Larval Development of the Rare Australian Aploactinid Fish 
*Matsubarichthys inusitatus* (Pisces: Scorpaeniformes)

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Jeffrey M. Leis, Amanda C. Hay and Anthony G. Miskiewicz (2004) Larval development of the rare Australian Aploactinid fish *Matsubarichthys inusitatus* (Pisces: Scorpaeniformes). Zoological Studies 43(3): 580-588. Larval development in the aploactinid velvetfish, *Matsubarichthys inusitatus*, previously known only from the holotype, is described using 15 larvae from plankton samples. Larvae were identified based on their unique meristics. Development is rapid, with all fins formed and the skeleton largely ossified by 4 mm standard length. The larvae are robust, and are characterized by large, early-forming pigmented pectoral fins, 20 or 21 myomeres, and blunt head spines that form following notochord flexion. Although this description results in the larval development of *M. inusitatus* being the best documented of any aploactinid, the species is known from only 1 post-settlement individual, reported herein; the adult habitat and morphology remain unknown.


**Key words:** Ontogeny, Aploactinidae, Larvae, Indo-Pacific.

Velvetfishes, family Aploactinidae, are a poorly known scorpaeniform group consisting of about 35 species in about 17 genera found only in the Indo-Pacific west of the Pacific Plate (Poss and Eschmeyer 1978, Poss 2000). Most velvetfish species are known from relatively few specimens. Larval development is, not surprisingly, very poorly known, with only a few publications describing partial series of a very few species (Kojima 1988, Leis and Carson-Ewart 2000). Perhaps the most poorly known species of the family is *Matsubarichthys inusitatus* Poss and Johnson 1991, which was described from a single, 8 mm specimen, apparently metamorphic, taken in a neuston tow at One Tree I. Lagoon on the southern Great Barrier Reef, Queensland, Australia.

Thus, we were intrigued by the discovery of a 2nd, apparently fully metamorphosed, settled, 6.4 mm specimen of *M. inusitatus* in northern New South Wales by an Australian Museum team led by Mark McGrouther. This prompted the identification of 15 larvae taken in plankton tows between Brisbane, Queensland (27°S) and Sydney, New South Wales (34°S) off the eastern coast of Australia. These larvae were readily identified as *M. inusitatus* by the species’ unique meristic characters. These occurrences imply that *M. inusitatus* may be subtropical in distribution, rather than tropical as are most species of the group.

Herein, we describe the development of this species, based on the most-complete developmental series known of any aploactinid, including settled individual. As a result, we find ourselves in the somewhat unusual position of knowing the larval development of a species for which the adult is unknown. We can only speculate as to the adult habitat. The holotype was captured at the surface in the lagoon of a coral reef, and the settled specimen was found in a rotenone collection among oyster-covered rocks and mangroves near the mouth of a large estuary about 700 km south of the type locality. The larvae were taken over the

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continental shelf, with a full range of sizes from a 1.8 mm preflexion individual to a 4 mm specimen with fully developed fins in a single plankton tow. Development of *M. inusitatus* is extremely rapid, based on the size of the larvae at various morphological milestones.

**MATERIALS AND METHODS**

The larvae were captured in plankton tows and fixed in 5%~10% formalin, and later transferred to 70% ethanol. Measurements and counts were taken with the aid of a dissection microscope at 8~50x. Definitions follow Leis and Carson-Ewart (2000). The illustrations were prepared with the aid of a camera lucida. After it was measured, one 4 mm larva was cleared and stained for visualization of bone and cartilage following Potthoff (1984). Larvae were assembled into a size series using the very low myomere and fin-ray counts, the long notochord tip, and the general morphology of aploactinids, particularly the early-forming pectoral-fins, the form of the dorsal fin, the thick skin, and the head spination (Leis and Carson-Ewart 2000). Larvae and the settled individual were identified as *M. inusitatus* by the highly restricted gill opening and the distinctive counts of myomeres 20-21; C 5+5; D II+ IV, 6; A II, 3-5; P1 15-16; and P2 I,1. The holotype, the only previously known specimen, was reported to have 21 vertebrae, C 5+5; D II+ IV, 6; A II, 4; P1, 15; and P2 I,1. We are aware of no other species in Australian waters, and certainly no other aploactinid, with these meristic characters.

All examined specimens are deposited in the Australian Museum, Sydney (and except the last one, all lots are larvae captured with plankton nets, and all n = 1 unless noted otherwise): I.26081-004, I.26112-034, I.26205-001 (n = 4), I.26213-005 (n = 4), I.29395-001 (holotype), I.36591-004, I.36601-006, I.36610-003, I.40938-004 (cleared and stained), and I.41289-011 (settled). (Table 1, Figs. 1-3), based on 15 larvae: 1.8~4.0 + 8.4 mm plus a settled fish of 6.4 mm.

