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Review

REVIEW OF AUSTRALIAN SPECIES OF *THEILERIA*, WITH SPECIAL REFERENCE TO *THEILERIA BUFFELI* OF CATTLE

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SUMMARY

This review describes 4 species of parasites in Australia generally regarded as Theileria. *The physiological and epidemiological characteristics of the species that occurs in cattle are discussed. Confusion still surrounds the relationship of this species with benign species of* Theileria *in other countries. Arguments are presented to support the proposal that the bovine species in Australia is correctly designated* Theileria buffeli *and that this name should apply to all the benign species of* Theileria *of cattle in Eurasia. The other 3 species considered in the review are proposed species from marsupials. Of these, only* Theileria tachyglossi *can confidently be included in the genus* Theileria, *because schizonts have yet to be detected in the other 2 species.*

INTRODUCTION

The genus *Theileria* comprises tick-transmitted protozoa characterised by schizonts in lymphoid cells and piroplasms in red blood cells of the vertebrate host. Transmission occurs trans-stadially within one tick generation. These features, together with certain aspects of the life-cycle in ticks differentiate *Theileria* from the closely related genus *Babesia* (Callow, 1984). Four species of *Theileria* have been described in Australia, namely *T. buffeli* (Dodd, 1910, as *T. mutans*) from cattle, *T. Tachyglossi* from echidna (Priestly, 1915), *T. ornithorhynchi* from platypus (Mackerras, 1959) and *T. peramelis* from several marsupials (Mackerras, 1959).

THE PARASITES

Theileria buffeli

Callow (1984) proposed that this *Theileria* parasite of cattle be called *T. buffeli* and we present arguments here to support that proposal.

Vectors

For many years *Boophilus microplus* was considered to be a vector of *T. buffeli* in Australia (Seddon, 1952; Albiston, 1967). Albiston (1967) suggested that the parasite was introduced into this country by either *B. microplus* or *Haemaphysalis bispinosa* (=*longicornis*) from India. On the other hand Hoogstraal *et al.* (1968) and Riek (1982) believed that *H. longicornis* was introduced into Australia from Japan, presumably bringing a species of *Theileria* with it. In view of recent findings (Uilenberg *et al.*, 1985; Stewart *et al.*, 1987a, b) and earlier observations (Callow and Hoyte 1961; Riek 1982) that indicate *H. Longicornis* is at best an inefficient vector of Australian *T. buffeli*, both these suggestions appear incorrect.

The main vectors of *T. buffeli* in Australia are now known to be *Haemaphysalis humerosa* and *Haemaphysalis bancrofti* (Stewart *et al.*, 1987a, b; Stewart *et al.*, 1989). Both are thought to be native ticks often found on bandicoots and wallabies. *Haemaphysalis bancrofti* frequently occurs on cattle (Roberts, 1970), and *H. humerosa* is capable of completing its life cycle on cattle, at least at the laboratory (Stewart *et al.*, 1987a,b). Under experimental conditions *H. longicornis, B. microplus, Ixodes holocyclus, Amblyomma triguttatum* and *Rhipicephalus sanguineus* have failed to transmit infection (Stewart *et al.*, 1987a, b; Stewart, 1990; Riek, 1982; Callow and Hoyte, 1961).

