First record of the ellobiopsid parasite *Thalassomyces marsupii* Kane, 1964, in a stegocephalid host, with a review of previous records

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Abstract

The ellobiopsid parasite *Thalassomyces marsupii* Kane, 1964, is for the first time reported from a stegocephalid host, viz. *Parandania boecki* from the Faroe islands. *T. marsupii* is now known from hosts from five different families of Amphipoda, all pelagic predators; all known records are reviewed.

Introduction

The taxonomic position of the Ellobiopsidae, enigmatic parasites of mostly pelagic Crustacea, has long been uncertain and has still not been resolved satisfactorily; the group may in fact not be a homogeneous one. Shields (1994) placed the Ellobiopsidae, with a certain hesitation, among the parasitic dinoflagellates, basing himself primarily upon the biflagellate zoospores discovered by Galt and Whisler (1970) in *Thalassomyces marsupii* Kane,1964. However, not all members of the family have zoospores with two flagellae (*Parallobiopsis* has uniflagellate spores (Hovasse, 1925).

The apparently non-parasitic, but epibiontic species in the genus *Ellobiocystis* Coutière, 1911, are primarily known as associates of the mouthparts of shrimps (cf. Shields, 1994). Very similar organisms also occur on the mouthparts of amphipods; they are common on the eusirid amphipod *Rhachotropis macropus* Sars in western Norway (Vader and Kane, 1968). These organisms were examined by the late H. Boschma (Leiden), who identified them as probably belonging to the genus *Ellobiocystis*. Similar organisms have been found on the mouthparts of *Podocerus septemcarinatus* Schellenberg by Monod (1926, sub. nom. *Platophium hystricoides*) from the Antarctic, and later by Wing (1975) on *Rhachotropis helleri* from the NE Pacific, and by Ortiz and Lalana (1992) on *Colomastix pusilla* from Cuba. In our experience these organisms are relatively common but overlooked symbionts on various amphipod species.

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All parasitic Ellobiopsidae on amphipods, with the single possible exception of a very small and stunted specimen of an unidentified ellobiopsid on the oxycephalid *Calamorhynchus pellucidus* Streets from the Adriatic Sea, reported by Hoenigman (1964), apparently belong to a single species *Thalassomyces marsupii*, originally described from *Parathemisto gaudichaudii* Guérin (Hyperiidae) from the Southern Ocean (Kane, 1964); this species is situated in the brood-pouch region of its host with the external parasite simulating a clutch of eggs. The mode of infection is unknown, but the parasite develops in the ventral nervous system of the host and the gonomeres break through the integument from the inside (Kane, 1964). Most of the infected specimens are seemingly immature (Kane, 1964; Tencati and Geiger, 1968), but it is unknown whether this is due to a predilection for young specimens or, perhaps more plausible, because the parasite inhibits the development of secondary sexual characters, as has been noted to occur in the hosts of other *Thalassomyces* species (see Shields, 1994).

Long before its official description *Thalassomyces marsupii* in fact had already been observed, but not recognized as a parasite. Sexton (1909), in a paper on amphipods from the Bay of Biscay, but in this case talking about comparative material from W. of Ireland, described the eusirid amphipod *Rhachotropis helleri* as having two types of eggs with those in smaller specimens ‘supported on long bulbous stalks, branching from a short central stem by which the mass is attached to the fifth segment.’ These, as also the added sketch shows clearly, are undoubtedly *T. marsupii* (see also Vader and Kane, 1968, p. 18). Another early reference is the one by Behning (1939) from *Parathemisto japonica.*

Hosts and distribution of Thalassomyces marsupii

At present Thalassomyces parasites have been reported from many species of *Parathemisto*, various Eusiridae, and single species of the Cyphocarididae, Cystosomatidae (?) and Stegocephalidae; its distribution is apparently almost world-wide. Only molecular studies can decide whether all these organisms indeed all should be classified as a single species, *Th. marsupii* Kane, 1964, as nowadays is customarily assumed, or if a group of closely related sibling species is present. A more detailed listing of hosts follows.

Cyphocarididae

Cyphocaris challengeri Stebbing, 1888.

