PRONYCTICEBUS NEGLECTUS — AN ALMOST COMPLETE ADAPID PRIMATE SPECIMEN FROM THE GEISELTAL (GDR)

by

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CONTENT

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ABSTRACT

In the course of the current revision of adapid primates from the Eocene Geiseltal, an almost complete specimen was found in the Geiseltal Museum collections. The fossil, the most complete adapid specimen so far discovered in Europe, has been determined as *Pronycticebus neglectus* n. sp. Ecology and locomotion as well as the likely phylogenetic position within the infraorder Adapiformes are discussed.

RESUME

Pronycticebus neglectus — un primate adapidé presque complet du Geiseltal (RDA).

A l'occasion d'une révision des primates adapidés de l'Eocène du Geiseltal un exemplaire presque complet fut trouvé dans les collections du musée. Le fossile, l'adapidé le plus complet en Europe, a été déterminé comme *Pronycticebus neglectus* n. sp. L'écologie et la locomotion sont discutées, ainsi que la position phylogénétique dans l'infraordre des Adapiformes.

KURZFASSUNG

Pronycticebus neglectus — ein fast vollständiger adapider Primate aus dem Geiseltal (DDR).

Die laufende Revision der adapiden Primaten aus dem eozänen Geiseltal hat zur Auffindung eines fast vollständigen Exemplars in den Museumsbeständen geführt. Das Fossil, bei dem es sich um den bis jetzt komplettesten Fund eines Adapiden in Europa handelt, wurde als *Pronycticebus neglectus* n. sp. bestimmt. Die Ökologie und Lokomotion, sowie die phylogenetische Stellung innerhalb der Infraordnung Adapiformes werden diskutiert.

INTRODUCTION

The earliest known Euprimates or "primates of modern aspect" (Simons 1963, Gingerich 1986) were widespread during the Eocene (54-35 my) in the Holarctic region (Szalay & Delson 1979). They are commonly allocated to two separate families, Omomyidae and Adapidae (e.g. Szalay & Delson 1979). The phylogenetic relationships of both groups remain uncertain. No plausible ancestors of either group are present in known European, Asian or North American faunas of late Paleocene age (Gingerich 1986). The adapids were recently interpreted as possible stem relatives of a monophyletic group containing modern lemurs and lorises (Beard *et al.* 1988), while omomyids are commonly interpreted to be at the base of the haplorhine radiation (Fleagle 1988).

The evolution of modern primates is still poorly understood, as the fossil record consists predominantly of dental evidence. The postcranial skeleton of North American adapids of the genera *Cantius*, *Notharctus* and *Smilodectes* is relatively well documented by articulated specimens (Beard & Godinot 1988, Gregory 1920, Rose & Walker 1985, Simons 1964), while among the European adapids, *Adapis parisiensis* and *Adapis (Leptadapis) magnus* are known from isolated, disarticulated postcranial remains allocated to those genera (Dagosto 1983). Four partial skeletons have been reported from the German site of Messel (Koenigswald 1979, 1985, Franzen 1987, 1988), but only one is associated with a skull permitting identification as *Europolemur koenigswaldi* FRANZEN, 1987. So far, no articulated skeleton including at least parts of the skull, dentition and representative body regions has been described for any European adapid.

The specimen reported here, allocated to the new species *Pronycticebus neglectus*, may serve as a test case for phylogenetic and paleoecological hypotheses based on the study of the fragmentary fossil record of extant primates.

SYSTEMATICS & TAXONOMY

Order **PRIMATES** LINNAEUS, 1758
Family **ADAPIDAE** TROUESSART, 1879

Pronycticebus neglectus n. sp.

Holotype: GMH L-2, an articulated and partially dislocated skeleton, including the crushed skull with upper and lower dentition and most of the postcranial skeleton (fig. 1, pl. 1, 2). Collection of the Geiseltalmuseum Halle (GMH), Martin-Luther-Universität Halle-Wittenberg (German Democratic Republic).
Etymology: The fossil was originally found in 1969, but its significance was not fully appreciated until much later (from Latin neglegere = to neglect, to leave unnoticed).
Type locality and horizon: Tagebau Geiselröhlitz, site L, Geiseltal near Halle (GDR), lower part of the Geiseltal brown coal, "Untere Mittelkohle", Middle Geiseltalian, MP level 12 (Franzen & Haubold 1987), Middle Eocene or Lutetian, respectively, in age.
Hypodigm: GMH XXII-1, right mandibular fragment with alveoli of C, P/2, and preserved P/3-4, M/1-3. Tagebau Neumark-Süd, site XXII, "Untere Mittelkohle" but slightly higher in stratigraphic position than the type. Formerly assigned to *Europolemur klatti* (Szalay & Delson 1979: 124, fig. 57B, D-E) or *Pronycticebus klatti* (Tattersall & Schwartz 1983: 7, fig. 5 "*Protoadapis klatti*").
Diagnosis: The morphology of the upper and lower dentition (fig. 2a-d) clearly indicates affinities with the members of the tribe Protoadapini (*Protoadapis*, *Agerinia*, *Europolemur*, *Mahgarita*, *Pronycticebus*) (Szalay & Delson 1979) in having a premolariform upper and lower P4, in lacking a postprotocone fold and in having a P/4 and P/3 subequal in height. Within this tribe, *Pronycticebus neglectus* differs from *Agerinia* species in being clearly larger in size (Szalay 1971) and from *Protoadapis curvicuspidens* in lacking a metaconule and in having a clearly defined hypocone on M1/ and M2/ (Russell *et al.* 1967). The hypoconulid lobe of M/3 is more developed in accordance with the distally more expanded M3/. *Protoadapis angustidens* is larger than *P. curvicuspidens* (Russell *et al.* 1967) and therefore larger than *Pronycticebus neglectus*, which is of comparable size to, or slightly smaller than, *P. curvicuspidens*. *Pronycticebus neglectus* differs from *Europolemur klatti*, *E. (Alsatia) dunaifi*, *E. collinsonae*, and *Mahgarita stevensi* in having an isolated developed hypocone, in lacking crested cinguli both lingually and buccally, in showing a less quadratic outline of M1/, M2/, and in having a relatively larger M3/. In *E. koenigswaldi*, the hypocone is only slightly developed on M2/ and lacking on M1/; a buccal cingulum is also present. *Pronycticebus neglectus* differs from *Pronycticebus gaudryi* in lacking a buccal cingulum on M1/ and M2/, and in the absence of a metaconule and an epicrista. The outline of the molars is very similar, however, especially in M3/, which is disto-lingually slightly expanded and has a small swelling in the pericone region. The specimen is therefore most similar to *Pronycticebus gaudryi* and is hence included in this genus as a new species.

