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RODENT SUBORDERS

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Abstract: For two hundred years the status of rodent suborders has been unstable. What are the natural groupings of extant rodent families? The formal recognition of rodent suborders has remained challenging and consensus has been elusive. Classically conceived rodent suborders are widely viewed as artificial, but no universally accepted classification has emerged to reflect the major features of rodent evolution. Over the last two decades molecular studies have established that extant rodents comprise three monophyletic clades. We review the molecular basis for these groups and recognize them as taxonomic units: Suborder Ctenohystrica Huchon et al., 2000, Suborder Supramyomorpha D'Elía et al., 2019, and a group of families clustered with Sciuridae. The latter differs from Sciuromorpha as traditionally conceived because the suborder includes Aplodontiidae but excludes Castoridae. We review morphological character complexes that are distributed broadly within these three clades, name the third group Eusciurida, new suborder, and find this three-fold division of extant Rodentia to reflect well the major features of rodent phylogeny. That some morphological features do not characterize all families within suborders, or are not unique to individual suborders, indicates major parallel innovations and reversals in rodent evolution. These incongruent morphologies invite future study.

Key words: Rodentia, suborder, classification, molecular evolution

Introduction

The polymathic career of Gerhard Storch embraced scientific studies, morphological and evolutionary, of many kinds of mammals, both living and extinct. The impact of Gerhard's scientific work cannot be summarized in a single study, so we focus on one aspect: how to deal with the Order Rodentia. Gerhard enlightened the systematics of diverse rodents of several families: murids, cricetids, eomyids, glirids, and other extinct groups. His work focused on minute distinctions between closely related species and genera, and on the major features of disparate lineages. Our present investigation touches on the systematic breadth of Gerhard's productive career by focusing on the question of how to group rodent families, that is, the contents of rodent suborders.

Whereas rodent families generally have useful diagnoses that facilitate association of extant genera within them, which yields stable classification at the family level, rodent suborders historically have been far from universally recognized, making their content (included families) controversial. Due in part to the high diversity of rodents and their evolutionary radiations with morphological divergence, it is difficult to discern characters useful in diagnosis of large suborder groupings. Features prone to secondary evolutionary modification occur unevenly across the members of the suborder. Increasingly it has become apparent that rodent suborders as classically conceived and based on one or two morphological characters do not reflect major rodent evolutionary radiations. Wood (1958) considered this problem and noted that while some groupings of families as suborders appear to be defensible, certain families might best be unassigned to reflect uncertain relationship.

Molecular evolution and phylogeny present another means of tracing relationship of extant families and recognizing major groups within living Rodentia. Chromosomal and genetic data provide information on the relatedness of extant rodents, and on the shared ancestry of families. Key studies (Nedbal et al. 1996, Huchon et al. 2000, Adkins et al. 2002) recognize a tripartite division of extant Rodentia that continues to be refined by

new molecular work (see below). The aim of the present study is to review currently-proposed groupings of extant rodent families as informed by molecular evidence. Given subordinal groupings of families based on molecular data, we can then recognize morphological features of family members that are useful in characterizing the suborders. We summarize recent advances in molecular studies of Rodentia and endorse formal names for major groups – suborders – and we note morphological character states that we observe to be shared by member families.

Historical notes

Major clusters of rodent families – suborders – have been perceived for two centuries. In early appreciation of rodent diversity, de Blainville (1816) recognized locomotory groups, but these were not "natural" in the sense that they reflected ecomorphology rather than phylogeny. It was decades later that Brandt (1855) applied the arrangement of the masticatory apparatus to propose related groupings. Brandt's (1855) Hystricomorpha were rodents with an enlarged infraorbital foramen through which much of the masseter muscle passed. Myomorpha showed a modification of this with the infraorbital foramen constricted ventrally by an outer portion of the masseter muscle. Brandt's (1855) Sciuromorpha differed with much of the masseter inserting in a deep fossa laterally on the snout above a small infraorbital foramen that transmits only nerve and blood vessels.

Tullberg (1899) pursued a different strategy. He saw that dentary (and lower incisor) structure revealed a key evolutionary innovation among rodents. He noted that some rodents display a derived condition: a lengthened pterygoid muscle correlated with displacement of the angle of the jaw lateral to the plane of the lower incisor. Rodent families with the outwardly deflected angle were grouped as Suborder Hystricognathi. These include the Hystricidae, African bathyergids, thryonomyids and petromurids, an array of South American rodents known as caviomorphs, and various extinct families. The remainder of extant rodent families, the paraphyletic Sciurognathi, shared unmodified jaw structure with the angle aligned with the plane of the lower incisor.

