The Genus *PENICILLIUM* and its teleomorphic states *Eupenicillium and Talaromyces*

JOHN I. PITT

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Preface

This study started in mid 1968, when I was offered a National Institutes of Health Postdoctoral Fellowship at the Northern Regional Research Laboratory, US Dept. of Agriculture, in Peoria, Illinois. Under the guidance of Dr. C. W. Hesseltine, I studied some hundreds of *Penicillium* isolates from cereals and flour, the object being the production of a document on common Penicillia for use in the cereal industry. One thing led to another: it must be recorded that what Dr. Hesseltine envisaged as a nine month project of limited scope has expanded remorselessly until it has occupied as many years.

I gratefully acknowledge my indebtedness to the following people and institutes, without whose cooperation this study would have been impossible: Dr. Hesseltine and the late Miss D. I. Fennell of NRRL, first for stimulating my interest in the genus *Penicillium*, and second for generously providing me with many lyophilised cultures from the NRRL collection, including those prepared and used by Dr. K. B. Raper; to Mr. A. Johnston and Dr. A. H. S. Onions of the Commonwealth Mycological Institute, Kew, Surrey, England for providing me with facilities, cultures, herbarium material and advice; and to Mr. M. V. Tracey, Chief, C.S.I.R.O. Division of Food Research, North Ryde, N.S.W., Australia, for permission to carry out this work and for his encouragement that it be completed.

I record my especial gratitude to Dr. D. L. Hawksworth of CMI for nomenclatural guidance and for editing much of this monograph in draft form; to Ms Ailsa D. Hocking, of C.S.I.R.O. Division of Food Research for professional assistance and for preparing the figures; and to my wife for typing the manuscript: and to all three for years of forbearance.

The scanning electron micrographs and line drawings are the work of Ms Hocking, while Mr. W. D. Rushton prepared the photographic prints.

I express my appreciation also to the many mycologists whose generous gifts of cultures provided so much new working material, especially Dr. H. K. Frank, Bundesforschungsanstalt für Lebensmittelfrischhaltung, Karlsruhe, W. Germany; Dr. R. A. A. Morrall, University of Saskatchewan, Saskatoon, Canada; Mr. M. D. Connole, Animal Research Institute, Yeerongpilly, Queensland, Australia; Dr. L. Leistner, Bundesanstalt für Fleischforschung, Kulmbach, W. Germany; Dr. B. J. Macauley, La Trobe University, Melbourne, Australia; and Dr. G. C. M. Latch, D.S.I.R., Palmerston North, New Zealand.

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Chapter 1

Introduction

Rare indeed must be the human individual who has not encountered fungi of the genus *Penicillium* or been affected by one of the many metabolites produced by them. Penicillia must be numbered among the most commonly occurring of all fungi, among the most numerous of all eukaryotic forms of terrestrial life. Their occurrence in soils is ubiquitous and their presence in the air and on decaying vegetation scarcely less so; in fact few terrestrial habitats are totally denied to them. During the past 30 years the spectacular success of one *Penicillium* metabolite as an antibacterial agent has ensured that the name *Penicillium*—or at least something akin to it—is universally recognised.

And yet how few human individuals are aware of what Penicillia really are, or of their astonishingly diverse infiuences on life on earth. In beginning his introduction to "The Penicillia", Charles Thom (1930) wrote "The molds of the genus *Penicillium* share with the Aspergilli and the Mucors a noisome preeminence as weeds. They rot our fruit, . . . injure our stored grain, . . . contaminate our pantries, . . . discolor fibres, wood, . . . stored paper and sometimes our books. In the laboratory they infest . . . every kind of culture operation, bacteriological, mycological, or phanerogamic". From the viewpoint of the food technologist, cook and microbiologist, Thom was right. But as our knowledge of ecology has broadened through the subsequent years, it has become apparent that the destructive role of Penicillia is also their great natural role, carrying a major share of the burden of recycling used organic matter of all types. To paraphrase Voltaire "If Penicillia did not exist, they would have to be invented"; for in their absence the diversification of other fungi or bacteria into their niches must occur, or the world drown in a morass of natural garbage.

