

Review article

Julia Machon, Jakob Krieger, Magali Zbinden, Juliette Ravaux and Steffen Harzsch*

Exploring brain diversity in crustaceans: sensory systems of deep vent shrimps

<https://doi.org/10.1515/nf-2020-0009>

Abstract: The current report focuses on shrimps from deep hydrothermal vents of the Mid-Atlantic Ridge that live in an environment characterized by high hydrostatic pressure, lack of sunlight, and with hot and potentially toxic emissions of black smoker vents. Malacostracan crustaceans display a large diversity of lifestyles and life histories and a rich repertoire of complex behavioral patterns including sophisticated social interactions. These aspects promote this taxon as an interesting group of organisms for those neurobiologists interested in evolutionary transformation of brain structures and evolutionary diversification of neuronal circuits. Here, we explore how analyzing the nervous system of crustacean species from extreme habitats can provide deeper insights into the functional adaptations that drive the diversification of crustacean brain structure.

Keywords: brain evolution; hydrothermal vent; neuroanatomy; place memory; *Rimicaris exoculata*

Zusammenfassung: Innerhalb der höheren Krebstiere (Malacostraca) finden sich Vertreter mit einer großen morphologischen und ökologischen Diversität, die sich außerdem durch eine Vielfalt an unterschiedlichen Lebenszyklen und komplexen Verhaltensweisen auszeichnen. Diese Diversität bietet sehr gute Voraussetzungen, um evolutive Transformationen von Gehirnstrukturen und Sinnessystemen im Spannungsfeld zwischen funktionalen und

phylogenetischen Zwängen zu analysieren. Insbesondere die Neurobiologie von Tieren aus extremen Lebensräumen kann uns neue Einblicke in funktionale Anpassungen ermöglichen, die die evolutive Diversifizierung von Gehirnstrukturen antreiben. In diesem Beitrag stellen wir die Sinnessysteme von Garnelen der Tiefsee vor, die eng assoziiert mit „black smoker“ hydrothermalen Quellen des Mittelatlantischen Rückens leben, einem lichtlosen und auf den ersten Blick lebensfeindlichem Habitat, dass durch hohen hydrostatischen Druck und die toxischen Emissionen der heißen Quellen geprägt ist.

Schlüsselwörter: Evolution des Gehirns; hydrothermale Quelle; Neuroanatomie; räumliches Gedächtnis; *Rimicaris exoculata*

Exploring the diversity of crustacean brains

Among the arthropods, crustaceans represent an important subgroup that displays a large diversity of sizes, morphologies, lifestyles, and life histories (for a review, see Schram, 2013). Specifically, members of the malacostracan crustaceans (Figure 1) have colonized habitats extending from the deepest ocean trenches and hydrothermal vents, through coastal, estuarine, to freshwater ecosystems. They also display a rich repertoire of complex behavioral patterns related to finding food, shelter, and mating partners; kin recognition and brood care; and orientation and homing. Complex social interactions include the establishment of dominance hierarchies, communal defensive tactics, the occupation of common shelters, and cooperative behavior during long-distance, offshore seasonal migration (reviewed by Breithaupt and Thiel, 2011; Derby and Thiel, 2014; Duffy and Thiel, 2007; Thiel and Walting, 2015). Their striking morphological, behavioral, and ecological diversity promotes this taxon as an interesting group of organisms for those neurobiologists interested in evolutionary transformation of brain

*Corresponding author: Steffen Harzsch, Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, D-17498, Greifswald, Germany, E-mail: steffen.harzsch@uni-greifswald.de. <https://orcid.org/0000-0002-8645-3320>

Julia Machon, Magali Zbinden and Juliette Ravaux: UMR CNRS MNHN 7208 Biologie des Organismes et Écosystèmes Aquatiques (BOREA), Equipe Adaptation aux Milieux Extrêmes, Sorbonne Université, Paris, France

Jakob Krieger: Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany

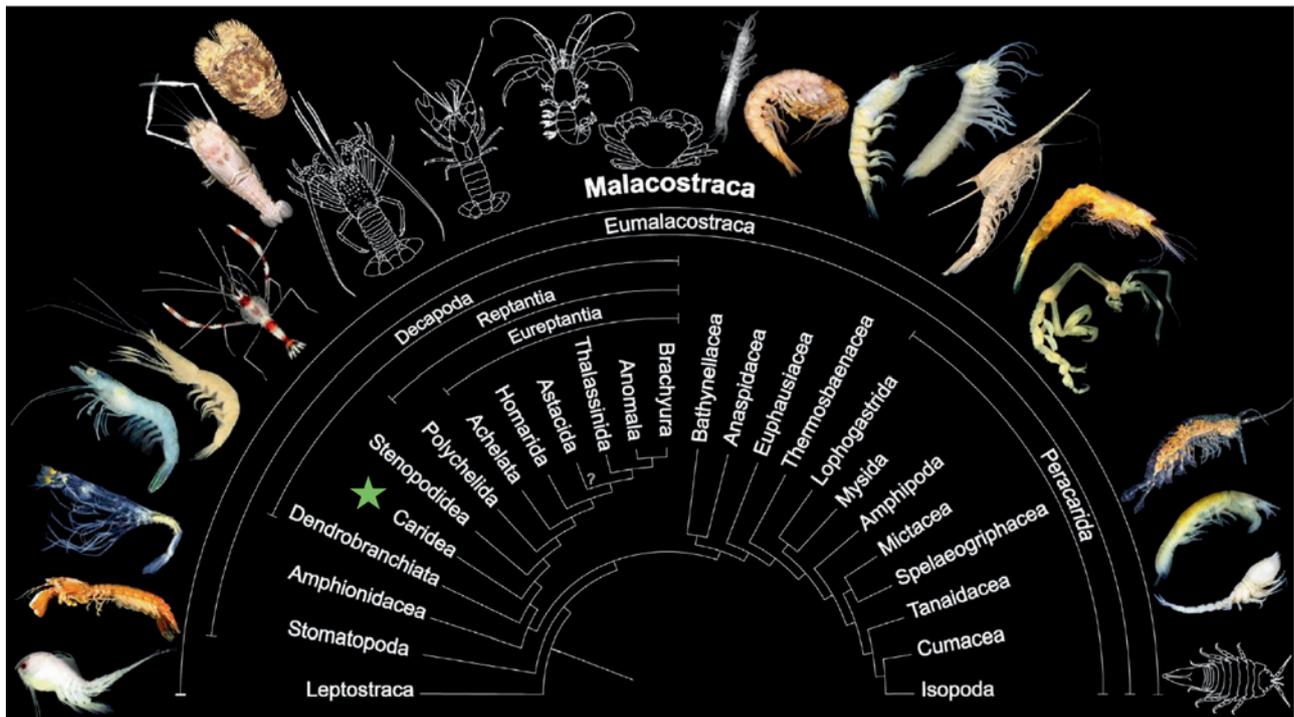


Figure 1: Phylogenetic relationships of malacostracan crustaceans (modified from Harzsch and Krieger, 2018; compiled after Richter and Scholtz, 2001; and Wirkner and Richter, 2010). The green asterisk show the phylogenetic position of the deep vent shrimp *Rimicaris exoculata* among Caridea.

structures and evolutionary diversification of neuronal circuits, specifically considering the antagonistic action of phylogenetic and functional constraints (Sandeman et al., 2014a, 2014b; Strausfeld, 2012). For example, crustaceans such as krill (*Euphausia superba*), which dominate the vast water bodies of the Southern oceans (Hempel, 1987), have evolved specific mechanisms of sensory-motor integration, which facilitates swimming in formation while schooling (Patria and Wiese, 2004). Cleaner shrimps, which are famous for their cleaning behavior of different species of coral reef fish and serve as iconic examples for communication across the vertebrate/invertebrate split (*Urocardirella sp.*, Becker et al., 2005), display specific adaptation in their central mechanosensory pathways (*Stenopus hispidus*, Krieger et al., 2019). Fiddler crabs of the genus *Uca* are characteristic crustaceans of equatorial intertidal mud flats and serve as models to analyze crustacean visual ecology and the neuroethology of homing behaviors (Tomšić, 2016; Zeil and Hemmi, 2006).

