of prolongation of the shield, the data points form a rather continuous line (Fig. 7), indicating an ontogenetic series without strong allometric changes.

### *Preservation of internal tissue*

Remains of cylindrical digestive tube preserved along the midline of the body (Fig. 8A).

## Discussion

### *Morphological details observed*

Our re-investigation, especially with use of composite fluorescence microscopy, reveals new details of the morphology of *Francoecaris grimmi*, allowing a restoration of the species in lateral view (Fig. 9). The massive sub-chela-forming thoracic appendage inserts on thoracic segment 7. Broili (1917) suggested, with question mark, that the enlarged appendage could arise from the last thoracic segment, but could not determine the exact position and how it was attached to the thorax. The endopod of this appendage is extremely elongated, reaching the anterior margin of the shield in lateral view, and is present in every specimen, more or less complete. As for the other thoracic appendages, only poor slender remains are preserved in some of the fossils (Fig. 3D, F).

The pleon segments of *Francoecaris grimmi* each form a dorsal sclerite (tergite) and a ventral sclerite (sternite; Figs. 4H, 6B). The elliptical structures present on pleon segments 1–5 are most likely scars of musculature of the pleopods, as seen in extant species (compare Fig. 4F, G). These are not to be confused with the so-called pleural plates, a ventral extension of the tergite found in some representatives of Mysida and Lophogastrida (Wittmann *et al.* 2014).

Different ontogenetic stages of *F. grimmi* are preserved (Fig. 2). However, there seem to be no substantial changes of the morphology throughout growth (Fig. 7). Although one specimen showed considerable difference (specimen SMNS 70520/2, Fig. 2N), this is probably due to imprecise measurements caused by very poor preservation. However, as this is also the smallest specimen of the study, it was important to keep it in the data set.

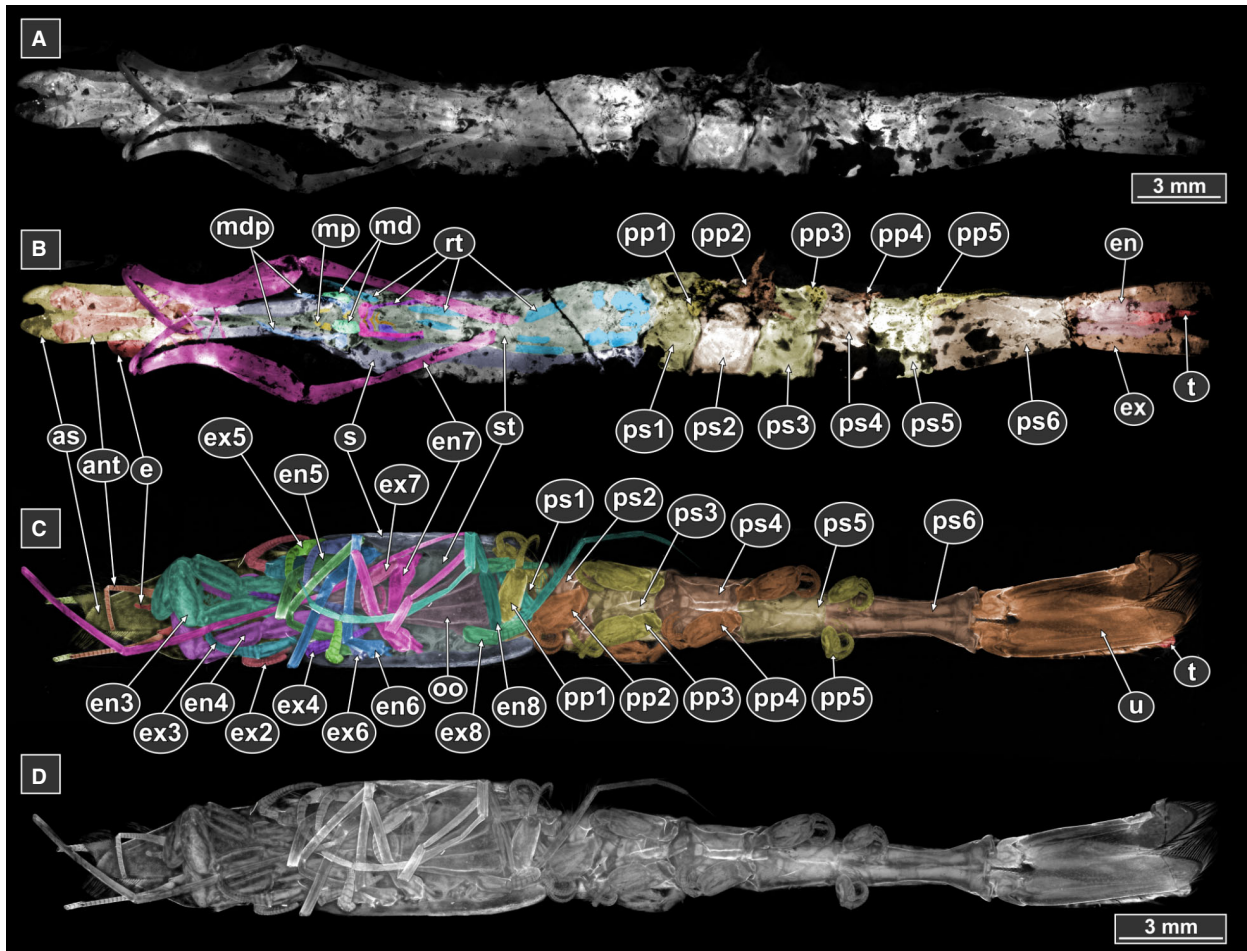


Fig. 6. Comparison of *Francocaris grimmi* and *Eucopia grimaldii* in ventral view; composite auto-fluorescence microscopy images. A, B, *F. grimmi*. C, D, *E. grimaldii*. Abbreviations: ant, antenna; as, antenna scale; e, eye; ec, eye cornea; en3–8, endopod of thoracopod 3–8; ep, eye peduncle; ex2–8, exopod of thoracopod 2–8; md, mandible; mdp, mandibular palp; mp, mouth parts; oo, oostegites; pp1–5, pleopod 1–5; ps1–6, pleon segment; rt, remains of thoracopods 1–6; s, shield; st, sternites; t, telson; u, uropods

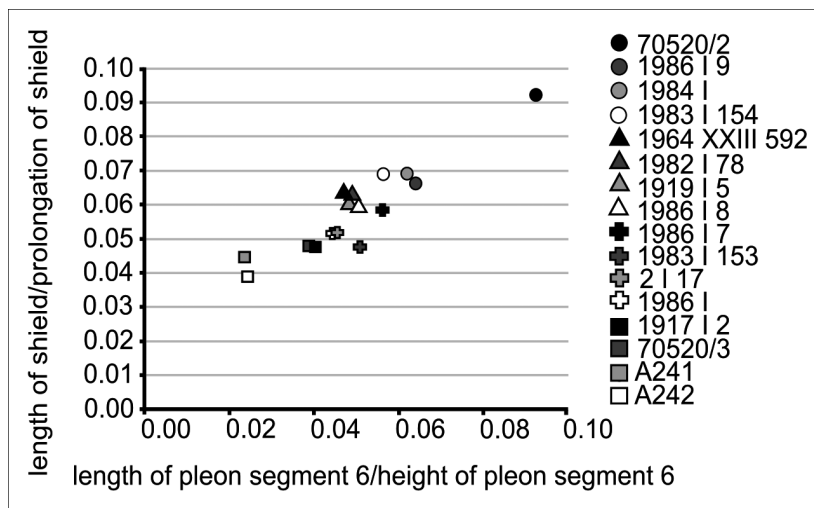


Fig. 7. Graphical representation of ontogenetic stages of *Francocaris grimmi* specimens used for this study. All values are normalized.

