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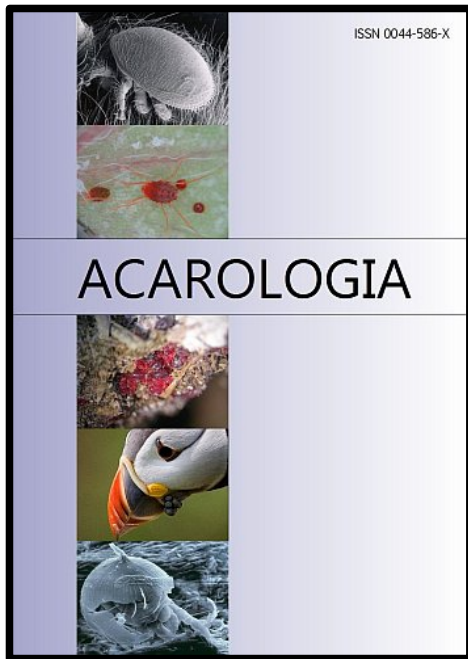
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The marine-associated lifestyle of ameronothroid mites (Acari, Oribatida) and its evolutionary origin: a review

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ABSTRACT — Existing literature on marine associated Ameronothroidea is reviewed and recapitulated. Although these littoral oribatid mites strongly resemble typical terrestrial mites, they have evolved different adaptations of various kinds to the marine littoral environment. In order to cope with intertidal wave action, most species show reduced and compact sensilla as well as sickle-shaped and elongated claws. Complex cerotegument based plastron mechanisms have evolved to allow breathing under flooded conditions and enabling these organisms to survive an average of more than a month completely submerged in saltwater. Behavioural adaptations include aggregations, diurnal and circatidal activity patterns, daily and seasonal migrations and thigmotaxis. Most taxa show no reproductive adaptations to the littoral habitat but some have developed ovoviviparity to protect the offspring and a few also have evolved distinct sexual dimorphism supposed to allow direct mating and secure sperm transfer in this constantly changing environment. Ameronothroid taxa are basically generalized feeders grazing on intertidal algae, lichens and fungi which also serve as microhabitat. Coastal areas all over the globe have been colonized and these mites can be found in a wide range of habitats: e.g. polar shores, rocky coasts, sandy beaches, tropical mangrove forests, brackish river estuaries and salt marshes. The families show a distinct climate related distribution pattern, with the Ameronothridae (Podacaridae included) in polar and cold temperate regions and the Fortuyniidae and Selenoribatidae in subtropical and tropical areas. Long distance transport to remote islands is supposed to be mainly achieved by bird phoresy in Ameronothridae and by dispersal via strong ocean currents in Fortuyniidae and Selenoribatidae. In literature there are basically two contrasting theories explaining the evolutionary invasion of marine associated habitats by ameronothroid mites, one favoring a monophyletic origin and a single land-to-sea transition event and another preferring an independent terrestrial ancestry and accordingly multiple invasions of the marine littoral environment. Recent molecular genetic studies support the latter theory and render the present superfamily of Ameronothroidea a polyphyletic taxon.

KEYWORDS — adaptations; plastron; biogeography; behaviour; reproduction; convergence; Ameronothridae; Fortuyniidae; Selenoribatidae

INTRODUCTION

The marine intertidal zone constitutes one of the most interesting ecosystems on earth. It represents the border of two completely different worlds, the marine and the terrestrial realms, where environmental parameters are changing constantly, hence

challenging the ability of organisms to cope with these extreme conditions.

Very few mite groups have been able to accomplish the land to sea transition, and they are scattered over various taxa. The prostigmatid Halacariidae represent a group that has even managed to

cross this line between land and sea completely having radiated in marine waters. They are cosmopolitan, occurring from shallow waters to the bathyal and even the abyssal (e.g. Bartsch 2004) and hence represent true marine organisms. Other mite groups have not crossed this barrier, though they have successfully invaded the littoral zone.

Among Mesostigmata, some genera of the family Ologamasidae, for example *Hydrogamasus* and *Psammonsella*, have adapted to intertidal marine habitats. Members of Halolaelapidae, e.g. *Halolaelaps* and *Halodarcia*, are also known to inhabit littoral algae and beach wrack in coastal zones. Representatives of Parasitidae and Laelapidae are likewise common predators in these habitats (e.g. Lindquist et al. 2009). The same applies to representatives of the prostigmatid families Bdellidae, Rhagidiidae and Erythraeidae (Walter et al. 2009). Littoral species that forage on marine algae can also be found in the endeostigmatic genus *Nanorchestes*, and the whole astigmatine family Hyadesiidae is composed of marine intertidal mites, occurring on virtually all coastlines (e.g. Schuster 1979). Last, several isolated oribatid mite species, for example *Hermannia subglabra* Berlese, 1910, *Acrotritia clavata* (Märkel 1964), *Passalozetes bidactylus* (Coggi, 1900), *Punctoribates quadrivertex* (Halbert, 1920), *Haloribatula tenareae* Schuster, 1957 etc. are associated with marine shores; they are thalassophilous or thalassobiont, meaning respectively that they occur in coastal areas or they have completely adapted to marine-associated environments (e.g. Schuster 1957, 1966, 1979, 1989; Luxton 1967, Syamjith and Ramani 2013). Other than Halacaridae, all the above mentioned groups are examples of infrequent marine associations within larger evolutionary clades suggesting that the invasion of coastal habitats happened repeatedly and relatively recently in geological time.

Only one group of oribatid mites stands out as supposedly representing an ancient, monophyletic taxon that evolved and radiated in the marine littoral environment, the superfamily Ameronothroidea. More than 90% of oribatid mite species living in intertidal habitats belong to this superfamily (Procheş and Marshall 2001) and they are

characteristic elements of the marine littoral fauna. The first member of this assemblage was discovered more than 140 years ago (Thorell 1871), and since then three families, 17 genera and approximately 84 species have been described (Subías 2004, update 2016). Despite a large literature concerning diverse aspects of this substantial group, the present state of knowledge still shows many gaps, relationships are largely unclear, and the evolutionary processes that led to the occupation of intertidal habitats are scarcely understood. Most of the literature is highly limited in scope, and only a few comprehensive studies include all members of Ameronothroidea (Wallwork 1964, Weigmann and Schulte 1977, Behan-Pelletier 1997).

The aim of the present paper is to summarize and synthesize existing literature on ameronothroid mites and to provide a concise and coherent overview of the biological, ecological, zoogeographical and evolutionary aspects of the marine-associated lifestyle of this taxon. Additionally, theories about the evolutionary invasion of littoral habitats by ameronothroid mites are reviewed and evaluated based on recent findings.

MATERIALS AND METHODS

Data acquisition and illustrations

Data presented in this paper are based on published literature, but some unpublished photographs, electron microscopic images and distribution maps are added to illustrate various topics. Light photographs were made with an Olympus E5 digital SLR camera attached to either an Olympus BH-2 microscope (for micrographs) or to an Olympus SZX 12 stereo microscope (for normal photographs). Electron micrographs were taken at the Research Institute for Electron Microscopy and Fine Structure Research, Graz, University of Technology (FELMI) using a Leitz AMR microscope and a Zeiss Gemini Ultra 55. For this purpose specimens stored in 70% ethanol were dehydrated in ascending ethanol concentrations, mounted on aluminium stubs with double-sided sticky tape, and then sputter coated with gold-palladium.

Terminology

Brachypylina classification used in this text follows the broad outlines of Norton and Behan-Pelletier (2009). The term “Ameronothridae sensu stricto (s. str.)” refers to the northern hemispheric ameronothrid taxa (in the sense of Vitzthum 1942); the more inclusive term “Ameronothridae sensu lato (s. l.)” refers to this northern hemispheric component plus all southern hemispheric Podacaridae (in the sense of Wallwork 1964). These terms are only used in the Taxonomy and Systematics Section, in all other sections these groups are given as Ameronothridae and Podacaridae. A general overview of oribatid morphology is given by Norton and Behan-Pelletier (2009).

Species authors of all marine-associated ameronothroid mites are given in Table 2 and therefore they are not cited when they are mentioned for the first time in text. However, species authors for non-ameronothroid taxa are given in the text.

TAXONOMY AND SYSTEMATICS – A BRIEF HISTORICAL OVERVIEW

At present, different classifications of the superfamily Ameronothroidea can be found in the literature (Table 1), and several taxonomic issues are still unresolved. However, all of these classifications (e.g. Schulte and Weigmann 1977, Subías 2004, Norton and Behan-Pelletier 2009 etc.) acknowledge the Ameronothridae, Fortuyniidae and Selenoribatidae as ameronothroid families. The marine-associated

lifestyle of most members of this group was surely one of the main reasons for their unification, but this motivation resulted in some ambiguous or conflicting taxonomic arrangements that are best understood in a historical context.

The first marine-associated oribatid mites were discovered in the late nineteenth century, but were mostly classified in genera that have very different concepts today. Thorell (1871) described the first ameronothroid mite, *Ameronothrus lineatus* (in *Eremaeus*), from the polar Island Spitsbergen. In subsequent years, further littoral species of mainly polar and cold temperate coasts were found and described by the most renowned acarologists of that time (e.g. L. Koch 1879, Michael 1882, Oudemans 1903). Berlese proposed the first modern ameronothroid genera, *Ameronothrus* (Berlese 1896) and *Halozetes* (Berlese 1916) but included the former in Carabodidae. Years later Willmann (1931) recognized that *Ameronothrus* represents an independent taxon; accordingly Vitzthum (1942) cited Willmann, 1931 as the family author. However, Willmann did not mention the family name in his work and, following the rules of the code of nomenclature, only the author giving the name for the first time is to be seen as the taxon author. Consequently, Vitzthum (1942) is the author of Ameronothridae. In his essay on the classification of oribatid mites, Grandjean (1954) included *Halozetes* in Ameronothridae and confirmed the distinct status of this family. Only one year later, Grandjean (1955) described *Podacarus auberti*, another littoral species from an Antarctic island. He noted its systematic relationship to

TABLE 1: Four different classifications of the superfamily Ameronothroidea present in important publications on oribatid mite systematics (indicated by different numbers). + family accepted as member, - rejected or neglected.

| Author | | Ameronothroidea | | | | |
|---------------------------------|---|------------------------|-------------|--------------|-----------------|------------------|
| | | Ameronothridae s. l. | | | | |
| | | Ameronothridae s. str. | Podacaridae | Fortuyniidae | Selenoribatidae | Tegeocranellidae |
| Wallwork 1964 | 1 | + | + | + | + | - |
| Weigmann and Schulte 1977 | 2 | | + | + | + | - |
| Balogh and Balogh 1992 | 2 | | + | + | + | - |
| Behan-Pelletier 1997 | 3 | | + | + | + | + |
| Woas 2002 | 4 | + | | + | + | + |
| Subías 2004 | 2 | | + | + | + | - |
| Norton and Behan-Pelletier 2009 | 3 | | + | + | + | + |

Ameronothridae, but proposed the family Podacaridae based on divergent morphological features of the immatures of this species. Van der Hammen (1960) was the first to find an intertidal species in tropical regions and included this new taxon, *Fortuynia marina*, in Podacaridae. When van der Hammen (1963) proposed *Fortuynia yunkeri*, the second species of this genus, he also described its juvenile stages; their morphology diverged conspicuously from juveniles of Podacaridae, and accordingly he excluded *Fortuynia* from this family and proposed the family Fortuyniidae within Ameronothroidea. Shortly afterwards, Wallwork (1964) considered the proposal of Fortuyniidae justified, and included only *Podacarus*, *Alaskozetes* and *Halozetes* in his revision of Podacaridae. Nevertheless, Balogh (1965) ignored these changes and assigned the genus *Fortuynia* again to Podacaridae, regarding the obvious differences as only of generic significance. Luxton (1967) disagreed with Balogh's opinion and confirmed again the validity of Fortuyniidae bringing this debate for now to an end; since then, Fortuyniidae are commonly accepted as a distinct taxon of Ameronothroidea.

