

Fossils Explained 48

Placodonts

Placodonts were unusual benthic-feeding marine reptiles known only from the Triassic of Europe, the Middle East and southern China. Best known for their wide, often armoured bodies, dense bones and the flattened crushing teeth for which they were named, they have variously been characterized as reptilian analogues of walruses or rays or as turtle-mimics; clearly they would have differed substantially from their pelagic, flippered kin, the plesiosaurs. Placodont teeth were discovered as early as 1809 and the first skull was found in 1824. Though these fossils were initially thought to belong to unusual fish, in 1858 the British anatomist Richard Owen argued that they represented a new group of reptiles related to plesiosaurs.

Though this idea was challenged several times in the following decades, there is agreement today that placodonts were highly modified, basal members of the Sauropterygia, the marine reptile group that includes nothosaurs, plesiosaurs and their relatives (Fig. 1A). Experts agree that sauropterygians are part of the major reptile group called the Diapsida, but there is less agreement on where within Diapsida sauropterygian affinities lie.

Placodonts have traditionally been divided into two major groups, the unarmoured Placodontoidea and the armoured Cyamodontoidea, and there are three main groups of cyamodontoid (traditionally regarded as families): the Cyamodontidae, Placochelyidae and Henodontidae. While numerous features indicate monophyly of the cyamodontoids, placodontoids are paraphyletic (Fig. 1B) and, unlike cyamodontoids, had an elongate body lacking an extensive covering of armour plates, and a relatively tall and narrow skull. In contrast, the dermal armour of cyamodontoids became so extensive that they evolved a complete dorsal shield (or carapace) and at least some of them also possessed a ventral shield (or plastron). Consequently they must have superficially resembled marine turtles. Although some recent studies have suggested a close relationship between turtles and sauropterygians, it is apparent that the similarities between turtles and cyamodontoids represent evolutionary convergence and the two groups differ profoundly in their morphological details.

Most were between 1–2 m long and the largest forms may have reached or just exceeded 3 m. All were quadrupedal robust animals of nearshore or lagoonal environments. Both armoured and unarmoured placodonts first appear in the Scythian (Lower Triassic) and the youngest known placodonts – members of the cyamodontoid family Placochelyidae – are from the Rhaetian, the last stage of the Upper Triassic. There is one report of a Lower Jurassic placodont – a single tooth described in 1931 – but this specimen is thought to have been reworked from Triassic strata. Placodonts became extinct at or before the Triassic–Jurassic boundary and they left no descendants.

Placodont morphology

Placodonts had robust skulls that housed rounded, flattened teeth borne on the maxillae, palatines and dentaries (Figs 2–4). Excepting the internal nostrils and some foramina located posterior to the largest teeth, the placodont palate is complete and entirely closed. Ventral elements of the braincase butt against the rear of the palate, and presumably provided rein-

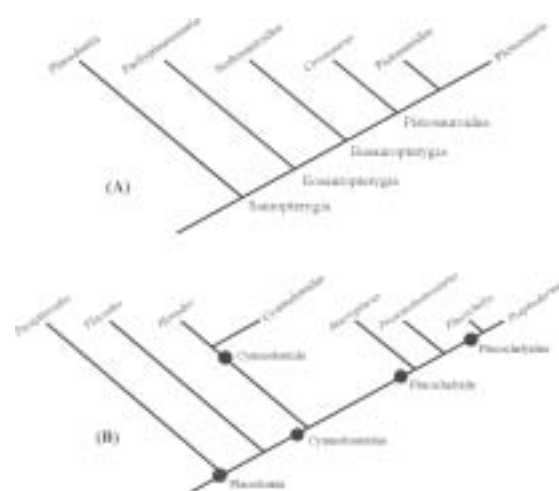


Fig. 1. Cladograms representing the relationships of placodonts. (A) Phylogeny of the Sauropterygia. (B) Inter-relationships of the main placodont groups. Based on Rieppel (2000, 2001) and other sources.

