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Phylogenetic relationships between Monotremata and Monotremaformes: parallelism with appendages and habits of aquatic moles

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For a long time, Monotremata included Mesozoic taxa such as *Steropodon* and *Teinolophos*, as well as Cenozoic species. However, fossil discoveries from the Cretaceous have revealed significant differences between Cenozoic monotremes and their ancestors, with Cenozoic monotremes being more closely related to each other than to earlier forms, thereby forming the crown group of Monotremata. Among extant mammals, moles exhibit several morphofunctional parallels with monotremes. These similarities may reflect comparable evolutionary trajectories. Here, we investigate evolutionary parallels between monotremes and Talpidae, aiming to determine whether their resemblances could indicate a similar evolutionary pathway and what implications this would have for our understanding of Monotremata's evolutionary history. Our objectives were to identify additional morphological characters to differentiate Monotremata from their ancestors and to outline possible evolutionary parallels between monotremes and Talpidae. To this end, specimens of monotremes and talpids housed in the collection of the Museu Nacional-UFRJ were analyzed, along with a literature review on the evolution, morphology, and fossil record of these groups. Among the non-dental morphological characteristics identified, we noted the presence of a lateral projection on the anterior portion of the mandible extending beyond the mandibular symphysis, forming the bony support of the "beak" in present-day monotremes, and the presence of a reinforced pectoral girdle with several hypertrophied bones and joints not observed in other tetrapods. The swimming method of platypuses, which involves a series of alternating strokes of the forelimbs, is highly similar to the digging or swimming motions observed in moles. Thus, it is possible that, like semi-aquatic moles, monotremes may have descended from an ancestor with a specialized fossorial lifestyle.

Key Words: Cretaceous, Eimer's organs, monotremes, Talpidae, *Teinolophos*.

Durante mucho tiempo, los Monotremata incluyeron taxones mesozoicos como *Steropodon* y *Teinolophos*, además de especies del cenozoico. Sin embargo, los descubrimientos fósiles del cretácico revelaron una diferencia importante entre los monotremas del cenozoico y sus ancestros, ya que los monotremas del cenozoico estaban más estrechamente relacionados entre sí que con formas anteriores, formando así el grupo corona de Monotremata. Entre los mamíferos vivos, los topos tienen una serie de paralelos morfofuncionales con los monotremas. Estos paralelos pueden reflejar trayectorias evolutivas similares. Nuestros objetivos fueron: encontrar caracteres morfológicos adicionales para diferenciar a los Monotremata de sus ancestros y rastrear posibles paralelos evolutivos entre ellos y Talpidae. Para ello, se evaluaron especímenes de monotremas y tálpidos almacenados en la colección del Museu Nacional-UFRJ, así como la investigación bibliográfica sobre la evolución, morfología y registro fósil de estos grupos. Entre las características morfológicas no dentales identificadas aquí están la presencia de una proyección lateral en la porción anterior de la mandíbula que se extiende más allá de la sínfisis mandibular, formando el soporte óseo del "pico" en los monotremas actuales y la presencia de una cintura escapular reforzada, con varios huesos y articulaciones hipertrofiadas no vistas en otros tetrápodos. El método de natación de los ornitorrincos, que implica una serie de golpes alternados de las extremidades delanteras, es muy similar al de los topos cuando excavan o nadan. Así, es posible que, al igual que los topos semiacuáticos, los monotremas desciendan de un ancestro con un estilo de vida fosorial especializado.

Palabras clave: Cretácico, monotremos, Talpidae, *Teinolophos*, órganos de Eimer.

Monotremes, the egg-laying mammals, are currently the only remaining members of the Yinotheria mammal lineage (Luo and Yuan 2007). Among living mammals, they are by far one of the most distinctive groups due to both their peculiar appearance and retention of several characteristics present in many Mesozoic mammals or even in previous synapsids such as egg laying, the presence of potentially venomous spurs on the hind legs, and a spread-out posture of the limbs (Hurum *et al.* 2006; Gambaryan and Kuznetsov 2013).

Due to the unique distinction of monotremes, for a long time represented by a scarce fossil record that was composed only of Cenozoic taxa closely related to living species, a strict definition of them in relation to the other groups of mammals was not possible. However, older taxa of the Monotremata lineage were eventually discovered (Archer *et al.* 1985; Flannery *et al.* 1995; Rich *et al.* 1999). These new fossil species were readily classified as members of the order Monotremata but given the great morphological differences between some of these taxa and their modern relatives, such as the possession of teeth in the anterior region of the mandible, including incisors and canines, the presence of a Meckel's groove in the posterior part of the mandible, and the probable absence of a "beak" (Archer *et al.* 1985; Musser 2003; Rich *et al.* 2016), it was necessary to revise the definitions of Monotremata.

Initially, the apomorphies used to differentiate monotremes from other Yinotheria were the presence of a partially enlarged mandibular canal, the marked separation in size between the last premolar and the first molar, the absence of a paraconid cusp on the lower first molar, and the presence of large and wide talonids (Pian *et al.* 2016). Following this definition, the order Monotremata included genera such as *Kollikodon,* a large Cretaceous mammal with bunodont teeth (Flannery *et al.* 1995), *Steropodon*, a peculiar animal with teeth similar to tribosphenic teeth and which was initially and erroneously interpreted as basal platypus (Archer *et al.* 1985), and *Teinolophos,* the oldest known member of this lineage, around 123 million years old, and all species of Cenozoic monotremes (Rich *et al.* 1999).

The new fossil discoveries have revealed significant differences between Cenozoic monotremes and their Cretaceous ancestors (Rich *et al.* 2016). Cenozoic monotremes are much more closely related to each other than they were to any of the Cretaceous ones, forming the crown group Monotremata Chimento *et al.* (2023). The broader group containing the Monotremata and older forms such as *Teinolophos*, *Kollikodon*, and *Steropodon* was named Monotremaformes. The analysis that based this arrangement was exclusively based on dental morphology, disregarding any non-dental character.

Chimento *et al.* (2023)'s proposal was made considering the possession of low dilambdodont molar teeth, expanded mesodistally, with the anterior lobe equivalent to the trigonid positioned lower than the posterior lobe, which would correspond to the talonid. The talonid is composed of two transverse lophs instead of one and lacks a labial cingulid. Thus, Chimento *et al.* (2023) did not include a broader analysis that encompassed non-dental characters of this group. While tooth morphology is an essential trait for the taxonomy of many mammalian groups, other types of characters—such as the mandible, middle ear, and scapular girdle—are also crucial, particularly in groups with highly specialized morphologies like monotremes.

