

HABITAT USE, FEEDING AND REPRODUCTIVE TRAITS OF ROCKY-SHORE INTERTIDAL MITES FROM BERMUDA (ORIBATIDA: FORTUYNIIDAE AND SELENORIBATIDAE)

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ABSTRACT — Ecological aspects of the intertidal fortuyniid oribatid mites *Alismobates inexpectatus* and *Fortuynia atlantica* and the selenoribatid *Carinozetes bermudensis* and *Carinozetes trifoveatus* were studied in the Bermuda islands. All species are stenotopic inhabitants of the marine littoral zone. *Fortuynia atlantica* and *C. trifoveatus* dwell predominantly in the lower eulittoral zone of rocky shores, *A. inexpectatus* prefers the median eulittoral area of exposed rocky coasts and *C. bermudensis* inhabits median and upper ranges of boulder beaches and mangrove forests. All species are algivorous showing certain food preferences but they are also opportunistic feeders. Indirect sperm transfer could be demonstrated in *A. inexpectatus* and *C. bermudensis*. Both species typically produce stalked spermatophores, although *A. inexpectatus* deposits spermatophores singly and *C. bermudensis* in groups. Occasional spermatophagy could be observed by specimens of *A. inexpectatus*. Oviposition was observed for all species and time from deposition to eclosion ranged from 15 to 30 days. Egg shell structure differs considerably between Fortuyniidae and Selenoribatidae. *Fortuynia atlantica* and *A. inexpectatus* showed aggregation behaviour, but no direct function or triggering stimulus could be detected. All species are fast-moving and excellent climbers. *Fortuynia atlantica* exhibits a special "floating behaviour" and *C. bermudensis* exhibits "levitation"; both phenomena are likely to facilitate hydrochorous dispersal.

KEYWORDS — Fortuyniidae; Selenoribatidae; spermatophores; exochorion; behaviour

INTRODUCTION

Oribatid mites are primarily terrestrial species, most of which inhabit soil, litter, bark and foliage. Certain oribatid taxa have also managed to conquer the marine environment but are restricted to littoral zones suggesting that they have not completely transgressed the ecological barrier between marine and terrestrial environments (Procheş and Marshall, 2001). More than two-thirds of the oribatid mites dwelling in marine-associated

habitats are representatives of the superfamily of Ameronothroidea, which contains the families Ameronothridae, Selenoribatidae and Fortuyniidae (Procheş and Marshall, 2001). The Tegeocranellidae, which are closely related to the Fortuyniidae and Selenoribatidae, have been placed within the Ameronothroidea (Behan-Pelletier, 1997) but differ from the other members in being exclusively associated with semi-aquatic habitats of terrestrial environments.

However, most of the Ameronothroidea are

characteristic elements of the littoral fauna and inhabit intertidal zones of rocky shores, boulder beaches, salt marshes and mangrove forests. The ecological traits of these mites are of special interest for evolutionary biologists as they show adaptations to both terrestrial and marine environments. The study of these taxa may therefore provide important insights into selective constraints imposed by both realms.

Although a substantial amount of literature dealing with diverse aspects of these intertidal oribatid mites exists, behavioral and life histories adaptations are poorly known and have been primarily studied in the Ameronothridae. Investigations on feeding habits of this group revealed that these mites are mainly algivorous, feeding on marine microphytes which include diverse algae and cyanobacteria (Luxton, 1966; Schulte *et al.*, 1975; Schulte, 1976; Pugh and King, 1985; Svik, 2004). Aggregations of adults and moulting aggregations of juveniles have been observed in many species (Schulte *et al.*, 1975; Schulte, 1976; Convey, 1994; Bcking *et al.*, 1998; Svik, 2004) and are hypothesized to prevent dislodgement by waves (Schulte *et al.*, 1975; Bcking *et al.*, 1998; Svik, 2004). Schulte (1973) and Pugh and King (1986) demonstrated circadian and circatidal activity rhythms in several members of the Ameronothridae and larviposition is suggested to be the main mode of parity in this taxon (Luxton, 1967; Bcking *et al.*, 1998; Svik, 2003). In contrast to the Ameronothridae, the ecology of the exclusively littoral Fortuyniidae and Selenoribatidae has been widely neglected. Schuster (1977) and Krisper and Schuster (2008) gave some information on feeding and aggregation behaviour, and recent publications (Pfingstl, 2013a, 2013b) have provided the first detailed insights into the biology and life history of these littoral mites.

The present paper represents a compilation of observations conducted during a year-long project on fortuyniid and selenoribatid mites from the archipelago of Bermuda and intends to increase our knowledge of the ecology of these animals. The results are compared with data on the life history traits of the Ameronothridae in order to ascertain if different families have evolved similar or diver-

gent mechanisms to cope with the intertidal environment.

