Acta Soc. Zool. Bohem. **77**: 145–158, 2013
ISSN 1211-376X

The giant African millipede, *Archispirostreptus gigas* (Diplopoda: Spirostreptida), a model species for ecophysiological studies

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Received 12 December 2012; accepted 16 June 2013
Published 5 August 2013

Abstract. Several species of large millipedes are kept as pets and generally called giant millipedes or giant African millipedes. There is often confusion over the species names of these millipedes due to difficulties with their exact determination. Their large body size and the relative ease with which they can be kept under laboratory conditions means they are suitable subjects for experimental investigations. *Archispirostreptus gigas* (Peters, 1855), the giant African millipede, is one of the largest species, growing up to 32 cm in body length. It is widespread from Mozambique to Kenya, mainly along the east coast of Africa rather than further inland, occurring in tropical and arid forest as well as savanna. A short review of different aspects of the conditions required for breeding it in the laboratory, its ontogeny and use in ecophysiological and physiological studies is presented for it and other representatives of the order Spirostreptida. Spirostreptid millipedes are recommended as model species for studies on chemical ecology, parasitology, microbial ecology of digestive tract, embryology and postembryonal development, biochemistry and physiological mechanisms, including digestion, metabolic physiology and others.

Key words. Spirostreptidae, giant millipedes, digestive enzymes, methane, gut microflora, ontogeny, physiological methods.

The popularity of keeping different soil invertebrates has increased over the last few years and the numbers of people keeping these animals is steadily growing (Sigling 2010). Some of the larger species of millipedes are often kept as pets. They are generally called giant millipedes or giant African millipedes. There is often confusion over the exact species of the several species available in shops or boutiques selling pets. The most common species is probably *Archispirostreptus gigas* (Peters, 1855). It is one of the largest species growing up to 32 cm in length (Sigling 2010). This short review presents the basic data available on these invertebrates. In addition, it provides an overview of the most important ecological and physiological topics that species of the genus *Archispirostreptus* and other members of the family Spirostreptidae, have been or may be used in the future for such studies under laboratory conditions.

Distribution and taxonomy of *Archispirostreptus gigas*

There are about fourteen species of giant millipedes in two genera, the genus *Archispirostreptus* Silvestri, 1895 with ten species and the newly established genus *Cacuminostreptus* Mwabvu, 2010 with four South African species (Mwabvu et al. 2010). The genus *Archispirostreptus* occurs mainly in the eastern half of Africa (Fig. 1). Although both genera are recorded in savanna woodland, forests and at high altitudes, they have allopatric distributions. *Archispirostreptus gigas* occurs widespread from Mozambique to Kenya, more along the east coast of Africa than further inland. The present distribution of the genus *Archispirostreptus* suggests that it was widely distributed in

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Presented at the 11th Central European Workshop on Soil Zoology, České Budějovice, Czech Republic, 11–14 April 2011.

the past before parts of Africa became drier in the late Pliocene or early Pleistocene. Now these animals occur in tropical and arid forests as well as savanna (Mwabvu et al. 2010).

The species identification of living specimens of giant millipedes based on external morphology is difficult due to some intra-specific variation in colour. Body colour of *A. gigas* is black or brown, as are the legs and antennae (Mwabvu et al. 2010). Reddish brown legs and antennae of some animals (Fig. 2) seems to correspond to the description of the smaller (body length 130–150 mm) species, *Archispirostreptus divergens* Krabbe & Enghoff, 1978, reported from Kenya (Mwabvu et al. 2010). However Sigling (2010) states that the antennae and legs of *A. gigas* are usually mahogany to rusty brown and often a little brighter than the rest of the body. Nevertheless to accurately determine the species one needs to examine the morphology of the gonopods of males, and in order to do this they have to be removed from the body cavity. Thus, in most of the studies that use live specimens in experiments it is uncertain whether the species have been correctly identified.

Fig. 1. The distribution of giant millipedes in Africa. Genus *Archispirostreptus* – striped and black areas, genus *Cacuminostreptus* – dark grey area. Black field represents distribution of *Archispirostreptus gigas*. Modified according to Mwabvu et al. (2010).

Fig. 2. A pair of *Archispirostreptus gigas* millipedes used for ecophysiological investigations at the Institute of Soil Biology (left – male, right – female). The photographs of adults (Figs. 2 and 3) obtained using a Canon EOS 600D camera, other photographs (Figs. 3AB and 4–7) were taken using an Olympus ZX61 stereomicroscope equipped with a DP20 camera.

