REVIEW ARTICLE

Echinococcus species in African wildlife

M. HÜTTNER* *and* T. ROMIG

University of Hohenheim, Department of Parasitology, Emil-Wolff-Strasse 34, 70599 Stuttgart, Germany

(*Received 7 April 2009; revised 7 May 2009; accepted 8 May 2009*)

SUMMARY

Cystic echinococcosis, caused by different species of the *Echinococcus granulosus* complex, is an important zoonotic disease with a particular impact on pastoralist societies. In addition to the widespread taxa with synanthropic transmission, a number of *Echinococcus* species were described from African wild carnivores early in the 20th century. For lack of study material, most of these were later tentatively synonymized with *E. granulosus*. Early infection experiments with wildlife isolates gave ambiguous results due to the use of unspecified parasite material, and only recently molecular methods provided the opportunity to shed light on the confusing scenery e.g. by characterizing *E. felidis* from the African lion. Here we will summarize the convoluted history of *Echinococcus* research in sub-Saharan Africa and highlight the necessity of molecular surveys to establish the life cycles and estimate the zoonotic potential of these parasites.

Key words: *Echinococcus*, Africa, wildlife parasites, zoonosis.

INTRODUCTION

The classification of the zoonotic cestode genus *Echinococcus* is presently undergoing a major revision. The recognition of *E. granulosus*, *E. multilocularis*, *E. vogeli* and *E. oligarthra*† as species was, among other criteria, inspired by the growth form of the metacestode and the family of definitive hosts. Within *E. granulosus*, the morphological diversity of the adults and distinct biological features of various 'strains' have long been recognized (Thompson and McManus, 2002), but this name was still retained for all taxa with cystic metacestodes due to uncertainty about the variability of separating characters, specifically host-induced variation (Rausch, 1967). By now, a wealth of genetic data has confirmed the distinctness of some of these strains, and phylogenetic approaches based on extensive sequence data of mitochondrial and nuclear genes in combination with morphological and biological characters lead to the separation of *E. equinus*, *E. ortleppi*, *E. canadensis* and *E. felidis* from *E. granulosus sensu stricto* (Thompson and McManus, 2002; Nakao *et al*. 2007; Hüttner *et al*. 2008; Saarma *et al*. 2009).

The species of this '*Echinococcus granulosus*-complex' (Table 1) are maintained in a variety of life cycles. Most of these are based on domestic animals, with the domestic dog as definitive host and various species of livestock (sheep, goats, cattle, yak, buffaloes, camels and pigs) as intermediate hosts. In many instances, wild mammals are marginally involved in transmission. Wild cycles independent from transmission in domestic animals are rare. In Australia *E. granulosus sensu stricto* has shifted from the dog-sheep transmission to a cycle involving wild dogs (dingoes) and wallabies, kangaroos and feral pigs (Jenkins and Macpherson, 2003; Jenkins and Morris, 2003). In southern Argentina a cycle between an indigenous fox species (*Pseudalopex culpaeus*) and introduced European hares (*Lepus europaeus*) has been described, which, however, might not be independent from the sheep-dog cycle in the same area (Schantz *et al*. 1972). In the northern hemisphere, a taxon of *Echinococcus* is transmitted between wolf and cervids which was originally known as the 'northern form' of *E. granulosus*. For a long time, this wildlife form was considered ancestral to the various domestic forms, which were thought to have derived from it after the domestication of livestock (Rausch, 1967). Molecular data tell a different story (Table 1): the 'northern form' is part of a species,

* Corresponding author: Tel: 0049 711 45923072. Fax: 0049 711 45922276. E-mail: huettner@uni-hohenheim.de

† Usually referred to as *E. oligarthrus*. However, the species was originally described as *Taenia oligarthra* ('few joints') (Diesing, 1863). The component *–arthra* is the plural of *arthron* (joint). The name is therefore not an adjective, but a noun in apposition, which does not change its ending according to the gender of the genus name. This was recognized earlier (Abuladze, 1964), but subsequently ignored.

