

# Early Evolution of Whales

## A Century of Research in Egypt

Philip D. Gingerich

### Introduction

Living whales are fully aquatic and belong to two suborders of Cetacea: Mysticeti (baleen whales) and Odontoceti (toothed whales). Both of these modern suborders appeared when Earth changed from a 'greenhouse' earth to an 'icehouse' earth at in about the beginning of the Oligocene epoch (Zachos et al., 2001). Early whales, from the 'greenhouse' Eocene, all belong to a distinct paraphyletic suborder Archaeoceti. Archaeocetes differ from later modern whales in retaining many characteristics of land mammals, including complexly occluding cheek teeth, ear bones well integrated with the rest of the cranium, longer necks, less specialized forelimb flippers, and hind limbs with feet and toes. Archaeocetes are, in essence, the transitional forms documenting the origin of whales from an earlier land-mammal ancestry (Gingerich, 2005).

The first archaeocete fossil to be studied scientifically was a very large vertebral centrum collected in 1832 near the Ouachita River in Caldwell Parish, Louisiana. This measured some 35 cm in length and was but one of a series of 28 vertebrae found together there. The animal represented was named *Basilosaurus* or 'king lizard' because of its size and presumed reptilian heritage (Harlan, 1834). At the time the British anatomist Richard Owen was busy studying the large reptiles he eventually called dinosaurs. To solve the mystery of *Basilosaurus*, Owen secured additional remains and showed that it was a mammal because its cheek teeth are double-rooted. Owen (1839) deemed the name *Basilosaurus* to be inappropriate and proposed *Zeuglodon* or 'yoked teeth' as a replacement name. Relationship to whales was codified when Owen (1841) added the specific epithet *Zeuglodon cetoides*.

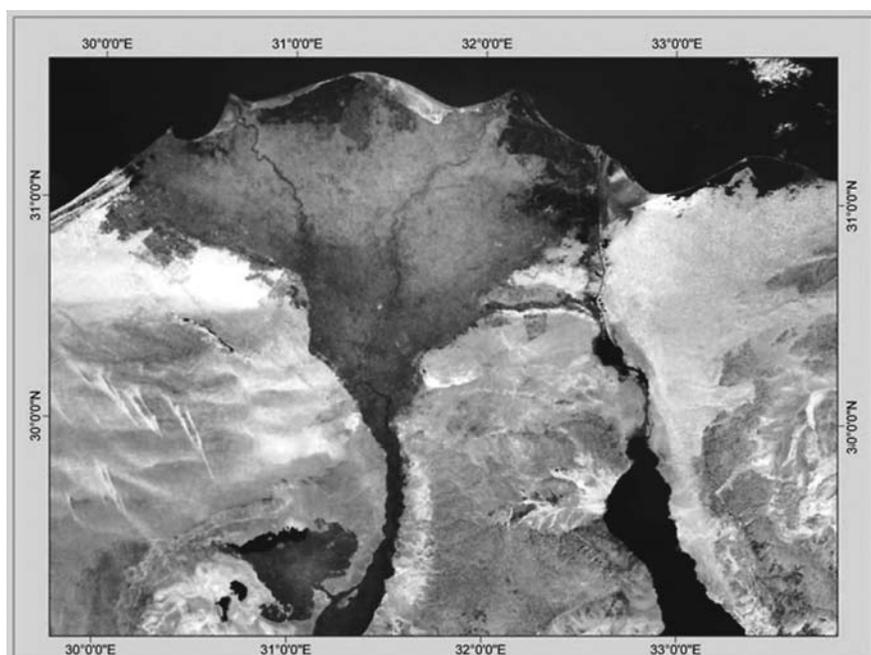
Additional archaeocete fossils were found in North America later in the nineteenth century, including the type specimen of *Dorudon serratus* Gibbes

---

Philip D. Gingerich  
Museum of Paleontology and Department of Geological Sciences, The University of  
Michigan, Ann Arbor, MI 48109-1079  
gingeric@umich.edu

(1845) and the type of *Zygorhiza kochii* (Reichenbach, 1847). These species were first classified in Basilosauridae by Cope (1868). Later all specimens known at the time were reviewed in a great monograph on Archaeoceti (Kellogg, 1936). This new monograph was important for the anatomical information it summarized, but also, on close reading, for the substantial gaps it revealed in our knowledge of archaeocetes: (1) no archaeocete was known from a complete axial skeleton, and it was impossible to say how many vertebrae any archaeocete had; (2) no archaeocete had the carpus and manus represented, and hence, conformation of the forelimb flipper was unknown (Gidley, 1913, and Kellogg, 1936, fabricated these using hands of sea lions as models); and (3) no archaeocete was known to have retained hind limbs with feet, and the innomates of *Basilosaurus* were mounted as if they still articulated with the vertebral column. Kellogg (1936) correctly inferred that advanced archaeocetes like *Dorudon* and *Zygorhiza* swam using upward and downward strokes of a powerfully-muscled and fluked tail (Uhen, 1996, 2004; Gingerich, 2003).

In recent years many of the gaps in our knowledge of archaeocetes have been filled by recovery of new and better archaeocete specimens from Egypt (Fig. 1)



**Fig. 1** Landsat image of present-day Egypt showing the location of Eocene archaeocete whale sites at Gebel Mokattam (site 1), Geziret el-Qarn (site 2), Qasr el-Sagha escarpment (site 3), Birket Qarun escarpment (site 4), Wadi Hitan (site 5), and Khashm el-Raqaba in Wadi Tarfa (site 6)

and from Pakistan. These include specimens with complete skulls, axial skeletons, forelimbs, hind limbs, and tails. The Egyptian archaeocetes include specimens classified as Basilosauridae (*Basilosaurus*, *Dorudon*, *Saghacetus*) and specimens classified as Protocetidae (*Protocetus*, *Eocetus*). The taxonomic history and stratigraphic distribution for each Egyptian archaeocete species is summarized in Table 1 and Table 2. Protocetidae and Basilosauridae represent different grades of adaptation to life in water, with early protocetids being semiaquatic foot-powered swimmers, while later basilosaurids were fully aquatic tail-powered swimmers (Gingerich, 2003). Of relevance here, the Egyptian and Pakistan field work was encouraged and facilitated, directly or indirectly, by Professor Elwyn Simons, and he was an active participant in recovery of the first whale hind limbs when these were found on *Basilosaurus*.

**Table 1** Summary of the history of names for the genera and species of archaeocete whales found in Egypt. Stratigraphic distribution of each species is shown in Table 2

| Egyptian form                | History of names                   | Author                     | Geographical distribution |
|------------------------------|------------------------------------|----------------------------|---------------------------|
|                              | <i>Basilosaurus</i> (no species)   | Harlan (1834)              | North America             |
|                              | <i>Zeuglodon</i> (no species)      | Owen (1839)                | North America             |
|                              | <i>Zeuglodon cetoides</i>          | Owen (1841)                | North America             |
|                              | <i>Dorudon serratus</i>            | Gibbes (1845)              | North America             |
| <i>Saghacetus osiris</i>     | <i>Zeuglodon osiris</i>            | Dames (1894)               | Egypt                     |
|                              | <i>Zeuglodon osiris</i>            | Slijper (1936)             | Egypt                     |
|                              | <i>Dorudon osiris</i>              | Kellogg (1936)             | Egypt                     |
|                              | <i>Saghacetus osiris</i>           | Gingerich (1992)           | Egypt                     |
| <i>Protocetus atavus</i>     | <i>Protocetus atavus</i>           | Fraas (1904a)              | Egypt                     |
| <i>Eocetus schweinfurthi</i> | <i>Mesocetus schweinfurthi</i>     | Fraas (1904a)              | Egypt                     |
|                              | <i>Eocetus schweinfurthi</i>       | Fraas (1904b)              | Egypt                     |
| <i>Basilosaurus isis</i>     | <i>Zeuglodon isis</i>              | Beadnell in Andrews (1904) | Egypt                     |
|                              | <i>Zeuglodon isis</i>              | Slijper (1936)             | Egypt                     |
|                              | <i>Prozeuglodon isis</i> (in part) | Kellogg (1936)             | Egypt                     |
|                              | <i>Basilosaurus isis</i>           | Gingerich et al. (1990)    | Egypt                     |
| <i>Dorudon atrox</i>         | <i>Prozeuglodon atrox</i>          | Andrews (1906)             | Egypt                     |
|                              | <i>Prozeuglodon isis</i> (in part) | Kellogg (1936)             | Egypt                     |
|                              | <i>Prozeuglodon isis</i>           | Moustafa (1954)            | Egypt                     |
|                              | <i>Dorudon atrox</i>               | Gingerich and Uhen (1996)  | Egypt                     |
| <i>Dorudon stromeri</i>      | <i>Prozeuglodon stromeri</i>       | Kellogg (1928)             | Egypt                     |
|                              | <i>Dorudon stromeri</i>            | Kellogg (1936)             | Egypt                     |
| <i>Ancalocetus simonsi</i>   | <i>Ancalocetus simonsi</i>         | Gingerich and Uhen (1996)  | Egypt                     |

