Advances in Taxonomy, Ecology, and Biogeography of Dirivultidae (Copepoda) Associated with Chemosynthetic Environments in the Deep Sea

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Abstract

**Background:** Copepoda is one of the most prominent higher taxa with almost 80 described species at deep-sea hydrothermal vents. The unique copepod family Dirivultidae with currently 50 described species is the most species rich invertebrate family at hydrothermal vents.

**Methodology/Principal Findings:** We reviewed the literature of Dirivultidae and provide a complete key to species, and map geographical and habitat specific distribution. In addition we discuss the ecology and origin of this family.

**Conclusions/Significance:** Dirivultidae are only present at deep-sea hydrothermal vents and along the axial summit trough of mid-ocean ridges, with the exception of *Dirivultus dentaneus* found associated with *Lamellibrachia* species at 1125 m depth off southern California. To our current knowledge Dirivultidae are unknown from shallow-water vents, seeps, whale falls, and wood falls. They are a prominent part of all communities at vents and in certain habitat types (like sulfide chimneys colonized by pompei worms) they are the most abundant animals. They are free-living on hard substrate, mostly found in aggregations of various foundation species (e.g. alvinellids, vestimentiferans, and bivalves). Most dirivultid species colonize more than one habitat type. Dirivultids have a world-wide distribution, but most genera and species are endemic to a single biogeographic region. Their origin is unclear yet, but immigration from other deep-sea chemosynthetic habitats (stepping stone hypothesis) or from the deep-sea sediments seems unlikely, since Dirivultidae are unknown from these environments. Dirivultidae is the most species rich family and thus can be considered the most successful taxon at deep-sea vents.

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Introduction

Copepoda are estimated to contribute more than 15% to the total number of animal species known from deep-sea hydrothermal vents worldwide [1]. Almost 80 species are currently described from the orders Harpacticoida, Calanoida, Cyclopoida, Pocillostomatoida and Siphonostomatoida, but many more species await identification and description [2]. The Dirivultidae, a family belonging to the Siphonostomatoida, is the most diverse one of all animal families at vents with 50 described species. The most diverse genus is *Lepetodrilus* (13 known species). Similar diverse faunal groups at deep-sea hydrothermal vents are Gastropoda with about 100 described species, including the prominent family Lepetodrilidae with 20 species and within this family the large genus *Lepetodrilus* (13 known species). Polychaeta are also represented with currently 111 species and the Polynoidae including 24 species [3].

In hard substrate ecosystems like many hydrothermal vents, copepods can be the most abundant and diverse meiofaunal taxon [4,5]. Copepods in general play an essential role in various ecosystems, being usually the second dominant higher meiofauna taxon following the nematodes [6]. They are known from marine and freshwater plankton, marine sediments, cryptic habitats (soil, forest litter, terrestrial mosses, tree holes), subterranean habitats (springs, pools in caves), anchialine caves, deep-sea vents, and as animal and plant associates [7]. Their ecological importance is high and in some ecosystems as e.g. in the plankton, copepods are the main primary consumers. Copepods are essential for nutrient recycling and their fecal pellets are a central source for detritus feeders, but also the animals themselves are an abundant feeding source for macrofauna [7].

Dirivultidae are found in frequent and diverse numbers at hydrothermal vents around the globe. For this review we developed a simple identification table which should help scientists to identify these copepods easy in future. Ecological aspects such as abundance and diversity patterns are evaluated. We also provide an update on current distribution patterns of this unique family and discuss the origin of Dirivultidae.
Methods

We reviewed the literature of Dirivultidae, including all species descriptions and ecological studies. Original species descriptions were used to develop a key to genera and species. We investigated the occurrence of dirivultids in chemosynthetic habitats such as hydrothermal vents, cold seeps, wood falls and whale falls in the deep sea to provide a complete overview of the distribution of this unique family. In addition, we also considered trophic interactions and compared abundance and diversity patterns of Dirivultidae in various ecosystems and habitat types to gain insight into the ecology of these copepods. Biogeographical patterns were analyzed by separation into four large regions: the Atlantic, North East Pacific, East Pacific, and West Pacific, following the definition of Desbruyères et al. [3]. We use the thus obtained information to discuss the origin of the Dirivultidae.

Results and Discussion

Taxonomy

Dirivultidae belong to the siphonostomatoid copepods and their morphological characteristics include: The body is cyclopiform with length ranging from 0.5 to 1.8 mm (Figure 1A, Figure 2). The prosome is 4 segmented, the urosome 4–5 segmented in females and 5–6 segmented in males. The first urosomite bears the leg 5. The oral cone is short and robust formed by labrum and labium (Figure 1D). In addition to the oral cone in the genera Ceuthoecetes, Dirivultus and Nilva a cutting borer is formed by the labium (Figure 1E). Mandible, maxillule, maxilla, and maxilliped are present (Figure 1A, 1D, 1E). Rami of legs 1 to 3 and exopod of leg 4 are 3-segmented (Figure 1G). Endopod of leg 4 is 2-segmented (Figure 1H). The development is as follows: females carry two egg sacs each containing one, frequently two (rarely more) large, yolky eggs; nauplii hatch as non-feeding lecithotrophic larvae, lacking mouth and labrum, and lacking a naupliar arthrite on the coxa of the antenna [8]. The exact number of naupliar stages is unknown; the lecithotrophic nauplius may moul in directly into the first copepodid stage. Five copepodid stages with well developed mouth parts and gut follow, the sixth stage being the adult.

The presumably derived characters distinguishing Dirivultidae from Ecbathyriontidae and other siphonostomatoids are the 2-segmented endopod of leg 4 (is 3-segmented in Ecbathyriontidae) and many other siphonostomatoids (and the fusion of ancestral segments 3–8 in the proximal part of the antennule into one compound segment which is armed with 6 pairs of setae. Morphological observations suggest that Ecbathyriontidae, a family consisting of a single species (a new species and genus is in preparation, pers. com. VNI) (Ecbathyrion prolacticauda, Humes 1987) and found at hydrothermal vents, can be considered the only sister-group of Dirivultidae [9]. The synapomorphy of the taxon Ecbathyriontidae – Dirivultidae is the presence of a double segment in the female antennule. This double segment is armed with 2 pairs of setae and formed by fusion of two segments which correspond to the ancestral segments 15 and 16 [10].