Within living memory, the influence of *Penicillium* on man has dramatically broadened. The discovery of penicillin in 1928, its introduction as a chemotherapeutic agent in the 1940s, the search for high yielding strains, and the development for its manufacture of industrial processes on an unprecedented scale, surely mark a turning point in the history of man's struggle with his environment. However, the story of penicillin is quite beyond the scope of this text. Further information may be found in works such as "In search of penicillin" (Wilson, 1976).

The second great impact of *Penicillium chrysogenum* on mankind is only now becoming clear. The universal use of penicillin has contributed to a dramatic decline in human mortality, an equally dramatic increase in human population, and concomitantly a drastic unbalancing of world ecology. It is ironical that this humble fungus, hailed as a benefactor of mankind, may by its very success prove to be a deciding factor in the decline of the present civilization. The primary role of *P. chrysogenum* in nature is as an agent of decay.

The success of penicillin caused an intensive search for other antibiotics: patulin, citrinin, griseofulvin and penicillic acid were soon discovered and their antibacterial potential established. However most turned out to be too toxic to be used as drugs. Today only griseofulvin remains in use as a chemotherapeutic agent.

In the 1960s the Western world finally become aware that the production of toxic metabolites by microfungi was of more than academic interest. This story began with deaths of turkeys and trout, with toxic peanut and cottonseed meal, with *Aspergillus flavus* and aflatoxin. Then there came ochratoxin and islanditoxin, citreoviridin and luteoskyrin, cyclopiazonic acid and cyclochlorotine. The toxic "antibiotics" patulin, citrinin and penicillic acid were added to the list and the general term "mycotoxin" coined for them. All those listed above except aflatoxin are produced by Penicillia. When names of other *Penicillium* toxins are added—rugulosin, rubratoxin, penitrem, roquefortine, verruculogen—it is evident that the Penicillia have a further claim to notoriety: production of the widest range of mycotoxins of any fungal genus. The study of the impact of these compounds on man and animals is still in its infancy. It can safely be stated, however, that early predictions that mycotoxins were laboratory curiosities, dramatised by chemists and mycologists in search of "relevancy", are unlikely to prove accurate in the decades to come.

Another point is perhaps worth making here. It was extraordinary that the mould which led Alexander Fleming to antibiotics was *Penicillium chrysogenum*, which produces penicillin, the only antimicrobial *Penicillium* metabolite which remains free of suspicion as an agent of mammalian toxicity. Suppose—and this is in no way an unreasonable supposition—that Fleming had seen antibacterial activity in a colony of *Penicillium patulum, P. citrinum, P. viridicatum, P. islandicum, P. expan-*

sum, or *P. purpurogenum*? Would we now enjoy the benefits that penicillin has brought? Far more probably research on fungal antimicrobial agents would have been rapidly halted because of sickness brought on by whichever metabolite had been tested. In hindsight, it must now be stated that penicillin is a mycotoxin which affects only bacteria, rather than saying that antibiotics from *Penicillium* have generally proved too toxic for use in human therapy.

Attempts to harness Penicillia for beneficial purposes have mostly been concerned with the use of enzymes and nontoxic metabolites. Since the late 1930s, chemists have discovered an amazing variety of chemical compounds produced by Penicillia. Some are of industrial importance; the list of known metabolites and possible uses is still growing.

Uses of living Penicillia, however, remain few. Often cited examples are the production of cheeses of the Camembert and Roquefort types. Because of excessive sporulation and the threat of mycotoxigenesis, uses such as single cell protein manufacture are unlikely.

Why should we attempt to identify Penicillia? To again quote Thom (1930), "their presence is thrust upon us so frequently that some means of identifying them is very desirable". With enquiries from ecologists and food technologists on one hand, and chemists and mycotoxicologists on the other, the need for accurate identifications of *Penicillium* species is no longer "very desirable" but pressingly urgent. After half a life time of study, Thom in 1930 wrote, "At best, it is possible to present only a very unsatisfactory scheme of classification of this difficult group". Forty nine years later, this new volume is offered as another step towards accurate classification of fungi belonging to the genus *Penicillium*.

