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The plasticity of gill raker characteristics in suspension feeders: Implications for Pachycormiformes

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Abstract

Pachycormids apparently represent part of the first radiation of the total group of teleosts, and therefore are important in understanding stem teleost phylogeny. Gill rakers (or fanunculi) are elements of the gill skeleton (branchial basket) in fishes that function primarily to protect respiratory lamellae, and sometimes have a secondary role in feeding. Characteristics of gill rakers have been used for taxonomic diagnosis and cladistic analysis of the interrelationships of Pachycormiformes, with particular importance for *Leedsichthys* and *Asthenocormus*. The material on which these determinations have been based is reviewed, along with the validity of the use of gill rakers in analyses of extinct fishes in general, based on their utility in extant fishes, following the presentation of a standardized nomenclature for these structures. Gill rakers are demonstrated to be an unreliable source of taxonomic characters in suspension feeders. The assignment of specimen PETMG F34 to *Leedsichthys*, solely based on the presence of elaborated but dissimilar gill rakers, is rejected, as there are no osteological resemblances to any other specimen of that taxon. The characters used to erect *Leedsichthys notocetes* are demonstrated to be artifacts generated by erosion and fracture, and this material is consequently synonymised within *Leedsichthys problematicus*.

Introduction

Pachycormids are a poorly understood group of Mesozoic actinopterygians that may represent part of the first radiation of the total group of teleosts (ARRATIA 1999, 2004), and therefore are important in understanding stem teleost phylogeny. Of all the taxa in the family Pachycormidae, the most poorly known is the enigmatic Callovian–Kimmeridgian genus *Leedsichthys*. When A. S. WOODWARD (1889a, 1889b) first reported and named the taxon *Leedsichthys problematicus*, he was fully aware that it was a difficult taxon to describe. Found amongst the vertebrate material collected from the Oxford Clay by A. N. Leeds, some of its bones had already been published under the misidentification of stegosaur armour (HULKE 1887). Since WOODWARD's description of the Peterborough and Normandie Oxford Clay material, different elements of its remains have been published on a further two occasions as belonging to a stegosaurian dinosaur, and it has been misidentified as fossil plant material on another (LISTON 2010). Conversely, some of the more obscure bones of other taxa (e.g. pliosaurs, NOÈ et al. 2003) have also been attributed to it in its role as an Oxford Clay 'wastebasket taxon' for vertebrate remains that are uncommon or unusual. Material sold to Liverpool Museum as *Leedsichthys* by A. N. LEEDS was later misguidedly reidentified as *Ophthalmosaurus* and "Reptilia indet." (NEAVERSON 1935). The recurrent pattern of a near-complete lack of understanding of the osteology of this animal has three underlying causes: firstly, the large (but indefinite) size of the animal has made interpretation of the remains difficult; secondly, these remains are most commonly crushed flat and broken into fragments, disguising their true in vivo shape and size; thirdly, the remains are invariably partial (often simply consisting of a few isolated elements) and do not represent an entire individual. All three of these causes are at least partly the result of the reduced ossification prevalent throughout the skeleton of *Leedsichthys*. This set of problems with the material (isolated, disarticulated, scattered, fragmentary, disjunct) has meant that, in spite of its size, this animal has had a set of barriers obstructing the understanding of its nature, similar to those surrounding conodont animals (ALDRIDGE 1986).

Although initially described in 1889, it was not until 1895 that A. S. WOODWARD declared that *Leedsichthys* was not related to the sturgeons or 'acipenseroids' (as he had previously stated, WOODWARD 1889a, 1889b), but was a member of the family Pachycormidae (WOODWARD 1895). It is perhaps, therefore, of little surprise that following WOODWARD's attempt to shorten the name he had designated for the fish (introducing the nomen nudum of *Leedsia problematica* – despite having already published the original name four times himself in WOODWARD 1889b, c, 1890a, WOODWARD & SHERBORN 1890), it was fully ninety eight years before another attempt was made to revisit the description or taxonomy of this animal. MARTILL (1988) amended WOODWARD's diagnosis to state that it was a "fish of gigantic proportions", and noted dimensions relating to gill rakers, the gill basket, the caudal fins and an uncollected ?pectoral fin ray. The use of absolute sizes in a diagnosis is rarely helpful, as (provided the specimen upon which the description is based can be determined to be an adult) it hinders the identification of sub-adult and juvenile material, and makes it difficult to distinguish between convergence and synapomorphy. Although knowledge that *Leedsichthys* was able to grow to a given size (and the estimated size of the fish has been a matter of some debate, with estimates ranging from 9 m (WOODWARD 1917; and see also LISTON & NOÈ 2004) to over 27 m (MARTILL 1986)) is of use for understanding an animal's ecology, statements of relative or proportional lengths are of more universal utility in matters of diagnosis.

Eight years after MARTILL published his modification to WOODWARD's diagnosis of the taxon, MICHELIS et al. (1996) amended MARTILL's revised diagnosis on the grounds of the histology of material found in the Callovian Oxford Clay or 'Ornatenton' of northern Germany.

The concept of histology as having a diagnostic role within fossil fish material has a long history (e. g. see ENLOW & BROWN 1956 for a review). MICHELIS et al. (1996) examined some of the material from the north German specimen of *Leedsichthys*, noting the presence of very fine blood vessels running parallel to the external bone surface and the 'absence of a compacta'. They then sought to demonstrate that *Leedsichthys* could be distinguished from 'higher' vertebrates and diagnosed on the basis of these characters. However, RICQLES et al. (1991) specifically noted that 'peculiarities' of bone histology cannot be regarded as having taxonomic significance, and FRANCILLON-VIEILLOT et al. (1990) expressly stated that the presence or absence of compacta is not diagnostic of precise anatomical or ontogenetic origins. This dismissal of that means of diagnosis was also inadvertently validated by MICHELIS et al. themselves, as they went on to misidentify a hypobranchial of *Leedsichthys* as a tail-spine of a stegosaurian dinosaur, using their compacta-based methodology to rule the element out from being a part of the *Leedsichthys* skeleton (1996). Compact bone is present in *Leedsichthys*, albeit in a very much reduced thickness for the comparatively large size of the bones concerned (LISTON 2010). This is a reflection of the reduced ossification of the skeleton that occurs as a phyletic trend across the Pachycormidae; not only have specific elements of the skeleton not ossified at all, but the majority of the rest of the skeleton has only ossified with a very thin superficial layer of compact bone over extensively resorbed and remodelled cancellous bone. This means that the bones of *Leedsichthys* from the Oxford Clay are most commonly preserved crushed and flattened (if not fragmented), unless exceptional preservation (e. g., within a concretion) occurred. (Noteworthy exceptions that commonly survive relatively intact due to their denser compact bone layer are the hyomandibulae and the ceratohyals.)

A. S. WOODWARD's species name of *problematicus* reflected his own uncertainty regarding the identification of the bony remains of *Leedsichthys* – underlined when he wrote some years later (LEEDS & WOODWARD 1897) that of the eight bones that he had identified in his original description, he could only really be certain of the osteological identity of two of them: the gill rakers and the fin rays (lepidotrichia). Indeed, in the hundred years since the remains of *Leedsichthys* were first noted in the collection of A. N. LEEDS (HULKE 1887), the only elements of its skeleton to be figured were two fragments of gill rakers from the holotype specimen NHMUK P.6921 (WOODWARD 1890b) (Fig. 1A).

Institutional abbreviations: GLAHM, Hunterian Museum, University of Glasgow, Scotland; **I,** Museo Regional de Antofagasta, Antofagasta, Chile; **LEIUG**, Leicester University, Geology Department, Leicester, England; **NHMUK**, Natural History Museum, London, England; **PETMG**, Peterborough Museum, Peterborough, Cambridgeshire, England; **SHL**, Tiergarten und Fossilium, Bochum, Germany; **SMNK**, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

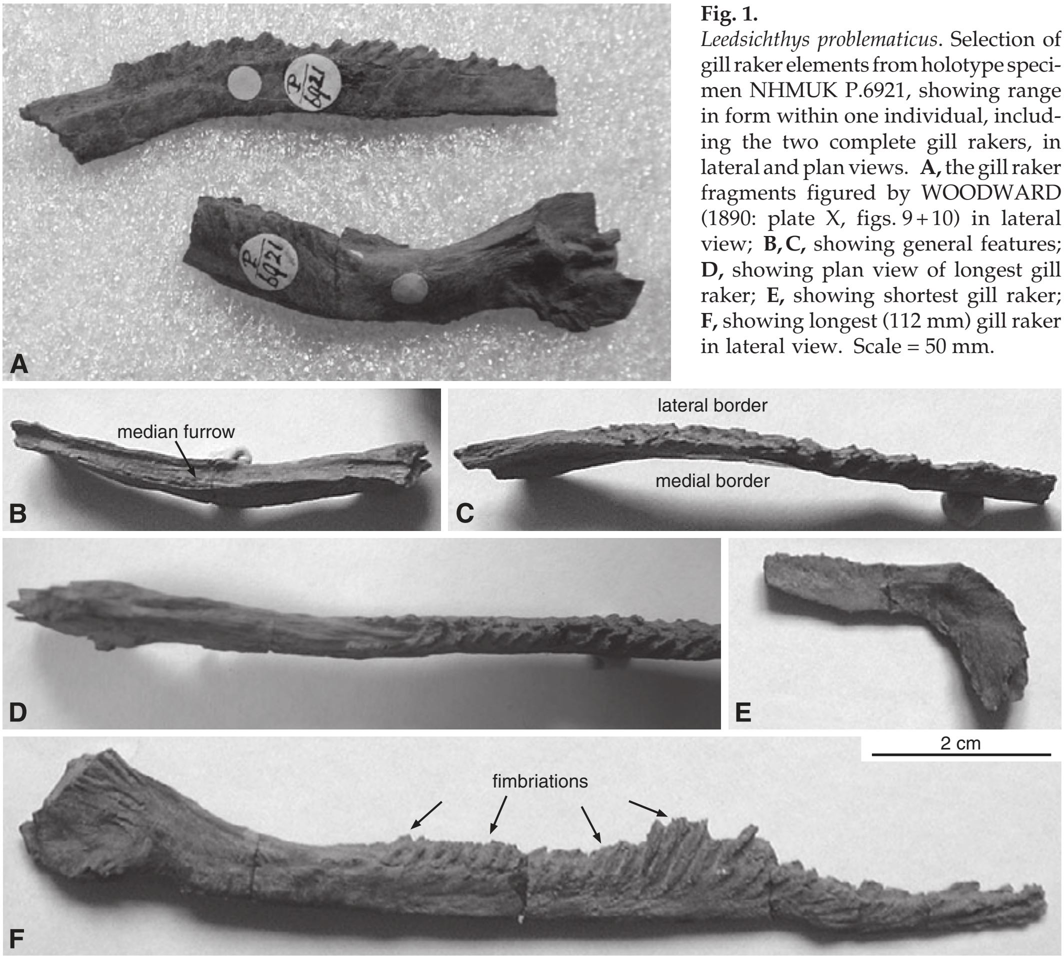

Fig. 1.
Leedsichthys problematicus. Selection of gill raker elements from holotype specimen NHMUK P.6921, showing range in form within one individual, including the two complete gill rakers, in lateral and plan views. **A,** the gill raker fragments figured by WOODWARD (1890: plate X, figs. 9 + 10) in lateral view; **B, C,** showing general features; **D,** showing plan view of longest gill raker; **E,** showing shortest gill raker; **F,** showing longest (112 mm) gill raker in lateral view. Scale = 50 mm.

