Richard ESTES

Lower vertebrates from the Golden Valley Formation, Early Eocene of North Dakota (U.S.A.)

[With plates XX—XXIII and 4 text-figs]

Fauna niższych kręgowców z wczesnego eocenu Golden Valley w Północnej Dakocie
(Stany Zjednoczone Ameryki)

Abstract. The Wasatchian (early Eocene) lower vertebrate fauna from the Golden Valley Formation (Stark County, North Dakota, U. S. A.) includes the fishes *Amia fragosa*, *A. uintaensis* (*Amiidae*), *Atractosteus occidentalis* (*Lepisosteidae*), and *Teleostei* indet., uniden- tified anurans, and the salamanders *Batrachosauroides gotoi* (*Batrachosauroididae*) and *Chryso- riton tiheni* (*Dicamptodontidae*). The latter species has an elongated, aquatic body, forming the first such adaptation recorded for the *Ambystomatoidea*. Reptiles include the turtles *Bapte- mys tricarinata* (*Dermatemydidae*), *Echmatemys testudinea* (*Emydidae*) and *Plastomenus* sp. (*Trionychidae*), the lizards cf. *Xestops* sp. (*Anguidae*), ?*Glyptosaurinae*, and *Saniwa*, cf. *S. en- sidens* (*Varanidae*), and the crocodilians *Chrysochampsa mlynarskii* gen. sp. n., *Allognathosuchus* sp. (*Alligatoridae*), and *Crocodylidae* indet. *Chrysochampsa mlynarskii* gen. sp. n. resembles most closely such species as *Alligator prenasalis* from the North American Oligocene, but it also has some resemblances to extant *Alligator* and the caimans. The lower vertebrates from the Golden Valley Formation represent a segment of the midcontinental fauna of North America that persisted from at least Late Cretaceous through the Wasatchian. However, except for the fishes, there is little generic similarity between the Golden Valley lower vertebrates and those from the Paleocene and Cretaceous. The assemblage includes primarily aquatic or ri- parian forms.

I. INTRODUCTION

Study of a widely distributed North American lower vertebrate chronofauna of Cretaceous and Paleocene age has produced considerable data bearing on the evolutionary and ecological history of many modern groups of lower verte- brates, especially lizards and amphibians (ESTES, 1964, 1976; ESTES and BER- BERIAN, 1970; ESTES and SANCHÍZ, 1982; GAUTHIER, 1982). This fossil fauna lived on the lowlands associated with mid-continent epicontinental seas, as well as on the residual floodplains formed after the retreat of these seas, and has its closest similarities environmentally (but only in part faunistically) with the Austroriparian Biotic Province of the eastern Gulf coast today.

In order to trace in greater detail the evolution of the Recent North American lower vertebrate fauna it is of interest to obtain fossils from similar localities

bridging the gap between Paleocene and Recent time. A few localities of Eocene or Oligocene age have produced well-preserved and diverse samples (GAUTHIER, 1982; BARTELS, 1983), and continued work on Miocene and Pliocene localities of this type have begun to fill in the later Tertiary record (e. g., WILSON, 1968; HOLMAN, 1976; HOLMAN and SULLIVAN, 1981).

A local fauna of Wasatchian age from the Golden Valley Formation, Stark County, western North Dakota (JEPSEN, 1963), provides additional knowledge of Early Eocene lower vertebrates; the fish, amphibians, and reptiles from this locality have produced some early records, new taxa, and extensions of ranges of considerable interest.

All of the lower vertebrate fossils have been obtained from the White Butte site, SW 1/4 sect. 29 and NW 1/4 sect. 32, T 139 N, R 97 W (JEPSEN, 1963). The trionychid material and one of the *Baptemys* specimens (P. U. 16798) came from three inches above the hard siliceous (HS) layer: all other specimens were found two to five inches below this layer.

The Princeton University collections are now housed at the Peabody Museum, Yale University, New Haven, Connecticut.

It is a pleasure to dedicate this article to Professor Marian MŁYNARSKI, in honor of his extensive work on lower vertebrates from the European Cenozoic.

II. SYSTEMATIC PALEONTOLOGY

Osteichthyes
Holostei
Amiidae

Amia fragosa (JORDAN, 1927)

PU 18567, right vomer (pl. XX: C), right second coronoid, anterior vertebra, and three unnumbered tooth-bearing fragments do not differ from elements

of this species described in Cretaceous and Paleocene samples (ESTES et al., 1969; BORESKE, 1974; ESTES, 1975).

Amia uintaensis (LEIDY, 1873)

PU 17270, a left dentary (pl. XX: A); 18568, posterior end of basioccipital (pl. XX: B); many unnumbered vertebrae. These elements are indistinguishable from those of the early Cenozoic species *Amia uintaensis*. Much larger than *A. fragosa*, *A. uintaensis* appears to be near the ancestry of the living *A. calva* (BORESKE, 1974).

Lepisosteidae

Atractosteus occidentalis (LEIDY, 1856)

PU 18569, scales, vertebral fragments, and fragments of skull are all indistinguishable from those of this species described by ESTES (1964). The convex outline of one of the dentary fragments indicates a wide-snouted gar, and the tooth pits of the internal row of dentary teeth indicate that this row of enlarged fangs ended abruptly far forward of the termination of the external row. These features have been treated as diagnostic for the Cretaceous and early Cenozoic gar *A. occidentalis* (ESTES, 1964), a species closely related to the living *A. spatula* (WILEY and STEWART, 1977), although the polarity of these characters remains to be determined.

This species was originally based on inadequate scale material from the Campanian Judith River Formation of Montana, but the extensive material from the Lance and Hell Creek formations of Wyoming and Montana has been used to produce a diagnosis (ESTES, 1964; ESTES et al., 1969). Nevertheless, it needs to be determined whether or not other Judith River material has the same diagnostic characters; a neotype should also be designated. WILEY (1976) gave reasons why this species should be referred to *Atractosteus* rather than *Lepisosteus*. I accept this opinion for the present, although there are some difficulties with applying WILEY's criteria to fossil material.

Teleostei indet.

PU 18570, two amphicoelous trunk vertebrae, cannot be identified more accurately at this time, and only indicate the presence of at least one small teleost in the vertebrate fauna of the Golden Valley Formation.

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Amphibia
Lissamphibia
Caudata
Proteoidea
Batrachosauroididae

Batrachosauroides gotoi ESTES, 1969

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PU 18012, holotype posterior trunk vertebra; 17275, almost complete
(? sacral) trunk vertebra; 17400 a—b, right dentaries, broken posteriorly;
unnumbered fragments of four trunk vertebrae. This salamander species was
described and figured by ESTES (1969); it is a primitive species of the genus,
but closely related to the Miocene *Batrachosauroides dissimulans* from Texas
and Florida. Figure E on Plate XXI gives a view of a dentary not figured by
ESTES (1969); its delicacy and strong expansion of the symphysis region confirm
reference to *Batrachosauroides*; the dentaries of the related *Lisserpeton* (ESTES,
1976) are more robust and have a lesser expansion of the symphysis. ESTES
(1976, 1981) referred the *Batrachosauroididae* to the *Proteoidea*.

<div align="center">

Ambystomatoidea
Dicamptodontidae

Chrysotriton tiheni ESTES, 1981

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PU 17314, holotype series of vertebrae, most of which are articulated or
only slightly dislocated from a natural position. A dicamptontid differing from
all other fossil and Recent species of the family in having a wing-like ventral
lamina and a single rib bearer of the transverse process, and larger, more well —
developed basapophyses than in other ambystomatids. At present generic and
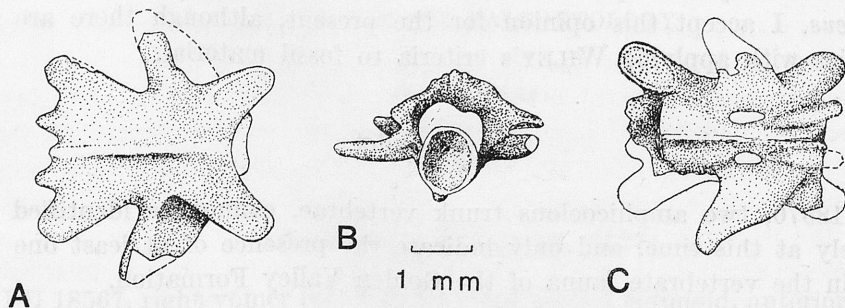specific diagnoses are identical.

