Turtles as diapsid reptiles

OLIVIER RIEPPEL

Rieppel, O. (2000). Turtles as diapsid reptiles. — *Zoologica Scripta 29*, 199–212.
Recent molecular studies of amniote relationships show turtles to be diapsid reptiles, related to the archosauromorph branch of saurian phylogeny. This conflicts with palaeontological data which shows turtles to be related either to anapsids, or to the lepidosauromorph branch within diapsids. Archosauromorph relationships of turtles have previously been proposed on the basis of neontological (mostly soft anatomy) characters. This paper reviews the neontological character evidence for turtle relationships and shows that most, but not all, of these characters are invalid in the reconstruction of turtle relationships within Amniota.

Olivier Rieppel, Department of Geology, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605–2496, USA. E-mail: rieppel@fmnh.org

Introduction

The structure of the temporal region of the skull and its bearing on reptile classification remained a controversial issue at the end of last century (Cope 1893; Baur 1889, 1895; and references therein). When the idea of classifying reptiles on the basis of the pattern of temporal fenestration of the skull began to take shape, Osborn (1903) suggested that the class Reptilia should be subdivided into two main branches, the Synapsida (with no or a single temporal fenestra) which eventually would give rise to mammals, and the Diapsida (with two temporal fenestrae) which would give rise to birds. The ancestral synapsid condition would be characterized by the absence of temporal fenestration, as represented by 'cotylosaurs' and turtles. That the turtle skull would primitively exhibit a completely closed temporal region was a statement in line with opinions expressed earlier (Baur 1889, 1895; Cope 1893), and which was later sustained by Hay (1905), Watson (1914), and Williston (1917). Where a reduction occurred in the dermal roofing of the temporal region of the turtle skull, as is, indeed, the case in most extant species, it was viewed as the result of emargination from the ventral, and/or posterior, margins of the cheek region of the skull, rather than of temporal fenestration. Williston's (1917) highly influential paper provided what was to be a long-lived framework for reptile classification, as he introduced the name Anapsida to refer to those reptiles with a closed temporal region of the skull, i.e. the 'Cotylosauria' and the Chelonia (Testudines).

However, this view did not remain unchallenged. Goodrich (1916) claimed that reptiles do not form a monophyletic assemblage. He recognized the Sauropsida (including birds) and the Theropsida (including mammals) as two separate amniote lineages that originated from a 'protosaurian' branch. The presence of a hooked fifth metatarsal, and heart structure, placed turtles within the sauropsidan lineage. Although Goodrich (1916: 273) considered it more likely that the temporal region of the turtle skull was secondarily closed, he admitted that the view might still be held that turtles 'may have branched off from the Sauropsidan stem when the heart and metatarsal had become specialized, but the roofing [of the skull] had not yet been pierced.' In his monograph on vertebrate structure and development, Goodrich (1930) emphasized differences of bone configuration in the temporal region of true anapsids and turtles in support of his claim that a complete roofing of the temporal region is secondarily acquired in turtles where it occurs.

In an address delivered to the French Academy of Sciences in Paris, Boulenger (1918) emphasized that the closed temporal region of turtle skulls does not compare to the pattern observed in stem reptiles, and he used the fenestrated pelvis and the hooked fifth metatarsal in support of affinities of turtles with diapsids such as *Sphenodon*. Broom (1924: 50) concluded that 'Those who regard the structure of the temporal region of the skull as the safest guide to affinity will naturally place the chelonians either with the primitive mammal-like reptiles or the cotylosaurs; those who hold that more reliance can be placed on the structure of the girdles and limbs will be more impressed with the affinities to the primitive diapsids such as *Sphenodon*.' Accepting the Diapsida, Synapsida, and Cotylosauria (with a fully roofed skull) as valid subgroups of Reptilia, Broom (1924) recognized a fourth group, derived from an 'ancestor of the diapsidan line' (Broom 1924: 62) which

would include turtles along with placodonts and sauroptery-gians. Among neontologists, a diapsid status of turtles was supported by Lakjer (1926) on the basis of the jaw adductor musculature, whereas Hofsten (1941), like deBeer (1937) before him, specifically suggested archosaurian (crocodiles and birds) affinities of turtles on the basis of several characters, most notably the developmental fate of the proatlas pleurocentrum, and the secondary subclavian arteries.

Discrepancies of opinion such as these set the stage for a comprehensive investigation of turtle relationships within reptiles, both fossil and extant, by Gregory (1946). He not only compared living and fossil turtles with placodonts and pareiasaurs, but also with diadectomorphs and captorhinids, then perceived as basal amniotes and included with pareiasaurs and procolophonids in the 'Cotylosauria', and even with the anamniote seymouriamorphs. He concluded, like some earlier authors, that Testudines were derived from Palaeozoic 'cotylosaurs', arguing however, that among 'cotylosaurs', pareiasaurs approached Triassic turtles more closely than diadectids. A diadectid origin of turtles was shortly thereafter proposed by Olson (1947). In the wake of these studies, the anapsid condition of the turtle skull became accepted throughout the palaeontological community. Romer (1968), in a loose sense, suggested procolophonids as turtle ancestors, while modern cladistic analyses showed turtles to be related either to captorhinids (at the base of his Eureptilia, including synapsids and diapsids: Gaffney 1980), or to pareiasaurs (Lee 1995, 1997a), or procolophonids (Laurin & Reisz 1995), respectively, within the Parareptilia (*sensu* Gauthier *et al.* 1988a). Predicated on the assumption that turtles are anapsid, all of these studies restricted the analysis of phylogenetic interrelationships of turtles to Palaeozoic reptiles. However, broadening the basis of comparison by inclusion of Mesozoic and extant reptile clades in the analysis echoed Broom's (1924) conclusions as turtles were found to be related to Saurop-terygia (Mesozoic marine reptiles), the two clades nesting at the base of the lepidosaurian lineage which includes *Sphenodon*, the squamates, and all their fossil relatives (deBraga & Rieppel 1997; Rieppel & Reisz 1999). This result is in partial agreement with other, neontological studies which place turtles within diapsids (Løvtrup 1977, 1985; Gardiner 1993), but it differs from these analyses, and in particular from recent phylogeny reconstructions based on molecular data (Platz & Conlon 1997; Kirsch & Mayer 1998; Zardoya & Meyer 1998; Hedges & Poling 1999; Mannen & Li 1999; Mindell *et al.* 1999), which all relate turtles to the archosaurian lineage (crocodiles and birds and all their fossil relatives) of the Diapsida.

One of the latest molecular analysis of turtle relationships (Kumazawa & Nishida 1999) quotes deBeer (1937), and Ax (1984), for morphological evidence in support of archosaur affinities. These latter authors specifically identify the Triassic fossil reptile *Trilophosaurus* as a potential turtle relative, as it

secondarily lost the lower temporal fenestra (Gregory 1944). The present paper reviews the neontological characters which have been claimed to support archosaur affinities of turtles (deBeer 1937; Remane 1959; Løvtrup 1977, 1985; Gardiner 1993; Ax 1984). These statements of primary homology (*sensu* dePinna 1991) have also been discussed from a different angle by Gauthier *et al.* (1988a) in their review of the purported monophyly of Haematothermia.

Characters that support archosaur affinities of turtles

The proatlas

In adult reptiles, the proatlas, if present, is represented by paired (fused in crocodiles) neural arch elements located between the occiput and the atlas neural arch (Romer 1956). The development and ultimate fate of the pleurocentrum (centrum) and hypocentrum (intercentrum) of the proatlas have remained somewhat controversial, and require critical reassessment (Bellairs *et al.* 1981). Currently, it is assumed that the hypocentral component either degenerates, or fuses into the occiput (Starck 1979). By contrast, earlier literature summarized in Goodrich (1930) suggests that the odontoid process of the axis of *Sphenodon* (reptiles), *Echidna* and *Bradypus* (mammals) incorporates not only the atlas centrum, but a second chondrification centre which is interpreted as pleurocentrum of the proatlas. Goodrich (1930) suggested that this is the general amniote pattern, although Hayek (1924) had concluded that the pleurocentrum of the proatlas fuses to the odontoid process in squamates, *Sphenodon* and mammals, whereas it forms the occipital condyle in turtles, crocodiles, and birds. DeBeer (1937) referred to the fact that the basal plate of the embryonic neurocranium lies hypochordal in *Sphenodon* and squamates (see Kamal 1965; for variability of this relation), but parachordal in turtles, crocodiles and birds. This results in the development of the occipital condyle below the notochord in lepidosaurs, whereas the notochord is enclosed in the occipital condyle in turtles, crocodiles and birds. From these topological relations deBeer (1937) concluded that the proatlantal pleurocentrum fuses to the odontoid process in lepidosaurs (and mammals), whereas it is incorporated into the occipital condyle in turtles, crocodiles and birds, and that the occipital condyle in these two groups therefore is not homologous.

In reptiles which show the notochord passing through the developing occipital condyle there usually persists a notochordal pit on the posterior surface of the ossified condyle, which is not only present in many stem-group reptiles of both parareptilian and eureptilian affinity (as well as in synapsids: R.R. Reisz, personal communication), but also in juvenile skulls of turtles and crocodiles. A notochordal pit on the occipital condyle is also present in basal saurop-terygians, a clade considered to be related to turtles (deBraga &

Rieppel 1997; Rieppel & Reisz 1999), and given its distribution, must represent the plesiomorphic amniote condition. The parachordal development of the occipital condyle therefore does not support the monophyly of a clade including turtles and archosaurs. Instead, the hypochordal development of the occipital condyle is a synapomorphy of Lepidosauria (*Sphenodon*, squamates, and their fossil relatives).

