Identification of *Leptocephalus acuticeps* Regan as the Larva of the Eel Genus *Avocettina*[1]

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REGAN (1916:140, pl. 7, fig. 5) based the description of a distinctive new eel larva, *Leptocephalus acuticeps,* on a single 47-mm specimen from the South Atlantic. He did not attempt to allocate this larva within the eel classification, but D'Ancona (1928:109) and Bertin (1936:7) assigned it to the Congridae. Although no additional specimens of *L. acuticeps* appear to have been reported since the brief original description, Bertin re-examined the original larva and gave important supplementary information on it, and an additional illustration.

Recent accessions of eel larvae from the eastern tropical Pacific in the Scripps Institution of Oceanography fish collection include two specimens that closely match the major known characters of *Leptocephalus acuticeps.* The present paper describes these larvae and assigns them to *L. acuticeps.* Comparative study indicates that *L. acuticeps* belongs to the *Avocettina* section of the family Nemichthyidae, and suggests that it is best interpreted as the general kind of larva that characterizes all of the avocettinas as a group.

DESCRIPTION OF NEW SPECIMENS

Collection data. The two larvae of *Leptocephalus acuticeps* from localities in the eastern tropical Pacific have the following collection data:

(1) SIO62–639–26A; from "Scot" expedition, Scripps Tuna Oceanography Program, Station No. 36; 6° 30′ N, 95° 54.8′ W; May 9, 1958; total length 124 mm. (2) SIO62–387–26A; same expedition, Station No. 59; 5° 34′ N, 81° 28.5′ W; May 18, 1958; total length 107 mm.

Morphology. These are moderately slender larvae, with a long, straight gut, and a short tail (Fig. 1). The smaller specimen has a total length of 107 mm; snout to anus, 97 mm; tail, 10 mm. The larger has a total length of 124 mm; snout to anus, 111 mm; tail, 13 mm. The maximum height is about 8% of the total length on the 107-mm larva, about 7% on the 124-mm larva. The head proportions are quite generalized, neither markedly elongated nor unusually shortened, compared with other leptocephali in general (Fig. 2). The rounded eyes lack the thick white supporting pad ("iridochoroid process") that sheaths the eyeball of certain other leptocephali (notably, most congrids). The snout profile is moderately concave. The jaws are moderately long and their tips are approximately even. The larval dentition, presenting no unusual features, consists of 12 or 13 lanciform teeth on each side of the upper jaw, and 11 or 12 on each side of the lower jaw. The rather small first upper tooth on each side is attached to one of the pair of sliver-like rudimentary premaxillary bones that are close together on the upper tip of the ethmoid cartilage. The other upper teeth border the maxillary and comprise 6 or 7 large ones followed by 5 or 6 distinctly smaller ones. These size classes are more sharply defined in the 107-mm larva. The teeth on the lower jaw decrease in size more evenly. The small, subtriangular nasal capsule lies directly adjacent to the upper anterior quarter of the eye margin. The rounded anterior nostril is smaller than the vertically ovoid posterior one; both are well defined, though small. The moderately large tongue rises well upward from the floor of the mouth, but neither its tip nor its sides project freely. The moderately large gill arches bear well-defined margi-

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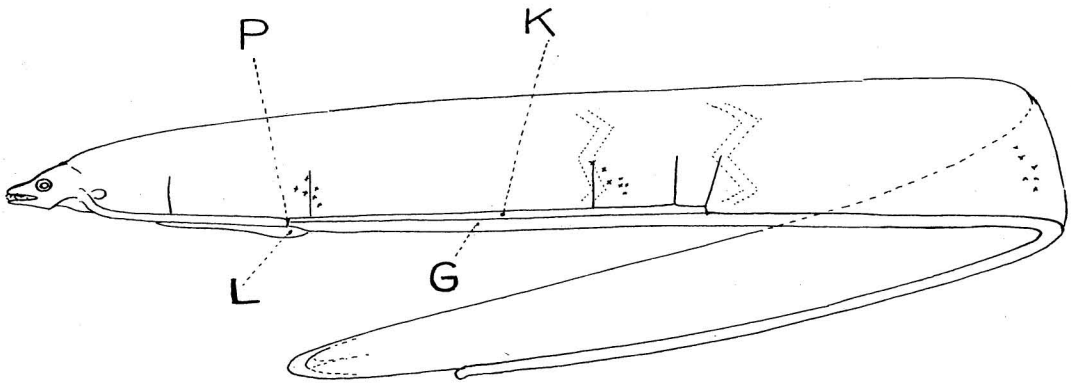

FIG. 1. *Leptocephalus acuticeps*. Outline of 107-mm larva. Shows internal three-spot pattern and associated morphological characters; rest of pigmentation omitted. Somites 50 and 63 outlined to show their general configuration; rest of somites omitted.

G, gut; *K*, kidney; *L*, liver; *P*, pylorus.

nal flaps but no definite respiratory filaments. Both larvae have well-developed pseudobranchs. The pectoral fins are moderately small. On the 107-mm larva the fin base is on the fourth somite, and the adpressed edge of the fin membrane reaches about halfway across the sixth somite. On the 124-mm larva the pectoral is one somite farther forward; its base is on the third somite and its free edge reaches the fifth. The caudal fin (Fig. 3) is well defined but the narrow hypurals are not very heavily chondrified, and their combined vertical diameter is only slightly greater than that of the notochord and spinal cord together. The three or four caudal rays quite fully occupy the available space, and hence few if any additional rays are likely to form on older larvae. The last basal elements of the dorsal and anal fins are in contact with the hypurals. The dorsal fin begins as a barely perceptible thickening at about the 149th somite on the 107-mm larva, and at about the 153rd somite on the 124-mm larva. (Position of a structure or color-pattern element in relation to a numbered somite is determined by extending a vertical line from the feature in question and counting the somite that forms its midlateral angle where this vertical line meets the body axis.) The somites total 182–187, of which 158–161 (about 86% of the total) are preanal and 24–26 are postanal. A major vertical artery extends down from the aorta to the viscera at the 16th or 17th somite, and another one (or two very close together) at the 26th or 27th somite. The narrow liver is moderately long, very thinly tapered anteriorly and slightly thicker toward its more bluntly pointed posterior end. It begins at the 13th somite in the 107-mm larva and at the 8th somite in the 124-mm larva; in each it ends at about the 27th somite. Since the pylorus is at the 25th somite in each larva, the liver subtends about 12 and 17 prepyloric somites, respectively. The gut is a simple straight tube, with no undulations or regional enlargements. The slightly thickened kidney parallels the top of the gut for about 36 or 37 somites behind the pylorus, to somite 61 or 62 (Fig. 4). There is a conspicuous vertical artery at somites 50–51 (damaged on the 124-mm larva). The major renal artery leaves the body axis at somite 58 or 60, and the renal portal vein at somite 63 or 64. The artery is vertical, but the vein slants forward. Behind its junction with the renal portal vein, the kidney narrows abruptly to form the thin, scarcely visible duct that continues along the top of the gut for an additional 97–99 somites and terminates directly behind the anus, between somites 158 and 161.

