PHYLOGENETIC ANALYSIS OF
THE COTTID GENUS ARTEDIUS
(TELEOSTEI:SCORPAENIFORMES)

by

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ABSTRACT

The genus Artedius Girard (Cottidae:Scorpaeniformes) is revised. Artedius hankinsoni is synonymized with Artedius lateralis, since the defining characters of Artedius hankinsoni (Hubbs, 1926) fail to separate it from Artedius lateralis. Evidence of the diphyletic condition of Artedius Girard is presented. Based on the character analysis in this study, five of the seven nominal species are hypothesized to represent a monophyletic group (A. corallinus, A. lateralis, A. harringtoni, A. fenestralis, and A. notospilotus) hereafter referred to as Artedius sensu strictu. Two Artedius species, Artedius creaseri and Artedius meanyi, do not share any of the synapomorphies of Artedius sensu strictu, therefore the genus Ruscarius Jordan and Starks is resurrected to include Ruscarius meanyi and Ruscarius creaseri. Evidence is presented for the monophyly of Ruscarius, which is hypothesized to be more closely related to Chitonotus and Icelinus than it is to Artedius.

Phylogenetic analysis of the adult data (including Artedius, Ruscarius, Oligocottus, Clinocottus, Chitonotus, Orthonopias, Icelinus and Hemilepidotus) yielded three cladograms. These differ only in the placement of Chitonotus. The results from this study are compared with those of Bolin (1947). A larval data matrix for Washington's (1982) study is reconstructed and three larval cladograms are presented.

Finally, an analysis of taxonomic congruence is attempted using the consensus technique of Adams (1972). Two trees were

prepared, one showing the consensus of the adult trees, one showing the consensus of the larval trees. The larval consensus tree was then compared with the adult consensus tree to give an overall consensus tree. This final consensus tree recognizes two generic groups: one composed of Artedius, Clinocottus and Oligocottus, and one composed of Ruscarius and Icelinus. Thus both adult and larval classifications support the removal from Artedius of creaseri and meanyi to the genus Ruscarius in a clade with Icelinus separate from the clade including Artedius, Oligocottus and Clinocottus.

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INTRODUCTION

The Cottidae are a Scorpaeniform family composed of sixty-seven genera (Nelson, 1976). Forty of the sixty-seven genera are found between the Aleutian Islands and Baja California. The taxonomic limits of the family are poorly defined and its monophyletic status has not been demonstrated. A major factor contributing to this confusion is the absence of sound systematic studies of the genera, including taxonomic analyses of the appropriate species. Even if the Cottidae is a natural taxon, it is likely that a number of genera are not monophyletic and that many species within those genera are invalid.

Given that our present knowledge of the genera is relatively incomplete, this study has four goals: (1) a taxonomic revision of the genus Artedius, (2) definition of the genealogical relationships of the species within Artedius, (3) an examination of the relationship of Artedius to other Cottid genera, and (4) a test of taxonomic congruence using data from larval and adult stages.

The genus Artedius Girard is distributed from the Aleutians Islands to Baja California. The genus is well-represented in museum collections and a large collection of larvae is also available for study.

HISTORICAL REVIEW

The genus Artedius was established by Girard in 1856 to accomodate two species of scaled cottids, Artedius lateralis (previously described as Scorpaenichthys lateralis by Girard in 1854), and Artedius notospilotus (Calcilepidotus lateralis Ayres 1854 and Hemilepidotus nebulosus Girard 1856 - though the latter was Ayres' unpublished name).

In 1882, Jordan and Gilbert placed both Artedius lateralis and Artedius notospilotus in the genus Icelus Kroyer, in the family Icelidae, along with other cottid species which were "more or less scaly" (p. 683). In their description of A. notospilotus, they remark that the northern specimens "represent a distinct variety." In 1883 they recognized this "northern variety" as a distinct species, Artedius fenestralis. However, due to the large number of species that had been transferred to and from Artedius since Girard erected the genus, they despaired of separating Artedius from Icelus, and deferred to their previous (1882a) decision placing all Artedius species in Icelus.

In 1895 Jordan and Starks described Ruscarius meanyi from Puget sound. Its affinities apparently lay with Chitonotus Lockington 1882, from which it was distinguished by a scallier back and weaker preopercular armature. Jordan and Starks (1895) also removed Artedius fenestralis to a new genus, Astrolytes, based on its rougher, more scaly cranium and stronger preopercular armature. Artedius notospilotus was subsequently

transferred to Astrolytes in 1896 by Jordan and Evermann.

In 1896 Starks described two new species, Artedius asperulus and Axyrias harringtoni, both from Puget Sound. Bean and Weed (1920) later described a new genus and species from the same region, Pterygiocottus macouni. This they suspected was the male of Axyrias harringtoni Starks, with which it was synonymized by Bolin in 1944.

Regan (1913), in his treatment of the Scleroparei (those fishes with the third suborbital extended backward onto the preopercle, forming a "suborbital stay"), placed both Artedius and Astrolytes in the family Cottidae and placed the family in the division Cottiformes. No mention was made of Ruscarius, but both Icelus and Icelinus were also included in the Cottidae.

Within his series Cottiformes, Jordan (1923) restricted the Cottidae to those genera that lacked scales. Thus Artedius, Astrolytes, Axyrias, Ruscarius, Ruscariops, and Pterygiocottus were united with Chitonotus, Orthonopias, Stelgistrum, Icelus, Icelinus, and twenty-seven other scaled genera and placed in the Icelidae.

No new Artedius-like species were described until 1926 when Hubbs described three species that were apparently related to Artedius. He placed each species in a monotypic genus. He considered Parartedius hankinsoni (a single specimen from Point Loma, California) and Allartedius corallinus (also a single specimen, from Point Lobos, Monterey County) closely related to Artedius. The third species, Ruscariops creaseri (from San Diego County), was related to Ruscarius meanyi of Jordan and Starks

(1895). Hubbs favored monotypic genera and in 1926 he removed A. notospilotus from Astrolytes and placed it into a new genus: Paraastrolytes.

In 1940, L.S. Berg reverted to Regan's (1913) treatment of Artedius and its relatives and placed them back in the Cottidae. The family Icelidae he reserved for Icelus. The remaining members of Jordan's Icelidae were reassigned to the Cottidae.

One year later, in 1941, Taranets completed his comprehensive treatment of the anatomy and relationships of the Cottidae. He divided the Scleroparei into twelve families and erected within the Cottidae thirteen subfamilies. His subfamily Oligocottinae contained two large generic groups: those with bony plates (scales) and lacking an anal papilla (Artediini), and those with an anal papilla and lacking bony plates (Oligocottini). The former included Artedius, Allartedius, Paraastrolytes, Axyrias and Orthonopias. Ruscarius and Ruscariops were removed to a subfamily, Icelinae, along with Icelus, Icelinus and Stelgistrum. This he justified by their common possession of two rows of bony plates which occur "one along the lateral line, and one at the base of the dorsal fin. In addition, plates are usually found in other parts of the body." (p.4). This description is hardly accurate, as Ruscarius, Ruscariops, and Stelgistrum all possess rows of scales covering the area between the lateral line and the dorsal fin bases. By his own definition, these three genera belong in the subfamily Oligocottinae along with Artedius and not in the Icelinae.

The last species to be assigned to the genus Artedius was A. delacyi, described from Alaska by Hubbs and Schultz in 1941. They cited its thicker lips and steeper snout as features distinguishing it from Artedius lateralis which was not known from Alaska at that time.

Except for Artedius which contained three species (A. asperulus, A. delacyi, and A. lateralis), all the remaining genera were monotypic and remained separate until 1944, when Bolin gathered Ruscariops, Astrolytes, Parartedius, Parastrolytes and Axyrias into Artedius, and placed Artedius asperulus in synonymy with Artedius fenestralis. He retained as subgenera Ruscariops (A. creaseri), Astrolytes, (A. fenestralis and A. notospilotus), Axyrias (A. harringtoni) and Artedius (A. corallinus, A. lateralis and A. hankinsoni). Neither Ruscarius meanyi nor Artedius delacyi was included in the taxonomic analysis. Bolin (1947) presented a branching diagram of the California members of the genus Artedius, including A. delacyi. This is the only phylogenetic dendrogram based on adult characters for Artedius and its close relatives (Fig. 23).

