Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain

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Chapter 4

British Tertiary fossil bird GCR sites

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INTRODUCTION

A general description of Tertiary stratigraphy and the British sedimentary setting of that time is provided in Chapter 3, and an outline of bird evolution is given in Chapter 1.

BIRD EVOLUTION IN THE BRITISH TERTIARY SUB-ERA

The time-span represented by the stratigraphical units that have produced bird fossils, from the Early Eocene to Early Oligocene sedimentary record, encompasses some major changes in bird faunas. Most of the British fossil birds belong to modern orders, although there are a few surprises, such as the early Oligocene ostrich *Proceriavis*. Most modern groups, from ducks and game birds to gulls, falcons and kingfishers, are represented as fossils, but the commonest birds today, the Passeriformes – perching birds or songbirds – are poorly known, because they radiated explosively in the Miocene Epoch, and sediments of that age are virtually absent in Great Britain. A possible early passeriform is *Primoscens*, from the London Clay Formation. Archaic bird groups are also represented, in particular the 'toothed' Odontopterygiformes of the Eocene Epoch. The main characters of the different Tertiary bird groups are given by Feduccia (1999) and, more briefly, by Benton (2005), and these two general books provide good introductions to the wider literature on bird anatomy and the fossil record of birds.

The fossil record of birds from Great Britain is good, including over 60 species, but the record is not so rich as that of mammals (see Chapter 3). It is often said that birds have an impossibly bad fossil record, but this is incorrect (Unwin, 1993), and people are often surprised at how much is known about the early history of the modern groups. The avifauna of the Early Eocene London Clay Formation appears to be as rich as in any modern temperate-climate location (Walker, 1980). However, in view of the tropical nature of the climate recognized to have existed in southern England, it is highly unlikely that the fossil record has sampled the full diversity of birds at the time.

Fossil birds were first reported from the London Clay Formation as long ago as 1825 (Koenig, 1825), and numerous other Victorian accounts were given of new specimens from that stratigraphical unit (e.g. Owen, 1841b, 1870, 1873, 1878; Bowerbank, 1854; Lydekker, 1891; Andrews, 1899) and occasionally from other Tertiary units (e.g. Newton, 1886). There was then a long gap of time during which very little research was done on British fossil birds, until the extensive and fruitful co-operation of Colin J.O. Harrison and Cyril A. Walker in the 1970s and 1980s (Harrison, 1971, 1980b, 1982a–c, 1983, 1984a,b, 1985, 1986; Harrison and Walker, 1971, 1972, 1975, 1976a–c, 1977a,b, 1979a,b; Walker, 1980). More recently, Gareth Dyke has begun a programme of description of new materials from the London Clay (Dyke and Cooper, 2000; Dyke, 2001a,b; Dyke and Waterhouse, 2001; Dyke and Gulas, 2002).

BRITISH TERTIARY BIRD SITES

The distribution of fossil birds in Great Britain was outlined by Walker (1980), but a number of further records have been published since then. Nonetheless, this work forms the basis for the county-by-county summary of fossiliferous bird sites given here. Fossil birds are found in many of the same Tertiary units that yield mammal specimens, but there is more emphasis on the London Clay Formation, which is, surprisingly perhaps, richer in birds and reptiles than it is in mammals.

Fossiliferous sites (Figure 4.1) are located predominantly in extensive coastal sections, most of them in the London Clay Formation along the northern and southern banks of the Thames Estuary, and others along the south coast of Hampshire and the north and north-western coasts of the Isle of Wight. Other sites have been quarries or temporary construction sites. An outline of the main locations is noted here, together with the name of the fossiliferous unit. Localities are arranged according to their occurrence in the London Basin (Middlesex, Suffolk, Essex, Surrey, Sussex, Kent, Hertfordshire, Berkshire) or the Hampshire Basin (Hampshire, Isle of Wight, Dorset).

GREATER LONDON: St James's Park, London (TQ 29 79; *Pediorallus barbarae*; division C, London Clay Formation; Wetherell, 1836; Walker, 1980): Chalk Farm, Primrose Hill, railway tunnel (TQ 266 841–TQ 277 842; *Proherodius oweni* type specimen; Early Eocene divisions B–C, London Clay Formation;

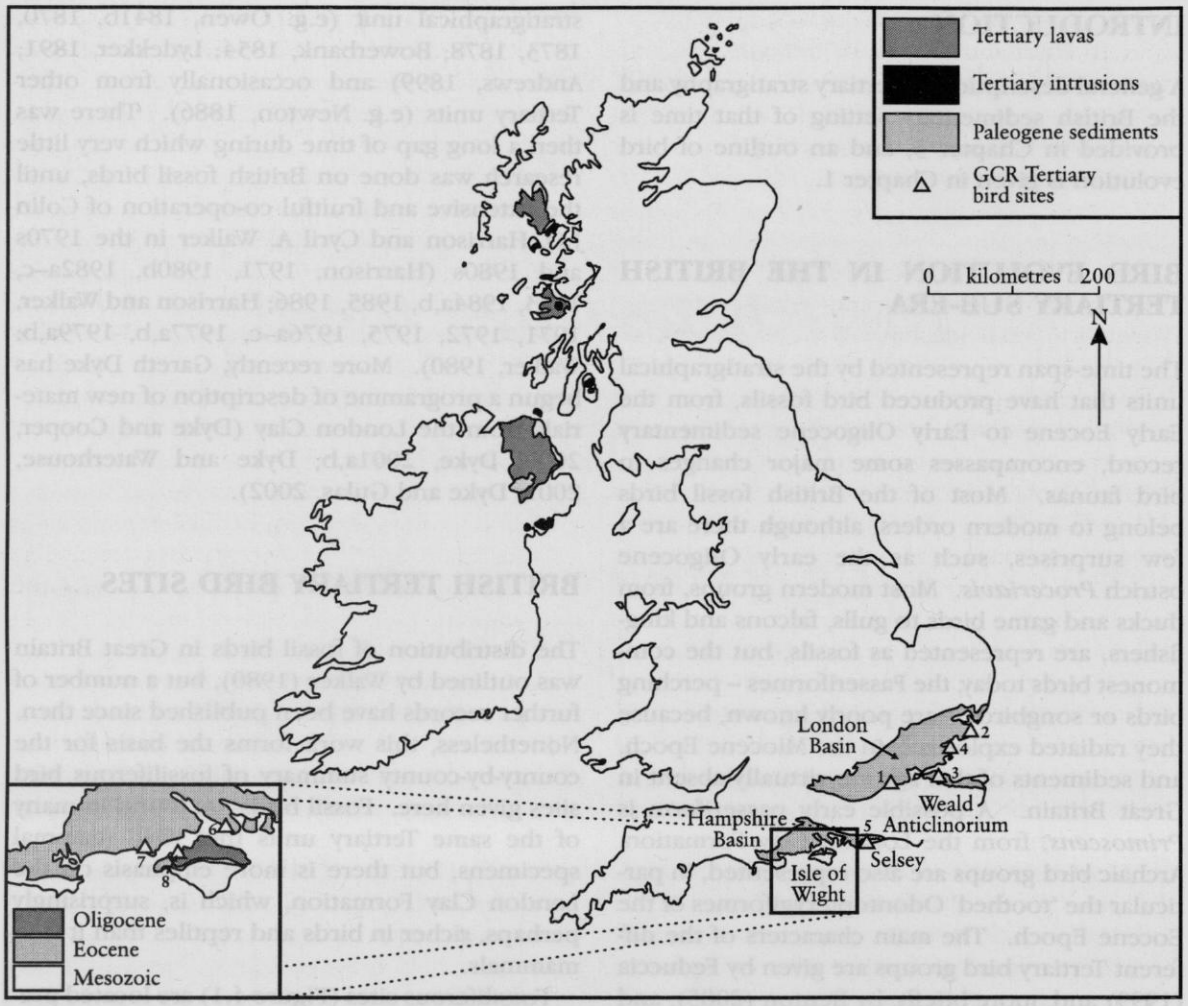


Figure 4.1 Map showing the distribution of Tertiary rocks in Great Britain. GCR Tertiary bird sites: (1) Abbey Wood; (2) Walton-on-the-Naze; (3) Warden Point and the Isle of Sheppey; (4) Burnham-on-Crouch; (5) Bognor Regis; (6) Lee-on-the-Solent; (7) Hordle Cliff; (8) Bouldnor Cliff.

Lydekker, 1891; Harrison, 1979; Harrison and Walker, 1977a, 1978; Dyke, 2001b): Abbey Wood (see GCR site report)

SUFFOLK: Orford (TM 415 500; *Diomedea anglica*; early/mid Pliocene Coralline Crag; Lydekker, 1891): Foxhall, near Waldringfield (TM 11 52; *Diomedea*; mid Pliocene Red Crag; Lydekker, 1886).

ESSEX: Grange Farm, South Ockendon (TQ 611 833–TQ 615 833; *Eostrix vincenti*, type specimen, a small gamebird, a pigeon and a small wader; Early Eocene division A, London Clay Formation; George and Vincent, 1978; Harrison, 1980b, 1983): Ongar (TL 562 024; *Pediorallus barbarae* type specimen, *Litoripes medius*; Early Eocene division C, London Clay Formation; Daniels, 1971; Harrison and Walker, 1977a; 1979a; Walker, 1980): Walton-on-the-Naze (see GCR site report): Burnham-on-Crouch (see GCR site report).

SURREY: Croydon (TQ 340 655; *Gastornis klaasseni*, type specimen; Early Eocene Woolwich Shell Beds, Woolwich Formation; Klaassen, 1883; Newton, 1886; Walker, 1980).

SUSSEX: Bognor Regis (see GCR site report).

KENT: Herne Bay (TR 187 683–TR 197 684; *Pediorallus barbarae*; Early Eocene division B, London Clay Formation; *Pseudodontornis tenuirostris*; Early Eocene Oldhaven Formation;

Cooper, 1977; Walker, 1980; Harrison, 1985): Warden Point and the Isle of Sheppey (see GCR site report).

BERKSHIRE: Arborfield (SU 767 654: possible bird bone; Early Eocene London Clay Formation; Cooper, 1976a).

HAMPSHIRE: Yateley (SU 826 611; *Litoripes medius*; early Middle Eocene (Lutetian) Earnley Formation, Bracklesham Group; James and Ward, 1976; Curry *et al.*, 1978; Walker, 1980): Highcliffe and Barton (SZ 367 899; *Villetus grandis*, type specimen and *Villetus waltoni*, type specimen; late Middle Eocene (Bartonian) Barton Clay Formation; Burton, 1929; Harrison and Walker, 1976c, 1977a; Walker, 1980): Dummer's Copse, Westend, near Southampton (SU 4585 1546; rolled and broken bird limb bones; Early Eocene Wittering Formation, Bracklesham Group; Kemp, 1984; Bone *et al.*, 1991): Hordle Cliff (see GCR site report): Lee-on-the-Solent (see GCR site report).

ISLE OF WIGHT: Yarmouth (SZ 367 899; *Proceriavis hamsteadensis*, *Paracygnopterus scotti*, *Oligocathartes olsoni*, *Argillipes magnus*, *Geranopsis hastingsiae*, *Palaeopapia hamsteadensis*; Early Oligocene Bembridge Marls Member of the Bouldnor Formation; Lydekker, 1891; Harrison and Walker, 1979b; Dyke, 2001b): Thorness Bay (SZ 464 945; *Oligocathartes olsoni*, mould of feather; Early Oligocene Bembridge Marls Member; Daley, 1973; Daley and Edwards, 1974; Jarzembowski, 1976; Harrison and Walker, 1979b; Walker, 1980): Burnt Wood, Thorness Bay (SZ 442 930; *Headonornis hantoniensis*; Early Oligocene Bembridge Marls Member; Lydekker, 1891; Daley, 1973; Walker, 1980): Bouldnor Cliff (see GCR site report).

From these potential locations, eight are selected as GCR sites for their fossil bird remains (Figure 4.1), five being Early Eocene in age (Abbey Wood, Walton-on-the-Naze, Warden Point, Burnham-on-Crouch, Bognor Regis), one Middle Eocene (Lee-on-Solent), one Late Eocene (Hordle Cliff) and one Early Oligocene (Bouldnor Cliff). Three of these sites (Abbey Wood, Hordle Cliff, Bouldnor Cliff) are also selected for the GCR for their fossil mammals, and full descriptions of the geology are given in Chapter 3 and not repeated here.

1. Abbey Wood, Greater London (TQ 480 786). Early Eocene (Ypresian) Blackheath Beds.
2. Walton-on-the-Naze, Essex (TM 263 230–TM 268 245). Early Eocene (Ypresian) Harwich (division A1) and Walton (division A2) members, London Clay Formation.
3. Bognor Regis, West Sussex (SZ 920 979–SZ 924 983). Early Eocene (Ypresian) Aldwick Beds (division B), London Clay Formation.
4. Warden Point and Isle of Sheppey, Kent (TM 263 230–TM 268 245). Early Eocene (Ypresian) London Clay Formation, divisions C–E.
5. Burnham-on-Crouch, Essex (TQ 290 968–TQ 922 966). Early Eocene (Ypresian) London Clay Formation, division D.
6. Lee-on-the-Solent, Gosport, Hampshire (SU 551 016–SZ 569 999). Middle Eocene (Lutetian) Selsey Formation and Elmore Member, Barton Clay Formation.
7. Hordle Cliff, Hampshire (SZ 254 925–SZ 270 921). Late Eocene (Priabonian) Totland Bay Member, Headon Hill Formation.
8. Bouldnor Cliff, Isle of Wight (SZ 375 902–SZ 403 919). Early Oligocene (Rupelian) Hamstead Member, Bouldnor Formation.

ABBEY WOOD, GREATER LONDON (TQ 480 786)

Introduction

The fossiliferous strata at Abbey Wood have produced a wide variety of vertebrate remains, including mammals, birds, reptiles and fishes. Over recent years the collecting emphasis has been placed on bulk sampling, and many significant new finds have come to light, including three fragmentary bird specimens (Harrison and Walker, 1977a). The site has potential for continued excavation and recovery of new fossil material.

Description

The stratigraphy and occurrence of the fossils are outlined in Chapter 3.

Fauna

In addition to an extensive fauna of fishes, reptiles and mammals (Cooper, 1932a,b; Simons, 1962; Van Valen, 1965; Kühne, 1969; Hooker,

1979, 1980, 1996c; Hooker *et al.*, 1980; Dineley and Metcalf, 1999), remains of one bird species have been recovered from Abbey Wood.

