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HEINRICH ERNST KARL JORDAN

1861-1959

KARL JORDAN, affectionately known for very many years by those most closely in touch with him as 'K.J.', was born the youngest of seven children of farming stock in the small village of Almstedt near Hildesheim in Hanover on 7 December 1861. As a child he had to help on the farm, yet found time to indulge a lively interest in the wild life of his surroundings. At the age of five he lost his father, and but for the generosity of an uncle who enabled him to attend the Hildesheim High School, his massive contributions to the study of entomology might never have been forthcoming. In 1882 he entered the University of Göttingen and four years later took his degree in botany and zoology, passing Summa cum Laude. Two years later, after securing a teaching diploma and putting in a year's military service (not without hardship), he was appointed a master at Münden Grammar School. Here he remained five years and here it was that he became known to two men whose acquaintance was to shape his whole future career. One was A. Metzger, Professor of Zoology at the Academy of Forestry, the other Count Berlepsch, an enthusiastic amateur ornithologist. In 1891 he married Minna Brünig with whom he had fallen deeply in love whilst both were still in their teens. It proved a profoundly satisfying marriage, broken only by her death in 1925. Although he quite rapidly acquired a British, indeed an international outlook, she remained to the end German, yet stoically bore the distresses this caused during the 1914-1918 world war.

Hardly had Jordan taken up his duties as teacher of mathematics, physics and natural history at the School of Agriculture in Hildesheim, in 1892, than, through the strong recommendation of his two good friends he received from Dr Hartert (recently appointed Director of Walter (later Lord) Rothschild's Museum at Tring) an invitation to join the staff of that Museum as entomologist. As Miriam Rothschild has written (Rothschild, M., 1955, p. 2): 'It is difficult to envisage a queerer state of affairs than that which K.J. found at Tring when he arrived there in 1893. Walter Rothschild was then twenty-four years of age and a most eccentric figure. He was always just about to leave the Rothschild banking house in disgrace, not for any serious misdeed, but because he displayed a quite remarkable lack of business acumen . . . and—worst of all—while pretending to attend the House of Commons actually spent all his time at the Natural History Museum . . . Another equally disconcerting aspect of the situation at Tring was the complete lack of facilities for working with a microscope. Walter Rothschild's



father had recently erected two cottages on the outskirts of the park in which his son was supposed to house his museum, but there was no space to accommodate the beetles which K.J. was engaged to "arrange, determine and classify". This gigantic overflow was stacked in boxes at random and in fearful confusion, in sheds and hired rooms scattered about Tring. K.J. had not even a suitable desk at which to work, and found it necessary to retire to the landing window-sill if he required sufficient light by which to use so much as a powerful lens. But this weird state of affairs in no way disconcerted him; with characteristic objectivity he appreciated the immense opportunities Tring had to offer. Here was the chance for both interesting and creative work. He took it.

'It is an almost incredible fact that within a year the collections of over 300000 beetles (60000 species) were arranged and classified—in the more conspicuous families named down to genera and species—while by the end of the following year over 400 new species had been described. K.J. was quick to realize that one aspect at least of Walter Rothschild's mania for size was both important and valuable. It was only a large collection such as this, containing both a great number of species and very long series of specimens, which could give him the facts he required.'

Normal hours of work were far exceeded. Living only a stone's throw from the Museum Dr Jordan quickly contracted the habit, which stayed with him till after his ninetieth birthday, of working on in the Museum after dinner well into the night. For recreation, he would take long walks or cycle rides and, later, took to gardening—the writer of this note well remembers seeing him vigorously wielding a pick in a recalcitrant corner of his rock-garden at the age of 91.

