Comparative craniological systematics of the "Tenrecomorpha" (Mammalia: Insectivora)

Peter Giere

Anke C. Schunke

Ulrich Zeller

Introduction

Insectivore systematics has long been of special interest for mammalogists in the belief that a member of this group represents the ancestral eutherian stock. Despite this attention, the establishment of a phylogenetic classification based on shared derived characters proved to be difficult due to the heterogeneity of the group and the paucity of such characters (cf. BUTLER 1988, MACPHEE and NOVACEK 1993). In part, this is also true for the taxa identified within the Insectivora. Here, a closer look will be taken at the "Tenrecomorpha", consisting of the Malagasy tenrecs and the central and west African otter shrews.

Based mainly on palaeontological data, BUTLER (1972) distinguished the "Tenrecomorpha" from the Erinaceomorpha, Soricomorpha and Chrysochlorida. Due to a misidentification of the original material, this division of the insectivores was abandoned (BUTLER 1988), and both tenrecs and otter shrews are now subsumed under the Soricomorpha (BUTLER 1988; cf. MACPHEE and NOVACEK 1993; MCKENNA and BELL 1997). The label "Tenrecomorpha" is used here to facilitate denoting tenrecs and otter shrews and could be used inter-

changeably with "Tenrecidae" as in HUTTERER (1993) or "Tenrecoidea" as in MCKENNA and BELL (1997). It is *not* used here to distinguish the tenrecs and otter shrews as a higher level taxon to be separated from other insectivore higher taxa.

The two genera of otter shrews, *Potamogale* and *Micropotamogale* are generally placed within the Tenrecidae (e.g. CABRERA 1925; MCDOWELL 1958; CORBET 1971; HUTTERER 1993; MCKENNA and BELL 1997). This classification stems from morphological similarities of *Micropotamogale* with rice tenrecs, Oryzorictinae, (HEIM DE BALSAC and BOURLIÈRE 1955; GUTH *et al.* 1959; 1960) and tenrecs *sensu stricto*, Tenrecinae (cf. CORBET 1971). It is striking, however, that little emphasis was given to distinguishing between plesiomorphic and apomorphic character states (MCKENNA 1975). Here, ontogenetic data of members of the "Tenrecomorpha" are reviewed and, in conjunction with new data, are used for comparison with data from other insectivore, eutherian and metatherian taxa in order to discuss their polarity.

Material and methods

Serial histological frontal sections (6-100 µm distance between sections) of five tenrec and otter shrew species of various ontogenetic stages were studied, together with *Erinaceus europaeus*, *Tupaia belangeri*, and *Monodelphis domestica* as out-groups for the Insectivora, Eutheria and Metatheria, respectively (table 1). Histological sections were used in order to include soft tissue data that otherwise is lost in studies of macerated museum material, whereas ontogenetic series (available to varying extent in most species studied) offered the opportunity to identify temporary and changing characters.

Graphic reconstructions or plate models of entire skulls or parts thereof were available for *Hemicentetes semispinosus* (14 mm headlength [hl]; SCHUNKE and ZELLER, in prep.); *Potamogale velox* (20 mm hl; BEHRENS 1998); *Erinaceus europaeus* (13 mm hl, 18 mm hl, adult; GIERE and ZELLER 1998, and unpublished data) and *Tupaia belan-*

Classification	*Species*	Approximate, inferred headlength
Insectivora: "Tenrecomorpha"	*Echinops telfairi*	18 mm
Insectivora: "Tenrecomorpha"	*Echinops telfairi*	32.8 mm [1?]
Insectivora: "Tenrecomorpha"	*Hemicentetes semispinosus*	14 mm
Insectivora: "Tenrecomorpha"	*Hemicentetes semispinosus*	23 mm
Insectivora: "Tenrecomorpha"	*Tenrec ecaudatus*	48 m [1?]
Insectivora: "Tenrecomorpha"	*Micropotamogale lamottei*	8.5 mm
Insectivora: "Tenrecomorpha"	*Potamogale velox*	20 mm
Insectivora: "Tenrecomorpha"	*Potamogale velox*	25 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	6.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	8.7 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	13 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	18 mm [2]
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	25.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	18 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	23.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	n/a [1]
Scandentia: Tupaiidae	*Tupaia belangeri*	several [3]
Marsupialia: Didelphidae	*Monodelphis domestica*	15.5 mm