AVES
Procellariiformes
Marinavidae
Marinavis longirostris Harrison and Walker, 1977a

The bird remains occur as scattered bone fragments that show little evidence of transport-induced abrasion. The holotype of *Marinavis longirostris* is an imperfect right dentary, broken at both ends, and an associated posterior fragment of a left rostrum (Figure 4.2), both collected by David Ward in 1972. Other material referred to this taxon includes the terminal hook of a premaxilla (paratype), also collected by David Ward in 1972, and a left carpometacarpus, collected by Stuart Baldwin in 1973.

Interpretation

Interpretation of the sedimentary environment is given in Chapter 3.

Marinavis longirostris was probably a seabird, perhaps a procellariiform or a pelecaniform, but probably the former (Harrison and Walker, 1977a). In some regards, the beak bones resemble the modern shearwater, *Puffinus tenuirostris*. These limited remains were made the foundation of not only a new genus and species, but also of a new family, Marinavidae (Harrison and Walker, 1977a). No further remains have been reported, and it is difficult to assess the validity of the new taxonomic names and their postulated relationships (Brodkorb, 1978; Unwin, 1993).

Comparison with other localities

Bird localities from the beginning of the Eocene Epoch are relatively few and far between, and most of them produce only isolated specimens. A distant relative of *Marinavis*, the bony toothed pelecaniform *Pseudodontornis tenuirostris*, has been reported from the Oldhaven Formation (Early Eocene) of Herne Bay, Kent (Harrison, 1985). The only other British earliest Eocene bird locality is in Croydon, Surrey, from which Newton (1886) reported remains of the large flightless bird *Gastornis klaasseni* from the somewhat older Woolwich Formation. Farther afield, earliest Eocene birds are not abundant but are known from a number of localities in North America, Central Asia and Europe (Harrison, 1980a; Unwin, 1993). Among the continental European localities, the Conglomérat de Meudon has yielded a gastornithid. The Landen Formation of Mesvin, near Mons, Belgium, is also the source of a gastornithid.

Chapter 3 gives further comparisons, especially of the more extensive mammal faunas.

Conclusions

British earliest Eocene bird fossils are rare, and Abbey Wood has produced the most recent reasonably good specimens. If the original description is correct, these specimens represent a new genus and species of seabird and also a new fam-

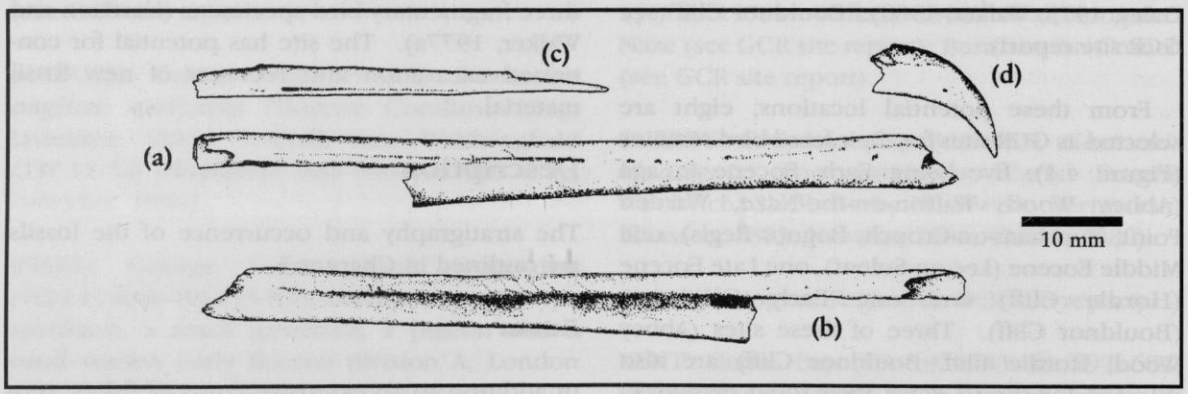


Figure 4.2 Specimens of *Marinavis longirostris* from Abbey Wood. An incomplete right dentary in external (a) and internal (b) views and parts of a premaxilla: posterior fragment (c) and and the terminal hook of the beak (d). (Based on Harrison and Walker, 1977a.)

ily. The site is selected mainly because of its potential for future finds. The impersistent nature of the vertebrate-bearing lenses means that carefully controlled excavation programmes will be required to prevent overworking and destruction of the site. The efforts of the Tertiary Research Group should ensure that the Lessness Shell Bed continues to be a rich source of bird, mammal, reptile and fish remains for many years to come.

THE LONDON CLAY FORMATION

The richest deposits of fossil birds in Great Britain are in the London Clay Formation (Early Eocene in age), particularly of the London Basin but also of the Hampshire Basin (Figure 4.1). This is an offshore marine unit, consisting mainly of dark-coloured muds but with occasional silty and sandy bands and rare pebble bands. The sediments contain abundant marine invertebrates, microfossils and sharks, as well as marine turtles and crocodiles, driftwood and rare bird skeletons. The London Clay Formation was deposited generally in water 20–100 m deep in gentle marine conditions, with occasional storms depositing the coarser clastic units.

Fossil vertebrates from the London Clay Formation are relatively abundant and diverse. The first finds to be reported were turtle remains, noted in 1811, and many reports of superb specimens appeared throughout the 19th century. Active collecting today produces a continuing and steady stream of excellent vertebrate specimens. Taxa reported so far (Hooker, 1994a; Hooker *et al.*, 1980, 1999; Benton and Spencer, 1995) include some 50 or more species of sharks, four species of chimaeroids, 15 species of turtles, a snake, a crocodile and 30 species of birds, but only very rare reports of mammals (including the plesiadapiforms *Platychoerops* and *Toliapina*, the pantodont *Coryphodon*, the creodont *Argillotherium* and the early equoids *Hyracotheriums* and *Pliolophus*). Most of the fossils come from the upper divisions (C–E), but largely because those are the horizons exposed on the Isle of Sheppey, which for two centuries has been the most prolific source of finds.

The bird faunas were most extensively described by Colin Harrison and Cyril Walker in many papers, from 1971 to 1986, and these two authors have established many new species on the basis of often rather incomplete remains. Their work has been criticized, especially on the grounds that many of the assignments to modern groupings have been based on rather doubtful evidence (e.g. Olson, 1985; Houde, 1988; Mayr and Daniels, 1998), and some of the criticisms have been vigorous and rather bitter (e.g. Steadman, 1981). However, much of the work by Harrison and Walker still stands without specific challenge by someone who has re-examined their specimens and re-assigned them confidently; the critical comments are rather that the materials are 'undiagnostic' or 'uncertain'. Thus, for the purposes of the present work, we rely on the published record and tentatively accept most of the Harrison and Walker taxa; specific counter opinions are given, where appropriate. A further complication is that large new collections of birds are being made from the London Clay Formation by private collectors (e.g. Daniels, 1994), but the material is not being described formally in refereed journals and so cannot be mentioned here. Feduccia (1999, pp. 165–7) gave a useful outline summary of the faunas, based on published and unpublished materials, and Dyke (Dyke and Cooper, 2000; Dyke, 2001a, b; Dyke and Waterhouse, 2001; Dyke and Gulas, 2002) has begun a programme of revision of the London Clay Formation birds.

After years of confusion and the establishment of many independent local stratigraphical schemes, the London Clay Formation was revised comprehensively by King (1981) and a unified scheme of divisions was proposed (Figure 4.3). This scheme allocated the so-called 'Basement Bed' and other lower units to the Oldhaven Formation. The London Clay Formation then encompassed the remainder of the succession. The Oldhaven and London Clay formations together were then referred to as the Thames Group. The London Clay Formation in the London Basin is succeeded by the Virginia Water Formation. The situation is more complex in the Hampshire Basin, where the London Clay Formation is thinner, lacking much of division C, and divisions D and E in the west, but being more complete in the east. The missing upper parts of the London Clay Formation are made up by fluviatile clastic facies ascribed to the Poole Formation in the west and the Wittering Formation (partly marine, partly brackish) in the east.

The London Clay Formation is divided into five divisions (A–E), based on five major trans-

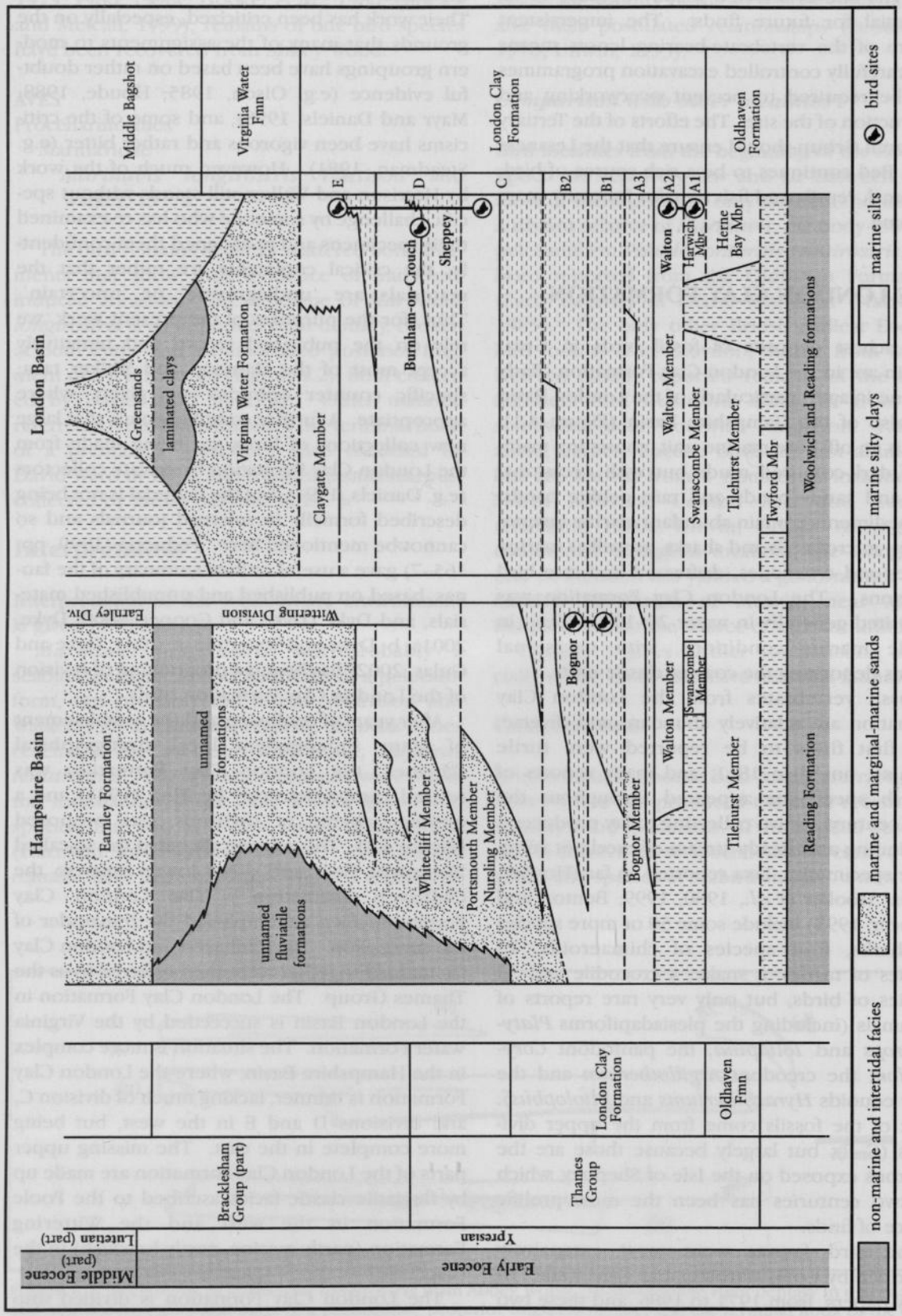


Figure 4.3 Stratigraphy and facies relationships of the London Clay Formation in the Hampshire and London basins, with tentative correlations and assignment to standard global chronostratigraphy. Sedimentary discontinuities are shown by horizontal broken lines. The major bird sites are indicated. (Based on King, 1981.) Since this work was published, most of the unnamed formations in the Hampshire Basin have been named (see Figure 3.2).

gression–regression cycles. Divisions A and B are further subdivided into A1–3 and B1–2 (Figure 4.3). Some of these divisions have been given member names as well, so that, for example, division A2 in the London Basin is also termed the Walton Member, and division A1 in north Essex is also termed the Harwich Member; and these are the units from which the superb bird specimens at Walton-on-the-Naze come.

The various divisions of the London Clay Formation can all be dated very precisely, because abundant biostratigraphically useful fossils are known throughout and there is a good magnetostratigraphical record (King, 1981; Ali *et al.* 1993). The entire formation is dated to the Ypresian Stage (Early Eocene), although the London Clay Formation overlies earlier Eocene deposits (namely Blackheath Beds, Oldhaven, Woolwich and Reading formations) (see Chapter 3). In all, the London Clay Formation spans time equivalents of the Planktonic Foraminifer Zones P6b (part), P7 and P8 (part) and Nannoplankton Zones NP10 to NP12 (lower part) and contains most of six microplankton zones (Powell, 1992).

WALTON-ON-THE-NAZE, ESSEX (TM 263 230–TM 268 245)

Introduction

The sea cliffs and foreshore at Walton-on-the-Naze expose a section of high division A1 and division A2 of the London Clay Formation (Figure 4.4; King, 1981, text-fig. 14). The sediments seen here have been divided further into 11 units. Units 10–11 belong to division A2, the rest to A1. The lithologies are dominated by clays and silts, with ash bands in A1, and have been dated to Early Eocene times (Ypresian Stage; George and Vincent, 1977).

Vertebrate fossils are commonly found at Walton-on-the-Naze, and these include fishes, reptiles and birds. This is one of the most productive sites in Britain for fossil bird remains, and more than 40 sets of associated remains have been recovered (George and Vincent, 1977). These include a small falconid (Harrison, 1982a) and a specimen hailed as the world's oldest parrot fossil (Harrison, 1982b), a primitive swift (Dyke, 2001a), as well as other types. Extensive collections of excellent bird fossils have been made more recently at Walton-on-the-Naze (Daniels, 1994; Feduccia, **1999**; Dyke and Cooper, 2000), but they remain in private collections and have not been studied extensively (except for Mayr and Daniels, 1998).

