·Review·

# Sleep alterations in mammals: Did aquatic conditions inhibit rapid eye movement sleep?

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Abstract: Sleep has been studied widely in mammals and to some extent in other vertebrates. Higher vertebrates such as birds and mammals have evolved an inimitable rapid eye movement (REM) sleep state. During REM sleep, postural muscles become atonic and the temperature regulating machinery remains suspended. Although REM sleep is present in almost all the terrestrial mammals, the aquatic mammals have either radically reduced or completely eliminated REM sleep. Further, we found a significant negative correlation between REM sleep and the adaptation of the organism to live on land or in water. The amount of REM sleep is highest in terrestrial mammals, significantly reduced in semi-aquatic mammals and completely absent or negligible in aquatic mammals. The aquatic mammals are obligate swimmers and have to surface at regular intervals for air. Also, these animals live in thermally challenging environments, where the conductive heat loss is approximately ~90 times greater than air. Therefore, they have to be moving most of the time. As an adaptation, they have evolved unihemispheric sleep, during which they can rove as well as rest. A condition that immobilizes muscle activity and suspends the thermoregulatory machinery, as happens during REM sleep, is not suitable for these animals. It is possible that, in accord with Darwin's theory, aquatic conditions in the elimination of REM sleep with time. In this review, we discuss the possibility of the intrinsic role of aquatic conditions in the elimination of REM sleep in the aquatic mammals.

Keywords: aquatic mammals; aquatic adaptation; mammalian sleep; phylogenetic evolution

### 1 Introduction

Two distinct sleep states, non-rapid eye movement (NREM) and rapid eye movement (REM) sleep, are present only in mammals<sup>[1]</sup> and birds<sup>[2]</sup>. In other vertebrate groups such as fishes, amphibians and reptiles, sleep is unitary in nature<sup>[3-6]</sup>. Similar to birds and mammals, fishes<sup>[7]</sup>, amphibians<sup>[4]</sup> and reptiles<sup>[3]</sup> periodically undergo sleepwake states but display spike-like activity in the electroencephalogram (EEG) during sleep and low-amplitude waves

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when awake. In birds and mammals, the EEG exhibits a synchronized pattern of high-amplitude slow waves during NREM sleep and a desynchronized pattern of high-frequency waves of low amplitude during wakefulness and REM sleep. These parameters, along with behavioral observation, help to characterize vigilant states in animals<sup>[1,8]</sup>. Further, sleep-wakefulness in almost all organisms is regulated by two independent mechanisms: circadian and homeostatic<sup>[9]</sup>. Although sleep in invertebrates and lower vertebrates shares several behavioral and functional properties with mammalian and avian sleep, it also has some fundamental differences. For example, sleep in invertebrates and lower vertebrates resembles avian and mammalian sleep in the daily timing of inactivity, periods of increased arousal

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threshold, and rebound after sleep loss<sup>[10]</sup>. However, the different stages of NREM and REM sleep, along with state-specific electrophysiological correlates, have evolved only in mammals and birds. It is believed that the complex nature of sleep in birds and mammals might have evolved gradually from the sleep state of lower organisms<sup>[2]</sup>.

Since the discovery of REM sleep, a number of studies have been performed to understand how and why it evolved only in birds and mammals. Current knowledge suggests that ancient or basal birds like the ostrich<sup>[11]</sup>, and mammals such as platypus<sup>[12]</sup>, opossum<sup>[13]</sup> and ferret<sup>[14]</sup>, manifest a large amount of REM sleep. On the other hand, reptiles (precursors of birds and mammals) exhibit only a single sleep-like state<sup>[15]</sup>. REM sleep or a REM sleep-like state has not been persuasively demonstrated in reptiles, suggesting that it has evolved in parallel and independently in mammals and birds. Further, semi-aquatic and aquatic mammals such as fur seals, dolphins and white whales have shed a significant amount of REM sleep and/or have eliminated it completely (Fig. 1). It is not known, however, why REM sleep is present in terrestrial mammals and birds and substantially reduced or eliminated in aquatic mammals. In this review, we primarily discuss the nature of sleep in aquatic and terrestrial mammals and the possible impact of aquatic conditions on the evolution of REM sleep.