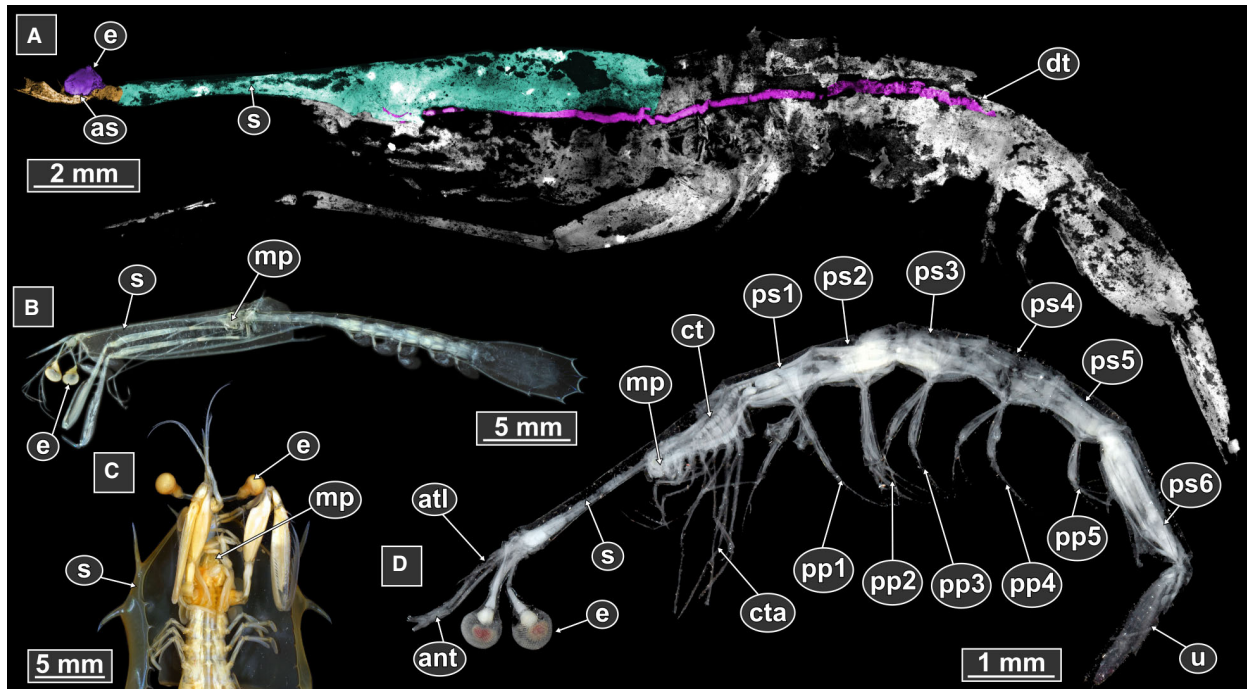


Fig. 8. Comparison of *Francocaris grimmi* with similar appearing crustaceans. A, composite auto-fluorescence image of *F. grimmi* in lateral view; note the preserved digestive tube. B, C, composite macro-photography images of mantis shrimp larvae. D, composite macro-photography image of a prawn (*Lucifer* sp.). ant, antenna; as, antennal scale; atl, antennula; ct, cephalothorax; cta, cephalothorax appendages; dt, digestive tube; e, eye; mp, mouth parts; pp1–5, pleopod 1–5; ps1–6, pleon segment 1–6; s, shield; u, uropods.

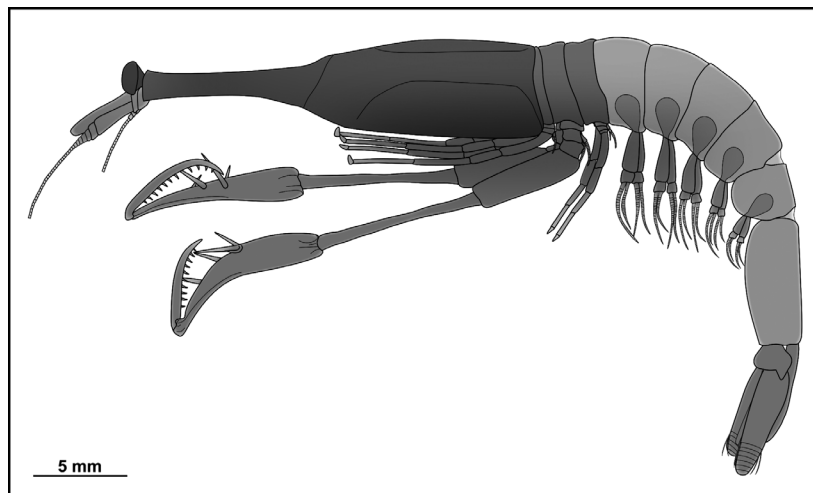


Fig. 9. Restoration of *Francocaris grimmi* Broili, 1917.

### *Systematic position of Francocaris grimmi: the historical view*

Broili (1917) described *F. grimmi* as a small crustacean with a very thin exoskeleton, which appeared poorly calcified. He assigned this fossil to the group ‘Thoracostraca’, today no longer considered to be a natural group. At the time, the group included shrimps, lobsters and similar crustaceans that

possessed a shield enveloping all or nearly all thoracic segments (post-ocular segments 6–14). From this group, he considered the fossil more closely related to Mysidacea (including Lophogastrida, Mysida and Stygiomysida). He based this decision on the shield being only formed by (‘attached to’) the anterior segments of the thorax but he expressed reservations due to the absence of modified posterior thoracic appendages, as present in *F. grimmi*, in



many (or most) extant species of Mysidacea. He therefore considered extant groups that possess such specialized appendages as, for example, species of *Stylocheiron*, a euphausiacean, commonly known as krill, as well as species of *Lucifer*, a decapodan prawn, which have an extremely elongated anterior region of the head (Fig. 8D). However, Broili (1917) also argued against a closer relationship of *F. grimmi* to Euphausiacea and Decapoda due to the organization of the cephalothorax, embracing all thoracic segments in the (adult) forms of these two groups.

