DESCRIPTION AND ULTRASTRUCTURE OF *LANKESTERELLA* SPECIES INFECTING FROGS IN KENYA

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Summary :

Two species of *Lankesterella* are described from Kenyan frogs. In the first, *Lankesterella ptychadeni* n. sp. from the frog *Ptychadena mascareniensis* (Dumeril & Bibron) found in the Lake Victoria region of Kenya, oogony and sporogony take place in the gut epithelium and in the lamina propria. Oocysts yield eight sporozoites which accumulate in both the gut mucosal epithelium and in the lamina propria. In the same frog merogony stages were traced in the liver, and sporogony stages, with eight sporozoite progeny, occurred in detached endothelial cells in the blood, alongside sporozoites in the erythrocytes. These stages represent either a different generation of the same species or belong to a different species.

The second, *Lankesterella dicroglossi* n. sp. recovered from *Dicroglossus occipitalis* (Gunther), in a spring south of Lake Baringo in Kenya, walled oocysts are formed in the reticulo-endothelial cells of the liver, spleen, and lungs and in the blood-vessel endothelium. Infected endothelium detaches into the blood stream. Oocysts yield over 40 sporocysts. The latter were seen accumulating in macrophage centers, as were invading circulating erythrocytes.

An ultrastructural study of *L. ptychadeni* oocysts and sporozoites reveales features in common with previously ultrastructurally studied *Lankesterella* spp., together with unique fine-structural features in the oocysts not reported to date: a large, rolled mitochondrion, an electron-dense tubulo-vesicular network, expanded Golgi-adjunct structures and endoplasmic reticulum filled with coarse granules.

KEY WORDS : *Lankesterella ptychadeni* n.sp., *Ptychadena mascareniensis*, *Lankesterella dicroglossi* n. sp., *Dicroglossus occipitalis*, Kenya, oogony, sporogony, gut epithelium, lamina propria, reticulo-endothelium, blood, ultrastructure.

RÉSUMÉ : DESCRIPTION ET ULTRASTRUCTURE D'ESPECES DE *LANKESTERELLA* INFECTANT LA GRENOUILLE AU KENYA

Deux espèces de Lankesterella *sont décrites chez des grenouilles du Kenya. La première,* Lankesterella ptychadeni *n. sp., de la grenouille* Ptychadena mascariensis *(Dumeril & Bibron) a été trouvée dans la région du Lac Victoria ; oogonie et sporogonie ont lieu dans l'épithélium digestif et la lamina propria. Les oocystes donnent huit sporozoïtes qui s'accumulent à la fois dans l'épithélium digestif muqueux et la lamina propria. Chez la même grenouille, les stades mérogoniques sont retrouvés dans le foie, et les stades sporogoniques, donnant huit sporozoïtes, se produisent dans des cellules endothéliales sanguines, à côté des sporozoïtes des érythrocytes. Ces stades représentent soit une génération différente de la même espèce, soit appartiennent à une espèce différente.*

La seconde espèce, Lankesterella dicroglossi *n. sp., a été observée chez* Dicroglossus occipitalis *(Gunther), dans une source au sud du Lac Baringo au Kenya. Des parois d'oocystes se forment dans les cellules réticulo-endothéliales du foie, de la rate et des poumons, ainsi que dans l'endothélium vasculaire. L'endothélium infecté se détache dans le courant sanguin. Les oocystes libèrent plus de 40 sporocystes. Ces derniers s'accumulent dans le centre des macrophages, et envahissent les érythrocytes circulants.*

L'étude ultrastructurale des oocystes et sporozoïtes de L. ptychadeni *révèle des caractères communs avec les* Lankesterella *spp. précédemment étudiées sous cet aspect, ainsi que des caractères propres à la structure fine des oocystes non rapportés à ce jour : mitochondrie large et enroulée, réseau tubulovésiculaire dense aux électrons, appareil de Golgi étendu et réticulum endoplasmique empli de granules.*

MOTS CLÉS : *Lankesterella ptychadeni n.p., Ptychadena mascareniensis, Lankesterella dicroglossi n. sp., Dicroglossus occipitalis, Kenya, oogonie, sporogonie, épithélium digestif, lamina propria, réticulo-endothélium, sang, ultrastructure.*

INTRODUCTION

Mansour and Mohammed's (1962) description of *Lankesterella bufonis* is the only detailed report available on *Lankesterella* from anurans of the African continent. There are two notes quoted by Bray, 1964, on *Lankesterella* sp. stages in the blood, by Awerizew (1914) and Rousselot (1953); Awerizew's note could also be describing a species of *Dactylosoma*. Species of *Lankesterella* have been described from anurans from Europe (Nöller, 1912), North and South America (Desser *et al.*, 1990; Lainson & Paperna, 1995), and from Australia (Stehbens 1966*a, b*). The last three quoted studies also include fine structural data.

