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Big Birds and Their Brains: Paleoneurology of the New Zealand Moa

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Key Words
Ratites · Wulst · Hyperpallium · Olfactory bulb · Encephalization · Dinornithiformes

Abstract
The moa (Dinornithiformes: Aves) are an extinct group of ratites from the North and South Islands of New Zealand. The ancestors of both the moa and the kiwi were isolated from other Gondwanan fauna as much as 80 million years ago and evolved in the absence of large mammalian predators. As such they represent a natural experiment in the removal of mammalian predation pressure on the encephalization of these two groups of ratites. We have used endocranial and skull morphometry in conjunction with high resolution CT scanning of the skulls of 8 species of moa to assess encephalization and brain morphology in moa and compare these features with extant ratites. Absolute brain size among the moa ranged from 17.0 ml for *Euryapteryx curtus* to 60.0 ml for female *Dinornis robustus*. Values for encephalization quotients (EQ) of moa ranged from 0.205 for *Euryapteryx gravis* of the southern North Island to a mean (± SD) of 0.475 (± 0.026) for *Anomalopteryx didiformis*, partially overlapping values for extant non-New Zealand ratites (emu: 0.402 ± 0.042; rhea: 0.496 ± 0.016; ostrich: 0.474 ± 0.084). Nevertheless, mean ± SD EQ for all moa examined (0.379 ± 0.065) was significantly lower than EQ for extant non-New Zealand ratites (0.539 ± 0.141). Bending of the endocranial axis was much less among moa than either the kiwi or non-New Zealand ratites, consistent with the caudal position of the foramen magnum and the horizontal carriage of the head and upper neck during life. Endocranial morphology of the moa species examined was similar to that for non-New Zealand ratites, with proportionally similar sizes of the olfactory bulb, Wulst, vagal and maxillomandibular foramina, suggesting that the moa occupied similar diurnal niches with comparable sensory specializations to the emu, rhea and ostrich. No evidence of olfactory specialization (i.e., enlarged olfactory bulbs and increased surface area of the olfactory nasal cavity or cribriform plate) was evident in any of the moa skulls, in contrast to the remarkable nasal and olfactory bulb specializations evident in the skull and brain of the little spotted kiwi *(Apteryx owenii)*. We cannot exclude that isolation in the absence of highly encephalized mammalian predators might have contributed to the lower EQ among moa, but it certainly did not lead to any significant reduction in EQ for kiwi; rather the kiwi embarked on a remarkable path of neurological specialization, which allowed them to exploit a niche usually occupied elsewhere by mammals.

Introduction

When New Zealand separated from the south-eastern coast of Gondwana approximately 80 million years ago [Sutherland, 1999], the ancestor/s of two modern groups of ratites became isolated on the evolving New Zealand archipelago. The moa were the tallest birds ever known to have existed and came to occupy the browsing niches filled by marsupial and eutherian mammals in other fragments of Gondwana. Molecular dating of mitochondrial

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DNA from moa remains suggests that they diverged from other ratites approximately 82 mya [Cooper et al., 2001] and that the most recent common ancestor of the Holocene moa existed after the Oligocene [Baker et al., 2005]. Radiation of the moa lineages probably occurred between 4 and 13 million years ago [Cooper et al., 2001; Baker et al., 2005]. All 10 Recent species of moa [Bunce et al., 2003, 2005] became extinct by the 15th century AD, largely as a result of human hunting [Holdaway and Jacomb, 2000], but, during the Pleistocene and Holocene (and probably before), these giant birds apparently filled an ecosystem without any mammalian predators [although evidence of a small Miocene mammal has recently been found in the South Island; Worthy et al., 2006]. The only known predator of moa was the large Haast's eagle *(Harpagornis moorei)*, which is thought to have killed moa of even adult size (200 kg). Haast's eagle is believed to be a recent arrival in New Zealand's South Island and to have been derived within the past 1.8 mya from a small Asian/Australian *Hieraatus* eagle [Bunce et al., 2005].

The other ratite group evolving in isolation on the New Zealand archipelago includes the ancestors of the still extant kiwi (Casuariiformes: Apterygidae). The flightless kiwi occupy a niche similar to that of eutherian and placental mammalian insectivores and exhibit anatomical and neurological specializations that are consistent with nocturnal insectivores [Martin et al., 2007].

Progressive increase in encaphalization quotients (EQ) of birds and mammals during the Cenozoic has been attributed to on-going competition between predators and prey [Jerison, 1973]. The absence of mammalian predators in Quarternary New Zealand, in contrast to other Gondwanan fragments (i.e., Africa, South America, Australia, New Guinea), provides the opportunity to assess the effect of selection pressure by highly encephalized mammalian predators (or its absence) on the encephalization of prey species. Therefore one of the aims of our study was to determine if the moa were less encephalized than ratites from other remnants of Gondwana (e.g., Africa), where ratites have been exposed to highly encephalized mammalian predators for many millions of years.

We analyzed CT scans of moa skulls to allow the assessment of likely behavior and sensory specialization of moa. Owen's original assessment of *Dinornis giganteus* in 1849 was that moa possessed better sight than kiwi and were diurnal, although they were also considered of a 'less delicate perception' than modern ratites and 'duller and more stupid than the dodo' [Owen, 1849, see also review in Anderson, 1989]. Several authors have suggested that moa shared the kiwi olfactory specializations (i.e., enlarged olfactory chambers and olfactory bulbs) [Anderson, 1989; Tennyson and Martinson, 2006], but this remains controversial and has never been assessed by modern high resolution CT analysis [Anderson, 1989]. The second aim of our study was therefore to examine the interior of moa skulls virtually sectioned by CT to compare interior features associated with sensory function (olfactory bulb volume, cribriform plate area, optic foramen area, Wulst area, maxillomandibular foramen area) with those in other ratites and kiwi.

Materials and Methods

We used Breazile and Kuenzel [1993] for all endocranial terminology as modified [Reiner et al., 2004; Jarvis et al., 2005]. The findings of the present study are based on analysis of the skulls of 45 moa from 8 species, 15 kiwi from 3 species and 17 non-New Zealand ratites from 5 species. Material was from the Canterbury Museum (Christchurch), Otago Museum (Dunedin), the Australian Museum (Sydney) and University of New South Wales Zoology Department (Sydney).

Endocranial volume (ECV) was measured by either the dried mustard seed technique (all specimens in tables 1 and 2) [Stewart, 1947] or from pixel counting of high-resolution spiral CT (Madena X program) on selected specimens (see table 3). Re-measurement of ECV by the mustard seed technique showed that estimates were reproducible within ± 0.25 ml and there was good agreement between estimates for those specimens for which both mustard seed and CT pixel counting data were obtained. In the present study, ECV was considered to be equivalent to brain weight for a given species (E_i), as has been used by previous authors for avian skulls [Jerison, 1973; Iwaniuk and Nelson, 2002]. The presence of the impressions of cerebral and cerebellar fissures on the insides of moa skulls indicated that brain volume corresponded closely (i.e., within a few percent) with ECV even allowing for the pituitary fossa and orifices of foramina. Specific gravity of the brain was assumed to be 1 g/ml [Jerison, 1973; Larsson et al., 2000].

Mid-shaft femoral circumference (C_f) was measured for those specimens where matching femora were available and body mass (W) in kg was estimated using the power function $W = 0.16C_f^{2.73}$ [Anderson et al., 1985; Murray and Vickers-Rich, 2004]. Femoral circumference was measured by wrapping a length of cotton around the circumference of the femur at its narrowest point, drawing this tight and marking the cotton ends in contact with a fine felt pen. The cotton length between the dots was subsequently measured with a caliper. A recent thesis comparing methods of body weight estimation concluded that femoral circumference is a better estimator of body weight than measurements of the tibiotarsus [Dickison, 2007]. For those kiwi specimens where no femora were available, W was estimated from foramen magnum area using the regression of foramen magnum area against W for those kiwi where femora were available. Where matching femora were not available for moa, the range of W for that taxa was used to calculate the range of likely EQ and a midrange body mass used when it was necessary to calculate a single EQ value for each specimen.

