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Paleocene Amphibians from Cernay, France

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The early fossil record of European amphibians is not well known. Before the Eocene, the salamanders are represented by *Hylaeobatrachus croyi* Dollo (1884) from the early Cretaceous (Wealden) of Belgium, and by a few late Paleocene forms from Walbeck, Germany: *Wolterstorffiella wiggeri*, *Geyeriella mertensi*, and *Koaliella genzeli*, all described by Herre (1939; 1950). *Koaliella* is clearly a member of the Salamandridae, but the systematic position of the other genera is less certain.

Pre-Eocene European frogs are even more scarce than salamanders. They are represented only by the poorly preserved *Montsechobatrachus gaudryi* and the little-known *Eodiscoglossus santonjae* (see Hecht, 1963), both from Spain. Family relationships are not known for either of these species, though the latter is related to the ascaphids or discoglossids according to Hecht (1963).

Additional material of Paleocene amphibians is thus welcome for the light that it may shed on the ancient European herpetofauna. The presence of amphibians in the Cernay deposits was first noted by V. Lemoine (1889). The Lemoine Collection (now in the Muséum National d'Histoire Naturelle, Paris) contains only a few insignificant amphibian remains. The present study is based on specimens from more recent col-

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lections made by Dr. D. E. Russell, M. Pierre Louis of Reims, and Dr. Jean Braillon of Beauvais. In spite of these recent additions, amphibian specimens still form only a small percentage of the total vertebrate fauna from the Cernay deposits.

The "Conglomérat de Cernay" was first described by Aumonier and Eck (1873). Three principal localities have yielded amphibian fossils, as well as other vertebrate material:

Cernay (Lemoine Quarry, on the northwest part of Mont de Berru)

Berru (Mouras Quarry, on the northeast part of Mont de Berru)

Rilly (on the north slope of the Montagne de Reims, 10 kilometers south of Reims; collection of P. Louis)

Within the deposit, these localities may be considered as virtually synchronous, but they correspond to different facies: conglomeratic at Cernay, sandy and argillaceous at Berru, and predominantly argillaceous at Rilly (Russell, 1964).

During the last quarter of the nineteenth century, Victor Lemoine (a physician of Reims) first described the Cernay fauna, and the mammals were later revised by Teilhard de Chardin (1921-1922). Since 1951, new fossiliferous localities have been discovered and exploited by some excellent amateur collectors, including Mme. R. Lasseron and M. Pierre Louis of Reims, and Dr. Jean Braillon of Beauvais. Dr. D. E. Russell has made major collections since 1958, including several thousand mammalian teeth and many other skeletal remains. This new material shows that 25 genera and 29 species of mammals were members of the Cernay fauna.

A correlation with the North American Paleocene has established the aspect and age of the Cernay fauna as essentially Tiffanian but with a certain element reminiscent of the Clarkforkian (Russell, 1964). In contrast to the mammals, the other Cernaysian vertebrates are still poorly known. Only the fish (Priem, 1908; Janot, 1966) and a few reptiles (especially the dominant element, *Simoedosaurus* Gervais, 1877) have been studied in detail.

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Figures 1, 2, 5-7 were prepared by Mr. Fred Maynard; figure 3 was done by Mr. Chester Tarka, and figure 4, by Miss Tehrie Holden.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History

C.R., Cernay specimens in the Muséum National d'Histoire Naturelle, Paris

M.C.Z., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

GEOLOGIC SETTING

During the late Paleocene (Thanetian=early Landenian), the sea progressively invaded the northern part of the Paris Basin and formed a gulf that ultimately extended to the east slightly beyond the city of Reims. The essentially arenaceous deposits of this Thanetian sea are transgressive on the eroded surface of the Campanian chalk and are collectively designated the Sables de Bracheux. Basally there may be a green flint conglomerate, a "tuffeau" (Tuffeau de la Fère), or a frequently glauconitic clay. The fossils (mollusks, fish, calcareous algae) indicate a warm sea with, however, some cold currents, as revealed by the presence of the mollusk *Cyprina*. Near Reims the marine sediments of Thanetian age pass laterally (southward and eastward) and vertically (upward) into continental facies. West of Reims the sediments are relatively thick and contain an abundant marine fauna (Sables de Jonchery, Sables de Châlons-sur-Vesle). Toward the east and south they thin, become faunistically poorer, pass into almost unfossiliferous, quartzitic, white sands (Sables de Rilly), and finally disappear.

In the same region, the terminal Thanetian is represented by the so-called Conglomérat de Cernay which overlies and channels into the Sables de Rilly. It is a detrital deposit having quite variable facies and thicknesses and in fact rarely merits the name "conglomerate." Although it is generally argillaceous and in many places lignitic, it can become very sandy or conglomeratic. Thus at Cernay (5 kilometers east of Reims) it consists of beds of coarse sand alternating with beds of limestone concretions and rolled elements of diverse nature. This variety of facies corresponds to quite different conditions of sedimentation. The deposit, in its type locality (the Lemoine Quarry, near Cernay), contains numerous marine shells and shark teeth associated with fresh-water and terrestrial elements and is a deltaic deposit. More to the east (Mouras Quarry, near Berru) the marine fauna disappears, and the deposit becomes strictly fluvatile. Throughout its extent, however, the sediments contain numerous remains of vertebrates: mammals, birds, reptiles, amphibians, and fish. The best vertebrate localities occur on the slopes of the Mont de Berru, a Tertiary hill rising from the Cretaceous plain several kilometers east of Reims; the villages of Cernay, Berru, and Nogent-l'Abesse encircle it. This erosional remnant has been separated from the Tertiary heights occurring west and south of Reims. The Conglomérat de Cernay extends to these slopes. Lemoine found it notably at Rilly (10 kilometers south of Reims), Merfy, and Marzilly (8-12 kilometers northwest of Reims), but it is there much less fossiliferous than at Mont de Berru.

More to the south, in the region of Rilly, a lake formed at the end of the Thanetian. Its deposits are the marls and limestones of the Calcaires de Rilly and contain fresh-water as well as brackish-water mollusks.

Still farther south, the Travertin de Sézanne, of the same age, has furnished an excellent flora indicating a warm climate. Information is thus provided on the climatic conditions that prevailed on the land bordering the Thanetian sea (de Saporta, 1868).

SYSTEMATICS

At least three salamanders and two frogs are represented in the Cernay collection. The terminology followed in the discussion below is that of Estes (1964) for the salamander vertebrae, that of Francis (1934) for the salamander skull elements, and that of Hecht and Estes (1960) and Estes and Tihen (1964) for the frog elements.

ORDER CAUDATA

FAMILY SALAMANDRIDAE?

PALAEOPROTEUS HERRE, 1935

Palaeoproteus gallicus, new species

DIAGNOSIS OF SPECIES: In comparison with the type species (*Palaeoproteus klatti*), *P. gallicus* has a weaker atlantal intercotylar process, or none, a relatively shorter first trunk vertebra, a maxilla with a roughened articulation surface dorsally and nutrient structures that left the maxilla through a notch on the posterior surface rather than a foramen. The bones of *P. gallicus* are also slightly more robust than those of *P. klatti*.

TYPE SPECIMEN: C.R. No. 6692, trunk vertebra, somewhat abraded; the neural arch and spine are broken posteriorly. See table 1 for hypodigm.

