# SPECIAL PUBLICATIONS
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No. 12

February 1977

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The purposes of this paper are several: to report many new localities in the Huastecan Province of Tamaulipas and San Luis Potosí, México, of the cave derivatives of the Mexican tetra, *Astyanax mexicanus* (Figs. 1-3); to discuss several aspects of the center of cave characin distribution, the Sierra de El Abra, and surrounding areas, especially as they apply to attempts to understand the evolution of the cave fishes; to describe briefly all of the cave characin localities; to correct some errors and misconceptions in the previous *Astyanax* literature ranging from very minor to major; and to comment on the evolutionary implications of the new cave records. Taken together, these discussions become a general, initial report on our studies of these blind fishes, which have been in progress for several years.

Since their discovery 41 years ago in a cave of the Sierra de El Abra (Fig. 4), these fishes have continued to be the subject of varied researches in several laboratories throughout the world. There are now almost 200 papers in the literature that deal wholly or in some substantive way with these animals (see Wiley and Mitchell, 1971). Their attractiveness in research is due to several reasons. Not only are they easily maintained in the laboratory, but they also reproduce readily in captivity, the only known cave fishes in the world to do so. They are among the very few cave-adapted animals that are traceable to an extant surface ancestor, an ancestor that today inhabits streams in the vicinity of the fish caves. Importantly, the cave forms remain interfertile with their surface ancestor. The fishes are "young" as cave-adapted animals, not yet having aquired the whole array of characteristics typical of long-evolved cave species. Some populations are readily accessible, and large numbers of individuals are obtainable, unlike so many other cave-adapted species which are so uncommon that sample size restricts their usefulness in research. Thus, these cave fishes, together with their ancestral form, provide unique opportunities for a great variety of approaches to the understanding of adaptation in general and of adaptation to subterranean environments in particular, including the much-debated process of "regressive" evolution.

Even though there is now a rather large body of published information on these fishes, very few papers have dealt with basic, essential field studies, studies required for final and meaningful extrapolation of laboratory data. It should be obvious that any detailed accounting of the ecology and evolutionary history of a particular species demands, among other things, an intimate knowledge of the range and specific habitats of that species. Researches, which have been basically experimental or otherwise laboratory confined, have lacked the reinforcement

provided by adequate knowledge of the fishes in nature, their habitats, and the region of their occurrence, primarily the Sierra de El Abra.

Until recently, it was thought that the Mexican eyeless characins were restricted to caves of the Sierra de El Abra, but we now know that this is not true—they have now been discovered in caves of adjacent areas: the Sierra de Guatemala to the north of the Sierra de El Abra, and the Micos area adjacent to the Sierra de Colmena and the northern Sierra de Nicolás Pérez, both to the west of the Sierra de El Abra. Even though the Sierra de El Abra remains the center of concentration of known blind-fish caves, it is appropriate to introduce into the literature another term to denote the larger area of their occurrence. We shall use "Huastecan Province." This name is widely used to designate that part of the Sierra Madre Oriental and adjacent coastal plain long inhabited by the Huastecan Indians. Fortuitously, it includes all of the known blind-characin caves, and because of local geology, it is not likely that such caves will be found outside this area. Fig. 5 shows a substantial part of the Huastecan Province, but it is limited to that portion in which blind-fish caves are presently known.

The name inseparably linked with studies of these fishes is C. M. Breder, Jr. Chiefly in the 1940's, he and his associates (Atz, Bridges, Cahn, Gresser, Hafter, Rasquin, and Schlagel) at the American Museum of Natural History contributed greatly to our knowledge of the eyeless characins in a series of some two dozen papers dealing with a wide variety of researches (see Wiley and Mitchell, 1971). Without detracting from the general contributions of this group, it may be said that this wealth of papers conveys the distinct impression that adequate, if not intensive, field research was done. But the fact is that the early field studies of his group in the Sierra de El Abra were quite limited, leading to the description of but a single cave and, unfortunately, to some unusual statements about the Sierra de El Abra and its caves. It is a matter of coincidence, but the single cave they described in the literature, La Cueva Chica, is perhaps the most atypical eyeless-characin locality of them all, and this fact has had its consequences in much that has been written about these fishes.

The first Mexican cave characin was described in 1936 by Hubbs and Innes as *Anoptichthys jordani* and was based on specimens collected earlier in that year by Sr. Salvador Coronado in La Cueva Chica, a small cave located 3/4 km. N El Pujal, San Luis Potosí. Ten years later, Alvarez (1946) described a second species, *A. antrobius*, from La Cueva de El Pachón, also a small cave, located at the southern edge of the village of El Pachón, Tamaulipas. The following year, Alvarez (1947) described still a third species, *A. hubbsi*, from a large cave, La Cueva de Los Sabinos, located approximately 12 1/2 km. NE Ciudad Valles, San Luis Potosí. It was these three "species" to which so much study was devoted by C. M. Breder and his associates. In fact, essentially all studies of these fishes have been restricted to these nominal species, and particularly to the first, *A. jordani.*

The reality of the genus *Anoptichthys* and even of the three described species has long been questioned. Even the authors of the genus, Hubbs and Innes (1936), were quick to state that "*Anoptichthys* agrees with the genus and subgenus *As-*

FIG. 1.—Cave-adapted *Astyanax* from La Cueva de El Pachón, Tamaulipas.

*tyanax* in all apparent characters other than those associated with blindness and subterranean life." Taxonomic emphasis upon eyelessness and depigmentation in cave animals has frequently served only to obscure relationships, as Mitchell and Reddell (1965) and Mitchell (1968) have discussed. Although the years following the original cave characin discovery saw many researchers repeatedly demonstrate the complete interfertility of the cave forms among themselves and with epigean *Astyanax mexicanus*, there has lingered a compelling hesitation to sink the genus *Anoptichthys*. There are probably several reasons for this, the basic one being that an animal lacking eyes and pigment simply presents a bizarre appearance. But this in itself may be of the most superficial significance in establishing true relationships. For present purposes, we shall address ourselves only to cave populations of *Astyanax mexicanus*, as has been done earlier by Şadoğlu (1957) and more recently by Wilkens (1970a, 1970b, 1970c, 1971, 1972). It should be emphasized that the purely taxonomic problems posed by the fishes are of little importance; it is the evolution of the fishes that is the cogent problem.

Apart from the type localities of the three described "species," *A. jordani*, *A. antrobius*, and *A. hubbsi*, only two other cave localities of these eyeless characins have been long known. These are El Sótano del Arroyo and El Sótano de la Tinaja, which were located in 1946 by Benjamin Dontzin and Edwin Ruda, who were commissioned by the American Museum of Natural History (Breder and Rasquin, 1947) to collect additional eyeless characins. These two caves are located near the previously known La Cueva de Los Sabinos.

A period of some 20 years elapsed before field studies related to these fishes were resumed in the Sierra de El Abra, this again probably being a consequence

FIG. 2.—Head of cave-adapted *Astyanax*.



FIG. 3.—Head of epigean *Astyanax*.

FIG. 4.—La Sierra de El Abra, viewing northword from near the Nacimiento del Río Choy toward the high point of the range near the Tamaulipas-San Luis Potosí border. Note the steep eastern face rising abruptly from the coastal plain, the rather narrow, flat crest, and the less abrupt western face.

of the apparent thoroughness of the earlier work of Breder *et al.* In the mid-1960's, as a result of activities by various members of the Texas-based Association for Mexican Cave Studies in the Sierra de El Abra, there began to appear sightings of blind fishes in newly discovered caves. These reports came at the same time that our interests in the Sierra de El Abra cave fauna generally were increasing. Since that time, an ever increasing amount of our research effort has been directed specifically toward the cave fishes.

In spite of the fact that we have known of some of the new localities for several years now, we refrained from early publication knowing that our continuing visits to the area were likely to add still more cave fish localities. In 1969, we made an extensive aerial survey of the Sierra de El Abra. As a result of this highly productive effort, we felt at last that probably almost all of the obvious blind fish caves finally had been discovered. The emphasis on obvious must be stressed. The obscurity of the entrances of some of the new localities—found by the sheerest chance events—suggests that countless other localities await discovery, their entrances small or hidden by the dense thorn scrub and tropical deciduous forest cover of the Sierra de El Abra. At about that time when we were satisfied that our efforts to discover additional blind-fish caves were reaching the point of diminishing returns and that publication was in order, eyeless-fish caves were discovered in two areas outside the region of our concentrated efforts, the Sierra de El Abra. These discoveries, which will be elaborated later, neces-

sitated still further field work. Even as this manuscript was in final preparation, a blind-fish cave was discovered in still another new area outside the Sierra de El Abra. It is now apparent that the discovery of new eyeless-characin caves will probably go on for years, but we feel it appropriate now to publish the data we have accumulated to date, placing emphasis on that area which we know the best and in which the majority of the fish caves are located, the Sierra de El Abra.

## Physiography and Geology

This discussion emphasizes the Sierra de El Abra because it is here that the fish caves are concentrated. (It should be noted that *de* and *El* do not contract in this name because *El* is part of the proper name "El Abra"). Pertinent information about this range may be found in Bonet (1953, 1963a, 1963b, 1963c), Boyd (1963), Rose (1963), Russell and Raines (1967), and Mitchell (1969). That of Bonet (1953) is the most thorough.

The Sierra de El Abra has long been known to be highly cavernous, but not until recent years has the true extent of its cavern development become apparent. It is known now to contain some of the longest and most complex cave systems in México. For example, surveyed passage lengths in the Sótano del Arroyo now exceed 7000 meters. Also, some of the numerous pits located in the higher elevations, most of which we have presently seen only from the air, will rival in depth the deepest known pits in the Western Hempisphere. Also highly cavernous, but not at all studied until quite lately, is the Sierra de Guatemala (Fig. 5), a much higher range to the north of the Sierra de El Abra. Several blind-fish caves now are known from this range. More recently discovered are the blind-fish caves in the western Micos area (Fig. 5), a region which is not yet as well known geologically as the Sierra de El Abra and Sierra de Guatemala. The most recently discovered blind-fish cave is located in a still little-investigated area, the northern portion of the Sierra de Nicolás Pérez (Fig. 5).

Beyond their obvious appeal to students of cavern formation and development, the caves of the Huastecan Province are now known to contain some of the most biologically important caves in the world. Accounts of the cave fauna of the Sierra de El Abra may be found in Osorio Tafall (1943), Mitchell (1969, 1970), Reddell and Mitchell (1971b), and in Reddell and Elliott (1973a); that of the Sierra de Guatemala, in Reddell and Mitchell (1971c) and Reddell and Elliott (1973b). Citations to all earlier publications on the cave faunas of the Sierra de El Abra and the Sierra de Guatemala may be found in Reddell (1971). Many new species of invertebrate cavernicoles have been described recently from these areas; they may be found in Reddell and Mitchell (1971a) and Mitchell and Reddell (1973).

The Sierra de El Abra lies approximately 150 kilometers from the coast of the Gulf of México and extends for some 125 kilometers in a generally north-

Fig. 5.—The region of the Sierra de El Abra, or that portion of the Huastecan Province in which the eyeless-characin caves are located. This map portrays most of those essential physical features, which are discussed in the text.

# LA REGIÓN DE LA SIERRA DE EL ABRA

**CARTOGRAPHER**

William H. Russell

**DRAFTED BY**

William R. Elliott,
William H. Russell &
Robert W. Mitchell
September, 1973

**LEGEND**

| | |
|---|---|
| ▥ | TOWN |
| 〜 | ROAD |
| ⊸ | HIGHWAY WITH KILOMETER POST |
| ⊤⊤⊤ | DROP |
| /|\ | SLOPE |
| ∴ | SWAMP |
| ● | BLIND FISH CAVE |
| ○ | RESURGENCE |
| +345 | ELEVATION ABOVE SEA LEVEL IN METERS |
| ▨ | CAVERNOUS LIMESTONE |
| ★ | EYED FISH LOCALITY |
| △ | BENCHMARK |

south direction. Its greatest elevation, not known precisely but between 450 and 650 meters, occurs just south of the Tamaulipas-San Luis Potosí border. Northward from this high point, the range gradually subsides until, almost sinking to the level of the coastal plain to the east, it again slopes gently upward to merge shortly with the abruptly rising Sierra de Guatemala. Southward from its high point, the range again gradually subsides, finally to disappear into the Río Tampaón at an elevation of about 40 meters. South of the river, El Abra Limestone makes two rather unimpressive reappearances, first as the Tantobal Dome, and farther south as the Salsipuedes Dome, a hilly area of low relief containing a spring that is a partial water source of the Río Coy.

The eastern face of the Sierra de El Abra is well defined as a very steep escarpment rising above the coastal plain (Fig. 6). The crest is almost flat and is very narrow ranging from about 3 kilometers at the Cañon Servilleta in the north to over 5 kilometers just south of the Tamaulipas-San Luis Potosí border. The crest abounds with large sinks, some of which are scores of meters across, and pits with black entrances indicating great depth. The crest has largely defied attempts to locate its caves from the ground; dense vegetation restricts—almost prevents—exploration. It would be of great value to locate blind-fish caves in the far eastern part of the El Abra Limestone, that is, beneath the crest of the range, but not only are the caves here difficult to locate, their depths to water would range from 400 to 600 meters.

The western face of the Sierra de El Abra is also fairly well defined but is more irregular, rolling, and less steep than the abrupt eastern face. This western face slopes away into a valley, the Valle de Antiguo Morelos (Fig. 5), bordered along most of its western side by the Sierra de Nicolás Pérez, but for a short distance in its southern portion by the Sierra de Colmena. Through this valley runs about 95 kilometers of Highway 85. This valley, important in considerations of the *Astyanax* problems, will be discussed later in connection with surface drainages.

The Sierra de El Abra lies on the boundary of two strikingly different physiographic provinces, the Gulf Coastal Plain to the east and the Sierra Madre Oriental to the west. The coastal plain is an almost flat plain, which slopes imperceptibly eastward to the sea. The Sierra de El Abra and the two ranges to the west, the Sierra de Nicolás Pérez and the Sierra de Colmena (Fig. 5), form a relatively low interruption in the otherwise massive Sierra Madre Oriental, which in the Sierra de Guatemala to the north reaches elevations in excess of 2200 meters and which to the south in the vicinity of Xilitla, San Luis Potosí, has peaks of over 3000 meters.

The Sierra de El Abra, as well as other ranges having eyeless-characin caves, is comprised of a dense, mid-Cretaceous limestone, the El Abra Limestone, which originated not as a single massive structure but rather as an aggregation of wave-washed shell banks, or reefs, separated by interreef areas where calcareous muds were deposited (Bonet, 1963*a*). The eastern edge of this reef complex faced the sea, and along this boundary fine material was removed by wave action leaving coarse shell to accumulate forming a dense, essentially unbedded limestone, the Taninul Member of the El Abra Limestone. Originally this frontal wave-washed

Fig. 6.—The eastern face of the Sierra de El Abra.

zone was about 8 kilometers in width. Farther westward behind the reef front there was less shell material and more lime mud and other fine particles that formed a bedded, backreef limestone, the El Abra Member of the El Abra Limestone. The El Abra reef thus grew for several millions of years resulting in the accumulation of hundreds of meters of limestone as deposition in shallow water kept pace with subsidence.

During much of Cretaceous time, the El Abra reef formed the eastern edge of a large shallow platform (Rose, 1963; Carrillo-Bravo, 1971; Bonet, personal communication) extending to the north of Ciudad Victoria, Tamaulipas, west to near San Luis Potosí, San Louis Potosí, and south to the vicinity of Zimapán, Hidalgo. The platform has been termed "La Plataforma Valles-San Luis Potosí" by Carrillo-Bravo (1971). The clear, shallow waters of this platform were favorable for the growth of carbonate reefs, and numerous reefs similar to those of the eastern face of the platform, though generally smaller, developed on this platform to the west of the face. Late in Cretaceous, gradual uplift of the continental interior began, and clastic materials to the west of the El Abra reef face at first mixed with large amounts of calcareous sediments, but as uplift continued, terrigenous sediments increased in volume and encroached eastward onto the growing reef narrowing the zone of limestone deposition. Finally toward the end of Cretaceous time clastic deposits buried the entire reef, thus ending limestone deposition.

The clastic deposits contributed to three formations: the Agua Nueva, San Felipe, and Méndez. The Agua Nueva, formed first, is a thin-bedded, dark lime-

Fig. 7.—An exposure of San Felipe Formation near the village of Montecillos, San Luis Potosí. Note its flaggy structure.

stone containing relatively little clastic material. Above this and lapping further eastward over the reef deposits is the San Felipe Formation (Fig. 7), comprised of flaggy beds of agrillaceous limestone characteristically about 20 centimeters in thickness and separated by thin zones of yellow shales and marls that color the outcrop. The entire El Abra reef was finally overlain by the Méndez Formation, a generally indistinctly bedded, poorly resistant shale. To the east of the reef, this formation is a few thousand feet thick, but the reef itself was probably not deeply buried. In fact, Rose (1963) stated that the crestal part may never have been buried.

During the Laramide Orogeny, the Huastecan area was uplifted and warped into a series of north-south trending anticlines. These anticlines characteristically have much steeper dips along their eastern flanks, and the structure of the Sierra de El Abra conforms to this general pattern with dips on the west flank of 10 to 20° and dips on the steeper east flank of 30 to 40°.

Much controversy has surrounded the structure of the Sierra de El Abra, especially that of its steep eastern face. Heim (1940), who did extensive work in the area before 1935, summarized the early work as follows: "In earlier reports the eastern border of the Sierra de El Abra from Quintero [Tamaulipas] to beyond the Río Tampaón was mapped as a fault. Such a fault may be present locally; for example, at Quintero between Mante and Cantón [El Abra, Tamaulipas] but wherever there are good outcrops no such fault was visible, the Tamabra [El Abra Limestone] dipping normally under the San Felipe or Méndez beds." He concluded (1940:344): "From there [the south end of the Sierra de Guate-

mala] the low El Abra range east of the Antiguo Morelos syncline forms the mountain front for 120 K as far as the Río Tampaón. It is a complex low Tamabra [El Abra Limestone] anticline with the steeper limb facing the plain." However, the steepness of the east face continued to suggest a fault, and Muir (1936: 35) emended Heim's cross sections to include a fault at the Hotel Taninul located near the southern pass through the Sierra de El Abra. Bonet (1953:246) stated that the eastern face "está constituída por un gran plano de falla, o mejor de una serie de fallas 'en echelon' cuyo plano, que se aproxima a la vertical, es paralelo al plano axial del anticlinal y muy próximo a él." Maps suggesting an anticlinal structure for the Sierra de El Abra are Murray's (1961) tectonic map of the coastal provinces in eastern México and the tectonic map of México of de Ceserna (1968). Rose (1963:61) stated that "at the paso de El Abra the massif is an asymmetrical anticline."

Other ideas have been advanced to explain the steepness of the eastern slope of the Sierra de El Abra. Heim (1940) realized that the El Abra reef represented the boundary between deep water and shallow water, and Rose (1963) felt that "the precipitous eastern front was merely an abrupt steep platform edge." This idea was further enlarged by Griffith *et al.* (1969) who stated that "as in some other prominent reef fronts, such as the Mississipian and Virgillian bioherms in the Sacramento Mountains of New Mexico and the Permian reef front of West Texas, the El Abra reef facies corresponds to the present escarpment." That is, erosion has removed the soft Méndez Formation that filled the area to the east of the reef, leaving the reef limestone standing above the coastal plain. However, if this were true, then the wave-washed reef zone in the El Abra reef would had to have been no more than a few hundred meters wide because the present exposure of Tanunul Member along the escarpment is but a few hundred meters wide. It is unlikely that the reef zone was so limited in width because wells drilled to the east of the Sierra de El Abra have encountered Taninul Member limestone (Rose, 1963), and to the north in the Sierra de Guatemala where the entire reef sequence is exposed, the Taninul Member is about 8 kilometers wide.

The idea of faulting is appealing because of the steepness of the slope, and it is difficult to refute inasmuch as exposures are generally poor. However, it is unlikely that a fault could follow exactly the undulating contact between the Taninul Member and the El Abra Member, which is aligned with the undulating face of the scarp as we have noted at several locations along the length of the range. It is this alignment of the east face of the Sierra de El Abra and the western edge of the Taninul Member that indicates that the growth of the Cretaceous reef and the structure of the present Sierra de El Abra are related. It is likely that the growth of the El Abra reef along the edge of the platform was controlled by a deep-seated structure now buried beneath the Cretaceous sediments. This structure, possibly a relatively high area of basement rock, was able to resist deformation and formed the edge of the carbonate platform. Upon this structure grew many hundreds of meters of massive reef limestone while structurally weaker limestone was deposited to the west and soft shales to the east.

It may be suggested that when the area was compressed during the Laramide Orogeny, the massive reef and its underlying structure resisted deformation, and the weaker, bedded, backreef limestones were folded against the massive Taninul Member. The Taninul Member was deformed only locally where it integrated with the El Abra Member, and the western edge of the Taninul Member was rotated upward to form the steeply dipping eastern edge of the Sierra de El Abra. Bedding planes in the Méndez and San Felipe Formations adjacent to the escarpment agree with the generally indistinct bedding planes in the Taninul Member of 30 to 40° indicating that the Taninul dips are dips off of the eastern limb of the anticline and not large-scale cross-bedding as might be expected to occur in the forereef talus formed originally a few kilometers to the east. Furthermore, the steepness of the slope of the escarpment has been enhanced in favorable localities as solution has removed material from the base of the escarpment. Concentration of water on the adjacent, flat coastal plain has caused the solutional encroachment of the plain into the scarp. For example, at the Nacimiento del Río Santa Clara (Fig. 5) this encroachment has progressed about one-half kilometer as demonstrated by the extension of the Taninul Member eastward from the base of the escarpment.

The present surface of the Sierra de El Abra is an almost perfectly stripped structural surface. There has been so little modification of this surface that in places traces of drainage systems that once existed on the overlying impervious strata may still be seen from the air.

The broader anticline forming the Sierra de Guatemala rises out of the northern end of the Valle de Antiguo Morelos (Fig. 5). It is physically continuous with both the Sierra de El Abra and the Sierra de Nicolás Pérez. North of Chamal, Tamaulipas, the Sierra de Guatemala rises rapidly, and west of Encino, Tamaulipas, it reaches elevations of about 2200 meters. The range then declines slightly toward the north where the narrow canyon of the Río Guayalejo crosses the anticline. The western boundary of the range is a relatively low valley that extends northward from Ocampo, Tamaulipas, to the Río Guayalejo. The western slope is developed on the bedded El Abra Member, the eastern front on the Taninul Member. The latter member extends several kilometers to the west, unlike its limited extension in the Sierra de El Abra, but its exact extent is not yet well known because of the great difficulty in moving about in this rugged range.

The limestone of the Sierra de Guatemala has been designated in the past as "Tamaulipas" and "El Doctor." Tamaulipas Limestone is, however, thin-bedded limestone that was deposited in deep water to the east of the Cretaceous reef front, and in the Sierra de Guatemala it is restricted to the eastern edge of the range north of the Nacimiento del Río Frío. The term "El Doctor Limestone" is defined so broadly that it essentially designates the whole collection of mid-Cretaceous reef limestones found in the Sierra Madre Oriental. We have chosen to apply the name "El Abra Limestone" to the rocks that comprise the bulk of the Sierra de Guatemala because they are identical in origin with those found in the Sierra de El Abra; indeed they are a part of the same reef aggregation. We should

also add that another reef of El Abra Limestone existed to the southeast of the El Abra region. This reef, now entirely buried, is known well because its western front forms the world-renowned, oil-producing "Faja de Oro."

The region containing some of the more recently discovered characin caves, the Micos area, is not yet as well known as the two previous Sierras, but our recent work in the area permits some considerations. Immediately to the west of the Sierra de Colmena in the vicinity of Micos, San Luis Potosí, there is a narrow range extending from a wide area of limestone outcrop to the south (Fig. 5). Structurally, this ridge is a northward continuation of the thrust fault that forms the frontal range of the Sierra Madre Oriental in the vicinity of Aquismón, San Luis Potosí, 40 kilometers to the south. Almost dying out in the Micos area, the ridge nevertheless continues northward to merge eventually with limestones to the west of the Sierra de Guatemala. This ridge is lithologically similar to the limestone of the Taninul Member. Although the flaggy San Felipe Formation overlies a thick-bedded El Abra Member 2 kilometers to the west, it does not overlie this ridge. The absence of the San Felipe here is due possibly either to deposition of massive reef limestone at this locality while San Felipe was being deposited elsewhere, or to thrusting of a sheet of limestone of Taninul lithology into the Micos area from its original position to the west. Whatever might be the explanation, the absence of the San Felipe Formation from this ridge is of great consequence because this Formation usually forms flanking slopes and hills that protect the El Abra Limestone from solutional attack.

The most recently discovered eyeless-characin cave is in still another area located outside the Sierra de El Abra, the Sierra de Nicolás Pérez. This range is a rather low-lying one forming most of the western boundary of the Valle de Antiguo Morelos. In its southern half, the Sierra de Nicolás Pérez still is covered by San Felipe Formation, but this Formation has been removed from the northern half, exposing El Abra Limestone, which, as in the Sierra de El Abra, merges with the El Abra Limestone of the Sierra de Guatemala.

In the intermountain valleys in the region of the Sierra de El Abra, there still persist large outcrops of Méndez marls and shales now mostly removed from the mountains themselves. Also persisting in some areas, especially along the western side of the Sierra de El Abra, is the relatively insoluble San Felipe Formation. The impervious Méndez and San Felipe are of great importance in the area because they have permitted the development of surface streams. El Abra Limestone, by contrast, is so permeable that it is essentially devoid of any surface drainage.

A point should be made about our usage of the term "Sierra de El Abra." In Fig. 5, the heavy lines are not contour lines but are trend lines outlining exposed formations. Basically, in this simplified version of our highly detailed map of the area, the trend lines separate exposures of cavernous and noncavernous formations. However, most of these trend lines also outline rather well the local sierras. This is not true though for the western edge of the Sierra de El Abra, shown by the western row of slope lines in Fig. 5. Of course, only that part of the El Abra outcrop located between the eastern and western faces is locally termed a "sierra."

