Ostrich-like eggshells from a 10.1 million-yr-old Miocene ape locality, Haritalyangar, Himachal Pradesh, India

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We report fossil ratite eggshells from the site, Dharamsala of Dhok Pathan Formation (Middle Siwaliks), dated to 10.1 Ma. A comparative analysis reveals that in their combination of eggshell surface, pore, pore canal morphology and cross-sectional features, the Indian eggshells show closest affinity with the widely distributed Neogene fossil taxon *Struthiolithus*, and as such are assigned to cf. *Struthiolithus*. We have carried out a parsimony analysis of all relevant extinct and extant palaeognathous birds of the southern continents, as ingroup taxa. *Genyornis*, an extinct bird from Australia, and *Gallus gallus* (chicken) were also used in this analysis as ingroup (Neornithes) taxa. The result supports monophyly of Palaeognathae. The present cf. *Struthiolithus* eggshell and *Aepyornis* were found to be sister taxa and their forbearers had a common ancestry with Afro-Arabian *Struthio* and *Diamantornis*. The Indian subcontinent now has an extended fossil record of struthionid eggshells from the Late Miocene to the Late Pleistocene, implying dispersals through intercontinental migration corridors. Our stable carbon isotope ($\delta^{13}C_{PDB}$) value of –10.4‰ of the present eggshells suggests that the ratite bird had a diet mainly of C_3 plants.

Keywords: Eggshells, Miocene ape locality, ostrich.

MONOPHYLY of palaeognathous birds (ratites and tinamous) is now widely accepted on the basis of molecular[1,2], skeletal morphological[3,4] and oological studies[5,6]. Ratites (flightless paleognathous birds) are widely regarded to be of Gondwanan origin, and their present-day distribution is most probably the consequence of continental drift (Figure 1)[2,3,7]. The 'out-of-India' dispersal hypothesis[8,9] proposes that several amphibian, mammal, reptile and ratite taxa dispersed into Eurasia from the Indian Subcontinent with India–Asia collision some 55–60 Ma ago, including the ostrich (*Struthio*)[2]. This view of ostrich dispersal is supported by fossil evidence. For example, the oldest species of Struthionidae (to which the present-day ostrich, *Struthio camelus* belongs) known so far, *Eleutherornis helveticus*, comes from the Eocene sediments of Switzerland[10]. Another example is that of *Palaeotis weigelti*, which is considered close to the ostriches by some workers (but disputed by others), recovered from the Middle Eocene of Europe[11].

There are few published records of fossilized skeletal remains of ostriches and their presence in Africa, Middle

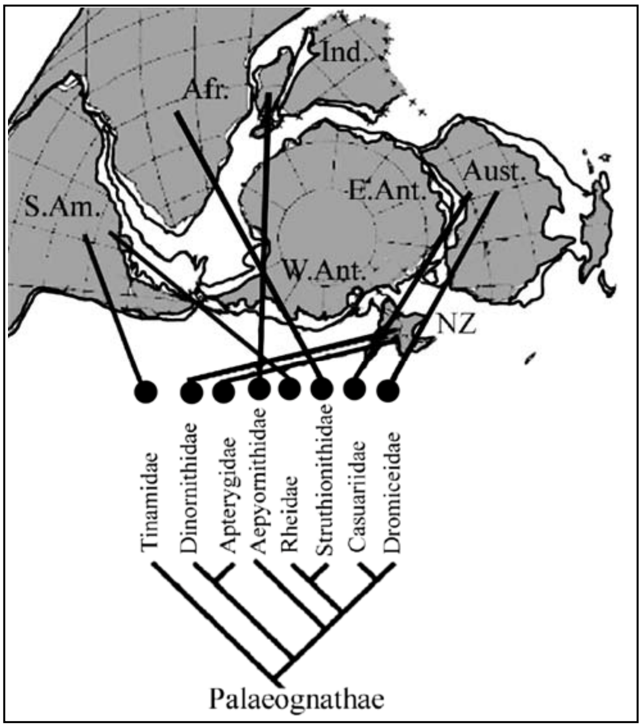

Figure 1. Relationship among Palaeognathae mapped onto an early Cretaceous (120 Ma) reconstruction of the southern continents (modified from Cracraft[3]).

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East, Europe, and Central and southern Asia in prehistoric times based largely on fossil eggs and eggshell fragments. Eggshell structure-based taxonomy is termed 'ootaxonomy' and has been used to identify dinosaur and ratite eggs[12,13]. Characteristic ratite or 'palaeognatheous' eggshell morphotypes[12] are found in the ostrich (Struthionidae), rhea (Rheidae), emu (Dromaiidae), cassowary (Casuariidae), moa (Dinornithidae), kiwi (Apterygidae) and the extinct Malagasy elephant bird (*Aepyornis*, Aepyornithidae). The eggs of these ratites can be differentiated on the basis of their pore pattern and eggshell microstructure[5,6,13–16]. Recently, comprehensive character-based studies of eggshell mega and microstructures revealed their usefulness in constructing phylogenetic relationships among extinct and extant ratites[5,6].

Ratite eggshells are generally classified as either 'struthionid-like', with needle pore pattern similar to that of *Struthio camelus*, the African ostrich (Figure 2 *a*), and 'aepyornithid-like', with dagger pore pattern similar to that of *Aepyornis maximus*, the giant extinct bird of Madagascar (Figure 2 *b*). The largest birds were the extinct elephant birds of Madagascar, *Aepyornis*. They weighed between 333 and 563 kg and reached around 2.5 m in height[17,18]. African fossil struthionid-like ootaxa include *Struthiolithus oshanai* from Namibia[19], renamed as *Namibornis oshanai*[20,21]. *Psammornis* has been recorded from Egypt and Arabia[13,15,22]. *Struthio karingarabensis*[23] and *Struthio daberasensis*[21] were described from the Namibian latest Miocene and Pliocene deposits respectively. Stidham[24] recently reported *S. daberasensis* from Late Pliocene sediments of Malawi. Harrison and Msuya[25] have discussed the biostratigraphic significance of Mio–Pliocene taxa *Struthio* cf. *karingarabensis* and *Struthio kakesiensis* from Laetoli. Skeletal remains of a new species, *Struthio coppensi* have been found associated with aepyornithoid eggshells from the Early Miocene deposits of Namibia[26,27]. Middle Miocene skeletal remains of *Struthio* are known from Kenya, Tunisia, Algeria, Morocco and Tanzania[26]. *Diamantornis corbetti*, *Diamantornis wardi*, *Diamantornis laini* and *Namornis oshanai* have been described from Namibia[21].

