

# Exceptionally preserved ostracods from a Middle Miocene palaeolake, California, USA

I.P. WILKINSON<sup>1</sup>, P.R. WILBY<sup>1</sup>, M. WILLIAMS<sup>2</sup>, D.J. SIVETER<sup>2</sup>, A.A. PAGE<sup>3</sup>,  
L. LEGGITT<sup>4</sup> & D.A. RILEY<sup>2</sup>

<sup>1</sup>*British Geological Survey, Keyworth, Nottingham NG12 5GG, UK (e-mail: ipw@bgs.ac.uk)*

<sup>2</sup>*Department of Geology, University of Leicester, Leicester LE1 7RH, UK*

<sup>3</sup>*Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2  
3EQ, UK*

<sup>4</sup>*Department of Earth and Biological Sciences, Loma Linda University, Loma Linda,  
CA 92350, USA*

**Abstract.** Exceptionally well-preserved specimens of a new cypridid ostracod (Crustacea), *Raepula ira* sp. nov., are described from palaeolake sediments of the Middle Miocene Barstow Formation of the Mud Hills, southern California. This is only the second occurrence of exceptionally preserved ostracods from the Miocene. Based on ages obtained from associated volcanic tuffs the palaeolake sediments were deposited between 16.3 and 15.8 Ma. The ostracods form one element of a diverse lake community dominated by fairy shrimps, copepods, diatoms, larvae of diving beetles, flies and mosquitoes, and body fossils and ephippia of branchiopods and anomopods. The ostracods are preserved three-dimensionally with their soft anatomy replicated in microcrystalline silica. Sub-micron scale details such as sensory setae are preserved, surpassing the resolution of most other ostracod-bearing lagerstätten and allowing their biology to be compared with extant taxa.

**Key words:** Ostracoda, Miocene, morphology, taphonomy, California

**Supplementary material:** Red-blue anaglyphs of the exceptionally preserved ostracods are available at <http://www.geolsoc.org.uk/SUP00000>.

Of the estimated 30,000 species of fossil ostracods only about 20 species are known from their soft anatomy. Rare mummified Quaternary ostracods have been recorded (e.g. Schmidt & Sellman 1966; Horne *et al.*, 1990) and records of soft-parts from older geological deposits extend back to the Palaeozoic (see Smith 2000; Siveter *et al.* 2003, 2007; Siveter 2008). Most are of marine ostracods (e.g. Siveter *et al.* 2003, 2007), although exceptionally preserved non-marine ostracods have been reported, for example from Eocene Baltic amber (Keyser & Weitschat 2005) and from lake sediments of the Middle Miocene of the Antarctic (Williams *et al.* 2008a; Lewis *et al.* 2008). The taxonomy of living freshwater ostracods is based principally on soft-part anatomy such as appendages and genitalia, with shell morphology taking a secondary role. Rare occurrences of soft anatomy preservation in the fossil record are an important way of testing whether shell-based taxonomies are realistic (see Siveter 2008; Williams *et al.* 2008b, for discussion of this problem). Here we report a new exceptionally preserved ostracod fauna from Middle Miocene palaeolake sediments of southern California (Fig. 1).

### **Neogene freshwater ostracods from southwest USA**

Ostracod faunas from Neogene palaeolakes are widely documented from the southwest part of the USA (e.g. Swain *et al.* 1971), but studies have largely focussed on taxonomic appraisal of shell material, rather than on interpretation of the palaeoenvironmental significance of the faunas: none of these deposits have yielded ostracods with soft anatomy. These palaeolake successions yield faunas of about 20 ostracod species (e.g. Swain 1987, 1990; Swain & Wagoner 1979, 1985), although diversity in any single sample

is between two and ten species. More than 40 ostracod species have been described from the Oligocene and Miocene Indian Well and Humboldt formations of north-eastern Nevada (Swain 1986). A succession of Miocene through Holocene freshwater ostracod faunas has been recognised in the Colorado Plateau and Great Basin (Swain and Wagoner, 1985), where the Early and Middle Miocene is characterised by species of *Tuberoocypris* and *Heterocypris*.

### **The Barstow Konservat Lagerstätte**

The Middle Miocene Barstow Formation of California is an approximately 1000m thick succession of lacustrine and fluvial deposits divided into the lower Owl Conglomerate Member and the informal 'Middle' and 'Upper' members (Woodburne *et al.* 1990) (Fig. 2). Ostracods with preserved soft anatomy occur in the 'Middle' Member (*ca* 570 m thick), which comprises grey and green-grey fluvial conglomerates and conglomeritic sandstones that pass laterally eastwards into low energy sandstones and lacustrine grey and green-grey mudstones with infrequent limestone and concretion horizons.

A number of volcanic tuff horizons distributed throughout the formation have provided a basis for geochronology (Woodburne *et al.* 1990). The base of the 'Middle' Member is locally defined by the Rak Tuff (16.3 $\pm$ 0.3 Ma). The concretions that bear ostracods with soft tissues occur 62.5m above the Rak Tuff, and approximately half way between it and the Oreodont Tuff (15.8 $\pm$ 0.3 Ma). The silicified ostracods therefore probably date to the latest Burdigalian, although an earliest Langhian age cannot be ruled out (= Hemingfordian Stage of local American usage).

The microfauna of the Barstow Konservat Lagerstätte has yielded three-dimensionally preserved insects including diving beetle larvae (*Schistomerus californensis*), flies (*Dasyhelea australis antiqua* and *Culicoides*), mosquitos (Anopheles), midges, thrips and wasps (*Hymenoptera*), together with abundant fairy shrimps (Anostraca), wolf spiders (Lycosidae), copepods, diatoms (*Craticula*, *Dimidiata*, *Amphora*, *Nitzschia* and *Anomoeoneis*) and body fossils and ephippia of zooplankton such as Branchiopoda and Anomopoda (Palmer & Bassett 1954; Palmer, 1957; Park 1995; Belk & Schram 2001; Park & Downing 2001; Miller & Lubkin 2001; Leggitt 2003, 2005, 2006; unpublished data). During the history of the lake, the faunal composition and insect diversity changed significantly, probably due to differences in water chemistry, a shift of the shoreline due to shallowing and increased aridity (Park & Downing 2001).

Within the 'Middle' Member several stratigraphical levels yield carbonate concretions (Park, 1995, Park & Downing, 2001). The ostracods reported here are from a single horizon of concretions at a site 17km north of Barstow in the "Rainbow Basin Canyon" in the Mud Hills, (grid reference North 35.023716 West 117.040819; Fig. 1). This locality is near to the type section of the Barstow Formation. The concretions yielded an ostracod fauna of one or possibly two species; the possible second species is known from only very rare and poorly preserved specimens. The ostracod diversity of the concretion horizon from palaeolake Barstow is, therefore, similar to other Neogene samples from the American Southwest.

## **The palaeoenvironment of Lake Barstow**

Both the palaeontological and sedimentological evidence indicate that Lake Barstow was a shallow, poorly-mixed, saline-alkaline lake in a warm temperate environment (Park & Downing 2001). The concretion-bearing sediments contain zeolites, borates, sulphates and low-Mg calcite, and are associated with evaporite beds and diatomites. The brine pathways postulated for these concretion-bearing deposits indicate high salinity and dysaerobic conditions (Park 1995). The presence of fairy shrimp, midges, diatoms and ostracods is consistent with this palaeoenvironmental interpretation. Fairy shrimp are restricted to environments lacking endemic predators, such as vernal pools or alkaline lakes (Pennak 1989); they are not known from waters with pH below 6.8 and some species may withstand up to pH 9.5. Fairy shrimp require a minimum salinity of 3% NaCl, and may withstand extremely high salinities (Ward 1992). Though the juvenile stages of the biting midge *Dasyhelea* favour saline environments, they can only tolerate salinities below 14% NaCl (Ward 1992). Likewise, presence of the diatoms *Craticula halophila* and *Dimidiata saccula* suggest a saline-alkaline lake environment (Hajos 1974; European diatom dataset 1996). A poorly-mixed, shallow lake environment is in accord with the presence of biting midges and ostracods (Pennak 1989), and the presence of non-biting midges is consistent with low oxygenation. Changes in faunal composition, sedimentology and isotopic data all indicate an increase in aridity and evaporation during the time in which the concretion bearing horizons were deposited (Park 1995; Park & Downing 2001); the widespread gypsum deposits overlying the youngest

concretion horizon in the Calico Mountains indicate the onset of more dominantly playa lake conditions.

Lake Barstow was probably ecologically similar to the Recent saline-alkaline lakes of the western United States (Park & Downing 2001), such as Mono Lake (California), Big Soda Lake (Nevada) and Soap Lake (Washington), and the lateral continuity of lake sediments is more consistent with a permanent lake rather than a vernal pool (Park 1995). The allochthonous fauna and flora suggest the area surrounding the lake was dominated by grassland (*Euscelis*, *Miogonates*, etc.) with small, scattered patches of woodland (indicated by the termite *Cybocelus*) located in a California slightly cooler and wetter than the present day (Park & Downing 2001). Tufas and volcanic rocks occur in adjacent coeval deposits, and the presence of borates in the lake deposits indicates both a hydrothermal and volcanic influence on lake chemistry (Park 1995; Park & Downing 2001; Smith & Medrano 1996). Considering this, and that the lake formed at a time of active tectonic extension (Woodburne *et al.* 1990), the lakes of the East African Rift Valley may also provide a good analogue for the geological setting.

The ecological requirements of *Raepula ira* gen. et sp. nov. are difficult to determine without recourse to the associated fauna and sediments, because the Family Cyprididae occupies a variety of mileux, including temporary water bodies, and tolerates a broad spectrum of salinities, alkalinities and oxygen content. Based on the palaeoenvironmental setting and associated biota, *Raepula ira* was probably polythermophilic and rheophobic (*sensu* Meisch, 2000), and occupied permanent saline-alkaline

lakes, in shallow, poorly mixed, dysaerobic waters, with a salinity between 3 and 14% NaCl and a pH greater than 6.8.

### **Systematic Palaeontology**

Figured specimens prefixed OUMNH are deposited in the University of Oxford Museum of Natural History, Parks Road, Oxford OX1 3PW and those prefixed LACMIP have been placed in the Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles CA 90007.

Class Ostracoda Latreille, 1806

Order Podocopida Sars 1866

Suborder Cypridocopina Jones 1901

Superfamily Cypridoidea Baird 1845

Family Cyprididae Baird, 1845

Subfamily Eucypridinae Bronstein, 1947

Genus *Raepula* gen. nov.

Type species: *Raepula ira* gen. et sp. nov.

*Derivation of name:* Latin, *rarus* (rare) + *epula* (a feast); alluding to the scarcity of ostracod fossils with preserved soft-parts; and *ira* (rainbow), referring to the type locality. Gender, feminine.

*Diagnosis:* Carapace laterally elongate and sub-reniform with seven elongate adductor muscle scars. First antenna large, with a sub-rectangular basipod and six podomeres. Second antenna has an endopod comprising three podomeres and a tiny, slender exopod. The first podomere bears a 'baseball bat' shaped aesthetasc.

Mandible has a large elongate sub-triangular coxa and an endopod comprising three podomeres. First maxilla has a large basipod; an endopod with one long and one short podomere; three curved endites; and a crescent-shaped branchial plate bearing at least eleven marginal setae. Second maxilla has an endite with at least ten distal setae and a tapered endopod terminating in possibly three setae in the female and a hook in the male. Sixth appendage has a large, curved basipod geniculate with a ramus consisting of four podomeres, the fourth having two stout apical setae and terminating in a large curved claw. Seventh appendage consists of a basipod and ramus with three podomeres, the terminal one bearing a small pincer organ and two elongate setae. Furca consists of a proximally fused pair of un-segmented rami, each with two large distal claws.

*Remarks:* The 'baseball bat' morphology of the aesthetasc on the second antenna supports the assignment of *Raepula* to the Cypridoidea, its morphology being an apomorphy for Cypridocopina (Kaji and Tsukagoshi, 2008). *Raepula* has a smooth carapace; it lacks a distal triangle on the furca; the posterior seta of the furca is relatively close to the base of the terminal claw; and the basal segments of the 6th appendage bears two setae. *Raepula* is therefore placed in Subfamily Eucypridinae. The distal podomere of the maxillula is not elongate, but about as broad as it is long and the natatory setae on the second antenna are well developed, reaching beyond the tip of the terminal claw. *Raepula* therefore resembles *Trajancypris*, but differs in having a sub-reniform rather than clavate carapace and in showing distinct sexual dimorphism, particularly in the structure of the second maxilla.

*Raepula ira* gen. et sp. nov.

Fig. 3a-j, Fig. 4a-i

*Holotype*: OUMNH NT.154, a carapace with soft anatomy (Fig. 3b).

*Material*: About 20 specimens (including OUMNH NT.154-NT.164), most with soft anatomy; a few specimens are detached from their carapace.

*Locality and stratigraphy*: Barstow Formation, 'Middle Member'; Mid Miocene (probably latest Burdigalian Age); Rainbow Basin, Mud Hills, California, USA (grid North 35.023716 West 117.040819; see Fig. 1).

The following description of soft anatomy is based on those specimens that have well-preserved appendage anatomy. Typically, carapaces of these specimens are between 0.6 and 0.8mm long, indicating that they represent pre-adult (probably A-1 and A-2) instars.

The carapace is elongate and sub-reniform in lateral view and approximately twice as long as high; greatest length is 972 $\mu$ m, greatest height is 583 $\mu$ m just anterior of mid-length (Fig. 3a). Dorsal outline gently arched, ventral outline straight or very weakly concave; posterior margin broadly rounded; anterior margin obliquely rounded. Adductor muscle scars (Fig. 5a, c-d) form an irregular grouping immediately anterior of mid-length and just below mid-height, comprising seven elongate scars, each one subdivided into two by weak sutures. Four indistinct dorsal muscle scars are also present (Fig. 5b).