Dr Jordan's incredible industry is at no period better exemplified than by the product of his first few years at Tring. Between 1893 and 1895 he not only reduced the chaotic insect collections to order but saw the first instalment of the Revision of the Papilios of the Eastern Hemisphere, consisting of some 300 pages, actually published. True it is that the main text of this very important work was by Rothschild, but there are many notes by Jordan who also provided all the drawings of anatomical details. Much light is shed upon the nature of the collaboration between Rothschild and Jordan by Jordan himself in his tribute to Lord Rothschild published in 1938 (Nov. Zool. 41, 1-14), from which the following passages are quoted. 'Walter Rothschild worked in many instances quite independently, neither discussing the subject with the curators, nor submitting the manuscript' . . . he . . . 'had never taken kindly to the microscope and microtome. Structural details easily escaped him. Like an artist, he perceived the animal as a whole and not the details . . . which would have been revealed by the cold lenses of a microscope.' Yet one of the outstanding features of all their joint work, as of Jordan's alone, is the insistent attention paid to structural details, no few of which were utilized by them for the first time.

Jordan's introductory note to this first major product of the Tring Museum

in the field of entomology is of particular interest as it sets out for the first time the taxonomic concepts and general principles which guided all his work, with but relatively trifling modifications and improvements in later years. As Eugene Munroe has so aptly written (Munroe, E., 1955, p. 69): 'Jordan's notes on Papilio, written ten years before the rediscovery of Mendel's laws, and forty years before the modern synthesis of taxonomy and population genetics, can be read virtually without reservation to-day. Here we find emphasis on the importance of series and, more, of adequate samples from every part of the geographic range. Here is a worker in possession of hitherto unrivalled material, who might well have been excused a touch of complacency, but who instead borrows specimens from almost every important collection, and bemoans the inadequacy of the accumulated resources of the world. Here, too, we find a clear understanding of the importance of types as standards of identification; here is a perfectly modern concept of the population as the basic unit in taxonomy, and a clear relegation of environmental and individual variation to a subordinate place; here is recognition of the plasticity and local variation that exist within larger and more definitely characterized populations; here are a mature appreciation of the process of geographic speciation, a firm and definite subspecies concept, and a recognition of the importance of vicarious species. These clear ideas are reflected in an equally clear nomenclatorial practice: the trinomen is explicitly reserved for the subspecies; indeed we find Jordan urging the taxonomic co-ordinacy of the nominate subspecies with other subspecies, and its nomenclatorial treatment as a trinomen, on his as yet reluctant co-editors, Rothschild and Hartert!' Here for the first time in lepidopterology, as Jordan has himself remarked (1938, Nov. Zool. 41, 9), geographical races described by various authors as distinct species were almost consistently (as much as the material at hand warranted) reduced to the rank of subspecies and the classification thereby much clarified.

Miriam Rothschild remarks how quickly one grows accustomed to scientific advances and how easily one takes them for granted. It will perhaps help to put Jordan's views in perspective by remembering that they were elaborated at a time when scorn and derision were still being poured on the theory of mimicry; when the occurrence of polymorphism such as exists in the African swallow-tail butterfly *Papilio dardanus* was still regarded by many leading entomologists as an impossibility; and when A. G. Butler in the British Museum and F. Moore in India had barely stopped describing as new species large numbers of Terias which, according to Jordan's concepts, could only be regarded as, and in fact were, seasonal forms or poorly differentiated geographical races. One must remember, however, that in those days the truth of another of Jordan's dicta was not generally realized: two or three specimens were considered adequate material on which to base a 'species': the need for long series, more and ever more material, was constantly stressed by Jordan, even though the material available to him at Tring was outstandingly greater than that of any other museum or private collection then in existence. Lord Rothschild once remarked to the writer that 'he never had any duplicates'!

Much has been heard during the past two or three decades of the 'new systematics' born of the discovery of Jordanian systematics by followers of other biological disciplines, notably the geneticists. Throughout his long career Jordan was a forthright champion of what this writer prefers to call the true systematics; and he could be scathing. 'Classification, as we know, has the reputation of being as dry as our cabinet specimens . . . and of interest only for those who work on the special group of animals classified. There are even biologists of fame who, in their misguided wisdom, scoff at systematics and look down upon this kind of work as more or less fruitless ... I take the opportunity ... of stating emphatically that sound systematics are the only safe bases upon which can be built up sound theories as to the evolution of the diversified world of live beings' (1911, Proc. Int. Ent. Congress, p. 385). It is curious that neither here (which would be rather early for it) nor later does Jordan make any reference, or only the most cursory references, to the work of the geneticists. Its possibilities can hardly have escaped him. In later years he often spoke with appreciation of the evolutionary geneticists and with regret that their important fields had not been opened up earlier.

