



**FAUNA**  
*of*  
**AUSTRALIA**



**42. BIOGEOGRAPHY AND  
PHYLOGENY OF THE  
CROCODYLIA**

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The living crocodylians give no hint of the vast range of diversity of those now extinct. This contribution is intended primarily to provide some appreciation of the evolutionary history and range of diversity of pre-eusuchian crocodylians, and also to outline the history of crocodylians in Australia and the southwestern Pacific region.

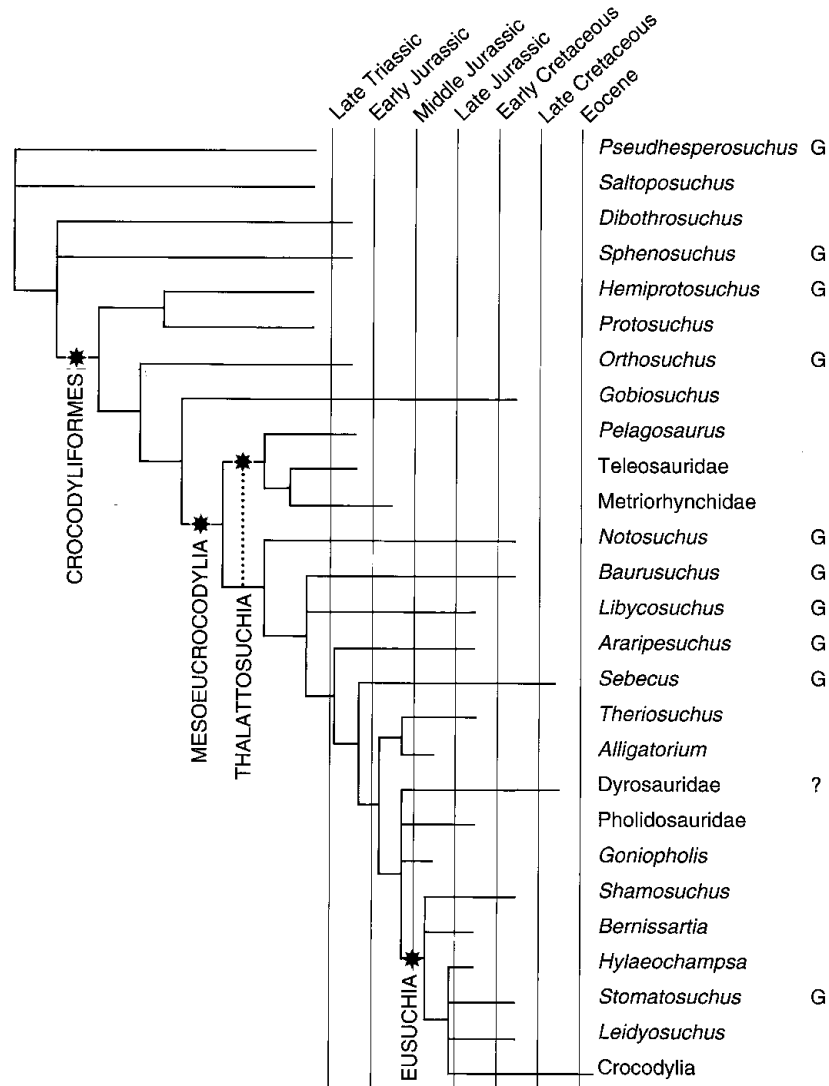
Recent phylogenetic analysis has substantially altered the classification of crocodylians. The Protosuchia and Mesosuchia have been abandoned as formal taxa: the Mesosuchia has been combined with part of the Eusuchia which together constitute the Mesoeucrocodylia (Table 42.1; Benton & Clark 1988). The terminology has changed also. The animals previously called crocodylians are now termed crocodylomorphs, and the term 'crocodylian' is restricted to the common ancestor of the living taxa and its descendants (Fig. 42.1; Benton & Clark 1988). Here the term 'crocodylians' will also be used, informally, in its more traditional sense.

**Table 42.1** Equivalent old and new terms (for example, Benton & Clark 1988) in crocodylian higher taxonomy.

Old terms	New terms
Crocodylia + Sphenosuchia	Crocodylomorpha
Crocodylia	Crocodyliformes
Mesosuchia + Eusuchia	Mesoeucrocodylia
Eusuchia (unaltered)	Eusuchia
Crocodylidae + Alligatoridae + Gavialidae	Crocodylia

Crocodylomorphs arose from the plexus of primitive archosaurs known as thecodonts. They have changed less from thecodonts than any other advanced group of archosaurs (Olshevsky 1991). Because crocodylians and birds are the only surviving archosaurs, our understanding of the Archosauria owes much to the study of these groups. Both are characterised by a craniofacial pneumatic system which extends into the snout, and is indicated skeletally (at least plesiomorphically) by the antorbital fenestrae (Witmer 1987). This relationship of the pneumatic system to the antorbital fenestra fits in with the long-standing use of the antorbital fenestra as a defining character of archosaurs (Carroll 1988b), and suggests that the origin of the rostral part of the pneumatic system marked the origin of the Archosauria.