#### 2 Discovery of REM sleep

Aserinsky and Kleitman, in 1953, observed for the first time a unique sleep stage in humans (both children and adults) when the eyes rolled in a regular fashion. They noted that the eyes of sleeping subjects were moving at a regular interval during which the EEG was similar to the waking condition<sup>[16]</sup>. Since the eyes were moving rapidly while the subject was still asleep, they named this new sleep stage "rapid eye movement (REM) sleep". They also found that most subjects were dreaming and the respiratory rate was augmented during REM sleep<sup>[16,17]</sup>. Later, they also found an increased heart rate during REM sleep<sup>[18]</sup>. Following Aserinsky's work, Dement and Kleitman reported in 1957 that during REM sleep, there were almost

no gross body and limb movements (postural muscle atonia), although numerous jerky limb and digital movements occurred<sup>[19]</sup>. In subsequent years, the REM sleep state and its associated phenomena were recorded in several experimental animals. For example, Dement in 1958 identified a sleep state of low-voltage EEG with eye movements in cats<sup>[20]</sup>. Jouvet's group in 1959 found a similar sleep stage occurring after slow-wave sleep, which comprised rapid low-voltage cortical activity with no muscle tone but rapid eye movements with jerky paw and tail movements<sup>[21]</sup>. They characterized this stage as 'paradoxical stage of sleep' because the EEG resembled that during wakeful-



Fig. 1. Correlation between REM sleep (% total recording time, TRT, in A; % total sleep time, TST, in B) and adaptation to terrestrial, semiaquatic and aquatic environments in mammals. The percentages of REM sleep relative to total recording time and total sleep time in mammals showed a significant inverse correlation with adaptation to an aquatic medium (n = 94). All data points used for analysis are listed in Table 1.

	Mammals	REM sleep (% TRT)	REM sleep (% TST)	References
	Terrestrial mammals			
1	Platypus	33.33	56.33	[12]
2	Virginia opossum	30.58	44.97	[74]
3	Latrine opossum	27.21	33.67	[75, 76]
4	Giant armadillo	25.42	33.71	[75, 76]
5	Ferret	24.42	40.41	[14]
6	Southern opossum	23.54	29.12	[13]
7	Large hairy armadillo	18.67	21.94	[41]
8	Big brown bat	16.25	19.79	[77]
9	Nine-banded armadillo	14.83	19.81	[78]
10	Golden hamster	14.63	23.43	[79, 80]
11	Thirteen-lined ground squirrel	14.21	24.71	[80]
12	Arctic ground squirrel	14.08	21.02	[81]
13	Cat	13.42	24.34	[82]
14	Collared lemming	13.29	21.00	[83]
15	Little pocket Mouse	13.12	15.70	[84]
16	Belding's ground squirrel	12.54	19.00	[85]
17	Siberian chipmunk	12.25	24.09	[86]
18	Western european hedgehog	12.00	28.57	[87]
19	Brandt's hedgehog	11.75	27.33	[88]
20	Golden-mantled ground squirrel	11.50	19.01	[85]
21	Kangaroo rat	11.33	17.00	[89]
22	Pig	10.96	29.13	[90]
23	Common tree shrew	10.79	16.40	[91]
24	Norway rat	10.75	19.48	[80]
25	Mountain beaver	10.21	17.01	[87]
26	Red fox	10.00	24.51	[92]
27	Lesser mole rat	9.96	22.53	[93]
28	Common tenrec	9.75	15.00	[87]
29	Northern short-tailed shrew	9.58	15.44	[94]
30	Mongolian jird	9.08	16.60	[95]
31	Star-nosed mole	9.04	21.03	[96]
32	Eastern mole	8.79	24.97	[96]
33	Djungarian hamster	8.63	14.47	[97]
34	House shrew	8.33	15.62	[94]
35	African giant pouched rat	8.33	24.09	[98]
36	Little brown bat	8.29	9.98	[99]
37	Human	7.92	23.75	[98]

### Table 1. Percentage of REM sleep out of total recording time (TRT) and total sleep time (TST) in terrestrial, semi-aquatic and aquatic mammals