Fig. 5 shows that most of the blind-fish caves are located at varying distances from the Sierra proper, actually being located in the Valle de Antiguo Morelos. Because these caves, however, are formed in El Abra Limestone elevated as a "sierra" to the east, we find it convenient to speak of the caves as occurring in the "Sierra de El Abra" (as all past researchers also have done). But the fact remains that the location of these caves is in a valley, not a sierra, and this is of great importance.

It also should be noted that locally the name "Sierra de El Abra" is of limited use, being applied only to that part of the range in the vicinity of the southernmost pass. In its midportion, the range is locally called the Sierra de Tanchipa but in its northern reaches it is known as the Sierra de Cucharas.

There is no widely accepted name for that range which we term the Sierra de Guatemala. Locally it is called the Sierra de Chamal and the Sierra de Gómez Farías, but this is confusing because these names are applied only to small, local parts of the larger range near the indicated towns. On old maps of México, this entire range has been designated La Sierra de Guatemala, and it seems to us useful to revive this name.

## Surface Drainages

In view of the fact that surface waters in the region are populated by *Astyanax mexicanus*, it is surprising that so little attention has been given to surface drainages in the literature, although they were discussed briefly by Bonet (1953). The basis for this inattention almost certainly derives from the unwarranted emphasis placed on the Río Tampaón in all past cave characin research. Although it seems well established that surface fishes from the Río Tampaón enter subterranean waters, this is without significance except as it pertains to the exceedingly interesting, but local, problem of hybridization occurring in La Cueva Chica and another nearby cave, Los Cuates. Presently, the site (s) of original colonization remain the subject of speculation, so the nature of surface drainages in the area, past and present, assumes great importance. As potential colonization sites, it is logical to look in part to stream captures in the area, of which there are several.

As previously mentioned, the El Abra Limestone itself does not support a surface drainage, but this fact, rather than diminishing, increases the importance of the nearby surface streams that do exist. Those streams that are of the most direct significance to the study of the eyeless characins are developed primarily upon the impervious Méndez and San Felipe Formations overlying El Abra Limestone. Briefly, though it will be elaborated later, wherever a surface stream has eroded downward through an impervious stratum to make contact with El Abra Limestone, it has been captured more or less immediately by the subterranean drainage of the El Abra. These captures are important in the evolutionary history of the cave *Astyanax* as they serve to introduce the epigean form into the underground drainage. Early, such a phenomenon initiated cave fish evolution; later, it resulted in local hybridization.

Of great importance are the surface drainages in the Valle de Antiguo Morelos. Northward from about the level of the northern El Abra pass, an area of about

450 square kilometers, the valley is floored by the Méndez Formation. In the remaining southern portion, an area of about 1600 square kilometers, the valley widens and is floored by Méndez to the west, San Felipe and Agua Nueva in the midregion, and El Abra Limestone (El Abra Member) in the east. Surface streams are developed on the impervious Méndez, San Felipe, and Agua Nueva, which together comprise about 1750 square kilometers of the total area of the valley which is approximately 2050 square kilometers. About 300 square kilometers in the eastern part of the valley are floored by El Abra Limestone.

Two separate drainages are developed in this valley. Breder and Rasquin (1947:325), in reference to La Cueva de El Pachón at about 22°37', stated that "Mr. C. E. Mohr . . . determined that it [Pachón] was actually in the same drainage valley as the others [La Cueva Chica and the "Sabinos" caves]." Although the cave at El Pachón is near the valley, examination of a good map of México will show that streams near El Pachón belong to a drainage separate from that in the southern reaches of the valley. Fig. 5 depicts these two drainages, one draining the northern portion of the valley, the other draining the southern portion. The drainage divide occurs near the Tamaulipas-San Luis Potosí border at about 22°26'.

The major trunk of the northern system is the Arroyo Lagarto, which drains about 550 square kilometers of the Valle de Antiguo Morelos. It is largely an intermittent stream carrying water only during the wet season when water fills many small tributaries reaching toward the Sierra de El Abra to the east. One such tributary, in fact, brings surface *Astyanax* to within 100 meters of (but well below) the entrance of La Cueva de El Pachón. Some of the waters of this system may be regarded as semipermanent because it is usually possible to find fishes in numerous deeper holes in streambeds at any time of the year.

The Arroyo Lagarto did not always continue bearing northward as it now does. Rather it once turned to the east at about 22°35' where it eroded a deep cut through the Sierra de El Abra. This pass is now abandoned and is used by Highway 85. The pass was abandoned when the Arroyo Lagarto was pirated by tributaries of the northern Río Boquilla, a result of more rapid erosion of the Méndez than of the El Abra.

Presently, the Arroyo Lagarto joins the Río Boquilla to the north just as the latter enters its river cut through the Sierra de El Abra, the Cañon Servilleta. This is the only pass through the Sierra de El Abra still carrying a surface stream. The Río Boquilla emerges from this cut with a local name change as the Río Comandante. The Río Comandante continues eastward to join the Río Frío, which arises spring-fed to the north, and their short, common trunk then joins the great Río Guayalejo, which winds down to the coastal plain from the deep interior of the Sierra Madre Oriental. After the confluence of the Río Frío, the Río Guayalejo takes a strong turn toward the east where other of its tributaries drain the local coastal plain. The major trunk, which continues across the coastal plain to empty finally into the Gulf of México at Tampico, is named the Río Tamesí. It is convenient and useful to think of this drainage as the Tamesí System, although it is customary to include it as a part of the vast "Red Hidrográfica Pánuco."

The major stream draining all of that part of the valley from the divide to the south is the Río Puerco. The upper reaches of this system empty into a large artificial lake at about 22°15' formed by the Presa [dam] La Lajilla. South from this lake, the Río Puerco receives many small tributaries, especially from the east. This trunk finally joins the Río Valles just to the northwest of Ciudad Valles. Several small, south-trending streams drain the extreme southern portion of the valley directly into the Río Valles. In these tributaries of the Río Valles, including the Río Puerco, water moves only during the wet season. But, as in the northern drainage, some pools in the streambeds are more or less permanently maintained, at least to the extent that surface fish populations may usually be found year-round. Bonet (1953:240) was in error when he stated that the Río Valles crosses the southern extreme of the valley "sin recibir ningún tributario superficial del mismo [the valley]" and that "la mayor parte de los 1500 km² de superficie ocupada por el valle [from Antiguo Morelos south to Ciudad Valles] carece de drenaje superficial." In reality, almost 90 per cent of this valley is surface drained. As will be elaborated below, only the eastern portion in which the El Abra Limestone is exposed is without a surface drainage.

The Río Valles is a permanent river, the primary water sources of which are the Río Mesilla draining the valley between the Sierra de Nicolás Pérez and the Sierra de Colmena and the Río Naranjo, which arises in the Sierra Madre Oriental to the west. The ancient Río Valles, similar to the Arroyo Lagarto, once crossed the Sierra de El Abra. It formed the pass to the east of Ciudad Valles now used by Highway 110. The Río Valles was in time pirated by tribuatries of the more southern Río Tampaón, which it now joins immediately west of the highway bridge at El Pujal, San Luis Potosí. The Río Tampaón is the eastern portion of a prominent river, the Río Santa María, which cuts through the whole of the mass of the Sierra Madre Oriental to the west. So much confusion surrounds the naming of the river herein called the Río Tampaón that probably no "correct" name for it actually exists. Maps may show it designated as the Río Tampaón, Río Santa María, Río Tantuán, or Río Tamuín. But to regard it as the Río Tampaón is advisable because this name already is established in the *Astyanax* literature and because the river is called locally (at El Pujal) the Río Tampaón. The same stream near the town of Tamuín to the east is called, quite naturally, the Río Tamuín. The river continues eastward on the coastal plain soon to join the Río Moctezuma from the south forming the Río Pánuco, which enters the Gulf of México at Tampico.

The large, northern Río Tamesí System and the even larger Río Pánuco System, which remain entirely separated in their upper reaches, finally unite by their major trunks at Tampico, and the entire drainage network is termed the Red Hidrográfica de Pánuco. The point should be made that the waters of these two systems are physically continuous, but the location of the point of union is so far removed from the minor tributaries of each, which drain the Valle de Antiguo Morelos, that it seems probable that the fish populations in these respective tributaries essentially are isolated from one another, perhaps as well as if the two systems had no connection whatever. Although more discussion of this problem follows, it is worth mentioning in passing that there are inputs of surface

*Astyanax* into subterranean waters from both the northern and the southern drainages. The evolutionary implications of the foregoing are obvious.

### Subsurface Waters of the Sierra de el Abra

Cavern development in the Sierra de El Abra probably began during the Cretaceous, resulting in a cavernous porosity that was not destroyed by later burial. This is evidenced by oil production data from the El Abra Limestone of the Faja de Oro to the southeast. Here oil has been encountered in cavernous porosities at depths of about 600 to 700 meters. One of these wells, the Aguila No. 4 Potrero del Llano, had a production of 100,000 to 110,000 barrels per day, and when allowed to flow would cause an almost immediate pressure decline in other wells as far away as 5.5 kilometers (Boyd, 1963). Another well, Huasteca No. 4 Cerro Azul, had a production of 200,000 barrels per day (Rose, 1963). Production such as this must be essentially from an oil-filled cave, indicating that cavernous porosity can withstand burial to depths probably greater than that previously undergone by the presently exposed El Abra Limestone.

As removal of the original Méndez cover began, this porosity greatly enhanced the ability of underground water to form large phreatic caverns because it enabled ground water easily to reach areas especially susceptible to solution, even though far removed from point of input. As more and more of the cover was removed, the limestone took still more water, forming additional solution spaces as previously formed ones continued to enlarge. More importantly, increasing input of water finally began to integrate previously isolated caverns into larger systems. It is likely that such solution continued for a long period during Tertiary time, probably beginning at least as early as Miocene, so that pre-Pleistocene integration was extensive.

Water moving through the limestone of the Sierra de El Abra resurges along the eastern face of the range. Resurgences, which are prominent enough to have been named, are nine in number. Three others, which occur at the base of the Sierra de Guatemala, should be included in this discussion, for even though they discharge little or no Sierra de El Abra water, their waters are probably those encountered in the northernmost blind-fish caves.

In México, these resurgences are known as "nacimientos" (*birth, origin, source of a river*) and the northernmost of them are the Nacimiento del Río Nacimiento, Nacimiento de la Florida, and the Nacimiento del Río Frío at the base of the southern part of the Sierra de Guatemala south of the town of Gómez Farías. These three nacimientos are within one kilometer of each other and the waters that they discharge form the Río Frío. This river flows southeastward to join the Río Tamesí System via the Río Guayalejo at this river's major bend near the town of El Limón.

The most northern resurgence in the Sierra de El Abra is the small Nacimiento de Riachuelo (*rivulet*) taking its name from the small stream that it forms. This stream shortly enters the Río Comandante just after the latter has exited the Cañon Servilleta. Water from the Río Riachuelo thus also joins ultimately the Río Tamesí System. Progressing southward, the next resurgence is found at the

base of the range at a point to the west-northwest of Ciudad Mante. This is the Nacimiento de San Rafael de Los Castros, deriving its name from that of a nearby village. Its stream joins the Río Guayalejo just east of El Limón finally to enter the Río Tamesí. The Río Mante arises from the next southmost resurgence, the Nacimiento del Río Mante (Fig. 8), the largest of the El Abra resurgences. Such is the discharge of this great spring that it may be regarded as a significant water source for the lower reaches of the Río Tamesí System.

Many kilometers of the Sierra de El Abra face are passed before encountering the next spring, a small one, the Nacimiento del Río Santa Clara, at about 22°32′. The small Río Santa Clara proceeds rather indistinctly eastward to join the Río Tamesí System. Farther south on the state line is the Nacimiento del Río Tantoán, the waters of which form a small stream flowing across the coastal plain to the Río Tamesí System. A short distance to the south, at about 22°21′, is a small wet-weather resurgence, the Nacimiento del Arroyo Seco. The Arroyo Seco shortly joins the Río Tantoán. The next resurgence to bear a name is located far to the south, almost due east of Ciudad Valles at about 21°58′. This, the Nacimiento del Río Choy (Fig. 9), is the only other major resurgence discharging Sierra de El Abra water, but its discharge is only about one-third that of the Nacimiento del Río Mante to the north. The Río Choy flows at first northeastward finally to bend to the southeast whereupon it disappears into a swampy area on the coastal plain near Tamuín. It reappears draining this swamp, the Ciénaga El Lavadero, to the south and shortly enters the Río Tamuín [ = Río Tampaón]. South of the Nacimiento del Río Choy is another resurgence, the Fuente de Taninul, the thermal, sulfurous waters of which spring in part from levels far below those populated by the cave fishes. It is also likely that there is some limited input of these thermal waters into those discharged by the nearby Nacimiento del Río Choy. Near the southern end of the Sierra de El Abra, at about 21°51′, is another small wet-weather resurgence, the Nacimiento del Rancho Viejo.

South of the Sierra de El Abra is the Nacimiento del Río Coy, located in the Salsipuedes Dome at about 21°43′. The discharge of this spring far exceeds that which could be accounted for by uptake of rainfall on the small El Abra Limestone exposure where the spring is located. Through pecularities in local geology, the greater part of its discharge probably derives from limestones in the mountains to the west.

Almost all springs along the eastern face of the Sierra de El Abra of any consequence are named. Those which are not are exceedingly small and are few in number. By flying the east face several times it has been possible for us to discern only three such springs, one at about 22°09′ between the nacimientos Tantoán and Choy, the other two a very obscure pair at about 21°53′ between the Nacimiento del Río Choy and the Río Tampaón. One of these is probably the wet-weather resurgence called the Nacimiento del Rancho Viejo. Only two or three other suggestions of springs have been seen, but these were probably only very small areas of somewhat denser vegetation resulting from highly concentrated, local runoff down the east face. Small springs are located also in the villages of Quintero and El Abra, Tamaulipas. The major points in discussing these

Fig. 8.—The Nacimiento del Río Mante.



Fig. 9.—The Nacimiento del Río Choy.

several small resurgences are, first, that there are simply few resurgences of any consequence save the Mante and the Choy, and, second, those few that do exist suggest the possibility of there still being some limited aquifer separation in the limestone of the Sierra de El Abra.

Most of the waters discharged from the Sierra de El Abra issue from the two largest resurgences, the Nacimiento del Río Mante and the Nacimiento del Río Choy, and a consideration of some specific flow rate data of these two springs contributes immensely to an understanding of the hydrology of the Sierra de El Abra. As yet, we lack sufficient data for a highly detailed treatment of this problem, but at least enough data are now available to illustrate some major points and to pose some interesting questions. Where is the source of the waters discharged by the El Abra's nacimientos? The narrow width and rather low crestal elevation of the Sierra de El Abra in the vicinity of the Nacimiento del Río Mante at first might suggest that the waters of this great spring derive from outside the Sierra. In fact, Enjalbert (1964:42) stated: "Pour les Nacimientos du Mante et du rio Frio la zone principale d'alimentation se situé selon toute vraisemblance a 30 ou 40 km a l'oueste sur les plateaux a entonnoirs et á poljes de la Húasteque montagneuse." He cited no evidence whatever to justify this assumption, nor are there "plateaux" ("plateau calcarie" of his map) 30 to 40 kilometers to the west, but only north-south trending mountains.

Our data demonstrate a plausible relationship between the amount of nacimiento discharge and the potential for recharge of the Sierra de El Abra aquifer occurring through direct infiltration of the El Abra outcrop and stream capture. Approximately 718 square kilometers of El Abra Limestone (in the Sierra de El Abra proper and in the eastern part of the adjacent Valle de Antiguo Morelos) are exposed to direct infiltration of rainfall, and there are about 51 square kilometers of impervious substrate in the Valle de Antiguo Morelos, the drainage of which is captured by caves (Fig. 10) formed in El Abra Limestone (to be elaborated later). Thus, excepting losses through evaporation and transpiration, the entire rainfall on an area of about 769 square kilometers is available for recharge of the aquifer. Based on data from several stations located in the lower areas surrounding the range, a figure of 1200 millimeters may be taken as a fair approximation of the average annual rainfall in the region. Thus, about 923 million cubic meters of rain fall annually upon the infiltration area of 769 square kilometers. This figure is in close agreement with a rainfall calculation of Bonet (1953:240). He cited a total area of 1500 square kilometers for the Valle de Antiguo Morelos (an underestimate) and calculated that on this area a total annual rainfall of 1650 million cubic meters fell.

The Nacimiento del Río Mante discharges about 335 million cubic meters per year; the Nacimiento del Río Choy, about 141 million per year (six-year averages from unpublished data, Dirección de Hidrología, Secretaria de Recursos Hidráulicos, México, D.F.). Discounting output from the remaining small resurgences, there is an annual discharge from the Sierra de El Abra of some 476 million cubic meters per year. The difference between the amount of rainfall and the combined Mante and Choy discharges suggests a loss through evaporation and transpiration

of about 48 per cent, which does not seem to be an unreasonable figure. We know of no evapotranspiration data available for this area, but because El Abra Limestone substrate is so permeable, a high value should not be expected. Some error is introduced by failure to consider the output of the smaller, ungauged nacimientos and the fact that rainfall is probably greater in the higher portions of the Sierra, but these would tend to be offsetting biases. Although these data are rather crude, they are consistent with the suggestion that waters resurging from the Sierra de El Abra are not derived to any extent from sources outside the outcrop.

Subsurface water movement in the Sierra de El Abra is not through small porosities in the limestone but rather through large conduits (Fig. 11). This is suggested by the structure of the caves themselves and is supported further by some flow rate data of the two large resurgences. In 1936, the flow rate of the Nacimiento del Río Mante had held constant at 11.6 m.$^3$/sec. from 14 to 18 August. On 18 August, a heavy rainstorm struck the Sierra de El Abra, and on the 19th the flow rate had risen to 27.8 m$^3$/sec. Peak flow occurred the following day at 171 m$^3$/sec (the greatest peak flow on record) decreasing on 21 August to 127 m$^3$/sec. On the 22nd, flow rate dropped sharply to 62 m$^3$/sec and on the 25th had fallen to 36 m$^3$/sec. At the Nacimiento del Río Choy a flow rate of 4.77 m$^3$/sec was recorded on 18 September 1967, and also on this same day a heavy rainfall began. The next day the flow rate was only slightly greater, 4.83m$^3$/sec, to be followed on 20 September by a rate of 22 m$^3$/sec. Flow rate rose sharply the following day to 102 m$^3$/sec and peaked on 22 September at 137 m$^3$/sec. On the 23rd, the rate was still high at 130 m$^3$/sec. There was gradual decline through the following several days, and, on the 29th, the flow rate was 23.7 m$^3$/sec. Many more data similar to the preceding should permit us eventually to discuss this hydrology in more detail. But for present purposes, the data demonstrate that following rainfall on the El Abra Limestone outcrop, resurgence discharge increases almost immediately, more rapidly at the Mante than at the Choy, however. The conclusions are obvious: subterranean water of local origin is moving rather unrestricted through large water passages in the El Abra Limestone, and this movement is more rapid in the northern El Abra than in the southern portion because the Mante responds more rapidly than does the Choy.

If it is true that waters discharged from the Nacimiento del Río Mante and the Nacimiento del Río Choy are not derived to any extent from sources outside the Sierra de El Abra, then an interesting problem is posed. The Nacimiento del
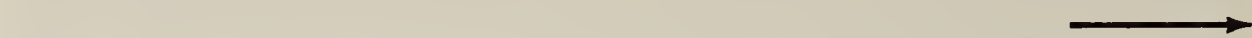
Fig. 10.—Proposed infiltration and capture areas for those waters discharged from the nacimientos Mante and Choy. Outlined area delineates El Abra Limestone outcropping in the Sierra de El Abra and adjacent Valle de Antiguo Morelos. Shaded areas represent approximated surface drainages captured by various blind-fish caves. Upper arrow indicates that point in the Valle de Antiguo Morelos where waters to the north drain to the Río Tamesí System and to the south to the Río Pánuco System. Lower arrow indicates the approximate point where a subsurface drainage divide may exist in the cavernous limestone. Square kilometer values at each divide indicate total area north and south, respectively, of water uptake by infiltration and capture, or both. See text for further explanation.
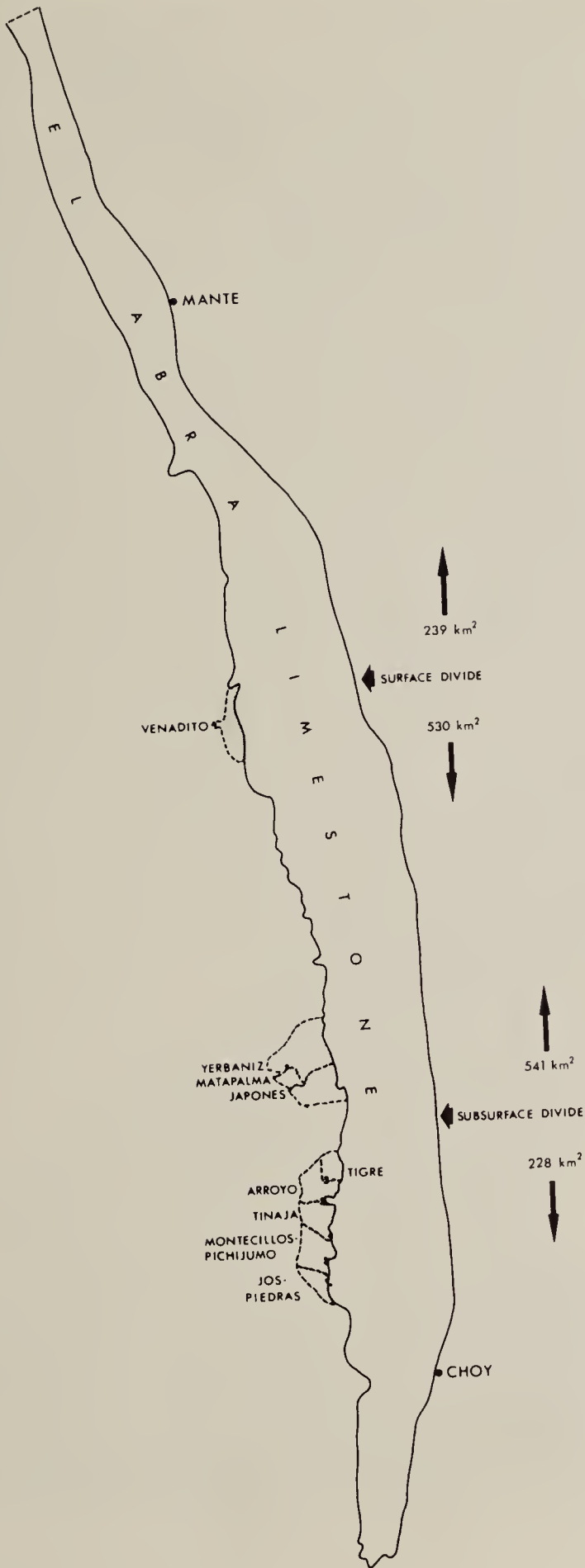
Río Mante in the north lies at an elevation of 80.5 meters; the Choy in the south lies at 34.0. The Mante is thus 46.5 meters higher than the Choy yet its discharge is about 2 1/3 times as great as that of the Choy. It seems evident that there is an internal drainage divide in the Sierra de El Abra. This unusual circumstance is apparently a result of differential Pleistocene, and possibly Recent, uplift of the Sierra de El Abra that increases toward the north. Uplift of the Sierra and surrounding areas in relatively recent times is indicated by Pleistocene lacustrine deposits that cap a small hill just south of Quintero, Tamaulipas (Bonet, 1963c, personal communication). This lacustrine limestone probably was deposited in an essentially sea level lagoon, but it now lies more than 100 meters above sea level. A relatively low pre-Pleistocene elevation of the Sierra de El Abra probably promoted the development of a large internal drainage system with greater northward flow. Solutional development since the uplift apparently has not yet been sufficient to reverse the greater part of the drainage toward the south, resulting in the apparent paradox in flow rates presented by the nacimientos Mante and Choy.

Where then is the internal drainage divide? Assuming that the nacimientos Mante and Choy discharge largely local waters, the divide must lie much closer to the Choy. The Choy discharges 30 per cent of the combined Mante-Choy output, and a similar percentage of recharge area in the southern Sierra de El Abra (discounting the Tantobal and Salsipuedes Domes) occurs south of N latitude 22°08' (Fig. 10), or within that portion of outcrop lying between the Los Sabinos cave cluster and the Yerbaniz cave cluster (Fig. 5). Although it is somewhat difficult to think of a drainage divide lying so far to the south, our data, if interpreted correctly, seem to bear this out.

If an internal drainage divide occurs in the southern reaches of the Sierra de El Abra, then there is no correspondence between it and the superficial drainage divide that lies at about N latitude 22°27', or just north of the Sótano de Venadito (Figs. 5, 10). Too many problems are posed if one assumes that these two divides should occur at approximately the same latitude. If the internal divide corresponded in location to the superficial divide, then the Nacimiento del Río Mante would receive less water originating from infiltration of permeable outcrop in the Sierra de El Abra than it discharges. This spring would have to be discharging a considerable amount of water originating outside the Sierra de El Abra, something greater than one-half its total discharge. Taken alone, this might be a plausible argument, but it creates illogical circumstances in the south. The Choy would then discharge far too little water than it should relative to the amount of recharge area south of the superficial drainage divide. One could only correlate Choy discharge and recharge data under such circumstances by assuming an evapotranspiration rate of nearly 80 per cent, a value that is surely too high considering the permeability of the outcrop and the fact that some recharge occurs rapidly by stream capture. To avoid this problem, one could suggest that some of the waters recharging the El Abra are resurging at springs outside the range, an idea without any other evidence to recommend it. We therefore suggest the occurrence of an internal drainage divide in the southern portion of the Sierra de El Abra at

FIG. 11.—Upper level passageway in the Sótano de Pichijumo, a typical water conduit in the El Abra Limestone.

roughly that point shown in Fig. 10, a divide unrelated in location to the superficial drainage divide. Independent evidence for the existence of such an internal divide as well as its location at the approximate point stated is presented in another section of this paper and in Fig. 21.