Table 1. ECV and EQ of moa

Species/specimen	ECV ml	Estimated W[a] or range of W[b], kg	EQ/range of EQ
Anomalopteryx didiformis			
AV8548 (Cant.)	26.5	19.0 – 73.0	0.338 – 0.725
AV16410 (Cant.)	21.5	30.3	0.417
AV3688 (Otago)	26.0	19.0 – 73.0	0.332 – 0.712
AV3690 (Otago)	23.0	19.0 – 73.0	0.293 – 0.629
AV3691 (Otago)	23.0	19.0 – 73.0	0.293 – 0.629
AV3692 (Otago)	26.0	19.0 – 73.0	0.332 – 0.712
AV3696 (Otago)	24.0	19.0 – 73.0	0.306 – 0.657
AV3697 (Otago)	25.5	19.0 – 73.0	0.325 – 0.698
AV6039 (Otago)	23.5	19.0 – 73.0	0.300 – 0.643
AV7491 (Otago)	24.5	19.0 – 73.0	0.313 – 0.670
Mean ± SD	24.4 ± 1.6		0.475 ± 0.026
Dinornis robustus			
AV8713 (Cant.)	60.0	F: 76.0 – 242.0	0.388 – 0.748
AV8717 (Cant.)	51.5	F: 76.0 – 242.0	0.333 – 0.642
AV14366 (Cant.)	48.5	F: 76.0 – 242.0	0.314 – 0.605
AV29786 (Cant.)	43.0	M: 34.0 – 85.0	0.503 – 0.846
A50:89 (Otago)	55.0	F: 76.0 – 242.0	0.356 – 0.686
AV3806 (Otago)	54.0	F: 76.0 – 242.0	0.349 – 0.673
AV3808 (Otago)	53.0	F: 76.0 – 242.0	0.343 – 0.661
Mean ± SD	52.1 ± 5.3		0.432 ± 0.044
Dinornis novaezelandiae			
AV3811 (Otago)	48.8	167.0	0.389
Emeus crassus			
AV8305 (Cant.)	22.0	36.0 – 79.0	0.268 – 0.419
AV8327 (Cant.)	22.0	106.8	0.226
AV8360 (Cant.)	19.5	70.8	0.253
AV13774 (Cant.)	21.5	111.2	0.216
AV3701 (Otago)	22.0	36.0 – 79.0	0.268 – 0.419
AV3704 (Otago)	21.5	36.0 – 79.0	0.262 – 0.410
AV3707 (Otago)	24.0	36.0 – 79.0	0.293 – 0.457
AV3752 (Otago)	24.0	36.0 – 79.0	0.293 – 0.457
AV3776 (Otago)	20.0	36.0 – 79.0	0.244 – 0.381
AV3785 (Otago)	27.0	36.0 – 79.0	0.329 – 0.514
AV3786 (Otago)	29.5	36.0 – 79.0	0.360 – 0.562
Mean ± SD	23.0 ± 3.0		0.314 ± 0.066
Euryapteryx curtus			
AV3798 (Otago)	17.0	31.0	0.353
Euryapteryx gravis			
AV9285 (Cant.)	23.5	142.9	0.205
A81.32 (Otago)[c]	27.0	52.0 – 109.0	0.274 – 0.418
AV3762 (Otago)[c]	23.5	52.0 – 109.0	0.239 – 0.363
AV3765 (Otago)[c]	24.0	52.0 – 109.0	0.244 – 0.371
AV3770 (Otago)[c]	25.5	52.0 – 109.0	0.259 – 0.394
AV3771 (Otago)[c]	21.5	52.0 – 109.0	0.219 – 0.332
AV3772 (Otago)[c]	26.5	52.0 – 109.0	0.269 – 0.410
Mean ± SD	24.7 ± 2.1		0.298 ± 0.025
Pachyornis australis			
AV36430 (Cant.)	31.0	44.0 – 90.0	0.351 – 0.527
OR151 (Cant.)	33.8	44.0 – 90.0	0.383 – 0.574
Mean ± SD	32.4 ± 2.0		0.438 ± 0.026
Pachyornis elephantopus			
AV3676 (Otago)	30.0	73.0 – 96.0	0.328 – 0.383
AV3679 (Otago)	29.5	73.0 – 96.0	0.322 – 0.376
AV3680 (Otago)	31.5	73.0 – 96.0	0.344 – 0.402
AV3682 (Otago)	29.0	73.0 – 96.0	0.317 – 0.370
AV3685 (Otago)	29.0	73.0 – 96.0	0.317 – 0.370
AV4661 (Otago)	30.5	137.8	0.271
Mean ± SD	29.9 ± 1.0		0.332 ± 0.032

F = Female; M = Male.

[a] Estimated by the power function relating body weight (W) to femoral shaft circumference (C_f): $W = 0.16C_f^{2.73}$ [Anderson et al., 1985; Murray and Vickers-Rich, 2004].

[b] Range of body weights given by Tennyson and Martinson [2006].

[c] These specimens are catalogued under the older name of *Euryapteryx geranoides*.

Table 2. Encephalization of non-moa ratites

Species	n	ECV, ml	Range of BW, kg	Mean EQ ± SD
Apteryx australis	3	11.7 ± 1.2	2.97–3.60	0.861 ± 0.053
Apteryx haastii	3	9.7 ± 0.8	1.80–2.86	0.871 ± 0.195
Apetryx owenii	10	6.9 ± 0.6	0.65–2.31	0.943 ± 0.167
Casuarius casuarius	3	31.2 ± 1.8	38.3–45.3	0.550 ± 0.020
Dromaius novaehollandiae	6	21.9 ± 2.7	35.5–41.8	0.402 ± 0.042
Pterocnemia pennata	1	11.0	3.6	0.773
Rhea americana	3	18.3 ± 1.9	16.9–23.6	0.496 ± 0.016
Struthio camelus	4	41.4 ± 3.3	80.00–128.5	0.474 ± 0.084

Table 3. Summary of Quantitative Analysis of CT scans

Specimen	Species	ECV by seed ml	ECV by CT ml	Volume of fore- and midbrain, ml (% of ECV)	Volume of hindbrain ml (% of ECV)	Volume of pituitary fossa, ml (% of ECV)	Volume of olfactory bulb, ml (% of ECV)	Area of Wulst, mm^2 (% of fore- and midbrain surface area)	Optic foramen area mm^2	Vagal foramen area mm^2	Maxillo-mandibular foramen area mm^2
AV8548	*An. didiformis*	26.5	25.7	19.4 (75.5)	5.72 (22.3)	0.56 (2.2)	0.16 (0.62)	321.6 (9.22)	0.09	0.06	0.12
AV29786	*D. robustus* (M)	43.0	41.6	30.0 (72.2)	11.4 (27.3)	0.22 (0.05)	0.40 (0.96)	855.0 (18.3)	0.17	0.09	0.10
AV8713	*D. robustus* (F)	60.0	59.3	44.6 (75.2)	13.7 (23.0)	1.08 (1.8)	0.50 (0.84)	1111.8 (18.3)	0.26	0.14	0.16
AV3811	*D. novaezelandiae*	NA	48.8	33.9 (69.5)	14.1 (28.9)	0.78 (1.6)	0.47 (0.96)	698.0 (13.8)	0.21	0.11	0.15
AV8305	*Em. crassus*	22.0	21.3	15.9 (74.7)	5.02 (23.6)	0.36 (1.7)	0.08 (0.38)	440.4 (14.4)	0.15	0.09	0.11
AV3798	*Eu. curtus*	17.0	15.6	11.7 (75.0)	3.53 (22.6)	0.37 (2.4)	NA (–)	388.8 (15.6)	0.07	0.04	0.07
AV3772	*Eu. gravis* (Sth)	26.5	25.9	18.7 (72.3)	6.65 (25.7)	0.51 (2.0)	0.18 (0.70)	604.4 (17.7)	0.18	0.11	0.13
AV9285	*Eu. gravis* (Nth)	23.5	23.3	18.3 (78.6)	4.68 (20.1)	0.31 (1.3)	0.12 (0.52)	457.8 (13.6)	0.15	0.09	0.09
AV36430	*Pachyornis australis*	31.0	30.6	22.0 (71.9)	8.12 (26.5)	0.48 (1.6)	0.10 (0.33)	654.0 (17.2)	0.15	0.12	0.16
OR151	*Pachyornis australis*	NA	33.8	24.7 (73.1)	8.26 (24.5)	0.84 (2.5)	0.24 (0.71)	593.4 (14.5)	0.11	0.10	0.09
AV3680	*P. elephantopus*	31.5	32.2	20.5 (63.7)	11.08 (34.4)	0.62 (1.9)	0.21 (0.65)	553.2 (15.3)	0.15	0.10	0.13
S535	*Apteryx owenii*	7.2	7.3	5.48 (75.0)	1.66 (22.7)	0.17 (2.3)	0.84 (11.5)	NA (–)	0.02	0.03	0.05
A6246	*Dr. novaehollandiae*	20.5	20.2	15.3 (75.9)	4.41 (21.8)	0.46 (2.3)	0.38 (1.88)	496 (16.6)	0.18	0.07	0.07
O65426	*R. americana*	20.5	19.8	15.0 (75.7)	4.35 (22.0)	0.46 (2.3)	0.17 (0.87)	419.6 (14.3)	0.22	0.12	0.13
S941	*S. camelus*	40.0	41.0	31.7 (77.3)	8.09 (19.7)	1.22 (3.0)	0.29 (0.71)	663.2 (13.7)	0.29	0.14	0.11

NA = Not assessable.

The EQ for a given specimen i (EQ_i) was calculated using $EQ_i = E_i/0.1371W_i^{0.568}$ using allometric constants for brain volume (E_i) versus body mass (W_i) derived from measurements of 1,482 species of birds (r = 0.939) [Iwaniuk and Nelson, 2003].

