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A CONSIDERATION OF INFRASPECIFIC CATEGORIES IN THE GENUS *ECHINOCOCCUS* RUDOLPHI, 1801 (CESTODA: TAENIIDAE)

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ABSTRACT: *Echinococcus granulosus* (Batsch, 1786) and *E. multilocularis* Leuckart, 1863, have been considered polytypic species, nine and three subspecies, respectively, having been recognized mainly on typological grounds. However, limits of taxonomically significant morphological and physiological variation have not been defined, nor do we know the degree to which such variation is influenced by species of host. With the probable exception of *E. g. canadensis* Cameron, 1960, the recognized subspecies of *E. granulosus* occur sympatrically with the nominate subspecies, *E. g. granulosus*, of European origin. Because there are no well-defined predator-prey relationships which would ensure their ecological isolation, seven of these subspecies are not reproductively segregated and therefore must be considered taxonomically invalid. Two subspecies of *E. multilocularis* are allopatric, but may represent two extremes of a cline; the status of the third is uncertain. Different populations (variants or physiological strains) of *Echinococcus* spp. might be more appropriately designated informally as strains or forms.

Attempts have been made in recent years to demonstrate the occurrence of polytypic species in the genus *Echinococcus* Rudolphi, 1801. Such studies have been complicated by two factors: the undefined limits of taxonomically significant morphological and physiological variation in cestodes, and the inadequate knowledge of the degree to which such variation is influenced by species of host.

Also bearing upon this difficult problem is the basic taxonomic concept of the subspecies. This has been defined by Mayr (1963, p. 348): "A subspecies is an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species." For species of *Echinococcus* and other cestodes whose life cycles are similar, different host assemblages may be considered the equivalent of different subdivisions of the range. Therefore, in defining subspecies of such cestodes, evidence must be presented to show that populations occurring in assemblages of sympatric hosts are indeed segregated.

Proceeding on this basis, the present study evaluates criteria utilized in the definition of subspecies of *Echinococcus* spp. and reviews the taxonomic status of subspecies that have been distinguished.

Species of *Echinococcus*

In recent revisions of the genus, not more than four species of *Echinococcus* have been

considered to be valid (Rausch and Nelson, 1963; Verster, 1965). Only two, *E. granulosus* and *E. multilocularis*, are comparatively well known. The recognized species are:

E. granulosus (Batsch, 1786) (syn. *E. cameroni* Ortlepp, 1934; *E. felidis* Ortlepp, 1937; *E. intermedius* López-Neyra and Soler, 1943; *E. longimanubrius* Cameron, 1926; *E. lycaontis* Ortlepp, 1934; *E. minimus* Cameron, 1926; *E. ortleppi* López-Neyra and Soler, 1943).

E. multilocularis Leuckart, 1863 (syn. *E. sibiricensis* Rausch and Schiller, 1954).

E. oligarthrus (Diesing, 1863) (? syn. *E. cruzi* Brumpt and Joyeux, 1924) (in wild felids in South America).

E. patagonicus Szidat, 1960 (in wild canids in Patagonia). *E. oligarthrus* and *E. patagonicus* are not considered further in the present paper.

Recognized subspecies of *E. granulosus*

Europe: Verster (1965) pointed out that the type locality of the nominate subspecies of *E. granulosus* is in Germany. More specifically, it appears to be in the vicinity of Quedlinburg, southwest of Magdeburg, in Sachsen, where the material studied by Goeze (1782) was evidently obtained. The type host is the domestic sheep. A single form of *E. granulosus* (the nominate subspecies) presumably is present in the agricultural regions of Europe, while the form occurring within the tundra zone of Eurasia appears to be distinguishable ecologically (Rausch, 1967). The status of the latter form is discussed below.

Cestodes from a red fox, *Vulpes vulpes* Linnaeus, in England, were identified by Cameron (1926) as *E. granulosus*. This material had been studied earlier by Ortlepp (1934, see p. 102), who made the same determination. Upon comparing the cestodes from the fox with specimens identified as *E. granulosus* from dogs in the vicinity of Pretoria, South Africa, Ortlepp (1934) concluded that the former were specifically distinct, and designated the species *E. cameroni*. After comparing some of the original specimens from the fox with *E. granulosus* from various regions, Rausch (1953) concluded that the two were morphologically indistinguishable, making *E. cameroni* a synonym of *E. granulosus*. Contrary to what is usually observed, *E. granulosus* in Great Britain is capable of maturing and producing eggs in red foxes.