In this communication two new species of *Lankesterella* are described from East African frogs. The first,

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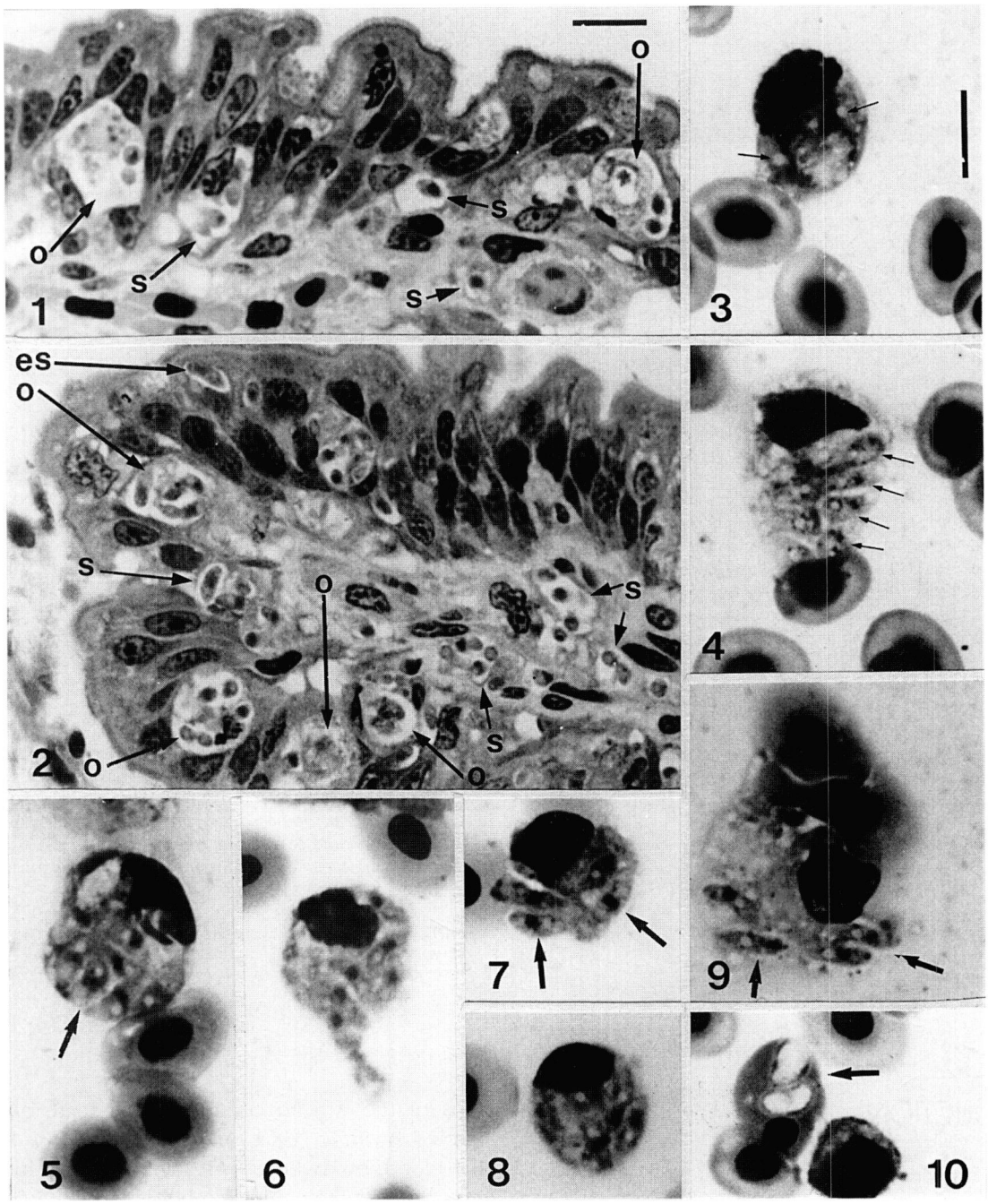


Figs. 1. and 2. — Oocysts and sporozoites of *Lankesterella ptychadeni* n. sp. in a histological section of *Ptychadena mascareniensis* gut; *es*, intraepithelial sporozoites; *o*, sporulating oocysts; *s*, sporozoites in the lamina propria cells (× 1,300).

Figs. 3 to 10. — Lankesterellid stages in the blood of *P. mascareniensis*, Giemsa stained (× 1,500): 3. Non-divided oocyst in detached endothelial cell (arrows- nuclei with refractile bodies). 4. Same type cell with dividing oocyst (arrows: emerging sporozoites). 5,6. Same type cells, each with sporozoites released from sporulated oocyst. 7,8. Monocytes with progenies of sporulated oocysts. 9. Sporozoites abondoning their endothelial host cell. 10. Sporozoites inside an erythrocyte.

found in *Ptychadena mascareniensis* exhibits unique features which have not been observed in the previously studied members of this genus, whereas the second, from *Dicroglossus occipitalis*, conforms with the generic general features and structural patterns.