Problems for such groupings of rodent families include homoplasy, omission of some families from the scheme, and morphological overprinting through which some character states cease to distinguish some group members. Wood (1955) and Korth (1994) provided thorough reviews of efforts toward a usable rodent classification up to the time of their writings. In a later classification McKenna and Bell (1997) modified the previous systems and recognized four suborders: Sciuromorpha, Myomorpha, Anomaluromorpha, and Hystricognatha.

In synthesizing the vast amount of research presented in **Evolutionary Relationships Among Rodents**, Luckett and Hartenberger (1985) perceived a fundamental dichotomy in rodent evolution (albeit with question marks) in which hystricognaths plus Family Ctenodactylidae comprised one branch of rodent evolution, and most other rodents shared a separate origin among an extinct group called the Ischyromyoidea. They thus endorsed the importance of the hystricognath jaw in pointing to an early split among rodents. Hystricognath monophyly was later confirmed by molecular features of the mitochondrial 12S rRNA gene (Nedbal et al. 1996). Marivaux et al. (2004) also recognized a basic rodent dichotomy in their study based on morphology. Their extensive cladistic analysis of dental and osteological features in fossil and living taxa traced crown plus stem groups into the Paleogene record. They retrieved a close relationship of hystricognaths, ctenodactylids, diatomyids, and other Paleogene rodents, endorsing placement of them in the taxon Ctenohystrica named by Huchon et al. (2000). The Marivaux et al. (2004) analysis also found monophyly for a group containing most of the remaining rodent families (as in the proposal of Luckett and Hartenberger 1985) and formally proposed for them "Ischyromyiformes". Certain basal rodents were excluded from either major group. Ctenohystrica and Ischyromyiformes were not given explicit taxonomic rank in that work.

Among Ischyromyiformes, Marivaux et al. (2004) recognized two monophyletic subgroups of rodents, which have been retrieved repeatedly in molecular studies, not always as sister taxa. One clade associated living sciurids and aplodontioids (Hopkins 2016 endorsed the corrected spelling Aplodontiidae) with fossil ischyromyids, and basal to them the extinct theridomyids. The second cluster groups most remaining crown families, including muroid families and the living glirids, with extinct sciuravids basal to these. These two major divisions were demarcated by distinct nodes on figure 2 of Marivaux et al. (2004) but were unnamed.

Complementary molecular evidence was accumulated to better distinguish rodent divisions. Nuclear genes were sampled across rodent families widely enough to propose higher taxa and, crucially, their relationships. Huchon et al. (2000) surveyed the von Willebrand factor nuclear gene in 28 rodents from 15 families. As in the Marivaux et al. (2004) study based on morphology, three rodent clades were apparent, their newly minted Ctenohystrica comprising a terminal clade. For Huchon et al. (2000) several phylogenetic details remained unresolved, and while the Ctenohystrica (embracing ctenodactylids plus hystricognaths) appeared reliably monophyletic, other nodes were weakly supported at that time.

Adkins et al. (2002) combined data from the nuclear genes GHR (growth hormone receptor) and BRCA1 (a breast and ovarian cancer gene) and distinguished the ctenohystricans as well as sciuroid and muroid clades. The composition of the latter clades differed in some details from the study of Marivaux et al. (2004), and the sciuroid clade was found to be basal to sister ctenohystrican and muroid clades.

Huchon et al. (2007) published a broader analysis that included the then-newly-recognized extant Family Diatomyidae. They used four nuclear (GHR, alpha 2B andrenergic receptor ADRA2B, interphotoreceptor retinoid binding protein IRBP, von Willebrand factor vWF) and two mitochondrial genes (cytochrome b and 12S rRNA), which resulted in a better resolved tree. (Yet we note that multiple mitochondrial genes do not yield independent phylogenetic information (Ruvolo 1997)). Both sciurognath families Diatomyidae and Ctenodactylidae were included in Ctenohystrica (Huchon et al. 2007), and Ctenohystrica appeared as sister to combined sciuroid and muroid clades. In this analysis glirids sorted with sciuroids, but interrelationship

of the three clades was not well differentiated. *Anomalurus* and *Pedetes* aligned with the muroid clade.

