DESCRIPTION OF *HAEMONCHUS PLACEI* (PLACE, 1893) (NEMATODA, TRICHOSTRONGYLIDAE, HAEMONCHINAE), IDENTIFICATION AND INTRA-SPECIFIC MORPHOLOGIC VARIABILITY

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Summary :

Haemonchus placei in cattle has never been completely described, possibly due to great morphological similarity with small ruminants *Haemonchus contortus*. It is newly described on one isolate from Argentina. It has clear distinct morphological features from sheep and goats *Haemonchus contortus* and presents only two female morphotypes (linguiform and knobbed) instead of three recorded in *H. contortus*. A key is proposed to identify females. Female as well as male *Haemonchus placei* from New World (Argentina, Mexico, USA) are morphologically different from those of Old World (Africa: Burkina-Faso, Mauritania and Ivory Coast) or Australia, possibly due to local evolution since their introduction several centuries ago from Africa or India. We propose to differentiate three sub-species, *H. placei placei* in Australia, *H. placei africanus* in western Africa and *H. placei argentinensis* in the New World.

KEY WORDS : *Haemonchus placei*, description, *Haemonchus contortus*, identification, morphologic variability, subspecies.

Résumé : *HAEMONCHUS PLACEI* (PLACE, 1893) (NEMATODA, TRICHOSTRONGYLIDAE, HAEMONCHINAE), DESCRIPTION ET VARIABILITÉ MORPHOLOGIQUE INTRA-SPÉCIFIQUE

Haemonchus placei chez les bovins n'a jamais été complètement décrit, sans doute en raison de grandes similitudes morphologiques avec *Haemonchus contortus* des petits ruminants. Il est ici décrit chez un isolat d'origine argentine. Il a des traits morphologiques différents de ceux d'*H. contortus* parasite d'ovins et de caprins; seuls deux morphotypes femelles (linguiforme et boutoné) sont recensés au lieu de trois chez *H. contortus*. Une clé est proposée pour la diagnose des femelles. Les mâles ainsi que les femelles sont morphométriquement différents entre le Nouveau Monde (Argentine, Mexique et USA) et le Vieux Monde (Afrique: Burkina-Faso, Côte-d'Ivoire et Mauritanie) et l'Australie. Nous proposons d'en faire trois sous-espèces, *H. placei placei* pour l'Australie, *H. placei africanus* en Afrique de l'Ouest et *H. placei argentinensis* pour le nouveau Monde. Ces différences entre les trois sous-espèces sont probablement le résultat d'adaptations locales d'*H. placei placei*, après son introduction il y a plusieurs siècles de l'Afrique ou de l'Inde.

MOTS CLÉS : *Haemonchus placei*, description, *Haemonchus contortus*, diagnose, variabilité morphologique, sous-espèces.

INTRODUCTION

The abomasal worms *Haemonchus placei* and *Haemonchus contortus*, are important parasites of domestic ruminants world-wide. *Haemonchus placei* infects primarily cattle, whereas *H. contortus* is mainly a parasite of sheep, but the two species are sympatric in several parts of the world. The absence of strict specificity (Jacquet *et al.*, 1998) indicates need for ways to identify these two species as they might be found together in small ruminants or cattle. *Haemonchus contortus* was described by Rudolphi (1803) from ovine. Place (1893) named the strongylid-like nematodes he found in the abomasum

of calves suffering from anemic diarrhea as *Strongylus placei* in Southern Australia (Adelaide). Ransom (1911) changed the name of *Strongylus placei* to *Haemonchus placei*. Later, Gibbons (1979) regarded this species as a synonym of *H. contortus* adding to the confusion. Numerous investigations have differentiated the two species. Bremner (1955, 1956) examined the ovine and bovine species of *Haemonchus* spp. and found that the chromosome number for both was $2n = 11$ in the male and $2n = 12$ in the female; he also reported that in the sheep species all the chromosomes were of similar size, whereas in the cattle species the male had two very large chromosomes. Molecular evidence likewise suggests that *H. placei* and *H. contortus* are distinct species (Christensen *et al.*, 1994; Zarlenga *et al.*, 1994; Stevenson *et al.*, 1995; Blouin *et al.*, 1997). Interbreeding experiments (Le Jambre, 1979) have demonstrated that they are distinct species. Roberts *et al.* (1954), Lichtenfels *et al.* (1988, 1994) found that cattle and sheep *Haemonchus* spp. were different in the mean length of the spicules and the position of the barbs on these

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spicules. Jacquet *et al.* (1997, 1998) differentiated *H. placei* and *H. contortus* using discriminant functions based on spicules length. The percentage of body length covered by synlophe (pattern of surface cuticular ridges) was a criterion used by Lichtenfels *et al.* (1986, 1994).

