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GEOLOGIC FRAMEWORK—*Continued*

BIBLIOGRAPHIES

The Pliosaurid *Megalneusaurus*: A Newly Recognized Occurrence in the Upper Jurassic Naknek Formation of the Alaska Peninsula

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ABSTRACT

A fragmentary humerus of the pliosaurid *Megalneusaurus*, from the Upper Jurassic Naknek Formation of the Alaska Peninsula, represents the only plesiosaurian known from Alaska and only the second Jurassic pliosauroid occurrence reported from the modern Arctic region. Elsewhere, *Megalneusaurus* is known only from Wyoming. The restricted geographic occurrence of *Megalneusaurus*, in the absence of any well-known European genera of Jurassic plesiosaurians or ichthyosaurs in marine strata from northwestern North America, suggests that there may have been biogeographic provincialism among Late Jurassic marine reptiles.

INTRODUCTION

In June of 1922, W.R. Smith of the U.S. Geological Survey (USGS) received from Jack Mason two large fossil bone fragments collected along the Kejulik River in the Alaska Peninsula (fig. 1). The specimens, proximal and distal ends of a large humerus, came from siltstone in the Upper Jurassic Naknek Formation. The fragments were accessioned with the United States National Museum (USNM, now the Smithsonian Institution's National Museum of Natural History) under the number 372857, and they were assigned a specimen number of USNM 418489. Two cards accompany these specimens. The first is a USGS locality information card stating that the specimens are from locality F 38, which is "sh [shale] in uppermost Naknek" located "On Kejulic River. N.E. of Becharof Lake. Found by Jack Mason." The second is a USNM card with much of the same information.

The only published reference to the plesiosaurian material here described is in a list of fossils from the Naknek Formation (Martin, 1926, p. 215), where a plesiosaurian is noted from locality F 38. This reference is obscure, and later workers (such as Tarlo, 1960; Persson, 1963) apparently were unaware of the existence of an Alaskan Jurassic plesiosaurian. The present paper places this geographically important material more obviously within the formal literature.

GEOGRAPHIC LOCATION AND STRATIGRAPHIC HORIZON

Martin (1926, p. 212) stated that the pliosaurid fossil was found "near mouth of Kejulik River" by "W.R. Smith, 1922." This taxonomic assignment was based on an unpublished report, dated October 30, 1922, provided to W. R. Smith by J.W. Gidley of the U.S. National Museum. Gidley reported that the specimens were found "near mouth of Kejulic River" in "shales" from the "Upper Jurassic, Upper Naknek." The collector was listed as W.R. Smith and the field locality as F 38. Gidley concluded that: "The pieces of this lot belong to a large species of plesiosaur, probably of the *Baptanodon* group [i.e., of Middle Jurassic Cordilleran affinity]. The large piece seems to be the distal end of a humerus. The genus and species cannot be determined on this material."

W.R. Smith and A.A. Baker were involved during the summer of 1922 in USGS geologic and topographic mapping of the Alaska Peninsula. Smith (Field Notebook II, 1922, p. 8) made the following field notes regarding the discovery of these bone fragments. "June 21. Fog. Walked to head of Ugashik Creek. Mason Bros. gave me some fossils from Garcolik River bank. One a piece of dinosaur bone." Presumably the "dinosaur bone" was one of the pliosaurid bone fragments because no other bone fragments were accessioned with the USNM. The Garcolic (also spelled Garkolik) River is an earlier alternate name for the Kejulik River of current usage (see Capps, 1923, p. 88, 103).

A. A. Baker (Field Notebook 22ABII, 1922, p. 10, entry for 24 June) provided a bit more information about this discovery: "Jack Mason reports an anticline in the Kejulics. As he described it to me the Kejulic River runs through the structure which follows the same structural

trend as the Cold Bay country or possibly a little more southerly. The rock is a hard, bluish gray shale with thin ss [sandstone] beds which Mason says is uppermost Naknek. He found a gastropod and some bones in this formation."

Two USGS field parties, one including Smith and the other including Baker, had their camps situated close to Pearl Creek dome, southeast of Mount Peulik, at the time the Mason brothers donated their fossil specimens. However, it is unclear what relationship other than proximity the Mason brothers might have had with the USGS parties working in the area at that time. It seems plausible that the brothers were involved with oil exploration and drilling being conducted in this region on the Pearl Creek dome. Certainly they had been involved previously in mineral exploration, for Smith (1925, p. 207) recorded that "in 1915 placer gold was discovered by Fred and Jack Mason in a small stream about 2 miles in length rising in the snow fields of Mount Kubugakli and entering the strait at the point of the cape just west of the southwest boundary of the Katmai National Monument."