1. Adult specimen; 2. specimen incomplete; 3. Cf. Zeller 1987.

Table 1
Species and specimens examined.

geri (cf. ZELLER 1983; 1987). Models aided in the positional interpretation of the cranial characters involved, whereas graphic reconstructions were mainly used to examine skull details, e.g. the paraseptal cartilage (unpublished data).

Results and discussion

Prior to the description of morphological data available from the study of histological sections, a brief review of representative diagnostic characters (as presently used) for each tenrecs and otter shrews species and the "Tenrecomorpha" is given. In various recent classifications of (African) insectivores, resolution ends at the family level and excep-

tions for sub-families from the characters given for the Tenrecidae are noted (McDowell 1958; Findley 1967; Lawlor 1976; Yates 1984). Only an identification manual for African mammals (Meester and Setzer 1971) differed in providing a separate entry for Potamogalinae (Corbet 1971) in the chapter on Tenrecidae (Genest and Petter 1971). A similar approach is taken here in not distinguishing between Geogalinae, Oryzorictinae and Tenrecinae when looking at "tenrecs" as opposed to otter shrews. This, however, does not imply a supposed underlying phylogeny.

Recent tenrecs are diagnosed as possessing a clavicle and completely free or webbed hind toes, whereas otter shrews lack a clavicle and have second and third hind toes that are joined basally (Cabrera 1925; Guth *et al.* 1960). Cranial diagnostic characters for the otter shrews include an osseous auditory bulla with a large contribution of the basisphenoid (Heim de Balsac 1954, Guth *et al.* 1959) and the presence of a condyloid canal not found in other tenrecs (McDowell 1958). According to Heim de Balsac (1954), tenrecs do not possess a bulla similar to that of the Potamogalinae. This view is not entirely shared by MacPhee (1981), who can only see minor differences in his phylogenetic interpretation of bullar characters. Unfortunately, no published interpretation on the postcranial characters could be found. Nevertheless, a multiple origin can be assumed for the reduction of the Clavicula and the development of syndactyl toes (e.g. Carnivora and Macropodidae, respectively).

A character identified by the histological approach in an embryo of *Potamogale velox* is the absence of a nasolacrimal duct (Behrens 1998) which was also found to be missing in *Micropotamogale lamottei* in this study. This reduction of the canal linking the eye with the nasal cavity may be considered apomorphic for otter shrews since the duct is present in *Hemicentetes semispinosus* (Schunke and Zeller, in prep.), *Tenrec ecaudatus*, *Erinaceus europaeus* and *Tupaia belangeri* (own observation; Zeller 1983). These data suggest the presence of a nasolacrimal duct in the insectivore morphotype, which, nevertheless, needs to be verified with data of the other Insectivore taxa.

The reduction of the nasolacrimal duct in a semi-aquatic animal might be regarded as an adaptation to the limnic habitat. However, in other semi-aquatic animals such as beavers (*Castor fiber* and *Castor*

canadensis), this canal is present (FRAHNERT 1998), which questions this interpretation.