Development in the vector

A developmental cycle has recently been described for *T. buffeli* in *H. bancrofti* showing the developmental stages of *T. buffeli* in the gut, haemolymph and salivary glands of the tick (Stewart, 1990). However, it was not possible to demonstrate conclusively the occurrence of sexual stages or syngamy as seen in other species of *Theileria* (Young *et al.*, 1980). Stewart (1990) observed close morphological similarities between the developmental cycle of *T. buffeli* and Japanese *Theileria sergenti* described by Higuchi (1986, 1987) and Higuchi *et al.* (1987). Vermicules of *T. buffeli* were found only during or after the nymphal moult, whereas those of other *Theileria* species, including *T. annulata* and *T. velifera*, were frequently found before the nymphal moult (Schein, 1975; Warnecke *et al.*, 1979). Vermicules of *T. mutans* were usually found considerably later in the adult tick (Young *et al.*, 1978). The development of *T. buffeli* in salivary glands (Stewart, 1990) was also similar to that of *T. sergenti* as described by Higuchi (1986)), and *T. taurotragi* (Young *et al.*, 1980). However, it differed considerably from the development of *T. mutans,* in which larger sporozoites were produced (Purnell *et al.*, 1975). In the light of current knowledge whereby there is doubt that *H. longicornis* is a vector of Australian *T. buffeli*, it is difficult to explain an observation by Riek (1966) of the development of *T. mutans* (= *T. buffeli*) in the salivary glands of *H. longicornis*. It is possible the ticks used by Riek (1966) were either *H. bancrofti* or *H. humerosa* and were wrongly identified as *H. longicornis*. Alternatively, the phenotype of *T. buffeli* may have changed, thus making it difficult for the parasite to cross the gut barrier of some ticks as suggested by other workers (Fujisaki unpub. observations; Sugimoto *et al.*, 1991).

Course of infection in cattle

Until recently the only known developmental stages of *T. buffeli* infections were confined to erythrocytes. Dodd (1910) described ring and rod shaped forms in bovine red blood cells, and gave them pathological significance. Stewart *et al.* (1988) studied the development and morphology of *T. buffeli* in the bovine host after experimental transmission with *H. humerosa.* Macroschizonts were demonstrated in Giemsa stained smears prepared from lymph nodes draining the site of tick attachment for between 6 and 20 days following infestation. The same authors confirmed the presence of schizonts in lymph node smears by immunofluorescence using antischizont *T. buffeli* antiserum. Microschizonts were seen infrequently. The schizonts and piroplasms of *T. buffeli* were morphologically similar to those reported by Uilenberg *et al.* (1985) for *Theileria orientalis* and by Minami *et al.* (1990) for *Theileria sergenti.*

Distribution in Australia

Theileria buffeli is widespread in Australia as are its tick vectors although the exact distribution is not defined (Callow, 1984). A recent serological survey (Stewart *et al.*,

1992) indicated that *T. buffeli* is ubiquitous in Queensland and has a wider distribution than previously reported by Riek (1982). The prevalence is higher in northern and coastal regions of Queensland, decreasing towards the south-west, and herd and animal sero-prevalences for *T. buffeli* are 75 and 41% respectively. The distribution of *T. buffeli* in the remainder of Australia is unclear. In New South Wales it has been reported to occur up to several hundred kilometres from the coast (Callow, 1984). Unpublished reports also indicate it may be present in Victoria, western Australia and the Northern Territory. There are no records of *T. buffeli* occurring in South Australia or Tasmania although it may be present in these States, since both the vectors (D. H. Kemp, pers comm) and bovine host occur there. Callow (1984) thought that at least one species of *Haemaphysalis* is more widely distributed in Australia than is generally known, and suggested a survey for ticks belonging to this genus. The distributions of *H. humerosa* and *H. bancrofti* have never been properly defined in Australia. However, each State has similar coastal and inland habitats which are favoured by these ticks. This combined with the large number of vertebrate hosts (Roberts, 1970) suggests that both ticks would have much wider distributions throughout Australia than those previously reported.

Pathogenicity

Diagnosis of theileriosis in cattle in Australia may be complicated by the presence of babesiosis and anaplasmosis (Callow, 1984); nevertheless losses due to *T. buffeli* are unusual. However, *T. buffeli*, or a closely related *Theileria* species, has been reported to cause sickness and death, particularly in imported cattle, in several eastern Asian countries (Uilenberg, 1981). Rogers and Callow (1966) described 3 deaths in mature dairy cattle in south-eastern Queensland over a 3 to 4 year period. In all 3 cases, parasitaemia approached 100% of erythrocytes and there was generalised icterus; the main microscopic changes were centrilobular necrosis and haemosiderosis in the liver, and lymphatic exhaustion of the spleen and lymph nodes. The 3 cases are the only documented cases reported from Australian cattle, and the development of fatal infections in a few mature cattle in a region are exposed to *T. buffeli* early in life suggests immune failure of the host rather than an escalation of virulence of the parasite.