Chapter 2

Penicillium as History

The generic name *Penicillium* (Latin, *penicillus* = little brush) was first published by Link in his "Observationes in Ordines plantarum naturales" in 1809. Link (1767–1851) described three species, *P. glaucum*, *P. candidum* and *P. expansum*. Thom (1910), in his first major treatise on *Penicillium*, pointed out the impossibility of equating the first two with modern concepts. However, Link described *P. expansum* from rotting fruit and in 1905, Thom (1930 : 10) made a survey of native fruits on sale in Berlin which convinced him that *P. expansum* was the same as the common apple rot fungus in that area. Thom (1910: 27) therefore treated *P. expansum* as the type species of the genus.

The problem of *Penicillium* Fr. Under the International Code of Botanical Nomenclature (Stafleu *et al.*, 1972) valid publication of names of *Fungi caeteri* start on 1 Jan. 1821; the name *Penicillium* Link cannot stand alone because it was published in 1809. For a name to be validly published (Art. 13f), it must be accepted by an author post 1 Jan. 1821 and, furthermore, prestarting point names accepted by Fries in his "Systema Mycologicum" (1821–32) must be given priority over any earlier names for the fungus.

Hawksworth and Sutton (1974: 563) pointed out that Fries (1829), in accepting *Penicillium* in that publication, typified it not by one of Link's species but by reference to *Mucor crustaceus* Linnaeus. It was further shown by Hawksworth *et al.* (1976) that the Linnaen species was most unlikely to be a *Penicillium* in the accepted sense, as Linnaeus (1753) referred his species to an illustration by Micheli (1729) of a *Botrytis*-like fungus. Tab. 91 of Micheli (1729) contains two figures labelled "Fig. 3", one of which is probably a *Penicillium*, and it seems likely that Fries intended using the name *Penicillium* in its current sense but made a *lapsus*.

In order to maintain current usage of *Penicillium*, Hawksworth *et al.* (1976) have proposed the conservation of *Penicillium* Link ex Gray (type: *P. expansum* Link ex Gray) against *Penicillium* Fr. (type: *Mucor crustaceus* L., *nom. dub.*). This proposal will be considered by the XIII International Botanical Congress in 1981.

Penicillium glaucum. Link (1824) abandoned the use of *Penicillium expansum* and grouped all green Penicillia under the name *P. glaucum*. This has no nomenclatural significance, but the taxonomic impact has been profound. For many years green Penicillia, i.e. most of those species with which we associate the name *Penicillium* today, were known simply as *P. glaucum*. In discussing this problem Thom (1930: xi) wrote "... we have in mind an elaborate piece of biochemical work upon a particular activity of '*P. glaucum* Link'. The chemist when asked for his culture confessed he had lost it and referred us to the one who had furnished it to him who replied, '—asked for a green *Penicillium*, we will guarantee that the culture was a *Penicillium* and that it was green—that's all we know about it' ".

All modern authors who have discussed the identity of *Penicillium glaucum* have agreed that typification is impossible and that its usage has been hopelessly confused. Under Art. 69 this name is considered a *nomen dubium* and rejected.

The Dark Ages. Although Link and Gray established a concept of *Penicillium* similar to that in current usage, many years passed before the genus as we know it today emerged as an unmistakable entity. This is scarcely surprising. Until the advent of pure culture microbiological techniques, mycologists illustrated and described only from natural sources, a technique singularly unsuited to *Penicillium* species with their minute, delicate, ephemeral structures.

During the years 1830 to 1900, many mycologists, among them Corda, Fresenius, Bonorden, Preuss, Rivolta and Spegazzini, described many *Penicillium* species. Most can be seen from the original illustrations to belong to *Cladosporium* or other dematiaceous hyphomycetes. A few are probably true Penicillia, but because of lack of information they remain unrecognisable. Even where herbarium material still exists, identification is almost always impossible. Both Biourge (1923) and Thom (1930) reported extensive observations on herbarium specimens, but with disappointing results. *Penicillium* taxonomy awaited an infusion of ideas from the bacteriologist.

Renaissance: early cultural studies. The first milestone in the rebirth of *Penicillium* taxonomy came from Brefeld (1839–1925), with his life history of "*Penicillium glaucum*" (1874). It is probable (Langeron, 1922; Stolk and Scott, 1967) that Brefeld was working with mixed cultures, and this would be hardly surprising. Among the fungi which he described and illustrated with considerable care were species with biverticillate penicilli; one, from a coremium on an apple, with terverticillate penicilli and recognisable as *P. expansum*; and a perfect state now classifiable in *Eupenicillium*. The development of a sclerotioid cleistothecium and its eventual production of asci and ascospores was illustrated in detail.

