
Warden Point and the Isle of Sheppey, Kent

[TQ 955 738]–[TR 024 717]

Introduction

The London Clay Formation (of Early Eocene age) is exposed on the northern and eastern shores of the Isle of Sheppey and is seen in the cliffs and on the foreshore (King, 1981, 1984; (Figure 4.8)). These exposures have produced a wide range of fossil vertebrates, including fishes, reptiles and birds. Commonly the bird bones occur as isolated ends of longbones, but occasionally articulated partial skeletons are preserved in phosphatic nodules that require careful mechanical preparation (Harrison, 1984a). The site has been collected from for many years and is still producing significant numbers of specimens.

Warden Point came to the attention of palaeontologists early, with reports of fossil turtles in 1811. Fossil birds were first noted from the London Clay Formation of the Isle of Sheppey in 1825 (Koenig, 1825), and many more specimens were reported over the years as they were delivered to London by the local collectors (e.g. Owen, 1841b, 1870, 1873, 1878; Bowerbank, 1854; Lydekker, 1891; Andrews, 1899). The tradition continues today, and numerous new specimens come to light all the time, giving rise to an extensive literature (Harrison, 1980b, 1982c, 1984a, 1986; Harrison and Walker, 1971, 1972, 1975, 1976b,c, 1977a; Walker, 1980; Dyke and Gulas, 2002; Mayr, 2002).

Description

The London Clay Formation has a maximum thickness of approximately 153 m, although only the top 53.5 m are exposed on the Isle of Sheppey (Davis, 1936; King, 1981). On the Isle of Sheppey, divisions A to lower C (King, 1981, 1984) are known only from boreholes, and divisions upper C, D and E are exposed. King (1984) identified 14 lithostratigraphical units (SH-1 to SH-14, in ascending order), sometimes separated by lines of septarian nodules.

(Table 4.4) Description of the London Clay Formation on the Isle of Sheppey based on King (1984)

Thickness (m)	
Virginia Water Formation	
Well-defined junction with SH-14, although not marked by a break in deposition or an erosion surface	10
London Clay Formation	
Division E	
SH-14. Silty clay/clayey silt; well-defined impersistent silt and sand partings, especially near the base and top	3.55
SH-13. Silty sand grading into sandy silt, intensely bioturbated, no primary sedimentary structures seen	1.00
SH-12. Silty and very silty clays, sandy horizon near the base (SH-12b), increase in prominent sandy lenses towards the top, base marked by septarian nodules	12.10
SH-11. Silty clays (SH-11a), sharp base with prominent layer of septarian nodules; irregularly spaced septarian nodules at higher levels; grades up into sandy silty clays (SH-11b) with occasional rounded septarian nodules	3.25
SH-10. Sandy clayey silt, transitional base, occasional lenticular septarian nodules near the top	c. 2.35
SH-9. Silty clay with sandy partings in upper part, tabular septarian nodules just above the base, small phosphatic nodules common in highest 0.8 m	c. 2.85

Division D

- SH-8. Very silty clay with pockets and lenses of very silty sand, base very poorly defined, top sharper c. 1.90
- SH-7. Silty clay, irregular septarian nodules in upper part, sharp base c. 3.70
- SH-6. Sandy clayey silt, poorly defined transitional basal junction, irregular and widely spaced band of lenticular septarian nodules near base, scattered nodules approximately 0.85 m below the top of the unit c. 2.80
- SH-5. Silty clays with a central subunit (SH-5b) of siltier clays and silt pockets and lenses, base marked by lenticular septarian nodules, nodule layers at higher levels underlain by pyritic brown clay, thin lenses of red-brown claystone at the base of SH-5b c. 7.95

Division C

- SH-4. Sandy clays and fine grained glauconite especially near the top c. 2.80
- SH-3. Silty clays, central layer of septarian nodules, small ovoid phosphatic nodules at base c. 2.00
- SH-2. Sandy clayey silts, small ovoid phosphatic nodules frequent at the top 7.20
- SH-1. Lowest level normally exposed, silty clays, five layers of septarian nodules. An unknown thickness of very silty clay, glauconitic near base, (SH-0) occurs below, on the foreshore. 6.30

Most of the fish, reptile and bird fossils have been collected from the foreshore without any stratigraphical data. The main source of the larger specimens is probably the phosphatic nodules found in SH-1 (King, 1984). King (1981, p. 53) noted that W.J. Quayle collected vertebrate specimens from nodule layers 5–10 m above the base of the exposed section, and he speculated that most of the museum specimens may have come from the same level.

