Ilse Bartsch | **Hamburg**

Halacaridae (Acari) in the Deep-Sea: list of species, characters, distribution, adaptation

Keywords Marine mites, Acari, deep-sea, number of species, characters, adaptations

Abstract The family Halacaridae is an aquatic representative of the mainly terrestrial arthropod class, the Chelicerata. The majority of the halacarids live in the sea, some few are found in fresh and/or brackish water. At the end of 2022, 1121 species, accepted as valid, belonged to marine and brackish water halacarid genera. All instars of halacarids are benthic; they can be found in all depth zones, from the upper tidal fringe to deep-sea basins. Ninety-two named species, in 18 genera, have one or more records from a depth between 480 and 6800 m. The species are listed in a table together with distributional data and morphological characters which may be of importance in respect to a life in the depth. The 18 genera and, in parentheses, their number of named deep-sea species are: *Acanthohalacarus* (1), *Agaue* (9), *Agauides* (2), *Agauopsis* (5), *Atelopsalis* (1), *Bathyhalacarus* (11), *Bradyagaue* (4), *Colobocerasides* (2), *Copidognathus* (23), *Halacarellus* (4), *Halacarus* (15), *Lohmannella* (4), *Pelacarus* (1), *Scaptognathus* (1), *Simognathus* (1), *Thalassarachna* (5), *Werthella* (2), and *Werthelloides* (1). The genus *Bathyhalacarus* is almost exclusively spread in the deep-sea; 11 of the known 12 species, or 92 % of all presently accepted *Bathyhalacarus* species, are from this zone. The in general numerically dominant halacarid genus *Copidognathus,* which stands for almost one-third of all halacarid species, is in the deep-sea represented by 23 species; that number equals 25 % of all deep-sea and 6 % of all *Copidognathus* species. Of the genera *Agaue, Bradyagaue, Halacarus, Thalassarachna,* and *Werthella* about

Author's Address Ilse Bartsch, Forschungsinstitut Senckenberg, c/o DESY, Notkestr. 85, 22607 Hamburg, Germany, ilse.bartsch@senckenberg.de

20–30 % of the species described and named have deep-sea records. If species with their characters shortly outlined but still un-named are included, *Lohmannella* should also be listed as a genus in which about 20 % of its species are found in great depth. The number of species in the deep-sea is certainly much higher, perhaps three times that presented in the list. In their external morphology, many deep-sea species are strikingly similar to halacarids from shallow water areas, in case the habitats in the different depth zones offer a similar texture and adequate nutritional sources. Deep-sea halacarids are neither larger nor smaller than shallow water species. Shape and length of the legs seem to be primarily an adaptation to the substratum and life-style, not to the depth. The plates of species expected to be psammobionts have a similar ornamentation, independent of the depth inhabited. The surface structure of halacarids living near oil or gas fields, vents or vent plumes are similar to that of species collected from shallow water epibios. Apart from the external features, both shallow and deep water species demonstrate a few rarely found internal character states, namely enlarged genital acetabula and an oviform excretion body in combination with a small anus. The dataset of number of species and specimens, their distribution and habitats are the result of a very restricted number of collections and also influenced by extraction and sorting methods. It offers only small glimpses of the halacarid life in the deep-sea; it is no solid basis for reliable discussions on spreading, role and adaptation of halacarids in these depths.

Zusammenfassung

Die aquatisch lebende Milbenfamilie Halacaridae gehört zur überwiegend terrestrischen Klasse der Chelicerata. Ende 2022 waren 1121 Arten gemeldet, die im Meer oder Brackwasser verbreiteten Gattungen zugeordnet werden. Von den aus über 480 m Tiefe genannten Arten werden 92 als gültig eingestuft. Die angetroffenen Gattungen und, in Klammern, die Zahl der Arten sind: *Acanthohalacarus* (1), *Agaue* (9), *Agauides* (2), *Agauopsis* (5), *Atelopsalis* (1), *Bathyhalacarus* (11), *Bradyagaue* (4), *Colobocerasides* (2), *Copidognathus* (23), *Halacarellus* (4), *Halacarus* (15), *Lohmannella* (4), *Pelacarus* (1), *Scaptognathus* (1), *Simognathus* (1), *Thalassarachna* (5), *Werthella* (2) und *Werthelloides* (1). Die 92 Arten, deren geographische Verbreitung sowie morphologischen Merkmale, die mit den Lebensbedingungen in der Tiefsee in Verbindung stehen könnten, sind in einer Tabelle zusammengefasst. Die Zahl der die Tiefsee besiedelnden Arten ist sicherlich wesentlich höher, vielleicht mehr als das dreifache der in der Liste genannten. Von den 18 aufgeführten Gattungen ist *Bathyhalacarus* fast ausschließlich aus der Tiefsee gemeldet; 11 der 12 Arten sind Tiefseebewohner; das sind 92 % aller *Bathyhalacarus*-Arten. Andererseits ist die Gattung *Copidognathus,* die weltweit fast 1/3 der Halacariden-Arten stellt, in Tiefen von mehr als 480 m mit 23 Arten zwar die art-häufigste Gattung, stellt aber nur 6 % aller Tiefseearten. Auch bei den Gattungen *Agaue, Bradyagaue, Halacarus, Thalassarachna* und *Werthella* entspricht die in der Tiefsee angetroffenen Anzahl an die 20–30 % der von der jeweiligen Gattung gemeldeten Arten. Wenn die bisher namenlosen, von der Tiefsee genannten *Lohmannella* Arten einbezogen werden, sind auch bei dieser Gattung 20 % ihrer Arten Tiefseebewohner. Die äußeren morphologischen Unterschiede zwischen Tief- und

Flachwasserarten sind hinsichtlich der Körpergröße, Form, Struktur der Platten und Beinlängen gering, sofern die Milben jeweils eine ansonsten ähnliche Habitatstruktur und Nahrungsbedingungen vorfinden. Abgesehen von ungewöhnlichen äußeren sind auch bei inneren Merkmalen von Flach- und Tiefenbewohnern Ähnlichkeiten zu finden. Beispiele sind, vergrößerte Genitalnäpfe und große, eiförmige, in konzentrischen Schichten aufgebaute Exkretionskörper. Das letztere Merkmal ist mit einer reduzierten Größe des Anus verbunden. Das Wissen ob der Verbreitung und Lebensweise der Tiefsee-Halacariden ist zu gering, um verlässliche Aussagen hinsichtlich der Rolle der Halacariden und einer Spezialisierung an ein Leben in großen Tiefen zu machen. Die dargestellten Ergebnisse der doch recht wenigen Aufsammlungen, zudem mit unterschiedlichen Extraktions- und Sortiermethoden bearbeiteten Proben, lassen kaum Aussagen über horizontale, vertikale oder umweltbedingte Verbreitungsgrenzen zu.

Introduction

Once one expected the deep-sea floor to be barren and empty. How should creatures be able to exist at low temperature, high pressure, steady darkness, and in respect to food relying on the sparse and highly unpredictable organic material that came from above, as marine snow or carcasses. Slowly one realized, there is an active life even in depths of more than 550 m. Recovered telegraph cables were found to be colonized by several species, samples taken with grabs or dredges from great depth held benthic organisms. Direct observations of deep sea areas followed; in 1934 a manned bathysphere reached a depth of almost 1000 m and in 1960 the submersible TRIESTE went down to the bottom of the Mariana Trench, to almost 11.000 m depth (Wikipedia 2022). Even here, close to the greatest depth, creatures passed by. What did the deep-sea animals, classified as consumers, feed on? According to general concepts, primary production was dependent on light, on solar radiation, this was used by organisms which via photosynthesis could build up organic material. The answer came 1977, while studying the Galapagos Rift and trying to locate a temperature anomaly in about 2500 m depth. For three minutes there was a spike in the water temperature and for this period the pictures showed the lava was covered with hundreds of white clams, alive (Ballard 1977). Other hydrothermal vent areas, as well as hydrocarbon seeps, held beside mussel beds long worms and crabs, hard substrata were overgrown by bacterial mats which in turn were inhabited by a diverse fauna. These communities contradicted the stories of poor conditions on the bottom of the deep-sea; many of the organisms used organic matter produced by chemoautotrophic endosymbiotic or free living bacteria (Williams et al. 1981; Brooks et al. 1987). Later, one realized that hot and cold water vents, as well as oil seep areas, often were colonized by a rich fauna, also halacarids, the consumers relying on the activity of chemoautotrophic microorganisms.

The first samples from the deep-sea were taken with grabs, dredges or epibenthic sleds, consequently hardly any details were available about the small-scale habitats used by the

meiofaunal organisms found when sorting the residues of a sample. In the meantime many studies are made with remotely operated vehicles (ROVs) equipped with cameras and robot arms which can take subsamples from a community but also deposit and re-collect adequate substrata. The list of deep-sea inhabitants is steadily growing.

Material and Methods

Described and named halacarid genera and species are listed in an alphabetical order (Table 1). Excluded are species not given a name, nomina nuda and species inquirenda. For each species the original and more detailed recent descriptions are cited. Synonyms are added. The short diagnoses, presented for each one of the species, do not include typical generic characters. Such characters are outlined in Bartsch (2006). Since those days a few changes have been made on generic level, namely definition and splitting of a few genera (Bartsch 2015a, 2016a). For instance, the genus *Arhodeoporus* sensu Newell 1947 is splitted (Bartsch 2016a). Species, new but still unnamed, because adequate specimens for a description were not at hand-e. g., adults damaged or incomplete or only the very first juvenile instars were present-are omitted.

The terminology in respect to a halacarid's morphology largely follows that in Newell (1984) and Bartsch (2006). The given diagnoses are primarily restricted to characters which in the one or other way may turn out to be correlated with life in great depths. References mentioned are the first description as well as more recent ones which added further data or a summary of morphological details. Sex and instars are included. A short list of synonyms is given, more details are in Viets (1956) and Bartsch (2009). Informations on horizontal and vertical distribution and, if known, ecological data, such as substratum and associated fauna, are added. Short notes inform about important morphological characters of deep-sea species, similar looking species, distinguishing details, and geographical and ecological data. Unless stated otherwise, these data are extracted from the papers cited.

The length of the idiosoma is that measured along a median line; a frontal spine, if present, is included in the given dataset. The width represents the greatest width. In general, the anal cone, at the end of the idiosoma, includes a pair of distinct anal sclerites (common state) but in a few species the sclerites are obscured by enlarged anal valves. The length of the gnathosoma is that from the tip of rostrum to the basal margin of the gnathosomal base; the width is measured in the widest part of the gnathosomal base. In the given length of legs, the claws are excluded. The term pectines is used only for tines along the shaft of claws but excludes those on an accessory process. Length, width and ratios in adults are extracted from published descriptions, from the text, calculated from the figures, and/or personal annotations made when studying specimens. If only data of juveniles are given, one should be aware of that characters may change from one instar to the other. Descriptions of halacarid mites are often prepared on the basis of mounted specimens, accordingly the mite's outline may have changed somewhat, due to compression

and evaporation of the mounting medium. Setae arranged around the genital opening are called perigenital setae. The term outlying seta is used for perigenital setae distanced from similar other setae. The outlying setae may be on the genitoanal plate but also outside the plate, within the striated integument. Adult halacarid mites have four pairs of legs, numbered I to IV from anterior to posterior. Gland pores, dorsal or marginal on the idiosoma, are numbered from I to V, from anterior to posterior. In respect to presence or absence of villi or filaments, those on perigenital, anal and/or tarsal setae are in parentheses or omitted. Characters hard to recognize are also in parentheses. Distribution and morphological character data which may be correlated with the species' life in the deep-sea are summarized in Table 1. Some few species are omitted because of uncertain records and/or identity. Abbreviations used in Table 1 are mentioned in the legends.

Where begins the deep-sea? The continental shelf has a depth of generally 250 m or less, then follows the continental slope. Locally the shelf area may extend to about 500 m (Ramirez-Llodra 2020). In some few publications, the 200 m line is accepted as a boundary to the deep-sea (Wilson & Hessler 1987, Ramirez-Llodra et al. 2010, Saeedi et al. 2020, Abel et al. 2021). Following WoRDSS (World Register of Deep-Sea Species), the 500-m line has been chosen as a main boundary to the deep-sea. At this depth seasonal variations in many physical and chemical parameters (e. g., temperature, salinity as well as the influence of sunlight) becomes minimal (Thistle 2003). Such boundaries differ of course due to local conditions and should not be handled too strictly. Newell (1971) described several halacarid species from deep-sea hauls from 485 m. These species will certainly also be found in greater depth and should hence not be excluded. In the following list of species, records from a depth of about 480 m or more are included. The list of halacarids is far from complete because mites are often ignored when collecting and sorting meiofauna.

Results

Halacaridae: shape, life-style, reproduction

Halacaridae inhabit both marine and limnic areas; they have no terrestrial instars. Halacarids are small-sized, most adults are within a length range of about 140 to 2000 µm. The few studies on halacarid anatomy, biology, ecology, and reproduction have been done with species inhabiting areas of about 0–20 m depth but not with species from the deep-sea. Halacarids are benthic, if disturbed they show no tendency to hit for the water column. If removed from the substratum inhabited, the mites will spread their legs and be ready to cling to everything they can get in touch with. In the sea, they can be found in all zones, from the very upper one, only irregularly washed by splash water (Bartsch 2000, 2003a, 2013a) to the bottom of deep-sea trenches in almost 7000 m (Jankovskaja 1978).

Adults and juveniles mainly share their habitats, though juveniles are often found more widely spread, also outside areas used by adults. Halacarids show no distinct daily or

seasonal migrations, as observed in other meiofauna taxa, e.g., in harpacticoid copepods and ostracods (Kolesnikova et al. 1995; Macquart-Moulin 1999; Teasdale et al. 2004; Walters 1988). Dispersal or resting stages are not known. Halacarids withstand unfavourable conditions often better than co-occurring meiofaunal arthropods, as proven by experiments and observations in field (Wieser & Kanwisher 1959; Bartsch 2021b, unpublished observations). They survive low and high temperatures, salinities, pH values (Bartsch 1974b; Lancaster & Pugh 1987; Pugh 1996; Siemer 1996), and they withstand anaerobiosis (Wieser & Kanwisher 1959).

The majority of halacarid species studied have a single generation per year. At present just one genus *(Isobactrus)* is known to have two or three generations (Bartsch 1972; Siemer 1996). The individual life span of most females is somewhat more than one year. Sperm transfer is via spermatophores. These are fixed to the substratum inhabited and each one includes a sperm sac (Kirchner 1969). Females deposit fertilized eggs in the substratum. Halacarids run through one larval and one to three nymphal stages till the adults appear (Straarup 1968; Bartsch 1972; Green MacQuitty 1987). The fecundity is low, hardly more than 10–20 eggs per female, except for parasitic forms. We can expect the adults to live about 6 to 9 months. According to the few data, a single generation per year seems to be true also for at least some of the species which live in cold (cold-temperate to arctic) and warm (warm temperate to tropical) waters (Bartsch 1996a; Nikitina 2013). In 'young' populations of shallow water species with most adults just hatched, males may slightly dominate but at least a few weeks later, females outnumber the males (Bartsch 1972). Moreover, females have a longer life span than males (Kirchner 1969; Bartsch 1972). In a population of subtidally living *Thalassarachna basteri* (Johnston, 1836), kept in the laboratory, Kirchner (1969) found 83 females but only 58 males, and females had a life span of up to 250 days, males one of 130 days. Reproduction rate and sex ratio in deep-sea populations are not known.

Halacarids are found in a variety of substrata, in sandy deposits, on, between and in other organisms, algae and a macrofauna, e.g., decapods, bivalves and echinoderms (Newell 1956; Števčić 1968; Bartsch 1989a; Pepato et al. 2005; Guerao et al. 2011; Krapivin 2012; Normant et al. 2013) In shallow water algae they can be very abundant and stand for more than 90 % of the meiofauna (Bartsch 1979c), but generally their part is less than 5 %. In sediments, halacarids are usually found in median grained or coarse, unsorted deposits (Schmidt 1968; Hulings 1974; Bartsch 1992a, 1999a). Mass occurrence in sediments is found and, though rarely, halacarids may stand for about 50–60 % of the meiofauna (Schmidt 1968; Bartsch 1999a). Many of the species and also genera from such sediments are perfectly adapted to use the void volume between the sediment particles. Halacarids inhabit the surface and the volume between colonial organisms; most important seems to be the structure not the taxon of the substratum (Bartsch 1979c).

List of deep-sea halacarid species

The following pages and Table 1 present 92 species, in 18 genera, with records from the deep-sea together with information on the collecting data and a few morphological characters which in the one or other way may be correlated with life in the given habitat. An Addendum includes another 20 species and adds two genera. The species are either unnamed adults or last nymphal instars which could not be identified reliably. If more material for study is available, the one or other may turn out to belong to one of the known species.

Acanthohalacarus reticulatus Bartsch, 2001

References Bartsch 2001a: 119–124, figs 1A-G, 2A-H, 3A-G (females, males, deuto-, protonymphs, larva).

Characters Idiosomal length of females 510–541 µm, of males 450–520 µm. Length:width ratio ca 1.6:1. Surface of dorsal plates reticulate, of ventral plates punctate. Corneae lacking. Anterior epimeral plate with five pairs of setae; each one of posterior epimeral plates with about 11 setae. Female genitoanal plate with 10 perigenital setae, males with 42–57 perigenital setae, of these 32–46 setae close around genital opening, the others in peripheral position. Gnathosoma slender, length:width ratio ca 1.9:1 and length ratio gnathosoma:idiosoma equalling 0.3:1. Rostrum extending to end of third palpal segment. Legs slender; leg I 1.2 times longer than idiosoma. Tibiae and telofemora I-IV, basifemora II-IV and trochanters III and IV with numerous short, spiniform, 'hollow' setae; on tibiae and telofemora these setae arranged in four lines. Such 'hollow' setae still lacking on legs of larvae. Pectines of claws with very delicate tines.

Remarks The general shape of the idiosoma, gnathosoma and legs is similar to that present in *Bathyhalacarus* and *Halacarellus* species. Most striking are the legs with numerous short spines, in addition to the few, slender dorsal setae.

Collecting data North Atlantic, Great Meteor Seamount, 30°N, 28°W, amongst sediment on a plateau in 511 m depth. The samples also included sponges (Bartsch 2001a).

Agaue abyssorum (Trouessart, 1896)

References *Halacarus abyssorum* Trouessart 1896: 104 (females, males, nymphs); Trouessart & Neumann 1896: 334–337, pl. 9, 1a-1d (females, males, nymphs).

Agaue abyssorum, Bartsch 1978a: 61.

Characters Length of adults, with gnathosoma included, 670–700 µm. Length of idiosoma ca 470–500 µm. Length:width ratio ca 1.5-1.6:1. Integument of idiosoma and legs covered by numerous villi. Dorsal plates foveate. Ocular plates with corneae and eye pigment. Posterodorsal plate with pair of narrow costae. Gnathosoma slender, length about twice the width; length ratio gnathosoma:idiosoma slightly more than 0.3:1. All legs slender, rather similar in size. Length ratio of leg I:idiosoma about 0.9:1. Tarsi with fossa membranes. Basal half of paired claws with distinct tines.

Remarks Bartsch (1978a) removed the species from the genus *Halacarus* because the genu of leg I is distinctly shorter than tibia and telofemur I and the four pairs of legs are almost equal in shape whereas in *Halacarus* the genua I are about as long as both tibiae and telofemora (cf. Bartsch 2006) and leg I is wider and larger than the following legs and has ventral spines. Because of its slender idiosoma, arrangement of corneae and eye pigment, slender gnathosoma and legs, tarsi with distinct fossa membranes, and tines of pectines restricted to the basal part of claws, the species seems to belong to *Agaue.*

Collecting and habitat data North Atlantic, Bay of Biscay (Golfe de Gascogne), 46°N, 6°W; extracted from samples of sediment and corals taken at a depth of 400 and 1410 m (Trouessart & Neumann 1896). Martinez et al. (2021) and García-Gómez et al. (2022) mentioned a shallow water record (4–7 m depth) from the Spanish Mediterranean coast. Since only a juvenile was found which is coded as having lamellae on the legs, the identity of this shallow water record needs verification. The shallow water record is not included in Table 1.

Agaue agauoides (Lohmann, 1907)

References *Halacarus (Polymela) agauoides* Lohmann 1907a: 9, 10; Lohmann 1907b: 376, pl. 35, figs 1–7 (females, male, deuto-, protonymphs).

Agaue agauoides, Viets 1931: 8; Newell 1984: 71, 72, figs 140–142 (females); Bartsch 1993: 96–98, fig. 37A-E (females); Bartsch 2016b: 133, 134. fig. 1A-G (females, male).

Agaue debilis var. *consobrina* André, 1933: 153–157, fig: 11Pm, E, I, and figs 12–13 (nymph).

Characters Length of females 575–750 µm, of males 530–640 µm. Length:width ratio 1.4-1.5:1. Dorsal and marginal plates and legs with prominent hyaline, cerotegumental lamellae in honeycomb-like arrangement. Frontal margin arched. First pair of gland pores not on anterodorsal but on dorsal part of anterior epimeral plate. Ocular plates with corneae. Striated integument of idiosoma with cerotegumental papillae. Gnathosoma slender; length:width ratio 1.9-2.0:1. Length ratio gnathosoma to idiosoma 0.3-0.4:1. Dorsal seta on second palpal segment of females wide and bifurcate, that of males slender, tapering. Rostrum slightly longer than gnathosomal base and extending beyond third palpal segment. Length ratio leg I:idiosoma 0.8:1. Telofemora with large and long cerotegumental lamellae; on leg I height of dorsal part of lamellae almost same as that of the segment, ventral part mostly less than half the height. On all legs, telofemoral lamellae extending from basal to apical part. Claws with accessory process and pectines; the latter with numerous tines.

Remarks The most striking characters of *Agaue agauoides* are the presence of large cerotegumental lamellae with cellular structure and the position of first pair of gland pores. None of the other *Agaue* species has such large lamellae and the gland pores in that position.

Collecting and habitat data Records are from South Sandwich Islands, King George I, off Graham Land, Georg V coast, Terre Adelie, Gauss-Station, Palmer Peninsula (Bartsch 2016b). The species is primarily circum-Antarctic. A sub-Antarctic record seems to be that from St. Paul, namely of a species once called *Agaue debilis* var. *consobrina* which most likely is a synonym of *A. agauoides* (Newell 1984). Presently known depth records of *Agaue agauoides* extend

from 30 to 680 m. *Agaue agauoides* is expected to colonize the epibios which settled on various hard substrata (Newell 1984).

Agaue corollata Bartsch, 1978

References *Agaue corollata* Bartsch 1978a: 56–60, figs 22–31, 32–41 (females, males); Bartsch 1982a: 45, 46, figs 1, 2 (females, males, deuto- and protonymphs, larvae).

Characters Length of females 580–725 µm, of males 587–685 µm. Length:width ratio 1.2:1. Dorsal plates and striated integument with up to 8 µm long epicuticular spicules. Gland pores on anterodorsal plate small, on ocular plate within raised 'wart'-like dome; 'wart' up to 65 µm in diameter. Each 'wart' with gland pore and corona-like cuticular membrane. Posterior pair of gland pores on tube-like cones near posterior margin of posterodorsal plate. Posterior epimeral plate with three setae both dorsally and ventrally. Females with 8–10 perigenital setae, males with about 150 such setae. Gnathosoma slender, ratio length:width 2.7:1; length ratio gnathosoma:idiosoma 0.4:1. Rostrum longer than gnathosomal base. Legs very slender. Surface of basifemora to tibiae with densely arranged villi, with debris trapped amongst the villi. Leg I 1.1 times longer than idiosoma. Tibia I with six ventral setae. Paired claws long and slender; no pectines recognized.

Remarks The species is characterized by its 'warts' on the ocular plates and the position of pair of tube-like projections near the posterior margin of posterodorsal plate. In closely related species the shape and position is different.

Collecting data North Atlantic, within a depth range from 1427 to 3610 m; its horizontal range includes the Labrador Basin, 59°N, 53°W, 3610 m; North American Basin, 38°N, 70°W, 3264–3356 m; Gulf of Biscay, 44°N, 4°W, 2006 m; Azores-Cape St Vincent Ridge, 37°N, 27°W, 3663 m; Guyana Basin, 10°N, 56°W, 3392–3429 m; and Angola Basin, 9°S, 10°E, 4223 m, 9°S, 12°E, 1427–1643 m (Bartsch 1978a, 1982a).

Agaue hirtella Bartsch, 1982

References *Agaue hirtella* Bartsch 1982a: 47, 50, 51, figs 12–15 (deutonymph).

Characters Length of idiosoma (deutonymph) 450 µm. Idiosoma and legs with delicate villi. Anterodorsal plate with small frontal spine. Three pairs of gland pores on tube-like projections, one each on anterodorsal plate in posterior half of plate, on ocular plates in their middle, and on posterodorsal plate in anterior half, situated anterior to fifth pair of dorsal setae, respectively. Gnathosoma slender, length:width ratio 2.4:1; length of gnathosoma equalling 0.4 times that of idiosoma. Deutonymphal legs longer than length of idiosoma.

Remarks *Agaue hirtella* belongs to the *corollata* group and is herein the only one with a frontal spine. Unique is the arrangement of the tubes on the dorsal plates. In adults the tubes may be wider, the length:width ratio will differ from that of the deutonymph.

Collecting data South Atlantic, East of the Falkland Islands, 52°S, 57°W, 520–530 m (Bartsch 1982a).

Agaue obscura Bartsch, 1987

References *Agaue obscura* Bartsch 1987: 1343–1345, figs 1–6, 7–11 (females, deutonymph); Bartsch 2010: 165–167, figs 18–26 (females, males, deuto-, protonymphs).

Characters Length of females 575–755 µm, of males 595–700 µm; length:width ratio 1.3:1. Anterior margin of anterodorsal plate arched, no frontal spine present. Margins of plates and tube-like processes with numerous delicate filaments, major part of plates with small epicuticular spinelets. Striated integument both dorsally and ventrally with filaments. Each ocular plate with tube-like process that includes a gland pore. Posterodorsal plate with single tube-like process with two fused afferent canals of gland pores. Tube positioned in anterior half of plate, anterior to fifth pair of dorsal setae. Posterior epimeral plates each with three dorsal and three ventral setae. Female genitoanal plate with six ventral setae. Ovipositor long, extending beyond genital plate. Gnathosoma slender, length:width ratio 2.4:1, length ratio gnathosoma:idiosoma 0.4:1. Rostrum longer than gnathosomal base. In females, dorsal seta on second palpal segment short, spine-like and bipectinate, in males that seta longer, not bipectinate. Legs slender, longer than idiosoma. Tibia I with six ventral bristles. Claws long and slender; claw pectines of posterior tarsi with few delicate tines in middle of claw.

Remarks In *Agaue obscura* the gland pores are not arranged within warts but in tube-like structures. In contrast to the other species, the tube of the posterodorsal plate is in the anterior half of the plate.

Collecting data Records are from western and eastern Antarctica, from the Amundsen Sea, 71–74°S, 105–110°W, 477–1486 m (Bartsch 2010), off the South Shetland Islands, 61°S, 56°W, from 360 m depths, and the Ross Sea, 72°S, 178°E, 344–351 m and 76°S, 170°W, 71–87 m (Bartsch 1987).

Agaue parva (Chilton, 1883)

References *Halacarus parvus* Chilton 1883: 190, 191, pl. 22B. fig. 1, 1a, 1b.

Agaue parva, Lohmann 1889: 279, 318, 354; Viets 1927a: 91–93, figs 2–7 (female); Newell 1984: 73–76, figs 158–166 (females, males, nymphs); Bartsch 1990a: 188, figs 12–16 (females, males, deuto-, protonymphs); Bartsch 1993: 100–103, fig. 39A-F (females, males, deuto-, protonymphs); Bartsch 2016b: 134–136, fig. 1 (females, males, deutonymphs).

Leptospathis bouvieri Trouessart, 1907 in Trouessart & Neumann 1907: 4–8, figs 1–3 (male).

Halacarus (Polymela) occultus Lohmann, 1907b: 375, fig 1 (2, 3), pl. 33, figs 2–4, 6, 7 (females, males, proto-, deutonymphs, larvae).

Agaue occultus var. *setifera* Womersley, 1937: 13, pl. 3, figs 1–6 (female?; male).

Halacarus (Polymela) pilosus Gimbel, 1919: 108–112, figs 1–7 (females, males, deuto-, protonymphs).

Agaue affinis Sokolov, 1962: 192, 193, fig. 2 (male).

Characters Length of females 690–1200 µm, of males 615–1025 µm; length:width ratio 1.6:1. Cerotegumental costae faintly raised and reticulate/foveate; remaining of dorsal plates foveate. Anterodorsal plate laterally expanded, reaching to trochanters I and ending with a porus.

Plate wider than long. Each ocular plate with two distinct corneae but without eye pigment. Posterodorsal plate with pair of costae. Female genitoanal plate with more than 10 pairs of perigenital setae, males with more than 100 setae. Gnathosoma slender, 2.7 times longer than wide. Length of rostrum more than twice that of gnathosomal base. Length ratio gnathosoma:idiosoma 0.4:1. Dorsal seta on second palpal segment in females wide, palmate, in males slender, seta-like. Legs slender; ratio length leg I:idiosoma 0.8-1.0:1. All telofemora with slightly raised cerotegumental panelling. Paired claws with pectines.

Remarks *Agaue parva* can be separated from other *Agaue* species on the basis of its laterally protruding anterodorsal plate and the intense, but not raised, cerotegumental panelling on telofemur I.

The species has been described several times, under different names; synonyms are listed in Viets 1950; Newell 1984; Bartsch 1993, 2009). Viets (1927a) had studied a type specimen, deposited in the Canterbury Museum, Christchurch, New Zealand, and presented a re-description which also included details not mentioned by Chilton but exactly fitted to that later described by Newell (1984). The present author once had asked for type specimens of *Halacarus parvus.* The slide only held basifemur, telofemur, genu, and tibia of a leg which partly was covered by sealing agent. The leg did not resemble that of adult *Agaue parva,* as described by Newell (1984).

Newell (1984) had studied series of *Agaue parva* from several localities and found the characters to vary in respect to length of telofemora, size of posterodorsal plate and number of setae on female genital plate. A thorough study of specimens from various localities is recommended to get a better idea of the identity of *Agaue parva* and possible cryptic species.

The species by Gimbel (1919) called *Halacarus (Polymela) pilosus* and by Newell (1984) accepted to be a junior synonym of *Agaue parva* was, according to Gimbel (1919: p. 111), densely covered with villi, though sometimes they were hardly recognizable. Such pilosity may be a form of fouling, just as described by Trouessart & Neumann (1907: p. 8, 9) in respect to '*Leptospathis scriptor*' (couvert de poils fins et assez longs) which turned out to be remnants of a fouling. Nowadays *L. scriptor* is accepted as junior synonym of *Agaue tenuirostris* (Lohmann, 1907).

Collecting and habitat data *Agaue parva* is one of the most widely spread halacarid species around Antarctica (cf. Bartsch 1993: map 4; Bartsch 2016b). Sub-Antarctic records are from the Kerguelen Islands and New Zealand (Chilton 1883; Newell 1984). Most samples with *A. parva* are from the lower tidal to about 300 m depth, one record is from 805–1061 m depth (Newell 1984). Different substrata were inhabited, e. g., muddy bottom, kelp holdfasts, hydrozoa, porifera, and bryozoa.

Agaue plutonia Bartsch, 1996

References *Agaue plutonia* Bartsch 1996b: 160, 161, figs 1–13 (female).

Characters Length of female 650 µm; length:width ratio 1.6:1. Dorsal plates reticulate; striated integument with filaments, 20–30 µm in length. Anterodorsal plate with short frontal spine. Ocular plates irregularly rounded; neither corneae, nor eye pigment present; each plate

with two gland pores. Posterodorsal plate 2.1 times longer than wide. Ventral plates and striated integument with filaments. Genitoanal plate with three pairs of perigenital setae. Posterior epimeral plate with one dorsal and three ventral setae. Gnathosoma slender, its length 0.4 times that of idiosoma. Slender rostrum distinctly longer than gnathosomal base, reaching to end of third palpal segment. Legs slender; surface with filaments. Leg I longer than idiosoma. Tibia I with six ventral setae. Paired claws with pectines, their tines delicate.

Remarks *Agaue plutonia* can be separated from other *Agaue* species because of its frontal spine. Unusual is the presence of two gland pores on each ocular plate. Once more specimens are available for study, the species may have to be moved to another genus.

Collecting and habitat data Mid-Atlantic Ridge, Lucky Strike, 38°N, 30°W, 540–919 m. Beside halacarids the sample held hydrozoans, polychaetes, aplacophorans, and other molluscs, amphipods, brachiopods, gorgonids, and crinoids (Bartsch 1996b).

Agaue tenuirostris (Lohmann, 1907)

References *Halacarus (Polymela) tenuirostris* Lohmann 1907a: 10; Lohmann 1907b: 1375, pl. 32, figs 1, 3, 4, pl. 32, figs 1, 5, 8 (female, male, deuto-, protonymph, larva).
Leptospathis scriptor Trouessart 1907 (in Trouessart & Neumann 1907): 8, 9 (male).
Agaue tenuirostris, Viets 1940: 68; Newell 1984: 72, 73, figs 143–157 (females); Bartsch 1993: 103–105, fig. 40A-E (females, males, deutonymphs, protonymph).
Agaue longissima Sokolov, 1962: 189–191, fig. 1A-V (deutonymph).

Characters Length of females 1165–1310 µm (up to 1550 µm according to Newell 1984), of males 1100–1260 µm. Length:width ratio about 1.7:1. Idiosoma marginally with narrow cerotegumental lamellae. Dorsal plates with raised, honeycomb-like arranged cerotegument. Each ocular plate with two corneae. On posterodorsal plate raised area U-shaped. Remainder of plates panelled. Gnathosoma very slender, length ratio gnathosoma:idiosoma 0.4–0.5:1. Slender rostrum reaching to middle of fourth segment. Its length twice that of gnathosomal base. Legs slender, leg I 1.1 times longer than idiosoma. Telofemora with honeycomb-like sculptured cerotegumental lamellae. Height of lamellae less than that of telofemora. Paired claws with accessory process, else almost smooth.

Remarks *Agaue tenuirostris* can be distinguished from the similar sized *A. parva* because of its slenderer idiosoma and the large honeycomb-textured lamellae on the telofemora. Further differences are in the shape of the anterodorsal plate, in *A. parva* abruptly widened at the level of insertions of leg I, in *A. tenuirostris* only slightly divergent.

Collecting and habitat data Known records exist from circumpolar Antarctic and a few from sub-Antarctic areas (Bartsch 1993: map 3). The species is expected to live primarily epibenthic and epizoic. Records are from a depth range of 20–622 m (Newell 1984; Bartsch 1993).

Agaue verrucosa Bartsch, 1982

References *Agaue verrucosa* Bartsch 1982a: 46, 47, figs 3–11 (female); Bartsch 1990a: 190, figs 28–30 (female); Bartsch 1993:107, fig. 42A-D (female).

Characters Length of females 835–910 µm; length:width ratio 1.5:1. Striated integument and plates covered with epicuticular spinelets. Gland pores on anterodorsal plate present but not in conspicuous cones. Each ocular plate with wart-like cone, 40–50 µm in diameter and including a gland pore. Another pair of pores on slightly raised cones near posterior margin of posterodorsal plate. Each posterior epimeral plate with three dorsal and three ventral setae. Female genitoanal plate with six pairs of perigenital setae. Length of gnathosoma 0.3 times that of idiosoma. Rostrum slender, reaching to middle of fourth palpal segment. Legs slightly shorter than idiosoma. Claws smooth.

Remarks The species is characterized by the arrangement and position of the gland pores on the dorsal plates.

Collecting and habitat data Found amongst flocculent sediment. Records are from the Southern Oceans, Argentine Basin, 37°S, 53°W, 2707 m (Bartsch 1982a), off the South Sandwich Islands, 60°S, 27°W, 1200–1450 m (Bartsch 1990a); a shallow water one, from 201 m, is from the Scotia Sea, 54°S, 41°W) (Bartsch 2010). A larva, listed as *Agaue* aff. *verrucosa,* has been taken in the Drake Passage, off the South Shetland Islands, 61°S, 54°W, in 2893 m depth (Bartsch 2005).

