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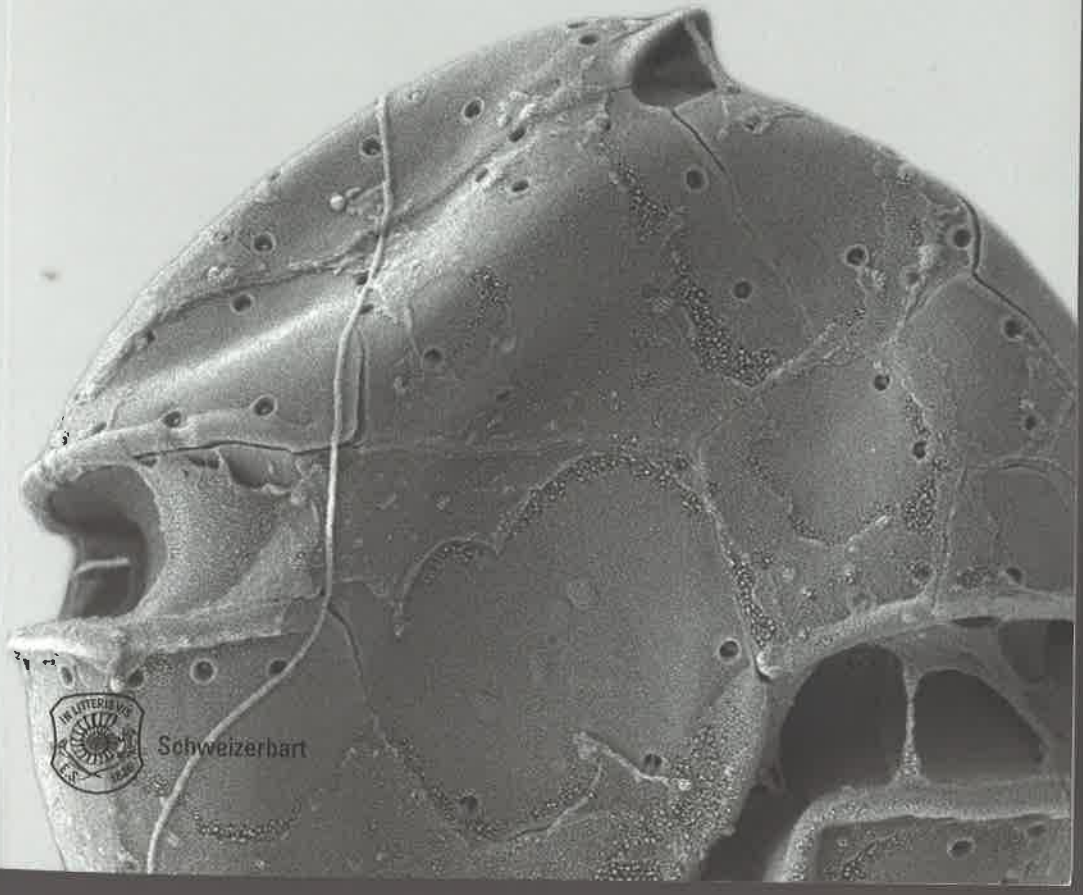
Mona Hoppenrath, Shauna A. Murray, Nicolas Chomérat, Takeo Horiguchi

Marine benthic dinoflagellates

– unveiling their worldwide biodiversity



Schweizerbart

Dinoflagellates are important primary producers, symbionts, but, at the same time, also consumers and parasites. The species composition in benthic habitats is quite distinct from planktonic habitats. The lack of comprehensive taxonomic studies of these taxa has complicated our progress in understanding dinoflagellate biodiversity, biogeography, and ecology. In recent years, benthic harmful algal blooms have attracted increasing interest because of the impact of ciguatera, the most important food-borne disease of nonbacterial origin worldwide, which is caused by benthic dinoflagellate species. These taxa seem to have widened their distribution lately.

This book summarizes the knowledge about the currently known benthic dinoflagellate species for the first time.

It presents the first comprehensive identification help for benthic dinoflagellates and is a basic contribution to improve monitoring efforts worldwide. About 190 species in 45 genera are presented, illustrated with more than 200 color images, about 150 scanning electron micrographs, and more than 250 drawings.