Pigmentation. The pigmentation is unusual, compared with that of other leptocephali in general, both in the complexity of its pattern

and in the small size and dense spacing of its melanophores (see Figs. 2–4). The uppermost element in the pattern is a middorsal band of melanophores in the skin. It begins at the third somite on the 107-mm larva but is not visible until the 15th somite on the 124-mm larva. In each the row extends to the tail tip. For most of its length, this stripe has an irregularly varying width of from one to several cells. When it meets the anterior end of the dorsal fin (about somites 149–153), the row narrows to a single file, which extends along the tops of the basal elements within the fin. Thus, the pigment cells come to lie progressively deeper inward from the surface as the thin edge of new fin tissue grows upward above the basals. An internal supraspinal row of small, densely spaced melanophores runs along the top of the spinal cord from the hindbrain to the tail tip, where the row ends just ahead of the hypurals. The cells are evenly spaced and of uniform size. Another internal row of melanophores, between the kidney and the top of the gut, extends from about the 16th somite to the anus. Anteriorly, it comprises a single line of cells, but at about the 50th somite the row begins to double, and thence continues more or less regularly doubled for the rest of its course. An external midventral row of tiny melanophores extends from the anterior end of the pericardium to the anus. This row shows strong zonation in cell abundance (compare Figs. 2 and 4). The melanophores form a wide, densely crowded patch below the pericardium, and a single densely spaced row from there to about the 27th somite (below the posterior end of the liver). Beyond the liver, the row thins out rapidly and its cells are widely spaced and inconspicuous until they again crowd together a short distance anterior to the anus. Although this ventral row underlies the gut very closely, it is in the skin rather than on internal surfaces. There are no melanophores along the midlateral surfaces of the somites, where many other kinds of eel larvae bear a conspicuous longitudinal row of black cells. Three rather inconspicuous patches of internal pigment (Fig. 1) lie between the midlateral axis and the lower edges of the somites, in approximately the anterior half (about 50 to 56%) of the total length. They are situated in the vertical connec-

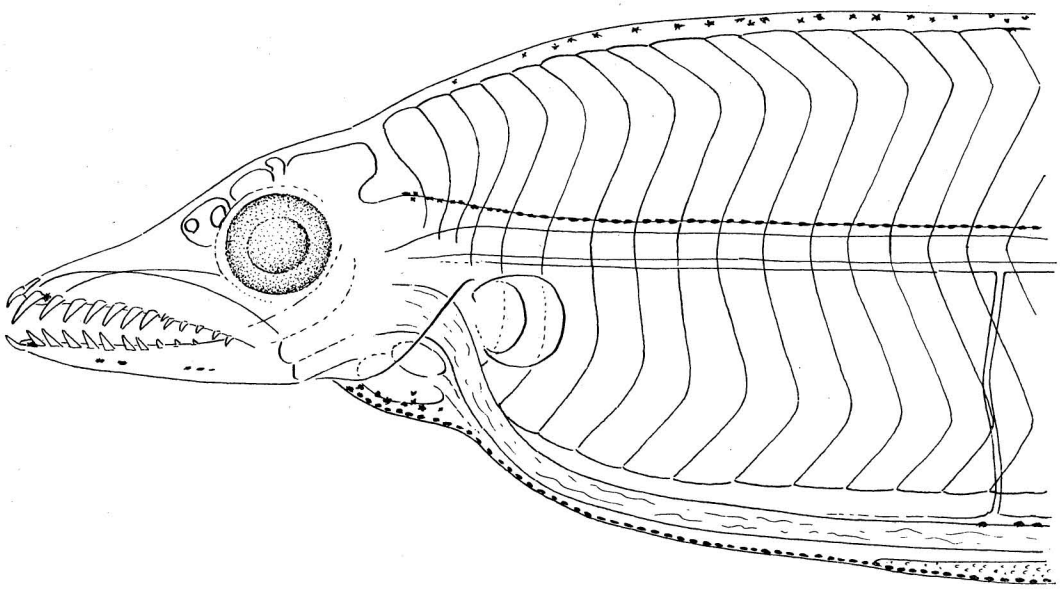

FIG. 2. *Leptocephalus acuticeps*. Morphology and pigmentation of head and anterior end of body of the 107-mm larva, through somite 16. Somite 4 includes base of pectoral fin; somite 13 marks origin of liver; somite 16 includes origin of a major vertical artery.

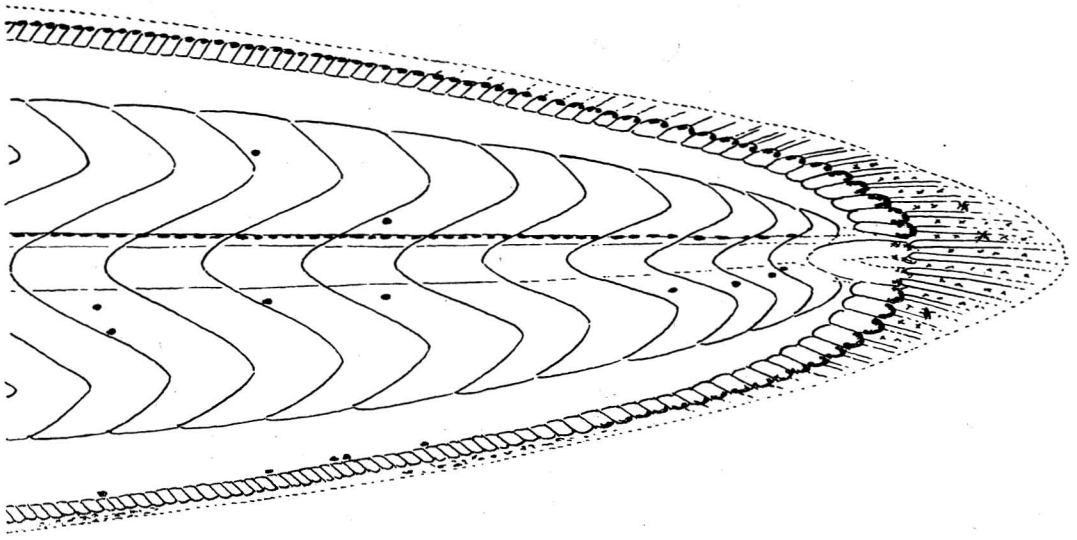

FIG. 3. *Leptocephalus acuticeps*. Tail tip and last 10 somites of the 124-mm larva.

tive tissue between the right and left muscle layers, and each patch or spot consists of an oblique or more or less vertical cluster of small, contracted, and rather widely spaced melanophores. On each specimen the first spot is at somites 25–26, the second at somites 50–52, and the third at somites 85–86. Each of the first two spots is close to a vertical blood vessel (Fig. 4). In addition to these three aggregations of melanophores, the median connective-tissue zone bears occasional very small, inconspicuous, separate melanophores scattered irregularly at wide intervals. Most of these cells are below the level of the notochord, but a very few are above it. The predominant pattern on the short tail (Fig. 3) consists of continuations of the supraspinal and middorsal rows. A midventral row, symmetrical with the latter, is developing along the outer edges of the posterior anal-fin basals. There are occasional melanophores along the inner edges of the anal basals, and scattered melanophores in the median connective-tissue zone (both above and below the midlateral axis), especially in the posterior half of the tail. The caudal fin is liberally dotted with very minute melanophores. The head is sparingly pigmented, except for the solidly dark eyes. There are a few tiny melanophores in the tip of each jaw, and a few along the lower-inner edge of the lower jaw. The heavy midventral band of pigment below the pericardium begins sufficiently far forward (Fig. 2) that it might also be regarded as a part of the head pattern.

