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145

Fossil tadpoles from the Miocene of Turkey

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We describe two exceptionally well-preserved anuran larvae from the Middle Miocene of central Turkey. Among extant taxa from Europe and Asia Minor, these specimens most closely resemble tadpoles of the genus *Pelobates*. Many non-mineralized tissues, such as the keratinized beaks, are preserved. Some of these structures are ambiguous for taxonomic assignment, and key diagnostic features, such as spiracular position and organization of oral denticles, are not observable.

INTRODUCTION

In 1968, the Turkish-American botanist Baki KASAPLIGIL discovered a fossil-rich site in the Gürcü Valley of Turkey, about 90 km north of Ankara (KASAPLIGIL, 1977, 1981). On that and subsequent trips KASAPLIGIL and associates encountered an "abundance of frustules of pennate fresh-water diatoms, Cyprinid fish fossils, frogs, salamanders, mosquito larvae, Nematoceran flies, dragon flies, bees and beetles" (KASAPLIGIL, 1981: 97). Before his death in 1992, Dr. KASAPLIGIL asked us to study some remarkably well-preserved fossil tadpoles from the site, and we present the results of our study here.

At first the site was listed as Pliocene (KASAPLIGIL, 1977), but later the age of the fossil deposits was determined through K/Ar isotope analysis to be ± 14.1 million years and said to be Upper Miocene (KASAPLIGIL, 1981). However, the dating makes the site Middle Miocene.

MATERIALS AND METHODS

There are two fossil tadpoles available for study; KASAPLIGIL knew of the existence of more vertebrate remains but was unable to locate them. Both specimens have been catalogued into the collection of the University of California Museum of Paleontology (UCMP) in accord with the wishes of Dr. KASAPLIGIL. The specimens are preserved in a laminated diatomite. One specimen (UCMP 139183) is a ventral impression of a complete tadpole, ventral side up. The matrix of this specimen is firm and dense. This specimen has the following accompanying data: Ankara, Güven, Beşkonak, Karga Creek, alt. 1300 m, October 4, 1986. The other specimen (UCMP 139184) is a more fragmentary head and body preserved as an impression and a counterpart. The soft matrix is fissile, and flakes easily. Both parts are mounted on stiff board. They have the following accompanying data: Güven, Gürcü Valley, Aköz Site, alt. 1200 m, August 30, 1976. We comment briefly on one additional specimen available to us only in the form of a photograph.

DESCRIPTION OF FOSSIL TADPOLES

SPECIMEN UCMP 139183

External form and dimensions

This specimen is superbly preserved; it reveals the virtually complete form of a tadpole, including head, body and tail (figs. 1-3). The specimen is preserved flat, with a small amount of relief visible in oblique light. The ventral surface is up. The keratinized beaks are conspicuous at the rostral end of the specimen. The maximum width of the beaks is 3.5 mm. The beaks are relatively thin and the lower beak forms a very broad "U" rather than a "V".

The keratin of the beaks is extremely fragile and the margins of the beaks are not adequately preserved to resolve serrations. Isolated specks of keratin around the beaks may be fragments of the beaks or isolated denticles. However, in this specimen those specks are neither sufficiently numerous nor symmetrically arranged so as to define denticle rows.

Measurements (in mm): total length 69.2; head-body length 28.3; tail length 40.9 (as much as 10 % of the terminal tip of the tail may be missing); maximum width of the body at the abdomen 19.6; maximum length of thoracoabdominal portion 14.8; maximum width of body at the branchial baskets 21.7; maximum width of specimen at level of eyes 18.4; maximum diameter of eyes 2.7 (left) and 3.0 (right); interocular distance 10.6; internarial distance ca. 3.9.



Fig. 1. — A Miocene tadpole from Turkey (UCMP 139183).