Agauides cryosi Bartsch, 1988

References *Agauides cryosi* Bartsch 1988a: 356–359, figs 10–19 (female); Bartsch 1989b: 466, fig. 60 (female).

Characters Length of female 768 µm; length:width ratio 1.4:1. Dorsal and ventral aspect dominated by large areas of striated integument. Dorsal plates uniformly reticulate; marginal parts of plates with delicate porosity. Ocular plates wider than long; corneae lacking. Single pair of gland pores near anterior margin of posterodorsal plate. Genitoanal plate with 6–7 perigenital setae in either half of plate. Between plates large areas with intensely wrinkled striated integument. Ventral plates with small pores. Gnathosoma slender, length 0.3 times of that of idiosoma. Two pairs of short setae inserted close together near basis of rostrum. Legs slender. Ratio length of leg I:idiosoma ca 0.8:1. Leg IV slightly longer than leg I. All tarsi with a somewhat claw-like dorsal seta. Paired claws smooth.

Remarks Similar to *Agauides pacifica;* differences are mentioned below.

Collecting and habitat data Northwest Atlantic Ocean, off Portugal, 37°N, 10°W. Extracted from sediment with remnants of foraminifera and pteropoda. Collected from a depth of 1505–1540 m (Bartsch 1988a).

Agauides pacifica Bartsch, 1989

References *Agauides pacifica* Bartsch 1989b: 464, 466, figs 52–60 (female).

Characters Length of female 620 µm; length:width ratio 1.5:1. Dorsum dominated by areas with striated integument. Dorsal plates reticulated. Anterodorsal plate pentagonal. Ocular plates small; wider than long. Posterodorsal plate rectangular; with pair of gland pores in anterolateral corners. Anterior epimeral plate with 12 setae; each posterior with one dorsal,

marginal and ventral seta. Genitoanal plate with 4–5 pairs of perigenital setae. Length of gnathosoma 0.3 times that of idiosoma. Two pairs of maxillary setae minute and situated close together at the rostral basis. Palps short, only slightly longer than rostrum. Legs shorter than idiosoma. Setae with filaments. Tibia I with seven ventral bristles. On tarsi I and II dorsal one of three fossary setae spiniform. Corresponding setae on tarsi III and IV slenderer. Claws smooth.

The female *Agauides pacifica* held a single large egg, 204 µm in length, i.e. 1/3rd of the length of the female idiosoma.

Remarks Two *Agauides* species are known, *A. cryosi* and *A. pacifica.* Both are similar in size, general shape and ornamentation of dorsal and ventral plates. The most marked difference is in the shape of the claws; they are slenderer in *A. pacifica* than in *A. cryosi.*

In both species the dorsal and ventral aspect is dominated by the large areas with striated integument. These areas are obviously still far from their maximum extension (fig. 16 in Bartsch 1988a).

Collecting data South Pacific, south of New Caledonia, 23°S, 167°E, from a depth of 570 m (Bartsch 1989b).

Agauopsis bathyalis Bartsch, 1989

References *Agauopsis bathyalis* Bartsch 1989b: 462, 464, 465, figs 43–51 (female).

Characters Length of female 360 µm. Length:width 1.8:1. Anterodorsal plate with frontal spine. Dorsal plates coarsely reticulate and punctate. Antero- and posterodorsal plates with longitudinal ridges which include scattered pores. Ocular plates without corneae. Ratio length of gnathosoma:idiosoma 0.4:1. Rostrum extending to end of palps. Leg I shorter than idiosoma, length ratio 0.9:1. Telofemur to tibia I with 2, 1, 3 ventromedial spines and 1, 1, 2 ventral spines, respectively. Except for very few delicate tines paired claws on tarsus I smooth; those on following tarsi with delicate tines.

Remarks *Agauopsis bathyalis* shares characters with species of the *conjuncta* group (cf. Bartsch 1986a). Its frontal spine separates this species from others of this group.

Collecting and habitat data South-western Pacific, Southwest of Lifou, 21°S, 167° E. The species was extracted from sediment samples from 1380 m depth (Bartsch 1989b).

Agauopsis costata Newell, 1971

References *Agauopsis costatus* Newell 1971: 29, 30, figs 69, 171–176 (females); Newell 1984: 226.

Characters Length of female 357–374 µm. Length:width ratio 1.5:1. Anterodorsal plate with frontal spinelet. Plate with two prominent ridges and one porose panel. Ocular plates without corneae. Posterodorsal plate with pair of well delimited, posteriad converging costae, these with single row of porose panels. Integument between costae with uniformly scattered pores, not panelled. Length:width ratio of gnathosoma 1.8:1. Rostrum extending beyond third palpal segment. Number of ventral setae: 3 (spiniform) on telofemur I; 1 (spiniform) plus 1 (setiform) on genu I; and 3 (spiniform) plus 1 (setiform) on tibia I. Claws almost smooth but a few delicate tines may be visible. Long dorsal setae on telofemora III and IV with long, delicate filaments.

Remarks Similar to *Agauopsis producta* Newell, 1971. Distinguishing characters are mentioned below.

Collecting data South-eastern Pacific Ocean, 26°S, 80°W, 550–950 m (Newell 1971).

Agauopsis producta Newell, 1971

References *Agauopsis productus* Newell 1971: 28–29, figs 64–68, 165–170 (females, deuto- and protonymph, larvae); Newell 1984: 227 (female).

Characters Length of females 313–392 µm. Length:width ratio 1.5-1.6:1 (frontal spine included). Length of frontal spine slightly less than 1/3 of anterodorsal plate. Posterodorsal plate with V-shaped ridge, its surface without distinct pores or panels. Surface between ridges uniformly porose. Length:width ratio of gnathosoma 2.0:1. Rostrum slender, extending beyond basis of fourth palpal segment. Spine on third palpal segment tapering. Leg I larger than following legs. Telofemur to tibia I with 3, 1, 3 strong, bluntly ending ventral spines.

Remarks With frontal spine and chaetotaxy of leg I similar to that of *Agauopsis costata,* but the frontal spine of *A. producta* is longer than the width at its basis. A rather long frontal spine is also present in *A. bathyalis.* The three species differ in the ornamentation of the dorsal and ventral plates and in the number, shape and arrangement of the spines on genua and tibiae I. In the majority of *Agauopsis* species the anterior margin of the idiosoma is truncate, arched, bi- or tricuspid, a single process, if present, is rectangular or spiniform, but not longer than the width at its basis.

Collecting data The type locality is in the South-eastern Pacific Ocean, 26°S, 80°W, 950 m. Further records from almost the same area are from 550–600 m depth (Newell 1971). At present there are no shallow water records.

Agauopsis racki Newell, 1984

References *Agauopsis racki* Newell 1984: 239–240, figs 671–675 (female).

Characters Length of female 585 µm; length:width ratio 1.5:1. Raised areas of dorsal plates with porose areola or costae, remainder of plates faintly reticulate and with fine pores. Anterodorsal plate with H-like, posterodorsal plate with slender costae. Ocular plates with corneae. Length:width ratio of gnathosoma 1.7:1 and length ratio gnathosoma:idiosoma 0.3:1. Rostrum slightly shorter than length of gnathosomal base and reaching to tip of palps. Tibia I with one ventral and three ventromedial spines; of the latter the two basal ones contiguous.

Remarks *Agauopsis racki* is a member of the *microrhyncha* group (cf. Bartsch 1986a, 1996a; Otto 1999) or Key group 7000 (cf. Newell 1984). The most easily recognized character of species of these groups is the number, size and arrangement of the ventral spines on tibia I.

Collecting data Off southern Argentina, 56°S, 66°W, 439 m, 55°S, 65°W, 247 m and South Pacific Ocean, 54°S, 140°W. The species was also extracted from 362–567 m depth (Newell 1984).

Agauopsis valida Bartsch, 2001

References *Agauopsis valida* Bartsch 2001b: 68–73, figs 13–25 (female, deuto-, protonymph).

Characters Length of female 467 µm, length:width ratio 1.5:1. Frontal spine short, triangular. Antero- and posterodorsal plate each with pair of costae, these with faintly developed rosette pores; remainder of plates delicately pitted. Each ocular plate with cornea and faint eye pigment. Gnathosoma short; length:width ratio 1.8:1; ratio length of gnathosoma:idiosoma 0.3:1. Rostrum shorter than gnathosomal base and almost extending to end of palps. Last palpal segment with single seta. Leg I much wider and longer than following legs. Leg I slightly shorter than idiosoma; ratio 0.9:1. Basifemur I with one apically dentate ventral spine. Basifemur, telofemur, genu, tibia, and tarsus I with 1/0, 2/3, 1/1, 2/3, 0/1 ventral/ventromedial solid, apically dentate spines. Spines basally flanked by short lamellae. Ventral setae on basi- and telofemora II to IV, as well as parts of segments with filaments. Paired claws of tarsus I slightly shorter than those of following tarsi. All paired claws without pectines.

Remarks *Agauopsis valida* is characterized by its legs I which are much wider and longer than the following legs and its spiniform ventral seta on basifemur I. This spine is present also in the nymphs.

Collecting and habitat data Northeast Atlantic Ocean, Great Meteor Seamount, 30°N, 28–29°W, 302–488 m depth (Bartsch 2001b). A second record (unpublished) is that of a protonymph, taken with an epibenthic sledge on the Great Meteor Seamount, 30°06'N, 28°23'W, 511 m, in the course of Cruise 42/3, R. V. Meteor.

Atelopsalis tricuspis Trouessart, 1896 (in Trouessart & Neumann 1896)

References *Atelopsalis tricuspis* Trouessart & Neumann 1896: 345–347, pl. 10, figs 2a, b, pl. 11, fig. 4 (female); Bartsch 1973a. 75, 76, figs 98–109 (females).

Characters Length of females 218–235 µm, length:width ratio 1.7:1. Dorsal plates panelled and with porose areolae. The latter with modified rosette pores. Anterodorsal plate with less than 10 such rosette pores. Posterodorsal plate with demarcated pair of costae with single row of pores. Pores small at the surface, followed by widened alveolus which is surrounded by a few, delicate canaliculi. Ocular plate with two corneae. Porose areolae in marginal parts of ventral plates with modified rosette pores. Anterior epimeral plates with pair of vesicles. Gnathosoma very short, hardly longer than wide and only 0.2 times the length of idiosoma. Leg I wider than following legs; length ratio leg I:idiosoma 0.9:1. Integument of telofemur I panelled. Pectines of paired claws of tarsi II to IV with numerous delicate tines.

Remarks From the Mid-Atlantic at present four species of *Atelopsalis* are known, i. e., *A. atlantica* Pepato & Tiago, 2004 (24°S), *A. meteorensis* Bartsch, 2002 (in Bartsch 2002b) (30°N), *A. newelli* Bartsch, 1973 (in Bartsch, 1973a) (37°N), and *A. tricuspis* (37 and 46°N) (Pepato & Tiago 2004, Bartsch 2002b, Bartsch 1973a, Trouessart & Neumann 1896). Differences are in the ornamentation of the plates, from slightly foveate *(A. newelli)* to surface of plates panelled and presence of porose areolae which enclose a few *(A. tricuspis)* or numer-

ous distinct rosette pores *(A. atlantica)*. Another species, *A. pacifica* Bartsch, 1985, first recorded from The Philippines (Bartsch 1985a), was recently mentioned from the Mediterranean (Durucan & Boyaci 2017).

Collecting and habitat data South-eastern Atlantic Ocean; recorded from the Bay of Biscay (Golfe de Gascogne), 1410 m depth, and the Josephine Bank (37°N, 14°W) from surface sediment in 256 and 291 m depth (Trouessart & Neumann 1896; Bartsch 1973a).

Bathyhalacarus abyssiculus Bartsch, 1982

References *Bathyhalacarus abyssiculus* Bartsch 1982b: 209–211 µm, figs 1–10 (females, deuto-, protonymphs, larva).

Characters Length of females 409–502 µm, length:width ratio 1.1:1. Large areas with striated integument between reticulated dorsal plates. Anterior margin of anterodorsal plate truncate, without frontal spine; plate much wider than long, with one pair of dorsal setae adjacent to anterior margin of plate. Ocular plates elongate; each with a gland pore in both anterior and posterior end. Each posterior epimeral plate with three dorsal and two ventral setae. Genitoanal plate with three pairs of perigenital setae. Anal sclerites small. Gnathosoma 1.7 times longer than wide. Length ratio gnathosoma:idiosoma equalling 0.3:1. Short triangular rostrum slightly extending beyond middle of second palpal segment. Legs slender, longer than idiosoma. Tibia I with three pairs of ventral setae. Tarsi III and IV each with three dorsal setae. Claws slender, smooth.

Remarks Most *Bathyhalacarus* species in the Atlantic Ocean have a frontal spine, in *B. abyssiculus* it is lacking.

Collecting data North Atlantic Ocean, Newfoundland Basin, 41°N, 46°W, 4400 m (Bartsch 1982b).

Bathyhalacarus acanthophorus Bartsch, 1982

References *Bathyhalacarus acanthophorus* Bartsch 1982b: 211–213, figs 11–18, 19–24 (female, males, deuto-, protonymphs).

Characters Length of female 486 µm, of males 434–450 µm. Length:width ratio of idiosoma (male) 1.4:1. Dorsal plates strongly reticulated. Anterodorsal plate with short frontal process, posterior margin wide, truncate. Instead of one pair of elongate ocular plates two pairs of short plates present, each with a gland pore. Corneae lacking. Each of posterior epimeral plates with three dorsal and three ventral setae. Genitoanal plate of male larger and longer than that of female. Males with 72 perigenital setae, females with six setae (three pairs). Anal sclerites extending beyond anal valves. Length of gnathosoma 0.3 times that of idiosoma. Length:width ratio of gnathosoma 1.6:1. Rostrum reaching to middle of second palpal segment. Length of leg I slightly less than that of idiosoma (length ratio 1.0:1). Tibia I with six ventral setae. Claws slender, smooth.

Remarks A unique combination of characters of *Bathyhalacarus acanthophorus* is: anterodorsal plate wide; posterior margin as wide as anterior one; ocular plates divided.

Collecting data South Atlantic Ocean, eastern part of Angola Basin, 9°S, 12°E, 1427–1643 m (Bartsch 1982b).

Bathyhalacarus aculifer Bartsch, 1982

References *Bathyhalacarus aculifer* Bartsch 1982b: 213–215, figs 25–30, 31–37 (female, male, deuto-, protonymphs, larva).

Characters Length of female 680 µm, of male 663 µm. Length:width ratio in female 1.4:1. Dorsal plates reticulated. Frontal spine of anterodorsal plate very small; plate as long as wide; its posterior margin shorter than anterior one. Anterior and posterior parts of ocular plates fused via narrow bridge or divided; both parts with gland pores; corneae absent. Posterior epimeral plates each with three dorsal and three ventral setae. In female and male plate corresponding to genital plate almost circular. Plate of female with four pairs of perigenital setae; male with 91 setae. Anal sclerites distinct, extending beyond anal valves. Length of gnathosoma 0.3 times that of idiosoma. Rostrum extends just beyond middle of second palpal segment. Leg I somewhat shorter, leg IV longer than idiosoma. Tibia I with three pairs of ventral setae. Claws slender, smooth.

Remarks This and the above mentioned *Bathyhalacarus acanthophorus* have the ocular plates divided into an anterior and posterior part. The anterodorsal plate of *B. aculifer* is about as long as wide, in *B. acanthophorus* it is distinctly wider than long.

Collecting data South Atlantic, Argentine Basin, 44°S, 49°W, 5208–5223 m (Bartsch 1982b).

Bathyhalacarus acutus Bartsch, 1982

References *Bathyhalacarus acutus* Bartsch 1982b: 215–217, figs 38–47 (females, deuto-, protonymphs).

Characters Length of females 378–490 µm; of holotype 422 µm; its length:width ratio about 1.5:1. Surface of dorsal plates reticulated. Anterodorsal plate with short frontal spine; plate wider than long. Either side with one single oblong ocular plate, both with a gland pore near anterior and posterior margin; corneae absent. Each posterior epimeral plate with three dorsal and three ventral setae. Female genital plate with three pairs of perigenital setae. Anal sclerites distinct, extending beyond anal valves. Length ratio gnathosoma:idiosoma 0.3:1. Length:width ratio of gnathosoma 1.6:1. Rostrum short, hardly extending beyond level of middle of second palpal segment. Leg I almost as long as idiosoma, leg IV somewhat longer. Tibia I with three pairs of ventral setae. Claws slender, with very delicate tines.

Remarks Six *Bathyhalacarus* species are known from the Atlantic Ocean (Bartsch 1982b, 2005), of these, *B. abyssiculus* and *B. acutus* have a pair of elongate, broadly fused ocular plates. In contrast to *B. abyssiculus* the anterodorsal plate of *B. acutus* has a frontal spine and the posterior half of the plate is about as wide as the anterior one whereas in *B. abyssiculus* the plate is wide in anterior half but then the margins rapidly converge.

Collecting data South Atlantic, Argentine Basin, 36–37°S, 52–53°W, 2041–2707 m depth (Bartsch 1982b). Two juveniles, similar to *B. acutus,* have been found off the South Shetland Islands, at 61–62°S, 61°W and 2875–2900 m depth (Bartsch 2005).

Bathyhalacarus anomalus Bartsch, 2005

References *Bathyhalacarus anomalus* Bartsch 2005: 32–35, figs 2–7, 8–14, 15–17 (females, protonymphs, larva).

Characters Length of female 364 µm, length:width ratio 1.4:1. Dorsal plates uniformly reticulated. Anterodorsal plate with short frontal spine; plate much wider than long, posteriorly narrowed, posterior margin short. Ocular plate with an anterior and posterior part separated by striated integument. Each part with a gland pore; corneae absent. Posterior epimeral plate with one dorsal, one marginal and two ventral setae. Genitoanal plate with three pairs of perigenital setae. Anal sclerites small, surpassed by anal valves. Gnathosoma 1.6 times longer than wide. Length of gnathosoma 0.3 times that of idiosoma. Rostrum short, reaching to middle of second palpal segment. Legs slender. Leg I 1.1 times longer than idiosoma, leg IV longer than leg I. Tibia I with two pairs of ventral setae. Claws long and slender; without pectines.

Remarks The posterior epimeral plate of most *Bathyhalacarus* species bears three dorsal and two or three ventral setae, in *B. anomalus* each plate has one dorsal, one marginal and two ventral setae. Another singularity in *B. anomalus* is the presence of no more than four ventral setae on tibia I, instead of the general number of six (to eight, number of setae in *Bathyhalacarus quadricornis* Sokolov & Jankovskaja, 1968 not known). Also the number of setae on the other legs is lower than in the majority of adult *Bathyhalacarus* species.

Collecting data South Atlantic Ocean, Western Antarctica, off the South Shetland Islands; 61–62°S, 61–62°W, 2875–2917 m (Bartsch 2005).

Bathyhalacarus atlanticus Bartsch, 1982

References *Bathyhalacarus atlanticus* Bartsch 1982b: 217, 218, figs 48–56 (females, deutonymph).

Characters Length of females 406–446 µm, length:width ratio 1.3:1. Dorsal plates faintly reticulated. Anterodorsal plate with short frontal spine; plate much wider than long, posteriorly narrowed, posterior margin short. Anterior and posterior part of ocular plate fused via very narrow bridge. Posterior epimeral plate with three dorsal and two ventral setae. Anal sclerites distinct, extending beyond anal valves. Length of gnathosoma 1.7 times the width; ratio gnathosoma:idiosoma 0.4:1. Rostrum hardly extending beyond level of middle of second palpal segment. Legs slender. Leg I somewhat, leg IV distinctly longer than idiosoma. Tibia I with three pairs of ventral setae. Claws slender, smooth.

Remarks The anterior and posterior parts of each ocular plate are fused via a very narrow bridge; in females of other *Bathyhalacarus* species these parts are either fused via wide bridges or completely separated by striated integument.

Distribution North Atlantic Ocean, North American Basin, 38°N, 70°W, 3264–3356 m (Bartsch 1982b).

Bathyhalacarus dictyotus Bartsch, 1989

References *Bathyhalacarus dictyotus* Bartsch 1989b: 456, 457, figs 1–9 (male).

Characters Length of male 477 µm, length:width ratio 1.4:1. Dorsal plates reticulated. Anterodorsal plate with small, upward turned frontal spine; plate much wider than long; posterior

margin wide, truncate. Ocular plate elongate, posterior part caudiform; with a gland pore both in anterior and posterior part. Posterior epimeral plates with five to six dorsal and three ventral setae. Genitoanal plate pentagonal; anterior margin truncate. Genital opening surrounded by almost 150 perigenital setae. Anal sclerites distinct, extending beyond anal valves. Length of gnathosoma 0.3 times that of idiosoma. Palps long; rostrum far from reaching to end of second palpal segment. Legs slender; leg I 1.1 times longer than idiosoma. Tibia I with six ventral bristles. Paired claws slender. Those on posterior legs with delicate tines.

Remarks *Bathyhalacarus dictyotus* is at present the only *Bathyhalacarus* species with more than three dorsal setae on the posterior epimeral plates.

Collecting data Pacific Ocean, northeast of New Caledonia, 21°S, 166°E. Collected from a depth of 1410 m (Bartsch 1989b).

Bathyhalacarus humboldti (Newell, 1967)

References *Thalassarachna humboldti* Newell 1967: 701–704, figs 18–35 (deutonymph, larva); Newell 1971: 12 (protonymph).

Bathyhalacarus humboldti, Bartsch 1982b: 209, 219.

Characters Length of deutonymph 461 µm. Length:width ratio of deutonymph 1.7:1. Small dorsal plates separated by large areas with striated integument. Anterodorsal plate with small frontal spine. Anterior and posterior part of ocular plates fused; each part with a gland pore. Posterior epimeral plate with two dorsal and three ventral setae. Deutonymphal genital plate separated from anal plate. Anal sclerites distinct. Rostrum short, reaching to middle of second palpal segment. Legs slender. Legs I and IV 1.2 and 1.6 times longer than idiosoma, respectively.

Remarks The species had been described on the basis of its deutonymph. At present, little is known about change in shape of plates and number and arrangement of setae on the legs during growth from one instar to the next, e. g., the number of setae on posterior epimeral plates and size of ocular plates may differ from that in adults.

Collecting data South-eastern Pacific, 29°S, 80°W, 3680–4100 m and 22°S, 82°W, 1760–1830 m. Collected with a dredge from a bottom with red clay, volcanic ash and manganese nodules (Newell 1967, 1971).

Bathyhalacarus quadricornis Sokolov & Jankovskaja, 1968

References *Bathyhalacarus quadricornis* Sokolov & Jankovskaja 1968: 486–488, figs 1 and 2 (female); Sokolov & Jankovskaja 1969: 113–114 (female); Sokolov & Jankovskaja 1970: 427–431, figs 1(1–10), 2(1–3) (female); Jankovskaja 1978: 295–299 (deutonymph).

Characters Length of females 500–630 µm, length:width ratio of a 570 µm-long female 1.6:1. Dorsal and ventral plates strongly reticulated. Striated integument with delicate pores and short filaments (according to Sokolov & Jankovskaja 1968, fig. 1. 3). Anterodorsal plate wide, anterior margin truncate, without frontal spine. First pair of gland pores on 'horns'. Pair of ocular plates elongate, anterior and posterior part fused. Anterior part with bul-

bous (?), posterior part with gland pore on tube-like 'horn'. No corneae present. Anterior part of genitoanal plate semi-circular. Length ratio gnathosoma:idiosoma 0.4:1. Rostrum not reaching to end of second palpal segment. Legs slender, length ratio leg I:idiosoma 0.8:1, leg IV longer than leg I, almost as long as idiosoma. Claws slender, almost smooth.

Remarks The species is characterized by its two pairs of horns, one pair on the anterodorsal plate, the second one on the posterior part of ocular plate. Each horn enclosing an afferent duct.

Collecting data Pacific Ocean, Kuril-Kamchatka Trench, 56°S 155° E., 5090–5100 m (Sokolov & Jankovskaja 1968, 1969) and Idzu-Bonin Trench (Izu-Ogazawara Trench), 28°S, 143°E, 6770–6850 m (Jankovskaja 1978).

Bathyhalacarus sordidus Bartsch, 1989

References *Bathyhalacarus sordidus* Bartsch 1989b: 458, 459, figs 10–21 (female, deutonymphs, larvae).

Characters Length of female 558 µm; length:width ratio 1.1:1. Dorsal aspect dominated by areas with striated integument. Idiosoma hardly extending beyond the level of insertion of leg IV. Surface of dorsal plates with very fine epicuticular filaments. Anterodorsal plate widest in its middle part, anterior margin arched, posterior margin short, truncate. Frontal spine lacking. Ocular plates elongate, narrow. Posterodorsal plate not seen. Each posterior epimeral plate with three dorsal and three ventral setae. Genitoanal plate almost circular, with three pairs of perigenital setae. Genital sclerites small. Ovipositor short. Anal sclerites small, surpassed by anal valves. Length ratio gnathosoma:idiosoma 0.4:1. Rostrum extending beyond second palpal segment. All legs slender; longer than idiosoma. Length ratio leg I:idiosoma 1.4:1. Telofemora with delicate epicuticular filaments. Tibia I with four pairs of ventral bristles, the ventromedial ones delicately bipectinate. All tarsi with three dorsal setae. Claws slender; tines of pectines not seen.

Remarks The idiosoma of *B. sordidus* is short and extends hardly beyond the insertion of legs IV, its length:width ratio is 1.1:1. Moreover, *B. sordidus* has eight ventral setae on tibia I instead of the generally found six ventral setae.

Collecting data Western Pacific Ocean, southwest of Lifou, 21°S, 167°E; 1380 m (Bartsch 1989b).

Bathyhalacarus speciosus Bartsch, 1989

References *Bathyhalacarus speciosus* Bartsch 1989b: 460, 461, figs 22–33 (females, males).

Characters Length of females 416–497 µm, of males 416–478 µm; length:width ratio 1.6:1. Dorsal plates reticulated. Anterodorsal plate slightly wider than long; anterior margin rounded; frontal spine lacking. Ocular plates large, elongate, posterior part caudiform; with a gland pore both in anterior and posterior part. Posterodorsal plate in females about 1.2 times longer than wide, in males at least 1.5 times. Ventral aspect dominated by its finely porose plates. Posterior epimeral plate with three dorsal and three ventral setae. Female genitoanal plate longer than wide, bearing two pairs of perigenital setae. Ovipositor in rest, hence internal, extending beyond the level of anterior margin of genitoanal plate. Posterior pair of genital acetabula enlarged. Male genitoanal plate oviform, slightly larger than in female, about 100 perigenital setae arranged around genital opening. Anal sclerites dis-

tinct. Length of gnathosoma 0.3 times that of idiosoma. Its length:width ratio 2.5:1. Parallel-sided rostrum 2.5 times longer than wide and extending beyond end of third palpal segment. Legs slender; leg I about as long as idiosoma. Tibia I with three pairs of smooth ventral bristles. Claws slender; pectines with very delicate tines.

Remarks *Bathyhalacarus speciosus* can be separated from congeners by the combination: dorsal and ventral aspect dominated by plates; in females posterodorsal plate distinctly smaller than in males; female genitoanal plate with two pairs of perigenital setae, rostrum parallel-sided and longer than gnathosomal base.

Collecting data Western Pacific Ocean, southwest of New Caledonia, 23°S 167°E, 570 m (Bartsch 1989b).

Bradyagaue aspidionis Newell, 1984

References *Bradyagaue aspidionis* Newell 1984: 82, 84, figs 186–189 (female).

Characters Idiosomal length of female 831 µm; length almost twice the width. Gnathosoma 2.4 times longer than wide. Tibiae III and IV each with three ventral setae, each seta on a setigerous process.

Remarks According to Newell (1984) similar to *B. drygalskii* but with a shorter posterodorsal plate.

Collecting data Antarctica, Near Victoria Land, 67°S, 164°E, 1442–1444 m (Newell 1984).

Bradyagaue drygalskii (Lohmann, 1907)

References *Halacarus (Polymela) drygalskii* Lohmann 1907a: 9; Lohmann 1907b: 377, 378, pl. 34, figs 1–6 (females, males, proto-, deutonymphs, larvae).
Leptospathis Alberti antarctica Trouessart & Neumann, 1907: 4–6, figs 1–5.
Bradyagaue drygalskii, Newell 1971 (10); Newell 1984: 82–84, figs 180–185 (female, male); Bartsch 1993: 116–118, fig. 46 A-F (females, males, deuto-, protonymphs, larvae); Bartsch 2016b: 136–139, fig. 2 A-C (females, males, deuto-, protonymphs, larvae).

Characters Length of female idiosoma 750–1000 µm, that of males 740–1000 µm. Idiosoma slender, length:width ratio about 1.9-2.2:1. Dorsal plates with faint, almost smooth layer of cerotegument. Each ocular plate with two corneae and eye pigment. Opposing margins of anterodorsal and posterodorsal plates acuminate. Female genitoanal plate with 6–11 perigenital setae on either side of genital opening, males with about 150 setae densely arranged around genital opening. Perigenital setae of males smooth to slightly tufted. Gnathosoma slender, its length twice the width. Length ratio gnathosoma:idiosoma 0.3:1. Legs slender. Ratio length leg I:idiosoma 0.8-0.9:1. Tibiae III and IV with three ventral setae; each seta on setigerous process. Cerotegument on telofemora I and II moderately developed, on telofemora III and IV faintly. Each lateral claw with accessory process and a long pecten, the latter with numerous tines.

Remarks A dozen *Bradyagaue* species are known from the southern hemisphere (Bartsch 2009). *Bradyagaue drygalskii* is characterized by the shape of its dorsal plates, namely opposing margins of anterodorsal and posterodorsal plates acuminate (versus semi-circular) and tibiae III and IV generally with three ventral bristles (versus four). The range of variants is not known.

Collecting and habitat data: Circum Antarctic. Records are from off the South Sandwich Is, Elephant I., South Shetland Is, King George I., Ross Sea, Victoria Land (Cape Hallett), Georg V Land (Commonwealth Bay), Terre Adélie, and Gauss Station (Lohmann 1907b; Viets 1952; Newell 1984; Bartsch 2008, 2016b). The species is also known from sub-Antarctic regions, e. g., Kerguelen Is, Macquarie I., Falkland Is (Viets 1952; Newell 1971, 1984). The known depth range extends from the lower shoreline to 1674 m depth. The species has generally been extracted from stoloniferous organisms; e. g., clinging on stolons of hydrozoa.

Bradyagaue quadriseta Newell, 1971

References: *Bradyagaue quadriseta* Newell 1971: 11–12, figs 16, 94–102 (females, males, deuto-, protonymphs, larvae).

Characters: Idiosomal length of females 600–618 µm, of males 679–687 µm; length:width ratio about 1.9-2.1:1. Posterior and anterior margins of antero- and posterodorsal plates rounded. Ocular plates with two corneae each. Females with 9–10 pairs of smooth perigenital setae. Males with 77–94 perigenital setae; these setae branched. Legs of males longer and slenderer than those of females. No cerotegumental lamellae developed. Tibiae IV with four ventral setae arising from setigerous processes. Tibiae and tarsi III and IV curved. Claws with pectines.

Remarks: *Bradyagaue quadriseta* has four ventral setae on tibia IV, this is shared with *B. stocki* (diagnosed below) whereas the Antarctic and Sub Antarctic species *B. aspidionis* and *B. drygalskii* have three setae.

Collecting and habitat data: The type locality is in the south-eastern Pacific Ocean; 26°S, 80°W; 160–170 m. Further records are from 33°S, 72°W, 485 m and 34°S, 79°W, 62 m. The records are from the shelf and slope area off Chile (Newell 1971).

Bradyagaue stocki Bartsch, 1992

References: *Bradyagaue stocki* Bartsch 1992b: 81–84, figs 1a-e, 2a-e (female).

Characters: Length of idiosoma 595 µm, length:width ratio 1.8:1. Surface of integument covered by villose cerotegument. Each ocular plate with two small corneae obscured by thick layer of cerotegument. Eye pigment not seen. Gnathosoma slender, its length:width ratio 2.3:1; length ratio gnathosoma:idiosoma 0.3:1. Rostrum slender, almost three times longer than gnathosomal base. Basal pair of maxillary setae wider and much longer than adjacent distal pair. Legs slender, length of leg I 1.1 times that of idiosoma. Surface of telofemora villous. Tibiae III and IV with four ventral bristles, each one on a setigerous process. Paired slender claws with numerous delicate tines.

Remarks: Tibiae III and IV of *Bradyagaue stocki* have four ventral setae, just as those of *B. quadriseta.* The setae arise from processes not set off as sharply as in *B. quadriseta,* the gnathosoma seems to be shorter than in the south-eastern Pacific species. No villi on the telofemora are mentioned in Newell (1971).

Collecting data: North-eastern Atlantic Ocean, near Cape Verde Islands, 17°N, 25°W, 1200 m (Bartsch 1992b).

Colobocerasides auster Bartsch, 1998

References *Colobocerasides auster* Bartsch 1998a: 228–230, figs 13–21, 22–28 (female); Bartsch 2016b: 139, 140, fig. 2D-H (deutonymph).

Characters Length of female 470 µm, length:width 1.9:1. Dorsum with wide areas of striated integument between plates. Surface of plates reticulate. Two pairs of ocular plates, none with cornea but anterior pair with small gland pore. Gnathosoma 1.9 times longer than wide; length ratio gnathosoma:idiosoma 0.4:1. Rostrum and chelicerae stylet-shaped. Rostrum slightly shorter than gnathosomal base. Palps four-segmented. Length ratio leg I:idiosoma 0.7:1. Telofemur IV with two ventral spines. Tibiae I to IV with 3, 2, 2, 3 ventral setae, of these 1, 1, 1, 0 delicately bipectinate. Each tarsus with pair of slender claws and a distinct median claw. Paired claws III and IV with delicate tines.

Remarks Differences between this and a second Atlantic species (*C. koehleri* Trouessart, 1896) are mentioned below.

Characters such as gnathosoma with wide pharyngeal plate, rostrum and chelicera stylet-shaped, body content dark, hint at an ecto-parasitic life style, though most likely temporarily. It would be worth to check polychaetes, tanaidaceans and other co-occurring macrofauna if halacarids are attached and feeding on them.

Collecting and habitat data Antarctica, off Elephant Island, 61°S, 57°W, 460–480 m and Weddell Sea, 72°S, 12°W, 211 m (Bartsch 1998a, 2016b). Found amongst octocorals with polychaetes and tubes with tanaidaceans.

Colobocerasides koehleri (Trouessart, 1896)

References *Coloboceras koehleri* Trouessart 1896: 105 (female); Trouessart & Neumann 1896: 348–351, pl. 11: fig. 1a-d (female).

Colobocerasides koehleri, Viets 1950: 30, 31 (female); Bartsch 1998a: 225–227, figs 1–3, 4–12 (female).

Characters Length of female 610(-680) µm; length about twice the width. Dorsum with wide areas of striated integument between plates. Surface of dorsal plates with delicate epicuticular granules, these forming a reticulate or maze-like ornament. Each half of body with two ocular plates; anterior plate with gland pore. Corneae lacking. Ventral plates with delicate porosity. Gnathosoma 1.9 times longer than wide and 0.3 times of length of idiosoma. Stylet-shaped rostrum about as long as gnathosomal base. Palps three-segmented. Legs slender; length of leg I equalling 0.6 times that of idiosoma. Telofemur IV without ventral seta. Tibiae I to IV with 4, 5, 4, 3 ventral setae, 3, 4, 3, 1 of these setae delicately pectinate. Each tarsus with pair of slender claws and a distinct median claw. Paired claws on tarsi III and IV with delicate tines.

Remarks *Colobocerasides koehleri* is larger than *C. auster,* the anterior part of the posterodorsal plate is triangular (versus semi-circular), tibiae I to IV have a larger number of ventral setae, and telofemora IV lack ventral setae.

Collecting data North-eastern Atlantic Ocean, Bay of Biscay (Golfe de Gascogne), 46°N, 6°W, 1410 m (Trouessart 1896).

Copidognathus abyssiculus Bartsch, 1982

References *Copidognathus abyssiculus* Bartsch 1982c: 162–165, figs 1–6, 7–13 (females, protonymphs, larvae).