It is appropriate to recall here that the principal summary of local hydrology that blind-fish researchers have had to work with all these years is that of Breder and Rasquin (1947:325) who stated that, "the underground drainage of this dry valley [the Valle de Antiguo Morelos] is into the Rio Tampaón."

## Stream Capture

The capture of a surface drainage by a subterranean system is an important, though localized, phenomenon in the Sierra de El Abra. Fourteen of the 20 known eyeless-characin caves here represent such captures. As mentioned, the El Abra Limestone outcrop itself is so permeable that it supports no appreciable surface drainage of its own. The captured streams, then, are developed off the El Abra Limestone on impervious strata, principally the San Felipe Formation, but occasionally on the Méndez Formation. Capture demands that erosion deepen a streambed to the interface of the impervious stratum and the El Abra Limestone. Such streambeds have then been maintained for only relatively short distances on the El Abra Limestone before making contact with a solution space, usually a vertical shaft.

The development of the Arroyo Japonés and its capture by the Sótano de Japonés illustrate this phenomenon well. Fig. 12 shows this arroyo several hundred meters from its point of capture where it is shallow and developed entirely upon the San Felipe Formation. Closer to the cave entrance, the arroyo finally contacts the El Abra Limestone-San Felipe Formation interface as evidenced by the appearance of large, dense masses of limestone in the bed of the arroyo (Fig. 13). Closer still to the entrance the arroyo becomes bedded entirely upon El Abra Limestone (Fig. 14), becomes deeper (Figs. 15, 16), and is shortly intercepted by the pit entrance of the cave (Fig. 17).

The structure of the El Abra Limestone has been very conducive to the formation of shafts, and they occur throughout the exposure both in the Sierra and in the valley, where in the latter those associated with surface streams form important recharge sites of the El Abra aquifer. These caves with vertical entrance shafts, whether or not associated with a surface stream, are known locally in northern México as *sótanos*, although in the Spanish language generally they are termed *simas* or if they take surface waters, *sumideros*.

There are two principal groups of blind-fish caves in the Sierra de El Abra that capture surface streams. These are nine of the 11 fish caves of the Los Sabinos area and three of the Yerbaniz area (Fig. 5). Other, isolated, captures in the Sierra de El Abra are represented by the Sótano de Venadito and by La Cueva Chica (Fig. 5). In the Sierra de Guatemala, all of those fish caves near the town of Gómez Farías (Fig. 5) capture surface drainages. In the Micos area two of the three blind-fish caves (Fig. 5) may be regarded as capturing surface streams. The only known blind-fish cave in the Sierra de Nicolás Pérez, the Sótano de Vásquez

(Fig. 5), also captures a surface arroyo. Even though the majority of the known blind-characin caves capture surface drainages, the captures are highly localized suggesting that very particular conditions must prevail before this phenomenon can occur. This is true, but the specific conditions permitting capture differ somewhat among the different sites.

Along the western edge of the Sierra de El Abra, the El Abra Limestone disappears under the San Felipe Formation flooring the Valle de Antiguo Morelos in the south and under the Méndez Formation in the north. The thickness of these impervious formations increases progressively to the west in this valley. The slope of the eastern part of this valley dictates, for the most part, a westward direction of surface stream flow (Fig. 5). The small streams between 22°15′ and 22°25′ illustrate well, in a negative way, some requirements for capture. Because these streams trend westward, they are developed on impervious San Felipe of ever-increasing thickness. Although downstream from their origin they do erode deeper and deeper, they also are becoming farther removed vertically from the underlying El Abra Limestone, and, consequently, they have never contacted the El Abra-San Felipe interface. Their waters, then, finally pass into the Río Puerco and on to the Río Pánuco.

In the Los Sabinos area, the captured streams trend to the south, not to the west (Fig. 5). The southward trend of these streams probably indicates that they were once tributaries of the stream that formed the southern El Abra pass (Fig. 5). The significance of this direction of surface water movement lies in the fact that these streams, developed on the San Felipe but very near to the El Abra Limestone outcrop, did not then course over San Felipe of ever-increasing thickness as the west-trending streams. Instead, the streambeds developed on San Felipe along a route where the San Felipe cover over El Abra Limestone is thin. This thin San Felipe cover presented ideal circumstances for capture as the nine captures here attest. It is of particular interest to note that south of the Sótano de Palma Seca at about 22°02′ (Fig. 5), the margin of the El Abra Limestone outcrop moves slightly eastward but the south-trending drainages, captured so frequently to the north, continue on, now developed on thickening San Felipe, without another capture finally to enter the Río Valles.

Apparently, there was once but a single major stream in this drainage, but it and all its main tributaries eventually were captured. There are also three instances of multiple stream capture of the same stream segment in the Los Sabinos area. This has happened through more recent upstream capture of a stream previously captured by an older downstream opening. The Sotanito de Montecillos represents a very recent, and very partial, capture of a stream segment completely captured by the downstream Sótano de Pichijumo. The Sótano de Joz now captures most of the water in a streambed that earlier was captured completely by the downstream Sótano de las Piedras. The earliest stages of stream capture are represented by the Sótano de la Roca, the very small entrance of which takes little water, and then only at flood stage, in a streambed captured entirely by the great Sótano del Arroyo.

Within the Los Sabinos area it is possible to see everything from very ancient to the most recent of captures. Relative ages of the captures may be seen not only

Fig. 12.—The Arroyo Japonés, several hundred meters upstream from the Sótano de Japonés, developed entirely upon the San Felipe Formation.



Fig. 13.—The Arroyo Japonés at that point where erosion has first exposed underlying El Abra Limestone, seen here as those large, dense slabs in the left side of the arroyo.

FIG. 14.—The Arroyo Japonés seen further downstream where development is now entirely upon the El Abra Limestone.
Montecillos



FIG. 15.—The Arroyo Japonés much nearer the cave entrance, showing deepening of the arroyo.

FIG. 16.—The Arroyo Japonés very near the cave entrance, showing even more deepening of the arroyo. Note also the bedding planes in the limestone that distinguish the El Abra Member from the Taninul Member in El Abra Limestone.

from the size to which the opening of the capturing solution space has been enlarged by the movement of water into it, but also from the structure of the bed of the captured stream. Early in capture, it may be presumed that the opening was so small that most water carried in the stream simply passed over, or by, the opening. The Sotanito de Montecillos, although deep, is only a minor opening in the streambed and is a good example of this early stage of development. Through time, the openings of other captures have enlarged to take more and more of the surface drainage, ultimately taking it all. In these later stages, there finally began to develop differential erosion of the bed upstream from the opening and that downstream from the opening. As soon as capture became complete, erosion almost ceased on the downstream side leaving the upstream bed to continue to deepen as its waters poured into the opening. Obviously then, the streambed comes to lie at different elevations on each side of the capture, and this difference may be pronounced as at the Sótano del Arroyo where about 55 meters separate the two. That side of the solution shaft beneath the abandoned downstream segment and facing the deeper upstream segment is termed the "headwall," and comparison of headwall heights thus offers some relative measure of capture times (all other things being equal, which is unlikely). Also useful as a time index to past events is the depth (or distinctness) of the streambed downstream from a complete capture. If this segment is shallow it indicates a short life of the original surface stream prior to the beginning of capture. In the Los Sabinos area, downstream segments associated with the largest and deepest sótanos are quite indis-

FIG. 17.—The entrance, or stream-capturing pit, of the Sótano de Japonés.

tinct but are readily discernable from the air. It should also be mentioned that frequently the downstream segment immediately adjacent to the capture is subjected to back-erosion so that for a short distance this segment slopes upward from the headwall. Fig. 18 diagrams the sequential development of a capture, and Fig. 19 shows a classical capture, the entrance pit of the Sótano de Pichijumo.

The Yerbaniz captures (Fig. 5) represent a somewhat different process in the establishment of streambed contact with the El Abra Limestone. The captured streams in the Yerbaniz area trend westward as do many others elsewhere, which remain uncaptured for the reasons previously cited. However, in the Yerbaniz area, some minor folding occurred involving both the covering San Felipe and the underlying El Abra Limestone. The streams now have eroded into these folds contacting the cavernous limestone.

The capture at the Sótano de Venadito is of a rather short, isolated stream, which also cuts into a fold. In similar fashion, La Cueva Chica also captured a small stream (separate and apart from its indirect connection to the Río Tampaón).

The northern two-thirds (linear) of the Sierra de El Abra is with but a single stream capture. Approximately the northern one-third (linear) of the El Abra Limestone outcrop is limited essentially to the Sierra proper (Fig. 5), and furthermore, the northern part of the Valle de Antiguo Morelos retains a near complete Méndez cover. This then suggests that any El Abra Limestone at lower elevations in this area is more deeply buried than in the south.

Another concentration of stream-capturing caves occurs near the base of the Sierra de Guatemala in the vicinity of Gómez Farías, Tamaulipas. Eyeless-chara-

Fig. 18.—Diagrammatic representation of the developmental sequence of a stream capture. A, Surface arroyo has developed on an impervious stratum beneath which is cavernous limestone. A solution space has formed at the intersection of a vertical joint and a bedding plane along which a horizontal tunnel is forming. Solid arrow indicates direction of water flow. B, Arroyo has eroded through the impervious stratum contacting the cavernous limestone. Vertical joint is now enlarging as it takes water from the arroyo. Horizontal joint is likewise enlarging, especially downstream, as it too carries more water. This stage of development is illustrated fairly well by the Sotanito de Montecillos. C, The capturing pit has enlarged sufficiently so that essentially all water carried in the arroyo enters the pit. Upstream and downstream segments of the arroyo are isolated now and the upstream segment has begun to downcut. Dashed arrow indicates slight back erosion of the downstream segment immediately adjacent to the pit. Differential erosion is beginning to result in headwall formation on the downstream side of the pit. This stage of development is illustrated fairly well by the Sótano de Yerbaniz and the Sótano de Jos, although at these two caves heavy flooding causes some water to pass across or by their entrances. D, Solution has enlarged the pit, and the arroyo is deepening considerably upstream. Headwall is higher. This stage of development is illustrated well by several of the blind-fish caves, among them the sótanos Palma Seca, Tigre, and Venadito. E, Pit has become very large and arroyo has downcut deeply. This stage of development is illustrated well by the Sótano de Pichijumo and the Sótano del Arroyo. F, Downcutting has been so great that the upstream arroyo has eroded to the level of the horizontal tunnel forming a deep canyon ending at the vertical headwall of the old capturing pit. This stage of development is illustrated well by the Sótano de la Tinaja.
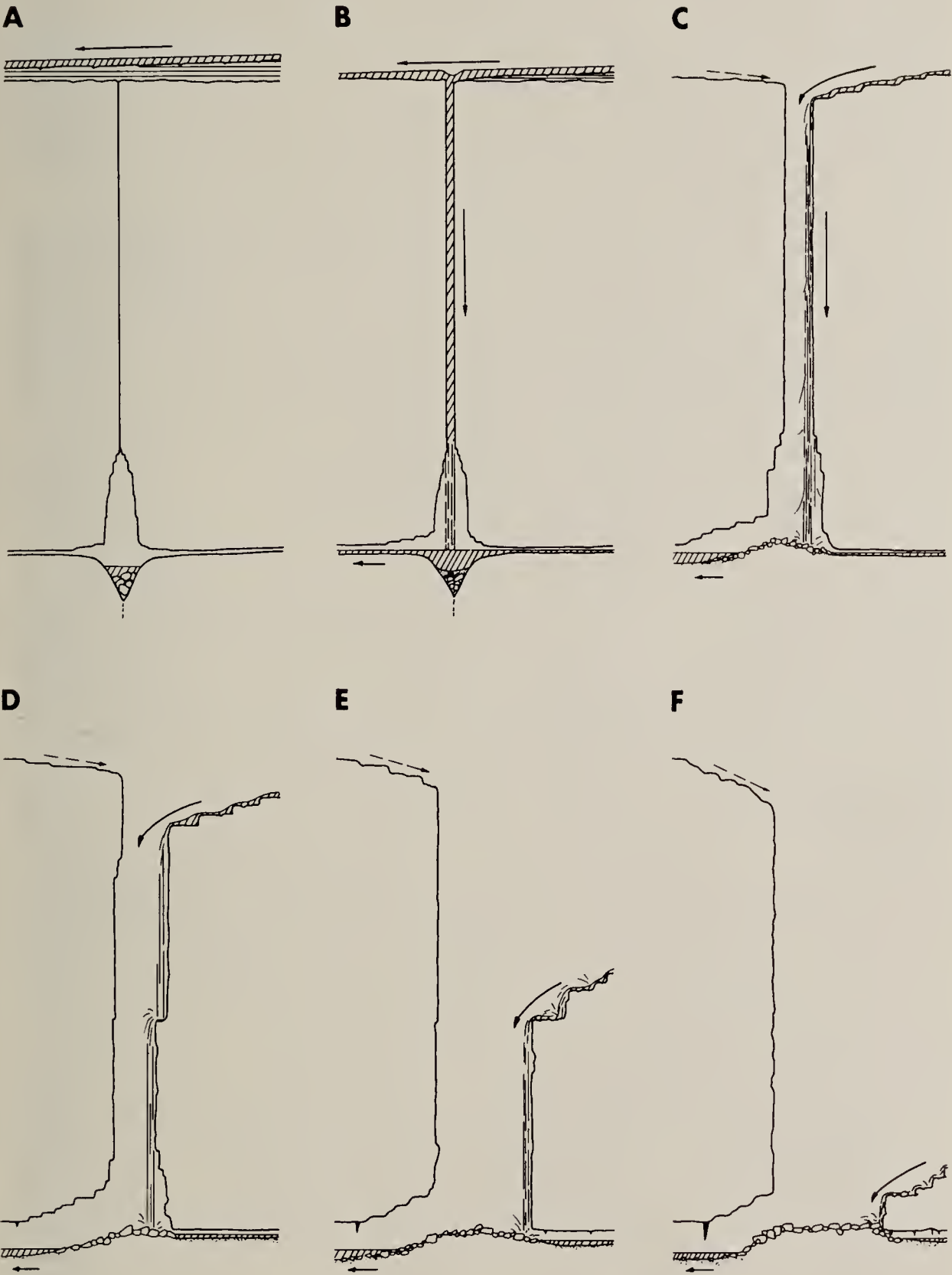
cin populations have been found in three of these deep caves and will probably be found in most of the others when exploration is complete. Stream capture in this area owes to the presence of a narrow ridge, upon which is built the town of Gómez Farías, surrounded by outcropping El Abra Limestone. This ridge, the Sierra de los Mangos, is formed of a Méndez base, and it has persisted because of the protection afforded by a Tertiary lava cap. The entire run-off from the impervious strata of this ridge enters the flanking El Abra Limestone. All of the blind-fish caves here represent captures of small streams that are a part of this localized drainage.

In the Micos area, the conditions leading to stream capture are almost exactly the reverse of those at Gómez Farías. At Micos, a ridge of dense limestone rises from a swampy (during the wet season) lowland, and because the ridge is unprotected by a cover of San Felipe Formation, water directly attacks the limestone around the perimeter of the outcrop. The effects of this solutional undermining are several. The flanking slopes of the ridge are frequently steepened abruptly just above base level. In places, this contact solution has been so extensive as to cut completely through the ridge breaking the once continuous limestone outcrop into a series of narrow hills. Similarly, this solution has intercepted previously formed cavernous spaces within the limestone. All of the Micos blind-fish caves are examples of such interception, and at two of them there has been the development of surface drainages leading to their entrances. At La Cueva del Río Subterráneo, particularly, a rather extensive and well-developed surface drainage has eroded a rather prominent arroyo leading to the cave.

The single blind-fish cave in the Sierra de Nicolás Pérez, the Sótano de Vásquez, is particularly interesting because it captures an arroyo on the crest of this narrow range. This short, a few hundred meters, arroyo owes its existence to a fold. It developed on the San Felipe Formation but rather quickly eroded through this stratum to contact underlying El Abra limestone whereupon it was captured shortly by the cave.

It is important to note that although 20 of the 29 blind-characin caves capture surface streams, few of these surface drainages support fish populations today. Most of the captured drainages contain water only very temporarily after heavy rains, and thus contain no fish fauna whatever. However, it has been mentioned that the Micos caves take drainage from a lowland, and somewhere in this system there are *Astyanax* that enter the caves. The only classical capture in which the upstream segment is populated with *A. mexicanus* occurs in the Yerbaniz area.

There should probably not be too much significance attached to the fact that the majority of the blind-fish caves are those that capture surface streams. One is tempted at first to conclude that this is precisely the reason why these particular caves contain blind-fish populations. It is likely, however, that the correct explanation is that stream capturing caves are simply the easiest types of caves to find in the area, either by ground or aerial survey.

FIG. 19.—Entrance of the Sótano de Pichijumo, an old capture site. Note the deep upstream segment of the captured arroyo, the high, vertical headwall, and (in the upper right) the shallow, back-eroded downstream segment of the arroyo.

## Caves Inhabited by Eyeless Characins

Following are listed and briefly discussed the 29 caves now known to be inhabited by cave-adapted *Astyanax*. Most of the accompanying descriptions are brief serving only to introduce the new localities. We are, however, preparing detailed descriptions, complete with maps, of each cave to be issued later in a series of separate papers. Some brevity is imposed because some of the caves remain poorly explored and studied. A few of the discussions grow in length because of particularly interesting features of some of the caves.

In addition to brief physical descriptions of the caves, we have included such additional information as may, in a variety of ways, lend to a better understanding and appreciation of the caves and the area. The very nature of the efforts demanded in exploring the local sierras requires mention of those persons associated with the discoveries of the caves and their blind-fish populations. "Discovery," of course, refers to discovery by any of those of us pursuing studies of caves and cave faunas; most of the caves are well known to the local populace. It is furthermore our intention in these brief descriptions to give the correct name of each cave (that is, correct in accord with proper spelling, accentuation, and grammatical construction). Too many errors already exist in the literature. All of the cave names, but one, are Mexican. Many are sufficiently prominent and well known locally to have acquired a name, and it is usually inappropriate to give an English name to a Mexican cave.

Of the several words in the Spanish language used to denote various types of caves, only two have been incorporated into the names of the blind-fish caves. As previously explained, *sótano* is equivalent to *pit* and is used to describe any cave with a vertical entrance regardless of its depth. *Sótano* always carries a written accent; its diminutive form, *sotanito*, does not. *Cueva* describes a cave with a horizontal, walk-in entrance.

Because of the large number of eyeless-characin caves now known, it is convenient for purposes of discussion to group them according to their location. Therefore, the Southern El Abra Caves include those four rather dispersed caves in that part of the Sierra de El Abra lying to the east and south of Ciudad Valles, San Luis Potosí. The Los Sabinos Caves include those 11 that, with one exception, are associated with that south-trending drainage between the Rancho de Los Sabinos and the villages of Montecillos and León García, San Luis Potosí. The Yerbaniz Caves include those three associated with west-trending drainages north of the Sabinos caves and west of Highway 85. The Northern El Abra Caves include those two located in the Sierra de El Abra in the state of Tamaulipas. The Micos Caves include those three south of the town of Micos, San Luis Potosí, and west of the Sierra de Colmena. The Nicolás Pérez Caves include but a single presently known locality in the northern part of the Sierra de Nicolás Pérez. The Chamal Caves include those two located in the southern, low-lying part of the Sierra de Guatemala just north of the town of Chamal, Tamaulipas. The Gómez Farías Caves include those three located near the town of Gómez Farías, Tamaulipas, and about the perimeter of the Sierra de los Mangos.

## Southern El Abra Caves

*La Cueva Chica.*—Because of its frequent mention in the literature during the past 35 years, La Cueva Chica probably is known better to more biologists than any other cave. It is well known as the cave where the first eyeless-characin fishes were discovered, and it remains the only characin cave to have had a widely distributed, detailed description (Bridges, 1940; Breder, 1942). This is an ironic and unfortunate situation because a good argument may be made that La Cueva Chica is the most atypical of all of the eyeless-characin caves. Its peculiar features have biased many studies of the fishes. In itself, the cave presents some interesting problems worthy of study, but with regard to the general problem of cave-characin evolution in the area, the existence of La Cueva Chica is essentially immaterial.

This cave is located at about 21°52′ N latitude and 89°56′ W longitude, near the village of El Pujal, San Luis Potosí. The name, meaning *little cave*, is used by the local populace to contrast to a nearby, larger, dry cave, La Cueva Grande. The original discovery of the cave and the initial fish collection from it were made about 1 November 1936 (Hubbs and Innes, 1936) by Sr. Salvador Coronado who at that time was employed by the Dirección General de Pesca e Industrias Conexas, Secretaria de Marina de México (Osorio Tafall, 1943). The first description of the cave was by Coronado in a letter written to Mr. C. Basil Jordan of the Texas Aquaria Fish Company of Dallas, Texas, the person for whom Coronado made the original collection (Jordan, 1937). This letter is interesting as a historical document and in demonstrating the emotional effect that caves (and cave animals) frequently have on people (biologists not excluded), which, in turn, often biases interpretative judgment if not the mere recollection of simple observations. Translated excerpts from this letter are given by Hubbs and Innes (1936) and by Jordan (1937). The fact that these two translations do not bear much resemblance to each other alters little the point being made.

La Cueva Chica was studied by the well-known New York Aquarium expedition of Breder and associates in 1940. Results of this expedition are detailed primarily by Bridges (1940) and Breder (1942). As a part of those studies, the cave was surveyed and the plan and profile were included in each of the two preceding papers. Although a transit purportedly was used in the survey, Breder's plan is but an approximation and the profile is distorted.

The cave was resurveyed in January 1970, March and May 1971, and May 1974 by William Elliott, Mel Brownfield, Jerry Cooke, William Russell, Russell Harmon, and Suzanne Wiley. The cave is comprised of a main passage, in which are located the waters inhabited by the fishes, and four smaller side passages, which do not contain water. The small entrance (1.5 by 3.5 meters) opens in a shallow arroyo and lies at an elevation of 49 meters. From the entrance, the main passage trends SSW for a total distance of about 320 meters. In a step-wise fashion, the passage continually pitches downward. The first permanent waters are encountered slightly more than 91 meters from the entrance. These are Pools I and II (designations of Bridges, 1940, and Breder, 1942) and each lies 4 meters

beneath the entrance. At Pool II, the passage bends slightly, continuing almost due south. Beyond Pool II and for a distance of about 50 meters, water cascades over a series of rimstone dams forming several small pools. Above these pools, there is a dome housing a moderate-sized bat colony ("Minor Bat Roost" of Breder's map). Water moving through these pools next falls over a 2-meter drop (not 25 feet according to Breder's survey) into Pool III. This "pool" is better described as a stream segment about 27.5 meters in length that passes over some small drops from its level of 13.5 meters beneath the entrance at its beginning to a level at its end of 15. Water from Pool III flows down a steep, 1.5 meter slope into another pool (not designated by Breder), which is nearly 25 in length. Its level is 17 meters beneath the entrance. Water then passes down another sloping drop into Pool IV, which lies 18 meters beneath the entrance. The cave ends at this pool. The "end" of the cave is evidently a siphon (point where ceiling disappears into the water). A dome in that segment of passage between pools III and IV houses a large bat colony ("Major Bat Roost" of Breder). Most available surfaces are guano covered for a great distance in the terminal part of the cave. Bridges (1940) adequately pictured this portion of the cave as "a nightmare of slime and the stench of bats." These details of the cave, though briefly described, are essential in understanding some Cueva Chica-related problems to be discussed later in this paper.

Early, it was ingrained in the literature that an unusual temperature situation prevailed in La Cueva Chica, and this idea probably has not yet been dispelled adequately. The temperature of Cueva Chica waters ranges between about 24 and 27°C (from data of Bonet, 1953; Osorio Tafall, 1943; our data). Water temperatures in other caves of the Sierra de El Abra are comparable, although considerable variation results from differences in particular structure among the caves. Breder had a poor understanding of the cave environment as revealed by his statement: "The caves which they [*Astyanax*] inhabit are warm, an unusual circumstance, because caves are normally cold even in the tropics" (Breder, 1943*b*:169). He attributed the temperature of Cueva Chica's waters to "the proximity of the underlying magma" (Breder, 1942:10). From this he extrapolated the idea that "La Cueva Chica is able to support a population of temperature limited characins by virtue of nearby thermal waters which prevent the subterranean waters from falling below a relatively high value" (Breder, 1942:14). There are two faults here. First, there is not the least thing "abnormal" about the temperature of the water in the cave. All recorded temperatures are quite close to the annual mean surface temperature as Osorio Tafall (1943) pointed out in the statement: "en las cuevas de la región de Valles lo se apartara mucho de 26°, que es la media anual de dicha zona." It is, of course, well known that cave temperatures closely approximate the mean annual temperature in the surrounding epigeum. Second, although the Characidae is a family of generally warm-water fishes, it is common knowledge that *Astyanax mexicanus* thrives in a wide temperature range as its distribution indicates. Hopefully, it may now be discounted that there are unusual temperature phenomena associated with this cave.

The aquatic fauna of La Cueva Chica is fairly diverse and well studied, including copepods, ostracods, and decapods. A listing of the species and citations pertinent to them may be found in Reddell (1971) and Reddell and Mitchell (1971*b*).