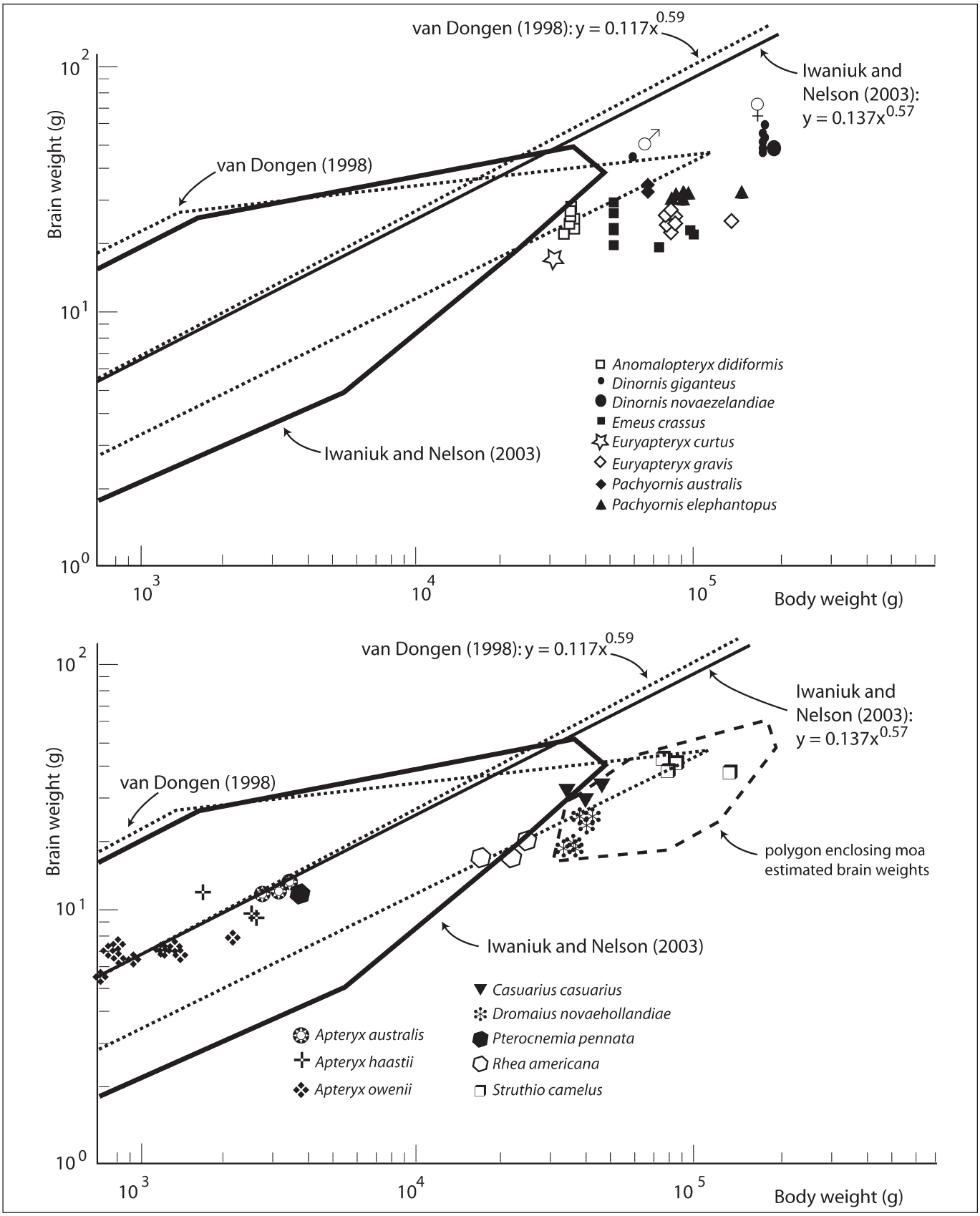
CT scans were performed on 15 specimens of moa and other ratites (ostrich – *Struthio camelus*, emu – *Dromaius novaehollandiae*, rhea – *Rhea americana*, little spotted kiwi – *Apteryx owenii*) at Christchurch (Christchurch Radiology Group, St George's Hospital, Siemens Somatom Definition, 120 kV, 400 mA, 0.6 mm slice thickness), Dunedin (Dunedin Hospital, Phillips Brilliance Big Bore, 120 kV, 200 mA, 0.8 mm slice thickness) and Sydney (WalesCT, Prince of Wales Hospital, Toshiba Aquilion 16 slice 0.6 mm slice thickness). Sagittal sections were used to estimate total ECV and the volumes of various subregions (combined fore-and midbrain; hindbrain – cerebellum, pons and medulla; pituitary fossa). Foramina for cranial nerves could also be identified and their area measured as seen in the sagittal plane. These included the optic foramen (II), maxillomandibular foramen (V2, V3); and the vagal foramen (IX, X, XI) [Bellairs and Jenkin, 1960; Bubien-Waluszewska, 1981]. Olfactory bulb volume was estimated from analysis of coronal sections where the cribriform plate defines the medial and lateral extent of the bulb. The surface area of the Wulst was also estimated from coronal sections, where the lateral extent of the hyperpallium is clearly demarcated in all moa and non-New Zealand (NZ) ratites by the prominent vallecula ridge on the inside of the skull.

Results

Estimation of EQ for Moa, Kiwi and Non-New Zealand Ratites

ECV (estimated brain mass) for most of the moa fell outside the minimum side convex polygons enclosing plotted values for brain and body weights of other bird species [221 bird species of van Dongen, 1998; or 1482 bird species (including Struthioniformes) of Iwaniuk and Nelson, 2003] (fig. 1a). Values for the non-NZ ratites measured in the present study also either fell within the minimum side convex polygon enclosing values for moa (ostrich, emu and some cassowary; fig. 1b) or in the case of rheas (fig. 1b) were at a similar distance below the regression lines obtained for birds [van Dongen, 1998; Iwaniuk and Nelson, 2003]. By contrast, all three kiwi species examined had estimated brain weights falling within the minimum side convex polygons for birds [van Dongen, 1998; Iwaniuk and Nelson, 2003].

Fig. 1. Brain size and body weight in moa (**a**), and for kiwi and non-NZ ratites (**b**). Two minimum side convex polygons derived from the data sets of other authors have been included for modern birds [221 species: van Dongen, 1998; 1482 species: Iwaniuk and Nelson, 2003]. The van Dongen data, although based on fewer species, includes specimens of higher body weight which provide a better comparison with moa. The respective regression lines for the two data sets are also indicated. The corner of the van Dongen polygon which lies among the moa data represents values for an ostrich. The dashed line in **b** represents the minimum side convex polygon enclosing moa brain weight estimates. Body weight values for those moa without accompanying femora are midpoints for the body weight range for that species [Tennyson and Martinson, 2006].


van Dongen (1998): y = 0.117x^0.59
Iwaniuk and Nelson (2003): y = 0.137x^0.57
van Dongen (1998)
Iwaniuk and Nelson (2003)
Brain weight (g)
Body weight (g)
10^2
10^1
10^0
10^3
10^4
10^5
♀
♂
Anomalopteryx didiformis
Dinornis giganteus
Dinornis novaezelandiae
Emeus crassus
Euryapteryx curtus
Euryapteryx gravis
Pachyornis australis
Pachyornis elephantopus
van Dongen (1998): y = 0.117x^0.59
Iwaniuk and Nelson (2003): y = 0.137x^0.57
van Dongen (1998)
polygon enclosing moa estimated brain weights
Iwaniuk and Nelson (2003)
Brain weight (g)
Body weight (g)
Apteryx australis
Apteryx haastii
Apteryx owenii
Casuarius casuarius
Dromaius novaehollandiae
Pterocnemia pennata
Rhea americana
Struthio camelus