Normal (sensillum) pores are scattered across the lateral surface of the valve, but with an apparent concentration along the antero-ventral and anterior margins (Fig. 3e-g). These pores are about 1.8 $\mu$ m in diameter and surrounded by a raised rim, each with a single seta up to 8 $\mu$ m long. Where

the valve has been dissolved away during preparation, the sensillum pores are preserved as silica casts and stand proud of the lateral surface, maintaining the pore structure (Fig. 3g). In several examples, the simple inner part of the pores is preserved to about 1 $\mu$ m length. The pore then widens abruptly into a lobed, spheroidal “pocket” about 3 $\mu$ m diameter.

The first antenna protrudes anteriorly from the body and comprises a large, sub-rectangular basipod and six podomeres (Fig. 3b-d, h-j; Fig. 4a, b, d, e). The 1st podomere is sub-quadrate, with one dorsal sub-apical seta. The 2nd podomere is narrower, elongate and has one seta dorsally near mid-length and two setae on the apical ventral edge. The 3rd podomere is sub-rectangular and bears two setae on the apical ventral edge, and one long seta on the apical dorsal edge. The 4th podomere is slightly narrower, sub-rectangular and bears two setae on the apical-ventral edge. The 5th podomere is sub-rectangular, narrower and also bears two setae on the apical-ventral edge, and at least one seta on the apical-dorsal edge. The 6th podomere is small, elongate and terminally bears a cluster of at least three setae.

The second antenna comprises a limb stem (curved basipod and possible coxa), an endopod comprising three podomeres, and a tiny, slender exopod (Fig. 3b-d, f, h-j; Fig. 4a-e). It is not possible to determine whether the structure of the exopod is similar to other Cyprididae (e.g. Karanovic 2008). The 1st podomere is large, elongate, with a ‘baseball bat’-shaped aesthetasc ventro-proximally (Fig. 3j) one long seta on the apical ventral edge and at least five setae on the apical inner face: the long setae on the apical inner face have been broken-off distally. The 2nd podomere is elongate, about half

the size of the first, with at least two setae at ventral mid-length, at least one seta on the sub-apical outer face, and at least three large claws terminally. The 3rd podomere is much smaller, sub-quadrate and has at least two claws and three setae.

The labrum is convex, broadly triangular in shape with a rounded margin at the atrium oris (Fig. 3b, c). The holotype, 780µm long, has a labrum about 100µm long.

The mandible consists of a large, elongate sub-triangular coxa, a sub-quadrate basipod with a single seta, and an endopod that protrudes at the side of the labrum and comprises three podomeres (Fig. 3b, c, h, j; Fig. 4c, f). The 1st podomere is short and has at least two setae at the apical ventral edge. The 2nd podomere is sub-rectangular, with at least three setae distally. The 3rd podomere is small, tapers distally and has a cluster of setae and at least three claws terminally.

The first maxilla comprises a large basipod and a possible proximal endite, an endopod consisting of one long podomere and one much shorter podomere, three curved endites and a crescent-shaped branchial plate bearing at least eleven marginal setae (Fig. 3b, c, h). The endopod has at least three setae on the outer apical side of the 1st podomere. The 2nd podomere is small, sub-quadrate with five apical setae. The endites decrease in size: the large third endite has at least six apical setae; the second endite has three apical setae; the small first endite has setae but is mostly obscured.

The 2nd maxilla consists of a large basipod, an endite with at least ten setae distally, and a tapered endopod ending in possibly three setae (Fig. 3b,

c, h; Fig. 4c, f). In one specimen the endopod terminates in a hook, indicating a male (Fig. 3h-i).

The 6th appendage comprises a ramus geniculate with a curved basipod (Fig. 4b-e). The ramus has a large, elongate, sub-rectangular 1st podomere. Podomeres two and three are smaller, sub-rectangular, and have at least one sub-apical ventral seta. The small, distally tapering 4th podomere terminates in a large curved claw.

The 7th appendage (Fig. 4a) comprises an elongate basipod approximately 45% of the length of the appendage; an elongate 1st podomere, about half the length of the basipod; a 2nd podomere of similar proportions crossed by three grooves; a 3rd diminutive and distally tapering podomere bearing three setae. It is not possible to determine whether the 2nd podomere comprises a fused EII and EIII, as seen in, for example, *Eucypris* and *Cryptocandona* (e.g. Meisch, 2000, fig. 10). The setae on the distal podomere comprise a very short h1, possibly associated with a poorly preserved pincer organ, and elongate h2 and h3 setae, of similar length.

The furca comprises a proximally fused pair of un-segmented curved rami, each with two large distal claws and an adjacent seta (Fig. 3a, h, j; Fig. 4b, d).

*Remarks.* The use of acid for extracting the specimens from the rock has resulted in the loss of the original shell material and ornament. Reconstructing the precise ontogeny of the ostracod is therefore not possible. The largest specimens - those greater than 0.8mm long - are assumed to be adults. Some specimens less than 0.8mm long, representing probable instars, have also been used to describe the soft-anatomy of *R. ira*. Smith & Martens (2000)

have documented considerable changes in appendage morphology between instars of the living cypridid ostracod *Eucypris virens* and Smith (2000) has used the same approach for the description of exceptionally preserved ostracods from the Cretaceous of Brazil.

*Raepula ira* has typical cypridine muscle scars (Fig. 5), comprising a group of five elongate adductor muscle scars and two elongate mandibular scars. A group of ill-defined dorsal muscle scars, comprising at least five scars, are also present.

### **Ostracod Taphonomy**

Unlike their calcified carapaces, which are resilient and have a long and well documented fossil record back to the Early Ordovician (Salas *et al.* 2007), the soft anatomy (non-biomineralised cuticle) of ostracods has a low preservation potential. Details of the body and/or appendages are known for about 20 fossil taxa (see summary in Smith, 2000) and eight sub-Recent species (see Matzke-Karasz *et al.* 2001). These occurrences share little in common in terms of their modes of preservation, and include examples of phosphatisation (Smith 2000), pyritisation (Williams *et al.* 2008a; Farrell *et al.*, 2009), organic preservation (Orr *et al.* 2008), inclusion in amber (Keyser & Weitschat 2005) and void fills in calcite (Siveter *et al.* 2003; Siveter *et al.* 2007). Such variability reflects the diversity of aquatic environments occupied by ostracods and, hence, the range of taphonomic regimes to which they may potentially be exposed post-mortem.

Barstow offers a unique example of silicified ostracod soft anatomy (though see mention of potential example in Müller, 1979). The soft anatomy

occurs in association with agape, closed and (rarely) isolated valves, and typically preserves submicron-scale details, such as sensory setae and setules (Fig. 3g). Silicification is biased towards the paired first antennae (e.g. Fig. 3d; Fig. 4g), though preservation may extend to a near full complement of appendages (e.g. Fig. 4b); some carapaces are empty. In most specimens, the appendages are preserved in near life position. However, in several cases they have collapsed and are disorganised (e.g. Fig. 3h-j), or they remain attached but are displaced outside of the carapace (Fig. 4h), possibly due to the partial separation of the inner lamella (cf. Orr *et al.* 2008). In both situations, the ostracods are typically infested with open filamentous networks of micro-organisms, and diatoms adhere in large numbers. Such characteristics are consistent with a more protracted period of decay prior to burial and silicification, though confirmatory experimental taphonomic data are generally lacking for ostracods (although see Langer 1973).

The style of preservation is broadly comparable to that of phosphatised fossil ostracods (for which see Smith 2000). It predominantly consists of a fine-scale replacement or penetrative impregnation of the integument by quartz, locally obscured by crude quartz overgrowths (Fig. 4g). The cuticle is the only tissue preserved: no visceral organs have been observed. The sub-micron scale precision with which the integument is replicated, and the preservation of structures wholly comprised of epicuticle (e.g. setules) indicate that at least this outermost layer of the cuticle is silicified. However, the apparent total thickness of the preserved cuticle, as seen in broken sections through hollow appendages, exceeds that of the epicuticle alone. Therefore, it seems likely that part of the underlying procuticle is also preserved, or that

selective decomposition of the procuticle allowed centripetal silicification to proceed in the vacated space.

In contrast, the carapace is seen principally as an internal mould, formed by interlocking, comparatively coarse (up to 200 $\mu$ m), prismatic quartzes that terminate in the domicilium (e.g. Fig. 3a, d). As such, the muscle scars are visible on the external surface of the specimens (Fig. 5); the calcitic carapace itself is presumed to have been present prior to acid preparation of the material. Hence, the generally observed margins of the carapace actually represent a cast of the vestibulum. As with the soft integument, the epicuticle of the carapace (see Yamada *et al.* 2004) is preferentially silicified. It forms a very thin (<1 $\mu$ m) discontinuous layer, often with detritus attached, separated from the internal mould by a gap which defines the *in vivo* thickness of the carapace (Fig. 3a).

The presence of large drusy quartz crystals and quartz overgrowths indicate that preservation was not silica-limited. Instead, the preferential preservation of certain anatomical features (e.g. first antennae) probably reflects their inherent decay resistance (cf. Orr *et al.* 2008). Silicification locally extends a short distance into the sediment along specific (organic-rich?) laminae, indicating that it took place after burial. It likely occurred episodically, thus accounting for the observed overgrowths, and may have continued up to the onset of development of the enclosing pre-compactional carbonate concretions: locally, silica overgrowths of calcite crystal terminations (now dissolved) are present. Stellate crystals forming the preserved surface of one ostracod carapace (Fig. 4i) resemble opal-CT

platelets (see Stein 1982, fig. 4b) and suggest original replication by opaline silica.

Though silica frequently pseudomorphs shelly fossils (Schubert *et al.* 1997) and preserves a range of ancient bacteria (see Westall *et al.* 2001), fungi (Taylor *et al.* 2004) and plants (Edwards 2004), it is rarely associated with soft-tissue preservation in animals (Carson 1991). Most documented examples are from hydrothermal sinters (though see Voigt 1988; Lin *et al.* 2006) such as the Devonian Rhynie chert complex where a variety of arthropods, including crustaceans, is encased within silica deposited from supersaturated fluids (Anderson & Trewin 2003); a bird is known from a comparable sub-Recent setting (Channing *et al.* 2005). The Barstow ostracods may have occupied a lake with a hydrothermal or volcanic influence, but their preservation style differs markedly from that of sinter fossils: crucially, the ostracod soft anatomy is predominately replaced, rather than encrusted and/or permineralized as is typical of sinter fossils. This suggests a profoundly different process of silicification, driven by heterogeneous nucleation on specific organic substrates, probably from a silica-undersaturated solution (see Leo & Barghoorn 1976). Certainly, the general absence of encrustations suggests that the dissolved silica concentration remained below the level required for homogeneous (spontaneous) nucleation of opal-A microspheres in the ambient pore waters (see Channing & Edwards 2004).

The contribution of microbes to silica precipitation, particularly sinter development, has been much debated (see discussions in Konhauser *et al.* 2004; Lalonde *et al.* 2005). In Barstow they probably played a significant

indirect role. Incipient microbial degradation of the ostracod cuticle may have facilitated silica infiltration (cf. Channing & Edwards 2004) and created new favourable nucleation sites, thereby enhancing the tissue's reactivity and preservation potential. Additionally, it may have locally decreased the pH and created a microenvironment conducive to silicification (Carson 1991; Briggs 2003); buffering by the calcite carapace may explain its preservation as a mould rather than a replacement.

## **Conclusion**

Concretions from the Middle Miocene Barstow Formation in the Mud Hills of southern California yield exceptionally preserved arthropods, including specimens of a cypridid ostracod, *Raepula ira* gen. et sp. nov. This material represents a rare occurrence of fossil ostracods with preserved soft tissues and is only the second such occurrence from the Neogene. The associated palaeolake fauna suggest that *R. ira* occupied permanent saline-alkaline lakes similar to those of the present western United States and East African Rift Valley.

Taphonomically the ostracods are unique, in that the soft anatomy is preserved as silica, typically with submicron-scale details, such as sensory setae and setules. The ostracod soft anatomy is predominantly replaced, rather than encrusted and/or permineralized as is typical of sinter fossils, leading to the conclusion that heterogeneous nucleation took place on specific organic substrates, probably from a silica-undersaturated solution.

IPW & PRW publish with permission of the Executive Director of the British Geological Survey (N.E.R.C.). The authors wish to thank Dr D.J. Horne and the anonymous second reviewer for their helpful comments.

## References

- ANDERSON, L. I. & TREWIN, N. H. 2003. An Early Devonian arthropod fauna from the Windyfield chert, Aberdeenshire, Scotland. *Palaeontology*, **46**, 467-510.
- BAIRD, W. 1845. Arrangement of the British Entomostraca, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the club. *Transactions of the Berwickshire Naturalists' Club*, **2** (13), 145-158.
- BELK, D. & F. R. SCHRAM. 2001. A new species of anostracan from the Miocene of California. *Journal of Crustacean Biology*, **21**, 49–55.
- BRIGGS, D.E.G. 2003 The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Sciences*, **31**, 275-301.
- BRONSTEIN, Z.S. 1947. Freshwater Ostracoda. *Zoologicheskiiy Institut Akademii Nauk SSSR*, **31**, 1-339.
- CARSON, G.A. 1991. Silicification of fossils. In: ALLISON, P.A. and BRIGGS, D.E.G. (eds) *Taphonomy: Releasing the data locked in the fossil record*. Plenum Press, New York, 453-499.

