Description and taxonomic discussion of eimerian coccidia from African and Levantine geckoes

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Two new genera are proposed to accomodate new and previously described species of eimerian coccidia from reptiles which undergo endogenous development either in the bile epithelium — *Choleoeimeria* n. gen., or in the microvillous zone of the intestinal epithelium — *Acroeimeria* n. gen. Endogenous development is described from 3 species, all from geckoes: *C. turcicus* (syn. *Eimeria turcicus* Upton, McAllister and Freed, 1988) from *Hemidactylus turcicus* in Israel; *C. pachydactyli* n. sp. from *Pachydactylus capensis* in South Africa and *A. lineri* (syn. *Eimeria lineri* McAllister, Upton and Freed, 1988) from *H. turcicus*, Israel and *H. mabouia,* South Africa. Biliary epithelial cells infected by *Choleoeimeria* become hypertrophic and are displaced to the surface of the epithelial layer. Oocysts are cylindroid to oval, lack a stieda body and sporulate in the gall bladder. The developing endogenous stages of *Acroeimeria,* enclosed in the microvillous border of the host cell, expand into the intestinal lumen. Oocysts are oval-spherical, lack a stieda body and sporulation is exogenous.

Twee nuwe genera word voorgestel vir nuwe sowel as reeds beskryfde spesies van reptiel Coccidia wat endogene ontwikkeling in òf die milt — *Choleoeimeria* n. gen., òf in die mikrovilli-sone van die intestinale epiteel — *Acroeimeria* n. gen. ondergaan. Endogene ontwikkeling word vir drie spesies beskryf wat almal in geitjies voorkom, d.i. *C. turcicus* (sin. *Eimeria turcicus* Upton, McAllister en Freed, 1988) van *Hemidactylus turcicus* in Israel; *C. pachydactyli* n. sp. van *Pachydactylus capensis* in Suid-Afrika en *A. lineri* (sin. *Eimeria lineri* McAllister, Upton en Freed, 1988) van *H. turcicus,* Israel en *H. mabouia,* Suid-Afrika. Galepiteelselle, besmet met *Choleoeimeria,* word hipertrofies en na die oppervlak van die epiteellaag verplaas. Oösiste is silindries tot ovaal, die stieda-liggaam is afwesig en sporulasie kom in die galblaas voor. Die ontwikkelende endogene stadium van *Acroeimeria,* ingesluit in die rand van die mikrovilli van die gasheerselle, verleng tot in die intestinale lumen. Die oösiste is ovaal-sferies, 'n stieda-liggaam is afwesig en sporulasie is eksogeen.

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The peculiar relationship between gall bladder eimerians and the host epithelium which leads to hypertrophy and displacement of the host cell, has been mentioned in a number of taxonomic descriptions of reptilian coccidia (Fantham 1932; Setna & Bana 1935; Brygoo 1963; Bovee & Telford 1965a; Cannon 1967; Vetterling & Widmer 1968; Bovee 1969; Clark 1970). But none of these studies regarded this as a distinctive characteristic of taxonomic relevance. The same situation applies to eimerians which develop in the microvillous zone of the intestinal epithelium in reptiles. This type of host parasite relationship is indicated from the description of *Eimeria sceloporis* (by Bovee & Telford 1965b). Two new genera are proposed to accomodate reptilian eimerians developing either in hypertrophic cells of the bile epithelium or in the microvillous zone of the intestinal epithelium. In the present communication we describe endogenous development of two already named and a third new species from geckoes, which are representative of the proposed two genera. Fine structural studies of the endogenous developmental stages of these species are reported in Paperna (1989) and Paperna & Landsberg (1989).

Materials and Methods

Geckoes were kept for several days after capture to obtain faeces. The presence of oocysts in the faeces was determined by direct microscopic examination of a suspension prepared from macerated faeces in tap water. Infected geckoes, 14 *Hemidactylus turcicus* L. 1766, out of 28 collected from urban and rural locations throughout Israel, two *Hemidactylus mabuia* (Moreau de Jonnes 1818) and one *Pachydactylus capensis* Smith 1846, captured from suburban dwellings near Pretoria, South Africa, were necropsied for the study of endogenous stages. Samples from the intestine, liver and gall bladder of the necropsied geckoes were fixed for histology in 10% buffered neutral formalin and embedded in glycolmethacrylate (Lulham 1979). Sections 3–4 μm thick, cut with a JB4 Sorvall glass knife microtome were stained with either Meyer's haemalum and counterstained with phloxine and eosin (*vide* H–E) or in Schiff's Periodic Acid method (*vide* P.A.S.). Histological data were also obtained from semithin sections of epon-embedded tissue prepared for transmission electron microscopy (TEM, for methods see Paperna, Landsberg & Feinstein 1986) and stained with 1% toluidine blue.

Measurements were obtained with an ocular micrometer at ×780 magnification from at least five specimens of each endogenous stage (from histological preparations) and ×400 magnification from 9–27 (Tables 1, 2) unfixed oocysts (in tap water), from each of the described species and hosts.

Results

Examination of *Hemidactylus turcicus* (28) from Israel revealed two species of eimerians, one from the gall bladder (in seven geckoes) and one from the intestine (in

Table 1 Morphometric data on oocysts and sporocysts of *Choleoeimeria turcicus* and *C. pachydactyli* compared with Setna & Bana (1935) data on *C. flaviviridis*. (S. index: Length/Width)

	Species, location and host species		
	C. turcicus Israel (USA) *H. turcicus*	*C. pachydactyli* South Africa *P. capensis*	*C. flaviviridis* India *H. flaviviridis*
Oocysts			
No. measured	17	9	
Length			
mean	36,0 (38,2)	28,3	
SD	1,2	1,7	
range	33–39 (35–41)	25–31	25–34
Width			
mean	18,3 (17,9	13,9	
SD	1,0	1,4	
range	15–20 (17–20)	11–17	11–14
S. index			
mean	2,07 (2,1)	2,05	
SD	0,18	0,24	
range	(1,9–2,3)		1,8–2,4
Sporocysts			
Length			
mean	9,9 (11,0)	11,4	
SD	1,1	1,0	
range	8,4–11,8 (10–12)	10,14–12,6	7–9
Width			
mean	8,3 (8,8)	6,9	
SD	0,3	0,3	
range	7,8–8,9 (8,4–9,4)	6,5–7,2	5–7
Sporozoites			
Length range	9–10 (12–14)		9–13
Width range	3–4 (2,4–3,2)		1,04–1,04