Neither the pliosaurid nor gastropod collection locality is shown on the geologic map of the Kejulik River valley that was published with the results of work for that year (Smith and Baker, 1924, pl. IX), nor is either locality described in that work. However, Smith, on October 24, 1922, submitted a request for examination of invertebrate fossils to T.W. Stanton of the USGS that included the fossil gastropod (*Amberleya*) mentioned by Baker. Smith provided field data for this specimen under field locality F 37 (cited in Martin, 1926, p. 212, 214 as USGS Mesozoic locality 11363), which he described as "Naknek. Shale on bank of Kejulic River, N.E. of Becharof Lake. With vertebrates found by Jack Mason." This statement might imply that locality F 37 was the same as locality F 38. Yet Martin (1926, p. 214) gives slightly different site descriptions for F 37 (=11363) and F 38, suggesting that the collection sites were different. Thus, although it is certain that the pliosaurid bone fragments were found somewhere along the banks of the Kejulik River (fig. 1), most likely near its mouth, we can neither locate precisely where they were found nor say for sure if they were found together with the specimen of *Amberleya*.

Although the original USGS locality information card states that these fossils came from the "uppermost Naknek," recent mapping suggests that the uppermost Naknek does not occur along the Kejulik River. Instead, the Kejulik River valley is largely floored by rocks of the Snug Harbor Siltstone Member, which lies near the middle of the Naknek Formation (Detterman and others, in press; Wilson and others, in press). This member of the Naknek has been dated as late Oxfordian to Kimmeridgean in age (Detterman and others, in press).

TAXONOMY

The two fragments (fig. 2) are proximal and distal ends of a plesiosaurian humerus. The two fragments do not make contact with each other, so it cannot be rigorously demonstated that they pertain to the same animal. However, the pieces are not overlapping, are from the same size animal, have color and texture that are identical, and come from the same locality. Therefore, it is very likely that these two pieces represent opposite ends of the same bone (fig. 3). The proximal fragment has a robust and rounded head, a pronounced lateral tubercle centered medially in dorsal view, and a stout but rounded shaft. The distal end is only modestly expanded when compared to other plesiosaurians. These characteristics are diagnostic for the superfamily Pliosauroidea (Tarlo, 1960, p. 181), which includes plesiosaurians with large heads, short necks, and barrel-shaped bodies (fig. 4). Traditionally, the superfamily Plesiosauroidea includes all other plesiosaurians, which are forms with long necks and much smaller heads. However, Bakker (1993) has argued convincingly that the Plesiosauroidea is polyphyletic and thus in need of taxonomic revision.

The Pliosauroidea are grouped either within the single family Pliosauridae (Tarlo, 1960; Carroll, 1988) or as three families (Persson, 1963). In the latter classification, some forms are placed in the family Pliosauridae, but others are placed in the families Rhomaleosauridae and Polycotylidae. Among the Rhomaleosauridae, the humeri of the Late Jurassic taxa *Simolestes* and *Leptocleidus* have distal ends that are more expanded than in the Alaskan specimen and proximal heads that are much less robust and less expanded (Tarlo, 1960, pl. 27; Andrews, 1922, pl. 15). The Polycotylidae are known only from the Cretaceous (Persson, 1963). Thus, the specimens at hand belong in the family Pliosauridae by either taxonomic system.

Among genera universally placed in the Pliosauridae, only the Late Jurassic North American genus *Megalneusaurus* provides a close match to the Alaskan material, both in its general appearance and in the details of the cross-sectional shape of the head and the tubercle. Even so, there are three discernible differences: (1) The crest of the tubercle on the Alaskan specimen is not quite as high in profile as it is in the type of *Megalneusaurus*. (2) Although the distal end of the Alaskan humerus shows a degree of lateral expansion similar to that seen in *Megalneusaurus* in dorsal view, in lateral view its relative thickness seems to be slightly less. (3) The type humerus of *Megalneusaurus rex* is nearly twice as large as that of the Alaskan specimen. While the observed differences might represent a species level of distinction between the type humerus of *Megalneusaurus* and the specimen from the Naknek Formation, they more probably represent allometric variation due to age or individual variation. As isolated plesiosaurian humeri are

considered diagnostic at the generic level of taxonomy but not at the species level (Tarlo, 1960, p. 149), it is pointless to assign taxonomic significance to the observed minor differences on the basis of one specimen.