In 1877 van Tieghem (1839–1914) reported similar observations with *Penicillium aureum* van Tiegh., a species classifiable as a *Talaromyces*. His fungus was growing on a seed: when placed in a moist chamber conidial structures were produced together with novel, cottony, yellow ascocarps in which ascospores, $5 \times 3\ \mu m$, developed. By culturing conidia and ascospores separately on bread and orange quarters, van Tieghem was able to demonstrate the complete life cycle.

The next signicant advance was made in 1891, when Delacroix (1858–1907) described *Penicillium duclauxii* in pure culture. He maintained his isolates as living cultures and distributed them as type material. The last strains of his *P. duclauxii* isolate were not lost from world collections until at least 1950. This work appears to be the first recognition of the value of distributing cultures for taxonomic purposes.

At about this same time, studies on the biochemical properties of *Penicillium* species commenced. Wehmer (1858–1935) published his genus *Citromyces* (now regarded as congeneric with *Penicillium*) for fungi producing citric acid and his work was later incorporated into Lafar's "Technische Mykologie" (1906). Wehmer also described *P. italicum*, the blue mould of *Citrus* fruits.

Dierckx and Biourge. More—much more—has been written about what Dierckx wrote on *Penicillium* than he himself contributed to the public record. His only publication on *Penicillium* (Dierckx, 1901) was the text of a short address to the Belgian National Academy. In this he stressed the need for pure cultures, descriptions under standardised conditions and distribution of living material. He also described some 25 new species, by far the largest number in a single contribution to *Penicillium* taxonomy at that time. It is obvious from this lecture that he understood both the revolutionary nature of his studies and the basic information needed to begin classifying *Penicillium* species.

It was most unfortunate that his work was never completed. A student of Dierckx described (Biourge, 1923: 34) how virtually all of Dierckx' cultures were lost while he was travelling and how, discouraged, he never returned to the study of *Penicillium*. All that remained were 25 meagre published descriptions and extensive notes, drawings and water colour paintings from which Biourge endeavoured to salvage something.

A single culture of Dierckx', however, did survive: the original isolate of *Penicillium griseoroseum*. This is still in maintenance and has the distinction of being the oldest *Penicillium* in culture, for a period of more than 75 years.

Biourge, whose monograph on *Penicillium* was published in 1923, built on the foundations provided by Dierckx. He neotypified as many of the Dierckxian species as he could recognise, provided the first subgeneric classification of the genus and emphasised again the need for pure culture techniques. Recording his observations from 13 different media, he provided descriptions of 125 species, of which about 60 were described as new.

Biourge (1923) also published a "Liste Onomastique du genre *Penicillium* (sensu latissimo)" in which he recorded all *Penicillium* species described up to 12 January 1923. His "sensu latissimo" was broad indeed: as well as *Citromyces* species, Biourge transferred into *Penicillium* the names of species which produced some form of penicillus—including ones in *Spicaria, Scopulariopsis, Isaria, Stysanus, Haplographium, Oidium* and other genera. These names are recorded here in the Species Lists; the synonymy of many of them is traced in this monograph for the first time.

Charles Thom. Thom (1872–1956) began work on *Penicillium* soon after the time of Dierckx' publication, in 1904, and devoted much of his lifetime to the study of *Penicillium* and *Aspergillus*. His first paper, "Fungi in cheese ripening" appeared in 1906; in this he described *P. roquefortii* and *P. camembertii*. In 1910 came the much longer and very important work "Cultural studies of species of *Penicillium*". Here emphasis was placed on the necessity for comparative study of species on standardised media; he provided the first key to the genus and also described 13 new species. Furthermore, he recognised the practical importance of temperature as a parameter controlling growth of spoilage fungi and provided the first temperature relations data for *Penicillium* species. Thom's work culminated in 1930 with publication of "The Penicillia", a compendium of all species published to date with descriptions of 300 species, keys to their identification, and some indications of synonymy. He divided the genus into four divisions (= subgenera) and subdivided each into sections and subsections, creating the first orderly overall classification of the genus. In old age he collaborated with K. B. Raper to produce "A Manual of the Penicillia".