MATERIALS AND METHODS

All investigations were carried out in the years 2011 and 2012 at the Bermuda Institute of Ocean Sciences (BIOS) Inc. Specimens of the truly littoral fortuyniid oribatid species, *Alismobates inexpectatus* Pfingstl and Schuster, 2012, *Fortuynia atlantica* Krisper and Schuster, 2008 and the selenoribatid *Carinozetes bermudensis* Pfingstl and Schuster, 2012 and *C. trifoveatus* Pfingstl and Schuster, 2012 were collected from different coasts of the archipelago of Bermuda. Bermuda lies at a latitude of 32°N and shows a subtropical climate with mean air temperatures ranging from 18.5 °C in February to 29.6 °C in August (Thomas, 2004). The tidal range on Bermuda is approx. 1 metre, and intertidal zones were defined as follows: lower eulittoral = 0 – 33 cm above the median low water level (MLL), median eulittoral = 34 – 66 cm, and upper eulittoral = 67 – 100 cm above the MLL. At present, the four investigated species are only known to occur on the islands of Bermuda, but there are records of closely related congeners from several Caribbean Islands, e.g. Jamaica, Barbados (Pfingstl, 2013a), and a wider geographic distribution of the respective species is supposed. Detailed information on seasonal dynamics, development, life histories, sex ratio and number of eggs per female of *F. atlantica*, *A. inexpectatus* and *C. bermudensis* are provided by Pfingstl (2013b). The life cycle of these intertidal mites has the following basic stages: egg, larva, protonymph, deutonymph, tritonymph and adult. A total of 115 samples (patches approx. 10 cm²) of diverse algae (*Bostrychia tenella* Agardh, 1863; *Bostrychia montagnei* Harvey, 1853; *Gardnerula* De Toni, 1936; *Herposiphonia secunda* Ambronn, 1880; *Lyngbya majuscula* Harvey ex Gomont, 1892 and *Rhizoclonium riparium* Harvey, 1849) in different intertidal zones were scraped of rocks and mangrove roots with a knife mostly during low tide. These algae represent a three-dimensional microhabitat, thus extraction is necessary to reveal the presence of mites. Adults and juveniles were extracted with a Berlese-Tullgren apparatus. For rearing and observational purposes, living specimens

TABLE 1: Frequency distribution and association with intertidal algae for the four investigated species. A – abundance in eulittoral zone and substrate given as percentage of 115 samples (e.g. *Fortuynia atlantica* was found in 25 % of all samples in the lower eulittoral zone); B – abundance on diverse algae given as percentage of the respective alga sample (e.g. *Fortuynia atlantica* occurred in 13 % of all *Bostrychia tenella* samples).

A	eulittoral zone				substrate	
	lower	median	upper	rocks	boulders	mangroves
Fortuyniidae						
<i>F. atlantica</i>	25	37	37	88	12	0
<i>A. inexpectatus</i>	5	39	56	82	13	5
Selenoribatidae						
<i>C. bermudensis</i>	15	35	50	27	32	41
<i>C. trifoveatus</i>	36	36	27	89	11	0

B	intertidal alga					
	<i>B. tenella</i>	<i>B. montagnei</i>	<i>H. secunda</i>	<i>R. riparium</i>	<i>Gardnerula</i> sp.	<i>L. majuscula</i>
Fortuyniidae						
<i>F. atlantica</i>	13	0	8	0	75	0
<i>A. inexpectatus</i>	87	24	63	50	25	38
Selenoribatidae						
<i>C. bermudensis</i>	16	100	33	88	25	63
<i>C. trifoveatus</i>	19	0	33	13	25	25

(adults and juveniles) were put into cylindrical plastic boxes lined with plaster of Paris and pieces of algae (of the respective sample) were added to provide food. No specific feeding experiments were performed but mites were observed feeding on specific algae and the results of these preliminary observations are presented in this paper. Species were reared separately and each box contained 10 to 20 individuals. Boxes were kept at room temperature (ca. 25 °C) and checked every day. Cultures were kept until the last specimen in the box died (maximum time approx. nine months). In several cases, dead animals were put into lactic acid and investigated in temporary slides to determine the sex. Photographs were made with a Canon Powershot D10 digital camera. For SEM-investigations, the eggs were dehydrated in ascending ethanol concentrations, air-dried, mounted on aluminium-stubs with double sided sticky tape, and then sputter-coated with gold-palladium. SEM-micrographs were taken

at the Research Institute for Electron Microscopy and Fine Structure Research, Graz, University of Technology using a Zeiss Gemini Ultra 55.

RESULTS

Habitat

The typical habitat of *A. inexpectatus* is mats of the filamentous red alga *B. tenella* growing on cliffs and bare rocks, which may be exposed to strong wave action. *F. atlantica* prefers rocky coastlines in sheltered bays or flat shores. Typical locations for *C. bermudensis* are sheltered bays with boulders overgrown with algae and shores with dense coastal vegetation or mangrove forests. *C. trifoveatus* prefers sheltered rocky bays like *F. atlantica*. Frequency distribution data for each of the defined shore zones and substrates are given in Table 1.

All species were found in high abundance (>50 specimens in 10 cm² algal cover), except for *C. tri-*