Humeri of other genera of described pliosaurids are much less similar in appearance to the Alaskan material. The genus *Pliosaurus* has a tubercle that is nearly equal in size to the head of the humerus (Tarlo, 1959a), while

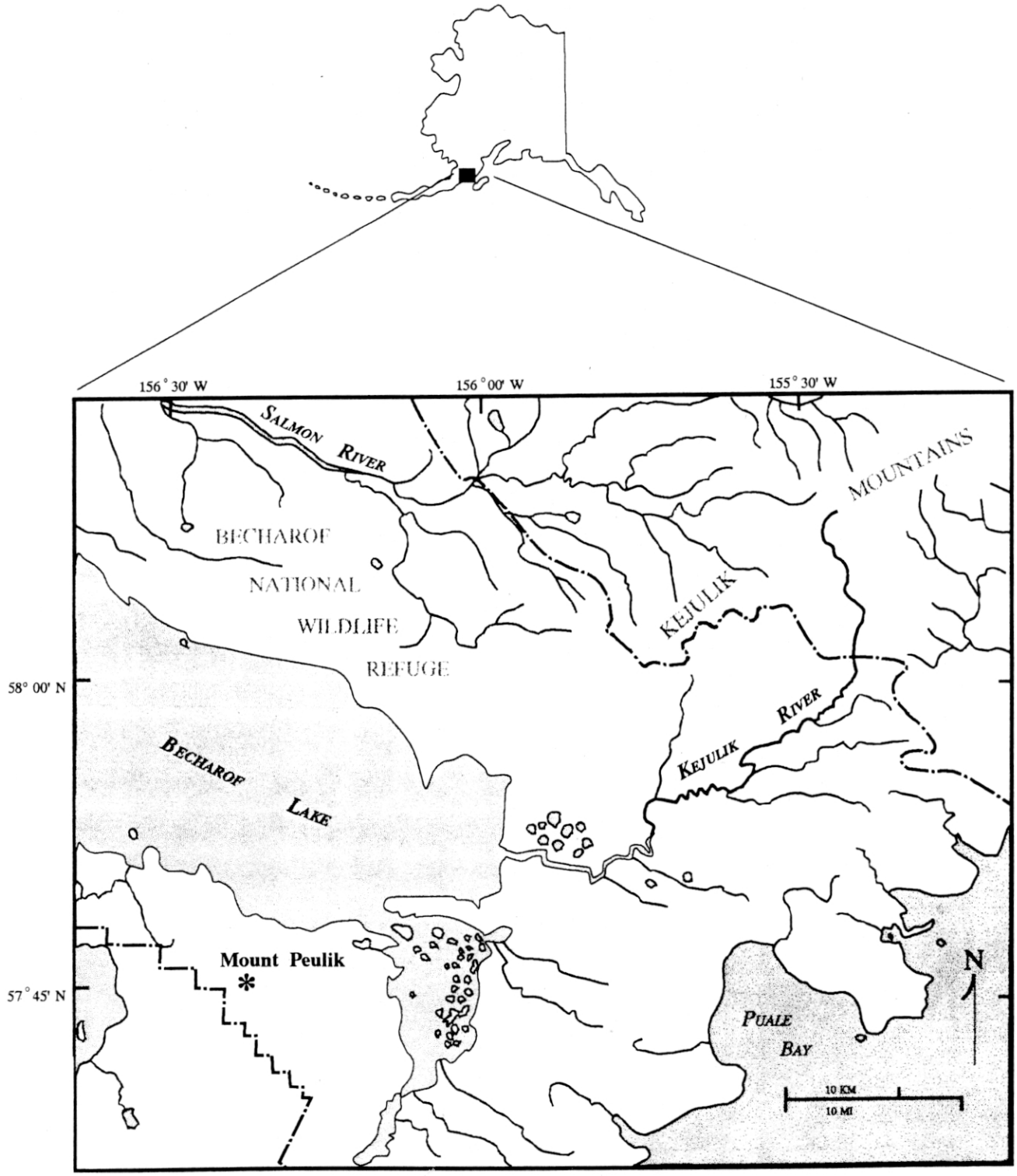

Figure 1. Map showing location of the Kejulik River on the Alaska Peninsula. A fragmentary pliosaurid humerus (*Megalneusaurus* sp.) was recovered from the banks of this river in strata of the Upper Jurassic Naknek Formation. Dashed lines mark the boundaries of the Becharof National Wildlife Refuge.