E. g. equinus was described in Great Britain by Williams and Sweatman (1963), who distinguished it morphologically from *E. granulosus* occurring in New Zealand. Williams and Sweatman (p. 403) concluded that *E. g. equinus* is sympatric with the nominate subspecies in Great Britain. Assuming that this cestode is the same as that studied by Cameron and Ortlepp, the subspecific designation *cameroni* thus would have priority over *equinus*.

North America: *E. granulosus* of European origin could have been introduced into North America during the early colonial period. The earliest record in the literature, however, appeared much later; the larval cestode was observed in domestic animals in Canada by Osler (1882), who also mentioned data published in 1845 concerning infected swine in Ohio. Further reports (Salmon, 1901) and specimens in the collections of the U. S. National Museum indicate that *E. granulosus* was prevalent in domestic animals in the United States prior to 1900 (Rausch, 1967). At present, *E. granulosus* of presumed European origin is restricted to certain endemic areas, mainly in the southern part of the United States.

That the indigenous mammalian fauna was involved in the life cycle of *E. granulosus* in North America was first noted by Riley (1933), who found infected wolves, *Canis lupus* Linnaeus, and moose (= elk), *Alces alces* Lin-

naeus, in Minnesota. However, the form occurring in the wild mammals has been considered to be the same as that found in domestic animals farther south (Magath, 1954).

Cameron (1960) determined that the form of *E. granulosus* present in northern North America differs biologically from the "typical" form of European origin, and he proposed that it be designated *E. granulosus* var. *canadensis*. This cestode was later recognized as a subspecies, *E. g. canadensis*, by Webster and Cameron (1961). The larval stage is found in wild ruminants (wild reindeer, or caribou, *Rangifer tarandus* Linnaeus, and moose), as well as in man, but appears to be incapable of development in domestic animals other than domestic reindeer. Clinical differences also have been noted through the study of infections in the aboriginal peoples of Canada and Alaska (Meltzer et al., 1956; Wilson et al., unpublished data).

The subspecies *E. g. borealis* Sweatman and Williams, 1963, was described from material obtained from wolves and deer in Canada. Concluding that *E. g. canadensis* had been introduced by means of domestic reindeer and dogs imported from Norwegian Lapland, Sweatman and Williams (1963) considered *E. g. borealis* to be the indigenous North American form. The distinction of *borealis* was based upon morphological characteristics as well as upon findings in experimentally infected animals.

New Zealand: Sweatman and Williams (1963) and Williams and Sweatman (1963) determined that the nominate subspecies occurs in New Zealand and, presumably, in Australia, having been introduced into these regions with domestic animals imported from Europe (Rausch, 1967). However, Verster (1965) found that cestodes from New Zealand differed morphologically from *E. g. granulosus*, and the former were consequently designated *E. g. newzealandensis* Verster, 1965.

Africa: The cestode from South African dogs identified by Ortlepp (1934) as *E. granulosus* was made the type of a new species, *E. ortleppi*, by López-Neyra and Soler (1943). Accepting Ortlepp's original determination, Rausch and Nelson (1963) placed *E. ortleppi* in synonymy with *E. granulosus*. After studying some of Ortlepp's material, Verster (1965)

concluded that these specimens were morphologically distinguishable at the subspecific level and thereupon designated them *E. g. ortleppi* López-Neyra and Soler, 1943.

Verster (1965) recognized the occurrence of the nominate subspecies in South Africa and assigned subspecific rank to two previously described species of *Echinococcus*, *E. felidis* and *E. lycaontis*, which had been considered synonymous with *E. granulosus* by Rausch and Nelson (1963). Besides these, *E. g. africanus* Verster, 1965, was distinguished, primarily on morphological grounds. Dailey and Sweatman (1965) reported both the nominate subspecies and *E. g. equinus* in domestic animals in Syria and Lebanon, in Asia Minor.

Nine subspecies of *E. granulosus* have been recognized.

Recognized subspecies of *E. multilocularis*

Three subspecies of *E. multilocularis* have been distinguished. The nominate subspecies, of which the type locality is southern Germany, has a restricted geographic range in central Europe. This form presumably occurs over much of the territory of the Soviet Union.

Vogel (1957) proposed that the cestode occurring in Alaska be considered a separate geographic race or subspecies of *E. multilocularis* "Auf Grund gewisser Unterschiede in der Hakengrösse, Wirtsspezifität und Lokalisation der Larvenstadien . . ." (p. 452). The type locality of *E. m. sibiricensis* is St. Lawrence Island, in the Bering Sea.

The third subspecies, *E. m. kazakhensis* Shul'ts, 1961, distinguished by the ability of the larval stage to develop in ungulates, evidently has been recorded only from Kazakhstan.

