# BIOSPÉOLOGIE

## FRESHWATER CAVERNICOLE PLANARIANS FROM MEXICO : NEW TROGLOBITIC AND TROGLOPHILIC DUGESIA FROM CAVES OF THE SIERRA DE GUATEMALA (1),

by Robert W. MITCHELL and Masaharu KAWAKATSU.

## Analyse.

In this paper are presented descriptions of freshwater cavernicole planarians from Mexico including the first true troglobitic species of the genus Dugesia. The troglobites Dugesia typhlomexicana and D. barbarae are described from La Cueva de la Mina and La Cueva de la Capilla, respectively, while the troglophile D. guatemalensis is described from La Cueva de las Perlas. All of these caves occur in the higher elevations of the Sierra de Guatemala of Tamaulipas. Also described are non-sexual specimens of an additional troglophile population inhabiting La Cueva de la Capilla and of an epigean population inhabiting a lowland stream near Gómez Farias, Tamps. The affinities of these planarians are discussed, and several suggestions are made regarding their cave colonization and evolutionary history.

Cette note présente les descriptions de Planaires obscuricoles dont certaines constituent les premières espèces hypogées connues du genre Dugesia. Dugesia typhlomexicana et D. barbarae, toutes deux troglobies sont décrites respectivement des grottes de la Mina et de la Capilla, tandis que D. guatemalensis, forme troglophyle, provient de la grotte de las Perlas. Toutes ces grottes sont situées en altitude (1500 à 2000 mètres). Dans la Sierra de Guatemala du Tamaulipas, sont également décrits des spécimens immatures d'une autre population de Planaires troglophyles localisées dans la grotte de Capilla et d'épigées récoltées dans un ruisseau de plaine près du Gómez Farias, au Tamaulipas. Les affinités de ces Planaires sont discutées et diverses suggestions sont proposées concernant leur colonisation des grottes et l'historique de leur évolution.

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#### Introduction.

The purpose of this paper is to present the descriptions and to discuss the affinities of some new species of troglobitic and troglophilic planarians inhabiting limestone caves in the Sierra de Guatemala of Tamaulipas, Mexico.

The freshwater planarian fauna of Mexico is practically unstudied. Prior to the discovery of the planarians upon which our study is based, there existed but a single literature reference to the occurrence of cavernicole planarians in Mexico. Villalobos (1960) mentions the presence of transparent planarians cohabiting pools with a troglobite amphipod, Bogidiella tabascensis, in Las Gruta de Cocona, Teapa, Tabasco. Mitchell and Kawakatsu (1972) recently described this distinctive planarian as a new genus and species, Dimarcus villalobosi, and erected for it a new triclad family, the Dimarcusidae. The existence of other Mexican cavernicole planarians was brought to light about three years ago during the course of continuing studies by the senior author and his students on the cavernicole fauna of the Sierra de El Abra and the Sierra de Guatemala. At this time, the presence was noted of a small-eved planarian inhabiting pools in La Cueva de la Capilla, Municipio de Jaumave, Tamaulipas. Mr. James R. Reddell discovered a quite small, eyeless, depigmented planarian in a pool in La Cueva de la Mina, Municipio de Gómez Farias, Tamaulipas. A limited sample of the eyeless species was prepared for study in the laboratory of the senior author, and while the specimens proved to be sexual, the slides were of insufficient quality to permit good description.

The occasion of the Libbie H. Hyman Memorial Symposium held in Chicago in December of 1970 fortunately brought the two of us together permitting a cooperative survey of the planarian caves of the Sierra de Guatemala, the first visit to these caves since initial discovery of the worms. The two planarians discovered earlier were recollected and two new populations were also found. The specimens obtained were prepared in the laboratory of the junior author, and their study revealed that all were undescribed species of the planariid genus Dugesia. Included were sexual individuals of two different troglobites (obligate cavernicole) and one troglophile (facultative cavernicole). Non-sexual specimens of an additional troglophile, probably conspecific with the sexual troglophile, were also taken. We further obtained several non-sexual specimens of an epigean Dugesia from a small surface stream near the town of Gómez Farias, Tamaulipas. All of these planarians are described herein.

#### Collection data.

Following are listed the several groups of planarians upon which this paper is based together with pertinent collection data. The numbers designating each sample are those employed by the junior author in his permanent recording system.

Specimen Lot No. 1075. This collection comprises four animals taken from a small epigean stream located about six km east of the town of Gómez Farias, Tamaulipas, Mexico. This intermittant stream is a tributary of the Rio Sabinas (a tributary of the large Rio Guayalejo which empties into the Gulf of Mexico at Tampico), and the collection of planarians was made at the point where the stream is crossed by Highway 85 (at about Km 138). The collection was made 9 January 1971. Water temperature was about 20°C at the time of collection, but the nature of the stream would make its temperature highly susceptible to large fluctuations. Altitude at the collection site is about 100 m. All individuals taken were sexually immature and diagnosable only to genus. Consequently, this species is referred to in this paper as «Dugesia sp. (species of Gómez Farias)». The collection was made by M. Kawakatsu, R. W. Mitchell, J. R. Reddell, W. H. Russell, and other members of Mitchell's laboratory.

Specimen Lot No. 1076. This collection comprises seven specimens of a small, eyeless, depigmented troglobitic *Dugesia* taken from a small pool in La Cueva de la Mina, Municipio de Gómez Farias, Tamaulipas, Mexico. This new species will be described subsequently in this paper as *Dugesia typhlomexicana*. Its cave habitat is also described in more detail in a later section. The collection was made on 10 March 1969 by J. R. Reddell and R. W. Mitchell.

Specimen Lot No. 1077. This sample comprises 21 individuals of *Dugesia typhlomexicana* n. sp. taken from the same pool in La Cueva de la Mina which yielded the preceding collection. These planarians were collected 10 January 1971 by M. Kawakatsu, R. W. Mitchell, and some other members of Mitchell's laboratory.

Specimen Lot No. 1078. This sample comprises 37 individuals of a small-eyed, troglophilic *Dugesia* taken from pools in La Cueva de la Capilla, Municipio de Juamave, Tamaulipas, Mexico. None of these worms was sufficiently mature to permit diagnosis, but in all likelihood the species will finally prove to be conspecific with *Dugesia guatemalensis* n. sp. described later in this paper. For the present, though, this species is herein referred to as «*Dugesia* sp. (species of La Cueva de la Capilla) ». The habitat will be described in more detail in another section of this paper. This collection was made 11 January 1971 by M. Kawakatsu, R. W. Mitchell, J. W. Cooke, S. Wiley, and other members of Mitchell's laboratory.

Specimen Lot No. 1079. This sample comprises five specimens of a small, eyeless, depigmented, troglobitic *Dugesia* taken from small pools in the preceding mentioned cave, La Cueva de la Capilla. This new species will be described subsequently in this paper as *Dugesia barbarae*. In all, eight individuals of this species have been taken. The first specimen by was collected on 11 January 1971 by S. Wiley, and shortly after its examination in the cave by the junior author, it disintegrated. The five specimens upon which the description is based were taken on 14 January 1971 by J. W. Cooke and M. K. Brownfield. These were not seen in life by the junior author since they were collected after his departure from Mexico. Later, on 16 May 1971, two additonal specimens were collected in this cave by S. Wiley, A. Sturdivant, and R. W. Mitchell. One of these disintegrated as a result of manipulations during photography.

ANNALES DE SPÉLÉOLOGIE, tome 27, fasc. 4, 1972.

641

Specimen Lot No. 1080. This sample comprises 17 specimens of a small-eyed troglophilic *Dugesia* taken from small pools in La Cueva de las Perlas, Municipio de Juamave, Tamaulipas, Mexico, a cave located quite close to La Cueva de la Capilla. This new species will be described subsequently in this paper as *Dugesia guatemalensis*. The habitat is also discussed in more detail in a later section. The collection was made on 15 January 1971 by S. Wiley, A. Sturdivant, and R. W. Mitchell. The junior author has not observed this species in life since the animals were collected after his departure.

#### Methods.

The animals of Specimen Lot No. 1076 were killed in 3 % nitric acid and were fixed in Bouin's fluid. Serial sagittal sections were stained with Mallory's triple stain. The remainder of the animals (Specimen Lot Nos. 1075, 1077, 1078, 1079, and 1080) were killed and fixed in Bouin's Fluid. Serial sections of several orientations were stained with Delafield's hematoxylin and eosin.

Altitudes of the cave entrances were determined with an American Paulin System Terra Surveying Altimeter, Model T-5, measuring in 5 ft increments with the reference base station being a benchmark, coded H-45, located at the Rio Sabinas bridge about 6 km east of Gómez Farias at an elevation of 99.286 m.

#### Species descriptions.

## Order TRICLADIDA. Suborder PALUDICOLA OF PROBURSALIA. Family Planariidae. Genus Dugesia Girard, 1850.

#### Dugesia typhlomexicana Mitchell and Kawakatsu, n. sp. (2).

#### Figs. 1 - 3, 9, 13, 14, 22, 24 - 27.

**DESCRIPTION.** — The general appearance of this species is indicated by Figs. 1 - 3, 9, 13, 14, and 22. This is a small, slender, rather delicate species measuring about 8 mm long and 0.5 mm wide. In the normally gliding animal, the head is triangular, with moderately developed and rather pointed auricles. The anterior end of the head is bluntly pointed. Behind the auricles, the body widens and soon reaches its greatest width at the pharyngeal region. Behind the pharynx the body tapers to a bluntly pointed posterior end. The pharynx is situated behind the middle of the body ; the mouth, at the beginning of the last one-fourth of the body ; and the genital pore, midway between the mouth and the posterior end.

There are no eyes in this species (Figs. 1, 2, 22) and no pigment. The head is almost transparent and the remainder of the body is white except for the contents of the intestine which may be visible through the body wall. These external characteristics demonstrate clearly that this species is a true troglobitic planarian.