Chemotherapy

Callow (1984) stated there was no justification for attempting to control *T. buffeli* in Australia. However, circumstances in the laboratory may warrant chemotherapy. In Australia, the production of highly effective vaccines containing *Babesia bovis, B. bigemina* and *Anaplasma centrale* (so called tick fever vaccines) depends on obtaining high parasitaemia in splenectomised calves. Stewart *et al.* (1990c) reported the depression of parasitaemia in *B. bovis* and *A. centrale* infections in splenectomised calves due to concurrent infection with *T. buffeli.*

Calves becoming infected with *T. buffeli* in the first few months of life (Riek, 1982) are unsuitable as donors for the production of tick fever vaccines. Thus, there has been considerable interest in methods to eliminate benign theilerial infections from calves being prepared for vaccine production.

Primaquine and other 8-aminoquinoline compounds have been shown to be active against the intraerythrocytic piroplasms of pathogenic and benign species of *Theileria* (Neitz, 1950; Callow, 1984). Stewart *et al.* (1990b) found that primaquine phosphate when used alone was incapable of eliminating infections of *T. buffeli* even after 9 treatments at 2 $mg kg^{-1}$ body weight. Relapses of *T. buffeli* were observed in all 19 calves between days 32 to 145 after treatment, irrespective of the number of treatments administered. Zhang (1987), however, describes successful elimination of *T. annulata* piroplasms with low doses of primaquine phosphate. Two other groups of compounds are active against intralymphocytic schizonts of pathogenic *Theileria* spp. In the first group the activity of the quinazolinone anticoccidial, halofuginone hydrobromide, was first reported by Schein and Voigt (1979) and confirmed by Uilenberg *et al.* (1980). Dolan (1986) subsequently described the activity of a less toxic analogue, halofuginone lactate, during acute clinical disease. The other group of compounds, the hydroxynaphthoquinones, includes menoctone (McHardy *et al.*, 1976), parvaquone (McHardy *et al.*, 1983) and buparvaquone (McHardy *et al.*, 1985).

Concurrent treatment with buparvaquone and primaquine phosphate (Stewart *et al.*, 1990a) or halofuginone lactate and primaquine phosphate (Stewart *et al.*, 1990b) has successfully eliminated infection with *T. buffeli* from cattle in most cases. Since *T. buffeli* does not produce pathogenic schizonts, and its major effect is destruction of erythrocytes, Callow (1984) believed the administration of an 8-aminoquinoline compound alone may be justified in clinical cases, should they occur.

Taxonomy of T. buffeli

In the past, the name *T. mutans* was applied to almost all *Theileria* spp. of low pathogenicity occurring in cattle (Uilenberg, 1986) although Uilenberg *et al.* (1977) had shown the Australian parasite to differ serologically from African *T. mutans* which is transmitted by *Amblyomma* ticks. Today confusion surrounds the taxonomy of benign bovine species of *Theileria* throughout the world.

Benign species of *Theileria* isolated from cattle in various continents and regions including Australia, New Zealand, Britain, Japan, Korea, Iran, United States of America, Ethiopia and Burundi, are similar serologically in the indirect fluorescent antibody test (Uilenberg, 1981). The morphology of their piroplasms and associated structures within infected red blood cells is also similar (Becerra *et al.*, 1983; James *et al.*, 1984; Kiltz *et al.*, 1986). Piroplasms 1·0 to 2·5 μm long occur in a multiplicity of forms, but Wenyon (1926) described them as round, ovoid, comma-shaped, bacilliform, coccal, dumb-bell-shaped, ring and cross forms. In the 3 countries where schizonts have been described, namely Korea, Australia and Japan, their morphology appeared to be identical (Uilenberg *et al.*, 1985; Stewart *et al.*,1988; Minami *et al.*, 1990). Moreover, the Australian parasite can be transmitted from buffalo to cattle (Callow *et al.*, 1976). On this basis, use of the name *T. buffeli*, described from buffalo in Indo-China (Neveu-Lemaire, 1912), for all of these parasites can be defended.