DESCRIPTION & COMPARISONS

A detailed morphological description and comparisons of all preserved elements (fig. 1a) will be published elsewhere. This paper concentrates on the dentition and on certain postcranial elements that are of particular interest.

SKULL & DENTITION

The skull and face are badly crushed. Anteriorly, the margin of the orbit ends before P4/, as in European *Pronycticebus gaudryi*, *Europolemur klatti* (Weigelt 1933), *Caenopithecus lemuroides* and North American *Smilodectes gracilis*. This contrasts with the European *Adapis parisiensis* and *Adapis (Leptadapis) magnus* and with North American *Notharctus tenebrosus* and *Mahgarita stevensi*, in which the orbit ends over M1/. The diameter of the orbit has been calculated from available fragments to be about 14-15 mm. This is comparable to that of *Hapalemur griseus* [880 g (Jungers 1985)] among recent primates, with a body size comparable to *P. neglectus* (800-850 g, tab. 2) and to that of the Eocene *Adapis parisiensis*, the latter being twice as heavy as *Pronycticebus neglectus*. Based on the relationship between orbit diameter and skull length, *A. parisiensis* has been supposed to be diurnal (Gingerich & Martin 1981).

The dentition is worn, obscuring morphological features to some degree. The upper dentition (fig. 2a) preserves on the right side P3/, the roots of P4/, M1/ (length x width = 4.5 x 5.0 mm), a broken M2/ and a partially covered but complete M3/ (3.5 x ?), on the left side P2/ and P3/ (visible in the X-ray), P4/ (3.4 x ?), M1/ (4.6 x ?), M2/ (4.7 x ?) and M3/ (3.5 x ?). No P1/ was present; upper incisors and canines are not traceable. P2/ is a single-rooted and very small single-cusped tooth. P3/ possesses a paracone, a small protocone (fig. 2a) and a cingulum forming small para- and distostyles. The same elements are characteristic for P4/, except that the development of the protocone is much more marked and a proper talon is present. M1/ (fig. 2a, d) and M2/ (fig. 2a) are very similar in morphology, though M2/ is somewhat better developed. The protocone is the largest cusp on the trigon. A hypocone is clearly developed at the lingual end of the distal cingulum. No so-called "*Nannopithex*-fold" (postprotocingulm) is present and the cusp is therefore a true hypocone. A protoconule is present, whereas the metaconule is absent. The crests are clearly defined, but not so sharply defined as in *Pronycticebus gaudryi* or *Europolemur klatti* and *E. dunaifi*. The anterior cingulum ends beneath the protocone; a buccal cingulum is lacking. The M3/ (fig. 2a) is relatively broad and short. The metacone is the smallest of the main cusps; a hypocone is lacking. The anterior cingulum surrounds the tooth on the lingual side and turns distally in a slight but clearly recognizable expansion of the tooth. The trigon is not very deep, but a postprotocone crista is present demarcating the trigon and the distal expansion. This is stated here to be typical for *Pronycticebus* species. On the buccal side, traces of a cingulum are present, but it is not developed along the whole tooth.

The symphysis of the lower jaw is unfused (fig. 2c). The right mandible (fig. 2a, b) is nearly complete but broken. It preserves the alveolus of I/2, the canine (length = 2.8 mm), the root of P/2, P/3 except for the top of the protoconid (l = 3.9), P/4 (l = 4.3), M/1 (l = 4.7), M/2 without the broken paraconid (l = 4.7 estimated), and M/3 (l = 5.7). A P/1 was probably not present, but a gap that is present between the canine and P/2 would have allowed enough room for this tooth, which is suggested to be variably present as a persistent milk tooth in *Protoadapis* species (Simons 1962). The dentition of the left mandible is complete, from I/1 to M/3; I/1-2, C and P/2 are visible, while the rest are documented in the X-ray. I/1 and I/2 (fig. 2c) are spatulate. The canine clearly extends above the occlusal plane and is curved. There is no similarity to a tooth-comb