Wing (1975) collected *Th. marsupii* from this host regularly during a year’s sampling in southeastern Alaska, with prevalences varying from <1 % in winter to 5-10 % in August.

Cystisomatidae

Cystisoma sp.

Wing (1975) mentioned that Dr T. Bowman (Smithsonian Inst., Washington, pers. comm.) had mentioned finding "a similar parasite" (to *Th. marsupii*) on a specimen of *Cystisoma* sp. in the northern Pacific. To our knowledge, this record has never been published.

Eusiridae

Eusirus leptocarpus G.O.Sars

Two infected specimens of this rare amphipod were collected (240 m) in hyperbenthic sledge hauls from Raunefjorden in western Norway in 1966 and 1967 (Vader and Kane, 1968). One of the specimens carried two well-developed parasites. Subsequently, a few more infected specimens of *E. leptocarpus* have been found in the Hjeltefjord N. of Bergen, at 300 m depth (W. Vader, pers. obs.; Tromsø Museum, Ell.14).

Eusirus longipes Boeck

Two infected specimens of this locally common species were collected from Raunefjorden near Bergen, the same locality and the same sledge haul where one of the infected *E. leptocarpus* was collected (Vader and Kane, 1968). Three more were later collected from the Hjeltefjord N. of Bergen, at 300 m depth, again together with infected *E. leptocarpus* (W. Vader, pers. obs.). Even though we have collected numerous specimens of the host, we have yet to observe *Th. marsupii* on *E. longipes* from shallower water.

Rhachotropis aculeata (Lepechin)

Two infected specimens of this species were collected by Dr. P. Brunel (Montreal) in the Baie de Chaleurs, Gulf of St Lawrence, Canada in 1954 (Vader and Kane, 1968).

Rhachotropis helleri Boeck

As mentioned earlier, Sexton (1909) found what were undoubtedly multiple specimens of *T. marsupii* in a large sample of *R. helleri* from the west coast of Ireland. Unfortunately, these specimens were lost with the entire '*Helga*' collection (see Vader and Kane, 1968). Also in this case 'immature specimens', i.e. those without secondary sexual characters, were the ones preferentially infected.

Rhachotropis macropus G.O.Sars

This common bathypelagic species, which occurs often at high densities in Norwegian fjords over mud bottoms, is regularly infected with *T. marsupii*. In the Korsfjorden near Bergen, W. Norway, at 680 m depth, prevalence was ca 10 % (Vader and Kane, 1968), which is much higher than we have found elsewhere. Most of the infected hosts were immature, whereas a number of adult hosts possessed brownish scars ventrally on the pereion, indicating a prior infection with the ellobiopsid. Infected specimens of *R. macropus* have been found elsewhere in W. Norway, as well as in N. Norway east to the Varangerfjord (W. Vader, unpubl. obs.). Apparently multiple infections, with two external parasites on the same host, occur regularly. It is of course difficult to be absolutely certain that two different root systems are involved, but clearing of specimens in clove oil strongly indicated that this was the case.

Recently, infected specimens of *R. macropus* have also been collected from off the coast of NE Greenland (J.Berge, pers. obs.)

Hyperiidae

Parathemisto abyssorum Boeck

Two infected specimens were caught in a

midwater trawl near Bergen, W. Norway (Vader and Kane, 1968); a third was collected from the same area a few years later (Tromsø Museum, Ell. 7). Tencati and Geiger (1968) found a prevalence of nearly 25 % in *P. abyssorum* from northeast Greenland, but only 1.3 % in the Beaufort Sea. Those authors noted that infected females never showed well-developed broodplates, while the situation in infected males was less clear: some showed no modifications at all, others lacked both a penis and well-developed testes. Perhaps the variation in sterilization is a function of infection with less obviously sterilized animals having been infected more recently. Mean size was the same between infected and non-infected *Parathemisto*.

Parathemisto gaudichaudii (Guérin)
This is the type host of *T. marsupii*. Kane (1964) reported on the distribution and abundance of a large number of specimens from the Southern Ocean, the Benguela Current and the north-western Atlantic. Infected hosts have also been found in the northern North Sea (McHardy in Wing, 1975, sub nom. *P. gracilipes*). Kane described the development and internal structure of *T. marsupii* in some detail, and opined that the parasite "does not seriously upset normal development" of the host amphipod.