Shortly thereafter, Blanga-Kanfi et al. (2009) published an analysis employing six nuclear genes (GHR, ADRA2B, IRBP, vWF, cannabinoid receptor CB1, recombination activating gene RAG2). They noted that the genes are unlinked genetically (separate chromosomes) and there are no reports of protein interactions among them to complicate interpretation. Blanga-Kanfi et al. (2009) again found a robust Ctenohystrica as sister to the muroids (mouse-related clade) plus *Anomalurus* and *Pedetes*. Basal to both was a grouping of sciuroid and glirid rodents (squirrel-related clade). By this time, it had become clear that rodent evolution was not simply dichotomous but involved at least three clades.

Honeycutt (2009) arranged the three well-supported clades, showing "Hystricomorpha" (we prefer Ctenohystrica) as sister to a "Mouse-like" clade; a "Squirrel-like" clade was basal to these. All living rodents were seen to fall into three clades, but the clades were not assigned formal ranks, and their interrelationships were still controversial.

While some analyses (Bininda-Emonds et al. 2007, Fabre et al. 2018) saw the three taxa similarly, a squirrel-like clade basal to sister ctenohystrican and mouse-like clades, Montgelard et al. (2008) placed the mouse group basal to the others. Gatesy et al. (2017) noted that subtleties of interpretation are influenced by DNA substitution models, coalescence models, and tree search routines.

Churakov et al. (2010) suspected another complicating factor at work. While they found a basal squirrel-like clade, they interpreted the data to propose a fascinating case of introgression of that clade with ctenohystricans early in their history. Introgression would complicate perception of which two of the three clades are closer and would cloud the perceived age difference between lineage split and gene origin. Churakov et al. (2010) did note an alternative hypothesis of incomplete lineage sorting.

Rodent suborders

A tripartite division of extant Rodentia is clear, yet uncertainty remains on interrelationships of the three groups of living rodents – which is basal to the others? D'Elía et al. (2019) note that today this remains unresolved. Introgression (Churakov et al. 2010) among early clade members, if a reality, would cloud this relationship, but also would imply closeness of the groups. We treat the three groups at the same taxonomic level. Higher categories should reflect closeness of the contained families to make rodent classification a useful tool. The three rodent clades represent major evolutionary radiations and we interpret them as suborders. Here we specify the family level content of each, noting morphological features shared by most or all families in each suborder. Shared features characterize suborder members, but few are diagnostic. We note inconsistencies and exceptions below.

Suborder Ctenohystrica Huchon et al., 2000

The large division Ctenohystrica of Huchon et al. (2000) has endured scrutiny and subsequent analyses and is a useful group, distinct from the extant squirrel-like and mouse-like family clusters. Suborder Ctenohystrica (see Appendix) includes the Hystricognathi Tullberg, 1899 (infraordinal rank) plus two family-level outgroups, Ctenodactylidae and Diatomyidae. The latter two show the plesiomorphic sciurognathous rodent jaw structure, which would occur in basal members of the suborder. The hystricognathous jaw structure is derived with respect to sciurognathy, and while characterizing Hystricognathi, by far the majority of Ctenohystrica, that character state evolved within the suborder after its origin. Following McKenna and Bell (1997) the Hystricognathi are considered an infraorder containing families Hystricidae, Erethizontidae, Thryonomyidae, Petromuridae, Bathyergidae, various extinct phiomorphs of Africa, and diverse South American families derived from a Paleogene hystricognath radiation (Rowe et al. 2010). The South American families within Hystricognathi are the monophyletic Caviomorpha Wood, 1955, a taxon comparable to the Caviida of Bryant and McKenna (1995).

All ctenohystricans are hystricomorphous (with an enlarged infraorbital foramen accommodating passage of a portion of the masseter muscle), but hystricomorphy occurs outside the suborder. Ctenohystrican families other than the ctenodactylids and diatomyids are hystricognathous. All are also derived in the enamel microstructure of their enlarged gnawing incisors. The enamel has a highly organized system of interlocking prisms referred to as multiserial enamel, with decussating prisms forming adjacent enamel bands that are several prisms thick. This organized system is derived with respect to the pauciserial enamel character state, which occurs in earlier Paleogene rodents (Wahlert 1968). The multiserial character state occurs outside this suborder as a homoplasy only in Pedetidae (see below).

Cheek tooth features typical of Ctenohystrica include presence of a hypocone in upper molars and deciduous 4th premolar, and rectangular lower cheek teeth, primitively with a hypoconulid. In most lineages, the cuspate cheek teeth become lophodont, and some become high crowned. Several closely related but independent hystricognath lineages suppress replacement of deciduous premolars, so that the adult dentition is DP4/4, M1–3/1–3.