The type genus of the Dirivultidae is Dirivultus Humes & Dojiri, 1980, and the other 12 genera are Aphopontius Humes, 1987; Benthoxynus Humes, 1984; Ceuthoecetes Humes & Dojiri, 1980; Chasmatopontius Humes, 1990; Exrima Humes, 1987; Fissuricola Humes, 1987; Humesipontius Lamberti & Ferrari, 2003; Humesipontius Humes, 1987; Rhogobius Humes, 1987; Rimipontius Humes, 1996; Sotocetes Humes, 1987; and Stygiopontius Humes, 1987 (Table 1). The genera can be mainly distinguished by the setation of the endopod of leg 4 (Figure 1H). The genera Chasmatopontius and Fissuricola are considered as basal due to the existence of 5 inner setae on the distal (second) endopodal segment of leg 4. These 3 setae indicate that the ancestor had three endopodal segments on leg 4. The distal (third) and middle (second) segments of a 3-segmented condition are fused into a distal double-segment in the 2-segmented condition. The presence of this former middle segment on the endopod of leg 4 is evidenced by the retention of 1 inner proximal seta of this segment (2 setae are indicated for the ancestor of siphonostomatoids). Ten other genera of dirivultids are characterized by a remarkably uniform 2-segmented endopod of leg 4. The distal endopodal segment of the 2-segmented endopod is armed with 2 setae at most, 1 terminal and 1 inner. The inner seta is lost in several genera of dirivultids. The proximal endopodal segment of leg 4 in dirivultids is armed with 1 inner seta at most as in the ancestral state of siphonostomatoids (this seta is lost in several genera of dirivultids). The endopod of leg 4 is lost completely in the monotypic genus Humesipontius. Table 1 is a key to genera featuring setation and some additional characters allowing genus identification. Schematic drawings of dirivultid morphology and important characters for identification are given in Figure 1.

Fifty species belong to the 13 dirivultid genera (Table 2, Table 3, and Table 4) [11–24]. Six genera (Chasmatopontius, Fissuricola, Humesipontius, Rimipontius, Nilva, and Sotocetes) are monotypic; 3 genera (Benthoxynus, Dirivultus, Exrima) contain 2 species; Rhogobius holds 3 species and Ceuthoecetes 4 species. Most diverse genera are Aphopontius and Stygiopontius with 10 and 21 species, respectively. In addition, our collection contains 2 species of Stygiopontius and 1 species of Chasmatopontius which are new to science but undescribed yet (SG, VNI pers. obs.). Tables 2 to 4 provide keys of genus specific characters allowing species identification within genera. Synonyms are as followed: Aphopontius rapunculus (Humes and Segonzac, 1998) was transferred to Rhogobius rapunculus (Humes, 1987) [2]; IVN in prep.; A. temperatus (Humes, 1997) was synonymized with A. allantus [2]. Stygiopontius luminiger (Humes, 1989) and S. bulbisetiger (Humes, 1996) were synonymized with S. senitfer and S. pectinatus, respectively [2].

Interestingly, only females or males are known in certain species despite the collection of sometimes thousands of specimens in a sample (see Table 5). For example, only females of Stygiopontius pectinatus, a species associated with the shrimp Rimicaris exoculata were found after inspection of more than 7400 individuals [20]. Whether the lack of finding both sexes has a biological background (e.g. parthenogenesis) or is simply due to wrong classification because of an acute sexual dimorphism remains to be studied, for example by life mating observations or by using genetic tools. Indeed, COI analyses of Stygiopontius hispidulus helped to find the male of that species (SG in prep.).

Ecology

Occurrence. Dirivultidae occur at deep-sea vents but have not been found in other chemosynthetic habitats such as shallow vents, seeps, whale falls (see Table 6) or wood falls nor in deep-sea or shallow-water sediments (PMA pers. obs.). At vents, however, they are not restricted to areas with vent flow, but can also survive away from vents on the bare basalt along the axial summit trough. Several species were encountered about 10 meters away from vents on the bare basalt along the axial summit trough. Despite the collection of sometimes thousands of specimens in a sample, the occurrence of dirivultids in chemosynthetic habitats such as shallow vents, seeps, wood falls and whale falls in the deep sea to provide a complete overview of the distribution of this unique family. In addition, we also considered trophic interactions and compared abundance and diversity patterns of Dirivultidae in various ecosystems and habitat types to gain insight into the ecology of these copepods. Biogeographical patterns were analyzed by separation into four large regions: the Atlantic, North East Pacific, East Pacific, and West Pacific, following the definition of Desbruyères et al. [3]. We use the thus obtained information to discuss the origin of the Dirivultidae.
Figure 1. Schematic drawings of dirivultid morphology and important characters for identification on genus and species level. The figure was created by selecting drawings of previous publications and adding additional information to illustrate the key to genera (Table 1) and to species (Tables 2, 3, 4). A: lateral view of a dirivultid (length ~ 1 mm) [3]. B–H ventral view of: B: antenna of *Stygiopontius lauensis* [18]. C: antenna of *Vent Copepoda (Dirivultidae)*.
seep sediments. However, while surfaces of tubeworms, mussels and other foundation species are colonized by dirivultids at vents, they are not inhabited by dirivultids at seeps. Further, whale bones and wood providing large surfaces for colonization are also devoid of dirivultids. We think that the large, continuous area of suitable substrate might play an important role for dirivultids to flourish at midocean ridges, but prevents them from colonizing relatively small patches of hard substrate of biotic origin (e.g. tubes, shells, bones, wood), which are surrounded by soft deep-sea sediments.

The occurrence of dirivultids is restricted to vents and the surrounding axial summit trough, which is in contrast to other meiofauna taxa. Harpacticoid copepod genera found at seeps and vents are usually unknown from deep-sea sediments, but their genera and sometimes even the species are known from shallow water sites (for more details see Martínez Arbizu et al. in prep.). Nematode genera detected at vents and seeps have been reported from deep-sea sediments but also from shallow regions (for more details see Vanreusel et al. in prep).