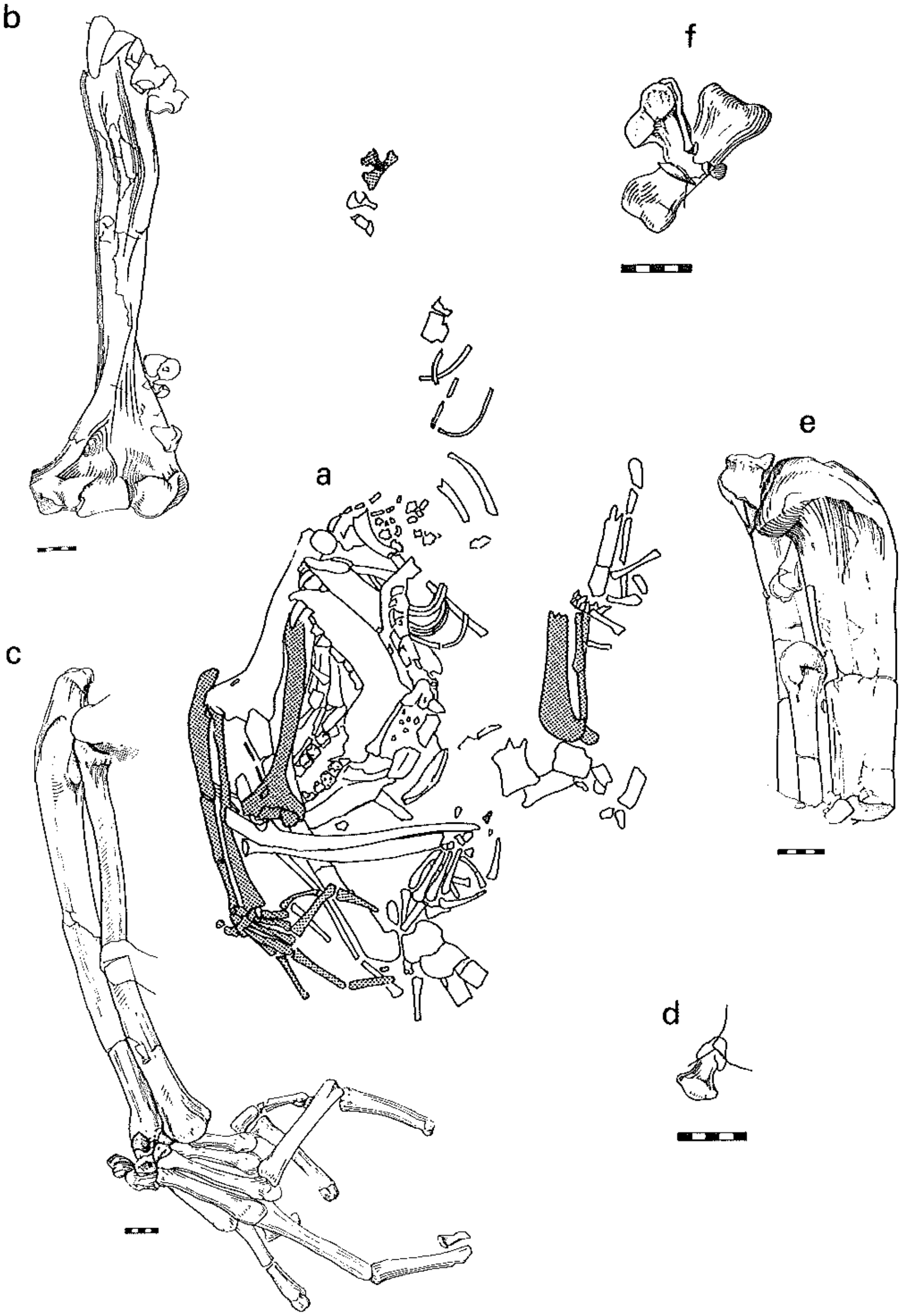

Figure 1. – Type specimen of *Pronycticebus neglectus* (GMH L-2) showing details of the postcranial skeleton (shaded). a: general state of preservation drawn from an X-ray. b: left humerus (anterior view). c: right forearm with ulna, radius and incomplete hand. d: distal phalanx of right thumb. e: proximal right fragments of tibia, fibula, and a metatarsal. f: proximal and distal phalanges of right hallux. Scale divisions in mm.

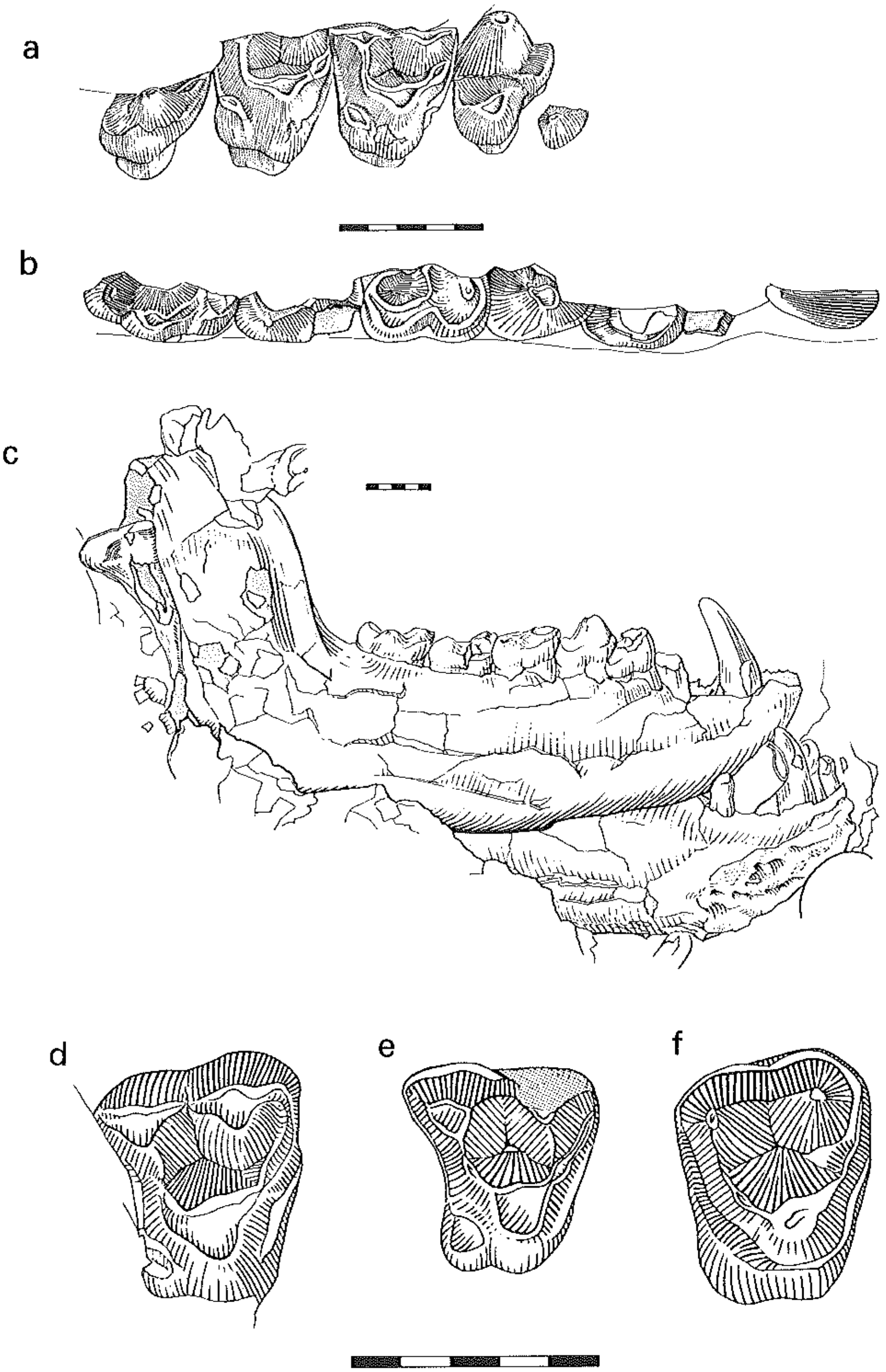

Figure 2. – Dentition of *Pronycticebus neglectus* (GMH L-2) and comparison of M1/ between different European adapids. a: left P3/-M3/ in occluso-lingual view, partially obscured (reversed drawing). b: occlusal view of right P/3-M/3, root of P/2, C, lingually obscured. c: right and left mandible with unfused symphysis. d: right M1/ of *Pronycticebus neglectus* (GMH L-2). e: *Pronycticebus gaudryi* (type, MNHN 1893). f: *Europolemur (Alsatia) dunaifi* (NHMB Bchs 648). Scale divisions in mm.