No further specimens of Ruscarius meanyi were collected until 1963, when Rosenblatt and Wilkie collected nine specimens in British Columbia. Redescribing the species, they referred it to Artedius Girard on the basis of Bolin's redefinition of Girard's genus. It was subsequently collected from Alaska (Peden and Wilson, 1976), British Columbia (Peden, 1972), Puget Sound (Moulton, 1977) and California (Lea, 1974).

Since Hubbs and Schultz' (1941) defining characters failed to separate putative A. delacyi from Alaskan A. lateralis, Hubbard and Reeder (1965) and Quast (1968) concluded that Artedius delacyi was not distinct from Artedius lateralis.

Recent classification schemes have differed little from that of Berg (1940). Nelson (1976) and Greenwood et al. (1966) both place Artedius in the Cottidae along with Oligocottus Girard and Clinocottus Gill, while Icelus is retained as the only member of the Icelidae.

In recent years a great deal of information on the morphology of larval cottids has accumulated, but only two studies have attempted to use these larval data in reconstructing phylogeny. Richardson (1981) recognized six phenetically derived groups within the cottid genera for which larvae are known. Her "group one" includes Artedius, Orthonopias, Clinocottus and Oligocottus. Icelus and Icelinus were included in "group two", along with Paricelinus, Triglops and Chitonotus. These groupings were primarily based on shared states of preopercular spines, snout and body shape, pigmentation, and different diverticula of the gut. These character states do not persist in adults. Meristic characters, which do persist in adults, were used for the purpose of identification.

Richardson's (1981) "group one", including Artedius, was characterized by a unique preopercular spine pattern, in all likelihood synapomorphic for that group, if the shared states are indeed homologous. However, no attempt was made to

establish any inter-generic relationships. Washington (1982) did attempt such an analysis for Artedius, Clinocottus and Oligocottus. She suggested that, on the basis of an I,2 pelvic state (one spine, two soft rays), A. meanyi should be removed to Icelinus, which also has an I,2 state. All other Artedius have an I,3 state. Under this scheme, A. creaseri would then become the sister group of an A. meanyi-Icelinus clade and an A. meanyi-Icelinus-A. creaseri clade would be the sister group of Artedius (less A. creaseri and A. meanyi) plus Oligocottus plus Clinocottus.

Within the genus Artedius three problems have emerged. First, there has been some difficulty in recognizing valid species. Usually this has been resolved by closer study and the only species now in question is Artedius hankinsoni. The status of this species is discussed later in this study. Second, there has been some question as to whether or not these species constitute a monophyletic group. Third, the relation of that group to Artedius and other scaled Cottid genera has not been resolved. The last two problems have remained unsolved primarily because researchers have attempted to justify groups on the basis of plesiomorphic characters. Witness Bolin's (1947) list of characters defining Artedius: "comparatively large head, normal structure of the pelvic fins and by the unadvanced anus."

These characters, taken as whole, supposedly serve to differentiate the genus at hand from other genera defined in a similar fashion. However, no one synapomorphic character has

ever been proposed to serve as justification for the monophyly of Artedius. This omission has resulted in: (1) the transfer of species to and from Icelus; (2) the suggestions (Bean and Weed, 1920, Howe and Richardson, 1978) that Orthonopias should actually be included in Artedius; and (3) the referral of Ruscarius meanyi to Icelinus by Washington (1982). When no synapomorphy is recognized different groupings and schemes of relationship cannot objectively be defended (Wiley, 1981).

The obvious solution is to test the hypothesis of monophyly of Artedius by searching for justification in the characters (Hennig, 1965, 1966; Rosen, 1974; Wiley, 1975, 1979, 1981, 1982). A natural group must be supported by synapomorphies at the appropriate level of universality. Plesiomorphic characters will not do, if the delineation of natural taxa is our goal (Nelson, 1971, 1972, 1973, 1979), as they inevitably lead to paraphyletic taxa (Farris, 1979a,b). Such taxa are classes and therefore timeless abstractions. Such taxa cannot participate in natural processes and should be avoided by those attempting to discover the pattern of natural order (Wiley, 1977, 1979, 1981, 1982; Rosen 1974).

METHODS

Adult Specimens

All specimens were preserved in either isopropanol (37.5% or 50%) or ethanol (70%). Cleared and stained specimens were prepared using the method of Dingerkus and Uhler (1977). Cleared and stained specimens were stored in 100% glycerin with thymol added to retard decomposition. Photographs of cleared and stained fish were made through a Bausch and Lomb dissecting microscope, with a Nikon F 35 mm camera and Nikon microscope adapter.

Institutions providing specimens were: California Academy of Sciences (CAS and SU), Los Angeles County Museum of Natural History (LACM), Scripps Institution of Oceanography Fish Division (SIO), University of British Columbia Fish Museum (BC), National Museum of Canada (NMC), University of Michigan Museum of Zoology (UMMZ), University of Washington Fish Collection (UW), and the United States National Museum (USNM).

Larval Data

Information on larval morphology was taken from Washington

(1982). Larval specimens were not examined in the present study.

Meristics

For both preserved and cleared and stained specimens all elements were counted. The one exception was the caudal fin count which included only principal rays.

Systematic Method

"If we find that the ascertainment of the order of nature is facilitated by one terminology or one set of symbols rather than another, it is our clear duty to use the former." T.H. Huxley, quoted in Jordan and Kellogg, 1907.

In constructing a general reference system (Hennig, 1966) for comparative biology (sensu Nelson, 1970) we must choose that method which best allows us to infer the historical course of evolution. Phylogeny is the history of life and that is what we are in business to discover. This involves specifying the genealogical relationships of natural taxa. Obviously, the primary problem is justifying the natural status of the groups

at hand. As Wiley (1979) noted, the only necessary and sufficient criterion of natural status is unique genealogy. Characters, which are our only directly observable evidence, are only secondary reflections of unique historical relationships. If we are to link characters to genealogy we need bridge principles (sensu Hempel, 1965) since characters exhibit two phenomena precluding their use as necessary and sufficient criteria of a group's natural status: ontogeny and character modification during phylogenetic descent (Wiley, 1978). If all characters remained unchanged throughout ontogeny and through the course of phylogenetic descent, they would constitute not only necessary but also sufficient evidence for the natural status of a group. Since they can be modified during the course of ontogenesis and phylogenesis we need bridge principles to move from that which we observe (characters) to that which we wish to infer (genealogy). Put simply, characters cannot be divorced from the concept of evolutionary homology (Wiley, 1981).

Our method should involve a search for evolutionary novelties which serve to define natural (monophyletic) taxa (Hennig, 1966, Wiley, 1979, 1981). Such characters are termed apomorphies if, at the level of analysis under study, they are hypothesized to be the derived state of an ancestral, relatively generalized homologue. An apomorphic character found in only one taxon is termed an autapomorphy. Shared apomorphies are termed synapomorphies. Only synapomorphies may be used to delimit natural, monophyletic groups.

The relatively generalized state of that homologue is termed a plesiomorphy and when shared by two or more taxa, a symplesiomorphy (Hennig 1966). Notice that all characters when they are evolutionary novelties, delimit a natural, monophyletic group. Thus at some level of universality all character states are apomorphic, delimiting a natural taxon. They cannot be used to diagnose other taxa at a level of universality at which they are not apomorphic (Hennig, 1966, Wiley, 1979, 1981). Note that apomorphy and plesiomorphy are relative terms and are meaningful only if the level of universality being considered is strictly specified.

The critical part of any such analysis is the determination of hypothesized plesiomorphic and apomorphic states for each character. Hennig (1966) discusses four methods: chorological (biogeographical), holomorphological (out-group comparison), geological precedence and ontogenetic precedence. Of these four, the first and third have generally been discarded due to their reliance on a priori assumptions about the pattern of character change in time and space. These assumptions may or may not be justified, depending on the particular circumstances. Because of this, outgroup and ontogenetic analyses are preferred. In outgroup analysis, character states shared with the outgroup are judged to be plesiomorphic at that level, while the alternative state is hypothesized to be apomorphic. In Nelson's (1978) formulation, the ontogenetic criterion follows from von Baer's law which states that relatively generalized states give rise to specialized ones as ontogeny progresses.

