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CAUSAL AGENTS OF BOVINE THEILERIOSIS IN SOUTHERN AFRICA

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SUMMARY

One pathogenic and 4 mild bovine Theileria *strains from southern Africa, all transmitted by* Rhipicephalus appendiculatus, *were compared amongst themselves as well as to bovine and buffalo strains of the* T. parva *complex from eastern and southern Africa and to bovine strains of* T. taurotragi *from Tanzania considered to be derived from eland antelope. Criteria used were parasitological, clinical, serological and cross-immunity characters.*

The mild strains are similar to bovine T. taurotragi. *Serological evidence suggested that* T. taurotragi *is also infective to sheep. The pathogenic strain belongs to the* T. parva *complex; the latter consists of a series of types with different behaviour ranging from the* lawrencei-*type (of buffalo) causing Corridor disease, through the* bovis-*type causing Rhodesian malignant theileriosis to the* parva-*type causing classical East Coat fever. Seven cattle-tick passages of a* bovis-*type strain did not result in transformation into a* parva-*type.*

Four species of bovine Theileriae *are now known to occur in southern Africa:* T. parva (lawrencei- *and* bovis-*types) and* T. taurotragi, *both transmitted by* R. appendiculatus, *and* T. mutans *and* T. velifera *both with* Amblyomma *spp. as vectors.*

INTRODUCTION

In Africa south of the Sahara there has recently been considerable development in our knowledge of the taxonomic relationships of the *Theileria* spp. involved in bovine theileriosis. In the work described here the opportunity has been taken to compare 5 isolates of *Theileria* spp. recently isolated in southern Africa with characterised strains of *Theileria* spp. of buffalo and cattle from South, Central and East Africa.

MATERIALS AND METHODS

Theileria strains

Theileria spp. from Zimbabwe. Three mild strains (Lawfield, Chiltington and McIlwaine) isolated by Lawrence and MacKenzie (1980).

Theileria sp. (Tzaneen). Isolated from ticks off the vegetation in farms in the Tzaneen area, northern Transvaal, Republic of South Africa (A. J. de Vos, unpub.)

Theileria sp. (Boleni). Isolated from a bovine animal on the Boleni farm in Zimbabwe where there had been a severe outbreak of theileriosis (Lawrence and MacKenzie, 1980).

These strains were compared to:

T. taurotragi. Two strains (Idobogo and Mwanza) isolated from cattle in Tanzania (Uilenberg, Schreuder, Mpangala and Tondeur, 1977).

T. parva. Six strains isolated from classical East Coast fever (ECF) in cattle: the Muguga strain from Kenya (Brocklesby, Barnett and Scott, 1961), the Kiambu 5 strain from Kenya isolated by Irvin, Purnell, Brown, Cunningham, Leger and Payne, (1974), the Pugu 1 and Pugu 3 strains isolated during field trials in Tanzania (Uilenberg, Schreuder, Mpangala, Silayo, Tondeur, Tatchell and Sanga, 1978), the Schoonspruit strain from South Africa (isolated in 1936 and maintained since then by over 100 cattle-tick passages at Onderstepoort) and a strain which we designate as Uganda 1 isolated in north-western Uganda in 1976 by L. Siefert (unpub.).[5]

T. bovis (Nyakizu) from Rwanda isolated from a case of bovine theileriosis by R. W. Paling.

T. lawrencei isolated from buffaloes in Tanzania: the Manyara strain (Schreuder, Uilenberg and Tondeur, 1977) which causes classical Corridor disease and the Serengeti "transformed" strain which has been adapted to cattle in the laboratory (Purnell, Young, Brown, Burridge and Payne, 1974).

All strains arrived in Utrecht in infected *R. appendiculatus.* Cattle were infected either by subcutaneous injection of sporozoite stabilates from ground-up ticks preserved in liquid nitrogen (Cunningham, Brown, Burridge and Purnell, 1973) or by feeding infected *R. appendiculatus* on the ears in cloth bags. In all cases nymphal ticks were used to acquire the infection resulting in infective adults.

Strains were compared on parasitological, clinical and serological behaviour. They were also tested in cross-immunity experiments in calves spontaneously recovered or immunised by an infection and treatment method using oxytetracycline (Radley, Brown, Burridge, Cunningham, Kirimi, Purnell and Young, 1975) or halofuginone (Schein and Voigt, 1979; Uilenberg, Jongejan and Perié, 1980). The minimum interval between initial infection and challenge was a month.

Ticks

Rhipicephalus appendiculatus. Six strains from Tanzania, Kenya, Zimbabwe, South Africa and Rwanda. One of these was the Kenyan Burguret strain (Lourens, 1979) of which males have abnormally shaped adanal shields and which appears to be of low vitality; this is possibly due to a mutation.

All tick strains at Utrecht were maintained by feeding on the ears of cattle and rabbits. Oviposition, hatching and moulting were carried out at 27°C and 90% relative humidity (rh), quiescent stages being kept at 20°C and 90% rh.

Experimental ruminants

Friesian calves weighing 100 to 200 kg were obtained at markets in the central Netherlands. Some were splenectomised prior to the experiments and corticosteriods were administered to suppress immunity. A sheep of the Texel breed bought at Utrecht was also used; it was splenectomised.

