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What is a truly marine oribatid mite?

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An interesting and important study recently published by Norton *et al.* (2025) describes a new family of oribatid mite, demonstrating evolutionary paedomorphism. Additionally, this paper makes the assertion that the single species described for this family, *Paedonothrus reductus*, represents the first truly marine oribatid mite. We argue here that insufficient data are given in the paper to confirm the marine existence of this mite, and that such an existence is well demonstrated in several other oribatid mite lineages. The suggestion of a marine existence of *P. reductus* is seemingly founded on its proposed independence of air breathing and by living on a drift algal/seagrass mat, nearby a tropical Indian Ocean island; the described functional morphology also suggests an aquatic lifestyle. Below we explain why this behaviour and 'habitat' are not compelling evidence for a marine existence, hoping that this correspondence will remove confusion around what constitutes a marine mite or a marine oribatid mite.

The habitat of the described mite is improperly defined. The authors report that seven individuals were collected from 'a floating mixed mat of seagrass (*Halophila* sp.) and seaweed (*Sargassum*)', which represent components of different marine ecosystems. Seagrasses inhabit soft substrata (muddy sediments of estuaries and lagoons) and seaweed typically attaches with a holdfast to hard (usually rocky) surfaces. Surveys of algae and seagrasses in the Lakshadweep Archipelago (Nobi *et al.* 2011; Shabeena *et al.* 2023) fail to record either *Halophila* or *Sargassum* from the island where *Paedonothrus* was collected, suggesting these plants may have been washed to the island from further afield. Although the authors might believe that the species is truly marine, its occurrence on marine plant debris points to possible displacement from an adajcent or even more distant terrestrial or freshwater environment. Such displacement is further suggested by the collection in the study of only thelytokous females, a strategy of mites and insects for effective colonization of novel environments (Pequeño *et al.* 2021; Queffelec *et al.* 2021). A prominent mechanism for the colonization of oceanic islands by small secondary marine and terrestrial invertebrates involves rafting on seaweed and organic debris masses, disloged during storms and high seas (Abe *et al.* 2013; Pfingstl 2017).

The behaviour and restriction of air-breathing in rafting small invertebrates is generally unclear and understudied. Raft floatation implies that hitchhikers could be afforded air-breathing (those at the upper surface of the raft), rather than being compelled to breathe underwater. But, in any case, oribatid mites have very low oxygen demand levels, which are typically met by direct diffusion across the integument (Hoy 2008). There are several demonstrations for an array of oribatid species surviving prolonged submersion, which might relate to their most common edaphic habitat becoming temporarily waterlogged (Bardel *et al.* 2018). Submersion tolerance predisposes oribatid mites to dispersal by means of oceanic rafting.

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Furthermore, the requirement of air breathing is probably the weakest of arguments when considering the likelihood of an organism being marine. Indeed, a very high proportion of aquatic and marine animals across the taxonomic spectrum of molluscs, arthropods, insects and vertebrates (Kramer 1988) depend on air breathing; examples include, high-shore gastropods, mosquito larvae, mangrove fishes (mudskippers), turtles, cormorants, seals and dolphins. Marine existence is thus better explained by an ability to interact solely with this environment and invariably feed and reproduce in this environment. Charismatic species such as whales and dolphins are not denied truly marine status based on air breathing, however, nor would this be denied to organisms such as sea turtles that still require access to land for reproduction. The evolutionary transitions that have brought these organisms back to the sea are profound (Procheş *et al.* 2014), and their integration into marine ecosystems is compelling. Neither marine feeding nor reproduction are demonstrated in the case of *P. reductus*.

In contrast, several situations within the Oribatida clearly indicate evolutionary transition from a terrestrial to a marine existence. This is well exemplified by members of the superfamily Ameronothroidea (Ameronothridae, 52 species Fortuyniidae, 30 species, Selenoribatidae, 44 species; Procheş & Marshall 2001; Pfingstl 2017; GBIF 2025), for which recent phylogenetic analyses suggest at least four independent marine incursions (Pfingstl *et al.* 2023; Cordes *et al.* 2024). Speciation within marine ecosystems is seen by vertical zonation in several *Halozetes* species across sub-Antarctic island rocky shores (Marshall *et al.* 1999; Mercer *et al.* 2000; Barendse *et al.* 2002; Marshall & Chown 2002). The pattern of species preference to specific peritidal zones (the low-shore red algae/*Porphyra* zones, the mid-shore *Verrucaria* zone, and the upper-shore and supratidal *Mastodia/Caloplaca* zones) is repeated across the sub-Antarctic islands for different *Halozetes marinus* is a low shore inhabitant, and is only temporarily exposed to air during brief low tide periods (Mercer *et al.* 2000; Marshall & Chown 2002).

This is, however, not to say that assigning a marine existence to an oribatid mite taxon is always straightforward. Fairly unusual to the animal kingdom is species representation of the same genus in both the marine and terrestrial realms. This is observed by *Halozetes*, with some species being transitional and others having reverted to a terrestrial existence. Halozetes belgicae occurs in supratidal habitats on sub-Antarctic islands but extends into the terrestrial biotope in the higher latitudinal maritime Antarctic (notably the taxonomy of this species is in flux, with several subspecies having been described; Coetzee 2000; Marshall & Convey 2004; Mortimer et al. 2011). Halozetes fulvus and H. crozetensis exemplify independent ecological reversions to a terrestrial existence on different sub-Antarctic islands (Marshall et al. 1999; Barendse et al. 2002; Marshall & Chown 2002). The waters become muddled and assigning marine existence is more difficult for lower latitudinal (tropical) oribatid mites, especially those inhabiting mangroves. Determining precisely the habitat occupied by terrestrially originated arthropods in a mangrove ecosystem is complicated by the narrow spatial separation (less than one metre) between the terrestrial (branches and leaves) and marine realms (pneumatophores), suggesting a high probability of ecological displacement. Moreover, many highly motile terrestrial invertebrates (particularly flying or rapidly crawling individuals) transit tropical intertidal zones during the low tide, without biotically interacting with other organisms.

What then is a true marine mite? We propose that true marine existence is represented by the permanence of a species in a clearly defined marine habitat. By implication (or observation), such a species interacts biotically (feeding) with other marine organisms, and individuals typically reproduce, develop and form populations within the habitat. By implication (or observation), such a species has usually acquired the capacity to tolerate periodic or continuous seawater immersion (salinity exceeding zero parts per thousand), likely through evolutionary acquisition of some

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capacity for osmoregulation (Charmatier *et al.* 2009). This correspondence is written in a spirit of good will, to remove confusion by future researchers that the Oribatida is represented in marine ecosystems by a single species. We believe the authors of the *Paedonothrus* description would be in favour of clearing any such confusion. This correction of context is not intended to and does not detract from their otherwise remarkable paper describing the morphological evolution of a new oribatid mite family.

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