This method has two immediate drawbacks: non-terminal addition of character states and instances of de-differentiation effectively refute von Baer's "law" making the attendant character analysis suspect (Brooks, 1984 in press; Kluge, 1984 in press). Nelson (1978) claimed, in his formulation, that ontogenetic analysis can proceed independently of outgroup comparison, but Wiley (1980) noted that in cases of non-terminal addition meaningful character analysis can only be attained by resort to outgroups. Fink (1982) pointed out that paedomorphosis can further confound character analysis by making derived characters appear primitive, again necessitating the use of outgroups as a check.

Polarizing characters becomes more difficult when two or more apomorphic states exist at a given level of analysis. These multistate characters present special difficulties in establishing transformation series. Mickevich (1983) distinguished four types of multistate characters based upon their distribution on a previously-derived cladogram. These are:

1. Additive characters, for which Farris optimization (a parsimony technique - see Farris 1974 for a description) is possible. These allow construction of a character state tree.
2. Non-additive characters, in which optimization leads to multiple possibilities for transformation series. At best these allow resolution of subsections of a tree.
3. Convergent characters, in which it is equally likely that one state was derived from different conditions.

These are of minimal use in the resolution of trees.

4. Disjoint characters, in which no transformation can be hypothesized to link whole subsets of character states, although transformation series may be established within the individual subsets. These may allow sections of the tree to be resolved, but the relationships between these sections remain ambiguous.

Once character analysis is complete a cladogram may be constructed, linking sister taxa (those hypothesized to share an immediate common ancestor) by means of synapomorphies. Rarely do all the characters indicate the same relationships due to homoplasy (non-homologous similarity). In such an event, the cladogram with the least number of conflicting characters (the fewest number of steps or character state changes) is chosen as best representing the data; it is the least refuted hypothesis. Parsimony considerations force us to minimize the number of conflicts, each of which requires an ad hoc explanation. This leads to a preference for the tree with the minimum possible number of steps for a particular data set.

It is precisely this parsimony requirement that "classical" evolutionary taxonomy of Mayr (1942, 1969) and Simpson (1945, 1961) fails to satisfy. Their reliance on overall similarity and adaptive divergence results from attempts to infer a pattern (phylogeny) from a particular process (Darwinian evolution). The use of overall similarity fails to separate plesiomorphic from apomorphic information and, as a result, characters are not applied strictly at the level at which they constitute a

critical test of the hypothesis at hand (Wiley 1981). The notion of process was the mold into which the information on pattern was fitted, resulting in paraphyletic groups (grades) which are not defensible constructs in a system which attempts to reconstruct the genealogical history of monophyletic groups. We must then ask: If we are seeking to discover the order in nature, is this the appropriate methodology?

This pattern/process dichotomy in systematics is reflective of a higher-level structure/function controversy (see Eldredge and Cracraft, 1981). The question that arises is, can an understanding of a particular process be attained without prior examination of the parts (patterns) involved? Churchland (1982) thought not; though his discussion centers on the study of cognition, he finds an isomorphism with natural science and in both, function and process are to be studied as emergent properties with an understanding of them contingent upon a priori structural analysis. Churchland (1982) discussed the failings of a functionalist approach which he labels "top-down". He considered such an approach to be faulty for two reasons. First of all, it aims at analyzing the common attributes (functions) of a group of entities without reference to the factors which produced them. Secondly, it may focus our explanatory efforts on perceived groupings which may in fact be unrelated to the properties (structures, and by extension, genealogy) of their members.

"In the event, and as in our own history, such inquiry

(bottom-up) deepens, and changes, our initial conception of what it is we should be trying to simulate. But if such inquiry is denied any central significance, and if our primitive initial conceptions are explicitly given the a priori status of a stipulative functional specification of the domain of phenomena at issue, then we threaten to make a prison of our own ignorance." (Churchland, 1982, italics his).

Within a functionalist paradigm, systematic information cannot be used for critical tests of competing hypotheses of process, since these patterns already reflect the process-level bias of the systematist. Cladistic analysis, on the other hand, does not assume any particular process of change, only that change (descent with modification) occurs and that characters are passed on, modified or not (Wiley, 1981 p. 78). Characters are used to delimit natural groups only at the level at which they are apomorphic. Notions of functional efficiency (adaptiveness) are never used to justify the natural status of a particular group.

Another existing method in use in systematics today has come to be known as phenetics (Sneath and Sokal, 1973). Ironically, since it does not pretend (usually) to estimate phylogeny, this amalgam of numerical techniques has fallen into the same trap (grouping by overall similarity) as has evolutionary taxonomy, which does claim to reconstruct phylogeny. Since phenetic techniques arose from pre-existing statistical methods never intended for use in biological

systematics, it is hardly surprising that they fail to separate the derived from the generalized components in their measures of overall similarity. If the derived component is not separated, the genealogy of life will escape largely unnoticed (Farris 1977). Only if there is no homoplasy and homogeneous rates of change during any given time period will phenetic analysis yield the same classification as a cladistic analysis. Cladistic analysis on the other hand, is a powerful tool for estimating phylogeny even in the presence of homoplasy and differential rates of change.

The Wagner program in the PHYSYS package of Farris and Mickevich (1983) was used to analyze the data matrix obtained by Hennigian character analysis. It is entirely phylogenetic in nature and is described in detail in Farris (1970) and Farris, Kluge and Eckardt (1970). In any event, the results of a Wagner analysis and hand computation are invariably the same. The program was used in this study in two instances: to check the cladogram derived by hand and to re-analyze the re-coded larval data of Washington (1982). These two results were then used to generate a consensus tree (sensu Adams, 1972) in an analysis of taxonomic congruence.

Comparison of Classifications

Adults

A phylogenetic tree was extracted from Bolin's (1947) analysis of the Cottidae. Two measures were employed to assess the tree's validity as an hypothesis of phylogeny. Firstly, the character data from this study were mapped onto Bolin's (1947) tree and the number of steps needed to account for the data counted. Secondly, since it is not possible to directly compare a classification with a data matrix from which it was not constructed, the data matrix from this study was converted to a Manhattan distance matrix (where the the Manhattan distance between two taxa is the number of character state differences between taxa divided by the number of characters). Both my Wagner tree and Bolin's tree were assessed for goodness of fit by calculating the cophenetic correlation coefficient (R). Since Bolin did not include Ruscarius meanyi in his analysis this species was deleted for the purposes of comparison from the present analysis.

Larvae

Before a congruence study could be attempted it was necessary to ensure that the best tree for the larval data had

been calculated. Satisfying this desideratum was initially difficult since Washington (1982) published no data matrix and one had to be reconstructed from the body of the text. A Wagner analysis was then performed on the reconstructed data matrix and the resulting tree compared with two trees derived from Washington's (1982) study: the dichotomous cladogram which was presented and the implied polytomous tree which resulted from collapsing all of the unsupported branches to the node below. These trees were then compared in the same way as the adult trees (i.e. by counting the number of steps and by fit to the Manhattan distance matrix).

Taxonomic Congruence

If there is truly only one genealogy of life, then congruence will necessarily be a consequence of any method which sets out logically to discover that history, though different data sources may allow reconstruction of that history to greater or lesser degrees.

Taxonomic congruence, as defined by Mickevich (1978), provides a measure of the degree to which the "classifications of the organisms remain stable as various lines of evidence are considered". This stability is a consequence of classificatory method and is often cited as being the sole property of one or another competing algorithm (Farris, 1971, 1982; Fink 1979, Mickevich 1978, 1980). The importance of a stable classification lies in hypothesis testing: new sources of information should never be interpreted as refuting previous

hypotheses of relationship unless the new information is actually contradictory (Farris 1971; Mickevich 1978, 1980). These different sources may be of the same type of data from different life stages, such as larvae and adults, or from different types of characters, such as behavior and morphology.

Taxonomic stability is also a requisite property of methods claiming to provide the best general reference system for comparative evolutionary biology (Mickevich, 1978), one that represents all characters as well as possible (Fink, 1979; Mickevich, 1980).

"Without congruence tests there is no way of determining whether classification represents a repeatable, natural order, or instead portrays only the idiosyncracies of one suite of observations" (Mickevich 1980).

