REPÚBLICA FEDERATIVA DO BRASIL
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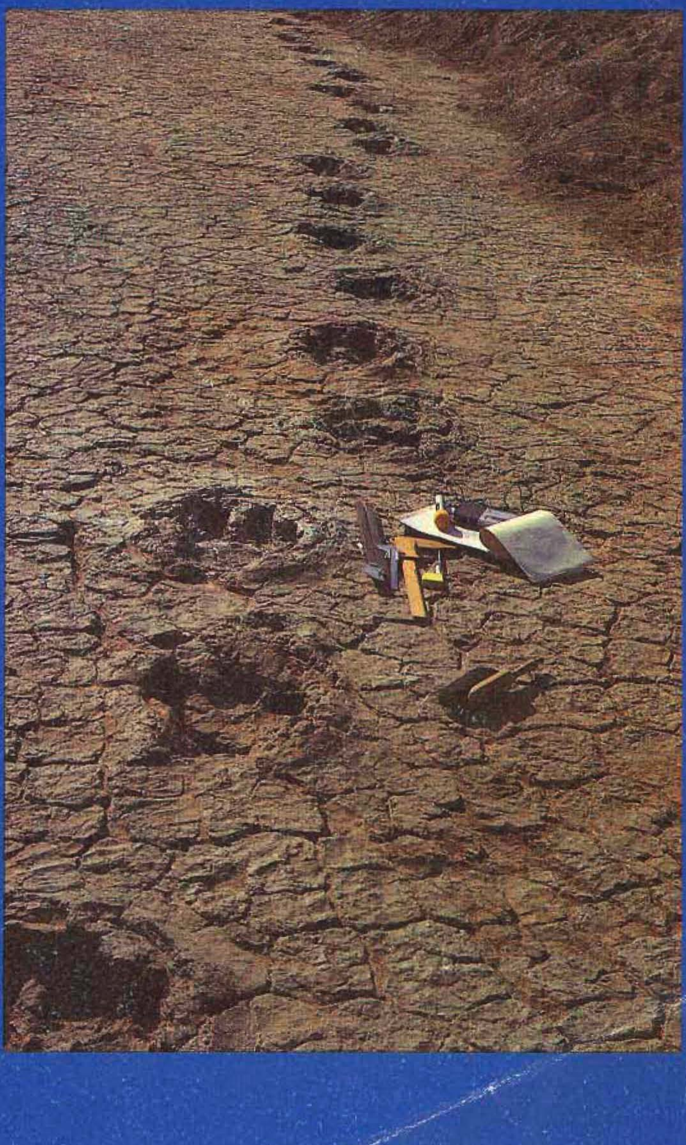
Glossary and Manual of Tetrapod Footprint Palaeoichnology



Organizado por
Giuseppe Leonardi

Foto de capa:

Pegadas de *Sousaichnium pricei* (Leonardi, 1979), atribuidas a Iguanodontidae.
Formacao Sousa, bacia do Rio de Peixe, K. inf.; Sousa - PB - Brasil.

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Glossary and Manual of Tetrapod Footprint Palaeoichnology

Edited by GIUSEPPE LEONARDI

(Conselho Nacional de Desenvolvimento Científico e Tecnológico – Brasil)

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BRASÍLIA – BRAZIL

1987

Publicação do
Departamento Nacional da Produção Mineral
Setor de Autarquias Norte, Quadra 1, Bloco B
70040 Brasília, DF
Brasil
Telex 0611116

Depósito Legal
Biblioteca Nacional do Rio de Janeiro
Instituto Nacional do Livro

Tiragem: 1.500 exemplares

ESTE VOLUME FOI PREPARADO PARA IMPRESSÃO NO
SERVIÇO DE EDIÇÕES TÉCNICAS – SETEC
DA COMPANHIA DE PESQUISA DE RECURSOS MINERAIS – CPRM

Brasil. Departamento Nacional da Produção Mineral.
Glossary and Manual of Tetrapod Footprint Palaeoichnology por Rodolfo M. Casamiquela, Georges R. Demathieu, Hartmut Haulbold, Giuseppe Leonardi e William A.S. Sarjeant. Brasília, 1987.
117p. il.
Edited by Giuseppe Leonardi
1. Palaeoicnologia–Glossários. 2. Tetrápodes–Glossários. I. Casamiquela, M. II. Demathieu, G.R. III. Haulbold, H. IV. Leonardi, G. V. Sarjeant, W.A.S. VI. Título.

CDD: 567.9103

In Memoriam
LUCIANO JACQUES DE MORAES

Apresentação

Dentro de sua filosofia de promover a difusão do conhecimento geológico do país, através da edição de obras de interesse especial da comunidade, sente-se o Departamento Nacional da Produção Mineral – DNPM altamente orgulhoso em publicar este Glossário e Manual sobre Rastros e Pegadas de Tetrápodes, matéria ainda pouco divulgada no Brasil, apesar de alguns magníficos sítios paleontológicos aqui existentes.

O editor desta obra, Giuseppe Leonardi, é cientista bastante conhecido no país e internacionalmente pelos seus inúmeros trabalhos de pesquisa paleontológica, especialmente no denominado "Vale dos Dinossauros", na Paraíba. Assim, ao proporcionar à classe científica as informações aqui contidas, está este Departamento contribuindo para a união de esforços em prol da Geologia do Brasil, o que constitui um dos pilares de sua atual administração.

Brasília, julho de 1987.

José Belfort dos Santos Bastos
Diretor-Geral do DNPM

Foreword

The diffusion of the country's geological connaissance – through the edition of books and papers of special interest of the scientific community, is one of the Departamento Nacional da Produção Mineral main objectives. So, DNPM is proud on publishing this Glossary and Manual on tetrapods trackways and footprints, matter which is poorly divulged in Brazil, despite the existence of some magnificent paleontological sites here.

The editor of this volume, GIUSEPPE LEONARDI, is a well known scientist in Brazil and other countries, through his many works on paleontological research, specially in the "Vale dos Dinossauros" (Dinosaur Valley) in Paraíba state, northeastern part of the country. On putting to the public the informations of this book, DNPM is also contributing for the strengthening of efforts for Brazilian geosciences, which is one of the philosophical bases of this administration.

Brasília, July 1987.

José Belfort dos Santos Bastos
General Manager

Preface

Les travaux lexicographiques
n'ont point de fin

LITTRÉ

Prehistoric man, who depended on hunting for food, certainly would have had a varied terminology for animal tracks, as indeed do the surviving primitive tribes. Contemporary hunters can define a track based upon many parameters, while using technical terms. Good hunters, especially the primitive ones, are able to determine the species, sex, age, conditions of health, gait and other information about the animal, based on empirical observations of trackways and the trackmakers.

Technical terminology for trackways has been used in scientific publications since the first half of the nineteenth century. However, the systematization of these therms took place much later, in general only whithin the last few decades. Probably the first published listing of terms is the very short one, published (in English) by Frank E. Peabody in 1948 and revised in 1959. The first glossary in French was published by Heyler and Lessertisseur (1963) and is more extensive than the preceding one. It includes some information on measurement techniques. Also in French is the glossary and manual found in the introduction to an important monograph by Demathieu (1970).

In German there are good listings of terms in the introduction of two works by Haubold (1971 a,c), as well as in his book "Saurierfährten" (1984). Casamiquela (1964) formalized an ichnological terminology in Spanish; in the same work he established methods of study and interpretation of tracks. Sarjeant's review of the tetrapod footprints (1975) is remarkable; it contains important considerations on the measurement, analysis, interpretation and terminology of footprints. M.T. Antunes (1976) presented a study on tracks of dinosaurs from Lagosteiros (Portugal); and first used technical terms in Portuguese.

The first attempt at a comparative glossary in seven languages was compiled by G. Leonardi (1979). The glossary put side by side the majority of terms used in English, French, German, Spanish, Italian, Portuguese and Latin; and a list of terms was presented for the first time in a systematic way in the three last languages.

Initial contacts for the present work were made in 1977 at the iniciative of this editor. Work started in 1979 and has taken eigth years. It encompasses more than 2500 terms (2588 altogheter; 1271 ichnological; 218 anatomical; 417 biomechanical; 149 on the substratum; 533 statistical. 361 in Spanish; 373 in German; 305 in English; 317 in French; 312 in Italian; 296 in Latin; 326 in Portuguese; 298 in Russian). It was by no means an easy task to unify methods of study and measurement. The patience of my good friends and colleagues in filling out forms, lists and questionnaires was infinite. The contribution of each is specified under the title of each chapter and also, in an abridged form, in the columns of terms for each language. Bill Serjeant carefully revised the text in English. English was the language chosen for the text because, unfortunately, there is no neutral language. English can be understood by all the ichnologists. Clearly, it would be impossible to publish the text in many languages.

The glossary deals with the ichnology of the tetrapods; with trackways and footprints, but not with other vertebrate traces such as eggs, coprolites and dens. The work is presented in following order. First a lengthy introduction to the history of the ichnology of vertebrates (with a selective bibliography) by Bill Sarjeant. Secondly the glossary of terms is presented in eight languages, i.e. the seven languages accepted by the International Code of Zoological Nomenclature and also Portuguese, because it is the language of this editor and of the country (Brazil) where the work will be published. In Brazil, ichnology has lately received considerable support from the cultural and political milieux, and from the institutions providing financial help for research, especially the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Departamento Nacional da Produção Mineral (DNPM). The subject has aroused great interest also among the Brazilian press and the general public, due to its great fascination.

The columns of terms, from left to right, are in alphabetical order of the names of the different languages: from "Castellano" to "Russian". (For "Spanish" we preferred the more correct name of "Castellano", in English, "Castilian" – as distinct from "Catalan").

In each column, the terms are not entered in alphabetical order; instead they are divided into areas (Ichnology, Anatomy, Biomechanics, Substratum, Statistics) since this was felt to be more potentially helpful.

In the first section there is a logical order, with general terms first, then with the terms concerned with the trackway, the footprint, and the morphological details of the footprint. The order in each section is not arbitrary, as it may seem at first. It aims to introduce first the basic terms, which are necessary to the understanding and usage of the terms that follow. The position of one or another term is sometimes debatable and might have been done differently. The alphabetical index simplifies location of terms in the glossary and in the discussion.

The choice of terms for the substrate (in English) was the work of Bill Sarjeant. The terms for Statistics were chosen by Georges Demathieu; consequently they appear in the French alphabetical order. The Statistics section is probably too large: some of the authors found it disproportionate compared to the other sections. Nevertheless I decided to publish it anyway. The difficulty we had in finding equivalent terms in the different linguistic columns convinced us that a statistical glossary in eight languages probably does not exist. Consequently, this section may make easier the reading and linguistic correlation of terms not only for ichnologists but also for paleontologists at large, and maybe even for other researchers. It is an "extra" that we offer to the scientific community! Furthermore, statistics is a science that has only recently been applied to ichnology: some terms, methods and concepts that are not employed in our field yet may be utilized in the near future.

Besides the terms already widely used, we introduced some new terms formed by analogy with other languages or by simply transforming adjectives into nouns (as in the example: mesaxonic – mesaxony – axony). Ichnology is a living science, growing rapidly today, so it is understandable that neologisms develop.

It was not possible to include all the terms in every column, in part because sometimes we could not find equivalents, but more often because the author responsible for the column did not think it opportune to include in his own language a term that migth be perfect in the other languages, but did not sound right to him. In Latin (that of the scientific milieu and of the western catholic Church) we could not find neologisms that could express some concepts. We have also created some new terms – not in excess, however!

The terms cannot always be simply translated, since there are significant conceptual and logical differences between the different languages. Note, for instance, the term "pace" in English. The author responsible for the English language in our glossary thinks that it already includes the concept of "oblique" which, in other languages, has to be made explicit.

Those terms which are commonly used in the existing literature but which should be avoided because they are either improper or confusing, are placed in parentheses. Optional complements are placed within brackets.

In the third section, there is a lengthy discussion of the meaning of the terms. Besides explaining the terms and discussing the relationship between the languages whenever necessary, there is also a discussion concerning the correct way of making the measurements. Included also are some considerations and suggestions on the study of footprints in general. We had to face up to many semantic difficulties in our attempt to unify the methods of the different countries and schools during the preparation of this text.

The numbering of items in the chapter "Discussion etc." is obviously the same as the lists of terms. Each number or item refers to a term or a group of terms.

Some special topics follow in an appendix – apparent limbs; thickness of footprint-relief and its significance; research on the distribution of the weight upon the autopodia; and a table of the phalangeal formulae of the reptiles.

To conclude, I would like to sumarize briefly our objectives we pursued in publishing this work. As already mentioned, ichnology is expanding and an increasing number of papers on this subject are being written in different languages. Correlating terms is not always an easy task; and descriptive methods are often different from school to school, and from country to country. This work is an attempt to unify methods and to correlate terminologies in eight languages. The utilization of our glossary in future study on vertebrate ichnology shall make possible, to ichnologists in different parts of the world, the understanding of the methods of measurement and study used in any particular paper and of the exact meaning of the terms employed. The future translation and publishing of our lists of terms in other languages by other authors may further widen the common international platform for our field. We hope we have rendered useful service to the ichnological community. Maybe because we are only a few around the world, we constitute a friendly community where everyone knows each other. Our hope is that some day we may all come to use the same methods and in this way, come to understand each other better.

Brasília, October 12, 1986.

Giuseppe Leonardi
Editor

Acknowledgements

The editor wishes to thank the other four authors for their patient and competent collaboration. It was a great honour and a great pleasure to have as co-authors those who were his masters when he started, somehow belatedly, the study of fossil tracks.

The editor and the other authors wish to acknowledge their deepest gratitude to those who generously collaborated in their work.

The following people kindly supplied useful lists of terms and/or definitions: prof. Ricardo N. Alonso (University of Salta, Argentina; lists of terms in Spanish); the geologist Diogenes de A. Campos (DNPM of Rio de Janeiro, Brazil; list of terms in Portuguese and discussions about their meaning); Father Reginald Foster, a famous latinist from the Ufficio Centrale di Statistica della Chiesa – Segreteria di Stato – Città del Vaticano who wrote out the list of statistical terms in Latin, as well as revising and enlarging other sections of the Latin glossary. We were fortunate in having his collaboration thanks to Mgr. Pietro Silva and to Fr. Diego Beggiao of Rome, Italy. Prof. José Carlos Garcia-Ramos (University of Oviedo, Spain; list of terms in Spanish); Prof. Lucio Malfi (University of Padua, Italy; list of statistical terms in Italian); Prof. Carlos Romero (mathematician of the Fundación Ameghino of Viedma, Argentina, who worked with R.M. Casamiquela in the preparation of the statistical glossary in Spanish); Prof. Mario Spezzamonte (Venice, Italy; list of terms in Italian).

Special thanks to Dr. Boris J. Fessenko, first secretary, and Dr. Andrei A. Sletov, private secretary to the Ambassador, both of the Soviet Embassy in Brasilia, who kindly collaborated in revising and preparing the final version of the list of terms in Russian.

We wish also to acknowledge the collaboration of friends and colleagues with whom we discussed objectives, methods and details of our glossary and manual:

Prof. José F. Bonaparte (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina); Dr. Maria Alessandra Conti (Università degli Studi, Rome, Italy); Dr. Maria Leonardi (Venice, Italy); Prof. Dr. Piero Leonardi (University of Ferrara, Italy) who, among other things, introduced his son – the editor of this work – from an early age to the research and study of fossil tracks; Dr. Umberto Nicosia (Università degli Studi, Rome, Italy); and Prof. Philippe Taquet (Director at the Muséum National d'Histoire Naturelle de Paris, France).

This Glossary was presented as a preprint during the First International Symposium on Dinosaur Tracks and Traces (Albuquerque, New Mexico, May 1986). On this occasion we received many suggestions and observations. We wish to thank sincerely the convenors, Dr. David D. Gillette (New Mexico Museum of Natural History, Albuquerque) and Dr. Martin G. Lockley University of Colorado at Denver) for the space and time we obtained; and some of the attending ichnologists for helping us with complete revisions of this work; specially Prof. Ricardo N. Alonso; Dr. Walter P. Coombs (Western New England College, Springfield, Massachussets); Dr. Philip J. Currie (Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada); Prof. James O. Farlow (Indiana University – Purdue Univ., Fort Wayne, Indiana); Dr. Martin G. Lockley and Dr. Mary Wade (Brisbane).

We would like to acknowledge our gratitude to Dr. Maria Alessandra Conti and Dr. Umberto Nicosia of the University of Rome (Italy), Dr. Dong Zhiming of the Academia Sinica (Beijing, China), Dr. Martin G. Lockley, Dr. Jairo Mojica of the Universidad Nacional (Bogotá, Colombia), the Nova Scotia Museum and Dr. Jim W. Warren of the Monash University (Clayton, Victoria, Australia) for their kindness in making available some of the photographs of the plates.

Ms. Cecilian L. Löwen (Ponta Grossa, PR; Brazil) typed the various phases of the glossary and Mrs. Linda Dietz (Saskatoon, Canada) typed the historical section; Mr. José William da Silva carefully typed the two final versions and Mrs. Maria Helena Araújo Mendonça did the final version of the illustrations (both from the National University of Brasilia, Brazil. Mr. William Presada (São Paulo, Brazil) did the great favour of translating the text of certain chapters into English. To everyone our heartfelt gratitude.

We offer our sincerest thanks to the Departamento Nacional da Produção Mineral and specially to Dr. Carlos Oiti Berbert and Dr. Benedito Waldir Ramos for the publication of this study in the Journal "Geologia".

Last but not least, the financial support was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq of Brazil, to whom also we acknowledge our esteem and gratitude.

Contents

The Study of Fossil Vertebrate Footprints A Short History and Selective Bibliography

by William A. S. Sarjeant

PREAMBLE

To attempt a world overview of the development of vertebrate palaeoichnology is an especially dangerous venture. Many crucially important papers are to be found, not in standard international scientific journals, but in the less widely available journals of local geological and natural history societies. (In Liverpool, England, for example, significant papers were contributed to no less than five local journals, runs of which are not even to be found in the major British university libraries!) Significant information is also contained in survey reports and general accounts of the geology of particular regions; such incidental mentions are readily missed. Thus I must request the forbearance of readers who come across errors and omissions in the review that follows; and I would be happy to be informed of those mistakes, in order to prevent their repetition.

I should emphasize also that this review is selective; it does not pretend to encompass all the published work of which I am aware. More complete accounts of footprint study in the British Isles are given by Sarjeant (1974) and Delair and Sarjeant (1985), in eastern Canada by Sarjeant and Mossman (1978) and in South America by Leonardi (1981a).

THE EARLIEST SCIENTIFIC DISCOVERIES

Fossil vertebrate footprints must have been noticed intermittently throughout the history of humankind and may well have been responsible, along with fossil bones of large size, for the persistent legends of dragons and other fabulous monsters encountered world-wide. However, the first scientific study of these trace-fossils was inaugurated in Scotland around 1824, when the Reverend Henry Duncan of Ruthwell was presented with a footprint-bearing slab from a quarry at Corncockle Muir in Annandale, Dumfries-shire. This came from the New Red Sandstone, then of uncertain geologic date but now known to be Permian. Duncan was interested enough to seek for further footprints in the quarry. His discoveries were reported to the Royal Society of Edinburgh on January 7th, 1828 but, though immediately summarized in two popular journals, were not fully published until three years later (Duncan, 1831).

Before this, Duncan had sent an account of the discovery to the Reverend William Buckland, Reader in Geology of the University of Oxford. Buckland, vastly intrigued, conducted a series of experiments to try to simulate the prints by setting a tortoise to walk on pie-crust, wet sand and soft clay. These were the earliest of all palaeoecological experiments and, though occasioning some amusement among observers (Murray, 1919; see also Sarjeant, 1974, p. 268-270), demonstrated that the gait of chelonians did indeed produce a pattern of footprints similar to those of the New Red Sandstone. Buckland's interest stimulated further collecting in the Corncockle Muir quarry, work that was to attain its acme in the handsome and expensive hand-coloured illustrations of these Scottish footprints at one-to-one scale by Sir William Jardine (1853). By that time, footprints had been found not only in the New Red Sandstone of several other Scottish counties, but also in Germany, England and the United States.

It is likely that the first discoveries of pre-Permian footprints were also made in Scotland. In George Fairholme's *General Geology of Scripture* (1833), a fairly full account is given of some footprints from the Craigleith Sandstone of Midlothian. Unfortunately, however, these footprints were not illustrated and appear not to have survived (See discussion in Sarjeant, 1974, p. 276-277.)

The dramatic story of the scientific study of fossil footprints in Germany seems to have had as starting-point a (published) letter sent in 1834 by F.K.L. Sickler to the eminent Hanoverian anatomist Johann Friedrich Blumenbach. In this was reported the discovery of vertebrate footprints in the Triassic red sandstones – so called, though more usually buff in colour – of Thuringia. This report excited much interest and speculation concerning the affinity of the trackmaker, alternatively christened *Chirotherium* or *Chirosaurus* in 1835 by J.F. Kaup: unfortunately the first, less appropriate name has priority. The story of the subsequent interpretations and misinterpretations of these tracks has been often told (e.g. by Peabody, 1947; Ley, 1951; Kramer and Kunz, 1966; and Sarjeant, 1975b, p. 300-303) and needs no repetition here. Its highlight was the remarkably accurate reconstruction of the trackmaker by Wolfgang Soergel in 1925, a reconstruction confirmed much later by discoveries of skeletal remains in the Triassic of Switzerland (Emil Kuhn-Schnyder and Bernhard Peyer, 1965; Bernhard Krebs, 1966). The German Triassic footprints have been perhaps more thoroughly studied than those of any other system in any region of comparable geographic extent; leading researchers have included H. Rühle von Lilienstern (1938 and other papers) and, more recently, Hartmut Haubold (1966, 1969, 1971a and other papers).

Triassic footprints were probably discovered in the Cheshire region of England as early as 1824, but their serious study did not commence till 1828, with a lecture to the Liverpool Mechanics' Institution by the Scottish zoologist Robert Edmond Grant: this was reported in a newspaper that year ([Grant], 1838), the report being republished in a natural history journal in 1839. Members of a number of local societies – the Liverpool Natural

History Society, the Liverpool Literary and Philosophical Society, the Liverpool Geological Society, the Liverpool Geological Association and the Liverpool Biological Society – were prominent in the research on these footprints. Although found also at a variety of other localities, the footprints came primarily from the Storeton Quarries near Birkenhead, Cheshire; fine specimens from Storeton, especially of *Chirotherium,* are to be seen in major museums world-wide. This work found its apotheosis in Henry Charles Beasley, whose long series of publications, in particular his *Reports* to the British Association for the Advancement of Science (1896, 1904 etc.), brought together all that was known about British Triassic footprints up to the time of his death in 1919. Indeed, since that year, their study has been only very intermittent. Justin Delair's demonstration that footprints occurred not only in the Permian, but also in the Triassic rocks of Annandale, Scotland (1969) and a report of footprints from lower horizons in the English Triassic – the so-called English "Bunter" – of Worcestershire (Leonard J. Wills and W.A.S. Sarjeant, 1970) constitutes the only new record of significance.

A third region in which early attention was paid to footprints long thought to be a Triassic age, but recently shown to be at least in part early Jurassic, is the Connecticut valley of the eastern United States. The earliest scientific study of these footprints was made by Edward Hitchcock of Amherst College, Massachussetts. Hitchcock believed originally that most or all of them were bird footprints, styling them "ornithichnites" and their study "ornithichnology" (1836): later, however, doubt crept in and he rechristened the discipline "ichnolithology" (1844). He was sedulous in striving to establish a sound taxonomy for these footprints (1845 and other papers) and sought continuosly to establish beyond doubt the identity of the trackmakers (e.g. 1848). His work culminated in the handsomely produced *Ichnology of New England* (1858) – another and more lasting rechristening of the discipline. In addition, Benjamin Silliman Sr. published a single paper on the Connecticut valley tracks in 1837 and Henry Darwin Rogers in 1841. Another early worker on them – indeed, a rival and, at times, an opponent of Hitchcock – was James Deane, whose studies were first published in 1844 and whose work culminated in another handsome volume, *Iconographs from the Sandstone of Connecticut River,* in 1861. Twenty years later, J. Eyermann (1886) and L.P. Gratacap (1886) reported tracks from New Jersey and A. Wanner reported them in 1887 from York County, Pennsylvania (see Wanner, 1889). Prominent among later workers have been Richard Swann Lull, whose scientific approaches to the study of the Connecticut Valley tracks and the reconstruction of the trackmakers (1915) marked a new epoch in this discipline, and Donald Baird, a less prolific but more careful student, especially of the footprints from New Jersey (e.g. 1957). A major study by Paul E. Olsen and Kevin Padian is presently in progress.

RECOGNITION OF PRE-PERMIAN FOOTPRINTS

A discovery in Nova Scotia, Canada in 1841 provided not only the first undoubted fossil footprints from the Carboniferous, but also the first clear indication of land-dwelling, air-breathing vertebrates in the Palaeozoic, the age of the New Red Sandstone being still a matter for controversy. William Edmond Logan, later to serve as first Director of the Geological Survey of Canada, found the footprints in a block of building stone at Horton Bluff. Unfortunately, when he displayed the footprints at a meeting of the Geological Society of London in 1842, they attracted much less interest than they merited and, indeed, gained only a brief and dubious mention in the Society's *Proceedings* (Logan, 1842). Not until twenty-one years later was an account of them published, and then not by Logan but by J. William Dawson (1863). By that time their significance had been reduced, since fossil bones had been found in the Carboniferous sediments of Germany and further vertebrate footprints in the Coal Measures of Pennsylvania (King, 1844). It was Dawson who was to write the first extended descriptions of Nova Scotia footprints (1872, 1876). His studies were followed up by those of George F. Matthew, who also made the first serious attempt to classify the footprints of the Coal Measures (1903). Matthew's last paper was published in 1905. After that, although the Nova Scotia footprints were given some taxonomic attention (e.g. by Hartmut Haubold, 1970) and mentioned in at least one field-excursion guide-book (R.L. Carrol *et al.,* 1972), no new discoveries were reported for over seventy years until Mossman and Sarjeant (1973) recorded two new types of tracks – one of a giant amphibian – from Horton Bluff.

A.T. King's first account of footprints from the Pennsylvanian Coal Measures was the prelude to four other papers, the most important in 1845. These discoveries in New England attracted the attention of Charles Lyell, who wrote short accounts both of the Connecticut Valley tracks (1842) and the Pennsylvanian footprints (1846), noting that some of the latter (though not all) were human artifacts. In a series of papers by Isaac Lea, further footprints from Pennsylvania were described: these were also Carboniferous (Mississippian) in age, though Lea miscorrelated them with the New Red Sandstone (1849, 1856). Henry Darwin Rogers wrote about these footprints also (1851, 1855), while W.D.H. Mason (1878) and Joseph Leidy (1879) recorded footprints from later strata, now considered to be of Late Pennsylvanian (Westphalian or Stephanian) date (D. Baird, *in litt.* to W.A.S.S.). Footprints of similar age from nearby Kansas were described by Benjamin F. Mudge (1873) and Othniel C. Marsh (1894). Handel T. Martin's record of giant amphibian tracks from the bed of a creek in that state (1922) was later discounted by Baird (1963), who suggested they might be stump-holes left by the decay of tree-trunks. Later, however, they were found to be recent artefacts, post-holes made with a crowbar in the soft sandstone by a farmer running his fence across the creek (D. Baird, *in litt.* to W.A.S.S.).

The records from Pennsylvania and Kansas were supplemented by one from Missouri, by Edward Butts (1891). However, though other discoveries followed in Pennsylvanian strata of those three states and others, it was not until 1908 that footprints were first reported from the Permian of the United States, from Texas by Samuel W. Williston. Later, Roy L. Moodie collected and described many more Permian reptilian footprints from that state (1929-1930; see also Sarjeant, 1971) and W.W. Dalquest described large amphibian footprints (1965). Charles W. Gilmore's accounts of fossil footprints of the Lower Permian of the Grand Canyon, Arizona (1926, 1927, 1928a) are of particular importance. Among the other reports of Late Palaeozoic footprints in North America are three accounts from West Virginia, by E. Tilton (1931), S. Happ and H. Alexander (1934) and D.H. Dunkle (1948), and the record of an extensive ichnofauna from Colorado by W.C. Toepelman and H.G. Redeck (1936). The tracks of a larval amphibian from the Pennsylvanian of Oklahoma (Sarjeant, 1976) possibly constitute the smallest fossil vertebrate footprints yet recorded.

RECOGNITION OF LATE MESOZOIC FOOTPRINTS

The first observations of fossil vertebrate footprints in the later Mesozoic were made by a clergyman, the Reverend Edward Tagart, in the Wealden sandstone (Early Cretaceous) of the Sussex coast. In his letter reporting these observations to the Geological Society of London, Tagart noted that "Dr. Harwood suspects them to be the footmarks of the iguanodon" (Tagart, 1846; A. Tyler, 1862). No illustration of any of Tagart's specimens was published until more than 120 years after his report (Sarjeant, 1974, fig. 31). However, many more dinosaur footprints were discovered in subsequent years, not only in the Wealden sandstones of Sussex and the Isle of Wight but also in the somewhat older Purbeck Beds (latest Jurassic – earliest Cretaceous) of Dorset. The history of these discoveries has been recounted in detail by Delair and Lander (1973) and Sarjeant (1974, p. 353-358), while the prolific finds of the last decade are described by Delair and Sarjeant (1985, p. 141-151) and Delair (1985, in press). Footprints considered to be made by *Iguanodon* have been found also in the Wealden of Belgium (Dollo, 1905) and Germany (C. Struckmann, 1880; M. Ballerstedt, 1905 and other papers), while dinosaur tracks have been found in beds of comparable age in Spain (L. Casanovas Cladellas and J.-V. Santafé Llopis, 1971) and on the island of Brioni (Brijuni), Yugoslavia (A. von Bachofen-Echt, 1926a, b). Dinosaur footprints of supposedly Cretaceous age reported from Italy by A. Fucini (1915) were shown later to be of Triassic (Ladinian to Carnian) date (M. Tongiorgi, 1980).

EARLY DISCOVERIES IN FRANCE

Oskar Kuhn, in his valuable review of *Ichnia tetrapodorum* (1963), included in the literature cited a paper by J.C. Delamétherie (1800) on "une empreinte d'oiseau dans un morceau de plâtre de Montmartre". Presumably Kuhn had not seen the paper for it describes, not a footprint but an impression in the Montmartre gypsum (almost certainly of inorganic origin) resembling a spread-winged bird. The earliest French description of fossil tracks appears to be Gabriel Daubrée's excellently illustrated account of Triassic footprints, presented to the geological section of the Académie des Sciences in 1835 but not published until 1857. Paul Gervais reported further Triassic footprints in 1857 and A. Delage published the first record from the French Permian in 1912. Thereafter the footprints in the red sandstones of France received scant attention for fifty years; papers by L. Christel (1945) and R.P. Charles (1949), both on Triassic footprints, are perhaps the only significant ones published during this time.

After 1945 Albert F. de Lapparent, with his researches on dinosaur trackways of France, Morocco, Spitsbergen, Portugal and Spain, gave a great impulse to the French Ichnology. Thanks to his influence, a revival of interest came in France during the 1960's and 1970's, principally as a consequence of the work of D. Heyler and J. Lessertisseur (1962, 1963); of Louis Courel, Georges, Germaine, and Pierre Demathieu, Georges Gand and their associates (L. Courel and G.G.P. Demathieu, 1963; L. Courel *et al.*, 1968; G. Demathieu, 1966, 1970 etc.; G. Demathieu and G. Gand, 1972; G. Gand, 1971, 1975b etc.); and by Paul and François Ellemberger (P. Ellemberger, 1958, 1972, 1974; F. Ellemberger and Y. Fuchs, 1965).

TERTIARY FOOTPRINTS

Though Delamétherie's specimen was not a footprint, nevertheless it was from the gypsum workings of Paris that the first Tertiary footprints were to be reported, by Jules Desnoyers in 1859. Stanislas Meunier recorded further tracks in 1906, but the closure and filling-in of the gypsum quarries ended these discoveries. The first Tertiary record from outside France came in 1879, when A. Portis recorded Eocene footprints from Piedmont, Italy. Seven years later, tapiroid tracks were reported from the early Tertiary of Germany by Georg Böhm (1898); these were redescribed by H. Tobien (1950). Since that time, records of Tertiary vertebrate tracks have been few, even on a world scale. Notable among those few are accounts of mammal tracks from the Paleocene of Montana by Charles W. Gilmore (1923b) and of Alberta, Canada, by R.L. Rutherford and Loris S. Russell (1914) and Russel (1930); from the Eocene of Spain by Eduardo Hernandez-Pacheco (1929) and M.L. Casanova Cladellas and J.-V. Santafé-Llopis (1982) and of Utah by H.C. Curry (1957) and Mounir T. Moussa (1968); from the Oligocene of Wyoming by Robert G. Chaffee (1943) and of South Dakota by P.R. Bjork (1976); from the Miocene of Hungary by Erich Thenius (1948) and of Roumania by N. Panin (1965); from the Late Tertiary of Kansas and California, respectively by George M. Robertson and George F. Sternberg (1942) and by Raymond M. Alf (1959, 1966); from the Pliocene of Oklahoma by Curtis J. Hesse (1936), of Texas by C.S. Johnston (1937) and of Argentina by Rodolfo M. Casamiquela (1974), a colour illustration of the latter appearing in Sarjeant and Mossman (1983); and from the Plio-Pleistocene of Mexico by A. Dugès (1894), of Arizona by Harvey H. Nininger (1941: see also L.F. Brady and Philip Seffi, 1959) and of Chile by Casamiquela and G.D. Chong (1975). The "footprints" from the Eocene of Italy reported by Carlo I. Migliorini (1947) were shown subsequently to be invertebrate burrows (G.C. Parea, 1964).

The tracks of lower Tetrapods have been reported only rarely from post-Mesozoic sediments. Indeed, the only records known to me are those from the Palaeocene of Montana and the Pliocene of California by Frank E. Peabody (1954, 1959).

The fossil tracks of birds have been reported from the Eocene of France by Jean-Claude Plaziat (1965) and of Utah by Bruce R. Erickson (1967) and Mounir T. Moussa (1968); from the Oligocene of Spain by J.F.M. de Raaf *et al.* (1965) and of Switzerland by S.W.G. de Clercq and H.K.H. Holst (1971): from Oligocene to Miocene sediments of Spain by Jean P. Mangin (1962) and of the south Shetland Islands, Antarctica, by V. Covacevich and C. Lamperein (1969); from the Miocene of Louisiana by Alexander Wetmore (1956) and of Roumania by N. Panin (1965); from the Pliocene of California by A.H. Miller and F. Ashley (1934) and of Argentina by J.F. Bonaparte (1965); and of Japan (Saburo Yoshida, 1967; Kelichi Ono, 1984); and from imprecisely dated Tertiary sediments of Argentina by R.M. Alonso *et al.* (1978). A general work on trace-fossils from the U.S.S.R. by O.S. Vialov (1966) includes accounts of mammal and bird footprints from the Tertiary and sets forth proposals for their classification.