Table 2 Morphometric data on *Acroeimeria lineri*

	Host species and location		
	H. turcicus		*H. mabuia*
	Israel	(USA*)	South Africa
Oocysts			
No. measured	27	24,8	18
Length			
mean	25,3		24,0
SD	2,2		2,0
range	22,5–28,1	21,6–28,8	21,5–26,5
Width			
mean	19,0	19,5	15,7
SD	2,6		2,5
range	14,1–22,5	18,4–21,6	11,6–19,0
Length/width ratio			
mean	1,33	1,3	1,53
range	1,25–1,6	1,1–1,5	1,39–1,8
Sporocysts			
Length			
mean	9,8	9,0	9,9
SD	0,77		1,65
Width			
mean	7,8	7,8	7,6
SD	1,80		1,82

11 geckoes). Double infections were found in four geckoes. From South Africa, both *Hemidactylus mabuia* were infected by an intestinal eimerian, while *Pachydactylus capensis* was infected by a biliary eimerian.

Taxonomy and descriptions

Choleoeimeria n. gen.

Syn: *Eimeria* Schneider, 1875, *pro parte: Goussia* Labbe, 1896, *pro parte.*

Diagnosis

With the characters of the family Eimeriidae Minchin, 1903. Oocyst cylindroid to oval with length/width ratio > 1,4 (usually 1,6–2,2), without a micropyle, containing four sporocysts, each with two sporozoites. Sporocysts bivalved and lack a stieda body. Endogenous stages, meronts and gamonts induce hypertrophy and displacement of the epithelial host cell from the original cellular layer; these infected cells remain attached by their basal end to this layer until the parasite reaches the oocyst stage. All recognized species undergo endogenous development in the gall bladders of reptiles. Sporulation is endogenous, in the gall bladder and in the lumen of the digestive tract.

Type species

Choleoeimeria turcicus (Upton, McAllister & Freed, 1988) n. comb.

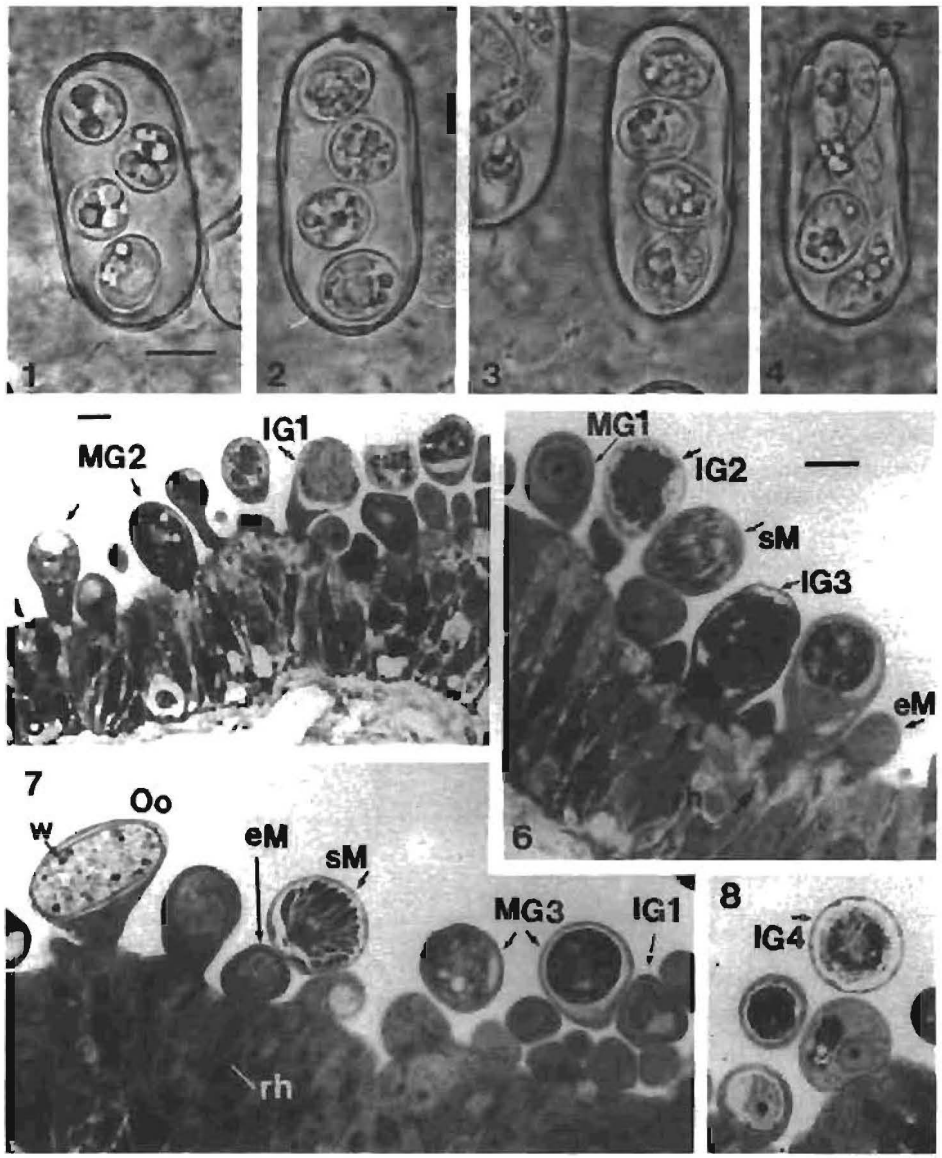
Choleoeimeria turcicus n. comb.

Syn: *Eimeria turcicus* Upton, MacAllister & Freed, 1988
Type host and locality: Hemidactylus turcicus L. Houston Zoological Gardens, Harris County, Texas, USA.
New localities (for type host): Houses and domestic habitats in Afula, Tel Aviv and Rehovot, Israel.

Description

Oocyst from the gall bladder and the intestine (Figures 1–4)

Measurements of oocysts and sporocysts are presented in Table 1. Oocysts are cylindroid, with a smooth surface and lacking a micropyle, oocyst residuum and polar granule. Sporulated oocysts already occur in the gall bladder (Figures 1, 2, 3). The spherical-ellipsoid sporocysts lack a stieda body, are bivalved and contain two sporozoites and a residuum. Cleavage of the sporocysts occurs in some oocysts while they are still in the gall bladder (Figure 4), while in others it is delayed till they are released in the faeces. However, release of sporozoites from the oocysts never occurred while in the gall bladder or in the digestive tract.