The epipterygoid

Lovtrup (1985: 466) lists 'epipterygoid joining parietal' as a synapomorphy of turtles and crocodiles. In fact, an ascending process of the palatoquadrate is vestigial or absent in crocodiles, such that their adult skull does not incorporate an epipterygoid ossification (Bellairs & Kamal 1981). The same is true for birds (deBeer 1937). Among basal archosauromorphs, *Trilophosaurus* shows a tall epipterygoid which is disarticulated, however. It might have contacted a groove on the lower surface of the parietal (Gregory 1944), but that same groove might also have accommodated the endocranial taenia marginalis instead. *Hyperodapedon*, a representative of rhynchosaurs which are again classified at the base of archosauromorphs, has been described to be similar to *Sphenodon* in that the narrow dorsal process of the epipterygoid closely approaches the parietal, probably separated from the latter by the taenia marginalis (Benton 1983).

By contrast, cryptodire turtles show a broad epipterygoid (not known for *Proganochelys* and pleurodires: Gaffney 1979, 1990), which together with a laterally descending flange of the parietal forms a secondary lateral wall of the braincase. Sauropterygians likewise show a broad epipterygoid — parietal contact (except in *Placodus*, where this contact is relatively narrow: Rieppel 1995). In the dried adult skull of *Sphenodon*, the dorsal head of the epipterygoid remains narrowly separated from the parietal by the neurocranial taenia marginalis which is intercalated between these two elements. In squamates other than snakes, the dorsal head of the epipterygoid usually contacts the parietal, the crista alaris of the pootic, or both.

A contact of the epipterygoid with the parietal thus does not support archosaurian affinities of turtles. On the basis of present knowledge, it supports monophyly of a clade including turtles and sauropterygians (deBraga & Rieppel 1997; Rieppel & Reisz 1999), and is convergently derived in squamates. In mammals, the epipterygoid is transformed by the addition of membrane bone (*Zuwachsknochen*) to form the alisphenoid, an element of the secondary lateral wall of the braincase (Presley & Steel 1976).

Relations of the interhyal process

DeBeer (1937) noted that turtles share with crocodiles, but not with *Sphenodon* or squamates, an embryonic connection of the columella auris with the posterior part of Meckel's cartilage (retroarticular process) via the pars interhyalis, a

character used in support of archosaurian relationships of turtles by Løvtrup (1985).

In turtles, the interhyal process of the insertion plate of the extracolumella is in a ligamentous connection with the retroarticular process of Meckel's cartilage. The development of the columella auris in crocodiles has been described in detail by Goldby (1925). The interhyal process of the extracolumellar insertion plate becomes connected with the developing ceratohyal (stylohyal of deBeer 1937), which in turn becomes temporarily connected to the retroarticular process of Meckel's cartilage, a primitive relation of these latter two elements for gnathostomes. A cartilaginous connection between the interhyal and ceratohyal in the fully formed structure is interpreted as epihyal (Bellairs & Kamal 1981).

Although there is connectivity between the extracolumellar insertion plate and the retroarticular process in turtles and crocodiles via the interhyal process, this connectivity is established differently in the two groups, and in itself may reflect a primitive gnathostome relation.

Vascular bone

Lovtrup (1985: 466) suggested the presence of vascular compact bone to be a character which unites turtles with crocodiles. He cited Enlow (1969) with respect to this character, but Enlow (1969: 51) stated that 'the bone itself conforms to the same basic plan of organization and undergoes the same process of remodeling that characterize the skeletal tissues of virtually all tetrapods.'

The typical reptilian long bone shows an outer cortex built of dense, laminar bone, surrounding the inner cancellous bone. The cortex may be composed of endosteal or periosteal bone. Endosteal cortex replaces inner cancellous bone at the metaphysis (the funnel-shaped end of long bones) during longitudinal growth of the element. Periosteal cortex is deposited on the surface of the bone as the elongated diaphysis increases in diameter (Enlow 1969; Figs 1, 2).

Turtle long bones show a well developed inner cancellous region surrounded by cortical bone of variable histology. The tissue may be composed of circumferential lamellae with little or no vascularization, or it may contain numerous primary vascular canals arranged in concentric circumferential rows (deRicqlès 1976: 127). Arrangement of primary vascular canals in circumferential concentric rows is a fundamental pattern of cortical bone for fossil anapsids, basal synapsids (pelycosaurs), and it is also found in sauropterygians (deRicqlès 1976). Conversion of primary periosteal cortex into endosteal trabecular bone takes place during continuous circumferential growth, and may result in turtles in secondary Haversian reconstruction (deRicqlès 1976).

The cortex of the long bones of crocodiles contains numerous circumferential lamellae with one or several rows

of longitudinal primary vascular canals. Haversian substitution may occur at the endosteal margin of the cortex (deRicqlès 1976).

Sphenodon resembles squamates, but differs from turtles and crocodiles, in that the shafts of the long bones are devoid of inner cancellous bone (present in the epiphyses), and the periosteal tissue is avascular, or contains only few primary vascular canals (deRicqlès 1976: 136). Non-ophidian squamates again show long bones which contain spongy bone tissue in the epiphyseal and metaphyseal region only, and with periosteal bone that is completely avascular (deRicqlès 1976).

As advocated by Gauthier *et al.* (1988a), the conclusion must be that vascular cortical bone is the plesiomorphic tetrapod condition, whereas the avascular periosteal bone of *Sphenodon* and squamates is a synapomorphy of lepidosaurs.

Epiphyses

Løvtrup (1985: 466) cites the presence of 'cartilaginous cones at end of long bones' as a character shared by turtles and crocodiles. This character reflects nothing but the absence of separate epiphyseal ossification centres in these two groups, a plesiomorphic character of amniotes (Gauthier *et al.* 1988a). Separate epiphyseal ossification centres are a synapomorphy of lepidosaurs within reptiles (Haines 1969; Gauthier *et al.* 1988b), and as such have no bearing on the analysis of turtle relationships. The presence of large cartilaginous cones at the end of long bones in turtles, crocodiles and birds was identified as a possibly primitive feature of tetrapods by Haines (1969), but is considered as nothing but a reflection of the geometry of the cartilage model of long bones by Gauthier *et al.* (1988a). It remains unclear why Løvtrup (1985) treats the presence of cartilage cells in the epiphyses of turtles and crocodiles as a separate character supporting close phylogenetic relationships of the two groups.

Thyroid and cricoid cartilages

Løvtrup (1985: 466) referred to the thyroid and cricoid cartilages in support of a relationship between turtles and crocodiles.

The laryngotracheal skeleton of reptiles is generally composed of the paired arytenoid cartilages, the unpaired cricoid cartilage, and tracheal rings (terminology *sensu* Göppert 1900, 1937). Tracheal rings are often not clearly separated from the cricoid cartilage. The cricoid generally forms an anterior, ventromedial process (processus ventralis medialis) which assumes different shapes and functions in the different groups. Not as consistently developed is an anterior dorsomedial process (processus medialis dorsalis) of the cricoid.

In turtles, the anterior dorsomedial process of the cricoid along with adjacent anteromediodorsal parts of the cricoid may separate from the main body of the latter (Göppert 1937). The laryngotracheal skeleton then consists of an unpaired anterior dorsomedial element, the procricoid, the main body of the cricoid, the paired arytenoid cartilages, and the tracheal rings (terminology of Göppert 1900, 1937). Henle (1839) homologized the procricoid with the cricoid of mammals, and the remaining larger part of the cricoid with the thyroid of mammals, and hence referred to the undivided cricoid of other reptiles as a 'cricoid-thyreoid'. Although this homology is not tenable on developmental grounds (Göppert 1937), the cricoid of turtles (*sensu* Göppert 1900) often continues to be termed thyroid or thyreocricoid, whereas the procricoid (*sensu* Göppert 1900) is often referred to as cricoid (Schumacher 1973).

The laryngotracheal skeleton of crocodiles has again been described as being composed of a cricoid (*sensu* Göppert 1900, 1937; thyreocricoid of Schumacher 1973), arytenoid cartilages and tracheal rings. An anterior dorsomedial process (processus medialis dorsalis) has not been reported for crocodiles. Instead, the anterior margin of the dorsal roof of the cricoid is recessed (Schumacher 1973). Likewise, a procricoid (*sensu* Göppert 1937) has never been reported for crocodiles. However, Söller (1931) has shown for *Alligator* and *Caiman* (Alligatoridae) that the cartilage of the recessed portion of the dorsal roof of the cricoid is discontinuous with the cartilage of the remainder of the cricoid ('*Zwischenknorpel*' of Söller 1931), although the entire cricoid is enclosed in a continuous perichondrium. Whether such a separation of the dorsal roof of the cricoid also occurs in other crocodiles remains unknown, but the morphology of the laryngotracheal skeleton of crocodiles does not show any special similarity to that of turtles.

Scales

Lovtrup (1977: 182) lists the 'type of scutes' as a shared derived character of crocodiles and turtles. This character is taken from Boas (1931), who referred to the incomplete separation or fusion of epidermal scutes on the head of crocodiles and turtles. Boas (1931) also compared the rhamphotheca of turtles to fused epidermal scutes. But whereas the latter character is an autapomorphy for turtles, the poor differentiation of epidermal scutes on the head in crocodiles and turtles reflects little more than the fact that these two taxa are not squamates, for which the differentiation of the epidermis is an autapomorphy.

