INTRODUCTION

The developmental processes inducing differentiations of limbs lie at the base of one of the most important evolutionary innovations, namely that variations in overall limb morphology reflect changes on a macroevolutionary level, i.e. they characterize higher level taxa (Futuyma, 1998). One of the macroevolutionary traits involved with limb morphology is the presence or absence of limbs. Limb reductions have occurred independently in many higher level taxa of vertebrate lineages, as for example teleosts (Bell, 1987; Nelson, 1989–90), amphibians (Duellman & Trueb, 1986), reptiles (Gans, 1975; Motani et al., 1996; Carroll, 1997; Pough et al., 1998), and even some mammals (Lande, 1978), all both in recent and fossil forms. Some intermediate forms, which could be a reflection of an evolutionary grade towards limb reduction and body elongation, do exist up to the interspecific level (e.g. in the genus Lerista within the Scincidae) (Lande, 1978; Greer, 1987, 1990). As this is still above the species level, it technically still involves processes underlying macroevolution (Futuyma, 1998; Carroll, 2001). As discussed by the latter authors, the notion of a gap between processes underlying micro- and macroevolution ranges between being substantial to nonexistent, depending on different methodological approaches (i.e. palaeontology vs. genetics, respectively). As Carroll (2001) mentioned: 'the distinction between macro- and microevolution in terms of morphological change is descriptive, not mechanistic'. Evidence is provided in this paper that even such a trait as the presence/absence of limbs can vary intra-

Intraspecific variation in limblessness in vertebrates: a unique example of microevolution

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The variation in limb reduction in vertebrates has generally been observed as characterizing higher-level taxa. Such structural changes are thus considered to reflect macroevolutionary processes. A statistical analysis of metric variables of some species of the African catfish family, Clariidae, suggests that fin reduction occurs at the microevolutionary level as well. In at least three species of that family intraspecific variation in the presence/absence of the pelvic fins was observed, and one species also showed similar variation for the pectoral fins. Discriminant function analysis confirmed that the variation is intraspecific, and even occurs within the same population. Sexual dimorphism could be excluded. This variation can be observed in the most anguilliform species of the clarid family, suggesting a link with body elongation (as is the case in tetrapods that show limb reduction). Pelvic fin loss appears to precede pectoral fin reduction during evolution. From the morphology it could be ascertained that the loss of the pelvic fins is coupled to the loss of the pelvic girdle, contrary to the case for the pectoral fins and girdle. Differences in functionality may explain this. Breeding results support the occurrence of intraspecific variation, as an F1 offspring showed a difference compared with the parents. For at least one species, the benefit from body elongation and limb reduction can be related to its highly specialized life style, as it lives subterraneanly in muddy soil of the Central African rainforest. © 2002 The Linnean Society of London, Biological Journal of the Linnean Society, 75, 2002, 367–377.

specifically in certain vertebrates and thus reflects both micro- and macroevolutionary processes.

In most vertebrate lineages characterized by limb reduction to limb loss the body undergoes marked elongation, which is considered as being an adaptation to burrowing and fossorial life styles (Gans, 1973, 1975; Withers, 1981). In teleost fishes, many strategies of burrowing behaviour exist in elongated species (Nelson, 1994), and one unique example is the clarid catfish family, in which a complete range of body forms exists from fusiform (with both pelvic and pectoral fins well developed) to anguilliform (with all paired appendages lacking) (Boulenger, 1908; Pellegrin, 1927). For some species, it had been noted that the pelvic and pectoral fins may be reduced or sometimes absent (Boulenger, 1911; Poll, 1942).

In this paper, we have used statistical means to support the hypothesis of interspecific, but more importantly intraspecific and even intrapopulation variation in the presence/absence of paired fins in several species of the Claridae. Evidence from the morphology suggests variation in an early triggering of fin development, whereas breeding results suggest a large degree of flexibility. Field observations support the hypothesis that within at least one of these species limb reduction and body elongation is related to a highly specialized fossorial habit, unique for teleost fishes.