Figures 1–8 Oocysts of *Choleoeimeria turcicus* from the gall bladder of *Hemidactylus turcicus*, containing already sporulated sporocysts (1–4) or already released sporozoites (4); Figures 1–4 same magnification. 5–8. Semithin section (2 μm) of *H. turcicus* gall bladder infected with endogenous stages of *C. turcicus*; toluidine blue stain; Figures 6–8 same magnification.

Endogenous stages in the gall bladder (Figures 5–9)

All infections were extremely heavy, with the lining epithelium of the gall bladder densely fringed with hypertrophic infected cells displaced to the surface of the epithelial layer (Figures 5–7). Infected cells usually contained a single nucleus, but occasionally contained two. Most cells were infected by a single parasite, but some contained two of the same (Figure 9i) or different developmental stages (Figure 9h). Hypertrophy and displacement of the host cell began already at an early stage of infection (Figures 7, 9a,b,c). Uninfected epithelial cells were 4–7 μm in width. Displaced host cells infected by young meronts were round or pear shaped (Figures 6, 7, 9a,b), 8,3–11,0 μm wide and by the time meronts completed differentiation, the host cell was 19–24 μm wide and displaced to a distance of 26-30 μm above the epithelial layer (Figure 9d). Meronts before segmentation (Figure 9d) were 14–24 × 13–22 μm. Segmented meronts (20–21 × 18–20 μm) contained 25–60 merozoites per cross section, 11–13 × 1–2 μm and were formed around a small residual body (Figures 6, 7). Free merozoites were 11 × 2 μm (Figure 9j). Host cells parasitized by gamonts and young zygotes were pear shaped, 14–24 μm wide and extended up to 37 μm above the surface of the bladder epithelium (Figures 5–7). Young microgamonts, already showing several nuclei (Figures 5, 7) were 11 × 13 μm. Fully grown microgamonts with numerous nuclei before differentiation (Figure 6) and already forming microgametes (Figures 8, 9e) were 17–21 × 13–15 μm. Microgamonts in the process of differentiation became deeply infolded (Figures 6, 9e). Macrogamonts, showing a distinct vesicular nucleus and large basophilic nucleolus (Figures 6, 8, 9c,f) reached 14–17 μm in diameter and, when mature, contained very distinct type 1 and type 2 wall-forming bodies (WF1 & WF2) (Figures 5, 7, 9f) (confirmed by TEM, Paperna & Landsberg 1989). Zygotes were round to oval, 13–18 ×

Key to abbreviations on figures

A	Amylopectin granules
C	Canaliculi
eM	Early meront
E	Host's mucosal epithelium
F	Microgamete's flagellum
H	Host cell/tissue
HN	Host cell nucleus
IG1	Young microgamont
IG2	Differentiating microgamont
IG3	Premature microgamont
IG4	Mature microgamont with microgametes
ig	Microgamete
L	Lipid vacuole
M	Mature macrogamont/Zygote (Figure 24)
MG1	Young macrogamont
MG2	Premature macrogamont
MG3	Mature macrogamont/Zygote
N	Nucleus
Oo	Oocyst
OW	Oocyst wall
R	Residual body (cytoplasm)
P	Trophozoite
r	Young stages (trophozoites)
rh	Basal end of displaced host cell
s	Sporocyst
sM	Meront segmented into merozoites
sz	Sporozoite
V	Vacuole
w & WF	Wall-forming bodies
WF1	Wall-forming bodies type 1
WF2	Wall-forming bodies type 2
Y	Young macrogamont (Figure 24)
Z	Zygote

Scales = 10 μm.

13–16 μm, loaded with translucent amylopectin bodies. WF1 were seen to aggregate beneath the cell wall while WF2 remained scattered within the cell (Figures 7, 9g). The latter persisted both in the zygote and young oocyst until their detachment, when they were already enclosed in hardened wall. Young oocysts before detachment and wall formation already assumed a cylindroid shape (29 × 13 μm, Figure 9k). The displaced hypertrophic cell became further expanded to accommodate the growing oocyst. Oocysts (29 × 11 μm) became enclosed by a thickened wall while still within their host cell, attached to the biliary epithelium (Figure 7, 9l). Detached oocysts were loaded with amylopectin granules. Division to sporoblasts occurred only in detached oocysts.