List of material studied

Asthenocormus titanius: SHL 1309.
Leedsichthys problematicus: GLAHM V3363; LEIUG 96087/24; NHMUK P.6921, NHMUK P.8610, NHMUK P.10000; NHMUK P.10156; NHMUK P.11823; PETMG F174.
Leedsichthys notocetes (= *L. problematicus*): I 8-02 11 73; I 19-1 21 73; SMNK 2573.PAL.
Martillichthys renwickae: NHMUK P.61563.
Osteichthyan indet.: PETMG F34.

Relationships of *Leedsichthys* to other pachycormids

These skeletal problems have similarly obscured the relationships between *Leedsichthys* and other pachycormids. Although a number of studies have featured *Pachycormus* or *Hypsocormus* as representatives within broader neopterygian or basal teleost relationships (GARDINER et al. 1996, ARRATIA 1999), only two earlier works have ever attempted to deal with the interrelationships of the members of the family Pachycormidae (although see ARRATIA & LAMBERS 1996 and ARRATIA & SCHULTZE this volume). In the first significant cladistic analysis of the pachycormids, MAINWARING (1978) excluded *Leedsichthys* from the family Pachycormidae, based on a misperception of there being a very limited diversity of skeletal elements represented in specimens of the taxon. LAMBERS (1992) reviewed MAINWARING's work, presenting the most recent hypothesis of the interrelationships of the group, and although he brought

Leedsichthys back into the family Pachycormidae, he experienced problems in obtaining useful characters for this genus. He presented only two such characters in his final analysis of the interrelationships of the family Pachycormidae: one of these was fin ray character (bifurcation without segmentation in the caudal fins), and the other was a gill raker character (the presence of 'needle teeth'). A third analysis by FRIEDMAN et al. (2010), later developed in FRIEDMAN (2011) was largely an incorporation of LAMBERS and MAINWARING into HURLEY et al. (2007). It also included unpublished data from LISTON (2007), which had excluded gill raker characters: the reasons why those characters were felt to be unsafe for phylogenetic use will be demonstrated in this current work, along with the further implications for other specimens, extant and extinct. ARRATIA & SCHULTZE (this volume) reviewed many of the characters used in previous phylogenetic analyses and concluded that the available information does not support Pachycormiformes as teleosts.

Characters that can be used only with significant caution for contemporary fishes as a component of a broader suite of characters (e. g., POPPER 1982) are sometimes successfully used in isolation for fossil taxa (KELLER et al. 2002, GAUDANT 2003). In the light of this, it is worth assessing the stability of gill rakers, to determine their robustness and potential suitability for use as a source of diagnostic characters. The use of gill rakers as a source of characters will be reviewed within and outside the family Pachycormidae, because a second species of *Leedsichthys* has been erected solely on the basis of characteristics apparent in a cluster of disarticulated and isolated gill rakers (*Leedsichthys notocetes* MARTILL et al., 1999). The nature of that specimen similarly requires that the functional anatomy associated with gill raker structure also be critically examined, and the terminology in the literature stabilized. The implications for specimens casually referred to *Leedsichthys* in the past will then be explored.

Gill rakers in fishes

Gill rakers (fanunculi) sit as either single or paired structures on the buccal aspect of the branchial arch in osteichthyans and chondrichthyans, sometimes also occurring in modified form within epibranchial organs (HOWES 1981, LAZZARO 1987). Their basic form is governed by their primary function, which is to protect the delicate respiratory surfaces of the gill lamellae/filaments from potential damage by particulate matter in the water taken in to the buccal cavity during respiration. They occur in most, but not all fishes (KYLE 1926, MAGNUSON & HEITZ 1971), and with varying degrees of distribution throughout the branchial arches, but the first arch is usually the main site. They have been noted in fossil fishes from the Oxford Clay other than *Leedsichthys* (WOODWARD 1897).

The form of gill rakers varies widely across many groups of fishes (IMMS 1904). Regardless of relative sizes of different elements, the basic structure of a gill raker follows the same general pattern (Fig. 2):

A broad base (PEIRONG 1989), which can be bifid, forms the site of insertion for raker abduction muscles (interbranchiales abductores of WINTERBOTTOM 1974, abductor branchiospinalis of VAN DEN BERG et al. 1994a) originating on the branchial arch component. From this base, a stalk (KAZANSKI 1964, PEIRONG 1989) extends from the base into the interarch gap, where it terminates as a tip.

The stalk may or may not carry accessory/secondary structures on its lateral and medial surfaces (e. g., branchiospinules GIBSON 1988, SANDERSON et al. 1996b) or on its dorsal surface ("process" of YASUDA 1960, "barbs" of PECK 1893, "denticles" of DE CIECHOMSKI 1967, "branchiospinules" of FRIEDLAND 1985, "teeth" of GIBSON 1988). These secondary structures on gill rakers are distinct from the dermal ossifications known as microbranchiospines or microgillrakers, which sit within the epidermis of the gill arch close to its base, and should not be confused with them (BEVERIDGE et al. 1988).

In some fishes, the function of gill rakers as a defensive barrier has been refined to include a role in trapping and extracting suspended food particles from the water for ingestion. In a functional

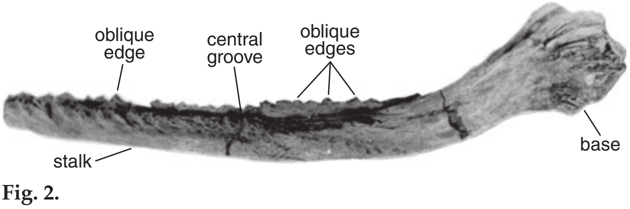

Fig. 2.
Gill raker of *Leedsichthys problematicus* (NHMUK P.8610) showing its main features; length = 81 mm. Oblique edge (WOODWARD 1889b) = "process" (YASUDA 1960) = "lateral plications" (MARTILL et al. 1999); stalk (PEIRONG 1989; KAZANSKI 1964) = ramus (MARTILL et al. 1999); base (PEIRONG 1989), the site of insertion of raker abducting muscle (interbranchiales abductores, WINTERBOTTOM 1974; abductor branchiospinalis, VAN DEN BERG et al. 1994a). Photograph by D. M. MARTILL.

sense, their form and frequency has often been correlated to the diet of the fish (e. g., NIKOLSKY 1963, YASUDA 1960, IWAI 1964, HELFMAN et al. 1997), with spacing of rakers being regarded as particularly diagnostic in this regard (ALEXANDER 1967). HYATT, however, noted (1979) that although fishes with closely spaced gill rakers are plankton feeders and those with coarsely spaced gill rakers are not, fishes can still be effective plankton feeders without closely spaced gill rakers.

For those fishes with gill rakers, VAN DEN BERG et al. (1993) suggested that the more comb-like (or "setiform"; IMMS 1904) the raker, the more random the orientation of the fish's prey was likely to be. SANDERSON et al. (1994) similarly noted that the character of the gill raker implied the feeding style of the fish: the thinner and more comb-like the raker (e. g., *Polydon spathula*, *Cetorhinus maximus*; IMMS 1904), the lower the buccal flow velocity; the larger the raker, the more it was able to cope with a higher buccal flow velocity, not by actively retaining prey, but by redirecting current flow to other retention areas (see also CHEER & KOEHL 1987). In comparing the structure of gill rakers as relating to a planktivorous diet, JOBLING (1995) described "fine filamentous gill rakers" being used as traps for prey, and how some fishes have a fine enough mesh of gill rakers to feed not just on zooplankton, but on smaller phytoplankton as well (e. g., *Engraulis ringens*; *Brevoortia* can collect particles as small as 13–16 microns; some *Tilapia* species can also filter phytoplankton). RYTHER (1969) also noted clupeids with specially modified gill rakers for herbivory. GRANDE & BEMIS (1991: 43) interpreted the diet of an extinct paddlefish on the similarity of its gill raker form to that of particular living paddlefishes.

Although sieving through a comb-like structure is a means of prey retention for the suspension feeding fishes, it is far from the only process employed. The exact mechanics of the process are unknown for most fishes: for 70 species in 21 families in 12 orders that suspension feed (CHEER et al. 2001), SANDERSON et al. (1996b) noted 56 species in 16 families for which the particle retention mechanism was unknown. Some suspension feeders can feed on small particles without well-developed gill rakers (e. g., *Tilapia melanotheron* feeding on 50–100 micron particles; HYATT 1979), and others are entirely unaffected in their ability to suspension feed when their gill rakers are surgically removed (e. g., mango tilapia *Sarotherodon galilaeus*, in SANDERSON et al. 1996b). For those fishes for which the process of trapping and extracting suspended food particles from the water for ingestion has been determined, the mechanisms vary widely (GERKING 1994). A functional continuum exists from pure sieving (BEMIS et al. 1997), through cross-flow filtration (SANDERSON et al. 2001), to trapping and extraction solely through the use of mucus (GOODRICH et al. 2000). Throughout these mechanisms, the role of the gill raker varies from merely directing water flow, either towards the roof of the mouth (SANDERSON et al. 1991) or towards the main current flow through the oral cavity (SANDERSON et al. 1996a), to sieving particles (SANDERSON et al. 1998), or to acting as a cross-flow surface (SANDERSON et al. 2001).

