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BACCIO BACCETTI AND THE COMPARATIVE SPERMATOLOGY OF INSECTS

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Reconstructing the history of a scientific career is always a difficult task because there is the risk of ignoring events and achievements that may seem of minor importance to us but which to the person in question involved great commitment and dedication. Concerning Baccio Baccetti, however, there is no risk involved if we state that one of his major contributions to science was in the field of comparative spermatology, a topic that brought him to the attention of the international scientific community and rewarded him with honours and glory.

During his research work in Florence's Agricultural Entomology Station in the early 1960s, Baccetti, who already enjoyed the attention and kindness of Antonio Melis, Director of the Research Station, was able to take advantage of the enormous resolving power of transmission electron microscopy in the field of entomology. With uncommon farsightedness, Melis understood the innovative contribution of the new methodology and, thinking highly of Baccetti's abilities and ingenuity, decided to buy a small electron microscope, sensing that the new technology would lead to the advancement of knowledge in agricultural entomology. In 1959-1960, there were two electron microscopes in Florence: the small Hitachi HS·6 in the Agricultural Entomology Station in Via Romana and a Siemens Elmiskop in the Institute of Histology of the University's Faculty of Medicine at Careggi, directed by Prof. Allara.

To learn the necessary fundamentals of the new technique, Baccetti went to the Institute of Anatomy in Milan, directed by Prof. Aurelio Bairati, a famous professor of that city's University. There he learned the basic techniques for preparation of materials and for interpretation of the results; he also met colleagues with whom he shared his first experiences and early successes in a field of Biology that would soon produce important results. Indeed, electron microscopy provided the opportunity to investigate and describe the internal organization of cells and organs, and from this knowledge to understand their functions. In Milan, Baccetti met Bairati's son, Nanni, with whom he began to collaborate on the structure of germ cells and on the spermatogenesis of *Drosophila* and the dipteran agricultural pest *Dacus (Bactrocera) oleae*. I had recently returned from military service and I was asked to illustrate the flagellar complex of this dipteran described by the two Authors (1964), a drawing later published in Redia (Fig. IA). Unfortunately for me, it was not the custom at that time to cite the author of the drawing. These were the first reconstructions of the structure of a spermatozoon, an important basis for the functional interpretation of flagellar movement, first hypothesized by B.A. Afze1ius in 1959 and later confirmed by P. Satir and J. Gibbons (1963-1965). The movement of the spermatozoon occurs through the interaction of the dynein arms present on subtubule A of each axonemal doublet and subtubule B of the adjacent doublet, with consequent reciprocal sliding of the microtubules involved.

Nevertheless, this first approach to spermatology was not immediately followed up because Baccetti preferred to explore different topics, fully exploiting the resolving power of the new methodology. In the 1960s, he worked tirelessly and published important contributions on the fine structure of the myosin filament, on the ultrastructure of the intestine of insects, on the nervous system, on the supporting stroma of some organs, on the collagen fibre, on Malpighian tubules, and on the structure of the eyes of a spider. All these works helped Baccetti make a name for himself internationally. The first results on the structure of sperm cells also gave him the opportunity to describe the effects of sterilization of males of insect agricultural pests by the use of ionizing radiation. He obtained an Inatom contract with which he expanded the small electron microscopy laboratory he had set up in the back of the lecture hall in Via Romana and he hired a technician for the preparation of materials (Paolo Salvatici).

In 1964, Baccetti won the competition for a chair of Zoology. He was to move to Padua, but by an agreement with the University of Padua and the consent of Prof. Pietro Omodeo, Professor of Zoology in the University of Siena, Omodeo went to Padua and Baccetti to Siena, as Professor of Biology and Zoology. Baccetti took up his new post in 1966 and the small Hitachi electron microscope went with him, the first electron microscope in the city of the Palio. The new methodology, together with the fervour that drove Baccetti to form a school of young researchers, attracted many followers, some of whom formed the first nucleus of the staff of the renewed Institute of Zoology of the Faculty of Mathematical, Physical and Natural Sciences. I had arrived in Siena the previous year, as assistant along with Paolo Salvatici, and we had been given the task of organizing the laboratories, including that of electron microscopy. The small Hitachi microscope was in constant use in the various lines of research but the instrument allowed only low resolution. Baccetti was keenly aware of this limitation and set out to purchase a new, more appropriate electron microscope. He tried to solve the problem by bringing an old Siemens to Siena from the Milan laboratory, but that choice did not improve the situation. He then bought a new Siemens Elmiskop IA electron microscope. Unexpectedly, Baccetti decided that the new instrument could only be used by himself and his associate Floriana Rosati. This produced a certain discontent and disaffection with research by some of the researchers. For me, they were very difficult months because I wanted to continue my ultrastructural studies but required the new microscope for the analysis of the flagellum of some spermatozoa. Hence, I was forced to use

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it only after the Institute remained deserted, late in the evening. The next morning, everything in the lab had to be in the same condition in which it had been left the previous day. I worked a lot in those months, and I was piling the many electron micrographs I had printed on a piece of furniture in my office on the upper floor of the Institute. One day, Baccio entered the room unannounced, saw the pictures and wanted to know what they were. When I explained that they were the result of months of clandestine work, he realized the deprivation he had forced on me, and using a Florentine expression, he laughed it off, as he always did when in difficulty. Baccio was like that: capable of unprecedented severity, but also of reparative gestures, even if they were late in coming.

In Siena, Baccetti came to know the writings of Gustaf Retzius (1906-1909), monumental works accompanied by splendid plates of the sperm of more than 400 species, half of them vertebrates, conserved in the Museum of the Fisiocritici Academy. At that time, the museum's rooms were adjacent the Institute of Zoology and thus it was easy to have access to the library. I am sure that Retzius's works on comparative spermatology, along with the more recent and fundamental work by Ake Franzén (1956) on spermatogenesis, sperm cells and fertilization in invertebrates, had a great influence on Baccetti's decision to undertake the ultrastructural study of the sperm of different animal phyla, particularly those of insects in order to reconstruct the phylogeny of the group. I remember a visit to Terminillo (Rieti) at the Carlo Jucci Apennine Genetics Centre in August 1967, where we went each year to collect faunal specimens for the various researchers who accompanied him (Giusti, Baroni-Urbani, Lazzeroni, Lovari and I, along with the Baccetti family, with the young Nicola and Cosimo; Baccetti was convinced that in order to become good researchers in entomology, each researcher should master a systematic group). Late one afternoon, Baccetti called us into the centre's lovely library and read to us, so as to have our comments, what he had written on the structure of the sperm of insects as an index of the phylogeny of the group. What he described to us became the subject of the talk he gave to the 7th Italian Congress of Entomology in Verona (Fig. IB). I have a perfect memory of that day because it coincided with the birth of my daughter Luisa. Baccio wanted me to be present in Verona in spite of the delicate moment and urged the gynaecologist treating my wife to ensure that the baby would be born before the Congress.