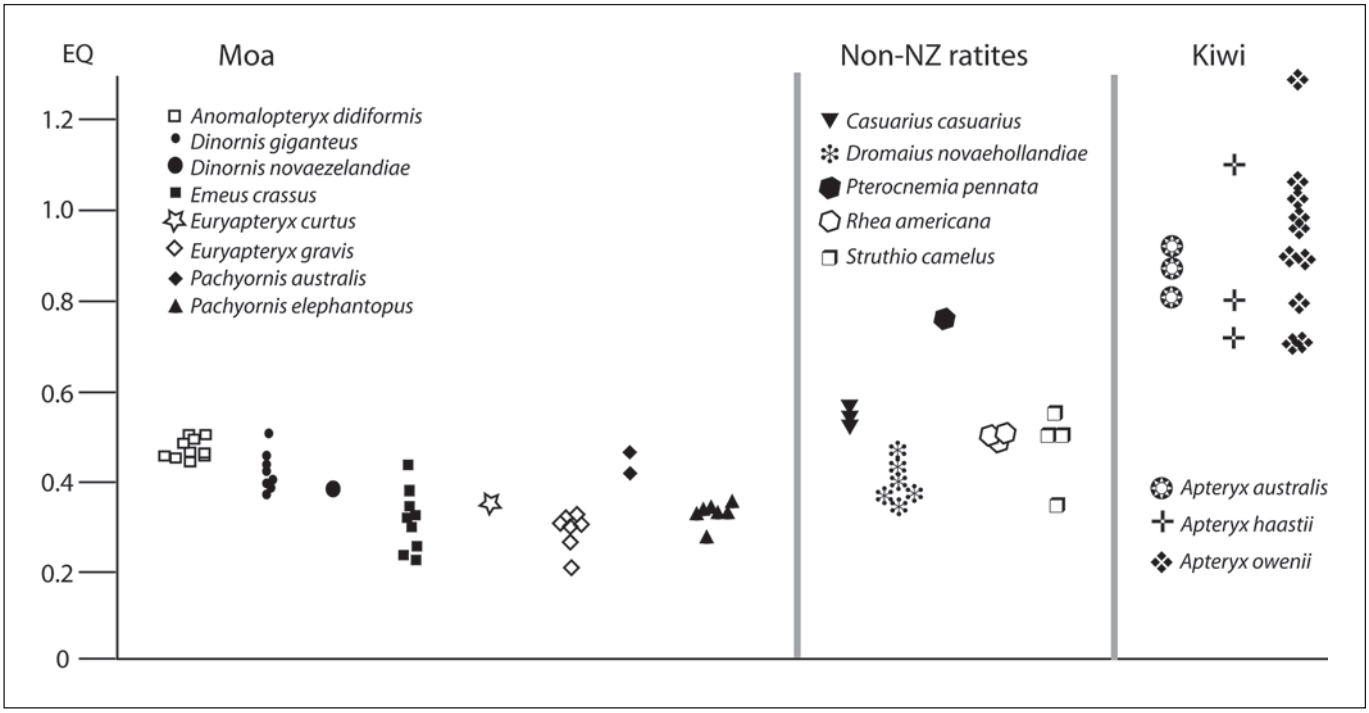


Fig. 2. Line diagram illustrating EQ of moa species compared to kiwis and non-NZ ratites. Each point represents a single bird. EQ values for those moa without accompanying femora are calculated using body weight values which are midpoints for the body weight range for that species [Tennyson and Martinson, 2006].

Values for EQ of moa and other ratites are shown in figure 2 and in tables 1 and 2. There was no consistent relationship between EQ and body weight among the moa, with high EQ values among both the smaller *Anomalopteryx didiformis* (19 to 73 kg) and the very large female *Dinornis robustus* (76 to 242 kg) [Tennyson and Martinson, 2006]. The range of EQ for all moa examined (0.204 to 0.513) was partially co-extensive with the range of EQ for non-NZ ratites (0.351 to 0.773) but the mean EQ (± SD) for 8 moa species of 0.379 (± 0.065) was significantly lower than the sample of 5 non-NZ ratites (0.539 ± 0.141) by the Mann-Whitney test (d.f. = 11, p = 0.023). There was also a significant difference in EQ between moa and non-NZ ratites when the van Dongen allometric constants were applied [van Dongen, 1998].

Endocranial Morphology of Moa Skulls

The overall shape of the endocranial cavity of the examined moa was broadly similar at the rostrocaudal level of the optic chiasm (fig. 3) and the optic lobe (fig. 4) and showed some significant differences and similarities when compared to little spotted kiwi *(Apteryx owenii)* and non-NZ ratites (ostrich, emu, rhea) crania examined at the same levels. Both the moa and the non-NZ ratites all showed prominent impressions on the endocranium corresponding to the Wulst or Eminentia sagittalis (dorsal pallium or hyperpallium) with a pronounced ridge (vallecula) marking its lateral border (fig. 3), whereas no vallecula ridge was visible on the interior of the kiwi skull. The proportion of the endocranial surface occupied by the Wulst appeared to be similar for all the non-NZ ratites and the moa. Some moa skulls (best illustrated by *Pachyornis elephantopus*, fig. 3n) showed a small ridge demarcating the boundary between the medial hyperpallium and the hippocampal region. The fossa for the optic chiasm (chiasma opticum) and anterior pituitary (hypophysis anterior) appeared to be deeper in the non-NZ ratites than in most of the moa, although that for *Emeus crassus* measured up to 10 mm dorsoventrally, which is comparable to that in the rhea.

At the level of the optic lobe (fig. 4, corresponding to the rostrocaudal level of the trigeminal ganglion and the exit of the maxillomandibular foramen), all the non-NZ ratites had a deep fossa for the optic lobe with a bony shelf

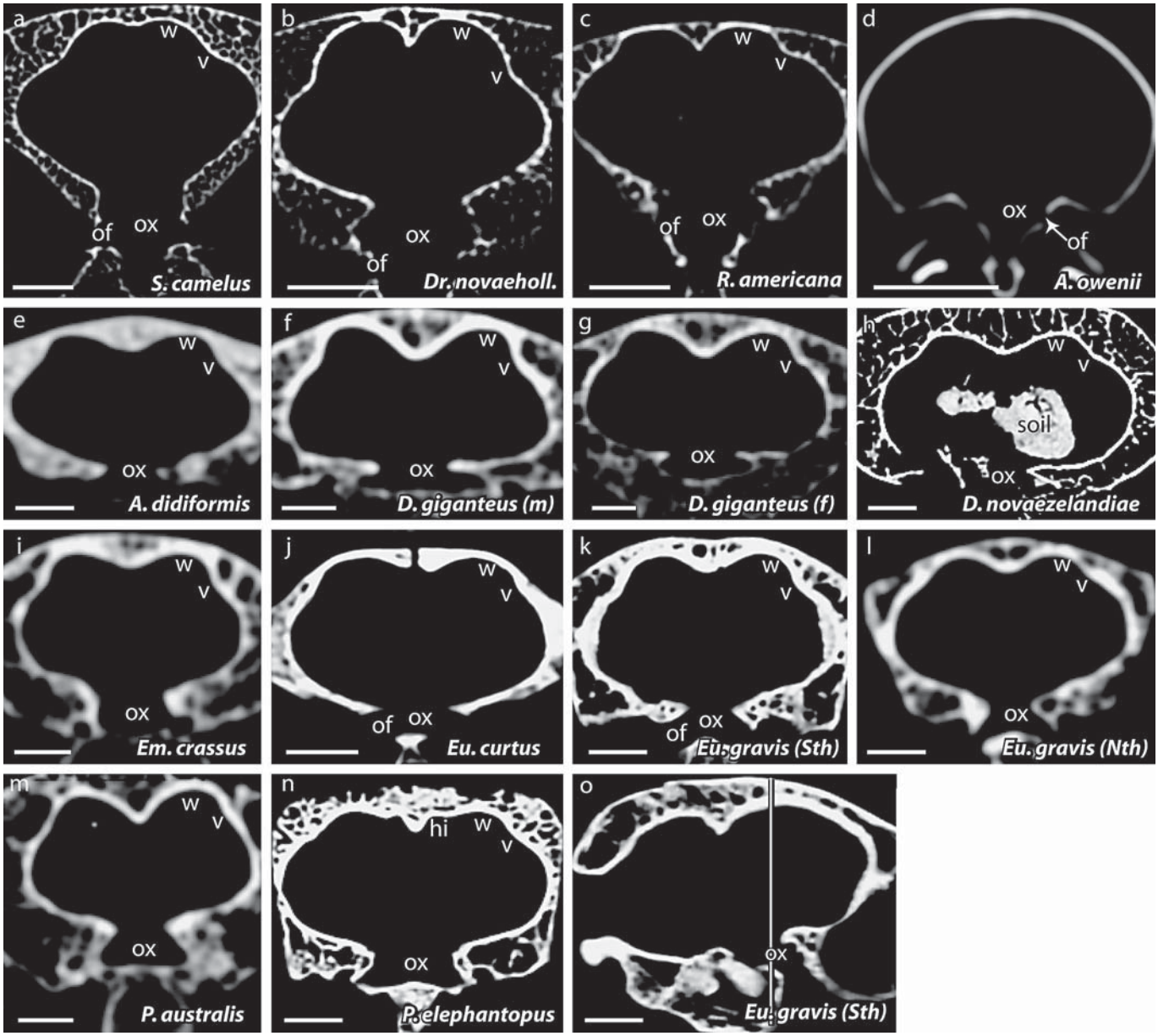


Fig. 3. Coronal CT scans through the endocranial cavity at the level of the optic chiasm (ox) for non-NZ ratites (**a–c**), a kiwi (**d**) and moa (**e–n**). Note that both South and North Island specimens of *Euryapteryx gravis* are illustrated (**k** and **l**, respectively). Scale bar in each image indicates 10 mm. Plate **o** shows the rostrocaudal level of the section as seen in a sagittal scan. hi = Hippocampus; of = optic foramen; w = Wulst; v = ridge corresponding to the vallecula.

demarcating the optic lobe from the overlying medial pallium (including the parahippocampal area) in the emu and rhea (fig. 4b, c). By contrast, the little spotted kiwi (fig. 4d) showed no evidence of an endocranial impression corresponding to the optic lobe. Most moa also showed prominent bony ridges separating the optic lobe from a presumptive parahippocampal region (e.g., *Anomalopteryx didiformis*, fig. 4e; both *Dinornis* species, fig. 4f–h; *Euryapteryx gravis* (North Island), fig. 4l; both *Pachyornis* species, fig. 4m, n), but the lateral margin of the forebrain extended much further beyond the optic lobe in all moa species compared to the situation in the