Three main variants of *Haemonchus* spp. vulval types have been recorded, i.e., those with a linguiform process, those with a knoblike projection, and those with no vulval projection (Chitwood, 1957). Our own unpublished data (morphological and molecular) in *H. placei* showed that only two types of females are found: linguiform and knobbed, which agrees with the proportions of morphotypes in natural infections already published (Roberts *et al.* 1954; Tod, 1965).

The original description of Place (1893) in Australia was very limited, and no type specimens were deposited, and later, further additional characters were mentioned only to identify *H. placei* from *H. contortus* males or females, but no full description of *H. placei* is available. This is the first aim of the paper. The other objective is to study morphometric variability between Australian, African and New World *H. placei*, as all cattle has been introduced from Africa to the New World centuries ago (Curasson, 1934) or from South Africa or India to Australia in the last century.

MATERIALS AND METHODS

HAEMONCHUS PLACEI IDENTIFICATION

Males

The available discriminant function for males based on spicule morphology was used (Jacquet *et al.*, 1997) as well as the length of body covered with synlophe (Lichtenfels *et al.*, 1994) which extended from 38 to 46 % (Argentina I) corresponding typically to *H. placei*.

Females

Three parameters were used to differentiate females of *Haemonchus placei* from those of *Haemonchus contortus*: the distance of anus to tail's tip, the width of tail and the proportion of the nematode body length covered by synlophe. The measurements were performed on four isolates (20 females for each one) of *Haemonchus contortus*: sheep isolate Zaire (Bunia, Ituri), sheep isolate France (Toulouse), goat isolate Caribbean (Guadeloupe), sheep and goat isolate Malaysia (Selangor), and seven isolates of *Haemonchus placei* (10 females for each one of biometrical study). Five *Haemonchus similis* (cattle isolate Martinique) were measured as in practice they might be found commonly in cattle. Analysis of variance (Anova) and discriminant analysis was performed using the Stat-Itcf program (1988).

DESCRIPTION

The worms were collected from the abomasum of two *Bos taurus*. The redescription was done on 10 males, 10 linguiform females, and 10 knob females of isolate Argentina I from the locality of Pergamino (Buenos Aires Province) (Muséum National d'Histoire Naturelle, France, accession number: MNHN 170 MQ). The measurements are given in micrometers unless stated otherwise, with the ranges in parentheses. The nomenclature used for the study of the caudal bursa and synlophe is that of Durette-Desset & Chabaud (1981) and Durette-Desset (1985), respectively. The sublateral hypodermal chords (Lichtenfels & Wergin, 1994) and bilateral perivulvar cuticular pores (Lichtenfels *et al.*, 1995) were not included as they are difficult to see and as they did not discriminate between *Haemonchinae* species.

BIOMETRIC STUDIES

Each isolate was studied on specimens collected in one or several bovines. Whole specimens were studied in temporary mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute alcohol). At least 10 males of every population of putative *Haemonchus placei* were differentiated of *Haemonchus contortus* using the discriminant function of Jacquet *et al.* (1997, 1998): the studied specimens were thus unequivocally ascribed to *H. placei*. This was further evaluated in two serial laboratory sheep passages: all male specimens were evidently *H. placei* based on the same criteria.

The parasites of eight cattle isolates were obtained from Pergamino (Argentina, Buenos Aires) isolate Argentina I; Las Parejas (Argentina, Santa Fe) isolate Argentina II; Mérida (Yucatan, Mexico) isolate Mexico I; Baton Rouge (United States, Louisiana), isolate USA I; Toumodi (Ivory Coast), isolate Ivory Coast; Bobo-Dioulasso (Burkina Faso), isolate Burkina Faso; Nouakchott (Mauritania) isolate Mauritania, and South-Queensland (Australia) isolate Australia. Larvae from several cattle isolates were passaged once (Mauritania, Burkina Faso, Argentina II) or during many years (Australia isolate) in sheep. Eight morphological features were measured for 10 males in each of the eight isolates, i.e., body length, body width, oesophagus length, distance from head to cervical papillae, length of spicule, distance from hook to tip of right and left spicules, and gubernaculum length. The following eight measurements were recorded for 10 females in each of the eight isolates, i.e., body length, body width, distance vulva-tail, oesophagus length, distance from head to cervical papillae, synlophe length, distance from anus to posterior extremity and width of tail. All the measurements were made using standard light microscopy and a semi-auto-

matic image analyser. The proportion of the nematode body length covered by synlophe was made using interference-contrast light microscopy. Discriminant analyses were performed on male and female measures using the Stat-Itcf program (Stat-Itcf, 1988).