Three orders of insects provided Jordan with the basis of all his taxonomic work, the butterflies and moths (Lepidoptera), the beetles (Coleoptera) and the fleas (Siphonaptera). Beetles attracted him most and, among these, the Anthribidae, a large family of 'long-horned' weevils displaying a truly bewildering range of variation, fascinated him. Over the years he published 145 papers on this single family and described 150 genera and some 1900 species and subspecies, representing nearly half the known genera and twothirds of the known species. All this, however, he regarded quite properly as merely preliminary work essential for the provision of a sound classification of the family, remarking that it would have saved taxonomists an enormous amount of laborious drudgery if Noah had 'imprinted an inheritable name on the bodies of the millions of species he saved from extinction by drowning'. Jordan could always see both the wood and the trees, the immediate needs and the distant objective. At the very end of his career he was still seeking logical explanations of the seemingly chaotic riot of variation displayed by these, his favourite, beetles. One is tempted to wonder why, with so much material so richly endowed with features well calculated to arouse speculation on evolution, taxonomy and cognate matters, Jordan hardly ever broached these subjects in any of his writings on Anthribidae. The reason is almost certainly that which confronts every taxonomic entomologist, no matter what his group, with a few exceptions: however extensive his material, it is hardly ever more than a small fraction of what he needs as a basis for satisfying work.

About the turn of the century Lord Rothschild gradually parted with all his Coleoptera, except the Anthribidae, so channelling his entomological

curator's activities towards the Lepidoptera, in which he was especially interested, altering the nature but by no means reducing the volume of Jordan's output. Of all the insects, the Lepidoptera are undoubtedly the most familiar and most collected. And of all the Lepidoptera by far the best known sixty years ago, as now, were precisely those groups which Rothschild, with Jordan's help, decided to monograph-the swallow-tailed butterflies, the hawk moths and the Charaxidini. Fairly abundant material of these was available (though it entailed searching most of the museums and private collections of Europe), and something was known of the bionomics of a good many of the species. The Revision of the Eastern Papilios, already referred to above, was based on the examination of some ten thousand specimens distributed amongst the 239 species which the authors recognized. This was followed by A Monograph of Charaxes and the allied prionopterous genera. The four parts of this appeared in 1898, 1899, 1900 and 1903, were profusely illustrated and ran to 375 pages. It is astonishing that simultaneously (in 1903) the Revision of the lepidopterous family Sphingidae, a work of over 1000 pages, illustrated by 67 plates, also was published. Sheer volume provides no criterion of value but when the quality of these works is considered, their production in so short a space of time is little short of phenomenal. In originality, breadth of outlook, accuracy and sound judgment they far surpassed all previous publications of a like nature, and little of a similar comprehensive character and permanent value has been published since. These are still the standard works on the subjects of which they treat; only here and there have modifications had to be made in the light of later discoveries.

It was not until 1906 that Rothschild and Jordan brought out the second part of their projected monograph of the swallow-tailed butterflies, dealing with the American Papilios. In many ways this was a greater achievement than their treatment of the oriental species, for the state of confusion that had till then reigned in the group was greater, the available material and information much less and the taxonomic problems more complex. Moreover, owing to the nature of the South American continent, material was available only from a limited number of points, such as the neighbourhood of the larger towns, and the banks of the rivers. The intervening areas were unknown. In spite of this Jordan was able to show on morphological grounds that many 'species', recorded from these widely separated areas, were truly only subspecies. He returns again, in the introduction, to his definitions of varieties, rather unnecessarily labouring the point one would say nowadays, until it is remembered that at that time the acceptance of his views and their expression in appropriate scientific terms and forms of nomenclature was still far from universal. Incidentally, he calls attention to a fact that must be little known to zoologists, namely, that it was Esper in his essay De varietatibus (1781, p. 18) who first introduced the term subspecies and defined it as 'that kind of variety which is an incipient species'. 'Therefore', says Jordan, 'the term subspecies is employed by us for nothing else but the geographical variety' since 'according to our researches the incipient species