**Table 2** Stratigraphic distribution of middle and late Eocene archaeocete whales from Egypt. Taxonomic history for each genus and species is summarized in Table 1

| Formation                        | Taxon  | Locality (Figure 1) |
|----------------------------------|--|---------------------|
| <b>Priabonian (late Eocene)</b>  |  |                     |
| Qasr el-Sagha Formation          | <i>Saghacetus osiris</i> (Dames, 1894)               | 3                   |
|                                  | <i>Dorudon stromeri</i> (Kellogg, 1928)              | 3                   |
| Birket Qarun Formation           | <i>Basilosaurus isis</i> (Beadnell in Andrews, 1904) | 2, 4, 5             |
|                                  | <i>Dorudon atrox</i> (Andrews, 1906)                 | 2, 4, 5             |
| <b>Bartonian (middle Eocene)</b> |  |                     |
| Giushi Formation                 | <i>Eocetus schweinfurthi</i> (Fraas, 1904a)          | 1                   |
| Gebel Hof Formation              | Undescribed skeletons                                | 6                   |
| <b>Lutetian (middle Eocene)</b>  |  |                     |
| Mokattam Formation               | <i>Protocetus atavus</i> Fraas, 1904a                | 1                   |

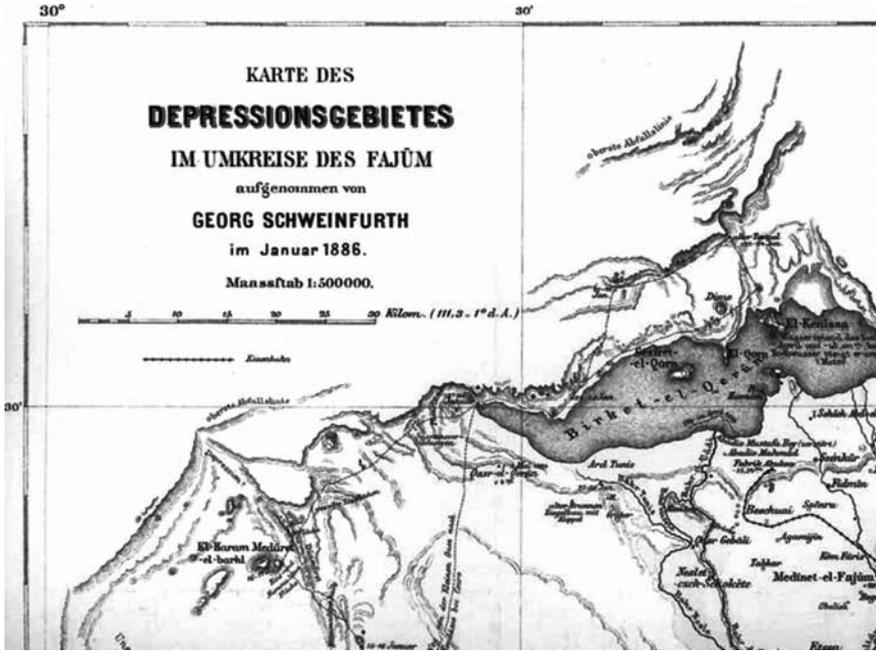
## Chronology of Egyptian Research

Egyptian archaeocetes were not the first archaeocetes to be found, but they include a number of early species (Table 1). Further, new specimens from Egypt are proving to be so complete and important for our understanding of early whale evolution that the history of their discovery deserves review.

### *Schweinfurth and Dames*

Georg August Schweinfurth [1836–1925] was a German botanist who spent three years in the Eastern Desert of Egypt and Sudan from 1863 to 1866 while compiling his botanical dissertation *Beitrag zur flora Äthiopiens* (1867). In 1868 he was commissioned by the Alexander von Humboldt Foundation of Berlin to explore more of Central Africa, which he did from 1869 to 1871. Publication of *Im Herzen von Afrika* in 1874 secured Schweinfurth's reputation as an African explorer.

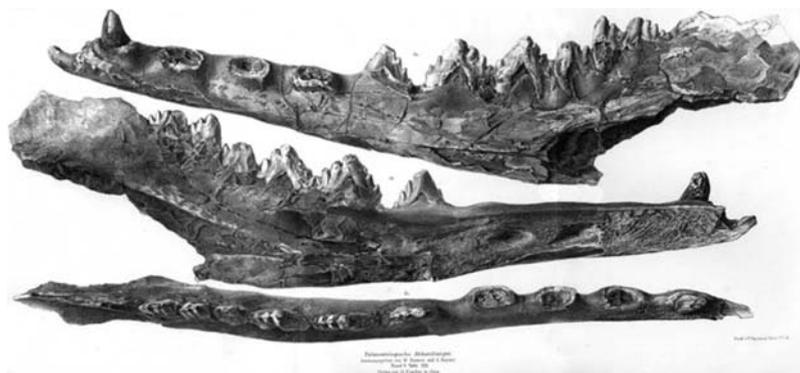
Schweinfurth lived in Cairo for 14 years from 1875 through 1889, and it was during this time that the first Eocene mammal fossils were described from Gebel Mokattam (site 1 in Fig. 1) near Cairo (the first was the sirenian *Eotherium aegyptiacum*, now *Eotheroides aegyptiacum*; Owen, 1875). While living in Cairo, Schweinfurth continued to explore locally, and in 1879 discovered the first vertebrate fossils in Fayum and the first archaeocete whales in Egypt. These were found on the island of Geziret el-Qarn (site 2 in Fig. 1) in the middle of lake Birket Qarun. In 1884 and again in 1886, Schweinfurth visited Qasr el-Sagha and the Qasr el-Sagha escarpment (site 3 in Fig. 1) on the north side of Birket Qarun. This is the time, too, when Schweinfurth published two studies



**Fig. 2** Georg Schweinfurth's map of Fayum showing the path of his 1886 expedition through Wadi Rayan and north of Birket Qarun. Schweinfurth found the type specimen of *Zeuglodon osiris* (now *Saghacetus osiris*) at the site near his January 21–22 camp (Garet el Esh). He camped at Garet Gehannam on January 16–17, but never found the archaeocete skeletons there nor those in Wadi Hitan several kilometers to the west

important for Egyptian stratigraphy and archaeocete paleontology: 'On the geological stratification of Mokattam near Cairo' (Schweinfurth, 1883), and 'Travel in the depression circumscribing Fayum in January, 1886' (Schweinfurth, 1886). On the expedition described in the latter (Fig. 2), Schweinfurth came within a few kilometers of discovering Zeuglodon Valley, or what is now called Wadi Hitan, but turned back because of difficulties with his camels and staff.

Schweinfurth's fossils from both expeditions, the 1879 expedition to Geziret el Qarn and the 1886 expedition to Wadi Rayan and the north side of Birket Qarun, are conserved in the Humboldt University *Museum für Naturkunde* in Berlin, where they were studied by Wilhelm Barnim Dames [1843–1898]. Fossils from Geziret el Qarn include a diversity of isolated vertebrae from what are now called uppermost Gehannam and lower Birket Qarun formations (see also Seiffert, this volume). Preliminary notices of these were published by Dames (1883a, b). Fossils from north of Birket Qarun include a well preserved dentary from the Qasr el-Sagha escarpment that became the type of the first archaeocete named from Egypt: *Zeuglodon osiris* (or now *Saghacetus osiris*; Fig. 3).