The animals on experiment were monitored by taking the rectal temperature daily and by examining blood smears and lymph node biopsy smears, first of the regional parotid node draining the site of infection once it started to enlarge; then when schizonts were found of both parotid and prescapular nodes. Blood and lymph node smears were taken 5 to 7 days a week. All smears were fixed in methanol and stained in Giemsa's stain. Calves were bled once a week for serum for serological testing.

[5] This Ugandan strain has been erroneously described as originating from Entebbe by Uilenberg and Zwart (1979).

TABLE I

Parasitological and clinical observations. Mild strains

Theileria strain	Animal[1] no.	Method of infection	Schizonts[2] 1st day, highest number	Piroplasms[3] 1st day, %, peak	Remarks[4]
Lawfield	295	Ticks	17 +	21, 0·1% (22–25)	Recovered after temporary alarming symptoms
	297 (s)	Ticks	16 (+)	48, 1% (91–98)	Prednisolone acetate 2 mg/kg, i.m., days 23 and 25
	305 (s)	Ticks	17 (+)	28, 5% (80–87)	
	327 (s)	Stabilate	13 (+)	21, <0·1% (40)	
Chiltington	311 (s)	Ticks	11 ++	35, 5% (68–83)	
	308	Stabilate	14 (+)	15, 1% (17–21)	Recovered after marked clinical symptoms
	321	Stabilate	– –	15, 0·5% (35)	Scanty schizonts in peripheral blood day 14, none found in lymph nodes Mild clinical symptoms
	322 (s)	Blood i.v.[5]	– –	17, 1% (32)	
McIlwaine	306 (s)	Ticks	14 ++	17, 1% (41–97)	
	320 (s)	Stabilate	16 (+)	25, 0·5% (51)	
Tzaneen	333 (s)	Ticks	12 (+)	19, 1% (34)	
	330 (s)	Stabilate	14 (+)	15, 0·5% (42–53)	
	352 (s)	Stabilate	13 (+)	– – –	Died day 16 with high parasitaemia of *Eperythrozoon wenyoni* since day 12
	355 (s)	Stabilate	– –	17, 2% (37–38)	
T. taurotragi (Idobogo)	278	Ticks	15 ++	19, 0·5% (25)	
	287	Ticks	10 +	20, 1% (53–73)	
	275 (s)	Stabilate	– –	30, <0·1% (?)	No recognisable peak parasitaemia
	326 (s)	Stabilate	– –	17, 0·5% (63)	Dexamethason Na-phosphate 0·2 mg/kg i.m. daily, days 31–36
T. taurotragi (Mwanza)	280	Ticks	15 (+)	– – –	280 was not infective to ticks

[1] (s) splenectomised.

[2] First day after infection when schizonts were detected in regional lymph node. (+), scanty; +, fairly numerous; ++, numerous; +++, very numerous. These symbols refer to the maximum number reached in 1 or more lymph nodes.

[3] First day after infection when piroplasms were detected in blood with approximate maximum percentage of infected red cells and day(s) after infection when the parasitaemia was at this peak.

[4] Mild infections, followed by recovery, in all animals, except where otherwise indicated.

[5] 90 ml of blood from calf 311 with a parasitaemia of approximately 0·1% were injected intravenously into calf 322.

Serological test

The indirect fluorescent antibody test (IFAT) was used to detect antibodies to *Theileria.* Both piroplasm antigen (Burridge, 1971) and cell culture grown schizont antigen (Burridge and Kimber, 1972) derived from various strains were used for *T. parva;* only piroplasm antigen was prepared of *T. taurotragi* (Idobogo) and from each of the strains Lawfield, Chiltington, McIlwaine and Tzaneen. Only schizont antigen of *Theileria* sp. (Boleni) was used. Serum dilutions were 2-fold starting from 1:40.

RESULTS

Mild strains

The Lawfield, Chiltington, McIlwaine and Tzaneen strains proved to be benign parasites (Table I). Apart from 1 splenectomised calf which died of intercurrent infection with *Eperythrozoon wenyoni* all animals recovered spontaneously. Only 2 out of 14 showed temporarily alarming clinical symptoms of theileriosis. Hyperthermia was invariably present during the period that schizonts were found, with a maximum of about 40°C only (range 39·5–40·6°C) and subsequently subsided. The type of infection resembled that seen in animals reacting to bovine *T. taurotragi* (Table I) with low numbers of schizonts and piroplasms. Schizonts and piroplasms appeared on average later than in *T. parva* infections and the peak parasitaemia was often considerably delayed and prolonged. Neither splenectomy nor synthetic immuno-