Fig. 1. *Chrysotriton tiheni*. A — posterior, B — ventral, and C — dorsal view of three vertebrae
from PU 17314, holotype

Supplementary description

The specimen now consists of two separate and partially overlapping blocks of matrix mounted in plaster, one of which shows seventeen trunk vertebrae, the other nine trunk vertebrae and one caudal. Both of these groups of vertebrae were originally part of a single group. Several vertebrae are slightly removed from the main group and their original position is unknown. Another vertebra (Fig. 1A, B) was removed and cleaned so that ventral and posterior views could be drawn. Most of the vertebrae are crushed and slightly dislocated, but almost all of them have some area that is well-preserved, so that by studying different aspects of a number of vertebrae most of the vertebral structure can be made out.

The vertebrae are all relatively compact in form; none are elongated. The centrum is basically simple, amphicoelous, and has a prominent keel ventrally. The cotyles are rounded anteriorly but have a slightly elongate inverted teardrop shape posteriorly. A pair of robust basapophyses protrude anteriorly beyond the border of the centrum. At the roots of the basapophyses there is usually a prominent pair of subcentral foramina, one on each side of the keel. The transverse processes are unicipital, and arise at about the midpoint of the centrum. On all vertebrae in which these processes are not broken there is a thin, winglike ventral lamina that curves forward to meet the anterior border of the centrum. The neural arch has a low median neural ridge, and the posterior border has a spinous projection on each side of the midline. The zygapophyses are robust, and strongly projecting from the centrum. Their medial edges are usually concave, the lateral edges convex. The posterior border of the neural arch projects about as far, or very slightly farther, than the posterior borders of the postzygapophyses.

Measurements of the vertebrae illustrated are as follows: Fig. 1 C: total length of neural arch from anterior border of anterior zygapophysis to posterior border of posterior zygapophysis = 3.7 mm; maximum width across anterior zygapophyses = 2.9 mm; width of neural arch at its narrowest point = 1.3 mm. Fig. 1 A, B: maximum midventral length of centrum = 2.6 mm; maximum length of neural arch (measured as above) = 3.6 mm.

Discussion

A preliminary description of this species was given by ESTES (1981). The general proportions of the vertebrae resemble the compact form seen in species of the dicamptodontid *Rhyacotriton*, as well as the ambystomatids *Rhyacosiredon* and the *tigrinum* or *mexicanum* groups of *Ambystoma* (TIHEN, 1958: 17). The projection of the neural arch to the same level as that of the post-zygapophyses is similar to that of the latter taxa, and the shape of the zygapophyses (widely separated, with concave medial edges) also resembles that of many ambystomatoid species. Presence of a spinal nerve foramen in the single caudal vertebra preserved and lack of such foramina in the trunk vertebrae indicates reference to the dicamptodontids (EDWARDS, 1976).
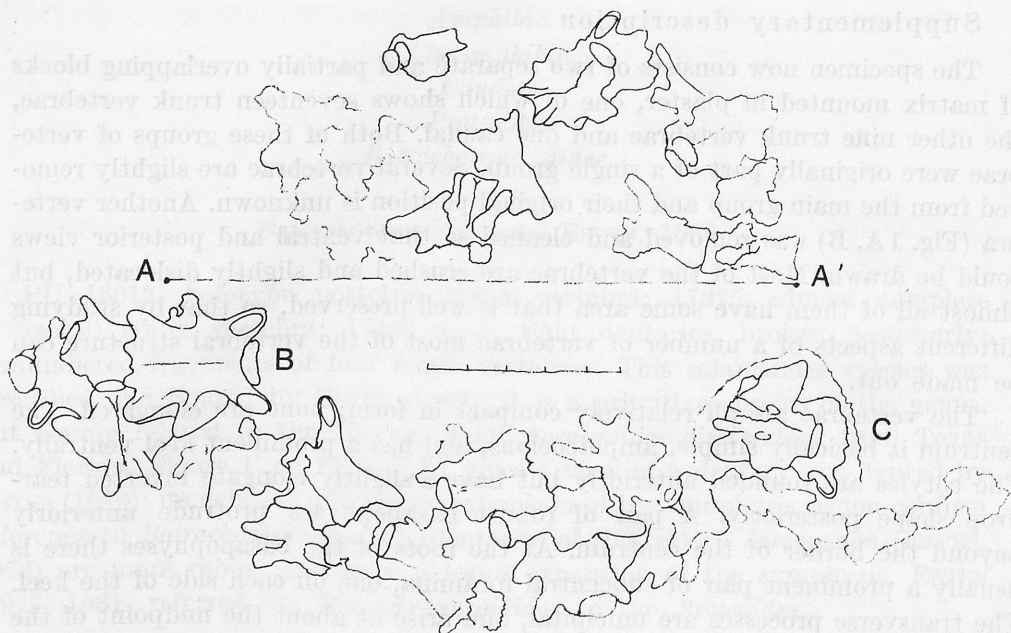
Fig. 2. *Chrysotriton tiheni*. PU 17314, holotype, outline of the two blocks of vertebrae. The position of the two blocks as preserved will be restored if the upper set of vertebrae is moved to the left until points A and A' are coincident. Line = 5 mm

Chrysotriton differs from dicamptodontids and ambystomatids in having a prominent subcentral keel and a single rib-bearer on the transverse process that is closely attached to the wing-like ventral lamina of the transverse process. This differs from the unicipital rib articulation of hynobiids in which the ends of the rib-bearers are dumb-bell shaped in lateral view and approach a bicipital condition. TIHEN (1958: 21) pointed out that some hynobiids have vertebrae with distinctly bicipital rib-bearers; these forms are quite similar in vertebral form to some of the more primitive ambystomatoids; family allocation of fossil material based on vertebrae alone may thus be open to question in some cases. Hynobiids that possess basapophyses have them placed far laterally on the anterior border of the centrum, while in those ambystomatoids possessing them they are nearer the median ventral line as in *Chrysotriton*. This condition resembles that of the sirenid salamanders *Siren* and *Habrosaurus*, and the batrachosauroidid *Prodesmodon* (ESTES, 1964, 1969; NAYLOR, 1979). This structure can be interpreted (by analogy with *Siren*) as an adaptation to a fully aquatic existence, in which ribs are reduced or absent. Whether *Chrysotriton* also had reduced limbs and an attenuated body form as in *Siren* is more speculative. However, if this specimen is interpreted as the remains of one individual, which the grouping of the remains suggests, then attenuation and consequent increase in vertebral number can be supported. The largest block of matrix has seventeen dorsals preserved in a more or less natural pattern (Fig. 2); the

relationship of the two blocks in the sediment is indicated in the legend in Fig. 2. If the vertebrae were of normal ambystomatid type, with double rib-bearers, the presence of two individuals might be suspected, because the usual vertebral count in *Ambystoma* ranges from eleven to fourteen and there are a total of twenty--eight vertebrae in the fossil specimen. However, the form of the transverse processes and the lack of regional differentiation in the preserved column, coupled with the absence of an "atlas" or sacral vertebra, strongly suggest an elongated body form with at least twenty-eight trunk vertebrae. In addition, it is impro-bable in this case that two individuals of the same species would be found to-gether in the same very small area of matrix; most of the remains from this deposit are completely disarticulated.

This is the first occurrence of an elongated, aquatic body form recorded for the *Ambystomatoidea*. This habitus is also found in *Sirenidae, Amphiumi-dae*, and *Batrachosaurididae* and perhaps in other fossil salamanders known now only from isolated vertebrae, and was a common body form among the salamanders represented in the primarily slack-stream, pond, or marshy deposits of Late Cretaceous and Early Cenozoic time.

Anura

Anura indet.

PU 18571, the proximal end of a urostyle (pl. XX: D) is of importance only in indicating the presence of frogs in the Golden Valley local fauna. All but a few frog families have the double urostylar articulation seen in this specimen, and it is found in both early and advanced groups. The maximum width across the articular surfaces is 2.7 mm.

