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Current aspects of the taxonomy and phylogeny of the genus *Echinococcus* Rudolphi, 1801

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After three decades of accumulating epidemiological, genetic, biochemical and geographic evidence, there are currently nine recognized species belonging to the genus *Echinococcus* Rudolphi, 1801 (Cestoda: Taeniidae). The causative agent of cystic echinococcosis, *Echinococcus granulosus* in the original sense (or sensu lato), is subdivided into five species: *E. granulosus* sensu stricto Batsch (1796) (genotypes G1 and G3, formerly 'sheep strain' and 'buffalo strain'), *E. equinus* Williams and Sweatman (1963) (genotype G4, 'horse strain'), *E. ortleppi* Lopez-Neyra and Soler Planas (1943) (G5 genotype, 'cattle strain'), *E. canadensis* Webster and Cameron (1961) (genotype G6, 'camel strain'; genotype G7, 'pig strain'; genotype G8, 'American cervid strain'; genotype G10, 'Fennoscandian cervid strain'), *E. felidis* Ortlepp (1937) ('lion strain'). In addition, agents of alveolar echinococcosis are *E. multilocularis* Leuckart (1863) and *E. shiquicus* Xiao et al. (2005). Polycystic echinococcosis is caused by *E. oligarthra* Diesing, 1863 and *E. vogeli* Rausch and Bernstein, 1972. A clade of the two latter neotropical species was located in a basal position of the mitochondrial and nuclear DNA phylogeny (Nakao et al., 2007; Hüttner et al., 2008; Knapp et al., 2011). Although the members of *Echinococcus* mostly utilise canids as definitive hosts, it is not yet resolved whether the ancestral definitive hosts were felids or canids (Nakao et al., 2013; Lymbery et al., 2017).

Compared with other taeniid genera, the close genetic relationships among the members of *Echinococcus* suggest that the genus is a younger group that has undergone relatively rapid speciation and global radiation (Knapp et al., 2011). Especially since the 60's and 70's of the last century it became clear that the currently classified *E. granulosus* s. l. contains a considerable number of variants with differences in host specificity, morphology, biochemical characteristics, developmental biology and geographical distribution (e. g., Beveridge, 1974; Kumaratilake and Thompson, 1982). Important contributions to the consolidation of the infraspecific categories were the studies of the mitochondrial cox1 and nad1 genes for seven strains of *E. granulosus*, *E. multilocularis*, *E. vogeli* and *E. oligarthra* conducted by Bowles et al. (1992) and Bowles and McManus (1993).

E. granulosus s. s. is the most common agent of human cystic echinococcosis worldwide, as 88.4% of the typed clinical isolates belonged to this species (Alvarez Rojas et al., 2014). The only exceptions are countries where this species is absent or rare in animals in favour of other *Echinococcus* spp. The contribution of *E. canadensis* to global human incidence is also not negligible given that 11.1% of human cases were implicated by G6 or G7 (only two cases by G8 or G10) (Alvarez Rojas et al., 2014).

The highest diversity is associated with the *E. canadensis* cluster, which is composed of two domestic strains, 'camel' (G6) and 'pig strain' (G7), and two sylvatic (or semi-domestic) 'cervid strains' (G8 and G10). There is ongoing debate and the main taxonomic issue in *Echinococcus* spp. to be resolved as to whether the related G6 and G7 should be ranked as a separate species, and what is the taxonomic status of the remaining variants. Reasonable proposals have been made to subdivide the cluster into three species: *E. intermedius* (G6/7), *E. borealis* (G8) and *E. canadensis* (G10) (Lymbery et al., 2015), in accordance with the mitochondrial evidence, and to the two species, G6/G7 and G8/G10, based on six nuclear loci, where species differentiation can be attributed to association with different host species (dog, wolves) and largely separated geographical distribution (Laurimäe et al., 2018). The open issue here is especially the maintenance of the species' genetic identity under sympatric conditions, which is fundamental in recognizing independent evolutionary origins of the three lineages (Romig et al., 2015; Vuitton et al., 2020). On this account, the strict ecological separation between the 'domestic' G6/7 and the 'sylvatic' G8, G10 has recently been questioned as G6 was found in wolves and reindeer in the Altai region and Yakutia, Russia (Konyaev et al., 2013), and G6/7 in reindeer in the Nenets Autonomous Okrug, Russia (Šnábel et al., 2022). In addition to more comprehensive information on biological and morphological characters, more data will be needed especially on nuclear gene loci from a greater number of geographically close isolates to assess putatively new species in the *E. canadensis* cluster (Romig et al., 2015; Hua et al., 2022).

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