FOSSIL FOOTPRINTS IN QUATERNARY SEDIMENTS

The earliest discoveries of fossil footprints in Recent sediments were made in the Mississippi valley by French explorers. These "human" footprints were first recorded, figured accurately and analysed by Henry R. Schoolcraft (1822) and attracted some attention, e. g. by Gideon Mantell. Their character remains unclear.

Almost fifty years elapsed before the next studies of fossil footprints in Quaternary sediments. These were made in New Zealand and were the tracks of a recently extinct group of flightless birds, the moas. The earliest account of such tracks was given to the Auckland Institute by T.B. Gillies in 1871 and published in 1872; later reports include that by H. Hill (1895), while Frederick W. Hutton recorded the fossil footprints of a kiwi-like bird (1898).

The next major discovery of Quaternary footprints occurred in Nevada – and caused a great deal of controversy. The footprints were formed in Pleistocene outwash sands, which, in the Eagle Valley near Carson City, were sufficiently consolidated to be quarried for building stone. Stones from the quarry came to be used for the construction of the Nevada State Prison alongside the floor of the quarry becoming the prison yard. It was the prison warden, William Garrard, who first noticed the tracks. Following his invitation , members of the California Academy of Sciences visited the quarry in July 1882. Two members, Harvey W. Harkness (1882) and Joseph Le Conte (1882), wrote accounts of their observations, while a third, Charles D. Gibbes (1882), published photographs and a careful map of the quarry floor. Later, an even more elaborate plan was published by Addison Coffin (1889). The tracks included those of mammoths, several different sorts of deer and antelopes, horses, two dog-like animals (one possibly a hyena), a large cat and a large ratite bird; but the most sensational tracks were several series of tracks taken at first to be those of sandal-wearing humans with particularly large feet! This concept was distrusted from the outset by Le

Conte, though he had no clear idea of the character of the track-maker. Rather surprisingly, the great vertebrate paleontologist Edward Drinker Cope, already a believer that man was a contemporary with mammals in the Pliocene – that earlier date was then thought likely for the Nevada tracks – enthusiastically welcomed the discovery of what he considered to be strong supporting evidence for this thesis (1883). His rival Othniel C. Marsh, predictably perhaps, took the opposite viewpoint, suggesting that the "human" tracks were in fact those of giant ground sloths (1883). This idea was lauded by William P. Blake (1884) and demonstrated to be correct, beyond reasonable doubt, by Chester Stock (1917, 1936). An account of the controversy was published recently by Jordan D. Marché (1984).

Also in 1882, "human" footprints were reported from the Little Cheyenne River, South Dakota, by Herbert B. Hubbell. These are equally suspect, but have not attracted the same degree of attention and do not seem to have been restudied. Undoubted Megatherioid footprints described from Monte Hermoso in the Province of Buenos Aires, Argentina, by Rodolfo M. Casamiquela (1983) confirmed the bipedal gait of these gigantic mammals. Footprints from Nicaragua, originally described as those of edentates by an anonymous author (1883), were subsequently stated to be human by Earl Flint (1884); their character also must be regarded as dubious.

Cave-bear footprints and scratch marks were reported from a cave in Germany by A. von Bachofen-Echt (1931) and bones, footprints and scratch-marks of a jaguar from a cave in Tennessee by George Gaylord Simpson (1941). Fossil bird tracks have been found in the Late Pleistocene sediments of Victoria, Australia (K.N. Bell and J.A. De Merlo, 1969).

The first authentic records of fossil human footprints came also from caves, specifically from grottoes in central France (H.V. Vallois, 1931). Fossil human footprints have been reported subsequently from Nicaragua (R.W. Brown, 1947), El Salvador (W. Haberland and W.H. Grebe, 1955) and South Africa (Mountain, 1966). They are also mentioned in many archaeological reports from Europe, Asia Minor and North America (e.g. Barneby, 1975, from Turkey). Footprints of earlier hominids have been discovered in East Africa (Mary D. Leakey and R.L. Hay, 1979; Anna K. Behrensmeyer and Léo F. Laporte, 1981), where tracks of the extinct horse *Hipparion* have furnished information concerning the gait of that animal (Elise Renders, 1984).

THE OLDEST FOSSIL TRACKS

A particular interest attaches to records of vertebrate footprints from the Devonian, the time when vertebrates were first emerging onto the lands. The most primitive track of all was discovered around 1927-1929, by officers of H.M. Geological Survey examining Old Red Sandstone strata on the island of Hoy, Orkney Islands (G.V. Wilson *et al.*, 1935). It consists of a belly-drag trace, with the impressions of fin-marks (or of fin-like footmarks) alongside. It appears to be the track of a rhipistid fish.

Several records of allegedly Devonian amphibian tracks were published last century, but most turn out to be either wrongly dated or spurious. Only two Devonian records can be viewed with confidence. The earlier of these is an impression of a single footprint (*Notopus petri*, G. Leonardi, 1983) from the Ponta Grossa Formation of Paraná, Brazil, discovered by Renato Castro and described by Giuseppe Leonardi (1982, 1983): a stratigraphically later, but ampler, record comes from the Late Devonian of Victoria, Australia (J.W. Warren and N.A. Wakefield, 1972).

Reports of footprints from the Carboniferous are still not numerous. The earliest discovery in Early Carboniferous (Mississippian strata was made in 1852, when C.B. Newenham noted footprints in a newly-laid paving-slab on a street in Cork, Ireland; it came from the Millstone Grit of Kilrush, County Clare. A description was published (Haines, 1852) but the specimen was never illustrated and appears lost. A few years later, a series of large, but poorly formed, amphibian footprints was noted in the Millstone Grit of Cheshire, England. These were described in 1856 by Edward W. Binney, but almost 120 years were to pass before illustrations of them were published (Sarjeant, 1974, p. 325-328). Smaller and better-preserved tracks were discovered in a sandstone within the Carboniferous Limestone of Northumberland and described by Thomas P. Barkas (1873); later discoveries from that region were also reported by Barkas, but never adequately described (1890). Indeed, no further descriptive work was done on British Carboniferous tracks for exactly a century until 1973, when a rich assemblage of footprints collected from the Keele Beds of Alveley, Shropshire, by Frank Raw was described by Hartmut Haubold and the writer (1973, 1974). Mississippian footprints from Virginia, USA, were described in 1910 by Edwin B. Branson. They have been reported from West Virginia by D.H. Dunkle (1948) and from Indiana by Edwin H. Colbert and Bobb Schaeffer (1947).

The major work on Late Carboniferous (Pennsylvanian) footprints has been done this century in the United States and Germany; yet, even from those countries, accounts are not numerous. Among the U.S. literature, papers worthy of particular note are on footprints from Colorado, by J. Henderson (1924); from Maryland, by Richard S. Lull (1924; Baird [1963] considered these to be pseudofossils); from Ohio, by Joel E. Carman (1927) and H.R. Mitchell (1931); from Alabama, by Truman H. Aldrich and W.B. Jones (1930); and from Rhode Island and Massachussetts, by B. Willard and A.B. Cleaves (1930). Their study in Germany appears to have been begun by Hanns Bruno Geinitz (1885). Later accounts include those by Richard Beck (1915), P. Kukuk (1926), Hermann Schmidt (1959, 1972), C. Hahne and D. Wolansky (1951) and H.W. Weingardt (1961). In recent years, a review by Arno H. Müller (1971) and the careful work of Hartmut Haubold have done much to enhance the usefulness of Carboniferous footprints to stratigraphers (1970, 1971b). Late Carboniferous footprints have also been reported from France by Georges Gand (1975a) and Jean Langiaux and Daniel Sotty (1976) and from Sardinia, Italy, by R. Fondi (1979, 1980). The "vertebrate" footprints reported by Joaquín Frenguelli (1950) from the Carboniferous of Argentina were shown subsequently by Rodolfo M. Casamiquela (1965) to have been made by horseshoe crabs (xiphosurans).

LATER WORK ON PERMIAN AND TRIASSIC FOOTPRINTS

The study of German Permian footprints was also begun by Hanns Bruno Geinitz, in his series of papers on what he termed the "Dyas" (e.g. 1861, 1863); but it was given order by the work of Wilhelm Pabst on the footprints of Tambach and other localities in Thüringia, in a series of papers beginning in 1895 and culminating in 1908. Pabst's work was followed up, in particular, by Arno H. Müller (1954, 1959). Among many other contributors to the study of German Permian footprints, Hermann Schmidt deserves mention for his studies of the Cornberg Sandstone (1952 and, in particular, 1959) and Hartmut Haubold, once again, for his successful employment of Permian footprints in stratigraphy (1970, 1971b, 1973; Haubold and G. Katzung, 1972); and Jürgen Fichter, for his work on latest Carboniferous to Early Permian tracks from Saarland-Pfalz (1983 b, c).

In England, Permian footprints were first recognized in Cumberland by George Varty Smith in 1884 and in Nottinghamshire in 1897; the complicated story of the latter discovery is told in Sarjeant (1974, pp. 332-334). Other finds came in Devonshire (A.W. Clayden, 1908), Warwickshire (R.D. Vernon, 1912) and Staffordshire (W.H. Hardaker, 1912). After fifty years of neglect of British Permian footprints, their study was begun anew by Justin B. Delair with a review of museum holdings of the footprints from Dumfries-shire, Scotland (1966) and an account of new discoveries in Cumberland (1967). Subsequently, footprints from the Lower Permian Enville Beds of Staffordshire, collected by Frank Raw many years earlier, were described by Hartmut Haubold and the writer (1973, 1974): and a new study of footprints from the Elgin region of Scotland was published by Michael J. Benton and Alick D. Walker (1985). Permian footprints have been reported from Italy by Ernst Kittl (1901), J.J. Dozy (1935), Friedrich von Huene (1940, 1941), Piero Leonardi (1951a, b, 1953), Paolo Mietto (1975, 1981), Giuseppe Leonardi (1974), Giuseppe Leonardi and Umberto Nicosia (1973) and M.A. Conti *et al.* (1975, 1977, 1980). There are records from Poland by T. Czyzewsta (1955), from Hungary by G. Majoros (1964) and András Raszap (1968), and from Iran by Kálmán Lambrecht (1938). Recent studies in France have included those by Daniel Heyler and Jacques Lessertisseur (1962, 1963), Heyler and Christian Montenat (1980) and Georges Gand (1981).

In southern Africa, the Karroo sediments have proved rich in footprints. They were first reported by H.G. Seeley from Cape Colony, now South Africa, in 1904 and discovered in Southwest Africa, now Namibia, by Georg Gürich (1926). Friedrich von Huene wrote a fuller account of the Southwest African finds ten years later (1925). The Stormberg series, of latest Triassic to Early Jurassic date, has become an especially fertile hunting-ground for vertebrate palaeoichnologists. There have been records of dinosaur and mammalian footprints from Basutoland (now Lesotho) by François and Paul Ellenberger and associates (F. and P. Ellenberger, 1960; F. Ellenberger, P. Ellenberger and L. Ginsburg, 1970; P. Ellenberger, 1970, 1972, 1974, 1975, 1976) and of dinosaur footprints, including hopping tracks, from just across the border in Cape Province, South Africa (D.E. van Dijk, 1978). *Chirotherium* footprints were recorded from the Triassic of Niger by Leonard Ginsburg, Albert F. de Lapparent and Philippe Taquet (1968). More recently, Late Triassic tracks were reported from Rhodesia (now Zimbabwe) by M.A. Raath (1972).

Fish trails are rarely found in the geological column. However, they were reported by Ann Anderson (1976) from the early Permian of South Africa.

It was Friedrich von Huene who first reported Triassic footprints from South America (1931b), specifically from the Rhaetian (Late Triassic) of Argentina. Later work on Argentinian Triassic assemblages has been done by Richard S. Lull (1942), Carlos Rusconi (1951; see also Frank E. Peabody, 1955a), Rodolfo M. Casamiquela (1964) and J.F. Bonaparte (1965). The finding of an *Isochirotherium* trail in the Antenor Navarro Formation of Brazil allowed Giuseppe Leonardi (1980c) to assign to that unit a Middle to Late Triasic date; however, both the identification and the dating were later discounted (G. Leonardi, *in litt.* to the writer). Middle Jurassic ichnofaunas consisting largely of dinosaur footprints have been reported from Patagonia by Casamiquela (1962, 1964).

A still more extensive ichnofauna was discovered by Leonardi in the Botucatu Formation, widely exposed in southern Brazil but of uncertain date – possibly latest Triassic, more probably Early Jurassic. This is a fauna of an arid environment. Although dinosaurs are present, advanced synapsid reptiles and/or proto-mammals overwhelmingly predominate (1977a, 1980d, 1981b; G. Leonardi and W.A.S. Sarjeant, 1986). Elsewhere, possible mammalian footprints have been reported from the Callovian to Oxfordian of Patagonia, Argentina by Rodolfo M. Casamiquela (1964), from the Middle Jurassic Stonesfield Slate of England by the writer (1975a) and, as mentioned above, from Lesotho: all other Triassic and Jurassic records are of reptile tracks.

Triassic footprints were first found in south Wales in 1878, by Thomas H. Thomas; they were described both by W.J. Sollas and, more fully, by their discoverer in 1879. Almost a century was to pass before a further rich find in the Welsh Triassic was reported, by Maurice E. Tucker and Trevor P. Burchette (1977). A footprint was found in 1881 in the Triassic of County Down, Ulster by John Ward and described to the Belfast Naturalist's Field Club by Robert Young (1882); the only subsequent find was made by Hallam Ashley in 1946. In Switzerland, Triassic footprints appear to have been discovered first in 1976, by Georges Bronner; they were recorded briefly by Bronner and Georges Demathieu (1977) and more fully by Demathieu and Marc Weidmann (1982). Vertebrate footprints were first reported from the Triassic of Spain by S. Calderón (1897) and Longinos Navás (1906). Subsequent work has been by Piero Leonardi (1959), Georges Demathieu and collaborators (Demathieu and J. Saiz de Omeñaca, 1976; Demathieu, A. Ramos and A. Sopeña, 1978) and M.L. Casanovas Cladellas *et al.* (1979). Dinosaur footprints reported by A. Fucini from Italy (1915), originally considered to be Cretaceous, were shown much later to be of Triassic (Ladinian to Carnian) age (see M. Tongiorgi, 1980). An early, brief record of footprints from Austria is by Othenio Abel (1904); later records have been few, the most important being perhaps that by Rainer Brandner (1973). Footprints were first reported from the Muschelkalk of the Netherlands by F.J. Faber (1958) and have been described more fully by Demathieu and Oosterinck (1982). A paper by Paolo Vinassa de Regny (1904) describes footprints from Montenegro, Yugoslavia.

Records from the Triassic of the western United States include the footprints described by Elmer S. Riggs (1904) from Arizona, by Edwin B. Branson from Wyoming (1947), by Frank E. Peabody from California (1946) and from Arizona and Utah (1948, 1956), by G. E. Lammers (1964) from Utah and by Donald Baird (1964) from New Mexico. Pierre Teilhard de Chardin and C.C. Young recorded footprints from the Triassic-Jurassic beds of Shansi, China (1929); the footprints found in 1939 by S. Sato in Manchuria (now northern China), and described by Tokio Shikama (1942), are also of somewhat uncertain date. In Australia, footprints were discovered in the Middle Triassic of New South Wales by Geoffrey Scarrott and reported by H.O. Fletcher (1948); later, Triassic footprints were located also in Queensland, by H.R.E. Staines and J.T. Woods (1964).

DISCOVERIES IN THE JURASSIC

Jurassic reptilian footprints were reported as early as 1831 from the Forest Marble (Middle Jurassic) of Wiltshire, England, by the vulcanologist George Poulett Scrope; they were not illustrated and, while they may correspond with specimens described more than a century later by the writer (1974, pp. 341-343), this is not certain. English records of Jurassic dinosaur footprints have been largely from the Middle Jurassic of the Yorkshire coast. A find by Mr. Rowntree in 1895, reported by J.A. Hargreaves in 1913, was unsupported by description or illustration. Consequently, the discoveries at Saltwick by Harold Brodrick (1907, 1909) mark the true starting-point of British Jurassic vertebrate palaeoichnology. Among later finds may be noted those reported by the writer (1970), M.A. Whyte and M. Romano (1984) and by Justin B. Delair and the writer (1985, p. 136-138). The only specimen from another locality is an imprecisely localized slab from Buckinghamshire (see Delair and Sarjeant, 1985, p. 138-141). Although a problematic specimen from Caithness is probably of Mesozoic date (see Sarjeant, 1974, p. 282), the first definite record of Mesozoic dinosaur footprints from Scotland is from the Middle Jurassic of the Isle of Skye, by J.E. Andrews and John D. Hudson (1984).

Dinosaur footprints were first described from the Jurassic of Portugal by J.P. Gomes (1916), but did not receive any searching study until the work of A.F. de Lapparent and his associates in 1951. Not until 1977 were dinosaur footprints recorded from the Jurassic of Spain, by J.C. García-Ramos and M. Valenzuela (1977a, b); a later record is by Hans Mensink and Dorothee Mertmann (1984). Dinosaur footprints were reported from the Triassic-Jurassic boundary strata of Germany by Oskar Kuhn in 1955 and from New Brunswick, Canada, by the writer and Peter Stringer (1978). Sauropod footprints were discovered for the first time in Europe at Barkhausen, Lower Saxony in 1972; they were first reported by F. Friese (1972) and described in detail by Mathias Kaever and Albert F. de Lapparent (1974). A major study from France is that by Albert F. de Lapparent and Christian Montenat, on Early Jurassic reptile footprints from la Vendée (1967). The tracks of a turtle have been recorded from the French Kimmeridgian by Paul Bernie *et al.* (1982), while a dinosaur footprint from the Portlandian of the Ile d'Oléron was noted by Lapparent and M. Oulmi (1964).

A rich Middle Jurassic ichnofauna, again largely of dinosaurs, was reported from Mexico by Israel V. Ferrusquia-Villafranca *et al.* (1978), while Late Jurassic dinosaur footprints have been described from two localities in Chile (Casamiquela and A. Fasola, 1968). Dinosaur footprints have also been reported from the Early Jurassic of central Iran by Albert F. de Lapparent and M. Davoudzadeh (1972), the Early to Middle Jurassic of Tadzhikistan, U.S.S.R. by A.K. Rozhdestvenski (1964) and the Middle and Late Jurassic of China, respectively by Yung Chung-Chien (1966) and by Zhen Shuonan *et al.* (1983).

Henry Faul and Wayne A. Roberts (1951) reported an ichnofauna of vertebrates and invertebrates from the Navajo Sandstone, presumed to be Lower Jurassic, of Colorado. Dinosaur tracks from the Jurassic of Arizona were described by S.P. Welles (1971) and Donald Baird (1980). Supposed pterodactyl tracks from that state (Stokes, 1957) were shown recently – and disappointingly! – by Kevin Padian and Paul E. Olsen (1984) to have been misinterpreted. In Queensland, Australia, dinosaurs footprints have been reported from Jurassic coal workings (Anon., 1952) and Jurassic to Lower Cretaceous fire-clay workings (H.R.E. Staines, 1954). Jurassic dinosaur footprints from Morocco are currently under study by the Japanese palaeontologist Shinoku Ishigaki. The track-bearing Morrison Formation limestones (Upper Jurassic) at the Purgatory River site (SE Colorado) provide the most spectacular and extensive exhibit of dinossaur tracks encountered in the Wertern U.S. Over 1300 footprints comprising at least 100 distinct trackways have been mapped in continuous outcrop along the southern bank (After M.G. Lockley, 1986).

LATER DISCOVERIES OF CRETACEOUS FOOTPRINTS

The Cretaceous, though it has furnished tracks of other vertebrates only meagrely to date, has provided an abundance of dinosaur tracks, not only in northwest Europe but also in several other regions. Their discovery in the high Arctic, on the island of Svalbard (Spitzbergen), was reported briefly by Albert F. de Lapparent (1960), Edwin H. Colbert (1964) and Anatol Heintz (1966); Natascha Heinz demonstrated that the footprints furnished evidence for polar wandering (1963). In Canada, dinosaur footprints were first described from Alberta by Charles M. Sternberg (1926). The plethora of dinosaur tracks in the Peace River canyon of western British Columbia, Canada, was first reported by F.H. McLearn in 1923 and first studied by Charles M. Sternberg (1930). After a lapse of almost fifty years, their examination was resumed under the direction of Philip J. Currie (Currie and Sarjeant, 1979; Currie, 1983); a major work on them is currently in preparation. Subsequently, dinosaur footprints have been reported from another, somewhat later stratum in British Columbia by John F. Storer (1975).

In Colorado and Utah, Cretaceous dinosaur tracks occur in natural outcrops and coal mines; they have been described by, among others, W. Peterson (1924), Barnum Brown (1938) and A. Look (1955). Recently they have been used to demonstrate hadrosaus locomotion and herding behaviour (Martin G. Lockley *et al.*, 1983). From South Dakota, dinosaur tracks were first reported by Summer M. Anderson (1939). In Texas, tracks were discovered widely in Late Cretaceous sediments, in particular in the beds of Hondo Creek, Paluxy Creek and other rivers. These were first described by Ellis W. Shuler (1917) and later by William E. Wrather (1922), Charles N. Gould (1927, 1929) and Sam H. Houston Jr. (1933). A long series was collected for the American Museum of Natural History by Roland T. Bird (1941) and furnished crucial evidence that the giant sauropods could walk on dry land (1944, 1954). As Christopher G. Weber (1981) and David H. Milne and Steven D. Schafersman (1983) have demonstrated, the supposed Cretaceous "human" footprints from that region consist, in part, of badly worn or incompletely exposed dinosaur footprints and, in part, of human artifacts. This whole controversy has been comprehensively reviewed in a special issue of the journal Creation/Evolution, edited by John R. Cole and Laurie R. Godfrey (1985).

An association of supposed "human" footprints with dinosaur footprints in the Cretaceous sediments of the southeastern Turkmen S.S.R., U.S.S.R., reported by K. Ammanniyazov (quoted in V. Rubtsov, 1983), deserves similar critical examination.

Cretaceous dinosaur footprints were first described from South America by L.J. Moraes sixty years ago, a chapter in his two-volume geological work *Serras e Montanhas do Nordeste* (1924) being devoted to dinosaur footprints from the Rio do Peixe basin of Brazil. Subsequently, Friedrich von Huene (1931a) described the same two trackways from Paraiba, Brazil, a region later studied by Giuseppe Leonardi (1979b, 1981a) and where a dinosaur museum, centered on footprints, is shortly to be brought into being. Discoveries from other south American localities were reported by R.S. Lull, 1942; R.N. Alonso, 1980a; and as summarized in G. Leonardi, 1981b. Dinosaur footprints have been reported also from the earliest Cretaceous of Chile by Rodolfo M. Casamiquela and A. Fasola (1968), from Bolivia by L. Branisa (1968) and G. Leonardi (1984).

The earliest record of fossil footprints in north Africa is by A. Péron and M. Le Mesle (1880), from southern Algeria; later studies from that country include that by P. Bellair and Albert F. de Lapparent (1948). Dinosaur footprints from Demnat, Morocco were reported by H. Plateau *et al.* (1937) and studied in great detail by E. Ennouchi (1953), Albert F. de Lapparent (1945) and J.M. Dutuit and A. Ouazzou (1980); they have been reported also from the latest Cretaceous near Agadir (R. Ambroggi and A.F. de Lapparent, 1954). Late Cretaceous footprints are known also from Spain (Llompart, 1979). Dinosaur footprints have been reported from Israel by Moshe A. Avnimelech (1963, 1966). In the U.S.S.R., they have been described by L.K. Gabunija from Georgia (1951) and by S.A. Zakharov from Tadzhikistan (1964). From Mongolia, they have been reported by O. Namnandorski (1957) and from Manchuria (now northern China) by H. Yabe *et al.* (1940a, b). Only recently have dinosaur footprints come to be reported from Japan – Early Cretaceous sediments by Masaki Matsukawa and Iwabo Obata (1985).

In Australia, dinosaur footprints were first reported from Queensland by L.C. Ball (1933, 1934, 1946): other records from that state include notes by F.H. Colliver (1956) and A. Bartholomai (1966) and a thorough study by Ricard A. Thulborn and Mary Wade (1984), who considered they had evidence for a "dinosaur stampede" (1979). Dinosaur footprints have been recorded also from western Australia, by Edwin H. Colbert and D. Merrilees (1967). A general account of Australian fossil footprint discoveries is to be found in R. Molnar's review of Australian late Mesozoic tetrapods (1980).

Early records of Mesozoic bird footprints have proved largely to be misinterpretations of dinosaur footprints. The first authentic record is that by Maurice G. Mehl (1931), from the Middle Cretaceous of Colorado. Somewhat older Middle Cretaceous bird footprints have been described recently by Philip J. Currie from the Peace River Canyon of British Columbia (1981).

OTHER ASPECTS OF FOOTPRINT RESEARCH

In many papers devoted primarily to the description and illustration of fossil footprints, comments are made on their taxonomy, their behavioral significance, the evidence they furnish concerning vertebrate evolution and their significance in palaeoecology and stratigraphy. However, a few papers on these topics deserve particular mention.

The propriety of applying Linnaean Binominal-style nomenclature to trace fossils of any kind has been questioned by some zoologists and palaeontologists; this matter is discussed at lenght by the author and W.J. Kennedy (1973) and need not be considered here. However, Henry Faul's reservations about this procedure (1951) led to the formulation by Faul and Roberts (1951) of a different approach need to be noted, as does Frank Peabody's reasoned response to that approach (1955). The elaborate classification of trace-fossils proposed by O.S. Vialov (1966, 1972) deserves study, for it accords particular attention to vertebrate traces.

If the information provided by footprints is to be utilized fully, a first step is the study of living animals of comparable type. Traditionally, the techniques of the hunters of today have been used in interpreting the behaviour of the animals of the past; but these have been valuably supplemented by a few careful studies of track patterns. Noteworthy among these are Frank E. Peabody's work on amphibian tracks (1959), Jürgen Fichter's analyses of amphibian and lizard tracks in different sedimentary substrates (1982, 1983a); the study of alligator tracks by Hans-Erich Reineck and James D. Howard (1978), Giuseppe Leonardi's examination of lizard trackways (1975) and Kevin M. Padian and Paul E. Olsen's work comparing the tracks of the living Komodo dragon with those of fossil reptiles (1984). A study by William K. Gregory (1912) of the principles of quadrupedal locomotion and of limb mechanisms in hoofed mammals remains valuable, while the perceptive work of Rodolpho M. Casamiquela (1964) on how patterns of mammalian footprints reflect their gait, and Norman Heglund and Richard Taylor's more detailed study of mammalian stride frequency and gait (1974) deserve mention. The laboratory and field studies of Edwin J. McKee (1947) and Leonard Brand (1979), of footprints formed in different substrates, are also of great importance.

An interesting demonstration of how the soft morphology of the foot of an extinct creature may be determined from its footprints was furnished by Wann Langston Jr. (1960), in his study of a hadrosaurian ichnite. The tracks of sauropods have indicated that the manus of sauropods may have retained a grasping function (G. de Beaumont and Georges Demathieu, 1980). Roland Birds's use of footprints to demonstrate that sauropod dinosaurs could walk on dry land proved to be a pivot for Robert R. Bakker's study of the ecology of the brontosaurs (1971). John H. Ostrom (1971) was the first person to elucidate the clear evidence provided by dinosaur footprints for herd and pack behaviour, thus showing convincingly that dinosaurs were so much more advanced in social behaviour than living reptiles as to deserve to be considered quite differently. The swimming ability of carnosaurs has been demonstrated from their footprints by W.P. Coombs Jr. (1980), while R. McN. Alexander (1976) and Georges R. Demathieu (1984) have formulated methods by which the speed of movement of dinosaurs may be calculated. (Most of these points are stressed in popular articles by Mossman and Sarjeant, 1983, and Lockley, 1984).

The use of footprints to determine changing behaviour, and thus to chart the course of evolution, was first attempted by Wilhelm Bock (1952) and has since been employed effectively by Hermann Schmidt (1959), Georges Demathieu and Hartmut Haubold (1974), and others.

As was first demonstrated by Daniel Heyler and Jacques Lessertisseur (1963), the impact of the foot of a vertebrate can not only affect the sediment on which it is walking but also the buried layers of sediment beneath, producing subtraces that simulate the shape of the footprints in part only and can thus mislead their discoverers. The result can be merely a disturbance of stratification, as in the hoofprints recorded from New Zealand beaches by G.J. Van der Lingen and P.B. Andrews (1969). Where heavy vertebrates are abundant, a reworking of the whole substrate may occur, as noted in Kenya by Léo F. Laporte and Anna K. Behrensmeyer (1980). Sole marks in the Triassic red beds of Wyoming have been shown by Donald W. Boyd and David B. Loope (1984) to be possibly attributable to the movements of a half-swimming quadruped.

The fullest account in English of the techniques of the study of fossil vertebrate footprints is still that written by the present writer ten years ago (1975). An important book on reptile footprints, written in German by Hartmut Haubold (1984), deserves translation, while his summary of *Ichnia Tetrapodorum et Reptiliorum fossilium* (1971b) remains valuable. A selection of "Benchchmark" papers on fossil vertebrate footprints was included by the writer in a survey of published work on *Terrestrial Trace Fossils* (1983) – the first work attempting to set footprints into the context of other palaeontological evidence from the terrestrial realm.

For many years the study of vertebrate footprints was considered by vertebrate palaeontologists to be unimportant; the writer has had the experience of seeing a paper rejected by a journal on the basis of a "review" by one such specialist which said: "I have not read this paper, but I am opposed to its publication since I consider studies of fossil footprints to be a waste of time". Now, ideas have changed. At the recent meeting of the Society of Vertebrate Paleontology in Berkeley, California (1984), vertebrate footprints were accorded their proper status as the major means by which the behavior of extinct vertebrates could be determined. This change in outlook is now very much in evidence. In 1986 the New Mexico Museum of Natural History hosted the First International Symposium on Dinosaur Tracks and Traces (Gillette, D.D., 1986) complete with a week long field trip through six States (Lockley, M.G., 1986). Plans now exist for further meetings in the area of vertebrate Ichnology.

The publication of the *Glossary* which follows will serve greatly to facilitate future research in this important field.

ACKNOWLEDGEMENTS

This account was written on the urging of my friend Giuseppe Leonardi, who has also read it critically and made valuable comments. In its preparation I was aided greatly by my research assistant, Mrs. Linda Dietz. The manuscript was also courteously read and commented on by Dr. Donald L. Baird (Princeton, New Jersey), Dr. Walter P. Coombs (Springfield, Massachusetts), Mr. Justin Delair (Oxford, England) and M. Georges Demathieu (Dijon, France), many of whose suggestions are incorporated. Mr. Alexander Dietz gave help with Russian papers. I am indebted to all of the above for their courtesy, but retain sole responsability for all opinions expressed herein.

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It must be stressed that, in the case of authors who have written a long series of papers devoted to one specific topic, only a few papers are selected for citation. The fact that there are others is indicated in the text by "(1886, etcetera)" or some equivalent phrase. The length of the list that follows will make evident the need for this selectivity. More extensive bibliographies are to be found in Kuhn (1963) and Haubold (1971, 1984); but there is need for a new and comprehensive bibliography of this field.