Tarsus of lower eyelid

Løvtrup (1985: 466) lists the absence of a cartilaginous disc embedded in the lower eyelid as a character uniting turtles and crocodiles. The lower eyelid of a typical nonophidian squamate contains a cartilaginous plate, the tarsus, and it is the lower eyelid which mostly effects closure of the eye (Underwood 1970). The same is true for *Sphenodon*, although the nature of the tarsus is specified as 'tough' only by Walls

(1942: 421). Turtles lack a tarsus in the lower eyelid, but as in lepidosaurs, it is again the latter which is covering the closed eye to the greater part. Crocodiles also lack a cartilaginous tarsus in the lower eyelid, but in this group it is the upper eyelid which mainly closes the eye, and it contains a bony tarsus (absent in turtles: Underwood 1970).

The eye lids of amphibians, where present, have no cartilaginous or fibrous tarsus. The lower eyelid of birds has a fibrous tarsus (except in parrots: Walls 1942), and in mammals both the upper and lower eyelid may have a fibrous tarsus (Rochon-Davigneaud 1972). Outgroup comparison therefore suggests that the presence of a fibrous tarsal plate in the lower eyelid is an amniote autapomorphy, its chondrification is a synapomorphy of squamates (or of lepidosaurs?), and its absence is a loss shared by turtles and crocodiles. Walls (1942) considered the loss of the tarsal plate to be correlated with aquatic habits. If correct, this character would likely be subject to convergence, and also would support the scenario for an aquatic origin of turtles developed by Rieppel & Reisz (1999). Gauthier *et al.* (1988a) found the distribution of tarsi, and their questionable homology with palpebrals and supraorbital bones, to be of limited value in phylogenetic analysis.

Jacobson's organ
Mammals, *Sphenodon* and squamates share the presence of a Jacobson's organ which develops as a medial or medioventral outpocketing of the nasal pit (Parsons 1970). Crocodiles and birds show the initial embryonic development of such an outpocketing, but it disappears during further development, and is absent in late embryos or adults. Turtles show no indication of a medial or medioventral outpocketing of the nasal pit at any time of their ontogeny. Gaffney (1980) considered the absence of Jacobson's organ a plesiomorphy of turtles, and its presence a potential synapomorphy linking synapsids and Diapsids (his Eureptilia). However, if turtles are included in diapsids on the basis of other evidence, it might be argued that the reduction (crocodiles, birds), or complete loss (turtles) of Jacobson's organ is a character supporting archosaur affinities of turtles (Ax 1984).

The nature of the nasovomeral organ, its definition, and its distinction from Jacobson's organ has previously received a lot of attention (Seydel 1895; Matthes 1934; Parsons 1970; Duellman & Trueb 1986). The most complete recent discussion of this character complex is that of Gauthier *et al.* (1988a), who concluded that archosaurs (crocodiles and birds) are diagnosed by the absence of all components of the nasovomeral organ in the adult, whereas a nasovomeral organ is present in turtles (Seydel 1896).

Tendon of nictitans to pyramidalis muscle
Løvtrup (1985: 466) cites the attachment of the tendon from the nictitating membrane to a pyramidalis muscle as a character shared by turtles and crocodiles. Underwood (1970) considers the nictitating membrane of amniotes to be homologous to the lower eyelid of amphibians, which itself has a tendon which arises from its margin and passes posteriorly around the eyeball and the retractor bulbi muscle to attach to the medial wall of the orbit. The tendon has a fibrous connection to the retractor muscle. The relations of the nictitating membrane are similar in *Sphenodon*, where the tendon first attaches to the lateral division of the retractor bulbi, from where it continues to the medial side of the orbit.

The retractor bulbi is split in *Sphenodon* (as it also is in turtles and crocodiles), and the bursalis muscle of squamates other than snakes is thought to be derived from the lateral division of the retractor muscle of *Sphenodon*. In nonophidian squamates ('lizards'), the tendon of the nictitans membrane is enfolded by the bursalis muscle from where it continues on to attach to the medial wall of the orbit.

The tendon of the nictitating membrane of crocodiles terminates in a pyramidalis muscle which inserts into the back of the eyeball, and which is innervated by the same cranial nerve (abducens) which also innervates the retractor bulbi. The tendon no longer reaches the medial wall of the orbit. Underwood (1970) considers it likely that the pyramidalis muscle again differentiated from the lateral division of the retractor bulbi. Essentially the same condition as seen in crocodiles is shared by turtles, where the pyramidalis muscle has a second tendon, however, which runs to the lower eyelid (Walls 1942). Birds have lost the retractor bulbi, but developed a fan-shaped bursalis muscle, and the tendon of the nictitating membrane is operated by a small pyramidalis muscle. In mammals, finally, the nictitating membrane is variably developed, but never related to musculature behind the eyeball as it is in Reptilia. Movements of the nictitans are passive in mammals (Walls 1942).

Given Underwood's (1970) homologization of the lower eyelid of amphibians with the nictitating membrane of amniotes (a homology disputed by Walls 1942), outgroup comparison would suggest that within amniotes, *Sphenodon* represents the most plesiomorphic condition (a conclusion also put forward by Walls 1942). This indicates that the differentiation of a pyramidalis muscle for the tendon of the nictitating membrane is a potential synapomorphy shared by turtles, crocodiles and birds (see also Gauthier *et al.* 1988a; who reached the same conclusion). The differentiation of a bursalis muscle is an autapomorphy of squamates (lost in snakes).

Another way to optimize these characters starts with the assumption that the nictitans is a neomorph of amniotes (as suggested by Walls 1942), and hence an autapomorphy of the group. Where present in mammals, the retractor bulbi is single or divided into four segments (Saban 1968).

Subdivision of the retractor bulbi into two compartments is a character of Reptilia. The lateral segment can be differentiated either as a bursalis (nonophidian squamates), or as a pyramidalis, which again remains a character uniting turtles with archosaurs.

Ciliary processes

Løvtrup (1985: 466), and Gardiner (1993), suggested the presence of ciliary processes to be another character uniting turtles with crocodiles. Differentiation of the ciliary body in the vertebrate eye makes it necessary to distinguish a ciliary fold from ciliary processes (Walls 1942). Although this distinction is primarily a quantitative one, it also accounts for different physiological functions. The ciliary body of amphibians differentiates ciliary folds only, except for a single mid-ventral fold large enough to be considered a process (Walls 1942). Ciliary processes are present in turtles, crocodiles, birds and mammals, and whereas Reptilia show fusion of the tips of the ciliary processes (where present) with the lens, mammals are distinguished by the differentiation of the ciliary web (Walls 1942: 668). Ciliary processes are absent in *Sphenodon* and squamates (the ciliary body is much reduced in snakes), which by outgroup comparison must be considered a secondary loss (as was also suggested by Underwood 1970), and as such a synapomorphy of lepidosaurs (Gauthier *et al.* 1988a). The presence of ciliary processes therefore does not support archosaur relationships of turtles.

Single penis

Hofsten (1941), Løvtrup (1977, 1985), and Gardiner (1993), suggested that the single penis with erectile tissue is a character which unites turtles and crocodiles. Amphibians have no true male intromittent organs; caecilians and the tailed frog *Ascaphus* use the everted cloaca for internal fertilization.

Sphenodon and most birds lack a male intromittent organ. Squamates differentiate paired hemipenes from the lateral walls of the cloaca, which constitute an autapomorphy of the group (Gauthier *et al.* 1988a). Turtles, crocodiles, and some basal birds differentiate a single penis from the ventral wall of the cloaca, enclosing paired corpora cavernosa composed of erectile tissue (Giersberg & Rietschel 1968).

The penis of mammals also differentiates from the ventral wall of the cloaca, but is more highly differentiated than that of Reptilia and the urethra is surrounded by a single corpus spongiosum. Nevertheless, similarities in early stages of development of the male intromittent organ in reptiles and mammals (Raynaud & Pieau 1970, 1978) suggest that the differentiation of a single penis from the ventral wall of the cloaca is a basal amniote character, as amniote reproduction necessitates internal fertilization. Absence of a male intromittent organ in *Sphenodon* and most birds would be secondary (Gauthier *et al.* 1988a).

Secondary subclavian artery

Hofsten (1941), Ax (1984), and Løvtrup (1985) championed the secondary subclavian artery as a character uniting turtles with crocodiles and birds. According to Hofsten (1941), the subclavian arteries, which supply the forelimbs, originate from the right aortic arch in *Sphenodon* and squamates other than snakes. In turtles, crocodiles, and birds, the origin of the subclavian arteries has been shifted rostrally, as they arise from the carotid arches. He accordingly referred to these vessels as secondary subclavian arteries.

The relationships of the subclavian arteries to the aortic arches and their derivatives is not as simple as suggested by Hofsten (1941; see also Gauthier *et al.* 1988a). Complications in the assessment of homologies of the subclavian artery arise from two factors. The embryonic limb bud is vascularized by several intersegmental arteries, as can be observed in the early chick embryo. In adult tetrapods, however, only a single artery persists, commonly referred to as arteria subclavia, although this vessel does not derive form the same intersegmental artery in various groups: in humans, the subclavian artery originates from the sixth intersegmental artery which originates from the neck region (Giersberg & Rietschel 1968). A second complication results from posterior displacement of the heart in the various tetrapod groups.