Reptilia

Testudinata

Dermatemydidae

Baptemys tricarinata HAY, 1908

PU 16798, crushed carapace and plastron; 17402, crushed carapace and pla-stron; isolated shell fragments; 17271, a crushed skull.

Description

The shells are badly crushed and distorted. Both specimens are incomplete posteriorly, above the peripheral bones. The carapace has median and flanking lateral keels. No complete counts can be made of neurals, costals, or periphe-rals.
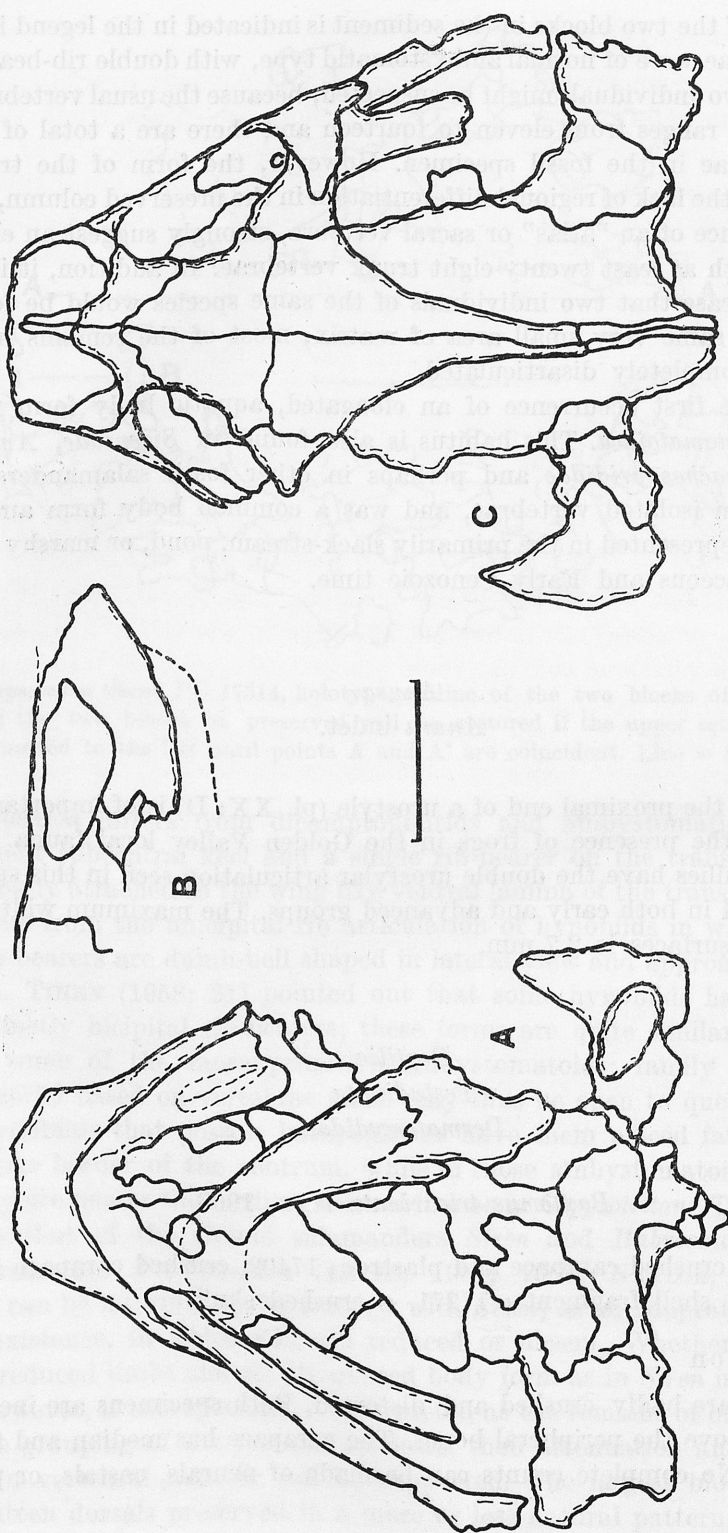
Fig. 3. *Baptemys tricarinata*? PU 17271, questionably referred skull in dorsal (A), ventral (B), and partial right lateral views (C). On the latter, the position of the lower jaw is indicated in dotted line. Line = 10 mm

The skull (Fig. 3) is crushed dorsoventrally. Few sutures can be made out, especially on the palate and postorbital portion of the skull. The orbits were well-exposed dorsally, with some reduction of the interorbital space. The anterior ends of the prefrontals are missing. The postorbital region is crushed and distorted, but a strong supraoccipital crest was present and the temporal region was strongly emarginate. The palate is crushed and occluded by the lower jaws, two hyoid bones (probably the right first branchial and the body of the hyoid, the latter crushed obliquely across the palate), and some unidentifiable bony material. The area of the pericapsular sac is exposed, but both ear regions are crushed and broken.

The descending processes of the prefrontals enclose a teardrop-shaped space between them for the olfactory tracts. The frontals are included in the orbit, but excluded from the temporal fenestra. The postorbital is large, and forms the well-developed postorbital arch. The quadrate does not enclose the stapes posteriorly. The anterior ends of the maxillae are expanded and anteriorly projecting, and, along with the premaxillae, form an essentially straight anterior border of the nares, which are elevated and dorsally oriented. There is a facet on the dorsal edge of the left maxilla, which indicates that the prefrontals originally covered (in part) the orbits dorsally. The maxillary triturating areas are of moderate size, the lateral maxillary borders are sharply defined, and the triturating surfaces have a single, short posteromedial ridge that does not contact the medial or lateral maxillary borders. The medial border is slightly raised but does not form a ridge. The anterior dentary triturating area is crushed flat against the primary palate, leaving the ascending processes of the vomers projecting. The dentary has a very narrow triturating surface anteriorly, and the posterior triturating surface cannot be seen. The dentary extends posteriorly over the surangular.

Discussion

The shell specimens are referred to *Baptemys tricarinata* on the basis of: (1) overall size smaller than in *B. wyomingensis*, (2) epiplastron expanded anterolaterally, (3) bridge region of plastron narrow and long, (4) posterior lobe tapers to a point and apparently not rounded, (5) carapace with three distinct and anteriorly persistent carinae. HUTCHISON (1980) has previously referred Golden Valley Formation specimens to this species. Dr. James DOBIE (Auburn University) is studying the Golden Valley *Baptemys* shells reported here.

A small piece of shell of *Baptemys* type was found near the skull, and reference of the latter to this species is probably correct, although there have been no shell-skull associations for *Baptemys tricarinata* and the present specimens are not directly associated. The dorsally-projecting snout configuration suggests possible use as a snorkeling adaptation, although the nasal region is crushed and the dorsal outline of the snout uncertain. The snout of *B. wyomingensis* resembles that of the Golden Valley Formation skull, although this is not

apparent from the figures in HAY (1908). A similar snout also occurs in the
extant *Dermatemys*; according to HUTCHISON and BRAMBLE (1981) the latter
genus can be derived directly from *Baptemys*. The Golden Valley specimen does
not resemble the skulls of *Trionychidae* and *Emydidae*, the other turtles repre-
sented here in the deposit, and there seems to be no problem in referring it
to *Baptemys tricarinata*. Skulls referred to *B. wyomingensis* by HAY (1908: 273)
differ from the present specimen in having a somewhat more elaborate masti-
catory surface, and possibly a relatively longer skull. Detailed study and compa-
rison of this specimen would be desirable, but are out of the scope of the present
paper.

Emydidae

Echmatemys testudinea (COPE, 1872)

PU 17057, nuchal plate; an unnumbered partial plastron. The lateral bor-
ders of the first vertebral scute diverge anteriorly on the nuchal, and nearly
reach its corners. The plastral fragments are emydid-like but does not have any
outstanding characteristics.

Shells of *Echmatemys* are frequently encountered in Eocene midcontinent
sediments in North America (e. g., GILMORE, 1945; ROBERTS, 1962), and the
shell fragments closely resemble those of *E. megaulax* from the early Eocene
of Wyoming, a species included in *E. testudinea* by HUTCHISON (1980).

Trionychidae

Plastomenus sp.