Sagittal, transverse, and frontal sections were prepared from a sample of 26 specimens (Specimen Lots 1076 and 1077). Almost all of these ani-

<sup>(2)</sup> From the Greek word, Typhlos, meaning blind.

mals were fully sexual. The dorsal epidermis is thicker than the ventral, and, as usual, the rhabdites are more abundant in the dorsal epidermis than in the ventral. The submarginal adhesive zone is conspicuous in this species. The secretion of the adhesive glands is granular and strongly eosinophilic. The pharyngeal muscles conform to the arrangement typical in the family Planariidae : the fibers of the internal zone forming two



FIG. 1. — Dugesia typhlomexicana from La Cueva de la Mina. Note the bluntly pointed anterior end, the transparency of the head, the rather pointed auricles, and the intestinal diverticula visible through the integument.

separate layers, an inner circular one and an outer longitudinal one. The anterior trunk of the intestine bears seven to eight lateral branches ; each posterior trunk, eight to ten short lateral branches.

The ovaries are located, as is typical, at the level behind the second or third lateral branch of the anterior intestinal diverticulum. The yolk glands occur throughout the body. The testes are of large size, as few in number as 14 pairs, and occupy the greater part of the dorsoventral space in the parenchyma between the intestinal diverticula. They extend in the lateral body regions from the level of the ovaries almost to the posterior end of the body. Behind the genital pore they are also found between the two intestinal trunks. At a short distance behind the ovaries, the testes may be dorsally located.

The copulatory apparatus is shown in sagittal view in Fig. 3. Photomicrographs of parts of the copulatory apparatus are shown in Figs. 24-27. The genital pore leads immediately into a small cavity, the common antrum (or the terminal part of the bursal canal). This cavity leads anteriorly into the male antrum, a conical cavity, wide anteriorly and tapering toward the common antrum. It is lined with a cuboid epithelium

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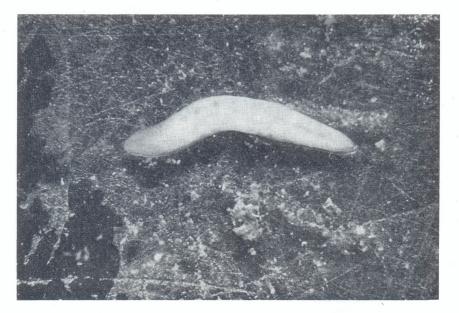


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The penis consists of an oval-shaped bulb and a moderately large, conical papilla of symmetrical shape. The appearance of the penis depicted



FIG. 2. — Dugesia typhlomexicana in pool in La Cueva de la Mina. Several individuals may be seen gliding on the substrate. Cohabiting these waters is the isopod *Brackenridgia bridgesi*.

in Fig. 3 is probably that of the organ in its normal, non-contracted state. Both the penis bulb and the papilla are weakly muscular. The bulb contains a cavity of elongated oval outline, the bulbar cavity (seminal vesicle), into which the sperm ducts open separately (e. g., the holotype, No. 1077 g). In some of the other specimens, however, the anterior part of the seminal vesicle is somewhat forked where the sperm ducts enter (Nos. 1076a and 1077p, Figs. 26, 27). The bulb has the usual coat of muscle fibers arranged in concentric layers. The bulbar cavity, lined with an epithelium of tall glandular cells projecting into the cavity, continues into the papilla as a rather wide canal, the ejaculatory duct, which opens at the tip of the papilla. The penis glands are weakly differentiated in this species. In every specimen examined, the two sperm ducts form the usual spermiducal vesicles on either side of the penis bulb at the level of the mouth. The outer wall of the papilla is covered with a cuboid epithelium of large cells. This epithelium tapers in thickness anteriorly. Below the epithelium there is a thick layer of circular muscle fibers followed by another thin layer of longitudinal fibers.

The copulatory bursa is a medium-sized sac closely fitted into the space between the penis bulb and the subepidermal musculature of the dorsal side of the body near the posterior wall of the pharyngeal chamber. It

has a wide lumen and the internal wall is lined by a tall, glandular epithelium. In this lumen, in some specimens (e. g., No. 1077g), masses of sperms were found enveloped in a coagulum of the secretion. The bursal stalk runs posteriorly over the posterodorsal side of the penis, and at the level of the genital pore it turns to the ventral side to then open at the pore. The bursal stalk has a nucleate epithelium. The ovovitelline ducts, accompanied by eosiniphilous glands, open separately into the bursal

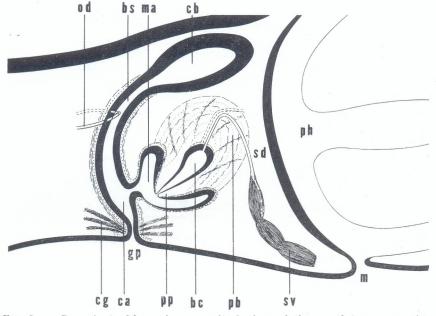


FIG. 3. — Dugesia typhlomexicana, sagittal view of the copulatory apparatus, No. 1077 g (Holotype). Abbreviations used to designate parts in this and all other figures are as follows : bc, bulbar cavity ; bs, bursal stalk ; cb, copulatory bursa ; ca, common antrum : cg, cement glands ; e, eye ; ed, ejaculatory duct ; gp, genital pore ; i, intestine ; m, mouth ; ma, male antrum ; od, ovovitelline pb, penis bulb ; ph, pharynx ; pp, penis papilla ; sd, sperm duct ; sv, spermiducal vesicle.

canal near the mid-part of the stalk. The terminal portion of the bursal stalk is somewhat wider than the anterior part of the duct, but a socalled vagina is not differentiated in this species. The muscular coat of the bursal stalk, consisting of inner circular and outer longitudinal fibers, is somewhat thicker in the posterior part of the organ than in the anterior part which connects with the bursa. Numerous eosinophilous glands are found around the distal part of the bursal stalk and the genital antrum near the genital pore.

The egg capsule, or cocoon, of this species is not known.

DIFFERENTIAL DIAGNOSIS. — Dugesia typhlomexicana differs from the other members of the genus by the following combination of characteristics : Troglobitic species lacking eyes and pigment. Size small, 8 mm in length in life. Auricles of moderate length, rather pointed. Testes large, only moderate in number, and occupying greater part of dorsoventral space between intestinal diverticula. Penis bulb moderate in size and weakly muscular. Sperm ducts opening separately into bulbar cavity. Penis papilla moderate in size, symmetrical, conical, and with wide ejaculatory duct. Copulatory bursa medium-sized. Two ovovitelline ducts entering bursal stalk separately.

TYPE SERIES. — Holotype, a set of serial sagittal sections (No. 1077g, one slide) deposited in the Division of Worms, U. S. National Museum. Two paratypes, a set of sagittal sections, (No. 1077p, one slide) and one whole mount (No. 1077u) also deposited in the U. S. N. M. The other paratypes (Nos. 1076a-f, 1077a-f, h-o, and q-t) retained in the authors' collections (Mitchell's laboratory in Lubbock and Kawakatsu's laboratory in Sapporo).

TYPE LOCALITY AND DISTRIBUTION. — La Cueva de la Mina, Municipio de Gómez Farias, Tamaulipas, Mexico. Known only from the type locality.

Additional discussion on the relationships of this species will follow in the section « Remarks on Affinities ».

## **Dugesia barbarae** Mitchell and Kawakatsu, n. sp. (3). Figs. 4, 5, 10, 15, 28 - 30.

DESCRIPTION. — Only five specimens of this form were available, but fortunately they were fully sexual. This new species is distinguished from the preceding species, *Dugesia typhlomexicana*, chiefly by the anatomy of the penis lumen. Although these two species are presently readily separable by their differences in penial anatomy, it is possible that when more is known of the cavernicole planarians of Mexico and adjacent regions, *D. barbarae* will become to be regarded as a subspecies of *D. typhlomexicana* (by virtue of page priority).

The appearance of this species is shown in Figs. 4, 10, and 15. This planarian is a small, slender, delicate troglobite. Eyes and pigment are lacking. The head is transparent and the remainder of the body white. Living specimens of the form bear a close resemblance to D. typhlomexicana externally, and in life the two species are probably not separable. Fully mature specimens measure about 8 mm long and 0.5 mm wide. The head is triangular, with moderately developed, rather pointed auricles. The anterior end of the head is somewhat pointed, seemingly more so than that of D. typhlomexicana. The body widens slightly behind the auricles, maintains a more or less constant width to the mid-region, then finally tapers gradually to a bluntly pointed posterior end. The pharynx is inserted behind the middle of the body. The copulatory apparatus, which could be seen vaguely from the ventral side in one preserved specimen prior to sectioning, occupies more than one-half the postpharyngeal region.

<sup>(3)</sup> We have named this species in honor of Mrs. Barbara Warburton, Director of the Biological Field Station of Texas Southmost College located at Rancho del Cielo, Municipio de Gómez Farias, Tamaulipas, Mexico.

The five specimens were sectioned sagittally and frontally. The rhabdites, the submarginal adhesive zone, and the pharynx do not present any special features. The anterior trunk of the intestine bears six to seven lateral branches ; each posterior trunk, eight to nine or more lateral branches.



FIG. 4. — Dugesia barbarae from La Cueva de la Capilla. Note the rather pointed anterior end and auricles and the transparent head.

The extraordinarily large ovaries occur at the level behing the third or fourth intestinal diverticula. The yolk glands are typical. The large testes begin immediately behind (or no more than just before) the ovaries. They are dorsally located at the anterior part of the pharyngeal region but frequently occupy the greater part of the dorsoventral space of the parenchyma between the intestinal diverticula. They extend throughout the body in a lateral tract on each side of the mid-line. Behind the genital pore, they are also found between the two intestinal trunks.

The copulatory apparatus is shown in sagittal view in Fig. 5 (anteroposterior axis in this figure inclined slightly to the right). Photomicrographs of parts of the copulatory apparatus are shown in Figs. 28 - 30.

At first it can be said that the size of the copulatory apparatus of *Dugesia barbarae* is larger than that of *D. typhlomexicana*. However, the copulatory apparatus of both of these species is similar in most details.

