

Jan Koteja - an extraordinary evolutionary and revolutionary coccidologist

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Abstract: This article summarises the extraordinary contributions to coccidology made by the late Professor Jan Koteja. During his 40 year career, he published over 110 articles on scale insects, including faunal surveys, studies of the taxonomy and morphology of extant groups, and more than 40 papers on scale insect palaeontology. His thorough studies in comparative morphology, especially of the mouthparts and sensilla, and his descriptions and illustrations of fossil scale insects are tangible legacies of his life's work. Furthermore, his ideas on scale insect evolution and classification, particularly his hypothesis on the early evolution of scale insects and his family-level classification of Morrison's Margarodidae, were revolutionary and inspirational. The breadth and high quality of Jan's research ensures that coccidologists will remember him always.

Key words: Koteja, biogeography, Poland, systematist, palaeontologist.

Introduction

Professor Jan Koteja was honoured *in absentia* at ISSIS-X in Turkey in 2004. He was presented with a plaque for his exceptional contributions to coccidology, but no review of his life, career and scale insect research was written at that time. At the current ISSIS-XI, Drs Ana Dziejzicka and Elżbieta Podsiadło have written a special tribute to the whole of Jan's amazing life. Here I attempt to summarise just Jan's contributions to coccidology, which are numerous and highly influential.

My first recognition of Jan's work was in 1975 when, during my PhD studies, Ms Helen Brookes, then at the Waite Agricultural Research Institute in Adelaide, handed me Jan's substantial papers (Koteja 1974, 1974b) on scale insect mouthparts to photocopy and read. Today, my students and I frequently still use those and subsequent publications (e.g., Koteja, 1976; Koteja & Liniowska, 1976). Similarly, Jan's two articles on scale insect sensilla (Koteja, 1974a, 1980) are masterpieces of comparative morphology. Jan's approach to morphology was to document similarities and differences among as many groups as possible and to suggest evolutionary trends in structural variation. Later I was to hear Jan's views on the early evolution of scale insects presented at ISSIS-IV in Hungary in 1983. His concise paper (Koteja, 1984b) entitled "Why the scale insects (Homoptera, Coccinea) are unusual", and his subsequent longer argument (Koteja, 1985b) "Essay on the prehistory of the scale insects (Homoptera, Coccinea)" had an enormous impact on my understanding of scale insect evolution, and this legacy persists today in my work. Jan proposed that the early evolution and radiation of scale insects occurred on the forest floor (hypogeal habitat) and that specialization for that habitat led to modifications, especially of the legs, wings and development, which became morphological constraints during later evolution.

Jan did not attend ISSIS-V in Italy but, as was his style, he contributed several papers, including a short article on why there are so many gall-inducing scale insects in my home country, Australia (Koteja, 1987b). Jan always had so many good ideas and, later when we all got onto email, Jan would correspond with his colleagues on all manner of discoveries and hypotheses. I always enjoyed reading his long and thoughtful email letters expounding his latest findings or opinions.

Jan organized and ran the ISSIS-VI meeting at Kraków, Poland, in 1990. He accepted the manuscripts of the participants early and by the meeting had published Part II of the