Regardless of mechanism, there is undoubtedly a high correlation among hypertrophy of rakers on gill arches, increase in their numbers per unit length of gill arch, and a tendency towards suspension feeding (SANDERSON & WASSERSUG 1990). Similarly, LINDSEY (1981) noted a "convergent suite of planktivore characteristics" in open-water plankton feeders, including high gill raker counts and long gill rakers, that had evolved at least three times. This pattern is sometimes additionally accompanied by the occurrence of edentulous jaws and also by the development of epibranchial organs (an accessory digestive structure; TAKAHASI 1957; NELSON 1967, 1970) at the expense of pharyngeal dentition, and has been noted in five different families of "lower" teleosts (SANDERSON & WASSERSUG 1993). LAZZARO (1987) interpreted the elaboration of gill rakers as part of a major evolutionary divergence from the basic teleost pattern of generalised predators, towards microphagy. In association with a trend towards replacement of teeth by elaborate gill rakers on branchial arches, he also found changes in the protrusibility of jaws, modification of some gill rakers in an epibranchial organ on the roof of the mouth, and a lengthening of the digestive tract (see also JUNE & CARLSON 1971, BONE et al. 1995) to process larger amounts of fine material without the digestive delay that is characteristic of macrophages. It is on this basis that acanthodiforms, with their edentulous jaws and possession of long gill rakers (e. g., *Acanthodes bronni*, in MILES 1973), have been interpreted as microphagous suspension feeders (JANVIER 1996, MOYLE & CECH 2000). Similarly, the few jaw components that have been identified for *Leedsichthys* are completely edentulous, and the gill rakers of this fish are of unusually (but not uniquely) large relative size, suggesting that a suspension feeding lifestyle is a reasonable model.

The plasticity and instability of gill rakers – factors ephemerally affecting gill raker morphology

Gill raker form varies greatly throughout the lifetime of an individual fish (JUNE & CARLSON 1971, SANDERSON & WASSERSUG 1993), even in terms of whether they are present or absent (BONE et al. 1995). GRANDE & BEMIS (1991), in their landmark review of paddlefishes, noted a niche shift as individuals of *Polyodon spathula* grew, with the gradual disappearance of its jaw teeth as its gill rakers developed, along with a behavioural change from carnivore to edentulous suspension feeder. Similarly, JUNE & CARLSON (1971) noted that the Atlantic menhaden *(Brevoortia tyrannus)* lost all of its teeth as its gill rakers developed, changing from a larval copepod feeder to a juvenile able to filter phytoplankton cells as small as 2 microns. Similar patterns of ontogenetic shift towards gill raker-assisted microphagy are also recorded by DE CIECHOMSKI (1967). Once a fish has acquired gill rakers, there are still variations in the nature of the gill rakers: length varies according to position on a gill arch (the longest raker usually being located at the upper arch/lower arch joint; MAGNUSON & HEITZ 1971, GIBSON 1988, SANDERSON et al. 1996a), and breadth of raker can also vary on a regular basis (PEIRONG 1989 noting that every 3rd–6th gill raker is broad in comparison to the preceding narrow forms in the silver carp *Hypophthalmichthys molitrix*). KLIEWER (1970), in reviewing lake whitefish (Coregonidae) across a series of lakes, noted that length of gill raker within a species could vary according to the proportion of the diet that was pelagic (longer) or benthic (shorter), similar to the way pharyngeal dentition develops according to available food (HYATT 1979). He also noted that gill raker length increased with the depth at which the specimen was caught, and that the number of gill rakers per gill arch varied positively with increasing proportions of benthic material in the diet, echoing LINDSEY's (1981: 1498) observation on the variation of both gill raker number and length being dependent on environment as well as age: "gill raker counts expand to fill the available niches."

Although gill raker numbers and length will generally increase with the age and standard length (SL) of the individual (e.g., *Clupea harengus* in GIBSON 1988, *Alosa pseudoharengus* in MACNEILL & BRANDT 1990), environmental as well as genetic factors can impinge on the resulting phenotype. In some species, gill raker numbers increase until the plateau of an 'adult level' has been reached (VILLALOBOS 2002), while in others, they continue to increase in number throughout life (KING & MACLEOD 1976, GIBSON 1988, LINDSEY 1988). LOY et al. (1999) noted the influence of salinity on gill raker number not just during embryonic development, but into adulthood, and stated that gill raker variation might well be ecophenotypic rather than adaptive. The number of gill rakers and their length may also decrease with age and size (e.g., *Seriola* in SANDERSON et al. 1996a).

HJELM & JOHANSSON (2003) noted that gill raker spacing in *Rutilus rutilus* responded to environmental change within five years, and covaried with the size of available zooplankton. MATSUMOTO & KOHDA (2001) similarly noted inter-raker spacing in local populations of *Goniistius zonatus* that appeared to reflect the size of available food at each location. Although the gaps between gill rakers are generally related to food, they can also increase isometrically (*Dorosoma cepedianum* MUMMERT & DRENNER 1986, cyprinids VAN DEN BERG et al. 1992). MAGNUSON & HEITZ (1971) even went so far as to present formulae for calculating inter-raker gaps for standard lengths of given species of scombrids and coryphaenids.

LISTON (2005) cautioned against the use of gill rakers as a source of diagnostic characters, noting their high lability and frequently convergent nature. As LOY et al. (1999) put it: "The use of gill rakers in systematic studies deserves special attention because variation may not be adaptive but purely ecophenotypic, and environmental conditions may act well beyond the embryo development." If parameters of spacing, length, frequency and number are not conserved within the adult life of the animal, how much taxonomic value can they really have?

Problems of historical use of gill rakers as a taxonomic tool

In spite of the above plasticity demonstrated in the characteristics of gill rakers, attempts have nonetheless been made to use them in taxonomic schemes for some contemporary fishes. For example, gill raker number and length have commonly been used as part of a suite of characters to diagnose individual species (e.g., *Bathyclarias* species; JACKSON 1959). YASUDA (1960) attempted to classify Japanese coastal fishes based on their gill raker shape. KAZANSKI (1964) erected a system for species-level diagnosis of cyprinid fishes based on the structure of the gill rakers, even going as far as to develop a pattern of descent based on characteristics of the gill raker and gill raker cushions. Similarly, IWAI (1963, 1964) established a classificatory scheme based on the histology of taste buds on gill rakers of teleosts.

On the concept of needle teeth

Although used as a character in LAMBERS' (1992) analysis of the interrelationships of the members of family Pachycormidae, the presence of "needle teeth" on the dorsal surface of gill rakers is not a pachycormid synapomorphy. It occurs on the gill rakers of other fishes; for example GIBSON (1988) referred to it as a feature of the gill rakers of herring, where it is extremely variable in its occurrence, and not present on the rakers of all gill arches. YASUDA (1960) referred to these structures as "processes", and noted that, as well as being variable in form around the gill basket in the mullet *(Mugil cephalus)*, they change with age in the mackerel *(Scomber japonicus)* and the sardine *(Sardinops melanosticta)* as their diets alter. DE CIECHOMSKI made similar observations in comparing gill raker ontogeny of two species of *Engraulis* (1967). VAN DEN BERG et al. (1994b) also noted preservational problems of "needle teeth" in contemporary fish populations, because of incomplete ossification of needles, which would clearly hinder assessment of their presence or absence within the fossil record. Suspension feeding can develop independently several times within a given clade of fish (NELSON 1967), appearing to be a common response to the availability of food suitable for microphagy (LAZZARO 1987). Similarly, the development of "needle teeth" on gill rakers in edentulous fishes appears to have occurred independently among different clades of suspension feeders, and as such its use as a taxonomic tool can only be a limited one.

The origin of the use of "needle teeth" specifically as a diagnostic character for pachycormids relates to the occasional use of basking sharks as modern analogues for *Leedsichthys*. In comparatively early studies on basking sharks, VAN DEINSE & ADRIANI (1953) noted the retrieval of some specimens of *Cetorhinus maximus* during the winter months without any gill rakers, and even tentatively suggested that a new form of basking shark might have been found, for which they provisionally proposed the name *Cetorhinus maximus infanuncula* nova forma. To counter this, PARKER & BOESEMAN (1954) hypothesised that *Cetorhinus maximus* simply shed its gill rakers during the winter, a hypothesis that has since been rejected (SIMS 1999). It was this hypothesis that was the model for MARTILL's (1988) suggestion that periodic shedding of "needle teeth" occurred from the gill rakers of *Leedsichthys*, because of variation in the gill rakers of *L. problematicus* recovered from the Oxford Clay, not all of which had "needle teeth". In fact, when the hypodigm for *Leedsichthys* is reviewed, only one specimen (that figured by MARTILL 1988: PETMG F34, consisting of a partial skull with damaged remains of skull roof, branchial basket and jaws) has ever been recovered with needle teeth present, despite the almost ubiquitous occurrence of gill rakers with specimens of this taxon. Therefore, it was decided to reexamine this specimen, to assess other aspects of its gill raker and general anatomy.

LAMBERS' (1992) analysis of the interrelationships of Pachycormiformes used the presence or absence of "needle teeth" on the gill rakers as a character. For his analysis he scored two taxa as possessing "needle teeth" – one, following MARTILL (1988), was *Leedsichthys* and the other was *Asthenocormus*. This latter genus is known from only a handful of 1–2 m long individuals from the Tithonian Solnhofen limestone, and only one of those specimens, in the Bochum Tiergarten Collection (SHL 1309), features putative gill rakers (see LAMBERS 1992). This identification, both in terms of whether or not they are gill rakers and whether or not they belong to *Asthenocormus*, has been questioned (LISTON 2007, 2012).

With the demonstrated weaknesses of gill raker morphology as a source of taxonomic characters, it is perhaps worth reexamining the validity of the second species of *Leedsichthys*, based solely on differences in gill raker structure from the "norm" for *Leedsichthys problematicus*, a scenario that recalls ALDRIDGE's (1986) comments on the dangers of 'parataxonomy'. MARTILL et al. (1999) based the new taxon of *Leedsichthys notocetes* from the Oxfordian of Chile on the characteristic fenestrae that occurred within the ramus of the gill rakers, absent from the gill rakers known from the Oxford Clay specimens of *Leedsichthys*. However LISTON (2005) observed that erecting a new taxon based solely on minor variations in gill raker structure was questionable: the presence of such fenestrae is counter-intuitive – why would a structure subjected to comparatively high hydrodynamic pressures during suspension feeding have such a structural weakness as holes, just at the level of the functional ridges, where it would be likely to fail and fracture? The gill raker would be expected to be subject to intense hydrodynamic distortion (MacNEILL & BRANDT 1990, WRIGHT et al. 1983) in high flow velocities and thus experience strong selection against anything that would structurally weaken the convex leading surface. Conversely, the presence of these fenestrae could be the manifestation of a natural shedding process, as proposed by MARTILL (1988). Recent work has demonstrated through the examination of marks of skeletal growth (LISTON et al. 2005) that gill rakers did not shed seasonally in *Leedsichthys*, but were retained for much of the life of the animal. The appearance of such fenestrae might be a sign of incipient shedding of the functional dorsal section (including the ridges) of the rakers of this animal, as new growth produced more bone to replace this structure. To assess this, the holotype block of gill rakers for *Leedsichthys notocetes* (SMNK 2573.PAL) was reviewed, and compared with the gill rakers that form part of the holotype specimen of *Leedsichthys problematicus*.