We are interested in determining how the sensory landscape that the animals analyze in their various habitats is mirrored in the phenotype of the sensory systems and the morphology of the primary sensory brain areas, and against this background, we have

previously studied the brains of a large diversity of malacostracan crustaceans (Figures 1 and 2). By describing the relative proportions of brain areas known to be involved in processing certain types of sensory input and comparing these proportions to other crustaceans' brains may reflect how important these senses are for the animals to analyze their environment (Sandeman et al., 2014a, 2014b). Specifically, analyzing the nervous system of crustacean species from extreme habitats may provide deeper insights into the functional adaptations, which drive the diversification of crustacean brain structure. One obvious example comes from crustacean living in lightless habitats, an environmental factor that promotes the simplification of visual systems (Ramm and Scholtz, 2017; Stegner et al., 2015). Representatives of the malacostracan crustaceans have also invaded terrestrial habitats multiple times independently (for a review, see Hansson et al., 2011) and representatives of isopod crustaceans survive and reproduce not only in our European forests and gardens but also in desert salt pans of North Africa. Neurobiological studies suggest that terrestrial isopod crustaceans have failed to evolve aerial olfaction during their evolutionary diversification from marine ancestors (Harzsch and Hansson, 2008), whereas representatives of terrestrial hermit crabs have invested

huge amounts of neuronal tissue in their olfactory pathway display a superb aerial sense of smell (Harzsch and Hansson, 2008; Krieger et al., 2010). Here, we explore what another example of crustaceans subjected to strong environmental constraints can teach us about the functional adaptations of crustacean sensory systems.

Introduction to vent shrimp sensory ecology

Since their discovery in the late 1980s, shrimps from deep hydrothermal vents have sparked interest among biologists because of their particular habitat and lifestyle. In addition to the high hydrostatic pressure and the absence of sunlight that characterize their environment, vent shrimps live in the surrounding areas of black smoker hydrothermal vents (Figure 3A, B). Hydrothermal fluids are hot (up to 350 °C) and rich in potentially toxic chemicals (Charlou et al., 2000, 2002, 2010). A key adaptation of the *Rimicaris exoculata* shrimps is their symbiotic association with chemoautotrophic bacteria that provide energy to their hosts by oxidizing the fluid chemicals. Hence, in light of their habitat, the fairly extreme conditions they must cope with, and their lifestyle, these vent shrimps are fascinating models to study biological adaptations to the environment.

An important question in vent shrimp ecology is to understand the sensory mechanisms that the animals use for orientation in their dark environment, to select a suitable habitat, to find food, to detect congeners, or to locate active smokers to supply their symbiotic bacteria with chemicals. Because they colonize the vicinity of black smokers, it has been suggested that they might exploit abiotic factors of the hydrothermal fluid as orientation cues (Sarrazin et al., 1999; Segonzac et al., 1993). The commonly considered factors are the fluid chemicals, temperature, and thermal radiation emitted by the hot fluids. The shrimp may have evolved specific abilities to detect these stimuli, and the related senses could play a major role in orientation within the habitat.

Therefore, analyzing the architecture of the peripheral and central sensory systems provides new insights into the sensory biology of vent shrimps (Figures 3 and 4), knowledge that is essential for learning their ecology and long-term evolutionary adaptations. Comparative studies with shallow water relatives are especially relevant in this context to reveal sensory adaptations to the habitat and related evolutionary processes (Derby and Weissburg, 2014).

A unique visual system

The first anatomical observations of vent shrimp specimens had led to the reassessment of the general belief that deep sea animals were entirely blind (Van Dover et al., 1989). Vent shrimps possess highly modified eyes, which, in *Rimicaris exoculata*, consist of large ocular plates located at the anterodorsal region of the cephalothorax (Figures 3C and 5A). Their retinal structure consists of a smooth cornea that covers a layer of photoreceptive rhabdoms, under which reflective cells of the tapetum are located (Figure 5B). Several authors have shown that the rhabdoms are hypertrophied, which would maximize the absorption of light (Chamberlain, 2000; Jinks et al., 1998; Machon et al., 2019; Nuckley et al., 1996; O'Neill et al., 1995). However, in the specimen presented here, the rhabdoms are degenerated, which appears to be a consequence of a dramatic deterioration of the retina following the intense light exposure during sampling, as shown by Herring et al. (1999). In addition, the dioptric apparatus, which is a characteristic of typical crustacean compound eyes, is lacking, indicating that these eyes cannot form images. Functional rhodopsin-like visual pigments were also identified in high quantities in the retina of *R. exoculata* (Van Dover et al., 1989) (Figure 5C). At the central nervous level, as in other malacostracans, vent shrimp present a suite of retinotopic visual neuropils (lamina, medulla, and lamina) (Figure 5D) that are strongly reduced in size and that are fused with the median brain (Figures 4 and 5A), coinciding with the absence of eyestalks (Machon et al., 2019).

Because selective pressure favors the reduction of unsolicited nervous tissues (Klaus et al., 2013; Moran et al., 2015; Niven and Laughlin, 2008), the presence of visual neuropils, together with a seemingly functional retina, is indicative of an effective visual system in vent shrimp, which implies that a light signal does occur in their environment. The prominent hypothesis is that vent shrimp might have evolved a highly sensitive retina, to the detriment of spatial resolution, to detect the very dim light of the thermal radiation emitted by the hot (up to 350 °C) hydrothermal fluids as they exit the black smoker (Pelli and Chamberlain, 1989; Van Dover and Fry, 1994; Van Dover et al., 1988, 1996).

A common olfactory system

Asking how the shrimps can detect active vent areas, biologists had previously proposed that they locate black smokers by chemotaxis, reacting to specific chemical compounds of the hydrothermal fluids (Segonzac et al.,

