



Review

A hundred years of controversy about the taxonomic status of *Echinococcus* species

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ABSTRACT

The parasitic diseases which we know today as cystic and alveolar echinococcosis are zoonoses known since antique times, and 1855, respectively. Whether the two clinically and morphologically distinct diseases were caused, according to a “unicistic” and a “dualistic” theory, by only one or two different cestode species was the subject of a fierce, 100 years long debate involving scientists from many countries. The natural life cycle of *Echinococcus granulosus* was fully clarified in 1855 after successful animal experiments. In contrast, the natural final and intermediate hosts of *Echinococcus multilocularis* remained unknown, and the advocates of either theory had to draw on a number of surrogate arguments to defend their positions. The seesaw of reasoning and mutual defeats of the two theories, and the final recognition of *E. multilocularis* as an independent species in the 1950s are described in this article.

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1. Background

The larval stages of the two tapeworm species *Echinococcus granulosus* and *Echinococcus multilocularis* cause two distinct diseases in humans and animals, cystic echinococcosis (CE) and

alveolar echinococcosis (AE), respectively. While CE was known as hydatid disease since ancient times (Table 1), AE was first recognized to be of echinococcal origin in 1852 and 1855 by the German pathologists Ludwig Buhl and Rudolf Virchow, respectively (Buhl, 1856; Virchow, 1856). It was Virchow however, who was the first to publish the correct conclusions (Tappe and Frosch, 2007). The question whether the two zoonoses were caused by variants of the same species, at that time called *Taenia echinococcus*, or by two different species, was to be debated in the scientific community for

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Table 1
Early descriptions of human liver lesions referring to CE, or resembling AE (cited from Vierordt, 1886 [1,3], Neresheimer, 1904 [2]).

(1) Hippokrates (~400 BC)	(2) Lazarus Rivierus (~1650), France	(3) Frederik Ruysch (1638–1731), The Netherlands
Quibus hepar aqua plenam in omentum erupit, his venter aqua repletur et moriuntur.	Rusticus quidam, hydropicus factus, abscessum passus est in dextra parte abdominis, eoque aperto, infinitus propemodum vesicularum aqua repletarum numerus egressus est, ut aucentarum numerum excederet, idque per plurium dierum spatium et sic omnino curatus est.	Anno 1696 Hydropici cadaver cultro anatomico subjeci, cujus hepar totum, quantum erat ex meris vesiculis constabat, quae materiam limosam pellucidam continebant.
He whose water-filled liver erupts into the omentum, his belly becomes filled with water and he dies.	A man from the countryside, suffering from dropsy, was operated on an abscessus on the right side of his abdomen. When it was opened, an almost infinite number of water-filled vesicles was emitted, which continuously died. This went on for days and he fully recovered.	In 1696, I dissected a corpse with dropsy whose whole liver completely consisted of vesicles, containing a gelatinous, translucent mass.

the coming 100 years. In CE, caused by larval stages (metacestodes) of the *E. granulosus*-complex, a slowly expanding hydatid develops (Fig. 1). The cycle of *E. granulosus* involves predominantly dogs as final hosts, and sheep, pigs, cattle, camels, and accidentally humans as intermediate hosts. The unilocular cystic lesions are most often located in the liver, but also in the lungs and in other organs. AE is caused by metacestodes of the fox tapeworm *E. multilocularis*. It is confined to the northern hemisphere and involves mainly foxes, but also dogs and other canids as final hosts. Rodents and accidentally humans serve as intermediate hosts. In AE, a multi-chambered (alveolar) parasitic tissue (Fig. 2) develops primarily in the liver, and

may infiltrate neighbouring tissues or even metastasize to distant organs.