**Fig. 3** Type specimen of *Zeuglodon osiris* Dames, 1894 [now *Saghacetus osiris* (Dames)] found by Georg Schweinfurth at a site near Garet el Esh (see Fig. 2), north of lake Birket Qarun in the Fayum Depression

Schweinfurth's specimens, including the type dentary of *Saghacetus osiris*, were reviewed and illustrated by Dames (1894).

### ***Blanckenhorn, Fraas, Markgraf, and Stromer***

The next group to investigate the marine Eocene north of Birket Qarun was also German. Max Blanckenhorn [1861–1947] started work for the Geological Survey of Egypt in 1897–1898, shortly after its founding, and he published several important reports on the stratigraphy of whale-bearing formations (Blanckenhorn, 1900, 1903). Eberhard Fraas [1862–1915] visited Egypt too, starting in 1897, where he engaged Richard Markgraf [1856–1916] as a private collector working first in the stone quarries of Gebel Mokattam, and later in Fayum. Markgraf was a Bohemian living in Egypt because of poor health.

During the winter of 1901–1902 Blanckenhorn was joined by Ernst Stromer von Reichenbach [1871–1952] of the *Königlich Bayerischen Akademie der Wissenschaften* in Munich. In January, 1902, they made an 11-day traverse starting at the temple ruin at Qasr Qarun near the west end of Birket Qarun. They went around the west end of Birket Qarun and then, following Schweinfurth's path, traveled eastward to Dimeh and Qasr el-Sagha on the north side of Birket Qarun. Stromer von Reichenbach (1903a) was generally disappointed by the results of this expedition, but he was able to describe a new skull and lower jaw of *Saghacetus osiris* (Dames) from what is now upper Qasr el-Sagha Formation. Later Stromer von Reichenbach (1903b) described a new species *Zeuglodon zitteli* from the type locality of *Saghacetus osiris*, but this has proven indistinguishable from Dames' species.

Markgraf made an important discovery in 1903 when he found the cranium and associated postcranial remains of a small archaeocete from the Mokattam Limestone of Lutetian, early middle Eocene, age, near the base of the Gebel Mokattam section (site 1 in Fig. 1). This was described by Fraas (1904a) as a new genus and species *Protocetus atavus*. The skull is primitive, with upper molars retaining protocones. Associated vertebrae include a partial sacrum with auricular processes indicating retention of articulation with a pelvis (the sacrum was originally interpreted as having consisted of a single centrum, but later comparisons indicate that the inferred reduction is an artifact of breakage).

A second skull of a different whale from Gebel Mokattam, recovered by Markgraf in 1904, was added to Fraas' 1904a publication, possibly at the proof stage. Fraas' name for this, *Mesocetus*, proved to be preoccupied, and the name *Eocetus* had to be substituted (Fraas, 1904b). The type of *Eocetus* came from what is now called Giushi Formation and is Bartonian, or late middle Eocene in age, from a level higher in the Gebel Mokattam section than that yielding *Protocetus* (site 1 in Fig. 1). The older and more primitive form, *Protocetus*, subsequently became the type of a new family of archaeocetes called Protocetidae (Stromer von Reichenbach, 1908). Protocetidae originally included just *Protocetus* and *Eocetus*, but the family now includes additional genera named in later years.

Stromer made a second trip to Egypt to collect Eocene whales and other vertebrates, starting in November 1903. This was a three-month expedition employing Markgraf and ranging widely. Two large archaeocete vertebrae were collected at Gebel Mokattam, and an archaeocete skull with jaws and vertebrae was collected north of Birket Qarun. Markgraf continued to collect fossil whales in Fayum, and later in 1904 he sent another specimen from the Qasr el-Sagha escarpment to Munich that Stromer von Reichenbach (1908) first identified as *Zeuglodon osiris*. This eventually became the type of *Dorudon stromeri* (Kellogg, 1928).

Eberhard Fraas made a final trip to Egypt to work with Markgraf in 1906. The trip started on March 11, and they reached Qasr el-Sagha on March 13. Camels were sent for water and fodder, and within days they moved to the west end of Birket Qarun (site 4 in Fig. 1). Here they excavated much of the skeleton of a large 'Zeuglodon' (*Basilosaurus isis*) with a 1.3-meter skull and a 10-meter section of the following skeleton comprising vertebrae and ribs (Fraas, 1906). This specimen, described by Slijper (1936), is in the *Staatliches Museum für Naturkunde* in Stuttgart.

### ***Beadnell and Andrews***

Hugh J. L. Beadnell [1874–1944] was British, and was employed by the Egyptian Geological Survey from the time it was founded in 1896 until 1906. Beadnell worked on various projects, and then started work in the Fayum in October, 1898. Beadnell started in eastern Fayum, and then extended his mapping first to

the escarpments north of Birket Qarun and then westward to Garet Gehannam during the spring of 1899. Charles W. Andrews [1866–1925] of the British Museum (Natural History) published the first note on Beadnell's paleontological discoveries (Andrews, 1899), and Beadnell himself (1901) provided a summary of Fayum stratigraphy that has guided most subsequent work. In April of 1901, Andrews joined Beadnell in the field for the first time to investigate bone beds discovered in 1898, and many new specimens including archaeocetes were found (Andrews, 1901). Collecting then continued during the winters of 1901–1902, 1902–1903, and 1903–1904. Sometime in this interval, Beadnell collected a very large dentary for the Cairo Geological Museum specimen that became the type of *Zeuglodon isis* Beadnell in Andrews, 1904 (now *Basilosaurus isis*). According to Beadnell (1905), this came from the Birket Qarun escarpment near the west end of the lake (site 4 in Fig. 1).

A second phase of mapping was carried out in the winter of 1902–1903, when Beadnell made a traverse from Garet Gehannam west and southwest 12 kilometers to a valley where large skulls and other remains of fossil whales were abundant (site 5 in Fig. 1). Very little was collected, but one skull recovered for the Cairo Geological Museum was made the type of *Prozeuglodon atrox* by Andrews (1906). This is now properly called *Dorudon atrox*. Andrews diagnosed *Prozeuglodon* as “intermediate between *Protocetus* and *Zeuglodon* proper,” but he seemingly did not recognize that the type is a juvenile with deciduous premolars. This led to confusion when it was recognized later, and for some time *Prozeuglodon atrox* was thought to be the juvenile form of *Zeuglodon isis*. Kellogg (1936), for example, combined these, and referred to both as *Prozeuglodon isis* (later recovery of skeletons of mature *Dorudon atrox*, see below, showed that they are clearly different from contemporary *Basilosaurus isis*). Surprisingly, following Beadnell's initial work in the valley 12 kilometers WSW of Garet Gehannam in 1902–1903, no serious collection and study of the whales there was carried out for eighty years.

## Osborn and Granger

Henry Fairfield Osborn [1857–1935] of the American Museum of Natural History in New York organized a 1907 collecting expedition to Fayum to follow in the footsteps of Blanckenhorn, Stromer, Beadnell, and Andrews. Osborn interpreted publication of Andrews' 1906 *Descriptive Catalog of the Tertiary Vertebrata of the Fayum, Egypt* to indicate that the area was now open for study by others, and Andrews himself (*in litt.*) encouraged Osborn to carry out further studies. Osborn's first published report on the expedition was submitted from Cairo and dated February 25. In this, Osborn coined the term ‘Zeuglodon Valley’ for Beadnell's valley 12 kilometers WSW of Garet Gehannam (Osborn, 1907a; site 5 in Fig. 1). He later called this “the most famous fossil locality in the Fayum” (Osborn, 1907b). Zeuglodon Valley has since been renamed Wadi

Hitan or 'Valley of Whales' to acknowledge synonymy of *Zeuglodon* with *Basilosaurus* and to provide an alternative in Arabic (Gingerich, 1992).