The taxonomic validity of infraspecific categories in cestodes of the genus *Echinococcus*

The comparatively great age of the species of mammals comprising the fauna of what is now Europe has been established from paleontological evidence (Charlesworth, 1957; Zeuner, 1958). Since adaptation of a cestode to its hosts involves a long evolutionary process (Baer, 1934, 1946; Stunkard, 1957), the species of cestodes occurring in these mammals must have existed as such since some time before the end of the last interglacial period

(Riss/Würm). Many of the species of mammals serving as hosts of *E. granulosus* and *E. multilocularis* at higher latitudes are holarctic in distribution (Rausch, 1963).

The life cycle of *E. granulosus* involved the wolf and wild ungulates of various species. By early postglacial time, the wolf was present extensively in Eurasia, but the ungulates serving as the intermediate host of *E. granulosus* were segregated to some degree both ecologically and geographically. The essential intermediate hosts within the tundra zone were the wild reindeer and probably the elk (moose). Farther south, in the European forested zone, the intermediate host of this cestode included several species (wild swine, *Sus scrofa* Linnaeus; aurochs, *Bos primigenius* Bojanus; red deer, *Cervus elaphus* Linnaeus, and others).

The dog (= wolf) was domesticated in Europe during late mesolithic time (Charlesworth, 1957; Clutton-Brock, 1963). With the domestication of ungulates of various species, conditions favoring the existence of a synanthropic cycle of *E. granulosus* came into being. The natural cycle involving the wolf and wild ungulates coexisted in Europe with the synanthropic cycle. With the extirpation of the wolf in Europe, the natural cycle of *E. granulosus* was largely destroyed, although the dog replaced the wolf to some extent as a source of infection for the remaining wild ungulates (deer and wild swine). The wolf-reindeer cycle has persisted at higher latitudes, although there also the dog and the domestic reindeer have partially replaced the natural hosts.

The nominate subspecies of *E. granulosus*, adapted in the larval stage to development in domestic animals, became widely distributed following the introduction of such animals into different regions of the world during the period of conquest and colonization in the 18th and 19th centuries (Rausch, 1967). This cestode had no doubt become established much earlier in Africa and southern Asia, but a succession of reintroductions must have taken place during the period of colonization. The northern form of *E. granulosus* could not have been distributed to any significant extent to other parts of the world, although cestodes possessing some of the characteristics of both forms might have been introduced occasionally with domestic animals originating in marginal

agricultural areas of northern Europe. After about 1890, infected reindeer and/or dogs could have been brought into Alaska and northern Canada, where presumably the northern form of *E. granulosus* was already present.

For *E. multilocularis*, foxes (*Vulpes* and *Alopex*) serve as the final host, and small mammals, particularly microtine rodents, contain the larvae. Under conditions modified by man, the dog also is an important final host. Although the pattern of geographic distribution of *E. multilocularis* is in some ways curiously restricted (Rausch, 1967), the original geographic range of this cestode seems not to have been extensively modified.

Subspecies of *E. granulosus*

Two biologically different forms of *E. granulosus* thus are seen to exist in western Eurasia, but from all evidence the two cannot be distinguished morphologically. The recognized subspecies of *E. granulosus* have been discussed below in reference to this hypothesis.

Modern taxonomic concepts preclude the sympatric existence of more than one subspecies of a single polytypic species. Assuming that different host assemblages are equivalent to different subdivisions of the geographic range of a free-living animal, conceivably two or more subspecies of *E. granulosus* could exist in sympatric hosts if segregated in different host assemblages by comparatively rigid predator-prey relationships. That such is the case in any area where two or more subspecies of this cestode have been recognized is not apparent.

In Great Britain, two sympatric subspecies of *E. granulosus* (*E. g. granulosus* and *E. g. equinus*) occur in the same hosts. The important final host is undoubtedly the dog, and the larval stage is found at least in horses and sheep if not in other ungulates (Williams and Sweatman, 1963; Cook and Crewe, 1963). *E. granulosus* in Great Britain can develop and produce eggs in red foxes, which probably serve as a source of infection for domestic animals. However, we cannot consider as realistic the proposal that a natural predator-prey relationship exists between foxes and the comparatively much larger ungulates. Both dogs and foxes must almost always become infected through feeding upon carrion or offal. The occurrence of gravid specimens of *E.*

granulosus in foxes of the genus *Vulpes* is not so unusual as was believed, in view of findings in other regions (Shumakovitch and Nikitin, 1959; Gorina, 1959; Malczewski, 1963). That *E. g. granulosus* and *E. g. equinus* are in any way segregated cannot be supported; therefore, the latter taxon must be considered invalid.

