

entrance (Decu *et al.*, 1998). Most species supposed to be strictly cavernicolous have been later found also outside caves. Even the rare *Hypoponera ragusai* considered by Tinaut (2001) to be limited to caves in Europe has been collected outside caves in France (Bernard, 1968) and in the Mediterranean islands of Lampedusa and Linosa (Mei, 1992, 1995).

This rarity of ants in caves concerns essentially temperate regions. Though limited, available evidence suggests that Formicidae might be much more frequent in tropical caves. More than sixty species have already been collected from the dark part of various caves of Southeast Asia (Roncin *et al.*, 2001, and unpublished data). Most of these species, well-known outside, are represented by isolated specimens in cave collections. But several are regular guano inhabitants, like *Hypoconerops confinis* in the Farm caves of Myanmar (Annandale *et al.*, 1913) and an unidentified species in the Mulu caves of Sarawak (Chapman, 1982). In fact, ants were present in most guano caves recently sampled in Southeast Asia, with *Hypoconerops* the dominant genus (Roncin *et al.*, 2001). They were sometimes found very far from cave entrance, living in loose colonies, foraging in or around the guano piles, where they are believed to prey on a rich fauna of micro- and meso-arthropods. None of these regular guano species are troglobiomorphic, and all were also collected outside caves. Among the hundreds of caves prospected so far in all regions of Southeast Asia (see Juberthie and Decu, 2001 for an overview), troglobiomorphic species were found only in Laos with *L. khammouanensis*.

Leptogenys khammouanensis was encountered far from the entrance in two big caves, Tham Nam Non (22 km long, the longest cave of continental Southeast Asia, Mouret, 2001) and Tham Thê (2.2 km long, Brouquisse, 1999). In spite of being 25 km apart and in different hydrogeological systems, both caves do belong to the same, uninterrupted, huge limestone unit. In Tham Nam Non, *L. khammouanensis* was collected at about 4.5 km of the entrance. These giant caves of the Khammouan karst host a rich troglobitic fauna, only recently discovered: microphthalmic crabs (*Erebusa calobates*, Yeo and Ng), various blind terrestrial Isopods, Araneids and Millipeds (Polydesmidae, Glomeridae), Campodeids, springtails, blind Nocticolid cockroaches, blind or microphthalmic *Diestrammena* sp., crickets (Besson *et al.*, 2001). As numerous species of *Leptogenys* are woodlice-hunters (for a full list of references see: Hölldobler and Wilson, 1990; Dejean 1997), the terrestrial isopods frequent in these caves could constitute a potential diet of *L. khammouanensis*, but this has to be confirmed.

The genus *Leptogenys* has already been found in caves. *Leptogenys jeanneli* Santschi, 1914 was described from a cave in Tanzania, and *Leptogenys diminuta* (Smith, 1857) was collected in the Batu Caves of peninsular Malaysia (Wilson, 1962; McClure, 1965). However, none of these species is cave-restricted, and none exhibits the combina-

tion of troglobiomorphic traits of *L. khammouanensis*.

Having analysed what was known about cave ants, Wilson (1962) hypothesized that social insects "never become truly troglobitic" because "they are unable to maintain sufficiently large cave demes" (implicitly because of food scarcity). The well-known link between troglobiomorphy and oligotrophic habitats (Deharveng and Bedos, 2000) certainly explains the extreme difficulty for ants to establish long-term colonies and to adapt to cave environment. This view is challenged today by the discovery of *L. khammouanensis* with its clear troglobiomorphic morphology. The unusually large underground voids of Laos may have given the opportunity for such an evolution to take place, by providing large food reservoirs on the long-term. To confirm this exciting hypothesis, it remains to document the peculiarities of the biology and social life of the new species (Tinaut and López, 2001).

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REFERENCES

- Andersen AN (2000) The ants of northern Australia. A guide to the monsoonal fauna. CSIRO Publishing, Collingwood
- Annandale N, Coggin Brown J, Gravely FH (1913) The limestone caves of Burma and the Malay Peninsula. J Proc Asiat Soc Bengal 9: 391–424
- Arnold G (1954) New Formicidae from Kenya and Uganda. Ann Mus Congo Belg Zool 1: 291–295
- Bernard F (1968) Les fourmis (Hymenoptera : Formicidae) d'Europe occidentale et septentrionale. Masson, Paris
- Besson JP, Deharveng L, Brehier F (2001) Laos. In "Encyclopaedia Biospeologica Tome 3" Ed by C Juberthie, V Decu, Soc Biospéologie, Moulis, pp 1883–1889
- Bingham CT (1903) The fauna of British India, including Ceylon and Burma. Hymenoptera. 2. Ants and Cuckoo-wasps. Taylor and Francis, London
- Bolton B (1975) A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian Region with a review of the Malagasy species. Bull Br Mus Nat Hist (Entomol) 31: 237–305
- Boutin C Organisms classification. In "Encyclopedia of cave and karst science", Ed by J Gunn, Fitzroy Dearborn Publishers, London (in press)
- Brouquisse F (1999) Catalogue of caves in the Lao peoples's Democratic Republic. Int Caver 25: 13–16
- Chapman P (1982) The ecology of caves in the Gunung Mulu National Park, Sarawak. Trans Br Cave Res Assoc 9: 142–162
- Christiansen KA (1962) Proposition pour la classification des animaux cavernicoles. Spelunca 2: 76–78
- Christiansen KA (1965) Behavior and form in the evolution of cave Collembola. Evolution 19: 529–537
- Culver D (1982) Cave life, evolution and ecology. Harvard Univ Press, Cambridge
- Decu V, Casale A, Scaramozzino PL, López F, Tinaut A (1998)