The subject of precisely where the cave continues beyond the siphon at the end of Pool IV is of importance because it is well known that the Cueva Chica fish population is a highly varied one being comprised of everything from typical eyeless, depigmented, cave fishes to typical surface *Astyanax*. Obviously, there is somewhere an input of surface fishes. This source of input has long been regarded as the Río Tampaón because of the proximity of that river to the terminal part of the cave. Breder (1943*a*) stated that the waters of Pool IV lay at the same elevation as the Río Tampaón. This was a guess on his part, but a good one. Our survey data show this pool to lie 18 meters below the entrance to the cave or at an elevation of 31 meters. Our calculated elevation of the Río Tampaón is 28.5 meters. Thus, the terminal pool is but 2.5 meters higher than the river. We should stress that all of our measurements of water surface elevations (in this area as well as elsewhere) were made during the height of the dry season and are thus low water measurements unbiased by any local, temporary high water conditions.

That surface fishes from the Río Tampaón might enter La Cueva Chica was first suggested by Bridges (1940) who gave Breder and E. B. Gresser credit for the idea. It was argued that the cave waters might either surface between the cave and the Río Tampaón or that they might enter the river directly as a subterranean spring in the streambed. Through the continuing series of papers on the eyeless characins by Breder and associates, there was such frequent mention of this Chica-Tampaón "connection" that it came to be regarded as a fact.

It should be made clear that early (Bridges, 1940) the entrance of the cave was ruled out as the point of surface fish input. A small arroyo leads directly into the entrance, but it carries water only during rains, and furthermore its drainage is very local. Breder (1943*a*) added the argument that "all of the *Astyanax* and other river fishes live at a level much below that of the cave, for miles around." This is actually not true as our data on surface-fish localities show (Fig. 5), but the nearest surface *Astyanax* (besides those in the Río Tampaón itself) to La Cueva Chica occur in a drainage different from that communicating with the entrance of the cave. It continues to seem evident that surface *Astyanax* do not enter through the mouth of the cave. In further support of surface fish entry into the terminal part of the system is the high proportion of surface *Astyanax* found in the siphon pool. This was best pointed out by Breder (1943*a*), and we have observed the same phenomenon at the present time.

We recall the preceding for two reasons. First, to attempt to solve the peculiarities of the mixed fish population in La Cueva Chica (to be elaborated elsewhere in this paper), it is essential to know the source of the cave's surface fishes. Second, our studies in the area lead to the same conclusion as that expressed by Breder, namely, the existence of some sort of connection between La Cueva Chica and the Río Tampaón. We have seen in Pool III two specimens of an unidentified

cichlid. The presence of such fishes argues for connection to surface waters, and at the same time avoids a problem inherent in using the presence of surface *Astyanax* to argue for the same connection. In other words, some might hold that the surface *Astyanax* in the cave have been maintained since the time of original colonization of the underground waters rather than being recent invaders of the system. One could hardly hold to such a view to account for the presence of the cichlids. We also have taken in the cave a large specimen of the river prawn *Macrobrachium jamaicensis*, and we have seen others (Breder, 1942, cited a similar record). This essentially confirms the existence of a cave-river connection.

Presently, the main problem seems not to be the presence or absence of a connection but the precise nature and location of that communication. We must state at first that no one has undertaken tracing techniques that might conclusively demonstrate the connection, but examination of the area leads to such an obvious conclusion that one becomes biased against further concern about the problem. Until we had examined closely the area around La Cueva Chica, we had not dispelled the idea that perhaps the waters of the cave resurged at some point along the eastern face of the Sierra de El Abra as do apparently all other such waters. The pair of very small springs mentioned earlier do, in fact, lie reasonably close to the cave. For the waters of the cave to resurge here would require that the cave passage make a rather drastic (about 90°) bend past the point of the Pool IV siphon. Because this is a point that presently neither can be proved nor disproved, it must still be admitted as a possibility. However, the cave trends southward about 280 meters beyond its entrance toward the Río Tampaón. Between the cave and the river, especially in the eastern part of the village of El Pujal, there are several water-filled sinks on the surface that suggest the presence of an underlying subterranean system. The first mention of this is given by Bridges (1940). Osorio Tafall (1943) discussed these surface features in more detail, but he spoke of a subterranean [and consequently direct?] connection between cave and river. To this problem he stated: "Asimismo, parece indudable la extencia de una o más comunicaciones subterráneas con el Río Tampaón" (p. 45). The idea of a direct connection was further converted into "fact" by such statements as that of Bridges (1943:90) who wrote: " . . . at the point where the underground waters of La Cueva Chica boil out into the bed of the Tampaon River." Recall that only three years before this statement was made that Bridges (1940) had referred to the "connection" only as "possibility."

Our studies in the area argue for an indirect connection between the cave and Río Tampaón. From the air, the riverbed of the Río Tampaón is clearly visible and sand bar patterns are distinct. There are no patterns in the riverbed south of the cave that would remotely suggest the presence of an undervater resurgence of subterranean waters from the north. It might be suggested that the waters resurge through small porosities rather than through large openings, but this is beside the point because such communications would not be navigable by large animals inhabiting the river.

The most likely point of entry of large animals, including *Astyanax*, from the Río Tampaón into the Cueva Chica system would seem to be a trio of small,

closely associated, tinajas (water-filled depressions) located in the eastern part of El Pujal and about 225 meters north of the Río Tampaón. From these tinajas, a rather prominent arroyo leads eastward for about 200 meters, where it then turns abruptly southward to continue a similar distance, whereupon it enters the channel of the Río Tampaón. By the time this arroyo has reached the river its bed lies scarcely more than a meter above low water level in the river. Erosion of this arroyo obviously has resulted from the intermittent discharge of subterranean waters from the tinajas during and after heavy rains. At high flood stage the Río Tampaón must at times fill this arroyo because the bed of the arroyo at the tinajas is but 3 meters above low water level in the Río Tampaón. Thus, the fauna of the Río Tampaón would seem to have fairly easy access to these tinajas, and if the subterranean waters discharged by them are continuous with those of La Cueva Chica, then a navigable communication between river and cave is established.

It is of value to cite the distance from La Cueva Chica to the Río Tampaón, or better from the Pool IV siphon in the cave to the tinajas in El Pujal. Breder (1942) estimated the distance between Pool IV and the river to be "about half a mile." This is quite close. From our aerial photographs of the area, resurvey of the cave, surface survey, and measurement of a standard on the ground (the length of the bridge over the Río Tampaón at El Pujal, 174 meters), we now know with some accuracy the distances between some of the more significant local features. The entrance of La Cueva Chica lies about 1353 meters north of the river (measured along an azimuth of 180°). Pool IV siphons at a point about 1079 meters north of the river (measured also along an azimuth of 180°, the trend of the terminal part of the cave). The trio of tinajas in El Pujal lies about 972 meters from the siphon at an azimuth of 162°. Thus, little demand is made upon the imagination to vizualize La Cueva Chica proceeding southward to the vicinity of El Pujal where its waters would then communicate with those that periodically resurge from the trio of tinajas.

One disconcerting fact remains. The water in La Cueva Chica flows continuously throughout the year, even at the height of the dry season. Apparently higher water in the surrounding limestone enters the more anterior part of the system through small fissures, although it is possible that some might enter the deep Pool I if this pool penetrates to base level. Even though La Cueva Chica waters flow continually, the tinajas in El Pujal are only of intermittent flow. If these tinajas do, in fact, penetrate the Cueva Chica system, their intermittent flow is exactly what would be expected because the water level in them (about one meter below their arroyo bed) is the same as the water level in Pool IV. But at low water there is no discharge from these tinajas even though water continues to move in La Cueva Chica. Therefore, there must be still another site(s) where these moving low waters resurge, however slight may be the discharge. The preceding suggestions then presuppose two types of exits for Cueva Chica waters, the tinajas in El Pujal (as well, perhaps, as other nearby solution features) that flow only at high water, and some unknown resurgence carrying the "normal" Cueva Chica flow.

This lengthy discussion of the probable communication between La Cueva Chica and the Río Tampaón has been necessary to lay the foundation for two additional discussions to follow, one dealing with the causes of the mixed eyed-eyeless fish population in this cave, the other dealing with the much discussed—and widely accepted—idea that original colonization of the subterranean El Abra waters was from the Río Tampaón via La Cueva Chica. In passing, it may be stated that the probable connection is critical to the first problem but is of little or no significance to the latter.

*Los Cuates.*—Los Cuates (= *the twins*) are located at 21°51′ N latitude and 89°55′ W longitude, about 1 km. NE El Pujal, San Luis Potosí, about 1 km. SE La Cueva Chica, and about 1 km. N Río Tampaón. As the name implies there are actually two caves here, their entrances but 9 meters apart. To separate them, we have designated the westernmost one as "El Cuate Oeste" and the easternmost as "El Cuate Este." The entrances, located on a slight local elevation, take no surface drainage. Los Cuates were located on 23 May 1971 by Robert Mitchell, William Russell, and Ann Sturdivant. On 23 and 26 May 1971, Mitchell and Russell descended the entrance pit of each cave, collected several fishes from small pools near the entrance drops of each, but did not determine the extent of passageway in either cave. The caves were explored and surveyed on 23-25 May 1974 by William Elliott, Andy Grubbs, Robert Hemperly, Neal Morris, John Prentice, Carmen Soileau, and Barbara Vinson. The latter group also collected fishes from other pools in El Cuate Oeste.

El Cuate Este is scarcely more than a pit. Its entrance, lying at an elevation of 59.5 meters, opens into a shaft that falls 25.5 meters to a short passage about 17 meters in length. In this passage is found a small pool at an elevation of 29 meters in which occur typical epigean *Astyanax*, hybrids, and eyeless fishes. This pool lies at approximately the same elevation as does the deepest pool in El Cuate Oeste, but the two are far removed laterally, and no communication navigable by man exists between the two caves.

The top of the entrance pit of El Cuate Oeste lies at an elevation of 61.5 meters, and the pit falls 22.5 meters to a narrow passageway trending almost exactly along a north-south line for slightly more than 400 meters. From the bottom of the entrance pit the passage slopes steeply southward ending after only about 20 meters at a small pool lying at an elevation of 30.5 meters. Beyond the entrance drop to the north, the passage continues almost in a straight line and at about the same elevation. About 70 meters beyond the entrance is found a small pool at an elevation of 32.5 meters, and about 50 meters beyond this point is a larger (4 by 13-meter) pool at an elevation of 31 meters. The fish collection made in this cave during May 1974 was from this pool and included eyed, eyeless, and hybrid fishes. About 190 meters beyond this pool, the passage drops abruptly about 10 meters to a series of small pools lying at an elevation of 29 meters. Extent of the passage beyond the fifth such pool is not known.

*El Sótano del Toro.*—This cave belies its name (*toro = bull*); it is the smallest and shallowest of the known eyeless-characin caves. The cave was discovered on 1 June 1969 by Kenneth R. John, William Russell, and Tom Albert, who were

guided to it by a local miner. It lies at about 21°54′ N latitude and 89°56′ W longitude, approximately 11 km. SE Ciudad Valles. On the first visit to the cave, a single blind fish was taken but others were seen. On the following day, seven more specimens were collected by Francis Abernethy, Robert Mitchell, and William Russell. Several subsequent visits have yielded but a single, minute fish. None of these fishes appeared to have hybridized with surface *Astyanax* even though La Cueva Chica is located only 5 kilometers to the south.

This cave is especially interesting because of its small size. From a shallow sink, 9 by 12 meters, there arise three tunnels. The southmost of these extends southward as a crawlway for 16.5 meters but does not descend to water. It is inhabited by ricinuleids, probably *Cryptocellus pelaezi* Coronado, 1970. An eastern tunnel bends southward extending as a 38.5-meter crawlway; it does not descend to water. The northernmost tunnel is a fissure 11 meters long and 4.5 deep. It is possible to stand in the entrance sink and, with a lamp, see the fishes in a small pool 4.5 meters below. This pool is only about ½ meter wide by 2.5 long, but it appears to be quite deep. Though the water is quite near the surface, it is so protected by overburden that it never receives direct sunlight.

The elevation of the cave entrance is 92 meters; the pool lies at 87.5. Thus, the pool is 43 meters above the entrance of the nearest blind fish cave, La Cueva Chica; 63.5 meters above river level at the Río Tampaón; and 58 above the level of the Nacimiento del Río Choy. These waters then represent a perched pool, and one which is probably small and fairly isolated because cave fishes have been so slow to make a reappearance since the original collection. Water temperature was 23.5°C on 2 June 1969.

The cave was surveyed on 4 and 10 July 1969 by William Elliott, Don Broussard, and James McIntire.

*La Cueva de la Curva.*—This cave is located 8 km. E Ciudad Valles, San Luis Potosí, and about 1 km. N villages of San Felipe and El Abra at 21°59′ N latitude and 89°56′ W longitude. The entrance is formed in the side of a dolina a few hundred meters east of the main San Felipe Formation-El Abra Limestone contact and lies at an elevation of 131.5 meters. The present name refers to the proximity of the cave to a bend (*curva*) in the Ciudad Valles-Estación Tamuín railway, and its usage was established before it was determined that it is probably the same cave referred to earlier as "La Cueva del Agua" (Villa R., 1966) and "El Sótano de Ferrocarril" (Reddell, 1967).

The cave was first located by our group on 31 May 1969 by Kenneth John, William Russell, and Tom Albert, who were guided to the entrance by a local miner. Blind fishes were observed on this visit and later on the same day collections were made by Robert Mitchell, William Russell, Richard Albert, and Kenneth John. Subsequent periodic visits have yielded some additional specimens.

The cave is essentially an enlarged joint with the wide, arching entrance passage perpendicular to the main tunnel. In recent years, local people have presumably moved aside many large cobbles that may have previously blocked access to the low water passage containing the fishes. Otherwise, it is difficult to imagine

that blind fishes could not have been reported by those earlier visits to the cave, if indeed it was visited earlier.

The main passage is about 183 meters in length and lies about 19 beneath the entrance. About 55.5 meters of the midportion of this passage contains water lying at an elevation of 112.5 meters, or 78.5 above the Nacimiento del Río Choy. Because this cave is so near to this resurgence and it waters so much higher, it is obvious that the cave waters are perched. Fishes are probably brought up into the cave with rising ground water during extremely wet periods.

The cave was surveyed on 8 July 1969 by Don Broussard, William Elliott, and James McIntire.

### Los Sabinos Caves

*El Sótano de Palma Seca.*—El Sótano de Palma Seca is located at 22°02′ N latitude and 89°57′ W longitude, about 7 km. NE Ciudad Valles and near the village of León García. The name (*dry palm*) refers to the palms that abound in the Sierra de El Abra. The cave was discovered from the air on 26 January 1969 by Robert Mitchell, William Russell, Francis Rose, and Richard Albert. On 31 January 1969, Mitchell, Rose, Albert, and William Elliott entered the cave and made the first blind-fish collections.

The entrance of the cave, at an elevation of 151.5 meters, captures the drainage of a small arroyo that is a part of the general south-trending drainage in the Los Sabinos area. Unlike most other such arroyos in the area, this arroyo is developed directly upon the El Abra Limestone outcrop. At that point where it is captured by the cave, the arroyo is about 12 meters wide and 9 deep. The cave captures a drainage area of about 1 square kilometer. This drainage area is limited because of the presence of another complete capture, the Sótano de las Piedras, of the same arroyo about 1 kilometer upstream from the Sótano de Palma Seca. The arroyo is without a fish fauna.

The entrance is about 7.5 by 10.5 meters and is 30.5 meters deep on the upstream side and 38 meters deep on the downstream side. The headwall is about 7.5 meters high. The main passage of the cave strikes W for 33.5 meters to the edge of a lake located 52.5 meters beneath the entrance. This lake is 7.5 meters wide and 21.5 long, and the ceiling above the lake is about 9 meters high. The main passage terminates about 9 meters beyond the lake. Between this lake and the entrance pit, another tunnel strikes southward for about 12 meters as a water passage. At this point, the passage bears southeast for another 49 meters where it abruptly siphons.

Blind fishes are abundant in both bodies of water. Water temperature was 19° C on 31 January 1969. Vampire bats inhabit the south-trending segment of the long water passage.

*El Sótano de Las Piedras.*—This cave (*piedras = rocks*) lies at 22°02′ N latitude and 89°57′ W longitude, about 7.5 km. NE Ciudad Valles. Its entrance is about 1 km. N Sótano de Palma Seca, 1 km. S of the Sótano de Jos, and at an elevation of 145 meters.

The cave was discovered from the air on 26 January 1969 by Robert Mitchell, William Russell, Francis Rose, and Richard Albert. On 31 January 1969 the cave was entered for the first time by Mitchell, Rose, Albert, and William Elliott, and a collection of fishes was made about 100 meters from the entrance. A second collection was made at this point on 15 July 1969 by Elliott, Don Broussard, James McIntire, and Stewart Peck. On the first date, water temperature was 19° C; on the second, it was 21°C.

The cave entrance is a pit completely capturing a small arroyo developed primarily on the San Felipe Formation but partly on El Abra Limestone. This arroyo drains about 4 square kilometers but no more than 0.5 square kilometers of drainage enters the cave because of another, nearly complete, upstream capture, El Sótano de Jos. At the point of capture the arroyo is about 9 meters wide and 9 deep. No fishes occur in the arroyo drainage.

The entrance of the cave is about 6 by 9 meters and drops about 18.5 on the upstream side and about 30.5 meters on the downstream side. The cave is basically a single passage about 400 meters long. From the entrance, this passage trends southwest as a 4.5-meter wide, 9-meter high, fissure for 43 meters turning then southeast for 40 meters and reaching 15 in height. At this point, 92 meters inside the cave, a pool is encountered that is 9 meters long and about 2 deep, lying 25.5 meters beneath the entrance, or at an elevation of 119.5 meters. Previous fish collections have been made from this pool and nearby ones. Beyond this pool the passage begins winding from northeast to southeast in roughly 12-meter sections. Several pools are located here. About 230 meters inside the passage, a lake about 10 by 10 meters is found lying 44 meters beneath the entrance, or at an elevation of 101. Beyond this lake the passage continues about 9 meters high and 15 wide and is floored with large cobbles. Large bat colonies occur here. The passage continues about 125 meters more, finally ending at another lake about 12 meters wide. This lake continues about 18 meters to where the passage siphons. This lake lies 46.5 meters beneath the entrance, or at an elevation of 98.5.

*El Sótano de Jos.*—This cave is located at 22°02′ N latitude and 89°57′ W longitude, about 8 km. NE Ciudad Valles. *Jos* is the name for a local tree, as yet unidentified. The cave was discovered on 31 January 1969 by William Russell and Tom Albert during a ground reconnaissance between Sótano de la Tinaja and Sótano de las Piedras. The cave was first entered on 26 May 1969 by William Russell and Tom Albert, who collected numerous blind fishes in water a short distance from the entrance.

The entrance, a long slot in the bed of an arroyo, lies at an elevation of 176 meters. Most of the drainage of this arroyo, about 3.5 square kilometers, is captured by the cave. At high flood stage some water probably moves across the entrance to be captured shortly by the downstream Sótano de las Piedras. No surface fishes live in this drainage.

The cave has been surveyed by John Fish and other members of the Association for Mexican Cave Studies. There are 338 meters of horizontal passage, and the deepest point lies at an elevation of 91.5 meters. There are three vertical drops, the entrance drop of 27, a second of 20.5, and a third of 15.5 meters.

*El Sótano de Pichijumo.*—This cave originally was known to us by the name of "Sótano de Montecillos," but in recent years it was learned that locally it is called "Sótano de Pichijumo." The word "pichijumo" is a spelling variation of the common name of a local leguminous tree, *Pithecellobium dulce* Benth., a plant known by other common names as well.

The cave is located at 22°03′ N latitude and 89°57′ W longitude, about 8 km. NE Ciudad Valles, 1.5 kilometers north of the village of Montecillos, and about 460 meters downstream from the entrance of Sotanito de Montecillos.

The entrance, an old, classical capture, lies at an elevation of 157.5 meters. It is about 23 by 15 meters and drops vertically 14 meters on the low upstream side and 38 on the high downstream side. This entrance completely captures an arroyo that drains an area of about 6 square kilometers. No fishes inhabit this surface drainage.

The cave was discovered and blind fishes observed by John Risinger on 23 December 1963. This was thus the first cave known to harbor such fishes since the discovery of the original five many years previously. The first collection of fishes from this cave was not made until some years later, however, when on 31 January 1968 the cave was visited by Robert Mitchell and Francis Rose. The collection was made in an upper level passage 16 meters beneath the entrance, or at an elevation of 141.5 meters. In these same waters on 20 November 1969, Valerio Sbordoni and Roberto Argano collected two typical, eyed, surface *Astyanax*. The source of these fishes still remains entirely unknown but must be discovered. In May 1971, William Elliott collected blind fishes in a large lake 68 meters below the entrance, or at an elevation of 89.5.

The cave was partially surveyed on 8 April 1965 by Chip Carney and Don Erickson. This map and a map of the Arroyo between the Sotanito de Montecillos and the Sótano de Pichijumo were published by Carney (1966). The two caves were surveyed in 1971 by members of the Association for Mexican Cave Studies, who established a connection between the two. According to an unpublished map, drafted by Neal Morris, there are about 1330 meters of surveyed passage in Pichijumo. The deepest point in the Pichijumo portion of this complex system lies 82 meters beneath the entrance, or at an elevation of 75.5 meters.

*El Sotanito de Montecillos.*—This cave is located at 22°03′ N latitude and 89°57′ W longitude, about 8.5 km. NE Ciudad Valles and 2 kilometers north of the village which name it bears. The cave was discovered and blind fishes observed on 23 December 1963 by John Risinger. On 31 January 1968, the first collection of fishes from the cave was made by Robert Mitchell and Francis Rose. In 1971, various members of the Association for Mexican Cave Studies surveyed this cave and the nearby Sótano de Pichijumo, during which time a connection between the two caves through a water-filled tunnel, or siphon, was established by Neal Morris, Craig Bittinger, Steve Bittinger, Jan Lewis, Roy Jameson, and Blake Harrison. Such a connection had long been suspected.

The entrance of this cave is at an elevation of 190 meters and it lies in the middle of an arroyo about 460 meters upstream from the entrance of Sótano de Pichijumo. The small 1.5 by 2.5-meter opening is covered and obscured partially by a

thick limestone slab. The entrance drop is 35 meters. The map of the Montecillos-Pichijumo system drafted by Neal Morris indicates that about 1741 meters of horizontal passage have been surveyed in the Montecillos portion of the system. Blind fishes have been found in pools from the 52 to the 91.5-meter levels beneath the entrance, or from elevations of 138 to 98.5 meters.

This cave is a good example of a very young stream capture. Although it does take some water, the opening is so small that the amount taken is surely negligible relative to that captured by the downstream Sótano de Pichijumo. No surface *Astyanax* inhabit this surface drainage.

An early, preliminary description of this cave has been done by McKenzie (1965).

*El Sótano de Soyate.*—This cave lies about 12.5 km. NE Ciudad Valles, about 4 km. E Arroyo Montecillos, and about 3 km. E San Felipe-El Abra Formation contact. The cave is named after surrounding soyate plants (*Beaucarnea carniosum*), woody monocotyledonous trees of the Liliaceae.

The cave's vertical entrance of 197 meters ranks it as the fifth deepest pit in the New World. For some time it was also the deepest, accessible blind-fish cave known, but that title has been relinquished now to a recently discovered cave in the Sierra de Nicholás Pérez. The entrance, about 9 by 13.5 meters, is well hidden by the surrounding thorn scrub, and because it occurs in an area of exposed El Abra Limestone, it exhibits no stream capture. Entrance elevation is 293 meters.

The entrance was located on 31 January 1969 by Tom Albert, James Reddell, William Russell, and Richard Smith, who were led to it by a local woodcutter. Although the cave appeared worthy of exploration, it was not until 27 May 1969 that it was revisited by Kenneth John, Robert Mitchell, and Tom Albert. The latter two entered the cave but had only sufficient rope to reach a small ledge about 90 meters beneath the opening. From there they timed falling rocks and estimated the total depth to be from about 180 to 245 meters.

On 6 July 1969, James McIntire and William Elliott, with the assistance of Don Broussard on the surface, reached the bottom of the cave and collected about 50 blind fishes in a large lake 238 meters beneath the entrance. On 14 August 1969, Broussard, Elliott, and McIntire reentered the cave, surveyed it completely, and collected additional fishes.

The large lake inhabited by the fishes is over 30 meters deep, and its surface, at an elevation of 55 meters, is probably near base-level in the Sierra de El Abra. Because the entrance of the Sótano de Soyate takes no flood waters and, furthermore, is far removed from other sources of debris input into El Abra waters, it was somewhat surprising to find this large cave inhabited by blind fishes, particularly in large numbers. The abundance of fishes in these seemingly "sterile" waters suggests that they are widely distributed and abundant throughout the base level waters of the Sierra de El Abra.

*El Sótano de la Tinaja.*—This great cave is located at 22°05' N latitude and 89°57' W longitude, about 10.5 km. NE Ciudad Valles on the Rancho de la Tinaja (*tinaja*=*pool*). The cave and its blind fishes were discovered by Benjamin

Dontzin and Edwin Ruda (Breder and Rasquin, 1947) in 1946. They had been commissioned by the American Museum of Natural History to search for such caves and to collect blind fishes. The cave seems to be part of a three-cave drainage network termed "La Sistema de Los Sabinos" (Fish, 1974), which also includes the Sótano del Arroyo and La Cueva de Los Sabinos.

From the structure of the entrance, it would be plausible to conclude that it is the oldest blind-fish cave opening in the Sierra de El Abra. Although the entrance is termed a "sótano," the cave does not have a simple, pit-type entrance characteristic of other sótanos in the area. Rather, the upstream side of the entrance has been downcut into an impressive canyon about 53 meters deep. This abrupt downcutting now has proceeded upstream to a point about 180 meters from the original entrance near which point the canyon receives a typical, small arroyo. Presently, the actual "entrance" to the cave is the opening into a horizontal tunnel lying at the bottom of what was once the original entrance, or stream-capturing pit. According to our altimeter data, the elevation of the floor of this entrance is 165.5 meters. This does not agree with the figure of Fish (1974) of 171 meters. The maximum surveyed depth of the cave beneath this point is 82, an elevation of 83.5 meters.