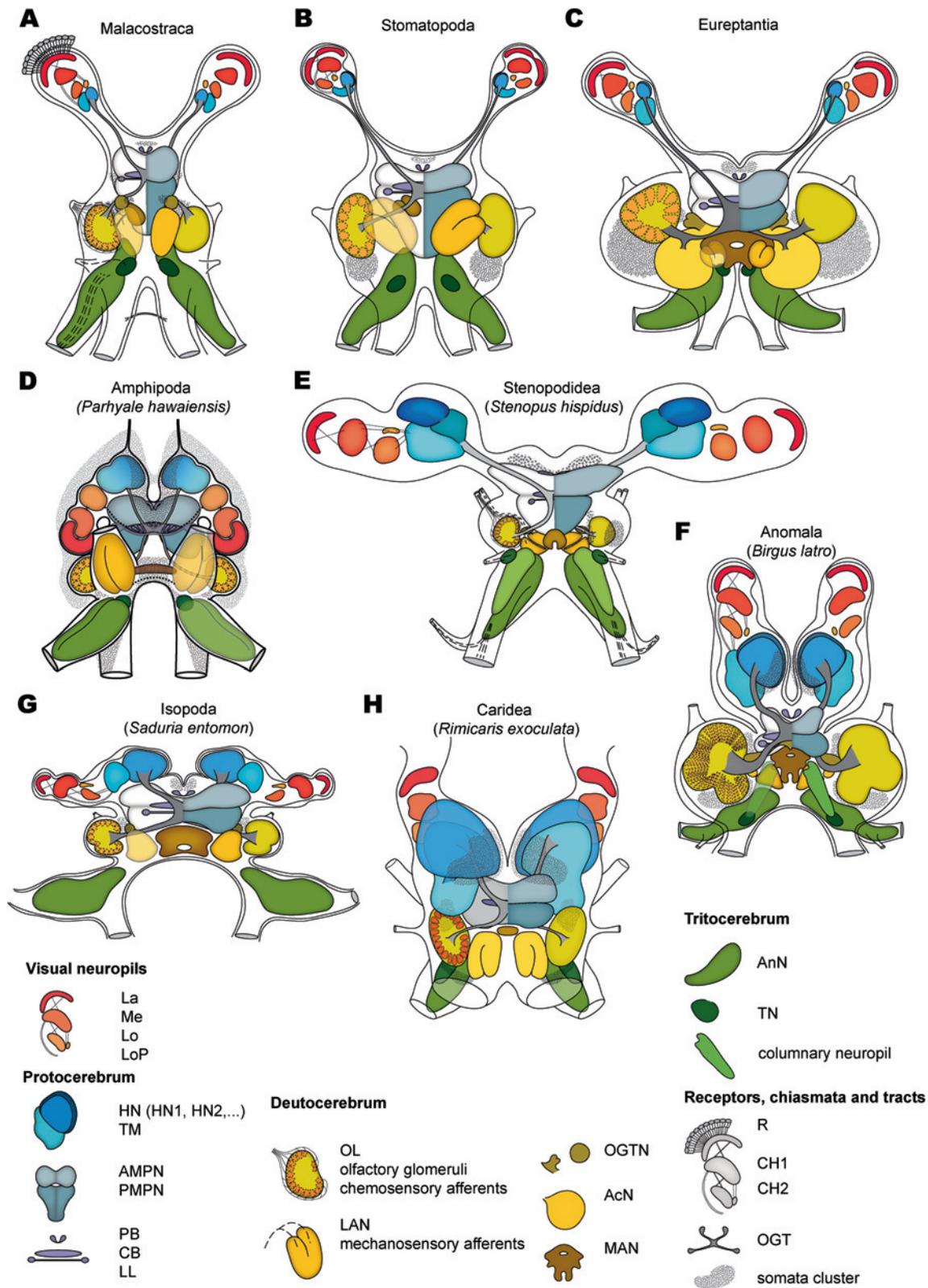


Figure 2: Brain anatomy of malacostracans (modified from Sandeman et al., 2014a, 2014b). The subdivisions of the proto-, deuto-, and tritocerebrum can be identified by their shape and color provided in the key. (A) Malacostraca. (B) Stomatopoda. (C) Eureptantia. (D) Amphipoda (*Parhyale hawaiensis*; from Wittfoth et al. 2019). (E) Stenopodidea (*Stenopus hispidus*; from Krieger et al., 2019). (F) Anomala (*Birgus latro*). (G) Isopoda (*Saduria entomon*). (H) Caridea (*Rimicaris exoculata*; from Machon et al., 2019).

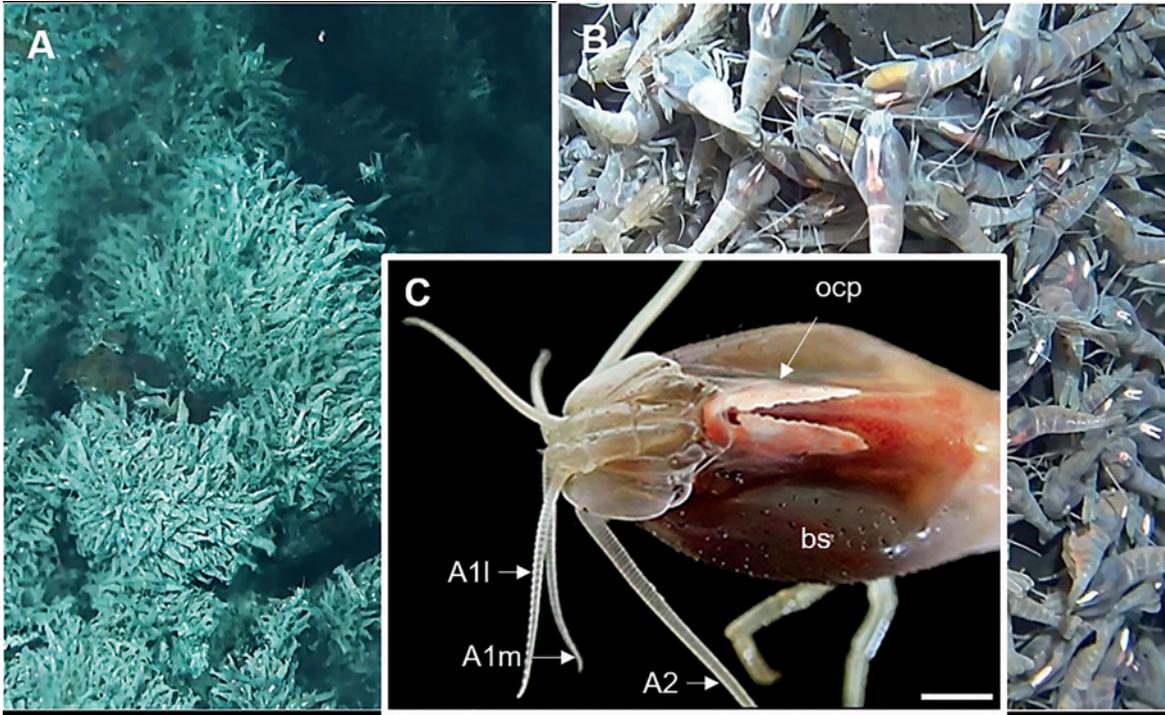


Figure 3: Swarms and morphology of the deep vent shrimp *Rimicaris exoculata*. A,B: Swarms of thousands of shrimp are surrounding the walls of black smoker hydrothermal vents at the TAG vent site (3600 m depth), Mid-Atlantic Ridge (©IFREMER/Nautilé6000, BICOSE 2018 cruise). C: Dorsal view of the cephalothorax showing voluminous gill chambers covered by the branchiostegites, dorsal eyes (namely the ocular plate) with two elongated retinæ fused in the anterior region, and sensory appendages (antennae 1 and 2). A1l, lateral flagellum of antenna 1; A1m, medial flagellum of antenna 1; A2, antenna 2; bs, branchiostegite; ocp, ocular plate. Scale bar = 5 mm. Modified from Machon et al. (2019).

1993). This hypothesis was soon supported by electrophysiological recordings of concentration-dependent sulfide sensitivity from the first antenna nerves of *R. exoculata* (Figure 6A), and the authors suggested that these shrimp may present enhanced olfactory abilities to detect naturally occurring sulfide gradients in the near field of the vents (Jinks et al., 1998; Renninger et al., 1995). The complexity of the animal's peripheral and central olfactory pathways may reflect these functional demands in that their chemical senses evolved to compensate for the underperformance of the visual system.

However, a comparative study of the first antenna and the specialized olfactory aesthetasc sensilla (Figure 6B, C) of *R. exoculata*, three other vent shrimp species, and a closely related shallow-water species revealed no specific adaptation between hydrothermal and coastal species regarding the

chemosensory organs morphology (Zbinden et al., 2017). Additionally, recent electrophysiological recordings from the antennae in the vent shrimp *Mirocaris fortunata* and a related member of the Caridea, the shallow-water shrimp *Palaemon elegans*, showed that sulfide detection is not specific to the vent species (Machon et al., 2018). Hence, no features indicative of a more sophisticated olfactory performance have been identified from the peripheral system of vent shrimp thus far. Nevertheless, a noticeable aspect of vent shrimp is the dense coverage of their antennae and aesthetasc sensilla by bacteria (Figure 6D), which were identified to be similar to known chemoautotrophic sulfur oxidizers and may thus influence the chemosensory system in several ways, but their specific roles are unknown yet (Zbinden et al., 2018).

Regarding the sensory centers, a thorough description of the brain neuroanatomy in *R. exoculata*

Abbreviations: Visual neuropils: La, lamina; Me, medulla; Lo, lobula; LoP, lobula plate neuropil. Protocerebrum: HN (HN1, HN2), hemiellipsoid body (subdivisions thereof); TM, terminal medulla; AMPN, anterior medial protocerebral neuropil; PMPN, posterior medial protocerebral neuropil; PB, protocerebral bridge; CB, central body; LL, lateral lobe. Deutocerebrum: OL, olfactory lobe; LAN, lateral antennular (antenna 1) neuropil; OGTN, olfactory globular tract neuropil; AcN, accessory lobe; MAN, median antennular (antenna 1) neuropil. Tritocerebrum: AnN, antennal (antenna 2) neuropil; TN, tegumentary neuropil; Receptors, chiasmata and tracts: R, retina; CH1, first visual chiasm; CH2, second visual chiasm; OGT, olfactory globular tract. Note that brain schemes are aligned according to their neuroaxis (not to their arrangement within the cephalothorax) and are not equally scaled.