To be continued

Continued				
38	Blind mole rat	7.92	15.27	[100]
39	Northern night monkey	7.58	10.72	[76]
40	Yellow-bellied marmot	7.54	10.39	[86]
41	Mexican volcano mouse	7.54	10.46	[101]
42	Brushtail possum	7.00	12.28	[102]
43	Chimpanzee	6.75	15.00	[76, 103]
44	Common marmoset	6.67	16.85	[104]
45	Dog	6.46	17.96	[105, 106]
46	Chinchilla	6.46	12.38	[80]
47	Stump-tailed macaque	6.33	15.96	[107]
48	Hispid cotton rat	6.16	13.09	[93]
49	Least shrew	5.83	15.38	[94]
50	Olive baboon	5.79	14.23	[93]
51	Gray mouse lemur	5.71	9.57	[108]
52	Common genet	5.42	21.31	[98]
53	Hamadryas baboon	5.25	12.80	[109]
54	House mouse	5.25	9.58	[80]
55	Pale-throated three-toed sloth	4.95	11.30	[110]
56	Greater short-nosed fruit bat	4.77	7.73	[111]
57	Rabbit	4.54	12.91	[112]
58	Barbary macaque	4.45	9.11	[113]
59	Pig-tailed macaque	4.42	11.04	[114]
60	Guinea pig	4.42	12.28	[115]
61	Bonnet macaque	4.37	11.45	[116]
62	Common squirrel monkey	4.29	11.28	[117]
63	Rhesus macaque	4.08	10.95	[118]
64	Yellow-spotted hyrax	3.79	17.16	[119]
65	Senegal galago	3.63	11.15	[120]
66	Patas monkey	3.58	7.93	[121]
67	Lesser dawn fruit bat	3.57	5.80	[111]
68	Black lemur	3.50	8.70	[122]
69	Horse	3.29	27.43	[39]
70	Yellow baboon	3.25	7.88	[123]
71	Cow	3.13	18.89	[39]
72	Goat	2.95	13.15	[40]
73	Long-nosed potoroo	2.58	5.81	[124]
74	Vervet monkey	2.50	5.80	[121]
75	Sheep	2.37	14.81	[39]
76	Rock hyrax	2.29	11.23	[119]
77	Guinea baboon	2.25	6.01	[109]

Continued					
78	Degu	2.16	7.51	[125]	
79	Tree hyrax	2.08	10.22	[119]	
80	Mongoose lemur	1.50	3.03	[122]	
	Semi-aquatic mammals				
81	Southern sea lion	9.71	39.29	[46]	
82	Gray seal	6.25	24.19	[52]	
83	Walrus	5.00	8.33	[48]	
84	Elephant seal	5.00	11.11	[51]	
85	Northern fur seal	4.70	12.46	[54]	
86	Cape fur seal	4.58	14.32	[45]	
87	Harp seal	3.2	12.83	[50]	
88	Sea otter	2.50	6.66	[44]	
89	Caspian seal	1.71	11.78	[49]	
	Aquatic mammals				
90	Amazon manatee	1	3.57	[64]	
91	Bottlenose dolphin	0	0	[60]	
92	Black sea porpoise	0	0	[61]	
93	White whale	0	0	[63]	
94	Amazon dolphin	0	0	[62]	

Note: Total sleep time in aquatic mammals is quantified by combining all slow-wave stages, such as moderate synchronization with sleep spindles and delta waves appearing individually in either hemisphere during unihemispheric sleep.

ness, whereas behaviorally the animal remained asleep<sup>[21]</sup>. In the same year, this sleep stage was also recorded in the rabbit<sup>[22]</sup>, and in subsequent years in the dog<sup>[23]</sup>, monkey<sup>[24]</sup>, rat<sup>[25]</sup>, mouse<sup>[26]</sup> and several other mammals (details in Table 1). The classic signs of REM sleep, such as fast low-voltage EEG, atonia, cessation of thermoregulation, and ponto-geniculo-occipital (PGO) spikes were discovered first in the cat, but tonic features associated with REM sleep were later recorded in most terrestrial mammals (for details see review<sup>[27]</sup>).

After the discovery of REM sleep in mammals, attempts were made to find it in non-mammalian species such as birds and reptiles. In 1964, two groups (Klein *et al.*, and Ookawa and Gotoh) reported a periodic recurrence of fast low-voltage EEG waves during behavioral sleep in birds<sup>[28,29]</sup>, which was later reconfirmed as REM/paradoxical sleep<sup>[30-33]</sup>. Interestingly, hippocampal theta activity (4–7

Hz), typical of mammalian REM sleep and equivalent to spontaneous mammalian PGO waves had not been reliably observed in birds<sup>[32]</sup>. Although some of the REM sleepassociated tonic features were not reliably recorded in birds, it was confirmed by several reports that REM sleep is present in birds<sup>[34]</sup>. In order to trace the phylogenetic correlates of REM sleep in lower vertebrates, attempts were made to characterize this sleep state in reptiles such as crocodiles, alligators, lizards, snakes and tortoises but REM sleep or a REM sleep-like state has never been observed or recorded in reptiles<sup>[7]</sup>. Although Huntley and associates and a few others have reported the presence of REM sleep in some reptiles<sup>[35]</sup>, clear confirmatory evidence is still lacking. Since the discovery of REM sleep, several studies have clearly demonstrated that it is found distinctly in birds and mammals and not in lower vertebrates such as reptiles, amphibians and fishes.