The first survey of the cave was a partial one done by an expedition sponsored by the American Museum of Natural History in 1947. This team surveyed the first 550 meters of the main passage, to a point where a drop is encountered, unclimbable without the aid of equipment. This map was never published. During the 1960's, members of the Association for Mexican Cave Studies began visiting the cave, and in 1964 intensive exploration was prompted by major discoveries by David McKenzie and John Risinger. During 1965 and 1966, about 4060 meters of passage were surveyed and a map drafted by David McKenzie was published in Russell and Raines (1967). Additional surveying in the ensuing years has brought the total to 4502 meters, with more explored passage trending toward the Sótano del Arroyo yet to be surveyed. An updated map has been published recently by Fish (1974).

Beyond the entrance, 12 wide by 6 meters high, the main passage trends east for about 671 meters. In its first 150 meters, it is about 9 wide and 4.5 meters high. It then attains widths and heights over 23 meters. In places, the floor is covered with large breakdown boulders often covered with the guano of vampire bats. In several places, and especially at a point about 340 meters inside the entrance, large amounts of organic debris are banked along the main passage. This debris supports an abundance of invertebrates (Elliott and Strandtmann, 1971). At about the 425-meter point in the main passage, a small lake, "Traverse Lake" (Fish, 1974), is encountered that always has been found to contain blind fishes. Beyond this lake, at a point about 550 meters from the entrance, is the 8-meter "Cable Ladder Drop" (which marks the end of the AMNH survey). From the bottom of this drop, a 7.5-meter high by 15-meter wide tunnel termed the "Sandy Floored Passage" meanders from northeast to northwest for about 1220 meters. This is an "upstream" passage that occasionally is fed by several inlets (Fish, 1974). About 60 meters from the beginning of this passage, there is the intersec-

tion of another tunnel that leads to a large room and then continues east-northeast descending sharply in a series of several one-meter drops until it reaches a large lake room 107 meters long, 9 wide, and 30 high. The surface of this lake marks the deepest surveyed point in the cave. This lake has yielded a beautiful troglobite shrimp, *Troglocubanus perezfarfanteae* (Villalobos, 1974), but, curiously, no blind fishes have been sighted here. This lake appears to be the major collecting point for flood waters (Fish, 1974).

About 70 meters east of the Cable Ladder Drop is the 19-meter "Siphon Pit" that leads into about 350 meters of decorated rooms and small passages, the "Siphon Pit Series." This is not an active flood route (Fish, 1974). About 670 meters beyond the beginning of the Sandy Floored Passage, there is the intersection of another major passage about 600 meters in length that at first trends northeast but eventually meanders to a westerly heading. Another major passage begins only about 45 meters inside the entrance. It drops down through boulders on the north wall and becomes the "Water Passage," a succession of pools covered with flood debris and inhabited by blind fishes. About 1000 meters of passage have been explored in this section, which contains a recently discovered upper-level inlet striking west and a succession of maze and tight crawlways leading through "Acupuncture Crawl" to a northwest-trending water passage that approaches the Sótano del Arroyo (Fish, 1974).

With the exception of the lake at the cave's deepest point, blind fishes have been encountered in many pools and lakes in all of the major passages. Water temperatures (taken in the Traverse Lake) are typical of those in other caves of the Los Sabinos area, 22.5 to 23°C.

The captured arroyo collects water from a drainage area of about 4.5 square kilometers. No surface fishes inhabit this drainage.

*El Sótano del Arroyo.*—This extensive cave is located at 22°06′ N latitude and 89°57′ W longitude, about 12.5 km. NNE Ciudad Valles and about 1.5 kilometers southeast of the village of Los Sabinos. The name is appropriate because the cave entrance captures a well-developed arroyo. Discovery of the cave and its blind fishes was by Benjamin Dontzin and Edwin Ruda in the spring of 1946 (Breder and Rasquin, 1947).

The entrance has the classical structure of an old capture site with the downstream portion of the captured arroyo deeply eroded, to a depth of about 60 meters at the point of capture. The headwall rises to an equivalent height above the opening. The 15-meter diameter entrance is vertical but not deep, about 15 meters, because of the extensive downcutting of the arroyo. Elevation of the entrance, at that point where the upstream segment of the arroyo is intersected by the vertical entrance, is 195 meters.

The cave was surveyed partially during the 1946 American Museum of Natural History expedition (Breder and Rasquin, 1947), but a map was never published. The cave again was partially surveyed, about 915 meters, in November 1961 by James Reddell, Bud Frank, Orion Knox, A. Richard Smith, Mills Tandy, and Tom White. In November 1962, a group of about 15 people from Austin, Texas, brought the survey to about 1616 meters and to a depth of 60. No addi-

tional surveying was done until December 1971 when a large group of people from Texas, Indiana, and Canada worked for several days within the cave. All known passages were resurveyed, and much new passage was discovered. Presently, the cave comprises 7200 meters of surveyed passage and is 133 meters deep. It thus contains more surveyed passage than any other cave in México. Recently, a map, based on the new survey, has been published by Fish (1974).

The following description is summarized from Fish (1974). Two passages lead from the entrance. The "Thirty Foot Level" begins 10 meters above the floor and meanders to the southwest for 224 meters to a point where it is almost blocked by flowstone, and it then continues for about 100 meters to a junction, through small holes, with the "Right-Hand Water Passage." The Right-Hand Water Passage traverses about 450 meters of pools and dams before entering the "Main Passage" at a point about 150 meters from the entrance. The Main Passage is large and strewn with mud and boulders. Two 10-meter drops are encountered 800 meters from the entrance. The "Left-Hand Passage" begins at the bottom of the second drop. It is a high canyon on the same level as the entrance sink. For the last 200 of its 450-meter length, this passage descends until it ends in a siphon 27 meters below the entrance. Here it may connect with the nearby Cueva de Los Sabinos.

About 100 meters past the Left-Hand Passage is the "Big Triangular Room," over 100 meters long, 30 high, and with large breakdown. The passage descends to a 16-meter drop into "Reddell's Lake" marking the beginning of the lower level where much mud and high $CO_2$ levels are encountered. The main lower level passage meanders from south to northeast for 1100 meters. Flooding apparently fills this and all side passages. At the end of this passage, in the extreme eastern part of the cave, there is a complex of passages totaling about 1000 meters. In this area, "Strickland's Bad Air Passage," an active floodwater route leads to a 30-meter drop into a large, unexplored passage. Here, $CO_2$ levels reach 4 per cent. This is the lowest point in the cave and, at an elevation of 62 meters, the lowest point yet encountered in any of the Los Sabinos caves. Fish (1974) suspected that this passage soon siphons.

One of the few literature references to this cave presents it in erroneous aspect. Breder and Rasquin (1947) stated that "the Arroya [sic] cave actually differs from all the rest [Chica, Tinaja, Sabinos, Pachón] in admitting light to an area inhabited by fishes." This cave is not so characterized except, perhaps, under unusual and temporary circumstances. It appears that occasional rains are sufficiently intense to backflood, or simply to fill beyond the capacity of its conduits to move water away as fast as the water is entering. The main passage then fills with water, even at the cave entrance. Suzanne Wiley and A. Richard Smith (personal communication) observed the cave under just these circumstances after a heavy rain in November 1967, at which time water had risen in the main passage to within 9 meters beneath the entrance drop. It seems likely that those persons, upon whose observations Breder and Rasquin were relying, visited the cave at such a time. Such flooding could carry fishes into an area (the entrance) where light would be admitted, but this would be only the most temporary situation be-

cause of the rapid drainage that occurs with cessation of rain. It is further possible that some fishes might become trapped in small pools at, or near (personal observation), the entrance, but these probably dry rapidly.

The arroyo captured by this cave drains an estimated 6.5 square kilometers, a drainage second only to that captured by the sótanos Yerbaniz and Matapalma. No surface fishes inhabit the Arroyo drainage.

*El Sótano de la Roca.*—This cave is located at 22°06′ N latitude and 89°57′ W longitude, about 13 km. NNE Ciudad Valles. The small entrance lies in the side of the same arroyo completely captured about 0.5 kilometers farther downstream by the Sótano del Arroyo. It takes its name from a prominent boulder in the arroyo that serves as a convenient landmark for locating the obscure entrance. The cave was discovered in July of 1970 by John Fish and Don Broussard.

The 1-meter diameter entrance, at an elevation of 240.5 meters, drops to the floor of a small room in which there is a slot-like opening into a tubular pit about 1 meter in diameter and about 40 deep. At the bottom of this pit, a fissure parallels the arroyo for about 12 meters to continue as a low crawlway leading to a pool. On 25 May 1971, William Elliott collected 35 blind fishes from this pool, which lies about 42 meters beneath the entrance (estimated from rope required to descend the pit), or at an elevation of about 198 meters. The cave is unsurveyed and incompletely explored. This cave deserves more attention because its waters apparently lie much higher above local base level than do those in any of the other blind-fish caves.

*La Cueva de los Sabinos.*—This cave is located at 22°06′ N latitude and 89°56′ W longitude, about 13 km. NNE Ciudad Valles and about 4 kilometers east of the village of Los Sabinos, from which it takes its name. Its first exploration and the first blind-fish collection made in it were on 3 April 1942 by C. Bolívar y Pieltain, F. Bonet, B. Osorio Tafall, D. Peláez, M. Correa, and J. Alvarez (Alvarez, 1946). It is the *Astyanax* population in this cave to which the name *Anoptichthys hubbsi* was given by Alvarez in 1947.

The entrance of the cave, about 30 meters wide and 15.5 meters high, is formed on the side of a rather indistinct branch of that arroyo captured by the Sótano del Arroyo. It is probable that the entrance never takes flood water. Even so, tree trunks and other organic debris make their appearance in the cave, offering support to the suggestion that this cave and the Sótano del Arroyo are connected. Entrance elevation is 239.5 meters, a value differing from that (125 meters) of Fish (1974).

The cave was partly surveyed by the American Museum of Natural History expedition in 1946. About 900 meters were surveyed to an indicated depth of 99 meters. The resulting map was never published. Bonet (1953) provided a map of the cave apparently done by compass and pace method. The cave was resurveyed in 1972 by John Fish, Don Broussard, and P. Thompson. This map (Fish, 1974) indicates a total length of 1502 meters and a maximum depth of 95.5, an elevation of 144 meters.

From the large entrance room, upper and lower levels trend northeast for 70 meters to a large shaft where they rejoin. The lower level continues on for 150

meters to the "Guano Room." Also from the entrance room is another passage, that trends southeast for about 60 meters to a point where a steeply sloping drop of some 33 meters is encountered. Beyond this drop, the passage enlarges to form a series of rooms extending about 150 meters to end apparently at a siphon. This siphon, at 177.5 meters, lies 9.5 above and only about 30 meters horizontally from the siphon in the Left Hand Passage of the Sótano del Arroyo (Fish, 1974; our elevation data). Because vertical control is not all that good in most cave surveys and because some discrepancy exists between our elevation data and those of Fish (1974), we suspect that the adjacent siphons in these two caves lie at the same elevation.

About 70 meters past the sloping drop is a pool that leads through a small constriction into a large water passage, "Elliott's Swim." After 250 meters of northeast-trending pools from 1 to 2 meters in depth, land is encountered, and the passage then continues about 200 meters to a siphon at the deepest point in the cave.

Water temperatures in the cave are typical of those in caves of the immediate area (23 to 24°C).

*El Sótano del Tigre.*—This deep pit is located at 22°07′ N latitude and 89°58′ W longitude, about 14.5 km. NNE Ciudad Valles. Like the three previous caves, it is located on the Rancho de Los Sabinos. The name (*tigre = jaguar*) is not purely imaginative because Mike Collins and others of the Association for Mexican Cave Studies saw and photographed a jaguar in the arroyo near the cave entrance in 1969.

It is not entirely certain when this cave was discovered by speleologists, but its first mention in the literature was by Bonet in 1953 who noted the existence of the cave but did not enter it. The cave was first entered on Christmas Day of 1963. Over the next three years, the cave was entered several times, but little explored beyond the impressive entrance drop. On 25 November 1967, Mike Collins, T. R. Evans, John Fish, Terry Plemmons, and Janie Evans returned to the cave, and Fish and T. R. Evans surveyed about 600 meters of passage on the first and second levels to a depth of 96 meters. On 27 November 1967, T. R. Evans, Janie Evans, Fish, and Plemmons reentered the cave surveying about 520 additional meters of passage. On this day, blind fishes were seen. This partial survey was drafted by Jim Weiler and distributed privately. On 1 February 1968, Robert Mitchell and James Reddell made the first fish collection in the cave at a level of 96 meters beneath the entrance, or at an elevation of 149.5 meters.

The entrance of the cave is one of the better examples of a classical stream capture to be found in the Sierra de El Abra. The captured arroyo drains an area of about 2.5 square kilometers, and as it approaches the cave entrance it becomes narrow and sheer-sided, being about 15.5 meters deep at the point of capture. It no doubt carries a formidable torrent of water into the cave during heavy rains. No surface fishes inhabit the surface drainage.

The entrance lies at an elevation of 245.5 meters and is 76.5 deep. Because of the existence of several levels of complexly developed passages, the cave is difficult enough to illustrate, much less to describe verbally. Basically, though, the cave may be said to be developed on three levels. On the first level (bottom of the

entrance drop), the main cave passage trends north for about 75 meters to a sloping drop of some 21 meters. Six side passages exit from this tunnel. After the 21-meter drop, the main passage turns and strikes south to lie beneath the first level, and it slopes to reach a depth of 96 meters. The passage then strikes west for about 60 meters to the top of a 9-meter drop from the bottom of which the passage then trends south containing a shallow pool about 60 meters long, which supports a large number of blind fishes. Water temperature here in June 1969 was 24°C. The passage continues on for hundreds of meters. Also from the bottom of the 9-meter drop, another passage trends northwest. It harbors a remarkable population of the ricinuleid *Cryptocellus osorioi*.

More recently, John Fish and members of the Association for Mexican Cave Studies have continued the survey of this cave. It is known now to consist of over 3000 meters of passageway and to reach a depth of 161.5 meters where long, horizontal, muddy passages suggest that base level is being approached.

## Yerbaniz Caves

*El Sótano de Japonés.* — This cave is located in the Arroyo Japonés at 22° 10′ N latitude and 89°59′ W longitude, about 19.5 km. NNE Ciudad Valles. The Arroyo is so-called locally because some years in the past a Japanese person was killed in an automobile accident at the bridge where Highway 85 crosses the arroyo (S. Herrera, personal communication). The cave was discovered from the air on 26 January 1969 by Robert Mitchell, Francis Rose, William Russell, and Richard Albert. The cave was first entered in March 1969 by Jimmy Jarl, Joe Sumbera, and several others who explored the maze passage at the bottom of the entrance drop. On 28 May 1969, Kenneth John, Robert Mitchell, and Tom Albert explored the main passage trending south, but they were halted after about 300 meters by a narrow pit requiring additional equipment to negotiate. On 27 July 1969, Don Broussard, William Elliott, and James McIntire descended this pit and continued down past three additional drops to a lake about 90 meters beneath the entrance. Here they collected about 70 blind fishes.

The cave entrance, lying at an elevation of 243 meters, captures the Arroyo Japonés. Depth of the entrance pit is 21.5 meters. The Arroyo Japonés drains a rather large area, about 5 square kilometers. No surface fishes inhabit the drainage.

Explorations by various members of the Association for Mexican Cave Studies have revealed the existence of a few thousand meters of passageway in the cave.

*El Sótano de Matapalma.*—This cave is located at 22°11′ N latitude and 89°59′ W longitude, about 21 km. NNE Ciudad Valles. *Matapalma* probably refers to the strangler fig, commonly known in México as the *matapalo* ( = *tree killer*), a member of the genus *Ficus*. The cave was discovered from the air on 26 January 1969 by Robert Mitchell, Francis Rose, William Russell, and Richard Albert. On 27 March 1969, Jimmy Jarl, Logan McNatt, Joe Sumbera, and Frieda Gail Webster partially explored the cave and collected two blind fishes in a rimstone pool. The cave was visited on 29 May 1969 by Robert Mitchell, Francis Abernethy, and Tom Albert who collected 12 more fishes, some of which were

typical eyeless forms whereas a few others appeared to be hybrids. On 4 August 1969, Don Broussard, William Elliott, and James McIntire collected 14 additional fishes in rimstone pools. In November of 1969, Ed Fomby, Logan McNatt, Brian Peterson, Joe Sumbera, and Mike Walsh surveyed a large part of the cave. A map of the cave has been published by Walsh (1972).

The cave entrance, a slot in the bed of the Arroyo Yerbaniz, completely captures this arroyo, but presently little water reaches this point because of the geologically later, upstream capture of the same arroyo by the Sótano de Yerbaniz. The entrance slot is particularly interesting because past geological developments in the arroyo can be visualized when looking up at the entrance from below. The passage into which the entrance pit descends lies beneath and parallel to the arroyo above. The downstream portion of the slot is large, and it developed parallel-sided as erosion progressed upstream. Then, rather abruptly, the slot narrows to about one-half its downstream width, this narrowing undoubtedly coinciding with the breakthrough of the Sótano de Yerbaniz into the arroyo farther upstream, a breakthrough which apparently rather quickly eroded to capture a sizable portion of the drainage of the arroyo. The narrowed slot then continued its progression upstream tapering but slightly, finally almost to close rather abruptly. This probably coincided with the final enlargement of the opening of the Sótano de Yerbaniz to near its present size. The most upstream portion of the slot is presently in the form of a small notch, probably eroded by a very local drainage and by the highly reduced amount of water that now moves past the Yerbaniz entrance during times of exceptionally heavy rains.

The entrance slot is about 46 meters long, 7.5 wide at its widest, and 64 deep. Entrance elevation has not been measured yet, but it lies slightly lower than the entrance of the Sótano de Yerbaniz at 242 meters. The cave is primarily one large, winding passage with few side passages. Total surveyed passageway is presently about 1725 meters with a small amount of passage remaining to be surveyed and numerous side passages yet unchecked.

The occurrence of hybrid fishes in this cave is of particular interest. This has resulted from the influx of eyed forms, which are abundant in the Arroyo Yerbaniz. The special problem of the occurrence of surface fishes in this arroyo, unlike the arroyos of the Sabinos area, will be elaborated in the discussion of the Sótano de Yerbaniz following.

It would not be just to those who have visited this cave to fail to make this one last comment. No blind-fish cave presents such frustrations in attempts to locate its entrance. Because the Arroyo Yerbaniz now carries so little water into the Sótano de Matapalma, the bed of the arroyo is overgrown completely with the densest of thorn scrub, a density almost matched as well by the thorn scrub of the surrounding hillsides. Usually the fish cave arroyos are sufficiently clean so that they may be walked easily. It is essentially impossible to follow the Arroyo Yerbaniz to the Sótano de Matapalma. This has forced attempts to traverse directly from the Sótano de Yerbaniz to Matapalma, an almost equally difficult chore. In their attempts to reach the cave, some have been turned back and others have been what seemed at the time to be inextricably lost. Many of the blind-fish caves

present their own particularly difficult internal problems, but this cave presents problems at the moment one sets out to visit it.

*El Sótano de Yerbaniz.*—This cave is located at 21°11' N latitude and 89°58' W longitude, about 21.5 km. NNE Ciudad Valles. The locally used name *yerbaniz* applies to a shrub, as yet unidentified, the flowers of which are used in religious ceremonies on the Día del Muerto (J. Gloria, personal communication). The cave was discovered from the air on 25 January 1969 by Robert Mitchell, Francis Rose, Richard Albert, and Tom Albert. Discovery was entirely by accident and occurred as a search was being made at dusk for a landing strip at the nearby Ponciano Arriaga. The cave was first entered on 28 January 1969 by Tony Mollhagen and Francis Rose who negotiated only the entrance pit. On 29 January 1969, Robert Mitchell, Francis Rose, and Richard and Tom Albert entered the cave, explored parts of the first and second levels, and collected typical, eyed, surface *Astyanax* in pools at the first level. On 31 January 1969 the cave was penetrated to its third level by Jerry Broadus, David Honea, Ann Lucas, Russell Harmon, Tony Mollhagen, and Joe Cepeda who collected several blind fishes in a large lake at the third level. On 2 February 1969, a sizable collection of blind fishes was made in the same lake by Robert Mitchell and William Russell. The cave was surveyed in July of 1969 by William Elliott, Don Broussard, and James McIntire.

The entrance of the cave is a slot about 16 meters long having a maximum width of about 3. It lies in the edge of the Arroyo Yerbaniz at an elevation of 241.5 meters. Although a relatively young opening, the entrance is of sufficient size to capture all of the water flowing in the Arroyo Yerbaniz except at high flood stage. That water can move past the entrance at these times was demonstrated in September 1969 when William H. Russell visited the cave entrance immediately after a very heavy rain. In spite of the size of the opening, so much water was being carried in the arroyo that the entrance could not accommodate all of it. Water of about 1 meter depth was passing by the opening where at one point there was a large whirlpool formed where water was entering and at another point where a vapor spout about 12 meters high occurred as a result of air being displaced rapidly by incoming water. The violence within the cave at such times can only be imagined, but large palm trunks wedged into small and remote passages attest to the force of the water.

The cave is complexly structured on three levels. The entrance pit penetrates to the first of these. The first level, consisting of several large rooms, small intersecting passages, and one long northeast-trending passage, lies about 56 meters beneath the opening. The second level, consisting of two large rooms, several small intersecting passages, one very long northwest-trending passage, and a shorter south-trending passage, lies about 69 to 85 meters beneath the entrance. The third level, consisting of one very large room (over 100 meters in length) and two long passageways structurally disassociated, lies about 91 meters beneath the entrance. The deepest points in the cave (surfaces of three lakes on the third level) lie 95 meters beneath the entrance, or at an elevation of 146.5 me-

ters. That these lakes lie at the same elevation and that each siphons suggests that they are at local base level.

Even though this cave is of rather recent discovery, it has now been entered many times, principally because of its rich and interesting fauna. A species of the rare, troglobite scorpion genus *Typhlochactas* has been described from the cave (Mitchell, 1971) as well as a new genus of schizomid (Rowland, 1971). Other entries into the cave have been made to examine the interesting relationships between the blind fishes and surface *Astyanax* swept into the cave by flood waters. Discussion of this problem will be deferred to a subsequent section of this paper where the mixed eyed-eyeless fish populations are specifically considered in some detail.

The Arroyo Yerbaniz drains the largest area of any of the arroyos captured by blind-fish caves, about 16 square kilometers. Surface fishes inhabit the arroyo in abundance. The arroyo does not, however, support a permanently flowing stream, but somewhere in its course there are certainly permanent waters in which the fish populations are maintained. We are not yet sure of the precise location and nature of these waters, but possibly they are deep pools in the bed of the arroyo in which we have collected fishes at the height of the dry season.

### Northern El Abra Caves

*El Sótano de Venadito.*—This cave lies at 22°25′ N latitude and 99°00′ W longitude, about 35 km. SSW Ciudad Mante and about 1.5 kilometers north of the Tamaulipas-San Luis Potisí border. It takes its name (*venadito* = *fawn*) from the now nonexistent village of El Venadito once located on Highway 85, five kilometers west of the cave.

The entrance to the cave was located on 22 January 1965 by Ed Alexander. On 24 January 1965, the upper level was explored by Terry Raines, John Fish, Janie Evans, and Ed Alexander. On 24 March 1968, the entrance area passageways were surveyed by Brian Peterson, James Jarl, Joe Sumbera, Martha Burk, Sharon Cathey, and James McIntire. Exploration to the 143-meter level yielded the first discovery of blind fishes in the cave by Brian Peterson, who collected two specimens. Another collection of fishes in the same remote pools was made on 11 July 1969 by Don Broussard, William Elliott, and James McIntire. The section of the cave leading to these first-discovered blind-fish pools was surveyed on 2 August 1969 by Elliott, Broussard, McIntire, and Jarl, at which time additional fishes were collected. Subsequent explorations in 1971 by Terry Raines, Jim Rodemaker, Julie Rodemaker, Hugo Victoria, David Honea, Craig Bittinger, Neal Morris, Roy Jameson, and Blake Harrison have resulted in the discovery of many new passages and large rooms. The latter four persons reached a depth of approximately 183 meters on 22 May 1971 and made another large collection of fishes. The lowermost passages are long, horizontal, and muddy, suggesting that local base level is being approached. Presently, about 760 meters of passage have been surveyed, but the cave is still very incompletely known. A map of the cave has been published by Walsh (1972).

The entrance, at an elevation of 312 meters, is a classical stream capture, and the arroyo captured drains an area of about 5.5 square kilometers. This drainage is highly isolated, contains water only temporarily, and supports no surface fishes.

*La Cueva de El Pachón.* — This cave is located at 22°37′ N latitude and 99°01′ W longitude, about 16 km. SW Ciudad Mante. It is named after the near-by village of El Pachón, part of which is now the Ejido Praxedis Guerrero. This cave, La Cueva Chica, and La Cueva de Los Sabinos comprise the group of blind-characin caves best known in biological literature. It was discovered and blind fishes collected from it on 7 December 1945 by R. Hernandez Corzo, C. Bolívar y Pieltain, A. Dampf, F. Bonet, and J. Alvarez (Alvarez, 1946). This population of eyeless *Astyanax* was named *Anoptichthys antrobius* by Alvarez in 1946. The cave was surveyed by John Fish, Terry Raines, Janie Evans, Danny Evans, Ed Alexander, and Jim Dunlap on 26 January 1965. A map of the cave drafted by Terry Raines was published by Russell and Raines (1967).

The entrance of the cave is a largely abandoned resurgence located well up on the western slope of the Sierra de El Abra at an elevation of 210.5 meters. The opening is 2.5 meters high and 6 wide, and the fact that it still serves as a wet weather resurgence for a very local area is evidenced by the presence of a shallow arroyo leading from the entrance down the steeply sloping side of the range. The cave is simple in structure, being essentially one passage that trends northeast from the entrance for a short distance to strike then abruptly southeast. About 160 meters inside the entrance a lake is encountered that is about 50 meters long. The cave terminates shortly beyond this lake near its end along the southwest wall of the passage. The surface of this lake lies but 8 meters beneath the entrance, or at an elevation of 202.5.