Uilenberg, Perie, Spanjer and van Vorstenbosch (unpub. observations in: Uilenberg, 1981) compared 4 non-pathogenic strains of *T. sergenti* (Japan) and *T. orientalis* (Britain, United States of America and Australia). They were unable to distinguish between them on morphological, serological or pathological grounds, and concluded that British and Australian parasites were the same, with the American and Japanese parasites being very closely related. However, Uilenberg (1981) was unsure whether the previous workers were dealing with one species or a complex of closely related species. Furthermore, Uilenberg (1981) suggested that benign species of *Theileria* occurring in domestic buffalo in areas where *T. annulata* or other well defined species are not known to occur might well belong to the same group. If this is the case the name *T. buffeli* (Neveu-Lemaire, 1912), would have priority over *T. sergenti* and/or *T. orientalis*. Furthermore, *sergenti*, by priority, belongs to a sheep parasite (Morel and Uilenberg, 1981; Callow 1984) and cannot serve to designate the benign *Theileria* of cattle in Eurasia. Morel and Uilenberg (1981) further stated that both these names would have to make way for *T. buffeli*, if and when the identities of the benign *Theileria* species of cattle and buffalo were established. Finally, based on the transmissibility of the Australian *Theileria* from buffalo (*Bubalus bubalis*) to cattle, Callow (1984) called the organism *T. buffeli*.

However, 2 arguments could be used to separate certain of these parasites as distinct species. First, experiments in India have reportedly shown that theilerial parasites of buffalo cannot be transmitted to cattle, using either blood passage or nymphal *H. bispinosa*. (Shastri *et al.*, 1985; U. V. Shastri, unpub observations). Schein (1923) also was unable to transmit species of *Theileria* of the buffalo to cattle or vice-versa in Indo-China by blood passage, but as Schein (1923) admitted readily, these experiments left much to be desired. If the specificity of certain parasites for the buffalo was to be confirmed, a case could possibly be made for considering these parasites as a species separate from those that infect both host species, such as the Australian parasite (Callow *et al.*, 1976). Because *T. orientalis* has been described from cattle and *T. buffeli* from buffalo, the logical conclusions would be to call the buffalo-specific parasites *T. buffeli* and the others *T. orientalis*. In that case the Australian parasite would be called *T. orientalis*.

This argument cannot be accepted until convincing results of strictly controlled transmission experiments are published. It is, moreover, a debatable argument, as there are examples of other haemoprotozoan parasite species which show strain-linked host-specificity. Differences in infectivity for man and for laboratory animals are well known within the *Trypanosoma brucei* group.

The Australian parasite has been transmitted easily by 2 Australian species of *Haemaphysalis* considered to be indigenous, namely, *H. humerosa* and *H. bancrofti*, while transmission by *H. longicornis* has been reported by Riek (1982). This last tick appears to be a main vector of *Theileria* sp. in Korea and Japan. It is also strongly suspected of being the vector of a *Theileria* in New Zealand, because no other tick parasitises livestock in that country (James *et al.*, 1984). The same is true in New Caledonia, where *H. longicornis* and *B. microplus* appear to be the only ticks found on cattle (G. Uilenberg unpub. observations). However, we do not think these observations can be the basis for considering the Australian parasite as a separate species.