1967 represents the beginning of a lovely and important scientific collaboration between Baccio and the group of young researchers he had chosen for the great project of forming a specialized school on animal reproduction. Following the reading of specific works by past authors, there were interminable discussions on the structure of the sperm of various groups of invertebrates. Each member of the research group was required to find representatives of the various arthropod groups and carry out an ultrastructural study of them. The work proceeded at a hectic pace and led to the first important results, presented at the 4th European Congress of Electron Microscopy held in Rome in 1968 and at the 13th International Congress of Entomology in Moscow in the same year. The latter work on "Phylogenetic considerations on Arthropoda on the basis of the ultrastructure of the spermatozoon", which Baccetti presented, received great attention from the international scientific community. In the same years (1969-1970), several papers on sperm cell ultrastructure in some insect orders (Ephemeroptera, Mallophaga, Psocoptera, Thysanoptera, Embioptera, Mecoptera, Neuroptera, Plecoptera, Trichoptera) were published in high-quality journals. These works and Baccetti's acquaintance with European and overseas specialists were the basis for the formation of a committee of experts in the field of spermatology and reproduction in general. The committee included: J. André (France), Don W. Fawcett (USA), B.A. Afzelius (Sweden) and Baccio, and later also J.M. Bedford (UK). These eminent scientists have the merit of creating a series of international spermatology meetings, resulting in over 10 congresses in a 40 year period (1969 to 2006).

Baccetti organized the 1st Congress, the inauguration being held in the summer of 1969 at the Lyncean Academy in Rome and the scientific work proceeding in Siena at the Institute of Zoology. It was an important event, whose scientific contributions were collected in a 600 page volume published by the Lyncean Academy and Academic Press, New York (Fig. IC). Several researchers in the Siena group presented their findings on the structure of the sperm cells of the Collembola, Pauropoda, Symphyla and Araneidae. Baccio spoke on "The sperm cell as index of Arthropod phylogenesis" and with this work he laid the foundations for an evolutionary interpretation of the components of the sperm cell.

The following year, the researchers and technicians of the Institute participated *en masse* in the 7th International Congress of Electron Microscopy in Grenoble (1970), with contributions on: the presence of ribonucleoproteins in the material forming the additional centriole, on the structure of the cell wall of spermatozoa, and on enzymatic localization in the flagellar axoneme. In 1971-72, the original group of researchers of Siena's Institute of Zoology was joined by the biochemist Vitaliano Pallini. His arrival led to the acquisition of new scientific expertise that gave a boost to the comparative spermatology studies; indeed, it allowed resolution not only of the fine structure but also of the chemical composition and functional significance of the various components of the spermatozoon. And those years saw the publication of two complex works of great importance: the first on the structure and function of the spermatozoon of *Bacillus rossius* and the second on that of *Tenebrio molitor*.

In 1972, Baccetti published a long paper in Advances in Insect Physiology, reporting recent findings on the spermatozoon of many insects (Fig. IIA). That substantial work was the result of many hours spent together discussing the various sperm cell models. After its publication, Baccio gave me one of the few available reprints in consideration of the assistance received. In 1973-1974, the results of studies on the ultrastructure of the sperm cells of the Protura, Diplura, Diptera Simuliidae, the cecidomyiid *Monarthropalpus buxi* and the diplopod *Polyxenus* were published (Fig. III). Some micrographs of the complex work on *Polyxenus*, accepted by the Journal of Morphology and dedicated to the extraordinary metamorphosis of the spermatozoon which has the form of a small barrel in the male genital tract and becomes ribbon-like in the spermatheca of the female, were publicly displayed at the journal's head office in New York.

1973 was also the year of the 2nd Congress of Comparative Spermatology in Stockholm, organized by Afzelius at the Wenner-Gren Institute. Baccetti and I were both invited to give a talk: Baccetti presented "Motility patterns in sperm with different tail structure" (Fig. IIB) and I spoke on "New models of arthropod aflagellate spermatozoa". The two talks were well accep-

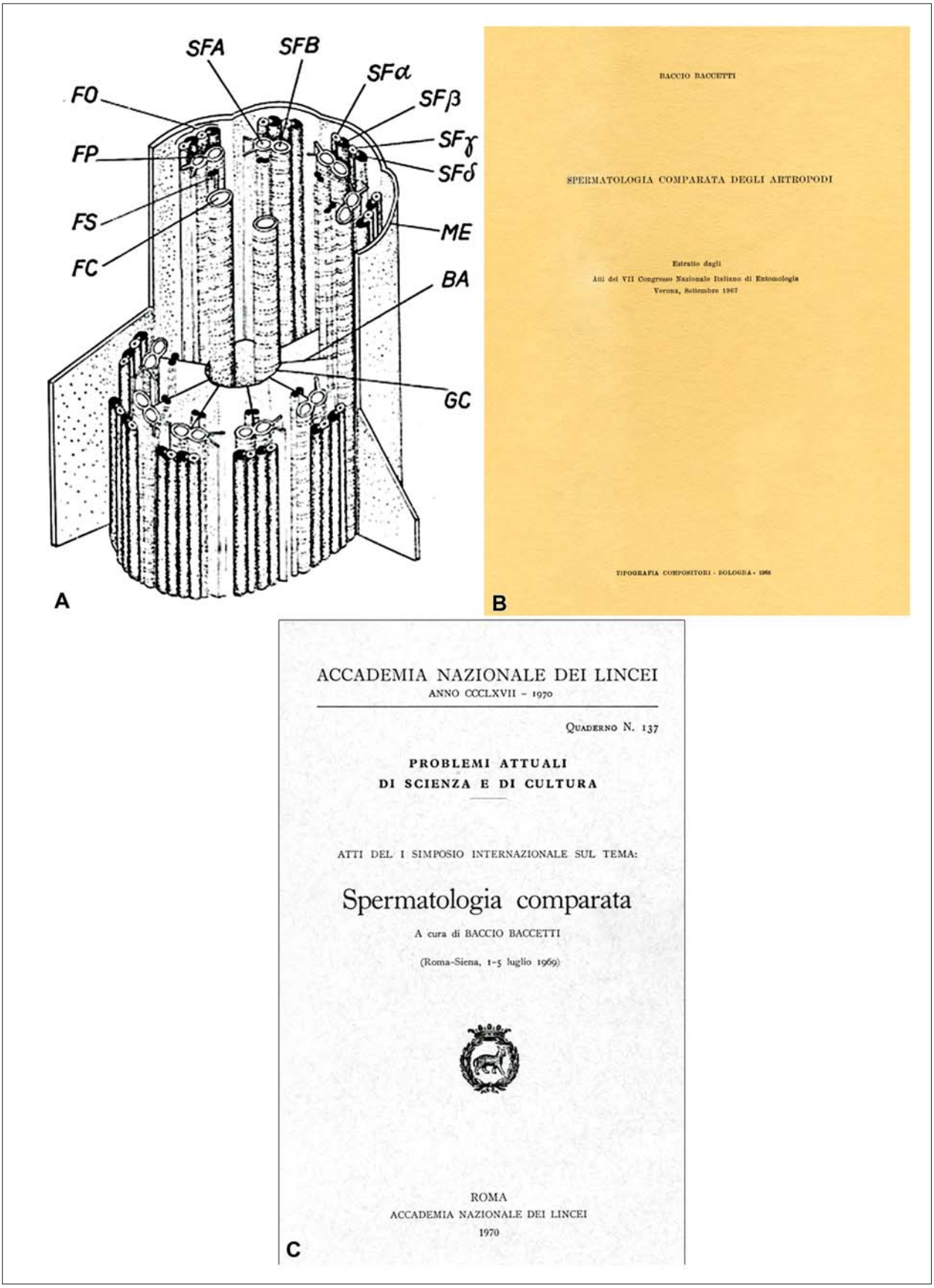

Fig. I

A - Schematic reconstruction of the flagellar axoneme of *Bactrocera* (= *Dacus*) *oleae*. The drawing performed by R. Dallai, illustrated the different microtubular components. B - cover of the paper by Baccetti on the "Comparative Spermatology of Arthropoda" which was the subject of his talk at the 7th National Congress of Entomology, held in Verona in 1967. C - Cover of the Proceedings of the 1st International meeting on "Comparative Spermatology", organized by Baccetti, held in Roma-Siena, 1969. The book was published by the Accademia Nazionale dei Lincei in 1970.