The common antrum, or terminal part of the bursal canal, leads into the male antrum. Both the cuboid epithelium of the wall of the male antrum and the two muscle layers below the epithelium are less developed in *D. barbarae*. The penis bulb is a large oval-shaped organ, but it is weakly muscular. The bulbar cavity (seminal vesicle) consists of a pair of moderately wide, elongated oval-shaped cavities located in the posterior part of the penis. These two cavities remain separate until near the tip of the penis papilla they unite forming a very short common cavity which opens into the male antrum at the tip of the papilla. In fact, an ejaculatory duct is not differentiated in this species. The penis lumen, consisting of the two separate bulbar cavities, is lined with a glandular epithelium of tall cells tapering in thickness toward the tip of the penis

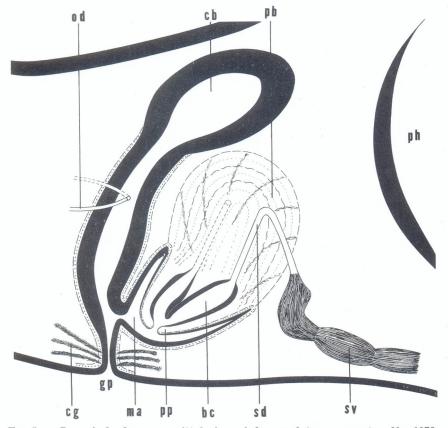


FIG. 5. — Dugesia barbarae, saggittal view of the copulatory apparatus, No. 1079c (Holotype). The anteroposterior body axis of this figure is inclined slightly to the right.

papilla. The penis glands are found in small numbers. The two sperm ducts penetrate the penis bulb from the anterolateral sides, and each opens into a cavity of the seminal vesicle (Figs. 29, 30). The spermiducal vesicles are well-developed in this species.

The penis papilla has a symmetrical, conical shape and is moderately large in size but weakly muscular. It is covered with the usual epithelium similar to that lining the male antrum, under which there are two muscle layers, an outer one of circular fibers and an inner one of longitudinal fibers. It was observed in every slide examined that both the epithelium

648

and the muscle layers of the male antrum and the papilla are less developed in *D. barbarae* than are those of *D. typhlomexicana*.

The copulatory bursa, a medium-sized sac located in the usual position, has a wide lumen, and the internal wall is lined by a glandular epithelium. The bursal stalk proceeds posteriorly near the posterodorsal side of the penis, widens considerably at its distal part, and opens at the genital pore. The bursal stalk has a nucleate epithelium. The two ovovitelline ducts open separately into the bursal canal near the mid-portion of the stalk. The muscular coat of the bursal stalk consists of inner circular and outer longitudinal fibers. These, however, are less developed in this species than in *D. typhlomexicana.* Eosinophilous glands are found around the genital antrum near the genital pore.

The egg capsule, or the cocoon, of this species is not known.

DIFFERENTIAL DIAGNOSIS. — Dugesia barbarae, closely related to Dugesia typhlomexicana, differs from the other members of the genus by the following combination of characteristics :

Troglobitic species lacking eyes and pigment. Size small, 8 mm in length in life. Auricles of moderate length, rather pointed. Testes large, located in dorsoventral space (essentially dorsal) between intestinal diverticula. Penis bulb large, weakly muscular. Seminal vesicle distinctly separated into two cavities, each entered by a sperm duct. Penis papilla moderate in size, symmetrical, conical, weakly muscular, and with wide cavity (posterior part of penis lumen). Copulatory bursa medium-sized. Two ovovitelline ducts entering bursal stalk separately.

TYPE SERIES. - Holotype, a set of serial sagittal sections (No. 1079c, 1 slide), deposited in the Division of Worms, U. S. National Museum. One paratype, a set of frontal sections (No. 1079d), also deposited in the U. S. N. M. The other paratypes (Nos. 1079a, b, and e) retained in the authors' collections (Mitchell's laboratory in Lubbock and Kawakatsu's laboratory in Sapporo).

TYPE LOCALITY AND DISTRIBUTION. — La Cueva de la Capilla, Municipio de Juamave, Tamaulipas, Mexico. Known only from the type locality.

Additional discussion on the relationships of this species will follow in the section « Remarks on Affinities ».

Dugesia guatemalensis Mitchell and Kawakatsu, n. sp. (4). Figs. 6, 16, 23, 31 - 37.

DESCRIPTION. — The appearance of this species (preserved) is shown in Fig. 16. This is a rather small, pigmented, troglophile with two small eyes.

The largest sexually mature specimen measures 10 mm long and 2 mm wide. In living specimens, the mobile head is triangular with moderately developed and pointed auricles. The anterior end of the head is rather

(4) Name indicates the occurrence of this planarian in the Sierra de Guatemala.

pointed. The two small eyes, separated by a distance of about one-third the head width at the level of the eyes, are each enclosed in a notably small, reniform, clear space (Fig. 23). The posterior one-half of the auricles is white in color. Behind the level of the auricles, the body widens, reaching its greatest width at the levels of pharynx and copulatory apparatus. The body then tapers to a bluntly pointed posterior end. The rather long pharynx is inserted behind the middle of the body and measures about one-fourth the length of the body. The genital pore is located midway between the mouth and the posterior end.

The general color of the dorsal surface is grayish brown with numerous pigment granules as shown in Fig. 16. A light, mid-dorsal, longitudinal stripe, limited to the anterior one-half of the body is inconspicuously present in some specimens. The anterior tip of the head and the body margins are of a lighter hue. The ventral side is lighter in color.

The six sexual specimens were sectioned both sagitally and transversally ; four were fully matured, two others were not quite mature. The dorsal epidermis is much taller than the ventral and much more heavily provided with rhabdites. The submarginal adhesive zone with eosinophilic glands is conspicuous. The internal muscle zone of the pharynx consists of two layers, an inner one of circular fibers and an outer one of longitudinal fibers. The anterior trunk of the intestine bears 15 or more lateral branches, each posterior trunk has 15 to 18 short lateral branches. The eyes, although small, are normal in their structure (Fig. 31).

The two ovaries occur in the usual anterior position, lying between the third and fourth intestinal diverticula. The numerous yolk glands (or vitellaria) occur throughout the body between the intestinal diverticula. The testes, not altogether well-defined in most specimens examined, occur in a lateral band on each side of the animal throughout the body length. They are essentially ventral being situated mostly below the level of the intestinal diverticula, but frequently they extend farther dorsally between the diverticula.

The copulatory apparatus is shown in sagittal view in Fig. 6, and photomicrographs of parts of the apparatus are shown in Figs. 32-37. The genital pore leads immediately into a small cavity, the common antrum. This cavity leads posterodorsally into the canal of the copulatory bursa and anteriorly into the male antrum. The male antrum is wide anteriorly. Its outer wall is lined with a tall, slender, glandular epithelium and is provided with two muscle layers, one circular and the other longitudinal.

The penis consists of a bulb embedded in the parenchyma and a free, well-developed papilla projecting into the male antrum. The penis bulb is spherical in shape, moderately muscular and contains a single bulbar cavity (seminal vesicle) from which a narrow canal (ejaculatory duct) continues to the tip of the papilla. There is no distinct separation between the seminal vesicle and the ejaculatory duct. The penis lumen is lined with a glandular epithelium, tapering in thickness anteriorly. The two sperm ducts penetrate the penis bulb from the anterolateral sides and run along either side of the bulbar cavity (Fig. 37). They then open into the posterior part of the seminal vesicle separately (Fig. 6). The penis bulb is pierced by numerous ducts of the penis glands. The usual spermiducal vesicles packed with sperms were not conspicuous in this species.

The symmetrical, muscular penis papilla is long, pointed, and conical. Its outer wall, especially in the basal region, is lined with a large, cuboid epithelium similar to that lining the male antrum. Below the epithelium there is a layer of circular muscle fibers followed by another of longitudinal fibers.

The copulatory bursa, situated in the usual position, is a medium-sized sac (in every specimen examined) with a wide lumen. The cavity of the bursa is lined by a very tall glandular epithelium. The bursal stalk, a long and rather wide cavity surrounded by a muscular coat consisting of inner circular and outer longitudinal fibers, runs posteriorly above the penis

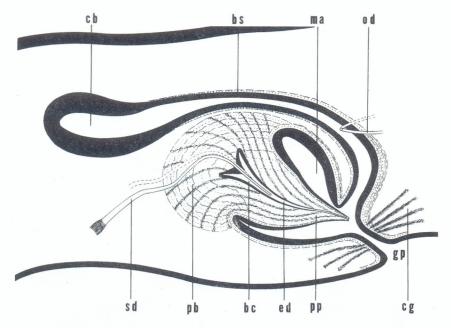


FIG. 6. — Dugesia guatemalensis, saggital view of the copulatory apparatus, No. 1080d (Holotype).

along the midline of the body, finally to curve ventrally and open into the common antrum. The bursal stalk has a nucleate epithelium. Just above its point of greatest curvature, the bursal stalk receives separately from both posterolateral sides the two ovovitelline ducts (Fig. 36). The ovovitelline ducts are accompanied by the usual trail of eosinophilous glands. The posterior, terminal portion of the bursal stalk is somewhat wider than the anterior part of the duct. The muscle coat of this part is also rather thicker than that of the anterior part of the bursal stalk. It consists of intermingled circular and longitudinal fibers only at the posterior portion of the stalk. A vagina is, however, not differentiated in this species. The walls of the distal part of the bursal stalk and the genital antrum near the genital pore are supplied with eosinophilous glands.

Specimens with supernumerary eyes and animals freshly regenerated after fission did not occur in our material. The egg capsule, or cocoon, of this species is not known. DIFFERENTIAL DIAGNOSIS. — Dugesia guatemalensis differs from the other members of the genus by the following combination of characteristics :

Troglophilic species with pigment and two small eyes. Size small, 10 mm in length in life. Auricles of moderate length. Testes numerous and essentially ventral. Penis bulb well-developed, moderately muscular, and with single bulbar cavity. Sperm ducts opening into seminal vesicle separately at basal part of penis lumen. Penis papilla symmetrical, conical, long, pointed, and with narrow ejaculatory duct. Copulatory bursa medium-sized. Two ovovitelline ducts entering bursal stalk separately.

TYPE SERIES. — Holotype, a set of serial sagittal sections (No. 1080d, 3 slides), deposited in the Division of Worms, the U. S. National Museum. Two paratypes also deposited in the U. S. N. M., one a set of transverse sections (No. 1080f, 10 slides), the other a whole mount (No. 1080g). The other paratypes, including sectioned material (Nos. 1080a-c and e) and whole mounts (No. 1080 group) retained in the authors' collections (Mitchell's laboratory in Lubbock and Kawakatsu's laboratory in Sapporo).