Another cranial character visible only on frontal histological sections was found by SCHUNKE and ZELLER (1996) for the Tenrecinae: *Hemicentetes semispinosus* and *Tenrec ecaudatus* possess, being macrosmatic animals (cf. STEPHAN *et al.* 1991), a *Recessus ethmoturbinalis* that is extended caudally if compared to otter shrews and other insectivores. This results in a lateral displacement and a dorsal extension of the *Cavum epiptericum*, which then forms a recessus lateral to the posterior part of the *Paries nasi* (SCHUNKE and ZELLER 1996). This ventral recessus of the *Cavum epiptericum* houses the sphenopalatine ganglion besides the second branch of the trigeminal nerve. SCHUNKE and ZELLER (1996) considered this to be an autapomorphic character for the tenrecs, a hypothesis that is supported for the Tenrecinae by the comparative data available in the present study. Judging from brain characteristics (STEPHAN *et al.* 1991), it can be assumed that both Oryzorictinae and Geogalinae possess a caudally extended *Recessus ethmoturbinalis* and thus a structure of the *Cavum epiptericum* similar to that of the tenrec species examined.

BUTLER (1972) based his new taxon "Tenrecomorpha" mainly on the long infraorbital canal present in otter shrews and a fossil tenrec, which, however, turned out to be based on a misidentified erinaceid (BUTLER 1988). Other cranial characters shared by tenrecs and otter shrews include zalambdodont molars ("pseudo-dilambdodont" in *Potamogale velox*; cf. GUTH *et al.* 1959; 1960), an incomplete zygomatic arch (jugal reduced), a modified entoglenoid process and the structure of the auditory bulla (FINDLEY 1967; YATES 1984). Zalambdodont teeth, which have long been used for classification (e.g. GILL 1889; VAN VALEN 1967), also occur in Solenodontidae and Chrysochloridae within the Insectivora as well as in *Notoryctes* (Metatheria: Notoryctidae) and BUTLER (1972) critically discusses the phylogenetic relevance of this character. No information on the remaining characters was found.

Histological sections provide some additional information in the examination of the "Tenrecomorpha". SCHUNKE and ZELLER (in prep.) found a missing connection between the paraseptal cartilage and the *Lamina transversalis anterior* in both tenrecs and otter shrews in their extensive histological study of these taxa. However, in the older spec-