PU 18714, a left xiphiplastron, and several plastral fragments are preserved.
The xiphiplastra met on a midline suture throughout their length. An exten-
sive plastron of this sort is known in several nominal species of fossil trionychid
turtles, which were grouped as the genus *Plastomenus* by COPE (1873). The
validity of this and many other described trionychid genera has been questio-
ned, and ROMER (1956: 514) included most of them in the synonymy of *Trionyx*.
Specimens having both solid and reduced plastra occur together as far back as
the Late Cretaceous. The name *Plastomenus* is retained here, pending revision
of the fossil forms, to emphasize the distinctive plastron, following ESTES
(1964) and HUTCHISON (1980). The complete plastron may indicate that this
group of trionychids was more amphibious than *Trionyx* (J. H. HUTCHISON
and W. BARTELS, pers. comm., 1987), perhaps more like *Lissemys* in adaptation.

Lacertilia
Anguidae
Glyptosaurinae

cf. *Xestops* sp.

PU 17274, left dentary; 18572, right pterygoid fragment, fragment of left maxilla, and osteoscutes (pl. XXI: D) indicate the presence of a relatively large anguid lizard. The tooth crowns are expanded and bulbous, with a striated cutting edge. The pterygoid bears a large, oval patch of small blunt teeth. The osteoscutes are keeled, the keel usually set at an angle to the long axis of the scute, and are covered with a tuberculate sculpture. A smooth gliding surface is present anteriorly, usually involving one-fourth to one-third of the scute area.

MESZOELY (1970) reviewed the North American anguid lizards, and SULLI-VAN (1979) revised the glyptosaurines. A number of glyptosaurine genera occur in the early Eocene; of these *Xestops*, *Arpadosaurus*, and *Melanosaurus* may have keeled scales and all three of these genera have expanded, bulbous teeth, although the degree of tooth expansion of the latter two taxa is greater than in the former. Body size is also greater in known specimens of *Arpadosaurus* and *Melanosaurus*, so that there may be an ontogenetic factor operating as well. The Golden Valley specimens could thus be referable to any of these three glyptosaurine genera. I have compared them with *Xestops*, the most generalized of the three taxa, because diagnostic materials of species of the other two genera do not occur in this sample.

?*Glyptosaurinae* incertae sedis

PU 17162, a broken left dentary (pl. XXI: B), and 17433, a left dentary fragment, are referable to *Anguidae* in having an intramandibular septum with free ventral border, a smooth sulcus dentalis, and a tendency for Meckel's groove to turn ventrad anteriorly. The teeth are pillar-like, thick walled, with blunt-conical crowns that are finely striated and slightly recurved. The teeth resemble those of "*Glyptosaurus*" *obtusidens* from the Wasatch Formation of Wyoming and New Mexico (Wasatchian, probably early Eocene; GILMORE, 1928). This species, as GILMORE noted, is founded on materials inadequate to confirm reference to *Glyptosaurus*, and is represented by individuals smaller than those of most known *Glyptosaurus* species. SULLIVAN (1979, 1986) has suggested that this species is a nomen dubium. The Golden Valley specimen is 14.4 mm long in total length as preserved, and five teeth occupy about 5.5 mm rather than 6.9 as in the type of "*G*". *obtusidens* so that this fossil is smaller (although not significantly) than known specimens of the latter species. The only other described glytosaurine that has bluntly pointed teeth of this type is *Helodermoides*, an Oligocene taxon. The Golden Valley specimen may be

a young ontogenetic stage of one of the Eocene glyptosaurines, although the bulbous tooth form of the latter is found in very small individuals. The PU specimens may also belong to a new taxon, but the material is inadequate for description.

Varanidae

Saniwa, cf. S. ensidens LEIDY, 1870

PU 17272, three trunk vertebrae (pl. XXI: C), and 17273, a right maxilla, broken anteriorly (pl. XXI: A) resemble those of varanids. Condyle and cotyle are broad, flattened, and face dorsad and ventrad respectively. The sides of the centrum are gently concave. There is no zygosphene or zygantrum.

The maxilla is broken anteriorly, and comes from an individual about half the size of the type specimen of the varanid *Saniwa ensidens*. There is no sulcus dentalis. The teeth are slender, pointed, slightly recurved and flattened cones, and have faint striations at their bases.

The upward-facing, flared condyle and concave-sided centrum with ventrally-facing cotyle indicate a varanid lizard. The maxilla differs in no way except smaller size from that of *Saniwa ensidens* LEIDY, from the Bridger Formation (Bridgerian, Middle Eocene, Wyoming). The dentition of *Saniwa* differs from that of parasaniwids (ESTES, 1964) in being formed of simple, slender, recurved cones, in contrast to the broader, more blade-like, and weakly falciform teeth of *Parasaniwa* and *Paraderma* and the high-crowned unstriated teeth of *Provaranosaurus* (ESTES, 1964, 1976). These specimens were not mentioned by ESTES (1983).

Crocodilia
Alligatoridae
Chrysochampsa gen. n.

Type species. — *Chrysochampsa mlynarskii* sp. n.
Etymology. — Greek, *chrysos*, gold (for the locality); *champsa*, crocodilian.
Diagnosis. — As for the type species.

Chrysochampsa mlynarskii sp. n.

Holotype. — PU 17258, a crushed shell, isolated vertebrae, and osteoscutes (pls. XXII and XXIII).
Referred specimens. — PU 17369, right dentary; 17370, maxillary fragments, maxilla, and premaxilla.
Etymology. — Patronym for Marian MŁYNARSKI, honoring his many years of work in paleoherpetology.

Diagnosis. — A taxon distinguished from all other alligatorid species except *Hispanochampsa muelleri* (KÄLIN, 1936, 1955) in the extremely narrow interorbital portion of the frontal and from all alligatorid species by the great posterior width of the frontal with respect to the proportions of the skull as a whole.

Description

Cracking and dislocation of the specimen make accurate measurement impossible, but the skull originally must have been about 40 cm in total length. Sutures are difficult to determine for the same reason, and crushing prevents
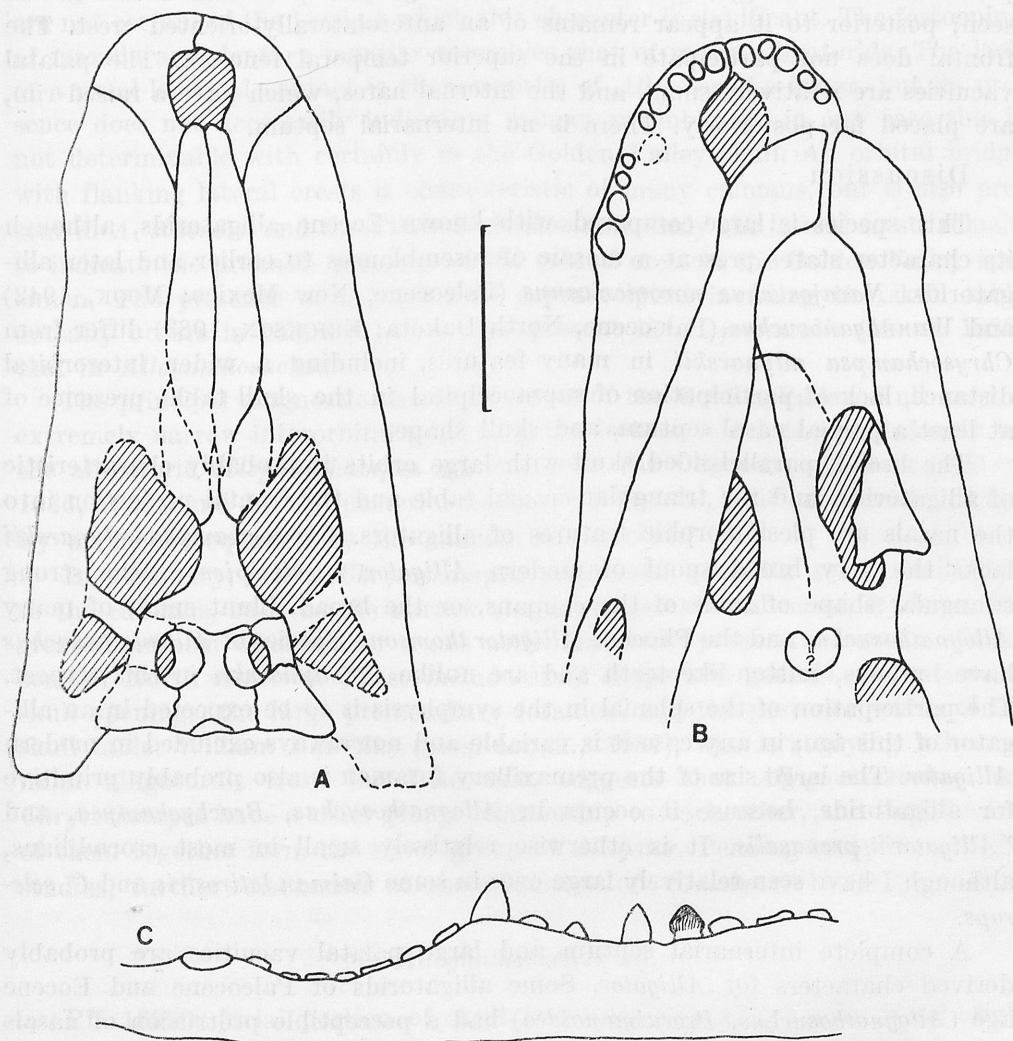