**Morphology**: The body is robust with a massive gut and large, broad head. Body depth is moderate (29%~41% BL, with the exception of 1 larva with a very full gut). Tail is moderately compressed, and until about 4 mm, is abruptly much

### Table 1. Morphometric (in mm) and meristic characters of *Matsubarichthys inusitatus* larvae. BL, body length; pAL, pre anus length; pDL, pre dorsal-fin length; BD, body depth; HL, head length; HW, head width; P1L, pectoral-fin length; Dsp2L, dorsal-fin spine 2 length; SnL, snout length; ED, eye diameter; OD, orbit diameter; D, A, P1, P2, and C, dorsal, anal, pectoral, pelvic, and caudal fins, respectively; d, damaged. For fin elements: parentheses ( ) enclose bases or anlagen, and brackets [ ] enclose incipient rays

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Fig. 1. Larval development of *Matsubarichthys inusitatus* from the western Tasman Sea off northern New South Wales and southern Queensland. In all specimens, the thick skin partially obscures the myomeres, and the illustrated myomeres are approximate. Crosshatching indicates the gill exhalent opening. Fin segmentation is shown only in the caudal-fin rays. Note that in A, B, and C, the more-or-less uniformly scattered melanophores of the pectoral fin have been omitted so as not to obscure the structure behind the fin. Note that in C, D, and E, sensory pores are shown on the head; the dorsal-most broken line in the branchiostegal area represents the interopercle and subopercle aligned tip-to-tip, whereas the other broken lines represent the branchiostegals, the ventral-most of which is not visible in lateral view; and the outermost, coarser broken line represents the edge of the branchiostegal membrane fused to the body.
(A) Preflexion larva, 1.8 mm (1.26205-001). Pectoral-fin pigment omitted. (B) Preflexion larva, 2.6 mm (1.26205-001). Pectoral-fin pigment omitted. This is the largest preflexion larva available; neither of the flexion larvae (2.6 and 2.8 mm) were suitable for illustration. (C) Postflexion larva, 3.1 mm (1.36610-003). Pectoral-fin pigment omitted. This is the smallest postflexion larva. (D) Postflexion larva, 3.8 mm (1.26205-001). Small teeth on the premaxilla are not visible in this lateral view. (E) Postflexion larva, 4.0 mm (1.26213-005). Teeth on the premaxilla are not visible in this lateral view. Broken lines anteriorly on the trunk (dorsal to the pectoral-fin base) indicate thickenings that are apparently incipient lateral-line scales. In the caudal fin, the dorsal-most and ventral-most rays are each procurent. (F) Dorsal outline of specimen E.
less deep than are the head and trunk. Skin is thick and granular, and particularly in smaller larvae, is inflated, especially over the head, and with a large subdermal space. Thick skin obscures details of the subdermal structures, and makes accurate myomere counts difficult. There are 20 or 21 myomeres, about 10–12 of which are postanal. The holotype was reported to have $9 + 12 = 21$ vertebrae (based on radiographs), but our cleared and stained larva has $9 + 11 = 20$. The prominent gut is coiled with a strongly descending posterior portion in the smallest larva. This morphology is retained until about 4 mm, when the body begins to become depressed. The large head is broad and rounded with a short snout (< eye width). The head becomes relatively larger with development, increasing from about 32% BL in preflexion larvae to 46% BL in the largest pelagic specimen. It becomes increasingly depressed from about 4 mm. The mouth is large and oblique. The maxilla reaches to about mid-eye. Canine teeth form following flexion, initially in the lower jaw. Eyes are initially large (31%–38% HL), but become progressively relatively smaller, especially following flexion (20%–27% HL). The eye is smaller than the orbit by 20%–30%. In conjunction with the depression of the head, the eyes move toward the dorsal profile of the head. Nostrils form following flexion: the inhalent nostrils form tubes by about 3.3 mm, and these project over the premaxilla by 4 mm. Gill membranes, even in the smallest (1.8 mm) larva are attached across the isthmus, and the exhalent opening is restricted to the upper portion of the base of the pectoral fin. The gill exhalent opening becomes progressively smaller and moves dorsally, so that by completion of flexion, it is restricted to a pore located dorsal to the opercle. The branchiostegals are conspicuous by about 2 mm, and their distal ends are progressively displaced dorsally. The interopercle and subopercle are strongly elongate (similar in shape to a branchiostegal), and aligned tip to tip, approximately parallel to the dorsal-most branchiostegal, extending dorsally. The subopercle passes under the opercle; the dorsal tip of the subopercle supports the outer periphery of the gill opening and is covered by a blunt, fleshy projection along the posterior edge of the gill opening.