DESCRIPTION: The type vertebra (fig. 1A-C, F, G) is robust and well ossified. The amphicoelus cotyles are teardrop-shaped and partially coated internally with what appears to be calcified tissue. Ventrally the centrum bears two robust basapophyseal crests, which begin posteriorly near the midline and become more pronounced and laterally divergent as they approach the anterior cotyle. The lower part of the anterior cotyle of the type is broken, but referred specimens show that the crests are continuous with blunt anterior basapophyses, which project below the anterior edge of the centrum. A deep fossa occurs between the basapophyseal crests, and no subcentral keel (hypapophysis) is present. The

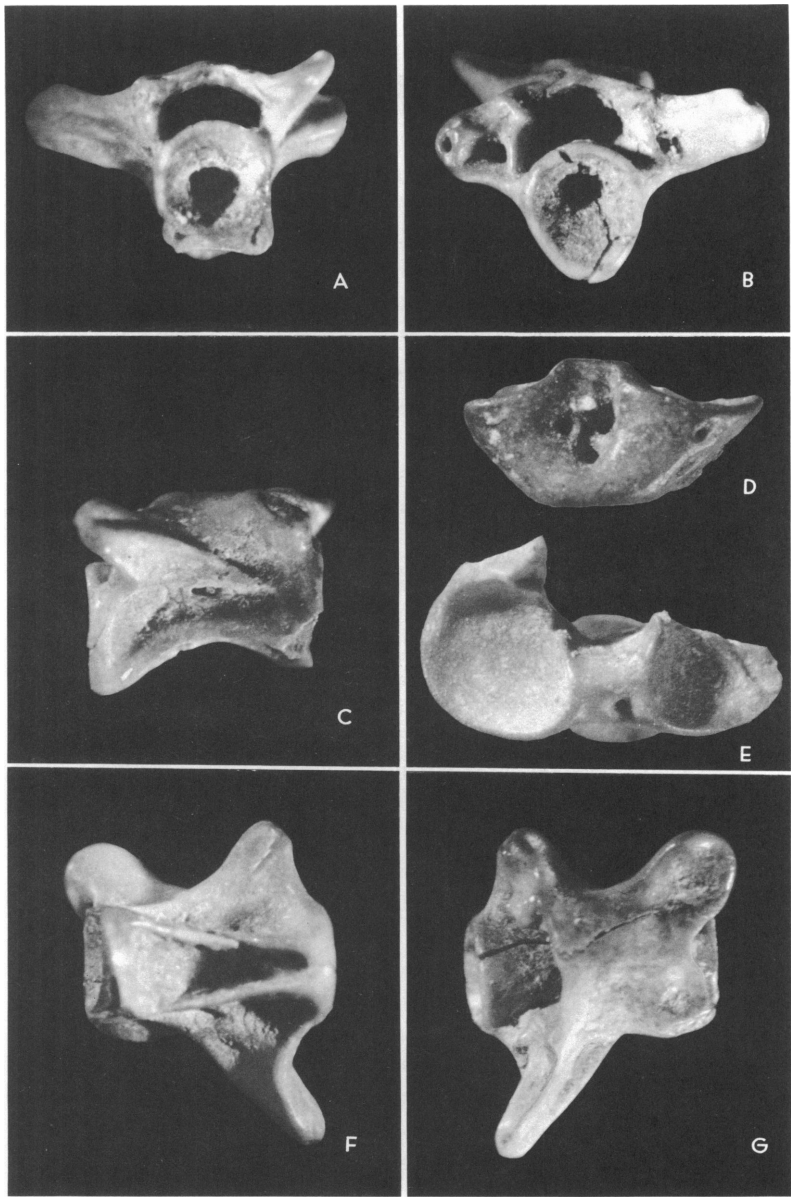


FIG. 1. *Palaeoproteus gallicus*. A-C, F, G. Type specimen, C.R. No. 6692. A. Anterior view. B. Posterior view. C. Right lateral view. F. Ventral view. G. Dorsal view. D. C.R. No. 6689, atlas, ventral view. E. C.R. No. 6688, atlas, anterior view. A, C, G slightly retouched. All $\times 10$.

neural arch is flattened and smooth dorsally, with little indication of a neural spine. The posterior border of the neural arch is broken. The zygapophyses are also broken, except for the left anterior one, which is small, oval, and projects laterally, forming a deep embayment between anterior and posterior zygapophyses. There is no distinct zygapophyseal ridge. The long, slender, transverse processes arise posteriorly close to the posterior zygapophyses and at about the level of the dorsal surface of the neural arch. Both rib-bearers on the type are close together but remain distinct to their tips, even though they are completely connected by bone. There is a narrow ventral lamina on the anterior face of the transverse process. The vertebra is broken, so that the only measurements that can be made are the total length of the centrum (3 mm.) and the minimum width of the neural arch between the anterior and posterior zygapophyses (1.8 mm.). The remaining trunk vertebrae are poorly preserved but show that on posterior vertebrae the transverse processes tend to develop flattened, ventral laminae. The type has only a small ventral lamina and is perhaps middorsal in position.

The first trunk vertebrae (fig. 2F) have relatively much shorter centra than the posterior ones, and a rounded or flattened subcentral keel is present (hypapophysis), widely separating the basapophyseal crests. The first trunk vertebrae also tend to have more calcified tissue in the anterior cotyle than is present in the posterior vertebrae.

The referred atlantes (fig. 1D, E) are robust and well ossified. The cotyles are nearly circular and partially separated by a downward projection of the neural canal. There is little or no intercotylar process. Ventrally there is a slight depression, in which two or three small foramina occur. The neural arches are missing on all specimens.

The symphyseal end of the figured dentary (fig. 3) is broken anteriorly. The bone was apparently relatively short, as is indicated by the referred specimens. The pedicels of 16 teeth are preserved. Though the tips of these are worn, the relatively regular height at which the crowns are missing indicates that the teeth were pedicellate. The Meckelian fossa is deep and is covered dorsally by a prominent projection of the tooth-bearing part of the bone. Posterior to the tooth row the jaw rises sharply to a distinct "coronoid" process. Beyond this point the jaw narrows and seems to have been short. Externally a single foramen is present at the level of the eighth tooth from the rear. Behind the foramen there is a weakly defined but distinct horizontal depression on the external surface of the bone. The maximum length of the figured specimen as preserved is 7.3 mm. Some of the other dentary specimens have the symphysis preserved, which is a simple, elongated oval and relatively little expanded.