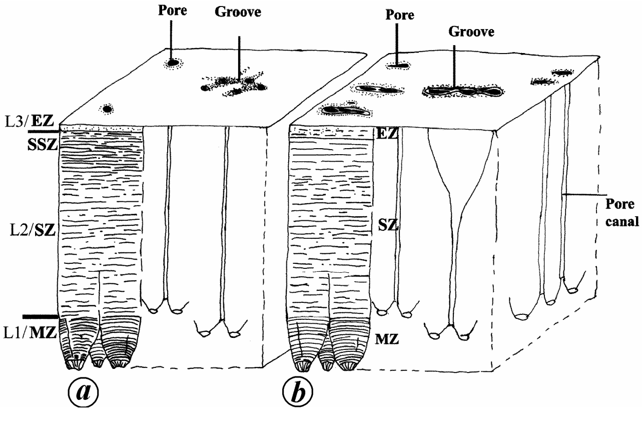

Figure 2. Schematic diagrams. ***a***, *Struthiolithus* sp. showing struthionid-like needle-point pore and pore canal pattern. ***b***, *Aepyornis* showing aepyornithid dagger-point pore and pore canal pattern. Layer 3 or EZ, External zone; Layer 2 or SZ, Spongy zone; Layer 1 or MZ, Mammilary zone. Figure is not to scale (modified after Sauer[15]).

Ostrich-like fossil eggs from eastern Europe, the Mediterranean region and Asia have been divided among five oospecies[13]: (1) *Struthiolithus chersonensis* from the Late Miocene (Meotian) to Late Pliocene of eastern Europe (Ukraine); (2) *Struthiolithus asiaticus* from the Late Miocene to Holocene of Central Asia (China, Mongolia, Transbaikalia, southern Turkmenistan); (3) *Struthiolithus transcaucasicus* from the Late Miocene and Late Pliocene of Transcaucasia, Turkmenistan and Kazakhsthan; (4) *Struthiolithus saueri* from Late Miocene to Late Pliocene of the Canary Islands, and (5) *Struthiolithus sarmaticus* from the Middle Miocene (Sarmatian) of Moldova. Three additional oospecies from Eurasia are known: *Struthio pannonicus* from Plio–Pleistocene (Villafranchian–Callabrian) deposits in Hungary[28]. This taxon was described in association with struthionid bone remains, but Mikhailov[14] has referred it to *Struthiolithus*. *Struthio anderssoni* and *Struthio mongolicus* were named by Lowe[29] from supposed latest Miocene (Pontian) deposits in China.

From southern Asia, Pakistani Siwalik sediments have yielded an almost continuous record of ratite remains ranging in age from Late Miocene to Middle Pleistocene[30]. As early as 1884, Lydekker[31] described skeletal remains (phalangeal bones, fibula, tibiotarsus and about 12 vertebrae) of *Struthio asiaticus* Milne-Edward 1871 from an unspecified locality in the Upper Siwaliks (Late Miocene Dhok Pathan Formation). Sauer[15] studied eggshell fragments (presently housed at the American Museum of Natural History) from the Dhok Pathan Formation at Hasnot, Pakistan, and found their aepyornithid-like pore pattern rather similar to that of the extinct elephant bird (*Aepyornis*) of Madagascar. Stern *et al.*[30] carried out isotope analysis on a successive record of Neogene and Quaternary ratite eggshells from Pakistan. They reported aepyornithid-like eggshells ranging from 11.35 to 1.25 Ma and struthionid-like eggshell fragments ranging in age from 2.25 to 0.58 Ma. Adams and Johnson[32] presented an abstract saying that these ratites from Pakistan first appeared at 10 Ma from Africa, followed by dispersals at 5.3, 3.3 and 1.5 million years. From India, Bidwell[33] described ostrich eggshell fragments from the Ken River in the Yamuna Valley near Banda, Uttar Pradesh. Later, these fossil ostrich eggshell fragments were recovered from over 40 Upper Palaeolithic sites in the Indian Peninsula ranging in age from 25,000 to 40,000 yrs BP[34,35] (S. A. Sali, unpublished). Ultrastructure, thin section and comparative studies of these Upper Palaeolithic eggshells supported the observation of Bidwell[33] that they show closeness to the East African form *S. camelus molybdophanes*[36,37]. It may be noted here that the allocation of Indian fossil ostrich eggshell frag-

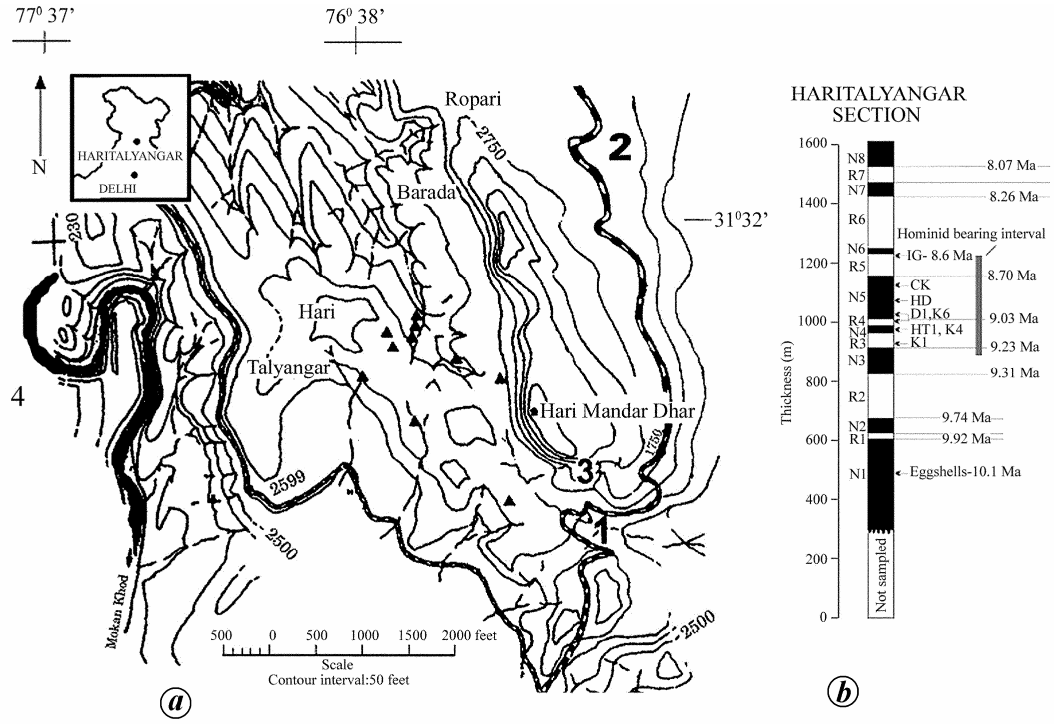

Figure 3. ***a***, Map showing cf. *Struthiolithus* sp. (4) and ape localities (1, 2 and 3). Triangles denote major hominoid localities. ***b***, Haritalyangar section (after Pillans *et al.*[38]).