Osborn did some prospecting for fossils during the time he was in Fayum, but he was accompanied by his wife and children and did no real collecting. The Egyptian Geological Survey assigned Hartley T. Ferrar [1879–1932], recently returned from Robert F. Scott's British National Antarctic Expedition of 1901–1903, to accompany and assist Osborn. The area that the American Museum party worked included Beadnell and Andrews' principal localities, in continental beds above the Qasr el-Sagha escarpment (north of site 3 in Fig. 1). Here American Museum quarries A, B, and later C were developed. From here, Osborn and Ferrar made a three-day camel march west to Garet Gehan-nam and Wadi Hitan on February 14–16 (site 5 in Fig. 1). As Osborn (1907b) wrote:

We found [Wadi Hitan] strewn with the remains of monster zeuglodonts, including heads, ribs and long series of vertebrae, most tempting to the fossil hunter, yet too large and difficult of removal from this very remote and arid point.

Osborn left the Fayum on February 18 to return to Cairo and New York, leaving Walter Granger [1872–1941] and Granger's assistant George Olsen [d. 1939] of the American Museum as the paleontologists responsible for all of the fossil collections to be made in Fayum. Granger and Olsen started work in Fayum on February 5 with a large team of Egyptian workers. They continued work at and near quarries A, B, and C through April 21, when they moved camp for three days to Qasr el-Sagha.

February 16, 1907, Granger had a chance meeting with Richard Markgraf, who was collecting fossils in the same area. Osborn met Markgraf on February 17 after his return from Wadi Hitan. At this time negotiations started for Markgraf to work the remainder of the season for the American Museum team. Two archaeocete specimens in the American Museum collection, a brain-case and frontal of *Basilosaurus isis* and a fine skull of *Saghacetus osiris*, were collected by Markgraf. The latter is illustrated in Kellogg (1936). These Markgraf specimens came from the Birket Qarun escarpment (site 4 in Fig. 1) and the Qasr el-Sagha escarpment (site 3 in Fig. 1), respectively.

The only archaeocete that the American Museum party found themselves was a partial skull of *Saghacetus osiris* collected on April 23 from 1–2 kilometers west of Qasr el-Sagha temple. Granger left Fayum for Cairo on April 25, and then returned to the field in Fayum again from May 2 through May 23.

## Phillips and Denison

Wendell Phillips [1925–1975], namesake and descendent of the nineteenth century abolitionist orator, was a young American, an enthusiastic Princeton undergraduate and University of California, Berkeley, graduate student in paleontology

who became an anthropologist, archaeologist, Arabian and African explorer, and later founder of Wendell Phillips Oil Company based in London. He participated in the first Pan-African Congress on Prehistory in 1947 and then organized the University of California African Expedition from Cairo to Cape Town, which was active from 1947–1950 (Phillips, 1948). Phillips also founded the American Foundation for the Study of Man, in Washington, D.C., in 1949.

Robert H. Denison [1911–1985], then of Dartmouth College, was the principal paleontologist during the Egyptian phase of the University of California African Expedition. He was assisted by Paul Deraniyagala of Ceylon, V. L. VanderHoff of Stanford University, and H. B. S. Cooke of the University of Witwatersrand. This group worked in Fayum from September 24 through December 14, 1947. Most of their time was spent prospecting and excavating in the vicinity of the earlier Beadnell-Andrews and American Museum excavations and prospecting on the Qasr el-Sagha excarpment (site 3 in Fig. 1).

On November 14, Denison and Deraniyagala drove westward with two U.S. Marine soldiers and reached Garet Gehannam and Wadi Hitan on November 15 (site 5 in Fig. 1). The group camped for two nights, and collected the well preserved left half of a *Basilosaurus isis* skull for the University of California at Berkeley. Deraniyagala (1948) published an illustrated account of the field work, including the trip to Wadi Hitan. Deraniyagala reported the whale skeletons in Wadi Hitan as Oligocene in age, which they are not, and recorded that some twenty skeletons lay with a radius of 1–2 kilometers of their camp, which is likely. However, his interpretation that such a density of skeletons “shows that even 35 million years ago schools of whales committed race suicide by stranding themselves” would require more detailed documentation than he provided.

### *Moustafa*

Y. Shawki Moustafa [n.d.] of Cairo University collected the cranium of a subadult archaeocete in 1950 from the lower part of the Birket Qarun Formation west of lake Birket Qarun (Moustafa, 1954, 1974; the specimen was found somewhere in or between sites 4 and 5 in Fig. 1). Following Kellogg (1936), Moustafa identified this as *Prozeuglodon isis*. However, with the experience of many seasons collecting archaeocetes in the Birket Qarun Formation (see below), the only archaeocete species found west of Birket Qarun for which numerous subadult individuals are known is *Dorudon atrox*, and the specimen described by Moustafa has the size and morphology of this species.

### *Simons and Meyer*

Elwyn Simons [b. 1930] was an American professor at Yale University when he started field work in Egypt. Simons carried out his first season of field work in

Fayum during the winter of 1961–1962, working north of the Qasr el-Sagha escarpment (Simons, 1968; north of site 3 in Fig. 1). Simons is now at Duke University, and the project continues to the present day with emphasis on recovery of late Eocene and Oligocene fossil primates. The manager of Simons' field work during the 1960s was Grant E. Meyer [d. 2004], who organized two trips to Wadi Hitan in 1965–65 and 1966–1967. During the first, Meyer was assisted by Jeff Smith and Tom Walsh, and during the second he was assisted by John Boyer and Lloyd Tanner. Collections from these expeditions are in the Cairo Geological Museum and the Yale University Peabody Museum of Natural History.

### *Simons and Gingerich*

Another American, Philip D. Gingerich [b. 1946], started working with Simons in 1983 to collect representative archaeocetes from the Qasr el-Sagha escarpment (site 3 in Fig. 1) and from Wadi Hitan (site 5 in Fig. 1). Initially the purpose was simply to acquire comparative specimens to facilitate research on archaeocetes being found in Pakistan, but both sites in Egypt proved to be so productive of exceptionally complete specimens that field research was focused here (Fig. 4). Field work was carried forward during six field seasons, in odd-numbered years from 1983 through 1993. Assistance was provided by Ali Barakat, Tom Bown, Will Clyde, Gregg Gunnell, Abd el-Latif, Alex van Nievelt, Bill Sanders, Holly Smith, and others in various years. Collections from these expeditions are in the Cairo Geological Museum and the University of Michigan Museum of Paleontology, and have been studied by Gingerich et al. (1990), Gingerich and Smith (1990), Gingerich (1992), Gingerich and Uhen (1996), and Uhen (1998, 2004).

The principal results of this work can be enumerated here:

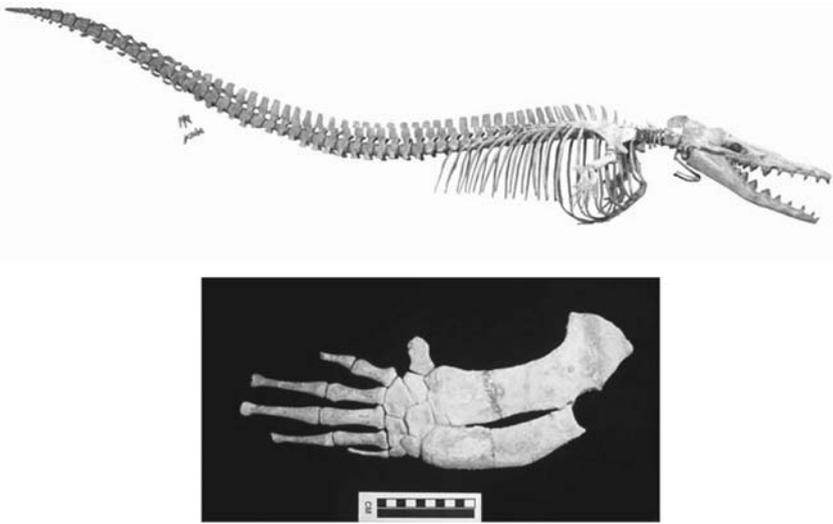
- (1) The only archaeocete species found commonly in the late Priabonian Qasr el-Sagha Formation of the Qasr el-Sagha escarpment (site 3 in Fig. 1) is the small ca. 3 meter-long *Saghacetus osiris*, which is known from skulls and several fairly complete axial skeletons.
- (2) There are two archaeocete genera and species found commonly in the early Priabonian Birket Qarun Formation of Wadi Hitan (site 5 in Fig. 1), which are the large ca. 18 meter-long *Basilosaurus isis* and the medium-sized ca. 5 meter-long *Dorudon atrox*. Both are known from virtually complete skeletons (e.g., Fig. 5).
- (3) Approximately 500 skeletons or partial skeletons of archaeocetes have been mapped in Wadi Hitan. Most specimens are *Basilosaurus isis* or *Dorudon atrox*. *B. isis* is a little more common than *D. atrox*, but skeletons of *B. isis* are also larger and therefore easier to map. All known *B. isis* specimens are mature adults, while *D. atrox* is approximately equally represented by