Basic information on biology, ecology and breeding conditions

In contrast to the popularity of this species among amateur breeders there is little information on different aspects of its biology published in the scientific literature. On the hand there is a lot of information of different levels of credibility dispersed in many different web pages, discussion forums, care sheets published by dealers and documents produced by breeders. The largest species, which belong to the genus *Archispiostreptus*, have been used as model species in many physiological studies. *A. gigas* reaches a body length of 130–320 mm, with an antennal length of 10–12 mm and maximum body width of 7–19 mm. Full-grown (adult) individuals have from 54 to 71 body segments. Adult males are smaller and darker than females, and their gonopods on the seventh segment are partially submerged into the body cavity.

A disadvantage of using these species in experiments may be their long life cycle. *A. gigas* is reported to have a lifespan of 5–7 (Oakland Zoo 2011) or even 7–10 years (McLeod 2011).

Archispirostreptus gigas occurs both in tropical and arid coastal forests or areas of coastal habitat with at least a few trees. It rarely reaches altitudes above 1000 m (Hoffman 2000). According to Sigling (2010) dry savannas with distinct dry and rainy seasons are also suitable habitats for this species. Giant millipedes are mostly active at night and live under rocks, in forest underbrush or burrow in the forest floor (Point Defiance Zoo 2011). The total abundance of spirostreptid species of millipedes in southern African savannas varies greatly between different types of habitat ranging from less than 1 to 35 individuals per square meter (Dangerfield & Telford 1996). A similar spirostreptid species to *Archispirostreptus* with a body mass of up to 20 g is *Alloporus uncinatus* Attems, 1914, which in rural areas of Zimbabwe can reach an abundance of 0.015 individuals per square meter (Mwabvu 1997). Most adult spirostreptids in savanna are active on the surface during the summer rainfall season in southern Africa (Dangerfield & Telford 1996).

For breeding *A. gigas* one does not have to supply them with water as they obtain this from their food providing the humidity is kept high. Some breeders suggest that one places a shallow dish of clean fresh water in the terrarium (Sigling 2010, McLeod 2011). The optimum width of the terrarium should be at least equal to the length of the biggest millipede and length at least twice that of the length of the biggest millipede and it is important that the substrate is about 10 cm deep as millipedes are burrowing animals. Sigling (2010) recommends that the substrate consists of wood or garden soil mixed with rotting hardwood litter and a small amount of sand and crushed cuttlefish bones or eggshells. The substrate should be regularly sprayed with water so that is always wet. Many breeders recommend a high temperature of between 24 and 28 °C, but it is also possible to keep millipedes at room temperature (e.g. 22 °C).

Defence strategies

Natural predators of giant millipedes seem to be birds, small mammals, frogs and reptiles. Defensive strategies of these animals include curling into a tight spiral and the secretion of an irritating liquid from repugnatory glands situated on the both sides of most body segments. The defence

Fig. 3. Curled up female of *Archispirostreptus gigas*. Details of (A) the position of the pore of a repugnatory gland opening on the side of a body segment marked by a white circle and (B) repugnatory glands in juvenile postembryonic stadium III.

glands consist of a paired spherical sac or reservoir that contains secretory cells, a simple duct and a valvular cuticular infolding that opens onto the lateral surface of the millipede via a pore (ozopore). This type of gland is present in millipedes belonging to the orders Callipodida, Spirobolida, Julida, Platydesmida and Polyzoniida (Hopkin & Read 1992, Ćurčić et al. 2009). These repugnatory glands are clearly visible under the lightly pigmented cuticle of freshly moulted juvenile stadia (Fig. 3). Benzoquinones and hydroquinones make up the main components of repugnatory secretions of millipedes belonging to the orders Julida, Spirobolida and Spirostreptida (Attygalle et al. 1993, Deml & Huth 1999, Arab et al. 2003). The chemical structures of these compounds are very similar (Deml & Huth 1999). The defensive fluid of *A. gigas* contains two benzoquinone components 2-methyl-3-methoxy- 1,4-benzoquinone and 2-methyl- 1,4-benzoquinone, as does that of *Archispirostreptus tumuliporus* (Karsch, 1881) and many other spirostreptid species (Barbier & Lederer 1957, Perissé & Salles 1970, Wood 1974, Smolanoff et al. 1975). It is likely that the secretions of the repugnatory glands of all spirostreptid millipedes have antifungal, antibacterial and anthelmintic properties as is recorded for particular species of this group of millipedes (Thomas 1957, Cohen et al. 1987, Williams et al. 1997). In the field the secretions of millipedes serve mainly as a defence against predatory arthropods and/or vertebrates (Eisner et al. 1978).