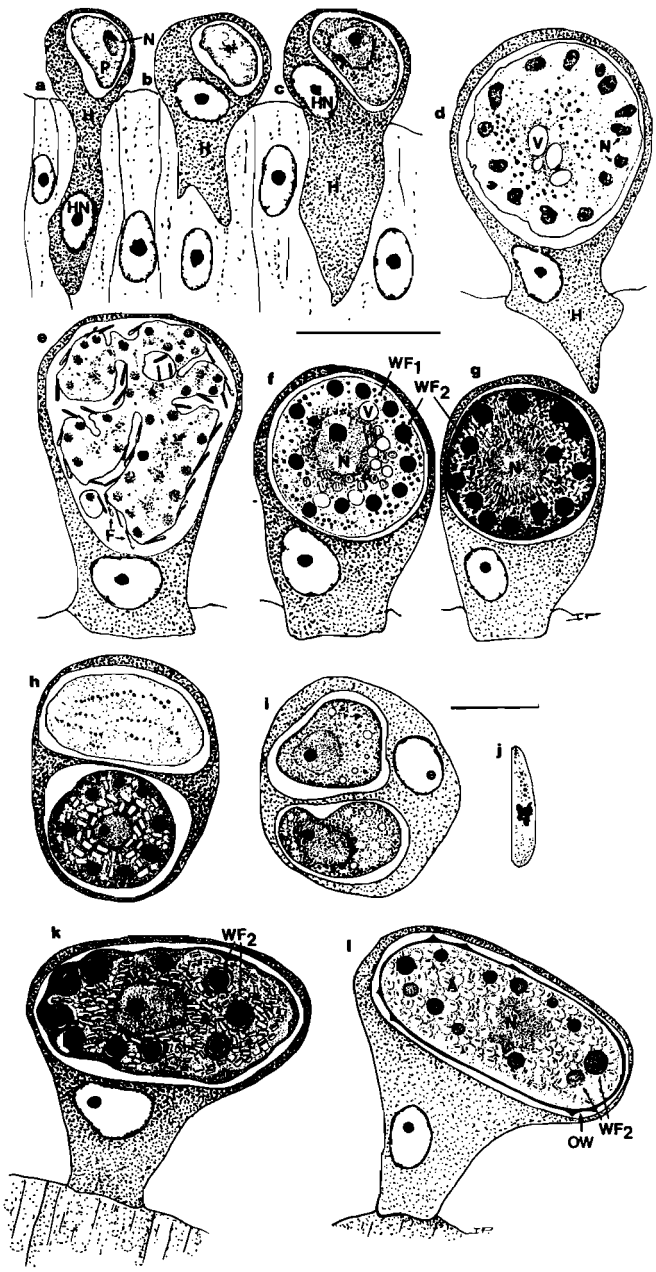


Figure 9 Detailed drawings of endogenous stages of *C. turcicus* from toluidine blue stained semithin sections of *H. turcicus* gall bladder: a, b. early stage of infection by young meronts, infected cells in gradual displacement from the epithelial layer; c. infection by young macrogamont; d. dividing meront; e. differentiating microgamont; f. mature macrogamont; g. young zygote; h. double infection of host cell by meront (top) and zygote. i. double infection of host cell by young macrogamonts; j. free merozoite irom the gall bladder lumen. k. late zygote; l. young oocyst already with hard wall.

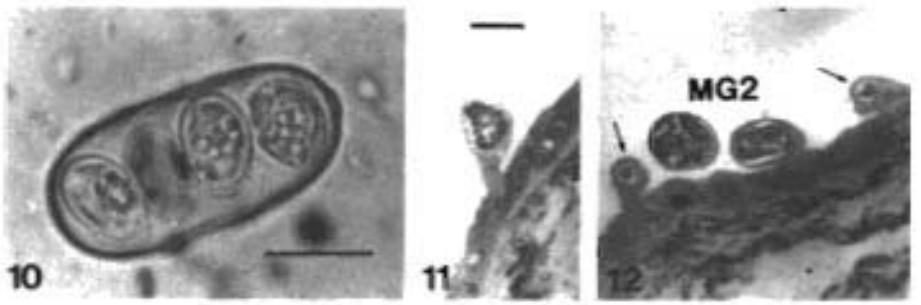
Choleoeimeria pachydactyli n. sp.

Hosts and Localities

Pachydactylus capensis Smith, South Africa: Outskirts of Pretoria.

Oocysts from the gall bladder and the intestine (Figure 10)

Measurements of oocysts and sporocysts are presented in Table 1. Oocysts are cylindroid, with a smooth surface and lacking a micropyle, oocyst residuum and polar granule. In a few oocysts a small knob occurred at one pole. Sporulated oocysts already occur in the gall bladder. Sporocysts are bivalved and lack a stieda body. Sporozoites released from sporocysts, within oocysts, were not suitable for measurements.



Figures 10-12 *C. pachydactyli* from gall bladder of *Pachydactylus capensis* 10. Oocysts with sporulated sporocysts from the gall bladder lumen. 11–12. Semithin sections, toluidine blue stained of gall bladder epithelium infected with endogenous stages; 11 & 12 same magnification.

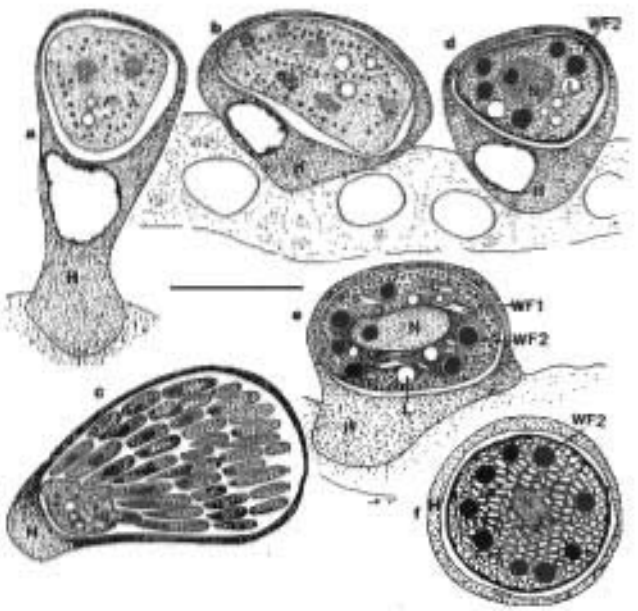


Figure 13 Detailed drawings of endogenous stages of *C. pachydactyli* from toluidine blue stained semithin sections of gall bladder of *P. capensis*: a, b. dividing meronts; c. meront segmented into merozoites; d. young macrogamont; e. mature macrogamont; f. zygote.

Endogenous stages in the gall bladder (Figures 11, 12, 13)

Infection in *P. capensis* was mild and not all developmental stages could be found in cross sections of the gall bladder. Infected cells were hypertrophic and displaced to the surface of the biliary epithelium (Figures 11, 12). Hypertrophic infected cells often retained a broad base attachment with the underlying layer of non-infected cells (Figure 9b,d,e). Young meronts with several nuclei (Figure 13a,b) were 9–11 × 8–9 µm. Meronts divided into merozoites (up to 68 were counted per section) (Figure 13c) reached 15–22 × 8–14 µm. Young microgamonts were 11–13 × 7–9 µm and mature 20 × 11 µm.

Young macrogamonts (Figure 13d) were 11–12 × 8–9 µm, while mature macrogamonts (Figure 11, 12, 13e) and early zygotes (Figure 13f) were 13,2–14,2 × 11,0–13,7 µm. The macrogamonts contained WF1s and WF2s, some vacuoles and toluidine blue resistant canaliculi (Figure 13e). Zygotes were loaded with translucent amylopectin bodies and contained several large WF2s. WF1s (as shown in TEM, Paperna & Landsberg, unpublished) aggregated into a dense marginal layer (Figure 13f).