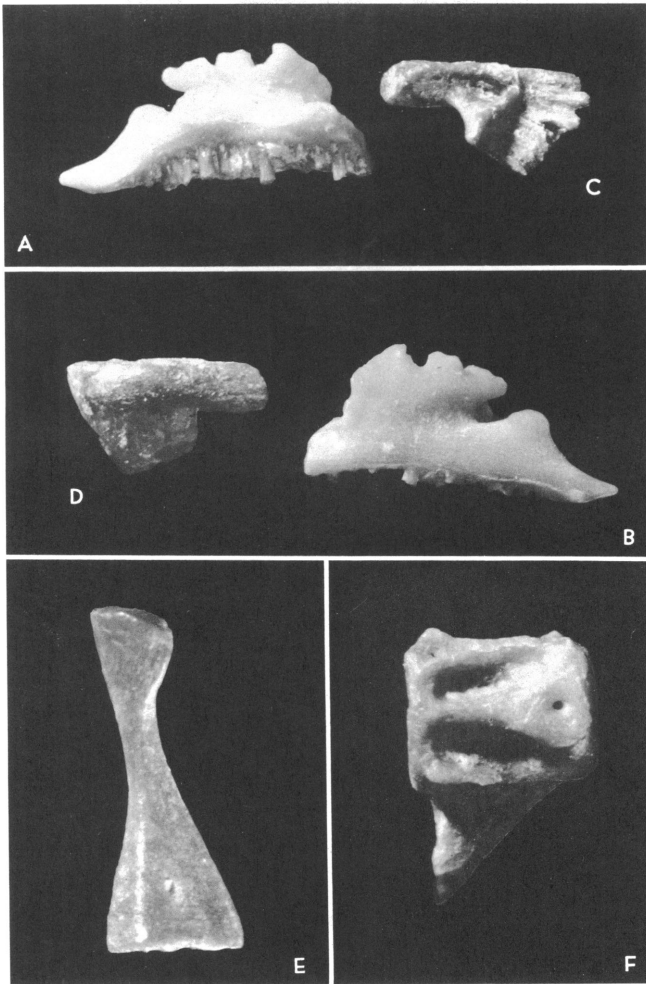


FIG. 2. *Palaeoproteus gallicus*. A, B. C.R. No. 6701, left maxilla. A. Lingual view. B. Labial view. C, D. C.R. No. 6700, left premaxilla. C. Ventral view. D. Dorsal view. E. C.R. No. 6721, first ceratobranchial, ventral view. F. C.R. No. 6693, first trunk vertebra, ventral view. All $\times 10$.

The Meckelian fossa opens in one specimen under the sixth and seventh teeth from the symphysis; in another this point is under the seventh and eighth teeth. Otherwise the specimens are too worn for comment.

The premaxilla (fig. 2C, D) has a smooth external surface and a broad pars dentalis, which shows the worn remains of six tooth pedicels. The pars dorsalis is narrow and subcylindrical and seems not to have en-

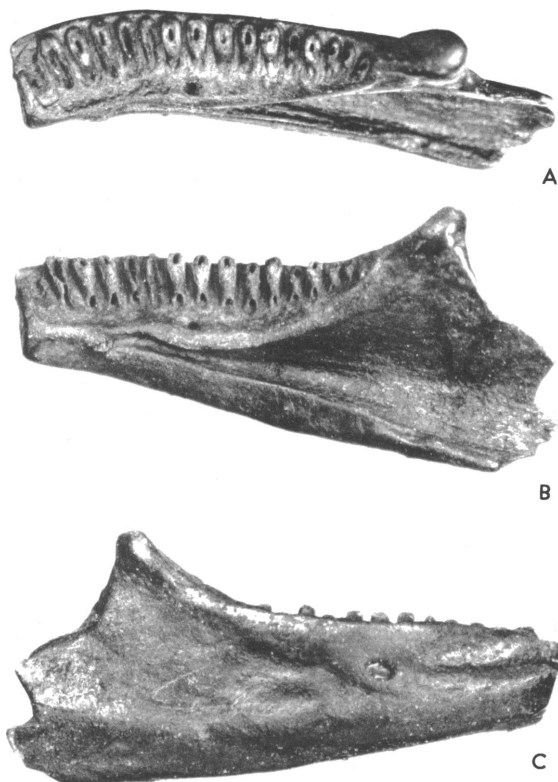


FIG. 3. *Palaeoproteus gallicus*, right dentary, collection of J. Braillon. A. Dorsal view. B. Lingual view. C. Labial view. $\times 10$.

closed a premaxillary gland. The pars dorsalis is broken at its tip. The greatest length of the specimen as preserved is 2.6 mm.

The maxilla (fig. 2A, B) is robust and has a strong pars facialis. The latter is roughened for articulation with more dorsal bones and is transected by a deep groove for vascular and nervous structures. Medially there is a prominent pars palatina, behind which a concavity in the bone perhaps indicates the lateral border of the internal choana. Posteriorly to this concavity a small, dorsally rugose, medial projection occurs immediately dorsal to the tooth row on the medial face of the pars facialis. The greatest length of the specimen is 4 mm.

The first ceratobranchial (fig. 2E) is short, stubby, dumbbell-shaped, and has flattened ends. Its maximum length is 4.2 mm.

DISCUSSION: The fossil remains discussed here clearly belong to the

genus *Palaeoproteus* Herre (1935). The type species is *P. klatti* from the middle Eocene Geiseltal deposits near Halle. One of us (Estes) has confirmed this identification by comparison with the hypodigm of the species in the Museum für Mitteldeutsche Erdgeschichte, Geologisch-Paläontologisches Institut, Halle (Saale). The atlas and several vertebrae were figured by Herre (1935, pl. 2, figs. 13b, e, f, g), and, though these sketches are not particularly clear, it is possible to see the distinctive configuration of the ventral surface of the first trunk vertebra and the equally distinctive, well-developed, basapophyseal crests (labeled hypapophyses by Herre) of the trunk vertebrae. No other described salamander possesses such well-developed crests throughout the vertebral column.

A number of characteristics indicate that the Cernay specimens belong to a species different from *Palaeoproteus klatti*; (1) the atlas has a weaker intercotylar process, or none; (2) the first trunk vertebra is relatively shorter; (3) the maxilla has a strongly developed articulation surface dorsally, and the large nutrient foramen on the maxilla is a notch on the posterior border rather than an enclosed foramen (cf. Herre, 1935, fig. 2); and (4) the bones of the Paleocene form are in general slightly more robust than those of *P. klatti*. None of these differences is sufficient in itself to indicate a specific difference but together seem to justify separation.

The body form of *Palaeoproteus gallicus* seems to have been similar to that of the elongated *P. klatti*. As in the latter, the anterior vertebrae have double-headed rib-bearers, with the two heads closely appressed. However, if the type of *P. gallicus* is actually middorsal in position, as suggested above, then this species has ribbed vertebrae farther posteriorly than in *P. klatti*. Whether the posterior vertebrae were ribless as in the German form cannot be determined on the present material.

The Cernay specimens resemble the North American Cretaceous and Paleocene salamander *Scapherpeton* (Estes, 1964) in having a relatively thin coating of endochondral hard tissue on the inside surfaces of the vertebral cotyles, and in the teardrop shape of the cotyle. The closely appressed rib-bearers of the anterior transverse processes most closely resemble those of anterior trunk vertebrae of *Opisthotriton* (Estes, 1964, fig. 41) and *Amphiuma*. The prominently ridged basapophyseal keels are different from those of any other known salamander. The atlantes are almost identical with those of *Opisthotriton*, except that the intercotylar process is less prominent or entirely lacking in *P. gallicus*, whereas it is usually present as a faint or well-developed ridge in the American form (Estes, 1964, fig. 38; A.M.N.H. No. 8110). The dentary resembles that of *Opisthotriton* in a general way, especially in the shape and distribution of

TABLE 1
LIST OF AMPHIBIAN SPECIMENS FROM THE CERNAY CONGLOMERATE, WITH THEIR LOCALITIES

Cernay, Lemoine Quarry	Mt. Berru, Mouras Quarry	Rilly
<i>Palaeoproteus gallicus</i> , new species		
C.R. Nos. 6688–6691, 6702–6704, atlantes	C.R. Nos. 6705–6708, 6722, atlantes	C.R. No. 6723–6728, atlantes
C.R. No. 6692, type vertebra	C.R. Nos. 6709, 6710, first trunk vertebrae	C.R. Nos. 6729–6738, trunk vertebrae
C.R. Nos. 6693, 6694, first trunk vertebrae	C.R. No. 6711, trunk vertebra	C.R. No. 6739, first ceratobranchial
C.R. Nos. 6713–6717, trunk vertebrae	C.R. No. 6712, dentary	
C.R. Nos. 6695–6699, 6718–6720, dentaries		
C.R. No. 6700, left premaxilla		
C.R. No. 6701, left maxilla		
C.R. No. 6721, first ceratobranchial		
Coll. J. Braillon, right dentary		
	<i>Koaliella</i> sp.	
C.R. Nos. 6740, 6741, trunk and caudal vertebrae		
	Cf. <i>Salamandra</i> sp.	
C.R. Nos. 6742–6744, trunk vertebrae		
C.R. Nos. 6745–6747, humeri		
	Discoglossidae	
C.R. No. 6748, left ilium		
C.R. No. 6749, vertebra		
C.R. No. 6750, left humerus		
	Neobatrachia	
C.R. No. 6752, vertebra		
C.R. No. 6753, right radio-ulna		
C.R. No. 5391, left humerus		

the tooth pedicels and the presence of a posteroexternal depression (Estes, 1964, fig. 39; A.M.N.H. No. 8104). The extreme projection of the “coronoid” process, the relatively short jaw, and the deep Meckelian fossa are especially well developed in the Cernay fossils, but it is worth noting that this general type of jaw occurs in many larval salamanders, each, however, having its own distinctive features.