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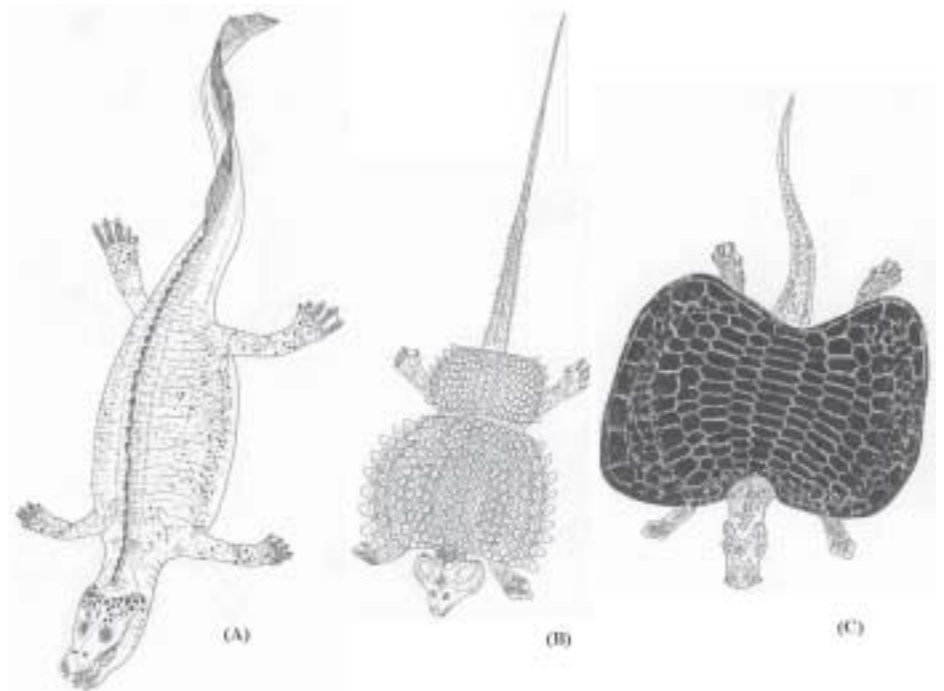


Fig. 2. Life restorations of a variety of placodonts. (A) *Placodus gigas* from the Middle Triassic of Germany (total length 3 m). (B) *Cyamodus* (based mostly on *C. hildegardis*) from the Middle Triassic of Germany, the southern Alps and Poland (total length 1.5–2.5 m). (C) *Henodus chelyops* from the Upper Triassic of Germany (total length approximately 1.5 m).

forcement during biting. While placodonts exhibit supratemporal fenestrae bordered by the postorbital, squamosal, parietal and, in non-cyamodontoids, post-frontal bones (*Henodus* (Fig. 2C) is unique in lacking supratemporal fenestrae), they are like other sauropterygians in exhibiting a ventral emargination on the temporal arch. This emargination is huge in

Paraplacodus (Fig. 4A) creating the impression that this primitive placodont had only recently descended from ancestors with a complete jugal-quadratojugal bar. More derived placodonts deepened the temporal bar, perhaps to increase both the weight and the area available for muscle attachment of the skull (Fig. 4B). In cyamodontoids, tubercular osteoderms decorate



Fig. 3. Virtually complete skeleton of the placochelyid *Psephoderma alpinum* from the Late Triassic of Italy. This specimen is 1.8 m long, is exhibited at the Museo della Vicaria di S. Lorenzo, Zogno (Bergamo, Italy) and was described by Renesto & Tintori. Note the three keels running part of the length of the carapace and the separate posterior plate covering the hips and tail base. Photo by kind courtesy of Silvio Renesto.