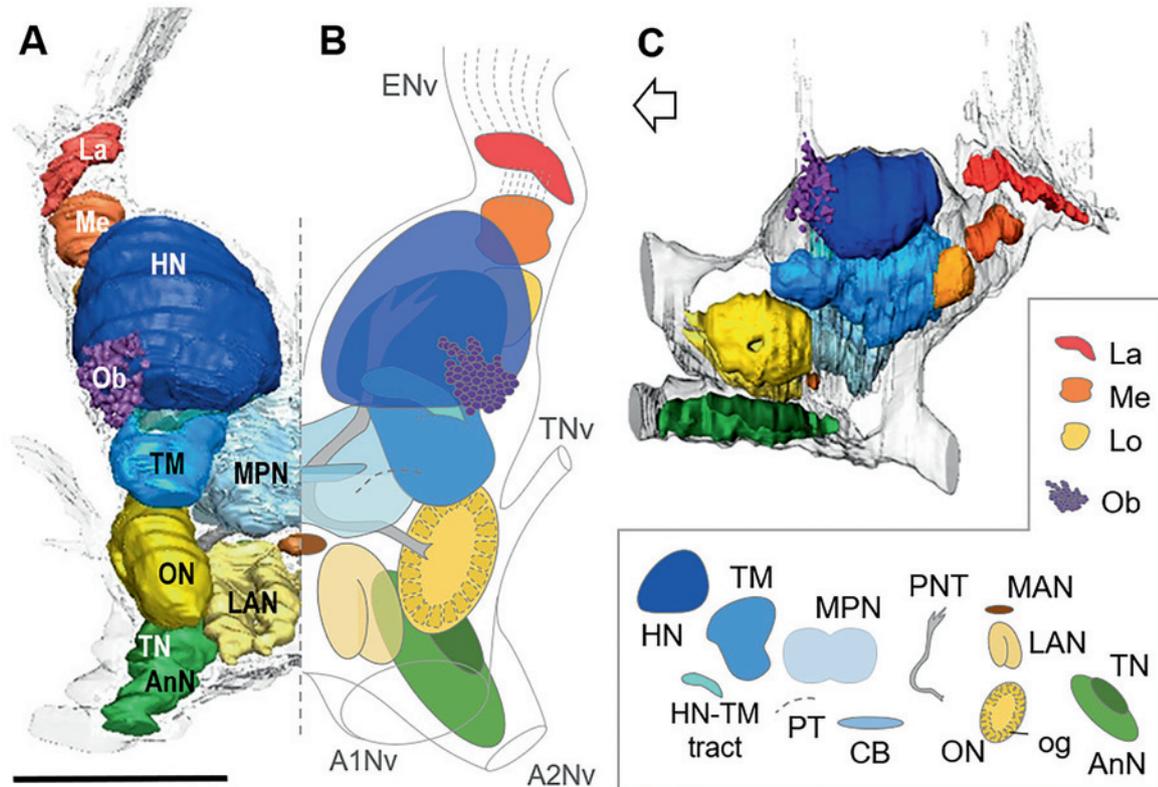


Figure 4: Brain architecture of the deep vent shrimp *Rimicaris exoculata*. 3D Reconstructions (A, C) and schematic representation (B) of the brain and neuropils, viewed from a dorsal, slightly anterior direction (A, B) and from the left (C). In C, the open white arrow point towards anterior of the body axis. The clusters of cell somata are not shown. The 3D reconstructions are based on an image stack obtained by serial sectioning of paraffin-embedded material. A1Nv, antenna 1 nerve; A2Nv, antenna 2 nerve; AnN, antenna 2 neuropil; CB, central body; ENv, eye nerve; HN, hemiellipsoid body neuropil; La, lamina; LAN, lateral antenna 1 neuropil; Lo, lobula; MAN, median antenna 1 neuropil; Me, medula; MPN, median protocerebral neuropil; Ob, onion bodies; og, olfactory glomerulus; ON, olfactory neuropil; PT, protocerebral tract; PNT, projection neuron tract; TM, terminal medulla neuropil; TN, tegumentary neuropil; TNv, tegumentary nerve. Scale bar = 500 μ m. Modified from Machon et al. (2019).

allowed to search for a differential investment in the olfactory neuropils that might reflect an enhanced olfactory performance (Machon et al., 2019). These neuropils are lobe-shaped and composed of olfactory glomeruli that are radially arranged around the periphery of a non-synaptic core (Figure 6E, F) and subdivided into three regions (Figure 6F) as observed in several decapod taxa (Harzsch and Krieger, 2018). Structural features that may be linked to the efficiency of the olfactory system were compared between *R. exoculata* and other malacostracan species, showing that the olfactory neuropils are not overly hypertrophied in the vent species. Overall, the structural complexity of the olfactory system does not suggest that *R. exoculata* presents adaptations to the specific chemosensory landscape at vents, and olfaction is probably not a particularly dominant sensory modality in vent shrimp.

The hemiellipsoid body, a higher integrative brain center

Higher integrative centers in the malacostracan brain provide the neuronal substrate for more sophisticated processing and receive input exclusively from second- or higher-order neurons but not from any primary sensory afferents. Interneurons within such centers typically respond to the stimulation of several different sensory systems (reviewed by Sandeman et al., 2014a, 2014b). In the malacostracan brain, the (bilaterally paired) complex of hemiellipsoid body and terminal medulla (HE/MT) is one of these higher integrative centers. It is targeted by the axons of the olfactory projection neurons as output pathway of the olfactory system and also receives input from the visual neuropils (for reviews, see Derby and Weissburg, 2014; Harzsch and Krieger, 2018; Schmidt, 2016). Substantial morphological modifications

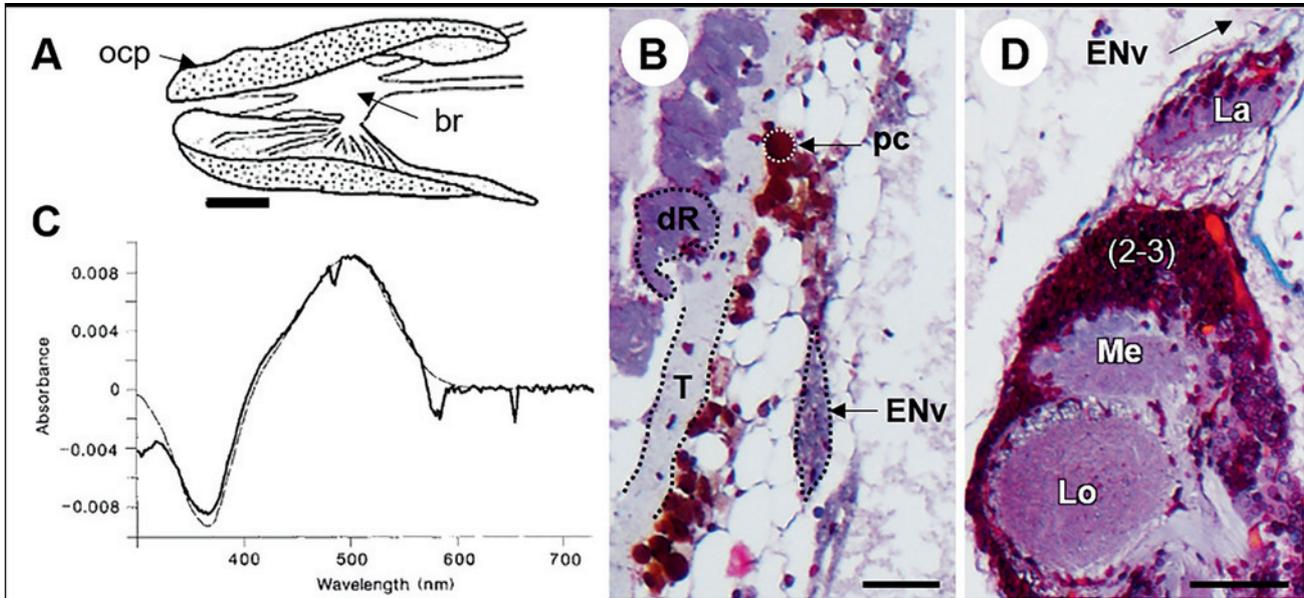


Figure 5: Visual system of the deep vent shrimp *Rimicaris exoculata*. A: Drawing showing the location of the visual organs and their connection to the brain (dorsal view; from Van Dover et al., 1989). B: Histological section of the retina. C: Bleaching difference spectrum of visual pigment in *R. exoculata* (solid trace) that maximally absorbs at 500 nm, typical of rhodopsin, and creates a new pigment at 367 nm, which corresponds to retinaloxime. The same features are seen in the difference spectrum of the frog rhodopsin (dashed line) (from Van Dover et al., 1989). D: Histological frontal section of the visual neuropils (from Machon et al., 2019). Scale bars = 100 μ m. (2–3), cell cluster 2–3; br, brain; dR, degenerated rhabdoms; ENv, eye nerve; La, lamina; Lo, lobula; Me, medulla; ocp, ocular plate; pc, pigment cell; T, tapetum.