FIG. 7. — *Dugesia* sp. (species of La Cueva de la Capilla). Note the small eyes and moderate pigmentation.

TYPE LOCALITY AND DISTRIBUTION. — La Cueva de las Perlas, Municipio de Jaumave, Tamaulipas, Mexico. Known with certainty only from the type locality.

Additional discussion on the relationships of this species will follow in the section « Remarks on Affinities ».

## **Dugesia** sp. (species of La Cueva de la Capilla). Figs. 7, 8, 11, 17 - 19, 38, 39.

DESCRIPTION. — We had only limited material of this species and none of the animals was fully mature. In only some of the specimens could even a part of the copulatory apparatus be traced. Therefore, this form is recorded in this paper as *Dugesia* sp. (species of La Cueva de la Capilla).

The living animals of the form (Figs. 7, 11) have a close resemblance externally to the preceding species, *Dugesia guatemalensis*, and it is highly likely that the two are conspecific. This planarian is a rather slender, small, pigmented troglophile. The largest partially mature specimen measures 10 mm long and 1 mm wide, with the typical appearance of the genus *Dugesia*; i. e., with a triangular head, prominent auricles, and elongated body tapering to the posterior end. The auricles are of moderate length. The pharynx, inserted behind the middle of the body, is long, measuring about one-fourth to one-third the length of the body. The geni-

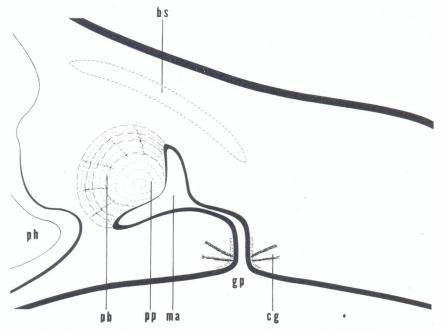


FIG. 8. — Dugesia sp. (species of La Cueva de la Capilla), saggital view of the copulatory apparatus, 1078b (specimen not fully mature).

tal pore, visible in some specimens, opens at the mid-portion of the postpharyngeal region. Externally, there is no difference in the position of the two small eyes and the coloration of the body between this form and *D. guatemalensis.* 

Of the 18 rather large specimens comprising the sample, a few were partially mature (No. 1078a-d, f, h, and m). The histology of the pharynx is typical of the family Planariidae. The anterior trunk of the intestine bears 18 or more lateral branches ; each posterior trunk bears 10 to 15 short lateral branches.

The non-mature ovaries, lying between the sixth and seventh intestinal diverticula, were found in some specimens (No. 1078b and others). The testes were also found in some slides, but mature sperms could not be detected.

All which could be determined of the structure of the copulatory apparatus is shown in sagittal view in Fig. 8 (No. 1078b), Fig. 39 shows a specimen with partially developed penis, male antrum, but lacking the genital pore. Fig. 38 shows a specimen with a shallow hole located at the level just behind the mouth (i. e., an early stage of the genital pore) accompanied by a number of eosinophilous glands around its wall.

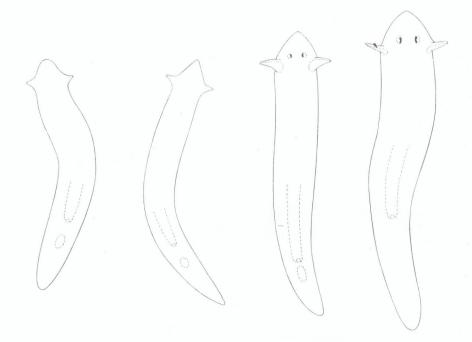


Fig. 9

Fig. 10

Fig. 12

FIG. 9. — Dugesia typhlomexicana, general view from life of mature specimen, No. 1077 group.

Fig. 11

FIG. 10. — Dugesia barbarae, general view from life of mature specimen. FIG. 11. - Dugesia sp. (species of La Cueva de la Capilla),

general view from life of partially mature specimen, No. 1078 group.

FIG. 12. — Dugesia sp. (species of Gómez Farias), general view from life of immature specimen, No. 1075 group.

As indicated by Fig. 8, the genital pore leads immediately into a small cavity, the common genital antrum. This cavity leads anteriorly into the male antrum. The outer wall of the common antrum is lined by a glandular epithelium below which are two muscle layers, one circular and

the other longitudinal. Both the penis bulb and papilla were found. The bursal stalk was evidenced only as a tract of cells. No suggestions were found of the sperm duct, bulbar cavity, ejaculatory duct, copulatory bursa and its stalk, or of the ovovitelline ducts.

MATERIAL. — Eighteen sets of sagittal, transverse, and frontal sections (No. 1078a-r) and a number of whole mounts (No. 1078 group) are retained in the authors' collections (Mitchell's laboratory in Lubbock and Kawa-katsu's laboratory in Sapporo).

## Dugesia sp. (species of Gómez Farias). Figs. 12, 20, 21.

DESCRIPTION. — The living animals (Fig. 12) of this form bear a close resemblance externally to Dugesia dorotocephala (Woodworth), one of the common species of the genus which occurs throughout the United States (Hyman, 1925, 1929, 1931 a and b, 1939 a, 1951, and others ; Kenk, 1935, 1944). There may, however, be slight differences between D. dorotocephala (of the U. S.) and this Mexican epigean species. The largest specimen which we examined measures about 10 mm long and 1.5 mm wide ; the other three individuals are but 5 to 8 mm long. The head is markedly triangular and rather pointed at the anterior end. There is a pair of elongated auricles in this form, but they are not so elongated, slender, and pointed as is usual in D. dorotocephala (compared with living specimens of this species from Buckhorn Spring in Oklahoma and several other localities in the U.S.) (cf. Kawakatsu, Teshirogi, and Yamada, 1968). The posterior one-half of each auricle is rather white in color but not conspiculously so. There are two eyes in the usual position. Their distance from each other is somewhat more than one-third the width of the head at the level of the eyes. A pigment-free area around each eye is conspicuous. Behind the auricles, the width of the body gradually increases to its widest at the level of the pharynx. A gentle narrowing of the head (neck) is not found in this form. The posterior end is bluntly pointed. The pharynx is inserted behind the middle of the body and measures almost one-fifth the length of the body (Figs. 12, 20).

The color of the dorsal surface is a dark brown with numerous, small, white, but conspicuous, spots. The ventral side is of a lighter color.

We have made sections of two large specimens, but each was sexually immature. It was seen that the internal muscle zone of the pharynx consists of two layers, circular fibers and longitudinal fibers, typical of the Planariidae.

MATERIAL. -- Two sets of serial sagittal sections (No. 1075a and b) and two whole mounts (No. 1075 group) are retained in Kawakatsu's laboratory in Sapporo.

#### Remarks on affinities.

The genus *Dugesia* Girard, 1850, (syn. *Euplanaria* Hesse, 1897) was defined by Hyman (1931 a, 1951) as follows : Head triangular with definite auricles ; eyes two (irregularities may occur) ; colored brown to black ; testes numerous, extending the body length ; penis with-developed bulb and papilla ; sperm duct entering a penis bulb

separately and enlarging therein to a bulbar cavity; copulatory sac sacciform; ovovitelline ducts entering a bursal canal; capsules spherical, stalked. Type : Dugesia gonocephala.

Inclusion of the eyeless and depigmented species described herein as well as some other species which violate other generic criteria will require the eventual rediagnosis of the genus.

The genus Dugesia has representatives in Europe, Asia. Africa, North and South America, and Australia (Kawakatsu, 1968, Fig. III - 1 ; revised world-wide distribution map of Dugesia will be found in Kawakatsu, In press - a). Lists of the known species of Dugesia and taxonomic discussions are found in the following papers : Europe — de Beauchamp, 1961, and others ; Dahm, 1967b ; Reynoldson, 1967. Asia — Ball, 1970; Ichikawa and Kawakatsu, 1964, 1967 ; Kawakatsu, 1965, 1966b, 1969b and d. Africa — Dahm, 1967a, Marcus, 1953, 1955a and b. North and South America - Ball, 1969a, 1971 ; de Beauchamp, 1939 ; Du Bois-Reymond Marcus, 1953 ; Hyman, 1939a, b, 1951, 1957, 1959, 1963, and others; Kenk, 1935, 1941, 1944, and others ; Marcus, 1946, 1948, 1954, 1960 ; Martins, 1970. Australia and the South Pacific Countries — Ball and Fernando, 1969 ; Kawakatsu, 1969a, c ; Nurse, 1950 ; Weiss, 1910. At present the genus comprises some 60 or more species, but this number may include some synonomies and uncertain species due to the difficulties in the systematics of the genus. It is apparently a very old and primitive genus (Kenk, 1941) and spreads from 0° to 60° S Lat. in the Southern Hemisphere and from 0° to 60° N. Lat. in the Northern Hemisphere (Kawakatsu, 1968, In press - a) (5). All

FIGS. 13, 14, 22. — Dugesia typhlomexicana, photographs from preserved specimens, No. 1077 group. Fig. 13, dorsal view ; Fig. 14, ventral view of same specimen ; Fig. 22, head of preserved specimen from whole mount (photomicrograph).

FIGS. 16, 23. — Dugesia guatemalensis, photographs of preserved specimens, No. 1080 group. Fig. 16, dorsal view; Fig. 23, head of preserved specimen from whole mount (photomicrograph).

FIGS. 17, 18, 19. — Dugesia sp. (species of La Cueva de la Capilla), photographs of preserved specimens, No. 1078 group. Fig. 17, dorsal view; Fig. 18, dorsal view; Fig. 19, ventral view of latter specimen.

FIGS. 20, 21. — Dugesia sp. (species of Gómez Farias), photographs of preserved specimens, No. 1075 group. Fig. 20, dorsal view; Fig. 21, ventral view of same specimen.

<sup>(5)</sup> Records of two introduced species are known in this genus. Dugesia tigrina, native to North and South America, has been introduced into European freshwaters (Dahm, 1955, 1958; Gourbault, 1969; Den Hartog, 1959, 1967; Hyman, 1951; Reynoldson, 1956) and has also been found in some aquaria of tropical fishes in Japan (Hirao, Kawakatsu, and Teshirogi, 1970; Kawakatsu and Hirai, 1968). According to Ball (1969 b, 1971), the European Dugesia polychroa (Reynoldson and Bellamy, 1970) was recently introduced into North American freshwaters. These introduced, curythermic species should be discounted in considering the zoogeography of the genus.

