areas, and lithology plays an important role in influencing cave morphology (Wadge & Draper, 1977a,b). Many of the larger peripheral caves, such as the spacious, old phreatic tunnel of Windsor Great Cave (Figure 2), have significant bat populations and have been commercially exploited for guano (Fincham, 1997).

The dramatic Cockpit Country landscape attracted the attention of 19th-century European geologists, such as J. Sawkins in 1869, but the first systematic geomorphological studies were undertaken in the 1950s by the Jamaica Geological Survey under the direction of V.A. Zans (Zans, 1951) and by visiting Europeans such as Herbert Lehmann, Marjorie Sweeting, and Harold Versey. In 1955, Zans and Sweeting traversed the Cockpit Country via the Troy-Windsor trail, an ambulation that convinced Sweeting (1958) that the terrain was the result of surface dissolution, rather than collapse or groundwater upwelling. Versey (1972) nevertheless continued to stress the mechanical significance of groundwater upwelling during heavy rainfall events, particularly in peripheral areas where large, complex depressions, such as Bamboo Bottom, have deeply alleviated floors with incised drainage channels and estavelles.

The surficial dissolutional origin is clearly complex, and it has been noted by Conrad Aub in particular that the vegetation canopy obscures the true irregularity of the cockpit slope surfaces, and that "rafting" of rain by the canopy results in approximately 14% more water reaching cockpit floors than the surrounding summits (Aub, 1969).

The Cockpit Country vegetation includes a range from wet to dry limestone forest, in which there is considerably floristic diversity and an extraordinary number of endemic species. The Cockpit Country fauna is also significant, including threatened species such as bats, snakes, frogs, and all but one of Jamaica's 28 endemic bird species.

Human influences have, to date, been limited by inaccessibility and lack of surface water, although there exists an extensive trail system, and many peripheral cockpits have been used for agriculture. In the 1700s, escaped slaves known as the Maroons used the Cockpit Country as a base for guerrilla activities against the British army. Treaties gave the Maroons a degree of autonomy that they have maintained ever since.

Since 1950, much of the Cockpit Country has been designated as a Forest Reserve, although there has been little enforcement of conservation directives. The immediate vicinity has a population of some 10 000 people, and is exploited for bauxite mining and agriculture. In the Forest Reserve, illegal logging, farming, hunting, and trapping for the pet trade are particular problems. More recently, the Cockpit Country has been proposed as a UN World Heritage Site, and there are currently plans to inscribe it as a national park.

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See also **Caribbean Islands; Cone Karst**

COLONIZATION

Colonization of a cave by an animal or plant species may be either primary or secondary. Primary colonization may be defined as the establishment of a population in an area not previously occupied by the species. A cave open to primary colonization may lack a species because of recent origin (e.g. during the karstification process), recent catastrophes (e.g. lava flows, glaciations), or geographic location (e.g. isolation). Secondary colonization is more characteristic of small locally confined areas less isolated from colonizing populations; in these areas the species disappeared following minor environmental alterations (e.g. marginal areas of a karstic massif after the retreat of a glacier, or polluted areas after recovery). Both primary and secondary colonization may be considered as continuous processes; nevertheless, colonization rates may increase or decrease owing to adverse climatic conditions, depletion of resources, high competition rates, or strong predation pressure.

In the biospeleological literature the term colonization refers mainly to the colonization of a cave by a surface population; however, subterranean organisms are active and apparently cognitive subjects, and their dispersal in new habitats, and hence the colonization of new caves, may be considered a relatively common event.

Considering the modalities of colonization, biospeleologists put great emphasis on active and passive colonization mechanisms. Usually active colonization is understood in the sense of colonization by means of the locomotory apparatuses and is the opposite of passive transport. However, some biospeleologists do not use the term "active" to refer to the mechanical method used to reach the subterranean environment, and view active colonization as synonymous with voluntary colonization. Indeed, one of the most common questions on colonization addressed by biospeleologists is not how epigean species colonized the subterranean domain, but why they did so. This is an old question due to the interpretation of the subterranean environment as a special one (the refugium model): caves have long been considered as refugia against climatic vicissitudes for the ancestors of troglobites, especially those of Pleistocene animals in temperate zones. Rouch & Danielopol (1987) challenged this idea, stating that there are no compelling forces to colonize the subterranean environment: the active colonization model replaced the refugium model. The refugium model is considered incompatible with the accumulated evidence that subterranean organisms occur on a worldwide scale, even in the absence of unfavourable climatic conditions; moreover, it does not explain the contemporary colonization processes of subterranean habitats and the fact that many hypogean animals are not relicts. The active colonization model proposes a unique scenario to explain colonization of subterranean habitats; for this reason, it was criticized by Botosaneanu & Holsinger (1991). They reported several examples for and against hypogean relicts and the refugial character of subterranean environments, stating that no unique explanation can be found to explain the colonization events. Finally, Stoch (1995) formulated an "adaptive zone model", suggesting that surface populations invade subterranean habitats to exploit a new set of resources; colonization may be followed by niche specialization and adaptive radiation. Most modern biospeleologists do not support the old hypothesis that the origin of subterranean animals must differ in certain instances from that of other animals: instead it is argued that caves are no more than one of several types of environments that ecologists deal with.