Among living placental mammals, some representatives of the family Talpidae (Laurasiatheria, Eulipotyphla) (true moles, shrew moles, and desmans) appear to exhibit a series of morphological and functional similarities with living monotremes, such as a modified rostrum containing specialized mechanosensory organs, which are essential for spatial orientation (Catania 2000), and a type of swimming driven by alternating movements of the forelimbs (Hickman 1984; Fish *et al.* 1997). Inasmuch as these similarities reflect convergent evolutionary trajectories, understanding the evolutionary history of moles could help understand the still obscure evolutionary history of monotremes. Therefore, we herein carry out a bibliographical review on the evolution and morphology of monotremes and their relatives in search of non-dental characters to be analyzed in the light of the phylogenetic proposal of Chimento *et al.* (2023).

In addition, we will also draw possible evolutionary parallels between monotremes and talpids, to determine whether their similarities could in fact represent a similar evolutionary trajectory, and what implications this would have for our understanding of the evolutionary history of the order Monotremata.

Materials and methods

Regarding monotremes and talpids, we based our character survey on those documented in the literature (detailed below) and in two skins and a skeleton of *Ornithorhynchus anatinus*, as well as two specimens of *Tachyglossus aculeatus*, and a skin and skull of *Desmana moschata*; four Myrmecophagidae and Manidae, variation in the shape of the mandibular symphysis was assessed from five articulated dentaries of *Tamandua tetradactyla* and two dentaries of *Manis sp*. All specimens are housed in the collection of the Museu Nacional (MN), Universidade Federal do Rio de Janeiro. The specimens were first analyzed macroscopically and then photographed using an Olympus OM-D E-M5 Mark II camera. Specimens deposited in the collection of the National Museum-UFRJ receive a numbering starting with the letters MN.

Regarding the monotremes and talpids, we observe morphological traits documented in the literature. For Myrmecophagidae and Manidae, variation in the shape of the mandibular symphysis was assessed from specimens in Museum to comparative purposes with that of echidnas.

Specimen provenances: the *Desmana moschata* specimen (MN 93184) originated from present-day Kazakhstan, formerly part of the USSR, with a collection label dated November 1931. The articulated mandibles of *Tamandua tetradactyla* evaluated in this study belong to the following specimens: MN 5883 from Santa Teresa, Espírito Santo; MN 9677 from Ilhéus, Bahia; MN 63499 from São Raimundo Nonato, Piauí; MN 68357 from Telêmaco Borba, Paraná; and MN 79449 from Duque de Caxias, Rio de Janeiro. The Monotremata specimens (MN 1 to MN 5) and the Pholidota specimens (MN 46 and MN 47) were purchased in Europe in the early XX century, and their exact geographical origins are unknown.

A comprehensive search of Google Scholar was conducted for data published between 1925 and 2025, using various combinations of keywords such as: Montramata + fossil; Monotremata + Shoulder Girdle; Monotremes + Evolution; Monotremata + middle ear; Monotremata + Eletroreception; Aquatic mole + Locomotion; Platypus + Locomotion; Echidna + Evolution. Priority was given to articles focusing on evolution, morphology (including jaw structure, shoulder girdle, and sensory organs), the fossil record of monotremes, other monotreme-like species, and semi-aquatic moles. Additionally, the bibliographic references of selected articles and books were thoroughly reviewed, with no restrictions on publication dates.

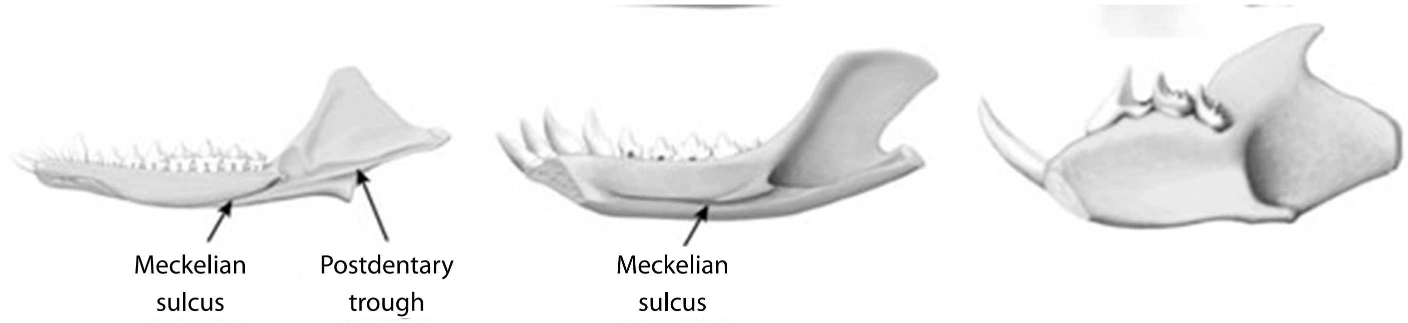

Figure 1. The three patterns of middle ear existing in mammals: (Right) *Morganucodon*, a postdentary attached ear: the jaw presents a Meckelian groove and a post-dental trough where the Meckelian cartilage and the post-dental bones would be inserted, respectively; (Center) *Lyaconodon*, a Meckelian-attached ear: a prominent Meckelian sulcus highlighting the possession of a Meckelian cartilage that may or may not be ossified and a lack of a post-dental trough. (Left) *Vilevolodon*, a detached ear, characterized by the complete absence of Meckelian groove or postdentary trough in the jaw. This stage represents the complete separation between the jaw and the bones of the mammalian ear (Modified from Wang *et al.* 2021)

Results

As a result of the bibliographic research, a total of 49 references on evolution, Monotreme morphology, and semi-aquatic moles were gathered and reviewed. These sources are divided into 40 articles and two notes published in journals, as well as seven book chapters. All these works found are cited and referenced below.

Middle Ear Patterns. Mammals can present up to three different types of middle ear patterns, which are defined by the level of connection between the dentary and the middle ear bones (Ramírez-Chaves *et al.* 2016; Wang *et al.* 2021). The mandibular middle ear of cynodonts (MMEC), in which the postdentary is attached in the mandible (Luo 2011) is the most primitive pattern, preceeding true mammals and being found in derived cynodonts. Additionally, in some primitive mammals such as *Henosferus molus* from the Lower Jurassic of Argentina (Rougier *et al.* 2007), the ear bones are fully fixed in the dentary, rendering them as a joint between the skull and the jaw. The bones are evidenced in incomplete fossils by the presence of a post-dental trough in the back of the jaw of these animals.

The second pattern is the partial mammalian middle ear (PMME), also known as "ear with Meckelian attachment" (Meng *et al.* 2011). In this pattern, the middle ear bones are still connected to the mandible by a Meckel's cartilage, which can be completely cartilaginous or ossified. The PMME can be inferred by a pronounced Meckel's groove in the dentary of incomplete fossils.