Hooker and Ward (1980, p. 5) noted that vertebrate fossils have come from a number of specific locations on the Isle of Sheppey, in the section from [TQ 955 738] to [TR 024 717], with specific finds noted from Minster [TQ 955 736], Royal Oak [TQ 967 757], Bugsby's Hole [TQ 974 725], Eastchurch Gap [TQ 997 730], Barrows Brook [TR 013 718] and Warden Point [TR 021 725]. Therefore museum collections must involve higher horizons than SH-1 too.

Most of the bird fossils preserved at this locality are single bones, often damaged. In exceptional circumstances, more-complete specimens have been preserved in phosphatic or calcareous nodules, for example the skull of *Odontopteryx toliapica* and the partial skeleton of *Prophaethon shrubsolei* (Harrison, 1984a).

Fauna

The London Clay Formation of the Isle of Sheppey is the source of many invertebrate and plant remains (King, 1981; Collinson, 1983a; Wilkinson, 1988), as well as fishes (Hooker *et al.*, 1980; Dineley and Metcalf; 1999), reptiles (Benton and Spencer, 1995, pp. 278–82) and rare mammals (see Chapter 3). The following listing of the avifauna is based on Walker (1980), updated from Harrison (1980b, 1982c, 1984a, 1986).

AVES

Palaeognathae

Lithornithidae

Lithornis vulturinus Owen, 184 lb

Parvigyps praecox Harrison and Walker, 1977a

Galliformes

(?) Phasianidae

Argillipes aurorum Harrison and Walker, 1977a

Argillipes paralectoris Harrison and Walker, 1977a

Percolinus venablesi Harrison and Walker, 1977a

Pelecaniformes

Prophaethontidae

Prophaethon shrubsolei Andrews, 1899

Pelagomithidae

Odontopteryx toliapica Owen, 1873

Macrodontopteryx oweni Harrison and Walker, 1976b

Pseudodontornis longidentata Harrison and Walker, 1976b

Dasornis londinensis Owen, 1870

Argillornis emuinus (Bowerbank, 1854)

Argillornis longipennis Owen, 1878

Procellariiformes

Hydrobatidae

Primodroma bournei Harrison and Walker, 1977a

Procellariidae

Neptuniavis miranda Harrison and Walker, 1977a

Neptuniavis minor Harrison and Walker, 1977a

Gruiformes

Rallidae

Parvirallus bassetti Harrison, 1984a

Parvirallus medius Harrison, 1984a

Parvirallus gassoni Harrison, 1984a

Charadriiformes

Glareolidae?

Precursor parvus Harrison and Walker, 1977a

Precursor magnus Harrison and Walker, 1977a

Precursor litorum Harrison and Walker, 1977a

Ciconiiformes

Threskiornithidae

Proplegadis fisheri Harrison and Walker, 1971

Falconiformes

Falconidae

Stintonornis mitchelli Harrison, 1984a

Strigiformes

Protostrigidae

cf. *Eostrix vincenti* Harrison, 1980b

Cuculiformes

Musophagidae

Promusophaga magnifica Harrison and Walker, 1977a

Apodiformes

Aegialornithidae

Primapus lacki Harrison and Walker, 1977a

Coraciiformes

Halcyornithidae

Halcyornis toliapicus (Koenig, 1825)

Piciformes

Primobucconidae

?*Primobucco olsoni* Feduccia and Martin, 1976

Incertae sedis

Leptosomidae

Plesiocathartes sp. [Mayr, 2002]

A remarkable reassignment of bird material from the Isle of Sheppey and other European and North American localities has established that a family of palaeognathous birds existed in northern Europe in Eocene times. Houde (1988) established the family Lithornithidae for two species from the Isle of Sheppey, *Lithornis vulturinus* Owen, 1841b, previously identified as a ciconiiform (stork relative), and *Parvigyps praecox* Harrison and Walker, 1977a, established as a falcon. *Lithornis vulturinus*, the first London Clay Formation bird to be named, was based on a partial postcranial skeleton ((Figure 4.9)a). *Parvigyps praecox* Harrison and Walker, 1977a, was established on the basis of the distal end of a humerus, and additional material (a partial pelvis and sacrum and a second partial sacrum) has been assigned to it. According to Houde (1988), other taxa described from the London Clay Formation should also be synonymized with *L. vulturinus*, namely *Neptuniavis minor* (pars), *Pediorallus barbarae* (pars) and *Promusophaga magnifica*, although Mayr *et al.* (2002) suggested that *Neptuniavis* may in fact be a pelagornithid pseudodontorn. The Lithornithidae were flying birds about the size of chickens, but Houde (1988) argued that they were close relatives of the living flightless palaeognathous birds such as ostriches and emus.