Suborder Eusciurida, new

The Suborder Eusciurida is a crown group, the least inclusive clade of all living "squirrel-like" Sciuridae, Aplodontiidae, and Gliridae (see Appendix). The name is based on squirrels and their relatives, plus the prefix "eu", Greek for "true, well". We follow the analysis of Marivaux et al. (2004) to include extinct Family Theridomyidae. Members have sciurognathous jaw structure, primitively lack hypocones on upper molars, and primitively have low crowned cheek teeth. Incisor enamel is derived, as highly organized and advanced as multiserial enamel, but in a different way. The decussating prism pattern, termed "uniserial enamel", is organized into thin bands, one prism thick, and is seen in all three extant families. (Extinct theridomyids, basal to the extant eusciuridans (Marivaux et al. 2004), have primitive pauciserial enamel as sampled by Wahlert (1968)).

Eusciurida families display different arrays of jaw muscle anatomy, showing independent evolutionary

paths. Aplodontiids have, arguably, the least derived jaw musculature, the masseter being unexpanded beyond the zygomatic arch. Sciurids are the namesake of the sciuromorphous condition in which the masseter seats broadly on the side of the snout in a distinct fossa that constricts the infraorbital foramen ventrally; it transmits only nerve and blood vessels. Glirids show independent modification of the musculature in which a primitively unexpanded masseter migrates onto the snout, in part through an enlarged infraorbital foramen (Vianey-Liaud 1985, Hautier et al. 2008). The extinct theridomyids are hystricomorphous (Marivaux et al. 2004).

Traditionally considered members of the old subordinal grouping Sciuromorpha, beavers (Castoridae) do have a sciuromorphous zygoma. Carleton (1984) realized that beavers are not closely related to squirrels, and subsequent studies consistently interpret the shared zygomasseteric morphology as a case of convergence. Because the content of Sciuromorpha has been so unstable, and Theridomyidae appear to be associated with it, we prefer a new name and utilize the prefix "eu" for Eusciurida.

Suborder Supramyomorpha D'Elía et al., 2019

Suborder Supramyomorpha (see Appendix) is the crown clade of myodonts (muroids plus dipodoids) with anomaluroids, pedetids, castorids (beavers), and geomorphs (the group for geomyids, heteromyids, and extinct eomyids). This clade supplants in part the classical Myomorpha, which has been used to contain myodonts, the geomorphs, and formerly in some classifications the glirids. The name invokes living myomorphous rodents but encompasses rodents with a wide array of structures. D'Elía et al. (2019) proposed this taxon at subordinal rank in their analysis of recent developments in rodent systematics.

Despite the name, only later muroids have myomorphous jaw musculature. Myomorphy is derived from hystricomorphy by inclination of the zygomatic plate (Lindsay 1977), which pinches the oval infraorbital foramen into a keyhole. Hystricomorphy appears to be primitive for myodonts, anomalurids and pedetids. On the other hand, geomorphs and beavers exhibit sciuromorphy (Korth 1994), and differ much from muroids in the sculpted fossa on the snout that seats the masseter muscle, with the small infraorbital foramen ventral to the fossa.

Supramyomorphs have primitive (sciurognathous) jaw structure. The incisor enamel is dominantly uniserial. Detailed variation in uniserial microstructure associates some muroid subgroups but, in other cases, suggests morphological homoplasy across that superfamily (Kalthoff 2000). One family, the Pedetidae, diverges from the others in displaying multiserial incisor enamel, apparently an independent acquisition. Like jaw musculature, incisor microstructure may show homoplasy (Wood 1955).

Many basal members of some clades (myodonts, early anomaluroids and early geomorphs) show a generalized molar structure, basically four-cusped with connecting lophs, called the "cricetid plan" (see Flynn et al. 1985). The "cricetid plan" includes presence of a hypocone on upper molars, which is seen in all groups, but the pattern is secondarily modified in geomorphs. A myodont

synapomorphy is reduction of the cheek tooth row from the usual 4/4 tooth formula: myodonts lack a lower premolar and only a few species retain a small last upper premolar.

Conclusion

Our purpose is to endorse formally as suborders the principle clades of living rodents as demonstrated in molecular analyses. The subordinal groupings of rodent families are based on genetic data developed in a rich literature (D'Elía et al. 2019) and briefly surveyed above. We add morphological features characteristic of most or all members of each: Suborder Ctenohystrica Huchon et al., 2000, Suborder Eusciurida, new, and Suborder Supramyomorpha D'Elía et al., 2019. The three-fold division of living Rodentia is robust and endures repeated molecular analyses. The arrangement of families into suborders as indicated by genetic data is partially consistent with morphological and palaeontological observations previously made, for example the cladistic analysis of Marivaux et al. (2004). Several key anatomical innovations of jaw structure and musculature sort with the suborders, as based on molecular evidence. Exceptions are likely instructive of homoplasy and overprinting by secondary evolution of structures.