Finally, the definitive mammal's middle ear (DMME) or "detached ear", has no direct connection between the ear bones and dentary since they completely migrated to the middle ear. The presence of this pattern is attested by the absence of both the postdentary trough and of Meckel's groove in the dentary (Figure 1); this is the condition found in all living mammals (Allin and Hopson 1992).

Both *Teinolophos* and *Steropodon* were originally interpreted as having post-dentary-attached (Luo *et al.* 2002; Rich *et al.* 2005). However, with the discovery of more complete materials of *Teinolophos*, it lacks a post-dental trough in its jaw and presents a very well-developed Meckel's groove in its dentary, indicating the presence of an ossified Meckel's cartilage, and a Meckelian-attached ear (Rich *et al.* 2016). Regarding *Steropodon*, a more in-depth analysis of the holotype revealed that its supposed postdentary trough was a pre-depositional break that the fossil had suffered. On the other hand, the mandible of *Steropodon* also presented a Meckelian groove, indicating an ear with a Meckelian-attached. The validity of this interpretation has been questioned by Ramírez-Chaves *et al.* (2016), but two additional jaw fragments of *Steropodon* described by Flannery *et al.* (2024) preserved a more posterior region of the jaw than that of the holotype. These additional specimens have a slight depression on the lingual surface of the dentary, which may be a remnant of a rudimentary Meckelian groove.

A possible additional taxon of Steropodontidae, the *Parvopalus clytiei,* probably had an ear detached, as it does not have a postdentary trough or even a Meckelian groove on its dentary (Flannery *et al.* 2024), so if its classification as a Steropodontidae alongside *Steropodon* is correct, it means that a detached ear may have arisen independently in different lineages of Monotremaformes.

The type specimen of the fossil taxon *Opalios splendens* has a possible Meckel's groove in its jaw; however, this is so reduced that it is likely that it was absent (Flannery *et al.* 2024).

All known taxa, living or extinct, of Ornithorhynchidae and Tachyglossidae have a detached ear, meaning their jaws do not show any trace of a postdentary trough or a Meckel's groove (Pascual 1992; Musser and Archer 1998; Rich *et al.* 2005; Chimento *et al.* 2023; Flannery *et al.* 2024). *Teinolophos* and *Opalios* are the closest taxa to the crown group of Monotremata and possibly have an ear Meckelian-attached, (Chimento *et al.* 2023; Flannery *et al.* 2024), while members of the crown group themselves have a detached ear. This suggests that this characteristic arose independently in this lineage in relation to the others (Figure 2).

The acquisition of a detached ear can be interpreted as a synapomorphy of the crown group of Monotremata among the Monotremaformes. Alternatively, if *O. splendens* does not possess a Meckelian groove, the presence of a detached ear could qualify as a synapomorphy of the lineage that includes both the crown group of Monotremata and its sister taxon *O. splendens*.

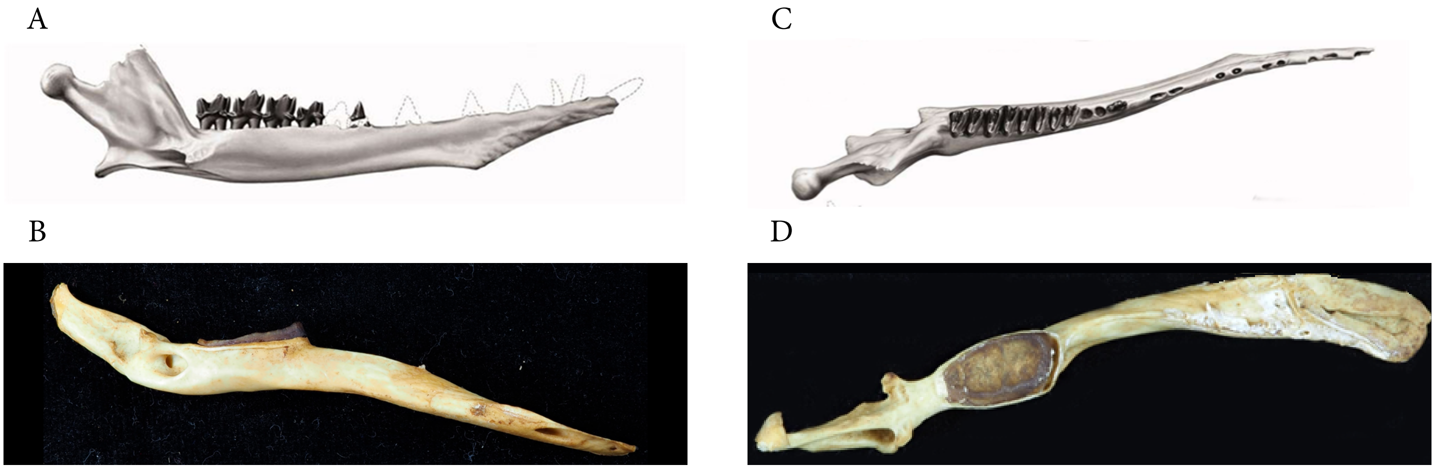

Figure 2. Lateral view of the jaws of a *Teinolophos trusleri* (A) and a platypus (*Ornithorhynchus anatinus*) (B). *T. trusleri* has a prominent Meckel's groove in the jaw, indicative of an ossified Meckel's cartilage. In contrast, the platypus does not have any trace of this structure (the middle ear is separate from jaw). (C) a superior view of the jaws of *T. trusleri* (Modified from Rich *et al*. 2016) and a platypus (D). The distal end of the jaws of *T. trusleri* projects inward to form the mandibular symphysis. In contrast, in the platypus, the distal end of the jaw curves outward, extending beyond the mandibular symphysis. Bar = 5 mm

Differentiation of the number of molars between Ornithorhynchidae and their predecessors. Cenozoic toothed monotremes such as *Monotrematum sudamericanum*, the species of the genus *Obdurodon,* and juveniles of the modern *Ornithorhynchus anatinus* have three pairs of molar teeth in their jaws, with a much-reduced M3, with only one tooth root holding it in the jaw. This same dental arrangement can be found in the fossil *Dharragarra aurora*, which is one of the characters contributing to its identification as an Ornithorhynchidae (Flannery *et al.* 2024), and as the oldest known member of the crown group of Monotremata.

Meanwhile, other Monotremaformes, such as *Teinolophos trusleri* and *Opalios splendens*, possess five pairs of molar teeth in their jaws with two tooth roots in all molars (Rich *et al.* 2016; Flannery *et al.* 2024). As these are the closest taxa to the crown group, one can assume that the reduction in the number of molars in the mandible, together with the significant decrease in the size of M3, may be synapomorphies of Monotremata.