Several colonization models have been developed to explain the origin of groundwater fauna, some of them dealing primarily with interstitial fauna (see Interstitial Habitats: Aquatic). Among several others, the following models are mentioned herein: regression model (Stock, 1980); zonation model (Iliffe, 1986); two-step model (Notenboom, 1991); "modèle biphase" (Coineau & Boutin, 1992); three-step model (Holsinger, 1994); and adaptive zone model (Stoch, 1995). Some of these models can also be applied to terrestrial fauna; however, detailed colonization models dealing separately with terrestrial habitats were developed for caves (three-step model, Juberthie, 1984) and lava tubes (adaptive shift, Ashmole, 1993).

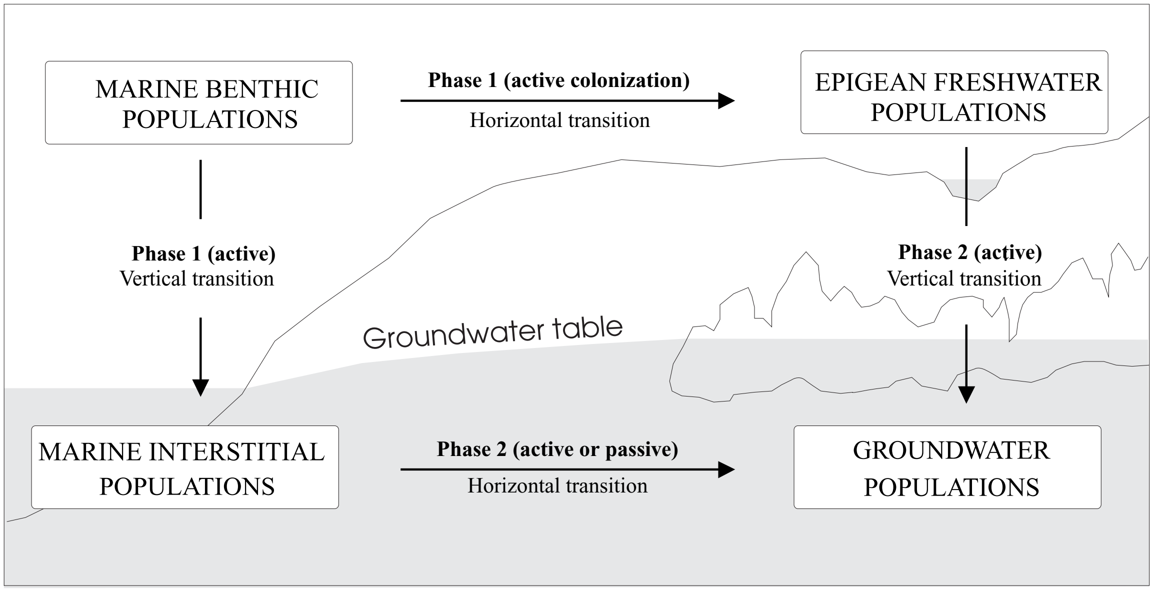
Coineau & Boutin (1992) synthesized most of the models outlined above for groundwater fauna. According to these authors, the stygobites living in inland subterranean waters belong to two groups: limnicoid stygobites, the marine ancestors of which lived in surface freshwaters before groundwater colonization, and thalassoid stygobites, which colonized continental groundwaters from the marine environment through the littoral interstitial zone during a marine regression. The two groups of stygobites settled into the inland groundwaters after two ecological and geographical transitions ("modèle biphase" or "two-step model") involving a "vertical transition" (active colonization of the littoral interstitial environments) and a "horizontal transition" (active or passive colonization of the continental interstitial groundwaters) (Figure 1).