## **3 REM sleep in the terrestrial, semi-aquatic and aquatic mammals: Comparative studies**

3.1 REM sleep in terrestrial mammals Sleep studies have mostly been performed in mammals and REM sleep has been electrophysiologically recorded in ~80 terrestrial species (Table 1). Phylogenetically, mammals fall into three sub-classes: (1) prototheria [egg-laving mammals: the echidna (Tachyglossus aculealus) and the duckbilled platypus (Ornithorhynchus anaticus)]; (2) metatheria (marsupials such as kangaroo and opossum); and (3) eutheria (placental mammals). In the mammalian lineage, it is believed that the prototheria might have evolved from reptiles, hence are ancient in origin and a connecting link between reptiles and mammals<sup>[36]</sup>. Some features of the echidna such as microchromosomes, filiform sperm, and egg-laving, closely resemble reptiles<sup>[36]</sup> and interestingly, REM sleep has not been found reliably in echidna and reptiles<sup>[7,35,37]</sup>. It was proposed, therefore, that REM sleep might have originated in recent metatheria and/or eutheria<sup>[37]</sup>. Siegel's group, however, later found that REM sleep is present in the duckbilled platypus<sup>[12]</sup>, thus refuting the hypothesis that REM sleep evolved relatively recently. They observed that the platypus not only exhibits REM sleep, but also displays the highest amount (5.8–8 h/day), more than any other animal studied so far<sup>[12]</sup>. Further, based on the firing properties of brainstem neurons in the echidna, the same group reported that echidna sleep may have features of combined REM and NREM sleep. It remains ambiguous whether the echidna has combined aspects of REM and NREM sleep or no REM sleep because only one study has reported some of the typical characteristics of REM sleep<sup>[38]</sup>.

Ancient mammals spend the most time in REM sleep (platypus: 33.33%; Virginia opossum: 30.58%; lutrine opossum: 27.20%; ferret: 24.41%) while relatively modern mammals spend varied amounts of time, ranging from 13.42% in the cat to 3% in the cow, goat and sheep (Table 1). A decreasing trend was further noted in the mongoose lemur, which spends only 1.5% of its time per day in REM sleep (the lowest amount of REM sleep in any terrestrial

mammal studied so far) (Table 1). These data suggest that REM sleep might have evolved in ancient mammals or their ancestors, but later, during the course of evolution, it remained high in some while it dwindled in others. Further, some mammalian species sleep notably less than others. For example, cow and goat sleep only 4–5 h/ day<sup>[39,40]</sup>, while the large hairy armadillo usually sleeps 20 h/day<sup>[41]</sup>. It can also be argued that animals that sleep less would exhibit less REM sleep. Although this could be true, an important interesting fact is that the majority of both long and short sleepers maintain REM sleep at a relatively constant  $16.87 \pm 0.009\%$  of the total sleep period. Species that show exceptionally different NREM/REM sleep proportions are the platypus, opossum and ferret, which have a very high proportion of REM sleep (25-56%) and some species of bat, monkey and lemur which exhibit a very low proportion (3-7%) of the total sleep period (details in Table 1). We do not yet have a clear understanding of why some terrestrial mammals have reduced their total sleep time, although some reasons could be energy conservation, survival strategy, ecological need or other evolutionary forces<sup>[42,43]</sup>.

3.2 REM sleep in semi-aquatic mammals Pinnipeds, semi-aquatic mammals, have adapted their sleep to the aquatic environment. They have a distinctive sleep pattern as they can sleep on land as well as in water. On land, their sleep is very similar to terrestrial mammals displaying both NREM and REM sleep with bihemispheric symmetry in slow-wave generation during NREM sleep. While in water, they exhibit inter-hemispheric asymmetry in the generation of slow-waves during NREM sleep and interestingly, a substantial decrease in REM sleep<sup>[44-48]</sup>. Some pinnipeds, such as Caspian seals (*Phoca caspica*)<sup>[49]</sup>, harp seals (Pagophilus groenlandica)<sup>[50]</sup> and elephant seals (Mirounga angustirostris)<sup>[51]</sup>, do not exhibit inter-hemispheric asymmetry in slow-wave generation during NREM sleep, suggesting that unihemispheric sleep is typical of fur seals and sea lions but not of all semi-aquatic pinnipeds.