Other species

Proposed also to be transferred into this new genus are nine species from the genus *Eimeria*, and one from the genus *Goussia* which infect the gall bladders of reptilian hosts, and which conform with the generic diagnosis of *Choleoeimeria* and also, in our opinion, *Tyzzeria chalcides* reported from the gall bladder of *Chalcides occelatus* from Egypt (Probert, Roberts & Wilson, 1988). The late stage of sporogony was overlooked, which led the authors to consider their species as *Tyzzeria*. Structural characteristics of the oocysts as well as the mode of endogenous development in the gall bladder are typical of *Choleoeimeria*.

The proposed species are:

Choleoeimeria (E.) ahtanumensis (Clark 1970) n. comb. [from *Sceloporus occidentalis*, USA].

Choleoeimeria (E.) bitis (Fantham 1932) n. comb. [from *Bitis lachesis (= arietans), South Africa]*.

Choleoeimeria (E.) cascabeli (Vetterling & Widmer 1968) n. comb. [from *Crotalus viridis viridis*, USA].

Choleoeimeria (T.) chalcides (Probert, Roberts & Wilson 1988) n. comb. [from *Chalcides ocellatus*, Egypt].

Choleoeimeria (E.) egerniae (Cannon 1967) n. comb. [from *Egernia whitii*, Australia].

Choleoeimeria (G.[E.]) flaviviridis (Levine 1983 [Setna & Bana, 1935]) n. comb. [from *Hemidactylus flaviviridis*, India].

Choleoeimeria (E.) noctisauris (Bovee & Telford 1965a) n. comb. [from *Klauberina riversiana*, USA].

Choleoeimeria persica (E.) (Physalix 1925) n. comb. [from *Natrix natrix* var. *persa*, Italy].

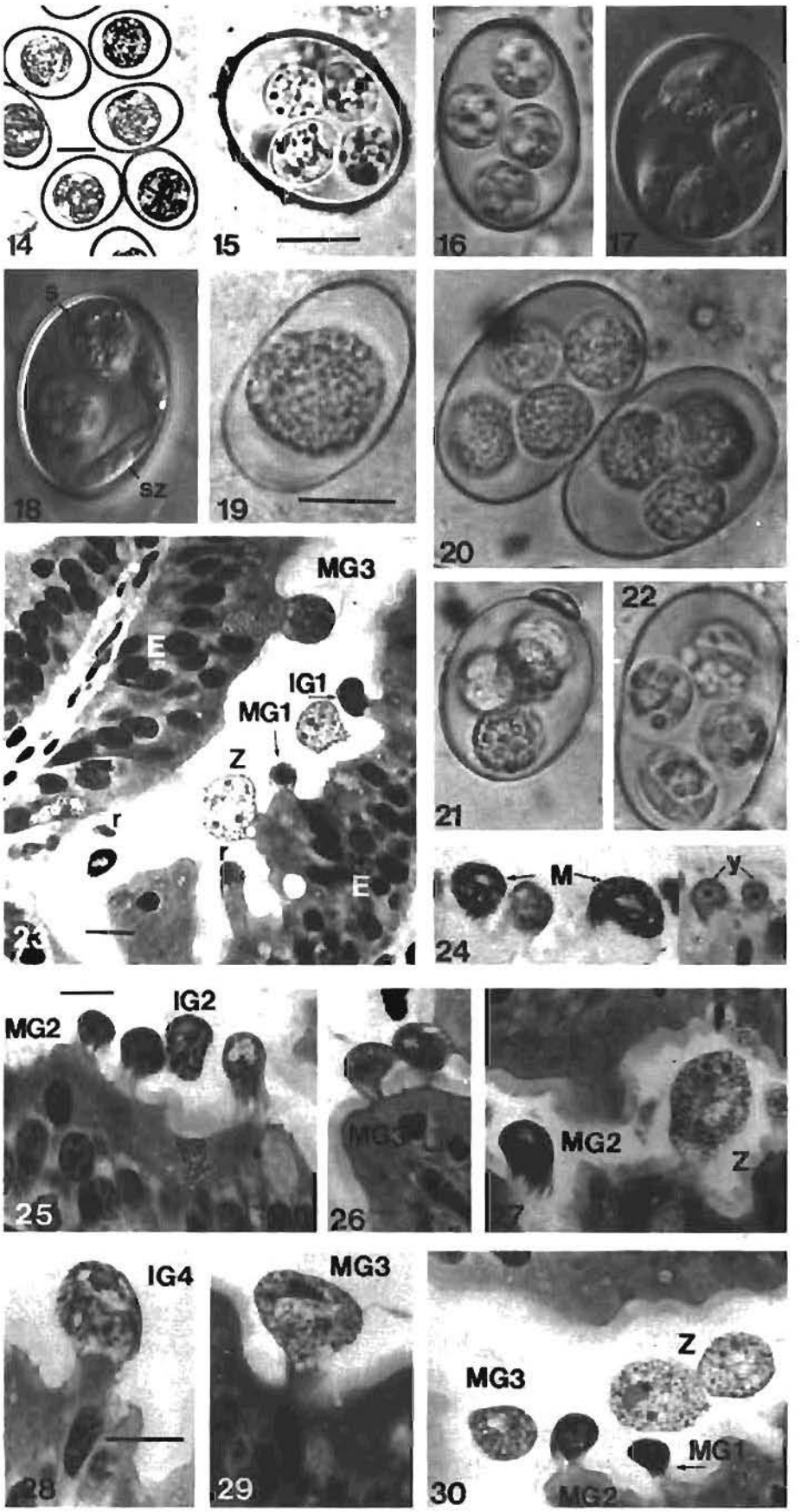
Choleoeimeria (E.) umis (Bovee 1969) n. comb. [from *Uma notata*, USA].

Choleoeimeria urosauris (Bovee 1966) n. comb. [from *Urosaurus graciosus* USA].

Choleoeimeria (E.) sp. of Brygoo 1963 [from gall bladders of cameleons, Madagascar].

Choleoeimeria (E.) 'sp.2' of Yamamoto 1933 [from gall bladder of *Hemidactylus frenatus*, Taiwan].