 © Cambridge University Press 2009
doi:10.1017/S0031182009990461 Printed in the United Kingdom

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

Table 1. Summary of the taxonomic status of the '*Echinococcus granulosus* complex' and other *Echinococcus* species

(Taxa recorded from sub-Saharan Africa are highlighted in bold)

Conventional taxonomy Species	Strain	Genotype	Molecular taxonomy* Species
E. granulosus	**Sheep strain**	**G1**	***E. granulosus sensu stricto***
	Tasmanian sheep strain	G2	
	Buffalo strain	G3	
	Horse strain	**G4**	***E. equinus***
	Cattle strain	**G5**	***E. ortleppi***
	Camel strain	**G6**	***E. canadensis****
	Pig strain	G7	
	Cervid strain	G8	
	?	G9	
	Fennoscandian cervid strain	G10	
	Lion strain	**—**	***E. felidis***
E. multilocularis			*E. multilocularis*
E. shiquicus			*E. shiquicus*
E. oligarthra			*E. oligarthra*
E. vogeli			*E. vogeli*

* Combined from Nakao *et al*. (2007) and Hüttner *et al*. (2008).
** The camel and pig strain might be split from *E. canadensis* as a separate species (Thompson, 2008; Saarma *et al*. 2009).

or species complex, – *E. canadensis* – which also includes domestic forms (the pig and camel strains)‡. Based on sequence divergence of mtDNA, the separation of the *E. canadensis* lineage from other *Echinococcus* taxa was estimated to have occurred more than two and a half million years ago (McManus, 2006). In the absence of a molecular clock calibrated for cestodes this figure might not be precise, but it is clear that the separation had occurred long before the domestication of livestock, which only began in the Neolithic period, approximately 9000 years ago. This strongly suggests that also the various cyst-forming *Echinococcus* species, or their ancestors, had existed long before the domestication of livestock. Except for *E. canadensis*, their ancestral wildlife cycles are apparently extinct, as there are few places in the world where stable ecosystems with large wild ungulates and their predators still exist. The one major exception is Africa.

ECHINOCOCCUS IN SUB-SAHARAN AFRICA

Most data on echinococcosis in sub-Saharan Africa have been gathered in the second half of the 20th century. There is no doubt, however, that these parasites were present much earlier. As an example, Gough (1908) put the following remark in his 'Notes on South African parasites': '*Taenia echinococcus*, v. Siebold. – Cysts of this cestode from a horse, from sheep and from man are in my possession. *Echinococcus* almost appears to me to be common in South Africa. I have been able to breed specimens from sheep in the saddle-backed jackal'. This indicates the existence of vigorous domestic life cycles, at least in South Africa, in the 19th century already. Which strains and species were involved at that time, whether they were indigenous, or from where and when they had perhaps been introduced, is not known. We can only assume that 'domestic' forms were introduced together with their hosts at various times in history, perhaps starting with the introduction of the first domesticated ruminants in ancient times, and continuing up to the present via the modern livestock trade. From what we know today, those invaders had met indigenous African forms, which were parasites of various species of wild animals.

The first historic record of an infected wild African animal seems to be the above cited report from a silver-backed jackal (*Canis mesomelas*), although as the result of an experimental infection with unspecified material. Interestingly, the first *Echinococcus* from Africa to be honoured with a detailed scientific description was of wildlife origin, recovered from an African wild dog (*Lycaon pictus*) in South Africa. On account of the long handle (or manubrium) of the small hooks, it was described as *E. longimanubrius* (Cameron, 1926). The African wild dog, almost extinct today, must have been widely available for parasitological research at that time, as some years later a different species, *E. lycaontis*, was described (Ortlepp, 1934) owing to the differences in the lengths of the large rostellar hooks.

‡ Some uncertainty remains on this – the pig and camel strains might have to be removed from *E. canadensis* as a closely related, but distinct species (Cruz-Reyes *et al*. 2007; Saarma *et al*. 2009).

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

Another discovery by the same author was *E. felidis* from South African lions (*Panthera leo*) (Ortlepp, 1937). He collected the parasites from a lion's intestine which was 'literally felted over' by these worms. He described that species on the basis of the marked rugosity of the rostellar hooks and its occurrence in a felid as definitive host. Lastly, experimental infections (Verster, 1965) showed that the 'subspecies' *E. g. granulosus*, *E. g. africanus* and *E. g. ortleppi* (see below) were infectious to silver-backed jackals, and *E. g. africanus* to Cape foxes (*Vulpes chama*). Therefore, of the 25 species and subspecies of *Echinococcus* that had ever been described, not less than 6 were reported to occur in African wild carnivores (Verster, 1965; Rausch and Bernstein, 1972; Kumaratilake and Thompson, 1982; Xiao *et al.* 2005).