Functionally, the close appression of the rib-bearers is probably related to the elongated body form and concomitant undulatory locomotion, as is shown by comparison with *Amphiuma means* and with an undescribed skeleton of the elongated *Opisthotriton kayi* from the Paleocene of Wy-

oming. The functional details of this situation are, however, as yet unknown (Auffenberg, 1959). The presence of strong anterior basapophyses is a resemblance to *Amphiuma* and to some ambystomatids, but otherwise the resemblance is slight.

Comparison with other elongated salamanders indicates that *Opisthotriton* was an obligate neotenic salamander, with a skull structure in general resembling that of *Gyrinophilus pallescens necturoides* or *Necturus*, except that large maxillae are present. The resemblance of *Palaeoproteus* dentaries to those of *Opisthotriton*, especially with respect to the strong "coronoid" process, the shape of the tooth-bearing area, and the conformation of the Meckelian fossa, is probably indicative only of the larval habitus of both animals. On the basis of the skull, it is probable that *Palaeoproteus* was at about the same stage of paedomorphosis as *Opisthotriton* or *Amphiuma*.

Herre (1935), in his original study, attempted to show that *Palaeoproteus* was most closely related to the modern genera *Necturus* and *Proteus*. Viewed from more recent knowledge of Recent and fossil salamanders, the similarity is superficial and relies principally on an elongated, perennibranchiate habitus to indicate closeness to *Proteus*. An important factor for Herre's placement of *Palaeoproteus* was the interpretation of the posterior projections of the otic capsules as opisthotics. He stated that these bones were fused with the parietals and showed no anterior suture with the prootics and so figured them: "Der hinteren Teil der Gehörblasen ist mit den Parietalia synostotisch verbunden. Es handelt sich um schalenförmigen Knochen, welche als Opisthotica aufzufassen sind. Diese Knochen springen nach hinten über die Condyli occipitales hinaus und bilden die äussersten Ecken des Schädels" (Herre, 1935, p. 8). Study of the actual specimens by one of us (Estes) confirmed the absence of sutures from the region in question, and there is thus no reason to believe that a separate opisthotic existed in *Palaeoproteus*. Herre's reconstruction of the animal is otherwise basically correct, although his restoration of the skull is diagrammatic and inaccurate in minor details.

Herre (1935, p. 65) attempted to make a case for a relationship of *Necturus* and *Proteus* to the "higher salamanders," specifically the Salamandridae. Other than the presence of the opisthotic, his suggestions were of a general nature and neither confirm nor deny the affiliation. As we note above, the relationship of *Palaeoproteus* to *Necturus* and *Proteus* cannot be substantiated at this time. However, there are a number of characters that indicate that *Palaeoproteus* may be related to the Salamandridae. These are: (1) the presence of more calcified tissue in the anterior cotyles of the anterior dorsal vertebrae, suggesting an approach to the

opisthocoelous condition; this condition is similar to that seen in salamandrid larvae or very young individuals before they become osteologically opisthocoelous; (2) the forked ribs described by Herre (1935, p. 24, fig. 18) occur only in the Salamandridae among recent salamanders (e.g., *Tylotriton*; see Herre, 1935, fig. 21); (3) the general shape and robust nature of the known skull bones resemble the condition in some salamandrids, but such resemblance is weak at best; (4) the wide separation between head and trochanter of the femur most closely resembles the situation in plethodontids and salamandrids (cf. Hecht and Estes, 1960, pl. 3; Herre, 1935, fig. 16b). One of Herre's figures (1935, fig. 16a) shows a different, rather *Necturus*-like configuration of the femur, but this specimen gives evidence of distortion, whereas the other (fig. 16b) does not.

It is always difficult to distinguish larval features of salamanders (whether they are facultative or obligate larvae) from those that distinguish the animals taxonomically. The characters discussed above are admittedly tenuous, but are as clear-cut as any that occur in such animals, and referral to the Salamandridae is not zoogeographically inconsistent. If this assessment of relationships is correct, *Palaeoproteus* is the first member of the Salamandridae to show body elongation. However, the Ambystomatidae, in which elongation had also not been known to occur, is now represented by an undescribed genus from the Eocene of North Dakota that shows elongation approximately similar to that of *Palaeoproteus*. As noted by Estes (1964, 1965), the extensive late Cretaceous and early Cenozoic coastal-plain waterways of North America seem to have supported a diverse fauna of elongated salamanders; perhaps, to some degree, those of the European continent may have as well.

KOALIELLA HERRE, 1950

Koaliella sp.

REFERRED SPECIMENS: C.R. No. 6740, a trunk vertebra; C.R. No. 6741, a first trunk vertebra. For localities, see table 1.

DESCRIPTION: The vertebrae are opisthocoelous and have a relatively compact build (fig. 4). The neural spine of C.R. No. 6740 is capped by a narrow band of dermal bone, which bears a delicate, pitted sculpture. The zygapophyses are small, compact, and set close to the neural arches. The only transverse process preserved (the right on C.R. No. 6740) is expanded and blunt at its tip and not forked into a double rib-bearer. Small but distinct basapophyses are present ventroposteriorly on C.R. No. 6740 but seem to be absent from the poorly preserved C.R. No. 6741.

The maximum length of the centrum of C.R. No. 6740 is 2 mm.; of C.R. No. 6741, 1.5 mm.

DISCUSSION: The combination of opisthocoealous centrum, relatively large neural arch, and the fact that the neural spine is capped by dermal bone indicate reference of these specimens to the Salamandridae.

Basapophyses have been stated to be absent from salamandrids (Teege, 1956; Auffenberg, 1961; Estes, 1964), but one of us (Estes) has recently found small basapophyses on some Recent salamandrids (e.g., *Salamandra salamandra hispanica*, M.C.Z. No. 8083), in addition to the evidence of this Cernay specimen. The structures are present in only a few individuals, however, and are thus not characteristic of the Salamandridae.