Characters Length of females 384–418 µm, length:width ratio 1.7:1. Surface of dorsal plates panelled, each panel subdivided. Rosette pores lacking. Corneae or eye pigment absent. Posterodorsal plate with slightly raised and panelled costae. Anal sclerites with epicuticular filaments. Length ratio gnathosoma:idiosoma 0.3:1. Gnathosoma about 1.6 times longer than wide. Rostrum rather short, not reaching to end of second palpal segment. Legs shorter than idiosoma. Length ratio leg I:idiosoma 0.7:1. Tarsi III and IV with four and three dorsal setae. Paired claws slender. Pectines of claws on posterior legs with delicate tines.

Remarks The surface structure of the plates is similar to that of the below outlined *C. abyssorum* but in *C. abyssiculus* the idiosoma and its plates are slenderer.

Collecting data Argentine Basin, 44°S, 49°W, 5208–5223 m (Bartsch 1982c).

Copidognathus abyssorum Bartsch, 1982

References *Copidognathus abyssorum* Bartsch 1982c: 165–169, figs 14–19, 20–23 (females, males, protonymphs, larvae).

Characters Length of females 403–446 µm. Idiosoma slender, length:width ratio 1.8:1. Length of males 412–471 µm. Dorsal plates panelled; without rosette pores. Posterodorsal plate with slightly raised costae. Corneae and eye pigment absent. Posterior pair of gland pores removed from posterior margin of posterodorsal plate. Anal cone prolonged. Marginal parts of idiosoma and anal sclerites often with a cover of delicate filaments and debris. Each one of male genital sclerites with three subgenital setae. Length of gnathosoma almost twice its width and 0.3 times that of idiosoma. Rostrum shorter than gnathosomal base and not reaching to end of second palpal segment. Leg I as long as idiosoma (1.0:1). Telofemur I panelled. Paired claws slender, pectines only seen at high magnification. Tarsi III and IV with four and three dorsal setae.

Remarks *Copidognathus abyssorum* is similar to *C. bruuni* Newell, 1971 but can be separated on the basis of shape of the plates, namely anterodorsal plate posteriorly arched (versus truncate), ocular plates posteriorly semi-circular (versus slightly acuminate) and posterodorsal plate about 1.7 times wider than anterodorsal plate (versus about twice that width).

Collecting data South Atlantic Ocean, Argentine Basin, 44°S, 49°W, 5208–5223 m (Bartsch 1982c).

Copidognathus alvinus Bartsch, 1994

References *Copidognathus alvinus* Bartsch 1994a: 484–487, figs 17–27 (females, males); Bartsch 1996b: 166 (male).

Characters Length of females 377–396 µm, of males 370–384 µm, length:width ratio of female 1.8:1, of male 1.7:1. Dorsal and ventral plates reticulate. Raised areas not distinctly delimited from remaining reticulate areas. No rosette pores in slightly raised areas. On anterodorsal plate raised area lambda shaped; posterodorsal plate with four costae. Ocular plates without corneae or eye pigment. Striated integument not squamate. Males with 11 pairs

of perigenital setae. Gnathosoma short. Length ratio gnathosoma:idiosoma 0.3:1. Length ratio leg I:idiosoma 0.7:1. Lateral flank of telofemora I and II reticulate. Pectines of paired claws with numerous minute tines.

Remarks *Copidognathus alvinus* is an inhabitant of hydrothermal vent areas but, according to its morphological characters, there is no close relationship to other vent species, e. g., *C. papillatus* Krantz, 1982 and *C. nautilei* Bartsch, 1997 (in Bartsch 1997a).

Two females held eggs. In one of the eggs a larva (prelarva?) was almost ready to hatch (Bartsch 1994a). In general, halacarids deposit their eggs for development in or on the substratum inhabited. In cold-temperate zones, the development from egg to larva may, dependent on e. g. temperature, take about two till five weeks (Kirchner 1969; Siemer 1996).

Collecting and habitat data Atlantic Ocean; Mid-Atlantic Ridge, Lucky Strike, 37°N, 32°W. The sample with the mites had been taken from rocky bottom in 1636–1685 m depth (Bartsch 1994a, 1996b).

Copidognathus anops Newell, 1971

References *Copidognathus anops* Newell 1971: 24–25, figs 52–54, 144–149 (female, larva); Newell 1984: 140, 148, 149, fig. 355 (female).

Characters Length of female 326 µm, length:width about 1.9:1. Dorsal plates with panels and areas with rosette pores. Anterodorsal plate anteriorly hooded; plate with two circular porose areolae fused via narrow bridge. Ocular plates without corneae; plate posteriorly acuminate (but without cauda). Narrow costae on posterodorsal plate with rosette pores. Gnathosoma with triangular tectum; length:width of gnathosoma 1.5-1.6:1. Rostrum not extending to end of second palpal segment. Ratio length of leg I:idiosoma about 0.6:1. Telofemur I short, its surface ornamented with polygonal reticulation. Tarsi III and IV with four and three dorsal setae, respectively. Claws of tarsi II to IV with pectines.

Remarks In contrast to other *Copidognathus* species known from this region, the telofemora I of *C. anops* are short. Further discriminating characters are given in Newell (1971).

Collecting and habitat data South-eastern Pacific ocean, off Peru, 13°S, 77°W. From a sample taken from rocky bottom in 1565 m depth (Newell 1971).

Copidognathus atlanticus Bartsch, 1982

References *Copidognathus atlanticus* Bartsch 1982c: 169–172, figs 24–28, 29–32 (females, protonymphs, larva).

Characters Length of females 327–348 µm. Length of idiosoma about twice the width. Dorsal aspect dominated by dorsal plates. These plates panelled; rosette pores lacking. On anterodorsal plate a median part slightly raised, posterodorsal plate with weakly developed costae. Posterior part of ocular plates caudiform. Corneae and eye pigment absent. Surface of costae almost smooth. Ventral plates with porose areolae; these with faintly developed rosette pores. Length:width ratio of gnathosoma 1.5:1, length ratio gnathosoma:idiosoma 0.3:1. Rostrum triangular, extending beyond middle of second palpal segment. Leg I wider than following legs. Length ratio leg I:idiosoma 0.7-0.8:1. Surface of telofemur I panelled. Paired claws on tarsi II to IV with distinct though delicate pectines. Tarsi III and IV with four and three dorsal setae, respectively.

Remarks The ocular plates of *Copidognathus atlanticus* are posteriorly elongate, in contrast to the shorter plates in *C. abyssorum* and *C. abyssiculus.* The three species are inhabitants of sandy deposits in the Argentine Basin.

Collecting and habitat data South Atlantic Ocean, Argentine Basin, 37°S, 53°W, 993–1011 m (Bartsch 1982c). Extracted from sandy deposits.

Copidognathus bituberosus Newell, 1971

References *Copidognathus bituberosus* Newell 1971: 19–20, figs 27–29, 126–132 (female, males); Newell 1984: 136–138.

Characters Length of female 329 µm, of males 348–365 µm, length:width ratio about 1.8:1. Integument of dorsal plates coarsely reticulate, their porose areolae with rosette pores. Middle of anterior dorsal plate with raised transverse areola due to fusion of two circular ones; another two areolae adjacent but not fused and in mounted specimens slightly extending beyond posterior margin of plate. Ocular plates without corneae. Posterior dorsal plate with pair of costae. Length:width of gnathosoma ca 1.6:1. Slender rostrum not directly reaching to end of second palpal segment. Tarsi III and IV with four and three dorsal setae. Claws of tarsi II to IV with delicate tines.

Remarks The species can be separated from other south-eastern Pacific species because of shape and arrangement of the porose areolae on the anterodorsal plate, namely a transverse areola in the middle of plate (by fusion of two circular ones) and two circular areas near posterior margin.

Collecting and habitat data South-eastern Pacific Ocean, off Chile, 33°S, 72°W. Found in a slope sample taken in 485 m depth (Newell 1971).

Copidognathus bruuni Newell, 1967

References *Copidognathus bruuni* Newell 1967: 704–708, figs 36–49 (male, protonymphs); Newell 1971: 22 (protonymph); Newell 1984: 182 (male).

Characters Length of a male 418 µm, length:width 2.1:1. Dorsal and ventral plates large, areas with striated integument narrow. Dorsal plates foveate to panelled; walls of panels with tubercles. Ocular plates posteriorly pointed. No cornea present. Posterodorsal plate very wide, its costae with deeply depressed panels. Elongate anal cone including anus and anal sclerites. Each anal sclerite with two short pairs of setae. Male with 25 perigenital setae; each genital sclerite with three subgenital setae. Length:width ratio of gnathosoma 1.8:1, ratio gnathosoma:idiosoma 0.3:1. Palps slender. Rostrum ending at about level with 2/3 of second palpal segment. Legs slender; all slightly shorter than length of idiosoma. Length ratio leg I:idiosoma 0.8:1. Surface of telofemora I and II panelled, walls of panels tuberculate. Trochanter I with filaments. Tarsi III and IV with four and three dorsal setae. Claws long and slender, smooth.

Remarks The majority of *Copidognathus* species have no prolonged anal cone, as present in *C. bruuni* and also in *C. abyssorum.* The most easily recognizable differences are: in *C. bruuni* is the posterodorsal plate wider than the anterodorsal plate (slightly more than twice ver-

sus 1.7 times in *C. abyssorum*) and the anal sclerites are enclosed in a tube-like anal cone (versus distinctly seen in dorsal and ventral aspect).

Collecting and habitat data South-eastern Pacific Ocean, 29°S, 80°W, 3680–4100 m. The mites had been taken with a dredge from a bottom with red clay, volcanic ash and manganese nodules (Newell 1967).

Copidognathus calidictyotus Bartsch & Rybakova, 2015

References *Copidognathus calidictyotus* Bartsch & Rybakova 2015: 178–182, figs 1–6, 7–15, 16–18 (females, males, protonymphs).

Characters Length of females 397–440 µm, of males 394–440 µm; length:width ratio of holotype male 1.9:1. Dorsal plates distinctly, ventral plates faintly reticulate; raised porose areolae with rosette pores. Antero- and posterodorsal plate with raised porose areolae. Anterodorsal plate with a median rectangular area, posterodorsal plate with a pair of short costae. Ocular plates without corneae or eye pigment. First pair of gland pores situated close together in anterior margin of areola on anterodorsal plate; first pair of dorsal setae distinctly removed from gland pores and in posterior half of plate. Ventral plates with demarcated porose areolae. Male genitoanal plate with 28–30 perigenital setae. Length:width of gnathosoma 1.6:1, length ratio gnathosoma:idiosoma 0.3:1. Rostrum in ventral aspect triangular; tip of rostrum extending to level of setae of second palpal segments. Legs rather slender, shorter than idiosoma. Length ratio leg I:idiosoma 0.7:1. Tarsi III and IV with four and three dorsal setae, respectively. Pectines on paired claws with delicate tines.

Remarks With characters such as first pair of gland pores rather close together near the anterior margin of anterodorsal plate, distanced from first pair of setae which is in the posterior half of the plate, ventral plates and gnathosoma with demarcated porose areolae, and legs slender *C. calidictyotus* resembles species of the *hartmanni* group (Bartsch & Rybakova 2015).

Collecting and habitat data Atlantic Ocean, Mid-Atlantic Ridge, Lost City, a cold water hydrothermal field. Samples with *Copidognathus calidictyotus* are from 30°N, 42°W, 736–847 m depth. It was the most abundant species amongst the halacarids collected in this area. The surface of the carbonate rocks is rich in crevices and interstitia. Parts which are in contact with hydrothermal fluids are colonized by Archaea and Eubacteria. Crevices and interstitia in and on the rocks harbour a rich meio- and macrofauna. Beside halacarid mites, arthropods were represented by ostracods, harpacticoids, amphipods, stomatopods, and decapods (Bartsch & Rybakova 2015).

Copidognathus corneatus Newell, 1971

References *Copidognathus corneatus* Newell 1971: 23, 24, figs 48–51, 138–143 (females, males protonymphs); Newell 1984: 146–148, figs 350–354.

Characters Length of females 305–331 µm, of males 305–313 µm; length:width ratio 1.7-2.0:1. Dorsal plates foveate, raised porose areolae with rosette pores. Anterior margin of anterodorsal plate arched; plate with lambda-shaped porose areola. Ocular plates with corneae, between these an area with rosette pores; posterior part of plates caudiform. Costae of

posterodorsal plate narrow, with rosette pores. Male genital plate with 13–15 pairs of perigenital setae around genital opening and a papilla between genital and anal opening. Each genital sclerite with three setae. Gnathosoma with triangular tectum. Ratio length:width of gnathosoma almost 1.7:1, length ratio gnathosoma:idiosoma 0.3:1. Rostrum close to reaching to end of second palpal segment. Length leg I:idiosoma 0.8:1. Telofemur I longitudinally panelled, each panel reticulated. Tarsi III and IV with four and three dorsal setae, respectively. Pectines on claws of these tarsi with delicate tines.

Remarks *Copidognathus corneatus* is a member of the *oculatus* group (cf. Bartsch 1977a), a group which is characterized by: males with postgenital papilla and no more than three pairs of subgenital setae; in female and male the anterodorsal plate with transverse or slightly lambda shaped porose areola, the posterior part of ocular plates caudiform, the posterodorsal plate with pair of costae. Species of the *oculatus* group are spread worldwide, from tidal to deep-sea zones, from cold- to warm temperate areas of the northern as well as southern hemisphere. In the halacarid fauna they seem to play numerically a greater role in the south than in the north (Bartsch 1977a, 1993, 1999b).

Collecting data South-eastern Pacific Ocean. Extracted from a sample taken on the upper slope area, 33°S, 72°W, from 485 m depth (Newell 1971).

Copidognathus curiosus Bartsch, 1982

References *Copidognathus curiosus* Bartsch 1982d: 444–446, figs 31–41 (female).

Characters Length of female 339 µm, ratio length:width 1.3:1. Anterodorsal plate with minute frontal spine. Dorsal plates with dome-like areolae with deep pores, area outside domes foveate/reticulate. Ocular plates without corneae. Posterodorsal plate with three pairs of small dome-like areolae; posterior pair situated on tube-like projections. All ventral plates fused to a ventral shield; this and gnathosoma may also be partly fused. Length of gnathosoma only slightly more than its width. Length ratio of part representing gnathosoma and idiosoma 0.2:1. Gnathosomal base with large pharyngeal plate. Rostrum very short. Tectum truncate, lamelliform. Legs slender; leg I almost as long as idiosoma (length ratio 0.9-1.0:1). Tarsi I and II with very long solenidia. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws of all tarsi slender, each claw with delicate accessory process. Pectines on claws of tarsi II to IV with delicate tines.

Remarks This is one of the very few deep-sea species with a ventral shield due to fusion of all ventral plates. Another one is *Copidognathus inusitatus* Bartsch, 1989, collected off Lifou, New Caledonia (Bartsch 1989b). In both, the ventral shield and gnathosoma may be fused. In addition to these, the author once received a photo with a general aspect of a halacarid in which, at least partly, ventral shield and gnathosoma seemed to be fused. That mite had been collected on the Condor Seamount, Azores, coll. Daniela Zepilli.

Collecting data Indian Ocean, off Mozambique, from 13°S, 45°E, 755–770 m (Bartsch 1982d).

Copidognathus dentatus Viets, 1940

References *Copidognathus dentatus* Viets 1940: 34–37, figs 52–56 I, II, III, IV, 57 (female, male); Green & MacQuitty 1987: 80, 81, fig. 29: A-E; Durucan 2019: 191, 193, fig. 3A-G (females, male).

Characters Length of females 360–435 µm, of males 387–410 µm. Length:width ratio 1.4-1.6:1. Dorsal plates panelled and with porose areolae; the latter with modified rosette pores, namely with foveae and numerous canaliculi. Anterodorsal plate with three such porose areolae, two posterior ones crescent-shaped. Posterodorsal plate with two pairs of costae, lateral ones very narrow. Ocular plates with corneae and eye pigment. Marginal parts of ventral plates with demarcated porose areolae. Length ratio gnathosoma:idiosoma 0.3:1; length:width ratio of idiosoma 1.7-1.8:1. Rostrum extending beyond tip of second palpal segment. Length of leg I 0.7 times the idiosoma. Both tibia I and II ventrally with two spiniform ventral lamellae. Tarsi III and IV with four and three dorsal setae, respectively. Pectines of claws on tarsi II to IV with distinct tines.

Remarks *Copidognathus dentatus* can be distinguished from the other Mediterranean and North Sea species on the basis of its two spiniform ventral lamellae on tibia I and II.

Collecting and habitat data Mediterranean, Adriatic Sea (Croatia), Levantine Sea (Turkey), and off Libya (Viets 1940; Durucan 2019; Bartsch 1988a). North-eastern Atlantic Ocean, The Netherlands and Great Britain (England) (Green & MacQuitty 1987; Bartsch & Smit 2006). The records from the North-eastern Atlantic, as also those from the Mediterranean, are from shallow water (0.1-3 m depth), from sediment and mats of green algae *(Cladophora, Enteromorpha)* and brown algae *(Padina)* rich in debris whereas the one, from off Libya (34°N, 15°E) is from 500–509 m depth. It was in a sample taken during a cruise of ATLANTIS II (Bartsch 1988a). Because of its corneae and eye pigment, *C. dentatus* is expected not to be a deep-sea species but accidentally became a part of the sample from 500–509 m depth.

Copidognathus flabelliferus Bartsch, 2011

References *Copidognathus flabelliferus* Bartsch 2011a: 98–103, figs 1–8, 9–14 (females, males, protonymph, larva).

Characters Length of females 460–540 µm, of males 475–500 µm, length:width ratio about 1.6-1.7:1. Dorsal plates reticulate and with demarcated porose areolae, the latter with rosette pores. Striated integument anastomosing, connecting bars raised. Anterodorsal plate with two porose areolae, one in middle of anterior margin, one, by fusion of a pair, in middle of plate. Each ocular plate with porose areola; corneae or eye pigment lacking. Posterodorsal plate with four costae, two on either side anteriorly almost fused. Major part of ventral plates punctate. Male genitoanal plate with 19–20 perigenital setae. Anal valves lamelliform, extending beyond anal sclerites. Length of gnathosoma 0.3 times of that of idiosoma. Length:width ratio of gnathosoma 1.8:1; tectum very short, semi-circular. Rostrum reaching almost to end of second palpal segment. Lateral flank of telofemur I with epicuticular droplets arranged in polygons, ventral margin of that segment delicately serrate. Length ratio leg I:idiosoma 0.7:1. Tarsi III and IV with four and three dorsal setae. Paired claws with pectines.

Remarks *Copidognathus flabelliferus* comes in its general aspect close to *C. papillatus* and *C. nautilei.* These species are known to live in or nearby chemotrophic communities.

Collecting and habitat data Gulf of Mexico, 26–27°N, 88–94°W, from gas seeps in 2190–2745 m depth (Bartsch 2011a). The halacarids are from samples taken with mussel pots which beside muddy sediment held a rich fauna with, e.g., sea urchins (*Sarsiaster* sp.), tubeworms and bivalves *(Bathymodiolus).*

Copidognathus inusitatus Bartsch, 1989

References *Copidognathus inusitatus* Bartsch 1989b: 466–468, figs 61–68 (male).

Characters Length of male 458 µm; length:width ratio 1.3:1. Idiosoma wide, ending with prolonged anal cone. Anterodorsal and posterodorsal plate large, surface reticulate. Posterior gland pores on posterodorsal plate on pair of domes. All ventral plates fused. Area corresponding to genital plate with five pairs of perigenital setae. Gnathosoma and ventral shield may be fused. Ratio length of part corresponding to gnathosoma to that of idiosoma 0.2:1. Rostrum short, hardly reaching to middle of second palpal segment. Right and left half of gnathosomal base with five and six maxillary setae. Scale-like tectum with serrate margin. Legs very slender, much longer than idiosoma; length ratio leg I:idiosoma 1.2:1. Genu and tibia IV with unusual long dorsal setae. Tarsi III and IV with four dorsal setae. Paired claws long and slender; no pectines seen.

Remarks *Copidognathus inusitatus,* just as the above mentioned *C. curiosus,* has the ventral plates fused and both species have a rostrum which is shorter than the gnathosomal base.

Collecting and habitat data South-western Pacific Ocean, off Lifou, 21°S, 167°E; sandy deposits extracted from of a slope area in 1508 m depth (Bartsch 1989b).

Copidognathus magniporus Bartsch, 1973

References *Copidognathus magniporus* Bartsch 1973a: 54, 55, figs 22–31 (female, male, protonymph, larva); unpublished material of cruise R.V. Meteor, Great Meteor Seamount, 29°54'N, 28°22'W, 332 m depth (females, males).

Characters Length of females 265–316 µm, of males 275–301 µm. Length:width ratio of idiosoma 2.1:1. Dorsal and ventral plates coarsely reticulated, each polygon with about 50 small pores. Posterior part of ocular plates tail-like; plates without corneae and eye pigment. Posterodorsal plate with two pairs of gland pores, each one connected with an internal gland. Anterior pair of internal glands spherical, about 20 µm in diameter, posterior pair oblong, length:width about 30:15 µm. Male genitoanal plate with 30 perigenital setae. Length ratio gnathosoma:idiosoma 0.3:1; length:width ratio of gnathosoma 1.7:1. Rostrum extending just beyond second palpal segment. Telofemora of legs panelled. Length of leg I 0.8 times that of idiosoma. Paired claws with accessory process; claws on tarsus I with few minute tines, those on tarsi II to IV with more and larger tines. Both tarsus III and IV with four dorsal setae.

Remarks In general aspect resembling *Copidognathus meridianus* Bartsch, 2003 (in Bartsch 2003b) but in *C. magniporus* the positions of gland pores on the dorsal plates are different (in

relation to setae) as also the number and arrangements of setae on the legs. *Copidognathus meridianus* has been extracted from sandy, shallow water deposits on the coast of north-western Australia (Bartsch 2003b).

Collecting and habitat data North-eastern Atlantic Ocean, Great Meteor Seamount, 30°N, 28–29°W, 302–488 m depth (Bartsch 1973a, and unpublished records from the Great Meteor Seamount, R. V. Meteor, Cruise 42/3, 332 m). Extracted from the upper sediment layer.

Copidognathus nautilei Bartsch, 1997

References *Copidognathus nautilei* Bartsch 1997a: 30–33, figs 1–8, 9–20 (females, males, protonymph, larva); Bartsch & Dovgal 2019: 197.

Characters Length of females 395–475 µm, length:width ratio 1.6:1. Length of males 421–452 µm. Porose areolae on dorsal plates with foveae which in turn are surrounded by canaliculi, remainder of plates reticulated. Integument between plates striated, striae with slightly raised connective bars. Short anterior lamella of anterodorsal plate irregularly dentate; plate with small porose areolae in anterior part and a larger, transverse areola in middle part. Posterodorsal plate with two pairs of porose costae, the median ones about two foveae wide, the marginal ones less obvious and shorter. Ocular plates without corneae. Anal valves slightly extending beyond anal sclerites. Ratio length of gnathosoma to idiosoma 0.3:1. Lateral parts of gnathosomal base coarsely foveate, adjacent an area with canaliculi. Triangular rostrum extending to end of second palpal segment. Legs shorter than idiosoma. Ratio length of leg I:idiosoma 0.8:1. Ventral margins of telofemora I and II delicately serrate. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws with delicate tines in their posterior part.

Remarks *Copidognathus nautilei* was extracted from hydrothermal vent areas and it shares characters with species collected near chemotrophic systems, namely *C. flabelliferus* and the below mentioned *C. papillatus*. These characters are: striated integument with connective bars, middle of anterodorsal plate with slightly transverse porose areola, ocular plates rather short, anal valves somewhat prolonged, and surface of telofemora I and II reticulated, the latter give the ventral margins a serrate aspect.

Collecting and habitat data Mid-Atlantic-Ridge, 15°N, 45°W, 3014–3050 m and 13°N, 45°W, 4087 m. From bivalves and sediment taken at the base of an active chimney (Bartsch 1997a; Bartsch & Dovgal 2010).

Copidognathus papillatus Krantz, 1982

References *Copidognathus papillatus* Krantz 1982: 1728–1731, figs 1–4, 5, 6 (females, protonymph); Bartsch 1991a: 790–792, figs 1–9 (females, males, protonymphs, larvae); Bartsch 2011a: 103, figs 21–23 (female).

Characters Length of females 395–453 µm, of males 395–428 µm; length:width ratio of female 1.6:1. Striated integument with raised, connective bars. Dorsal plates with foveate areas. Anterodorsal plate with one small anterior and a larger median area. Posterodorsal plate without distinctly demarcated costae and ocular plates without distinct corneae. Prolonged anal valves surpassing anal sclerites. Length:width ratio of gnathosoma 2.0:1, length ratio gna-

thosoma:idiosoma 0.3:1. Rostrum extending to end of third palpal segment. Leg I slightly shorter than idiosoma. Ventral margin of telofemur I dentate. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws with accessory process and pectines.

Remarks Striking characters of this species are: striated integument squamose due to raised connective bars; anal valves prolonged, surpassing the anal sclerites; ventral margins of telofemora I dentate. This combination of characters is also present in *C. flabelliferus* and *C. nautilei.*

Collecting and habitat data Pacific Ocean, Galapagos Rift, 1°N, 86°W, 2482 m depth. Extracted from a sample with mussels growing on the walls of a hydrothermal vent (Krantz 1982). Further records are from the Falu Fa Ridge, Lau Basin, 23°S, 177°W, 1914 m, North Fiji Basin, White Lady, 19°S, 173° W, 2750 m, East Pacific Ridge, 13°N, 104°W, 2630 m, Gorda Ridge, 43°N, 127°W, 2701 m, Juan Fuca Ridge 45°N, 130°W and 48°N, 129°W, 2220 m (Tsurumi & Tunnicliffe 2001; Kelly et al. 2007; Bartsch 2011a). A record from the Kuril-Kamchatka Trench, 40°N, 147°E, 5217–5229 m (Schwabe et al. 2015) is expected to be one of *Copidognathus papillatus.*

Copidognathus posticus Newell, 1971

References *Copidognathus posticus* Newell 1971: 22, 23, figs 34–47, 137 (females, males, protonymph, larva).

Characters Length of females 357–383 µm, of males 339–374 µm; length:width ratio 1.2-1.5:1. Dorsal plates with slightly raised areolae or costae with rosette pores, the latter with wide ostia. Anterodorsal plate wider than long; plate with middle pair of areolae closer to anterior than to posterior margin, pair of areolae distanced. Ocular plates short; neither cauda nor corneae present. Pair of gland pores in striated integument, not as usual on lateral margin of ocular plate. Posterodorsal plate with single pair of costae. Male with 13–17 perigenital setae on each side. Length:width ratio of gnathosoma 1.5-1.7:1. Rostrum close to reaching to end of second palpal segment. Legs slender. Leg I about 0.95 times the length of idiosoma. Surface of telofemur I with large elongate panels. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws on tarsi II to IV with pectines.

Remarks *Copidognathus* species in general have a gland pore on each ocular plate, in *C. posticus* this gland pore is in the striated integument adjacent to the ocular plate.

Collecting data South Pacific, Chilean slope, 33°S, 72°W, 485 m depth. Further records are from an abyssal area off Peru, 18°S, 79°W, 3200 m depth (Newell 1971). The type locality given in Newell (1984: 197) may refer to that of *C. coalescens* Newell, 1984).

Copidognathus procerus Bartsch, 2002

References *Copidognathus procerus* Bartsch 2002a: 77–80, figs 15–20, 21–26 (female, males).

Characters Length of female 250 µm, of males 252–261 µm; length:width ratio 2.3-2.4:1. Dorsal plates panelled and with porose areolae, the latter not raised but recognizable because of change in structure of surface, namely presence of numerous canaliculi. Anterodorsal plate remarkably wide in its posterior part, still plate slightly longer than wide; single

porose areola arched. Posterodorsal plate with pair of costae. Ocular plates with corneae; plates elongate, caudiform. Genitoanal plate posterolaterally with elongate porose areolae. Length:width ratio of gnathosoma 1.5:1, length ratio gnathosoma:idiosoma 0.2:1. Tectum triangular. Rostrum almost reaching to end of second palpal segment. Length of leg I equal to 0.6 times the length of idiosoma. Tarsus III with four, tarsus IV with three dorsal setae. Paired claws with accessory process and few delicate tines.

Remarks *Copidognathus procerus* can be distinguished from other species by the combination of characters: idiosoma very slender; dorsal plates panelled and punctate but without rosette pores; posterior part of anterodorsal plate wide; ocular plates narrow, long, caudiform.

Collecting and habitat data North Atlantic Ocean, Great Meteor Seamount, 30°N, 28°W, extracted from 511 m depth. In a sample taken with an epibenthic sledge (Bartsch 2002a).

Copidognathus richardi (Trouessart, 1902)

References *Halacarus (Copidognathus) richardi* Trouessart 1902: 69, 70.

Copidognathus richardi, Bartsch 1983: 285–288, figs 1–5, 6–9 (male); Bartsch 1991b: 1347–1348, figs 16, 17 (female, male).

Characters Length of adults 550–570 µm, of a male 558 µm; length:width ratio 1.4:1. Idiosoma and legs densely covered with filaments. Dorsal plates with raised areolae; surface of areolae with modified rosette pores, namely with foveae including numerous canaliculi. Anterodorsal plate with small anterior areola and a dumb-bell shaped one in middle of plate. Each ocular plate with two distinct corneae. Posterodorsal plate with two pairs of costae. Male genitoanal plate with 47 perigenital setae, arranged in two rows. Gnathosoma 1.6 times longer than wide; length ratio gnathosoma:idiosoma 0.3:1. Rostrum at its base convergent, towards its tip almost parallel sided. Rostrum extending to end of second palpal segment. Males with two pairs of maxillary setae on gnathosomal base and a third pair of setae in basal part of rostrum. Length ratio leg I:idiosoma 0.8:1. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws with pectines, each claw with numerous tines.

Remarks *Copidognathus richardi* is very similar to *C. granulatus* (Hodge, 1863) as described by Green & MacQuitty (1987). A few differences between the two species are mentioned in Bartsch (1983) though *C. richardi* may also turn out to be a junior synonym of *C. granulatus.* Studies on new material from the former collecting areas are needed.

Collecting data North Atlantic, off Svalbard (near Hopen Island, 76°N, 25°E, 48 m, north of Svalbard, 80°N, 10°E, 430 m and the Azores, from 599 m depth (Trouessart 1902).

Copidognathus triton Newell, 1971

References *Copidognathus triton* Newell 1971: 25, 26, figs 55, 56, 150–158 (females, males, protonymph, larva); Newell 1984: 197 (female).

Characters Length of females 400–435 µm, of males 400–452 µm. Length:width 1.7–1.9:1. Dorsal plates foveate to panelled and with porose areolae, the latter with rosette pores. In middle of anterior dorsal plate pair of ovate areolae completely fused. Pair of raised marginal are-

olae separated and extending beyond plate. Ocular plates with short cauda; corneae feebly developed. Posterior dorsal plate with two pairs of porose costae. Gnathosoma about 1.6–1.7 times longer than wide; its tectum rather long, triangular; rostrum not reaching to end of second palpal segment. Legs slender, length ratio leg I:idiosoma 0.8:1. Tarsi III and IV with four and three dorsal setae. Tines on paired claws of tarsi II to IV feebly developed.

Remarks Characters which separate *Copidognathus triton* from the other *Copidognathus* species known from the coast of Peru and Chile are the shape and arrangement of porose areolae and the costae on the dorsal plates. The anterodorsal plate has a rather large median areola (equal to two completely fused areolae) and a pair of large dome-like areolae, the posterodorsal plate has a second pair of costae along the lateral margins.

Collecting data Eastern Pacific Ocean, 13S, 77° W, from 550 and 570 m depth (Newell 1971).

Copidognathus tritoni Bartsch, 2013

References *Copidognathus tritoni* Bartsch 2013b: 240–244, figs 1–8, 9–15, 16–19 (females, male, protonymph).

Characters Length of females 395–450 µm, of male 410 µm, length:width ratio in female 1.4:1; in male 1.6:1. Surface of dorsal plates reticulate; within raised areas reticulation distinct, else plates with delicate porosity. Raised transverse area on anterodorsal plate in middle of plate. Posterodorsal plate with two pairs of costae. Ventral parts of ventral plates uniformly panelled, marginal parts reticulate. Male genitoanal plate with 17 pairs of perigenital setae. Length:width ratio of gnathosoma 1.5:1, length ratio gnathosoma:idiosoma 0.3:1. Rostrum reaching almost to the level of seta on second palpal segment. Length ratio leg I:idiosoma 0.8:1. Telofemora panelled; walls of these polygons with tubercles. Tips of tubercles ending in short filaments. Length:height ratio of telofemur I 2.5-2.6:1. Tarsi III and IV with four and three dorsal setae, respectively. Pectines of paired claws on tarsi II to IV with numerous small tines.

Remarks *Copidognathus tritoni* shares characters with the hydrothermal vent halacarids *C. papillatus* and *C. nautilei* and the cold seep mite *C. flabelliferus*. The first mentioned species seems to be wide-spread in the Pacific Ocean (in case the one or other record does not turn out to be a separate species), *C. nautilei* is known from the Mid-Atlantic Ridge, *C. flabelliferus* lives amongst the fauna in gas seep areas in the Gulf of Mexico. Characters the three species share are: anterodorsal plate with a transverse porose areola; ocular plates short, with rounded corners; rostrum slender, not extending beyond the end of second palpal segment; telofemora prominently panelled; both ventral setae on tibia IV smooth. Differences between the three species are in the ornamentation of the plates and the striated integument, position of dorsal setae, and shape and size of the anal cone (Bartsch 2013b).

Collecting and habitat data Pacific Ocean, East Pacific Rise, 10° N, 104° W, 2500–2542 m depth. Found within kitchen sponges which had been exposed for a few weeks till more than two years near the periphery of vent communities (Bartsch 2013b).

Copidognathus trouessarti (Voinov, 1896)

References *Halacarus trouessarti* Voinov 1896: 128, 129, figs 1, 2 (female); Voinov 1897: 94, 95, figs 1 and 2.

Copidognathus trouessarti, Bartsch 1991b: 1345, 1446, figs 8–15 (females, males).

Non *Copidognathus tricorneatus* Bartsch 1973b, 38, 39, figs 1, 2 (females, male); Bartsch 1973a, 53, 54, figs 1–7 (larva); Bartsch 1979a, 217–219, figs 1–7 (females, males).

Characters Idiosomal length of females 322–435 µm, of males 327–396 µm; length:width 1.6:1. Dorsal plates reticulated. First pair of gland pores situated rather close together near anterior margin but first pair of dorsal setae near posterior margin of anterodorsal plate. Ocular plates slender, each one with two corneae. Posterior cornea divided. Posterodorsal plate with two pairs of narrow costae. Plate of female distinctly slenderer than that of male. Ventral plates with demarcated porose areolae. Female genitoanal plate triangular to lingual shaped, that of male much wider, its anterior margin almost truncate. Male with 28–37 perigenital setae arranged in a ring around genital opening. Length:width ratio of gnathosoma 1.8-1.9:1. Length ratio gnathosoma:idiosoma 0.3:1. Rostrum slender, posterior part almost parallel-sided. Tip of rostrum extending just beyond third palpal segment. Legs slender; leg I slightly longer than idiosoma (1.0-1.1:1). Each one of tarsus III and IV with four dorsal setae. Paired claws with accessory process, their pectines with delicate tines.

Remarks *Copidognathus trouessarti* belongs to a natural group called *tricorneatus* group (cf. Bartsch 2013c). *Copidognathus trouessarti* is characterized by its long and slender almost parallel-sided rostrum and four setae on both tarsus III and IV. Most likely primarily with epizoic way of life.

Collecting and habitat data North-eastern Atlantic, Great Meteor Seamount and Josephine Bank, 30°N, 28–29°W and 37°N, 14°W, 311–511 m depth (Bartsch 1973a, b); Tenerife, Spain, 300 m (unpublished record, deposited in Zoologisch Museum Amsterdam); Mediterranean, Italy, Gulf of Naples, 1–2 m depth (Voinov 1896); French coast of English Channel (Bartsch 1979a). Extracted from colonies of hydrozoans, bryozoans, barnacles, and red algae.

Copidognathus uniareolatus Newell, 1971

References *Copidognathus uniareolatus* Newell 1971: 20–21, figs 30–33, 133–136 (male); Newell 1984: 138 (male).

