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FOSSIL AMPHIBIANS FROM THE MIOCENE OF THE NORTH CAUCASUS, U.S.S.R.

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ABSTRACT

A small late Miocene amphibian fauna from the northern Caucasus Mountains, U. S. S. R., includes *Mioproteus caucasicus*, a new proteid salamander more robust than the living *Proteus anguineus* and probably not troglobitic ; a small salamandrid indistinguishable from the living *Triturus marmoratus*, a discoglossid frog showing features resembling both *Discoglossus* and *Bombina*, and an unidentifiable procoelous frog. *Triturus* and the discoglossid *Bombina* live in the region today, but the presence of a proteid extends the known distribution of the family far to the east, and is the first valid fossil record of the Proteidae.

INTRODUCTION

There are few known occurrences of fossil lissamphibians in the U.S.S.R. and the specimens described here are thus of particular interest in giving some indication of the nature of the fossil amphibian fauna of the Northern Caucasus Mountain region during the late Miocene.

Although few in number, these fossils demonstrate the presence of four amphibian families. The best preserved and most abundant remains are of salamanders. They clearly demonstrate the presence of the family Proteidae for the first time in the fossil record ; a new genus and species *Mioproteus caucasicus* is described, closely related to the living genus *Proteus* and showing some similarities to the North American genus *Necturus*. Other fossil forms referred by previous authors to the Proteidae are suspect to one degree or another : *Orthophyia* is based on material now lost, *Proteus bavaricus* is based on material inadequately figured and described, *Comonecturoides marshi* is based only on a femur, and *Palaeoproteus klatti* was removed from the Proteida by Estes, Hecht, and Hoffstetter (1967). It is entirely possible that the Russian material described here may represent the genus *Orthophyia*, but as the type materials of the latter are lost confirmation of this possibility is impossible.

The other salamander remains are referable to the family Salamandridae and belong to the living genus *Triturus*. Their specific allocation is difficult to determine because of the small sample, but they are very close to the living species *T. marmoratus*.

Two specimens indicate the presence of two different frog families. An atlas is referable to the family Discoglossidae, a single vertebra is referable to one of the procoelous families.

SYSTEMATIC DESCRIPTION

Class	Amphibia
Subclass	Lissamphibia
Order	Caudata
Family	Proteidae

Mioproteus caucasicus, n. gen., n. sp.

Holotype : Zoological Institute, Academy of Sciences, Leningrad ZIL 240, anterior trunk vertebra, slightly broken. Maximum length of centrum 6.25 mm.

Referred specimens : Thirty-eight trunk and four caudal vertebrae ; an atlas ; fragments of hyobranchial skeleton including a ceratohyal, a first ceratobranchial, and a hypobranchial ; four right vomers ; fragments of three right and one left dentaries.

Diagnosis : A species of proteid differing from *Proteus anguineus* in having robust, well-ossified vertebrae with posterior basapophyses present ; neural arch relatively wider with wider forking of the neural spine ; ventral surface of centrum flattened, co-extensive with the basa-

pophyses. At present, generic and specific diagnoses are the same.

Description : Atlas with centrum flattened dorsoventrally ; cotylar areas narrow, elongated lateromedially, the cotylar surface flattened and confluent across the tiny intercotylar process ; prominent crests ventroposteriorly on centrum ; posterior cotyle amphicoelous.

Trunk vertebrae uniformly amphicoelous, small ones deeply so, large specimens tending to have the anterior cotyles ringed peripherally with calcification but the notochordal pit always present. Trunk centra with moderate ventromedial keels, sometimes flattened anteriorly and posteriorly ; usually more or less prominent basapophyses present posteriorly, issuing laterally from the flattened area on the ventro-posterior centrum surfaces. Centra deeply excavated laterally in region of transverse processes, the latter unicipital with no trace of rib articulation surface ; a prominent ventral lamina present on transverse process, its anterior edge generally prolonged into a point ; dorsal part of transverse process a vertically-oriented lamina originating on the prominent interzygapophyseal ridge and diminishing laterally until it joins the ventral lamina at its tip ; prominent pits anterior and posterior to the vertical lamina of the transverse process, these pits usually confluent with the subcentral foramina. Neural arch prominent but flattened ; zygapophyses well-defined and projecting widely ; neural spine present as a poorly-developed keel ; posterior surface of neural arch deeply forked, the two forks projecting laterally, widely separated, forming a space for muscle insertion between them. Centrum length ranges from 2.5—6.65 mm.