Dirivultidae were found mostly on hard substrates (basalt and sulfide precipitates) in aggregations of invertebrates, such as bivalves (*Bathymodiolus thermophilus*, *B. puteoserpens*, *Calyptogena magnifica*), vestimentiferan tubeworms (*Riftia pachytila*, *Ridgeia piscesae*), alvinellids

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**Figure 2. Stygiopontius pectinatus (female) SEM micrographs.** A: habitus, ventral view. B: habitus, dorsal view. C: oral cone and anterior appendages. Scale bars 100 μm. (A, B: [3]; C: by VNI). doi:10.1371/journal.pone.0009801.g002
Alvinella pompeiana, A. caudata, Paracalanilla sulfuscina, P. pandorae, P. grasslei, P. hessleri, and shrimps (Romicaric exoculata). A total of 24 species each was found within bivalve beds and vestimentiferan bushes. Ten species each were located in alvinellid and shrimp aggregations. Two species were found in bacterial mats growing on basalt, and 3 species were detected in the plankton above vents. Unfortunately, the specific habitat of 8 species (Aphotopontius baculigerus, Fissuricola caritus, Rhogobius pressulus, Stygiopontius appositus, S. brevispina, S. lauenstii, S. verruculatus) is unknown.

Most dirivultids are habitat generalists as they are able to live at different hydrothermal flux regimes and in different aggregates of megafauna. The majority of species was found in more than 2 different habitats, and only 30% of species were found in a single habitat (6 spp. at bivalves, 5 spp. at shrimps, 4 spp. at vestimentiferans, 1 sp. at alvinellids). 45% of species were detected in 2 habitats, most of them (11 from 19 spp.) in bivalve and in vestimentiferan habitats. 17% (7 spp.) were observed in three habitat types. Since it is known that those megafauna organisms

### Table 1. Genus key of Dirivultidae.

| genus              | # | 1st | 2nd | comment                                                                 |
|--------------------|---|-----|-----|-------------------------------------------------------------------------|
| Benthoxynus       | 2 | 0-0 | 0,0 | leg 3 exopod, 1st segment without setae (in contrast to Exrina, Rimipontius) |
| Exrina            | 2 | 0-0 | 0,0 | leg 3 exopod, 1st segment with setae (in contrast to Benthoxynus)          |
| Rimipontius       | 1 | 0-0 | 0,0 | caudal ramus with 5 setae (on contrast to 6 in other Dirivultidae)          |
| Ceuthoeetes       | 4 | 0-0 | 0,1 | A2 has hooklike claw, A1 10 segmented (in male and female)                |
| Dirivultus        | 2 | 0-0 | 0,1 | A2 has hooklike claw, A1 13 segmented (female) or 12 seg (male), oral cone with spines |
| Nilva             | 1 | 0-0 | 0,1 | A2 has hooklike claw, urosome with dorsal hump                           |
| Stygiopontius     | 21| 0-0 | 0,1 | leg 1 endopod is 3 segmented in female and male, leg 5 male normally developed (1 segment) |
| Scoecetes         | 1 | 0-0 | 0,1 | leg 1 endopod is 2 segmented in female, leg 5 in male reduced to small ridge with 3 setae |
| Chasmatopontius   | 1 | 0-0 | 0,3 | urosome 4 segmented in female, 5 segmented in male (in contrast to other Dirivultidae) |
| Aphotopontius     | 10| 0-1 | 0,1 | no lobes at anal somite                                                  |
| Rhogobius         | 3 | 0-1 | 0,1 | 2 lobes at anal somite (in contrast to Aphotopontius)                     |
| Fissuricola       | 1 | 0-1 | 0,1 |                                                                         |
| Humesipontius     | 1 | absent | absent |                                                                             |

Dirivultid genera and number of described species within each genus (#). Genera can be distinguished by the number of setae (Arabic numbers) and spines (Latin numbers) on their leg 4 endopod. 1° indicates setation of the first segment of leg 4 endopod, 2° indicates setation of the second segment of leg 4 endopod (see for example Figure 1H, showing leg 4 of Stygiopontius). The first step of genus identification is to analyze leg 4 endopod, afterwards the description of other characters should be followed. Other characters include number of segments and setation of other legs (terminology of different parts of legs see Figure 1A and 1G), number of setae on caudal rami and lobe presence/absence at anal somite (see for example Figure 1J showing Aphotopontius with 6 setae on caudal rami and anal somite without lobes), shape of antenna (A2) (Figure 1B shows a typical antenna of Dirivultidae; Figure 1C shows the antenna with a hook like claw as typical for the genera Ceuthoeetes, Dirivultus, and Nilva), and number of segments in antennule (A1).

### Table 2. Species key of Dirivultidae: Aphotopontius.

| Aphotopontius | caudal ramus l:w | f genital somite | m genital somite | other characters                                                                 |
|---------------|------------------|-----------------|-----------------|-----------------------------------------------------------------------------------|
| A. baculigerus| 14:1 (f) 9:1 (m) | with small S    | no info         | rostrum rounded, anal segment smooth                                               |
| A. limatulus  | 10:1 (f) 8:1 (m) | no S, rounded   | no S            | rostrum straight, anal segment with spinules                                       |
| A. faciciputus| 5:1              | no S, rounded   | no S            | broad genital somite, male leg 6 with 2 setae                                     |
| A. arcatus    | 5:1, concave     | with S          | no S            | mxp slender, male leg 6 with 1 seta, spinules at outer margin of caudal ramus      |
| A. flexispina | 4:1              | no S, rounded   | male unknown    | mxp: spine on second segment has curved tip, claw is pectinate                     |
| A. probolus   | 3:1              | with S          | no S            | prominent process between mxp and leg 1, spinules at outer margin of caudal ramus  |
| A. acanthinus | 2:1              | with S          | with S          | basis leg 1 mammilliform, m A1 5th seg with 1 spine                               |
| A. mammillatus| 2:1              | hourglass shaped| with S          | basis leg 1 mammilliform, m A1 5th seg with 2 spines                             |
| A. hydronautus| 2:1              | with S          | male unknown    | basis leg 1 rounded, mxp process not over leg 1                                  |
| A. atlanteus  | 2:1              | no S            | with S          | basis leg 1 rounded, body broader than A. hydronautus                             |

First, species of this genus can be distinguished by the ratio of length to width of the caudal ramus (caudal ramus l:w). Second, species can be discriminated by the presence or absence of spiniform processes (S) on the genital somite of female (f) and male (m) (e.g. Figure 11 shows A. acanthinus with a caudal ramus ratio of lengthwidth with 2:1; the female genital double somite has spiniform processes). Other species characters include the shape of various parts of the body (i.e. the maxillipeds (mxp), see Figure 1F).