In all the other species of *Eimeria* from the gall



Figures 14–30 14–18. Oocysts of *Acroeimeria lineri* from *H. turcicus*: 14. unsporulated oocysts from the intestine; 15–17. sporulated oocysts from faeces; 18. oocysts with cleaved sporocysts; Figures 15–18 same magnification. 19–21. Oocysts of *A. lineri* from *H. mabuia:* 19. unsporulated oocyst from the intestine; 20. oocyst in sporulation in faeces; 21, 22. sporulated oocysts in faeces; Figures 19–21 same magnification. 23. Endogenous stages of *A. lineri* in intestine of *H. turcicum,* methacrylate embedding, H–E. 24. Same, young (y) PAS– & mature (M) macrogamonts PAS+: PAS stain, same magnification as Figure 23. 25–30. Endogenous stages of *A. lineri* from intestine of *H. turcicus* methacrylate embedding, H-E; Figures 25–27 & Figures 28–30 same magnification.

bladders of reptiles, which have characteristic cylindroid oocysts of a length/width ratio > 1,4 (> 1,6–2,2) and sporocysts lacking a stieda body, endogenous developmental stages were not, or inadequately, described, thus their affinities with *Choleoeimeria* cannot be determined.

***Acroeimeria* n. gen.**

Syn: *Eimeria* Schneider 1875, *pro parte*

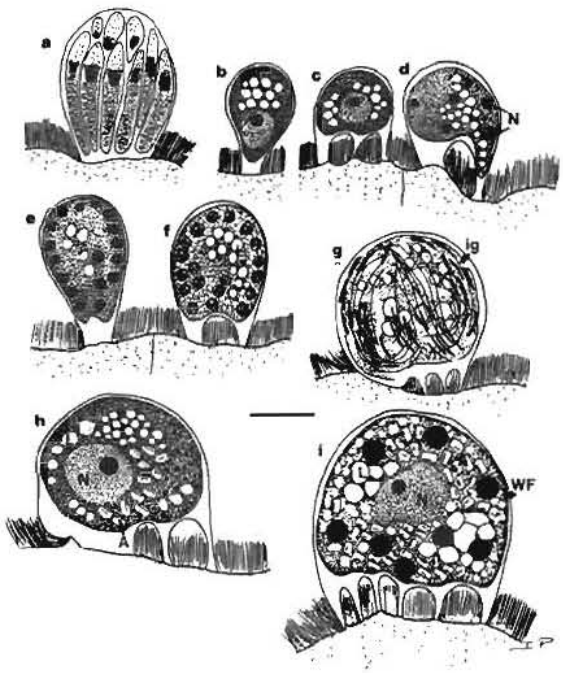


Figure 31 Detailed drawings of endogenous stages of *A. lineri* from *H. turcicus* intestine, methacrylate embedding, H–E: a. meront segmented into merozoites; b, c. young macrogamonts; d. young microgamont; e, f. multinucleate microgamonts; g. mature microgamont differentiated into microgametes. h. premature macrogamont. i. mature macrogamont or a zygote.

Diagnosis

With the characters of the family Eimeriidae, Minchin, 1903. Oocysts oval to round with a length/width ratio not exceeding 1:8, with or without micropyle, with four sporocysts each with two sporozoites. Sporocysts lack a stieda body. Endogenous stages, meronts and gamonts develop at the microvillous zone of the host cell and, enclosed in the host cell microvillous boundary, extend above the intestinal mucosal surface (Figure 10).

Type species: Acroeimeria lineri (McAllister, Upton & Freed, 1988) n. comb.

***Acroeimeria lineri* n. comb.**

Syn: *Eimeria lineri* McAllister, Upton & Freed 1988.
Eimeria (s.l.) sp. Paperna, 1989.

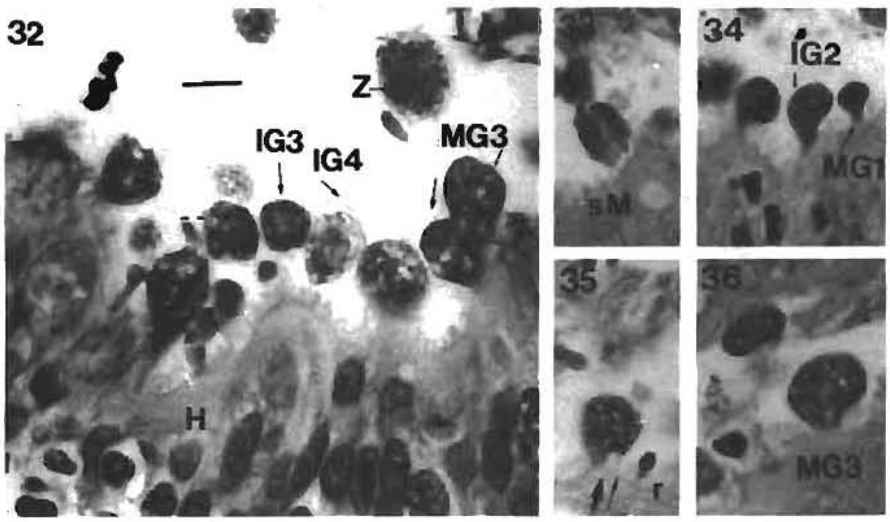
Type host and locality: Hemidactylus turcicus, Houston, Harris County, Texas, USA.

New hosts and localities: Type host: domestic habitats in Tel Aviv, Afula, Rehovot, Israel; *Hemidactylus mabouia,* outskirts of Pretoria, South Africa.

Description

Oocyst stages (Figures 14–22)

Sporulation is exogenous, all oocysts recovered from the posterior intestine contained an undivided cytoplasm (Figures 14, 19). In excreted faeces, oocysts sporulated (Figures 20, 21) within 48 h. Sporulated oocysts (Figures 15–18, 22) were ellipsoidal with a smooth outer surface. Micropyle and oocyst residuum were absent, in some oocysts there was a knob-like thickening at one pole of the wall (Figure 21). The four sporocysts were smooth, thin walled and lacked a stieda body (Figures 16–18, 22). Upon completion of sporulation each sporocyst contained two sporozoites and a residuum consisting of globular material. Sporocysts opened by a longitudinal slit (Figure 18). There was a wide variation in shape indices (length-width ratios) among oocysts recovered from both South African and Israeli hosts. Therefore,



Figures 32–36 Endogenous stages of *A. lineri* from intestine of *H. mabuia,* methacrylate embedding, H–E; all same magnification, arrows indicate 'rootlet like' connections.