MATERIALS AND METHODS

Anurans were collected during August-September 1994 from a number of localities in Kenya for a study on coccidioses and blood protozoa. Animals were killed with chloroform; blood samples drawn from the heart diluted in frog saline (0.5 %), and fresh tissue squash preparations from the intestine, liver, spleen and kidneys were examined under phase-contrast microscope for hematozoans and coccidians. Blood films, smears prepared from the intestine, and touch preparations from the liver, kidneys and spleen were air-dried and stained after fixation in absolute methanol with Giemsa. Only tissues from infected specimens were processed for histology and electron microscopy. The stages in the blood of *P. mascareniensis* were detected only in stained blood films, examined long after the necropsy and collection of tissue samples for histology and electron microscopy.

For histology, tissues were fixed in neutral buffer formalin and after dehydration in graded ethanols were embedded in glycol-methacrylate medium (GMA of Agar, UK). Sections, 3-4 µm, were cut with a glass knife on a Sorval JB4 microtome and stained with Mayer's hemalum-eosin. For electron microscopy, tissues were fixed in 2.5 % cacodylate (0,1 m, pH 7.4) buffered glutaraldehyde for 24 hours at 4 °C, repeatedly rinsed, postfixed in 1 % osmium tetroxide in the same buffer for one hour, rinsed, dehydrated in graded ethanols and embedded in Agar 100® (Agar, UK). Thin sections were cut on a Reichert « Ultracut » with a diamond knife, stained on grid with uranyl acetate and lead citrate and examined in a Jeol 100CX TEM.

RESULTS

Infection comprised of lankesterellid oocysts and sporozoites was recovered in one of four small (20 to 23 mm long, excluding legs) *Ptychadena mascareniensis* (Dumeril & Bibron) caught at Aheru in ricefield canals fed by a nearby stream in the hinterland of Lake Victoria in Kisumu, Kenya. Sporozoites of *Lankesterella* with no other stages were found in the blood and livers of a further five out of 27 frogs of the same and congeneric species (*P. anchietae* (Bocage) and *P. porosissima* (Steindacner)) examined from swamps fringing Lake Victoria at Kisumu. An additional 15 *Ptychadena* spp. from the Lake Baringo basin and seven from Sagana fish farm located north of Nairobi were free of lankesterellid infection. In one specimen of *Dicroglossus occipitalis* (Gunter), out of three examined, from a spring south of Lake Baringo, young and sporulated oocysts, and free sporozoites of a *Lankesterella* sp. were detected in the liver and the spleen, and intraerythrocytic sporozoites were found in the blood.

DESCRIPTION OF NEW SPECIES

Lankesterella ptychadeni, n. sp.

Type host: *Ptychadena mascareniensis* (Dumeril & Bibron).

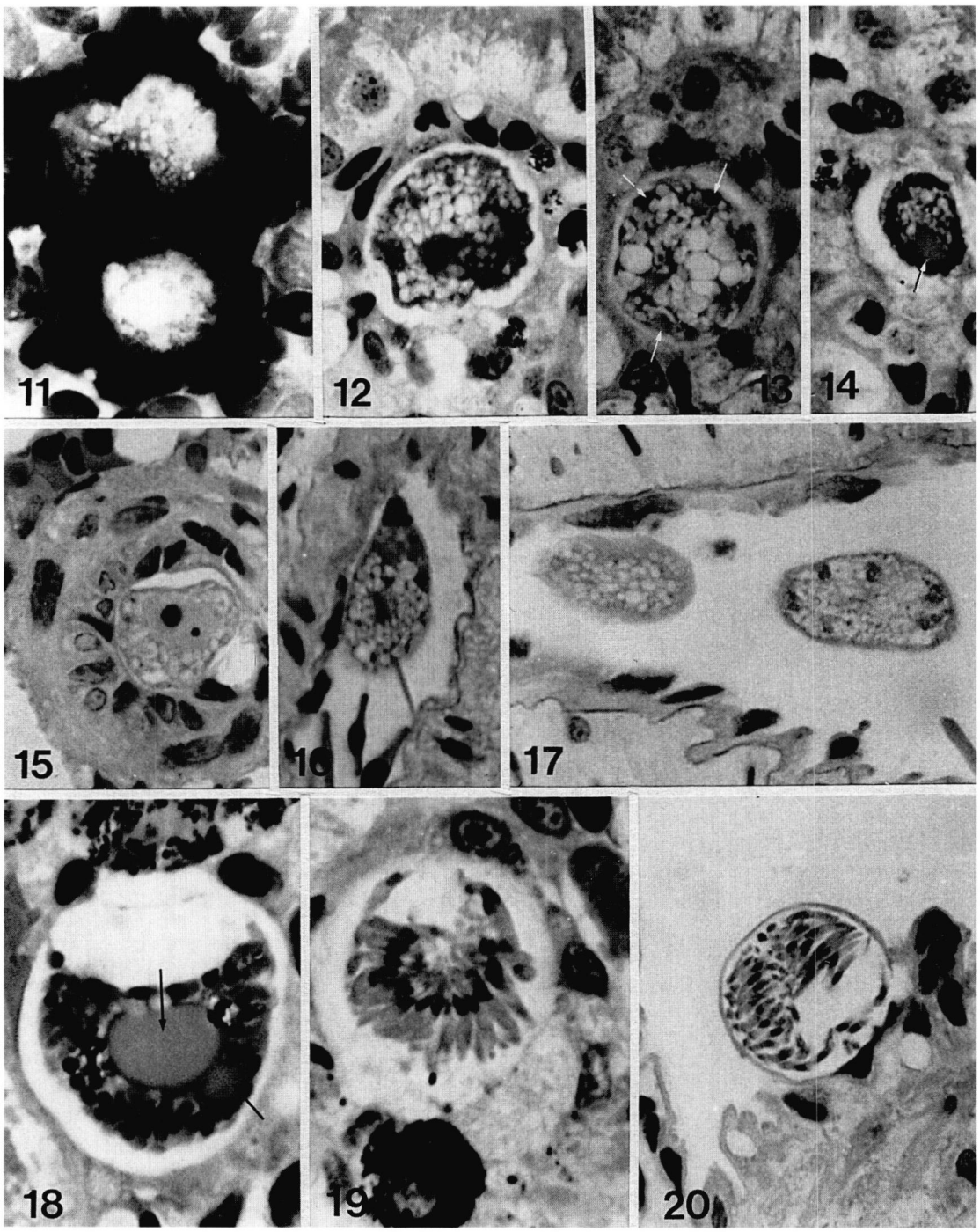
Type locality: Aheru rice fields, East of Lake Victoria in Kisumu, Kenya.