Three galliforms (game birds) have been named from Isle of Sheppey specimens: *Argillipes aurorum* Harrison and Walker, 1977a, based on a partial tarsometatarsus, as well as another tarsometatarsus and a partial humerus; *Argillipes paralectoris* Harrison and Walker, 1977a, based on a partial tarsometatarsus; and *Percolinus venablesi* Harrison and Walker, 1977a, based on a partial tarsometatarsus, as well as the cast of another. All three might represent a single taxon and, in any case, none of the specimens shows any diagnostic characters of the order. Dyke and Gulas (2002) preferred to refer all the material to 'Galliformes *incertae sedis*'.

The pelecaniforms from the Isle of Sheppey include perhaps seven species. *Prophaethon shrubsolei* Andrews, 1899, the first to be reported, was based on a remarkable near-complete skull ((Figure 4.9)b,c), as well as parts of the shoulder girdle, backbone and hindlimb (Harrison and Walker, 1976a, 1977a). Probably also included here are the bony toothed birds, the Pelagornithidae, (ex Odontopterygiformes) (Unwin, 1993), from the Isle of Sheppey, which were reviewed and described in detail by Harrison and Walker (1976b, 1977a). These authors concluded that there were six species from the Isle of Sheppey, distributed in three families: the Odontopterygidae, Pseudodontornithidae and Dasornithidae. *Odontopteryx toliapica* was described from a partial skull ((Figure 4.9)d,e) by Owen (1873), and a few leg bones also have been assigned to the species. *Macrodonopteryx oweni* was established by Harrison and Walker (1976b, p. 12) for another partial skull of a larger bird ((Figure 4.9)f,g) that originally had been ascribed to *Argillornis longipennis* by Owen (1880). A third species, *Pseudodontornis longidentata*, was founded by Harrison and Walker (1976b, p. 17) on a partial beak ((Figure 4.9)h) and a vertebra. Three further species, *Dasornis londinensis* Owen, 1870, *Argillornis emuinus* (Bowerbank, 1854) and *Argillornis longipennis* Owen, 1878, were grouped together in the new family Dasornithidae on account of their large size and other features. The type materials of these three are, respectively, two incomplete skulls, several humeri and other limb bones and several humerus fragments.

Three procellariiform birds, relatives of modern albatrosses and petrels, have been named on the basis of specimens from the Isle of Sheppey: *Primodroma bournei* Harrison and Walker, 1977a, based on the distal end of a right humerus, *Neptuniavis miranda* Harrison and Walker, 1977a, based on two partial tarsometatarsi ((Figure 4.9)i,j), and *Neptuniavis minor* Harrison and Walker, 1977a, based on a partial tarsometatarsus and a partial femur. The latter may be a synonym of the lithornithid *Lithornis vulturinus* (Houde, 1988).

Three gruiforms, the rails *Parvirallus bassetti* Harrison, 1984, *Parvirallus medius* Harrison, 1984a, and *Parvirallus gassoni* Harrison, 1984a, have been described from the Isle of Sheppey, the first two on the basis of one partial tarsometatarsus each, the last on the basis of a partial tibiotarsus and a partial femur.

The charadriiforms — shorebirds, gulls, auks and skuas — are represented on the Isle of Sheppey by three species: *Precursor parvus* Harrison and Walker, 1977a, based on a partial humerus from Bognor and a partial humerus from the Isle of Sheppey, *Precursor magnus* Harrison and Walker, 1977a, based on a partial tarsometatarsus, and *Precursor litorum* Harrison and Walker, 1977a, based on the distal end of a humerus.

A ciconiiform (a relative of modern storks and New World vultures), *Proplegadis fisheri* Harrison and Walker, 1971, is based on a partial humerus. A falconiform, *Stintonornis mitcheffi* Harrison, 1984a, was founded on a partial tarsometatarsus from the Isle of Sheppey. The owl *Eostrix vincenti*, described from a phalanx from South Ockendon,

Essex, also may be represented on the Isle of Sheppey by a partial tarsometatarsus (Harrison, 1980b).