Previously, the classification of crocodylians rested largely on two characters: the position of the choanae in the palate, especially in relation to the pterygoids, and the form of the vertebral centra, especially the acquisition of procoely. Modern work has greatly increased the number of morphological characters used, particularly regarding the structure of the braincase and associated regions of the skull (for example, Norell 1989). Within the past fifteen years biochemical characters and relationships to parasites have been used in studies of the relationships of living eusuchians. These characters have traditionally been applied to living forms, however, advances in molecular palaeontology (Rowley 1991) may lead to the application of similar techniques to extinct crocodylian groups, with potentially enlightening results.



**Figure 42.1** Phylogenetic relationships of selected crocodylomorphs, and their approximate time of origin. All taxa are extinct except for the Crocodylia. The major clades are identified by an asterisk. G=Gondwanan forms; ? = possible Gondwanan forms. (After Benton & Clark 1988; Willis 1993)

[W. Mumford]

## EVOLUTIONARY HISTORY AND ZOOGEOGRAPHY OF CROCODYLIANS

Crocodylians differ from other archosaurs in having a squamosal that overhangs the quadrate laterally, contact between the prootic and the quadrate, an extensive craniofacial pneumatic system in the region of the braincase and elongate proximal carpals; they lack the postfrontal bone. The sphenosuchians are the oldest and most primitive crocodylomorphs (Fig. 42.2A). As currently used (for example, Olshevsky 1991) sphenosuchians are a paraphyletic group (*cf.* Benton & Clark 1988), lacking any uniquely defining characters. The grade contains the sister groups of the more advanced crocodylomorphs (Crocodyliformes), which includes the genera *Pseudhesperosuchus*, *Saltoposuchus*, *Dibothrosuchus* and *Sphenosuchus* (Fig. 42.1). They lived during Middle Triassic to Early Jurassic times, from 240 to 105 million years ago, and have been found in Brazil, Argentina, South Africa, China, Arizona, England and Germany; thus they were essentially cosmopolitan in Pangaea. The oldest and most primitive

sphenosuchians are from South America, which suggests that crocodylians may have arisen in that part of Gondwana. Sphenosuchians appear to have been gracile, quick-moving terrestrial predators. Together with the protosuchians, they indicate that crocodylians originated as terrestrial predators, and only some 55 million years later did crocodylians adopt the amphibious mode of life that they exploited so successfully. When they originated, the 'crocodylian niche' of amphibious ambush predator was occupied by the phytosaurs, superficially crocodile-like archosaurs. Crocodylians exploited the amphibious lifestyle only after the extinction of the phytosaurs.