There have been a few such tests of congruence. To date, these have shown that phylogenetic systematics provides the most stable method for finding maximum congruence (Andersen, 1979; Baird and Eckhardt, 1972; Baverstock et al., 1979; Hood and Smith, 1982; Jensen and Barbour, 1981; Mickevich, 1978, 1980; Mickevich and Farris, 1981; Mickevich and Johnson, 1976; Miyamoto, 1981; Munding, 1979; Schuh and Farris, 1981; Shuh and Polhemus, 1980). This study attempts a congruence analysis using the larval data of Washington (1982) and the present analysis of adults.

THE GENUS ARTEDIUS GIRARD 1856Taxonomic Revision

Artedius Girard, 1856, p. 134.

(genotype by subsequent designation of Jordan and
Evermann 1896 Scorpaenichthys lateralis Girard)

Astrolytes Jordan and Starks, 1895

Axyrias Starks, 1896

Pterygiocottus Bean and Weed, 1920

Allartedius Hubbs, 1926

Parartedius Hubbs, 1926

Parastrolytes Hubbs, 1926

Artificial key to Artedius

1a. Scales present on the occiput..... 2.

2a. Preorbital cirrus present.....

Artedius harringtoni.

2b. No preorbital cirrus..... 3.

3a. Scales extend under anterior orbit.....

Artedius fenestralis.

3b. No scales under anterior orbit.....

Artedius notospilotus.

1b. No scales on the occiput..... 4.

4a. Cirri present above upper lip.....

Artedius corallinus.

4b. No cirri above upper lip.....

Artedius lateralis.

Diagnosis of Artedius

Recall that Bolin characterized Artedius (the only such attempt at diagnosis on record) as follows: "comparatively large head, normal structure of the pelvic fins and by the unadvanced anus." (1947, p. 161) Even slight familiarity with Cottids equips one to fit literally dozens of genera into the above description. In this light, the following is a list of diagnostic characters apomorphic for Artedius sensu stricto alone.

3. Scale ridge curving to become parallel with basal plate.
4. Generally darker background pigmentation of lateral body surface interrupted by circular areas of lighter pigmentation (same as ventral body surface, not white spots of Orthonopias). These lighter circles larger closer to ventral edge of dark areas. Largest, at margin, incomplete, producing a scalloped area above anal fin. Margins of each circle of light pigmentation crisp and well-defined.
12. In preserved specimens, a pattern of circular blotches of light background pigmentation interrupting darker pigmentation of ventral surface of head, extending backwards onto branchiostegal membrane.
27. Postcleithra absent.
35. Scale ridge a small semicircle.
45. Triangular flange at posterior edge of pterotic long, extending at least to posterior edge of cranium.

Artedius corallinus

Artedius corallinus (Hubbs 1926) (Fig. 1)

Range: Orcas Island (Washington) to Baja California.

Habitat: Rocky intertidal areas to 70 ft.

Synonymy

Allartedius corallinus Hubbs, 1926, p. 8; Point Lobos, Monterey County, California.

Artedius corallinus Bolin, 1937, p. 63 (description, first Baja record); Bolin, 1944, p. 53, fig. 20 (in key, description, distribution, relationships); Miller and Lea, 1972, p. 126, fig. p. 126 (in key, also distribution); Fitch and Lavenberg, 1975, p. 128 (name only); Howe and Richardson, 1978, p. 12 (in key, plus diagnosis, synonymy, meristic variation); Hubbs, Follett and Dempster, 1979, p. 18 (name only-California checklist); Eschmeyer, Herald and Hamman, 1983, p. 161, pl. 18.

Diagnosis

20. Cardiform teeth on dentaries, premaxillae, palatines and vomer.

26. Two to sixteen simple paddle-shaped flat cirri just above upper lip along its length. These located anywhere from end of maxilla forward, not distributed evenly on each side of head. Usually two small cirri on either side of premaxillary symphysis.

22. 43-46 rows of scales along body, extending from origin of first dorsal fin to base of ultimate or penultimate dorsal soft ray.

Specimens Examined

UMMZ 14168 1 (holotype) Monterey, Pt. Lobos; CAS 19453 1 Mexico:Baja; CAS uncat. 1 CA:Monterey; CAS W51-74 1 CA:Palos Verdes; CAS 28838 1 CA:Mendocino; CAS uncat. 1 Mexico:Baja; CAS 39853 1 CA:Monterey; CAS Acc.#1972:23 1 CA:Monterey; CAS 48958 2 CA:Orange Co.; SU 29536 1 CA:Monterey; SU 48970 7 CA:Orange County; SU 35365 1 CA:Monterey; SU 40881 1 CA:Pt. Lobos; LACM W53-395 1 Mexico:Coronado Island; LACM 1989 2 Mexico:San Martin Island; LACM W70-16 48 CA:Monterey; LACM W65-26 13 CA:Ventura Co.; LACM 9421-6 9 Mexico:San Nicolas Island; LACM 31301-1 34 CA:Diablo Cove; LACM W67-152 2 Mexico:Punta Banda; LACM 31937-8 1 CA:Humboldt Co.

Artedius fenestralis

Artedius fenestralis (Jordan and Gilbert 1882) (Fig. 2)

Range: Aleutian Islands to southern California.

Habitat: Intertidal to 180 feet.

Synonymy

Artedius notospilotus Jordan and Jouy, 1882, p. 6 (No. 27416); Bean, 1882a, p. 250; 1882b, p. 471 (not of Girard).

Icelus notospilotus Jordan and Gilbert, 1882b, p. 690.
(the "northern variety", not of Girard).

Icelus fenestralis Jordan and Gilbert, 1882b, p. 973.
(no locality given)

Artedius fenestralis Jordan and Gilbert, 1883, p. 577
(Commencement Bay, Washington); Jordan, 1887, p. 898 (name only); Bolin, 1944, p. 48, fig.18 (description, distribution and relationships); Wilimovsky, 1954, (name only - Alaska checklist); McAllister, 1960, p. 41 (name only--from Clemens and Wilby 1949); Clemens and Wilby, 1961, p. 298, fig. 186 (life history, distribution); MacPhee and Clemens, 1962, p. 33 (depth distribution); Wilimovsky, 1963, p. 182 (name only - Alaska checklist); Delacy, Miller, and Borton, 1972, p. 15

(name only); Miller and Lea, 1972, p. 126. Fig. p. 127 (in key and distribution); Quast and Hall, 1972, p. 20 (name only - Alaska checklist); Blackburn, 1973, (larvae: Cottid 4); Hart, 1973, p. 478 (life history, distribution); Fitch and Lavenberg, 1975, p. 128 (name only); Peden and Wilson, 1976, p. 235 (distribution- British Columbia); Richardson and Pearcy 1977, (larvae: Artedius sp. 2); Howe and Richardson, 1978, p. 13 (in key, plus diagnosis, synonymy, and meristic variation); Hubbs, Follett and Dempster, 1979, p. 19 (name only - California checklist); Pearcy and Myers, 1979, p. 212 (larvae - Yaquina Bay, Oregon); Richardson and Washington, 1980, (larvae: Artedius sp. 2); Washington, 1982, (larvae); Eschmeyer, Herald and Hamman, 1983, p. 162, pl. 18.

Astrolytes fenestralis Jordan and Starks, 1895, p. 807 (Puget Sound); Jordan and Evermann, 1898a, p. 1899 (in key, and distribution); Jordan and Gilbert 1899, p. 456 (name only); Gilbert and Thompson, 1905, p. 977 (description, synonymy); Evermannn and Goldsborough, 1907, p. 298 (distribution - Alaska); Starks, 1911, p. 188 (description, relationships); Gilbert and Burke, 1912, p. 36; Kincaid 1919, p. 30 (in checklist); Hubbs 1926, p. 1.

Artedius asperulus Starks, 1896, p. 553, (vicinity of Port Ludlow, Washington); Jordan and Evermann, 1898, p. 1903

Astrolytes notospilotus Jordan and Evermann, 1900, fig. 689a. (not of Girard)

Diagnosis

16. Three to ten simple short cirri in a line on top of each of transverse head tubercles.
17. No cirri located along suborbital stay.
28. A single row of scales extending forward to a point under anterior margin of orbit.
30. Body scales continuing onto the dorsal surface of the caudal peduncle, covering area extending from end of second dorsal base to origin of caudal fin.