Fig. 4. *Chrysochampsa mlynarskii* gen. sp. n., PU 17258, holotype skull and jaws. Restoration in A — dorsal, B — ventral views; C — lateral view of left dentary. Line = 10 cm for A and B; C not to scale

precise delineation of the skull in lateral view. The lateral margins of the orbits and the lower temporal fenestrae are missing, as are the posterior tips of the mandibles. The bluntly-tapered, delicately sculptured skull bulges anteriorly in the region of the fourth and fifth maxillary teeth.

All mandibular teeth occluded internally to the maxillary and premaxillary series. Of the five premaxillary teeth the fourth is the largest. There are fourteen or fifteen maxillary teeth, the fourth the largest. Most teeth are crushed or missing but appear to have been smooth in the anterior region and blunt and striated posteriorly. The mandibular margin is prominently festooned.

The anteroposteriorly-oriented, oval external nares include only a minute protrusion of the long, slender nasals. On the right, the prefrontal suture can be seen; posterior to it appear remains of an anterolaterally-oriented crest. The frontal does not participate in the superior temporal fenestra. The palatal vacuities are relatively small, and the internal nares, which have a raised rim, are placed far posteriorly. There is no internarial septum.

Discussion

This species is large compared with known Eocene alligatorids, although its character states present a mosaic of resemblances to earlier and later alligatorids. *Navajosuchus novomexicanus* (Paleocene, New Mexico; MOOK, 1942) and *Wannaganosuchus* (Paleocene, North Dakota; ERICKSON, 1983) differ from *Chrysochampsa mlynarskii* in many features, including a wider interorbital distance, lack of participation of supraoccipital in the skull table, presence of at least a partial nasal septum, and skull shape.

The broad, parallel-sided skull with large orbits is probably characteristic of alligatorids, and the triangular cranial table and the frontal projection into the nasals are plesiomorphic features of alligators. *Chrysochampsa mlynarskii* lacks the very broad snout of modern *Alligator mississipiensis*, the strong triangular shape of some of the caimans, or the broad, blunt snout of many *Allognathosuchus* and the Pliocene *Alligator thomsoni*. Species of *Allognathosuchus* have bulbous, button-like teeth and are unlike *C. mlynarskii* in this respect. The participation of the splenial in the symphysis is to be expected in an alligator of this age; in any case it is variable and not always excluded in modern *Alligator*. The large size of the premaxillary foramen is also probably primitive for alligatorids, because it occurs in *Allognathosuchus*, *Brachychampsa*, and *"Alligator" prenasalis*. It is otherwise relatively small in most crocodilians, although I have seen relatively large ones in some *Caiman latirostris* and *C. sclerops*.

A complete internarial septum and large palatal vacuities are probably derived characters for *Alligator*. Some alligatorids of Paleocene and Eocene age (*Allognathosuchus*, *Procaimanoidea*) had a perceptible protrusion of nasals into the external nares that is not seen in *Chrysochampsa mlynarskii*. Related to this is the general size of the naris. In alligatorids that have a partial or complete septum the total area occupied by the external nares is relatively large

and wide, and the nares may be placed far anteriorly. In *C. mlynarskii* and caimans, the nares are relatively small and laterally compressed. Accompanying this in the caimans and *Alligator* is a relatively deep snout and cranium elevated above the snout; the Golden Valley specimen is too crushed to determine this condition with certainly, but it appears to have been more flat.

The lateral sides of the skull table tend to be essentially parallel in *Alligator* and its allies (giving a squared-off appearance), and tend to diverge posteriorly in caimans, although in *A. prenasalis* a caiman-like shape occurs. The outline of the maxillopalatine suture has a squared-off appearance in *Alligator* (again excepting "*A.*" *prenasalis*), and balloons anteriorly in many caimans. *Chrysochampsa mlynarskii* resembles "*A.*" *prenasalis* in this caiman-like feature, but I am not certain of the level at which this character is significant. The festooning of maxilla and dentary margins resembles that of many alligatorids. The lack of a nasal-lacrimal contact is characteristic of *Alligator*-like forms, but its presence does not necessarily indicate a caiman resemblance; in any case this is not determinable with certainly in the Golden Valley skull. An orbital bridge with flanking lateral crests is characteristic of many caimans, but is also present in *A. sinensis*, and the Pliocene *A. thomsoni*. Only the lateral crests remain to indicate the probable presence of the orbital crest in the Golden Valley specimen. The presence of a sculptured supraoccipital invading the skull table dorsally occurs in caimans but is also present in *A. prenasalis* (MOOK, 1932) and in *Allognathosuchus*.

The principal diagnostic character states of the Golden Valley skull are the extremely narrow interorbital portion of the frontal, which is equalled only by the alligatorid *Hispanochampsa muelleri* from the Oligocene of Spain (KÄLIN, 1936, 1955), and by the posterior width of the frontal, which is approached but by no means equalled by the caiman *Paleosuchus*.

In summary, while *Chrysochampsa mlynarskii* presents some similarities to the caimans, such as the narrow shape of the external nares, it shares the greatest number of character states with "*Alligator*" *prenasalis* from the Oligocene of North America. These include skull shape and general proportions of skull openings, the large premaxillary foramen, and the posterior width of the skull table. William BARTELS (pers. comm., 1987), who is studying other similar alligatorids from the Paleocene, suggests that *Allognathosuchus* and *Chrysochampsa* have a sister group relationship to each other, and that the two of them together form the sister group of *Alligator*. Pending completion of his studies, further discussion of the affinities of *C. mlynarskii* is premature.

Allognathosuchus sp.

PU 16990, facial portion of skull and associated fragments; 16902, right and left dentaries; 16996, associated right and left dentaries; isolated left dentary, left premaxilla, and fragments. The skull is one of the best preserved specimens of this genus. The specimen is essentially uncrushed and all sutures are visible.

A number of specimens of this genus is now available (many of them in the Princeton University collection) and revision and study of this peculiar group of crocodilians will be necessary before any specific identification or discussion of these specimens can be attempted.

Crocodylidae indet.

PU 18694, isolated teeth, vertebrae, and osteoscutes. The anterior teeth are smooth and keeled as in *Leidyosuchus* and in some species of *Crocodylus*; the posterior teeth are ribbed, long, and spike-like. The largest of them is 13 mm in anteroposterior diameter, and 30 mm in crown height. The scutes are of commensurate size and have a coarse, deeply-pitted sculpture. The vertebrae, like the scutes, are referred on the basis of size. The specimens indicate the presence of a very large crocodylid (perhaps five meters long), in the fauna. William BARTELS (pers. comm., 1987) suggested to me that this material may be referable to *Leidyosuchus acutidentatus*.

III. SUMMARY AND CONCLUSIONS

Interpretation of the fauna

The Golden Valley local fauna is important for several reasons: (1) it represents a well-preserved sample of lower vertebrates from the early Eocene (Wasatchian), (2) its paleoecology seems to resemble that of the Lance and Medicine Rocks local faunas (ESTES, 1964, 1976b) and is close enough geographically to the latter two so that it can be interpreted as another segment in the Late Cretaceous through Wasatchian midcontinent riparian chronofauna discussed in the above papers, and (3) it gives some indication of the changes that occurred in that chronofauna with the advent of the "geomorphic phase between the forested floodplains of the Paleocene and the alternation of savannah and forest which marks the Early Eocene of the areas farther to the west" (JEPSEN, 1963: 682) that was the result of the rising Rocky Mountains.