and changes related to the relative proportion of types of input occurred during the evolutionary elaboration of the HE/MT complex (reviewed, e. g., by Harzsch and Krieger, 2018; Machon et al. 2019). Nevertheless, recent studies suggest that, despite many morphological differences, the MT/HE complex of crustaceans and the iconic mushroom bodies of insects share common architectural, physiological, and neurochemical features, suggesting a homology of their very basic neuronal circuitry (e. g., Maza et al., 2016; Wolff et al., 2012, 2017; Wolff and Strausfeld, 2015; Strausfeld and Sayre et al. 2020, Sayre and Strausfeld 2019). Considering such basal anatomical similarities of the crustacean hemiellipsoid body and insect mushroom body, Wolff et al. (2017) suggested an involvement of both structures in place memory. Furthermore, because of its close anatomical association with the olfactory system as target of the projection neuron tract, evolutionary (Sullivan and Beltz, 2001, 2004), and functional considerations (Harzsch and Krieger, 2018; Sandeman et al., 2014a, 2014b; Strausfeld, 2012) have focused on the possible roles of these centers in higher-order olfactory processing and have suggested that the structural elaboration and size of hemiellipsoid bodies largely mirror the importance of the central olfactory

pathway in a given brain (e. g., Harzsch and Hansson, 2008; Harzsch and Krieger, 2018; Krieger et al., 2010).

In the brain of *R. exoculata*, an inconspicuous and moderately developed olfactory neuropils (see previous section A common olfactory system) contrast with disproportionately large hemiellipsoid bodies (Figure 4). Because visual input also plays a minor role, Machon et al. (2019) suggested that the impressive hemiellipsoid body of *R. exoculata* may fulfill functions in addition to higher-order sensory processing in that they perhaps serve as the neuronal basis for a sophisticated place memory. For survival in the extreme, lightless habitat of *R. exoculata*, an excellent place memory may be essential for avoiding the dangerously hot vent chimneys and memorizing emission sites of hydrothermal fluids rich in those chemicals on which their endosymbiont bacteria depend (Machon et al. 2018). To test this hypothesis, other representatives of the taxon Alvinocarididae should serve as a model because behavioral experiments with *R. exoculata* are technically challenging because they need to be carried out in the pressurized aquariums. Other vent shrimp species such as *M. fortunata* also display pronounced hemiellipsoid bodies (see next section

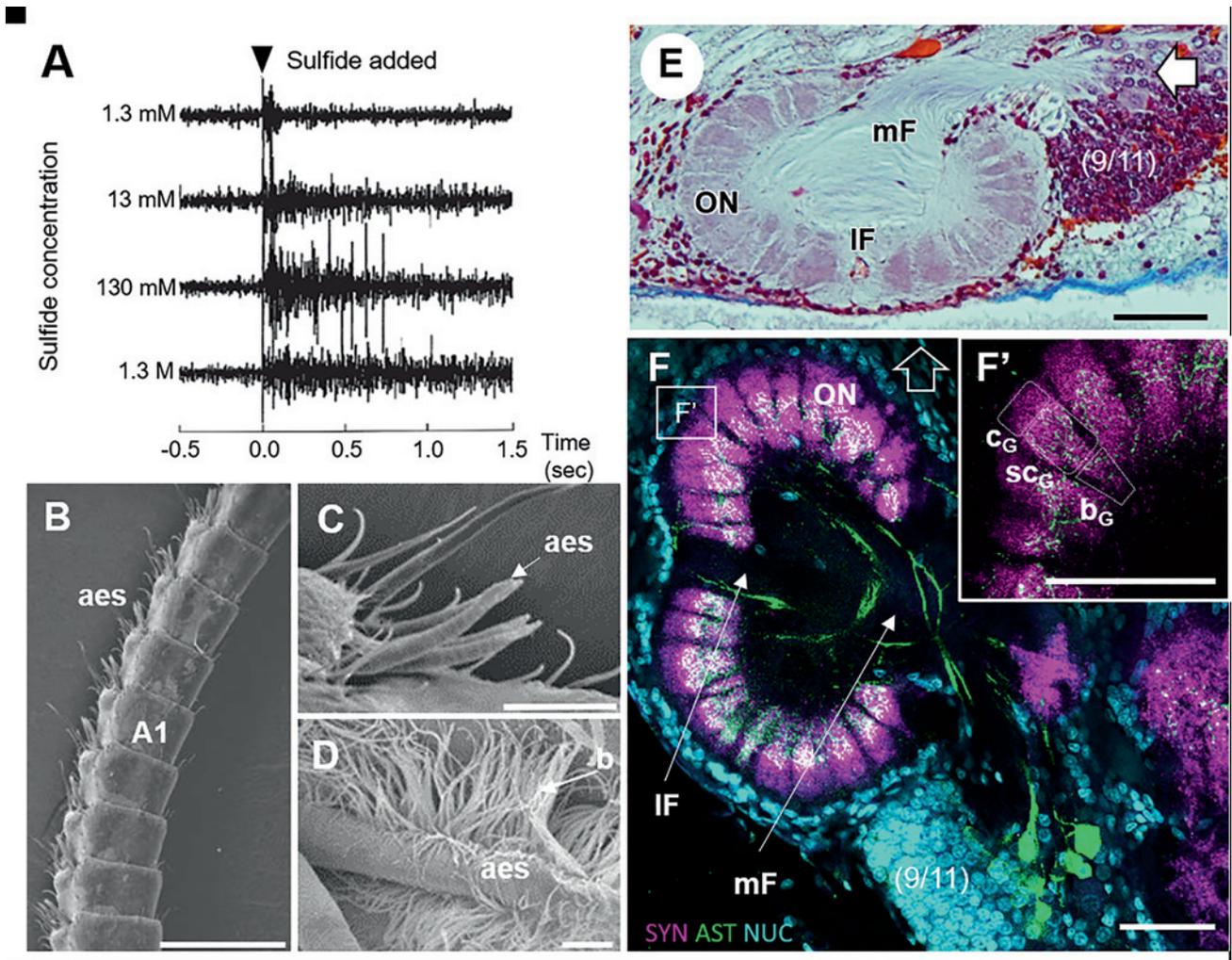


Figure 6: Olfactory system of the deep vent shrimp *Rimicaris exoculata*. A: Recordings from a bundle of nerve fibers in the lateral antenna 1 showing massed action potential generation in response to the application of different concentrations of sulphide (from Renninger et al., 1995). B–D: Electron microscopy images of the lateral flagellum of antenna 1 (B) bearing the aesthetasc olfactory sensilla (C), often associated with a bacterial coverage (D) (from Zbinden et al., 2017, 2018). E: Sagittal histological section of the olfactory neuropil. The white open arrow points towards anterior of the body axis. F: Horizontal immunohistological section of the olfactory neuropil, triple-labeled for synapsin immunoreactivity (SYN, magenta), allatostatin-like immunoreactivity (AST, green) and a nuclear marker (NUC, cyan). F' shows an enlargement view of the olfactory glomeruli (E and F from Machon et al., 2019). (9–11), cell cluster 9–11, A1, antenna 1; aes, aesthetasc; b, bacteria; bG, base region of the glomerulus; cG, cap region of the glomerulus; IF, lateral foramen; mF, medial foramen; ON, olfactory neuropil; scG, subcap region of the glomerulus. Scale bars B = 500 μm , C, E, F, F' = 100 μm , D = 20 μm .

Conclusions and perspectives), can be maintained at atmospheric pressure, and therefore are more suited for behavioral observations.