The situation is somewhat more complex in North America, where the geographic range of the indigenous form of *E. granulosus* encompasses at least the zones of tundra and boreal forest, while the southern limits are unknown (Rausch, 1967). *E. g. granulosus* of European origin was introduced into the agricultural regions of the United States and southern Canada, and after attaining maximum geographic distribution in domestic animals around 1900, has been largely eliminated through the control of abattoirs. These two forms of *E. granulosus* have remained essentially allopatric in their North American distribution, although some overlapping of their ranges probably occurred in marginal agricultural areas at about the latitude of the border between the United States and Canada. However, if such overlapping did occur, no evidence of intergradation between these forms has been detected. The status of *E. g. granulosus* in North America seems to be well defined.

In northern North America, however, two sympatric subspecies of *E. granulosus* have been recognized. Sweatman and Williams (1963) concluded that *E. g. canadensis* was introduced with reindeer and dogs from Norwegian Lapland, while *E. g. borealis* represents the indigenous North American subspecies. Again, two subspecies allegedly occur in sympatric hosts not segregated ecologically. If, as Sweatman and Williams believe, the form designated *E. g. canadensis* was introduced from Lapland, it would presumably be identical with the indigenous North American form, there being probably a single, holarctic form at higher latitudes. In any event, an introduced subspecies of *E. granulosus* could not retain its genetic identity in the absence of a segregating mechanism. Any genetic differences that might have existed would disappear in the resulting common gene pool, since by definition the different subspecies of a polytypic species interbreed if not segregated.

Thus, *E. g. canadensis* could not exist as an infraspecific entity; further, that a distinctive organism was in fact introduced is doubtful. Under these circumstances, only a single subspecies could be recognized. If the indigenous North American cestode were to be designated as a distinct subspecies, *E. g. borealis* on the basis of priority would have to be suppressed in favor of *E. g. canadensis*.

In another region, South Africa, the mammalian fauna would seem to be sufficiently varied to permit the existence of different host assemblages segregated by well-defined predator-prey relationships. The existence of polytypy within *E. granulosus* might thus be expected, but this in actuality does not appear to be the case. Verster (1965) recognized five subspecies of *E. granulosus* in the Transvaal region of South Africa, primarily on morphological grounds: *E. g. africanus*, *E. g. felidis*, *E. g. granulosus*, *E. g. lycaontis*, and *E. g. ortleppi*. With the possible exception of *E. g. felidis* in the lion (*Panthera leo* Linnaeus), about which little is known, a significant degree of ecological isolation or host specificity in the strobilar stages of these cestodes is not evident. Neither do the respective larval stages exhibit an appreciable degree of host specificity. Strobilae identified as those of *E. g. africanus* and *E. g. ortleppi* were obtained in experimentally infected canine animals from larvae from cattle, and cestodes identified as *E. g. africanus* and *E. g. lycaontis* were similarly reared from larvae from domestic sheep. Larvae of *E. g. granulosus* were obtained by Verster also from man and domestic swine. Larval *Echinococcus* were not recorded in the Transvaal from wild ungulates that comprise the major prey of the lion or of the hunting dog, *Lycaon pictus* Temminck. As in Kenya (Nelson and Rausch, 1963), *E. granulosus* appears to be propagated essentially by domestic animals, including the dog, in South Africa.

The view that more than a single subspecies of *E. granulosus* occurs in South Africa is supportable only by evidence of ecological segregation or marked host specificity. Lacking such evidence, as is the case, we must regard four subspecies (*africanus*, *felidis*, *lycaontis*, and *ortleppi*) to be synonyms of *E. g. granulosus*.

The remaining subspecies, *E. g. newzealandensis*, Verster (1965) found to differ

morphologically from *E. g. granulosus* from Germany. A well-documented history exists of introductions of domestic animals of European origin into New Zealand. This and our knowledge of the absence in New Zealand of an indigenous form of *Echinococcus* uphold the conclusion that the differences attributed to *E. g. newzealandensis* probably represent nonsignificant variation in cestodes belonging to the nominate subspecies.

Morphological data of impressive quantity are available on subspecies of *E. granulosus*. A review of these makes apparent that the systematic concepts upon which published work was based were largely typological, perhaps because the amount of material studied was insufficient to provide an understanding of the limits of morphological variation within local populations of *E. granulosus*. Relevant to this is the view of Mayr et al. (1953), who pointed out that populations of an animal may be statistically different, but not as a consequence necessarily taxonomically different.

