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Source: Zoological Science, 20(7) : 919-924

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.20.919

ZOOLOGICAL SCIENCE **20**: 919–924 (2003)

Leptogenys khammouanensis sp. nov. (Hymenoptera: Formicidae). A Possible Troglobitic Species of Laos, with a Discussion on Cave Ants

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ABSTRACT—The new species *Leptogenys khammouanensis* sp. nov. is described from two caves of the Khammouan karst (Laos). It is characterized by a set of striking morphological characters (reduced eyes, light pigmentation, slender body and very elongated legs and antennae), which recall the troglobiomorphic traits of cave arthropods. Relations between caves and ants are discussed at this occasion, in the light of the recent biological explorations of caves in Southeast Asia. The classical view that ants are rare and unimportant in caves is challenged. Ants are actually major and regular components of guano assemblages in many caves of the region, but none of these guano species exhibit cave-related adaptation in its external morphology. Conversely, ants are very rare in low-resources habitats, where only accidental occurrence of outside species are reported in Southeast Asia. *Leptogenys khammouanensis* has been found only in such an oligotrophic environment, very deep in the cave and far from any guano deposits. Its presence there, together with its troglobiomorphic traits, support the idea that *Leptogenys khammouanensis* might be the first truly troglobitic ant.

Key words: *Leptogenys*, taxonomy, troglobiomorphy, cave ants, Laos

INTRODUCTION

The pantropical genus *Leptogenys* presently includes 215 species of which 54 species and 28 subspecies are known from the Oriental region. African species have been revised by Bolton (1975) and Melanesian species by Wilson (1958). A revision of the Neotropical species by J. Lattke is on the way. No similar work exists for the Oriental region. Most species were described posteriorly to the only treatment of the Asian *Leptogenys* by Mayr (1879). The species of India have been keyed out by Forel (1900) and Bingham (1903), and Chinese fauna has recently been revised with several new species described (Xu 1996, 2000; Zhou 2001).

In this work, we describe *Leptogenys khammouanensis* sp. nov. collected in two caves of Laos. It exhibits the combination of morphological characters which defines troglobiomorphy in arthropods (Christiansen, 1965): reduced eyes, elongate appendages (legs and antennae), light color. The possible troglobitic status of the new species is discussed in the context of our knowledge of Southeast Asia cave ants.

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MEASUREMENTS AND INDICES

All measurements were made on specimens in alcohol using a Leitz Weitzlar Stereomicroscope at magnifications of ×150, ×100, and ×50 for total Length. Measurements (in millimeters) and abbreviations used here are based on Bolton (1975),Ward (1989) and Roncin (2002). Total Length (TL): Total length of an individual, from the mandibular apex to the gastral apex. Head Length (HL): Length of the head, excluding the mandibles. This measurement is taken in frontal view on the sagittal line from the foremost point of the clypeal margin (or its projection if situated laterally to the line) to the most posterior point on the occipital margin (or its projection). Head Width (HW): Maximum head width of the head measured in full-face view excluding the eyes. Scape Length (SL): Length of the first antennal segment, excluding the condylus. Cephalic index (CI): (HW / HL) × 100. Scape Index (SI): (SL / HW) × 100. Eye Diameter (EL): Maximal length of eye. Pronotal Width (PrW): Maximum width of pronotum in dorsal view. Mesosoma Length (ML): Diagonal length of the mesosoma, measured in lateral view from the point at which the pronotum meets the collare to the base of the propodeal lobes. Often called Weber's length of mesosoma. Petiole Height (PH): Height of the petiole measured in profile from the apex of the ventral (subpetiolar) process vertically to a line intersecting the dor-

salmost point of the node. Petiole length (PL): Length of the petiole from the anterior flanges to the posteriormost point of the petiole. Lateral Petiole Index (LPI): (PH / PL) × 100. Dorsal Petiole Width (DPW): Maximum width of the petiole, measured in dorsal view. Dorsal Petiole Index (DPI): (DPW / PL) × 100.

DESCRIPTION

Genus ***Leptogenys*** Roger, 1861

Leptogenys khammouanensis sp. nov.