Morphological observations on the gill rakers of suspension feeding Pachycormiformes

In order to assess the importance of gill raker morphological variations in pachycormids, the type material for both species of *Leedsichthys* and the figured material for gill rakers in both *Asthenocormus* and *Leedsichthys*, were reviewed.

Description of gill rakers of *Leedsichthys problematicus* (holotype NHMUK P.6921)

In order to assess how significant the morphological differences may be between *Leedsichthys problematicus* and specimens PETMG F34 and SMNK 2573.PAL, it is necessary to examine the series of 89 gill raker elements that constitute part of the holotype. Of this series, only two elements are complete (with base, stalk and tip intact), representing different extremes of size: the short gill raker is 39 mm long (Fig. 1E), and the long gill raker is 112 mm long (Fig. 1F). More than a century after this specimen was first described, only one intact gill raker within the hypodigm has been found that is shorter (a 35 mm raker in NHMUK P.10000), and only two that are longer (LISTON 2006). WOODWARD (1890b) figured two of the fragments, and repeated the account of them from his original description (1889b) as, "laterally compressed, slightly expanded at the basal extremity, and rarely straight, but irregularly bent or contorted. The surface is coarsely rugose, and one long border is rounded, while the other is cleft by a longitudinal median furrow. The rounded border is comparatively smooth, but the furrowed edge is coarsely serrated, a series of short oblique ridges terminating in points on each side." WOODWARD's (1890b) figure showed the features he described with his diagram 10a showing a plan view of the longitudinal median furrow (Fig. 1B) – the "dental groove" of MARTILL (1988). This furrow is shaped by the lateral and medial borders (Fig. 1C), which are formed by a series of fimbriations producing the effect of a pair of undulating external ridges (Fig. 1F), occasionally with intergrowth between fimbriae (Fig. 1A). This creates the effect of an undulating ridged flange on each side of the dorsal surface of the gill raker. The fimbriae may radiate at the tip to point directly into the inter-arch gap (Fig. 1F), growing in a long tongue-like fashion. In terms of YASUDA's (1960) scheme (following his table of "processes") these features curve up as biserial lateral growths resembling the 'processes' depicted for adult *Scomber japonicus* (YASUDA 1960: fig. 4A) flanking a groove.

There is, however, more than one gill raker morph present within the 89 gill raker fragments of the holotype. There are rakers (including the longest element present) that lack the groove described by WOODWARD (1890) (Fig. 1D), as though it has been occluded through the two lateral edges growing together. In some cases, this feature appears to become even more removed from the furrowed state, with the oblique ridges seeming to become a plane perpendicular to the axis of the stalk, with the lateral and medial edges of the ridges becoming less thick and oblique and more thin and vertical, resembling a sharp, elevated blade that runs transversely from one side of the raker to the other, as though fimbriae on opposite borders have grown together. This condition has also been noted on isolated gill rakers from the Callovian of Normandie (LISTON 2008a: fig. 7A) and the Kimmeridgian of Le Havre (LISTON 2008a: fig. 8, 2010), which have been referred to *Leedsichthys*. Within Peterborough Oxford Clay material, this character can also be seen in occasional raker fragments within specimens LEIUG 96087/24 and NHMUK P.8610. Within the latter two specimens and NHMUK P.6921, a continuum of forms exists between the two extremes.

In addition, it is worth noting that the isolated gill raker element from the Callovian of Normandie also appears to preserve traces in plan view of an extremely thin mesh above the gill raker, as though growing out from the tips of the transverse planes (LISTON 2008a: fig. 7B). It is probably simplest to regard this as a delicate component that is not preserved in the softer Oxford Clay around Peterborough.

Description of specimen PETMG F34, osteichthyan indet.

PETMG F34 is an enigmatic cranial fragment, previously referred to *Leedsichthys* (MARTILL 1988). However, this referral seems to have been purely on the basis of the presence of prominent and elaborate gill rakers in an Oxford Clay osteichthyan: PETMG F34 does not appear to have any definitive dermatocranial morphology to diagnose that it is *Leedsichthys*, is only partially freed from its clay matrix, and lacks distinctive perimeters to the bones of its skull roof. The specimen is a 475 mm by 175 mm block of two parts (Fig. 3), representing the bulk of the gill basket of a single individual with associated dermatocranial elements. Identifiable cranial elements on the dorsal aspect (Fig. 3A) include a 153 mm by 77 mm complete left parietal, and parts of a left maxillary fragmented through transverse shear. The jaw elements suffer from having the occlusal (potentially tooth-bearing) surfaces hidden or sheared away, so that it cannot be confirmed that these elements were edentulous. Although the parietal conforms to a recognisable shape, the maxilla cannot easily be related to the only known *Leedsichthys* maxilla (GLAHM V3363) or any other known jaw element. Assuming that these fragments are correctly identified, then the lower jaw is lost.

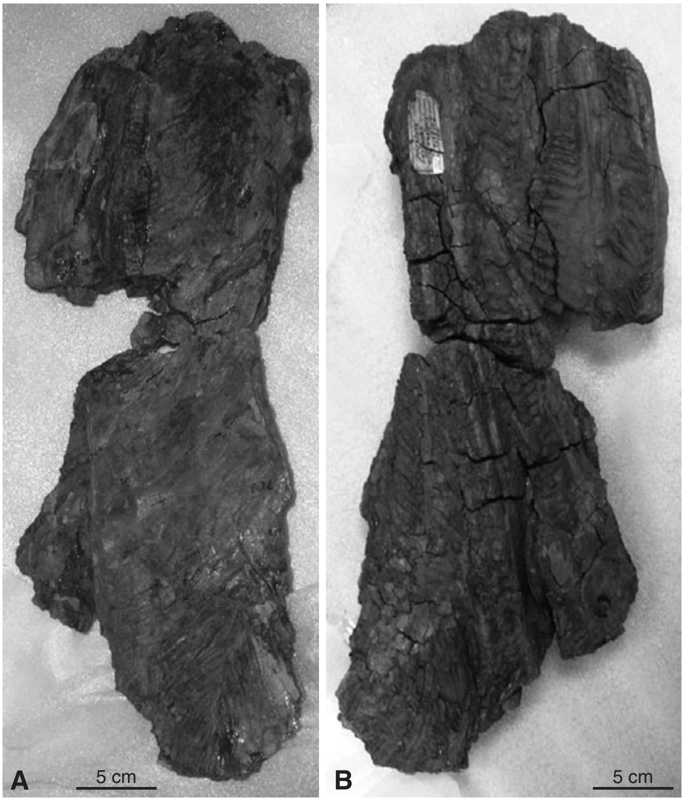

Fig. 3.
Osteichthyan indet., PETMG F34, gill basket with cranial elements. **A,** dorsal view of specimen. **B,** ventral view of specimen. Scale = 50 mm.

From the density of gill rakers per arch, and the ornamentation on each raker, it seems highly likely that this animal was a suspension feeder. However no specimen of the known Oxford Clay suspension feeders *(Leedsichthys* and *Martillichthys)* presents a similar form of gill raker (or even gill basket) structure to that presented by PETMG F34. The more diagnostic anterior parts of the gill basket (the hypobranchials, hypohyals and the anterior tips of the ceratobranchials) are missing, but the posterior extremities of right ceratobranchials I and II are characteristically present on the inferior surface of the posterior block (Fig. 3B) with associated, exceptionally long, gill rakers, as in the large adult gill basket of *Leedsichthys* (NHMUK P.10156; LISTON 2008b) and many other suspension feeding fishes. The ceratobranchials resemble those in the subadult specimen NHMUK P.11823 in form, although they are significantly smaller (a maximum width of 40 mm, compared with the maximum ceratobranchial width of 49 mm in the subadult specimen). The gill rakers between the ceratobranchials show an average spacing (KING & MACLEOD 1976) of 5.3–7.3 mm, which is not dissimilar to the figure for the gill basket specimen NHMUK P.10156 (6.6–8.2 mm) and the Antofagasta articulated partial gill basket I 19–1 21 73 (5.8–6.2 mm; LISTON 2010: fig. 11c). The gill rakers have a very similar orientation (angle subtended by the raker to the axis of the ceratobranchial is around 45 degrees) to those in the gill basket specimen NHMUK P.10156, but are considerably shorter, with an average length of around 45 mm instead of 75 mm. The extended gill rakers also differ significantly in their lengths, with a maximum length (at the posterior termination of ceratobranchials I and II) in PETMG F34 of 75 mm, and of 135 mm in NHMUK P.10156.