Water temperature (measured at different times over the course of three years) is 25.5°C. This temperature, comparable to that in La Cueva Chica, is slightly higher than are the temperatures recorded in most of the other blind-fish caves, particularly in those several caves of moderate depth and characterized by vertical shafts. The latter probably serve as rather efficient cold air traps thus lowering mean water temperatures a slight amount. The deepest of the vertical caves, how-ever, have slightly higher water temperatures (Soyate, 25°C; Tigre, 24°C) than do the shallower vertical systems. The point is that this rather high water temper-ature in Pachón does not reflect any gross regional pecularity, but rather results from the structure of the cave itself, a general statement which can be applied to the other blind-fish caves as well.

Some information on population size of the Pachón fishes is appropriate, es-pecially because of recent statements in the literature about it. Avise and Selander (1972) stated, in partial summary of their study that "reduced variability in the small populations of *Astyanax* occurring in cave pools is attributed primarily to genetic drift." That the Pachón population is "small" derives from their state-ment, "it is estimated that the populations sampled in pools in Pachon, Sabinos, and Chica caves consisted of only 200 to 500 individuals." Their "estimate," in reality, is a guess and is so in error as to discredit partly their thesis. William R. Elliott has done a two-census mark-recapture estimate of the population size in

Pachón obtaining a figure of 8502 fishes (with 95 per cent confidence limits of 1279 to 18,283). This population must then be one of the largest of eyeless *Astyanax* populations known, ranking with the great number of fishes in the Sótano de Yerbaniz (mark-recapture data) and in the Sótano de Soyate (observation only). The energy sources supporting the large Pachón population derive from bat colonies located above the cave water and from influx of plant debris that is carried into the system from some unknown source(s), but probably a local one located on the crest of the range.

### Micos Caves

*La Cueva del Río Subterráneo.* — This cave is located at 22°03′ N latitude and 99°14′ W longitude, about 26 km. WNW Ciudad Valles and about 10 kilometers SSW Micos, San Luis Potosí. The cave was located first by biologists working with the joint Mexican-American rabies control program sometime during the 1960's. Learning about the cave from this group, Horst Wilkens and J. Parzefall visited it in the spring of 1970. It was they who named it. Wilkens and Burns (1972) published a short paper (including a sketch map of the cave) on the fish population here. Wilkens informed us of the existence of this cave in April 1970, and subsequently we have visited it, surveyed it, examined the local geology and physiography, and sought more blind-fish caves in the area, finding two.

The entrance of the cave, at an elevation of about 230 meters, is located at the base of a ridge of limestone rising from a lowland to the west of the Sierra de Colmena. The cave has basically the form of a "U." From the entrance, a passage strikes south descending steeply over breakdown to a temporary pool 25 meters beneath the entrance, which, after flooding, completely blocks the passage. About 40 meters beyond this pool, a 3-meter drop leads to an apparently permanent pool at a depth of 32 meters beneath the entrance, or at an elevation of about 198 meters. Beyond this pool, the passage strikes southwest and then abruptly angles northwest. At the end of a branch of the northwest-trending passage, there is another pool, also at a depth of 32 meters. During extensive flooding, these low-lying passages almost certainly fill with water.

Floodwater is carried into the cave by an arroyo that originates on the western slope of the Sierra de Colmena, crosses the flat lowland, and ends at the entrance of the cave. The arroyo is dry during the dry season, and low water flow does not reach the entrance but rather sinks about 100 meters upstream where the arroyo first contacts the limestone ridge. At high water, though, there is movement down this last segment of the arroyo into the cave. As evidenced by their occurrence in the cave, surface *Astyanax* are carried into the cave by floodwaters. We do not yet know the source of these epigean fishes, but somewhere in the surface drainage there must exist permanent waters.

The temporary pool near the entrance has been found to contain only surface *Astyanax*. The first permanent pool has been seen to contain both eyed and eyeless fishes. No surface fishes have been seen in the most remote pool.

The cave was surveyed in June 1971 by William Russell and David McKenzie. Total surveyed passage is about 475 meters.

*La Cueva de Otates.*—This cave is located at 22°03′ N latitude and 99°14′ W longitude, about 26 km. WNW Ciudad Valles, about 10 km. SSW Micos, and about 0.6 km. E La Cueva del Río Subterráneo. The cave was located in June 1971 by William Russell and David McKenzie. *Otate* is the common name of a large, thorny bamboo, which is particularly abundant in the arroyo leading to the cave entrance.

The entrance to the cave is situated behind a talus pile at the base of the same limestone ridge where La Cueva del Río Subterráneo is located. Entrance elevation is about 239 meters. A shallow arroyo draining adjacent fields leads into the talus so that when water is carried in the arroyo it enters the cave. From the entrance, a short fissure leads to a 7-meter drop into the main cave. At the base of this drop there is a pool about 6 meters wide and 12 long, which is the source of a shallow stream that flows gradually downward through a long, low tunnel. Several small rooms adjoin this tunnel. The tunnel meanders southwest for approximately 240 meters to a point where bad air is encountered preventing further exploration. Just before this point, the stream disappears into the south wall of the tunnel. The stream lies 19 meters beneath the entrance, or at an elevation of about 220.

Both eyed and eyeless fishes have been collected in the cave where the latter are restricted primarily to the first pool. The source of the epigean fishes is no doubt permanent water in some larger drainage that connects with the arroyo at times of high water.

*La Cueva del Lienzo.*—This cave is located at 22°03′ N latitude and 99°15′ W longitude, about 26 km. WNW Ciudad Valles and about 11 km. SSW Micos. The name refers to a fence line that is followed when walking to the cave (*lienzo = fence line or survey line*). The cave was located by William Russell and David McKenzie in June 1971.

The entrance, lying at an elevation of about 236 meters, is a shelter on the northern end of a large limestone outcrop that extends for at least 20 kilometers to the south. North of the outcrop lies a flat valley separating this ridge from that containing La Cueva del Río Subterráneo and La Cueva del Otates. La Cueva del Lienzo is about 0.8 kilometers south of the former.

Within the shelterlike entrance is a fissure that shortly joins a solution tube, which pitches downward at about 40°. After about 16 meters, a vertical drop of 7 meters leads to a small pool about 1.5 meters wide and 3 long. Both eyed and eyeless fishes occur in the pool. The eyed fishes no doubt enter the cave in much the same way as they enter the previous two caves. Local drainage appears to be such that heavy rains could cause flooding into the fissure connecting with the solution tube. The pool lies 21 meters beneath the entrance or at an elevation of about 215.

## Nicolás Pérez Caves

*El Sótano de Vásquez.* — This cave is located at 22°50′ N latitude and 9° 14′ W longitude, about 6 km. ESE Ocampo, Tamaulipas. It was named for an inhabitant of Ocampo who first supplied the information leading to its discovery.

The cave was located in late November 1971 by Amador Cantú, Charles Fromen, and others, at which time the entrance drop was entered to a ledge at 13 meters. On 21 November 1972, Cantú, Jon Everage, and Ronnie Fiesler descended to the bottom of the approximately 104-meter entrance drop. Another large group of people further explored the cave during late December 1972 and early January 1973, reaching a depth of about 170 meters before halting. During the second week of February 1973, Peter Strickland, Don Coons, and Jim Rodemaker penetrated deeper into the cave, and Coons and Strickland reached the bottom level at a varying depth beneath the entrance of 259 to 275 meters. At the lowest level, they encountered a water passage containing an abundance of blind fishes, and they collected a sizable sample.

The entrance of the cave is located near the top of the narrow crest of the Sierra de Nicolás Pérez about 6 kilometers south of the merger of this range and the massive Sierra de Guatemala. Entrance elevation is about 422 meters. The opening is roughly circular, about 23 meters in diameter, and it completely captures a rather short (400 to 500-meter) arroyo. The presence of an arroyo near the crest of this range is interesting, first because it is not the most likely place for the development of an arroyo, and, second, because all other arroyos captured by blind-fish caves are lowland. The arroyo owes its existence to a local fold. The arroyo never carried water off the range but instead carried it into an abruptly rising closure at the south end of the fold. At precisely this point, it was ultimately captured by the cave. No surface fishes inhabit the arroyo.

This is the only blind-fish cave that has not yet been entered personally by one of us, so we shall attempt no secondhand accounting of its complex structure. Suffice to say that it is developed on several levels that are connected by vertical pits. At the 275-meter level in the terminal room is located the water passage inhabited by the fishes. This water lies at an elevation of about 147 meters. The passage extends about 40 meters and then siphons; water depth is about 1.5.

### Chamal Caves

*Bee Cave.*—This cave is located at 22°55′ N latitude and 99°09′ W longitude, about 8.5 km. NE Chamal, Tamaulipas, in the low-lying foothills of the southern slope of the Sierra de Guatemala. This deep sótano was reported by Alexander (1965*a*) to be called "Bee Cave" by local North American citrus growers, hence the English name. We, however, have heard the cave termed locally only as "El Sótano," a common occurrence when there is but a single prominent pit cave in a local area. In keeping with the practice of applying Mexican names to Mexican caves, Mitchell and Russell (1969) altered the name to "El Sótano de las Abejas" on their privately, but widely, distributed map of the El Abra region. Later it was learned that the bee which is so common in the entrances of so many sótanos is properly termed a *colmena* rather than an *abeja*. Rather than to alter the name for a third time, we have decided to revert to the original name, particularly because this name has been previously published.

This cave was located by Ed Alexander on 28 May 1965, but he did not enter it at that time because of lack of equipment (Alexander, 1965*a*). He finally en-

tered the pit on 28 December 1965 (Alexander, 1965*b*) and again on 10 April 1966 (Fish, 1966) when he was accompanied by Ross Felton, John Fish, and David McKenzie. It was on this latter date that three specimens of cave fishes were collected in a small pool at the 119-meter level. On 29 January 1969, John George, Robert Mitchell, and Francis Rose made the first sizable fish collection in the cave, about 15 specimens. The cave has been entered several times since that date, but the pool has never yielded more than two or three specimens per visit. The cave was surveyed on 10 August 1969 by Don Broussard, William Elliott, and James McIntire.

The entrance, about 24 by 53 meters, lies on the side of a small hill at an elevation of 248.5 meters. It takes no surface waters aside from rainfall. The large entrance pit falls about 85 meters to the floor of a passage about 240 meters in length. The passage is straight and lies on a southeast-northwest line. Near its southeast end, the passage slopes to its deepest point, 119 meters beneath the entrance. At this point the cave barely penetrates a permanent pool, which lies at the bottom of a mud sump. So little pool surface is exposed (about 1 square meter) that collection is difficult. This "pool" is evidently an exposed portion of a water passage intersected by the main cave passage. Entry into the water passage would be difficult and dangerous because of the lack of air space. The surface of these waters lies 43 meters above a cluster of small nacimientos (del Río Nacimiento, de la Florida, and del Río Frío) located about 13 kilometers north-northeast at the base of the Sierra de Guatemala and at an unknown elevation above the Nacimiento de Riachuelo, located about 8 kilometers southeast at the base of the Sierra de El Abra. It is not known where the waters found in this cave resurge.

The few fishes taken here indicate an interesting population. The eyes of some showed varying degree of development; one had quite large eyes. Pigmentation of the lateral stripe also was variable, being fairly obvious in some specimens. Evidently, there is some hybridization occurring with surface *Astyanax*, but as yet we have no good idea where a source of surface fish input might be. Surface *Astyanax* inhabit local streams when these contain water during the wet season, but neither Bee Cave nor the nearby Sótano de Caballo Moro take surface water. In fact, we know of no cave at all in this area that takes surface streams populated by fishes. We must point out, however, that this is still a very poorly known area because it is generally quite inaccessible.

We should note lastly that Bee Cave is the first eyeless-characin cave to be found outside the Sierra de El Abra.

*El Sótano de Caballo Moro.*—This cave is located at 22°55′ N latitude and 99°12′ W longitude, about 7.5 km. NW of Chamal. The name (*Caballo moro* = *dappled horse*) derives from that of a nearby clearing. The cave was discovered from the air by Richard Albert, Robert Mitchell, and William Russell in May 1969. This pit was first located on the ground in November 1969 by William and Carol Russell, T. R. and Janie Evans, Ron Rossburg, and Louis Henbry. Rain and lack of time prevented entry. In December 1969, William Russell, T. R. Evans, Ron Rossburg, Walter Gersh, Howard Crow, Ernest Garza, and a local

rancher entered the pit and collected three blind fishes in a lake at the bottom. On 3 January 1970, the cave was visited by Mitchell, Russell, John George, Perihan Şadoğlu, Jerry Cooke, Suzanne Wiley, Virginia Tipton, Richard Smith, William Elliott, and Russell Harmon. At this time, eyeless, hybrid, and eyed fishes were collected.

Entrance elevation is unknown presently, but it is likely to be slightly higher than the 248.5-meter elevation of nearby Bee Cave. The fissurelike entrance lies at the bottom of a 60-meter deep, steep-sided dolina. The entrance is a vertical drop of about 50 meters, and at its bottom a sloping floor leads sharply downward to the edge of a large lake approximately 18 by 90 meters. This lake lies about 65 meters beneath the top of the entrance drop, and its floor pitches to apparently great depth. The cave is constructed so that daylight penetrates to the near shore during the afternoon. A low water passage leads from the far side of the lake, but a strong current into it has so far discouraged exploration. The cave is very incompletely surveyed.

In several ways, this is a difficult cave. It is almost inaccessible by vehicle, and loose rocks on the dolina walls make the descent to the entrance dangerous. Flotation gear will be necessary to make sizable fish collections in the lake.

*Gómez Farías Caves*

*El Sótano Escondido.*—This cave lies at 23°04′ N latitude and 99°08′ W longitude, about 1 km. SW Gómez Farías, Tamaulipas. It was located by William Russell in January 1971 and first entered on 15 May 1971 by Jerry Cooke and William Elliott, who descended about 100 meters; lack of rope prevented further exploration. On 16 May 1971, it was entered again by Elliott and Mel Brownfield who explored it to its bottom. Here a pool was encountered containing an abundance of blind fishes, and a collection was made. Elliott, Greg Walker, and John Prentice surveyed the cave in June 1974.

The entrance is located on the lower western slope of the Sierra de los Mangos at an elevation of 302.5 meters. It is divided by a natural arch and is overgrown heavily with vegetation, hence the name (*escondido* = *hidden*). The cave is essentially vertical with only 100 meters of horizontal passage. Several drops, seven requiring equipment to negotiate, descend in a counter-clockwise fashion to a terminal room in which the fish pool is located. The pool lies 148 meters beneath the entrance, or at an elevation of 154.5 meters (about 68 meters above the Nacimiento del Río Frío). Water temperature is 23.5°C.

This blind-fish pool no doubt is perched above the primary fish-bearing waters in this region. First, it lies well above the deepest known fish-inhabited waters in the area, the terminal pool in the Sótano de Molino, an elevation of 125.5 meters. Second, most of the fishes seen here were small and of uniform size, indicating the probability that a very few fishes were transported upward by rising waters to be trapped in the pool where they then gave rise to the population discovered.

A shallow arroyo that takes runoff from the slope drains into the cave. No surface fishes inhabit this drainage.

*El Śotano de Molino.*—This cave lies at 23°05′ N latitude and 99°08′ W longitude, about 0.5 km. W Gómez Farías. The name (*molino = mill*) refers to a small sugar cane mill once located a short distance from the cave. The cave was first located and entered by Terry Raines in June 1964 and again by T. R. Evans on 24 December 1965 (Evans, 1965). On 2 January 1971, Logan McNatt discovered blind fishes in upper level pools. On 20 March, Mel Brownfield and William Elliott partially surveyed the cave and collected fishes from these debris-ladened waters. The two pools here lie 73 and 77 meters beneath the entrance and at elevations, respectively, of 195.5 and 191.5 meters (about 109 and 105 meters, respectively, above the Nacimiento del Río Frío). The entire cave was surveyed on 21 and 22 October 1971 and 27 November 1971 by Steve Bittinger, Jan Lewis, Logan McNatt, Terry Raines, Craig Bittinger, and Bob Stockton.

The large entrance of this cave lies in the flat surrounding the Sierra de los Mangos at an elevation of 268.5 meters. Depth of the entrance pit is 67 meters. A total of 163 meters of horizontal passage has been surveyed, and the deepest point lies 143 meters beneath the entrance. Blind fishes inhabit waters in this lowest portion of the cave, 125.5 meters in elevation, or about 39 meters above the Nacimiento del Río Frío.

A well-developed arroyo leads into the cave and receives wet weather runoff from surrounding fields and the western side of the Sierra de Los Mangos. This arroyo is several hundred meters in length and is the largest captured arroyo in the area. It is not inhabited by fishes. Erosion by the waters carried by the arroyo have produced a headwall height at the entrance of about 10 meters.

It is interesting that blind fishes were not discovered in the upper level pools of this cave when it was entered initially in 1964 and 1965. In all probability, these pools at that time contained no fishes. Before the fish discovery in 1971, there was probably a high rise in local subterranean water level carrying the fishes upward from lower, permanently inhabited waters.

*El Sótano de Jineo.*—This cave is located at 23°05′ N latitude and 99°08′ W longitude, about 1 km. NW Gómez Farías. It takes its name from a group of houses, the Plan de Jineo, located adjacent to the road from Gómez Farías to San Juan. The cave was discovered in January 1971 by William Russell and was first entered by Jerry Cooke and William Elliott on 17 May 1971 when lack of equipment prevented descent beyond about 100 meters. On 18 May 1971, Mel Brownfield and William Elliott descended to about 143 meters, where exploration ended at a mud sump. No water was encountered. On 24 and 25 November 1971, the cave was surveyed by Roy Brown, D. Christie, Jan Lewis, Logan McNatt, Terry Raines, Olga Reyes, and Bob Stockton. A previously undiscovered area in the lowest portion of the cave was found to contain water and blind fishes. A small collection was made.

The entrance of the cave, a pit, lies at an elevation of 292 meters. There are 303 meters of horizontal passageway, and the deepest point is 144 meters beneath the entrance. Nine drops requiring equipment are encountered in reaching this level. At 144 meters beneath the entrance, the pool thus lies at an elevation of 148 meters, or 62.5 meters above the Nacimiento del Río Frío. This pool, like

that in the Sótano Escondido, no doubt is perched above the primary fish-inhabited waters in the region.

A fairly well-developed arroyo about 100 meters in length drains a small local area into the cave during wet weather. No fishes inhabit this small drainage.

### BASE LEVELS AND ELEVATIONS OF CAVE WATERS

As is evident from the preceding cave descriptions, the vertical separation of fish populations could be important in their isolation. We therefore shall give considerable attention to our elevation data, especially as these pertain to local base levels, the vertical removal of fish pools above base level, and particularly to the relationships between the two. This discussion is confined to the Sierra de El Abra because it is this area that we know the best.

Our data on absolute elevation of cave waters (or deepest points in caves) derive from two sources, altimeter measurements and cave surveys. Altimeter data were gathered earlier in our studies with an American Paulin System Terra Surveying Altimeter, Model T-5, measuring in increments of five feet. Later we used an altimeter of the same manufacture, but a Micro Surveying Altimeter, Model M-2, measuring in increments of two feet.

With the altimeters we have determined entrance elevations of 27 of the 29 known fish caves as well as elevations of some of the important nacimientos. During our altimeter work we correlated measurements of points of unknown elevation with several of known elevation including the railroad bed at the Estación Ferrocarril in Ciudad Valles (76.5 meters), and Bench Marks H-45 (at the bridge over the Río Sabinas, 99.199 meters), H-9 (2 km. S Antiguo Morelos on a small bridge culvert, 201.1766 meters), G-15 (on a small bridge culvert where Highway 85 crosses the southmost of two branches of the Arroyo Yerbaniz, 278.5058 meters), and G-39 (at the bridge over the Río Tamapón, 42.885 meters). Earlier, Mitchell and Kawakatsu (1972) cited an elevation of 99.286 meters for Bench Mark H-45. The present value used is a revision obtained from the Comisión de Estudios del Territorio Nacional, México, D.F., source of the other bench mark data as well.

Most of our data were gathered at a time when the only elevations known to us were those of the Bench Mark H-45 at the Río Sabinas and of the railway bed at the station in Ciudad Valles. The other elevations cited were tied into our data at a later date with correspondence between our measurements and the established figures being excellent. We determined the elevation of Bench Mark H-9 to be 201.2 meters; its cited elevation is 201.1766 meters. We determined the elevation of Bench Mark G-15 to be 280.5 meters; its cited elevation is 278.5058. We determined the elevation of the roadbed on the bridge over the Río Tampaón to be 42.1 meters; elevation of Bench Mark G-39, elevated slightly less than one meter above this roadbed, is cited to be 42.885. We also worked from Bench Mark G-29 on the south edge of Ciudad Valles with a cited elevation of 79.621 meters. Our value for this station was 76.5 meters, which correlated with other known elevations (the railroad bed in Valles and Bench Mark G-39). We now believe the figure of 79.621 for Bench Mark G-29 to be in error (from tran-

scription or prior measurement). We have detailed the preceding data to support our belief that our altimeter data (rounded to the nearest 1/2 meter) are highly reliable.

Altimeter measurements were made with great care, and many points were measured repeatedly. Each time a measurement was made, the altimeter was first set at a base station of known elevation. Then, as quickly as possible, an unknown point was read followed again as quickly as possible by a rereading, or back check, on the base station. Time and temperature also were recorded with each reading of the altimeter. Back checking on the base station is essential in this type of elevation determination because of the effects of temporal changes in barometric pressure. Most of our cited elevations reflect back checks that were exact or were within increment capability of the instrument. At times, unknown points were sufficiently inaccessible to require considerable time in which to make a reading. In such instances, original and back check elevations would sometimes differ, requiring computational adjustment of the elevation of the measured point assuming linear change in barometric pressure during that interval between first and last readings at the base station, a standard procedure in altimeter work. Also according to standard procedure, adjustments were made for temperature because our altimeters were calibrated to give exact altitudinal differences at a temperature of 50°F.

Distances of cave waters beneath the entrances were taken from cave survey data. The caves were surveyed with Brunton-type transits or Suunto compasses and tapes. When carefully used, such instruments are accurate to about 1°. But on long sightings considerable error can be introduced. It generally is assumed that because of the many sightings required in most cave surveys positive and negative errors tend to cancel out. Transit error would only be a factor in depth measurement when used to measure slope between survey points. Pits and other vertical drops were tape-measured. In general, because of instrumentation and technique, depth measurements within the caves should probably be regarded as less reliable than elevations determined with a surveying altimeter. The water elevation data, which we shall present in this section, then should be accepted for what they probably are—good, especially for comparative purposes, but not necessarily exact.

From the cave entrance elevation data and the cave survey data, we have calculated the absolute elevations of many fish-inhabited waters, and these are summarized in Table 1. Cave entrance elevations, nacimiento elevations, and the elevations of some other points are included in Fig. 5.

Although the absolute elevational data of the cave waters suggest the potential for vertical isolation of some pools, these data cannot be used directly for comparative purposes because of differences in local base level and because of the probable shape of high water profiles within the El Abra Limestone during times of extensive water uptake. We shall turn our attention first to the problem of base level. Because nacimientos discharge water along the eastern face of the Sierra de El Abra, we know that there is a westward rise in base level, and because most El Abra water is discharged through two large nacimientos located far apart

TABLE 1.—Absolute elevations of waters in the blind-fish caves of the Sierra de El Abra.
Measurements are in meters.

| Cave | Elevation | Cave | Elevation |
|---|---|---|---|
| Cuates | 32.5 | Montecillos | 138.0 |
| | 31.5 | | 98.5 |
| | 30.5 | Soyate | 55.0 |
| | 29.0 | Tinaja | ~155 |
| | 29.0 | | 130.0 |
| Chica | 45.0 | | 83.5[2] |
| | 35.5 | Arroyo | 173.5 |
| | 34.0 | | 62.0[1] |
| | 32.0 | Roca | ~198 |
| | 31.0 | Sabinos | 177.5 |
| Toro | 87.5 | | 172.0 |
| Curva | 112.5 | | 144.0[1] |
| Palma Seca | 99.0 | Tigre | ~149 |
| Piedras | 119.5 | | 84.0 |
| | 101.0 | Japonés | ~153 |
| | 98.5 | Yerbaniz | 146.5 |
| Jos | 91.5 | Venadito | 169.0 |
| Pichijumo | 141.5 | | 129.0 |
| | 89.5 | Pachón | 202.5 |
| | 75.5[1] | | |

[1]Fish occurrence uncertain.
[2]Fish never observed.

and at different elevations, we know that base level must vary between the two. So we shall attempt to demonstrate both latitudinal and longitudinal base level profiles in the Sierra de El Abra.

Only in the Los Sabinos area do we have data from localities appropriate to the determination of an east-west base level profile (Fig. 20). This owes to the occurrence of the Sótano de Soyate at a position intermediate between the Los Sabinos caves and the face of the Sierra. At the latitude of Soyate, then, we used three datum points to demonstrate base level: elevation of the Nacimiento del Río Choy, elevation of the lake in Soyate, and elevation of the deepest point in the Sótano del Arroyo. We have long thought that the lake in Soyate must lie near local base level because it is but 21 meters above the Nacimiento del Río Choy, and because the deepest point in the Sótano del Arroyo must be near local base level at this longitude inasmuch as it is only 28 meters above the Nacimiento del Río Choy and the deepest point lies in a tunnel that Fish (1974) believed would be seen to siphon shortly (if the problem of high $CO_2$ content could be overcome to permit exploration).