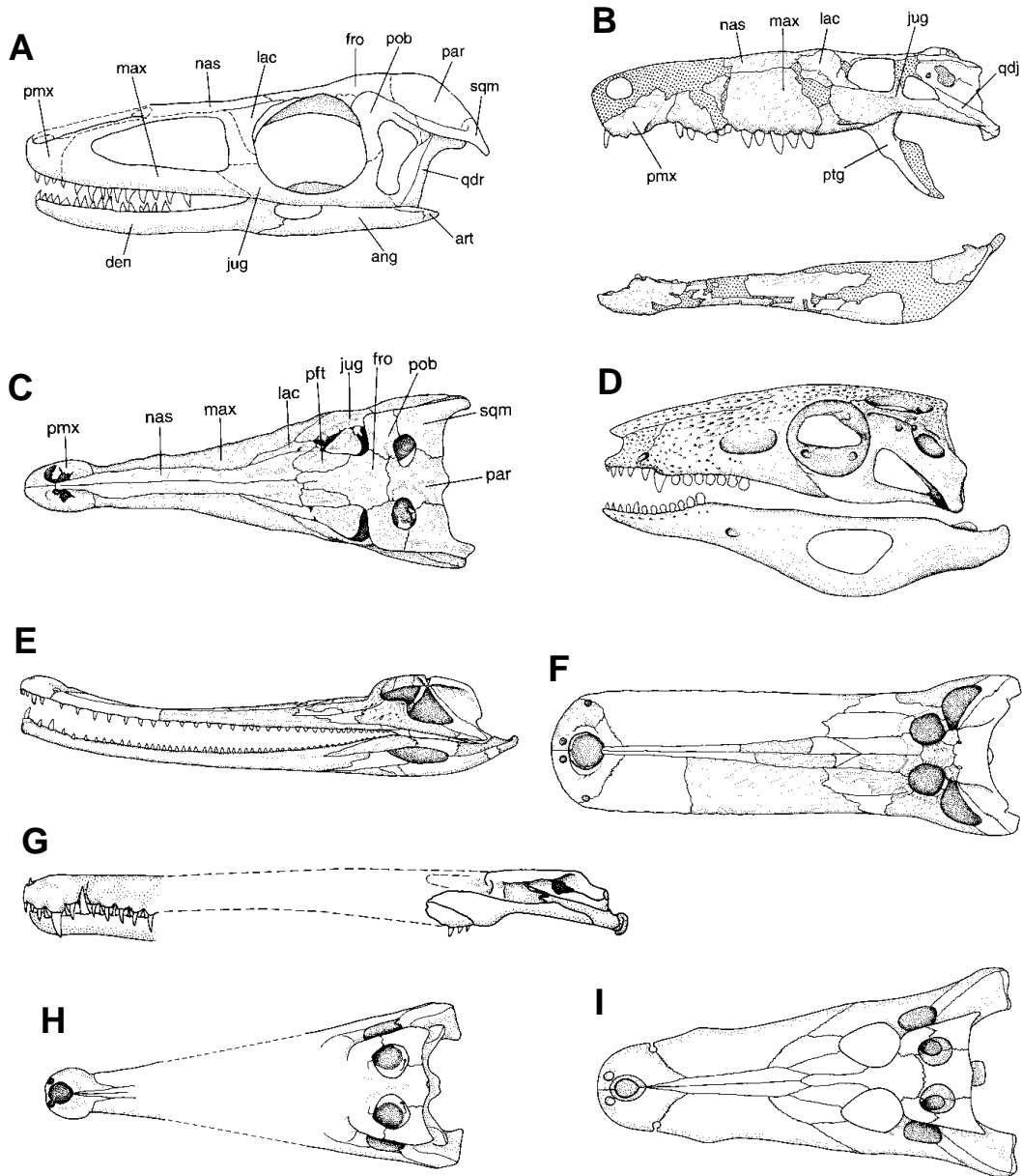
The protosuchians, once thought to be the earliest crocodylians, are now considered to be paraphyletic, consisting of the monophyletic Protosuchidae (includes *Hemiprotosuchus* and *Protosuchus*) and sister groups of the mesoeucrocodylians including the genera *Gobiosuchus* and *Orthosuchus* (Fig. 42.1). The protosuchids and their allies are similar in their level of evolution. Both have choanae anterior in the palate, between the maxillae and palatines, and show no indication of a bony secondary palate. Like most pre-eusuchians, they had amphicoelous vertebral centra. Most lived during the Early Jurassic, although there is a Late Triassic genus from Argentina. Protosuchians have been found in southern South America, southwestern and northeastern United States of America, South Africa and China. As with the sphenosuchians, these records suggest a cosmopolitan Pangaeian distribution, and the oldest and most plesiomorphic forms are found in North and South America.

The traditional mesosuchians are a paraphyletic group characterised by a more posterior location of the choanae between the palatines and pterygoids. The location of the choanae near the pharynx, where presumably they function as in modern crocodylians, is widely taken to reflect the adoption of amphibious habits. Mesosuchians are now included together with the Eusuchia, in the Mesoeucrocodylia (Table 42.1; Whetstone & Whybrow 1983). The Mesoeucrocodylia have a bony secondary palate formed of the maxillae and palatines, foramina for cranial nerves IX–XI well within the otoccipital and the canal for the temporo-orbital vein, and cranial nerve V walled by the quadrate, squamosal and otoccipital. The Mesozoic mesoeucrocodylians, too, were cosmopolitan in distribution, probably reflecting the equable climates of the Mesozoic (Buffetaut 1979).