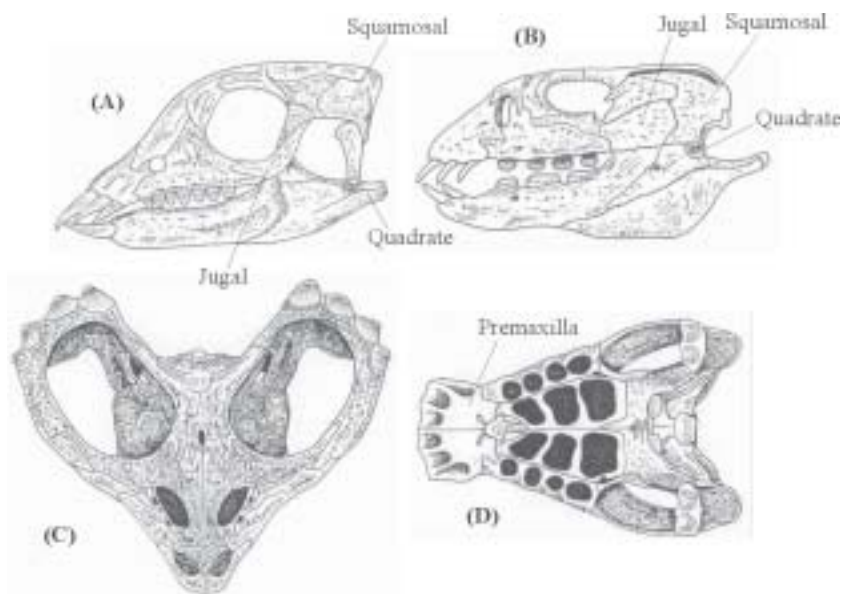


Fig. 4. Some representative placodont skulls. (A) Skull of the basal placodont *Paraplacodus broilii*. The emargination between the jugal and quadrate indicates that placodonts descended from diapsid reptiles with a laterotemporal fenestra enclosed ventrally by a bony bar. (B) *Placodus gigas* in lateral view. The enlargement of the jugal and squamosal in this form and other placodonts resulted in the loss of the ancestral ventral cheek emargination. (C) *Cyamodus* in dorsal view; note the enormous supra-temporal fenestrae (= openings of skull). (D) *Placodus gigas* in ventral view to show the enlarged palatal teeth. The premaxillary teeth are absent in this specimen. Not drawn to the same scale throughout. Redrawn from Rieppel (1995, 2000) and Nosotti & Pinna (1996).

the dorsal and lateral rear margins of the skull.

Pronounced muscle attachment sites at the rear of the lower jaw, on the pterygoids on the palate and on the squamosals and quadrates at the back of the skull, combined with the presence of a large coronoid process on the lower jaw, show that rapid jaw opening (probably employed in suction feeding, see below) and a powerful crushing bite were practised by most placodonts. Although derived cyamodontoids lost their premaxillary teeth, other forms had protruding teeth at the front of the jaws that appear to be suited for plucking shelled invertebrates from the sea floor (Fig. 4A, B).

Placodont ribs are thick and heavy, and those of some cyamodontoids are fused to the greatly elongated transverse processes. Those of *Paraplacodus* are distinctive as each has a prominent flange (an uncinate process) on its posterior margin that would have tightly overlapped the following rib and prevented lateral undulation of the body. The presence of a prominent basket of gastralia ('belly ribs'), and of processes between the vertebrae that did not permit much motion, not to mention the rigid carapaces of the cyamodontoids, also indicate that placodonts used their limbs and tails for propulsion and did not have flexible bodies.

The pectoral and pelvic girdles of placodonts were

composed of large flattened bones and the bony contacts with the vertebral column appear to have been weak. Insertion scars for large muscles are seen on the expanded heads of the proximal limb bones. The hands and feet are short and wide, and were probably paddle-like in life (Fig. 5). These features suggest that placodonts had ample limb musculature, employed their limbs in steering and paddling, but were not good at supporting their weight when on land. It remains unknown whether placodonts practised symmetrical or asymmetrical swimming motions with their limbs. Primitive placodonts like *Paraplacodus* have a long, laterally compressed tail that would have been moderately flexible, although it is not as deep as typically expected for an amphibious animal. Cyamodontoids evolved unusual tails, sometimes exhibiting rows of scutes. In some forms the tail was stiff and round in cross-section and so could not have been much use in swimming.

Placodont armour

Unarmoured placodonts had robust bodies that were rather square-shaped in cross-section. Cyamodontoids elaborated on this design by evolving a dorsoventrally compressed body in which hexagonal osteoderms on the animal's dorsal surface were tightly sutured together to form a carapace. In some forms the carapace consisted of two shields, the main one and a small posterior one covering the base of the tail. The

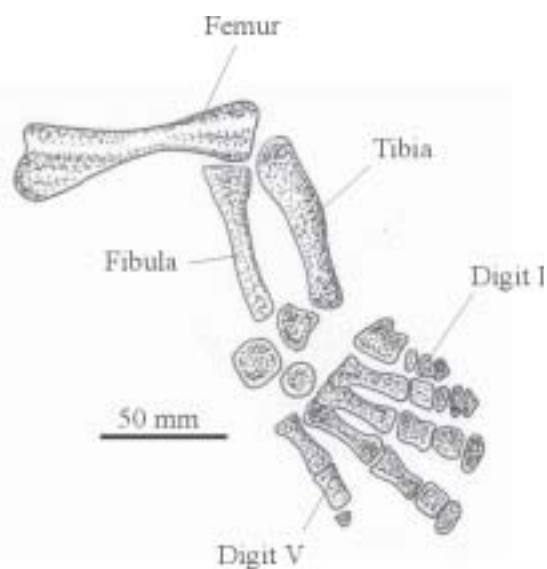


Fig. 5. Right hind limb of *Psephoderma alpinum* from the Late Triassic of Germany, the southern Alps and possibly England. The toes are rather short and, if encased in webbing, would have formed a paddle-like foot. Note that the last three digits do not bear claws. Redrawn from Renesto & Tintori (1995).

