12. Morphological Diversity in the Skulls of Large Adapines (Primates, Adapiformes) and Its Systematic Implications

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12.1 Introduction

The European Eocene adapiforms include two subfamilies, the Cercamoniinae, present in the early and middle Eocene, and the Adapinae, present in the late Eocene (Franzen, 1994; Godinot, 1998; Fleagle, 1999; Gebo, 2002). The large adapine species has a robust upper canine and other characters. It was named *Adapis magnus* by Filhol (1874), and was later placed in the genus *Leptadapis* by Gervais (1876). However, Gervais' choice was seldom followed by subsequent authors. Stehlin (1912) and Depéret (1917), for example, retained *Leptadapis* as a subgenus of *Adapis*. For Stehlin, a fossil species was equivalent to a living genus; he used the name *Adapis magnus* in his text and figures, and *Leptadapis magnus* in his final stratigraphic chart of the genus *Adapis* (p. 1280). A single genus, *Adapis*, is used by Genet-Varcin (1963), Simons (1972), and Gingerich (1977, 1981). Most recent authors (Godinot, 1998; Fleagle, 1999; Gebo, 2002) kept the genus *Leptadapis*, following Szalay and Delson (1979). Recent work by Lanèque emphasized the systematic complexity reflected by the skulls of *Adapis* sensu Szalay and Delson (1979) (Lanèque, 1992a, b, 1993), and also showed a marked heterogeneity in the larger adapine skulls (*Leptadapis*) (Lanèque, 1993). The radiation of these adapines is very complex (Godinot, 1998); there is an overlap in size between the large *Adapis* and the small *Leptadapis*. Furthermore, the dentally peculiar *Cryptadapis* (Godinot, 1984) lies in this zone of overlap. Deciphering the systematics and the phylogeny of the adapines is a long-term task.

One difficulty for adapine studies is that the systematics of Stehlin (1912) is based on skulls in the old Quercy collections, and these have no biochronological context. Even when specimen information includes the name of a village, these names are not sufficient because several fissure-fillings were exploited in most of these villages. It is impossible to know from which fissure the specimens were collected. Work started around 1960 by colleagues from the universities of Montpellier, Poitiers and Paris led to the recovery of many precisely located faunas, which have been placed in a good biochronological framework (Crochet et al., 1981; Remy et al., 1987; BiochroM'97, 1997). However, a difficulty remains because the newly collected material, from pocket remains or exploitation residue, is very poor in comparison with the old collections. This is especially true for the primates. The new collections include fragmentary primate material: jaws from a few localities, but more often isolated teeth. In contrast, the systematics of Stehlin (1912) was based on cranial characters, and the types he erected were crania without associated mandibles. It is very difficult to associate the new dental remains to the species defined by Stehlin. This work is nevertheless in progress, and it appears probable now that many *Adapis* species from the old collections belong to a late Eocene radiation of this genus (MP 19 reference-level in the European Paleogene Mammalian

Scale, Schmidt-Kittler et al., 1987). By contrast, several species of *Leptadapis* come from earlier localities, MP 17-18, Priabonian (Remy et al., 1987; Godinot, 1998). Here we will concentrate on the skulls of large size present in the old Quercy collections, and only briefly mention specimens found in one stratified locality.

The skulls of large size in the old Quercy collections have not been well treated in the literature. This probably goes back to Grandidier (1905) who identified a beautiful cranium and associated mandible as "*Leptadapis magnus*" (Figure 1), whereas this specimen was in fact quite different from the type specimen of *L. magnus* described by Filhol (1874). When he described specimens from the collections of Montauban, Munich, and Basel, Stehlin (1912) recognized differences between two pairs of specimens (Figure 1). He discussed the idea that these pairs might possibly be males and females of one species, however, because the size differences between their canines were very small, insignificant ("geringfügig"), he could not definitely endorse this hypothesis. Without a clear conclusion, Stehlin did not propose a systematic distinction between them. He kept the question open and left all the specimens in "*Adapis magnus*". However, Stehlin saw clear morphological and size differences between the Montauban 3 cranium and the others, and he named a new variety for this specimen: "*Adapis magnus* var. *Leenhardti*". For Stehlin, a "variety" was equivalent to an extant "species". We do not know why Stehlin did not come to Paris to include the Paris collection in his study. Did he have only a short visit to Montauban? In his work, the figures are "reconstructions", for the most part very reliable, showing in white the reconstructed parts and in grey the actual fossil; this way, it is possible to identify the specimens he used. However, sometimes his drawings compensate for specimen deformations, and they can be inaccurate for some details. Some specimens also may have been partly damaged or lost, rendering their identification difficult.

Gingerich (1977) started a systematic revision of European adapiforms. He interpreted differences between two groups of small-sized *Adapis* specimens as due to sexual dimorphism within a single species *A. parisiensis*. He suggested that differences between two groups of large-sized specimens reflect sexual dimorphism among the large "*Adapis*" *magnus*. He also considered the Quercy *A. parisiensis* as a descendant of "*A.*" *magnus* from the same region (Gingerich, 1977, 1981; Gingerich and Martin, 1981), in contrast with Stehlin's view of two distinct lineages (Stehlin, 1912, p 1280). Gingerich's suggestion was seldom followed. Szalay and Delson (1979) continued to see only one species, *L. magnus*, in the large Quercy skulls. In her study of orbital characters, Lanèque (1993) showed quite convincingly that two groups of *Leptadapis* could be distinguished based on interorbital breadth, however she did not pursue the systematic implications of this finding. On a stratophenetic diagram of biochronologically situated dental

assemblages, Godinot (1998) found that two lineages could be distinguished, which might correspond to the groups delineated by Lanèque.

Several factors played a role in preventing an easy systematic study of these fossils, including the fact that they are spread between several distant institutions, and they differ in their preserved parts. The specimens are large enough that direct comparison of their dentitions under a binocular microscope is awkward or impossible. At superficial examination, they seem to have a relatively similar dental pattern, however, a detailed examination of these skulls reveals differences in dental characters, some of which have to be meaningful. In this paper, we first briefly describe the eight best-preserved skulls of large adapines. We then explain why we propose to distinguish two major groups (genera). We review each group and suggest how many species should be distinguished. We comment on the phylogeny of these groups. Lastly we propose a first morphometric approach to studying this material.

12.2 Material: The Best Preserved Large Adapine Skulls (Table 12.1)

The most complete specimen is a cranium, QU 10870, with associated lower jaws (QU 10871, Paris Museum, MNHN). There is little doubt that this is the specimen figured by Grandidier (1905) as "*A. magnus*", "coll. Filhol, Muséum de Paris" (idem, p 141). It possesses basically the same parts. The associated jaw is similarly preserved: breakage of the angular process of the left side (Figure 12.1B), same part missing anteriorly with a gap on the left side and the same teeth preserved, M/3 to P/2 on both sides (idem, Figure 4). This skull remains one of the best preserved Eocene primate skulls ever found. Grandidier's figures, labelled "*A.*" *magnus* despite differences between it and the type specimen, were really a bad starting point for later work. Several of these figures were reproduced by Gregory (1920) and one by Piveteau (1957). This probably largely explains the failure of subsequent authors to recognize the groups distinguished below.

There are also some differences between the skull and the figures of Grandidier, revealing that those are not entirely accurate, and/or that the specimen possibly suffered some damage since 1905. The profile view of the left side (Figure 12.1B) shows that the sagittal crest was complete, whereas it is now broken (posterodorsal part missing); the zygomatic arch is shaped differently, the gap linked to a fissure in the anterior part being exaggerated in the figure. On the ventral aspect of the cranium, the same teeth are present on the actual specimen and in the figure (Figure 12.1E), the two canines showing breakage at a similar level, higher on the left than on the right canine. The left P3/ and M3/ are better preserved according to the figure than on the actual specimen. Were they
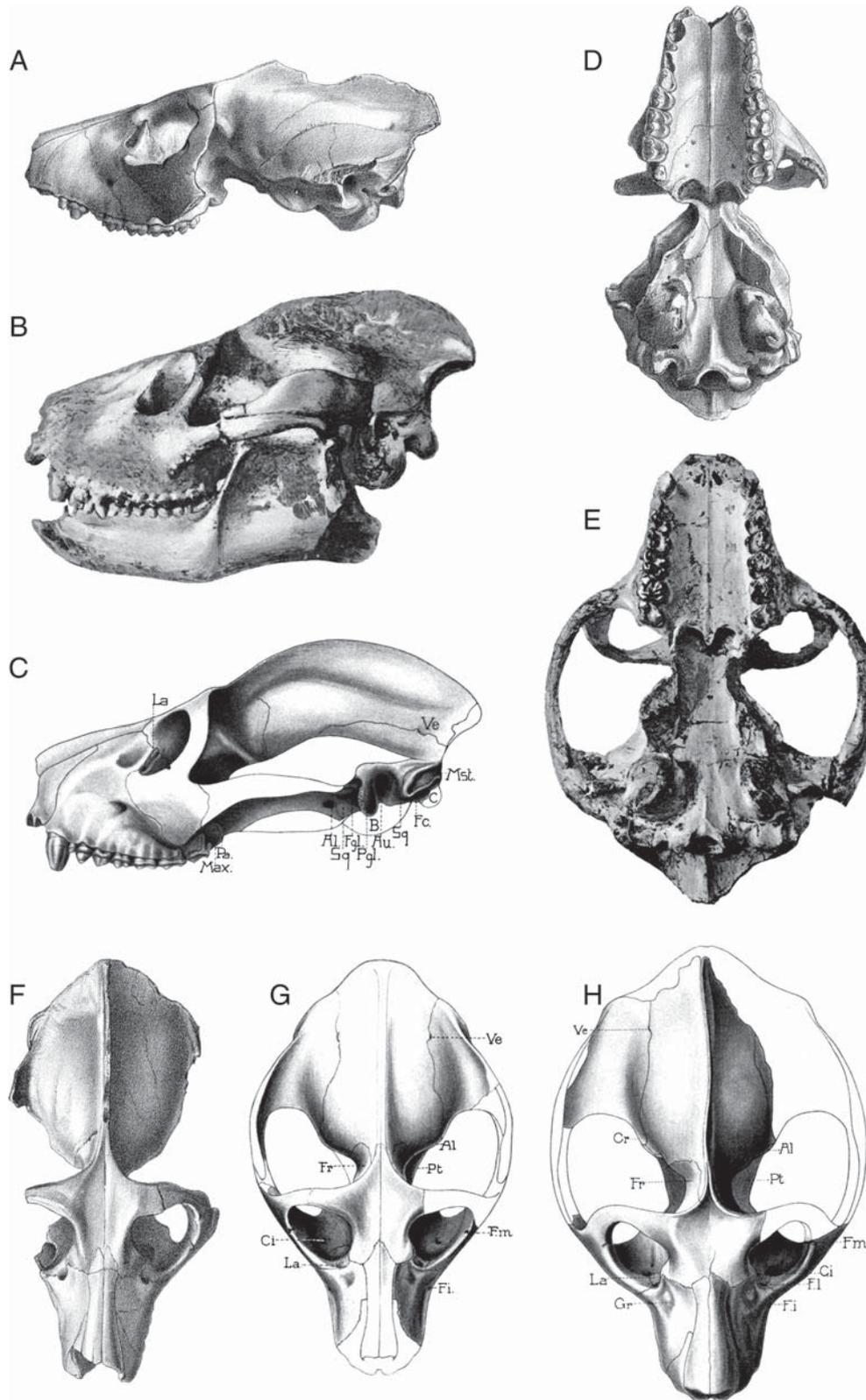
FIGURE 12.1. Illustrations of crania all ascribed to "*Adapis magnus*" by the authors who described them. A, D, F, the type specimen of *Leptadapis magnus*, QU 11002, three of the four drawings published by Filhol (1874), all inverted left/right on Filhol's engravings, now showing their natural side. A, left lateral view; D, ventral view; F, dorsal view (muzzle toward the top in Filhol, inverted here for comparison with Stehlin's figures). B, E, the skull QU 10870-10871 as figured by Grandidier (1905). B, lateral view of cranium (QU 10870) and mandible (QU 10871); E, ventral view of cranium. C, G, H, three illustrations from Stehlin (1912); C and H are reconstructions of MaPhQ 210 in lateral (C) and dorsal (H) views; G is the reconstruction of MaPhQ 211 in dorsal view. Not to scale, but G and H preserve their relative scale as present in Stehlin's illustrations. Differences in interorbital and muzzle breadth can be observed between F-G (*L. magnus*) and H (*Magnadapis fredi* n. gen. n. sp. in this paper), and differences in facial and muzzle height can be observed between A (*Leptadapis*) and B–C (two *Magnadapis* species).

TABLE 12.1. Listing of the specimens used in this study, indicating their preserved parts, aspects of their crests and canines, and their systematic allocation in this paper. Abbreviations for institutions are: MNHN, Muséum National d'Histoire Naturelle, Paris; MU, Montpellier University; NMB, Naturhistorisches Museum Basel; YPM, Yale Peabody Museum.

Specimen number	Preserved parts	Sagittal crest, nuchal projection, canine	Systematic allocation
MNHN QU 11002	Cranium lacking right postorbital bar and both zygomatic arches	High sagittal crest, strong nuchal projection, canine alveolus	Type of *Leptadapis magnus*
Montauban MaPhQ 211	Cranium somewhat distorted lacking left postorbital bar and both zygomatic arches	Broken probably high sagittal crest, strong nuchal projection, partial canine alveoli	*L.*aff. *magnus*
MU ACQ 209	Cranium with incomplete right zygomatic arch	Moderate sagittal crest and nuchal projection, partial left canine	Type of *L. filholi*
YPM PU 11481	Cranium with incomplete postorbital bars and zygomatic arches (reconstructed with plaster)	Very low sagittal crest, unknown nuchal projection, partial canine alveoli	Neotype of *L. leenhardti*
MNHN QU 10875	Cranium almost complete, lacking only right zygomatic arch	Low sagittal crest, weak nuchal projection, complete slender right canine	Type of *Magnadapis quercyi*
Leuven PLV 6	Muzzle with slightly deformed left orbit	Complete right canine	*M.*aff. *quercyi*
MNHN QU 10870-71	Complete cranium and mandible	High sagittal crest, strong nuchal projection, partial canines	Type of *M. intermedius*
MNHN QU 11035-36	Crushed cranium with complete left zygomatic arch and posterior extremity, and mandible	Posteriorly very high sagittal crest, strong nuchal projection, partial large canine alveolus	*M.*aff. *intermedius*
MU ACQ 214	Muzzle slightly crushed, without complete orbit	Complete large and robust left canine	*M. intermedius*
Montauban MaPhQ 210	Partial cranium, lacking zygomatic arches and posteroventral part	Very high sagittal crest, strong nuchal projection, almost complete large right canine	Type of *M. fredi*
NMB St.H. 1634	Crushed muzzle, palate	Almost complete partly deformed canines	*M. fredi*
MNHN QU 10872	Cranium lacking postorbital bars and zygomatic arches	Very low sagittal crest, moderate nuchal projection, broken bases of both canines	Type of *M. laurenceae*

damaged since, or restored on the figure? On this figure, the right P1/ should be more visible, and the right M2/ appears quite inaccurate in its rendering. Other aspects of the ventral view are also surprising. Small fissures at the same place on the zygomatic arches confirm that the specimen really is the same. However, a marked exaggeration of the concavity lying behind the left zygomatic arch suggests that a piece of bone is missing there, whereas it is present on the specimen: this demonstrates that the figure was modified, either by a poorly done cutting around the photograph, or through painting of the negative. A confirmation of the bad rendering of the outline is given by the interior of the left orbital aperture, which shows on the figure a long indentation not present on the specimen. Clearly, there was a heavy and partially inaccurate retouching of Grandidier's photographs, and not only on the outlines: the two occipital condyles are beautiful on the specimen, and poorly rendered on the same figure. Two other differences between the ventral view (Figure 12.1E) and the actual specimen must be taken with caution: on the figure, the back of the palate shows a marked posterior spine at its midline, and an osseous continuity between the right posterior end of the palate and the right median pterygoid lamina. These parts might have been broken since 1905, however they also might have been restored on the figure, the palatal spine by comparison with the type skull of *L. magnus*, on which it is conspicuous, and the continuous ptery-

goid plate by comparison with the crushed skull QU 11035, on which it shows a similar trajectory (different on other skulls, e.g., QU 10875, see below). Because no other skull pertaining to the same group (see below) shows such a palatal spine, and because the right pterygoid region of the figure suggests an inaccurate (asymmetric) external pterygoid plate, it seems that this figure also presents heavy and inaccurate retouching. The left bulla presents a slight crushing of its lateral wall, however the right one is perfectly preserved. Excessive retouching probably explains a more important and embarrassing aspect of Figure 2 in Grandidier (1905), in which the orbit is clearly too small, exaggerating the similarity between this specimen and *Adapis* (compare Figures 12.1B and 12.8C). The left postorbital bar shows a slight deformation, hence orbital characters should be measured on the right side. The right view gives a perfect outline of the orbit and the very peculiar zygomatic arch of a large adapine. A good photograph of this same specimen in dorsal view is given in Lanèque (1993, Figure 10a; in this paper the legend for Figure 10 is below Figure 9, and vice versa).