Caudal vertebrae with both sides of hemal arches connected ventrally ; anterior caudals with ventral centrum surface flattened and crested laterally.

Dentary fragments poorly preserved. Meckel's groove open widely almost to symphysis ; teeth widely separated, apparently sub-pedicellate ; symphysis region narrow, elongated anteroposteriorly. Vomers triangular, palatal shelf dorsally-curved at its medial side, evidently not reaching midline ; a slight projection laterally for attachment to nasal capsule and skull roof. Palatopterygoid fragment narrow, elongated, with anterior tooth patch and posterior edentulous expansion, teeth sub-pedicellate, a zone of weakness clearly present between crown and pedicel but the two parts not completely separated.

Ceratohyal boomerang-shaped, a prominent muscle attachment at the angle ; first ceratobranchial similarly shaped, more robust, a crest dorsally for muscle attachment ; hypobranchial relatively short, its extremities expanded.

Discussion : The recent species *Proteus anguineus* is characterized by the following features : very delicate, lightly-ossified vertebrae with many excavations and laminae present ; centra deeply amphicoelous ; no trace of basapophyses ; zygapophyses protuberant ; posterior border of neural arch deeply forked ; transverse processes unicipital, strongly webbed with bone ventrally ; ribs lacking ; ventral surface of centrum seldom if ever flattened.

The specimens from the northern Caucasus agree with vertebrae of *Proteus anguineus* except in having flattened ends of the ventral centrum surfaces, well-developed basapophyses, and a much wider neural arch ; they are also more robust and better ossified than those of the recent species. These differences are not great. Any one of them may show variation among closely-related species of salamanders, and the fossil and recent species are evidently closely related. Yet the series of differences taken together, and their consistent presence on all fossil specimens, indicates a taxonomic difference that approaches the generic level.

In addition, the lacustrine origin of the deposits in which the fossils are found, and the association with aquatic newts, two families of frogs, and more characteristically terrestrial forms such as lacertid lizards and colubroid snakes (not yet described), indicates a profound difference in mode of life between the Miocene species and the troglobitic *Proteus anguineus*. This, in conjunction with the morphological differences and the differences in age and geography indicate that a generic separation is reasonable.

In spite of the differences in vertebrae between the two species, the skull and hyobranchial elements of *Mioproteus caucasicus* indicate a degree of paedomorphosis similar to that of the recent species, although their relatively shorter form indicates a less elongated head than in *Proteus anguineus*. The sub-pedicellate dentition, widely-open Meckel's groove, the latter extending far anteriorly, the larvaform shape of the palatopterygoid tooth plate and triangular vomers are all similar to conditions in *Proteus* and *Necturus*. These features are common to other paedomorphic species, particularly members of the fossil family Batrachosauroididae (Estes, 1969 ; referred to Proteida by Estes, 1975) and *Palaeoproteus* (Herre, 1935 ; Estes, Hecht, and Hoffstetter, 1967). The detailed structure of the bones, however, resembles that of *P. anguineus* more than it does the other three genera mentioned. These three genera and the batrachosauroidids are the only known forms to have this particular arrangement of elements ; other paedomorphic forms have dentaries, vomers, and palatopterygoids modified in slightly different ways (see Larsen, 1963 : 123, pl. 26).

It is interesting that several features of *Mioproteus* resemble those of the North American genus *Necturus*. All of the vomers of *Mioproteus* are broken, but only slightly at the posterior end ; tooth counts on the four available specimens are 7, 8, 9, 9. One of the latter two specimens appears to be almost complete posteriorly,

for the teeth show decreasing size. This indicates that the total vomerine tooth count may have been on the order of 10-12 as in *Necturus* rather than the 24-26 seen in *Proteus*. The well-developed posteriorly-projecting palatal shelf of the vomer is also more like *Necturus* than *Proteus*, although the probably unrelated *Palaeoproteus* also approaches this condition (Herre, 1935). The more robust form and wider proportions of the vertebrae of *Mioproteus* are unlike the slender vertebral proportions seen in both *Proteus* and *Necturus*, although the presence of weak calcification in the anterior cotyles of *Mioproteus* vertebrae resembles conditions in *Necturus*. *Mioproteus* vertebrae also resemble those of the North American batrachosauroidid *Opisthotriton* in general habitus (Estes, 1975, figure 1).