RESULTS

HAEMONCHUS PLACEI IDENTIFICATION USING DISCRIMINANT FUNCTIONS

Males

Most isolates, sheep *H. contortus* from Guadeloupe (French West Indies; $n = 20$), South of France (Toulouse; $n = 5$), Malaysia ($n = 20$) and Congo-Zaire ($n = 20$) and cattle *H. placei* from Argentina I ($n = 40$), Argentina II ($n = 10$), Burkina-Faso ($n = 20$), or *H. similis* from Martinique ($n = 50$) were all correctly identified. Ivory Coast, Mexico, and USA I cattle isolates were respectively constituted of *H. placei* (20, 80 and 80 %) and *H. similis* (80, 20 and 20 %). The Mauritanian cattle isolate was composed of *H. placei* (90 %) and *H. contortus* (10 %).

Females

The synlophe length (Sy), distance anus to tail (Dt), and tail width (Tw) (Table I) were used to establish a discriminant function, as no single measure was able to discriminate well enough between the three species. Using only Sy, there was 15 % of missclassified, mostly *H. placei* identified as *H. similis* and conversely using Dt alone, 15 % were missclassified (mostly *H. placei* identified as *H. contortus* or vice versa). The first two axes (Y1 and Y2) in discriminant function, which are linear combinations of Sy, Dt and Tw, were significant ($P < 0.01$). The pseudo-F value of Y1 (341) was higher than F from any measure taken alone, which indicates that linear combination of measures was more efficient in discriminating species. The Sy (Anova: $F = 319$ for 2 and 152 degree of freedom) and Dt (Anova: $F = 141$ for $df = 2, 152$) were significant whereas Tw was not significantly different between the three species. Only one worm out of 155 was missclassified (one *H. placei* classified as *H. contortus*).

The discriminant functions are:

$$Y1 = -0.09 \times Sy + 0.002 \times Dt + 0.000624 \times Tw + 3.58$$

$$Y2 = 0.104 \times Sy + 0.0134 \times Dt + 0.00117 \times Tw - 11.47$$

The following identification key was established on the basis of discriminant analysis:

- 1 (2) $Y2 < -1.60$ *H. similis*
- 2 (3) $Y2 > -1.60$ *H. placei* or *H. contortus*
- 3-1 $Y1 > 0$ *H. placei*
- 3-2 $Y1 < 0$ *H. contortus*

Species	Synlophe length	Distance anus-tail	Tail width
<i>H. p.</i> Argentina I	41* (3)** 36-46***	539 (63) 472-640	114 (11) 96-133
<i>H. p.</i> Argentina II	36 (5) 29-43	626 (59) 515-699	127 (18) 102-170
<i>H. p.</i> Mexico I	37 (2) 33-40	581 (47) 516-671	103 (9) 89-117
<i>H. p.</i> USA I	40 (3) 38-48	563 (44) 474-619	127 (15) 101-151
<i>H. p.</i> Burkina Faso	46 (7) 34-61	469 (38) 402-516	108 (6) 97-117
<i>H. p.</i> Mauritania	39 (2) 35-42	497 (33) 445-556	113 (14) 92-137
<i>H. p.</i> Ivory Coast	41 (3) 38-48	524 (60) 417-619	97 (33) 83-130
<i>H. c.</i> Zaire	57 (4) 52-67	421 (42) 341-515	106 (10) 81-128
<i>H. c.</i> France	57 (3) 52-64	445 (40) 385-528	144 (192) 75-118
<i>H. c.</i> Caribbea	59 (3) 54-65	370 (37) 305-457	92 (13) 62-116
<i>H. c.</i> Malaysia	56 (3) 50-62	419 (42) 330-492	101 (11) 75-120
<i>H. similis</i> Caribbea	48 (4) 42-53	213 (24) 193-251	72 (7) 64-78

H. p. = *H. placei*.

H. c. = *H. contortus*.

* mean in μm , ** standard-deviation (in parentheses) and *** range.