Another exquisitely preserved cranium is QU 10875, also from the Paris collection. This specimen appears in three excellent photographs by Genet-Varcin (1963), two photographs on one plate by Saban (1963), in one lateral view by Simons (1972), and in one dorsal view by Lanèque (1993, Figure 9b – legend below Figure 10). The two

postorbital bars are even thinner than on QU 10870, and the left orbit shows a slight distortion, visible in anterior view; its right orbit seems undistorted. The right zygomatic arch is missing. The pterygoid laminae are almost complete. The teeth are quite well preserved; the small P1/ are lost, the right canine is complete, pointed and robust, showing the vertical grooves typical of these fossils. On the whole, this cranium including its teeth, resembles quite closely QU 10870, however there are also differences, which will be described below.

Another specimen preserving both postorbital bars is ACQ 209 from the University of Montpellier collection (UM). This specimen has probably never been previously figured (Figure 12.2). Its postorbital bars are thin and intact. Part of the right zygomatic arch is missing, however the left one is complete. There is slight deformation of the posterior part, visible in ventral view: the basioccipital appears pushed ventrally away from the bullar walls and above the more anterior ventral floor (probably the sphenoid). The bullae have experienced some deformation: the left one is less completely distorted than the right one. The pterygoid laminae are almost complete. A thick and short posterior palatal spine emerges at the confluence of two arcuate crests which border the palate posteriorly. On the dorsal side, the bone of the anterior part of the braincase is eroded on both sides, however, the sagittal crest, which is around 8 mm tall at its highest, is quasi intact, being one of the best preserved in all these skulls. It is very regularly round and its posterior part projects approximately 1 cm beyond the posterior border of the foramen magnum.
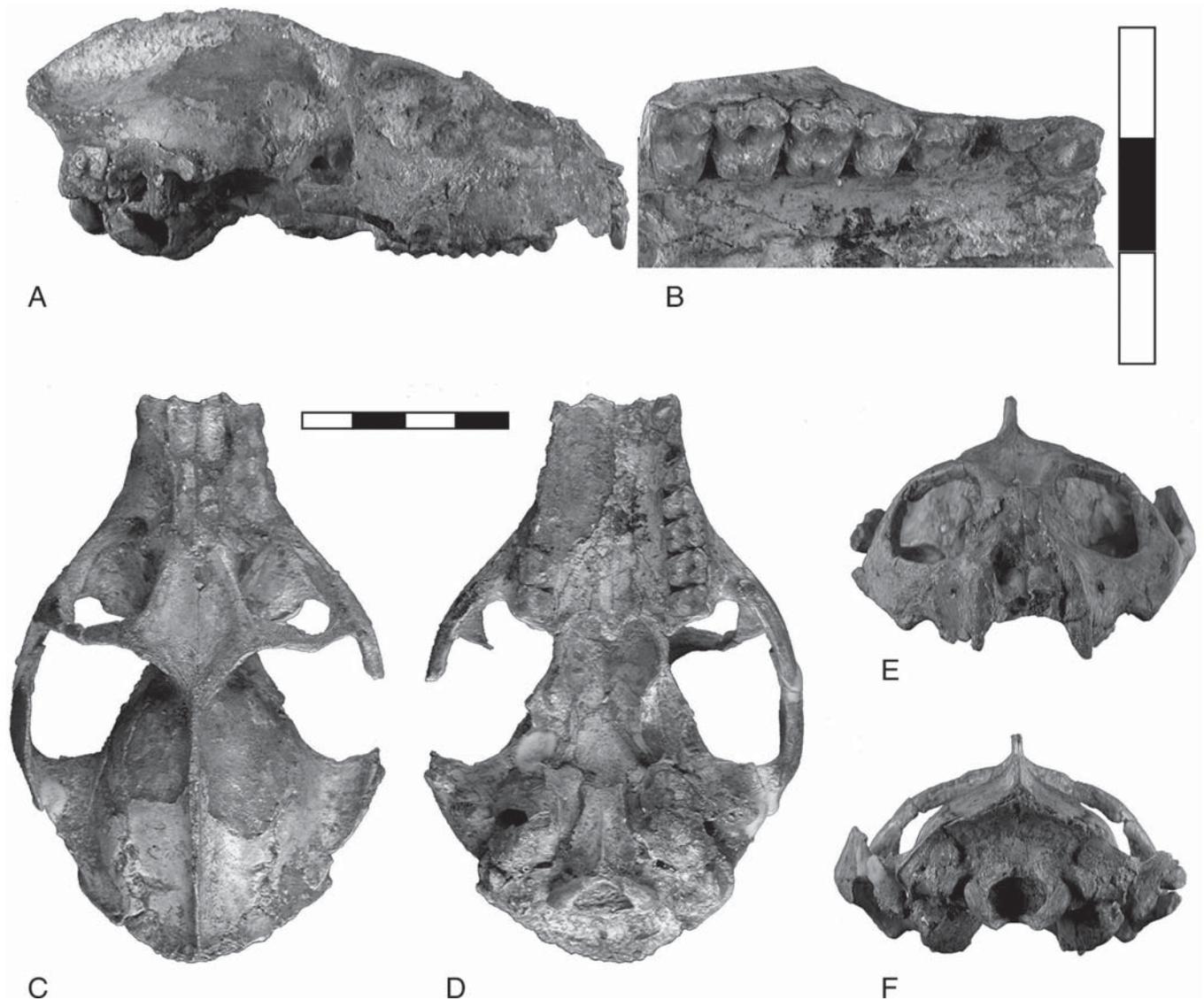
FIGURE 12.2. The cranium MU ACQ 209, type specimen of *Leptadapis filholi* n. sp., in lateral (A), dorsal (C), ventral (D), anterior (E), and posterior (F) views, all at the same scale (bar is 4 cm). The right part of its palate (B) is at a larger scale (bar is 3 cm).

The anterior part of the cranium is less well preserved. The right side of the muzzle is eroded (Figure 12.2). The anterior parts of the nasals are crushed against the palate. The premaxillae, the posterior parts of the nasals, and a small part of the frontal are missing. However, the left maxilla seems undistorted, allowing an estimate of the height of the muzzle without the nasals (the nasals make a thin straight ribbon in profile view on the similar *magnus*-type skull). The right dentition is relatively well preserved, from P3/ to M3/. The canine is moderate in size, partly eroded, and its outline in occlusal view is very rounded, almost as broad as it is long; P1/ is there and is relatively large; P2/ is missing. This specimen is very important because it is the only representative of the *Leptadapis* group as delineated below that has an intact zygomatic arch and that has the upper canine and the P1/ (see Figures 12.7, 12.9). Over many years of study, one of us (MG) wondered if this cranium could have been the one chosen by Stehlin (1912) as the type of his "variety *Leenhardti*". Some of the Montauban *Adapis* skulls were in a protestant college of theology and were later transferred to the Montpellier University collection, and this cranium resembles more closely Stehlin's figures than does any other present in the Montpellier or Montauban collections. Similarities include its small size, relative completeness, preservation up to the canine anteriorly and no further. However, there are also many discrepancies between the figures of Stehlin and this specimen, including a size discrepancy, this specimen being larger than that in Stehlin's figures (the scale is very accurate for the figure of the Montauban 2 specimen). This specimen preserves the left P4/, P3/ and P1/, which are absent in Stehlin's figure 297 [the right M1/ and P4/ of the figure could have been restored from those of the other side, and the right zygomatic likewise completed from the other side, as Stehlin's figures are "reconstructions"]. On the dorsal view (idem, Figure 296), the posterior extremity of the cranium is narrower and more salient than on the specimen, the posterior part of the temporal fossa is narrower and much more arcuate than on the specimen, and the orbits are more anteroposteriorly elongated. Although there are a few problems with some of Stehlin's reconstructions, these are very minor compared to the differences outlined above. There is no doubt for us that the type of the "variety *Leenhardti*", despite being similar to ACQ 209 in its general state of preservation, was actually not this specimen.

The last specimen that apparently preserves both orbits is YPM PU 11481, housed in the Yale University collection (Figure 12.3). This specimen comes from the former Princeton collection and may never have been figured. This specimen is the smallest of those studied here, and as such it is the closest to the type of the "variety *Leenhardti*". Its state of preservation looks superficially similar in dorsal view, only the nasals and premaxillae missing. On the ventral view, the same teeth are preserved, P4/ to M3/ on the right side, M1-3/ on the left side. The right bulla, open on the Yale specimen, could have been reconstructed based on the intact left bulla. The two canines, present on Stehlin's figure, might have been lost since.

Stehlin described the specimen as heavily deformed. This is not apparent on his reconstruction, and is not true of the Yale specimen. Furthermore, it is difficult to explain why Stehlin did not mention the Princeton specimen had he access to it. The specimen was, according to Yale records, purchased in the early to mid-1890s by Professor W. B. Scott from A. Rossignol in Caylus (W. Joyce, personal communication 2006). Many institutions have specimens labelled "Rossignol collection". This date refutes the hypothesis of a later purchase of the Montauban specimen, seen by Stehlin in or not long before 1912. A closer look at the Yale specimen confirms that it is different: it is actually heavily restored with plaster! Without the plaster, it would lack the right orbit, both zygomatic arches and its right and middle posterior extremity, as can be seen on CT scans of the specimen (Figure 12.3). The left orbit, almost complete, is anteroposteriorly shorter on the Yale specimen than on Stehlin's figure. In ventral view, if the canines had been lost since the drawing of the specimen, there would be breakages or big holes, which is not the case. Also, based on alveolar morphology, P2/ was single-rooted in the "variety *Leenhardti*" type specimen, whereas it was two-rooted on the Yale specimen. On the whole, although the Yale specimen is the closest to the type of Stehlin's variety in size and preserved teeth, for both historical and morphological reasons it cannot be the actual type. Further similarities in the outline in dorsal and ventral views suggest that the artist who did the plaster reconstruction probably used Stehlin's figures of the *Leenhardti* type as a model for making the reconstruction. This is why the plaster reconstruction looks realistic in dorsal and ventral views. However, he had no figure of a lateral view because Stehlin gave none, and he produced a very inaccurate reconstruction of the zygomatic arches in profile view: they are much too low and incorrectly proportioned for an adapine. The Yale specimen is still an important one, having an almost complete left orbit, a well preserved brain case and a very low sagittal crest. On its ventral side, the pterygoid laminae are complete anteriorly but incomplete posteriorly. The left bulla is slightly crushed, and the right one is open, showing the promontory. The teeth are little worn, suggesting that it was a young individual. The left M2-3/ are very well preserved, and the right M2-3/ are slightly damaged. The right P4/ is lacking two small chips which do not prevent the study of its morphology. On the whole, this specimen really could pertain to the same species as the "variety *Leenhardti*" of Stehlin, because it is by far the closest to its type specimen. The actual type is, as far as we know, lost. Therefore, we designate below YPM PU 11481 as a neotype for *L. leenhardti* Stehlin.

The type specimen of *Leptadapis magnus*, MNHN QU 11002, was described and illustrated by Filhol (1874). A photograph in dorsal view is given by Lanèque (1993, Figure 10b). It has a complete left orbit. Its postorbital bar is broader than that of any of the preceding specimens (Figures 12.1, 12.4, 12.6). Despite its missing parts, it is not distorted. The top of its muzzle is intact, and the left nasal appears to be complete. The left orbit is undistorted.
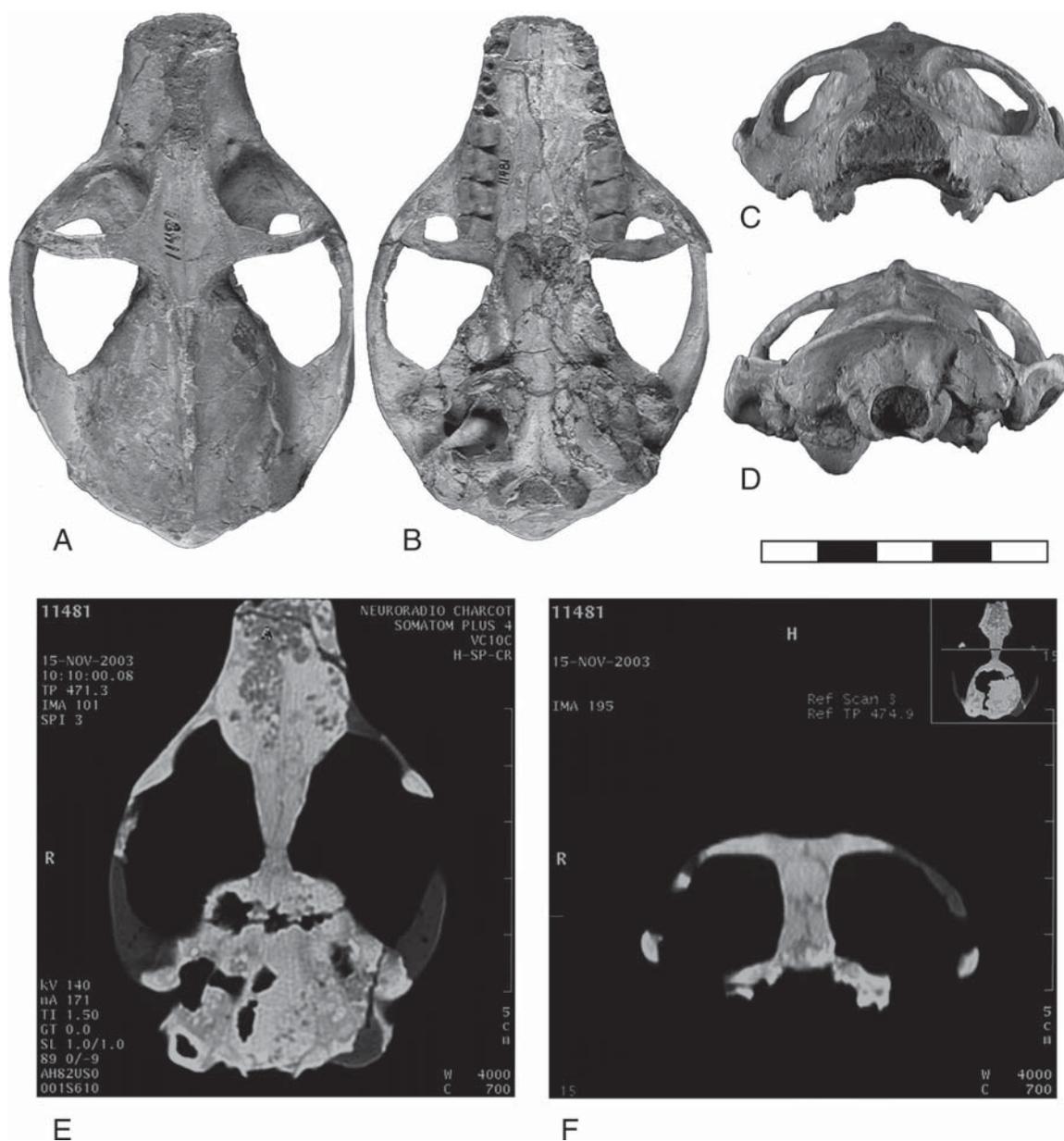
FIGURE 12.3. Cranium of YPM PU 11481, neotype of *Leptadapis leenhardti*, in dorsal (A), ventral (B), anterior (C), and posterior (D) views; all at the same scale (bar is 5 cm). Two scanner images of the same skull, in horizontal (E) and frontal (F) planes. The scanner images reveal parts reconstructed with plaster: zygomatic arches and right posterior extremity (E) and parts of the two postorbital bars (F). One can also see in D that the posterior extremity of the sagittal crest and the left nuchal crest are reconstructed with plaster.

A limited part of the high sagittal crest is missing, allowing a relatively accurate estimate of its shape. The posterior extremity of the cranium projects far behind the posterior rim of the foramen magnum (around 11 mm). The bullae are moderately distorted. The pterygoid laminae are quite well preserved posteriorly, but are incomplete anteriorly. This way, they do not prevent the observation in dorsal view of the marked postorbital narrowing of the skull, which is extreme on this specimen (Figure 12.4).

The two other relatively well preserved skulls are those from Montauban which were quite accurately described by Stehlin (1912) as Montauban 1 (now MaPhQ 210) and Montauban 2 (MaPhQ 211). However, Stehlin's figures were again reconstructions (Figure 12.1). These were on the whole accurate, and honest in the sense that they usually show in simple white outline the missing parts which were reconstructed. However, there are some differences, corresponding to actual specimen deformations which were compensated for in the drawings, and which are not shown in white and can be misleading. We mention some of them below and underline the need to study the original specimens and to use real photographs.

The right postorbital bar of MaPhQ 210 is deformed, whereas it is reconstructed undistorted on Stehlin's drawings. On the dorsal view, the posterior part of the right zygomatic arch appears more salient laterally and has a less arcuate outline on the specimen than on the figure, suggesting that the zygomatic arches might well have been more extended laterally than on the reconstruction (idem, Fig. 276). A comparison with the other very robust skull, QU 10870, shows that the flat area on the top of the posterior root of the zygomatic arch is anteroposteriorly more extended and mediolaterally flatter (less dorsally curved in posterior view) on MaPhQ 210 than on the other, again suggesting extremely laterally salient zygomatic arches, exceeding those of Stehlin's reconstruction. On the profile view, Stehlin showed the left side even though the right one is the one that preserves the orbit. The reconstruction shows the postorbital bar as having the same breadth along its entire length whereas the specimen narrows ventrally along its dorsal half. The reconstruction probably exaggerates slightly the height of the orbit (difficult to estimate due to deformation) and, in any case, misrepresents its ventral border. At the same time, it probably underestimates the vertical distance between the base of the orbit and the base of the zygoma. Stehlin, or his artist, seems to have reshaped the orbit with a very inclined anteroventral border, whereas that part does not appear to be deformed on the specimen, being more horizontal anterior to the anterior extremity of the zygoma. This partly diminished the extreme robusticity of the anterior zygomatic root. On this profile view (idem, Fig. 277), the shading suggests that the sagittal crest diminished in height posteriorly, whereas on the actual specimen the sagittal crest increases posteriorly, coming close to 2 cm in height (see Figure 12.8). This specimen has the largest sagittal crest of all. The ventral view shows longer portions of the zygomatic arches anteriorly on both sides: could some pieces have been broken since? On the contrary, posteriorly the zygomatic root is actually longer on the right side than represented in grey on Stehlin's figure, suggesting that these reconstructions should not be trusted. In the open right bulla, the drawing shows the tympanic ring, which is not present today.

