1

Introduction

Brent B. Nickol

Fifty years ago the second part of a two-part monograph on the Acanthocephala was published. The monograph, by Anton Meyer and called simply *Acanthocephala*, comprised the two *Lieferungen* of the *Zweite Buch* of the *Zweite Abteilung* of the *Vierter Band* of *Dr H.G. Bronn's Klassen und Ordnungen des Tierreichs*. Confusion surrounds the year of publication because each *Lieferung* was issued separately, one in 1932 and one in 1933. Afterwards, they were assembled as a complete volume to which the publisher affixed the later date (Van Cleave, 1948). Bound copies of the two parts frequently have a single title page, dated 1933, and a combined table of contents. Covers for the individual parts, however, bear the original 1932 and 1933 dates. This monumental work still stands as one of the principal reference works for the Acanthocephala. To commemorate its fiftieth anniversary, the present volume reviews and interprets many of the discoveries regarding the biology of the Acanthocephala that have been made after 1933.

As the fascinating recent discoveries are read in the following pages, it is appropriate to remember that pioneering work, such as that done by Rudolphi, Hamann, Kaiser, Lühe, Meyer, Travassos, Van Cleave and others, was a prerequisite to the more complete knowledge now amassed. In this era of explosive technology when history is not in vogue, when it is often considered irrelevant, and when ideas of what constitutes science and worthy scientific endeavor are dictated only by the latest issue of *Current Contents*, it is especially important to keep track of the past and to realize where we have been.

Meaningful information about the Acanthocephala is comparatively recent, certainly post-Linnaean and, for the most part, it dates from within the last 100 years. Modern views of the systematic relations of Acanthocephala have the fundamental arrangement of Otto Hamann

(1892) as their basis. Hamann was able to integrate detailed observations by his contemporaries, perhaps most notably those of J.E. Kaiser, into a comparative system. He was the first to evaluate differences at a level above those for separating species, to recognize several genera in place of the all-inclusive *Echinorhynchus*, and to formulate the concepts of acanthocephalan families (Van Cleave, 1948). Meyer added information from his own studies of ontogeny and morphological interpretations to the Hamann scheme to produce his monograph of all the then-known Acanthocephala.

Meyer was not the only early-twentieth-century pioneer to make lasting contributions to knowledge of the Acanthocephala. Beginning in 1913, H.J. Van Cleave made numerous contributions that outlined and defined the acanthocephalan fauna. In 1936 he visualized the concept of Eoacanthocephala, which reconciled incongruent elements in the system advocated by Meyer, and the Meyer–Van Cleave system of classification was formulated. This system provides the basis for most present views of acanthocephalan systematics.

During the three decades following publication of Meyer's monograph, a steady level of investigation continued to accumulate information regarding the diversity of the Acanthocephala and to define the fauna. During this period the first critical studies of life cycles and transmission (Ward, 1940*b*; Moore, 1946*a*, *b*; DeGiusti, 1949*a*) began uncovering some of the ecological facets of acanthocephalan biology. It was soon apparent that the Acanthocephala are ideal animals for the study of many parasitological relationships, especially those of populations and communities. Unlike the Platyhelminthes, they are dioecious, do not multiply within intermediate hosts, and have no free-living stage. The opportunities offered by these attributes were soon exploited.

In the 1970s there was a marked increase in the use of acanthocephalans in parasitological research. Not only did study of them result in new ecological understanding, but it also provided insight into the cellular, molecular, and regulatory biology of helminths and into the host–parasite relationships.

It is the intent of this book to summarize some of the knowledge that has accumulated during the last 50 years. Throughout, the systematic arrangement and nomenclature outlined in Chapter 4 by Omar Amin has been adopted. Synonyms, under which some of the information cited was published, are readily found in that chapter.