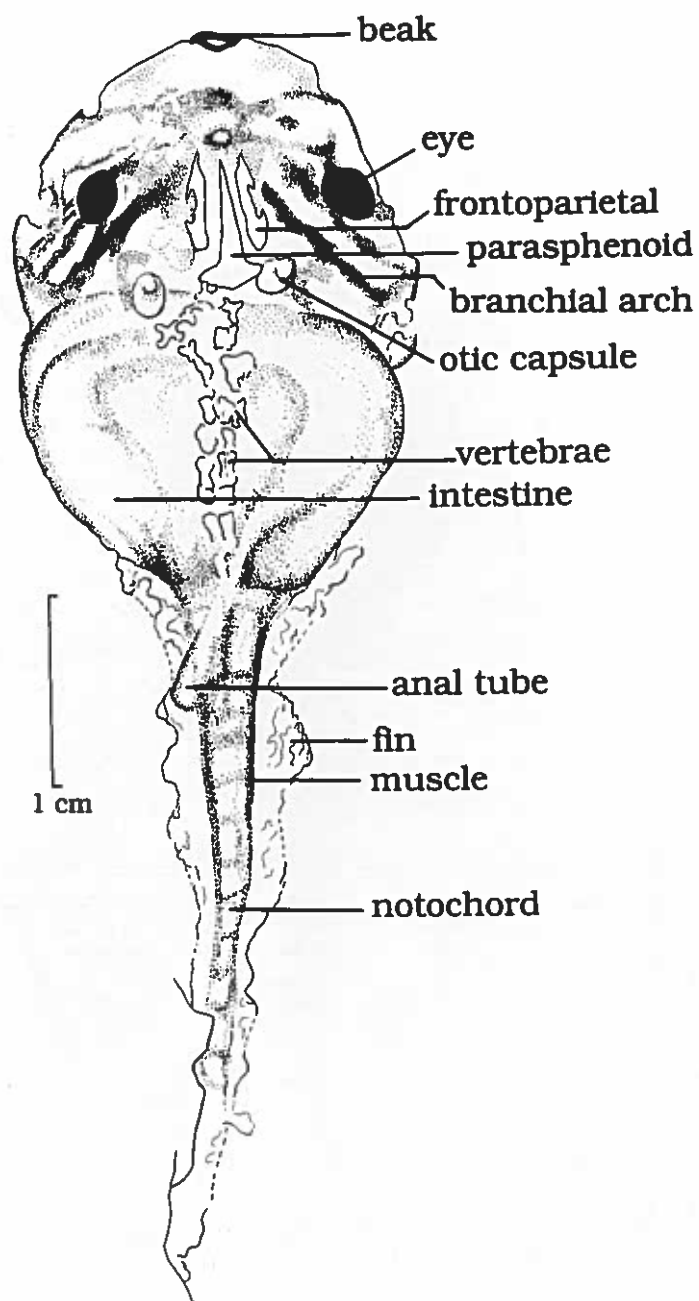


Fig. 2. — An outline drawing of fig. 1, with prominent features discussed in the text indicated.

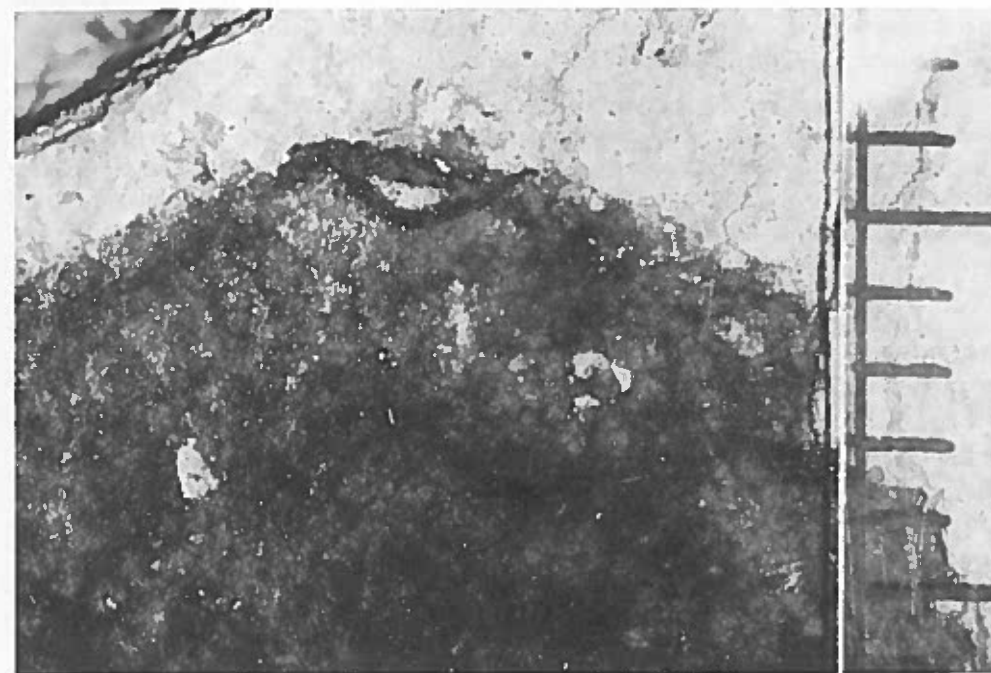


Fig. 3. — Enlargement of the beak region of fig. 1. Note the fossilized keratinous beaks. Remnant denticle rows are not visible in this illustration.