The lower vertebrates from the Golden Valley local fauna represent a segment of the midcontinent riparian chronofauna that persisted from at least Late Cretaceous through Wasatchian time in North America. This chronofauna is characterized by amiid and lepisosteid fishes, by a number of genera of aquatic salamanders (usually neotenic and elongated), by a varied group of lizards including a major component of *Anguidae*, by a relatively rich turtle and croco-

dilian fauna (especially in the Wasatchian, which equals the diversity in the Late Cretaceous of the same region; HUTCHISON, 1982), and by temporal trends involving loss of archaic taxa, new records of modern forms, and reduction of lizard diversity.

There is no record of sharks in the Golden Valley local fauna, in contrast with the other faunas noted above. Rays (*Myledaphus*) occur in a correlative Wasatchian fauna (ESTES, 1964) and in the Green River Formation (LOVE, McGREW, and THOMAS, 1963; GRANDE, 1984), some of which is Wasatchian in age. The reduction of sharks in Cenozoic localities appears to reflect the continued retreat of Cretaceous epicontinental seas, although isolated remains of land-locked sharks occur sporadically in other localities (LOVE, McGREW and THOMAS, 1963).

A major similarity between the Golden Valley local fauna and Lance and Medicine Rocks local faunas is in the presence in all of these samples of the fishes *Amia* and *Atractosteus*. These fishes are a persistent primitive link between the ancient chronofauna and the modern Gulf coastal plain ichthyofauna, in which *Amia* and *Atractosteus* also occur.

Other bony fishes do not seem to have been common. Sturgeons are absent from the Golden Valley assemblage and seldom occur in Cenozoic deposits, though they are common in many Cretaceous localities. They are limited in general today to the larger rivers and lakes, and to marine waters. The teleosts may have been abundant but are poorly represented in the Golden Valley sediments. As a group, freshwater teleosts do not become common as fossils in North America until the Green River Formation (Wasatchian-Graybullian; early Eocene).

A major difference between the Golden Valley local fauna and the earlier Lance and Medicine Rocks local faunas is evident in the absence of the salamanders *Habrosaurus*, *Opisthotriton*, *Scapherpeton*, and *Lisserpeton*. This relatively tightly-knit and long-persisting group of elongated and neotenic salamanders characterizes most riparian local faunas of Late Cretaceous and Paleocene age. The reasons for this abrupt change are not clear. The group is replaced in the Golden Valley local fauna by two other salamanders of apparently similar adaptations. Both are almost certainly neotenic and aquatic, and at least one (*Chrysotriton*) is elongated; the other (*Batrachosauroides*) is the earliest fossil record of a genus that persists through the Miocene on the Gulf coast. It is related to the Cretaceous and Paleocene genus *Opisthotriton* (ESTES, 1976). The absence of sirenids from the Golden Valley local fauna may be an artifact of collection or distribution, because GOIN and AUFFENBERG (1957) described *Siren dunni* from the early Eocene of Wyoming.

Among the turtles, *Baptemys* is known from Eocene sediments. *Echmatemys* occurs in a number of other North American Eocene localities. The referred remains of the latter genus clearly indicate the presence of a primitive pond turtle. Close relatives of the trionychid *Plastomenus* occur in the Late Cretaceous

and extend into the Eocene, so that at least the plastomenines form a link between the Golden Valley local fauna and that of the Lance Formation (HUTCHISON, 1982; HUTCHISON and ARCHIBALD, 1986). Thus the Golden Valley turtles are a mixture of persistent and later elements.

Only three genera of lizards occur in the Golden Valley local fauna, continuing a trend toward reduction in numbers and diversity of riparian lizards from Late Cretaceous to Eocene time noted by ESTES (1970). More terrestrial localities might show a different trend, but unfortunately relatively few of these are represented in Late Cretaceous and Early Cenozoic time. The best representation of a more terrestrial situation is the Wasatchian Four Mile local fauna (McKENNA, 1960). At least ten and perhaps more taxa of lizards occur here (including those cited by McKENNA (1960: 10)) and aquatic elements are rare. Nevertheless, within the aquatic and riparian habitats represented by Lance, Medicine Rocks, and Golden Valley localities, the trend towards reduction in numbers and diversity of lizards is marked.

Anguine and glyptosaurine lizards are consistently associated with Late Cretaceous and Early Cenozoic riparian assemblages, a fact which implies that their natural habitat was always near the edge of the water, and suggests that the crushing teeth of *Xestops* may have functioned in cracking the shells of molluscs or arthropods found in or near fresh water. Living lizards with teeth of this type, however, are generally omnivorous, whether or not shell crushing is part of the dietary regime (ESTES and WILLIAMS, 1984). *Saniwa* has been questionably cited as present in the Middle Paleocene of Wyoming (SULLIVAN, 1982; ESTES, 1983); while these latter specimens may be varanid, the Golden Valley specimens appear to be the earliest well documented record of the genus *Saniwa* in North America.

The Golden Valley crocodilians are less diverse than they apparently were in Lancian faunas (three vs. five; HUTCHISON, 1982), although Wasatchian crocodilian diversity as a whole is the same as in the Late Cretaceous (HUTCHISON, 1982). Except for the peculiar *Allognathosuchus* they are of more modern aspect than those from the other two localities.

As is clear from the above discussions, there is little generic similarity between the Golden Valley sample and those from the Paleocene and Cretaceous except for the fishes, in contrast to the much stronger similarity between the Cretaceous and Paleocene samples from Lance and Tongue River Formations (see e. g., ARCHIBALD and HUTCHISON, 1986). It seems apparent that to a degree the lower vertebrates of midcontinent Wasatchian time (with the exception of the lower fishes) paralleled the major changes in many mammalian faunas that occurred at this time (see e. g., JEPSEN, 1963: 675). The similarity between Wasatchian faunas of North America and correlative Sparnacian faunas of western Europe (see e. g., McKENNA, 1972) suggests that these changes may have been influenced by the possibility of intercontinental migrations until the end of the Wasatchian. However, the difference between North American Torrejonian and Tiffanian (Paleocene) and Wasatchian faunas may be less

noticeable when more is known about the former. Only a limited sample is presently available and contains a mixture of earlier Puercan-Torrejonian and Cretaceous types, Eocene types, and unique elements (ESTES, 1976).

Paleoecology

Amia uintaensis, which seems to have reached a size of approximately three meters, indicates that there were large bodies of permanent water available, either sluggish streams or lakes. The Recent *Atractosteus spatula* lives in large, sluggish, silty rivers. Because the fossil and this modern species are closely related, it is perhaps an indication that the Golden Valley habitat was of this type. The presence of both gars and amiids indicates quiet waters, and occurrence together of both amiids and elongated neotenic salamanders indicates absence of any influence by marine or brackish waters.

The turtles and crocodilians probably lived in or near these waters, and the lizards may have been essentially riparian. The frequency and relatively complete preservation of some of the turtle and crocodile material perhaps supports an hypothesis of relatively large and deep bodies of water, also suggested by the large fish, and perhaps indicates that they were buried close to their natural habitat, and were relatively undisturbed so that separation of the various bony elements did not occur.

The total picture presented by the lower vertebrate remains is of an essentially aquatic, amphibious, or riparian community, with little or no evidence of forms that would have lived very far away from the edge of the water.

Department of Biology
San Diego State University
San Diego, CA 92182, U.S.A.