As most descriptions were based on structural characters of adult worms whose variation within a parasite population, or between worms in different host species, was unknown, a period of reviews and synonymizations set in. The first was done in 1963, where the differences between most of these species were considered to be within the limits of normal variation (Rausch and Nelson, 1963). The authors only retained *E. granulosus*, *E. multilocularis*, *E. oligarthra*, *E. patagonicus* and *E. felidis*. In the latter case, it was the unique preference of felids as final hosts rather than convincing morphological differences that led to the retention of that species (Rausch and Nelson, 1963). Shortly after, a major revision of *Echinococcus* was published (Verster, 1965). Criteria for classification were the morphological characters of the adult worms like number of segments, arrangement of the sexually mature segment, number and distribution of the testes and, in addition, host specificity. Size and shape of the rostellar hooks, the foundation of some early descriptions, were not considered sufficiently stable to warrant taxonomic significance. By this approach, only *E. granulosus* and *E. multilocularis* retained their species status, and *E. oligarthra* from South America was considered a *species inquirendae*. All species which had been described by then from the African continent either were reduced to the rank of subspecies of *E. granulosus* (*E. felidis* and *E. lycaontis*, together with *E. ortleppi*, described for the first time 1943 from a domestic dog in the South of Spain (Lopez-Neyra and Soler Planas, 1943)), or were included in *E. g. granulosus* due to the lack of separating characters. An additional subspecies *E. g. africanus* was created for worms recovered from a dog from unknown locality and from 3 additional experimental infections of dogs and jackals, which had been fed with hydatid cysts of bovine and ovine origin. This subspecies was characterized by the difference in the number of testes and the shape of the seminal receptacle (Verster, 1965). Just 2 years later, the concept of *Echinococcus* subspecies was refuted, because at least some of these occurred sympatrically in the same definitive host species without any obvious reproductive isolation (Rausch, 1967). It was proposed to provisionally retain all these taxa in *E. granulosus* and suggested to designate the different forms of *E. granulosus* informally as strains until new information would become available to decide otherwise. Up to the present, this system eventually led to the distinction of 11 strains of *E. granulosus* (G1 to G10, and the 'lion strain'). Five of them, namely the sheep, horse, cattle, camel and the lion strains, were reported from sub-Saharan Africa. The recent availability of reliable genetic data, showing clustering of some strains and rather distant relationship of others, has brought about the next major reshuffle of the genus (Table 1) (Nakao *et al.* 2007). The horse and cattle strains were the first to be split from *E. granulosus* as *E. equinus* and *E. ortleppi*, respectively (Thompson and McManus, 2002), followed by the camel, pig and cervid strains (as *E. canadensis*) (Nakao *et al.* 2007) and finally the lion strain as *E. felidis* (Hüttner *et al.* 2008). Awaiting further biological and epidemiological data, the pig and camel strains might have to be split from *E. canadensis*, but there is still uncertainty on this (Thompson, 2008; Saarma *et al.* 2009).

Of all the species originally described from African wild carnivores, only *E. felidis* has survived the storms of time. It was therefore suggestive to attribute all previous reports of *Echinococcus* cysts from wild herbivores in natural African ecosystems to that species. Is this justified?

Looking at *Echinococcus* records from African wildlife, it is intriguing to note the long list of species which are known to act as hosts for these worms. Definitive hosts are quite few: silver-backed jackal (*Canis mesomelas*), golden jackal (*Canis aureus*), Cape fox (*Vulpes chama*), African wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*), African wild cat (*Felis silvestris lybica*) and lion (*Panthera leo*) (Ortlepp, 1937; Nelson and Rausch, 1963; Verster and Collins, 1966; Troncy and Graber, 1969; Dinnik and Sachs, 1972; Young, 1975*a*; Graber and Thal, 1980; Macpherson *et al.* 1983). In contrast, hydatid cysts could be isolated from a large number of different ungulates: 11 species of bovids, warthogs (*Phacochoerus* sp.), bushpig (*Potamochoerus larvatus*, *P. porcus*), hippopotamus (*Hippopotamus amphibius*), giraffes (*Giraffa camelopardalis*), zebras (*Equus quagga*, *E. zebra*), cape mole rats (*Georychus capensis*), baboons (*Papio* sp.) and colobus monkeys (*Colobus* sp.) (Dinnik and Sachs, 1969; Graber *et al.* 1969; Woodford and Sachs 1973; Young, 1975*a*, *b*; Graber and Thal, 1980; Macpherson *et al.* 1983, 1986; Krecek *et al.* 1990; Macpherson and Wachira, 1997).