Holsinger (1994) developed a "three-step model" of colonization of continental groundwaters; these steps (designated A, B, and C) are best regarded as components in a graded series or phases in a transition and not as rigid stops and starts. Species at step A are epigean benthic forms with little or no apparent troglomorphy, living in freshwater or in shallow littoral or sublittoral sea zones and demonstrate little specialization; most of these taxa remain potential epigean ancestors of stygobites. Species at step B are semi-hypogean organisms, with strong preadaptation to life in subterranean waters; eyes and pigment are typically rudimentary. Species at step C are stygobites; either limnostygobites or thalassostygobites, commonly troglomorphic and restricted to life in subterranean waters.

Ashmole (1993) summarized the theories on the origin of subterranean terrestrial species in volcanic islands, distinguishing between "ecological colonization" and "evolutionary colonization". Ecological colonization of lava flows commences as soon as the rock is cool; populations of "lavicolous" scavengers build up both on the surface and in cracks and dry caves, exploiting the "biological fallout", mainly windborne insects. On the other hand, evolutionary colonization of the deep cave zone (both mesocaverns and saturated caves) is the process by which some individuals from one type of habitat move into a different habitat that imposes new selection pressures, thus leading to adaptive divergence and speciation of the colonizing population. This "adaptive shift" may occur when preadapted epigean individuals accidentally penetrate cavities and form populations that are poorly or rarely influenced by gene flow. The shift involves rapid adaptive evolution in morphological and physiological characteristics.

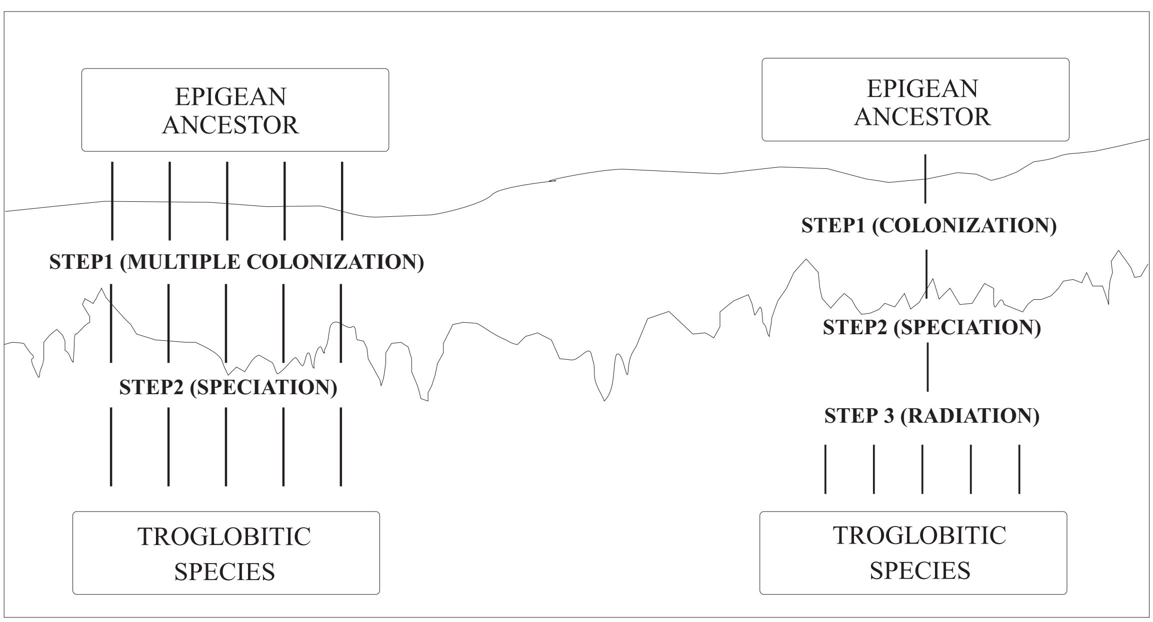
Juberthie (1984) illustrated the theories on colonization of cave habitats by terrestrial species, dealing mainly with the role of the MSS (Mesovoid Shallow Substratum: see Interstitial Habitats: Terrestrial). Juberthie's scenario is a three-step model. During the first step, some populations inhabiting soil litter or mosses colonize the lower layer of forest soils, becoming preadapted to the subterranean environment. Next, they invade the MSS: during this step, the colonizing populations inhabit both compartments. Finally, MSS populations invade the "deep hypogean compartment" (e.g. caves); the isolation of cave-dwelling populations is related to geographical location, degree of karstification, and history (e.g. glaciations).