Sweatman and Williams (1963) and Williams and Sweatman (1963) relied upon characteristics of rostellar hooks of both larval and strobilar stages as well as upon number of segments, relative position of the mature segment, number and distribution of testes, and structure of the cirrus sac and seminal vesicle. Verster (1965), on the other hand, found that the size of the rostellar hooks in the adult cestode varied with species of final host; moreover, she was unable to confirm that the ultimate size of rostellar hooks is fixed in the larval stage, as Sweatman and Williams (1963) believed. Verster depended largely upon number of segments, relative position of the mature segment, and distribution and number of testes, in order to distinguish subspecies of *E. granulosus*.

The apparent, though slight, differences that she observed in material obtained in experimentally infected animals evidently represented host-species induced variation, combined in some cases with physiological modifications. The series of animals utilized were in general too small to exclude as an influence the possible effects of dissimilarities in degree of susceptibility among animals of the same species. Although Verster expressed some reservations concerning the reliability of the

criteria she employed, she considered recognition of subspecies of *E. granulosus* to be appropriate until these bases were shown to be invalid. However, since the described subspecies of this cestode must be rejected on other grounds, the evaluation of morphological criteria at the infraspecific level is not essential here.

Subspecies of *E. multilocularis*

All of the recognized subspecies of *E. multilocularis* are allopatric. *E. m. multilocularis* and *E. m. sibiricensis* differ relatively in site of localization of the larva in the intermediate host and in host specificity of the strobilar stage (Vogel, 1957). The form of *E. multilocularis* in central North America may exhibit variations of similar magnitude (Rausch and Richards, unpublished data), and other variants may be recognized in the future, particularly in the Soviet Union.

E. m. kazakhensis was originally reported from sheep in Kazakhstan, where up to 8% of *Echinococcus*-infected animals contained larvae of alveolar type (see Abuladze, 1964, p. 358). The adult cestode occurs in dogs. More recently, the larval stage of *Alveococcus* (= *Echinococcus*) *multilocularis*, as well as that of *E. granulosus*, have been reported from wild swine, *Sus scrofa*, in the same region (Shol', 1963).

DISCUSSION

Our inadequate understanding of the limits of intraspecific variation in cestodes of the genus *Echinococcus* has been a source of uncertainty at both the specific and infraspecific levels. Smyth and Smyth (1964), for example, concluded that *E. granulosus* and *E. multilocularis* represent the two extremes of a character-gradient comprising an indefinite number of variants which may exhibit characteristics common to both. Their interpretation appears to be largely the result of placing emphasis on host-induced variation in larval cestodes developing in other than their natural hosts. The limits of normal intraspecific variation in these cestodes must be determined through the study of material from the natural hosts, i.e., those mammals which perpetuate the cestodes under conditions unmodified by man. Under natural conditions also the larval stages of these ces-

todes may develop in fortuitously infected mammals of species that obviously cannot be included in the respective host assemblages (e.g., the larval *E. multilocularis* in *Sorex*); however, the status of such accidental hosts can be readily determined by means of ecological investigations.

Intraspecific variation in *Echinococcus* might be made more understandable if certain uniform conditions were assured in experimental studies. Yamashita et al. (1958), for example, demonstrated that uniform strains of white mice varied widely in the degree to which they supported development of the larval *E. multilocularis*. Of similar magnitude might be the variation resulting in different genetic strains of domestic animals or even in wild animals of the same species originating from widely separated localities. Consequently, results of investigations in different parts of the world with animals of the same species are not necessarily comparable. Not only should experimental animals be uniform genetically, but differences in age and nutritional status may be reflected in the results. In infecting dogs of a pure strain (beagle) with *E. multilocularis*, I have found that the results are not always uniform in members of single litters which received the same quantity of infective material from a single source. When experimental studies involve small series of animals, either as final or intermediate hosts, apparent differences in results should be evaluated with caution.

As the recent investigations have shown, local populations of *E. granulosus* are intrinsically variable morphologically. Genetic variability of the cestodes in combination with effects related to species of host seems to account for the statistically demonstrable but taxonomically insignificant differences that have been described. The dissimilarities existing between the two comparatively well known forms or populations of *E. multilocularis* may be taxonomically significant. In view of the extensive geographic range of the species, the central European and Alaskan forms may represent two extremes of a cline. Until new information becomes available to indicate otherwise, it seems appropriate to designate different populations of *E. granulosus* and *E. multilocularis* informally, as strains or forms.

ACKNOWLEDGMENTS

To Professor Ernst Mayr, Museum of Comparative Zoology, Harvard University, and Dr. Francis H. Fay, Arctic Health Research Center, who read the manuscript of this paper, I express my thanks.

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