The numerous species of antelopes (wild bovids other than buffalo) appear to play a minor role as intermediate hosts. The prevalence of hydatid cysts

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

in these animals is low compared to other ungulates in the same surveys, whether due to low susceptibility or behavioural factors. In the Serengeti of Tanzania, 4 'antelopes' (sic) out of 350 were found infected (Dinnik and Sachs, 1969), in the Maasai Mara of Kenya 1 out of 17 wildebeest (*Connochaetes taurinus*) and none out of 47 other antelopes of 10 species had hydatid cysts (Nelson and Rausch, 1963), a survey in Uganda found no hydatids in 122 examined antelopes of 5 species (Woodford and Sachs, 1973), and in South Africa only 3 of 600 impalas (*Aepyceros melampus*) were infected (Young, 1975*a*). This is different with buffalos and warthogs, for which prevalences of 17% and 10–40%, respectively, were reported from Tanzania and Uganda. Cysts from warthogs contained protoscolices, but those from buffaloes were mostly non-fertile (Dinnik and Sachs, 1969; Woodford and Sachs, 1973). At least in South Africa, zebras seem to be an important host species: 60% of an unspecified number of Burchell's zebras (*E. quagga*) were found to be infected there (Young, 1975*a*).

In the absence of any recognized diagnostic feature of the cysts, it is unknown for any of these records if they reflect infections by *E. felidis*, by another as yet uncharacterized wildlife species (like those uncertain species described early on from *Lycaon pictus*), or constitute spill-overs from domestic cycles. In many parts of eastern and southern Africa, livestock and wildlife coexist in the same area or in close neighbourhood. Interaction between wildlife and domestic lifecycles could occur under several circumstances. Livestock grazed in or near conservation areas might acquire a form present in wildlife, and wild carnivores preying on livestock or scavenging carcasses might acquire 'domestic' forms. Even where large wild herbivores are extinct, jackals or hyenas can still partake in domestic cycles. In parts of Kenya it could even be shown that wild carnivores scavenge on human corpses. In the Turkana district of Kenya, where human infection is extremely frequent, the consumption of undercooked jackal intestines (which are eaten) was proposed as one of several important infection sources (Nelson and Rausch, 1963; Macpherson, 1983; Macpherson *et al*. 1983, 1985, 1989*a*).

In the past, some infection experiments were done to shed light on the epidemiology in wildlife. As mentioned above, silver-backed jackals were successfully infected in South Africa with hydatid material from human, cattle, pig and sheep; the worms obtained could be characterized as *E. g. granulosus*, *E. g. africanus* and *E. g. ortleppi* (Verster, 1965). N. F. Viljoen, in 1937 infected the same species successfully with protocolices from cattle (cited by Macpherson and Wachira, 1997). African wild dogs were also confirmed as definitive hosts of *E. g. lycaontis* (larvae derived from sheep) and *E. g. africanus* (larvae derived from cattle). An experimental infection with the latter larval material resulted also in the development of adult worms in Cape foxes (Verster, 1965). In the 1980s, an attempt to infect spotted hyenas with unspecified larval material of human origin in Kenya was unsuccessful (Macpherson *et al*. 1983). Another experiment was carried out by feeding beagles with cysts from warthog (*Phacochoerus africanus*) and red river hog (*Potamochoerus porcus*) from the Central African Republic. Two months later no adult *Echinococcus* could be found in the dogs (Graber and Thal, 1980). Negative results of infection experiments, however, should be taken with caution, as numerous factors could adversely influence the trial. The only experimental infection between two wildlife species was done in South Africa (Young, 1975*a*), where hydatid cysts of zebra origin were fed to a lion which was found to be highly susceptible. An additional infection experiment with cysts from zebra yielded *E. equinus* in dogs (see below) (Kumaratilake *et al*. 1986).

In summary, the results of these experiments, some done in a rather unsystematic way, or using parasite material which was neither morphologically nor genetically characterized, gave us a few pieces of the puzzle, but are not sufficient to resolve the epidemiological situation. This experimental approach is unlikely to be a practical method in future either, due to the effort, cost, biohazard and ethical considerations involved (most wildlife species are endangered and legally protected). In the absence of distinctive morphological features of the cysts, and of uncertainty about the taxonomic value of characters of the adults, only genetic characterization of isolates can solve this riddle. To provide some firm ground from where to begin this exploration, we summarize those records from sub-Saharan Africa which are unequivocally characterized either morphologically or genetically.

Echinococcus granulosus *s. s.*

The frequent occurrence of the common sheep strain (G1) of this species was confirmed by 2 molecular studies. In Kenya, a total of 248 samples from goat, cattle, camel, sheep, dogs and humans were examined by RFLP-PCR of the *its1* gene. *Echinococcus granulosus* s. s. could be diagnosed in all host species (Wachira *et al*. 1993). The second investigation was done with samples from Kenya and Sudan. A species- and strain-specific PCR-system based on the mitochondrial 12SrRNA gene was used, and the examination of 520 cyst samples from cattle, camels, sheep, goats, pigs and humans revealed the existence of *E. granulosus* s. s. in all these species (Dinkel *et al*. 2004). In addition to this, we have the morphologically based records of '*E. g. granulosus*' from various domestic animals in South Africa, and from successful infection

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

experiments with jackals, wild dogs and foxes (Verster, 1965).