Ridgway *et al.*, in 1975, for the first time studied sleep telemetrically in four adult gray seals (*Halichoerus grypus*)<sup>[52]</sup> and found that they can sleep under the water, on the sur-

face, and out of the water. They found that sleep in gray seals is distinct from that in terrestrial mammals in many ways: (1) REM sleep comprises 6.35% of total recording time, and is accompanied by rapid but regular heart and respiratory rates (which are usually irregular during REM sleep in terrestrial mammals); and (2) REM sleep appears before NREM sleep, whereas in other terrestrial mammals it normally follows NREM sleep<sup>[52]</sup>. Later, Mukhametov et al., while recording sleep polygraphically in three subadult northern fur seals (Callorhinus ursinus), observed a sleep pattern similar to that reported by Ridgway et al. in the gray seal<sup>[52]</sup>. Mukhametov et al. recorded 5.8% REM sleep in the northern fur seal<sup>[53]</sup>. Interestingly, they also showed, for the first time, an inter-hemispheric asymmetry in the generation of slow waves during NREM sleep in the northern fur seal<sup>[53]</sup>. Later, they further confirmed this unique event as 'the generation of inter-hemispheric asynchrony of slow wave activity' in the northern fur seal and suggested that this phenomenon is not specific to aquatic cetaceans<sup>[54]</sup>. Nevertheless, in two other pinnipeds (the Caspian seal and the harp seal, which are morphologically very close to the northern fur seal), inter-hemispheric asymmetry in slow waves has not been found<sup>[49,50]</sup>. Although the harp seal does not exhibit unilateral sleep, its sleep pattern exhibits a remarkable phenomenon. When harp seals sleep on land, they exhibit ~3.2% REM sleep, but in water they barely go into REM  $(0.5\%)^{[50]}$ . Castellini et al. compared sleep in northern elephant seal pups under dry and wet conditions and demonstrated that the length of REM sleep episodes significantly decreases under wet conditions<sup>[51]</sup>. Similar characteristics have also been recorded in northern fur seals<sup>[55]</sup>. When the northern fur seal sleeps on land, it exhibits ~5% REM sleep but when it sleeps in water, the proportion of REM sleep decreases considerably<sup>[55]</sup>. In order to find similar REM sleep patterns in other mammals that have adapted to constant living in the aquatic environment, Laymin et al. investigated the behavioral sleep pattern in sea otters (Enhydra lutris) and found that they exhibit REM sleep-like behavior in water as well as on land<sup>[44]</sup>, though it is not clear if the proportion decreases significantly when they sleep in water. Interestingly, it was noted that the longest episodes of REM sleep occurred on land<sup>[44]</sup>. Further, they studied the sleep patterns in the walrus, the only surviving representative of the family Odobenidae. When on land, the walrus exhibits 6.9% REM sleep, but in water this significantly decreases to  $1.1\%^{[47]}$ . This evidence thus suggests that REM sleep is not expressed at its full length if these animals sleep in water.

The three families of pinnipeds, Odobenidae, Otariidae and Phocidae, comprise 35 species. Among these, the sleep-wakefulness pattern has been studied in only 8, and REM sleep has been reported in all of these. Most of these animals [walrus<sup>[47]</sup> (Odobenidae), elephant seal<sup>[51]</sup> and harp seal<sup>[50]</sup> (Phocidae), and northern fur seal<sup>[55]</sup> (Otariidae)] exhibit either less REM sleep or shorter REM episodes in water than on land. In another four pinnipeds: gray seal<sup>[52]</sup> and Caspian seal<sup>[49]</sup> (Phocidae); cape fur seal<sup>[45]</sup> and sea lion<sup>[46]</sup> (Otariidae) the amount of REM sleep could not be characterized in both conditions, so it is undetermined whether these animals also exhibit differential REM sleep expression on land and in water. REM sleep was also found in another semi-aquatic mammal, the sea otter, which belongs to the Mustelidae and is adapted for constant living in the aquatic environment. Nevertheless, out of the nine semiaquatic mammalian species studied so far, the majority (five species) express more REM sleep when on land, but drastically curtail it while sleeping in water. Thus, it seems that aquatic conditions may not be favorable for REM sleep.