However, the discovery of further ameronothroid species in subsequent years led to a controversy about the systematic status of Podacaridae and Ameronothridae. Based on detailed morphological investigations, Schubart (1975) stated that these two families are likely to be two subfamilies of a single family. Weigmann and Schulte (1977) supported Schubart's hypothesis and included all former podacarid genera in Ameronothridae arguing that there is no decided gap among the taxa and that their groupings into separate monophyletic families are no longer justified. Some authors (Subías 2004, Norton and Behan-Pelletier 2009) accepted this taxonomic reorganization, others (Luxton 1990b, Woas 2002) still recognized Podacaridae and so both systematic groupings still are found in the literature.

The ameronothroid family Selenoribatidae, on the other hand, has never been seriously challenged. Strenzke (1961) described the first selenoribatid species, *Selenoribates foveiventris*, from coasts of the Red Sea, then Schuster (1963) proposed two years later Selenoribatidae, when he discov-

ered *Thalassozetes riparius*, another intertidal species from Mediterranean shores. Grandjean (1966) was the first to give a detailed diagnosis for this family and later (Grandjean 1968) provided further important taxonomic and systematic information strengthening the concept of Selenoribatidae. Since then the number of selenoribatid taxa quintupled and though there have been some problems at the generic or species level (e.g. synonymies, unjustified transfers; for details see Pfingstl and Schuster 2012a), the family remained a well delimited and established monophyletic group.

The last and probably the most overlooked ameronothroid family are the Tegeocranellidae which differ in their ecology from nearly all other members in being exclusively associated with freshwater habitats. The distinctness of this monogeneric taxon was never questioned but the position within the system of higher oribatids and especially its inclusion within the Ameronothroidea is still controversial. Balogh and Balogh (1992) included this taxon initially in the Polypterozetoidea, a superfamily characterized as eupheredermous Oribatida, which means the nymphs retain the exuvial scalp of the preceding stage after the moult. But nymphs of Tegeocranellidae do not retain scalps and are thus classified as apheredermous. Behan-Pelletier (1997) noticed this fundamental mistake and moreover demonstrated plausibly that the family Tegeocranellidae is indeed a member of the Ameronothroidea, closely related to Fortuyniidae and Selenoribatidae. Although Behan-Pelletier's reasoning was based on clear synapomorphic characters and thus conclusive, several authors seem to have simply neglected her excellent work. For example, in his annually updated checklist of oribatid mites, Subías (2004) includes the Tegeocranellidae in the superfamily Tectocephoidea without any explanation and therefore causes persisting confusion about the systematic relationship of this family.

In summary, a universally accepted systematic concept of Ameronothroidea is lacking and certain groupings, e.g. Podacaridae included in Ameronothridae (Weigmann and Schulte 1977) or Tegeocranellidae included in Tectocephoidea (Subías 2004), remain questionable.

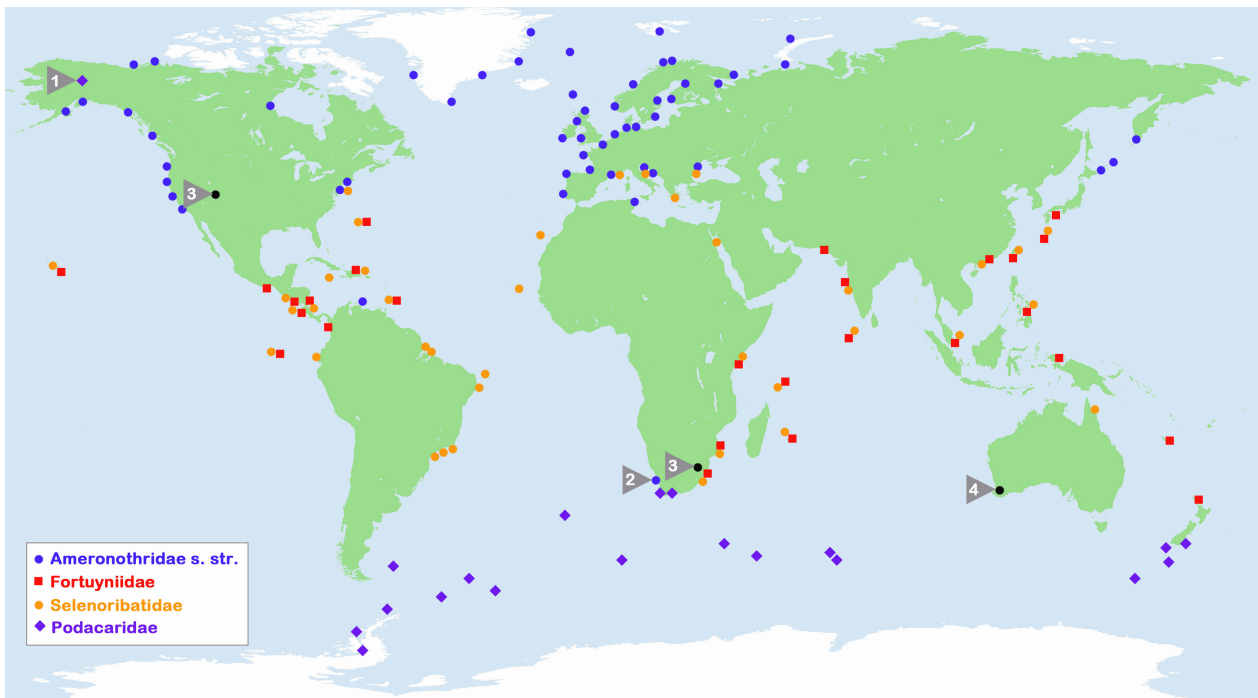


FIGURE 1: Global distribution of marine-associated ameronothroid mite families. Ameronothridae – blue circles; relictual terrestrial Ameronothridae – black circles; Selenoribatidae – orange circles; Fortuyniidae – red squares; Podacaridae – violet squares. Arrowheads pointing to occurrences of taxa specifically discussed in the text. 1 – *Alaskozetes coriaceus*; 2 – *Ameronothrus bilineatus*; 3 – *Aquanothrus*; 4 – *Chudalupia meridionalis*.

BIOGEOGRAPHIC DISTRIBUTION

Marine-associated Ameronothroidea can be found in all oceans, and their distribution extends from coasts of the Arctic to shores of the Antarctic (Figure 1). The occurrence of the families is strongly correlated with different climate zones, i.e. the Ameronothridae and Podacaridae are predominantly contained within cold-temperate regions around both poles (e.g. Procheş and Marshall 2001), and only a small fraction of northern hemispheric Ameronothridae can be found beyond the limits of these areas. *Ameronothrus bilineatus*, *A. marinus*, *A. schneideri* and *A. schusteri* may occur towards the transition-zone to the tropics (Schulte 1975) though only *A. maculatus* clearly stands out from the other cold-adapted taxa with records from coasts of Tunisia (Schulte 1975) and the tropical Caribbean Island Curaçao (Willmann 1936).

In contrast to the northern hemispheric Ameronothridae, the southern hemispheric Podacaridae include exclusively cold-adapted taxa

and are largely confined to Antarctic and Sub-Antarctic regions (Procheş and Marshall 2001). The only occurrence outside these polar areas is that of *Halozetes capensis*, a possible endemic species living on temperate shores of South Africa (Coetzee and Marshall 2003).

The families of Fortuyniidae and Selenoribatidae, on the other hand, are limited to shorelines of the subtropics and tropics (e.g. Schuster 1989) and hence they appear to be warm-adapted mites. Most members can be found in the tropical Eastern Pacific, the tropical Western Atlantic and the Indo-Pacific (Procheş and Marshall 2001, Pflingstl and Schuster 2014) while the least inhabited area is the Mediterranean-Atlantic region.

Besides the aerial climate, a few authors (Schuster 1966, Pflingstl and Schuster 2014, Pflingstl 2016) suggested that the temperature of large ocean currents may also shape distributional patterns. For example, warm-adapted selenoribatid mites occur abundantly on the South American Atlantic coast

where the warm Brazil Current flows southwards, whereas these mites are absent from the Pacific shore at the same latitudes where the cold Humboldt Current prevails (Pfingstl and Schuster 2014). A similar situation is found at the southern tip of Africa: cold-adapted ameronothrid species occur on the west coast where the cold Benguela current is present, and warm-adapted fortuyniid and selenoribatid taxa inhabit the east coast where the warm Agulhas Current flows (Pfingstl 2016).

However, aerial and oceanic climate are closely linked, and we do not know the relative importance of air or water temperature in the distribution of these taxa. But given the fact that stenotopic intertidal species are spending half of their lives in the seawater, it is likely that water temperature influences their biogeography.

Although the worldwide distribution of Ameronothroidea shows a relatively well-defined pattern, two exceptional records have seemed enigmatic. The first is the discovery of *Alaskozetes coriaceus* (Hammer 1955) from an arctic hill in Alaska. Marie Hammer described this species and proposed the genus *Alaskozetes* based on a single specimen that was given to her from that location. Surprisingly, this was the only *Alaskozetes* specimen ever found in the northern hemisphere, all others have been collected later in the southern hemisphere

from Sub-Antarctic and Antarctic areas, where this genus is abundant. Such a disjunctive distribution on opposite Polar Regions, with more than 10 000 km in between, is more than extraordinary. It was suggested that the finding in Alaska may have been caused by migratory birds flying from Pole to Pole with the mites attached to their feathers (Schuster 1966). The second biogeographic puzzle was the finding of *Ameronothrus bilineatus* specimens from the littoral zone of South Africa (Weigmann 1975b). Before that, this species was known to occur only in the northern hemisphere, namely on European coasts with a latitudinal distribution range from Scandinavia to Portugal. Although Weigmann (1975b) mentioned the possibility of birds having transported specimens from Europe to South Africa, he favored the idea of a continuous distribution from Southern Europe along the African west coast. Procheş and Marshall (2001), on the other hand, clearly classified the South African *A. bilineatus* population as introduced, but offered no potential explanation, so this biogeographic mystery also remains unsolved.

Vast coastlines of each continent are still largely uncharted in terms of intertidal oribatid mite occurrences and thus known biogeographic patterns may change considerably in the future.