Finally, it is impossible to introduce a review such as this without also speculating on the likely content of similar reviews 50 years in the future. Large voids in understanding the Acanthocephala result from the paucity of information on their genetics and their immunological relations with

hosts. Advances on these fronts undoubtedly will occur and with them will emerge more enlightened views on pathogenesis, host specificity, host resistance, phylogeny, and many other facets of biology. Increased understanding of cellular and molecular relationships might permit better success in *in vitro* cultivation and with it advances in fields dependent on that technique. A better defined fauna and computer-assisted analysis should produce more detailed and theoretical understanding of community structure and population dynamics. Perhaps puzzling instances of dispersal and distribution among hosts will be resolved.

Whether parasitological study follows these or other paths in future years, present appreciation of the potential held by the Acanthocephala as experimental animals indicates that knowledge of their biology will increase along with their contributions to research in helminthology.

2

Anton Meyer

D.W.T. Crompton

Anton Meyer was born on 28th September 1901 in Mies (now called Stříbro; southwest of Prague, 49.46N, 13.00E) in Bohemia.[1,2] His father, who was probably also called Anton,[1] was a tinsmith from Černošin and his mother, whose maiden name was Buberlová, came from Marienbad.[3] In an application form to the Rockefeller International Education Board,[1] Meyer's citizenship is given as Czechoslovakian and his languages as German, English and Czech in that order. This application form and other sources give no more information about his family and origins. He declared himself as unmarried in 1927[1] and in 1933 wrote 'I am still away from getting married'.[4] Meyer may have died about the time of the outbreak of World War II, possibly in a psychiatric hospital in Dobřany[3] which was destroyed, together with its medical files, by a bombing raid in 1943.[5] Attempts to check this suggestion have yielded nothing of substance, but something may be inferred from the publication in 1958 by another author, C. Spren, of a supplement entitled 'Nachtrag zu Dr Anton Meyer – Klasse: Acanthocephala, Akanthozephalen, Kratzer' in *Die Tierwelt Mitteleuropas*; presumably Meyer must have died.

The record of Anton Meyer's education and academic career is no easier to trace than his personal history. He attended the *Gymnasium*, which we may assume was in Mies, from 1912 to 1920 when he attained his certificate of maturity.[1] He then enrolled in the Faculty of Natural Sciences at the German University of Prague and was awarded his Doctoral Degree on 20th October 1924 for research on the embryology of *Macracanthorhynchus hirudinaceus* (Acanthocephala) under the supervision of Professor C.T. Cori.[1,6] Meyer remained at the German University of Prague as a Demonstrator at the Zoological Institute until he moved to the Department of Zoology at the University of Oxford in England in October 1927 on being awarded a Research Fellowship from the Rockefeller International

Education Board.[1] The Fellowship, which was offered for a year in the first instance, covered the costs of his travel between Czechoslovakia and England, and provided a stipend not to exceed more than US$120 per month.[7] Anton Meyer worked with Professor E.S. Goodrich[8,9] on various aspects of the biology of annelid worms and, after his Rockefeller Fellowship had been extended,[10] he moved in July 1928 to the laboratory of the Marine Biological Association of the United Kingdom at Plymouth where he stayed until February 1929.[11,12]

After his visit to England, Meyer appears to have intended to take up a post as Assistant at the Zoological Institute of the German University of Prague,[13] but these plans may not have been fulfilled. He undoubtedly worked at the Zoological Institute of the University of Leipzig[14] with financial support from the Notgemeinschaft der Deutschen Wissenschaft, an agency acknowledged by Meyer in several of his publications of this period. Anton Meyer next moved, perhaps towards the end of 1931 and apparently with continued financial support from the Notgemeinschaft der Deutschen Wissenschaft, to the Kaiser-Wilhelm-Institut für Biologie, Berlin-Dahlem. He was accommodated in the department headed by Dr Otto Mangold[15] where he worked on his monograph on the Acanthocephala.[16,17]