Stages in the intestine

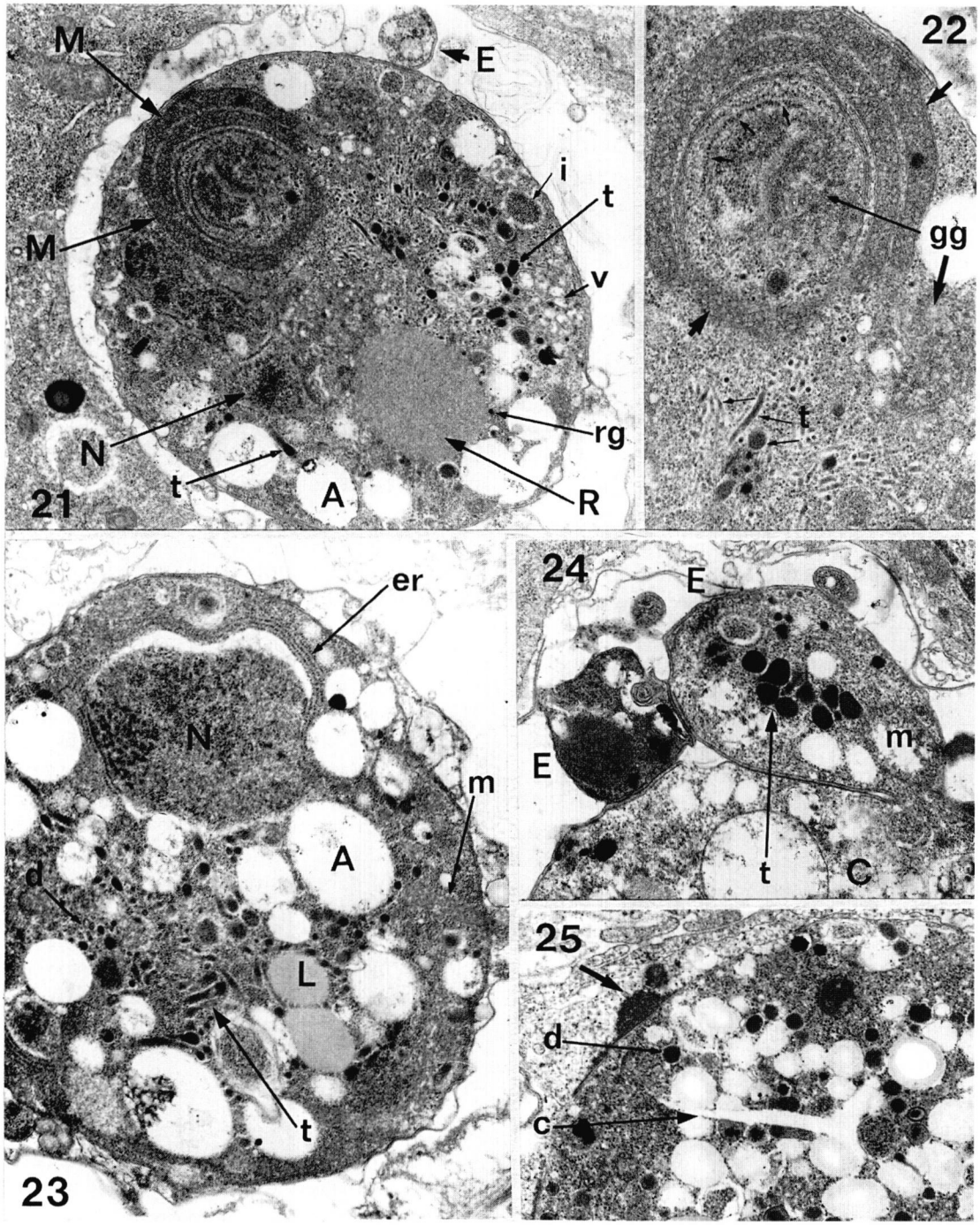
Young 7-8 µm in diameter and sporulated oocysts as well as numerous 6-8 x 1-2 µm sporozoites (with their characteristic refractile body) occurred both in the epithelium and in the lamina propria (Figs 1, 2). Oocysts and sporozoites formations (of up to six in histological sections) accompanied by an oocyst residue were located within large vacuolized, 11 x 11 to 16 x 24 µm enclaves — the remains of the hypertropied host cell, often fringed by a flattened nucleus. Both the epithelial layer and the lamina propria also contained many single extracellular sporozoites and host cells invaded by one to several sporozoites. The sporozoites were located in individual or merged parasitophorous vacuoles (PVs).