#### *Systematic position of Francocaris grimmi: expanded view*

Due to the overall body organization, an ingroup position of *F. grimmi* within Eumalacostraca seems beyond doubt. It furthermore does not possess any of the prominent characters of adults of Hoplocarida (movable rostrum, triflagellate antennula, enlarged pleon). Likewise, no specialized characters of Syncarida are apparent (most important, the very short shield).

One might now argue that by identifying *F. grimmi* as a eumalacostracan and by excluding Hoplocarida, Syncarida, Decapoda and Euphausiacea, a closer relationship to Neocarida seems likely. Yet, it is less simple than that. The presence of free thoracic tergites and a long shield is, of course nowadays, only found within Mysidacea, hence an ingroup of Neocarida and Peracarida, but both characters are plesiomorphies. Thus, in principle also many forms of the early evolution of Eumalacostraca branching off all the mentioned lineages will possess such a morphology. Still, we will concentrate in the following on identifying possible apomorphic characters for Mysidacea or one of its ingroups in *F. grimmi*.

The relationships of the three major ingroups of Mysidacea (Lophogastrida, Mysida and Stygiomysida) have been heavily debated in the last few decades (see Wittmann *et al.* 2014 for a review), especially due to the fact that phylogenetic reconstructions based on morphological characters (Wirnkner & Richter 2007, 2010) differ from the ones based on molecular data (Spears *et al.* 2005; Meland & Willassen 2007). Currently, the monophyly of Lophogastrida (Richter 2003) and Mysida (Wittmann 2013) is strongly supported. The monophyly of Stygiomysida is not clear, and its position within Mysida or as sister group of Mysida remains open (Meland & Willassen 2007; Meland *et al.* 2015).

Representatives of Mysidae (large ingroup of Mysida) possess a statocyst, a balance organ, in the proximal part of the endopods of the uropods (Wittmann *et al.* 2014). The lack of this character has been

used to separate lophogastridans from mysidans (Meland *et al.* 2015; Feldmann *et al.* 2017). However, this character alone only helps to exclude a species or specimen from being an ingroup of Mysidae. *Franco-caris grimmi* does not seem to possess a statocyst and is therefore unlikely a representative of Mysidae.

So far, known representatives of Mysida and Stygiomysida possess straight 'pediform' endopods on the posterior thoracopods. Although sub-chelate appendages occur in ingroups of Mysida (Petalophthalminae and Heteromysinae), these are positioned more anteriorly on the body, on thoracopods 1 and 2 in Petalophthalminae and on thoracopod 3 in Heteromysinae. Only Lophogastrida species are known to possess sub-chelate thoracic appendages arising far posterior on the body, comparable to those apparently present in *F. grimmi*.

#### *Lophogastrida*

The group Lophogastrida consists of four ingroups: Peachocarididae (with exclusively fossil representatives), Gnathophausiidae, Eucopiidae and Lophogastridae; the last three groups have extant representatives. These four groups are distinguished mainly (but not only) by the number of thoracic appendages with their distal elements forming sub-chelae (Wittmann *et al.* 2014).

Peachocarididae Schram, 1986 was erected to accommodate two fossil species from the Carboniferous of the United States of America, *Peachocaris strongi* (Brooks, 1962) and *Peachocaris acanthouraea* Schram, 1984 (Schram 1986). *Peachocaris strongi* was originally described as *Anthracophausia strongi* by Brooks (1962) and then renamed as *Peachella strongi* by Schram (1974). Yet, as the name *Peachella* was already occupied for a Cambrian trilobite, Schram (1976) changed the name again to *Peachocaris strongi*.

It is unlikely that Peachocarididae represents a natural group. In fact, it is even questionable that both fossil species are representatives of Lophogastrida at all. *P. strongi* was also considered to be a fossil representative of Euphausiacea (Brooks 1962) because of its caridoid appearance and all thoracopods being biramous and unmodified. Yet, it was reinterpreted as a lophogastridan (Schram 1974, 1976; 1986). The characters used for this interpretation are as follows: 'well-developed abdominal pleura, pleopods, and thoracopods (this last with a well-developed peduncle at the base of the exopods), and the apparent lack of uropodal statocysts' (Schram 1986, p. 124). As already pointed out, these characters are all plesiomorphies. The apparent lack of a statocyst tends to exclude the fossils from being a

representative of the ingroup Mysidae, but does not support a position within Lophogastrida.

*Peachocaris acanthoura* is based on isolated fossil remains of the last three pleon segments and the tail fan (Schram 1984). With this, it provides even fewer characters arguing for lophogastridan affinities than *P. strongi*. Peachocarididae is therefore not further considered here.

As mentioned above, the three groups of Lophogastrida with extant representatives are easily distinguished by the number of thoracic endopods with the distal elements forming a sub-chela. In representatives of Lophogastridae and Gnathophausiidae, the first and/or the second thoracopods are modified, forming a distal sub-chela; the remaining thoracic endopods are pediform, while in representatives of Eucopiidae, thoracopods 2–7 are modified, forming a sub-chela (Wittmann et al. 2014). Hence, as in *F. grimmi*, the thoracopod 7 bears a sub-chela in the latter.

### Eucopiidae

Eucopiidae includes eight species in the modern fauna, all in *Eucopia*. In all representatives of *Eucopia*, the first pair of thoracopods is modified into maxillipeds (Fig. 5H, I) and thoracopods 2, 3 and 4 are short, strong and sub-chelate (Fig. 5F, G), strongly contrasting with slender and elongate sub-chelate thoracopods 5–7 (Fig. 5D, E, J, K; Wittmann et al. 2014). Thoracopod 8 is also slender, but not as elongated as the previous ones and does not possess a sub-chela (Wittmann et al. 2014).

At least six fossil species have been interpreted as representatives of Eucopiidae: *Schimperella benecke* Bill, 1914, *Schimperella kessleri* Bill, 1914, *Schimperella accanthocercus* Taylor, Schram & Yan-Bin, 2001, *Yunnanocopia grandis* Feldmann, Schweitzer, Hu, Huang, Zhou, Zhang, Wen, Xie, Schram, Jones, 2017, *Yunnanocopia longicauda* Feldmann, Schweitzer, Hu, Huang, Zhou, Zhang, Wen, Xie, Schram, Jones, 2017, and *Eucopia praecursor* Secrétan & Riou, 1986. Yet, all these fossils do not clearly possess apomorphies of the group, but are characterized by plesiomorphies.