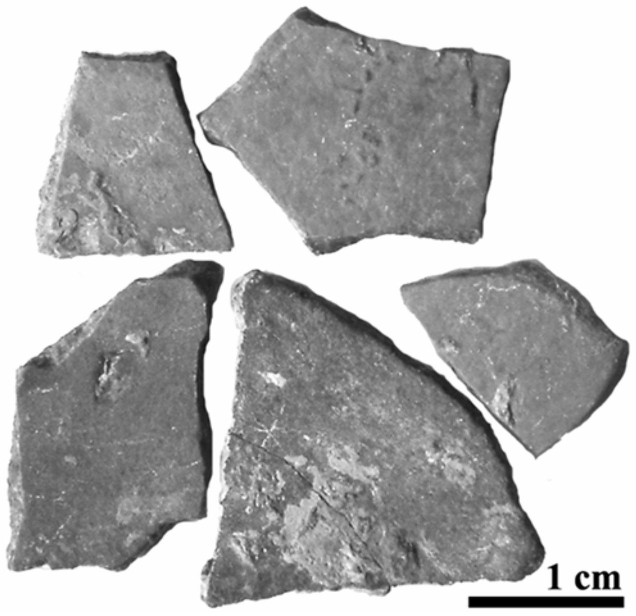

Figure 4. Eggshell fragments of cf. *Struthiolithus*.

ments up to subspecies level based on their comparison to the external characteristics of actual modern eggs of African ostriches is not widely accepted.

Here we describe the collected eggshell fragments and compare them with those of fossil and extant species of *Struthio*, *Struthiolithus*, *Aepyornis*, *Dromaius*, *Diamantornis* and *Genyornis*. Based on cladistic analysis, we also discuss the possibility of an affinity between the eggshells of extinct southern Asian ratites and those of the present-day African, Australian and South American ratites. We also throw some light on the palaeobiogeography of ostrich-like taxa and the palaeoclimatic conditions in which they lived.

Materials and methods

Forty-five eggshell fragments (specimen nos. VPL/BEG-1–45) were recovered from the locality of village Dharamsala (31°31′75″N; 76°36′72″E, Figure 3 *a*), which has recently been palaeomagnetically dated to 10.1 Ma (Figure 3 *b*)[38]. These eggshells (Figure 4) most probably belong to a single egg as they were collected from a small area (~40 cm^2) and are similar in thickness, colour and morphology. Some of the eggshell fragments were found to fit together. These deposits belong to the Dhok Pathan Formation of the Middle Siwaliks[38]. The eggshell fragments were studied under binocular and scanning electron microscopes (JSM model no. 6490). Freshly broken as well as polished eggshell radial surfaces were used in the study. We also made thin sections to study these eggshells under polarizing optical microscope. We used the cathodluminesence detector of the JSM 6490 to detect any diagenetic modifications. For CL analysis, the eggshells were polished and coated with platinum. For comparative study we used eggshells of *Aepyornis* (from Madagascar), *Struthio camelus* (sub-fossils from Fayum, Egypt), *Struthio* cf. *S. camelus molybdophanes* (Upper Palaeolithic of India), recent and fossil emu and *Genyornis* (Late Pleistocene of Australia), and *Diamantornis laini* (Baynunah Formation, United Arab Emirates) specimen number YPM (Yale Peabody Museum) 56715. We also compared the present specimens to eggshells of *Apteryx*, *Dinornis*, *Casuarius*, *Dromaius* and *Eudromia* based on published literature. In order to determine the polarity of character transformations, eggshells of chicken (*Gallus gallus*), sauropod (*Megaloolithus jabalpurensis*) and theropod (*Ellipsoolithus khedaensis*) were used in this study. We have followed eggshell terminology of Mikahilov[13]. The data matrix file was assembled using MacClade and parsimony analysis was conducted using both the branch-and-bound and heuristic search algorithm[39] of PAUP* 4.0b10. Stable isotope analysis of only one sample was carried out at the Cerlings Laboratory at the University of Utah. For stable carbon and oxygen analysis, ~50 μg of eggshell powder was digested in an phosphoric acid bath at 90°C. The products of the reaction are essentially H_2O and CO_2. The two are separated using traps. First is an ethanol CO_2 slurry, which traps the water. This is followed by a liquid nitrogen trap that traps CO_2. The CO_2 is then sent into the mass spectrometer and analysed in dual inlet mode[40].

Description

The eggshell surface showed sparsely distributed tiny pores similar to ‘needle-point’ pores (see Sauer[15]). The pores were tiny (0.05–0.1 mm in diameter, Figure 5 *b*–*d*), mostly isolated, but at a few places occurred as aggregate complexes in shallow depressions (Figure 5 *b* shown by black triangle). The pore canals are non-branching and straight (Figure 6 *a*). The outer surface of the eggshells was mostly smooth, but at few places irregular nodes were observed (Figure 5 *a*). The eggshell thickness averaged around 3 mm. In radial section, the shell displayed typical ratite microstructure with distinct layer 1 (mammilary zone – MZ), layer 2 (spongy zone – SZ) and layer 3 (external zones – EZ; Figure 5 *e* and *f*). L1 was ~0.75 mm thick and comprised long calcite wedges running radially (Figure 5 *f*). L1 had weak vesiculation (Figure 5 *g* and *i*), visible only when magnified. L2 (SZ) showed herring-bone pattern (Figure 5 *i*, black arrow). L2 also showed vesiculation (Figure 5 *h* and *i*). In thin section an outer layer of the spongy zone SSZ was seen (Figure 6 *a*), which is not evident in SEM images. This sub-layer appears to be a product of post-depositional diagenesis. Earlier workers[5,16] have used cathodoluminescence analysis to distinguish post depositional diagenetic changes in eggshells. We also were able to distinguish this additional subzone from the outermost layer (Figure 6 *d* and *e*) using cathodoluminescence detector fitted to the JEOL-SEM, JSM 6490. Thin section of the present specimens showed very thin (~0.1 mm) external zone and microcrystalline calcite wedges oriented vertically (Figure 6 *a*) as observed in *Struthio* (see Zelenistky and Modesto[6]).