Thom's impact on *Penicillium* taxonomy is difficult to overestimate. His first and last publications span 45 years; he brought order to the taxonomy of the genus; and many of his concepts on speciation and subgeneric classification still stand.

Raper and Fennell. Kenneth B. Raper and Dorothy I. Fennell (1916–1977) began work on *Penicillium* at the Northern Regional Research

Laboratory, US Dept. of Agriculture, about 1940. Raper had worked with Thom for the previous decade, and the urgent wartime USDA programme on penicillin production, with consequent increase in interest in Penicillia, provided motivation for a revision of *Penicillium*. "A Manual of the Penicillia" appeared in 1949. Although ostensibly coauthored by Raper and Thom, it was in fact largely written by Raper and Fennell, using Thom's records, descriptive material and advice as a guide.

This Manual represented a great advance. Raper systematically examined all species which were known in culture and reduced the majority of them to synonymy. The 137 species accepted were ordered in 4 sections and 41 series along the lines proposed by Thom. Emphasis was placed on practicality. That this Manual has now been in use for 30 years is a tribute to the conceptual acuity and thoroughness of its three authors.

Raper pioneered another, often overlooked, advance: the use of lyophilisation in mycology. He took care to ensure that all *Penicillium* cultures ex type and other important sources were preserved by this method. Raper's foresight has had a most important practical consequence: the present revision is based on his cultures, seen now as they appeared in the 1940s, providing a continuity of investigation which otherwise would not have been possible.

Other taxonomists. A history such as this would not be complete without mention of some other twentieth century mycologists who have contributed significantly to *Penicillium* taxonomy.

Over the years 1905 to 1914 Bainier, sometimes in collaboration with Sartory, introduced more than 30 new names in *Penicillium* and *Citromyces*. Many were well described and illustrated and are still recognisable, especially those of which cultures were distributed, and have been accepted here. But, as noted by Thom (1930: 15), a number of his descriptions were inadequate and remain of uncertain application.

Westling (1911) published a monograph of *Penicillium* species from Scandanavia, including 18 described as new. His descriptions were careful and he distributed cultures ex type; as a consequence many of his species have been accepted in later studies.

In the following year, Sopp (1912; formerly known as Olav Johan-Olsen) produced a similar monograph. Unfortunately he did not distribute cultures; only a few of his species have been recognised by later taxonomists.

Penicillium species from Polish forest soils formed the basis of the study by Zaleski (1927). He described 35 new species and one variety. Cultures were grown on neutral Raulin medium solidified with gelatin, and in consequence overemphasis was placed on substrate liquefaction and mycelial buckling. Several important soil fungi were first named by him.

From 1930 to 1965, George Smith (1895–1967) of the School of Public Health, University of London, published a long series of short papers on new species of *Penicillium.* Although he was clearly knowledgeable about *Penicillium* taxonomy, only rarely did he attempt to assess the relationships of his new species within the framework of the genus as a whole. Perhaps in consequence few of his new taxa have survived later scrutiny.

A study of soil fungi of Lunz, now in East Germany, was published by Armin von Szilvinyi (1941). Similar in concept to that of Zaleski, it was much less successful. Only a few of his cultures have survived and without them his new species are unrecognisable. He also introduced a great number of varieties, all with the epithet "*lunzinense*", which are equally unrecognisable today.

Soon after the publication of the Raper and Thom Manual, Abe (1956) published a reclassification based on it, but notable for the wide variety of morphological and biochemical properties taken into account. Abe's work was based almost entirely on his own cultures without comparison with type or authentic isolates and as a result his data must be treated with caution. Abe (1956) also described 32 new species and varieties, but failed to validly publish them. Most were examined by Smith (1962) and either validated or placed in synonymy.

A Russian text on *Penicillium* by Pidoplishko (1972) contained some recent names, but was mainly based on the Raper and Thom Manual.

