LETTERS

Jaws and teeth of the earliest bony fishes

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Extant jawed vertebrates, or gnathostomes, fall into two major monophyletic groups, namely chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes and tetrapods). Fossil representatives of the osteichthyan crown group are known from the latest Silurian period, 418 million years (Myr) ago, to the present. By contrast, stem chondrichthyans and stem osteichthyans are still largely unknown. Two extinct Palaeozoic groups, the acanthodians and placoderms, may fall into these stem groups or the common stem group of gnathostomes, but their relationships and monophyletic status are both debated. Here we report unambiguous evidence for osteichthyan characters in jaw bones referred to the late Silurian (423–416-Myr-old) fishes *Andreolepis hedei* and *Lophosteus superbus*, long known from isolated bone fragments, scales and teeth, and whose affinities to, or within, osteichthyans have been debated[1–11]. The bones are a characteristic osteichthyan maxillary and dentary, but the organization of the tooth-like denticles they bear differs from the large, conical teeth of crown-group osteichthyans, indicating that they can be assigned to the stem group. *Andreolepis* and *Lophosteus* are thus not only the oldest but also the most phylogenetically basal securely identified osteichthyans known so far.

Scales and minute bone fragments of *Lophosteus* and *Andreolepis* are classical fish remains from the Upper Silurian (423–416-Myr-old) limestone of the Baltic area[1–12]. They are now known elsewhere in the world, and *Lophosteus* occurs up to the early Devonian period (410 Myr ago)[8,9,13]. However, their affinities have long been a riddle. When first discovered, *Lophosteus* was tentatively referred to osteichthyans on the basis of its diamond-shaped scales[1,2], but its stellate ornamentation was later regarded as more suggestive of placoderms (armoured jawed vertebrates)[13] and its large fin spines suggested a relationship to acanthodians[5,8,10]. The latter are Ordovician to Permian (445–294-Myr-old) fishes that have been regarded as possible stem osteichthyans but lack the characteristic osteichthyan suite of large dermal bones and rows of shedding marginal teeth (acanthodian teeth, if present, are generally arranged in whorls or statodont rows; that is, non-shedding tooth rows growing by the addition of new teeth at one end). The relationships of *Andreolepis* have been more consensual. *Andreolepis* is generally regarded as a primitive actinopterygian (ray-finned fish)[3,6,9] on the basis of its ganoid scale structure (superimposed layers of dentine and enameloid), but it has also been supposed to share some derived characters with onychodontiform sarcopterygians (lobe-finned fishes) and acanthodians[7].

Although known from thousands of minute remains collected by dissolving limestone blocks in acid, *Lophosteus* and *Andreolepis* have until now yielded no skull-bone feature that would unambiguously anchor their relationships to the osteichthyan crown group. None of the dermal bones recorded so far unambiguously resembles a typical osteichthyan dermal bone, or shows the characteristic closed sensory-line canals of osteichthyans. No sensory-line bearing bone of *Andreolepis* is yet known, and those of *Lophosteus* only show broad sensory-line grooves[4,5,8,9]. Only one large dermal bone fragment of *Andreolepis* has been tentatively referred to a cleithrum, a dermal bone of the osteichthyan shoulder girdle[7]. We are therefore left with the ganoid scales of *Andreolepis*, including its possible fulcral scales that strengthened the leading edge of the fins, which are convincingly actinopterygian-like[6,7]. Nevertheless, no characteristic osteichthyan lepidotrich (bony dermal fin ray segment) has ever been recorded in association with either *Andreolepis* or *Lophosteus*, whereas they are common in Devonian (416–359-Myr-old) and younger osteichthyan-bearing sediments. This combination of characteristics indicates that both genera might belong to the osteichthyan stem group.