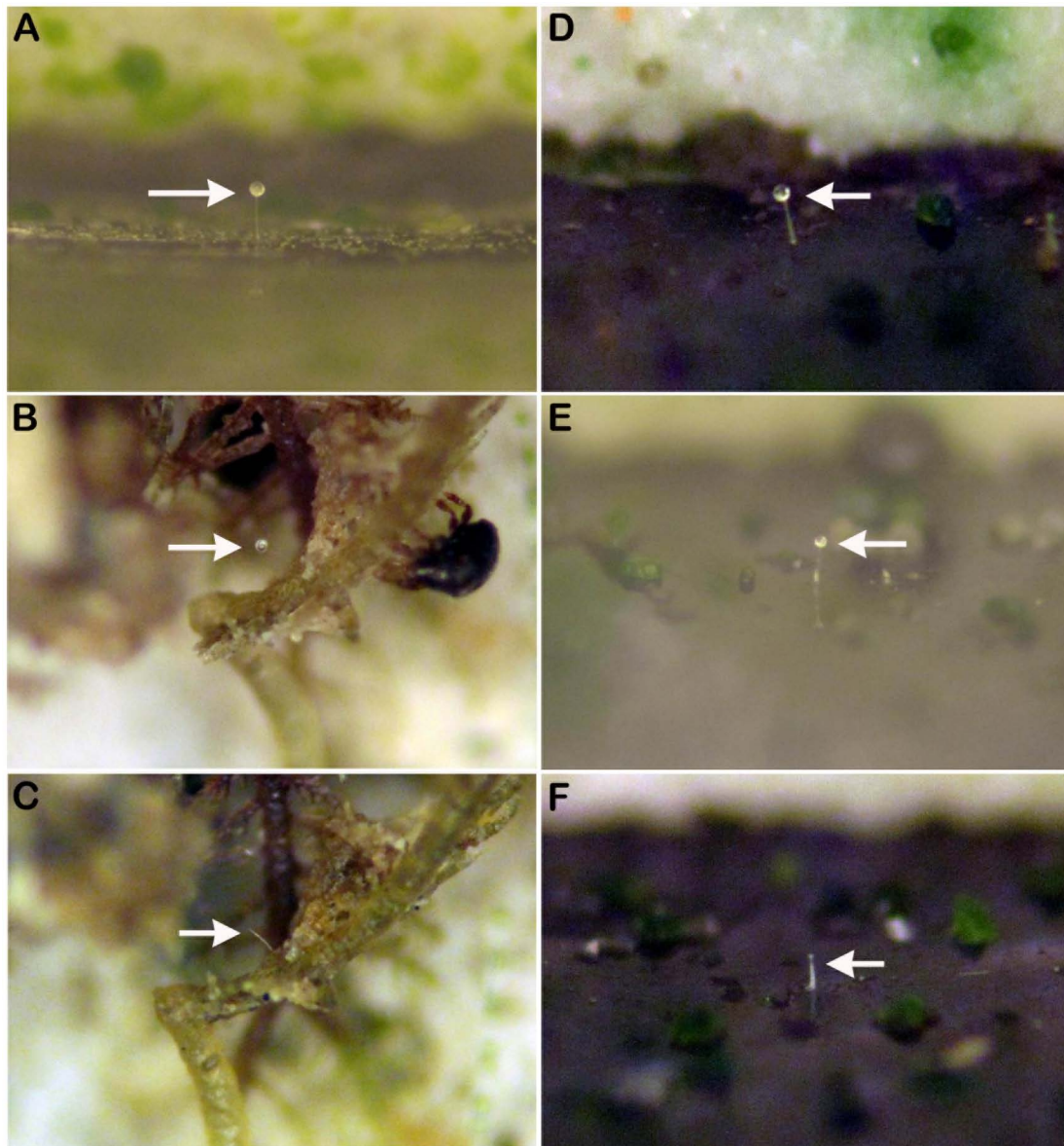


FIGURE 1: A-C – Spermatophores of *Alismobates inexpectatus*; A – deposited on lateral wall of plastic box; B – deposited on alga; C – bare stalk of spermatophore shown in B; D-F – spermatophores of *Carinozetes bermudensis*, D-E – deposited on lateral wall of box; F – bare stalk. Arrows pointing to spermatophores and bare stalks, respectively.