The cuculiforms are represented by one species, the musophagid *Promusophaga magnifica* Harrison and Walker, 1977a, based on an incomplete skeleton ((Figure 4.9)k) and two other blocks with partial postcranial skeletons. This species may, however, be a synonym of the lithornithid *Lithornis vulturinus* (Houde, 1988). The apodiforms are represented on the Isle of Sheppey by a right humerus referred to *Primapus lacki* Harrison and Walker, 1975, a small relative of modern swifts and hummingbirds described first from the London Clay Formation of Bognor Regis. The coraciiform *Halcyornis toliapicus* (Koenig, 1825), originally thought to be an early kingfisher, was the first London Clay Formation bird to be named, founded on an incomplete skull from the Isle of Sheppey. A further specimen, a partial tarsometatarsus from the Isle of Sheppey, was assigned tentatively to *Primobucco olsoni* Feduccia and Martin, 1976, by Harrison (1982c), but this has been reassigned. First, Mayr (1998) referred Primobucconidae to Piciformes, the woodpeckers, alongside much good material from Messel in Germany. He then assigned the London Clay specimen to the pseudasturid psittaciform *Pulchrapollia* Mayr 2002. Finally, Mayr (2002) assigned a partial tarsometatarsus to *Plesiocathartes* sp., related to *P. kelleri* from Messel, birds assigned to the Leptosomidae, a family of uncertain relationships.

In all, the Isle of Sheppey has been the source of type specimens of 22 birds, including the lithornithids *Lithornis vulturinus* Owen, 1841b; and *Parvigyps praecox* Harrison and Walker, 1977a; the galliforms *Argillipes aurorum* Harrison and Walker, 1977a; *Argillipes paralectoris* Harrison and Walker, 1977a; and *Percolinus venablesi* Harrison and Walker, 1977a; the pelecaniforms *Prophaethon shrubsolei* Andrews, 1899; *Odontopteryx toliapica* Owen, 1873; *Macrodontopteryx oweni* Harrison and Walker, 1976b; *Pseudodontornis longidentata* Harrison and Walker, 1976b; *Dasornis londinensis* Owen, 1870; *Argillornis emuinus* (Bowerbank, 1854); and *Argillornis longipennis* Owen, 1878; the procellariiforms *Primodroma bournei* Harrison and Walker, 1977a; *Neptuniavis miranda* Harrison and Walker, 1977a; and (?)*Neptuniavis minor* Harrison and Walker, 1977a; the gruiforms *Parvirallus bassetti* Harrison, 1984a; *Parvirallus medius* Harrison, 1984a; and *Parvirallus gassoni* Harrison, 1984a; the ciconiiform *Proplegadis fisheri* Harrison and Walker, 1971; the falconiform *Stintonornis mitchelli* Harrison, 1984a; the cuculiform (?)*Promusophaga magnifica* Harrison and Walker, 1977a; and the coraciiform *Halcyornis toliapicus* (Koenig, 1825).

Interpretation

The London Clay Formation has been interpreted as a shallow marine shelf deposit that accumulated in depths of up to 100 m. Variations in sediment grain size have been accounted for by inferring changes in relative sea level. The basal section of division D has been interpreted as a transgressive phase. By the end of division D, sea level was lowered (Islam, 1984). The upper sections of the London Clay Formation have been interpreted as being deposited under increasingly shallow conditions (King, 1984). The majority of the invertebrate taxa recorded from this site are thought to have inhabited the sea. The terrestrial taxa (plants and land animals) were washed in from the surrounding lands (Benton and Spencer, 1995).

The Lithornithidae, a family established by Houde (1988), represents an extraordinary biogeographical conundrum. Today, the flightless birds, the Palaeognathae or Struthioniformes are a southern continent group, being represented by ostriches, emus, cassowaries, rheas, the kiwi and the extinct moas. The Lithornithidae and their close relatives from the Paleocene and Eocene epochs, were widely distributed over Europe and North America. *Lithornis vulturinus* was described originally as a bird of prey. Although the type specimen was destroyed in the bombing of London during the Second World War, illustrations remain. From these, it was re-identified as an ibis (Harrison and Walker, 1977a), and then it was made the type of the new family Lithornithidae by Houde (1988). The type specimen of *Parvigyps praecox* originally was assigned to *Lithornis vulturinus*, but it was re-identified by Harrison and Walker (1977a) as a modern Old World vulture. Houde (1988) returned it to the Lithornithidae, a view accepted by others (Olson, 1985; Unwin, 1993).

The gamebirds *Argillipes aurorum* Harrison and Walker, 1977a, *Argillipes paralectoris* Harrison and Walker, 1977a, and *Percolinus venablesi* Harrison and Walker, 1977a, are assigned to the Phasianidae, the family including most gamebirds. All four taxa are small birds, comparable to modern partridge or quail in size and appearance (Harrison and Walker, 1977a).