Two new discoveries of dermal jaw bones strongly support the placement of *Andreolepis* and *Lophosteus* in the osteichthyan stem group. Like all the previous material they are isolated fragments but can confidently be assigned to their respective genera on the basis of their dermal ornament (see Supplementary Information). First, among the incomplete skull bones of *Andreolepis* collected from the island of Gotland (Sweden; see Supplementary Information) some years ago, several have been identified as fragments of dentary; that is, the dermal bone of the lower jaw that normally bears the lateral series of large conical teeth ('outer dental arcade') in osteichthyans. We show here the best preserved fragment (Fig. 1a–d). This dentary curiously lacks large teeth, its edge bearing only rows of enlarged denticles that laterally grade into the rounded tubercles of the external bone ornamentation (Fig. 1d). Its internal surface is similar to that of the dentary in Devonian actinopterygians and sarcopterygians but, contrary to actinopterygian dentaries, there is no evidence for a mandibular sensory-line canal (Fig. 1a; see Supplementary Information). This suggests that a ventral row of infradentaries carried the canal, as in sarcopterygians.

Second, a large denticle-bearing dermal bone, ornamented with the characteristic stellate tubercles of *Lophosteus*, was discovered recently in late Silurian erratic boulders from Germany (see Supplementary Information). Its posteriorly increasing depth recalls an osteichthyan maxillary, and its denticles, although small, are slightly more distinct from the external ornamentation than in the dentary of *Andreolepis* (Fig. 2a–c). However, they differ from the characteristic maxillary teeth of early actinopterygians and sarcopterygians in being organized in at least three, almost parallel, longitudinal rows that, when combined, form transverse denticle files (Fig. 2d). Minute fragments of denticle-bearing dermal bones of *Lophosteus* (notably a probable 'denticle whorl') have been mentioned previously[4,5], but the specimen described here is clearly identifiable as a maxillary, as a result of the presence of a narrow medial horizontal lamina (Fig. 2b, d) and a low anterior prolongation that bears a small anterior overlap area (Fig. 2a). As a whole it compares in

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outline with the anterior part of the maxillary of early actinopterygians (Fig. 1e) and certain early sarcopterygians, notably onychodontiforms (Fig. 2e, f). The overlap area may be for a short lacrymal bone (Fig. 2a, f) and there is a possible suture area for the premaxillary (see Supplementary Information).