More complete material of *Mioproteus caucasicus* would be needed to provide meaningful information on the relationships of the living proteid species, but those similarities mentioned above are consistent with the work of Larsen and Guthrie (1974), who summarize evidence bearing on the relationship of *Necturus* and *Proteus* : they conclude that the similarities between the two living genera are the result of relationship rather than parallelism, contrary to the suggestion of Hecht (1957). The work of Salthe (1967) on courtship patterns suggests a possible relationship of *Proteus* and the salamandrids, with *Necturus* more distantly related, yet detailed data for courtship patterns in *Necturus* are lacking. The pattern of calcification in the vertebral cotyles of *Mioproteus* is unlike that seen in salamandrids ; it seems more like that in the ambystomatoid line in forming a funnel of calcified material that remains open anteriorly, rather than the calcified cap or plug often seen in salamandrids. The batrachosauroidids also have the ambystomatoid type of vertebral cotyle calcification, suggesting that salamandrid relationship of the Proteida is less likely. Our own opinion is that present evidence is compatible with a relationship between *Necturus* and *Proteus*, and that parallelism of these genera has not been demonstrated. The presence of separate opisthotic ossifications, unique among salamanders to these two genera, suggests that proteids are more primitive than other salamanders, yet the related batrachosauroidids are more specialized than living cryptobranchoids (Estes, 1975), suggesting that the separate opisthotics may be a derived paedomorphic condition. An isolated position for Proteida (Regal, 1966) is preferable at this stage of knowledge than one in which any suggestion of relationship to salamandrids or to any other living salamander family is made.

Type locality : Lake deposits in the Maikop District, valley of the Belaya River, northern Caucasus Mountains, U. S. S. R.

Age : Late Miocene, Middle Sarmatian (Bessarabian). Some (particularly Russian) authors consider Bessarabian to represent part of the Middle Miocene.

Family Salamandridae

Triturus sp., cf. *T. marmoratus*

Specimens : ZIL 241, two trunk vertebrae.

Description : Vertebrae opisthocoelous, the condyle separated from the centrum by a distinct neck or cons-

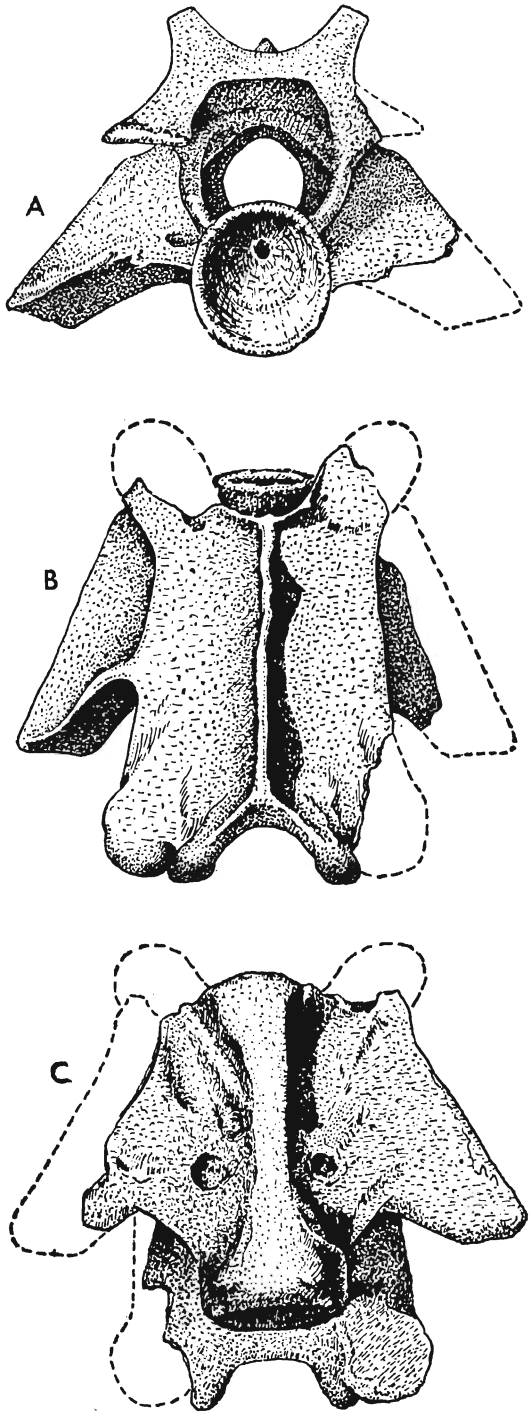

Figure 1. *Mioproteus caucasicus*, n. gen., n. sp. ZIL 240, holotype vertebra. A, posterior ; B, dorsal ; C, ventral views. ×8.5. Dotted line = restoration.

