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A case of a facultative life-cycle diversification in the fluke *Pleurogenoides* sp. (Lecithodendriidae, Plagiorchiida)

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Ein Fall einer fakultativen Diversifizierung des Lebenszyklus des Egels *Pleurogenoides* sp. (Lecithodendriidae, Plagiorchiida)

Zusammenfassung. Zahlreiche Exemplare des heimischen digenen Darmegels *Pleurogenoides* sp. (Lecithodendriidae, Plagiorchiida) – eine Gattung, die für die gleichzeitige Koexistenz von genuinen Adultstadien und progenetischen, Erwachsenen-ähnlichen Metazerkarien bekannt ist – wurden zufällig im Ösophagus einer kürzlich zuvor importierten, tropischen Rauhschuppen-Buschviper (*Atheris hispida*) parasitierend vorgefunden. Die Schlange war zuvor mit dem angenommenen Endwirt des Egels, heimischen Grünfröschen, zwangsgefüttert worden. Demgemäß scheinen Grünfrösche als zweiter Zwischenwirt oder als paratenischer Wirt für Pleurogenoides-Egeln zu fungieren; jedenfalls müssen diese Frösche progenetische Egellarven beherbergen, die sich zu genuinen Erwachsenen entwickeln, wenn sie in einen passenden, nachfolgenden Wirt übertragen werden, in den Ur-Endwirt, in ein Reptil.

Die Europäischen Pleurogenoides-Egelarten scheinen eine fakultative Diversifikation ihres Lebenszyklus zu entfalten, sie können ihre Entwicklungsstrategie entsprechend den unmittelbaren Übertragungsgelegenheiten anpassen. Diese phänotypische Plastizität lässt den Parasiten auf jede Veränderung in der Häufigkeit eines Wirts prompt reagieren; üblicherweise führt diese biologische Merkwürdigkeit zu einer Verkürzung des Lebenszyklus, die mit einer Elimination des Endwirtes einhergeht.

Summary. Numerous specimens of the native, intestinal digenean fluke *Pleurogenoides* sp. (Lecithodendriidae, Plagiorchiida), a genus known for the simultaneous coexistence of genuine adults and progenetic, adult-like metacercaria, were found by chance parasitizing in the oesophagus of a recently imported, tropical Bristly Bush Viper (*Atheris hispida*). The snake had before been force-fed with native water frogs, the assumed definitive host of these flukes. Hence water frogs act as the second intermediate host or as a paratenic host for Pleurogenoides flukes, as they must house progenetic fluke larvae, which develop to genuine adults when transmitted to an appropriate consecutive host, the ancestral definitive host, a reptile.

The European Pleurogenoides fluke species seem to display a facultative life-cycle diversification, they can adjust their life-history strategy according to their immediate transmission opportunities. This phenotypic plasticity allows the parasite to respond quickly to any changes in the abundance of a host; usually this biological oddity results in a life-cycle truncation by the elimination of the definitive host.

Key words: *Pleurogenoides* sp., progenesis, life-cycle truncation, *Atheris hispida*, Europe.

Introduction

Definitive host, the creature in which adult parasites reproduce sexually [1], and intermediate host, that is the host in which parasite larvae multiply asexually [1], seem to be axiomatic concepts in parasitology. Nevertheless, within the taxon Digenea, obligatory parasitic trematodes with primarily complex, multi-host life-cycles, progenesis, that is the precocious development of the reproductive system which leads to an early sexual maturity in juvenile stages [1], is a common oddity for the purpose of a life-cycle simplification [1]. Fluke species, in whose populations genuine adults and progenetic larvae co-exist simultaneously (= facultative progenesis), sometimes jointly within one host species, or even within one host individual, detract from this straightforward conceptual conceivability. Here we report a case of a native intestinal fluke of frogs with known facultative progenesis, growing up to genuine adults in the oesophagus of a tropical viper after having been force-fed with local water frogs.

