The myth of the Mesozoic cannibals

Victorian naturalists portrayed ichthyosaurs as fearsome beasts with a penchant for cannibalism. But another look at the bones shows how wrong they were

Michael Benton

Reptiles have long been regarded as morally corrupt, rather low sorts of creatures—witness Victorian natural history books with their tales of cold-blooded crocodiles and strange and terrible dinosaurs. And of all their alleged corruptions, it is cannibalism that holds the greatest fascination. But just how prevalent was cannibalism among the dinosaurs and their primeval colleagues? Palaeontologists have been debating this question for years, scouring the fossil record for clues. The focus of their attention has been the ichthyosaurs, dolphin-like animals that lived during the Mesozoic, between 245 and 65 million years ago.

Over the past 200 years, many examples have emerged of adult ichthyosaurs with juveniles trapped in their ribcages; the best come from Holzmaden, near Stuttgart, in Germany. The key question has been whether these juveniles are prey or embryos. Now, a study by Roland Böttcher, of Stuttgart's natural history museum, may have finally settled the matter. Having pored over the evidence, Böttcher finds the ichthyosaurs not guilty: the juveniles are unquestionably embryos, he says. Additional support for this verdict comes from an ichthyosaur fossil found recently in Britain, now on show in Bristol City Museum.

Böttcher's study is important because it deals a hefty blow to the whole notion of ancient reptiles as cannibals. Aside from the ichthyosaur skeletons, evidence that extinct reptiles ate members of their own species is extremely scarce. Indeed, there is only one unequivocal specimen, a skeleton of an adult Coelophysis discovered in New Mexico in 1947 and dated at about 220 million years ago (the late Triassic). Tellingly, the fossil harbours the skeleton of a second Coelophysis, not only curled up in a suspicious manner inside the adult's ribcage, but also far too large to be an embryo.

Böttcher's study also establishes beyond doubt that the ichthyosaurs bore live young instead of laying eggs, as is more usual for reptiles. It confirms what many palaeontologists have long suspected: that for ichthyosaurs, live birth would have been essential. Being confined to water, the creatures would have been unable to lay eggs in the sand as modern aquatic turtles and crocodiles do. And, being air-breathing, the embryos in any eggs laid under water would simply have suffocated. The acceptance of these ideas means that researchers can now start to make interesting comparisons between the ichthyosaurs and the many groups of modern lizards and snakes which have evolved viviparity (the ability to retain embryos in the oviducts until they have developed sufficiently to lead independent lives).

The first ichthyosaur carrying a juvenile came to light at Holzmaden as long ago as 1749. Yet the fossil was not described in print until 1824, and even then the author, Georg Friedrich von Jaeger, failed to spot the juvenile. It was only some 20 years later, following other finds, that the controversy began in earnest. Some naturalists were happy to accept the idea of ichthyosaurs giving birth to live young, while others immediately interpreted the "included" juveniles as evidence of cannibalism.

As more and more ichthyosaurs carrying young emerged, the debate gathered momentum. Since the 1840s Holzmaden has yielded several hundred skeletons of adult ichthyosaurs, of which some fifty appear to carry young, and researchers are still finding new specimens. Supporters of the embryo theory have always explained the high proportion of suspect fossils by arguing that pregnant females, especially those close to, or at, term were particularly vulnerable. But can such an argument account for all the specimens?

A German naturalist called Wilhelm von Branca believed not. In 1908 he published what became the authoritative account of why some of the skeletons within skeletons had to be prey. His argument rested on five observations: some adults contain juvenile skeletons of various sizes; some juveniles lie close to remnants of chewed food; most skeletons face the same way as the adult (which implies tail-first birth, something Branca considered unlikely); most skeletons lie away from the region of the uterus; and ribcages commonly contain up to 10 or 11 skeletons (Branca thought this significant because whales and dolphins generally give birth to a single, large calf).

Initially, the influence of Branca's study extended well beyond the ichthyosaurs themselves. It encouraged the belief that many, if not most, extinct reptiles had had cannibalistic tendencies, and even fuelled suspicions about modern reptiles. As naturalists learnt more about the habits and reproductive biology of modern reptiles, the study's influence waned, but the notion of the ichthyosaurs as cannibals persisted. Nobody bothered to challenge Branca's arguments in detail—that is, until Böttcher decided to reopen the case.