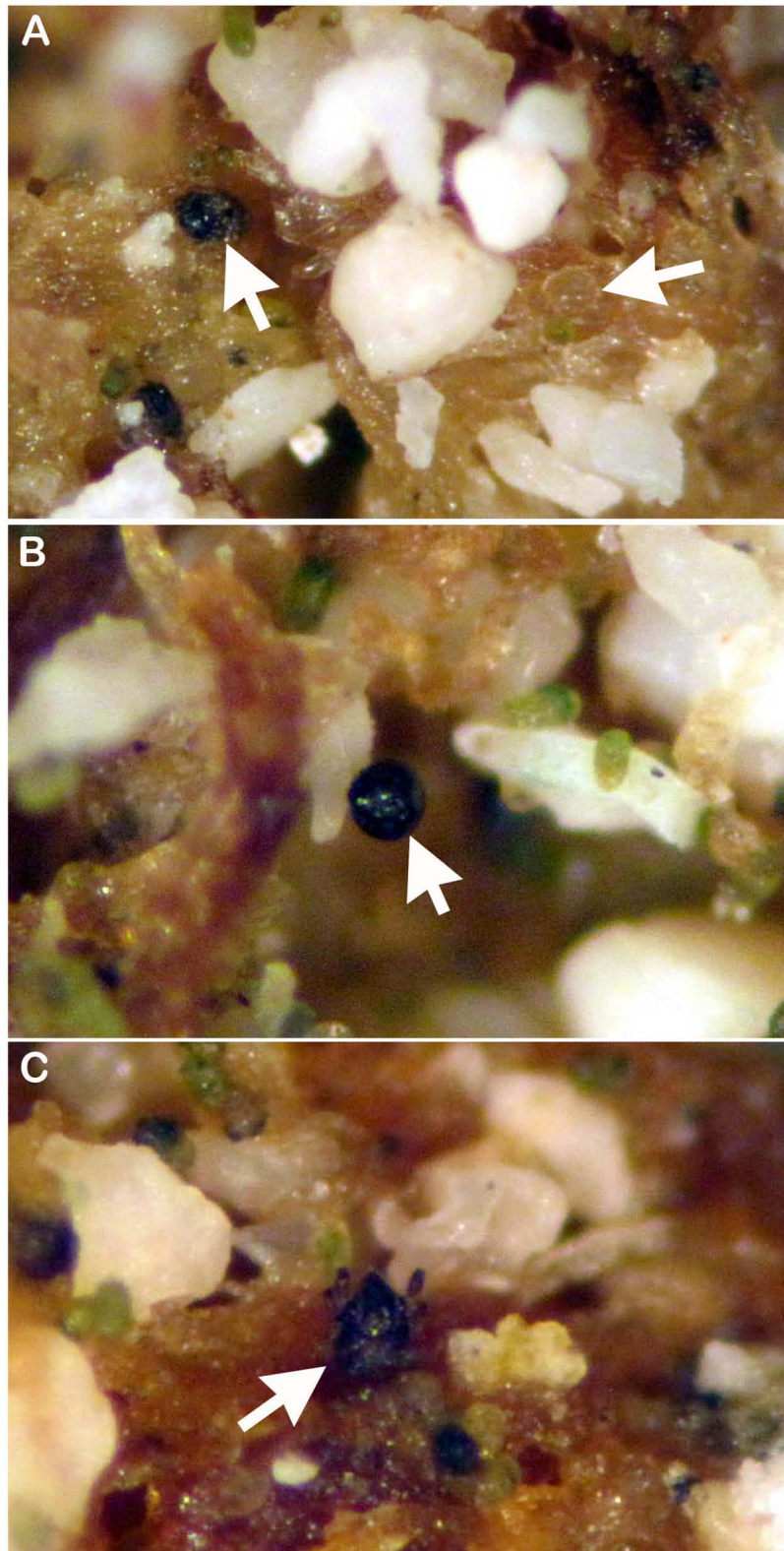


FIGURE 2: Eggs of *Alismobates inexpectatus* deposited into an algal mass, arrows pointing to eggs. A – left egg shortly before eclosion showing dark colour, right egg freshly deposited with lighter colour; B – algal mass removed from egg; C – larva hatching from egg.

foveatus. Of the 115 samples, there were 21 in which more than one species occurred together. Of these, *A. inexpectatus* and *C. bermudensis* co-occurred as pairs most often (nine times) and *F. atlantica* and *C. bermudensis* least (once). In three samples, three species could be found together with all possible species combinations, and in one sample, all four species were recorded together.

Food

Alismobates inexpectatus was observed feeding extensively on *B. tenella*, occasionally on *H. secunda* and in a few cases on *L. majuscula* and other unidentified filamentous green algae. *F. atlantica* was observed feeding on the green alga *Gardnerula* sp. and *C. bermudensis* fed on *R. riparium* Harvey, 1849 and *B. montagnei*. As *C. trifoveatus* was always found in small numbers, observations in rearing experiments were not numerous enough to make statements about their food habits.

Reproduction

Alismobates inexpectatus produces stalked spermatophores with a length of approximately 70 – 100 µm. The stalk is very thin with a fragile appearance and the head consists of a globular droplet of sperm (Figures 1A and 1B). The spermatophores were always deposited singly. Typically, each male deposited at least two spermatophores over the course of a few days followed by a pause of about a month. Spermatophores were frequently deposited in the absence of females. Observed time from deposition to uptake by females ranged from a few hours to four days and remaining bare stalks (Figure 1C) persisted for a few more days. In several cases, no stalks were left at all. Olfactory perception may be involved in the detection of spermatophores as on several occasions females walking close to a spermatophore were observed to stop abruptly, make obvious movements with the pedipalps and then head directly to the spermatophore to take it up. The opposite behaviour, avoiding contact with spermatophores, was also observed. Nevertheless, a few spermatophores were seemingly trampled down involuntary. I twice observed mites consuming spermatophores including the whole stalk. Un-

fortunately, the sex of these animals could not be determined as the consumption happened within seconds and the subsequent removal of these specimens failed. *A. inexpectatus* shows oviparity. Eggs were deposited into tiny hollow spaces and interstices of the algal substrate, so that the algal mass



FIGURE 3: Egg of *Fortuynia atlantica*, vertical row of pictures illustrating chronological development of egg stage. Arrow points to egg.

nearly completely enclosed the eggs (Figures 2A–C). Due to this camouflage, eggs could rarely be detected and consequently time from deposition to emergence of larva could not be recorded. However, eggs turned from yellow to nearly black two days before hatching (Figure 2B). Under SEM-examination the surface of the eggs is completely smooth and lacks conspicuous exochorion structures (Figures 5A and 5B).