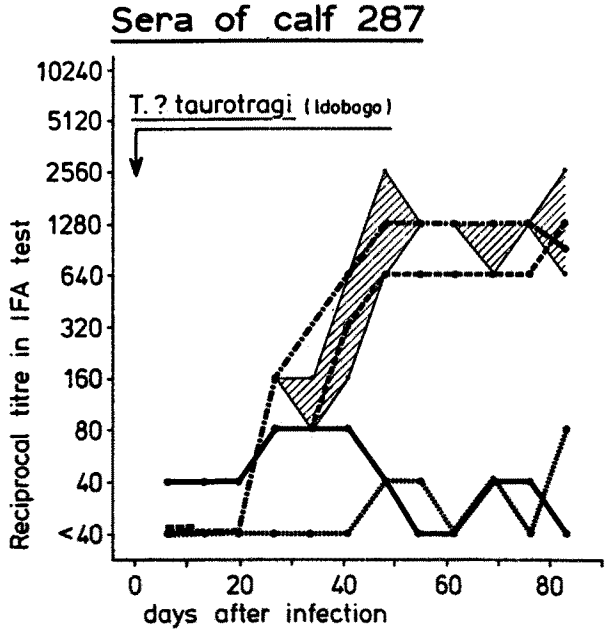

FIG. 1

FIGS 1 to 6. ——— *T. parva* piroplasm antigen; ——— *T. parva* schizont antigen; ------ *T. taurotragi* Idobogo piroplasm antigen; ·-·-·-Tzaneen antigen; ——— Lawfield antigen (Fig. 5 only) ------McIlwaine antigen (Fig. 5 only); ZZZZZ Field covered by combined results of antigens of the 3 Rhodesian strains, Lawfield, Chiltington and McIlwaine. (Except Fig. 4, as no Chiltington antigen was available any more for sera of animal 333.)

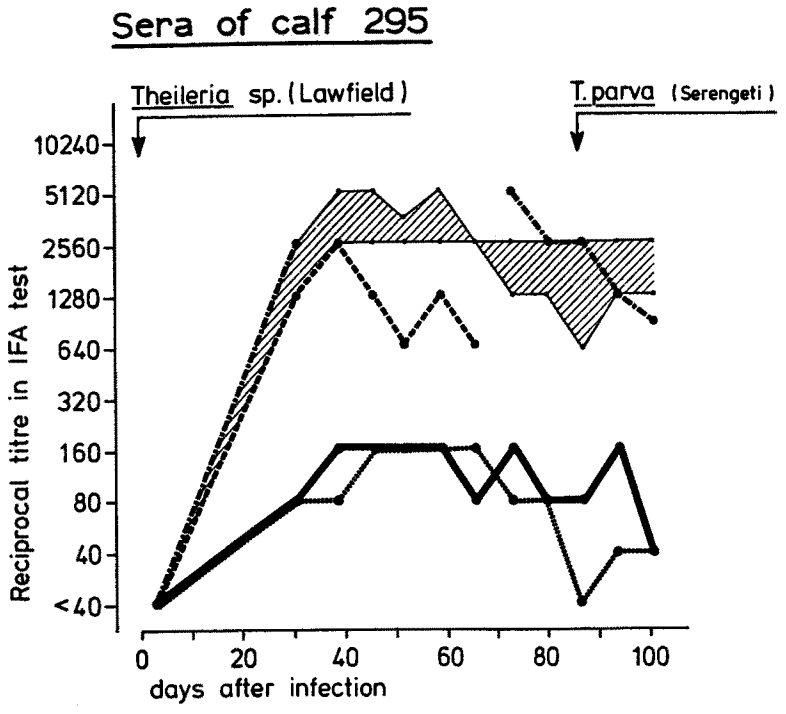
Sera of calf 295
Theileria sp. (Lawfield)
T. parva (Serengeti)
10240
5120
2560
1280
640
320
160
80
40
<40
Reciprocal titre in IFA test
0
20
40
60
80
100
days after infection

FIG. 2

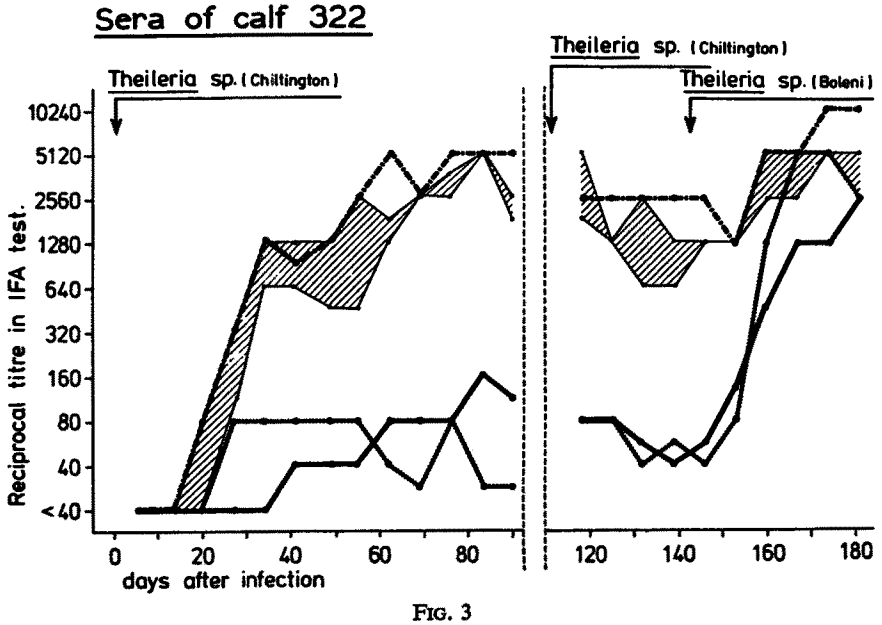
Sera of calf 322
Theileria sp. (Chiltington)
Theileria sp. (Chiltington)
Theileria sp. (Boleni)
10240
5120
2560
1280
640
320
160
80
40
<40
Reciprocal titre in IFA test.
0
20
40
60
80
120
140
160
180
days after infection