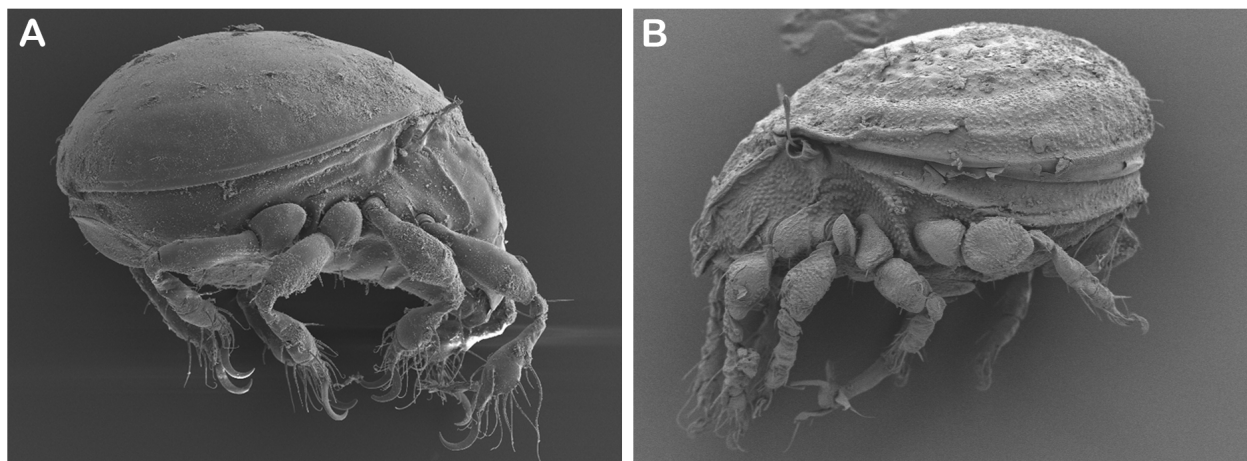


FIGURE 2: SEM-micrographs – juxtaposition of typical intertidal and typical terrestrial oribatid mites, showing no obvious differences (excepting tarsal claws much more prominent in intertidal species): A – *Alismobates inexpectatus*, inhabitant of rocky intertidal shores (Western Atlantic); B – *Scutovertex ianus*, found in moss (Central Europe).

EVOLUTIONARY ADAPTATIONS TO THE MARINE LITTORAL LIFESTYLE

Luxton (1990b) was correct in noting that marine-associated oribatid mites appear at first sight to show no modifications for life on the sea shore. Being air-breathing animals that have not completely transgressed the ecological barrier between marine and terrestrial environments, they strongly resemble typical terrestrial oribatid mites (Figure 2). Nevertheless, evolutionary adaptations to the intertidal lifestyle can be found in all biological aspects of these mites.

(1) Morphology

Daily tidal submergence is surely one of the main selective factors shaping the morphology of intertidal mites. Schubart (1971, 1975) noticed a causal correlation between frequent inundation and reduction of sensilli in the Ameronothridae. Species living predominantly in supralittoral zones (the upper-

most area of the littoral zone), like *Ameronothrus lineatus* or *A. maculatus*, in general have small sensilli while species dwelling in the intertidal zone, like *A. bilineatus* and *A. marinus*, have lost their sensilli and bothridia completely. A reduction of these sensory organs may prevent overstimulation when the mite is submerged and subject to strong tidal wave action and constantly moving water. Indeed, the majority of ameronothroid mites show relatively simple and short sensilli. Members of the genus *Fortuynia*, which live in the lower eulittoral area (e.g. Pflingstl 2013b), exhibit especially short and compact sensilli.

Another morphological trait affected by tidal wave action is the tarsal claws of the legs. Karasawa and Hiji (2004b) demonstrated that monodactylous species dominate in littoral environments and consequently they stated that a reduction in the number of claws may be an evolutionary adaptation to regular tidal flooding. All members of Fortuyniidae and Selenoribatidae, which are stenotopic inhabitants

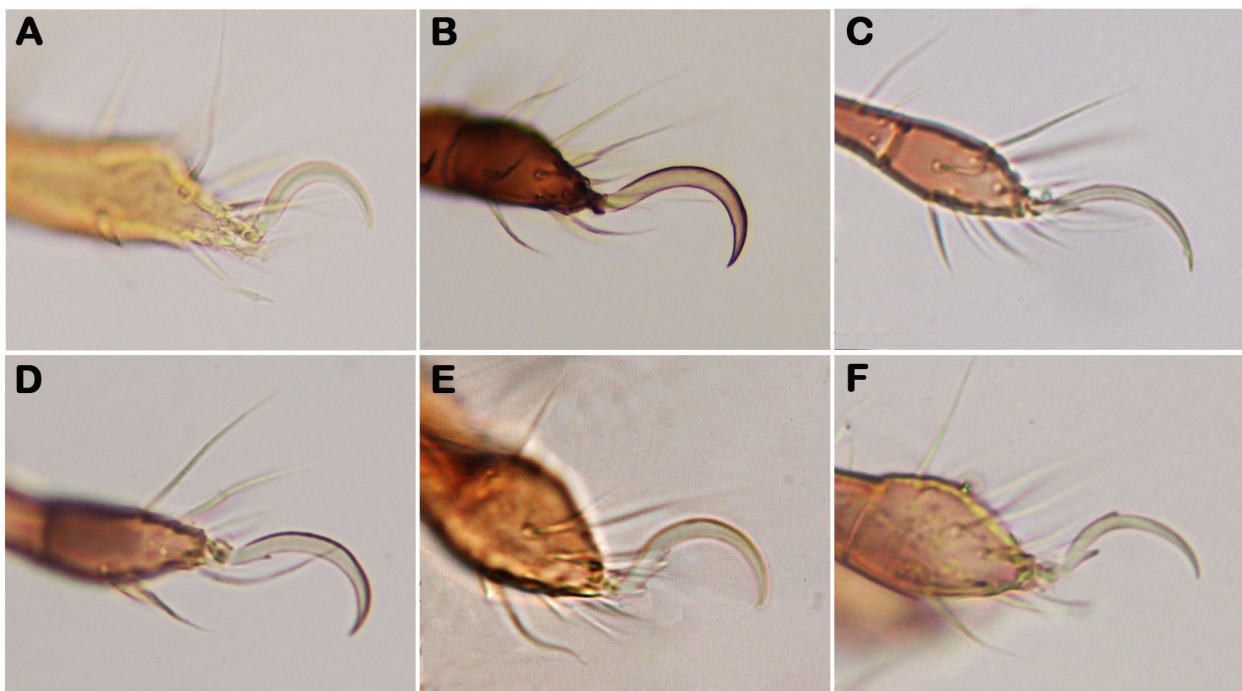


FIGURE 3: Types of tarsal claws present in intertidal oribatid mites. Upper row – different kinds of elongated sickle-shaped claws, lower row – claws with additional teeth: A – *Ameronothrus* sp.; B – *Fortuynia smiti*; C – Selenoribatidae gen. nov.; D – *Carinozetes bermudensis* (one proximoventral tooth); E – *Selenoribates arotroventer* (two proximoventral teeth); F – *Selenoribates satanicus* (one proximoventral and one proximodorsal tooth).

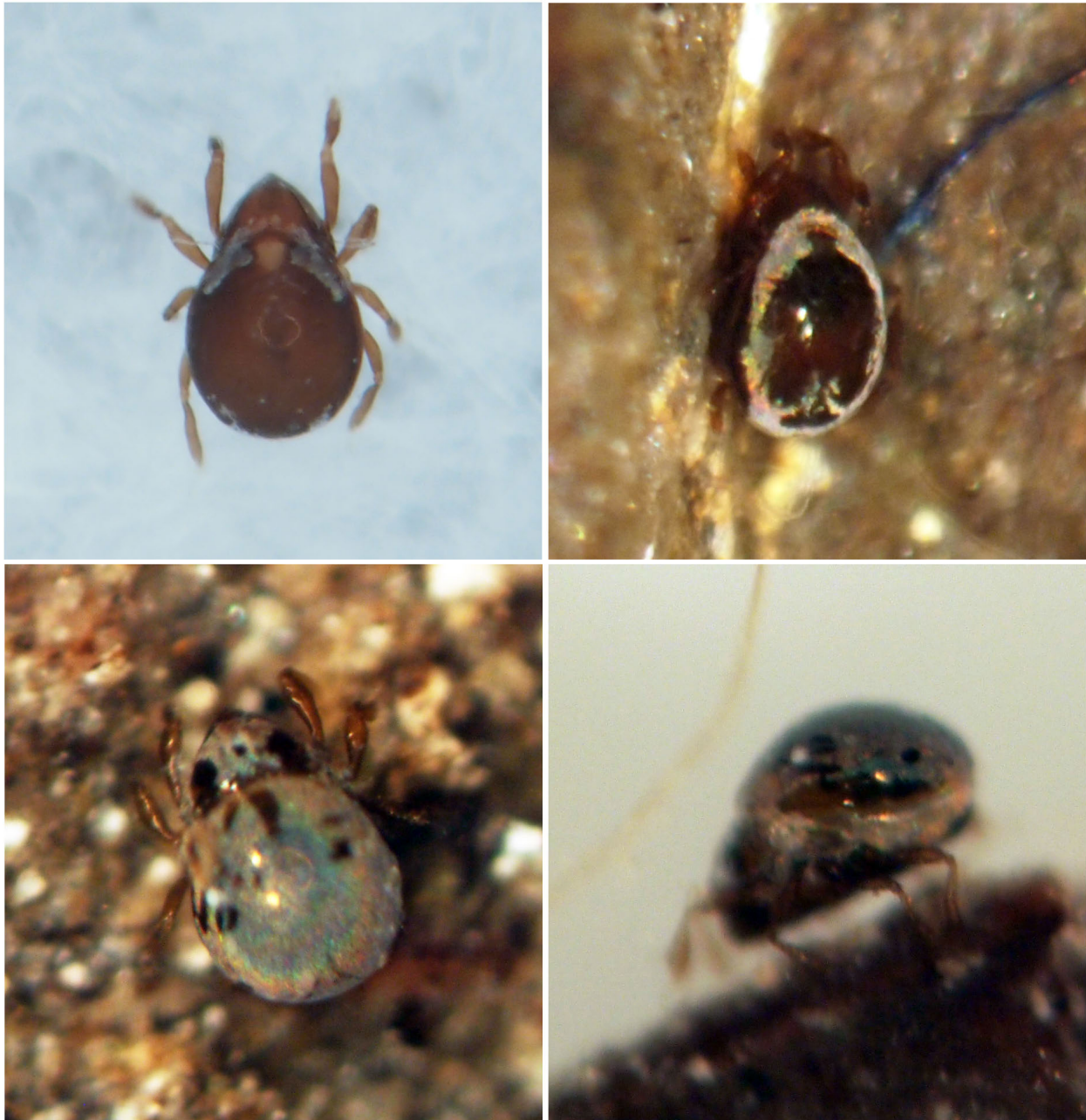


FIGURE 4: Photographs of flooded fortuyniid specimens from Bonaire Isl. Retained air can be seen as silvery shimmer on body surfaces.

of the intertidal zone, show only a single claw on their legs, whereas Ameronothridae and Podacariidae, which have both intertidal and non-intertidal representatives, possess either one or three claws. Concerning the latter, Schubart (1975) noted that *Ameronothrus* species living on hard substrates (e.g. rocks, shore fortifications) are tridactylous, while

species dwelling on soft substrates (e.g. salt meadows, silted rocks) are monodactylous, accordingly he postulated a correlation between type of substratum and claw number. Apart from the claw number, Pugh et al. (1987b) demonstrated that claws of intertidal *Ameronothrus* species are proportionally longer than those of congeneric supralittoral species. In-

deed, the majority of intertidal oribatid species possesses elongated claws (Figure 3) allowing them to grip the substrate more tightly during tidal flooding (Karasawa and Hiji 2004b); these claws may be equipped with spine-like structures (Figures 3D–F), as in most selenoribatid species (e.g. Strenzke 1961, Grandjean 1968, Pfungstl 2013c, 2015b).