A separate identity for the Australian *Theileria* would be very surprising since the parasite has certainly been introduced into the country with cattle from either Asia, where *H. longicornis* and several other species of *Haemaphysalis* are proven vectors of similar parasites or from Europe, in particular from Great Britain, where *H. punctata* is the proven vector (Uilenberg *et al.*, 1985). Alternatively it could have entered Australia in Brahman cattle from America where the vector is as yet unknown. An Australian stock of *Theileria* has been transmitted experimentally with *H. Punctata*, as have British and Iranian stocks (Uilenberg *et al.*, 1985). The Australian and British parasites are similar because the latter has also been transmitted by *H. longicornis* (Uilenberg *et al.*, 1985). The above suggests that more than one *Theileria* spp. may have been introduced into Australia. However, this suggestion was not confirmed by Stewart (1990) who performed transmission experiments using different geographically isolated strains of *T. buffeli* as well as strains of *H. longicornis* which originated in either Queensland, New South Wales or western Australia. It is more likely that there are strain-specific differences in the transmissibility by various species of the genus *Haemaphysalis*, a phenomenon which is recognised in vector-borne parasites and suggested previously as an explanation for apparent anomalies in transmission experiments by Stewart *et al.* (1987a).

Recent information emanating from Japan suggests that Japanese and Australian stocks of *Theileria* may differ phenotypically (Sugimoto *et al.*, 1991) and biochemically (Sugimoto *et al.*, 1992). However, it is unfortunate that different methods were employed to maintain these stocks in the laboratory. In the genus, *Babesia*, it has been demonstrated that different methods of maintenance can influence parasite morphology (Stewart *et al.*, 1986) as well as protein and antigen profiles (Kahl *et al.*, 1983; Timms *et al.*, 1990). Similar phenomena may have arisen during the studies of Sugimoto *et al.* (1991) and Sugimoto *et al.* (1992) due to the different methods of parasite maintenance employed. As new criteria become available at the genetic level to distinguish species of *Theileria* the situation should become clearer. Kawazu *et al.* (1992a, b) demonstrated genomic and antigenic differences between *T. sergenti*, *T. buffeli* and *T. orientalis*. Allsopp *et al.* (1993) also used biotechnological techniques to demonstrate differences between several species of *Theileria* occurring in Africa. This work is encouraging and warrants further investigation. However, until more evidence becomes available we conclude that there is no reason for the time being for distinguishing more than one species in this benign group of theilerial parasites and that it should be called *T. buffeli.*

Theileria tachyglossi

The first report of parasites of the genus *Theileria* infecting Australian native animals was given by Priestley (1915). He described parasites closely resembling *T. parva* in the blood of the echidna (*Tachyglossus aculeatus*), and proposed the name *T. tachyglossi*. Priestly (1915) observed that an echidna infected with *T. tachyglossi* was heavily infested with ticks identified as *Aponomma decorosum*. Subsequently, Mackerras (1959) suggested that *A. decorosum* and *Aponomma hydrosauri* were possible vectors of *T. tachyglossi*, but this remains to be confirmed.

Very little is known of the life-cycle of *T. tachyglossi* in the vertebrate host. However, Priestley (1915) described piroplasms in erythrocytes and schizonts in the liver, spleen and lungs, leaving little doubt that this parasite belongs in the genus *Theileria*. The pathogenicity of this parasite has never been studied in detail but it was believed to be associated with the death of 12 echidnas in Taronga Park Zoological Gardens, Sydney (Backhouse and Bolliger, 1957).

Theileria ornithorhynchi

Mackerras (1959) observed intraerythrocytic piroplasms in blood films from platypuses (*Ornithorhynchus anatinus*) from 2 different areas of Queensland and named this parasite *T. ornithorhynchi*. The development cycle of *T. ornithorhynchi* in the platypus is unknown. Mackerras (1959) failed to find schizonts either in blood films or in sections of liver, spleen and lung. Nevertheless Mackerras (1959) believed *T. ornithorhynchi* to be a *Theileria*, different from *T. tachyglossi*, and suggested *Ixodes ornithorhynchi* may be a vector. Collins *et al.* (1986) also considered that it could be a *Theileria*, their reasons being the presence of a cytostome within the piroplasm, similar ultrastructure to other species of *Theileria* and the presence of possible pre-schizont stages within white blood cells. It is not known if this parasite is capable of causing disease, and there is little likelihood of its pathogenicity being investigated because of the highly protected status of the host. In the absence of conclusive evidence for a schizont stage in *T. ornithorhynchi*, inclusion of this species in the genus *Theileria* must be tentative.