Material, methods and results

Recently from Uganda via Slovakia to Austria imported, 24 g weighting, female Bristly Bush Viper (*Atheris hispida* Laurent, 1955) died briskly five weeks after having been force-fed twice on

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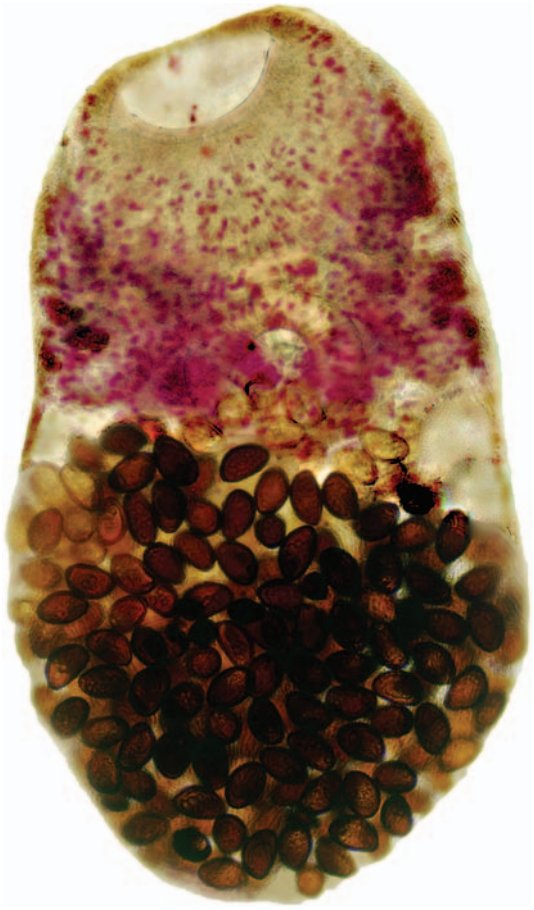

Fig. 1. A carminred-stained, genuine adult specimen of the native digenean fluke genus *Pleurogenoides*, having parasitized an artificial definitive host, the African Bristly Bush Viper (*Atheris hispida*). Fluke length: 1.2 mm

several, reportedly defrosted, but presumably just refrigerated, native water frogs (*Rana* sp.) with symptoms of a disseminating Monocercomonas infection [2]. Necropsy revealed cachexia, severe anaemia and an infestation with about three hundred opaque, exsanguinous flukes adhered to the mucosa of the oral cavity, oesophagus and stomach. The eye catching, but obviously minor pathogenic flukes were fixed in ethanol, stained with carminred and processed for conservation according to Best [2]. They were identified as *Pleurogenoides* sp., most probably *P. medians* (Olsson 1876) or *P. compactus* (Strom 1940), by morphological and biometrical criteria [3] (Fig. 1), as no reference data on a biochemical or genetic species determination are available.

Discussion

Pleurogenoides is a well-known and common genus of intestinal flukes of frogs in the Palaearctic only [4]. The feasible reasons for the unexpected finding of a native anuran fluke in recently imported African snakes intended to live as pets, and the implications on the Conservation Biology and Medicine are discussed in detail elsewhere [5]. To sum up, well-intended but improper force-feeding of the snake with native water frogs, infected with progenetic larvae of Pleurogenoides, is by far the most likely explanation.

The European species of the fluke genus Pleurogenoides (Travassos 1921) have been considered to pass through a straightforward, three-host life-cycle, including two consecutive intermediate hosts, freshwater snails (Lymnea, Bithynia, Planorbarius) and dragonfly larvae respectively, and European anurans, Rana, Hyla, Bufo, Bombina and Pelobates, as the definitive host (e.g. [4, 6, 7]). In Europe, the fluke genus distribution area obviously covers the one of the key host – water frogs of the genus Rana (*R. lessonae*, *R. ridibunda*, *R. kl. esculenta*, *R. perezi*, *R. epeirotica* and *R. shqiperica*). Surprisingly grown-up Pleurogenoides flukes were detected naturally parasitizing Egyptian chameleons [8, 9], Ukrainian Sand lizards (*Lacerta agilis*) [9] and, after experimental infection, Ocellated Skinks (*Chalcides ocellatus*) [9]. Bristly Bush Vipers have now to be added to the list of the artificial definitive host species [5].