The other Montauban cranium, MaPhQ 211 (Montauban 2 of Stehlin), is smaller and more deformed. Its right orbit is complete; some breakage makes it appear slightly smaller than in reality, however on the whole it is little distorted. There are fissures in the maxillae, nasals, and between the frontals. A part of the right premaxilla is still there, with a small part of the rim of the nasal aperture. The cranium was broken behind the orbits, however the left pterygoid lamina is relatively well preserved (incomplete further posteriorly). The right bulla is open, broken laterally, and shows the promontorium; the left bulla shows parts of its medial wall; some matrix remain inside the bullae. The braincase is not much distorted, except for its posterior extremity, which is pushed toward the right. Despite this displacement, one can see the extent of the nuchal projection (well marked, around 1 cm), and estimate the height of the sagittal crest, which must have

been well developed. The two zygomatic arches are missing. The figures of Stehlin for this specimen (Figure 275 [12.1G] for the dorsal view, and 280 for the ventral view) show some evidence of restoration, and also make us wonder about possible damage to the specimen. The drawing in dorsal view evidently compensated for the displacement of the posterior extremity, therefore the outline is uncertain; it also modified the outline of the orbit. It shows a much more complete right zygomatic arch. The ventral view shows the same teeth, alveoli, anterior breakage and missing half of the right M3/. It shows the right pterygoid wing in white, i.e., reconstructed. It shows again a right zygomatic arch much more complete than on the actual specimen which suggests that breakage occurred since. The two bullae are drawn intact; they were probably less completely prepared at Stehlin's time because normally when the promontorium was visible it was drawn. However, some reconstruction was probably also added. The preserved parts look slightly different (the sutures medial to the bullae are very simplified on the drawing).

Another skull used in our study and never described until now is QU 10872 from the Paris collection (see Figures 12.8, 12.10). This specimen requires further cleaning. It is relatively small and not as well preserved as the others because it has no complete orbit. However, the upper part and the lower part of the right orbit are intact, allowing an estimate of orbit size. The orbit appears quite small in comparison with other specimens of similar size, e.g., ACQ 209. The zygomatic arches are missing and the left orbital region is damaged. However, the right side of the muzzle is well preserved and the dentition is relatively complete (P2/-M3/ and broken base of canine on both sides, and broken base of I1/ and I2/ on the left side). Posteriorly, the ventral side is poorly preserved, without pterygoids or bullae. The braincase on the whole is not distorted, however there is a slight global deformation of the specimen, which has, in dorsal view, its posterior part slightly pushed toward the left side relative to the anterior part. On the dorsal side, this specimen has one of the two lowest sagittal crests (with two missing chips) of any large adapine; only the Yale specimen has a lower one (the sagittal crest is less than 5 mm high at its maximum, difficult to measure precisely because the junction with the braincase is curved). This small sagittal and the nuchal crests nevertheless produce a nuchal projection of around 8 mm.

Five other specimens will be mentioned. The very crushed skull QU 11035 from the Paris collection is from a very large individual. The muzzle and the anterior part of the braincase are missing. However, the left zygomatic arch is very complete. The posterior part of the skull is well preserved and is very low (Figure 12.6). The large bullae are intact, and are the best preserved of any adapine. This specimen also has an associated mandible. The mandible is fused at the symphysis and bears a right series that includes a small P/1, broken canine and alveoli for the two incisors. The left posterior part of the mandible is also well preserved.

Another crushed and less complete specimen from the Basel collection comes from Euzet-les-Bains, having thus a stratigraphic provenance. The species from Euzet-les-Bains (or Saint-Hippolyte-de-Caton) was described by Depéret (1917), who figured two palates, mandibles and a fragment of maxilla with the base of the orbit in profile (idem, Pl. 25). The crushed muzzle of Basel, NMB St.H.1634 (Figure 12.10), clearly shows the broad interorbital distance and the breadth of the muzzle, which are important characters for us. Depéret (1917) ascribed the species to *Adapis (Leptadapis) magnus*; he considered that a subgenus was enough to distinguish the large species. He basically followed Stehlin (1912) concerning adapine systematics.

Another specimen of interest is a muzzle with part of the right orbit, UM ACQ 214, with beautiful teeth on the right side, complete canine and base of I2/ on the left side. This specimen has the largest intact upper canine of any Quercy cranium. The palate has a dorsal curvature, exaggerated posteriorly due to crushing. The anterior part of the muzzle is only slightly distorted, the premaxillae being almost complete and the right side of the nasal aperture being almost undistorted (nasal slightly pushed under the premaxilla). The anterolateral base of the right orbit is intact, and the height of the anterior root of the right zygomatic arch can be estimated. Large parts of the frontals are also preserved, showing the beginning of the right postorbital bar as it narrows laterally, and also the large interorbital breadth. However, some crushing between the frontals and the muzzle, close to the maxillary suture, pushed the frontal part ventrally, artificially diminishing orbital height in anterior and profile views.

Another specimen is an incomplete muzzle with left postorbital bar and zygomatic root, PLV 6 from Leuven University, Belgium. We mention it because it has a beautiful right canine. However, the specimen needs further cleaning and restoration, and it will be described more completely in a future study of dental material.

The last specimen which should be included in our series in the future is the partial cranium and associated mandibles which are housed at the University Geological Museum in Moscow. The specimen was figured by Pavlova (1910, p. 166). It is part of a collection brought back by Kovalewsky, and was a gift from Gaudry (T. Kouznetsova, personal communication 1995). The specimen resembles QU 10870 and QU 11035 in shape and preservation. It will be interesting in the future to compare these crania. We wonder if some of them might come from the same field collection, possibly made in one locality, and would as such be important for documenting skull variability in one putative species of large adapine.

12.3   First Group of Generic Value: *Leptadapis*

In her study of orbital characters in adapines, Lanèque (1993) showed that *Leptadapis* skulls exhibit variation in interorbital breadth greatly exceeding the variation found in living species.

Scaling of this character (idem, Figure 8) clearly delineated two groups [her point 29 is an estimate, as ACQ 214 is a muzzle and has no associated condylobasal length]. Lanèque did not pursue the systematic implications of her study. We agree with her two groups, and we emphasize that other differences between them exist. These groups demand systematic recognition.

The first group includes four specimens: QU 11002, ACQ 209, MaPhQ 211, YPM PU 11481. These specimens have a smaller interorbital breadth (overlapping variations in living *Colobus* species in Lanèque's diagram). The dorsomedial rim of the orbit has a subrectilinear part directed slightly anteromedially and slightly extended on the muzzle. As a result, the frontal depression is bordered by two anteriorly converging rims, and is concave between the two orbits. In the other group the frontal depression is less extended anteriorly (Figures 12.2, 12.4). Specimens in the first group also have a much narrower muzzle (Figure 12.4). The palate is narrower, and the dental rows converge more anteriorly, with a canine alveolus protruding medially (ACQ 209 differs from the others in having a slightly broader muzzle and palate).

Several dental characters confirm this grouping: on all these specimens, there is a strong size contrast between a larger and especially longer M2/ and a smaller, narrower M3/; the P4/ has a more triangular outline, with a narrow lingual part. Only one of these specimens, ACQ 209, has an upper canine, which is partially worn, and a P1/. The P1/ seems larger than on specimens of the other group, and the canine seems to be smaller. This canine also seems simpler than on specimens of the other group, having less accentuated vertical grooves. In this group of specimens, only ACQ 209 shows a complete zygomatic arch, on its left side. This group includes QU 11002, which is the type specimen of *Leptadapis magnus*. Thus they must belong to the genus *Leptadapis*.

12.3.1   Comparison Between MaPhQ 211 and QU 11002

MaPhQ 211 is very similar to the type. Differences between them include the breadth of the postorbital bar, which is narrow on MaPhQ 211 whereas it is broader on the type (Figure 12.6). Possibly linked to this is the height of the anterior part of the zygomatic arch, below the orbit, which is greater on the type specimen than on MaPhQ 211. The ventral border of the nuchal projection is more horizontal on the type, but more inclined on MaPhQ 211. However, this part is deformed on the last specimen, making this difference of dubious value. The sagittal crests cannot be compared along most of their extent, however, in their anterior part, one can see clearly that the crest is higher on the type specimen than on the other. To properly observe this difference, it is necessary to look from the posterior side, in an antero- and slightly lateral direction; the distance between the border of the braincase and the top of the dorsal rim of the frontals is higher on the type specimen. In general the type specimen appears somewhat more robust than the other. This could be intraspecific variation, possibly
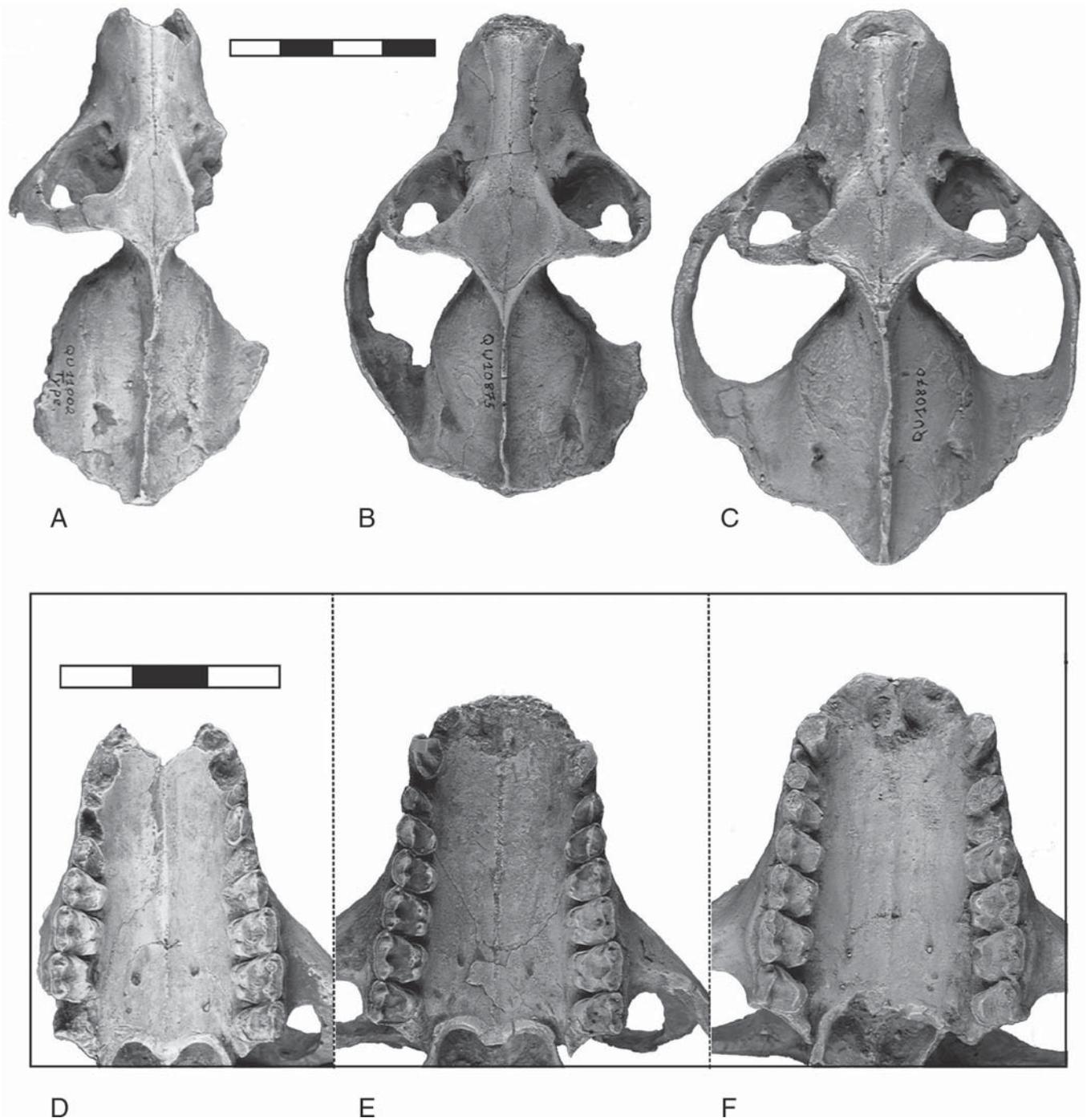
FIGURE 12.4. Crania of *Leptadapis* (A) and two *Magnadapis* species (B, C) in dorsal views (A–C) at the same scale (bar is 4 cm), and ventral views of their palates (D–F) at another scale (bar is 3 cm). QU 11002 is the type specimen of *L. magnus* (A, D); QU 10875 is the type specimen of *M. quercyi* n. gen. n. sp. (B, E), and QU 10870 is the type specimen of *M. intermedius* n. gen. n. sp. (C, F). Note differences in interorbital breadth, medial orbital rims and muzzle breadth between the two genera in A–C, and differences in palate breadth and anterior outline in D–F.

linked to age or sexual dimorphism; it could also reflect a small phylogenetic difference. Differences can be seen on the teeth. On MaPhQ 211, M1-2/ have a continuous lingual cingulum, whereas it is interrupted on the type specimen. M1/ on MaPhQ 211 appears more square, its posterior half is wider in comparison with the anterior half relative to the type specimen. On the type specimen, the crista obliqua seems slightly better developed. P4/ on the type specimen has a more triangular

outline, and it has a distinct crista obliqua; on MaPhQ 211, P4/ is slightly broader lingually and there is no crista obliqua; the posterior cingulum is also isolated from the protocone at its lingual extremity. This extremity is slightly thickened on the right P4/, as if there were an incipient hypocone. On the right P4/, it seems that the cingulum was continuous on the lingual side, not very clearly seen because the tooth is eroded, whereas on the left side the lingual cingulum is clearly interrupted. The link between the protocone and the posterior cingulum is more continuous on the type specimen. P3/ on MaPhQ 211 is narrower in its lingual part, with a cingulum and no protocone cuspule, whereas on the type specimen the lingual part is slightly broader and there is a small recognizable protocone, with a short labial slope. These differences may slightly exceed intraspecific variability, however, they are not strong. The M2/ has a very similar outline. Hypocone size, which decreases from M1/ to M2/ to M3/ (tiny thickening of the cingulum on the type specimen; nothing on the other), appears very similar on both specimens. The differences could indicate just a very small distance within a single lineage. The continuous lingual cingulum on the molars and almost continuous on P4/, as well as the loss of the crista obliqua on P4/, could indicate a more derived stage for MaPhQ 211 than for the type specimen of *L. magnus*. In this case, the P3/ would be in the process of simplification, losing its protocone. However, at this moment, we refrain from naming a new species on such small differences without a better understanding of dental variability in *Leptadapis* species. The differences in cranial superstructures described above could also have evolutionary significance, and in that case would not reflect sexual dimorphism. We need to learn more about dental variability to better interpret these cranial differences. MaPhQ 211 is left in open nomenclature as *L.* aff *magnus*.

12.3.2 Comparison Between YPM-PU 11481 and QU 11002

The teeth of the Yale skull, YPM PU 11481, are similar to those of the *L. magnus* type specimen, QU 11002. M1/ is narrower in its posterior half, with a lingual flexus between the protocone and the hypocone, as on the type. There are still some differences: the M2/ of the Yale specimen has a complete lingual cingulum and a slightly smaller hypocone than does the type. Its M3/ is peculiar too: it is transversely short (a peculiarity of the "variety *Leenhardti*" type specimen noted by Stehlin) and is narrower in its lingual part. The P4/ of the Yale specimen has a triangular outline, slightly narrower lingually than the P4/ of QU 11002, without a postprotocrista, and with an anterior cingulum. On this P4/, the paracone is markedly higher than the metacone, whereas the two cusps are more similar in height on QU 11002 (with variation: the contrast is higher on the left than on the right side of the type; however, neither side has a metacone as reduced as on the P4/ of the Yale specimen). There are also differences in the alveoli of the anterior teeth. The Yale specimen has two

alveoli for P2/, the posterior one is larger than the anterior. The alveolus for P1/ is small. On QU 11002, there is only one alveolus for P2/; it is broader posteriorly and is slightly larger. On the whole dental differences between the Yale specimen and the *L. magnus*-type pertain to P4/ and M3/. They tend to confirm a specific distinction between them, however their polarity is not straightforward.

Concerning the cranium, the Yale specimen is smaller than QU 11002, and they differ markedly in proportions. In ventral view, they differ little in palate size and tooth size (this is consistent with intraspecific variability). The palate is longer on the type; its posterior arcuate rim is at the level of the posterior margin of M3/. The rim is further anterior, clearly between the two M3/, on the Yale specimen. This could be due to the Yale individual being a younger at death one. The distance between palate and bullae is only slightly larger on the type than on the other. On the Yale skull, the pterygoid plates are interrupted anterior to the bullae. The right lateral plate is partly deformed, and breakage of the posterior part of these plates can be suspected. On the right side at the base of the pterygoid plate a smooth rounded surface shows the natural original interruption of the plate corresponding to the relatively large foramen pterygospinosum. On the left side, the small bony ridge which is an extension of the plate, possibly broken, would in any case have surrounded the foramen. Low and straight relief on the bulla might well indicate breakage of the pterygoid plate joining the bulla as in all other adapine skulls (this should be checked against the original). The apparent interruption between the pterygoid plate and the bulla on both sides, which would have been very unusual, is probably an artifact.