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are found at distinct flux regimes (alvinellids and shrimp at high flow with temperatures >50°C, tubeworms at vigorous flow with moderate temperatures <30°C), bivalves at low flow (<15°C) [31,32], most dirivultids must be able to tolerate a wide range of hydrothermal fluid flux regimes.

Information on where exactly and how dirivultids live is rare, since this often requires direct observations. Up to 10 copepods were counted per shrimp (Rimicaris exoculata) on the Mid-Atlantic Ridge. They were located on the mouthparts among dense bacteria growth, in the gill chambers, and/or probably were also crawling on alvinellid tubes colonizing sulfide chimneys at the East Pacific Rise (SG, MB pers. obs.). In this habitat type, temperatures were investigated more in detail and exhibited high hemoglobin concentrations can be above 1000 μM and oxygen is depleted [33,34]. Two of those dirivulitid species, Benthoxynus spiculifer and Ceuthoecetes introrsus (both found in association with Paralvinella spp.), were investigated more in detail and exhibited high hemoglobin concentrations, with a very high and temperature sensitive oxygen affinity. This could be one of the crucial adaptations to live in low-oxygen environments [35,36].

**Abundance and diversity.** Quantitative data on copepod (and dirivulid) abundances are only available thusfar for the East Pacific Rise (EPR), Juan de Fuca Ridge (JFR), and Mid-Atlantic Ridge (MAR). Copepod abundance at deep-sea hydrothermal vents is on average below 80 ind. 10 cm⁻², and ranging from 36 to 474 ind. 10 cm⁻² at alvinellids [5,25], 1 to 50 ind. 10 cm⁻² at tubeworms [4,5], and 13 to 41 ind. 10 cm⁻² at mussels [29,37]. They make up 37±23% of total meiofauna communities associated with meagala aggregations on hard substrates. Dirivulidae are the main copepod family with usually a dominance of 80% (Table 6) [4,5,29,37–39].

Interestingly, there are often less males than females in dirivulid populations. For example, the female to male ratio at JFR was 7.6:1 for Stygopontius quadrirugatus, 10.6:1 for Aphotopontius forcipatus, and 1.5:1 for Benthoxynus spiculifer [5]. Also, many species from tubeworm and mussel associated communities from the Northern EPR showed a female bias or even completely lacked males (Aphotopontius hydronauticus, A. probolus, A. acanthinus). But also, certain species such as Ceuthoecetes acahanthothrix, C. introrsus, and Scoetoecetes introrsus were male dominated [39].

In other chemosynthetic habitats no dirivultids have been found and instead harpacticoids were dominant. Similar to vent epifauna, seep epifaunal communities showed a relatively high dominance (34±27%) of copepods within the meiofauna communities. Copepods comprised 10–43% of the meiofauna in tubeworm associated communities, and 17–99% in mussel associated communities [40]. Relative abundance of copepods is lower in sediments from seeps and vents compared to epizooic communities from these habitats. In seep sediments, the relative abundance of copepods was usually <15% within the meiofauna community [Table 6; 41–54]. Only 4 samples showed a higher relative abundance [47,49]. In one sample, in the center of a mud volcano, copepods highly dominated [53], and in another study on bacterial mats the relative abundance of copepods was 33±21% [55]. Vent infauna (most studies are from shallow-water vents) composition is highly variable with relative abundances of copepods ranging from 0 to 68% [38,56–60].

Dirivulid copepod communities are less species rich at high flow alvinellid habitats than at low flow mussel and tubeworm habitats. Copepod communities associated with the alvinellid Paralvinella sulfincola at high temperature vents (communities sampled 4 cm away from 255°C peaks) at JFR were highly dominated by Stygopontius quadrirugatus (80%), followed by Benthoxynus spiculifer (almost 20%) [5]. A similar dominance pattern was also found at high temperature vents of the EPR, where S. hispidulus was the most successful species in alvinellids Alvinella pompejana and A. caudata habitats [25]. In total 10 species are known from the alvinellid habitat (Table 5).

In contrast, diversity of dirivulid was relatively high at sites with lower temperatures (∼10–20°C). At JFR B. spiculifer reached a

| Table 3. Species key of Dirivultidae: Benthoxynus, Ceuthoecetes, Dirivultus, Exrima, Rhogobius. |
|---|
| **Benthoxynus** characters |
| B. tumidoseta | A1 f 11-segmented (m unknown), caudal ramus lw 7:1 |
| B. spiculifer | A1 f 18-segmented, A1 m 11-segmented), caudal ramus lw 5:1 |
| **Ceuthoecetes** characters |
| C. introversus | leg 1, exopod 3rd segment with inward spine (in contrast to other C), maxilla length 1st to 2nd segment 1:1 |
| C. acanthothrix | maxilla length 1st to 2nd segment 1:1, spine on 2nd seg of leg 3 exopod much longer than segment (other C – same length) |
| C. cristatus | maxilla length 1st to 2nd segment 1:1.5 |
| C. aliger | mpx slender (in contrast to very a broad one in other C), maxilla length 1st to 2nd segment 1:1.5 |
| **Dirivultus** characters |
| D. spinulatus | prosome has triangular shape, oral cone with 4 prominent posteroventral spines |
| D. dentaneus | prosome has rectangular shape, oral cone with 2 prominent posteroventral spines |
| **Exima** characters |
| E. dolichopus | length ratio caudal ram: last urosomite 1:2, f genital segment triangle shape |
| E. singula | length ratio caudal ram: last urosomite 1:2, f genital segment rectangular shape |
| **Rhogobius** characters |
| R. contractus | genital segments equally developed, leg 5 2-segmented |
| R. pressulus | genital segment broad with 2 posterolateral processes, very small segment after genital somite, leg 5 2-segmented |
| R. rapunculus | leg 5 1-segmented |

Used abbreviations: antennule (A1), female (f), male (m), length (l), width (w), maxilliped (mxp), segment (seg). doi:10.1371/journal.pone.0009801.t003
A conspicuous successional pattern in diversity was found by studying new, mature, and senescent vents at JFR. New vents were mainly colonized by the dirivultid *Aphotopontius forcipitatus* (80%), and mature vents were characterized by a more even distribution of several copepods but with a dominance of dirivultid species. At senescent vents, with no vent flux, dirivultids were low in abundance. These communities were dominated by a cyclopid species (*Barathricola rimensis*) and various harpacticoid and calanoid copepods [5]. It should be mentioned that there is no information on hydrothermal vent flux temperature from new and mature vents.