Commensals and parasites

Spirostrepid millipedes often have commensalistic, paraphagic or phoretic mites on their body surfaces (Fig. 4). These mites are often imported into Europe together with the millipedes (Salmane & Telnov 2007). Most of these paraphages are probably mites belonging to the order Mesostigmata (e.g. Iphiopsididae), which are known to be common associates of spirostreptid millipedes, mainly species of the genus *Julolaelaps* Berlese, 1916 (Fain 1987, Ryke 2009, Farfan 2010). The feeding habits of these mites (parasitism or paraphagy) are uncertain (Hunter & Rosario 1988). At least four species of the genus *Julolaelaps* are reported as associates of *A. gigas* (Uppstrom & Klompen 2005, Kontschán 2005, Farfan 2010). All post-larval instars of these mites actively move around the body surface of the host and hide between the legs of the host when disturbed (Yoder & Klompen 2001).

Nematodes are also recorded as parasites of spirostreptid species. There are three new species of rhigonematid nematodes, *Brumptaemilius justini* Adamson & Anderson, 1985, *Waerebekeia simoni* Adamson & Anderson, 1985 (Rhigonematida, Rhigonematidae and Carnoyidae) and *Thelastoma gueyei* Koubková, Baruš, Matějusová, Hodová & Koubek, 2006 (Oxyurida, Thelastomatidae) recorded as parasites of *A. tumuliporus*. Species of the genus *Brumptaemilius* Dollfus, 1952 are specific parasites of the family Spirostreptidae, which only occur in Africa. Rhigonematid nematodes belonging to the genus *Abirovulva* Hunt 2002 also occur in the digestive tract and faecal pellets of some specimens of *A. gigas* (Baruš pers. comm.).

Feeding, digestion and gut microflora

The food of giant millipedes in the field probably consists of mainly decaying plant matter and some fallen fruits and leaves, and rarely dead animals (Ziegler 2003, McLeod 2011). In captivity millipedes can be fed rotten fruit and vegetables such as the leaves of lettuce, cucumber, tomatoes, melon, peaches, bananas and some grains (Ziegler 2003). According to Sigling (2010) this species is omnivorous accepting all the food reported above. Laboratory observations reveal that millipedes prefer fresh or decaying vegetables to European leaf litter (oak and maple). A suitable source of calcium should be added to the diet (McLeod 2011). A wide range of food is utilized by savanna diplopods in southern Africa (Dangerfield & Telford 1996) from that of relatively poor quality to nutrient rich sources, such as, soil, tree leaf or grass litter, *Aloe* litter, algae, faeces, dead invertebrates and cotyledons of *Acacia* seedlings.

In order, to account for the wide range of feeding preferences information on the digestive enzymes of this species is needed. A rich array of enzymest is reported in another member of the Spirostreptidae family, the American giant desert millipede *Orthoporus ornatus* (Girard, 1953). The following enzymes are active in the digestive tract of this species: mellibiase, raffinase, lactase, saccharase, maltase, trehalase, melezitase, salicylase, amylase, cellobiase, carboxymethyl cellulase and xylanase (Nunez & Crawford 1976). Most cellulose and hemicellulose degradation occurs in the midgut and pectin degradation occurs mainly in the hindgut. The hemicelluloses, β-glucosidases, Cx-cellulase and pectinase present in the gut of *O. ornatus* are probably of microbial origin, because treatment with antibiotics reduced ^{14}C cellulose breakdown (Taylor 1982). According to Hopkin & Read (1992) it is unlikely that millipedes have a permanent cellulolytic symbiotic microflora like termites and other insects, although they do have some sort symbiotic relationship with microorganisms (Byzov 2006).