(2) Plastron respiration

Intertidal ameronothroid mites are air-breathing animals respiring with a tracheal system, therefore they had to evolve special adaptations in order to survive daily tidal flooding. Ameronothroid mites are known to use plastron respiration when flooded. A plastron is an alternative respiration system absorbing oxygen from the surrounding water via a thin layer of air trapped by hydrophobic hairs or other cuticular projections (definition after Fielden et al. 2011) and is known to occur in many aquatic and semi-aquatic arthropod taxa, like insects and spiders. Plastrons of intertidal ameronothroid mites (Figure 4) are associated with cuticular and/or cerotegumental structures (e.g. Pugh et al. 1987a, 1990; Messner et al. 1992, Pfungstl and Krisper 2014). It was demonstrated by Pugh et al. (1987a) that the cerotegument of *Ameronothrus marinus* contains approximately 21 % airspace and that of *A. maculatus* even 60%. Although the air-retaining surface structures are more or less similar in all investigated taxa, the specific mode of plastron respiration differs considerably among them. For example, in flooded fortuyniid and selenoribatid adults the retained layer of air always communicates with the tracheal system (Pfungstl and Krisper 2014), whereas in submerged *Ameronothrus* individuals no such connection was found, and diffusion of oxygen from the plastron is assumed to occur across the weakly sclerotized cuticle instead via the tracheae (Pugh et al. 1987b, 1990). Similarly, in juvenile Fortuyniidae and Selenoribatidae air is retained in certain large lateral and ventral folds of the soft integument, and these folds are equipped with series of pores leading into tracheal structures supplying the internal organs with oxygen (Pfungstl and Krisper 2014). In *Ameronothrus* nymphs, on the other hand, the folding pattern is conspicuously different, tracheal

structures are absent and gas transfer is assumed to take place across the whole soft integument (Messner et al. 1992).

Adults of Fortuyniidae have furthermore evolved a unique complex system of lateral cuticular taenidia, also called van der Hammen's organ (e.g. Hammen 1963, Travé 1986, Pugh et al. 1990) (Figure 5). This system of taenidia connects the dorsal and ventral plastron area and is thought to facilitate rapid equilibrium of pressure changes between the respiratory system and the surrounding environment caused by rough wave movements (Pugh et al. 1990). Although present in all fortuyniid members, the specific configuration of taenidia slightly varies among the genera (e.g. Pfungstl and Schuster 2012b, Pfungstl and Krisper 2014).

Several authors investigated the efficiency of plastron respiration in certain ameronothroid taxa and demonstrated that these mites are able to survive astonishingly long periods of time under flooded conditions (Table 3). *Alismobates inexpectatus*, *Fortuynia atlantica* and *Carinozetes bermudensis* specimens survived an average of one month under water (Pfungstl 2013a), *A. lineatus* and *A. marinus* specimens more than two months (Schuster 1979, Pugh et al. 1987a) and *A. maculatus* tolerated inundation for more than one month (Schuster 1966). Maximum survival times ranged from nearly two to eight months in these species (Schuster 1966, 1979; Pfungstl 2013b).

(3) Behaviour

Intertidal mites are confined to a relatively few microhabitats, such as rocky shore lichens, kelp holdfasts, etc., which provide protection from direct and indirect stresses of severe wave action (Pugh and Mercer 2001), but behavioural adaptations further minimize these stresses. Several marine-associated oribatid mites are relatively quick and active climbers (Pfungstl 2013a); this allows them to escape rising tide and retreat into crevices or other protected spots. There may be a relation among the speed of this locomotion, the substrate and the mite's vertical occurrence in the littoral area (Pfungstl 2013a). Species dwelling on rocky exposed substrate in the lower eulittoral, such as *F. atlantica*, are

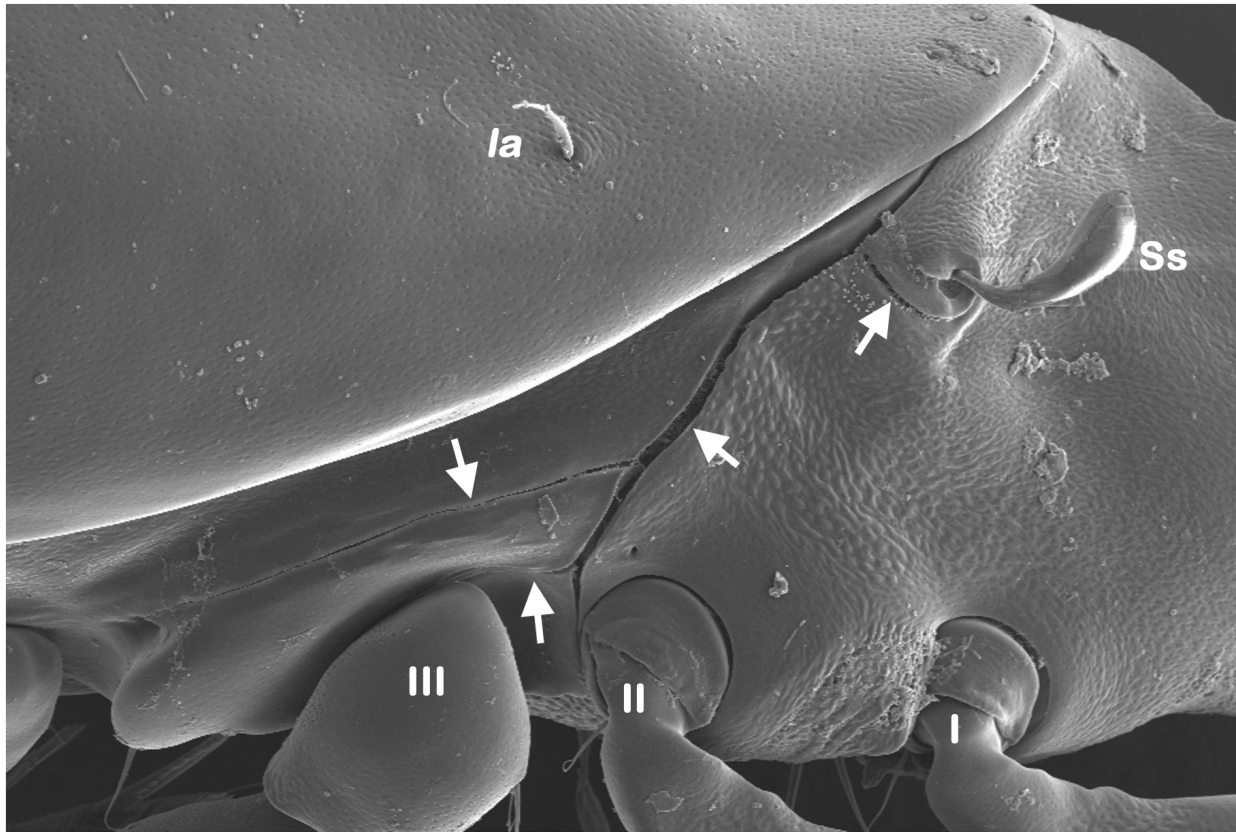


FIGURE 5: SEM-micrograph of *Fortuynia maledivensis*, lateral view, demonstrating the configuration of Van der Hammen's organ. Arrows point to each lateral cuticular channel of this organ; Ss – sensillus, la – lateral anterior notogastral seta, I–III – legs.

very fast climbers (Pfingstl 2013a), while species living in the upper and more vegetated eulittoral area, e.g. *Halozetes otagoensis*, *Ameronothrus schneideri* and *Alaskozetes antarcticus*, are moderate or even sluggish runners (Luxton 1966, 1990a, Strong 1967, Goddard 1979). The more exposed and closer the animals are to the water's edge, the more quickly they must react and move to avoid being washed away.

Another behavioural strategy to prevent dislodgement by waves is aggregation. This has been observed often and in many intertidal taxa, e.g. Fortuyniidae (Krisper and Schuster 2008, Pfingstl 2013a), Ameronothridae (Schulte *et al.* 1975, Schulte 1976b, Bücking *et al.* 1998, Søvik 2004) and Podacaridae, (Peckham 1967, Goddard 1979, Convey 1994b) where hundreds of individuals of different age are crouched next to and on top of each other (Figure 6A). Protection against wave action is a pri-

mary function of this behaviour, but in some instances aggregations may aid mate location (Block and Convey 1995) and synchronization of moults (Søvik 2004).

Certain fortuyniid and selenoribatid species show thigmotactic behaviour (Pfingstl 2013a) by entering narrow crevices and small depressions when these are present. This behaviour is advantageous in a periodically flooded environment because it limits the time the animals spend in open areas, exposed to the tidal surge. Intertidal oribatid mites usually are either inactive (e.g. Schulte 1973, Behan-Pelletier and Eamer 2007) or show low activity when flooded (Pfingstl 2013a). Pugh and King (1986) demonstrated that intertidal mites have activity cycles synchronized with diurnal and circatidal patterns, so that they are most active during periods of low tide and bright daylight. Individuals of

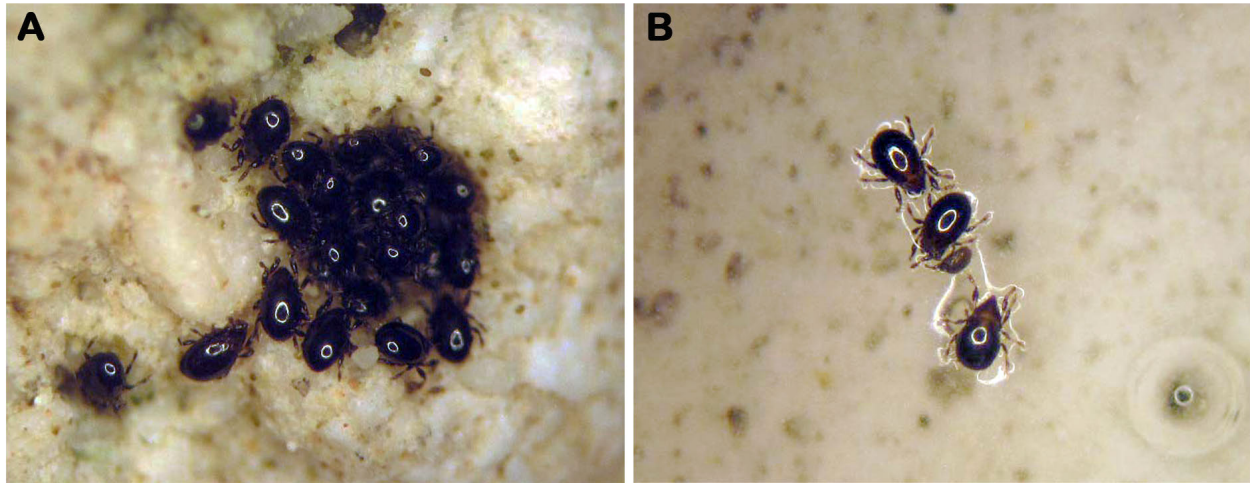


FIGURE 6: Photographs illustrating characteristic behaviors intertidal *Fortuynia atlantica*: A – Adult specimens aggregating in a small depression of substrate; B – Three adults and larva rafting on water surface – “floating behavior” (white rings on mites are reflections of ring-light illuminator).

A. marinus even perform rhythmic daily vertical migrations to avoid tidal flooding. In this way, they reduce the time of submergence and extend the time of possible food intake (Schulte 1973).

The temperate species *A. lineatus* shows another interesting strategy to reduce or avoid the mechanical stress of wave movement. In summer, when reproduction reaches its peak, adults migrate into the uppermost eulittoral where they lay eggs; offspring develop there for the next two months, then deutonymphs move back to the littoral zone where development is completed (Bücking et al. 1998). By these seasonal vertical migrations the dangers of the tidal cycle are avoided for at least the most vulnerable stages: eggs, larvae and protonymphs.