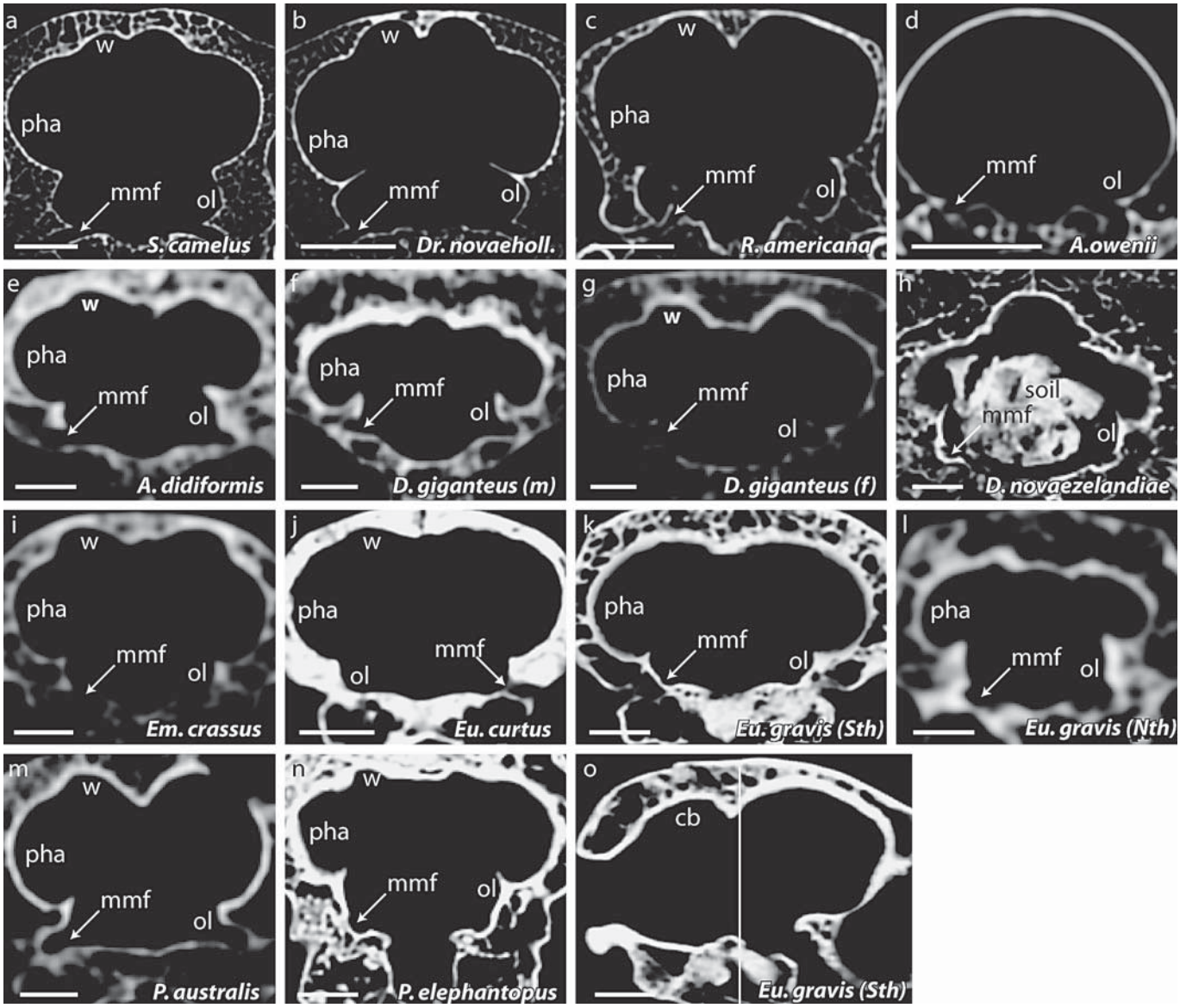


Fig. 4. Coronal CT scans through the endocranial cavity at the level of the opening of the maxillomandibular foramen (mmf) and optic lobe (ol) for non-NZ ratites (**a–c**), a kiwi (**d**) and moa (**e–n**). Plate **o** shows the rostrocaudal level of the other scans as seen in a sagittal scan. Scale bar in each image indicates 10 mm. cb = Cerebellum; pha = parahippocampal area; w = Wulst.

non-NZ ratites. All the endocranial cavities of the moa also appeared to be more dorsoventrally compressed than the ostrich, emu, or rhea. The maxillomandibular foramen was a prominent feature on the interior of the skulls of all the ratites, usually arising from the lower part of the optic lobe impression where the trigeminal ganglion should also have been situated (fig. 4).

Reconstructions of the interior of the left half of the skull (fig. 5) as viewed from the opposite side showed that the flexion of the endocranial cavity of all moa was substantially less than that for the other ratites examined. In fact, *Euryapteryx gravis* (North Island) and *Pachyornis australis* showed retroflexion of the endocranial axis of –9.4° and –15.0°, respectively (fig. 5j, k). Olfactory bulbs were not obviously enlarged in any of the moa examined and, as noted above from coronal sections, the pituitary fossa was usually shallower than in the ostrich (fig. 4a).

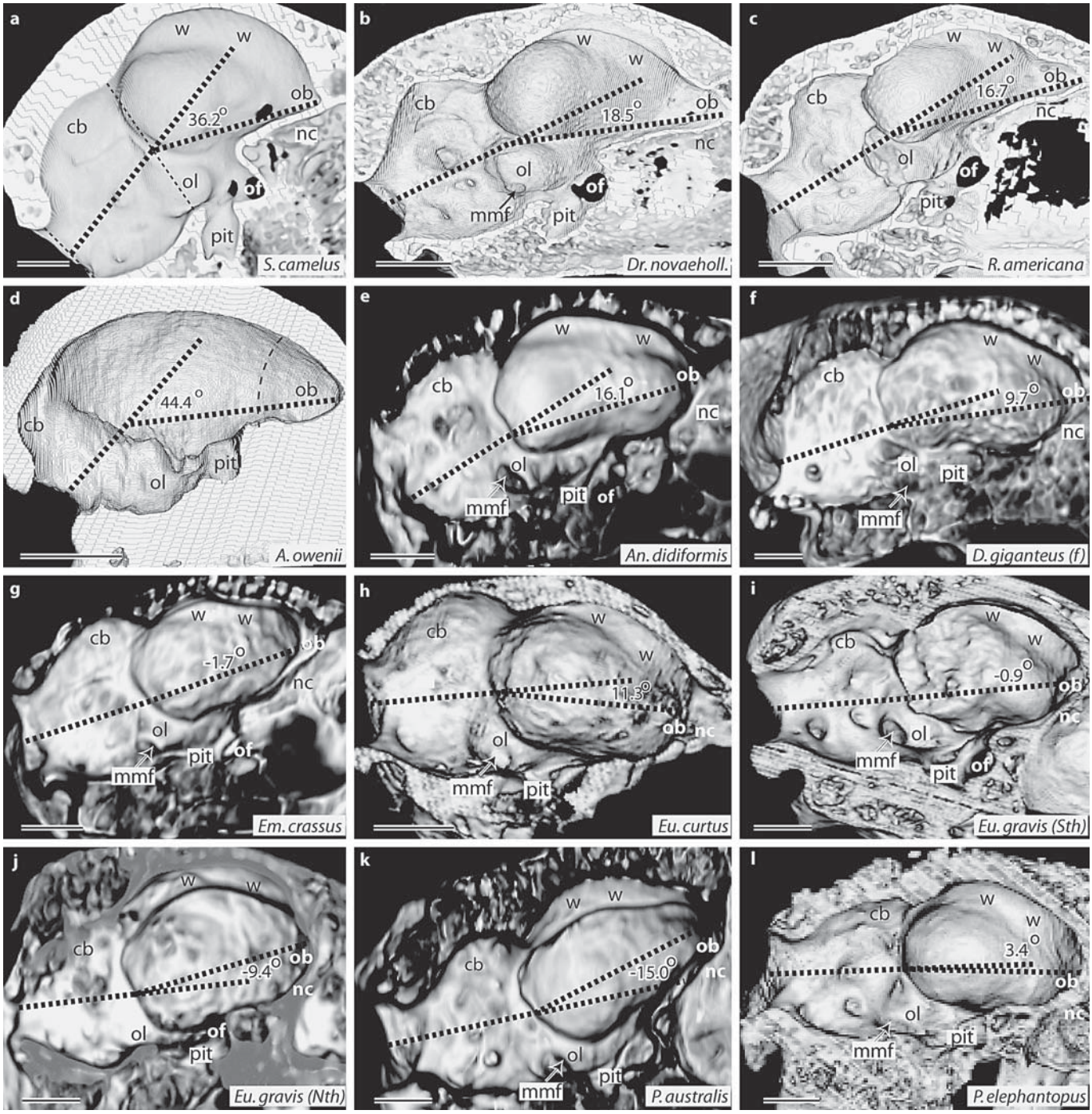


Fig. 5. Interior of the left half of the reconstructed skull of three non-NZ ratites (**a–c**), a kiwi (**d**) and selected moa (**e–l**). ob = Position of olfactory bulb; pit = pituitary fossa; nc = nasal cavity. Other abbreviations as for previous figures. Heavy dashed lines indicate the path of the endocranial axis from the tip of the olfactory bulb to the midpoint of the isthmic constriction and thence to the midpoint of the foramen magnum. Both the isthmic constriction and foramen magnum are indicated by light dashed lines in figure **a**. Scale bars indicate 10 mm.

