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Irish and British cave biology, mid-19th to the early 20th century: forgotten beginnings and historical insights

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Abstract: Between 1895 and 1906, naturalists associated with the Dublin Science and Art Museum (now the National Museum of Ireland) collected fauna (and some flora) from Mitchelstown Cave, Marble Arch Cave, and several other caves across the island of Ireland. The resulting preliminary inventory reflects biota commonly encountered in Irish caves and represents the first such survey undertaken anywhere in the British Isles. Almost nothing of note is recorded from Great Britain during this period. Members of the Irish group also speculated about the evolution of blind cave animals within a Darwinian framework – an unusual perspective at the time – and proposed a simple empirical ecological classification of cave fauna. Interest in the subject declined after the turn of the century, and thereafter the political situation ensured that it did not recover. It is suggested that it was the political situation and the social environment that were the major reasons for failure to capitalize on what might have become a promising start. Whilst the results of this pioneering work were to all intents and purposes forgotten, they do perhaps suggest a reason behind the historical delay in adoption of neo-Darwinian thinking by leading speleobiologists. It is also argued that they contribute some insight into the roots of an over-emphasis on troglobites in cave ecology.

Separate from investigations of true cave fauna, the years 1896 to the outbreak of war in 1914 produced sundry British and Irish records of the threshold-dwelling European Cave Spider, *Meta menardi*.

Keywords: Boho caves, Carpenter, cave ecology, Collembola, Coolarkin Cave, Dunmore Cave, evolution, Halbert, Lyster Jameson, *Lipura*, Marble Arch Cave, *Meta menardi*, Mitchelstown Cave, natural selection, troglobites, troglodytes, Scharff.

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"[Mitchelstown Cave] is the only grotto in England, Scotland, or Ireland where, up to the present time, there have been found animals peculiar only to caverns."
Édouard-Alfred Martel, 1896.

Introduction

The present paper is a contribution to a study of speleobiology in Britain and Ireland, approached from a 'history of biology' perspective. It presents a detailed account of the history of *cave* biology in the United Kingdom from 1859, the year in which *On the Origin of Species* (Darwin, 1859) was published, to the establishment of the Irish Free State in 1922. The latter date is appropriate because the only investigations of substance relevant to cave biology during this period were conducted in Irish caves.

The paper begins by reviewing the status of cave biology in the United Kingdom as it stood in 1859. It then provides a detailed chronological account of investigations undertaken in Irish caves from that year until activity declined in the early 20th century, framed within the political, social, and institutional environment. It is suggested that it was the political situation and the social environment that were the major reasons for failure to capitalize on what might have become a promising start. This is followed by a review of the much more limited activity that occurred in Great Britain during the same period. The paper is a case study in the history of speleobiology. Using early cave biology in Ireland and Britain it illuminates how science can be driven by false hypothesis, and the impact of institutions and political change on the development of scientific ideas

Subsequently it is argued that the insights that arise from this study help to explain the an apparent historical delay in the adoption and application of neo-Darwinian thinking by leading speleobiologists. They also contribute some understanding of the roots of the longstanding undue emphasis on troglobites in studies related to cave ecology.

For completeness, a list of *contemporary* cave occurrence records of the threshold-dwelling Cave Spider, *Meta menardi*, from the British Isles is included.

Terminology

Sometimes in the associated literature, the term ***cave biology*** has been employed in a flexible and broad context to encompass ***speleobiology*** as a whole. In contrast, where it appears in the present paper, it is used in its more restricted sense, relating only to the biology of ***caves***, as distinct from that related to groundwater and other subterranean habitats. This usage recognizes that, prior to the Great War, biological investigations of caves and groundwater environments had developed as separate fields of study and, as such, they were approached independently. Only later was the biotic and physical continuity of subterranean environments more-fully recognized (Moseley, 2021, p.27; 2024, p.14).

The term ***Great War*** is used in preference to First World War, in conformity with contemporary usage in the historical period under consideration. Similarly, although never done nowadays, capitalization of a species epithet in a source publication (e.g. *Wrightii*) is retained, in conformity with original usage. Also, when the term *troglodyte* appears in contemporary literature referring to cave fauna, there is a temptation to treat it as synonymous with the modern and widely adopted term *troglobite*. Although its usage clearly implies blind animals restricted to cave environments, *troglodyte*, unlike the modern term, was never defined and thus might not be strictly equivalent in meaning. For reasons of historical accuracy, the term is therefore retained here in its original, somewhat ambiguous, sense.

The cave referred to by the 20th century naturalists as Mitchelstown Cave was discovered during quarrying in 1833 and is also known as Mitchelstown New Cave. Naturalists who investigated its fauna during the late 19th century were unaware of an adjacent cave referred to variously as Old Mitchelstown Cave or Desmond Cave (Baker, 1906).

Ireland refers throughout to the pre-1922 country. It therefore incorporates the present Republic (Éire) and Northern Ireland.

The historical background: British and Irish cave biology before 1859

In 1859 very little was known or understood about subterranean environments, and they were still widely regarded as hostile and largely inhospitable to life. Caves were generally assumed to be isolated, bounded spaces and, as yet, there was no understanding of the ecological continuity between caves and groundwater systems accessed through wells and other water sources (Malard *et al*., 2023; Moseley, 2024). The only animals thought truly to "belong" underground were blind, depigmented species. Unlike on the European continent, where Schiödte (1851) had already described caves as ecological units, British and Irish naturalists showed little interest in cave-dwelling organisms other than bats.

By 1859, less than thirty years after the chance discovery in Carniola (a Balkan region located almost entirely within present-day Slovenia) of the beetle *Leptodirus hochenwartii*, the first known blind cave insect, investigations in continental Europe and the United States had revealed the existence of previously unknown and zoologically diverse communities of blind animals inhabiting deep, lightless caves (Schmidt, 1832a, b, 1847; Polak, 2005; Romero, 2009; Moseley, 2021). These pale, blind organisms, able to survive and thrive in an environment long assumed to be uninhabitable, generated considerable interest, including in Great Britain and Ireland. In 1857, only two years before publication of *On the Origin of Species*, entomologists from Edinburgh and Dublin conducted brief, largely unsuccessful, searches in England and Ireland respectively. These pioneers were creationists whose worldview allowed for the possibility that God had created analogous blind species in the British Isles, just as He had elsewhere in Europe and in North America. A specific comment to this effect appears in Anon (1857) ***[Note 1]***.

Of these attempts to find troglodytes in the British Isles, the first was that of the Scottish naturalist Andrew Murray, who visited Blue John Cavern (Derbyshire) in 1855 (Moseley, 2015). Soon afterwards, the distinguished Anglo-Irish entomologist Alexander Henry Haliday and his younger colleague Edward Perceval Wright collected invertebrates in Mitchelstown Cave, County Tipperary, near the border with County Cork (Murray, 1857; Wright *in* Wright and Haliday, 1857; DeArce, 2012; Moseley, 2021).

Neither Wright nor Haliday possessed directly relevant experience, and collecting underground, relying on hand-held candles, presented significant practical difficulties. The cave was visited only once, in August 1857. It can reasonably be assumed that these early investigators hoped to find blind beetles, millipedes, springtails, or other cave-adapted forms comparable to those described and illustrated by Schiödte (1851) from the Carniolan caves. Consequently, they must have been disappointed when no such organisms, apart from springtails, were encountered. The flies, spiders, and other animals that they undoubtedly observed were presumably dismissed as non-cavernicolous.

Only two species – both of them springtails (Collembola) – were collected and reported. One, found near the cave entrance, was dismissed as a stray. The second, collected near drip pools deep within the cave (Anon, 1857) was considered a possible troglodyte and tentatively identified, albeit with reservations, as *Lipura stillicidii*, one of the species known from the Carniolan caves. At that time, study of the taxonomy of Collembola remained in its infancy (Lubbock, 1873), and the identification relied upon consideration of the cave habitat, analogy with the Carniolan species, and hopeful-expectation, rather than on robust taxonomic evidence. *L. stillicidii* remains a valid species, but, as Haliday quickly realized, it was a misidentification ***[Note 1]***. The specimens were more likely *Deuteraphorura inermis*, a widespread springtail, abundant in caves and surface habitats throughout Britain and Ireland. Nevertheless, the Mitchelstown Cave examples being eyeless, the mistaken assumption that it was a troglodyte persisted.

Because caves in the British Isles contain few blind animals, these efforts proved unsuccessful, yielding only the single doubtful "troglodyte" *L. stillicidii,* and they were not immediately repeated (Moseley, 2015; 2021). There was no further collecting in Irish caves until the mid-1890s. Multiple factors, outside the scope of the present paper, appear to have been involved, although the disappointing results of the early searches undoubtedly reflect one major cause: in Ireland, the two decades *circa* 1870 to *circa* 1890 were years of near stagnation in entomology overall (Beirne, 1985). And, as pointed out by the great French cave explorer Martel, this lack of interest was also true of all aspects of British and Irish speleology except for archaeology at that time (Martel, 1897, pp.500–501). But then, following this long hiatus of nearly forty years, Wright's report of a putative collembolan troglodyte, although a mistake, bore unexpected fruit by sparking the first cave fauna survey in the British Isles.