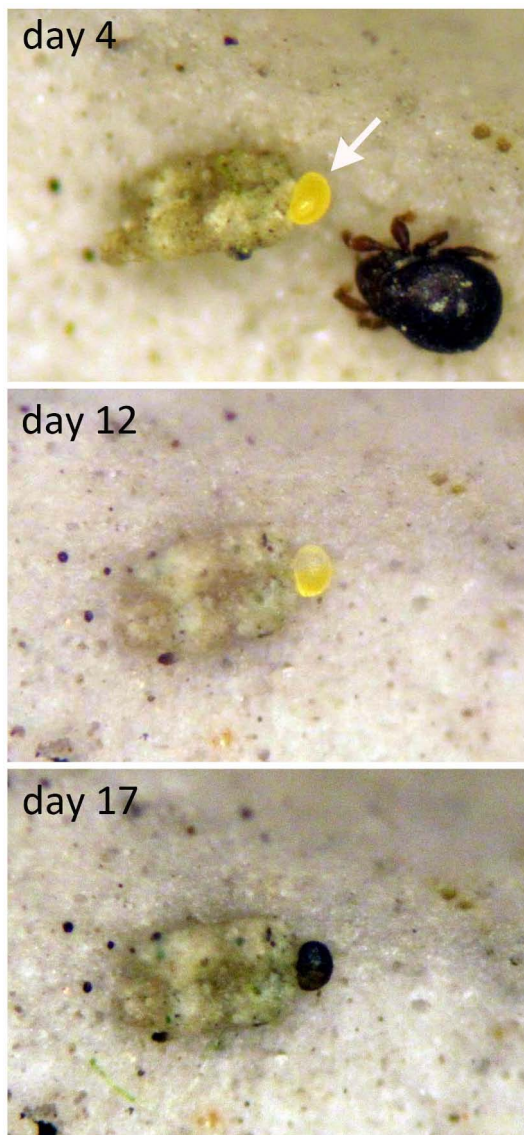


FIGURE 4: Chronological development of egg stage of *Carinozetes bermudensis*. Egg attached to a grain of sand. Arrow points to egg.

Spermatophores or mating behaviour were not detected in *F. atlantica*, although this species successfully reproduced in the rearing boxes. *F. atlantica* is also oviparous and eggs were laid singly into crevices or fissures of the substrate. The eggs seemed to be glued to the substrate, as specimens walking past and touching the eggs did not change the eggs' positions. Time from deposition to eclosion ranged from 25 to 32 days (Figure 3). Young eggs displayed a yellowish white colour. After ten days a clear polarization of the mass within the egg could be observed, which means that one pole became darker and the other lighter, nearly transparent. Approximately two days before eclosion eggs turned dark brown, nearly black, and the larva could be recognized through the egg shell (Figure 3). The surface of the eggs of this species is also completely smooth under SEM (Figures 5C and 5D).

Carinozetes bermudensis produces stalked spermatophores with a length of approximately 50 – 80 μm . The stalk is thin, but with a robust appearance (Figures 1D and 1E). The spermatophores were always deposited in groups (four to nine spermatophores), separated from each other by about 1 mm. Uptake of sperm droplets happened very soon after deposition as in most cases only the bare stalks (Figure 1F) were detected during the daily box checks. The bare stalks were very resistant; in one case they persisted for three weeks, even though many active animals were contained in the respective box. No spermatophagy was observed in this species. *C. bermudensis* deposited eggs singly into interstices and fissures of the substrate, where they were slightly glued to the ground or to grains of sand. Duration of the egg stage ranged from 17 to 22 days. Newly laid eggs were yellow. After approximately ten days a polarization of the mass within the egg was noticed and, shortly before eclosion, eggs became dark brown (Figure 4). Under SEM, the egg shell of this species is uneven showing a dense gauze-like structure (Figures 5E and 5F).

No observations of spermatophores or oviposition by *C. trifoveatus* were made.