FIG. 3

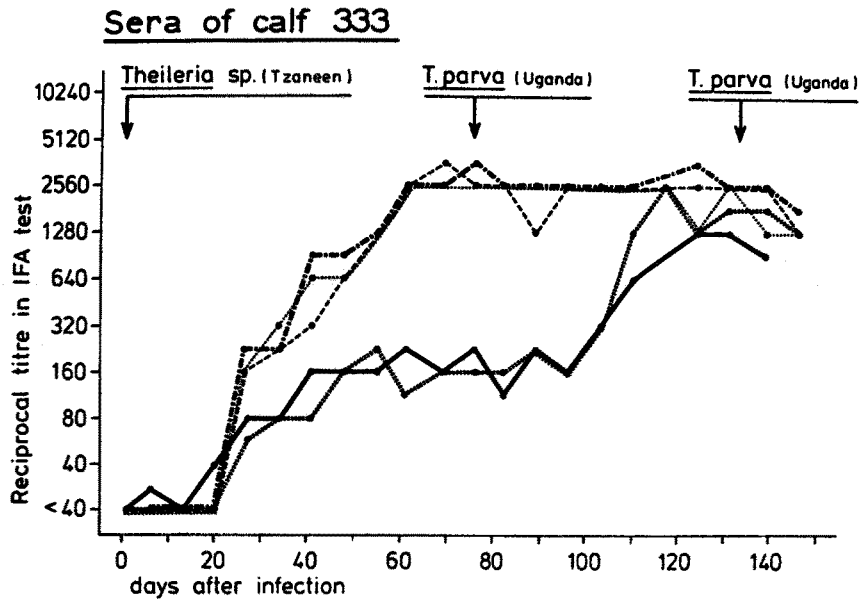
Sera of calf 333
Theileria sp. (Tzaneen)
T. parva (Uganda)
T. parva (Uganda)
Reciprocal titre in IFA test
10240
5120
2560
1280
640
320
160
80
40
< 40
0
20
40
60
80
100
120
140
days after infection

FIG. 4

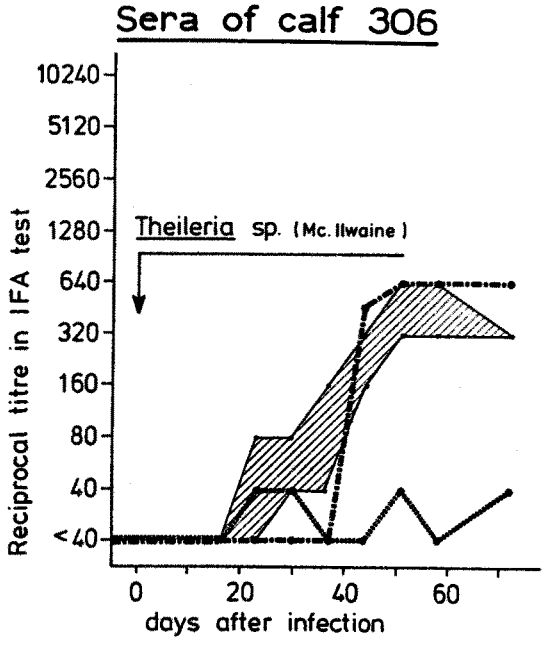
Sera of calf 306
Theileria sp. (Mc. Ilwaine)
Reciprocal titre in IFA test
10240
5120
2560
1280
640
320
160
80
40
< 40
0
20
40
60
days after infection

FIG. 5

suppressive steroids appeared to influence the infection in a consistent way. The animals remained carriers, piroplasms being detectable in blood smears continuously or intermittently as long as observations were continued (from a few weeks to several months).

Microschizonts were not seen with certainty. Macroschizonts and piroplasms resembled those of *T. taurotragi* in cattle, macroschizonts being indistinguishable from small *T. parva* schizonts and piroplasms being predominantly round and oval with far less rod- and comma-shaped forms present than in *T. parva* infections. There was no intra-erythrocytic bar and/or veil, associated with the piroplasms.

The Lawfield, Chiltington, McIlwaine and Tzaneen strains were indistinguishable from *T. taurotragi* (Idobogo strain) in the IFAT (Figs 1–6). Antigens and antisera were fully cross-reactive. They were also similar in their reaction to *T. parva* antigens and sera. Antigens of all these strains reacted strongly with sera recovered from *T. parva* infection but sera from animals recovered from the Zimbabwean and South African strains showed only low titres to *T. parva* antigens.