Theileria peramelis

A species of *Theileria* of bandicoots was first observed in *Thylacis abesulus* (= *Isoodon* *macrourus*) and *Perameles nasuta* by Mackerras *et al.* (1953) and later named *T. peramelis* by Mackerras (1959). Mackerras (1959) did not detect schizonts but found indications of marked destruction of red blood cells and anaemia, including anisocytosis, polychromasia and nucleated red cells. In a more recent study Weilgama (1979) claimed to have successfully transmitted *T. peramelis* with *Ixodes tasmani.* However, the evidence presented is not convincing because the splenectomised bandicoots used as recipients were not tested serologically for infection before the experiments and experienced only low parasitaemias. Since no schizonts were observed, it is possible that splenectomy induced a patent relapse of a pre-existing, chronic infection. Piroplasms in the type specimen of *T. peramelis* held at the Queensland Museum, Brisbane, Australia observed by one of the authors (N. P. Stewart) had morphological similarities to other species of *Theileria.* However, until a schizont stage is conclusively demonstrated, there currently appears to be no justification to classify this parasite within the genus.

We conclude that of the *Theileria* spp. reported from monotremes and marsupials only *T. tachyglossi* can presently be included in the genus *Theileria.* The authors are aware of the problems associated with observing parasites in native animals. The lack of information in the literature confirms this point. However, more work is required in order to determine the taxonomy and pathogenicity of the parasites infecting monotremes and marsupials. In our experience, the parasite previously referred to as *T. peramelis* is probably pathogenic and thus warrants further investigation.

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REVUE DES ESPECES AUSTRALIENNES DE *THEILERIA* AVEC UNE ETUDE PARTICULIERE DE *THEILERIA BUFFELI* PRESENTE CHEZ LE BETAIL

Résumé–Cette revue décrit les 4 espèces de parasites considérées habituellement comme des *Theileria* en Australie. Les caractéristiques physiologiques et épidémiologiques de ces espèces, présentes chez le bétail, sont ici discutées. La relation entre ces espèces et des espèces bénignes de *Theileria* dans d'autres pays reste confuse. Des arguments sont présentés en faveur du fait que l'espèce bovine en Australie est correctement identifiée comme *Theileria buffeli* et que ce nom devrait être utilisé pour les espèces bénignes de *Theileria* chez le bétail en Eurasie. Les 3 autres espèces présentées dans la revue sont des espèces proposées issues de Marsupiaux. Parmi ces dernières, seule *Theileria tachyglossi* peut être inclus dans le genre *Theileria*, car des schizontes doivent être observés pour les 2 autres espèces.

REVISION DE LAS ESPECIES AUSTRALIANAS DEL GENERO *THEILERIA* CON ESPECIAL REFERENCIA A *THEILERIA BUFFELI* DEL GANADO VACUNO

Resumen–Este artículo describe las 4 especies de parásitos incluídas normalmente en el género *Theileria* que se encuentran en Australia. Se discuten las características fisiológical y epidemiológicas de las especies que infestan el ganado vacuno. Existe todavía confusión acerca de la relación de dichas especies con otras especies benignas del mismo género que se encuentran en otros paises. Se presentan argumentos que apoyan la opinión de que la especie que se encuentra en el ganado vacuno en Australia debe designarse como *Theileria buffeli* y que este nombre debería aplicarse también a todas las especies benignas de *Theileria* que se encuentran en el ganado vacuno en Eurasia. Las otras 3 especies que se proponen en este artículo se encuentran en animales marsupiales. De todas ellas, sólo la especie *Theileria tachyglossi* puede ser incluída con certeza en el género *Theileria*, puesto que todavía no se han detectado esquizontes en las otras dos.