*Schimperella kessleri* and *Schimperella benecke* come from the Triassic (Olenekian to Anisian, ~251 to 245 Ma) of France. A relationship to Eucopiidae was based on the fact that ‘medium thoracic legs are the longest, and the dactylus is formed as a strong and slightly curved claw’ (Bill 1914, p. 313; translated from German original). Yet, the joint responsible for the maximum curvature of the supposed claw appears to be between the carpus and propodus, not between the propodus and dactylus. The joint

between dactylus and propodus appears straight, as seen in pediform appendages. In addition, the surface of the appendages is smooth, not armed with spines. A similar arrangement seems present in *Schimperella accanthocercus* (Taylor et al. 2001) and *Schimperella* sp. (Larghi & Tintori 2007; Kri nar & Hitji 2010).

*Yunnanocopia grandis* and *Yunnanocopia longicauda* were both described from the Anisian (~245 Ma, Middle Triassic) of China (Feldmann et al. 2017). Unfortunately, thoracopods are not preserved in any of the two species. The characters used for the association with Eucopiidae represent similarities and are all plesiomorphies within Peracarida. These are, for instance, absence of pleural plates, presence of pleopods and at least six pairs of oostegites (specialization of thoracic epipods of females that support the brood pouch).

*Eucopia praecursor* is from the Callovian (~165 Ma, Middle Jurassic) of France. The species is known only from two specimens from the La Voulté Lagerstätte. It is a small shrimp-like crustacean, about 20 mm long, which possesses three to four free thoracic segments and elongated and slender thoracopods. The combination of these two characters was used to place *E. praecursor* within Eucopiidae (Secrétan & Riou 1986). Unfortunately, the distal portion of the thoracopods is not well preserved. Therefore, it remains unclear whether it possesses sub-chelae.

Hence, none of the supposed fossil representatives of Eucopiidae shows clear apomorphic characters of this group. For species of *Schimperella*, it remains unclear whether they are representatives of Peracarida at all. Their habitus is compatible with several positions within Eumalacostraca. The species of *Yunnanocopia* can be identified as representatives of Peracarida based on the presence of oostegites, yet any further narrowing down remains impossible. The species *praecursor* Secrétan & Riou, 1986 could in principle be in fact an ingroup of Eucopiidae and *Eucopia*, based on the elongate thoracopods, yet without preservation of the distal elements this remains a rather weak character. Given the uncertainties of all so far supposed fossil representatives of Eucopiidae, we restrict further comparison to the more informative extant forms.

### Could *Francocaris grimmi* be a representative of Eucopiidae?

*Francocaris grimmi* shares with modern representatives of Eucopiidae, hence those of *Eucopia*, the presence of an elongated thoracopod 7 with a sub-chela formed by propodus and dactylus, both elements being armed with spines. There are no clear apomorphic characters of Neocarida, Peracarida, or

Lophogastrida visible in *F. grimmi*, yet the observable details are at least compatible with such an interpretation.

Unfortunately, it remains unclear how the distal parts of thoracopods 2–6 were organized in *F. grimmi*. It is possible that all of them were sub-chelate (as in representatives of *Eucopia*), yet we simply lack this detail. The complexity of the shared character – sub-chelate, elongate thoracopod 7 armed with prominent spines – provides at least a conclusive indication of a close relationship of *F. grimmi* and *Eucopia*, yet it depends on a number of assumptions on the morphology of *F. grimmi* that have not been directly observed. This does not only account for the distal parts of the anterior thoracopods, but also, for example, for a marsupium formed by oostegites in females.

Furthermore, if accepting a possible sister group relationship of *F. grimmi* and *Eucopia* there are still two possibilities for the reconstruction of character evolution: (1) the stem species ( $\approx$  last common ancestor) of both could have possessed three elongate thoracopods (5–7) and this condition was retained by *Eucopia*, while the presence of only one long sub-chelate appendage is an autapomorphy of *F. grimmi*; (2) the stem species could have had only one long appendage, *F. grimmi* retained the long thoracopod 7, and the presence of three of such appendages is an autapomorphy of *Eucopia* (Fig. 10).

Based on the discussion of the morphology of *F. grimmi* and different ingroups of Eumalacostraca above, we propose that *F. grimmi* is a representative of the Lophogastrida ingroup Eucopiidae.

### Comparative morphology: morphological peculiarities of *Francocaris grimmi*

There are three morphological aspects of *Francocaris grimmi* that demand further consideration in a comparative frame:

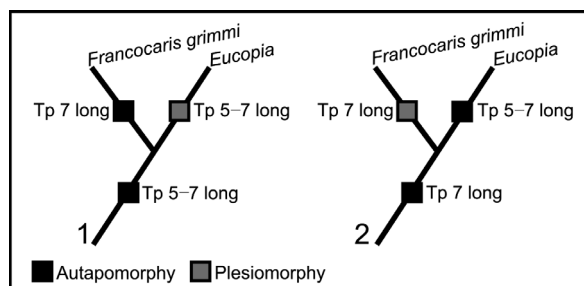


Fig. 10. Two hypotheses about the presumed character evolution on the lineage towards *Francocaris grimmi* and the species of *Eucopia*. Tp, thoracopod.

*The elongation of the anterior head region.* – Comparing *F. grimmi* to its possible closer relatives, the elongation of the anterior head region is clearly an autapomorphic character of this species. However, such elongations by which the segments of the eyes, antennulae and antennae are separated by a long distance from the next segment, that is that of the mandibles, are known in some other representatives of Eumalacostraca.

As Broili (1917) noted, such a morphology is known in prawns of the group *Lucifer* (Fig. 8D). Other groups of Eumalacostraca show such an elongation especially in their larval forms, for example the alima-type larvae of mantis shrimps (Fig. 8B, C), although in adults mantis shrimps the distance between the antennae and the mandibles is also quite large (Haug *et al.* 2012). Other larvae with an elongated anterior region of the head are those of spiny and slipper lobsters (Palero *et al.* 2014), and of the species *Amphionides reynaudii* (Kutschera *et al.* 2012).

It is interesting to note that this character appears to have independently evolved in at least three different types of larvae. Also, the adults of *Lucifer* appear larviform overall and are regularly misidentified as larvae in many plankton samples (own observations from different museum collections). It is therefore tempting to suggest that the extreme elongation in *F. grimmi* is originally a type of larval character retained into adulthood. Yet, as it is an ingroup of Peracarida, its ontogeny does not include a pronounced larval phase. Hence, there is no support for such assumption. Moreover, the reverse, the elongation extending over ontogeny, appears to be unlikely too, based on the known preserved specimens forming part of the ontogeny.

*The structure of the sub-chela.* – The propodus and dactylus of thoracic appendage 7 form a prominent grasping structure. The principle arrangement is generally categorized as a sub-chela. Yet, the propodus is not straight, and it is curved laterally, changing some of its functional aspects. ‘Normal’ sub-chelae with straight propodi have to grasp around the to-be-grasped object as the angle of opening is directed strongly backwards. A true chela can grasp an object from behind, as the opening angle is oriented forward.