Cross-immunity tests are summarised in Table II. Animal no. 308 immune to 2 strains of *T. parva* was fully susceptible to the Chiltington strain and showed clinical symptoms associated with this group of strains. Animal no. 326 recovered from *T. taurotragi* (Idobogo) was immune to challenge with the Chiltington strain. The experiments also confirmed the lack of protection against *T. parva* after recovery from the Tanzanian bovine strains of *T. taurotragi*. The 4 strains from Zimbabwe and South Africa were similar in this respect also, although 2 of the animals recovered from the Chiltington strain and 1 of those infected with the Tzaneen strain survived *T. parva* challenge (including 1 challenged with the Boleni strain which has proved to be *T. parva*).

A splenectomised sheep was infected with the Lawfield strain by subcutaneous injection with the tick-derived stabilate which had proved to be infective to a calf. Although the regional prescapular lymph node became swollen no schizonts were

TABLE II
Cross-immunity tests with mild strains[1]

Animal no.	Recovered from	Challenged with	Results
295	Lawfield	*T. parva* (Serengeti)	ECF, killed in extremis day 16
305	,,	*T. parva* (Pugu 1)	ECF, killed in extremis day 24
311	Chiltington	*T. parva* (Muguga)	ECF, killed in extremis day 23
321	,,	*T. parva* (Serengeti)	Severe ECF, recovered
322	,,	Boleni strain	Severe theileriosis, recovered
306	McIlwaine	*T. parva* (Muguga)	Died of ECF day 23
330	Tzaneen	*T. parva* (Uganda)	Died of ECF day 19
333	,,	*T. parva* (Uganda)	Very mild reaction, recovered
275	Idobogo	*T. parva* (Pugu 3)	Died of ECF day 24
287	,,	*T. parva* (Pugu 3)	ECF, killed in extremis day 24
326	,,	Chiltington strain	No reaction
326	Idobogo & Chiltington	Boleni strain	Died of theileriosis day 18
280	Mwanza	*T. parva* (Pugu 3)	Died of ECF day 26
308	*T. parva*[2]	Chiltington strain	Marked clinical symptoms, recovered

[1] All animals were challenged with stabilates of batches of which the infectivity had been proved in other animals except for 287 and the Boleni challenge of 326, where ticks were used.
[2] 308 had been immunised with the Pugu 1 and the Serengeti strains.

TABLE III
Parasitological and clinical observations. Boleni strain

Theileria strain	Passage no.[1]	Animal no.[2]	Schizonts[2] 1st day, highest number	Piroplasma[2] 1st day, highest number	Remarks[3]
Boleni	I	329 (s)	11 (+)	18, 1%	Died day 21
	II	324	9 +	?, 5%	Killed in extremis, day 34[4]
	II	322 (s)	13 +	?, <0·1%	Severe reaction, spontaneous recovery
	III	337	9 ++	16, 1%	Died day 20
	III	326 (s)	11 +++	18, 0·1%	Died day 18
	III	335	9 +++	14, 0·2%	Died day 14
	IV	341	7 +++	– –	Died day 13
	IV	343	9 +++	18, 0·1%	Died day 19
	V	350	10 (+)	17, 1%	Killed in extremis, day 22
	VI	363	12 ++	18, 0·1%	Killed in extremis, day 19
	VII	374	9 ++	14, 0·1%	Killed in extremis, day 21[5]

[1] Number of tick-cattle passages in Utrecht (see Fig. 7).
[2] See legend to Table I.
[3] All animals were infected by ticks apart from 322 and 335 which received stabilate.
[4] The first day of the parasitaemia could not de determined in these animals as they were patent, recovered carriers of other species of *Theileria*.
[5] Treated with halofuginone, 1 mg/kg, on day 14 which failed to prevent the fatal outcome.

TABLE IV
Serology of sheep infected with Lawfield strain

	Titre[1]
Before infection	<40
Weeks post-infection	
2	160
3	320
4	640
5	640–1280
6	640–1280
7	640
8	1280
9	640
10	80–160

[1] Reciprocal titre in IFAT using McIlwaine antigen.

found in biopsy smears made from day 8 to day 18 but abnormally high numbers of lymphoblastoid cells and of dividing cells were observed on days 12 and 13. No piroplasms were found in blood smears during an observation period of nearly 5 months. Serological evidence (Table IV) suggested, however, that the sheep had acquired a latent infection.

The Boleni strain

Fig 7 summarises the transmissions carried out with this strain excluding animals cured by oxytetracycline or halofuginone. It proved to be highly pathogenic causing fatal theileriosis in 10 out of 11 cattle (Table III). Rectal temperatures reached 41°C except in the animal that recovered (40·7°C) and persisted until the end. Piroplasm parasitaemia remained low while schizonts were numerous only in animals receiving the 3rd and 4th passage (Table III). Prepatent periods to schizonts were similar to those seen in animals infected with *T. parva*.