**Trophic interactions.** Most dirivultid species can be considered primary consumers and are grazing on bacterial mats and detritus [26,39]. This could be inferred by analyses of mouthparts and by the finding of partly dissolved bacteria and mucus in the foregut of specimens [26,38]. Copepods associated with shrimps were feeding on bacteria located on the shrimp mouthparts or on bacteria in the water column [20]. Detailed stable carbon and nitrogen isotopes in combination with fatty acid composition and morphological examination proved that *Stygiopontius quadrispinosus* and *Bathylaophonte azorica* are mainly bacterivorous and, interestingly, food partitioning at the same trophic level occurred between these two species. *S. quadrispinosus* had a smaller mouth opening (~5 μm) and its diet was based on specific bacterial strains, composed of autotrophic bacteria. In contrast, *B. azorica* had a larger mouth opening (~20 μm) and was feeding on various autotrophic and heterotrophic bacteria, [6].

Only members of the genera *Ceuhtocoeetes*, *Dirivultus*, and *Nilva* have a different form of feeding, and are thought to feed on vestimentiferans [26]. The oral cone of these parasites is cylindrical and the labium is transformed into a cutting borer.

### Table 4. Species key of Dirivultidae: *Stygiopontius.*

| **Stygiopontius** | exo 4, 3rd | coxal setae | other characters |
|-------------------|------------|-------------|-----------------|
| S. appositus      | III, I, 4  | none        | peg-like structure on cephalothorax |
| S. appositus      | III, I, 4  | none        | peg-like structure on cephalothorax, shorter claw on mxp (contrast to S. appositus) |
| S. quadrifidus    | III, I, 4  | none        | leg 3 endopod 3rd segment with setation 1, 1, 3 (other S. 1, I, 3), extremely short innermost terminal seta at caudal ramus |
| S. quadrifidus    | III, I, 4  | leg 2       | A1 serrate, leg 1 intercoaxial plate with 2 little knobs |
| S. stabilis       | III, I, 4  | leg 2       | A1 smooth, leg 1 intercoaxial plate smooth |
| S. latulus        | III, I, 4  | leg 2       | A1 smooth with large spine on 4th segment, very broad body |
| S. cladorus       | III, I, 4  | leg 2, 3    | (no spiniform processes at genital segment) |
| S. brevispinus    | III, I, 4  | leg 1, 2    | 2 short spine-like setae on end of A2, short claw on mxp |
| S. sentifer        | III, I, 4  | leg 1, 2    | maxilliped with very large thorn |
| S. flexus         | III, I, 4  | leg 1, 2    | leg 3 endopod 3rd segment with setation 1, 1, 3 (other S. 1, I, 3) |
| S. hispidulus     | III, I, 4  | leg 1, 2    | caudal rami smooth, leg 1 basis with spines |
| S. laevis         | III, I, 4  | leg 1, 2    | caudal rami with spines, leg 1 basis smooth |
| S. mirus          | III, I, 4  | leg 1       | mxp with elongated 1st segment |
| S. pectinatus     | III, I, 4  | leg 1, 2, 3 | A2 claw like, mxp pectinate |
| S. verruculatus   | II, I, 4   | none        | knob on mxp, large genital segment |
| S. rimivagus      | II, I, 4   | leg 1       | 1 pair postlateral spiniform processes at genital segment |
| S. cinctiger      | II, I, 4   | leg 1, 2    | 2nd postgenital segment extremely short |
| S. lomonosovi     | II, I, 4   | leg 1, 2    | broader cephalothorax in contrast to S. teres |
| S. teres          | II, I, 4   | leg 1, 2    | more narrow cephalothorax in contrast to S. lomonosovi |
| S. mcruciferus     | II, I, 4   | leg 2       | mxp with spines (instead of setae in other S.) on 1st and 2nd segment |

First, *Stygiopontius* species can be distinguished by the setation of the 3rd exopodal segment of leg 4 (exo 4, 3rd) (setae are represented by Arabic numbers, spines by Latin numbers). Second, the number of coxal setae (if present, and on which leg it is present) has to be determined (see Figure 1G as an example of a coxal seta). Third, there are some additional characters allowing the final species identification of *Stygiopontius*. Used abbreviations: antennule (A1), antenna (A2), female (f), male (m), maxilliped (mxp).

**Notes:**
- Please refer to the table for a detailed list of species and their specific characteristics.
- The table includes information on the setation and coxal setae for each species, with additional notes on their morphological features.
- The study highlights the diversity and feeding habits of dirivultid species in hydrothermal vent environments, emphasizing their role as primary consumers or grazers on bacterial mats and detritus.