Stages in the blood

Enlarged, up to 21 x 15 µm, presumably detached endothelial cells (Figs. 3 to 6, 9) either contained oocysts with up to eight nuclei accompanied by a distinct, round, blue refractile body, but with no defined outlines of zoites (Fig. 3), or oocysts where the sporozoites division was incomplete remaining in part interconnected (Fig. 4), or with formations of up to eight 6-7 x 1-2 µm sporozoites (Figs. 5 to 6, 9). The sporozoite formations occupied the major portion of the host-cell cytoplasm. Sporozoites contained a deep staining red nucleus and one, exceptionally two, pale-blue-staining refractile bodies. Monocytes, and exceptionally other types of leukocytes contained few (up to six) or one slender 5.6-6.5 × < 1,2 µm sporozoite (Figs. 7, 8). Single robust (4.2 × 2,8 µm), or slender (5.6-7.7 ×, 1,4 µm) sporozoites also occurred in some erythrocytes (Fig. 10).



Figs. 11 to 20. — *Lankesterella dicroglossi* n. sp. in *Dicroglossus occipitalis* (11, in Giemsa-stained smears [× 1,300], the rest in histological sections — 12, 13 × 1,250; 14, × 800; 15-17, × 1,330; 18, 19 × 2,000, 20, × 1,500).
11. Walled sporulated oocysts in the spleen. 12, 13. Zygote or young oocyst in the liver; 14. Sporoblast in the liver, with divided nuclei at the periphery and a central refractile body. 15. Macrogamont in an endothelial cell in a lung venule. 16. Late macrogamont or young oocyst in a detaching endothelial cell in a venule in the lungs. 17. Detached young oocysts in the lung venule. 18. Sporulated oocyst in the liver, arrows: residual refractile bodies. 19. Oocyst yielding sporozoites formation in the liver. 20. Sporozoite yield of sporulated oocyst in an endothelial cell in the lung.



Figs. 21 to 25. — Electron microscopic images of zygote-young oocysts of *Lankesterella ptychadeni* in the gut of *Ptychadena mascareniensis*. 21. Young oocyst with, one (or two?) nuclei (N), and an extension (E), showing a refractile body (R) with electron-dense droplets (*rg*), a rolled mitochondrion (M), a tubulo-vesicular system (*t*), a Golgi-adjunct globular aggregates (*gg*), amylopectin granules (A), inclusions (*i*) and an array of vesicles (v) (× 12,800). 22. Enlarged view showing details of the rolled mitochondrion (thick arrows), enclosing the specialized ER (fine arrows), note details of the tubulo-vesicular system (*t*) and the Golgi-adjuct -globular complex (*gg*) (× 26,000). 23. Zygote with a large nucleus(N), amylopectin granules (A) and lipid vacuoles (L), revealing small mitochondria (*m*), concentric, circumnuclear ER (*er*), tubulo-vesicular system (*t*) and electron-dense granules (*d*) (× 15,500). 24. Details of the oocyst (C) extension (E) with a variety of cytoplasmic organelles including a mitochondrion and electron-dense vesicles (*t*) (× 14,000). 25. Oocyst with electron-dense material deposited on its wall (bold arrow); note also canaliculi (*c*), electron dense granules (*d*) and amylopectin granules (A) (× 20,000).

The few sporozoites traced in the liver were within red blood cell, none were seen in the spleen or the kidneys.

Sporozoites found in erythrocytes of frogs of the same species in the Lake Victoria fringe swamps were 8-14 × 2.1-2,8 µm (n = 5).

Lankesterella dicroglossi n. sp.

Type host: *Dicroglossus occipitalis* (Gunter).