Skeletal elements

Although the specimen appears to be premetamorphic, some skeletal elements are evident. Cartilage of the chondrocranium is represented as dark brown staining of the underlying rock. The vague outline of the cranial base and ethmoidal region is visible. More distinct are three obliquely oriented ceratobranchials on each side. These gill bars define the branchial baskets, each of which is about 9 mm long and 8 mm wide.

The parasphenoid is well-developed and its outline is clear. The bone has the shape of an inverted "T," with the cultriform process gradually but continuously tapering rostrally, to a sharp point. The alar processes are relatively narrow, parallel-sided, and blunt-tipped. The parasphenoid is 7.6 mm long and 4.1 mm wide. The maximum width of the cultriform process is 0.9 mm, and the maximum rostrocaudal dimension of the alar processes is 1.1 mm. The caudal margin of the parasphenoid forms a shallow "V" on the midline.

Elliptical ossifications of the prootic are evident. On the right side of the specimen the prootic lies immediately lateral to the alar processes of the parasphenoid, while on the left

the bone is displaced further laterally a short distance. The bones measure 2.3 mm rostrocaudally and are 1.5 mm wide. The prootic ossification on the left is rotated with its lateral portion facing rostrally. Each prootic has a hemispheric elevation filling the lateral half; we interpret these thickened areas as mineral deposits in the endolymphatic sacs.

Paired frontoparietal bones are conspicuous lateral to the cultriform process of the parasphenoid. These elongate elements taper to rostral points but are blunter posteriorly. The bones are 5.0 mm long and 1.4 mm wide at the widest point (about three-fourths of the distance back from their rostral tip). Each bone has a distinct elevated strip, now facing laterally; this zone may represent matrix-filled evacuations, because they are symmetrical and thus likely derive from the normal anatomy of the tadpole. They lie in the middle third of each bone and are about 2 mm long and 0.5 mm wide. In life these may have faced each other across the dorsal midline of the skull, delimiting a frontoparietal fontanelle; if so, they have undergone postmortem rotation around their longitudinal axis.

Preservation in the region of the craniovertebral joint is poor. Whereas each exoccipital-first vertebral articulation can be discerned, resolution is insufficient to interpret the shape of the condyles and cotyles.

A number of vertebrae are present, with the more anterior being better preserved, probably because of more extensive ossification. A precise count is not possible because of fragmentation. The first two vertebrae are slightly shifted off the midline, but the third is displaced far to the left and somewhat rostrally, behind the prootic. What may be the fourth and fifth vertebrae are fragments displaced to the right and left respectively. The next five vertebrae are located in sequence and more or less along the midline. Thus, either nine or ten vertebrae are present, depending on interpretation of the fragments. The first three vertebrae display neural arch elements and centra; they are spool-shaped with amphicoelous ends. Vertebrae six through ten are also spool-shaped, but they consist mainly of neural arch elements, and these fade caudally so that the last element consists only of paired, slightly concave impressions. Vertebrae six and seven appear to have ossified centra.

No appendicular elements are observed. That feature, by itself, suggests that the tadpole is at an early free-swimming stage. However, the fact that the parasphenoid, exoccipital, prootic and many vertebral elements are ossified indicates that this tadpole must be at a later stage of development. The ossification schedules of *Xenopus* (TRUEB & HANKEN, 1992), *Bombina* (HANKEN & HALL, 1984, 1988), *Rana* (ERDMANN, 1933; KEMP & HOYT, 1969), and *Spea* (WIENS, 1989) all suggest that this specimen is close to GOSNER's (1960) stages 36-38, i.e. a more mature but still premetamorphic larva.

Additional features

The eyes are clearly visible as two black spots, possibly resulting from retinal melanin. They are located within the outline of the head but rather far laterally.