Description

The history of stratigraphical studies at Walton-on-the-Naze has been outlined by George and Vincent (1977). The site was first described by Prestwich (1854), who considered the sediments to reach a thickness of some 27.5 m. Further accounts, for example Whitaker (1877), Holmes (1890, 1891) and Stopes and Dalton (1880), did not add a great deal new to the geological and palaeontological description of the locality. Davis and Elliott (1951) recorded the presence of a blue clay beneath the Red Crag. Cooper (1970) described the section shown in Table 4.1 below. Table 4.2 shows the composite section recorded by George and Vincent (1977, p. 84).

The succession at Walton-on-the-Naze extends from the upper part of the Harwich Member (A1) to the Walton Member (A2) of the London Clay Formation (King, 1981, p.50). The Walton Member belongs to the *Wetzeliella astra* and *W. meckelfeldensis* dinocyst zones.

Vertebrate fossils have been recovered from many of the units described by George and

Table 4.1 Section at Walton-on-the-Naze (Cooper, 1970)

	Thickness (m)
2. Silty to very silty clays, logs often preserved in concretions	10.0
1. Sandy clayey silts and clayey sandy silts, especially sandy at the top, contains erosive scours up to 30 cm deep and 3 m wide infilled with finely laminated silty fine sands. Small-scale ripple-cross-stratification occurs locally. Occasional small rounded flint pebbles are found, usually close to the upper junction. Intense bioturbation seen on weathered surfaces	at least 1.5

Figure 4.4 The London Clay Formation at Walton-on-the-Naze. (Photo: Dave Evans.)

Table 4.2 Composite section at Walton-on-the-Naze (George and Vincent, 1977, p. 84)

	Thickness (m)
Above 11 alternating slightly silty clay bands (0.60 m thick) and clay bands (0.30 m thick) are seen in the cliff	
11. Grey clay. Very low silt fraction. Wood and nodules occur, but no other fossils observed	seen to 0.30
10. Silty clay. Woody pockets still occur and occasionally large logs may be seen. Black flint pebbles and small nodules in this bed	0.61
9. Green silt band	0.05
8. Very silty clay. Wood fragments and woody accumulations are common. Small rounded black-coated flint pebbles also occur	0.45
7. Green silt band	0.05
6. Silty clay. Approximately 0.07 m into this unit is a discontinuous nodule band. The nodules are usually quite small, very hard and formed around pieces of wood containing much pyrite. Pieces of wood and woody pockets are common. Black pebbles occur. Shelly nodules probably come from this horizon	0.40
5. Blue-grey clay	0.85
4. Blue hard clay. Sometimes represented by mattings of bioturbation	0.05
3. Blue-grey clay with woody fragments and pockets	0.23
2. Blue hard clay. Sometimes represented by mattings of bioturbation	0.05
1. Blue-grey clay with isolated pockets of vegetation. A band of whitish soft nodules may be seen at the top of this unit in close proximity to Unit 2	0.30

Vincent (1977), and they generally are preserved in small pockets within the London Clay Formation. The more common vertebrates are fishes (units 8, 4, 3 and 1) and reptiles, for example articulated turtle fossils (unit 6).

The bird remains from Walton-on-the-Naze

occur as groups of associated bones that may be referable to single individuals. It has been suggested that these associations of bones were preserved in small hollows in the sea bed (Harrison, 1983). The average number of bones for each specimen ranges from 2 to 30 (George and Vincent, 1977). The musophagid bones were found in a woody pocket in Unit 10 (basal division A2). Bird remains also occur in unit 8 and are often concentrated some 0.75 m below the upper boundary of the bed (division A1). Two associations of bird bones have been recovered from woody accumulations beneath the nodules in unit 6 (George and Vincent, 1977).

Fauna

Walton-on-the-Naze has yielded a mixed fauna of fishes (mainly sharks, Hooker *et al.*, 1980), turtles (Benton and Spencer, 1995, p. 277) and birds (Harrison, 1982a,b, 1983). Associated fossils include insects, other arthropods, gastropods, bivalves, echinoderms, foraminifera and abundant plant remains (George and Vincent, 1977). The faunal list is from Harrison (1983, 1984b), with modifications from Dyke and Cooper (2000), Dyke (2001a, b), and Dyke and Gulas (2002).

AVES
Galliformes
?Gallinuloididae
Paraortygoides radagasti Dyke and Gulas, 2002
Anseriformes
Anatidae
Anatalavis oxfordi Olson, 1999
Procellariiformes
Procellariidae
two procellariids
Gruiformes
large rail '*Pediorallus*' sp.
Charadriiformes
two waders
Columbiformes
Columbidae
a pigeon
Falconiformes
Falconidae
Parvulivenator watteli Harrison, 1982a
Accipitridae
a small accipitrine bird of prey
?Caprimulgiformes
?Caprimulgidae
?a caprimulgid
Apodiformes
Apodidae
Eocypselus vincenti Harrison, 1984b
Laputavis robusta (Dyke, 2001a)
Coliiformes
Eocolius walkeri Dyke and Waterhouse, 2000
Psittaciformes
Pseudasturidae
Pulchrapollia gracilis Dyke and Cooper, 2000
Psittacidae
[*Palaeopsittacus georgei* Harrison, 1982b]
three parrot species (species A, B and C of Mayr and Daniels, 1998)
Coraciiformes
three coraciiform specimens
Cuculiformes
Parvicuculidae
Procuculus minutus Harrison and Walker, 1977a
Musophagidae
a large musophagid

Most of the bird remains from Walton-on-the-Naze have been identified to ordinal, or familial, level only. The 20 or so specimens collected by W. George and S. Vincent and identified by Harrison (1983) are mainly isolated limb bones. Some of the specimens provided further important information, showing the existence of large rails of the genus *Pediorallus*, although the specimen might belong to the palaeognathous bird *Lithornis*, according to the revisions of Houde (1988). In addition, the Walton-on-the-Naze sediments produced the type specimens of a small falconid, *Parvulivenator watteli*, based on a partial tarsometatarsus (Harrison, 1982a; Figure 4.5), and the supposed parrot *Palaeopsittacus georgei*, based on a set of 11 postcranial elements (Harrison, 1982b), but which Dyke and Cooper (2000) regarded as *incertae sedis*. These authors named a new parrot based on different specimens from the same location, *Pulchrapollia gracilis*. Further type specimens from Walton-on-the-Naze are the duck *Anatalavis oxfordi*, the mousebird *Eocolius walkeri*, and the swifts, *Eocypselus vincenti* Harrison, 1984b and *Laputavis robusta* (Dyke, 2001a) (N.B. *L. robusta* was first placed in the genus *Laputa*. When this name was found to be preoccupied by a fish, it was changed to *Laputavis* (Dyke, 2001c))

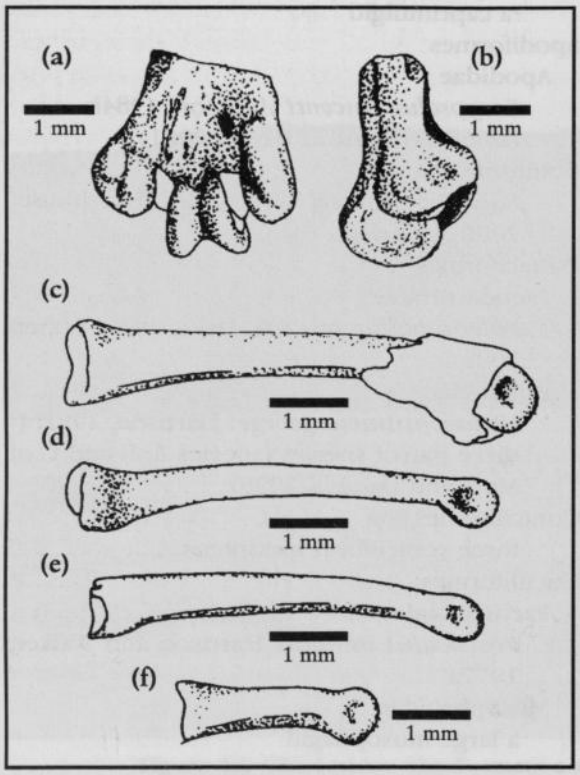


Figure 4.5 The small raptor *Parvulivenator watteli* from the London Clay Formation of Walton-on-the-Naze. (a,b) Lower end of the tarsometatarsus in posterior (a) and internal (b) views. (c–f) External views of four toe bones; (c) the basal phalanx of the third digit; (d) the basal phalanx of the first digit; (e) a possible second phalanx of the second or third digit; (f) the basal phalanx of the second digit. (After Harrison, 1982a.)

Interpretation

The Harwich Member (division A1) of the London Clay Formation is a silty clay with ash bands and occasional concretions containing marine fossils, indicating shallow marine conditions.

The Walton Member (division A2) of the London Clay Formation consists of clayey silts and silty clays, with thin bands of fine-grained sand and silt and bioturbated fine-grained sand (*Chondrites*). Some bivalves and shark teeth have been reported, as well as abundant pyritized diatoms and lignitic debris, logs and twigs. This facies is interpreted (King, 1981) as indicating a low-energy marine environment of deposition. The bioturbated horizons indicate slow deposition, and the thin coarser clastic units point to periodic storm events. The lignitic plant debris is probably the remains of driftwood. Vertebrate fossils include various shark, marine turtles, a single mammal specimen and the bird specimens, all of which make sense in terms of the shallow marine habitat indicated by the sediments.

Harrison (1983) noted a 'small game bird' from Walton-on-the-Naze, and Dyke and Gulas (2002) named this as the type of the species *Paraortygoides radagasti*. The specimen consists of associated vertebrae from the neck and pelvis area, parts of the shoulder girdle and wing and partial hindlimbs. It is a close relative of *P. messelensis* Mayr, 2000 from the mid Eocene Messel deposits in Germany, and falls low in the cladogram of Galliformes. *P. radagasti* is one of the oldest galliform birds on record.

The duck *Anatalavis oxfordi* Olson, 1999 is based on an incomplete specimen, one of the most complete from the London Clay, comprising parts of the skull, vertebral column, shoulder girdle, pelvis, and wings. Olson (1999) suggested that *Anatalavis* was a member of the Family Anseranatidae, and hence a relative of the living Australian Magpie goose. On the basis of a more extensive cladistic analysis, Dyke (2001b) allied *Anatalavis* with the living true ducks, the Family Anatidae, and the fossil flightless duck-like *Presbyornis*.

The swifts *Eocypselus vincenti* Harrison, 1984b and *Laputavis robusta* (Dyke, 2001a) were named on the basis of an associated pair of humeri, a coracoid and a partial ulna and radius (Harrison, 1984b) and an associated sternum, coracoids, humerus, radius, wing and vertebral elements (Dyke, 2001a) respectively. In Dyke's (2001a) cladogram, *Eocypselus* is sister group to the modern Apodidae, while *Laputavis* falls low in the cladogram as the most basal apodiform. Mayr (2001a) was highly critical of Dyke's (2001a) cladistic analysis, and later (Mayr, 2003) offered a revised version, in which *Eocypselus* falls low in the Apodiformes, but *Laputavis* is not included.

When it was described, *Palaeopsittacus georgei* was the oldest known parrot in the world, and it is recorded as such by Unwin (1993). Some doubts were, however, expressed about the identification (Olson, 1985, pp. 120–1), and Mayr and Daniels (1998, pp. 164–5) stated unequivocally that it is not a parrot, whereas Dyke and Cooper (2000) confirmed that the specimens are not diagnostic at ordinal level. They did not, however, assign it else-

where. Mayr and Daniels (1998, pp. 162–4) did describe three postulated species of parrots, termed species A, B and C, from Walton-on-the-Naze, and Dyke and Cooper (2000) named the new parrot genus and species *Pulchrapolliagracilis* from Walton-on-the-Naze. Mayr (2001a, 2002) was critical of some of Dyke and Cooper's interpretations of *Pulchrapollia*, and he assigned it to the related psittaciform family Pseudasturidae. The next oldest parrots are from the Mid Eocene deposits of the Messel site, Germany (Mayr and Daniels, 1998), and the Late Eocene sediments of France. An even older parrot recently has been reported from the Late Cretaceous Lance Formation of North America (Stidham, 1998), but the record is suspect (Dyke and Mayr, 1999).

The birds include a couple of marine procellariids and a wader, but the remainder, the birds of prey, the gamebird, the pigeon, the parrots, the ?caprimulgid (nightjar), the musophagid (touraco or plantain-eater), the coraciiforms (rollers, kingfishers) and the swifts, are all either arboreal, ground-dwelling or associated with fresh waters. These terrestrial birds must all have been blown out to sea by storms, or perhaps their carcasses were washed into the sea.

Some of these bird groups are typical of Europe today, but others (the parrots and touracos) are distinctly tropical, being known today from Africa. In earliest Eocene times, Great Britain lay a little farther south, and climates were much warmer than today.

Comparison with other localities

The nearest comparable bird fauna is from Grange Farm, South Ockendon, Essex (TQ 611 833–TQ 615 833), also in division A of the London Clay Formation, from which isolated specimens of the owl *Eostrix vincenti* Harrison, 1980b, a small gamebird, a pigeon and a small wader have been reported (George and Vincent, 1978; Harrison, 1980b, 1983). Note, however, that the identity of the owl has been challenged by Peters (1992a) in his description of an owl from the Middle Eocene Messel site in Germany.

Some earliest Eocene avifaunas are known from continental Europe, but diversity is low. In France, the Sables de Laon of the Paris Basin have produced specimens of the large flightless bird *Diatryma*, and the Lower Eocene 1 Fehmarn Clay of Katharinenhof, Schleswig-Holstein, in Germany, is the source of a possible phoenicopteriform. The only reasonable avifauna with which the Walton-on-the-Naze fauna may be compared comes from the Mo Clay (Fur Formation) of Denmark. This is the source of an accipitrid (?), a phasianid (pheasant), a rallid (rail) and a musophagid (touraco), all of which are groups represented at Walton-on-the-Naze.

Conclusions

The cliffs and foreshore at Walton-on-the-Naze expose an excellent section of the upper Harwich Member (division A1) and the Walton Member (division A2) of the London Clay Formation. The avifauna consists of 14 different bird groups, and it is the most extensive earliest Eocene bird fauna known in Europe, and probably the world. The cliffs at Walton-on-the-Naze continue to be eroded, renewing the sections for collectors, although under certain conditions the London Clay Formation outcrop may become obscured by clay slips.

