K-strategy and adaptative specialization in *Steneofiber* from Montaigu-le-Blin (dept. Allier, France; Lower Miocene, MN 2a, ±23 Ma): first evidence of fossil life-history strategies in castorid rodents

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Abstract

The fresh-water limestone deposits of Montaigu-le-Blin yielded a small pocket containing almost exclusively cranial and post-cranial elements of the castorid *Steneofiber*. A full inventory of these skeletal remains makes it possible to recognize an assemblage of two adults and eight juveniles of two different ages. It corresponds well to a family group of the extant beaver, usually consisting of an adult breeding pair together with a variable number of yearlings and kits; consequently this pocket is interpreted as a fossil burrow containing the catastrophic death-assemblage of a *Steneofiber* family, and we infer a K-strategy model of reproductive pattern for this genus. Moreover, a minute fossil ungual phalanx corresponds well to the "combing-claw" of the extant beaver and suggests the development of non-wettable fur, an important adaptation to a semiaquatic way of life. The shape of the fossil caudal vertebrae, without the wing-like transverse processes of *Castor*, indicates that the tail of *Steneofiber* was cylindrical, however.

1. Introduction

Oligo-Miocene fresh-water indusial limestone deposits cover a wide area in the Limagne basin (French Massif Central) and have been excavated for cement for a long time; Geoffroy-Saint-Hilaire (1833) was the first author to describe mammalian remains in the Miocene of Saint-Gérand-le-Puy. During more than 150 years, an abundant fossil fauna, particularly aquatic avifauna, was collected from the numerous quarries that covered the area around the two localities of Montaigu-le-Blin and Saint-Gérand-le-Puy (Cheneval, 1989; Hugueney et al., 1990). In his paper, Geoffroy-Saint-Hilaire (1833) created the genus *Steneofiber*, thus recog-

nizing the affinity of this form with the extant castorid rodent *Castor fiber*.

It is worth noting that *Steneofiber* is not the most ancient castorid genus known in Europe because it is preceded by *Asteneofiber* (Kretzoi, 1974), with the species *A. butselensis* from Hoogbutsel (Misonne, 1957), known as early as the beginning of the Oligocene (±34 Ma). The family Castoridae appeared almost simultaneously in North America with the genus *Agnotocastor* and is reported in the Oligocene of Asia with the genus *Propalaeocastor* (Stirton, 1935; Hugueney, 1975). Today, this family contains only the genus *Castor*, well adapted to an amphibian way of life but, due to human activities, seriously reduced or

even disappeared over most of its former range both in America and in Eurasia. During the Tertiary, this family was much more diversified: nearly ten genera are known from Europe (Kotsakis, 1989) and, during the Early Pliocene, four different genera could coexist in the same locality (Franzen and Storch, 1975). In North America, where a dozen genera are known from the Tertiary, an Early Miocene evolutionary radiation of the family led to a number of forms adapted to burrowing in dry sandy uplands where they dig the helicoidal structures named *Daimonelix* (Martin, 1987, p. 73).

In the Saint-Gérand-le-Puy area, most of the earlier collected material was in the form of isolated pieces, found by chance by quarrymen and generally sold to paleontologists; more scientific collecting started recently and has shown that all the fillings were not equivalent, some providing a mixture of mostly aquatic forms, others predominantly terrestrial ones and even some pockets containing almost exclusively the remains of a unique species (Bucher et al., 1985).

Recently, in Les Pérards quarry, near Montaigu-le-Blin, a new small undisturbed pocket was discovered about half way up the roughly 30-m-high cliffs (by a young man practising roping down). As he saw cranial remains crushed on the walls (Fig. 1a), he collected all the sediment contained in the pocket; the washing and screening (through a 0.5 mm meshed sieve) of these greenish marls provided almost exclusively bones and teeth of *Steneofiber* (with some bones of aquatic birds) including minute skeletal elements; their attribution to *Steneofiber* can be confidently assumed as a unique species is represented, and, moreover, as there is great similarity with the corresponding bones of the extant *Castor*.

The study of this material provided an opportunity to approach the population structure and to have a better knowledge of the adaptative modifications in the post-cranial skeleton of *Steneofiber*.

2. Bone assemblage and population reconstruction

In the material of *Steneofiber*, recovered from Les Pérards, numerous cranial and postcranial elements were mixed together (skull fragments, maxillae, mandibles, isolated teeth, vertebrae, ribs, limb bones, phalanges of both right and left sides), mandibles, humeri and femora being the most abundant; it was obvious that they represent the remnants of the entire skeletons of several animals which had been burried simultaneously. A full inventory of these skeletal remains was undertaken to answer the question of how many individuals were represented.