Cave biology in Ireland 1859–1922

Neither Wright nor Haliday published anything further on cave fauna. Haliday, a member of the Anglo-Irish professional class and a leading figure in Irish entomology, was already 50 years old by 1857 and moved to Italy in 1861 because of ill health (Nash and O'Connor, 2011). In contrast, Wright was still in his mid-twenties and presumably physically able to continue field investigations in caves, but his scientific interests and commitments were broad. Nevertheless, he maintained a peripheral interest in caves, visiting the speleobiologically important Postojna Cave in 1861 and later becoming a founding member of the Société de Spéléologie, established in 1895 by Édouard-Alfred Martel (Anon, 1909; Shaw, 1999).

[Note 1]: Wright made the correction in a presentation to the British Association for the Advancement of Science (Anon, 1857). Considering that the *L. stillicidii* had a wide geographical range in continental Europe, it had not at first seemed unlikely that it also occurred in the British Isles. However, on careful examination, Haliday had found that the Irish specimens were eyeless in contrast to those described from Europe which had ocelli (he was likely referring to pseudocelli) and other morphological differences. In answer to a question from the audience, he opined that these animals were distinct species "*created for the special circumstances in which they were found*."

Interest in cave biology in Ireland was revived only during the final years of the 19th century, driven by a younger generation of naturalists. Between 1895 and 1906, a closely connected group of field naturalists and museum curators associated with the Natural History Division of Dublin Science and Art Museum (now the National Museum of Ireland) and the Field Clubs, collected fauna from Mitchelstown Cave, Marble Arch Cave, and from several other cave sites. Although their investigations were preliminary and narrow in scope, they constitute the only inventory of cave fauna from any region of the British Isles before formation of the British Speleological Association in 1935. Members of this group also discussed the evolution of blind cave animals within a Darwinian framework, and proposed a simple ecological classification of cave fauna, both of which aspects are considered below.

Cave biology in late 19th and early 20th century Ireland cannot be characterized simply as an Irish rather than British undertaking. Despite emancipation of the Roman Catholic majority in 1829, Ireland remained a Protestant-run country ***[Note 2]***. Irish natural history was largely still the preserve of Anglo-Irish and English naturalists, whether resident in or visiting Ireland, and Irish-born Protestant clergymen and other middle-class professionals (Beirne, 1985; Blackstock, 2013; Jarrell, 2016) ***[Note 3]***. In the specific case of cave biology, most of the principal figures were British naturalists working in Ireland together with their Anglo-Irish colleagues. One important exception was Henry Paul William Lyster Jameson, who came from an Anglican Irish family (Craven, 2012; Evans, 2021).

The renewed interest in the possibility of finding more cave animals in Ireland coincided with a broader revival of entomological activity during the period from approximately 1890 to 1900 (Beirne, 1985). Much of the ensuing cave work was published in *The Irish Naturalist*, a journal established in 1892 through the efforts of Dublin naturalists. Similar in purpose and scope to local natural history journals in Britain, it published records of Irish flora and fauna, local species lists, and reports of field club activities. Its circulation, however, remained modest and primarily domestic (Scharff, 1922; Wyse Jackson and Wyse Jackson, 1992).

Four men were the most prominent in the investigation of cave fauna. These were Dr Robert Francis Scharff (1858–1934), George Herbert Carpenter (1865–1939), James Nathaniel Halbert (1872–1948), and, the youngest, Henry Paul William Lyster Jameson (1875–1922). Other names identified from the literature as associated peripherally with cave fauna are (in alphabetical order) Alfred Cort Haddon (1855–1940), Francis Ignatius Neale (*unknown–unknown*), Albert Russell Nichols (1859–1933), Robert Lloyd Praeger (1865–1953), Henry Joseph Seymour (1873–*unknown*), and Richard John Ussher (1841–1913). The clergyman and amateur bryologist Reverend David McArdle (sometimes spelled M'Ardle) (1849–1934) also collected mosses and liverworts from cave entrances during broader botanical work.

[Note 2]: Beirne (1985, p.8) commented wryly in relation specifically to Irish entomology: *"Up to 1920 there was only one author (of a single note, in 1893) whose surname began with an O'."* Carpenter (1901) observed, revealingly, that *"…* [in Irish Field Club work]*, as in many other walks of life where the initiative must be taken by the people, the North has led the way. But for the support of national scientific institutions we must depend upon a department of the government and these institutions have naturally grown up in that city which the government regards as the Capital of Ireland, namely Dublin."*

[Note 3]: One example was the prominent entomologist Reverend Arthur Ricky Hogan (1832–1880). After moving to England in 1856, he became an important figure in early investigations of well-shrimps (Moseley, 2021, p.28).

[Note 4]: The committee was preceded by a British Association committee, appointed to explore the caves of the South of Ireland (BAAS, 1880).

Figure 1*: Dr Robert Francis Scharff (1858–1934).*
[From the Irish Naturalists' Journal, Vol.5(6), (1934), Plate 13. Reproduced with permission, Irish Naturalists' Journal Ltd.]

Scharff and the Dublin Science and Art Museum

Robert Francis Scharff (Fig.1) was an English zoologist born in Leeds, West Yorkshire, who moved to Ireland when appointed to a position at the Dublin Natural History Museum, and became widely known for his contributions to Irish natural history: Beirne (1985, p.22) described him as *"a naturalist of many interests and wide vision who was to be a constructive influence on entomology in the* [Museum] *for some 35 years."* He was a committed advocate of Darwinian natural selection (Jarrell, 1983; Adelman, 2005).

In 1887 Scharff was appointed Assistant Naturalist at the then Natural History Museum, and Curator (i.e. Head of the Museum) in 1887. In 1891 Natural History was incorporated as a Division of the newly opened Museum of Science and Art, and his title changed to Keeper of the Natural History Division. He was promoted to Acting Director of the Museum in 1916. After reaching retirement age in 1921, he took his pension and, following the establishment of the Irish Free State in 1922, returned to England (Anon, 1934; Jarrell, 1983; Shaw, 1999; Leaney, 2009; Nigel T Monaghan [National Museum of Ireland; Retired], pers.comm., 2026).

Scharff's interests in Irish natural history were broad and eclectic, extending to Irish caves. He played an important role in facilitating cave research, particularly in archaeology and palaeontology. He chaired the *Committee Appointed to Explore Irish Caves*, established jointly by the Royal Irish Academy and the British Association for the Advancement of Science ***[Note 4]***. The principal emphasis of their work was the archaeology and palaeontology of Ireland's many small caves. Because these shallow sites offered little prospect for the discovery of blind cave fauna, their investigations had limited relevance for cave biology beyond occasional observations of bat colonies. But Scharff also served as Chairman of the Royal Irish Academy (RIA) Flora and Fauna Committee, which became a source of support and funding for speleobiological research (Ussher, 1902; Scharff, 1902; Scharff *et al*., 1906, 1919; Shaw, 1999).

Taxonomic placement	Collected by Wright & Haliday, 1857	Collected by combined field clubs, 06 July 1894				Collected by Lyster Jameson, 22 – 25 July 1896					Most likely identity
		Anon 1894	Carpenter 1895	Friend 1895	Friend 1896	Lyster Jameson 1896	Anon 1896	Carpenter 1897a	Carpenter 1897b	Carpenter 1902	
Collembola, Onychiuridae	*Lipura stillicidii (?)*	*Lipura stillicidii*	*L. stillicidii*								*Deuteraphorura inermis*
Collembola, Onychiuridae			*Lipura Wrightii* sp. nova			*L. Wrightii*				*Lipura inermis*	*Onychiurus* sp. *sensu lato*
Collembola, Entomobryidae		*Templetonia crystallina*	*Sinella cavernicola* sp. nova					*Templetonia cavernicola*		*Heteromurus margaritatus*	*Heteromurus nitidus*
Collembola, Entomobryidae						*Sinella cavernicola*		*Cyphoderus Martelli* sp nova	*Cyphoderus (?Sinella) cavernicola*	*Pseudosinella cavernarum*	*Pseudosinella* sp.
Collembola, Tomoceridae						*Tomocerus tridentiferous*		*T. tridentiferous*			*Tomocerus minor*
Collembola, Hypogastruridae								*Achorutes armatus*			*Ceratophysella armata*
Collembola, Neanuridae								*Anurida granaria*			*Anurida granaria*
Collembola, Arrhopalitidae								*Smynthurus coecus*		*S. coecus*	*Arrhopalites caecus*
Araneae, Linyphiidae		*Porrhomma myops*	*P. myops*			*P. myops*					*Porrhomma* sp.
Araneae, Linyphiidae						*Leptyphantes pallidus*	*L. pallidus*				*Palliduphantes pallidus*
Acari, Parasitidae		unidentified gasmid	*Gamasus attenuatus*			*G. attenuatus*					*Eugamasus* sp.?
Oligochaeta, Lumbricidae			earthworm	*Allurus flavus*	*Allurus tetraedrus*						*Eiseniella tetraedra*
Oligochaeta, Lumbricidae					*Allurus* sp(p). Imm.						*Eiseniella tetraedra*
Diplopoda, Polydesmidae						*Brachydesmus superus*					*Brachydesmus superus*
Coleoptera, Carabidae						*Trechus micros*					*Trechus micros*
Coleoptera, Staphylinidae						*Ancyrophorus omalinus*					*Ochthephilus omalinus*
Coleoptera, Carabidae						*Pterostichus vulgaris*					*Pterostichus* sp.
Diptera, Mycetophillidae						*Sciara sp.*					*Sciara* sp.
Mollusca, Oxychiliidae						*Hyalina contracta*					*Oxychilus cellarius*

