PREFACE

The genus Gregarina was created by Dufour in 1828 for "un nouveau genre de ver qui vit en troupeau dans les intestins de divers insectes". These unicellular parasites were discovered before the cell theory was developed by Schwann & Schleiden in 1839 and completed by Virchow in 1855, and therefore, Dufour supposed that they were helminths. He named *Gregarina ovata* and *G. cuneata*, the two first known species found in earwigs and beetles respectively. Many other species were further described over the whole world, aided by the easy detection of their large extracellular stages, even with simple binocular magnifiers, and by their abundance in a wide range of invertebrates, especially insects. The first major contributions to our knowledge of gregarines are due to Kölliker (1850–60), Lankaster (1860–85), Schneider (1875), Mingazzini (1891–93), and Siedlecki (1899) including the first observation of the process of fertilization in the cyst of *Lankesteria ascidae*. The occurrence of Microsporidia inside marine gregarines was established by Caullery & Mesnil (1897–1919). Léger (1904–1910) accurately described the gametogenesis of *Stylocephalus longicollis* and other species. In the first part of the 20th century, the occurrence of an asexual schizogonic process was demonstrated in marine gregarines by Brasil (1904–1910). Various classifications were proposed by Pixell-Goodrich (1915–1950), Ray (1930), Ganapati and coworkers (1937–46), Kamm (1922), Reichenow (1929–32) and other authors.

The chapter *Gregarines* written in 1953 by Pierre-Paul Grassé (*Traité de Zoologie*, Tome I, Masson Ed.) was the masterwork of what was known about this parasitic group at the middle of the 20th century, both in its biology, cytology at the light microscopic level and systematics. Since then, the development of methodological tools has considerably improved our knowledge of Gregarines and their place in the evolution of the Apicomplexa. The present revised and updated edition of the chapter *Gregarines* covers more than 60 years of publications, recording scientific investigations conducted in both cell biology and systematics of marine and terrestrial gregarines. In the early 60's, electron microscopy became the determinant for defining the cellular organization of these parasites. During that period, two main schools emerged in France, one focused on the ultrastructure of marine gregarines under the leadership of Emile Vivier at Lille University, the other on the ultrastructure of terrestrial gregarines under the direction of Pierre-Paul Grassé in the Laboratory 'Évolution des êtres organisés' (Faculty of Sciences, Paris). Since 1953, gregarine systematics were emphasized by Geus (1969) and Levine (1988) in book chapters and more recently by Clopton & Perkins (2000) in the *Illustrated Guide of Protozoa* (Lee, Leedale & Bradbury Ed.).

The Apicomplexa (Levine, 1970) are able to parasitise the majority of animal taxa due to their ability to develop outside and also inside host cells. The extracellular development of most gregarines explains their morphological variability and the predominance of their sexual reproduction with many gametes in large size gamonts.

In contrast the Coccidia and Hematozoa are able to enter and develop intracellularly in their vertebrate hosts, while their pathogenicity appears as a consequence of their asexual proliferation, a process additional to the formation of small intracellular gamonts. The systematics of gregarines is based on morphological, biological and molecular criteria that appear to be correlated with their localization in their hosts and to reflect their adaptation to the large diversity of environments, as well as the feeding behaviours and development of their invertebrate hosts. The emphasizing on the distribution of the different gregarines taxa in marine, freshwater and terrestrial hosts is therefore an important theme of this publication. The data presented in chapters III and IV is intended to facilitate the identification of species encountered by those who do not specialise in these parasites.

An important part of the information herein reported was collected from 1970 to 1980 by Jean Théodoridès for a supplement of the first edition of the *Traité de Zoologie*. The supplement remained unpublished after the death of P. P. Grassé, in 1985. This volume is dedicated to the memory of Jean Théodoridès (1927–1999) and Emile Vivier (1923–2011), for their contribution to the knowledge of Gregarines.