It was also obvious at first sight that there was a mixture of juvenile and adult bones. It was possible to divide the mandibles (and maxillaries) into three age classes: (1) adult mandible with permanent tooth (P4) in use; (2) juvenile mandible with erupting P4; (3) juvenile mandible with lacteal tooth (D4) in use (Fig. 1). The measurements of the few complete jaws do not show any clearcut size variation that could be related to a sexual dimorphism: in the two adult maxillaries, the length of left P4 – M2 is 120 and 122 mm, respectively. In extant beavers, the female is usually slightly larger than the male, but, as the individual growth lasts at least four years, it is not possible to recognize a sexual dimorphism on the size.

Immature fossil bones, with incompletely fused epiphyses, were abundant and distributed into two size classes, the length of the smaller being roughly two thirds of the bigger ones. They can confidently be interpreted as corresponding respectively to the two classes of juvenile jaws. The numerical analysis of the more characteristic bone elements present in the sample is shown in Fig. 2. The minimum number of individuals, taking into account the age classes, is 10, 2 adults and 8 juveniles of two different ages (3 with erupting P4—yearlings, 5 with D4—kits).

The extant beavers are known to live in family

Fig. 1. (a) Adult cranium (left), juvenile cranium with erupting P 4 (right), isolated incisor and proximal end of a right femur of *Steneofiber*; all these skeletal remains were crushed on the pocket wall, constituted of an aggregate of small mollusc shells bound together by a calcareous crust (no. FSL 97870, Univ. Lyon coll.). (b) Juvenile mandible with brachyodont D4 in use (kit); labial view (b) and occlusal view (b') (no. FSL 97871, Univ. Lyon coll.). (c) Juvenile mandible with erupting hypsodont P4 (yearling); labial view (c) and occlusal view (c') (no. FSL 97872, Univ. Lyon coll.). Scale bars represent 1 cm.

N in each class of age	adults		yearlings			kits				
	1	2	1	2	3	1	2	3	4	5
Total N of individuals	1	2	3	4	5	6	7	8	9	10
right upper jaw	+	+	+	+						
left upper jaw	+	+	+							
right lower jaw						+	+	+	+	+
left lower jaw			+	+		+	+			
right humerus			+	+	+	+	+			
left humerus			+			+	+			
right ulna						+	+			
left ulna		+			+					
right femur						+				
left femur			+	+		+				

Fig. 2. Minimum number of individuals reconstructed after the number of representative remains.

groups formed of an adult breeding pair with yearlings and kits; beavers have from one to eight kits (usually four or five) and one litter is born per year; the juveniles remain with their parents until the second breeding season following birth and then disperse from their natal group. In lakes or ponds beavers build lodges, but in rivers they usually dig burrows into the river banks and floods can adversely affect beaver populations (Mc Laughlin, 1984). Thus the fossil assemblage corresponds well to a beaver family and is consistent with a model of a catastrophic death assemblage: many young and middle-aged individuals and few old individuals (Korth and Evander, 1986); a likely hypothesis is that catastrophic flooding could have killed this castorid family in his bank den and have been responsible for the simultaneous burial of the skeletons. In the state of the art, it seems that a fossil family group of beavers is recognized for the first time. We have to notice, however, that in the Lower Miocene of North America, remains of fossil fossorial beavers were found in the horizontal parts of the helicoidal burrows called *Daimonelix* and it was concluded that they were used as living chambers (Martin and Bennett, 1977). Moreover, Martin and Bennett mentioned "on the basis of the discovery of remains of young beavers within them, we can

also infer that young were raised in this type of living chamber" (Martin and Bennett, 1977, p. 186). However, even if they suppose parental investment in the breeding of the young, we have to emphasize that, in Montaigu-le-Blin, a two-years-long parental care system can be demonstrated (Fig. 3). As the number of yearlings is less than that of kits, we can also get an idea of the juvenile mortality, hypothesizing a constant litter size.

The finds of Montaigu-le-Blin give us an insight into a number of components of the life-history strategy of *Steneofiber*:

- fecundity: one litter per year;
- litter size: at least five kits;
- juvenile mortality: $\pm 40\%$;
- degree of parental care: a two-year parental investment;
- age at first reproduction: 2nd year after birth.