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Glossary in Eight Languages

(see the Preface for symbology and explanations)

CASTELLANO (ESPAÑOL) R.M.C.	DEUTSCH H.H.	ENGLISH W.A.S.S.	FRANÇAIS G.R.D.
1. TERMINOS ICNOLOGICOS	ICHNOTERMINI	ICHNOLOGICAL TERMS	TERMES ICHNOLOGIQUES
1.1 GENERALIDADES	ALLGEMEINES	GENERAL	GÉNÉRALITÉS
1. incologfa	Ichnologie	ichnology	ichnologie
2. neoicnologfa	Neoichnologie	neoichnology	néoichnologie
3. paleoicnología	Palichnologie	palaeoichnology	paléoichnologie
4. icnofauna	Ichnofauna	ichnofauna	ichnofaune
5. icnocenosis	Ichnozönose	ichnocoenose (ichnocoenosis)	ichnocénose
6. icnofósil	Ichnofossil	ichnofossil	ichnofossile
7. icnogénero	Ichnogenus	ichnogenus	ichnogenre
8. icnoespecie	Ichnospezies	ichnospecies	ichnoespèce
9. morfofamília	Formfamilie, Fährtenfamilie	morphofamily, form-family	morphofamille
1.2 PISTAS	DIE FÄHRTE	THE TRACKWAY	LA PISTE
10. pista, rastro, rastrillada, andada, (huellas)	Fährte, Fährtenfolge, Spur, Geläuf	trackway, tracks (trail)	piste, voie
11. morfología del rastro, carácter de la pista	Fährtenmuster, -anordnung, Trittbild	trackway pattern	aspect de la piste
12. pista: recta atravesada regular irregular	Fährten: schüren schränken regular irregular	trackway: – – regular irregular	voie: droite croisée regulière irregulière
13. autor del rastro	Fährtenerzeuger, (Fährtentier)	trackmaker	auteur des traces
14. punto de referencia puntos homólogos punto de medida centro [de la huella] –	Referenzpunkt Homologer Punkt Messpunkt Mittelpunkt –	reference point homologous points – midpoint –	point de repère points homologues – centre [de l'empreinte] –
15. línea media eje central –	Mittellinie – (Hilfslinie)	midline – –	– axe de la piste, de la voie –
16. paso doble, (zancada)	Doppelschritt "Stridelänge" einseitiger Schritt	[length of] stride	[longueur de l'] enjambée
17. paso [simple]	Schritt	[length of] pace	[longueur du] pas

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ H.H.
TERMINI ICNOLOGICI	ICHNOLOGICA VERBA	TERMOS ICNOLÓGICOS	Ихнологическая терминология
GENERALITÀ	GENERALIA	GERAL	Общие термины
Icnologia	Ichnologia	Icnologia	Ихнология
Neoicnologia	Neoichnologia	Neoicnologia, Neicno- logia	Неоихнология
Paleoicnologia	Paleoichnologia	Paleoicnologia, Palic- nologia	
icnofauna	ichnofauna	icnofauna	Ихнофауна
icnocenosi	icnocenosis	icnocenose	ихноценоз
icnofossile	ichnofossilis	icnofóssil	ихнофоссилии
icnogenere	ichnogenus	icnogênero	ихнород
icnospecie	ichnospecies	icnoespécie, icnospécie	ихновид
morfofamiglia	morphofamilia	morfofamília	формальное семейство
LA PISTA	VESTIGIA	A PISTA	след
pista	vestigia	pista, (pegadas), (andada)	след
stile della pista	caracter vestigiorum	padrão da pista	рисунок (система паттерн) следов
pista: – – regolare irregolare	vestigia: – – aequabilia enormia	pista: – – regular irregular	след:однорядный, шнуровидный многорядный; регулярный нерегулярный
autore delle orme	– –	autor das pegadas, responsável pelas pegadas	продюсер (животное, оставившее след)
punto di riferimento punti omologhi punto di misura punto medio –	punctum rationis puncta homologa punctum mensurae punctum medium signum	ponto de referência pontos homólogos ponto de medição ponto médio –	точка отсчета гомологичная точка точка измерения центр,срединная точка –
linea media asse della pista –	linea media axis vestigiorum –	linha mediana eixo da pista –	средняя линия ось следа
doppio passo	passus	passo duplo, (passada)	сдвоенный (двойной) шаг
passo	gradus	meio passo	шаг

CASTELLANO (ESPAÑOL) R.M.C.	DEUTSCH H.H.	ENGLISH W.A.S.S.	FRANÇAIS G.R.D.
18. paso oblicuo	"rechts-links Schritt", Schrittlänge (einfacher Schritt)	[oblique] pace (length of step)	pas oblique, (envergure)
19. distancia mano-pie	Abstand Hand-Fuss	distance between manus and pes	distance main-pied
20. ancho del paso, (ancho del rastro	Schrittweite (-breite)	width of pace	écartement des pattes
21. ancho exterior del rastro	Gang-, Spur-, Fährtenbreite, aussen	[external] trackway width, breadth	largeur exterieure de la piste, largeur totale de la piste
22. ancho interior del rastro	Gang-, Spur-, Fährtenbreite, innen	breadth between tracks	largeur interieure de la piste (de la voie)
luz del rastro	–	–	lumière de la piste
23. distancia entre manos distancia entre pies –	Abstand zwischen Hand- bzw. Fusseindrücken, Spurbreite der Hände und Füsse	intermanus distance interpedes distance	distance entre les mains distance entre les pieds
luz entre pisadas de la mano y del pie	–	–	–
24. ángulo de paso	Schrittwinkel	pace angulation, step angle	angle du pas
25. –	(Winkelfolge)	(angulate pattern)	–
26. adelantamiento, anteposición, sobrepaso	Übertreten, Übereilen, Beitritt, Kreuztritt	overstep	dépassement prégression
27. sobreposición, superposicíon,	Übertreten	overlap	superposition, empiètement
supraposición			
grados de s.:	Grad des Übertretens:	degrees of o.:	degrés de s. ou e.:
primaria	primär	primary	primaire
secundaria	sekundär	secondary	secondaire
terciaria;	tertiär;	tertiary;	tertiaire;
marginal	randlich	marginal	marginal
parcial	teilweise, (partiell)	partial	partiel
total	total, ganz	total	total
28. divergencia de la pisada	–	divarication of foot from midline	–
ángulo de los pies;	Neigungswinkel der III	foot angulation	angle du pied avec l'axe de la piste
desvío del pie;	Zehen zur Mittellinie;		
diagonalización del pie	Fuss-und Handstellung		
ángulo positivo	Auswärtsdrehung (+plus)	outward or positive rotation	angle positif
ángulo nulo		nil, zero angle	angle nul
ángulo negativo	Einwärtsdrehung (-minus)	inward or negative rotation	angle negatif
1.3 PISADAS	DER EINDRUCK	THE FOOTPRINT	L'EMPREINTE DE PAS
29. huella, pisada, (impresión), (impronta),	Eindruck, Fuss-, Handabdruck, Fussspur, Tritt, Trittsiegel, Stapfe, (Fährte, Spur)	footprint, footstep, footmark, imprint, impression, print	empreinte [de pas], impression, trace [de patte], patte, pas
icnita	–	(ichnite)	(ichnite)

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ Н.Н.
passo obliquo	gradus obliquus, gradus transversus	passo oblíquo	диагональное расстояние между правым и левым следом, длина шага
distanza mano-piede	distantia manus pedisque	distância mão-pé	расстояние рука-нога
scartamento delle zampe	latitudo passus	bitola das patas	ширина шага
larghezza esterna della pista, larghezza della pista "fuori tutto"	latitudo externa vestigiorum	largura exterior da pista, largura total da pista	внешняя ширина следа
larghezza interna della pista luce della pista	latitudo interna vestigiorum lumen vestigiorum	largura interna da pista vão da pista, luz da pista	внутренняя ширина следа
distanza tra le mani distanza tra i piedi	distantia inter manus distantia inter pedes	distância inter manus distância inter pedes	расстояние между рядами следов рук или ног
–	–	–	
angolo del passo	angulus passus	ângulo do passo	угол шага
–	–	–	угол хода
sorpasso	precursio	ultrapassagem	перекрытие
sovrapposizione	superpositio	sobreposição	перекрытие
gradi di s.:	gradus superpositionis:	graus de s.:	степень перекрытия
primaria	primaria	primária	первичная
secondaria	secundaria	secundária	вторичная
terziaria	tertiaria	terciária	третичная
marginale	s. marginis	marginal	краевая
parziale	ex parte	parcial	частичная
totale	plena	total	полная
divergenza dell'orma angolo asse piede-asse pista	– angulus inter axem pedis et axem vestigiorum	divergência da pegada ângulo eixo do pé – eixo da pista	положение ног и рук угол наклона к средней линии
angolo positivo	angulus positivus	ângulo positivo	вывернутое положение
angolo nullo	angulus nullus	ângulo nulo	
angolo negativo	angulus negativus	ângulo negativo	обращенное во внутрь положение
L'ORMA	VESTIGIUM	A PEGADA	ОТПЕЧАТОК
impronta, impressione, orma	vestigium, pedicata, impressio, passus	pegada, pisada, rastro, rasto, impressão	отпечаток (ноги, руки)
(icnite)	(ichnites)	(icnite)	

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30. impresión en hueco	Vertiefung	hollow	empreinte en creux
impresión original	original Eindruck	original print	empreinte originale
(impresión positiva)	(Positivabdruck)	(positive print)	(empreinte positive)
molde	Abdruck	mould (U.K.), mold (U.S.A.)	–
epirelieve cóncavo	Epirelief, konkav	concave epirelief	epirelief concave
31. impresión en relieve	(Fährtenrelief)	–	empreinte en relief, en bosse
	(Fährten-) Relief		
–	Gegendruck	(reverse print)	contre-empreinte
calco [natural]	Ausfüllung, Ausguss	[natural] cast	moulage naturel
(impresión negativa)	(Negativabdruck)	(negative print)	(empreinte negative)
hiporelieve convexo	Hyporelief, konvex	convex hyporelief	hyporelief convexe
32. par [de pisadas]	Trittpaar, (Einzelfährte, -fährtenpaar), Hand-Fuss Paar, linkes, rechtes Laufpaar	set [of footprints]	couple
33. eje longitudinal	Längs-, Longitudinalachse	long axis, longitudinal axis	axe longitudinal
34. eje transversal	Quer-, Transversalachse	transverse axis	axe transversal
35. eje metapodio-falangeal	Metapodial-Phalangen Achse	metapodial-phalangeal axis	axe digito-metapodial
metacarpo-falangeal	Metacarpal-Phalangen Achse	metacarpal-phalangeal axis	axe digito-métacarpien
metatarso-falangeal	Metatarsal-Phalangen Achse	metatarsal-phalangeal axis	axe digito-métatarsien
–	Kreuzachse	(cross axis)	–
36. largo de la pisada	Eindrucklänge	footprint length	longueur de l'empreinte
37. ancho de la pisada	Eindruckbreite	footprint width, breadth	largeur de l'empreinte
38. palma	Handfläche	palm	paume
39. largo de la palma	Handfläche Länge	palm length	longueur de la paume
40. ancho de la palma	Handfläche Breite	palm width, breadth	largeur de la paume
41. planta	Sohle	sole	plante
42. largo de la planta	Sohlenlänge	sole length	longueur de la plante
43. ancho de la planta	Sohlenbreite	sole width, breadth	largeur de la plante
44. dedo, dígito, I-II-III-IV-V	Zehe I-II-III-IV-V	digit I-II-III-IV-V	doigt ou rayon I-II-III-IV-V
–	Finger, Zehe [Vorderfuss, Hand]	finger [of fore-foot]	doigt [de la main]
–	Zehe [Hinter-Fuss]	toe [of hind foot]	orteil [du pied]
45. eje del dedo, eje del dígito	Zehenachse, Fingerachse	digit axis, finger axis, toe axis	axe du doigt, axe de l'orteil
46. hypex	Hypex	hypex	hypex
47. largo del dígito, largo del dedo, longitud del dígito, etc	Zehenlänge, Fingerlänge	digit length, finger length, toe length	longueur du doigt, de l'orteil, du rayon
48. largo libre del dedo, del dígito	Länge des freibeweglichen Zehenteils	free length of digit, finger, toe	longueur de la partie libre des doigts, des orteils, des rayons

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impronta impronta originale (impronta positiva) – epirilievo concavo	vestigium vestigium originale (vestigium positivum) – epieminentia concava	pegada pegada original (pegada positiva) – epirrelevo côncavo	оттиск углубление первичный отпечаток позитивный отпечаток эпирельеф
	vestigium eminens	pegada em relevo	выпуклый рельеф
controimpronta calco naturale (impronta negativa) iporilievo convesso	contravestigium exemplar naturaliter fictum (vestigium negativum) hypoeminentia eminens	contramolde molde natural (pegada negativa) hiporrelevo convexo	противоотпечаток выполнение (негативный отпечаток) гипорельеф
coppia mano-piede	par	par, par mão-pé	пара следов, пара рука-нога
asse longitudinale	axis in longitudinem	eixo longitudinal	продольная ось
asse trasversale	axis transversus	eixo transversal	поперечная ось
asse metapodial-falangeale asse metacarpal-falangeale asse metatarsal-falangeale –	axis metapodialis-phalangealis axis metacarpalis-phalangealis axis metatarsalis-phalangealis –	eixo metapódio-falangeal eixo metacarpo-falangeal eixo metatarso-falangeal –	 скрещение осей
lunghezza dell'orma	longitudo vestigii	comprimento da pegada	длина отпечатка
larghezza dell'orma	latitudo vestigii	largura da pegada	ширина отпечатка
palma, (palmo)	palma	palma	ладонь
lunghezza della palma	palmae longitudo	comprimento da palma	длина ладони
larghezza della palma	palmae latitudo	largura da palma	ширина ладони
pianta	planta	planta	подошва
lunghezza della pianta	plantae longitudo	comprimento da planta	длина подошвы
larghezza della pianta	plantae latitudo	largura da planta	ширина подошвы
dito I-II-III-IV-V – –	digitus I-II-III-IV-V – –	dedo I-II-III-IV-V dedo [da mão] dedo, artelho [do pé]	палец (I-II-III-IV-V) палец (передней ноги, руки) палец (задней ноги)
asse del dito	axis digiti	eixo do dedo	ось пальца
hypex	hypex	hypex	гипекс
lunghezza del dito	longitudo digiti	comprimento do dedo	длина пальца
lunghezza del dito libero	longitudo digiti liberi	comprimento do dedo livre	длина свободно дви- гающейся части пальца

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49. –	–	(communal length)	–
50. largo de la porción falangeal del dígito	Phalangenlänge	length of the phalangeal portion of the digit	longueur de la partie phalangienne du doigt
51. largo real del dedo, del dígito	reelle-Zehenlänge	true lenght of digit, finger, toe	longueur réelle du doigt, de l'orteil, du rayon
52. uña garra, zarpa casco, pezuña	Nagel Klaue Huf, Schale	nail claw hoof	ongle griffe onglon, sabot
53. – almohadilla palmar almohadilla plantar	Sohle, Ballen Polster – –	sole-pad, sole-callus – –	– coussinet palmaire coussinet plantaire
54. almohadilla, cojinete, callosidad subdigital, nudillo	[Zehen-, Phalangen-] Polster	[digital] pad, node	coussinet digital, pelote
55. talón, calcáneo	Ferse	heel	talon
56. divergencia de los dígitos ángulo interdigital parcial: I-II; II-III; III-IV; IV-V; II-IV total: I-V constante variable	Zehendivergenz Zehenwinkel teilweise: I-II; II-III; III-IV; IV-V; II-IV total: I-V konstant variabel	divarication of digits interdigital angle, angle of divergence, digit angle partial: I-II; II-III; III-IV; IV-V; II-IV total: I-V constant variable	divergence des doigts angle interdigital partiel(le): I-II; II-III; III-IV; IV-V; II-IV total(e): I-V constant(e) variable
57. ángulo de cruzamiento	Kreuzachsenwinkel	cross-axis angle	obliquité
58. membrana interdigital membrana natatoria	– Schwimmhaut	[interdigital] web, webbing –	palmure [interdigitale] membrane natatoire
59. huella de cola	Schwanzspur	tail drag	trace de la queue
60. rastro, impresión, huella, marca	Spur, Marke, Eindruck, Abdruck	mark, impression, print, spoor	trace, marque, impression
61. dactilia	Dactylie, Zehenzahl	dactyly	dactylie
62. monodactilia bidactilia tridactilia tetradactilia pentadactilia	Monodactylie (1 Zehigkeit) Bidactylie (2 Zehigkeit) Tridactylie (3 Zehigkeit) Tetradactylie (4 Zehigkeit) Pentadactylie (5 Zehigkeit)	monodactyly didactyly tridactyly tetradactyly pentadactyly	monodactylie bidactylie tridactylie tetradactylie pentadactylie

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–	–	–	
lunghezza della porzione falangeale del dito	longitudo partis phalangealis digiti	comprimento da porção falangeal do dedo	длина фаланги
lunghezza reale del dito lunghezza del dito *s.s.*	longitudo digiti vera longitudo digiti *s.s.*	comprimento real do dedo comprimento do dedo *s.s.*	реальная длина пальца
unghia artiglio zoccolo	unguis unguis ungula	unha garra casco	ноготь коготь
– cuscinetto palmare cuscinetto plantare	pulvinus pulvinus palmaris pulvinus plantaris	almofada, coxim almofada palmar almofada plantar	подушка подошвы
cuscinetto [digitale]	pulvillus	almofadinha, coxinete	подушка пальца
tallone, calcagno	talus, calx, calcaneum	talão, calcanhar	пятка
divergenza delle dita angolo interdigitale parziale: I-II; II-III; III-IV; IV-V; II-IV totale: I-V constante variabile	divortium vel divergium digitorum angulus interdigitalis ex parte: I-II; II-III; III-IV; IV-V; II-IV totalis(-e): I-V constans(-e) variabilis(-e)	divergência dos dedos ângulo interdigital parcial: I-II; II-III; III-IV; IV-V; II-IV total: I-V constante variável	расхождение (дивергенция) пальцев Угол между пальцами частные: I-II; II-III; III-IV; IV-V; II-IV общий: I-V устойчивый, постоянный изменчивый
angolo dell' incrocio assi	angulus crucis	ângulo do cruzeiro	угол скрещения осей
membrana interdigitale membrana natatoria	membrana interdigitalis– –	membrana interdigital membrana natatória	плавательная перепонка
traccia della coda	caudae vestigium	rastro [etc.] da cauda	отпечаток хвоста
traccia, impressione, impronta	vestigium	traço, vestígio, impressão, rastro,	намек следа
dattilia	dactylia	datilia, dactilia	дактилия, число пальцев
monodattilia bidattilia tridattilia tetradattilia pentadattilia	monodactylia bidactylia tridactylia tetradactylia pentadactylia	monodatilia bidatilia tridatilia tetradatilia pentadatilia	монодактилия(однопалость) дидактилия(двупалость) тридактилия(трехпалость) тетрадактилия(четырехпалость) пентадактилия(пятипалость)

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63. pisada monodigitada bidigitada tridigitada tetradigitada pentadigitada or: monodáctila, etc.	Eindruck: monodactyl bidactyl tridactyl tetradactyl pentadactyl	footprint: monodactyl didactyl tridactyl tetradactyl pentadactyl	empreinte: monodactyle bidactyle tridactyle tetradactyle pentadactyle
64. axonia	Axonie, (betonte Achse)	axony	axonie
65. entaxonia mesaxonia paraxonia ectaxonia	Entaxonie Mesaxonie Paraxonie Ectaxonie	entaxony mesaxony paraxony ectaxony	entaxonie mesaxonie paraxonie ectaxonie
66. pisada: entaxónica mesaxónica paraxónica ectaxónica	Eindruck: entaxonisch mesaxonisch paraxonisch ectaxonisch	footprint: entaxonic mesaxonic paraxonic ectaxonic	empreinte: entaxonienne mesaxonienne paraxonienne ectaxonienne
67. gradismo	Fuss-, Handhaltung	grady	gradie
68. plantigradismo semiplantigradismo digitigradismo semidigitigradismo unguligradismo calcigradismo	Plantigradie, (Sohlengang) Semiplantigradie Digitigradie, (Zehengang) Semidigitigradie Unguligradie, (Hufgang) Calcigradie	plantigrady semi-plantigrady digitigrady semi-digitigrady unguligrady calcigrady	plantigradie semiplantigradie digitigradie semidigitigradie unguligradie calcigradie
69. pisada: plantígrada semiplantígrada digitígrada semidigitígrada ungulígrada calcígrada	Eindruck: plantigrad semiplantigrad digitigrad semidigitigrad unguligrad calcigrad	footprint: plantigrade semi-plantigrade digitigrade semi-digitigrade unguligrade calcigrade	empreinte: plantigrade semiplantigrade digitigrade semidigitigrade onguligrade calcigrade
70. heteropodia	Heteropodie	heteropody	hétéropodie
71. homopodia	Homöopodie	homopody	homopodie
72. derecha e izquierda	Rechts and Links	right and left	droite et gauche
2. TERMINOS ANATOMICOS	ANATOMISCHE BEGRIFFE	ANATOMICAL TERMS	TERMES ANATOMIQUES
73. largo del tronco distancia gleno-acetabular	Rumpflänge, Länge der Dorsalregion Abstand von glenoid und acetabular Fossa	body length, length of the dorsal region gleno-acetabular distance	longueur du tronc distance gléno-acétabulaire
74. longitud relativa del tronco; razón de la longitud tronco-miembros	Relation von Rumpf- und Extremitätenlänge	coupling value	longueur relative du tronc par rapport à la longueur des membres

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orma: monodattila	vestigium: monodactylum	pegada: monodátila	след:монодактильный(однопалый)
bidattila	bidactylum	bidátila	дидактильный(двупалый)
tridattila	tridactylum	tridátila	тридактильный(трехпалый)
tetradattila	tetradactylum	tetradátila	тетрадактильный (четырехпалый)
pentadattila	pentadactylum	pentadátila	пентадактильный(пятипалый)
		or: monodáctila etc.	
assonia	axonia	axonia	аксония(выделеииость одиой оси)
entassonia	entaxonia	entaxonia	энтаксония
mesassonia	mesaxonia	mesaxonia	мезаксония
parassonia	paraxonia	paraxonia	параксония
ectassonia	ectaxonia	ectaxonia	эктаксония
orma: entassonica	vestigium: entaxonicum	pegada: entaxônica	отпечаток:энтаксонический
mesassonica	mesaxonicum	mesaxônica	мезаксонический
parassonica	paraxonicum	paraxônica	параксонический
ectassonica	ectaxonicum	entaxônica	эктаксонический
gradia	gradia	gradia	поза(постановка)ноги,руки
plantigradia	plantigradia	plantigradia	плантиградия
semiplantigradia	semiplantigradia	semiplantigradia	семиплантиградия
digitigradia	digitigradia	digitigradia	дигитиградия(пальцехождение)
semidigitigradia	semidigitigradia	semidigitigradia	семидигитиградия
unguligradia	unguligradia	unguligradia	унгулиградия
calcigradia	calcigradia	calcigradia	кальциградия
orma: plantigrada	vestigium: plantigradum	pegada: plantígrada	след:плантиградический
semiplantigrada	semiplantigradum	semiplantígrada	семиплантиградический
digitigrada	digitigradum	digitígrada	дигитиградический
semidigitigrada	semidigitigradum	semidigitígrada	семидигитиградический
unguligrada	unguligradum	ungulígrada	унгулиградический
calcigrada	calcigradum	calcígrada	кальциградический
eteropodia	heteropodia	heteropodia	гетероподия(разноногость)
omopodia	homopodia	homopodia	гомоподия(равноногость)
destra e sinistra	dextera ac sinistra	direita e esquerda	правый и левый
TERMINI ANATOMICI	ANATOMICA VERBA	TERMOS ANATÔMICOS	АНАТОМИЧЕСКИЕ ТЕРМИНЫ
lunghezza del tronco	longitudo trunci	comprimento do tronco	длина тела, длина дорзальной области
distanza gleno-acetabolare	distantia glenoacetabularis	distância gleno-acetabular	расстояние между плечевым и бедренным сочленениями
lunghezza relativa del tronco	longitudo trunci relativa	comprimento relativo do tronco	соотношение между длиной корпуса и конечностей

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75. grados de la cupla animal: con cupla corta con cupla larga con cupla muy larga	 Tier: kurzbeinig oder langbeinig in Beziehung zum Schulter-Beckenabstand	degrees of coupling animal: short coupled long coupled very long coupled	– animal à courts, longs, très longs membres par rapport au tronc
76. pie, pata –	Fuss –	foot paw	pied –
77. mano pie delantero, anterior manus	Hand Vorderfuss, Vorderlauf manus	hand front foot, forefoot manus	main pied anterieur manus
78. pie pie trasero, posterior pes/pedes	Fuss Hinterfuss, Hinterlauf pes/pedes	foot hind foot pes/pedes	pied pied postérieur pes/pedes
79. autopodio	Autopodium/-a	autopodium/-a	autopode
80. radius/-ii radio	Radius/-ii Strahl	radius/-ii	radius/-ii rayon
81. miembro aparente largo aparente del brazo largo aparente de la pierna	Extremitätenlänge (scheinbare) Armlänge (scheinbare) Beinlänge (scheinbare)	apparent limbs apparent fore limb apparent hind limb	membre apparent longueur apparente du membre antérieur longueur app. du membre posterieur
82. ángulo de marcha	Schreitwinkel	angle of gait	angle de marche
83. fórmula falangeal	Phalangenformel	phalangeal formula	formule phalangienne
84. digitación	Zehenmuster	digitation	digitation
85. medial	medial	medial	médial
86. lateral	seitwärts	lateral	latéral
87. distal	distal	distal	distal
88. proximal	proximal	proximal	proximal
89. mediano	mittler	median	médian
90. extremo	äussert	outer	extrême
3. TERMINOS BIOMECANICOS	BIOMECHANISCHE BEGRIFFE	BIOMECHANICAL TERMS	TERMES BIOMÉCANIQUES
91. locomoción: cuadrúpeda semibípeda bípeda	Lokomotion: Quadruped; quadruped Semibiped, semibiped Biped, biped	locomotion: quadrupedal semibipedal bipedal	locomotion: quadrupède semi-bipède bipède

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			длинноногий или коротконогий (в связи с расстоянием между плечевым и тазовым поясами)
piede –	pes –	pata –	нога
mano piede anteriore manus	manus pes anterior –	mão pata dianteira, anterior mahus	рука передняя нога
piede piede posteriore pes/pedes	pes pes posterior –	pé pata traseira, posterior pes/pedes	нога задняя нога
autopodio	autopodium/-a	autopódio	автоподий
radius/-ii raggio	radius/-ii –	radius/-ii (raio)	луи
arto apparente – –	membrum apparens – –	membro aparente – –	длина конечности (видимая)
angolo di marcia	angulus incessus	ângulo de marcha	угол между ногами
formula falangeale	formula articulorum (phalangium)	fórmula falangeal	формула фаланг
digitazione	digitatio	digitação	расположение пальцев
mediale	medialis	medial	медиальный
laterale	lateralis	lateral	боковой
distale	distalis	distal	
prossimale	proximalis	proximal	
mediano	medianus	mediano	средний
estremo	extremus	extremo	крайний
TERMINI BIOMECCANICI	BIOMECHANICA VERBA	TERMOS BIOMECÂNICOS	БИОМЕХАНИЧЕСКИЕ ТЕРМИНЫ
locomozione: quadrupede semibipede bipede	processus: quadrupes semibipes bipes	locomoção: quadrúpede semibípede bípede	передвижение: четвероногий двуногий

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92. cuadrupedalismo semibipedalismo bipedalismo	Quadrupedie Semibipedie Bipedie	quadrupedaly semibipedaly bipedaly	quadrupédie semi-bipédie bipédie
93. tetrápodo	Tetrapod	tetrapod	tétrapode
94. posición de los miembros: miembros: parasagitales transversales horizontales	Gliedmassenstellung: Gleidmassen: vollaufgerichtet halbaufgerichtet schubkriechen	position of the limbs: limbs: parasagittal transversal horizontal	position des membres: membres: parasagittaux transversaux horizontaux
95. andar, marcha, progresión	Gang, Lauf, Gangart	[manner of]gait, progressive motion	allure, demarche attitude de marche
96. andar: esparrancado erguido	Gang: kriechend aufrecht	gait: sprawling erect	allure: rampante (reptation) érigée, dressée
97. andar: caminado de carrera brincado, saltado, a saltos	Gang: gehen rennen, laufen springen, hüpfen	gait: walking running jumping, hopping	allure: du pas de course par sauts, bonds
98. tipos de andares (de marcha):	Gangarten:	manners of gait:	modes d'allure:
paso [alternado]	gehen	normal pace	pas [alterné]
ambladura		amble	amble
trote	trotten, traben	trot	trot
galope	galoppieren	gallop	galop, fuite
saltos, brincos	hoppeln, hüpfen	springs	sauts, bonds
richochet, brinco bipedal	springen	richochet, saltation	sauts
marcha serpenteante, andar serpenteante	schlängeln	serpentine progression	progression serpentine
seminatación	rudernd; Schwimmfährte	half-swimming	semi-natation
vuelo – decolaje y aterrizaje	Flug – Start und Landung Sprungfährte und Landefährte	flight – take off and landing	vol – envol et atterrissage
99. recto curvo	geradeaus Krümmung, Bogen, Kurve	straight crooked, bent	droit déjeté
100. abducción	Abduktion, (Abziehen)	abduction	abduction
101. aducción	Adduktion, (Anziehen)	adduction	adduction
102. base: unipedal bipedal tripedal quadripedal angosta ancha	Basis: uniped, 1 füssig biped, 2 füssig triped, 3 füssig quadruped, 4 füssig schmal breit	base: unipedal bipedal tripedal quadripedal narrow wide	base: unipède bipède tripède quadrupède étroite large
103. batida	Auftreten	footfall	pose
104. levantamiento	Abtreten, Abheben	retraction	rétraction (retrait)
105. período, tiempo	Zyklus, Phase	cycle	période, cycle

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ Н.Н.
quadrupedia semibipedia bipedia	quadrupedia semibipedia bipedia	quadrupedía semibipedia bipedia	
tetrapode	tetrapus, -podis	tetrápode	
posizione delle membra: membra: parasagittali transversali orizzontali	membrorum status: membra: parasagittalia transversa ad libellam directa	posição dos membros: membros: parasagitais transversais horizontais	
andatura, marcia	incessus	andar, andadura, andamento, marcha	походка, ход
andatura: strisciante eretta	incessus repens incessus erectus	andar: arrastado, rastejante erguido	походка: ползающий ход прямой (прямохождение)
andatura: al passo di corsa a salti	incessus cursus incessus saliens	andar: caminhado corrido saltado	походка: хождение бег прыжок
tipi di andatura: passo [alternato] ambio trotto galoppo salti – andatura serpentina	incessus modi: incessus tolutilis gradus quadrupedus cursus saltus – incessus serpens	tipos de andar: passo [alternado] passo esquipado, esquipança trote galope pulos ricochete andadura serpentina	походка: диагональный ход иноходь рысь, бежать рысью галоппировать скакть прыгать тащиться, волочиться
seminuoto volo – decollo e aterraggio	seminatatio volatus – evalatio et descensus	seminatação vôo – decolagem e aterrissagem	
diritto uncinato, curvo	rectus flexus	reto curvo	прямо по кривой
abduzione	abductio	abdução	абдукция
adduzione	adductio	adução	аддукция
base: unipedale bipedale tripedale quadripedale stretta larga	basis: unipedalis bipedalis tripedalis quadipedalis angusta lata	base: unipedal, unípede bipedal, bípede tripedal, trípede quadripedal, quadrípede estreita larga	осанка:унипедальная,одноногая бипедальная,двуногая трипедальная,трехногая квадрипедальная, четырехногая узкая широкая
battuta	percussio	batida	поза
sollevamento	sublatio	levantamento	поднятие, вставание
periodo, ciclo	periodus, cyclus	período	цикл, фаза

CASTELLANO (ESPAÑOL) R.M.C.	DEUTSCH H.H.	ENGLISH W.A.S.S.	FRANÇAIS G.R.D.
106. bípedo: diagonal lateral	diagonale Bipedie einseitige Bipedie	limb pair: diagonal limbs lateral limbs	bipède: diagonal lateral
4. TERMINOS RELATIVOS AL SUBSTRATO	TERMINI ZUM SUBSTRAT	SUBSTRATE TERMS	TERMES RELATIFS AU SUBSTRATUM
107. substrato duro	hart Substrat	hard substrate	substrat dur
108. substrato firme	fest Substrat	firm substrate	substrat ferme
109. substrato blando	weich Substrat	soft substrate	substrat mou
110. substrato elástico	nachgiebig Substrat	yielding substrate	substrat élastique
111. substrato cohesionado	kohäsiv Substrat	cohesive substrate	substrat cohésif
112. substrato arenoso	sandig Substrat	sand substrate	substrat sableux
113. substrato arcilloso	tonig Substrat	clay substrate	substrat glaiseux
114. substrato fangoso	schlammig Substrat	mud substrate	substrat boueux
115. substrato arcilloso	argillitisch Substrat	argillaceous substrate	substrat argileux
116. substrato pantanoso	wasserhaltig Substrat	waterlogged substrate	substrat humide
117. substrato sumergido	überschwemmt Substrat	submerged, overflowed subs.	substrat submergé
118. substrato seco, árido	trocken, arid Substrat	dry, arid substrate	substrat sec
119. s. medanoso, de duna	äolisch Substrat	dune substrate	substrat dunaire
120. s. de estratific. cruzada	Kreuzgeschichtet Substrat	cross bedded substrate	s. à stratification entrecroisée
121. substrato deltaico	Delta-fluviatil Substrat	delta, deltaic substrate	substrat deltaïque
122. rebaba, rebada, reborde	Wulst	displacement rim	bourrelet, talus de rejet
123. medialuna de arena	Sand-Sichel	sand crescent	croissant de sable
124. subtraza, infratraza, pisada fantasma	Undertrack	subtrace, under track "ghost print"	sous-trace
5. TERMINOS ESTADISTICOS	STATISTISCHE BEGRIFFE	STATISTICAL TERMS	TERMES STATISTIQUES
125. análisis de la variancia	Varianzanalyse	analysis of variance	analyse de la variance
126. asimetría	Asymmetrie	asymmetry	asymétrie – dissymétrie
127. sesgo	Bias	bias	biais
128. binomial	Binomial	binomial	binomiale (distribution)
129. acotar	einschränken	to bound	borner
130. chi cuadrado	chi Quadrat	chi square	khi deux
131. intervalo de confianza	Konfidenzintervall, Vertrauens grenzen	confidence interval	intervalle de confiance

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ Н.Н.
bipiede: diagonale laterale	artus diagonales artus laterales	membros diagonais membros laterais	боковая двуногость диагональная двуногость
TERMINI RELATIVI AL SUBSTRATO	TERMINI DE SOLO	TERMOS DO SUBSTRATO	ТЕРМИНЫ ДЛЯ СУБСТРАТА (седиментологические)
substrato duro	solum durum	substrato duro	
substrato coerente, saldo, stabile	solum solidum	substrato firme	
substrato molle	solum molle	substrato mole	
substrato elastico	solum lentum	substrato elástico	
substrato coesivo	solum glutinosum	substrato grudento	
substrato sabbioso	solum arenosum	substrato arenoso	
substrato argilloso	solum argillosum	substrato argiloso, argiláceo	
substrato fangoso	solum lutulentum, lutosum	substrato barrento	
substrato argilloso	solum argillosum	substrato argiloso, argiláceo	
aquitrinoso, impregnato d'acqua	solum madefactum, scaturiginosum	encharcado; pantanoso	
substrato sommerso	solum submersum	substrato submerso	
substrato secco, arido	solum siccum, aridum	substrato seco, árido	
substrato di duna	arenae congestus	substrato de duna	
s. a stratificazione incrociata	–	s. de estratificação cruzada	
substrato deltaico	–	substrato deltaico	
cercine, bordo di rimpiazzo		borda, rebordo	
mezzaluna [di sabbia]	lunula arenae	meia lua [de areia]	
subimpronta	–	subpegada	
TERMINI STATISTICI	VERBA STATISTICA	TERMOS ESTATÍSTICOS	СТАТИСТИЧЕСКИЕ ТЕРМИНЫ
analisi della varianza	variationis inquisitio	análise da variação (da variância)	Дисперсионный Анализ
assimmetria	inaequalitas	assimetria	Асимметрия
bias	proclivitas	viés	
binomiale (distribuzione)	binominis (partitio)	binomial	Биномиальный
–	circumcludere	–	Ограничить
chi quadrato	chi quadratum	chi quadrado	Хи-квадрат
intervallo di confidenza	fidei intervallum	intervalo de confiança	Доверительный интервал

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132. continuo	Stetig	continuous	continu
133. correlación	Korrelation	correlation	corrélation
134. coeficiente de correlacción	Korrelationskoeffizient	correlation coefficient	coefficient de corrélation
135. covariancia	Kovarianz	covariance	covariance
136. grados de libertad	Freiheitsgrad	degree of freedom	degré de liberté
137. dependencia	Abhängigkeit	dependence	dépendance
138. discontinua (distribución)	Unstetig, unstetige Verteilung	discontinuous (distribution)	discontinue (distribution)
139. discreta (variable)	diskret	discrete (variate)	discrète (variable)
140. dispersión	Spannweite, Dispersion	dispersion	dispersion
141. distribución	Verteilung	distribution	distribution
142. función de distribución	Verteilungsfunktion	distribution function	fonction de répartition
143. autovalor	Eigenwert	eigen value	valeur propre
144. error	Fehler	error	erreur
145. estimación, estima	Schätzung	estimation	estimation
146. evento, suceso	Ereignis	event	evênement
147. esperanza (matemática)	Erwartung (swert)	expectation (value)	espérance (mathématique)
148. ajuste	Anpassung	fit	ajustement
149. frecuencia	Haüfigkeit	frequency	fréquence
150. función de densidad	Wahrscheinlichkeitsdichte	frequency function	densité de probabilité
151. distribución de frecuencia	Haüfigkeitsverteilung	frequency distribution	distribution de fréquence
152. histograma	Säulendiagramm	histogram	histogramme
153. independencia	Unabhängigkeit	independence	independance
154. intervalo	Intervall	interval	intervalle
155. cuadrados mínimos	kleinste Quadrate	least square	moindres carrés
156. riesgo	Niveau	level	seuil
157. matriz	Matrix	matrix	matrice
158. máxima verosimilitud	Maximum likelihood (Methode)	maximum likelihood (method)	maximum de vraisemblance
159. media	Mittelwert	mean	moyenne
160. medible	messbar	measurable	mesurable