Elevations and depressions in the abdominal region (best seen with oblique lighting) suggest intestinal coils. These are most evident as a weakly elevated and more lightly

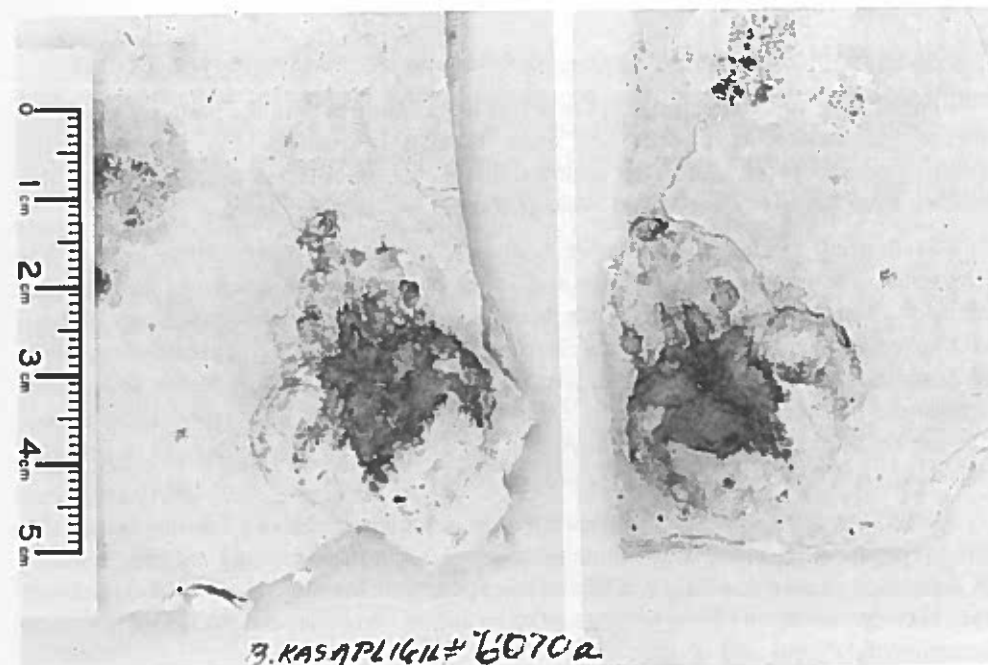


Fig. 4. — A Miocene tadpole from Turkey (UCMP 139184). The photographs are oriented with the snout of the specimen at 11 o'clock on both the cast and the counterpart. The eyes, beaks and abdomen are easily visible on both parts. The greater width of the abdomen compared to the head is probably a postmortem artifact.

stained area along the left margin of the specimen and an arched depression in the lower left quadrant of the abdomen (i.e. on the anatomically right side of the specimen). The depression first follows the curve of the abdomen but then bends caudally to the anal region where it terminates. The topography suggests that the depression was produced by the distal portions (colon and rectum) of the alimentary canal.

SPECIMEN UCMP 139184

External form and dimensions

This specimen consists of an imprint and a counterpart of the head and body of a tadpole without the tail (fig. 4). The size of this specimen, the position of its eyes and mouth, and the similarity of its skeletal elements to those of UCMP 139183 leaves little doubt that the two are specimens of the same species at nearly the same stage of development.

Measurements (in mm): maximum length of head + body 37.6; maximum width of specimen (across abdomen) 28.3; maximum length of cranium 17.9; maximum width of head at the eyes 18.5; maximum eye diameter 3.8.

Skeletal elements

In general this specimen displays fewer soft tissue features than the previous specimen, but the bony elements present are more extensively ossified. No outline of the chondrocranium can be seen. Our description focuses on features that distinguish this specimen from UCMP 139183, and comparisons are to that specimen.

The imprint of the beak is more complete, and while most of the keratin has deteriorated, the imprints show upper and lower beaks that are deeper in rostrocaudal dimension. The maximum width of the beaks is 4.1 mm. The exterior surfaces of both beaks have fine ridges and very finely serrated margins. Keratinized fragments of the beaks and denticles are displaced both rostral and caudal to the beaks. Close to the beaks, both rostrally and laterally, there are two to seven specks of keratin in tight rows. These appear to be the keratinized remains of denticles, but the rows are so fragmentary as to preclude determination of the number of rows present in life.