Despite these strategies, intertidal mites surely are surprised often by waves and washed away, and for such an event the tropical *F. atlantica* has evolved an interesting behaviour. When exposed to a sudden flood, specimens immediately splay the legs, so that they float like a raft on the surface of the water until they again reach firm substrate (Pfungstl 2013a) (Figure 6B). By this so-called “floating behaviour” the mites increase their chances of survival in the open water and successful dispersal by ocean currents (Pfungstl 2013a).

(4) Reproduction

As noted, aggregation may facilitate finding mates (Block and Convey 1995) or deposition of eggs in areas far above tidal range (Bücking et al. 1998), but there are several other reproductive traits that have evolved as adaptations to the marine environment. For example, most Ameronothridae are ovoviviparous (for a detailed discussion of this phenomenon see Norton 1994), with the larva having developed within the mother’s body and hatching from the egg immediately (larviparity) or within a few hours after deposition (Luxton 1966, Weigmann 1975a, Bücking et al. 1998, Søvik 2003, Søvik et al. 2003). This way, the vulnerable egg stage is extremely shortened and the mobile larva can promptly escape tidal waves. The tropical Fortuyniidae and Selenoribatidae, on the other hand, are oviparous; their egg stage takes approximately 15–35 days, similar to those of typical terrestrial oribatid mites (Pfungstl 2013a). However, they protect their eggs from tidal movement by either gluing them into tiny crevices of the substrate, as for example in *F. atlantica*, or they push them deep into the intertidal algae so that the algal mass completely encloses and protects the eggs, e.g. as in *A. inexpectatus* (Pfungstl 2013a).

Spermatophores of males appear even more

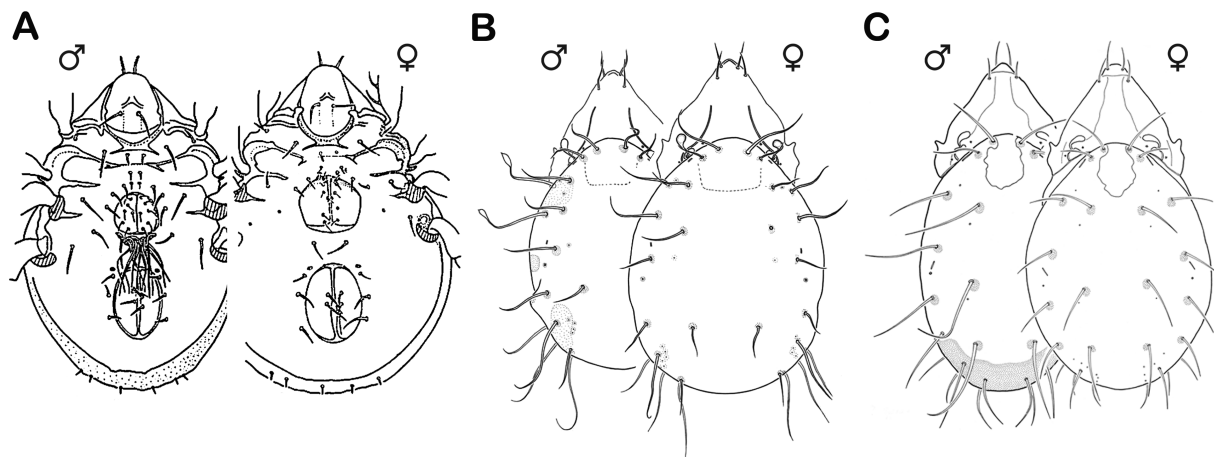


FIGURE 7: Examples of distinct sexual dimorphism in littoral ameronothroid mites (see text for explanation): A – *Alaskozetes antarcticus* (modified after Wallwork 1962); B – *Fortuynia atlantica* (modified after Krisper and Schuster 2008); C – *Fortuynia dimorpha* (modified after Pfungstl 2015a).

fragile structures that are easily destroyed by the mechanical effects of the tides, but no special littoral adaptations are known, which Alberti (1974) already demonstrated for Trombidiformes. Typical stalked spermatophores were found in Ameronothridae (Luxton 1966, Schuster 1979, Søvik 2004), Fortuyniidae and Selenoribatidae (Pfungstl 2013a). Pfungstl (2013a) suggested that spermatophore deposition, detection and utilization by females may happen quickly during the short time frame of low tide. In this way spermatophores would not come in contact with water and hence would be safe.

Distinct sexual dimorphism is present in a small percentage of ameronothroid species, where it is expressed to different degrees and in various regions of the body (Pfungstl 2015a, Behan-Pelletier and Eamer 2010, Behan-Pelletier 2015) (Figure 7). In *A. lineatus* and *A. nigrofemoratus*, males exhibit conspicuously longer legs than females (e.g. Schubart 1975) whereas in the podacarid species *Podacarus auberti*, *Halozetes belgicae* and *Alaskozetes antarcticus* males show a remarkable aggenital neotrichy which is absent in females (e.g. Wallwork 1964). Not a single case of sexual dimorphism is known in selenoribatid mites, whereas a handful of fortuyniid species have elaborate sexually dimorphic characters. *Fortuynia yunkerii* males show only slight modi-

fications of the fourth leg (Hammen 1963) but males of *F. atlantica* possess certain lanceolate notogastral setae, enlarged notogastral porose areas and a pair of obvious lateral protuberances on the notogaster (Krisper and Schuster 2008); in males of *F. dimorpha* the posterior part of the gastronotic region is completely covered with a porose area and several notogastral setae are conspicuously elongated (Pfungstl 2015a). The function of these modified characters is unknown but if they are linked to dermal glands like the octotaxic system of brachypyline mites (Alberti et al. 1997, Norton and Alberti 1997, Norton et al. 1997) and porose areas of mixonomatid Collohmanniidae (Norton and Sidorchuk 2014), they probably play a role in semiochemical communication linked with associative mating (Pfungstl 2015a, Behan-Pelletier 2015). Although never observed, direct sperm transfer in the littoral environment would be clearly advantageous because it reduces the stress for the sperm package in this intermittently dry and wet habitat.

However, at least two fortuyniid species have managed to completely avoid the stress of tidal inundation on spermatophores by simply not producing them. In *Fortuynia hawaiiensis* and *Fortuynia maledivensis* males are completely absent and females reproduce via thelytoky (Pfungstl and Jagersbacher-Baumann 2016). This reproductive

mode entails a few advantages because it reduces costs of producing males, mate finding and sperm transfer in the extreme conditions of intertidal environments and furthermore it facilitates the colonization of new coastlines.

(5) Feeding

As far as known, marine-associated oribatid mites are generalized feeders with various degrees of specialization (e.g. Schulte 1979, Pfungstl 2013a), and usually the substrate serves them both a habitat (or protection against desiccation and dislodgment) and a food source (Bücking et al. 1998, Pfungstl 2013a) (Figure 8). Most Ameronothridae, Podacaridae and several Fortuyniidae and Selenoribatidae have been observed feeding on diverse types of green algae, as for example the microphytes *Pleurococcus* sp. or *Chlorococcus* sp., the filamentous algae *Lyngbia* sp. or *Rhizoclonium riparium*, macrophytes *Enteromorpha* sp. or *Prasiola crispa* and seaweed *Porphyra* sp. (Peckham 1967, Schulte 1976b, Pugh 1995, Pfungstl 2013a). Lichens are also an important food source for intertidal mites (e.g. Block and Convey 1995), but the mites feed predominantly on the phycobionts, i.e. the algal cells, of the lichens (e.g. Schulte 1976b, Bücking et al. 1998). In some cases *Ameronothrus* species were reported to feed on fungi (Luxton 1966, Schulte 1976b). Certain fortuyniid and selenoribatid species as well as the ameronothrid *A. maculatus* are known to primarily graze on cyanobacteria (Schuster 1979, Søvik 2004, Krisper and Schuster 2008). Carnivory has not yet been confirmed in any intertidal oribatid species. Schuster (1977) once inferred that Selenoribatidae may be carnivorous as he found pieces of tardigrades in their guts, but soon after he withdrew his idea (Schuster 1979).

Food preferences may differ among the developmental stages (Luxton 1966). Adults and tritonymphs of most *Ameronothrus* species feed on micro- and macroalgae, while the larvae, proto- and deutonymphs feed exclusively on microalgae. This sometimes leads to a spatial separation of the stages, with the younger ones staying in higher littoral areas (Schulte 1976b, Bücking et al. 1998). In most *Ameronothrus* species a correlation between habitat

and type of food can also be observed, accordingly: (1) inhabitants of rocky intertidal shores predominantly feed on epilithic algae (algivorous), (2) mites dwelling on hard substrates in supralittoral areas prefer lichens (lichenivorous) and (3) species occurring in salt marshes mostly graze on fungi (fungivorous) (Schulte 1976b).

Feeding activity and defecation of *Ameronothrus* species follow a tidal rhythm, with maxima between the high tides (Schulte 1976b, Pugh and King 1986). This suggests that they feed as much as possible during low tide and then rest during high tide when they are submerged. Schulte (1976a) demonstrated that inhabitants of the lower eulittoral, exposed to longer periods of submergence, start feeding earlier and feed more quickly during low tide than do populations of the upper eulittoral, which are subject to shorter periods of inundation and hence have more time to feed.

(6) Physiology

There is a large amount of literature – enough to fill a book – dealing with physiological adaptations of ameronothroid mites but more than 90 % of it focuses on the ability of Antarctic Podacaridae to survive the extreme low temperatures and conditions of polar areas. These studies (e.g. Sømme and Block 1984, Convey 1994a, Block and Convey 1995, Worland and Lukešová 2000, Worland and Convey 2001, Deere and Chown 2006, Hawes et al. 2007, Benoit et al. 2008) are important to understand the mechanisms of survival in such cold environments, but studies investigating physiological adaptations to the marine environment are few, so our knowledge is sketchy.

Intertidal oribatid mites are resistant to salt and fresh water and as mentioned above, they can survive inundation for weeks and sometimes months (e.g. Schuster 1979, Pfungstl 2013b) (Table 3). How osmoregulation works in these animals is unclear but probably they possess the ability of hypertonic regulation to water of lower osmotic values than their hemolymph, such as fresh water, and to water of higher values, i.e. salt water, they are probably poikilosmotic (Schuster 1979). It has been suggested that littoral mites use their coxal glands for os-

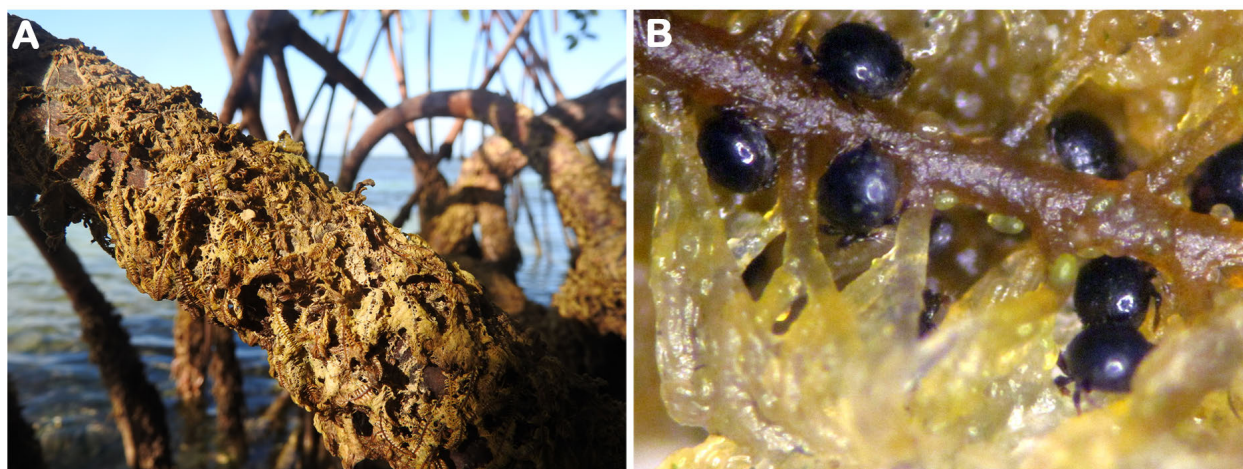


FIGURE 8: Algal habitat as substrate and food resource: A – Intertidal alga *Bostrychia* sp. growing on mangrove root (El Limón, Dominican Republic). B – Enlarged view of *Bostrychia* sp. showing *Alismobates inexpectatus* individuals foraging on alga and depositing fecal pellets.

moregulation (Alberti and Storch 1977) or that they reduce ion resorption from excretory waste filtrate if their coxal glands are degenerated (Woodring 1973).