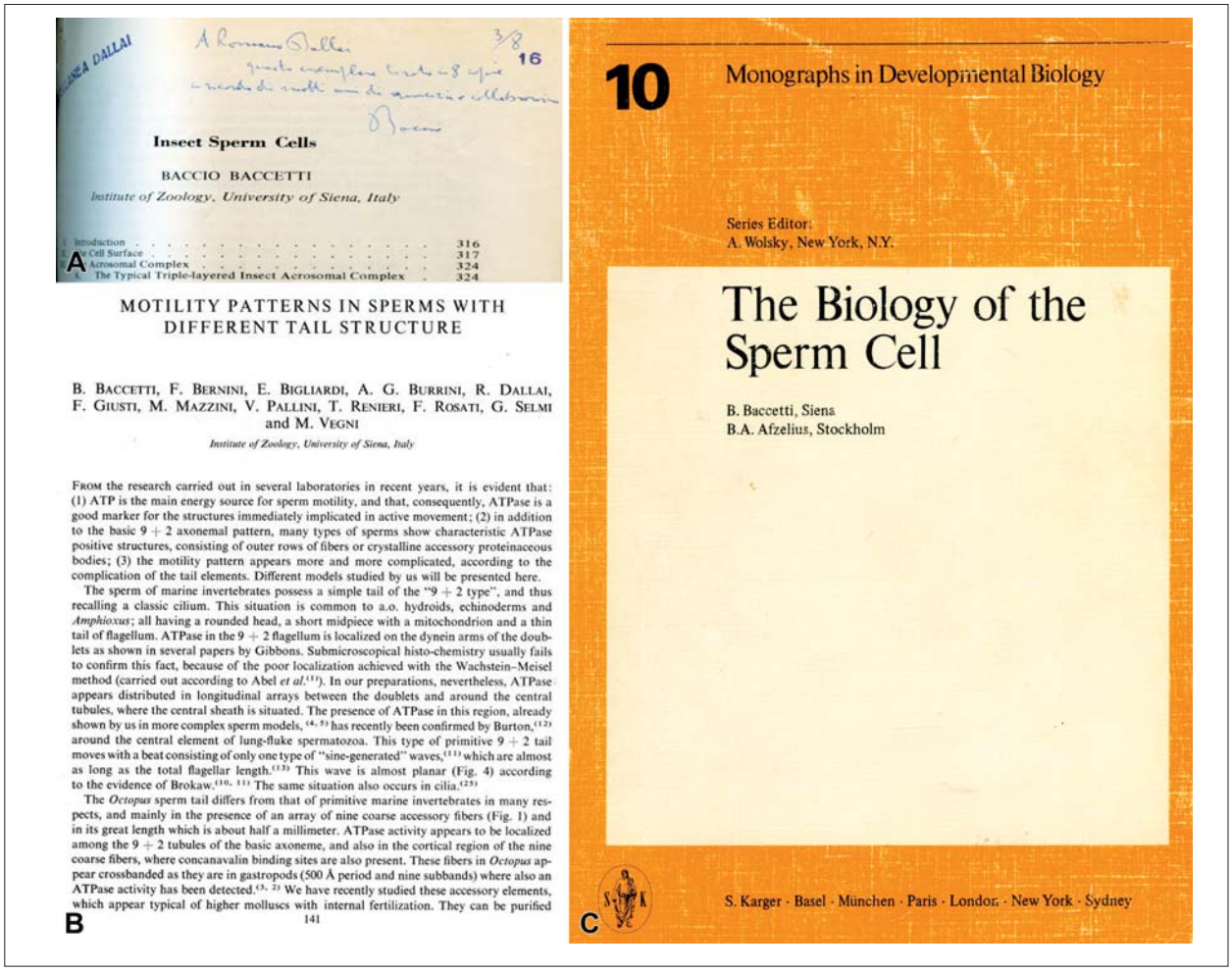

Fig. II
A - The first page of the paper by Baccetti on "Insect Sperm Cell" published in 1977 on Advances of Insect Physiology. B - The talk by Baccetti at the 2nd International meeting of "Comparative Spermatology" held in Stockholm in 1973. C - The cover of the important book by Baccetti and Afzelius on the " The Biology of Sperm Cell" edited by Karger Press in 1976.

ted by the many participants and also received the compliments of Afzelius, Fawcett and Anderson, some of the most respected specialists in the field. In the evening, Baccio and I decided to stay in the hotel lobby to relax after the stresses accumulated in the previous days. As we toasted our success, Baccio said to me "You know, Romano, today we've made a name for ourselves in international research. Now we can really compete with the best schools". I was very touched by his words because we had expended so much energy in the previous months, he in his study on the ground floor and I in mine on the top floor of the Institute, continually telephoning each other to tell the other what we had written. After the Congress, we decided to put the names of all the researchers of the group on each of the two talks. The two works were published with several authors, as if we were a football team. Baccio had, like me, a passion for this sport, which we occasionally played, albeit without much success, in friendly university matches. Those years were the best ones of our collaboration: with great dedication to research and much satisfaction for the international recognition our work received and for the friendship that had grown between us.

In 1975, Baccio published a paper on the contribution of the Golgi apparatus during spermatogenesis. He also gave special attention to this organelle later when he used it as a guide trait for animal phylogeny (l979) in a paper in Current Topics in Developmental Biology.

In 1976, the constant presence of Bjorn Afzelius in Siena gave Baccetti the opportunity to plan the fundamental work "The Biology of the Sperm Cell" for Karger Press, Basel, written by the two specialists (Fig. II C). This text was and still is a reference for all those intending to study spermatozoa.

Again in 1976, Baccio and I began a fruitful collaboration with Bjorn Afzelius, who had become an esteemed guest, leading first to the identification of giant mitochondria in the spermatozoon of *Notonecta glauca* (1976) and later, thanks to the collaboration of Pallini and Rosati, to the characterization of a novel protein contained in these mitochondria, called crystallomitin. The paper was accepted by the Journal of Cell Biology (1977) (Fig. IV).

Pallini's biochemical expertise and the tireless efforts of Anna Burrini, who had practically become his technician, made it possible to describe the chemical composition of the accessory fibres of mammals and cephalopods, establishing also that the structures were rich in sulphur and zinc. Moreover, three lines of research were set up in parallel: one on the aberrant structure of the sperm of the Cecidomyiidae (1976), a second on the sperm of the Ony-