Other Monotremaformes such as *Steropodon* and *Parvopalus* also have three molars in their jaws (Archer *et al.* 1985; Flannery *et al.* 2024); however, *Steropodon* has at least a very different dental morphology from that found in *T. trusleri* or in species of the crown group of Monotremata (Flannery *et al.* 2022; Chimento *et al.* 2023). Regarding *P. clytiei*, no other materials are known besides the holotype. As it only consists of a toothless jaw, its dental morphology is unknown, and its number of molar teeth is only known due to the dental alveoli present in the holotype (Flannery *et al.* 2024).

Kollikodontidae taxa, such as *Kollikodon ritchiei* has four molar teeth per quarter of the jaw, its M4 being significantly reduced, with only one tooth root (Pian *et al.* 2016; Flannery *et al.* 2022). This condition is not very different from the M3 of the Ornithorhynchidae; however, its tooth morphology is markedly different from that seen in other Monotremaformes or even in other mammals (Flannery *et al.* 1995; Pian *et al.* 2016). Therefore, the reduction in the number of molars probably occurred in separate ways in different lineages of Monotremaformes.

Rostrum Commonly Referred to as "Beak" or "Bill". One of the most striking characteristics of living monotremes is the possession of a rostrum that is generally referred to as a leathery "beak" full of electroreceptors and mechanoreceptors, which these animals use to locate their prey (Pettigrew 1999). To transmit environmental information from the "beak" to the brain, these animals increased the size of their mandibular nerves, resulting in the formation of an enlarged mandibular canal in their jaws (Musser and Archer 1998; Asahara *et al.* 2016; Rich *et al.* 2016). Given this functional correlation between the presence of an enlarged mandibular canal and the possession of a "beak", the presence of the former has been used as an indication of the presence of the latter (Figure 3).

Thus, all Mesozoic members of the monotreme lineage that had an enlarged mandibular canal, such as *Steropodon*, *Teinolophos*, and *Kollikodon*, were automatically interpreted as having a "beak", similarly to their living relatives (Musser and Archer 1998; Rowe *et al.* 2008). This line of thought was predominant for a long time, as the fossils of these Mesozoic taxa were very fragmentary, with only incomplete jaw remains that consisted only of the posterior part of the jaw (Flannery *et al.* 2022). This such an association was questioned after the discovery of a complete jaw of *Teinolophos trusleri* by Rich *et al.* (2016), who reported that despite the presence of an enlarged mandibular canal in the dentary *T. trusleri* did not present the characteristic "beak" of living monotremes. Its mandibular symphysis extends to the tip of their mandible, as in most other mammals, as opposed to modern platypuses whose anterior portion of the mandible extends beyond the symphysis and projects laterally outward, forming the bony support for its "beak". This indicates that *T. trusleri* did not have a "beak" (Figure 2). In both *Teinolophos* and *Obdurodon*), therefore, the presence

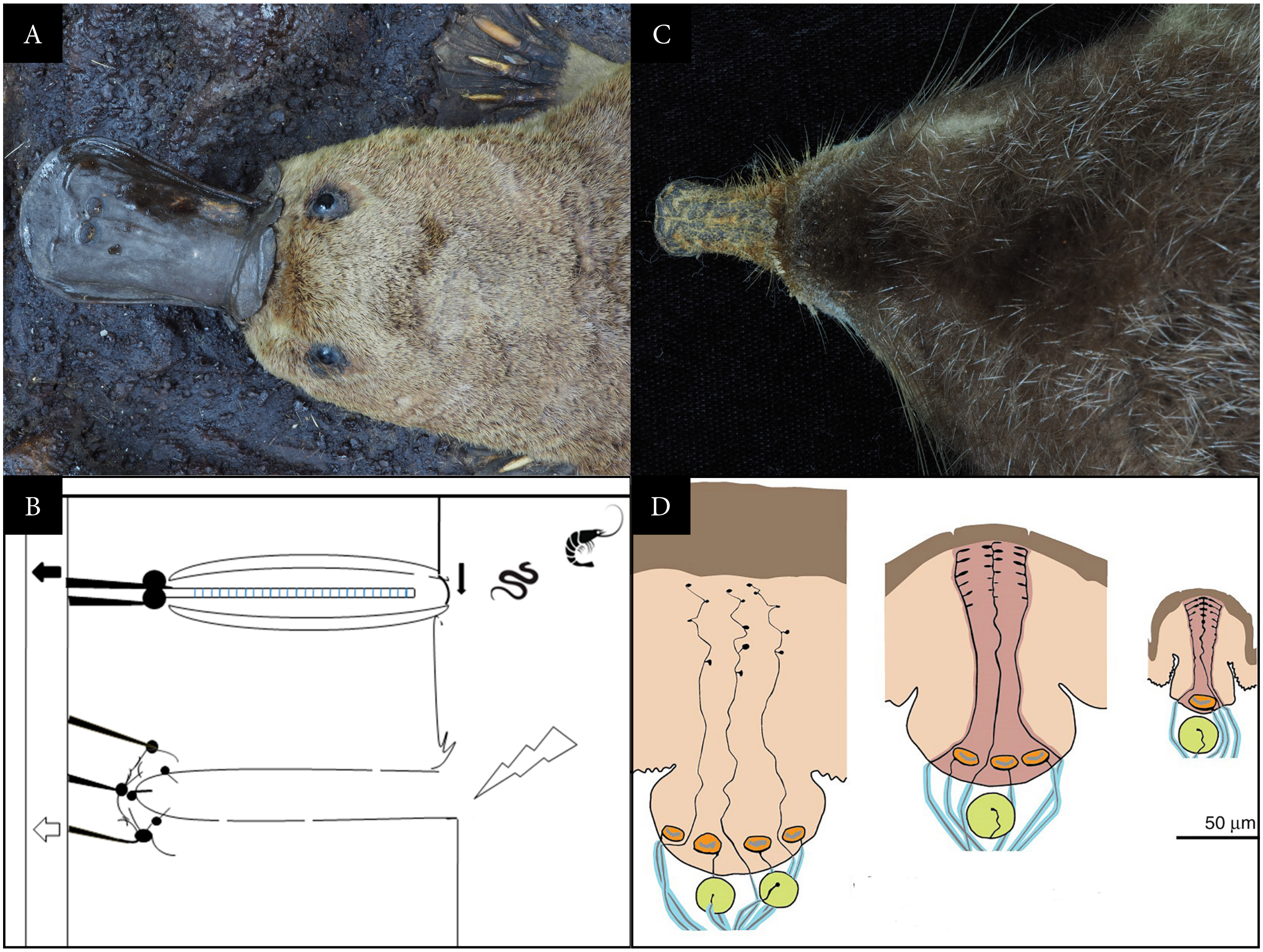

Figure 3. Upper: Top view of the rostrums of a platypus (*Ornithorhynchus anatinus*) (A-MN 2) and a Russian desman (*Desmana moschata*) (C-MN 93184). Both animals have a laterally wide rostrum covered by naked and highly sensitive skin. Lower: representations of the specialized sensory structures in the rostrums of both animals (B), (Modified by Fish *et al.* 1997) and D (Modified by Catania *et al.* 2020), with emphasis on the mechanoreceptor structures that are very similar to each other.

of an enlarged mandibular canal should not be interpreted as unequivocal evidence of the possession of this structure.