MATERIAL AND METHODS

MEASUREMENTS

Using digital callipers (0.05 mm accuracy), 30 metric measurements were taken on 473 specimens belonging to nine clarid species: *Clarias gariepinus* (Burchell, 1822), *Clarias salae* Hubrecht, 1881, *Clariellabes longicauda* (Boulenger, 1902), *Gymnallabes alvarezi* Roman, 1970, *G. typus* Günther, 1867, *Platyallabes machadoi* Poll, 1977, *Platyallabes tihoni* (Poll, 1944), *Channallabes apus* (Günther, 1873) and *Dolicallabes microphthalmus* Poll 1942. Specimens were obtained from the collections of the MRAC (Musée Royal d’Afrique Central, Belgium), BMNH (British Museum of Natural History), MNHN (Musée National d’Histoire Naturel, Paris), MHN (Musée d’Histoire Naturelle, Geneve), NMW (Naturhistorisches Museum, Wien), MCZ (Museum of Comparative Zoology, Harvard), ZMB (Museum fur Naturkunde, Berlin) and RMNH (Rijksmuseum van Natuurlijke Historie, Leiden). Measurements taken were: (1) total length, (2) standard length, (3) preanal length (4) pre-dorsal-fin length, (5) distance between the dorsal fin and the supraoccipital process, (6) caudal peduncle depth, (7) abdominal depth, (8) maxillary barbel length, (9) internal mandibular barbel length, (10) external mandibular barbel length, (11) nasal barbel length, (12) skull length, (13) skull width, (14) skull height, (15) preorbital skull length, (16) orbital skull width, (17) orbital skull height, (18) length of the supraoccipital spine, (19) width of the supraoccipital spine, (20) interorbital distance, (21) distance between the anterior nostrils, (22) distance between the posterior nostrils, (23) orbital diameter, (24) snout length, (25) snout height, (26) distance between the snout and the hyoid fold, (27) distance between the internal mandibular barbel bases, (28) distance between the external mandibular barbel bases, (29) mouth width, and (30) caudal fin length. For a drawing of the taken measurements, we refer to Teugels (1986).

STATISTICAL ANALYSIS

Backward stepwise Discriminant Function Analyses (DFA) were performed using Statistica (Statsoft, Inc.), with the number of variables for each analysis depending on the amount of correlation between variables, and correlation between means and variance (correlated variables and variables with a high correlation >0.9) between means and variance were removed from the analysis. The first analysis involved all species, which were categorized into 13 groups (based on the configuration of the paired fins) as follows: (1) *Cg*: *Clarias gariepinus* (*N* = 21), (2) *Cs*: *Clarias salae* (*N* = 41), (3) *Cl*: *Clariellabes longicauda* (*N* = 41), (4) *Ga*: *Gymnallabes alvarezi* (*N* = 12), (5) *Ga-v*: *G. alvarezi* lacking pelvic fins (*N* = 5), (6) *Gt*: *Gymnallabes typus* (*N* = 31), (7) *Pm*: *Platyallabes machadoi* (*N* = 17), (8) *Pt*: *Platyallabes tihoni* (*N* = 53), (9) *Ca*: *Channallabes apus* (*N* = 4), (10) *Ca-v*: *C. apus* lacking pelvic fins (*N* = 155), (11) *Ca-vc*: *C. apus* lacking both pectoral and pelvic fins (*N* = 76), (12) *Dm*: *Dolicallabes microphthalmus* (*N* = 3), and (13) *Dm-v*: *D. microphthalmus* lacking pelvic fins (*N* = 14). Of all these groups, these not designated as ‘–v’ or ‘–vc’ thus possessed both pectoral and pelvic fins (in some rare cases where specimens only had one pectoral or pelvic fin these were grouped with those having both contralateral fins). For the analysis of the geographical variation in *C. apus*, five populations were used in which specimens with and specimens without paired fins could be observed: (1) *Bt*: Boloko, western part of the Middle Zaire river system (Likouala river, Congo Brazzaville), (2) *Bm*: Bumba, northern part of the Middle Zaire river system (Congo Republic), (3) *LD*: Loundjili, coastal river system (Congo Brazzaville), (4) *TM*: Tchimenji, Kasai river system (Angola), and (5) *WO*: Woleu, Woleu–Ntem river system (Gabon). The coding ‘–v’ and ‘–vc’ follows that as above. For the analysis of possible sexual dimorphism, five groups could be defined: (1) *m*, male specimens having both
pectoral and pelvic fins, (2) m-v, males lacking only pelvic fins, (3) m-vc, males lacking both pectoral and pelvic fins, (4) f-vc, females lacking only pelvic fins, and (5) f-vc, females lacking both pectoral and pelvic fins. Only one female specimen with both pectoral and pelvic fins present was available. It was thus not included in this analysis.