Table I. – Female measures needed for identification of *Haemonchus placei*, *H. contortus* and *H. similis*.

DESCRIPTION OF *HAEMONCHUS PLACEI ARGENTINENSIS* N. SUB-SPECIES

Body filiform. Head without cephalic vesicle, with a buccal cavity with a lancet-shaped, dorsal neodont formation (Figs. 1B, C). In apical view, buccal aperture hexagonal ring, 2 small amphids, 6 externo-labial papillae and 4 cephalic papillae. Presence of 4 cephalic plates, crescent-shaped, situated behind median externo-labial papillae (Fig. 1D).

Synlophe of type I, present only in anterior part of body, in various proportions: 41 (40.9-41.1) percent; about 36 ridges in male, 34 in females at oesophageal-intestinal level, of more or less equal height and orientated perpendicularly to body surface (Fig. 1E).

Excretory pore situated just posterior to nerve ring. Hook-shaped deirids, posterior to excretory pore,

Fig. 1. – *Haemonchus placei argentinensis* n. sub-species in *Bos taurus*. Female. A, anterior extremity, ventral view. B-D, head, B, ventral view, C, right lateral view, D, apical view. E, synlophe, transverse section of the body, at the esophago-intestinal junction. F, detail of the nerve ring, excretory pore and deirids, ventral view. G, tail, ventral view. H-I, vulvar region. H, linguiform process and ovejector, right lateral view, I, knob process; r: right side. A, G, H: 200 µm; B-D: 20 µm; E: 50 µm; I, J: 100 µm.

Fig. 2. – *Haemonchus placei argentinensis* n. sub-species in *Bos taurus*. Male. A, caudal bursa, ventral view. B, genital cone, papillae 0 and 7, dorsal view. C, genital cone, ventral view. D, gubernaculum, ventral view. E-F, spicules, ventral view, E, right spicule, F, left spicule. A, 200 µm; B, C: 50 µm; D-F: 100 µm. The dorsal rays were coded from 2 to 8.

situated very anteriorly, in the first quarter of oesophagus length (Fig. 1A, F). Male: Length 15.2 (14.7-15.7) mm, width at mid-body 167 (152-182), deirids 411 (386-436) from cephalic extremity. Oesophagus 1,595 (1464-1726) long. Caudal bursa with ornate ventral surface mainly between extremities of rays 2 to 8, composed of 2 large lateral lobes and a reduced dorsal lobe situated on left (Fig. 2A). Ray 2 and 3 with very long, common stem, curved ventrally with extremities separated from each other. Ray 4 straight, extremities almost equidistant from those of ray 3 and 5. Ray 5 and 6 parallel with extremities curved dorsally. Ray 8 straight and thin. Dorsal ray stout, divided half-way down in 2 branches, each branch divided again into 2, internal (rays 10) longer than external (ray 9). Genital cone prominent, bearing on ventral lip sharp papilla "zero" (Fig. 2C) and 2 curved papillae "7" on dorsal lip (Fig. 2B). Spicules thick, unbranched, subequal, 512 (491-533) long. Each spicule had one distally small protuberance (Figs. 2E, F). Distance between right and left protuberance and tip of spicule was 56 (51-61) and 26 (24-28) respectively. Gubernaculum spindle-shaped in ventral view, 253 (237-269) long (Fig. 2D).

Female: according to presence or absence of a process at vulvar level, the morphometric data are as follows: Females with linguiform process: Length 21 (19-22) mm, width at mid-body 275 (248-302). Deirids 471 (444-498) from cephalic extremity. Oesophagus 193

(170-216). Vulvar opening at 71 %. Thick-walled vagina vera directed forwards parallel to body. Linguiform process, about 400 µm, situated above the vulvar opening (Fig. 1H). Rounded tail, without spine, 599 (546-652) long and 131 (120-142) wide at its base (Fig. 1G). Females with knob process: Length 20 (19-21) mm, width at mid-body 273 (257-289). Deirids 457 (430-484) from cephalic extremity. Oesophagus 165 (145-185) (Fig. 1A). Vulvar opening at 76 %. Thick-walled vagina vera directed forwards obliquely to body. Knob process, about 150 × 150 µm, situated on left side on body (Fig. 1I). Rounded tail, without spine, 561 (538-584) long and 122 (116-128) wide at its base.