FIG 15. — Dugesia barbarae, photograph from preserved specimen. No. 1079 group.

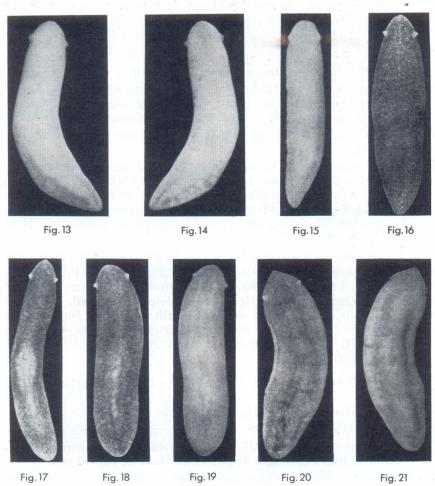


Fig. 17

Fig. 18

Fig. 20

Fig. 21

657



Fig. 22

Fig.23

Annales de Spéléologie, tome 27, fasc. 4, 1972.

44

of the known species of the American *Dugesia* are listed in Ball's 1969 paper, except for two Brazilian forms recently described. It is here appropriate to list the American species of *Dugesia* and their synonyms.

The North American Dugesia are as follows :

Dugesia tigrina (Girard, 1850) (syn. Planaria maculata Leidy, 1847; Planaria lata Sivickis, 1923; Euplanaria novangliae Hyman, 1931) from the entire United States and Canada.

- Dugesia microbursalis Hyman, 1931, from Connecticut and Massachusetts.
- Dugesia dorotocephala (Woodworth, 1897) (olim Planaria; syn. Planaria agilis Stringer, 1909; Euplanaria philadephica Hyman, 1931; Dugesia diabolis Hyman, 1956, from Devil's Hole, Nevada), from Pennsylvania and Virginia westward to the Pacific coast); (also in some Central American countries; Ball, 1971).

The taxonomy and systematics of the Caribbean and South American *Dugesia* are still not settled (Ball, 1969a, 1971). Although the specimens used for some of the old descriptions were sexual, some of these forms remain, nevertheless, incompletely described. De Beauchamp's (1939) classification of some South American *Dugesia* has not received wide acceptance among the American triclad specialists (Hyman, 1951, 1957; Du Bois-Reymond Marcus, 1953; Marcus, 1946, 1948, 1960).

The Caribbean and South American species of *Dugesia* are as follows :

Dugesia antillana Kenk, 1941, from Puerto Rico.

Dugesia aurita (Kennell, 1888) (olim Planaria) from Trinidad.

Dugesia arimana Hyman, 1957, from Trinidad and Caracas in Venezuela (includes new and unpublished data of Kawakatsu).

- Dugesia longistriata (Fuhrmann, 1914), (olim Planaria) from Colombia.
- Dugesia paramensis (Fuhrmann, 1914), (olim Planaria) from Colombia.

Dugesia polyorchis (Fuhrmann, 1914), (olim Planaria) from Colombia.

- Dugesia cameria (Fuhrmann, 1914), (olim Planaria) from Colombia.
- Dugesia festai (Borelli, 1898), (olim Planaria Festae and P. F. var albolineata; non Planaria aurita Kennell, 1888; syn. Dugesia titicacana Hyman, 1939; Euplanaria aurita sensu de Beauchamp, 1939) from the Andes of Bolivia, Peru, Ecuador, Colombia, Curaçao, and Caracas in Venezuela (including new and unpublished data of Kawakatsu).







659

Fig. 28



Fig. 25



Fig. 26



Fig. 27



Fig. 29



Fig. 30

FIGS. 24 - 27. — Dugesia typhlomexicana, photomicrographs of sagittal sections of copulatory apparatus. Fig. 24, No. 1077e; Fig. 25, No. 1077g, Holotype; Fig. 26, No. 1077p; Fig. 27, No. 1076a.
FIGS. 28 - 30. — Dugesia barbarae, photomicrographs of sagittal and transverse sections of copulatory apparatus. Fig. 28, sagittal section, No. 1079c, Holotype; Figs. 29, 30, transverse sections, No. 1079b.

#### R. W. MITCHELL AND M. KAWAKATSU.

Dugesia chilla Marcus, 1954, from Chile.

Dugesia rincona Marcus, 1954, from Chile.

Dugesia dimorpha (Böhmig, 1902), (olim Planaria) from Chile.

- Dugesia sanchezi Hyman, 1959, from central Chile, Argentina, and Brazil.
- Dugesia iheringii (Böhmig, 1887), (olim Planaria Iheringii) from Brazil.

Dugesia nonatoi Marcus, 1946, from Brazil.

Dugesia arndti Marcus, 1946, from Brazil.

Dugesia hypoglauca Marcus, 1948, from Brazil.

Dugesia jimi Martins, 1970, from Brazil.

Dugesia veneranda Martins, 1970, from Brazil.

Dugesia tigrina (Girard, 1850), from Brazil (Marcus, 1946).

Dugesia anceps (Kenk, 1930), (syn. Planaria dubia Borelli, 1895) from Paraguay.

Dugesia andina (Borelli, 1895), (olim Planaria) from Argentina.

In addition to these species, it is highly probable that some species described in the genus *Cura* Strand, 1942, (syn. *Curtisia* Von Graff, 1916) may be transferred into the genus *Dugesia* (Ball, 1971).

According to Marcus (1946, p. 173), *Dugesia tigrina* from Brazil (Sao Paulo and its vicinity and Porto Alegre in South Brazil) may be native to that country, but there is no continuity of distribution of this species between North and South America. Moreover, there are some slight differences in the genital anatomy between the animals from each continent.

Several uncertain species whose descriptions are based on nonsexual specimens are also recorded from the Americas. The following forms probably belong to the genus *Dugesia*, although their true generic assignment is impossible : *Planaria similis* Böhmig, 1902, from Chile ; *Planaria laurentiana* Borelli, 1897, from Argentina ; *Dugesia* sp. of Hyman, 1957, from Barro Colorado Island, Canal Zone. According to Hyman (1957, p. 4), the latter, long auricled *Dugesia* could possibly be *D. cameliae* or *D. antillana*.

All of these preceding Caribbean and South American species of *Dugesia* occur in epigean waters.

Our paper is one of the first to report on the freshwater planarian fauna of Mexico. Hyman (1957) identified as «*Planaria fissipara*» Kennell, 1888, some small planarians found in aquaria in the American Museum of Natural History which contained freshwater fishes from Mexico. According to Hyman's discussion, it is impossible to state-with certainty that these non-sexual planarians came from Mexico, but this would seem to be highly probable. «*Planaria fissipara*», the type locality of which is Trinidad, is also known from the Amazon and other rivers of northern Brazil (Marcus, 1948). Ball (1971), as a consequence of examination of Hyman's planarian material at the American Museum of Natural History, records for

660

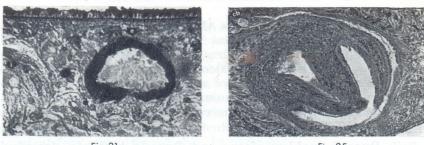


Fig. 31

Fig. 35



Fig.32

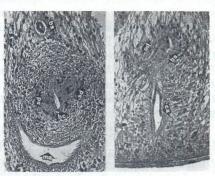


Fig. 36

Fig. 37



Fig. 33





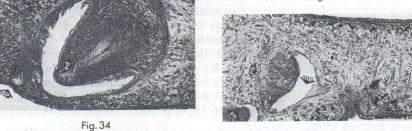


Fig. 39

FIGS. 31 - 37. — Dugesia guatemalensis, photomicrographs of sagittal and transverse sections of anterior part of body and copulatory apparatus. Fig. 31, sagittal section, No. 1080b; Fig. 32, sagittal section, No. 1080d, Holotype; Fig. 33, sagittal section, No. 1080a; Fig. 34, sagittal section, No. 1080b; Fig. 35, sagittal section, No. 1080e; Figs. 36, 37, transverse sections, No. 1080f.

FIGS. 38 - 39. — Dugesia sp. (species of La Cueva de la Capilla), photomicrographs of sagittal sections of copulatory apparatus. Fig. 38, No. 1078b; Fig. 39, No. 1078d. Dugesia dorotocephala (p. 14) « AMNH 737, Fish Tanks, AMNH, Mexico ? » Benazzi and Giannini (1971) have recently described Cura azteca from an epigean stream at El Zarco, Puerto de Las Cruces, about 30 km SW of Mexico City. As mentioned, Villalobos (1960) recorded the occurrence of a white planarian in the waters of Las Grutas de Coconá. This animal, an interesting marine relict, was recently described as Dimarcus villalobosi by Mitchell and Kawakatsu (1972).

Both Dugesia typhlomexicana and Dugesia barbarae, described herein, are white, eyeless species inhabiting cave waters, and, as such, they stand in sharp contrast to all other New World Dugesia which are pigmented, eyed species inhabiting springs or strictly epigean waters. Prior to the discovery of these troglobitic Dugesia, the only troglobitic planarians known in the New World, aside from Dimarcus villalobosi, were the several species of the genus Sphalloplana and the one species of the related genus Kenkia confined to the United States (for a complete listing of the species in these genera, see Mitchell, 1968, and Kenk, 1970).

In the genus *Dugesia*, only three oriental forms are reported as lacking pigment. These are as follows :

Dugesia burmaensis (Kaburaki, 1918), from a muddy bottom of Inle Lake (about 3 m in depth) in Burma.

Dugesia batuensis Ball, 1970, from Batu Caves in Malaya.

Dugesia sp., an undescribed form a well in Matsuyama City, Shikoku, Japan (Kawakatsu, 1960, p. 620; 1965, p. 365; 1966a, pp. 54-57, Fig. 1; 1967, p. 134; 1969d, p. 47, Table 1; Kawakatsu and Itô, 1963, p. 234).