morphology in the anterior dentition. P/2 is a small single-cusped tooth, with the cusp placed mesially. The only cusp of P/3, the protoconid, is also mesial. The mesial edge is therefore steeper than the distal part of the tooth, with its moderate posterior cristid forming a small talonid cuspule. On both sides of the posterior cristids are two small shallow shelves. P/4 contrasts with P/3 in having a small but distinct metaconid joined with the protoconid by a protocristid and in having an anterior cingulum. The mesial edge of the anteriorly placed protoconid is as steep as the distal cristid, giving way to a talonid cuspule. On both sides of the posterior cristid, two marked shelves are present; the lingual one is deeper and larger. The M/1 trigonid was clearly higher than the talonid. The paralophid is of reduced size compared to the protocristid and the paraconid is very small if not absent. The talonid is broader than the trigonid and the talonid basin is deep. The hypoconid is slightly mesial compared to the entoconid. The kind of wear suggests a high oblique cristid and a deep V-shaped postcristid between hypo- and entoconid. A buccal cingulid extends from the middle of the tooth along the trigonid to its mesial half. A distal cingulid at the base of the hypoconid is present. M/2 is damaged in the trigonid region and most of the tooth is covered by postcranial elements. A paraconid was not developed. The distal cingulid is worn down. The trigonid of M/3 is also higher than the talonid and reduced in its longitudinal extension and somewhat compressed in its width compared to the talonid. A distinct high hypoconulid lobe is developed and located lingually, the talonid basin being relatively deep. The postcristid, connecting hypoconulid and hypoconid, is deeply V-shaped. A buccal cingulid surrounds the trigonid from the mesial base of the hypoconid sloping up along the trigonid to its mesial half.

The dental formula was probably 2.1.3.3/2.1.3.3. The overall functional morphology of the tooth-row is reminiscent of *Notharctus* or *Protoadapis*, with an emphasis on piercing rather than on slicing as in *Adapis parisiensis* (Gregory 1920). The condyle of the mandible (fig. 2c) shows the same general morphology as *Notharctus*, although it is not so strongly developed. It turns somewhat backward and downward on the inner moiety, allowing freer movement of the jaw than in *Adapis parisiensis* with its more transversal articulation (Gregory 1920).

POSTCRANIAL SKELETON

The axial skeleton is incompletely preserved, but nearly all regions are represented to some extent. The caudal vertebrae indicate a long tail with strong muscle attachments near the sacrum. In the shoulder girdle the well developed clavicle shows exactly the same form as in Malagasy lemurs and galagines, with a single curve and contrasts sharply with the S-shaped clavicle of slow-moving lorisines (Thalmann 1986). The humerus (length = 60 mm) is straight (fig. 1b). The tuberculi are lower than the rounded caput. The shape of the trochlea in the distal articulation is conical and separated by a trochleo-capitular ridge from the rounded and prominent capitulum. The olecranon fossa is shallow. These features reflect the morphology of North American *Cantius* (Gebo 1987a), *Smilodectes*, *Notharctus*, and European *Europolemur koenigswaldi*. A fossa epitrochlearis (Conroy 1976) is lacking on the medial condyle. This fossa is well developed in *Plesiadapis*, in *Adapis (Leptadapis) magnus*, and in Fayum haplorhines, variably expressed in *Adapis parisiensis*, slightly developed in *Cantius*, absent in *Notharctus* (but see also Ford 1988) and in *Smilodectes* (tab. 1). In extant primates, this fossa is lacking in all strepsirhines and catarrhines, but is well marked in almost all platyrrhines. The ulna (fig. 1c) has a well developed olecranon and is curved in the proximal third. The head of the radius (l = 57-58 mm) is rounded, the distal articulation forming the major part of the carpal articulation. The digital formula is

III, IV, II, I, V. The dominance of the third digit is typical for pentadactyl mammals and the haplorhine primates, whereas in modern lemurs and lorises the fourth digit dominates (Etter 1974, Jouffroy & Lessertisseur 1979). Three flattened, arrow-shaped terminal hand-phalanges indicate fingernails on all digits, the phalanges of which are curved. The pelvis is not preserved, and from the femora only distal parts are present in very poor condition. The tibia (l = 82 mm) and fibula were unfused (fig. 1e), the tibia being straight, in contrast to *Notharctus*, and medio-laterally flattened. The feet are dislocated and covered by the mandibles. No inference can be made concerning a toilet-claw on the second toe, which is typical for living strepsirhines (but see *Daubentonia*) and *Tarsius* (2nd and 3rd toe). The distal part of the calcaneus is relatively elongated, as in primates generally except *Adapis parisiensis* and *Adapis (Leptadapis) magnus* (Martin 1979). The big toe (fig. 1f) was opposable, judging from the shape of the proximal phalanx and the apparent presence of a nail.

Fossil	f. epi.	References
Pronycticebus neglectus	-	this paper
Archontan humerus AMNH 89519	+	Szalay & Dagosto (1980)
Plesiadapis walbeckensis	+	Szalay & Dagosto (1980)
Plesiadapis tricuspidens	+	Szalay *et al.* (1975)
Plesiadapis gidleyi	?	Szalay *et al.* (1975)
Saxonella crepaturae	(+)	Szalay & Dagosto (1980)
Omomyidae AMNH 29126	(–)	Szalay & Dagosto (1980)
Notharctus osborni AMNH 11474	-	Gregory (1920)
Notharctus tenebrosus AMNH 1727	-	observed on cast
Smilodectes gracilis AMNH 11484	-	observed on cast
Cantius	+	Rose & Walker (1985)
Adapis parisiensis	+ to -	Thalmann (1986)
Adapis (Leptadapis) magnus	+	Thalmann (1986)
Aegyptopithecus zeuxis	+	Schön-Ybarra & Conroy (1979)
Homunculus patagonicus	+	observed on cast

Table 1. – Distribution of the fossa epitrochlearis (f. epi.) in fossils. + = present, – = absent, ( ) = uncertain, ? = unknown, AMNH = American Museum of Natural History.