Finally Stoch (1995) clearly separated the colonization process from the speciation process (see Speciation), and developed



Colonization: Figure 1. The two ways of colonization of continental groundwaters according to the "two-step model" (modified after Coineau & Boutin, 1992): transition via surface freshwaters (limnicoid stygobites) and transition via littoral interstitial waters (thalassoid stygobites).

a multiple step model (called "adaptive zone model") to explain the origin of subterranean biodiversity following two different methods: colonization—speciation-adaptive radiation (e.g. rapid phylogenetic diversification via niche differentiation) or multiple colonization-speciation (when radiation does not occur) (Figure 2). Both active and passive colonization mechanisms are allowed by the adaptive zone model, but the refugium model is clearly ruled out. Following this model, climatic fluctuations and other events such as marine regressions clearly enhanced colonization rates, but speciation is not a consequence of colonization and an increase in the rate of colonization is not necessarily followed by increased speciation rates. Generalist colonizers accomplish



Colonization: Figure 2. Origin of troglobitic species according to the "adaptive zone model" (Stoch, 1995); two different ways are possible: multiple colonization followed by speciation, and colonization by a single ancestor followed by speciation and adaptive radiation.

the expansion of their range due to efficient dispersal adaptations and, after arrival, the establishment of a viable population at the new site. Repeated colonizations into the same site are likely to occur and colonization rates may be high. But generalist colonizers do not appear to speciate: the efficiency of colonization effectively prevents the accumulation of genetic differences from the source, and a speciation event in this case is unlikely. Following the adaptive zone model, only stochastic colonization by a founder with preadaptation to the new site is an event conducive to speciation.

Several hypotheses have been proposed to date the colonization processes, for example marine regressions, the Messinian salinity crisis for the Mediterranean area (Hsü, Ryan & Cita, 1973), and glaciations for temperate zones. Unfortunately, in most models based on historical events the age of colonization is confused with the cause of colonization. For example, some biospeleologists advocated that the Mediterranean salinity crisis (when most of the Mediterranean Basin dried up) forced isopods and amphipods to colonize groundwaters where they remained "stranded" ("regression model" developed by Stock, 1980). Following this model, the age and cause of colonization are determined by the same historical event, but an alternative explanation is possible. According to the adaptive zone model, Stoch (1995) supposed that the Messinian event simply interrupted the genic flux between brackish water and marine populations; epigean brackish water species may have colonized surface freshwaters and subsequently cave waters following the development of karstic areas. Therefore, these stygobitic species may be considered a recent limnicoid stygobite instead of older thalassoid stygobites, and an active colonization model may be advocated opposed to a refugium model.

Unfortunately, most of the theories dealing with the colonization process remain highly speculative and untested: for this reason, the debate between active colonization and refugium model supporters is still a central focus in the current biospeleological literature.

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See also **Adaptation; Evolution of Hypogean Fauna; Speciation**

COMMUNICATIONS IN CAVES

On deep or wet pitches, communicating by means of whistle-blasts is an established practice and, in many situations, this or perhaps a loud voice will be sufficient. However, for cave rescue, expedition management or the execution of projects such as photography in a large chamber, communication by radio or telephone is often essential.

Possibly the first use of a telephone in a cave was during the exploration of Lamb Leer Cavern (Mendip, United Kingdom) in 1880 (Williams, 1995). Despite the disadvantage of having to lay a cable, telephones continue to be used because they are simple and robust. A variety of other cable-based systems exist—single-wire telephone, "guide wire" radio, and optical fibre. True "wireless" communication is difficult because rock, being conductive, absorbs radio waves. For line-of-sight work within cave passages, high-frequency (HF) walkie-talkies and CB radios are used, but magnetic induction equipment is usually necessary for communication through the rock itself. The technique of "earth current injection" was developed during World War I but is rarely used now although an enhancement, using a low-frequency (LF) carrier, is the basis for the latest high-performance induction radio/earth-current "hybrids" now used in the United Kingdom and Europe.

The single-wire telephone (SWT) (also known as an earth-return telephone) uses the conductivity of the ground to provide a return path for the current. The obvious advantage is that only half the weight of cable has to be carried. The devices used by cavers feature electronic amplification and will often operate without any specific earthing other than through the caver's body. SWTs are cheap, rugged, easy to build by amateurs, and are preferred to the traditional army field telephone. They are