BOGNOR REGIS, WEST SUSSEX (SZ 920 979–SZ 924 983)

Introduction

The London Clay Formation is exposed on the foreshore at Bognor Regis, West Sussex. Vertebrate remains have been recovered from the outcrops on the beach and in pyritous debris pools on the shoreline; these pools concentrate scattered fossil remains (Figure 4.6). Bulk sediment sampling and processing of the beach sediments has been attempted (Dineley and Metcalf, 1999).

Six bird species have been reported from Bognor Regis, and one of these is of great potential international importance (Harrison, 1975, 1984b; Harrison and Walker, 1975, 1977a). This is the record of a possible early Tertiary passeriform (songbird), perhaps the oldest in the world, if the identification is confirmed, and occurring some 25 million years before the major songbird group began to radiate worldwide.

Description

The London Clay Formation is exposed along the coast from Bognor Regis westwards to Aldwick and Pagham. The exposure is not con-

Figure 4.6 The fossiliferous London Clay Formation at Bognor Regis. (Photo: Dave Evans.)

tinuous, consisting of discontinuous foreshore esposures of silty muds and sands. The strata dip at a low angle towards the south-west. The succession was described by Venables (1962) and revised according to the new stratigraphical scheme by King (1981, pp. 71–5). The succession runs from the Oldhaven Formation, up through divisions A2, A3, B1, B2 and the lower part of division C. The junction between the London Clay Formation and the overlying Bracklesham Group is not seen (Daley, 1999a).

The section shown in Table 4.3 is based on the studies of King (1981) and Venables (1962).

The Aldwick Beds (London Clay Formation, division B) of Bognor Regis has produced a variety of vertebrate taxa, including fishes, reptiles and birds. The material generally is well preserved. The vertebrate fossils come from the Upper and Lower Fish-tooth Beds, which lie in the Upper Aldwick Beds and Lower Aldwick Beds respectively, and from the Beetle Bed in the Lower Aldwick Beds (King, 1981; Harrison, 1982b).

To date, in excess of 200 bird bones have been found at Bognor Regis. Most have been found from three horizons. Limb bones are found most often; cranial bones have not been recovered from this site (Venables, 1962).

Fauna

In addition to abundant shark remains, mainly teeth, some fossil turtle remains have been found at Bognor Regis (Hooker *et al.*, 1980; Dineley and Metcalf, 1999), as well as the birds.

AVES
Palaeognathae
  Lithornithidae
    Lithornis hookeri (Harrison, 1984c)
Pelecaniformes
  Pelagornithidae
    Argillornis longipennis Owen, 1878
Charadriiformes
  ?Glareolidae
    Precursor parvus Harrison and Walker, 1977a
Columbiformes
  Columbidae
    Microena goodwini Harrison and Walker, 1977a

Cuculiformes
  Parvicuculidae
    Procuculus minutus Harrison and Walker, 1977a
Apodiformes
  Aegialornithidae
    Primapus lacki Harrison and Walker, 1975
Passeriformes
  Primoscenidae
    Primoscens minutus Harrison and Walker, 1977a

The London Clay Formation at Bognor Regis has produced a modest fauna of birds compared with the list of materials from the Isle of Sheppey. The struthioniform *Lithornis hookeri* is recorded here on the basis of an end of humerus found in the Fish-tooth Beds at Bognor referred to the so-called rail, named *Pediorallus hookeri* by Harrison (1984c, p. 21). It was reassigned by Houde (1988) to the genus *Lithornis*, a palaeognathous bird related to the modern flightless birds of the Southern Hemisphere.

The toothed bird *Argillornis longipennis* Owen, 1878, was named from material found on the Isle of Sheppey, but an indeterminate bird limb bone found at Bognor Regis by E.M. Venables also has been assigned to this species (Harrison and Walker, 1977a, pp. 20–1). The charadriiform *Precursor parvus* Harrison and Walker, 1977a (Figure 4.7) was based on the distal end of a left humerus and part of the shaft, with a paratype also from the Isle of Sheppey. This was a small bird, related to modern wading birds, gulls and auks. The columbiform *Microena goodwini* Harrison and Walker, 1977a, was based on a left tarsometatarsus, and it came from a small pigeon-like bird.

The cuckoo *Procuculus minutus* Harrison and Walker, 1977a, was named on the basis of a partial tarsometatarsus from the Lower Fish-tooth Beds, and this is the only known specimen (Harrison and Walker, 1977a, pp. 44–5; Harrison, 1982c).

The apodiform *Primapus lacki* Harrison and Walker, 1975, was based on the distal end of a right humerus from the Fish-tooth Beds. This is a relative of modern swifts and hummingbirds (Harrison and Walker, 1975, 1977a; Harrison, 1984b).

The passeriform *Primoscens minutus* Harrison and Walker, 1977a, was based on a partial right carpometacarpus from the Fish-tooth beds. If identified correctly, this is the oldest

Table 4.3 Succession of the London Clay Formation at Bognor Regis after King (1981) and Venables (1962)

	Thickness (m)
London Clay Formation	
Division C (of King, 1981)	
5. Upper Clay (of Venables, 1962)	
Undescribed deposits	6.1
Grey clay with plant remains	0.9
Undescribed deposits	3.5
Pagham Rock	0.6
Clay (partly described, sparsely fossiliferous)	18.6
Cainocrinus Bed	1.2
Pholadomya Bed	0.6
Clay, partly described, with basal glauconitic pebble bed	3.7
Division B (of King, 1981)	
4. Barn Rock Bed (of Venables, 1962)	2.4
3. Middle Clay (of Venables, 1962)	
Base of Barn Rock	1.2
Undescribed deposits	1.2
Craigwell Bed	1.5
Undescribed deposits	3.0
3.3. Upper Aldwick Beds (of Venables, 1962)	
Clay with pyritized plant remains	2.4
Two septarian bands	0.6
Clay with pyritized plant remains	1.2
Septarian band (with *Artica planata* in clay)	0.3
Upper Fish-tooth Bed	1.5
3.2. Clay, unfossiliferous, with septarian band 1 m above base	3.7
3.1. Lower Aldwick Beds (of Venables, 1962)	
Beetle Bed. Clay with septarian band	1.2
Lower Fish-tooth Bed. Earthy clay, with clay pellets and basal black flint pebble bed	0.6
Division A3	
2. Bognor Rock Group (of Venables, 1962), Bognor Member (of King, 1981)	
Bognor Rock Bed. Interbedded unconsolidated grey sand and partially cemented, fine glauconitic sandstone	6.7
Sandy Clay and soft sandstone	3.0
1. Lower Clay (of Venables, 1962)	
Septarian band, with white clay, iron stained	0.6
'*Cyprina*' Bed	5.5
Starfish Bed	1.8
Clay	1.2
Astarte Bed	2.4
Division A2, Walton Member (of King, 1981)	
Friable clay	2.7
Clay with occasional pyritized plant remains	2.7
Sandy layer	0.3
Clay, partly described	4.6
Septarian band, with white clay, iron stained	0.3
Dark-grey, silty clay	0.6+
Oldhaven Formation (of King, 1981)	
Decalcified glauconitic sandy silts obscured by alluvium	3.0+

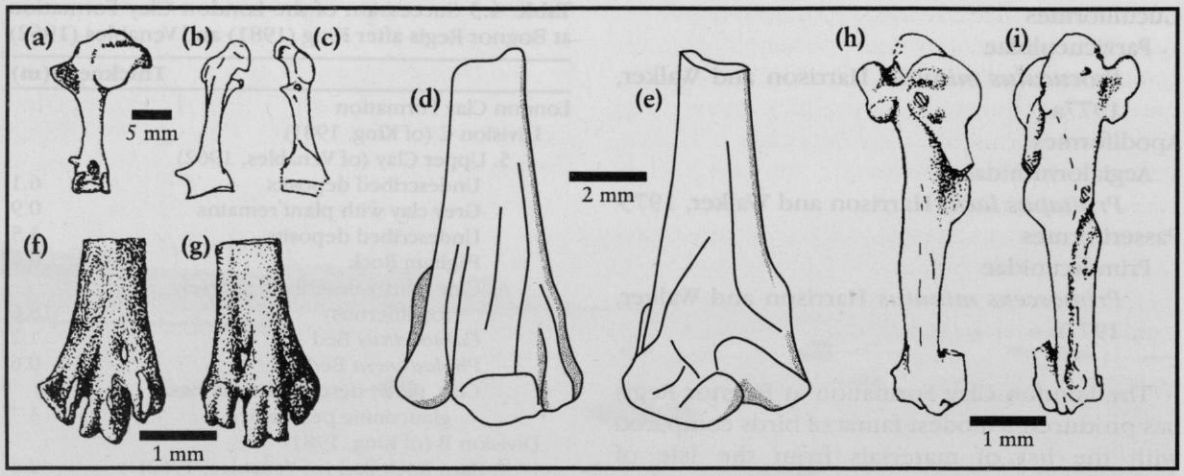


Figure 4.7 Specimens of fossil birds from the London Clay Formation of Bognor Regis. (a–c) The swift *Primapus lacki*; humerus in palmar view (a), and coracoid in ventral (b) and dorsal (c) views. (d,e) Distal end of the left humerus of the charadriiform *Praecursor parvus* in anconal (d) and palmar (e) views. (f,g) distal end of the right tarsometatarsus of the cuckoo *Procuculus minutus* in posterior (f) and anterior (g) views. (h,i) Carpometacarpus of the postulated songbird *Primoscens minutus* in proximal (h) and palmar (i) views. (After Harrison, 1973, 1982b,c; and Harrison and Walker, 1977a.)

perching bird. However, isolated postcranial elements of passeriforms cannot be distinguished readily from those of piciforms (the woodpeckers), and the identification of this and other putative early songbirds (e.g. Boles, 1997) are all hotly debated.

Bognor Regis has been the source of holotypes of five species, the charadriiform *Precursor parvus* Harrison and Walker, 1977a, the columbiform *Microena goodwini* Harrison and Walker, 1977a, the cuculiform *Procuculus minutus* Harrison and Walker, 1977a, the apodiform *Primapus lacki* Harrison and Walker, 1975, and the passeriform *Primoscens minutus* Harrison and Walker, 1977a.

Interpretation

The coarsening-upward cycles seen in divisions A and B of the London Clay Formation are indicative of transgressive and regressive cycles. The sediments were deposited in a shallow sea, and the majority of fossils are marine, with occasional inputs from the nearby land masses. The bird remains probably were transported from nearby land or resulted from death over the sea and were buried in the marine sediments.

The floral assemblages indicate a paratropical-like vegetation that grew in a humid, warm, low seasonality climate (Collinson, 1983a; Collinson and Hooker, 2003). Insect remains are abundant and well preserved and suggest a nearshore environment of deposition (Jarzembowski, 1992).

The three orders Charadriiformes, Columbiformes and Apodiformes are unique to Britain during Early Eocene time, the next records being from the Middle Eocene Messel site in Germany and then generally the Oligocene and Miocene epochs elsewhere. There is some doubt about the validity of *Procuculus minutus* Harrison and Walker, 1977a, which Olson (1985, p. 135) asserted cannot be a cuckoo for anatomical reasons and might turn out to be a synonym of the swift species *Primapus lacki* Harrison and Walker, 1975. He noted a more complete skeleton from the Early Eocene Green River Formation of Wyoming, which also might be assignable to *Primapus lacki*. Dyke (2001a) accepted the validity of *Primapus* and found it is a basal member of Apodiformes, related to *Scaniacypselus* and *Aegialornis*.

The record of a songbird *Primoscens minutus* Harrison and Walker, 1977a, from Bognor is hotly debated. It was ascribed to the new family Primoscenidae by Harrison and Walker (1977a, pp. 47–8) and Harrison (1982c), and an unnamed Middle Eocene bird from Messel also has been ascribed to the family (Unwin, 1993, p. 734). If *Primoscens* truly is a passeriform, it predates the general radiation of the order in the Miocene Epoch by some 25 million years. It is

not, however, clear whether it really is a songbird, and the Family Primoscenidae is listed under *Incertae sedis* by Unwin (1993, p. 734). Olson (1985, pp. 139–41) noted the oldest certain passeriforms from the late Oligocene and early Miocene deposits of Europe, and a more recent discovery (Boles, 1997) suggests that the songbirds may have originated as early as Early Eocene times in Australia.

Comparison with other localities

The London Clay Formation of Bognor Regis, where the bird fossils come from division B, is not directly comparable in age with the other bird GCR sites, which are either older (Walton-on-the-Naze, divisions A1 and A2) or younger (Isle of Sheppey, divisions C–E and Burnham-on-Crouch, division D). However, the avifauna from Bognor Regis is a subsample of the larger one from the Isle of Sheppey, with all the main groups shared by both. Some of the species also are shared, although some are unique to Bognor Regis. Olson (1985, p. 135) noted an American specimen from the Early Eocene Green River Formation of Wyoming that might belong to *Primapus lacki*.

Conclusions

The coastline at Bognor Regis is one of the few sites in Britain where the lower section of the London Clay Formation (divisions A–C) is exposed (Venables, 1962). The vertebrate fauna is abundant and diverse and includes seven species of Early Eocene birds, five of them having type specimens from the site. The site is exposed and undergoes erosion, so fresh finds will always be possible. It is probable that continued use of bulk sampling techniques will further our knowledge of the vertebrates from this locality.

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,

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.)

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

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

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.