DISCUSSION

ECOLOGY AND LOCOMOTION

Pronycticebus neglectus lived in the Eocene Geiseltal, characterized as an environment with a subtropical warm lowland and open savannah-like woodland. Around waterholes, some of which persisted during the dry season, the vegetation was probably denser. Due to the high latitude, seasonality in daylength and a long twilight period were present. Alternating rainy and dry seasons over the year have been suggested (Mai 1976).

In this general context, the postcranial skeleton permits a number of ecological interpretations: body weight is related to diet, and morphology together with limb proportions reveal pivotal information concerning locomotion. Leaping, climbing, suspensory, quadrupedal and bridging displacement are major forms of locomotor behaviour in primates. They vary in importance from species to species. In strepsirhines, two major groups can be distinguished, the slow-moving lorisine nonleapers often bridging to overcome gaps, and the rest of the strepsirhines leaping at least to some degree (Gebo 1987b). A maximal intermembral index ([humerus + radius]/[femur + tibia] x 100 < 73 %) has been estimated for *Pronycticebus neglectus* by taking the same value for the femur as for the tibia, as no living strepsirhine (Walker 1967) or known adapid (Koenigswald 1979, 1985, Walker 1967) has a longer tibia than femur. Among living primates, non-leapers show several characteristics such as a high intermembral index (83-94 %) (Walker 1967), hand morphology allowing strong gripping, an S-shaped clavicle promoting freer movements in the shoulder girdle (Thalmann 1986), and a reduced tail. None of these features can be seen in *Pronycticebus neglectus*, and the locomotor type "slow-moving arboreal quadruped" is excluded. The hindlimb dominance indicated by the low intermembral index suggests leaping abilities, but the unfused sacrum indicates only limited stability in the pelvic girdle, and leaping may not have been of major importance. The shoulder joint was constructed as in recent quadrupedal lemurs, and full extension at the elbow joint was impossible. The humerus-radius articulation guaranteed good pronation/supination movement in the forearm, and judging from the presence of nails on hand and feet, grasping was of great importance. The locomotor pattern is concluded to be of the "grasp-leaping" type (Szalay & Dagosto 1980), with a high degree of grasp-climbing and quadrupedal displacement in a thin branched arboreal milieu including both canopy and undergrowth.

Measurement	g	r	References
humerus + radius (length)	850	.989	Jungers (1981)[1)]
humerus (length)	1000	.979	"
radius (length)	690	.989	"
tibia (length)	520	.971	"
M1/ (length x width)	2350	.946	Gingerich (1982)
M/2 (length)	1960	.949	Kay & Simons (1980)

Table 2. – Body weight estimation (g) for *Pronycticebus neglectus* calculated using allometric correlation of teeth and longbone measurements. r: correlation coefficient. [1)] based on allometric correlations for lemurids.

The body weight (tab. 2) has been estimated by direct comparison with living forms of comparable size and proportions. The most accurate model is the Malagasy lemur *Hapalemur griseus*. This species has a body weight of 880 g (Jungers 1985), and is slightly larger in overall body dimensions than *Pronycticebus neglectus*, which is therefore estimated to be about 800-850 g. Long bone length regressions (Jungers 1985) yielded values between 520 and 1000 g. Allometric regressions from measurements of the molar teeth M1/ (Gingerich *et al.* 1982) and M/2 (Kay & Simons 1980) yielded body weights of 2350 and 1960 g, respectively. The estimates based on teeth dimensions probably represent an overestimate, as direct comparison of overall body dimensions is regarded as a more reliable indicator. In recent primates, a relationship between body weight and diet exists (Kay & Simons 1980, Kay & Covert 1986). Insectivores typically weigh less than 1 kg, and only the smallest species are predominantly insectivores. Most modern primates species in the size range of *Pronycticebus neglectus* are frugivorous and eat insects as a protein source. The apparent overestimation of body weight using tooth dimensions suggests that *P. neglectus* had relatively large teeth, and relatively large teeth are typical for insectivores and primarily insectivorous primates such as *Tarsius* (Gingerich *et al.* 1982). The cusp morphology of the dentition and the high trigonid relative to the talonid also suggest important puncture-crushing functions and the freer movement of the mandibular articulation indicates quite well developed masticatory abilities. It is therefore concluded that *P. neglectus* was a frugivore/insectivore, having a very large proportion of insects in its diet, probably depending on seasonal availability.

A clear inference in favour of nocturnal or diurnal activity period cannot be made on grounds of orbit size, as the relationship between orbit diameter and skull length used to infer nocturnal or diurnal habits (Gingerich & Martin 1981) cannot be estimated with sufficient accuracy.

PHYLOGENY

Two questions are of major interest concerning the phylogenetic relationship (fig. 3) of a fossil: which are its closest relatives and what new information can we extract for interpretation of other taxa? As indicated by the diagnosis and the name, the closest known relative of *Pronycticebus neglectus* is suggested to be *P. gaudryi*, although *P. gaudryi* is much younger (late Eocene [Szalay & Delson 1979]) than *P. neglectus* and more primitive in the dental formula ?.1.4.3 (Grandidier 1904), making a direct ancestor – descendant relation unlikely. A possible common ancestor for the two species of *Pronycticebus* would be *Protoadapis* or *Europolemur*. *Protoadapis* species have a reduced lingual cingulum and usually (but not always) lack a hypocone on the molars (Russell *et al.* 1967). The hypocone of *Pronycticebus* is well developed at the lingual end of the distal cingulum. Dentally, *Pronycticebus* could have evolved from *Protoadapis* through formation of an isolated hypocone from the lingual end of the distal cingulum as a derived feature. *Europolemur klatti* is characterized by a crestiform continuous lingual cingulum, at least on the M2/, forming a hypocone cusp at the disto-lingual corner. Franzen (1987) suggests that this specific morphology evolved from a species of *Protoadapis* through an intermediate form such as *Europolemur koenigswaldi* and finaly to *E. klatti*. This may have occurred through simultaneously developing a continuous cingulum on the lingual side and the cusp of a hypocone. The different morphology and probably different formation processes of the hypocones in *Pronycticebus* and *Europolemur klatti* make a close direct relationship of the two unlikely. Thus, *Pronycticebus* is more likely to have evolved from a *Protoadapis* stock and not from *Europolemur*.