INTRA-SPECIFIC VARIABILITY OF *H. PLACEI* ISOLATES

The different isolates were slightly different according to the morphological characteristics (Tables II and III). All the characters were significant using analysis of variance ($P < 0.01$). The identification based on eight morphometrics characters using discriminant analysis was able to classify correctly only 72 % and 74 % of males and females into the right isolate, respectively. Conversely, three groups were clearly delineated (95 % of males and 85 % of females were well classified) in this analysis: male (79 % of inertia in the significant two axes) or female (75 % of inertia in the significant two axes) *H. placei* from Australia, Africa and America

Isolates	Body length	Body width	Oesophagus length	Cervical deirids*	Length of spicule	Right hook to tip of spicule	Left hook to tip of spicule	Gubernaculum
Argentina I	15,189 (496)	167 (16)	1,595 (139)	411 (27)	513 (23)	56 (6)	27 (3)	254 (17)
Argentina II	14,276-15,760 16,330 (1,357)	147-198 178 (7)	1,393-1,911 1,561 (53)	383-458 418 (22)	485-551 485 (19)	46-65 53 (4)	24-34 26 (3)	222-279 247 (10)
Mexico I	13,700-17,800 14,140 (1,465)	167-188 167 (12)	1,464-1,624 1,453 (112)	385-447 372 (42)	455-520 473 (17)	46-58 51 (3)	22-31 25 (2)	225-257 243 (11)
USA I	11,400-16,100 15,580 (1,006)	152-183 173 (17)	1,331-1,632 1,536 (78)	280-437 397 (31)	446-509 477 (16)	47-57 50 (2)	22-27 25 (3)	217-256 245 (16)
Burkina	14,000-17,200 13,325 (567)	149-209 141 (8)	1,377-1,685 1,317 (73)	342-434 397 (8)	441-492 459 (15)	48-54 51 (2)	20-29 26 (3)	228-273 233 (10)
Mauritania	12,500-13,900 14,070 (497)	131-151 153 (16)	1,234-1,401 1,367 (67)	385-405 401 (16)	435-472 461 (10)	48-53 49 (4)	21-29 26 (3)	224-250 239 (8)
Ivory Coast	13,200-14,700 13,440 (1,697)	119-170 156 (17)	1,266-1,512 1,415 (99)	366-426 385 (14)	441-470 430 (19)	42-55 48 (3)	22-31 21 (3)	229-254 223 (18)
Australia	10,400-15,600 17,539 (1,306)	126-178 182 (7)	1,229-1,504 1,727 (81)	368-406 456 (31)	397-455 489 (14)	43-52 52 (3)	16-25 29 (2)	191-256 225 (10)
	14,709-19,475	170-191	1,609-1,873	399-496	467-521	47-58	26-31	208-239

* Distance from head to cervical deirids.

Table II. – Male morphometric characteristics (mean in µm, standard-deviation and range) of eight isolates of *Haemonchus placei*.

Isolates	Body length	Body width	Distance vulva-tail	Oesophagus length	Cervical deirids*	Synlophe length**	Distance anus-tail	Tail width
Argentina I	18,160 (1,726)	187 (12)	3,148 (460)	1,694 (57)	427 (26)	41 (3)	539 (63)	114 (11)
Argentina II	15,427-21,049 23,370 (1,999)	170-205 191 (23)	2,423-3,760 3,950 (334)	1,589-1,804 1,685 (136)	371-459 452 (35)	36-46 36 (5)	472-640 626 (59)	96-133 127 (18)
Mexico I	20,100-26,400 19,710 (1,504)	139-215 183 (14)	3,500-4,600 3,520 (545)	1,467-1,935 1,566 (128)	398-513 387 (32)	29-43 37 (2)	515-699 581 (47)	102-170 103 (9)
USA I	18,000-21,900 21,160 (971)	167-214 216 (18)	3,000-4,800 3,550 (422)	1,337-1,810 1,622 (93)	324-443 435 (28)	33-40 40 (3)	516-671 563 (44)	89-117 127 (15)
Burkina	19,800-22,800 15,030 (1,641)	189-245 185 (12)	2,700-4,100 2,750 (127)	1,481-1,812 1,386 (67)	395-482 377 (20)	38-48 46 (7)	474-619 469 (38)	101-151 108 (6)
Mauritania	12,800-18,900 18,600 (867)	170-208 180 (14)	2,500-3,000 3,410 (331)	1,276-1,459 1,443 (82)	348-414 410 (15)	34-61 39 (2)	402-516 497 (33)	97-117 113 (14)
Ivory Coast	17,300-19,900 19,130 (2,139)	160-199 180 (25)	2,700-3,900 3,280 (442)	1,329-1,607 1,562 (104)	388-437 407 (25)	35-42 41 (3)	445-556 524 (60)	92-137 96 (33)
Australia	17,000-22,600 22,400 (2,745)	125-216 203 (9)	2,500-3,900 4,342 (260)	1,440-1,744 1,739 (86)	344-436 443 (24)	38-48 40 (2)	417-619 598 (58)	11-130 138 (9)
	14,771-24,310	192-222	3,816-4,710	1,571-1,828	409-479	37-44	503-698	123-152