Mesoeucrocodyles exhibited great diversity (Buffetaut 1982). Some, such as goniopholidids, were the first crocodylians to adopt the lifestyle of amphibious ambush predator. Thalattosuchians successfully adapted to marine life, where a long snout developed, associated with massive jaw-closing muscles, flippers and a heterocercal tail. Hsisosuchians and sebecids seem to have been terrestrial predators. They acquired deep, laterally compressed snouts and trenchant, serrate teeth (known as ziphodont teeth) like those of carnivorous dinosaurs (Fig. 42.2B, C). The relatively short-snouted notosuchians (a paraphyletic group) were also apparently terrestrial. The blunt, intricately fluted cheek teeth of the uruguaysuchians (Rusconi 1932) resembled those of herbivorous dinosaurs and lizards, suggesting they were also herbivorous (Fig. 42.2D). Others, including an unnamed taxon from Malawi, had heterodont dentition, with cheek teeth like those of some contemporaneous mammals (Clark, Jacobs & Downs 1989). Notosuchians were South American and African forms which may yet be discovered in Australia.

The Gondwanan crocodylians of the Late Mesozoic seem to have evolved independently of those in Laurasia. But in early Tertiary times, Laurasian eusuchians established themselves in Africa and South America and perhaps caused the extinction of some of the more plesiomorphic southern taxa (Buffetaut 1979).





**Figure 42.2** Selected skulls of extinct crocodylians. **A**, the sphenosuchian, *Barberenasuchus brasiliensis*, from the Middle Triassic of Brazil, is the oldest known well-preserved crocodylian, and suggests that crocodiles originated in Gondwana (lateral view); **B**, the ziphodont, *Sebecus icaeorhinus*, from the Eocene of Argentina, may have been a terrestrial carnivore (lateral view); **C**, dorsal view of *Sebecus icaeorhinus*; **D**, the tooth-row of the brevirostrine, *Uruguaysuchus aznarezi*, of the Late Cretaceous of Uruguay is almost mammal-like in its differentiation and may have been herbivorous (lateral view); **E**, lateral view of the nettosuchian, *Mourasuchus atopus*, from the Miocene of Columbia; **F**, dorsal view of *Mourasuchus atopus*; **G**, the longirostrine, *Harpacochampsa camfieldensis*, from the Miocene of the Northern Territory appears not to be closely related to other endemic Australian crocodylians (lateral view); **H**, dorsal view of *Harpacochampsa camfieldensis*; **I**, the mekosuchine, *Australosuchus clarkae*, from the Miocene of South Australia presumably resembled the stem group animals of the mekosuchines (dorsal view). **ang**, angular; **art**, articular; **den**, dentary; **fro**, frontal; **jug**, jugal; **lac**, lacrimal; **max**, maxilla; **nas**, nasal; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pob**, postorbital; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **sqm**, squamosal. (After A, Mattar 1987; B,C, Kuhn 1968; D, Rusconi 1932; E, F, Langston 1965; G, H, Megirian *et al.* 1991; I, Willis & Molnar 1991b) [T. Wright]

Although the phylogenetic relationships among crocodylians are reasonably clear, there are few forms that actually exemplify transitions between major groups. For example, the gap between protosuchian and thalattosuchian levels remains unbridged, nor is there any better understanding of the process by which some groups of ziphodont crocodylians (hsisosuchians, sebecids) originated. However a brevirostrine (short snouted) lineage, from which others diverged, seems to have persisted from the sphenosuchian period almost until the origin of the eusuchians (*cf.* Buffetaut 1982; Benton & Clark 1988). Some of the diverging lineages evolved snout proportions like those of modern alligators or crocodiles, such as the goniopholidids, but others became longirostrine (long snouted) or ziphodont.

The eusuchians are the only traditional crocodylian group that survived the test of phylogenetic analysis. They are characterised by pterygoids which surround the choanae entirely. The Crocodylia are those eusuchians in which the anterior and posterior margins of the scapula are nearly parallel (Benton & Clark 1988). The oldest eusuchians date from the Early Cretaceous (approximately 130 million years ago), whilst the oldest crocodylians (*sensu* Benton & Clark) are difficult to date, although they may be no older than Eocene, about 50 million years (Fig. 42.1; summarised in Densmore & Owen 1989).

Morphologically, eusuchians are more uniform than earlier mesoeucrocodylians, and differ mainly in skull form, especially that of the snout. Among the living species, the differences between the broad, and moderately broad-snouted, forms (*Alligator*, *Caiman*, most species of *Crocodylus*, *Melanosuchus*, *Osteolaemus*, and *Paleosuchus*) and the narrow-snouted fish-eaters (*Gavialis*, *Tomistoma*, *Crocodylus cataphractus*, and *C. johnstoni*) are well known. The living eusuchians are divided in two families, the Alligatoridae and Crocodylidae, with the position of the gavials being uncertain (Norell 1989), as discussed later. Extinct taxa, however, included the ziphodont pristichampsines, which were apparently terrestrial predators of Asia, Europe and North America, and convergent forms with very long and broad snouts (*Stomatosuchus* and *Mourasuchus*; Fig. 42.2E, F) (Langston 1965, 1966). Langston (1965) suggests these latter may have engulfed small floating animals, or even plants, whilst cruising slowly through the water, or perhaps scooped up bottom life. Both genera inhabited Gondwanan continents (Africa and South America respectively), and perhaps they, or similar forms, lived in Australia.