Characters Length of male idiosoma 418 µm. Length:width 1.5:1. Single transverse porose areola with rosette pores on anterior dorsal plate. Ocular plates wide; corneae lacking. Costae on posterodorsal plate with rosette pores. Male genitoanal plate with 12–13 perigenital setae in each half. Anal cone rather long. Length:width of gnathosoma 1.8:1; length ratio gnathosona:idiosoma 0.3:1. Rostrum extending beyond basal 2/3rd of second palpal segment. Tectum bluntly rounded. Palps long, slender; length of slender second papal segment about 0.55 of that of gnathosoma. Legs slender. Telofemur I with rectangular panels. Tarsi III and IV with four and three dorsal setae, respectively. Pectines hardly visible.

Remarks *Copidognathus uniareolatus* has a rather wide idiosoma whereas its legs are slender.

Collecting and habitat data: The holotype male has been extracted from a slope area in 550–600 m depth, South Pacific Ocean, 26°S, 80°W. A larva with long and slender palps which may be referable to *C. uniareolatus,* has been taken at 1565 m depth (Newell 1971).

Halacarellus auzendei (Bartsch, 1990)

References: *Agauopsis auzendei* Bartsch 1990b: 70–73, fig. 1A-K (female, deutonymph).
Halacarellus auzendei, Bartsch 1994a: 480–482, figs 1–3, 4 (females, males, deuto-, protonymphs).

Characters: Length of females 562–675 µm; length:width ratio 1.6:1. Length of males 502–560 µm. Surface of dorsal plates reticulate; striated integument with minute epicuticular spikes. Corneae lacking. Posterodorsal plate with pair of narrow costae. Female genitoanal plate with two pairs of perigenital setae. Length of gnathosoma equal to 0.3 times length of idiosoma. Gnathosoma slender, length 1.7 times the width; rostrum reaching to end of second palpal segment. Length of leg I 0.8 times that of idiosoma. Leg I somewhat wider that the other legs and on ventral flank bearing long, bluntly ending spines. Telofemur, genu, tibia, and tarsus I with 5, 2, 5, 1 such spines, respectively. Following legs with setae but no spines. Pectines on claws II to IV with distinct tines.

Remarks: Leg I is wider than the following legs and has long, bluntly ending setae. These characters are shared with shallow water inhabitants of the *H. subterraneus* group. Long, bluntly ending setae are also present in the deep sea inhabiting *H. bandyi* (Newell, 1984).

Collecting and habitat data: Atlantic Ocean, Mid-Atlantic-Ridge, 23°N, 45°W, 3478 m. From sediment taken at the base of an active chimney (Bartsch 1990b, 1994a) and 37°N, 32°W, 1700 m (Cuvelier et al. 2014). Several mites were infested by the suctorian *Corynophrya* sp. (Bartsch & Dovgal 2010). Most of the *Halacarellus auzendei* individuals had a fouling on the setae of the legs, namely tufts of filaments or small encrustings, the latter fixed to the setae like beads on a string (Bartsch 1994a).

Halacarellus bandyi (Newell, 1967)

References: *Thalassarachna bandyi* Newell 1967: 696–701, figs 1–17 (female, deutonymph); Newell 1984: 117.
Halacarellus bandyi, Bartsch 1988b (812, 816).

Characters: Length of female idiosoma 648 µm; length:width ratio 1.4:1. Dorsum and venter dominated by wide areas with striated integument. Dorsal and ventral plates present though reduced in size. Anterior dorsal plate and epimeral plates broadly fused. Ocular plates small; corneae absent. Anterior epimeral plate with four pairs of setae. Female genitoanal plate posteriad extending beyond anal cone; plate with five pairs of setae. Basis of gnathosoma and rostrum hirsute. Gnathosoma short, length:width ratio 1.8:1 and length ratio gnathosoma:idiosoma 0.25:1. Palps long and slender but rostrum short, hardly reaching to middle of second palpal segment. Legs slender, leg I 1.6 times, leg IV 1.9 times longer than idiosoma, respectively. All legs arising from protuberances. Several of the legs' setae stiff, spike-like. Paired claws with very delicate tines.

Remarks The species is characterized by its large genital plate, in mounted specimens protruding beyond the anal cone, and the very long legs, all longer than the idiosoma and bearing stiff setae. The generic position is uncertain (Bartsch 1988b, 1997b), most likely close to *Halacarellus.*

Collecting and habitat data South-eastern Pacific Ocean, 29°S, 80°W, 3680–4100 m, samples taken with a dredge from a bottom with red clay, volcanic ash and manganese nodules (Newell 1967).

Halacarellus decipiens (Newell, 1984)

References *Thalassarachna decipiens* Newell 1984: 96–98, figs 228–232 (females, males, deutonymph).
Halacarellus decipiens, Bartsch 1986b: 559; Bartsch 1990a: 204–206, figs 94–98 (females, males).

Characters Idiosomal length of females 770–800 µm, of males 699–810 µm. Length:width ratio 1.5:1. Surface of plates with canaliculi but no panels. Anterodorsal plate with minute frontal spine. Each ocular plate with two gland pores; corneae absent. Posterodorsal plate with pair of narrow costae. Posterior epimeral plates each with three dorsal and three ventral setae. Gnathosoma slender; its length 2.4 times the width. Length of gnathosoma 0.3 times of that of idiosoma. One pair of maxillary setae on gnathosomal base, a second, very short pair in distal third of rostrum. Rostrum parallel-sided, reaching to end of third palpal segment. Legs slender; leg I as long as idiosoma (1.0:1). Tarsus I with high number of paired ventral setae. Claws with delicate tines.

Remarks *Halacarellus decipiens* is related to the southern ocean species *H. eltanini* Newell, 1984 and *H. vajetus* (Bartsch, 1974) (in Bartsch 1974a). Characters they share are: anterior margin of anterodorsal plate with minute frontal spine (versus arched or truncate); posterodorsal plate with pair of narrow costae (versus one or two pairs of rather wide and generally porose costae; rostrum long, parallel-sided and basal pair of maxillary setae on gnathosomal base, much shorter apical pair of setae in posterior fifth of rostrum, versus gnathosoma triangular and no such distance and difference in length between basal and apical maxillary setae (Bartsch 1990a, 2021b).

Collecting data Macquarie Rise, 54–55°S, 158–159° E, 79–549 m; 51°S, 162°E, at 415 m. Near Antipodes Island 50°S, 179°E, at 103 m (Newell 1984).

Halacarellus epimeralis (Newell, 1984)

References *Thalassarachna epimeralis* Newell 1984: 108, 111–113, fig. 273 (deutonymph); Bartsch 1997b: 1230.
Bathyhalacarus epimeralis, Bartsch 1988b: 815.
Halacarellus epimeralis, Bartsch 2009: 84.

Characters Length of deutonymph 557 µm. Ocular plates elongate, corneae lacking; each plate with two gland pores near posterior margin. Posterior epimeral plate with two dorsal and three ventral setae. Claws of tarsus III with delicate tines.

Remarks The information to this species is sparse and relies on a deutonymph. The deutonymph has two dorsal setae on the posterior epimeral plate; we can expect the adults to have

three dorsal setae on each plate. The ocular plates are elongate and each plate has two gland pores near the posterior margin. In adults the number and arrangement of the pores will be similar. There is no information to the position of the apical pair of maxillary setae (tritorostrals according to Newell 1984). As long as no adult instar has been found, any close relationship to the one or other genus cannot be proven. Bartsch (1988b) mentioned the species as *Bathyhalacarus epimeralis* but later, in Bartsch (1997b), it was listed as *Thalassarachna,* in order to keep stability in the nomenclature. The most easily recognized character of adult *Thalassarachna* is the increased number of dorsal setae on the tarsi I and II of adults, but no adult *epimeralis* is available. *Thalassarachna* species may have up to four pairs of gland pores, one on the anterodorsal plate, one in the striated integument in a more or less marginal position, one on each ocular plate and one near the posterior margin of the posterodorsal plate. None of the presently described species has two gland pores per ocular plate. In the genus *Halacarellus,* species with one as well as two gland pores on the ocular plates are known. Moreover, a few *Halacarellus* species have an increased number of dorsal setae on the posterior epimeral plates. The species *epimeralis* Newell, 1984 does not contradict the character combination of *Halacarellus.* New material and other diagnostic techniques may bring light into the species taxonomic position.

Collecting data South-eastern Pacific Ocean, 46°S, 84°W, found in a sample from 742 m depth (Newell 1984)

Halacarus actenos Trouessart, 1889

References *Halacarus actenos* Trouessart 1889: 239, 240 (female); Lohmann 1893: 83, 84, pl. 10, figs 1, 2 (female, male); Trouessart & Neumann 1894: 146, 147, 156, pl. 10, fig. 2a, a', a'' (female); Trouessart & Neumann 1896: 340, 341; André 1946: 60–62, figs 28–30 (female); Newell 1947: 82, 87, figs 94–102 (female, male, deutonymph); Bartsch 1980: 38, 39, figs 2–15 (females, males, deuto-, protonymphs, larvae); Green & MacQuitty 1987: 110, 111, fig. 44A–C; Pepato 2010: 17, 157, 158, 165, 180, figs 23, 24; Bartsch 2011b: 24–27 (females, males); Durucan et al. 2018: 85–88 (male, deutonymph).

Characters Length of females and males from the eastern Atlantic 785–870 µm and 555–670 µm, respectively, from the western Atlantic (according to Newell 1947) 519 µm (female) and 422 µm (male). Length:width ratio 1.5-1.8:1. Dorsum dominated by areas with striated integument. Idiosoma, gnathosoma and legs with delicately reticulate epicuticula. Anterodorsal plate with medium-sized triangular frontal spine; posterior part of plate slender, triangular. Ocular plate present but hardly visible; plate dominated by cornea. Posterodorsal plate absent. Female genitoanal plate with rather uniform cerotegumental cover, not divided into right and left half; genitoanal plate with one to two perigenital setae on either side of genital opening and one pair of outlying setae in striated integument anterior to plate. Males with about 68–83 perigenital setae. Length of gnathosoma about twice its width (2.0:1), length ratio gnathosoma:idiosoma 0.3:1. Rostrum reaching to end of second palpal segment. Length of leg I similar to that of idiosoma. Telofemur, genu and tibia I with 2, 2, 4 smooth, rather slender spines. Males with plumose parambulacral

setae. Tarsi III and IV with 4/2 and 3/2 dorsal/ventral setae, respectively. Paired claws of tarsi I–IV with accessory processes.

Remarks *Halacarus actenos* has given name to a group of *Halacarus* species which are characterized by absence of a posterodorsal plate in both female and male, small or reduced ocular plates, uniformly structured female genitoanal plate, 1–2 pairs of perigenital setae on either side of genital opening and a pair of outlying setae in the striated integument. This combination is shared with 22 *Halacarus* species of the *H. actenos* group (Bartsch 2011b; Pepato & Da Silveira 2013). Three species of this group have records from the deep-sea (according to the definition of a depth of almost 500 m or more).

Collecting data Records are from the Mediterranean and North Atlantic Ocean, from Spain (García-Gómez et al 2022), from the eastern part of the Atlantic Ocean from the Cape Verde Islands (Cabo Verde), Canary Islands, Tenerife (Spain) to Ireland (Republic of Ireland) (Viets 1956; Green & MacQuitty 1987; Somerfield 1991; Durucan et al. 2018, 2023), and the western North Atlantic, from Florida (United States of America) (Newell 1947). Since the specimens from Florida are somewhat smaller than the eastern Atlantic ones and differences in the faunas of the eastern and western North Atlantic are known (Bartsch 1982e, 1989c, 2004a, 2009) a careful examination and comparison of individuals of both areas, the eastern and western part of the Atlantic, is recommended.

Most records of *H. actenos* are from shallow water areas (inter- and subtidal), Trouessart & Neumann (1896: 340) added a record of a female from 400–500 m depth but mentioned that the record is outside the depth else typical for this species. *Halacarus actenos* may have to be removed from the list of deep-sea species.

Halacarus arnaudi Newell, 1984

References *Halacarus arnaudi* Newell 1984: 43, 44, figs 64–68 (females, males, protonymphs); Bartsch 1993: 25–27, figs 2A-E, 3A, B (female, male); Bartsch 2016b: 140, fig. 3A (females, males).

Characters Length of female 640 µm, length:width ratio 1.9:1, length of male 550–600 µm. Epicuticula on dorsal plates with maze-like structure. Frontal spine apically rapidly converging and turned upward. Posterior part of anterodorsal plate triangular, its margin semi-circular. Ocular plates present, small, with cornea. Posterodorsal plate in females slender, its narrow triangular tip levelling with pair of gland pores IV. In male this plate longer and wider, just extending beyond fifth pair of dorsal setae and enclosing pair of gland pores IV. Female genitoanal plate evenly structured; anterior margin almost truncate; one pair of perigenital setae on genitoanal plate and one pair in striated integument. Male genitoanal plate oviform; one pair of perigenital setae near anterior margin of plate, 30–34 setae on each side of genital opening. Length of gnathosoma twice the width; length ratio gnathosoma:idiosoma 0.3:1. Ratio length of leg I:idiosoma 0.9:1. All ventral bristles on tibiae slender, tapering, none spiniform, none distinctly bipectinate. Tarsi III and IV with 3/0 dorsal/ventral setae.

Remarks In size and shape of the dorsal plates rather similar to *Halacarus nanus* Gimbel, 1919 and accordingly *H. arnaudi* may be a junior synonym of *H. nanus. Halacarus nanus* has been

collected near the Gauss-Station, Antarctica, 67°S, 89°E, an area in which one can expect to find *H. arnaudi.*

Collecting and habitat data: Off South Shetland Islands, 63°S, 56°W, 370 m and Terre Adélie, Point Géologie, 67°S, 140°E, shallow subtidal (Newell 1984); Wedell Sea (Halley Bay) 75°S, 30°W, 500 m (Bartsch 2016b). Extracted from holdfasts of kelp with Hydrozoa (Newell 1984).

Halacarus atlanticus Bartsch, 1981

References: *Halacarus atlanticus* Bartsch 1981a: 203, 204, figs 1–9, 10–17 (females, males, deuto-, protonymphs).

Characters: Length of females 430–500 µm, of males 388–453 µm; length:width ratio of a female 1.7-1.8:1. Anterodorsal plate with spatulate frontal spine, spine somewhat notched and anteriorly slightly wider than in basal part. Ocular plates and corneae absent. Gland pores III and IV situated on small platelets in striated integument. Posterior dorsal plate triangular, in female reaching just beyond the level of gland pores IV. In males that plate slightly larger. Female genitoanal plate rectangular but with rounded corners; plate with two pairs of perigenital setae on genital plate close to genital opening. Circular genitoanal plate of males with 63–76 perigenital setae scattered around genital opening. In addition, both females and males with one pair of outlying perigenital setae in striated integument. Length ratio idiosoma:gnathosoma 0.3:1; length:width ratio of gnathosoma about 2.1:1. Rostrum reaching to end of second palpal segment. Leg I 1.1 times longer than idiosoma; its segments wider than those of following legs. Telofemur to tibia I ventrally with 2, 2, 3 long, stout ventral spines and 0, 0, 1 setae. Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae, respectively. Paired claws on tarsi II to IV long, slender, smooth.

Remarks: The species is most similar to the South Pacific *Halacarus spathulifer* Newell, 1971. The differences between the two species are rather small and are summarized after the presentation of *H. spathulifer.*

Collecting data: *Halacarus atlanticus* was extracted from the Guyana Basin, 8°S, 54 W; from 508–523 m (Bartsch 1981a).

Halacarus dictyotus Bartsch, 1981

References: *Halacarus reticulatus* Bartsch 1981b: 40–44, figs 10–15, 16–19, 20, 21 (females, males); Bartsch 1982d: 435–437, figs 1–3 (males, deuto-, protonymphs, larva).
Halacarus dictyotus, Bartsch 1988c: 221.

Characters: Idiosomal length of female 475 and 675(?) µm, that of male 410–493 µm. Length:width ratio in holotype male 1.7:1. Frontal spine of anterodorsal plate slender, its length half that of the plate; posterior part of anterodorsal plate almost semi-circular. Ocular plates completely reduced, neither cornea nor eye pigment present. In males gland pores IV situated within posterodorsal plate, in female in striated integument. Female genitoanal plate with pair of reniform cerotegumental swellings and (two to) three pairs of perigenital setae. Males without such swelling; genital opening surrounded by 66–75 perigenital setae. Length:width ratio of gnathosoma 1.9:1, length ratio gnathosoma:idiosoma 0.3:1.

Rostrum longer than gnathosomal base. Leg I slightly longer than idiosoma. Telofemur, genu and tibia I with 2, 2, 4 smooth spines. Tarsi III and IV with 4/3 and 3/2 dorsal/ventral setae. Paired claws smooth.

Remarks This is one of the *Halacarus* species in which females as well as males have an antero- and posterodorsal plate but no ocular plates.

Collecting and habitat data Indian Ocean, north-eastern part of Mozambique Channel, close to Glorieuse Islands and Mayotte island, 11–13°S and 45–47°E. Records are from 250–620 m depth, from coarse, calcareous sediment (Bartsch 1981b, 1982d).

Halacarus echinatus Newell, 1984

References *Halacarus echinatus* Newell 1984: 50–52, figs 89–96 (female, male, deutonymph).
Halacarus sp. B Newell 1971: 8, figs 8 and 9 (deutonymph).

Characters Length of female idiosoma 861 µm, of male 696 µm; length:width ratio 2.1:1. Frontal spine almost reaching to tip of rostrum. Ocular plates small, each one including a cornea. Gland pores III in striated integument posterior to ocular plates. Posterodorsal plate absent in both female and male. Margins of female genitoanal plate with thick cerotegumental layer. Female with two short perigenital setae on either side of genital opening; male with about 100 setae close around genital opening. Both female and male with one pair of outlying perigenital setae in striated integument anterior to genitoanal plate. Length:width ratio of gnathosoma 2.4:1. Length ratio gnathosoma:idiosoma 0.3:1. Leg I almost as long as idiosoma. Tarsi III and IV with 4/1 and 3/1 dorsal/ventral setae. Paired claws long and slender, with minute accessory process but no pectines.

Remarks The species is characterized by its long and slender frontal spine and long, smooth claws, and in both female and male the posterodorsal plate is lacking. Leg I of deutonymphs have long, curved, tapering ventral setae, as the adults.

Collecting data Southeast Pacific, 53°S, 75°W, 64 m and off southern Argentina, 53°S, 75°W, 40–49 m (Newell 1984) as well as from off Chile, 33°S, 72°W, 485 m (Newell 1971).

Halacarus excellens Lohmann, 1907

References *Halacarus excellens* Lohmann 1907a: 11, 12; Lohmann 1907b: 383, txt-fig. 10 1, 2, pl. 38 1–3, 6 (females, deuto-, protonymph); Newell 1984: 39, figs 50–53 (deutonymph); Bartsch 2010: 158–163, figs 1–9, 10–17 (females, males, deutonymphs).

Characters Length of females 1150–1360 (1470?) µm, of males 976–1010 µm. Length:width ratio of females 1.6-1.8:1. Dorsal plates punctate; surface of plates with irregularly reticulate epicuticula. Frontal spine slender, shorter than remainder of anterodorsal plate. Ocular plate small, with cornea and eye pigment. Posterodorsal plate in females shorter than in males; in both sexes anteriad not extending to fourth pair of gland pores. Fifth pair on horn-like projections extends beyond anal cone. Surface of horns with a few minute spicules. Anal valves and sclerites small. Female genitoanal plate circular. With 4–5 pairs of perigenital setae on either side of genital opening plus one pair of outlying setae in striated integument. Male genitoanal plate ovate; one pair of outlying setae near anterior

margin of plate and about 90 setae arranged around the genital opening. Gnathosoma slender, length:width ratio 2.2:1, rostrum longer than gnathosomal base. Legs slender; leg I 1.0-1.1 times longer than idiosoma. Telofemur, genu and tibia I with 1, 1, 2 pairs of slender, smooth spines. Tarsi III and IV with 4/1(-2) and 3/1(-2) dorsal/ventral setae (number of ventral setae somewhat variable). Claws slender, especially those on the hind legs.

Remarks *Halacarus excellens* is one of the large-sized *Halacarus* species in which females reach a length of more than 1000 µm, other species with such a length are *H. lamellipes* Newell, 1984, *H. longior, H. profundus* Newell, 1984, and *H. setifer* Newell, 1984. In *H. excellens* the posterior pair of gland pores end on prolonged cones, in the other four species the cones hardly extend beyond the anal cone. More discriminating characters are listed in Bartsch (2010). Lohmann (1907b) presents a length of 1470 µm; it is likely that in this length the gnathosoma is included.

Biology A few individuals contained an ovoid, stratified body of accumulated excretory material. Similar ovoid excretory bodies have been found in a few other halacarid species, e.g., in *Rhombognathus amplus* Bartsch, 2013, an inhabitant of marine upper tidal areas (Bartsch 2013a) and in several *Limnohalacarus* species which live in fresh and low saline brackish water (Bartsch 2018). All these species have unusual small anal openings. In the majority of halacarid species, the waste products are not stored in an ovoid body but in a dorsomedian, narrow bar and regularly defecated.

Collecting data Around Antarctica; records are from the GAUSS Station, 66°S, 90°E, 385 m, and the Amundsen Sea, 74°S, 105°W, 490–509 m (Lohmann 1907b; Bartsch 2010).

Halacarus lamellipes Newell, 1984

References *Halacarus lamellipes* Newell 1984: 67–69, figs 126–134 (female, male).

Characters Length of female 1098 µm (Newell 1984), of male 1095 µm (unpublished pers. observ.), length:width ratio of female 2.1:1. Aspect of dorsum dominated by areas with striated integument. Idiosoma, gnathosoma and legs (except for tibiae and tarsi) with conspicuous cerotegumental layers, accordingly surface of dorsal plates roughly wrinkled (cf. Newell 1984: fig. 131). Anterodorsal plate with slender frontal spine. Ocular plates and corneae absent. Posterodorsal plate triangular, short, far from reaching to gland pores IV. Gland pores ending on small papillae. Female genitoanal plate wider than long; marginally with cerotegument. Plate with two pairs of perigenital setae close to genital opening and one pair of setae distanced in striated integument (Newell 1984: fig. 129). Male genitoanal plate circular, with about 150 perigenital setae on the plate plus three pairs of outlying setae in striated integument, two of them close to the plate. Gnathosoma 2.2 times longer than wide. Rostrum almost reaching to end of second palpal segment. Legs slender. Tibia I with six rather short and slightly curved ventral spines. Claws smooth.

Remarks *Halacarus lamellipes* is one of the large-sized species with antero- and posterodorsal but no ocular plates and three pairs of ventral setae on tibia I. Unusual are the thick cerotegumental layers on idiosoma, gnathosoma and legs.

Collecting data Southern Argentina, 56°S, 66°W, 439 m (Newell 1984) and 54°S, 52°W, 419–483 m, 1966, ELTANIN Cruise 22/1521 (new, unpublished record).

Halacarus laterculatus Viets, 1950

References *Halacarus laterculatus* Viets 1950: 7–9, fig. 2A-E (female, deutonymph); Newell 1984: 60–62 (females, males, deutonymph); Bartsch 1993: 32–35, figs 7A-E, 8A, B (females, males).

Characters Length of females 626–853 µm, length:width ratio 1.9:1; length of males 596–644 µm. Anterodorsal plate with triangular, only slightly upturned frontal spine; posterior part of plate triangular. Ocular plates small; with cornea. In female posterodorsal plate far from extending to the level of gland pores IV, in male plate longer and wider but not reaching to the level of gland pores IV. Anterior margin of female genitoanal plate almost truncate, lateral parts of plate not markedly set off from anterior part; one pair of outlying perigenital setae in striated integument and one pair on genitoanal plate close to genital opening. In males genitoanal plate ovate, its anterior margin truncate; pair of outlying perigenital setae situated in genitoanal plate; genital opening surrounded by 88 perigenital setae. Length of gnathosoma 1.9 times its width. Length ratio gnathosoma:idiosoma 0.2:1. Rostrum longer than gnathosoma wide. Legs rather stout. Epicuticula of legs punctate-reticulate. Length ratio leg I:idiosoma 0.8:1. Telofemur, genu and tibia I with 2, 2, 4 slender, smooth ventral spines. Tarsi III and IV with four and three dorsal but no ventral setae. In males parambulacral setae on tarsus IV plumose. Paired claws with accessory processes but no pectines.

Remarks In dorsal aspect similar to *H. arnaudi* but, in contrast to *H. laterculatus,* females and males of *H. arnaudi* have distinctly larger posterodorsal plates. The size relationship of idiosoma and its plates can be influenced by the body content, hence examination of several specimens is recommended.

Collecting and habitat data Falkland Islands (Berkeley Sound and Port William), 52°S, 58°W, 16–22 m, sand, broken shells, algae; off the Falkland Islands, 52°S, 57°W, 746 m; South Georgia (Cumberland Bay), low tide zone; Palmer Peninsula, Anvers Island, 65°S, 64°W, 9 m; Chile, Fuerte Bulnes, barnacles and coralline red algae association, low tide zone (Viets 1950; Newell 1984; Bartsch 1993).

Halacarus leptopus Bartsch, 2002

References *Halacarus leptopus* Bartsch 2002b: 36–41, figs 28–37, 38–44 (females, males, deutonymphs, protonymph).

Characters Length of females 580–653 µm, of a male 562 µm. Length:width ratio in female 1.3:1. Frontal spine slender, as long as remaining part of anterodorsal plate. Pair of small corneae present, situated in striated integument. Eye pigment lacking. Posterodorsal plate lacking in both female and male. Female genitoanal plate with rather uniform cerotegumental swellings; anterior margin of plate arched. Pair of outlying perigenital setae in striated integument, well removed from genitoanal plate. Genitoanal plate of male ovate; approximately 70 perigenital setae arranged around genital opening. Pair of outlying perigenital

setae in striated integument close to genitoanal plate. Length ratio gnathosoma:idiosoma 0.3:1. Gnathosoma long, its length:width ratio 2.3:1. Rostrum longer than gnathosomal base. Rostrum extending beyond third palpal segment. Legs slender. Epicuticula with parallel striae. Leg I about 1.1 times longer than idiosoma. Tarsi II-IV with four ventral setae each, tarsi III and IV with four and three dorsal setae, respectively. Claws on leg I shorter than those of following legs. The latter with minute accessory process, else smooth.

Remarks The species is characterized by a combination of: posterodorsal plate and ocular plates reduced but corneae present, first pair of dorsal setae close to first pair of gland pores, female genitoanal plate with rather uniform cerotegumental cover, two pairs of perigenital setae close to genital opening, leg I with long, tapering spines, tarsi II-IV with four long ventral setae.

Collecting data North-eastern Atlantic Ocean, 30°N, 28°W, 332 m (Bartsch 2002b) and an unpublished record from the Great Meteor Seamount, 30°06'N, 28°23'W, 511 m. Extracted from biogenic calcareous sediment including porose limestone.

Halacarus longior Bartsch, 1981

References *Halacarus longior* Bartsch 1981a: 204–208, figs 18–24, 25–31 (females, males, deuto-, protonymphs); Bartsch 2005: 38 (female).

Characters Length of females 965–1225 µm, of males 790–995 µm. Length:width ratio in a male 1.9:1. Dorsal aspect dominated by areas with striated integument. Dorsal plates with delicate pores. Frontal spine long, slender. Anterior and posterior parts of anterodorsal and posterodorsal plates triangular. Ocular plates and corneae absent. Anterior margin of female genitoanal plate arched; plate with 6–8 perigenital setae on either side of genital opening and a pair of small setae in striated integument (omitted in Bartsch 1981a, fig 18). In males circular genitoanal plate with more than 150 perigenital setae. Pair of outlying setae in striated integument. Gnathosoma slender, length:width ratio 2.2:1. Length ratio gnathosoma:idiosoma about 0.3:1. Rostrum extending just beyond second palpal segment. Length of legs I and IV about 1.1 times length of idiosoma; legs II and III as long as idiosoma. Telofemur to tibia I with 2, 2, 4 rather short, slender spines. All claws slender, smooth. Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae. In males parambulacral setae on tarsus IV plumose.

Remarks This is one of the large species, most females are more than 1000 µm long, males often somewhat smaller.

Collecting data Atlantic Ocean, North American Basin, 38°N, 70°W, 3264–3356 m (Bartsch 1981a), Mid-Atlantic Ridge, 36°N, 34°W, 2275 m and 14°N, 45°W, 3014 m (Bartsch 2010), Angola Basin, 10°S, 11°E, 2644–2754 m; Argentine Basin, 37°S, 53°W, 2195–3343 m (Bartsch 1981a); and Drake Passage 61°S, 54°W, 2893 m (Bartsch 2005); Mid-Atlantic Rift, site Logatchev, 15°N, 45°W, 3014 m (unpublished).

Halacarus peregrinus Bartsch, 1981

References *Halacarus peregrinus* Bartsch 1981a: 212–214, figs 45–51, 52–55 (females, males, deuto-, protonymphs, larva).

Characters Length of females 483–539 µm, of males 384–393 µm. Length:width ratio in females 1.9-2.2:1, in a male 1.8:1. Frontal spine medium-sized, triangular. Ocular plates minute; corneae lacking. In females posterodorsal plate lacking, in males this plate wider than long; its truncate anterior margin anteriad not reaching to the level of gland pores V. Female genitoanal plate wide, its anterior margin arched, marginally plate extending to the dorsum. Male genitoanal plate circular. Both females and males with a pair of outlying perigenital setae, positioned in striated integument; females with another pair of perigenital setae close to anterior margin of genital opening; males with 56–72 perigenital setae scattered around genital opening. Gnathosoma slender, length 2.2 times the width. Length ratio gnathosoma: idiosoma 0.3:1. Rostrum almost reaching to end of third palpal segment. Legs almost as long as idiosoma (ratio 1.0:1). Telofemur to tibia I with 2, 2, 4 ventral spines. Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae. Paired claws slender. Claws of tarsi of anterior legs with very delicate accessory process, the other claws almost smooth.

Remarks This is one of the species in which males, but not females, have a posterodorsal plate. In the female the marginal parts of the genital plate extend to the dorsum.

Collecting data Southern Atlantic, Argentine Basin, 37°S, 53°W, 993–2707 m (Bartsch 1981a).

Halacarus profundus Newell, 1984

References *Halacarus profundus* Newell 1984: 39–43, figs 54–60, 61–63 (females, males, deutonymphs).

Characters Length of female idiosoma 1449–1474 µm, of male 1068–1220 µm. Length in females almost twice their width (1.9:1). Frontal spine acuminate and of moderate length. Posterior part of anterodorsal plate abruptly narrowing. Ocular plates and corneae absent. Posterodorsal plate rather short, anterior half triangular, both in females and males. Anterior margin of female genitoanal plate semi-circular, marginal parts with thick cerotegumental layer; one pair of perigenital setae in striated integument and 9–12 (or more) perigenital setae on either side of genital opening. Male genital plate more elongate, anterior margin notched; posterolateral part with cerotegument. Genital opening surrounded by 79–86 pairs of perigenital setae; one pair of outlying setae in anterior margin of genital plate. Gnathosoma 2.4 times longer than wide. Rostrum slightly longer than gnathosomal base. Length ratio leg I:idiosoma 0.8:1. Telofemur, genu and tibia I with 2, 2, 4 ventral spines (according to Newell 1984: 42) but 2, 2, 3 spines (according to Newell 1984: fig. 60), respectively. Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae. Paired claws smooth.

Remarks *Halacarus profundus* is one of the large-sized *Halacarus* species in which females reach a length of more than 1000 µm.

Collecting data Ross Sea, 75°S, 176°W, 2212–2306 m (Newell 1984).

Halacarus prolongatus Bartsch, 1996

References *Halacarus prolongatus* Bartsch 1996b: 162–165, figs 14–21, 22–27 (female, males).

Characters Length of female 750 µm, of males 615 and 760 µm. Length:width ratio of male idiosoma 2.5:1. Anterodorsal plate with long frontal spine, posterior part of plate long and slender. Plate with very delicate, reticulate ornamentation. Ocular and posterodorsal plate absent. Female genitoanal plate covered by thick layer of cerotegument. Two pairs of perigenital setae close to genital opening, one pair (outlying setae) in striated integument. Male genitoanal plate with 72 perigenital setae around genital opening and two outlying setae in striated integument. Gnathosoma slender, its length:width ratio 2.6:1 and length of gnathosoma:idiosomal 0.3:1. Rostrum longer than gnathosomal base, anteriad extending beyond end of second palpal segment. Legs slender; leg I somewhat longer than idiosoma (1.0–1.1 times). Telofemur, genu and tibia I with 2, 2, 4 tapering ventral spines. Tarsi III and IV with 4/4 and 3/4 dorsal/ventral setae. Tarsus IV of males with plumose parambulacral setae. Paired claws with accessory process but no pectines.

Remarks *Halacarus prolongatus* is characterized by its long frontal spine, absence of ocular plates and posterodorsal plate,, and one pair of perigenital setae anterior to genitoanal plate in both female and male. Except for absence or presence of very small ocular plates and number of ventral spines on tibia I the given combination of characters is found in species of the *actenos* group (cf. Bartsch 2011b).

Collecting and habitat data Mid-Atlantic Ridge, Site Menez-Gwen, 38°N, 32°W, 845 m (Bartsch 1996b). The sample included a rich vent fauna with hydrozoans, bivalves, polychaetes, gastropods, copepods, ostracods, amphipods, isopods, tanaidaceans. A few years later (in 2001), another male was extracted from the same vent area at 38°N, 32°W, 824 m (unpublished record).
The legs of the holotype male are covered by an amorphous layer which includes angular and black particles and 10–25 µm long filaments of bacteria (?).

Halacarus spathulifer Newell, 1971

References *Halacarus spathulifer*Newell 1971: 7, 8, figs 1–5, 80–83 (female, deuto-, protonymphs, larvae); Newell 1984: 64.

Characters Length of female idiosoma 470 µm; length:width ratio 1.7:1. Anterior and posterior dorsal plates distinct, ocular plates absent. Anterior dorsal plate with spatulate frontal spine. Genitoanal plate with three pairs of perigenital setae, two pairs immediately adjacent to genital opening, one pair in striated integument anterior to genitoanal plate. Genital opening ending at margin of genitoanal plate. Length:width ratio of gnathosoma about 1.9:1. Length ratio gnathosoma:idiosoma 0.3:1. Leg I almost as long as idiosoma (frontal spine included). Telofemur and genu I ventrally with 2, 2 bluntly ending spines, tibia I ventrally with three bluntly ending spines and one slender ventral seta. Legs III and IV with filaments. Tarsi III and IV with four and three dorsal setae. Paired claws smooth.

Remarks *Halacarus spathulifer* shares with *H. atlanticus* the spatulate shape of the frontal spine. Differences between the two species are: *H. atlanticus* has a slenderer frontal spine and

posterodorsal plate and the distance between first pair of dorsal setae and gland pore is larger (cf. Bartsch 1981a: fig. 2 versus Newell 1984: fig. 3), the female genitoanal plate extends beyond the genital opening (Bartsch 1981a: fig. 3 versus Newell 1984: figs 2 and 83). But the number of individuals studied is small and several characters are not mentioned in the descriptions. A faunal exchange via seaways between the Atlantic and Pacific Ocean was given during periods of the Palaeogene (Adams 1981). Further examinations will have to prove the status of *H. atlanticus;* is or isn't *H. atlanticus* a junior synonym.

Collecting data South-eastern Pacific Ocean, 33°S, 72°W, 485 m depth (Newell 1971).

Halacarus spiniger Bartsch, 1973

References *Halacarus spiniger* Bartsch 1973a: 52, figs 1–10 (protonymph); Bartsch 2002b: 41–43, figs 47–58 (female).

Characters Length of female 390 µm, length:width almost 2.1:1. Anterodorsal plate with triangular frontal spine, wide at its basis. Ocular plates and corneae absent. Posterodorsal plate triangular in outline. Equivalent to third pair of gland pores lacking. Female genitoanal plate with three pairs of perigenital setae, two pairs close to genital opening, one pair immediately adjacent to anterior margin of genitoanal plate. Length:width ratio of gnathosoma 2.0:1; length ratio idiosoma:gnathosoma 0.3:1. Rostrum extending to basis of fourth palpal segment. Leg I almost as long as idiosoma and much wider than following legs. Telofemur to tibia I with 2, 2, 4 short, wide spines. Most of spines apically blunt but their tips denticulate; only apical one of ventrolateral spines on tibia I tapering towards the tip. Each of tarsi III and IV with three dorsal but no ventral setae. Claws smooth.