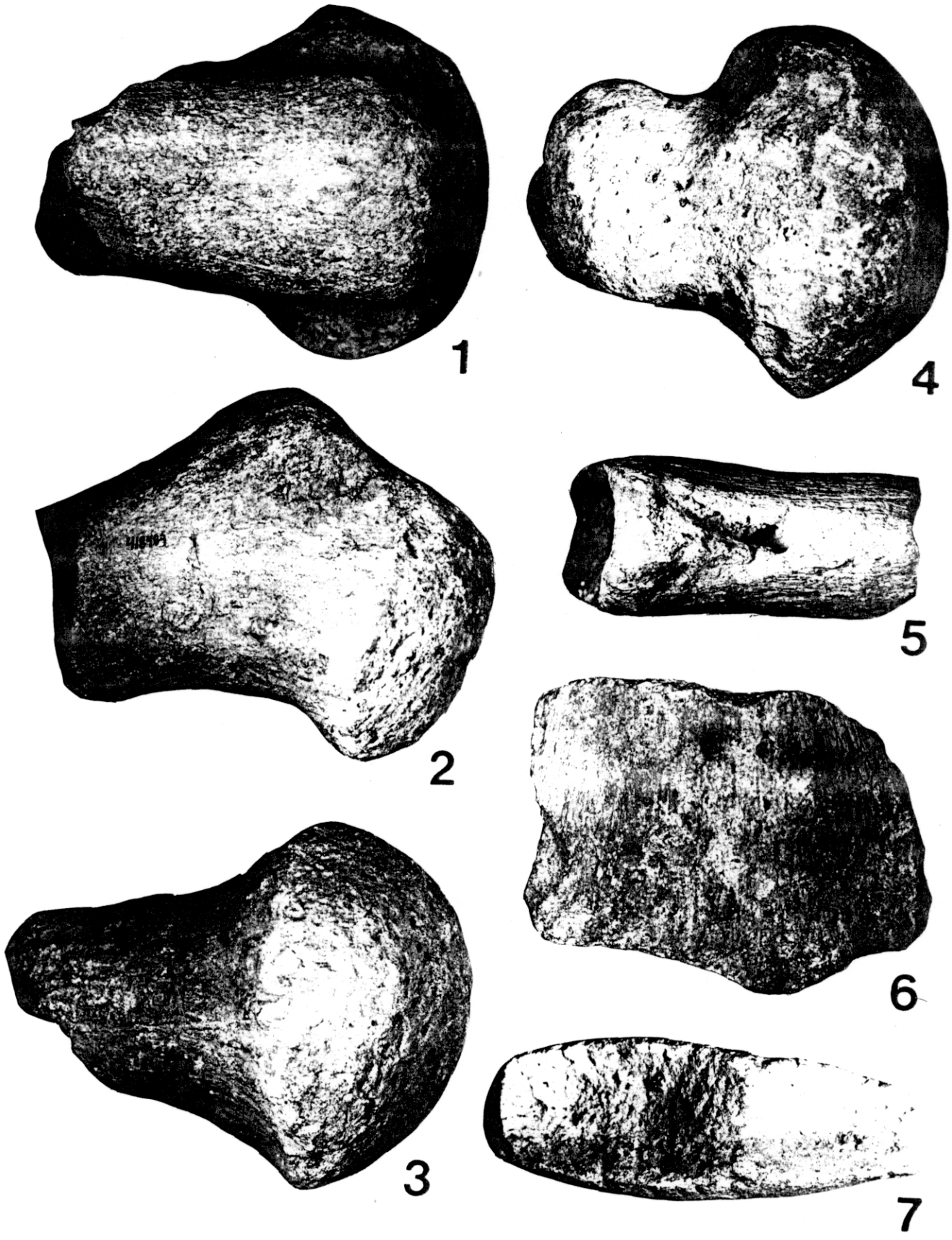

Figure 2. *Megalneusaurus* sp. (USNM 418489) from the Naknek Formation. 1-4, Dorsal, lateral, ventral, and proximal views of proximal end of humerus. 5-7, Lateral, dorsal, and distal views of distal end of humerus. All views ×0.5.