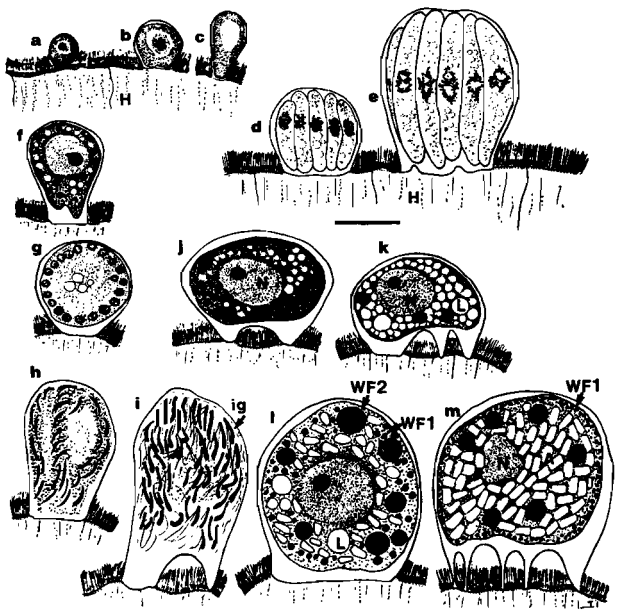


Figure 37 Detailed drawings of endogenous stages of *A. lineri* from intestine of *H. mabuia,* methacrylate embedding, H–E: a–c. young stages (meronts or gamonts); d, e. meronts segmented into merozoites (e. tangential section?); f. young macrogamont; g. young microgamont; h. microgamont before final differentiation; i. differentiated microgamont into microgametes; j, k. premature macrogamonts; l. mature macrogamont; m. zygote.

although calculated means for oocysts of either host differed (1,33 *vs.* 1,56), the shape indices of the two groups were grossly overlapping (1,25–1,60 *vs.* 1,39–1,80). Oocyst mean shape index of the USA geckoes was 1,3 (1,1–1,5). Comparison of the oocyst morphometry from the two hosts is presented in Table 2.

Endogenous stages in the intestinal epithelium (Figures 23–37)

All endogenous stages developed at the microvillous portion of the intestinal epithelium and were enclosed in the microvillous border of their host cell which expanded into the lumen (Figures 23–37). Low to medium infections were restricted to the anterior portion of the intestine, heavy infections extended to the mid-intestine. In both host species infection was encountered either at the peak of the gamogony or even at the onset of the oogony. There were no shape and size differences between corresponding stages from *H. turcicus* and *H. mabuia.* Newly attached stages, juvenile meronts and early gamonts (Figures 23, 35, 37a,b,c) were 2–4 × 1–3 μm. Meronts already divided into 12–16 merozoites (Figures 31a, 33, 34d,e) were 7–12 × 5–7 μm (size differences between Figures 37d and 37e cannot result from different section planes). Merozoites were 7–9 × 2 μm. Non-differentiated microgamonts containing numerous nuclei (Figures 25, 31d,e,f, 32, 34, 36, 37g) were 8–11 × 8–9 μm. Mature microgamonts, already differentiated into flagellated microgametes (Figures 28, 31g, 32, 37h,i) reached 11–15 × 7–11 μm. Young and immature macrogamonts (5–11 × 4–11 μm) were recognized by their large nucleus and distinct nucleolus (Figures 24, 25, 30, 31b,c, 37,f,j,k). Premature and mature macrogamonts (9–15 × 8–13 μm) (Figures 23, 26, 31h, 36, 37l) contained WF1s, WF2s, lipid vacuoles and PAS positive amylopectin granules. Both young and mature macrogamonts appeared to be connected with the host cell through rootlet-like connections (Figures 23, 25, 26, 35), which are in fact cross-sections through deeply infolded sides of the parasitophorous bulge of the host cell (confirmed by scanning electron microscopy, unpublished data). Mature macrogamonts/zygotes (12–18 × 11–13 μm) (Figures 23, 27, 29, 30, 31i, 37m), were loaded with translucent PAS positive amylopectin bodies (Figure 24), still retained a number of WF2s (Figures 23, 27) and sometimes marginal aggregates of WF1s (Figure 37m). Part of the zygotes were detached, released into the intestinal lumen (Figure 30). Young thin-walled oocysts in the intestinal lumen were 18–22 × 13–14 μm (in cross-section).

Other species

Acroeimeria (Eimeria) sceloporis (Bovee & Telford, 1965b) n. comb. [from *Sceloporus clarki boulangeri, S. occidentalis biseriatus, S. magister,* USA].

Data on *E. mitraria* (Laveran & Mesnil 1902) suggest development at the microvillous end of the host cell, but are not suffient to determine generic affinities.

Discussion

Length-width indices of oocysts

Bovee & Telford (1965b) recognized two distinct groups of *Eimeria* species among lizards, which differed distinctly in the shape of the oocyst. The oocysts of the first group have a long-ellipsoid or cylindrical form and the second group have a spherical or rounded form. Species with oocysts of the first type invariably underwent endogenous development in the gall bladder or biliary ducts, while species with oocysts of the other type inhabited the epithelium of the small intestine. A length/breadth index of 1,4 was set up to define the limit between the two groups (Bovee & Telford 1965b; Bovee 1971). *A. lineri* is exceptional among intestinal species in producing along with the usual rounded oocyst (with shape index > 1,4) also elongated, with shape index up to 1,8. Such values inevitably may overlap shape indices of some of the gall bladder species which form more rounded oocysts such as *C. urosauris* (Bovee, 1966) and *E. gehyrae* Cannon 1967 with shape index of 1,6 or *E. sinaita* Kasim & Shawa 1988 with shape index of 1,56. All this might suggest that length/breadth index cannot be applied too rigidly for grouping reptilian eimerians.

Genus *Choleoeimeria*

In all instances of endogenous development in the gall bladder epithelium (Setna & Bana 1935; Bovee 1969; Bovee & Telford 1965a; Brygoo 1963; Cannon 1967: Clark 1970; Fantham 1932; Vetterling & Widmar 1968 and present study), it followed a similar pattern where

parasite development involved hypertrophy and displacement of the host cell. This unique form of host-parasite relationship together with a characteristic oocyst morphology and development (i.e. elongate-cylindroid oocysts, bivalved sporocyst without a stieda body and endogenous sporulation) clearly separates these bile inhabiting species from eimerians infecting reptilian intestines. This type of relationship with the host cell is also unknown among coccidia infecting mammals or birds, including those species inhabiting the gall bladder (see Pellerdy 1974). All this justifies in our opinion the creation of the new genus *Choleoeimeria* for these species.