TABLE 2
VERTEBRAL INDICES [(LENGTH OF CENTRUM/TOTAL VERTEBRAL HEIGHT) \times 100]
OF VARIOUS SALAMANDRIDS

Taxon	Specimen	First Dorsal	Tenth Dorsal
<i>Neurergus crocatus</i>	M.C.Z. No. 24182	84	114
<i>Koaliella</i> sp.	C.R. No. 6740	74	—
	C.R. No. 6741	—	109
<i>Koaliella genzeli</i>	Herre (1950, fig. 14)	85	—
	Herre (1950, fig. 15)	—	107
<i>Tylototriton andersoni</i>	M.C.Z. No. 22515	63	102
<i>Cynops ensicaudus</i>	M.C.Z. No. 518	78	90
<i>Notophthalmus viridescens</i>	M.C.Z. No. 1146	79	97
	M.C.Z. No. 32402	74	74
	M.C.Z. No. 32404	70	91
<i>Notophthalmus meridionalis</i>	M.C.Z. No. 5231	69	89

The general shape of the specimens as well as the narrow extent and fine texture of the dermal cap on the neural spine resembles the condition in the Recent genera *Cynops*, *Notophthalmus*, and *Neurergus*, but shows closest accord with the last. *Neurergus* also agrees with *Koaliella* in the blocky, compact, vertebral shape. Vertebral indices of the fossil and selected Recent individuals are compared in table 2. The first dorsal (second vertebra) of salamanders has a relatively higher neural spine and relatively shorter centrum than other vertebrae in the same vertebral column. It can thus be identified by its index (relative to more posterior vertebrae) as well as by a number of other morphological characteristics such as the angle of the transverse processes and the distribution of the dermal bone (if present). This situation is similar both in late premetamorphosed and postmetamorphosed individuals.

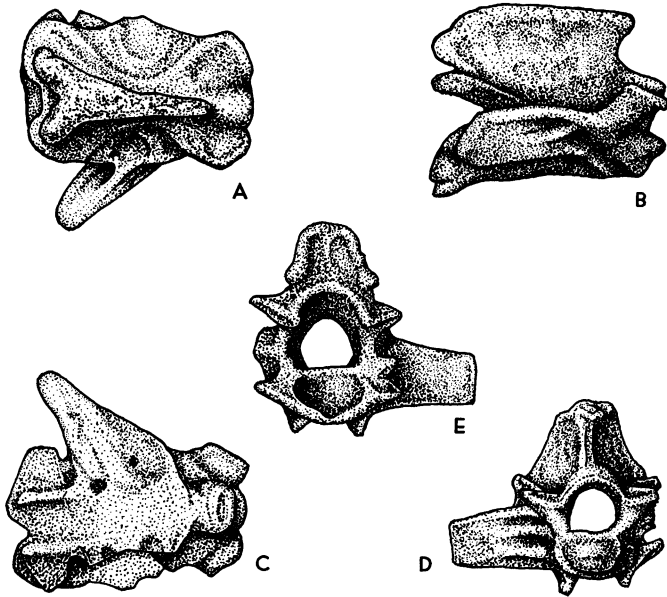


FIG. 4. *Koaliella* sp., trunk vertebra, C.R. No. 6740. A. Dorsal view. B. Right lateral view. C. Ventral view. D. Anterior view. E. Posterior view. $\times 10$.

It is interesting to note that trunk vertebrae of *Cynops* and *Notophthalmus* have ratios ranging from 74 to 97 as a result of their relatively high neural arches throughout the column, whereas the supposedly primitive *Neurergus* and *Tylototriton*, and the Cernay specimen, have relatively lower spines and higher ratios. An admittedly questionable ratio derived from Herre's figure of the Walbeck salamandrid *Koaliella genzeli* (Herre, 1950, fig. 15) is in the same general range as the last-mentioned specimens. Though it is certainly dangerous to derive quantitative data from figures of specimens, this index is probably accurate within the order of magnitude dealt with here. In any case, the Cernay specimen C.R. No. 6740 has a relatively lower neural spine than does any available Recent salamandrid of comparable sort, except *Neurergus*, and in this respect seems also to resemble the Walbeck specimen. Among Recent newts, *Neurergus* shows the closest resemblance to *Koaliella* and is perhaps most closely related to it.

Thus, in general shape, small, closely set zygapophyses, and relatively low neural spine with a thin crest of dermal bone, the Cernay specimens show greatest resemblance to the Walbeck salamandrid *Koaliella genzeli* Herre (1950) and are in all probability referable to that genus. Such

reference is not inconsistent with other faunal similarities between Cernay and Walbeck noted by Russell (1964).

Based on the single preserved transverse process, the Cernay specimen differs from the Walbeck specimens in having an unforked rib-bearer, but without more material this difference is difficult to interpret. In some Recent specimens the normal bipartite rib-bearer of the transverse process is single and blunted on a given vertebra. This condition is also characteristic of the first postsacral vertebra, which is otherwise often similar to the more anterior trunk vertebrae.

The presence of basapophyses on the Walbeck specimens is suggested by Herre's rather generalized figures, but he said nothing in the text to indicate their presence. Unfortunately the specimens have been temporarily mislaid, so that the condition cannot be confirmed at this time.

Cf. *Salamandra* sp.

REFERRED SPECIMENS: C.R. Nos. 6742, 6743, trunk vertebrae; 6744, caudal vertebra; 6745, 6746, proximal humeri; 6747, distal humerus. For localities, see table 1.

DESCRIPTION: The vertebrae are opisthocoelous, but the condylar ball of C.R. Nos. 6742 (fig. 5B, C) and 6744 is not completely ossified anteriorly. The neural spine of the trunk vertebra, C.R. No. 6742, is faint, no dermal ornamentation is present, and it has a small fossa at the posterior border. The comparable area on the other vertebrae is not preserved. Basapophyses are absent; both vertebrae are smooth ventrally. The humeri (fig. 5A, D, E) are broadly expanded proximally and have prominent trochanters. Their proximal articulation surfaces are broken at the tips. The maximum length of C.R. No. 6742 is 3.5 mm.; of C.R. No. 6743, 2.7 mm.

DISCUSSION: These vertebrae are distinguished from all vertebrae of *Palaeoproteus* by the absence of basapophyseal keels and by opisthocoely; from those of *Koaliella* they differ in being of larger size and in lacking a dermal ornament or neural spine. The flattened condylar end of C.R. No. 6742 appears to differ strongly from the constricted condyle of C.R. No. 6743 (cf. fig. 5B, F), but such a lack of ossification appears occasionally as an individual variant in modern salamandrids, especially in the anterior caudal region. The lack of condylar ossification on C.R. No. 6742 and the reduced dorsal rib-bearer on C.R. No. 6743 may indicate that both were first post-sacral vertebrae, by analogy with recent species, but the material is so poor that no decision can be made with any confidence.