Type locality: Spring system, southeast of Lake Baringo.

Oocysts encased in a thin but firm wall were most numerous in the liver and lungs, but also occurred in the spleen (Figs. 11 to 14). Infection was also recovered in the endothelial lining of arterioles and venules in the lungs and mesenteries; infected cells and free oocysts were sloughed into the blood circulation (Figs. 15 to 17). Macrogamonts (14-15 µm in diameter) contained a large central nucleus with a distinct nucleolus (Fig. 15). Oocysts varied in size from 14 × 11 to 21 × 19 µm, and with a few, in the liver reaching up to 28-35 µm in diameter (Figs. 12, 13). The ones released from the endothelium into the blood were 14-25 × 10-15 µm. Non-divided oocysts were loaded with amylopectin granules, with faint outlines of a nucleus and a few scattered eosinophilic bodies (wall-forming-like bodies?) (Fig. 13). Some oocysts were overlaid with a dense eosinophilic layer or deposit. One oocyst yields over 40 sporozoites (Figs 18-20). Divided nuclei were seen to accumulate along the oocyst margins (Fig. 14) and eventually differentiated into 7-9 × 1-1,4 µm sporozoites. The latter were arranged around a residuum comprised of the remains of the amylopectin granules and a large eosinophilic inclusion, apparently the remains of the oocyst refractile body (Fig. 18). The released sporozoites occurred free in the liver and spleen, or accumulated inside macrophages (up to six per cell). Intracellular sporozoites were somewhat wider (2,8 µm) than the free ones; all sporozoites contained one anterior and one posterior refractile body. Sporozoites were particularly numerous in macrophage centers. Erythrocytes contained only single sporozoites.

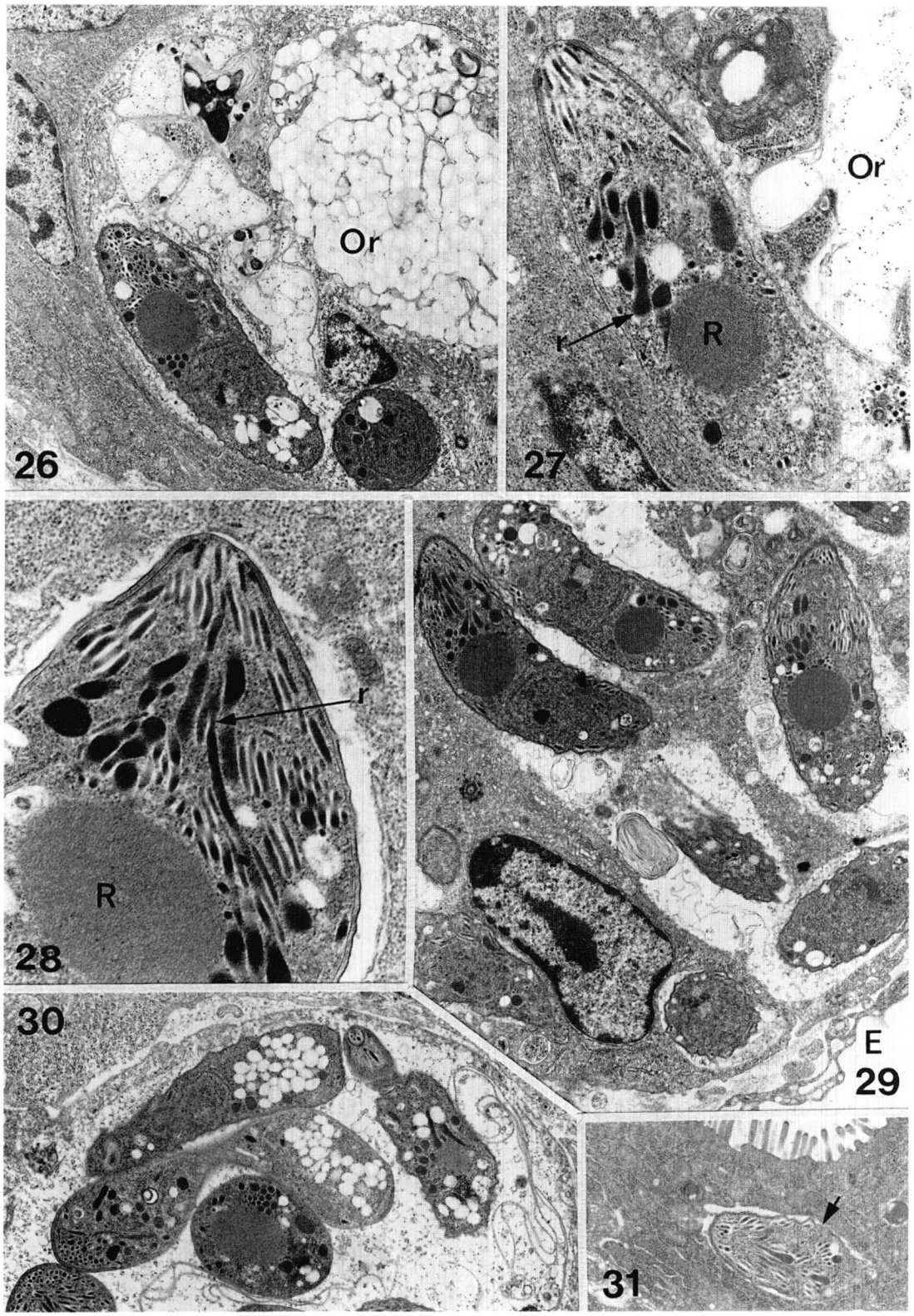
Fine structure of *Lankesterella ptychadeni* from the gut tissue