Remarks In contrast to the general number of five pairs of gland pores only four pairs were found in *H. spiniger* and tarsi III and IV have three dorsal setae each, instead of a combination three on tarsus IV but four on tarsus III.

Collecting and habitat data North Atlantic Ocean; Great Meteor Seamount, 30°N, 28–29°W, from sediment extracted from 332–448 m depth (Bartsch 1973a, 2002b). An unpublished record of a deutonymph is from the Great Meteor Seamount, 30°06' N, 28°23'W, from 511 m depth). That sample had been taken with an epibenthic sledge.

Lohmannella abyssalis Bartsch, 2005

References *Lohmannella abyssalis* Bartsch 2005: 38–40, figs 22–30, 31–37 (female, deutonymph).

Characters Length of female 385 µm; ratio length:width 1.3:1. Surface of plates almost smooth; striated integument with delicate canaliculi. Corneae lacking. All five pairs of gland pores small. Genitoanal plate of female with 17 perigenital setae. Length:width ratio of gnathosoma 2.2:1; length ratio gnathosoma:idiosoma 0.6:1. Rostrum longer than gnathosomal base. Pair of palps distanced from each other by about the width of basal palpal segment. Second palpal segment with cuticular spine. Ratio length leg I:idiosoma 0.7:1. Tibiae I and II with five and four ventral setae, respectively, all setae bipectinate. Tarsi III and IV with four and three dorsal setae. Paired claws smooth; accessory process or pectines not recognized.

Remarks This *Lohmannella* is at present the only one which has the palps separated by a distance equalling about the basal segment's width.

Collecting data West Antarctica, off the South Shetland Islands; 61°S, 54°W, 2893 m (Bartsch 2005).

Lohmannella cygna Bartsch, 1988

References *Lohmannella cygna* Bartsch 1988b: 818, 819, 1–10 (female).

Characters Length of female 515 µm; length:width ratio 1.2:1. Surface of plates smooth. Anterodorsal plate wide, hexagonal. First pair of gland pores slightly enlarged, following pairs as well as dorsal setae very small. Neither corneae nor eye pigment present. Anal cone enlarged; with a pair of minute setae on its inner flank. Genitoanal plate with 18 perigenital setae. Gnathosoma very slender, length ratio gnathosoma:idiosoma 0.9:1. Rostrum much longer than gnathosomal base. Palps slender, curved. Leg I hardly longer than idiosoma (1.0:1). Genu and tibia I ventrally with five and eight bipectinate setae. Tarsi III and IV with four and three dorsal setae. Paired claws smooth.

Remarks A unique character of *L. cygna* is the prolonged anal cone and its very small setae. Other easily recognized characters rarely found in *Lohmannella* species is the combination of: legs long and five and eight bipectinate setae on genu and tibia I, respectively.

Collecting data South Atlantic Ocean, Angola Basin, 9°S, 12°E, dredged with an epibenthic sled in about 1427–1643 m depth (Bartsch 1988b). A very similar looking individual had been collected in the South-western Pacific Ocean, North Fiji Basin Pacific Ocean, 17°S, 174°W, 2000 m (Bartsch 2021a).

Lohmannella falcata (Hodge, 1863)

References *Leptognathus falcatus* Hodge 1863: 302, 303, figs 6, 7.
Lohmannella falcata, Trouessart & Neumann 1901: 250; Viets 1927b: 29, figs 71, 72) (female, male); Fountain 1953: 363, 364, fig. 3 (female); Newell 1947: 190, 191, figs 327–330 (male); Bartsch 1972: 218 (females, males, deutonymphs, protonymphs); Bartsch 1977b: 142, 143, 152, figs 1–9 (females, males); Bartsch 1979b: 57 (females, males, deutonymphs, protonymphs); Green and MacQuitty 1987: 140, 141, fig. 57A-D.
Non *Lohmannella falcata* Bartsch 1978a: 60, fig. 42.

Characters (According to Fountain 1953, Bartsch 1977b and Green & MacQuitty 1987): Length of females 270(?)–515 µm, of males 335–490 µm. Length:width ratio 1.3:1. Surface of plates almost smooth. Pair of ocular plates with corneae. Gnathosoma slender, its length about twice the width. Length ratio gnathosoma:idiosoma about 0.5-0.6:1. Rostrum longer than gnathosomal base. Length of leg I about 0.7 times that of idiosoma (mainly according to Hodge 1863: fig. 6; Fountain 1953: fig. 3). Genu and tibia I with four and (five to) six bipectinate ventral setae, respectively. Both tarsus III and IV with four dorsal setae each. Claws with minute accessory process.

Remarks *Lohmannella falcata* is one of the few species with four dorsal setae on both tarsus III and IV, instead of solely three setae on tarsus IV, as present in the majority of species.

Collecting and habitat data: Widely spread in the North Atlantic Ocean and adjacent basins; records are from the coast of North America and Europe, from the White Sea in the north to the Mediterranean/Black Sea in the south (Bartsch 2021a). Most records are from shallow water areas. Deep-water records from 400–500 m and 1410 m, Bay of Biscay, had been published by Trouessart & Neumann (1896) but the authors were not sure about the individuals' identity (a male and a larva). The male, from 400–500 m depth, had a robust rostrum and rather short legs. The larva, from 1410 m depth, was characterized by a very short rostrum (Trouessart & Neumann 1896). Specimens from off Norway, from 2500–3000 m depth (Bartsch 1978a) proved not to belong to *L. falcata* (Bartsch 2003c) but to an undescribed species. *Lohmannella falcata* has been extracted from hydrozoans, bryozoans, algae, and sediment.

Lohmannella fukushimai Imamura, 1968

References: *Lohmannella fukushimai* Imamura 1968: 472–475, pl. 1: figs 1–4, pl. 2: figs 1–5 (male, deutonymph); Bartsch 1993: 153–155, fig. 60A-E (females, males); Bartsch 2010: 168 (females, male); Bartsch 2016b: 143, fig. 3F, G (female, males, deutonymphs).

Characters: Length of females 495–560 µm, of males 491–582 µm. Length:width ratio 1.3-1.5:1. Dorsal and ventral plates with delicate epicuticular granules. Idiosoma with protruding anal cone. Third and fourth pair of gland pores replaced by minute setae. Ocular plate with eye pigment and one distinct and one faintly delimited cornea. Gnathosoma almost as long as idiosoma. Legs slender, slightly longer than idiosoma. Tarsi III and IV with four and three dorsal setae, respectively. Paired claws slender, each one with accessory process, else almost smooth.

Remarks: The species is characterized by its long anal cone, gnathosoma and legs. In its habitus, *Lohmannella fukushimai* is similar to *L. cygna* but in *L. fukushimai* two pairs of its gland pores are replaced by minute setae, the dorsal plates are not smooth but covered by delicate epicuticular granules and the sixth pair of idiosomal setae are on the lateral flank of the anal cone.

Collecting and habitat data: Southern Oceans: Circum-Antarctic and sub-Antarctic with records from the Weddell Sea, off Prince Harald Coast, the Ross Sea, and Amundsen Sea. Present depth range extends from about 190 to 1047 m depth (Imamura 1968; Bartsch 1993, 2010, 2016b).

Pelacarus aculeatus (Trouessart & Neumann, 1896)

References: *Agaue aculeata* Trouessart & Neumann 1896: 341–345, pl. 10 fig. 1a-c, pl. 11 fig. 3 (male).
Agauopsis aculeata, Viets 1927a: 94.
Werthella aculeata, Newell 1984: 204, 205; Morselli & Mari 1985: 211–215, fig. 4a-d, 5 Z1–Z5 (females, male).
Pelacarus aculeatus, Bartsch 1986c: 215–219, figs 12–22, 23–33 (females, male, deutonymph).

Characters: Length of females 415–450 µm; length:width ratio 1.4:1, length of male 362–409 µm. Idiosoma, gnathosoma and legs with tufts of delicate epicuticular filaments. Dorsal areas with striated integument and plates almost equal in size. Striated integument with connective bars between striae. Raised areas on plates with a reticulum, in these areas each polygon

corresponds to a rosette pore. Integument outside panelled areas foveate. Anterodorsal plate with an ovate areola which anteriad continuous into a short frontal process, a second median areola in about middle of plate and a pair of small areolae in posterior margin. Pigment spots present but no corneae. Posterodorsal plate with pair of costae, each one with a few rosette pores. Panels of ventral plates with porosity within demarcated areas. Anterior epimeral plate with pair of distinct epimeral pores. Females with three, males with 16–22 pairs of perigenital setae. Gnathosoma short, length:width ratio 1.6: 1. Rostrum in ventral aspect triangular. Length ratio gnathosoma:idiosoma 0.3:1. Tectum in shape of transverse lamella. Palps short. Second palpal segment with a tuft of short filaments. Rostrum extending to end of palps. Length of leg I 0.7 times of that of idiosoma. Setae of several leg segments with epicuticular filaments. Telofemora panelled. Paired claws smooth. Each of these claws with accessory process but no pectines.

Remarks This is at present the only species of the genus *Pelacarus.* Newell (1984) and Morselli & Mari (1985) expected the species to belong to the genus *Werthella.* Important differences between *Werthella* and *Pelacarus* are in the position of the solenidion on tarsus II (dorsolateral in *Werthella,* dorsomedial in *Pelacarus*) and a deutonymphal instar (absent in *Werthella,* present in *Pelacarus*).

Collecting data North-eastern Atlantic Ocean, Bay of Biscay (Golfe de Gascogne), 46°N, 6°W, 1220–1440 m (Trouessart & Neumann 1896); and Mediterranean, coastlines of Spain, France and Italy, 4–35 m depth (Martinez et al. 2021; Garcia-Gómez et al. 2022; Bartsch 1986c; Morselli & Mari 1985).

Scaptognathus minutus Bartsch, 1973

References *Scaptognathus minutus* Bartsch 1973a: 72, 73, figs 72–84 (females, deutonymphs, protonymph, larva); Bartsch 1982d: 451, 452, figs 61–67 (females, deuto-, protonymphs); Bartsch & Rybakova 2015: 182–184, figs 19–21 (female).

Characters Length of females 145–178 µm; length:width ratio 1.3:1. Dorsal plates reticulate to foveate. Anterodorsal plate larger than posterodorsal one. Ocular plates minute; no corneae present. Female genitoanal plate bipartite; anterior part circular. Gnathosoma slightly shorter than idiosoma (0.9 times the latter's length). Length:width ratio of gnathosoma 1.9-2.1:1. Length of leg I 0.8 times the idiosoma. Paired claws with minute accessory process, else smooth.

Remarks *Scaptognathus minutus,* with a body length of less than 200 µm, is one of the small-sized *Scaptognathus* species (cf. Abé 2021).

Collecting and habitat data North-eastern Atlantic Ocean, documented from the Josephine Bank, 37°N, 14°W, 216–291 m, Great Meteor Seamount, 30°N, 28–29°W, 325–580 m depth and Lost City (Mid-Atlantic Ridge), 30°N, 42°W, 700–800 m (Bartsch 1973a; Bartsch & Rybakova 2015), and from the Indian Ocean, from a reef area off Mozambique, 13°S, 45°E, 755–770 m, 12°S, 47°E, 330–550 m and 11°S, 47°E, 335–390 m (Bartsch 1982d). The specimens from the seamounts are from sandy deposits; those from the Mid-Atlantic Ridge from bacterial mats in a cold water hydrothermal field and the ones from the Indian Ocean from a reef area.

Simognathus serratus Bartsch, 2004

References *Simognathus serratus* Bartsch 2004b: 186–190, figs 17–24 (female, deutonymph, larva).

Characters Length of female 526 µm, width 310 µm; length:width ratio 1.7:1. Dorsal and ventral plates foveate. Foveae of ventral plates more delicate than those on dorsum. Ocular plates small; corneae lacking. Length:width ratio of gnathosoma 1.3:1, length ratio of gnathosoma:idiosoma 0.3:1. Tectum scaliform. Rostrum short, conical. Second palpal segment with ventral protuberance and seta. Legs rather long and slender. Length ratio leg I:idiosoma 0.8:1. All telofemora slender; length:height ratio of telofemur I 2.7:1, that of following telofemora 2.5-2.6:1. Paired and median claw on tarsus I almost equal in length but paired claws very slender, almost seta-like. Median claw on tarsi II to IV minute; paired claws similar in length but much wider than claws on tarsus I. Claws on tarsi II and III with delicate tines.

Remarks In contrast to other *Simognathus* species the telofemora of *Simognathus serratus* are unusual slender.

Collecting data North-eastern Atlantic Ocean, Great Meteor Seamount, 30°N, 28°W, 476 and 511 m depth. The samples had been taken with an epibenthic sledge (Bartsch 2004b).

Thalassarachna alvina (Bartsch, 1994)

References *Halacarellus alvinus* Bartsch 1994a: 482–484, figs 6–16 (female, deutonymph); Bartsch 1996b: 165, 166, figs 28–32 (females, males, deutonymph).
Thalassarachna alvina, Bartsch 1997b: 1229.

Characters Length of female idiosoma 544–665 µm; length:width ratio 1.8:1. Length of males 502–582 µm. Large areas of dorsum with striated integument. Surface of anterodorsal plate almost smooth, that of posterodorsal plate reticulated. Anterior margin of anterodorsal plate arched. Plate without frontal spine. Ocular plates reduced to small, circular platelets. Ventral plates punctate. Each of posterior epimeral plates with one dorsal and two ventral setae; a third pair of ventral setae in striated integument. Female genital plate circular; with three pairs of perigenital setae. Genital opening of male surrounded by 47–51 perigenital setae. Length ratio gnathosoma:idiosoma 0.3:1. All legs shorter than idiosoma; length of leg I 0.8 times that of idiosoma. Tibia I with four pairs of ventral setae, two pairs slightly spiniform, two pairs bristle-like. Tarsi I to IV with 5, 4–5, 3, 3 dorsal setae (solenidia omitted). Paired claws with accessory process but without pectines.

Remarks This species and the below mentioned *T. caecoides* (in Bartsch 1978a) look similar. Distinguishing characters are outlined after the presentation of the latter species.

Collecting data North Atlantic Ocean, Mid-Atlantic Ridge, Lucky Strike, sites Tour Eiffel, Isabel and Pagode, 37°N, 32°W, 1636–1727 m (Bartsch 1994a, 1996b); Mid-Atlantic Ridge, Rainbow, 36°N, 32°W, 2200 m (unpublished record).

Thalassarachna caecoides (Bartsch, 1978)

References *Halacarellus caecoides* Bartsch 1978a: 48–52, figs 1–8, 9, 10 (female).
Thalassarachna caecoides, Bartsch 1997b: 1229.

Characters Length of female idiosoma 730 µm; length twice the width. No frontal spine present. Dorsal aspect dominated by large areas with striated integument. Dorsal plates reticulated. Ocular plates present but small, circular. Corneae lacking. Anterodorsal plate rectangular, posterodorsal plate triangular. Each posterior epimeral plate with two ventral setae; another pair of ventral setae in striated integument. Genital plate with 2–3 pairs of perigenital setae. Length of gnathosoma one-third of that of idiosoma. Legs slender. Leg I slightly less than length of idiosoma (ratio 0.9:1). Tarsi I to IV with 4, 4, 3, 3 dorsal setae (solenidia on tarsi I and II omitted). Paired claws smooth; no pectines seen.

Remarks This is one of the *Thalassarachna* species in which the ocular plates are strongly reduced in size, similar as in the above mentioned *T. alvina.* An easily recognized difference is that *T. caecoides* has a longer posterodorsal plate, the interval between the anterior tip of the plate and the fifth pair of the dorsal setae equals that between fifth and sixth pair of the dorsal setae whereas in *T. alvina* the length of the first-mentioned interval equals 1/3 of the posterior one.

Collecting and habitat data North Atlantic Ocean, Norwegian Basin, 64°N, 1°E, 2615 m. The sample was rich in sponges and hydrozoans (Bartsch 1978a).

Thalassarachna mollis Bartsch & Rybakova, 2015

References *Thalassarachna mollis* Bartsch & Rybakova 2015: 185–188, figs 27–34, 35–44 (female)

Characters Length of female 620 µm, length:width ratio 1.7:1. Dorsal plates faintly reticulated. Dorsum with large areas of striated integument between plates. Anterior margin of anterodorsal plate truncate to arched. Ocular plates slender, elongate, with a gland pore in posterior part. No cornea present. Second, third and fourth pair of dorsal setae longer than first and fifth pair. Each one of posterior epimeral plates with one dorsal and two ventral setae; a third pair of ventral setae in striated integument. Female genitoanal plate circular, with three pairs of perigenital setae. Gnathosoma slender, length 1.9 times the width and one-third of length of idiosoma. Rostrum shorter than gnathosomal base, anteriad extending just beyond second palpal segment. Leg I shorter than idiosoma, length ratio 0.9:1; leg IV about as long as idiosoma. Tibiae I with eight ventral bristles. Tarsi I and II with seven dorsal setae each, tarsi III and IV with four setae each. Paired claws on tarsus I smaller than on following tarsi. All paired claws with accessory process and pectines. Tines of pectines of claw I shorter than those on following claws.

Remarks *Thalassarachna mollis* is rather similar to *Thalassarachna alvina* and *T. caecoides* The three species have a rather slender idiosoma and small ocular plates, all three species are known from depths of the North Atlantic Ocean (Bartsch 1978a, 1994a). Discriminating characters of *T. mollis* are, the ocular plates are elongate, three times longer than wide, in the other two species they are reduced in size, almost circular, and the tarsi I to IV have 7, 7, 4, 4 dorsal setae in *T. mollis* but less in the two other species.

Collecting and habitat data: North Atlantic Ocean, Mid-Atlantic Ridge, cold water vent field Lost City, 875 m; extracted from carbonate sediments from the basis of a carbonate tower (Bartsch & Rybakova 2015).

Thalassarachna reticulata (Bartsch, 1978)

References: *Halacarellus reticulatus* Bartsch 1978a: 52–56, figs 11–15, 16–21 (male).
Thalassarachna reticulata, Bartsch 1997b: 1229.

Characters: Length of male 380 µm, ratio length:width 1.3:1. Dorsal plates large, their surface reticulated. Anterior margin of anterodorsal plate truncate. Ocular plate somewhat shorter than anterodorsal plate; each ocular plate with a cornea. Second, third and fourth pair of dorsal setae situated in striated integument. Male genitoanal plate with 106 perigenital setae. Length:width ratio of gnathosoma 2.2:1. Length relation gnathosoma:idiosoma about 0.4:1. Rostrum slender, its lateral margins parallel-sided, its tip extending beyond end of third palpal segment. Rostrum slightly longer than gnathosomal base. Legs slender; leg I 1.2 times longer than idiosoma. Tibiae I to IV with 6, 5, 5, 4 ventral bristles. Tarsi I to IV with 5, 4, 3, 3 dorsal setae (solenidia and famuli omitted). Pectines of paired claws with numerous small tines.

Remarks: In contrast to the other *Thalassarachna* species from the Northern Atlantic Ocean, the dorsal plates are rather large, strongly reticulated and the rostrum slender. A similar slender rostrum is present in *T. robusta* (Bartsch, 1978) (in Bartsch 1978b).

Collecting data: North Atlantic Ocean, North-eastern Atlantic Basin, 48°N, 8°W, 805 m (Bartsch 1978a).

Thalassarachna setulosa Bartsch & Rybakova, 2015

References: *Thalassarachna setulosa* Bartsch & Rybakova 2015: 188–192, figs 45–53, 54–57, 58–63. (male).

Characters: Length of male 560 µm, length:width ratio 1.4:1. In a few areas integument of dorsal plates with minute pores, else surface of plates reticulated. Anterodorsal plate with truncate anterior margin. Each ocular plate short, slender, with a gland pore but no cornea. Second, third and fourth pair of dorsal setae longer than first and fifth setae. Surface of ventral plates uniformly punctate. Each one of posterior epimeral plates with one dorsal and two ventral setae, a third pair of ventral setae in striated integument. Male genitoanal plate circular, with ca 160 slender perigenital setae. Gnathosoma slender; length ratio gnathosoma:idiosoma 0.3:1, length:width ratio of gnathosoma 2.1:1. Triangular rostrum almost reaching to end of third palpal segment. All legs slender, longer than idiosoma. Leg I 1.6 times longer than idiosoma. Telofemora, tibiae and tarsi I with a high number of ventral setae, namely 13–14, 18–19, 14–15 setae, respectively (pair of parambulacral setae excluded). Tarsi I to IV with 6, 6, 3, 3, dorsal setae (solenidia and famuli excluded). Paired claws with delicate tines arranged from arc to basis of claw.

Remarks: Compared to congeners, the number of ventral setae on the telofemora, tibiae and tarsi is unusual high. Compared to other halacarid genera, an even higher number is present in *Acanthohalacarus* and a somewhat lower number in *Enterohalacarus.* Details and observations of the life-style are not available. Bartsch (2001a) reflected on that such spines

may not protect the mites from predators but prevent the mites from a contact to harmful mechanical or chemical components of the substratum inhabited.

Collecting and habitat data North Atlantic Ocean, Mid-Atlantic Ridge, 750–900 m depth, cold water field Lost City, 30°N, 42°W; bacterial mats on sediment and rocks (Bartsch & Rybakova 2015).

Werthella atlantica Bartsch, 1986

References *Werthella atlantica* Bartsch, 1986c: 212–214, figs 1–11 (females, protonymph).

Characters Length of females 428–471 µm; length:width ratio about 1.6:1. Idiosoma, gnathosoma and legs with delicate epicuticular filaments. Dorsal plates with raised areolae which are panelled and porose. Anterior margin of anterodorsal plate slightly hooded; plate with one small area in anterior half, one larger in posterior half and a pair of small areolae in posterior margin. Width of ocular plates more than twice the length. Corneae lacking. Posterodorsal plate with pair of slightly swelled costae. Anterior epimeral plate with elongate epimeral pores. Length of gnathosoma 1.8 times its width. Length ratio gnathosoma:idiosoma 0.3:1. Tectum rather large, scale-like. Legs slender; leg I shorter than idiosoma, length ratio 0.8:1. Long dorsal setae on tibiae III and IV and genu IV plumose, covered with long filaments. Tarsi I and II both with 3/1 dorsal/ventral setae (solenidia and famuli excluded). Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae. Paired claws slender, smooth.

Remarks *Werthella atlantica* is most similar to the below outlined *W. plumifera* Newell, 1971. Morphological differences are mentioned below.

Collecting data South Atlantic Ocean, Argentine Basin, 37°S, 53°W, 2195–2323 m, and Angola Basin 9°S, 2°E, 1427–1643 m (Bartsch 1986c).

Werthella plumifera Newell, 1971

References *Werthella plumifera* Newell 1971: 31, 32, figs 71, 182–187 (females, males, protonymphs, larvae); Newell 1984: 210–212, fig. 588.

Characters Length of females 426–566 µm, of males 400–513 µm; length:width ratio about 1.6:1. Anterodorsal plate with two panelled areolae, an anteromedian and posteromedian one. Ocular plates lack corneae. Costae on posterior dorsal plate with two pairs of swellings. Striated integument with asteriform papillae, each one with long filaments. Legs slender. Length ratio leg I:idiosoma 0.6-0.7:1. Genu IV and tibiae III and IV each with a plumose dorsal seta. Tarsi I and II with 3/1 and 3/0 dorsal/ventral setae, respectively (solenidia and famuli excluded).Tarsi III and IV with 4/0 and 3/0 dorsal/ventral setae, respectively. Paired claws smooth.

Remarks *Werthella plumifera* and *W. atlantica* are very similar. Differences are: the ocular plates of *W. plumifera* are not as wide as in *W. atlantica,* the swellings on the posterodorsal plate seem to be larger and tarsus I to be longer in *W. plumifera* than in *W. atlantica,* and the number of dorsal/ventral setae on the tarsi I and II is different. Moreover, the pair of porose areolae in the posterior margin of anterodorsal plate of *W. atlantica* is not mentioned in the description of *W. plumifera.*

Collecting data South-eastern Pacific, Chilean Slope, 33°S, 72°W, 485 m. Further records are from off Peru, from 13°S, 77°W, 1565 m, 16°S 78°W, 2640–2780 m (Newell 1971, 1984)

Werthelloides bathyalis Bartsch, 1986

References *Werthelloides bathyalis* Bartsch 1986c: 219–222, figs 34–45, 46–54 (female, male, deutonymph).

Characters Length of female 725 µm, of male 725 µm; length:width ratio 1.2:1. Surface of plates and striated integument of idiosoma as well as gnathosoma and legs with dense layers of delicate filaments. Large areas of dorsum with striated integument; venter dominated by ventral plates. Integument of dorsal plates with numerous foveae and delicate porosity. Anterior margin of anterodorsal plate arched. Ocular plates without corneae but each plate with a seta. Female genitoanal plate with 18 perigenital setae. Male genitoanal plate larger than that of female; small genital opening surrounded by about 100 delicate setae. Gnathosoma slender, 1.9 times longer than wide. Its length about 0.3 times that of idiosoma. Largely parallel-sided rostrum extending to end of second palpal segment. Legs slender; leg I 1.1 times longer than idiosoma. Tibia I with four bipectinate ventromedial and two to three smooth ventrolateral setae. Paired claws rather short, each one with distinct accessory process.

Remarks At a first glance, *Werthelloides* shares several characters with species of the Halixodinae, namely with the genera *Agaue* and *Halixodes*. The most important difference is the position of the solenidion on tarsus II, namely dorsomedial in the Halixodinae but dorsolateral in *Werthelloides*.

The large body, in dorsal aspect dominated by striated integument, suggests that this species can store large amounts of food, in case an adequate source has been found. This may be an adaptation to life in an environment with spatially and temporally limited supply of food.

Collecting data Indian Ocean, off Réunion, 21°S, 55–56°E; 1050–1600 m (Bartsch 1986c).

Addendum

Four species are omitted from the above given list because of their uncertain identity and/or locality. These are *Agaue magellanica* Newell, 1971, its depth records are contradicting, *Copidognathus oculatus* (Hodge, 1863) (in Trouessart 1896, called *Halacarus oculatus*), *C. quadricostatus* (Trouessart, 1894) (in Trouessart 1894 and Trouessart & Neumann 1894 called *Halacarus gracilipes* var. *quadricostatus*), and *Maracarus gracilipes* (Trouessart, 1889) and by Trouessart called *Halacarus gracilipes*. The three last-mentioned species with deep-sea records are from the French Atlantic coast, their true identity is not known.

Included in the addendum are records of unnamed adults and/or last nymphal instars taken in depths of more than 500 m. The characters of the species have been shortly outlined and illustrated but the species have not been given a name. The nymphal instars

included are either the proto- (genera *Copidognathus* and *Werthella*) or deutonymphs (the other genera). Juvenile halacarids are not just tiny copies of adults; size and length:width ratios of the plates may differ, as well as the shape and length ratios of appendages (cf. e. g., Bartsch 1998b, 2007b, 2015a, b; Pepato & Tiago 2005, Pepato et al. 2005).

Still, if the local fauna is known, the instar preceding the adult generally can be assigned to an adult. As to adults, if no adequate material for a solid description was at hand, they often remained unnamed. The species mentioned belong to the genera *Anomalohalacarus, Atelopsalis, Bathyhalacarus, Copidognathus, Halacarus, Lohmannella, Scaptognathides, Scaptognathus, Simognathus,* and *Werthella.*

Anomalohalacarus sp.

References *Anomalohalacarus* sp. in Bartsch 2003c: 114 and new record of a female.

Characters Length of female idiosoma 232 µm; length:width ratio 1.9:1. Antero- and posterodorsal plates reduced in size, ocular plates lacking; aspect of dorsum dominated by areas with striated integument. Gnathosoma slender. Ratio length of gnathosoma:idiosoma 0.4:1. Rostrum extending to end of fourth palpal segment. Ratio leg I:idiosoma about 0.8:1. All legs slender.

Remarks The genus *Anomalohalacarus* is exclusively psammobiontic, its species are regularly found in sandy deposits from 0 to about 60 m depth (Bartsch 1985b).

The body is adapted to life in the void volume between more or less spherical particles. The idiosoma is slender, oblong, its dorsal and ventral plates are reduced in size, the areas of striated integument between the plates are large. The gnathosoma with its slender palps and the body with long and slender legs form a slightly curved, crescentic entity. The mites can quickly run on the more or less spherical surface of the sand but not on a plain one, they can use and turn around in small interstities amongst the particles but will hardly be able to push themselves through narrow fissures. Nineteen species are named.

Collecting data North Atlantic, Great Meteor Seamount, 476 m (Bartsch 2003c) and 30°06' N, 28°23'W, 511 m depth (unpublished record). The latter sample had been taken with an epibenthic sledge.

Atelopsalis sp.

References *Atelopsalis* sp. in Bartsch 1982d: 442–444, figs 23 and 24 (female).

Characters Length of damaged female 214 µm. Surface of dorsal plates covered with foveae. Legs I longer and wider than following legs. Telofemur I with three cuticular spines. Claws on tarsi II to IV with distinct pectines, each with numerous tines.

Collecting and habitat data Indian Ocean, reef area off Mozambique, 13°S, 45°E, 750 m (Bartsch 1982d).

Bathyhalacarus sp. 1

References *Bathyhalacarus* sp. A in Bartsch 1994a: 487–489, figs 28–32 (deuto-, protonymph).

Characters Length of deutonymph 412 µm. Length:width ratio 1.8:1. Dorsal plates reticulate. Antero- and posterodorsal plates rectangular, both plates with truncate anterior margin. Ocular

plates elongate, with gland pores both anteriorly and posteriorly. Length ratio of gnathosoma:idiosoma equalling 0.4:1. Rostrum not reaching to end of second palpal segment. Legs slender. Tibia I with three ventral setae. Claws with accessory process.

Remarks The *Bathyhalacarus* juveniles could not be assigned to any of the *Bathyhalacarus* species described.

Collecting data Atlantic Ocean. Mid-Atlantic Ridge, Snake Pit, 23°N, 45°W, 3520 m (Bartsch 1994a).

Copidognathus sp. 1

References *Copidognathus* sp. A in Bartsch 1989b: 468–469 (protonymph).

Characters Length of protonymph 385 µm. Plates with rosette pores. Anterodorsal plate hooded. Ocular plates with corneae. Gnathosoma with spiniform tectum. Legs short; telofemora with lamellae.

Remarks The species belongs to the *Copidognathus gibbus* group (cf. Bartsch 1994b). This is a natural group, wide-spread in tropical and warm-temperate areas but also found along cold-temperate coastlines.

Collecting data South-western Pacific. Off New Caledonia, 23°S, 167°E, 570 m (Bartsch 1989b).

Copidognathus sp. 2

References *Copidognathus* sp. B in Bartsch 1989b: 469, figs 69 and 70 (protonymph including a male).

Characters Length of protonymph 303 µm. Dorsum with heavily sclerotized striated and foveate integument, no distinct margins between plates and striated integument. Anterodorsal, ocular and posterodorsal plates present. Length ratio gnathosoma:idiosoma 0.3:1. Rostrum slender, longer than gnathosomal base, with parallel lateral margins. Tip of rostrum extending beyond third palpal segment. Legs stout. Claw pectines with few, strong tines.

Remarks The slender rostrum hints at an at least partly ectoparasitic way of feeding.

Collecting data South-western Pacific, northeast of the Island Lifou, 21°S, 167°E, 1420 m (Bartsch 1989b).

Copidognathus sp. 3

References *Copidognathus* sp. A in Bartsch 2011a: 103, 104, figs 24 and 25 (female).

Characters Length of female 415 µm, length:width ratio about 1.6:1. Anterodorsal plate with internal A-shaped apodeme extending into triangular frontal spine. Pair of ocular plates elongate, with corneae and dark eye pigment. Posterodorsal plate with pair of slightly sigmoid costae. Surface of costae with rosette pores; integument outside costae reticulated. Adjacent parts of anteroventral epimeral and genitoanal plates separated in the middle but fused in their lateral angles. Length of gnathosoma slightly less than one-third of the idiosoma. Tectum crest like. Trochanters III and IV with triangular dorsal process, telofemora with large articular lamellae.

Remarks The species belongs to the *Copidognathus-gibbus* group (cf. above mentioned *Copidognathus* sp. 1). Because of the intense eye pigment, this species is certainly no typical deep-sea inhabitant.

Collecting and habitat data: Gulf of Mexico, 28°N, 88°W, from gas seeps in 2185 m depth (Bartsch 2011a). Extracted from a sample with tubeworms.

Copidognathus sp. 4

References: *Copidognathus* sp. B in Bartsch 2011a: 104, 105, figs 26 and 27 (male, protonymph).

Characters: Length of male 332 µm, length:width ratio about 2.0:1. Dorsal plates reticulate. Anterodorsal plate with short hood-like lamella and lambda-shaped, raised areola. Each ocular plate with eye pigment and two corneae. Posterodorsal plate with pair of narrow costae. Genital opening in posterior part of genitoanal plate, removed by 2.8 times its length from anterior margin of plate. Twenty-three perigenital setae closely arranged around genital opening. Gnathosoma 1.6 times longer than wide. Legs slender. Claws with tines.

Remarks: The species shares several characters with *C. nemenus* Bartsch, 1984, a species known from the Caribbean Sea (Bartsch 1984).

Collecting and habitat data: Gulf of Mexico, 28°N, 91°W, from gas seeps in 571–2185 m depth. Found in samples with tubeworms (Bartsch 2011a).

Halacarus sp. 1

References: *Halacarus* sp. A in Newell 1971: 8, figs 6 and 7 (deutonymph); Newell 1984: 38, 39 (deutonymph).

Characters: Length of idiosoma 340 µm. Anterior margin of anterodorsal plate with tapering spine. Each ocular plate with cornea. Posterodorsal plate small. Paired claws with accessory processes but no pectines.

Collecting and habitat data: South-eastern Pacific ocean, off Chile, 33°S, 72°W. Found in slope samples taken in 485 m depth (Newell 1971).

Halacarus sp. 2

References: *Halacarus* sp. in Bartsch 1982d: 439 (deutonymph).

Characters: Length of idiosoma 397 µm.

Collecting data: Indian Ocean, reef area off Mozambique, 13°S, 45°E, 755–770 m (Bartsch 1982d).

Halacarus sp. 3

References: *Halacarus* sp. in Bartsch 1989b: 462, figs 36–42 (deutonymph).

Characters: Idiosoma 428 µm long, i.e. 1.2 times longer than wide. Antero- and posterodorsal plates present, ocular plates lacking. Anterior part of anterodorsal plate constricted. Length ratio gnathosoma:idiosoma 0.4:1. All legs longer than idiosoma. Ventral spines on leg I short. Paired claws very slender. No pectines seen.

Remarks: In contrast to other *Halacarus* species the anterior part of the anterodorsal plate of this species is constricted by wide marginal parts of the epimeral plates; there is no frontal spine.

Collecting data: South-western Pacific Ocean, 23°S, 167° E, 570 m (Bartsch 1989b):

Lohmannella sp. 1

References *Lohmannella* sp. A in Newell 1971: 34 and 35 (deutonymph), Newell 1984: 263 and 264 (deutonymph).

Characters Length of idiosoma 287 µm. Antero- and posterodorsal plates and ocular plates with distinct gland pores. Ocular plates without corneae. Genital plate with three pairs of perigenital setae. Length ratio gnathosoma:idiosoma 0.9:1. Paired claws with minute accessory processes; pectines lacking.

Remarks The deutonymphal gnathosoma is almost as long as the idiosoma and we can expect in adults the proportions to be similar to those in deutonymphs.

Newell (1971: 35 and 1984: 249) mentioned another *Lohmannella* species, two larvae taken in the South-eastern Pacific Ocean, 26°S, 80° W, from 950 m depth. Length of the idiosoma is 230 µm. The gland pores are small. A posterodorsal plate is lacking. The ocular plates are minute. The length ratio of gnathosoma:idiosoma is 0.7:1. These larvae and the above mentioned deutonymph are representatives of two different species.