Originally, the subclavian arteries branch off from the unpaired dorsal aorta, as is the case in urodeles. Through basal bifurcation of the aorta, the subclavian arteries become vessels of the aortic arch (arcus aortae), as is the case in frogs (Hafferl 1933; Stephan 1950).

Reptiles other than birds retain paired aortic arches. The paired carotids (carotis communis of the left and right side, each in turn giving rise, by bifurcation, to the internal and external carotids) branch off the right aortic arch in all reptiles, either separate, or with a common stem (carotis primaria). After the origin of the paired carotids and of the vertebral arteries, the subclavian arteries originate from the right aortic arch, either separately, or with a common root, both in *Sphenodon* and nonophidian squamates (Hafferl 1933).

In crocodiles, paired arteriae anonymae (anonymous arteries) originate from the truncus arteriosus at the very base of the right aortic arch. The right one bifurcates dorsal to the coracoid, giving rise to the subclavian artery and the right external carotid. Before it bifurcates into these same vessels, the left anonymous artery gives rise to the carotis subvertebralis, which in its middle section represents the fused internal carotids (Hafferl 1933). The root of the right internal carotid usually degenerates, or may be retained in a vestigial condition. The carotis subvertebralis bifurcates below the first cervical vertebra, giving rise to the paired cerebral carotids (carotides dorsales of Hafferl 1933).

In turtles, two large vessels originate from the proximal part of the right aortic arch, termed trunci anonymi. These

subdivide, each giving rise to the subclavian artery and the carotis communis (Hafferl 1933). Hofsten (1941) compares turtles to crocodiles in the sense that the origin of the subclavian artery is shifted craniad in both these taxa, i.e. from the aortic arch (as in *Sphenodon* and non-ophidian squamates) on to the root of the carotid arches. Details of the circulatory pattern in these two groups are quite different, however.

In birds, two collateral anonymous arteries, also termed arteria brachiocephalica dextra et sinistra, originate from the base of the aortic arch. These in turn soon bifurcate to give rise to the left and right carotids (carotis communis) and subclavian arteries.

Hafferl (1933) hypothesized that embryonic turtles and crocodiles still retain the root of a vessel branching off from the right aortic arch which vascularizes the limb bud. Later, this vessel would establish a secondary anastomosis with the base of the third aortic arch which represents the base of the carotid system. After degeneration of the primary connection to the right aortic arch during subsequent development, the subclavian artery retains a single common root with the carotid arch, i.e. the arteria (truncus) anonyma(us). This, indeed, is the developmental pattern observed in birds.

Mammals differ from Reptilia in that they retain the left, rather than both or only the right (birds) aortic arch. The branching pattern of vessels originating from the left aortic arch in mammals is variable: both carotids and both subclavian arteries can have separate origins from the aortic arch; the carotis and the subclavian arteries of the right or of both sides can share a common root (truncus brachiocephalicus); the carotids can share a common root while the subclavian arteries originate separately from the aortic arch; or the subclavian arteries can have a separate origin from the common root of the carotids (see Barone 1972; for further details). In monotremes, the right carotid and the right subclavian artery have a common stem, whereas the corresponding vessels from the left side originate separately from the aortic arch; in marsupials, both carotids have a common stem with the right subclavian artery, whereas the left subclavian artery has a separate origin from the aortic arch (Hafferl 1933). Throughout mammals, however, variation of this character complex is extensive, and may affect even closely related species.

In summary, the differentiation of the origin of the subclavian arteries from the aortic arches or from the carotid arches is highly variable, and its systematic significance needs critical reassessment. Outgroup comparison with amphibians, as well as the ontogeny criterion of character polarization, suggest that the rostral shift of the origin of the subclavian arteries from the aortid arch to the carotid arch is a derived character shared by turtles, crocodiles, and birds. Mammals, however, demonstrate the plasticity of this character complex, and the potential for convergence. Variability has also

been recorded for turtles, as a specimen of *Emys* showed the carotis communis to branch off directly from the aortic arch (Bojanus, quoted in Göppert 1900) The ultimate criterion of homology would be the identification of the intersegmental artery from which the subclavian artery originates in the various groups. The extensive variation observed in mammals raises concerns as to the utility of this character complex for higher level phylogeny reconstruction, and calls for a more extensive survey of this character complex within Reptilia.

Egg caruncle
Løvtrup (1977) thought the absence of a true egg tooth, i.e. the presence of an egg caruncle, to be a character which unites turtles with crocodiles. This character is invalid, because the hatching Sphenodon also pierces the egg membrane with a horny caruncle (Moffat 1985; Gauthier et al. 1988a).

Lime impregnated shell
Løvtrup (1977) used the lime-impregnated egg shell as a synapomorphy linking turtles with crocodiles (and by extension, with birds).

The lime-impregnated shell of most geckos (and *Dibamus*) is certainly separately derived within lepidosaurs, because *Sphenodon* (Moffat 1985), as well as nonscleroglossan squamates, have no calcareous egg shell matrix. Nevertheless, most squamate egg shells show a superficial encrustation with calcium-carbonate (Schleich & Kästle 1988).

The egg-shells of turtles, crocodiles and birds are lime-impregnated, but in turtles the calcium carbonate of the egg shell is in the form of aragonite, whereas in crocodiles, birds, and gekkonine squamates, the calcium carbonate of the egg shell is in the form of calcite (Kelly 1901; Krampitz *et al*. 1974; Ewert 1985; Ferguson 1985). The amino acid composition of the egg shell also differs between turtles and crocodiles: with respect to the amount of histidine, for example, crocodiles differ markedly from turtles but resemble ratite birds (Krampitz *et al*. 1974). On the basis of these data, egg shell composition does not specifically support archosaur affinities of turtles.

Gardiner (1993) added the presence of pore canals in the egg membrane (membrana testacea) as a special similarity shared by turtle and archosaur eggs. The innermost surface of the egg membrane of crocodiles shows pores which represent the inner openings of a complex system of vacuities or spaces (cavity systems of Kriesten 1975) enclosed in the egg membrane that relate the content of the egg to the external environment (Ferguson 1985). By contrast, the inner surface of the egg membrane of turtles has been described as 'featureless' (Packard 1980; Ewert 1985), although turtles incorporate in their egg membrane similar complex spaces as crocodiles and squamates (Kriesten 1975). Kriesten (1975)

does report some similarities in the egg membrane of turtles and crocodiles, such as fusion of fibers resulting in aggregates, and the particular differentiation of the cavity system, but other characters such as the shape of the osmiophilic cores are shared by *Alligator* and *Iguana*. At the bottom line, not enough is known about the properties of the egg membrane in support of archosaur affinities of turtles.

The thymus

Løvtrup (1985: 466) referred to the nonlobed thymus in support of archosaur affinities of turtles. In fact, the thymus of turtles is lobulated, as is that of crocodiles and birds (Bockman 1970). The thymus of *Sphenodon* and squamates is generally nonlobulated, but variations may occur: a lobulated thymus has been recorded for *Psammodromus* (Bockman 1970). The thymus of mammals also is lobulated (Arvy 1973), as is that of urodeles and caecilians (Giersberg & Rietschel 1968; Duellman & Trueb 1986).

As concluded by Gauthier *et al.* (1988a), outgroup comparison suggests that the lobulate thymus is plesiomorph at the level of amniotes, and the non-lobulate thymus is a synapomorphy of lepidosaurs, with the potential of reversal within that group.

The pituary gland

Løvtrup (1985: 466), quoting Wingstrand (1951), refers to the sinus cavernosus as a synapomorphy shared by turtles and crocodiles. Wingstrand (1951) quoted Shindo (1915), who found that embryos of reptiles and mammals share a primordial vessel located behind Rathke's pouch that links the vena capitis medialis of both sides (vena retrohypophysea; see also Goodrich 1930: 533). In birds, a sinus cavernosus is derived from the retrohypophyseal vein, and as such is not (Wingstrand 1951), or only partially homologous with the mammalian sinus cavernosus (i.e. sinus intercavernosus posterior: Enemar 1960; the sinus cavernosus proper of mammals is derived from the vena capitis medialis [Shindo 1915]).

For birds, the sinus cavernosus is defined as a paired structure, located on either side of the fossa hypophysialis in the floor of the braincase (sella turcica), and connected with each other by two transverse veins passing in front and behind the hypophysis (Baumel 1993: 447). The cavernous sinus drains the hypothalamic region of the brain and the hypophysis. Wingstrand (1951) described the sinus cavernosus of birds as a cavernous system surrounding the hypophysis, with its greatest extension along the latter's lateral sides. Wingstrand (1951: 294) hypothesized that the 'sinus cavernosus of birds might correspond to the median parts of the vena (retro-) hypophysea in reptiles, and when a sinus cavernosus is formed as in chelonians and crocodiles it may be regarded as homologous with the avian one'.

The term sinus cavernosus as used by Wingstrand (1951) for birds denotes a structure derived entirely from the retrohypophyseal vein, and hence does not refer to the same structure in mammals, where the sinus cavernosus is derived from the vena capitis medialis (Shindo 1915). The latter is, however, the meaning of the term 'sinus cavernosus' as used by Bojanus & Rathke (cited in Grosser & Brezina 1895) in the description of the cephalic venous system of turtles and crocodiles.