Oocysts

Oocysts revealed one or several nuclei, and some already contained a refractile body (Figs. 21 to 25). They were bound by a trilaminated cell wall, the outer lamina being the thickest, the middle one thin and fragile (Figs. 22, 24). Some oocysts were also enclosed by an additional loose, bilaminated membrane (Fig. 23). The walls of other oocysts contained deposits of a heavy electron-dense substance (Fig. 25). Electron-dense deposits also occurred along the boundary of the PV. The PV was limited by a bilaminated wall membrane. The oocyst produced cytoplasmic, membrane-bound extensions into the PV lumen (Figs. 21, 24). In addition the PV lumen contained membranous aggregates. The oocyst cytoplasm contained one large refractile body, amylopectin granules, lipid and food vacuoles, canaliculi and a variety of other inclusions (Figs. 21 to 25). At its boundary the refractile body contained the same electron-dense droplets (Fig. 21) reported in the rims of the refractile bodies in other *Lankesterella* spp. oocyst (Desser *et al.*, 1990; Lainson & Paperna, 1995). A large, elongated, rolled mitochondrion enclosed a cytoplasm rich in ribosomes, which contained a conspicuous endoplasmic reticulum (ER) and Golgi-adjunct-like structure. The latter seems to be the extension of a complex of Golgi-adjunct plates and globular aggregates which occupy the section area between the nucleus and the large mitochondrion (Figs. 21, 22). The cytoplasm contained numerous tubules terminating in vesicles filled with electron-dense substance reminiscent of micronemes or rhoptries (Figs. 21 to 23); the ER tubules were filled with regularly spaced granules. The ER also formed concentric loops around the nucleus (Fig. 23). The cytoplasm also contained additional small mitochondria, and a few to numerous granules with various densities of electron-dense particles reminiscent of type-1 wall-forming bodies (but could also be cross sections of the tubulo-vesicular organelles, Figs. 23, 25). The cytoplasm of the oocyst extensions was continuous with the oocyst contents and revealed mitochondria, very expanded electron-dense tubulo-vesicles, a few amylopectin granules and other vesicles (Fig. 24). The oocyst and host cell demonstrated various degrees of cytological damage which could have resulted from impaired processing. With the maturation of the oocyst, host cells evidently degenerated (detectable also in histological material). The necrotic material formed around the oocyst could have impeded the entry of TEM fixatives or the impregnation process.

Sporozoites

Sporozoites were observed either at their site of differentiation next to the residue of their oocyst (Figs. 26, 27), or established within cells of the gut epithelium (Fig. 31) and the lamina propria (Figs 28, 29, 30). Oocyst residue consisted mostly of amylopectin granules. Sporozoite fine structure conformed with that of previously described, lankesterellids and eimerians in general: bound by a pellicle, with an elaborate apical complex — a conoid, rhoptries, micronemes (Fig. 28), at least 20 microtubules, a single nucleus, at least a single large mitochondrion, a food vacuole and a variable number of amylopectin granules (Figs. 27 to 30). All



Figs. 26 to 31. — Electron microscopic images of sporulated oocysts and sporozoites of *Lankesterella ptychadeni* in the gut of *Ptychadena mascareniensis*. 26. Site of sporulated oocysts with sporozoites alongside oocyst residuum (Or) (× 7,200). 27. Enlarged view of a newly differentiated sporozoite (R, refractile body; *r*, rhoptries, × 10,630). 28. Anterior end, with the apical complex of a sporozoite (× 29,600). 29. Sporozoites established inside individual PVs in a cell of the lamina propria adjoining the endothelium (E) (× 8,200). 30. Infected host cell in a state of disaggregation, sporozoites are located within a common space; arrow: residues of the PV limiting membranes (× 9,600). 31. Sporozoite inside an epithelial enterocyte (× 5,800).

cross sections revealed only one refractile body located beween the apical complex and the nucleus (Fig. 29). Sporozoites were initially located within individual PVs. The latter were filled densely or loosely with flocculent or particulate material, globules and membranous residue. Gradual disaggregation of the rims of the PV often leads to the eventual incorporation of the individual PVs into one expanded parasitophorous enclave (Fig. 30), and ultimately to the dissolution of the entire host cell and release of the sporozoites.