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ Н.Н.
continuo (agg.), continuum (sost.)	continuus (adiect.) continuum (subst.)	contínuo	непрерывный
correlazione	congruentia	correlação	корреляция
coefficiente di correlazione	causa congruentiae	coeficiente de correlação	коэффициент корреляции
covarianza	variatio conjuncta	covariância	ковариация
grado di libertà	libertatis modus	grau de liberdade	степень свооодьı
dipendenza	consecutio	dependência	зависимость
discontinua (distribuzione)	intermissa (partitio)	descontínua (distribuição)	разрыв, дискретное распределение
discreta (variabile)	discreta (variatio)	discreta (variável)	дискретньи
dispersione	dispersio	dispersão (amplitude)	рассеянность дисперсия
distribuzione	partitio	distribuição	распределение
funzione di distribuzione	partitionis munus	função de distribuição	функция распределения
valore proprio	proprium pondus	valor próprio, autovalor	сообственное значение
errore	error	erro	ошибка; погрешность
stima	aestimatio	estimativa	оценка
evento	eventus	evento	событие
aspettativa, previsione	fides (mathematica)	esperança matemática (probabilidade fiducial)	математическое ожидание
rettifica	correctio	ajuste	критерий различия
frequenza	crebritas	freqüência	частота
funzione di frequenza	crebritatis munus	função de freqüência	плотность распределения
distribuzione di frequenza	crebritatis partitio	distribuição de freqüência	статистическое распределение
istogramma	histogramma	histograma	гистограмма
independenza	libertas	independência	независимость
intervallo	intervallum	intervalo	интервал
minimi quadrati	minima quadrata	mínimos quadrados	наименьшие квадраты
livello	gradus	nível	уровень
matrice	forma	matriz	матрица
massima verosimiglianza	summa probabilitas	variação máxima	метод правдоподобия
media	media ratio	média	среднее (значение)
misurabile	computabilis	mensurável	измеримый

CASTELLANO (ESPAÑOL) R.M.C.	DEUTSCH H.H.	ENGLISH W.A.S.S.	FRANÇAIS G.R.D.
161. mediana	Zentralwert	median	médiane
162. momento	Moment	moment	moment
163. distribución normal	Normalverteilung	normal distribution	distribution normale
164. número (de elementos)	Zahl (der Einheiten)	number (of units)	effectif (nombre d'éléments)
165. parámetro	Parameter	parameter	paramètre
166. correlación parcial	partielle Korrelation	partial correlation	correlation partielle
167. población	Population	population	population
168. potencia	Potenz, Mächtigkeit	potency	puissance
169. probabilidad	Wahrscheinlichkeit	probability	probabilité
170. proceso	Prozess	process	processus
171. azar	Zufall	random	hasard
172. variable aleatoria	Zufallsgrösse, -variable	random variable	variable aléatoire
173. rango	Rang	rank	rang
174. razón	Verhältnis	ratio	rapport
175. regresión	Regression	regression	regression
176. muestra	Stichprobe	sample	echantillon
177. conjunto	Menge	set	ensemble
178. significación	Signifikanz	significance	signification
179. desviación standard	Standardabweichung; Streuung	standard deviation	écart-type
180. error standard	Standardfehler des Mittelwertes	standard error	erreur-type de la moyenne
181. estadística	Statistik	statistic	statistique
182. tabla	Tafel	table	tableau
183. test, prueba	Test	test	test
184. variabilidad	Variabilität	variability	variabilité
185. variable	variable	variable	variable
186. variancia	Varianz	variance	variance
187. vector	Vektor	vector	vecteur

ITALIANO G.L.	LATINUS G.L.	PORTUGUÊS G.L.	РУССКИЙ Н.Н.
mediana	mediana ratio	mediana	медиана
momento	momentum	momento	момент
distribuzione normale	communis partitio	distribuição normal	нормальное распределение
numero (dei casi)	numerus (rerum)	número (de elementos)	число (единиц)
parametro	parametrum	parâmetro	параметр
correlazione parziale	congruentia imperfecta	correlação parcial	частичная корреляция
popolazione	incolae	população	популяция
potenza	potentia	potência	степень; мощность
probabilità	probabilitas	probabilidade	вероятность
processo	processus	processo	процесс
caso	casus	acaso, aleatoriedade	случай
variabile casuale	variatio anceps	variável aleatória	случайный вариант
classe	genus	classe	ранг
rapporto	ratio	razão (quociente)	отношение, (частное)
regressione	regressus	regressão	регрессия
campione	specimen	amostra	выборка
insieme	summa	conjunto	множество (совокупность)
significatività	significatio	significância	значимость
scarto quadratico medio	media quadrata declinatio	desvio-padrão	стандартное отклонение
errore standard della media	communis error mediae rationis	desvio médio	стандартная ошибка среднего значения
statistica	statistica	estatística	статистика
tabella	tabella, tabula	tabela	таблица
test	periclitatio	teste	тест; критерий; испытание
variabilità	mutabilitas	variabilidade	изменчивость
variabile	mutabilis	variável	переменная
varianza	variatio	variação, variância	дисперсия
vettore	vector	vector, vetor	вектор

Discussion of the Terms and Methods

by Giuseppe Leonardi
(with the collaboration of the other authors)

1 – ICHNOLOGY. The study of the traces of the activity of organisms.

2 – NEOICHNOLOGY. The study of the traces of activity, produced by organisms presently living (modern biogenic structures).

3 – PALAEOICHNOLOGY. The study of the fossil traces of the activity of organisms formerly living (fossil biogenic structures). "... we really mean that we are interested in the goodness of fit between recent and ancient traces and tracemakers: the kind of creatures that made the traces; the conditions under which these organisms lived; how, where and when the traces were made and preserved; what influences these processes had upon other organisms and the chemical and physical environment; and how all this information can best be used to enrich our practical knowledge of geology and biology" (Frey, 1975, page 13).

Palaeoichnology can be divided into: palaeoichnology of plants, of vertebrates and of invertebrates. The topic of this glossary is the palaeoichnology – and in particular the footprints – of the tetrapods, that is, of the vertebrates exclusive of the fish and fish-like classes.

4 – ICHNOFAUNA. A fauna whose composition is indicated (wholly or largely) by the traces of the activity of its component animal species. When speaking only of fossil traces it might be more proper to use "palichnofauna" (or palaeoichnofauna). "Ichnofauna" has an ampler meaning than "ichnocoenose": it can be used for the trace fossil association either from one level or from a complete series.

5 – ICHNOCOENOSE (or ICHNOCOENOSIS). An assemblage of fossil traces representing the activities of an association of living organism. In our case we can talk more correctly of a palaeoichnocoenose (or palichnocenose, or palichnocenosis), which means an assemblage of trace fossils, showing evidence of an assemblage of formerly living tetrapods, some of which may have left no other fossil evidence of their existence. "Ichnocoenose" is properly used for the trace fossil association from the same level only.

6 – ICHNOFOSSIL (or "trace fossil" or "lebensspur"). The evidence of the activity of a fossil organism preserved in an inorganic or organic substrate. The ichnofossils that are the objects of this glossary and manual are impressions made by parts of the body (principally the feet) of active tetrapods (excluding taphoglyphs, the passive impressions into a sediment of the whole or part of the bodies of dead animals).

7 – ICHNOGENUS. A parataxon (or ichnotaxon) that contains one or more ichnospecies. Its name is a substantive in the singular number, or a word treated as such. Its definition is wholly morphological and implies no definite taxonomic relationship. The ichnofossils of a certain ichnogenus may not correspond to a trackmaker of only one genus, but may be the evidence of similar activity by trackmakers of two or several genera. In the palaeoichnology of tetrapods, as in palaeontology in general, the tendency is to give greater importance to the genus than to the species; thus the fundamental ichnotaxon is the ichnogenus.

8 – ICHNOSPECIES. The ichnotaxon of the lowest level normally recognized (though Sarjeant and Kennedy, 1973 recognize also the varietas or variety). The name of an ichnospecies is a binary combination, consisting of the name of the ichnogenus followed by a single specific epithet; this may be in adjectival form and agreeing with the generic name grammatically, or it may be in genitive form. It is not always easy to define exactly an ichnospecies because of the variability of the extramorphological parameters. A "splitter" might institute various ichnospecies (or even ichnogenera) for only one trackway of a variable pattern, especially if it should be found divided up into isolated fragments, or should indicate variable behaviour (walking with all digits impressed, running with only one or few digits impressed, jumping or just sitting).

9 – MORPHOFAMILY (or form-family). A group of ichnogenera that presents morphological affinities. The morphofamily does not necessarily include trackways whose makers belong to the same family, or even order, of Linnaean systematics and nomenclature *sensu stricto*, because the criteria of classification in our case is fundamentally morphological and based on relatively marginal characters. The term is rarely used; and indeed Sarjeant and Kennedy (1973) considered that there should be no formal groupings of ichnotaxa above the ichnogeneric level.

10 – TRACKWAY (plates I; II; III; IV, A; IX, A-J; X, A-D). A series of successive footprints left by an animal on the move. In a technical sense, a trackway is usually understood to consist of a minimum of three sequential sets of footprints in quadrupeds and three sequential footprints in bipeds. With only two consecutive sets or footprints, the direction of the gait of the trackmaker and the width of the trackway can be extrapolated from the relative orientation of the footprints. With merely one set or a single footprint, the pattern can hardly ever be reconstructed. In French, the term "voie" is used for a group of two consecutive sets (left-right or right-left). The trackway is thus a succession of "voies".

11 – **TRACKWAY PATTERN.** The trackway pattern is the complex of characteristics of the trackway (with the exception of those characteristics belonging specifically to the manus and pes). It includes the relative position and orientation of the prints, the width of the trackway, the presence and character of tail traces, etc.

In some languages, such as Italian and Latin, there is no satisfactory translation for "pattern". Borrowed through analogy from structural geology, "stile" in Italian seems to be suitable. For lack of a better word in Latin, "caracter" is accepted. In Portuguese, "fisionomia" is satisfactory.

12 – Hunters in different countries use various terms to indicate the **CHARACTERISTICS OF THE TRACKWAYS (plate III).** The first term on the list for this item (for ex.: Schnüren) refers to trackways in which sets or footprints are all crossed by the midline (the Cervidae; many theropods; some chirotherians) (plate III, F). The second (for ex.: Schränken) indicates trackways in which the sets are shown alternately to the left and the right of the midline; this is the most common type in fossil trackways (plate III, E). The third term (regular) refers to trackways in which the sets are separated by equal distances (plate III, A-B); the fourth term (irregular) refers to the opposite case (plate III, C-D).

13 – **TRACKMAKER.** This term is used when referring to the animal that produced the trackways, by means of active contact with the substrate (plate IV).

14 – **REFERENCE POINTS (plate I).** Any homologous points can be used as points of reference or of measurement. Normally the best reference points are the distal extremities of digit III, the mid-points of the metapodial-phalangeal pads of the III radius or the mid-point of the segment joining the hypexes of the III digit. When dealing with long digits, it is better to use the mid-point of the pad referred to above, owing to the flexibility of such digits. In some cases, it is better to choose the geometrical **MID-POINT** of the footprints, as, for example, when measuring the foot-hand distance or when it is necessary to measure trackways in which the footprints are poorly impressed or preserved, obscuring morphological details (plate I, 3rd set).

15 – **MIDLINE.** An imaginary trace of the sagittal plane of the trackmaker onto the substrate (plates I-II). This imaginary line is equidistant between the footprints of a rectilinar trackway. However, when dealing with a curvilinear trackway or with trackways of animals with a sprawling gait or a serpentine motion, this line may present periodic sinusoidal curves.

16-18 – Each of the terms discussed here presents different problems in different languages. There exist words in the popular or technical vocabulary of some of the languages to describe the pendular motion of the leg, from the lifting to the planting of the foot, as well as words to describe the distance between corresponding foot positions or footprints. In English, for example, "stride", a term employed by the early surveyors, is used. In French, "enjambée" is accepted. In Latin, "passus", of military origin and understood in the expression "milia (passuum)", is the accepted term. (It is interesting to note that it is from "milia" that "mile" was derived, originally meaning a distance of a thousand strides). In languages in which suitable specific terms cannot be found, modifiers must always accompany the noun. This adjective-noun phrase is treated as one term. In some cases, the adjective-noun (or noun-adjective) structure was adopted through its usage in the common or technical vocabulary for non-ichonological purposes. (To illustrate the point, in Spanish "paso doble" was originally a military term and subsequently applied to a dance). As a result of the improper use of these three terms, there exists a good deal of confusion. Therefore, it is extremely important that, once their use and meaning have been established, they be used only in that manner.

16 – **STRIDE (plates I-II).** In a general sense, this is a pendular movement of the leg which is completed when the foot regains its starting position; or the distance covered during this movement. From an ichnological point of view, a stride is the measure of the segment that unites two corresponding reference points of two consecutive footprints on the same side. This segment is more or less parallel to the midline; measured in that direction, it is equal to twice the pace (see next no.). In some languages there are various terms possible; however, it is recommended that one be chosen and used in a consistent fashion, to avoid possible ambiguity of meaning. The length of stride is very often constant in the trackways. However, it is variable in relation to the type of gait and to the speed of movement within the same gait. This last relationship is indicated by the formula: $\lambda / h \pm 2.3(v^2/gh)^{0.3}$, where λ = stride length; h = height of the hip from the ground; v = the velocity of the animal; g = the acceleration of free fall (Alexander, 1976).

17 – **PACE (plates I-II).** The distance that separates two corresponding reference points in two consecutive footprints of a left pes and a right pes (or left manus and right manus), projected upon the midline. This measurement appears of little value, since its average corresponds to half the length of an average stride. The use of the words corresponding to pace in the different languages can still be maintained; but these terms should generally be clarified by "oblique" or corresponding terms when referring to the measurement to be discussed next. In Portuguese, "meio passo" should be used, since it is unequivocal, even though there are still some obvious flaws: as it stands, one "passo duplo" (literally: double pace) might be expected to equate to four "meio passo" (literally: half-pace), whereas, obviously, it is equal to only two. In English, however, "pace" is always (or almost always) used in the meaning of no. 18.

18 – **[OBLIQUE] PACE (plates I-II).** The distance between the impression of the right manus (or right pes) and the left manus (or left pes): measurement of pace length is thus oblique to the midline of the trackway. In Portuguese, Italian and Latin, the terms "passo", "passo", and "gradus" respectively have a very general meaning and should always be modified by the adjectives "obliquo", "obliquo" and "obliquus", or "transversus" (respectively) to clarify when they are meant to indicate the measure of the distance (oblique in relation to the midline) between reference points of the opposite members. The same does not apply in English, where "pace" will suffice. The French term "envergure" does not seem appropriate as, when correctly used, it indicates the maximum span between the tip of two members (especially wings and arms, and to a lesser extent, legs), whereas generally this is not the implication.

19 – **DISTANCE BETWEEN MANUS AND PES (plates I-II).** The distance between the projections upon the midline of the centres of the autopodia of a set. In this case, the reference points must be the mid-points (no. 14) of the footprints, because homologous points between a hand and a foot do not truly exist. The value of this measurement must appear as a negative number in the case of overstep. In the case of large quadrupeds like sauropods, the hind foot may obliterate much of the impression of its associated manus track. In that case, the manus-pes distance can be measured using the anterior edges of the manus and pes as reference points. However, if the pes is substantially larger than the manus, measuring the manus-pes distance in this manner will give lower values than when track centres are used as reference points. When possible, it is desirable to measure the manus-pes distance both ways. This would enable one to convert measurements

based on track margins to estimates where the latter measurement cannot be made directly. The total length of the set, measured parallel to the midline, could also be considered (Heyler & Lessertisseur, 1963).

20-22 - The WIDTH OF A TRACKWAY (plates I-II) can be measured in several ways, all of which will be reviewed here. In some cases, indeed, it is useful to record the trackway width in several different ways. Once again it is important that, once the meaning of these terms be established, they be used consistently; and it is very desirable to agree upon an unanimous and coherent use at an international level. The choice between the different methods for this measurement depends on the state of the impression and the conservation of the material.

20 - WIDTH OF PACE (plates I-II). The distance between the mid-points of two consecutive footprints of two hands (or two feet) of the opposite side, projected upon an axis perpendicular to the midline. The terms in the French, Italian and Portuguese columns are taken from railroad vocabulary.

21 - EXTERNAL TRACKWAY WIDTH (plates I-II). The total width, i. e. the distance between the exterior (lateral: see no. 86) tangents to the footprints, taken parallel to the midline. However, whilst in theory the tangents in a trackway are parallel, in practice this is not always the case. It is therefore useful to take several measurements of the trackway width and to record the average of these measurements. This applies also to the measurement discussed in numbers 20, 22 and 23.

22 - BREADTH BETWEEN TRACKS (plates I-II). The measurement of the distance between the parallel, interior (medial; see no. 85) tangents to the closest footprints of two consecutive sets of opposite sides. In agile animals, especially bipeds, the internal width of the trackway is often zero or less than zero; in this last case, these values should be recorded as negative numbers. The Portuguese words "vão" and "luz", the Italian "luce", the Latin "lumen" and the French "lumière", which normally apply to bridges and windows, etc., are excellent for expressing this concept.

23 - INTERMANUS OR INTERPEDES DISTANCE (plates I-II). The measure of the distance between the internal (medial) parallel tangents to two consecutive left-right footprints of either the hand or the foot. Instead of the term "interpes" proposed by Peabody (1948), it is better to use "interpedes" for Latin grammatical reasons ("intermanus" is a valid and grammatically correct term). It is obvious that, in each trackway, the intermanus, or alternatively the interpedes, distance corresponds to the internal width of the trackway (breadth between tracks).

24 - PACE ANGULATION (plates I-II). The angle that is constituted by the segments joining corresponding points (preferably the centre of the metapodial-phalangeal pad of digit III) of three consecutive footprints of the pes (or of the manus), i.e. right-left-right or left-right-left. Its value, on the same trackway, is frequently constant, at least whilst the same type of gait is maintained; but its value is directly proportional to that of the velocity. This relationship is similar to that which exists between stride length and velocity (indicated above, no. 16). The study of modern trackways shows that, in the same species, the value of the pace angulation depends on age, sex, state of health, bone fractures, etc., and on the gait; but the measure does not generally present important differences between individuals. The angle of the pace is low on wide trackways with short strides; it is high on narrow trackways with long strides (rising in some theropod trackways to 180^{o}). The angle of the pace of the hand is bigger than that of the foot when (as is usual) the forefeet are closer to the midline than the hindfeet are. Only in rare instances (with therapsids especially) is the opposite the case.

25 - The series of alternating angles between the footprints in a track forms an **ANGULATE PATTERN** representing average pace angulation (Peabody, 1959, page 6). It seems to us undesirable to use "angulate pattern", since the corresponding terms "stride pattern", "pace pattern" etc. are neither used nor necessary. It is always best to work with the average values of the various measurements thus far discussed, whenever there is sufficient material to work with. We consider it easier to speak of the average stride, average pace, average pace angulation, etc. and to represent the values with the following symbols for use in charts, graphs, etc.: $\overline{\text{M}}$ stride, $\overline{\text{M}}$ pace, $\overline{\text{M}}$ pace angulation, and so forth.

26 - OVERSTEP (plate V, H). The overstep of the foot in relation to the hand print, *sensu lato*, can either be primary, secondary, or tertiary. Taken *sensu stricto*, however, this term applies only to primary overstep; namely, the situation in which, in the same set, the print of the pes is so placed as to appear ahead of the print of the manus.

27 - OVERLAP (plate V, A-D). "Placing of the pes upon part or all of the manus impression: **(a) PRIMARY.** Normal overlap of short-coupled body in which the pes is implaced on part or all of the manus impression, immediately following retraction of manus; **(b) SECONDARY.** Overlap such as occurs in long-coupled animals, in which the glenoacetabular distance is so long relatively that at the instant of emplacement, the pes is one full stride behind the manus but nevertheless eventually overlaps the manus impression; **(c) TERTIARY.** Overlap such as occurs in animals so extremely long-coupled that, at the instant of emplacement, the pes is two full strides behind the manus (Peabody, 1959, page 6). The overlap can be **MARGINAL, PARTIAL,** or **TOTAL** (plate V, B-D) if the footprint marginally covers, partially covers, entirely covers the hand print.

28 - DIVARICATION OF FOOT FROM MIDLINE (plate I). This is the convex angle formed by the longitudinal axis of the foot (refer to no. 33) with the midline (refer to no. 15). The vertex can be located either posteriorly or anteriorly to the direction of the trackway, depending on whether the foot is pointed outwards or inwards. The value of this measurement can be positive, zero, or negative. We propose to consider as positive the outward divarication and as negative the inward divarication. One must make the distinction between the orientation of the longitudinal axis of the entire footprint and the direction in which the digits are pointed.

29 - FOOTPRINT (plate V, F-G; VI; VII; VIII, G-H). This term defines the impression in the substrate of the autopodium (no. 79), or of part of the autopodium, of a tetrapod. This impression presents itself as a **CONCAVE EPIRELIEF** (plate VI, A-1) on the upper surface of a stratum. In ichnological practice, usually we use this term also to indicate the cast, the convex impression on the lower surface of the adjacent superior stratum, which presents itself as a **CONVEX HYPORELIEF** (plate VI, A-2). Some terms in the different languages are used specifically to indicate single foot impressions, as for example, "footprint" or "orma". However, there are terms that are, in themselves, less specific and must be clarified, as for example "empreinte *de pas*" in French. In Portuguese, "pegada" is used to indicate foot impressions, yet it can be used also, in either the singular or the plural, to refer to an animal's trackway. In Portuguese also, "rastro" and "rasto" have a general meaning and are used also to refer to those impressions made by other parts of the body, such as the tail. If "rastro" and "rasto" appear in the plural form, they may ever refer to the trackway. The German word "Fährten", widely used in specialized literature to designate isolated footprints, is correctly applied only to a trackway. (Epirelief, hyporelief: after Seilacher, 1953).

30-31 - MOULD AND CAST (plate VI, A). To indicate these concepts, some languages have explicit nouns, as for example the

English language; in other languages, it is necessary to add an adjective. It is desirable to avoid, in all languages, the concepts and terms "positive" and "negative" impressions, because these are ambiguous and inexact. In reality, the mould is the negative of the animal's foot and the cast is its positive copy. It is simpler to note that the mould is always a concave epirelief; the cast is always a convex hyporelief.

32 – SET (plate V, E). The footprints of the hand and the foot of the same side, impressed in the same cycle of movement. In the trackways of very long-coupled animals, beside the real sets, there are generally pseudo-sets in which hand and foot belong to different cycles (set *sensu lato, sensu* Peabody, 1959). The term "lote" in Spanish should be avoided and reserved only to indicate a different phenomenon (cf no. 102). The term "pair" in some columns is not perfect because it should indicate two equivalent impressions, whereas the prints of the hand and foot only may look alike or are analogical; but it is used in default of a better term.

33 – FOOTPRINT LONG AXIS (plate V, F). As a rule, the axis of a footprint is not a true axis of symmetry, but rather a conventional axis that is used merely as a basis for measurements. The measurements of the length and width of the footprint, of palm and sole and of the divarication of the foot from the midline, depend on this axis. There is as yet no agreement on how to establish the longitudinal axis of a footprint. We propose that the footprint long axis should always correspond with the axis of digit III (in accordance with definition no. 45).

Because of the variety of morphologies encountered, the following additional rules are presented: (i) In the event that digit III appears only as a round distal pad (or claw impression) isolated from the sole pad, the long axis of the foot should be taken as the line that passes through the centre of the round pad (or claw) of digit III and through the centre of the sole pad; (ii) If digit III does not appear in the impression, or if it is too short to give an indication of the axis, the long axis of the foot becomes the anterior-posterior axis of symmetry of the footprint; (iii) In cases where only the round distal pads of the digits are present (the sole pad is absent), the axis becomes the line which passes through the pad of digit III and which corresponds best with the anterior-posterior axis of symmetry of the footprint.

Naturally there exists a great deal of subjectivity especially in the ideal rectification of digit III when it is bent. However, this limitation is outweighed by the fact that constant reference, direct or indirect, of all the measurements mentioned above, is made to the footprint long axis, which is in turn related only to digit III. It is always convenient to illustrate in any publication, by means of drawings, which is the longitudinal axis of any particular footprint according to the author's understanding.

34 – TRANSVERSE AXIS (plate V, F). This is the axis perpendicular to the long axis. Parallel to the transverse axis, the following measurements are taken: width of the footprint and width of the palm and sole.

35 – METAPODIAL-PHALANGEAL AXIS (Cross axis) (plate V, F). This axis is conceptually different from the transverse axis (although at times they may correspond). This axis is the straight line that crosses as close as possible to the center of the metapodial–phalangeal pads of digits I-IV (and occasionally I-V). This axis allows measurement of the cross-axis angle (refer to no. 57) and defines the anterior limit of the palm and sole. To prevent confusion, it is best to employ this term and not to use the term "cross axis" (Peabody, 1948, fig. 1), since the latter term does not have an unequivocal anatomical basis.

36 – FOOTPRINT LENGTH (plate V, F). The distance between the most anterior point and the most posterior point of the footprint, measured parallel to the long axis of the footprint (refer to no. 33). The true footprint length can be masked by heel drag or by scrape-marks of nails (claws) in the substrate. According to the definitions given below (see nos. 39, 42, 50), the sum of the palm or the sole and the length of the phalangeal portion of digit III may differ from the length of the footprint.

37 – FOOTPRINT WIDTH (plate V, F). The distance between the furthest medial point and the furthest lateral point of the footprint. It is measured parallel to the transverse axis of the footprint (see no. 34); that is, at right angles to the long axis (see no. 33). See also nos. 85-86.

38 – PALM (plate V, F). The surface between the posterior, medial and lateral (see numbers 85 and 86) margins of the forefoot (manus) print and the metacarpal-phalangeal axis.

39 – PALM LENGTH (plate V, F). The distance between the furthest anterior and the furthest posterior points of the palm, measured parallel to the long axis of the footprint (refer to no. 33).

40 – PALM WIDTH (plate V, F). The distance between the furthest lateral and the furthest medial points of the palm, measured parallell to the transverse axis of the footprint (refer to no. 34).

41 – SOLE (plate V, F). The surface between the posterior, medial and lateral (see nos. 85 and 86) sides of the hindfoot (pes) print and the metatarsal-phalangeal axis.

42 – SOLE LENGTH (plate V, F). The distance between the furthest anterior point and the furthest posterior point of the sole, measured parallel to the long axis of the footprint (refer to no. 33).

43 – SOLE WIDTH (plate V, F). The distance between the furthest lateral and the furthest medial point of the sole, measured parallel to the transverse axis of the footprint (refer to no. 34).

44 – DIGIT (plate V, G). In languages where this is possible, it is easier to use the generic term ("digit" in English) when no special reference is made either to front or hind legs. However, when wishing specifically to refer to the digits of the fore or hind feet, the appropriate terms should be used ("fingers" and "toes" in English and their corresponding terms). The Roman numerals I, II, III, IV, and V should be used when referring to digits. Digit I is furthest medial (pollex; thumb or hallux); digit V is furthest lateral (little finger or toe).

45 – DIGIT AXIS (plate V, G). The imaginary line that passes through the centre of the metapodial-phalangeal pad (or, if that pad is not present, the mid-point of the furthest proximal section of the digit) and that: (i) If the digit is straight, serves also as its (approximate) axis of symmetry; (ii) If the proximal section of the digit is straight and the distal section bent, serves also as the axis of symmetry (approximate) of that proximal section; (iii) If the digit is completely bent, corresponds to the axis of symmetry of the digit, ideally rectified. In this last case it is evident that, in choosing the axis, there is much subjectivity on the part of the investigator. Determination of the axis of the digit is necessary in order to measure the length of the digit. The axis of digit III defines the axis of the autopodium and/or the footprint and thus facilitates the making of any other measurements. It is important to indicate the axis used by means of drawings.

46 – HYPEX (plate V, G). "The apex of the re-entrant angle between digits" (Peabody, 1948, page 299). This term can be used in all the languages in this glossary. Plural: "hypexes" or "hypices".

47-51 – (plate V, G). We find various ways in which **LENGTH OF THE DIGITS** is measured in different ichnological publications. It is not possible always to measure by one method; different criteria must be considered, according to the shape of the footprint and its preservation. Therefore, it is always important to indicate the method employed by means of drawings. Whenever possible, it is better to measure the length of the phalangeal portion of the digit (refer to number 50). In some cases it may be advantageous to utilize several different methods of measurement.

47 – DIGIT LENGTH (or length of digit) (plate V, G). This is the measure of the line that unites the point of the nail (or claw or hoof) with the hind point of the last visible digital pad belonging to the digit under consideration. This measurement is not the real length of a crooked digit since, in such case, the measurement should be made along the chord and not parallel to the digit's axis.

48 – FREE LENGTH (plate V, G). This refers to the measure (taken along the chord) of the segment that joins the distal extremity of the digit to the mid-point of the distance between two adjacent hypices. In the case of digits I and V, (digits II and III in most of the tridactyl footprints), which have only one adjacent hypex, this last point can be readily substituted by the mid-point of the line perpendicular to the axis of the digit that passes through the adjacent hypex.

49 – (COMMUNAL LENGTH) (plate V, G). This term, introduced by Peabody (1948, fig. 1) corresponds to the difference between the measurements of the digit length (see no. 47) and of the free length (see no. 48). Its use must be avoided, because it has neither anatomical significance nor any practical usefulness.

50 – LENGTH OF THE PHALANGEAL PORTION OF THE DIGIT (plate V, G). This length is the measure of the segment that joins the distal extremity of the digit with the corresponding mid-point of the metapodial-phalangeal pad. When the imprint of this pad is present and clearly marked, it is helpful to quote this measurement, since it is very significant from an anatomical view point. It is measured along the chord.

51 – TRUE LENGTH OF THE DIGIT (or length of digit *sensu stricto*) (plate V, G). This is the length of the phalangeal part of the digit (refer to no. 50) when the digit is straight. This measurement should be taken, whenever possible, because it corresponds most closely to the anatomical length of the digit.

51 bis – WIDTH OF THE DIGIT IMPRINTS. This is not an important figure. There is a great deal of variation even when dealing with one individual animal, since its gait and the type of soil it passes or has passed over will influence this value. An average of several measurements does have some relative value, since it gives an indication of the relative width of the digits of the same autopodium.

52 – NAIL, CLAW, HOOF (plate VII, A-C). Each of these three terms should be used specifically in the specific cases. A nail is a blunt structure terminating a digit; a claw is a sharply pointed structure; a hoof is a greatly broadened and very blunt structure emplaced in absence (usually) of any digital pad impression.

53-54 – PAD (plate VII, D; see also, for ex., plate V, E). In some languages there exist proper and different terms for palm/sole pads and for digital pads. In other languages (for example in English), it is necessary to add a qualifying adjective to the noun to clarify the usage.

55 – HEEL (plate V, F). This term should be used in the proper sense only when talking about the footprints of animals that are plantigrade (those that place their heel on the substrate). It is sometimes used in an ampler sense, ichnologically, with reference to the end margin of the footprint (even in digitigrade footprints!). In such cases, the term should be employed between inverted commas.

56 – DIVARICATION OF DIGITS (plate V, G; VI, B-D). The angle between two digit axes on the same autopodium or the same footprint. Normally the angles between adjacent digits are measured (partial divarication). Beside these, the angle between digits II and IV (in tridactyl footprints) and the angle between digits I and V (total divarication) are measured. The angles can be acute, right or obtuse; they can have zero or negative values as well (albeit rarely). The interdigital divarication, especially of big footprints, can be measured by means of a contact goniometer. It is highly desirable to show on a diagram the angles measured (plate VI, B-D).

57 – CROSS-AXIS ANGLE(plate V, F). This angle is defined as the angle between the metapodial-phalangeal axis (cross axis) and the long axis of the footprint. Of the four angles formed by these two axes, the cross-axis angle is the lateral and anterior one. It is an important parameter because it is constantly connected with the anatomy of the autopodiu m The measurement taken should be indicated by means of a drawing.

58 – [INTERDIGITAL] WEB. (plate VII, G). This is characteristic of partially or wholly aquatic animals; because of this, it is an indicator of the environment and an important classification element of the trackmaker. The interdigital web should be recorded as present only when the footprints are of high quality, since frequently the pressure of the adjacent digits in very moist substrates produces pseudo-impressions of interdigital webs. An interdigital web is also present between the thumb and the II finger of apes and humans.

59 – TAIL DRAG (plate III, A and C). A very common phenomenon in the trackways of animals of sprawling gait. It is principally found in small animals, but is, in contrast, extremely rare in the larger reptiles, for example in bipedal or even quadrupedal dinosaurs. (Even in sauropod trackways, only exceptionally are tail drags impressions present). In all probability, the bipedal animal's body in progression stayed parallel to the ground and the tail was lifted up, either parallel to the ground or "en trompette", whilst the quadrupedal dinosaurs seem also to have kept their tail elevated.

60 – MARK, etc.. These are generic terms that should be applied to any impression of a part of an active animal's body in the substrate, other than the autopodia.

61 – DACTYLY (plate VII, E – I). The number of toes of a footprint and/or corresponding autopodium.

62-63 – NUMBER OF DIGITS (plate VII, E – I). The terms cited in this item are used when referring to the autopodium, or by extension to the footprint. When a footprint with impressions of, say, four digits, is judged, by its structure, to belong to an animal with pentadactyl feet, it is better not to speak simply of a tetradactyl footprint, but to use the expression "functionally tetradactyl" or something similar. The different forms in Spanish, Portuguese and Russian can be used indifferently.

64 – AXONY (plate VII, J – M). The fact or the effect of a footprint having the axis in a determined direction. The axis, in this case, is not the long axis (the basis for measurement, according to definition no. 33) but rather the axis of the most important digit. This corresponds generally to the axis that receives the greatest load and, at times, coincides with the long axis.

65-66 – POSITION OF THE AXIS (plate VII, J – M). ENTAXONIC is applied to a footprint whose most important digit is medial (no. 85) (digit II or I); the entaxonic condition, present in human feet, is very rare in other animals. **MESAXONIC** is applied to a footprint whose most important digit is the central digit, generally digit III. This is quite common in Archosauria. The **PARAXONIC** footprint is that which is either bidactyl or tetradactyl and whose digits III and IV appear to be equally important. This condition occurs only rarely in reptils – *Isochirotherium* is almost paraxonic – but is universal, for example, in artiodactyl mammals. **ECTAXONIC** can define a footprint whose most important digit is external or lateral (no. 86) (most often digit IV), as is very common in Lepidosauria.