- CHANNING, A. & EDWARDS, D. 2004. Experimental taphonomy: silicification of plants in Yellowstone hot-spring environments. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 503-521.
- CHANNING, A., SCHWEITZER, M.H., HORNER, J.R. & MCEANEY, T. 2005. A silicified bird from Quaternary hot spring deposits. *Proceedings of the Royal Society B*, **272**, 905-911.
- EDWARDS, D. 2004. Embryophytic sporophytes in the Rhynie and Windyfield cherts. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 397-410.
- European Diatom Database. 1996. Available at:  
<http://craticula.ncl.ac.uk/Eddi/jsp/>
- Farrell, U.C., Martin, M.J., Hagadorn, J.W., Whiteley, T. & Briggs, D.G.E. 2009. Beyond Beecher's Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician Taconic foreland basin. *Geology*, **37**(10), 907-910.
- HAJOS, M. 1974. Faciological and stratigraphical importance of the Miocene diatoms in Hungary. *Nova Hedwigia*, **45**, 365-376.
- HORNE, D. J., LORD, A. R., ROBINSON, J. E. AND WHITTAKER, J. E. 1990. Ostracods as climatic indicators in interglacial deposits or on some new and little-known British Quaternary Ostracoda. *Courier Forschungsinstitut Senckenberg*, **123**, 129-140.
- JONES, T.R. In: CHAPMAN, F. 1901. On some Fossils of Wenlock Age from Mulde, near Klinteberg, Gotland. *Annals and Magazine of Natural History* (7) **7**, 141-160 [pp. 146-147: a table by T. R. Jones].

- KAJI, T. & TSUKAGOSHI, A. 2008. Origin of the novel chemoreceptor Aesthetasc “Y” in Ostracoda: morphogenetical thresholds and evolutionary innovation. *Evolution and Development*, **10**, 228-240.
- KARANOVIC, I. 2008. A new species of the genus *Candonopsis* (Crustacea, Ostracoda) from Western Australia. *Records of the Western Australian Museum*, **24**, 411-419.
- KEYSER, D. & WEITSCHAT, W. 2005. First record of ostracods (Crustacea) in Baltic amber. *Hydrobiologia*, **538**, 107-114.
- KONHAUSER, K.O., JONES, B., PHOENIX, V.R., FERRIS, F.G. & RENAUT, R.W. 2004. The microbial role in hot-spring silicification. *Ambio*, **33**, 552-558.
- LALONDE, S.V., KONHAUSER, K.O., REYSENBACH, A.-L. & FERRIS, F.G. 2005. The experimental silicification of Aquificales and their role in hot spring sinter formation. *Geobiology*, **3**, 41-52.
- LANGER, W. 1973. Zur ultrastruktur, mikromorphologie und taphonomie des Ostracoda-carapax. *Palaeontographica, Abteilung A*, **144**, 1-54.
- LEGGITT, V.L. 2003. Silicified microfossils from Black Canyon: Miocene Barstow Formation, San Bernardino County, California. *Geological Society of America, Seattle Annual Meeting (November 2–5, 2003), Abstracts with Programs, Volume 35* (6) (September 2003), 495.
- LEGGITT, V.L. 2005. Cladocerans (Branchiopoda: Anomopoda) from the Miocene Barstow Formation: San Bernardino County, California. *Geological Society of America, Salt Lake City Annual Meeting (October 16–19, 2005), Abstracts with Programs*, **37** (7), 368.

- LEGGITT, V.L. 2006. Lacustrine ostracoda and other microcrustaceans with preserved appendages from the Miocene Barstow Formation. *Geological Society of America, Abstracts with Programmes*, **38**, 64.
- LEO, R.F. AND BARGHOORN, E.S. 1976. Silicification of wood. *Botanical Museum Leaflet, Harvard University*, **25**, 1-47.
- LEWIS, A.R., MARCHANT, D.R., ASHWORTH, A.C., HEDENÄS, L., HEMMING, S.R., JOHNSON, J.V., LENG, M.J., MACHLUS, M.L., NEWTON, A.E., RAINE, J.I., WILLENBRING, J.K., WILLIAMS, M. & WOLFE, A.P. 2008. Major mid-Miocene cooling and extinction of tundra in continental Antarctica. *Proceedings of the National Academy of Sciences (PNAS)*, **105**, 10676-10680.
- LIN, J.-P., SCOTT, A.C., LI, C.-W., WU, H.-J., AUSICH, W.I., ZHAO, Y.-L. & HWU, Y.-K. 2006. Silicified egg clusters from a Middle Cambrian Burgess Shale-type deposit, Guizhou, south China. *Geology*, **34**, 1037-1040.
- MATZKE-KARASZ R., HORNE D C., JANZ, H., GRIFFITHS, H I., HUTCHINSONN, W. F. & PREECE R. C. 2001. 5,000 year-old spermatozoa in Quaternary Ostracoda (Crustacea). *Naturwissenschaften*, **88** (6), 268-272.
- MEISCH, C. 2000. *Freshwater Ostracoda of Western and Central Europe*. 522pp. [Spektrum Akademischer Verlag, Heidelberg]
- MILLER K.B. AND LUBKIN S.H. 2001. *Calicovatellus petrodytes*, a new genus and species of primitive vatelline diving beetle (Coleoptera: Dytiscidae: Hydroporinae: Vatellini) from the Miocene Barstow Formation, Southern California, USA. *Journal of Paleontology*, **75**, 890-894.
- MÜLLER, K. J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. *Lethaia*, **12**, 1-27.

- ORR, P.J., BRIGGS, D.E.G. & KEARNS, S.L. 2008. Taphonomy of exceptionally preserved crustaceans from the Upper Carboniferous of southern Ireland. *Palaios*, **23**, 298-312.
- PALMER, A. R. 1957. Miocene Arthropods from the Mojave Desert California. United States Geological Society Professional Paper, **294-G**, 237-280.
- PALMER, A. R., & BASSETT, A. M. 1954. Nonmarine Miocene Arthropods from California. *Science*, **120**, 28-29.
- PARK, L. E. 1995. Geochemical and paleoenvironmental analysis of lacustrine Arthropod-bearing concretions of the Barstow Formation, southern California. *Palaios*, **10**, 44-57.
- PARK, L. E. & DOWNING, K. F. 2001. Paleoecology of an exceptionally preserved arthropod fauna from lake deposits of the Miocene Barstow Formation, southern California, USA. *Palaios*, **16**, 175-184.
- PENNAK, R.W. 1989 *Freshwater invertebrates of the United States: Protozoa to Mollusca* (3rd ed). John Wiley and Sons, New York: 656p.
- SALAS, M. J., VANNIER, J. M. C. & WILLIAMS, M. 2007 Early Ordovician ostracods from Argentina: their bearing on the origin of the binodicope and palaeocope clades. *Journal of Paleontology*, **81**, 1384-1395.
- SARS, G.O. 1866. Oversigt af Norges marine ostracodes. *Norske Videnskaps-Akademiens Forhandlinger*, **1865**, 1-130.
- SCHMIDT, R. A. M. & SELLMAN, P. V. 1966. Mummified Pleistocene ostracods in Alaska. *Science*, **153**, 167-168.
- SCHUBERT, J.K., KIDDER, D.L. & ERWIN, D.H. 1997. Silica-replaced fossils through the Phanerozoic. *Geology*, **25**, 1031-1034.

- SIVETER, D. J. 2008 Ostracods in the Palaeozoic? *Senckenbergiana Lethaea* **88**, 1-9.
- SIVETER, DAVID J., SUTTON, M.D., BRIGGS, D.E.G. & SIVETER, DEREK J. 2003. An ostracod crustacean with soft parts from the Lower Silurian. *Science*, **300**, 1749-1751.
- SIVETER, DAVID J., SIVETER, DEREK J., SUTTON, M.D. & BRIGGS, D.E.G. 2007. Brood care in a Silurian ostracod. *Proceedings of the Royal Society of London, Series B*, **274**, 465-469.
- SMITH, R J. 2000. Morphology and ontogeny of Cretaceous ostracods with preserved appendages from Brazil. *Palaeontology*, **43**, 63–98.
- SMITH, G.I. & MEDRANO, M.D. 1996. Continental Boarte deposits of Cenozoic age. In: GREW, E.S., AND ANOVITZ, L.M. (eds). Boron: mineralogy, petrology and geochemistry. *Reviews in Mineralogy*, **33**: 263-298.
- STEIN, C.L. 1982. Silica recrystallization in petrified wood. *Journal of Sedimentary Petrology*, **52**, 1277-1282.
- SWAIN, F. M. & WAGONER, J. L., 1979. Biostratigraphy and paleoecology of freshwater Ostracoda from Esmeralda Formation (Neogene) of western Nevada. In: KRSTIC N. (Ed.) *Taxonomy, Biostratigraphy and Distribution of Ostracodes; Proc. VII Int. Symp. on Ostracodes*. Serbian Geol. Soc., Beograd, 191-196.
- SWAIN, F. & WAGONER, J.L., 1985. Some freshwater Ostracodas from Esmeralda Formation (Neogene) of western Nevada. *Revista Española de Micropaleontología*, **17**, 123-149.

- SWAIN, F. M., 1986. Some Middle Cenozoic freshwater Ostracoda from northeastern Nevada. *Revista Española de Micropaleontología*, **18**, 181-227.
- SWAIN, F. M., 1987. Some Oligocene and Miocene freshwater Ostracoda from central and southern Nevada and southwestern Texas. *Revista Española de Micropaleontología*, **20**, 413-449.
- SWAIN, F. M., 1990. Miocene and Pliocene freshwater Ostracoda from California, Nevada and Oregon. *Revista Española de Micropaleontología*, **22**, 143-159.
- SWAIN, F.M., BECKER, J., DICKINSON, K.A., 1971. Paleoecology of Tertiary and fossil Quaternary non-marine ostracoda from the Western Interior United States. *In: OERTLI, H.J. (Ed.), Paléoécologie des Ostracodes*. Bulletin du Centre de Recherche Pau-SNPA (Suppl. 5), 461–487.
- TAYLOR, T.N., KLAVINS, S.D., KRINGS, M., TAYLOR, E.L., KERP, H. & HASS, H. 2004. Fungi from the Rhynie chert: a view from the dark side. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 457-473.
- VOIGT, E. 1988. Preservation of soft tissues in the Eocene lignite of the Geiseltal near Halle/S. *Courier Forschungsinstitut Senckenberg*, **197**, 325-343.
- WARD, J.V. 1992. *Aquatic Insect Ecology, 1: Biology and Habitat*. John Wiley and Sons, New York: 483p.
- WILLIAMS, M., SIVETER, D.J., ASHWORTH, A.C., WILBY, P.R., HORNE, D.J., LEWIS, A.R. & MARCHANT, D.R. 2008a. Exceptionally preserved lacustrine ostracods from the Middle Miocene of Antarctica: implications for high latitude

palaeoenvironment at 77° south. *Proceedings of the Royal Society of London, Series B.*, **275**, 2449-2454.

WILLIAMS, M., SIVETER, SALAS, M., D.J., VANNIER, J.M.C., POPOV, L.E. & GHOBADI POUR, M. 2008b. The earliest ostracods: the geological evidence. *Senckenbergiana Lethaea*, **88**, 11-21.

WOODBURNE, M. O., TEDFORD, R. H. & SWISHER, C. C. 1990. Lithostratigraphy, biostratigraphy and geochronology of the Barstow Formation, Mojave Desert, southern California. *Geological Society of America, Bulletin*, **102**, 459-477.

YAMADA, S., TSUKAGOSHI, A. & IKEYA, N. 2004. Ultrastructure of the carapace in some *Semicytherura* species (Ostracoda: Crustacea). *Micropaleontology*, **50**, 381-389.

## Figure captions

Figure 1. Location of the ostracod-bearing concretion horizon, Mud Hills, southern California.

Figure 2. Correlation of the Barstow Formation of Mud Hills, southern California with a succession in the Calico Mountains.

Figure 3. Morphology of *Raepula ira* gen. et sp. nov. a, LACMIP 13642, carapace, right lateral view.. Note, preferential silicification of the carapace epicuticle (light grey) and comparatively coarse quartz prisms (medium grey) forming an internal mould. b, c, OUMNH NT.154, holotype carapace, ventral (stereo-pair) and detail of anterior appendages (stereo-pair). d, LACMIP 13643, carapace, dorsal view. Note the preferential replacement of the antennae and contrasting crude preservation of the carapace as an internal mould by comparatively coarse quartzes. e, f, OUMNH NT.155, carapace oblique ventral (stereo-pair) and detail of anterior appendages (stereo-pair). g. OUMNH NT.156, sensory setae extending from the margins of a valve preserved as an internal mould. Basal thickenings represent casts of pores in the valve (dissolved). h-j, OUMNH NT.157, ventral view (stereo-pair) and anterior details of appendages (h, j). Note, the appendages have collapsed and are partially disorganised, and microbial filaments occupy the posterior margin of the right valve. Abbreviations: a1, first antenna; a2, second antenna; a6, sixth appendage; a7, seventh appendage; ba, basipod; cl, claw; en, endopod; ex, exopod; fu, furca; hi, hinge; il, inner lamella; la, labrum; lv, left valve; ma, mandible;

ml, first maxilla; 2<sup>nd</sup>ml, second maxilla; rv, right valve; se, setae; at, aesthetasc; sp, sensory pore with sensillum.

Scale bar (µm) = a) 300, b) 230, c) 150, d) 330, e) 260, f) 130, g) 11, h) 240, i) 300, j) 170.