We can infer that, as early as the Early Miocene, *Steneofiber* favoured maximum efficiency in the use of resources by high parental investment in the production of a few highly competitive offspring with delayed maturity; the evolution of its reproductive strategy was finished and completely fits with the model of K strategy defined by Mac Arthur and Wilson (1967); in this case, the possibility to evolve on a continuum r–K (Pianka,
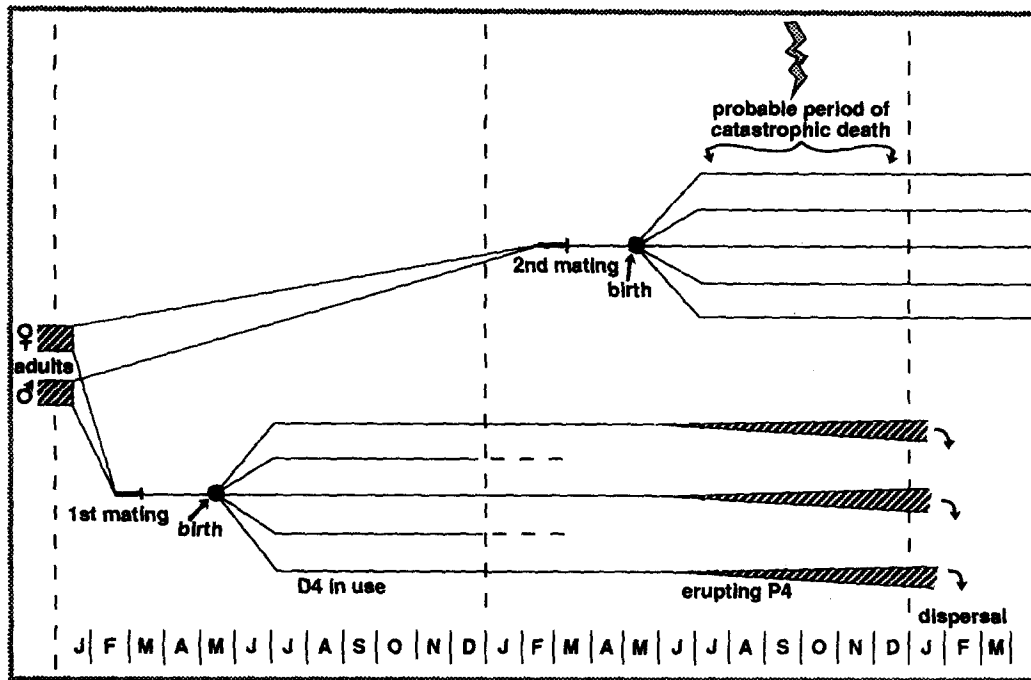
Fig. 3. The two-year long breeding pattern of *Steneofiber* with an approximate timing of the development of the youngs and of the catastrophic death.

1970) seems to be definitely excluded as the reproductive pattern of the castorids remained stable up to now. Thus, this exceptional fossil record provides a temporal evidence of behavioral evolution and demonstrates that fixed kinds of behavior can persist over long periods of evolutionary time and that care of current offspring with fitness consequences provides an advantage in long-term reproductive success; but, concurrently, beavers lose their plasticity for selection and become unable to respond to major environmental variations. As ecological variables and behavioral strategies are interdependent, we can infer that this evolution of social behavior toward monogamous pairing and cooperative breeding was related to a locally stable but saturated habitat offering limited access to breeding territory. The evolution in life-history strategies of castorids led them to become habitat specialists with the selection of habitat structures that have been retained up to now (bank burrows). As the "Indusial Limestone Formation" of Montaigu-le-Blin is known to be of fluvio-lacustrine origin and as the few other fossils found

in the pocket together with *Steneofiber* are hydrophilic vertebrates (aquatic birds: gulls, ducks, flamingos, crakes and fishes) we can infer that the fossil beaver burrow was close to a body of fresh water; at the moment, however, there is no evidence whether it was a streamside burrow, as is often the case in modern beavers, nor that *Steneofiber* used to build dams with the help of its family as beavers do nowadays.

It is interesting to emphasize that roughly at the same time (Late Oligocene–Early Miocene) North American castorids underwent extensive radiation that led them to develop a variety of fossorial adaptations and to select a completely different environment, i.e. dry and sandy uplands. Thus, at that moment, the castorids were still able to respond to presumably different evolutionary pressures and to select two completely opposite habitats. Of these two branches of specialization, the fossorial one vanished rapidly (end of the Arikarean, ±20 Ma; Martin, 1987) while the aquatic one flourished during the Miocene and is continuing its evolution today.