Utilizing gene-based suborder categories is far more useful than artificial groupings that are clearly inferior (Wood 1958). The three extant rodent suborders originated during the Paleogene. These crown groups contain all living and some extinct families. Perhaps all Neogene fossil rodents belong to living suborders but the crown groups based on molecular data that we observe across extant families do not necessarily encompass the entirety of rodent evolution in the early Cenozoic. Some extinct clades, particularly basal groups, do not fall readily into these high-level clusters. Such vestiges of early rodent evolution, e.g. Alagomyidae represented by extinct *Tribosphenomys* Meng et al., 1994 and classified presently as "Rodentia, incertae sedis", may eventually form a basis for recognizing extinct suborders.

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Appendix

Extant rodent suborders and included rodent families, after Honeycutt (2009) and D'Elía et al. (2019) with additions.

Order Rodentia Bowdich, 1821

Suborder Eusciurida, new
Family Sciuridae Fischer [de Waldheim], 1917
Family Aplodontiidae Brandt, 1855 (including extinct Mylagaulinae Cope, 1881)
Family Gliridae Thomas, 1897
Family Theridomyidae[1] Alston, 1876

Suborder Supramyomorpha D'Elía, Fabre et Lessa, 2019
Family Castoridae Hemrpich, 1820
Family Geomyidae Bonaparte, 1845
Family Heteromyidae Gray, 1868
Family Eomyidae[2] Winge, 1887
Family Anomaluridae Gervais in d'Orbigny, 1849
Family Zenkerellidae Matschie, 1898
Family Pedetidae Gray, 1825
Infraorder Myodonta Schaub, 1958
Family Dipodidae Fischer [de Waldheim], 1917
Family Zapodidae Coues 1875
Family Sicistidae Allen, 1901
Family Platacanthomyidae[3] Alston, 1876
Family Spalacidae[4] Gray, 1821
Family Calomyscidae[5] Vorontsov, Kartavtseva et Potapova, 1978
Family Nesomyidae Forsyth Major, 1897
Family Cricetidae Fischer [de Waldheim], 1917
Family Muridae Illiger, 1811

Suborder Ctenohystrica Huchon, Catzeflis et Douzery, 2000
Family Ctenodactylidae Gervais, 1823
Family Diatomyidae Mein et Ginsburg, 1997
Family Tsaganomyidae[6] Matthew et Granger, 1923
Infraorder Hystricognathi Tullberg, 1899
Family Hystricidae Fischer [de Waldheim], 1917
Family Bathyergidae Waterhouse, 1841
Family Heterocephalidae Landry, 1957
Superfamily Thryonomyoidea Pocock, 1922
Family Thryonomyidae Pocock, 1922
Family Petromuridae Tullberg, 1899
Parvorder Caviomorpha Wood, 1955[7]
Family Agoutidae[8] Gray, 1821
Family Dasyproctidae Gray, 1825
Family Caviidae Fischer [de Waldheim], 1917
Family Hydrochoeridae Gray, 1825
Family Erethizontidae Bonaparte, 1845
Family Dinomyidae Peters, 1873
Family Chinchillidae Bennett, 1833
Family Abrocomidae Miller et Gidley, 1918
Family Octodontidae Waterhouse, 1839
Family Ctenomyidae Lesson, 1842
Family Capromyidae Smith, 1842
Family Echimyidae Gray, 1825
Family Myocastoridae[9] Ameghino, 1902

[1] Extinct group placed here in the analysis of Marivaux et al. (2004).

[2] Extinct family placed with geomyoids by consensus (e.g. Wood 1955, Korth 1994).

[3] Position endorsed by Jansa et al. (2009).

[4] Spalacidae includes four subfamilies, extant Spalacinae, Rhizomyinae, and Myospalacinae, and following Wang and Qiu (2018) the extinct Tachyoryctoidinae Schaub, 1958.

[5] Recent work finds Calomyscidae basal to Nesomyidae plus higher muroids (Steppan and Schenk 2017).

[6] Extinct Tsaganomyidae Matthew et Granger, 1923 are placed here following Bryant and McKenna (1995).

[7] Vucetich et al. (2015) differ somewhat in family recognition, and list several extinct clades.

[8] Agoutidae Gray, 1821 predates Cuniculidae Miller et Gidley, 1918 (McKenna and Bell 1997).

[9] Included in Echimyidae by McKenna and Bell (1997).