The pelecaniiforms are one of the larger groups represented. Included here is *Prophaethon shrubsolei*, which seems to show a mix of characters, mostly pelecaniiform, but others procellariiform or charadriiform. This was a large seabird, with a skull some 115 mm long, implying a wingspan of over 1 m. Perhaps it looked something like a gannet. The bony toothed birds, the Pelagornithidae (= Odontopterygidae), probably also belong here. They were seabirds, characterized by the remarkable tooth-like projections along the sides of their beaks ((Figure 4.10)a–c). These were not true teeth (birds had lost their teeth in the Mesozoic Era), but they probably functioned somewhat like teeth, perhaps in securing and holding slippery fish. The Isle of Sheppey specimens vary enormously in size, with skull lengths from 150 mm to 0.5 m. The larger species then must have had wingspans of 5–6 m (Harrison and Walker, 1976b). Their skulls superficially resemble some of the modern seabirds ((Figure 4.10)d–j), but the extinct forms all have more massive lower jaws. Harrison and Walker (1976b) proposed that the bony-toothed birds should be placed in their own families — the Odontopterygidae, Pseudodontopterygidae and Dasornithidae — and in their own order — the Odontopterygiformes. Olson (1985, pp. 194–201) argued, however, that all these families should be included in the Pelagornithidae, an extinct family of large seabirds that falls in the Order Pelecaniformes, and that the apparent diversity in the London Clay Formation has probably been overestimated.

The three rails from the Isle of Sheppey, *Parvirallus basseti* Harrison, 1984a, *Parvirallus medius* Harrison, 1984a, and *Parvirallus gassoni* Harrison, 1984a, were all small birds, resembling in size and appearance perhaps the modern little stint *Calidris minutus*. The ciconiiform *Proplegadis fisheri* is similar in many ways to modern ibises such as *Geronticus calvus* and *Eudocimus ruber* (Harrison and Walker, 1971; Harrison, 1986). Note, on the other hand, that Olson (1985, p. 162) did not believe that any of these specimens could be referred with confidence to the rails.

The supposed owl *Eostrix vincenti* Harrison, 1980b, is uncertainly identified: the remains do not match those known for the American species of *Eostrix*, nor the Middle Eocene owl *Palaeoglaux* from Messel (Peters, 1992a). Olson (1985, p. 13) is uncertain of their true identity. The cuculiform *Promusophaga magnifica* Harrison and Walker, 1977a, has been reinterpreted by Houde (1988) as a ratite (a flying palaeognathous bird).

The coraciiform *Halcyornis toliapicus* (Koenig, 1825) was first interpreted by Koenig (1825) as a gull, then Owen (1846) recognized it as a kingfisher, but Lydekker (1891) re-classified it as a gull, before Harrison and Walker (1972, 1977a, pp. 46–7) finally assigned it again to Coraciiformes as a stem member of the order, but in its own family, Halcyornithidae. Olson (1985, p. 125) tentatively agreed with this finding.