**MORPHOLOGY**

The morphology of the pectoral and pelvic fins and girdle was studied using cleared and stained material. Clearing and staining followed Taylor & Van Dyke (1985). Specimens used for the clearing came from a single sample of the MRAC (KMMA 88–5-P-2192–227). Breeding results come from spontaneous reproduction of two individuals that were commercially obtained.

**RESULTS**

**STATISTICAL ANALYSIS**

A first discriminant function analysis was undertaken to determine to what degree the metric variables could be used to reflect interspecific variation, as well as to evaluate the relative position of the intraspecific groups (with specimens having a different number of paired appendages). A plot of the 13 groups (N = 473), based on 30 variables reflects a cluster structure, supported by what is to be expected from the general morphology and taxonomy: all species (not groups) differ significantly from each other (P < 0.001 for all pairwise contrasts between species, with the exception of P = 0.003 for Ga-v/Ca, Fig. 1a). The squared Mahalanobis distances (D²-values) between species ranged between 14 (for Gt/Ca) and 542 (for Cg/Dm, Table 1). Root 1 reflects the degree of anguilliformity (supported by the factor structure). The fusiform *Clarias gariepinus* has the lowest root 1 values, whilst *Clarias salae* also has a slightly elongated body (reflected in the taxonomic position in the subgenus *Anguillolabes* (Teugels, 1986). A chain of consecutive clusters along root 1 includes (starting with the less anguilliform): *Platyclarias machadoi*, *Platyllabes tihoni*, *Gymnallabes alvarezi*, *G. typus*, *Channallabes apus* and finally the extremely elongated *Dolichallabes microphthalmus*. The species *P. tihoni* is separated from this cluster along root 2 as a result of the anterior-placed dorsal fin. Of importance is the relation between the intraspecific groups: all groups with a different number of paired fins cluster together according to the species they belong to. The lowest D²-values were observed between the groups of *C. apus* and those of *D. microphthalmus*, where none were significantly different from one other: 1.7 between *Ca* and *Ca-v* (P = 0.899), 5.6 between *Ca* and *Ca-vc (P = 0.107), 8.1 between *Dm* and *Dm-v* (P = 0.192). Although the latter groups (*Dm* and *Dm-v*) lie separate on the plot of root 1 vs. root 2, this is not the case for plots of other roots. The groups *Ca-v* and *Ca-vc*, as well as the groups *Ga* and *Ga-v*, were significantly different (P <