Specimens Examined

USNM 27206 1 (Holotype) WA:Puget Sound; BC 63-252 2 Alaska; BC 63-245 3 Alaska; BC 53-74 12 Burrard Inlet; BC 63-154 4 Alaska; BC 62-989 5 Alaska; BC 62-555 4 Alaska; BC 60-226 3 BC:Vancouver Id.; BC 62-291 2 BC:Gardner Canal; BC 62-589 7 Alaska; BC 61-501 1 Alaska:Lynn Canal; BC 53-232a 1 BC:Joassa Channel; BC 53-232b 1 BC:Joassa Channel; BC 59-484 2 Alaska:Zachar Bay; BC 53-210 2 BC:Gale Passage; BC 61-497 3 Alaska:Auke Bay; BC 62-574 2 Alaska:Pt. Armstrong; BC 61-495 2 Alaska:Auke Bay; BC 54-447 6 BC:Saturna Id.; BC 53-86 5 BC:English Bay; BC 55-359 2 WA:San Juan Id.; BC 62-881 6 BC:Sooke; BC 62-637 7 BC:Howe Sd.; BC 62-731 2 BC:Saxe Pt.; BC 53-156 3 BC:Echo Bay; CAS 17765 6 CA:Sonoma, Bodega Bay; SU 16676 15 CA:Del Norte Co.; CAS 40354 7

Oregon; CAS 16662 10 CA:Del Norte Co.; CAS 40403 3 OR:Cape Perpetua; SU 40882 1 CA:Humboldt Bay; LACM 31700-4 5 CA:Diablo Cove; LACM 4339 1 WA:Skagit Co.; LACM 4391 1 WA:Skagit Co.; UW 17208 4 WA:San Juan Island; UW 5450 15 WA:Edmonds; UW 980 5 WA:West Seattle.

Artedius harringtoni

Artedius harringtoni (Starks 1896) (Fig. 3)

Range: Kodiak Island to southern California

Habitat: Intertidal to 70 feet, usually in rocky areas, especially abundant in kelp beds.

Synonymy

Axyrias harringtoni Starks, 1896, p. 554, pl. 74 (vicinity of Port Ludlow, Washington); Jordan and Evermann 1898a, pl. 904 (in key, and distribution); Kincaid, 1919, p. 30 (in checklist); Schultz and DeLacy, 1936, p. 78 (annotated checklist).

Axyrias harringtonii Bean and Weed, 1920, p. 72

(except mature males).

Pterygiocottus macouni Bean and Weed, 1920, p. 73, pl. 3 (Ucluelet, British Columbia); Jordan, 1923, p. 212 (name only).

Artedius harringtoni Bolin, 1944, p. 45, fig. 17 (description, distribution); McAllister, 1960, p. 41 (name only--from Clemens and Wilby 1949); Clemens and Wilby, 1961, p. 296, fig. 185 (distribution, life history); MacPhee and Clemens, 1962, p. 33 (depth distribution - Puget Sound); DeLacy, Miller and Borton, 1972, p. 15 (name only); Miller and Lea, 1972, p. 128, fig. p. 128 (in key, and distribution); Quast and Hall, 1972, p. 20 (name only - Alaska checklist); Blackburn, 1973, (larvae: Cottid 6); Hart, 1973, p. 473 (life history, distribution); Fitch and Lavenberg, 1975, p. 128 (name only); Peden and Wilson, 1976 p. 235 (distribution- British Columbia); Richardson, 1977, (larvae: Artedius sp.1); Richardson and Percy, 1977, (larvae: Artedius sp. 1); Howe and Richardson, 1978, p. 14 (in key, plus diagnosis, synonymy, and meristic variation); Hubbs, Follett, and Dempster, 1979, p. 19 (name only - California checklist); Percy and Myers, 1979, p. 212 (larvae - Yaquina Bay Oregon); Richardson, Laroche, and Richardson, 1980, (larval distribution - Oregon Coast); Richardson and Washington, 1980, (larvae); Washington, 1982, (larvae); Eschmeyer, Herald and Hamman, 1983, p. 162, pl. 18.

Diagnosis

- 20. In adult males, teeth on vomer and palatines cardiform; those on dentaries and premaxillae irregularly canine, with numerous distinctively longer canine teeth on both upper and lower jaws.
- 21. Seven branchiostegal rays, one additional on ceratohyal.
- 22. 43 to 46 scale rows above lateral line.
- 23. Incised membrane of anal fin convex in males, concave in females.
- 24. In males, anal fin covered with an hexagonal latticework of light pigmentation on a darker background.
- 25. Penis present, in form of small cone.
- 30. Dorsal body scales continuing onto dorsal surface of caudal peduncle.
- 31. One very large cirrus anterior to orbit, plumose in mature males.
- 32. No cirri in the region between the pectoral fin base and the lateral line.
- 34. Seven to twelve simple cirri along preopercular margin, not confined to preopercular spines.

Specimens Examined

SU 5047 1 (Holotype) WA:Port Ludlow; BC 63-936 1 BC:Jervis

Inlet; BC 65-43 16 AK:Kodiak Island; BC 61-301 3 BC:Bute Inlet;
 BC 62-637 6 BC:Howe Sound; BC 65-43 x AK:Kodiak Id.; CAS 29521 5
 CA:Mendocino; CAS 29488 8 CA:Mendocino; CAS 25889 5 CA:Pacific
 Grove; LACM 31937-8 1 CA:Humboldt Co., Trinidad; LACM 31938-12 8
 CA:Del Norte Co.; LACM 1679 12 CA:San Luis Obispo; LACM 7909 20
 CA:San Luis Obispo; UW 18020 ser. WA:San Juan Island; UW 3020 4
 WA:Cape Johnson; UW 17208 4 WA; UW 18020 6 WA:San Juan Island;
 UW 14303 1 WA:San Juan Island.

Artedius lateralis

Artedius lateralis (Girard 1854) (Fig. 4)

Range: Kodiak Island to Baja California.

Habitat: Intertidal to 45 feet. Especially abundant in tidepools.

Synonymy

Scorpaenichthys lateralis Girard, 1854 p. 145
 (Monterey and San Luis Obispo, California).

Artedius lateralis Girard, 1856, p. 134; 1857, p. 14,

(not plate 22a), figs. 5, 6; Gunther, 1860, p. 174 (diagnosis, synonymy); Jordan and Jouy, 1881, p. 6 (name only - in checklist); Jordan, 1887, p. 898 (name only) ; Eigenmann and Eigenmann, 1892, p. 355 (distribution); Jordan and Starks, 1895, p. 807; Jordan and Evermann, 1896, p. 437 (name only, in checklist); Jordan and Evermann, 1898, p. 1902 (in key, and distribution); Greeley, 1899, p. 19 (color description, habitat); Osgood, 1910, p. 20 (name only); Starks, 1911, p. 190 (description, relationships); Halkett, 1913, p. 99 (name only, in checklist); Kincaid, 1919, p. 30 (name only, in checklist); Bean and Weed, 1920, p. 72 (not 24765); Hubbs 1926, p. 7; Budd, 1940, figs. 58-74 (eggs, larval development); Hubbs and Schultz, 1941, p. 4; Bolin, 1944, p. 55, fig. 21 (in key, and distribution); McAllister, 1960, p. 41 (name only - from Clemens and Wilby 1949); Clemens and Wilby, 1961, p. 299, fig. 187; MacPhee and Clemens, 1962, p. 33 (depth distribution); Hubbard and Reeder, 1965, p. 507 (distribution, synonymy, first verified Alaskan record); Quast, 1968, p. 485 (description, distribution); DeLacy, Miller and Borton, 1972, p. 15 (name only, in checklist); Miller and Lea, 1972, p. 126, fig. p. 126 (in key, and distribution); Quast and Hall, 1972, p. 20 (name only - Alaska checklist); Hart, 1973, p. 481 (in key, also life history and distribution); Fitch and Lavenberg, 1975 p. 128 (name only); Marliave, 1975 (larvae); Peden and Wilson, 1976, p. 235 (distribution- British Columbia); Howe and Richardson, 1978, p. 14 (in key, plus diagnosis, synonymy and meristic variation); Hubbs, Follett, and Dempster, 1979, p. 19

(name only, in California checklist); Washington, 1982, (larvae); Eschmeyer, Herald and Hamman, 1983, p. 162, pl. 18.

Icelinus lateralis Jordan and Gilbert, 1883, p. 689.