Conclusions and perspectives

The case of the vent shrimp discussed here provides new insights into aspects of the evolutionary transformation of crustacean brains and their associated sensory organs. Layered visual neuropils are present within *R. exoculata*

brains with an arrangement similar to that of phylogenetically related shallow water shrimps with fully developed compound eyes, although much smaller. The compound eyes of *R. exoculata* ancestors, during the evolutionary diversification of this group, were transformed to a flattened but seemingly functional retina without notable spatial resolution but most likely can detect the very dim light of the thermal radiation (Pelli and Chamberlain, 1989; Van Dover and Fry, 1994; Van Dover et al., 1988, 1996). The fact that, despite these major modifications of sensory input, the number and

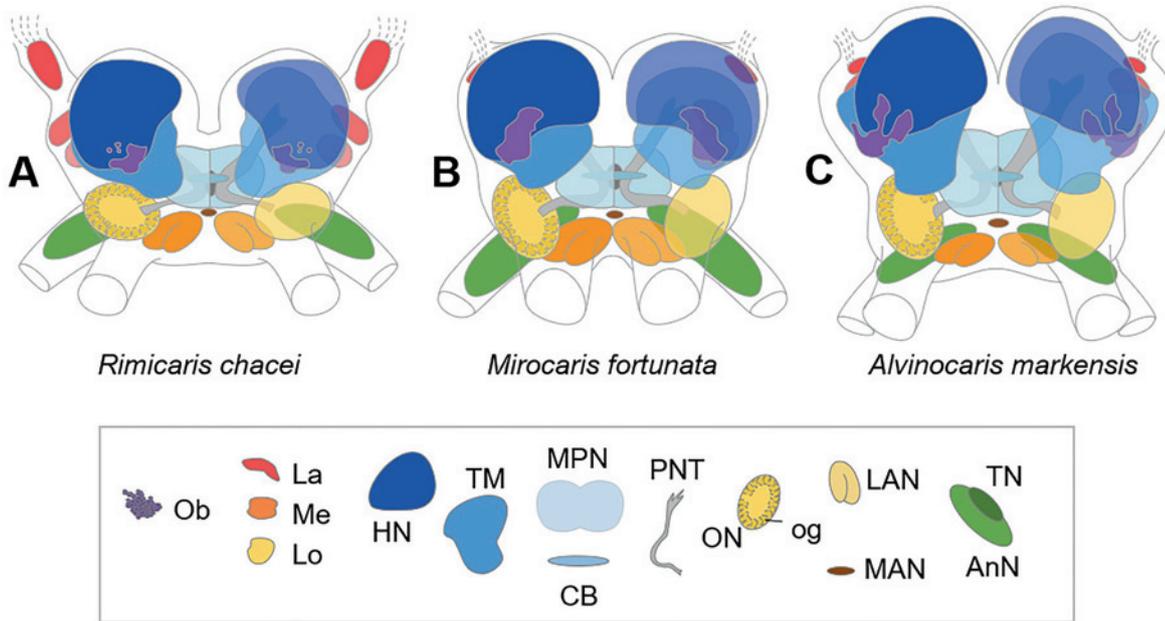


Figure 7: Brain architecture of other Alvinocarididae vent shrimp species. A: *Rimicaris chacei*. B: *Mirocaris fortunata*. C: *Alvinocaris markensis*. Abbreviations: Ob, organ of Bellonci. Visual neuropils: La, lamina; Me, medulla; Lo, lobula. Protocerebrum: HN hemispherical body; TM, terminal medulla; MPN, medial protocerebral neuropil; CB, central body. Deutocerebrum: OL, olfactory lobe; og, olfactory glomerulus; LAN, lateral antennular (antenna 1) neuropil; MAN, median antennular (antenna 1) neuropil. Tritocerebrum: AnN, antennular (antenna 2) neuropil; TN, tegumentary neuropil. Note that brain schemes are aligned according to the neuroaxis (not to their arrangement within the cephalothorax) and are not equally scaled.

principal arrangement of the three visual neuropils remain conserved is remarkable and suggest a selective pressure acting to retain this arrangement. Concerning the HE/MT complex, the brain of *R. exoculata* has taught us that the structural elaboration of these neuropils may be less dependent on olfactory input than we previously thought and instead points to other functions that were previously less in the focus of crustacean neurobiologists (Machon et al., 2019).

Future studies in the field of research exposed in this paper should, in addition to qualitative aspects of brain structure, pay more attention to numerical and volumetric aspects. For example, determining across-species variations in numbers of olfactory sensory neurons and olfactory interneurons as well as glomerular numbers and volumes can be instructive for discussing functional aspects of crustacean olfactory systems such as the wiring logic from receptor to glomerulus (Harzsch and Krieger, 2018). We expect that determining neuropil volumes and neuronal numbers of other sensory systems and comparing these across species will be essential as a basis for new insights into brain adaptations related to ecological complexity of the habitat, lifestyle, and locomotion, and perhaps also biological processes such as invasiveness,

sexual dimorphisms, sociality, and aging. As for crustaceans from extreme habitats, the related vent shrimp species from the Mid-Atlantic Ridge within the Alvinocarididae, which include *Rimicaris chacei*, *M. fortunata*, and *Alvinocaris markensis* (Gebruk et al., 2000), should be suitable for such comparisons, although they are less numerous than *R. exoculata* and are, therefore, even more difficult to sample. Preliminary results suggest that all these species present an overall similar brain pattern as in *R. exoculata* (Figure 7). Other vent crustaceans, such as the hydrothermal crab *Segonzacia mesatlantica*, could be also good models for future investigations (Charmantier-Daures and Segonzac, 1998; Matabos et al., 2015).

Acknowledgments: The authors thank the chief scientists of the Momarsat 2011, 2012, and 2016 cruises (Mathilde Cannat and Pierre-Marie Sarradin), of the Biobaz 2013 cruise (François Lallier), and of the Bicosse 2018 cruise (M-A. Cambon), who allowed the sampling of hydrothermal shrimps. This work was partially supported by the European Union Seventh Framework Programme (FP7/2007-2013) under the MIDAS project (grant agreement no. 603418).