These aberrant observations are explained most convincingly with the assumption of an occurrence of progenetic fluke larvae in small tree-, water- and brown frogs, which later on were gorged by reptilian predators. Facultative progenesis is indeed a known phenomenon in the Pleurogenoides genus [11, 12]. Yet, this thesis enforces parasitologists to accept that water frogs act as the second intermediate host of these flukes, at least occasionally. Snails or other molluscs cannot be substituted or skipped as a host in a digenean life-cycle [1] – they represent the archetype of the first, intermediate host. The dragonfly larvae act actually as a paratenic host (= a substitute of an intermediate host, in which no ontogenetic development of the parasite occurs) and as a transport vehicle. This stage may even be skipped completely in some life-cycles of the flukes as water frogs as well as other anurans do not need dragonflies to get in contact with freshwater snails. As any confutative data on host necessities are unknown to us, we deduce, that the life-cycle of Pleurogenoides is ductile to a large extend. The purpose may be a significant reduction of the risks associated with rare events, e.g. the finding of an adequate consecutive host with a low abundance.

This suggestion implicates, that a life-cycle abbreviation or a transmission-act elimination is a derived feature, currently evolving from the more complex ancestral status. Indeed, deletion of the definitive host by progenesis of the parasite is the most common way in which life-cycles of flukes are simplified [1]. In the genus Pleurogenoides, the metacercaria even attain such a degree of maturity that they do not only produce viable eggs, but cannot be distinguished from genuine adults morphologically [11], fulfilling thereby the definition of a neotenic species. The observation of a "host-induced" morphological variability of *P. medians* supports the assumption of an existence of morphologically variable precocious metacercaria within water frog populations [13]. If this thesis is true, reptiles, squamata, are the ancestral definitive host of the European Pleurogenoides species. The flukes are currently abbreviating their life-cycle by eliminating hosts, at least one, either the dragonfly larvae or the squamata, or even both simultaneously. Furthermore they may be considered as members of a curious genus which is in a phase of an evolutionary reorientation of the life-cycle by a functional

substitution of the definitive host. The European Pleurogenoides flukes seem to display facultative life-cycle modifications as alternative survival strategies, with normal, modified and abbreviated cycles simultaneously present in the parasite populations.

There are two adequate hypotheses on the evolutionary forces behind a life-cycle truncation, both built up on the conclusive postulation of infrequent transmission acts.

The rare or missing host hypothesis, which assumes, that one host in the life-cycle will be unavailable periodically, e.g. by seasonal migration or by other limited fluctuations in its abundance. This also accounts for predation rates so low that the predator might as well be almost completely absent to a parasite larva waiting inside a prey [14]. Waiting stages, especially the metacercarial stage, are generally seen as a sophisticated addition in the evolution of a fluke life-cycle, enhancing the chances of transmission to a consecutive, but rare host [15].

The developmental time hypothesis, which assumes, that an internal developmental clock ticks inside a parasite stage. If a parasite life-stage has to wait too long for its transmission to the consecutive host, it must continue its ontogenetic development, especially by starting precociously an egg production [12]. This is only an indirect result of a low frequency of transmission acts, the real cause is the ageing of the parasite inside an intermediate host. A subsequent transmission of the precocious larva put the life-cycle simply back on track – as observed in our Bush Viper case. This hypothesis explains the cases of facultative progenesis in a fluke species infecting an intermediate host that outlive the parasite [15], which seems to be an appropriate fiction in case of perennial water frogs.

Although Pleurogenoides flukes of the Palaearctic do definitely not infect mammals including man [9], population decline or extinction of them may cause some public health and welfare problems. If the survival of Pleurogenoides is strongly associated to water frogs as the key host within the life-cycle, Pleurogenoides might soon become a vanishing genus at least in Europe because of the current widespread frog population decline [16]. In that case the absence of Pleurogenoides larval stages in the snails will open free ecological niches – chances to use these snails as hosts – for other flukes. This might increase significantly the populations of such flukes, which infest and molest man, especially flukes causing cercarial dermatitis.

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Conflict of interest

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