Schizonts resembled those of *T. parva* as did piroplasms the majority of which were rod-shaped, comma-shaped or oval. The Boleni strain proved indistinguishable from *T. parva* in the IFAT. Sera from animals recovered from infection by the Boleni strain gave high titres to *T. parva* antigens and schizont antigen of the Boleni strain reacted as strongly with *T. parva* sera as did *T. parva* schizont antigen. Cross-immunity tests confirmed the identity of the Boleni strain with *T. parva*. Animals recovered from Boleni infection did not react or reacted very mildly to challenge with the Muguga, Pugu 1 or Serengeti strains of *T. parva*. Challenge with the Boleni strain caused no or mild reactions in animals immunised against the Pugu 1, Muguga or Uganda strain. However, Boleni-recovered animals reacted severely to challenge with the Uganda or Nyakizu strain but these 2 strains also caused severe reactions in animals immune to the Schoonspruit, Muguga, Manyara, Pugu 1, or Kiambu strains of *T. parva*. Idobogo and Chiltington strains conferred no protection against Boleni challenge (Table II).

Seven cattle-tick passages of the Boleni strain were carried out between November 1978 and April 1980 (Fig. 7). The results are summarised in Table III, showing that, although the numbers of schizonts were higher in the 3rd and 4th passage, no consistent increase in piroplasm parasitaemia was achieved and the strain had not significantly changed its behaviour.

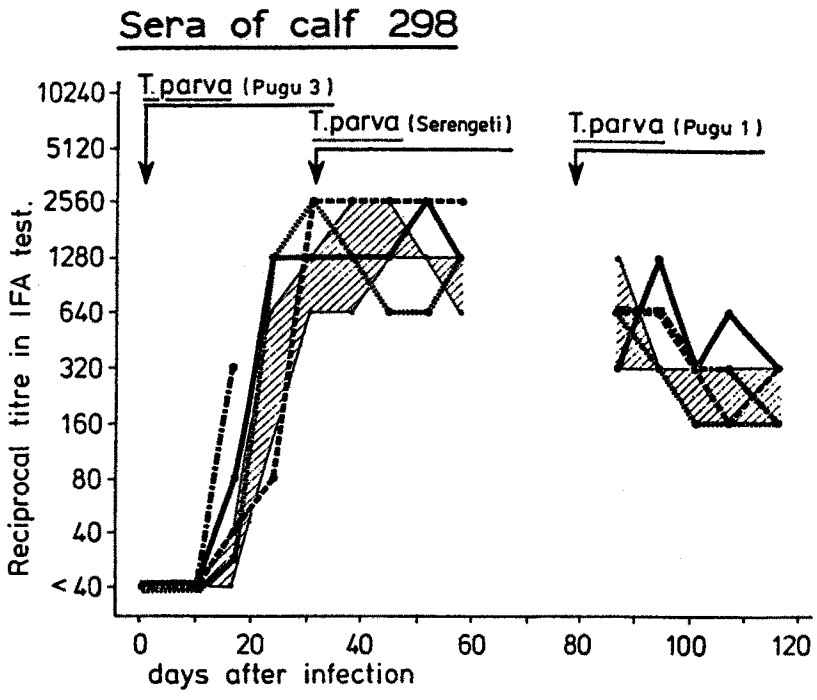

FIG. 6

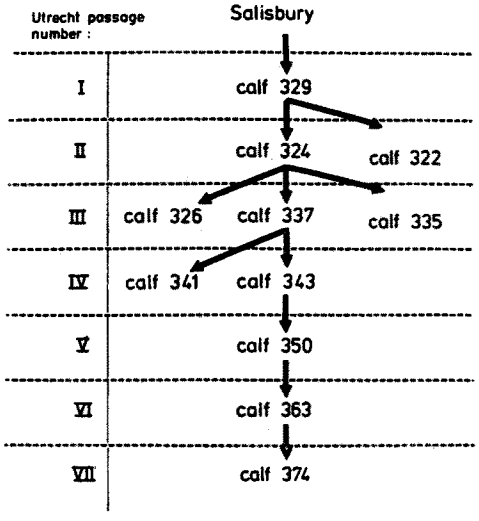

FIG 7. Tick-borne passages of Boleni strain.

DISCUSSION

To date there have been 6 causal agents of bovine theileriosis identified in southern Africa. *T. parva* was introduced into Rhodesia (now Zimbabwe) and South Africa in 1901. This parasite is transmitted between cattle by *R. appendiculatus* and causes ECF,

a disease manifested by the presence of large numbers of intra-lymphocytic schizonts and intra-erythrocytic piroplasms. In addition 2 closely related parasites also transmitted by *R. appendiculatus* have been recorded in southern Africa. *T. lawrencei* (Neitz, 1955) was described from South Africa having been first recognised in Southern Rhodesia by Lawrence in 1933 (Neitz, 1957). This was considered to be a parasite of buffalo (*Syncerus caffer*) transmissible to cattle in which few schizonts and rare piroplasms could be detected. The disease in cattle, Buffalo disease or Corridor disease, was always associated with the presence of buffalo, transmission between cattle rarely if ever being recorded. A third parasite *T. bovis*, able to maintain itself in cattle without contact with buffalo, causing the disease Rhodesian malignant theileriosis or January disease, was recognised by Lawrence in 1935 (Neitz, 1957). In this disease fewer schizonts and piroplasms are present than in ECF. *T. bovis* was, however, synonymised with *T. lawrencei* when it was discovered that the latter could be transmitted between cattle by Neitz, 1957, who also reported cross-immunity between *T. parva* and *T. lawrencei* and *T. bovis* respectively. Barnett and Brocklesby (1966) confirmed the immunological relationship between *T. parva* and *T. lawrencei* and were able to change the behaviour of *T. lawrencei* by cattle-tick passages so that it became indistinguishable from classical *T. parva*. Serological evidence (Burridge, Young, Stagg, Kanhai and Kimber, 1974) confirmed the identity of the 2. Accordingly Uilenberg (1976) proposed that *T. parva* and *T. lawrencei* should be considered as biological subspecies and Lawrence (1979) added *T. bovis* as a third candidate subspecies, *viz. T. parva parva*, *T. parva lawrencei* and *T. parva bovis*.