Mantis shrimps optimize their prey catching by the principle Z-shaped arrangement of the entire appendage. By this arrangement, the angle of opening becomes shifted further anteriorly. The sub-chela of *F. grimmi* probably allowed to grasp around an object in a similar way to mantis shrimps. The propodus, laterally curved outwards, provides an



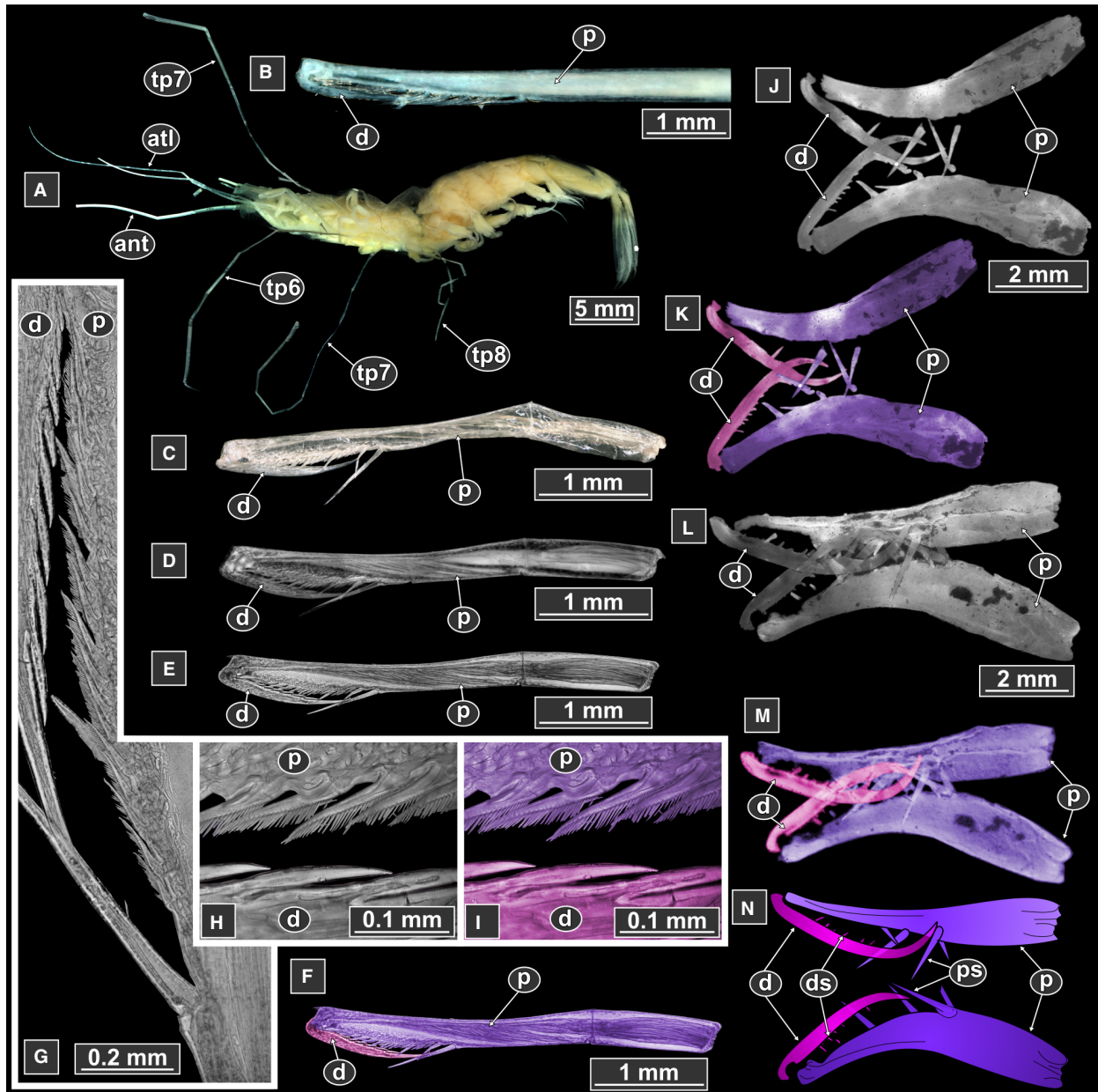


Fig. 11. Comparison of the sub-chelae of thoracopod 7 of different species. A, B. *Eucopia crassicornis*. A, overview. B, close-up of sub-chela. C–I, *Eucopia grimaldii*. G–I, high magnification images (60× objective, resulting in c. 600× magnification) of the sub-chela, showing the inner row of spines of the dactylus and inner row of spine-like-setae of the propodus. J–N, *Francoecaris grimmeri*. Abbreviations: ant, antenna; atl, antennula; d, dactylus; ds, dactylus spines; p, propodus; ps, propodus spines; tp6–8, thoracopod 6–8.

arrangement distantly comparable to the Z-shaped appendages in mantis shrimps.

Similarities in size, equipment with massive spines, and the optimization of the opening angle of *Francoecaris grimmeri* and mantis shrimps provide an indication that *F. grimmeri* likewise used its appendages for grasping prey items. Unfortunately, we do not know details about the feeding behaviour of extant representatives of *Eucopia* which could provide additional indications for the feeding biology of *F. grimmeri*.

Although also heavily armoured, the sub-chelae in representatives of *Eucopia* are significantly smaller than those of *F. grimmeri* also indicating differences in possible prey size (Fig. 11).

*Position of the appendage bearing the sub-chela.* – Sub-chelate appendages occur in various lineages of Euarthropoda (Fig. 12). Yet, those of *F. grimmeri* are remarkable in that they are so far posterior. Within Euechelicerata, sub-chelate appendages are known on