Comparisons

We begin with comparing the present eggshells to those of palaeognathous birds followed by comparison to those of *Genyornis*, *Gallus*, *Megaloolithus* and *Ellipsoolithus*. The overall pore and pore canal pattern and shell microstructure of the present eggshells resembled most closely those of the eggshells of *Struthiolithus* described from Pakistan[5]. *Struthiolithus* eggshells, according to Grellet-Tinner[5], are characterized by straight pores with round or slit-like aperture on the same eggshell surface. *Struthiolithus* eggshells from Pakistan is oval to sub-spherical in shape, measuring 176.19 × 132.20 mm in length and diameter, and has a rugose outer surface and thin (1.7 mm) eggshells[5]. Eurasian *S. chersonensis*, *S. sarmaticus* and *S. transcaucasicus* can be differentiated from present eggshells in having slightly thinner eggshells (2.6–2.7 mm, see Mikhailov[13]). Likewise, *S. anderssoni* and *S. mongolicus* differ from the present eggshells in having significantly thinner shell[28], averaging around 2 mm. The thickness of the eggshells of *S. pannonicus*[27] ranges between 2.6 and 3.4 mm. This range encompasses that of the present eggshells. Absence of further diagnostic information on *S. pannonicus* makes further comparison impossible at this point. *S. asiaticus* eggshells are similar to the present eggshells in retaining the needle pore pattern throughout the Neogene[13], but differ in having thinner eggshells (2.2–2.4 mm). The present eggshells are quite distinct from those of *S. camelus* in having non-branching straight pore canals and thick eggshells. *S. camelus* eggshells show both straight (Figure 6 *b*) as well as branched (Figure 7 *a*) pore canals. The eggs of the five extant subspecies of *S. camelus*, i.e. *S. c. camelus*, *S. c. spatzi*, *S. c. australis*, *S. c. massaicus* and *S. c. molybdophanes* (*S. c. syricus* is excluded here because it is now extinct from Arabia) have, to a certain degree[13], distinct pore pattern and their thickness averages around 2 mm[41]. Eggs of *Aepyornis* are almost twice as big (310.5 × 222 mm) as those of *Struthiolithus* from Pakistan. The former taxon also has eggshells twice as thick (3–4 mm) as those of the latter taxon. Compared to the present eggshells, *Aepyornis* eggshells are thicker (Figures 6 *g* and 8 *a*) and show slit-like pore apertures. L3 of *Aepyornis* eggshells is often divided into 2–3 sub-layers (Figure 8 *a* and *c*) and L1 has fairly straight wedges (Figure 8 *b*). Pore canal in *Aepyornis* sometimes bifurcates (Figure 8 *e*) (contra Grellet-Tinner[5], p. 178). *Diamantornis* is characterized by complex, circular, funnel shaped megapores