Table 1*: Fauna collected from Mitchelstown Cave, County Tipperary, Ireland (1857–1894).*

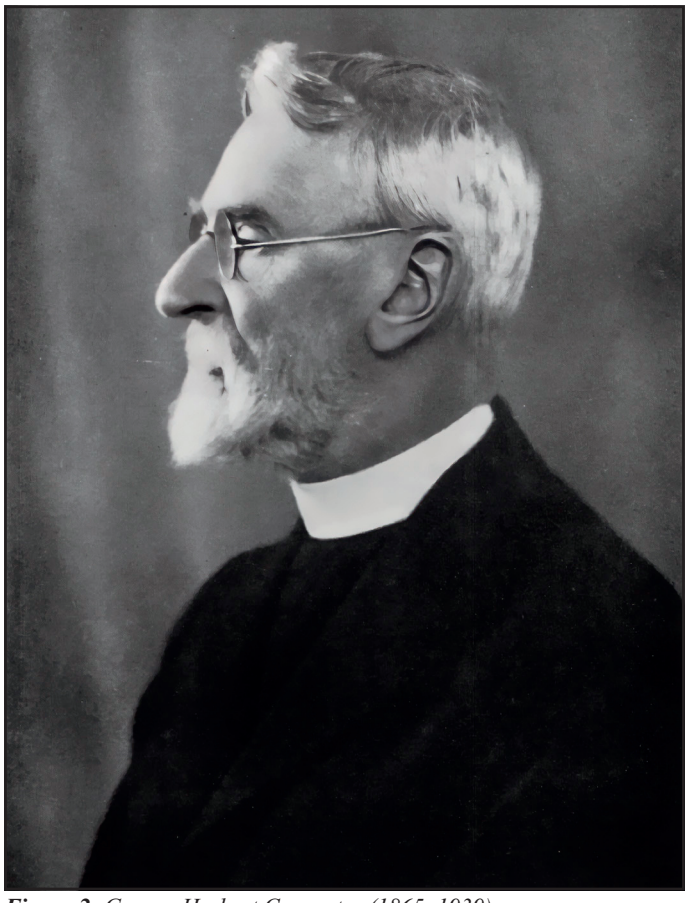


Figure 2*: George Herbert Carpenter (1865–1939). [From the Irish Naturalists' Journal, Vol.7(5), (1939), Plate 5. Reproduced with permission, Irish Naturalists' Journal Ltd.]*

Searching for troglodytes in Mitchelstown Cave: Carpenter, July 1894

In contrast to the many small caves that, as mentioned above, were of little or no speleobiological importance, deeper caves – commonly hydrologically active and less easily accessible – presented a greater possibility of harbouring blind cave animals. Among these was Mitchelstown Cave, where Wright and Haliday had previously reported a putative collembolan troglodyte. Since its discovery during quarrying in 1833, the cave had become increasingly well-known and could now be explored with the assistance of experienced local guides. Scharff became interested in pursuing the earlier observations and determining whether they could be confirmed and perhaps extended.

In 1894, George Herbert Carpenter (Fig.2), Assistant in the Natural History Division of the Science and Art Museum, led a joint excursion of the Dublin, Cork, and Limerick Field Clubs to the district surrounding Fermoy, County Cork. The 3-day excursion, held from 05–07 July, involved a large party of naturalists ***[Note 5]*** and included a visit to Mitchelstown Cave. One of the stated aims of this visit was to rediscover *Lipura stillicidii* and, if possible, to find "*some other inhabitants of the place*", a phrase that can reasonably be interpreted as referring to putative troglodytes (Anon., 1894; Carpenter, 1895, p.26). Apparently, the participants were unaware that Haliday and Wright had realized long ago that their cave springtail was not *L. stillicidii* (see above). This correction was almost entirely overlooked in the literature until much later; even Lubbock (1873) appears not to have been aware of it.

Carpenter was a young English naturalist and entomologist who had been appointed to the Museum in 1888 after a period working as a clerk at the British Museum (Natural History).

[Note 5]: The party consisted of more than thirty members of the Field Clubs, and was joined by additional participants from England.

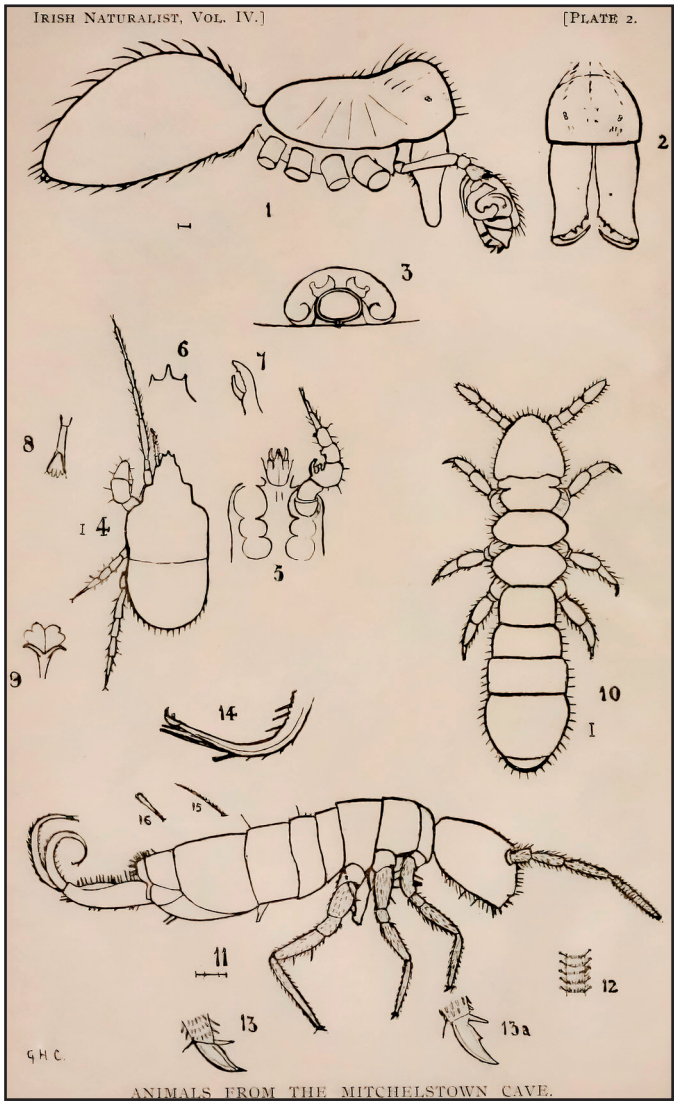


***Figure 3**: Illustrations of animals collected from Mitchelstown Cave by Carpenter and others in 1894.*
*Porrhomma myops, **1**: lateral view of ♂; **2**–3: morphological details.*
*Gamasus attenuatus, **4**: dorsal view of ♂; **5**–**9**: morphological details.*
*Lipura Wrightii, **10**: dorsal view.*
*Sinella cavernicola, **11**: lateral view; **12**–**16**: morphological details.*
[Reproduced from The Irish Naturalist, Vol.IV, No.2(1895), Plate 2.]