3. Adaptations to aquatic life

As soon as they arrived in Europe at the beginning of the Oligocene, castorids seem to have a preference for wet habitats; in Hoogbutsel the dark grey marls with black bones imply a humid habitat ("paysage poldérien" in Quinet and Misonne, 1965) and during the Oligocene they are generally associated with stratified limnic layers, with the exception of the *Steneofiber* of Gaimersheim which is perhaps the only aquatic castorid to be found in karstic fillings. But castorids are very rare during the Oligocene and it is only at the beginning of the Miocene that they become abundant and that they offer an opportunity for a better understanding of them.

The majority of the long bones of *Steneofiber* have been known for a long time; Gervais (1852) was the first author to mention some characteristics of its humerus, femur and tibia, noticing the similarities of the humerus with that of the extant *Castor*.

The numerous bones recovered from the Saint-Gérand-le-Puy area allowed Filhol (1875) and, more recently, Schreuder (1929, 1951) to carry out studies of the cranium and limb bones of *Steneofiber* based on fairly abundant material and to quote more observations that reinforce the overall correspondence between the two genera; nevertheless they emphasized the fact that the hind limb was proportionally longer in *Steneofiber* than in *Castor* (Fig. 4). Therefore most paleontologists have assumed that the fossil form had a mode of life similar to that of the extant species with the legs used for locomotion, the hind-limb carrying out the main work of propulsion, but additional characteristics of swimming efficiency were unknown.

3.1. Auto-grooming

An important advance in the adaptation to a semi-aquatic way of life is the development of non wettable fur which makes it possible to increase buoyancy by retaining air bubbles and thus reduces body density. Like many other amphibian animals, the extant beaver scratches its fur with its feet (auto-grooming) and coats it with the oily secretion of its anal glands. For this purpose, the second toe—and not the second and third as Grassé said
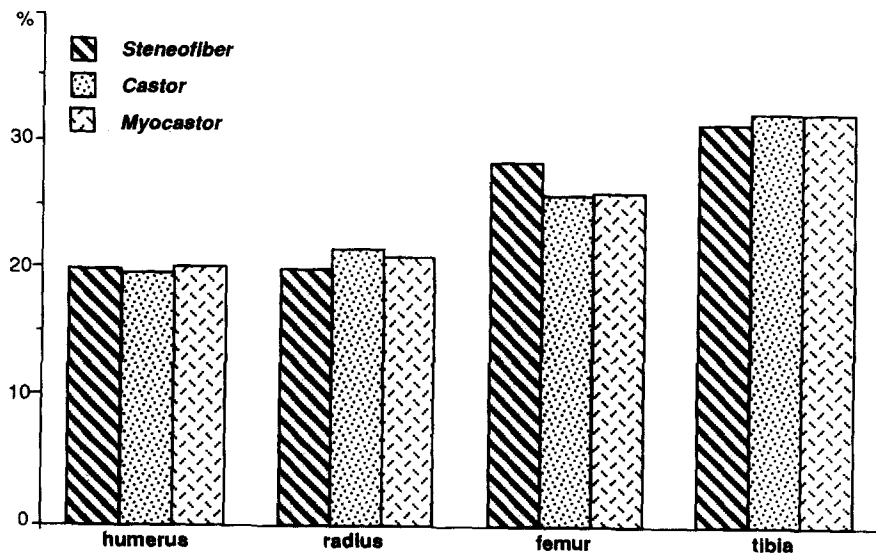