Size differences between the Yale specimen and QU 11002 are more marked posteriorly. The space between the bullae and the articular condyles is clearly larger on the type than on the Yale specimen. Adding these differences in length, the type appears markedly longer than the Yale specimen, whereas they differ little in breadth. This length difference is accentuated in dorsal view due to the strong posterior projection of the sagittal and nuchal crests on the type. This is absent on the Yale specimen. The braincase is clearly closer to the anterior part of the skull and the postorbital narrowing is slightly less expressed on the Yale specimen than on the type. The braincases of the two specimens seem to be similar in size. A big difference between them is the very strong development of the sagittal and nuchal crests, projecting further posteriorly on the type (more than 1 cm beyond the posterior margin of the foramen magnum) than on the Yale one (reconstructed with plaster in this part). The Yale individual has a very low sagittal crest. Even if this crest is slightly worn, one can see very clearly in the anterior part of the braincase the two frontal lines converging posteriorly just on the top of the braincase. This demonstrates that the crest is very low on the Yale individual. By contrast, on the type, the frontal lines join almost 1 cm above the anterior part of the braincase (the smallest distance between

braincase and dorsal rim of frontals, along a dorso-anteriorly inclined line, is 8 mm). Hence there is a very strong difference between the two specimens in the development of the sagittal crest and the distance between the braincase and the frontal plane, which are both very reduced on the Yale specimen. Can such huge differences be explained by growth, sexual dimorphism, or both? The canine alveoli of the Yale specimen are too poorly preserved to be used in assessing differences in canine size. In lateral view, the zygomatic arches of the Yale specimen are disturbing because they are poorly restored in plaster. However, the anterior part of the zygomatic arch is intact: it is more gracile on the Yale individual. The anterior view clearly confirms that the zygomatic root, below the orbit, is higher on the type than on the Yale specimen, making the cranium look higher in profile view (Figure 12.6).

The Yale individual has a definitive P4/ and M3/, and only slight wear of the major crests on M1/ and M2/. It is probably a young adult, and certainly not a juvenile. The *L. magnus* type skull is an adult, however its teeth are little worn, so that it cannot be a very old individual. These individuals could not have been very different in age at death. Consequently, most of their morphological differences cannot be explained by growth. Might some of these differences be due to sexual dimorphism? If all the differences in size and cranial superstructures between these specimens were due to sexual dimorphism, this dimorphism would be extreme for a primate of that size, and one would expect the putative male, the type, to have enormous canines. Such is not the case based on its canine alveoli. More importantly, the distance between the braincase and the frontal rims reveals a marked difference in skull structure and not simply a difference in growth as could be expected between males and females. We acknowledge that a degree of sexual dimorphism in *Leptadapis* would explain a small part of the differences in crest development. However, on the whole, we think that the sum of the differences in size, cranial structure and cranial superstructures goes much beyond intraspecific variability, and must have an evolutionary significance. The two specimens very probably pertain to two different, closely related, species. As the Yale specimen is in its major characters close to *L. leenhardti*, and we do not want to excessively complicate the nomenclature of this group, we designate the Yale cranium as neotype for *L. leenhardti*.

12.3.3 Comparison Between MU ACQ 209 and MNHN QU 11002

The Montpellier cranium ACQ 209 differs from the *L. magnus* type specimen QU 11002 in several ways. The weaker development of its sagittal and nuchal crests could be due to a difference in age or sex, however both appear to be young adults and there is no indication from the canine alveolus of the type that the canine was larger than that of ACQ 209. The type has a peculiar broad postorbital bar; ACQ 209

has a narrower one. The anterior zygomatic root is slightly higher on the type; both roots present an anterior ventral spine almost at the level of the dental row. However, other differences appear more significant. In anterior view, the zygomatic arches project farther laterally on ACQ 209; this appears linked to the larger orbits of ACQ 209, which are more circular in anterior view, higher and more anteroposteriorly elongated in profile view (Figure 12.6). The infraorbital foramen is slightly more anterior on ACQ 209 in profile view. The most dramatic differences between them are in the height of the muzzle. The muzzle is higher anteriorly on ACQ 209 than on the type. Its interorbital breadth is slightly greater, and in ventral view its palate is markedly broader. In dorsal view, the braincase of ACQ 209 is further anterior. This is linked to its smaller sagittal crest. The anterior part of the braincase reaches less than 5 mm below the rims of the frontal depression. This is a clear difference in the lateral view of the two crania (Figure 12.6). The anterior slope of the muzzle is more inclined in relation to the tooth row in QU 11002, which appears to have a lower anterior muzzle. On the whole, differences in cranial superstructures and cranial elongation cannot be related to sexual dimorphism, because there is no evidence of canine size difference, and other marked differences exist in muzzle height and palate breadth. We think that such differences probably exceed intraspecific variability, however we admittedly have little reference in comparable skull morphologies.

There are differences in the teeth of the two specimens. On ACQ 209, M1/ is especially broad in its lingual part, due to the unusually large size of its hypocone lobe in occlusal view, and it has a more voluminous hypocone than does QU 11002 (Figure 12.5). The posterior extension of the hypocone is also present on M2/, which also shows a more salient and extended crest posterior to the protocone. The tooth has an anteroposteriorly elongated outline, which is derived for the group. The M3/ differs in some details. The lingual cingulum is complete on the type, which has a very weak hypocone (slight swelling of the cingulum), whereas the cingulum is interrupted on ACQ 209, which has a distinct cingular hypocone linked to the posterior crest of the protocone. This renders the M3/ of ACQ 209 broader lingually than on the type. The P4/ of the two specimens are similar for several characters, including a distinct crista obliqua. Both have a posterior crest descending from the protocone, joining the posterior cingulum on the type, but interrupted before the cingulum, which is more extended lingually, on ACQ 209. However, on ACQ 209, the P4/ metacone is especially small, being only a thin cusp on the crest descending from the high paracone (Figure 12.5). Both cusps are more equal in size on the type. Another difference between them is that P4/ is transversely less extended and lingually broader on ACQ 209. The P3/ does not show a clear difference. In general, the differences on the molars and P4/ are probably significant. This dental evidence reinforces our conclusion concerning cranial characters, and we conclude that ACQ 209 is a species of *Leptadapis* different from *L. magnus* and *L. leenhardti*.
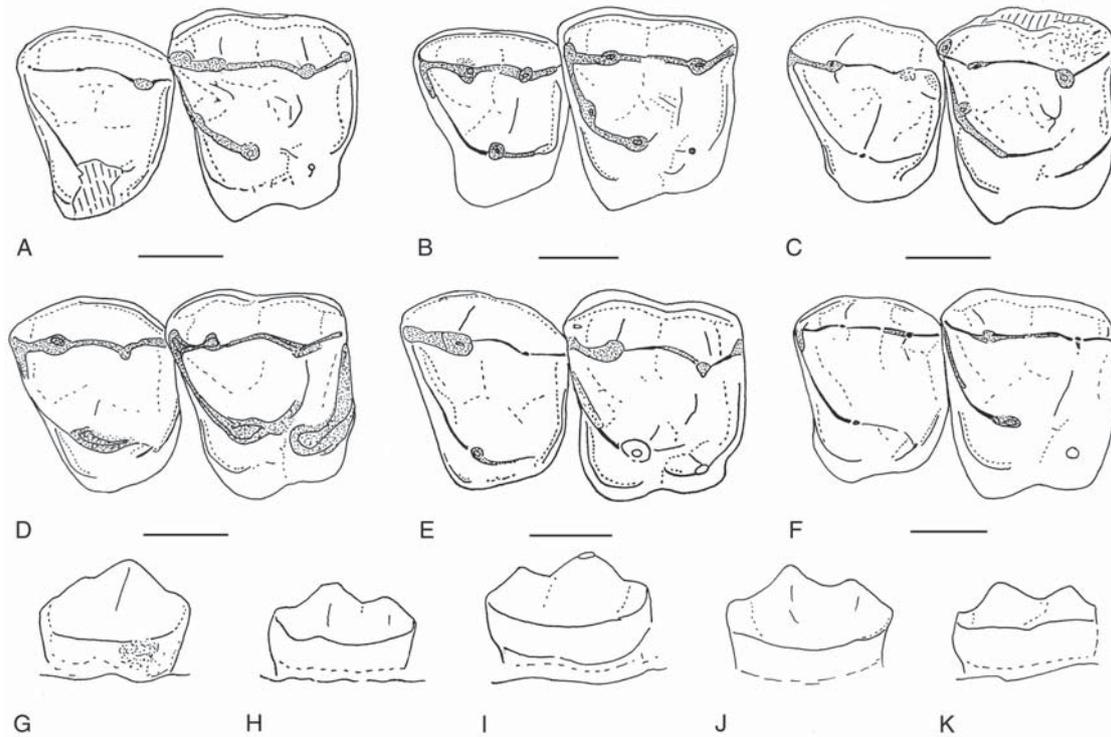
FIGURE 12.5. Schematic drawings of the occlusal views of P4/ and M1/ (A–F), and of the labial views of P4/ (G–K), in selected large adapines. Not to scale; all M1/ were drawn at the same maximal transversal breadth, and P4/ vary accordingly (scale bar is 3 mm). A is YPM PU 11481, neotype of *Leptadapis leenhardti*; B and H are MNHN QU 11002, type specimen of *L. magnus*; C and G are MU ACQ 209, type specimen of *Leptadapis filholi* n. sp.; D and I are MNHN QU 10875, the type specimen of *M. quercyi*, n. gen. n. sp.; E and J are MNHN QU 10870, the type specimen of *M. intermedius*, n. gen. n. sp.; F and K are MaPhQ 210, the type specimen of *M. fredi* n. gen. n. sp. Note that the M1/ vary in outline from markedly asymmetrical (B) to more subquadrate (E), and their hypocones vary from small and crested (B, E) to larger and round (F), or very large and moderately crested (C); there are also variations of the lingual cingulum. The P4/ are generally smaller and lingually narrower in *Leptadapis* species (A–C), and two have a well-developed crista obliqua (B and C); P4/ are generally larger and lingually broader in *Magnadapis* species (D–F); increasing lingual breadth can be observed from A and B to E and F (note incipient hypocone in F). Molarization of P4/ on its labial side can be seen from G (dominating paracone, metacone barely isolated), to K, the most molarized, with a lower paracone and well isolated metacone, through intermediates (H–J). Several specimens are left-right inverted for comparison in A–F, but not in G–K.

Is ACQ 209 also different from other previously named species? The maxilla of *L. assolicus* (Richard, 1940) bears molars which are incomplete but well enough preserved to show important differences from all the large adapines studied here. The P4/ is large compared to M1/. It is simple, very narrow lingually and unlike all the P4/ of the other large adapines. M1/ is difficult to analyze because pieces of enamel are missing. M2/ has a large and high hypocone, relatively close to the summit of the protocone. This morphology recalls that of *Cryptadapis tertius* and clearly differs from all the other large adapines analyzed here. The species *assolicus* is not a *Leptadapis* as defined here, and neither does it pertain to the group defined below.

It was suggested in a stratodimensional diagram that the species *A. stintoni*, proposed as a descendant of *L. magnus* by Gingerich (1977) and having a size similar to *assolicus*, could be a synonym of the latter (Godinot, 1998: Figure 5).

However, a re-examination of the type material confirmed that it is a large species of *Adapis*. It is not a *Leptadapis* species nor is it a *Cryptadapis* species.

Lastly, the M3/ of ACQ 209 also differs from the M3/ described by Crusafont-Pairo (1967) as *"Arisella" capellae*, and later transferred to *Leptadapis capellae* by Szalay and Delson (1979). The M3/ of *L. (?) capellae* has a marked narrowing of its posterior half, a large paraconule, no lingual cingulum and no enlargement of the posterior cingulum corresponding to the location of a hypocone. These differences clearly exceed intraspecific variation of the M3/, and ACQ 209 cannot belong to the species *L. (?) capellae*. Hence ACQ 209 is a new species, which requires a new name. Our study of crania and teeth leads us to formally recognize three species in the genus *Leptadapis*, including a new species.

12.3.4 Systematics of the *Leptadapis* Species

Adapinae Trouessart 1879

Leptadapis Gervais, 1876

Type-species: *Leptadapis magnus* (Filhol, 1874)

Included species: *L. leenhardti* (Stehlin, 1912), *L. filholi*, n. sp.

Diagnosis: large adapines with crania possessing a relatively narrow interorbital breadth, narrow muzzle, salient posterior palatal spine; muzzle generally lower than in *Magnadapis* species; M1/ and M2/ with a well-developed hypocone, M3/ with a postprotocrista and a well-developed posterior cingulum; P4/ usually narrow in its lingual half; canines smaller than in *Magnadapis* species; no diastema between upper canine and I2/.

Leptadapis magnus (Filhol, 1874)

Type specimen: cranium MNHN QU 11002, Muséum National d'Histoire Naturelle, Paris (Figures 12.1, 12.4–12.7).

Horizon and locality: unknown; old collections, Quercy region, south France.

Emended diagnosis: *Leptadapis* with large sagittal and nuchal crests, marked distance between the braincase and the frontal plane, producing a relatively elongated skull.

Referred specimen: cranium MM MaPhQ 211 (described and figured by Stehlin, 1912, as "Montauban 2").

Leptadapis leenhardti Stehlin, 1912

Type specimen: cranium "Montauban 3" described by Stehlin (1912), now lost. Neotype: cranium YPM PU 11481, Yale Peabody Museum (Figures 12.3, 12.5, 12.6).

Horizon and locality: unknown; old collections, Quercy region, south France.

Diagnosis: *Leptadapis* smaller than *L. magnus*, having a very low sagittal crest, weaker anterior zygomatic root than in *L. magnus*; frontal plane lying just above the braincase; skull anteroposteriorly short; P4/ simple and especially narrow lingually.

Leptadapis filholi, new species

Type specimen: cranium UM ACQ 209, Montpellier University (Figures 12.2, 12.5–12.7, 12.9).

Derivatio nomini: in honor of Henri Filhol, who named the species *L. magnus* and made substantial contributions to our knowledge of fossil mammals.

Horizon and locality: unknown; old collections, Quercy region, south France.

Diagnosis: *Leptadapis* with a higher muzzle and a broader palate than in *L. magnus* and *L. leenhardti*; sagittal and nuchal crests moderate in size (well developed but smaller than in *L. magnus*); distance between braincase and frontal plane intermediate between *L. magnus* and *L. leenhardti* (closer to the latter); the three molars are broader lingually than in the two other species; M1/ has an especially broad hypocone.

FIGURE 12.6. The four crania of *Leptadapis* in lateral views at the same scale (bar is 4 cm). Type specimen of *L. filholi*, MU ACQ 209 (A); type specimen of *L. magnus*, QU 11002 (cast, B) showing the highest sagittal and nuchal crests, and a thickened postorbital bar; the neotype of *L. leenhardti*, YPM PU 11481 (C) has a very low sagittal crest, and its posterior extremity and zygomatic arch are reconstructed with plaster; another *L. magnus*, MaPhQ 211 (D).
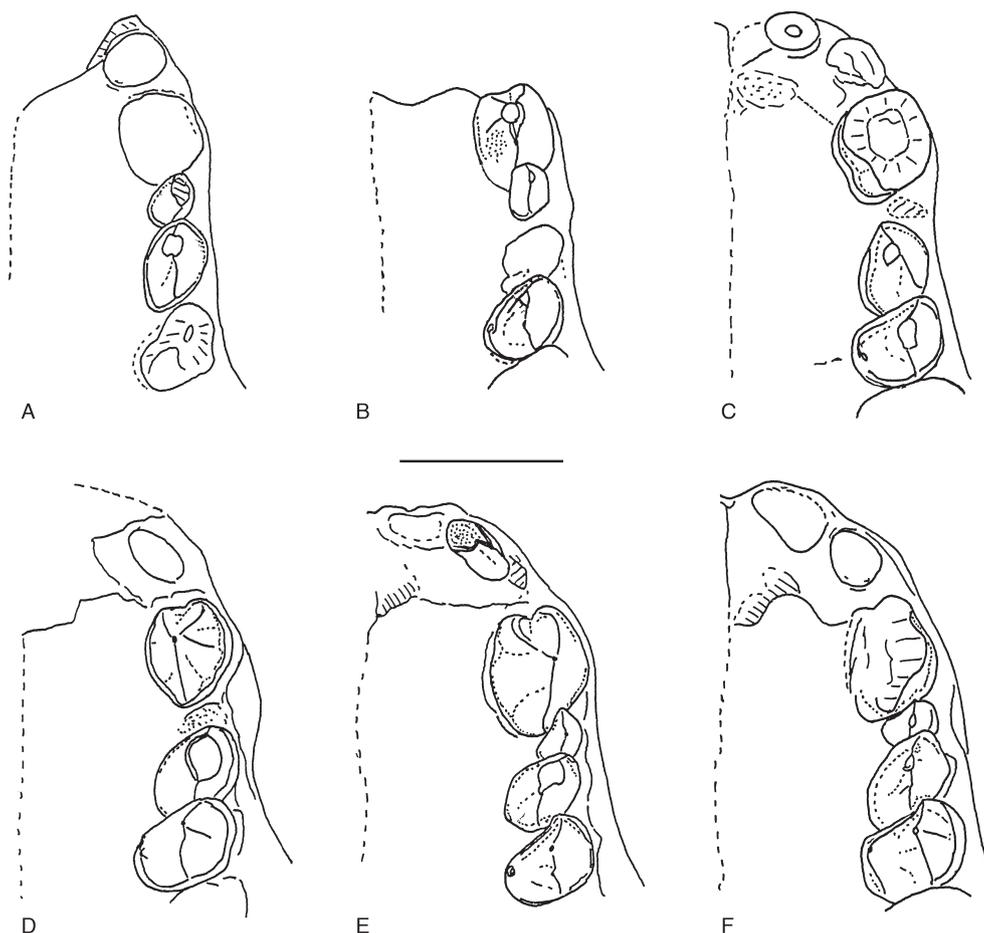
FIGURE 12.7. Drawings of the left anterior part of the muzzles of large adapines, showing the canine or its alveolus, P1/ to P3/ or alveoli, and incisor remnants or alveoli when preserved. Placing complete canines as vertical as possible inclines the nearby premolars, their labial sides being favored and their lingual side being diminished. All drawn at the same scale (bar is 1 cm). A is QU 11002, type of *Leptadapis magnus*; B is ACQ 209, type of *L. filholi*, n. sp.; C is QU 10872, type of *Magnadapis laurenceae*, n. gen. n. sp.; D is QU 10875, type of *M. quercyi* n. gen. n. sp. (inverted left-right; right side); E is ACQ 214, *L. intermedius* n. gen. n. sp.; F is MaPhQ 210, the type of *M. fredi*, n. gen. n. sp. Note that canines vary in size and outline (that in B is partially worn). Rare preservation of the incisor region shows that the alveolus of I2/ is close to that of the canine in *Leptadapis* (A), whereas incisors or alveoli are separated by a short diastema and slightly shifted medially in *Magnadapis* species (C–F); incisor alveoli are best preserved in F (canine is better preserved on the other side, but incisor alveoli are less clear); a partially worn I2/ is present in E and the root of I1/ is present in C.