A detailed study of the histology of the gut of *A. gigas* based on transmission electron microscopy and immunostaining revealed cell apoptosis and necrosis of the columnar digestive cells in the epithelium of its midgut (Sosinka & Rost-Roszkowska 2010). While the foregut of millipedes is poorly populated with microorganisms and the peritrophic membrane in the midgut prevents micro-organisms gaining access to the midgut epithelium, the hindgut is a suitable environment for microbes (Byzov 2006). In the cuticle of the hindgut of Spirostreptidae (*O. ornatus*) there are numerous projections and depressions in which bacteria reside (Crawford et al. 1983). Oravecz et

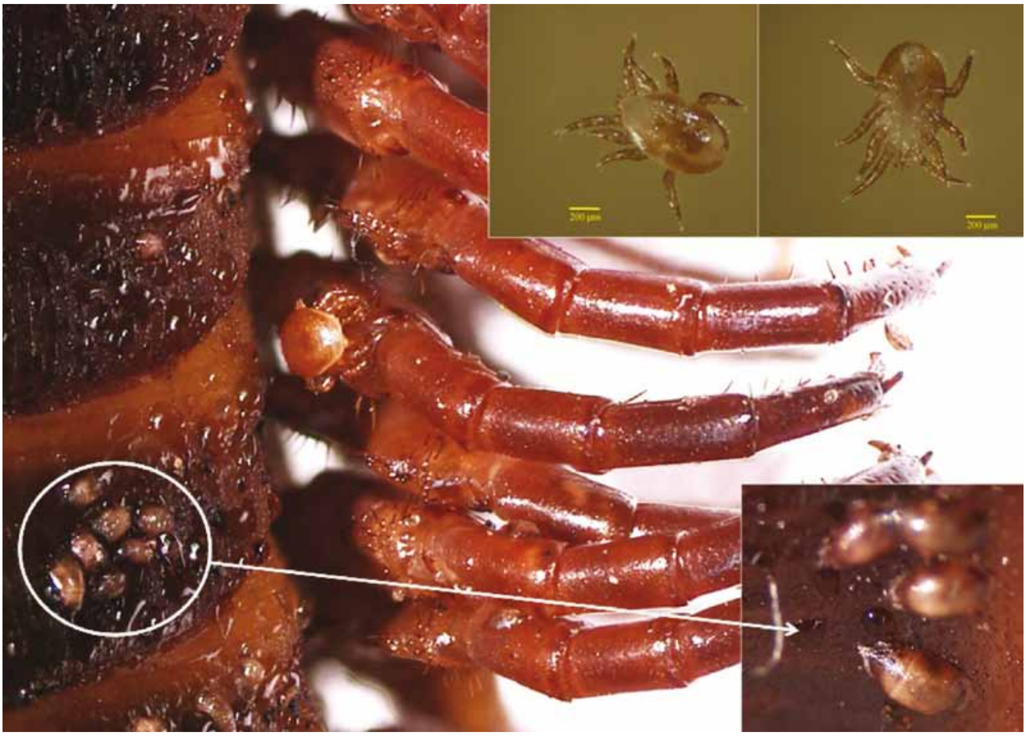

Fig.4. Phoretic mites (cf. *Jululaelaps* sp.) on the body surface of an adult *Archispirostreptus gigas*.

al. (2002) characterized bacterial isolates from the faecal pellets of an undetermined spirostreptid millipede from Morocco using amplified ribosomal DNA-restriction analysis (ARDRA) and by sequencing the 16S rRNA gene. The faecal microbial community is dominated by members of the class Actinobacteria, with most of the strains belonging to the genera *Rhodococcus*, *Cellulomonas* and *Leifsonia*. Many of these species in the intestine of millipedes can potentially break down complicated food polymers, such as cellulose, lignin and chitin. Byzov (2006) only mentions the methanogenic and cellulolytic microflora of spirostreptids in his review of the intestinal biota of millipedes. Further research in this field is needed.

Methane production and methanogenic microorganisms

Giant millipedes are suitable model species for studies on the role of invertebrates in methane production. Methane is produced in the digestive tract of invertebrates by microorganisms (anaerobic methanogenic Archaea) (Hackstein & Stumm 1994). This is also the case for large tropical millipedes. Two members of the Spirostreptidae, *Orthoporus* sp. and *Rhapidostreptus virgator* (Silvestri, 1907) produce methane and hydrogen. The hindguts of these species contain free methanogenic bacteria and protozoa (*Nyctotherus* type ciliates) with intracellular methanogens (Hackstein & Stumm 1994). Each ciliate cell contains more than 4000 methanogens, which are also present in the cysts of ciliates (Hackstein et al. 2006). Recently the millipede *A. gigas* was used as a model species in a project studying the production of methane and microbial ecology of methanogenic Archaea living in the digestive tract of invertebrates.