DISCUSSION

Lankesterella ptychadeni found in *Ptychadena mascareniensis* in Kenya differs from all previously described species not only in its unique site of development and its fine structural features (outlined above), but also by the following conventional criteria for differentiation: its oocysts yield eight sporozoites, as compared with 16-32 and up to 50 sporozoites in *L. minima* from *Rana esculenta* from Germany (Noller, 1912), 70 from the same species from *Rana catesbeiana* from Canada (Desser *et al.*, 1990) and up to 32 in L. *petiti* from *Bufo marinus* from the Amazonian region, Brazil (Lainson & Paperna, 1995). A progeny of eight is also characteristic of *L. hylae* from the Australian tree frog *Hyla (Littoria) caerulea* (Stehbens 1966a); conspecificity is, however, unlikely due to differences in host species and geographical location.

The single sporozoites seen in the erythrocytes probably represent the final stage in the sporulation process of this gut *Lankesterella*. It is not certain, however, if the sporulating oocysts circulating in the blood within detached endothelial cells seen in the same host are *L. ptychadeni*. This, inspite of the apparent similarity in progeny size (eight) and the presence of a single refractile body in the sporozoite.

The new species *Lankesterella dicroglossi* found in the Kenyan frog *Dicroglossus occipitalis* sporulates in the reticulo-endothelial cells of the lungs, liver and spleen, and like *L. minima* and *L. petiti* forms oocysts with firm walls (Desser *et al.*, 1990; Lainson & Paperna, 1995). The sporozoite progeny numbers of over 40 resembles that of *L. minima* from European frogs. Conspecificity with the latter species is, however, unlikely due to generic and family-level differences in the hosts.

Sloughing of infected endothelial cells into the blood stream was observed in both lankesterellid infections, in *P. mascareniensis* and *D. occipitalis*, and also earlier, in *L. petiti* (Lainson & Paperna, 1995). This phenomenon appears to be common to species of *Lankesterella* developing in the endothelial cells of their hosts.

Oocysts development and accumulation of sporozoites in the gut epithelium and lamina propria, as seen in *L. ptychadeni* infection, is characteristic of *Schellackia* spp. rather than of *Lankesterella*. In the remaining species of *Lankesterella*, including that presently reported from *D. occipitalis*, the endogenous development occurs in the reticulo-endothelial system of the visceral organs. In *L. hylae*, sporozoites may enter the lamina propria, but development takes place in the reticulo-endothelial cells (Stehbens, 1966*a*). Nonetheless, fine structural data of the presently described young oocysts reveal little resemblance to *Schellackia*: they lack the characteristic type-1 and -2 wall-forming bodies characteristic of the latter genus (Ostrovska & Paperna, 1987) and shared also with all species of reptilian, avian and mammalian *Eimeria* (Scholtyseck *et al.*, 1971). The observed oocysts formed cytoplasmic extensions into the PV, and heavy electron-dense material was deposited on the boundary wall of some oocysts. These, and the electron-dense droplets seen at the rim of the refractile body have been reported in previously ultrastructurally studied *Lankesterella* spp. (Desser *et al.*, 1990; Lainson & Paperna, 1995). The electron-dense granules reminiscent of type-1 wall-forming bodies also occur at some stage in the differentiation of *L. petiti* oocysts (Lainson & Paperna, 1995). The latter similarities favor the affiliation of the presently described coccidium with the genus members of *Lankesterella* — despite of the unusual site of oogenesis.

Finding sporozoites inside the gut epithelial layers is exceptional, even for those *Schellackia* spp. whose oogenesis occurs in the gut mucosa. The infection in the frog was very high, thus the excessive numbers of sporocyst formed might have delayed their clearance from the epithelium into the lamina propria.

Further peculiarities unique to the presently described coccidium were the rolled mitochondrion, the electron-dense tubulo-vesicular network, and the ER filled with granular substance.

The present findings further emphasise the invalidity of using the family Lankesterellidae as a common taxon for both *Schellackia* and *Lankesterella*.

It is therefore proposed to reinstate Grasse (1953) system separating Schellackidae Grasse, 1953 from Lankesterellidae Noller, 1920. Contrary to the relatively homogenous nature of *Schellackia* species which are characteristic eimeriids with heteroxenous life history, the taxonomic affinities of *Lankesterella* still need to be defined. Our knowledge of *Lankesterella*'s life history remains based on a very restricted number of known species. More species appear to exist, many of which are known only from intraerythrocytic sporozoites. The taxonomic affinities of *Lankesterella* (=Atoxoplasma) reported from avian hosts (Lainson, 1959; Khan & Desser, 1971) as well as of *Lainsonia* spp. (Landau, 1973, 1974) remain unconcluded, in

the absense of fine structural data on the macrogamont stages. The species of *Schellackia* reported from anuran amphibia (Le Bail & Landau, 1974; Paperna & Lainson, 1995), although fine structural data are lacking, seem to conform with the congeneric species described from reptiles. Their status, may, however, change when their fine structure is revealed.

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