12.3.5 Phylogeny of *Leptadapis* Species

Our systematic interpretation of the four *Leptadapis* skulls is to classify them in three different species. Can a phylogenetic interpretation of those be proposed? In the most evident character, cranial superstructures and robusticity, there is a clear morphocline. *L. leenhardti* has a very low sagittal crest, the braincase lying just beneath the frontal depression, the anterior zygomatic arch is lower than on the other specimens. Next is *L. filholi*, which has an intermediate sized sagittal crest and a braincase still anterior but several millimeters beneath the frontal rims; the anterior zygomatic arch is as high as in *L. magnus*. Lastly, *L. magnus* has a strongly developed sagittal crest, the sagittal and nuchal crests project much farther

beyond the occipital plane, and the braincase is pushed backward (distinctly more isolated from the anterior part of the skull). The postorbital bar is clearly thicker on the *L. magnus* type specimen than on the other specimens.

In terms of superstructures and robusticity, there is a clear morphocline *leenhardti-filholi-magnus*. The increased development of the masticatory musculature is accompanied by a lengthening of the space between the frontal region and the braincase (the postorbital narrowing being stronger) and an accentuation of the posterior projection of the nuchal crests. Both aspects produce a marked lengthening of the whole skull in *L. magnus* in comparison with the two other species. However, some of the other observable skull characters do not fit into a similar morphocline. This is especially true of

the breadth of the palate and muzzle, which is greater in *L. filholi* than in the two other species. This also seems to be true of muzzle height. This is visible despite the incompleteness of the nasal region on *L. leenhardti*. Little is missing between the two maxillae, and the height of its muzzle on the right side must be very close to the original state. Clearly the muzzle is much lower on *L. leenhardti* than on *L. filholi*: again *L. filholi* does not appear to be intermediate between the two other species in terms of muzzle morphology.

Concerning dental characters, there are no big differences between *L. leenhardti* and *L. magnus*, however those present can be interpreted. The lingual narrowness of M3/ and the double-rooted P2/ in *L. leenhardti* can be primitive (or variability?). On the P4/ of *L. leenhardti*, the absence of the crista obliqua and the less equally-sized labial cusps make this tooth appear simpler, and labially less molarized. *L. leenhardti* may well be primitive relative to *L. magnus* for dental and cranial characters, leading to the most parsimonious hypothesis that it is a possible ancestor of the latter (see Figure 12.11). We mentioned that characters of the M1/ in *L. filholi* (length, very large hypocone) are derived in comparison with the two other species. The P4/ however is not more derived than that of *L. magnus*. It could be at the same time derived in its transverse shortness and lingual breadth, and primitive in retaining a very small metacone. As is true of cranial characters, dental characters of *L. filholi* suggest a lineage independent of *L. magnus*. This leads to the view that two lineages of *Leptadapis* are present in the Quercy region. In this context, we cannot say anything concerning possible sexual dimorphism in *Leptadapis* species. We cannot say for sure if the *L. magnus* type specimen is a male and the *L. filholi* is a female, differences in cranial superstructures between the two species might be less accentuated. However we cannot show this through canine size. The two specimens attributed to *L. magnus* have small differences in cranial superstructures, which could reflect either a small amount of dimorphism or a small evolutionary distance. Available specimens do not give positive evidence of sexual dimorphism in *Leptadapis* species. Do some of the skull characters of *L. leenhardti* indicate that it might be a juvenile? The specimen, however, has a definitive P4/ and M3/, and the *L. magnus* type specimen has P4/ and M1/ which have only a small degree of wear. The difference in age at death between these two specimens must have been small, indicating that growth cannot account for most of the differences found in cranial superstructures. On the whole, *Leptadapis* species as redefined here are incompletely known: their anterior dentition is poorly documented; only one of them, *L. filholi*, shows a complete zygomatic arch, a canine and a P1/. No specimen has an associated mandible. It will be important to search in the biochronologically situated assemblages for mandibles which can be attributed to *Leptadapis* species.

12.4   Second Group of Generic Value: *Magnadapis* n. gen.

The other group of specimens includes the skull QU 11035-11036, the crania QU 10870, QU 10872, QU 10875, MaPhQ 210, the two muzzles PLV 6, ACQ 214, and specimens from Euzet-les-Bains. As explained above, they represent several species sharing a number of significant characters. These species need to be distinguished from the preceding group at the generic level, and we coin a new genus for them. Because this group has never been properly recognized before, we name several new species, for the skull morphologies which appear to us to warrant such systematic recognition. We first give names and diagnoses for the clearly recognizable species, and explain our choices and hesitations concerning other specimens in the following discussion.

12.4.1   Systematics

Magnadapis, new genus
   Type-species: *Magnadapis quercyi*, new species.
   Derivatio nomini: from *magnus*, large, and *Adapis*, because this group includes the largest known adapine species.
   Diagnosis: species of *Magnadapis* differ primarily from species of *Leptadapis* by a broader interorbital breadth, associated with a broader muzzle; the palate is also broad, and the dental rows are less convergent anteriorly than in *Leptadapis* species (except *L. filholi*, which also has a broad palate); there is no posterior palatal spine. I2/ is small and isolated from the canine by a small diastema; the canines are very large and marked by deep vertical grooves; the P1/ seems comparatively smaller than in *Leptadapis*; P4/ often lingually broader than on *Leptadapis* species, and never presenting a crista obliqua interrupting the trigon basin; upper molars with hypocones generally smaller than in *Leptadapis* species, sometimes absent on M2/; M3/ transversely broad, with the trigon basin open posteriorly (no crista obliqua, usually no posterior cingulum). Several *Magnadapis* specimens are somewhat larger than *Leptadapis* specimens.
   Other included species: *Magnadapis fredi* n. sp., *M. laurenceae* n. sp, and *M. intermedius* n. sp.
   Magnadapis quercyi, new species
   Type specimen: MNHN QU 10875, cranium from the Muséum National d'Histoire Naturelle, Paris (Figures 12.4, 12.5, 12.7–12.9). Cranium figured by Genet-Varcin (1963), Saban (1963) and Simons (1972).
   Derivatio nomini: in reference to the South-France province where all the large adapine skulls were found in a well known paleokarst.
   Horizon and locality: unknown; old collections, Quercy region, south France.
   Diagnosis: cranial superstructures weakly developed, root of zygomatic arch higher than in *M. laurenceae*; large orbits and narrow postorbital bar; height of muzzle tapering anteriorly
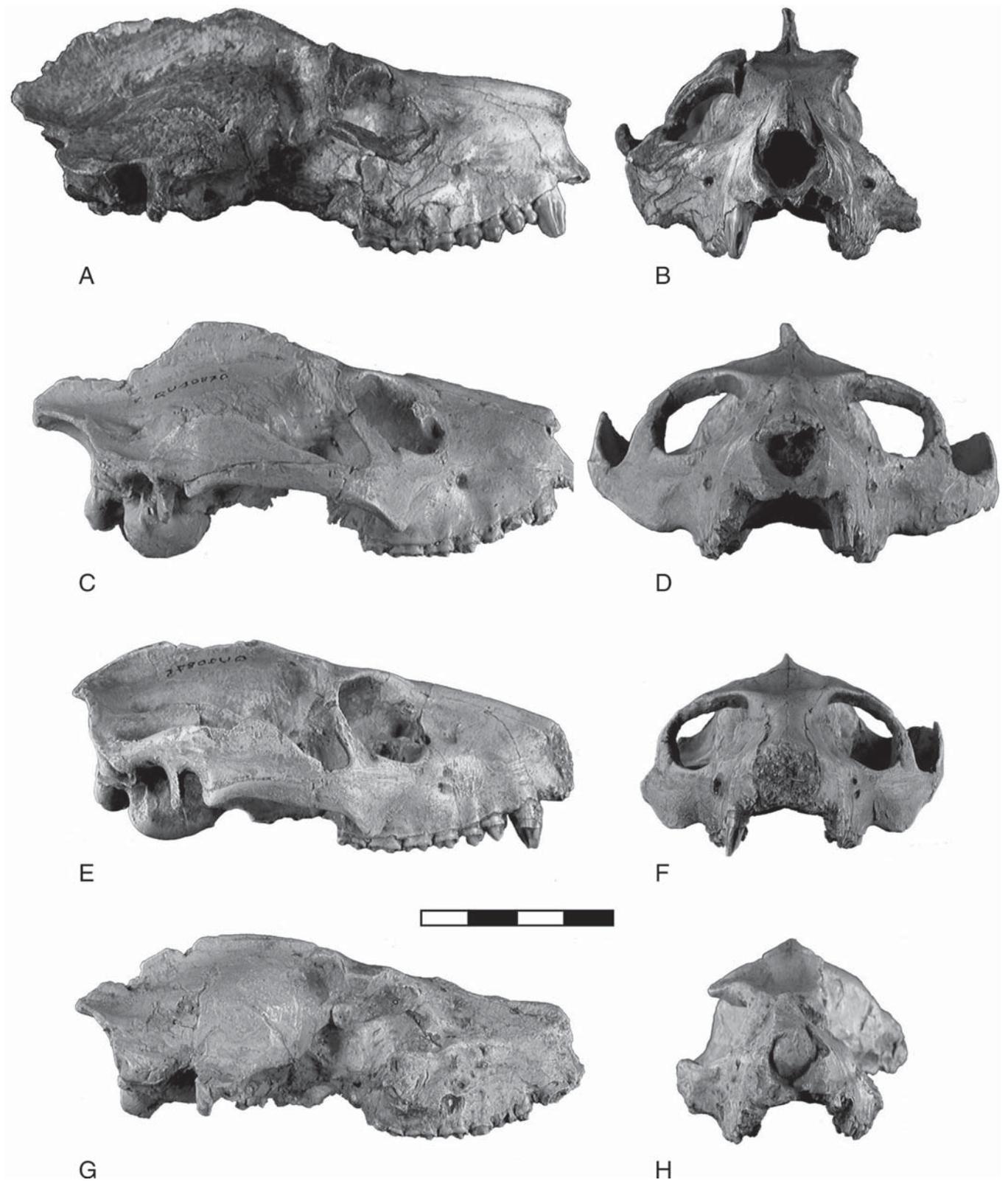
FIGURE 12.8. Four crania illustrating the four different *Magnadapis* species, in lateral (A, C, E, G) and in anterior (B, D, F, H) views, all at the same scale (bar is 4 cm). Type specimen of *M. fredi* n. gen. n. sp., MaPhQ 210 (A, B); type specimen of *M. intermedius* n. gen. n. sp., MNHN QU 10870 (C, D); type specimen of *M. quercyi*, MNHN QU 10875 (E, F); type specimen of *M. laurenceae*, MNHN QU 10872 (G, H). They are arranged with cranial superstructures increasingly developed from bottom to top, but the nuchal projection is more accentuated in G than in E. Note an accompanying increase in facial and anterior muzzle height.
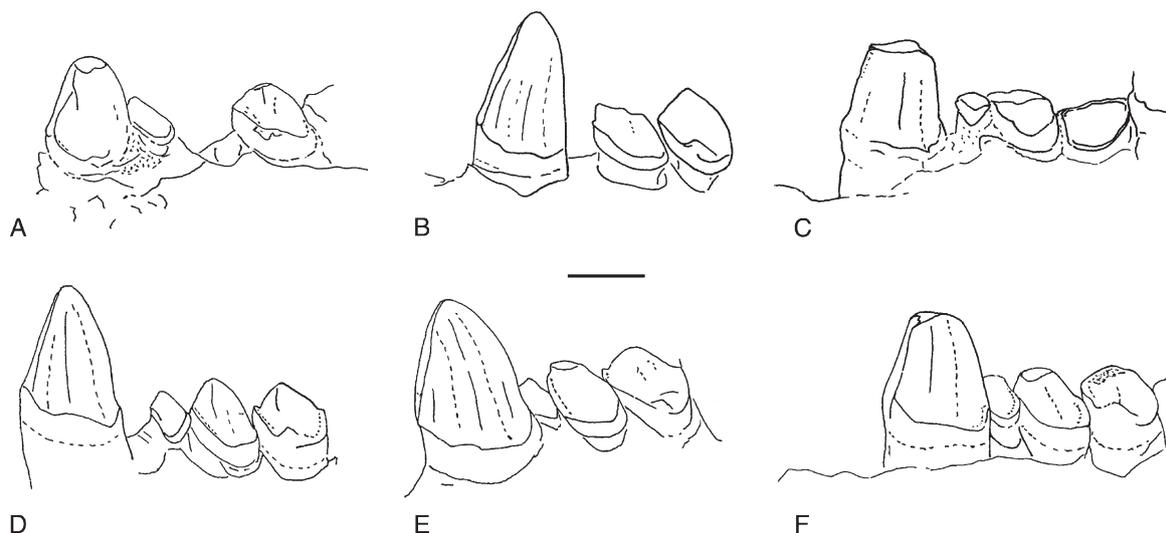
FIGURE 12.9. Schematic drawings of left upper canine to P3/ in lingual view in several large adapines, all at the same scale (bar is 5 mm). A is ACQ 209, type of *Leptadapis filholi*, n. sp.; B is QU 10875, type of *Magnadapis quercyi* n.gen. n. sp.; C is QU 10870, type of *M. intermedius* n. gen. n. sp.; D is PLV 6, referred to as *M*. aff. *quercyi*; E is ACQ 214, referred to *M. intermedius*; F is the type of *M. fredi*, n. gen. n. sp. Although the canine in A is partially worn, its anterior vertical groove and its lingual cingulum are partially preserved, showing a clear difference in size and shape between the only upper canine preserved in a *Leptadapis* species (A) and the more numerous upper canines of *Magnadapis* species. Note also increasing molarization of P3/ from A to B, E, to D, and to F, where the protocone lobe is broad and high.

much more than in *M. fredi*; canine moderate in size; P2-3-4/ less developed lingually, less molarized than in *M. fredi*; M2/ with small recognizable, cuspidate hypocone.

Referred specimen: muzzle PLV 6 from Leuven University, Belgium.

Magnadapis laurenceae, new species

Type specimen, MNHN QU 10872, incomplete cranium from the Muséum National d'Histoire Naturelle, Paris (Figures 12.7, 12.8, 12.10).

Derivatio nomini: in honor of Laurence Lanèque, in recognition of her important dissertation work on adapine skulls.

Horizon and locality: unknown; old collections, Quercy region, south France.

Diagnosis: weakly developed cranial superstructures; very low sagittal crest; frontal lines joining more posteriorly than on all other large adapine skulls; correlatively braincase closer to the anterior part of the skull than in other *Magnadapis* species; nuchal crests projecting further posteriorly than in *M. quercyi*; muzzle narrower, orbits smaller and anterior zygomatic root lower than in *M. quercyi*; premolars similar to those of *M. quercyi* in terms of molarization; canine relatively large and unusual in its great labio-lingual breadth (crown subcircular instead of anteroposteriorly elongated as in other species); M2/ with complete lingual cingulum and no hypocone.

Magnadapis fredi, new species

Type specimen: MM MaPhQ 210, cranium of the Montauban Natural History Museum (Figures 12.5, 12.7–12.10); recon-

struction figured as "*Adapis magnus*, Montauban 1" by Stehlin (1912).

Derivatio nomini: in honor of Frederick S. Szalay, Fred to his close colleagues and friends, in recognition for his extensive contributions to primate paleontology and his commitment to theoretical questions.