Reproduction and development

In captivity *A. gigas* reproduces readily if provided with a moist substrate and kept in warm conditions (Sigling 2010). Mating behaviour of this species, including meeting, courting, insemination and release, is reported by Mazer (1996) and filmed and analyzed in detail by Moresco et al. (2004). The whole mating sequence takes about 35 minutes. Mating occurs only in spring and autumn (Ziegler 2003). Probably their reproduction is synchronized with particular seasonal changes (Dangerfield & Telford 1996). Egg laying can be triggered by simulating a short period of drought followed by an increase in moisture (Sigling 2010). Eggs are deposited in holes burrowed into the substrate and every egg is contained in a separate capsule (Ziegler 2003). Probable function of this capsule (ootheca) may be protection against desiccation and whether it provides any protection against microbial infection is questionable because dead eggs of *Plusioporus setiger* (Broelemann, 1901) covered by fungus inside their ootheca have been recorded (Fontanetti & Zirondi 2000). The ootheca is most probably created at least partly from faecal material (Fontanetti & Zirondi 2000) and may contain intestinal microflora.

However, some eggs may be found lying free on the substrate without a capsule. The eggs have a diameter of about 2.5 mm and are yellow-white and glossy (Fig. 5). They need about 1–2 months (Sigling 2010) or even up to six weeks (Ziegler 2003) to complete their development.

A morphological investigation of the head of an embryo of a species of *Archispirostreptus* from South Africa was published at the beginning of the twentieth century (Robinson 1907). The morphological changes during ontogenesis and their timing have not been fully described so far for *A. gigas*. The course of early postembryonal development in *A. gigas* is similar to that described by Fontanetti & Zirondi (2000) for the spirostreptid species *P. setiger*. For other species of spirostreptids, Bercovitz & Warburg (1985) record the developmental patterns in two populations of *Archispirostreptus syriacus* (Saussure, 1859) in Israel and Crawford et al. (1987) the life histories of three subtropical spirostreptids from arid regions: *O. ornatus*, *Archispirostreptus tumuliporus judaicus* (Attems, 1927) and *Harpagophora nigra* (Attems, 1914). The body size of *A. gigas* makes it an ideal subject for detailed studies on individual development. The pupoid that emerges from an egg is surrounded by an embryonic cuticle, is white, almost motionless but rapidly increases in volume and has an ocular spot and rudiments of both antennae and three pairs of legs (Fig. 6). First juvenile stages of spirostreptids remain inside the ootheca (Fontanetti & Zirondi 2000). It is possible to see the adding of new body segments, repugnatory glands and changes in the arrangement of ocelli in the juvenile stages of *A. gigas* (Fig. 7). The first four body segments bear five pairs and each of the following segments two pairs of legs. Several apodous rings (without pairs of legs) often form a hardly distinguishable "growth zone" in the posterior region of each new instar (Fontanetti & Zirondi 2000). The number of body rings added in each subsequent moult fluctuates around five. After moulting the exuviae are consumed by larvae probably to recycle calcium and other substances. The postembryonic development of spirostreptids is most probably hemianamorphic (Fontanetti & Zirondi 2000). The whole development from egg to maturity is reported to take about two years (Ziegler 2003). In the early stages one row of ocelli is added at every moult with the number increasing by one after each ecdysis. Ocelli in the ocular field form an almost regular triangle (Fig. 7).

The eye fields in millipedes are of the "row by row type" present in Trilobita and Xiphosura (Harzsch & Hafner 2006). This form of development corresponds to the general scheme observed in other millipedes reviewed by Blower (1985) and Enghoff et al. (1993). Specifically in *A. gigas* the increase in numbers of ocelli results in a triangular eye field with the peak (the oldest ocellus) posterior and somewhat ventral to the base of the antennae (Harzsch et al. 2007). At every moult

Fig. 5. Egg of *Archispirostreptus gigas* lacking a soil capsule.