Head spination is well-developed, but difficult to characterize because much of it is obscured by the thick skin. Most of the spines are blunt rather than pungent. Development of the head spination is intimately connected with the early development of sensory pores and tubes on the head. The 1st head ornamentation to form is the supraocular ridge, late in the preflexion stage. This becomes progressively more prominent, and irregular in profile from about 4 mm, although no spines form. Sensory pores and underlying tubes are present on the medial edge of the supraocular ridge in postflexion larvae. The 1st opercular spine begins to form just prior to flexion; from the flexion stage, 2 opercular spines are present, which are joined at the base and arrayed at nearly a right angle to one another. They are pointed, but the free tips are neither long nor robust. The preopercular ridge is first visible when flexion is complete at about 3 mm, and at this point in development, 3 pores are present along the lower limb, but no spines are visible externally. On both inner and outer borders of the cleared and stained specimen (4.0 mm), there are 3 subdermal spines on the lower limb and 1 on

Fig. 2. Metamorphic larva of *Matsubarichthys inusitatus*, 8.5 mm (holotype, I.29335-001, reproduced with permission from Poss and Johnson 1991) from a neuston tow at One Tree Island Lagoon, Great Barrier Reef.
the upper limb, but 2 of the lower-limb spines are joined (inner to outer) to form the sensory tubes. Pores are interspersed with spines along the preopercular border. In the most-advanced 4 mm larva (Fig. 1E), the 2 spines on either side of the preopercular angle are enlarged, pointed, and clearly visible externally, whereas the other spines are visible only as blunt protuberances. There are no spines on the splint-like interopercle or subopercle. The infraorbitals are present as an irregular shelf over the maxilla in the smallest postflexion larva. This irregularity becomes more pronounced, and in the most-advanced 4 mm larva, 3 blunt spines are present on the lachrymal, alternating with pores. Posteriorly, 2 pores form at about 4 mm, and a very blunt elevation marks the anterior end of the extension of the suborbital stay to the preopercle. On the dentary, a pair of pores forms by the end of flexion, and a low ridge associated with them is present by 3.8 mm. A low, blunt post-temporal spine forms shortly after flexion, and a pore just anterior to its base is present by 3.8 mm. In the most-advanced 4 mm larva, a pore just anterior to a low pterotic ridge is also present. In the cleared and stained larva, a sensory tube and associated low ridge are present on the tabular, and a buried supracleithral spine is present as are 2 buried cleithral spines. No spination on the parietal was evident. All head spines of the settled individual are covered by skin. The most prominent are the preopercular spines, the blunt lachrymal spination and ridge, and the ridges of the suborbital stay and of the pterotic-post temporal.

The smallest larva has large, well-developed pectoral fins, with most rays already formed. A full complement of 15 or 16 pectoral-fin rays is present in the largest postflexion larva. The uniquely arranged dorsal fin is first present as an anlage in postflexion larvae as small as 2.2 mm. All elements but the 1st spine of the fin are present in the smallest postflexion larva (3.1 mm), and the full complement of elements is present by 3.3 mm. All fin elements form in place, without migration, so the gap between spines II and III is present from when the fin first forms. Spines I and II of the dorsal fin are on the head, although the origin of the fin remains posterior to the eye. The anal fin forms simultaneously with the dorsal, but all our postflexion specimens have a full complement of elements. The caudal-fin rays begin to form from about 2.2 mm. Notochord flexion begins at about 2.6 mm, and is complete by 3.1 mm. The notochord tip is very long, and is retained following flexion until about 4 mm. In the cleared and stained larva, the base of the notochord tip is ‘S’-shaped as if folding back on itself just dorsal to the urostyle. This tip disappears very quickly (judged on the basis of size): it is present and still large in the 4 mm cleared and stained larva, but has disappeared in the most-advanced 4 mm larva. All 5+5=10 principal caudal rays are present in postflexion larvae, and a single dorsal and ventral procurrent ray begins to form at about 3.8 mm, formation being complete by 4.0 mm. The pelvic fin is first visible as a thickening ventral to the base of the pectoral fin at about 2.6 mm in the largest preflexion larva. The smallest postflexion larva has a single soft ray in the pelvic-fin bud, and the single spine is present by 3.2 mm, completing the fin.