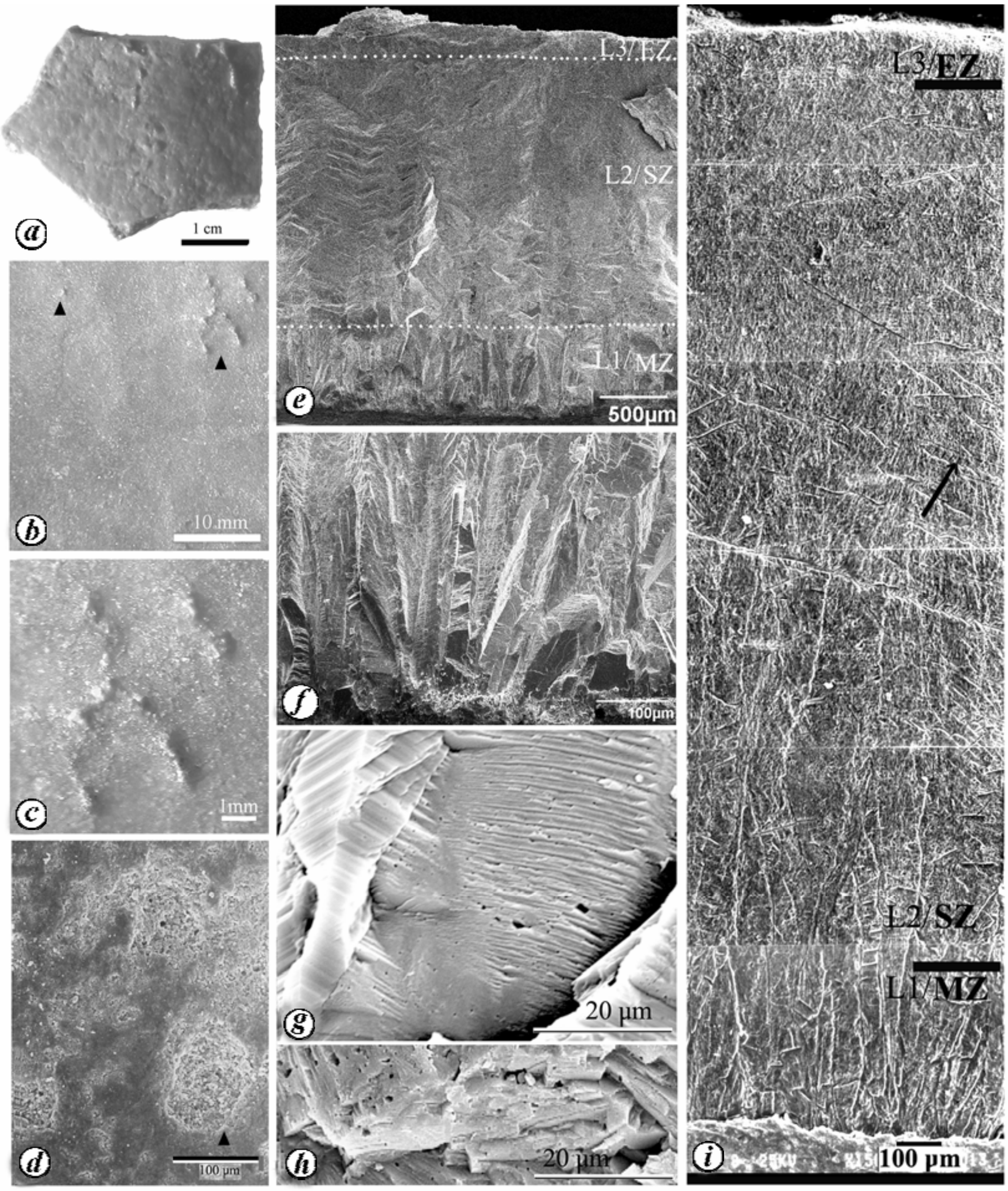

Figure 5. Cf. *Struthiolithus*. ***a***, Outer surface of an eggshell fragment; ***b***, Outer surface showing isolated pores and pores in groups (marked by black triangles); ***c***, A pore group shown on ***b*** is magnified; ***d***, SEM showing pores; ***e***, SEM of freshly broken radial surface; ***f***, Layer 1 or mammilary zone enlarged; ***g***, Mammilary zone wedge crystallite magnified showing vesicles; ***h***, Spongy zone crystallite magnified showing vesicles and ***i***, SEM of polished and etched radial section.

with numerous pores and branching pore canals[20,21]. *Diamantornis* shells (thickness, 2.6–4.1 mm) are three layered, L1 and L2 are highly vesiculated, L3 is very thin and prismatic in nature and boundary between layers are abrupt (Dauphin *et al.*[42], Plate II; Figure 7 *b*). *Dromaius* eggshells on the other hand are thinner (0.9 mm), have an additional layer, L4, round pore apertures and branched pore canals (Figures 8 *d* and 7 *c*). *Rhea* eggshells are thinner (0.9 mm), have three aprismatic layers, and straight pore canals with round openings (Figure 6 *a–d*)[5]. Similarly, *Dinornis* eggshells are three-layered, thinner (1 mm), have straight pore canals, but slit-like pore apertures (figure 17)[5]. *Apteryx* has very thin (0.4 mm), three-layered eggshells, and straight and round pores (figure 20 *a–c*)[5]. *Genyornis* eggshells are thin (1.2 mm) and lack layer 3, have straight pore canals and slit-like pore apertures[5] (Figure 7 *d*). *Gallus* eggshells on the other hand, are very thin (0.4 mm), have three distinct prismatic layers, and straight and round pores (Figure 8 *f*). *Megaloolithus jabalpurensis*[43], the sauropod dinosaur from India, has eggshells with thickness around 2.5 mm, one layer (Figure 7 *e*), straight pore canals and round pore apertures.

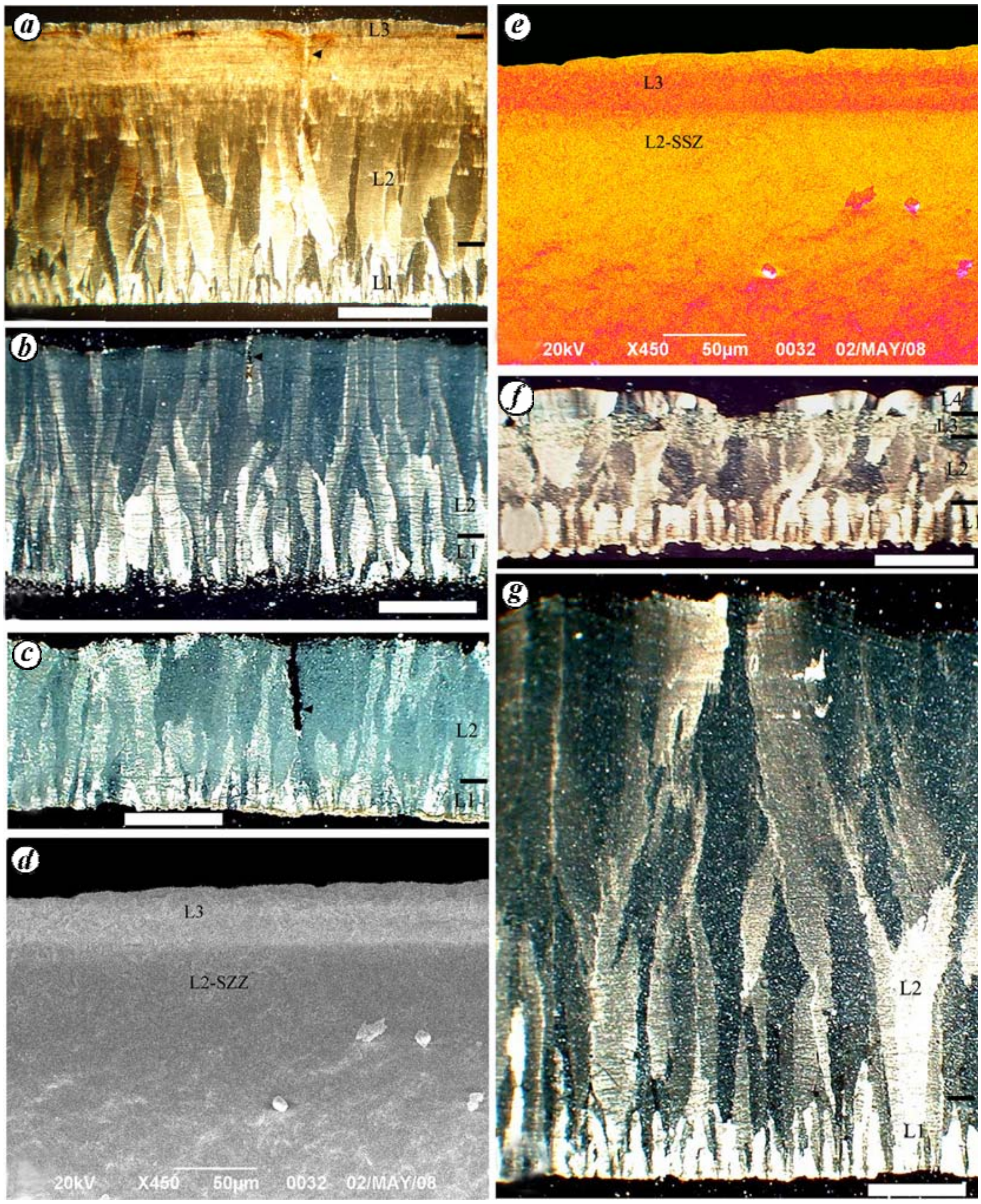

Figure 6. Thin radial sections under crossed nicols and SEM images. ***a***, Cf. *Struthiolithus* sp.; ***b***, *Struthio camelus camelus*; ***c***, *Genyornis*; ***d***, cf. *Struthiolithus* CL image in black and white; ***e***, cf. *Struthiolithus* CL image in false colour; ***f***, *Dromaius* and ***g***, *Aepyornis*. L, Layer. Scale bar represents 1 mm.