This is, worldwide, the most widespread form of *Echinococcus* in domestic animals and it is well known that various wild animals can be involved in the transmission. If a true wildlife cycle of *E. granulosus* s.s. exists in Africa, is not known. The potential for this is shown by the above-mentioned experimental infections and by a recently confirmed natural *E. granulosus* s. s. infection of a wild warthog from the Queen Elizabeth National Park in Uganda (Hüttner *et al*. 2009).

Echinococcus equinus

E. equinus represents the 'horse strain' of *E. granulosus*, or G4, which seems to use exclusively equids as intermediate hosts (Thompson *et al*. 1995). There are no molecular data confirming its presence in Africa. However, in south-western Africa adult worms were recovered from the intestine of a dog which had been fed with a hydatid cyst from a mountain zebra (*Equus zebra*). The worms were identified morphologically as *E. equinus* (Kumaratilake *et al*. 1986). Disregarding some unspecified records of cysts from horses and donkeys, this is the only firm evidence that *E. equinus* occurs in Africa in wild or domestic animals.

Echinococcus ortleppi

The 'cattle strain', or G5, was first recorded in South Africa (Verster, 1965) by re-examining material from dogs, which was previously identified as *E. granulosus* (Ortlepp, 1934). Apart from dogs, silver-backed jackals were found susceptible for this species (Verster, 1965). The infection of cattle with hydatid cysts is no indication for the presence of this species, as cattle can also harbour cysts of *E. granulosus* s.s., although those are usually infertile (Thompson *et al*. 1984; Dinkel *et al*. 2004). Its existence was proven with molecular techniques in an unspecified species of zebra from Namibia, which constitutes the only proven record in a naturally infected wild animal (Obwaller *et al*. 2004), and in cattle from Sudan and a domestic pig from Kenya (Dinkel *et al*. 2004).

Echinococcus canadensis

There are important camel-raising regions in the north of sub-Saharan Africa, and the presence of the 'camel strain' (G6) is therefore not surprising. However, camels are also infected with other forms of *Echinococcus*, and molecular characterization is needed to confirm the nature of the parasite. The species was found to be frequent in Kenya and in Sudan, where goat, cattle, camel, sheep and pig, as well as dogs, were found infected (Wachira *et al*. 1993; Dinkel *et al*. 2004). Human patients are also known from these regions, but cases appear to be much rarer than with *E. granulosus* s.s., despite its frequency in livestock (Dinkel *et al*. 2004).

Echinococcus felidis

The first *Echinococcus* specimens found in lions were described as a new species (Ortlepp, 1937). Later, 5 of 7 South African lions were found harbouring these tapeworms (Verster and Collins, 1966), and a similar situation was reported from Uganda where lions were found to be commonly infected (Dinnik and Sachs, 1972; Woodford and Sachs, 1973). A later report of 4% of 75 faecal samples from lions found to be positive for *Echinococcus* spp. in the Serengeti and Ngorongoro Crater, Tanzania, needs confirmation, as the animals were examined with an immunodiagnostic test of unclear specificity (Müller-Graf, 1995). Recent studies on the genome of this parasite, based on *Echinococcus* eggs from Ugandan lion faeces, and preserved South African worms that had been determined by A. J. Verster in the 1960s, confirmed the distinctiveness of *E. felidis*, and established its status as a sister taxon of *E. granulosus* s. s. (Hüttner *et al*. 2008). The faecal prevalence of *E. felidis* in the small lion population from this park was 72% and confirmed the persistence of this parasite at least in this refuge. In addition to lions, *E. felidis* eggs could be identified in 1 of 5 faecal samples from spotted hyenas (Hüttner *et al*. 2009). Concerning intermediate hosts, there is only 1 molecularly characterized infection in a warthog from the Queen Elizabeth National Park in Uganda (Hüttner *et al*. 2009).