COMPARISONS

A. *Leptocephalus acuticeps*

The specimen on which Regan based the larval name *Leptocephalus acuticeps* was collected in the South Atlantic (21° S, 37° 50′ W) by the "Terra Nova" expedition. The data and illustrations in Regan (1916) and Bertin (1936), when combined, characterize *L. acuticeps* unusually completely, and show it to be very distinctive and more confidently identifiable than are most other described leptocephali. The given data on somite counts are even sufficiently complete to reveal several useful proportional characters that both authors had overlooked. In the following discussion of this specimen, the characters that pertain to somite numbers and positions are calculated from Regan's original counts. Bertin omitted the first two somites, which appeared to be incomplete ventrally. My own counts on specimens examined include all discernible anterior somites regardless of

whether they seem to extend completely to the ventral margin of the musculature.

The total length of the original specimen of *L. acuticeps* was 47 mm. The maximum height was about 8.5% of the total length. The dorsal profile of the head was markedly concave; the jaws bore about seven upper and six lower teeth on each side; Regan's illustration shows sufficient space behind these for the addition of more, perhaps smaller, teeth during larval growth. The tip of the lower jaw protruded slightly. The somites totalled 207, of which 174 (84%) were preanal and 33 were postanal. The gut was a long, straight, simple tube, with no apparent specializations. An enlargement of the liver occurred at about the 30th somite (hence, the 30th somite can be considered the approximate location of the pylorus). There were major vertical blood vessels anteriorly at somites 16 and 27, and farther back at somites 61, 71, and 76. The kidney terminated at about the 76th somite, and there were therefore about 46 somites between the pylorus and the posterior end of the kidney, and about 100 between the latter position and the anus. Although Regan did not describe the tail, his illustration shows that the fleshy part was obtusely rounded, with a distinctly rayed tip. Bertin mentioned that the hypurals were scarcely visible and that the caudal was pointed. The vague definition of these characters certainly stems at least partly from the relatively young stage of the specimen. The known pigmentation of this original specimen included an internal row of minute, densely spaced melanophores along the top of the spinal cord, a similar row along the top of the gut beginning at about the 30th somite (probably at or near the pylorus) and extending to the anus, and another row (probably external) along the ventral surface from the heart region to at least the pyloric region. The sides of the tail bore a few small scattered melanophores, both above and below the level of the notochord. There were three internal spots visible through the lower halves of the somites, each spot composed of a loosely clustered, roughly linear group of small melanophores. The first spot was at somites 27–30, the second at somites 61–62, and the third at somites 104–107. The first and second spots were each near a major vertical blood vessel.

The two eastern Pacific larvae described in the present paper match the determinable characters of Regan's Atlantic larva of *L. acuticeps* so closely that there is no doubt of their close relationship to it, and therefore I have assigned them to *acuticeps*. So far as known, they differ from the Atlantic specimen only in details of the sort that are readily subject to variation among very closely related larvae or between growth stages of a single form. The Scripps specimens share the general format and visceral characters of *acuticeps,* but they are much larger and have about twice as many teeth, the head profile is straighter, and the tips of the jaws are even. The Scripps larvae have somewhat lower somite counts and the preanal somites constitute a slightly higher percentage of the total number. In addition, the pylorus is about five somites farther forward in the Scripps larvae than its estimated position in the original *acuticeps,* the posterior end of the kidney and the main renal blood vessels are about 12–14 somites farther forward, and there are about 10 or 11 fewer

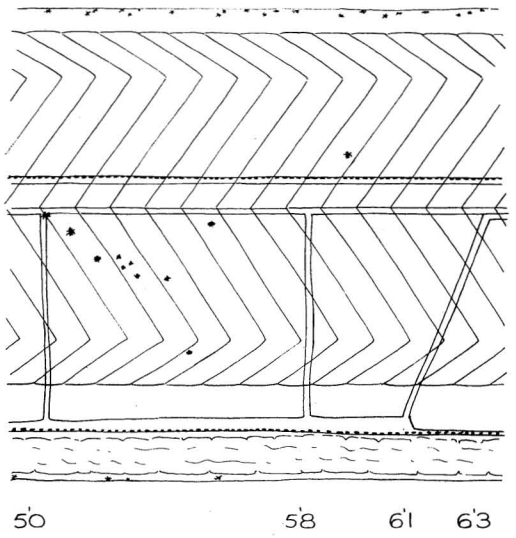

FIG. 4. *Leptocephalus acuticeps.* Section between somites 50 and 63 of the 107-mm larva. Numbers designate somites. Somite 50 includes origin of vertical artery at anterior limit of the cluster of melanophores that comprises the second of the three internal spots; somite 58 includes origin of main renal artery; somite 61 marks posterior limit of kidney; somite 63 includes origin of renal portal vein.

somites between the pylorus and the posterior end of the kidney. There is close agreement in the number of somites between the posterior end of the kidney and the anus. The differences in visceral proportions are consistent with the lower total somite count and the consequently shorter gut in the Scripps specimens.

The pigmentation of the eastern Pacific larvae closely matches the known pattern of the Atlantic specimen. The internal supraspinal row of melanophores has essentially the same extent; the internal supra-intestinal row apparently extends farther forward (Regan did not show any prepyloric pigment in this row); and the external midventral row is apparently more complete (Regan showed no postpyloric pigment here). The original references did not indicate any middorsal pigment on the Atlantic larva. In the Scripps larvae the three internal spots are placed somewhat farther forward in relation to somite numbers, but (as will be discussed in a later section) they have essentially the same position in relation to the viscera and to certain blood vessels. Regan did not mention these spots in the original description, but Bertin discovered them, described them in detail, and figured one of them. These markings comprise an unusual pattern element which, so far as I can determine, is known elsewhere only in the larvae of *Nemichthys* (see discussion below). The descriptions did not mention scattered internal melanophores anterior to the anus in addition to the three aggregate spots, but they did indicate that the tail bore small melanophores both above and below the median axis, and in Regan's illustration this speckling forms essentially the same pattern as it does on the Scripps specimens.