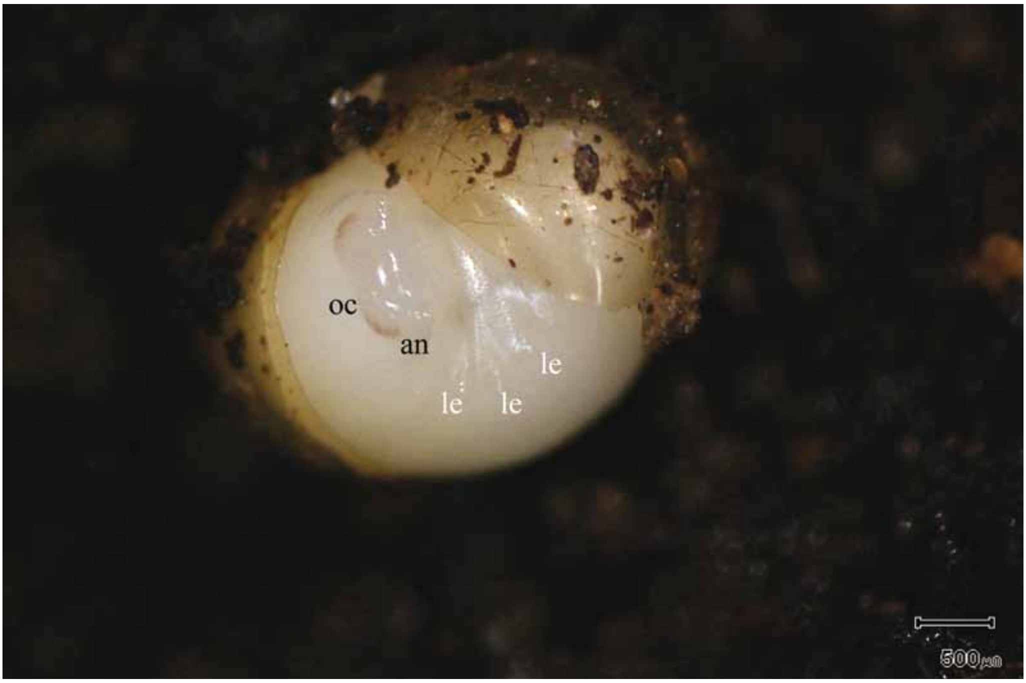

Fig. 6. Pupoid stage of *Archispirostreptus gigas* with ocular spots (oc) and rudiments of antennae (an) and three pairs of legs (le).

another row of ocelli develops at the base of the ocular field containing one more ocellus than in the previous row. The shape of the ocular field becomes half moon like and surrounds the base of the antennae in older stages. Harzsch et al. (2007) recorded the proliferation of cells in the developing eyes of *A. gigas* by in vivo labelling using the mitosis marker bromodeoxyuridine.

The results of this study of this species of millipede indicate that it is a suitable model for morphogenetic studies. Janssen & Damen (2006) were the first to isolate the Hox genes from a millipede and determine their patterns of expression, which determine the identity of each segment. Recently one of these genes (Ubx) was sequenced for *A. gigas* (Ronshaugen et al. 2002).

Another aspect of individual development are the physiological mechanisms regulating the energy demands of morphogenetic processes. Moulting of millipedes is frequently synchronized with climatic conditions (Fontanetti & Zirondi 2000). The control of the moulting cycle is probably hormonal but the responsible hormones and sites of their production are unknown (Hopkin & Read, 1992). Five types of neurosecretory cells have been identified in the brain of *A. syriacus* using cytochemical techniques and electron microscopy (Warburg & Rosenberg 1983).

Because of its large size it is likely that *A. gigas* requires large amounts of energy for development. The energy budget and metabolic aspects of development, however, have only been studied for another species of spirostreptid. The respiration rate decreases before moulting in *O. ornatus*. The total annual respiratory metabolism of this species is estimated to be 1332 cal×g^{-1}×year^{-1}.

Fig. 7. The juvenile stadium III of *Archispirostreptus gigas* with exuvium of the previous stadium. Details of legs on the posterior part of the body (A), repugnatory glands (B) and ocular field with pigmented ocelli (C).

Seasonal changes in the rate of respiration seem to follow annual changes in ambient temperature (Wooten & Crawford 1974).