Eggshells of *Ellipsoolithus khedaensis*[44] are two-layered (Figure 7*f*), 1.2–1.6 mm thick and have lineartuberculate ornamentation.

A comparative analysis shows that cf. *Struthiolithus*, *Aepyornis* and *Struthio* are very similar to each other. The present cf. *Struthiolithus* is characterized with eggshells having a rugose surface, tiny rounded pores, straight pore canals, abrupt layer boundaries and mammillae longer than wide. *Aepyornis* is distinct from cf. *Struthiolithus* in having slit shaped apertures. *Struthio* on the other hand can be differentiated from cf. *Struthiolithus* by having a smooth surface, and both branched and straight pore canals. Presence of a round aperture (struthionid, see Figure 2) similar to that of the extant ostrich, is the key in calling the present eggshells as ‘ostrich-like’.

Cladistic analysis

The following is a list of 17 eggshell characters (C1–C17) used in the phylogenetic analysis. C1–C13 are after Grellet-Tinner[5] and C14–C17 are from Zelenistky and Modesto[6]. The primitive state is designated as (0) and the derived states as (1, 2, 3, 4). All the 17 characters were of the type ‘ordered’ (Wagner) and had equal weights. Fifteen characters were parsimony-informative and two were parsimony-uninformative. Multistate taxa interpreted as polymorphism.

(1) Surficial eggshell ornamentation – present (0); absent (1).
(2) Ornamentation morphologies: nodular (0); lineari-tuberculate (1); smooth (2); rugose (3); granular (4).
(3) Pore canal shape: straight bifurcating (0); oblique (1); straight (2); branched, tree-like (3); pore canal not connected between layers 3 and 4 (4).
(4) Pore aperture: round aperture (0), slit-like aperture (1).
(5) Spherulite: acicular rhombohedric calcite crystallites (0); short, blade-like calcite crystallites (1); long, blade-like calcite crystallites (2).
(6) Layer 3: absent (0), present (1).
(7) Layer 4: absent (0), present (1).
(8) Layer 3 morphology: layer 3 absent (0), amorphous (1), blocky (2), porous (3).
(9) Transition between L1 and L2 – No L2 (0), gradual/prismatic (1), abrupt/aprismatic (2).
(10) Transition between L2 and L3 – No L3 (0), gradual/prismatic (1), abrupt/aprismatic (2).
(11) Transition between L3 and L4 – No L4 (0), abrupt/aprismatic (1).
(12) L1/L2 ratio – No layer 2 (0), ratio above 0.80 (1), ratio between 0.50 and 0.80 (2), ratio below 0.50 (3).
(13) L3/L2 ratio – No layer 3 (0), ratio above 0.1 (1), ratio below 0.1 (2).
(14) Pore orifices: occluded with plug (0), unoccluded (1), covered with resistant zone or layer 3 (2).
(15) Mammilla proportions: wider than high (0), or higher than wide (1).
(16) Vesiculation in L2 (SZ): present (strong) (0), or absent (weak) (1).
(17) Vesiculation in L1 (MZ): present (strong) (0), or absent (weak) (1).

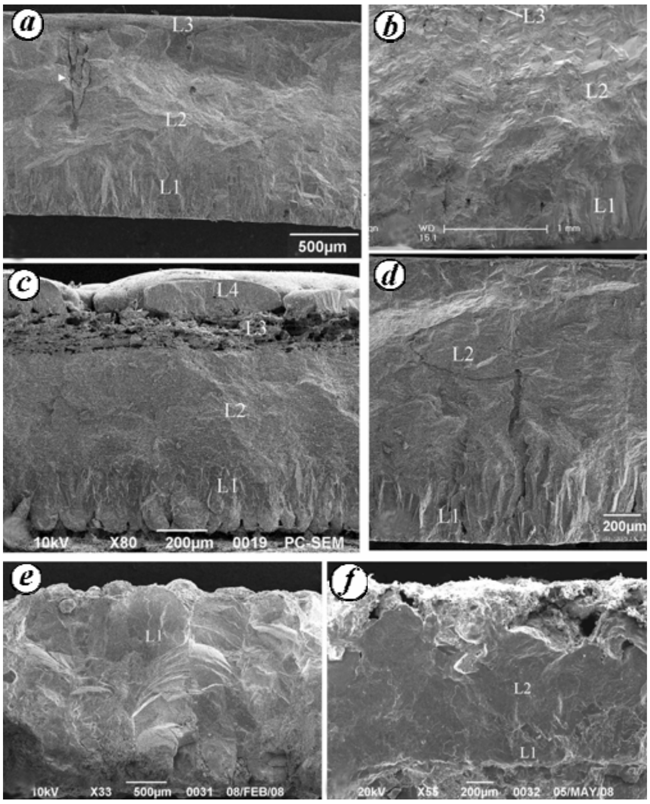

Figure 7. *Struthio camelus*. ***a***, SEM of freshly broken radial surface; ***b***, *Diamantornis laini* eggshell radial surface; ***c***, *Dromaius* eggshell showing freshly broken radial surface; ***d***, *Genyornis* eggshell showing freshly broken radial surface; ***e***, *Megaloolithus* eggshell showing freshly broken radial surface; ***f***, *Ellipsoolithus* eggshell showing freshly broken radial surface.