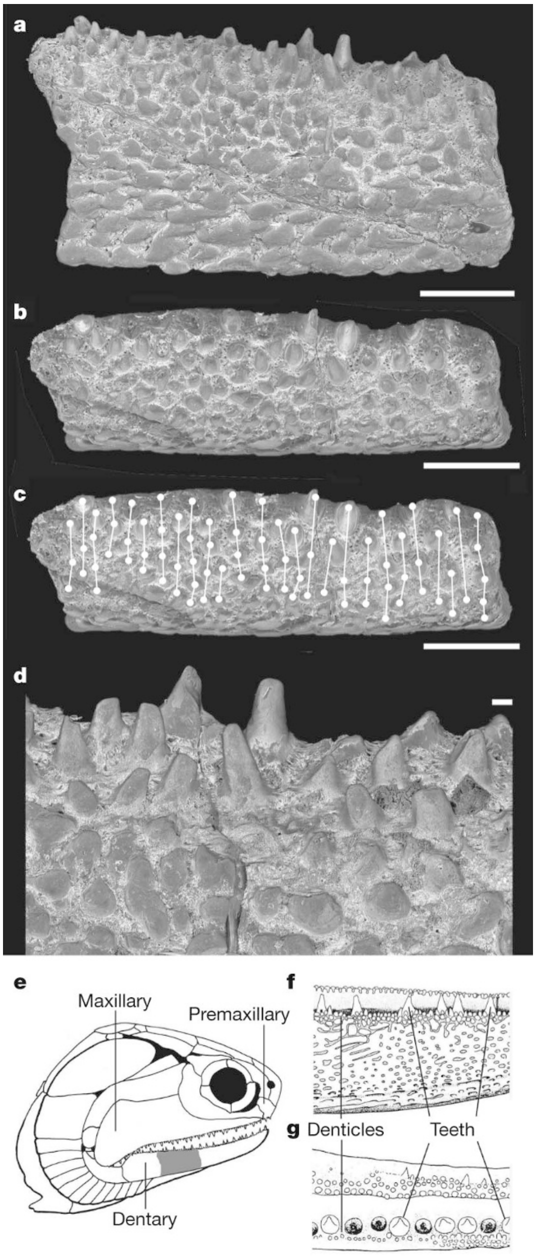

Figure 1 | Comparison of the dentary of *Andreolepis* with that of an actinopterygian. a–c, Incomplete right dentary of *Andreolepis hedei*, Upper Silurian (Ludlow) of Gannes, Gotland, Sweden (Lund University LOG87-301DF; scale bars, 1 mm (**a**–**c**) and 0.1 mm (**d**); scanning electron micrographs); **a**, Lateral view. **b**, **c**, Dorsal view showing the transition between the tooth-like denticles of the dorsal edge and the external ornamentation of the bone (**b**) and the possible arrangement of the denticles into files with alternating denticle initiation (**c**). **d**, Detailed view of the denticles in the middle part of the bone. **e**–**g**, Comparative illustration of the late Devonian (380-Myr-old) actinopterygian *Moythomasia* (from ref. 27; not to scale). **e**, Head showing the portion of the dentary (grey) corresponding approximately to the dentary fragment of *Andreolepis* in **a**–**d**. **f**, **g**, Lateral (**f**) and dorsal (**g**) views of the dentary showing the monolinear series of true conical teeth (absent in *Andreolepis*) and the labial series of denticles grading into the ornamentation, comparable to the denticles of *Andreolepis*.

The dentary of *Andreolepis* and the maxillary of *Lophosteus* both differ from their homologues in younger osteichthyans in lacking the series of large, conical teeth that are conspicuous in basal actinopterygians (Fig. 1f, g) and sarcopterygians (for example *Onychodus*; Fig. 2e, f), except for lungfishes, which have lost the marginal tooth rows[14]. In early actinopterygians and sarcopterygians, these large teeth are nevertheless bordered laterally by series of pointed denticles that gently grade into the external ornamentation (Fig. 1f, g) and are thus suggestive of the denticles on the dentary of *Andreolepis* and the maxillary of *Lophosteus*. In both forms, these denticles are similarly curved towards the jaw margin and show a marked gradient in size, the medialmost ones being larger than the lateral ones (Fig. 2d).

The presence of osteichthyan marginal jaw bones in *Andreolepis* and *Lophosteus*, coupled with the absence of the characteristic osteichthyan linear shedding tooth rows, is most readily interpreted as reflecting a phylogenetic position in the osteichthyan stem group (Fig. 3). Consequently, the ganoid scale structure of *Andreolepis*, long