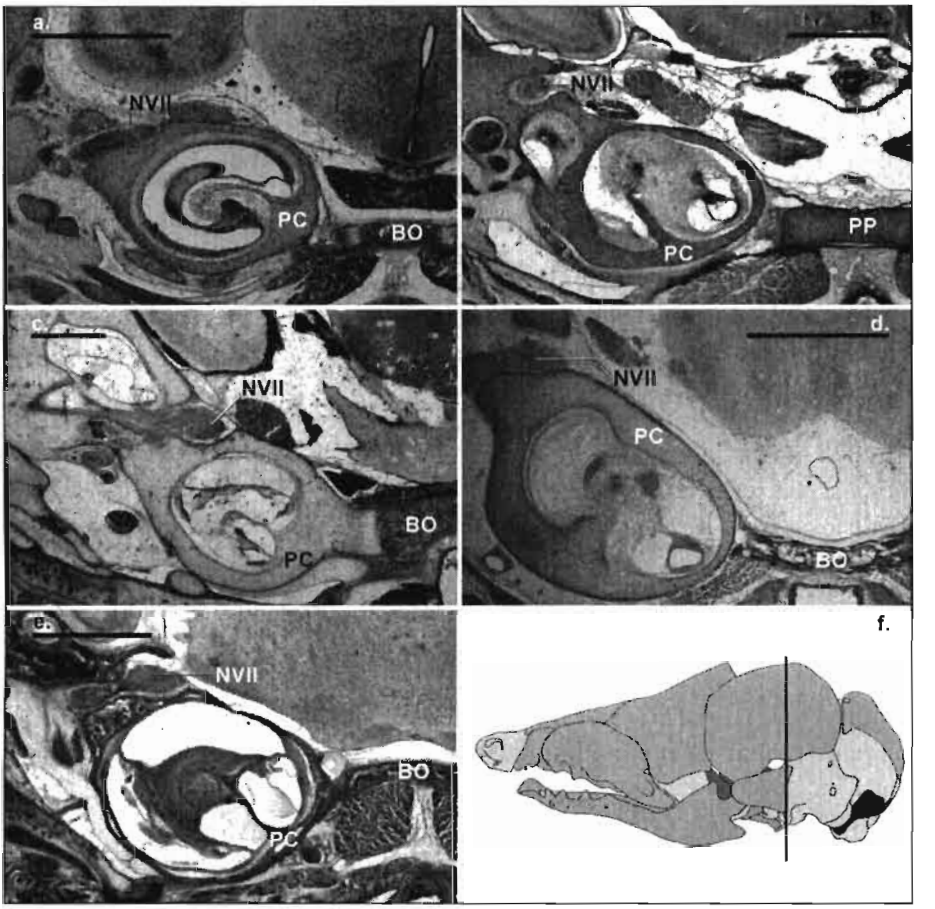

Figure 1
Frontal sections through the *Pars cochlearis* of the auditory capsule of:
a. *Hemicentetes semispinosus*;
b. *Potamogale velox*;
c. *Erinaceus europaeus*;
d. *Tupaia belangeri*;
e. *Monodelphis domestica*; Horizontal bars equal 1 mm;
f. Lateral view of a reconstruction of *Hemicentetes* (modified after Schunke and Zeller 1996), vertical bar indicates approximate plane of sections at the internal opening for the *Nervus facialis*.
Abbreviations:
PC: *Pars cochlearis;*
PP: parachordal plate;
BO: Basioccipitale;
NVII: *Nervus facialis.*

imen of *Potamogale velox*, these cartilaginous structures are joined (SCHUNKE and ZELLER, in prep.). Viewed in the light of the greater ontogenetic database available for the erinaceids in this study (prenatal and postnatal stages including the adult), this character is recognized as undergoing substantial changes during ontogeny, i.e. in *Erinaceus europaeus*, the paraseptal cartilage is linked to the *Lamina transversalis anterior* during embryogenesis and is separated in the adult. Thus, it must be cautioned that unless it is clear that the characters concerned do not change during ontogeny, only ontogenetic stages which are at a similar developmental level may be compared when analyzing embryonic data.

Nevertheless, further evidence was found for the "Tenrecomorpha" in the sectioned material. In all tenrec and otter shrew specimens examined, the *Pars cochlearis* of the ear capsule formed a low angle with the parachordal plate / Basioccipitale, resulting in an almost horizontal position of this structure (figure 1). This character was retained throughout ontogeny. In addition, the medio-ventral side of the *Pars cochlearis* maintains the angle given by the ventral side of the parachordal plate, a character that is obscured in macerated material. This character was found in all specimens except *Echinops telfairi*. In all species used as out-groups, the *Pars cochlearis* is angled against the horizontal plane and the medio-ventral side of this structure forms an angle with the parachordal plate. Thus, these characters can be regarded as apomorphies for the "Tenrecomorpha", assuming a similar composition of the inner ear in the Oryzorictinae and Geogalinae.

Concluding from the evidence compiled here, despite the ontogenetic apomorphies presented and several shared (but not necessarily) derived characters, not much evidence for the "Tenrecomorpha" is found. This corresponds partly to the results of a recent study on tenrecid phylogeny, where some tree topologies failed to indicate monophyly of the Tenrecidae (ASHER 1999). A cladistic review of the characters originally used to link otter shrews and tenrecs is necessary to establish the monophyly of the "Tenrecomorpha" as used here. For the Insectivora, this was achieved by BUTLER (1988) and, more explicitly, by MACPHEE and NOVACEK (1993). However, the morphological evidence is scanty and more characters are needed, which may be supplied by studies of serially sectioned specimens. This is necessary in the light of recent molecular studies of eutherian phylogeny

(SPRINGER *et al.* 1997; STANHOPE *et al.* 1998; EMERSON *et al.* 1999) that question insectivore monophyly by separating Tenrecidae and Chrysochloridae into a newly established clade, the "Afrosoricida" (STANHOPE *et al.* 1998). Unfortunately, neither of the molecular studies included data from otter shrews, thus no molecular evidence for the "Tenrecomorpha" is available.

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