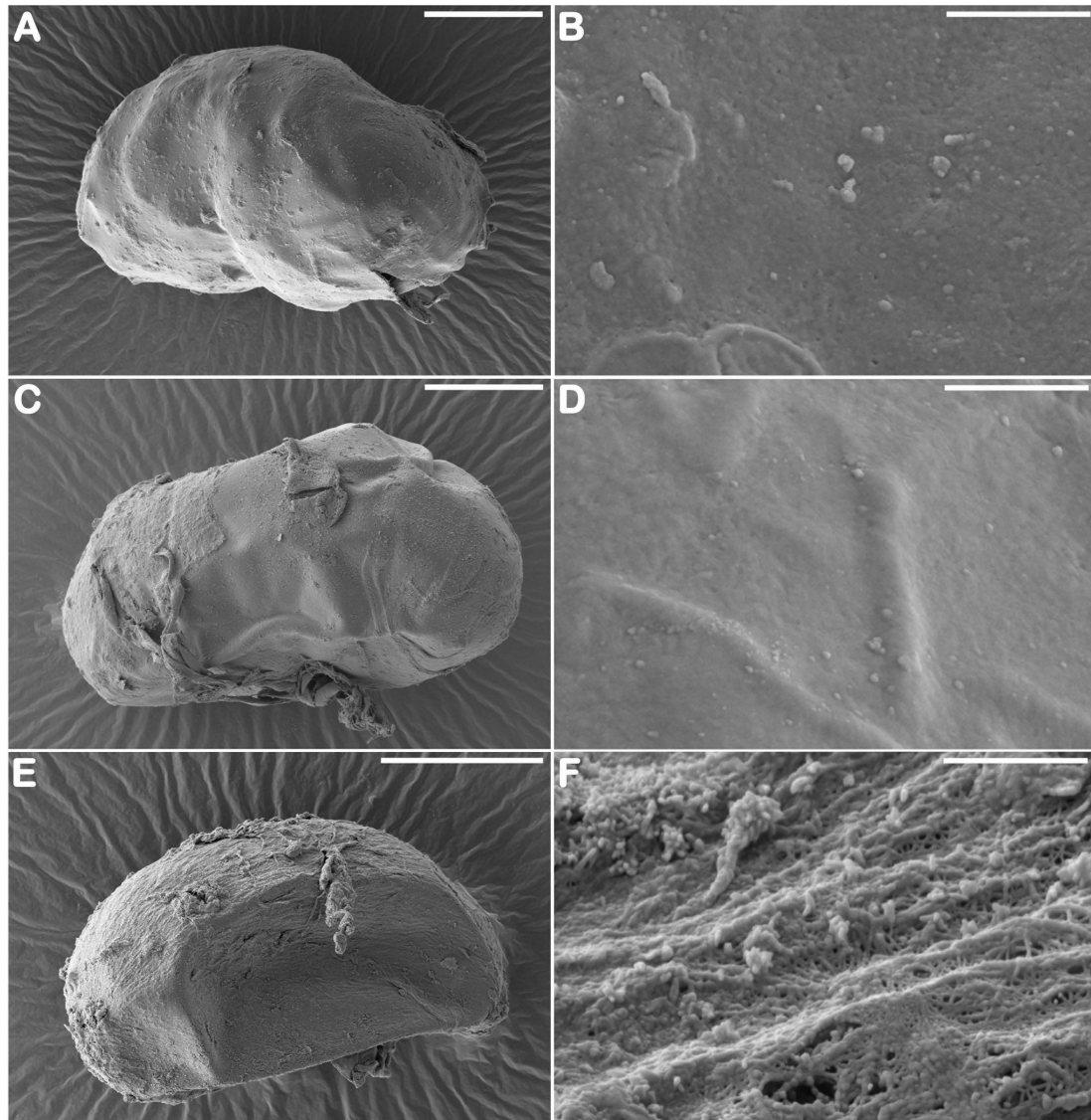


FIGURE 5: SEM-micrographs of exochorion structures; scale bar of left column 40 µm, scale bar of right column 1 µm. A – *Alismobates inexpectatus* egg; B – detailed surface view of egg shown in A; C – *Fortuynia atlantica* egg; D – detailed surface view of egg shown in C; E – *Carinozetes bermudensis* egg; F – surface details of egg shown in E.

Moulting

Moulting aggregations were not observed in any of the investigated species; however, in one alga sample numerous exuviae of *F. atlantica* juveniles were found in a very limited area. In the rearing boxes, larvae and nymphs basically retreated solitarily in holes or other protected spaces before entering the quiescent pre-moult state.

I observed moulting in *A. inexpectatus*, *C. bermu-*

densis and *C. trifoveatus* and this process took three to seven hours. After opening the ecdysial cleavage line, animals pushed the dorsal and ventral part of the exuvia slowly apart. Short periods of activity were followed by longer periods of rest. Finally, the juveniles emerged from the exuvia in reverse.

In a few cases the dorsal scalp stuck to the emerging mite but was lost after a short while.

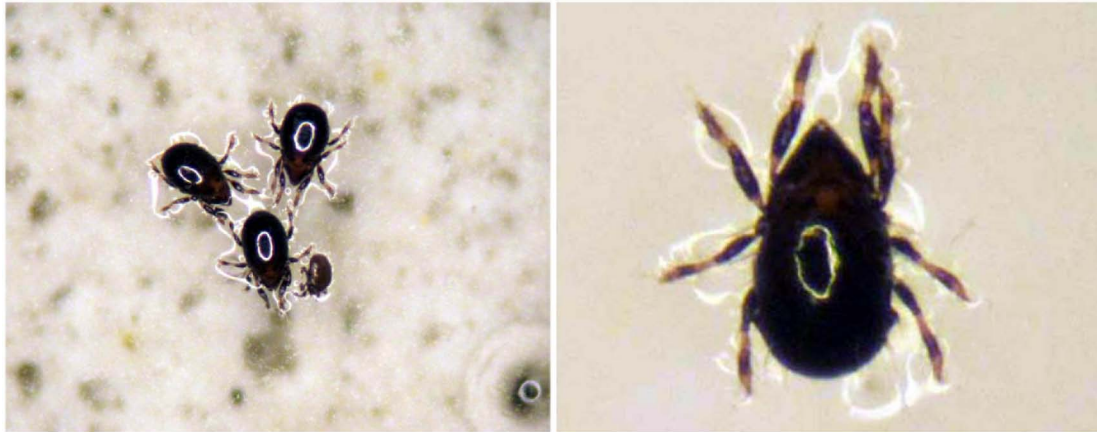


FIGURE 6: Photographs illustrating "floating behaviour" shown by *Fortuynia atlantica*; specimens floating with splayed legs on the water surface.

Locomotion

Fortuynia atlantica is a fast-moving species, with excellent climbing skills. The animals were able to climb a two centimetre high vertical smooth plastic wall in 1-2 seconds. The animals showed increased activity when exposed to strong light or reduced moisture. Decreased activity was recorded when the specimens were completely flooded with sea-water. Thigmotactic behaviour (movement of an organism towards an object) was frequently observed, in which animals entered small and narrow crevices and stayed there motionless for a while. Aggregation was shown by juveniles and adults of this species but I could detect no triggering stimulus or direct function of this behaviour. The animals crouched next to each other and on top of each other and stayed in this position for a few days. *F. atlantica* specimens immediately splayed their legs when exposed to sudden flood and floated motionless on the surface of the water (Figure 6) until they reached firm substrate, which they then tried to climb. This special behaviour was only shown by this species and is called "floating behaviour" by the author.

Alismobates inexpectatus is less agile than *F. atlantica*, but still more mobile than a typical terrestrial oribatid mite. This species also became more active when exposed to light or reduced moisture. When the animals were completely flooded, activity was reduced. Thigmotaxis was also present in

this species. Both adults and juveniles aggregated frequently, and again no trigger or function for this behaviour, e.g. synchronized moulting or mating, could be detected. Sometimes the animals remained aggregated for more than a week. In one case two specimens died within the crowd and even began to decompose without the aggregation dissolving; only stimulation with a fine brush dispersed the animals. *A. inexpectatus* individuals did not show any "floating behaviour" and soon sank when put into water.