Paraxonic footprints are symmetrical, mesaxonic ones are almost symmetrical and ectaxonic ones are markedly asymmetrical, with the digits increasing in length from I to IV. In the entaxonic condition, internal or medial digits predominate, so that these are also asymmetrical. The entaxonic, mesaxonic, paraxonic, and ectaxonic condition of a footprint can be respectively named **ENTAXONY, MESAXONY, PARAXONY** and **ECTAXONY.**

67 – GRADY (plate VII, N – R). The fact or the effect, of a foot having a certain position, either more or less leant on the ground or raised from the ground during the progression and/or in the rest position. This term is usually applied also to the footprints and thus to the trackways.

68-69 – POSITION OF THE FOOT (plate VII, N – R). The terms here discussed refer to the position of the foot during motion. However, they may also be correctly applied to footprints, as happens frequently in ichnological literature. A footprint is **PLANTIGRADE** when the impression is that of a complete autopodium; **SEMIPLANTIGRADE** is the condition where all the footprint but the heel is impressed; **SEMI-DIGITIGRADE** is the condition intermediate between "plantigrade" and "digitigrade", i. e. with only the front portion of palm or sole impressed. (One may employ the terms **PALMIGRADE** and **SEMI-PALMIGRADE** when dealing with fore-feet, but these terms are encountered rarely). The condition described as **DIGITIGRADE** is where only the impression of the entire digits appears; and finally the **SUBDIGITIGRADE** condition is when only part of the digit appears in the impression. **UNGULIGRADE** is used to describe the footprints of animals that use only the tip of the last phalanges for support; the tip is usually covered with a nail or a hoof (= *ungula* in Latin). The word **CALCIGRADE** describes footprints in which the point of deepest impression is the heel. These footprints are generally made while the animal is standing still. Any attempt to distinguish between the various types is affected by some degree of subjectivity on the part of the investigator. The plantigrade, semiplantigrade, semi-digitigrade, digitigrade, subdigitigrade, unguligrade and calcigrade conditions of a footprint (and of a foot) can be named respectively: **PLANTIGRADY, SEMIPLANTIGRADY, SEMI-DIGITIGRADY, DIGITIGRADY, SUBDIGITIGRADY, UNGULIGRADY, CALCIGRADY.**

70 – HETEROPODY (plate VII, T). The condition in which the hand and the foot are dimensionally and morphologically different. This is the most common circumstance (e.g in man, frogs, rabbits).

71 – HOMOPODY (plate VII, U). The condition in which the hand and the foot are dimensionally and morphologically the same. This is a rare circumstance in the reptiles (Therapsida) but is more frequent in mammals (Artiodactyla, some Perissodactyla, Carnivora, etc.).

72 – RIGHT AND LEFT. In the cast or reverse print, the right and left side are obviously inverted. In cases in which this is not clear from the context, it is well to specify the print's position and to use these adjectives consistently.

73 – BODY LENGTH (GLENO-ACETABULAR DISTANCE) (plate VIII, C-F). From the anatomical point of view, this is the distance between the centre of the glenoid cavity and the centre of the acetabular cavity. From the ichnological point of view, the (approximate) measurement of the body length is done in the following way (obviously only for quadrupedal trackways): **(i)** In the case of a primitive alternate pace, at the moment in which the support of the animal changes from one diagonal limb pair to another, all four members are supported on the ground. It can be considered that the body length is, above the midline, the segment that unites the intersection points of the line of the reference points of the hands (the segment that joins homologous points in two successive fore-footprints of the opposite side) and the line of the reference points of the feet with the midline. Starting with the elements of the trackway, the body length (BL) is the same as a half stride (St/2), enlarged by the hand-foot distance (D) or: BL = St/2 + D; **(ii)** When the feet of the same diagonal limb pair are not synchronized in their movement, the animal rests constantly during its progression on three supports. The body length cannot be estimated by using formula i. Observation shows that the glenoid articulation is vertical to one of the anterior autopodia, while the acetabular is found upon the middle point of the line that unites the hind-feet. On the trackway, choosing a section with three sets, the body length can be estimated as the length of the segment of the midline which joins the two following points: a. the projection of the reference point of the more advanced fore-foot to: b. the intersection of the midline with the line that joins the reference points of the two hind-feet of the other two sets. The theoretical value of the body length is equal to 3/4 of the stride length, enlarged by the length of the hand-foot distance, or BL = 3/4St + D; **(iii)** If it is clear that the trackmaker walked in an amble, the body length is the distance between the intersections with the midline of the line of the hands (the segment that joins homologous points in two sucessive fore-footprints of the opposite side) and of the line of the feet (which are not necessarily those that follow immediately the hands); these two lines are more or less parallel. Sometimes there could be a case of pregression of the hand, because the apparent hand-foot sets are not always formed by two footprints emplaced in the same cycle of the progression. The body length is the same, for the amble, as one hand-foot distance (in the case of a short body, the hands of a cycle are closer to the feet of the following cycle, and behind them) or of a hand-foot distance plus a stride, if the hands of two contiguous sets lie slightly beyond the feet of the set that immediately preceeds the two sets referred to above: BL = S + St; **(iv)** Finally, some trackways might have been made by very long-coupled animals (see nos. 74-75), so that the apparent hand-foot sets do not correspond to the same periods of the progression. Whether the animal walked in an amble or an alternate pace, we have to add one or two stride lengths to the body length estimated from above formulae, according to the hypothesis made when talking about, respectively, secondary or tertiary overlap.

The determination of the body length cannot be done exactly, but one may arrive at approximate numeric results. The option between the different hypothesis can be chosen only after a careful examination of the trackways. There are no absolute general rules; each case must be studied separately.

74-75 – COUPLING VALUE (plate V, A). A number derived by dividing the length of the dorsal region (gleno-acetabular distance) by the sum of the length of fore limb and hind limb (apparent limb length, refer to no. 81). This indicates whether the animal is short-, medium- or long-coupled (cf Peabody, 1959, page 6). This value is readily determined in studies of living forms but, in the case of fossil tracks, serious inaccuracies in calculations can arise and the resultant values are of questionable utility. As an example of the relationship between the terms "short-coupled, etc." and the numerical values of the coupling value, the data given by Peabody in his report about salamanders may be mentioned: (1959, fig. 5): *Taricha torosa,* coupling value = .70: short-coupled animal; *Aneides lugubris lugubris,* c.v. = .94: medium-coupled animal; *Aneides flavipunctatus* c.v. = 1.36 to 1.40: long-coupled animal; *Plethodon elongatus* c.v = 1.60 and *Batrachoseps* (several species): c.v. = 2.00 to 2.60: very long coupled animals. Long and very long coupled animals are very rare.

76 – FOOT, etc.. These are general terms indicating either the fore or hind autopodium of a quadrupedal animal. The English word "paw" is used equally either for the hand or for the foot of a quadruped but is should be applied to only a padded foot with claws, as with the cat or dog, not to a hoofed foot.

77-78 – In almost all the languages of this glossary, it is common and correct to use the terms "hand" and "foot", and corresponding terms, when speaking respectively of the front and hind autopodia of animals and of man. In Italian, however, "mano" is generally used only for man: the feet of animals are always referred to as "piede". The term "mano", however could be introduced into the ichnological jargon for practical purposes.

77 – HAND, etc. This term refers to the front autopodium of a tetrapod. If the specific term "hand", or its corresponding terms in other languages, is not used, it is necessary to add to the word "foot" (and to its non-English counterparts) the prefix "front" or "fore". In all languages, the Latin "manus" (plural "manus") may be used to indicate either the anterior autopodium or the corresponding footprint.

78 – FOOT, etc. This term refers to the posterior foot of man and to both autopodia of animals. However, it is too vague when applied specifically to the hind foot of an animal. To avoid ambiguity, therefore, it is wise to clarify it with the prefixes "hind" or "rear". In Portuguese, "pé" can be used opposite "mão", since the common term is "pata". Of course, in all languages the Latin "pes" (plural "pedes") can be used.

79 – AUTOPODIUM. A word of Greek origin that refers to a foot, namely, the sum of **BASIPODIUM** (carpus or tarsus), **METAPODIUM** (metacarpus or metatarsus) and **ACRO PODIUM** (phalanges). It would be improper to use this term to indicate a footprint. Its meaning is general and it should be used either when not wanting to refer specifically to the hand or the foot or in opposition to the leg.

80 – RADIUS/–II, etc. etc. These terms indicate the set of a metapodial and the corresponding digit, or their relative impressions. In Portuguese texts, it would be more appropriate to use the Latin term, although "raio" is acceptable. This applies also in Italian. The English word "digit" may also correspond to radius. The term "radius" should be avoided, in some languages, because it is potentially confusing.

81 – APPARENT LIMBS (plate VIII, A – B). The apparent limb is the length of the straight segment that joins the acetabulum (or the glenoid cavity) to the base of the foot (or the hand) on the ground when, during locomotion (walking gait), the elongation of the legs from the vertical is at maximum. See special chapter in the appendices.

82 – ANGLE OF GAIT (plate VIII, A – B). The angle formed between two associated apparent members (see item 81) in a pace, projected upon the sagittal plane. In a live animal this is very easily calculate but, in considering the trackway of a fossil animal, iet is much more difficult. The extrapolation is done by comparison of the parameters of the trackway with the osteological and biomechanical data of the animals to which the trackways are attributed. The principal data are: the type of articulation of the stylopodia in the girdles, the amplitude of the maximum angle which one member can make above the articulation without dislocating itself, and the different gaits. See also appendices.

83 – PHALANGEAL FORMULA (plate X, G; Table in appendix). A schematic method of representing the number of phalanges of the digits of an autopodium. This is done by listing the number of the phalanges of each digit in order from I to V and separating each number with a hyphen or comma. For example, the fundamental phalangeal formula of the hand of the reptiles is represented as: 2-3-4-5-3. In well impressed and clearly conserved footprints, the phalangeal formula can be often calculated, if the relation that exists between the folds of the skin of the digits and the articulations between phalanges in the animal groups are studied. This calculation can not be made when the digit is covered by a hoof or callus. In some instances (for example, in many Therapsida, the number of phalanges corresponds to the fundamental formula of the reptiles: 2-3-4-5-3(4); but, from a functional point of view, there is a great reduction because many phalanges are reduced to thin discs of bone.

It is obvious that, in a subdigitigrade footprint, the formula can be calculated only in an incomplete form. In this case, mathematical symbols such as $<$, $\geq$, etc. can be introduced into the phalangeal formula. This is very variable in amphibians; in many reptiles it is 2-3-4-5 for the first four digits, but the number of phalanges is variable in the digit V; it is regularly 2-3-3-3-3 in mammals. As for the reptiles, see table in appendix.

84 – DIGITATION. An appendix or an impression of an appendix, with the form of a digit but which is not a digit.

85 – MEDIAL (plate VIII, G – H). This term is applied to the margin of a foot that is nearer to the sagittal (median) plane of the animal body; and to the margin of a footprint that is nearer to the midline of the trackway. Evidently, as this term has an anatomical meaning, it applies always to the margin occupied by the I digit (II in tridactyl autopodia and footprints) and applies also in the cases in which the footprint is bent inward or outward, the nearest margin being the anterior or posterior (cranial or caudal; distal or proximal).

86 – LATERAL (plate VIII, G – H). This term is applied to the margin of a foot that is most distant from the sagittal (median) plane of the animal body; and to the margin of a footprint that is most distant from the midline of the trackway. For the sake of coherence, since this term has an anatomical meaning, it is applied always to the margin occupied by the V digit (IV in tridactyl autopodia and footprints).

87 – DISTAL (plate VIII, G – H). The part of the segment of an extremity that is most distant from the trunk.

88 – PROXIMAL (plate VIII, G – H). The part of the segment of an extremity that is nearest to the trunk.

89 – MEDIAN (plate VIII, G – H). One calls digit III the median digit; the three digits II – IV may be termed "median" in a pentadactyl foot or footprint.

90 – OUTER (plate VIII, G – H). One calls "outer" the digits I and V in a pentadactyl foot or footprint; the II and IV in a tridactyl one.

91 – LOCOMOTION (plates IX; X, A-D). An animal is **QUADRUPEDAL** or **BIPEDAL** when it progresses (or stands still) respectively, on all four limbs or on its hind limbs only; it is **SEMIBIPEDAL** when it is generally bipedal, but the fore limbs are sometimes placed on the ground in the slow gait. These terms apply to the corresponding trackways also.

QUADRUPEDAL TRACKWAY (plates I; II, A, C-D; III, A – F; IX, B – D, G, I – J; X, B-D). The footprints are impressed on both sides of the midline, in hand-foot sets, generally with an alternate rhythm. When the pace is very long, and principally during the gallop, the footprints lie very close together in groups (plate V, H; IX, G, J, K).

SEMIBIPEDAL TRACKWAYS (plate IX, A). The fore-footprints appear on the ground only during slow gait, when the animal stops or sometimes, when it changes directions.

BIPEDAL TRACKWAY (plates II, B; IX, E-F, H, O). The left and right hind footprints are alternate, one in front of the other, on each side of the midline.

Trackways with three feet (rare) represent the passage of crippled quadrupedal animals. One occurrence is known, in the Botucatu Formation (Brazil).

92 – QUADRUPEDALITY, SEMIBIPEDALITY, BIPEDALITY. These terms apply to the condition of an animal (and of a trackway) that is quadrupedal, semibipedal or bipedal.

93 – TETRAPOD. One calls tetrapods all the animals of the classes Amphibia, Reptilia, Aves, Mammalia, whose general structure (actual or original) contains four limbs. Man is a tetrapod, though generally bipedal; so also are whales and snakes. Terms such as "quadrupedal" and "bipedal" point to the posture and gait; the term "tetrapod" has a structural and phylogenetic meaning.

94 – POSITION OF THE LIMBS. Limbs are defined **PARASAGITTAL** when their movement in the gait occurs along vertical or subvertical (parasagittal) planes; **TRANSVERSAL** when the stylopodium (humerus and femur, respectively) moves in a horizontal plane; **HORIZONTAL** when the whole limb moves in a horizontal or subhorizontal plane (Vialleton, 1924).

95 – GAIT. The progression of an animal that results from a succession of paces or bounds made successively in a determined direction. Generally, the animal moves forward; only rarely are trackways that represent a retrocession registered.

96-98 – MANNERS OF GAIT (plates IX – X). SPRAWLING GAIT (plates III, A – D; IV). A gait in which the legs are very far apart; the base being wide, the pace angulation tends to be low. A type of trackway with these characteristics points to a lizard-like animal or to a heavy, slow animal of primitive structure, with legs in a horizontal or transversal disposition.

ERECT GAIT (plate IX, D – E; X, C-D). A gait in which the legs are situated below the trunk and move in a parasagittal plane. The base is narrow and the pace angulation is high, with values that rise to 180°. This gait is proper to agile and rapid pedestrians.

WALKING GAIT (plates I; II, A – D; III, A – B; IX, B; X, B-D). The normal progression, more or less slow, in which the animal (either quadruped or biped) supports itself on the ground, with a variable number of feet. In this gait at least one foot is in contact with the ground at all times. The fundamental types of walking gait are the pace and the amble, in which the support is respectively diagonal and lateral. The walking gait, within the characteristics referred to above, can be slower or more rapid. The trackway is regular and the sets follow each other cyclically and alternately (left, right, left, etc.). With increasing speed, the strides are longer, but the general pattern of the trackway remains the same.

RUNNING GAIT (plate IX, C – E, G, J-K). A rapid progression in which the animal attains a faster speed than even the more rapid walking gait permits. During running, there are moments in which the animal is completely off the ground, whilst at other times it is supporting itself on the ground with a variable number of feet. The trunk of the quadruped passes through curving and extension phases; this gives added energy to that of the legs. In quadrupedal trackways produced by this gait, the footprints are generally united in periodic groups, separated by more or less long spaces. In bipedal trackways, the footprints (of the hind feet) are farther apart one from another than in the walking gait. In trackways of the running gait, generally the autopodium is supported only in part on the substrate: for example, animals that are plantigrade in the walking gait become semiplantigrade or digitigrade when in the running gait. The fundamental types of running gait are the trot and the gallop. Trackways of quadrupedal running gaits are rare in paleoichnology; however, there are good examples in the Jurassic of Patagonia (Casamiquela, 1964) and Brazil (Leonardi & Godoy, 1980).

JUMPING GAIT (plate IX, F, H). A bipedal gait, in which the animal proceeds by jumping on its two hind feet, which can either be side by side or diagonally placed. Sometimes this movement is helped by the tail which serves as a support and propulsion element. Fossil trackways of this type are rare; however they are relatively common in the Botucatu Formation, formed in an arid environment in Brazil (Leonardi & Godoy, 1980). For dinosaurian jumping gait, see Bernier et al., 1984.

[NORMAL] PACE: the most common type of walking gait in quadrupeds. It consists in the shifting forward of a hind leg on one side (for example the left) and the fore leg of the other side, the right in this case (diagonal limb pair), while the fore and hind members of the other diagonal limb pair (respectively right and left in this case), turned backward, push the body ahead.

In reality things are not so simple. Shifting of the diagonal limb pair forward is not always simultaneous for both of the limbs, so that the feet need not touch the ground at the same time. The lower tetrapods include in this pace a phase in which all their four feet lean on the ground, at the moment of change of the diagonal support. In this phase, two feet (for example the right fore-foot and the left hind foot) have plantigrade support; the others have digitigrade support.

The higher tetrapods, which are good walkers, never rest on their four feet simultaneously during the walking pace; there is a phase-displacement between the movements of the fore and hind members of the opposite sides. This permits some species to impress tracks in which the foot is impressed over the hand. In this case, at a quiet pace, the body almost always rests on three supports.

AMBLE. A rarer type of walking gait. The animal shifts forward the two legs on the same side (lateral support) at the same time, while the other two legs sustain the body and thrust it ahead. Really, in the actual ambling gait, a slight phase-displacement exists in the movements of the legs of the same lateral limb pair: the foot shifts with little advancement in relation to the hand. This gait is practised by giraffes, elephants, camels and occasionally by bears, dogs and horses (plate VIII, E-F). Fossil trackways of camelids present this type of progression (Webb, 1972).

TROT. This intermediate gait between the pace and the gallop is characterized by the footfalls being regulary spaced and made alternately by each diagonal limb pair. It is a two-stage gait, separated by an instant of suspension in which the animal is completely clear of the ground. There are various types of trots: principally, the gentle trot and the steady trot.

GALLOP (plate V, H; IX, G, J, K). A rather complex quadrupedal running gait that presents numerous variants. It is the most rapid form of progression. It is developed in four stages. In the case of the horse, for example, it is carried ou in the following sequence: left hind leg, diagonal limb pair, right fore leg, suspension time with the four feet simultaneously in the air. The supports for the animal are constituted in the above stages by two, one, or no autopodia. In the French language, one distinguishes between gallop and "fuite", that is a gallop combined with irregular bounds. Fossil trotting and galloping trackways are very rare.

SPRINGS, RICOCHET, SALTATION, SALTATORY LOCOMOTION. See above under "jumping gait".

SERPENTINE PROGRESSION (plate X, A-B). This is peculiar to animals (principally amphibians and reptiles) that have long bodies and short legs and which advance supporting themselves on the belly, by a wavy movement of the body. It is an extreme form of the sprawling gait. In the snakes and in limbless lizards, this gait attains its most complete expression, following a complete loss (functional or anatomical) of the legs. Fossil trackways of this type are rare, but they are represented, for example, in the Triassic of France (Demathieu, 1977) and in the Jurassic of Patagonia (Casamiquela, 1964).

HALF-SWIMMING (plate IX, L-O). The progression of animals that float in shallow waters and make progress by setting the tips of their feet against the bottom (the submerged substrate). The corresponding trackways are frequently incomplete and irregular. Prints of this type could be made also by animals fully immersed, i.e. "over his head" in water, as hyppos kick along bottom in this way, fully submerged. The footprints consist principally of scratches or indentations left by the claws, digits or hooves. Fossil trackways of this type are common in red-beds of Permian and Triassic Age. Trackways of half-swimming theropods were found in the Connecticut Valley (Coombs, 1980) and in Paraíba, Brazil (Godoy and Leonardi, 1985); hadrosaur trackways of this type occur in the Middle Cretaceous of the Peace River Valley, British Columbia (Sarjeant, 1981). The term "semi-natation", from which corresponding terms in other languages were derived, was proposed by D. Heyler (oral communication).

FLIGHT - TAKE-OFF AND LANDING. Flying animals leave normal trackways when they walk or hop on the sediment. However, in the phases of take-off and landing, a characteristic track may be impressed which includes the hind footprints, generally side by side, and sometimes the impression of the points of the wings, hitting the ground either to increase the take-off energy or to cushion the landing. No fossil tracks of this type have been discovered yet.

99 - STRAIGHT; BENT AND CROOKED: These terms are appliable above all to the digits. The digit can be rectilinear (plate V, E) completely curved (plate VII, H) or crooked (plate VII, S) i.e. rectilinear in the proximal portion and bent is the distal parts; or only the claws may be bent (plate V, B, III digit of the foot). Such curvature (or, alternatively, bending) can be in the medial direction (inward) or in the lateral direction (outward); the latter is less common. (For the way in which to measure curved or crooked digits, see no. 47).

100 - ABDUCTION. The situation of an extremity, digit or any organ (structurally) diverging away from the plane of symmetry (the sagittal plane). In ichnology it is usually applied to digit V, when that digit is diverging away from the symmetry plane of the autopodium.

101 - ADDUCTION. The action that approaches an extremity, or any organ, to the plane of symmetry or to the sagittal plane. It applies to digit V, when it approaches the symmetry plane of the autopodium.

102 - BASE. The limb or limbs which are placed simultaneously on the ground and which constitute the support of the animal at that instant. Such a base can be provided by 1 (unipedal base), 2 (bipedal base) (plate IX, F, H), 3 (tripedal base) or 4 (quadripedal base) feet. If the base is narrow – the step angle then tends to be high – the implied gait is erect and, for this reason, the animal must be agile; if the base is wide – the step angle then tends to below – the implied gait is generally sprawling and the animal an inefficient pedestrian.

103 - FOOTFALL. Application to the ground of one or more members simultaneously.

104 - RETRACTION. One or more members leaving the ground simultaneously.

105 - CYCLE. The lapse of time between two retraction or between two footfalls.

106 - LIMB PAIR. Any couple of limbs. They may be lateral (hand and foot of the same side) or diagonal (hand and foot opposite one another).

Substrate and Footprints

by W.A.S. Sarjeant and G. Leonardi

Footprints are moulds of the feet in the substrate over which the animal passed. A too hard and firm substrate (nos. 107 and 108) will not allow the formation of footprints. If the upper surface of a layer is quite fine grained and cohesive (no. 111), neither too dry (no. 118) nor too wet, an exact impression of the undersurface of the feet may be produced. Not only the major morphological features such as claws, nails or hoofs, but also less promitent ones such as scales or even bristles, may be shown clearly in the mould. When the substrate is too coarse or dry, these details will not be shown (plate X, E-F). When too wet (no. 116) or too yielding (no. 110), the impression may be deformed. If the substrate is submerged (no. 117), the footprints may be severely marred or completely obliterated. In any event, footprints impressed into beaches or in shallow estuaries will be very probably washed out by the next rising or receding tide, whilst prints impressed into sand dunes (nos. 112 and 119) are generally (though not always) obliterated by winds and sandslides.

The best circumstances for preservation are at the end of a phase of flood or high water, when fine sediments in suspension are slowly deposited and then progressively dried and sun-baked. When an inrush of suspension-laden waters follows a cloud-burst, the already hardened footprints may be filled up by the new sediments before they are washed out. Such natural casts, being formed by a coarser and more solid material, have a greater survival potential that the original mould in the argillaceous substrate (no. 115) (plate VI, A).

Soft and wet clay substrates (nos. 109, 113 and 115) may adhere to the animal's feet, causing sucker effects and deforming or destroying the footprints. When walking on a mud substrate (no. 114), the animal's feet normally produce a displacement rim around the footprints (no. 122). When crossing the foreset of a dry sand-dune, the animal's feet always produce sand crescents (no. 123) that point to the dip of the foreset.

On bedding planes beneath the primary footprint bearing surface, subtraces (or "under tracks", also called "ghost prints") may be impressed (no. 124) (plate VI, A-3).

Use of Statistical Methods in Palaeoichnology

by Georges R. Demathieu
(with the collaboration of W.A.S. Sarjeant)

Footprints are not body fossils, as are ammonites, but images of body parts of animals, here the undersurfaces of feet or hands (autopodia). Thus, even in one trackway, the sizes and the measurements of the imprints can vary. This variation is due to: (a) the grain size of the sediment; (b) its physical state (wetness, elasticity, plasticity); (c) the hazards affecting the locomotion of the trackmaker; (d) the effects of diagenesis and (e) errors of measurement. These factors are themselves intricate and, when interacting, they may produce a cumulative result. If the footprints being studied are really well preserved, such factors can have had little influences; consequently, sizes and measurements may show only a small degree of variation.

For the reasons stated above, a single well-preserved footprint cannot be considered as an unvarying object but merely as a representative of a population (hypodigma), i.e. a set of footprints which have the same morphological characters. For statistical purposes, one series of measurements, based on a single footprint, would not be significant. However, where enough footprints are available for measurement, a statistical study is the proper completion to the morphological study. The statistics used need only to be elementary. For each character, one determines (i.) the mean of the sample; (ii.) its standard deviation; (iii.) the coefficient of variability; and (iv.) the confidence interval for the mean (at the 5% level); then one uses (v.) a test to verify or disprove the homogeneity of the sample, i.e. whether the distribution fits the normal law. For this latter purpose two tests can be used: "chi square" of Pearson or the Cramer test. The latter is easier to compute than the former.

The coeficient of variation (= [100 x Standard deviation]/mean) gives an indication of the spread of the distribution, but its mean value can have three different possible implications. A high value ($>25\%$) can signify either (a) that the imprints are badly preserved, (b) that the population is heterogeneous, or (c) that the sample contains animals of very different sizes. In the case of traces made by animals of the same species but of different sizes, it is about 12 to 18%; however, in the case of allometric growth it can reach 25 to 30%. In a single trackway, the coefficient of variation will be low (4 to 9%). It should be noted that the interdigital angles – they are theoretically independent of the size – show generally a higher value for the coefficient of variation than the dimensions, but the cross-axe angles are generally stable. Concerning the length of the digits, a comparison of the variabilities can indicate the importance of a digit in foot support. For example, among the chirotheriids the variability of digit III is often only half of that of digit V; this means that digit V plays a smaller part in foot support than III.

The confidence interval for the mean, at 5% level, gives an indication on the reliability of the mean. It is a parameter more useful for the trackway than for an assemblage of isolated footprints. In the case of allometric growth its value is only an indication of the value of the median size. In this latter case and for comparison purposes, it is better to compute the ratios of the dimensions two by two (for example: length of digit III/length of digit I or whole length/whole width, etc.). By this means, the differences due to size or allometric growth are minimized and thus the calculated coefficient of variation must have been produced by external factors. In addition, the means of two samples can be usefully compared by the Student's test.

If means of ratios are significantly different, one can conclude that the two sets of impressions constitute two ichnospecies. Correlations between characters are interesting also because they give information of the quality of the footprints. It is undoubtedly the case that, in a living animal, there are correlations between the proportions of the different parts of the body. A failure of correlations may be the result of the bad preservation of imprints; where this is not the case, a distribution may have been biased by an external factor. This is particulary true for widths, which are very sensitive to differences in the physical state of the sediment.

Other methods can be used: histograms to represent the distributions; cartesian graphs with two variates, which can give good indications of the relationships between characters; and a variety of others. Thanks to their ready interpretation, such diagrams are useful. They can be employed at the same time as the statistical study.

One could use more sophisticated methods of multivariate analysis: cluster analysis, increasing hierarchical classification, principal component analysis, correspondence analysis, discriminant analysis. However, these methods require computers of high capacity and, from our own attempts to use them, seem not to give results as fine and clear as the others.

Appendices

Apparent Limbs

by Georges R. Demathieu

The notion of apparent limbs was defined first by Soergel (1925). It is the lenght of the straight segment that joins the acetabulum (or the glenoid cavity) to the base of the foot (or the hand) on the ground when, during locomotion (walking), the elongation of the legs from the vertical is at maximum (plate VIII, A–B).

The length of the limb can be estimated first in multiplying the apparent limb by a coefficient. The length of the limb depends on the size of the animal considered and its limb posture. It is higher for small than for tall animals and for hind limbs than for the front. It is higher too among those animals that have a sprawling gait than among the ones which have erect limbs. The observations on skeletons give for this coefficient the following results (fore-limb; hind-limb): cat: (1.1; 1.2); hound: (1.05; 1.1); horse: (1.07; 1.1): ox: (1.04; 1.09); bear: (1.03; 1.07).

Among reptiles and amphibians for the hind limb we have found *Varanus komodoensis:* 1.3; *Triturus vulgaris:* 1.6.

For the estimation of the lenght of the limb it is necessary to add the lenght of the foot (or hand) impression.

We can see that the apparent limb among animals with erect limbs is not very different from the length of the part of the limb that is put on the ground. The difference is not greater than 10% in the extreme cases for animals of median or great size.

The notion of apparent limb is a very important one. It permits the estimation of the limbs and the height of the hip. It is bound with the length of the pace (plate VIII, A-B: AB) (1 pace = 1/2 stride) and the angle of gait (= angle de marche = Schreitwinkel [Soergel, 1925]) (see no. 82). The length of the pace is known by means of the data furnished by the trackways; for this purpose, it is better to take the mean of a trackway rather than one single pace.

The angle of gait must be assumed after the study of some trackways of the same ichnospecies.

If the gait appears slow (short paces) this angle is low (30° – 40°) and if the gait seems to increase in speed it grows; but for the Mesozoic archosaurs and for Cenozoic or modern mammals in walking gait it does not exceed 60°. For other reptiles or amphibians it is greater (60° – 90°) because the limbs are folded during the locomotion (plate VIII, B).

If we call 2β the angle of gait (in a walking gait) the lenght of the apparent limb is given by the following formula, in the case of erect posture of limbs:

$$(1) \qquad OA = OB = \frac{AB}{2 \sin\beta}$$

If the limbs are not erected (sprawling gait), the value of the apparent limb is:

$$(2) \qquad OA_1 = OB_1 = \frac{AB}{2}\sqrt{\frac{1}{\sin^2\alpha} + \frac{1}{tg^2\beta}}$$

where 2α is the measure of the pace angulation (Peabody, 1948) (tg = tan [USA]).

The height of the hip is given by the same formula for the two cases:

$$(3) \qquad OH = \frac{AB}{2}\, tg\beta$$

These formulae can give a better approach of the size of the limbs of animals if we have different trackways of the same ichnospecies. The ichnospecies *Chirotherium barthii* Kaup, 1835 gives us a good example. In a walking gait, the mean of the length of the stride is 1100mm (data from Haubold, 1971). In an accelerated walk the length of the same parameter is 2000mm (Demathieu & Leitz, 1982). As the animals appear to have the same size, because the footprints are approximately equal, the difference must come from the angle of gait in each case, and the limbs must have about the same length.

We find the following results: the lenth of the hind limb of the trackmaker is comprised between 920 and 1060mm, with angles of gait of 30 – 35°, in the slow walk and 58° – 66° in the accelerated walk. As 66° is a very high angle of gait for an accelerated walk, the hind apparent limb cannot measure less than 920mm. Its probable value is about 990mm.

When β is put down, β' is given by:

$$\sin \beta' = \frac{A'B'}{AB} \sin \beta$$

2β is the angle of gait for the pace AB and $2\beta'$ that of the pace A'B'; A'B' and AB are data of the trackways. In all event, the choice of 2β depends on the characters of the trackway.

In the figures we have considered that the apparent limbs and the pace made an isosceles triangle (AÔB). This approaches the reality though it is not exactly correct, but for our research these approximations are sufficient. (After Demathieu 1970, p. 29-31).

Thickness of the Footprint-Reliefs and its Significance: Research on the Distribution of the Weights upon the Autopodia

by Georges R. Demathieu

Fossil footprints are semi-reliefs on the surface of a bed of stone. If they are on the top surface they usually form a hollow, a mark called a "concave epirelief" (Seilacher, 1953), and at the base (sole) of a bed they form a ridge, a cast, called a "convex" (Seilacher 1953). In the first case these reliefs are more or less deep impressions and in the second they are more or less raised areas. In both cases we will use the word "thickness of the relief".

An animal that walks on a muddy soil makes more or less deep imprints. This depth may depend on the physical state of the substrate and imprints, if it contains more or less water. But for quadrupedal trackways in the same substrate we must remember that the traces of the fore-limbs and those of the hind limbs cannot have the same depth, because the fore part of the body bórne by the fore limbs does not generally have the same weight as does the hind part of the body borne by the hind limbs.

Small manus and large pes signify a heavy "rear axle" and a light "front axle".

In living mammals there are often differences between the surfaces of the fore and hind autopodia. Generally in these animals the manus has a larger surface than the pes. This is the case in the majority of the fissipeds, artiodactyls and perissodactyls. This difference signifies that the centre of gravity in each of these animals is situated nearer to the "front axle" than to the "rear axle".

In contrast, reptiles and a few mammals (bear, rabbit, kangaroo) have greater hind autopodia than fore. This signifies, the centre of gravity is in this case nearer the "rear axle" than the front and indicate these animals, not only can attain an erect posture but also might walk with a bipedal gait. The bipedy is dependent by the place in the body of the centre of gravity. Every reptile that has a long and heavy tail and a short neck and small head is well fitted to be bipedal.

The study of vertebrate footprints can give us some approximate information concerning the location of the centre of gravity of the trackmaker and of the distribution of the mass of the animal body; thus we may gain ideas concerning the length of the neck, the importance of the head, of the pelvic region, of the tail.

A comparison of the thickness of the reliefs can give us such information. For this research it is necessary to utilize only well preserved tracks. In a manus-pes set of impressions it is highly probable that the sediment had the same physical and granulometric state. It is useful to consider not just one set but several, if possible. In a plastic sediment, the thickness of the reliefs is not truly proportional to the pressure but follows more complicated physical laws. The problem is not so easy but, if we do not expect very precise information and if we consider only some traces in a single trackway, we can suppose that the thickness is proportional to the pressure.

If r_1 is the maximum thickness of the manus relief, a_1 the areal measure of the surface area of the manus imprint and F_1 the force (= the weight) exerted on it, it is possible to write the equation:

$$r_1 = k\,F_1/a_1$$

k is a parameter depending on the characters of the sediment.

For the pes, with the corresponding notations:

$$r_2 = k\,F_2/a_2$$

We assume k has the same value for manus and pes in a set.

These two equations imply:

$$\frac{F_1}{F_2} = \frac{a_1\,r_1}{a_2\,r_2} \qquad (1)$$

a_1, a_2 are data of the trackways and are measured with a grid covered tracing-paper (each square is 1mm long). r_1, r_2 are measured on the footprints with a slide gauge (slide caliper).