Böttcher overturns each of Branca's arguments and marshals more evidence to support the opposite view. First, the way the young are preserved points to their being in the uterus rather than in the gut, he argues. There are signs that in certain specimens the gases released by the decomposition of the adult's flesh have forced one or more of the embryos out of the cloaca tail first. In some cases the embryo's head remains lodged between the pelvic bones, while its body lies outside. Had the juveniles been swallowed, gases within the adult would have pushed them in the opposite direction, up into the ribcage. Only partly digested specimens in the intestine would have been within reach of the pelvic area—and no such fossils have been discovered.

Some specimens appear to contradict this interpretation, as they contain juveniles at the front of the adults' ribcages. Böttcher's explanation is that this position is close to that of the oviducts of living reptiles. By analogy with modern
Viviparous lizards and snakes, he argues, ichthyosaur oviducts probably expanded during gestation to occupy both sides of the ribcage as far forward as the shoulder area. The right oviduct extended further than the left, and the embryos probably moved from side to side to make best use of the available space. According to specimens that preserve traces of internal organs, the stomach, heart and lungs lay below the oviducts. Any young contained in the stomach would end up lying nearer the underside of the ichthyosaur skeletons.

A third piece of evidence comes from the way the skeletons lie. Some of the very small skeletons are curled up as though confined by an egg membrane, but most of the larger skeletons are stretched out, parallel to the backbone of the adult. Had they been swallowed whole, they would be more disordered. It seems that the ichthyosaurs had evolved beyond the first stage of bearing live young, in which the mother retains her eggs inside her body to provide a kind of protective nest, with the yolk sac providing all nutrition. At least at larger sizes, it would appear, ichthyosaur young were nourished by maternal nutrients that passed through a placenta. Further support comes from the fact that the eggs of many modern groups of lizard have components which function as a kind of placenta and which have evolved quite independently of the better-known mammalian placenta.

The fact that the heads of the young skeletons nearly always point forward is in itself an important clue. Böttcher notes that modern animals which devour their prey whole, such as snakes and fishes, tend to swallow them head first. Branca’s interpretation was quite different. Based on the behaviour of modern animals, he argued that ichthyosaurs must have given birth to their young head first, and that the small skeletons were therefore pointing the wrong way to be embryos. This reasoning turns out to be flawed: mammals that usually give birth to a single, large juvenile follow the “head-first” rule, but mammals that bear large numbers of less-developed young show no preferred orientation.

The behaviour of other aquatic animals also casts doubt on Branca’s interpretation. Viviparous bony fishes give birth both ways, while young sharks are usually born tail first. The coelacanth’s preference has changed during the course of evolution. The young of the living fish Latimeria are born tail first, but the young of the extinct coelacanth Undina were born head first, according to fossil evidence. Limited observations suggest that the young of whales and hippopotamuses are also born tail first.

Tail-first birth is an obvious adaptation for air-breathing animals confined to water. The supply of oxygen from the mother is relinquished only at the last minute, giving the
Prime suspect: one of the fifty or so ichthyosaur skeletons from Holzmaden that carry young ichthyosaurs in their ribcages. A small skeleton has been expelled from the ribcage by gases released during the decomposition of the adult’s flesh.

Most “caged” ichthyosaurs lie closer to the supposed oviduct areas, on either side of the backbone, than to the stomach regions. During gestation, the embryos probably moved from side to side.

Just 16 centimetres long, this fetus from Somerset is the smallest ichthyosaur embryo found to date. It was probably expelled from its mother after she had fallen to the seabed.

the relationship would be expected to blur for the largest adults, who would tend to eat both small and large prey. Branca made much of the fact that a few adult ichthyosaurs do contain young of wildly different sizes. But these could in fact be embryos at different stages of development.

In any case, Böttcher resolves any doubts by showing that the adult ichthyosaurs and their respective young obey an established equation governing the sizes of reptiles and their hatchlings. The equation, first proposed by Phil Currie of the Royal Tyrrell Museum of Palaeontology in Alberta and Bob Carroll of McGill University in Montreal, is purely empirical but holds true for 120 species of living lizards and crocodilians. It would be remarkable if adult ichthyosaurs had chosen to feed only on juveniles whose sizes match those predicted for their offspring at term.