Fig. 20 shows that we have not used the absolute elevations for the Choy and Arroyo in projecting local base level. Instead we have used values for these two points adjusted to the Soyate latitude because the Sierra de El Abra is so narrow and because our three datum points do not lie at the same latitude. We obtained our adjusted figures (39.5 meters for the Choy rather than 34 meters and 60
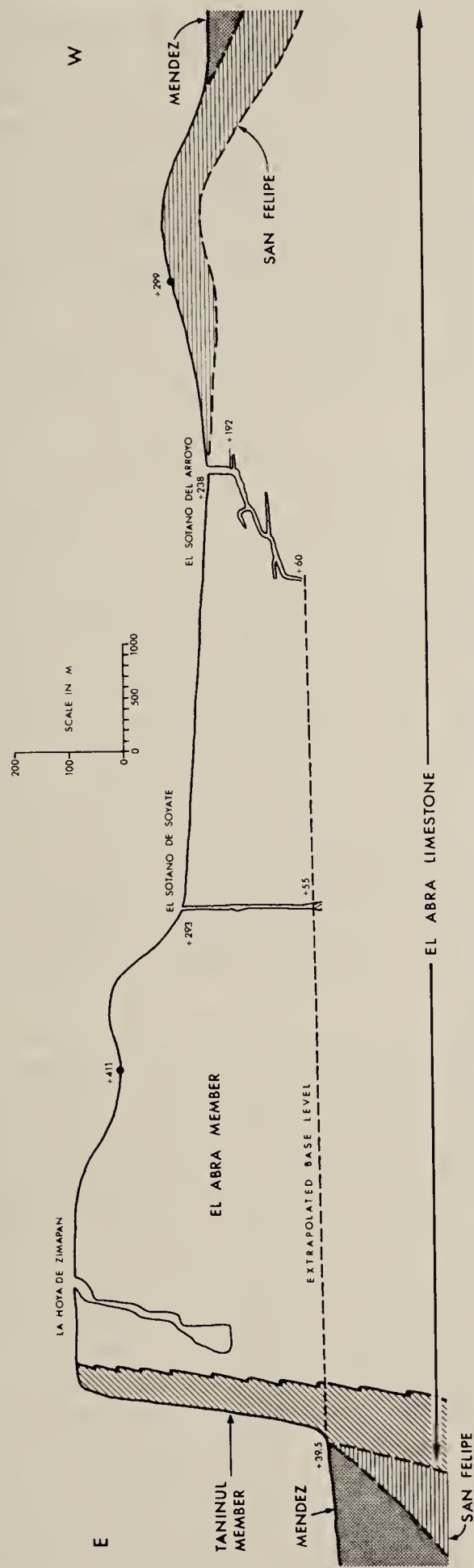
FIG. 20.—Diagrammatic cross-section of the Sierra de El Abra at approximately the latitude of the Sótano de Soyate. Vertical scale is exaggerated by a factor of five relative to horizontal scale. Shown are the typical formations of the area, Méndez and San Felipe in the coastal plain and Valle de Antiguo Morelos, and El Abra Limestone in the Sierra and adjacent Valle de Antiguo Morelos. Dashed line indicates approximate base level of groundwater in the El Abra Limestone as extrapolated from the illustrated points. See text for further discussion.

meters for Arroyo rather than 62 meters) by assuming a linear rise in the longitudinal base level profile between the nacimientos Choy and Mante. This manner of adjusting these two points is actually not entirely appropriate because we shall demonstrate that the longitudinal base level profile is anything but linear, but still the adjustments may be justified in that they lead to somewhat more accuracy than would use of absolute elevations of the three datum points. In reality, these adjustments (or others one might make using any other plausible method) make little difference anyway because there is little difference between the adjusted values and the absolute values. Any trio of figures, absolute or logically adjusted, come very close to plotting a straight line, and one of essentially the same slope as another. We therefore believe that our data demonstrate a nearly linear westward rise in base level profile (in the Los Sabinos area) of slightly more than 2 meters (2.2) per kilometer.

Determination of a longitudinal base level profile presents an altogether different problem. The Nacimiento del Río Choy lies at 34 meters and the Nacimiento del Río Mante at 80.5 meters, but our earlier discussion of subsurface waters in the Sierra de El Abra and Fig. 10 already indicate that the base level change between these two nacimientos is not linear inasmuch as there appears to exist an internal drainage divide. Here we shall attempt to demonstrate the longitudinal base level profile in the Sierra de El Abra using several datum points that we know, or believe, to be at or near local base level. These figures should reveal longitudinal base level including the internal drainage divide, if it exists. Importantly, these data provide a method of both indicating and locating the divide in a way entirely independent of the method we have used previously in suggesting the existence and location of such a divide. Fig. 21 illustrates our extrapolated longitudinal base level profile and, more closely than one could hope, also indicates a drainage divide at the same location as does Fig. 10, an illustration derived from independent data (ratios of nacimiento discharge and uptake area).

The base level profile in Fig. 21 was derived from eight datum points, the elevations of the nacimientos Choy and Mante and the elevations of the deepest points in six caves. The Choy and the Mante are obviously base level, and we have already given our justification for regarding the deep points in Soyate and Arroyo as at or near base level. Exploration in the Sótanos Tigre and Venadito has approached base level as evidenced by long, horizontal, muddy passageway. Actual base level in these two caves probably has not been reached quite yet. The deepest point in the Sótano de Japonés is probably near, but not quite at, local base level inasmuch as the deep point is a very long, horizontal passage. Base level probably has been reached in the Sótano de Yerbaniz as evidenced by the occurrence of three lakes that all siphon at the same elevation. Actually, five datum points suffice to indicate the general nature of the longitudinal base level profile, elevations of the two nacimientos and elevations of the deep points in Soyate, Arroyo, and Yerbaniz. Existence of a profile of this general shape is reinforced strongly by the other three datum points, elevations of the deep points in Tigre, Japonés, and Venadito. Especially important is the elevation of the
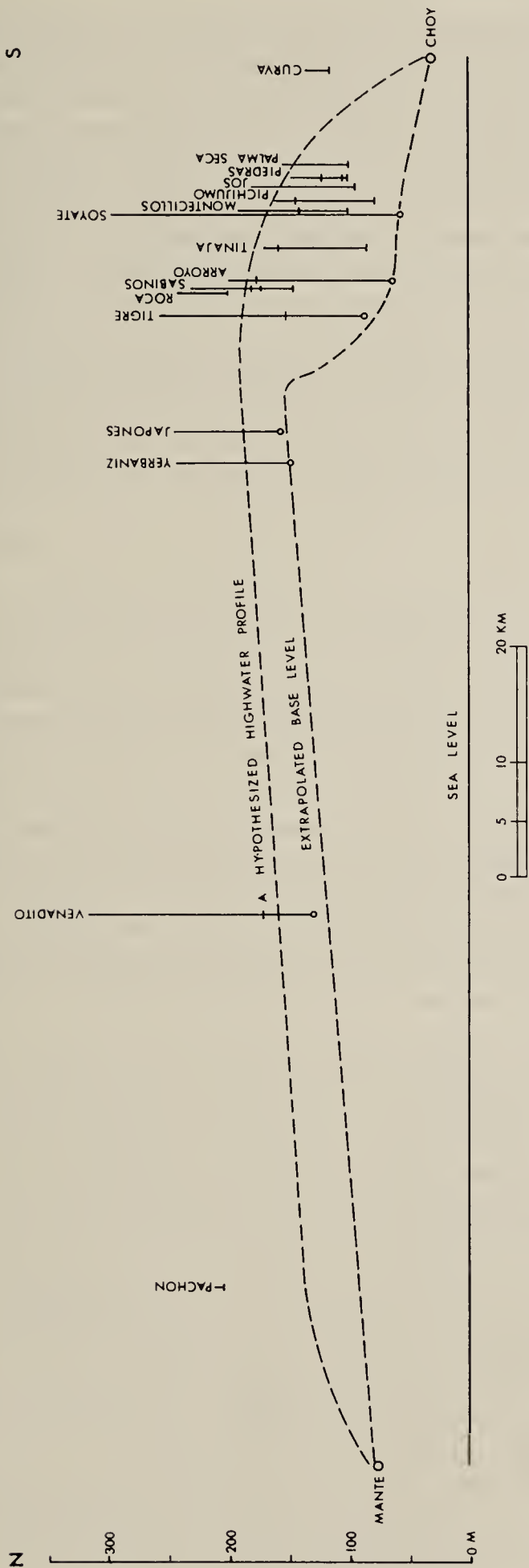
Fig. 21.—Longitudinal base level and high water profiles in the Sierra de El Abra. Vertical scale greatly exaggerated (about 100×). Points at, or near, base level are indicated by open circles; fish-inhabited pools by horizontal bars; and cave entrances by the letter **E**. The high point of the base level profile was taken from Fig. 10. See text for further discussion of this point and for the shape of the high water profile.

deepest point encountered in the Sótano de Venadito. Had this point been higher than the elevation of the lakes in Yerbaniz, obviously our projected profile would have been destroyed. But the deep point in Venadito is precisely where it should be if we have correctly demonstrated the base level profile. We should add here two further comments about Fig. 21. The vertical scale is exaggerated vastly (by about 100 ×) so that the shape of the base level profile is clearly evident. Also, the latitude of the highest point on the profile is taken from Fig. 10 and is thus the only nonindependent datum used in drawing the profile in Fig. 21. But had this datum not been used, the high point would then have been drawn near the deep point in the Sótano de Japonés, which would not have altered the shape of the profile but would only have shifted its suggested high point a very short distance to the north. Because we now have independently agreeing data, we are confident that an internal drainage divide occurs somewhere in that short distance intervening between the Los Sabinos cave cluster and the Yerbaniz cave cluster.

We may now turn our attention to the problem of vertical isolation of various cave waters. It should be clear by now that one cannot speculate as to the vertical isolation of a cave pool on the basis of its absolute elevation because, if for no other reason, local base level varies. But, unfortunately, a comparison of cave waters on the basis of their elevations above local base level cannot be used with confidence either. That the latter is true owes directly to the flow characteristics of the El Abra aquifer. We already have pointed out that heavy rainfall causes a high water rise in the El Abra Limestone, which then lowers as water is discharged through the resurgences on the east face of the Sierra, principally the nacimientos Choy and Mante. Of course, water rises in the limestone to a greater or lesser extent depending upon the amount of water uptake. But whether a high, moderate, or low rise, the shape of the high water profile should be reasonably constant as determined by the longitudinal base level profile and especially by the differential response of the nacimientos Choy and Mante as they discharge their waters.

We have demonstrated already that the Mante reaches its peak discharge much more quickly than does the Choy and that the Mante further diminishes from its peak much faster than does the Choy. As we have stated, this indicates a better integration of that part of the aquifer draining to the north than of that draining to the south. This profoundly affects the high water profile in the limestone. In Fig. 21 we have drawn a speculated high water profile. Although two datum points have been used to set the height of this line (high water marks observed in the sótanos Arroyo and Yerbaniz), they do not figure materially in our shaping of the line. The profile then is almost altogether hypothetical, its shape deduced from the response times of the Mante and Choy. Our argument for its shape is simply that there must be considerably more "pile-up" of water, or a steeper profile, toward the Choy than toward the Mante.

It is now evident that to consider the extent to which a cave pool may be vertically isolated one must look not to the absolute elevation of that pool nor to its height above local base level, but to its position relative to the height and shape

of high water profiles. In Fig. 21, we have indicated the positions of many fish-inhabited waters. One can now see the relationship between pool position and shape of the high water profile. Water reaching the height we have indicated by the profile, if we have interpreted the profile more or less correctly, would cause flooding by rising water of most of the fish-inhabited waters in the Los Sabinos area. Only the waters in the Sótano de la Roca and La Cueva de la Curva remain above this particular profile. But to the north, the waters in La Cueva de El Pachón lie far above this particular high water line even though they lie somewhat closer to local base level than do some waters in the Sótano del Arroyo and La Cueva de Los Sabinos. The waters of Pachón are thus the most isolated cave waters by far, and those of Curva are also well isolated (though not as much as those of Pachón as can be understood if one pictures high water three-dimensionally in the limestone). It must, therefore, require an exceptional water uptake to cause the flooding of Pachón. In fact, one is even led to wonder if the Pachón population arose independently when the cave was abandoned as a resurgence.

## DISTRIBUTION OF LOCAL EPIGEAN ASTYANAX

*Astyanax mexicanus* is well known to be a common and widespread characin, but some brief comments on its local distribution are appropriate because of the implications of this distribution on cave colonization and cave-fish evolution to be discussed.

Basically, our collection data show that *A. mexicanus* occurs in essentially all local epigean waters of a permanent nature as well as in temporary streambeds having a direct connection with a permanent stream (Fig. 5). The fishes are common in both of the major drainage systems, the Tamesí and the Pánuco, the tributaries of which ramify throughout the Huastecan Province.

As discussed elsewhere, *A. mexicanus* inhabits some waters that, during flooding, enter certain caves carrying fishes into the subterranean systems. With a single exception, however, fishes do not occur in any of those streams completely captured by an eyeless-characin cave. The exception is the Arroyo Yerbaniz, partly captured by the Sótano de Yerbaniz and completely captured by the downstream Sótano de Matapalma. Although we do not know where yet, somewhere in this relatively large drainage (about 16 square kilometers) there are permanent, fish-inhabited waters. *A. mexicanus* may be collected readily in the arroyo anytime rains fill it, and heavy flooding causes fishes to be swept into the capturing caves. The complete capture effected by the Sótano de Matapalma isolates the Arroyo Yerbaniz population of *A. mexicanus*.

Three other specific epigean *A. mexicanus* localities merit mention. These are cave localities, La Cueva de El Mante near the Río Tampaón, La Cueva del Rancho Viejo on the east face of the Sierra de El Abra near its southern end, and La Cueva Chica del Arroyo Seco on the east of the Sierra de El Abra near its midregion (Fig. 5).

It is curious that we have not collected cave fishes in La Cueva de El Mante because it lies near La Cueva Chica and Los Cuates, but the cave evidently con-

tains only epigean fishes. There is nothing further to suggest that this population has been long isolated. On the contrary, the cave is so near to the Río Tampaón that fish replacement probably occurs with some regularity.

On the east face of the Sierra de El Abra about four kilometers north of the Río Tampaón is a small, wet weather resurgence, the Nacimiento del Rancho Viejo. About 100 meters to the north of this and about 10 meters above the coastal plain is the entrance of La Cueva del Rancho Viejo. A pool, about 10 meters beneath the entrance, in the first room of the cave contained epigean *A. mexicanus*. Epigean *A. mexicanus* and cichlids (unidentified) were collected also in a small pool at the end of the cave (about 100 meters long) lying about 10 meters beneath the entrance. Because the pools in this cave are essentially at base level, it would seem that epigean fishes probably gain access to them through the nearby nacimiento whenever there is stream flooding on the coastal plain.

La Cueva Chica del Arroyo Seco, at about 22°31', opens on the east face of the Sierra de El Abra about 15 meters above the coastal plain. It appears to be a largely abandoned resurgence that now discharges only at times of high water rise in the El Abra Limestone. Beneath its entrance, the Arroyo Seco shortly joins the Río Santa Clara. Abandonment of this cave (as well as others along the east face of the range) as a more active resurgence has resulted from downcutting of the adjacent coastal plain. Within the cave, there are waters which, judging from the descent required to reach them, probably lie at the level of the coastal plain. We speculate that epigean fishes enter these waters through small fissures in the limestone whenever flooding carries water up the Arroyo Seco to the face of the Sierra.

Lastly, we recall the discovery by Valerio Sbordoni and Roberto Argano of two typical epigean *A. mexicanus* in an upper level passage in the Sótano de Pichijumo. We do not know the source of these fishes, but it is obviously important to discover it.

## Mixed Fish Populations

Epigean *Astyanax mexicanus* gain entry into some of the blind-fish caves where hybridization occurs, the extent of which depends on certain features of the particular cave. At least some hybridization occurs in the southernmost El Abra caves (La Cueva Chica, Los Cuates), the Micos caves (La Cueva del Río Subterráneo, La Cueva de Otates, and La Cueva del Lienzo), two of the Yerbaniz caves (El Sótano de Yerbaniz, El Sótano de Matapalma), and the Chamal caves (Bee Cave, El Sótano de Caballo Moro).

The celebrated cave in which hybridization occurs is La Cueva Chica, the only such cave known prior to the beginning of our studies in the area. The complete intergradation of cave and surface *Astyanax* here was discovered by the New York Aquarium expedition in 1940 led by Breder (Bridges, 1940; Breder, 1942). Since that time, most researchers have presumed this gradient to be the result of hybridization between a previously evolved cave form and the surface form, although some (for example, Kosswig, 1965) have suggested the possibility that this population only recently has started to evolve cave adaptations.

The hybrid swarm in La Cueva Chica is extensive and is likely a long-term phenomenon that will persist as long as present physical and biological factors prevail in the cave. Combining to cause and maintain this hybridization are a source of epigean fishes, a source of cave fishes, and a large energy input into the system. As we have argued earlier, surface fishes probably enter the Cueva Chica system whenever the Río Tampaón floods a group of tinajas located somewhat less than 1000 meters south of the last accessible pool (Pool IV) in the cave. Any rise of the Río Tampaón of over three meters above normal dry season flow would bring water to the tinajas. Continual cave fish input into the system probably is assured by way of the lower pools, which no doubt communicate with a more extensive, base level aquifer.

Continual input of surface and cave fishes into a system do not alone insure extensive hybridization as occurs in La Cueva Chica. Examination of some other mixed fish caves in the region demonstrate this point. The peculiar feature of La Cueva Chica that promotes the hybridization and maintenance of a large hybrid swarm is the substantial energy input into the system deriving from two large bat roosts located immediately above the fish-bearing waters. Although bats occur in all of the fish caves, there are no other mixed fish caves in which large bat colonies exist directly over the fish pools. Especially in contrast to other mixed fish caves, it is apparent that in La Cueva Chica the abundant food supply reduces the selective advantages of the cave forms to a point where the surface forms can survive sufficiently long to interbreed with the cave forms. In all probability, the cave form-to-hybrid-to-surface form ratio shifts from time to time as both cave fish and surface fish input varies.

As has already been pointed out by Bridges (1940) and Breder (1942), there is a greater abundance of cave forms at the front of the cave. Two phenomena cooperate to produce the gradient observable through the length of the cave, one physical, the other biological. At normal water conditions, surface fishes, which enter the end of the cave from the Río Tampaón, and cave fishes, which enter from the underlying aquifer, are prevented from moving to the more anterior pools because the pools step upward (the differential between Pool IV and Pools I and II being 14 meters). However, La Cueva Chica at times floods (how often we do not know) making continuous the otherwise semi-isolated pools. Such a condition has occurred at least once during our studies in the area (Harmon, personal communication). During such a time, fishes in the end of the cave can penetrate the system as far as Pools I and II. But in these waters, there is not the energy input that occurs in the waters beneath the bat roosts, and, moreover, water flow is carrying food materials originating at the bat roosts downstream and away from the anterior pools. Any surface fishes progressing to the anterior parts of the system evidently cannot compete well with the cave forms under the prevailing energy conditions and thus are eliminated in time, a situation directly comparable to that in the Sótano de Yerbaniz discussed following.

Mixed fish populations also occur in nearby Los Cuates (Este and Oeste). We do not have sufficient collections of fishes yet from Los Cuates to comment on the relative abundance of cave forms, hybrids, and surface forms. Suffice to say, based on little study of Los Cuates, that it is reasonable to assume that surface

fishes enter Cuates in much the same way as they enter La Cueva Chica and that at least some hybridization occurs.

El Sótano de Yerbaniz supports large numbers of cave fishes and also receives an enormous input of surface forms. In fact, there are far more cave fishes here than in La Cueva Chica and evidently a far greater surface fish input. Yet in this cave there is very limited hybridization, so limited, in fact, that several trips were made into the cave before any obvious hybrids were ever encountered, and then only two specimens. One acquainted with the hybrid swarm in La Cueva Chica, or with the literature on it, should at first find the situation in the Sótano de Yerbaniz surprising, particularly because there seems to be here every quantitative opportunity for hybridization. Cave fishes are especially abundant. In the largest lake in the cave, William R. Elliott used a two-census, mark-recapture technique to estimate the total number of fishes to be 8671 (with wide 95 per cent confidence limits, however, of 1810 to 15,534). And we know from personal observations that great numbers of surface forms enter the cave. As we have discussed, the Arroyo Yerbaniz is the largest surface drainage to be captured by a fish cave. This drainage is sufficiently large (draining about 16 square kilometers) to support somewhere in its reaches a permanent and isolated (by virtue of complete downstream capture by the Sótano de Matapalma) population of epigean *A. mexicanus.* Flooding of the Arroyo Yerbaniz brings hundreds (personal observations), if not thousands, of surface fishes into the cave. Why then is there no appreciable hybridization? Two phenomena probably combine to account for this. First, the cave forms are especially abundant. Second, energy input into this cave is relatively low (compared to the situation in La Cueva Chica with its bat roosts above the fish-bearing waters), being derived mostly from seasonal influx of flood detritus. Under such conditions, the cave-trapped epigean fishes do not thrive. Our collections indicate rather the contrary. As the dry season progresses, entrapped surface fishes develop signs of starvation and their numbers decline rapidly. In short, in the Sótano de Yerbaniz epigean fishes probably serve more as food for the agressive cave forms than as mates.

We also have collected hybrid fishes in the downstream Sótano de Matapalma, the cave which finally completes capture of the Arroyo Yerbaniz. We have not studied this great cave system as thoroughly as some of the others and are thus limited to a few comments about its mixed fish population. It is likely that surface fish input is not as extensive here as in the Sótano de Yerbaniz because it would take a sizable flooding of the Arroyo Yerbaniz to cause water to move partly uncaptured across the entrance of the Sótano de Yerbaniz. But this can occur, as William H. Russell has seen. Under such conditions, surface fishes must surely enter the Sótano de Matapalma. In light of study of the Sótano de Yerbaniz it is curious that we have found a greater percentage of hybrids in the Sótano de Matapalma. Perhaps in the latter cave, flooding causes cave and surface fishes to be trapped together in small pools in disproportionate numbers favorable to some limited interbreeding. Studies of the remote portions of the Sótano de Matapalma (which we have not done yet) should assist in explaining the occurrence of some hybrids in this cave because the main fish-bearing waters are located here.

Surface fishes also are introduced into the three fish caves located near Micos, San Luis Potosí. We have not thoroughly examined the fish populations in these caves as yet, but one of them (La Cueva del Río Subterráneo) has been reported on by Wilkens and Burns (1972). These authors believed that the fishes in this cave represent a population of cave forms in "*statu nascendi.*" They based this judgement on observing that the eye vestiges of these fishes are larger and more variable than those of the Pachón and Sabinos fishes but smaller and less variable than those of the fishes comprising the hybrid swarm in La Cueva Chica. They also stated that "melanin pigment seems to be almost unafflicted [*sic*] by regressive mutations." There are certainly no *a priori* reasons to think that somewhere there may not be an established population in the earlier stages of cave adaptation, but we think it dangerous to regard this population as such because of the epigean fish input into the cave. It seems just as likely—if not more so—to us that the Micos fishes are simply other populations where hybridization is occurring between cave and surface forms, but forms derived from gene pools new to blind-fish researchers.

The epigean fishes in the Micos caves do not represent a well-established population of surface forms but rather are the result of recent introductions, as evidenced from the studies of Wilken and Burns (1972). Almost all of the surface fishes they collected in the cave showed signs of malnutrition, recalling our observations of epigean fishes trapped in the Sótano de Yerbaniz. Also, they recovered fish remains (unidentifiable) from the stomachs of some cave fishes but no such remains from the stomachs of any entrapped epigean fishes. In spite of the fact that the remains were unidentifiable, this would seem to support our contention that under conditions of relatively low energy input (and in total darkness) entrapped epigean forms are at such a pronounced selective disadvantage that in time they themselves become food (even though some degree of interbreeding may occur in the meanwhile).

The precise source of the epigean *Astyanax* entering the Micos caves is presently unknown, but the fishes probably enter the caves' main entrances (unlike the situation at La Cueva Chica) because two of them have arroyos leading to the entrances (La Cueva del Río Subterráneo and La Cueva de Otates), and the other (La Cueva del Lienzo) is evidently subject to flooding as we have discussed previously. In all likelihood, the surface fishes are derived from smaller tributaries of the Río Santa María to the south, which is a part of the Río Pánuco System.

The remaining mixed fish caves are those two in the southern foothills of the Sierra de Guatemala in the vicinity of Chamal, Tamaulipas. Although we have not studied the Sótano de Caballo Moro in detail yet, it appears from limited collections and observations that hybridization here is moderate, much more than that occurring at the Sótano de Yerbaniz, but less than that occurring at La Cueva Chica. Energy input would appear to be quite minimal in this cave because there are no large bat colonies, and the cave does not even flood periodically as does the Sótano de Yerbaniz. Based on this alone, it would appear that hybridization here should be nil or that we have not correctly deduced the reasons for the disparity in hybridization between the Sótano de Yerbaniz and La Cueva Chica.

There is, however, a peculiar feature of the Sótano de Caballo Moro that distinguishes it from the other mixed fish caves. The entrance pit of this cave is constructed so that even though the cave is deep, the large lake containing the fishes is lighted dimly during a part of the day. Although epigean *A. mexicanus* are not obligate visual feeders, there can be little question that their feeding efficiency is improved by the presence of light. We suggest, therefore, that the dim lighting in the Sótano de Caballo Moro reduces the selective disadvantage that otherwise would be imposed on the epigean fishes permitting them to survive—perhaps for long periods—but at least long enough to interbreed considerably with the cave forms.

It is disturbing to us that we do not know yet the site of epigean fish input into the Sótano de Caballo Moro. It is not the cave entrance because it does not capture a stream, nor is it a nearby cave that does capture a stream because this stream is intermittent and is isolated from fish-bearing waters. During the wet season, tributaries of the Río Boquillas fill with water and fishes, and these reach to the vicinity of the cave. So somewhere in the area, which we still know very poorly because of the difficulties of moving about in the region, these tributaries must be intercepted by solution features or must at times overflow into such features.