Fig. 4. Morphology of *Raepula ira* gen. et sp. nov. a. OUMNH NT.158, detached body and appendages, right lateral view (stereo-pair). b, c, OUMNH NT159, detached body and appendages, left lateral view (stereo-pair) and details of anterior appendages (stereo-pair). Basipod and podomeres 1 to 3 of the 2<sup>nd</sup> antenna are identified. The position of the base of the tiny exopod, here broken off, is marked by the circle. d, OUMNH NT160, detached body and appendages, left lateral view (stereo-pair), especially showing the large basipod and 6 podomeres of the first antenna. e, f, OUMNH NT161, detached appendages and body, right lateral view (stereo-pair) and close up of mandible (stereo-pair). Note porous areas where silicification is incomplete and preservation can be seen to be a replacement of the cuticle, rather than coating or infill. g OUMNH NT.162, left lateral view of carapace, showing antennae with crude quartz overgrowth and domicilium occupied by comparatively coarse quartz prisms. Note space at hinge-line recording former (dissolved) calcitic carapace, now internally moulded and with a thin external coating. h, OUMNH NT.163. Specimen preserved as a single valve with appendages displaced outside and infested with a network of microbial filaments. i, OUMNH NT.154, close-up of holotype carapace showing stellate crystals

reminiscent of opal-CT platelets. Abbreviations as for Plate 1, except: bp, brachial plate; cox, coxa; end, endite.

Scale bar (microns) = a) 180, b) 200, c) 130, d) 240, e) 260, f) 110, g) 290, h) 330, i) 9.

Figure 5. Muscle scars of *Raepula ira* gen. et sp. nov. 3a-c, carapace OUMNH NT.164: 3a, left lateral view; 3b, dorsal scars 3c, adductor muscle scars. 3d. reconstruction of the adductor and mandibular muscle scars as a composite of all available specimens. Scale bar a) 100  $\mu\text{m}$ , b-c) 200  $\mu\text{m}$ .

## **Supplementary material**

Supplementary material 1: red-blue anaglyph of the right lateral view of the mandible. Note porous areas where silicification is incomplete and preservation can be seen to be a replacement of the cuticle, rather than coating or infill. Specimen OUMNH NT161 (See also Fig.4 e-f for details). (Photograph RC138a)

Supplementary material 2: red-blue anaglyph of the ventral view and anterior details of appendages. Note that the appendages have collapsed and are partially disorganised. Microbial filaments occupy the posterior margin of the right valve. Specimen OUMNH NT.157 (See also Fig. 3 h-j for details). (Photograph RCO502L1)

Supplementary material 3: red-blue anaglyph of the holotype carapace, ventral view. Specimen OUMNH NT.154 (See also Fig. 3 b for details). (Photograph RCO519\_520)

Supplementary material 4: red-blue anaglyph of the holotype carapace, ventral view, showing the detail of the anterior appendages. Specimen OUMNH NT.154 (See also Fig. 3 c for details). (Photograph RCO523\_522)

Supplementary material 5: red-blue anaglyph of a detached body and appendages, right lateral view. Note 1st, 2nd, 6th and 7th appendages are particularly well preserved. Specimen OUMNH NT.158 (See also Fig. 4 a for details). (Photograph RCOJ126a)

Supplementary material 6: red-blue anaglyph of detached body and appendages, left lateral view. Note the furca is well preserved on this specimen. Specimen OUMNH NT.159 (See also Fig. 4 b-c for details). (Photograph RCOJ129a)

Supplementary material 7: red-blue anaglyph of a carapace in oblique ventral view. Specimen OUMNH NT.155 (See also Fig. 4 e for details). (Photograph RCOJ1031)

Supplementary material 8: red-blue anaglyph of a carapace in oblique ventral view showing the detail of the anterior appendages. Specimen OUMNH NT.155 (See also Fig. 4 f for details). (Photograph RCOJ1091)

Supplementary material 9: red-blue anaglyph of detached appendages and body, right lateral view. Specimen OUMNH NT.161 (See also Fig. 4 e for details). (Photograph RCOJ1241)

Supplementary material 10: red-blue anaglyph of the anterior details of appendages in ventral view. Specimen OUMNH NT.157 (See also Fig. 3 j for details). (Photograph RCOJ1331)

Supplementary material 11: red-blue anaglyph of the anterior details of appendages in ventral view. Note the partially collapsed appendages and microbial filaments. Specimen OUMNH NT.157 (See also Fig. 3 h for details). (Photograph RCOJ1361)

Supplementary material 12: red-blue anaglyph showing the details of the 2<sup>nd</sup> antenna, mandible and maxilla, left lateral view. Specimen OUMNH NT.159 (See also Fig. 4 c for details). (Photograph RCQ149a)

Supplementary material 13: red-blue anaglyph of a detached body and appendages, left lateral view. Note the podomeres of the first antenna are especially well preserved. Specimen OUMNH NT.160 (See also Fig. 4 d for details). (Photograph RCQ152a)