The parameters for the equation vary according to reproductive strategies. Robin Andrews of the Virginia Polytechnic

juvenile ample time to swim to the surface to fill its lungs for the first time. Also, studies of modern animals show that the heaviest part of the body often lies lowest in the uterus and so is born last. For whales and ichthyosaurs, unlike land-dwelling mammals, this is the front part of the body because the hind limbs and hip, no longer needed for walking, are comparatively small.

If the young are embryos, there ought to be a relationship between their sizes and those of the adults. This is exactly what Böttcher finds: in general, the bigger the adult ichthyosaur, the bigger its juveniles. Although a similar trend could result from cannibalism—bigger predators can tackle bigger prey—
The relationship between adult body length and hatching length (right). The thick lines are for individual reptile groups; the fine line gives the overall correlation for 120 species. The ichthyosaurs' straight line proves their innocence. Gradients vary according to reproductive strategy. Snakes lay few eggs (top, right) and so have a steeper gradient than turtles, (top, left)

Institute and State University, Virginia, has found that the parameters are slightly different for each group of living reptiles. The hatching sizes of crocodilians and turtles vary little with adult size, probably because these creatures lay extremely large clutches of eggs (up to 200). Fewer eggs at a sitting

means that larger mothers can invest more per egg and produce larger hatchlings. Lizards lay 5 eggs on average, and most snakes lay between 1 and 20 eggs. The parameters for ichthyosaurs are close to those of lizards and snakes.

The final piece of evidence is based on the anatomy of the gut. The ichthyosaur's stomach appears simply too small and complex to have accommodated the indigestible fruits and seeds of naked seeds. Bothecher doubts that an ichthyosaur could have digested such large, bony prey, and the behaviour of modern crocodilians bears this out. Large prey animals get stuck in the throats of crocodiles until the parts in the stomach have been digested. If ichthyosaurs really did eat large juveniles, one would expect to find adults with juvenile skeletons poking out of their mouths.

None of the fossils contains evidence of partially digested juveniles. Studies show that ichthyosaurs ate small cephalopods and fishes, which were rapidly broken down into a sludgy mess inside the stomach. The hard bits of a prey animal, such as the chitinous booklets of the cephalopods, were retained in the stomach; small fish bones were probably dissolved by the digestive juices. It would have been quite impossible for complete skeletons of young ichthyosaurs to pass into

Caring, sharing dinosaurs bury old prejudices

THE myth of the wicked reptile is dealt a further blow by palaeontologists working in the US and in Mongolia who have found evidence of caring group behaviour among dinosaurs.

John Horn, of Montana State University, has been excavating dinosaur nesting sites in Montana for nearly 15 years. He discovered early on that these dinosaurs, herbivorous hadrosaurs and hypsilophodontids, laid their eggs in batches of 20 to 30 in large circular nests which they scraped out in the sand. The female, it seems, scooped a hollow about 1 metre wide and laid her eggs in concentric circles. She then covered them with sand and sometimes with leaves and twigs: as with some modern crocodilians, the rotting vegetation would have helped to warm up the nest and incubate the eggs.

Horn found that the Montana dinosaurs nested communally—like many modern birds—spacing their nests out so that no mother dinosaur could quite reach the neighbouring ones. By digging down beneath the nests, he found successive layers of burned rock with nests, suggesting that the dinosaurs returned to the same nesting site year after year.

Many of the nests still contain eggs, some of which are unhatched. One hypsilophodontid egg contains a tiny embryo which would have been just 20 centimetres long, compared to an adult length of 5-6 metres. Horn argues that

these tiny hatchlings were too small and poorly developed to move far from the nest, and that their parents must therefore have fed and protected them.

Further evidence that dinosaurs reared their young comes from skeletons of adult and juvenile hadrosaurs, of the genus *Maasaura* ("good mother reptile"), which Horn found near the nests. The juveniles

from the American Museum of Natural History. Yet another detail was done on these finds until Konstantin Mikhailov, of the Palaeontological Institute in Moscow, and Karov Sabath, of the Palaeontological Institute in Warsaw, began their studies.