The completeness of ossification of the humeri indicates that they

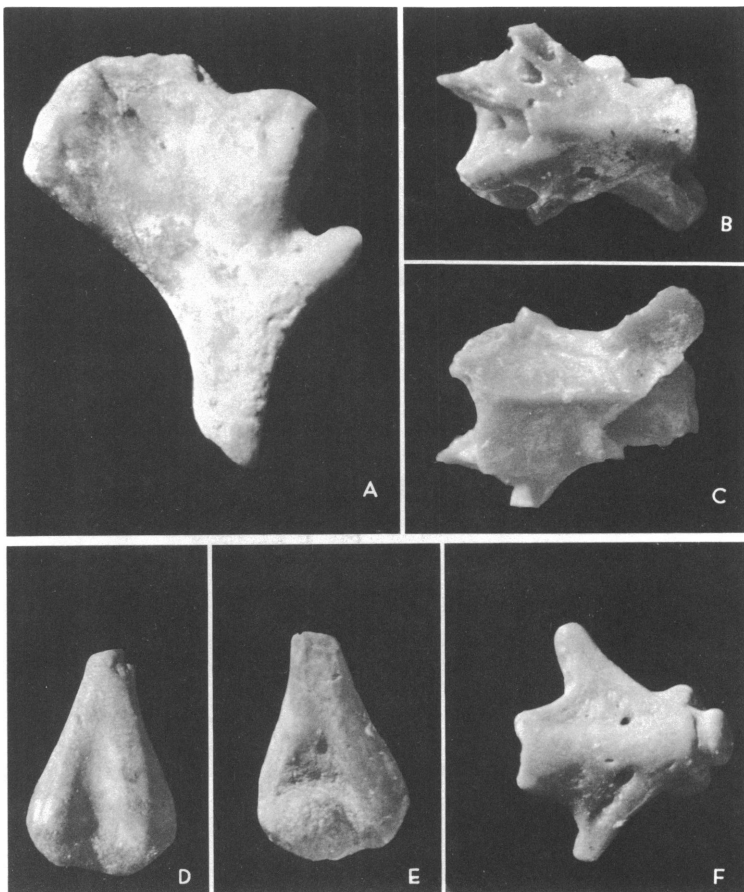


FIG. 5. Cf. *Salamandra* sp. A. Proximal right humerus, C.R. No. 6746, lateral view. B, C. Trunk vertebra, C.R. No. 6742. B. Ventral view. C. Dorsal view. D, E. Distal humerus, C.R. No. 6747. D. Medial view. E. Lateral view. F. Trunk vertebra, C.R. No. 6743, ventral view. All $\times 10$.

probably belonged to fully metamorphosed adults, for it is characteristic of larvae of terrestrial forms as well as of perennibranchs that the humerus is small and poorly ossified terminally. The humeri of *Palaeo-proteus klatti* are subcylindrical without noticeable processes (Herre, 1935, p. 24), and the Cernay specimens are too large to be referred to *Koaliella*.

It is worth noting here that the distal humerus of salamandrids resembles that of frogs if the articular ball is well ossified (see fig. 5D, E). Since the ball (even if ossified) is relatively small, it appears superficially

similar to that of frogs of the family Pipidae, and in an early stage of this study was in fact identified as belonging to that family. However, the pronounced fossa on the dorsal (posterior) surface of the humerus distinguishes the salamander humerus from that of any frog.

Among the Salamandridae only *Salamandra*, *Mertensiella*, and *Chioglossa* have vertebrae with flattened neural arches. Other salamandrids develop noticeable neural spines (e.g., *Triturus*) which may be capped with dermal bone (e.g., *Notophthalmus*). These fragmentary specimens indicate the presence of a metamorphosed salamandrid of the *Salamandra* type. The related *Mertensiella* and *Chioglossa* tend to have more delicate, elongated vertebrae than does *Salamandra*, and the fossils agree with the latter in this respect. Beyond this the specimens are too fragmentary for discussion, and are here compared only with *Salamandra*.

ORDER SALIENTIA

SUBORDER ARCHAEOBATRACHIA

FAMILY DISCOGLOSSIDAE

Indeterminate genus and species

REFERRED SPECIMENS: C.R. Nos. 6748, left ilium; 6749, vertebra; 6750, humerus. For localities, see table 1.

DESCRIPTION: The distal ilial shaft is missing, the iliopubic symphysis is badly abraded, and the dorsal prominence is broken. The ilium has a prominent iliac synchondrosis, a prominent dorsal prominence characterized by a bipartite dorsal protuberance, and a large acetabular region which extends to the posterior border of the very small ventral acetabular expansion (fig. 6A, B). The ventral border of the acetabulum is about 2.8 mm. long, and the anterior dorsal protuberance is about 1.6 mm. long. No other complete measurements can be made.

The vertebra has a weak transverse process which extends perpendicularly to the anteroposterior vertebral axis and is thus either the fourth or fifth vertebra, most probably the fourth. It is amphicoelous, with a persistent notochordal canal. The length of the centrum is about 1 mm.; the width across the transverse processes, about 4 mm.

The humerus is incomplete proximal to the prominent olecranon scar. The humeral ball is prominent, rounded, and has a diameter slightly less than 2 mm. The lateral and medial epicondyles are abraded, but the medial condyle seems to have been only slightly more prominent than the lateral one (fig. 6C, D).

DISCUSSION: The prominent iliac synchondrosis is characteristic of the

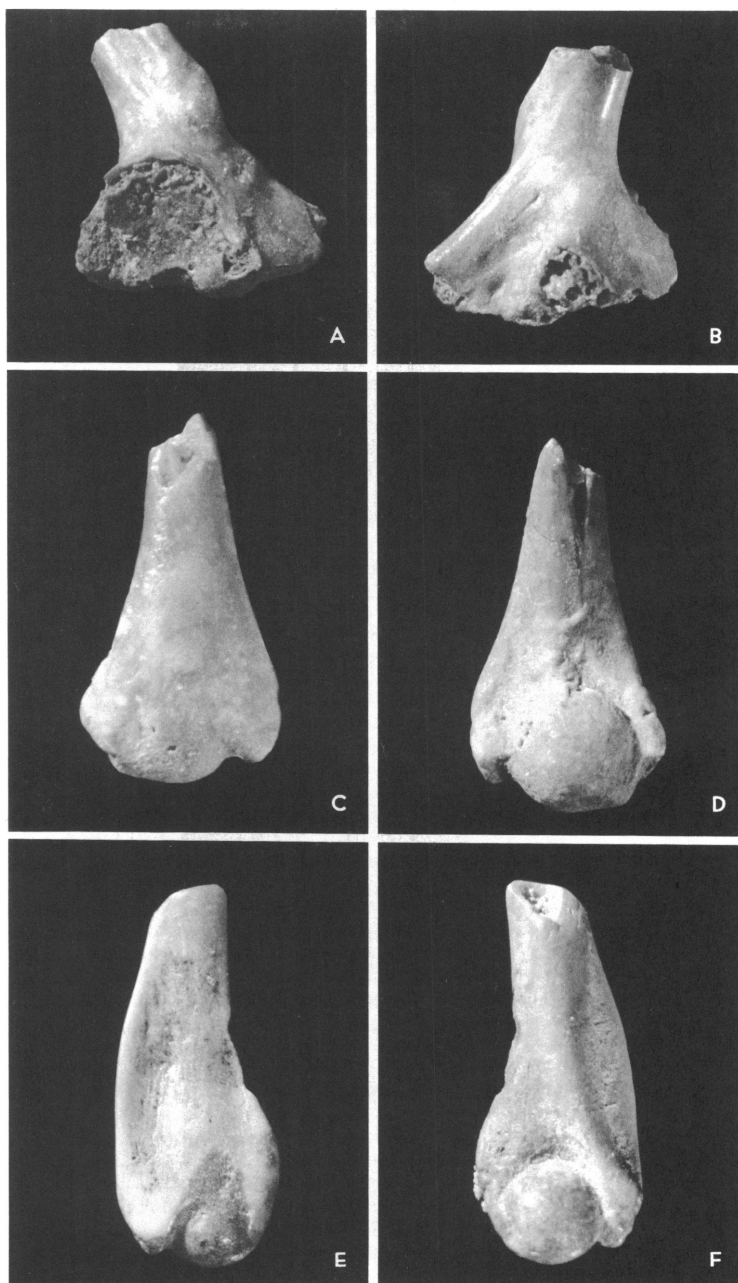


FIG. 6. A-D. Discoglossidae. A, B. Proximal left ilium, C.R. No. 6748. A. Lateral view. B. Medial view. C, D. Questionably referred left distal humerus, C.R. No. 6750. C. Medial view. D. Lateral view. E, F. Neobatrachia, left humerus, C.R. No. 5391. E. Medial view. F. Lateral view. All $\times 10$.