It is better to take measurements on several sets and to calculate the mean of these data in order to obtain a good estimates. When these values have been calculated, it is possible to find the approximate position of the centre of gravity, after the theorem of the levers:

(2) $$\frac{a_1 r_1}{a_2 r_2} = \frac{F_1}{F_2} = \frac{O_2 G}{O_1 G}$$

with G centre of gravity, O_1 the glenoid cavity and O_2 the acetabulum. To make the calculation easier we assume that the three points lie in a straight line: the resultant error is not significant.

For example: *Isochirotherium coureli* (Demathieu 1970) (*). The surfaces of the pes and manus measure respectively 117 and 18cm^2 and the reliefs have a thickness of 0.6 and 0.5cm. Thus we have

$$\frac{a_1 r_1}{a_2 r_2} = \frac{O_2 G}{O_1 G} \approx \frac{9}{70}$$ that implicate

$$O_2 G = \frac{9}{70} O_1 G$$

This equation signifies that the centre of gravity lies at a distance from the acetabulum equal to the $\frac{9}{79} \simeq \frac{11}{100}$ of the length of the gleno-acetabular distance. For *Iso. coureli* the gleno-acetabular distance is estimated as being 76cm. From our calculation, the centre of gravity of the trackmaker must lie at about 8.5cm from the acetabulum. This result is necessarily approximate. A better approach can be made using the interval 8–9cm. It indicates the strong trend for the animal to have an erect posture and bipedal gait. This last character is only rarely observed among *Isochirotherium coureli* tracks. If we consider formula 2, the result indicates that the "rear axle" bears about 89% of the weight of the animal and the front 11%. Probably the interval 80–90% is more correct in the first case and 10–20% in the second, because errors arise in the measurements and in the calculation of the means.

Two other examples will show the interest of these estimates. The tracks *Brachychirotherium circaparvum* Demathieu 1971 show an animal where $\frac{O_2 G}{O_1 G} \simeq \frac{1}{3}$

In this case the centre of gravity is at a distance from the acetabulum about equal to 1/4 of the gleno-acetabular distance. We can conclude that the bipedal trend is less strong than in *Iso. coureli*. In fact the tracmaker of *Br. circaparvum* has not left bipedal tracks.

The case of *Rhychosauroides peabodyi* (Faber 1958) is peculiar. The imprint of the manus (plantigrade) has a surface of 1025mm2 and the surface of the pes (digitigrade) measures 1125mm2. As the reliefs of manus and pes have a thickness respectively of 3.5mm and 3mm, OG_2/OG_1 is about equal to 1.06. This signifies that the centre of gravity of this animal is about at the middle of the gleno-acetabular distance. However, the entire pes was larger than the manus and consequently the hind limb was more important than the fore.

The consequence is that the head of the trackmaker and its neck must have been heavy. The use of the thickness of the reliefs was proposed by Soergel (1925), but that author did not propound the method for calculation.

All the results must be considered not as exact values, but as indications. The precision can vary from 5 to 10%.

All that is written above illustrates, if anyone wishes to have a good impression of the trackmaker, the utility of the formula (2). Though the results are approximate, the distributions of the loads on the anterior or posterior limbs reveal, to a considerable degree, the size and the proportions of the body of the animal being considered through its footprints.

(*) $a_1 = 18cm^2; a_2 = 117cm^2; r_1 = 0.5cm; r_2 = 0.6cm$
$a_1 \times r_1 = 9cm^3; a_2 \times r_2 = 70.2cm^3$ i.e. $70cm^3$
$a_1 \times r_1/a_2 \times r_2 = 9/70 = O_2G/O_1G$. Then $O_1G = 70/9 \times O_2G$
$O_1G + O_2G = O_1O_2 = 70/9 \times O_2G + O_2G = 70/9 \times O_2G + 9/9\, O_2G$.
$O_1O_2 = 79/9 \times O_2G$. Then $O_2G = 9/79\, O_1O_2$.

The estimate of the gleno acetabular distance O_1O_2 for this form is about 76cm; also $O_2G = 9/79 \times 76 = 8.658cm$ i.e. 8.5cm. One can conclude that O_2G is comprised between 8 and 9cm, and the center of gravity is much nearer the acetabulum than the glenoid cavity.

The Phalangeal Formulae of the Reptilia (plate X, G)

by Giuseppe Leonardi
(with the collaboration of Walter P. Coombs, Hartmut Haubold and Martin G. Lockley)

The phalangeal formula is given as a series of five hyphenated arabic numbers corresponding to digits I-II-III-IV-V (see no. 83). When the formulae for manus and pes are very different, they are given separately, but when there is no difference, except in digit V, the number of phalanges in the pes of digit V is given in parentheses at the appropriate position in the series. For ex.: 2-3-4-5-3(4), that is:

I – II – III – IV	–	V	
2 – 3 – 4 – 5	–	3	(4)
manus and pes		manus	pes

In the case of variability in the number of phalanges of a digit within a group (order, etc.) the maximum-minimum number of phalanges is given, in the appropriate position in the series; for ex.: -4 or 5-; -3 to 0-; etc.

COTYLOSAURIA	2-3-4-5-3(4) but: Procolophonidae: Manus: 2-3-4-5-3 Pes: 3-3-4-5-4 Pareiasauridae: Manus: 2-3-3-3-2 Pes: 2-3-3-4-3
TESTUDINES (generally)	2-3-3-3-3 but excepc.: 2-3-4-5-3(4) in one case: 2-2-2-2-1
EOSUCHIA (including ARAEOSCELIDIA)	2-3-4-5-3(4) but *Champsosaurus*: 2-3-4-4-3 (manus)
LACERTILIA	2-3-4-5-3(4) with reductions and exceptions; hyperphalangy in Mosasauridae
RHYNCHOCEPHALIA	2-3-4-5-3(4) but Rhynchosauria: 2-3-4-5-3 (3 or 4) Askeptosauridae 2-3-3(4)-4-3(4) or 2-3-4-4-3(4)
THECODONTIA	2-3-4-5-3(4) with reductions in bipedal forms
CROCODILIA	2-3-4-4-2 or 3(0); but Protosuchidae: 2-3-4-5-3(4)
PTEROSAURIA	Manus: 2-3-4-4-0; Pes: 2-3-4-5-3 to 0
THEROPODA	Manus: 2-3-4 to 0-?2 to 0-0 Pes: 0 to 2-3-4-5-0 (generally)
PROSAUROPODA	Manus: 2-3-4 and high variability in IV-V digits Pes: 2-3-4-5-0 or 1
SAUROPODA	Manus: strong reduction, up to 2-2-2-1-1 or 2-1-1-1-1 Pes: 2-3-4(or 3)-2-1
ORNITHOPODA	Manus: highly variable: 2 to 0-3-4(or 3)-(3 or 2)-4 to 0 Pes: from 2-3-4-5-0 to 0-3-4-5-0
STEGOSAURIA	Manus: 2-3-4 and IV-V presumably reduced Pes: 2-3-4-5-0
ANKYLOSAURIA	Manus: 2-3-3 or 4-3 to 0-3 to 0 Pes: 2 or 0-3-4-4 or 5-0
CERATOPSIA	Manus: 2-3-4-3-2 or 1 Pes: 2-3-4-5-0
NOTHOSAURIA	2-3-4-5-3(4) but: *Ceresiosaurus* 2-3-5-6-6 (pes) Pachypleurosauridae: manus: 1-2-3-3-2 pes: 2-3-4-4-3 and hyperphalangy in some other forms
PLESIOSAURIA	Hyperphalangy
ICHTHYOSAURIA	Hyperphalangy; Hyperdactily or, in other cases, reduction of the number of digits
PROGANOSAURIA	2-3-4-5(or 6)-3(4)
PELYCOSAURIA	2-3-4-5-3(4) but: *Cotylorhynchus* and other Caseidae: 2-2-3-3-2
PHTHINOSUCHIA	probably 2-3-4-5-3(4)
GORGONOPSIA	generally 2-3-4-5-3(4), with shortened phalanges
CYNODONTIA	often 2-3-4-4-3, with shortened phalanges
THEROCEPHALIA	2-3-3-3-3
BAURIOMORPHA	2-3-3-3-3
ANOMODONTIA	2-3-3-3-3

Index

(organized by Cláudia V. de Lima and Francisco Henrique de O. Lima – Brasília, Brazil)

All terms appearing in the glossary are indexed; however the Russian equivalents are not indexed since they are given in the Cyrillic. Numbers used refer to those in the columns of terms and also in the Chapter "Discussion of the terms and of the methods". The numbers are followed by letters, that indicate the different languages (c = Castellano or Spanish; d = Deutsch or German; e = English; f = Français or French; i = Italiano or Italian; l = Latinus sermo or Latin; p = Português or Portuguese). The statistical terms, listed in a separate index, follow. An author index is not included, owing to the fact that this is mainly a glossary. Adjectives are entered with the endings more often employed. Groups of names and/or adjectives that are very similar in the different languages, are entered only by their stem, without suffixes (e.g.: plantigrad- for plantigrade, plantigrady, plantigradum, plantigrado, plantigradia etc.) though sometimes with the necessary orthographic variants (e.g.: ic(h)nolog-).

B

C

D

E

F

G

W

Z

Index of the Statistical Terms

Plates

PLATE I

The trackway. See text, nos. 10–28.
Measurements of a trackway (*Phalangichnus perwangeri* Conti *et al.*, 1977; Permian of Italy. Quadrupedal trackway, redrawn and modified, after G. L., 1974 and 1979. Numbers used before the terms refer to those in the columns of terms and in their discussion.

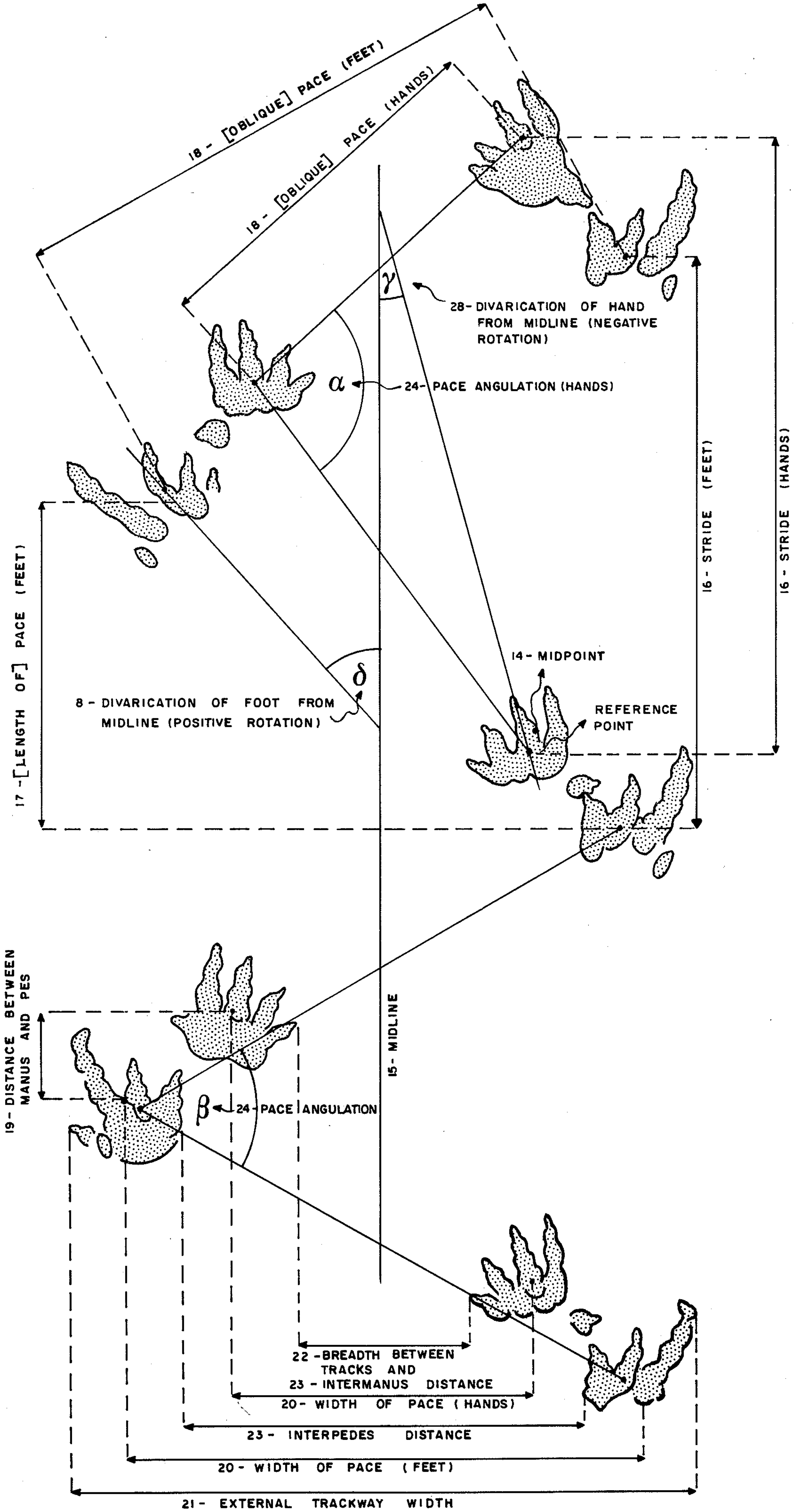
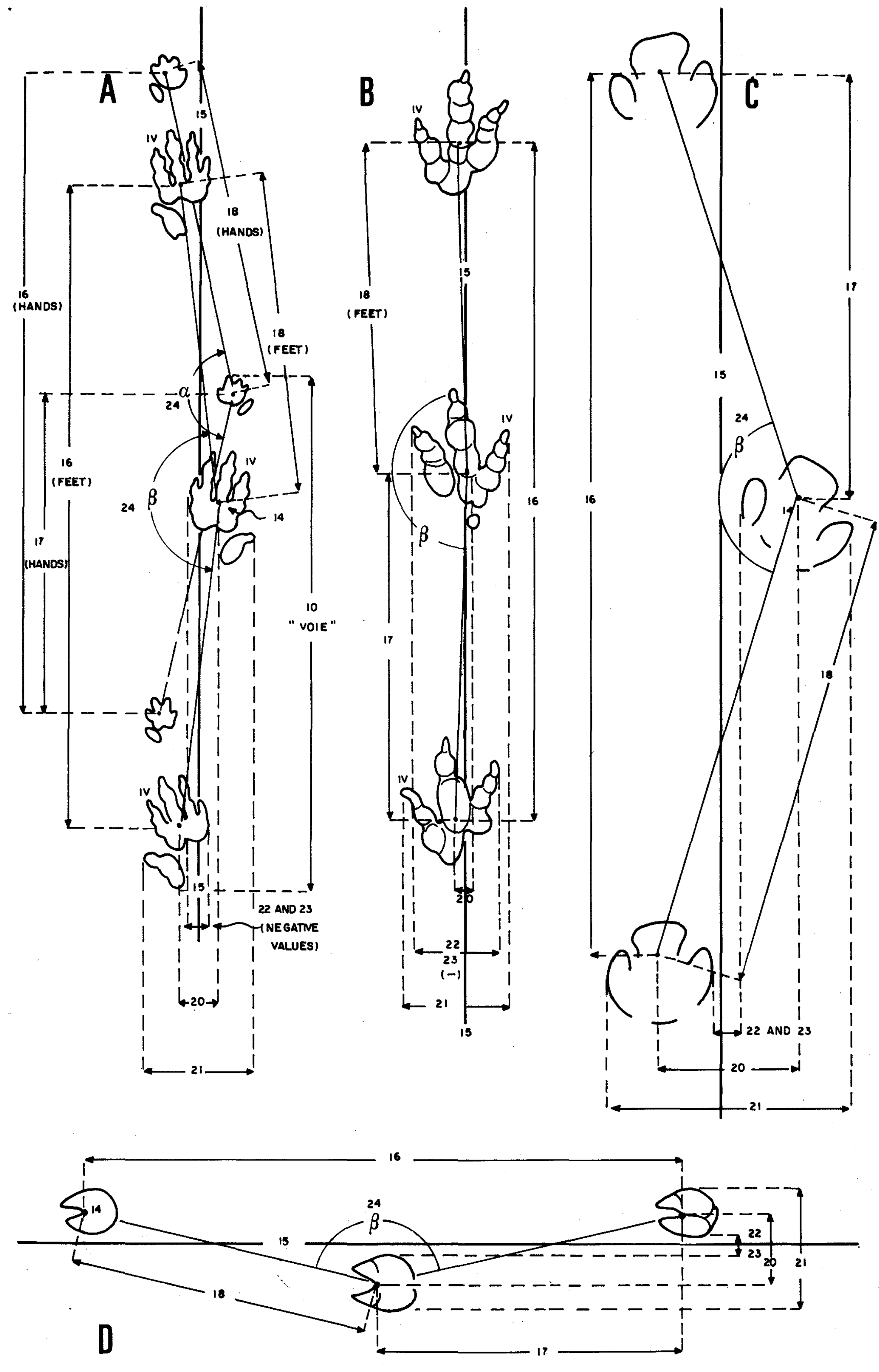

18 - [OBLIQUE] PACE (FEET)
18 - [OBLIQUE] PACE (HANDS)
28- DIVARICATION OF HAND FROM MIDLINE (NEGATIVE ROTATION)
24- PACE ANGULATION (HANDS)
16 - STRIDE (FEET)
16 - STRIDE (HANDS)
17 - [LENGTH OF] PACE (FEET)
8 - DIVARICATION OF FOOT FROM MIDLINE (POSITIVE ROTATION)
14 - MIDPOINT
REFERENCE POINT
19 - DISTANCE BETWEEN MANUS AND PES
15 - MIDLINE
24 - PACE ANGULATION
22 - BREADTH BETWEEN TRACKS AND
23 - INTERMANUS DISTANCE
20 - WIDTH OF PACE (HANDS)
23 - INTERPEDES DISTANCE
20 - WIDTH OF PACE (FEET)
21 - EXTERNAL TRACKWAY WIDTH

PLATE II

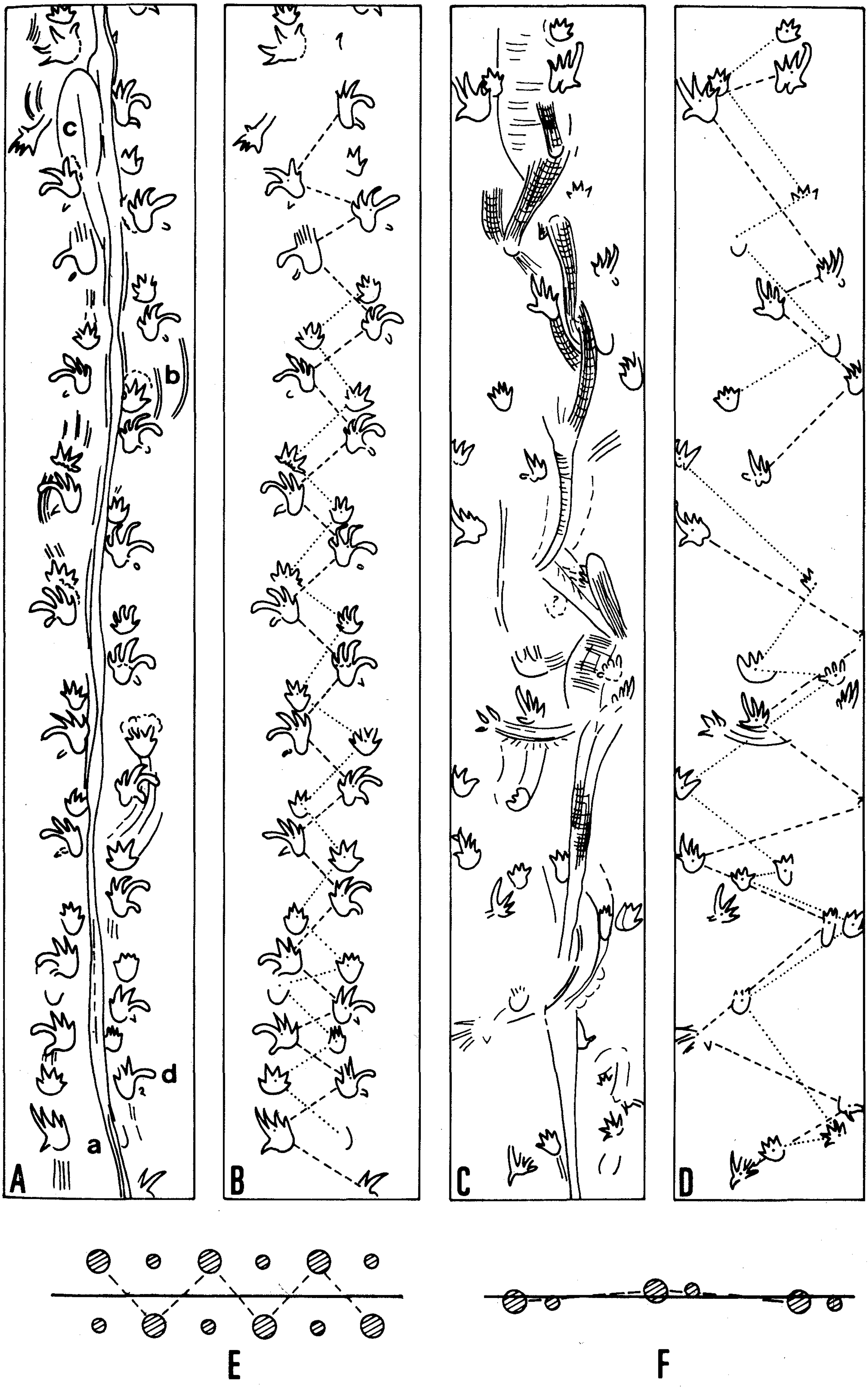
The trackway. See text, nos. 10-28. Measurements of some others trackways.
A: Quadrupedal trackway, *Chirotherium* Kaup, 1835; Triassic of Germany. Redrawn and modified from H.H., 1971a.
B: Bipedal trackway of a theropod. Lower Cretaceous of Brazil. Original drawing by G.L.
C: Quadrupedal trackway with total overlap. *Ronzotherichnus voconcense* Demathieu *et al.*, 1984; a fossil Rhinocerotidae from the Oligocene of France.
D: Quadrupedal trackway with total overlap. *Bifidites velox* Demathieu *et al.*, 1984. Fossil artiodactyl from the Oligocene of France.
Numbers used before the terms refer to those in the columns of terms and in their discussion.



A
15
IV
18
(HANDS)
16
(HANDS)
18
(FEET)
α
24
16
(FEET)
24
β
IV
14
17
(HANDS)
10
" VOIE "
IV
15
22 AND 23
(NEGATIVE
VALUES)
20
21
B
IV
18
(FEET)
15
IV
16
β
17
IV
20
22
23
(−)
21
15
C
17
15
24
β
16
14
18
22 AND 23
20
21
D
16
24
β
14
15
22
23
20
21
18
17

PLATE III

Characteristics of the trackway. See text, nos. 11–12.
A–D: Different trackways of the same individual of the south american lizard *Tupinambis teguixin* Linnaeus, 1758 (Teiidae). After G.L., 1975.
A–B: Regular trackway.
C–D: Irregular trackway.
A and C: Note also the tail drags (no. 59), the scrape – marks of the digits; and a belly imprint. Respectively: a), b), c).
E–F: See no. 12 in the text. Redrawn and slightly modified, after H.H., 1971c.



A
B
C
D
E
F
a
b
c
d

PLATE IV

The trackmaker. See text, no. 13. Example of a reconstruction of the reptile to which the trackway of plate I most probably belongs to, based on measurements and study of the trackway. Attributed to Cotylosaurs. After G.L., 1974.

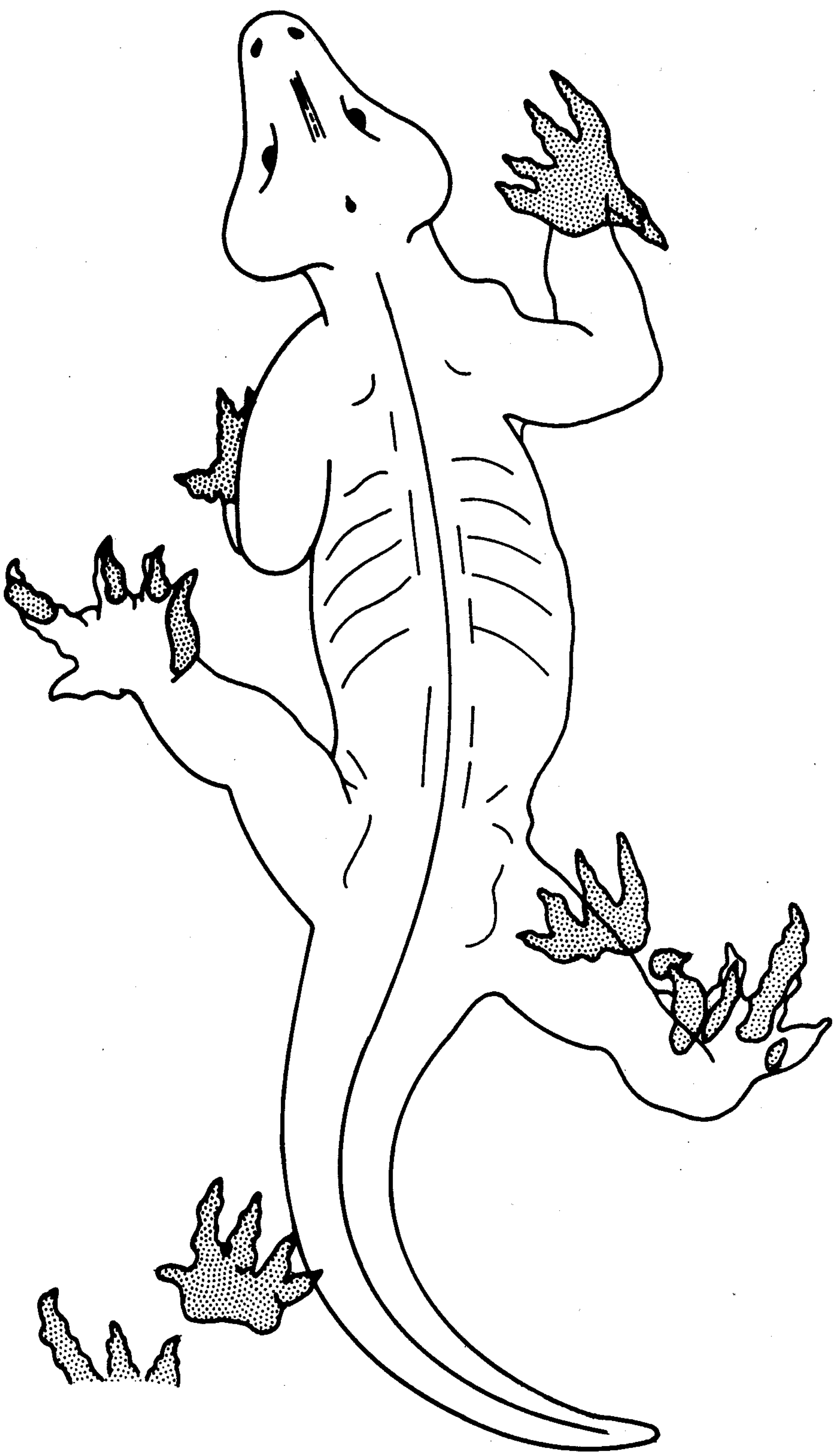
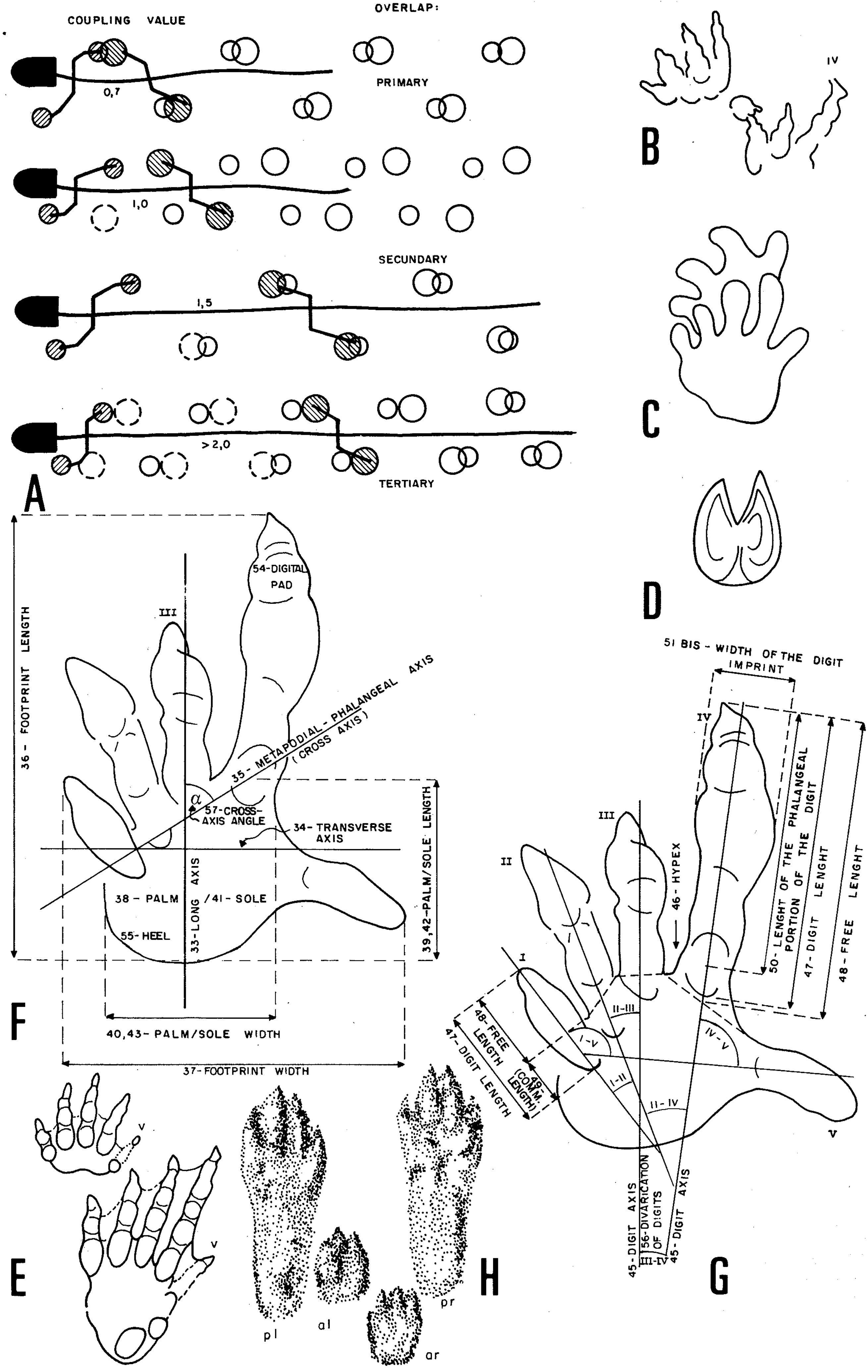


PLATE V

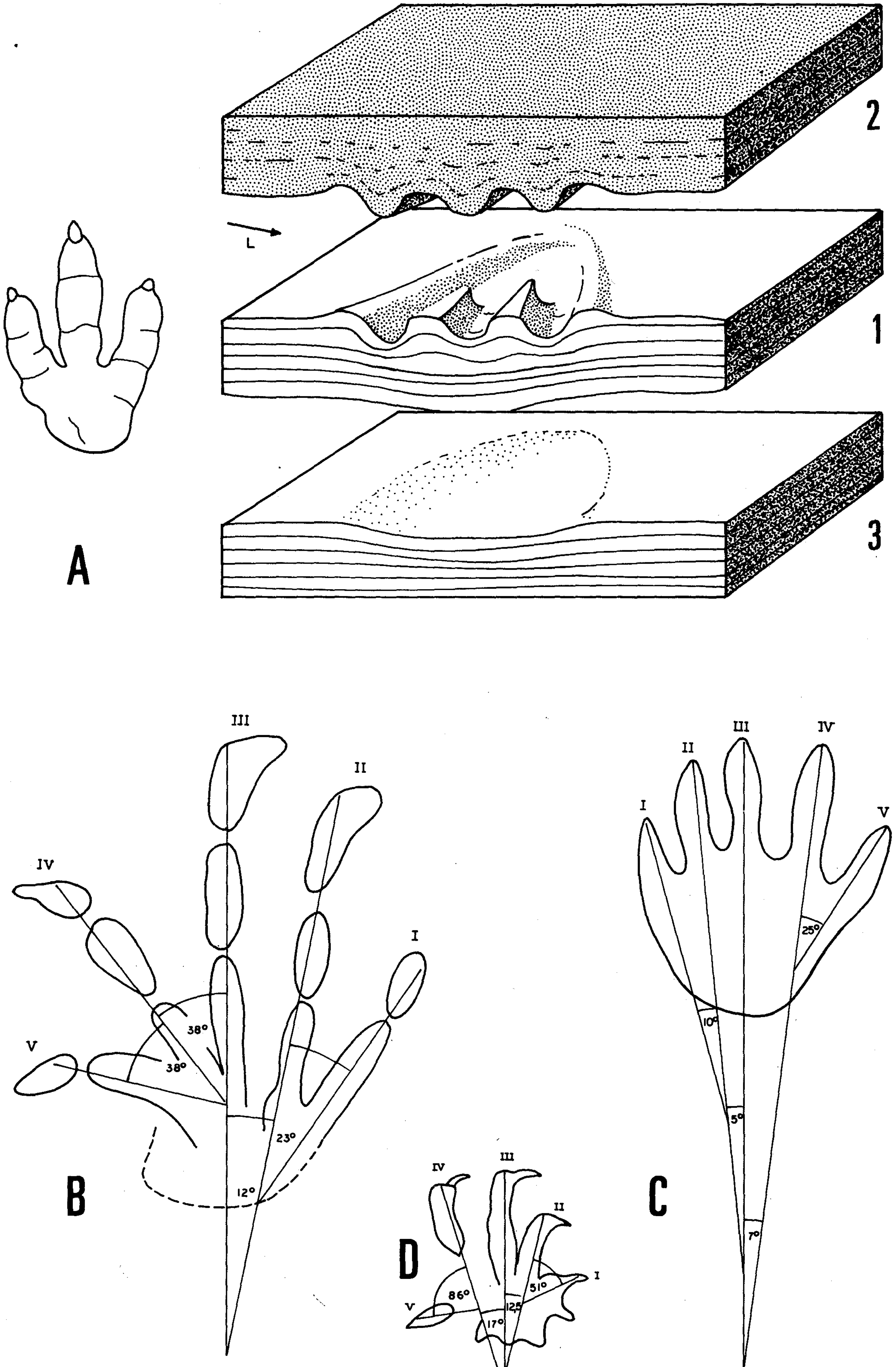
A: Coupling value and degrees of coupling. See text, nos. 74-75. Redrawn and modified, from Peabody, 1959 and H.H., 1971c.
B–D: Cases of overlap. See text, no. 27. B: marginal overlap; a set of *Phalangichnus perwangeri* (as above). C: partial overlap; a schematic set of *Limnopus* Marsh, 1894; D: total overlap: placing of pes upon all of manus impression. *Bifidites velox* (as above).
E: A set. See text, no. 32. *Apatopus lineatus* (Bock), 1952; redrawn from Baird, 1957.
F–G: Measuremensts of a footprint, *Dromopus lacertoides* (Geinitz), 1961; modified from G.L., 1974 and 1979.
F: General parameters of the footprints; G: parameters of the digits. See text, nos. 29–57. Numbers used before the terms refer to those in the columns of terms and in their discussion.
H: Overstep in a trackway (gallop) of a present day hare. Text, no. 26. al = anterior left; ar = anterior right; pl = posterior left; pr = posterior right.