is represented by the geographical race . . . no other variety forms the basis of the development of a species into several species'. In the matter of the nomenclature of infrasubspecific varieties, he champions a system which almost inevitably will one day be adopted, under which each peculiarity will be known 'by a special morphological term'. He points out the inconvenience, if not the absurdity, of calling, for example, the uniformly black variety of one swallow-tail ab. *niger*, of another ab. *wilsonae*, of a third ab. *schmidtii*, and so on. 'The describing and cataloguing of "species" are certainly the basis of systematics, but also the lowest degree in this science. After that comes classification, or in other words, research in relationship.'

Simultaneously, during this period of the monographs, Jordan published numerous shorter papers describing the new discoveries which Rothschild's collectors were constantly making in the East Indies and particularly New Guinea. This activity, which Jordan always regarded as rather menial, however essential, continued into the 1950's but with the emphasis shifting gradually to the Anthribidae and Siphonaptera. At the same time several papers of a purely morphological nature appeared from his pen; for example, on the antennae of butterflies (1898), on the mesosternite of butterflies (1902), on a peculiar sexual character found among Geometridae (1905), on the basal spine on the forewing of Saturniidae (1911). Much of this work, however, is hidden in longer taxonomic papers, preparation of which necessitated it. It was almost exclusively Jordan's work on the Lepidoptera that provided him with the basis of all his more philosophical papers.

Jordan's interest in fleas dated from about 1898, or earlier, and was inspired by a schoolboy, Charles Rothschild, Walter Rothschild's younger brother. 'Before K.J. had won himself a desk on the ground floor of the Museum Cottage he was sometimes joined at the landing windowsill (his only work bench!) by a modest but very enthusiastic schoolboy for whom he instantly conceived a great liking' (M.R., 1953, p. 4). Elsewhere Miriam Rothschild records (1953, Hopkins, G. H. E. and Rothschild, M. Cat. Fleas, 1, 5) how these two laid the foundations of the Rothschild flea collection through a successful setting of two traps one evening at Tring in search of Typhlopsylla agyrtes. Thereafter Jordan published, either alone or jointly with Rothschild, upwards of 140 papers on fleas, running to over 1450 pages and including descriptions of at least 75 new genera and 480 new species and subspecies. To illustrate this massive contribution Jordan prepared 1280 drawings, besides executing 375 others for papers published by Charles Rothschild alone. The uniformly high standard of all this work would again be regarded as quite remarkable, were it not that, after very little contact with Jordan's work, one learns to expect it. An admirable summary of Jordan's work on the fleas has been written by Robert Traub (1955, pp. 33-42). After calling attention to the many morphological features and important concepts in the fields of distribution, taxonomy and host-relationships to which Jordan was the first to draw attention, Traub writes: 'Probably Jordan's greatest contribution to the study of Siphonaptera has

been the development of a system of classification of the higher categories, thereby ending literal chaos. This significant advance in systematics is based upon his sound background in morphology, coupled with an imaginative insight which enabled him to place new and fertile interpretations upon the relationships of genera, and the ability to consider new approaches as well as established methodology. The Order Siphonaptera seems unique concerning the enormous differences of opinion regarding familial assignment of major genera . . . The status of many other genera in the Order has been just as perplexing. The first taxonomic key which even attempted to cope with the many aberrant groups of fleas was that of Jordan in 1948, and this actually is a superb outline of the classification of fleas. Although by definition the key is not wholly inclusive, since the book dealt with arthropods of medical inportance, Jordan somehow managed to include in the key the great majority of the subfamilies of fleas. As a result, this chapter has been of incalculable assistance in the identification of fleas from remote areas since many exotic fleas simply would not fit anywhere in previous systems of classification. It cannot be overemphasized that the taxonomic characters used in this key were, to a great extent, wholly original and were not even mentioned by earlier workers, and are examples of Jordan's unusual interpretive powers. Among these original features are all save one of those listed for the superfamilies, and such structures as the vincula of the thorax, apical spines on the metanotum, and a transparent collar over the base of the anal tergum, all of which were formerly completely overlooked or disregarded. The path opened by the pioneer was readily followed by other workers, and Hopkins and Miriam Rothschild based their excellent classification upon that introduced by Jordan in 1948 and upon unpublished notes especially prepared for them at their request . . .