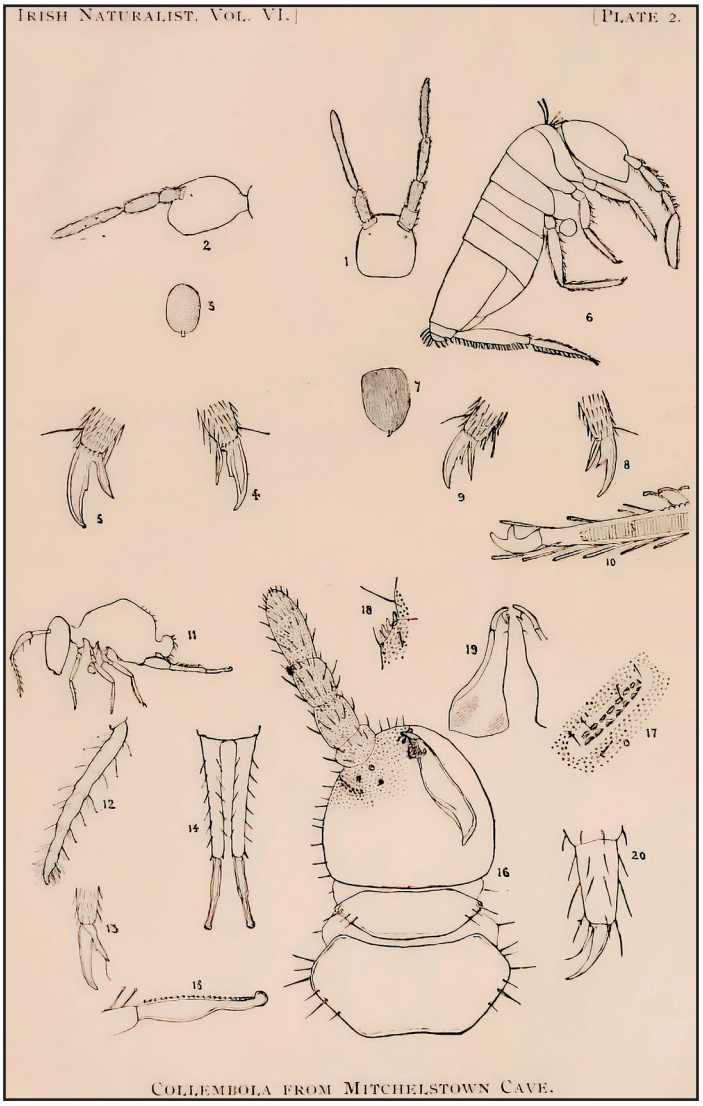


***Figure 4**: Collembola from Mitchelstown Cave.*
***1**–**5**: Templetonia cavernicola, morphological details.*
***6**: Cyphoderus Martelli, habitus; **7**–**10**, morphological details.*
***11**: Smynthurus coecus, habitus; **12**–**15**, morphological details.*
***16**: Lipura Wrightii, habitus; **17**–**20**, morphological details.*
[See Table 1 for updated taxonomy]
[Reproduced from The Irish Naturalist, Vol.VI, No.9 (1897), Plate 2.]

Born and educated in London, he had completed a BSc at King's College and worked as an engineers' draftsman (1880–1884). While undertaking further studies at the Royal College of Science in Dublin he developed a strong interest in natural history, which his appointment at the Dublin Museum enabled him to indulge. Eventually becoming an influential figure in Irish entomological circles, his contributions included promoting entomology as a university discipline, co-founding *The Irish Naturalist*, and supporting the development of Irish natural history in many other ways. His principal interests were insects and arachnids, economic entomology, and zoogeography. Upon establishment of the Irish Free State, he returned to England and accepted a position at Manchester Museum (Anon, 1939; Bolger, 1997; Andrews, 2009).

Although the Mitchelstown Cave visit had been intended as a priority event of the excursion, unforeseen delays meant that only a short period on the afternoon of 06 July was available for underground work. Collecting conditions were difficult because illumination depended entirely upon hand-held candles. Nevertheless, with assistance from Halbert, Neale, Nichols, and other members of the party, Carpenter succeeded in obtaining a small collection of specimens (Halbert, 1895).

Several examples of the presumed *Lipura stillicidii* were collected from the cave's deeper areas, together with two additional springtail species (one described by Carpenter as a new form under the name *Lipura Wrightii*), a gamasid mite, and a small linyphiid spider. Notably absent were the Diptera commonly found resting on cave walls and ceilings: Culicidae, Mycetophilidae, Sciaridae, and Heleomyzidae. This is consistent with the idea that the collectors were searching only for troglodytes and based their expectations on the Carniolan fauna described by Schiödte (1851), which excluded Diptera. Near the entrance, an earthworm was collected and forwarded to Hilderic Friend for identification ***[Note 6]***. Friend identified it as *Allurus flavus*, a species he had described from England in 1893, although he later acknowledged that it might simply represent a form of *Allobophora* (now *Eiseniella*) *tetraedra* (Friend, 1895, 1896). Subsequent work suggests that the latter interpretation was correct. *Eiseniella tetraedra* is a widespread and common earthworm frequently encountered in caves.

Carpenter attempted to identify the remaining material and later published descriptions and illustrations in *The Irish Naturalist* (Anon., 1894, p.183; Carpenter, 1895, 1897a, 1897b, 1902a, 1902b) (see also Figs 3 and 4), Table 1 and ***Note 7***).

[Note 6]: Friend was an oligochaetologist who also identified several English subterranean aquatic microdrile species (Moseley, 2024, 13–14).

[Note 7]: Rediscovery of the supposed *Lipura stillicidii* initiated Carpenter's life-long interest in Collembola, publishing many papers on this group (Carpenter, 1917, p.68). Although he undertook no further cave collecting, he did describe springtails from tropical caves sent to him by correspondents (Carpenter, 1924, 1933).

***Figure 5**: Henry Paul William Lyster Jameson (1875–1922). [Courtesy of Mersea Museum, West Mersea, Essex.]*

The specimens belonged to taxonomically difficult groups in which he possessed inadequate specialist experience, and consequently many of his identifications cannot be accepted uncritically. He still accepted *L. stillicidii*, although this erroneous identification had already been noticed (see above). The identity of *L. Wrightii* has never been resolved and it remains a *species dubia* (Gisin, 1960, p.151). The records of these and the other taxa are summarized and revised taxonomically, where possible, in Table 1.

With the exceptions of the mite and the earthworm, Carpenter concluded, optimistically, that the reduced pigmentation and absent or reduced eyes of the springtails and spider ***[Note 8]*** indicated that they were true cave animals: *"They all present the characters of true troglodytes"* (Carpenter, 1895, p.32). He therefore interpreted the material as evidence for a terrestrial community of blind cave fauna within the cave.

Although this interpretation proved erroneous, this apparent discovery of a terrestrial troglobitic biota in the British Isles would have represented a finding of considerable significance. In Ireland the report was seen as important, although it appears to have attracted little attention in Britain, perhaps because it was published in a journal with limited circulation. The same lack of wider attention also affected Carpenter's accompanying discussion of the possible evolutionary origins of blind cave animals, considered later in this paper.

***[Note 8]**:* Interestingly, the spider collected by Carpenter might have been *Porrhomma rosenhaueri*, a troglobitic species subsequently recorded from other caves in Tipperary and Clare. This species is pale in colour and possesses greatly reduced or absent anterior median eyes (Locket and Millidge, 1953; Růžička, 2018).

Dr Scharff certainly saw the potential significance of the Mitchelstown discoveries. In the next issue of *The Irish Naturalist*, he emphasized it, and proposed a systematic inventory of Irish caves as a basis for future biological and archaeological investigations. He compiled an initial list of twenty-three cave sites that he was aware of (Scharff, 1895; Shaw, 1999, p.24). This inventory was later supplemented by Ussher (1895), Coleman (1895), Lyster Jameson (1896b), and Praeger (1896).

By a fortunate coincidence, Scharff did not have to wait long for an opportunity to advance the study of Irish cave biology further. Such an opportunity arose almost immediately.

Lyster Jameson, Martel, and the RIA Flora and Fauna Committee

By early 1895, the celebrated French cave explorer Édouard-Alfred Martel was preparing for a visit to the British Isles. As part of his preparations, he contacted colleagues in England and Ireland, seeking information about important cave sites and making arrangements for his travels. Among those he approached was Robert Francis Scharff, whom he asked to recommend someone local who could accompany him during exploration of caves in Ireland ***[Note 9]***.

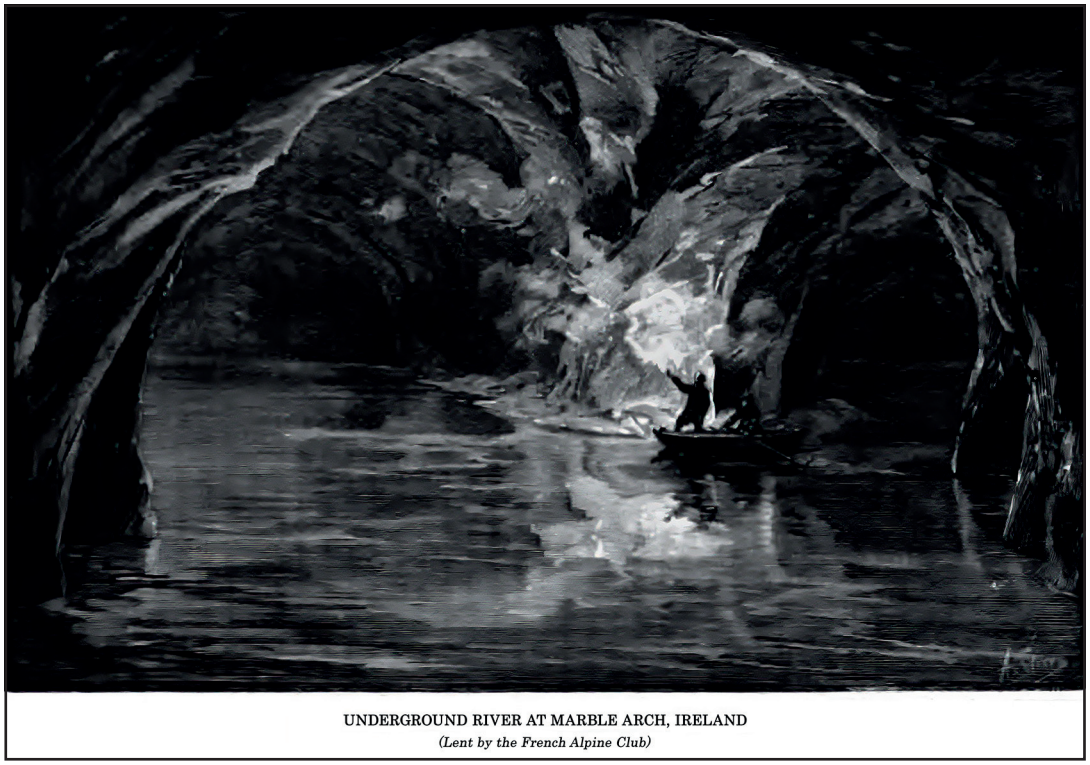
Recognizing that Martel's visit presented an exceptional opportunity to advance the investigation of Irish caves and their fauna, Scharff approached a young zoology undergraduate Henry Paul William Lyster Jameson of Dublin University to determine whether he would be interested in participating (Fig.5). Lyster Jameson (as he liked to be known) accepted enthusiastically. At twenty years of age, he was physically fit, adventurous, and had already begun to develop an interest in bats (Lyster Jameson, 1897). Born into an Anglican family in County Louth, where his father served as rector of Killencoole parish, he had shown an early interest in zoology and, at only seventeen years of age, had already contributed ornithological notes to the first volume of *The Irish Naturalist* (1892) (Anon, 1922; Scharff, 1922a, b; Craven, 2012). He appears to have been a sensible and appropriate choice ***[Note 10]***.