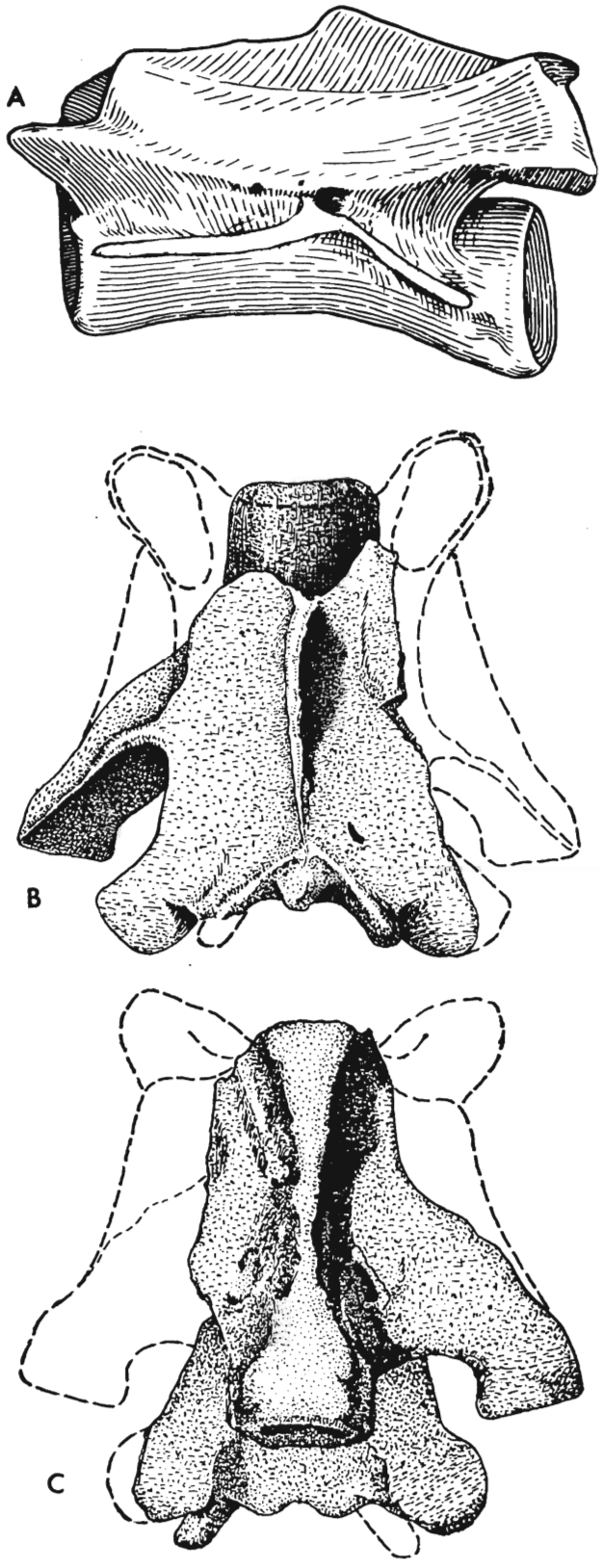

Figure 2. *Mioproteus caucasicus*, n. gen., n. sp. A, trunk vertebra, lateral view, ×10. Whitened area on transverse process indicates breakage. B, dorsal and C, ventral views of another trunk vertebra, ×8.8. Dotted line=restoration.