'The reader may be surprised that Jordan's epochal classification was not published until some fifty years after he first became interested in Siphonaptera. However, this apparent procrastination to a great extent explains why this scheme of systematics is so superior. Jordan deliberately waited as long as possible so that the maximum number of missing links and intermediate forms would be discovered. In the interim he went over the Tring collection many, many times, noting and studying every possible structure that might indicate relationship rather than similarities. This was enormously difficult, since so many fleas lack close relatives, and since similar morphological traits seem to occur spontaneously in apparently unrelated genera, while seemingly close forms often differ strikingly in a few particulars. Colleagues who visited Tring were astounded at Jordan's tremendous memory for detail, which enabled him to note an obscure characteristic in a species seen for the first time and then unerringly to point out, seemingly without effort, how the same feature occurred sporadically elsewhere in the order. Recitation of detail, however, did not interfere with his making sound generalizations as well. Only when all these pieces eventually began to fit in the puzzle did Jordan decide it was not premature to publish his ideas of classification.

'We are also much indebted to Jordan for exquisitely illustrating evolutionary trends within the Order Siphonaptera in 1950, and for simultaneously citing morphological details of use in determining the original affinities of this rather anomalous group of insects. Such an interesting and learned article could be written only by one who knew the comparative morphology of insects in general and was thoroughly familiar with the external anatomy of all types of fleas . . . This article is crammed with expert generalizations posing questions that will stimulate the students of the Order for years.'

An oft-told story, in which Dr Jordan played a leading part is that concerning plague and the systematics of the genus *Xenopsylla*. It is well told by Traub. 'In 1926 he pointed out that the Advisory Commission on Plague ... assumed that *all* pale fleas were X. *cheopis*, the vector of plague. One reason why the theory of transmission of plague by X. cheopis met opposition was that there was no plague in areas such as Madras where X. cheopis was common. However, as long ago as 1908, Jordan and Rothschild theorized that more than one species of fleas had been present in the experiments undertaken by the Commission. It remained for N. C. Rothschild to demonstrate that there were two other Xenopsylla common on rats in India, X. astia and X. brasiliensis, and Hirst then speculated that the distribution of these fleas might be connected with the distribution of plague. The Tring specialists thereupon showed that the "pale flea" in the non-endemic areas was generally X. astia, an inefficient vector of plague. A similar condition occurred when plague authorities in Africa identified the local vector as X. astia. It seemed strange that X. astia could be an inefficient vector in India and a highly efficient one in Africa, but the mystery was solved when Jordan and Rothschild proved that these African X. astia were in reality X. nubicus.'

In concluding his analysis of Dr Jordan's work on fleas, Traub emphasizes that the papers written by him when he was in his eighties and nineties were 'the finest he has ever done as regards concepts of classification and relationships of fleas . . . the only truly satisfactory classification of fleas was published during this period'. There cannot have been many zoologists who at this age could still utilize their accumulated knowledge and experience with unabated mental ability.

Early in his career at Tring Jordan had been impressed by the comparative isolation of entomology from the main stream of zoological thought and activity. His broad training rebelled at the attitude to entomologists held by so many professional zoologists of standing who should have been well aware of the contribution which entomology could make to the science. This intellectual isolation of entomology from the rest of zoology was, however, accompanied at that time by an insularity, one might call it, amongst entomologists themselves. In his travels about Europe Jordan discovered that very few of the scientific men he met were personally known to each other, and that, as often as not, their attitude to one another was competitive rather than co-operative. The size of the entomological field, too, holding more than three-quarters of all the known species of animals in the world, was of itself a factor tending to split entomology into a number of subsidiary 'camps', the occupants of which hardly knew each other either.