In the same way, *Opalios splendens* does not have projections on the mandible extending beyond the mandibular symphysis. However, *O. splendens* has some mandibular characteristics seen in platypuses, such as a torsion of the horizontal ramus of the dentary, the presence of a deep hemispherical pit for enlarged masseter and the possession of a very evident horizontal flattening in the anterior portion of the mandible (Flannery *et al.* 2024). This may indicate that *O. splendens* perhaps had some intermediate structure between a basic mammalian snout and a "beak" derived from monotremes. This is one of the reasons why it is classified as the closest taxon to the Ornithorhynchidae (Flannery *et al.* 2024), and by extension, the crown group of Monotremata.

Among the known Monotremaformes, the closest taxa to the crown group of Monotremata (*Teinolophos* and *Opalios*), do not have a true "beak", which strongly suggests that this feature was not present in other Monotremaformes from the "middle Cretaceous". Therefore, this structure must only be present in members of the crown group of Monotremata and could consequently be a synapomorphy of this clade.

Both *Patagorhynchus* and *Monotrematum* do not have known complete jaw remains and, therefore, it is not known whether they had a lateral projection that extends beyond the mandibular symphysis. However, both taxa have teeth which are morphologically almost identical to the teeth of *Obdurodon*, are found in sediments of ancient bodies of freshwater (Chimento *et al.* 2023). In addition, *Monotrematum* presents postcranial remains that show adaptations for swimming (Forasiepi and Martinelli 2013). These traits suggest that they present a typical general morphology of a platypus and, by extension, a lateral projection of the mandible that extends beyond the mandibular symphysis.

It should also be noted that echidnas (Tachyglossidae) do not have a lateral projection of the mandible that extends beyond the mandibular symphysis like platypuses, but they still have a "beak" (Pettigrew 1999; Augee *et al.* 2006). However, despite the absence of concrete fossil

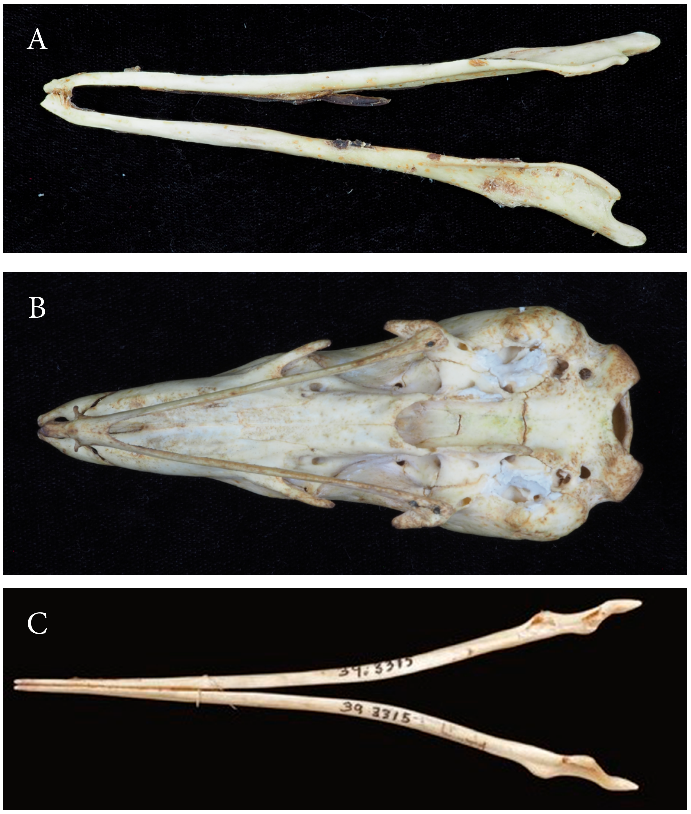

Figure 4. (A) Ventral view of the jaws of a southern tamandua (*Tamandua tetradactyla* MN 68359), (B) an Asian pangolin. (*Manis sp.* MN 47), and a long-beaked echidna C. (*Zaglossus brujinii*) modified from Helgen *et al.* 2012. The distal ends of the echidna jaws do not have an inward curvature to form the mandibular symphysis as in other myrmecophagous; instead, the jaws extend parallel to their distal end forming a long mandibular symphysis also seen in platypuses.

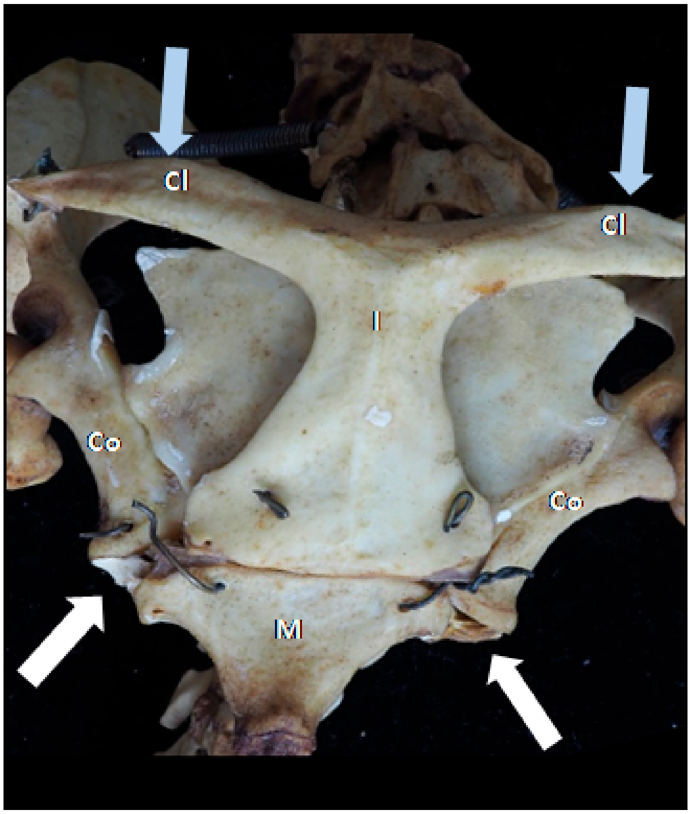

Figure 5. Ventral view of the shoulder girdle of the modern platypus (*Ornithorhynchus anatinus*, MN 3). Gray arrows point to clavicles parallel to the interclavicle, white arrows point to the articulation between the coracoid, manubrium and interclavicle. Captions: Cl = Clavicle; I = Interclavicle; Co = Coracoid; M = Manubrium. Photo: João Alves de Oliveira.

evidence (Camens 2010), echidnas evolved from ancestors very similar to platypuses (Phillips *et al.* 2009; Flannery *et al.* 2022) and, therefore, both share morphological characteristics.