Between 1933 and 1938, after the publication of his monograph, Meyer does not seem to have had any permanent or even temporary laboratory address. His contribution to *Die Tierwelt Mitteleuropas*, which was published in 1938, gives his address as 'in Mies i Böhmen'. In two letters,[4,18] which mark the beginning and end of this period, it is clear that he had had several arguments with colleagues, editors and publishers about the length of his manuscripts and the significance of his research. For example, he wrote 'Also my monograph of the Acanthocephala became somewhat shortened and deprived of the preface which would have been very necessary, as to secure a right understanding of the disposition of the whole. I had heavily to cross with the publisher...'[4] In the same letter he writes as if recovering from a state of nervous exhaustion and perhaps, although this is merely a speculative suggestion, he was by the end of 1933 beginning to suffer from the illness which may have led to his death in the hospital in Dobřany.

Anton Meyer was remembered by Dr D.P. Wilson[19] as 'a quiet pleasant young man, an earnest and meticulously careful worker'. They corresponded after Meyer's departure from Plymouth[4,19] and, as a token of friendship and respect, Meyer sent Dr Wilson a copy of M.E. Boyle's book *In Search of Our Ancestors* (1927, London, Bombay & Sydney: George G. Harrap & Co. Ltd) in which he wrote 'Dear Mr Wilson. With best

wishes for Christmas I send you this book as a small expression of my gratitude. Yours truly Ant. Meyer.' Professor W.E. Ankel[20] recalled Meyer as a typical outsider whom he would have described as a nonconformist. He could not remember where they met, but thought it could well have been at the Zoological Station in Naples. There is no record of Meyer's having worked at Naples,[21] but he could have worked there; he visited the Marine Stations in Helgoland[1] and Messina.[13] Dr H. Kumerloeve[14] clearly remembered Meyer 'as dark-haired, small and with glasses and as a rather shy person who had almost no contact with other scientists' in the laboratory at Leipzig. He gave a seminar there and 'was known as a highly specialized scientist'. From these fragments of direct evidence, Anton Meyer (Fig. 2.1) emerges as an intense, sensitive, dedicated and lonely man. He does not seem to have worked in collaboration with others (see list of publications below), he could not be traced

Fig. 2.1. Anton Meyer. This photograph, which was kindly provided by Dr D.P. Wilson, was accompanied by a handwritten inscription, 'Marienbad, August 1939, Drinking Ambrosias'.

as having been a member of the relevant scientific societies of his day (e.g. Kaiser-Wilhelm-Gesellschaft and Zoologische Gesellschaft), there is no obvious obituary notice, he is not mentioned in the *Biologorum*, there is no record of him in the archives of the Berlin Document Centre and he does not appear to have served as an editor or editorial-board member for any of the prominent scientific journals of the time.[22,23]

During his career (1920–?1939), Anton Meyer achieved much in the fields of acanthocephalan and annelid biology (see list of publications below). In Professor Ankel's view, Meyer's 'most exciting contribution at that time' was his work on flagellated cells in annelids.[20] Professor Cori,[6] whose opinions were endorsed by Professor G.N. Calkins,[24] regarded Meyer as a gifted scholar of unusual maturity and scientific judgement who had already done very creditable work on the cytological aspects of fertilization.[13] Paradoxically, Meyer's researches on annelids, which provided most information about his history, seem to have lost their early impact (for example, his work is given little attention in the relevant volume on *Traité de Zoologie*, edited by P-P. Grassé, Paris: Masson et C[ie]) while his acanthocephalan contributions, which have so far revealed little about the author, have remained fundamental to our present understanding of the phylum.[25]