HABITATS AND ECOLOGY

Ameronothroid mites have colonized various microhabitats of the marine littoral, even though this represents only a spatially restricted habitat. Ameronothridae and Podacaridae show various degrees of association with the intertidal ecosystem, including (1) typical intertidal species, e.g. *A. marinus*; (2) so-called transition species, able to dwell in both environments, e.g. *A. lineatus*; and (3) typical terrestrial species, as for example *P. auberti* (Schulte and Weigmann 1977) (see Table 2). There is a distinct latitudinal component to this habitat specificity: species at lower latitudes in each hemisphere are restricted to littoral environments while species found at higher latitudes show a greater affinity for terrestrial habitats (Schulte et al. 1975, Marshall and Convey 2004). Furthermore, several northern hemisphere Ameronothridae are also able to colonize brackish and freshwater habitats, such as marine ponds and estuaries (e.g. Schulte et al. 1975). Especially *A. maculatus* shows high freshwater tolerance and can frequently be found on the shores of coastal rivers (e.g. Schulte et al. 1975, Schuster 1986); in one case individuals were found in a small river 50

km upstream from the Mediterranean coast (Travé 1963). Some members of Ameronothridae can also be found far inland in typical terrestrial habitats, as for example the high arctic *Ameronothrus lapponicus* (Dalenius 1963) or the Scandinavian *Ameronothrus dubinini*, which was discovered a few kilometers inland (Laine et al. 1988). Within the littoral environment, Ameronothridae may occur on sediment-free rocky coasts (e.g. Bücking et al. 1998), on sediment-rich hard substrates (e.g. Schulte et al. 1975), in salt-marshes (e.g. Luxton 1966) and in washed-ashore flotsam or tidal debris (e.g. Schulte et al. 1975, Pugh and MacAlister 1994). There are also reports of quite unusual habitats. For example, the Antarctic *Alaskozetes antarcticus* was found near seal wallows or around penguin rookeries (Peckham 1967, Block and Convey 1995) but also on dead birds and well-rotted seal carcasses (Goddard 1979); *Ameronothrus lineatus* was collected from the nests of three different seabirds on Spitsbergen (Coulson et al. 2009) and *Antarcticicola georgiae* and *Halozetes belgicae* were sampled from whale bones on sub-Antarctic coasts (e.g. Goddard 1979, Pugh and MacAlister 1994). Independent of microhabitat and taxon, investigations have shown that intertidal and terrestrial species show generally high niche specificity whereas transition species are eurytopic and may occur in a wide range of niches (Schulte et al.

1975, Marshall et al. 1999).

In contrast to Ameronothridae and Podacaridae, the subtropical and tropical Fortuyniidae and Selenoribatidae are stenotopic inhabitants of the littoral area, i.e. transition species or terrestrial species

are lacking in these taxa. Collectively, Selenoribatidae species may inhabit a wide variety of intertidal habitats, e.g. sandy beaches, boulder beaches, rocky cliffs and mangrove roots (e.g. Karasawa and Aoki 2005, Pflingstl 2013a). Mangrove forests are one of

TABLE 2: List of predominantly marine-associated ameronothroid species and their ecological classification. *associated with aquatic and/or terrestrial habitats; transition = occurring from the littoral to terrestrial areas, intertidal = restricted to the eulittoral zone; ? no information available.

| Taxon | ecological class |
|--|------------------|
| Ameronothridae | |
| <i>Ameronothrus bilineatus</i> (Michael, 1888) | intertidal |
| <i>A. dubinini</i> Sitnikova, 1975 | terrestrial |
| <i>A. lapponicus</i> Dalenius, 1963 | terrestrial |
| <i>A. lineatus</i> (Thorell, 1871) | transition |
| <i>A. maculatus</i> (Michael, 1882) | transition |
| <i>A. marinus</i> (Banks, 1896) | intertidal |
| <i>A. nidicola</i> Sitnikova, 1975 | transition |
| <i>A. nigrofemoratus</i> (Koch, 1879) | transition |
| <i>A. oblongus</i> Sitnikova, 1975 | transition |
| <i>A. schneideri</i> (Oudemans, 1903) | intertidal |
| <i>A. schubarti</i> Weigmann & Schulte, 1975 | intertidal |
| <i>A. schuberti</i> Schubart, 1970 | intertidal |
| <i>Aquanothrus montanus</i> Engelbrecht, 1975 | terrestrial* |
| <i>Chudalupia meridionalis</i> Wallwork, 1981 | terrestrial* |
| Podacaridae | |
| <i>Antarcticola meyeri</i> (Wallwork, 1967) | terrestrial |
| <i>Alaskozetes antarcticus</i> (Michael, 1903) | transition |
| <i>A. bouvetoyaensis</i> Pletzen & Kok, 1971 | transition |
| <i>A. coriaceus</i> Hammer, 1955 | terrestrial |
| <i>Halozetes bathamae</i> Luxton, 1984 | intertidal |
| <i>H. belgicae</i> (Micheal, 1903) | transition |
| <i>H. capensis</i> Coetzee & Marshall, 2003 | intertidal |
| <i>H. crozetensis</i> (Richters, 1908) | transition |
| <i>H. edwardensis</i> Pletzen & Kok, 1971 | intertidal |
| <i>H. fulvus</i> Engelbrecht, 1975 | terrestrial |
| <i>H. impeditus</i> Niedbala, 1986 | transition |
| <i>H. intermedius</i> Wallwork, 1963 | intertidal |
| <i>H. littoralis</i> Wallwork, 1970 | intertidal |
| <i>H. maquariensis</i> (Dalenius, 1958) | terrestrial |
| <i>H. marinus</i> (Lohmann, 1907) | intertidal |
| <i>H. marionensis</i> Engelbrecht, 1974 | intertidal |
| <i>H. necrophagus</i> Wallwork, 1967 | transition |
| <i>H. otagoensis</i> Hammer, 1966 | transition |
| <i>H. plumosus</i> Wallwork, 1966 | transition |
| <i>H. scotiae</i> (Trouessart, 1912) | ? |
| <i>Podacarus auberti</i> Grandjean, 1955 | terrestrial |
| <i>Pseudantarcticola georgiae</i> (Wallwork, 1970) | terrestrial |

TABLE 2: Continued.

| Taxon | ecological class |
|--|------------------|
| Fortuyniidae | |
| <i>Alismobates inexpectatus</i> Pfungstl & Schuster, 2012 (2012b) | intertidal |
| <i>A. keniaensis</i> Pfungstl, 2016 | intertidal |
| <i>A. pseudoreticulatus</i> Pfungstl, 2015 (2015c) | intertidal |
| <i>A. reticulatus</i> Luxton, 1992 | intertidal |
| <i>A. rotundus</i> Luxton, 1992 | intertidal |
| <i>Circellobates venustus</i> Luxton, 1992 | intertidal |
| <i>Fortuynia arabica</i> Bayartogtokh, Chatterjee, Chan & Ingole, 2009 | intertidal |
| <i>F. atlantica</i> Krisper & Schuster, 2008 | intertidal |
| <i>F. dimorpha</i> Pfungstl, 2015 (2015a) | intertidal |
| <i>F. elamellata</i> Luxton, 1967 | intertidal |
| <i>F. hawaiiensis</i> Pfungstl & Jagersbacher-Baumann 2016 | intertidal |
| <i>F. inbambanensis</i> Marshall & Pugh, 2002 | intertidal |
| <i>F. longiseta</i> Pfungstl, 2015 (2015c) | intertidal |
| <i>F. maculata</i> Luxton, 1986 | intertidal |
| <i>F. maledivensis</i> Pfungstl, 2015 (2015c) | intertidal |
| <i>F. marina</i> Hammen, 1960 | intertidal |
| <i>F. rotunda</i> Marshall & Pugh, 2002 | intertidal |
| <i>F. sinensis</i> Luxton, 1962 | intertidal |
| <i>F. smiti</i> Ermilov, Tolstikov, Mary & Schatz, 2013 | intertidal |
| <i>F. taiwanica</i> Bayartogtokh, Chatterjee, Chan & Ingole, 2009 | intertidal |
| <i>F. yunkerii</i> Hammen, 1963 | intertidal |
| Selenoribatidae | |
| <i>Arotrobates granulatus</i> Luxton, 1992 | intertidal |
| <i>A. lanceolatus</i> Luxton, 1992 | intertidal |
| <i>Carinozetes bermudensis</i> Pfungstl & Schuster, 2012 | intertidal |
| <i>C. mangrovi</i> Pfungstl, Lienhard & Jagersbacher-Baumann, 2014 | intertidal |
| <i>C. trifoveatus</i> Pfungstl & Schuster, 2012 | intertidal |
| <i>Pseudobates uncutunguis</i> Luxton, 1992 | intertidal |
| <i>Rhizophobates shimojanai</i> Karasawa & Aoki, 2005 | intertidal |
| <i>Schusteria littorea</i> Grandjean, 1968 | intertidal |
| <i>S. melanomerus</i> Marshall & Pugh, 2000 | intertidal |
| <i>S. nagisa</i> Karasawa & Aoki, 2005 | intertidal |
| <i>S. saxea</i> Karasawa & Aoki, 2005 | intertidal |
| <i>S. ugraseni</i> Marshall & Pugh, 2000 | intertidal |
| <i>Selenoribates arotroventer</i> Pfungstl, 2015 (2015b) | intertidal |
| <i>S. asmodaens</i> Pfungstl, 2015 (2015b) | intertidal |
| <i>S. divergens</i> Pfungstl, 2015 (2015b) | intertidal |
| <i>S. elegans</i> Pfungstl, 2013 (2013c) | intertidal |
| <i>S. foveiventris</i> Strenzke, 1961 | intertidal |
| <i>S. ghardaqensis</i> Abd-el-Hamid, 1973 | intertidal |
| <i>S. mediterraneus</i> Grandjean, 1966 | intertidal |
| <i>S. nicus</i> Pfungstl, 2015 (2015b) | intertidal |
| <i>S. quasimodo</i> Pfungstl, 2013 (2013c) | intertidal |
| <i>S. satanicus</i> Pfungstl, 2013 (2013c) | intertidal |
| <i>Thalassozetes barbara</i> Pfungstl, 2013 (2013d) | intertidal |
| <i>T. riparius</i> Schuster, 1963 | intertidal |
| <i>T. tennisetosus</i> Bayartogtokh & Chatterjee, 2010 | intertidal |

the most important environments for tropical intertidal oribatid mites (Karasawa and Hijii 2004a) and some species, e.g. *Carinozetes mangrovi*, seem to be exclusively associated with these habitats (Pfungstl et al. 2014). Fortuyniidae species, on the other hand, display a very narrow range of habitats. Nearly all of them inhabit rocky shores; only three out of 20 species have been reported to occur occasionally in mangrove forests (e.g. Pfungstl 2015c). Pfungstl (2015c) suggested that the homogeneous morphology of the genus *Fortuynia* may be associated with this limited habitat preference. Several *Fortuynia* species may also dwell in empty barnacles or oyster shells, and are the only intertidal mites known to do so (Hammen 1963; Aoki 1974; Luxton 1990a, 1992; Marshall and Pugh 2002; Krisper and Schuster 2008). There is one record of *F. smiti* found in a riverine environment which represents the most unusual occurrence of this taxon (Pfungstl 2015c).