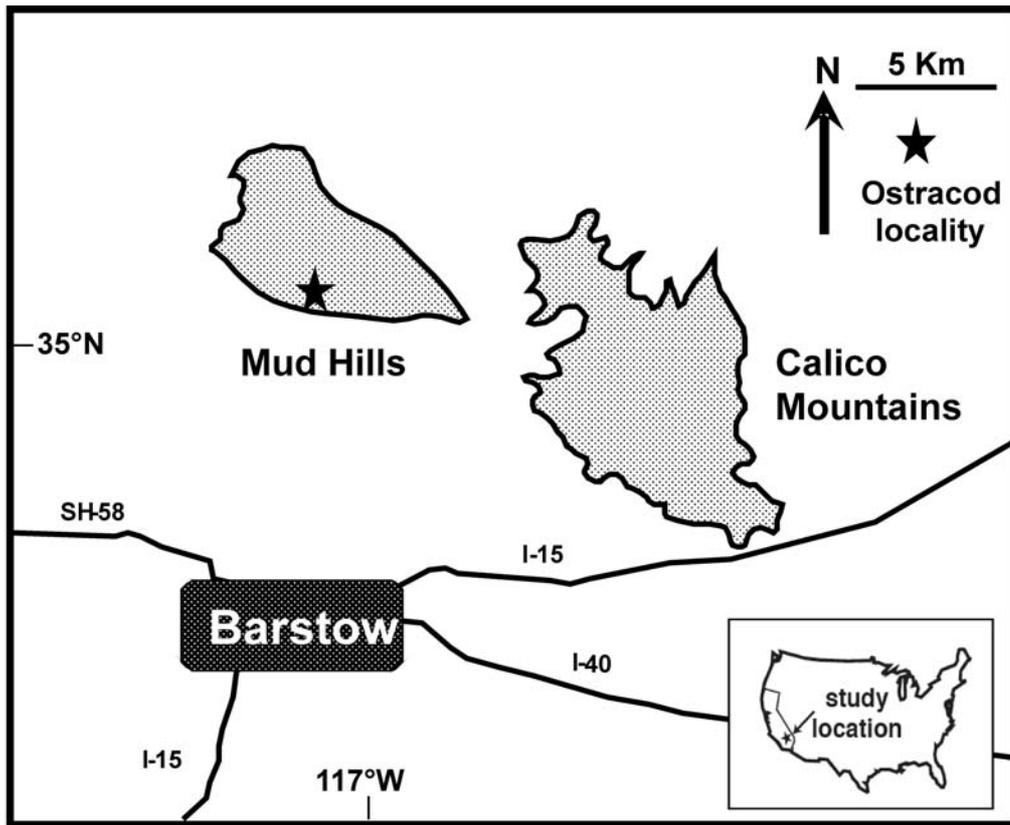


Fig. 1

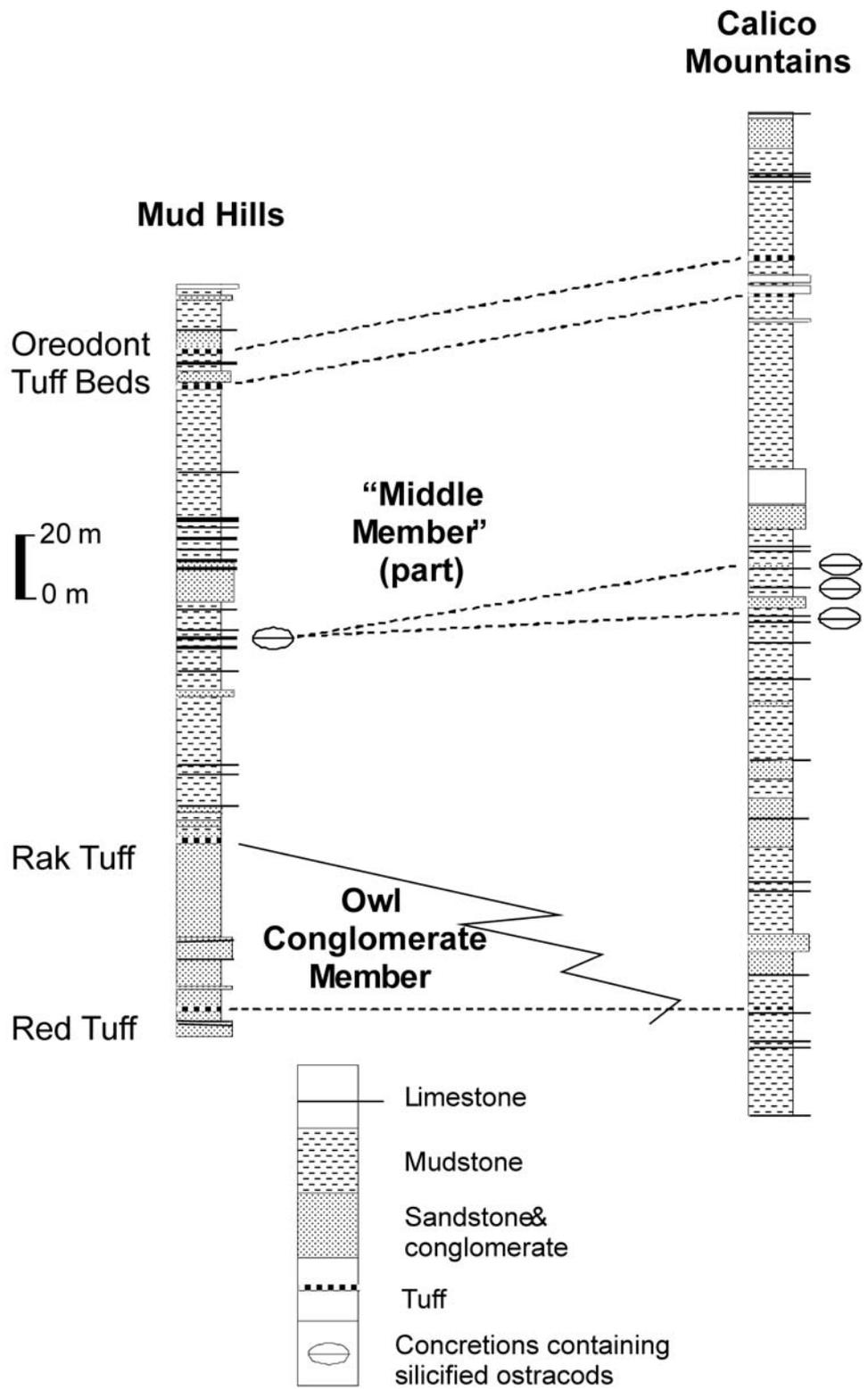


Fig. 2



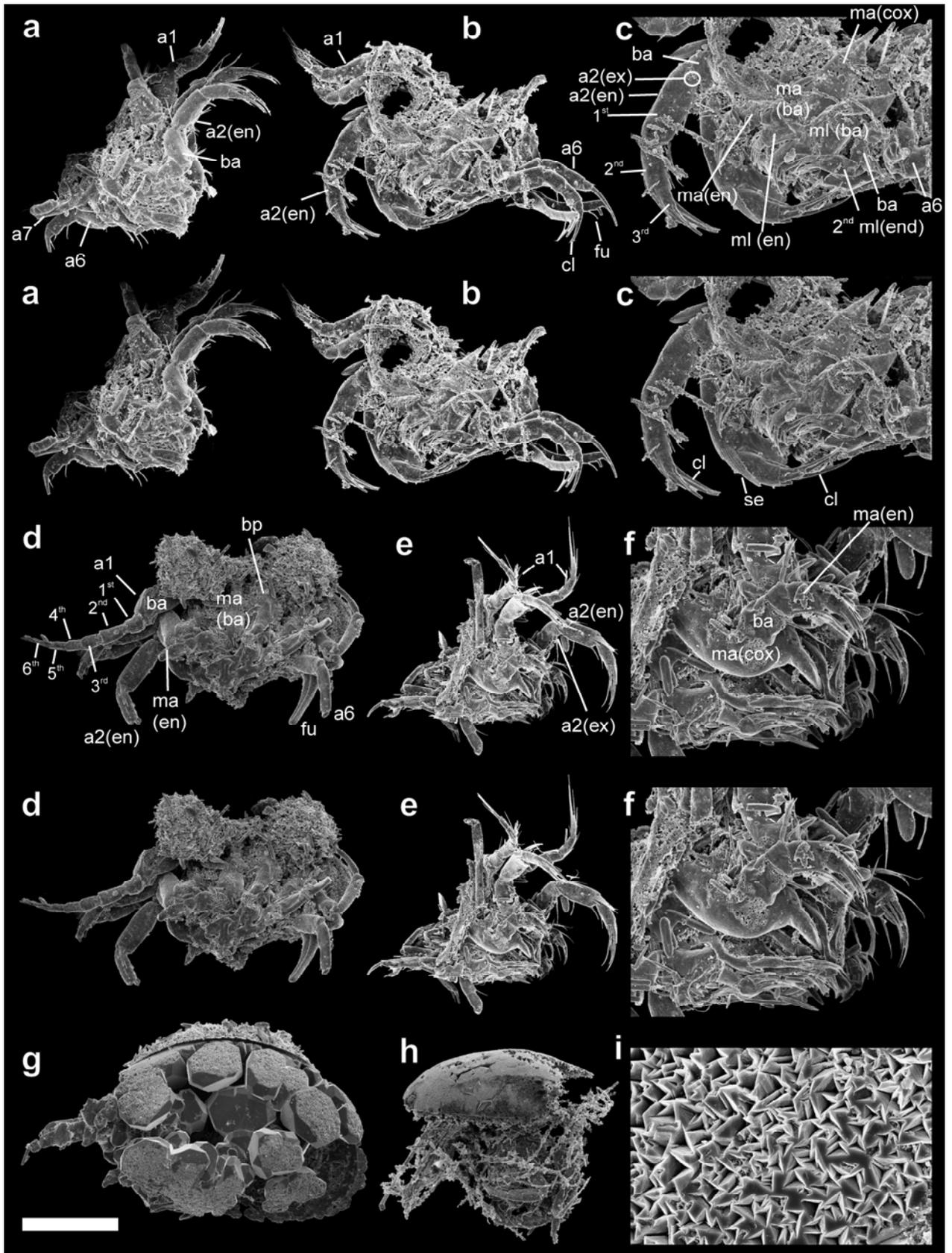


Fig. 4

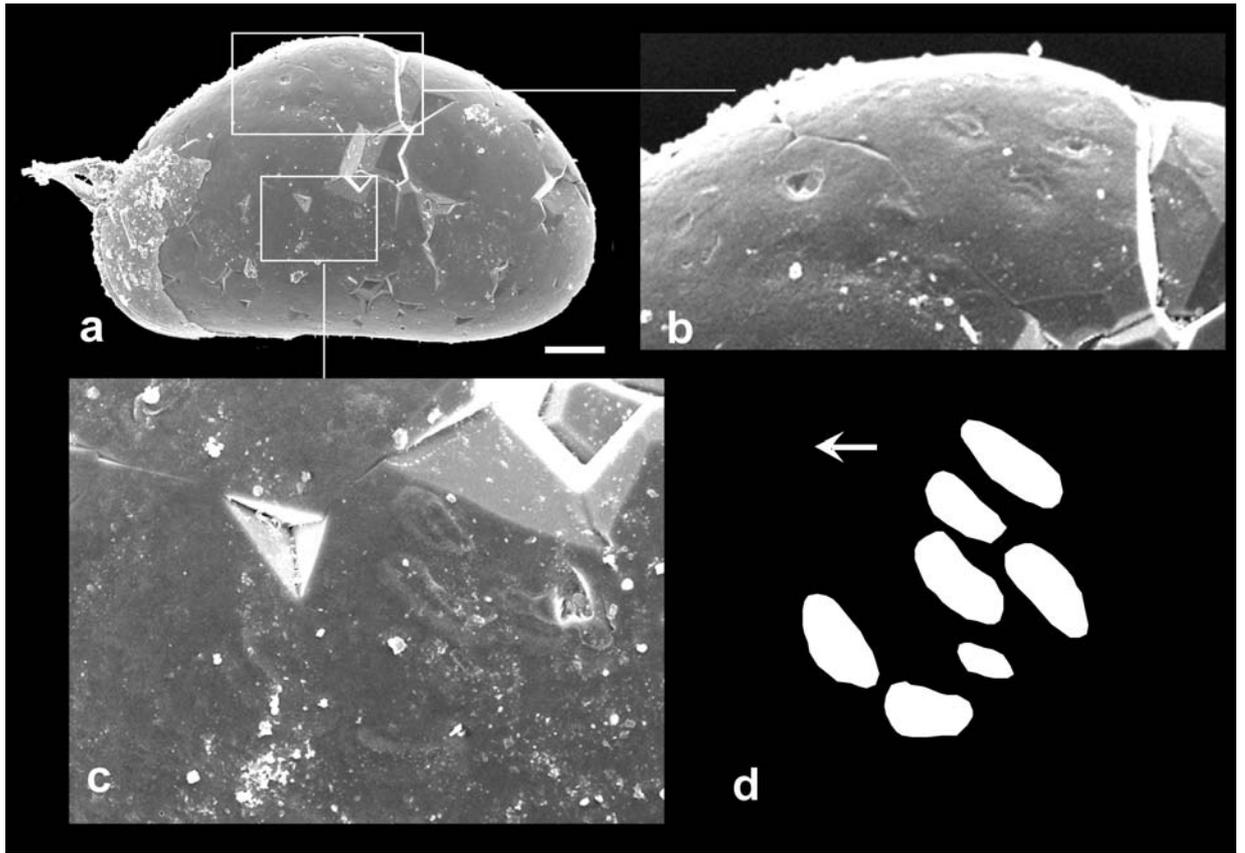
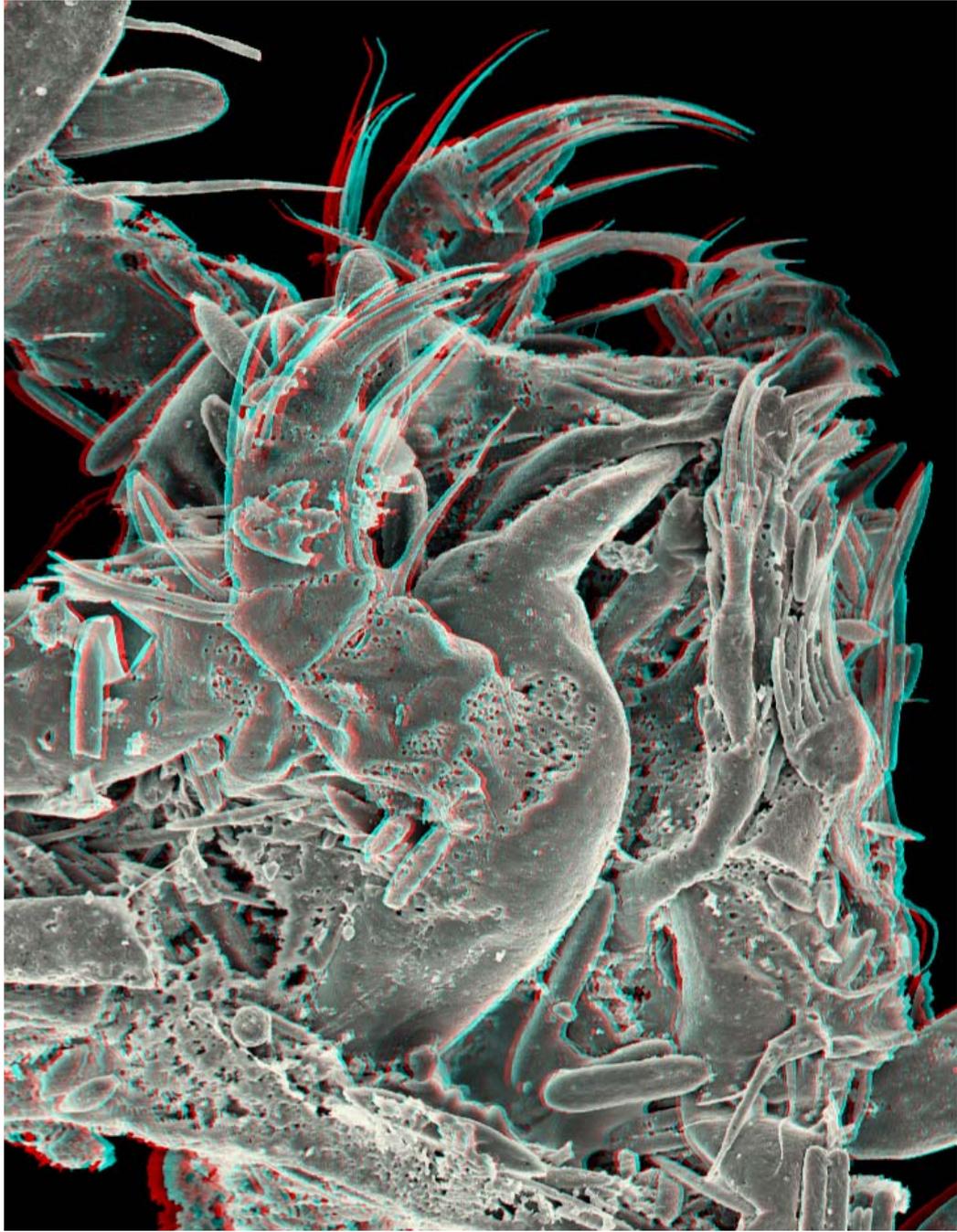
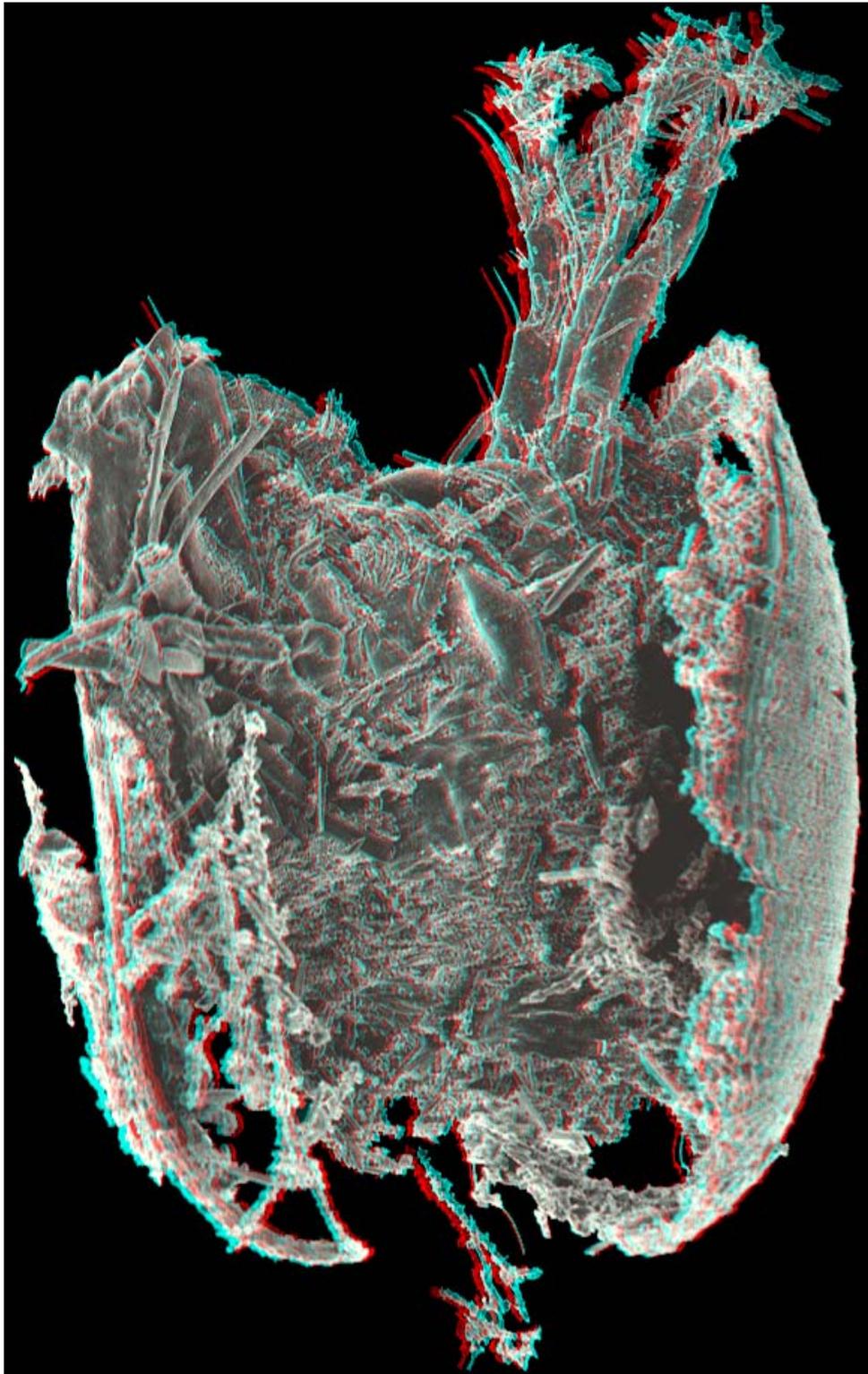