Thus extinct eusuchians and other mesoeucrocodylians exhibited a wide range of cranial forms, not represented among the surviving taxa.

## **GENERAL FEATURES OF CROCODYLIAN EVOLUTION, ZOOGEOGRAPHY AND EXTINCTION**

There are no recent comprehensive reviews of crocodylian evolution or palaeozoogeography, although some phylogenetic studies have been made (Benton & Clark 1988; Norell 1989). The several recent studies of zoogeography (cited in Taplin & Grigg 1989) concern only crocodylians, generally accepted as having a relictual distribution.

Mesoeucrocodylian lineages repeatedly adopted similar cranial forms. The piscivorous longirostrine skull evolved at least eight times (thalattosuchians, pholidosaurids, tethysuchians, *Thoracosaurus*, *Euthecodon*, gavials, *Toyotamaphimeia*, *Crocodylus cataphractus*). Ziphodont structure developed at least four times (hsisosuchians, sebecosuchians, pristichampsine crocodylids, and some mekosuchian crocodylids), possibly more (*cf.* Benton & Clark 1988). And, as mentioned previously, a broad, flat, 'duck-like' snout evolved independently in at least two lineages. These parallelisms usually occurred as a series of temporal replacements, although taxa exhibiting parallelisms did

sometimes exist simultaneously in different regions, for example, among longirostrine forms (Buffetaut 1979). There is also a series of replacements among the terrestrial groups, at least in Laurasia. Sphenosuchians were replaced by protosuchids, followed by the sequential appearance of atoposaurs in Europe and hsisosuchians in China, *Gobiosuchus*, and finally pristichampsines.

Crocodylians seem not to have been greatly affected by the mysterious Cretaceous-Tertiary extinctions (Buffetaut 1979). Instead, because crocodylians are unable to reproduce at low temperatures (Magnusson, Vliet, Pooley & Whitaker 1989), extinctions have generally been accepted as having been caused by increasingly colder climates. The major crocodylian extinctions occurred later, in the Late Tertiary, and seem to have been caused by the lower temperatures of the Late Cenozoic glaciations (Buffetaut 1979). Until the Late Tertiary, crocodylians seem to have become extinct in a piecemeal fashion, related more to trophic competition than to any general environmental deterioration.

Regional endemism was evident on the southern continents after the mid-Mesozoic. Endemic genera and families inhabited both South America (peirosaurids, various notosuchian groups, dolichochoampsids, sebecids, *Charactosuchus*) and Africa (libycosuchids, *Stomatosuchus*, *Aegyptosuchus*, *Euthecodon*) during the Cretaceous and Tertiary. Some of these groups were replaced by crocodylids on both continents during the Cenozoic.

Crocodylian palaeozoogeography can be used in reconstructing ancient climates since crocodylians are limited in their ranges by environmental temperatures. However, care must be taken in such interpretations as alligators are able to survive under temporary ice cover (Brisbin 1989), and perhaps some extinct taxa were also able to do so. Thus the occurrence of crocodylian remains in the Early Cretaceous of southern Victoria (Rich & Rich 1989), need not contradict the reported near-freezing (presumably winter) ground water temperatures (Rich & Vickers-Rich 1992). The presence of crocodylians however seems to be a good indication that climates were not more rigorous than the occasional winter snowfall or freeze.

Another point of interest is the ability of eusuchians to disperse through salt water. Taplin & Grigg (1989) presented an interpretation of crocodylid evolution based on their studies of osmoregulation. The function and efficacy of the osmoregulatory organs are closely related to the ability to disperse through salt water, and hence to the role of oceans and seas as a barrier to or avenue of dispersal by crocodylians. Taplin & Grigg (1989) contended that effective osmoregulatory structures developed early in eusuchian history and so these animals were not restricted in their dispersal by oceans. However, intriguing though this interpretation is, no outgroup comparison was included in the phylogenetic analysis, so there remains some doubt that effective osmoregulatory structures were developed early in eusuchian history.