DISPERSAL MECHANISMS

Given the strong ecological connection of ameronothroid mites to the littoral zone habitat, dispersal by active migration would be possible only along the coastline, but the fact that these

mites have also reached geologically young and remote oceanic islands clearly shows that there are other ways of dispersal. There are several dispersal mechanisms that may be responsible for long-distance transport of these flightless arthropods, but the scarcity of evidence has allowed no consensus on their reality or relative importance. An overview of these possible dispersal mechanisms follows.

(1) Anthropogenic dispersal seems unlikely as intertidal mites do not occur on commercially used plants or soils. Although the transport of these mites in bilge tanks of large vessels cannot be excluded, shipping activities are recent in geological times and may not have seriously influenced present distribution and population patterns. Nevertheless, with growing globalization activities this mode of dispersal may well have an impact on patterns in the near future.

(2) Aerial dispersal (anemochory) is another possible mechanism but experimental data on this topic are rare and controversial. In an early study (Glick 1939), in which insect traps were installed on airplanes, mites were trapped on various occasions at different altitudes, but nearly all trapped

TABLE 3: Observed survival times of ameronothroid mites experimentally submerged in salt water. LT 50 = median lethal time, max = maximum survival time.

| | LT 50 | max | reference |
|---------------------------------|----------------------|---------------------------|----------------|
| Ameronothridae s. str. | | | |
| <i>Ameronothrus lineatus</i> | 74 days / > 2 months | 249 days / > 8 months | Schuster 1979 |
| <i>A. maculatus</i> | - | 104-108 days / > 3 months | Schuster 1966 |
| | 43 days / > 1 month | 160 days / > 5 months | Schuster 1979 |
| <i>A. marinus</i> | - | 138 days / > 4 months | Schuster 1966 |
| | 68 days / > 2 months | 143 days / > 4 months | Schuster 1979 |
| Podacaridae | | | |
| <i>Halozetes marinus</i> | >20 / < 1 month | - | Pugh 1995 |
| Fortuyniidae | | | |
| <i>Alismobates inexpectatus</i> | 21 days / < 1 month | 55 days / > 1 month | Pfungstl 2013a |
| <i>Fortuynia atlantica</i> | 40 days / > 1 month | 143 days / > 4 months | Pfungstl 2013a |
| Selenoribatidae | | | |
| <i>Carinozetes bermudensis</i> | 19 days / < 1 month | 51 days / > 1 month | Pfungstl 2013a |

specimens belonged to phoretic mite taxa that use insects as transport hosts. In a later study (Gressitt and Yoshimoto 1974), using fine mesh aerial nets in Alaska, a few oribatid mites were caught drifting in the wind, and a more recent study (Lehmitz et al. 2011) demonstrated that oribatid mites can be dispersed by wind up to at least 160 m above ground level, though the majority of these wind-transported mites consisted of species usually found in tree habitats. In contrast, a similar survey found no evidence of wind dispersal of mites (Coulson et al. 2003). Moreover, powerful storms would be necessary to propel flightless arthropods long distances of a few thousand kilometers and even if this would happen, these animals would not survive the extreme conditions, such as low pressure and freezing temperatures at high altitudes (Pugh 2003). Intertidal oribatid mites are neither phoretic on insects, nor do they inhabit trees and therefore aerial dispersal is a quite unlikely mode of long-distance transport for them.

(3) Bird-mediated transport has been discussed as another possible way of reaching and colonizing remote islands (e.g. Schatz 1991, 1998; review by Lebedeva and Lebedev 2008) but again, evidence is scarce and authors are of different minds as to the importance of this mode of distribution. In a long-term study of birds in polar areas, several terrestrial mites were found on a few occasions, either in bird nests or plumage (Lebedeva and Lebedev 2008, Lebedeva 2012) and hence birds are believed by these authors to be the main suppliers of soil mites to isolated archipelagos.

Considering the terrestrial nature of high Arctic and Antarctic Ameronothridae, it is indeed possible that dispersal occasionally occurs in this way. For example, it would explain the already mentioned mysterious findings of *Alaskozetes coriaceus* and *Ameronothrus bilineatus* in hemispheres opposite from their main distributions (Schuster 1966, Weigmann 1975b). In the above-mentioned study of seabird nesting colonies on Spitsbergen, *A. lineatus* individuals were found in a few nests (Coulson et al. 2009), hence the basic prerequisite for

dispersal by birds was met. Nevertheless, the same study could find no evidence of the mites being actually transported by birds. Pugh (1997) dismissed a priori bird-mediated transport of oribatid mites to oceanic islands, arguing that mites dispersed by birds usually show specific morphological adaptations to attach to the bird's body. Marine-associated ameronothroid mites show no morphological modification for phoresy, though their long hook-like claws may facilitate such transport. While transport in bird plumage remains a possible, if improbable, dispersal mechanism for Ameronothridae, it almost certainly has no role for Fortuyniidae or Selenoribatiidae: species of these exclusively intertidal families do not dwell in the vicinity of seabird nests or colonies.

(4) Another potential method to reach remote islands is through transport by ocean currents (hydrochory). First evidence was provided by a study in which pleuston nets on boat trips between the islands of the Galápagos archipelago were used after a heavy storm, and a remarkable number of living oribatid mite individuals was found floating in debris or directly in the sea (Peck 1994). To survive such a transport, tolerance of long periods of submersion is necessary, which littoral mites possess, as discussed above (e.g. Schuster 1979, Pugh et al. 1987a). Coulson et al. (2002) further demonstrated that even terrestrial arthropods with different biologies are able to survive in salt water for over 14 days and therefore transoceanic dispersal by mites and collembolans may be a common phenomenon. Based on mean survival times of Bermudian intertidal oribatid mite species, individuals are able theoretically to survive transport in seawater along the Gulf Stream over a distance of 3,000 km (Pfungstl 2013b). Moreover, the floating behaviour of certain *Fortuynia* species (Pfungstl 2013a) as well as the possession of buoyancy-giving plastrons in supposedly all ameronothroid taxa, would contribute to their hydrochorous dispersal. Therefore, most authors (e.g. Schatz 1991, 1998; Coulson et al. 2002; Pfungstl 2013b) agree that long-distance dispersal of oribatid mites to oceanic islands is mainly hydrochorous.

EVOLUTION OF THE INTERTIDAL LIFESTYLE

An extensive fossil record since the Middle Devonian ($388 \pm 3,8$ mya) indicates that oribatid mites are an ancient taxon (Norton et al. 1988). A molecular genetic study (Schaefer et al. 2010) even suggests that oribatid mites were among the first terrestrial colonizers and had already originated in the Precambrian (571 ± 37 mya). The colonization of land started in the interstitial zone of coastal habitats and finally resulted in the occupation of all terrestrial habitats on earth. Marine-associated mites as well as the exclusively marine halacarid mites demonstrate that some of them not just evolved from water to land but later also from land to water.

Current hypotheses

Schuster (1966) was the first to theorize about the origin of the intertidal lifestyle in oribatid mites. He suggested two possible ways: (a) terrestrial ancestors successively colonized the fringe of freshwater bodies, then brackish water habitats and finally the marine littoral; (b) fully terrestrial ancestors began to feed on washed-ashore flotsam, rich in organic matter, and subsequently specialized on other food resources present in the intertidal zone. Schuster admitted that both scenarios could have been concurrent, but considered it more likely that at least the Ameronothridae took the former evolutionary pathway. Indeed, certain members of *Ameronothrus* can be found regularly in estuaries (e.g. Schulte et al. 1975) and can withstand long periods of inundation not only with salt water but also with fresh water (Schuster 1979). Pfungstl (2013b) also discovered an unexpectedly high fresh water tolerance in the exclusively intertidal selenoribatid *Carinozetes bermudensis* and suggested it may be a relictual trait. A high general water tolerance was without a doubt a preadaptation necessary for mites to invade aquatic habitats, but it provides no evidence of evolutionary pathway, since some typical terrestrial species, e.g. *Euzetes globulus*, also can tolerate long periods of inundation (Schuster 1966).

Schulte and Weigmann (1977) provided another evolutionary scenario (Figure 9A) hypothesizing that

a terrestrial ancestor of ameronothrid mites, inhabiting cold and wet soils, occupied larger portions of the world's land masses and a warming of the world's atmosphere scattered these animals to cooler locations. Subsequent glaciation events pushed these mites closer to the shore and finally forced them to invade polar coastlines. The chances of survival were higher near the warmer sea and so these coastal species radiated in the littoral environment and spread along the coast to warmer climates and this spreading happened independently in the Northern and Southern hemisphere. Marshall and Convey (2004) agreed that all ameronothroid lineages must ultimately have had an earlier terrestrial ancestry but they argued that at least recent colonization patterns of podacarid mites of the southern hemisphere cannot be explained with the aforementioned hypothesis. They stated that species living exclusively in intertidal habitats of the Antarctic and Sub-Antarctic are more primitive than those in supralittoral/terrestrial environments of coastal areas and proposed that colonization by ameronothrid (podacarid) mites in the southern hemisphere has proceeded from marine habitats to terrestrial areas following glacial retreat. However, a molecular genetic investigation of several Antarctic species of Podacaridae (*Halozetes*, *Alaskozetes*, *Podacarus*) found no evidence of speciation from an intertidal to a terrestrial group or vice versa (Mortimer et al. 2011). Although the above-mentioned theories (Schuster 1966, Schulte and Weigmann 1977, Marshall and Convey 2004) offer different opinions on recent evolutionary patterns, all agree on a monophyletic origin of the Ameronothroidea and their littoral lifestyle.

Procheş (2001), on the other hand, suggested that land-to-sea transition in secondary marine organisms, including ameronothroid mites, took place independently in three distinct latitudinal bands (northern cold-temperate, tropical, southern cold-temperate) (Figure 9B). He suggested that species interactions, i.e. competition, drove the origin of marine association in subtropical and tropical selenoribatid and fortuyniid mites, while glaciation is thought to be responsible for that of polar ameronothrid/podacarid mites (e.g. Schulte and Weigmann 1977, Procheş and Marshall 2001).