Proceedings, as a stimulus for discussion. That volume contains 44 papers and Jan had planned to publish a Part I later (but other events intervened). During ISSIS-VI, Jan's emblem on the cover of the Proceedings was adopted as the logo for future ISSIS meetings. The Kraków meeting was highly memorable and Jan was a congenial host. I especially remember being given a tour of his laboratory and inspecting various amber fossils of scale insects. Jan's research on fossil scale insects started to appear in print from the 1980s (Koteja, 1984d, 1985a,b, 1986, 1987, 1987a,d, 1988, 1988b-d, 1989, 1989b, 1990, 1990a, 1996, 1996b-d, 1997a-e, 1998, 1998a, 1999, 2000, 2000c, 2001, 2001a,c, 2004; Koteja & Żak-Ogaza, 1988, 1988a, 1989; Koteja & Azar, 2001; Koteja & Ben-Dov, 2003; Koteja & Poinar, 2001, 2005). He erected eight extinct families (Albicoccidae, Burmacoccidae, Electrococcidae, Grimaldiellidae, Inkaidae, Jersicoccidae, Kukaspididae and Labiococcidae) and many new species and genera based on fossil scale insects, and always provided insightful discussion of scale insect evolution in his papers. Jan is the only person ever to have made significant contributions to scale insect palaeontology. His work is synthetic in nature and morphologically detailed, and clearly benefited from his superb knowledge of the morphology and taxonomy of extant taxa. All of Jan's earliest papers, from 1964 to 1985, reported either on the comparative morphology (mentioned above) or taxonomy of extant species, especially but not exclusively in the Coccidae (e.g., Koteja, 1966, 1966a, 1969, 1970, 1971, 1978, 1979, 1979a, 1980a,b, 1984; Dziedzicka & Koteja, 1971, 1985; Koteja & Rosciszewska, 1970; Koteja & Żak-Ogaza, 1972, 1979, 1981; Koteja & Howell, 1979; Koteja & Kozár, 1979; Koteja & Brookes, 1981), or on faunal studies of Polish scale insects (e.g., Koteja, 1964, 1969a, 1970a, 1971a, 1972; Koteja & Żak-Ogaza, 1966, 1969, 1983). He continued faunal studies throughout his career (e.g., Koteja, 1984e, 1985, 1986b,c, 2000a,d; Lagowska & Koteja, 1996) but the few later studies of extant groups (e.g., Koteja, 1986e,g, 1988a, 2001b) were replaced with his prolific studies of scale insect compression fossils and amber inclusions.

Jan followed from a long line of distinguished Polish entomologists, including A.W. Jakubski, K.L. Boratynski, Z. Kawecki and B. Żak-Ogaza, whose names are well known to contemporary coccidologists. Jan was one of Professor Kawecki's many students. There seems no doubt that the Polish cochineal insect, now known as *Porphyrophora polonica* (Linnaeus), and its early literature (some even before the time of Linnaeus), engendered their interest in scale insects (see preface to Jakubski, 1965; Davies & Williams, 1982; Dziedzicka, 1984a).

Altogether Jan published more than 110 articles on scale insects, and some of them substantial tomes. The genius of his work was to combine knowledge of modern scale insects with a thorough understanding of fossils. Very few palaeoentomologists are also neontologists, but Jan was familiar with all scale insect families and all instars, including the adult male, from the early Mesozoic to the present.

One of Jan's most important contributions to coccidology was his foresight in recognising that the margarodids *sensu* Morrison (1927, 1928) "are relics of an ancient, abundant and diverse group" [see his reviewer's remark on page 47 of Kozár & Kosztarab (1988)]. In a series of papers (Koteja, 1974, 1990a, 1996a, 2000b), Jan classified the extant margarodids *sensu lato* into a number of distinct families, namely Callipappidae, Coelostomidiidae, Kuwaniidae, Marchalinidae, Margarodidae *sensu stricto*, Matsucoccidae, Monophlebidae, Pityococcidae, Steingeliidae and Xylococcidae. Recent works (e.g. Foldi, 2005a,b; Hodgson & Foldi, 2006; Miller *et al.*, 2007) support this multi-family classification and thus gradually coccidologists are accepting a view that Jan first proposed over 30 years ago. Clearly Jan was ahead of his time in his ideas and phylogenetic thinking, even though he never had

access to DNA data or analysed any morphological data on a computer, other than the one in his head.

At time of his death in August 2004, Jan was working with Dany Azar on a large paper documenting the scale insects from Lower Cretaceous amber of Lebanon. Fortunately, this important work, which describes new taxa, including three new extinct families, should be published soon (Koteja & Azar, 2008). We dearly miss Jan as a colleague and our discipline has lost an extraordinary evolutionary and revolutionary scientist.

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References

For full reference details, please refer to publications by Jan Koteja listed in ScaleNet (Veilleux *et al.*, 2006); dates and letter codes (e.g., Koteja, 1974, 1974a, etc.) cited in the text above are the same as in ScaleNet. Other cited references also can be accessed via ScaleNet except Miller *et al.* (2007) and Koteja & Azar (2008).

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