SENCKENBERG
world of biodiversity

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Impressum

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Volume 54: Marine benthic dinoflagellates – unveiling their worldwide biodiversity
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Front cover: *Herdmania*, the taxon was named to honor E.C. Herdman, who did the pioneering studies about marine sand-dwelling dinoflagellates (1921–1924).

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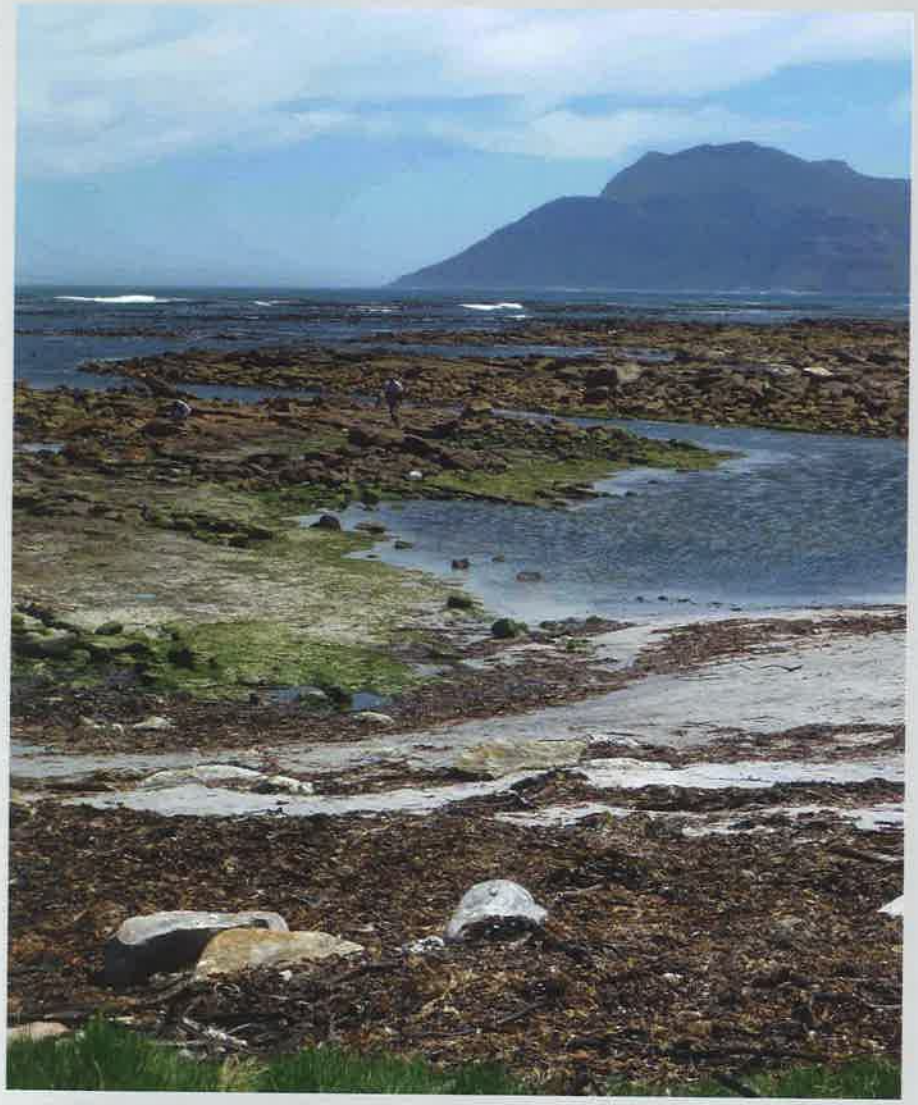

Kommetjie, Cape Town, South Africa. Diverse habitats at one site: sandy beach, rocky shore containing tide pools, and floating macroalgae.