**Fig. 4** Elwyn Simons helping to excavate the hind limb of a specimen of an 18-meter-long individual of *Basilosaurus isis* in Wadi Hitan in 1989. The vertebral column is articulated, and each individual centrum shown here measures about 30–33 cm in length. In contrast, a complete tibia, shown in situ here, is less than 15 cm long. Hind limbs and feet of Wadi Hitan *Basilosaurus isis*, the first for a cetacean, were described by Gingerich et al., 1990)

mature adult and immature specimens. Some immature *D. atrox* skulls exhibit bite marks made by a large predator, possibly *B. isis*.

- (4) A third archaeocete species, *Ancalocetus simonsi*, is the size of *Dorudon atrox* and represented by a single partial skeleton (Gingerich and Uhen, 1996). There are seemingly two or three additional archaeocete genera and species present in Wadi Hitan.
- (5) *Basilosaurus isis* and *Dorudon atrox* skeletons both retain flexible elbows but have wrists with blocky, tightly-packed carpals. The carpus consists of a separate scaphoid, lunar, and cuneiform in the proximal row; and a reduced trapezium, fused trapezoid-magnum, and large unciform in an alternating distal row. A small superficial centrale articulated with the scaphoid. The pollex is greatly reduced but not lost, and the pisiform is large, flat, and projecting (Gingerich and Smith, 1990; Uhen, 2004). This pattern differs somewhat from that of *Zygorhiza kochii* described by Kellogg (1936), which has relatively smaller carpals.
- (6) *Basilosaurus isis* has 7 cervical vertebrae, 18 thoracics, and about 42 lumbo-caudals (Gingerich et al., 1990), while the vertebral formula for *Dorudon atrox* was 7.17.20.21 (Uhen, 2004; lumbar and caudals are distinguished



**Fig. 5** Virtually complete skeleton of *Dorudon atrox* collected in 1991 from Wadi Hitan. Note the forelimbs modified as flippers, expanded and robust lumbocaudal vertebral series, and reduced *Basilosaurus*-like hind limbs separated from the axial skeleton and embedded in the ventral body wall. All are characteristics of modern whales with a tail fluke and associated with aquatic propulsion by caudal undulation and oscillation (Uhen, 1996, 2004; Gingerich, 2003)

by the presence or absence of chevron facets). Skeletons of both genera and species lack any clear evidence of an intervening sacrum in the lumbocaudal vertebral series; both evidently retained pelvis well separated from their vertebral column, and both were fully aquatic tail-powered swimmers. Both retained well-formed hind limbs and feet that were much reduced in size compared to the rest of the skeleton.

### ***Gingerich, Fouda, and Attia***

A new cooperative project was initiated in 2004 involving the Egyptian Environmental Affairs Agency (represented by Moustafa M. A. Fouda [b. 1950]), the Egyptian Mineral Resources Authority (including the Egyptian Geological Survey and Geological Museum; represented by Yousry Attia [n.d.]), and the University of Michigan (represented by Philip D. Gingerich). Field work was restarted to substantiate the importance of Wadi Hitan for understanding early whale evolution, which contributed to the site being designated a UNESCO World Heritage Site in 2005. New fossils have been collected, but these have not as yet been prepared or studied, and there are as yet no new scientific results to report.

### *Bianucci and Others*

Giovanni Bianucci [n.d.] and others in Italy illustrated and exhibited the skeleton of a protocetid archaeocete recovered by stonecutters in Italy while cutting decorative limestone imported from Egypt (Bianucci et al., 2003). There are additional unpublished reports of archaeocetes and primitive sirenians being found in limestones imported to Europe from Egypt. Investigation in 2006 indicates that these specimens are coming from the Gebel Hof Formation or equivalent, of Bartonian late middle Eocene age, from a site at 28E 27' N latitude and 31E 50' E longitude, north of Khashm el-Raqaba in Wadi Tarfa, Eastern Desert of Egypt (Fig. 6). More work will be required to devise a way to find, recover, and prepare such specimens for scientific study. They are potentially very important for filling a gap between reasonably well known Lutetian early middle Eocene protocetids and classic Priabonian late Eocene basilosaurids. This gap is the time of transition from foot-powered to tail-powered swimming in archaeocetes.



**Fig. 6** Truck hauling middle Eocene limestone from a major quarry complex at 28E 27' N latitude and 31E 50' E longitude, north of Khashm el-Raqaba in Wadi Tarfa, Eastern Desert of Egypt. This limestone is exported to Europe and elsewhere as decorative building stone. Some is archaeocete-bearing, as indicated by the specimen illustrated by Bianucci et al. (2003)

## Significance

Egyptian fossil localities and specimens are fundamental for understanding the early evolution of whales. Egyptian archaeocetes are found in four stratigraphic intervals spanning much of the middle and late Eocene, and all four intervals have been known for fully 100 years. Likewise, five of the six major sites in Fig. 1 have been known for fully 100 years. Wadi Hitan has been particularly important during the past twenty years because it is here that we have been able to answer many of the questions left unanswered by Kellogg's (1936) classic monograph on Archaeoceti. We now have several archaeocetes with virtually complete axial skeletons, and we know their vertebral formulae. We know the size, proportions, and articulation of the forelimb, wrist, and hand for *Basilosaurus* and *Dorudon*, and we know much about the size, proportions, and articulation of the hind limb, tarsus, and foot for both genera.

Further, the success of our research on skeletons of late Eocene archaeocetes in Wadi Hitan inspired a return to investigation of protocetid archaeocetes in Pakistan, where protocetids are now represented by equally complete skeletons with skulls, axial skeletons complete to the end of the tail, forelimbs with wrists, hands, fingers, and hooves, and hind limbs with ankles, feet, and toes. Recovery of ankle bones associated with protocetid skeletons demonstrated the artiodactyl ancestry of whales, solving a major mystery and controversy in mammalian phylogeny (Gingerich et al., 2001).

Finally, to close, this is an appropriate place to acknowledge and thank Elwyn Simons for encouraging and facilitating research on early whale evolution in Egypt. Simons said several times during his career that what surprised him about fieldwork in Egypt and elsewhere was that new discoveries rarely conform to expectation. This has been my experience studying early whale evolution too. I never expected that archaeocetes living 15–20 million years after the origin of whales would still retain well formed hind limbs and feet, long after they ceased to walk; and I never expected that whales would prove to be the direct descendants of artiodactyls. Field work in Egypt and Pakistan has shown both to be true. This means two things: first, we are still at a stage where emphasis on exploration and discovery now will greatly enhance reliable interpretation in the future; and second, it is probably futile to try to infer the paths of morphological transformation, adaptation, and phylogenetic relationships of whales (or primates) in much detail beyond what we can trace in the fossil record.

Inference from the present works in some instances, as in prediction that whales and artiodactyls should be related (starting with Boyden and Gemeroy, 1950), but animals living today are a small subset of those that have lived in the past, limiting what we can learn of the past from the present. Van Valen (1966) explained Boyden and Gemeroy's inference of a whale-artiodactyl relationship in terms consistent with what we knew of the fossil record at the time, but here, to my surprise, new fossils showed he was wrong. If inferential methods had much power, we would more often find what we expect in the fossil record.