and $Ga-v$ difference between the groups is very low, as is reflected in the
the other groups. It remains clear that the distance
mens, this in contrast to the much higher number for
viewed with caution as
Again,
data set (with the exception of an inverted root 1).
the distribution
specimens (Fig. 1b). True intraspecific
variation is again suggested because the distribution
of the
Channallabes apus
might be masked by the total interspecific variation
could be ruled out, based on a DFA of only the
DFA.
other possible factors underlying the variability in
fin development, as for example geographical varia-
tion between populations or sexual dimorphism, could
be ruled out as well. A DFA of five geographically
separated populations (not only regionally, but also
by river system), suggests that even within a single
population the number of paired fins may vary
(Fig. 1c). As could be expected, some populations
cluster more closely together than others, but it is the
relation within the populations that is important.
Within four of the populations the groups with a
different number of paired appendages could not be dis-
tinguished ($P > 0.1$, Table 3) and cluster closely
together: Boloko population ($D^2 = 0.7$), Bumba popu-
lation ($D^2 = 2.4$), Loadjili population ($D^2 = 1.4$), and
Tchimenji population ($D^2 = 0.5$). Only the Woleu
population showed two distinct groups ($P < 0.001$,
$D^2 = 20.7$), largely based on a narrower supraoccipital
width. However, the results for this population should
be treated with caution, as the group with taxa having
all paired fins contained only two specimens.
Analysis of the two sexes ($N = 149$) showed no indi-
cation of a strict sexual dimorphism in paired fin
development (Table 4). High $P$ values ($>0.01$) indicated
a non-significant distinction between sexes for $m$ and
$f-v$, for $m$ and $f-vc$, for $m-vc$ and $f-vc$. For some of them, even the $D^2$-values were extremely
low (e.g. 0.018 between $f-vc$ and $m-vc$).

**Breeding results**
The hypothesis of true intraspecific variation within
Channallabes apus was confirmed by the production

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**Table 1.** Values of $P$ (upper right) and Squared Mahalanobis distances ($D^2$, lower left) of all 13 groups, reflecting the
significant discrimination between the species, but not between groups within a single species

<table>
<thead>
<tr>
<th></th>
<th>$Ca$</th>
<th>$Ca-v$</th>
<th>$Ca-vc$</th>
<th>$Cg$</th>
<th>$Cl$</th>
<th>$Cs$</th>
<th>$Dm$</th>
<th>$Dm-v$</th>
<th>$Ga$</th>
<th>$Ga-v$</th>
<th>$Gt$</th>
<th>$Pm$</th>
<th>$Pt$</th>
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<td>$Ca$</td>
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<td>0.107</td>
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<tr>
<td>$Ca-v$</td>
<td>$2$</td>
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<td>$Ca-vc$</td>
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<td>$2$</td>
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<tr>
<td>$Cs$</td>
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<td>144</td>
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<td>92</td>
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<tr>
<td>$Dm$</td>
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<td>511</td>
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<tr>
<td>$Ga$</td>
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<td>55</td>
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<td>30</td>
<td>230</td>
<td>85</td>
<td>74</td>
<td>74</td>
<td>86</td>
<td>31</td>
<td>17</td>
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<td>**</td>
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<tr>
<td>$Pm$</td>
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<td>115</td>
<td>141</td>
<td>223</td>
<td>64</td>
<td>92</td>
<td>187</td>
<td>229</td>
<td>77</td>
<td>85</td>
<td>91</td>
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</tr>
<tr>
<td>$Pt$</td>
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<td>121</td>
<td>136</td>
<td>266</td>
<td>127</td>
<td>139</td>
<td>132</td>
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<td>73</td>
<td>102</td>
<td>87</td>
<td>106</td>
<td></td>
</tr>
</tbody>
</table>

* $P < 0.01$; ** $P < 0.001$; $D^2 < 20$ underlined.

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**Table 2.** Values of $P$ (upper right) and Squared Mahalanobis distances ($D^2$, lower left) of the Channallabes apus
groups

<table>
<thead>
<tr>
<th></th>
<th>$Ca$</th>
<th>$Ca-v$</th>
<th>$Ca-vc$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Ca$</td>
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</tr>
<tr>
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<td></td>
</tr>
<tr>
<td>$Ca-vc$</td>
<td>6</td>
<td>2</td>
<td></td>
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</tbody>
</table>

* $P < 0.01$; ** $P < 0.001$. 

0.001), however, the $D^2$-value was very low (2.3 and 19, respectively). Comparable low $D^2$-values could be
observed between some groups of different species: $Ga-v$ and $Ca$ (16), $Gt$ and $Ca$ (14), $Cs$ and $Cl$ (16), and
$Ga-v$ and $Gt$ (17) (all $P < 0.001$, except for $Ga-v$ and $Ca$ with $P = 0.003$).