From the data summarized above it is evident that the epidemiology of *Echinococcus* spp. in African wildlife is only known in sketches. The value of morphological descriptions of the past is acknowledged, but future research priorities have to include the molecular and biological characterization of isolates from wild host species, and the comparison with isolates from domestic animals and human patients living in close neighbourhood. This will serve to identify the host range and geography of the various species, the possible identification of 'cryptic' forms which had been described from wild carnivores (e.g. *E. lycaontis*), and the putative linkage between domestic and sylvatic life cycles. An important aspect will be the appraisal of the potential of wild carnivores as transmitters of zoonotic agents. *E. felidis* is most closely related to *E. granulosus* s. s., the major agent for human echinococcosis worldwide. The pastoralist peoples living in the vicinity of East Africa's conservation areas (e.g. the Maasai) show a mean prevalence of cystic echinococcosis higher than 1% (Macpherson *et al*. 1989*b*), and not all these cases might be caused by the domestic

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

forms of *Echinococcus*. A recent re-examination of 412 cyst samples from humans, cattle, camels, sheep and goats from eastern Kenya only found *E. granulosus* s. s. and *E. canadensis* (G6/7), but isolates from the vicinity of conservation areas were few in that sample (Hüttner *et al*. 2009). Vice versa, there might be a possible detrimental impact of domestic *Echinococcus* forms to endangered wild mammals, as has been reported from Australia (Barnes *et al*. 2008). Large African wildlife species, even in conservation areas, vanish rapidly due to population pressure, bad governance and civil strife. This is especially true for the large predators, some of which are even on the verge of extinction in the wild (cheetah and wild dog). Parasites are not only agents of disease, but an integral part of the ecology of these areas, and those with complex life cycles, involving various host species, are even more vulnerable than their hosts. If we don't look now, we might not have another chance.

FINANCIAL SUPPORT

This work was partially supported by the Eiselen Foundation Ulm; by the graduated grant (LGFG) of Baden-Württemberg (M.H.) and by the DFG project R03753 1-1 (M.H., T.R.).

REFERENCES

Abuladze, K. I. (1964). Taeniata of animals and man and diseases cause by them. In *Essentials of Cestodology*. *Vol. IV* (ed. Skrjabin, A. K. I.), Israel Program for Scientific Translations, 1970, Jerusalem.

Barnes, T. S., Goldizen, A. W., Morton, J. M. and Coleman, G. T. (2008). Cystic echinococcosis in a wild population of the brush-tailed rock-wallaby (*Petrogale penicillata*), a threatened macropodid. *Parasitology* **135**, 715–723.

Cameron, T. W. M. (1926). Observation on the genus *Echinococcus* Rudolphi, 1801. *Journal of Helminthology* **IV**, 13–22.

Cruz-Reyes, A., Constantine, C. C., Boxell, A. C., Hobbs, R. P. and Thompson, R. C. (2007). *Echinococcus granulosus* from Mexican pigs is the same strain as that in Polish pigs. *Journal of Helminthology* **81**, 287–292.

Diesing, K. M. (1863). Revision der Cephalocotyleen. Abteilung: Paramecocotyleen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse, Abteilung 1* **48**, 200–345.

Dinkel, A., Njoroge, E. M., Zimmermann, A., Wälz, M., Zeyhle, E., Elmahdi, I. E., Mackenstedt, U. and Romig, T. (2004). A PCR system for detection of species and genotypes of the *Echinococcus granulosus*-complex, with reference to the epidemiological situation in eastern Africa. *International Journal for Parasitology*, **34**, 645–653.

Dinnik, J. A. and Sachs, R. (1969). Cysticercosis, echinococcosis and sparganosis in wild herbivores in East Africa. *Veterinary Medical Review* **2**, 104–114.

Dinnik, J. A. and Sachs, R. (1972). Taeniidae of lions in East Africa. *Zeitschrift für Tropenmedizin und Parasitologie* **23**, 197–210.

Gough, L. H. (1908). Notes on South African parasites. In *Report of the South African Association for the Advancement of Science Sixth Meeting* (ed. Schönland, S.), pp. 167–170. African Book Company, LTD., Grahamstown, South Africa.

Graber, M. and Thal, J. (1980). L'échinococcose des artiodactyles sauvages de la République Centralafricaine: Existence probable d'un cycle lion-phacochère. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux* **33**, 51–59.

Graber, M., Troncy, P., Tabo, R., Service, J. and Oumatie, O. (1969). L'echinococcose-hydatidose en Afrique centrale. I. Echinococcose des animaux domestiques et sauvages. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux* **22**, 55–67.

Hüttner, M., Nakao, M., Wassermann, T., Siefert, L., Boomker, J. D., Dinkel, A., Sako, Y., Mackenstedt, U., Romig, T. and Ito, A. (2008). Genetic characterization and phylogenetic position of *Echinococcus felidis* (Cestoda: Taeniidae) from the African lion. *International Journal for Parasitology* **38**, 861–868.

Hüttner, M., Siefert, L., Mackenstedt, U. and Romig, T. (2009). A survey of *Echinococcus* species in wild carnivores and livestock in East Africa. *International Journal for Parasitology* **39**, 1269–1276.