**References:**
- [20] Detailed stable carbon and nitrogen isotopes in combination with fatty acid composition and morphological examination proved that *Stygiopontius quadrispinosus* and *Bathylaophonte azorica* are mainly bacterivorous and, interestingly, food partitioning at the same trophic level occurred between these two species. *S. quadrispinosus* had a small mouth opening (~5 μm) and its diet was based on specific bacterial strains, composed of autotrophic bacteria. In contrast, *B. azorica* had a larger mouth opening (~20 μm) and was feeding on various autotrophic and heterotrophic bacteria, [6].
- Only members of the genera *Ceuhtocoeetes*, *Dirivultus*, and *Nilva* have a different form of feeding, and are thought to feed on vestimentiferans [26]. The oral cone of these parasites is cylindrical and the labium is transformed into a cutting borer.
Table 5. Information on all dirivultid species including authorship, known sexes, biogeography, and habitat preference.

| Species                  | Authors                  | Sex | A | NEP | EP | WP | biv | ves | alv | shr | bac | pla | ref # |
|--------------------------|--------------------------|-----|---|-----|----|----|-----|-----|-----|-----|-----|-----|------|
| Aphotopontius acanthinus | Humes & Lutz 1994        | m, f|   | x   | x  | x  |     |     |     |     |     |     | [25] |
| Aphotopontius arcuatus   | Humes 1987               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [16,22,25,29,30] |
| Aphotopontius baculigerus| Humes 1987               | m, f|   |     |   | x  |     |     |     |     |     |     | [16] |
| Aphotopontius flexispina | Humes 1987               | f   |   |     | x  | x  | x   |     |     |     |     |     | [4,30] |
| Aphotopontius forcipatus | Humes 1987               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [4,16,22,27,29] |
| Aphotopontius limatulus  | Humes 1987               | m, f|   |     |     | x  | x   |     |     |     |     |     | [4,16,22,27,29] |
| Aphotopontius probolus   | Humes 1990               | m, f|   |     |     | x  | x   |     |     |     |     |     | [4]  |
| Aphotopontius atlanteus  | Humes 1996               | m, f|   |     |     | x  |     |     |     |     |     |     | [22,29] |
| Benthoxynus spiculifer   | Humes 1984               | m, f|   | x   | x  | x  |     |     |     |     |     |     | [5,16] |
| Benthoxynus tumidisetia  | Humes 1989               | f   |   |     |     | x  |     |     |     |     |     |     | [4]  |
| Ceuthoecetes acanthothrix| Humes & Dojiri 1980      | m   |   |     | x  | x  |     |     |     |     |     |     | [4,16,22,29,30] |
| Ceuthoecetes cristatus   | Humes 1987               | m   |   |     | x  | x  |     |     |     |     |     |     | [16,30] |
| Ceuthoecetes introversus | Humes 1987               | m   |   |     | x  | x  |     |     |     |     |     |     | [4,25] |
| Chasmatopontius thescalus| Humes 1990               | m, f|   |     | x  |     |     |     |     |     |     |     | [18] |
| Dirivulus denteneus      | Humes & Dojiri 1980      | m, f|   |     |     | x  |     |     |     |     |     |     | [18] |
| Dirivulus spingulatus    | Humes 1999               | m, f|   |     |     | x  |     |     |     |     |     |     | [4]  |
| Exima dolichopus         | Humes 1987               | f   |   |     | x  | x  |     |     |     |     |     |     | [29,30] |
| Exima singula            | Humes 1987               | f   |   |     | x  | x  |     |     |     |     |     |     | [30] |
| Fissuricola cantus       | Humes 1987               | f   |   |     |     | x  |     |     |     |     |     |     | [4]  |
| Humesipontius arthuri    | Ivanenko & Ferrari 2002  | f   |   |     |     | x  |     |     |     |     |     |     | [4]  |
| Nilva torifera           | Humes 1987               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [16,29,30] |
| Rhogobius contractus     | Humes 1987               | m, f|   |     |     | x  |     |     |     |     |     |     | [15,16,29,30] |
| Rhogobius pressulus      | Humes 1989               | f   |   |     | x  |     |     |     |     |     |     |     | [16] |
| Rhogobius rapunculus     | Humes & Segonzac 1998    | f   |   |     | x  | x  |     |     |     |     |     |     | [4,29] |
| Rimipontius mediosinifer | Humes 1996               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [22,24,28,29] |
| Scotoecetes intransus    | Humes 1987               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [30] |
| Stygiopontius appositus  | Humes 1989               | m   |   |     |     | x  |     |     |     |     |     |     | [30] |
| Stygiopontius brevispina | Humes 1991               | m, f|   |     | x  |     |     |     |     |     |     |     | [22,30] |
| Stygiopontius cinctiger  | Humes 1987               | f   |   |     | x  |     |     |     |     |     |     |     | [22,30] |
| Stygiopontius cladarus   | Humes 1996               | m, f|   |     | x  | x  | x   |     |     |     |     |     | [24,28] |
| Stygiopontius flexus     | Humes 1987               | f   |   |     | x  | x  | x   |     |     |     |     |     | [4,22,25] |
| Stygiopontius hispidulus | Humes 1987               | f   |   |     | x  | x  | x   |     |     |     |     |     | [4,22,30] |
| Stygiopontius latulus    | Humes 1996               | m   |   |     | x  |     |     |     |     |     |     |     | [4]  |
| Stygiopontius laevis     | Humes 1991               | m, f|   |     | x  |     |     |     |     |     |     |     | [4]  |
| Stygiopontius lomanosovi | Ivanenko et al. 2006     | m, f|   |     | x  |     |     |     |     |     |     |     | [22] |
| Stygiopontius minus      | Humes 1996               | m   |   |     | x  | x  |     |     |     |     |     |     | [22] |
| Stygiopontius mucroniferus| Humes 1987               | f   |   |     | x  | x  |   |     |     |     |     |     | [4,22] |
| Stygiopontius paullifer  | Humes 1989               | m   |   |     | x  | x  |     |     |     |     |     |     | [22,25] |
| Stygiopontius pectinatus | Humes 1987               | f   |   |     | x  | x  | x   |     |     |     |     |     | [5,16,20,24,28] |
| Stygiopontius quadrapinosus| Humes 1987              | m, f|   |     | x  | x  | x   |     |     |     |     |     | [5,16] |
| Stygiopontius regius     | Humes 1996               | m, f|   |     | x  |     |     |     |     |     |     |     | [22] |
| Stygiopontius rimivagus  | Humes 1997               | m   |   |     | x  | x  |     |     |     |     |     |     | [22] |
| Stygiopontius semifer    | Humes 1987               | f   |   |     | x  | x  |     |     |     |     |     |     | [22,29,30] |
| Stygiopontius sematus    | Humes 1996               | m, f|   |     |     | x  |     |     |     |     |     |     | [4,30] |
| Stygiopontius stabilitus | Humes 1990               | f   |   |     | x  | x  | x   |     |     |     |     |     | [14,22] |

Sex is given for male (m) and female (f). We distinguished between four biogeographic regions: Atlantic (A), East Pacific (EP), North East Pacific (NEP), and West Pacific (WP). Habitat preferences were differentiated into bivalves (biv), vestimentiferans (ves), alvinellids (alv), shrimp (shr), bacterial mats (bac), and plankton (pla). X indicates presence. In addition to the authors’ information, also other references are given for findings of each species (ref/#).