Another theilerial species *T. mutans* was described in South Africa as being benign and readily transmissible by blood inoculation (Theiler, 1906). What was thought to be *T. mutans* was subsequently transmitted by *R. appendiculatus* (Theiler, 1909) but it was later found that a parasite similar to that originally described as *T. mutans* was transmitted by species of *Amblyomma: A. variegatum* (Uilenberg, Robson and Pedersen, 1974), *A. cohaerens* (Young, Burridge and Payne, 1977), *A. gemma* (Paling, Grootenhuis and Young, 1981) and *A. hebraeum* (de Vos and Roos, 1981); this parasite could not be transmitted by *R. appendiculatus*. However, the benign theilerial strains from Zimbabwe and South Africa, which we have shown in this paper to be similar to the Idobogo strain of *T. taurotragi*, are transmissible by *R. appendiculatus* but not *A. hebraeum* (A. J. de Vos, unpub; Lawrence and MacKenzie, 1980).

Another non-pathogenic theilerial species, *T. velifera* (Uilenberg, 1964), widely distributed in Africa south of the Sahara has recently been found to occur in South Africa (Berger, 1979) and Mozambique (Vilhena and Arnold, in press). This parasite is transmitted by at least 3 *Amblyomma* spp.: *A. variegatum* (Uilenberg and Schreuder, 1976), *A. hebraeum* (Schein and Uilenberg, in van Vorstenbosch, Uilenberg and van Dijk, 1978) and *A. lepidum* Dönitz, 1909 (Uilenberg in van Vorstenbosch *et al*, 1978).

All results of the comparative studies of the Lawfield, Chiltington and McIlwaine strains from Zimbabwe and the Tzaneen strain from South Africa show their specific identity with the Tanzanian Idobogo strain for which the name *T. taurotragi* appears to be justified. It could be argued that the correct name for these parasites is in fact *T. mutans* as it was thought since 1909 that *T. mutans* was transmitted by *Rhipicephalus* spp. The *Amblyomma*-transmitted *Theileria* should then be given a new name and the eland *Theileria* would have to be designated as *T. mutans* instead of *T. taurotragi*. However, Theiler (1906) described *T. mutans* as readily transmissible to intact cattle by blood inoculation and as causing anaemia. These characteristics apply to the *Amblyomma*-transmitted parasite not to the *Rhipicephalus*-transmitted strains. Although we did transmit the Chiltington strain once by intravenous injection of

blood to a splenectomised animal (Table I), an attempt by J. A. Lawrence to transmit the Lawfield strain with blood to a splenectomised calf failed and de Vos was unable to induce patent infection in intact cattle by blood inoculation with the Tzaneen strain. The *Amblyomma*-transmitted strains produce readily detectable parasitaemias in intact cattle following blood inoculation even when the subcutaneous route is used; peak parasitaemia commonly reaches 1% or more in intact animals and usually at least 10% in splenectomised cattle. Furthermore the *Amblyomma*-transmitted parasites often cause anaemia even in intact cattle contrary to those having *Rhipicephalus* ticks as vectors.

T. taurotragi may be to some extent related to *T. parva* considering their partial serological relationship, their transmission by the same vector and the morphological similarity of the macroschizonts. Their differences are immunological (absence of cross-immunity), serological (partial), differences in the infection rate in the vector and in the developmental cycle in the tick (Young, Grootenhuis, Leitch and Schein, 1980), morphological (more rod- and comma-shaped piroplasms in *T. parva*) as well as differences in the infectivity for the eland. This antelope has so far not been shown to be susceptible to *T. parva* although the few experiments reported in the literature Grootenhuis, 1979) are certainly not conclusive and were not done with eland born and bred in tick-free conditions.

T. taurotragi has in our single experiment caused latent infection in a splenectomised sheep, an observation which confirms Neitz' (1957) findings.

Theileria sp. (Boleni) is undoubtedly a strain of *T. parva* with characteristics intermediate between those of the classical *parva*-type (ECF) and those of the buffalo-associated *lawrencei*-type (Corridor disease).[6] Dr S. F. Barnett (pers. comm.) suggested that rapid tick-cattle passages may be necessary for full transformation of such intermediate *bovis*-type strains and that the reason why such strains do not further transform in southern Africa may be that the vector only undergoes 1 developmental cycle per year so that there is only 1 annual passage of the parasite. Nearer to the equator *R. appendiculatus* produces more than 1 generation annually and tick-cattle passages occur more frequently. It should be remembered of course that classical ECF was introduced into southern Africa from equatorial regions although buffalo and possibly the *lawrencei*-type of *T. parva* were present in southern Africa long before that. So far seven rapid passages have not appeared to change the characters of the Boleni strain.