**Acknowledgment** I thank Elwyn Simons for encouraging and facilitating research on early whale evolution in Egypt, and for the same, less directly, in Pakistan. John G. Fleagle provided important encouragement too when we started research in 'Zeuglodon Valley.' The editor and two anonymous reviewers provided comments improving the manuscript. Field research in Egypt was made possible by a succession of grants from the Committee for Research and Exploration of the National Geographic Society, and more recently by the U.S.-Egypt Joint Science and Technology Program and the U.S. National Science Foundation (OISE-0513544).

## References

- Andrews, C. W. (1899). Fossil Mammalia from Egypt, Part I. *Geol. Mag.* 6: 481–484.
- Andrews, C. W. (1904). Further notes on the mammals of the Eocene of Egypt, Part III. *Geol. Mag.* 1: 211–215.
- Andrews, C. W. (1906). A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum (Natural History), London. p. 324.
- Beadnell, H. J. L. (1901). The Fayum depression: A preliminary notice of the geology of a district in Egypt containing a new Palaeogene vertebrate fauna. *Geol. Mag., London* 8: 540–546.
- Beadnell, H. J. L. (1905). The topography and geology of the Fayum Province of Egypt. Survey Department of Egypt, Cairo. p. 101.
- Bianucci, G., Nocchi, C., Sorbini, C., and Landini, W. (2003). L'Archeoceto nella Roccia alle origini dei Cetacei. Museo di Storia Naturale e del Territorio, Università degli Studi di Pisa, Pisa. pp. 1–17
- Blanckenhorn, M. (1900). Neues zur Geologie und Paläontologie Aegyptens. II. Das Palaeogen. *Z. Deut. Morganland. G.* 52: 403–479.
- Blanckenhorn, M. (1903). Neue geologisch-stratigraphische Beobachtungen in Aegypten. *Sitzungsberichte der Mathematisch-physikalischen Classe der Königlichen bayerischen Akademie der Wissenschaften, München* 32: 353–433.
- Boyden, A. A., and Gemeroy, D. G. (1950). The relative position of the Cetacea among the orders of Mammalia as indicated by precipitin tests. *Zoologica- New York* 35: 145–151.
- Cope, E. D. (1868). An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States. *P. Acad. Nat. Sci. Phila.* 19: 138–156.
- Dames, W. B. (1883a). Ein Epistropheus von Zeuglodon sp. *Sitzungsberichte der Gesellschaft naturforschender Freunde, Berlin* 1883: 3.
- Dames, W. B. (1883b). Ueber eine tertiär Wirbelthierfauna von der westlichen Insel der Birket-el-Qurun. *Sitzungsberichte der Königlich-preussischen Akademie der Wissenschaften, Berlin* 1883: 129–153.
- Dames, W. B. (1894). Über Zeuglodonten aus Aegypten und die Beziehungen der Archaeoceten zu den übrigen Cetaceen. *Geologische und Paläontologische Abhandlungen, Jena* 5: 189–222.
- Deraniyagala, P. E. P. (1948). Some scientific results of two visits to Africa. *Spolia Zeylanica* 25: 1–42.
- Fraas, E. (1904a). Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo. *Geologische und Paläontologische Abhandlungen, Jena* 6: 197–220.
- Fraas, E. (1904b). Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Cairo. *Geologisches Zentralblatt, Leipzig* 5: 374.
- Fraas, E. (1906). Wüstenreise eines Geologen in Ägypten. *Kosmos, Handweiser für Naturfreunde, Stuttgart* 3: 263–269.
- Gibbes, R. W. (1845). Description of the teeth of a new fossil animal found in the green-sand of South Carolina. *P. Acad. Nat. Sci. Phila.* 2: 254–256.

- Gidley, J. W. (1913). A recently mounted *Zeuglodon* skeleton in the United States National Museum. *Proceedings of the U.S. National Museum* 44: 649–654.
- Gingerich, P. D. (1992). Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *University of Michigan Papers on Paleontology* 30: 1–84.
- Gingerich, P. D. (2003). Land-to-sea transition of early whales: Evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. *Paleobiology* 29: 429–454.
- Gingerich, P. D. (2005). Cetacea. In: Rose, K. D. and Archibald, J. D. (eds.), *Placental mammals: origin, timing, and relationships of the major extant clades*. Johns Hopkins University Press, Baltimore, pp. 234–252.
- Gingerich, P. D., Haq, M., Zalmout, I. S., Khan, I. H., and Malkani, M. S. (2001). Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science* 293: 2239–2242.
- Gingerich, P. D., and Smith, B. H. (1990). Forelimb and hand of *Basilosaurus isis* (Mammalia, Cetacea) from the middle Eocene of Egypt. *J. Vertebr. Paleontol.* 10A: 24.
- Gingerich, P. D., Smith, B. H., and Simons, E. L. (1990). Hind limbs of Eocene *Basilosaurus isis*: Evidence of feet in whales. *Science* 249: 154–157.
- Gingerich, P. D., and Uhen, M. D. (1996). *Ancalocetus simonsi*, a new dorudontine archaeocete (Mammalia, Cetacea) from the early late Eocene of Wadi Hitán, Egypt. *Contrib. Mus. Paleontol., Univ. Mich.* 29: 359–401.
- Harlan, R. (1834). Notice of fossil bones found in the Tertiary formation of the State of Louisiana. *T. Am. Phil. Soc.* 4: 397–403.
- Kellogg, R. (1928). The history of whales—their adaptation to life in the water. *Q. Rev. Biol.* 3: 29–76, 174–208.
- Kellogg, R. (1936). A review of the Archaeoceti. *Carnegie Institution of Washington Publications* 482: 1–366.
- Moustafa, Y. S. (1954). Additional information on the skull of *Prozeuglodon isis* and the morphological history of the Archaeoceti. *Proceedings of the Egyptian Academy of Science* 9: 80–88.
- Moustafa, Y. S. (1974). Critical observations on the occurrence of Fayum fossil vertebrates. *Annals of the Geological Survey of Egypt* 4: 41–78.
- Osborn, H. F. (1907a). The Fayum expedition of the American Museum. *Science* 25: 513–516.
- Osborn, H. F. (1907b). Hunting the ancestral elephant in the Fayum desert. *Century Magazine* 74: 815–835.
- Owen, R. (1839). Observations on the teeth of the *Zeuglodon*, *Basilosaurus* of Dr. Harlan. *Proceedings of the Geological Society of London* 1839: 24–28.
- Owen, R. (1841). Observations on the *Basilosaurus* of Dr. Harlan (*Zeuglodon cetoides* Owen). *Transactions of the Geological Society of London* 2: 69–79.
- Owen, R. (1875). On fossil evidences of a sirenian mammal (*Eotherium aegyptiacum*) from the nummulitic Eocene of the Mokattam cliffs, near Cairo. *Quarterly Journal of the Geological Society of London* 31: 100–105.
- Phillips, W. (1948). Recent discoveries in the Egyptian Fayum and Sinai. *Science* 107: 666–670.
- Reichenbach, H. G. L. (1847). Systematisches. In: Carus, C. G. (ed.), *Resultate geologischer, anatomischer und zoologischer Untersuchungen über das unter dem Namen Hydrarchos von Dr. A. C. Koch zuerst nach Europa gebrachte und in Dresden angestellte grosse fossile Skelett*. Arnoldische Buchhandlung, Dresden and Leipzig, pp. 13–15.
- Schweinfurth, G. A. (1883). Ueber die geologische Schichtengliederung des Mokattam bei Cairo. *Zeitschrift der Deutschen Geologischen Gesellschaft, Stuttgart* 35: 709–737.
- Schweinfurth, G. A. (1886). Reise in das Depressionsgebiet im Umkreise des Fajum im Januar 1886. *Zeitschrift der Gesellschaft für Erdkunde zu Berlin* 21: 96–149.
- Seiffert, E. R. (this volume). Geology, paleoenvironment, and age of Birket Qarun Locality 2 (BQ-2), Fayum Depression, Egypt. In: Fleagle, J. G. (ed.), *Elwyn L. Simons: Mapping the Progress of Primate Evolution*. Plenum Press, New York.