Horizon and locality: unknown; old collections, Quercy region, south France.

Diagnosis: *Magnadapis* with enormous cranial superstructures, braincase slightly more than 1 cm below frontal rims, and pushed posteriorly relative to the anterior part of the skull; postorbital narrowing correlatively strong; very high sagittal crest in the posterior part of the skull, more than 1.5 cm high; cranium extended posteriorly further beyond the external auditory meatus than in other species; anterior zygomatic root higher than in all other species, and muzzle higher in its anterior part than in all other species of *Magnadapis*; nasofrontal suture shorter, much less posteriorly wedged between the frontals; P2-3-4/ lingually well developed, more molarized than in the three other *Magnadapis* species; M2/ with recognizable and cuspidate hypocone.

Magnadapis intermedius, new species

Type specimen: MNHN QU 10870/1, cranium and associated mandible (10871) from the Muséum National d'Histoire Naturelle, Paris (Figures 12.4, 12.5, 12.8, 12.9); figured by Grandidier (1905).

Derivatio nomini: to reflect the fact that its morphological characters are in several respects intermediate between those of *M. quercyi* and *M. fredi*.
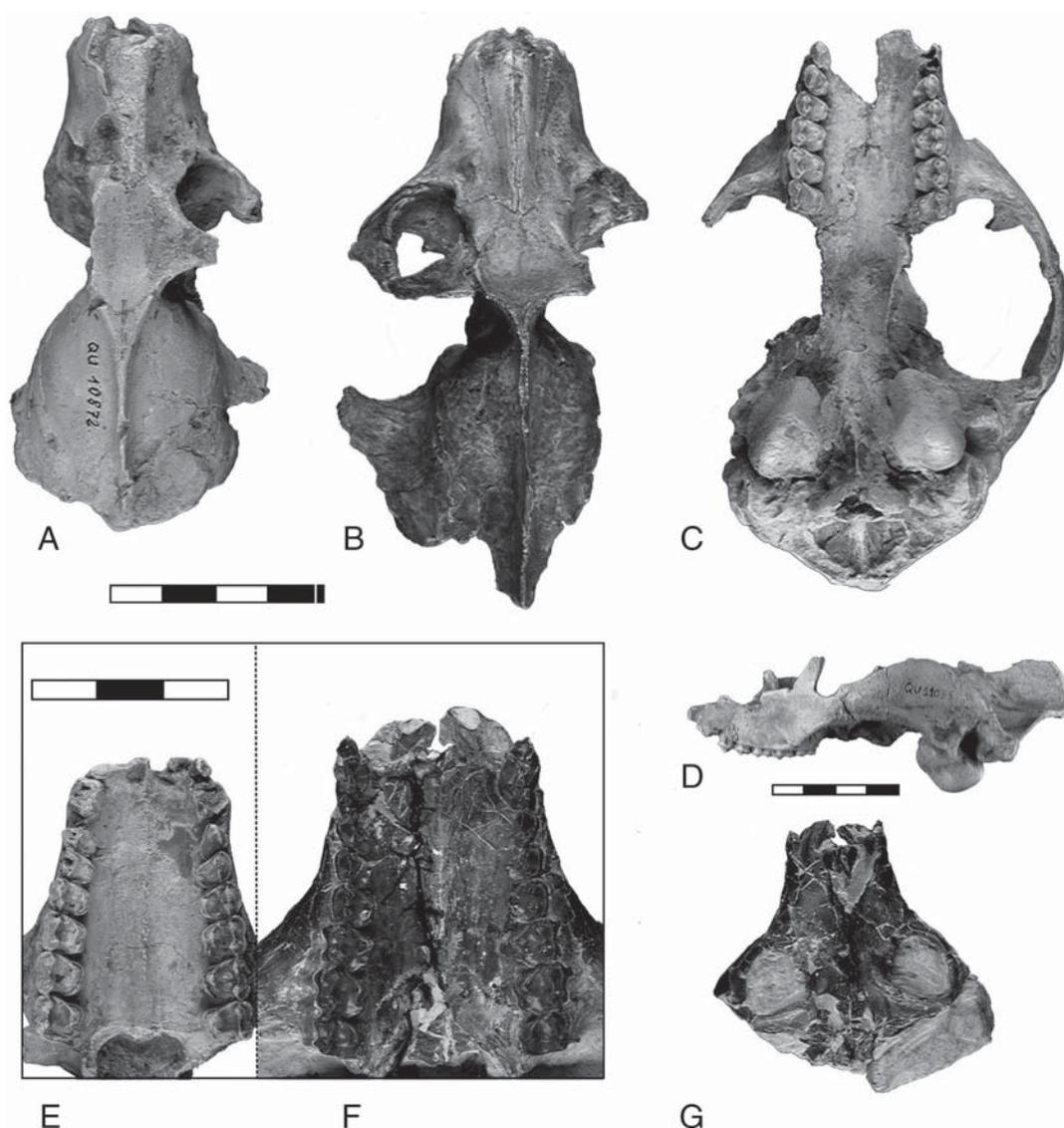
FIGURE 12.10. Two crania, one partial cranium and one muzzle of different *Magnadapis* species. Dorsal views of the type specimen of *M. laurenceae* n. gen. n. sp., MNHN QU 10872 (A), and the type specimen of *M. fredi* n. gen. n. sp., MaPhQ 210 (B); ventral view of MNHN QU 11035, *M*. aff. *intermedius* (C), and lateral view of the same (D); ventral views of the palates of *M. laurenceae* QU 10872 (E) and of the crushed muzzle BM St. H. 1634 from Euzet, referred to *M. fredi* (F); dorsal view of the same muzzle St.H. 1634 (G). At different scales: A–C and D, G, bars are 4 cm; E, F, bar is 3 cm. The two crania in A and B illustrate minimal (A) and maximal (B) cranial superstructure development in *Magnadapis* species. The posterior part of QU 11035 (D) probably approximates how the broken posterior part of *M. fredi* (B) may have looked like; notice the extremely high posterior part of the zygomatic arch.

Diagnosis: *Magnadapis* with well developed cranial superstructures, flaring zygomatic arches, sagittal and nuchal crests projecting far behind the foramen magnum, making a triangular posterior projection in dorsal view; postorbital constriction more accentuated than in *M. quercyi*; skull longer than in *M. quercyi*; cranial superstructures generally less extreme than in *M. fredi*; canines larger than in *M. quercyi*.

Referred specimens: partial cranium MNHN QU 11035 (Figure 12.10) and associated mandible (11036), muzzle ACQ 214 (Figures 12.7, 12.9).

The four crania used to name these four species can be arranged in a morphocline according to the general development of cranial superstructures (Figure 12.8). However, several peculiarities of *M. laurenceae* set it apart, and later we will discuss its possible significance. The partial cranium QU 11035 is somewhat intermediate between the type specimens of *M. intermedius* and *M. fredi*, and the muzzles PLV 6 and ACQ 214 also pertain to the same group. A parsimonious phylogenetic interpretation of this evidence is that these species constitute a lineage marked by increasing robusticity and

cranial superstructure development, starting with *M. quercyi* and ending with *M. fredi* (an hypothesis which implies a chronological succession). However, the number of species to be distinguished between these two extremes is not straightforward, due to the possible role of sexual dimorphism in the morphological differences between the specimens.

12.4.2 Comparison Between QU 10870 and QU 10875

The most interesting case is QU 10870/1, the type specimen of *M. intermedius*. It is slightly larger than the *M. quercyi* type specimen QU 10875, and presents markedly more developed sagittal and nuchal crests, an increased nuchal projection, and its zygomatic arches are more flared laterally (Figure 12.4). These specimens show quite similar degrees of tooth wear, indicating that age cannot be responsible for their morphological differences. The difference between them in canine size is difficult to evaluate because the two canines of QU 10870 are incomplete and partially worn; the left one is more complete and preserves remnants of its basal cingulum: it was slightly larger than that of QU 10875 (Figure 12.9). If there were sexual dimorphism in large adapines, these two specimens could be considered a female (QU 10875) and a male (QU 10870) of the same species. Their orbital morphologies are remarkably similar. Size differences in sagittal and nuchal crests could exist between males and females as in some living anthropoids, however to what degree could they exist in Eocene strepsirhines? In fact, close inspection shows that they differ by some important skull characters; looking at these skulls in a posterolateral view, one sees that the minimal distance between the anterior part of the braincase and the frontal plane (the two converging frontal rims) is between 2 and 3 mm on QU 10875, and is 7–8 mm on the left side of QU 10870 (around 4 mm on the right side, where a bony plate artificially lengthens the braincase anteriorly). In dorsal or lateral view, the braincase of QU 10870 is posteriorly shifted behind the frontal region, accentuating its postorbital narrowing, and also increasing its skull length (Figures 12.4, 12.8). Related to its posterior shift, the posterior part of QU 10870 shows a more accentuated posteroventral inclination of the braincase relative to the anterior part of the skull (i.e., a higher degree of basal flexure or klinorhynchy). There is also a difference in the anterior part of the skull, the muzzle of QU 10870 being higher in its posterior part than on QU 10875 (Figure 12.8). This difference resides in the infraorbital height, greater on QU 10870. This difference in height is also present in the anterior part of the muzzle, thinner on *M. quercyi*. Strangely, in this context one would suspect that the orbit might be more vertical on QU 10870, and in fact the contrary is true: the orbit has a more posterior inclination on the higher of the two skulls, QU 10870 (Figure 12.8). On the whole, the huge difference in the size of their sagittal and nuchal crests, the marked nuchal projection on QU 10870, only incipient on QU 10875 (Figure 12.8), the increased flaring of the zygomatic

arches on QU 10870, and its higher anterior zygomatic roots, are accompanied by a marked anteroposterior lengthening of the skull, an increased distance between braincase and frontal plane, and a clear difference in muzzle height. Such differences markedly exceed those found in species of *Alouatta*, the most dimorphic platyrrhine (which is roughly similar in size). If *Magnadapis* species had a higher degree of sexual dimorphism than highly dimorphic anthropoids, one would expect this to be reflected by very big canines in males. However, the difference in size of the canines observed between the two specimens is small (Figure 12.9). In this context, an evolution of cranial superstructures linked to dietary adaptation seems much more likely than an extreme degree of unusual sexual dimorphism. Even if a small part of the marked morphological differences between these two crania might be due to sexual dimorphism, we feel that they need to be placed in two different species.

12.4.3 Comparisons of QU 11035 and the Muzzles PLV 6 and ACQ 214

At this moment, it is difficult for us to find dental characters which would clearly delineate species of *Magnadapis*. The teeth of the *M. quercyi* type specimen seem primitive, due to the square outline of M1/, the simple, lingually narrow P4/, and the very small protocone of P3/. Its canine is also relatively slender. However, the muzzle PLV 6, which would fit very well with *M. quercyi* because it has a similar orbit and a similarly slender anterior zygomatic root, has less square M1/, clearly broader in its anterior than in its posterior half. This muzzle also retains a well preserved canine, more robust than that of the *M. quercyi* type. Is this evidence of possible canine dimorphism, usual intraspecific variability, or slight evolution toward more robust upper canines? We cannot clearly answer this question without more information on intraspecific dental variability in large adapines. We leave PLV 6 in open nomenclature as *M*. aff *quercyi*.

The incomplete skull QU 11035/6 raises another interesting question. In its preserved parts, the crests are extremely developed and in this way it resembles MaPhQ 210, the *M. fredi* type specimen. However, the anterior root of its zygomatic arch is much lower than on MaPhQ 210. Its P3/ is also less molarized than on MaPhQ 210. Its P2/ is remarkably little extended lingually and is also less molarized than on MaPhQ 210. Hence this skull is clearly closer to QU 10870 than to the *M. fredi* type specimen. We cannot find clear dental characters separating QU 11035 and QU 10870, whereas such characters exist for QU 11035 and MaPhQ 210. QU 11035 is slightly larger than QU 10870, the *M. intermedius* type specimen. Its zygomatic arches flare more widely and its nuchal crests and the posterior extremity of its sagittal crest are more extended than on QU 10870. In dorsal view, QU 10870 shows a salient posterior triangle due to these crests (Figure 12.4), whereas QU 11035 has a more

regular outline (Figure 12.10), due to the increased lateral development of its nuchal crests. In QU 11035, the zygomatic arch is higher, remarkably robust in its posterior part (Figure 12.10), and it seems to have even greater basicranial flexure than QU 10870. The profile view also shows the very steep departure of the sagittal crest above the nuchal projection, not preserved on QU 10870. These differences concern crests, muscular attachments, and their possible correlates. The anterior zygomatic roots have only a small difference (slightly higher on QU 11035), easily accommodated in intraspecific variability. Hence these two specimens, QU 10870 and QU 11035 could possibly illustrate sexual dimorphism in *M. intermedius*, the type specimen being a female and QU 11035 being a male. However, other differences between the two specimens might also point toward some evolutionary distance between them instead. The base of the skull is slightly more extended posteriorly on QU 11035 than on QU 10870. In ventral view, the area posterolateral to the bullae and surrounded by a ribbon-like area continuous with the nuchal plane (presumably for a more extensive area of nuchal musculature attachment), is larger on QU 11035 than on QU 10870. Another difference, more clearly seen, is the much larger bullae on QU 11035 than on QU 10870 (visible even in lateral views, Figures 12.8, 12.10). Whereas we cannot definitely rule out that sexual dimorphism would explain some of these differences, we consider likely that QU 11035 represents a more advanced stage in a lineage affected by developing cranial superstructures, an increasing basicranial flexure and inflating bullae. Because the interpretation is difficult and we do not want to excessively multiply species names, we leave QU 11035 in open nomenclature as *M*. aff *intermedius*.

Canine size was not directly used in the preceding comparison because QU 11035 only retains a partial alveolus for its left canine. This seems to have accommodated a large tooth, and the muzzle ACQ 214 may add some information here. Its anterior zygomatic root is more similar to that of QU 10870 than to that of QU 11035 (thus it is very distinct from the *M. fredi* type specimen), and this muzzle bears a very large canine (Figure 12.9). This canine is clearly larger than those of QU 10870: it could fit in the alveolus of QU 11035. This agrees with both interpretations of the last specimen: in the case of sexual dimorphism, it would illustrate a marked canine size dimorphism in *M. intermedius* (both QU 11035 and ACQ 214 being males); in the case of different evolutionary stages, it would add to the preceding evolutionary changes an increase in canine size (in agreement with the very robust canine of *M. fredi*). In the other parts of its dentition, one can see that the P3/ protocone is larger than that of QU 11035 and QU 10870 (and more marked on the right than on the left side). This favors an evolutionary stage going toward *M. fredi*, the species which can be recognized by its clearly more molarized premolars. Because it is far from having the enormous zygomatic root of the *M. fredi* type specimen, we also refer ACQ 214 to *M. intermedius*, noting that, if the

zygomatic root height were a very reliable character, ACQ 214 would be closer to the *M. intermedius* type specimen than to QU 11035. It might then illustrate a marked canine size dimorphism. If P3/ molarization were a better systematic indicator than zygomatic root height, ACQ 214 would be a more derived evolutionary stage, confirming at the same time the value of canine size as an indicator of evolution in this *Magnadapis* lineage.

12.4.4 Comparison of MaPhQ 210

The Montauban cranium MaPhQ 210, chosen as the type of *M. fredi*, has cranial superstructures further increased over the state seen in *M. intermedius*. The braincase is slightly more distant from the frontal plane (around 10 mm), and the two frontal lines converge sharply, which results in a short and very narrow frontal triangle (Figure 12.10). The postorbital narrowing is again slightly increased over that of QU 10870. The posterior part of the sagittal crest is enormous (around 18 mm visible) and seems more extended than on QU 10870 (though the latter is broken). The missing posterior part is not very extensive: the nuchal projection may be the authentic one (to be verified on the original), and the right lateral extremity of the nuchal plane is preserved. The most posterior part of the skull is more extended than on QU 10870. In ventral view, the osseous area posterior to the bulla is clearly more extensive on MaPhQ 210 than on QU 10870, and slightly more than on QU 11035. Likewise in lateral view, the part of the skull posterior to the external auditory meatus is very short on QU 10870 (as on *M. quercyi*), and is clearly more extended on MaPhQ 210. QU 11035 is similar to MaPhQ 210 in this view, and its lateral aspect probably gives a relatively good approximation of how the crests of *M. fredi* would have looked (Figure 12.10). Among the peculiarities of MaPhQ 210 are that the nasofrontal sutures protrude posteriorly into the frontals much less, the increased height of the anterior part of its muzzle, and especially the incredibly exaggerated height of its anterior zygomatic root (Figure 12.8). In lateral view, it seems also that MaPhQ 210 has a smaller orbit than the others. This is difficult to show, due to deformation: the postorbital bar has two pieces that are displaced and badly adjusted. However, in this view, the very high zygomatic root of MaPhQ 210 leaves a strong impression that the orbit was smaller and less posteriorly inclined than on the other skulls.

Many of the above-mentioned characters clearly distinguish the types of *M. fredi* and *M. intermedius*, but they cannot be compared with QU 11035 because the dorsal part of QU 11035 is crushed. However, dental characters also clearly separate MaPhQ 210 from all the preceding specimens: its P3/ is clearly broader and more extended lingually than on other specimens, having a more voluminous protocone (Figures 12.7, 12.9); the whole premolar series is more molarized and confirms a probably more derived evolutionary stage. In this context, there is no reason to wonder if QU 11035 might have been a female of *M. fredi*, and the latter species appears well justified.