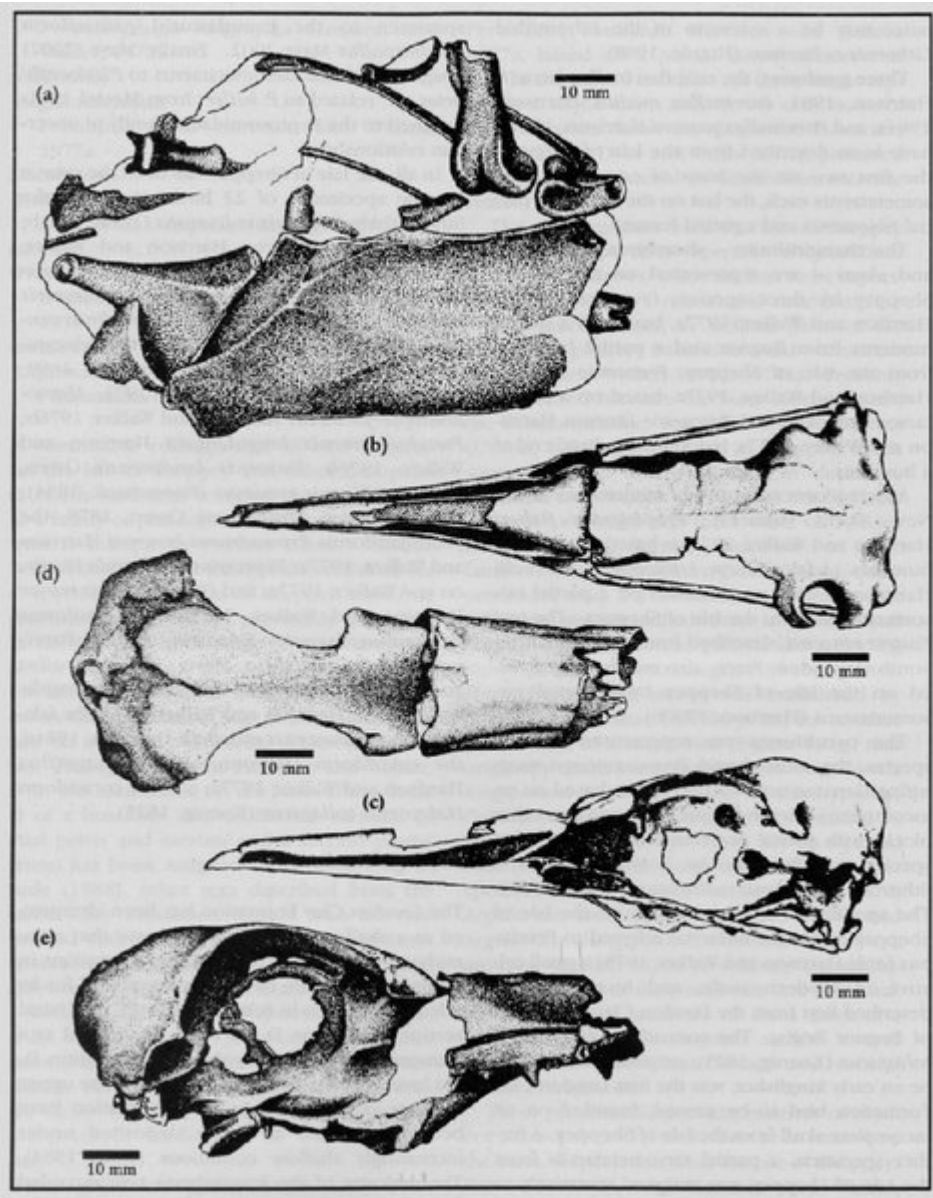
Comparison with other localities

Comparisons can be made with various British sites, including material from London Clay Formation division C in London and south Essex, division B at Herne Bay and Bognor Regis and division A1 and A2 at Walton-on-the-Naze (Harrison, 1983). The Isle of Sheppey avifauna includes many of the elements seen in the older units at Walton-on-the-Naze, but the Isle of Sheppey site has produced a much more diverse bird fauna. Farther afield, the only really comparable bird fauna is known from the Early Eocene Green River Formation of Wyoming, where some exquisite complete specimens are known (Olson, 1985). Feduccia (1999, p. 168) gives a useful list of the Green River Formation bird taxa, consisting of just under 40 species, and many of the groups, and even genera, are shared with the London Clay Formation. Comparative units in continental Europe have been outlined in the Walton-on-the-Naze GCR site report, but none of these avifaunas even approaches the diversity of the Isle of Sheppey localities (Harrison, 1980a).

Conclusions

The avifauna preserved at Warden Point and the Isle of Sheppey in general, is exceptionally diverse and abundant. Of particular interest are the large numbers of small species of non-passerine birds that appear to have occupied the ecological niches characteristic of many modern passerine species. The Isle of Sheppey is the source of the richest and most diverse fossil bird fauna in Britain, and the best in the Early Eocene record of Europe. Extensive exposure and continuing erosion mean that fresh finds are made all the time, and the potential for further finds is considerable.