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STRESZCZENIE

Fauna niższych kręgowców z wczesnego eocenu (wasatch) formacji Golden Valley (hrabstwo Stark, Północna Dakota, Stany Zjednoczone Ameryki) jest reprezentowana przez ryby *Amia fragosa*, *A. uintaensis* (*Amiidae*), *Atractosteus occidentalis* (*Lepisosteidae*) i *Teleostei* indet., nieoznaczone płazy bezogonowe, płazy ogoniaste *Batrachosauroides gotoi* (*Batrachosauroididae*) i *Chrysotriton tiheni* (*Dicamptodontidae*), żółwie *Baptemys tricarinata* (*Dermatemydidae*), *Echmatemys testudinea* (*Emydidae*) i *Plastomenus* sp. (*Trionychidae*), jaszczurki cf. *Xestops* sp. (*Anguidae*), ?*Glyptosaurinae* i *Saniwa* cf. *S. ensidens* (*Varanidae*), oraz krokodyle *Chrysochampsa mlynarskii* gen. sp. n., *Allognathosuchus* sp. (*Alligatoridae*) i *Crocodylidae* indet. *Chrysochampsa mlynarskii* gen. sp. n. przypomina najbardziej *Alligator prenasalis* z oligocenu Ameryki Północnej, ale

również współczesne gatunki rodzaju *Alligator* oraz kajmany. Niższe kręgowce z Golden Valley stanowią typową faunę śródkontynentalną, która przetrwała w Ameryce Północnej od co najmniej późnej kredy do wczesnego eocenu. W składzie fauny przeważają formy mniej lub bardziej związane ze środowiskiem wodnym.

Plate XX

A, B — *Amia uintaensis*. A — medial view of PU 17270, left dentary; B — ventral view of PU 18568, basioccipital. C — *Amia fragosa*, PU 18567, fragment of vomer showing pillar-like teeth. D — PU 18571, anterior view of anuran urostyle
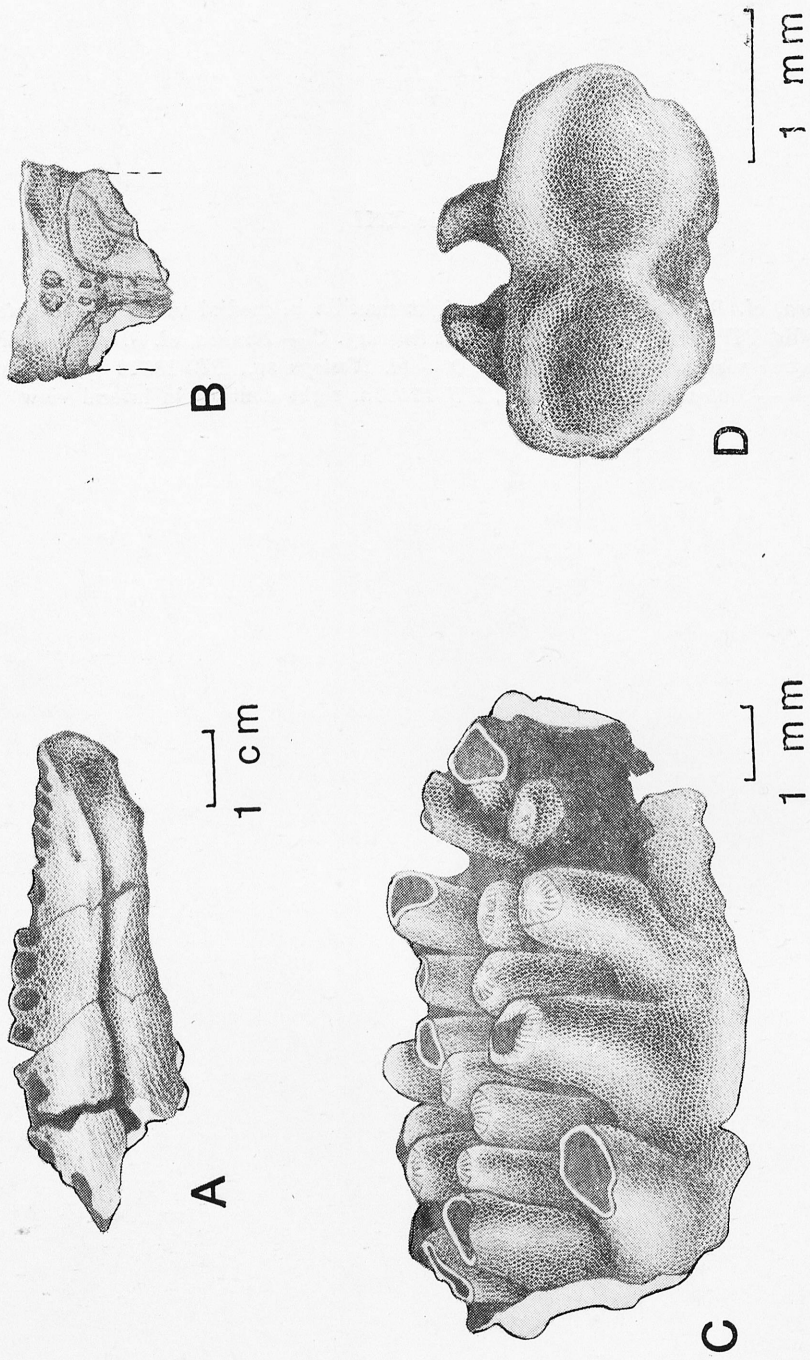
A — *Saniwa, cf. S. ensidens*, PU 17273, right maxilla in medial view. B — *Glyptosaurinae incertae sedis*, PU 17162, medial view of left dentary. C — *Saniwa, cf. S. ensidens*, PU 17272 (part), ventral view of trunk vertebra. D — cf. *Xestops* sp., PU 18572 (part), osteoscute. E — *Batrachosauroides gotoi*, PU 17400a, right dentary in lateral view
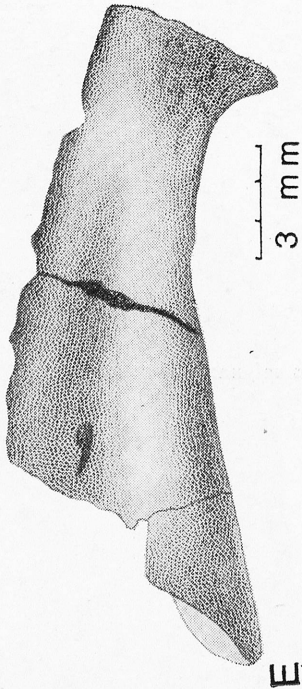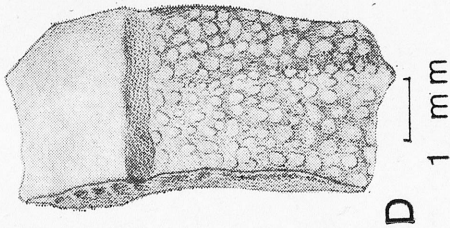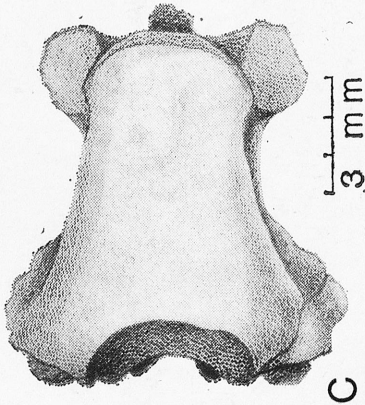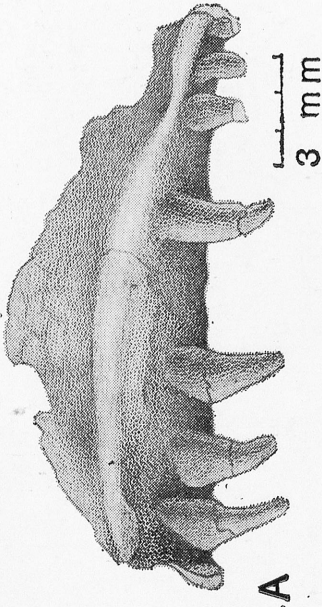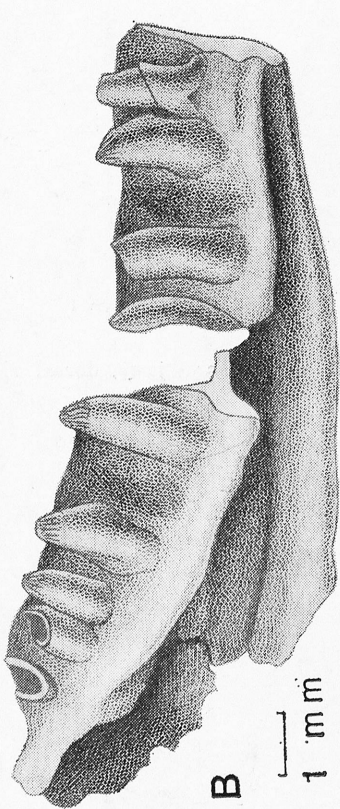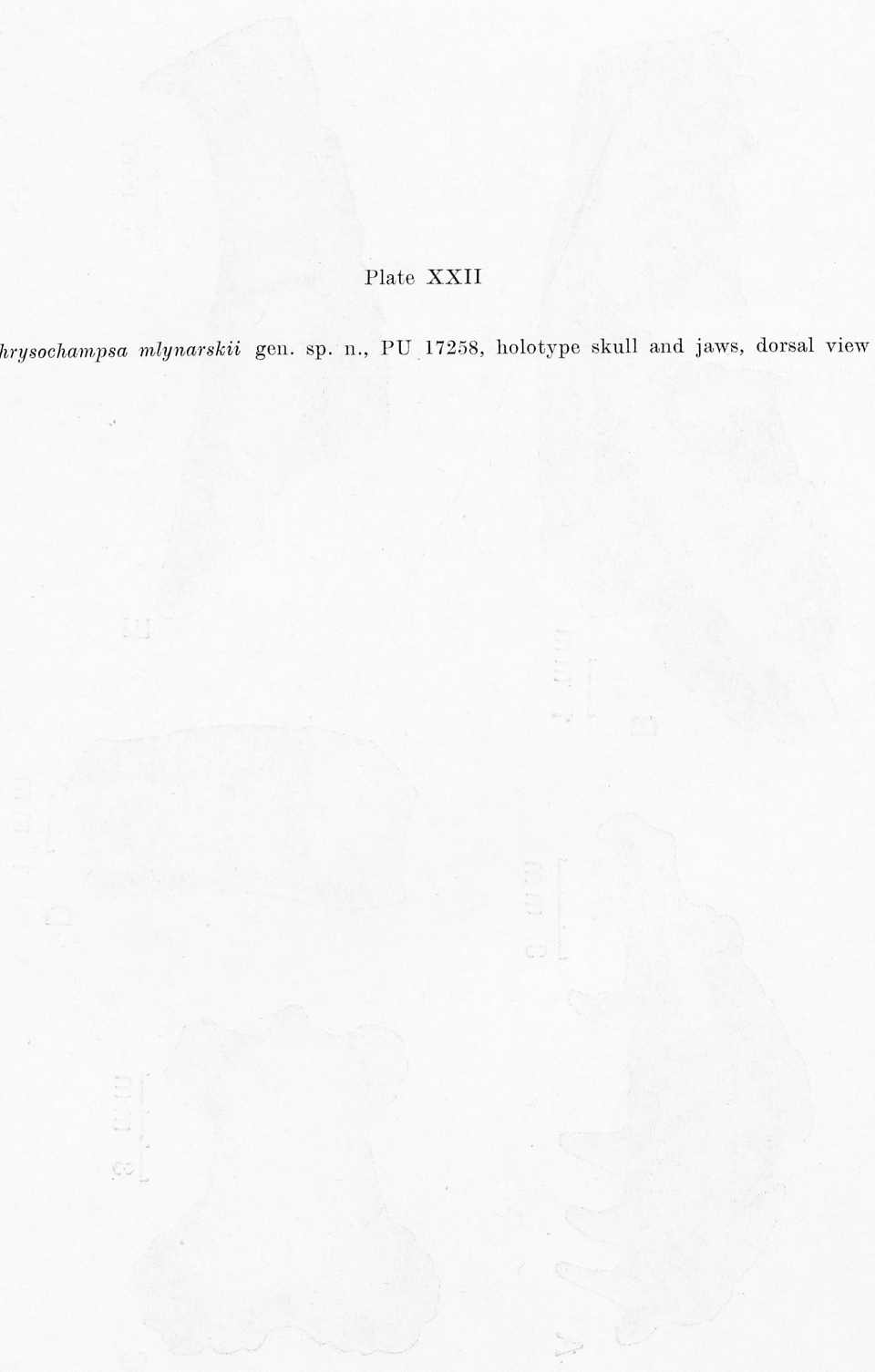
Plate XXII