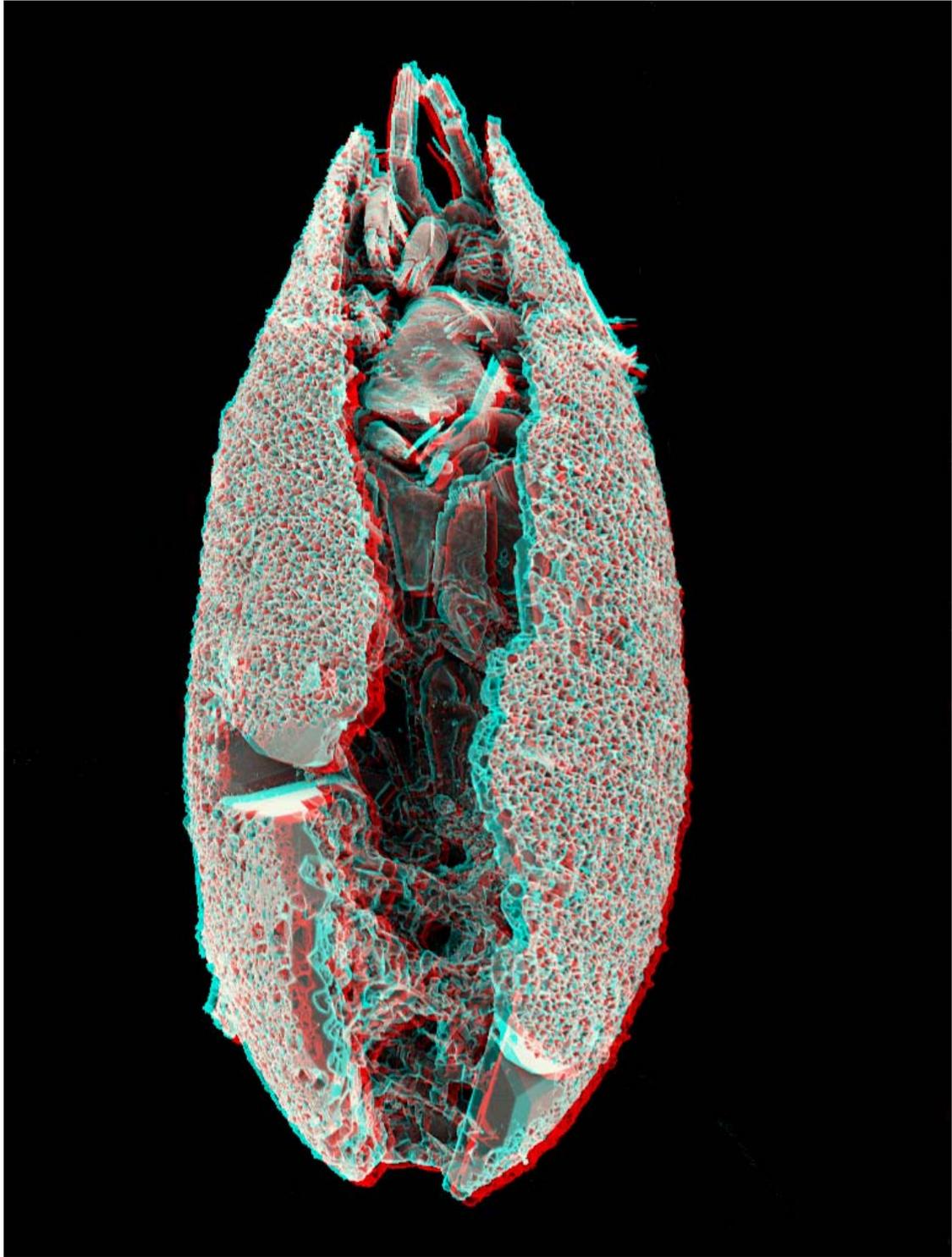
Fig. 5



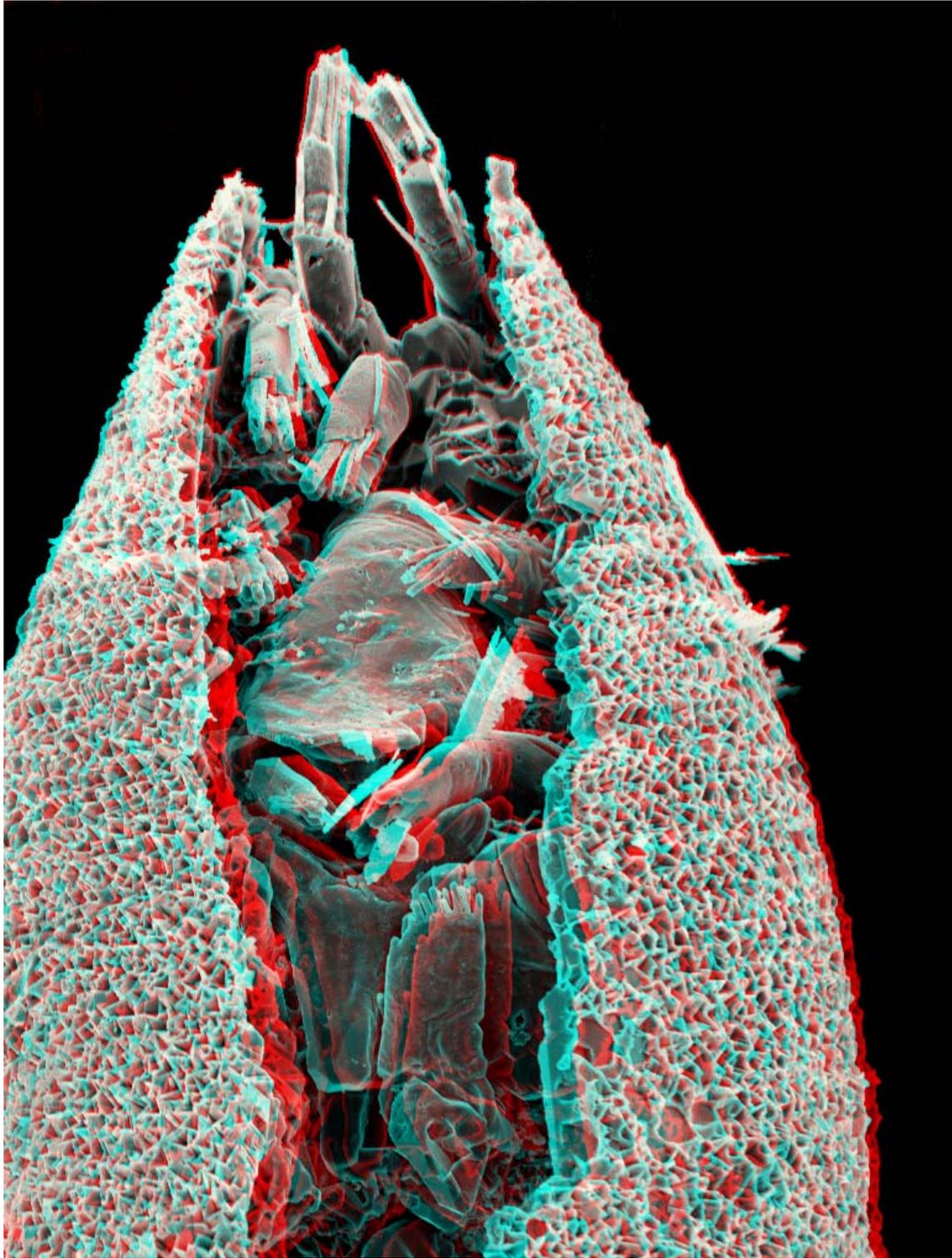
Supplementary material 1



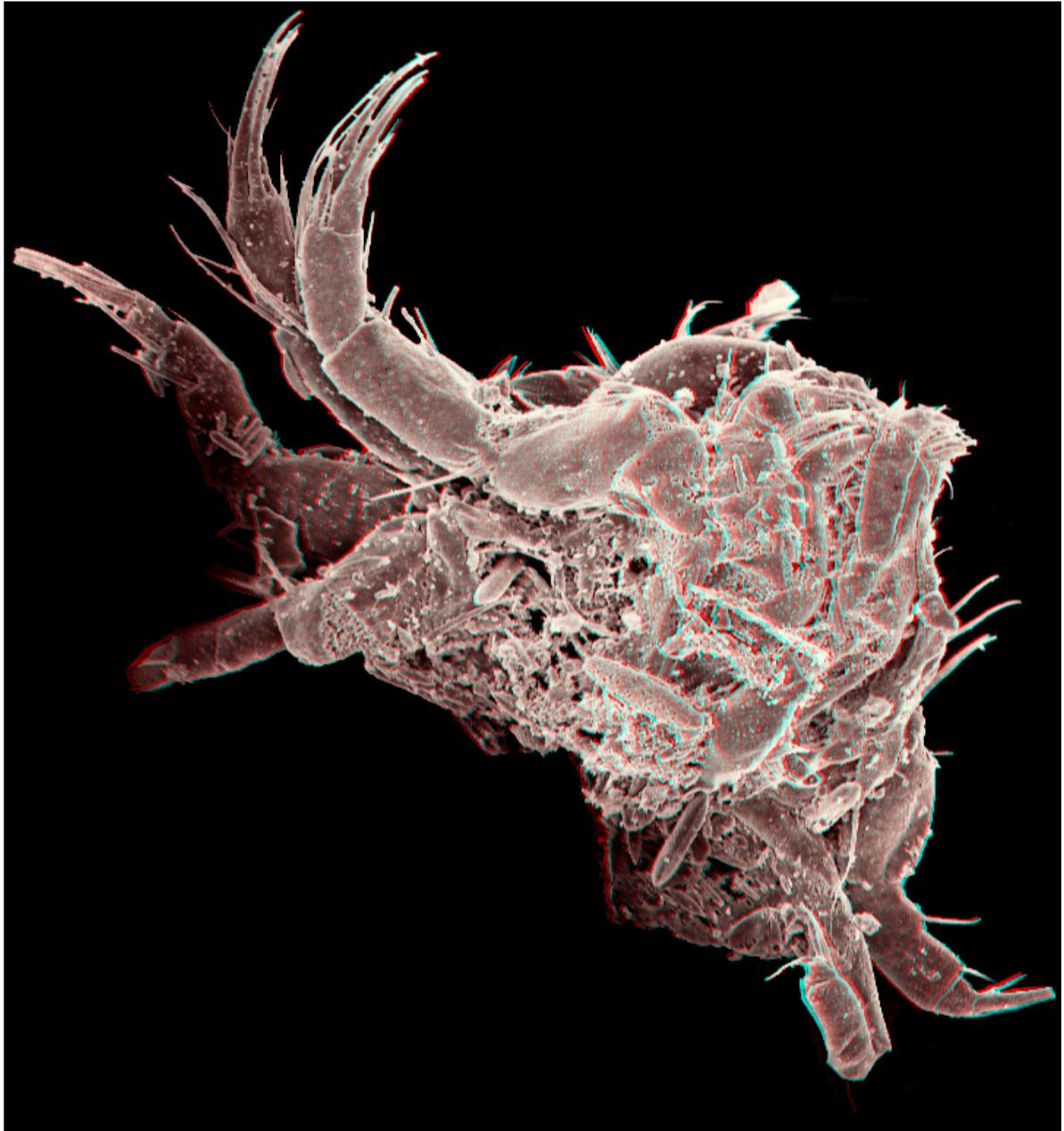
Supplementary material 2



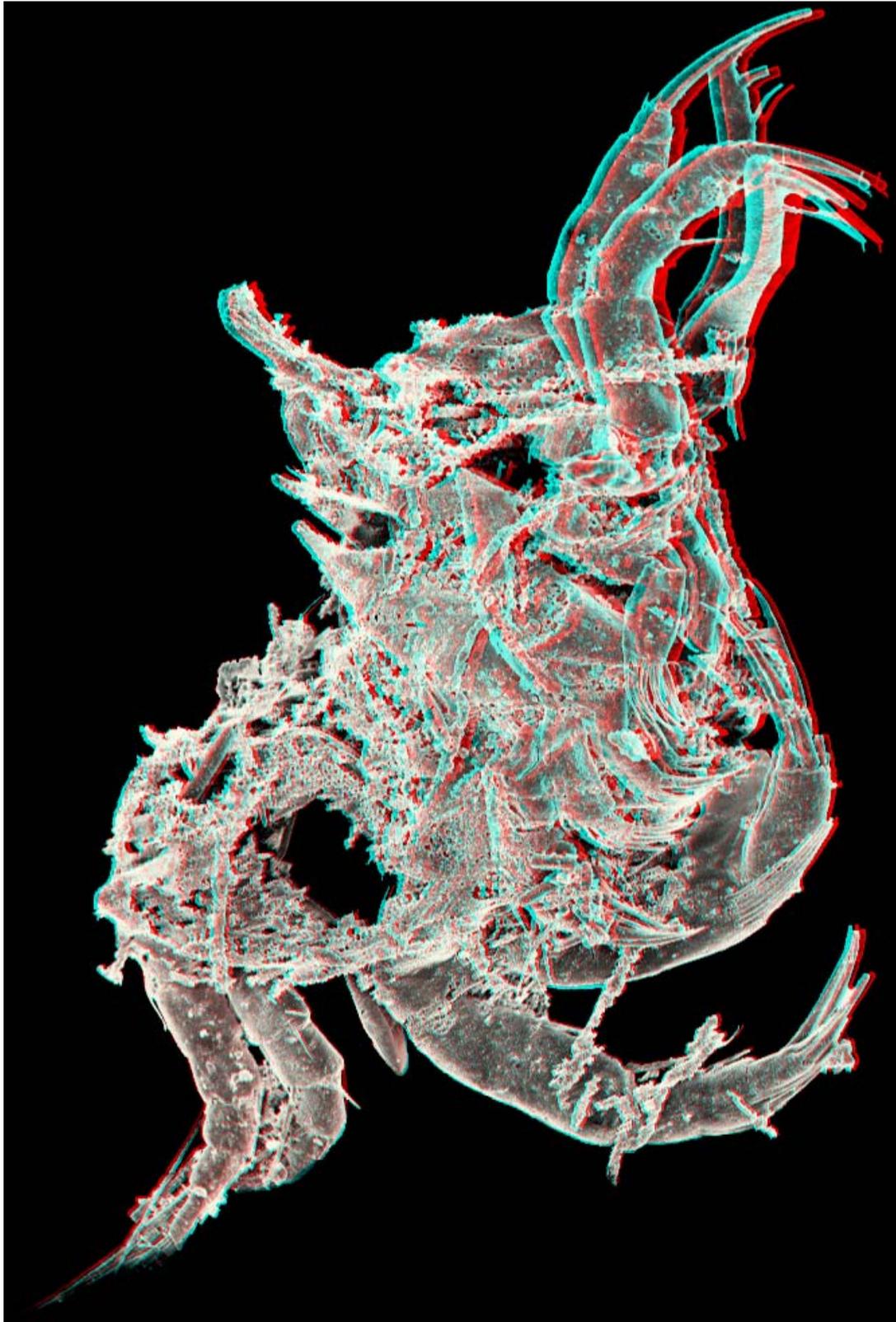
Supplementary material 3