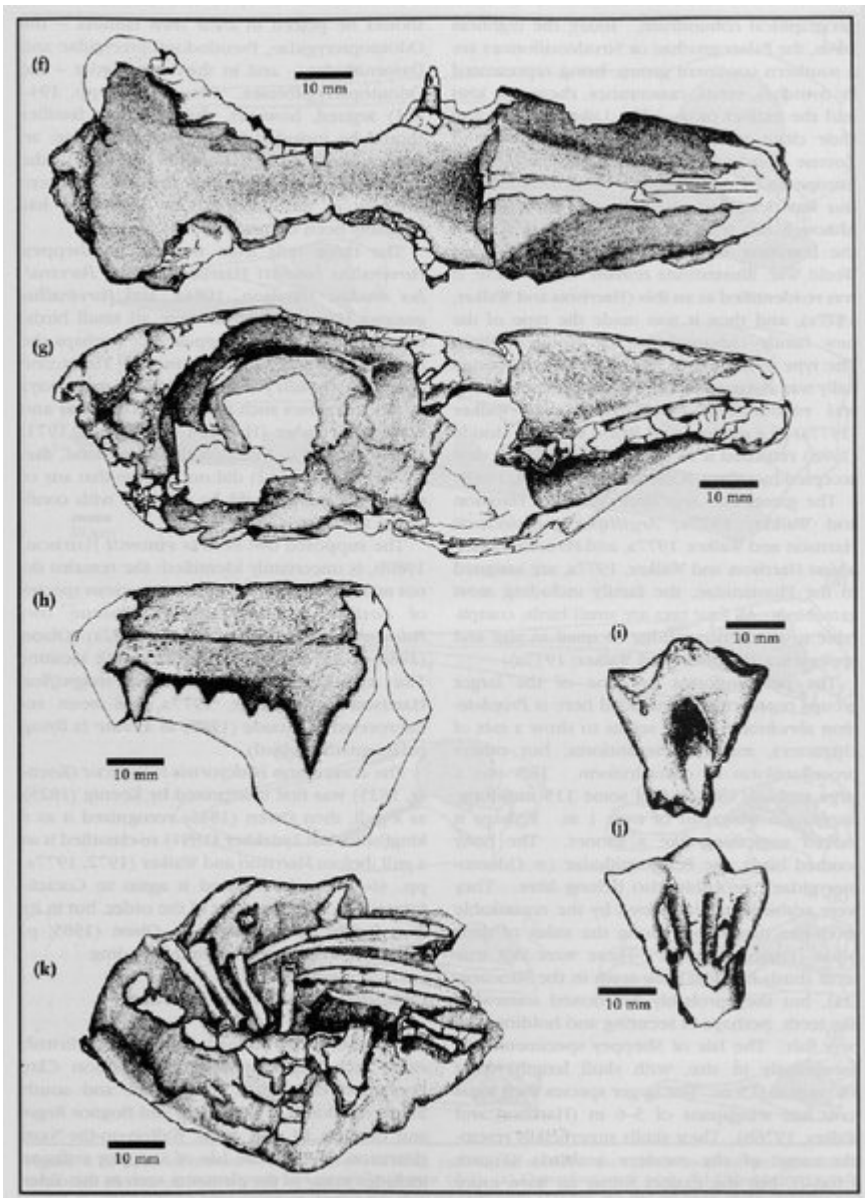
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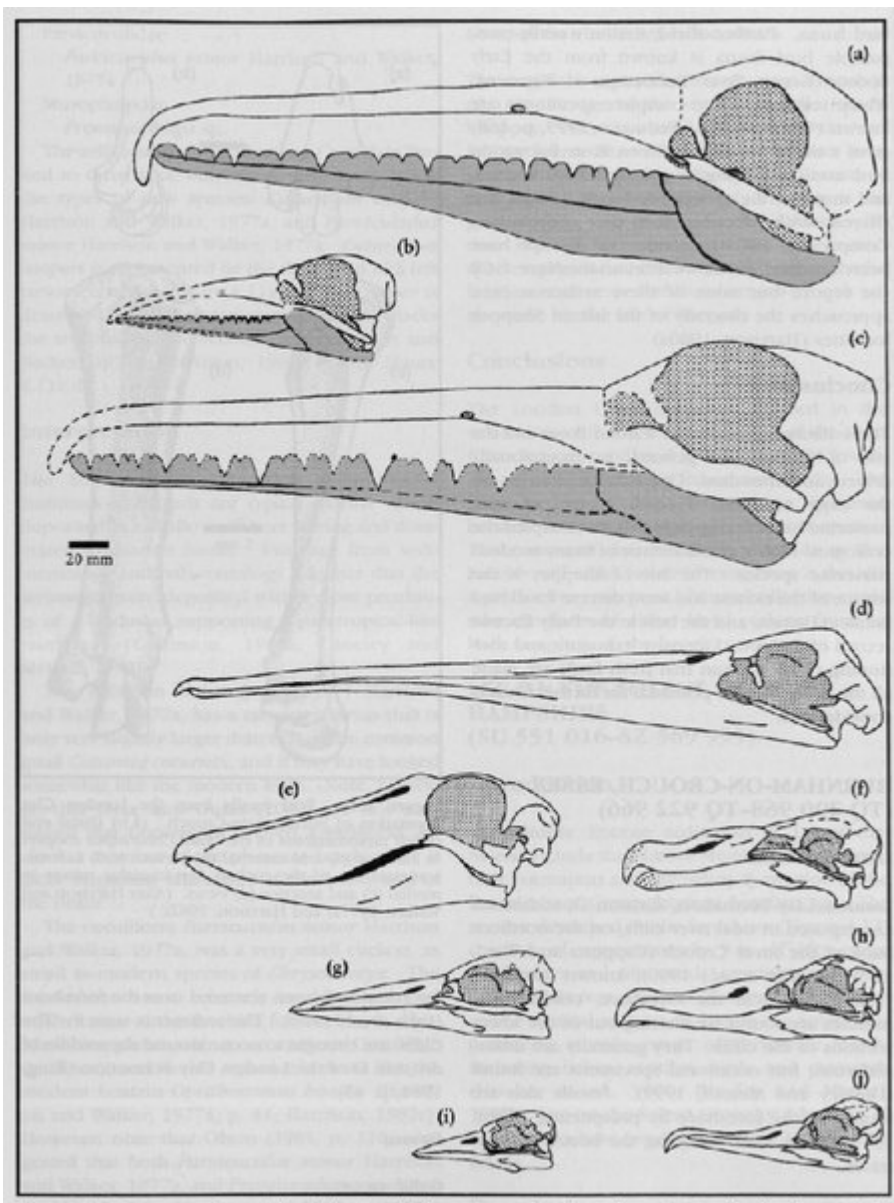
(Figure 4.8) The London Clay Formation exposed at Warden Point, Isle of Sheppey, showing collapsed cliffs and fossil-bearing material on the foreshore. (Photo: D.J. Ward.)