Chrysochampsa mlynarskii gen. sp. n., PU 17258, holotype skull and jaws, dorsal view
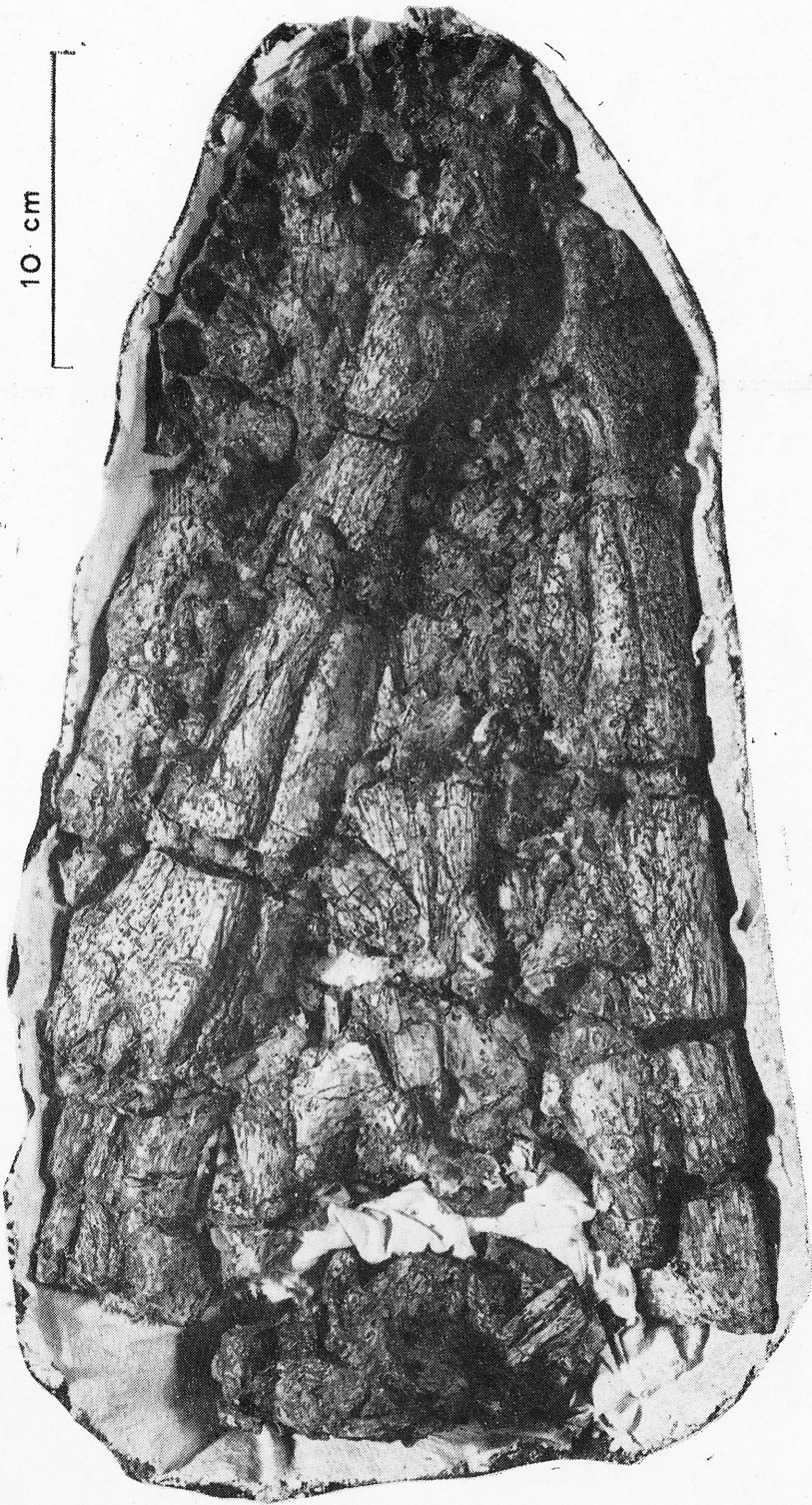
R. Estes

Plate XXIII

Chrysochampsa mlynarskii gen. sp. n., PU 17258, holotype skull and jaws, ventral view

10 cm

R. Estes