Parartedius hankinsoni Hubbs, 1926, p. 4 (Point Loma, California).

Artedius delacyi Hubbs and Schultz, 1941, p.4.; Bolin, 1947, p. 162; Wilimovsky, 1954, p. 285 (name only - Alaska checklist).

Artedius hankinsoni Bolin, 1944, p. 57, fig. 22.

Comments:

Artedius hankinsoni is here formally synonymized with Artedius lateralis. In Hubbs' (1926) characterization of A. hankinsoni, two features were cited as being diagnostic: the low scale count and the multifid upper preopercular spine. Bolin (1944) adds no new characters, but includes the species in Artedius, which Hubbs had not.

In Artedius, there is considerable variation in the upper preopercular spine within each species, indeed even between the left and right spines of one individual. In the putative A. hankinsoni examined in this study, none save the type specimen displayed anything worthy of being called "multifid". The remainder are indistinguishable from the normal range of variation found in Artedius lateralis.

Apart from the spine, only the low scale count on the body remains. Examination of larger series of lateralis in this study yielded a few additional "A. hankinsoni" types, in

addition to numerous specimens intermediate between A. *lateralis* and A. *hankinsoni*. All of these specimens, A. *hankinsoni* included, are indistinguishable from A. *lateralis* in every other respect. The existence of these intermediates, coupled with the relative scarcity of A. *hankinsoni*, leads to the conclusion that A. *hankinsoni* represent A. *lateralis* in which the scale development is incomplete. The type specimen seems to have been unique in possessing a multifid preopercular spine, a feature not shared by other putative A. *hankinsoni*.

Diagnosis

22. Twenty-four to twenty-six rows of scales along dorsal body surface, extending from second or third dorsal spine to penultimate or antepenultimate dorsal soft ray.

29. No scales on body behind pectoral fin base.

Specimens Examined

UMMZ 126491 1 AK:delacyi paratype; UMMZ 126490 1 AK:delacyi holotype; USNM 117494 1 AK:delacyi *delacyi* paratype; UMMZ 55001 1 hankinsoni holotype; BC 53-295 16 CA:Morro Bay; BC 62-589 4 BC:Sooke; BC 62-731 2 BC:Saxe Pt.; BC 53-38 1 BC:Nanaimo; BC 53-

232 1 BC:Joassa Channel; BC 53-40 2 WA:Cape Johnson; BC 53-296
 32 CA:San Luis Obispo; BC 53-88 6 BC:Nanaimo; BC 54-452 2
 BC:Saturna Island; BC 59-286 1 BC:Burrard Inlet; BC 62-42 1
 BC:Saturna Island; BC 54-448 2 BC:Saturna Island; BC 54-96 1
 BC:Stanley Park; BC 53-88 8 BC:Nanaimo; BC 60-238 4 Washington;
 CAS 50393 17 CA:San Nicholas Id.; CAS 27316 16 CA:Duxbury Reef;
 CAS 50391 13 CA:Carmel; CAS 50392 12 CA:Santa Barbara; CAS 50388
 4 OR:Cape Arago; SU 68852 4 CA:Duxbury Reef; LACM 23612 1
 Mexico:Baja; LACM W71-9 3 CA:Monterey; LACM 21132 9 OR:Yaquina
 Light; LACM 8310 1 CA:Palos Verdes (hankinsoni); LACM 1679 14
 CA:San Luis Obispo; LACM 33709-3 6 CA:Arena Cove; LACM 21133 2
 Mexico:Baja, Santo Tomas; LACM 876 1 CA:Pacific Grove; LACM
 31860-2 23 CA:San Luis Obispo; UW 3019 16 WA:Cape Johnson; UW
 3020 4 WA:Cape Johnson; UW 2312 4 Cleared and stained; UW 15741
 ser. AK:Kodiak Island (delacyi); UW 17412 5 WA:San Juan Island.

Artedius notospilotus

Artedius notospilotus Girard 1856 (Fig. 5)

Range: Puget Sound (Washington) to Baja California.

Habitat: Intertidal to 170 feet.

Synonymy

Calcyepidotus lateralis Ayres, 1855, p. 77 (not of Girard).

Hemilepidotus nebulosus Girard, 1856, p. 134. (refers to Ayres previously unpublished name).

Artedius notospilotus Girard, 1856, p. 134 (Tomales Bay, California); 1857, p. 535, pl. 24, figs. 5,6; 1858, p.71; Gill 1862, p. 279 (name only); Jordan and Gilbert, 1881, p. 454 (in checklist, and distribution); Jordan and Jouy, 1881, p. 6 (name only, in checklist); Jordan, 1887, p. 898 (in part); Eigenmann and Eigenmann, 1892, p. 355 (distribution); Bolin, 1944, p. 50 (in key, description, distribution, relationships); DeLacy, Miller and Borton, 1972, p. 15 (in checklist : Puget Sound); Miller and Lea, 1972, p. 127, fig. p. 126 (in key, and distribution); Fitch and Lavenberg, 1975, p. 128 (name only); Howe and Richardson, 1978, p. 15 (in key, plus diagnosis, synonymy, meristic variation); Hubbs, Follett, and Dempster, 1979, p. 19 (name only, in California checklist); Eschmeyer, Herald and Hamman, 1983, p. 163, pl. 18.

Artedius lateralis Girard, 1858, p. 71, pl. 22b, figs. 5, 6 (specimen no. 366, collected by Ayres, figure based on this specimen only); Bean and Weed, 1920, p. 72 (27645 only).

Icelus notospilotus Jordan and Gilbert, 1882b, p. 690 (in part).

Astrolytes notospilotus Jordan and Evermann, 1896, p. 436 (in key, and distribution); 1898a, p. 1899, 1900, fig. 689 (not fig. 689a); Jordan, 1905, p. 442, fig. 382 (mature male, Puget Sound); Starks and Morris, 1907, p. 219 (name only, record of Jordan and Gilbert, 1881, p. 61); Jordan, 1925, p. 653, fig. 551 (mature male, Puget Sound, same specimen figured in Jordan 1905).

Parastrolytes notospilotus Hubbs, 1926, p. 2.

Diagnosis

10. Additional short, rounded spinelets encrusting two or three main upper preopercular spines.

18. In adults, lower preopercular spines serrated at posterior edge, extended dorso-ventrally along preopercular margin.

19. Six to twelve irregularly spaced pores in groove bounded anteriorly by ethmoid hump, posteriorly by orbital margin, not divided evenly by midline.

39. In adults, head tubercles raised dorsally, adorned with irregular groups of knoblets.

40. Serrations present on posterior posttemporal and upper border of supracleithrum.

Specimens Examined

USNM 329 1 (Holotype) CA:Tomales Bay; USNM 27206 1 (Originally syntype of Artedius fenestralis); USNM 26865 6 CA:Santa Barbara; CAS 27317 17 CA:Duxbury Reef; CAS 50390 1 CA:San Francisco; CAS 50389 2 Mexico:Baja; CAS W53-398 1 CA:Los Angeles; CAS Acc.# 1958-VI:9 1 San Francisco; CAS Acc.# 1972-I:24 1 No Data; CAS 13469 1 CA:San Francisco; SIO 55-34 1 CA:San Luis Obispo; SIO H52-164 1 Mexico:Punta Roca; SIO 55-105 8 CA:San Luis Obispo; SIO H52-168 4 Mexico:Playa Maria; SIO 74-122 1 CA:Pt. Conception; SIO 63-1052 1 Mexico:Bahia San Quintin; SIO 63-1054 2 Mexico:Bahia San Quintin; SIO 63-1056 2 Mexico:Bahia San Quintin; SIO 73-101 12 CA:El Segundo.

THE GENUS RUSCARIUS JORDAN AND STARKS 1895Taxonomic Revision

Ruscarius Jordan and Starks, 1895. Artedius Bolin (in part), 1944.

Artificial key to Ruscarius

1a. Scales on eye.....

Ruscarius meanyi.

1b. No scales on eye.....

Ruscarius creaseri.

Based on the phylogenetic analysis, meanyi and creaseri, both formerly included in Artedius, are shown to comprise a separate monophyletic lineage, as they share none of the characters which are hypothesized to be apomorphic for Artedius. Conversely, the character states uniting meanyi and creaseri are not shared with Artedius sensu strictu. Since meanyi was originally described by Jordan and Starks in 1895 in the genus Ruscarius, it is here proposed that this genus be resurrected to include Ruscarius meanyi and Ruscarius creaseri. These two species have never been diagnosed as a monophyletic unit. Such a diagnosis is here provided, in addition to diagnoses for each of the species.