Carinozetes bermudensis shows moderate climbing skills and is basically less active than the fortuyniid species. However, this species reacted instantly to exposure to light and thigmotactic behaviour was observed frequently. The animals rarely aggregated and the observed aggregations contained only a few individuals. When flooded, the specimens struggled hectically for a while, but it seemed that the loss of ground contact rather than the contact with water induced this behaviour. After a while the animals stopped moving and drifted with the whole body submerged upside down adhering to the water surface. The living specimens were extremely buoyant and drifted up to two weeks before sinking. In a few cases bubbles aggregated after a while in the gut of flooded specimens, adding to the floating ability of this species.

In contrast to the other species, *C. trifoveatus* was very active and agile under flooded conditions

and showed less activity when exposed to reduced moisture. One specimen of this species was observed running unperturbed on the water's surface.

DISCUSSION

Habitat and food

The present results confirm the intertidal character of the investigated species, as all of them occurred solely in the eulittoral range. According to Schulte *et al.* (1975), they should be classified as stenotopic inhabitants of the marine littoral zone, confined exclusively to the coast. The Fortuyniidae and Selenoribatidae differ in this respect from the marine associated Ameronothridae, which are known to show increasing habitat specificity with decreasing latitude, in both the southern and northern hemisphere (Schulte, 1975; Marshall and Convey, 2004). Although the fortuyniid and selenoribatid species from Bermuda are restricted to the intertidal zone and sometimes occurred syntopically, they exhibit divergent preferences concerning vertical zonation and coastal configuration (substrate, exposition, wave action). These differences may be related to the spatial distribution of the algae, which serves as substrate and food resource at the same time. According to Schulte (1976) variations in the vertical distribution of littoral algae may determine the local occurrence of ameronothrid mites and the same may apply to the taxa of the present investigation. *A. inexpectatus*, *F. atlantica* and *C. bermudensis* are clearly algivorous and although Schuster (1977) found body parts of tardigrades in the guts of undetermined selenoribatid species, supposing them to be carnivorous as well, my observations of feeding could not confirm this assumption. The investigated species show certain food preferences, but they are also opportunistic feeders. This nutritional flexibility and the occasional syntopic occurrence of these taxa indicate that competition for food is unlikely to be a limiting factor in the intertidal environment.

Reproduction

Concerning the reproduction of littoral oribatid mites, a detailed study does not exist. Indi-

rect sperm transfer has been previously reported in marine-associated mites. Luxton (1966) found stalked spermatophores in the hermanniid *Hermannia pulchella* Willmann, 1952 living in a salt-marsh, Svik (2004) observed the same in the ameronothrid *Ameronothrus lineatus* (Thorell, 1871) and Alberti (1974) stated that the morphology of spermatophores produced by littoral Trombidi-formes, although differing among genera, did not show any special adaptations to the intertidal habitat. The latter is also the case in *A. inexpectatus* and *C. bermudensis*; both produce stalked spermatophores typical of terrestrial oribatids although the detailed structure is slightly different. However, no obvious structural adaptations to the quickly changing intertidal environment were found. Sperm droplets mostly burst when contacted by salt water and considering these fragile structures, it must be assumed that sperm transfer must happen fast and during low tide. The supposed olfactory perception of spermatophores in *A. inexpectatus* may allow rapid detection and absorption, whereas the deposition of groups of spermatophores in *C. bermudensis* may also increase the chance of sperm transfer during the short time frame of low tide.

Turk (1988) observed a male of the erythroid *Erythraeus phalangoides* De Geer, 1778 feeding on its own spermatophore and supposed this to be an aberrant behaviour. Spermatophagy in *A. inexpectatus* was observed twice in different rearing boxes, therefore a specific function of this behaviour should be assumed. Females of certain species of the insect order Orthoptera are also known to feed on a non-sperm-bearing spermatophylax, which is hypothesized to be a kind of gustatorial courtship (Dettner and Peters, 2003). Sperm competition, with males trampling down spermatophores of other males, has been observed in many arthropod taxa (Proctor, 1998). This may also be the case in *A. inexpectatus* with males feeding on the spermatophores of other males. However, further studies are necessary to assess whether this behaviour represents gustatorial courtship or sperm competition.

The reproductive mode of *F. atlantica*, the third investigated species, remains unknown. Krisper

and Schuster (2008), observing specimens of this species in laboratory cultures, neither detected spermatophores nor a typical adult sexual behaviour and the same applies to the present study. The strong sexual dimorphism of this species, with males showing large lateral protuberances and leaf shaped notogastral setae (Krisper and Schuster, 2008), suggests that some kind of mating behaviour may be involved although direct sperm transfer could not be detected. A strong sexual dimorphism in conjunction with physical contact during mating is also shown in the terrestrial collohmanniid *Collohmannia gigantea* Sellnick, 1922 (Schuster, 1962) and in the galumnid *Pilogalumna* sp. (Estrada-Venegas *et al.*, 1996). Direct sperm transfer in *F. atlantica* possibly happens very quickly and while the mites are retreated into crevices in order to avoid submerged conditions. This may also explain why mating has not yet been observed.