shape and surface texture of placodont osteoderms is variable, and they range from flat with a pitted or grooved surface to pyramidal or tubercular. They may be solid or largely hollow and diverse osteoderm morphologies may be present on a single individual. In *Psephoderma*, osteoderms with raised midline keels form three distinct ridges running the length of the carapace (Fig. 3). In those cyamodontoids with a plastron (*Henodus*, *Placochelys* and *Psephosaurus*), osteoderms also fused together along the sides of the body to form a lateral wall linking the plastron and carapace.

The presence in cyamodontoids of a turtle-like shell opens up several interesting areas of speculation. Modern turtles with hard shells are known to be extremely resistant to fluctuations in salinity compared to other amphibious reptiles, simply because the shell acts as a superb osmotic barrier. An indication that cyamodontoids were similarly resistant comes from the environment in which *Henodus* is preserved, a lagoonal-brackish lake subjected to influxes of fresh water and to marginal desiccation resulting in extreme hypersalinity. This idea of 'tolerant placodonts' is also supported by the longevity of cyamodontoids compared to other Triassic marine reptile lineages. While most sauropterygians became extinct at the end of the Carnian (related perhaps to a series of marine transgressions and regressions), cyamodontoids persisted as late as the Rhaetian.

Placodont armour may also have served a defensive purpose. However, while two juvenile *Cyamodus* specimens have been reported from the stomach contents of the nothosaur *Lariosaurus*, most placodonts inhabited environments where predators large enough to have preyed on them were absent. An alternative, though not mutually exclusive, suggestion is that the carapace may have improved hydrodynamic efficiency. This may have been particularly true for keel-shelled *Psephoderma*, where the keels may have helped to control the flow of water around the body, and help make the animal faster and more stable when swimming.

Unarmoured placodonts

Paraplacodus, the most basal known placodont, is represented by only one species, *P. broillii* Peyer, from the Grenzbitumen-horizon (Anisian-Ladinian boundary) of Monte San Giorgio in the Southern Alps. It has three elongate, forward-pointing teeth in each premaxilla and two elongate teeth at the tip of each dentary (Fig. 4A). There are seven rounded crushing teeth on each maxilla, four larger and more rectangular teeth on each half of the palate, and seven rounded teeth on each dentary. *Saurosphargis voltzi* from the Lower Anisian of Poland, known only from

a single skeleton destroyed in World War Two, re-called *Paraplacodus* in its rib morphology and may have been a close relative, but, unlike *Paraplacodus*, it had at least some osteoderms.

Placodus Agassiz is one of the best known and most common of all placodonts and many species have been named, all from the Lower and Upper Muschelkalk (Anisian-Ladinian) of Germany. Like *Paraplacodus*, *Placodus* has three forward-pointing teeth in each premaxilla (Fig. 4B), but, unlike those of *Paraplacodus*, these teeth are robust and spatulate. The three palatal teeth of *Placodus* are huge and highly distinctive, being expanded (they take up almost the entire palatal surface) and rectangular in shape (Fig. 4D). *Placodus* was large (to 3 m), bulky, and with a long tail (Fig. 2A).

Cyamodontids – wide skulls, wide carapaces

Cyamodontids are represented only by *Cyamodus* Meyer, a genus for which four species from Anisian and Ladinian times are present. These differ in the width and length of the skull as well as in other features, and some workers have suggested that new genera should be erected for all those species other than *C. rostratus*, the type species. It has also been argued that *Cyamodus* does not form a clade and that some species are more closely related to placochelyids than are others. Recent research does not support these views. Phylogenetic studies indicate that

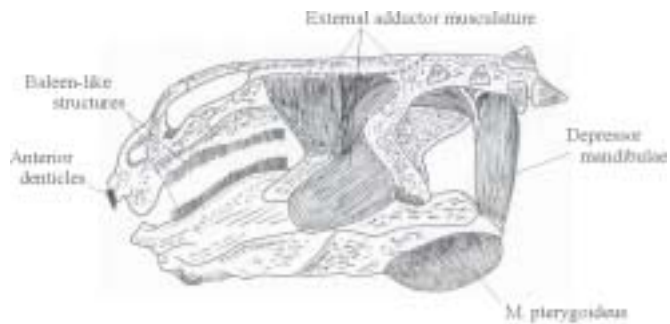


Fig. 6. The bizarre skull of *Henodus chelyops* in lateral (with baleen-like structures and some of the more important musculature reconstructed), and dorsal views. Note also the denticles on the premaxillary flange, the anterior location of the nostrils and eye sockets and the absence of supratemporal fenestra. Redrawn from Rieppel (2001, 2002).