Anton Meyer's life and achievements are all the more interesting and remarkable because they took place during a period of major change and instability in Europe. In 1901, when he was born, Bohemia was a province of the Austro-Hungarian Empire.[26] By 1920, when he went to the University of Prague, the fragmentation of Europe during World War I had occurred and the state of Czechoslovakia had been formed from the provinces of Bohemia, Moravia, Silesia, Slovakia and Ruthenia. This amalgamation produced an apparently economically strong country with an important strategic position, but also a population of several languages and divided loyalties.[26] Some looked to Vienna for leadership, others to Budapest and no doubt the German-speaking residents of the Sudetenland,[27] like Meyer, felt drawn towards the rising power of the new Germany as the Weimar Republic (1919–1933) was overtaken by Hitler's National Socialist Workers' Party which advocated anti-semitic, anti-communist and anti-parliamentary policies.[26,28,29] At the end of Anton Meyer's career, and probably of his life, Europe was again on the verge of destruction and terror as World War II approached. Throughout this period, the political uncertainties and power struggles and the collapse of the German economy in the 1920s,[30] when Meyer would have been seeking grants to support his highly academic research, could hardly have helped to create a secure environment for a young and sensitive scientist.

Unless serendipity intervenes, much more research will be needed to elucidate the life history of Anton Meyer and explain how his interest in the Acanthocephala was aroused. Perhaps he should remain as a shadowy figure and perhaps his private life, his hopes and fears, his ambitions and disappointments should not be disclosed. Science is our common heritage and scientists come and go, but I wish we knew more about him.

> Time will say nothing but I told you so,
> Time only knows the price we have to pay;
> If I could tell you I would let you know.
>
> *If I could tell you*, W.H. Auden,[31] October 1940

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Publications of Anton Meyer

1924 Über die Segmentalorgane von *Tomopteris helgolandica* nebst Bemerkungen über das Nervensystem und die rosettenförmigen Organe. *Zoologischer Anzeiger*, **60**, 83–8.

1926 Die Segmentalorgane von *Tomopteris catharina* (Gosse) nebst Bemerkungen über das Nervensystem, die rosettenförmigen organe und die Cölombewimperung. Ein Beitrag zur Theorie der Segmentalorgane. *Zeitschrift für Wissenschaftliche Zoologie*, **127**, 297–402.

1927 Über Cölombewimperung und cölomatische Kreislaufsysteme bei Wirbellosen. Ein Beitrag zur Histophysiologie der secundären Liebeshöhle und ökologischen Bedeutung der Flimmerbewegung. *Zeitschrift für Wissenschaftliche Zoologie*, **129**, 153–212.

Ist *Parergodrilus heideri* (Reisinger) ein Archiannelide? *Zoologischer Anzeiger*, **72**, 19–35.

1928 Die Furchung nebst Eibildung, Reifung und Befruchtung des *Gigantorhynchus gigas* (Ein Beitrag zur Morphologie der Acanthocephalen). *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **50**, 117–218.

1929 Die Entwicklung der Nephridien und Gonoblasten bei *Tubifex rivulorum* Lam. nebst Bemerkungen zum natürlichen System der

Oligochäten. *Zeitschrift für Wissenschaftliche Zoologie*, **133**, 517–62.

Über Cölombewimperung und cölomatische Kreislaufsysteme bei Wirbellosen. II. Teil. (Sipunculoides, Polychaeta Errantia). Ein Beitrag zur Histophysiologie und Phylogenese des Cölomsystems. *Zeitschrift für Wissenschaftliche Zoologie*, **135**, 495–538.

On the coelomic cilia and circulation of the body-fluid in *Tomopteris helgolandica*. *Journal of the Marine Biological Association of the United Kingdom*, **16**, 271–6.

Ein atavistischer *Tubifex*-Embryo mit überzähligem Gonoblastenpaar und seine Bedeutung für die Theorie der Segmentstauchung bei den Oligochäten. *Zoologischer Anzeiger*, **85**, 321–9.

Zur Segemtierungsanalyse und Stammesgeschichte der Oligochäten. *Zoologischer Anzeiger*, **86**, 1–16.

Tomopteris anadyomene nov. spec. ein Nachweis Phylogenetischer Umwandlung von Nephridialtrichtern in leuchtorgane bei den Polychäten. *Zoologischer Anzeiger*, **86**, 124–33.