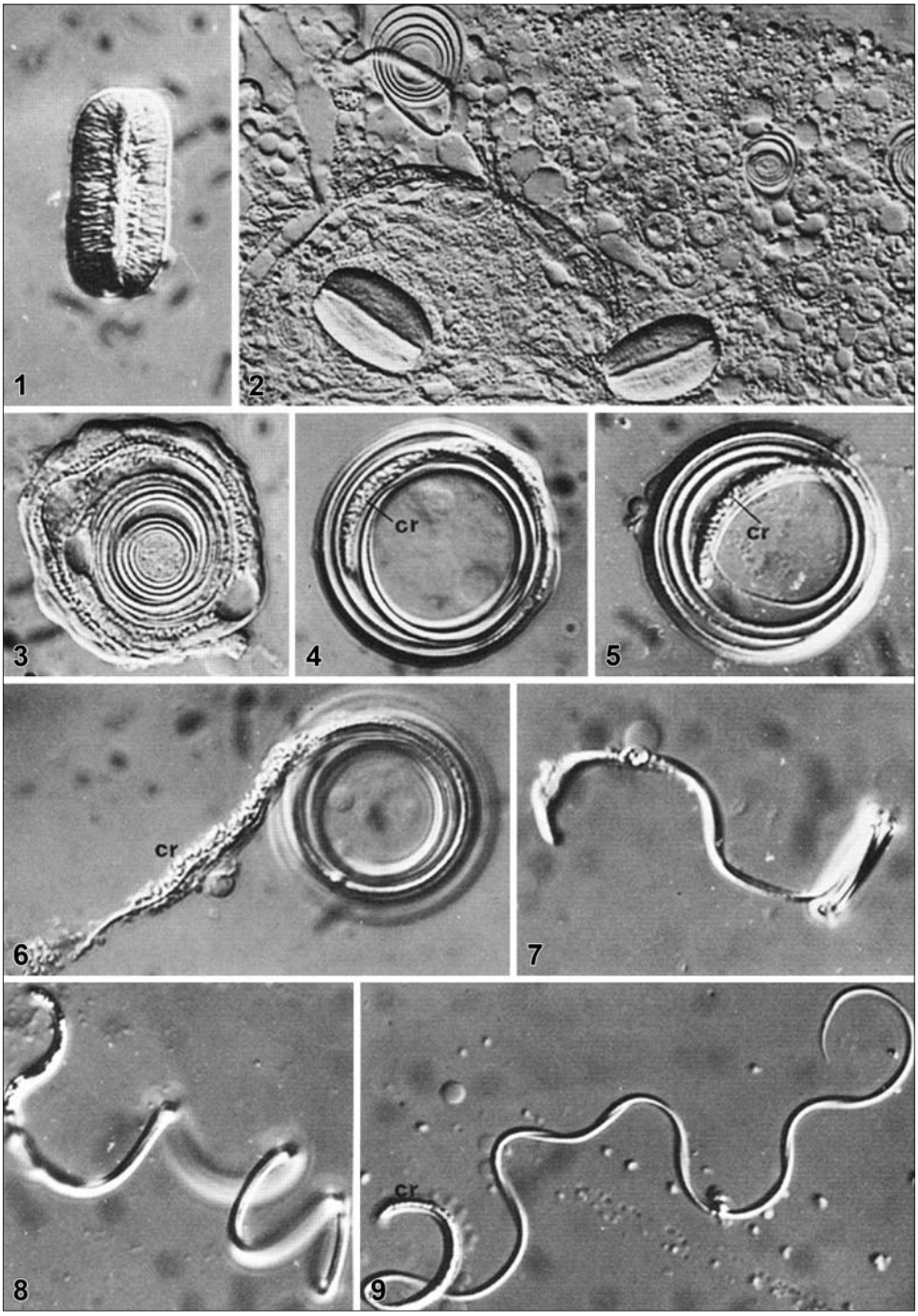

Fig. III
Living spermatozoa form *Polyxenus lagurus* testis (1) where the sperm cell is barrel-shaped, and the progressive transformation of the germ cell (2 – 8) into the female spermatheca. In the final step the sperm becomes an elongated cell (9). The process was identified as a sperm metamorphosis (Baccetti et al., 1974)

chophora (1976, 1977), and a third on the sperm of the Myriapoda (1977). These works were published in high-quality journals and received broad consensus that led to invitations to both researchers to give talks in various conferences.

In 1977, our friend Michael White sent some specimens of *Mastotermes darwiniensis* to us from Australia. We began to study the ultrastructure of the sperm cells of this termite, but the work proceeded slowly due to the difficulty in isolating the reproductive apparatus without compromising its integrity. The species, like the rest of the Isoptera, hosted various Hypermastigida protozoa, and this curbed our enthusiasm at first. We had, in fact, identified multiflagellate cells in the male genital tract and to ensure that this finding was due to peculiar sperm cells we had to exclude the possibility of contamination. For this reason,

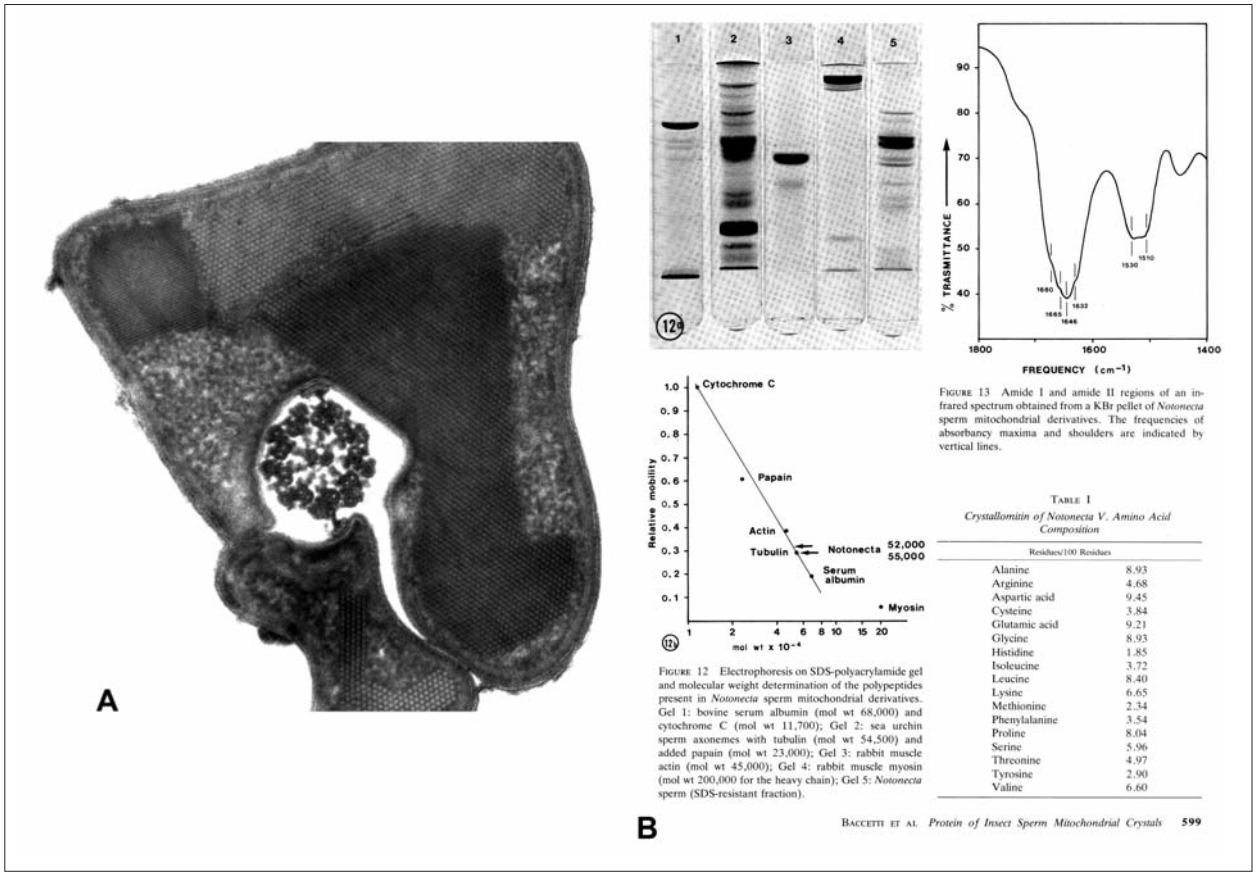

Figure 13 Amide I and amide II regions of an infrared spectrum obtained from a KBr pellet of *Notonecta* sperm mitochondrial derivatives. The frequencies of absorbancy maxima and shoulders are indicated by vertical lines.