Dugesia burmaensis was described from preserved animals only, Kaburaki (1918, p. 187) wrote of its color as follows : « The ground color of the dorsal surface is usually light drab. There exist no pigments. — on the dorsal side a light grayish-olive colour due to the gut content, the position of the pharynx and copulatory organs being marked by clear brownish colouration ; the ventral surface is of a much lighter colour, except the genital-end organs which appear of a blackish colour. — The species is wholly destitute of colourless areas corresponding to the auricular sense organ ». Judging from the description cited above and the black and white drawing of D. burmaensis (Kaburaki, 1918, Pl. 27, Fig. 1), this form may be a species of low pigmentation. It is highly probable that bleaching of the material could have occurred from overexposure to the fixative if the fixative contained acid (Ball, 1970, p. 282). Dugesia burmaensis has a pair of eyes.

According to its original description, *Dugesia batuensis* is a twoeyed, non-pigmented species, and in life the animal appears creamy white (Ball, 1970, p. 278). The junior author has material from Batu Caves (the type locality of this species) collected by Dr. S.-I Ueno

662

and Dr. M. Hirano on August 6, 1967 (Kawakatsu's specimen Lot No. 764). According to information from Dr. Ueno, the living specimens of this form were white in general appearance (in litt). Examination with a high power binocular microscope shows that the animal is a low pigmented form (material preserved in Bouin's fluid and relaxed in 70 % ethyl alcohol with a small quantity of lithium chloride). The usual clear space around each eye is not conspicuous in this species, but a pair of auricular sense organs is apparent as pigment-free areas (Kawakatsu, In press-b).

Dugesia sp. (species of Matsuyama) is a small, pigmentless form inhabiting subterranean waters and is closely related to a common Japanese freshwater planarian, Dugesia japonica Ichikawa and Kawakatsu, 1964, as evidenced by the shape of its body. About 40 non-sexual specimens were collected by the junior author, Dr. K. Matsumoto, and Dr. H. Sugino from a driven well in Matsuyama City (October 24 and 25, 1958; Kawakatsu's Specimen Lot No. 265). Most of these animals have two remarkably small eyes in the usual position, but a number of eyeless animals also occur in the population (Kawakatsu, 1960, p. 620; Kawakatsu and Itô, 1963, p. 234). Three subterranean isopods, Asellus iyoensis Matsumoto, 1960, A. shikokensis Matsumoto, 1960, Mackinia japonica Matsumoto, 1956, have also been recorded from this locality (Matsumoto, 1960).

Thus, the two Mexican Dugesia, D. typhlomexicana and D. barbarae, described in this paper are unique in this large and widespread genus in that they are true troglobites (i.e., white and eyeless).

In the arrangement and number of testes and the structure of the copulatory apparatus, D. typhlomexicana and D. barbarae are distinct from the other North American species of Dugesia (D. tigrina, D. dorotocephala, D. microbursalis). Instead, these two Mexican troglobitic species bear some slight resemblance to some South American species in the details of their genital anatomy, especially D. veneranda from Brazil and D. andina from Argentina, species which have dorsal testes, penis of symmetrical shape, and a wide bulbar cavity into which sperm ducts open separately. These two species differ, however, from D. typhlomexicana and D. barbarae in the size of the body, pigmentation of the dorsal side of the body, presence of eves, and by the occurrence in *D. veneranda* of an extraordinarily wide bulbar cavity and the presence or a rather well-developed vagina in D. andina. D. chilla, occurring in central and southern Chile, also has dorsal testes and a wide bulbar cavity, but this species is distinguishable by its infranucleate epithelium of the bursal stalk.

Dugesia guatemalensis, the third new Mexican species of the genus described in this paper, is a pigmented species with two eyes which inhabits caves waters in La Cueva de las Perlas. Although this species lives in subterranean pools in darkness, the animals do not have the specialized characteristics of true cave planarians except for a slight degree of lighter coloration of the body and possession of rather small eyes. It is highly probable that *Dugesia* sp. (species of La Cueva de la Capilla) recorded in this paper is identical with *D. guatemalensis*; the distance between the entrances of La Cueva de las Perlas and La Cueva de la Capilla is only about 100 m (Fig. 44). We fully expect to encounter *D. guatemalensis* in other caves of the Sierra de Guatemala.

Of all the new world Dugesia, D. guatemalensis appears to be most similar to D. dorotocephala, but the two, nevertheless, are separable. D. guatemalensis, lightly colored and with less developed eves, is smaller and more slender in the sexually mature state more bluntly pointed at the anterior end, and shorter in the length of its auricles than D. dorotocephala (6). The arrangement of testes in Dugesia guatemalensis differs to some extent from that of D. dorotocephala. In the slides of D. dorotocephala which we examined (Buckhorn Spring in Oklahoma and Powder Mill Spring, Shannon County, Missouri) (7), the ventrally located testes are small and are extraordinarily numerous (Hyman, 1925, and others ; Kenk, 1935, 1944). In D. quatemalensis the sperm ducts enter the seminal vesicles separately while in D. dorotocephala the sperm ducts typically expand to form seminal vesicles prior to the union of these into a single lumen. However, Ball (1971) attaches little importance to this character since such a bifid seminal vesicle sometimes occurs in D. tigrina and is likewise known for one population of D. dorotocephala (AMNH 735, Fort Davis, Texas). Although D. guatemalensis and D. dorotocephala are quite similar, we regard them as distinct species, as, for example, are D. dorotocephala and D. tigrina, species in which the anatomical and karyological differences are not very pronounced (Ball, 1971; Benazzi, Giannini, and Puccinelli, 1970; Kenk, 1944, p. 20). Because of their structural similarity, it would seem guite likely that D. guatemalensis is a near relative of D. dorotocephala.

Dugesia guatemalensis differs from the other two North American Dugesia (D. tigrina, D. microbursalis) and from all of the Caribbean and South American Dugesia in the size and form of the body, pigmentation of the dorsal side of the body, small eyes, the arrangement of the testes (ventral in D. guatemalensis), and in structure of the copulatory apparatus.

<sup>(6)</sup> Photographs of living specimens of *D. dorotocephala* may be found in the following papers: Kawakatsu, Teshirogi, and Yamada (1968, pp. 444-449; loc. Buckhorn Spring, Sulfur City, Oklahoma), Kenk (1935, Pl. 45, Fig. 3; loc. Big Spring near Kerr's Creek, Virginia), and several other papers on breeding behavior and experimental psychology of this species (Jenkins, 1964, and others; McConnell, 1965, and others).

<sup>(7)</sup> The Oklahoma material (Kawakatsu's Specimen Lot Nos. 443 and 444) was received from Dr. James V. McConnell and is being studied at the University of Michigan (Dr. McConnell's laboratory) and at Madison College in Virginia (Dr. Marie M. Jenkins' laboratory). The Missouri material (Kawakatsu's Specimen Lot no. 1086) was received from Dr. Roman Kenk,

As discussed earlier, the Mexican epigean species, Dugesia sp. (species of Gómez Farias) is closely related to the North American Dugesia dorotocephala in general appearance, but there are minor differences between them. The occurrence of D. dorotocephala in the southern states of the United States has been recorded by Kenk (1941) and Ball (1971). According to Dr. Kenk, this species occurs in California, New Mexico, and Texas. Ball (1971) has studied sexual material from Fort Davis, Jeff Davis County, Texas (AMNH 735). Jenkins and Brown (1963, p. 177, addendum : see also Jenkins, 1964, p. 48; loc. Roaring Springs, according to unpublished data of Mr. K. Mattox) have also recorded the occurrence of D. dorotocephala in Texas. Taxonomic studies of this latter Texas form are not vet published. We have examined living specimens from six populations of Dugesia in Texas from the following localities : a small stream in Yellowhouse Canyon within the corporate limits of the city of Lubbock (altitude, about 975 m; Kawakatsu's Specimen Lot. No. 1073), Beaver Creek at Highway 87, Mason County (altitude, about 425 m; Kawakatsu's Specimen Lot No. 1074), Amanitos Creek, 10 miles SE Presidio, Presidio County (altitude, about 780; Kawakatsu's Specimen Lot No. 1087), stream in Limpia Canyon, Fort Davis, Jeff Davis County (altitude about 1500 m; Kawakatsu's Specimen Lot No. 1088). Glenn Spring, south of Chisos Mts. in Big Bend National Park, Brewster County (altitude, about 780 m; Kawakatsu's Specimen Lot No. 1089), and Dripping Spring, north of the Chisos Mts. in Big Bend National Park (altitude about 780 m). No sexually mature specimens were collected from these localities, but they are very possibly all D. dorotocephala. If these forms are, in fact, D. dorotocephala, it is then not difficult to imagine that the range of this species continues on southward. This, together with structural similarity, would make it even more likely that the nonsexual specimens of Dugesia sp. (species of Gómez Farias) are D. dorotocephala.

Ball (1971) has made a detailed examination of several species of *Dugesia* (*D. dorotocephala*, *D. tigrina*, *D. diabolis*, *D. arimana*, and *D. antillana*) from North, Central, and South America including the Caribbean countries. He proposed that *D. diabolis* be considered a synonym of *D. dorotocephala*. He also stated that the possibility exists that his non-sexual specimens from the vicinity of Guatemala City were *D. dorotocephala*. In summarizing the distributional data of this species, Ball (1971) stated, «*Dugesia dorotocephala* thus extends from central and western North America down to Texas and possibly Mexico and the central American states ».

As pointed out some time ago by de Beauchamp (1939) and more recently by Ball (1971), the New World *Dugesia* form a well-defined group within the genus. Characteristics of the newly discovered Mexican cavernicole species do not invalidate this fact. Thus the differences — those associated with cave adaptation — seen in the

Mexican troglobitic planarians, *D. typhlomexicana* and *D. barbarae*, and the troglophilic species, *D. guatemalensis*, do not reflect their derivation from basically different evolving ancestral stocks, but rather reflect the disparity in time of cave colonization by their respective ancestral forms. This phenomenon has been of common occurrence in the evolution of cave-adapted animals (Mitchell and Reddell, 1971; Mitchell and Smith, 1972).