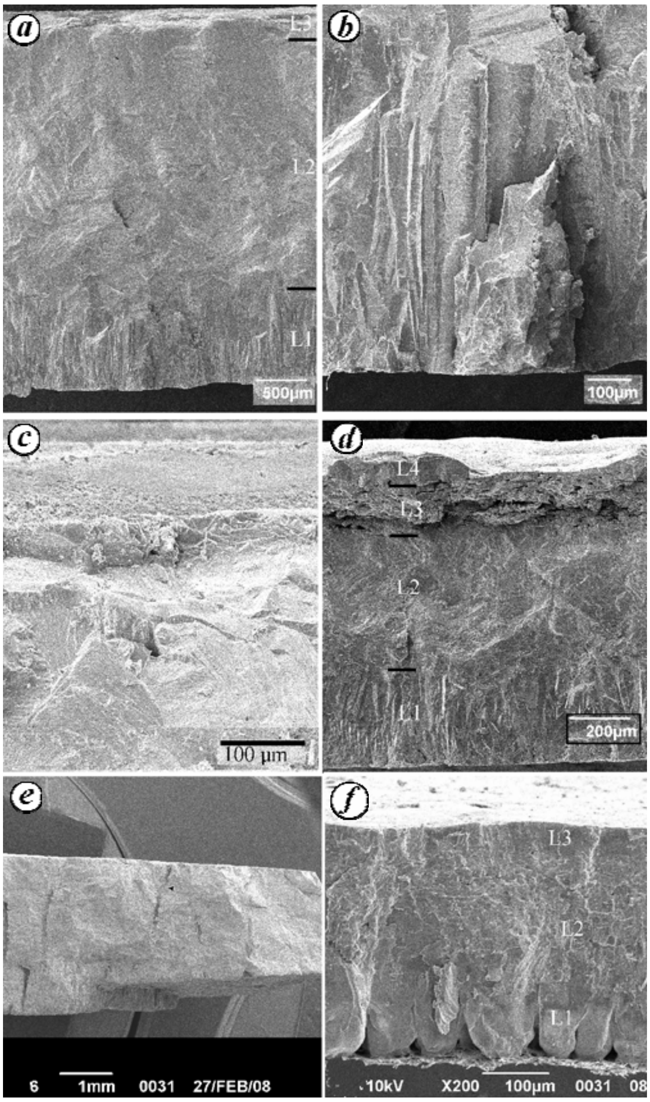

Figure 8. ***a–c***, *Aepyornis* sp. ***a***, SEM freshly broken radial surface; ***b***, Layer 1 or mammilary zone enlarged; ***c***, Layer 3 or external zone enlarged. ***d***, Freshly broken radial surface of eggshell of fossil *Dromaius*; ***e***, *Aepyornis*-black arrow indicates the point where the pore canal is brached; ***f***, *Gallus*.

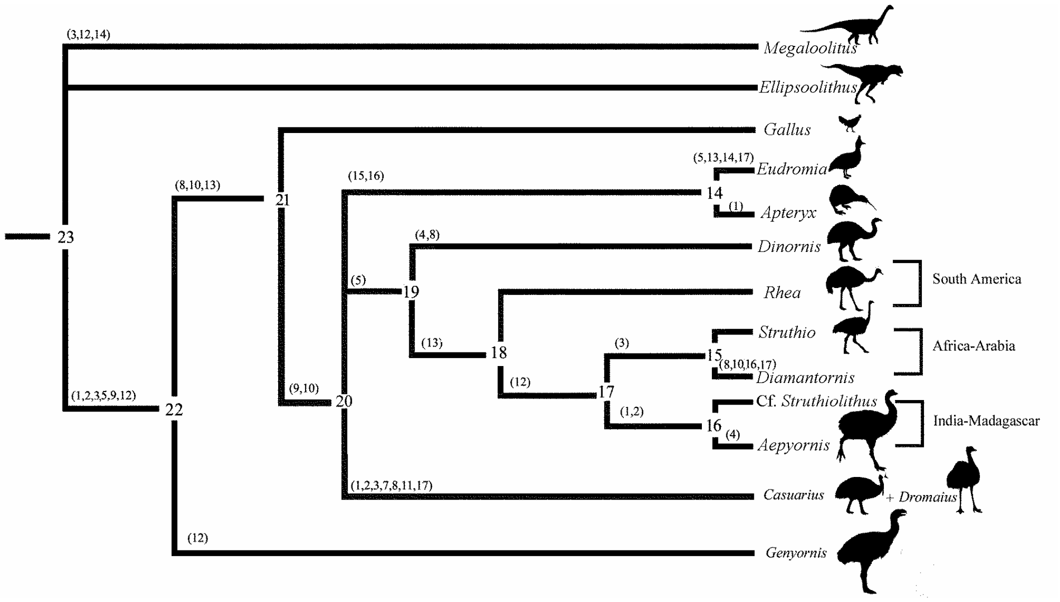

Figure 9. Cladogram showing inter-relationship among various bird and Indian dinosaur taxa. The matrix (Table 1) is composed of 13 taxa and 17 characters. All searches were performed using both branch and bound and heuristic search algorithm of PAUP* 4.0b10. Nodes supported by characters are shown in parentheses. Tree length = 52; consistency index (CI) = 0.6538; Homoplasy index (HI) = 0.3846; Retention index (RI) = 0.6667; Rescaled consistency index (RC) = 0.4359.

We selected *Megaloolithus* and *Ellipsoolithus* as out group taxa and all the Palaeognathae and neognathae birds in the ingroup.

Results

We found that *Dromaius* and *Casuarius* had equivalent scores for all 17 characters and so were combined into a single operational taxonomic unit (*Casuarius* + *Dromaius*). In order to obtain the most parsimonious tree, we undertook branch and bound algorithm method. This produced six most parsimonious trees with 52 steps. A heuristic search also returned the same result. A strict consensus of these six trees is shown in Figure 9.

Discussion and conclusion

Phylogeny

The final tree (Figure 9) is more or less similar to those deduced from skeletal[4], molecular[4] and eggshell[5,6,45] characters. This tree favours monophyly of Palaeognathae (node 20), which is supported by characters 9 and 10, but not of Struthioniformes (*Eudromia* comes out as the sister taxon to *Apteryx*). South American *Eudromia* and *Apteryx* of New Zealand are united by characters 15 and 16 and share a polytomy with *Casuraius–Dromaius*, and a clade comprising *Dinornis*, *Rhea* plus African and Indian ratites (nodes 19 and 18). Afro-Arabian taxa *Struthio* and *Diamantornis laini* are sister taxa (supported by character 3) and cf. *Struthiolithus* and *Aepyornis* are sister taxa (supported by characters 1 and 2), all four forming a clade supported by character 12 (node 17). South American *Rhea* is attached to this clade, which is supported by character number 13. Besides the rejection of monophyly for Struthioniformes, a second problematical result is the paraphyly of the two included neognathes *Genyornis* and *Gallus*. *Genyornis* (a waterfowl) is most probably deeply rooted within Neornithes and node 22 that unites it to other neornithes is supported by characters 1, 2, 3, 5, 9 and 12. Characters 8, 10 and 13 unite the palaeognathous and neognathous birds at node 21.

