representatives of the family were in an evolutionary stage represented by the extant *Geochelone emys* of Southeast Asia. They were large, low shelled, plantigrade, nomadic, frugivorous tortoises living in mesic tropical evergreen forests. Much of the evolutionary history of tortoises reflects adaptations to grazing in semiarid, subtropical grassland and thorn forest. The change in habits and ecology is reflected in several major morphologic evolutionary trends (Hay 1908, Williams 1950a, 1950b, Loveridge and Williams 1957).[1]

1) The high, convex shell of almost all extant testudinids is evolved from one that was low and similar to that in *Chrysemys*. The depressed shell of a few Recent species of tortoises is probably a specialization related to shelter utilization. Two reasons have been suggested for the major trend in changing shell shape: 1) carnivorous land animals cannot span the greater convexity of a domed shell with their jaws as readily as a more flattened shell, and 2) the vaulted shell provides greater space for the lungs. Several workers (Koch 1934, *et al.*) have shown that the capacity of the lungs of testudinids is somewhat greater than that of equal sized emydids (except *Terrapene*, which has a life style similar to that of testudinids).

2) In emydids the neurals are usually hexagonal, with the broader end directed anteriorly. The earlier species of tortoises also exhibit this condition, though in occasional individuals the second neural is octagonal (sometimes a rare variant in other families of turtles[1]). Among later fossil testudinids a high degree of neural differentiation is the rule, usually an alternation of octagonal and tetragonal elements at least anteriorly. In some fossil and Recent species the hexagonal neurals have the broad end directed posteriorly. This is a specialized condition (Fig. 2). Some extant tortoises retain the emydid condition, except that few neurals may be tetragonal as in *Homopus*.

3) Considerable modification has taken place in the pleurals during the evolution of tortoises. In almost all other turtles the proximal and distal ends of the second through the sixth pleurals are nearly the same width. In almost all testudinid species the proximal ends of the second, fourth, and sixth pleurals are much narrower than the proximal ends of

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[1] For anatomy of turtles, including tortoises, see Bojanus 1821, Jackson 1837, Parker 1868, Gray 1873c, 1873d, 1873e, Furbinger 1874, Rutimeyer 1874, Zittel 1887-90, Hoffman 1890, Bauer 1891, Bruhl 1896, Siebenrock 1897, 1898, 1899, 1909, Wieland 1900, Sieglbauer 1909, Williston 1925, Beer 1926, Nopsca 1926a, 1931, Ruckes 1929a, 1929b, Bolk *et al.* 1931-8, Thompson 1932, Versluys 1936, Kuhn 1937, Schepers 1938, 1939, 1948, Zangerl 1939, Walls 1942, Romer 1945, 1956, Walker 1947, Schumacher 1954, 1955, George and Shah 1955a, 1955b, 1959a, 1959b, Golby and Gamble 1957, Parsons 1959, Williams 1959, McDowell 1961, Shah and Patel 1964, Zug 1966, Pawley 1968.

[1] Shell anomalies are discussed by Meyer 1867, Parker 1901, Coker 1910, Lynn 1937, Grant 1946, Lynn and Ullrich 1950, Mlynarski 1956, Zangerl and Johnson 1957, Staesche 1961, and others.