The crushed muzzle NMB St.H. 1634 from Euzet-les-Bains has a broad interorbital region, a broad palate, large canines and its premolar series is highly molarized, making it very similar to the type of *M. fredi* (Figure 12.10F). Its hypocone is quite small on M2/, whereas this cusp is well developed and more voluminous on MaPh Q 210. However, this specimen from Euzet has markedly worn molars, rendering cusp size estimation difficult. It will be important to make a detailed study of dental variations in the Euzet assemblage, and compare it with the morphology of the M. *fredi* type specimen. Pending such a study, we provisionally refer the Euzet assemblage to *M. fredi*. This is important because Euzet is placed in the European biochronological scale (MP 17a), which gives a good idea of the age of the *Magnadapis* lineage, close to MP 16 – MP 17.

12.4.5   Comparisons of QU 10872, *M. Laurenceae*

The very peculiar *M. laurenceae* has the thinnest anterior zygomatic root and the lowest sagittal crest of all *Magnadapis* crania. Paradoxically, its nuchal crests project posteriorly beyond the foramen magnum further than in QU 10875. The only way it could fit in the preceding lineage of species would be as a species more primitive than *M. quercyi*, with even weaker cranial superstructures. However, other characters suggest a more complex relationship. Concerning cranial superstructures, QU 10872 has an anteriorly very low sagittal crest, as in *M. quercyi*, and its two frontal lines join even further posteriorly than in that species (Figure 12.10). This gives the impression that the braincase is slightly closer to the anterior part of the skull in *M. laurenceae* than in *M. quercyi* (correcting for the slight deformation of QU 10872 would possibly increase that impression). For that very posterior frontal junction, this specimen is an extreme within the large adapines, and it resembles *Notharctus* and other fossil primates. Could it be primitive for adapines? Posteriorly, the sagittal and nuchal crests project relatively far beyond the occipital plane (around 8 mm), clearly further back than in *M. quercyi*. Some variability or dimorphism can be expected there. However, it is strange to have the projection more accentuated on the slightly smaller, and possibly more primitive specimen. The anterior root of the zygomatic arch is slightly less robust in *M. laurenceae*, in proportion with its slightly smaller size. For these cranial superstructures, *M. laurenceae* appears possibly more primitive and in line with the preceding lineage, however the other cranial characters appear more problematic. In dorsal view, its muzzle is narrower than in *M. quercyi*. In anterior and lateral views, QU 10872 clearly appears to have a smaller orbit than *M. quercyi* and QU 10870 (Figure 12.8). In lateral view, the profile of the muzzle seems slightly concave, which would be unusual for adapines. However, this part of the skull is badly preserved and it is sediment instead of real bone which suggests this profile. In lateral view, the alveolar rim appears

ventrally convex and markedly curving upward anteriorly, as in other *Magnadapis*. The ventral view confirms that the skull is proportionately shorter than in *M. quercyi*, the braincase and the anterior part being closer to each other. The palate is narrower and also seems somewhat shorter. On the whole, all these differences in skull characters show *M. laurenceae* to be quite distinct from other *Magnadapis* species. Because for several of these differences, it resembles *Leptadapis* species, further interpretation of its characters is relevant to the relationships between the two genera. These are discussed below.

For dental characters, *M. laurenceae* also shows differences from other *Magnadapis* species. The hypocone of its molars is especially small, being completely absent on M2/, which has a continuous lingual cingulum well separated from the postprotocrista, and small on M1/. It seems that M1/ and M2/ have a straighter centrocrista than on QU 10875 (M2/ is partly worn labially on the left side, where the molars are best preserved). The P4/ appears to be slightly more transverse, or slightly less anteroposteriorly elongated (with paracone and metacone closer, less equal) than on *M. quercyi*. P3/ appears quite similar on both specimens. The same is true for P2/. There seems to be a marked difference on the canines, seen in the unusual outline of the left canine in *M. laurenceae*. This tooth is broken, however the outline of its base is intact, and one can see the posterior part of the lingual cingulum, with a much more accentuated concavity. On the right side, the base of the canine is lingually worn, and the outline of the tooth is unclear. It is possible to place side by side the left canine of QU 10872 and the right canine of QU 10875. Their outlines are different (Figure 12.7). In *M. laurenceae*, the canine is broader in its anterior part (below the anterior groove). It is also linguo-labially broader in its median part, and it is less posteriorly extended (less oval). The canine of *M. quercyi*, more oval in occlusal outline, is similar to the canines of other large adapines. In contrast, the canine of *M. laurenceae* has a more circular outline (similar grooves can be deduced from the outline and the base at least anteriorly and posterolingually). The root of the left I1/ can be seen; it seems relatively small in comparison with the alveoli as preserved in *M. fredi*. We are cautious with regard to the significance of this because no I1/ is preserved in the large adapines studied here, and well preserved alveoli are also rare in this group. In sum, differences in dental characters reflect the uniqueness of *M. laurenceae*, and, like cranial characters, raise questions about character polarities. If a small hypocone on M1/ and no hypocone on M2/ were constant in *M. laurenceae*, it would be an autapomorphic character. The P4/ and the relatively straight centrocrista of M1-2/ would suggest primitive dental character states, possibly the relatively quadrangular M1/ also. We feel that these dental characters will need a more detailed and quantified study including assemblages from known localities, to get an idea of dental character variability. Perhaps we are overemphasizing small dental characters which may vary a lot within large adapine species.
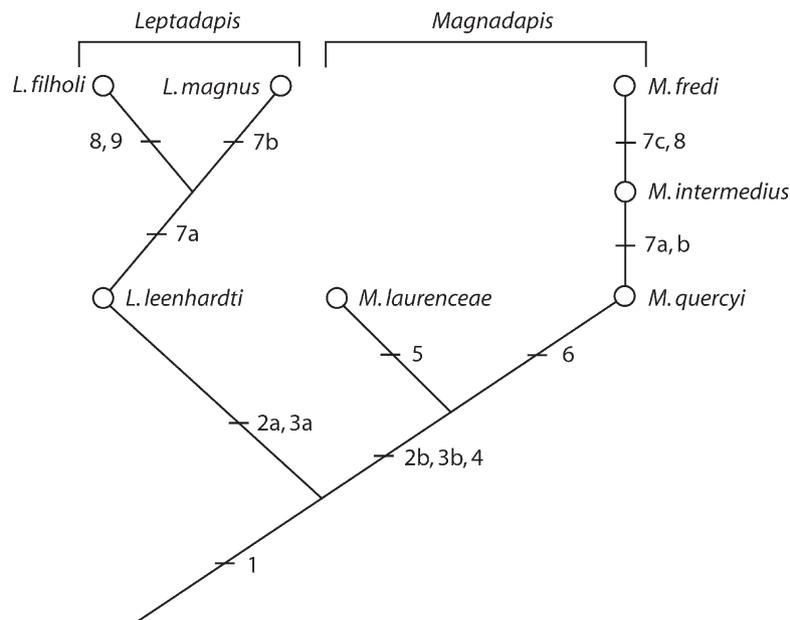
FIGURE 12.11. Schema showing our working hypothesis for large adapine phylogenetic relationships primarily based on cranial characters, with the addition of some dental traits. The characters corresponding to numbers are: orbits larger than in *Adapis* (1); weak interorbital breadth (2a) and greater interorbital breadth (2b); moderate hypocone size on molars (3a), and a decrease in hypocone size (3b); enlargement of M3/ (4); decrease in orbit size (5); broadening of the muzzle (6); moderate (7a) and more marked (7b) development of cranial superstructures, and very strong cranial superstructures including an exaggerated height of the anterior zygomatic root (7c); molarization of the upper premolars (8); lengthening and increase in size of the hypocone on M2-3/ (9).

12.5 Character Polarity and Relationships Between *Leptadapis* and *Magnadapis*

Comparing species of *Leptadapis* and *Magnadapis* might suggest something about character polarity and possible ancestral states. We found in both genera a morphocline from smaller animals having less developed cranial superstructures and an anteroposteriorly shorter skull (primitive) to species of larger size, more developed superstructures and long skulls (derived). These morphoclines would be *M. laurenceae-quercyi- fredi* and *L. leenhardti-filholi-magnus*. For reasons explained above, these morphoclines cannot be simple lineages of species. However, by comparing the most primitive species in each genus, or species having characters intermediate between the two genera, we might try to suggest hypotheses for other characters. *L. filholi* has a broad palate and a broader and higher muzzle than other *Leptadapis* species. Could this be a link with *Magnadapis*? We do not think so. As seen quite clearly with dental characters, especially the M1/ (Figure 12.5), we consider *L. filholi*, which has moderate cranial superstructures, as autapomorphic for its dental and muzzle characters (Figure 12.11).

Comparison of the primitive *L. leenhardti* to *M. laurenceae* does not suggest a place for the latter. Both have a very low sagittal crest, generally weak cranial superstructures, and a relatively narrow muzzle and palate. Both are anteroposteri-

orly short. For all these characters, they are likely primitive. However, the two genera were already well separated, as shown by the broad interorbital breadth, the higher muzzle, and the alveolar rim arcuate and curving upward anteriorly in *M. laurenceae*. *M. laurenceae* has a transversely elongated M3/ and a lingually broad P4/, as do other species of the genus. The bizarre character of *M. laurenceae* is its smaller orbit, which is also smaller than in other *Magnadapis* species (except possibly *M. fredi*). By comparison with *Adapis*, and because it is associated with the very posterior frontal line junction, it could be primitive for large adapines. However, in that case, convergence would have occurred for orbit size increase in both genera. This is not parsimonious. Branching of *M. laurenceae* before the split between *Magnadapis* and *Leptadapis* would appear even less parsimonious, implying convergence in all the derived characters defining *Magnadapis*. More probably, a secondary decrease in orbit size, a reversal, appeared in the lineage leading to *M. laurenceae* (Figure 12.11).

We did not fully elaborate on the polarity of dental characters. This appears as a complex task. The inclusion of *Paradapis ruetimeyeri*, which is the oldest large adapine species, might suggest polarities opposed to those chosen by us for some dental characters. This species has molars with very large hypocones, and the P4/ is highly molarized (Stehlin, 1916). However, these teeth differ from those of the crania studied here. They are not close enough to suggest a reversal of our dental polarities, which

would imply a reversal in cranial trends. The resulting cranial gracilization required in large adapines seems very unlikely to us. Figure 12.11 shows our working hypothesis for the phylogeny of these species. It is primarily based on cranial characters, with the addition of some probably meaningful dental evidence. It is not yet placed in a stratigraphic frame, and future work might make it more complex (e.g., if the Euzet assemblage turned out to differ from *M. fredi*).

12.6   Preliminary Morphometric Study

The preceding systematic analysis is based on one quantitative analysis, the allometric approach of interorbital breadth by Lanèque (1993), and otherwise entirely on qualitative observations. In order to more quantitatively assess our material, we tried two different approaches using geometric morphometrics: (1) one using the seven fossil crania possessing a postorbital bar, to see if a quantitative approach would confirm our groups or not; and (2) a second one including our fossil sample and living species, to see if, by comparison with intraspecific variability in skull shape, we might have overestimated the number of species.

All data acquisition was done by taking three-dimensional coordinates of landmarks, using an Immersion Microscribe, three-dimensional point digitizer. For the first analysis, 38 points were digitized on the fossil skulls (Figure 12.12). Some points were missing on the most incomplete specimens. Some methods now are available for morphometrics with missing data and fossil reconstruction (Gunz et al., 2004). However, these methods require a reference-specimen (while none of our specimens can be considered as a reference), and are not appropriate for small samples. As the method used for this study does not work with missing points, we chose, when breakage of specimens did not allow real measurements, to visually estimate where the missing landmarks would have been. To attenuate the subjectivity introduced by these estimates, all measurements and estimates were done twice and each specimen used as two different individuals. This on one hand artificially increases the sample, and on the other hand reveals uncertainties due to estimation by showing, for the most incomplete skulls, an increased distance between the two points of one specimen (Figures 12.13, 12.14). Data were treated by Generalized Procrustes Adjustment, and Procrustes residuals were used in a principal component analysis (PCA, Gower, 1975). The first three axes of the PCA explain 33.86% (first axis), 25.39% (second axis) and 11.23% (third axis) of the total variance. Scatter diagrams of the specimens along the first two axes are given in Figure 12.13. We tested the possible effect of autocorrelation introduced by using each specimen two times. The same analysis was performed with one point for each specimen. It gave similar results and scatter diagrams. The difference in the variance explained by the axes in the two analyses is between 2.4% and 4.9% of the total variance. With an effect lower than 5%, we consider that

autocorrelation is not a serious problem of our analysis. A hierarchical classification analysis was performed in order to evaluate the influence of estimated landmarks. Both measurements of each specimen were always grouped together, testifying that error due to landmark estimation is very low in comparison with interspecimen morphological variation. Lastly, we realized that the distribution along the two principal axes appeared driven by two specimens, MaPhQ 210 and MaPhQ 211, which are clearly less well-preserved than the others. The two points for each specimen are more separated than for other specimens, suggesting the influence of missing point reconstruction. Hence we performed an analysis without these two specimens (Figure 12.13B). It is discussed below.

In order to understand the meaning of the first axes, we extracted the variables driving them (weight over 0.7) and we studied their correlation with size. In the first analysis including the two damaged Montauban specimens, the first axis shows a significant correlation with size (correlation coefficient of 0.70; $p < 5\%$), whereas the second axis is not significantly correlated with size (0.32). For the first axis, the negative pole is influenced among others by three landmarks linked to the breadth of the posterior part of the palate (13, 16, 17), and two landmarks linked to interorbital breadth (19, 24), suggesting that *M. fredi* differs from other *Magnadapis* in being extreme for these characters. The positive pole raises the question of a possible difference in the height of the posterior part of the skull (33, 34, 35), which needs to be confirmed. The second axis separates *Magnadapis* specimens, below, from the specimens ascribed to *Leptadapis* above (with MaPhQ 211, distorted specimen, probably pushed more distantly by missing points). The negative pole of the second axis is influenced by the height between palate and orbits (12, 16, 17, 21, 18, 28), and by the anteroposterior length of the bullar region (9, 34, 35, 36). The positive pole seems influenced by the overall breadth of the skull (3, 4, 5) and also raises a question concerning a possible difference in height of the frontal line (3, 4, 23).

The scatter of specimens along the third axis (not shown here) spreads individuals between the *L. magnus* type specimen (positive pole) and QU 10870 (negative pole), specimens which are not distorted (however the former has no intact zygomatic arch). This axis better separates *L. leenhardti* and *L. filholi*, which were close to each other on the preceding diagram; it also widely separates QU 10875 and QU 10870, which were very close on the other diagram. There is probably some interesting signal here. Among the characters influencing this axis are, for the negative pole, M1/-M2/ length (16, 17), height of the posterior plane (6, 7), and for the positive pole canine projection (15), breadth of the postbullar region (34, 36).

The analysis performed without the two most damaged specimens (Figure 12.13B) shows an overall similar scatter, but with some interesting differences. Along axis one, QU 10875 is now well separated from QU 10870 (differences between *M. quercyi* and *M. intermedius*). Two other speci-
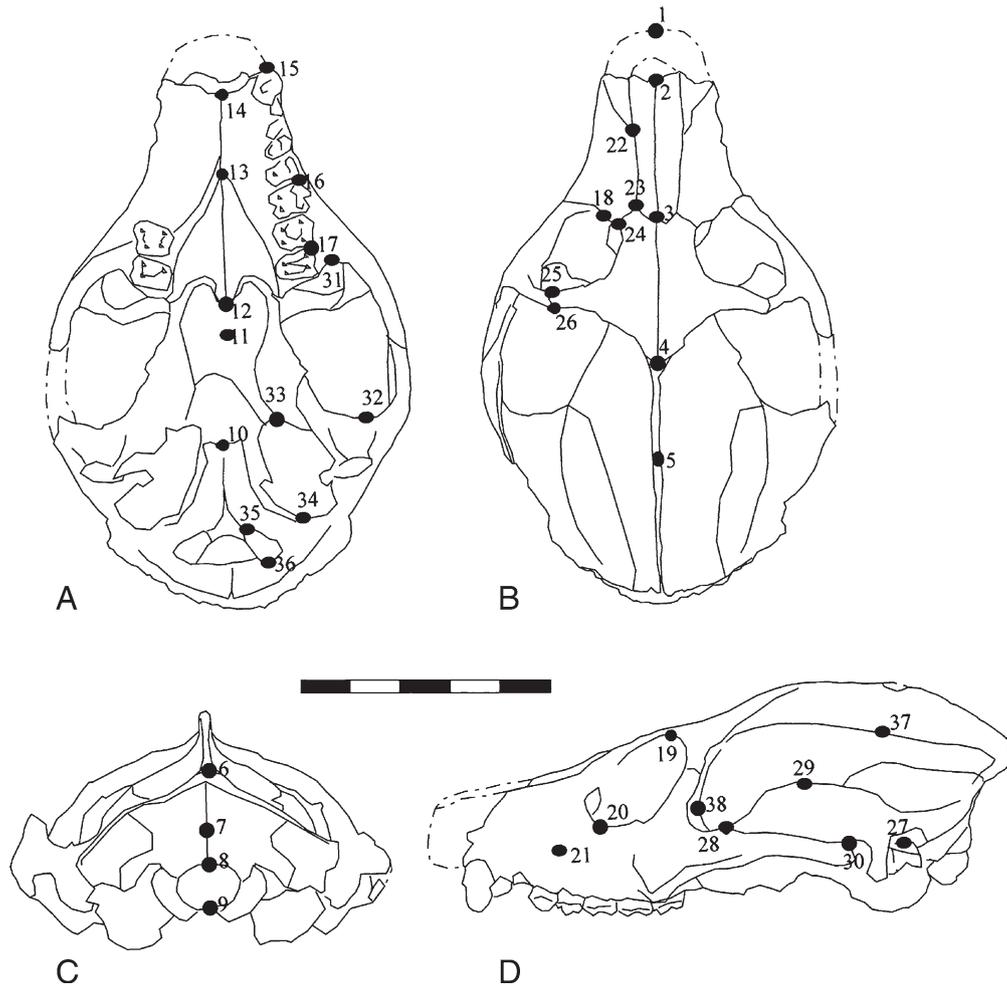
FIGURE 12.12. Schematic drawings of a *Leptadapis* cranium in ventral (A), dorsal (B), posterior (C), and lateral (D) views, showing all the landmarks used in the morphometric study (listed in Table 12.2). Scale bar is 5 cm.