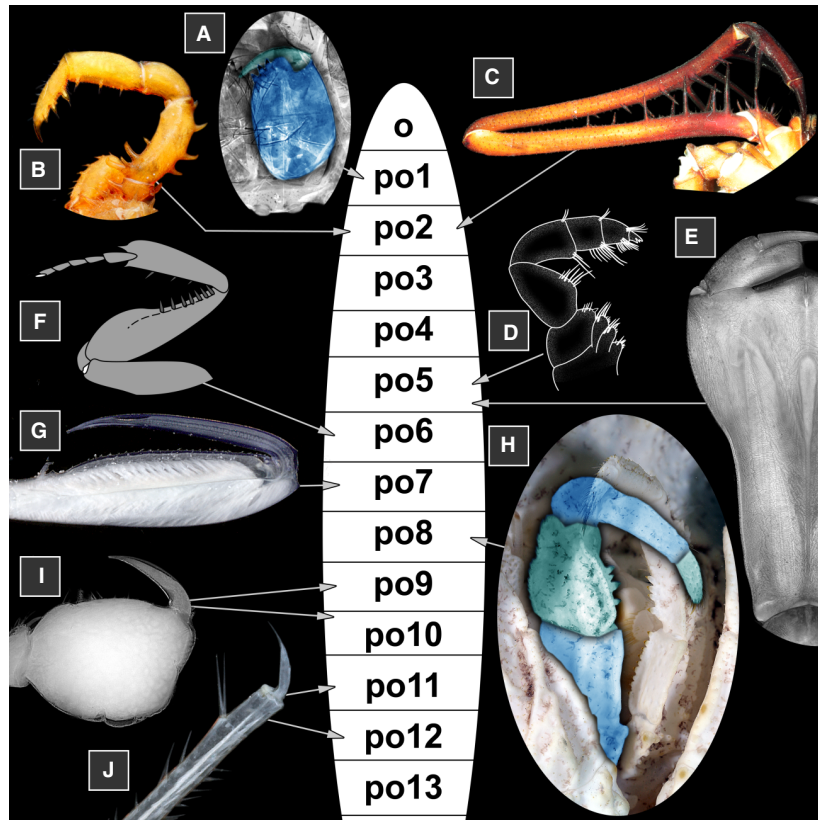


Fig. 12. Schematic drawing of the head and thoracic region of a euarthropod, illustrating the position of grasping appendages in different groups. A, chelicera of a web spider. B, pedipalp of an armoured harvestman. C, pedipalp of a whip spider. D, maxilla of a remipedian; from Haug *et al.* (2014b). E, labium of a dragonfly larva. F, raptorial leg of a fossil cockroach, from Dittmann *et al.* (2015). G, I, raptorial leg of stomatopod larvae. H, maxilliped 3 of a slipper lobster. J, raptorial appendage of a phyllosoma larva. Abbreviations: o, ocular segment; po1–13, post-ocular segment 1–13.

post-ocular segment 1, for example the chelicera in web spiders (Araneae), and also on post-ocular segment 2, for example the pedipalp in armoured harvestmen (Opiliones, Laniatores), dwarf whip scorpions (Schizomida) and whip spiders (Amblypygi).

Further rather anterior sub-chelate appendages are present in remipedian crustaceans on post-ocular segments 4, 5 and 6, that is maxillula, maxilla and maxilliped. Many representatives of Insecta also have sub-chelate appendages on these segments. The 'raptorial mask' of odonatan larvae is in principle arranged as two sub-chelae, as this derived labium represents the conjoined appendages of post-ocular segment 5. Numerous examples can be found for sub-chelate appendages on post-ocular segment 6, for example in mantises (Mantodea) and their closer relatives (Dittmann *et al.* 2015), water scorpion bugs (Nepidae, Belostomatidae), mantis lacewings (Mantispidae) and many others. In mantis shrimps, this appendage has also a small sub-chela, yet it is clearly not used for grasping, but for cleaning.

The most anterior functional sub-chelate appendage in mantis shrimps arises from post-ocular

segment 7. The following segments, post-ocular segments 8–10, have sub-chelate appendages as well. Comparably, the sub-chelate 'gnathopods' of amphipodan crustaceans arise from post-ocular segments 7 and 8. More rarely also some forms of Insecta have sub-chelate appendages on post-ocular segment 7, such as gladiators (Mantophasmatodea) or predatory bush crickets (Saginae), and on post-ocular segment 8 (larval forms of Trichoptera).

*Francocaris grimmi* is hence rather unusual in having a sub-chelate appendage on post-ocular segment 12. As pointed out, modern forms of *Eucopia* also have a sub-chela on this segment. Other examples are 'podotrematan' brachyuran crabs and phyllosoma larvae of spiny and slipper lobsters. 'Podotrematan' crabs use the sub-chelate appendages on post-ocular segment 12 and 13 to carry objects allowing them to hide or better camouflage under them (Guinot & Wicksten 2015). Phyllosoma larvae appear to grab prey with their sub-chela-like appendages on post-ocular segments 9–12 (Jefferies 2007).

Therefore, besides *F. grimmi* only extant species of *Eucopia* and phyllosoma larvae appear to use sub-

chelate appendages on post-ocular segment 12 for feeding. Like in *F. grimmi*, these are very elongated. Yet, unlike in *F. grimmi*, in phyllosoma larvae several pairs of appendages are involved in preying, while it appears that *F. grimmi* relied primarily on this elongated appendage. This appears to be a so far unique type of morphology and supposed feeding strategy.

## Conclusions

In this re-description of *Francoecaris grimmi* Broili, 1917, we report new details of the species concerning its systematic interpretation, its evolution and its morphology:

- 1 The presence of the elongated and sub-chelate thoracic appendage 7 appears to be a synapomorphy of *F. grimmi* and *Eucopia*, hence an autapomorphy of Eucopiidae, including *F. grimmi*. Other characters of *F. grimmi* are in concordance with this suggestion, such as well-developed pleopods and pleon segments without projecting pleurae.
- 2 Due to the lack of apomorphic characters, most supposed fossil representatives of Eucopiidae should be treated with caution.
- 3 The presence of a massive sub-chela, heavily armoured with spines, suggests that *Francoecaris grimmi* was a predator.
- 4 The use of mainly the appendages of post-ocular segment 12 for preying would so far be unique for Euarthropoda.

*Acknowledgements.* – We thank Alexander Nützel and Mike Reich from the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Matthias and Marina Wulf, Rödelsee, Martin Sauter, Freising, Roger Frattigiani, Laichingen, and Udo Resch, Eichstätt, for providing the fossil specimens that made this study possible. We thank also Stefan Friedrich and Roland Melzer from the Zoologische Staatssammlung München for kindly loaning the extant material of *E. grimaldii*, and Laure Corbari from Muséum national d'Histoire naturelle, Paris, for providing access to the specimen of *E. crassicornis*. We are grateful to the institutions who kindly funded this project: Capes/Doctoral Program (Process n° 88887.161379/2017-00; PGP), Dept. Origines et Evolution, MNHN (project PerSysT; CJ), Deutsche Forschungsgemeinschaft (DFG Ha 6300/3–2; JTH), LMU (LMUexcellent; CH) and Volks-wagen Foundation (Lichtenberg professorship; JTH). We thank Rodney Feldmann and an anonymous reviewer for their very helpful comments on an earlier version of this paper. P. G. Pazinato and C. Jauvion contributed equally to the paper.