(Fig. 1: a–d)

Description of Holotype (worker). TL 7.6, HL 1.54, HW 1.01, CI 65, SL 1.99, SI 197, EL 0.09, PrW 0.71, ML 2.55, PH 0.46, PL 0.77, LPI 59, DPW 0.32, DPI 0.40

Head elongate, quite narrow, slightly broadened anteriorly, broadest across the eyes, the sides feebly convex. Occipital margin passing to lateral margin by a regular curve. A low nuchal carina present. Eyes small, oval, composed of 15–20 ommatidia. Maximum diameter of eye 0.093 mm, about 0.09 × HW, that is less than the maximum width of the scapes (0.127 mm). Eyes well in front of the middle of head sides, with their posterior borders situated on the same level than the posterior end of the frontal carinae in full face view. Eyes position frontal, not overlapping the outlines of head sides in full-face view. Circumocular groove strongly developed. Mandibles not striated, weakly shining, with feeble punctures more numerous near masticatory border. Masticatory margin of mandibles with 14 teeth: the two apical ones well developed and followed by three denticles, one tooth and a series of 8 small teeth and denticles. Basal margin of mandibles close to the basal tooth of the apical margin with small crenulations. Clypeus triangular, projecting anteriorly as a distinct lobe closing tightly against the basal border of the mandibles, and with its foremost part broadly truncated. A wide longitudinal carina present on the median portion of clypeus. Anterior border of clypeus bidentate due to two massive enlarged central setae and laterally a row of normal and straight setae, all much shorter than other cephalic setae. Antennal scapes extremely long surpassing the occipital margin by almost half their length, with numerous erect to subdecumbent hairs, most of them being half the scape width. Funicular segments elongate : length of segments 1–3 ca 0.254, 0.422, 0.355 respectively (the partly visible condylar bulb of the first antennal segment is exclude from this measurement). Funicular segment 11: length 0.232; width 0.131.

Mesosoma elongate. Pronotum widest behind the middle, narrower in front than behind. Mesonotum markedly elongate (dorsal length of mesonotum 0.659 mm, taken at the level of the anterior border of metathoracic spiracles) and approximately of the same length than pronotum length (collare excluded) in dorsal view. Mesosoma shallowly depressed between mesonotum and propodeal dorsum but without any trace of the transverse metanotal suture. A transverse carina present on the posterior end of the declivitous face of propodeum surrounding insertion of petiolar peduncle. A low longitudinal median carina is present on the mesosternum and is crossed by small wrinkles. Legs extremely long, with metafemur length (2.10 mm) exceeding gaster length.

Node of the petiole in dorsal view much longer than broad. Anterior part of the node with a carina separating it from the true anterior peduncle which is indeed very short. Dorsal outline of the anterior part of the node concave in lateral view. The node is widening progressively backward, giving to the anterior part of the node an aspect of false peduncle.

Gaster constricted between its first and second segment. Sting relatively short.

All body sculpture smooth. Body color light orange-yellow with small brown spots regularly spaced at the basis of body setae. Callow individuals yellow. Body with a dense pilosity especially on head, gaster and coxae, and with the longest hairs situated on clypeus, ventral surface of the head capsule and procoxae.

Gyne and male unknown.

Etymology. From “Khammouan”, a province of Laos with beautiful calcareous landscapes, uncountable caves and subterranean rivers.

Type material. Holotype worker, Laos: Tham (= cave) Nam Non (18.0270° N, 104.6883° E, coordinates from Brouquisse, 1999), alt. 185 m, several km inside the cave, hand collecting, 15.II.1999, (LAO-070), J. Lordon and J.F. Vacquié.

Paratypes workers: 2 workers, same data; collected with holotype.

Other material: 4 workers, Laos: Ban Nakok: Tham Thê cave (17.9964° N, 104.4482° E, coordinates from Brouquisse, 1999), 11.II.1998, (LAO-016), collected at about 500 m from cave mouth, hand collecting, L. Deharveng and A. Bedos.

Standard measurements: workers. TL 7.0-7.8, HL 1.54-1.65, HW 0.98-1.05 CI 64-65, SL 1.94-2.12, SI 197-201, EL 0.09, PrW 0.66-0.74, ML 2.42-2.64, PH 0.45-0.50, PL 0.76-0.84, LPI 58-59, DPW 0.29-0.32, DPI 0.38-0.40

One worker from the type locality possesses on the right side an abnormal eye of circular shape reduced to a single large ommatidia of 0.041 mm diameter.

The holotype of the new species is deposited in the Museum National d’Histoire Naturelle de Paris (MNHN) and the paratypes in the author’s collection.

Remarks. The general habitus of *Leptogenys khammouanensis* with very elongate head, mesosoma, petiole, antennae and legs is very similar to that of *Leptogenys assamensis* Forel, 1900, a species that seems to be known only from the type series collected by Long in the Garó hills in Assam (E. India), and to *Leptogenys ergatogyna* Wheeler, 1922, a forest species known from Zaire, Uganda and Cameroun and which presents few affinities to other African species (Bolton, 1975). However, *Leptogenys assamensis* and *Lep-*