The strain of *R. appendiculatus* did not appear to have any significant influence in our experiment on the evolution and the severity of different theilerial strains. Moreover as southern strains of *R. appendiculatus* have shown themselves for more than half a century to be effective vectors of introduced classical East African ECF and as Corridor disease as well as the *bovis*-type of strain (Nyakizu) are maintained in the equatorial regions by the local strains of tick, it is unlikely that particular types of *T. parva* are associated with and influenced by different vector strains. The aberrant Burguret strain also proved capable of transmitting *T. parva*. Apart from the fact that we know that a *lawrencei*-type of strain can be adapted to cattle we do not yet know how stable the behaviour is of different types of such adapted strains. We do believe that one should keep in mind that wherever strains of the *lawrencei*- or *bovis*-types occur the possibility of classical ECF re-emerging spontaneously cannot be ruled out.

[6] In evaluating the type of strain one should take into account the existence of very virulent strains of classical *parva*-type which may kill their host too quickly for the parasites to become numerous and thus may on occasion simulate *bovis*- or even *lawrencei*-types of strain.

CONCLUSION

At the moment we distinguish in Zimbabwe and South Africa the following theilerial parasites of cattle:

Theileria spp.	Main local vectors
T. parva (*lawrencei*- and *bovis*-types)	*R. appendiculatus*
T. taurotragi	*R. appendiculatus*
T. mutans	*A. hebraeum*, *A. variegatum*
T. velifera	*A. hebraeum*, *A. variegatum*

Of the 5 parasites isolated from southern Africa, in this study the Boleni strain from Zimbabwe would be classified as *T. parva* (*bovis*) and the Lawfield, Chiltington and McIlwaine strains from Zimbabwe and the Tzaneen strain from South Africa as *T. taurotragi*.

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AGENT DE LA THEILERIOSE BOVINE EN AFRIQUE AUSTRALE

Résumé—Une souche pathogène et quatre souches bovines bénignes de *Theileria* d'Afrique australe, toutes transmises par *Rhipicephalus appendiculatus* ont été comparées entre elles, puis avec des souches de bovins et de buffles du complexe de *T. parva* de l'Afrique australe et orientale et enfin avec des souches bovines de *T. taurotragi* de Tanzanie considérées comme originaires de l'Elan du Cap. Les critères utilisés ont été d'ordre parasitologique, clinique, sérologique avec recherche des caractères d'immunité-croisée.

Les souches bénignes sont similaires à *T. taurotragi*. La sérologie a suggéreré que *T. taurotragi* est également infectieuse chez le mouton. La souche pathogène appartient au complexe de *T. parva* ; ce complexe consiste en une série de types présentant divers comportements depuis le type *lawrencei* du buffle causant l'affection "Corridor", et le type *bovis* cause de la theileriose maligne de Rhodésie jusqu'au type "*parva*" cause de l'East Coast Fever classique. 7 passages bétail-tique d'une souche de type *bovis* n'ont pas réussi à la transformer en type *parva*. 4 espèces de Theileries bovines sont maintenant connues en Afrique australe : *T. parva* (types *lawrencei* et *bovis*) et *T. taurotragi* toutes deux transmises par *R. appendiculatus*, *T. mutans* et *T. velifera* avec toutes deux *Amblyomma* spp. comme vecteurs.

AGENTES CAUSALES DE THEILERIOSIS EN EL SUR DE AFRICA

Resumen—Se compararon 5 cepas de *Theileria* del sur de Africa, 1 patógena y 4 benignas, todas transmitidas por *Rhipicephalus appendiculatus*, entre si y también con cepas derivadas de bovinos y búfalos, del complejo *T. parva*, del sur y este de Africa, y con cepas bovinas de *T. taurotragi* de Tanzania derivadas de antílope eland. Los criterios de evaluación utilizados fueron parasitológico, clínico, serológico, utilizando también los caracteres de inmunidad cruzada.

Las cepas benignas son similares a *T. taurotragi* de bovinos. Las pruebas serológicas indicaron que esta última es también infectiva para ovejas. Las cepas patógenas pertenecen al complejo *T. parva;* este último consiste de un rango de tipos con diferente comportamiento que van desde el tipo *lawrencei* (búfalo) que causa la enfermedad Corridor, a través del tipo *bovis* que causa la theileriosis maligna de Rodesia, hasta el tipo *parva* que causa la típica Fiebre de la Costa Este. Siete pasajes a través de bovinos y garrapatas de un tipo *bovis*, no produjo transformación alguna al tipo *parva*.

Se conocen entonces 4 especies de *Theileriae* bovina en el sur de Africa: *T. parva* (tipos *lawrencei* y *bovis*) y *T. taurotragi*, ambas transmitidas por *R. appendiculatus*, y *T. mutans* y *T. velifera*, ambas transmitidas por *Amblyomma* spp.