Collecting data South-eastern Pacific Ocean, off Chile, 33°S, 72° W, 485 m (Newell 1971).

Lohmannella sp. 2

References *Lohmannella* sp. in Bartsch 1982d: 449–451, figs 53–60 (female, gnathosoma lacking), *Lohmannella* sp. A, Bartsch 2021a: 221.

Characters Length of female 545 µm; length:width ratio 1.2:1. Dorsal plates with very faint epicuticular reticulation. Corneae lacking. Posterodorsal plate ending with horn-like projection. Pair of gland pores IV replaced by small setae. Trochanters I and II flanked by epimeral plates. Legs long and slender; leg I 1.2 times longer than idiosoma. Tibia I with eight and tarsus I with four bipectinate ventral setae. Tarsi II to IV with 3–4, 6, 4–5 solid ventral setae, respectively. Claws slender.

Remarks A horn-like projection on the posterodorsal plate, like that in this species, is else unknown within the genus *Lohmannella* whereas a replacement of gland pores IV by minute setae is also found in the above mentioned *L. cygna* and *L. fukushimai.*

Collecting data Indian Ocean, Mozambique Channel, 13°05'S, 45°08'E, 400–520 m (Bartsch 1982d).

Lohmannella sp. 3

References *Lohmannella falcata* in Bartsch 1978a: 60, fig. 42 (females, deutonymphs), Bartsch 2003c: 106 (female).

Lohmannella sp. B in Bartsch 2021a: 221 (females).

Characters Idiosomal length of two females 412–417 µm. Length of gnathosoma 232–243 µm. Length ratio gnathosoma:idiosoma equalling 0.6:1. Legs slender. Genua and tibiae I ventrally with two to three and five to six bipectinate setae, respectively. Tarsi III and IV with four and three dorsal setae, respectively.

Remarks Bartsch (1978a) called these specimens tentatively *Lohmannella falcata.* In the meantime, the knowledge of character variability of *Lohmannella* species has increased. Characters such as the shape and chaetotaxy of the legs do not support a conspecificity of these deep-sea individuals with *L. falcata.*

Collecting and habitat data: Eastern North Atlantic Ocean, Norwegian Basin, 64–69°N, 0–10°E. Extracted from hydrozoans and sponges dredged in 2538–2957 m depth (Bartsch 1978a).

Lohmannella sp. 4

References: *Lohmannella* sp. 1 in Bartsch 2013b: 245 (female).
Lohmannella sp. C in Bartsch 2021a: 221 (female).

Characters: Length of female 560 µm. In shape of dorsal and ventral plates, arrangement of setae and gland pores, prolonged anal cone with pair of nipper forceps, long and slender gnathosoma and legs very similar to *L. cygna.*

Remarks: Differences to *L. cygna* are in the number of bipectinate ventral setae on genua and tibiae I, *Lohmannella* sp. 4 bears four to five and seven setae, respectively, *L. cygna* five and eight setae. The individual from the North Fiji Basin may be conspecific with *L. cygna* since in the genus *Lohmannella* the number of bipectinate ventral setae is known to vary.

Collecting data: South-western Pacific Ocean: North Fiji Basin, 17°S, 174°'W, 2000 m. Taken in the course of the French-Japanese project STARMER II Cruise (Bartsch 2013b).

Lohmannella sp. 5

References: *Lohmannella* sp. 2 in Bartsch 2013b: 245.
Lohmannella sp. D in Bartsch 2021a: 221, 222 (female).

Characters: Length of female 510 µm; width 216 µm, length:width ratio 1.2:1. Surface of plates almost uniformly smooth, except for porose areolae, namely, a pair of ovate areas and a median unpaired area on posterodorsal plates, and a marginal pair on posterior epimeral plates. Corneae absent. Length of gnathosoma 350 µm, length:width ratio 2.6:1. Length ratio gnathosoma:idiosoma 0.7:1. Rostrum slender. P-2 8.4 times longer than its basal width. Length of leg I about 0.7 times of idiosomal length. Tibiae I to IV with 7, 5, 5–6, 5 ventral setae; on tibia I all seven setae bipectinate. Each one of paired claws with tiny accessory process.

Remarks: With the shape of dorsal and ventral plates, position of setae and gland pores, length of gnathosoma and chaetotaxy of legs, the species comes close to *L. kerguelensis,* but according to the description of *L. kerguelensis,* there should be no porose areolae on the dorsal plates.

Collecting data: Eastern Pacific Ocean, South-East Pacific Rise, 9°51'N, 104°18'W, 2500 m (Bartsch 2013b).

Lohmannella sp. 6

References: *Lohmannella* sp. E in Bartsch 2021a: 222 (female).

Characters: Length of female 248 µm, width 216 µm, length:width ratio 1.2:1. Gnathosoma slender; length 208 µm, 2.6 times longer than wide. Ratio length of gnathosoma:idiosoma 0.8:1. Second palpal segment with cuticular ventral spine. Legs slender. Length ratio leg I:idiosoma equalling 0.8:1. Basal part of trochanter I partly surrounded by epimeral plate I. Tarsi III and IV with 4/1 and 3/1 dorsal/ventral setae. Claws slender.

Remarks: The species has a spiniform ventral process on the second palpal segment. Such spines are found in several southern hemisphere species but rarely in northern populations. In

its general shape, the species comes close to *L. subfalcata,* but that species has no such spines.

Collecting data Eastern North Atlantic Ocean; Great Meteor Seamount, 30°05'N, 28°23'W, 511 m (Bartsch 2021a).

Simognathus sp.

References *Simognathus* sp. in Bartsch & Rybakova 2015: 185 (protonymph including a deutonymph).

Characters Length of protonymph 400 µm. Surface of dorsal and ventral plates foveate. Ocular plates lack corneae. Length ratio gnathosoma:idiosoma 0.2:1. Second palpal segment without ventral protuberance; ventral seta with basal knob. Surface of legs reticulate. Ventral spine on tibia I slender and evenly tapering.

Collecting data Atlantic Ocean, Mid-Atlantic Ridge, Lost City, RV 'Academic Mstislav Keldysh, Cruise 50, Station 4803, 30°N, 42°W, 750–900 m (Bartsch & Rybakova 2015).

Scaptognathides sp.

References *Scaptognathides* sp. in Bartsch 2003c: 110–112, figs 25–33 (deutonymph).

Characters Length of deutonymphal idiosoma 193 µm, length:width ratio 1.3:1. Surface of dorsal plates with epicuticular droplets. Anterodorsal plate with one pair of gland pores in lateral corners of anterior margin. Ocular and posterodorsal plates each with two gland pores in lateral margins. Length of gnathosoma half that of idiosoma; its length:width ratio 1.8:1. Rostrum slender, longer than gnathosomal base. Length of leg I 0.6 times that of idiosoma. Telofemur I distinctly longer than the other segments of leg I and longer than this segment on the following legs. Tines on paired claws of tarsus I in umbrella shaped arrangement.

Remarks Adults of this species may have a length of about 200 µm. This size and the character combination, namely dorsal plates ornamented with epicuticular droplets, ocular plates with two gland pores, ocular plate not very slender, rostrum longer than gnathosomal base, and telofemur I remarkably long and wide, are not given in any of the other *Scaptognathides* species.

Remarks Most records of the genus *Scaptognathides* are from shallow water sandy deposits along warm-temperate and tropical coastlines. This one is at present the only record from the Eastern Atlantic Ocean and from a deep-water area.

Collecting data Atlantic Ocean, Great Meteor Seamount, 30°06' N, 28°23'W, 511 m depth (Bartsch 2003c). The sample had been taken with an epibenthic sledge.

Scaptognathus sp.

References *Scaptognathus* sp. in Bartsch & Rybakova 2015: 184, 185, figs 22–26 (deutonymph).

Characters Length of idiosoma 244 µm; length:width ratio 1.4:1. Dorsal plates reticulated; each polygon divided. Anterodorsal plate anteriorly truncate, posterior part triangular. Ocular plates small. Posterodorsal plate short, rectangular. Genital plate bipartite. Gnathosoma as long as idiosoma; its width half that of the length. Leg I slightly longer than idiosoma, fol-

lowing legs shorter. Tibia I with three bipectinate ventral setae. Each one of paired claws with minute accessory process.

Remarks The juvenile instar (deutonymph) may belong to *Scaptognathus tridens* Trouessart, 1889. The differences listed are within the range expected to be found between deutonymphs and adults.

Collecting data Atlantic Ocean, Mid-Atlantic Ridge, Lost City, 30°N, 42°W, 736–845 m (Bartsch & Rybakova 2015).

Werthella sp.

References *Werthella* sp. in Bartsch 1986c: 214 (protonymph incuding a female).

Characters Length of protonymph 645 µm. Anterodorsal plate with pair of small porose areolae. Ocular plates slightly circular; corneae absent. Posterodorsal plate with two pairs of ovate raised areolae. Anterior epimeral plate with pair of large elongate epimeral pores. Surface of legs with villi. Claws of tarsi long and slender:

Remarks The skin of the protonymph is very dilated, active protonymphs will certainly be smaller.

Collecting data Mid-Atlantic, Angola Basin, 9°S, 12°E, 1427–1643 m (Bartsch 1986c).

Discussion and Conclusion

Number of species

The most recent compilations of halacarids with records from the deep-sea are in Bartsch (2009) and Chatterjee (2021). Both used the 1000-m depth line as a boundary to the deep-sea. The deepest record of a halacarid mite is from 6850 m (Jankowskaja 1978). Table 1 presents a list of 92 accepted species extracted from the seafloor within a range from 480 to 7000 m; added are informations on a few morphological characters and the depth data. Twenty unnamed species, in 10 genera, are listed in an Addendum. Summarized in Table 2 are the genera with three or more records of species, independent if the genus is mainly restricted to the deep-sea or also lives in shallow waters. The table presents the number of deep-sea species of these genera, the percentage of the species extracted from great depths compared to the world-wide number of congeners.

At the end of 2022, 1121 species, belonging to marine and brackish water halacarid genera, were accepted as valid. More recent descriptions of new marine species (e. g., Lee et al. 2023), as well as species of mainly fresh water inhabiting halacarid genera are omitted. Also excluded are nomina nuda, doubtful subspecies and species with fragmentary descriptions of juveniles. No more than 92 species, i. e. 8 % of the above mentioned number of species in marine genera, are from deep-sea samples. Three of the species are solely represented by and had been described on the basis of juveniles, namely last nymphal instar. About half of the 92 species listed (48 %) have been collected just once, extracted from the material of the same haul or at least from the same area. A few of the deep-

sea species listed are obviously wide-spread, longitudinally from the North- to the South Atlantic Ocean *(Agaue corollata, Halacarus longior)* and from the North- to the South Pacific Ocean *(Copidognathus papillatus),* or circum polar (Antarctica and adjacent areas) *(Agaue parva, Halacarus arnaudi, Lohmannella antarctica, L. fukushimai).* More collections will certainly extend the list and the percentage of wide-spread species.

Eighteen of the 92 deep-sea species have records both from the littoral (depth range of about 0–200 m) and the deep-sea (deeper than 480 m). If we accept the deep-sea to begin at 1000 m (cf. Gage et al. 1984; Bartsch 2009; Chatterjee 2021) then almost 50 species are inhabitants of that zone (because of doubts in identification exact number is not known). Striking is that the genus which stands for almost one-third of all worldwide known halacarid species, namely *Copidognathus* (Bartsch 2009), is distinctly underrepresented in the deep-sea. Twenty-three species are listed, that equals one-fourth (25 %) of the 92 deep-sea inhabiting halacarid species and 6 % of all world-wide known *Copidognathus.* Three of the 23 *Copidognathus* species in Table 1 *(C. dentatus, C. richardi, C. trouessarti)* have records from both shallow (0–48 m) and somewhat more than 500 m depth. It is not known, if they regularly can be found beneath the 480 m depth line. In contrast to *Copidognathus,* the genus *Bathyhalacarus* seems to be specialized for life in great depth, 11 of its 12 species, i. e., 92 % of the worldwide accepted *Bathyhalacarus* species (WoRMS 2023), have records from great depth. Actually, more *Bathyhalacarus* species are known, e. g., one (unnamed), represented by a nymphal instar, is listed in the Addendum). All *Bathyhalacarus* species have slender legs, whereas in deep-sea *Copidognathus* species some few have long and slender legs, in others the legs are short, their telofemora and tibiae rather wide. In the genera *Agaue, Bradyagaue, Halacarus, Thalassarachna,* and *Werthella* about 20–30 % of the named species have records from the deep-sea. According to Table 2, the part of deep-sea *Lohmannella* species, compared to the number of congeners, is about 10 % but if the five or six species mentioned in the Addendum are added, the percentage will run up to somewhat more than 20 % of all congeners. Different numbers depend on the status of *Lohmannella* sp 4, is it a 'synonym' or a species of its own?

Completely lacking in the deep-sea are genera which have been summarized in the ecological group rhombognathines (cf. Bartsch 2003d). The group includes four genera, *Isobactrus, Metarhombognathus, Rhombognathides,* and *Rhombognathus.* The 149 species are mainly or exclusively phytophagous. In case the 200-m line is accepted as a boundary to the deep-sea, then the genus *Rhombognathus* may have to be added to the list of deep-sea halacarids. Coralline nodules use to be inhabited by *Rhombognathus* (pers. observ.) and corallines have been found in a depth of 268 m (Littler et al. 1985). Nodules from depth of more than 200 m have not been studied in respect to halacarid inhabitants.

The number of collections from the deep-sea with data on halacarids is small. Generally halacarids were just by-catch. Neither the extraction nor sorting methods were designed for this meiofaunal taxon. From shallow water areas distinctly more data sets of ecological parameters are available, from different localities, habitats and various substrata. The

author expects that careful collecting, extractions and sorting of deep-sea samples will result in three times higher numbers of deep-sea halacarid species than known today.

Life and morphology of deep-sea species

Sex ratio and reproduction

For each species listed, the sex of the adults and the developmental state of the juveniles mentioned has been added. Three of the 92 species were present only with nymphal instars, 49 species with both females and males. Of the remaining 40 species five species were represented by males, 35 by females. These data do not automatically hint at a very distinct numerical dominance of females. Many of the samples held no more than a single adult individual.

Shallow water inhabiting populations from coldtemperate coastlines, studied once a month for more than a year, demonstrated, most species had a single generation per year and often a restricted period of reproduction; more females than males were counted (Kirchner 1969; Bartsch 1972). In populations held in the laboratory, the life span of females was almost twice that of males (Kirchner 1969). Accordingly, differences in the numbers of females and males can both be due to a general higher number of female embryos and a female's longer life span.

The data from the depths of the seas do not hint at a slower or faster reproduction and the sex ratio seems to be rather similar to that of populations in littoral zones.

Shape and size of the idiosoma

Do deep water halacarid mites show characters else not registered in shallow water inhabitants? Amongst the 92 species listed a single one, *Bathyhalacarus sordidus,* is unusual in its shape. Its idiosoma ends immediately posterior to the level with insertion of legs IV and is only slightly longer than wide. But in general, deep-sea halacarids have a shape and length:width range similar to that common in shallow water species, namely the idiosoma extends posteriad beyond the insertion of leg IV and is about 1.2 to 2.1 times longer than wide. An abruptly ending idiosoma, as in *B. sordidus,* is else not known, neither in deep nor in shallow water species. There are no informations on details of the substratum colonized by *B. sordidus.* The idiosoma, abruptly cut immediately posterior to insertion of legs IV, is certainly no anomaly in this single specimen. Character anomalies are sometimes found in halacarids, mainly in those collected along severely polluted coastlines. In such mites, right and left half of the body show differences (Bartsch 2015c). We can expect the reduction of the posterior part of idiosoma to be an adaptation to life in a special substratum which in turn is not bound to any hydrostatic pressure.

Deep-sea organisms are often said to demonstrate dwarfism or gigantism (Roberts et al. 2007; Ramirez-Llodra et al. 2010; Danovaro et al. 2017). The idiosoma of more or less free-living adult halacarids reach a length of about 140 to 1500 µm. Females are often

slightly larger than males. The largest-sized marine halacarid, with a length of somewhat more than 2000 µm, is the parasitic living species *Enterohalacarus minutipalpus* Viets, 1938. The mite was found in a sea urchin that lived in 240 m depth on grey mud and fine sand (Viets 1938; Mortensen 1940). Amongst the deep-sea species, the genus *Agaue* holds two, *Bradyagaue* a single and *Halacarus* four species in which the idiosoma reaches a length of 1000 µm or more (Table 1). Similar length data exist in shallow water species. For instance, one of the six presently known Mediterranean *Halacarus* species reaches a length of more than 1000 µm (Bartsch 2007a). On the other hand, *Halacarus setifer* Newell, 1984, with a body length of 1342 µm, is an example of a large-sized species recovered from shallow water (148 m depth) (Newell 1984). Accordingly, there is no striking difference in body length of free-living shallow versus deep water forms.

The at present smallest-sized halacarid species extracted from deep-sea samples, *Scaptognathus minutus,* has a length of 145–178 µm. The known depth range inhabited by this species is 335–900 m. A juvenile *Scaptognathides* that was represented by the last nymphal stage, 193 µm in length, was extracted from a depth of 511 m (eastern Atlantic, Great Meteor Seamount) (Bartsch 2003c). Also of small size is an *Actacarus* male, 189 µm in length, collected in the Western Atlantic, in 400 m depth (Bartsch 1977c).

At least, in respect to halacarid mites, any deep-sea gigantisms or dwarfisms are not proven.

Plates' size, surface structures and ornamentation

The idiosoma of halacarids bears plates which in general are separated from each other by striated, hence flexible integument. The distance between the plates may be narrow and the striated integument include rather few, parallel striae or be wide, the striae densely wrinkled or anastomosing. One of the columns in Table 1 informs, if in dorsal aspect the surface of the idiosoma is dominated by plates or by striated integument. The affiliation to a given genus seems to play a greater role than any depth data. Large or fused plates give a solid exoskeleton, they allow the mite to press itself through a substratum but also prevent it from being crushed by surrounding particles or predators. On the other hand, large plates will set limits to both a mite's motility and body volume whereas striated or densely wrinkled integument allows more flexibility and a rapid increase of volume if amount of food is ready to be engulfed. The flexibility of a body with reduced plates is best demonstrated by species of the genus *Anomalohalacarus.* Presence or absence of such species seems to be correlated to grain size and void volume, not to any bathymetric pressure.

The densely wrinkled integument of *Agauoides* is expandable and allows substantial intake of food, similar as it has been proposed to be the case in the shallow water halacarid *Halixodes* (Bartsch 1986d), as well as in juvenile oribatid mites (Acari: Oribatida) (Smrž 2007). Also the squamose integument of *Copidognathus papillatus,* and species with similar integument, may be expandable but also used for camouflage in the lightless depth, in that sonar signals sent out by predators are irregularly reflected and may be incorrectly interpreted.

A halacarid cuticula consists of a thick procuticula which is covered by a thin epicuticula (Crowe & Camara 1973). Several shallow water halacarids have pronounced, solid integumental structures, mainly on the surface of the dorsal and lateral plates. Such ornamentation is in the form of costae, domes, simple pores or in an arrangement called rosette pores. The integument with rosette pores has small caverns which are surrounded by canaliculi (Newell 1947; Crowe & Camara 1973). Detailed studies of the structures of the halacarid integument are rare.

Species from lenitic or low-saline areas often have a rather weak ornamentation compared to closely related species which live in wave exposed marine areas (30S‰ and more) or in habitats rich in dissolved organic and inorganic matter (Bartsch 1999c, 2018). In all, shape and ornamentation may be indicators in respect to special environmental parameters but not to life in a certain depth zone.

The ornamentation of species collected from sandy deposits in deep and shallow water is rather uniform. The surface of the plates of e.g., *Bathyhalacarus* and *Copidognathus,* is rather evenly reticulate, punctate or almost smooth, without very distinct rosette pores. Species of the genus *Halacarus,* both shallow and deep-water inhabitants, generally have a thin epicuticula with fingerprint-like or parallel striae or a porose texture. Details of the microstructure of the integument in deep-sea halacarids are hardly known.

In a high percentage of the deep-sea species the surface of the integument bears cerotegumental lamellae, spikes, epicuticular droplets, villi, and/or filaments arranged in line, concentrated in clusters or fused to lamellae. Villi or filaments are found on the plates as well as on the striated integument, on the idiosoma, legs or on the setae. Often debris are trapped in these ornamental structures. Lamellae, tubercles, villi, or filaments are present on the integument of instars still inside the skin of the preceding instar (Newell 1971; Bartsch 2015c). We do not know if villi and filaments always represent genuine halacarid material or are remnants of an epibios (cf. Trouessart & Neumann 1907).

Such surface structures are not restricted to deep-sea species. In halacarids inhabiting the upper tidal zone, epicuticular tubercles or villi are expected to reduce desiccation and/or the impact of UV radiation (Bartsch 2000, 2015c). Plumose setae or a coating with filaments are often present in species which live in a muddy substratum, both in those inhabiting shallow and deep water. Warts and tube-like knobs are commonly found in *Agaue*-species, in general on the ocular plates but also on the antero- or posterodorsal plate. Four of the nine deep-sea *Agaue* species have such knobs or tubes. Each one includes an afferent canal which ends with a porus at the surface. Tubes or horns on the dorsal plates are also known in shallow water species, also in other genera (e.g., *Copidognathus, Halacarus, Maracarus*). Accordingly, such knobs are not restricted to deep-sea species.

As mentioned above, the surface structure of the plates varies from warts and horns to almost smooth surface, the integumental structure itself from elaborate porose areolae (e.g., rosette pores) to very uniform and faint ornamentation, the surface of the integument may be uniformly smooth or porose, bear filaments or villi, cerotegumental lamellae, the striated integument may be squamose or very regularly striated. Surface structures

may act as camouflage, both in shallow and deep-water areas, predators on search for prey, namely small, ovoid bodies as e.g., halacarids, harpacticoid copepods, ostracods, can use chemical as well as sonar signals to find a prey. The debris amongst the surface structures may suppress chemical clues and mask the true outline of the body. It is not known if species with raised structures often are found in (or prefer) a muddy environment.

Corneae and eye pigment

According to Table 1, 25 of the deep-sea species have corneae, one has feebly developed ones, 65 species lack them. In one species no informatio is given. Presence versus absence of eye pigment has been excluded from the list of characters since most of the specimens studied had been stored for an unknown period and the influence of the storing medium and period on the pigment is not known. Shallow water halacarids, regularly exposed to light, generally have ocular plates with both corneae and eye pigment close to the corneae. A third pigment spot is beneath the anterior part of the anterodorsal plate. Halacarids inhabiting the groundwater, caverns or the mesopsammal lack both corneae and pigment but there exist many 'intermediate' forms, species in which the pigment spots from individual to individual varies from faint but still recognizable to almost completely vanished. Similar situation is found in respect to the corneae. A cornea may be almost spherical or a flattened lens; in a few species only a smooth, hyaline area in the integument is present.

Halacarids which constantly live in darkness obviously tend to reduce corneae and eye pigment, independent if they live in shallow or deep water. The question is, how many generations are needed for such a reduction? We can expect that at least a few of the deep-sea species with distinct corneae and eye pigment, mentioned in Table 1 and the Addendum (e.g., *Copidognathus dentatus* and *Copidognathus* sp. 3), actually are shallow water inhabitants.

Sexual dimorphism

Halacarid females and males may differ in shape, size, number, and arrangement of setae in their genital region and, of course, presence versus absence of the internal ovipositor or spermatopositor, else most other parts of the mites are similar in general aspect. In only a few genera and species females and males show differences in the size and shape of both dorsal and ventral idiosomal plates and number and shape of setae on gnathosoma and legs (Bartsch 1994c, 2006; Chatterjee & Guru 2012). Sexual dimorphism is demonstrated in more than a dozen halacarid genera, in the one or other species, independent if the species live in shallow or deep-sea regions; examples are *Agaue, Anomalohalacarus, Arenihalacarus, Bathyhalacarus, Copidognathus, Halacarellus, Halacaroides, Halacarus, Isobactrus, Phacacarus, Rhombognathus, Scaptognathus, Simognathus,* and *Thalassarachna.* Several descriptions of deep-sea species, but also of shallow water ones, have been prepared on the basis of a single specimen, hence presence of dimorphism is not known.

Gnathosoma

The gnathosoma of all deep-sea halacarids consists of a base, a rostrum that partly encloses a pair of chelicerae and, attached to the gnathosomal base, a pair of two- to four-segmented palps. None of the 92 species with records from below 480 m has extremely reduced palps, solely represented by a few setae. The rostrum forms a trough in which the chelicerae can move to and fro. The chelicerae are meant for cutting or piercing cells, not for crushing or brushing. Halacarids feed by sucking up the pre-digested material. Details are not known. We can expect the deep-sea species mainly to be secondary and tertiary consumers and to feed on the associated micro-, meio- and macrofauna as well as carcasses, fungi and bacteria. The very few studies on feeding have been done with shallow water species. Sometimes the shape of rostrum and palps can give hints. The impact of dissolved organic matter is unknown.

Except for very few species, the gnathosoma of shallow water halacarids resembles that of deep water species. *Spongihalacarus longiscutatus* Otto, 2000 is the most striking exception. In this species, extracted from a shallow water sponge, the palps are represented by a few setae, else the palpal segments are reduced (Otto 2000: fig. 3). The sponge lives in about 1 m depth, in a symbiotic association with red algae (sponge weed) which in turn obviously is used by the mite.

Legs and claws

Halacarid mites have four pairs of legs, except for their larvae which solely have three pairs. The legs are fixed to the idiosoma in a lateral to dorsolateral position. The two anterior pairs are directed forward, the two (single one in larvae) posterior pairs backward. There is a gap between insertion of the second and third pair of legs. The tips of the tarsi of the first and second pairs of legs bear sensory setae; they are expected to respond on chemical and tactile clues. Direct observations of how halacarid mites use their front legs, when walking or catching food, are rare. Independent if the mites live in shallow or deep water, we can expect that at least in the majority of species all four pairs of legs primarily are used for walking. The first two pairs of the legs are often shorter and slightly wider than the posterior pairs (e. g., in several *Copidognathus*). In other genera the shape of legs I and II differ, e. g., legs I are wider and longer than legs II, its telofemora are wider and legs I bear spines. In these species, e. g., representatives of the genera *Agauopsis, Halacarus* and *Thalassarachna,* leg I will also play a major role in catching and holding a wriggling prey (cf. Lohmann 1893; Kirchner 1969; Bartsch 1974b; Krantz 1970). Long first pair of legs can also be used to explore the surroundings in front of the mite. A few long-legged deep-sea species demonstrate an increase of setae or spines on the legs. The highest number of ventral and dorsal setae on basi-, telofemora and tibiae is found in *Acanthohalacarus reticulatus.* Many of these setae or spines are short and obviously hollow. A high number of setae are also found on the legs of the parasitic *Enterohalacarus minutipalpus* and in a few *Thalassarachna* species. Unusual long and numerous setae are found on legs IV of *Copidoganthua inusitatus* (illustrated in Bartsch 1989b: fig. 68). It is

not known if these setae are an anomaly because else *Copidognathus* species are characterized by an almost constant number of setae per segment.

A tarsus generally ends with a pair of claws (often called lateral claws), each articulating with the central sclerite (Newell 1947; Bartsch 2006). The latter ends with a claw-like process which often is much smaller, rarely almost as large as or even wider than the paired claws. The paired claws can be short, rather compact, their length less than that of the tarsi or long and slender, almost as long as the tarsi. Paired claws often bear an accessory process and pectines, namely a row of small or large tines extending from the apex to the basis; in other species the claws are rake-like, the tines arranged along the margin of a laterally extending process. Such rake-like shape of claws and their pectines can be used as indicator in respect to turbulences in the habitat; they are present in colonizer of substrata in strongly agitated water (Bartsch 1978c; Pugh et al. 1987). In respect to tarsus I, the shape of its claw or claws is also expected to be correlated with feeding, mainly catching prey. Long, slender claws on tarsi II to IV will facilitate locomotion in a brittle substratum or soft ooze with only a few irregularly, horizontally, vertically, or diagonally arranged fragments to grip or to step on and thus prevent uncontrolled sinking (cf. Bartsch 2007a). The effectiveness of long toes and claws is demonstrated by Rallidae (order Gruiformes, Aves) when they pass reed- or grass-land areas.

In respect to deep-sea halacarids, many of them have claws with small, hardly recognizable tines but the claws of species extracted from the vicinity of hydrothermal vent areas are in their size and shape most similar to those of mites from colonial shallow water organisms with a rich epibios, e.g., with hydrozoans, barnacles or/and corallines. A character of vent fluids is, they use to be rich in minerals, and these are certainly needed to create solid claws. Long and slender claws are present both in deep and shallow water inhabitants.

Summarizing the data, then the mites life-style and environmental conditions like turbulence, substratum, availability of solid food particles as well as dissolved organic and inorganic matter, will play a role but not the actual depth. Neither character combinations nor presence in deep-sea samples are enough to assign anyone of the halacarids to be exclusively an inhabitants of that zone.

Internal characters

Congeneric deep-sea and shallow water halacarids share external but also rarely occurring internal characters. For example, halacarids are known to accumulate waste products in a narrow dorsal bar which is defecated through the anus (Thomae 1926). In a few species, instead of a bar an oviform body with accumulated material can be seen. The body is almost uniformly transparent, dark or dominated by concentrically arranged dark and hyaline striae. The presence of such an excretory body is correlated with small anal sclerites. Amongst deep-water species a small anus, flanked by small anal sclerites, is found in *Bathyhalacarus abyssiculus, B. anomalus, B. sordidus,* and *Halacarus excellens.* Not known is, if these species have an oviform excretory body. Such excretory bodies exist in shallow water halacarids, both in marine and freshwater species (cf. Bartsch 2018).

Another rare character state, found in both marine and freshwater halacarids is that one or more of the genital acetabula are enlarged. Genital acetabula, as also epimeral pores, include ion-permeable areas (Bartsch 1973c, 1974b) and microscopical analyses revealed characteristics for osmoregulatorily active cells (Alberti 1979). Adults of most marine genera have three pairs of genital acetabula.

Also in freshwater species of else marine genera, the acetabula (as also epimeral pores) may be enlarged, obviously to fulfil the role of osmoregulation. But a similar enlargement is also, though rarely, found in species collected in marine habitats. It has been speculated that the acetabula or vesicles contain bacteria (Bartsch 1991c) or the different size of the acetabula in females and males may be correlated with periods of oviposition, but nothing could be proven (Bartsch 1986e). In general, the acetabula of females and males differ in size (Bartsch 2004c). Whatever the reason for any enlargement is, in *Bathyhalacarus sordidus* the posterior pair of the genital acetabula is enlarged.

According to present data of external and internal morphology, there are almost no differences between shallow water and deep-sea species, provided they live in similar substrata.

How and when did halacarids reach the deep sea?

Halacarids are not known to leave the substratum inhabited and periodically enter the water column. They are benthic. Special phoretic instars are not described. Transport seems to be primarily coincidentally, being attached to marine aggregates (marine snow, faecal pellets), to a macrofauna, colonial organisms, algal fronds, wooden material adrift, and on rafts after heavy storms, tsunamis, or submarine landslides. As proven by man-made litter (plastic, etc.) which within the passed decades accumulated in the deep-sea (Bergmann & Klages 2012; Woodall et al. 2014; Van Cauwenberghe et al. 2013; Abel et al. 2021) and in the meantime by local organisms is accepted as a substratum to settle on. Galgani et al. (2022) demonstrated a rapid transport of plastic fragments through the water column. According to them, globular plastic particles, about 100 µm in diameter and incorporated in biogenic material, may sink to 600 m depth within one to two weeks; larger particles may even be faster. Halacarids are somewhat larger and tend to cling to whatever they get in touch with. According to these data, the mites have a chance to reach a new adequate habitat without being captured by planktivorous organisms. Still, more likely seems to be that not just a few drifting particles or thalli of algae but solid rafts with a rich epibios offered halacarid populations a chance for a long-way transport. Halacarids are often found associated with benthic species and washing of macrofauna is a common method to collect halacarids (Lohmann 1893; Bartsch 1974a, 1979b; Newell 1984; Pepato et al. 2005). Hidden in structures (e. g., gills), the mites have a chance for a long-term stay on their 'vehicles' and finally reach a new habitat. Most likely seems to be that solid rafts with a rich epibios offered halacarid populations a chance for a long-way transport, both vertically and horizontally.

The oldest record of a fossil mite is from the Devonian (Hirst 1923), it corresponds to an age of almost 400 million years. According to molecular studies, halacarids have existed at least since the Late Triassic, since about 200 million years (Pepato et al. 2018). Their distribution, in shallow or deep water, is not known but we cannot exclude that halacarid species, if already present in the deep-sea, as other creatures survived extensive hypoxic periods, e.g., during the late Cretaceous and early Tertiary (cf. Kiel & Little 2006).

Most halacarids studied have a low reproduction rate; if this is true also for deep-sea halacarid populations, we cannot expect them to quickly invade an area, even if in the beginning, the number of competitors may be small and predators not specialized on these new colonists' size, taste and behaviour. The mites had thousands to millions of years to settle in and get adapted to a new environment. They could withstand numerous failures. An example of a rapid invasion is that of a European shallow water *Isobactrus* species in south-eastern Australian mangroves (Bartsch & Gwyther 2004; Bartsch 2014).

Studies on the halacarid fauna from various localities and survival experiments proved, many a halacarid species can live in a wide range of habitats, environmental parameters and withstand stress outside the range normally experienced (Wieser & Kanwisher 1959; Bartsch 1974b; Lancaster & Pugh 1987; Pugh 1996; Siemer 1996). But these data sets were achieved with shallow water species and the experiments were run over short periods of a few hours, weeks or months.

The present-day populations may be derived from single populations but also the result of multiple colonisation of the deep-sea. The species of the genera listed in Table 1, namely, *Agaue, Agauopsis, Bathyhalacarus, Copidognathus, Halacarellus, Halacarus,* and *Thalassarachna,* belong to different natural lineages. Since halacarids have a low reproduction rate, most of the deep-sea mites are expected to have rather slowly, step by step, colonized the deep-sea.

One should keep in mind, the biotic conditions in great depths are not as harsh as, centuries ago, Man believed them to be. For halacarids the life in great depth seems to be rather comfortable. In contrast to shallow water (0–200 m) inhabiting halacarids those in the deep-sea have neither to withstand large daily or seasonal changes in temperature, salinity, acidity, UV radiation, oxygen availability, nor dislodgement because of irregular periods of breaking waves and/or emergence. Moreover, the influence of catastrophes, e.g., impact events, volcanic eruptions, widespread anox conditions, may in the depth have been less dramatic than in shallow water areas (cf. Kiel & Little 2006).

When did the first halacarids settle in the deep-sea? The deep-sea is no recent realm and we can expect several of its inhabitants to be of ancient origin, once, in the Mesozoic, widely spread. On the basis of fossils and techniques such as molecular clocks, it seems to be likely that some of the present day deep-sea taxa extend back to the mid-Cretaceous (Harasewych & McArthur 2000; van Dover et al. 2002; Kiel & Little 2006). As to halacarids, fossils are not known and the molecular data are still restricted to a few species.

In contrast to distributional data of other meiofaunal taxa, those of halacarids demonstrate striking similarities in the faunal composition even on opposite sides of the globe,

with a high percentage of same or almost identical species. Bartsch (1996c, 2007c) expects some of the widely spread halacarid species to have existed since the Mesozoic or even Pre-Mesozoic. According to Pepato et al. (2018), the halacarid genus *Lohmannella* may date back to the Late Triassic (Early Mesozoic).

Nowadays, introduced species can be found almost everywhere. Numerous alien species successfully invaded niches, changed their life-style, reproduced and are now a steady part of the local fauna. The same will be true for many a recent deep-sea species.

Conclusion

Amongst the else mainly terrestrial class of Arachnida (Zhang 2011), the family Halacaridae is the only one in which its more than 1200 species spend all their life in water. Larvae, nymphs and adults colonize all depth zones, from the supralittoral, wetted by splash, to the bottom of deep-sea trenches. Terrestrial phases are as yet not known and perhaps have never existed during evolution of halacarids. There are no striking morphological differences between deep-sea and shallow water inhabiting halacarids. Several of the species listed in Table 1 are known from just one locality, extracted from material of the same haul or at least the same area; only a few of the deep-sea species listed are wide-spread. But, we should be aware that only a small part of the halacarid deep-sea fauna is known: and more samples and adequate extraction, sorting and identification methods will raise the number of deep-sea records and species. The author expects the number of species to be more than three times higher than known today.