In an effort to remedy this state of affairs, Jordan conceived the plan of organizing a series of international entomological congresses, inspired perhaps by the zoological congresses which he had attended at Cambridge and Berlin. Little of his early world-wide correspondence on this project now exists, but in one of these early letters (from Bengtsson) there is the illuminating sentence, 'Es ist leider so gewiss, was Sie sagen, dass unsere schöne liebe Wissenschaft ein Stiefkund der Zoologie geworden ist und dass die Stellung der Entomologie nicht der Wichtigkeit der wissenschaftlichen und praktischen Ergebnisse derselben entspricht'. To cut a long story short, the combination of Iordan's industry, tact and sound practical good sense, inspired the Belgian entomologists enthusiastically to take up the idea and to organize the first Congress in Brussels in 1910. The second, Oxford 1912, was only saved from last-minute collapse, through the illness of the secretary, by the personal intervention of Jordan himself. From then on Jordan was the king-pin, in fact, if not always in name, the permanent secretary of the organization and twice resurrected it from the ruins of war. In 1948 at the Stockholm Congress, when too deaf to take part effectively in discussion, but still more audible than the great majority of speakers, he was elected Honorary Life President of the Congresses. If it is doubtfully true, as many maintain, that such congresses serve any great purpose in the furtherance of science, it is unquestionably true that the opportunities they provide for personal contacts are often of very great value. Even if entomologists held differing and sometimes seemingly antagonistic theories, they all sought the hidden truths which the study of differences between species both illuminated and obscured, and the making of friendships could, and often did, provide agreeable opportunities for reconciling them.

Another international field in which Jordan gave great service was that of zoological nomenclature. For about a hundred years from the time of the publication of the 10th edition of Linnaeus's *Systema Naturae*, all seemed well in this rather special field, so great had been the relief afforded by the introduction of the binominal system of naming species. However, by this time, national rivalries and isolation were beginning to cause such confusion that the need for rules of nomenclature was becoming all too evident. Various sets of rules were proposed; for over twenty years argument raged without conclusive result, even within the special Commission which had been set up expressly to produce an acceptable code. By 1913 when the Commission met at Monaco concurrently with the Zoological Congress the situation was critical. It was here that Jordan, quietly but with Lord Rothschild's forthright backing, saved the day by introducing a proposal that the Commission should be given plenary powers to suspend the rules in certain specified cases. This statesmanlike compromise satisfied both opposing camps and has been

a major contribution to the stability of zoological nomenclature. It is also a notably successful example of the application of the completely dispassionate and strictly objective scientific approach to the realm of human affairs. It not only 'saved the day' but it has been of the greatest assistance in the settlement of many knotty problems of nomenclature ever since. Jordan remained a member of the Commission till 1950, holding the office of President for just over nineteen years. His farewell letter to the Commission contains the following characteristic passages:

'One or other of the Commissioners may at times be inclined to regret the hours spent on the consideration of nomenclatorial questions which do not directly concern his own field of study; but the thought should ever be present in our minds that nomenclature is an international language and the only international undertaking on the basic principle of which all biologists agree; the same name for the same animal in science throughout the globe. I know that there are highly intelligent biologists who look upon nomenclature with disdain because the great fact has escaped them, that in the present spiritual turmoil in which humanity finds itself one point of general agreement, like the basic principle of nomenclature, renders general agreement in other matters a possibility and gives humanity some hope.'