Fig. 4. Relative length of each limb bone in *Steneofiber*, *Castor* and *Myocastor*, given as percentage of the total length of the four bones: the length of the humerus remains relatively constant; the proportions are very similar in *Castor* and *Myocastor*, whereas the femur is distinctly longer in *Steneofiber*; data from Filhol (1879) for *Steneofiber* and from two *Castor* and one *Myocastor* of the collection of the *Université Claude-Bernard*, Lyon.
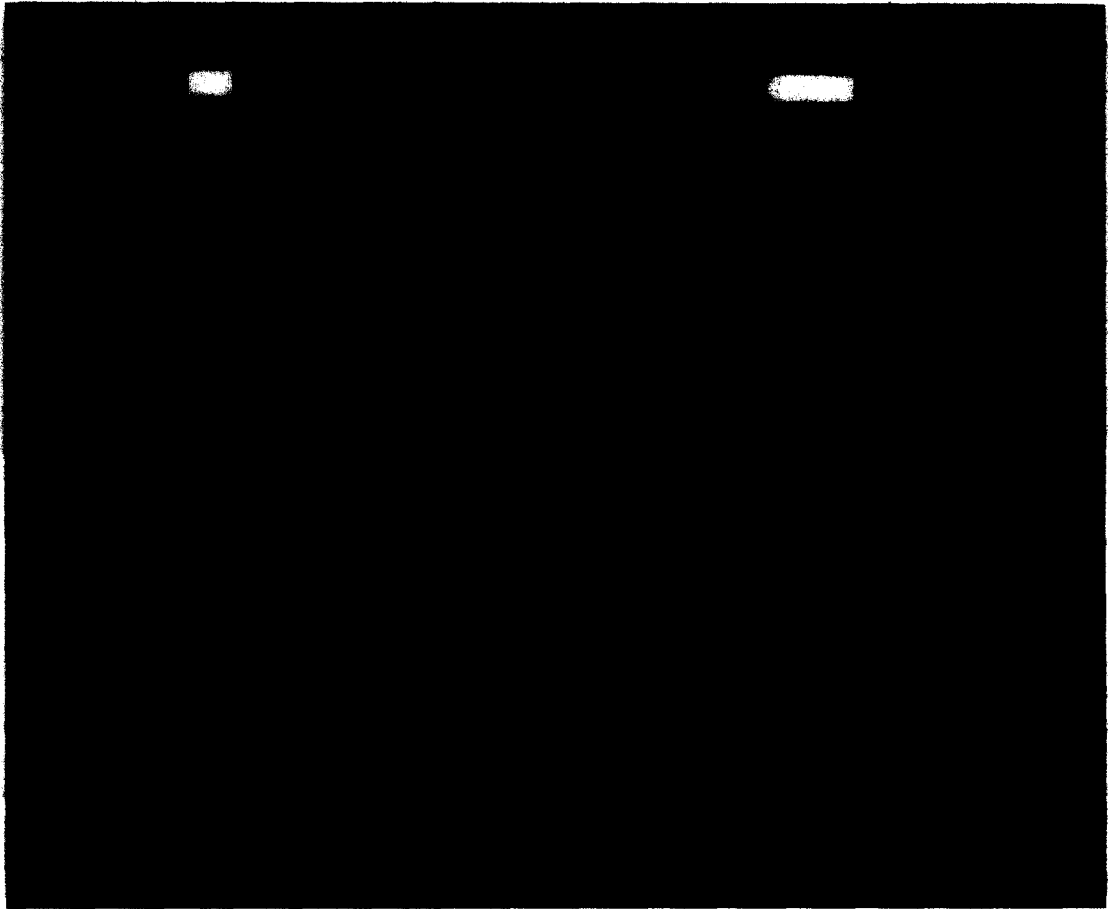
Fig. 5. Ungual phalanx of left digit II of *Castor* (left) and *Steneofiber* (right; no. FSL 97873, Univ. Lyon coll.): (a, b) medial view, proximal is up; (a', b') proximal view; plantar surface is up. Scale bars represent 1 mm.

(Grassé and Dekeyser, 1955, p. 1330) has developed "combing-claws", i.e. peculiar double nails, both parts of each being movable. This adaptation produces skeletal modifications: the second phalanx of digit II shows a pronounced longitudinal torsion with a strongly asymmetrical distal part; but a more pronounced modification is to be seen on the ungual phalanx of this digit II: in this case the articular surface, instead of being smoothly rounded, is deeply and asymmetricaly excavated with a foramen at the bottom of the hollow; as none of the other ungual phalanges of *Castor* exhibit such a foramen, we have to infer an important remodeling of this part of the phalanx in order to enclose additional circulatory and nervous supply. This disposition, associated with an internally curved distal end, provides this phalanx with a very distinctive habitus (Fig. 5a,a').