* Distance from head to cervical deirids.

** Percentage of synlophe length on the body length.

Table III. – Female morphometric characteristics (mean in μm and standard-deviation) of eight isolates of *Haemonchus placei*.

were different (Fig. 3). Only one isolate from Australia was studied and we focused on New World and African data where several isolates were studied. *H. placei* found in New World (North and South America) and Old World (Africa) were different when their morphometrics was compared (Figs. 4 and 5): 94 % of males and 89 % of females were well identified to their African or American origin.

DISCUSSION

Species of *Haemonchus* have veterinary significance and it is important to have accurate species identification. There are nine or ten species and five sub-species of which four are from domestic ruminants (*H. longistipes*, *H. contortus*, *H. similis* and *H. placei*) (Gibbons, 1979). The differentiation of males by measurement of spicules (Jacquet *et al.*, 1997) was a simple good criteria for individual identification between *Haemonchus contortus* and *Haemonchus placei*, in our isolates. The differentiation of females based on length of synlophe, width and length of tail was completely efficient for the different isolates.

Morphometrics of males and females were related to their Australian, African or New World location. There has been introduction of probably infected cattle in the last four centuries in the Carribea either from Africa (Curasson, 1934) or India, where *H. placei* is common.

Fig. 3. – Male and female morphological differences between African, American and Australian isolates using discriminant analysis. Only the gravity centers of American (square), African (circle) and Australian (triangle) isolates are shown.

Fig. 4. – Male morphological differences between African and American *Haemonchus placei* isolates using discriminant analysis. The isolates were coded as Argentina I –1, Argentina II –2, Mexico I –3, USA I –4, Burkina Fasso –5, Mauritania –6, and Ivory Coast –7. ○ = African isolates. □ = American isolates; shaded circle and square correspond to gravity centers of each isolate.

Fig. 5. – Female morphological differences between African and American *Haemonchus placei* isolates using discriminant analysis. The isolates were coded as Argentina I –1, Argentina II –2, Mexico I –3, USA I –4, Burkina Fasso –5, Mauritania –6, and Ivory Coast –7. ○ = African isolates. □ = American isolates; shaded circle and square correspond to gravity centers of each isolate.

Further introductions of cattle from the Caribbean to Central or South America did occur which might explain the presence of *H. placei* in South America. The origin of *H. placei* in Australia might relate to Indonesian introductions (LeJambre, personal communication, 1999). The different origin *H. placei* in America evolved for several centuries (probably for African introduced *H. placei*) or less than a century (*H. placei* from massive Indian *Bos indicus* importation at the very beginning of this century). At that stage, we suggest that the isolate from Australia should be considered as a subspecies called *H. placei placei* whereas the subspecies found in America and Africa should be called *H. placei argentinensis* n. sub-species and *H. placei africanus* n. sub-species, respectively. More detailed studies using genetic markers on a larger number of isolates could eventually trace the migrations of *H. placei* which could explain the differences between African, Australian and American isolates. Only one isolate from Australia (repeatedly bred for years in sheep) was used to characterise the continent and cattle isolates from several regions should be studied to confirm the particularities of the Australian isolate we described. The existence of several subspecies tends to indicate that *H. placei* might evolve relatively rapidly. This would not be the first case rapid evolution as it has been recorded in another trichostrongylid, *Heligmosomoides polygyrus*, after introduction from Europe to North America at the colonizing period. In less than five centuries, differences in morphological features (Durette-Desset *et al.*, 1972), hosts preferences (Quinnell *et al.*, 1991; N'Zobadila, 1994), and biological characteristics or genetic markers (N'Zobadila, 1994) were evidenced in *H. polygyrus* and they were separated into *H. p. polygyrus* (Europe) and *H. p. bakeri* (North America).

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