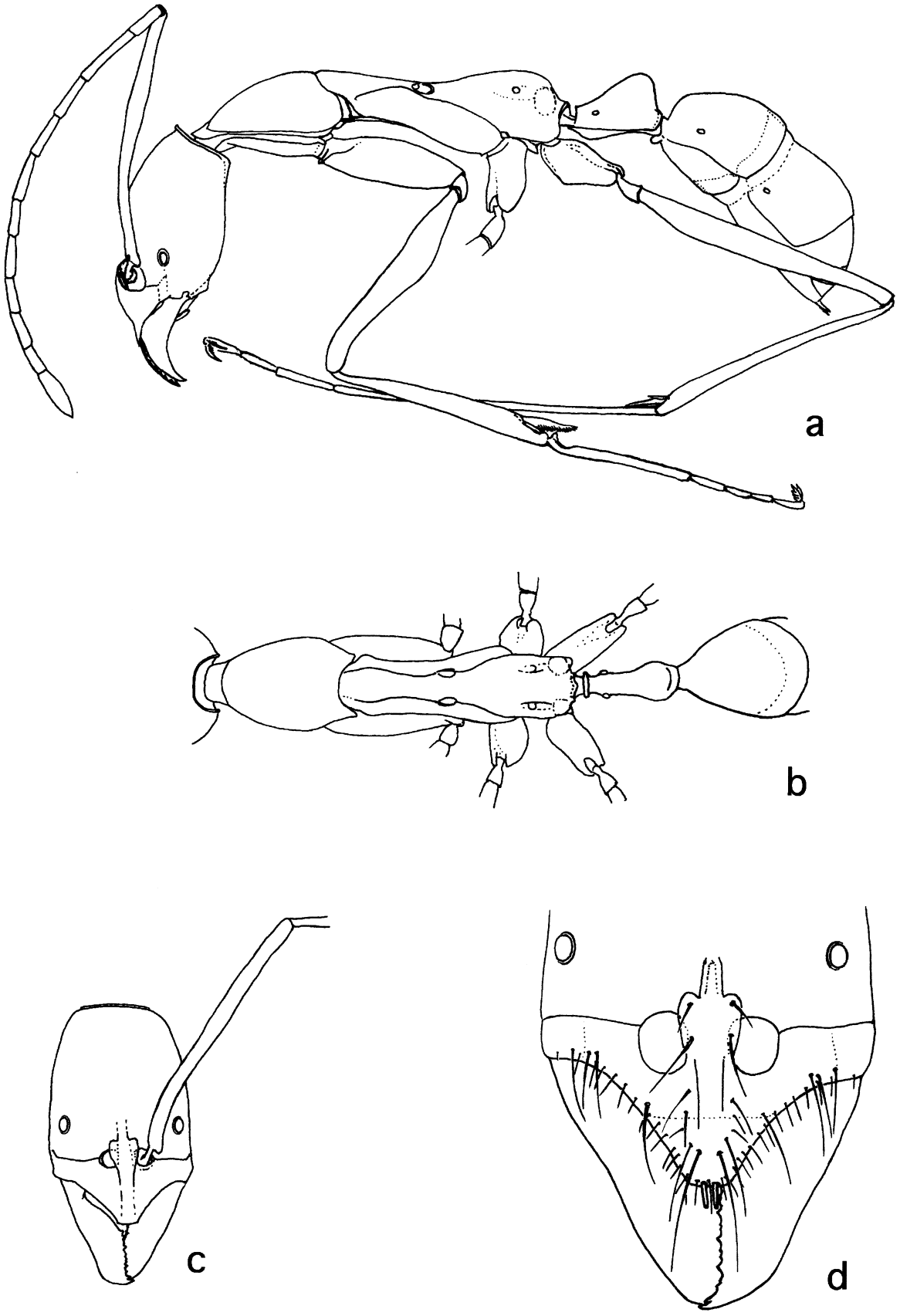

Fig. 1. *Leptogenys khammouanensis* sp. nov. a–d, holotype worker. a, lateral view; b, dorsal view; c, head in frontal view; d, anterior part of head with clypeal setae figured.

togenys ergatogyna differ from *L. khammouanensis* by the presence in both species of the metanotal suture, the absence of a pair of enlarged, straight and hard setae on the clypeal lobe border, less mandibular teeth (no mandibular teeth in *L. assamensis* and only two apical teeth in *L. ergatogyna*) and by other characters (color, eyes size) discussed in the paragraph below concerning troglobiomorphic characters in *Leptogenys*.

DISCUSSION

The combination of reduced eyes, very pale color and elongate appendages isolates *Leptogenys khammouanensis* in its genus. Short of a revision of Oriental *Leptogenys*, it is impossible to assess its affinities, especially because these conspicuous morphological traits are adaptive to hypogean life. For this reason, however, they are of great interest, as they point to an unusual mode of life for an ant. The possibility of troglobitic life for ants has long puzzled specialists (see Wilson, 1962), and is still a matter of debate (Tinaut and López, 2001). Compared to other ant candidates to troglobitic life, *L. khammouanensis* is one step ahead in terms of morphological characters linked to cave life. This question of troglobitic and troglobiomorphic ants will be discussed below, taking into account recent literature and the rich material of cave ants we have gathered in Southeast Asia.