- Simons, E. L. (1968). Early Cenozoic mammalian faunas, Fayum Province, Egypt. Part 1. African Oligocene mammals: introduction, history of study, and faunal succession. *Bulletin of the Peabody Museum of Natural History, Yale University* 28: 1–21.
- Slijper, E. J. (1936). Die Cetaceen, Vergleichend-Anatomisch und Systematisch. *Capita Zoologica* 6–7: 1–590.
- Stromer von Reichenbach, E. (1903a). Bericht über eine von den Privatdozenten Dr. Max Blanckenhorn und Dr. Ernst Stromer von Reichenbach ausgeführte Reise nach Aegypten. Einleitung. Ein Schädel und Unterkiefer von Zeuglodon osiris Dames. *Sitzungsberichte der Mathematisch-physikalischen Classe der Königlichen Bayerischen Akademie der Wissenschaften, München* 32: 341–352.
- Stromer von Reichenbach, E. (1903b). Zeuglodon-Reste aus dem oberen Mitteleocän des Fajum. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Vienna* 15: 65–100.
- Stromer von Reichenbach, E. (1908). Die Archaeoceti des ägyptischen Eozäns. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Vienna* 21: 106–178.
- Uhen, M. D. (1996). *Dorudon atrox* (Mammalia, Cetacea): Form, function, and phylogenetic relationships of an archaeocete from the late middle Eocene of Egypt. Ph.D. dissertation, University of Michigan, Ann Arbor, p. 608.
- Uhen, M. D. (1998). Middle to late Eocene basilosaurines and dorudontines. In: Thewissen, J. G. M. (ed.), *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea*. Plenum Press, New York, pp. 29–61.
- Uhen, M. D. (2004). Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the middle to late Eocene of Egypt. *University of Michigan Papers on Paleontology* 34: 1–222.
- Van Valen, L. M. (1966). Deltatheridia, a new order of mammals. *B. Am. Mus. Nat. Hist.* 132: 1–126.
- Zachos, J. C., Pagani, M., Sloan, L. C., Thomas, E. and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.

**Gingerich, P. D. 2007. Early evolution of whales: a century of research in Egypt. In J. G. Fleagle and Christopher C. Gilbert (eds.), *Elwyn Simons: A Search for Origins*, Springer, New York, pp. 107-124.**

**Six figures prepared for publication in this chapter are included on the following pages. Inexplicably, a different set of figures was used in the chapter printed by Springer, and no proof copies of text or figures were sent to authors.**

**Fig. 1** Landsat image of present-day Egypt showing the location of Eocene archaeocete whale sites at Gebel Mokattam (site 1), Geziret el-Qarn (site 2), Qasr el-Sagha escarpment (site 3), Birket Qarun escarpment (site 4), Wadi Hitan (site 5), and Khashm el-Raqaba in Wadi Tarfa (site 6).

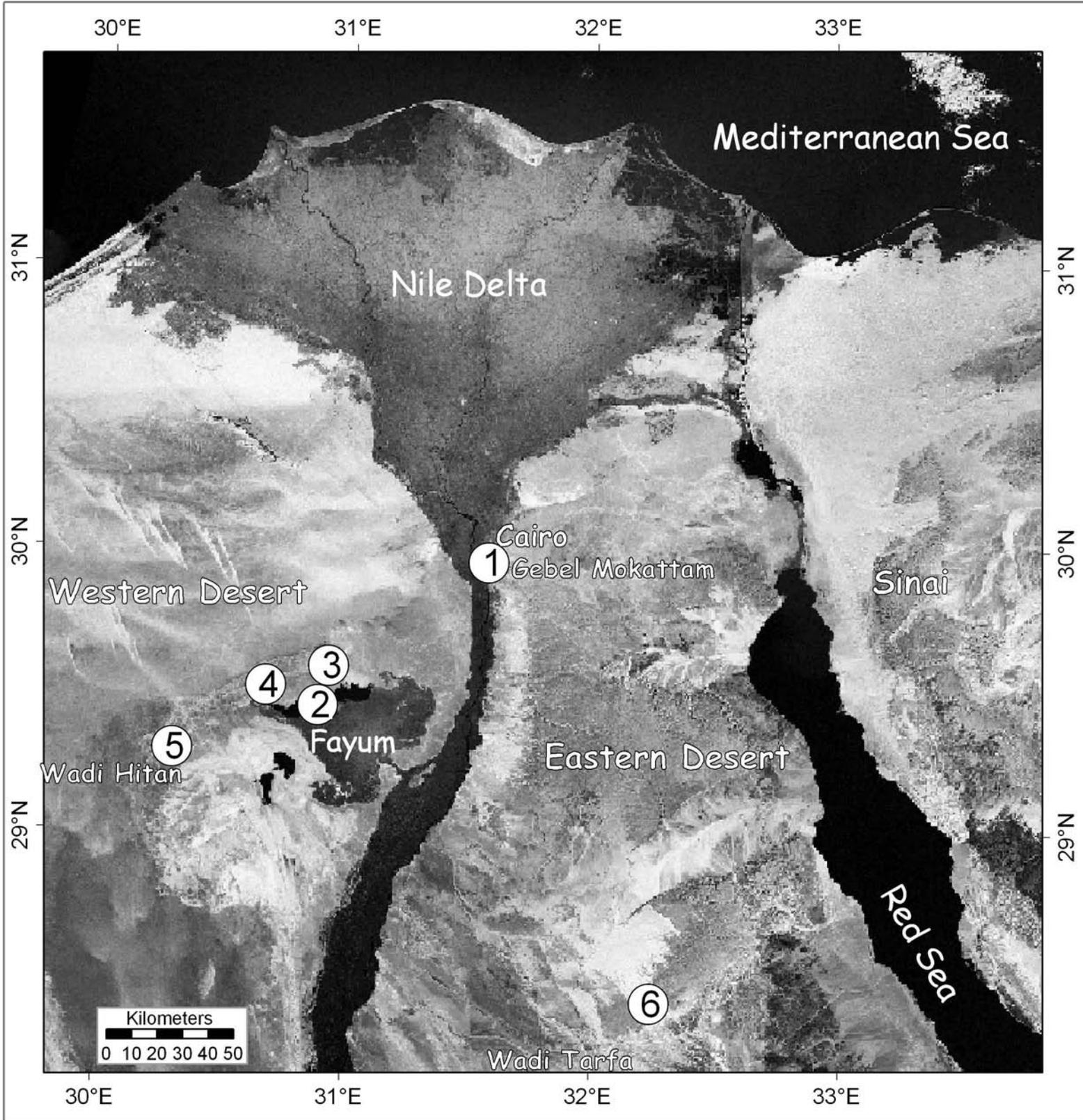
**Fig. 2** Georg Schweinfurth's map of Fayum showing the path of his 1886 expedition through Wadi Rayan and north of Birket Qarun. Schweinfurth found the type specimen of *Zeuglodon osiris* (now *Saghacetus osiris*) at the site near his January 21–22 camp (Garet el Esh). He camped at Garet Gehannam on January 16–17, but never found the archaeocete skeletons there nor those in Wadi Hitan several kilometers to the west.

**Fig. 3** Type specimen of *Zeuglodon osiris* Dames, 1894 [now *Saghacetus osiris* (Dames)] found by Georg Schweinfurth at a site near Garet el Esh (see Fig. 2), north of lake Birket Qarun in the Fayum Depression.

**Fig. 4** Elwyn Simons helping to excavate the hind limb of a specimen of an 18-meter-long individual of *Basilosaurus isis* in Wadi Hitan in 1989. The vertebral column is articulated, and each individual centrum shown here measures about 30–33 cm in length. In contrast, a complete tibia, shown in situ here, is less than 15 cm long. Hind limbs and feet of Wadi Hitan *Basilosaurus isis*, the first for a cetacean, were described by Gingerich et al., 1990).

**Fig. 5** Virtually complete skeleton of *Dorudon atrox* collected in 1991 from Wadi Hitan. Note the forelimbs modified as flippers, expanded and robust lumbocaudal vertebral series, and reduced *Basilosaurus*-like hind limbs separated from the axial skeleton and embedded in the ventral body wall. All are characteristics of modern whales with a tail fluke and associated with aquatic propulsion by caudal undulation and oscillation (Uhen, 1996, 2004; Gingerich, 2003).