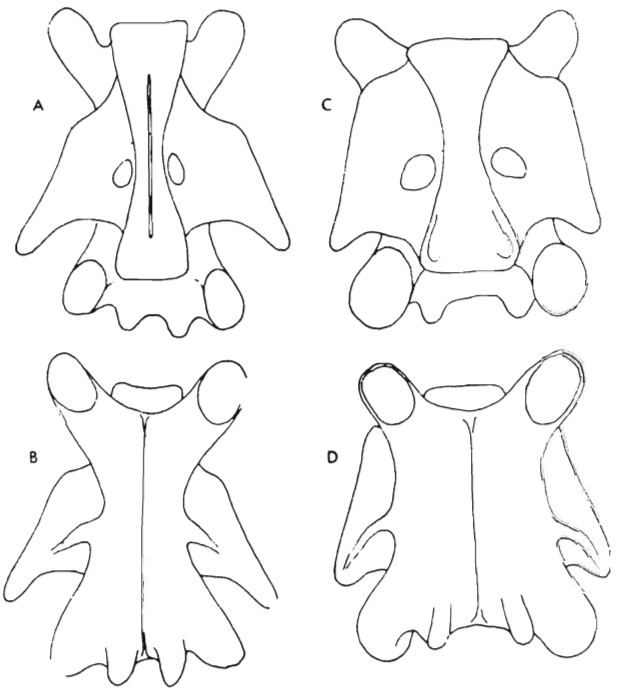

Figure 3. Comparison of *Proteus anguineus* and *Mioproteus caucasicus*, n. gen., n. sp. A, ventral and B, dorsal views of middle trunk vertebra of *P. anguineus*, ×12. C, ventral and D, dorsal views of trunk vertebra of *M. caucasicus*, somewhat restored based on other specimens, ×10·5.

triction; centra rather narrow; transverse processes bicipital; subcentral foramina widely opening ventrally; neural arch well-developed; neural spine forming a low but distinct lamina anteriorly, no deposition of dermal bone or flattened area on it dorsal surface. Maximum length of centrum 3.1 and 3.7 mm.

Discussion: The low-spined condition of these characteristically *Triturus*-like vertebrae most closely resembles that of the primitive newt species *T. marmoratus* and *T. cristatus*, especially the former, as the crests in the latter are extremely faint (if developed at all). *T. cristatus* has vertebrae more similar to those of *Salamandra* than do other newts, because of having a rather domed neural arch posteriorly; it is consequently less similar to the Caucasian fossil form than is *T. marmoratus*. The two fossil vertebrae cannot at present be separated from those of recent *T. marmoratus*, and closely resemble late Miocene fossils near that species from La Grive-St. Alban, France (Estes and Hoffstetter, 1976). They differ slightly from the latter in having relatively more open subcentral foramina, but they are so close to vertebrae of the recent species that a much larger sample of both recent and fossil species would be necessary to demonstrate if a specific or subspecific difference is involved. *Triturus cristatus* lives today in the area from which the fossils were derived.

Age and Locality: Same as for *Mioproteus caucasicus*.