In the material of Montaigu-le-Blin, recovered by washing and screening, two twisted phalanges could be interpreted as second phalanx of the second toe, permitting us to infer the presence of combing-claws, but none of the ungual phalanges contained in this material corresponded to the morphological design of the combing-claw of *Castor*. A thorough search in the undeterminate material of the "Saint-Gérand" collection in Lyon University led us to recognize a very similarly shaped phalanx, unfortunately damaged at the distal end; its deeply hollowed articular surface, provided with a nutritional foramen, the shape of the ventral process for insertion of tendons of the
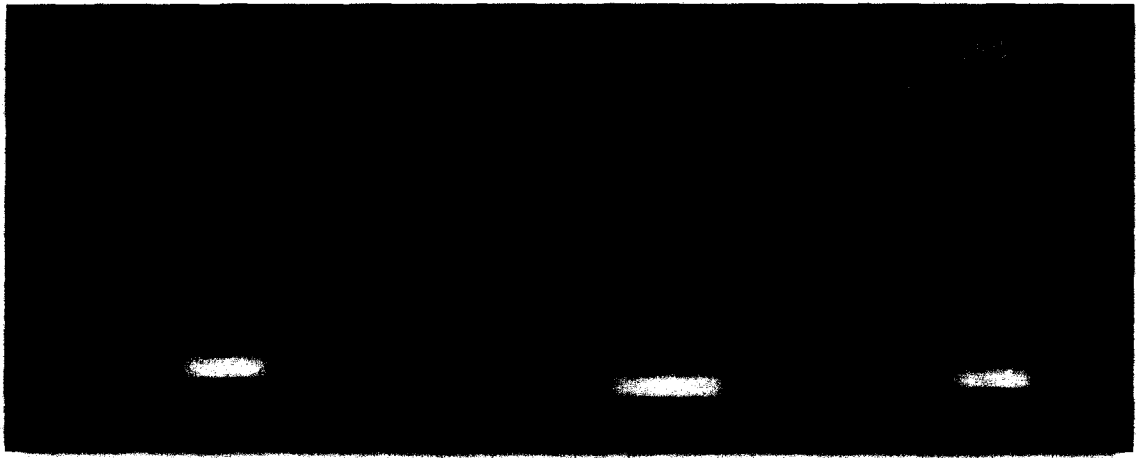
Fig. 6. Caudal vertebrae. (a) *Castor* (18th) showing the lateral wings; (b) immature *Steneofiber* (approximately 12th–15th; no. FSL 97874, Univ. Lyon coll.); and c = *Myocastor* (12th), showing short, flattened transverse processes. Dorsal view; anterior is up. Scale bars represent 5 mm.

digital flexor, its curved habitus and its size closely related to the size of the distal end of phalanx II correspond almost without doubt to *Steneofiber* (Fig. 5b,b′). As it bears also a close resemblance to the corresponding combing-claw of *Castor* we can infer that, as early as the beginning of the Miocene, *Steneofiber* had probably completed the development of a non-wettable fur that permitted it to maintain a nearly horizontal body orientation during swimming without intervention of the forelimbs; like *Castor* and other semi-aquatic mammals, its swimming efficiency was certainly increased by exclusive hind-limb paddling (Fish, 1993).

3.2. Tail habitus

Another autapomorphic feature of *Castor* consists of its flattened tail, a manifold tool used in swimming, in the construction of lodges and dams and also as warning system; morphologically, skeletal modifications of the caudal vertebrae are to be seen and especially, as high as the seventh or eighth caudal vertebrae, the development of winglike transverse processes that persist to the extremity of the tail; they develop, generally, at the proximal part of the vertebral body but, in many cases, there is a doubling of the transverse process by the development of a caudal formation that can fuse with the anterior process (Fig. 6a).

Among the recovered fossil caudal vertebrae, 42 lack the vertebral foramen, which is the case in *Castor* at approximately the eighth caudal vertebra, at the same level as the first wing-like transverse process appears; none of these fossil vertebrae documents the presence of large wings as seen in *Castor* (Fig. 6b). Nevertheless, they are not rapidly reduced to a stick-like vertebral body as it is the case in many other vertebrates; rather they closely resemble the caudal vertebrae of the nutria, *Myocastor coypus* (Fig. 6c), whose tail is cylindrical but whose caudal vertebrae show short flattened transverse processes along the whole length of the vertebral body at the beginning of the tail and then diminish progressively. So the very specialized flattened tail of the beaver was not developed and this is in good agreement with the fact that the *Steneofiber* family was found in a burrow and not in a self-made lodge.

Conclusions

Finally, these recent discoveries show that a 23 Ma old *Steneofiber* family exploited its environment in the same skilful way as the extant beaver,

with a parental care system that produced an interaction pattern, and an advantage for all parties from the shared activities: opportunity for the young to learn about food sources from the parents and from the yearlings, and, for the parents, retention of helpers. They demonstrate also the antiquity of life-history strategies in this family and that such fixed behavior can persist over long periods of time.

This case study demonstrates furthermore that a more accurate and scientific exploitation of old quarries can bring outstanding results and how the study of osteological remains can make significant contributions to our understanding of past life and events.

Acknowledgements

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