Figure 12 Electrophoresis on SDS-polyacrylamide gel and molecular weight determination of the polypeptides present in *Notonecta* sperm mitochondrial derivatives. Gel 1: bovine serum albumin (mol wt 68,000) and cytochrome C (mol wt 11,700); Gel 2: sea urchin sperm axonemes with tubulin (mol wt 54,500) and added papain (mol wt 23,000); Gel 3: rabbit muscle actin (mol wt 45,000); Gel 4: rabbit muscle myosin (mol wt 200,000 for the heavy chain); Gel 5: *Notonecta* sperm (SDS-resistant fraction).

Table I
Crystallomitin of Notonecta V. Amino Acid Composition

	Residues/100 Residues
Alanine	8.93
Arginine	4.68
Aspartic acid	9.45
Cysteine	3.84
Glutamic acid	9.21
Glycine	8.93
Histidine	1.85
Isoleucine	3.72
Leucine	8.40
Lysine	6.65
Methionine	2.34
Phenylalanine	3.54
Proline	8.04
Serine	5.96
Threonine	4.97
Tyrosine	2.90
Valine	6.60

Fig. IV
A, B – In 1976 Baccetti, with the collaboration of Afzelius, Dallai, Pallini and Rosati, published the important paper on Journal of Cell Biology on the new protein "crystallomitin" which constitutes the component of the sperm mitochondrial derivatives of *Notonecta glauca* (A). The biochemical characteristics of this protein and its aminoacid composition is reported (B).

we decided to conduct a study on the spermatogenesis of the species. The result was confirmation of the presence of functional sperm with about one hundred flagella, a unique case in the animal kingdom (Fig. V; Fig. VI A). Recent work conducted with my colleague G. Callaini (2009) on this species confirmed that the unusual number of flagella is due to uncontrolled multiplication of the centrioles in the young spermatid (Fig. VI B, C). Our finding was published as a short note in the Comptes Rendus de l'Académie des Sciences of Paris, sponsored by P.P. Grassé (1977), and then as a full paper in the Journal of Cell Biology (1978). With Baccetti, we also examined the immobile spermatozoa of the Aleyrodidae and, through the study of the spermatogenesis of these insects, we described the progressive degeneration of the flagellar axoneme (1977). Also in 1977, Baccetti published a paper on the spermatozoa of the Sipunculidae in the journal of the Lyncean Academy and a note on an "Unusual feature of insect spermatogenesis" in International Cell Biology. In the same year, with Burrini and Pallini, we began to study the molecular characterization of the dynein arms of the flagellar axoneme of insects. Through exhausting dissections of the cecidomyiid *Diplolaboncus tumorificus* from the Modena plain, a species provided with a giant axoneme with a thousand microtubule doublets equipped with the external arm alone, we were able to obtain a pellet of sperm sufficient for biochemical investigations (Fig. VII). They led to the identification of a peculiar electrophoretic pattern, illustrated in a paper published in the Journal of Cell Biology (1979). In the same period, we also began research on the spermatozoa of Myriapoda (1978), with particular attention to those of the Diplopoda. The results of these studies were published in "Myriapod Biology" edited by Marina Camatini (1979). The many spermatological data were published in the journal of the Lyncean Academy (1978) and then combined in a long paper by Baccetti in "Arthropod Phylogeny" edited by A.P. Gupta (1979).

1978 was the year of the 3rd Congress of Comparative Spermatology organized by Don W. Fawcett in Boston-Woods Hole, in which various members of the Siena group participated. I had been invited to give one of the plenary lectures and inexplicably that displeased Baccetti. The topic asked of me was: "The evolution of the spermatozoon of insects" (1979). Baccetti, instead, gave a nice talk on the evolution of the acrosomal complex and another, with Pallini and Burrini, on the first results of a study on a polypeptide rich in cysteine present in the mitochondria of mammalian sperm (1979).

In 1982, the 4th Congress of Comparative Spermatology was held in Seillac (France), organized by J. André. Baccetti presented "The sperm structure and function in 70 year old humans". In those years, Baccio had begun research on human spermatology with attention to health issues, also involving some of his colleagues.

At the 5th Congress of Comparative Spermatology in 1986 in Fujiyoshida, near Mount Fuji in Japan, organized by H. Mohri, Baccio presented a communication on

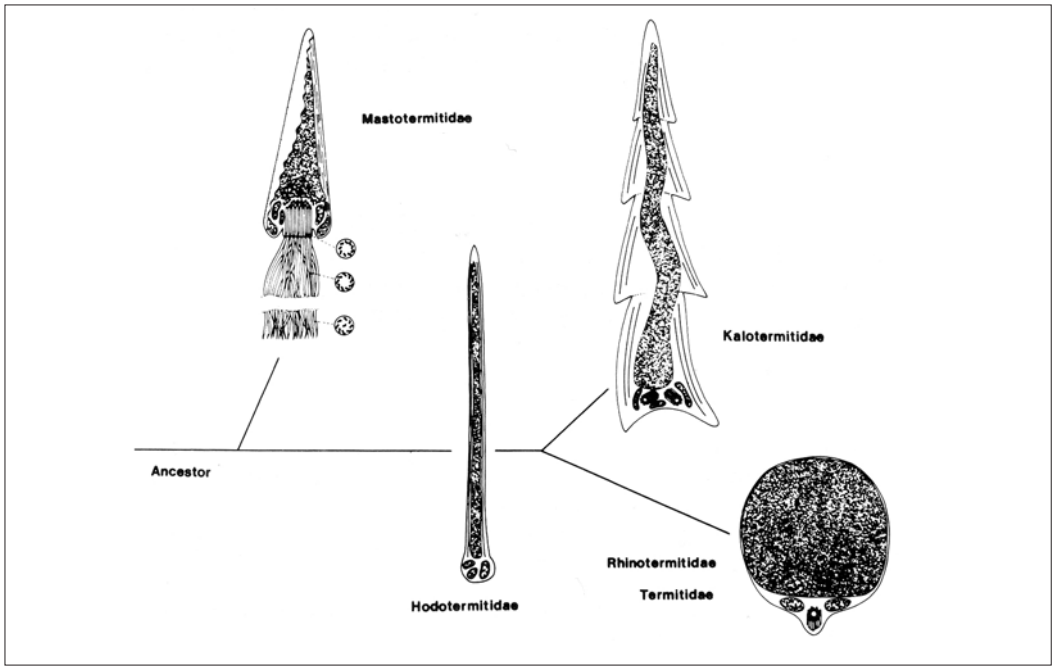

Fig. V
Schematic drawing to show the isopteran phylogeny according to the sperm structure (Baccetti et al., 1981).