Assessing the troglobitic status of a taxon is not easy. However, troglomorphy (Christiansen, 1962), or better troglobiomorphy (Boutin, in press), i.e. the set of morphological traits characteristics of cave organisms, is always a strong indication of troglobitism (while the opposite is not always true). Troglobiomorphy in arthropods is defined by four morphological traits: loss of wings in winged arthropod groups, reduction of eyes, reduction of tegumentary pigment and elongation of appendages (Vandel, 1964; Christiansen, 1965; Culver, 1982; Marques and Gnaspini, 2001). All known specimens of *L. khammouanensis* are workers, which are always apterous in ants. We do not know therefore the state of the first character in the new species, but the last three traits are present.

Troglobiomorphic characters in *Leptogenys*

The small eyes and light color of *L. khammouanensis* recall those of the group of *L. processionalis* sensu Taylor (1969) (= *fallax*-group of Andersen, 2000), which comprises three Australian species, *L. fallax* (Mayr, 1876), *L. tricosa* Taylor, 1969 and *L. fortior* Forel 1900, and the Oriental species *L. myops* (Emery, 1887), *L. crassicornis* Emery, 1895 and *L. processionalis* (Jerdon, 1851). Species of this group possess also light color and reduced eyes varying from a single (*L. tricosa*) to about fifteen facets, but antennae are short, and size is small. Such a morphology appears as a classical adaptation to endogeous, not to cave life. At least several African species in the *guineensis*- and the *nitida*-group also possess small eyes, and are yellow brown to dark brown. However their head and appendages are so not elongated.

In its slender habitus (very elongate head, mesosoma, petiole, antennae and legs), *Leptogenys khammouanensis* is similar to *Leptogenys ergatogyna* Arnold 1954 from Africa (redescribed in Bolton, 1975) and to *L. assamensis* Forel, 1900 from Assam (redescribed by Bingham, 1903). But both species differ from *L. khammouanensis* by their black color and larger eyes, and cannot be considered as troglobiomorphic.

No species of *Leptogenys* therefore approaches *L. khammouanensis* in its combination of troglobiomorphic characters.

Troglobiomorphic ants

Only one species of Formicidae, *Aphaenogaster cardenai* Espadaler, 1981, could be associated to subterranean habitats (Decu *et al*., 1998, Tinaut and López, 2001). This rare Spanish species has always been collected in cryptic habitats: under big rocks, galleries of rodents and caves. However in this latter habitat no nests have ever been found, which led these authors to postulate that *A. cardenai* is more probably an inhabitant of the MSS (“Milieu Souterrain Superficiel” of Juberthie *et al*., 1980, “superficial underground compartment” in Humphreys, 2000), than a strictly cave dwelling species.

A. cardenai is related to *A. splendida* (Roger, 1859), *A. ovaticeps* (Emery, 1898) and *A. muelleriana* Wolf, 1915. All have reduced eyes, slender body, elongate appendages and often pale color, compared to other species of the genus. Bernard (1968: 136) stressed the peculiar morphology of the species then known and noted that they have “un faciès aphaenopsien de cavernicole” (“an *Aphaenops*-like morphology of cave species”). He supposed they inhabit hypogean habitats, probably deep cracks that they rarely leave, hence their rarity in collection. However a few captures from surface habitats (Forel, 1911; Wheeler and Mann, 1916) could indicate nocturnal activity more than hypogean life.

Leptogenys khammouanensis is therefore the second example in Formicidae with the *Aphaenogaster* of the *splendida*-group, and the first Ponerinae, which combines hypogean life with microphthalmy, light color, and elongated appendages, i.e. the typical adaptive characters of cave inhabiting arthropods. None of the *splendida*-group species of *Aphaenogaster* is cave-restricted. Conversely, *L. khammouanensis* was observed only in deep parts of caves and in rather significant numbers, bringing an exciting question to the fore: is *L. khammouanensis* the first truly troglobitic ant?

Cave ants

Though frequently cited from caves, ants have not provided so far any unambiguously troglobitic species. Most records (Wilson, 1962; Tinaut and López, 2001) concern in fact accidental occurrences, generally not far from cave

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 *Hypoponera 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 *Hypoponera* 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 woodlices-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 combination 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).

ACKNOWLEDGEMENTS

We thank the members of the 1998 and 1999 French caving expedition to Laos, who provided the specimens, especially Anne Bedos, Jérome Lordon, and Jean-François Vacquié. Bernard Kaufmann and Hervé Jourdan made useful comments on the manuscript. We further thank Penelope Greenslade and Robert Taylor for style improvment of large parts of the manuscript.

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(Received July 12, 2002 / Accepted March 12, 2003)