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, 1841b
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
Pelagornithidae
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 4.9a). *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 4.9b,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 4.9d,e) by Owen (1873), and a few leg bones also have been assigned to the species. *Macrodontopteryx oweni* was established by Harrison and Walker (1976b, p. 12) for another partial skull of a larger bird (Figure 4.9f,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 4.9h) 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 4.9i,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 mitchelli* 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 4.9k) 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 bio-

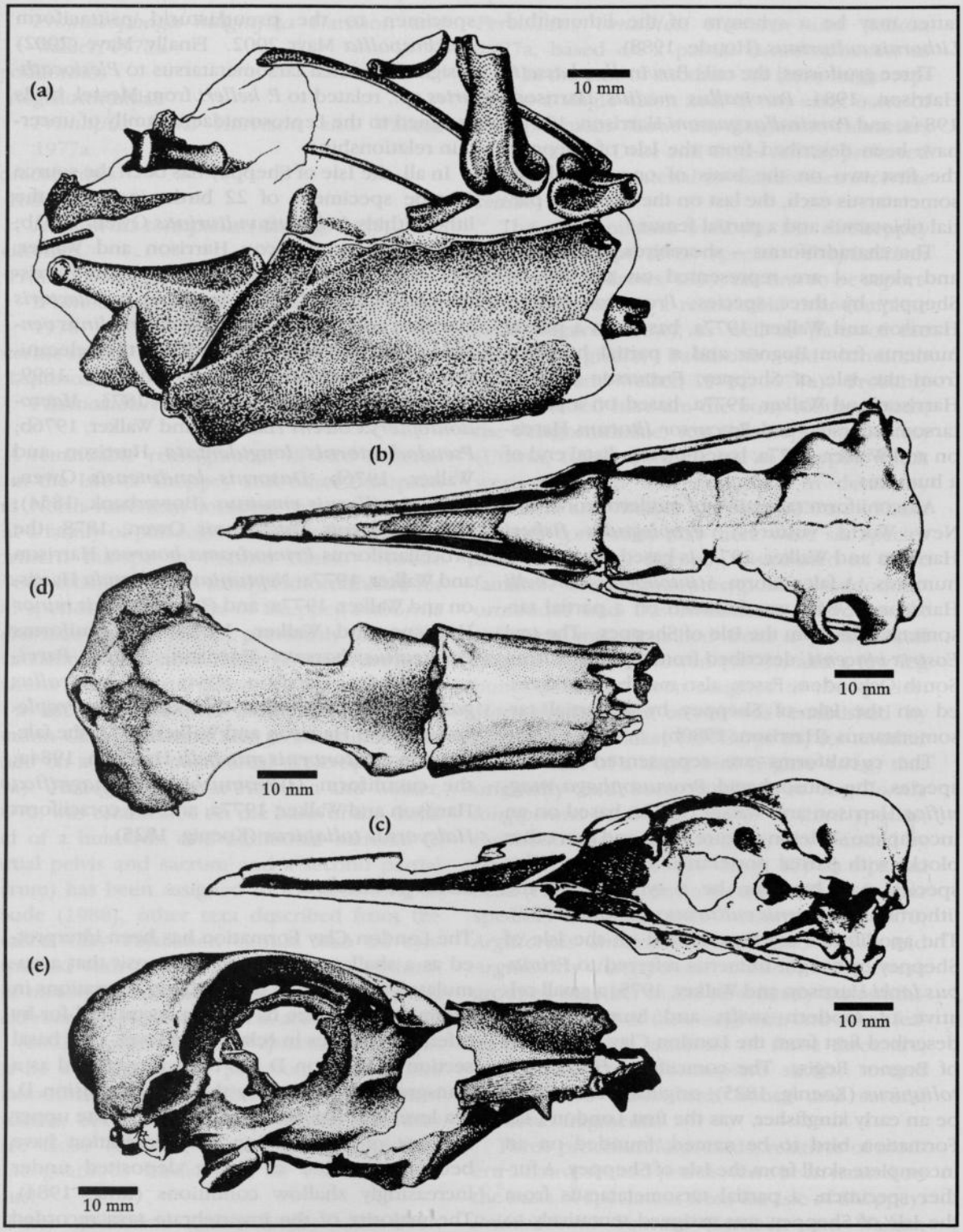
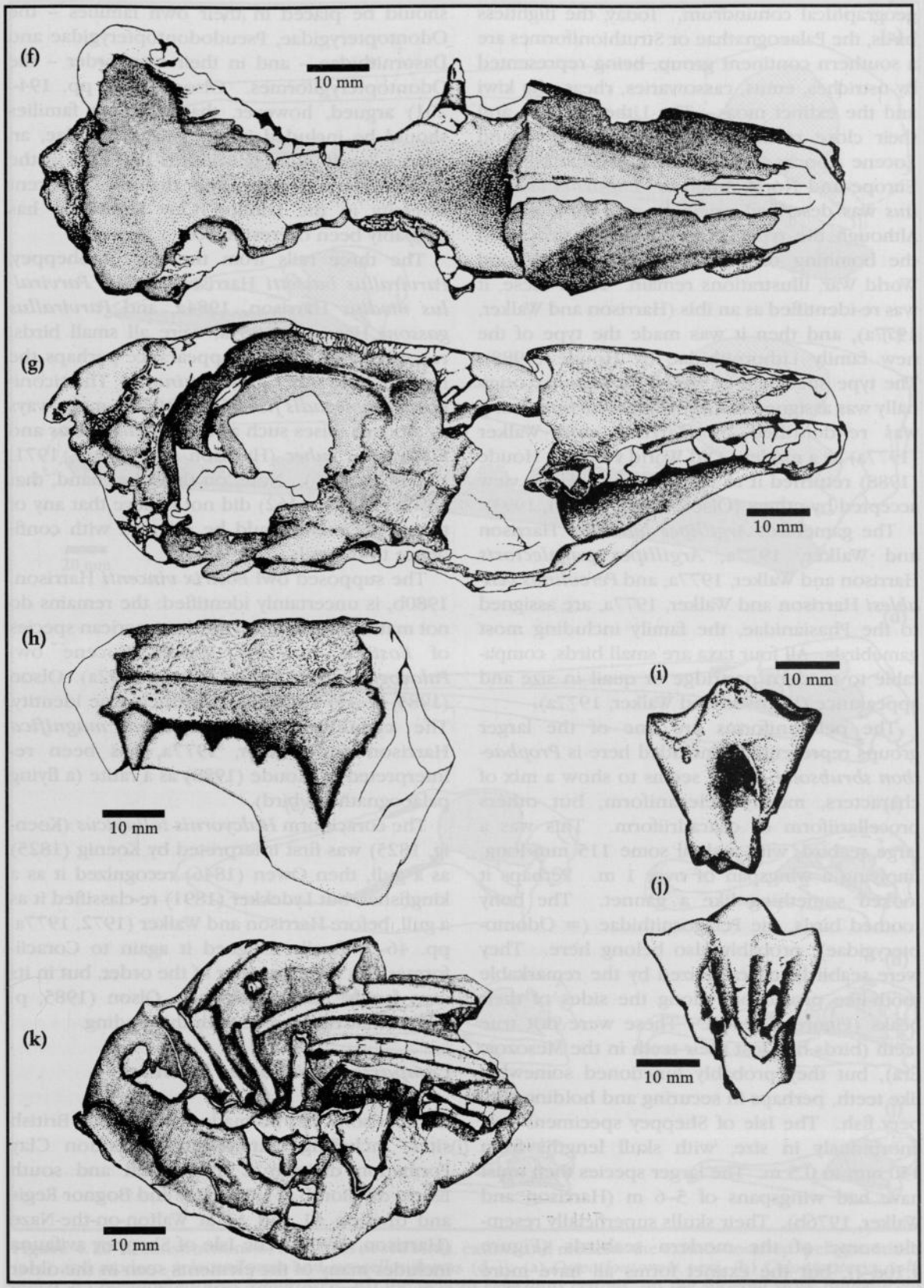


Figure 4.9 Specimens of fossil birds from the London Clay Formation of Warden Point, Isle of Sheppey. (a) Thoracic region of the lithornithid *Lithornis vulturinus*, mainly in left lateral view. (b,c) Skull of the prophaethontid *Prophaethon shrubsolei* in dorsal (b) and left lateral (c) views. (d,e) Skull of the pelagornithid *Odontopteryx toliapica* in dorsal (d) and right lateral (e) views. (f,g) Skull of the pelagornithid *Macrodontopteryx 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.)


(f)
10 mm
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geographical 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 pelecaniforms are one of the larger groups represented. Included here is *Prophaethon shrubsolei*, which seems to show a mix of characters, mostly pelecaniform, 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 4.10a–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 4.10d–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 bassetti* 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 calcus* 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

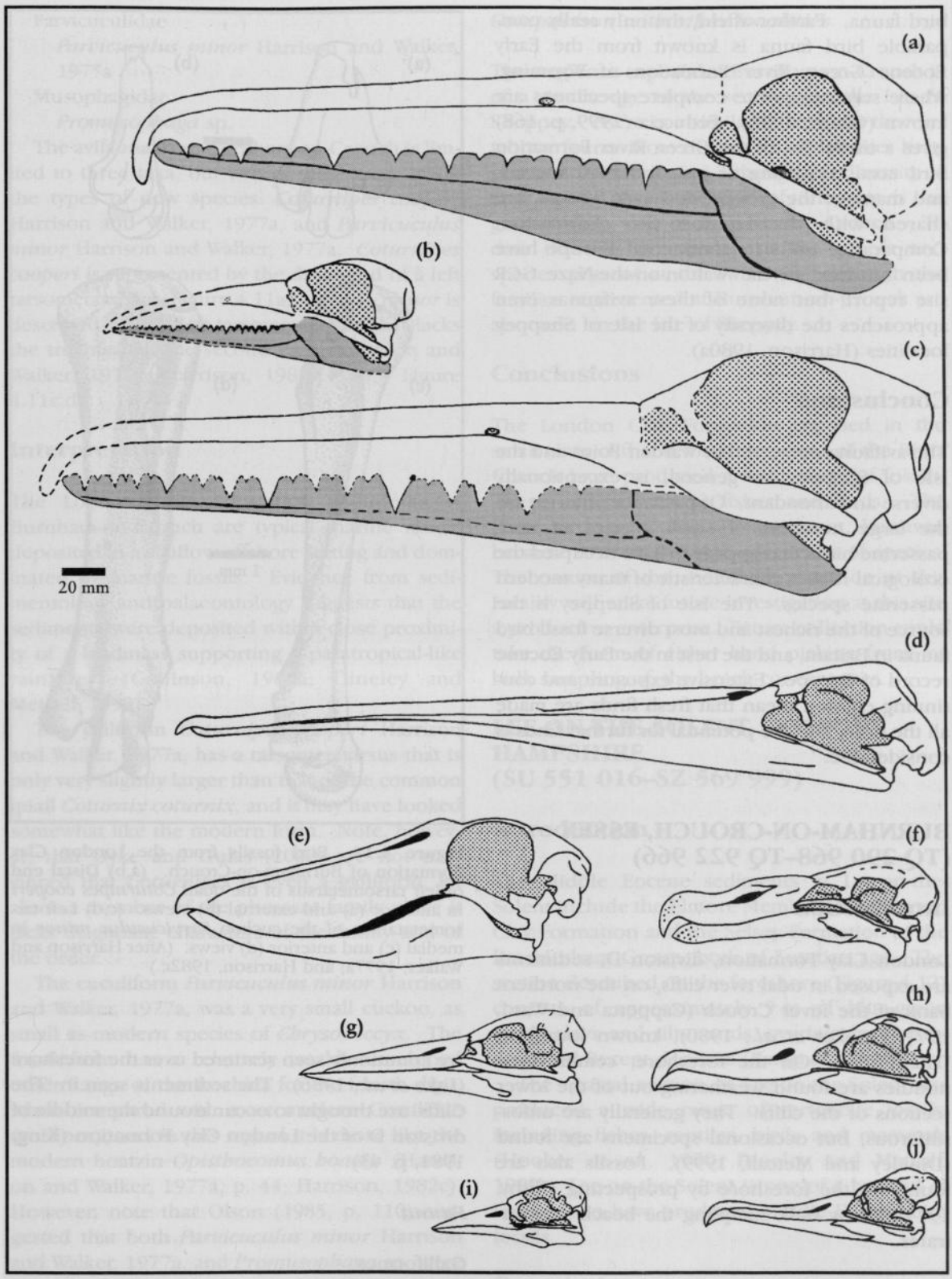

Figure 4.10 Reconstructions of the skulls of sea birds, extinct and modern: the extinct 'toothed' pelagornithids (a–c) and modern pelecaniforms and procellariiforms (d–j). (a) *Osteodontornis orri*, (b) *Odontopteryx toliapica*, (c) *Pseudodontornis longirostris*, (d) the pelican *Pelecanus crispus*, (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.)

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.

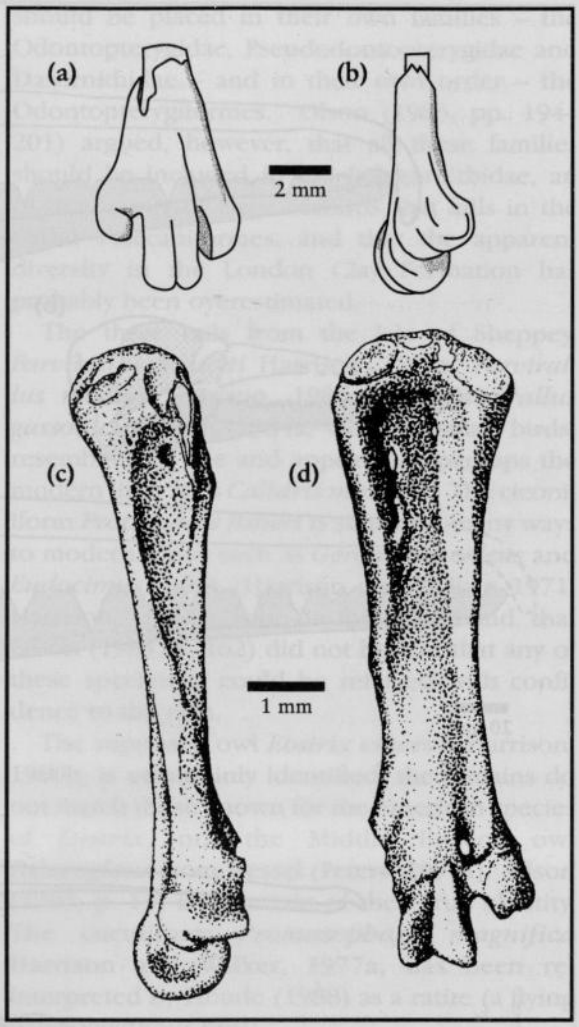

Figure 4.11 Bird fossils from the London Clay Formation of Burnham-on-Crouch. (a,b) Distal end of left tarsometarsus of the quail *Coturnipes cooperi* in anterior (a) and external (b) views. (c,d) Left tarsometatarsus of the cuckoo *Parvicuculus minor* in medial (c) and anterior (d) views. (After Harrison and Walker, 1977a; and Harrison, 1982c.)

BURNHAM-ON-CROUCH, ESSEX (TQ 290 968–TQ 922 966)

Introduction

London Clay Formation, division D, sediments are exposed in tidal river cliffs, on the northern bank of the River Crouch (Cappetta and Ward, 1977; Hooker *et al.*, 1980), known locally as 'The Cliffs'. On the foreshore, cementstone nodules are found weathering out of the lower sections of the cliffs. They generally are unfossiliferous, but occasional specimens are found (Dineley and Metcalf, 1999). Fossils also are found on the foreshore by prospecting (Kirby, 1974), or by bulk sampling the beach concentrates.