2. Concepts of echinococcosis before Virchow's discovery in 1855

Until 1855, CE in humans and animals was frequently diagnosed in many regions of Europe, where Iceland had the highest endemicity, and also in Russia, North Africa, South America, and Australia (Posselt, 1900). The larval nature of the hydatid cysts had been hypothesized already in 1767 by Pallas and had been confirmed in 1782 by Goeze (Hosemann, 1928), who described in detail the protoscoleces in liver cysts. The term *Echinococcus* originally referred to the invaginated protoscoleces and was used for the various larval "forms": *E. veterinorum* (Rudolphi) for simple cysts in animals, and *E. hominis* (Rudolphi) for the composite cysts containing daughter cysts or brood capsules in human viscera. A series of experiments was conducted simultaneously by Carl Theodor von Siebold, Breslau, and Friedrich Küchenmeister, a physician from Zittau. They fed metacestodes from sheep to dogs using *E. veterinorum*, which led to the discovery of the strobilar stage. Von Siebold called it *Taenia* (*T.*) *echinococcus* (Von Siebold, 1853). The life cycle of the parasite, later called *E. granulosus*, was further clarified by feeding eggs from feces of infected dogs to sheep (Haubner, 1855), which resulted in fertile liver cysts in the latter. The origin of CE cysts in humans, however, remained unclear (Kugler, 1930). An experiment with such cysts fed to dogs had failed in 1853 (Küchenmeister, 1855). Shortly before Virchow's publication, Küchenmeister, who did not believe in the rigid host restriction of simple or composite cysts, introduced the names *E. altricipariens* and *E. scolecipariens* referring to the occurrence of scolex formation (Küchenmeister, 1855). Thus, the entity of hydatid disease and the unity of the species called *E. granulosus* today had not been clarified sufficiently at that time. Of note, species validation is still in progress for some genotypes of the *E. granulosus*-complex today (see last chapter).

3. The onset of a long scientific dispute

In 1855, at the autopsy of a patient from the Bürgerspital in Würzburg, Germany (Fig. 3), Virchow excised a tumorous lesion from the liver consisting of high numbers of vesicles, mostly not greater than millet-seeds, containing a gelatinous mass. Each was surrounded by a laminated layer similar to that of the common *Echinococcus*. In a few of these vesicles, Virchow was able to identify some protoscoleces (Virchow, 1856). He then reanalyzed the published data of previous cases described as "alveolar colloid" or "gelatinous cancer" of the liver, and concluded that some of

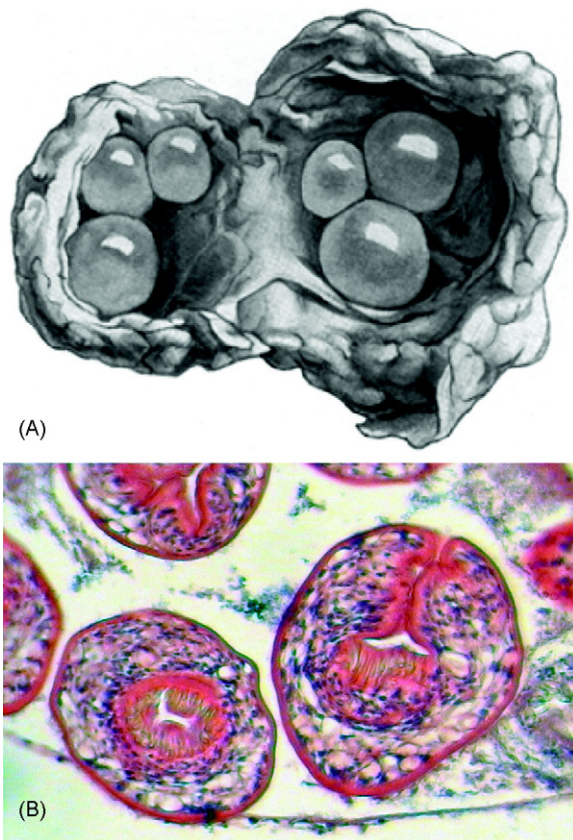


Fig. 1. Cystic echinococcosis, common hydatid disease. (A) Six daughter cysts are shown within an opened hydatid. Drawing from 1932, taken from Schmieta (1932). (B) Brood capsule arising from the germinal layer on the inner surface of the vesicles. Within the brood capsule, many protoscoleces develop. Original magnification 400 \times , haematoxylin and eosin stain.

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