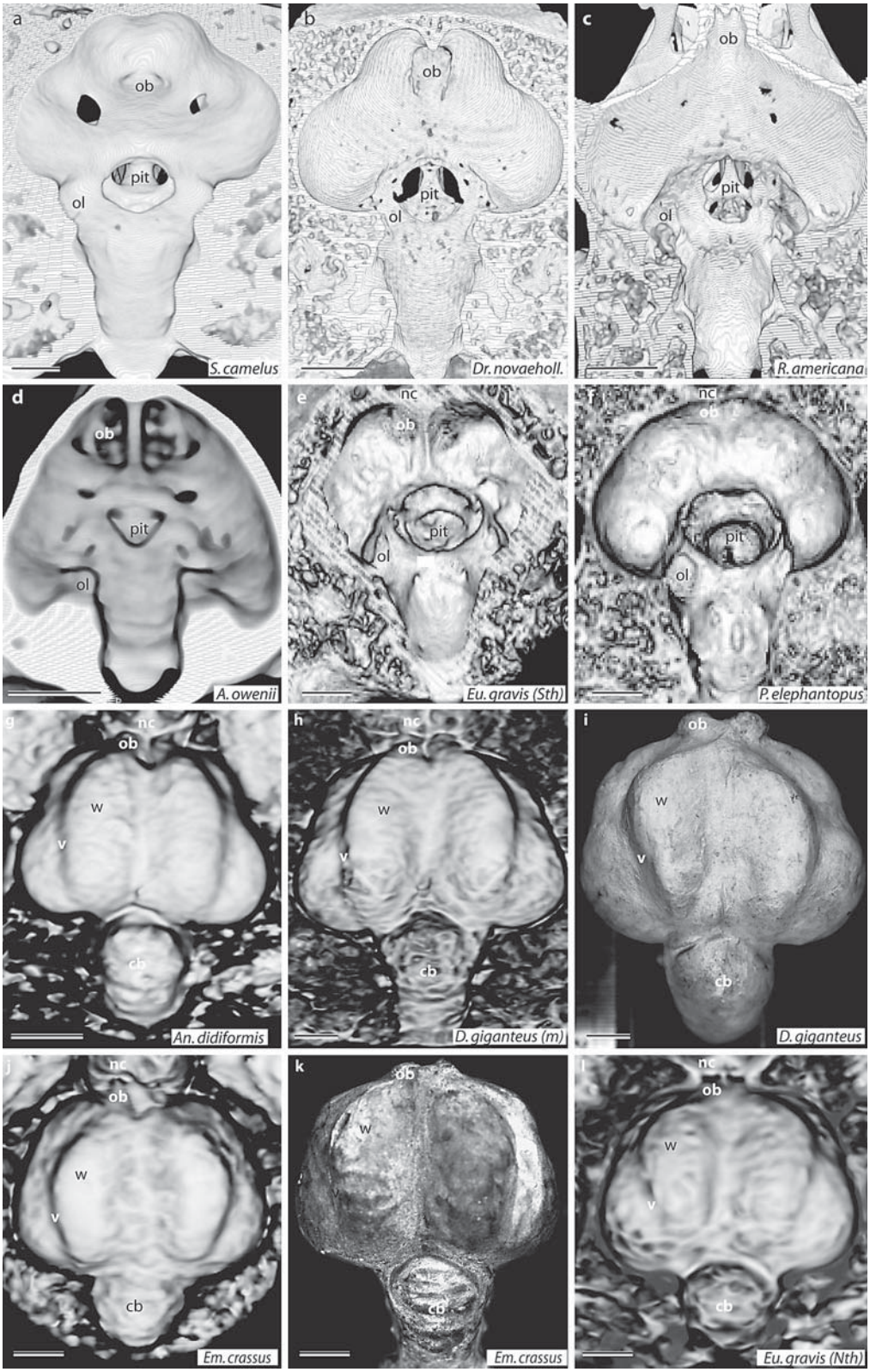


Fig. 6. Views of the floor (**a–f**) and roof (**g**, **h**, **j**, **l**) of the endocranial cavity in reconstructed skulls from non-NZ ratites (**a–c**), a kiwi (**d**) and selected moa (**e–l**). Figures **i** and **k** show views of the dorsal surfaces of the cranial endocasts of two moa in the Canterbury Museum collection. Abbreviations as for previous figures. Scale bars indicate 10 mm.

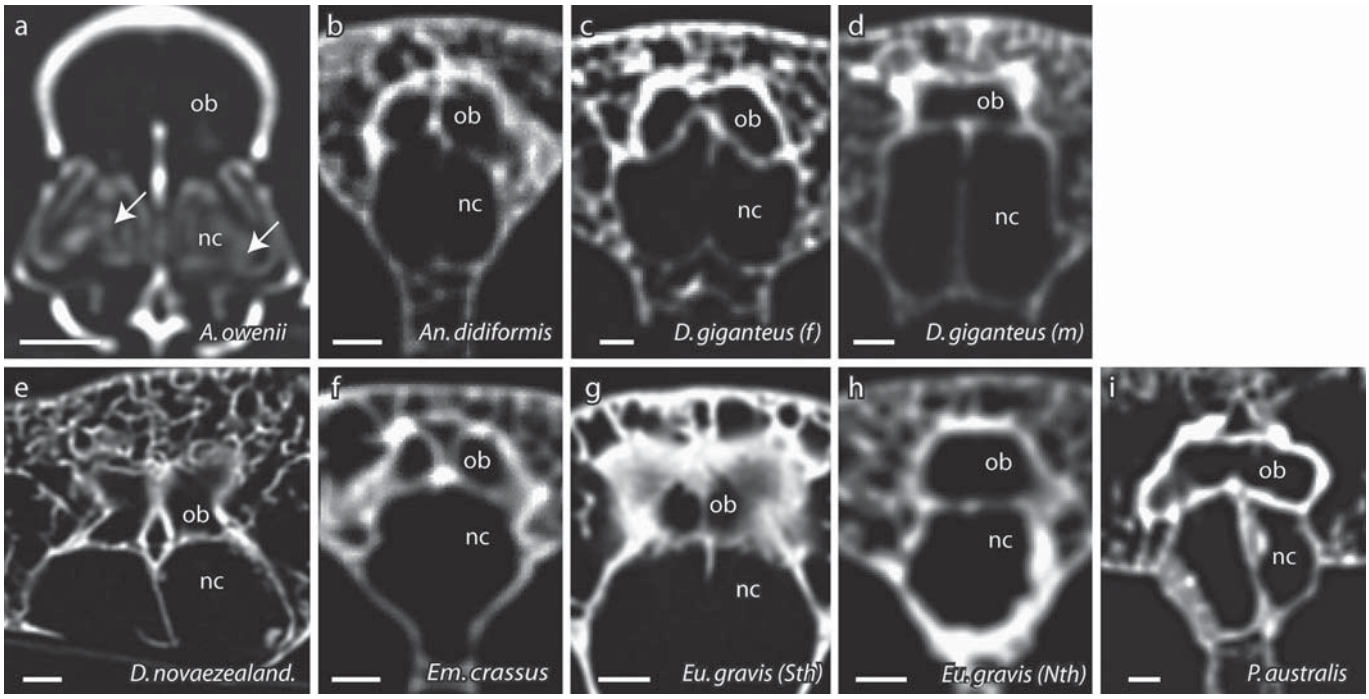


Fig. 7. Coronal CT scans through the olfactory bulb and nasal cavity of a kiwi (**a**) and selected moa (**b–i**). nc = Nasal cavity. Arrows in **a** indicate turbinates. Scale bars indicate 5 mm for all images.

Reconstructions of the floor or roof of the endocranial cavity are shown for selected moa and other ratites in figure 6. The view of the floor highlights the relative size of the cribriform plate (and hence the degree of olfactory specialization) in non-NZ ratites (fig. 6a–c), the little spotted kiwi (fig. 6d), and selected moa (fig. 6e, f). It has been pointed out that moa are unique amongst birds in having an olfactory chamber housing the olfactory capsule which is in turn completely enclosed by other bones of the skull [Worthy and Holdaway, 2002]. In some of the moa, the size of the olfactory bulb is most easily assessed by examining the dorsal view of an endocast (fig. 6i, k) or the dorsal interior of the endocranial cavity (fig. 6g, h, j, l). Despite this, in all the available material, the olfactory bulbs, cribriform plates and Wulsts of the moa were of a similar proportional size to that seen in non-NZ ratites.