The possibility that true intraspecific variation might be masked by the total interspecific variation
could be ruled out, based on a DFA of only the Channallabes apus specimens (Fig. 1b). True intraspecific
variation is again suggested because the distribution
of the C. apus groups is comparable to that of the total
data set (with the exception of an inverted root 1).
Again, $D^2$-values between the groups remain very low:
0.9 ($P = 0.447$) between $Ca$ and $Ca-v$; 5.8 ($P = 0.001$)
between $Ca$ and $Ca-vc$; and 2.2 ($P < 0.001$) between
$Ca-v$ and $Ca-vc$ (Table 2). The seemingly significant
difference between $Ca$ and the other groups has to be
viewed with caution as $Ca$ contained only four speci-
mens, this in contrast to the much higher number for
the other groups. It remains clear that the distance
between the groups is very low, as is reflected in the
$D^2$-values and the large overlap of the polygons on the DFA.

of offspring. Two surviving larvae of spontaneous reproduction in an experimental aquarium exhibited a different paired fin morphology from that of their parents. Although both parents lacked both pectoral and pelvic fins, the larvae developed pectoral fins, although pelvic fins were absent (Fig. 2).

**MORPHOLOGY**

The general morphology of the pelvic fins and associated girdle in clariids closely resembles the plesiomorphic condition in catfishes, with the central plate of the basipterygium bearing two rostral processes (Shelden, 1937). Radial elements are absent. This configuration can be found in both the fusiform *Clarias* and the anguilliform *Gymnallabes*. In *Channallabes* the anterior processes appear to be absent with the pelvic fin rays being supported by a simple basipterygial element (Fig. 3a). In the *C. apus* specimens bearing both pelvic fins, both fins are supported by such basipterygial elements. When both pelvic fins are absent the basipterygial elements are also lacking (Fig. 3c). The strict relation between fin development and girdle development is demonstrated in a specimen which lacks only the right pelvic fin: only the right basipterygial element is absent. The left one has a comparable morphology to that of normal girdle (Fig. 3b).

The pectoral girdle in clariids is well developed, as it is for most catfishes (Tilak, 1963). It consists of a large cleithral bone, which is attached to a large coracoid bone. Both bones form ventral interdigitations with their counterparts, thus fortifying the pectoral girdle. Laterally the cleithrum bears a notch into which fits the pectoral spine. This spine is generally well developed in clariids, but may be small to rudimentary in anguilliform species. Such a rudimentary spine can be observed in *Channallabes apus* specimens that have pectoral fins (Fig. 4a-b). In those specimens lacking a pectoral fin, no traces of a protruding pectoral spine can be observed (Fig. 4c-d). The pectoral girdle, however, is still well developed with strong midline suturing.

**DISCUSSION**

**VARIABILITY IN LIMB REDUCTION AND ANGUILLIFORMITY**

The occurrence of variability in paired fin loss appears to be related to the degree of anguilliformity. In the DFA of all species root 1 represents the degree of anguilliformity: lowest root-values correspond to the fusiform body shape of *Clarias gariepinus*, whereas highest root-values correspond to the extremely elongated body of *Dolichallabes microphthalmus* (Fig. 1a). For all groups lacking pelvic and/or pectoral fins the centroids have positive root 1-values (only Ga has a negative value). Not only is the variability in presence/absence of paired fins observed only in anguilliform species, this intraspecific variability is

also related to the degree of anguilliformity: within all three species showing this variance (i.e. Gymnallabes alvarezi, Channallabes apus and D. microphthalmus), the more paired fins that are absent, the higher the root 1-values for the centroids of the subgroups.

From this DFA it also becomes clear that in the (micro- and macro-) evolutionary process of body elongation, it is always the pelvic fins that are the first to disappear. In the three species studied here which show the intraspecific variation in limb development, all have specimens lacking pelvic fins. All paired fins are present in the less anguilliform specimens of Channallabes apus (based on the position of the centroid in the DFA). On the other hand, in the most anguilliform specimens all paired fins are absent, whereas in the intermediate group only the pelvic fins are lacking; a situation that supports our hypothesis.