Palaeobiogeography

The present topology (Figure 9) clearly shows that the Indian-Madagascar forms align close to African-Arabian forms, implying a Late Neogene India–Arabia–Africa–Madagascar biogeographic link. This is indicative of presence of a province that was occupied by ancestral stocks of *Struthiolithus*, *Aepyornis*, *Dimantornis* and *Struthio*. This palaeobiogeographic link corroborates other lines of evidence for faunal migration between southern Asia and Africa since the Middle Miocene. Several authors[32,46–50] have proposed an intercontinental dispersal corridor between southern Asia and Africa from Middle Miocene to Pleistocene. Discovery of a dominantly African fauna from 6–8-Ma-old sediments of Abu Dhabi, UAE[50], and including *Diamantornis*[51], further fortifies the link. Mourer-Chauvire *et al.*[26] have argued that the genus *Struthio* appeared in Africa prior to the Miocene and *Struthio* with an aepyornithid-like pore pattern spread to

Table 1. Character matrix

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17
Megaloolithus (Sauropod)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Ellipsoolithus	0	0	1	1	0	1	0	0	0	0	0	1	0	1	1	1	1
Gallus	1	2	2	0	1	1	0	1	1	1	0	2	1	1	1	1	1
Genyornis	1	2	2	1	1	0	0	0	1	0	0	3	0	1	1	1	1
Eudromia	1	2	2	0	0	1	0	1	2	2	0	2	2	0	0	0	0
Dinornis	1	2	2	1	2	1	0	2	2	2	0	2	1	1	1	1	1
Rhea	1	2	1&2	0	2	1	0	1	2	2	0	2	2	1	1	1	1
Struthio	1	2	3	0	2	1	0	1	2	2	0	3	2	1	1	1	1
cf. *Struthiolithus*	0	3	2	0	2	1	0	1	2	2	0	3	2	1	1	1	1
Diamantornis	1	2	3	0	2	1	0	2	2	1	0	3	2	1	1	0	0
Aepyornis	0	3	2	1	2	1	0	1	2	2	0	3	2	1	1	1	1
Casuarius	0	4	4	0	1	1	1	3	2	2	1	2	1	1	1	1	2
Dromaius	0	4	4	0	1	1	1	3	2	2	1	2	1	1	1	1	2
Apteryx	0	1&2	2	0	1	1	0	1	2	2	0	2	1	1	0	0	1

Eurasia sometime in Middle Miocene. Furthermore, they proposed that another lineage comprising *Namornis*, *Diamantornis* and oospecies of *Struthio* gave rise to present day African *Struthio* with the spread of struthionid-type pore pattern to Eurasia in the Late Miocene. Contemporaneous eggshells from Africa are represented by *Diamantornis wardi*[52], which differs from the present cf. *Struthiolithus* in its greater thickness and extremely large pore complexes (‘mega-pores’ ranging from 2 to 8 mm in diameter)[20]. A plausible scenario based on the fossil data may indicate that after their initial dispersal into Eurasia during the Eocene; Struthionidae, like several mammal taxa, may have also spread into Africa sometime in the Oligocene[53]. Later, during the Middle to Late Miocene they may have expanded their geographical distribution to Saudi Arabia and South Asia.

Palaeoclimate

Carbon isotope fractionation between eggshell (carbonate) and consumed plants, by metabolism in modern ostriches[54] is ~16‰. That is, an ostrich with predominantly C3 plant diet (δ^{13}C value of between –35‰ and –22‰)[55] will have eggshell $\delta^{13}C_{PDB}$ (PDB-Peedee belemnite; reference/standard) values of less than –6‰. The African ostrich (*S. camelus*) is described as an opportunistic omnivorous browser[56] and in general their diet is low in C4 grasses[54]. Isotopic studies on sub-fossil *Aepyornis* eggshells indicate that they had a habitat dominated by C3 vegetation[57,58]. Siwalik ratite eggshells indicate a C3 diet when C3 plants dominated the ecosystem (before 7 Ma), and a mixed C3–C4 diet when C4 vegetation was dominant (after 6 Ma) in the Siwaliks[30]. Our result of –10.4‰ $\delta^{13}C_{PDB}$ in the struthionid eggshell (only one sample was analysed) reflects a dominantly C3 diet. Though high 3‰ $\delta^{18}O_{PDB}$ value for the present eggshell, may reflect a water source in highly arid conditions[59], we need to carry out more analyses to evaluate its significance.

Variations in the struthionid-like pore patterns documented through the Neogene may be linked to fluctuating climatic conditions, perhaps linked to the marked global cooling trend characteristic of this time interval[60]. Mikhailov[14] proposed that with increasing aridity from the Late Miocene to the Pleistocene, ancient struthionid eggshells would have become thinner. The Siwalik Group ranging in age from ~18 to 0.2 Ma provides an excellent opportunity to learn about the antiquity of monsoonal conditions in the past. The Miocene locality of Haritalyangar has yielded diverse faunal assemblages besides the famous fossil apes. The well-known fossils include those of apes such as *Sivapithecus*, *Gigantopithecus* (*Indopithecus*), monkeys (*Pliopithecus*), adapid primate (*Sivaladapis*), horse (*Sivalhippus*), mouse deer (*Dorcatherium*), suid (*Propotamochoerus*), rodents (*Sayimys*, *Rhizomyides*), insectivores and other vertebrates. The overall fauna, sedimentary structure and palaeosol is indicative of mosaic environment comprising streams, gallery forests floodplain with thick forests cover with patches of grasslands. By the Late Miocene (8.5 Ma ago), these apes disappeared from the Siwalik sediments. Their sudden exit coincides with major tectonic and climatic events in southern Asia[61]. Tibeto-Himalayan uplift at around 12–9 Ma probably altered the heat budget, causing an intensification of the monsoon system in southern Asia[59–66]. Ancient soils, well preserved in the Siwaliks, also indicate marked seasonality in rainfall at this time[67,68]. Sanyal *et al.*[69] have also observed monsoon intensification at around 10 Ma. A major change in the diversity of muroid rodents (from cricetid-dominated to murid-dominated) at ~9–8 Ma has been attributed to an intensification of the monsoons[70]. Another factor influencing shrinking of forests is the advent of Late Miocene global cooling inducing arid conditions[71,72]. It seems quite plausible that such a change towards more seasonality would have led to an expansion of open conditions which may have aided ostriches to disperse into southern Asia.

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