Greetings

At present fewer than two million species are known to inhabit the biosphere, but experts estimate that between 5 to 50 times as many species are actually living on our planet. The relatively unexplored deep sea is fascinating for the public by its unknown biodiversity. But there is no need to search those far reaches to discover new species, they can be found "right in front of the door". To understand marine habitats, a lot of effort has been put into phytoplankton inventories worldwide. In particular, Harmful Algal Blooms (HABs) caused by diverse dinoflagellate taxa, are a major, socially and economically relevant field of research. In recent years the importance of benthic HABs is increasingly recognized because of the impact of ciguatera, which is the most important food borne disease of non-bacterial origin in the world and is caused by benthic dinoflagellate species. Benthic dinoflagellates are understudied, and the known species diversity has nearly doubled in the past 15 years, with new taxa discovered every year – including new genera. This book is the first comprehensive summary of their worldwide biodiversity and biogeography, covering a total of 189 species in 45 genera. With its excellent illustrations it will certainly help to identify and monitor these species and to assess potential risks of HABs causes by some of them. Hopefully, this book will also broaden the awareness of these fascinating, tiny, single-celled marine organisms and motivate students to study them.

The authors, who are among the very few expert taxonomists for these dinoflagellates (responsible for over a third of the taxon descriptions), illustrate through their long-term research that systematics and compiling inventories of life is a demanding and complex science requiring many years of experience and patience as well as advanced laboratory techniques.

My congratulations go to the four authors of this timely and important monograph, which certainly will serve as a standard work for many years to come. Senckenberg is proud to have supported this great project.

Volker Mosbrugger
Senckenberg Gesellschaft für Naturforschung

Foreword

It is a pleasure to introduce *Marine benthic dinoflagellates – unveiling their worldwide biodiversity*. The complicated taxonomy of benthic dinoflagellates is summarized using the most recent information from combinations of detailed microscopic observations, genetic approaches and careful, patient field studies. This work provides new and useful clues on the biogeography, systematics and ecology of this group, including some of the organisms causing harmful outbreaks, and concurrently highlights the unresolved difficulties and challenges for the thorough comprehension of the benthic dinoflagellates. This effort benefitted not only from recent technological advances, but especially, from the youth and diversity (from Germany, France, Australia and Japan) of the co-authors. The expertise of these young, motivated researchers holds much promise for the future of dinoflagellate taxonomy. At the beginning of the XXIst century, taxonomy is essential not only to establishing the worldwide biodiversity of benthic dinoflagellates, but to identify particular harmful taxa. Indeed, a main aim of this effort is to help monitoring programs prevent and mitigate the consequences of harmful events affecting human and ecosystem health. Finally, the thorough treatment of the benthic dinoflagellates provided in this book constitutes a solid basis for future studies on the structure and dynamics of benthic dinoflagellate communities.

This publication is especially timely because it comes to press in the spring of 2014, ten years after Professor Ramon Margalef passed away. Margalef would be particularly delighted reading it given his special admiration for dinoflagellates, as he clearly expressed in his contribution to the VIIIth Conference on Harmful Algae" held in Vigo on 1997: "*Dinoflagellates are admirable in their organization and behaviour*" (Margalef 1997). This book provides excellent images of this wonder of nature. The high quality and resolution of the microphotographs illustrate what it would be defined in Margalef's terms as "a comprehensive dictionary" of benthic dinoflagel-

lates or using the author's words, "the unveiled worldwide biodiversity", of this group. As was Margalef, we are certain the authors have experienced the pleasure of observing nature and the major gratification will be to communicate the fruits of the long hours of meticulous and inspired work. More importantly, this book will introduce scientists to the beauty, complexity, and importance of dinoflagellates for generations to come.

We congratulate M. Hoppenrath, S.A. Murray, N. Chomérat and T. Horiguchi on their fine publication. It is certain this volume will be a success and we hope that it will not be the last joint effort to bring the heretofore neglected benthic dinoflagellates to the forefront.

Elisa Berdalet, Raphael Kudela, Patricia A. Tester
February 2014

GEOHAB
Global Ecology and Oceanography of Harmful Algal Blooms

International Council for Science
SCOR
Scientific Committee on Oceanic Research

United Nations Educational, Scientific and Cultural Organization

Intergovernmental Oceanographic Commission

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Acknowledgements

This book was a "project" for Mona Hoppenrath (MH) but all co-authors had to work on it alongside, so that we want to thank our colleagues and students for their patience during busy writing times.