Philippine genus *Barbourula* and an as yet undescribed genus from the early Oligocene (Tongrian) of Belgium (Hecht and Hoffstetter, 1962). The specimen further resembles the Belgian form in the presence of the bipartite dorsal protuberance. The anterior portion of the dorsal protuberance was probably the point of attachment of the iliofemoralis. A narrow groove separates this area from the posterior portion, and the latter was probably the point of attachment of the iliofibularis (Noble, 1922). The presence of the bipartite dorsal protuberance differs from the single specimen of *Barbourula busuangensis* available to us (M.C.Z. No. 25656) and indicates that the early Oligocene fossils noted above, the fossil described here, and the late Cretaceous specimen described and questionably referred to *Barbourula* by Estes (1964) may be congeneric, since all of them possess this character.

A complete trunk vertebra and a humerus can be allocated to the Discoglossidae on a tentative basis. The vertebra is similar to vertebrae of specimens referred to the *Barbourula*-like discoglossid from the Tongrian of Belgium mentioned above. The humerus is not distinctive, but resembles the humeri of discoglossids in general in the shape and orientation of the olecranon scar.

SUBORDER NEOBATRACHIA

FAMILY INDETERMINATE

Various specimens belonging to this suborder are discussed *seriatim* below.

1. The distal half of a left humerus, C.R. No. 5391, is about 2.5 mm. long. The humeral ball is hemispherical and has an approximate diameter of 0.8 mm. in the distal-proximal axis and 0.75 mm. in the medio-lateral axis. The prominent medial epicondyle is clearly demarked from the humeral ball. The lateral epicondyle is reduced to a slight ridge which expands proximally into a large flange, which joins the main shaft above the deep but indistinctly demarked fossa cubitus ventralis. Similarly, from the proximal part of the medial epicondyle, there develops a flange that is less prominent than the lateral epicondylar flange but attains a greater length. This flange gradually joins the main axis at the level of the proximal end of the specimen. The olecranon scar is small and is about 0.75 mm. at its greatest length and about 0.9 mm. at its greatest width (fig. 6E, F).

The chief characteristics of this specimen are its prominent medial epicondyle, reduced lateral epicondyle, deep but not clearly demarked fossa, well-developed ball, and large epicondylar flanges. The development

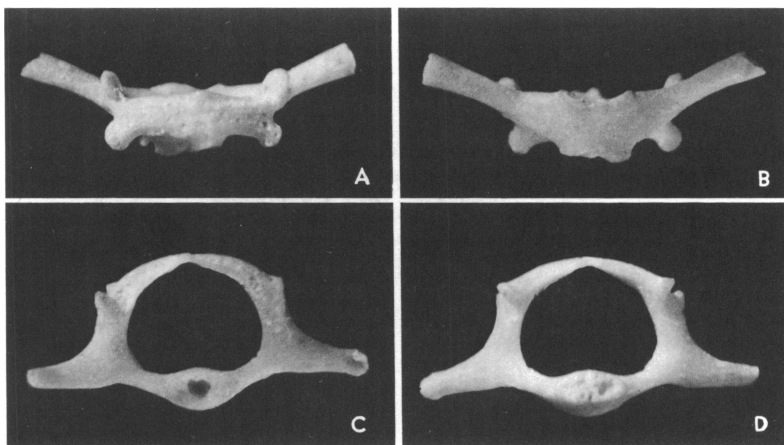


FIG. 7. Neobatrachia, vertebra, C.R. No. 6752. A. Dorsal view. B. Ventral view. C. Anterior view. D. Posterior view. $\times 10$.

of the flanges may be merely a sexually dimorphic feature perhaps indicating that the specimen was a male. In the remaining combination of features the fossil resembles members of the Ranidae, the Hyperoliidae, and the Microhylidae.

2. A right proximal radioulna, C.R. No. 6753, may be neobatrachian but is not distinctive enough for discussion.

3. A second(?) vertebra, C.R. No. 6752, is procoelous and bears a small pit in the cotyle which is perhaps an indication of a persistent notochord. The vertebra has a relatively short centrum and transverse processes which arise at the level of the ventral surface of the centrum. The centrum is incomplete, and the condyle surface is abraded. The dorsal portion of the neural arch has a maximum length of 0.6 mm. The maximum width of the vertebra across the transverse processes is about 4.5 mm. (fig. 7).

The procoelous centrum indicates relationship to a limited number of living families. The presence of a notochordal pit may indicate that the fossil came from a young animal, since a persistent notochord is not usual in adult members of the living procoelous families of frogs. The narrow neural arch apparently did not overhang the posterior vertebra. The transverse processes of the fossil arise at the level of the ventral surface of the centrum, a condition indicating the anterior position of this vertebra in the column, but in only one of approximately 30 species (in 12 genera) of hylids examined was the position as low as it is in the fossil. The combination of characters found in this fossil indicate that

the specimen may be referable to the Hylidae or to a related family, but no formal allocation is made here.

In summary, the Cernay neobatrachian fossils indicate similarities to the Hylidae, the Rhacophoridae, the Ranidae, the Microhylidae, and the Phrynomeridae, but the material is insufficient for formal allocation to be made to any of these families.

ZOOGEOGRAPHY AND PALEOECOLOGY

The Cernay fishes include sharks, rays, and amiids. The last-named occur today only in North America. Regardless of the presence of marine sharks, the amiids and amphibians indicate strictly fresh-water deposition of the sediments. The geology, as noted above, indicates that the site of deposition was near the boundary of the Thanetian sea in the Reims area. It is probable that the predominantly marine sharks and rays were entering the local fresh waters or being landlocked in lakes, as noted for the fauna in the Paleocene Waltman Lake in Wyoming by Love, McGrew, and Thomas (1963) and the Cretaceous of Wyoming by Estes (1964).

The short limbs and concomitant undulatory locomotion of *Palaeoproteus* indicate that the conditions of preservation and deposition must be associated with permanent water. *Koaliella*, on the basis of its resemblance to Recent aquatic newts, was also probably an aquatic form. Since some modern newts occur in relatively warm, lowland areas (especially some of the Oriental forms), they cannot be used to indicate climatic conditions, even though many of the recent species are found in cooler mountainous areas. The reference to cf. *Salamandra* is too tenuous to be used in paleoecological analysis. The resemblance of the discoglossid frog to the modern aquatic *Barbourula* indicates that at least one of the fossil frogs described here was of probably aquatic habit. Discoglossids seem to have always been a Northern Hemisphere group. They barely reach into the tropical regions today and are associated with a humid, permanently watered habitat.

The presence of a *Barbourula*-like discoglossid, with the similar Cretaceous and Oligocene forms described by Estes (1964) and Hecht and Hoffstetter (1962), respectively, indicates that distribution of this group of discoglossids was once Holarctic.

Palaeoproteus, *Koaliella*, and cf. *Salamandra* are consistent with the present-day occurrence of salamandrids. If there is any relationship of *Koaliella* and the Recent *Neurergus* it would tend to strengthen an Asian aspect of the Paleogene European herpetofauna, since *Tylotriton* is already

TABLE 3
COMPARISON OF SELECTED CERNAY AND LANCE FORMATION LOWER VERTEBRATES
OF THE SAME TAXON OR OF COMPARABLE ECOLOGY

Lance Formation	Cernay Conglomerate
Elasmobranchs of anadromous type	Elasmobranchs of marine type
Sting rays	Eagle rays
Amiids	Amiids
<i>Lepisosteus</i>	Not present in the Cernay conglomerate but does occur in associated Thanetian marine deposits (Priem, 1908)
<i>Opisthotriton</i> , <i>Habrosaurus</i>	<i>Palaeoproteus</i>
—	<i>Koaliella</i>
—	Cf. <i>Salamandra</i>
Cf. <i>Barbourula</i> (see text)	Discoglossidae (see text)
<i>Champsosaurus</i>	<i>Simoesosaurus</i>
Crocodylians	Crocodylians
Lizards	Lizards
Turtles	Turtles

known from the Eocene (Herre, 1935), and *Andrias* is common in the Oligocene and Miocene of Europe.