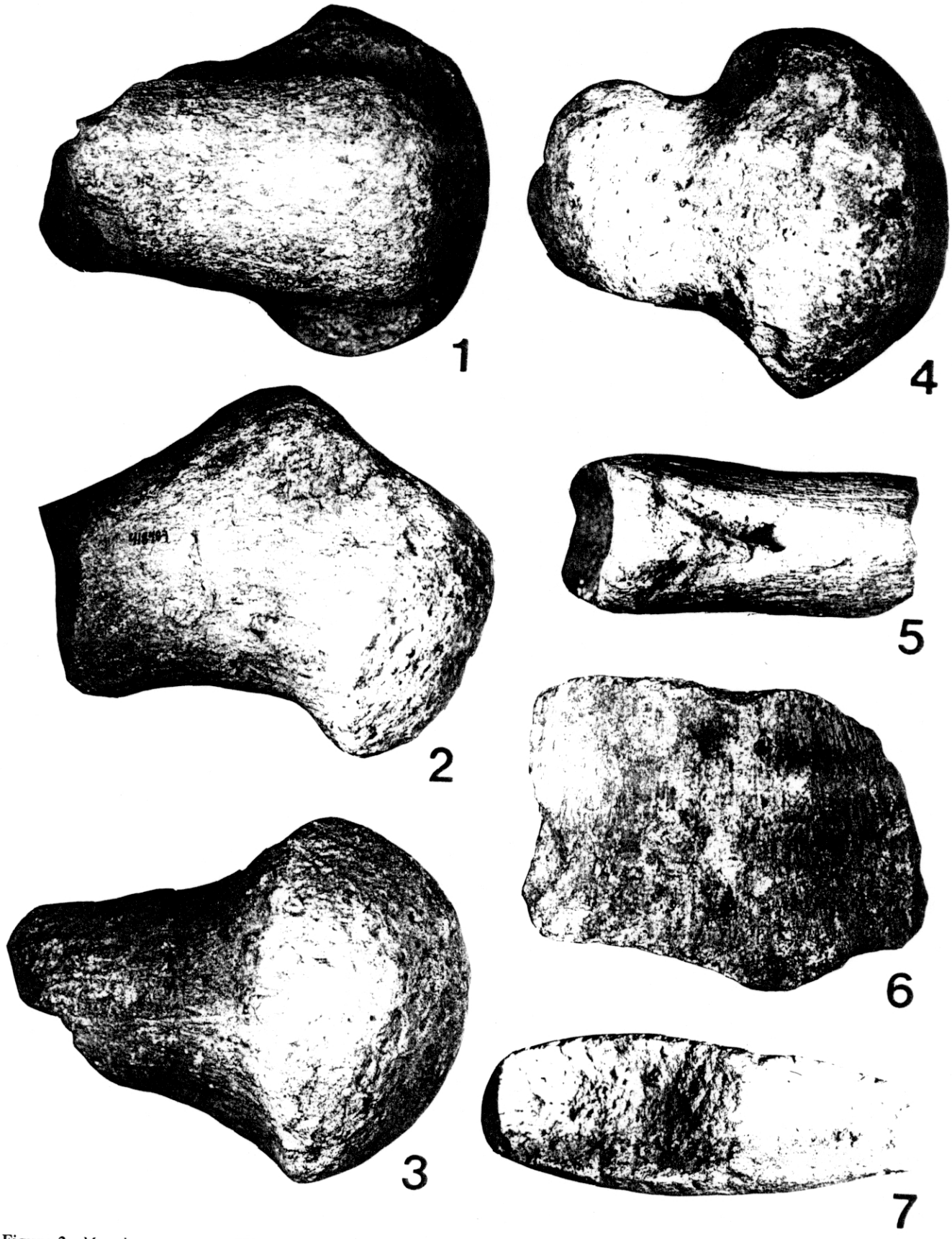

Figure 2. *Megalneusaurus* sp. (USNM 418489) from the Naknek Formation. 1-4, Dorsal, lateral, ventral, and proximal views of proximal end of humerus. 5-7, Lateral, dorsal, and distal views of distal end of humerus. All views ×0.5.