The traditional interpretation of adapiform phylogeny recognized two distinct subfamilies, the Eocene Notharctinae and Adapinae, later joined by a third group, the Miocene Sivaladapinae of Asia (Gingerich & Sahni 1984, Thomas & Verma 1979). The Adapinae were regarded as monophyletically derived from a primitive, probably *Cantius*-like, North American ancestor that had invaded Europe by the early Eocene. The landbridge between North America and Europe disappeared at the beginning of the middle Eocene (Savage & Russell 1983), and there was an impressive subsequent radiation of adapiforms in Europe. The background for the dichotomy of the Eocene forms has been greatly influenced by historical factors. When only a few fossils were

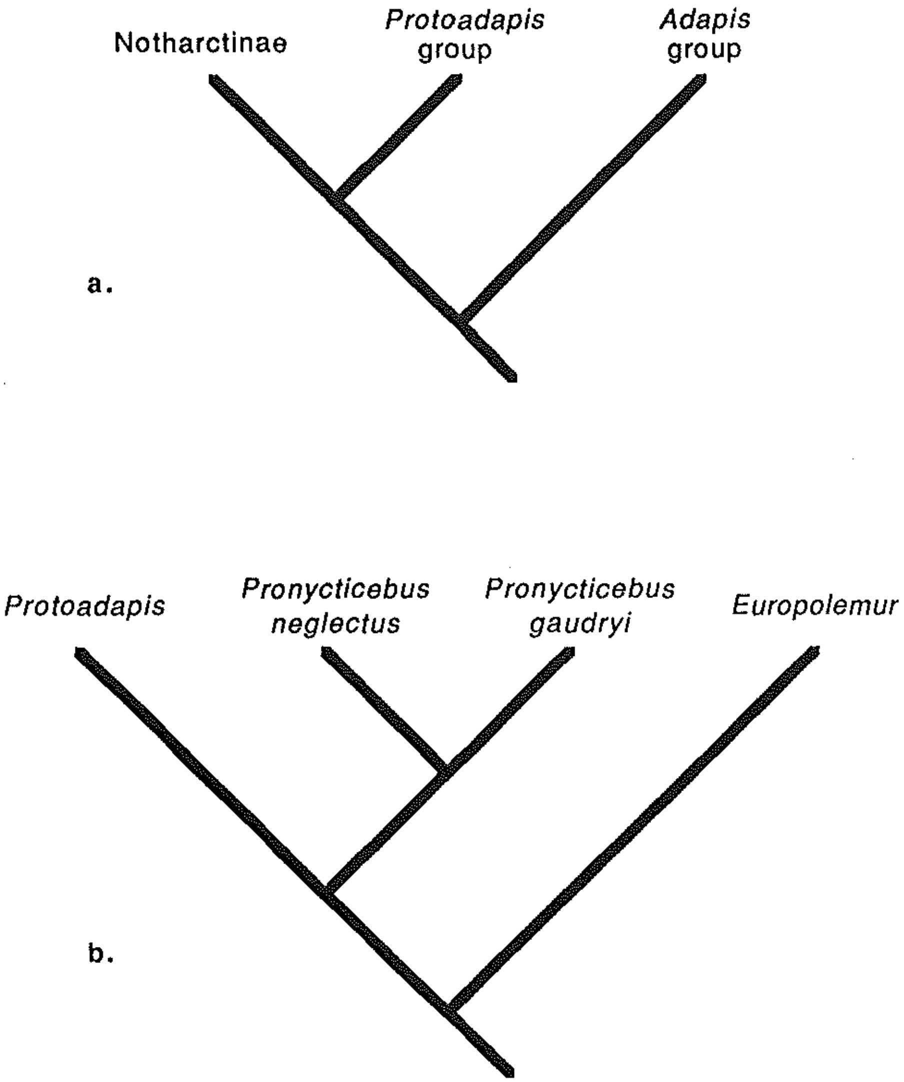

Figure 3: Phylogenetic hypotheses. Suggested relationships for a: higher North American and European adapid taxa of the Eocene, and for b: *Pronycticebus neglectus*.

known, the best argument for the distinction of the two groups was the hypocone, developed as a real hypocone from the cingulum in adapines, but as a pseudohypocone (a derivative of the protocone) in notharctines. All further fossils were usually pressed into this scheme, stressing the paleogeographic argument.

This division is questionable for two reasons: *Mahgarita*, a North American form from the upper middle or lower late Eocene (Uintan; Savage & Russell 1983, Szalay & Delson 1979) has been suggested to be closely related to European adapines such as *Europolemur* (Wilson & Szalay 1976). Second, the postcranial skeleton of *Pronycticebus neglectus* and the Messel fossils (Franzen 1987, Koenigswald 1979, 1985) is much more similar to that of *Cantius*, *Notharctus*, and *Smilodectes* than to postcranial elements attributed to *Adapis parisiensis* and *Adapis (Leptadapis) magnus*

(Dagosto 1983, Thalmann 1986).

Provided that *Mahgarita* is an adapine in the traditional sense, with affinities to the Protoadapini, there are two explanations for its appearance in southern North America (Texas): (1) *Mahgarita* evolved from unknown adapine ancestors in North America. This would imply that North American adapines had already split from notharctines by the early Eocene. (2) *Mahgarita* could have invaded North America from Europe by an unknown landbridge, although North America and Europe are thought to have been completely separated by the Atlantic ocean by the beginning of the middle Eocene (Savage & Russell 1983). If *Mahgarita* is not an adapine at all but a notharctine, the developement of a real hypocone instead of a pseudohypocone in *Mahgarita* must be interpreted as a result of convergence. A third possibility arises that *Mahgarita* is neither an adapine nor a notharctine, but a member of an as yet undefined group.