The gill rakers also differ markedly in form from those found with *Leedsichthys*: the stalks project at right angles to the arch, with a bifid base connecting them to the ceratobranchial. This is in stark contrast to the gently curved transition from a leaf-shaped base seen in gill rakers of *Leedsichthys* and *Martillichthys* (LISTON 2008b: fig. 9). The stalk in PETMG F34 consists of a thin blade bearing a single row of 'needle teeth' on its buccal margin (Fig. 4A), rather than the robust ramus constituting the stalk in *Leedsichthys* and *Martillichthys*. In this regard, it is worth noting that although the latter taxon (as represented by NHMUK

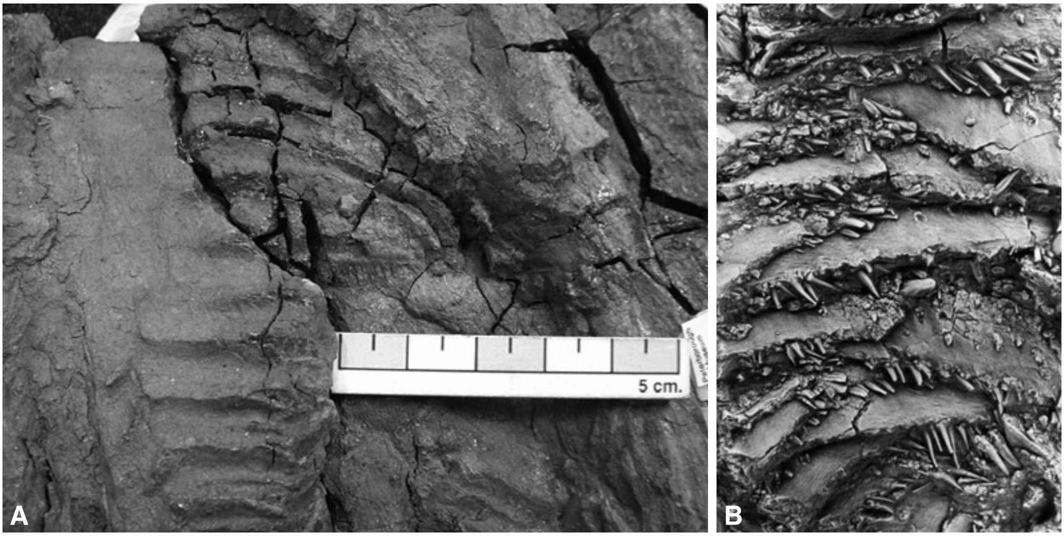

Fig. 4.
Osteichthyan indet., PETMG F34, gill basket with cranial elements. **A,** detail of ventral surface, showing gill rakers with acus fanunculorum. Scale = 50 mm. **B,** detail of fragment from PETMG F34, coated with ammonium chloride. **E**, edge; **S**, socket. Field of view = 17 mm wide. Second photograph courtesy of D. M. MARTILL.

P.61563) has a head smaller than that of PETMG F34 (370 mm total head length, as compared with 475 mm for the partial cranial fragment), the gill rakers nonetheless are of the robust form, although smaller than the blade-like rakers of PETMG F34.

It is worth noting that MARTILL's (1988) original illustration of a gill raker of *Leedsichthys problematicus* (reproduced here as Fig. 5A with the original pre-publication caption) was entirely based on PETMG F34. The only modifications that appear to have been made to this are the introduction of an oblique angle to the "needles" and the presentation of a general surface growth texture over the PETMG F34 stalk as equivalent to the high-relief oblique edges in *L. problematicus* (Fig. 2). It is noteworthy that the illustration based on PETMG F34 bears no resemblance to the gill raker of *L. problematicus* photographed in the same paper (without needles or a bifid base; MARTILL 1988: fig. 1a; Fig. 2). These differences are significant, as they skew the concept of gill raker form for *L. problematicus*, when compared to those of this fish.

Some gill rakers exhibit signs of a slightly raised edge medial and lateral to the line of "needle teeth" that may be the start of development of a shallow median groove (Fig. 4B, centre of image). Frequently, if a "needle" has become detached from its gill raker, a socket-like recess is revealed (Fig. 4B, centre left and centre right of image). Although following YASUDA's (1960) scheme the "needle" is very similar to the long and pointed morph of *Seriola quinqueradiata* depicted by YASUDA (1960: fig. 4D), it appears that, being centrally rather than laterally or medially located on the dorsal surface, the "needle teeth" are not homologous structures to the dorsal surface structures described as "processes" (YASUDA 1960), "barbs" (PECK 1893), or "teeth" (GIBSON 1988) in other fishes. To distinguish them from these other structures, the term acus fanunculorum (needle of the raker) will be used to describe the pointed central structure set within a socket, in some areas appearing almost "gripped" by the slightly serrated or peg-like edge of the lateral outgrowths on the gill raker (which are the true homologue of the features of PECK 1893, YASUDA 1960 and GIBSON 1988), the pegs alternating with each acus (Fig. 4B: centre of image).

These significant departures for PETMG F34 from the gill raker morphology observed in other specimens of *Leedsichthys* could be argued to be part of a juvenile phase on the grounds of its size, which could ultimately have resulted in the more recognized adult form. However PETMG F34 consists of a well-ossified skull with well-fused dermatocranial elements, a more developed condition than that found in considerably larger specimens of *Leedsichthys*, which is evidence against it being a juvenile representative. Nor does the condition of the matrix lead one to believe that this specimen is a case of exceptional preservation, as it is very much like any Peterborough Member Oxford Clay vertebrate. In comparison with *Leedsichthys*,

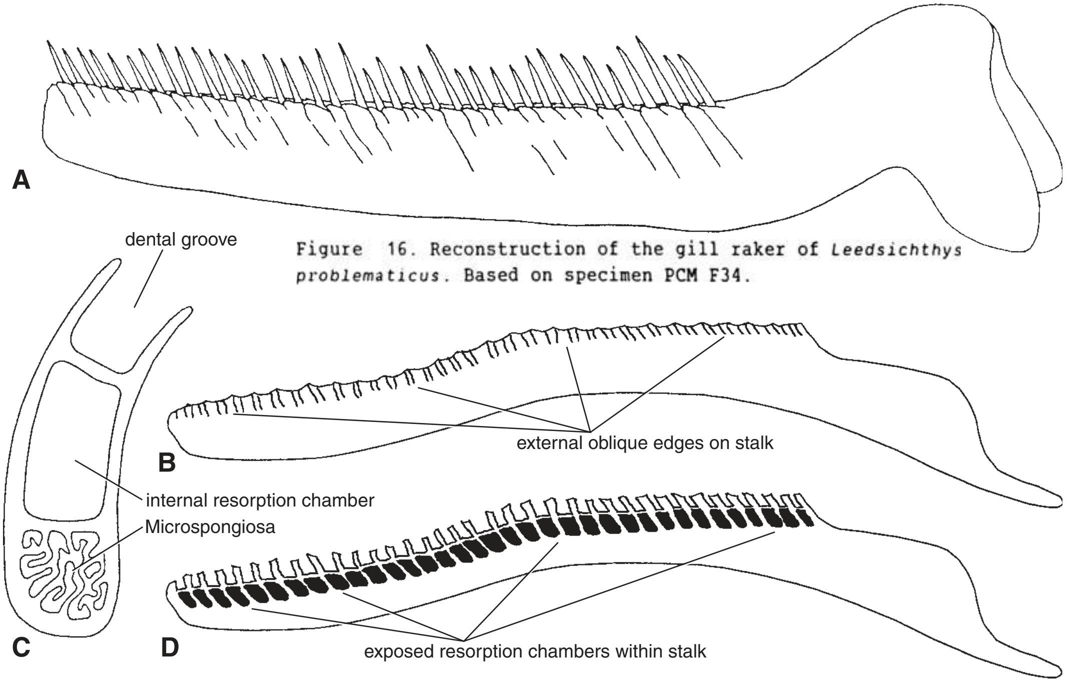

Fig. 5.
Leedsichthys notocetes (= L. problematicus). Original line drawings from MARTILL (1988) and MARTILL et al. (1999), corrected and annotated. **A,** gill raker illustration used in MARTILL (1988: fig. 4), showing original pre-publication caption. Note oblique angle of single central row of 'needles', bifid base and external lines on stalk. **B,** actual lateral view of composite gill raker, after MARTILL et al. (1999: fig. 4b). **C,** cross-section of gill raker with added label for internal resorption chamber, annotated after MARTILL et al. (1999: fig. 4c). **D,** longitudinal section of gill raker, modified after 'lateral view' of MARTILL et al. (1999: fig. 4b).

it is unusual that it has been possible to collect the branchial elements present as a partially articulated unit, and it is unique to excavate them with dermatocranial elements articulated. Although it could be that the unusual retention of the parietal with the carcass has led to this acting as a shield, limiting the post-mortem disruption of the branchial basket, this alone would be insufficient to explain the degree to which the hundreds of gill rakers present have been retained in life position with acus fanunculorum intact, compared to what is seen in the more than seventy other specimens of *Leedsichthys* (LISTON 2010), of which only NHMUK P.10156 (preserved in a concretion) retains some gill rakers in position. All other specimens have ceratobranchials that are preserved devoid of gill rakers. One could speculate that with increasing size, the greater thickness of the connective tissue and epithelia covering the ceratobranchials means that the gill rakers more easily detach from them after death, but there is not enough evidence to support this contention.

In the light of these observations, the lack of skull elements that can diagnose this animal as even a pachycormid merely confirms that this specimen cannot be identified as *Leedsichthys* or *Martillichthys*. Further conservation and full preparation of this specimen will be necessary for the full description required of what appears to be an entirely new taxon.

Comments on the gill rakers of specimen SHL 1309 of *Asthenocormus*

Specimen SHL 1309 of *Asthenocormus* contains clusters of disarticulated fragments in the general area of the head of a complete individual (LAMBERS 1992), some bearing tooth-like points that have been identified as possible gill rakers with 'needle teeth' (LAMBERS 1992: chapter 7, pl. 2b; LISTON 2012: fig. 7c) of a form similar to a swollen-based version of the morph for *Seriola quinqueradiata* depicted by YASUDA (1960). Although previously suggested (LISTON 2007) to be ectopterygoid dentition or pharyngeal tooth plates,