MH acknowledges a research scholarship from the Deutsche Forschungsgemeinschaft (DFG), as well as funding by the National Science Foundation (NSF), the National Science and Engineering Research Council of Canada (NSERC), and the Canadian Institute for Advanced Research (CIfAR). Shauna Murray (SM) wants to thank the Australian Research Council for funding her salary and the Australian Biological Resources Study (ABRS) for funding two field trips to Broome. Takeo Horiguchi (TH) wishes to thank the Ministry of Education, Culture, Sports, Science and Technology in Japan (MEXT) and also by the Japan Science and Technology Agency (JST, Strategic International Research Cooperative Programme) for financial support for benthic dinoflagellate projects.

We want to thank our colleagues Dr. Maria Saburova (Kuwait Institute for Scientific Research, Kuwait), Dr. Maria Faust (National Museum Natural History, Smithsonian Institution, USA), Dr. Elisabeth Nézan (IFREMER, France), Dr. Miriam Weber (HYDRA Institut für Meereswissenschaften, Germany), Dr. Alain Couté (Muséum National d'Histoire Naturelle, France), Dr. Loïc Ten-Hage (University Paul Sabatier, France), Dr. Piet Houpt (Vlissingen, The Netherlands), Dr. The Ho Van (Institute of Oceanography, Viet Nam), Dr. Ngoc Lam Nguyen (Institute of Oceanography, Viet Nam), and our former students Sarah Sparmann (University of British Columbia, Canada), Nadine Borchhardt (University of Oldenburg, Germany), Drs Maiko Tamura and Yoshihito Takano (Hokkaido University, Japan) for providing images. MH is thankful for the long-term benthic dinoflagellate collaborations with Dr. Marina Selina (Far Eastern Federal University, Russia), Dr. Brian Leander (University of British Columbia, Canada), and Dr. Yuri Okolodkov (Universidad Veracruzana, Mexico). Dr. Maria Saburova is thanked by MH and Nicolas Chomérat (NC) for sharing her benthic dinoflagellate findings / samples and collaboration. NC wants to acknowledge Dr. Maurice Loir (Gouesnach, France) for sampling and long-time collaboration as well as Drs Jean-Pascal Quod and Jean Turquet (Agence pour la Recherche et la Valorisation Marines, France) for samples from the Indian Ocean. SM and MH want to express their appreciation of the support by Dr. David J. (Paddy) Patterson (University of Sydney, Australia) and SM also wants to thank him for introducing her to systematics and being a mentor. Dr. Malte Elbrächter (Senckenberg, Germany) initiated MH's work about benthic protists and encouraged her taxonomy enthusiasm, thanks a lot for supervising. TH wishes to thank for the long-term dinoflagellate collaborations with Dr. Mitsuo Chihara (Tsukuba University, Japan) and Dr. Richard N. Pienaar (University of the Witwatersrand, South Africa). Dr. Carmen Zinßmeister's (Senckenberg am Meer, Germany) information about *Bysmatrum* cysts has been appreciated. Dr. John McNeill (Royal Botanic Garden, Scotland, U.K.) is thanked for nomenclatural advice and help to formally correct work with the ICN.

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I. Introduction

The first studies of dinoflagellates inhabiting in sandy sediments were conducted early last century (Kofoid and Swezy 1921, E.C. Herdman 1922, 1924a, b, Balech 1956), however, few studies were conducted in the decades after these. Further investigations started in the 1980s (e.g. Saunders and Dodge 1984, Larsen 1985, Dodge and Lewis 1986, Horiguchi and Pienaar 1988a, Horiguchi 1995, Faust 1995). Faust and Horiguchi had a continuous interest in benthic dinoflagellates, exploring mangrove and coral reef habitats and tide pools (e.g. Faust 1993a, b, 1997, 1999, Horiguchi and Chihara 1983a, 1988, Horiguchi and Pienaar 1994a, Horiguchi et al. 2000, 2011, 2012). Comprehensive studies of sand habitats occurred in the 2000s (Hoppenrath 2000b, Murray 2003, Tamura 2005, Mohammad-Noor et al. 2007b, Al-Yamani and Saburova 2010). These studies showed that a species composition quite distinct from planktonic habitats was present in benthic habitats. Less than 10% of the about 2000 described extant dinoflagellate species appear to be benthic (Taylor et al. 2008). They occur in different types of habitats (see chapter II) and appear to be adapted to a benthic life style in their morphology, in their behavior, and some also in their life cycles (see ecology chapter VI).