Apparently, no scales form in this species other than the well-developed tubular scales along the lateral line. These are present in the metamorphic holotype, and thickenings that are apparently precursors to these tubes are present in the most-advanced 4 mm larva. The settled individual has an arrangement of scales very similar to that of the holotype.

Post-settlement development

The single known settled individual is, at 6.4 mm, 2 mm smaller than the largest pelagic individual. We do not know if this reflects individual variation or shrinkage associated with metamorphosis. The depression of the head and increase in its relative length continue in this specimen, so it is likely

Fig. 3. Settled Matsubarichthys inusitatus, 6.4 mm (I.41289-011) from a rotenone collection near the mouth of the Clarence River, northern New South Wales. Photo by K. Parkinson.
the adult has a depressed, very large head, approaching 50% of SL. The specimen is tadpole-like in overall appearance (Fig. 3). The mouth remains large, as does the pectoral fin.

**Pigment**: Pigment is apparently variable among individuals, and changes in pigment take place over small size intervals. The most-striking feature of the larvae until the early postflexion stage is the heavy pigmentation of the large pectoral fin (not shown in Fig. 1A-C). Over this developmental interval, the fin is more-or-less uniformly covered with small melanophores. After about 3.5 mm, this pigment becomes more restricted, and eventually forms vertical bands from about 3.9 mm. These bands are absent from the largest pelagic specimen (the holotype). The most-consistent pigment on the body is a concentration of melanophores on the ventral surface, especially on the gut. A series of very fine melanophores on the ventral surface of the tail is present in small larvae, but may be absent from the late preflexion stage. A few scattered melanophores are present on the ventral finfold, and these initially increase in number once the fin rays form, but then disappear. Scattered melanophores are present dorsally and laterally on the trunk, and these increase in number with development. Similar melanophores form on the tail, but these are more confined to the ventrolateral surfaces and form later than those on the trunk. There is very little pigment on the head until 4 mm, when some individuals may be heavily pigmented on the head and trunk. Interestingly, the largest pelagic specimen has very little pigment, and unlike the other pelagic specimens, the pigment is not present as small, scattered melanophores, but as a few very dense, larger melanophores mostly on the dorsal surfaces of the head, trunk, and tail. Therefore, the holotype has less pigment, and the pigment is distributed somewhat differently than that of either the next smallest available larvae or the settled individual.

The settled specimen is darkly and more-or-less uniformly pigmented on the head and trunk and somewhat less so on the tail, with a darker band at the base of the caudal-fin rays. This overall pattern corresponds with the heavier pigment that develops in most pelagic larvae. The dorsal and anal fins match the body color. The caudal fin is transparent. The pectoral fin is lightly pigmented except at the base, with a partial band at about 2/3 the length of the upper rays. Ventrally, the entire body color approximately matches that laterally on the tail.

**Osteology**: The 4 mm cleared and stained specimen is remarkably well ossified for such a small larva. All the vertebrae (9+11=20), hemal and neural arches, and spines are ossified. The vertebral count differs from the description of the holotype (9+12=21), based on soft x-rays: it is unclear if the x-rays were misleading, or if there is variation among individuals in vertebral count. There are 7 epineural ribs, all ossified. The fin pterygiophores are all present and cartilaginous, but not ossified, except the pterygiophore of the 1st spine, that forms, in dorsal view, a broad, arrow-shaped element pointing posteriorly with the shaft extending between the eyes. The "Ahlstrom formula" for interdigitation of fin pterygiophores and neural spines is 1+1/1/1/1/1/1/1. The neural spine of the 1st centrum is closely applied to the back of the skull, and the tips of neural spines 5 and 6 nearly meet across the gap between them (which lacks a pterygiophore). All fin elements are present and ossified, except some rays distally. Nearly all of the bones of the skull are fully ossified (including the 6 branchiostegals), as are the bones of the pectoral girdle. A row of strong teeth in the lower jaw are fully ossified, as are a few forming teeth in a 2nd row. The somewhat-smaller teeth of the premaxilla are also ossified. Some other details of ossification of this specimen are included in the description of morphological development, above. The fin-ray counts are: D II+IV,6; A II,4; P1 16, P 2 I,1; C 1+5+5+1. These correspond to the holotype, but we found some variation in these counts among the other specimens: D II+IV or V, 6; A II,3~5; and P1 15 or 16.