In the past decade several papers on *Penicillium* taxonomy have been published by mycologists at the Centraalbureau voor Schimmelcultures, Baarn, Netherlands. Most have dealt with perfect states and are discussed in Chapter 3. One study, by Samson *et al.* (1976), revised subsect. *Fasciculata* of sect. *Asymmetrica* Raper and Thom: it is discussed in Chapter 10, which deals with subgen. *Penicillium.*

To broaden the range of characters on which *Penicillium* taxonomy could be based, Pitt (1973, 1974) introduced the techniques of incubating cultures at high and low temperatures (37°C and 5°C) and on a medium of reduced water activity. As an estimate of growth under these and traditional incubation conditions, colony diameters were measured after a specific time interval, seven days. Data obtained showed a high infraspecific correlation, but often with useful differences between species. Apparently based on stable physiological characters, these techniques have now been tested successfully on several thousand isolates. Incubation under standardised conditions underlies the descriptions of colony morphology on which this monograph is based.

Chapter 3

Teleomorphic States of *Penicillium*

I. History of *Eupenicillium*

It is over 100 years since Brefeld first described the production of a teleomorphic* state by a *Penicillium* species. In "Die Entwicklunggeschichte von *Penicillium*", published in 1874, Brefeld described sclerotioid cleistothecia and their maturation to produce chains of asci, which in turn contained ornamented ellipsoidal ascospores. These germinated by dehiscence along the longitudinal axis. He reported the fungus studied as "*Penicillium crustaceum* Fries, *Penicillium glaucum* Link".

Winter (1887), in his important account of the central European pyrenomycetes, included an extract of Brefeld's description and figures and applied the name "*Penicillium crustaceum* (L.) Fr." to Brefeld's fungus. Based on Winter's account, Ludwig (1892) introduced the new generic name *Eupenicillium* for the perfect state described by Brefeld and applied the name "*Eupenicillium crustaceum* (L.) Fr. (*P. glaucum*)". Under the provisions of the International Botanical Code (Art. 59), the

* In accordance with recent recommendations by Hennebert and Weresub (1977), the term "anamorph" will be used throughout this work to refer to asexual mitotic diasporic (imperfect) fungal states; "telemorph" will refer to ascocarpic (perfect) states; and the term "holomorph" will refer to the entire fungus.

correct name for Brefeld's fungus is *Eupenicillium crustaceum* Ludwig, as stated by Stolk and Scott (1967). It is to be typified by Brefeld's fungus and not treated as a new combination based on the name in *Penicillium*. This is fortunate, as given the state of *Penicillium* taxonomy during the nineteenth century, the identity of the anamorphic state belonging to Brefeld's fungus is unknown. It is highly unlikely to have been the popular concept of "*Penicillium crustaceum*" which was usually considered to be a similar fungus to *P. expansum* (Raper and Thom, 1949: 515).

The name *Eupenicillium* was ignored or overlooked for many years. Langeron (1922) independently introduced the name *Carpenteles* for *Penicillium* species producing sclerotioid cleistothecia. Like *Eupenicillium*, this genus was based on Brefeld's fungus, but Langeron chose the name *Carpenteles glaucum*, correctly cited as *C. glaucum* Langeron, as his type.

Considering that *Carpenteles glaucum* was indeterminable, Shear (1934) proposed the further new name *Carpenteles asperum* for Brefeld's species. He reported isolation of a teleomorphic fungus which he identified with that of Brefeld. That Stolk and Scott (1967) showed Shear's fungus to differ from Brefeld's is nomenclaturally irrelevant as Shear clearly regarded Brefeld's organism to be the type for his new name.

Benjamin (1955) accepted the name *Carpenteles* and transferred to it several other teleomorphic species with *Penicillium* names which had been described in the intervening years.

Stolk and Scott (1967) revived the use of the name *Eupenicillium* Ludwig, based on a portion of the illustrations by Brefeld (1874) as lectotype. They transferred the previously described species of *Carpenteles* to *Eupenicillium* and in a series of subsequent papers (Scott and Stolk, 1967; Scott, 1968a; Stolk, 1968), described 16 new species.

Scott (1968b) published a monograph of *Eupenicillium*, with descriptions of, and a key to, 26 species. The key, based on mature teleomorphic states, was difficult to use because maturation of some species requires many weeks. Because of this, Pitt (1974) developed a synoptic key to *Eupenicillium* species, and added to it a number of sclerotigenic *Penicillium* species. Based primarily on cultural and anamorphic state characters, that synoptic key remains the basis for *Eupenicillium* species determination in the current monograph.

II. History of *Talaromyces*

Just three years after Brefeld reported the association of *Penicillium* with a cleistothecial ascomycetous state, van Tieghem (1877) found on a