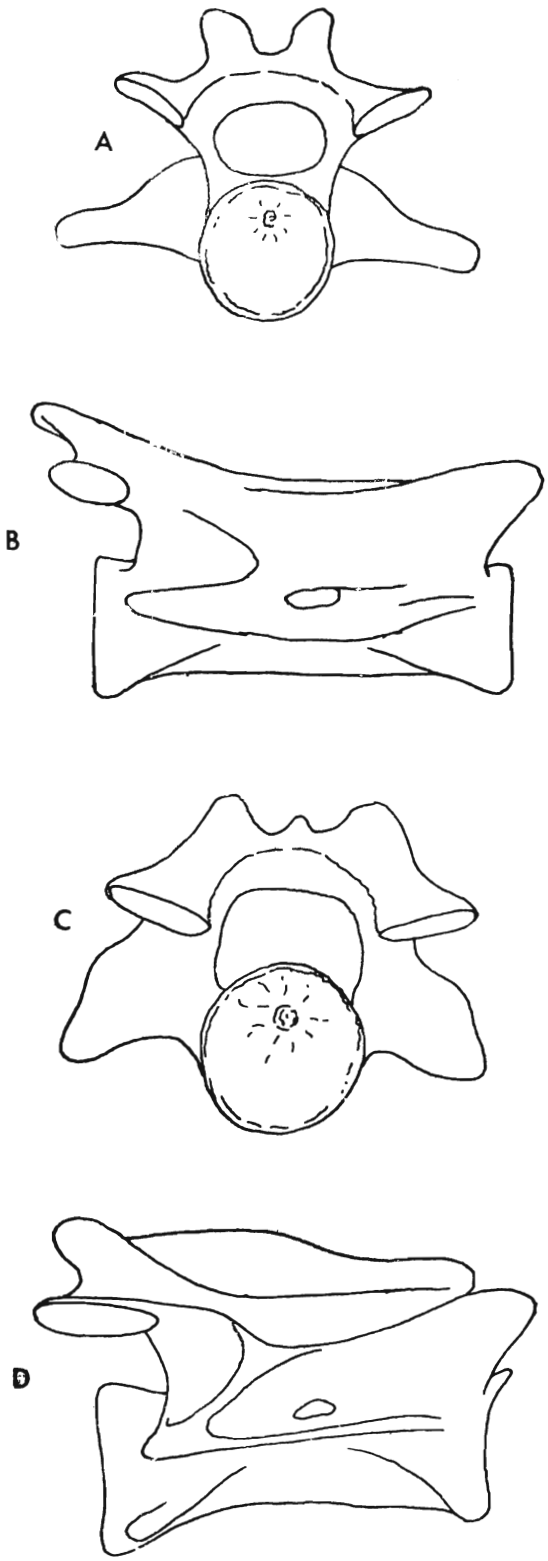

Figure 4. Comparison of *Proteus anguineus* and *Mioproteus caucasicus*, n. gen., n. sp. A, posterior and B, right lateral views of middle runk vertebra of *P. anguineus*, ×17. C, posterior, and D, right lateral views of trunk vertebra of *M. caucasicus*, somewhat restored based on other specimens, X17.

Order Salientia
Family Discoglossidae

unidentified genus and species

Specimens : ZIL 242, an atlas.

Description : Neural arch of atlas missing ; centrum of atlas flattened, ventral centrum surface with prominent anteroposterior keel ; posterior cotyle smoothly rounded ; anterior articular cotyles well-separated on the midline. Maximum width across articular cotyles 3.7 mm.

Discussion : The opisthocoelous condition of the vertebrae indicates a frog of the families Discoglossidae or Pipidae. No authenticated record of the latter has yet been found in the Northern Hemisphere, and the general appearance of the atlas is different from that of pipids. The specimen lacks the strong flattening and horizontal orientation of the anterior cotyles seen in *Alytes*, and resembles that of *Bombina* and *Discoglossus* more closely. The general proportions of the specimen, especially the relatively short centrum and the wide separation of the anterior cotyles, resemble conditions in species of *Bombina*. A ventral keel, however, is lacking in *Bombina* seen by us, but occurs in many examples of living *Discoglossus pictus*. *Bombina* lives in the northern Caucasus today but known fossil and recent distribution of *Discoglossus* is farther to the south and west. Without more complete material the specimen is identifiable only to family.

Age and locality : The same as for *Mioproteus caucasicus*.

CONCLUSION

Only one fossil lissamphibian, *Zaissanurus belajaevaei*, has so far been described from the Soviet Union. Known only from the lower jaw, it is a *nomen nudum*, as it has not been properly characterized (Chernov, 1959). It is probably a synonym of the common late Cenozoic European and North American cryptobranchid salamander *Andrias*.

Although few in number, the fossils described here are of interest in providing additional documentation on the fossil amphibian fauna of the U. S. S. R. In the Miocene, the Caucasus were separated from more northern and western regions by an epicontinental seaway ; it is thus probable that *Mioproteus* reached the Caucasus from the Balkan region via Asia Minor, unless it is a holdover of an early Cenozoic migration utilizing a more direct route. Additional specimens of *Mioproteus*, probably the same or a closely related species, occur in the middle Miocene (Helvetian) locality at Appertshofen bei Inglostadt, Germany (Dehm, 1961).

The few suggestions of similarity between *Mioproteus* and *Necturus* are consonant with evidence given by Larsen and Guthrie (1974) suggesting that *Necturus* and *Proteus* are in fact related. Hecht and Edwards (1976), however, have carefully reanalyzed the characters that have been

used to relate *Necturus* and *Proteus* and find most of them of relatively low significance. Only the karyotype similarities between the two genera are admitted as possibly showing a derived common state between them, yet even this is equivocal, since without more detailed biochemical and karyological studies independent derivation from ancestors possessing higher numbers of chromosomes is not ruled out (Morescalchi, 1975). Both Morescalchi on the one hand, and Hecht and Edwards on the other, agree that the monophyletic hypothesis is the most parsimonious at present. Morescalchi accepts this as a working hypothesis ; Hecht and Edwards, lacking resolution of the karyotype problem and having no other positive evidence of monophyly, have chosen to consider the genera polyphyletic. Our data do not clarify this issue, but with Morescalchi we choose the monophyletic derivation as a working hypothesis, simply based on parsimony (which Hecht and Edwards point out rightly may not always lead to correct conclusions) and on the fact (again recognized by Hecht and Edwards) that if separated, the two genera would be placed in two families that would be essentially impossible to diagnose.

The modern species *Triturus cristatus* and *T. vittatus* live in the Caucasus today as does the discoglossid *Bombina*. Vertebrae of species close to the living *T. marmoratus* occur widely in the European Oligocene and Miocene fossil record and this primitive species was apparently once widespread compared with its present distribution. The Caucasus specimens, belonging to *T. marmoratus* or a close relative, extend the distribution of this group of salamanders far to the east.

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