The status of the remaining species infecting reptilian gall bladders where endogenous development is presently unknown will remain unresolved. However, their relationship with the new genus is strongly suggested.

Differentiation to species level in *Choleoeimeria* can be based at present only on the morphometry of oocysts and sporocysts as with species of *Eimeria.* Oocysts and sporocysts' mean dimensions from the bile bladder of the autochthomous Israeli population and the population of *H. turcicus* (Upton *et al.* 1988) introduced into the USA, differed slightly, but their size ranges were closely overlapping. Shape indices were the same. There is no doubt that these two populations are conspecific. Oocysts of *C. turcicus* are the largest among those oocysts formed by bile-inhabiting species of *Choleoeimeria* and *Eimeria* of geckoes. Oocysts and sporocysts of comparable size to those of *C. turcicus* have been recorded from *Choleoeimeria* from North American lizards *C. ahtanumensis* (Clark 1970), *C. noctisauris* (Bovee & Telford 1965a) and *C. urosauris* (Bovee 1966). The oocyst to sporocyst length ratio in *C. turcicus* (3,5–3,6) is the same as in the smaller oocysts of *C. flaviviridis* (Setna & Bana 1935), while in *C. pachydactyli* (with oocysts similar in size to *C. flaviviridis*), sporocysts are considerably larger (with a ratio of 2:5) than those of *C. flaviviridis.* Similar in oocyst and sporocyst size to *C. pachydactyli* are *Eimeria gehyrae* Cannon 1967 (from the gall bladder of the gecko *Gehyra variegata* from Australia), *E. japonicus* Bovee 1971 (from the gall bladder of the gecko *Gekko japonicus* from Japan) and *C. egerinae* from an Australian skink (Cannon 1967). Nevertheless, owing to differences in hosts, at both the generic and suprageneric levels and geographical origin, the above-listed species are, in our opinion, unlikely to be regarded conspecific with either *C. turcicus* or *C. pachydactyli* despite apparent similarities in their oocyst and sporocyst dimensions. The endogenous developmental process has not yet been studied in detail in a sufficient number of species to give suitable comparative parameters for infrageneric differentiation. The structure, as well as the sizes of endogenous stages (meronts, gamonts and zygotes) are similar in *C. turcicus, C. pachydactyli, C. flaviviridis* (Setna & Bana 1935) and *C. egerinae* (Cannon 1967). In *C. noctisauris* both meronts and gamonts (within the hypertrophic displaced host cell) are somewhat larger (Bovee & Telford 1965a).

The number of produced merozoites is similar (about 60–70), in *C. turcicus* and in *C. pachydactyli;* in *C. flaviviridis* meronts were reported to contain 16–40 merozoites (Setna & Bana 1935). In species from hosts other than geckoes the number of produced merozoites ranged from 16 to 50 (in *C. ahtanumensis, C. cascabebli, C. chalcides, C. noctisauris* and *C. umis*), or is unrecorded (in *C. bitis, C. egerini* and *C. urosauris).*

Genus *Acroeimeria*

Localization of the meronts and gamonts at the microvillous zone of the intestinal epithelium host cell, as occurs in the presently described coccidia from the gecko, has been described in several piscine coccidia (Leger & Hollande 1922; Lom & Dykova 1982). This type of host-parasite relationship has not yet been found in eimerian infections in mammals and birds. Dykova & Lom (1981) formed a new genus *Epieimeria* for piscine eimerians which develop in the microvillous zone. Superficially, endogenous stages of the piscine and the presently described reptilian 'epieimerians' appear very similar. Piscine *Epieimeria* species however, show a close relationship with other piscine coccidia, they lack true wall-forming bodies and form a fragile oocyst wall (Lom & Dykova 1982; Molnar & Baska 1986). The 'epieimerian' coccidium described here from the gecko demonstrates clear affinities with other reptilian coccidia (Ostrovska & Paperna 1987; Paperna & Landsberg 1989), most notably, by the presence of two types of wall-forming bodies and the formation of a hard oocyst wall and therefore differ from 'epieimerian' piscine coccidia. Oocysts with a length/width of ratio of 1,2–1,6 are not exclusive to 'epieimerians' and are also formed by eimerine species of reptiles, including geckoes which develop like typical *Eimeria* spp. i.e. within the host cell (*E. ablephari,* Cannon 1967; *E. geckonis,* Tanabe 1928; *E. koidzumii,* Matsubayashi 1941; *E. lampropholidus* and *E.leiolopismatis,* Cannon 1967; *E. najae,* Ray & Das Gupta 1936). Many other eimerian species from reptiles, including geckoes (*E. boveroi,* Carini & Pinto 1926; *E. cicaki,* Else & Colley 1975; *E. helenae,* Bray 1981; *E.* sp. Yamamoto 1933) with the same oocyst length / width ratio are known, but only from oocyst stages. Differentiation of *Acroeimeria* species from species of other reptilian eimerine genera with similar oocyst dimensions is therefore not feasible unless the mode of their endogenous development is known. Apart from *A. lineri* an apparent 'epieimeria' development can only be demonstrated in one species, *E. sceloporis* Bovee & Telford 1965 (and maybe also in *E. mitraria* Laveran & Mesnil 1902).

Oocysts of *A. sceloporis* (Bovee & Telford 1965) are of a similar size but rounder (length/width ratio $< 1,25$) and the sporocysts are smaller than those of *A. lineri.* Differences in hosts (on a family rank) and geographical location (North America *vs.* Afroasia) are, however, in favour of regarding the two as distinct species. *E. boveri* (redescribed by McAllister & Upton 1989), the only other species of *Eimeria* described from *Hemidactylus mabuia,* differs from *A. lineri* in having considerably smaller oocysts. The validity of the proposed conspecifity betweens *Acroeimeria* of *H. turcicus* and that of *H. mabuia* from South Africa may be questioned in view of

the apprent differences in calculated mean shape index for oocysts of the two populations. The shape indices for individual oocysts from the two populations are, however, overlapping. Some differences in mean and range of shape indices also exist between oocysts from the recently introduced into the USA *H. turcicus* and those from the autochthomous Israeli population in Israel. Interspecific variations in oocysts' dimensions and length-weight ratios are not exceptional among eimerine coccidia (Parker & Duszynski 1986). In addition, no differences could be demonstrated in the morphology, size and fine structure (Paperna 1989) of the endogenous stages of *A. lineri* from Israel and South Africa.

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