Description

The river cliffs expose a section 2–3 m thick. On the north side of the river cementstone nodules are commonly seen scattered over the foreshore (Lake *et al.*, 1986). The sediments seen in 'The Cliffs' are thought to occur around the middle of division D of the London Clay Formation (King, 1981, p. 43).

Fauna

Galliformes
  Phasianidae
    Coturnipes cooperi Harrison and Walker, 1977a
Cuculiformes

Parvicuculidae
Parvicuculus minor Harrison and Walker, 1977a
Musophagidae
Promusophaga sp.

The avifauna from Burnham-on-Crouch is limited to three taxa, but two of these were made the types of new species: *Coturnipes cooperi* Harrison and Walker, 1977a, and *Parvicuculus minor* Harrison and Walker, 1977a. *Coturnipes cooperi* is represented by the distal end of a left tarsometatarsus (Figure 4.11a,b) and *P. minor* is described from a left tarsometatarsus that lacks the trochlea for the second digit (Harrison and Walker, 1977a; Harrison, 1982c, 1983; Figure 4.11c,d).

Interpretation

The London Clay Formation sediments at Burnham-on-Crouch are typical marine muds, deposited in a shallow offshore setting and dominated by marine fossils. Evidence from sedimentology and palaeontology suggests that the sediments were deposited within close proximity of a landmass supporting a paratropical-like rainforest (Collinson, 1983a; Dineley and Metcalf, 1999).

The galliform *Coturnipes cooperi* Harrison and Walker, 1977a, has a tarsometatarsus that is only very slightly larger than that of the common quail *Coturnix coturnix*, and it may have looked somewhat like the modern form. Note, however, that Dyke and Gulas (2002) are not convinced that *Coturnipes* is even a galliform, let alone a member of the pheasant family, since it lacks diagnostic characters of the family and of the order.

The cuculiform *Parvicuculus minor* Harrison and Walker, 1977a, was a very small cuckoo, as small as modern species of *Chrysococcyx*. The fossil form has a relatively weakly developed outer flange of the trochlea for the fourth digit, when compared with most modern Cuculidae (cuckoos), and in this regard it is more like the modern hoatzin *Opisthocomus hoazin* (Harrison and Walker, 1977a, p. 44; Harrison, 1982c). However, note that Olson (1985, p. 110) suggested that both *Parvicuculus minor* Harrison and Walker, 1977a, and *Promusophaga* sp. were misidentified by Harrison and Walker (1977a) and that they belong to different bird orders. Unwin (1993), on the other hand, retained *P. minor* as a valid cuckoo record.

Comparison with other localities

The sequence exposed at Burnham-on-Crouch is of a similar age to the sections on the Isle of Sheppey. There is a similarity between the vertebrate faunas from these sites. Both sites have produced bird remains, although the diversity of taxa known from the Isle of Sheppey is far greater than that of Burnham-on-Crouch. To date there is no overlap in the genera and species present at the two sites, although the families represented at Burnham-on-Crouch are also seen on the Isle of Sheppey.

Conclusions

The London Clay Formation exposed in the small river cliff and foreshore areas of the River Crouch have produced a wide range of fossils. These include various fishes and birds. The three bird specimens are important, however, because two are the type specimens of species. The nature of the sedimentary section at this locality will make future investigation at this site a productive enterprise. Future collection could take the form of either hand picking from, or bulk sampling.of, the beach concentrates.

LEE-ON-THE-SOLENT, GOSPORT, HAMPSHIRE (SU 551 016–SZ 569 999)

Introduction

The Middle Eocene sediments at Lee-on-the-Solent include the Elmore Member of the Barton Clay Formation and the Selsey Formation of the Bracklesham Group, both of Lutetian age. The section described on the foreshore (Figure 4.12) consists of approximately 9 m of blue-green sandy clays and silty sands, overlain by Pleistocene and Recent deposits (Kemp *et al.*, 1979).

The coastal section at Lee-on-the-Solent has produced a wide range of vertebrate fossils, including fishes, reptiles, birds and mammals (Hooker *et al.*, 1980; Dineley and Metcalf, 1999). Lee-on-the-Solent is one of a handful of localities to have produced Middle Eocene bird fossils.

Description

The main exposure of the Elmore Member is on the beach at Elmore between SU 5635 0013 and

Figure 4.12 General view of the Lee-on-the-Solent GCR site, which provides foreshore exposures of Middle Eocene sediments, one of the very few Middle Eocene fossil bird localities. (Photo: Dave Evans.)

SZ 5657 9965 (Figure 4.12). Smaller exposures also are seen at SZ 5670 9974 and SZ 5678 9963. The beds have a low angle of dip (approximately 2°) to the south-east and are visible only at low tide. The base of the Elmore Member and the contact with the underlying '*Nummulites variolarius* bed' of the Selsey Formation are hidden by a Pleistocene channel-fill deposit. The upper levels of the Elmore Member also are obscured by Pleistocene and Recent sediments (Kemp *et al.*, 1979). Also known as the Huntingbridge division, the Elmore Member originally was accorded the rank of formation but later was reduced to member status (Hooker, 1986). The succession outlined in Table 4.5 is taken from Kemp *et al.* (1979).

The Selsey Formation is best seen in the lower sections of the foreshore between Knight's Bank, Monk's Hill (SU 5510 0135) and Marine Parade East car park (SU 5622 0026). The basal bed (the 'Campanile Bed') is not seen in the foreshore section, although it is exposed at Crofton Cliff (SU 5472 0186). At the south-eastern end of the section, the upper bed is the '*Nummulites variolarius* Bed' (Kemp, 1985). A description of the Selsey Formation sediments taken from Kemp (1985, pp. 35–8) is shown in Table 4.6 .

The Elmore Member sedimentary facies are almost completely decalcified, with the exception of the 'Coral Bed' (unit 6). This is the lowest horizon in the section that has an identifiable macrofauna, which is composed of solitary corals, bivalves and serpulids. The stratigraphically younger '*Rimella canalis* Bed' (units 7–11) contains poorly preserved moulds of bivalves, gastropods and scaphopods. Phosphatic nodules from unit 7 contain crustacean remains and rare pyritized gastropods. The sequence also contains microfossils, for example diatoms and agglutinating foraminiferans (Kemp *et al.*, 1979). The underlying Selsey Formation is also well exposed at sea level (Kemp, 1985).

The vertebrate remains have been found in the foreshore sands and clays of the Selsey Formation, and of the Elmore Member of the Barton Clay Formation. Bird fossils are rare and are normally fragmentary (Kemp *et al.*, 1979). Vertebrates have been noted by Kemp *et al.* (1979) in beds L3vi, L5i, L5ii, L7ii and L9.

Table 4.5 Succession of Elmore Member sediments at Elmore, Lee-on-the-Solent modified from Kemp *et al.* (1979)

	Thickness (m)
Barton Clay Formation	
Elmore Member	
'*Rimella canalis* bed'	
11. Sandy clay, pale blue-green, pyritic, glauconitic with clay-filled burrows and mollusc-bored lignite	0.52
10. Clay, pale blue, stiff, pyritic	0.46
9. Clay, pale blue-green, laminated, with very fine glauconitic sand. Tabular siltstones at upper contact	0.35
8. Clay, pale blue, stiff, pyritic, slickensided at upper contact	0.80
7. Sandy clay, pale blue-green, nodular claystones and siltstones throughout. Probably the source of some of the vertebrate remains	0.42
'Coral bed'	
6. Sandy clay, pale blue-green, shelly, with bivalves, serpulids and corals, interspersed siltstones	0.90
Unnamed beds	
5. Clay, pale blue-green, stiff, slightly sandy, slickensided at upper and lower contacts, glauconitic in lower part	2.15
4. Sandy clay, mid-green, finely glauconitic, with some medium-grained quartz and glauconite	0.60
3. Sand, green, silty, glauconitic, clay-filled burrows	0.32
2. Clay, pale blue, stiff, increasingly sandy and glauconitic downwards, slickensided in lower part	1.54
1. Sandy clayey silt, mid-green, glauconitic	0.98
Selsey Formation	
'*Nummulites variolarius* Bed'	
Shelly sandy clay, glauconitic, with abundant molluscs and nummulites	*c.* 1.35

Identifiable bird bones have been recovered from the Selsey Formation sediments: *Milvoides kempi* from beds L3vi to L5ii and *Percolinus proudlocki*, *Parvirallus gracilis*, *Latipons gardneri* and *Latipons robinsoni* from beds L5i to L5ii. Indeterminate bird fossils are known from all of the Selsey Formation beds (Kemp, 1985). In addition, a few that are tentatively identified to family level have been found in the Elmore Member (Kemp *et al.*, 1979, p. 102)

Fauna

Fossil vertebrates from Lee-on-the-Solent include 53 species of sharks, five chimaeroids and some isolated mammal remains (e.g. *Propalaeotherium* cf. *parvulum*, cf. *Palaeotherium* sp., *Lophiodon* cf. *cuvieri*) (Hooker, 1986, 1996b; Dineley and Metcalf, 1999). The birds from the Selsey Formation of Lee-on-the-Solent were described by Harrison and Walker (1979a).

AVES
Galliformes
Phasianidae
Percolinus proudlocki Harrison and Walker, 1979a
Litoripes medius Harrison and Walker, 1979a
Falconiformes
Accipitridae
Milvoides kempi Harrison and Walker, 1979a
Gruiformes
Rallidae
Parvirallus gracilis Harrison and Walker, 1979a
Latipons gardneri Harrison and Walker, 1979a
Latipons robinsoni Harrison and Walker, 1979a

The six birds from the Mid Eocene Selsey Formation record of Lee-on-the-Solent were collected by D.J. Kemp and R. Gardner, and the collection was described by Harrison and Walker (1979a). The gamebirds *Percolinus proudlocki* Harrison and Walker, 1979a, and *Litoripes*

Table 4.6 Succession of Selsey Formation sediments at Lee-on-the-Solent, north-west of Elmore, from Kemp (1985, pp. 35–8)

		Thickness (m)
Selsey Formation		
'*Nummulites variolarius* Bed'		
L11iii.	Grey, weathering yellow-brown, glauconitic sandy clay, packed with *Nummulites variolarius*, molluscs and lignitized driftwood	0.51
L11ii.	Grey stiff clay with rare molluscs	0.05
L11i.	Green-grey sandy clay with patches of silty sand with fine glauconite, abundant *Nummulites* and large molluscs	0.50
'Brook Bed'		
L10.	Grey-green stiff slickensided clay, molluscs and *Nummulites* concentrated in small sandy lenses	1.06
L9.	Green-grey sandy clay–silty sand, fine glauconite; thin burrows filled with pyritic sand, becoming more sandy in middle; diverse invertebrate fauna; vertebrates	0.76
'*Pinna* Bed'		
L8.	Grey, stiff, slickensided clays with brown patches	0.39
L7iii.	Grey-green stiff sandy silty clays with well-preserved bivalves throughout	2.40
L7ii.	Grey-brown stiff sandy clay, slightly slickensided at top, fine glauconite present, with large flat-oval concretions in upper part, many of which surround colonies of *Pinna* sp. and concentrated *Nummulites variolarius*; small molluscs common throughout, rare vertebrates concentrated in green sand pockets	1.80
L7i.	Dark green-grey glauconitic sandy clay–silty sand, intensely bioturbated at base, with occasional round black pebbles and large molluscs above	0.57
'*Miocardia* Bed'		
L6iii.	Grey–dark-green clayey glauconitic sand, rare bivalves and small gastropods	0.63
L6ii.	Light brown–grey stiff silty sand, fine glauconite, with rare small bivalves and occasional *Nummulites* sp.	0.45
L6i.	Grey-blue silty sand with fine glauconite, large (100 mm diameter) calcareous concretions often containing bored drifted logs near upper contact, rare bivalves and occasional *Nummulites* sp.	0.60
'*Amusium corneum* Bed'		
L5ii.	Blue-grey sandy clay, with fine glauconite, becoming more sandy and glauconitic near upper contact; molluscs and vertebrate remains	0.64
L5i.	Grey-green stiff sandy clay, rare glauconite with thin burrows filled with fine pyritic sand and occasional concretions throughout; frequent vertebrate remains (shark, ray, teleost)	1.60
L4.	Green–dark-green clayey, silty glauconitic sand, many bivalves, burrows infilled with glauconite	0.50
'Silt Bed'		
L3vi.	Dark green-grey silty glauconitic sand, invertebrate, vertebrate and plant fossils, intense bioturbation at upper contact, rare black pebbles throughout	0.99
'Campanile Bed'		
L3v.	Grey laminated clayey silt	0.02
L3iv.	Grey-green silty glauconitic sand, bioturbated	0.58
L3iii.	Grey-green silty sand with fine glauconite, bioturbated	1.57
L3ii.	Grey sandy silt with fine glauconite	1.60
L3i.	Grey silty glauconitic sand becoming more sandy towards base	0.46
L2.	Grey laminated silty clay	0.11
L1.	Grey glauconitic sand with abundant molluscs	augered 0.25

medius Harrison and Walker, 1979a, were each based on a tarsometatarsus (Figure 4.13a–c), although an additional partial tarsometatarsus and a partial femur also were ascribed to the first. The falconiform *Milvoides kempi* Harrison and Walker, 1979a, also was based on a partial tarsometatarsus (Figure 4.13d), and referred material includes two partial carpometacarpi and a partial ulna. The three rails, *Parvirallus gracilis* Harrison and Walker, 1979a, *Latipons gardneri* Harrison and Walker, 1979a, and *Latipons robinsoni* Harrison and Walker, 1979a, were founded on a partial left humerus, a partial right tibiotarsus and a partial left tibiotarsus respectively (Figure 4.13e–i). In addition, an incomplete ulna was referred to *L. gardneri* and a second partial tibiotarsus and a partial ulna to *L. robinsoni* (Harrison and Walker, 1979a).