Some taxa are known to produce toxins impacting humans, particularly those occurring in tropical and subtropical regions (see chapter VII), which has caused an increase in research interest in benthic dinoflagellates. The study of harmful benthic dinoflagellates started in late 1970s with the discovery that a benthic species, later named *Gambierdiscus toxicus*, was thought to be responsible for ciguatera fish poisoning, a type of human poisoning linked to the consumption of certain species of tropical reef fish (Yasumoto et al. 1977). As ciguatera fish poisoning incidences are increasing, and the distribution of toxin producing benthic taxa seems to expand, an understanding of the species diversity and their identification is becoming more and more important. Blooms of harmful benthic dinoflagellates can cause serious human and environmental health problems. Recently the potentially toxic species have been subject of intense research activities (e.g. Litaker et al. 2009, Laza-Martínez et al. 2011; reviews: Parsons et al. 2012, Hoppenrath et al. 2013a).

The lack of comprehensive taxonomic investigations of benthic dinoflagellates complicates progress in our understanding of their biodiversity, biogeography and ecology, and motivated us to compile current information into this book. One hundred and eighty-nine species belonging to 45 genera are described and their known distribution recorded herein. The distribution section for the species lists the references in the following order: Arctic Ocean, North Atlantic (e.g., UK, North Sea, France, Spain, Portugal, east USA, Gulf of Mexico, Caribbean Sea), South Atlantic (e.g., Cape Town, South Africa), Mediterranean Sea, Arabian/Persian Gulf, Indian Ocean (e.g., Viet Nam, Malaysia, West Australia, South Africa), North Pacific (e.g., Sea of Japan, Korea, Japan, BC Canada, California), South Pacific (e.g., East Australia, New Caledonia, French Polynesia, New Zealand). It is the first comprehensive treatise on the group, and it is our intention that it will facilitate further studies.

The classification of dinoflagellates is currently changing and is far from being settled, with the discovery of new species and genera, and the rearrangements of systematic entities. Many benthic dinoflagellate genera have unusual morphologies and appear to be not closely related to known planktonic taxa, and molecular phylogenetic analyses frequently show low statistical support for any relationship (see chapter IV). They show unique thecal plate arrangements when compared to planktonic species, e.g. *Adenoides, Amphidiniella, Cabra, Planodinium, Rhinodinium, Sabulodinium* (see taxonomy chapter III). Therefore, no higher classification was used in this book and the genera (and species within a genus) are presented in alphabetical order. No keys were provided but information about similar species with which a taxon can be confused is given.

A good introduction to dinoflagellates is the Tree of Life web project page (http://tolweb.org/Dinoflagellates/2445). Summaries of main dinoflagellate characteristics were published in Hoppenrath et al. (2009a, 2013a) and of their diversity in F.J.R. Taylor et al. (2008). The cell orientation is explained in figure 1. For the thecal plate designation, the Kofoid system as modified and described in Fensome et al. (1993) was followed (Fig. 2). Some benthic taxa have thecal tabulations difficult to interpret and sometimes different designations (plate formulae) have been published for one taxon.

As our understanding of the morphological and genetic diversity of dinoflagellates has increased in recent years, some original descriptions of species may no longer be adequate to identify a taxon. Cryptic species diversity has been detected already (Murray et al. 2012), and it is highly likely that further cryptic species will be found. Furthermore, some old taxonomic concepts are no longer valid. For example within the unarmoured (athecate, naked) dinoflagellate genera some genus delimitations are unsatisfactory, and reclassification is still ongoing. For instance, the genera *Amphidinium*, *Gymnodinium*, and *Gyrodinium* were redefined (Daugbjerg et al. 2000, Flø Jørgensen et al. 2004a, Murray et al. 2004). As a consequence of the redefinitions many species can no longer be classified in the genera, need reinvestigation, reclassification or classification within new genera. For practical reasons and not to make them "nameless", the old generic names were used in this book, and the genera were separated into sensu stricto (s.s.) and sensu lato (s.l.) species.