Halacarids have existed at least since the Early Mesozoic, they had plenty of time to get adapted to life in the deep-sea. Shallow water inhabiting halacarid species are known to survive in an environment in which the parameters differ from that the mites are used to. Accordingly, halacarids had a good chance to spread and colonize the globe, also the deep-sea. Especially conditions of life in the deep-sea may cause less stress than one in the tidal and upper littoral zone.

We do not know if there are differences in the life cycles between shallow and deep-water inhabiting species. Rather few and vague data from cold-temperate or polar, almost constantly ice covered coastlines hint at maintenance of a one-year cycle in suppressing one of the nymphal instars (cf. Bartsch 2021b). Noteworthy is, *Copidognathus alvinus,* from more than 1500 m depth, held a larval (prelarval?) instar. Is this another way to reduce the period of juvenile development?

Most important for a successful settlement in a new environment, e.g., the deep-sea, are long-term constant conditions, adequate food resource and substratum. In contrast, short-term repetitive catastrophes, extreme changes in temperature, enrichment of sulphides, will finally be lethal.

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References

Abé, H. (2021): Taxonomic review of the subfamily Lohmannellinae (Acari: Trombidiformes: Halacaridae) with morphological comparison among genera. Zootaxa 4980: 201–255. https://doi.org/10.11646/zootaxa.4980.2.1

Abel, S. M., Primpke, S., Int-Veen, I., Brandt, A. & Gerdts, G. (2021): Systematic identification of microplastics in abyssal and hadal sediments of the Kuril Kamchatka trench. Environ. Pollut. 269: 116095. https://doi.org/10.1016j.envpol.2020.116095

Adams, C. G. (1981): An outline of Tertiary palaeogeography. In: The evolving earth, L. R. M. Cocks (ed.), pp. 221–235. Cambridge, Cambridge University Press.

Alberti, G. (1979): Fine structure and probably function of genital papillae and Claparède organs in Actinotrichida. In: Recent advances in acarology. II, Rodriguez, J. (ed.), pp. 501–507. Academic Press, New York.

André, M. (1933): Contribution á l'étude des Acariens marins des îles Kerguelen et Saint-Paul. Ann. Inst. Océanogr., Paris, n.s. 13: 137–161.

André, M. (1946): Halacariens marins. Faune Fr. 46: 152 pp.

Ballard, R. D. (1977): The discovery of hydrothermal vents. Oceanus 20: 35–44.

Bartsch, I. (1972): Ein Beitrag zur Systematik, Biologie und Ökologie der Halacaridae (Acari) aus dem Litoral der Nord- und Ostsee. I. Systematik und Biologie. Abh. Verh. Naturw. Ver. Hamburg (NF) 16: 155–230.

Bartsch, I. (1973a): Halacaridae (Acari) von der Josephinebank und der großen Meteorbank aus dem östlichen Nordatlantik. II. Die Halacaridae aus den Bodengreiferproben. Meteor Forsch.-Ergebn. D 15: 51–78.

Bartsch, I. (1973b): Halacaridae (Acari) von der Josephinebank und der großen Meteorbank aus dem östlichen Nordatlantik. I. Die Halacaridae aus den Schleppnetzproben. Meteor Forsch.-Ergebn. D 13: 37–46.

Bartsch, I. (1973c): *Porohalacarus alpinus* (Thor) (Halacaridae, Acari), ein morphologischer Vergleich mit marinen Halacariden nebst Bemerkungen zur Biologie dieser Art. Ent. Tidskr. 94: 116–123.

Bartsch, I. (1974a): *Agaue vajeta* n. sp., Beschreibung einer Halacaride (Acari) von Südafrika. Rev. Zool. Bot. Afr. 88: 175–179.

Bartsch, I. (1974b): Ein Beitrag zur Systematik, Biologie und Ökologie der Halacaridae (Acari) aus dem Litoral der Nord- und Ostsee. II. Ökologische Analyse der Halacaridenfauna. Abh. Verh. Naturw. Ver. Hamburg (NF) 17: 9–53.

Bartsch, I. (1977a): Zur *oculatus*- und *gibbus*-Gruppe der Gattung *Copidognathus* (Halacaridae, Acari). Entomol. Mitt. Zool. Mus. Hamb. 6: 1–12.

Bartsch, I. (1977b): New species of *Lohmannella* (Halacaridae, Acari) from the Roscoff area, Brittany. Cah. Biol. mar. 18: 141–153.

Bartsch, I. (1977c): Eine neue *Actacarus*-Art (Acari, Halacaridae) aus dem Bathyal vor der Küste von North Carolina, USA. Zool. Scr. 6: 323–326.

Bartsch, I. (1978a): Halacaridae (Acari) aus der Tiefsee des atlantischen Ozeans. Cah. Biol. Mar. 19: 47–62.

Bartsch, I. (1978b): Halacaridae (Acari) von Gezeitenstränden Nordnorwegens. Mikrofauna Meeresboden 70: 1–22.

Bartsch, I. (1978c): Die Krallen der Meeresmilben geben Auskunft über den Lebensraum. Mikrokosmos 67: 197–200.

Bartsch, I. (1979a): Ergänzungen zur *Copidognathus*-Fauna (Halacaridae, Acari) der Bretagne-Küste. Acarologia 20: 217–234.

Bartsch, I. (1979b): Halacaridae (Acari) von der Atlantikküste Nordamerikas. Beschreibung der Arten. Mikrofauna Meeresboden 79: 1–62.

Bartsch, I. (1979c): Verbreitung der Halacaridae (Acari) im Gezeitenbereich der Bretagne-Küste, eine ökologische Analyse. II. Quantitative Untersuchungen und Faunenanalysen. Cah. Biol. Mar. 20: 1–28.

Bartsch, I. (1980): Halacaridae (Acari) aus der Bucht von Morlaix (Bretagne). Acarologia 21: 34–45.

Bartsch, I. (1981a): Fünf neue Arten der Gattung *Halacarus* (Acari, Halacaridae) aus dem Atlantik. Zool. Scr. 10: 203–215.

Bartsch, I. (1981b): Halacaridae (Acari) aus dem Kanal von Moçambique. Cah. Biol. Mar. 22: 35–63.

Bartsch, I. (1982a): Zur *corollata*-Gruppe der Gattung *Agaue,* Verbreitung und Beschreibung von zwei neuen Arten. Acarologia 23: 45–53.

Bartsch, I. (1982b): Zur Gattung *Bathyhalacarus* (Acari, Halacaridae), nebst Beschreibung fünf neuer Arten. Zool. Scr. 11: 209–220.

Bartsch, I. (1982c): Drei Arten der Gattung *Copidognathus* (Acari, Halacaridae) aus dem Argentinischen Becken. Entomol. Mitt. Zool. Mus. Hamb. 7: 161–174.

Bartsch, I. (1982d): Weitere Halacaridae (Acari) aus dem Kanal von Moçambique. Cah. Biol. Mar. 23: 435–457.

Bartsch, I. (1982e): Halacaridae (Acari) von der Atlantikküste des borealen Nordamerikas. Ökologische und tiergeographische Faunenanalyse. Helgol. Meeresunters. 35: 13–46.

Bartsch, I. (1983): *Copidognathus richardi* Trouessart (Halacaridae, Acari), eine Wiederbeschreibung. Acarologia 24: 285–288.

Bartsch, I. (1984): New species of the genus *Copidognathus* (Halacaridae) from the Caribbean region. Stud. Fauna Curaçao 67: 1–14.

Bartsch, I. (1985a): Zur Halacaridenfauna (Halacaridae, Acari) der Philippinen. Beschreibung von drei neuen Arten. Mitt. Hamb. Zool. Mus. Inst. 82: 269–277.

Bartsch, I. (1985b): Notes on the Halacaridae (Acari) from Yorkshire. Naturalist 110: 4–48.

Bartsch, I. (1986a): Zur Gattung *Agauopsis* (Acari, Halacaridae), Beschreibung zweier Arten und Übersicht über Verwandtschaftsgruppen. Zool. Scr. 15: 165–174.

Bartsch, I. (1986b): New species of Halacaridae (Acari) from New Zealand. N.Z. J. Zool. 12: 547–560.

Bartsch, I. (1986c): Zur Gattung *Werthella* Lohmann, *Pelacarus* n. gen. und *Werthelloides* n. gen. (Halacaridae, Acari). Cah. Biol. Mar. 27: 211–223.

Bartsch, I. (1986d): A new species of *Halixodes* (Halacaridae, Acari) and a review of the New Zealand species. J. Roy. Soc. N.Z. 16: 51–56.

Bartsch, I. (1986e): Lohmannellinae (Halacaroidea, Acari) aus dem Mittelmeer. Entomol. Mitt. Zool. Mus. Hamb. 8: 231–244.

Bartsch, I. (1987): *Agaue obscura* n. sp. (Acari, Halacaridae), a new circumpolar Antarctic mite. Can. J. Zool. 65: 1343–1345.

Bartsch, I. (1988a): Halacariden (Acari) im Nordatlantik. Beschreibungen von *Halacarus balgimus* sp. n. und *Agauides cryosi* gen. et sp. n. Cah. Biol. Mar. 29: 353–359.

Bartsch, I. (1988b): Deep-sea halacarids (Acari) and description of a new species. J. Nat. Hist. 22: 811–821.

Bartsch, I. (1988c): Arenicolous Halacaridae (Acari) in Hawaiian waters. Proc. Hawaii. Ent. Soc. 28: 213–228.

Bartsch, I. (1989a): *Copidognathus brifacius* n. sp. (Halacaridae, Acari) und Bemerkungen zu weiteren Bewohnern des Seeigels *Spatangus purpureus* (Echinoidea). Mitt. Hamb. Zool. Mus. Inst. 86: 315–328.

Bartsch, I. (1989b): Deep-sea mites (Halacaridae, Acari), from the south-western Pacific. Cah. Biol. Mar. 30: 455–471.

Bartsch, I. (1989c): Marine mites (Halacaroidea: Acari): a geographical and ecological survey. Hydrobiologia 178: 21–42.

Bartsch, I. (1990a): Antarctic Halacaroidea (Acari): Genera *Agaue, Bradyagaue,* and *Halacarellus.* Antarct. Res. Ser. 52: 185–217.

Bartsch, I. (1990b) Hydrothermal vent fauna: *Agauopsis auzendei* n. sp. (Acari, Halacaridae). Bull. Mus. Hist. Nat., Paris, 4e sér. 12, Sect. A: 69–73.

Bartsch, I. (1991a): *Copidognathus papillatus* Krantz (Acari, Halacaridae), a hydrothermal vent mite in the Pacific Ocean. Zool. Sci. 8: 789–792.

Bartsch, I. (1991b): On the identity of some North Atlantic halacarid species (Acari). J. Nat. Hist. 25: 1339–1353.

Bartsch, I. (1991c): Arenicolous Halacaridae (Acari) from Hong Kong. Asian Mar. Biol. 8: 57–75.

Bartsch, I. (1992a): Two new species of arenicolous *Agauopsis* (Acari: Halacaridae) from Hong Kong. In: The Marine Flora and Fauna of Hong Kong and Southern China III (Morton, B., ed.), Vol. 2. University Press, Hong Kong. Pp 891–897.

Bartsch, I. (1992b): *Bradyagaue stocki* nov. spec., a deep-sea halacarid mite (Halacaridae, Acari) from the Atlantic Ocean. Bull. Zoöl. Mus. Amsterdam 13 (8): 81–84.

Bartsch, I. (1993): Synopsis of the Antarctic Halacaroidea (Acari). Synopses of the Antarctic Benthos 4: 176 pp. Koeltz, Koenigstein.

Bartsch, I. (1994a): Halacarid mites (Acari) from hydrothermal deep-sea sites. New records. Cah. Biol. Mar. 35: 479–490.

Bartsch, I. (1994b): *Copidognathus* (Halacaridae: Acari) from western Australia. Description of twelve species of the *gibbus* group. Rec. West. Aust. Mus. 16: 535–566.

Bartsch, I. (1994c): Sexualdimorphismus bei Meeresmilben (Halacaridae, Acari). Übersicht und Beschreibung des Männchens von *Phacacarus flavellus.* Zool. Anz. 232: 61–74.

Bartsch, I. (1996a): Halacarines (Acari: Halacaridae) from Rottnest Island, Western Australia: the genera *Agauopsis* Viets and *Halacaropsis* gen. nov. Rec. West. Aust. Mus. 18: 1–18.

Bartsch, I. (1996b): Halacarid mites (Acari) from the Mid-Atlantic Ridge. New records. Cah. Biol. Mar. 37: 159–167.

Bartsch, I. (1996c): Halacarids (Halacaroidea, Acari) in freshwater. Multiple invasions from the Paleozoic onwards? J. Nat Hist. 30: 67–99.

Bartsch, I. (1997a): *Copidognathus nautilei* (Acari: Halacaridae) a new mite from a hydrothermal vent field in the Mid-Atlantic Ridge. Cah. Biol. Mar. 38: 29–33.

Bartsch, I. (1997b): *Thalassarachna* and *Halacarellus* (Halacaridae: Acari): two separate genera. J. Nat. Hist. 31: 1223–1236.

Bartsch, I. (1998a): *Colobocerasides koehleri* (Trouessart) und *C. auster* n. sp. (Arachnida: Acari: Halacaridae), Beschreibung der Arten. Mitt. Mus. Natkd. Berlin, Zool. Reihe 74: 225–232.

Bartsch, I. (1998b): A new species of the *Copidognathus pulcher* group (Acari: Halacaridae) from Western Australia: Description of adults and juveniles and notes on developmental pattern. Species Divers. 3: 187–200.

Bartsch, I. (1999a): *Actacarus ponticus,* a new marine mite from the Black Sea (Arachnida: Acari: Halacaridae). Senckenberg. biol. 78: 141–151.

Bartsch, I. (1999b): *Copidognathus* (Halacaridae: Acari) from Western Australia: five species of the *oculatus* group. Rec. West. Austr. Mus. 19: 299–321.

Bartsch, I. (1999c): Freshwater *Copidognathus* (Halacarinae, Acari) in Europe: a re-evaluation. Mitt. hamb. zool. Mus. Inst. 96: 169–179.

Bartsch, I. (2000): A new species of *Isobactrus* from the Black Sea (Acari, Halacaridae, Rhombognathinae). Cah. Biol. mar. 41: 407–411.

Bartsch, I. (2001a) A new halacarid genus (Acari: Halacaridae: Halacarinae) from the Great Meteor Seamount, Eastern North Atlantic. Species Divers. 6: 117–125.

Bartsch, I. (2001b): *Agauopsis* (Arachnida, Acari, Halacaridae) from the Northeastern Atlantic, description of two species, *A. minor* (Trouessart) and *Agauopsis valida* sp. nov. Mitt. Hamb. Zool. Mus. Inst. 98: 63–75.

Bartsch, I. (2002a): Halacaridae (Acari) from the Great Meteor Seamount (Northeastern Atlantic). description of two new *Copidognathus* species. Entomol. Mitt. Zool. Mus. Hamb. 14: 71–82.

Bartsch, I. (2002b): Halacarids from the Great Meteor Seamount (Northeastern Atlantic). Description of new species of *Agauopsis, Atelopsalis* and *Halacarus* and redescription of *H. spiniger* Bartsch (Arachnida: Acari: Halacaridae). Mitt. Hamb. Zool. Mus. Inst. 99: 29–45.

Bartsch, I. (2003a): Mangrove halacarid fauna (Halacaridae, Acari) of the Dampier region, Western Australia, with description of five new species. J. Nat. Hist. 37: 1855–1877.

Bartsch, I. (2003b): A new arenicolous *Copidognathus* (Halacaridae: Acari) from Dampier, Western Australia. In: The Marine Flora and Fauna of Dampier, Western Australia, Vol. 1, Wells, F. E., Walker, D. I. & Jones, D. S (eds), pp. 281–289. Western Australia Museum, Perth.

Bartsch, I. (2003c): Lohmannellinae (Halacaridae: Acari) from the Great Meteor Seamount (Northeastern Atlantic). Description of new species and reflections on the origin of the seamount fauna. Mitt. Hamb. Zool. Mus. Inst. 100: 101–117.

Bartsch, I. (2003d): The subfamily Rhombognathinae: developmental pattern and re-evaluation of the phylogeny (Arachnida, Acari, Halacaridae). Senckenberg Biol. 82: 15–57.

Bartsch, I. (2004a): Geographical and ecological distribution of marine halacarid genera and species (Acari: Halacaridae). Exp. Appl. Acar. 34: 37–58.

Bartsch, I. (2004b): Halacaridae (Acari) from the Great Meteor Seamount (Northeastern Atlantic). Description of *Simognathus* species. Mitt. Hamb. Zool. Mus. Inst. 101: 185–196.

Bartsch, I. (2004c): *Acarothrix ampliata* (Arachnida: Acari: Halacaridae), a new halacarid mite from Florida, with notes on external genital acetabula. Spec. Div. 9: 259–267.

Bartsch, I. (2005): Halacaridae from the depths of Western Antarctica (Archnida: Acari). Senckenberg Biol. 85: 31–41.

Bartsch, I. (2006): Halacaroidea (Acari): a guide to marine genera. Org. Div. Evol. 6, Electron. Suppl. 6: 1–104. (http://www.senckenberg.de/odes/06-06.htm)

Bartsch, I. (2007a): *Halacarus longiunguis* Police, 1909 (Acari: Halacaridae), a new record a century later, re-description and notes on Mediterranean *Halacarus* species. Entomol. Mitt. Zool. Mus. Hamb. 14: 393–403.

Bartsch, I. (2007b): The freshwater mite *Porolohmannella violacea* (Kramer, 1879) Acari: Halacaridae), description of juveniles and females and notes on development and distribution. Bonner Zool. Beitr. 55: 47–59.

Bartsch, I. (2007c): Freshwater Halacaridae (Acari) from New Zealands rivers and lakes, with notes on character variability. Mitt. Hamb. Zool. Mus. Inst. 104: 73–87.

Bartsch, I. (2008): Halacaridae (Acari) from Western Antarctica. New data. Entomol. Mitt. Zool. Mus. Hamb. 15: 53–61.

Bartsch, I. (2009): Checklist of marine and freshwater halacarid mite genera and species (Halacaridae: Acari) with notes on synonyms, habitats, distribution and descriptions of the taxa. Zootaxa 1998: 1–170.

Bartsch, I. (2010): *Halacarus excellens* Lohmann, 1907 (Acari: Halacaridae), a new record a century later, re-description and notes on this and other Antarctic halacarid species. Entomol. Mitt. Zool. Mus. Hamb. 15: 157–170.

Bartsch, I. (2011a): Marine mites (Acari: Halacaridae) from deep-sea gas seeps in the Gulf of Mexico. Meiofauna Marina 19: 97–108.

Bartsch, I. (2011b): *Halacarus socius* (Acari: Halacaridae), description of the male and diagnoses of species of the *Halacarus actenos* group. Zootaxa 2800: 18–40.

Bartsch, I. (2013a): Upper littoral rhombognathines (Acari: Halacaridae) from Singapore: description of a new species. Acarologia 53: 305–313.

Bartsch, I. (2013b): A new species, genus *Copidognathus* (Acari: Halacaridae), from a hydrothermal vent area of the East Pacific Rise. Cah. Biol. Mar. 54: 239–246.

Bartsch, I. (2013c): *Copidognathus andhraensis* (Halacaridae: Acari), a new record from Singapore, supplemental description and notes on the habitat. Entomol. Mitt. Zool. Mus. Hamb. 16 (190): 111–119.

Bartsch, I. (2014): Die Meeresmilbe *Isobactrus uniscutatus* (Acari: Halacaridae), ein "Europäer" in australischen Gewässern. Verh. Naturwiss. Ver. Hamburg N. F. 48: 177–188.

Bartsch, I. (2015a): The genital area of Halacaridae (Acari), life stages and development of morphological characters and implication on the classification. Zootaxa 3919: 201–259.

Bartsch, I. (2015b): *Thalassarachna basteri* (Acari, Halacaridae), description of external Characters:of larva, nymphs and adults and outline of discriminating characters of larvae. Ecologica Montenegrina 4: 33–45.

Bartsch, I. (2015c): Halacaridae (Acari) amongst an epiflora and fauna on trunks, branches, roots, and pneumatophores on the coast of Singapore. A survey. Raffles Bull. Zool., Suppl. 31: 96–138.

Bartsch, I. (2016a): *Arhodeoporus, Camactognathus, Plegadognathus,* and *Winlundia* (Acari: Halacaridae), re-evaluation and geographical distribution. Acarologia 56: 553–571.

Bartsch, I. (2016b): Antarctic Halacaridae (Acari), new records, these species characteristics and an updated list of species. Pol. Polar Res. 37: 131–154.

Bartsch, I. (2018): Freshwater halacarid mites (Acari: Halacaridae) from Madagascar — new records, keys and notes on distribution and biology. Bonn Zool. Bull. 67: 79–99.

Bartsch, I. (2021a): The halacarid genus *Lohmannella* (Halacaridae, Acari), list of species, notes on characters, distribution, ecology, and a tabular key. Acarina 29: 189–232.

Bartsch, I. (2021b): The genus *Halacarellus* (Halacaridae, Acari), analysis of distribution, ecology, systematic, and description of *H. balticus.* Mar. Biodivers. 51: 1–22. https://doi.org/10.1007/s12526-020-01143-y

Bartsch, I. & Gwyther, J. (2004): A non-indigenous halacarid species in Victoria, south-eastern Australia, *Isobactrus uniscutatus* (Rhombognathinae, Halacaridae, Acari). Proc. Roy. Soc. Vict. 116: 201–206.

Bartsch, I. & Smit, H. (2006): Een checklist van de Nederlandse Zeemijten (Acari: Halacaroidea). Nederl. Faun. Meded. 25: 25–32.

Bartsch, I. & Dovgal, I. V. (2010): A hydrothermal vent mite (Halacaridae, Acari) with a new *Corynophrya* species (Suctoria, Ciliophora), description of the

suctorian and its distribution on the halacarid mite. Eur. J. Protistol. 46: 196–203.
Bartsch, I. & Rybakova, E. (2015): Halacaridae (Arachnida: Acari) from Lost City, the Mid-Atlantic Ridge, description of new species. Cah. Biol. Mar. 56: 177–193.
Bergmann, M. & Klages, M. (2012): Increase of litter at the Arctic deep-sea observatory HAUSGARTEN. Mar. Pollut. Bull. 64: 2734–2741.
Brooks, J. M., Kennicutt II, M. C., Fisher, C. R., Macko, S. A., Cole, K., Childress, J. J., Bidigare, R. R. & Vetter, R. D. (1987): Evidence for energy and nutritional Carbon sources. Science 238 (4830): 1138–1142. DOI: 10.1126/science.238.4830.1138.
Chatterjee, T. (2021): A checklist of deep-sea halacarid mites (Acari, Halacaridae) found from more than 1000 m depth. Persian J. Acarol. 10: 341–346. https://doi.org/10.22073/pja.v10i3.67563
Chatterjee, T. & Guru, B. C. (2012): Sexual dimorphism in halacarid mites (Acari, Halacaridae): an updated overview. Acta Biol. 19: 97–112.
Chilton, C. (1883): On two marine mites. Trans. Proc. N. Z. Inst. (Zool.) 15: 190–192.
Crowe, J. H. & Camara, C. G. (1973): Studies on acarine cuticles—I, Cuticular pores in a marine mite. Comp. Biochem. Physiol. 45A: 757–766.
Cuvelier, D., Beesau, J., Ivanenko, V. N., Zeppilli, D., Sarradin, P-M. & Sarrazin, J. (2014): First insights into macro-and meiofaunal colonisation patterns on paired wood/slate substrata at Atlantic deep-sea hydrothermal vents. Deep Sea Res., Oceanogr. Res. Pap. 87(01): 70–81. DOI:10.1016/j.dsr.2014.02.008.
Danovaro, R., Corinaldesi, C., Dell'Anno, A. & Snelgrove, P. V. R. (2017): The deep-sea invertebrate under global change. Curr. Biol. 27: R461-R465.
Durucan, F. (2019): New records of *Copidognathus* (Acari: Halacaridae) from Antalya, Turkey. Persian J. Acarol. 8: 189–210.
Durucan, F. & Boyaci, Y. C. (2017): First record of the genus *Atelopsalis* (Acari: Halacaridae) from Turkey. Nat. Engin. Sci. 2:10–13. DOI:10.28978/nesciences.348327.
Durucan, F., Range, P. & Boyaci, Y. Ö. (2018): First record of *Halacarus actenos* Trouessart, 1889 (Halacaridae, Acari) from Portugal. J. Eğirdir Fish. Fac. 14: 84–88.
Durucan, F., De La Paz, J. C. & Hernández-Teixidor, D. (2023): Halacaridae (Acari) from Tenerife (Canary Islands). Persian J. Acarol. 12: 1–19.
Fountain, H. C. (1953): An examination of the original slides of marine Acari of Hodge, 1863. J. Mar. Biol. Ass., U.K. 32: 357–364.
Gage, J. D., Pearson M., Bilett D. S. M., Clark A. M., Jensen M., Paterson G. L. J. & Tyler P. A. (1984): Echinoderm zonation in the Rockall Trough (NE Atlantic). In: Proceedings of the Fifth International Echinoderm Conference, Keegen B. F. & O'Connor, B. D. S. (eds), pp. 31–36. Galway. Balkema, Rotterdam.
Galgani, L., Goßmann, I., Scholz-Böttcher, B., Jiang, X., Liu, Z., Scheidemann, L., Schlundt, C. & Engel, A. (2022): Hitchhiking into the deep: how microplastic particles are exported through the biological carbon pump in the North Atlantic Ocean. Environ. Sci. Technol. 56: 15638–15649.
García-Gómez, G., Garcia-Herrero A., Sánchez, N., Pardos, F., Izquierdo-Muñoz, A., Diego Fontaneto, D. & Martínez, A. (2022): Meiofauna is an important, yet often overlooked, component of biodiversity in the ecosystem formed by *Posidonia oceanica*. Invertebr. Biol. 141, e12377 DOI:10.1111/ivb.12377.
Gimbel, O. (1919): Über einige neue Halacariden. Mitt. Zool. Mus. Hamburg 36: 105–130.
Green, J. & MacQuitty, M. (1987): Halacarid Mites. Synopses of the British Fauna, New Series 36: 178 pp.
Guerao, G., Andree, K. B. & Rotllant, G. (2011): Direct evidence of parasitism by *Copidognathus stevcici* (Acari, Halacaridae) in crabs *Maja squinado* and *M. brachydactyla* (Brachyura, Majidae) in the laboratory. Aquacult. 316: 136–138.
Harasewych, M. & McArthur, A. (2000): A molecular phylogeny of the Patellogastropoda (Mollusca: Gastropoda). Mar. Biol. 137: 183–194. https://doi.org/10.1007/s002270000332
Hirst, S., 1923: On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). Ann. Mag. Nat. Hist. 12: 455–474.
Hodge, G. (1863): Contributions to the marine zoology of Seaham Harbour. On some undescribed marine Acari. Trans. Tyneside Nat. Fld Cl. 5: 298–303.
Hulings, N. C. (1974): A temporal study of Lebanese sand beach meiofauna. Cah. Biol. Mar. 15: 319–335.
Imamura, T. (1968): A new species of halacarid mites from the Antarctic Ocean. Acarologia 10: 472–476.
Jankovskaja, A. I. (1978): The first finding of ultra-abyssal Halacaridae (Acarina) in the Pacific. Zool. Zh. 57: 295–299.
Johnston, G. (1836) Illustrations in British zoology. Mag. Nat. Hist. 9: 353–357.
Kelly, N., Metaxas, A. & Butterfield, D. (2007): Spatial and temporal patterns of colonization by deep-sea hydrothermal vent invertebrates on the Juan de Fuca Ridge, NE Pacific. Aquat. Biol. 1: 1–16.
Kiel, S. & Little, C. T. S. (2006): Cold-seep mollusks are older than the general marine mollusk fauna. Science 313 (5792): 1429–1431. DOI: 10.1126/science.1126286
Kirchner, W. P. (1969): Zur Biologie und Ökologie von *Halacarus basteri basteri* Johnson 1836 (Acari, Trombidiformes). Oecologia 3: 56–69.
Kolesnikova, Ye.A., Povchun, A. S. & Serenko, I. V. (1995): Migration of meiobenthos in the inshore zone of the Black Sea. Hydrobiol. J. 31: 45–54.
Krantz, G. W. (1982): A new species of *Copidognathus* Trouessart (Acari: Actinedida: Halacaridae) from the Galapagos Rift. Can. J. Zool. 60: 1728–1731.
Krapivin, V. A. (2012): Symbionts of *Mytilus edulis* in the littoral and sublittoral zones of the Kandalaksha and Onega Gulfs of the White Sea. Parazitol. 46: 203–225.
Lancaster J. & Pugh, P. J. A. (1987): The effect of salinity, pH, and temperature on *Rhombognathus notops* (Gosse) (Rhombognathinae: Halacaridae: Prostigmata). J. Exp. Mar. Biol. Ecol. 111: 23–35.
Lee, J., Shin, J. H. & Chang, C. Y. (2023): New records of the *Copidognathus gibbus* group (Acari, Halacaridae) from Korea, with descriptions of *C. levicosta-*

tus n. sp. and *C. vicinus*. J. Mar. Sci. Engin. 11, 964. https://doi.org/10.3390/ jmse11050964.

Littler, M. M., Littler, D. S., Blair, S. M. & Norbis, J. N. (1985). Deepest known plant life discovered on an uncharted sea mount. Science 227: 57–59.

Lohmann, H. (1889): Die Unterfamilie der Halacaridae Murr. und die Meeresmilben der Ostsee. Zool. Jb. Syst. 4: 269–408.

Lohmann, H. (1893): Die Halacarinen der Plankton-Expedition. Ergebn. Atlant. Ozean Planktonexp. Humboldt Stift. 2. G. a: 11–95.

Lohmann, H. (1907a): Über einige faunistische Ergebnisse der Deutschen Südpolar-Expedition unter besonderer Berücksichtigung der Meeresmilben. Schr. Naturwiss. Ver. Schleswig-Holstein 14: 1–14.

Lohmann, H. (1907b): Die Meeresmilben der Deutschen Südpolar-Expedition 1901–1903. Dt. Südpol. Exped. 1901–1903 9. pp. 361–413. G. Fischer, Jena.

Macquart-Moulin, C. (1999): Diel vertical migration and endogenous swimming rhythm in *Asterope mariae* (Baird) and *Philomedes interpuncta* (Baird) (Crustacea Ostracoda Cypridinidae). J. Plankton Res. 21: 1891–1910. https://doi.org/10.1093/plankt/21.10.1891

Martínez, A., García-Gómez, G., García-Herrero, Á., Sánchez, N. & Pardos, F. (2021): Habitat differences filter functional diversity of low dispersive microscopic animals (Acari, Halacaridae). Hydrobiologia 848: 2681–2698. DOI: 10.1007/s10750-021-04586-x.

Morselli, I. & Mari, M. (1985): Ricerche sugli alacaridi delle coste Livornesi. IV. – Osservazioni su alcune specie raccolte su fondi sabbiosi della zona di Piombino. Atti Soc. Tosc. Sc. Nat., Mem. (B) 91: 201–220.

Mortensen. Th. (1940): Report of the Echinoidea collected by the United States Fisheries Steamer "Albatross"' during the Philippine Expedition 1907–1910. Part 2. The Echinothuridae, Saleniidae, Arbaciidae, Aspidodiademidae, Micropygidae, Diadematidae, Pedinidae, Temnopleuridae, Toxopneustidae, and Echinometridae. Smithson. Inst. U.S. Natl. Mus. Bull. 100, vol. 14: 1–52.

Newell, I. M. (1947): A systematic and ecological study of the Halacaridae of eastern North America. Bull. Bingham Oceanogr. Coll. 10: 1–232.

Newell, I. M. (1956): A parasitic species of *Copidognathus* (Acari: Halacaridae). Proc. Hawaii. Ent. Soc. 16: 122–125.

Newell, I. M. (1967): Abyssal Halacaridae (Acari) from the southeast Pacific. Pacif. Insects 9: 693–708.

Newell, I. M. (1971): Halacaridae (Acari) collected during cruise 17 of the R/V Anton Bruun, in the southeastern Pacific Ocean. Anton Bruun Rep. 8: 1–58.

Newell, I. M. (1984): Antarctic Halacaroidea. Antarctic Res. Ser. 40: 1–284.

Nikitina, M. P. (2013): Sezonnaâ dinamika čislennosti i žiznennye morskih klešči litoralnih fykoidov v okrestnostâh BBS. Moskovskii Gosudarstvennii Universitet imeni M. B. Lomonosova. Biologiceskii fakultet, Moskau, pp. 207–210, Table 1.

Normant, M. A., Zawal A., Chatterjee T. & Wójcik, D. (2013): Epibiotic mites associated with the invasive Chinese mitten crab *Eriocheir sinensis* – New records of Halacaridae from Poland. Oceanologia 55: 901–915. doi:10.5697/oc.55-4.901

Otto, J. C. (1999): Halacarid fauna of the Great Barrier Reef and Coral Sea: the genera *Agauopsis* and *Halacaropsis* (Acarina: Halacaridae). Mem. Qld. Mus. 43: 797–817.

Otto, J. C. (2000): *Spongihalacarus longiscutatus* n.gen., n.sp., a marine mite (Acari: Prostigmata: Halacaridae) associated with an alga-sponge symbiosis from the Great Barrier Reef Lagoon in Australia. Int. J. Acarol. 26: 279–283.

Pepato, A. R. (2010): Posiçao filogenética dos ácaros Actinotrichida (Chelicerata) e espermatologia comparada dos Halacaridae (Actinotrichida). PhD Thesis, Universidade de Sao Paulo. http.//www.teses.usp.br/teses/disponiveis/41/41133/tde-02032010-110711/

Pepato, A. R. & Tiago, C. G. (2004): *Atelopsalis atlantica* sp.n., a new species of halacarid mites from the south-eastern Brazilian coast (Acari, Halacaridae). Revist. Iber. Aracnol. 10: 146–148.

Pepato, A. R. & C. G. Tiago (2005): Two new species of *Agauopsis* (Acari, Halacaridae) from southeastern Brazil. Zootaxa 994: 1–12.

Pepato, A. R., Santos, C. & Tiago, G. C. (2005): Two new closely related species of *Copidognathu*s (Acari: Halacaridae) associated with crabs. Cah. Biol. Mar. 46: 69–79.

Pepato, A. R. & Da Silveira, P. S. A. (2013): Two new species of *Halacarus* (Acari, Prostigmata) from Brazil. Zootaxa 3670: 591–600.

Pepato, A. R., Vidigal, T. H.D. A. & Klimov, P. B. (2018): Molecular phylogeny of marine mites (Acariformes: Halacaridae), the oldest radiation of extant secondarily marine animals. Mol. Phyl. Evol. 129: 182–188.

Pugh, P. J. A. (1996): Using artificial substrata to monitor how cryptofaunal acari colonize littoral algae on sub-Antarctic South Georgia. Acarologia 37: 189–200.

Pugh, P. J. A., King, P. E. & Fordy, M. R. (1987): Possible significance of the claw structure in the Rhombognathinae (Halacaridae: Prostigmata: Acari). Acarologia 28: 171–175.

Ramirez-Llodra, E. (2020): Deep-Sea Ecosystems. Biodiversity and anthropogenic impacts. Chapter 2. In: The law of the seabed: Access, uses and protection of seabed resources, Banet, C. (ed.). pp. 36–60. Brill Nijhoff. DOI: https//doi.org/10.1163/9789004391567_004

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A. & Vecchione, M. (2010): Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosci. 7: 2851–2899.

Roberts, H., Carney, R., Kupchick, M., Fisher, C., Nelson, K., Becker, E., Goehring, L., Lessard-Pilon, S., Telesnicki, G., Bernard, B., Brooks, J., Bright, M., Cordes, E., Hourdez, S., Hunt Jr., J., Shedd, W., Boland, G., Joye, S., Samarkin, V., Bernier, M., Bowles, M., MacDonald, I., Niemann, H., Petersen, C., [[Morrison, C.]]