In order to assess the development of the olfactory apparatus in moa, CT scans through the rostrocaudal level of the olfactory bulb and presumptive olfactory region of the nasal cavity were compared with those of the same regions in the kiwi and non-NZ ratites. In most moa the olfactory bulb was located immediately dorsal to the caudal nasal cavity (fig. 7) as seen in the kiwi, whereas the olfactory part of the nasal cavity lay rostral to the olfactory bulb in the emu and rhea. The specialization of the olfactory region of the nasal cavity of the kiwi was strikingly obvious (fig. 7a) with extensive turbinate formation visible. No such specializations were seen in any of the moa skulls (fig. 7 b–i), even where the nasal cavity was well preserved. Similarly, the little spotted kiwi has a strikingly large olfactory bulb, as large as or even larger than moa that are as much as 100 times the body weight and 8 times the brain weight.

Quantitative Analysis of CT Scans

The ECV as measured from CT scans agreed well with ECV as measured by dried mustard seed (table 3). The volume of the fore- and midbrain as a percentage of total ECV in the moa ranged from 63.7 to 78.6% (mean of 72.7%) as against 75.0% for the little spotted kiwi and 75.7–77.9% for the non-NZ ratites. The proportion of ECV occupied by the pituitary fossa ranged from 0.05 to 2.5% across the moa species examined; those were mostly lower than values for the kiwi (2.3%) and non-NZ ratites (rhea: 2.3%; ostrich: 3.0%; emu: 2.3%). The volume of the olfactory bulb as a proportion of ECV was similar for the moa (0.33–0.96%) and non-NZ ratites (rhea: 0.87%; ostrich: 0.71%; emu: 1.88%) and much higher in the kiwi

(11.5%). Another indicator of olfactory bulb size used previously [Cobb, 1960; Bang and Cobb, 1968] is the ratio of transverse olfactory bulb diameter to maximal transverse forebrain diameter. Values for the moa ranged from 18.1% for *Euryapteryx gravis* (South Island) to 30.4% for one of the *Pachyornis australis* specimens, somewhat higher than the range for non-NZ ratites (rhea: 19.8%; ostrich: 22.1%; emu: 17.3%) but substantially lower than the kiwi we examined (48.8%).

The area of the Wulst could not be assessed in the kiwi skull because a vallecula ridge was absent, but quantitative analysis of the other ratites confirmed the impression noted earlier that the Wulst in moa is similar in proportional area to that in the non-NZ ratites. Wulst area was strongly correlated with ECV for moa, rhea, ostrich and emu ($r = +0.897$, d.f. = 12, $p < 0.001$) and, when expressed as a percentage of the fore- and midbrain surface area, ranged from 9.22 to 18.3% for the moa. In most moa the Wulst area was between 13.6 and 18.3% of the fore- and midbrain area which was very similar to values for non-NZ ratites (rhea: 14.3%; ostrich: 13.7%; emu: 16.6%), with only *Anomalopteyrx didiformis* lying well below this. It might be significant that *A. didiformis* also had a small optic foramen, because a substantial proportion of the Wulst is concerned with vision. It was also noted that the range and mean of optic foramen areas for the moa (0.07–0.21 mm^2, mean of 0.163 $\pm$ 0.048 mm^2) was lower than that for non-NZ ratites (0.18–0.29 mm^2, mean of 0.230 $\pm$ 0.056 mm^2), but not significantly different (Student's t test, $p = 0.156$).

The areas of the maxillomandibular and vagal foramina were measured as indicators of neurological specialization towards trigeminal somatosensation (V2 and V3 branches) and control of the syrinx (X), respectively. The areas of both these canals were moderately correlated with ECV among all the ratites studied ($r = +0.727$, d.f. = 13, $p < 0.01$ for vagal foramen area; $r = +0.671$, d.f. = 13, $p < 0.01$ for maxillomandibular foramen area). The area of the vagal foramen was broadly similar for the moa (0.04–0.14 mm^2) compared to non-NZ ratites of similar body mass (rhea: 0.12 mm^2; ostrich: 0.14 mm^2; emu: 0.07 mm^2). Similarly, maxillomandibular foramen area of moa (0.07–0.16 mm^2) was co-extensive with the range of values for the non-NZ ratites (rhea: 0.13 mm^2; ostrich: 0.11 mm^2; emu: 0.07 mm^2). Hypoglossal foramen area (as an indicator of hypoglossal nerve cross-sectional area and hence control of tongue musculature) could not be measured reliably in our material, but it was certainly not enlarged in any of the moa.

Discussion

Encephalization of Moa: Comparison with Other Ratites

In the present study we have used EQ to compare the encephalization of moa with other ratites. EQ are notorious for their limitations [Striedter, 2005], the principal of these being that different values for EQ might be obtained if different allometric constants (slope and intercept of the power function describing the comparison set) are used. For this reason EQ estimates should be seen only as intuitive and convenient tools for comparing the relative brain size of birds of different body weight and not as defining characteristics. In the present study EQ was calculated using allometric constants derived from the largest available avian brain volume data set [Iwaniuk and Nelson, 2003]. When the allometric constants of the van Dongen dataset [van Dongen, 1998] were used, slightly lower EQ were obtained for the moa. Nevertheless, regardless of the allometric constants used, the EQ of the 8 moa species examined were significantly lower than that for non-NZ ratites by non-parametric statistics.

Although our data indicate that encephalization of the moa was less than that for most birds, the values for EQ of moa as a group were broadly similar to those for other ratites. In particular, the encephalization of modern emus is comparable to that for many moa species, with the exception of *Emeus crassus*, *Euryapteryx gravis* (both North and South Island) and *Euryapteryx curtus*. Nevertheless, we did find a statistically significant difference of about 30% between the EQ of all moa and non-NZ ratites, meaning that we cannot exclude the possibility that absence of predation by more highly encephalized mammals has contributed towards a reduction of EQ in this group.

On the other hand, our observations of kiwi encephalization do provide refutation of the hypothesis that removal of mammalian predation pressure results in decreased encephalization. Values of EQ for the three kiwi species examined ranged from 0.721 to 1.260. No data were available on the encephalization of the ancestors of the modern kiwi, but EQ for *Archaeopteryx* based on an estimated ECV of 0.92 ml and minimum and maximum body weight estimates of 310 and 500 g [Jerison, 1973] yielded a range of 0.198 to 0.260. This suggests that the lineage of birds leading to modern kiwi has undergone a 4- or 5-fold increase in relative brain size since the late Jurassic, with much of this presumably occurring after the separation of New Zealand from the rest of Gond-