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### Table 6. Relative abundance of dirivultid and harpacticoid copepods in chemosynthetic environments.

| Location          | depth (m) | habitat               | Copepoda (% of meio) | Dirivultidae (% of cope) | Harpacticoida (% of cope) | ref # |
|-------------------|-----------|-----------------------|-----------------------|--------------------------|---------------------------|-------|
| **Seep infauna**  |           |                       |                       |                          |                           |       |
| Denmark           | 10 to 12  | reduced sediments     | no info               | no info                  | no info                   | [41]  |
| Santa Barbara     | 15        | bac mats              | 0–1%                  | 0                        | 100                       | [42]  |
| Santa Barbara     | 18        | bac mats              | 7–14%                 | 0                        | 100                       | [43]  |
| Santa Barbara     | 18        | bac mats              | 2%                    | 0                        | 100                       | [44]  |
| Santa Barbara     | 19        | bac mats              | 6%                    | no info                  | no info                   | [46]  |
| Gulf of Mexico    | 72        | bac mats              | 0–46%                 | 0                        | 100                       | [47]  |
| Gulf of Mexico    | 72        | bac mats              | 1–16%                 | no info                  | no info                   | [48]  |
| Black Sea         | 182-252   | bac mats              | 0–59%                 | no info                  | no info                   | [49]  |
| Norwegian margin  | 733       | Sclerolinum           | 5%                    | 0                        | 100                       | [54]  |
| Norwegian margin  | 733       | reduced sediments     | 12%                   | 0                        | 100                       |       |
| off Oregon        | 800       | bac mats              | 0–1%                  | no info                  | no info                   | [52]  |
| Sagami Bay        | 1100–1200 | under calms           | 1–13%                 | no info                  | no info                   | [50]  |
| Blake Ridge       | 2154–2158 | bac mats              | 0–54%                 | 0                        | 100                       | [55]  |
| Gulf of Mexico    | 692–2238  | bac mats              | 19–37%                | 0                        | 100                       | [55]  |
| Barents Sea       | 1255      | bac mats              | 5%                    | 0                        | 100                       | [54]  |
| Barents Sea       | 1286      | sediment center       | 95%                   | 0                        | 100                       | [53]  |
| Barents Sea       | 1288      | Sclerolinum           | 7%                    | 0                        | 100                       |       |
| Barbados Trench   | 5000      | sediment center       | 0%                    | no info                  | no info                   | [45]  |
| Barbados Trench   | 5000      | under clams           | 1%                    | no info                  | no info                   |       |
| Gulf of Mexico    | 1400–2800 | ass. vestimentifera   | 10–43%                | absent (po SG)           | majority (po, SG)         | [40]  |
| **Seep epifauna** |           |                       |                       |                          |                           |       |
| **Vent infauna**  |           |                       |                       |                          |                           |       |
| Indonesia         | 3         | reduced sediments     | 40–70%                | no info                  | no info                   | [60]  |
| New Zealand       | 8 to 11   | bac mats              | no info               | no info                  | present                   | [56]  |
| Papua New Guinea  | 0 to 27   | bac mats              | 12–20%                | 0                        | 12–29%                    | [57]  |
| Mediterranean Sea | 5 to 10   | bac mats              | no info               | 0                        | 100                       | [58]  |
| Guaymas           | 2000      | bac mussels           | 13%                   | no info                  | present                   | [38]  |
| North Fiji Basin  | 2000      | mussel sediment       | 0–3%                  | 0                        | 0–3%                      | [59]  |
| **Vent epifauna** |           |                       |                       |                          |                           |       |
| Guaymas           | 2000      | ass. diverse fauna    | 60%                   | 99%                      | a few                     | [38]  |
| Juan de Fuca Ridge| 2300      | ass. Paralvinella     | no info               | ~>80%                    | a few                     | [5]   |
| East Pacific Rise | 2491–2690 | ass. mussel           | 18–75%                | present (po PMA)         | no info                   | [37]  |
| East Pacific Rise | 2500      | ass. Vestimentifera   | 2–58%                 | 75–100%                  | 0–25%                     | [4]   |
| Mid Atlantic Ridge| 3492      | ass. mussel           | 35±4%                 | 91%                      | 9%                        | [29]  |

Location, depth, habitat type (bac mats = bacterial mats; ass. = associated with) and relative abundance of Copepoda within the meiofauna community (% of meio), relative abundance of Dirivultidae within the copepod community (% of cope), and relative abundance of Harpacticoida within the copepod community (% of cope) are given. Reference (ref #) is given for each record. po personal observation.
Photographs of vestimentiferans showed round wounds in the tentacular crown which were thought to be inflicted by *Dirivultus dentaneus*. However, it is also stated that indentations could be an artifact caused by the fixation [12]. *Dirivultus spinigulatus* was observed feeding on vestimentiferan plume filaments [21].

Dirivultids are a food source for macrofauna. Stable isotope studies on *Paralvinella* showed that copepods were part of its diet. It was hypothesized that copepods were consumed along with debris while the animal was grazing on the chimney surface [61]. It is unknown yet, but highly probable, that also many other macrofauna species feed on dirivultids.

**Biogeography**

Dirivultids are highly successful in their distribution since they are known from 4 main biogeographic regions, the Atlantic (A), North East Pacific (NEP), East Pacific (EP), and West Pacific (WP) (Figure 3; Table 5; [4,5,9,11–25,27–30]). A total of 13 genera with 50 species are currently known and most are endemic to a single region. Only five species occur in 2 regions and those belong to the two most diverse dirivultid genera *Stygiopontius* and *Aphotopontius*. We are not aware of any other region studied, in which dirivultids did occur. It has be taken into account that the majority of studies was historically carried out in the East Pacific. Therefore we expect that future collections will improve our knowledge of the distribution patterns in this family.