COUPLING VALUE
OVERLAP:
0,7
PRIMARY
1,0
SECUNDARY
1,5
>2,0
TERTIARY
A
IV
B
C
D
36 - FOOTPRINT LENGTH
54-DIGITAL PAD
III
35 - METAPODIAL - PHALANGEAL AXIS (CROSS AXIS)
α
57-CROSS-AXIS ANGLE
34- TRANSVERSE AXIS
33-LONG AXIS
38 - PALM /41 - SOLE
55- HEEL
39,42-PALM/SOLE LENGTH
40,43- PALM/SOLE WIDTH
37-FOOTPRINT WIDTH
F
51 BIS - WIDTH OF THE DIGIT IMPRINT
IV
III
II
I
V
46 - HYPEX
50- LENGHT OF THE PHALANGEAL PORTION OF THE DIGIT
47- DIGIT LENGHT
48- FREE LENGHT
48- FREE LENGTH
49 (COMM. LENGTH)
47- DIGIT LENGTH
II-III
I-V
IV-V
I-II
II-IV
45- DIGIT AXIS
56-DIVARICATION OF DIGITS
III-IV
45- DIGIT AXIS
G
V
V
E
pl
al
ar
pr
H

PLATE VI

A: Footprints and substrate. See text, nos. 30–31 and 122, 124.
Slab 1: the original print, or mould of a theropod footprint, as a concave epirelief. Note also the displacement rim (no. 122).
Slab 2: the cast, or convex hyporelief.
Slab 3: a subtrace, or "ghost print" (no. 124). After G.L., 1984.
B–D: The divarication of digits. See text, no. 56. After W.A.S.S., 1966, 1971 and 1975b.



2
1
3
L
A
III
II
IV
I
V
38°
38°
23°
12°
B
IV
III
II
I
V
86°
125
51°
17°
D
I
II
III
IV
V
25°
10°
5°
7°
C

PLATE VII

Different manners of footprints. See text, nos. 52–54, 58, 61–71.
A–C: Claws, nails and hoofs (no. 52). Respectively, unclassified theropod, after G.L., 1984; footprint of *Dasypus* L., pes; original drawing by G.L.; *Ronzotherichnus vonconense* (as above).
D: Sole-pad and digital pads (nos. 53–54). Early ornithopod, after Demathieu & Weidmann, 1982.
E–I: Dactily. Nos. 61–63. Footprints (from left to right) monodactyl (horse); bidactyl (cow); tridactyl (goose); note the interdigital web (no. 58); tetradactyl *(Notopus petri* G.L., 1983, *?Ichthyostegalia*); pentadactyl (cfr *Dimetropus berea* (Tilton), 1931, after G.L., 1974).
J–M: Axony. Nos. 64–66. Footprints (from left to right): entaxonic (Neanderthal man, cave of Toirano, Ligury, Italy; original drawing by G.L.); mesaxonic (Anatidae, Tertiary of King George Island, South Shetland; simplified, from Covacevich & Rich, 1977); paraxonic (schematic fore footprint of *Arachichnus dehiscens* E. Hitchcock, 1858); ectaxonic (lacertoid footprint, after G.L. 1974).
N–R: Grady. Nos. 67–69. Footprints (from left to right): plantigrade *(Pachypes dolomiticus* P. Leonardi *et al.,* 1975); semiplantigrade (Anomodontia indet., after Conti *et al.,* 1977); digitigrade (chirotherian, after G.R.D. & H.H., 1974); subdigitigrade (theropod, after Courel & G.R.D., 1976); unguligrade (therapsid; after Schmidt, 1959). Note the relationship between the autopodium and the footprint.
Q, H and S: Respectively, straight, bent and crooked digits (S: *Rhynchosauroides schochardti,* after H.H., 1971c); no. 99.
T–U: Heteropody and homopody, nos. 70–71. T: heteropody *(Chirotherium barthii* Kaup, 1835 after H.H., 1971c); U: homopody *(Dicynodontipus,* (Rühle v. Lilienstern, 1944), modified from H.H., 1971a).

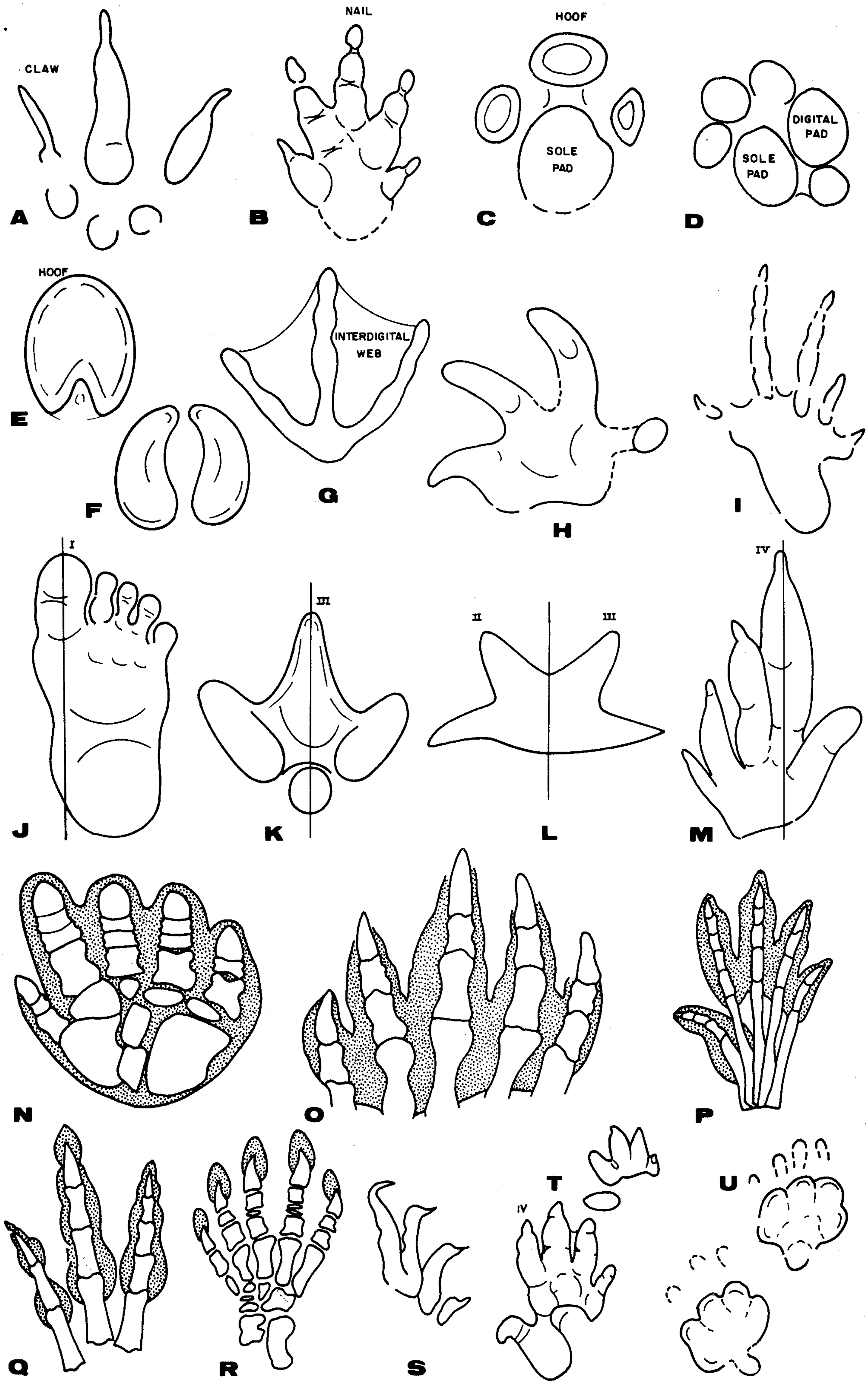
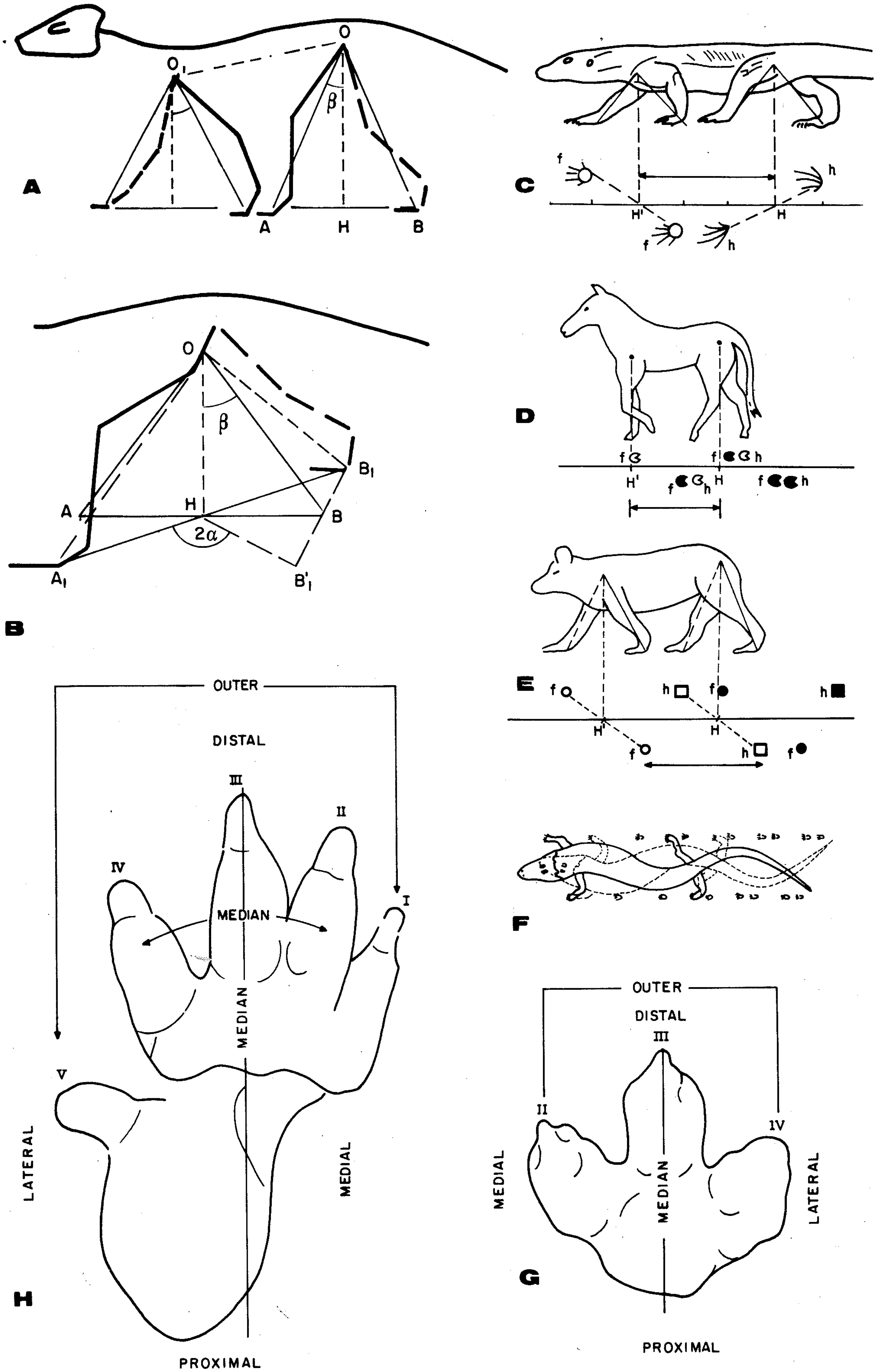

CLAW
NAIL
HOOF
SOLE PAD
DIGITAL PAD
SOLE PAD
A
B
C
D
HOOF
INTERDIGITAL WEB
E
F
G
H
I
I
III
II
III
IV
J
K
L
M
N
O
P
IV
Q
R
S
T
U

PLATE VIII

A–B: Apparent limbs and angle of gait. See text, nos. 81–82. See also the special chapter in the appendix.
The sketches show the relationship between apparent limbs and real limbs. In the case of alternate pace: A – for an animal of vertical limbs; OA, OB apparent members. B – for an animal in sprawling gait: AB, pace; A_1 B_1, oblique pace; A_1 H B'_1, pace angulation. After G.R.D., 1970, modified.
C–F: Calculation of the body length or gleno-acetabular distance, in different manners of gait. See text, nos. 73, 94 and 96–98.
After G.R.D., 1970, modified. C: primitive alternate pace (no. 73/i): support on diagonal limb pairs, changing periodically the support. The body-length (BL) is the segment H–H' on the midline. f = fore; h = hind.
D: Alternate pace (no. 73/ii): the animal rests constantly, during its progression, on three supports. H–H' = body length.
E: Amble (no. 73/iii): the body length (H–H') is the same as the distance of a set impressed in the same cycle.
F: The very long-coupled animal *(Eogyrinus)* walks in an amble. The body–length is almost three strides long.
G–H: Anatomical terms applied to the footprint and to its digits. Note the difference between "medial" and "median". See text, nos. 85–90.
G: *Amblydactylus kortmeyeri* Currie and Sarjeant, 1979.
H: *Isochirotherium marshalli (Peabody, 1948).*



A
O
O1
β
A
H
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β
B1
A
H
B
2α
A1
B'1
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h
H'
H
f
h
D
f
f
h
H'
H
f
h
f
h
E
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h
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h
H'
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G
OUTER
DISTAL
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LATERAL
PROXIMAL
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OUTER
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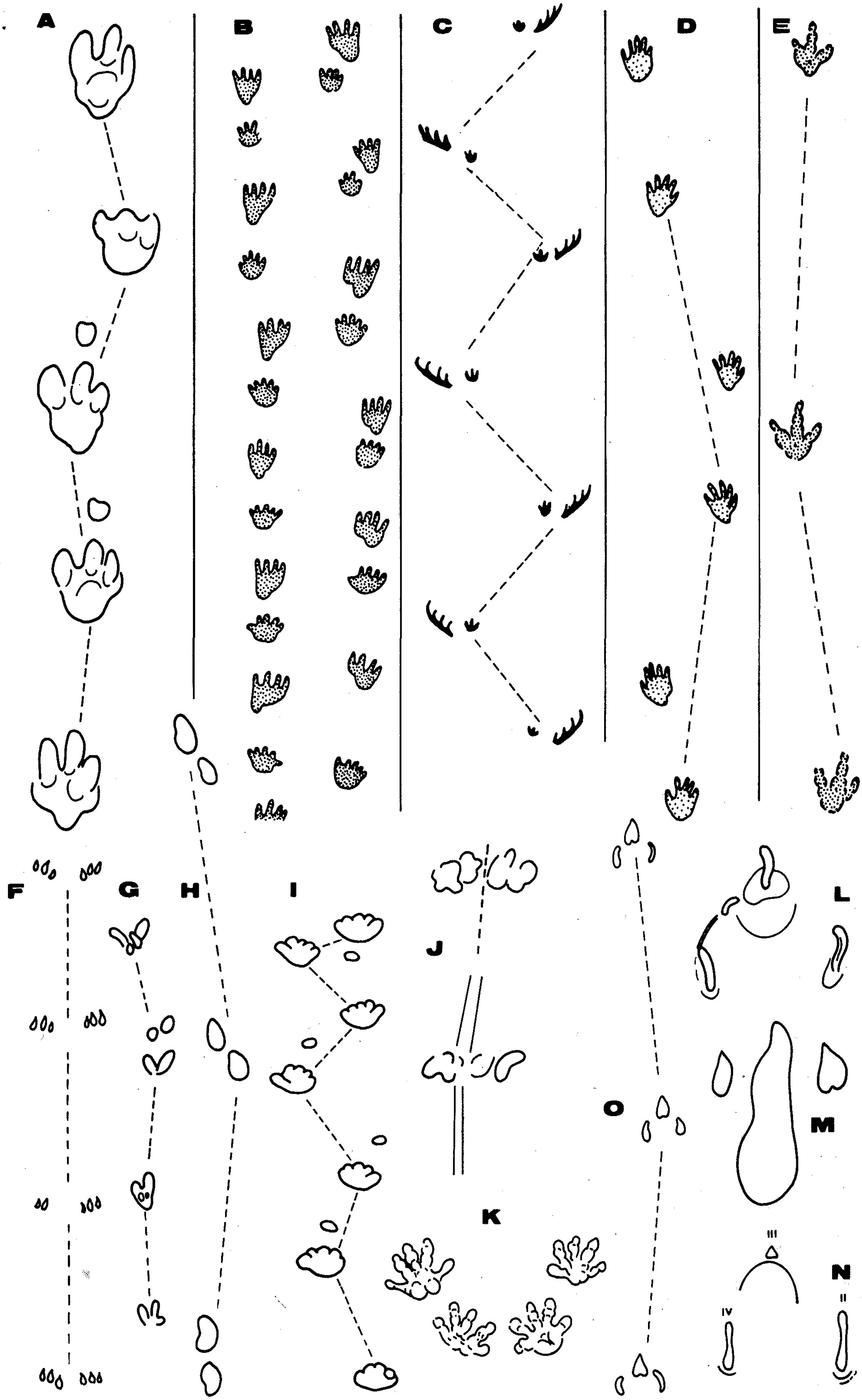
IV
I
V
MEDIAN
LATERAL
MEDIAL
PROXIMAL

PLATE IX

Different gaits, as illustrated by trackways. See text, nos. 91–92 and 96–98.
A: *Sousaichnium pricei* G. Leonardi, 1979. Semibipedal; trackway narrow and regular. The ornithopod was walking slowly, sometimes leaning upon the front feet on the ground. Lower Cretaceous; Paraíba, Brazil. Drawing by G.L.
B: *Megapezia praesidentis* Schmidt, 1956. Plantigrade tracks of a quadruped: trackway broad and rather irregular; stride short – an inefficient walker. Upper Carboniferous; Germany.
C: *Rhynchosauroides schochardti* (Rühle v. Lilienstern, 1939). Digitigrade tracks of a quadruped: trackway broad, but stride quite long and much more regular – a running track evidencing greater efficiency in movement. Triassic; Germany.
D: *Dicynodontipus geinitzi* (Hornstein, 1876). Plantigrade tracks of a quadruped: trackway narrow; stride long and regular – a highly efficient walker. Triassic; Germany.
E: *Anomoepus sp.* Semidigitigrade tracks of a biped: trackway very narrow; stride long – also an efficient walker. Triassic; France.
B–E: Respectively, after Schmidt, 1956; H.H., 1971a; Ellemberger, 1965; all of them in W.A.S.S., 1975.
F: Hopping gait (ricochet); subdigitigrade trackway of a small theropod or, more probably, of a mammal. Jurassic; Brazil. After G.L. & Godoy, 1980.
G: An early gallop, attributable to mammals. Ibid.
H: Hopping gait, idem. Ibid.
I: *Brasilichnium elusivum* G. Leonardi, 1981. Plantigrade trackway of a small quadruped mammal; Ibidem. Extreme heteropody. The hand-foot distance increases when the speed of the gait decreases. Idem, ibidem. After G.L., 1981.
J: *Ameghinichnus patagonicus* Casamiquela, 1964. Gallop; track with two quadripedal sets and tail drags. Middle Jurassic of Patagonia, Argentina. After R.M.C., 1964.
K: A quadripedal set of the same species. Idem, ibidem.
L–O: Tracks of half-swimming theropods. L, M, O from the Lower Cretaceous of the Paraíba, Brazil; L–M: after G.L., 1984; O: original drawing of G.L.
N: Liassic of the Connecticut, USA; after Coombs, 1980.


A
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J
K
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III
IV
II

PLATE X

A–D: Different gaits, as illustrated by trackways. See text, nos. 91–92 and 96–98.
A: *Parophidichnium triassicum* Demathieu, 1977, Serpentine progression.
After a photo in G.R.D., 1977. Triassic; France.
B: *Rogerbaletichnus aquilerai* Casamiquela, 1964. Quadrupedal trackway, semi-erected gait, heavy podal drags – an inefficient walker. Triassic of Patagonia. Argentina. Original drawing by G.L.
C: *Ligabueichnium bolivianum* G. Leonardi, 1984. Quadrupedal trackway with total overlap, walking gait; attributed to an Ornithischian. Upper Cretaceous of Bolivia. After G.L., 1984.
D: *Caririchnium magnificum* G. Leonardi, 1984. Quadrupedal, regular trackway, with high heteropody. Walking gait. Lower Cretaceous; Paraíba, Brazil. Ibid.
E–F: Footprints and substrate (nos. 107–124). Two sets of the same individual of *Tupinambis teguixin* L., 1758 (Teiidae, Lacertilia) impressed in laboratory on different substrate; respectively moist and cohesive river-mud, and moist sand. Same scale.
G: Phalangeal formula (no. 83) and digital pads (no. 54). *Tupinambis teguixin* (as above). Vertical section of the left side feet digits, with their restored skeleton; medial view. The vertical line indicates the beginning of the free digits (no. 48). Note the general correspondence between pads and articulations in reptiles. E–G after G.L., 1975.

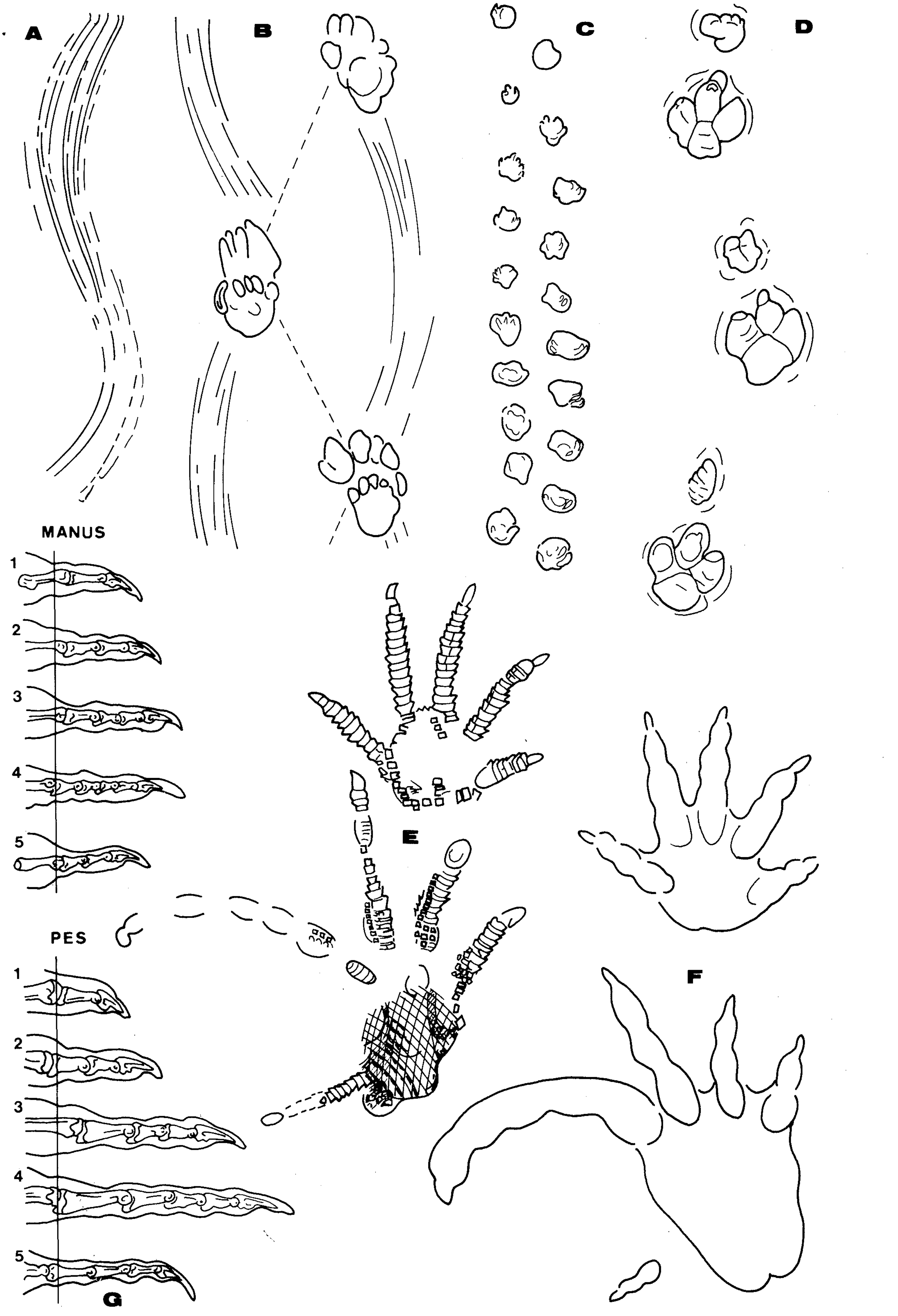

A
B
C
D
MANUS
1
2
3
4
5
E
PES
1
2
3
4
5
F
G

PLATE XI

UPPER DEVONIAN

A: The trackway from the Devonian of Hoy Island, Orkney Islands, Scotland: a belly-drag trace, with the impressions of fin-marks alongside. It appears to be the track of a rhipidistid fish. Old Red Sandstone. External trackway width:~3cm. After W.A.S. Sarjeant, 1974.

B: Bedding plane in sandstone of the Genoa River Beds, with two trackways of devonian amphibians. Eastern Victoria, Australia.

1: belly-drag trace, with the impressions of heteropod footprints alongside.

2: plantigrade broad tracks of a quadruped; stride short; marginal overlap. Arrows indicate direction of movement. Graphic scale in cm and inches. Photo courtesy of Dr. Jim W. Warren.

C: Impression of a single tetradactyl footprint (cast), holotype of *Notopus petri* Leonardi, 1983, from the Ponta Grossa Formation, São Domingos Member, of Tibaji, Paraná, Brazil. Attributable to ?Ichthyostegalia. Specimen no. 1417–R, Seção de Paleontologia DNPM, Rio de Janeiro. Scale in cm. Photo courtesy of the same Secção.

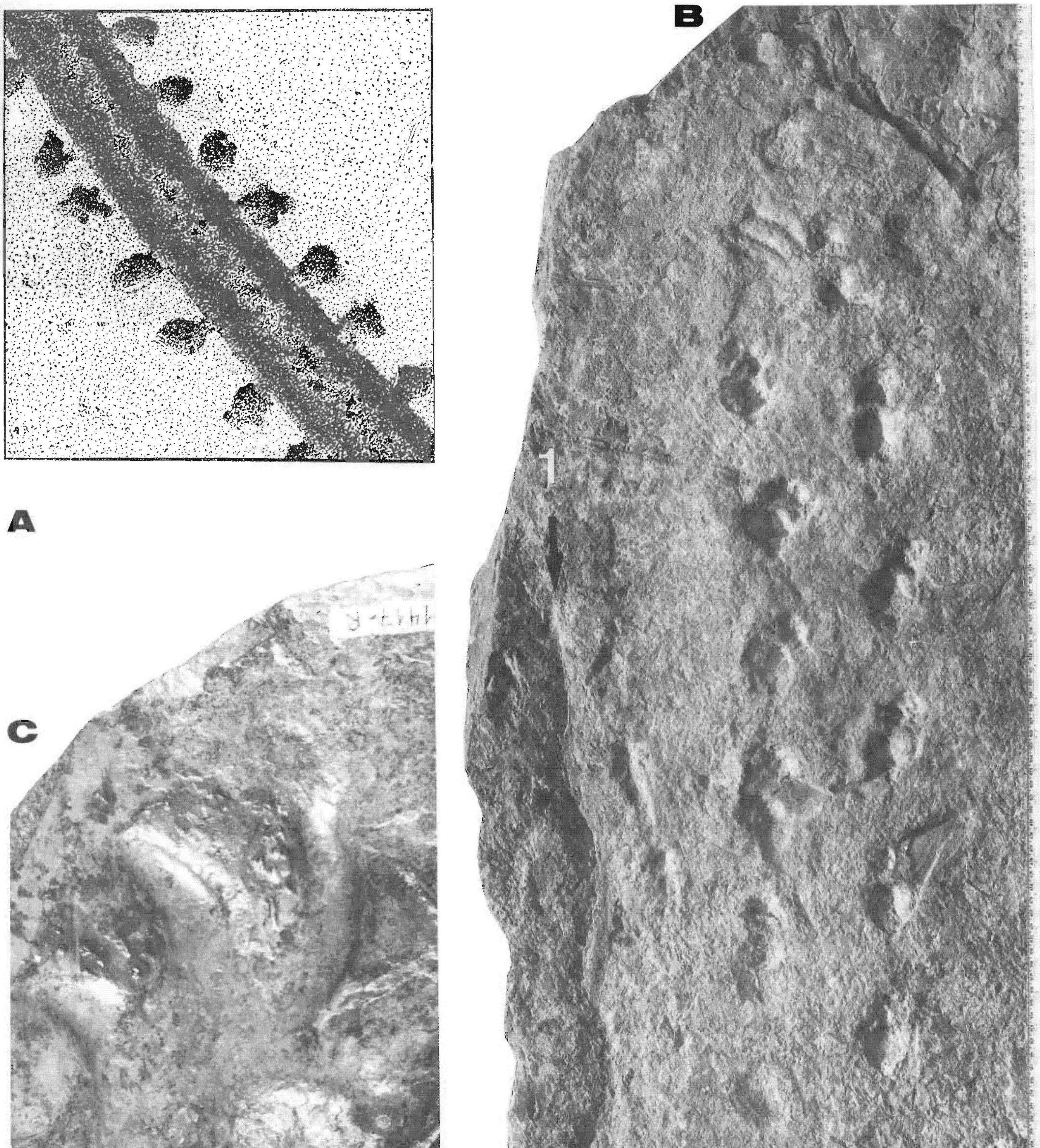

A
B
C
1
2

PLATE XII

CARBONIFEROUS

Trackway of a large amphibian *(Baropezia* sp.) on west bank of the Avon River estuary near low tide level. Top of Bell's "D2" unit or base of his "C" member; North of the light house. Horton Bluff Formation (Mississippian), Nova Scotia, Canada. A Nova Scotia Museum crew prepare to make a cast of the trackway. Photo courtesy of the Nova Scotia Museum.

PLATE XIII

PERMIAN. Scales in cm.
A: Footprint (cast) attributed to the Pareiasauridae: *Pachypes dolomiticus* P. Leonardi *et al.,* from the Arenarie di Val Gardena Formation (Upper Permian, Uppermost Capitanian or, more likely, Lower Abadelian) of the Bletterbach canyon, Bolzano, Italy. Photo courtesy of the Dept. of Geology of the University of Rome.
B: Therapsidian footprint of *Dicynodontipus* Rühle v. Lilienstern, 1944 (cast). Ibidem. Photo: as above (A).
C: Trackwy attributable to *Laoporus* Lull, 1918 (Caseidae). Coconino sandstone, Northern Arizona. Collections of the Museum of Northern Arizona. Photo: the Editor.
D: *Laoporus (Barypodus)* footprints. Ibidem, ibidem. Note the sand crescents. Photo: the Editor.

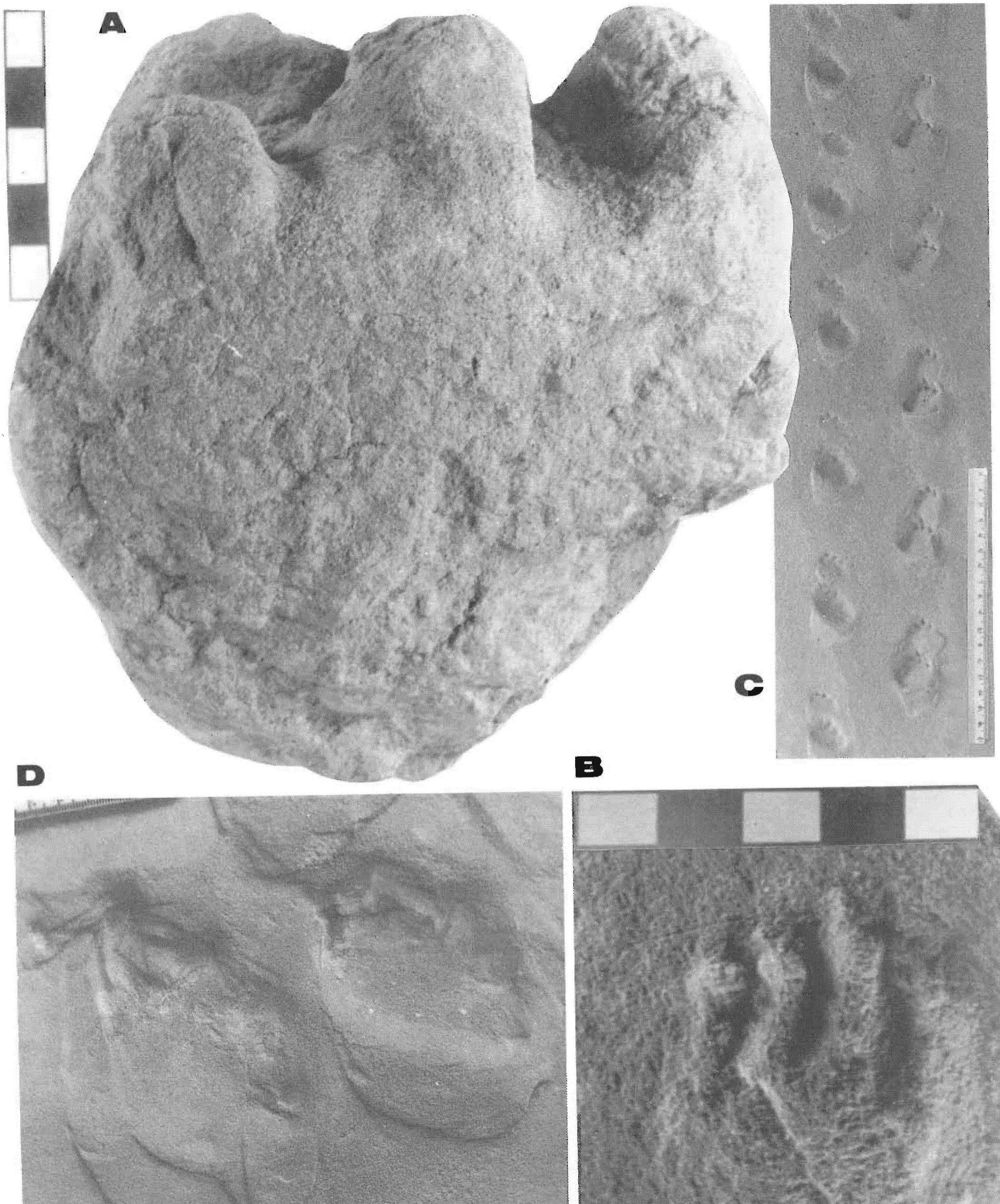

A
B
C
D
BARYPODUS
Coconino Sandstone Permian
Northern Arizona

PLATE XIV

TRIASSIC. Scales in cm.
A: A set (cast) of *Chirotherium barthii* Kaup, 1835, attributed to Thecodontia, from Upper Moenkopi Formation of Northern Arizona. Museum of N.A., no. G2.2127. Photo: the Editor.
B: A set (cast) of *Isochirotherium felenci* from the Middle Triassic of Largentière, Ardeche, France. Photo: G.R. Demathieu.
C: *Batrachopus* cf *dewey* (E. Hitchcock), 1843, from the Ata Canyon, 10km SSE of Prado, Tólima, Colombia. Saldaña Formation, Upper Norian to Lower Rhaetian. *In situ.* Photo courtesy of Dr. Jairo Mojica.
D: A trackway (cast) attributed to therapsids, holotype of *Gallegosichnus garridoi* Casamiquela, 1964. From an unnamed Formation, "Complejo porfírico" *auctorum,* Norian to Lower Rhaetian, of Tscherig quarry, Los Menucos, Río Negro Province, Argentina. Collections of the Museo de La Plata, no. MLP 60–XI–31–7. Photo: the Editor.
E: *Chirotherium storetonense* Morton, 1863 (= *Chirotherium barthii* Kaup, 1835), a specimen in the Liverpool Museum collections, photographed by Henry C. Beasley c.1900. From Beasley's photograph.