Although the maximum sizes that the Atlantic and Pacific larvae attain are still unknown, simple individual or growth-stage variation could account for most of the evident differences between the available Pacific larvae and the described Atlantic specimen. The smaller number of teeth, more concave head profile, slightly protruding lower jaw, slightly deeper body, and poorly defined hypurals of the original specimen of *acuticeps* are developmental features that are commonly seen in young stages of leptocephali. Whether the minor color pattern differences represent growth-stage characters will remain uncertain until more complete developmental series are available. The difference in somite counts is the principal feature which suggests that the populations in the two regions may differ at the species level, but more data are needed before this difference can be evaluated.

It is now pertinent to discuss the place of *L. acuticeps* in the eel classification. Apparently only two authors have compared *acuticeps* with other larvae (*L. oxycephalus* Pappenheim and *L. magnaghii* D'Ancona), and only two have attempted to assign it to a category in the eel classification (both to the same family, the Congridae). Elsewhere, however, one can find clues that clearly point to the proper taxonomic position of *acuticeps*.

B. *Leptocephalus oxycephalus*

Pappenheim (1914:190, pl. 9, figs. 3, 5) based his brief description of *L. oxycephalus* on seven Atlantic larvae that measured 177–193 mm in total length, and he placed about 40 additional smaller and less well-preserved specimens from the Atlantic and Indian oceans in *oxycephalus* with less certainty. He credited this larval form with total somite counts of 220–230, of which 180–190 were preanal. At about the 30th somite, he noted a structure that he tentatively identified as the liver anlage. He listed only two other characters, both rather uninformative: the head was low and the caudal fin was normal. Pappenheim did not mention pigmentation, and none is definitely apparent in his photographs of *L. oxycephalus,* but this does not necessarily mean that pigment cells actually were totally absent. It is quite possible that pigment had faded before he received the collection, or that the individual melanophores were too small to show on the photographs. In his descriptions of other leptocephali in the same paper, he tended to omit pigment characters or to treat them very superficially. Hence he may have considered the color pattern too insignificant to require detailed description. In Pappenheim's illustrations the general format of *L. oxycephalus* rather closely resembles that of the Scripps specimens of *L. acuticeps,* but it also looks much like a very generalized congrid larva, and the characters discernible in the photographs are insufficient to permit definite discrimination. Regan (1916) considered his new *L. acuticeps* to be very simi-

lar to *L. oxycephalus,* and he mentioned no differences other than the somewhat lower somite count of *acuticeps.* D'Ancona (1928) rejected affinity of *oxycephalus* to *acuticeps* because of the ostensible lack of pigment in *oxycephalus.* Bertin (1936) doubted that they are related, but he gave no reasons. On present knowledge, I consider *L. oxycephalus* too incompletely known to be identified with certainty.

C. *Leptocephalus magnaghii*

D'Ancona (1928:109) rejected Regan's view that *L. acuticeps* resembles *L. oxycephalus,* and suggested instead that *acuticeps* should be compared with his own newly described leptocephalus from the Red Sea, *L. magnaghii* (op. cit.: 44; pl. 3, figs. 4, 5). He stated that the somite counts of *acuticeps* and *magnaghii* show no essential difference (*acuticeps,* total 207, preanal 174; *magnaghii,* total 205–219, preanal 157–161, excluding a metamorphosing larva with shortened gut). He suggested that *acuticeps* might even be considered a younger stage of *magnaghii,* but he decided to recognize both forms because of a difference in lateral pigmentation that he did not think could be explained by either individual or growth-stage variation; i.e., the presence of a midlateral longitudinal row of melanophores along each side in *magnaghii* and the absence of such rows in *acuticeps.*

L. acuticeps and *L. magnaghii* differ more widely than D'Ancona realized. *L. magnaghii* does resemble *acuticeps* in total somite count, in its long straight gut, and in the low number of caudal rays, but it differs in virtually all other significant features of morphology and pigmentation that can be compared. D'Ancona was unaware that *acuticeps* has the unusual pattern of three internal blotches, for Regan did not mention or figure these spots and Bertin's comments on them had not yet been published. The Scripps fish collection includes extensive series of *magnaghii*-like larvae from the eastern tropical Pacific. These leptocephali are identifiable as heterocongrid eels on the basis of compared somite and vertebral counts, congrid characters of metamorphosing specimens, and remnants of the larval color pattern that are retained by juveniles of *Taenioconger* sp. in the Scripps collection. The close agreement of the Scripps larvae with D'Ancona's detailed description and excellent illustrations of *magnaghii* (including a metamorphosing specimen) suggests that this larval name was based on heterocongrid larvae, possibly of two species.

The relatively greater importance of characters other than the somite count, in the critical comparison of *L. magnaghii* and *L. acuticeps,* exemplifies the paradox that data on somite counts can be both essential and misleading. The eels comprise such a large and complex group that totally unrelated forms may independently have the same, or broadly overlapping, ranges of variation in vertebral counts. For example, at least ten families[3] are already known to contain species with vertebral counts that fall within the range of about 145–155. Thus, an unidentified leptocephalus that has a somite count within this range might belong to any one of at least ten families. The successful identification of eel larvae requires the use of many additional characters. The visceral anatomy supplies more informative clues to the family affinities of a leptocephalus than does the somite count.

D. Congrid Larvae

Characters of congrid larvae. So far as I can find, only D'Ancona and Bertin have tried to assign *Leptocephalus acuticeps* to a family in the eel classification. Each author considered it to be a congrid, but neither stated his reasons. A detailed comparison of *acuticeps* with congrid larvae should reveal whether it properly belongs with them, but two formidable difficulties hamper this comparison: the wide disagreement among taxonomists as to the composition of the family Congridae, and the resultant uncertainty over the criteria for defining congrid vs. noncongrid larvae. The present paper is hardly the place for an attempt to settle the natural boundaries of this family, yet some sort of limits must be indicated in order to permit useful larval comparisons.

The type genus, *Conger,* is the base line for comparison of larval stages as well as of adults

[3] Heterenchelidae, Muraenidae, Synaphobranchidae, Ilyophidae, Nessorhamphidae, Echelidae, Ophichthidae, Congridae, Muraenesocidae, Serrivomeridae.