## Data availability statement

Original images of this study are available in the MorphDBase digital repository: <<http://morphdbase.de>>

## References

- Arratia, G., Schultze, H.P., Tischlinger, H. & Viohl, G. 2015: *Solnhofen – Ein Fenster in die Jurazeit*, 620 pp. Dr Friedrich Pfeil Verlag, München.
- Barthel, K.W. 1978: *Solnhofen. Ein Blick in die Erdgeschichte*, 393 pp. Ott Verlag, Thun.
- Barthel, K.W., Swinburne, N.H.M. & Conway Morris, S. 1990: *Solnhofen: A Study in Mesozoic Palaeontology*, 236 pp. Cambridge University Press, Cambridge.
- Bill, P.C. 1914: Über Crustaceen aus dem Voltziensandstein des Elsasses. *Mitteilungen der Geologischen Landesanstalt von Elsaß-Lothringen* 8, 289–338.
- Broili, F. 1917: Eine neue Crustaceen-(Mysidaceen-)Form aus dem lithographischen Schiefer des oberen Jura von Franken. *Centralblatt für Mineralogie, Geologie und Paläontologie* 19, 426–429.
- Brooks, H.K. 1962: The Paleozoic Eumalacostraca of North America. *Bulletins of American Paleontology* 44, 163–335.
- Dittmann, I.L., Hörnig, M.K., Haug, J.T. & Haug, C. 2015: *Raptoblatta waddingtonae* n. gen. et n. sp. – an Early Cretaceous roach-like insect with a mantodean-type raptorial foreleg. *Palaediversity* 8, 103–111.
- Feldmann, R.M., Schweitzer, C.E., Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., Schram, F.R. & Jones, W.T. 2017: Earliest occurrence of lophogastrid mysidacean arthropods (Crustacea, Eucopiidae) from the Anisian Luoping Biota, Yunnan Province, China. *Journal of Paleontology* 91, 100–115.
- Garassino, A. & Schweigert, G. 2006: The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions (infraorders Astacidea, Thalassinidea, and Palinura). *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia naturale in Milano* 34, 1–64.
- Guinot, D. & Wicksten, M.K. 2015: Camouflage: carrying behaviour, decoration behaviour, and other modalities of concealment in Brachyura. In Castro, P., Davie, P.J.F., Guinot, D., Schram, F.R. & Von Vaupel Klein, J.C. (eds): *Decapoda: Brachyura (Part 1), Treatise on Zoology-Anatomy, Taxonomy, Biology*, volume 9C–I, 583–638. Brill, Leiden and Boston.
- Haug, J.T. & Haug, C. 2013: An unusual fossil larva, the ontogeny of achelatan lobsters, and the evolution of metamorphosis. *Bulletin of Geoscience* 88, 195–206.
- Haug, J.T. & Haug, C. 2015: 'Crustacea': Comparative aspects of larval development. In Wanninger, A. (ed): *Evolutionary Developmental Biology of Invertebrates 4: Ecdysozoa II: Crustacea*, 1–37. Springer, Vienna.
- Haug, J.T. & Haug, C. 2016: 'Intermetamorphic' developmental stages in 150 million-year-old achelatan lobsters – The case of the species *tenera* Oppel, 1862. *Arthropod Structure & Development* 45, 108–121.
- Haug, J.T. & Haug, C. 2017: A new glimpse on Mesozoic zooplankton—150 million-year-old lobster larvae. *PeerJ* 5, e2966.
- Haug, J.T., Haug, C. & Ehrlich, M. 2008: First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). *Palaediversity* 1, 103–109.
- Haug, C., Haug, J.T. & Waloszek, D. 2009a: Morphology and ontogeny of the Upper Jurassic mantis shrimp *Spinosculda ehrlichi* n. gen. n. sp. from southern Germany. *Palaediversity* 2, 111–118.
- Haug, J.T., Haug, C., Waloszek, D., Maas, A., Wulf, M. & Schweigert, G. 2009b: Development in Mesozoic scyllarids and implications for the evolution of Achelata (Reptantia, Decapoda, Crustacea). *Palaediversity* 2, 97–110.
- Haug, J.T., Haug, C., Maas, A., Kutschera, V. & Waloszek, D. 2010: Evolution of mantis shrimps (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. *BMC Evolutionary Biology* 10, 290.
- Haug, J.T., Haug, C., Waloszek, D. & Schweigert, G. 2011a: The importance of lithographic limestones for revealing ontogenies in fossil crustaceans. *Swiss Journal of Geosciences* 104, 85–98.
- Haug, J.T., Haug, C., Kutschera, V., Mayer, G., Maas, A., Liebau, S., Castellani, C., Wolfram, U., Clarkson, E.N.K. & Waloszek,