Scharff recommended Lyster Jameson, and also secured financial support for him through the RIA Flora and Fauna Committee. This funding enabled him to spend two weeks in the field, from 11–25 July 1895, accompanying Martel during exploration of caves near Enniskillen, County Fermanagh, and at Mitchelstown Cave, while also carrying out independent investigations at several additional cave sites (Lyster Jameson, 1896a; Martel, 1897; Scharff, 1922a, b; Shaw, 1999, p.24).

Lyster Jameson travelled first to the Boho district in County Fermanagh where, assisted by the local Anglican rector Reverend A Knight as guide, he spent two days exploring the Boho cave system and Coolarkin Cave, while collecting fauna. Following Martel's arrival in Fermanagh on 15 July, the two men investigated Noon's Hole and Pollanafrin in the Enniskillen area. On the following day they carried out the first exploration of the subterranean river within Marble Arch Cave, using Martel's portable folding canvas boat. Approximately 300m of the underground river passage was mapped (Fig.6). They also conducted the first exploration of the nearby Cradle Hole.

***[Note 9]**:* In 1895 Scharff became a corresponding member of the *Société de Spéléologie*, established that year by Martel (Shaw, 1999). Interestingly, Shaw reports Wright as a founding member, so it is possible that it was Wright who drew Scharff's attention to the cave Collembola.

***[Note 10]**:* Carpenter might seem the more obvious candidate, being still only thirty years old at the time, and there may have been unrecorded reasons why he was not involved in the field investigations. He did, however, undertake the important task of identifying much of the invertebrate material collected.



UNDERGROUND RIVER AT MARBLE ARCH, IRELAND
(Lent by the French Alpine Club)

***Figure 6**: Drawing, made by E-A Martel, of the underground river in Marble Arch Cave, County Fermanagh, Northern Ireland. [E-A Martel, Public domain, via Wikimedia Commons. Reproduced from Martel, E-A, 1897. British Caves and Speleology. The Geographical Journal, Vol.X(5), p.503.]*

The investigation of the fauna of Mitchelstown Cave remained Lyster Jameson's principal objective. He devoted three days (22–23 and 25 July) specifically to this work, while spending the intervening day assisting Martel in exploration and mapping of the cave (Fig.7) (Lyster Jameson, 1896a; Martel, 1896). Unlike Carpenter, who had concentrated largely on Collembola and other small invertebrates thought likely to represent troglodytes, Lyster Jameson adopted a broader view of cave fauna. In addition to springtails, he collected beetles, millipedes, snails, a frog, and other organisms encountered during his investigations. Many of these belonged to taxonomic groups that were comparatively well known and relatively straightforward to identify.

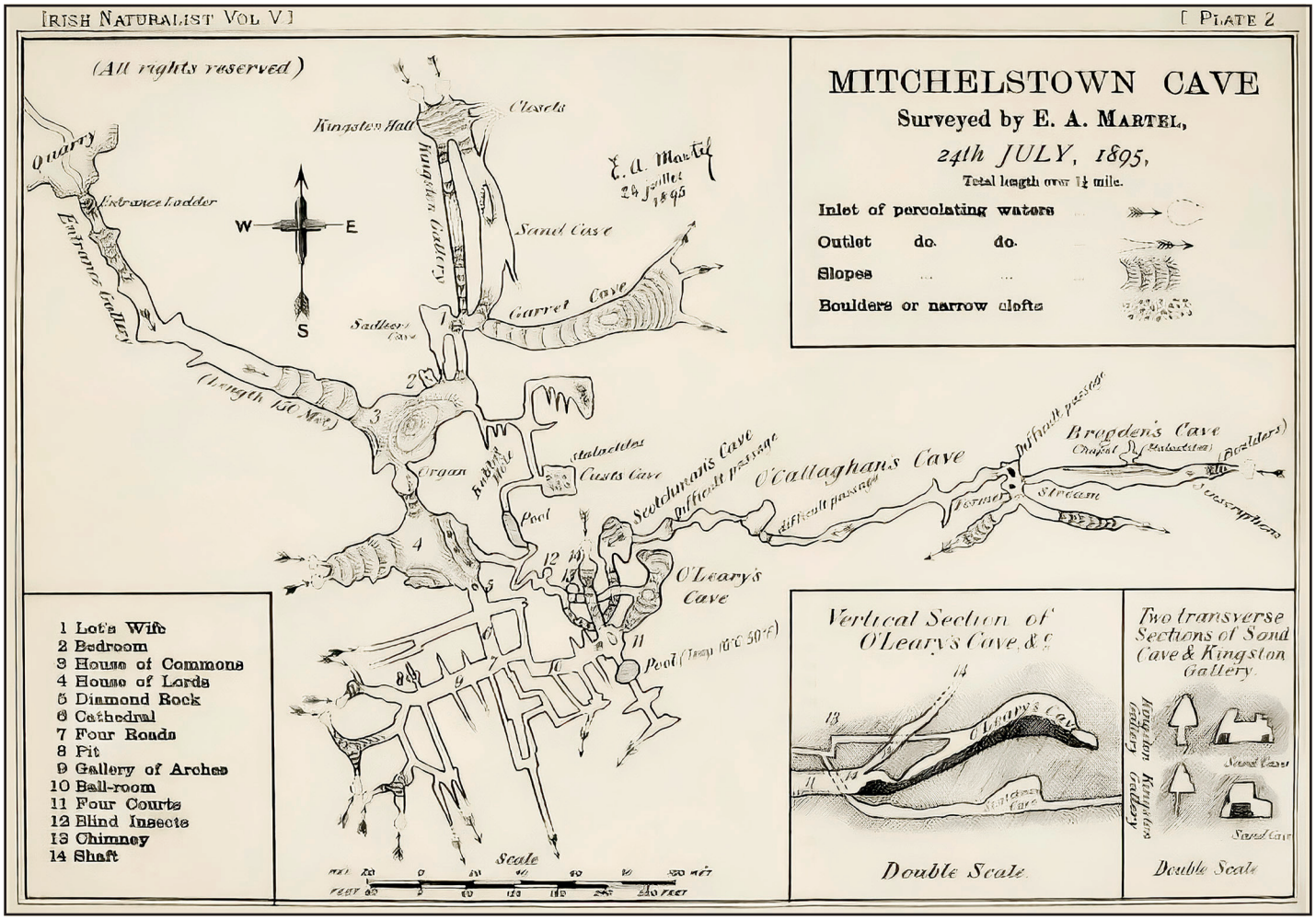


***Figure 7**: Martel's 1895 map of Mitchelstown Cave. Reproduced from The Irish Naturalist, Vol. V (1896), Plate 2. Note that a location where blind insects were found is indicated at "12".*

Taxonomic placement	Locality	Reported by			Most likely identity
		Lyster Jameson 1896	Carpenter 1902	Pack-Beresford 1920	
	BOHO CAVES				
Araneae, Tetragnathidae		*Meta menardi*			*Meta menardi*
Araneae, Tetragnathidae		*Meta merianae*			*Meta merianae*
Diptera, Limoniidae		*Erioptera sp*			*Erioptera* sp.
Diptera, Limoniidae		*Molophilus sp*			*Molophilus* sp.
Hemiptera, Veliidae		*Velia currens*			*Velia caprai*
Chiroptera, Vespertilionidae		*Vespertilio daubentonii*			*Myotis daubentonii*
	COOLARKIN CAVE				
Collembola,Tomoceriidae		*Tomocerus tridentiferous*			*Tomocerus minor*
Aranea, Linyphiidae		*Porrhomma microphthalma*			*Porrhomma* sp.
Diplopoda, Polydesmidae		*Brachydesmus superus*			*Brachydesmus superus*
Diplopoda, Julidae		*Iulus pilosus*			*Ophyiulus* sp?
Coleoptera, Carabidae		*Bembidium rufescens*			*Ocys harpaloides*?
Coleoptera, Staphylinidae		*Ancyrophorus omalinus*			*Ochthephilus omalinus*
Coleoptera, Scirtidae		*Helodes marginata*			*Elodes marginata*
Coleoptera, Staphylinidae		*Coprophilus striatulus*			*Coprophilus striatulus*
Diptera, Sciaridae		*Sciara thomae*			*Sciara* sp.
Hemiptera, Veliidae		*Velia currens*			*Velia caprai*
	MARBLE ARCH				
Collembola, Tomoceridae		*Tomocerus tridentiferous*			*Tomocerus minor*
Araneae, Linyphiidae		*Porrhomma microphthalma*		*Porrhomma Thorelli*	*Porrhomma* sp. prob. *convexum*
Diplopoda, Polydesmidae		*Brachydesmus superus*			*Brachydesmus superus*
Coleoptera, Carabidae		*Clivina fossor*			*Clivina fossor*
	DUNMORE CAVE				
Collembola, Entomobryidae			*Heteromurus margaritatus*		*Heteromurus nitidus*
Collembola, Entomobryidae			*Pseudosinella alba*		*Pseudosinella* sp.
Collembola, Tomoceridae			*Tomocerus tridentiferous*		*Tomocerus minor*