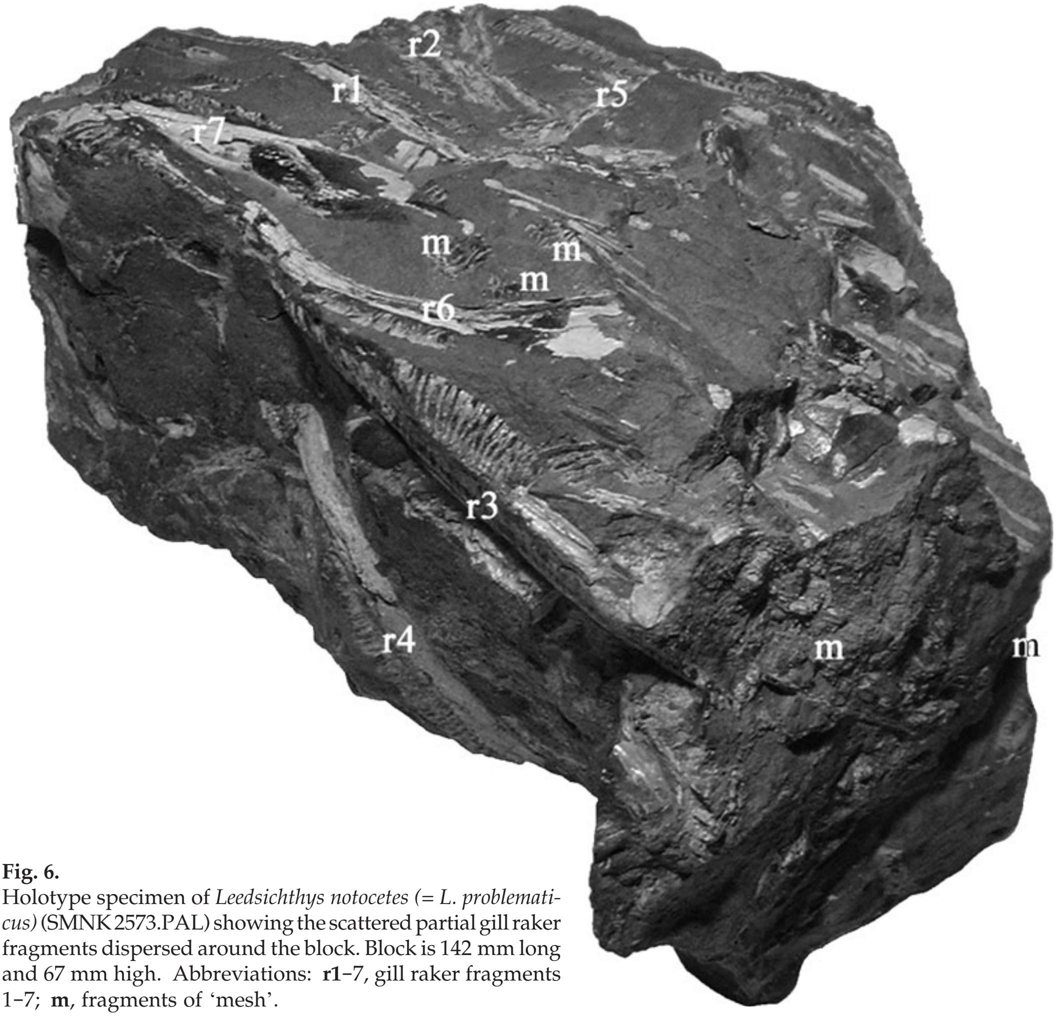

Fig. 6.
Holotype specimen of *Leedsichthys notocetes (= L. problematicus)* (SMNK 2573.PAL) showing the scattered partial gill raker fragments dispersed around the block. Block is 142 mm long and 67 mm high. Abbreviations: **r1**–7, gill raker fragments 1–7; **m**, fragments of 'mesh'.

they appear to be extremely fragmentary gill rakers (LISTON 2012), but the degrees of both preservation and preparation do not allow a decision as to whether these are accessory/secondary stalk structures or acus fanunculorum. The "needle like structures" of *Asthenocormus* are unusual in that the gill raker fragments indicate that they project beyond the tip of the gill raker into the interarch space, in contrast to those of specimen PETMG F34.

This is the only specimen of *Asthenocormus* to have been reported to have gill rakers (with or without "needle teeth"), despite all specimens of this genus coming from the exceptionally well-preserved material in the Kimmeridgian–Tithonian Solnhofen Lithographic Limestone. In this regard, the specimens in the museum of Dresden and the Jura-Museum are particularly conspicuous in not having any traces of these elements.

Description of gill rakers of *Leedsichthys notocetes* (holotype SMNK 2573.PAL)

Initially misidentified as a taphonomic accumulation of dentaries of *Pterodaustro* sp. (FREY pers. comm.), this specimen from the Atacama Desert in Chile consists of a cluster of partial gill rakers. The six surfaces of the block are extremely irregular, and around 38 gill raker fragments are visible on the outer surface of the block (Fig. 6). From an initial examination, it is clear that none of the gill rakers on the block is complete: in comparison to the plan of a generic gill raker (Fig. 2), none of the fragments has all of the basic components present; hence, MARTILL et al. had to create a composite reconstruction from several of the fragments on the block (MARTILL et al. 1999: fig. 4). The fimbriated character of the lateral and medial surfaces is again evident, displaying the same long, curling, tongue-like growth at the tips (Figs. 7B,D). In YASUDA's (1960) scheme (following his table of "processes") these features curve up as biserial lateral growths flanking a groove, resembling the "processes" depicted for adults of *Scomber japonicus* (YASUDA 1960: fig. 4A), as with the gill rakers of *Leedsichthys problematicus*. The base of the gill rakers presents as a leaf-like shape, as with *L. problematicus*, the extent to which the thin lamina reaches a full diamond shape being dependent on the preservational regime (the bases are rarely complete in the Oxford Clay, pers. observ.) as well as on the position of the individual raker within the branchial basket.

MARTILL et al. (1999) described the "sub-oval fenestrae" as a character of the lateral surface of the gill rakers, with a fenestra situated at the base of each plication along the length of the stalk (sensu KAZANSKI 1964 and PEIRONG 1989) of the gill raker. The gill raker fragments on the block do not universally share the fenestral character; indeed, the fenestrae are only clearly evident on areas of four of the fragments (Fig. 7). Even the most extensive of these fragments (Fig. 7A) does not present the fenestrae as described by MARTILL et al. (1999) in their composite diagram. In reality, the fenestrae are only visible in sections of the gill rakers, and when they are present, they appear to grade smoothly into a regular raker only a few oblique ridges farther along the stalk. Within the height of an average ridge-bearing stretch of the gill raker stalk, the oblique ridges occupy about 3 mm out of the 9 mm height of the element (Fig. 7A), with 2 mm of it below where the fenestrae might manifest, and a more solid 4 mm of stalk below that (Fig. 7A). Although the fenestrae shown in the diagram of MARTILL et al. (1999) would ideally be formed by the oblique ridges anterior and posterior to them, in reality these walls commonly are incomplete, with the rim of the fenestra being of variable thickness, and anterior or posterior walls often partially or completely absent (Figs. 7A–D).

On close examination it can be seen that the sections where the fenestrae appear to be are actually at a different topographic level than the rest of the remains on a given gill raker (Fig. 7A). This is because the gill raker is an area of weakness within the calcilutite block, and the block has preferentially split through, rather than around, the periosteal surface of the gill rakers. This means that the outer surface is rarely preserved intact, as has also been observed with other material from a different region of the Atacama Desert in Chile (ARRATIA & SCHULTZE 1999; LISTON 2004a, 2010), where the harder matrix surrounding the more fragile gill rakers and other fossilised bones generally fractures through the fossil material, rendering excavation and reconstruction of the fossil material extremely problematic (LISTON 2010). Thus there is longitudinal damage to each and every fragment – in no gill raker fragment is the external surface visible or intact, and the bone always shows signs of breakage. The "sub-oval fenestrae" are an artefact on the specimen (STEEL, pers. comm. 08/2004), formed by fracturing and/or erosion penetrating the thin gill raker walls between the oblique ridges to partially expose the internal gill raker cavity (Fig. 8B). The internal gill raker cavity is formed by extensive bone resorption, and is irregularly exposed across the gill raker, depending upon the gill raker's topographic exposure and vulnerability to erosional or mechanical damage. This model is further supported by other similar gill raker material from the Oxfordian of Chile (ARRATIA & SCHULTZE 1999; LISTON 2008a, 2010: fig. 11b,c), which preserves the same characteristics as displayed on the SMNK 2573.PAL block, including intermittent and occasional "fenestrae" on its ventral as well as lateral and medial surfaces (Fig. 8A). They occur on the ventral surface in this specimen because the rakers are not isolated, but are lying stacked en echelon more or less vertically, as they would have been in life. This caused there to be more erosional attack from above (on to the ventral as well as the lateral surfaces), as the gill rakers form a fracture plane through the rock.

If the fenestral level of the gill raker is regarded as a "box" formed of an upper surface (the bone forming the base of the "dental groove" of MARTILL et al. 1999: fig. 4c), a lower surface (the bone covering over the "microspongiosa" of MARTILL et al. 1999: fig. 4c), a left surface (lateral or medial wall of raker), a right surface (the opposite wall of the raker), and anterior and posterior partial planes of bone (the four oblique ridges forming the four verticals of the box), then each gill raker has had either the left or right wall excised through fracturing or erosion. As noted by MARTILL et al. (1999), the stalk of the raker is "thin-walled and hollow dorsally, comprising two parallel sheets of bone." It is the centres of these thin lateral walls of each subacular chamber that have broken away under shear, revealing the matrix-filled hollow dorsal chamber described. The reason why anterior and posterior bony rims partially appear as apparent struts is because they represent the internal thickening of the oblique ridges of WOODWARD (1889b, 1890b) or plications of MARTILL et al. (1999).