Ruscarius Jordan and Starks, 1895.

Ruscarius diagnosis

3. Scale ridge almost perpendicular to basal plate, ctenii curving very little.
4. Lateral body surface covered with light stippling of darker pigmentation, interrupted by well-defined areas without any darker pigmentation.
5. A small patch of ten to twenty scales located just caudad to dorsal edge of axilla.
7. Upper preopercular spine narrow and extended caudally. This spine bifid, forking only in posterior quarter of its length.
11. Adult males with dusky black pigmentation covering lower jaw, throat, ventral body surface and all fins except caudal.
6. Scattered scales on snout above upper lip, on tip of ethmoid hump and above ascending processes of premaxillae.
28. Single row of scales extending forward under anterior orbit.
31. One to four cirri located at upper anterior orbital margin.

Ruscarius creaseri

Ruscarius creaseri (Hubbs 1926) (Fig. 6)

Range: Carmel Bay (California) to central Baja California.

Habitat: Intertidal to 90 feet.

Synonymy

Ruscariops creaseri Hubbs, 1926, p. 12. (Bird Rock, San Diego County. Paratypes from White Point, Los Angeles County, and Point Lobos, Monterey County, California).

Artedius creaseri Bolin, 1944, p. 43, fig. 16 (description, relationships); Miller and Lea, 1972, p. 126, fig. p. 126, (in key, and distribution); Fitch and Lavenberg, 1975, p. 128 (name only); Howe and Richardson, 1978, p. 13 (in key, plus diagnosis, synonymy and meristic variation); Hubbs, Follett and Dempster, 1979, p. 18 (name only - California checklist); Washington, 1982, (larvae); Eschmeyer, Herald and Hamman, 1983, p. 162, pl. 18.

Diagnosis

9. Three to ten simple cirri in a cluster at dorsalmost posterior edge of opercle, just anterad to fleshy flap which makes up its posterior margin.

33. One to ten simple cirri in cluster anterad to uppermost preopercular spine.

32. One to three simple cirri in cluster midway between top of pectoral base and lateral line.

Specimens Examined

UMMZ 141866 1 Bird Rock, San Diego (holotype); BC 63-979 3 Mexico:Baja; CAS 19800 2 CA:Bird Rock, San Diego; CAS 19671 1 Mexico:Baja; CAS 50119 1 Mexico:Baja; CAS 19516 2 CA:San Diego; CAS 19797 2 CA:San Diego; CAS 25382 1 CA:Santa Catalina Island; CAS 19626 3 Mexico:Baja; LACM 6587-5 39 CA:Palos Verdes; LACM 4917 3 CA:San Luis Obispo; LACM 32082-1 3 Mexico:Baja; LACM 32045-3 4 Mexico:Cedros Island; LACM 32053-11 3 Mexico:Baja; LACM 32041-9 1 Mexico:Cedros Island.

Ruscarius meanyi

Ruscarius meanyi Jordan and Starks 1895 (Fig. 7)

Range: Alaska to Arena Cove (California).

Habitat: Intertidal to 269 feet.

Synonymy

Ruscarius meanyi Jordan and Starks, 1895, p.805, pl. 80 (Port Orchard Puget Sound, Washington); Jordan and Evermann, 1898, p. 1908 (in key, and distribution); Halkett, 1913, p.99 (name only, in checklist); Kincaid, 1919, p. 29, fig. 66 (checklist - Puget Sound); Hubbs, 1928 (name only, in checklist); Schultz and De Lacy, 1936, p.127 (in checklist, and distribution); Schultz, 1936, p. 177 (key).

Artedius meanyi Rosenblatt and Wilkie, 1963 (redescription, distribution: first British Columbia record); Peden, 1972, p. 168 (distribution - British Columbia); Quast and Hall, 1972, p. 20 (name only - Alaska checklist); Blackburn, 1973, (larvae: Cottid 3); Hart, 1973, p. 483 (figure, life history, distribution); Lea, 1974 (first California record); Fitch and Lavenberg, 1975, p. 128 (name only); Peden and Wilson, 1976, p. 235, (first Alaskan record);

Moulton, 1977 (Puget Sound: habitat, depth distribution); Richardson, 1977, (larvae: Icelus sp. 1); Richardson and Pearcy, 1977, (larvae: Icelus sp. 1); Howe and Richardson, 1978, p.14 (in key, plus diagnosis, synonymy, meristic variation); Hubbs, Follett, and Dempster, 1979, p. 19 (name only, in California checklist); Richardson and Washington, 1980, (larvae: Icelus spp.); Washington, 1982, (larvae); Eschmeyer, Herald and Hamman, 1983, p. 163, pl. 18.

Diagnosis

1. In adult males, urogenital opening abuts origin of anal fin.
8. One spine and two soft rays in pelvic fins.
37. Maximum adult size 50 mm.
38. In adult males, first three anal rays thickened and short.
44. No cirri on nasal spine.
47. Scales cover upper one-fifth of surface of eye, never covering pupil.

Specimens Examined

SU 3127 2 WA:Cotypes; CAS 37281 1 BC:Saenich Inlet; CAS 27695 2 CA:Mendocino; BC 62-495 1 BC:Sooke; LACM 38248-1 3 BC:Blind Bay; LACM 38247-1 3 BC:Raymond Island; NMC 77-0148 27 BC:Klaquack

Channel; NMC 68-0373 1 BC:Queen Charlotte Islands; SIO 63-599 2
BC:Howe Sound; SIO 73-227-55 1 CA:Arena Cove; UW 20721 1 WA:Shaw
Island; UW 20720 1 WA:Seattle; UW uncat. 2 cleared and stained.

PHYLOGENETIC ANALYSIS

List of Adult Characters

1. Position of anus
2. Shape of snout
3. Form of scale ridge
4. Body color pattern
5. Scales above axilla
6. Scales on snout
7. Shape of upper preopercular spine
8. Number pelvic rays
9. Cirri on opercle
10. Spinelets on main preopercular spine
11. Male color
12. Chin coloration
13. Mandibular pore pattern
14. Pores on lateral line scales
15. Form of head scales
16. Cirri on transverse head tubercles
17. Cirri on suborbital stay
18. Form of preopercular spine
19. Nasal pores
20. Form of teeth
21. Branchiostegal number
22. Number of scale rows above lateral line

23. Anal fin membrane
24. Anal fin pigmentation
25. Penis
26. Cirri on upper lip
27. Postcleithra
28. Scales under anterior of orbit
29. Scales behind axilla
30. Scales on caudal peduncle
31. Preorbital cirri
32. Cirri above axilla
33. Cirri anterad to upper preopercular spine
34. Cirri on preopercular margin
35. Scale ridge shape
36. Scale ridge placement
37. Adult size
38. Anal ray form (males)
39. Form of head tubercles
40. Serrations on posttemporal and supracleithrum
41. Size of circles on body
42. White throat pigmentation
43. White spots on body
44. Cirri on nasal spine
45. Pterotic flange
46. Ossification of opercle
47. Scales on eye

List of Larval Characters

1. Number of preopercular spines
2. Relative size of preopercular spines
3. Basal preopercular spines
4. Inner shelf preopercular spines
5. Skin bubble on nape
6. Dorsal gut diverticula
7. Parietal spines
8. Nape melanophores
9. Snout shape
10. Hindgut length
11. Number of pelvic rays

Adult Character Analysis

Character 1. Position of anus.

State 0: urogenital opening located slightly anterad to origin of anal fin base.

State 1: in adult males, urogenital opening abuts origin of anal fin.

An anterior anus is found in adults of Clinocottus, Triglops, Blepsias and Orthonopias. Ruscarius creaseri and

Artedius sensu stricto have the plesiomorphic condition (state 0). The condition in Ruscarius manyi (state 1) is not found in any of the outgroups and is therefore hypothesized to be autapomorphic for Ruscarius manyi.

Character 2. Snout shape.

State 0: snout long; distance from anterior edge of orbit to upper lip about equal to orbital width.