Neither the cultriform nor the alar processes of the parasphenoid are fully intact, and while the preserved portion of the bone measures 7.0 mm in length and 3.7 mm in width, this element evidently was larger in life in this specimen than in the other. The relatively large alar processes in this specimen, for example, have a maximum rostrocaudal dimension of 1.7 mm and obscure the exoccipital region from view.

Prootic elements are not preserved, but circular impressions on both the primary cast and the counterpart indicate the position of the mineral deposits in the endolymphatic sac. Both sacs, with diameters of about 1.6 mm, are displaced rostrally, one sufficiently far forward and lateral to contact the posterior edge of the eye.

The only other cranial elements preserved are the frontoparietals. These lie approximately parallel to the long cultriform process of the parasphenoid, but they have been subjected both to shear and torsion so that one is closer to the parasphenoid and contacts it while the other is displaced laterally a third of the distance to the eye. The maximum length of the frontoparietals is 5.8 mm; maximum width is 1.5 mm. These elements are less well preserved than in the other specimen; they are wider posteriorly and more ossified. The lateral emarginated zone described in the other specimen is not evident. On the other hand, the frontoparietals in this specimen have a thickened ridge along their lateral margins which we interpret as a flattened ventral ridge.

Parts of at least nine vertebrae are evident. The most fully preserved, in the middle of the vertebral column, are rotated around the long axis of the body and display both elements of the neural arch and the centrum. The more rostral vertebrae are displaced laterally and appear to have been forced forward, partly under the skull, where they have left impressions directly in the alar processes of the parasphenoid. The most caudal vertebra is represented only by its split neural arch, one side more posterior than the other.

Remarkably, both the primary and counter impressions reveal the clear outline of the notochord, which extends about two vertebral lengths (3.6 mm) behind the last vertebra. It also can be seen continuing rostrally through the fragments of two vertebrae. The notochordal impression is lost within the remains of the next most rostral vertebra but then reappears and extends forward to within one vertebral length of the occiput.

As in the other specimen, the greatest postmortem disturbance of the axial skeleton is in the immediate postcranial region. Consequently, it is difficult to resolve critical features in that anatomical region, such as a pectoral girdle or limb rudiments, which would help stage this specimen. We also find no evidence of hind limbs or the pelvic girdle. Nevertheless, the amount of ossification suggests that this tadpole, like UCMP 139183, was at GOSNER's (1960) developmental stage 36-38 when it died.

ADDITIONAL MATERIAL

According to information provided by Dr. KASAPLIGIL (pers. comm.) and his published observations (KASAPLIGIL, 1977, 1981), there are additional fossil amphibian specimens, both anuran and urodele, in the collections he made from the site reported here. These have been unavailable to us. However, Dr. KASAPLIGIL provided us with a photograph of one additional tadpole (labeled as B.K. 5629), possibly now in the collection of the Natural History Museum of the Mineral Research and Exploration Institute of Ankara. We present his photograph (fig. 5), with the following comments: in terms of size, degree of ossification, and developmental stage, this specimen appears to be taxonomically identical to the two specimens described above. However, the specimen is preserved in a more lateral view, with the head missing anterior to the parasphenoid, and the distal half of the tail is also missing. The parasphenoid is ossified. There are at least eight, and possibly nine, vertebrae but, as in the other specimens, the preservation in the immediate postcranial area is inadequate to permit a precise description of skeletal elements in this region.

DISCUSSION

Fossils of tadpoles and adult frogs were reported from the Miocene of Turkey by PAICHELER et al. (1978), also from the Gürcü Valley, near the site of the fossils described herein. These authors figured a fossil tadpole and assigned their specimens to *Pelobates* sp. However, their brief and general account contains no description and mentions no diagnostic features other than size and the presence of a beak. We believe that these specimens are from the same strata as those described here and are taxonomically identical. Reasons for our taxonomic assignment are presented below.