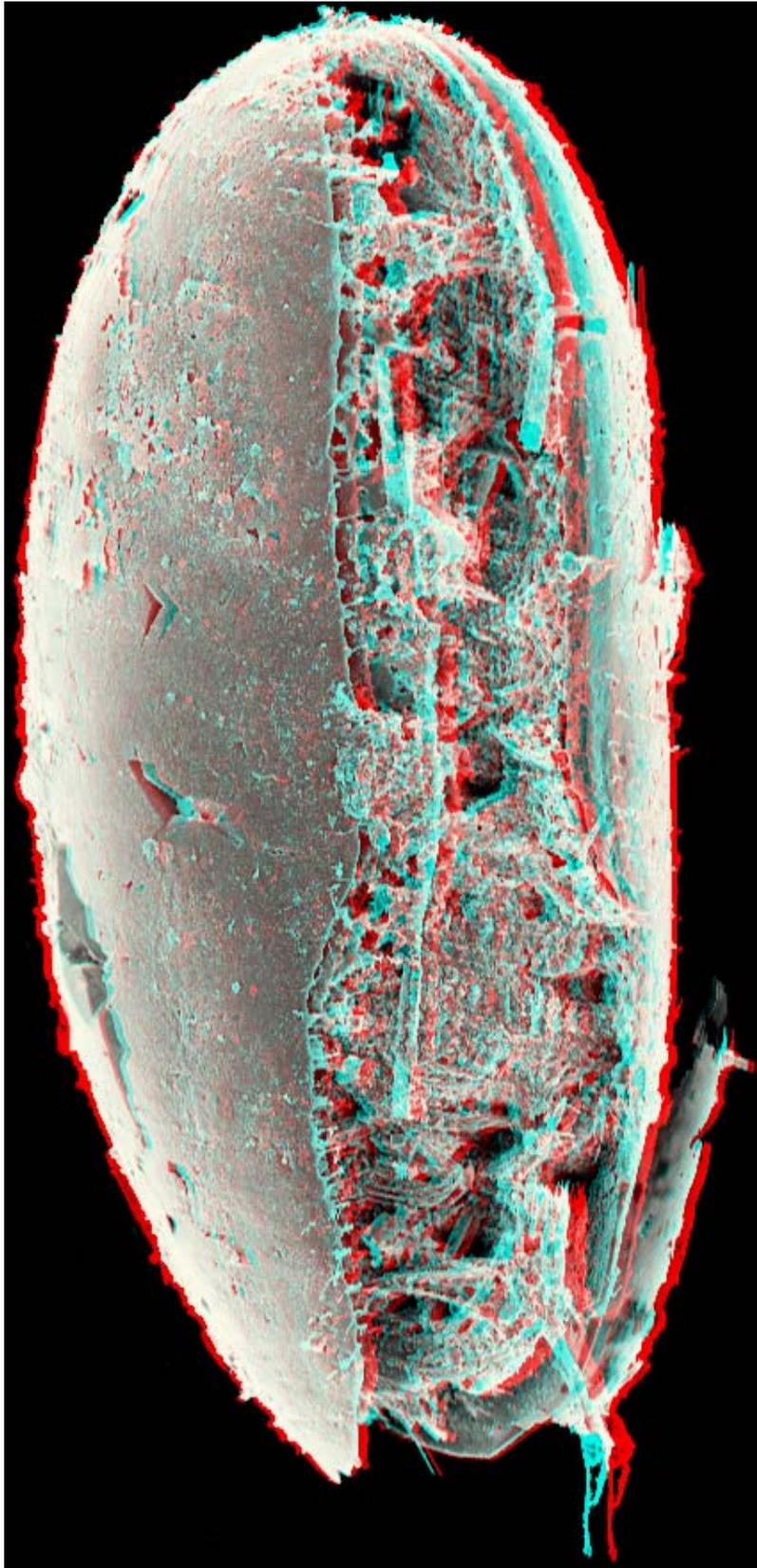
Supplementary material 4



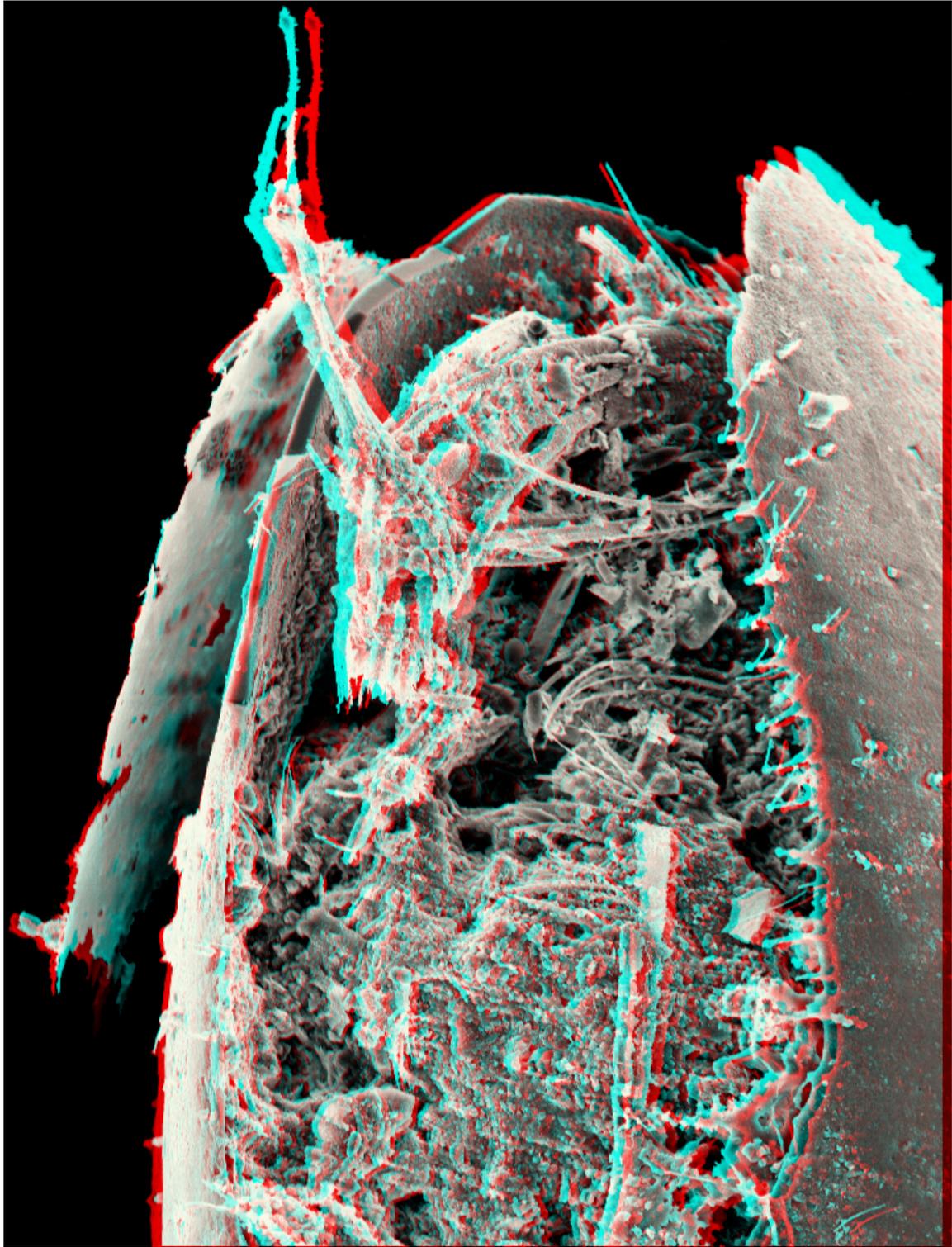
Supplementary material 5



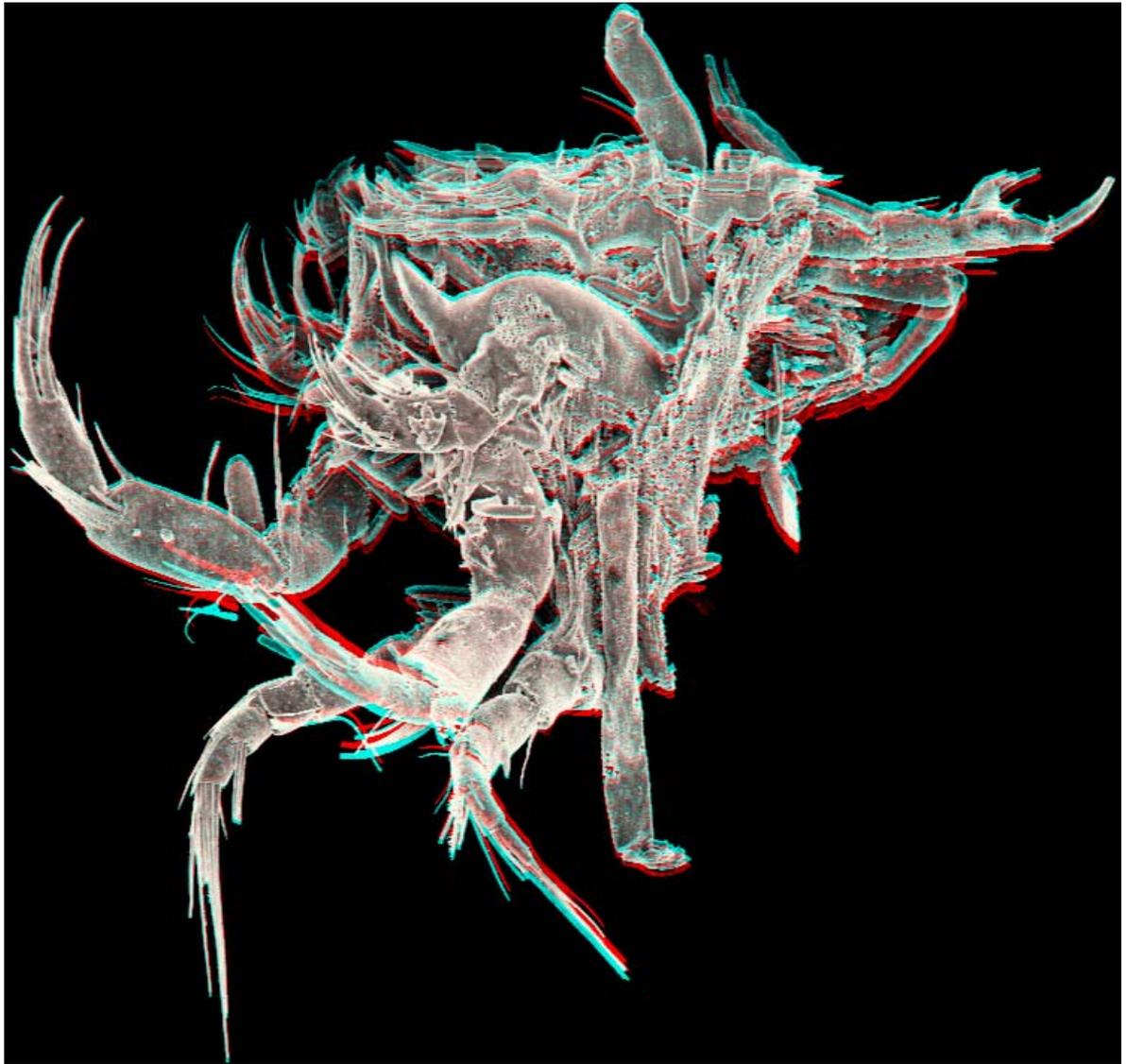
Supplementary material 6



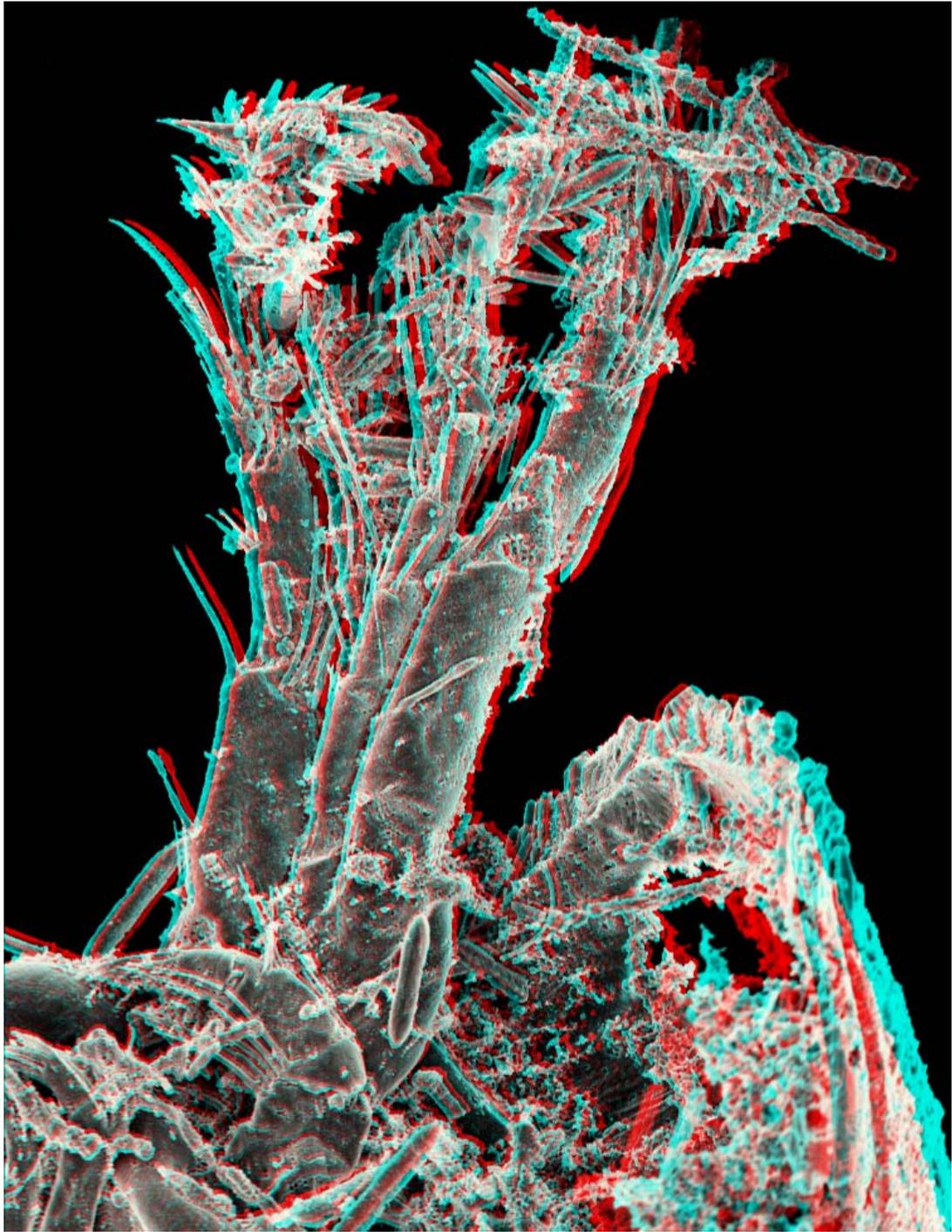
Supplementary material 7