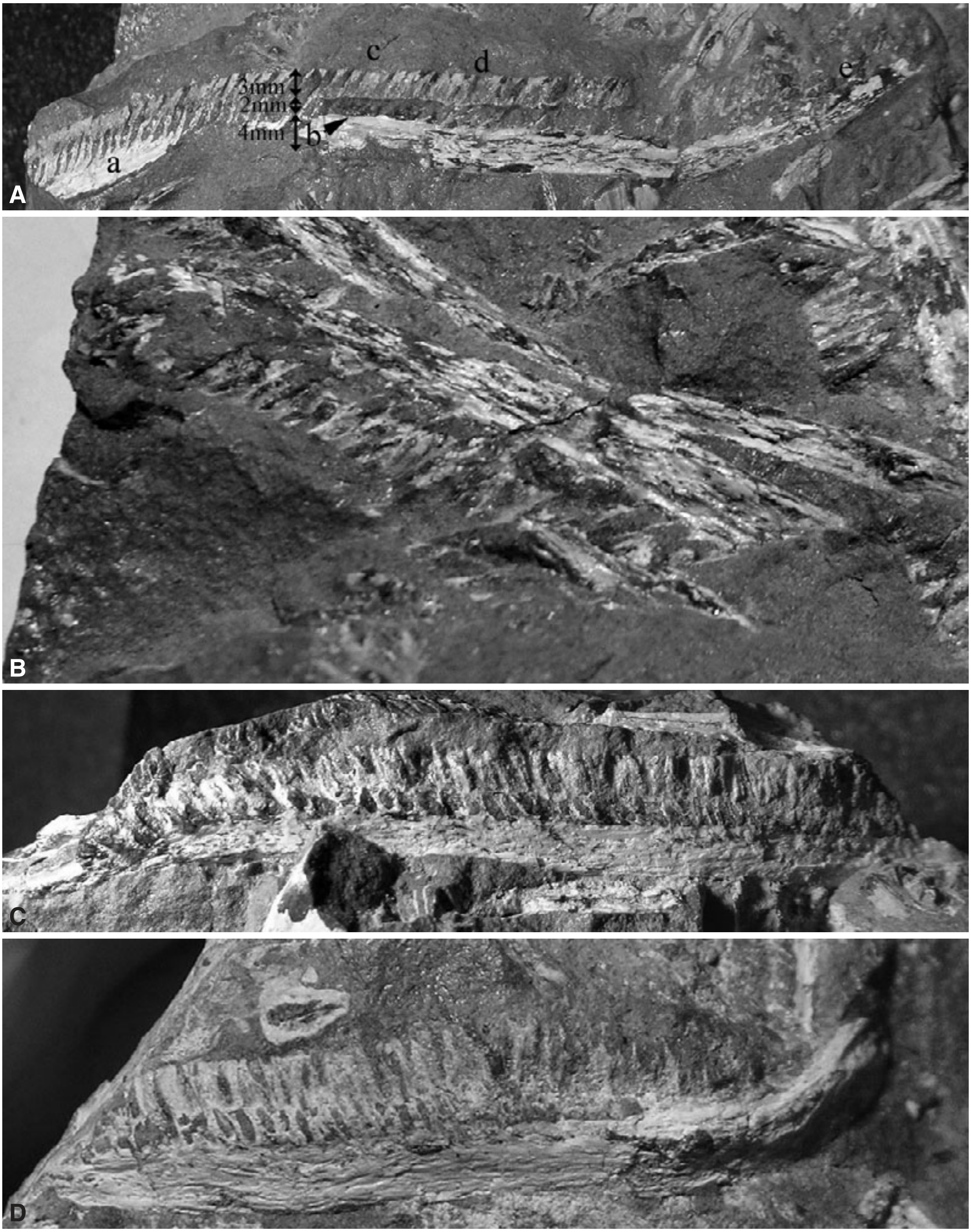

Fig. 7.
Closeups of gill raker fragments of holotype specimen of *Leedsichthys notocetes (= L. problematicus)* (SMNK 2573. PAL). **A,** gill raker fragment 1 (**r1**), field of view = 90 mm. See text for legend for points **a**–**e**. **B,** gill raker fragment 2 (**r2**), field of view = 15 mm. **C,** gill raker fragment 3 (**r3**); field of view = 75 mm. **D,** gill raker fragment 4 (**r4**), field of view = 60 mm.

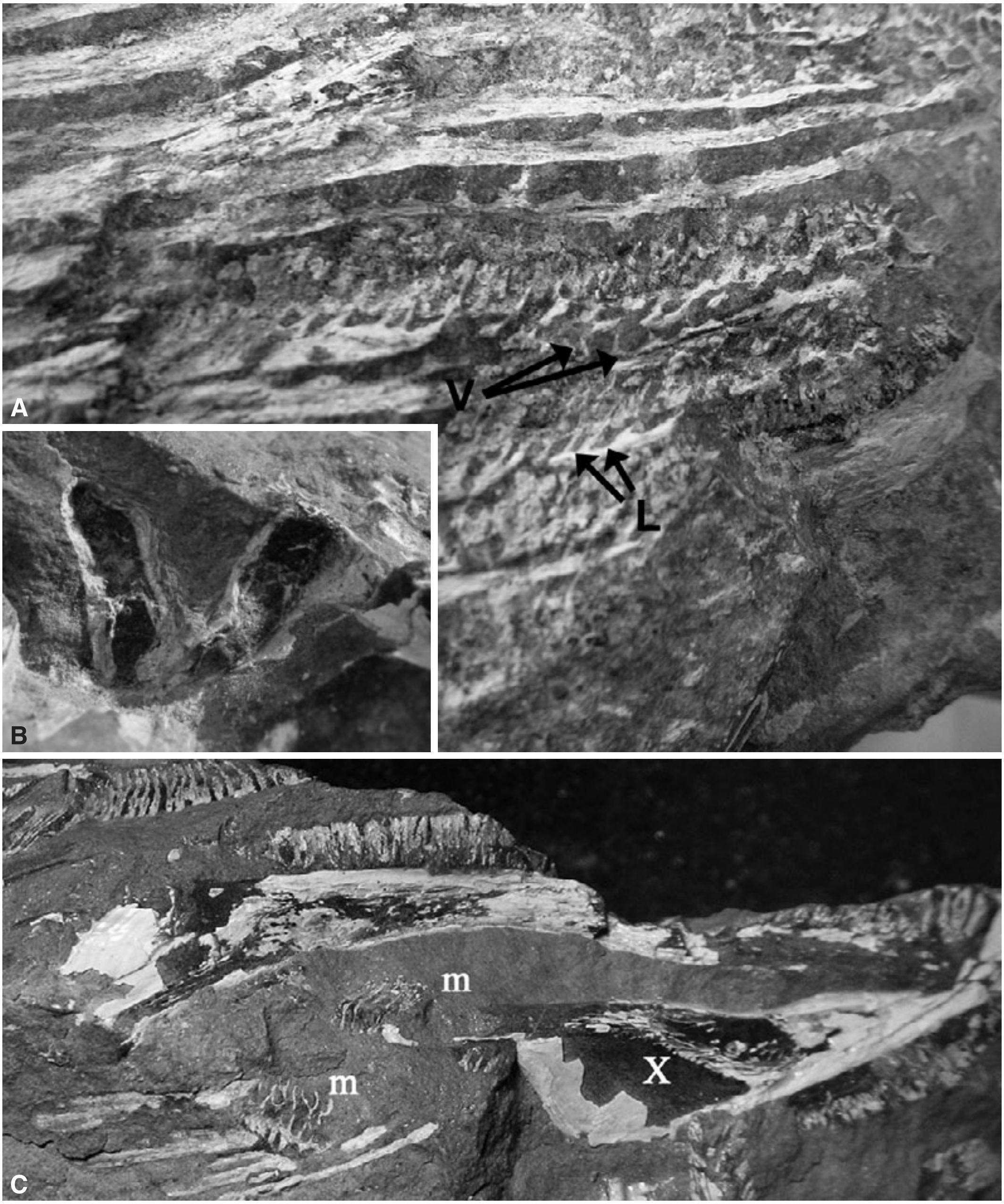

Fig. 8.
Details of gill raker fragments of *Leedsichthys notocetes (= L. problematicus)*. **A,** ventral fenestrae with lateral fenestrae on block of articulated gill rakers, specimen I 8-02 11 73, collected in the Atacama desert east of Antofagasta in February 1973. Field of view = 70 mm wide. **B,** Transverse cross-section of two gill rakers from SMNK 2573.PAL with extensive internal resorption. Field of view = 15 mm wide. **C,** Black contact area (**X**) on gill raker fragment 7 of SMNK 2573.PAL with nearby fragments of 'mesh.' Abbreviations: **r1–7**, gill raker fragments 1–7; **m**, fragments of 'mesh'; **V**, ventral fenestrae; **L**, lateral fenestrae. Field of view = 80 mm.

The level at which the fracturing has occurred has determined how thick the "walls" of the fenestrae (the "frames" around the "windows") appear. This also explains why that (circa 2 mm) level of the gill raker lateral or medial surface grades from bony external wall, to parallel oblique ridges, to fenestrae, to sediment that extends uninterrupted through the internal gill raker cavity at the level of the ridges: the fracture sheared through the raker at an angle close to (but not quite) the axis of the gill raker, removing an entire side of ridges and penetrating farther into the middle of the gill raker as it progressed. An analogy might be helpful: if one sectioned through the hull of a ship longitudinally, one is far more likely to cut through the bulkheads that partially separate different sections of the ship's hull than through the thickness of the port or starboard hull. The "bulkheads" in the gill raker are the internal thickenings to support the oblique ridge on the external surface of the gill raker, which is why the angle of the ridges reflects the orientation of the fenestrae. The patchy exposure of fenestrae on each raker that exhibits them reflects the degree of internal resorption within the bone of the gill raker, as well as the fracturing and differential delamination of the raker eroding in a harsh desert weathering regime (as opposed to a frequently water-logged Oxford Clay, which is more likely to separate around rather than through a fragile structure such as a gill raker), thus giving the impression of regularly spaced fenestrae.

To clarify this, the original gill raker illustrations of MARTILL et al. (1999) are reproduced here in corrected form (Figs. 5B–D), with the figure originally labeled "lateral view" corrected to be read as a longitudinal section (Fig. 5D). A lateral view is also presented (Fig. 5B).

This interpretation is further supported by another area of evidence: on this block, if bone has been in direct contact with the calcilutite, and has then broken away, it leaves behind a black contact mark (Fig. 8C). On the most prominent example of a gill raker with fenestrae on the upper surface of the block, the lateral aspect is against the matrix, with medial aspect uppermost (Fig. 7A). Taking into account the relief in the raker, it is evident that it is the inner surface of the lateral wall of the gill raker that is visible proximally (Fig. 7A, area A) for the most part, displaying the ridges separated only by slits of matrix. It is only at an area of high relief (Fig. 7A, starting at area B), where the fracture is passing through a more medial part of the raker, that the fenestrae become visible. The above trend can be seen from fenestrae on a high relief section with black areas showing (Fig. 7A, area C) where more complete areas of bone once completely and partially (depending on which chamber is being referred to) enclosed the chambers (Fig. 7A, area D), to parallel ridges on the most distal (Fig. 7A, area E) extent of the raker stalk.

It appears that it is the differences in matrix and exposure regime that have led to this material presenting differently to that from strata of Callovian–Kimmeridgian age. Another difference is that the material from Chile can also present a finely preserved ultrastructure intimately associated with the gill rakers (variably visible on some areas on the block, see Figs. 6 and 9, as well as a separate fragment and thin sections showing it in transverse and plan views; LISTON 2008a: figs. 5, 6). This unusual ultrastructure bears some resemblance to the suspension feeding meshes of the contemporary fishes *Rhincodon typus*, the whale shark (GUDGER 1941: fig. 8), and the advanced suspension feeding silver carp *Hypophthalmichthys molitrix* (VERIGIN 1957: fig. 1), and may be associated with increased efficiency of suspension feeding (WILAMOVSKI 1972) through extraction of finer organic material. This latter species (OSHIMA 1919) is one of many suspension feeders that have independently evolved epibranchial organs (SANDERSON & WASSERSUG 1993). It has a remarkable internal "3-way extraction system" (PEIRONG 1989, GERKING 1994), enabling it to feed on phytoplankton as well as suspended bacteria (SANDERSON & WASSERSUG 1993). This mesh feature or characteristic has partially been observed in only one specimen of *Leedsichthys* from the Callovian-Kimmeridgian clay deposits, perhaps due to preservational factors. This specimen, from the Callovian of Normandie, can show an identical plan view (fig. 7B of LISTON 2008a) to the mesh above the gill rakers in the Oxfordian material from Chile. Further work to reconstruct this apparent "supra-fanuncular mesh" atop the gill rakers in *Leedsichthys* may well give indirect evidence of the predominant prey size in the environment, a rare indication in our sparse knowledge of the geological record of planktonic lifeforms (CRESSEY & PATTERSON 1973).