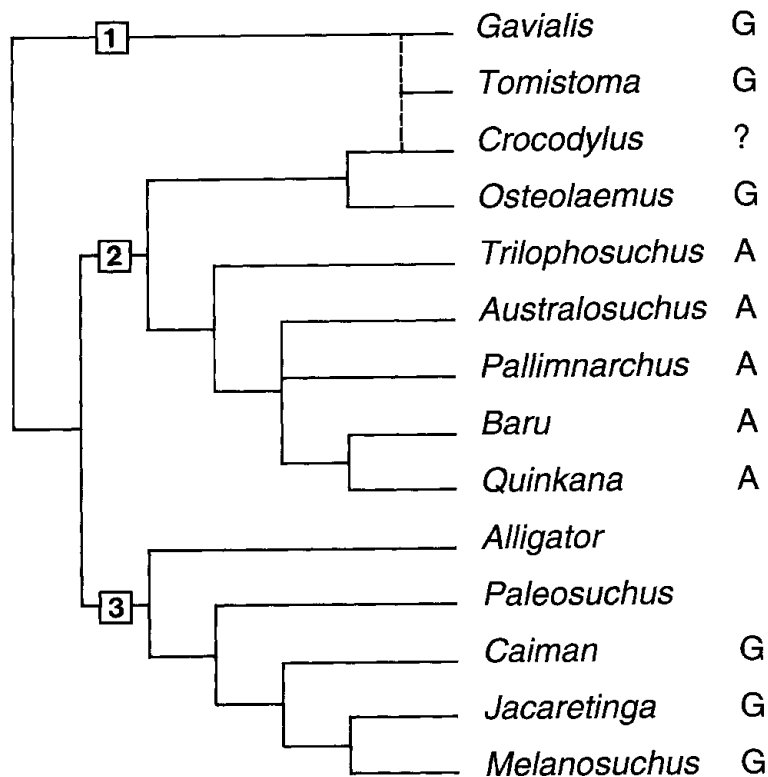
## **RELATIONSHIPS OF *GAVIALIS* AND *TOMISTOMA***

There is some contention amongst taxonomists regarding the relationships of the living longirostrine crocodylians, *Tomistoma* and *Gavialis* (Fig. 42.3). Palaeontologists of the last century generally considered the two genera to be closely related, but more recently Kälin (1955) and Telles Antunes (1961) both considered them to be independently derived convergent forms. This view was not accepted by all workers. For example, Langston (1965) pointed out similarities between early gavials and *Tomistoma*. More recently the application of biochemical and immunological methods suggested that *Gavialis* and *Tomistoma* are closely related (Densmore & Dessauer 1984; Hass, Hoffman, Densmore & Maxson 1992). This view has been accepted by some, such as Buffetaut (1985), but strongly contested by others. Buffetaut has argued that

fossil gavials such as *Eogavialis* are very similar to *Tomistoma*, and that the differences arose late in gavial evolution and hence do not indicate a long-standing separation of the two lineages.

A dissenting view was held by Tarsitano (1985), Tarsitano *et al.* (1989) and a few other workers. Tarsitano (1985) regarded *Gavialis* as having been distinct from all other eusuchian lineages for a long time, presumably since the early Cenozoic. He noted major differences in the structure of the braincase, which in most eusuchians has been 'verticalised'. This term refers to the deepening of the basisphenoid and basioccipital such that they face posteriorly, rather than ventrally. It occurs after the first year of life and so is not seen in hatchlings. In *Gavialis*, the braincase retains its plesiomorphic condition. Major differences in the musculature of the hind limb and tail of gavials have also been reported (Frey *et al.* 1989).

Although cogently argued, this view is not generally accepted. Tarsitano's interpretation does not account for the biochemical data, and it assumes that the unusual features of gavials reflect their ancestry rather than being autapomorphies. In a paper apparently unknown in the west, Aoki (1976) argued that the absence of 'verticalisation' in the braincase of *Gavialis* is a pedomorphic character, a retention into adulthood of the condition at hatching. In addition, as Tarsitano admits, 'verticalisation' is a convergent character in archosaurs, as it occurred in several Mesozoic pre-eusuchian crocodylians and even in large theropod dinosaurs, such as *Tyrannosaurus*. So it may have evolved convergently among eusuchians and not indicate a long period of separation of the gavial lineage from those of the other eusuchians.