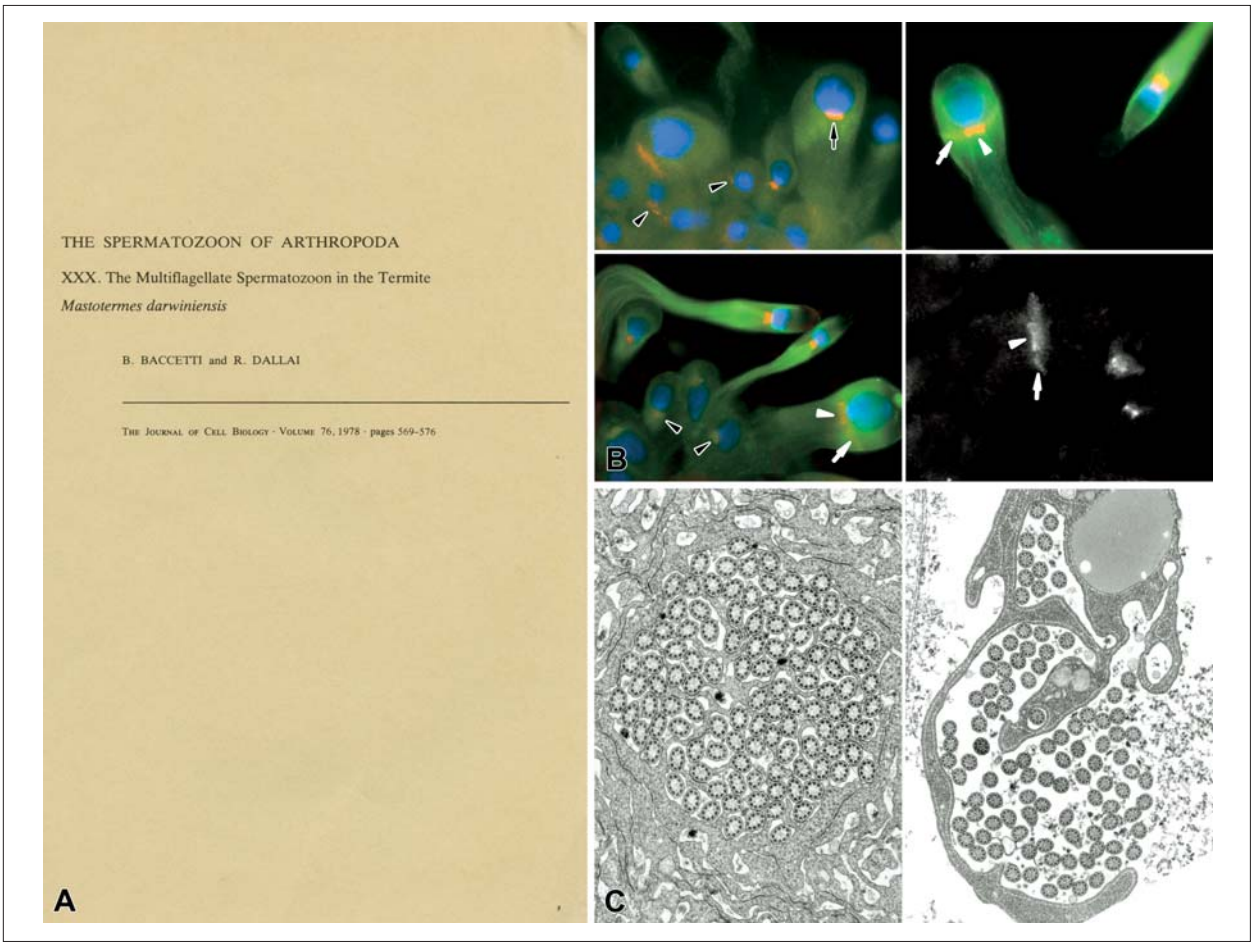

Fig. VI
A – Cover of the paper by Baccetti and Dallai (1978) on the multiflagellated structure of *Mastotermes darwiniensis*. B – Localization of the γ-tubulin (upper figures) and centrosomin (bottom figures). Microtubules are green, centrosomal antigens are yellow and the DNA in blue. In the bottom right picture the centrosomin staining alone is reported. Both centrosomal proteins show the same distribution. In early spermatids the centrosomal protein is less evident (black arrowheads) (Riparbelli et al., 2009). C – Two cross sections through successive levels of *Mastotermes* sperm showing the numerous flagella (Riparbelli et al., 2009).

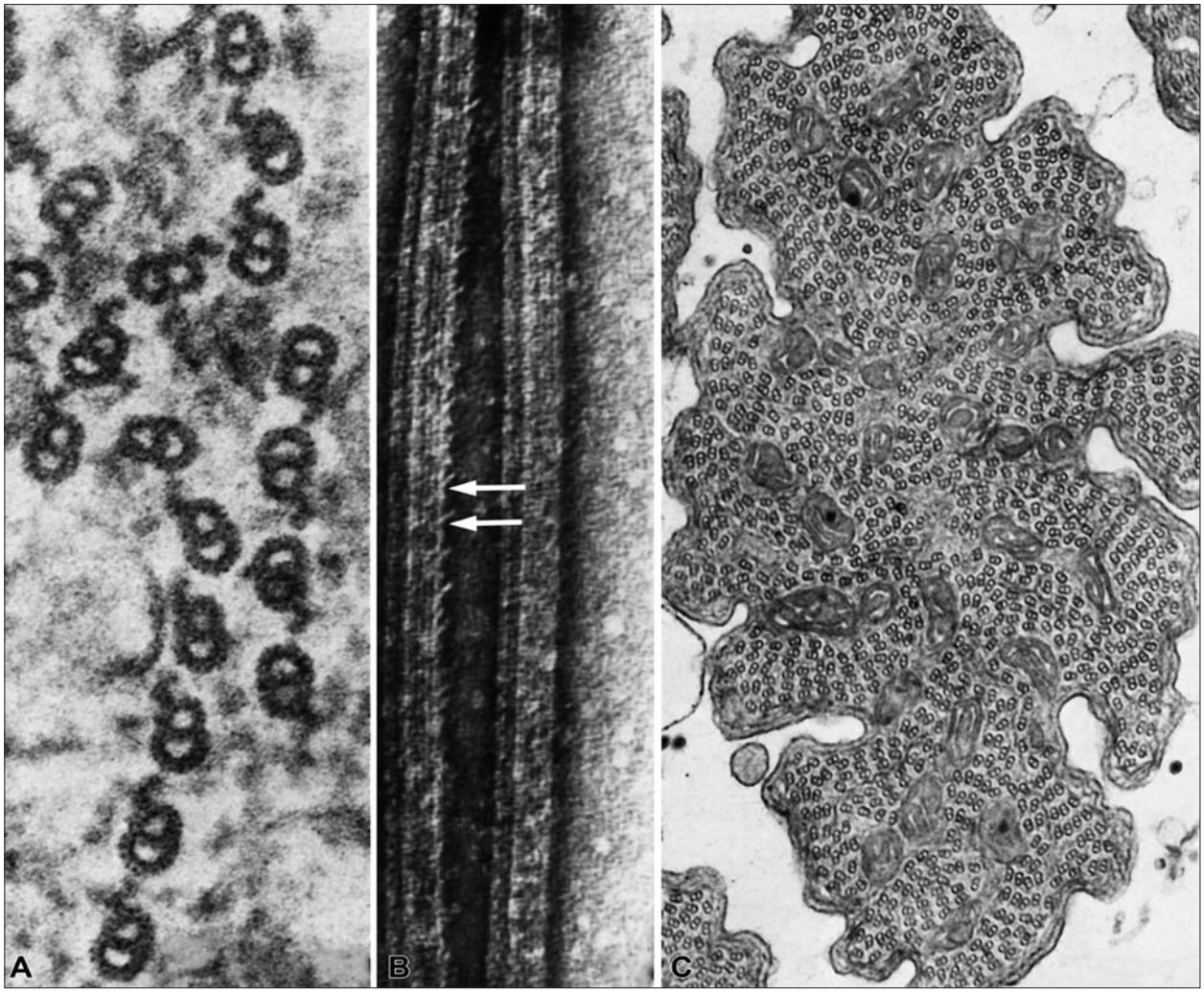

Fig. VII
A, B, C – *Diplolaboncus tumorificus* spermatozoa. In A a detail of a series of axonemal doublets provided with only the outer dynein arms; in B, a negative staining to show the dynein arms along microtubule doublets; in C, a cross section of the sperm flagellum showing numerous microtubules doublets (Baccetti et al.,1979).