in this heterogeneous group. Fortunately, the larvae of its type species, *C. conger* (Linnaeus), and of two closely related eels from the Atlantic and Mediterranean are known. The latter two species have had (and are still having) a confused nomenclatorial history, but they are identifiable under the commonly used names *Ariosoma balearica* (de la Roche) and *Congermuraena mystax* (de la Roche). The similarities among the definitely identified leptocephali of these three nominal genera provide a basic standard for defining true congrid larvae, and their differences indicate some of the kinds of variational trends that one can expect to find in related larvae. I have examined Pacific larvae of the *Ariosoma balearica* and *Congermuraena mystax* groups, but have not yet seen *Conger* larvae. The larvae of this central group of indisputable congrids share essentially the same basic format. Its conspicuous features include the long, straight, simple gut (without regional enlargements or other specializatons), and the short tail with a well-defined caudal fin that typically comprises 6–10 caudal rays. These larvae differ among themselves in size, proportional details, somite counts, and in anatomical characters of the sort that I have used above in the description of *Leptocephalus acuticeps* (position of the pylorus, length of the kidney, etc.). The quite different color patterns of these three kinds of larvae indicate that the true congrids have undergone considerable evolutionary diversification in larval pattern. *Conger conger* has a pair of ventrolateral rows of melanophores, apparently external, paralleling the gut; a midlateral row, also apparently external, on each side of the body axis; and several large melanophores on each side of the pericardium. *Congermuraena mystax* has the ventrolateral and pericardial pigment, but lacks the midlateral row. In both of these larvae, the melanophores are relatively large and conspicuous. *Ariosoma balearica* differs sharply, both in the pattern itself and in the very small size and dense spacing of the melanophores. This pattern includes densely crowded rows of tiny melanophores externally along the middorsal and anterior midventral surfaces, and internally along the top of the gut. In place of the simple longitudinal row of large melanophores along the midlateral surface, *A. balearica* has an elaborate lateral surface pattern composed of a uniform series of short, oblique, parallel black lines just below the midlateral axis along nearly the full length of the larva. Each of these short black lines consists of a dense row of minute melanophores placed lateral to the myocomma between two contiguous somites. Since the row of cells marks the section of the myocomma that lies just below the midlateral axis, the row therefore conforms to the oblique ventrocaudal orientation of this part of the myocomma. The diagrammatically repetitive composition of the pattern results from the regular presence of a row of cells on almost every myocomma.

A typical congrid larva is readily identified as such, for it has morphological and color-pattern characters that are consistent with the trends indicated in this basic group of known larvae. For example, the Scripps collection includes many eastern Pacific leptocephali that are easily allocated to the Congridae, and it is evident that they include at least a dozen different kinds though few of these can yet be identified with named adults. The color patterns of most of these kinds of larvae are simple modifications of the *Conger conger* type.

It is not known whether larvae of all true congrids conform strictly to the format of this basic group of identified larvae, or how widely a larva may depart from this type in morphological and pattern characters and still retain recognizable evidence of congrid affinity. However, some idea of the limits within which congrid larvae might evolve (and, thus, whether *Leptocephalus acuticeps* might belong here) can come from study of the problem groups that have been interpreted variously by different authors. The heterocongrid eels are an instructive example. Whether the heterocongrids (the garden eels, or tube eels) are best retained in the Congridae or interpreted as a separate but closely related family is still under debate in the literature. Known heterocongrid larvae (*Leptocephalus magnaghii* from the Red Sea, and closely similar larvae from the eastern tropical Pacific) differ from larvae of the *Conger-Congermuraena-Ariosoma* complex in some respects (e.g., higher somite counts, relatively shorter gut, and more anterior origin of the

dorsal fin), yet they retain an unmistakable structural similarity to these basic congrid larvae and their pigmentation is a simple variant of the *Conger conger* type of larval pattern. The heterocongrids probably should be considered genetically close to the typical congrids, no matter how one may choose to juggle their nomenclature. The nettastomid eels, which are still sometimes included in the Congridae (e.g., Ginsburg, 1951), exemplify the opposite extreme. Their known larvae differ strikingly from the typical congrid larvae in both morphology and pigmentation. The head and jaws are usually very elongated, the viscera are exceptionally short and complexly specialized, and the color patterns are unusual. These and other specializations indicate that these larvae have evolved along distinctive lines and suggest that the nearest relationships of the nettastomids are to stocks that are remote from the congrids. Several groups of genera in addition to the nettastomids seem far too discordant with the type genus, *Conger,* in both adult and larval characters, to be retained within the same family. These include the dysommids, especially if the larva that Grassi (1913:170, pl. 10, figs. 1, 5) assigned to *Todarus brevirostre* was correctly identified, and the muraenesocids. I agree with authors who have elevated each of these groups to family rank. It seems to me that certain other genera (e.g., *Hoplunnis, Oxyconger,* and *Gavialiceps)* that are sometimes placed in the Congridae should also be excluded, but their larvae are still unknown and their adult stages are too incompletely described to support effective discussion of affinities. Some of these forms may prove to be muraenesocids, when the limits of that family are better understood, but others (notably, *Gavialiceps toeniola* Alcock) perhaps represent phyletic lines that are distinctive enough to justify family rank.

These examples help to establish criteria for the probable limits within which the larvae of true congrids have evolved, but a more precise understanding must await the specific identification of many more larvae, particularly in the less well-known genera that are of questionable status. Although present knowledge precludes a more authoritative discussion, this summary at least provides some basis for evaluating the possible affinity of *Leptocephalus acuticeps* to the typical Congridae.

Comparison of Leptocephalus acuticeps *with congrid larvae.* Neither D'Ancona nor Bertin gave his reasons for considering *Leptocephalus acuticeps* to be a congrid, but they probably noticed the characters of long, unspecialized gut and short tail that it shares with the congrids and with certain other leptocephali. It is also likely that they noticed the partial similarity of its pigmentation to that of the *Ariosoma balearica* larva, for both of them had reported on larvae of the *balearica* group. However, comparative study indicates that *acuticeps* does not belong here, even though the limited present knowledge reveals few absolute distinctions that firmly exclude it from the Congridae. There are some rather subtle morphological differences between *L. acuticeps* and typical congrid larvae. In *L. acuticeps* the nasal capsule is conspicuously smaller, the eyeball lacks the white (or partly pigmented) supporting sheath that most but not all known congrid larvae have, and the tongue is fully adherent, in contrast to its usually free tip and edges in congrid larvae. The hypurals are narrow and rather weakly chondrified, and there are only 3 or 4 caudal rays compared with the 6–10 generally reported for congrid eels. The somite counts of *L. acuticeps* exceed the vertebral counts of the better known congrids, most of which fall between 130–160, but this is not an excluding character, for a few congrids are known to have counts that overlap or even exceed the known somite counts of *L. acuticeps.* For example, Asano (1962) listed vertebral counts of 173–181 for *Congrina retrotincta* (Jordan and Snyder), and 203–206 for *Uroconger lepturus* (Richardson). The Scripps collection contains unidentified Indo-Pacific congrid leptocephali with somite counts as high as 230. The similarities in pigmentation between *L. acuticeps* and the larva of *Ariosoma balearica* include the very small size and dense spacing of the melanophores, and the presence of middorsal and anterior midventral surface rows and an internal row along the top of the gut. There are important differences in the rest of the pattern. *L. acuticeps* has a complete row of internal supraspinal melanophores and the distinctive three oblique internal spots, and lacks lateral

surface pigment. Few congrid larvae are known to have any trace of internal supraspinal pigment. The internal three-spot pattern of *acuticeps* has no known counterpart in congrids. Numerous differences in morphological characters indicate that *acuticeps* is not related to *Ariosoma balearica.*

At present, the best evidence that supports the exclusion of *L. acuticeps* from the Congridae is its close resemblance to the definitely identified larvae of a different family, the Nemichthyidae.