In the foregoing paragraphs an attempt has been made to indicate the volume of Dr Jordan's contributions to entomology, zoological nomenclature and international co-operation. The full impact of this work and the modernity of his major contributions to the philosophy of evolution and systematics (and their intimate relationships) is only now, after a lapse of more than half a century, being fully appreciated. One reason for this may well be that his most important essays in this field were published either incidentally in the course of systematic monographic treatments of Lepidoptera, or in journals rarely consulted by the general zoologist. His 1896 paper on mechanical selection and other problems appeared in the Tring Museum journal, Novitates Zoologicae, which consisted almost entirely of systematic revisions and descriptions; his 1905 paper on the difference between geographical and non-geographical variation appeared in German in the Zeitschrift fur Wissenschaftliche Zoologie and is very little referred to in the English literature. Moreover, he worked with insects, which like his methods were not in favour amongst the laboratory biologists of his time. Another and more personal reason was, in the writer's opinion, due to an element of shyness: he was not the type to stump the country in support of any theory or to engage in polemics. Sure of his own position and equally sure that it was right, he seemed always content to let others argue among themselves, in the certain belief that his view could not fail in the end to win acceptance. If this sounds like conceit, it was humble conceit nevertheless. As Lord Rothschild remarked: 'The fellow is always right!' His single-minded purpose was the pursuit of truth; personal prestige interested him not at all.

The whole of Jordan's vast output was consistently directed towards

well-defined and easily recognizable objectives, the elucidation of the course and nature of evolution through the most thoroughgoing examination of existing species from every aspect available to him. In the process he set himself to demonstrate that taxonomy, far from being the Cinderella of the biological sciences, held the key to the understanding of evolution and, in its truest expression, was a synthesis of many biological disciplines. 'Jordan had learned as a zoology student at the university that the taxonomist has a great deal of information of vital significance to the general biologist . . . for long it seemed like a hopeless endeavour to bring this point home, but the increasingly close collaboration between taxonomists and experimental biologists during the past two decades proves that the point has finally been made—Jordan has contributed his share toward the victory of the idea that every taxonomist must have a broad training in general biology, and that every biologist must know and understand the important generalizations that come from the field of systematics.' (Mayr, 1955, p. 47.) In championing this cause it was against the superior beings who, de haut en bas, looked down on taxonomists as a lower order of zoologists that he inveighed; criticism of his less gifted colleagues was always kindly. But he was careful to point out that the theorist may be all too easily led astray by bad systematics, as Darwin himself was in the case of the birds of Madeira and the Canary Islands.

Jordan's longer papers on systematics have already been mentioned above. One of his most perfect gems, however, is quite a short paper modestly and inadequately entitled 'Notes on Arctiidae' (Nov. Zool. 23, 124-150). In the compass of some 26 pages, Jordan provides a masterly example both of straightforward taxonomy and of the direct application of the resulting conclusions to the much wider field of evolutionary thought. He concludes, in fact, with one of the earliest and clearest statements on the subjects of synpatric and allopatric speciation: '... I have dealt with insects corresponding to two species of the Lep. Phal. of Hampson, Ammalo insulata and Sychesia dryas (as Elysius dryas in Hampson). We have seen that under the garb of insulata three species are concealed, and that there are nine species of Sychesia instead of one (Hampson, dryas) or three (Rothschild, dryas, *pseudodryas* and *omissus*). The conclusion to be drawn from the results of our investigation is obviously this: In order to arrive, without evidence from breeding, at fairly accurate systematics it is insufficient to study only the external aspect of the specimens . . .

'The differences between the species above described being essentially such as are not visible outwardly, the specific distinguishing characters cannot have developed by means of selection on the part of insectivorous enemies.