The sinus cavernosus of turtles is located medial to the epipterygoid, but lateral to the dorsum sellae and sella turcica housing the hypophysis, as it is floored by the sulcus cavernosus on the dorsal surface of the pterygoid. The sulcus cavernosus essentially floors the cavum epiptericum, which in turtles is an intracranial (but extramural) space because of the formation of a secondary lateral braincase wall by the epipterygoid (cryptodires) and parietal (pleurodires). The veins of the nasal and orbital region drain into the sinus cavernosus, which wraps around the roots of the maxillary and mandibular branches of the trigeminal nerve, passing essentially below and medial to the latter. Posteriorly, the venous system leaves the cavum epiptericum through the foramen cavernosum leading into the canalis cavernosum which houses the lateral head vein (Gaffney 1972). In turtles therefore the vena capitis medialis persists in the orbitotemporal region (cavum epiptericum), but is replaced posteriorly, i.e. lateral to the otic capsule (lateral to the facialis, glossopharyngeus and vagus nerves) by the vena capitis lateralis during embryonic development (Goodrich 1930).

Grosser & Brezina (1895) note close similarities in the organization of the orbitotemporal veins in nonophidian squamates as compared to turtles. The orbital veins drain into a sinus which in nonophidian squamates relates to the trigeminal nerve in an identical manner as in turtles, and which again represents a persisting part of the vena capitis medialis (Grosser & Brezina 1895; Goodrich 1930). More posteriorly, the vein comes to lie lateral of the facialis and vagus nerves, and therefore constitutes a vena capitis lateralis. The only difference between nonophidian squamates and turtles noted by Grosser & Brezina (1895) is the extracranial position of the persisting part of the vena capitis medialis in nonophidian squamates, compared to the supposedly intracranial position of the sinus in turtles. However, as noted above, the sinus lies extramural but intracranial in turtles, in the cavum epiptericum which is enclosed by a secondary lateral braincase wall. In nonophidian squamates, the sinus lies medial to the epipterygoid in the extracranial cavum epiptericum, which is the anterior continuation of the cranioquadrate passage in both groups, nonophidian squamates and turtles.

Green (1951) describes a plexus of veins surrounding the posterior part of the hypophysis in turtles and *Alligator*, which may be compared, in part, to the sinus cavernosus in birds,

and which is represented by a simple enlarged transverse vein in Lepidosauria (Saint Girons 1970). An annular structure as it exists in birds has not been described for turtles and crocodiles, however, and the presence of a sinus cavernosus in crocodiles has been denied by Hochstetter (1906: 103) and Shindo (1914: 372). Variability and assessment of homology of the venous system as it relates to the hypophysis needs critical reassessment based on embryological studies. O'Donoghue (1921) for example described for *Sphenodon* an anastomosing vein which receives lateral hypophyseal veins and which connects the median cephalic veins with one another in front of the hypophysis.

The adrenal

Løvtrup (1985: 466), citing (Gabe 1970), referred to the retroperitoneal position of the adrenal in turtles and crocodiles as a shared derived character.

According to Gabe (1970), the adrenal gland of turtles lies against the kidney, and its dorsal limit is incompletely separated from the renal parenchyma, which is regularly penetrated by islets of interrenal and adrenal tissue. The adrenal gland is ventrolaterally attached to a peritoneal fold which ensheathes the gonads, forming the male mesorchium and the female mesovarium. Ventrally, the adrenal is covered by a parietal (somatopleural) fold of the peritoneum.

In lepidosaurs, the adrenal lacks a direct contact with the kidney, and is fully ensheathed by the mesorchium or mesovarium of the gonads, with no direct contact with the peritoneum. In crocodiles, the adrenal is entirely retroperitoneal, i.e. not suspended from mesenteries. The gland lies dorsal to the gonad and lateral to the genital duct, and its posterior end is insinuated into the parietal peritoneum. In birds, the adrenal again lies closer to the gonads than to the kidney, as is true of crocodiles and lepidosaurs.

From these topological relations, Gabe (1970: 272) concluded that the adrenal of lepidosaurs is intramesenteric (ensheathed by the mesorchium and mesovarium, respectively), but retroperitoneal in turtles and crocodiles. Using this character as a potential synapomorphy of turtles and crocodiles is problematical for several reasons. First, the mesorchium and mesovarium are not true mesenteries, as they are not derived from the median dorsal mesenterium which originally separates the two peritoneal cavities from one another (Broman 1937). This is illustrated by turtles, which show an adrenal not ensheathed but attached to a peritoneal fold which forms the mesorchium and mesovarium, respectively. Secondly, the adrenal of turtles retains a close association with the kidney, whereas the adrenal of crocodiles, as well as that of lepidosaurs and birds, is closely associated with the gonads (Lawton 1937; Gabe 1970). By outgroup comparison with amphibians (urodeles and anurans), and mammals, the association of the adrenal with the

kidney is the plesiomorphic condition (Berkelbach van der Sprenkel 1934; Gauthier *et al.* 1988a). And thirdly, histological details of the adrenal do not support a turtle — crocodile relationship (Gabe 1970; Gauthier *et al.* 1988a). Løvtrup (1977) interprets Gabe (1970) as to imply that the adrenal tissue of turtles is intermediate between that of *Sphenodon* and that of crocodiles (and birds). However, Gabe (1970: 309) stated that: 'The cytological data therefore agree well with current ideas on reptilian classification. Turtles, lepidosaurs and archosaurs show quite distinct patterns, while that of crocodilians resembles the pattern seen in birds.'

Blood proteins

Referring to Dessauer (1970), Løvtrup (1977) used blood proteins in support of a turtle–crocodile relationship. Although Dessauer (1970) did mention a signal for a 'very remote affinity between turtles and crocodiles' as compared to a fairly close relationship of 'lizards' and snakes which together have widely diverged from turtles and crocodiles, the picture is not so simple as this sweeping statement would seem to imply (Dessauer & Fox 1964). Furthermore, the use of electrophoretic data for reptile systematics in these papers is based on phenetic methods, and hence carries no phylogenetic information content.

Discussion

Although an impressive list of characters has been presented in favour of archosaur affinities of turtles (Hofsten 1941; Remane 1959; Løvtrup 1977, 1985; Ax 1884; Gardiner 1993), few hold up against critical scrutiny. Some of these characters need critical reassessment based on the application of modern methods of investigation, such as the developmental fate of the proatlas. It is important to note in this context that a major motivation for deBeer (1937) and earlier authors to study the development of the vertebrate head was the investigation of cranial segmentation, which introduced a bias into this research (Rieppel 1985). If corroborated, however, the incorporation of the proatlas pleurocentrum into the occipital condyle would be an important character linking turtles with crocodiles and birds.

The nature of the secondary subclavian arteries and their phylogenetic information content likewise requires critical reassessment both by ontogenetic investigations as well as studies of variation across the major taxa invoked in this debate. The same is true for the venous sinuses in the hypophyseal area in turtles and crocodiles, and their relation to the sinus cavernosus of birds.

Other characters fail the test of similarity (Patterson 1982) and hence cannot be proposed as hypotheses of primary homology (dePinna 1991), such as the dorsal relations of the epipterygoid, the relations of the interhyal process, the thyroid and cricoid cartilage, the type of scales, the egg

shell characters, and the adrenal. Of these characters, the dorsal contact of the epipterygoid with the parietal adds to the evidence (deBraga & Rieppel 1997) supporting a relationship of turtles to sauropterygians, rather than to archosauromorphs.

Other purported syapomorphies of turtles and crocodiles have been wrongly polarized (see also Gauthier *et al*. 1988a), and turn out to be symplesiomorphies based on outgroup comparison with amphibians and mammals such as the vascular cortical bone, the cartilaginous cones at end of long bones (i.e. the absence of separate epiphyseal ossification centres), the nature of the tarsus in the lower eyelid, the presence or absence of Jacobson's organ, the presence or absence of ciliary processes, probably the presence of a single male intromittent organ developed from the ventral wall of the cloaca, the egg caruncle, and the lobulate thymus. Support for archosaur affinities of turtles on the basis of blood proteins is based on a phenetic approach. The character that does, on the basis of present knowledge, unequivocally support a relationship of turtles to archosaurs is the differentiation of a pyramidalis muscle for the tendon of the nictitating membrane. However, other characters indicate affinities of turtles with anapsid reptiles (Lee 1995, 1997a), or with lepidosauromorphs within diapsids (deBraga & Rieppel 1997; Rieppel & Reisz 1999).

Neontological characters which place turtles outside the archosauromorph-lepidosauromorph dichotomy and hence support their anapsid status include the association of the adrenal with the gonads as discussed above. As noted by Benton (1985; see also Starck 1979; Gauthier *et al*. 1988a), the forebrain of turtles shows a sessile olfactory bulb, whereas the olfactory bulb is claimed to be separated from the cerebrum by a distinct peduncle (olfactory tract) in lepidosaurs and crocodiles (the olfactory bulb of birds and mammals is sessile). This is an oversimplified representation of the distribution of this character, however. It is true that the plesiomorphic condition is a sessile olfactory bulb as seen in turtles, mammals and birds, but this condition is also found in most lizards and all snakes (Senn & Northcutt 1973). Another putative diapsid synapomorphy is Huxley's foramen defined by processes originating from the extracolumella (deBeer 1937; Benton 1985; Gauthier *et al*. 1988a), but modern developmental data would seem highly desirable to establish the primary homology of this structure where it occurs. Gauthier *et al*. (1988a) cite the loss or suppression of the urea-cycle as another potential synapomorphy of diapsids excluding turtles. Other, osteological characters that relate turtles to anapsids are those of Lee (1995, 1997a).