"News on phylogenetical and taxonomical spermatology" and one on "The action of gossypol on mammalian spermatozoa".

However, Baccetti also returned from time to time to the comparative spermatology of insects. In fact, he published a paper on the structure of the sperm of various species of termites which I sent to him from Somalia, where I had gone to teach the course in Agricultural Zoology in the Faculty of Agriculture of Mogadishu (1981), as well as others on the sperm of *Galloisiana* (Grylloblattodea) and, in collaboration, on the motility of the sperm of the Coccidae (1982), on the sperm of some sandfly species (1984), of the Curculionidae (1985), of the Phasmatidae (1986), of the Orthopteroidea (1987), of the Chrysomelidae (1988), of the Strepsiptera (1989), and on the aflagellate and immobile sperm of the Coleoptera Ptiliidae (1989).

In 1985, Baccetti published a major work on the evolution of the spermatozoon for the volume of Ch. Metz and A. Monroy, "Biology of Fertilization", published by Academic Press, N.Y.

Profiting from the presence of the Gibbons (husband and wife) as guests of the Institute of Zoology, Baccio became interested in the movement of the spermatozoa of the eel, provided with a type 9+0 flagellar axoneme (1983-1985), and later of that of the sperm cells of the Tephritidae, demonstrating their ability to move backwards (1989). He also published some notes on the sperm of different groups of insects: in 1983 and 1985 on the Nematoda, and in 1987 on the Tardigrada.

In 1988, Baccio presented a plenary lecture on "The value of sperm and egg structure in insect systematics" at the 18th International Congress of Entomology in Vancouver, while at the 19th International Congress of Entomology in Beijing in 1992, he spoke on "Modern trends in Insect spermatology", as well as on the spermatozoa of the Blattaria and the evolution of the spermatozoa of the Coleoptera.

At the 20th International Congress of Entomology in Florence (1996) (Fig. VIII), which he organized with great success, Baccio presented a plenary lecture on "Comparative spermatology in Insect phylogeny and taxonomy", which was also the topic he dealt with in "Insecta" volume 11C edited by F.W. Harrison and M. Locke for the series Microscopic Anatomy of Invertebrates (1998).

Nevertheless, his major focus was on the health aspects of human spermatology and on sperm pathologies underlying human infertility. He published a great deal in

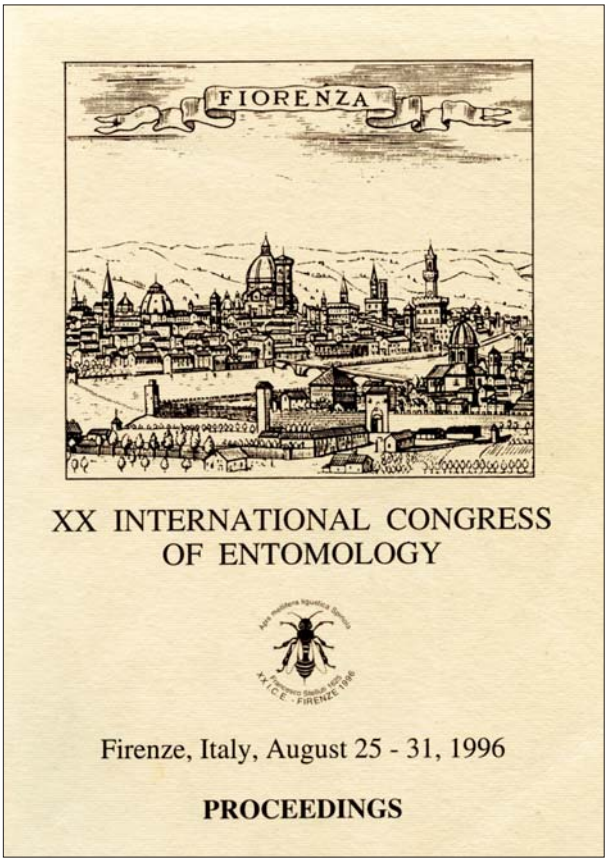

Fig. VIII
Cover of the Proceedings of the 20th International Congress of Entomology held in Florence in 1996 and organized by Baccetti.

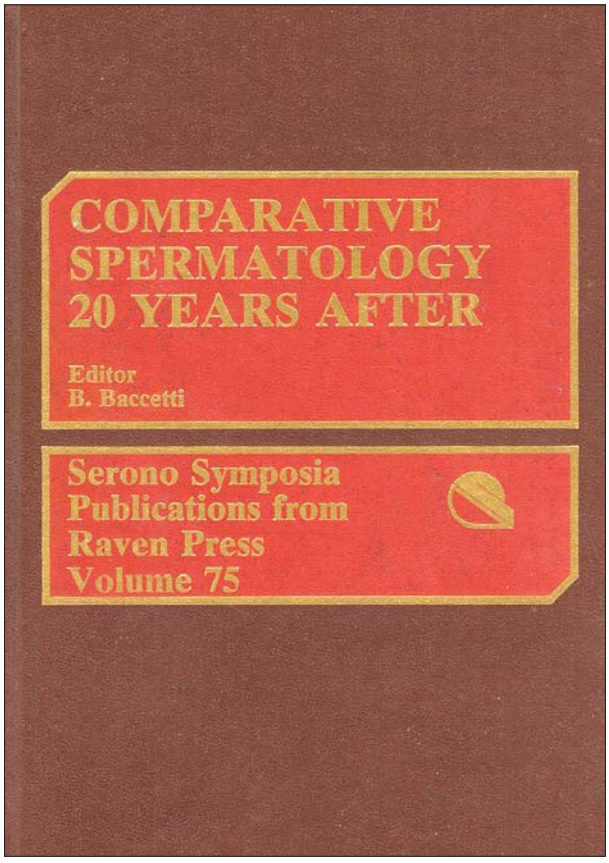

Fig. IX
Cover of the book on "Comparative Spermatology 20 years after" organized by Baccetti in 1990. edited by Raven Press.

this area in collaboration with physicians and clinicians. Some of his papers were of great international importance, such as the one in the Journal of Cell Biology on the presence of the HIV-I virus in the sperm of AIDS patients, or the one on the method for a mathematical evaluation of sperm malformations, or the one on spermatological defects in blood relatives.

In 1990, Baccio organized the symposium "Comparative Spermatology 20 years after" in Siena to celebrate the 6th Congress of Comparative Spermatology (Fig. IX). His inaugural speech, later reported in the preface to the large volume of the proceedings, clearly showed his awareness of the enormous progress made by the scientific community in the study of germ cells, as well as his pride in having significantly contributed to the success of this branch of Biology.

The change in direction of his research was also explained by his transfer to the Faculty of Medicine of the University of Siena (1988-1989) and by his separation from the original group of researchers of the Institute of Zoology in order to give life to the new Institute of General Biology.