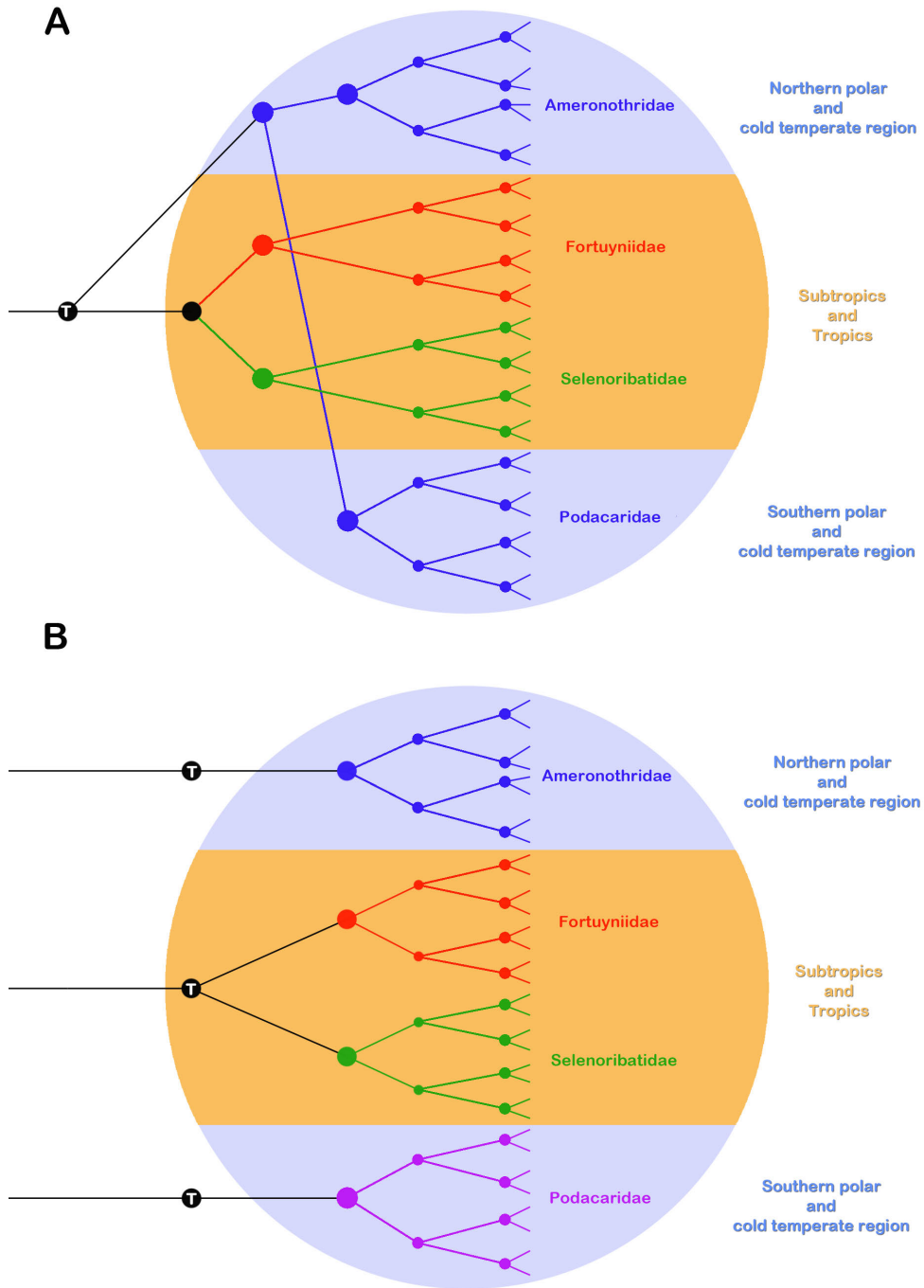


FIGURE 9: Simplified schemes illustrating two different evolutionary theories explaining origin of marine-associated Ameronothroidea: A – Monophyletic origin of Ameronothroidea implying single land-to-sea transition event (e.g. supported by Schulte and Weigmann 1977); B – Polyphyletic Ameronothroidea and three independent invasions marine littoral (e.g. supported by Procheş 2001). T = last terrestrial ancestor, invading littoral environment. (Schemes are not to be seen as phylogenetic trees, length of lines does not correspond with time or number of evolutionary changes).

Flaws in current hypotheses, and evidence from preliminary molecular studies

Schulte and Weigmann (1977) provided a thoughtful hypothesis concerning the monophyletic origin of the intertidal lifestyle which lead to the taxonomic unification of Ameronothridae and Podacaridae. The authors plausibly demonstrated that there are not enough morphological features separating these two taxa and indeed, presently there are only two characters which do not overlap: the presence in all *Ameronothrus* species (but absence in all Podacaridae) of brachytracheae in legs and the absence of setae *it* on leg IV of all Podacaridae (versus the presence in Ameronothridae). From a morphological point of view, the monophyly of this group seemed to be validated.

However, the molecular genetic study of Schäffer et al. (2010), encompassing selected oribatid mite species from diverse families, including *A. maculatus* and *P. auberti*, demonstrated a paraphyletic position of the two taxa, which clearly contradicts the conclusion of Weigmann and Schulte (1977). Wallwork (1964) had already argued that certain similar traits of the Podacaridae and Ameronothridae may have evolved independently. Both taxa inhabit predominantly cold and temperate regions and similar environmental properties may have led to similar convergent morphologies. The biogeographic distribution of Ameronothridae and Podacaridae – in opposite hemispheres without a noteworthy overlap – may point to an independent origin rather than to a common ancestry. The two often neglected and exceptional monotypic genera *Aquanothrus* and *Chudalupia*, occurring in ephemeral rock pools at modest elevations in semi-arid or arid regions of North America, South Africa and Western Australia, have been considered relictual ameronothrid species (Norton et al. 1997) that might have been linked biogeographically in the distant past. But there is evidence from another molecular genetic study (Mortimer et al. 2011) that *Aquanothrus* is not closely related to Podacaridae as the ceratozetoid genus *Magellozetes* intervenes between *Aquanothrus* and the Podacaridae. Consequently, these data also indicate that Ameronothridae and Podacaridae are supported as different

groupings and that the current disjunct distribution, in opposite areas of the world, may not be associated with the relictual occurrences of *Aquanothrus* and *Chudalupia*. The biogeographic pattern of Ameronothroidea rather supports the theory of Procheş (2001), in which land-to-sea transitions took place independently in three distinct latitudinal bands, with the Ameronothridae in the northern cold-temperate, the Fortuyniidae and Selenoribatidae in the tropical, and the Podacaridae in the southern cold-temperate region. This theory is further supported by results of Krause et al. (2016) who investigated the evolution of aquatic life by oribatid mites using molecular genetics. They concluded that Fortuyniidae and Selenoribatidae colonized salt water habitats only once whereas the Ameronothridae invaded these habitats independently and hence they suggested that Ameronothroidea are a polyphyletic taxon.

Behan-Pelletier and Eamer (2007) argued that the evolution of respiratory organs in Oribatida was a critical step in the invasion of aquatic habitats, and indeed the development of plastron respiration was surely one of the most important adaptations allowing the colonization of the intertidal zone. Comparing plastron respiration systems in Ameronothroidea further supports the theory of independent land-to-sea transition events. Fortuyniidae and Selenoribatidae use similar plastrons and breathe with tracheal organs while submerged (Pfungstl and Krisper 2014), whereas Ameronothridae use different plastron organs and breathe across the thin weakly sclerotized cuticle during submergence (Pugh et al. 1987a, 1990; Messner et al. 1992).

In summary, biogeographic, molecular genetic and plastron respiration data contradict the theory of a monophyletic Ameronothroidea in its current sense, and suggest multiple independent origins of their marine-associated lifestyle.

Nevertheless, biogeographic patterns are largely incomplete and many new taxa and occurrences remain to be found (Pfungstl and Schuster 2014). Furthermore, the recent molecular genetic studies (Schäffer et al. 2010, Mortimer et al. 2011, Krause et al. 2016), while informative, are certainly preliminary, as they include very few ameronothroid

taxa and concentrated on different research questions. Finally, plastron structures were investigated in very few species, none of which was a member of Podacaridae.

The semiaquatic Tegeocranellidae and their relationship to marine-associated mites

Several authors (e.g. Subías 2004, Marshall and Pugh 2002) do not accept the monogeneric Tegeocranellidae as a member of Ameronothroidea because they do not consider the juvenile morphology to be important for systematic considerations. Given the above-mentioned doubts about the monophyly of Ameronothroidea, it may seem reasonable to agree with these authors. Nonetheless, Behan-Pelletier (1997) provided seven synapomorphies supporting a relationship among Tegeocranellidae, Fortuyniidae and Selenoribatidae. The most obvious synapomorphy is certainly the shared type of juvenile plication, namely a centrodorsal gastronomic plate framed by deep lateral and ventral folds and wrinkles, only present in immatures of these three taxa. Pfungstl and Krisper (2014) demonstrated that this specific type of plication plays an important role in plastron respiration of juvenile fortuyniid and selenoribatid mites. Though not investigated yet in tegeocranellid immature stages, they may use the same plastron mechanism and this could be a further indication of a common origin. Another morphological character associated with plastron respiration may also support a close relationship between Tegeocranellidae and Fortuyniidae. The already-mentioned van der Hammen's organ of fortuyniid mites is part of the plastron system, and Behan-Pelletier (1997) noticed similar structures in Tegeocranellidae but refrained from considering these traits homologous. Considering a close relation between Tegeocranellidae and Fortuyniidae/Selenoribatidae, occupation of semiaquatic freshwater habitats may represent the more ancestral ecology. Based on these indications, the following scenario might be considered: a terrestrial ancestor colonized semiaquatic and aquatic freshwater habitats, e.g. ponds and streams, then some descendants diversified within these environments, evolving the Tegeocranellidae, and others

colonized the marine littoral either by migrating downstream into brackish waters or by inhabiting coastal freshwater bodies that eventually became connected to the open ocean and evolved there to the Fortuyniidae and Selenoribatidae.

CONCLUDING REMARKS

Ameronothroid intertidal oribatid mites have successfully colonized all shorelines, from biologically depauperate ice-cold polar coasts to lush humid tropical shores. Although air-breathing and similar in overall morphology to typical terrestrial taxa, they have evolved specific adaptations to the marine littoral, as for example modified tarsal claws, plastron respiration and ovoviviparity. Daily tidal cycles and associated wave action are the most important stress factors shaping these adaptations. Hydrochorous dispersal is considered the main long-distance transport mechanism in fortuyniid and selenoribatid mites, whereas bird-mediated transport may be responsible for dispersal events in northern ameronothroid mites.

Based on recent findings it is suggested that the families currently included in Ameronothroidea do not share a proximate common ancestry. They probably have colonized coastal environments at least three times, once in northern hemispheric polar and temperate areas by the Ameronothridae, once in the Tropics by ancestors of Fortuyniidae and Selenoribatidae and once in Antarctic and Sub-Antarctic regions by the Podacaridae. Accordingly, the family Ameronothridae *sensu lato* – i.e. *sensu* Weigmann and Schulte (1977) – is a polyphyletic grouping, and the unification of Ameronothridae with Podacaridae no longer seems justified. The two families probably evolved parallel in opposite Polar regions. The Fortuyniidae, Selenoribatidae and Tegeocranellidae, on the other hand, may still represent a monophyletic lineage which has evolved from a tropical ancestor that already showed an association with freshwater habitats.

As Marshall and Convey (2004) already pointed out, a more complete understanding of the evolution of marine-associated mites will require thorough morphological and molecular phylogenetic in-

vestigations. Moreover, a comprehensive and holistic approach is needed to reveal natural relationships among alleged members of Ameronothroidea and to reconstruct their evolutionary pathway from a terrestrial ancestor to the sea.

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