**FIN DEVELOPMENT AND FIN LOSS**

In many teleosts lacking pelvic fins, the endoskeletal pelvic girdle remains present (Nelson, 1994). Exceptionally, a large variation in the degree of pelvic fin and girdle reduction has been observed independently in many populations of several gasterosteid teleosts, especially from lakes in recently deglaciated regions (Nelson & Atton, 1971; Bell, 1987, 1994; Bell *et al*., 1993). In these gasterosteids almost all degrees of

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**Figure 2.** Larval Channallabes apus showing the well-developed pectoral fins (although those of the parents were absent). (A) Lateral view of the head, and (B) detail of the pectoral fin.
morphological intermediates between fully developed and absent structures were observed, although the sequence in which elements of the pelvic complex are lost is strikingly similar among populations (Bell, 1987). In Channallabes apus, however, this is not the case. Specimens with two pelvic fins have their pelvic fin rays supported by a basipterygial element. The loss of a fin also implies the loss of the entire girdle-half at that side. Such a condition is not present in the pectoral girdle, as it always retains its normal form when the pectoral fin is absent. The fact that no intermediate stages were observed and that the pelvic fins in mature C. apus are very small (compared to other clariids), indicates that a minimal threshold of relative size might exist. This has been observed in tetrapods (Lande, 1978), and appears to be the case for C. apus as well, as the pelvic length did not go below 13% of the skull length (nor did it for the other clariid species studied). Such a threshold was not observed in the pectoral fin (its size ranged between 1% and 50% of the skull length).

The difference in the degree of development in the pelvic and pectoral fins and girdles may be the result of a different timing of a triggering mechanism, which inhibits fin formation in relation to functional demands. In teleosts it has been demonstrated that the chondrogenic condensation of the pelvic girdle immediately results in an adult pattern, whereas the pectoral girdle experiences a kind of larval metamorphosis (Grandel & Schulte-Merker, 1998). In relation to functional demands and natural selection the complete loss of the pelvic girdle, in contrast to the conservation of the morphology of the pectoral girdle, is to be expected. Although some secondary functions of the pelvic fins such as in the formation of an egg pouch are known in some catfishes, its primary function is restricted to supporting the pelvic fin (Kohda et al., 1995). The pectoral girdle, however, is of more importance in other crucial biological roles. The pectoral girdle participates in the mechanics of buccal expansions associated with respiration and feeding, as well as protecting the heart (Lauder & Liem, 1989; Liem, 1991). This multi-functional difference may be reflected in the fact that the first paired fin to disappear is always the pelvic. In gasterosteids, the reduction of pelvic elements (especially the spine) could be related to the absence of predatory fishes, but in a complex way involving other factors like calcium levels as well (Bell et al., 1993). In clariids, predation will be of little importance, since the pelvic fins have no protective function. A link with its life style may be more plausible (see below).

Figure 3. External (top row) and internal (two bottom rows) morphology of the pelvic fins and girdle in Channallabes apus (ventral view). (a) Both pelvic fins present; (b) right pelvic fin present; and (c) pelvic fins both absent. Blue arrowhead indicates the position of the anterior margin of the anal fin; white arrowhead indicates the position of the anal opening; and red arrowhead indicates the position of the pelvic girdle. Scale bar = 1 mm.
The breeding results indicated that the genetic determination of pectoral fin loss may be variable, since the larvae had well developed pectoral fins although both parents did not. To what degree the pectoral fin development as well as the minimal pelvic fin length threshold is regulated genetically requires further study. A partial genetic control of intraspecific pelvic fin variability has, however, been demonstrated in gasterosteid species (Nelson, 1977; Bell et al., 1993). By analogy with snakes and lizards limb reduction in anguilliform clariids may be attributed to body elongation (Greer, 1990), which is associated with the expansion of Hox-gene expression domains along the body axis (Cohn & Tickle, 1999). If so, a significant dif-