Luxton (1967) reported that oribatid mites inhabiting the areas of a salt meadow below the limits of high spring tides were viviparous and suggested that the mechanical effect of the tide is important in regulating the occurrence of egg laying mites in this habitat. Members of the littoral Ameronothridae are also known to be mainly larviparous (Luxton, 1966; Bücking *et al.*, 1998; Svik, 2003) and this trait is supposed to be related to this aquatic and semiaquatic mode of life (Norton, 1994). In contrast, the Fortuyniidae and Selenoribatidae of the present study show oviposition with egg stage durations of 15 days to a month. The regular tidal flooding obviously does not pose a serious threat to the egg stage of *A. inexpectatus*, *F. atlantica* and *C. bermudensis*. These mites protect their eggs against the mechanical effects of tidal flow by laying them in small crevices or within the algal mass. Only little information exists about egg shell structure in intertidal oribatid mites in literature. Grandjean (1955) reported that the surface of the eggs of the littoral ameronothrid *Podacarus auberti* Grandjean, 1955 is conspicuously granular and Krisper *et al.* (2008) demonstrated a remarkable exochorion structure in the epilittoral scutoverticid *Scutovertex arenocolus* Pfingstl and Schffer, 2009, with mushroom-like formations covered by an additional external layer.

The latter authors supposed that these structures act as protection against osmotic stress and help keep a layer of air around the egg during inundation. The exochorion of *C. bermudensis* clearly differs in its specific structure from the above mentioned examples, but the gauze-like formation with its hollow spaces may also allow air retention under flooded conditions. The surface of the eggs of *F. atlantica* and *A. inexpectatus*, on the other hand, are lacking external structures completely, thus air is not covering the egg during high tide. This demonstrates that the families of Fortuyniidae and Selenoribatidae have evolved different mechanisms to cope with daily tidal inundation of the eggs.

Aggregation

Many authors (Schulte *et al.*, 1975; Schulte, 1976; Convey, 1994; Bcking *et al.*, 1998; Svik, 2004) have observed aggregations in littoral Ameronothridae, and Krisper and Schuster (2008) also reported similar behaviour in *F. atlantica*. These aggregations are hypothesized to be protection against wave action (Schulte *et al.*, 1975; Bcking *et al.*, 1998; Svik, 2004), but also to aid mate location (Block and Convey, 1995) and to ease synchronized moults (Svik, 2004). The present data confirms the existence of this behaviour in the fortuyniid species, but the function of these aggregations could not be ascertained. Neither moulting juveniles nor reproductive behaviour were observed, thus protection against dislodgement by waves may be the most likely explanation.

In the selenoribatid *C. bermudensis* aggregating mites were more or less absent. This species predominantly inhabits boulder beaches overgrown with algae or mangrove forests not exposed to strong surf and these habitats may provide more refuge spaces compared with bare rock. These mites are also smaller than *A. inexpectatus* and *F. atlantica* specimens and may therefore enter smaller crevices and find shelter more easily.

Locomotion

All species, investigated in this study, are fast moving animals and active climbers, especially *F. atlantica* and *C. trifoveatus*. These locomotive skills

probably represent an adaptation to fast changing intertidal environment and there may be a correlation between vertical occurrence, substrate and speed of locomotion. According to the present results, species dwelling on rocky substrate in the lower eulittoral zone are able to move faster than species living in sandy or vegetated areas of the upper eulittoral. This hypothesized correlation is supported by the fact that the intertidal mycobatid *Punctoribates quadrivertex* Halbert, 1920, established in lower regions of coastal marshes, is also known as a fast runner and climber (Luxton, 1966), while the ameronothrid *Halozetes otagoensis* Hammer, 1966 and *Ameronothrus schneideri* (Oudemans, 1903), dwelling in the upper eulittoral and the supralittoral respectively, are slow moving species (Luxton, 1966, 1990).

The "floating behaviour" observed in *F. atlantica* is unique among intertidal oribatid mites. Pfingstl (2013a) demonstrated that hydrochorous dispersal is the most likely mode of long distance transport in this species and the floating behaviour clearly facilitates dispersal along ocean currents. The other fortuyniid species, *A. inexpectatus*, has not evolved such a behavioural mechanism; however, these mites can often be found in dense algal mats and attached to a piece of floating algae; long distance transport is therefore still feasible. *C. bermudensis* also lacks behavioural adaptations for hydrochorous dispersal, but this species shows remarkable floating abilities due to a layer of air retained to the body surface while being submerged (Pfingstl, 2013a). The occasional formation of bubbles in the gut, observed in this study, further increases buoyancy making this species more or less unsinkable. Newell (1945) discovered upward movement in the water column due to air bubbles in the midgut in aquatic *Hydrozetes* species and named this phenomenon "levitation". He suggested that levitation would allow animals that have been dislodged to escape starvation and death by anoxia that would occur at the dark bottom of a pond. In the intertidal *C. bermudensis* it seems unlikely that these mites would fall to anoxic depths of the ocean, therefore this mechanism more likely facilitates hydrochorous dispersal.

CONCLUDING REMARKS

The present study demonstrated that the intertidal families of Ameronothridae, Fortuyniidae and Selenoribatidae have evolved several different mechanisms to cope with daily tidal inundation. For example, oviparity is the common mode in Fortuyniidae and Selenoribatidae and these mites lay their eggs in deep fissures to protect them from wave action, whereas in Ameronothridae the eggs develop sheltered in the mother's body and larviparity is shown. Detailed comparisons between the families are yet not feasible as information on spermatophores, egg shell structure, and hydrochorous dispersal of ameronothrid mites is lacking. Further investigations on more species of Ameronothridae, Fortuyniidae and Selenoribatidae from various geographic areas are necessary to reveal and compare the evolutionary histories and specific ecological adaptations of these intertidal families.

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