**Figure 42.3** Phylogenetic relationships within the Crocodylia indicating, the uncertain family status of the Gavialidae (1), and the Crocodylidae (2) and Alligatoridae (3). G = Gondwanan forms; A=Australian endemics. (After Benton & Clark 1988; Willis 1993) [W. Mumford]



The problem of the relationships of *Gavialis* and *Tomistoma* is part of a larger problem of the relationships of all longirostrine crocodylians. Until recently, the relationships of the Mesozoic longirostrines have been unsettled, and even among living taxa the relationship of *Gavialis* and *Tomistoma* is not the only one in doubt. Some taxonomists (for example, Aoki 1976) consider *Crocodylus cataphractus* to belong to the monospecific genus, *Mecistops*. The longirostrine habitus has evolved independently at least eight times, and it simply is not clear which characters of these crocodylians are associated with the development of the longirostrine habitus, and which reflect ancestry.

## CROCODYLIANS IN THE SOUTHWESTERN PACIFIC REGION

It is useful to look at the crocodylians of the south-western Pacific region to appreciate Australian crocodylians, for these taxa share the same zoogeographic and phylogenetic patterns. In this region, the distributions of insular endemic *Crocodylus* species form a pattern 'superimposed' on the much broader range of *C. porosus*. The latter occurs throughout the region, occasionally as far as Ponape (Allen 1974), 480 km north of New Zealand (Robb 1980) (Fig. 42.4). The insular endemics are possibly derived from populations of *C. porosus* that invaded the inland waters (*cf.* Ross & Magnusson 1989). They include *C. novaeguinae* in New Guinea, *C. johnstoni* in Australia, *C. raninus* in Borneo (Ross 1990) and *C. mindorensis* on several of the southern Philippine Islands (Luzon, Mindoro, Masbate, Samar, Negros, Busuanga, Mindanao and Jolo; Ross & Magnusson 1989). There seems to be an Indonesian freshwater crocodile of unknown taxonomic affinities (Ross 1986), and possibly a second endemic in Papua New Guinea (Ross & Magnusson 1989).

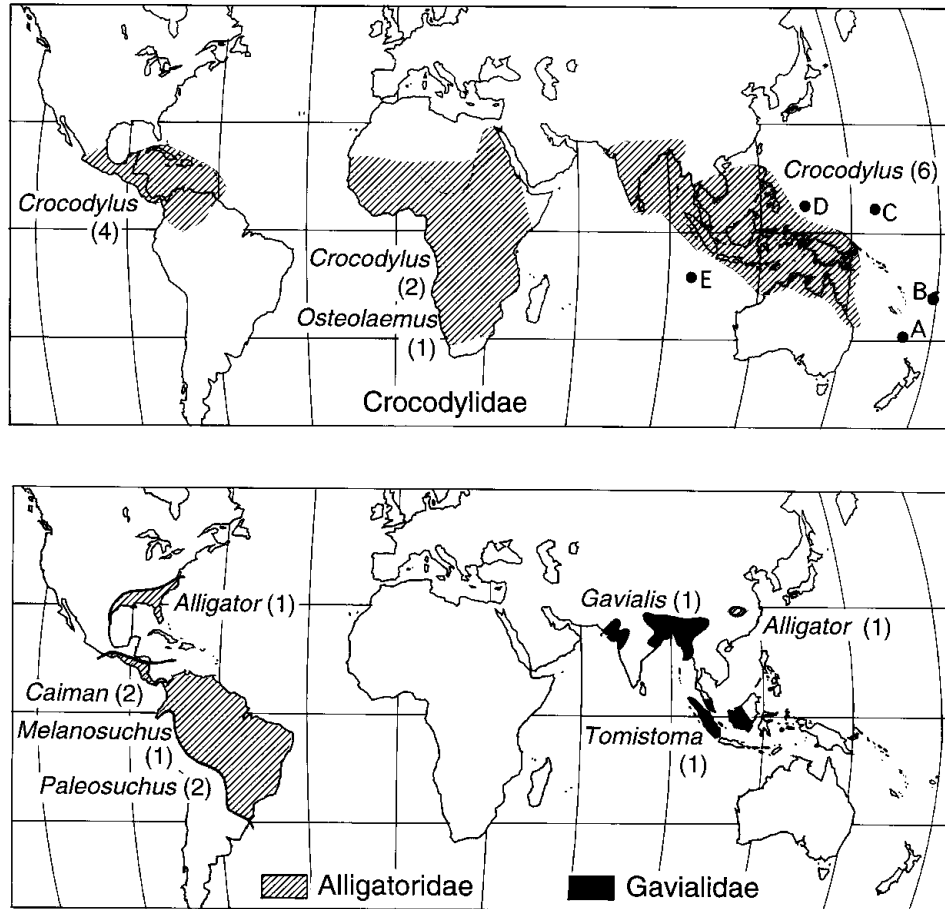
Such a pattern probably persists from the past and endemic crocodylians might have lived on other southwestern Pacific islands. For example, the New Caledonian *Mekosuchus inexpectatus* became extinct less than two millennia ago. It was a plesiomorphic eusuchian with unusual derived features (Balouet & Buffetaut 1987; Balouet 1989); its ancestors probably diverged from the eusuchian line near the beginning of the Tertiary. It is believed to have fed on snails.