Some characteristics present in echidnas may suggest that their ancestors had jaws like those of platypuses. The possession of a lateral twist of the jaws greater than that of other myrmecophagous mammals, such as in anteaters and pangolins, is not very different from the condition in platypuses. The two sides of the echidna's jaws do not contort inward to form the mandibular symphysis but instead run parallel to the tip of the mandible, in a very similar way to the mandibular symphysis of platypuses, but without the post-symphysis projections (Figure 4). Thus, the absence of these projections in modern echidnas is due to their derived facial morphology and does not affect the possession of a "beak" as a synapomorphy of Monotremata.

Shoulder girdle. Mammals are divided into two major groups: Yinotheria and Theriimorpha. These groups can be distinguished based on the structure of the pectoral girdle. Yinotheria possess a rigid and reinforced pectoral girdle that retains all the bones found in earlier therapsids, whereas the Theriimorpha have a mobile pectoral girdle with a lighter and more simplified suspension, exhibiting a significant reduction in the number of bones (Augee *et al.* 2006; Luo and Yuan 2007). Within Yinotheria, monotremes have the most reinforced pectoral girdle, featuring a hypertrophied interclavicle whose upper portion almost entirely overlaps the extent of the clavicles. Additionally, they possess a hypertrophied (meta)coracoid that extends to the manubrium-interclavicle joint, forming an articulation with these respective bones (Luo and Yuan 2007; Luo 2015) (Figure 5).

The reinforced arrangement of the shoulder girdle of monotremes provides additional support for the powerful shoulders and forelimbs of these animals. In general, the reason for the existence of such a structure is attributed to the digging habits of these mammals, which were secondarily co-opted to carry out the swimming movements of semi-aquatic platypuses. To date, there are no known remains of the shoulder bones of any of the pre-Cenozoic fossil monotremaformes, and as the only other Yinotheria whose shoulder girdle is known are the Shuotheriidae from the Middle Jurassic of Asia. There's a gap of more than 100 million years between a primitive Yinotheria shoulder girdle and the Monotremata shoulder girdle (Luo and Yuan 2007; Luo 2015; Flannery *et al.* 2022).

Because all fossil monotremes from the Upper Cretaceous to early Cenozoic were semi-aquatic (Phillips *et al.* 2009; Chimento *et al.* 2023), it is possible that the reinforced shoulder structure of these animals evolved to allow the execution of their unique swimming movements (Fish *et al.* 1997). Therefore, it could be possible to infer that the reinforced shoulders of modern monotremes may have evolved along with a semi-aquatic lifestyle, as among the Monotremaformes only monotremes have semi-aquatic forms (Flannery *et al.* 2022; Chimento *et al.* 2023). The reinforced shoulder could qualify as a synapomorphy of this clade, however, given the large gap in the fossil record of these animals, this proposal must be taken with caution, as new discoveries could completely change this reconstruction of the evolutionary history of these animals.

Sensitive snouts and unusual swimming. One of the most striking characteristics, which can be found in both talpids and monotremes, is the possession of a highly sensitive snout full of mechanosensory organs. Monotremes have a highly specialized snout, superficially similar to the beak of a bird, that is full of mechanoreceptors and electroreceptor (see Figure 3), while moles have a procumbent snout, similar to a proboscis, filled with a set of specialized mechanoreceptive organs known as Eimer's organs. Desmans (a group of aquatic moles) have an extensive network of Eimer's organs aligned in a complex configuration of rosettes, with a micro-vibrissa located within each rosette (Catania 2000; Catania 2020).

The mechanoreceptive organs of monotremes and the Eimer's organs of talpids are remarkably similar both morphologically and functionally. In addition, aquatic talpids (*Desmana*, *Galemys* and *Condylura*), have an even more modified snout than their terrestrial and fossorial relatives, with star-nosed moles having a series of nasal tentacles, while desmans have an elongated snout like a proboscis that has a notable morphological similarity to the "beak" of platypuses (Catania 2000; Catania 2020).

Among extant aquatic mammals, platypuses exhibit a unique swimming motion characterized by a series of alternating strokes of their forelimbs (Fish *et al.* 1997). These swimming movements closely resemble the motions performed by moles and other fossorial mammals while digging. Notably, semi-aquatic moles, such as the star-nosed mole (*Condylura cristata*), display a swimming pattern highly similar to that of platypuses, using a series of predominantly alternating strokes with their forelimbs to propel themselves through water. These movements closely resemble those used by these and other moles for soil excavation; however, unlike platypuses, star-nosed moles also employ their hindlimbs, to a lesser extent, for additional underwater propulsion (Hickman 1984).

Despite their vaguely beaver-like form, platypus tails do not play an active role in locomotion. Instead, they serve other functions, such as transporting nesting materials and storing fat (Guiler 1983; Fish *et al.* 1997; Thomas *et al.* 2017). The fat-rich tails of platypuses were highly valued by Indigenous Australian peoples, particularly during winter (Robinson and Plomley 1966; University of New South Wales, Sydney [Accessed May 18th, 2025]).

Desmans also swim using a series of alternating limb movements; however, unlike platypuses and star-nosed moles, desmans utilize their hindlimbs for aquatic propulsion, in addition to their long, laterally flattened tails (Ivlev *et al.* 2010). Given that the few mammals that move through water via alternating limb strokes originate from fossorial species and possess a relatively well-documented evolutionary history, this may suggest that other mammals with similar swimming styles have followed comparable evolutionary trajectories. Although predominantly terrestrial, echidnas are nonetheless adept swimmers, capable of crossing rivers and occasionally even swimming in the ocean (Augee *et al.* 2005; Phillip *et al.* 2009). They can dive underwater, which aids their survival during sudden flooding events. When caught in such situations, an echidna reduces its heart rate from 60 beats per minute to just 12 beats per minute, conserving oxygen for its heart and brain—the organs most sensitive to oxygen deprivation. Laboratory data have revealed that the cardiovascular system of an echidna resembles that of a seal (Augee *et al.* 2005), further supporting the hypothesis that this trait is inherited from ancestors, similarly to the platypus. When swimming, echidnas, like platypuses, engage in alternating strokes of their forelimbs. However, their swimming rhythm is slower, and their hindlimbs also contribute to additional propulsion.