Dinoflagellates are protists that historically have been treated in accordance with the International Code of Botanical Nomenclature (ICBN) and the International Code of Zoological Nomenclature (ICZN) – ambiregnal taxa. It has been agreed on solely applying the botanical code for dinoflagellates in future, and we here follow the latest version of the International Code of Nomenclature (ICN) for algae, fungi, and plants – the Melbourne Code (McNeill et al. 2012). Some species epithets (names) have been corrected, following article 32.2: "Names or epithets published with an improper Latin termination but otherwise in accordance with this *Code* are regarded as validly published; they are to be changed to accord with Art. 16–19, 21, 23, and 24, with-

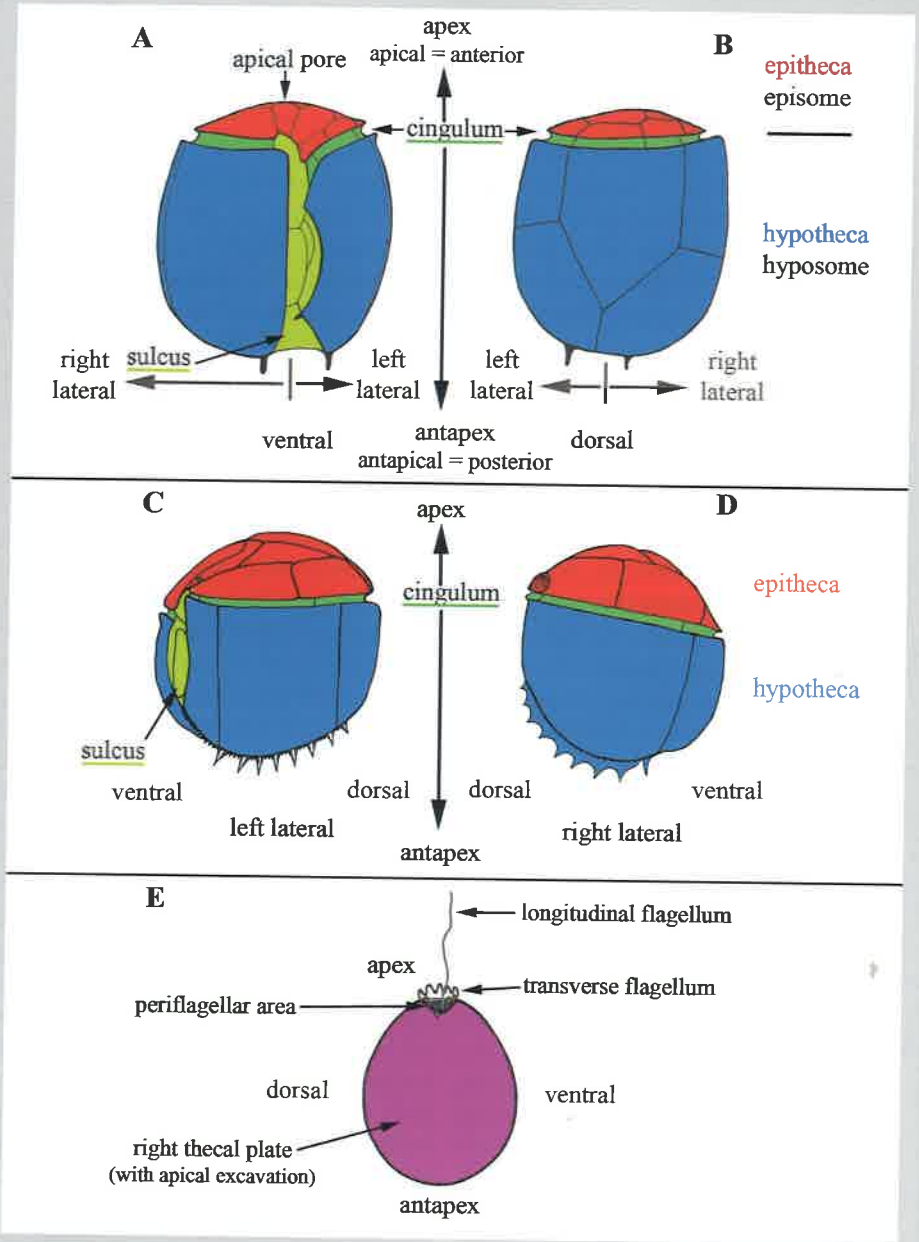