Cyamodus is monophyletic and shares unique skull features with *Henodus*. Consequently, cyamodontids and *Henodus* have been united in a cyamodontoid subgroup termed the Cyamodontida (Fig. 1B).

Cyamodus has a remarkable skull that has been described as 'heart shaped.' It is anteroposteriorly short, with a reduced snout and face, but unusually wide, with enormous supratemporal fenestrae usually more than twice as wide as the eye sockets (Fig. 4C). There are either two or three small maxillary teeth and two or three palatine teeth, the most posterior of which is much larger than the more anterior one. Unlike *Henodus* and the placochelyids, *Cyamodus* possessed two small, projecting teeth in each premaxilla. Juveniles appear to have had one extra tooth on the palate or maxilla compared to adults. The body of *Cyamodus* was broad and flattened with a carapace composed of hexagonal to subcircular osteoderms and subconical osteoderms also decorated the skull, limbs and tail (Fig. 2B). Because *Cyamodus* had stronger limbs and a deeper body than the placochelyids, it has been suggested that it might have been less bottom-dependent and more mobile than these forms, perhaps living in rougher waters in a more rocky environment.

Bizarre, square-snouted *Henodus*

Henodontids, named for *Henodus chelyops*, are known only from the Gipskeuper deposit of Tübingen-Lüstnau (Carnian, early Upper Triassic), southern Germany. Because the Gipskeuper is believed to represent a semi-enclosed brackish lagoon, *Henodus* is the only placodont known to have inhabited a non-marine environment. The skull of *Henodus* looks rather surreal with its broad, squared-off rostrum, hypershortened pre-orbital region and broad flat skull table (Fig. 6). The nostrils and orbits are located close to the snout tip and because the skull is curved when viewed from the side, the nostrils and orbits face forwards.

The dentition is strongly reduced with only one pair of small teeth located far to the rear on the palatine bones and another on the dentaries. Gutter-like grooves run along the edges of the upper and lower jaws. The lower jaw is surprisingly deep and heavy, but its low coronoid process suggests that *Henodus* did not have the awesome crushing bite of other cyamodontoids. However, features indicative of musculature allowing rapid jaw opening are present while prominent hyoid bones imply that *Henodus* had a distensible throat. In its postcranial anatomy, *Henodus* is not that different from *Cyamodus*. It does, however, have an even wider carapace (Fig. 7) as well as a plastron and a lateral wall.

Given these features, how and what *Henodus* ate has always been controversial. A popular idea has

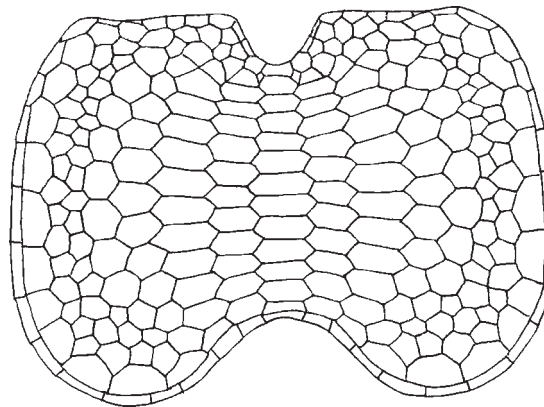


Fig. 7. The broad carapace of *Henodus chelyops* in dorsal view showing the reconstructed pattern of osteoderms. Redrawn from Westphal (1976).

been that it grubbed around in the mud for crustaceans. However, the rediscovery in the 1990s of striations within the jaw grooves (originally reported in 1936) indicate that *Henodus* had baleen-like material fringing its jaws. Furthermore, long overlooked is that the premaxillae support a ventrally projecting flange with a sharp cutting edge and, most surprising of all, that this cutting edge exhibits a row of tooth-like denticles along its anterior surface (Fig. 6). When considered together and compared with the feeding adaptations of turtles, these features suggest that *Henodus* was a filter feeder that employed depression of the heavy lower jaw and expansion of the throat to suck in food particles. It may have engulfed swimming invertebrates, filtered burrowing forms out from the substrate, or used the premaxillary flange and denticles to scrape algae off rocks or to cut off pieces of other kinds of aquatic vegetation. Clearly, reappraisal of this bizarre placodont has revealed hitherto unsuspected diversity in the ecology of Mesozoic marine reptiles.