Discussion

Non-dental synapomorphies of Monotremata. In addition to the dental characters described by Chimento *et al.* (2023), the crown group of Monotremata can be distinguished from the other Monotremaformes by a suite of characters: (1) the absence of a Meckel groove in the posterior part of the dentary, a lateral projection in the anterior portion of the mandible that is extends beyond the mandibular symphysis (Rich *et al.* 2016; Flannery *et al.* 2024); (2) a reduction in the number of molars in the mandible, with a marked simplification of M3, which has only one tooth root (Flannery *et al.* 2024), and (3) the possession of a reinforced shoulder girdle with expanded interclavicles that completely overlap the clavicles and a hypertrophied (meta) coracoid that extends to the joint between the manubrium and interclavicles (Augee *et al.* 2006; Luo and Yuan 2007; Luo 2015).

Based on dental morphology, Chimento *et al.* (2023) recovered *Teinolophos trusleri* as the closest relative to the crown group Monotremata, but the subsequent discovery of *Opalios splendens*, changed this view. In addition to sharing several unique characteristics with *T. trusleri*, such as the possession of five molars in the jaw, *O. splendens* also shares some derived characters present in monotremes, such as a flattened snout and perhaps a prominent ear (Flannery *et al.* 2024). Thus, it probably represents an intermediate form between the Teinolophidae and the Monotremata, being a sister taxon of this last. It is worth highlighting that *O. splendens* may not be the ancestor of the crown group, as it was contemporary with the platypus *Dharragarra aurora,* the oldest known member of the crown group of Monotremata (Flannery *et al.* 2024).

Therefore, the old synapomorphies used to define monotremes cited in Pian *et al.* (2016) should not be discarded, but rather repositioned, as although they are not enough to define what Monotremata is, they can still be used to define what Monotremaformes are.

Definitive Middle Ear and Chewing. To date, few studies have been conducted on why different lineages of mammals independently evolved a detached ear. Grossnickle (2017) in his work proposed that in Cladotheria mammals (placentals, marsupials, and Meridiolestida), the evolution of a detached ear would be associated with the predominant transverse chewing movement present in this group, as the ossified Meckel's cartilage present in several lineages of earlier mammals would considerably restrict the jaws from performing these mediolateral movements. Thus, the first Cladotheria significantly reduced Meckel's cartilage, so that it did not limit the ability to move their jaws, allowing them to move their jaws without limitation.

In addition to the Cladotheria, another very well-known group of mammals that developed a detached ear were the Allotheria represented by Euharamyida, Multituberculata, and Gondwanatheria (Kielan-Jaworowska 1997; Krause *et al.* 2020; Mao 2023). These rodent-like mammals were among the most abundant and diverse mammals of their time (Krause *et al.* 2021), some of them like *Vilevolodon diplomylos* had ear ossicles very similar to those of living monotremes (Wang *et al.* 2021). However, unlike Cladotheria, Allotheria did not have transverse chewing movement but rather a palinal chewing movement (Lazzari *et al.* 2010; Zheng *et al.* 2013; Schultz *et al.* 2014), similar to that of many contemporary herbivorous dinosaurs such as ceratopsids and hadrosaurids (Varriale 2016). Therefore, the transverse chewing movement itself cannot be considered the only event by which mammals could have developed a detached middle ear.

Basal Monotremaformes such as *Teinolophos* and *Steropodon* had a chewing movement that was substantially ortal rather than transverse due to the accessory complements of the mandible (ossified Meckel's cartilage) and the molar teeth deeply rooted in the mandible. On the other hand, the Monotremata have a predominantly transverse chewing movement that can be evidenced by the extensive transverse wear on the molars of species of the genus *Obdurodon* (Ashwell 2013). Monotremata and Cladotheria possess a prominent angular process, positioned at the posterior part of the mandible (Rich *et al.* 2016; Grossnickle 2017). The presence and location of this structure were also noted by Grossnickle (2017) as being correlated with the evolution of transverse mastication and, by extension, with the distinct middle ear. Multituberculates and other Allotheria lack an angular process in their mandibles (Kielan-Jaworowska 1997). Based on this evidence, we propose that, as in Cladotheria, the reduction and subsequent loss of ossified Meckel's cartilage in Monotremaformes is probably associated with a predominantly transverse chewing movement performed by the jaws of these animals.

Additional evidence for the platypus-like ancestry of echidnas. As previously stated, today we know that echidnas are derived from terrestrial platypuses, with several aspects of their biology referring to their aquatic ancestry (Phillips *et al.* 2009; Flannery *et al.* 2022). We propose two additional morphological characteristics that corroborate the proposal that echidnas diverged from platypuses (Figure 4): (1) the presence of a well-marked lateral curvature in their jaws, not recorded in other mammals with similar facial morphology, such as pangolins and anteaters, and (2) the shape of the mandibular symphysis. In most mammals, including the myrmecophagous forms already mentioned, the distal end of the jaws curves inwards, forming the mandibular symphysis; however, in echidnas, this pattern is very similar to that seen in platypuses. Based on this evidence, we propose that, despite extensive cranial specializations for myrmecophagy, echidnas still possess the same base jaw shape as their platypus-like ancestors.

The "Bill" of the Platypus and the Proboscis of the Mole. It has been proposed that the electroreceptive and mechanoreceptive senses of the Monotremaformes evolved in the polar forests of southern Gondwana during the Early Cretaceous (Flannery *et al.* 2022). These conditions enabled the highly sensitive snouts to locate the small invertebrates on which they fed. As the senses of electroreception and mechanoreception are more efficient in an aqueous environment than on dry land, it is not surprising that, over time, some of these Monotremaformes adopted a semiaquatic lifestyle.

In the water, these animals were able to make even more use of their electrical and tactile senses using their typical mammalian snouts on extensive platforms full of electroreceptors and mechanoreceptors, thus forming the characteristic "beak" of members of the order Monotremata (Pettigrew 1999; Asahara *et al.* 2016). A similar process occurred in a later lineage, the mole family Talpidae.