Pleistocene Java was home to two extinct crocodiles. *Crocodylus ossifragus*, a broad-snouted species, and *Gavialis bengawanicus*, which occurred near the eastern end of the range of the genus. This range may have extended even further east, as fragmentary remains from Murua (Woodlark) Island (*Gavialis papuensis*) include portions of a rostrum and jaws with laterally directed alveoli. Once thought to indicate a *Euthecodon*-like form (Molnar 1982), they may derive from a malformed individual of *G. bengawanicus* (Aoki 1988).

The southwestern Pacific reflects the situation of crocodylians in Australia, showing a greater past diversity now reduced to members of only the single genus *Crocodylus*. (Fig. 42.4).

The most ancient known Australian crocodile is a relatively small animal, of uncertain affinities, from the Early Cretaceous deposits at Lightning Ridge, New South Wales (Etheridge 1917). Little is known of this form, if indeed only a single taxon is represented. Procoelous vertebrae are present (Molnar 1980) indicating that it was either a eusuchian or was closely related to eusuchians.

A longirostrine form, known only from a jaw, from the Queensland Eocene (Willis & Molnar 1991a) suggests that crocodylians were diverse in Australia early in the Cenozoic. Another Eocene jaw from Queensland represents a species of more typical cranial proportions. Many of the later Australian fossil crocodylian taxa are united by a series of characters which include the reduction or absence of the anterior process of the palatine, large anteriorly located



**Figure 42.4** Distribution of the extant crocodylian families Crocodylidae, Alligatoridae and Gavialidae. The labelled dots represent reported sightings of individuals of *Crocodylus porosus*. A, 480 km north of North Cape, New Zealand; B, Fiji; C, Ponape; D, Palau; and E, Cocos (Keeling) (Sources: A, Robb 1980; B, D, E, Schmidt 1957; C, Allen 1974) (After Alderton 1991) [W. Mumford]

palatine fenestrae, a large triangular exposure of the supraoccipital on the skull roof, well-developed alveolar processes in both jaws (Willis, Molnar & Scanlon 1993), and a marked disparity of alveolar size in the jaws (Fig. 42.2G). These features are possessed by *Mekosuchus* (Willis *et al.* 1993), suggesting an indigenous radiation of Australian and southwestern Pacific crocodylians. Willis and co-authors called this the mekosuchine radiation. Its members were diverse, and several genera are represented in some deposits (Archer, Hand & Godthelp 1991). They adopted a variety of forms. Some species, including *Pallimnarchus pollens*, had very broad, low skulls reminiscent of those of temnospondyl amphibians, others were ziphodont (*Quinkana fortirostrum*) or semi-ziphodont (*Baru darrowi*; Willis, Murray & Megirian 1990). There were small terrestrial predators (*Trilophosuchus rackhami*), and others that resembled typical crocodylids such as *Australosuchus clarkae* and *Kambara murgonensis*.

However, it is not clear that all pre-Pliocene Australian crocodylians were mesosuchines. *Crocodylus* has been reported from the Miocene Waite Formation of the Northern Territory (Woodburne 1967), but this material needs further study in the light of recent discoveries. A longirostrine crocodylian, *Harpacochampsia camfieldensis*, from the Miocene Camfield Beds in the Northern Territory (Megirian, Murray & Willis 1991) may not have been a mekosuchine (Fig. 42.2H, I).

#### 42. BIOGEOGRAPHY AND PHYLOGENY OF THE CROCODYLIA

Non-mekosuchine crocodylians were present in the late Tertiary. *Crocodylus porosus* first appears in the Allingham Formation of the Pliocene in north-eastern Queensland (Molnar 1979). Fossils of *Crocodylus johnstoni* appear in the Pleistocene of Queensland's Gulf country (Willis & Archer 1990) shortly after, in geological terms, the native mekosuchine crocodylians apparently became extinct. This extinction has been attributed to competition with the 'invaders' from Asia (Archer *et al.* 1991) leaving the present impoverished crocodylian fauna of Australia.

Throughout the southwestern Pacific region a diversity of endemic mekosuchine crocodylians has become extinct, to be replaced by a pattern of endemic species of *Crocodylus*, superimposed on the range of seagoing *C. porosus*.