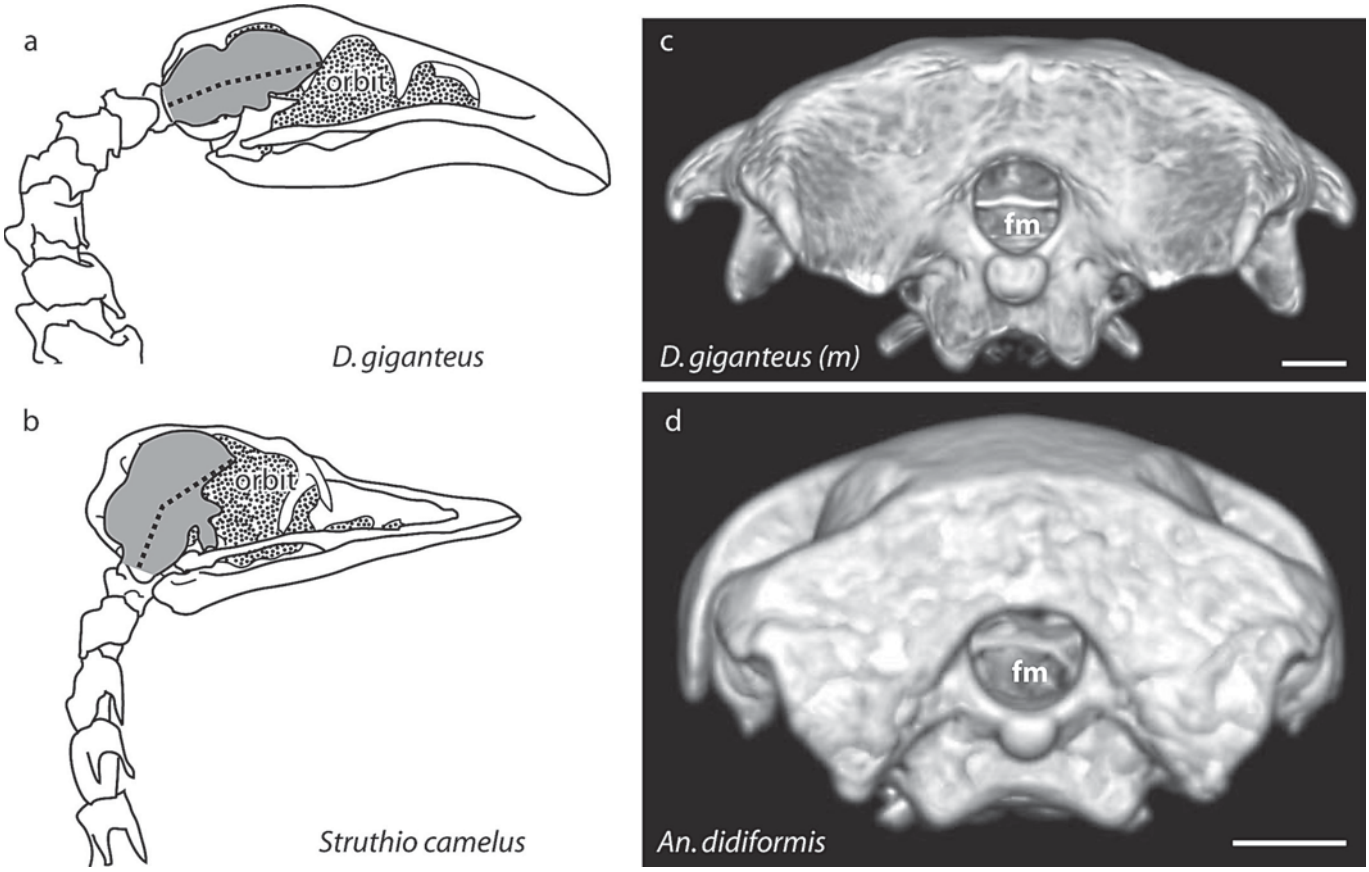


Fig. 8. Carriage of the head and orientation of the endocranial axis in *Dinornis giganteus* (**a**) contrasted with that in *Struthio camelus* (**b**). The endocranial cavity and endocranial axis are superimposed on lateral views of the head and neck in the two species. The attachment of the neck to the back of the skull in moa is accompanied by a posteriorly positioned foramen magnum (fm) in both large (**c**) and small (**d**) moa. Scale bar indicates 10 mm in **c** and **d**.

wana. There are two possible explanations for this. Firstly, the remarkable neurological adaptations of the kiwi to a nocturnal niche may have driven expansion of central centers associated with the relevant sensory specializations (in particular olfaction, but perhaps also trigeminal somatosensation); but, apart from some cytoarchitectural and chemoarchitectural analyses of the olfactory bulb and brainstem [Martin et al., 2007], no detailed studies concerning the central organization of olfactory or trigeminal pathways in kiwi are available to test this hypothesis. Secondly, the observed EQ of kiwi might be the result of a profound reduction in somatic size without a corresponding reduction in brain weight. A similar explanation has been proposed for the large size of kiwi eggs relative to the body of the female [Calder, 1979].

Endocranial Morphology of Moa in Comparison with Other Ratites

Qualitative analysis of endocranial morphology of the moa shows that despite some striking differences in the degree of endocranial flexure, the endocranium is broadly similar in morphology to that of other non-NZ ratites, in particular emus. The low values for brain flexion among moa are consistent with the horizontal deportment of the upper neck as in more modern skeletal reconstructions [see discussion in Worthy and Holdaway, 2002]. This horizontal deportment and its resulting effect on brain orientation and foramen magnum position are illustrated in figure 8. The proportional size of the Wulst and olfactory bulb in moa was similar to Australian ratites, suggesting that diurnal habits and sensory organization were comparable to those of emus.

Quantitative Analysis of Moa Endocrania: Comparison with Other Ratites and Birds

Calculation of forebrain volume alone was not possible from moa skulls, but comparison of combined fore- and midbrain volume with other ratites and birds was both feasible and informative. Among the moa we examined by CT, combined fore- and midbrain volume as a percentage of ECV ranges from 63.7–78.6%, whereas using the same methodology we obtained values of 75.0% to 77.3% for the non-moa ratites. Based on measurements by other authors [Boire and Baron, 1994], values for proportional fore- and midbrain volume for Galliformes (supposedly the least neurologically advanced birds apart from ratites) ranged from 70.0–82.1% (mean of 78.1%). Almost all other bird orders have values higher than either ratites or Galliformes (penguins: 78.9%; pelicans: 78.0%; cranes/storks: 81.9%; pigeons/doves: 78.1–81.3%; parrots: 85.5–88.7%; perching birds: 83.5%). We can exclude the possibility that the proportion of fore- and midbrain volume is biased by allometric scaling because, although fore- and midbrain volume correlates strongly with brain weight ($r = +0.998$), we found that fore- and midbrain volume as a percentage of ECV correlates poorly with brain weight ($r = +0.022$) over an extensive range of bird brain weights (0.12–19.9 g) [data from Boire and Baron, 1994]. Burish and colleagues [2004] have shown that the telencephalic volume fraction is strongly correlated with social complexity. This suggests that moa might have been less capable of higher cognitive functions than even other living ratites. This has important ecological implications as it is some of the best evidence for the lack of a complex social system. A complex social system, with creching behavior in chicks as well as migration, has been suggested by some authors, who have also hypothesized that this led to the rapid demise of the moa after human arrival [Holdaway and Jacomb, 2000]. It has been suggested that, if moa were highly social and flocked together, this might have made hunting easier for the early Polynesians and thereby made the group's so called 'blitzkrieg extinction' easier.

Quantitative analysis of structures associated with sensory specializations strongly suggests that moa and emu had similar sensory abilities. Olfactory bulb volume in moa is similar to that in non-NZ ratites and both Wulst morphology and area are comparable to that in diurnal ratites. Our findings therefore support Owen's original conclusions concerning moa biology and do not support significant use of olfaction by the group. The Cobb index (ratio of olfactory bulb to hemisphere transverse diameter) [Cobb, 1960; Bang and Cobb, 1968] ranged from 18.1–30.4% for the moa and was 48.8% for the little spotted kiwi. This compares with ranges of 18.0–37.0% for Procellariiformes (petrels, shearwaters and albatrosses), 18–22% for Columbiformes (pigeons) and 3.0–18.0% for Passeriformes (songbirds) [Bang and Cobb, 1968]. Nevertheless, the Cobb index might not be an appropriate indicator of olfactory bulb size in moa because of the greater degree of dorsoventral flattening of the bulb in moa, in comparison to other birds.

A rarely quoted paper [Worthy, 1989] has stated that the olfactory chamber of the moa is extraordinarily large and attributes this to possible elevated olfactory acuity in moa. However, our study indicates that this olfactory chamber is actually an apparently unique ethmoid capsule and the uniqueness of this structure and the lack of a correspondingly large olfactory bulb suggest that this organ had some role other than olfaction in moa. One possibility is that the chamber developed to resonate sounds in the dense forest environment that moa inhabited or that an organ evolved to extract salt or some other toxin from the moa's diet.

Atkinson and Greenwood [1989] postulated that moa had large eyes and a poor sense of smell and thus color and form were important in food choice. They suggested that this lack of olfactory acuity was demonstrated evolutionarily in New Zealand by the fact that palatable and non-palatable plants (easily separable by animals with a good sense of smell) looked very similar. Our data suggest that, because moa appear to have visual acuity similar to other diurnal ratites and an apparently poor olfactory ability, this hypothesis is valid.

Glacial/Interglacial Body Size Change and Its Relationship to EQ and Olfactory Bulb Size

Like mammals elsewhere, moa taxa have reduced in mean individual size since the last Glacial maximum, probably due to climatic and competition pressures [Worthy and Holdaway, 2002]. Such rapid decline in body size is likely to have made a significant change in EQ which should be reflected in comparative EQ measurements from the two epochs. Our data did not allow direct comparison between the EQ of Pleistocene and Holocene specimens of the same taxa, but there is evidence to suggest that *Pachyornis australis* (a close relative of *Pachyornis elephantopus*) became extinct following the last Glacial maximum [Worthy and Holdaway, 2002] meaning that any specimen of *Pachyornis australis* sampled would be Pleistocene. Although the sample was small, our data show that EQ and the olfactory bulb are proportionally larger in *Pachyornis australis* than *Pachyornis elephanto-*

pus and thus there is some evidence for Glacial/Interglacial body size change affecting EQ and comparative brain function. We suggest that further study of these phenomena might reveal more evidence for mechanisms related to Glacial/Interglacial body size changes and suggest contributory causes for these differences.

Evolutionary Considerations

Ratites (both kiwi and moa) have evolved in isolation on the New Zealand archipelago for 80 million years and analysis of their endocranium reveals that these two groups have followed quite different paths of brain evolution. From our study of the endocranial morphology of the moa it would appear that the sensory specializations of these ratites were most like those of the modern emu, ostrich and rhea. There was no evidence of olfactory specializations in either olfactory bulb development or in the enlargement of the surface area of the olfactory nasal cavity. On the other hand, the kiwi show striking specializations for both olfaction and trigeminal somatosensation, as reflected in the pronounced turbinates, large olfactory bulb, and 'whisker-like' feathers around the base of the beak [Martin et al., 2007]. The moa, along with non-NZ ratites, appear to have undergone only a modest increase in EQ compared to Mesozoic birds and other Maniraptorans, although absolute brain size among the largest moa is more than 60 times that of *Archaeopteryx*. It remains uncertain at this stage what factors might have driven the increase in EQ among the kiwi, although a combination of somatic reduction not accompanied by reduction in brain size (decoupling of brain and somatic mass) and sensory specialization appears to be the most likely explanation.

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