Moles in general have a unique characteristic, the Eimer's organs (Figure 3); these are a set of tactile organs located on the surface of the nasal epidermis, which give the animal an extraordinary sense of touch. In terms of structure and function, Eimer's organs are very similar to the mechanoreceptor organs of monotremes and their ancestors (Catania 2000), thus being an example of convergent evolution. Given the morphological and functional similarity between both structures, it is possible to draw certain parallels between the evolutionary history of Monotremaformes and that of talpids.

The first moles were small animals that lived above ground and foraged in the leaf litter of the ancient forests of Asia during the Paleogene, in a similar way to early Monotremaformes of the lower Cretaceous like *Teinolophos trusleri*. Like these, when foraging in the dense forest environment and in low light, the moles were able to make use of the sharp mechanosensory system, to locate their prey. A few basal talpids still maintain this ancestral lifestyle.

The shrew moles of the subfamily Uropsilinae are the most primitive living talpids, forming a sister lineage to all other moles. These animals lack the typical adaptations for the fossorial lifestyle of their relatives, still retain external auricles, and have the most rudimentary Eimer's organs of their family. Over time, most moles became fossorial and began to use their Eimer's organs to locate earthworms and other invertebrates underground. However, at least two mole lineages, the Condylurini and the Desmanini, have a semiaquatic lifestyle and can therefore utilize even more complex sensory structures like monotremes (Shinohara *et al.* 2003; Wan *et al.* 2013; Bannikova *et al.* 2015).

The star-nosed mole *(Condylura cristata)* is the only semi-aquatic mole native to North America, as well as the only living representative of the tribe Condilurini (Wan *et al.* 2013; Bannikova *et al.* 2015). It lives mainly in regions with humid soil, such as in swamps and on the banks of rivers and lakes.

In general, star-nosed moles spend most of their time digging, but they also forage in water, particularly in the winter. To pick up signals from their prey in their moist environments, these moles use a series of nasal appendages that increase the surface area of their snouts, giving them one of the most developed mechanosensory systems of any other mole (Hamilton 1931; Hickman 1984).

The "desmans", two species native to northern Eurasia members of the Desmanini tribe (Wan *et al.* 2013; Bannikova *et al.* 2015), are the most morphologically modified talpids for a semiaquatic lifestyle. Similarly to the star-nosed mole, desmans further developed their mechanosensory systems in response to their aquatic lifestyle; they utilized their snout into a true proboscis that is wide laterally and compressed vertically (Richard and Vallette Viallard 1969), which makes it visually very similar to the "beak" of aquatic monotremes such as the platypuses. Although thinner, this proboscis has an extensive network of Eimer's organs aligned in a complex configuration of rosettes, with a micro-vibrissa located inside each rosette, which gives the animal not only the ability to find its prey underneath water, but also to detect and avoid submerged obstacles (Catania 2000), in the same way as the "beaks" of platypuses.

A Reinforced Shoulder for Swimming and Digging. Due to the significant scarcity of postcranial remains of Mesozoic Yinotherian mammals, the precise timing of the emergence of the reinforced shoulder structure found in modern monotremes remains unknown. However, the foundational arrangement of this structure was already present in basal Yinotheria, such as *Pseudotribos robustus* (Luo and Yuan 2007), a Middle Jurassic Shuotheriidae from Asia. *P. robustus* is known from a partial skeleton, including pectoral girdle elements such as a large and robust interclavicle, whose anterior portion extensively overlaps the clavicles. This pectoral girdle arrangement has been associated with a fossorial lifestyle.

Kryoryctes cadburyi is the only known representative of Mesozoic Monotremaformes with postcranial remains, specifically a single humerus. This humerus exhibits significant morphological similarity to that of echidnas, to the extent that *Kryoryctes* was initially interpreted as a basal Tachyglossidae (Pridmore *et al.* 2005). Consequently, it was proposed that *K. cadburyi* had a specialized fossorial lifestyle.

To test the hypothesis that *Kryoryctes* was indeed fossorial, Hand *et al.* (2025) analyzed the bone microstructure of the only known specimen of this taxon. Their results indicated that, despite its external morphology closely resembling fossorial species, the humerus of *K. cadburyi* exhibits a bone microstructure highly similar to that of extant aquatic mammals, featuring a particularly thick cortex and a significantly reduced medullary cavity. Based on these findings, the authors proposed a semi-aquatic burrowing lifestyle for this taxon. As a semi-aquatic burrower, *Kryoryctes* would benefit significantly from the reinforced shoulder structure found in Monotremata.

Therefore, it would not be unreasonable to suggest that this structure evolved to facilitate more efficient swimming. Since within Monotremaformes only Monotremata includes semi-aquatic species, the reinforced shoulder structure could be considered a synapomorphy for the clade. The only postcranial fossil evidence of aquatic locomotion in Cenozoic monotremes is a humerus from *Monotrematum sudamericanum*, which exhibits morphology nearly identical to that of modern platypuses and likely shared a similar lifestyle (Forasiepi and Martinelli 2013).

Among extant aquatic mammals, platypuses—and by extension early Monotremata—are characterized by a unique swimming motion involving a series of alternating strokes of the forelimbs (Fish *et al.* 1997). Among all living mammals, only one species is known to employ a similar movement for underwater propulsion: the star-nosed mole. This small fossorial and semi-aquatic mammal uses a series of predominantly alternating strokes of its forelimbs to move through water. These movements closely resemble those used by moles for digging; however, unlike platypuses, star-nosed moles also utilize their hindlimbs to a lesser extent for additional underwater propulsion (Hickman1984).

Thus, the reinforced shoulder structure has played a fundamental role throughout the evolutionary history of these groups, influencing their ability to occupy various habitats and often contributing to their survival in transitional and dynamic environments.

In conclusion, we describe four morphological characteristics, in addition to dental morphology, that can be identified as synapomorphies of the crown group of Monotremata, namely: the absence of a Meckel groove in the posterior part of the dentary, the presence of a lateral projection in the anterior portion of the mandible that extends beyond the mandibular symphysis, the reduction in the number of molars in the mandible, with marked simplification of the M3, and probably due to the possession of a reinforced shoulder girdle with expanded interclavicles that overlap entirely with the clavicles, and a hypertrophied (meta) coracoid which extends to the joint between the manubrium and the interclavicles.

We propose that as in Cladotheria mammals, the evolution of a prominent ear in Monotremata is related to a transverse chewing movement. We also suggest that the shape of the echidna's jaw remains remarkably like that of its ancestors, despite the evident morphological changes associated with myrmecophagy. Finally, we observed that the evolutionary history of monotremes in fact has several parallels with the evolutionary history of aquatic moles. Based on this, we propose that, like the Desmanini and Condylurini, monotremes are descendants of ancestors with a specialized fossorial lifestyle.

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