& Potter, J. (2007): Alvin explores the deep northern Gulf of Mexico slope. EOS 88: 341–342.
Saeedi, H., Simões, M. & Brandt, A. (2020): Biodiversity and distribution patterns of deep-sea fauna along the temperate NW Pacific. Progr. Oceanogr. 183: 102–296.
Schmidt, P. (1968): Die quantitative Populationsdynamik des Mesopsammon am Gezeiten-Sandstrand der Nordseeinsel Sylt. I. Faktorengefüge und biologische Gliederung des Lebensraumes. Int. Rev. Ges. Hydrobiol. 53: 723–779.
Schwabe, E., Bartsch, I., Błażewicz-Paszkowycz, M., Brenke, N., Alexei V., Chernyshev, A. V., Elsner, N. O., Fischer, V., Jażdżewska, A., Malyutina, M. V., Miljutin, D., Miljutina, M., Kamenev,, G. M., Karanovic, I., Maiorova, A. & Würzberg, L. (2015): Wood-associated fauna collected during the KuramBio – expedition in the North West Pacific. Deep-Sea Res. II 111: 376–388.
Siemer, F. (1996): Untersuchungen zur Verteilung, zur Biologie und zum Lebenszyklus mariner Halacaridae (Prostigmata: Acari) im ästuarinen Felslitoral. PhD-Thesis, Universität Bremen, 165 pp.
Smrž, J. (2007): "Nymphes plissées" structure of the cuticle of juveniles of some oribatid mites (Acari: Oribatida). Eur. J. Entomol. 104: 619–629:
Sokolov, I. I. (1962): [New species of the halacarids from the Antarctic.] Issled. Fauny Morei 1: 190–195. (In Russian)
Sokolov, I. I. & Jankovskaja, A. I. (1968): Perwyi abissal'nyi predstavitel' Halacaridae (Acari) iz raina Kurilo-Kamčatskoi wpadiny. Dokl. Akad. Nauk SSSR 179: 486–488.
Sokolov, I. I. & Jankovskaja, A. I. (1969): New genus and species of Halacaridae (Acari) from the abyssal region of the Kuril-Kamchatka Trench. In: Proceedings of the 2nd International Congress of Acarology, pp. 113–114, Owen G. (ed.). Budapest.
Sokolov, I. I. & Jankovskaja, A. I. (1970): [An abyssal representative of Halacaridae (Acari) of the Kuril-Kamchatka Region.] Trud. Inst. Okeanol. 86: 427–431.
Somerfield, P. (1991): Additional records of marine Halacaridae (Acari: Prostigmata) from Ireland. Bull. Ir. Biogeogr. Soc. 14: 2–23.
Števčić, Z. (1968): Parasiten und Kommensalen des Brutraumes der Seespinne (*Maja squinado* Herbst). Thalassa Jugoslavica 4: 5–10.
Straarup, J.-O. (1968): On the life cycles of halacarids (Acari) from the Öresund. Ophelia 5: 255–271.
Teasdale. M., Vopel K. & Thistle D. (2004): The timing of benthic copepod emergence. Limnol. Oceanogr. 49: 884–889.
Thistle, D. (2003): The deep-sea floor: An overview. Chapter 2, pp. 5–38. In P. A. Tyler (ed.), Ecosystems of the Deep, Elsevier Science B. V., Amsterdam, The Netherlands, 569 pp.
Thomae, H. (1926): Beiträge zur Anatomie der Halacariden. Zool. Jb. Anat. 47: 155–190.
Trouessart, E. L. (1889): Revue synoptique de la famille des halacaridae. Bull. Scient. Fr. Belg. Sér. 3, 20: 225–251.
Trouessart, E. (1894): Notes sur les acariens marins (Halacaridae) dragués par M. P. Hallez dans le Pas-de-Calais. Rev. Biol. N. Fr. 6: 154–184.
Trouessart, E. (1896): Note préliminaire sur les acariens marins dragués à de grandes profondeurs par M. Koehler dans le Golfe de Gascogne (Août – Septembre 1895). Bull. Soc. Zool. France 21: 102–105.
Trouessart, E. (1902): Note préliminaire sur les acariens marins (Halacaridae) recueillis par S.A.S. le Prince de Monaco, dans les mers arctiques. Bull. Soc. Zool. France 27: 66–70.
Trouessart, E.& Neumann, M. G. (1894). Note sur les acariens marins (Halacaridae) récoltés par M. Henri Gadeau de Kerville sur le littoral du département de la Manche (Juillet-Août 1893). Bull. Soc. Amis Sci. Nat. Rouen 9: 139–175.
Trouessart, E. & Neumann, M. G. (1896): Halacariens. Résultats scientifiques de la Campagne du 'Caudan' dans le Golf de Gascogne. Ann. Univ. Lyon 26: 325–353.
Trouessart, E. & Neumann, G. (1901): Note sur les Acariens marins (Halacaridae) récoltés par M. Henri de Gadeau de Kerville dans la région d'Omonville-la-Rogue (Manche) et dans la fosse de la Hague. Bull. Soc. Amis Sci. Nat. Rouen, Sér. 4, 14: 247–266.
Trouessart, E. L. & Neumann, G. (1907): Acariens marins. In: Expédition Antarctique Française (1903–1905), commandée par le Dr. Jean Charcot, Sci. Nat.: Docums scient. pp. 1–9. Masson, Paris.
Tsurumi, M. & Tunnicliffe, V. (2001): Characteristics of a hydrothermal vent assemblage on a volcanically active segment of Juan de Fuca Ridge, northeast Pacific. Can. J. Fish. Aquat. Sci. 58: 530–542.
Van Cauwenberghe, L., Vanreusel, A., Mees, J. & Janssen, C. R. (2013): Microplastic pollution in deep-sea sediments. Environ. Pollut. 132: 495–499.
Van Dover, C. L., German, C. R., Speer, K. G., Parson, L. M. & Vrijenhoek, R. C. (2002): Evolution and biogeography of Deep-Sea vent and seep invertebrates. Science 295: 1253–1257.
Viets, K. (1927a): Die Halacaridae der Nordsee. Z. Wiss. Zool. 130: 83–173.
Viets, K. (1927b): Halacaridae. Tierwelt N.- u. Ostsee XI.c: 1–72.
Viets, K. (1931): Hydracarinen der Fauna Arctica. Fauna Arct. 6: 1–8.
Viets, K. (1938): Eine merkwürdige, neue, in Tiefsee-Echiniden schmarotzende Halacaridengattung und -Art (Acari). Z. Parasitkd. 10: 210–216.
Viets, K. (1940): Meeresmilben aus der Adria (Halacaridae und Hydrachnellae, Acari). Arch. Naturgesch. (N.F.) 9: 1–135.
Viets, K. (1950): Die Meeresmilben (Halacaridae, Acari) der Fauna Antarctica. Further Zool. Results Swed. Antarct. Exped. 4: 1–44.
Viets, K. (1952): Nachträge zu "Die Meeresmilben (Halacaridae, Acari) der Fauna Antarctica". Further Zool. Results Swed. Antarct. Exped. 4: 1–11.
Viets, K. (1956): Die Milben des Süßwassers und des Meeres. Katalog der Halacaridae, Meeresmilben. II. Abschnitt. In: Viets, K. (ed.). Die Milben des Süßwassers und des Meeres. Hydrachnellae et Halacaridae, pp. 641–870. Fischer Verlag, Jena,
Voinov, D. N. (1896): *Halacarus Trouessarti*. Nouvelle espèce d'Halacaridae de la Méditerranée. Bull. Soc. Zool. Fr. 21: 128–129.

Voinov, D. N. (1897): O specie noua halacarid. Bul. Soc. Sti. Buc. 6: 92–95.
Walters, K. (1988): Diel vertical migration of sediment-associated meiofauna in subtropical sand and seagrass habitats. J. Exp. Mar. Biol. Ecol. 117: 169–186. https://doi.org/10.1016/0022-0981(88)90224–9
Wieser, K. & Kanwisher, J. (1959): Respiration and anaerobic survival in some sea weed-inhabiting invertebrates. Biol. Bull. 117: 594–600.
Wikipedia (2022): en.Wikipedia.org/. Accessed at 2022.
Williams, P. M., Smith, K. L., Druffel, E. M. & Linick, T. W. (1981): Dietary carbon sources of mussels and tubeworms from Galápagos hydrothermal vents determined from tissue 14C activity. Nature 292: 448–449.
Wilson, G. D. F. & Hessler, R. R. (1987): Speciation in the deep sea. Ann. Rev. Ecol. Syst. 18: 185–207.
Womersley, H. (1937): Acarina. Australasian Antarctic Expedition 1911–1914, Sci. Rep. Ser. C, 10: 1–24.
WoRDSS (2022): The World Register of Deep-Sea Species. Glover, A. G., Higgs, N. & Horton, T. (eds). Accessed at 2022–07-14 https://vvv.marinespeciesorg/deep sea org DOI 1014284/352
WoRMS (2023) World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2022
Woodall, L. C., Sanchez-Vidal, A., Canals, M., Paterson, G. L. J., Coppock, R., Sleight, V., Calafat, A. & Rogers, A. D. (2014): The deep sea is a major sink for microplastic debris. R. Soc. Open Sci. 1:140317. https://doi.org/10.1098/rsos.140317
Zhang, Z.-Q. (ed.) (2011): Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 1–237.

Table 1. Deep-sea Halacaridae (Acari), list of presently 92 accepted species with states of morphological characters and depth distribution. To each one of the 18 genera the number of world-wide registered species is added [in square brackets]. (Abbreviations used: abs, absent; AD, anterodorsal plate; arch, arched; catch, catching; catch+walk, used both for catching and walking; cer, cerotegumental; DN, deutonymph; elon, elongate; equal, in dorsal aspect, areas with striated integument and solid plates almost equal in size; flank, sclerites flanked by large valves; fov, foveate; fov/panel, partly foveate, partly panelled; fov/retic, partly foveate, partly reticulate; hirs, hirsute; hone-com, honeycomb like structure; hood; with hood or hooded; (no), interpretation of character state not sure; norm, normal sized, used in respect to shape of anal cone if anal sclerites surpass the anal valves; obscu, obscured; OC, ocular plate(s); panel, panelled, coarsely reticulate; PD, posterodorsal plate; pgs, perigenital setae; plat, plate; point, pointed; pres, present; (pres) present but feebly developed; rais, raised; red, largely reduced; retic, reticulate; sho, short; sligh, slightly; (smooth), claws with accessory process but any pectines not described; spike, spikes; spin, spine; squam, squamose; (squam), striated integument only delicately squamose; stri, striae; trun, truncate; walk, walking; walk/catch, used both for walking and catching; -, no information given).

Table 1 genera *Acanthohalacarus* to *Agauopsis*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, orna-mentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
Acanthohalacarus [1]											
reticulatus	450–541	510–541	450–520	1.6:1	plat	AD, OC, PD	trun	retic	no	abs	abs
Agaue [44]											
abyssorum	470–500	470–500	470–500	1.5–1.6:1	plat	AD, OC, PD	trun	fov	yes	abs	pres
agauoides	530–750	575–750	530–640	1.4–1.5:1	plat	AD, OC, PD	arch	cer, lam	yes	abs	pres
corollata	580–725	580–725	587–685	1.2:1	stri-plat	AD, OC, PD	arch	spike	no	abs	abs
hirtella (DN)	DN = 450	—	—	—	—	AD, OC, PD	—	—	—	—	abs
obscura	575–755	575–755	595–700	1.3:1	stri	AD, OC, PD	arch	spikes, villi	no	abs	abs
parva	615–1200	690–1200	615–1025	1.6:1	plat	AD, OC, PD	arch	retic	yes	abs	pres
plutonia	650	650	—	1.6:1	plat	AD, OC, PD	spin	retic	yes	abs	abs
tenuirostris	1100–1310	1165–1310	1100–1260	1.7:1	plat	AD, OC, PD	arch	hone-com	yes	abs	pres
verrucosa	835–910	835–910	—	1.5:1	stri	AD, OC, PD	trun	spikes, villi	no	abs	abs
Agauides [2]											
cryosi	768	768	—	1.4:1	stri	AD, OC, PD	trun	retic	yes	abs	abs
pacifica	620	620	—	1.5:1	stri	AD, OC, PD	arch	retic	no	abs	abs
Agauopsis [91]											
bathyalis	360	360	—	1.8:1	plat	AD, OC, PD	spin	retic	yes	abs	abs
costata	357–374	357–374	—	1.5:1	plat	AD, OC, PD	spin	porose	yes	abs	abs
producta	313–392	313–392	—	1.5–1.6:1	plat	AD, OC, PD	spin	porose	yes	abs	abs
racki	585	585	—	1.5:1	plat	AD, OC, PD	spin	retic	yes	abs	pres
valida	467	467	—	1.5:1	plat	AD, OC, PD	hood/spine	pitted	yes	pres	pres

Table 1 genera *Acanthohalacarus* to *Agauopsis*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
Acanthohalacarus												
reticulatus	abs	no	abs	sho	norm	1.9:1	0.3:1	1.2:1	walk	tiny	delicate	511
Agaue												
abyssorum	pres	no	—	sho	norm	ca 2.0:1	0.3:1	0.9:1	walk	pres	distinct	400–1410
agauoides	pres	no	abs	sho	norm	1.9–2.0:1	0.3–0.4:1	0.8:1	walk	pres	pres	30–680
corollata	pres	yes	pres	sho	norm	2.7:1	0.4:1	1.1:1	walk	abs	abs	1427–4223
hirtella (DN)	—	yes	pres	—	norm	—	—	—	walk	—	—	520–530
obscura	pres	yes	pres	elon	norm	2.4:1	0.4:1	1.2:1	walk	pres	small	71–1486
parva	pres	(no)	abs	sho	norm	2.7:1	0.4:1	0.8–1.0:1	walk	pres	pres	0–1061
plutonia	pres	no	abs	sho	norm	—	0.4:1	1.1:1	walk	pres	delicate	540–919
tenuirostris	pres	no	abs	sho	norm	—	0.4–0.5:1	ca 1:1	walk	pres	delicate	20–622
verrucosa	pres	yes	pres	sho	norm	—	0.3:1	0.9–1.0;1	walk	abs	smooth	201–2893
Agauides												
cryosi	—	no	abs	sho	norm	—	0.3:1	0.8:1	walk	smooth	abs	1505–1540
pacifica	pres	no	abs	sho	norm	—	0.3:1	0.8:1	walk/catch	smooth	abs	570
Agauopsis												
bathyalis	—	no	abs	sho	norm	—	0.4:1	0.9:1	walk/catch	delicate	delicate	1380
costata	pres	no	abs	sho	norm	1.8:1	—	—	walk/catch	—	delicate	550–950
producta	pres	no	abs	sho	norm	2.0:1	—	—	walk/catch	—	—	550–950
racki	—	no	abs	sho	norm	1.7:1	0.3:1	—	walk/catch	delicate	—	247–567
valida	pres	no	abs	sho	norm	1.8:1	0.3:1	0.9:1	walk/catch	abs	abs	302–511

Table 1 genera *Atelopsalis* to *Bradyagaue*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, ornamentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
Atelopsalis [8]											
tricuspis	218–235	218–235	—	1.7:1	plat	AD, OC, PD	hood	panel	yes	pres	pres
Bathyhalacarus [12]											
abyssiculus	409–502	409–502	—	1.1:1	stri	AD, OC, PD	trun-arch	retic	no	abs	abs
acanthophorus	434–486	486	434–450	1.4:1	plat	AD, OC, PD	spin	retic	no	abs	abs
aculifer	663–680	680	663	1.4:1	stri	AD, OC, PD	spin	retic	no	abs	abs
acutus	378–490	378–490	—	1.5:1	stri	AD, OC, PD	spin	retic	no	abs	abs
anomalus	364	364	—	1.4:1	stri	AD, OC, PD	spin	retic	no	abs	abs
atlanticus	406–446	406–446	—	1.3:1	stri	AD, OC, PD	spin	retic	no	abs	abs
dictyotus	447	—	447	1.4:1	stri	AD, OC, PD	spin	retic	no	abs	abs
humboldti (DN)	DN = 461	—	—	—	—	AD, OC, PD	sho spin	retic	no	abs	abs
quadricornis	500–630	500–630	—	1.6:1	stri	AD, OC,?	trun	—	—	abs	abs
sordidus	558	558	—	1.1:1	stri	AD, OC	arch	porose	no	abs	abs
speciosus	416–497	416–497	416–478	1.6:1	plat	AD, OC, PD	arch	retic	no	abs	abs
Bradyagaue [17]											
aspidionis	831	831	—	2.0:1	equal	AD, OC, PD	trun	uniform	no	abs	pres
drygalskii	740–1000	750–1000	740–1000	1.9–2.2:1	equal	AD, OC, PD	trun	uniform	no	abs	pres
quadriseta	600–687	600–618	679–687	1.9–2.1:1	equal	AD, OC, PD	trun	uniform	no	abs	pres
stocki	595	595	—	1.8:1	equal	AD, OC, PD	trun	retic	no	abs	abs

Table 1 genera *Atelopsalis* to *Bradyagaue*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
Atelopsalis												
tricuspis	abs	no	abs	sho	norm	0.9–1.1:1	0.2:1	0.9:1	catch	pres	minute	256–1410
Bathyhalacarus												
abyssiculus	—	sligh rais	abs	very sho	small	1.7:1	0.3:1	1.1:1	walk	delicate	abs	4400
acanthophorus	—	sligh rais	abs	sho	norm	1.6:1	0.3:1	1.0:1	walk	minute	delicate	1427–1643
aculifer	pres	(no)	abs	sho	norm	—	0.3:1	1.0:1	walk	—	smooth	5208–5223
acutus	—	no	abs	sho	norm	1.6:1	0.3:1	ca 1.0:1	walk	pres	delicate	2041–2707 (2900)
anomalus	abs	no	abs	obscu	small	1.6:1	0.3:1	1.1:1	walk	delicate	abs	2875–2917
atlanticus	abs	no	abs	sho	—	1.7:1	0.4:1	1.1:1	walk	smooth	abs	3264–3356
dictyotus	pres	(no)	abs	sho	norm	—	0.3:1	1.1:1	walk	minute	delicate	1410
humboldti (DN)	—	no	abs	—	norm	—	—	1.2:1	walk	—	—	1760–4100
quadricornis	pres	yes	pres	sho	—	—	0.4:1	0.8:1	walk	—	—	5090–6850
sordidus	pres	no	abs	obscu	small	—	0.4:1	1.4:1	walk	abs	abs	1380
speciosus	—	no	abs	sho,obscu	norm	2.5:1	0.3:1	1.0:1	walk	minute	delicate	570
Bradyagaue												
aspidionis	—	no	abs	sho	norm	2.4:1	—	—	walk	—	—	1442–1444
drygalskii	abs	no	abs	sho	norm	2.0:1	0.3:1	0.8–0.9	walk	pres	pres	0–1674
quadriseta	(on pgs)	no	abs	sho	norm	—	—	—	walk	pres	pres	62–485
stocki	pres	no	abs	sho	norm	2.3:1	0.3:1	1.1:1	walk	pres	pres	1200

Table 1 genera *Colobocerasides* to *Copidognathus*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, ornamentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
Colobocerasides [2]											
auster	470	470	—	1.9:1	stri	AD, OC, PD	trun	uniform	no	abs	abs
koehleri	610–680 (?)	610–680 (?)	—	ca 2.0:1	stri	AD, OC, PD	trun	uniform	no	abs	abs
Copidognathus [374]											
abyssiculus	384–418	384–418	—	1.7:1	plat	AD, OC, PD	arch	retic	yes	abs	abs
abyssorum	403–471	403–446	412–471	1.8:1	plat	AD, OC, PD	arch	panell	yes	abs	abs
alvinus	370–396	377–396	370–384	1.7–1.8:1	plat	AD, OC, PD	arch	retic	yes	abs	abs
anops	326	326	—	1.9:1	plat	AD, OC, PD	hood	panel	yes	pres	abs
atlanticus	327–348	327–348		ca 2.0:1	plat	AD, OC, PD	hood	panel	yes	abs	abs
bituberosus	329–365	329	348–365	1.8:1	plat	AD, OC, PD	hood	retic	yes	pres	abs
bruuni	418	—	418	2.1:1	plat	AD, OC, PD	hood	Fov/panel	yes	abs	abs
calidictyotus	394–440	397–440	394–440	1.9:1	plat	AD, OC, PD	arch	retic	yes	pres	abs
corneatus	305–331	305–331	305–313	1.7–2.0:1	plat	AD, OC, PD	hood	fov	yes	pres	pres
curiosus	339	339	—	1.3:1	plat	AD, OC, PD	spinelet	fov/retic	(yes)	abs	abs
dentatus	360–435	360–435	387–410	1.4–1.6:1	plat	AD, OC, PD	hood	panel	yes	pres	pres
flabelliferus	460–540	460–540	475–500	1.6–1.7:1	plat	AD, OC, PD	hood	retic	yes	pres	abs
inusitatus	458	—	458	1.3:1	plat	AD, OC, PD	arch	retic	no	abs	abs
magniporus	265–316	265–316	275–301	2.0–2.1:1	plat	AD, OC, PD	hood	retic	—	abs	abs
nautilei	395–475	395–475	421–452	1.6:1	plat	AD, OC, PD	hood	retic	yes	pres	abs
papillatus	395–453	395–453	395–428	1.6:1	plat	AD, OC, PD	arch	fov	(no)	abs	abs
posticus	339–383	357–383	339–474	1.2–1.5:1	plat	AD, OC, PD	hood	fov	yes	pres	abs

Table 1 genera *Colobocerasides* to *Copidognathus*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
Colobocerasides												
auster	abs	no	abs	sho	norm	1.9:1	0.4:1	0.7:1	walk	pres	pres	211–480
koehleri	abs	no	abs	sho	norm	1.9:1	0.3:1	0.6:1	walk	pres	pres	1410
Copidognathus												
abyssiculus	pres	no	abs	sho	norm	1.6:1	0.3:1	0.7:1	walk	pres	delicate	5208–5223
abyssorum	pres	no	abs	elon	norm	2.0:1	0.3:1	1.0:1	walk	pres	delicate	5208–5223
alvinus	abs	no	abs	sho	norm	—	0.3:1	0.7:1	walk	pres	minute	1636–1685
anops	abs	no	abs	sho	norm	1.5–1.6:1	—	0.6:1	walk	—	pres	1.565
atlanticus	—	no	abs	sho	norm	1.5:1	0.3:1	0.7–0.8:1	walk	pres	pres	993–1011
bituberosus	abs	no	abs	sho	norm	1.6:1	—	—	walk	pres	pres	485
bruuni	pres	no	pres	long	norm	1.8:1	0.3:1	0.8:1	walk	abs	abs	3680–4100
calidictyotus	abs	no	abs	sho	norm	1.6:1	0.3:1	0.7:1	walk	pres	pres	736–847
corneatus	abs	no	abs	sho	norm	1.7:1	0.3:1	0.8:1	walk	pres	delicate	485
curiosus	abs	yes	pres	elon	norm	1.2:1	0.2:1	0.9–1.0:1	walk	pres	delicate	755–770
dentatus	abs	no	abs	sho	norm	1.7–1.8:1	0.3:1	0.7:1	walk	pres	pres	0–509
flabelliferus	squam	no	abs	elon	flank	1.8:1	0.3:1	0.7:1	walk	pres	pres	2190–2745
inusitatus	—	yes	abs	long	norm	1.3:1	0.2:1	1.2:1	walk	abs	abs	1508
magniporus	abs	no	abs	sho	norm	1.7:1	0.3:1	0.8:1	walk	pres	pres	302–488
nautilei	(squam)	no	abs	sho	norm	—	0.3:1	0.8:1	walk	pres	delicate	3014–4087
papillatus	squam	no	abs	elon	flank	2.0:1	0.3:1	0.9–1.1:1	walk	pres	pres	1914–5229

Table 1 genera *Copidognathus* to *Halacarus*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, ornamentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
Copidognathus **continued**											
procerus	250–261	250	252–261	2.3–2.4:1	plat	AD, OC, PD	arch	panel	yes	abs	pres
richardi	550–570	550–570	558	1.4:1	plat	AD, OC, PD	trun	faint	yes	pres	pres
triton	400–452	400–435	400–452	1.7–1.9:1	plat	AD, OC, PD	arch	panel	yes	pres	(pres)
tritoni	395–450	395–450	410	1.4–1.6:1	plat	AD, OC, PD	point	retic	yes	pres	—
trouessarti	322–396	322–435	327–396	1.6:1	plat	AD, OC, PD	trun	retic	yes	pres	pres
uniareolatus	418	—	418	1.5:1	plat	AD, OC, PD	arch		yes	pres	abs
Halacarellus [50]											
auzendei	502–675	562–675	502–560	1.6:1	plat	AD, OC, PD	arch	retic	—	abs	abs
bandyi	648	648	—	1.4:1	stri	AD, OC, PD	arch	smooth	—	abs	abs
decipiens	699–810	770–800	699–810	1.5:1	plat	AD, OC, PD	spinelet	smooth	yes	abs	abs
epimeralis (DN)	DN = 557	—	—	—	—	AD, OC, PD	arch	—	—	abs	abs
Halacarus [76]											
actenos	555–870	(519?)–870	(422?)–670	1.5–1.8:1	stri	AD, OC	spin	no	no	abs	pres
amaudi	550–640	640	550–600	1.9:1	stri	AD, OC, PD	spin	no	no	abs	pres
atlanticus	388–500	430–500	388–453	1.7–1.8:1	stri	AD, PD	wide spin	no	no	abs	abs
dictyotus	410–675(?)	475–675(?)	410–493	1.7:1	stri	AD, PD	long spin	retic	no	abs	abs
echinatus	696–861	861	696	2.1:1	stri	AD, OC	long spin	no	no	abs	pres
excellens	976–1360	1250–1360	976–1010	1.6–1.8:1	stri	AD, OC, PD	long spin	no	no	abs	pres

Table 1. genera *Copidognathus* to *Halacarus*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
Copidognathus **continued**												
posticus	—	no	abs	sho	norm	1.5–1.7:1	1.0:1	1.0:1	—	pres	pres	485–3200
procerus	—	no	abs	sho	norm	1.5:1	0.2:1	0.6:1	walk	pres	delicate	511
richardi	pres	no	abs	sho	norm	1.6:1	0.3:1	0.8:1	walk	pres	pres	48–599
triton	abs	no	abs	sho	norm	1.6–1.7:1	—	0.8:1	walk	pres	delicate	550–570
tritoni	abs	no	abs	sho	norm	1.5:1	0.3:1	0.8:1	walk	pres	pres	2500–2542
trouessarti	abs	no	abs	sho	norm	1.8–1.9:1	0.3:1	1.0–1.1:1	walk	pres	delicate	1–511
uniareolatus	—	no	abs	sho	norm	1.8:1	0.3:1	—	walk	pres	delicate	550–1565
Halacarellus												
auzendei	abs	no	abs	sho	norm	1.7:1	0.3:1	0.8:1	catch+walk	pres	pres	1700–3478
bandyi	hirs	no	abs	sho	obscu	1.8:1	0.3:1	1.6:1	walk	pres	delicate	3680–4100
decipiens	abs	no	abs	sho	norm	2.4:1	0.3:1	1.0:1	walk	pres	delicate	79–549
epimeralis (DN)	—	no	abs	sho	—	—	—	—	—	—	—	742
Halacarus												
actenos	abs	no	abs	sho	norm	2.0:1	0.3:1	1.0:1	catch+walk	pres	?	0–500
arnaudi	abs	no	abs	sho	norm	2.0:1	0.3:1	0.9:1	—	—	—	ca 5–500
atlanticus	abs	no	abs	sho	norm	2.1:1	0.3:1	1.1:1	catch+walk	(pres)	abs	508–523
dictyotus	abs	no	abs	sho	norm	1.9:1	0.3:1	1.2:1	catch+walk	abs	abs	250–620
echinatus	abs	no	abs	sho	red	2.4:1	0.3:1	ca 1.0:1	catch+walk	pres	abs	40–485
excellens	abs	no	abs	sho	small	2.2:1	—	1.0–1.1:1	catch+walk	abs	abs	385–509

Table 1. genera *Halacarus* to *Pelacarus*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, ornamentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
***Halacarus* continued**											
lamellipes	1095–1098	1098	1095	2.1:1	stri	AD, PD	long spin	no	no	abs	abs
laterculatus	596–853	626–853	596–644	1.9:1	stri	AD, OC, PD	spin	no	no	abs	pres
leptopus	562–662	580–653	562–662	1.3:1	stri	AD, corneae	long spin	no	no	abs	pres
longior	790–1225	965–1225	790–995	1.9:1	stri	AD, PD	spin	no	no	abs	abs
peregrinus	384–593	483–593	384–393	1.8–2.2:1	stri	AD, OC, [PD]	spin	no	no	abs	abs
profundus	1068–1474	1449–1474	1068–1220	1.9:1	stri	AD, PD	spin	no	no	abs	abs
prolongatus	615–760	750	615–760	2.5:1	stri	AD	long spin	no	no	abs	abs
spathulifer	470	470	—	1.7:1	stri	AD, PD	wide spin	no	no	abs	abs
spiniger	390	390	—	2.1:1	stri	AD, PD	long spin	no	no	abs	abs
Lohmannella [39]											
abyssalis	385	385	—	1.3:1	plat	AD, OC, PD	trun	no	no	abs	abs
cygna	515	515	—	1.2:1	plat	AD, OC, PD	arch	no	no	abs	abs
falcata	270(?)–515	270(?)–515	335–490	1.3:1	plat	AD, OC, PD	trun	no	no	abs	pres
fukushimai	491–582	495–560	491–582	1.3–1.5:1	plat	AD, OC, PD	trun	no	no	abs	pres
Pelacarus [1]											
aculeatus	362–450	415–450	362–409	1.4:1	equal	AD, OC, PD	sho hood	fov	yes	pres	abs

Table 1. genera *Halacarus* to *Pelacarus*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
***Halacarus* continued**												
lamellipes	abs	no	abs	sho	norm	2.2:1	—	—	—	abs	abs	419–483
laterculatus	abs	no	abs	sho	norm	1.9:1	0.2:1	0.8:1	catch+walk	abs	abs	9–746
leptopus	abs	no	abs	sho	norm	2.3:1	0.3:1	1.1:1	catch+walk	pres	pres	332–511
longior	abs	no	abs	sho	small	2.2:1	0.3:1	1.1:1	catch+walk	abs	abs	2195–3356
peregrinus	abs	no	abs	sho	norm	2.2:1	0.3:1	1.0:1	catch+walk	pres	abs	993–2707
profundus	abs	no	abs	sho	norm	2.4:1	—	0.8:1	catch+walk	abs	abs	2212–2306
prolongatus	pres	no	abs	sho	norm	2.6:1	0.3:1	1.0–1.1:1	catch+walk	pres	abs	824–845
spathulifer	pres	no	abs	sho	norm	1.9:1	0.3:1	—	catch+walk	—	abs	485
spiniger	—	no	abs	sho	norm	2.0:1	0.3:1	1.0:1	catch+walk	abs	abs	332–511
Lohmannella												
abyssalis	abs	no	abs	sho	norm	2.2:1	0.6:1	0.7:1	walk+catch	abs	abs	2893
cygna	abs	no	abs	sho	norm	—	0.9:1	1.0:1	walk+catch	abs	abs	1427–1643 (–2000?)
falcata	pres	no	abs	sho	norm	2.0:1	0.5–0.6:1	0.7:1	walk+catch	pres	—	2–500(?) (–1410?)
fukushimai	pres	no	abs	elon	norm	1.3–1.5:1	ca 1.0:1	1.0–1.2:1	walk+catch	pres	(smooth)	190–1047
Pelacarus												
aculeatus	pres	no	abs	obscu	norm	1.6:1	0.3:1	0.7:1	walk	pres	abs	4–1440

Table 1. genera *Scaptognathus* to *Werthelloides*

genus/species	idiosoma, length of adults (µm)	idiosoma, length of female (µm)	idiosoma, length of male (µm)	length: width	dorsal aspect dominated by	dorsal plates present	AD, shape of anterior margin	PD, ornamentation	PD with costae/ lamellae	rosette pores on dorsal plates	corneae
Scaptognathus [31]											
minutus	145–178	145–178	—	1.3:1	plat	AD, OC, PD	trun	fov/retic-	no	abs	abs
Simognathus [44]											
serratus	526	526	—	1.7:1	plat	AD, OC, PD	arch	fov	no	abs	abs
Thalassarachna [16]											
alvina	502–665	544–665	502–582	1.8:1	stri	AD, OC, PD	arch	retic	no	abs	abs
caecoides	730	730	—	2.0:1	stri	AD, OC, PD	trun	retic	no	abs	abs
mollis	620	620	—	1.7:1	stri	AD, OC, PD	trun	retic	no	abs	abs
reticulata	380	—	380	1.3:1	plat	AD, OC, PD	trun	retic	no	abs	pres
setulosa	560	—	560	1.4:1	stri	AD, OC, PD	trun	retic	no	abs	abs
Werthella [10]											
atlantica	428–471	428–471	—	1.6:1	stri	AD, OC, PD	sho hood	—	yes	abs	abs
plumifera	400–566	426–566	400–513	1.6:1	stri	AD, OC, PD	—	fov	yes	abs	abs
Werthelloides [1]											
bathyalis	725	725	725	1.2:1	stri	AD, OC, PD	arch	fov	no	abs	abs

Table 1. genera *Scaptognathus* to *Werthelloides*

genus/species	epicuticular villi, lamellae, spikes, etc.	gland pores on 'horns'	wart-like cones or tubes on OC	anal cone	anal sclerites and valves	gnathosoma length: width	length ratio gnathosoma:idiosoma	length ratio leg I:idiosoma	leg I used for	tarsi II to IV, accessory process of claws	pectines on tarsi II to IV	depth (in m)
Scaptognathus												
minutus	abs	no	abs	sho	norm	1.9–2.1	0.9:1	0.8:1	walk	pres	abs	216–800
Simognathus												
serratus	abs	no	abs	sho	norm	1.3:1	0.3:1	0.9	catch	pres	delicate	476–511
Thalassarachna												
alvina	abs	no	abs	sho	norm	—	0.3:1	0.8:1	walk	pres	abs	1636–2200
caecoides	abs	no	abs	sho	norm	—	0.3:1	0.9:1	walk	abs	smooth	2615
mollis	abs	no	abs	sho	norm	1.9:1	0.3:1	0.9:1	walk	pres	pres	875
reticulate	abs	no	abs	sho	norm	2.2:1	0.4:1	1.2:1	walk	abs	pres	805
setulosa	abs	no	abs	sho	norm	2.1:1	0.3:1	1.6:1	walk	pres	pres	750–900
Werthella												
atlantica	pres	no	abs	sho	norm	1.8:1	0.3:1	0.8:1	walk	abs	smooth	1427–2323
plumifera	pres	no	abs	obscu	norm	—	—	0.6–0.7:1	walk	abs	smooth	485–2780
Werthelloides												
bathyalis	pres	no	abs	sho	norm	1.9:1	0.3:1	1.1:1	walk	pres	abs	1050–1600

Table 2. List of halacarid genera extracted from the deep-sea, included are genera with at least three records of species from deep and/or shallow water (column 1); number of species from the deep-sea (column 2) and all depth zones (column 3); ratio of deep-sea species of a genus to sum of all presently known deep-sea species, namely 92 (column 4) and to congeners from all depth zones (column 5).

Halacaridae	**number of named species from**		**ratio deep- sea species of a given genus to all deep-sea halacarid species (in %)**	**ratio of deep-sea species to congeners from all depth zones (in %)**
Genus	the deep-sea (485–7000 m)	all depth zones		
Agaue	9	44	9.8	20.5
Agauopsis	5	90	5.4	5.6
Atelopsalis	1	8	1.1	12.5
Bathyhalacarus	11	12	12.0	91.7
Bradyagaue	4	17	4.3	23.5
Copidognathus	23	374	25.0	6.1
Halacarellus	4	50	4.3	8.0
Halacarus	15	76	16.3	19.7
Lohmannella	4	39	4.3	10.3
Scaptognathus	1	31	1.1	3.2
Simognathus	1	44	1.1	2.3
Thalassarachna	5	16	5.4	31.2
Werthella	2	10	2.2	20.0