**3.3 REM sleep in aquatic mammals** Aquatic mammals belonging to two families, Cetacea and Sirenia, have a notable sleep pattern: one half of the brain remains active while the other half sleeps, and each half exhibits ~4 h of slow-wave sleep per day<sup>[56]</sup>. John Lilly for the first time noted that dolphins sleep with one eye open and the other closed<sup>[57]</sup>. He assumed that the dolphin scans its environment all the time by keeping one half of the brain always active<sup>[57]</sup>. His finding may have led to the discovery of unihemispheric sleep in dolphins<sup>[56]</sup>.

Mukhametov and his team (in 1975) recorded EEG in the bottle-nose dolphin for the first time and reported occasional asynchronous development of EEG slow waves in both hemispheres<sup>[58]</sup>. In addition, they noted that the dolphin does not show any polygraphic signs of REM sleep<sup>[58]</sup>, though an earlier study by Shurley *et al.* (in 1969) reported episodes of REM sleep in the pilot whale<sup>[59]</sup>. In all subsequent physiological studies, however, it was confirmed that REM sleep is absent from the Cetacea bottle nose dolphin<sup>[60]</sup>, black sea porpoise<sup>[61]</sup>, amazon river dolphin<sup>[62]</sup> and beluga whale<sup>[63]</sup>, while in the amazon manatee (Sirenia), only a few episodes of REM sleep were recorded<sup>[64]</sup>. Although sleep has been studied extensively in only a few cetaceans and REM sleep is absent in most of them, further studies are needed to confirm whether REM sleep or its associated signs are indubitably absent in Cetacea. Lyamin et al. pointed out in their review that the traditional criteria used to identify REM sleep may not be appropriate for cetaceans because if dolphins have REM sleep of short duration, it could remain unnoticed<sup>[56]</sup>. Another reason for unidentified REM sleep in cetaceans could be the possibility that they have a modified form of REM sleep<sup>[56]</sup>. The latter, however, seems unlikely because the semi-aquatic pinnipeds exhibit the conventional form of REM sleep and its associated signs, living in similar conditions in water and on land. The difference in REM sleep in water and on land is that pinnipeds have significantly less REM sleep in water. It is likely that during the course of divergent evolution, REM sleep may not necessarily be required, and thus was eliminated in all aquatic mammals.

### 4 Do aquatic conditions disfavor REM sleep continuity?

Sleep in some semi-aquatic mammals is unique because it changes from bihemispheric on land to unihemispheric in water. It is noteworthy that when on land, sleep in fur seals generally resembles that of most terrestrial mammals, i.e. the sleep cycle alternates between NREM and REM sleep and the bilateral EEG exhibits synchronization during NREM sleep and desynchronization during REM sleep. But when the fur seal is in water, the occurrence of REM sleep declines to the extent that there may not be even a single episode<sup>[46]</sup>. It is not known how the brain switches from terrestrial bihemispheric to aquatic unihemispheric sleep in semi-aquatic mammals. In fact, it has been suggested that sleep in fur seals defies the principle of homeostatic regulation, since no rebound of lost REM is seen when it returns to land after staying several weeks in water<sup>[42]</sup>. Unihemispheric and bihemispheric sleep have their own specific properties, probably regulated by different mechanisms. A neuronal mechanism activated in animals when they are in water could induce the distinctive unihemispheric aquatic sleep and simultaneously eliminate REM sleep. Hence, one would not expect a REM rebound once the organism regained bihemispheric terrestrial sleep.

The amount of REM sleep in mammals may depend on their degree of adaptation to the aquatic and non-aquatic environments. REM sleep in completely aquatic mammals such as the dolphin, porpoise, white whale and manatee is either completely absent or present in a negligible amount (dolphin and white whale: 0%; manatee: 1%)<sup>[64,65]</sup>. Semiaquatic mammals such as seals exhibit comparatively more REM sleep than aquatic mammals but less than terrestrial mammals. The amount of REM sleep (% of total recording time and % of total sleep time) in 94 mammalian species is listed in Table 1. When we correlated the percentage of REM sleep out of total recording time (Fig. 1A) and also out of total sleep time (Fig. 1B) with adaptation to aquatic, semi-aquatic and terrestrial conditions for these 94 mammals, the correlations were significantly negative. Most terrestrial mammals exhibit a high amount and proportion of REM sleep compared to semi-aquatic mammals, while aquatic mammals either do not have REM sleep or even if they have it, it is very little. This suggests that when animals remain in water, aquatic conditions somehow restrain the genesis of REM sleep.