European adapines are generally considered to be monophyletic, but the relations within the group remain unclear. Most authors recognize at least two well distinguished groups (Gingerich 1977, Godinot 1984, Szalay & Delson 1979). The long-snouted adapines of the genus *Adapis*, on the one hand, have a primitive dental formula 2.1.4.3. combined with a highly molarized P4. The short-snouted adapids of the *Protoadapis* type, on the other hand, commonly show a reduced dental formula and there is a relatively sharp morphological contrast between premolars and molars.

Relatively little is known about the postcranial skeleton of European adapids, given the relatively large number of different species that have been recognized. Again, two groups can clearly be distinguished, the *Adapis parisiensis* group on one hand, and the fossils from Messel together with the Geiseltal specimen on the other. The identified specimens from Messel and the Geiseltal are both member of the *Protoadapis* group. They are much more similar to the North American notharctines than to *Adapis parisiensis* and *Adapis (Leptadapis) magnus*. This has been concluded from comparison of limb proportions (Dagosto 1983), foot morphology, especially calcaneus proportions (Martin 1979), and humeral morphology (Dagosto 1983, Thalmann 1986). These similarities suggest a close phylogenetic relationship between one part of the European adapines (Geiseltal, Messel) and North American notharctines, and make a monophyletic derivation of all European adapids questionable.

This interpretation is further supported by the fossa epitrochlearis. Its wide distribution among living primates and the fossil evidence (tab. 1) clearly indicate that the presence of this fossa should be interpreted as a primitive feature. The last possible common ancestor of North American and European adapids, *Cantius*, has a slightly developed fossa. This fossa is lacking in some later forms such as *Notharctus* (vs. Ford 1988), *Smilodectes* and *Pronycticebus neglectus*, but is well marked in *Adapis (Leptadapis) magnus* and is variable in the heterogeneous sample of *Adapis parisiensis* humeri (well marked to absent). This distribution may be interpreted in different ways: (1) *Pronycticebus neglectus* and *Protoadapis*-like relatives were derived independently or together with the rest of the North American adapids from a *Cantius*-form as separate group, or (2) they stem from a form with morphological features similar to those of *Adapis (Leptadapis) magnus*. The latter explanation is highly unlikely because the typical adapines of the *Adapis* type appear with some retained primitive features in the cranium and postcranial skeleton late in the fossil record at the beginning of the upper Eocene and are not known from earlier deposits of Europe. However, in the absence of a more detailed understanding of morphological features, it is difficult to draw clear conclusions regarding the phylogeny of the adapids.

Nevertheless, there is now much evidence indicating that European adapids are not monophyletic, but at least paraphyletic (fig. 3a). The abruptly appearing typical adapines of the upper Eocene (e.g. *Adapis*) seem not to be closely related phylogenetically to the European forms and probably immigrated from a yet unknown place, probably Asia (Tong 1979, but see also Szalay 1982) or possibly Africa (Franzen 1987).

The detailed revision of all the Geiseltal primate dental and postcranial material now in progress, together with further comparative analyses of he postcranial skeleton of the adapids in a functional context, should help to clarify the present confusing situation regarding the phylogeny, paleoecology and paleogeography of the Adapiformes.

SUMMARY

The most complete European adapid specimen from the Middle Eocene brown coal deposits in the Geiseltal near Halle (German Democratic Republic), determined as *Pronycticebus neglectus* n. sp., was an animal weighing about 800-850 g. It was an insectivore/frugivore, emphasizing the arthropod component of its diet. The locomotor pattern can be described as of the "grasp-leaping" type, probably in a fine branch milieu. The postcranial skeleton suggests a close relationship to specimens from the Messel site and to North American forms such as *Cantius*, *Notharctus*, and *Smilodectes*.

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LEGENDS OF PLATES

PLATE 1

Photograph of *Pronycticebus neglectus* n. sp., holotype: partial skeleton from the "untere Mittelkohle", Geiseltal near Halle (GDR). Geiseltalmuseum Halle [GMH] L-2. Scale divisions in cm.

PLATE 2

X-ray of *Pronycticebus neglectus* n. sp., holotype. Scale division in cm.

Legend for Plate 1 and 2:

1: mandible. 2: maxilla and upper dentition. 3: crushed face and skull. 4: fragments of cervical, thoracic, and lumbar vertebrae; ribs. 5: sacral vertebrae. 6: caudal vertebrae$^{2)}$. 7: clavicle$^{1)}$. 8: crushed scapula$^{2)}$. 9: humerus. 10: ulna. 11: radius. 12: hand. 13: femur. 14: tibia. 15: fibula. 16: fragmentary metatarsals of right foot. 17: incomplete left foot (tarsals, metatarsals, and phalanges)$^{2)}$. 18: left proximal and distal hallucial phalanx.
a = right; b = left; $^{1)}$ only indicated in table 1; $^{2)}$ only indicated in table 2.