E. *Nemichthys* Larvae

Characters of Nemichthys *larvae.* The distinctive larvae of *Nemichthys* (family Nemichthyidae) have been described and illustrated under several leptocephalus names, for their various size-groups and stages in metamorphosis have repeatedly been considered new kinds of larvae. Data on metamorphosis enabled Roule and Bertin (1929:61) and Beebe and Crane (1937:357) to assign all of these varying larvae to *Nemichthys.* It is possible that the extensive described material may also include larvae of *Nematoprora* or *Cercomitus,* for these genera are closely related to *Nemichthys* and probably closely accord with it in larval characters. A complete review of the literature on the *Nemichthys* group is not essential to the present paper, however, for the two references cited above give adequate surveys of the literature on the larvae up to 1937, and very little that is pertinent to this paper has been published since then. The discussion that follows is based both on the literature and on *Nemichthys* larvae from the eastern Pacific in the Scripps collection.

Larvae of the *Nemichthys* group may attain a total length of at least 359 mm before metamorphosis (Roule and Bertin, op. cit.), and they are therefore among the largest known leptocephali. Total length is a rather deceptive measure of their size, however, for they are also among the slenderest of the known leptocephali (except during their more conventionally proportioned earliest stages), and hence they look smaller than the length indicates. The general form of the well-grown *Nemichthys* larva is a long narrow ribbon that has a nearly uniform width along much of its length and ends in a very thin, pointed tip without a well-defined caudal fin. The slenderness of the larva becomes more exaggerated as the total length increases. The gut is a straight, simple tube that extends exceptionally far back, and the preanal somite count is therefore unusually high. The bulging cranium, strongly concave snout profile, and slender jaws give the head distinctive and somewhat birdlike contours. The forms of *Nemichthys* have the highest vertebral counts known in the eels, and both of the references cited above suggested that additional somites and vertebrae probably continue to form at the tail tip throughout life, in contrast to the definitive growth pattern known in other eels. The narrowness and dense spacing of the terminal segments make a precise count difficult, especially on the smaller larvae. A 147-mm larva in the Scripps collection (SIO62–640–26A) has 225 preanal somites and about 50 postanal somites, making an approximate total of 275. Beebe and Crane (1937:363) reported that the total number may reach 450 before metamorphosis, and the same authors (op. cit., p. 351) recorded a vertebral count of 660 in an adult *Nemichthys.*

Roule and Bertin (1929:61) and Beebe and Crane (1937:357) had two kinds of nemichthyid larvae, which they termed "A" and "B." These probably represent different species, and possibly different genera, but the nomenclatural details need not be explored in this paper. Roule and Bertin found that the "Dana" collections contained 664 larvae of type A and only 26 of type B, and included a sufficient range of growth stages of each type to demonstrate that the two kinds do differ and are not themselves stages in a continuous series. The type B larva reaches a greater total length (to 359 mm) than type A, and has a higher number of preanal somites (maximum known, 320). An internal row of very small melanophores along the top of the spinal cord and a similar row along the top of the gut both begin at about the 10th somite. The smaller type A larva (maximum length before metamorphosis, about 253 mm) has fewer preanal somites (maximum known, 248), and its internal rows of minute supraspinal and supraintestinal melanophores begin farther back, at about the 25th somite. Type A has an important color-pattern character that the authors did not find in type B. This

comprises three small internal black spots that show through the somites. Roule and Bertin stated that on younger larvae each of the three spots is large, branched, and extends over the width of several somites. On the 147-mm larva in the Scripps collection, each spot consists of a loose cluster of from two to several cells. Roule and Bertin found that the spots become much less conspicuous on the larger larvae, but traces of them remain on some of the metamorphosing specimens. In gross appearance, the spots are farther forward on larger larvae than on small ones. This does not represent an actual displacement of the markings, however, but is a passive proportional modification that results from the continued addition and lengthening of somites posteriorly. The spots continue to occupy fixed positions (discussed in detail below). Roule and Bertin (op. cit., p. 74) found that in the extensive "Dana" material the three spots occupy average locations at somites 39, 73, and 116 respectively.

Comparison with Leptocephalus acuticeps. The combination of excessively attenuated form and extremely high somite count tends to isolate larvae of *Nemichthys* from other leptocephali and to mask any similarity to them, but a critical examination of details reveals characters that link *Nemichthys* closely with *Leptocephalus acuticeps.* Direct comparison of these larvae shows that their most conspicuous differences correlate rather simply with their greatly different somite counts and tail-tip structure. In *Nemichthys* the visceral anatomy borders a greater number of somites, so that the various organs are associated with more posterior somites than is true of their counterparts in *L. acuticeps,* but the visceral proportions are much the same as in *acuticeps.* The two kinds of larvae differ markedly in tail-tip structure. *L. acuticeps* has a bluntly rounded tail tip with a well-defined caudal fin; the *Nemichthys* larva has a thin filament-like tail tip with little or no apparent definition of fin elements. The *Nemichthys* larva and *L. acuticeps* both have internal rows of supraspinal and supraintestinal melanophores (which are relatively uncommon in eel larvae), and they agree in the small size and dense spacing of the cells in these rows. The most significant shared pigment character is the presence and similar placement of the unique pattern of three internal spots. It seems suprising that when Bertin (1936) redescribed the original larva of *L. acuticeps* he did not mention the resemblance of its internal three-spot pattern to that of *Nemichthys,* which he (with Roule) had described in detail only a few years before. Apparently, however, Bertin considered the extreme elongation and high somite counts of the *Nemichthys* larva to be primary characters of sufficient importance to outweigh any resemblances to other leptocephali. Perhaps, also, he had not yet studied a sufficiently wide variety of larval color patterns to realize the uniqueness of this one. *L. acuticeps* differs from *Nemichthys* in having melanophores along the middorsal surface and in having more extensive pigment midventrally from the pericardium to the anus. *Nemichthys* appears to lack the scattered, isolated melanophores in the median connective-tissue zone which, in *L. acuticeps,* supplement the three aggregate spots.

In respect to somite numbers, the three internal spots are somewhat farther forward in *L. acuticeps* than in *Nemichthys,* but in relation to the total length the reverse condition eventually occurs because of the differences in the nature of the proportional changes during growth. Both kinds of larvae are subject to lengthening through enlargement of somites, but in addition *Nemichthys* lengthens through the continued formation of new somites posteriorly. Thus, in *Nemichthys* the posterior end literally grows away from the spot pattern. A superficial examination of the spot positions reveals only that the two kinds of larvae differ, but a comparison of the spot positions with visceral "landmarks" instead of simply with somites reveals a striking agreement. Although the first spot averages about 10–14 somites farther back in *Nemichthys* than in the Scripps larvae of *acuticeps,* in both forms the spot occurs above or just behind the pylorus, close to or overlapping the position of a median vertical artery that extends down from the aorta to the viscera. The second spot averages about 20–23 somites farther back in *Nemichthys* than in *acuticeps,* but in both kinds the spot occupies the same morphological position about 10–12 somites ahead of the posterior end of the kidney, near or overlapping the

vertical artery that precedes the main renal artery (Fig. 4). The location of the third spot averages about 30 somites farther back in *Nemichthys,* but in both kinds of larvae it is situated in the same region about 24–31 somites behind the posterior end of the kidney. The internal morphological affinities of the third spot are not clear from the present data, but may be determinable from histological examination or from study of the anatomical changes that occur in this region during metamorphosis. From Bertin's data one can diagram the positions of the spots and of the major blood vessels in the holotype larva of *L. acuticeps,* and the result is essentially the same as in the Scripps larvae of *acuticeps* and in *Nemichthys:* the first spot coincides with the position of a median vertical artery in the pyloric region, and the second coincides with a similar vessel about 10 somites anterior to the main renal artery. Bertin's illustration (his fig. 4) includes this spot and artery.