**DISCUSSION**

Development of *Matsubarichthys inusitatus* is typical of the few other aploactinids for which larvae are known, with large, early forming pectoral fins, an initially rounded head that develops significantly, if generally blunt, spination at about the time of flexion, and thick, granular (or perhaps vesicular) skin. In contrast to other aploactinid species, developmental milestones in this species are reached at very small sizes: notochord flexion is completed by 3 mm, and a full complement of fin rays is present at 3.3 mm. Previously, the only aploactinid for which preflexion stages were described was *Erisphex pottii* (Kojima 1988), and in that species, preflexion specimens as large as 4.6 mm are known. Settlement in *M. inusitatus* apparently takes place at the very small size of...
6–8 mm. The fact that the settled larva is 2 mm smaller than the neustonic holotype implies that there is individual variation in settlement size or shrinkage during metamorphosis. Alternatively, the holotype may represent a benthic juvenile stage that returns dielhy to surface waters to forage in a gradual transition between pelagic and benthic habitats (H.G. Moser, pers. commun.).

Several speculations arise from the mode of development of *M. inusitatus*. The small size at which all fins formed and the skeleton ossified might indicate that swimming abilities form rapidly in larvae of this species. The small size of the larvae at settlement might imply that the pelagic phase is short. A short pelagic period combined with early development of swimming abilities could lead to limited dispersal during the pelagic phase of this aploactinid. If so, such limited dispersal may help explain the high species diversity and relatively limited species ranges found in the Aploactinidae.

In *M. inusitatus* larvae, a very long notochord tip is retained for a period following flexion. This is not a common feature of scorpaeniform larval development, but is commonly encountered in some other robust larvae with few myomeres such as callionymids and some lophiiform and tetraodontiform species. It is tempting to suggest that such a notochord extension is an indication that the low number of myomeres is derived from a greater number in an ancestor.

The thick skin of aploactinids interferes with examination of the underlying structures, and in some of the specimens, it is rather inflated, with a significant subdermal space. It is not clear if this is an artifact of preservation or is reflective of the condition of live larvae. This variation in inflation, combined with variation in fullness of the massive gut, results in a large range in body depths.

The present description is the most complete for any aploactinid, but given how few species are known from larvae, we do not know how typical of the family it is. Poss and Johnson (1991) were unsure of the relationships of *M. inusitatus* when they described the species, and could not unequivocally assign it to either aploactinid subfamily. We must await the description of the ontogeny of more aploactinid species, but most of the features of the development of *M. inusitatus* are similar to those of the few aploactinid larvae that have been described. Differences, particularly the precocial development of *M. inusitatus*, are difficult to interpret. Discovery of the adult of *M. inusitatus* is eagerly awaited, and may shed light on a number of ambiguities. *Matsubarichthys inusitatus* has some of the lowest meristic values found in the family, and combined with its precocious larval development, leads us to suggest it may be a dwarf species among aploactinids.

The early (during flexion) constriction of the gill opening to a small, dorsal pore is unusual. The dorsal position of the gill opening implies that settled individuals either partially bury themselves in soft sediment, or that they live in environments with much suspended sediment or detritus in the water column. This could help explain why adults remain unknown. The numbers of larvae captured indicate that, although *M. inusitatus* is not abundant, it is more common than its absence in museum collections of adults would lead one to expect.

Aploactinids are similar to the larvae of a number of scorpaeniform groups, including congiopodids, and the `morph A` scorpaenids of Leis and Rennis (2000). The principal difference between aploactinids and the other groups is the development of the head spination: in aploactinids, it forms later (at or after notochord flexion) and is generally more poorly developed, and the spines are blunt rather than pungent. The very early-forming pectoral-fin rays, the small size at most developmental landmarks, the arrangement of the spines of the dorsal fin, the long notochord tip, and the very low meristic values will help to distinguish the larvae of *M. inusitatus* from any others. Early larvae of some lophiiform fishes, particularly those with early-forming pectoral fins, might be confused with early *M. inusitatus* larvae, but in lophiiform larvae, the exhalent opening of the gill is located at the lower edge of or below the pectoral-fin base.

Larvae taken off southern Queensland/northern New South Wales were all captured in surface plankton-net taws, in spite of the fact that oblique taws were also made at the same locations, and the holotype was taken in a neuston tow, all indicating a preference by *M. inusitatus* larvae for the surface. Only the specimen from off Sydney, the southernmost occurrence, was not taken at the surface: it was captured at 15-30 m. The cleared and stained larva (also the Sydney specimen) had 3 calanoid copepods in its gut, providing limited insight into its feeding. The large, early-forming pectoral fins of *M. inusitatus* larvae are probably used in labriform swimming, but might also be useful in feeding, perhaps herding food organisms to within easy reach of the mouth.

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