PLATE 1

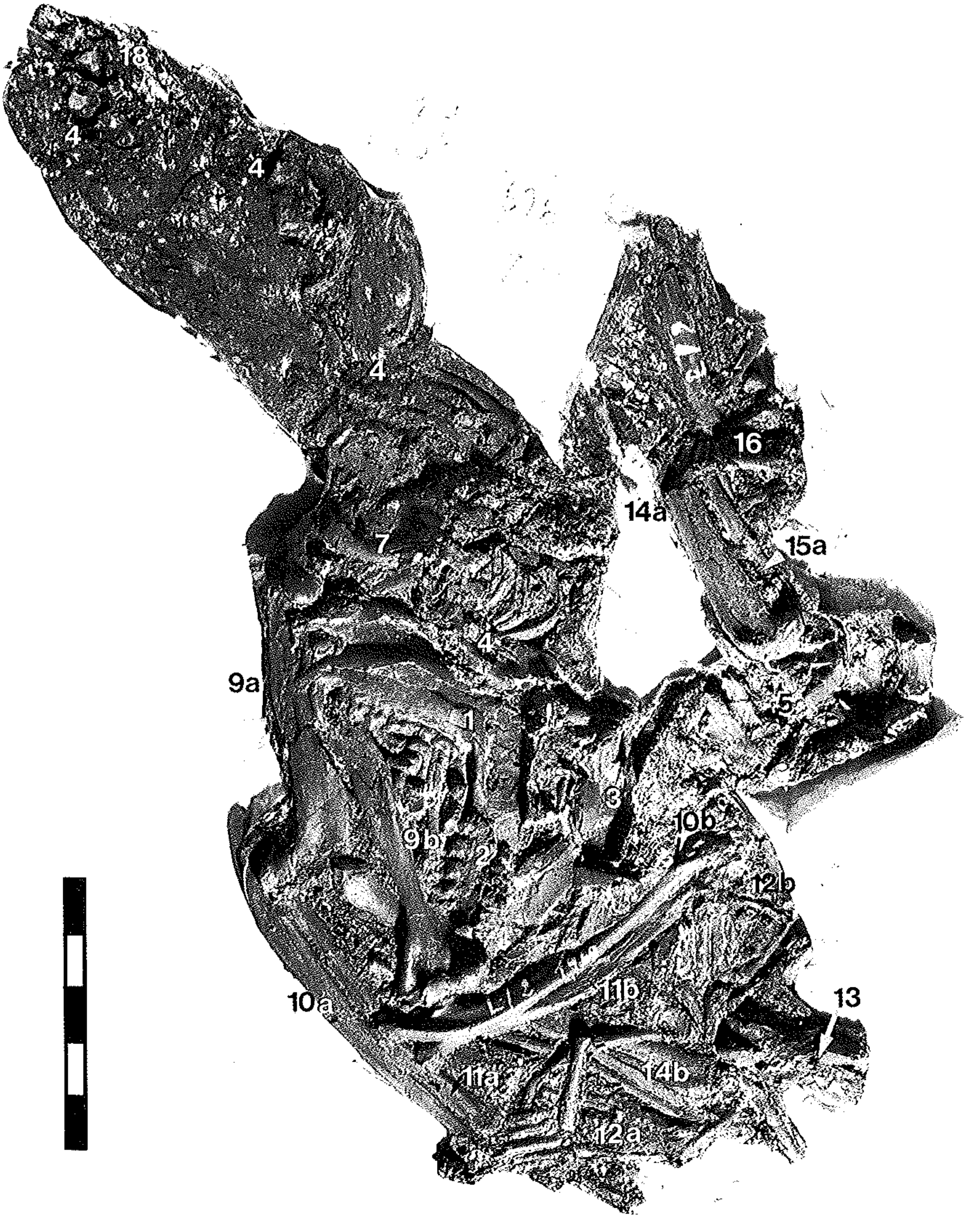
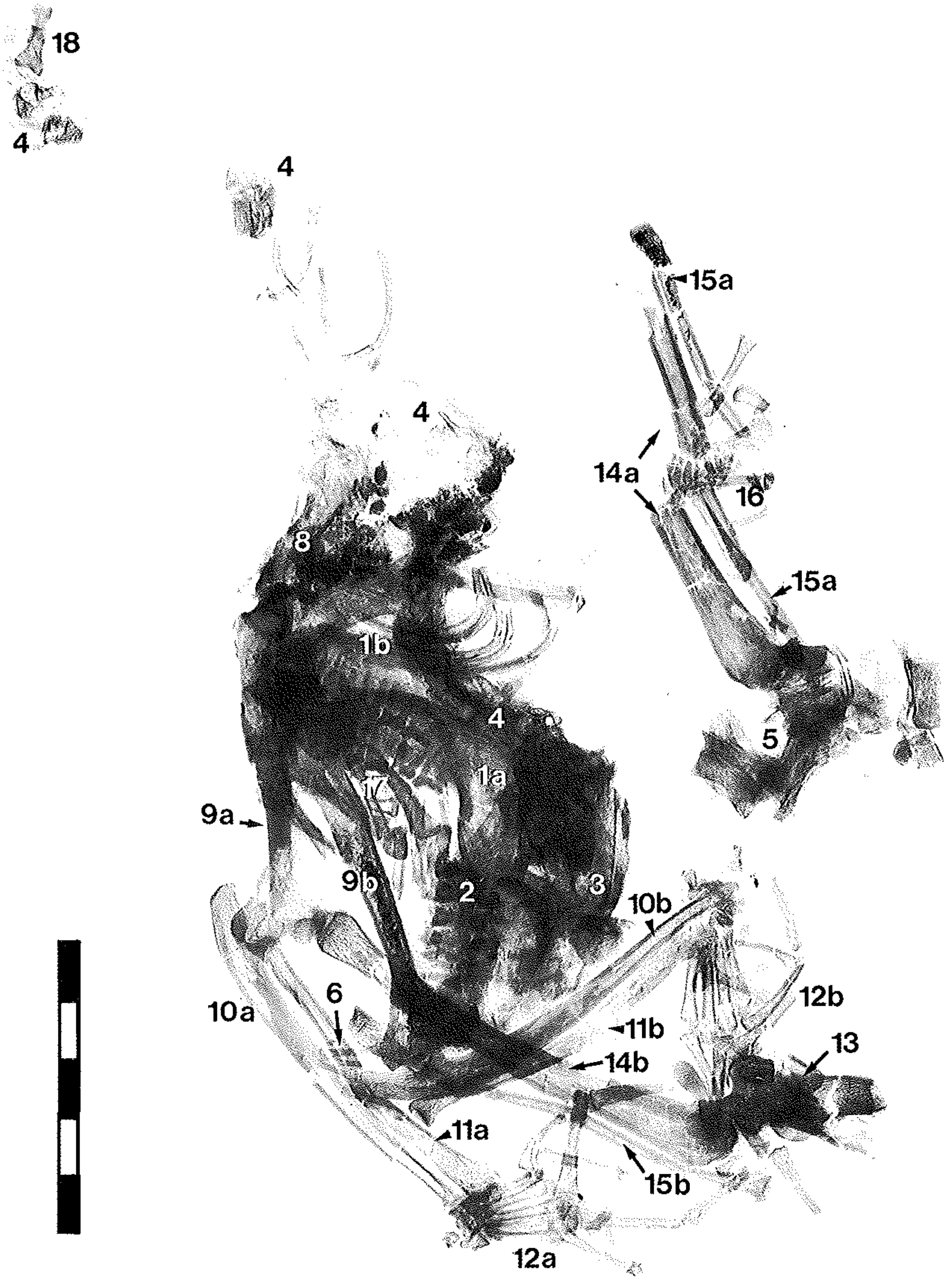


PLATE 2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