Table 2*: Irish cave fauna collected by Lyster Jameson in 1894 (excluding those Mitchelstown Cave collections that are listed in Table 1).*

The fact that many of these species possessed normal pigmentation and fully developed eyes, and therefore clearly occurred outside caves, indicates that Lyster Jameson recognized that organisms found in caves could still be ecologically relevant, even if they were not strict cave specialists. The fauna collected (Tables 1 and 2) was subsequently identified by Carpenter and published and discussed by both men (Lyster Jameson, 1896a; Anon., 1896; Carpenter, 1897a, b, 1902).

Drawing upon his field observations and the accumulated collection records, Lyster Jameson (1896a, 99–100) proposed a simple ecological grouping of cave animals, discussed later in this paper. He concluded that those organisms interpreted, following Carpenter, as troglodytes were confined to Mitchelstown Cave (Lyster Jameson, 1896a). This conclusion reflected the widespread contemporary assumption that cave faunas consisted of isolated populations confined to individual cave systems. However, evidence suggests that he later came to recognize that the supposed Mitchelstown troglodytes actually represented species with broad European distributions in surface habitats (Baker, 1906, p.36).

Ireland 1900–1922

After completing his degree in Dublin, Lyster Jameson moved to England to study at the Royal College of Science in London. Meanwhile in Ireland interest in cave fauna gradually declined. Nevertheless, Scharff attempted to encourage further investigation. In 1900, he secured funding through the RIA Flora and Fauna Committee for James Nathaniel Halbert to investigate the fauna of Dunmore Cave (Praeger, 1903). In 1892, at the age of twenty, Halbert had joined the Science and Art Museum as a Labeller. He became Assistant in 1904, remaining at the Museum until 1923. His earliest publications consisted of brief notes on Coleoptera and Lepidoptera in the first issue of *The Irish Naturalist* (1892). He also worked on several additional insect groups, particularly Neuroptera and Hemiptera, as well as on freshwater mites (Praeger, 1949 p.92; Baker and Bayliss, 2005).

Dunmore Cave was a well-known limestone cave approximately 400m in length and notable as a site of discovery of Viking-age human remains. On 01 December 1900, Halbert visited the cave with Haddon, Seymour, and Praeger, collecting invertebrates from what was clearly the dark zone of the cave. In a preliminary verbal report presented to the Dublin Naturalists' Field Club, he described the fauna as including springtails, myriapods, and spiders, many resembling forms previously reported from Mitchelstown Cave. With the exception of the springtails, which Carpenter examined subsequently, the complete results of the investigation were never published formally (Anon., 1901a, b; Carpenter, 1902; Praeger, 1918; Table 2 herein).

The Dunmore investigation proved to be an isolated effort and was not followed by additional work. Some new records of fauna, together with the first records of cave flora, appeared incidentally during a broader biological survey of Lambay Island. This island, approximately 2.5 km² in area and situated in the Irish Sea off the coast of County Dublin, was visited repeatedly during 1905 and 1906 by an informal group of naturalists undertaking a comprehensive zoological and botanical survey.

***Table 3**: Fauna and flora recorded from Lambay Island, County Dublin, 1905–1906.*

Fauna recorded from a small cave in cliffs on the southern coast at Sunk Island Bay (Site a). *T. fulvus* is a coastal beetle known to occur in maritime caves.	
DIPTERA	*Culex pipiens* [abundant] (Grimshaw, 1907)
COLEOPTERA	*Trechus fulvus* (as *T. lapidosus*), [common in shingle], (Halbert, 1907);
ARANEAE	*Micryphantes innotabilis* [1 adult ♂],
	Porrhomma micropthalma [2 adult ♂, 1 adult ♀]*,
	Meta merianae [adult ♂♀] (Pack-Beresford, 1907).
	*Corrected to *P. thorellii* by Pack-Beresford (1920)
Flora recorded from unnamed sea caves on the northern coast (Site b). The presence of *S. maritimum* and *A. serpens*, both known to tolerate nearshore conditions, is consistent with a partly tidal sea cave.	
BRYOPHYTA (mosses) (McArdle, 1907a)	*Schistidium maritimum (*as *Grimmia maritima)*
	Welssia rupestris
	Pleuropus sericeus
	*Oxyrrhynchium speciosum (*as *Eurhynchium speciosum)*
	Amblystegium confervoides
	A. serpens
	Hypnum elodes
	H. commitatum
	H. molluscum
	Hylocomium splendens
HEPATICAE (liverworts) (McArdle, 1907b)	*Lophocolea cuspidata*
	Pellia epiphylla
	Conocephalus conicus

Scattered among the published results were records of animals from a small cave at Sunk Island Bay on the island's southern coast, together with records of flora from coastal caves on the northern coast (Carpenter *et al*., 1907; Grimshaw, 1907; Halbert, 1907; McArdle, 1907a, b). These observations appear to have passed unnoticed as speleobiological records. For reference, they are compiled and summarized in Table 3 of the present paper. The only additional records of cave flora were made in 1906 when the amateur bryologist David McArdle collected mosses and liverworts from Pigeon Hole Cave in County Mayo (McArdle, 1907c) (Table 4).

This effectively marked the end of cave biology in Ireland until the middle of the 20th century. What initially appeared to be a promising beginning ultimately produced little lasting development, and subsequently much of the work carried out during this period was forgotten.

After 1910 entomological activity declined substantially in Ireland, and depended increasingly upon those resident entomologists whose careers had begun in the 1880s and 1890s (Beirne, 1985). Among these were Carpenter and Halbert. The years from 1916 to 1921 were also marked by civil unrest and political upheaval. By 1922 many of the naturalists most closely associated with cave biology had retired or returned to England.

Having reached retirement age in 1921, Scharff retired and returned to England following establishment of the Irish Free State in 1922. Halbert also retired shortly afterwards, in 1923. Carpenter likewise left Ireland and accepted a position at Manchester Museum. *The Irish Naturalist*, already struggling financially and affected by the wider political situation, survived only a few more years before ceasing publication in 1924 (Scharff, 1922; Wyse Jackson and Wyse Jackson, 1992). It was succeeded in 1925 by the successful *Irish Naturalists' Journal*, published in Belfast, Northern Ireland (Monaghan, 2025).

Cave biology in England 1859–1914

Little of significance in cave biology occurred in Great Britain during this period. The available records are few and generally insubstantial, and they had little discernible influence on the development of speleobiology. As noted previously, Andrew Murray had spent several hours in a Derbyshire cave in 1855 searching unsuccessfully for blind insects (Murray, 1857). Beyond this, only isolated reports appeared prior to the Great War.

One report, which mentioned a spider collected from Wookey Hole, emerged from a taxonomic study published in 1894. Another report involved cave-fauna collecting undertaken in Derbyshire by the Irish naturalist Lyster Jameson while he was temporarily in England pursuing further studies. He did not publish his findings, and they are known only indirectly through secondary accounts. Together, these fragmentary records constitute almost the entirety of documented cave biological activity in Great Britain during this period.

Pigeon Hole is a small stream cave in limestone entered via a steep narrow gully. McArdle collected from the shaded walls of the gully, an area that can be considered threshold.	
BRYOPHYTA (mosses)	*Oxyrrhynchium speciosum (as Eurhynchium speciosum)*
	Amblystegium serpens
	Microeurhynchum pumilum (as Eurhynchium pumilum)
	Rhychostegiella teneriffae (as Eurhynchium Teesdalei)
	R. tenella (as Eurhynchium Tenellum)
HEPATICAE (liverworts)	*Marchesinia mackaii (as Lejeunea Mackaii)*
	Conocephalum conicus
	Metzgeria furcata

***Table 4**: Flora recorded from Pigeon Hole, near Cong, County Mayo, 1906 (McArdle, 1907c).*

Frederick Octavius Pickard-Cambridge (1860–1905) was a Dorset-born clergyman, arachnologist, and scientific illustrator who collected spiders in Wookey Hole near Wells, Somerset, in May 1894 ***[Note 11]***. The only species he reported were numerous adult and immature specimens of *Porrhomma egeria*, apparently representing a permanent or semi-permanent population within the cave; his wording suggests that these spiders were collected from the dark zone (Pickard-Cambridge, 1895, p.37). Several members of this small linyphiid genus are associated with cave habitats, but *P. egeria* itself is encountered infrequently. This genus is taxonomically difficult, and Pickard-Cambridge's description is inadequate by modern standards, so the identification might have been incorrect. The more commonly occurring *P. convexum* has been observed in large numbers within caves (pers. obs.) and might represent the actual species collected at Wookey Hole.