Liopleurodon and *Peloneustes* both have heads much less expanded and less rounded than the head of the Alaskan specimen (Linder, 1913, pl. 35, fig. 7 *per* Tarlo, 1960, p. 167; Andrews, 1913, p. 57). The Alaskan specimen compares rather favorably to *Stretosaurus* in its general proportions (Tarlo, 1959b), but the shape of the proximal head, the lateral tubercle, and the distal end do not match in detail. The humerus is unknown for *Strongylokrotaphus* from Russia (Novozhilov, 1948, 1964), and for *Sinopliosaurus*, *Bishanopliosaurus*, and *Yuzhoupliosaurus* from China (Young, 1944; Hou and others, 1975; Zhang, 1985; Dong, 1980), so direct comparisons cannot be made with any of those genera. If any of these taxa eventually prove to be synonymous with *Megalneusaurus*, the American name has priority.

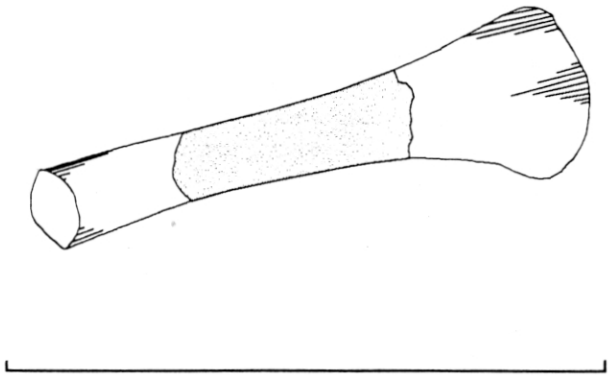

Figure 3. Estimation of the relative proportions of missing (stippled) and preserved bone for the Alaskan humerus specimen of *Megalneusaurus* sp. Missing portion shown here is estimated by comparison with the humerus of *Megalneusaurus rex* shown here in lateral view (Knight, 1898) (scale is for *M. rex*).

STRATIGRAPHIC RANGE OF *MEGALNEUSAURUS*

Persson (1963, p. 37) stated that *Megalneusaurus rex* came from the " "Como Stage" = Morrison Formation (Kimmeridgian-L. Portlandian). Natrona County (Wyoming)." Although the locality is correctly listed, the stratigraphic horizon is wrong. This error occurred because Knight (1898), in the same article that he described *Megalneusaurus*, also proposed that the beds containing this fossil be formally named the "Como group." However, W.B. Scott (1897) already had proposed the name "Como beds" for what today is called the Morrison Formation. Apparently, Knight was initially unaware of this; later, he changed his terminology and adopted Scott's term "Como beds" (as the "Como stage") for beds equivalent to the Morrison and renamed the *Megalneusaurus*-bearing beds as the "Shirley stage." The "Shirley" beds today are the upper part of the Sundance Formation (Imlay, 1952). Unfortunately, Knight never explicitly renounced his original usage of "Como group" for the upper part of the Sundance Formation (Knight, 1900; Wilmarth, 1957, p. 499). Because Knight (1900) later listed *Megalneusaurus* as a "Shirley" fossil, it is certain that he collected it from the upper part of the Sundance Formation of late Oxfordian age. However, Persson understandably but incorrectly assumed that that "Como stage" and "Como group" were synonymous concepts. In so doing, he unwittingly moved the provenance of *Megalneusaurus* out of the upper Oxfordian part of the Sundance Formation and into the Kimmeridgian part of the Morrison Formation.

The base of the Naknek Formation in the Kejulik River area is, like the upper part of the Sundance Formation, Oxfordian in age. But the Snug Harbor Siltstone