TAXONOMIC CONSIDERATIONS

The keratinized mouthparts immediately preclude assignment of these fossils to the Pipoidae or the Microhylidae. The fact that the botanical associates of these tadpoles are largely genera present in modern-day Turkey (KASAPLIGIL, 1977, 1981) suggests that these fossil tadpoles are likely to be members of genera extant in Asia Minor or neighboring regions. Among extant European and western Asian taxa (BAŞOĞLU & ÖZETİ, 1973), the

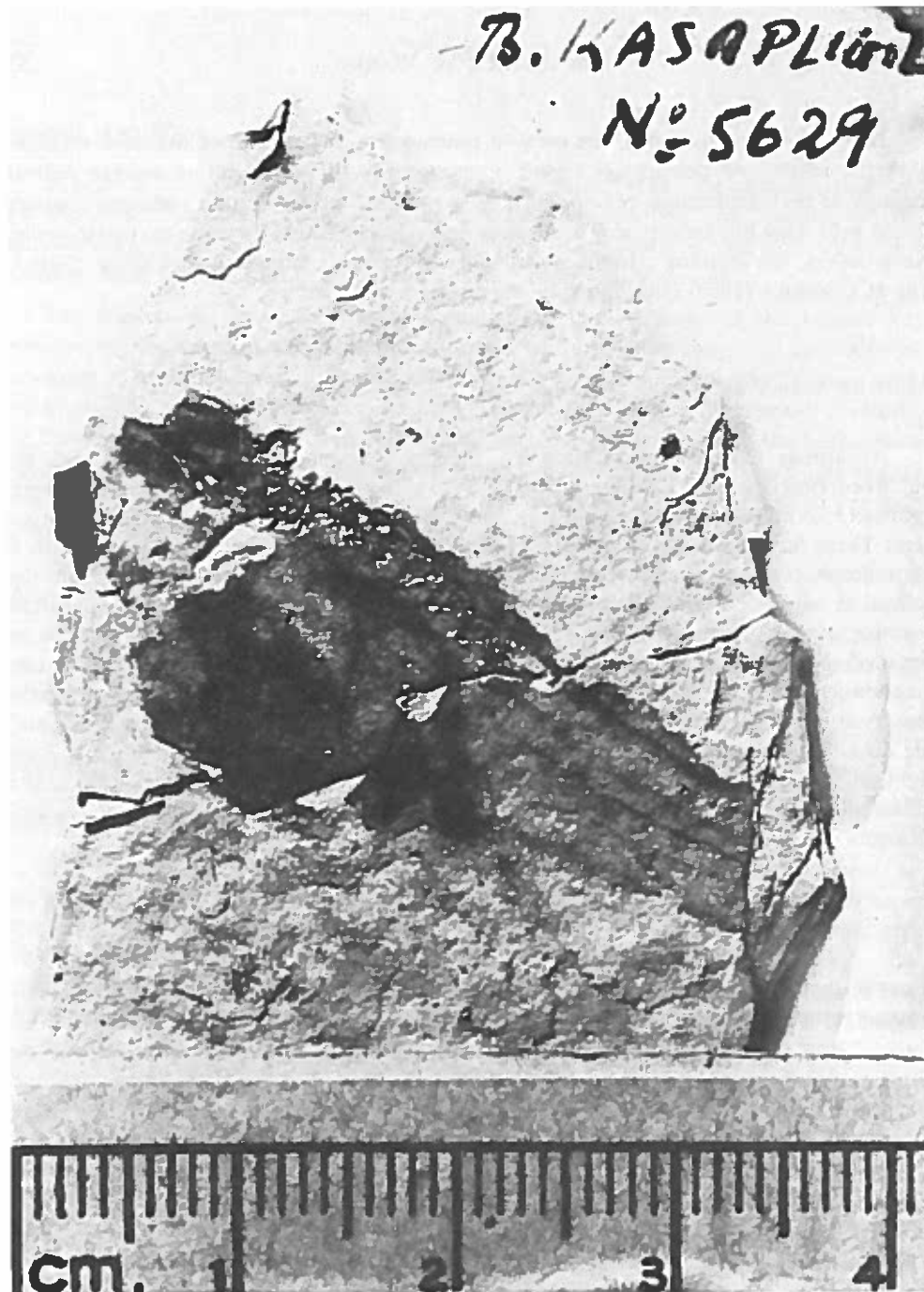


Fig. 5. — Photograph of an additional Miocene tadpole from the same deposit as those shown in figs. 1 and 2 (B.K. 5629). This photograph was provided by B. KASAPLIGIL. The specimen itself was not examined, but from the notes of B. KASAPLIGIL it seems likely that it may be in the collection of the Natural History Museum of the Mineral Research and Exploration Institute of Ankara. The tadpole is preserved on its side and in the photograph is oriented with the snout at 10 o'clock. This specimen closely resembles the specimens illustrated in figs. 1-4 in terms of size, shape, and extent of ossification.

large size of the fossil tadpoles precludes assignment to *Pelodytes*, *Discoglossus*, *Bombina*, *Bufo*, or the brown frogs within the genus *Rana* (for comparison, see descriptions and illustrations in BOULENGER, 1897, DELWIG, 1928 and GRILLITSCH et al., 1983). The other, larger *Rana* (i.e. the green frog group) have proportionately narrower bodies and longer tails than our most complete specimen UCMP 139183.