Jenkins, D. J. and Macpherson, C. N. L. (2003). Transmission ecology of *Echinococcus* in wild-life in Australia and Africa. *Parasitology* **127** (Suppl.), S63–S72.

Jenkins, D. J. and Morris, B. (2003). *Echinococcus granulosus* in wildlife in and around the Kosciuszko National Park, south-eastern Australia. *Australian Veterinary Journal* **81**, 81–85.

Krecek, R. C., Boomker, J., Penzhorn, B. L. and Scheepers, L. (1990). Internal parasites of giraffes (*Giraffa camelopardalis angolensis*) from Etosha National Park, Namibia. *Journal of Wildlife Diseases* **26**, 395–397.

Kumaratilake, L. M. and Thompson, R. C. (1982). A review of the taxonomy and speciation of the genus *Echinococcus* Rudolphi 1801. *Zeitschrift für Parasitenkunde* **68**, 121–146.

Kumaratilake, L. M., Thompson, R. C. and Eckert, J. (1986). *Echinococcus granulosus* of equine origin from different countries possess uniform morphological characteristics. *International Journal for Parasitology* **16**, 529–540.

Lopez-Neyra, C. R. and Soler Planas, M. A. (1943). Revision del genero *Echinococcus* Rud y description de una especie nuéva parasita intestinal del porro en Almeria. *Revista Ibérica de Parasitología* **3**, 169–194.

Macpherson, C. N. L. (1983). An active intermediate host role for man in the life cycle of *Echinococcus granulosus* in Turkana, Kenya. *The American Journal of Tropical Medicine and Hygiene* **32**, 397–404.

Macpherson, C. N. L., Craig, P. S., Romig, T., Zeyhle, E. and Watschinger, H. (1989*a*). Observations on human echinococcosis (hydatidosis) and evaluation of transmission factors in the Maasai of northern Tanzania. *Annals of Tropical Medicine and Parasitology* **83**, 489–497.

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press

Macpherson, C. N. L., Else, J. E. and Suleman, M. (1986). Experimental infection of the baboon (*Papio cynocephalus*) with *Echinococcus granulosus* of camel, cattle, sheep and goat origin from Kenya. *Journal of Helminthology* **60**, 213–217.

Macpherson, C. N. L., French, C. M., Stevenson, P., Karstad, L. and Arundel, J. H. (1985). Hydatid disease in the Turkana District of Kenya, IV. The prevalence of *Echinococcus granulosus* infections in dogs, and observations on the role of the dog in the lifestyle of the Turkana. *Annals of Tropical Medicine and Parasitology* **79**, 51–61.

Macpherson, C. N. L., Karstad, L., Stevenson, P. and Arundel, J. H. (1983). Hydatid disease in the Turkana District of Kenya. III. The significance of wild animals in the transmission of *Echinococcus granulosus*, with particular reference to Turkana and Masailand in Kenya. *Annals of Tropical Medicine and Parasitology* **77**, 61–73.

Macpherson, C. N. L., Spoerry, A., Zeyhle, E., Romig, T. and Gorfe, M. (1989*b*). Pastoralists and hydatid disease: an ultrasound scanning prevalence survey in East Africa. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **83** 243–247.

Macpherson, C. N. L. and Wachira, T. M. (1997). Cystic echinococcosis in Africa south of the Sahara. In *Compendium of Cystic Echinococcosis in Africa and in Middle Eastern Countries with Special Reference to Morocco* (ed. Andersen, F. L., Ouhelli, H. and Kachani, M.), pp. 245–277. Brigham Young University, Provo, Utah, USA.

McManus, D. P. (2006). Molecular discrimination of taeniid cestodes. *Parasitology International* **55** (Suppl.), S31–S37.

Müller-Graf, C. D. (1995). A coprological survey of intestinal parasites of wild lions (*Panthera leo*) in the Serengeti and the Ngorongoro Crater, Tanzania, east Africa. *The Journal of Parasitology* **81**, 812–814.

Nakao, M., McManus, D. P., Schantz, P. M., Craig, P. S. and Ito, A. (2007). A molecular phylogeny of the genus *Echinococcus* inferred from complete mitochondrial genomes. *Parasitology* **134**, 713–722.

Nelson, G. S. and Rausch, R. L. (1963). *Echinococcus* infections in man and animals in Kenya. *Annals of Tropical Medicine and Parasitology* **57**, 136–149.

Obwaller, A., Schneider, R., Walochnik, J., Gollackner, B., Deutz, A., Janitschke, K., Aspöck, H. and Auer, H. (2004). *Echinococcus granulosus* strain differentiation based on sequence heterogeneity in mitochondrial genes of cytochrome c oxidase-1 and NADH dehydrogenase-1. *Parasitology* **128**, 569–575.