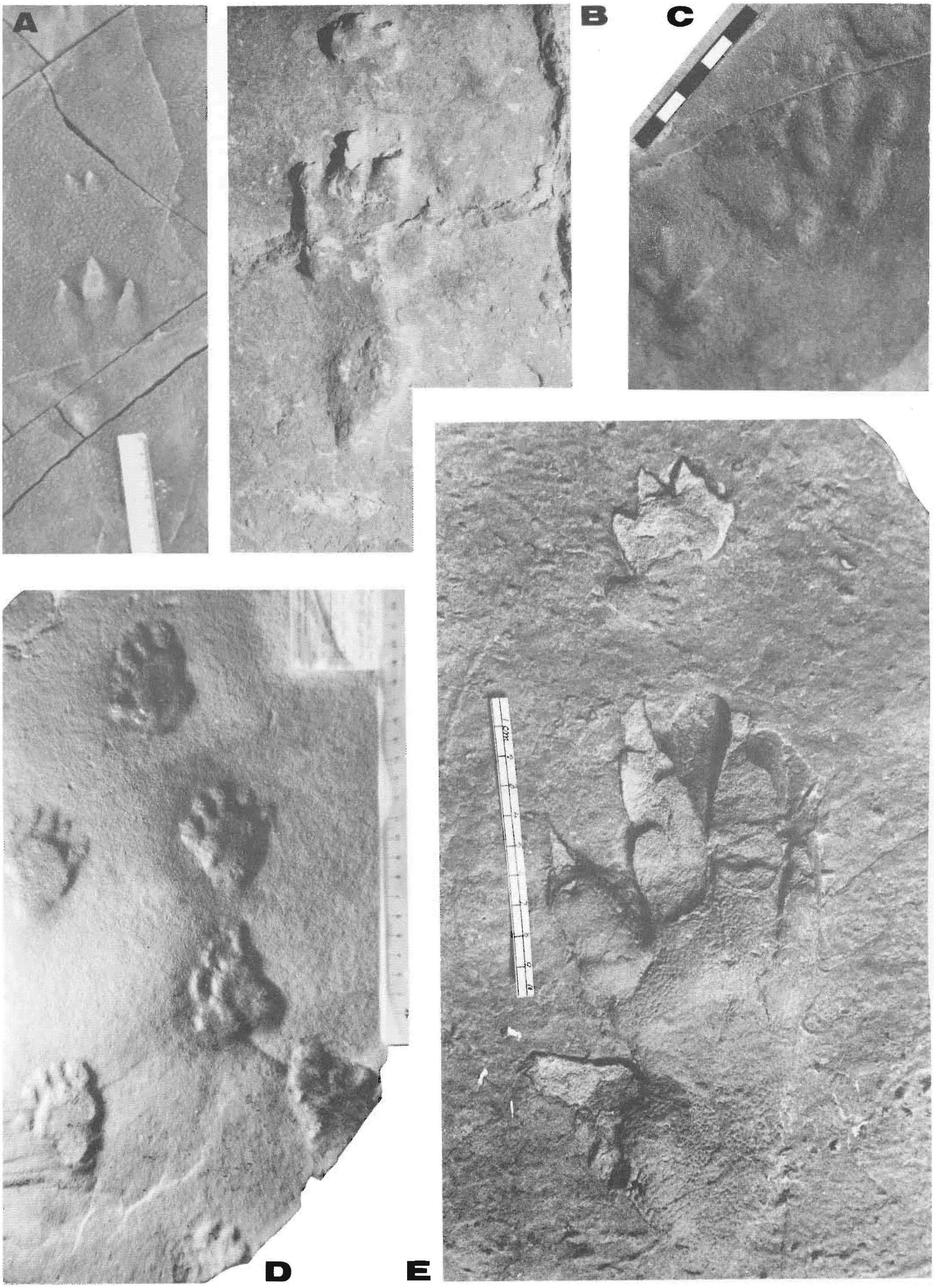

A
B
C
D
E

PLATE XV

JURASSIC – 1

A: Portion of a trackway (cast) collected from the sidewalk flagstone of São Carlos, State of São Paulo, Brazil. Attributable to ?Tritylodontoidea. Botucatu Formation, probably Lower Jurassic. Desert environment. Collections of the Seção de Paleontologia DNPM, Rio de Janeiro. Scale in cm. Photo: the Editor.

B–C: Hopping gait trackways from the Botucatu Formation (as above) of São Bento quarry, Araraquara, State of São Paulo, Brazil. Collections of the Museu Nacional, Rio de Janeiro. Scale in cm. Photos: the Editor.

D: A mammalian trackway pointing to a galloping gait. Ibidem. Collections of the Secção de Paleontologia DNPM, Rio de Janeiro. Scale in cm. Photo: the Editor.

E: Footprints attributable to cf *Batrachopus* E. Hitchcock, 1845 (but: cf W.L. Stokes and J.H. Madsen, 1979), from the Navajo Sandstone of Sand Flats, near Moab, Utah. Scale in cm. Photo: the Editor.

F: Closeup of the best set of footprints of *Pteraichnus saltwashensis* Stokes, 1957, from the Morrison Formation, Salt Wash Sandstone Member (Upper Jurassic) of NW Carrizo Mountains, Apache County, Arizona. Supposed pterodactyloid tracks, recently (1984) attributed by K. Padian and P.E. Olsen to a crocodilian. Scales in inches. From W.L. Stokes, 1957, in W.A.S. Sarjeant, 1975b.

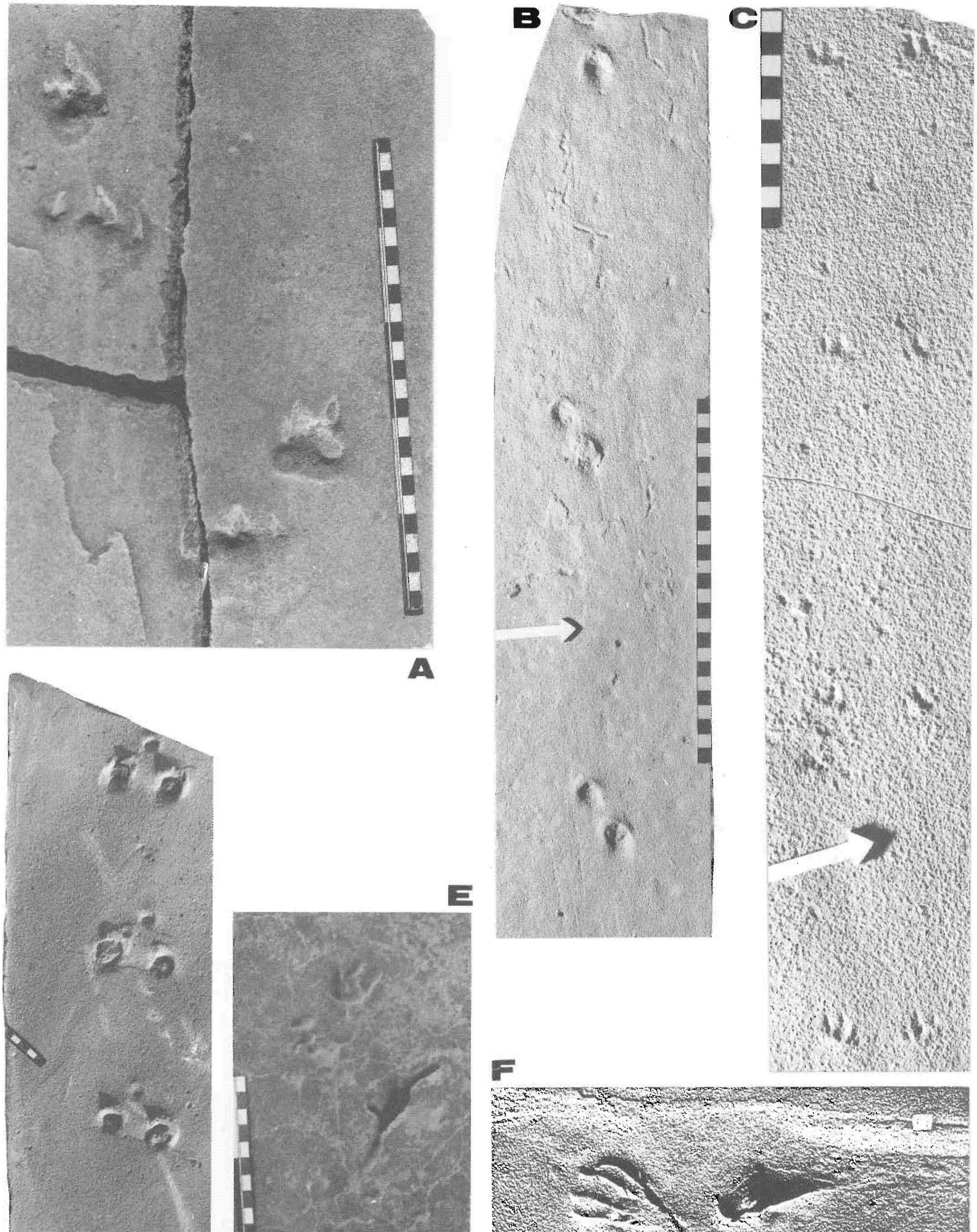

A
B
C
D
E
F

PLATE XVI

JURASSIC – 2. Scales in cm.
A: A footprint from a paratype of *Sarmientichnus scagliai* Casamiquela, 1964, attributed to a medium sized coelurosaur, with tridactylous feet, but functionally didactylous. From the La Matilde Formation, Upper Jurassic, Oxfordian, of Fazenda Laguna Manantiales, 140km SW of Jaramillo, Santa Cruz Province, Argentina. Collections of the Museo de La Plata, no. MLP 60–X–31–1–A. Photo: the Editor.
B: A galloping trackway of *Ameghinichnus patagonicus* Casamiquela, 1964, attributed to patriotheroid mammals. Ibidem, ibidem, no. MLP 60–X–21–10. External trackway width:~3cm. Photo: R.M. Casamiquela.
C: theropod left footprint (cast) from the Upper Jurassic of the Sichuan Basin, China. Photo courtesy of Dr. Dong Zhiming.
D: Large sauropod tracks from the Morrison Formation, Upper Jurassic, Purgatory valley, SE Colorado. Photo courtesy Dr. Martin G. Lockley.
E: Theropod right footprint (cast) from the Cayenta Formation of Northern Arizona (Lower Jurassic). Museum of Northern Arizona. Photo: the Editor.

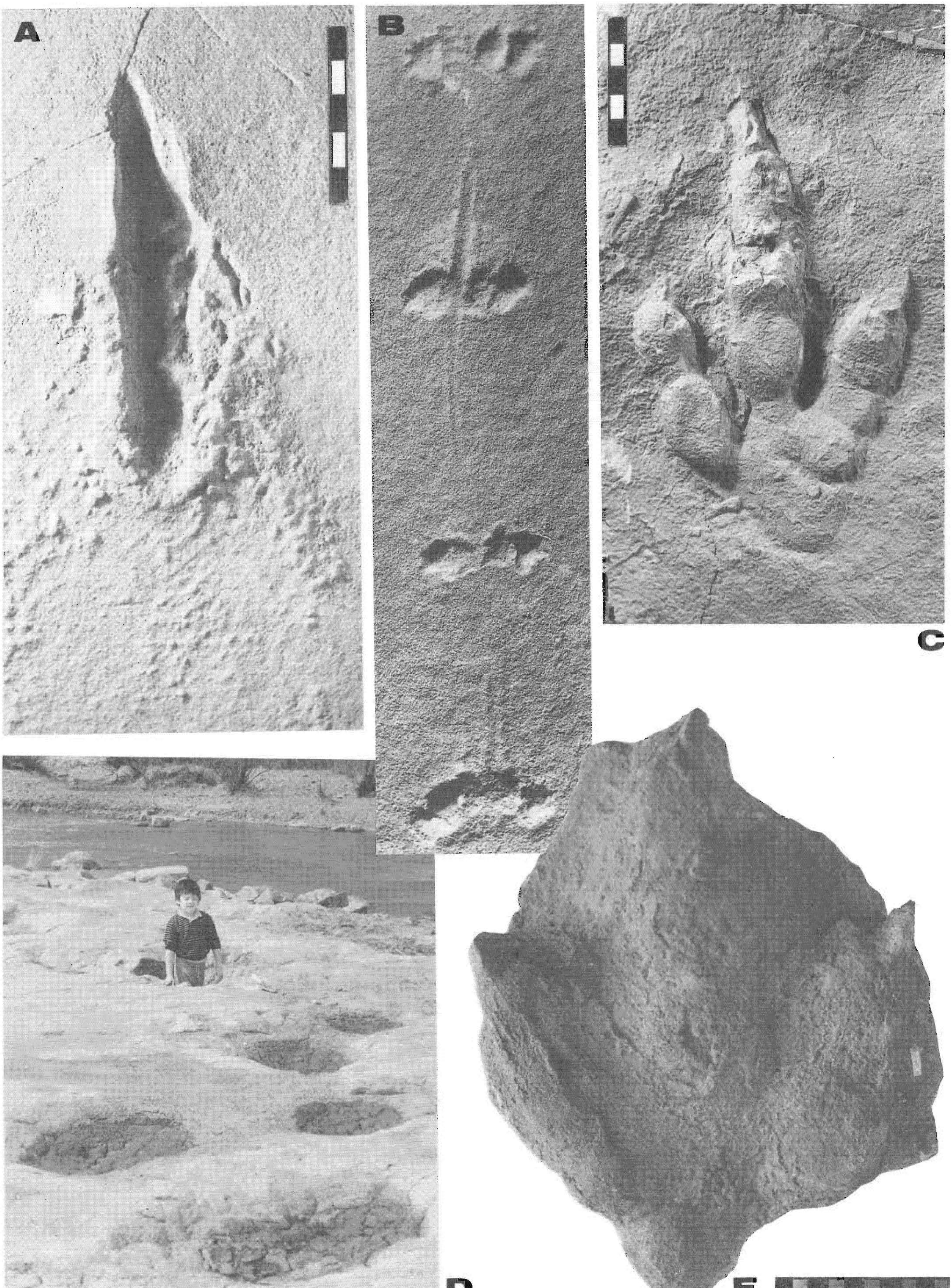

A
B
C
D
E

PLATE XVII

CRETACEOUS – 1. Photos: the Editor.
A: *Sousaichnium pricei* G. Leonardi, 1979, holotype, attributed to the Iguanodontidae. Sousa Formation, Lower Cretaceous of Sousa, Paraíba State, Brazil.
B: Carnosaur trackway. Ibidem.
C: Coelurosaur trackway from the Cenomanian limestones of Beth Zayit, 4km of Jerusalem.

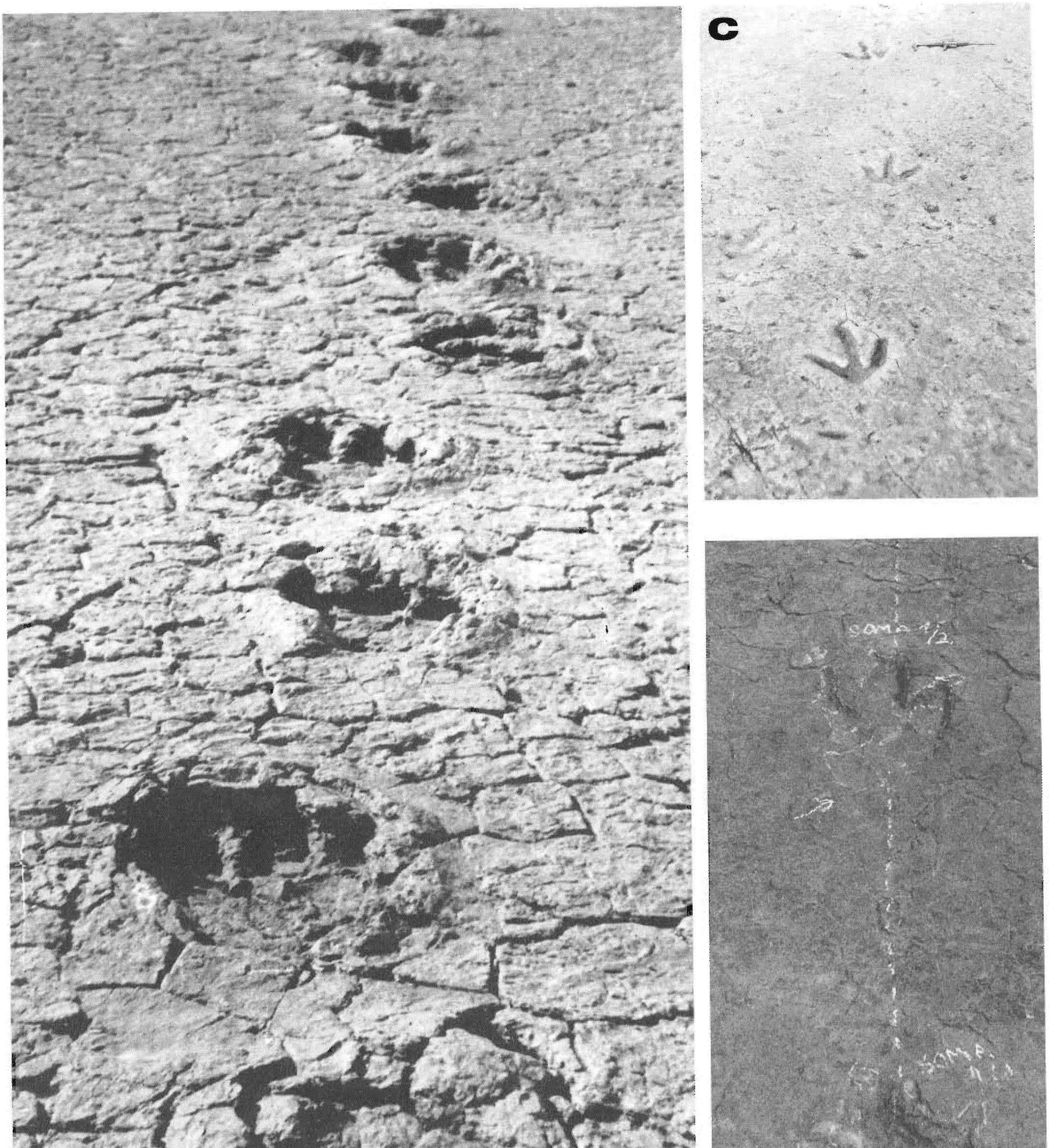

C
A
B

PLATE XVIII

CRETACEOUS – 2. Scales in cm.

A: Miscellaneous small tracks (cast) from the Doug Wilson collection, College of Eastern Utah Museum, Price, Utah; attributed to young hadrosaurs. Coal mines in the Mesaverde Group (Upper Cretaceous). Photo: Dr. Martin G. Lockley.

B: *Ligabueichnium bolivianum* G. Leonardi, 1984: large ornithischian trackway attributed to ?Ceratopsia, from the El Molino Formation (Upper Maastrichtian) of Toro-toro, Potosí, Bolivia. The track assemblage includes some 70 theropod trackways. External trackway width:~1.5m. Photo: the Editor.

C: Bird tracks (cast) from the Upper Maastrichtian of Monton–Il0, Río Negro Province, Argentina. Collections of the Museo Civico of Venice (Italy). Photo: the Editor.

D: Coelurosaur or bird tracks (cast) from the Mesaverde Group (Upper Cretaceous): Vicinity of Monticello, Utah. Photo: the Editor.

E: Theropod footprint from the Sousa Formation (Lower Cretaceous) of Caiçara farm, Sousa, Paraíba, Brazil. The bedrock surface displays rain drops. Borgomanero collection, Curitiba, Paraná, Brazil. Photo: the Editor.

F: A sauropod footprint from the trackway of Mont Arli, W of Agadès, Niger; from the "argiles de l'Irhazer", Lower Cretaceous. Photo: the Editor.

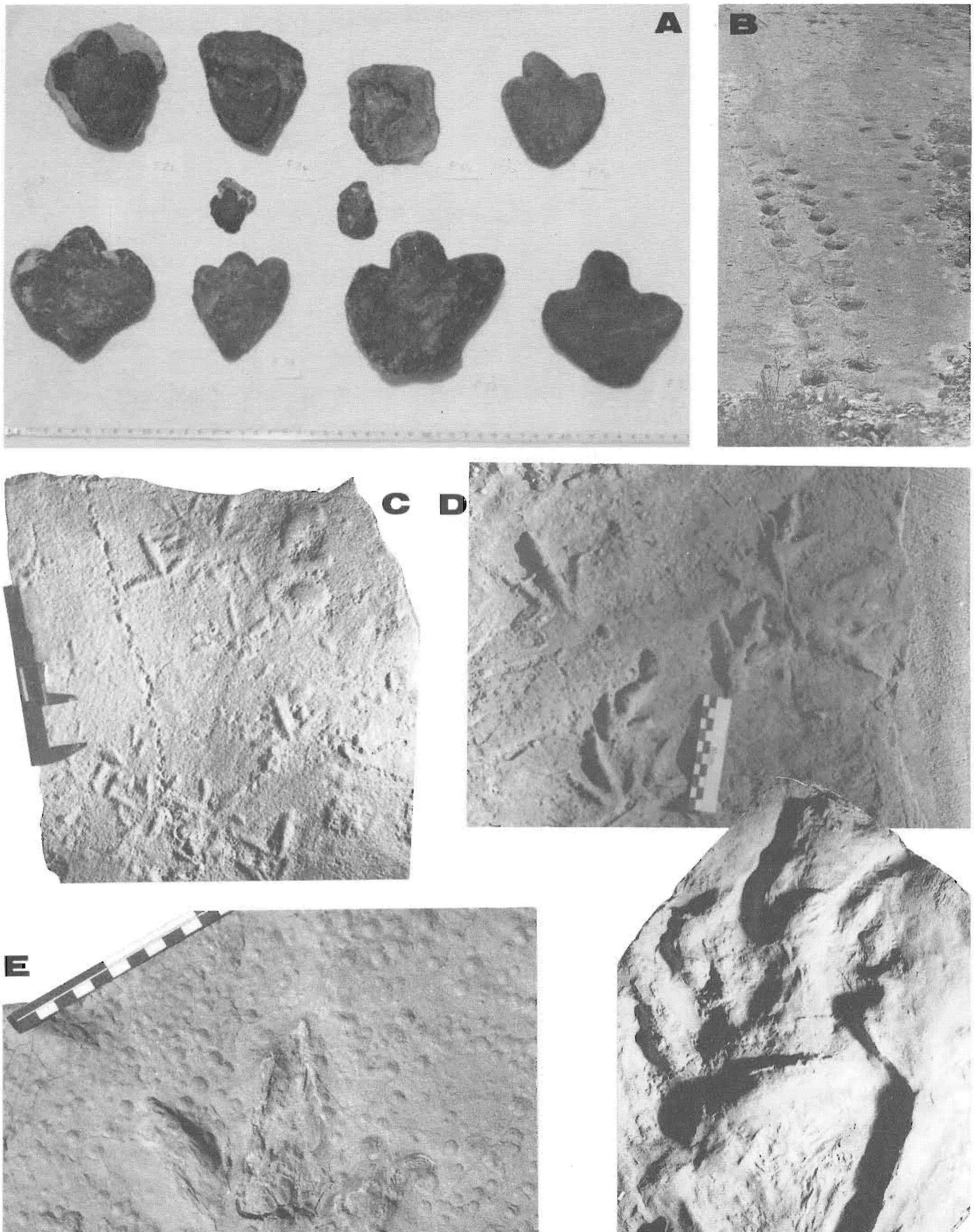

A
B
C
D
E
F

PLATE XIX

CAINOZOIC – 1. Photos: G.R. Demathieu. Scales in cm.
A: *Bifidites velox* Demathieu *et al.,* 1984, portion of a trackway, *in situ*. Attributed to a slight, medium size artiodactyl. Upper "calcaires de La Fayette, Lower Oligocene, Sannoisian of the Apt basin, 5km E of Apt, Vaucluse, France.
B: Closeup of a right footprint of the same.
C: A set of footprints of *Ronzotherichnus voconcensis* Demathieu *et al.,* 1984,attributed to the rhinocerotid *Ronzotherium.* Ibidem.
D: Bird tracks, among them *Pulchravipes magnificus* Demathieu *et al.,* 1984, related to the Order Ralliformes of Charadriformes. Ibidem.
E: Rhinocerotid tracks, *Ronzotherichnus vonconcensis,* as above (C).

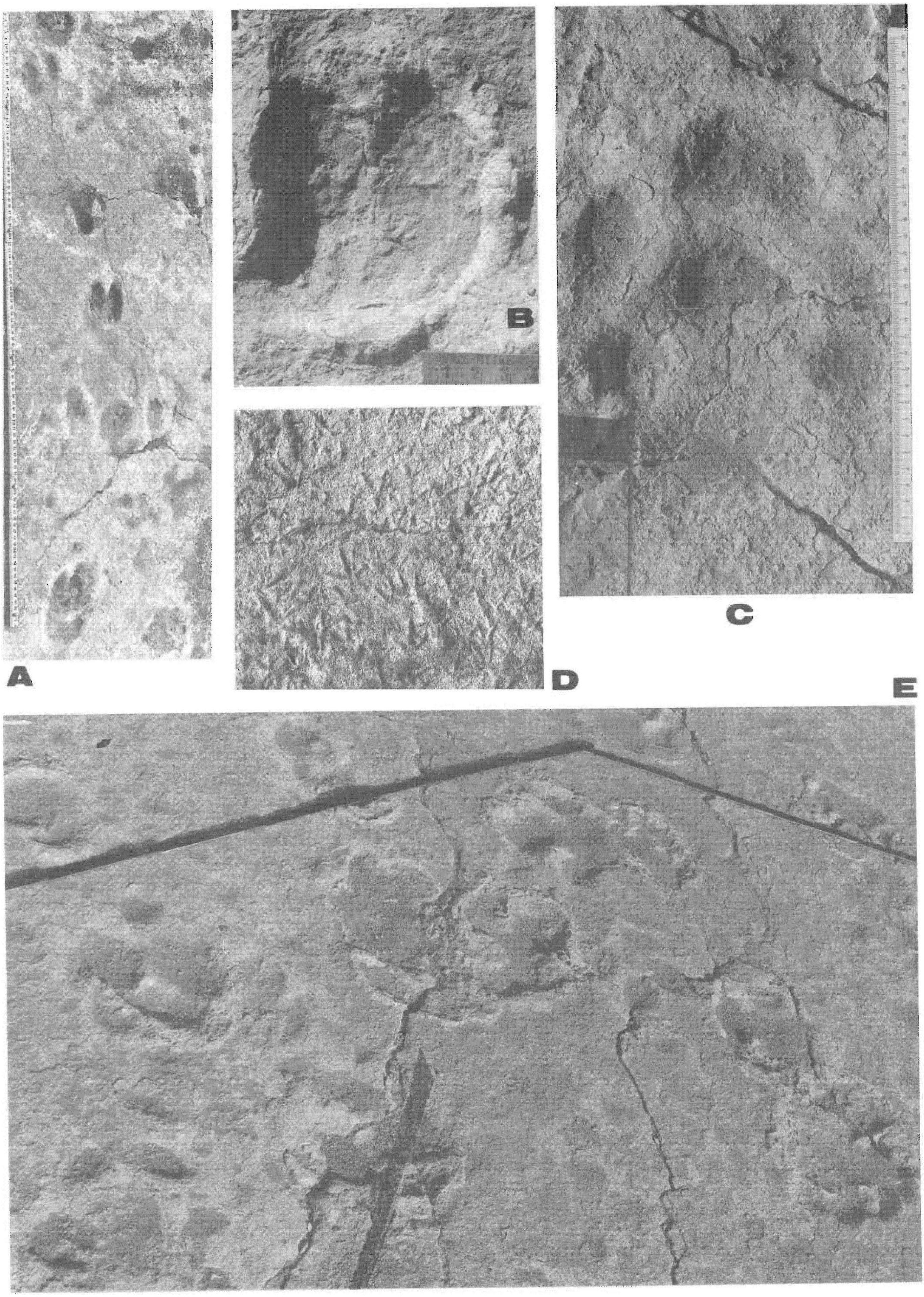
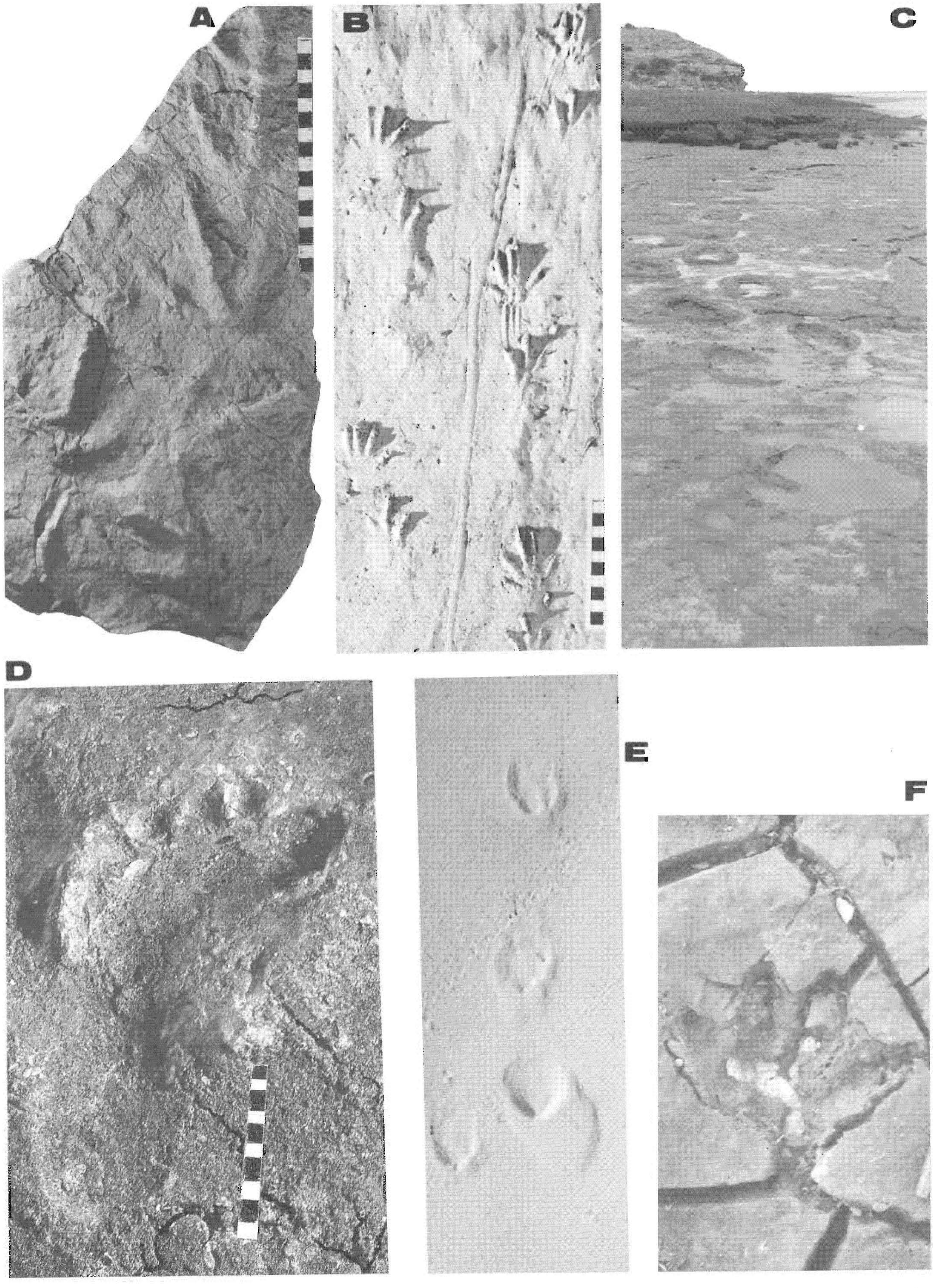

A
B
C
D
E

PLATE XX

CAINOZOIC – 2. Photos: the Editor. Scales in cm.
A: Bird tracks (cast), probably related to Palaeognathae, Rhaeiformes, from the Vinchina Formation or, more probably, Toro Negro Formation; Miocene or, respectively, Pliocene. Quebrada del Yeso, Northern extremity of the Sierra de Umango, La Rioja Province, Argentina. Collections of the Fundación Miguel Lillo, Tucumán, Argentina.
B: Trackway of the living South American lizard *Tupinambis teguixin* Linnaeus, 1758 (Teiidae). Plaster cast; laboratory experiment.
C: *Megatherichnum oportoi* Casamiquela, 1974: a large trackway from the Río Negro Formation, Pliocene or Pleistocene. Carmen de Patagones, Buenos Aires Province, Argentina.
D: A footprint of the Neandertal Man from an Italian cave.
E: Quadripedal base from the trackway of a galloping (living) jackal. Sinai desert. Note the sand crescents, and the Coleoptera trails.
F: The footprint of a living jaguar, from a mud-flat near Ponta Grossa, Paraná, Brazil.


A
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F

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