Parathemisto japonica Bovallius
Behning (1939), in a hitherto overlooked reference from Far East Russia, noted for the hyperiid *Parathemisto japonica*: “Now and then specimens were found with peculiar ‘grape-like structures’ (‘Traubenbildungen’) on the ventral side, which seemingly belong to a parasitic fungus.” (translated from German by the author.). This is clearly a *Thalassomyces,* and most probably *T. marsupii*.

Parathemisto libellula Lichtenstein
Wing (1975) collected 19 infected amphipods of this species among ca 2,000 specimens of *P. libellula* in south-eastern Alaska in Sept. 1966, although none were present among >5,000 *P. libellula* in August 1965.

Parathemisto pacifica Stebbing
Wing (1975) also collected a single parasitized specimen of *P. pacifica* (among ca 200 amphipods collected) in south eastern Alaska in Sept. 1966. The same species was found parasitized ‘regularly’ and was used for their studies of sporulation in ellobiopsids by Galt and Whisler (1970), working in Washington Sound, NW USA. These authors provided data on the biflagellate swarmers, and pictures of the vegetative thallus of the parasite.

Stegocephalidae
Parandania boecki (Stebbing)
A single 12 mm long immature specimen of the cosmopolitan pelagic species *Parandania boecki* was collected during the BIOFAR research programme in the water around the Faroe Islands (Berge and Vader, 1997, misidentified as *Euandania gigantea* Stebbing; Berge *et al.*, 2000; Vader and Berge, 2003); the locality BIOFAR st. 417 is 62°16’N, 10°58’W, 894 m. This speci-

Fig. 1. Thalassomyces marsupii *Kane, 1964 on* Parandania boecki *(Stebbing) (69°16'N, 10°58'W, 894 m). Young trophomeres ventrally on pereion.*

men carried a single young ellobiopsid parasite (Fig. 1), that in all particulars agrees with the descriptions of *Th. marsupii*.

This is the first record of an ellobiopsid parasite on a representative of the amphipod family Stegocephalidae

Discussion

Thalassomyces marsupii has a nearly world-wide distribution (Fig. 2), especially if one takes into account the cryptic nature of these easily overlooked, egg-mimicking parasites. Most records nevertheless seem to be in the temperate zones of both hemispheres, with a few reports from Arctic regions (Tencati and Geiger, 1968; Berge, pers. obs.). Interestingly, none have been found in the Antarctic nor have they been reported from the tropics.

Kane (1964) strongly indicated that *T. marsupii*, in contradistinction to some other *Thalassomyces* species, does not castrate its host and this is supported by Shields (1994). We, too, have observed ovigerous specimens of *Rhachotropis macropus* with scars indicating prior infection with *Thalassomyces.* Nevertheless, there are also strong indications that the presence of the