Ortlepp, J. R. (1934). *Echinococcus* in dogs from Pretoria and vicinity. *The Onderstepoort Journal of Veterinary Science and Animal Industry* **3**, 97–108.

Ortlepp, J. R. (1937). South African helminths. – Part I. *The Onderstepoort Journal of Veterinary Science and Animal Industry* **9**, 311–336.

Rausch, R. L. (1967). A consideration of infraspecific categories in the genus *Echinococcus* Rudolphi, 1801 (Cestoda: Taeniidae). *The Journal of Parasitology* **53**, 484–491.

Rausch, R. L. and Bernstein, J. J. (1972). *Echinococcus vogeli* sp. n. (Cestoda: Taeniidae) from the bush dog, *Speothos venaticus* (Lund). *Zeitschrift für Tropenmedizin und Parasitologie* **23**, 25–34.

Rausch, R. L. and Nelson, G. S. (1963). A review of the genus *Echinococcus* Rudolphi, 1801. *Annals of Tropical Medicine and Parasitology* **57**, 127–135.

Saarma, U., Jogisalu, I., Moks, E., Varcasia, A., Lavikainen, A., Oksanen, A., Simsek, S., Andresiuk, V., Denegri, G., Gonzalez, L. M., Ferrer, E., Garate, T., Rinaldi, L. and Maravilla, P. (2009). A novel phylogeny for the genus *Echinococcus*, based on nuclear data, challenges relationships based on mitochondrial evidence. *Parasitology* **136**, 317–328.

Schantz, P. M., Lord, R. D. and de Zavaleta, O. (1972). *Echinococcus* in the South American red fox (*Dusicyon culpaeus*) and the European hare (*Lepus europaeus*) in the Province of Neuquen, Argentina. *Annals of Tropical Medicine and Parasitology* **66**, 479–485.

Thompson, R. C. (2008). The taxonomy, phylogeny and transmission of *Echinococcus*. *Experimental Parasitology* **119**, 439–446.

Thompson, R. C., Kumaratilake, L. M. and Eckert, J. (1984). Observations on *Echinococcus granulosus* of cattle origin in Switzerland. *International Journal for Parasitology* **14**, 283–291.

Thompson, R. C., Lymbery, A. J. and Constantine, C. C. (1995). Variation in *Echinococcus*: towards a taxonomic revision of the genus. *Advances in Parasitology* **35**, 145–176.

Thompson, R. C. and McManus, D. P. (2002). Towards a taxonomic revision of the genus *Echinococcus*. *Trends in Parasitology* **18**, 452–457.

Troncy, P. and Graber, M. (1969). L'echinococcose-hydatidose en Afrique Centrale. III. Teniasis des carnivores a *Echinococcus granulosus* (Batsch, 1786 – Rudolphi, 1801). *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux* **22**, 75–84.

Verster, A. J. (1965). Review of *Echinococcus* species in South Africa. *The Onderstepoort Journal of Veterinary Research* **32**, 7–118.

Verster, A. J. and Collins, M. (1966). The incidence of hydatidosis in the Republic of South Africa. *The Onderstepoort Journal of Veterinary Research* **33**, 49–72.

Wachira, T. M., Bowles, J., Zeyhle, E. and McManus, D. P. (1993). Molecular examination of the sympatry and distribution of sheep and camel strains of *Echinococcus granulosus* in Kenya. *The American Journal of Tropical Medicine and Hygiene* **48**, 473–479.

Woodford, M. H. and Sachs, R. (1973). The incidence of cysticercosis, hydatidosis and sparganosis in wild herbivores of the Queen Elizabeth National Park, Uganda. *Bulletin of Epizootic Diseases of Africa* **21**, 265–271.

Xiao, N., Qiu, J., Nakao, M., Li, T., Yang, W., Chen, X., Schantz, P. M., Craig, P. S., Ito, A. (2005). *Echinococcus shiquicus* n. sp., a taeniid cestode from Tibetan fox and plateau pika in China. *International Journal for Parasitology* **35**, 693–701.

Young, E. (1975*a*). Echinococcosis (hydatodosis) in wild animals of the Kruger National Park. *Journal of the South African Veterinary Association* **46**, 285–286.

Young, E. (1975*b*). Some important parasitic and other diseases of lion, *Panthera leo*, in the Kruger National Park. *Journal of the South African Veterinary Association* **46**, 181–183.

https://doi.org/10.1017/S0031182009990461 Published online by Cambridge University Press