The diversity hotspot is the East Pacific with 33 species from 10 genera. Four genera with 4 species are known from the North East Pacific and 3 genera with 6 species from the West Pacific. In the Atlantic, a total of 3 genera with 12 species are currently recognized.

Nine of the 13 genera are endemic. Six genera are restricted to the East Pacific (*Ceuthoecetes* (4 spp.), *Exrima* (2 sp.), *Fissuricola* (1 sp.), *Niva* (1 sp.), *Rhogobius* (3 spp.), and *Socitoecetes* (1 sp.)). The genus *Chasmatopontius* is only known from the West Pacific (1 spp.), *Humesipontius* only from the North East Pacific (1 spp.), and *Rimipontius* only from the Atlantic (1 spp.) (Figure 3). 45 of the 50 described dirivultid species are endemic to a single biogeographic region (EP: 30 spp.; A: 8 spp.; WP: 4 spp.; NEP: 3 spp.) (Table 5).

The genus *Stygiopontius* has representatives in all four regions (EP: 11 spp.; A: 9 spp.; WP: 4 spp.; NEP: 1 sp.). *Aphotopontius* was found in the Atlantic (2 spp.), North East Pacific (1 sp.) and East Pacific (8 spp.). *Benthoxynus* is known with a single species each from the North East Pacific and the East Pacific, and *Dirivultus* from the West Pacific (1 sp.) and from off California (*Dirivultus dentaneus*; not at vents) (Figure 3). However, only five species are known from 2 regions. The Atlantic and East Pacific share the species *Stygiopontius mirus* and *S. rimivagus*, the Atlantic and the West Pacific have *S. pectinatus* in common, the Atlantic and North East Pacific *Aphotopontius forcipatus*, and the East Pacific and the West Pacific *S. stabilitus*.

Dispersal of copepods in the pelagial is often but not exclusively during their copepodid stage [6]. Adults and copepodid stages of *Rimipontius mediospinifer*, *Stygiopontius cladarus*, *S. pectinatus* were found in plankton at 80–300 m above vents in the Mid-Atlantic Ridge.
been possible due to long-distance dispersal via ocean currents. However, copepodids have also been sampled from tubeworm and mussel associations suggesting that at least part of the copepodid development is also possible within the benthos [39]. Although detailed studies on dispersal abilities (such as duration of nauplii and copepodid stages, their buoyancy and feeding strategies) lack, the first observations of copepods and their copepodids in the plankton give a hint that the global distribution of Dirivultidae may have been possible due to long-distance dispersal via ocean currents.

Origin and phylogenetic relationship

The distribution of extant dirivultids points to a pathway of immigration from shallow waters, and not from the deep-sea sediments, nor from other deep-sea chemosynthetic habitats as it has been suggested for many other vent animals [62,63]. Dirivultidae are only known from deep-sea hydrothermal vents and from the axial summit trough, but are unknown from deep-sea sediments. We conclude that other deep-sea chemosynthetic habitats did not facilitate immigration as stepping stones towards vents [64] or that dirivultids belong to the wide-spread sulphophilic fauna, because this family is unknown from seeps, whale falls, or any other reducing ecosystems. The only exception is the species Dirivultus dentaneus, which was once collected from the hydrothermal tubeworm Lamellibrachia bahamensis at 1125 m depth off southern California [12]. L. bahami is known from the subduction zone cold seeps on the North America continental margin and from a sedimented hydrothermal region at Middle Valley on the Juan de Fuca Ridge [3]. Due to its limited distribution, it is also unlikely that dirivultids recently originated from a widespread fauna of generalists. Whether dirivultids have a long-term in situ evolution remains to be tested. For small animals, immigration via their foundation species could be another option to invade the vent habitat. However, we suggest that alvinoacid shrimp, vestimentiferan tubeworms or bivalves did not act as ancestral carrier species. These megafauna species invaded the vent ecosystem via seeps, but dirivultids are not found there [63]. Alvinellid polychaetes are only found at vents, and the order Terebellida (to which alvinnelids belong to) is found in shallow waters [63]. We propose that it is most likely that the dirivultid ancestor immigrated from the shallow water, the habitat where nowadays most Siphonostomatoida are found in association with various invertebrates and vertebrates [65]. Maybe, invasion was possible via the hard substrate ecosystem of mid-ocean ridges from shallow waters towards greater depths.

Dirivultidae are considered to have a basal position within the large order Siphonostomatoida due to the presence of a simple oral cone with a loosely associated labrum and labium, instead of a complex oral structure called siphon (with a fused labrum and labium) as found in many other siphonostomatoids [66]. The Siphonostomatoida includes more than 40 families with clear morphological distinction from other copepods (by the formation of an oral cone) but with unresolved phylogenetic relationships [67]. Siphonostomatoida live in association with other animals and most of them are animal parasites exhibiting a siphon for cutting and/or sucking. Two thirds of the species (with a total of >1530) are described as parasites of fishes and mammals, the other third are parasites or associates of invertebrates such as ascidians, polychaetes, bryozoans, cnidarians, crustaceans, echinoderms, or sponges [7]. In contrast, most dirivultids are not parasitic, but are free-living and bacterivorous and often live in aggregations of invertebrates at hydrothermal vents [26,61]. The bacterivorous feeding type (as seen from the simple mouth structure) of dirivultids suggests that they are basal to the other siphonostomatoids.

Future perspectives

Dirivultidae is the most diverse taxon at deep-sea hydrothermal vents. With the discovery of new vent sites and with the study of sites where macrofauna species are already known but not the meiofauna, species number is expected to increase further. Although they can be highly abundant in some vent habitats, only a few studies include this family in a broader ecological context. One goal is to take this family into account and the here provided key should help scientists to do so. Biogeographic patterns are expected to change with future collections; especially knowledge from the West Pacific region and the Indian Ocean is very scarce at the moment, and the polar regions remain completely unstudied. Origin and evolutionary processes are unclear yet, and in the future, genetic analyses will help to understand species distributions and speciation processes.

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Author Contributions

Analyzed the data: SG VNI PMA. Wrote the paper: SG MB. Conception: SG MB. Revised article for intellectual content: VNI PMA.
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