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Isabelle Desportes and Joseph Schrével

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Foreword

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J. C. Pinder, R. E. Fowler, A. R. Dluzewski, L. H. Bannister, F. M. Lavin, G. H. Mitchell, R. J. M. Wilson & W. B. Gratzer, 1998. Actomyosin motor in the merozoite of the malaria parasite, *Plasmodium falciparum*: implications for red cell invasion. Journal of Cell Science 111, 1831–1839.
J. Schrével, G. Asfaux-Foucher, J. M. Hopkins, V. Robert, C. Bourgouin, G. Prensier & L. H. Bannister, 2008. Vesicle trafficking during sporozoite development in *Plasmodium berghei*: ultrastructural evidence for a novel trafficking mechanism. Parasitology 135, 1–12.

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J. F. Dubremetz, 1973. Étude ultrastructurale de la mitose schizogonique chez la Coccidie *Eimeria necatrix* (Johnson 1930). J Ultrastruct Res, 42, 354–76.
M. Lebrun, A. Michelin, H. El Hajj, J. Poncet, P. J. Bradley, H. Vial & J. F. Dubremetz, 2005. The rhoptry neck protein RON4 relocalizes at the moving junction during *Toxoplasma gondii* invasion. Cell Microbiol. 7, 1823–1833.
M. E. Francia, C. N. Jordan, J. D. Patel, L. Sheiner, J. L. Demerly, J. D. Fellows, J. C. de Leon, N. S. Morrissette, J. F. Dubremetz & B. Striepen, 2012. Cell division in apicomplexan parasites is organized by a homolog of the striated rootlet fiber of algal flagella. PLoS Biol. 10(12): e1001444

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N. Steere, V. Chae, M. Burke, F.-Q. Li, T. Takemaru & R. Kuriyama, 2012. A Wnt/beta-catenin pathway antagonist Chibby binds cenexin at the distal end of mother centrioles and functions in primary cilia formation. PLoS One 7, e41077.
N. Steere, M. Wagner, S. Beishir, E. Smith, L. Breslin, C. G. Morrison, H. Hochegger & R. Kuriyama, 2011. Multiple centrosomes are induced in CHO and DT40 cells in a cdk-dependent manner. Cytoskeleton 68, 446–458.
R. Kuriyama, M. Bettencourt-Dias, I. Hoffmann, M. Arnold & L. Sandvig, 2009. Gamma-tubulin-containing abnormal centrioles are induced by insufficient Plk4 in human HCT116 colorectal cancer cells. J Cell Sci. 122, 2014–2023.

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N. W. Charon & S. F. Goldstein, 2002. Genetics of motility and chemotaxis of a fascinating group of bacteria: the spirochetes. Annu. Rev. Genet. 36, 47–73. Review.
S. Goldstein, N. Charon & J. Kreiling, 1994. *Borrelia burgdorferi* swims with a planar waveform similar to that of eukaryotic flagella. Proc. Natl. Acad. Sci. 91, 3433–3437.

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G. Prensier, E. Vivier, S. Goldstein & J. Schrével, 1980. Motile flagellum with a '3+0' ultrastructure. Science, 207, 1493–94.
G. Prensier & C. Slomianny, 1986. The karyotype of *Plasmodium falciparum* determined by ultrastructural serial sectioning and 3D reconstruction. Journal of Parasitology, 72, 731–36.
G. Prensier, J. F. Dubremetz & J. Schrével, 2008. The unique adaptation of the life cycle of the coelomic gregarine *Diplauxis hatti* to its host *Perinereis cultrifera* (Annelida, Polychaeta): an experimental and ultrastructural study. Journal Eukaryotic Microbiology, 2008, 541–53.

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J. Vavra & V. Sprague (Editors), 1976, 1977. Comparative Pathobiology Vol. 1. (Biology of the Microsporidia), Vol. 2. (Systematics of Microsporidia.) Plenum Press.
J. Vavra & J. I. R. Larsson, 1999. Structure of the Microsporidia, in: The Microsporidia and Microsporidiosis, ASM Press, Washington DC
E. U. Canning & J. Vavra, 2000. Phylum Microsporida, in: An Illustrated Guide to the Protozoa, Society of Protozoologists, USA.
L. F. Solter, J. J. Becnel & J. Vavra, 2012. Research methods for entomopathogenic microsporidia and other protists. In: Manual of Techniques in Invertebrate Pathology, 2nd Ed., Academic Press.