Fig. 1: Cell orientation. A–D: Dinokont cells. A, B: Dorsoventrally flattened cell. C, D: Laterally flattened cell. E: Prorocentroids, desmokont cell.

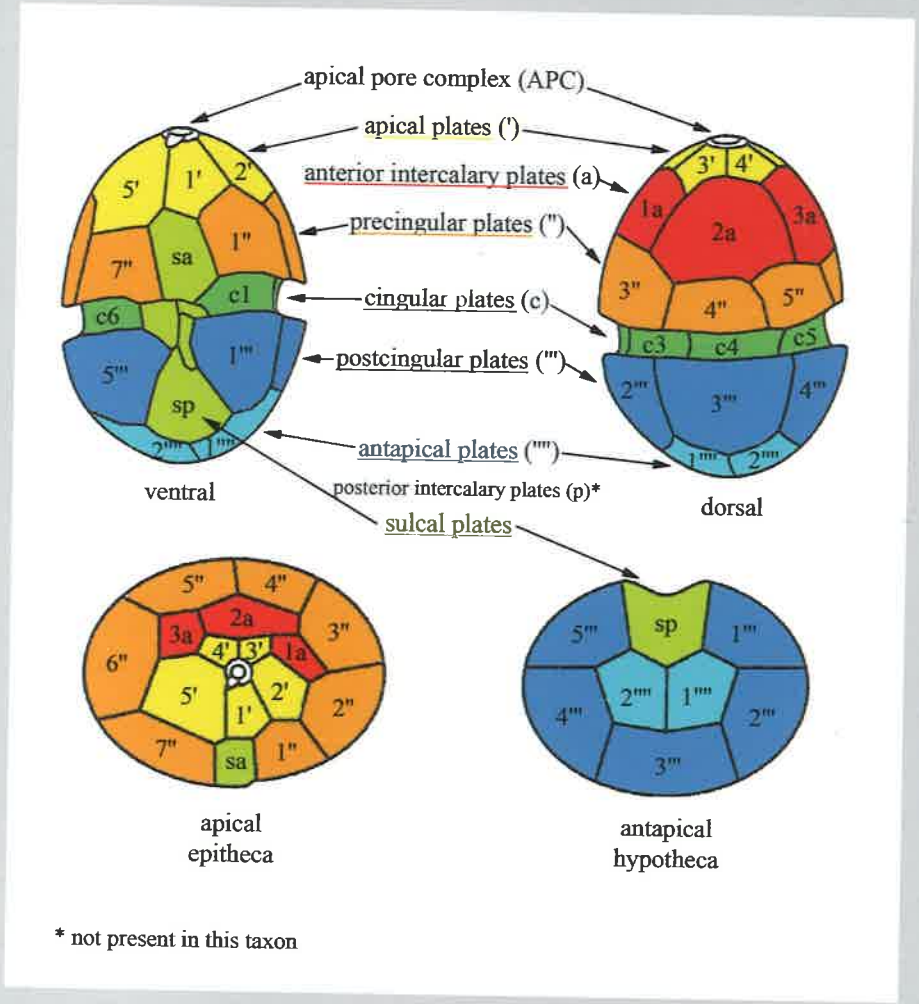

Fig. 2: Kofoid system of thecal plate designation.

out change of the author citation or date (see also Art. 60.12)." For the holotype designation in many published (past) new dinoflagellate species descriptions article 40.5 applied and still applies: "For the purpose of Art. 40, the type of a name of a new species or infraspecific taxon of microscopic algae or microfungi (fossils excepted: see Art. 8.5) may be an effectively published illustration if there are technical difficulties of preservation or if it is impossible to preserve a specimen that would show the features attributed to the taxon by the author of the name."