Characters which relate turtles to the lepidosauromorph branch of diapsids are those of deBraga & Rieppel (1997), and Rieppel & Reisz (1999). Among those, the ontogenetic repatterning of the proximal tarsus figures prominently, as it correlates with the development of an mesotarsal joint (Sewertzoff

1908; Rieppel 1993a, b). Crocodiles do not develop a meso-tarsal joint, but a cruro-tarsal joint instead (Brinkman 1981).

Laurin (1991: 90) defined the lepidosauromorph ankle joint as one where 'the fourth distal tarsal has a ventromedial process that fits under the astragalus' (see also Rewcastle 1980). A survey of cleared and stained as well as skeletonized non-ophidian squamates and turtles showed that the dimensions of this medioventral process on the fourth distal tarsal may vary between the groups, but that turtles and 'lizards' share the same basic complexity of their mesotarsal joint both in its cartilaginous, as well as in its ossified stage. Ax (1984) considered the mesotarsal joint as a potential synapomorphy of turtles, lepidosaurs and archosaurs, although he quoted Starck (1979: 589) who considered the mesotarsal joint to have convergently evolved in lepidosaurs and archosaurs, because it was not differentiated in basal 'eosuchians' and 'thecodonts.' Indeed, within archosauromorphs, the meso-tarsal joint is an ornithodiran (pterosaurs plus dinosaurs) synapomorphy (Sereno & Arcucci 1990; Sereno 1991).

Methodological problems in the analysis of turtle relationships

Analysing relative relationships over a broad array of taxa usually results in large data matrices which tend to transcend the expertise of single researchers. In addition, the degree of homoplasy discovered in morphological data is surprisingly high (Rieppel & Reisz 1999; and above), which indicates the potential for extensive convergence and/or reversals for a large number of (primarily) osteological characters. The level of homoplasy is also relatively high in large molecular data sets. The result is a relatively low stability of resulting hierarchies. As a consequence, the most parsimonious tree, or the equally parsimonious trees if there are several, are subjected to various statistical tests in an attempt to estimate their reliability. The more frequently used tests are the decay index (or Bremer support index: Bremer 1988), and the bootstrap (Felsenstein 1985; Sanderson 1989). However, the decay index can be low if only one or a few unambiguous synapomorphies (which an individual consistency index of 1) support a node but are combined with numerous homo-plastic characters. The same is true for bootstrap support methods. In a more general sense, test methods that are based on random models would seem to be inappropriate to place meaningful confidence limits on cladograms, if indeed the characters used in phylogeny reconstruction are intrin-sically hierarchical (Kitching *et al*. 1998).

Adherence to statistical support measures or confidence limits in the evaluation of multiple equally parsimonious cladograms reveals a quantitative, rather than a qualitative approach to phylogeny reconstruction. Furthermore, the Wilcoxon signed-rank test as implemented by Templeton (1983; see also Larson 1994) does indicate whether or not

two trees (from different sources) are significantly different from one another, but it does not indicate why. In the case of turtle relationships, this test showed that placement of turtles with sauropterygians among diapsids is not significantly different from the placement of turtles with pareiasaurs relative to the same data set (Wilkinson *et al.* 1997; Rieppel & Reisz 1999), but why this should be so remains obscure. Since the test depends on the number of characters/taxa relative to the number of transformation steps implied by alternative phylogenies, it cannot discriminate between homoplasy which represents random noise, or homoplasy which consists of two subsets of characters within the same matrix which support alternative hierarchies.

In order to investigate this point further, reverse successive weighting (Trueman 1998) was applied to the data set used to analyse turtle relationships (Rieppel & Reisz 1999). Including all characters in the analysis yielded two most parsimonious trees, both showing the turtles as sister-group of Sauropterygia nested at the base of the lepidosauromorph branch of diapsids (Rieppel & Reisz 1999; lack of resolution is restricted to basal Archosauromorphs). All the characters which perform as unequivocal synapomorphies ($ci = 1$) in this analysis (characters 4, 5, 13, 21, 34, 39, 40, 44, 57, 58, 71, 90, 93, 94, 102, 119, 121, 136, 148, 152, 156, 167) were identified and excluded from the matrix prior to a second run. Exclusion of these characters resulted in nine equally parsimonious trees, with reduced resolution in the strict consensus tree. However, turtles were still found to be the sister-group of a monophyletic Sauropterygia, with lepidosauriforms (kuehneosaurs, rhynchocephalians, and squamates) as successive sister-groups to that clade (i.e. the monophyly of Lepidosauriformes was lost). Bootstrap support for turtle relationships with the excluded characters is less than 50% (100 replications), however, and the turtle — sauropterygian clade breaks, as most other groupings, in a tree one step longer.

Characters which performed as unequivocal synapomorphies in this second search (18, 70, 84, 133, 142) were excluded in a third analysis which yielded a single most parsimonious tree which corresponds to the original tree as obtained in the first analysis with all characters included (archosauromorph relationships now fully resolved), but which shows turtles as sister-group of pareiasaurs among parareptiles. This tree topology retains two unequivocal synapomorphies, and the node which relates turtles to pareiasaurs breaks only in a tree three steps longer than the most parsimonious one, but its bootstrap support is again less than 50% (100 replications). Based on the decay index, this is the best supported tree topology, but that support derives form the deletion of contradicting evidence (character exclusion). Finally, excluding the characters 50 and 97 in a fourth analysis again yielded a single most parsimonious tree, identical to the previous tree, but none of the nodes is supported by an unequivocal synapomorphy any longer. The node relating turtles to pareiasaurs breaks in a tree one step longer, and its bootstrap support again is less than 50% (100 replications).

In summary, it can be concluded that the data matrix of Rieppel & Reisz (1999) does include subsets of characters which support two alternative hierarchies, one placing turtles as sister-group of pareiasaurs, the other placing turtles as sister-group of sauropterygians within diapsids, but the latter signal is stronger than the first, presumably because it is supported by a larger number of unequivocal synapomorphies.

Conclusions

Without exception, molecular data place turtles closer to archosaurs than to lepidosaurs (Platz & Conlon 1997; Kirsch & Mayer 1998; Zardoya & Meyer 1998; Hedges & Poling 1999; Mannen & Li 1999; Mindell *et al.* 1999; Kumazawa & Nishida 1999). This is intriguing in view of the neontological characters listed by deBeer (1937), Hofsten (1941), Remane (1959), Løvtrup (1977, 1985), Ax (1984) and Gardiner (1993), which have been postulated to also relate turtles to archosaurs. By contrast, one palaeontological data set shows turtles to be the sister-group of Sauropterygia nested at the base of the Lepidosauromorph clade, which in terms of extant taxa places turtles closer to *Sphenodon* and squamates than to crocodiles and birds (deBraga & Rieppel 1997; Rieppel & Reisz 1999), while other palaeontological data favour a relationships of turtles with anapsid parareptiles (pareiasaurs: Lee 1995, 1997a, b). This is an intriguing conflict, that poses a challenge to both palaeontologists and molecular systematists.

The molecular data appear to have some problems of their own, relating to the choice of outgroups, and to the choice of genes to be included in the analysis. A grouping of the lepidosaur taxon *Sphenodon* with archosaurs, as is obtained by molecular data (Hedges & Poling 1999), is certainly highly problematic from a palaeontological point of view. It is also worth noting that birds clustered with mammals in earlier molecular analyses (Hedges *et al.* 1990), and that removal of the 18S rRNA (which favours the bird–mammal grouping) from the analysis increases the support for a relationship of turtles with crocodiles and birds (Hedges & Poling 1999).

At the present time, however, the various attempts to resolve turtle relationships among reptiles result in a classic case of taxonomic incongruence, which raises interesting new questions with respect to the analysis of morphological characters the comparison of which has been neglected over the last few years.

Acknowledgements

reviewers for reading earlier drafts of this paper, providing much helpful criticisms and comments.

References

Arvy, L. (1973). Le thymus des mammifères. In P.-P. Grassé (Ed.) *Traîté de Zoologie*, Vol. 16, *Fasc. 4* (pp. 418–604). Paris: Masson & Cie.

Ax, P. (1984). *Das Phylogenetische System* (pp. 349). Stuttgart, Gustav Fischer.

Barone, R. (1972). Appareil circulatoire. In P.-P. Grassé (Ed.) *Traîté de Zoologie*, Vol. 16, *Fasc. 4* (pp. 704–921). Paris: Masson & Cie.

Baumel, J. J. (1993). *Handbook of Avian Anatomy*. Cambridge MA: The Club.

Baur, G. (1889). On the morphology of the vertebrate skull. *Journal of Morphology*, 3, 467–474.

Baur, G. (1895). Bemerkungen über die Osteologie der Schläfengegend der Höheren Wirbeltiere. *Anatomischer Anzeiger*, 10, 315–330.

Bellairs, A. d' A. & Kamal, A. M. (1981). The chondrocranium and the develpment of the skull in recent reptiles. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 11 (pp. 1–263). London: Academic Press.

Benton, M. J. (1983). The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Proceedings of the Royal Society of London, B 302*, 605–720.

Benton, M. J. (1985). Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84, 97–164.

Berkelbach van der Sprenkel, H. (1934). Nebenniere und Paraganglien. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch, (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 2.1 (pp. 777–816). Berlin: Urban & Schwarzenberg.

Boas, J. E. V. (1931). Schuppen der Reptilien, Vögel und Säugetiere. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 1 (pp. 559–564). Berlin: Urban & Schwarzenberg.

Bockman, D. E. (1970). The thymus. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2 (pp. 111–133). London: Academic Press.

Boulenger, G. A. (1918). Sur la place des chéloniens dans la classification. *Comptes Rendues À l'Académie Des Sciences, Paris*, 169, 605–607.

Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42, 795–803.

Brinkman, D. (1981). The origin of the crocodiloid tarsi and the interrelationships of thecodontian archosaurs. *Breviora*, 464, 1–23.

Broman, I. (1937). Cölom. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 3 (pp. 989–1018). Berlin: Urban & Schwarzenberg.

Broom, R. (1924). On the classification of the reptiles. *Bulletin of the American Museum of Natural History*, 51, 39–65.

Cope, E. D. (1893). On the homologies of the posterior cranial arches in the Reptilia. *Transactions of the American Philosophical Society, n. s.*, 17, 11–26.

deBeer, G. S. (1937). *The Development of the Vertebrate Skull*. Oxford, Clarendon Press.

deBraga, M. & Rieppel, O. (1997). Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society*, 120, 281–354.

dePinna, M. C. C. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7, 367–394.

deRicqlès, A. J. (1976). On bone histology of fossil and living reptiles, with comments on its fuctional and evolutionary significance. In A. d'A. Bellairs & C. B. Cox (Eds) *Morphology and Biology of Reptiles* (pp. 123–150). London: Academic Press.

Dessauer, H. C. (1970). Blood chemistry of reptiles: physiological and evolutionary aspects. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2 (pp. 1–72). London: Academic Press.

Dessauer, H. C. & Fox, W. (1964). Electrophoresis in taxonomic studies illustrated by analyses of blood proteins. In C. A. Leone (Ed.) *Taxonomic Biochemistry and Serology* (pp. 625–664). New York: Ronald Press.

Duellman, W. E. & Trueb, L. (1986). *Biology of Amphibians* (pp. 670). New York: McGraw-Hill.

Enemar, A. (1960). The development of the hypophysial vascular system in the lizards *Lacerta a. agilis* Linnaeus and *Anguis fragilis* Linnaeus and in the snake *Natrix n. natrix* (Linnaeus), with comparative remarks on the Amniota. *Acta Zoologica (Stockholm)*, 41, 142–237.

Enlow, D. H. (1969). The bone of reptiles. In C. Gans, T. S. Parsons & A. d' A. Bellairs (Eds) *Biology of the Reptilia*, Vol. 1 (pp. 45–80). London: Academic Press.

Ewert, M. A. (1985). Embryology of turtles. In C. Gans & F. Billet (Eds) *Biology of the Reptilia*, Vol. 14A (pp. 75–267). New York, John Wiley and Sons.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791.

Ferguson, M. W. J. (1985). Reproductive biology and embryology of the crocodilians. In C. Gans & F. Billet (Eds) *Biology of the Reptilia*, Vol. 14A (pp. 329–491). New York: John Wiley and Sons.

Gabe, M. (1970). The adrenal. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2 (pp. 263–318). London: Academic Press.

Gaffney, E. S. (1972). An illustrated glossary of turtle skull nomenclature. *American Museum Novitates*, 2486, 1–33.

Gaffney, E. S. (1979). Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History*, 164, 1–376.

Gaffney, E. S. (1980). Phylogenetic relationships of the major groups of amniotes. In A. L. Panchen (Ed.) *The Terrestrial Environment and the Origin of Land Vertebrates* (pp. 593–610). London: Academic Press.

Gaffney, E. S. (1990). The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, 194, 1–263.

Gardiner, B. G. (1993). Haematothermia: warm-blooded amniotes. *Cladistics*, 9, 369–395.

Gauthier, J. A., Kluge, A. G. & Rowe, T. (1988a). *Amniote phylogeny and the importance of fossils*. *Cladistics*, 4, 104–209.

Gauthier, J., Estes, R. & deQueiroz, K. (1988b). A phylogenetic analysis of Lepidosauromorpha. In R. Estes, R. & G. Pregill (Eds) *Phylogenetic Relationships of the Lizard Families* (pp. 5–98). Stanford: Stanford University Press.

Giersberg, H. & Rietschel, P. (1968). *Vergleichende Anatomie der Wirbeltiere*, 2. Jena: Gustav Fischer.

Goldby, F. (1925). The development of the columella auris in the Crocodilia. *Journal of Anatomy*, 59, 301–325.

Göppert, E. (1900). Der Kehlkopf der Amphibien und Reptilien. II. Reptilien. *Gegenbaurs Morphologisches Jahrbuch*, 28, 1–27.

Göppert, E. (1937). Kehlkopf und Trachea. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 3 (pp. 797–866). Berlin: Urban & Schwarzenberg.

Goodrich, E. S. (1916). On the classification of the Reptilia. *Proceedings of the Royal Society of London, B 89*, 261–276.

Goodrich, E. S. (1930). *Studies on the Structure and Development of Vertebrates* (pp. 837). London: Macmillan.

Green, J. D. (1951). The comparative anatomy of the hypophysis, with special reference to its blood supply and innervation. *American Journal of Anatomy, 88*, 225–311.

Gregory, W. K. (1944). Osteology and relationships of *Trilophosaurus*. *University of Texas Contributions to Geology, 4401*, 273–332.

Gregory, W. K. (1946). Pareiasaurs versus placodonts as near ancestors to turtles. *Bulletin of the American Museum of Natural History, 86*, 275–326.

Grosser, O. & Brezina, E. (1895). Über die Entwicklung der Venen des Kopfes und Halses bei Reptilien. *Gegenbaurs Morphologisches Jahrbuch, 23*, 289–325.

Hafferl, A. (1933). Das Arteriensystem. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 6 (pp. 563–684) Berlin: Urban & Schwarzenberg.

Haines, R. W. (1969). Epiphyses and sesamoids. In C. Gans, T. S. Parsons & A. d'A. Bellairs (Eds) *Biology of the Reptilia*, Vol. 1 (pp. 81–115). London: Academic Press.

Hay, O. P. (1905). On the group of fossil turtles known as the Amphichelydia; with remarks on the origin and relationships of the suborders, superfamilies, and families of Testudines. *Bulletin of the American Museum of Natural History, 21*, 137–175.

Hayek, H. (1924). Über das Schicksal des Proatlas und über die Entwicklung der Kopfgelenke bei Reptilien und Vögeln. *Gegenbaurs Morphologisches Jahrbuch, 53*, 137–163.

Hedges, S. B., Moberg, K. D. & Maxon, L. R. (1990). Tetrapod phylogeny inferred from 18S and 28S ribosomal RNA sequences, and a review of the evidence for amniote relationships. *Molecular Biology and Evolution, 7*, 607–633.

Hedges, S. B. & Poling, L. L. (1999). A molecular phylogeny of reptiles. *Science, 283*, 998–1001.

Henle, J. (1839). *Vergleichend-anatomische Beschreibung des Kehlkopfs mit besonderer Berücksichtigung des Kehlkopfs der Reptilien* (pp. 83). Leipzig: L. Voss.

Hochstetter, F. (1906). Beiträge zur Anatomie und Entwicklungsgeschichte des Blutgefässsystems der Krokodile. In A. Voeltzkow (Ed.) *Reise in Ostafrika in Den Jahren 1903-05*, Vol. 4, *Heft 1: Anatomie und Entwicklungsgeschichte* (pp. 1–139). Stuttgart: E. Schweizerbarthsche-Verlagsbuchhandlung (E. Nägele).

Hofsten, N. V. (1941). On the phylogeny of the Reptilia. *Zoologisca Bidrag Fran Uppsala, 20*, 501–521.

Kamal, A. M. (1965). On the cranio-vertebral joint and the relation between the notochord and occipital condyle in Squamata. *Proceedings of the Egypt Academy of Sciences, 19*, 1–12.

Kelly, A. (1901). Beiträge zur mineralogischen Kenntnis der Kalkausscheidungen im Tierreich. *Jenaer Zeitschrift für Naturwissenschaften, 28*, 429–492.

Kitching, I. J., Forey, P. L., Humphries, C. J. & Williams, D. M. (1998). *Cladistics, 2nd. Edition* (pp. 228). Oxford: Oxford University Press.

Kirsch, J. A. W. & Mayer, G. C. (1998). The platypus is not a rodent: DNA hybridization, amniote phylogeny and the palimpsest theory. *Philosophical Transactions of the Royal Society of London, B 353*, 1221–1237.

Krampitz, G., Böhme, W., Kriesten, K. & Hardebeck, W. (1974). Die Aminosäurenzusammensetzung von Reptilien-Eischalen in biochemischer und evolutiver Sicht. *Zeitschrift für Zoologische Systematik und Evolutionsforschung, 12*, 1–22.

Kriesten, K. (1975). Untersuchungen über die Ultrastruktur, Proteinmuster und Aminosäurezusammensetzung der Eischalen von *Testudo elephantopus, Caiman crocodilus*, und *Iguana iguana*. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere, 94*, 101–122.

Kumazawa, Y. & Nishida, M. (1999). Complete mitochondrial DNA sequences for the green turtle and blue-tailed mole skink: statistical evidence for archosaurian affinity of turtles. *Molecular Biology and Evolution, 16*, 784–792.

Lakjer, T. (1926). *Studien Über die Trigeminus-Versorgte Kaumuskulatur der Sauropsiden* (pp. 154). Copenhagen: C.A. Reitzel.

Larson, A. (1994). The comparison of morphological and molecular data in phylogenetic systematics. In B. Schierwater, B. Streit, G. P. Wagner & R. DeSalle (Eds) *Molecular Ecology and Evolution. Approaches and Applications* (pp. 371–390). Basel: Birkhäuser Verlag.