The remaining extant genera to be considered are *Alytes* and *Pelobates*. Unfortunately the diagnostic features of the denticles, spiracle, oral disc, anal tube position, tail fin shape, etc., are not observable in our specimens. Accordingly we are unable to assign our specimens with certainty to either of these genera. However, several lines of evidence lead us to make a tentative assignment to *Pelobates*.

The lateral eyes and nearly terminal mouth of the complete tadpole are more typical of *Pelobates* than of *Alytes* (see figures in BOULENGER, 1897). The general form of the body resembles that of tadpoles of *Pelobates fuscus* (e.g. figures in GRILLITSCH et al., 1983; SCHULZE, 1892). The denticles of the fossils are simple in structure and are neither multicusped nor cupped. If we assume that the few denticles retained in the specimens are complete (as they appear to be), they more closely resemble those of *Pelobates* (BOULENGER, 1897: fig. 43) than of *Alytes*.

Osteological features of the fossil tadpoles, especially the shape and arrangement of the parasphenoid and frontoparietal bones, resemble those of *Pelobates* (ROČEK, 1980: figs. 38 and 43) and metamorphic *Spea* (WIENS, 1989), a North American pelobatid, and contrast with those of many other extant anurans (as illustrated by DUELLMAN & TRUEB, 1985: figs. 13.17-18). The pointed, tapered cultriform process and the orthogonally oriented, blunt-ended alar processes of the parasphenoid of the fossils closely match these features of the parasphenoid in *Pelobates cultripes* and *Spea bombifrons* as illustrated by ROČEK (1980) and WIENS (1989), respectively. Furthermore, the spacing size and shape of the frontoparietals of the fossils, including the ventral ridge, match those features in the two extant pelobatids with which we have compared them. Taken together, these resemblances support our tentative assignment of the Turkish fossils to the pelobatid genus *Pelobates*. The fossil tadpoles are not identical to those of modern *Pelobates* in all discernible features, however. For example, the wider and thinner beaks of specimen UCMP 139183 are more like those of *Pelodytes* and *Alytes* than of *Pelobates*.

Pelobatid frogs are an ancient group; divergence of *Pelobates* from the *Scaphiopus-Spea* group in North America has been estimated at more than 100 million years, but the frogs retain great morphological similarity and have changed relatively little over vast periods of time (reviewed by SAGE et al., 1982). Given the geological age of our specimens and the absence of critical features used to discriminate tadpoles of living species, we consider it premature to assign the specimens we have studied to any species.

TAPHONOMIC CONSIDERATIONS

The fossils occur in very fine grained, laminated diatomaceous earth that is soft and crumbles readily. KASAPLIGIL (1977: 25) reports that "the laminated diatomaceous earth

was oriented vertically and the sheets of these spongy rocks were naturally split into book-size platelets. Due to absorption of rainwater we could pull out any piece with great ease, just like pulling out books from a library shelf". Elsewhere he speculates that fossilization occurred as a result of volcanic activity which poured lava and hot volcanic ash into the lake, causing rapid sedimentation of diatomaceous frustules. These, along with the accumulation of fine silt from streams flowing into the lake, formed the laminated diatomites and paper shales (KASAPLIGIL, 1981).

Frogs in this part of the world would be expected to breed in the winter and early spring (BAŞOĞLU & ÖZETİ, 1973). Based on the size and developmental stage of the fossils, we speculate that the tadpoles were killed in mid to late spring.

ECOLOGICAL CONSIDERATIONS

The particularly globose body and relatively short tail of specimen UCMP 139183 characterizes a generalized pond tadpole adapted to life in standing water. The terminal mouth and position of the eyes (more lateral than dorsal) characterize anuran larvae that are active in the water column and not strictly benthic. The large branchial baskets furthermore suggest that this Miocene form was an effective suspension feeder in life. Our interpretation of the morphology of the fossils is consistent with the taphonomy of these fossils and the associate plant fossils.

ACKNOWLEDGEMENTS

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