Physiological studies on spirostreptid millipedes

There are several studies on the effect of different factors on the metabolic rate of giant millipedes, in particular, body size and temperature (Dwarakanath 1971, Wooten & Crawford 1974, Penteado et al. 1991, Webb & Telford 1995), hypoxic conditions (Penteado 1987, Penteado & Hebligberaldo 1991), locomotory activity and photoperiod (Boccardo & Penteado 1995) and gender (Wooten & Crawford 1974, Penteado et al. 1991).

There is an increase in the concentration of sugar in the haemolymph and an associated decrease in glycogen and total carbohydrates and increase phosphorylase activity in the fat body of *Spirostreptus asthenes* Pocock, 1892 following the injection of crustacean hyperglycemic hormone, which indicates that the hormonal regulation of energy metabolism is similar in all arthropods (Reddy 1991). Measurements of the respiratory quotient of *O. ornatus* revealed seasonal differences in the use of different metabolic reserves (Wooten & Crawford 1974).

The haemolymph and hemocytes of spirostreptids are the subjects of many other physiological studies. The properties of haemolymph, such as protein content, electrophoretic variability of haemolymph proteins, osmolarity and pH are reported by (Xylander 2009a) and compared with those of other species of millipedes and centipedes. In the haemolymph of millipedes, including the spirostreptids *R. virgator* and *Triaenostreptus triodus* (Attems, 1909) there are antibacterial substances active against gram-positive and gram-negative bacteria (Xylander 2009b). Some properties of these antibacterial agents, such as their resistance to heat, molecular weight and lysozomal activity are reported by Xylander (2009b). These findings indicate that spirostreptid millipedes might be interesting models for studying the immune defence mechanisms of invertebrates.

Kusche & Burmester (2001) report the first sequence for a haemocyanin of a species of *Spirostreptus*. Haemocyanins are copper-containing respiratory proteins of Arthropoda, which previously were mainly studied in the Chelicerata and Crustacea. Although spirostreptids have a well developed tracheal system there is a large amount of haemocyanin in the haemolymph of species of *Spirostreptus* and two other related species. It is likely that haemocyanins occur in all Myriapoda (Kusche & Burmester 2001). Thus, unlike in insects, the evolution of a tracheal system in myriapods was not accompanied by the loss of haemolymph respiratory pigments. Molecular phylogenetic analyses of haemocyanin sequences reveal interesting information about the phylogeny of arthropods. These analyses indicate a monophyletic origin of all arthropod hemocyanins, most likely from a phenoloxidase-like ancestor.

The phenoloxidase system is an important defence mechanism of arthropods, which results in the polymerization and deposition of melanin around foreign particles. The phenoloxidase system of the spirostreptid *R. virgator* was studied by Xylander & Bogusch (1997).

Vitellogenin, the precursor protein of yolk and its product vitellin occur in the haemolymph, fat body of females and mature oocytes in *S. asthenes* (Prasath & Subramoniam 1991). The vitellogenesis in *S. asthenes* is similar to that in insects.

The adaptation of desert spirostreptids to dry and hot environments has attracted the attention of ecophysiologists. The ultrastructure of their integument plays an important role in determining their resistance to desiccation (Walker & Crawford 1980). The coordination of feeding and locomotory activity with changes in diurnal temperature by the desert millipede *O. ornatus* is reported by Wooten et al. (1975). The consumption of oxygen, evaporative water loss and other aspects of water balance and aestivation in *Alloporus bilobatus* Schubart, 1966 are reported by Webb & Telford (1995).

This extensive list of topics studied using several species of spirostreptids indicates the considerable potential of species of *Archispirostreptus* in further physiological studies. In addition to the recent investigations into the production of methane by the microbial microflora of *A. gigas* there have been several bioenergetical studies on the development of these large millipedes. These include studies on the mechanisms by which they digest resistant plant polysaccharides and the screening for new cellulases of animal origin. Other studies on respiration have focused on the role of haemocyanin and the tracheal system, genetical control of morphogenetic processes during development and immune responses including the antibiotic functions of haemolymph and that provided by the repugnatory glands, which are very interesting and perspective fields for future physiological research on these fascinating animals.

Acknowledgements

The authors thank Michelle Hamer and Tarombera Mwabvu (Durban, South Africa) for kindly providing literature, data on distribution and for valuable discussions on giant millipedes. This research was funded by project No. 526/09/1570 of the Czech Science Foundation. The language of the manuscript was kindly checked by Professor Anthony F. G. Dixon (Norwich, UK).

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