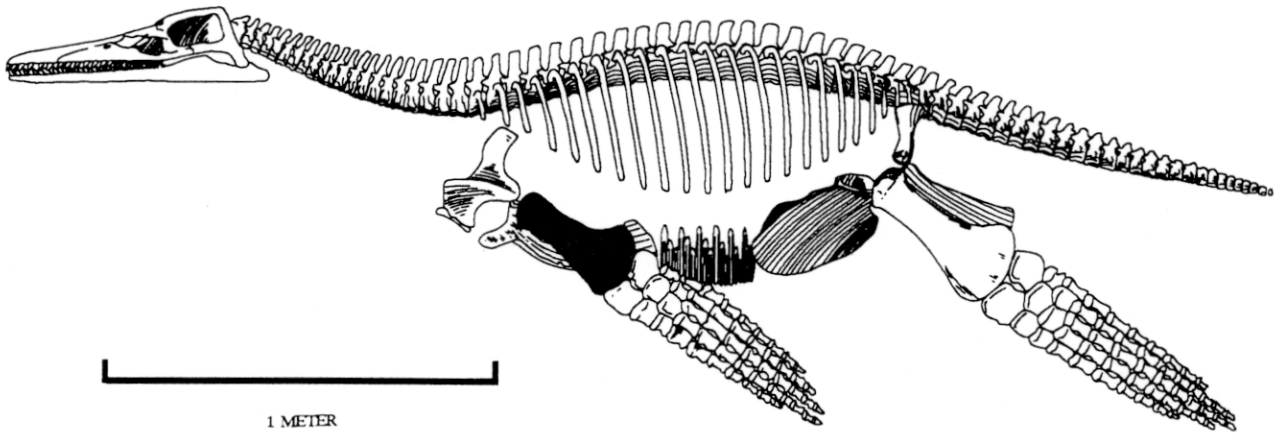

Figure 4. Restored skeleton of one of the better known small pliosaurids, *Peloneustes philarchus* (Seeley), as envisioned by Andrews (1913). The humerus is shown in black. The relatively longer humerus of *Megalneusaurus* (see fig. 3), as compared with *Peloneustes*, suggests that *Megalneusaurus* had a more powerful swimming stroke than *Peloneustes*.

Member of the Naknek, which floors the Kejulik River valley, also ranges upward into the Kimmeridgian stage (Detterman and others, in press). Thus the Alaskan specimen of *Megalneusaurus* could be either the same age as the Wyoming occurrences of *Megalneusaurus rex* or slightly younger. As the Late Jurassic has been considered to be a time of relative ecological and taxonomic stability among marine reptiles (Bakker, 1993), an Oxfordian to Kimmeridgian range for *Megalneusaurus* would not be surprising.

BIOGEOGRAPHIC AND PALEOECOLOGIC IMPLICATIONS

The occurrence of *Megalneusaurus* in Alaska has interesting implications for the biogeography of marine reptiles in the Late Jurassic. None of the plesiosaurian species described from the Upper Jurassic of northwestern North America are synonymous with European species, and assignments previously made to European genera are all questioned (Persson, 1963). Similarly, ichthyosaurs (another major group of Jurassic marine reptiles) are represented in the Upper Jurassic of western North America by species of the endemic genus *Baptanodon* (Gilmore, 1905, 1906) and two poorly known endemic species originally assigned (probably incorrectly) to *Ichthyosaurus* (Camp, 1942; Camp and Koch, 1966). Upper Jurassic ichthyosaur genera known from Europe (*Ophthalmosaurus*, *Grendelius*, and ?*Nannopterygius*) have not been reported from western North America (Carroll, 1988). This apparent provincialism among the western North American marine reptiles may be significant in view of the fact that invertebrate fossils from northwestern North America (for example, *Buchia* and *Amoeboceras*) are part of a distinct Late Jurassic biogeographic Boreal realm that differs markedly from the circumequatorial Tethyan realm invertebrate faunas found farther south (Khudoley, 1979, p. 60; Detterman, 1988, p. 8–9, 24; Hillebrandt and others, 1992, p. 351). The occurrence of *Megalneusaurus* widely across this province, both in Wyoming and Alaska but not elsewhere (fig. 5), hints that the marine reptiles within the Late Jurassic Boreal Realm may have been endemic to this province. A later Mesozoic biogeographic provincialism in the Pacific Coast region has been documented for plesiosaurians and mosasaurs in the Late Cretaceous (Russell, 1993), so it will be most interesting to see if future finds continue to suggest an earlier provincialism among Late Jurassic marine reptiles of the northern Pacific region.

There has been much controversy concerning the location of the Peninsular terrane and associated southern Alaskan terranes during the Mesozoic. On the basis of paleomagnetic data (for example, Packer and Stone, 1974; Stone and Packer, 1979; Stone and others, 1982), it has been suggested that these terranes lay far south of their present position during the Jurassic, perhaps even south of the equator. However, both the low diversity of the Naknek molluscan fauna and its strong similarity to molluscan faunas of similar age in Siberia, Franz Joseph Land, Arctic Canada, and Greenland offer compelling evidence that by Late Jurassic time the Peninsular terrane was located at or near its present position in a cool to cold boreal setting (Taylor and others, 1984; Detterman, 1988; Hillebrandt and others, 1992). Similarly, the scarcity of Upper Jurassic calcareous sediments in the Naknek Formation suggests that the Peninsular terrane was located in cool to cold water (Imlay, 1965, p. 1033). In contrast to the Naknek beds, the Oxfordian upper part of the Sundance Formation of Wyoming, which contains the other occurrence of *Megalneusaurus*, appears to have been deposited in somewhat warmer waters. The upper part of the