TABLE 12.2. Listing of the 38 landmarks digitized for each cranium (all the measurements were performed on the left side of the cranium). Asterisks indicate the 21 points which are used in the analysis of adapines and *Alouatta* species.

Number	Definition	Number	Definition
1*	Interincisors	21*	Infraorbital foramen
2*	Summit of the nasal opening	22	Suture nasal/maxilla/premaxilla
3*	Nasion	23	Suture nasal/maxilla/frontal
4*	Bregma	24	Suture maxilla/frontal on the rim of the orbit
5	Summit of the sagittal crest	25	Suture frontal/zygomatic on the lateral rim of the orbit
6*	Lambda	26	Suture frontal/zygomatic on the rim of the temporal fossa
7*	Inion	27*	Porion
8*	Opisthion	28*	Suture zygomatic/squamosal on the upper rim
9*	Basion		of the zygomatic arch
10	Suture basioccipital/basisphenoid on the midline	29	Summit of the zygomatic arch
11	Suture basisphenoid/ presphenoid on the midline	30*	Suture zygomatic/squamosal on the lower rim
12*	Suture of the palatines on the midline		of the zygomatic arch
13*	Suture maxillas/palatines	31	Anterior point of the temporal fossa
14	Suture maxilla/premaxilla on the palate	32	Posterior point of the temporal fossa
15	Suture maxilla/premaxilla on the face	33*	Anterior point of the tympanic bulla
16	Proximo-vestibular point of the P4/ alveolus	34*	Posterior point of the tympanic bulla
17	Proximo-vestibular point of the M3/ alveolus	35*	Anterior point of the occipital condyle
18*	Suture maxilla/zygomatic on the rim of the orbit	36*	Posterior point of the occipital condyle
19*	Summit of the orbit	37	Median point on the braincase (same height as point 5)
20*	Base of the orbit	38	Maximum of constriction between the braincase and the face
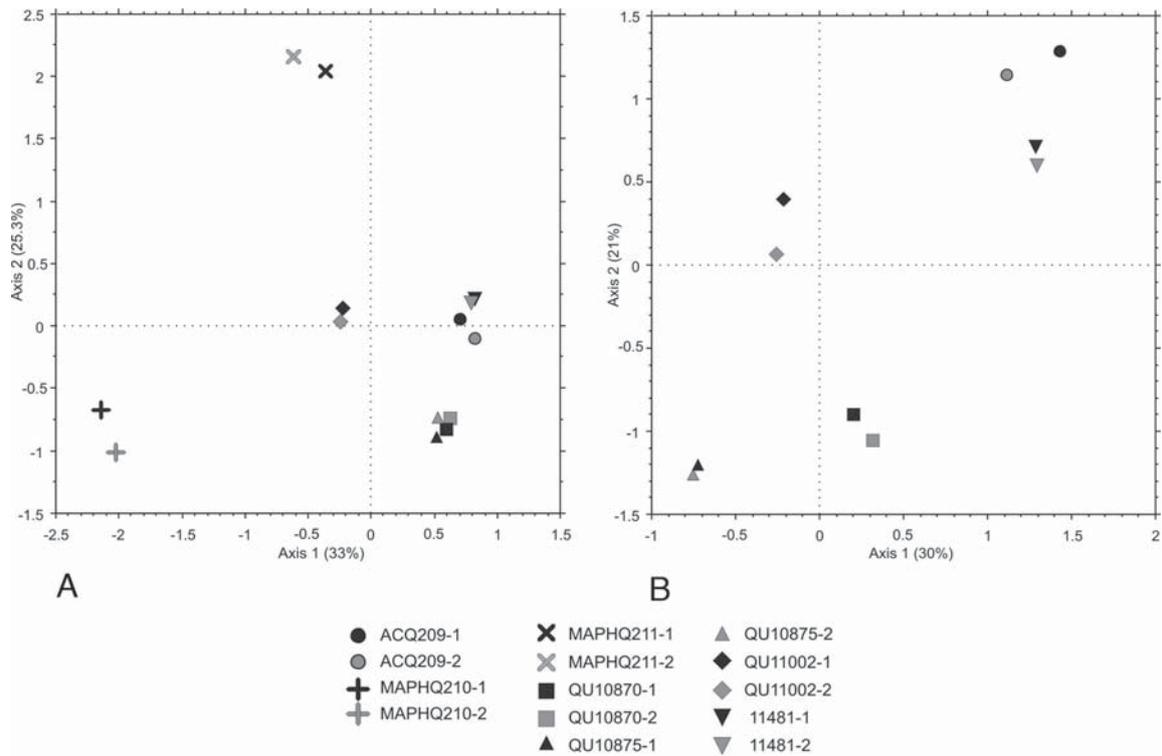
FIGURE 12.13. Scatter diagrams of large adapine crania along the two first axes of the principal component analysis of Procrustes residuals (38 landmarks); each cranium is represented by two points corresponding to two different sets of measurements. Analysis with the seven best preserved crania (A), in which the two points for MaPhQ 210 and MaPhQ 211 are relatively distant (influence of estimated missing points). Analysis without the two most damaged specimens (B). In both analyses, axis 2 separates *Leptadapis* specimens (top) from *Magnadapis* specimens (bottom).
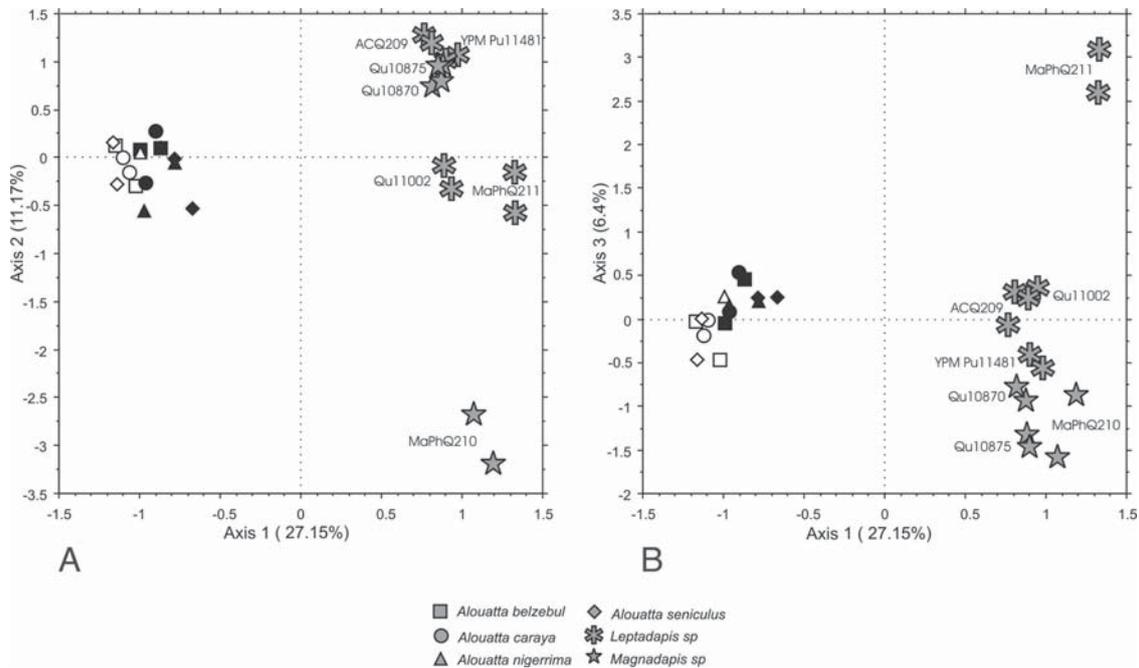
FIGURE 12.14. Scatter diagrams of a set of crania of four species of *Alouatta* and of the large adapine crania along the three first axes of the principal component analysis of Procrustes residuals (21 landmarks); first and second axes (A) and first and third axes (B). Female *Alouatta* are figured in white, and male *Alouatta* are figured in black; fossils are of unknown sex and are shown in grey.

mens now show a distance between their two measurements, ACQ 209 along axis one, and QU 1102 along axis two, revealing that estimated points still play a role. The two first axes explain a somewhat inferior percentage of the total variance, respectively 30% and 21%, and this time the first axis does not appear correlated with size. The variables driving the distribution were extracted (weight over 0.7). The negative pole of the first axis (*M. quercyi*) is again driven by a majority of seven variables in breadth (9, 10, 11, 13, 16, 17, 19), and also five variables in length. The positive pole better isolates two *Leptadapis* specimens. It is influenced by a great majority of eight variables in length (2, 5, 6, 13, 15, 23, 27, 35), against two in breadth and two in height. Axis two separates more clearly than in the preceding analysis the two *Magnadapis* specimens (below) from the three *Leptadapis* specimens (above). This is very interesting. The negative pole, toward *Magnadapis*, is influenced by seven variables in height, again suggesting differences between the palate and the orbit and infraorbital foramen (landmarks 12, 14, 15, 16, 17, 18, 21), five in length (including three posterior landmarks 9, 34, 36) and three in breadth. The positive pole, toward *Leptadapis*, gives an even clearer signal, with six variables in height, two in length and two in breadth. Almost all the variables in height are between the orbit and the frontal (landmarks 3, 4, 19, 20, 23). This analysis completes the distinction of the two genera. The latter were distinguished based on interorbital and muzzle breadth. This analysis adds shape differences in height between the dorsal frontal line, the base of the orbit and the palate. Visual inspection confirms marked differences in the anterior part of the cranium. Facial height is greater in *Magnadapis*, lower and tapering more anteriorly in *Leptadapis*. This is clearly seen in comparing specimens of similar length and cranial superstructures, as *L. magnus* (Figure 12.6B) and *M. intermedius* (Figure 12.8C).

Our second study attempts to compare these fossils with some living primates. Using the data base of one of us (S.C.) on living platyrrhines, we selected the genus *Alouatta* as being the most dimorphic platyrrhine genus, and the closest to large adapines in terms of overall size. Landmarks in common between the study of adapines and that of platyrrhines include 21 points (Table 12.2). In order to equilibrate the two samples, we used a sample of 15 adult *Alouatta*. A Generalized Procrustes Adjustment was done and a PCA analysis of Procrustes residuals. Scatter diagrams of specimens along the three first axes are given in Figure 12.14. In fact, we did a first analysis, not shown here, with a sample of 14 adult *Alouatta seniculus* (7 males and 7 females). The results were very similar. The only difference was that the *Alouatta* sample was more concentrated than in Figure 12.14, less spread along axis two. In order to increase the morphological variation in the living genus, we performed a second analysis with 15 individuals (7 females and 8 males) pertaining to four different species (Figure 12.14). Axis one clearly separates howling monkeys from large adapines. One third of the variables have a significant weight, almost all points are affected. This is not surprising: the morphologies of the two groups differ profoundly.

Along this axis, female *Alouatta* (on the left) are almost separated from the males (on the right), whereas species of *Alouatta* are not isolated. The distances between the extremes within the two groups are similar. Axis two separates large adapines into three groups which are clearly spread more distantly than the sample of four different howler monkey species (not separated on this axis either). Even taking into account that MaPhQ 210 is damaged, and the distance between its two points indicate some influence of reconstructed landmarks, there seems to be a clear signal: the distinction of *M. fredi* from all the others confirms our analysis of this species as being extreme in the morphocline of cranial superstructures and/or muzzle height, and suggests that it may warrant generic distinction. However, this axis does not separate our two proposed generic groups. Interestingly, despite the shift toward the right of MaPhQ 211 (deformed specimen), this specimen groups with the *L. magnus* type specimen, which agrees with our systematic choice. Axis three again shows the species of *Alouatta* grouped together, and the large adapines more regularly spread (with the exception of MaPhQ 211, probably linked to missing points). Along this axis (Figure 12.14B), the three *Magnadapis* specimens appear on one side, toward the bottom of the diagram, and the four *Leptadapis* specimens on the other side, above, suggesting a possible systematically meaningful signal. These results are appealing, however we need to be cautious because there is clearly a strong influence of missing points (MaPhQ 211 very isolated, and the two points for MaPhQ 210 quite apart from each other). We defer a more precise morphological interpretation to future analyses avoiding the influence of missing points.

On the whole, these first geometrical morphometric attempts show two probably significant results. The comparison of the large adapine skulls with those of several *Alouatta* species suggests that the large adapines show a higher morphological disparity than several living species of one genus, giving further quantitative confirmation that two genera can be distinguished among them. The two studies also suggest that the two proposed genera can be quantitatively separated by shape variables, along axis 3 in the second study, and along axis 2, independent of size, in the study including only adapines. The results helped the recognition of major differences in facial height between the two genera. Other results call for further examination of other quantitative characters. However, Procrustes methods are poorly suited to locate shape differences. Further elaboration on these results will require more precise analyses avoiding missing points, a search for new landmarks which would better reflect some of the peculiar morphological differences analyzed here (e.g., distance between braincase and frontal rims), and the use of other methods.

12.7 Summary and Perspective

The large adapine skulls are for the first time subjected to a global study. We propose to distinguish among them two genera, *Leptadapis* and *Magnadapis*, and seven species. We

also propose a first phylogenetic hypothesis for these species (Figure 12.11). The proposed lineage *M. quercyi – M. fredi* is parsimonious in minimizing the number of cladogenetic events. A different chronological succession would imply a higher number of lineages.

Our proposed lineage *M. quercyi – M. intermedius – M. fredi* stands in marked opposition with earlier hypotheses explaining cranial differences between the large adapines by sexual dimorphism (Gingerich, 1981; Gingerich and Martin, 1981). We emphasize that differences in this lineage affect not only cranial superstructures, but also facial height, which must result from phyletic evolution. Also, the differences in the canines of these species mainly reflect an evolution in canine robustness (length and breadth). There is no clear evidence between putative male and female cranial pairs of the strong canine size difference, including canine height, that should be present if large differences in cranial superstructures had been due to sexual dimorphism. This view agrees with the absence of canine dimorphism found in the largest adapine assemblage known from one locality, Euzet-les-Bains (Gingerich, 1977). We interpret the increase in canine size and robustness in this lineage as a phyletic trend paralleling the other cranial trends. However, some intraspecific canine size variability is suggested by the two muzzles. Canine dimorphism is still a possibility in large adapines, but in our opinion it would not be sufficient to explain the marked cranial characters that we used to define different species.

Our comparisons lead us to suspect that *"L." assolicus* is closely related to *Cryptadapis* and to return *"L." stintoni* to genus *Adapis*. This gives an interesting indication concerning the possible age of the largest *Adapis* species created by Stehlin (1912), and emphasizes the diversity of *Adapis* species in the latest Eocene (MP 19-20). It also restricts the known distribution of large adapines to older levels (MP 14-18).

The lineage *M. quercyi – M. fredi* may have been of relatively short duration. Its adaptive evolution and that of *Leptadapis* species possibly was a reaction to environmental change. The Perrière fauna (MP 17a) includes a large adapine and reveals the first signs of aridity, probable dry seasons, and less forested environments in the Quercy region (Legendre, 1987, 1989).

Our phylogenetic hypothesis will have to be confronted with other possible character interpretations. It will be important to study the possible effect of growth and aging on characters of the cranial superstructures, and also to further scrutinize the possible effect of sexual dimorphism on these characters. Until now, lack of provenance of the skulls of the old Quercy collections prevented a sound estimation of these factors, because we do not know how many samples they represent. Further scrutiny of the historical provenance of some might lead us to delineate possible assemblages (the Moscow skull and Paris specimens for example). Also, more complete phylogenetic analyses including *Adapis*-sized skulls should be done in the future. They might alter some of the character polarities which have been endorsed here.

The evolutionary history of large adapines appears as complex as that of the smaller adapines which diversified at the end of the Eocene (Lanèque, 1992a, b, 1993; Bacon and Godinot, 1998). Study of the dental material of the new Quercy collections and from some stratified localities will help to estimate the intraspecific variability and thus the systematic value of dental characters. It will also help us to understand the polarity of dental characters.

The dental record in its biochronological framework cannot provide a real Popperian test of hypotheses based on skull characters, because we are interpreting historical, and not experimental, data. Nevertheless, it should provide crucial arguments for the elaboration of understandable and parsimonious historical narratives of large adapine evolution during the late Eocene. This evolution already appears as a history of diversification, size increase, cranial superstructure development and dental specialization linked to diet. An increase in adapine lower molar cresting through time is documented, suggesting a folivorous adaptation, however the enormous cranial superstructures of some of them have yet to be fully explained. Certainly, more will be extracted from the study of this beautiful collection of Eocene primate skulls when analyses are extended to a richer dental record.

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