	Thickness (m)
Virginia Water Formation	
Well-defined junction with SH-14, although not marked by a break in deposition or an erosion surface	10
London Clay Formation	
Division E	
SH-14. Silty clay/clayey silt; well-defined impersistent silt and sand partings, especially near the base and top	3.55
SH-13. Silty sand grading into sandy silt, intensely bioturbated, no primary sedimentary structures seen	1.00
SH-12. Silty and very silty clays, sandy horizon near the base (SH-12b), increase in prominent sandy lenses towards the top, base marked by septarian nodules	12.10
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SH-9. Silty clay with sandy partings in upper part, tabular septarian nodules just above the base, small phosphatic nodules common in highest 0.8 m	c. 2.85
Division D	
SH-8. Very silty clay with pockets and lenses of very silty sand, base very poorly defined, top sharper	c. 1.90
SH-7. Silty clay, irregular septarian nodules in upper part, sharp base	c. 3.70
SH-6. Sandy clayey silt, poorly defined transitional basal junction, irregular and widely spaced band of lenticular septarian nodules near base, scattered nodules approximately 0.85 m below the top of the unit	c. 2.80
SH-5. Silty clays with a central subunit (SH-5b) of siltier clays and silt pockets and lenses, base marked by lenticular septarian nodules, nodule layers at higher levels underlain by pyritic brown clay, thin lenses of red-brown claystone at the base of SH-5b	c. 7.95
Division C	
SH-4. Sandy clays and fine grained glauconite especially near the top	c. 2.80
SH-3. Silty clays, central layer of septarian nodules, small ovoid phosphatic nodules at base	c. 2.00
SH-2. Sandy clayey silts, small ovoid phosphatic nodules frequent at the top	7.20
SH-1. Lowest level normally exposed, silty clays, five layers of septarian nodules. An unknown thickness of very silty clay, glauconitic near base, (SH-0) occurs below, on the foreshore.	6.30

(Table 4.4) Description of the London Clay Formation on the Isle of Sheppey based on King (1984)



(Figure 4.9) Specimens of fossil birds from the London Clay Formation of Warden Point, Isle of Sheppey. (a) Thoracic region of the lithornithid *Lithornis vulturinus*, mainly in left lateral view. (b,c) Skull of the prophaethontid *Prophaethon shrubsolei* in dorsal (b) and left lateral (c) views. (d,e) Skull of the pelagornithid *Odontopteryx toliapica* in dorsal (d) and right lateral (e) views. (f,g) Skull of the pelagornithid *Macrodonopteryx oweni* in dorsal (f) and right lateral (g) views. (h) Left external view of a fragment of the beak of the pelagornithid *Pseudodontornis longidenta*. (i,j) Proximal end of the right tarsometatarsus of the procellariid *Neptuniavis miranda* in anterior (i) and posterior (j) views. (k) Thoracic region of the cuckoo *Promusophaga magnifica*, mainly in left lateral view. (Based on Harrison and Walker, 1976b, 1977a.)



(Figure 4.10) Reconstructions of the skulls of sea birds, extinct and modern: the extinct 'toothed' pelagornithids (a-c) and modern pelecaniforms and procellariiforms (d-j). (a) *Osteodontornis orri*, (b) *Odontopteryx toliapica*, (c) *Pseudodontornis longirostris*, (d) the pelican *Pelecanus crispus*, (e) the shoebill stork *Balaeniceps rex*, (f) the giant petrel *Macronectes giganteus*, (g) the gannet *Sula bassana*, (h) the albatross *Diomedea chrysostoma*, (i) the tropic bird *Phaethon lepturus*, (j) the frigate bird *Fregata aquila*. (After Harrison and Walker, 1976b.)