Laurin, M. (1991). The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society, 101*, 59–95.

Laurin. M. & Reisz, R. R. (1995). A reevaluation of early amniote phylogeny. *Biological Journal of the Linnean Society, 113*, 165–122.

Lawton, F. E. (1937). The adrenal — autonomic complex in *Alligator mississippiensis. Journal of Morphology, 20*, 361–377.

Lee, M. S. Y. (1995). Historical burden in systematics and the inter-relationships of 'parareptiles'. *Biological Reviews, 70*, 459–547.

Lee, M. S. Y. (1997a). Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society, 120*, 197–280.

Lee, M. Y. S. (1997b). Reptile relationships turn turtle. *Nature, 389*, 245–246.

Løvtrup, S. (1977). *The Phylogeny of Vertebrata* (pp. 330). London: John Wiley.

Løvtrup, S. (1985). On the classification of the taxon Tetrapoda. *Systematic Zoology, 34*, 463–470.

Mannen, H. & Li, S. S.-L. (1999). Molecular evidence for a clade of turtles. *Molecular Phylogenetics and Evolution, 13*, 144–148.

Matthes, E. (1934). Geruchsorgan. In L. Bolk, E. Göppert, E. Kallius & W. Lubosch (Eds) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*, Vol. 2.1. (pp. 879–948). Berlin: Urban & Schwarzenberg.

Mindell, D. P., Sorenson, M. D., Dimcheff, D. E., Hasegawa, M., Ast, J. C. & Yuri, Y. (1999). Interordinal relationships of birds and other reptiles based on the whole mitochondrial genome. *Systematic Biology, 48*, 138–152.

Moffat, L. A. (1985). Embryonic development and aspects of reproductive biology in the Tuatara, *Sphenodon punctatus*. In C. Gans & F. Billet (Eds) *Biology of the Reptilia*, Vol. 14A (pp. 493–521). New York: John Wiley and Sons.

O'Donoghue, C. H. (1921). The blood vascular system of the Tuatara, *Sphenodon punctatus. Philosophical Transactions of the Royal Society of London, B 210*, 175–252.

Olson, E. C. (1947). The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana (Geology), 11*, 1–53.

Osborn, H. F. (1903). On the primary division of the Reptilia into two subclasses, Synapsida and Diapsida. *Science*, *17*, 275–276.

Packard, M. J. (1980). Ultrastructural morphology of the shell and shell membrane of eggs of common snapping turtles (*Chelydra serpentina*). *Journal of Morphology*, *165*, 187–204.

Parsons, T. S. (1970). The nose and Jacobson's organ. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2 (pp. 99–191). London: Academic Press.

Patterson, C. (1982). Morphological characters and homology. In K. A. Joysey & A. E. Friday (Eds) *Problems of Phylogenetic Reconstruction* (pp. 21–74). London: Academic Press.

Platz, J. E. & Conlon, J. M. (1997). Reptile relationships turn turtle ... and turn back again. *Nature*, *389*, 245–246.

Presley, R. & Steel, F. L. D. (1976). On the homology of the alisphenoid. *Journal of Anatomy*, *121*, 441–459.

Raynaud, A. & Pieau, C. (1970). Contribution à l'étude des premiers stades de la formation des organes copulateurs chez les reptiles. *Mémoires Du Muséum National d'Histoire Naturelle, A 58*, 1–187.

Raynaud, A. & Pieau, C. (1978). Morphogenèse des organes copulatuers et implications phylogénetiques chez les reptiles. *Bulletin de la Société Zoologique de France*, *103*, 205–218.

Remane, A. (1959). Die Geschichte der Tiere. In G. Heberer (Ed.) *Die Evolution der Organismen*, Vol. 1, 2nd. edn. (pp. 340–422). Stuttgart: Gustav Fischer.

Rewcastle, S. C. (1980). Form and function in the lacertilian knee and mesotarsal joint: a contribution to the analysis of sprawling locomotion. *Journal of Zoology, London*, *191*, 147–170.

Rieppel, O. (1985). The recessus scalae tympani and its bearing on the classification of reptiles. *Journal of Herpetology*, *19*, 373–384.

Rieppel, O. (1993a). Studies on skeleton formation in reptiles. Patterns of ossification in the skeleton of *Chelydra serpentina* Linnaeus (Reptilia, Testudines). *Journal of Zoology London*, *231*, 487–509.

Rieppel, O. (1993b). Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology*, *13*, 31–47.

Rieppel, O. (1995). The Genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology. *Fieldiana (Geology), N.S.*, *31*, 1–44.

Rieppel, O. & R. R. Reisz. (1999). The origin and early evolution of turtles. *Annual Review of Ecology and Systematics*, *30*, 1–22.

Rochon-Davigneaud, A. (1972). L'oeil et la vision. In P.-P. Grassé (Ed.) *Traîté de Zoologie*, Vol. 16, *Fasc. 4* (pp. 609–703). Paris: Masson & Cie.

Romer, A. S. (1956). *The Osteology of the Reptiles* (pp. 772). Chicago: Chicago University Press.

Romer, A. S. (1968). *Notes and Comments on Vertebrate Paleontology* (pp. 304). Chicago: Chicago University Press.

Saban, R. (1968). Musculature de la tête. In P.-P. Grassé (Ed.) *Traîté de Zoologie*, Vol. 16, *Fasc. 4* (pp. 230–471). Paris: Masson & Cie.

Saint Girons, H. (1970). The pituary gland. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2 (pp. 135–199). London, Academic Press.

Sanderson, M. J. (1989). Confidence limits on phylogenies: The bootstrap revisited. *Cladistics*, *5*, 113–129.

Schleich, H. H. & Kästle, W. (1988). *Reptile Egg-Shells SEM Atlas* (pp. 123). Stuttgart: Gustav Fischer.

Schumacher, G.-H. (1973). The head muscles and hyolaryngal skeleton of turtles and crocodiles. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 4 (pp. 101–199). London: Academic Press.

Senn, D. G. & Northcutt, R. G. (1973). The forebrain and midbrain of some squamates and their bearing on the origin of snakes. *Journal of Morphology*, *140*, 135–152.

Sereno, P. C. (1991). Basal Archosaurs: Phylogenetic Relationships and Funcional Implications. *Journal of Vertebrate Paleontology*, *4* (*Suppl.*), 1–53.

Sereno, P. C. & Arcucci, A. B. (1990). The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, *180*, 21–52.

Sewertzoff, A. N. (1908). Studien über die Entwicklung der Muskeln, Nerven und des Skeletts der Extremitäten der niederen Tetrapoda. *Bulletin de la Société Impériale Des Naturalistes de Moscou, n.s.*, *21*, 1–430.

Seydel, O. (1895). Über die Nasenhöhle und das Jacobson'sche Organ der Amphibien. *Gegenbaurs Morphologisches Jahrbuch*, *23*, 453–543.

Seydel, O. (1896). Über die Nasenhöhle und das Jacobson'sche Organ der Land- und Sumpfschildkröten. *Festschrift 70 Geburtstag Gegenbaur*, *2*, 385–486.

Shindo, T. (1914). Studien zur Kenntnis des Wirbeltierkopfes. 1. Das Chondrocranium von *Crocodilus*, mit Berücksichtigung der Gehirnnerven und der Kopfgefässe. *Anatomische Hefte*, *1*, 257–381.

Shindo, T. (1915). Über die Bedeutung des Sinus cavernosus der Säuger mit vergleichend anatomischer Berücksichtigung anderer Kopfvenen. *Anatomische Hefte*, *1*, 319–495.

Söller, L. (1931). Über den Bau und die Entwicklung des Kehlkopfes bei Krokodiliern (*Caiman*) und Marsupialiern (*Didelphys*). *Gegenbaurs Morphologisches Jahrbuch*, *68*, 541–593.

Starck, D. (1979). *Vergleichende Anatomie der Wirbeltiere Auf Evolutionsbiologischer Grundlage*, Vol. 2. Berlin, Springer Verlag.

Stephan, F. (1950). Morphologie générale du système circulatoire. In P.-P. Grassé (Ed.) *Traîté de Zoologie*, Vol. 12 (pp. 854–973). Paris: Masson & Cie.

Templeton, A. (1983). Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. *Evolution*, *37*, 221–244.

Trueman, J. W. H. (1998). Reverse successive weighting. *Systematic Biology*, *47*, 733–737.

Underwood, G. (1970). The eye. In C. Gans & T. S. Parsons (Eds) *Biology of the Reptilia*, Vol. 2. (pp. 1–97). London: Academic Press.

Walls, G. L. (1942). *The Vertebrate Eye and its Adaptive Radiation* (pp. 785). Reprinted 1967. New York: Hafner Publishers Co.

Watson, D. M. S. (1914). *Eunotosaurus africanus* Seeley, and the ancestry of the Chelonia. *Proceedings of the Zoological Society of London*, *1914*, 1011–1020.

Williston, S. W. (1917). The phylogeny and classification of reptiles. *Journal of Geology*, *25*, 411–421.

Wilkinson, M., Thorley, J. & Benton, M. J. (1997). Uncertain turtle relationships. *Nature*, *387*, 466.

Wingstrand, K. G. (1951). *The Structure and Development of the Avian Pituary* (pp. 316). Lund: C.W.K. Gleerup.

Zardoya, R. & Meyer, A. (1998). Complete mitochondrial genome suggests diapsid affinities of turtles. *Proceedings of the National Academy of Science*, *95*, 14226–14231.