- D. 2011b: Autofluorescence imaging, an excellent tool for comparative morphology. *Journal of Microscopy* 244, 259–272.
- Haug, C., Mayer, G., Kutschera, V., Waloszek, D., Maas, A. & Haug, J.T. 2011c: Imaging and documenting gammarideans. *International Journal of Zoology* 2011, 1–9.
- Haug, C., Sallam, W.S., Maas, A., Waloszek, D., Kutschera, V. & Haug, J.T. 2012: Tagmatization in Stomatopoda – reconsidering functional units of modern-day mantis shrimps (Verunipeltata, Hoplocarida) and implications for the interpretation of fossils. *Frontiers in Zoology* 9, 1–14.
- Haug, J.T., Ah Yong, S., Haug, C., Audo, D., Charbonnier, S. & Haug, C. 2013: Diversities of developmental patterns in achelate lobsters—today and in the Mesozoic. *Development Genes and Evolution* 223, 363–373.
- Haug, J.T., Ah Yong, S. & Haug, C. 2014a: Fossil malacostracan larvae. In Martin, J.W., Olesen, J. & Høeg, J.T. (eds): *Atlas of Crustacean Larvae*, 176–179. The Johns Hopkins University Press, Baltimore.
- Haug, C., Briggs, D.E.G., Mikulic, D.G., Kluessendorf, J. & Haug, J.T. 2014b: The implications of a Silurian and other thylacocephalan crustaceans for the functional morphology and systematic affinities of the group. *BMC Evolutionary Biology* 14, 1–15.
- Haug, C., Wiethase, J.H. & Haug, J.T. 2015: New records of Mesozoic mantis shrimp larvae and their implications on modern larval traits in stomatopods. *Palaeodiversity* 8, 121–133.
- Hessler, R.R. 1969: Peracarida. In Moore, R.C. (ed.): *Treatise on invertebrate paleontology. Part R. Arthropoda, volume 4*, 360–393. Geological Society of America, Boulder and University of Kansas Press, Lawrence.
- Jeffs, A. 2007: Revealing the natural diet of the phyllosoma larvae of spiny lobster. *Bulletin Fisheries Research Agency Japan* 20, 9–13.
- Klomp maker, A.A., Schweitzer, C.E., Feldmann, R.M. & Kowalewski, M. 2013: The influence of reefs on the rise of Mesozoic marine crustaceans. *Geology* 41, 1179–1182.
- Kri nar, M. & Hitji, T. 2010: Nevretenčarji (Invertebrates) Strelovski formacije. *Scopolia (Ljubljana)* 5, 91–107.
- Kutschera, V., Maas, A., Waloszek, D., Haug, C. & Haug, J.T. 2012: Re-study of larval stages of *Amphionides reynaudii* (Malacostraca: Eucarida) with modern imaging techniques. *Journal of Crustacean Biology* 32, 916–930.
- Larghi, C. & Tintori, A. 2007: First record of a decapod from the Meride Limestone: new data from one of the best Ladinian (Middle Triassic) taphonomic windows of a transitional environment. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 35, 68–69.
- Meland, K. & Willassen, E. 2007: The disunity of ‘Mysidacea’ (Crustacea). *Molecular Phylogenetics and Evolution* 44, 1083–1104.
- Meland, K., Mees, J., Porter, M. & Wittmann, K.J. 2015: Taxonomic review of the orders Mysida and Stygiomysida (Crustacea, Peracarida). *PLoS ONE* 10, e0124656.
- Oppel, A. 1862: Ueber jurassische Crustaceen. *Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates* 1, 1–120.
- Palero, F., Clark, P.F. & Guerao, G. 2014: Achelata. In Martin, J.W., Olesen, J. & Høeg, J.T. (eds): *Atlas of Crustacean Larvae*, 272–278. The Johns Hopkins University Press, Baltimore.
- Polz, H. 1972: Entwicklungsstadien bei fossilen Phyllosomen (Form A) aus den Solnhofener Plattenkalken. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 11, 678–689.
- Polz, H. 1973: Entwicklungsstadien bei fossilen Phyllosomen (Form B) aus den Solnhofener Plattenkalken. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 5, 284–296.
- Polz, H. 1996: Eine Form-C-Krebslarve mit erhaltenem Kopfschild (Crustacea, Decapoda, Palinuroidea) aus den Solnhofener Plattenkalken. *Archaeopteryx* 14, 43–50.
- Polz, H. 1998: *Schwegerella strobili* gen. nov. sp. nov. (Crustacea: Isopoda: Sphaeromatidea), eine Meeres-Assel aus den Solnhofener Plattenkalken. *Archaeopteryx* 16, 19–28.
- Polz, H. 2003: Eine neue Assel aus den Solnhofener Plattenkalken (Crustacea: Isopoda: Sphaeromatidea). *Archaeopteryx* 21, 3–12.
- Polz, H. 2004: Asselansammlung auf einer Wasserwanze aus den Solnhofener Plattenkalken. *Archaeopteryx* 22, 51–60.
- Richter, S. 2003: The mouthparts of two lophogastrids, *Chalaraspidium alatum* and *Pseudochalaraspidium hansenii* (Lophogastrida, Peracarida, Malacostraca), including some remarks on the monophyly of the Lophogastrida. *Journal of Natural History* 37, 2773–2786.
- Robin, N., Charbonnier, S., Bartolini, A. & Petit, G. 2013: First occurrence of encrusting nubeculariids (Foraminifera) on a mobile host (Crustacea, Decapoda) from the Upper Jurassic Eichstätt Lagerstätte, Germany: a new possible relation of phoresy. *Marine Micropaleontology* 104, 44–52.
- Röper, M. 2005: Lithographic Limestones and Plattenkalk Deposits of the Solnhofen and Mörnsheim Formations near Eichstätt and Solnhofen. *Zitteliana* B26, 71–85.
- Schram, F.R. 1974: The Mazon Creek caridoid Crustacea. *Feldiana, Geology* 30, 9–65.
- Schram, F.R. 1976: *Peachocaris*, a new name for *Peachella* Schram, 1974, non Walcott, 1910. *Journal of Paleontology* 50, 994.
- Schram, F.R. 1984: Upper Pennsylvanian arthropods from black shales of Iowa and Nebraska. *Journal of Paleontology* 58, 197–209.
- Schram, F.R. 1986: *Crustacea*, 606 pp. Oxford University Press, New York.
- Schweigert, G. 2007: Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 245, 117–125.
- Schweigert, G. 2011: The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: a historical review and some recent discoveries. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260, 131–140.
- Schweigert, G. 2015: Zehnfüßkrebse (Decapoda) und andere Krebstiere. In Arratia, G., Schultze, H.P., Tischlinger, H. & Viohl, G. (eds): *Solnhofen – Ein Fenster in die Jurazeit*, 271–291. Verlag Dr Friedrich Pfeil, München.
- Schweigert, G. & Garassino, A. 2004: New genera and species of shrimps (Crustacea: Decapoda: Dendrobranchiata, Caridea) from the Upper Jurassic limestones of Southern Germany. *Stuttgarter Beiträge zur Naturkunde B* 350, 1–33.
- Schweigert, G., Garassino, A. & Pasini, G. 2016: The Upper Jurassic Solnhofen decapod crustacean fauna: Review of the types from old descriptions. Part II. Superfamily Penaeoidea and Infraorder Caridea. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia naturale in Milano* 41, 3–40.
- Secrétan, S. & Riou, B. 1986: Les Mysidacés (Crustacea, Peracarida) du Callovien de la Voulte-sur-Rhône. *Annales de Paléontologie (Vert.-Invert.)* 72, 295–323.
- Spears, T., Debry, R.W., Abele, L.G. & Chodyla, K. 2005: Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). *Proceedings of the Biological Society of Washington* 118, 117–157.
- Taylor, R.S., Schram, F.R. & Yan-Bin, S. 2001: A new upper Middle Triassic shrimp (Crustacea: Lophogastrida) from Guizhou, China, with discussion regarding other fossil ‘Mysidaceans’. *Journal of Paleontology* 75, 310–318.
- Wirkner, C.S. & Richter, S. 2007: The circulatory system in Mysidacea – Implications for the phylogenetic position of Lophogastrida and Mysida (Malacostraca, Crustacea). *Journal of Morphology* 268, 311–328.
- Wirkner, C.S. & Richter, S. 2010: Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). *Cladistics* 26, 143–167.
- Wittmann, K.J. 2013: Comparative morphology of the external male genitalia in Lophogastrida, Stygiomysida, and Mysida (Crustacea, Eumalacostraca). *Zoomorphology* 132, 389–401.
- Wittmann, K.J., Ariani, A.P. & Lagardère, J.P. 2014: Orders Lophogastrida Boas, 1883, Stygiomysida Tchindonova, 1981, and Mysida Boas, 1883 (also known collectively as Mysidacea). In Vaupel Klein, J.C., Charmanier-daures, C. & Schram, F.R. (eds): *Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea, volume 4, Part b*, 189–396. Brill, Leiden.

## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Supplement S1.** Measurements of shield and last pleon segment of *Francocharis grimmii*. Raw values and values divided by body length.