Although Lyster Jameson published no further work on cave fauna following his Irish investigations, secondary sources indicate that he continued to maintain some interest in the subject. Baker (1903) records that he collected cave invertebrates in Speedwell Cavern, Derbyshire, during May 1901, while participating in the first exploration of the "Bottomless Pit" led by James William Puttrell (1868–1939) and members of the Kyndwr Club.

According to Baker's account, Lyster Jameson collected gnats, earthworms, beetles, springtails, and crustaceans interpreted as organisms that had wandered into the cave from surface habitats. Species he considered more likely to be established cave inhabitants included a blind mite, probably *Gamassus*, together with the springtails *Lipura ambulans* (presumably *Onychiurus ambulans*), *Lipura inermis* (now *Deuteraphorura inermis*), and *Tomocerus tridentiferus* (now regarded as a synonym of *T. minor*). He also reported finding what he believed to be the first troglodyte, a species of *Lipura*, recorded from England:

> "*The fauna of the cave, on the other hand, more than realised expectations. The most important specimen collected was a species of Lipura, perhaps the first example of a blind cave animal recorded from Great Britain*"
> (Wilkinson, 1902).

Additional aquatic organisms considered by Lyster Jameson to be cave inhabitants included two flatworms, *Planaria alpina* (now *Crenobia alpina*) and a *Polycelis* species misidentified as *P. cornuta* (a marine species), together with an almost colourless *Gammarus* water-flea, presumably *Gammarus pulex*.

Whereas the reliability of these identifications cannot now be determined, the list is broadly consistent with the fauna expected typically in a Derbyshire cave. In March of the following year (Shaw, 1999), Lyster Jameson also collected material from Peak Cavern, which is near, and connected to, Speedwell Cavern, but no known surviving account records what he found there.

After completing his studies in Dublin, Lyster Jameson spent a year at the Royal College of Science in London before entering the University of Heidelberg, where he completed his doctoral degree in 1898. Subsequently he worked at a pearling station in British New Guinea, investigating the causes of pearl formation. Later he continued this work at the Lancashire Sea Fisheries Station in Barrow-in-Furness, where he developed the parasitic theory of pearl formation in marine mussels. After contracting tuberculosis, he moved to South Africa, where he worked for the Natal Education Department and later lectured at the Technical College in Johannesburg. He never returned to Ireland and died from TB in 1922 at only forty-seven years of age (Anon., 1922; Scharff, 1922; Shaw, 1999; Craven, 2012).

From the perspective of cave biology, it is unfortunate that Lyster Jameson was either unable or unwilling to pursue his early interest in cave fauna further. He was a capable field zoologist who, as later discussion will show, developed noteworthy ideas regarding cave fauna.

Evolution of blind cave animals

Scharff, Carpenter and their colleagues approached the question of biological evolution within a Darwinian framework. Born in mid-century, these men were contemporaries who had come of age and learned their biology (and geology) in the decades following publication of the first edition of *On the Origin of Species*. But they were field and museum naturalists and taxonomists, so evolutionary theorizing was not of overriding concern to them in their professional activities. They reveal hardly anything about their own views on this topic in their published work.

Carpenter, however, did reveal something at a meeting of the Royal Irish Academy held on 30 November 1909 in commemoration of publication of Darwin's great work. In his presentation he pointed out:

> "*that Darwin himself was no believer in the 'all-sufficiency of Natural Selection' and that his disciples should preserve an open mind in face of modern advances in heredity and selection"*
> (Anon, 1910).

This open-minded stance was reasonable in the earliest years after the rediscovery of Mendelian genetics, but before the Modern Evolutionary Synthesis had been developed and generally accepted. While accepting that other processes might be involved, obviously he was not troubled by those *serious* doubts among his contemporaries about the validity of natural selection (Bowler, 1992), nor was he constrained by those metaphysical and religious worldviews that led many to reject Darwinism (Moseley, 2022, p.41).

Carpenter's views on the mechanisms of evolution are notable because he had previously discussed the origins of blind cave animals in evolutionary terms. In his 1895 paper (p.32) he outlines briefly the various theories that others had proposed as mechanisms for loss of eyes and pigment in cave animals, without drawing any definite conclusions himself. These mechanisms are:

(1) direct effect of development in the dark,
(2) natural selection, and
(3) cessation of natural selection.

His wording seems to imply that (2) and (3) might apply to different organs in the same species. In a review of these theories, he points out that bleaching and even loss of eyes might be a direct result of development in the dark. But, because these organs are useless in caves, their loss could be attributed to relaxation of selection, or perhaps – considering the limited food supply – their loss could be of considerable benefit (implying direct selection). The subsequent debate has continued to revolve mostly around the relative contribution of these same two alternatives i.e. natural selection versus passive genetic drift ***[Note 12]***. Carpenter's views placed within the context of the overall historical debate are considered later in this paper.

[Note 11]: Pickard-Cambridge developed his interest in natural history through the influence of his uncle, the distinguished arachnologist Arthur Wallace Pickard-Cambridge (1828–1917), with whom he has occasionally been confused. As far as is known, his visit to Wookey Hole was his only cave investigation. He experienced increasing psychological instability later in life and died by suicide at the age of forty-four (Bristowe, 1939; Hillyard, 1995).

[Note 12]: A third possible mechanism, selection acting on traits linked pleiotropically to pigment and/or eye loss, is now favoured by some evolutionary geneticists (e.g. Jeffery, 2010).
Of course, this possibility was not understood by anyone in 1895.

Ecological classification of cave-associated animals

It has already been noted that rather than concentrating exclusively on blind animals presumed to be permanent cave inhabitants, Lyster Jameson recognized that caves contained a broader assemblage of organisms with differing degrees of ecological association with subterranean environments. Based on his field observations and the accumulated collection records he grouped the animals so far collected in Irish caves as follows (1896a, 99–100):

(1) Species inhabiting the entrances to caves, near the light, using the cave as a convenient hiding place; such are the two species of Meta, perhaps Leptyphantes (sic) pallidus, and the bats.

(2) Species which have wandered into the caves, accidentally, perhaps, or have been washed in by floods, and are so to speak "fish out of water", examples of such are the water-bugs and crane-flies from Bohoe (sic); Iulus (sic), Velia, Sciara and the beetles from Coolarkin; Clivina fossor from the Marble Arch; and the frog, Pterostichus, Sciara, and Ancyrophorus from Mitchelstown.

(3) The Troglodytes; found only in Mitchelstown, e.g. Lipura, Sinella and Porrhoma (sic) myops.

(4) Those species which do not fall under any of these three groups seem to me to form a division intermediate in position between the last two.

This proposed classification of cave fauna, although preliminary and lacking precision, is similar to that proposed earlier by Schiödte (1851) based on where cave animals are actually found ***[Note 13]***. These early empirical approaches anticipated later ecological approaches to subterranean biology. Rather than defining cave organisms solely through striking morphological features such as blindness and depigmentation, they implicitly recognized that cave communities could include species differing in their dependence upon subterranean habitats. They are however distinct from the subsequent and widely-adopted Schiner–Racoviță approach which attempts problematically to classify cave-associated species according to their assumed specific degree of ecological dependence on the habitat (see Sket, 2008 for explanation).

Occurrence records of *Meta menardi* in caves

The years around the turn of the 20th century witnessed a minor flurry of published records of the European Cave Spider, *Meta menardi*. Interest in this species was largely independent of investigations of blind cave fauna. Rather, the spider attracted attention because of its conspicuous appearance and distinctive biology. It commonly inhabits damp, shaded environments such as cave entrances, cellars, and similar sheltered sites, and is particularly notable for its comparatively large size and its characteristic "cotton wool" egg cocoons. Published cave records from this period are summarized here for completeness.

The earliest cave records in the British Isles originated from Ireland (Lyster Jameson, 1896a) and Scotland (Evans, 1896, 1898a, b). The species was not recorded from caves in England until 1908, when it was discovered in the Dog Holes cave system in Lancashire during archaeological investigations conducted by Wilfred Jackson of Manchester Museum (Standen, 1908). This discovery was followed by additional reports from Lancashire (Airey, 1909; Standen, 1909a, b; Bailey, 1910; Jackson, 1912a) and from Westmorland (Jackson, 1912b). The first cave record from Yorkshire was subsequently reported by Falconer (1912). Standen (1909a) also cited records from the Isle of Man, Cumberland, Northumberland, Devonshire, and Dorset. However, he did not indicate whether these records referred specifically to cave localities.

[Note 13]: Schiödte (1851) classified the animals from Carniolan caves according to where they were to be found as (i) Shade-animals; (ii) Twilight-animals; (iii) Cave-animals; and (iv) Stalactite-cave-animals.