The bird specimens from the Elmore Member are a broken radius of ?Presbyornithidae, a broken carpometacarpus of Phasianidae and a broken tarsometatarsus of ?Psittacidae (Kemp *et al.*, 1979)

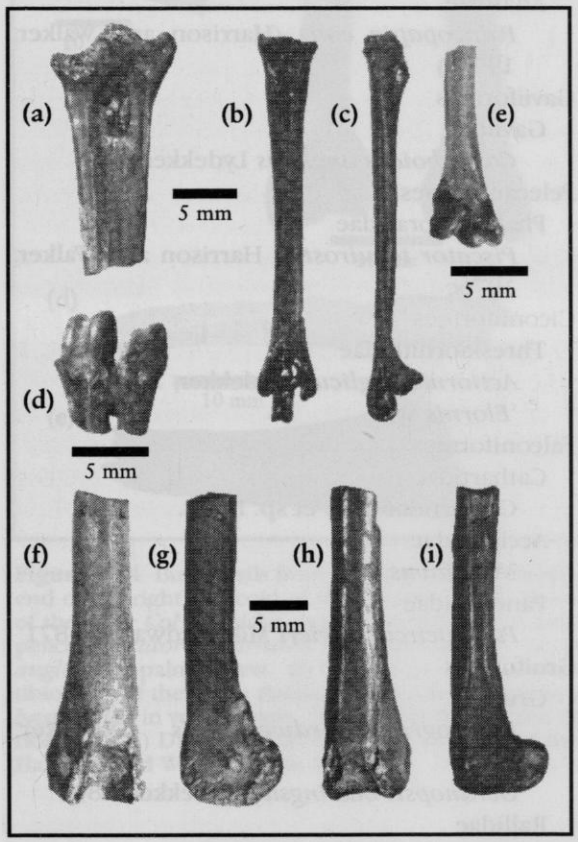

Figure 4.13 Bird fossils from the Middle Eocene Selsey Sand Formation of Lee-on-the-Solent, Gosport, Hampshire. (a) Tarsometatarsus of the gamebird *Percolinus proudlocki* in anterior view. (b,c) Tarsometatarsus of the gamebird *Litoripes medius* in posterior (b) and internal (c) views. (d) Distal end of the tarsometatarsus of the falconiform *Milvoides kempi* in anterior view. (e) Distal end of the humerus of the rail *Parvirallus gracilis* in anterior view. (f,g) Distal end of the tibiotarsus of the rail *Latipons gardneri* in posterior (f) and external (g) views. (h,i) Distal end of the tibiotarsus of the rail *Latipons robinsoni* in posterior (h) and external (i) views. (After Harrison and Walker, 1979a.)

Interpretation

The sediments at Lee-on-the-Solent are marine, as indicated by the abundant marine fossils throughout and the presence of glauconite. The vertebrate fauna is dominated by marine sharks, with only rare birds and mammals, the fragmentary remains of which presumably were washed in from neighbouring land masses.

The two gamebirds, *Percolinus proudlocki* and *Litoripes medius,* do not have a special affinity with forms adapted to wet conditions, although the tarsometatarsus of *Litoripes* suggests a bird with long, slender legs superficially similar to those of shorebirds (Harrison and Walker, 1979a). The three rails, *Parvirallus gracilis*, *Latipons gardneri* and *Latipons robinsoni*, are birds of shallow water and the water's edge. Rails today usually are associated with fresh and brackish, but not salt, water. Note, however, that Olson (1985, p. 162) was unhappy about referring any of these isolated Eocene bones to the family Rallidae.

Comparison with other localities

The Elmore Member and Selsey Formation are also exposed on the Isle of Wight in Alum Bay and Whitecliff Bay, but bird fossils have not been found in these units. The gamebird *Percolinus proudlocki* is a different species of a genus that is known otherwise from the Early Eocene London Clay Formation of the Isle of Sheppey (see GCR site report). *Litoripes medius* is also recorded from the Lutetian Earnley Formation site of Yateley (Walker, 1980), but the other taxa from Lee-on-the-Solent are unique to that locality at genus level. The only other British Middle Eocene bird site is Barton Cliff where late Middle Eocene (Bartonian) sediments have yielded two species (Harrison and Walker 1976c). In continental Europe there are very few avifaunas known of middle Eocene age. Harrison (1980a) noted just one, in the Sables de Bruxelles of

Etterbeek, near Brussels, Belgium, which has yielded a possible specimen of *Argillornis longipennis*, a species known from the London Clay Formation of the Isle of Sheppey. More recent finds from the Lutetian (Middle Eocene) deposits of Messel in Germany include about 20 species of birds, and these generally are superbly preserved complete specimens (Peters, 1992b; Feduccia, 1999, p. 168).

Conclusions

The sediments at Lee-on-the-Solent have produced a significant Middle Eocene avifauna. Many of the families seen here, for example the rails, are also known from the stratigraphically older Early Eocene sediments. The specimens include type specimens of six species – a highly significant total. Elsewhere in Europe there are very few bird faunas of this age known. The Lee-on-the-Solent section has recently suffered from sea-defence work. Hopefully, matters will improve and new finds will be possible in the future.

HORDLE CLIFF, HAMPSHIRE (SZ 254 925–SZ 270 921)

Introduction

Hordle Cliff (also termed Milford or Hordwell) has produced one of the richest Late Eocene bird and mammal faunas in the world. Other taxa, for example turtles, crocodilians, lizards and snakes, are also well represented (Benton and Spencer, 1995). This site is continuing to produce new material as the cliffs continue to be eroded. A brief review of the history of exploration at Hordle Cliff may be found in Chapter 3.

Fossil birds from Hordle Cliff were described by Lydekker (1891) and Harrison (1971, 1976) and reviewed by Harrison and Walker (1976c).

Description

The geology of Hordle Cliff is described in Chapter 3.

Despite the large collection of bird fossils described from Hordle Cliff, little is known about their precise stratigraphical position. Most of the material was collected during the middle part of the 19th century, when stratigraphical details were not always rigorously documented. Further information on the provenance of the vertebrate fossils is given in Chapter 3.

Fauna

The extensive faunas from various horizons at Hordle Cliff include molluscs, fishes, some 40 taxa of reptiles (Benton and Spencer, 1995), mammals (see Chapter 3) and birds.

AVES
Anseriformes
  Presbyornithidae
    Headonornis hantoniensis (Lydekker, 1891)
  Anatidae
    Palaeopapia eous (Harrison and Walker, 1976c)
Gaviiformes
  Gaviidae
    Colymboides anglicus Lydekker, 1891
Pelecaniformes
  Phalacrocoracidae
    Piscator tenuirostris Harrison and Walker, 1976c
Ciconiiformes
  Threskiornithidae
    Actiornis anglicus (Lydekker, 1891)
    '*Elornis* sp.'
Falconiformes
  Cathartidae
    Cathartidae gen. et sp. indet.
  Accipitridae
    ?*Aquifavus* sp.
  Pandionidae
    Palaeocircus cuvieri Milne-Edwards, 1871
Gruiformes
  Gruidae
    Palaeogrus hordwelliensis (Lydekker, 1891)
    Geranopsis hastingsiae Lydekker, 1891
  Rallidae
    Ibidopsis hordwelliensis Lydekker, 1891
Charadriiformes
  Recurvirostridae
    Kashinia magnum (Harrison and Walker, 1976c)
  Burhinidae
    Petropluvialis simplex Harrison and Walker, 1976c

The birds from Hordle Cliff were reviewed by Harrison and Walker (1976c), who identified 11

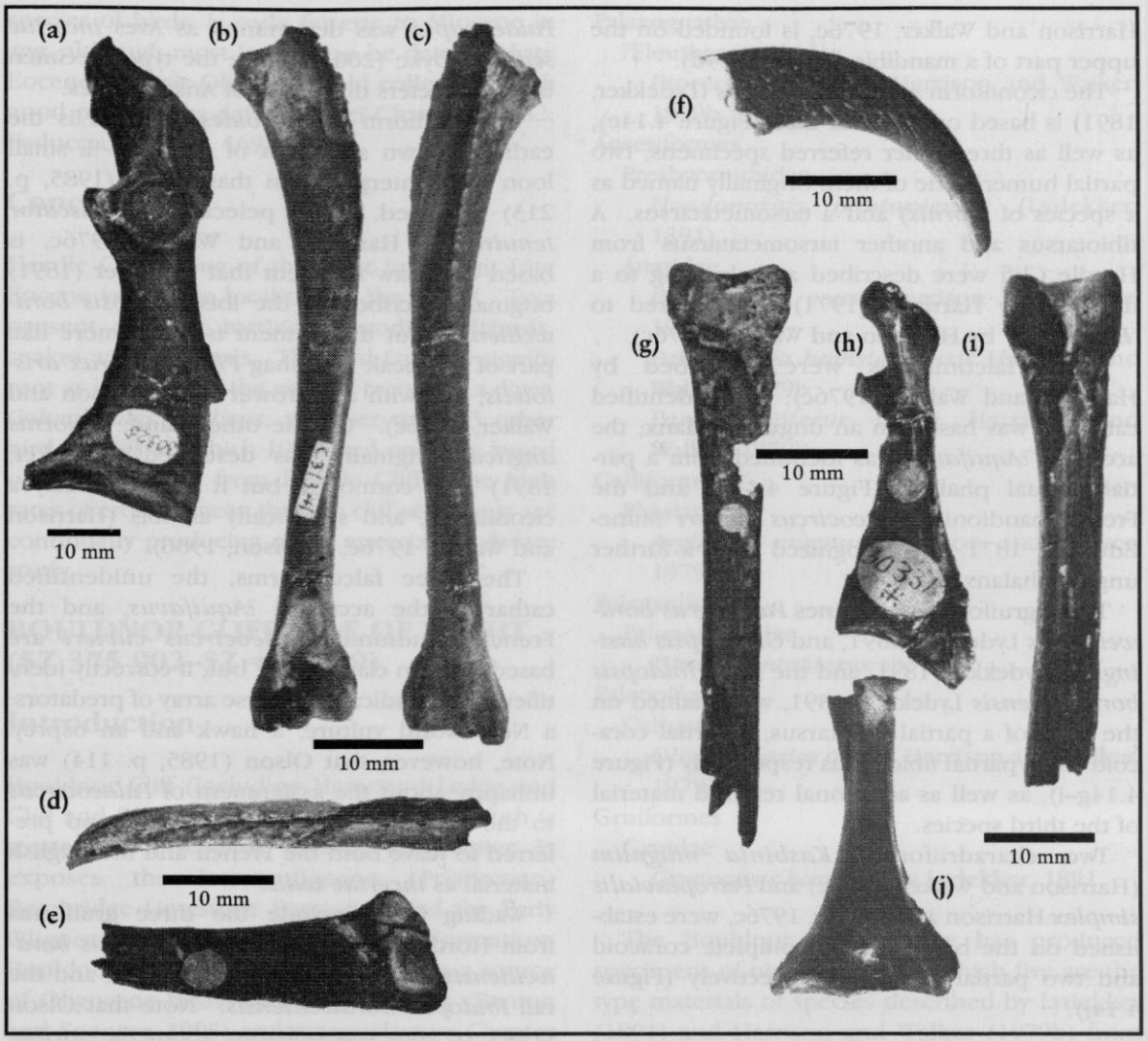

Figure 4.14 Bird fossils from the Late Eocene Headon Hill Formation of Hordle Cliff, Hampshire. (a) Proximal end of the right coracoid of the presbyornithid *Headonornis hantoniensis* in dorsal view. (b,c) Left humerus of the diver *Colymboides anglicus* in palmar (b) and anconal (c) views. (d) Upper portion of the beak of the pelican *Piscator tenuirostris* in left lateral view. (e) Proximal end of the right ulna of the ciconiiform *Actiornis anglicus* in palmar view. (f) Claw of the falconiform *?Aquifavus* in lateral view. (g) Distal portion of the right tibiotarus of the crane *Palaeogrus hordwelliensis* in anterior view. (h) Left coracoid of the crane *Geraniopsis bastingsiae* in ventral view. (i) Distal portion of the right tibiotarsus of the rail *Ibidopsis hordwelliensis* in anterior view. (j) Distal portion of the left coracoid of the thick-knee *Petropluvialis simplex* in ventral view. (After Harrison and Walker, 1976c.)

named species, 10 of them erected by Lydekker (1891) or by Harrison and Walker (1976c) (not including subsequent synonymies) on the basis of type specimens from Hordle Cliff. As with other British fossil bird localities, most of the taxa recorded from Hordle Cliff are known from only one or two bones.

The record of a presbyornithid anseriform *Headonornis hantoniensis* Lydekker, 1891, from Hordle Cliff is based on the holotype, a right coracoid (Figure 4.14a), as well as a right humerus and a partial femur. The duck *Palaeopapia eous* (Harrison and Walker, 1976c) was based on a partial sternum and a referred right coracoid from Hordle Cliff. The gaviiform (diver) *Colymboides anglicus* Lydekker, 1891, is known from a left coracoid, a left humerus (Figure 4.14b,c) and the frontal portion of a skull (Harrison, 1976; Harrison and Walker, 1976c). The pelecaniform *Piscator tenuirostris*

Harrison and Walker, 1976c, is founded on the upper part of a mandible (Figure 4.14d).

The ciconiiform *Actiornis anglicus* (Lydekker, 1891) is based on a partial ulna (Figure 4.14e), as well as three other referred specimens, two partial humeri (one of them originally named as a species of *Elornis*) and a tarsometatarsus. A tibiotarsus and another tarsometatarsus from Hordle Cliff were described as belonging to a flamingo by Harrison (1971) and referred to '*Elornis* sp.' by Harrison and Walker (1976c).

Three falconiforms were described by Harrison and Walker (1976c): an unidentified cathartid was based on an ungual phalanx; the acciptrid ?*Aquifavus* was identified from a partial ungual phalanx (Figure 4.14f); and the French pandionid *Palaeocircus cuvieri* Milne-Edwards, 1871, was recognized from a further ungual phalanx.

Three gruiforms, the cranes *Palaeogrus hordwelliensis* Lydekker, 1891, and *Geranopsis hastingsiae* Lydekker, 1891, and the rallid *Ibidopsis hordwelliensis* Lydekker, 1891, were named on the basis of a partial tibiotarsus, a partial coracoid and a partial tibiotarsus respectively (Figure 4.14g–i), as well as additional referred material of the third species.

Two charadriiforms, *Kashinia magnum* (Harrison and Walker, 1976c) and *Petropluvialis simplex* Harrison and Walker, 1976c, were established on the basis of an incomplete coracoid and two partial coracoids respectively (Figure 4.14j).

Interpretation

For an interpretation of the environment of deposition, see Chapter 3.