It might seem reasonable to suppose that color-pattern elements that are directly beside the somites are associated primarily with these immediately neighboring somites rather than with some other structure. The contrary explanation in the present example traces to the fact that the spots in question are internal rather than external to the somite surfaces. In eel larvae, the visceral complex is displaced far downward, usually completely below the lower edges of the somites. The essential links between the body axis and the viscera (blood vessels, supporting connective tissue, etc.) are greatly attenuated and occupy a thin median vertical plane sandwiched between the laterally compressed right and left halves of the somites. The available evidence indicates that position of the diagnostic internal three-spot pattern in this group of larvae is primarily a function of the visceral and arterial positions and therefore only indirectly dependent on somite number. Evolutionary changes that have shifted the critical internal landmarks farther forward or backward along the body have also shifted these characteristic spots correspondingly, and thus the markings have maintained their predictably constant relationship to the specific blood vessels and visceral organs. The more conspicuous positional association is with the pylorus and the end of the kidney, but experimental studies (if such work is ever feasible on deep-sea leptocephali) might show that the specific vertical blood vessels are the more direct determinants.

This problem demonstrates graphically the importance of noting precisely whether a color-pattern element that is "on the somites" actually occurs outside or inside of the transparent muscle layer. The morphological affiliations, and hence the evolutionary potentialities, of these two locations are quite different.

Once it is established that *L. acuticeps* and the *Nemichthys* larva share a uniquely integrated structural and color-pattern character in the predictable detail that hints genetic relationship, then the probable significance of the similarities and differences that they show in other characters becomes clear. The *Nemichthys* larva is, essentially, an exaggerated *acuticeps* that has specialized in extremely attenuated shape, very high somite count, and the probably continuous addition of new somites in its filament-like tail tip. These chief larval differences involve the same characters as do the differences that separate the adults of *Nemichthys* from those of certain related genera, and these characters suggest the probable correct generic placement for *Leptocephalus acuticeps.*

ASSIGNMENT OF *Leptocephalus acuticeps* TO *Avocettina*

Opinions on the generic composition and best nomenclatural treatment of the *Nemichthys* group differ greatly. Some authors divide the presumed relatives of *Nemichthys* into several families, and set the entire group apart from all other eels at the subordinal level. Others reduce the number of families, chiefly by lumping rather than by deletion from the group, and either accept or omit the subordinal category. Roule and Bertin (1929) proposed subordinal rank for these eels and, on the basis of small differences, divided them into six families: Nemichthyidae, Avocettinidae, Avocettinopsidae, Gavialicipidae, Cyematidae, and Serrivomeridae. Trewavas (1932) reduced this assemblage to three families: Serrivomeridae (including *Gavialiceps* in part; she placed *G. toeniola* in the nettastomid genus *Saurenchelys*), Cyemidae, and

Nemichthyidae. Böhlke and Cliff (1956), representing the trend toward more extreme lumping, recognized only the Nemichthyidae (including *Avocettina, Avocettinops,* and *Cyema*) and the Serrivomeridae (including *Gavialiceps*). The larvae of *Serrivomer* and *Cyema* are quite well known, particularly from the studies by Beebe and Crane (1936) and Bauchot (1959) on the former, and by Bertin (1937) on the latter. These larvae clearly have differentiated along quite different evolutionary lines than have *Nemichthys* and *Leptocephalus acuticeps,* and are outside the scope of the immediate larval problems discussed in the present paper. Thus, regardless of which way one thinks it best to delimit the family Nemichthyidae (a very inclusive, or a narrowly limited version), it is apparent that the adult stage of *L. acuticeps* can be sought in the more restricted group of forms that are thought to be phyletically the closest to *Nemichthys.* The forms in this limited group center around two principal genera, *Nemichthys* and *Avocettina.* Although the several pertinent genera are usually keyed out primarily on the basis of their lateral-line characters, a different grouping is more practical for the purposes of the present discussion, for it utilizes characters that can be determined on larvae as well as on adults. The widely distributed *Nemichthys* and the less well-known genera *Nematoprora* and *Cercomitus* comprise the more extremely attenuated of the snipe eels, with excessively high vertebral counts that may continue to increase throughout life, and a thinner and more whiplike tail that has little or no trace of a defined caudal fin. Reported vertebral counts of *Nematoprora* exceed 259 (Trewavas, 1932:649, for a specimen with an incomplete tail), and of *Nemichthys* range from 300 to as high as 660 (Beebe and Crane, 1937). The eels that may be grouped with *Avocettina* include *Labichthys* and, tentatively, the incompletely known *Avocettinops.* These eels are less extremely attenuated, have a better differentiated caudal fin, have much lower vertebral counts, and apparently develop a fixed number of vertebrae rather than adding new units indefinitely. The known vertebral counts of the *Avocettina* group are only moderately high, compared with other eels in general. Beebe and Crane (1937: 366, 375) reported a range of variation from about 170 to 198 in *Avocettina,* and from about 175 to 180 in *Labichthys.* Bertin (1942:106) reported a count of about 192 vertebrae in *Avocettinops.* The known caudal-ray counts are low, compared with eels as a whole: five rays in *Avocettina* (Beebe and Crane, 1937:371), and four in *Avocettinops* (Bertin, 1942:107).

The somite counts of 182 and 187 on the two eastern Pacific larvae of *Leptocephalus acuticeps* fall within the known range of variation in vertebral counts of *Avocettina.* The count of 207 on the Atlantic larva of *acuticeps* is a little higher than the known maximum adult vertebral count. If the questionable *Leptocephalus oxycephalus* Pappenheim should prove to belong to this group, its somite counts of 220 to 230 would indicate the existence of related populations that have vertebral counts substantially higher than the presently known maximum among the *Avocettina*-like eels. *L. acuticeps* resembles *Avocettina* also in its low caudal-ray count.