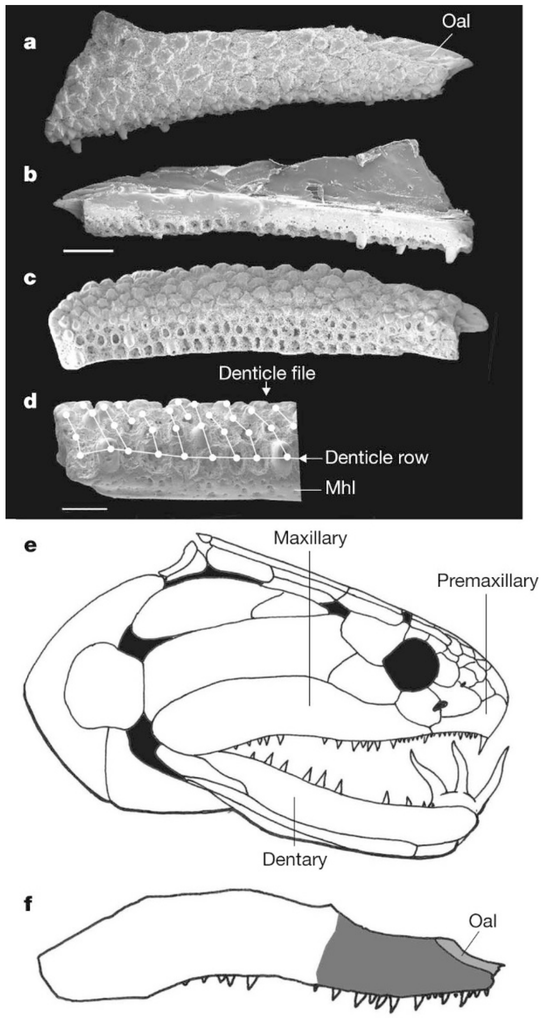

Figure 2 | Comparison of the maxillary of *Lophosteus* with that of a sarcopterygian. a–d, Right maxillary of *Lophosteus superbus*, Upper Silurian (Middle–Upper Pridoli) erratic boulder of Germany (Museum für Naturkunde, Berlin MB.f.17035; scale bars, 1 mm (**a**–**c**) and 0.1 mm (**d**); scanning electron micrographs). **a**, Lateral view. **b**, Medial view. **c**, Ventral view showing the transition between the denticles and the external ornamentation. **d**, Detail of the posterior end of the ventral edge showing the organization of the denticles into rows and files. **e**, **f**, Comparative illustration of the late Devonian (380-Myr-old) onychodontiform sarcopterygian *Onychodus* (from ref. 28, not to scale). **e**, Head in lateral view. **f**, Maxillary showing the portion (grey) approximately corresponding to the maxillary fragment of *Lophosteus* in **a**–**d**. Mhl, medial horizontal lamina; OaL, overlap area for the lacrymal.

regarded as an actinopterygian 'signature', is probably a more general character than previously believed, as also suggested by its presence in the supposed early Devonian actinopterygian *Dialipina*, whose anatomy is in fact strongly at odds with that of all early crown osteichthyans[15]. Moreover, the skull bones of the basalmost sarcopterygian *Meemannia* also possess a ganoine-like covering[16]. *Lophosteus*, *Andreolepis* and, potentially, *Dialipina* thus begin to define a character complement for the upper part of the osteichthyan stem group[17]. This will form a valuable basis for evaluating the relationships of forms such as acanthodians whose suggested similarities to osteichthyans are more tenuous. *Lophosteus* and *Andreolepis* also illuminate the evolution of the osteichthyan dentition.

Several theories have been proposed for the origin of gnathostome tooth patterning and replacement[18–23]. A recently favoured hypothesis suggests that the initial tooth patterning and replacement mechanisms are modular and derived from the pattern of the pharyngeal denticle whorls found in some fossil jawless vertebrates[19,20]. This accounts for the tooth replacement of sharks and early chimaeroids, and for the parasymphysial tooth whorls of acanthodians and primitive osteichthyans. In the tooth rows of the most primitive living actinopterygian, the bichir (*Polypterus*), and in living amphibians, new teeth grow medially to older ones in a transverse sequence. This mechanism is interpreted as primitive for osteichthyans[18], suggesting that patterning and replacement of these tooth rows are also fundamentally modular[21–23]. The organization of the jaw denticles of *Lophosteus* into parallel longitudinal rows and transverse files, which recalls that of the tooth 'families' (or files) of chondrichthyans and certain acanthodians[24], may thus illustrate an early stage of osteichthyan marginal tooth patterning. It is possible that each of these denticle files corresponds to an individual tooth 'capsule'; that is, a functional module[22,23]. The largest (and presumably youngest) denticles form the medialmost row, and new, larger and larger denticles appeared at the medial end of each denticle file as the maxillary grew. Although the denticles seem to grade into the tubercles of the external bone ornamentation, their pattern differs from the random distribution of the latter (Fig. 2c). The denticles of *Andreolepis* show the same medial-to-lateral size gradient as in *Lophosteus* and seem to be arranged in transverse files with alternating initiation of new denticles (Fig. 1b, c), suggesting a tooth initiation pattern somewhat like that in sharks[19].