Examination of the list of American Dugesia appearing earlier in this paper clearly demonstrates that the North American species of the genus were derived from an ancestral form invading from South America which was probably colonized from Africa prior to separation of the Gondwanian Land Mass. These northward colonizing movements in the New World are evidenced by the fact that in the present South American Dugesia fauna there is rather extensive speciation and considerable endemism, while in North America there are but few species, of which the most common, D. dorotocephala and D. tigrina, are fairly recently evolved, each being widespread and polymorphic species. Simply put, Dugesia has not existed long enough in North America for extensive speciation to occur.

Any attempt to account for the co-occurrence of troglobitic and troglophilic *Dugesia* in caves of the Sierra de Guatemala of Mexico must include the argument that this area was invaded twice, and at different times, by epigean forms ancestral to the cave species. In the briefest outline form, we may hypothesize the following sequence of events :

- 1) The Sierra de Guatemala was first colonized by an ancestral form which continued its northward invasion ultimately to give rise to the North American species of *Dugesia*.
- 2) While inhabiting the Sierra de Guatemala, this ancestor established cave populations.
- 3) Epigean populations of this ancestor were eliminated from the Sierra de Guatemala, probably by climatic events, thus isolating the cavernicole populations.
- 4) This subterranean isolation then permitted, or hastened, cave adaptation leading to the evolution of *D. typhlomexicana* and *D. barbarae*.
- 5) The ancestral form continued its spread, and limited evolution, in epigean habitats, principally in the United States.
- 6) One derivative of this ancestral form, *D. dorotocephala*, or perhaps its immediate progenitor, reinvaded the Sierra de Guatemala establishing epigean and cavernicole populations.
- 7) So recent has this second subterranean colonization occurred that the cavernicole derivative, *D. guatemalensis*, shows only the slightest cave adaptation.

It is appropriate to offer here an elaboration of the foregoing schedule of events including various alternatives to certain of the steps in the sequence and attempting to assign absolute times to some of the events though this is a problem of an altogether different magnitude than proposing a relative time sequence.

We may first suggest that the North American land mass was not invaded by a South American *Dugesia* until late Pliocene or, perhaps, even earliest Pleistocene. Although geological events in Middle America during Tertiary time are still a subject of some considerable controversy, it seems now to be well-established that the North and South American land masses were not completely united until the closure of the Panamanian-Colombian sea barrier at the end of the Tertiary (Myers, 1966). The various sea barriers which existed up until this time separating North and South America probably prevented the movement of South American *Dugesia* onto the North American continent since it has been well demonstrated that even the narrowest of straits are effective barriers to triclad dispersal (Ball, 1971).

As a second suggestion, we must admit to the possibility that there was an earlier, very slow northward movement of *Dugesia* through Middle America as various sea barriers closed even though others remained open for greater or lesser periods of time. As Ball (1971) has rightly argued in attempting to explain the biogeography of Carribbean *Dugesia*, successful dispersal does not demand a continuous land connection at any given point in time, but rather that refugia should persist while various connections are made and broken. If North America were colonized in this way by South American *Dugesia*, then it would be impossible for us to try to date the time of such colonization other than to suggest that it was probably an event of early to mid-Tertiary.

This suggestion is not without merit since Pierce (1960) pictures two fossil planariids from calcareous petroliferous nodules formed in a Miocene lake in the area which is now the Calico Mountains, San Bernardino County, California. The outline of these animals (of which no internal detail is evident) is somewhat Dugesia-like, but, of course, it is impossible to diagnose the genus of these worms. The objection may also be raised that the first proposal allows too little time for these planarians to have become so widely distributed in North American epigean habitats as is reflected by the ranges of D. dorotocephala and D. tigrina. This wide distribution is perhaps at first thought more in keeping with the second suggestion that invasion of North America by ancestral Dugesia was an earlier Tertiary event. Still, however, the hypothesis is contradicted by the limited evolution undergone by Dugesia in North America. Perhaps the dispersal of these planarians north of Mexico has been greatly facilitated by the abundance of waterways in the northern latitudes.

We agree with Ball (1971) that attempts to account for the distribution of American *Dugesia* as a consequence of passive over-water transport are unrealistic, but we suppose that such dispersal must still be admitted as a possibility, however unlikely. If North America were colonized in this way, it can only be said that it was probably an early to mid-Tertiary occurrence. To suggest that North America was not colonized until near the end of Tertiary time is to merely accept the simplest of explanations. While such reasoning in explaining biological phenomena is correct more often than not, we hasten to stress that often the least likely explanations are, in fact, the correct ones.

The beginning of the evolution of the troglobitic planarians D. tuphlomexicana and D. barbarae dates from within the Pleistocene, probably very early in the Pleistocene. This statement may be made irrespective of considerations as to when North America was colonized by Dugesia and essentially irrespective of the time when caves in the Sierra de Guatemala became available to potential colonizers. This owes to the fact that the evolution of the troglobite characteristics of these planarians was probably largely - or entirely - deferred until removal of the epigean parent populations from the immediate vicinity of the caves, i.e., higher altitudes of the mountaneous areas. Almost certainly it was not until the first glaciation marking the beginning of the Pleistocene that there was a climatic shift of sufficient severity to cause this removal. Of course, the southernmost edge of the ice sheet covering continental North America was far removed to the north of the Sierra de Guatemala, but accompanying this glaciation in the United States and Canada was montane glaciation in high altitude Mexico. Mountain ranges of elevations comparable to that of the Sierra de Guatemala were probably never directly subjected to glaciation themselves, but the higher reaches of the Sierra de Guatemala are certainly high enough to have undergone marked climatic change. The rich troglobite fauna of the caves in the Sierra de Guatemala (Reddell and Mitchell, 1971) attests to the widespread removal of the epigean fauna in this area. It might be disputed by some that our hypothesis allows too little time (from early Pleistocene) for the evolution of these troglobitic planarians. However, it has been well-established that many troglobites have evolved their adaptations since the beginning of the Pleistocene, indeed, even later (Mitchell and Reddell, 1971). The intense selection pressures characterizing the cave environment simply promote rapid rates of evolution.

If, according to our first speculation, *Dugesia* did not arrive in North America until near the end of Tertiary time, then cave colonization in the Sierra de Guatemala, removal of the epigean parent population, and the beginning of troglobite evolution in the cave derivatives all occurred within a relatively short period of time. If on the other hand, *Dugesia*, by some rather unlikely means, invaded North America much earlier, then there was probably some considerable lapse of time between the times of cave colonization and beginning of troglobite evolution. If these planarians colonized epigean habitats in Mexico during early to mid-Tertiary, then it is possible that caves in the Sierra de Guatemala were colonized as early as late Miocene, the earliest time that it is plausible to suggest cave availability in this area.

The Sierra Madre Oriental, of which the Sierra de Guatemala is a small part, was uplifted during the Miocene as a consequence of the Laramide Orogeny. The limestone (El Abra) in which the caves are formed gives evidence of not having been deeply buried by overlying late Cretaceous sediments, so with only a minimal amount of overburden to be erosionally removed it is probable that the cavernous limestone was exposed not too long after uplift (Mitchell, 1969; Mitchell, Russell, Elliott, in litt.). But it must still be emphasized that even if these caves were colonized by *Dugesia* as early as late Miocene, evolution of the troglobite planarians began much later upon removal of the epigean fauna.

We have suggested that the *Dugesia* ancestral to the troglobitic planarians colonized the caves of the Sierra de Guatemala during the course of its initial northward movements in North America and have further suggested that this form ultimately gave rise to the other North American epigean species.

An alternative hypothesis might assert that the troglobites were derived from one ancestral form while the remaining North American *Dugesia* were derived from a related, but altogether different invader from southern latitudes. This seems less acceptable than our initial proposal since it is a more complicated hypothesis and, more importantly, would require the troglobitic species to constitute the sole remnants of the earlier invaders. It is difficult to accept that there would not have persisted in some other habitats in northern latitudes other planarian species of even closer affinities to the troglobites than the presently known North American species.

Dugesia guatemalensis is obviously a derivative of some late epigean colonizer of the Sierra de Guatemala. The slight, but nevertheless positive, indications that this species is an evolving cave form suggest an interesting zoogeographical history in the Sierra de Guatemala. Because of its similarity to D. dorotocephala, it is not unreasonable to suggest that D. dorotocephala, itself, is the ancestral species. Even if one supposes that D. guatemalensis might have been derived from the immediate progenitor of D. dorotocephala, our thoughts following are not invalidated. For purposes of discussion, at any rate, we shall regard D. dorotocephala as ancestral to D. guatemalensis.

An initial point to be made is that while the troglobites, *D. typhlo-mexicana* and *D. barbarae*, were evidently derived from a southern invader, the troglophile, *D. guatemalensis*, was derived from a northern invader, or at least from an epigean species having evolved in North America. Perhaps *D. dorotocephala* evolved in latitudes to the north of the Sierra de Guatemala, its occurrence in Mexico and even more southern latitudes being a result of southward movements

during its dispersal. It should be recalled here, however, that the occurrence of *D. dorotocephala* in latitudes south of the continental United States has not yet been verified. Even so it certainly seems that the range of this species extends at least into Mexico (Ball, 1971, pp. 14-16).

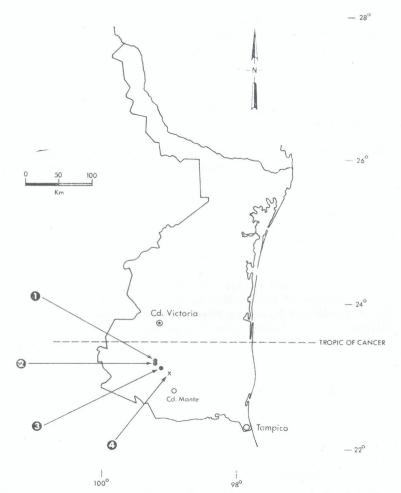


FIG. 40. — Tamaulipas, Mexico, showing location of the cavernicole planarian localities. 1, La Cueva de las Perlas, type locality of the troglophile, *Dugesia* guatemalensis. 2, La Cueva de la Capilla, type locality of the troglobite, *Dugesia barbarae*, and the troglophile, *Dugesia* sp. 3, La Cueva de la Mina, type locality of the troglobite, *Dugesia typhlomexicana*. 4, epigean locality of *Dugesia* sp. (species of Gómez Farias).