Discussion

Gill raker morphology

Gill rakers have been demonstrated to be a poor source of taxonomically valid characters: they change their form with age and in response to environmental stimuli. They are also a high-risk character on which to base new taxa due to the likelihood of ecophenotypic convergence in suspension feeders. In terms of

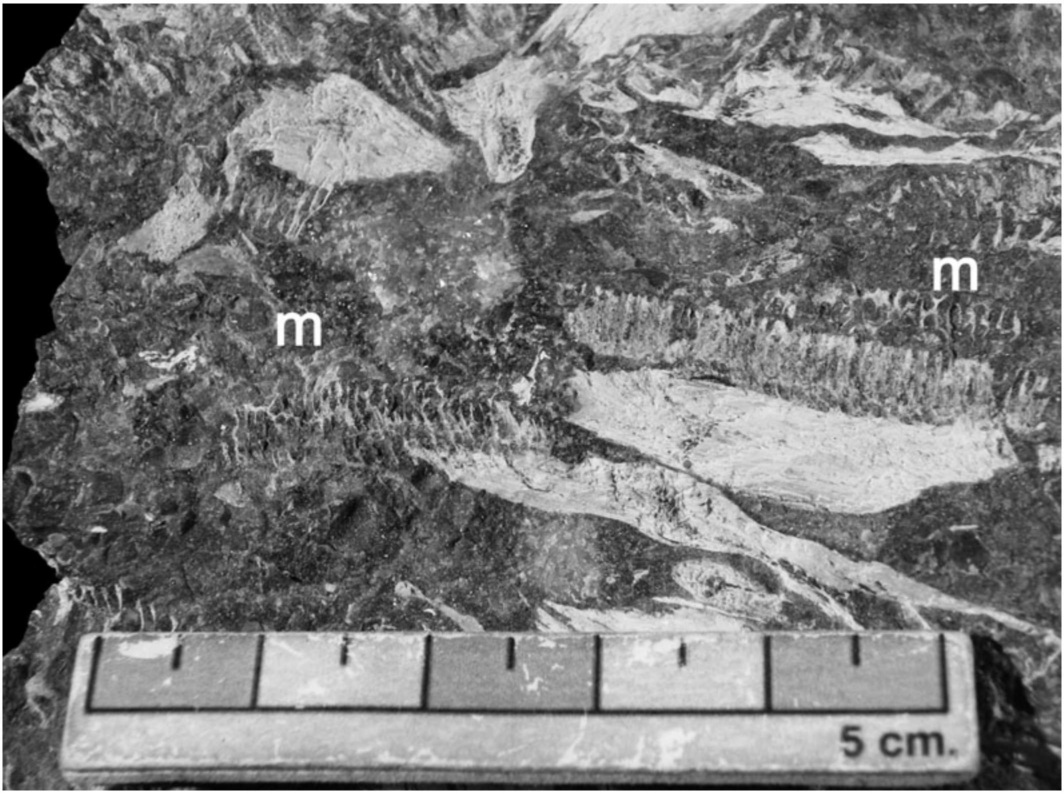

Fig. 9.
Detail of disarticulated gill raker block, specimen I 19−1 21 73, collected in the Atacama desert east of Antofagasta in January 1973, showing 'mesh' fragments of *Leedsichthys notocetes (= L. problematicus)*. Abbreviation: **m**, fragments of 'mesh'. Scale = 50 mm.

preservation, gill rakers are vulnerable to damage (resulting in artefacts), and can be obscured by other remains, making it difficult to assess both their presence and nature.

The presence or absence of "needle teeth" on gill rakers in pachycormids is a character that should be easiest to assess in the larger suspension feeding genera *Asthenocormus*, *Martillichthys* and *Leedsichthys*, for which the size of the fishes should make gill rakers easy to detect and examine, and yet only one specimen of *Asthenocormus* presents even equivocal evidence, and the other two genera appear to be devoid of such structures. Although possessing structures similar to "needles", *Asthenocormus* seems to have a very different type of gill raker, both in proportions of the 'needle-like structure' to the stalk, and in the proportions of the stalk itself. The 'needle-like structures' cannot be confirmed as aci fanunculorum without preparation and reconstruction. The few gill rakers present in *Martillichthys* have no "needles", and seem very similar in shape and proportions to those of *Leedsichthys*, although much smaller.

In his original use of the 'needle teeth' character for his matrix, there is no specific reference made by LAMBERS (1992) to the "needle-less" gill raker state in the other smaller pachycormids. As such, the presence/absence of these "needle teeth" is a character that cannot be rigorously or consistently demonstrated for either larger or smaller (e. g., *Sauropsis*, *Haasichthys*) representatives of the family.

Given the demonstrated problematic characteristics of gill rakers in contemporary fishes, the degree of variability in the character of needle presence/absence in the few cited examples of contemporary fishes, and the limited possibility of assessing the presence of this structure in most members of the family Pachycormidae, it was decided to exclude this character from the revised analysis incorporating LAMBERS' (1992) and LISTON's (2007) dataset in FRIEDMAN et al. (2010). This followed the removal of this character in earlier cladistic work, when it was noted that the character of presence/absence of gill raker "needle teeth" did not harm the linkage between *Asthenocormus* and *Leedsichthys*, and indeed the introduction of *Martillichthys* linked all three taxa together in 100 % of the most-parsimonious trees (LISTON 2007).

The "needle teeth" of gill rakers may not fully ossify in life (VAN DEN BERG et al. 1994b), and in specimen PETMG F34 it is unlikely that their presence is the result of exceptional preservation of an average specimen. Given that gill rakers of fishes go through many structural changes throughout ontogeny reflecting changes in diet, and that WEBB & BUFFRÉNIL (1990) noted that "… the larger the adult size, the larger the number of intermediate stages that might be expected" in the development of an animal, and with an animal capable of reaching the estimated lengths of *Leedsichthys* (see LISTON et al. this volume), it would be tempting to assume that PETMG F34 was indeed a juvenile form. However, invoking these structures as possible juvenile features when such structures are otherwise unknown in *Leedsichthys* does not justify the inclusion of this cranial fragment within the genus. With the lack of pachycormid osteological characters, and the absence of evidence that any specimen of *Leedsichthys* with a gill basket as small as that indicated by PETMG F34 would have a different form of gill raker, it seems most practical to refer to this specimen as an undescribed suspension feeding osteichthyan with hypertrophy of the gill rakers, of which two are already known (LISTON 2008b), to have inhabited the Oxford Clay sea.

Conversely, the gill raker material on the block SMNK 2573.PAL described as *Leedsichthys notocetes* seems identical to specimens referred to *L. problematicus*, with three caveats:

1. The suprafanuncular mesh (Fig. 9). There is some evidence for the presence of this in gill rakers of Callovian *Leedsichthys problematicus*, but it is hard to tell if the material is more developed in the Oxfordian material from the Atacama desert, or simply better preserved in that lithology. Alternatively, it may again be an ontogenetic stage, as with increasing age the animal develops a finer mesh to make its extraction of organic material from the water more efficient, and so support a larger body mass. This pattern of development is seen in the Silver Carp *Hypophthalmichthys molitrix* (WILAMOVSKI 1972).
2. The presence of the "fenestrae" erosional artefacts (Fig. 7A).
3. The degree of internal bone resorption and remodelling within the gill rakers (Fig. 8B). This internal resorption seems more extensive than in other gill rakers recently examined for analysis of growth rings (LISTON et al. 2005), but this may well be more a reflection of the different positions chosen to section the gill rakers for analysis, than on fundamental differences between the gill rakers themselves.

The species *L. notocetes* based on this material (SMNK 2573.PAL) is therefore a junior synonym of *L. problematicus*. More extensive material with similar gill rakers has been collected from elsewhere in the Oxfordian of Chile (ARRATIA & SCHULTZE 1999, LISTON 2004a, LISTON 2010) and is currently awaiting preparation. This new material should give a clearer indication of whether or not there are significant taxonomic differences between the European and the South American material of *Leedsichthys*. To create a separate taxon on the basis of the evidence currently available would be to unnecessarily increase taxonomic names on the basis of very little evidence (STRAND 1928, FOWLER 1930).

Conclusions

The referral of specimen PETMG F34 to *Leedsichthys* is unsupportable, as no skeletal elements of *Leedsichthys* are identifiable within the specimen. Given their demonstrated ecophenotypic plasticity in suspension feeding fish, gill rakers should not be used as a primary basis for diagnosis of such taxa. Gill rakers are complex and diverse structures, and it is difficult to use aspects of them as characters without having a clear understanding of their variations throughout a given gill skeleton, as well as variations throughout ontogeny. To fully determine the occurrence of "needle teeth" (whether acus fanunculorum or other forms) in pachycormids, as in other groups, a full knowledge of them in each taxon is necessary to determine how ephemeral they may be. Fortunately, there are some prospects for progress in this area, at least with regard to *Leedsichthys*. A specimen collected recently (PETMG F174) from Bed 14 (HUDSON & MARTILL 1994) of the Peterborough Member of the Oxford Clay in the Star Pit near Whittlesey (LISTON 2006) consists of many paired elements (including pectoral fins, preopercles and hyomandibulae) and a significant portion of the branchial basket. Many hundreds of gill rakers were collected and mapped, and this means that a future investigation into variability of gill raker morphology within a single individual will be possible, and might also reveal details of their disposition around the gill basket. It will be noteworthy if any of these retrieved gill rakers display the same white, possible mesh structure present in the Callovian material from Normandie. The gill raker material originally described as *Leedsichthys notocetes* is indistinguishable from that of *L. problematicus* on any grounds other than preservational. *Leedsichthys notocetes* is therefore synonymised with *L. problematicus*.

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