'In some of the species we find small but obvious morphological differences in the specimens from certain localities: geographical varieties or *subspecies*. In other forms which are also geographically separated the differences are so great that we must consider them specific; these species replace one another, one being a substitute for the other: vicariant species. And lastly, we have species the ranges of which overlap or are more or less the same, the species occurring side by side, often actually flying together: synpatric species. This graduation in the evolution is represented, for instance, by (1) Sychesia dryas dryas and S. dryas tupus, which exclude one another geographically, but are essentially the same insect; (2) Ammalo insulata, A. arravaca and A. aurata, which also inhabit separate geographical areas, but are so different that they might occur together without mixing and amalgamating; and (3) Sychesia dryas, S. subtilis and S. omissus, which occur together. If the differences in the first category become greater, we have the second. If the range of the second category extends, we have the third category of forms. This is true not only for insects, but also for other classes of animals, the exceptions appearing to me more seeming than real. The important part which geographical isolation plays in the evolution of the subspecies and vicariant species is so obvious that it is hardly necessary to dilate on it. Which, however, is the factor or group of factors that led to the appearance of the structural differences we have described? Mendelism cannot account for the geographical phenomenon embodied in the problem; selection by insectivorous enemies being likewise excluded, there remains the influence of the inorganic surroundings, which are different in the various geographical areas, in connexion with geographical isolation. If the geology of a continent or archipelago is known, i.e. the relative ages of the districts or islands, one can generally predict with a high degree of accuracy where subspecies and vicariant species will be found.

'I have assumed that the various species of Sychesia, and the three yellow Ammalo, have retained the colouring of the respective ancestors from which they are derived, and for this reason are externally so similar to one another. The opinion, however, might be advanced that these species were originally also different in colouring, and their present synchromatism is a secondary development due to mimicry. This cannot be a true explanation, because (1) most of the species are not synpatric, and (2) the subspecies of S. dryas and S. subtilis are alike in colour and different in structures in a similar way as are the species, but to a much lesser degree.'

Most of Jordan's major contributions to the elucidation of the problem of the factors of evolution, particularly speciation and micro-evolution, were made at a time when the role of the environment was little understood and nothing was known of the nature of genetic factors. It is remarkable, therefore, that in his early discussions of the role of natural selection in the production of mimicry in butterflies he arrived at a theory to account for mimetic polymorphism which has since proved acceptable to geneticists. In order to account for the well-known rarity of mimics, as compared with their models, 'he advanced a theory which—anticipating the recent selection experiments of Mather, Lerner and others—has a remarkably modern ring . . . almost fifty years have passed by before the analysis of gene complexes by Mather and others has led to a genetic confirmation of Jordan's views of the detrimental effects of one-sided selection.' (Mayr, p. 64.)

When the writer of this brief and inadequate tribute to the memory of Dr Jordan became interested in the systematics of the Rhopalocera, some fifty years ago, Jordan was already pre-eminent and indeed the acknow-ledged leader. His methods, his approach, and his belief in the importance of the role to be played by true systematics were already widely accepted standards. They were part of one's creed, as it were; indeed, they were largely taken for granted, and the extent to which they were due to the writings of Jordan, and to one's contacts with him was not then fully appreciated. Only now, looking back, does one realize what a debt is due to him. As Mayr has written, 'in his writings and through his contacts he exerted an influence on the development of systematics and on evolutionary thought that cannot be overestimated. Even though Jordan's name may not be cited as widely in textbooks of evolution and zoological systematics as it deserves, at least . . . most of the concepts which he pioneered and for which he fought have now been accepted by virtually every worker in the field'.

For Jordan the man, those who had the boon of his friendship could only feel the warmest affection. At international gatherings he would sweep aside rules, regulations and red-tape with tolerant disdain, coming direct to the thing to be done. Precedents that lay in the past did not concern him; it was only the future that mattered. At work in the Museum, seated at a desk that was to him in perfect order but to anyone else looked like chaos, he was invariably ready to counsel with equal courtesy the novice or the expert: nothing was too much trouble if it served in any way to advance knowledge. To meet him was always a delight, for he was so very human, so unexpectedly humorous, so helpful. At his home in Tring he welcomed entomologists from all parts of the world and the hospitality he dispensed left with all his visitors a sense of having shared something of his contentment in the long life of satisfying and happy achievement that was his.

Karl Jordan died on 12 January 1959.

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* Many of the notes in this paper are signed 'K.J.' It is obvious from internal evidence that a long introductory passage on pp. 168-182 is also by him and it is credited to him (not very clearly) by W. Rothschild at the bottom of p. 167. This introductory passage is of importance as Jordan's pioneer essay on methods of classification of Lepidoptera.

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124

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Biographical Memoirs

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126

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128

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