Discussion

The search for troglodytes and the influence of preconceptions

The repeated but largely unsuccessful search for "troglodytes" in the British Isles illustrates the powerful influence of prior expectations on scientific investigation. The earliest workers approached caves with the expectation that they would contain blind and highly specialized organisms analogous to those already reported elsewhere. These expectations influenced both the questions being asked and the interpretation of observations. Wright and Haliday's tentative identification of a very common springtail from Mitchelstown Cave as *Lipura stillicidii* illustrates this clearly. The identification rested on inadequate evidence and appears to have been influenced mainly by analogy with previously described cave animals from Carniola. This initial erroneous identification (and false assumption that *L. stillicidii* was a troglodyte) subsequently motivated Scharff and Carpenter who later interpreted a collection of other relatively ordinary cave invertebrates as evidence of a community of true troglodytes. Accepting and buoyed by this apparent success, Scharff and Lyster Jameson were motivated to carry forward investigations in Irish caves.

These mistaken, and compounded, interpretations might be criticized as groundless wishful thinking, but this particular chimeric quest for blind cave animals was by no means unique. There were repeated similar instances during the early years of the British Speleological Association/Cave Research Group survey in the mid-20th century. In the 1940s these included description of a "new" subterranean mite *Eugamasus anglocavernarum* (Moseley, 2022 and references therein); two supposedly new aquatic subterranean isopods *Asellus hazeltoni* and *Stenasellus hazeltoni*, and a third putative asellid that was even considered to represent an entirely new genus (Edney, 1953; Harding, 1977). Even in the late 1960s and early 1970s aquatic snails collected in Irish caves were thought provisionally to be stygobiotic *Bythiospeum* (Warwick, 1968). Also, three new cave-collected species of Acari – *Rhagidia vitzthumi*, *R. odontochela,* and *Bonzia brownei* – proved to be junior synonyms of known surface-dwelling species or *species dubia* (Zacharda, 1884; Moseley, 2022 p.42). There are further examples, not listed here.

The early emphasis in Ireland on so-called troglodytes foreshadowed and reflects a persistent tendency within speleobiology to focus disproportionately on highly specialized cave organisms at the expense of the wider subterranean fauna. This has had the unfortunate effect of drawing attention away from the significance of the British Isles as an excellent exemplar of an active post-glacial colonizing fauna (Chapman, 1993, p.115; Wood and Proudlove, 2005).

Ironically, however, the early investigations in Ireland unexpectedly produced valuable empirical results. Work initiated and driven largely through erroneous interpretations of common cave fauna generated the first and only inventory of cave biota from any region of the British Isles before the middle of the 20th century, and prompted the naturalists involved to think about the evolution and ecology of cave animals.

Yet, despite these favourable beginnings, the subject failed to bear fruit. This does not seem to have been because it was realized that the underlying results were erroneous. After all, Lyster Jameson believed he had found a troglodyte – a *Lipura* species – in England, and the Irish findings were never retracted. It might be that the lack of interest from elsewhere was a discouragement, and certainly publication in a relatively obscure journal rather than in a more widely read international forum restricted their readership and visibility. But the work was supported by energetic field naturalists, with institutional support from museums and scientific societies. It was the loss of these that was probably the single overriding factor. By 1922 the Anglo-Irish, British, and Protestant Irish naturalists who had been involved were gone or no longer active. Investigations ceased, and what had been achieved was subsequently overlooked.

Evolutionary interpretations of cave animals

Around the same time that Carpenter was thinking about the evolution of blind cave fauna (see above), another naturalist, Charles Chilton, was speculating independently about the evolutionary origins of New Zealand well-shrimps (aquatic subterranean isopods and amphipods). His views were similar to those of Carpenter, i.e. supportive of natural selection with the proviso that 'disuse' or direct environmental effects might also be involved (Chilton, 1894; Moseley, 2025).

So, although accepting the *possibility* of inheritance of acquired characters, both men were thinking within a Darwinian framework and were generally supportive of the contribution of selectionist processes in the evolution of blind cave animals. Such discussion contrasted both with earlier assumptions grounded in creationist thinking and with contemporary evolutionary opinion elsewhere within cave biology.

Speleobiologists have been slow to accept and incorporate many advances in mainstream biology and ecology, and resistance to the Modern Evolutionary Synthesis is particularly striking (Kane and Richardson, 1985; Christiansen, 1992, 469–470; Romero, 2009, Chapter 1; Mammola and Martinez, 2020; Mammola *et al*., 2020; Moseley, 2022). In America, exemplified by Alpheus Spring Packard (1839–1905) and his colleague Frederic Ward Putnam (1839–1915), the involvement of natural selection in troglobitic rudimentation (i.e. loss or reduction of eyes and pigment) was rejected in favour of neo-Lamarckian explanations, whereas continental European, primarily French, explanations likewise rejected neo-Darwinism, usually in this case in favour of orthogenesis and teleological processes (Bocking, 1988; Romero, 2009; Moseley, 2022). Not until the early 1960s did mainstream speleobiologists, first in the USA, attempt belatedly to bring the subject within the long-accepted neo-Darwinian synthesis (Culver and Pipan, 2015). The now classic studies of adaptive evolution of form in cave-dwelling Collembola (Christiansen, 1961, 1965) and adaptation in amblyopsid cavefishes (Poulson, 1963) appeared at this time.

Ironically, it was Darwin himself who resorted to "*long-continued disuse*" as the best explanation he had for the loss or reduction of structures such as the wings of the ostrich and the eyes of the mole. Unable to see how natural selection accounts for the loss of eyes in many cave animals, he also espoused "*disuse*" in this case (1859, 137–138 and all later editions). Romero (2009, pp.21 *et seq*.) makes the case that by giving undue credence to what amounts to a Lamarckian explanation of cave-associated rudimentation Darwin inadvertently held back theoretical evolutionary speleobiology by decades.

This vague term was unhelpful at best, but Romero might have overstated the case. The fact that naturalists including Carpenter and Chilton were nevertheless open to selectionist explanations suggests that Darwin was not the root cause of the problem. Furthermore, explanations of troglomorphic atrophy in cave animals consistent with natural selection had already been proposed by the late 19th century by two highly respected biologists, Weismann (1885, 1889) and Wallace (1889). So, Darwin's endorsement of non-selectionist explanations was not fatal and the question remains, why did no *influential* speleobiologist endorse selectionist explanations until so late?

The examples of Carpenter and Chilton bring into sharp focus that the long delay in accepting Darwinian processes was due primarily to chance: to the geographical accident that the hotspots of troglobiotic diversity that attracted the attention of naturalists happened to coincide with countries dominated intellectually by non-Darwinian beliefs. Those biologists, including Packard in the USA and European orthogeneticists such as Albert Vandel, were motivated by entrenched *a priori* views, which they would have held-to whatever Darwin said: not only in regard to blind cave animals (Romero, 2009; Moseley, 2022). Had there been rich communities of troglobites in the British Isles, or elsewhere, open to Darwinian thinking, the conceptual development of speleobiology would likely have followed an entirely different path.

Significance of Lyster Jameson's ecological classification

Lyster Jameson's ecological grouping of cave animals anticipated approaches that later became important within subterranean biology by recognizing that cave communities consist of organisms differing in their ecological relationships with caves. Although preliminary, this represented an early movement away from defining cave biology solely through the presence of blind or highly modified species.

Concluding comments

Unexpectedly, the investigations discussed above produced potentially useful empirical results. Work initiated and pursued through an erroneous interpretation of common cave fauna ultimately generated the first and only inventory of cave biota from any region of the British Isles before the middle of the 20th century. Such unexpected outcomes happen more frequently in the history of science than is generally recognized. As Lovejoy (1936 p.333) put it: "*the utility of a belief and its validity are independent variables; and erroneous hypotheses are often avenues to truth*."

These direct scientific achievements of the early investigations of cave fauna in Ireland admittedly were limited and subsequently overlooked for the most part. Nevertheless, they possess significance beyond the historical record itself. They contain several observations that contribute to a broader understanding of the conceptual development of speleobiology. In particular, they provide insight into changing ideas concerning the evolutionary origins of cave organisms, the nature of cave communities, and the interpretation of subterranean habitats.

Lyster Jameson's attempt to categorize cave animals provides a glimpse into early thinking about cave ecology. Carpenter's discussion of the evolutionary origins of blind cave animals demonstrates that selectionist interpretations of cave-associated evolution were being considered in Britain and Ireland as early as the 1890s. Together with comparable ideas proposed independently by Chilton in New Zealand, this suggests that the prolonged reluctance of leading speleobiologists to adopt evolutionary interpretations compatible with the Modern Evolutionary Synthesis arose less from any inherent conceptual difficulty than from historical and geographical circumstance. The principal geographical centres of troglobiotic diversity that attracted scientific attention happened largely to occur in countries where non-Darwinian viewpoints remained intellectually dominant and influential.

Finally, Robert Francis Scharff emerges from this historical review as a figure whose role in the development of Irish cave biology has been underappreciated. Although not himself a direct participant in any of the field investigations, he played an important part in facilitating and encouraging research through institutional support, organization, and the creation of opportunities for others. His influence helped establish, however briefly, what was the first coordinated attempt to investigate cave fauna in Britain and Ireland.

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