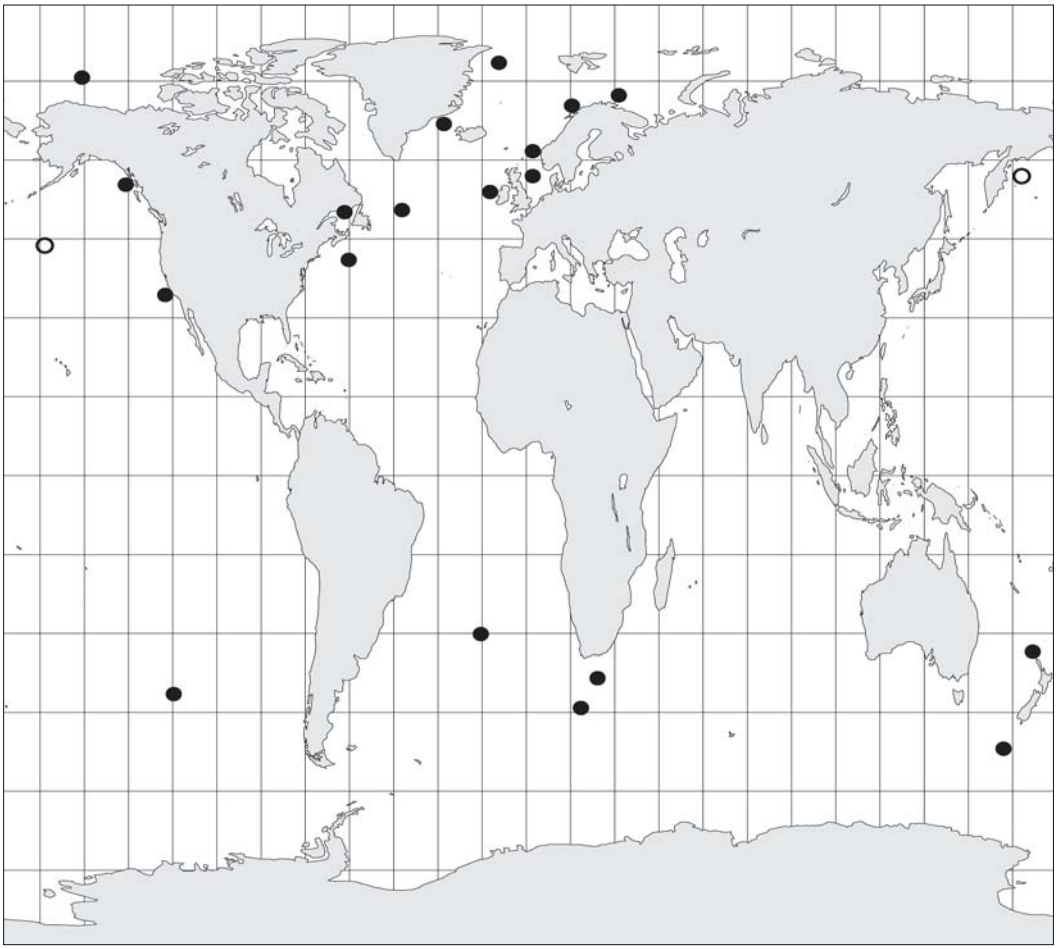

Fig. 2. *Distribution of* Thalassomyces marsupii. *(The open circles represent records where the exact locality is not known).*

parasite suppresses oviposition and development of secondary sexual characters in female hosts. For example, one never finds ovigerous amphipods that also carry the parasite, and in many host species, authors have recorded that the parasite preferentially infests 'immature specimens', even though there is no size-difference between infected and uninfected specimens (Sexton, 1909; Tencati and Geiger, 1968; Vader and Kane, 1968). Another line of evidence would be feminization; it would be evident in a skewed sex ratio for infected versus uninfected hosts; no such data are as yet available for these hosts, which in general show few secondary sex characters.

Thallasomyces marsupii is a host generalist and parasitizes a wide variety of hosts

among the Amphipoda, unless this is a species complex rather than a single species. Several other *Thalassomyces* species also infect a large range of hosts, e.g., *T. boschmai* Nouvel on Mysidacea, *T. fagei* (Boschma) on Euphausiacea , and *T. racemosus* (Coutière) on shrimps (Vader, 1973; Shields, 1994). The amphipod hosts of *T. marsupii* belong to widely different families, but they all share a similar biology. All are pelagic or bathypelagic predators of smaller zooplankton, although *Parandania boecki* may be foremost a predator of deep-water medusae (Moore and Rainbow, 1989; Coleman, 1990). We have never found ellobiopsid parasites on other bathypelagic amphipods, such as species of *Halice, Pardalisca* or *Arrhis* that also may occur in very high densities locally, but which are not predators. Perhaps this indicates an intermediate or paratenic host in the life cycle of the parasite.

The putative life cycle of *Th. marsupii* has been described and discussed by Galt and Whisler (1970) and Shields (1994). Although the exact means of infection remains unknown, the authors agree that 'the infection is presumably acquired via the ingestion of an infectious spore' (Shields, 1994: 263). All authors have assumed direct ingestion of the spores from the water, but the predatory nature of all known hosts of *T. marsupii* makes one wonder if this is necessarily true.

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