Although metamorphosing specimens are still lacking, the available data warrant the tentative identification of *Leptocephalus acuticeps* as a larval stage of the *Avocettina* group. The ostensibly extreme differences between the *Nemichthys* larva and *L. acuticeps* seem inevitable consequences of the basic differences between *Nemichthys* and *Avocettina.* From the known vertebral and caudal-fin characters of the adults of these two genera, one can predict that their larvae must differ in somite and tail-tip characters in precisely the way that *L. acuticeps* does differ from known larvae of *Nemichthys.*

The available evidence suggests that *acuticeps* is probably significant above the species level. Similar problems on other leptocephali indicate that eel larvae in general tend to show strong group resemblances and relatively small or obscure species differences. For example, *Anguilla* larvae conform to a distinctive and easily recognized generic format wherever they occur, but in the Indo-Pacific Jespersen (1942) found that they are difficult to separate into species to match the approximate dozen named species that are currently recognized for adults in that region. Similarly, Bauchot (1959) found that two named larvae, *Leptocephalus lanceolatus*

Strömman and *L. lanceolatoides* Schmidt, encompass larval populations that represent several species of *Serrivomer*. The available data suggest that *L. acuticeps* is probably also an indicator of group relationships. The many basic morphological and color-pattern characters that *acuticeps* and larval *Nemichthys* share have been sufficiently stable to withstand the amount of evolutionary divergence that now separates the genera *Avocettina* and *Nemichthys*. Hence the existing intrageneric variation in these characters undoubtedly has even narrower limits. Since all species in the *Avocettina* group (including *Labichthys* and, tentatively, *Avocettinops*) thus probably have very similar larvae, I have elected to treat *L. acuticeps* in a practical sense as a larval group category that designates, comprehensively, the general kind of larva that is characteristic of the avocettinas as a whole. This avoids the needless redundancy of establishing a new formal (but temporary) leptocephalus name for each ostensibly different minor population within the *Avocettina* group.

A more detailed understanding of larval differentiation within this group of eels awaits not only the study of more extensive larval collections but also additional taxonomic work on the adults. The number of valid species and genera of avocettinas is uncertain, and a worldwide revision of the group is needed. Problems that await study include the status of the genus *Avocettinops*. Is its single recognized species, *Avocettinops schmidti* Roule and Bertin, a distinct entity, or is it based on spawned-out, senile individuals of *Avocettina* spp. with regressive skeletal characters?

Much remains to be learned about the color-pattern characters of nemichthyid larvae, particularly with respect to developmental changes and population differences. The known larvae of the avocettinas (*Leptocephalus acuticeps*) are more heavily pigmented than are larvae of *Nemichthys*, both in the density of the markings that they share and in the presence of additional pattern elements. Since the evidence of evolutionary trends in color patterns commonly consists of simple modifications of a recurring basic pattern, the characters of these known nemichthyid larvae suggest some pattern variants that might reasonably be watched for among other closely related but still undiscovered larval populations. In such larvae, certain parts of the pattern might be less fully developed than they are in known larvae of *Nemichthys*, or the pattern might be still more complex than it is in the known specimens of *L. acuticeps*. The characteristic internal-spot pattern might be modified, or it might be totally absent, as has been reported for type "B" larvae of *Nemichthys* (Roule and Bertin, op. cit.). The scattered, inconspicuous internal melanophores that supplement these spots in the Scripps larvae of *L. acuticeps* might be more heavily developed in some related larval populations.

The assignment of *Leptocephalus acuticeps* to the *Avocettina* group provides information that is useful for various evolutionary studies. Since *L. acuticeps* has a more generalized format than do the extremely attenuated larvae of *Nemichthys*, *L. acuticeps* probably more nearly represents the basic nemichthyid larva and it is, consequently, the more important larva to treat in comparative studies on the evolutionary affinities of the nemichthyids to other eels. The ostensible morphological similarity between nemichthyid and congrid larvae is one of the problems that needs inquiry. Both *L. acuticeps* and the larva of *Nemichthys* show sufficient resemblance to congrid larvae, especially in the various proportional characters that are associated with the gut length, to suggest the need for a renewed study of the relationships of these two families, which are usually placed far apart in the classification. Although the available evidence does not warrant any assumption that these two families are more closely related than hitherto suspected, it does suggest that future work on leptocephali may profitably emphasize a more intensive comparative study of their basic anatomy so that the phyletic significance of their obviously diversified characters can be evaluated and used more effectively in eel systematics.

SUMMARY AND CONCLUSIONS

Regan (1916) based the South Atlantic eel larva, *Leptocephalus acuticeps*, on a single 47-mm specimen, which Bertin (1936) later reexamined and discussed in greater detail. The relatively complete published data and the unusual nature of certain of the characters set

acuticeps well apart and make it more confidently identifiable than are most other described leptocephali.

Two larvae from the eastern tropical Pacific in the Scripps Institution fish collection appear to be the first new material on *L. acuticeps* to be reported since the original specimen. They share the general format and the determinable visceral and pigmentation characters of the original specimen, and differ in details that apparently represent growth-stage differences and individual or population variation.

For unspecified reasons, D'Ancona (1928) and Bertin (1936) assigned *L. acuticeps* to the Congridae, but the studies reported in the present paper show that in both morphological and color-pattern characters *acuticeps* most closely resembles the larvae of *Nemichthys,* the type genus of the Nemichthyidae. The larva of *Nemichthys* differs from more conventional leptocephali in its greatly attenuated shape, very high somite count, and apparent continuous, life-long addition of new somites in its thin, filament-like tail tip. However, a detailed comparison of the *Nemichthys* larva with *Leptocephalus acuticeps* shows that these outwardly conspicuous differences mask fundamental resemblances in both morphological and color-pattern characters, and that the larva of *Nemichthys* is, essentially, an exaggerated *acuticeps.* The most significant of the pigment characters that they share is an internal three-spot pattern (visible through the transparent somites) that is not known to occur in any other leptocephali. These spots are in the anterior half of the body, occupying the level between the midlateral axis and the lower edge of the somites. Each spot consists of several small melanophores loosely grouped together in a more or less linear cluster, situated on the median connective tissue that is compressed between the right and left muscle layers. The spots are substantially farther back in *Nemichthys* larvae than in *L. acuticeps,* in relation to somite numbers. In both kinds of larvae, however, the first spot is above or slightly behind the pylorus, near or overlapping a vertical artery; the second spot is about 10–12 somites ahead of the posterior end of the kidney, adjacent to or overlapping the last vertical artery anterior to the main renal artery; and the third spot is about 24–31 somites behind the posterior end of the kidney. The anatomical significance of this third location is not clear from the present data. The predictable relationship between the internal three-spot pattern and the visceral anatomy suggests that these color-pattern and structural characters have operated as a very stable unit during phyletic changes.

Although metamorphosing specimens are still lacking, the available evidence places *Leptocephalus acuticeps* in the *Avocettina* section of the family Nemichthyidae. From the known adult characters of *Nemichthys* and *Avocettina,* one can predict that their larvae must differ in somite and tail-tip characters in precisely the way that *L. acuticeps* differs from larvae of *Nemichthys.* On present knowledge, *acuticeps* cannot be restricted to any single species, and it is probable that all species in the *Avocettina* group (including *Labichthys* and, tentatively, *Avocettinops*) have larvae of this general type. Thus, it seems best to treat *acuticeps* comprehensively as an informal group category that designates the kind of larva that characterizes the avocettinas as a whole. A more detailed understanding of differentiation in larval populations within the *acuticeps* complex must await not only the study of larger series of larvae but also a world-wide revisionary study of the adult avocettinas.

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