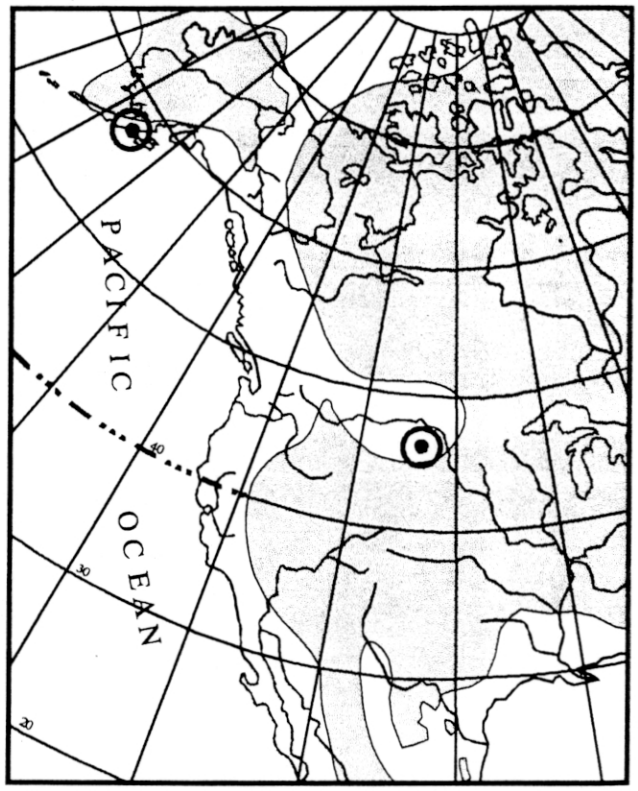

Figure 5. Late Jurassic paleogeography of western North America (modified from Imlay, 1984), showing the relative locations of the type area occurrence of *Megalneusaurus* in the Sundance Formation of Wyoming and the presently reported occurrence in the Naknek Formation of Alaska. Stippled area represents estimated extent of land during this time period. In this figure, Alaska is assumed to have reached nearly its present geologic configuration by the Late Jurassic. The transition between the circumequatorial Tethyan realm and the Boreal realm lies at about 40°N. latitude.

Sundance Formation has common bedded limestones, a much more diverse invertebrate fauna, and an abundant and taxonomically diverse population of the bivalve genus *Gryphaea*. The latter genus is totally unknown from Naknek fossil collections.

The presence of a large reptile such as *Megalneusaurus* on the Alaska Peninsula does not necessarily contradict the above cited faunal and sedimentological evidence. Although this is the first plesiosaurian known from Alaska, a Late Jurassic pliosaurid (*Peloneustes* cf. *philarchus*) also has been reported in the circumpolar region from Franz Joseph Land northeast of Norway (Persson, 1963, p. 35). According to recent paleogeographic reconstructions (Smith and others, 1993), both of these pliosaurid occurrences were higher than 60° paleolatitude in the Late Jurassic. It might be argued that pliosaurid reptile remains at very high paleolatitudes indicate that the Late Jurassic polar region was much warmer than today. However, it must be remembered that the only living fully marine reptile of remotely comparable bulk (the leatherback sea turtle *Dermochelys*) ranges north to Labrador, Iceland, and Alaska during the summer months (Ernst and Barbour, 1989). In cold water, leatherbacks can maintain body temperatures up to 18°C higher than that of surrounding water (Frair and others, 1972). It is quite possible that pliosaurids were comparable to *Dermochelys* in their wide-ranging habits and in their ability to survive in cool or cold waters. Massare (1987) has concluded that pliosaurids probably were opportunistic predators like modern killer whales. Based on one case of preserved stomach contents, some pliosauroids definitely preyed upon cephalopods. Their tooth morphology, however, suggests that they also could have caught and consumed fish, sea turtles, and (or) small ichthyosaurs as well. Thus, *Megalneusaurus* may have been a wide-ranging, opportunistic marine predator that visited the waters of the Alaska Peninsula only seasonally.

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