Studies on the sleep patterns in reptiles that have either adapted to aquatic life or live near water [such as the turtle, black iguanid lizard (*Ctenosaura pectinata*) and green iguanid lizard (*Iguana iguana*)] are limited. It is likely that the unitary form of sleep will be found in such animals. Sleep remains to be examined thoroughly in reptiles that stay away from water. This might provide clues regarding the evolution of the dual nature of sleep. Interestingly, REM sleep can be artificially abolished in terrestrial mammals using specific deprivation methods, such as disk-over water, multiple or single platform, and wiremesh grid platform in which water is used as the surrounding medium<sup>[66-69]</sup>. In the wire-mesh grid platform method, the animal is kept on a platform with a guard of wire mesh grid and the water level is kept 1 cm below the platform in a tank, so the animal cannot fall into the water and/or make contact with it. Merely keeping an animal in such a condition suppresses REM sleep. However, keeping an animal over water could be stressful and/or fear-inducing, and it is known that stress/fear suppresses REM sleep<sup>[70]</sup>. It is not clear what contributes to the elimination of REM sleep in these protocols, stress or the presence of water; but from the examples of sleep patterns in the semi-aquatic pinipeds, it seems that less REM sleep is expressed in aquatic conditions.

### 5 Possible advantages of REM sleep elimination in aquatic mammals

Significantly less REM sleep in semi-aquatic and some aquatic mammals and no REM sleep in cetaceans raise unanswered questions, such as whether the evolution of REM sleep in vertebrates was confined to life on land and/or whether adaptation to life in an aquatic environment inhibited the occurrence of REM sleep. It is possible that REM sleep serves a meaningful purpose only in terrestrial animals and hence its evolution is restricted to them. In the majority of terrestrial mammals, basic somatic features of REM sleep such as atonia, REMs and myoclonic twitches occur<sup>[71]</sup>. The dramatic atonic condition during REM sleep occurs because the motoneurons, which innervate muscle fibers, are actively inhibited<sup>[72]</sup>. The aquatic mammals are obligate swimmers and have evolved unihemispheric sleep, during which they can sleep with one half of the brain and simultaneously remain moving to sustain life. Therefore, a condition that could immobilize them or restrict their movement, as usually happens during REM sleep in terrestrial mammals, cannot be advantageous. In addition, it has been observed in terrestrial mammals that the thermoregulatory mechanism and response to thermal load remains suspended or inhibited during REM sleep<sup>[71]</sup>, so the responses are similar to those of poikilothermic animals.

The aquatic mammals live in thermally challenging environments and it is known that conductive heat loss is ~90 times greater in water than air. Since all mammals have distinctive thermoregulatory machinery, aquatic mammals do not differ in this from other mammals. If aquatic mammals had REM sleep, they would face the herculean task of managing their body temperature during REM sleep. There could, however, be several other reasons for doing away with REM sleep. Considering all, it seems that REM sleep may not be favorable for life in an aquatic environment and might have subsequently been reduced or eliminated in aquatic mammals.

### 6 Conclusion

We have limited information to understand the evolution of the dual nature of sleep in higher vertebrates. REM sleep has been characterized in birds and mammals only. Within mammals, however, REM sleep is absent in cetaceans and is drastically reduced in semi-aquatic mammals. Although in-depth sleep studies have only been performed in a limited number of aquatic and semi-aquatic species, the data consistently show less or no REM sleep in these animals. Since aquatic and semi-aquatic mammals live in a challenging environment, the presence of REM sleep could do more harm than good. Therefore, REM sleep might have been reduced or eliminated in the evolution of some mammals. This also indicates a great influence of selection/evolutionary forces on sleep characteristics. It has also been proposed that some aquatic mammals may survive for several weeks without sleep, while terrestrial mammals cannot survive long<sup>[73]</sup>. This suggests that the sleep patterns in aquatic and terrestrial conditions are basically distinct. Therefore, we need to develop a detailed understanding of the evolution of sleep and its functions.

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