It is well known that the alternating climates of the Pleistocene eliminated populations of many species of animals, caused major north-south shifts in the ranges of others, and also caused extensive

670

| 102° vertical migrations of still other populations inhabiting mountanous regions. We can visulaize that during the Pleistocene in the Sierra de Guatemala there were movements by epigean planarian populations downward with the progression of the glacial periods and upward movements during the ameliorating climates of the interglacials. We propose that late in the Pleistocene an epigean planarian, perhaps *D. dorotocephala*, was able to gain access to that area where *D. guatemalensis* now exists. At this time cave colonization occurred. This event is surely assignable to one of the later interglacials, otherwise *D. guatemalensis* would certainly show more evidence of cave adaptation.

Since D. guatemalensis shows some slight evidence of the beginnings of cave adaptation, it is logical, in accord with our earlier discussions, to argue that its epigean progenitor was likewise removed from the immediate vicinity of the caves, at least for some duration. Were the epigean freshwater planarian fauna of the Sierra de Guatemala and adjacent coastal plain better known, then it would be possible to speculate in more detail on the evolutionary history of this troglophilic species.

#### The cave habitats.

The caves yielding the planarians Fig. 40 described in this paper are quite remarkable for their cavernicole faunas, especially La Cueva de la Mina and La Cueva de la Capilla. A complete listing of the species identified to date from these caves may be found in the recent paper of Reddell and Mitchell (1971).

## LA CUEVA DE LA MINA.

This cave has a rich and diverse fauna, the best known of any cave of the Sierra de Guatemala, a circumstance owing to the fact that the cave yielded the world's first troglobite scorpion (Mitchell, 1968b). The several collecting efforts which have now been made in the cave have resulted in the identification of 41 species of cavernicoles of which 14 are troglobites, six with this cave as type locality. The troglobites include the planarian Dugesia typhlomexicana, the isopods Speocirolana pelaezi and Brackenridgia bridgesi, the scorpion Typhlochactas rhodesi, the pseudoscorpion Tyrannochthonius troglobius, the spiders Circurina mina and Euagrus cavernicola, the opilionid Hoplobunus inops, the millipedes Strongylodesmus harrisoni and Sphaeriodesmus sp., the gryllid cricket Paracophus caecus, the carabid beetle Mexisphodrus profundus, the catopid beetle Ptomaphagus troglomexicanus, and the staphylinid beetle Stenopholea reddelli. The cave will almost certainly yield other troglobite species, especially of spider, pseudoscorpion, beetle, and millipede.

La Cueva de la Mina (Fig. 41) is of only moderate size consisting primarily of one large, steeply sloping room and a lower-lying tunnel. During

#### R. W. MITCHELL AND M. KAWAKATSU.

the rainy season (mid to late summer) the cave is quite wet and small streams form along the sloping walls to fill many terraced pools. This water passes into the tunnel to finally disappear into an opening too small for entry. During the dry season almost all water evaporates from the pools even though the small entrance (< 1 m) greatly restricts venti-

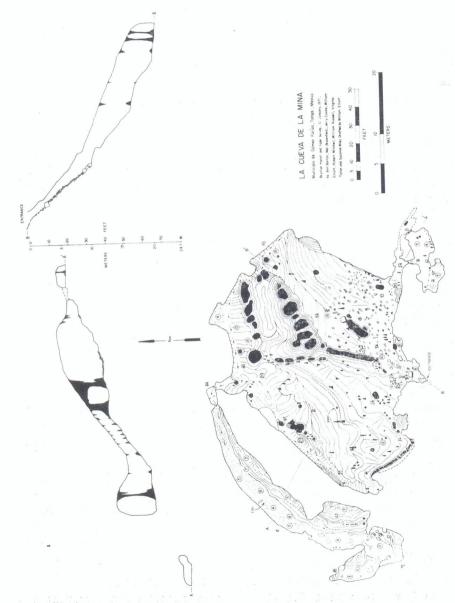


FIG. 41. — La Cueva de la Mina. Symbols used are those adopted by the Association for Mexican Cave Studies (Russell and Raines, 1967, p. 108-110).

lation. However, even at the height of the dry season, we have never found the cave to be completely dry. A few very small pools remain fed by drip-water. Notable among these is the pool (about 30 cm  $\times$  40 cm  $\times$  5 cm) from which the planarians have been taken (see Fig. 41, « pool »). Perhaps in the driest of years all pools in the cave disappear, however, Water temperature in this pool is stable at about 14.5°C (60° F as measured several times at different times of the year by Mitchell). This temperature, low for a cave found below the Tropic of Cancer (Fig. 40) owes to its high elevation, about 1527 m or 5006 ft. (entrance).

Energy input into the cave appears to be minimal. Some organic detritus enters the small room on the cave's southeast side by filtering through cracks in the overburden which is thin here. Some bats have at times been seen in the cave and while bat guano may be found there are no appreciable deposits. *Dugesia typhlomexicana* cohabits the waters of the pool with the isopod *Brackenridgia bridgesi* which in the high altitude caves of the Sierra de Guatemala is amphibious but spends most of its time in the water.

## LA CUEVA DE LA CAPILLA.

This cave has a wealthy fauna although it has not yet yielded as many species as La Cueva de la Mina. It has, however, not been visited as frequently as has the latter cave, largely a consequence of the difficulty in reaching it. The species it has yielded to the present, however, suggest a fauna comparable to that of La Cueva de la Mina. Twenty-five species have now been taken in this cave of which nine are troglobies, six with the cave as type locality. The troglobites include the planarian *Dugesia barbarae* ; the spiders *Cicurina mina*, *Euagrus cavernicola*, *Leptoneta capilla*, and *Metagonia capilla* ; the millipedes *Mexicambala* sp. and *Strongylodesmus harrisoni* ; the carabid beetle *Mexaphenops intermedius* ; and the catopid beetle *Ptomaphagus troglomexicanus*. Additional troglobites have been taken but their identifications have not been verified, and certainly others remain to be collected.

La Cueva de la Capilla (Fig. 42) is a fairly large cave consisting of one wide, irregular tunnel. At each end of the cave there is an entrance, the western one large and the eastern one scarcely large enough to permit entry. During the dry season, the western 100 m of the cave becomes quite dry, but the eastern portion remains more moist because of restricted ventilation caused by vertical constrictions of the tunnel. During the west season water moves over flowstone and through terraced pools in the eastern part of the cave apparently to sink into a large mud-floored area. While there is considerable evaporation during the dry season, at least some water has been observed to remain in most of the pools identified in Fig. 42. Water temperature is about  $12^{\circ}$ C or  $54^{\circ}$ F. That water temperature here is colder than that in La Cueva de la Mina results from the higher elevation of La Cueva de la Capilla, 2040 m or 6689 ft. (floor level, main entrance).

Energy input appears to be scant. Some organic detritus falls into the main entrance but the irregular floor would prevent its being

ANNALES DE SPÉLÉOLOGIE, tome 27, fasc. 4, 1972.

transported into the recesses of the cave. Very few bats have been seen. The eastern entrance is too small to permit much entry of organic detritus.

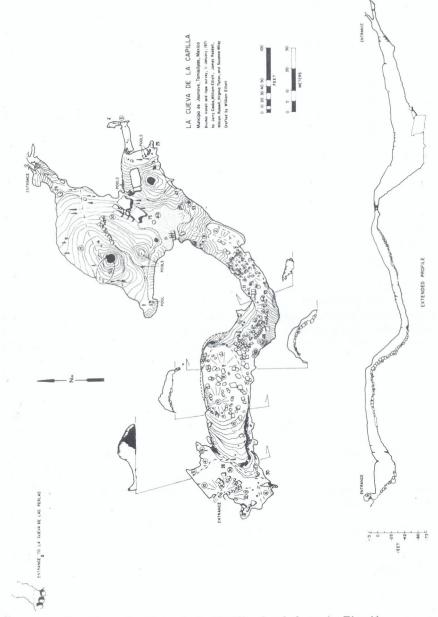


FIG. 42. -- La Cueva de la Capilla. Symbols as in Fig. 41.

674

Among all the pools in the cave, *Dugesia barbarae* cohabits the waters with an isopod, probably *Brackenridgia bridgesi*; two earthworms, *Eodrilus albus* and an undetermined species; an undetermined dytiscid beetle; and a troglophile planarian, probably *D. guatemalensis* as discussed earlier. The troglobite planarians seem to show a preference for the smaller pools even though they have been taken from the larger pools in the eastermost part of the cave.

The troglophile planarians show a distinct preference for the larger bodies of water (the largest about  $1 \text{ m} \times 5 \text{ m} \times 10 \text{ cm}$ ); they are absent from the small drip pools. The large earthworm, *Eodrilus albus* and the dytiscid beetle seem likewise to be so restricted in occurrence.

When the cave was visited by Mitchell, Kawakatsu, and others in January of 1971, the largest pools were filled to capacity, the troglophile planarian was very abundant, and no troglobite planarians were found here. In May, 1971, when the cave was again visited by Mitchell and others, the pools were almost dry, very few troglophile planarians were seen and these were small specimens, and two troglobite planarians were taken from the waters.

#### LA CUEVA DE LAS PERLAS.

The fauna of this small cave (Fig. 43), located quite near to La Cueva de la Capilla (Fig. 42), is without note except for the occurrence of the troglophile planarians *Dugesia guatemalensis*. The

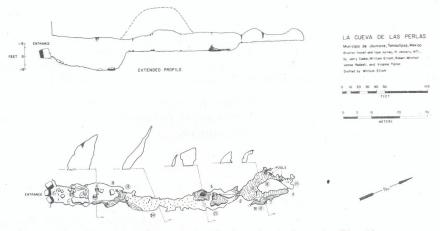


FIG. 43. - La Cueva de las Perlas. Symbols as in Fig. 41.

worms occur in several small pools near the end of the cave, the largest of which is about  $1 \text{ m} \times 2 \text{ m} \times 5 \text{ cm}$ . In January of 1971, the pools contained much water and the worms were fairly abundant but in May of 1971 the pools were completely dry. Probably the pools

dry each dry season due to the small size of the cave and its large entrance. Occurring also in the pools is a large earthworm, probably *Eodrilus albus*. Although carefully sought for, no troglobite planarians were found in this cave.

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