Authors' Addresses

Dr. Mona Hoppenrath

is a biologist/botanist. She studied at the University of Göttingen (Diploma 1995) and the University of Hamburg (PhD 2000). Her thesis was about the taxonomy and ecology of marine interstitial flagellates with an emphasis on dinoflagellates (Wadden Sea Station Sylt). As a postdoc (2000 to 2004) at the Biologische Anstalt Helgoland, AWI, she re-investigated the North Sea phytoplankton around Helgoland taxonomically, published as book in 2009 (Kleine Senckenberg-Reihe 49). From 2004 until the end of 2006 she was a research scientist at the University of British Columbia (UBC), Canada, working about the molecular phylogeny, morphology, and taxonomy of selected dinoflagellates. In 2007 she continued working at UBC as research scientist of the University of Maryland, USA, in an AToL project about an integrated approach to the phylogeny of dinoflagellates. Since 2008 she is a research scientist at the German Centre of Marine Biodiversity Research, Research Institute Senckenberg, in Wilhelmshaven, responsible for Marine Botany and the Centre of Excellence for Dinophyte Taxonomy (CEDiT, http://www.dinophyta.org/), and has a research focus on dinoflagellates. In 2009 she was an invited guest scientist at the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) in Concarneau, working together with N. Chomérat about the molecular taxonomy and phylogeny of benthic dinoflagellates from South Brittany. After habilitation at the Carl von Ossietzky University Oldenburg in 2012 she is now a private lecturer. Since her PhD study marine benthic dinoflagellates were her main research interest. She serves as Associate Editor for Protist and Phycological Research and is member of the Editorial Board of Botanica Marina and of the Board of Reviewers for The Journal of Eukaryotic Microbiology.

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Dr. Shauna A. Murray

is a biologist who studied at the University of New South Wales and the University of Sydney (PhD 2003) in Australia. Her PhD research focused on the molecular evolution and systematics of marine benthic dinoflagellates of southern Australia, including potentially toxic species and a phylogeny of the genus *Amphidinium*. After being awarded a grant from the Australian Biological Resources Study, she continued to work on marine benthic dinoflagellates from tropical Australian sites (2003 to 2005), and obtained a Japan Society for the Promotion of Science fellowship to the University of Tokyo in 2004 to work on the toxin producing benthic genus *Prorocentrum*. She worked briefly on the molecular evolution and ecology of vertebrates at the University of Sydney (2006 to 2007), before being awarded Vice Chancellor's and Australian Research Council (ARC) Fellowships at the University of New South Wales (2008 to 2012) to research the evolution, genetics and toxicity of the planktonic dinoflagellate genus *Alexandrium*, which produces paralytic shellfish toxins. She is currently an Associate Professor and ARC Fellow at the University of Technology, Sydney, with research interests into the molecular evolution, molecular ecology and toxicology of dinoflagellates.

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Fig. 93: The authors (from left to right): M. Hoppenrath, S. A. Murray, N. Chomérat and T. Horiguchi, at Senckenberg am Meer in Wilhelmshaven 2011. Photos V. Siegler, Senckenberg am Meer.

Dr. Nicolas Chomérat

is a biologist/phycologist. He studied in France at the University of Saint-Etienne and the University of Marseilles (Diploma in 2001, PhD in 2005). His thesis was about the ecology of brackish phytoplankton of a hypereutrophic lagoon from the French Mediterranean area, with an emphasis on potentially toxic cyanobacteria (*Planktothrix agardhii*) and dinoflagellates. After his PhD, he worked with A. Couté at the National Muséum of Natural History (Paris) on scanning electron microscopy of benthic dinoflagellates from the SW Indian Ocean, especially Glorioso islands and he specialized on the taxonomy of epiphytic and benthic dinoflagellates associated with ciguatera. Since 2006 he is a research scientist at the French Research Institute for the Exploitation of the Sea (Ifremer), at the Marine biological station of Concarneau and works with Elisabeth Nézan. His research focus is on taxonomy and molecular phylogeny of micro-algae, especially marine dinoflagellates. In South Brittany, he investigated the diversity of benthic dinoflagellates and described several new sand-dwelling taxa. He started international collaborations with