At the end of this historical reconstruction of the birth of the Comparative Spermatology of Insects, it is perhaps appropriate to remark on the results obtained by Baccetti and his school in this field of Biology. The findings on the structure of the spermatozoa of various groups of animals, especially insects, were numerous and revealed phylogenetic affinities that were unexpected and often conflicting with those derived from the external morphology; yet many of these findings have been supported by the results of molecular studies. To give just a few examples: the Protura are a group with aberrant sperm cells (equipped with an axoneme with several doublets and lacking a central complex) which probably is not on the phyletic lineage of insects; the Phasmatodea, which have lost mitochondrial derivatives, are a very apomorphic group, standing alone among the Polyneoptera; the Strepsiptera present small accessory bodies, and could be related to Coleoptera and not to Diptera; the Diptera Cecidomyiini and Asphondyliini share the presence of only one external dynein arm in the aberrant axoneme, while *Contarinia* and related genera, with immobile sperm, should be placed on a separate evolutionary branch different from that of the Cecidomyiidi and Lasiopteridi (Fig. X). Therefore, the spermatozoon, more than the general morphology of the body (which is more susceptible to external selection pressures), can reveal the true affinities among groups, even those apparently distant. This was Baccetti's conviction and the more recent works of comparative spermatology of insects seem to confirm this hypothesis.

In the 1970s, after returning from Copenhagen where he met George Karl Wingstrand, Baccetti told me of the work this great zoologist was doing, of his intuition about the phylogenetic position of some difficult zoological groups, and in particular of the importance that spermatozoal structure had in establishing that the phylum Pentastomida (or Linguatulida) was related to the Crustacea Branchiura rather than to the Protoarthropoda (Onychophora and

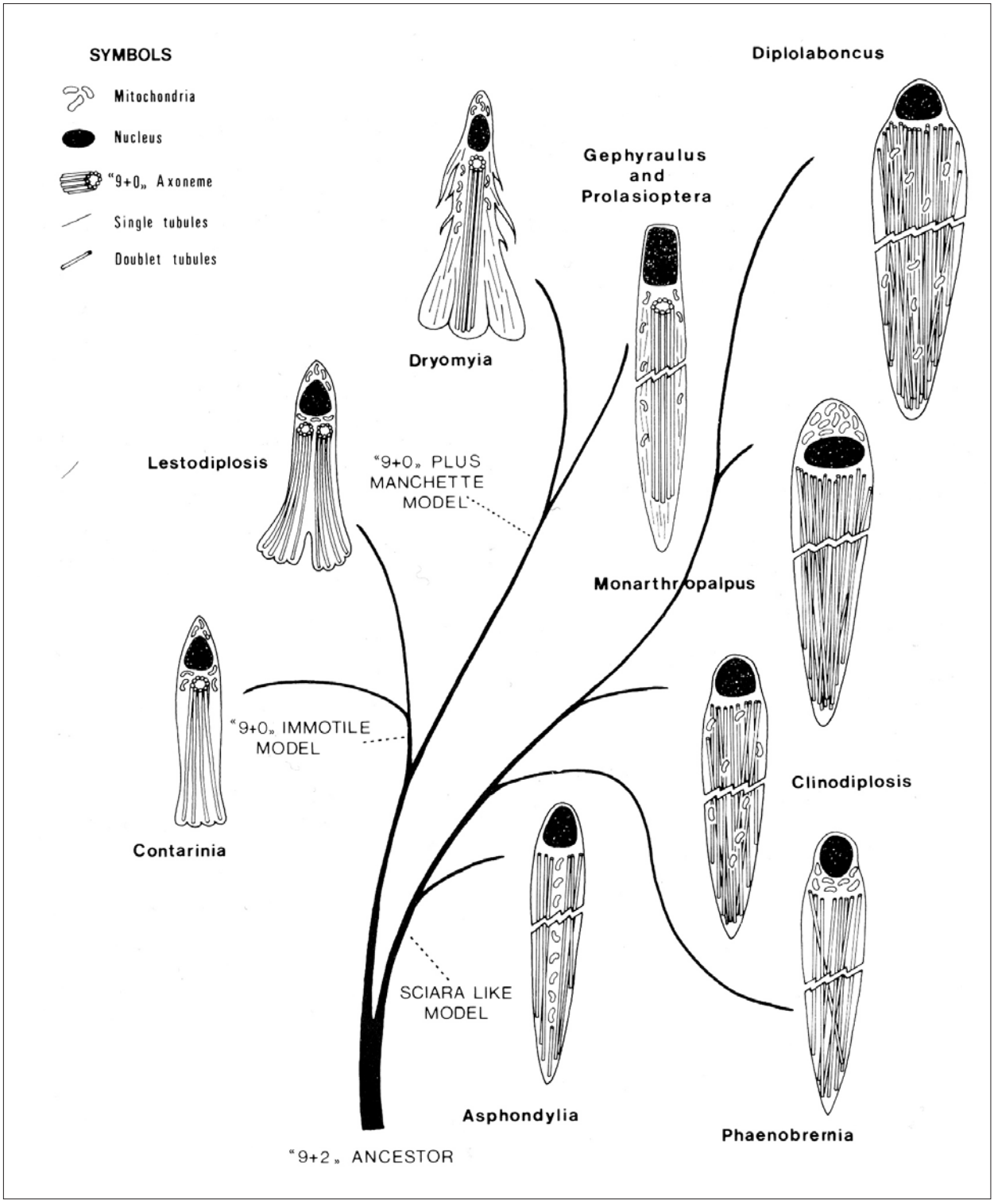

Fig. X
Schematic drawing of the sperm evolution in the gall-midge flies. Two independent evolutive trends are recognizable: one characterized by motile sperm flagella provided with giant axonemes (right) and a second with immotile sperm provided with microtubule doublets and singlets without dynein arms (left) (Baccetti et al., 1976).

Tardigrada). I believe that visit to Denmark also gave Baccio confirmation of the importance of ultrastructural studies of sperm cells for phylogenetic purposes.

Perhaps the conclusions reached by Baccio in his works were based simply on the sharing of structures found in the considered groups and not on a classic cladistic evaluation of spermatozoal traits, i.e. which ones are plesiomorphic and which ones apomorphic. Likewise, he did not take into due consideration the type of reproduction adopted by the examined species (monandry and polyandry) and the existence of sperm competition. However, the fact remains that many of his conclusions are still valid.

It is not easy to make a concise judgement of Baccio Baccetti, and it is especially difficult for someone like me who has matured scientifically next to him and thus has enjoyed and suffered his strong personality. Perhaps he was not the Mentor I would have desired, but certainly he was for everyone a formidable manager able to find the resources and personnel to realize a grand research project. One can say that he was an extraordinary man, but like so many he had his weaknesses and his passions, his fears and his enthusiasms, his intolerance of anything that wasted his time, his unexpected generosity. Certainly he was very determined to achieve the goals he had set for himself and to which he was dedicated, and he had no scruples in obtaining what he desired. A clear example of this is the tenacity with which he made and brought to a successful conclusion the request for an Italian CNR Centre in Siena.

A tireless worker, with an incredible facility for writing, Baccetti wrote about everything and everyone. Reading the list of his publications leaves one amazed at how he was able to pass from scientific data, be they naturalistic, taxonomic or ultrastructural, to obituaries, to historical reconstructions of entomology, to discussions of university policies, and even to humorous quotes.

I, who shared many years of work with him (publishing more than 40 works together), prefer to remember how we were back in the 1970s, when we were both animated by the same passion and fondness for research and we spent hours in the hall of the Institute of Zoology discussing the novelties we had observed with the electron microscope. And we always left the Institute together, late in the evening, happy and proud of our results.

Then our paths separated and each of us chose to take a different route, with other fellow travellers, to destinations that each considered more suitable to his way of being. With age, which in the words of Erri De Luca "makes the day rusty in early evening" and a light mist descends to cover all things and every story, there remains the regret of not being able to bring to term, together with him, a long scientific and human experience.