References

- Becker, J.H., Curtis, L.M., and Grutter, A.S. (2005). Cleaner shrimp use a rocking dance to advertise cleaning service to clients. *Curr. Biol.* *15*, 760–764.
- Breithaupt, T. and Thiel, M. (2011). *Chemical Communication in Crustaceans* (New York: Springer).
- Chamberlain, S.C. (2000). Vision in hydrothermal vent shrimp. *Philos. Trans. R. Soc. London B* *355*, 1151–1154.
- Charlou, J.L., Donval, J.P., Douville, E., Jean-Baptiste, P., Radford-Knoery, J., Fouquet, Y., Dapoigny, A., Stievenard, M., 2000. Compared geochemical signatures and the evolution of Menez Gwen (37°50'N) and Lucky Strike (37°17'N) hydrothermal fluids, south of the Azores Triple Junction on the Mid-Atlantic Ridge. *Chem. Geol.* *171*, 49–75.
- Charlou, J.L., Donval, J.P., Fouquet, Y., Jean-Baptiste, P., Holm, N., 2002. Geochemistry of high H₂ and CH₄ vent fluids issuing from ultramafic rocks at the Rainbow hydrothermal field (36°14'N, MAR). *Chem. Geol.* *191*, 345–359.
- Charlou, J.L., Donval, J.P., Konn, C., Ondréas, H., Fouquet, Y., Jean-Baptiste, P., and Fourné, E. (2010). High production and fluxes of H₂ and CH₄ and evidence of abiotic hydrocarbon synthesis by serpentinization in ultramafic-hosted hydrothermal systems on the Mid-Atlantic Ridge. *Geophys. Monogr. Ser.* *188*, 265–296.
- Charmantier-Daures, M. and Segonzac, M. (1998). Organ of Bellonci and sinus gland in three decapods from Atlantic hydrothermal vents: *Rimicaris exoculata*, *Chorocaris chacei*, and *Segonzacia mesatlantica*. *J. Crustac. Biol.* *18*, 213–223.
- Derby, C. and Thiel, M. (2014). *Nervous Systems and Control of Behavior* (New York: Oxford University Press).
- Derby, C. and Weissburg, M.J. (2014). The Chemical Senses and Chemosensory Ecology of Crustaceans. *Nervous Systems and Control of Behavior*. C. Derby and M. Thiel, eds. (New York: Oxford University Press), pp. 263–292.
- Duffy, J.E. and Thiel, M. (2007). *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms* (New York: Oxford University Press).
- Gebrek, A.V., Southward, E.C., Kennedy, H., and Southward, A.J. (2000). Food sources, behaviour, and distribution of hydrothermal vent shrimps at the Mid-Atlantic Ridge. *J. Mar. Biol. Assoc. UK* *80*, 485–499.
- Hansson, B.S., Harzsch, S., Knaden, M., and Stensmyr, M. (2011). The Neural and Behavioral Basis of Chemical Communication in Terrestrial Crustaceans. *Chemical Communication in Crustaceans*. T. Breithaupt and M. Thiel, eds. (New York: Springer), pp. 149–173.
- Harzsch, S. and Hansson, B.S. (2008). Brain architecture in the terrestrial hermit crab *Coenobita clypeatus* (Anomura, Coenobitidae), a crustacean with a good aerial sense of smell. *BMC Neurosci.* *9*, 58.
- Harzsch, S. and Krieger, J. (2018). Crustacean olfactory systems: A comparative review and a crustacean perspective on olfaction in insects. *Prog. Neurobiol.* *161*, 23–60.
- Hempel, G. (1987). The krill-dominated pelagic system of the Southern Ocean. *Environ. Int.* *13*, 33–36.
- Herring, P.J., Gatén, E., and Shelton, P.M. (1999). Are vent shrimps blinded by science? *Nature* *398*, 116–116.
- Jinks, R.N., Battelle, B.-A., Herzog, E.D., Kass, L., Renninger, G.H., and Chamberlain, S.C. (1998). Sensory adaptations in hydrothermal vent shrimps from the Mid-Atlantic Ridge. *Cah. Biol. Mar.* *39*, 309–312.
- Klaus, S., Mendoza, J.C., Liew, J.H., Plath, M., Meier, R., and Yeo, D.C. (2013). Rapid evolution of troglomorphic characters suggests selection rather than neutral mutation as a driver of eye reduction in cave crabs. *Biol. Lett.* *9*, 20121098.
- Krieger, J., Hörnig, M.K., Sandeman, R.E., Sandeman, D.C., Harzsch, S., 2019. Masters of communication: The brain of the banded cleaner shrimp *Stenopus hispidus* (Olivier, 1811) with an emphasis on sensory processing areas. *J. Comp. Neurol.* <https://doi.org/10.1002/cne.24831>.
- Krieger, J., Sandeman, R.E., Sandeman, D.C., Hansson, B.S., and Harzsch, S. (2010). Brain architecture of the largest living land arthropod, the Giant Robber Crab *Birgus latro* (Crustacea, Anomura, Coenobitidae): Evidence for a prominent central olfactory pathway? *Front. Zool.* *7*, 25.
- Machon, J., Lucas, P., Ravaux, J., and Zbinden, M. (2018). Comparison of chemoreceptive abilities of the hydrothermal shrimp *Mirocaris fortunata* and the coastal shrimp *Palaemon elegans*. *Chem. Senses* *43*, 489–501.
- Machon, J., Krieger, J., Meth, R., Zbinden, M., Ravaux, J., Montagne, N., Chertemps, T., and Harzsch, S. (2019). Neuroanatomy of a hydrothermal vent shrimp provides insights into the evolution of crustacean integrative brain centers. *ELife* *8*.
- Matabos, M., Cuvelier, D., Brouard, J., Shillito, B., Ravaux, J., Zbinden, M., Barthelemy, D., Sarradin, P.M., and Sarrazin, J. (2015). Behavioural study of two hydrothermal crustacean decapods: *Mirocaris fortunata* and *Segonzacia mesatlantica*, from the Lucky Strike vent field (Mid-Atlantic Ridge). *Deep Sea Res. II* *121*, 146–158.
- Maza, F.J., Sztarker, J., Shkedy, A., Peszano, V.N., Locatelli, F.F., and Delorenzi, A. (2016). Context-dependent memory traces in the crab's mushroom bodies: Functional support for a common origin of high-order memory centers. *Proc. Natl. Acad. Sci.* *113*, E7957–E7965.
- Moran, D., Softley, R., and Warrant, E.J. (2015). The energetic cost of vision and the evolution of eyeless Mexican cavefish. *Sci. Adv.* *1*, e1500363.
- Niven, J.E. and Laughlin, S.B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *J. Exp. Biol.* *211*, 1792–1804.
- Nuckley, D.J., Jinks, R.N., Battelle, B.A., Herzog, E.D., Kass, L., Renninger, G.H., and Chamberlain, S.C. (1996). Retinal anatomy of a new species of bresiliid shrimp from a hydrothermal vent field on the Mid-Atlantic Ridge. *Biol. Bull.* *190*, 98–110.
- O'Neill, P.J., Jinks, R.N., Herzog, E.D., Battelle, B.-A., Kass, L., Renninger, G.H., and Chamberlain, S.C. (1995). The morphology of the dorsal eye of the hydrothermal vent shrimp, *Rimicaris exoculata*. *Vis. Neurosci.* *12*, 861–875.
- Patria, M.P. and Wiese, K. (2004). Swimming in formation in krill (Euphausiacea), a hypothesis: Dynamics of the flow field, properties of antennular sensor systems and a sensory-motor link. *J. Plankton Res.* *26*, 1315–1325.
- Pelli, D.G. and Chamberlain, S.C. (1989). The visibility of 350 °C black-body radiation by the shrimp *Rimicaris exoculata* and man. *Nature* *337*, 460–461.
- Ramm, T. and Scholtz, G. (2017). No sight, no smell? – Brain anatomy of two amphipod crustaceans with different lifestyles. *Arthropod Struct. Dev.* *46*, 537–551.
- Renninger, G.H., Kass, L., Gleeson, R.A., Van Dover, C.L., Battelle, B.-A., Jinks, R.N., Herzog, E.D., and Chamberlain, S.C. (1995). Sulfide as a chemical stimulus for deep-sea hydrothermal vent shrimp. *Biol. Bull.* *189*, 69–76.
- Richter, S. and Scholtz, G. (2001). Phylogenetic analysis of the Malacostraca (Crustacea). *J. Zool. Syst. Evol. Res.* *39*, 113–136.