**Fig. 6** Truck hauling middle Eocene limestone from a major quarry complex at 28° E 27' N latitude and 31° E 50' E longitude, north of Khashm el-Raqaba in Wadi Tarfa, Eastern Desert of Egypt. This limestone is exported to Europe and elsewhere as decorative building stone. Some is archaeocete-bearing, as indicated by the specimen illustrated by Bianucci et al. (2003).



# KARTE DES DEPRESSIONSGBIETES

## IM UMKREISE DES FAJÛM

aufgenommen von

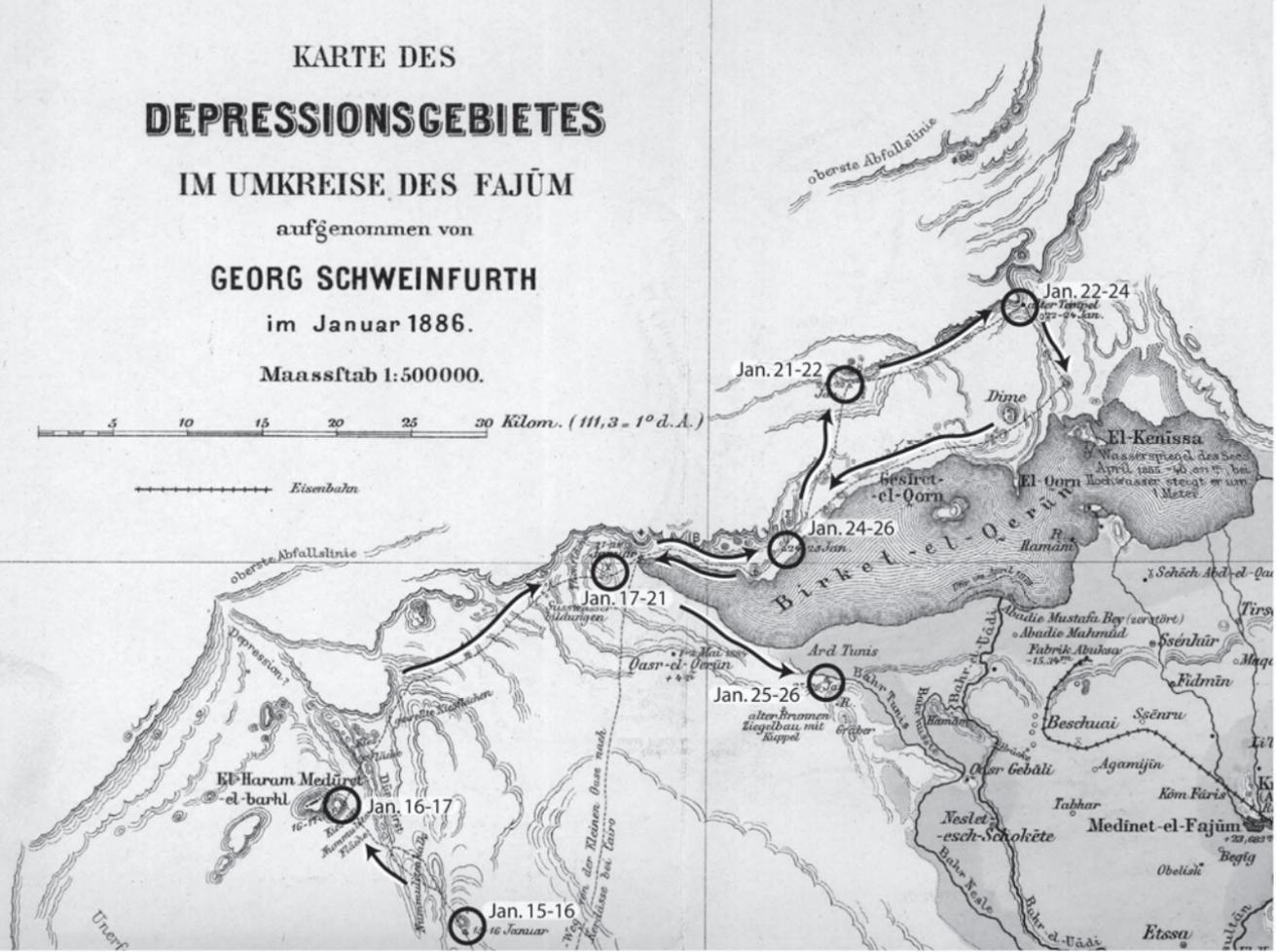
**GEORG SCHWEINFURTH**

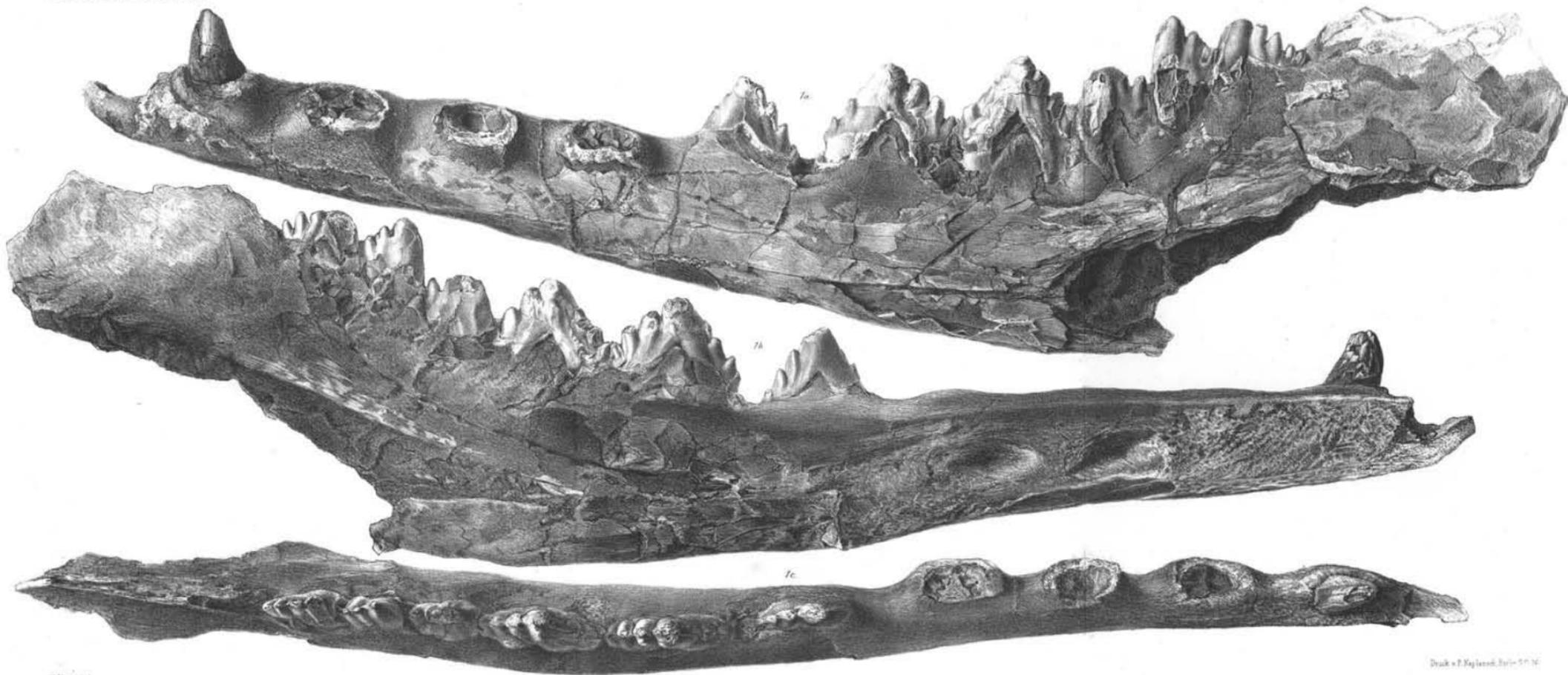
im Januar 1886.

Maassstab 1:500000.

5 10 15 20 25 30 Kilom. (111,3 = 1° d. A.)

+++++ Eisenbahn







Tibia

Articulated  
vertebrae