1930 Vergleichende Untersuchung der Segmentalorgane von Tomopteriden des Mittelmeeres, ein Nachweis eines Substitutionsprozesses. *Zeitschrift für Wissenschaftliche Zoologie*, **136**, 140–53.

1931 Das urogenitale Organ von *Oligacanthorhynchus taenioides* (Diesing), ein neuer Nephridialtypus bei den Acanthocephalen. *Zeitschrift für Wissenschaftliche Zoologie*, **138**, 88–98.

Urhautzelle, Hautbahn und plasmodiale Entwicklung der Larve von *Neoechinorhynchus rutili* (Acanthocephala). (Ein Beitrag zur Entwicklungsmechanik gebahnter organbildung.) *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **53**, 103–26.

Infektion, Entwicklung und Wachstum des Riesenkratzers (*Macracanth. hirudinac.*) im Zwischenwirt. *Zoologischer Anzeiger*, **93**, 163–72.

Gordiorhynchus, ein neues Acanthocephalengenus mit innerer ovarialer Pseudosegmentierung. *Zoologische Jahrbücher. Abteiling für Systematik, Ökologie und Geographie der Tiere*, **60**, 457–70.

Neue Acanthocephalen aus dem Berliner Museum. Bergründung eines neuen Acanthocephalensystems auf Grund einer Untersuchung der Berliner Sammlung. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*, **62**, 53–108.

Die Formbildungsmuster und Das Wirbelphänomen in der Cölombewimperung von *Nephthys*. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **14**, 222–54.

Das Häutgefasystem von *Neoechinorhynchus rutili* (Formbildung auf plasmodialer Grundlage). *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **14**, 255–65.

Cytologische Studie über die Gonoblasten und Andere Annliche Zellen in der Entwicklung von *Tubifex*. *Zeitschrift für Morphologie und Ökologie der Tiere*, **22**, 269–86.

Die Stellung des Genus *Heterosentis* Van Cleave 1931 im Acanthocephalensystem. *Zoologischer Anzeiger*, **94**, 258–65.

Die Acanthocephalen d. Arktischen Gebietes. *Fauna Arktica*, **6**, 9–20.

1932 Acanthocephala. In *Dr H.G. Bronn's Klassen und Ordnungen des* Tier–Reichs, Band 4, Abt. 2, Buch 2, Lief. 1, pp. 1–332. Leipzig: Akademische Verlagsgesellschaft MBH.

1933 Acanthocephala. In *Dr H.G. Bronn's Klassen und Ordnungen des Tierreichs*, Band 4, Abt. 2, Buch 2, Lief. 2, pp. 333–582. Leipzig: Akademische Verlagsgesellschaft MBH.

1934 Über Formbildung (Morphodynamik). *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **36**, 218–24.

Die Axiome der Biologie. *Nova Acta Leopoldina Halle*, **1**, 474–551.

1935 Eine regionale Protoplasmazentrierung als Ursache der Formbildung. *Biologia Generalis*, **11**, 122–34.

1936 Dynamese des cölomatischen Wimperfeldes von *Nephthys hombergii*. *Biologischen Zentralblatt*, **56**, 532–48.

Die plasmodiale Entwicklung und Formbildung des Riesenkratzers *Macracanthorhynchus hirudinaceus* (Pallas). I. Teil. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **62**, 111–72.

1937 Die plasmodiale Entwicklung und Formbildung des Riesenkratzers *Macracanthorhynchus hirudinaceus* (Pallas). II. Teil. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **63**, 1–36.

1938 Die plasmodiale Entwicklung und Formbildung des Riesenkratzers *Macracanthorhynchus hirudinaceus* (Pallas). III. Teil. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **64**, 131–97.

Die plasmodiale Entwicklung und Formbildung des Riesenkratzers *Macracanthorhynchus hirudinaceus* (Pallas). IV. Allgemeiner Teil. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **64**, 199–242.

Der Rogen (Spawn) und die Entwicklung der Trochophora von *Eulalia viridis* (Phyllodocidae). *Biologia Generalis*, **14**, 334–89.