The Cernay reptiles include the aquatic champsosaur *Simoesosaurus*, the lizard *Necrosaurus*, other lizards of smaller size (including lacertids and an amphisbaenid), crocodiles, and turtles.

In general the lower vertebrates suggest (as noted by Russell, 1964, p. 269, on the basis of the mammalian fauna) a riparian and aquatic assemblage living on a coastal plain. Permanent, rather quiet waters are indicated by the amiids and elongated salamanders. The general composition of the fauna somewhat resembles that from the Lance Formation (Estes, 1964; table 3, this paper) and probably reflects a similar physiographic situation, providing support for Russell's suggestions. The lower vertebrates are less abundant and diverse in relation to the higher vertebrates than they are in the Lance Formation, suggesting a warm-temperate climate as opposed to the more subtropical aspect of the Lance fauna, but, since ecological (near marine conditions) and depositional factors may also have been important in determining these proportions, this fact should not be used in paleoecological analysis. The climate during the early Eocene Geiseltal deposition was subtropical and the Geiseltal fauna also included *Palaeoproteus*. Moreover, Sittler and Millot (1964) indicated that on both sedimentary and paleobotanical grounds the Paleogene climate in France was tropical or subtropical from late Cretaceous to late Oligocene.

SUMMARY

The late Paleocene (Thanetian) salamanders from Cernay, France, include *Palaeoproteus gallicus*, new species, *Koaliella* sp., and cf. *Salamandra* sp. *Palaeoproteus* has been known formerly only from the middle Eocene Braunkohle near Geiseltal, Germany. Evidence indicates that this elongated perennibranch is perhaps a member of the Salamandridae; it is not related to *Necturus* or *Proteus*. *Koaliella* is known also from the late Paleocene Walbeck deposits of Germany and resembles *Neurergus* and *Tylotriton* among modern salamandrids. Cf. *Salamandra* is known from only a few specimens but most closely resembles the modern genus.

The frogs from Cernay include a discoglossid and unidentified neobatrachians. The discoglossid resembles *Barbourula* and indicates an extension back to the late Paleocene for this particular group of discoglossids in Europe.

Comparison of the Cernay and late Cretaceous Lance Formation lower vertebrates indicates a similar subtropical flood-plain setting near marine waters for both localities.

LITERATURE CITED

- AUFFENBERG, W.
1959. The epaxial musculature of *Siren*, *Amphiuma* and *Necturus* (Amphibia). Bull. Florida State Mus., vol. 4, pp. 253-265, 2 figs.
1961. A new genus of fossil salamander from North America. Amer. Midland Nat., vol. 66, pp. 456-465, 5 figs.
- AUMONIER, J., AND A. ECK
1873. Notice sur la constitution géologique de la montagne de Berru. Reims, Imprimerie Coopérative, xi + 68 pp.
- DOLLO, L.
1884. Note sur le batracien de Bernissart. Bull. Mus. d'Hist. Nat. Belgique, vol. 3, pp. 85-96, 3 pls.
- ESTES, R.
1964. Fossil vertebrates from the late Cretaceous Lance Formation, eastern Wyoming. Univ. Calif. Publ. Geol. Sci., vol. 49, pp. 1-180, 73 figs., 5 pls.
1965. A new fossil salamander from Montana and Wyoming. Copeia, 1965, no. 1, pp. 90-95, 4 figs.
- ESTES, R., AND J. TIHEN
1964. Lower vertebrates from the Valentine Formation of Nebraska. Amer. Midland Nat., vol. 72, pp. 453-472, 5 figs.
- FRANCIS, E.
1934. The anatomy of the salamander. London, Oxford University Press, xxxi + 381 pp.
- GERVAIS, P.
1877. Énumération de quelques ossements d'animaux vertébrés recueillis

- aux environs de Reims par M. Lemoine. Deuxième note. Jour. Zool., vol. 6, pp. 76-79, 3 figs.
- HECHT, M.
1963. A reevaluation of the early history of the frogs. Part II. Syst. Zool., vol. 12, pp. 20-35, 7 figs.
- HECHT, M., AND R. ESTES
1960. Fossil amphibians from Quarry 9. Postilla, Peabody Mus. Nat. Hist., no. 46, pp. 1-19, 3 pls.
- HECHT, M., AND R. HOFFSTETTER
1962. Note préliminaire sur les amphibiens et les squamates du Landénien supérieur et du Tongrien de Belgique. Bull. Inst. Roy. Sci. Nat. Belgique, vol. 38, pp. 1-30.
- HERRE, W.
1935. Die Schwanzlurche der mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluss der fossilen Formen. Zoologica, Stuttgart, vol. 33, no. 87, pp. 1-85, 36 figs., 7 pls.
1939. Ueber die Urodelenreste von Walbeck. Zeitschr. Naturwiss., Halle, vol. 93, pp. 117-120, 2 figs.
1950. Schwanzlurche aus dem Paleocän von Walbeck. Zool. Anz., Suppl., Klatt Festschr., vol. 145, pp. 286-301, 16 figs.
- JANOT, C.
1966. *Amia russelli* nov. sp., nouvel Amiidé (poisson holostéen) du Thanétien de Berru, près de Reims. Compt. Rendus Soc. Géol. France, fasc. 3, p. 142, 1 fig.
- LEMOINE, V.
1889. Considérations générales sur les vertébrés fossiles des environs de Reims et spécialement sur les mammifères de la faune cernaysienne. Compt. Rendus Congr. Internatl. Zool., Paris, vol. 1, pp. 233-279, 8 figs.
- LOVE, J., P. MCGREW, AND H. THOMAS
1963. Relationship of latest Cretaceous and Tertiary deposition and deformation to oil and gas in Wyoming. Mem. Amer. Assoc. Petrol. Geol., no. 2, pp. 96-208, 9 figs.
- NOBLE, G. K.
1922. The phylogeny of the Salientia. I: The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 1-89, 23 pls.
- PRIEM, F.
1908. Étude des poissons fossiles du bassin parisien. Ann. Paléont., Paris, pp. 1-144, 74 figs., 5 pls.
- RUSSELL, D. E.
1964. Les Mammifères paléocènes d'Europe. Mem. Mus. Natl. d'Hist. Nat., Paris, new ser., vol. 13, pp. 1-324, 73 figs., 16 pls.
- SAPORTA, G. DE
1868. Prodrome d'une flore fossile des travertins anciens de Sézanne. Mem. Soc. Géol. France, ser. 3, vol. 8, pp. 289-436, 15 pls.
- SITTLER, C., AND G. MILLOT
1964. Les climats du Paléogène français reconstitués par les argiles néo-

formées et les microfiores. *Geol. Rundschau*, vol. 54, pp. 333-343.

TEEGER, M.-J.

1956. Studien zur Entwicklung und Gestalt der Urodelenwirbel. *Zeitschr. Wiss. Zool.*, vol. 160, pp. 95-163, 29 figs.

TEILHARD DE CHARDIN, P.

1921-1922. Les mammifères de l'Éocène inférieur français et leurs gisements. *Ann. Paléont.*, Paris, vol. 10 (1921), pp. 171-176, 2 figs.; vol. 11 (1922), pp. 1-108, 40 figs., 8 pls.