The two researchers have now identified eggs and nests produced by all the major dinosaur groups, including the large herbivorous sauropods, the herbivorous horned ceratopsians, and the carnivorous theropods. At one of their Montana sites, they found nests in the sand made by two or three different kinds of dinosaurs, as well as one kind of bird, all on a beach as a lake. Mikhailov's findings suggest that the idea that dinosaurs nested communally and returned to the same nesting grounds each year.

Mikhailov made an even more startling discovery in the nest in Mongolia. Among the shell fragments were numerous bones of herbivorous ceratopsians and other small reptiles. The conditions of the site showed that these small bones had not been washed in, nor were the ceratopsians, being herbivores, feeding on the eggs. Mikhailov's interpretation is that the theropods had stacked the nest with small prey as food for their ravenous hatchlings. But this remains controversial because of the methods used to identify the eggs (This Week, 7 September).
The deepest regions of the stomach or into the intestine.

Only two observations are difficult to square with the embryo theory. The first is that some adults contain juveniles of various sizes. Böttcher's reply is that most of these juveniles lie above the gut. Instead of reflecting cannibalism, he argues, the size variation suggests ichthyosaurs carried young at different stages of development as do some modern viviparous reptiles. Alternatively, the smaller skeletons may be of young that died during development and became trapped. Some modern animals abort dead embryos only after the birth of their surviving siblings.

Secondly, why do the majority of specimens carry much fewer than the maximum number of young—an average of about 3 instead of 10 or 11? One possibility is that at the time of death most ichthyosaurs had already given birth to some young. Another is that a high proportion of embryos vanished during death, or afterwards during preservation and fossilisation.

The best evidence for an ingested juvenile comes not from Holzmaden but from southern England. An ichthyosaur fossil found in Somerset in 1846 contains a tiny skull covered by the contents of the creature's stomach. Whether the skull lies in the stomach itself or the uterus, however, is unclear: the fossil may thus be an accident of preservation. A similar fossil was apparently found in Holzmaden in the 1840s, but it has since been lost.

A more recent finding from Somerset, dated at about 200 million years ago, offers little comfort to the cannibalism camp. The fossil shows a tiny, curled fetus just behind the cloacal opening; it was probably expelled by decomposition gases. No other young are present, suggesting that the rest of the litter vanished during decay.

Given the lack of hard evidence, why has the cannibalism theory proved so resilient? Naturalists have always been rather zealous in looking for signs of cannibalism among "lower organisms", whether they be worms, sharks, reptiles or cave-men. This tendency has exaggerated the significance of what little evidence there is. Studies show that modern reptiles do indulge in cannibalism, but not nearly to the extent implied by some naturalists' tales.

One alleged offender is the world's largest lizard, the Komodo monitor (Varanus komodoensis). There have been many reports of the Komodo monitor digging up nests of eggs and eating hatchlings and juveniles of its own species. Yet, on closer inspection, the true extent of these activities appears quite limited. Some research suggests that 8 per cent of Komodo monitor droppings carry remnants of cannibalistic meals, but most put the figure at less than 2 per cent.

The alligator, though not completely innocent (dissected adults occasionally contain the remains of young alligators) has suffered similarly. Female alligators, for instance, assist their young out of the nest and into the water, crushing and swallowing rotten or infertile eggs while doing so. Predictably, casual observers have tended to interpret such behaviour as evidence of cannibalism. Even more unjust, female crocodiles often carry hatchlings, in their mouths, to the water for a first swim: a caring act, but one often misconstrued as a mother eating her own offspring.

The moralistic view of natural history prevalent in Victorian times no doubt encouraged such misjudgments. But at least for the ichthyosaurs, the spectre of cannibalism has now been laid to rest. With the acceptance of Böttcher's ideas about the trapped skeletons, researchers can at last begin to use the many excellent specimens to build up a fuller picture of the developmental biology of ichthyosaurs. The embryos may even shed light on the vexed question of the origin of the ichthyosaurs, and their acquisition of such advanced aquatic adaptations from a fully terrestrial ancestry.