A few hybrids have appeared in the small collections of fishes we have made in nearby Bee Cave. We are presently at a loss to attempt a plausible explanation for the occurrence of these hybrids other than to state that the "pool" in Bee Cave is obviously but a small point of access to a much larger, inaccessible aquifer, which is perhaps associated with the waters of the Sótano de Caballo Moro. The entire Chamal area is puzzling and in need of further study.

If nothing else, the preceding discussion of the mixed fish caves points up the existence of excellent, "made-to-order" conditions making it possible to study in nature the selective value conferred by "regressive" evolution.

### Morphometric Comparisons of Astyanax Populations

Through the use of multivariate statistical procedures we have tested for discreteness of several *Astyanax* populations. These first comparisons were not intended to be exhaustive but were made primarily to give us some initial appreciation of the extent of population divergence, if any, among the cave fishes and among surface fishes as well. To this end, we compared among themselves populations from the following eight caves: La Cueva de la Curva, El Sótano de Palma Seca, El Sótano de Jos, El Sotanito de Montecillos, El Sótano de la Tinaja, El Sótano del Arroyo, El Sótano del Tigre, and La Cueva de El Pachón. This group was selected largely because it includes fishes from several caves in proximity in the Los Sabinos area, another (La Cueva de la Curva) removed a short distance from the Los Sabinos cluster, and another (La Cueva de El Pachón) removed a great distance from all of the others. Moreover, some of the Los Sabinos area populations were from waters at approximately the same elevation in the limestone whereas the others were from waters of different elevations. The waters of La Cueva de El Pachón are furthermore the most vertically isolated (re-

lative to shape of the internal high water profile) of any of the fish-inhabited waters of the Sierra de El Abra as we have demonstrated (Fig. 21). The waters of La Cueva de la Curva are perched also. Three populations of surface fishes were compared among themselves. These included one from the southern portion of the Valle de Antiguo Morelos where drainage is ultimately into the Río Pánuco System, one from near the Nacimiento del Río Mante where drainage is into the Río Tamesí System, and the last, a highly isolated one, from the Arroyo Yerbaniz.

Morphometric characters compared included measurements of standard length, body depth, head depth, head width, gape, mandibular length, maxillary length, caudal peduncle length and depth, anal fin length, distance to origin of dorsal fin, and counts of gill rakers on upper and lower limbs of the first gill arch, thoracic and caudal vertebrae, and rays of all fins (limited to left side only for the paired fins). The nature of fragmentation and fusion of the infraorbital bones also was quantified and incorporated into these comparisons. Six such bones form each orbit ventrally and posteriorly, and in the cave fishes they have begun to regress accompanying regression of the eyes. If indeed the eyeless-characin populations are discrete, it would be logical to suspect that infraorbital bone regression would not proceed in the same manner in each population. Alvarez (1946), in fact, used differences in the morphology of these bones to assist in separating the three "species" known at that time. We therefore quantified fragmentation of each infraorbital (0 if entire, to $n$ pieces) and fusion of adjacent infraorbitals ($1 + 2$, $4 + 5$, $5 + 6$, and $4 + 5 + 6$ being the only types of fusions observed to date). Anomalies rarely occur among these bones in surface fishes, but the fact that they at least occasionally exist has permitted limited use of infraorbital morphology in surface fish comparisons. Altogether, about 50 characters were used in cave fish comparisons and about 40 in the surface fish comparisons, although in the latter the analyses were programmed to delete variables making little contribution to overall variation.

We made our original fish comparisons with the intention of working with sample sizes of about 20 to 25 individuals irrespective of sex. Even though one acquainted with these fishes usually can identify the sexes superficially, there is little obvious sexual dimorphism. In fact, absolute decisions as to sex must finally lie in examination of the gonads or examination of the anterior anal fin rays, which in the male bear small spines (the latter is not invariably diagnostic, however). Our first analyses tested for homogeneity of data between the sexes. In all populations, the two sexes proved to be highly dimorphic, and, interestingly, the characters contributing to dimorphism were different among all populations. In each of the eight cave populations, the single characters contributing the most to discrimination were, respectively, maxillary length, total number of entire infraorbital bones, number of gill rakers on the lower limb, number of fragments of right infraorbital bone 1, number of fragments of left infraorbital bone 1, number of fragments of right infraorbital bone 3, head width, and number of pectoral fin rays. The same was true for the three surface populations tested, and the single most discriminating characters were, respectively, number of pectoral fin rays,

TABLE 2.—*Posterior probability matrices summarizing the numbers of fishes of one population that "misclassify" into another population.*

| | Montecillos | Arroyo | Curva | Tigre | Jos | Palma Seca | Pachón | Tinaja |
|---|---|---|---|---|---|---|---|---|
| *Cave females (48 variables)* | | | | | | | | |
| Montecillos | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Arroyo | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| Curva | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 |
| Tigre | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 |
| Jos | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 |
| Palma Seca | 0 | 0 | 0 | 0 | 0 | 17 | 0 | 0 |
| Pachón | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 0 |
| Tinaja | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 |
| *Cave males (48 variables)* | | | | | | | | |
| Montecillos | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Arroyo | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 |
| Curva | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| Tigre | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 |
| Jos | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 |
| Palma Seca | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 |
| Pachón | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 |
| Tinaja | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |

| | Tamesí drainage | Arroyo Yerbaniz | Pánuco drainage |
|---|---|---|---|
| *Surface females (14 variables)* | | | |
| Tamesí drainage | 13 | 0 | 0 |
| Arroyo Yerbaniz | 0 | 10 | 0 |
| Pánuco drainage | 0 | 0 | 15 |
| *Surface males (10 variables)* | | | |
| Tamesí drainage | 12 | 0 | 0 |
| Arroyo Yerbaniz | 0 | 11 | 0 |
| Pánuco drainage | 0 | 0 | 8 |

number of thoracic vertebrae, and head length. Curiously, only one character, number of pectoral fin rays, served as the most important discriminator in more than one population. Among all of the populations there were so many characters reflecting (to a greater or lesser degree) sexual dimorphism that it was not possible to elimate these to consider then the remaining characters in samples of pooled sexes. Instead it was necessary to analyze the sexes separately. Before continuing, we should note that these preceding tests for intersex homogeneity already denote a great deal about discreteness of the populations.

We compared the preceding populations using a program (BMDO7M) of step-wise discriminate analysis incorporating canonical analysis (Seal, 1964) combined with posterior probability classification procedures (Cooley and Lohnes,

1971). Because in the later analyses the sexes were separated, sample sizes were not as large as would be hoped for. Nevertheless, each population proved to be discrete based upon analysis of data for both males and females. This discreteness is seen clearly in the posterior probability classification matrices (Table 2), which summarize the numbers of fishes belonging to one population which "misclassify" into another population. Population discreteness is obvious because in the summations in Table 2 there is not a single misclassification.

Our preliminary data have not been examined in statistical detail to determine degree of phenetic similarity and dissimilarity among the populations, but the preceding analyses suggest that the populations of La Cueva de la Curva and La Cueva de El Pachón (of the eight compared) are the most distinct. This is hardly surprising considering the vertical isolation of their waters.

## COMMENTS ON EVOLUTIONARY HISTORY

There appears often in the literature on the cavernicolous *Astyanax* the idea that surface colonizers populated the subterranean waters of the region from the Río Tampaón by way of its connection with La Cueva Chica and that the fishes then moved slowly northward through subterranean routes to populate the more northern caves. This became such a popular and widely accepted idea that for all practical purposes it became converted into fact by mere repetition. Leading, in large part, to this idea was the fact that the extensive local occurrence of epigean *A. mexicanus* in the region had been ignored or at least obscured.

Interestingly enough, the earliest comments on local *Astyanax* distribution were good statements of fact, and our data (Fig. 5) are merely supportive. Breder, as quoted by Bridges (1940), wrote: "It's a common fish in all the local surface streams." Osorio Tafall (1943) stated that *A. mexicanus* is a "pececillo abundante en las aguas de la cuenca hidrográfica del Pánuco." Alvarez (1946) wrote: "*Astyanax fasciatus mexicanus*, pez epigeo, muy abundante en toda la región." In reality, there are no better ways in which to summarize local *Astyanax* distribution.

The first expression of the previously stated hypothesis was by Breder and Rasquin (1947:343) who stated: "We may assume for purposes of discussion that river fish entered La Cueva Chica, the while undergoing optical and pigmentary reduction, and worked on up the valley [the Valle de Antiguo Morelos] underground." Although this hypothesis is the one that came to be generally accepted by Breder, his associates, and others, Breder and Rasquin, in the same paper (1947), put forward two alternative hypotheses (pp. 343, 344). They stated: "Another way in which one might suppose these caves became populated is to assume that before the waters sank below ground the now dry river bed [the collective drainage of the Valle de Antiguo Morelos] was a permanent stream well populated with the rather ubiquitous river form and that as the caves were formed various local populations sank into the ground in substantially their present location, the survivors giving rise independently to the present blind populations." Then, too, they stated: "It might even be presumed that the present underground populations have arisen from a successful establishment of an underground popu-

lation far up the valley, perhaps near Cueva del Pachon. Then these would be conceived of as gradually working down stream and finally hybridizing with fresh entrants from the river in La Cueva Chica."

It is curious, perhaps only in hindsight, that it was the first of these hypotheses that gained general acceptance, especially because the other two incorporate points that now seem more plausible. Prior to the Breder and Rasquin paper of 1947, Breder himself (1943a, b) had made statements in contradiction to the later hypothesis he came to hold. He stated (1943a) in response to apparent changes in the ratio of eyed and eyeless fishes in La Cueva Chica that "the most reasonable explanation [for the increase in eyed forms] would thus seem to be that some subterranean passage opened very recently which permitted the river fish to gain an easy access to the cave." He also stated (1943b) that "this kind of evolution [of the cave forms] could have conceivably taken place many times and it may well be that these two blind populations [La Cueva Chica and La Cueva de Los Sabinos—the only two known eyeless-characin caves at the time of this writing] are independent developments from the same basic stock and differ only in the accidental assortment of genotypes that gave rise to them."

It is not altogether clear-cut why the first Breder and Rasquin hypothesis was the one they came to accept nor why it generally came to be regarded as dictum. Two statements in the Breder and Rasquin paper (1947) were perhaps influential in causing acceptance of the first hypothesis, although they were not put forward in direct support of it. Early in their paper (p. 325) these authors stated: "The underground drainage of this dry valley [the Valle de Antiguo Morelos] is into the Río Tampaón." Nowhere is there any mention of the precise point where the authors believed this underground drainage enters the Río Tampaón, but the reader is left to assume that it is by way of the Cueva Chica-Río Tampaón connection so frequently mentioned in the literature to this time. Aside from the fact that we already have pointed out that this valley is neither "dry" nor is its underground drainage exclusively into the Río Tampaón (and, moreover, that exiting La Cueva Chica into the Río Tampaón is inconsequential), the statement is inadvertently misleading because it implies lack of surface fishes elsewhere in the area and thus lack of potential colonizing sites other than La Cueva Chica. In the same paper (Breder and Rasquin, 1947:325) they further stated that "the various cave openings are arranged in the following sequence [Chica, Tinaja, Arroyo, Sabinos, Pachón] from the nearest point on the Río Tampaon, which is the closest body of water and which is well populated with the eyed river form." Here again are implications similar to those of the previous statement.

Breder and Rasquin (1947) did counter somewhat their latter two hypotheses (and perhaps by default accepted the first) by stating these objections: "One is that there is a progressive reduction in optical equipment up the valley. Another is that hybrids between Chica and Sabinos fish are intermediate in both morphology and behavior, indicating that the two stocks are related. Such would certainly not be expected from two separate populations that have undergone morphological and behavioristically parallel changes associated with similar environments. Alvarez (1946), in comparing Chica, Sabinos, and Pachon fish taxonomically,

shows that fin ray counts and various body proportions form overlapping series as one passes up the valley through these three caves [Chica, Sabinos, Pachón], another item that agrees with the supposition that the fish worked their way up the valley under ground and one that strongly militates against the possibility of their having worked their way *down* the valley." Certainly when any type of study compares the fishes of the surface-Chica-Sabinos (or other such cave as the latter) series as has often been done, a progression toward some extreme (in reductions, for example) should be expected because there is extensive input of epigean fish genes into La Cueva Chica but not into La Cueva de Los Sabinos. Unfortunately, the statement that there is "progressive reduction in eye equipment up the valley" included by implication La Cueva de El Pachón. But the eyes of the Pachón fishes had not been studied at that time. Several years later, Şadoğlu (1957), working in Breder's laboratory, crossed Chica fishes, Sabinos fishes, and Pachón fishes with epigean fishes and measured eye diameters of the F1 hybrids. She stated that the mean diameter was progressively smaller moving from the Chica crosses to those of Sabinos to those of Pachón. She stated (p. 435): "This fact favours the assumption that the number of deleterious genes influencing eye size is higher in the population which is the most remote from the overground river [the Río Tampaón]." More recently, however, Wilkens (1970*a*, 1971) in detailed studies has provided convincing evidence that the eyes of Sabinos and Pachón fishes "exhibit practically no differences." Further studies may very well demonstrate that Pachón fishes do, in fact, show some degree more regression than others (in the series presently in question) as Alvarez' study (1946) of the infraorbital bones suggests. This would not be surprising at all, however, because the Pachón fishes are isolated altitudinally, a factor unrelated to horizontal distance from the Río Tampaón or any other surface waters.

In any event, from the time of the 1947 Breder and Rasquin paper there was general acceptance, perhaps insensible acceptance, of the idea of colonization from the Río Tampaón via La Cueva Chica, northward underground dispersal, and increased rgression with greater removal from "the river." For all practical purposes, time converted into "fact" a suggestion originally made "for purposes of discussion only." Literature examples of this are abundant and include the following examples: Dearolf (1956:210): "They are derived from a nearby river form and worked their way up the river valley underground in caves to develop independent but parallel blind fish populations." Cahn (1958:104): "This increased stability of the eye size in the fish from the two caves farthest from the river may indicate that some gene exchange between *Astyanax* and Chica populations may have been taking place, wheras the other caves were too far away from the river for this to occur." Franck (1964:96) wrote that "*Astyanax mexicanus*, der im Río Tampaón unweit der Höhle lebt. In benachbarten Höhlen wurder später andere Populationen ahnlicher Höhlenfische gefunden. In der am weitesten vom Río Tampaón entfernten Pachonhöhle lebt ein Characinide dessen Augen und Pigmente am stärksten reduziert sind." Şadoğlu (1967:541): "This cave fish lives in Cueva del Pachon which is the most remote cave being 54.5 miles from the Río Tampaón where the ancestral eyed, pigmented river fish, *Astyanax mexicanus* (Filippi), lives."

Had there been any appreciable early field studies by students of these cave fishes, the thinking regarding their colonization and evolution would not have become so rigid. Considering the amount of research devoted to these fishes by so many people since the time of their discovery, it is difficult to believe that the only intensive field work prior to ours, begun in 1968, was that of the Breder team in 1940, which was confined to La Cueva Chica and to the immediate vicinity of El Pujal. Of course, various people have collected these cave fishes through the years, but their efforts were directed at little else and were confined to the original five caves discovered, and especially to La Cueva Chica, La Cueva de Los Sabinos, and La Cueva de El Pachón.

Our studies of these fishes, their environments, and the general region of their distribution naturally lead us to suggest some answers to the questions posed regarding their colonization and evolution. The logical first question is: Should any credence be placed in the hypothesis that surface colonizers populated the subterranean waters of the region from the Río Tamapón by way of its connection with La Cueva Chica? The answer is no. This communication is recent, and the current influx of epigean *A. mexicanus* into the cave is of little consequence aside from the fact that it has led to considerable local interbreeding with an already evolved cave form (and to confusion in the literature). Several of our previous discussions (on geology and surface and subsurface waters) support this contention well.

Did the cave-adapted *Astyanax* arise through single or multiple colonization of the subterranean waters by epigean *A. mexicanus*? The existence of so many, and such widely scattered, cave localities seems at first to recommend the idea of multiple colonization, but to argue this idea on the basis of distribution alone is dangerous. It is possible that all of the present cave fish populations have been derived from a single successful invasion. That this is conceivable owes to the fact that the cavernous limestones inhabited by the fishes are continuous. A single colonization hypothesis would, however, call for extensive and circuitous movements underground, both lateral and vertical, to establish populations in some of the caves, those at Micos, for example. And, too, our studies of population discreteness suggest that even though water moves extensively and rapidly through El Abra Limestone, the fishes remain somewhat localized. Also, even though the cavernous limestones are continuous, our hydrological data demonstrate the existence of a subterranean drainage divide in the limestone of the Sierra de El Abra, and probably other such drainage divides exist because it is likely that the waters in the system accessible in the Micos caves and the waters accessible in the Gómez Farías caves do not resurge from any of the nacimientos of the Sierra de El Abra. Even though it is impossible to speculate on the extent to which subterranean drainage divides may isolate the cave fishes, they surely at least impede movement across them. The preceding, together with the fact that there are so many potential colonization sites, seems to make more plausible a multiple colonization hypothesis.

How many potential colonization sites exist? We emphasize that we are asking about possible sites of invasion, not about the number of successful colonizations

that might have occurred. Suggestions relative to this latter problem will have to await comprehensive comparative studies of the fish populations themselves. But we can state that there exist many potential colonization sites, and in all probability a large number of actual invasions have been made. There is no reason to assume that subterranean invasions by epigean *A. mexicanus* have not been going on for a protracted period in the past just as they still are today. It should be recalled that even now we know of several specific points of invasion, the communication between La Cueva Chica and the Río Tampaón and the entrances of the sótanos Yerbaniz and Matapalma and two Micos caves. Considering this large number of present invasion sites, it would seem reasonable at first to suggest that invasion by epigean *A. mexicanus* probably occurred at most of those caves that now capture a surface drainage. But this would assume that *A. mexicanus* has inhabited these drainages since the time that erosion removed sufficient overburden to expose the cavernous limestones, thus making capture possible. It is likely that some stream capturing began before *A. mexicanus* had populated epigean waters this far north in México. There are two indicators of this. First, because uplift of the area occurred in early Tertiary and because overlying sediments were thin, some cavernous limestone surely was exposed by mid-Tertiary time. Second, Myers (1966) pointed out that in all likelihood the primarily freshwater characins, of southern origin, did not gain access to Middle America until the North and South American land masses were completely united by closure of the Panamanian-Colombian sea barrier at, or near, the end of Tertiary time. *Astyanax mexicanus* has been the most successful characin in northward dispersal, but if it did not occur in Middle America until relatively recently, then it probably did not reach northern México until sometime in the Pleistocene. Wilkens (1971) also has used the Myers (1966) paper to argue that the hypogean populations of *A. mexicanus* were not established until sometime in the Pleistocene. It is likewise our contention that cave fish evolution certainly began no earlier than Pleistocene and probably not until the latter part of the Pleistocene or even later. Further supporting this is the fact that the cave and surface forms remain completely interfertile and the genic similarities of cave and surface forms demonstrated by Avise and Selander (1972). It is likely that by the time *A. mexicanus* arrived in the Huastecan Province, stream capturing was already in progress with some surface drainages having been isolated completely from noncaptured drainages and thus made inaccessible to epigean fishes. So, older captures were probably not sites of *A. mexicanus* invasion, but others, of unknown but large number, probably were invaded. It should be pointed out that there are doubtless many other potential invasion sites than those currently known to us as examination of detailed topographic maps, especially those of the area west of the Sierra de Colmena, suggest. Lastly, we point out that resurgences, past and present, are potential colonization sites. A functioning, base level resurgence is probably of little immediate consequence as a colonization site because epigean *A. mexicanus* probably can penetrate the subterranean system for only a short distance before vertical conduits in the system limit their movement. But during the past, as uplift or removal of materials adjacent to the cavernous limestones has

occurred, resurgences have been abandoned as their waters have sought lower base levels. Many such abandoned resurgences exist, particularly along the east face of the Sierra de El Abra. During the process of abandonment, epigean fishes could become entrapped and, if successfully established, could then move into lower, integrating systems. In summary, it would seem apparent that epigean *A. mexicanus* has invaded the subterranean waters of the El Abra Limestone at many points in time and space, but, again, it is impossible to speculate presently on the number of successful invasions.

How were invading epigean *A. mexicanus* isolated underground? The answer is obvious, stream capture and resurgence abandonment. The situation at the Sótano de Yerbaniz illustrates the former. Here epigean fishes living in the Arroyo Yerbaniz enter the cave with flood waters. In time, this arroyo will deepen sufficiently through erosion such that the resulting gradient will not permit maintenance of permanent waters. That this is the fate of the Arroyo Yerbaniz can be seen by examining other arroyos such as those captured by the sótanos Venadito, Tigre, and Arroyo. Such a capture therefore provides not only for introduction of potential colonizers but eventually eliminates continuing invasion, which would prevent, or greatly retard, adaptation because of swamping. La Cueva Chica del Arroyo Seco illustrates well how resurgence abandonment could result in isolation because continued downcutting of the adjacent coastal plain could cause its waters to become vertically separated from nearby surface waters.

Have the cave fishes dispersed through subterranean routes? The answer is yes, almost certainly. In spite of the fact that we have used several arguments to demonstrate that multiple colonization by the surface ancestor is a plausible hypothesis, no one would presume to suggest that all, or even most, of the cave localities represent an independent colonization. Although a multiple colonization hypothesis remains plausible, most present cave fish populations probably arose through subterranean dispersal. But these two ideas are not at all contradictory. Despite our demonstration of discreteness of several cave fish populations that indicates their local confinement, it is probable that subterranean water movements, especially violent ones, have carried, and are still carrying, fishes into new habitats. Such dispersal could at the same time be uncommon but still result in population of most local subterranean waters. Surely subterranean dispersal has resulted in all of those blind-fish populations in the Los Sabinos area. And the same thing surely can be said also for those populations in the Pujal, the Micos, the Chamal, and Gómez Farías areas. But what can be said about those individual, "isolated" cave localities? Very little except that some are perhaps isolated only in the sense that we have not yet found nearby, or intermediate, caves reaching water.

If these cave fishes inhabit waters in continuous, highly cavernous limestones, can any of them then be geographically isolated? The answer seems to be relative, some are more isolated than others although perhaps none is absolutely isolated. We have demonstrated the existence of an internal drainage divide in the Sierra de El Abra, and this divide should be at least a partial isolator. A more obvious isolator, however, is the vertical separation of fish-inhabited waters. As we have

detailed, many blind-fish populations are removed vertically from local base levels and at distances varying up to about 150 meters. But we have shown also that it is not this distance so much that is critical in isolation but the position of a cave pool relative to the shape and height of high water profiles within the limestone. Thus, the highest fish pool in the Sierra de El Abra, that in the Sótano de la Roca, is more susceptible to flooding from rising water than is La Cueva de El Pachón even though the water in Roca is about 28 meters higher above local base level than the Pachón waters. Even so, it is logical that the higher a pool is perched in the limestone the less often it will be flooded by rising water than a lower pool at the same latitude. Because of the shape of the high water profile toward the Nacimiento del Río Choy, it is likely that almost all of the fish pools in that region, excepting perhaps that in La Cueva de la Curva, flood with sufficient regularity to prevent marked population divergence. Flooding of high pools in caves near the Nacimiento del Río Mante in the north, however, probably occurs with much less frequency because of the shape and height of the high water profiles toward that nacimiento. Perched cave fish populations near the Nacimiento de Río Mante (which we presently know to exist only in La Cueva de El Pachón) probably have undergone more divergence than most of those populations in more southern areas.

Our studies to date on the eyeless characins have led to a much better understanding of them, but, even more importantly, they have led to the defining of many specific problems the solutions to which will tell us even more about the evolutionary history of these interesting animals.

and William Rhodes, for their long-time companionship and help in the field, and to William Atchley for assistance in the statistical analyses.

Many persons have assisted us, both directly and indirectly, in our blind-fish studies through being associated with various field and laboratory aspects of the work, including search for caves, exploration of caves, survey of caves, fish collecting, altitude determinations, and morphometric and skeletal study of fishes. We owe our appreciation to John George, John Mecham, Francis Rose, Kenneth Johnson, Perihan Şadoğlu, Bobbi Low, Mel Brownfield, Jerry Cooke, Suzanne Wiley, Fred Howell, Ann Sturdivant, Russell Harmon, John Prentice, Virginia Tipton, Andy Grubbs, Robert Hemperly, Neal Morris, Carmen Soileau, Barbara Vinson, Don Broussard, James McIntire, John Fish, Chip Carney, Don Erickson, Craig Bittinger, Steve Bittinger, Jan Lewis, Roy Jameson, Blake Harrison, David McKenzie, John Risinger, Bud Frank, Orion Knox, A. Richard Smith, Mills Tandy, Tom White, T. R. Evans, Janie Evans, Mike Collins, Terry Plemmons, Jimmy Jarl, Joe Sumbera, Jim Weiler, Frieda Gail Webster, Logan McNatt, Ed Fomby, Mike Walsh, Brian Peterson, Tony Mollhagen, Jerry Boradus, David Honea, Ann Lucas, Joe Cepeda, Terry Raines, Ed Alexander, Martha Burk, Sharon Cathey, Jim Rodemaker, Julie Rodemaker, Hugo Victoria, Roy Jameson, Danny Evans, Jim Dunlap, Amador Cantú, Charles Fromen, Jon Everage, Ronnie Fiesler, Peter Strickland, Don Coons, Ron Rossburg, Walter Gersch, Howard Crow, Ernest Garza, Greg Walker, Bob Stockton, Roy Brown, D. Christie, Olga Reyes, Tom Albert, Robert Mitchell, Jr., Sharon Mitchell, Carol Russell, Louis Henbry, Richard E. Smith, Jim Blassingame, Lucy Cogdill, and Glenn Campbell. Included in the preceding are most of those who have made substantial contributions to the many thousands of man-hours that have been invested in those efforts leading to our better knowledge of the eyeless characins. Lastly, we express our sincere appreciation to Robert Rush Miller for his thorough reading of our manuscript. To those whose names have been inadvertently omitted we apologize.

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