Placochelyidans, the 'reptilian rays' and allies

In marked contrast to short-snouted *Cyamodus* and *Henodus*, the exclusively Late Triassic members of the Placochelyida are united by an elongate rostrum. This has a concave ventral surface and a reduced or absent dentition. While the best known and most derived members of the Placochelyida, the placochelyids *Placochelys* and *Psephoderma*, exhibit extensive carapaces, the two most basal forms (*Macropalacus* from the Rhaetian of Germany and *Protenodontosaurus* from the Carnian of Italy) are known only from skull material and remain mysterious. Placochelyids also have a distinctly depressed skull, and an even longer and narrower rostrum than *Macropalacus* and *Protenodontosaurus*.

How placochelyids lived, and what they preyed upon, has been the subject of some controversy. Because their long, slender rostra do not seem powerful enough to have wrenched shelled invertebrates from

hard surfaces it is inferred that they probed for prey in soft sediments. Grooves run along the bottom of the rostrum, all the way from its tip to the internal nostrils on the palate. This implies that, while probing the sediment, placochelyids inhaled water and tested it for olfactory clues: such underwater olfaction has been recently proposed for plesiosaurs and may prove even more widespread in fossil marine reptiles. Once prey was located, a placochelyid may have employed suction to get the prey into its mouth. As noted earlier, placochelyids exhibit muscle attachment sites on the back of the skull and lower jaw which would have allowed them to generate powerful suction, simply by rapidly opening the jaws.

The flattened bodies and long, slim tails of placochelyids (Fig. 3) have led some experts to liken them to modern eagle rays. These hide from predators by burying themselves in the sea floor substrate, and dig for hard-shelled invertebrates in sand and mud. This seems unlikely though given that, unlike rays, placochelyids had an inflexible body and did not inhabit an environment where there were predators large enough to tackle them.

Placodonts that aren't

Two forms previously regarded as primitive, basal placodonts are no longer thought of as such. *Helveticosaurus zollingeri* from the Anisian of Switzerland, initially described as an extremely primitive placodont and even given its very own placodont subgroup (the Helveticosauroidae) in 1955, has turned out instead to be an unusual aquatic non-sauropterygian archosauromorph. Another supposed basal placodont, *Negevodus ramonensis* from the Middle Triassic of Israel, was described in 1986 on the basis of a fragment of upper jaw. Combining features not seen in other placodonts with those of basal placodonts and advanced cyamodontoids, *Negevodus* was finally reinterpreted in 1991 as a member of the Temnospondyli, a group of basal tetrapods regarded by some as the ancestors of modern frogs, salamanders and kin.

Placodont lifestyle and ecology

Their pavements of crushing teeth indicate that placodonts fed by crushing the shells of invertebrates and then feeding on the soft parts. Presumably, they crushed their prey by positioning them between the enormous palatal and mandibular teeth, spat out the bits of shell, and then swallowed the soft parts. Placodonts like *Placodus* have usually been regarded as predators of bivalves, but brachiopod fossils are also abundant at some placodont-bearing localities and broken masses of brachiopod shells have been

regarded by some experts as the remains of placodont meals.

Because of this shellfish-crushing lifestyle, placodonts have often been regarded as reptilian analogues of walrus. This is not entirely appropriate, however, as we now know that walrus do not crush their mollusc prey (it used to be thought that they did), but instead employ suction alone to remove the soft parts. Furthermore, it is incorrect to stereotype all placodonts as bivalve or brachiopod eaters because some placodont taxa occur in strata where such invertebrates are all but absent. Decapod crustaceans are generally abundant in these cases, however. As noted earlier, *Henodus* has been interpreted as a herbivore, filter-feeder or both.

Because all placodonts appear capable of at least some movement on land, it can be imagined that they were egg-layers that dug nests high on beaches. To date, however, nothing is known about placodont reproduction. Evidence for sexual dimorphism has not been reported.

Suggestions for further reading

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