The presbyornithid *Headonornis hantoniensis* Lydekker, 1891, is recognized at Hordle Cliff on the basis of the original material described by Lydekker (1891), as well as on the basis of a partial femur originally named as the new genus and species *Gigantibis incognita* Harrison and Walker, 1976c, interpreted first as representing a large ibis, but later (Harrison, 1976) re-assigned to *Headonornis hantoniensis*. This was a large wading bird, with a body as large as a swan, but much longer legs. Dyke (2001b) retained the type coracoid in *H. hantoniensis*, but noted that the humeri are most likely assignable to *Presbyornis isoni*, a ground-dwelling duck, and he suggested that *Headonornis* might in the end turn out to be a synonym of *Presbyornis*. *Palaeopapia* was determined as Aves *incertae sedis* by Dyke (2001b) since the type specimen lacks characters diagnostic of Anseriformes.

The gaviiform *Colymboides anglicus* is the earliest known specimen of a diver – a small loon – an interpretation that Olson (1985, p. 213) accepted. The pelecaniform *Piscator tenuirostris* Harrison and Walker, 1976c, is based on a jaw fragment that Lydekker (1891) originally ascribed to the ibis *Ibidopsis hordwelliensis*, but the element is much more like part of the beak of a shag *Phalacrocorax aristotelis*, but with a narrower bill (Harrison and Walker, 1976c). On the other hand, *Actiornis anglicus* originally was described (Lydekker, 1891) as a cormorant but it is more likely a ciconiiform, and specifically an ibis (Harrison and Walker, 1976c; Harrison, 1986).

The three falconiforms, the unidentified cathartid, the acciptrid ?*Aquifavus*, and the French pandionid *Palaeocircus cuvieri* are based only on claw bones, but, if correctly identified, these indicate a diverse array of predators: a New World vulture, a hawk and an osprey. Note, however, that Olson (1985, p. 114) was unhappy about the assignment of *Palaeocircus* to the Family Pandionidae (ospreys) and preferred to leave both the French and the English material as *incertae sedis*.

Wading birds include the three gruiforms from Hordle Cliff, the cranes *Palaeogrus hordwelliensis* and *Geranopsis hastingsiae*, and the rail *Ibidopsis hordwelliensis*. Note that Olson (1985, p. 163) was unhappy about the attribution of *Palaeogrus* to the cranes but believed that *Geranopsis* may indeed be a gruid. The charadriiforms *Kashinia magnum* and *Petropluvialis simplex* represent an early avocet and a thick-knee, further typical shorebirds today.

Comparison with other localities

The sediments at this site are directly comparable to the Totland Bay Member at Headon Hill, Isle of Wight, in terms of the mammal faunas preserved. However, birds have not been found in these age-equivalent units (Hooker *et al.*, 1980). In France, a relatively extensive fauna of 13 species of birds is known from the slightly younger Gypse de Montmartre in the Paris Basin (Harrison, 1980a), and the falconiform *Palaeocircus cuvieri* Milne-Edwards, 1871, is shared with Hordle Cliff. The famous Phosphorites du Quercy, source of a rich fauna of some 90

species of birds, is early Eocene to Miocene in age, although most faunas can be dated as Late Eocene or Early Oligocene; old collections lack good provenance data (Mourer-Chauviré, 1982; Feduccia, 1999, p. 169).

Conclusions

Hordle Cliff is one of the most important Late Eocene vertebrate localities in the world. Taxa present include turtles, crocodiles, lizards, snakes and mammals. The bird fauna is significant as it preserves the earliest record of a diver, *Colymboides anglicus*, together with 13 other bird species, of which 10 named ones are based on type material from Hordle Cliff. The high rates of erosion mean that the cliff sediments are continually producing more material for future study.

BOULDNOR CLIFF, ISLE OF WIGHT (SZ 375 902–SZ 403 919)

Introduction

Bouldnor Cliff (including Hamstead Ledge and Cliff and 'Yarmouth'; but note that Yarmouth is treated as a separate locality in Chapter 3) exposes the latest Eocene (Priabonian) Bembridge Limestone Formation and the Early Oligocene (Rupelian) Bouldnor Formation. Bouldnor Cliff is important globally as a source of Oligocene birds, as well as reptiles (Benton and Spencer, 1995) and mammals (see Chapter 3). Bird fossils from Bouldnor Cliff were first described by Lydekker (1891), and new materials were announced by Harrison and Walker (1979b). The cliffs are washed by the sea and it is likely that further bird specimens will be found in the future.

Description

The geology of the site and occurrence of vertebrate fossils are outlined in Chapter 3. The bird fossils probably came from the muds and clays of the Hamstead Member, as did the majority of reptile and mammal specimens.

Fauna

The Bouldnor Cliff avifauna is summarized here from the review by Harrison and Walker (1979b).

Palaeognathae
  ?Eleutherornithidae
    Proceriavis martini Harrison and Walker, 1979b
Anseriformes
  Presbyornithidae
    Headonornis hantoniensis (Lydekker, 1891)
  Anatidae
    Palaeopapia eous (Harrison and Walker, 1976c)
    Palaeopapia hamsteadensis Harrison and Walker, 1979b
    Paracygnopterus scotti Harrison and Walker, 1979b
Galliformes
  Phasianidae
    Argillipes magnus Harrison and Walker, 1979b
Pelecaniformes
  Pelagornithidae
    ?*Macrodontopteryx* sp.
Falconiformes
  Cathartidae
    Oligocathartes olsoni Harrison and Walker, 1979b
Gruiformes
  Gruidae
    Geranopsis hastingsiae Lydekker, 1891

The Bouldnor Cliff locality has produced specimens of nine species, of which five are the type materials of species described by Lydekker (1891) and Harrison and Walker (1979b) from Bouldnor Cliff. Bouldnor Cliff is just east of the town of Yarmouth. Some specimens of bird bones are labelled 'Yarmouth', and are likely to be from the western end of the Bouldnor Cliff locality, and relatively low in the sequence.

The flightless ratite bird *Proceriavis martini* Harrison and Walker, 1979b, was based on a partial cervical vertebra and a toe phalanx from Yarmouth (Figure 4.15a–c). The presbyornithid *Headonornis hantoniensis* (Lydekker, 1891) was described from the Late Eocene sediments of Hordle Cliff, and it is recognized from Bouldnor Cliff from a partial scapula (Figure 4.15d), a partial coracoid and a partial humerus. The anatid duck *Palaeopapia eous* (Harrison and Walker, 1976c) also was first noted from Hordle Cliff and is represented at Bouldnor Cliff by a coracoid (Figure 4.15e,f). Two additional anatid ducks, *Palaeopapia hamsteadensis* Harrison and Walker, 1979b, and *Paracyg-*

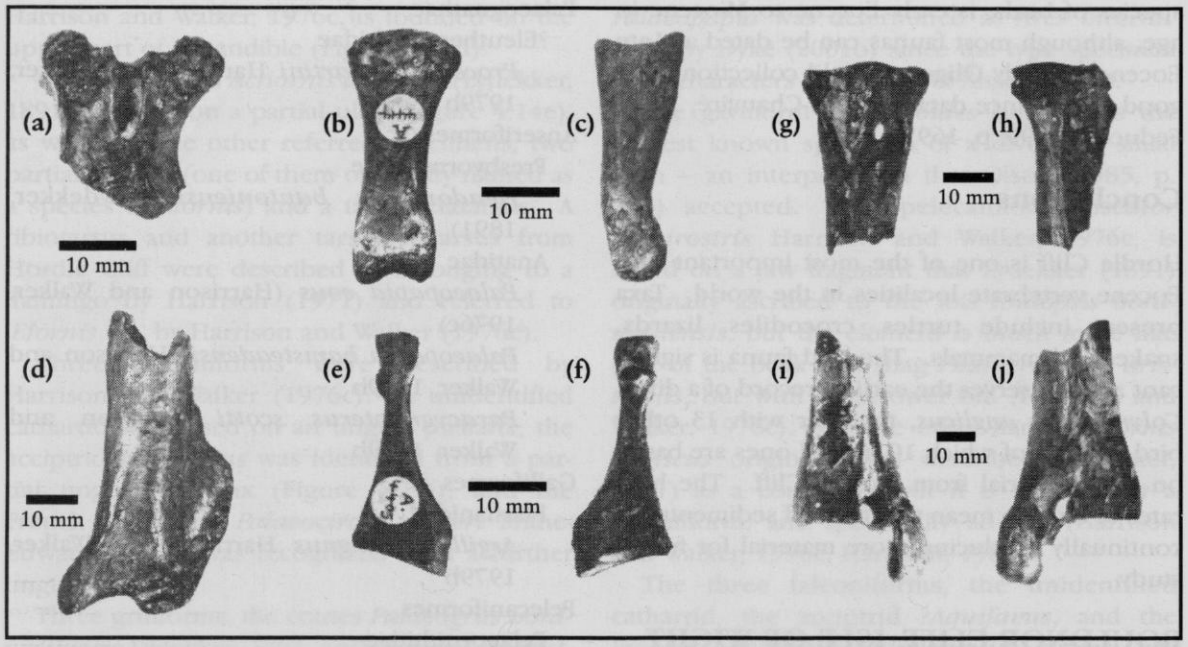

Figure 4.15 Bird fossils from the Early Oligocene Bouldnor Formation of Bouldnor Cliff, Isle of Wight. (a–c) Bones of the eleutherornithid *Proceriavis martini*; cervical vertebra in dorsal view (a), and basal phalanx of right digit 4 in ventral (b) and external (c) views. (d) Proximal end of the right scapula of the presbyornithid *Headonornis hantoniensis* in ventral view. (e,f) left coracoid of the right scapula of the duck *Palaeopapia eous* in ventral (e) and dorsal (f) views. (g,h) Proximal end of the left tarsometatarsus of the gamebird *Argillipes magnus* in posterior (g) and external (h) views. (i,j) Distal end of the left tarsometatarsus of the falconiform *Oligocathartes olsoni* in dorsal (i) and ventral (j) views. (After Harrison and Walker, 1979b.)

nopterus scotti Harrison and Walker, 1979b, also were established, based on type material from Yarmouth: a partial scapula and a partial coracoid respectively. The bony-toothed pelecaniform *Macrodontopteryx* was recognized tentatively from Bouldnor Cliff on the basis of a partial radius (Harrison and Walker, 1979b).

The galliform (gamebird) *Argillipes magnus* Harrison and Walker, 1979b, was based on a partial tarsometatarsus from Yarmouth and another tentatively referred tarsometatarsus from Bouldnor Cliff (Figure 4.15g,h). The falconiform *Oligocathartes olsoni* Harrison and Walker, 1979b was based on a partial tarsometatarsus (Figure 4.15i, j) and possibly also a partial coracoid, from Yarmouth and Thorness Bay respectively. The gruiform *Geranopsis bastingsiae* Lydekker, 1891, was founded on a partial coracoid from Yarmouth, as well as other limb bones from Yarmouth and one from Hamstead.

Interpretation

In the Hampshire Basin, a sequence of over 600 m of clastic sediments, with minor limestones, rests unconformably on the Chalk. These sediments represent a series of transgressions and regressions. Marine conditions predominated from soon after the beginning of the Eocene Epoch, until the end of Mid Eocene times in central and eastern parts of the basin, when non-marine environments became increasingly significant (Daley, 1989; Armenteros *et al.*, 1997).

Three main environments of deposition have been suggested for the Bembridge Marls Member. The lower part of the sequence, the 'Bembridge Oyster Bed', represents the main transgressive phase. Invertebrate faunas are typical of restricted marine conditions and accumulated in an estuary or brackish bay. This facies is overlain by a thick sequence of grey or blue-green clays, which may show laminations. These sediments are thought to have been deposited in brackish lagoons during the early part of a regression episode (Daley, 1972, 1973). Continued regression led to the deposition of the olive, brown and grey clays and associated sedimentary structures such as rootlet horizons and graded silt laminae, indicative of the upper

freshwater reaches of a lagoon (Collinson, 1983b).

The ratite *Proceriavis martini* shows affinities with modern ostriches and cassowaries, but the remains are too incomplete for further determination (Harrison and Walker, 1979b). This find of a ratite in England may seem unusual, but such flightless birds are relatively widespread in the Eocene and Oligocene deposits of Europe (Houde, 1988).

The three ducks *Palaeopapia eous* (Harrison and Walker, 1976c), *Palaeopapia hamsteadensis* Harrison and Walker, 1979b, and *Paracygnopterus scotti* Harrison and Walker, 1979b, are respectively comparable in size to a true goose of the genus *Branta*, the shelduck *Tadorna ferruginea* and a whistling duck of the genus *Dendrocygna*. Note, however, that Dyke (2001b) was not convinced that *Palaeopapia* has any diagnostic anseriform characters, nor whether *P. hamsteadensis* belongs to the genus. Dyke (2001b) was also unconvinced by the limited material of *Paracygnopterus scotti*, referring it also to Aves *incertae sedis*.

The gamebird *Argillipes magnus* Harrison and Walker, 1979b, was about the size of a domestic fowl *Gallus gallus*. The falconiform *Oligocathartes olsoni* Harrison and Walker, 1979b, was assigned to the family Cathartidae, containing today the New World vultures.

The birds are mainly representative of terrestrial and freshwater environments, except for the possible pelecaniform bony-toothed bird *Macrodontopteryx*, a thorough-going marine form best known from the Early Eocene London Clay Formation, and perhaps the presbyornithid *Headonornis hantoniensis* (Lydekker, 1891), a large wading bird (Harrison and Walker, 1979b).

Comparison with other localities

Early Oligocene bird fossils have been reported from the Hamstead Member of Bouldnor Cliff, (including Yarmouth) and Thorness Bay, on the Isle of Wight. No other British early Oligocene site can be compared with Bouldnor Cliff. Farther afield, an avifauna of six species has been reported from the Early Oligocene Boom Clay of the Rupel region in Belgium (Harrison, 1980a). Thirteen species have been recorded from another Early Oligocene locality in Belgium, Boutersem, of very similar age to that of the Upper Hamstead Member of Bouldnor Cliff (Mayr and Smith, 2001). The fauna comprises ducks, rails and shorebirds. There is only slight overlap with Bouldnor Cliff in that the duck *Paracygnopterus* occurs at both localities.

The presence of some of the Bouldnor Cliff bird taxa (*Headonornis hantoniensis*, *Palaeopapia eous*) in the Late Eocene record of Hordle Cliff indicates faunal continuity between the two time periods. Two of the genera (*Macrodontopteryx*, *Argillipes*) are also known from the Early Eocene London Clay Formation.

Conclusions

Bouldnor Cliff, near Yarmouth on the Isle of Wight, has yielded one of the best early Oligocene bird faunas in Europe and possibly the world. Nine bird species have been reported, of which five are type specimens of species named from the site. The cliffs are undergoing erosion, and the site has great potential for future finds.