Figure 4. Morphology of the pectoral fin in Channallabes apus. (a, b) Cleared and stained specimen, showing a small pectoral fin with spine and well-developed girdle. Black arrow indicates radials, white arrow indicates pectoral spine. (c, d) External morphology of a specimen lacking pectoral fins. Scale bar = 1 mm.
ADAPTATIONS TO A SPECIALIZED LIFE STYLE

What could be the driving force towards fin reduction in clariids? The answer presumably can be found in relation to their life style. A correlation between body elongation (by means of an increasing number of vertebrae (Hoffstetter & Gasc, 1969)) and limblessness has been demonstrated for several vertebrate lineages (Gans, 1975; Lande, 1978; Withers, 1981). It has even been suggested that in lizards body elongation preceded limb reduction during evolution, which appears to be the case in Clariidae as well (Pellegrin, 1927; Gans, 1975). In general, limblessness and body elongation have become associated with a burrowing or fossorial behaviour (especially head-first burrowing) where additional structural adaptations may involve the complete body musculature (Lee, 1998; O’Reilly et al., 1997). In anguilliform clariids the axial skeleton has an analogous structural advantage to that of tetrapod Caecilia, i.e. the ribs do not enclose the viscera latero-ventrally. In Clariidae body elongation involves the addition of caudal vertebrae, which do not support ribs that would stress the viscera during undulation (Cabuy et al., 1999). This is clearly in favour of extreme anguilliform or undulatory locomotion, which facilitates both aquatic and terrestrial locomotion (Gillis, 1996). Its beneficial result on energy management has also been suggested (Gans, 1975, 1986). The efficiency of terrestrial locomotion in Channallabes apus was observed in the field by one of the authors (D.A). Once on the soil, specimens progressed very quickly through vegetation by means of lateral undulations. However, it also appears that the driving force towards body elongation and limblessness in this species is related to burrowing adaptations as well. This species is found in Northern Gabon, to some degree living under similar conditions as Protopterus, the African lungfish (both species are syntopic (Teugels et al., 1991)). Channallabes apus appears to live in the moist soil of the rain forest of Central Africa where they could be caught by placing bait in a small, hand-made furrow (specimens were caught both during dry and rainy seasons). Within five to 20 minutes after placing the bait (earth worms) on a fish line, specimens were caught. This would indicate that C. apus is able to detect prey when it is subterranean and swims/crawls through the mud to catch it. During the dry season, when the swampy regions are largely dried up, water is restricted to below the surface layer of the soil (where the water presumably is in contact with small creeks in the neighbourhood). During the rainy season the area is covered with tiny, extremely shallow creeks and the soil is much more saturated. This ecological niche differs from that utilized by Protopterus, which is more restricted to dryer regions (closer to savannas).

Other adaptations to a fossorial habit include reduction of the eye, and may involve special modifications in the cranial morphology (for example skull miniaturization) (Cabuy et al., 1999; Devaere et al., 2001). Comparable body elongation as well as cranial adaptations, combined with a similar burrowing behaviour, have been suggested for some Asian clariids (Encheloclarias spp.) (Ng & Lim, 1993).

Variation in limb development in vertebrates is generally considered to represent major structural changes at the macroevolutionary level where such changes are believed to have a different basis than those at the microevolutionary level. In some species of the African catfish family Clariidae, however, variation in fin development appears to exist at the intraspecific level, thus representing a unique example of microevolutionary variability. In these species fin and/or girdle reduction can be linked to body elongation, which is also the case in most other elongated vertebrates. The process of paired fin loss in clariids always involves the initial loss of the pelvic fins, which may be followed by the loss of the pectoral fins in Channallabes apus. The loss of the pelvic fins is accompanied by the loss of the pelvic girdle. This is not the case for the pectoral girdle. This may well be a reflection of the differences in multi-functional importance of the girdles. As is the case for most limbless and elongated vertebrates, the loss of fins in clariids may possibly be related to the highly specialized fossorial life style.

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