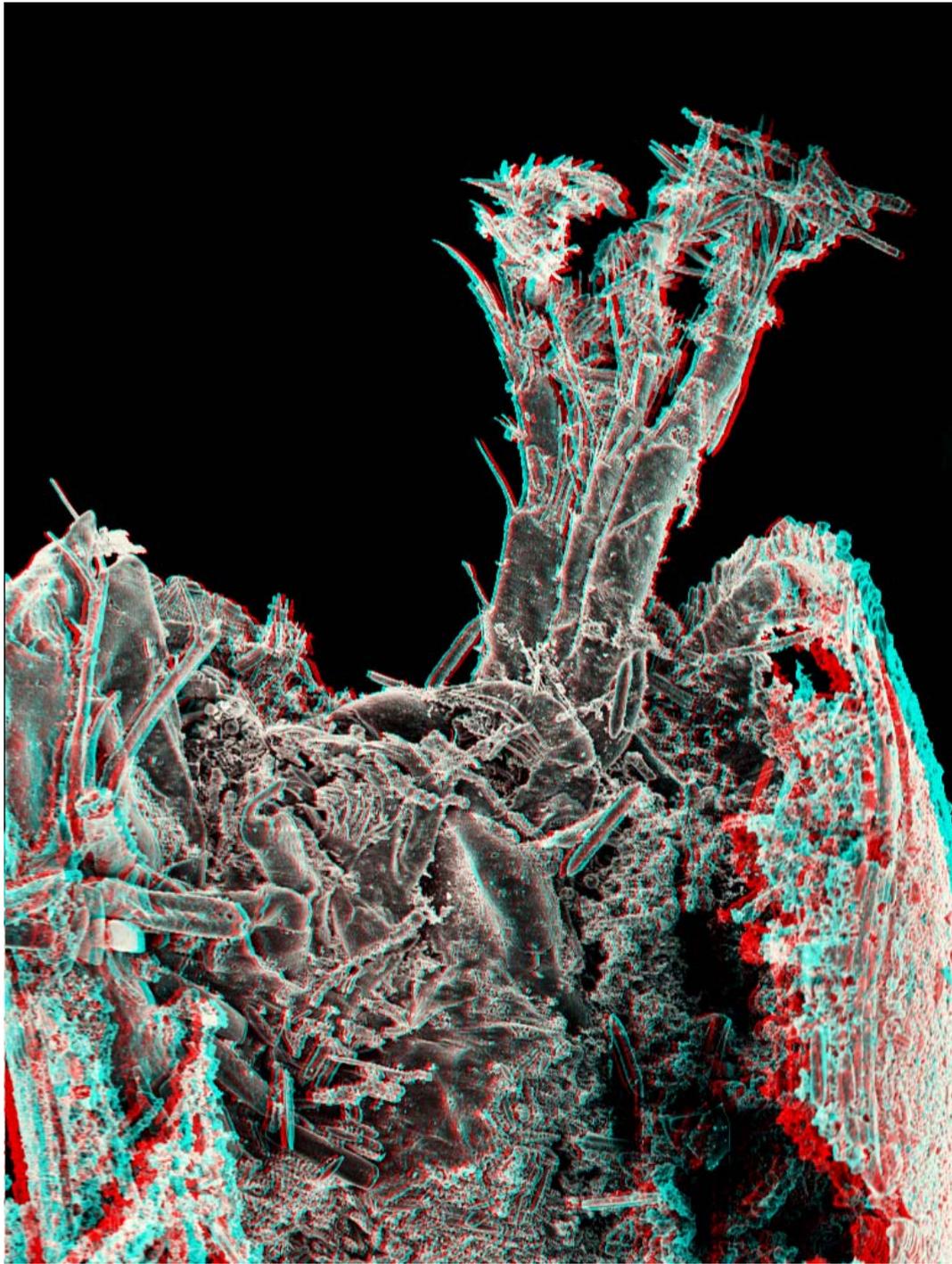
Supplementary material 8



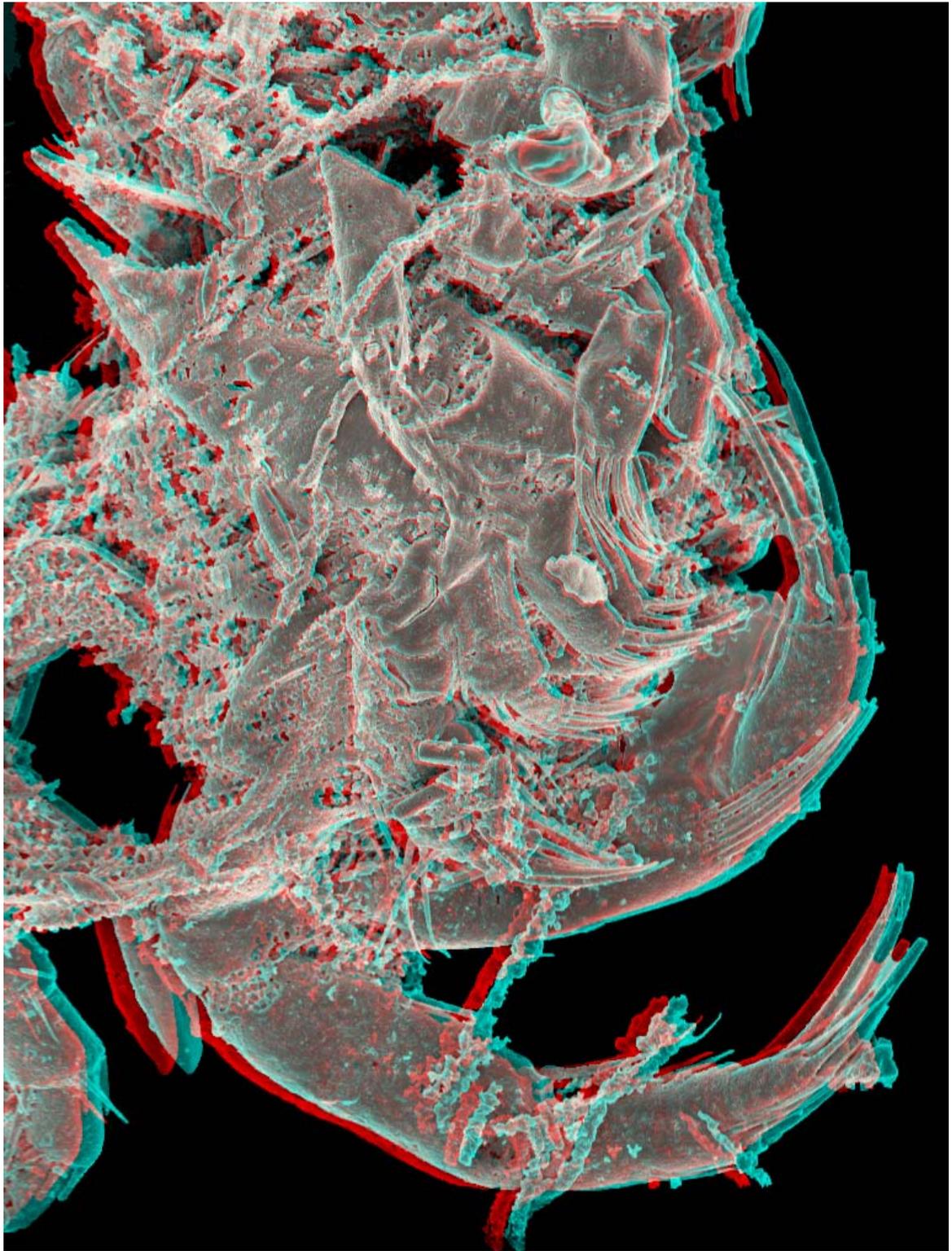
Supplementary material 9



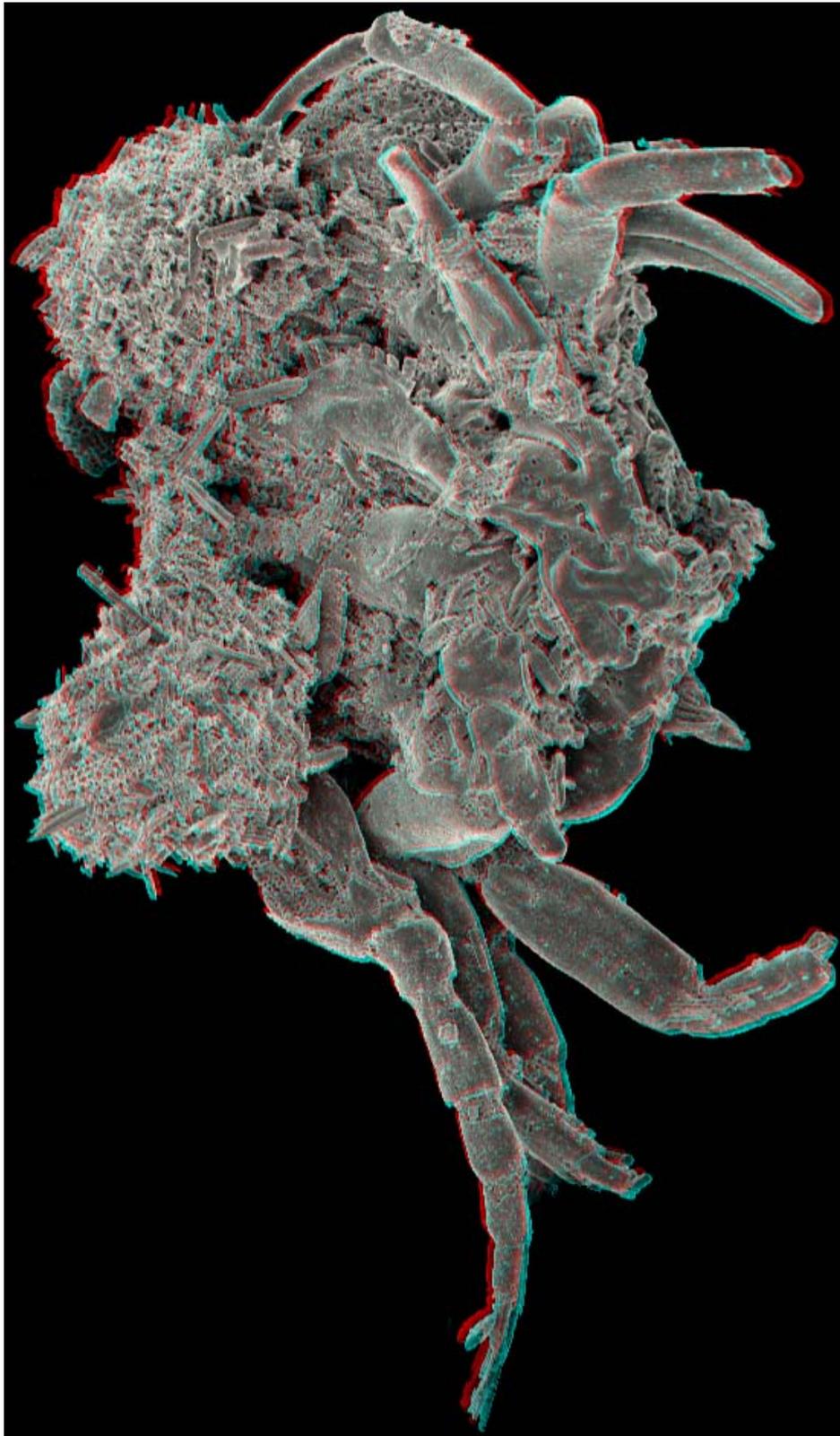
Supplementary material 10



Supplementary material 11



Supplementary material 12



Supplementary material 13