- Sandeman, D., Kenning, M., and Harzsch, S. (2014a). Adaptive trends in malacostracan brain form and function related to behavior. *Crustacean Nervous System and their Control of Behavior, Vol. 3*. C. Derby and M. Thiel, eds. (New York: Oxford University Press), pp. 11–48.
- Sandeman, D., Kenning, M., and Harzsch, S. (2014b). Adaptive Trends in Malacostracan Brain form and Function related to Behavior. *Crustacean Nervous System and their Control of Behaviour*. C. Derby and M. Thiel, eds. (New York: Oxford University Press), pp. 11–48.
- Sarrazin, J., Juniper, S.K., Massoth, G., and Legendre, P. (1999). Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, northeast Pacific. *Mar. Ecol. Prog. Ser.* 190, 89–112.
- Sayre, M.E. and Strausfeld, N.J. (2019). Mushroom bodies in crustaceans: insect-like organization in the caridid shrimp *Lebbeus groenlandicus*. *J. Comp. Neurol.* 527, 2371–2387.
- Schmidt, M. (2016). Malacostraca. Structure and Evolution of Invertebrate Nervous Systems. A. Schmidt-Rhaesa, S. Harzsch, and G. Purschke, eds. (Oxford: Oxford University Press), pp. 529–582.
- Schram, F.R. (2013). Comments on crustacean biodiversity and disparity of body plans. *Natural History of the Crustacea, Volume 1: Functional morphology and diversity*. M. Thiel and G.A. Wellborn, eds. *Natural History of Crustacea* (New York: Oxford University Press), pp. 1–33.
- Segonzac, M., De Saint Laurent, M., and Casanova, B. (1993). L'énigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale médio-atlantique. *Cah. Biol. Mar.* 34, 535–571.
- Stegner, M.E., Stemme, T., Iliffe, T.M., Richter, S., and Wirkner, C.S. (2015). The brain in three crustaceans from cavernous darkness. *BMC Neurosci.* 16, 19.
- Strausfeld, N.J. (2012). *Arthropod Brains: Evolution, Functional Elegance, and Historical Significance* (Cambridge: Belknap Press).
- Strausfeld, N.J., Wolff, G.H., and Sayre, M.E. (2020). Mushroom body evolution demonstrates homology and divergence across Pancrustacea. *eLIFE* 9, e52411.
- Sullivan, J.M. and Beltz, B.S. (2001). Neural pathways connecting the deutocerebrum and lateral protocerebrum in the brains of decapod crustaceans. *J. Comp. Neurol.* 441, 9–22.
- Sullivan, J.M. and Beltz, B.S. (2004). Evolutionary changes in the olfactory projection neuron pathways of eumalacostracan crustaceans. *J. Comp. Neurol.* 470, 25–38.
- Thiel, M. and Walting, L. (2015). *Lifestyles and Feeding Biology, the Natural History of Crustacea, Vol. 2* (New York: Oxford University Press).
- Tomsic, D. (2016). Visual motion processing subserving behavior in crabs. *Curr. Opin. Neurobiol.* 41, 113–121.
- Van Dover, C.L. and Fry, B. (1994). Microorganisms as food resources at deep-sea hydrothermal vents. *Limnol. Oceanogr.* 39, 51–57.
- Van Dover, C.L., Fry, B., Grassle, J.F., Humphris, S., and Rona, P.A. (1988). Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge. *Mar. Biol.* 98, 209–216.
- Van Dover, C.L., Szuts, E.Z., Chamberlain, S.C., and Cann, J.R. (1989). A novel eye in “eyeless” shrimp from hydrothermal vents of the Mid-Atlantic Ridge. *Nature* 337, 458–460.
- Van Dover, C.L., Reynolds, G.T., Chave, A.D., and Tyson, J.A. (1996). Light at deep-sea hydrothermal vents. *Geophys. Res. Lett.* 23, 2049–2052.
- Wirkner, C.S. and Richter, S. (2010). Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). *Cladistics* 26, 143–167.
- Wittfoth, C., Harzsch, S., Wolff, C., and Sombke, A. (2010). The “amphi”-brains of amphipods: new insights from the neuroanatomy of *Parhyale hawaiiensis* (Dana, 1853). *Front. Zool.* 16, 30.
- Wolff, G.H. and Strausfeld, N.J. (2015). Genealogical correspondence of mushroom bodies across invertebrate phyla. *Curr. Biol.* 25, 38–44.
- Wolff, G., Harzsch, S., Hansson, B.S., Brown, S., and Strausfeld, N. (2012). Neuronal organization of the hemiellipsoid body of the land hermit crab, *Coenobita clypeatus*: Correspondence with the mushroom body ground pattern. *J. Comp. Neurol.* 520, 2824–2846.
- Wolff, G.H., Thoen, H.H., Marshall, J., Sayre, M.E., and Strausfeld, N.J. (2017). An insect-like mushroom body in a crustacean brain. *eLife* 6.
- Zbinden, M., Berthod, C., Montagné, N., Machon, J., Léger, N., Chertemps, T., Rabet, N., Shillito, B., and Ravaux, J. (2017). Comparative study of chemosensory organs of shrimp from hydrothermal vent and coastal environments. *Chem. Sens.* 42, 319–331.
- Zbinden, M., Gallet, A., Szafranski, K.M., Machon, J., Ravaux, J., Léger, N., and Duperron, S. (2018). Blow your nose, shrimp! Unexpectedly dense bacterial communities occur on the antennae and antennules of hydrothermal vent Shrimp. *Front. Mar. Sci.* 5, 357.
- Zeil, J. and Hemmi, J.M. (2006). The visual ecology of fiddler crabs. *J. Comp. Physiol. A* 192, 1–25.

Bionotes



Julia Machon

UMR CNRS MNHN 7208 Biologie des Organismes et Écosystèmes Aquatiques (BOREA), Equipe Adaptation aux Milieux Extrêmes, Sorbonne Université, Paris, France

Julia Machon studied Biology at the Sorbonne University (Paris, France). She obtained her Ph.D. degree in 2018 in the team “Adaptation to Extreme Environments”, under the supervision of Dr. Magali Zbinden and Dr. Juliette Ravaux. Her research focused on sensory adaptations -mainly chemoreception- in shrimp from deep-sea hydrothermal vents, using various approaches such as morphology, behavior experiments and electrophysiology. She later worked with the team of Pr. Steffen Harzsch, at the University of

Greifswald (Germany) for a collaborative research project to investigate the brain architecture in these rare deep-sea invertebrates.



Jakob Krieger

Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany

Jakob Krieger is a scientific assistant and post doc in Steffen Harzsch's Lab at the Zoological Institute and Museum of the University of Greifswald. He studied Marine Biology in Rostock and received his Diploma in Biology and his PhD from the University of Greifswald. He worked on crustacean neuroanatomy with emphasis on the olfactory system as well as on behavioral aspects in different malacostracan crustaceans such as coconut crabs, brachyurans, or cleaner shrimps. He is currently analysing the neuroethology of terrestrial hermit crabs related to shell-choice behavior.



Magali Zbinden

UMR CNRS MNHN 7208 Biologie des Organismes et Écosystèmes Aquatiques (BOREA), Equipe Adaptation aux Milieux Extrêmes, Sorbonne Université, Paris, France

Magali Zbinden studied Biology at the University Pierre and Marie Curie (Paris, France) and obtained her Ph.D degree in Physiology in 2001. Since 2004: Associate professor at Sorbonne University, doing her research on deep-sea biology, and her teaching at the Zoology Department. 2017: French Scientific Habilitation in Life and Health Sciences. She carried out her postdoctoral research at the University of Liège, Belgium (European Ventox and FNRS grant). M. Zbinden works on the biology and physiology of animals associated with chemosynthetic ecosystems, in particular deep hydrothermal vents. Her main research field are: i) study of symbiosis with chemoautotrophic bacteria, ii) sensory perception in hydrothermal shrimp, using morphological, molecular and behavioral approaches and *in vivo* experiments in prototype pressurized aquarium developed by our lab (B. Shillito) dedicated to the study and maintenance of deep marine organisms.



Juliette Ravaux

UMR CNRS MNHN 7208 Biologie des Organismes et Écosystèmes Aquatiques (BOREA), Equipe Adaptation aux Milieux Extrêmes, Sorbonne Université, Paris, France

Juliette Ravaux studied Biology at the University Pierre and Marie Curie (Paris, France) and obtained her Ph.D degree in Invertebrate Physiology in 1999. Since 2000: Associate professor at Sorbonne University, doing her research on deep-sea biology, and her teaching at the Zoology Department. 2014: French Scientific Habilitation in Life and Health Sciences. Her main research topics focus on understanding the adaptations to deep-sea vent environments, and more specifically the strategies to cope with highly variable thermal environments, the adaptation to high hydrostatic pressure, and more recently the sensory functions (as part of the european project Managing Impacts of Deep-sea resource exploitation, Work program ENV.2013.6.2-8 Sustainable management of Europe's deep sea and sub-sea floor resources, P.I. Pr. Philip Weaver, Southampton, UK).



Steffen Harzsch

Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany
steffen.harzsch@uni-greifswald.de
<https://orcid.org/0000-0002-8645-3320>

Steffen Harzsch obtained his PhD in 1995 from the University of Bielefeld/Germany with a thesis on the development of crustaceans and continued to work on crustacean neurogenesis as a PostDoc at Wellesley College/Massachusetts. He then moved to the University of Ulm/Germany for comparative analyses of arthropod brains and promoted the discipline "neurophylogeny", a synthesis of neurobiological studies and phylogenetic aspects. He obtained his habilitation in 2001 and continued to work in Ulm on a Heisenberg stipend funded by the Deutsche Forschungsgemeinschaft. In 2006, Steffen Harzsch moved to Bill Hansson's group "Evolutionary Neuroethology" at the Max Planck Institute for Chemical Ecology in Jena/Germany as group leader in neuroanatomy focussing on the evolution of arthropod olfactory systems. In 2008, Steffen Harzsch obtained tenure as professor in Cytology and Evolutionary Biology at the Zoological Institute of the University of Greifswald/Germany