The dentition of *Lophosteus* is more obviously patterned in rows and files than that of *Andreolepis* and is therefore closer to the condition in crown osteichthyans: it could in principle be converted into a typical osteichthyan tooth row by introducing a shedding phase such that each tooth in a file was shed before its more mesial replacement was implanted. In contrast, the diversity and size of the fin spines referred to *Lophosteus* suggests a more primitive condition than *Andreolepis*, recalling that of acanthodians[4,5,8,10]. Paired and unpaired fin spines are also known in the early Devonian sarcopterygian *Psarolepis*[25], as well as in the earliest chondrichthyans[26], and are probably a general character of the crown-group gnathostomes, or even all jawed vertebrates if regarded as homologous to the spinal plates of placoderms (Fig. 3). Which of *Andreolepis* or *Lophosteus* is more closely related to crown-group osteichthyans cannot be determined until more complete specimens are found. Recent discoveries of the earliest crown-group osteichthyans from the early Devonian of China have considerably increased our understanding of the actinopterygian–sarcopterygian divergence and overturned some supposedly diagnostic characters of these groups[16]. Even though *Andreolepis* and *Lophosteus* possessed characteristic osteichthyan jaw bones with incipient osteichthyan tooth organization, the rest of their skull pattern may turn out to be quite different from that of crown-group osteichthyans.

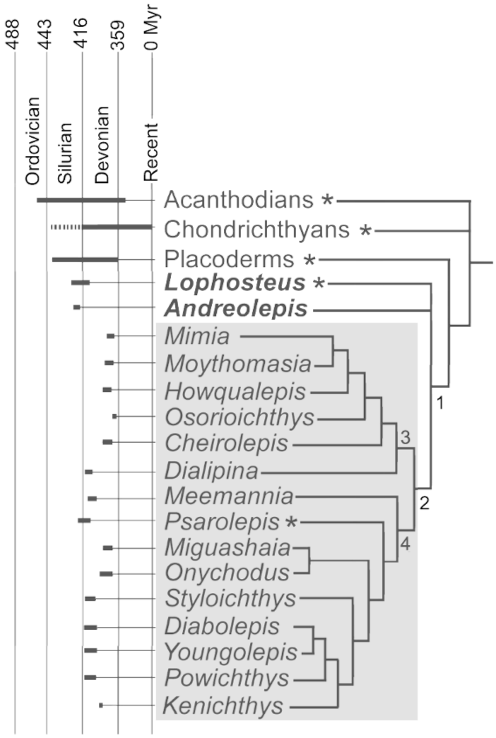

Figure 3 | Relationships of *Andreolepis* and *Lophosteus* to other jawed vertebrates. The diagram is taken from the tree in ref. 16, with *Andreolepis* and *Lophosteus* added; bold lines show distribution through time. The debated chondrichthyan record is dashed. Crown-group osteichthyans (grey) include here only the Devonian relatives of major living taxa, for example actinopterygians (*Mimia*/*Moythomasia*), coelacanths (*Miguashaia*), dipnoans (*Diabolepis*) and tetrapodomorphs (*Kenichthys*). Asterisks indicate taxa with fin spines or spinal plates. 1–4, Jawbone characters: 1, osteichthyans (denticles on edge of dentary, maxillary and possibly premaxillary); 2, crown-group osteichthyans (broad medial horizontal lamina of dentary and maxillary bearing larger monolinear tooth row); 3, actinopterygians (sensory-line canal in dentary); 4, sarcopterygians (largest teeth ('fangs') on coronoids, ectopterygoids, dermopalatine and vomers).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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