State 1: snout short and steep in profile; distance from anterior edge of orbit to upper lip about one-half width of orbit. (fig. 8)

Snout shape in the cottids is highly variable. A majority have a long, flat snout, but a very short snout is found in only a few genera, including Orthonopias, Gymnocanthus and Ocynectes (state 1). Artedius sensu strictu and Ruscarius have longer snouts (state 0).

Character 3. Form of scale ridge. (fig. 9)

State 0: scale ridge almost perpendicular to basal plate, with ctenii curving to an angle parallel with plate (fig. 9a).

State 1: scale ridge almost perpendicular to basal plate, ctenii curving very little (fig. 9b).

State 2: no scale ridge; ctenii originating directly from basal plate (fig. 9c).

State 3: scale ridge curving to become parallel with plate,

ctenii radiating from dorsal, ventral and caudal margins of ridge (fig. 9d).

State 4: scale ridge curving to become parallel with plate, ctenii radiating from caudal margin of ridge only. Antero-lateral edge of ridge without ctenii, forming a distinct shelf (fig. 9d).

State 5: no scale ridge, no ctenii.

The scales in cottids are not the usual teleostean cycloid or ctenoid bony ridge scale, rather they are bony structures consisting of a basal plate from which arise various projections. These projections (ctenii) may arise directly from the plate, or from an intervening ridge (spinous ridge). State 0 is found in Hemilepidotus hemilepidotus and Orthonopias, and is hypothesized to be plesiomorphic. The scale ridge in Orthonopias is not complete and decreases in height as it approaches the midline of the basal plate. As a result, the three or four ctenii which lie on or near the midline of the plate arise directly from the base, with no intervening ridge. State 1 is found in Ruscarius manyi and Ruscarius creaseri, and is hypothesized to be synapomorphic for Ruscarius. By comparison with the outgroups, state 3 is hypothesized to be synapomorphic for Artedius sensu stricto. State 4 is hypothesized to be synapomorphic for the subgenus Artedius, which includes Artedius harringtoni, Artedius lateralis, and Artedius corallinus. State 2 is found only in Chitonotus pugetensis.

Although this character serves to distinguish several

monophyletic lineages, it has a non-additive distribution at the higher level of analysis and is therefore of little value in determining inter-generic relationships, particularly with regards to the lineage including Ruscarius, Chitonotus, and Icelinus. There are nine equally-likely transformation series, none of which can be favored at present.

Character 4. Body color pattern. (Figs. 1-8)

State 0: in preserved specimens, the area bounded anteriorly by pectoral fin base, posteriorly by caudal fin, dorsally by rows of body scales, ventrally by a line dorsal to anal fin covered with uninterrupted darker pigment. This may be arranged in alternating stripes of relatively lighter and darker pigment (fig. 8).

State 1: lateral body surface covered with light stippling of darker pigmentation, interrupted by well-defined circular areas without any darker pigmentation (figs. 6 and 7).

State 2: generally darker background pigmentation of lateral body surface interrupted by circular areas lacking darker pigmentation (the latter the same as ventral body surface). Lighter circles become larger closer to ventral edge of dark pigmentation. The largest circles, at the ventral margin, are incomplete, producing a scalloped appearance above anal fin base. Margins of each circle crisp and well-defined (figs. 1-5).

The distinctive "Artedius" pattern of pigmentation (state

2) is found only in Artedius sensu strictu and not in any of the outgroups. It is therefore postulated to be synapomorphic for the genus Artedius. A similar type of coloration pattern occurs in the cottid genus Myoxocephalus, but on close examination this is seen to be a pattern of irregular yellow blotches on a darker background. These blotches continue to the anal fin base and do not extend above the lateral line: hence this is hypothesized to be a different state from that observed in Artedius. Irregular blotches of lighter pigment, similar to the Artedius circles, are also found in Clinocottus. However, these do not have the characteristically crisp outline of Artedius circles and they decrease in diameter as they continue down to the anal fin. In Oligocottus, the pattern is much the same as in Clinocottus: the margins of the spots are indistinct and they decrease in size ventrally. In Oligocottus, though, the middle portion of each spot is covered with darker black speckles.

In Chitonotus, Icelinus, and Ruscarius (state 1), the lateral body surface is covered with a stippling of black pigment, with widely-spaced melanophores. Below the lateral line, this stippling is broken up by areas without pigment. These areas are circular in Icelinus and Chitonotus, and form vertical bars in Ruscarius manyi and Ruscarius creaseri. The pattern varies within Icelinus, with Icelinus borealis, I. filamentosus and possibly I. burchami having roughly circular areas of light pigment, though they are more irregular than those in Artedius. In Icelinus cavifrons these seem to be roughly aligned in vertical bars, much as in Ruscarius.

This character has a disjoint distribution consisting of two transformation subseries: 0-1-2 and 3-4. Its main use in this hypothesis seems to lie in supporting the separate monophyly of Ruscarius and Artedius sensu strictu.

Character 5. Scales above axilla.

State 0: no scales located above axilla.

State 1: a small patch of ten to twenty scales located just caudad to dorsal edge of pectoral fin base, not arranged in rows.

This patch of scales (in Ruscarius creaseri and R. meanyi) is in a different location from the scale patch found in Hemilepidotus hemilepidotus, which is behind the fin and not above the axilla. The other pattern of scales behind the fin is one of parallel rows, not a patch (see character 39). This patch is not found in Artedius, Orthonopias, Icelinus, Stelgistrum, Ricuzenius or Chitonotus pugetensis, and is postulated to be synapomorphic for Ruscarius.

Character 6. Scales on snout.

State 0: no scales on snout.

State 1: scattered scales on snout above upper lip, at tip of ethmoid hump and above ascending processes of premaxillae.

Scales are found on the snout in Ruscarius meanyi and R. creaseri as well as two other genera (Chitonotus and

Ricuzenius). Farris optimization leads to a hypothesis of two independent origins for this feature: once in Ricuzenius and once in the lineage leading to Ruscarius and Chitonotus. These scales are not found in Artedius sensu strictu.

Character 7. Shape of upper preopercular spine.

State 0: upper (fourth) preopercular spine not extended caudally, having two to three prongs.

State 1: upper preopercular spine narrow and extended caudally. This spine bifid, forking only in posterior quarter of its length (figs. 6 and 7).

A narrow, caudally elongated preopercular spine is found in several cottid genera. A long, unbranched spine is typical of Porocottus and Myoxocephalus. Variations on the "antler-like" preopercular spine are found in Chitonotus, Gymnocanthus, Leptocottus, Enophrys, Icelinus and the Japanese genera Stlengis and Daruma. The number of times this "antler-like" spine has arisen in the family cannot be estimated until a phylogenetic hypothesis including all cottoid genera is generated. For the time being, then, only the state found in Ruscarius meanyi and Ruscarius creaseri (state 1) can be hypothesized to be a unique, derived trait. All of the species in Artedius sensu strictu have state 0.

Character 8. Number of pelvic rays.

State 0: one spine, three soft rays.

State 1: one spine, two soft rays.

There has been some contention as to whether Ruscarius meanyi actually has two or three pelvic rays, primarily caused by its small size and the difficulty of distinguishing individual rays without clearing and staining. Lea (1974) found only two rays in his specimens. Howe and Richardson (1981) re-examined Lea's (1974) specimens and found only one with two: the rest had three. Washington (1982) also re-examined Lea's specimens, this time clearing and staining. She found two rays in all of the fish she examined. I examined cleared and stained Ruscarius meanyi in this study and found them to have two rays, never three. Without clearing and staining, it is easy to mistake the branched end of the one thickened ray for two normal rays.

Two pelvic rays are also characteristic of the genera Icelinus and Stlengis. Washington (1982) suggested that Ruscarius meanyi be placed in a taxon with Icelinus based on this character. However, the state I,2 is hypothesized to have arisen independently in Ruscarius meanyi and Icelinus, since the present analysis indicates that Ruscarius creaseri (I,3) is the sister taxon to Ruscarius meanyi, and, further, that Chitonotus (also I,3) is the sister taxon to these two. An indication of the independent origin of this state comes from Washington (1982). Referring to Ruscarius meanyi, she stated: "cleared and stained specimens have I,2 pelvic fin rays. The outermost ray is greatly thickened and branched at the tip in all specimens

examined" (1982, p. 148). By contrast, she observed that, in Icelinus, "both fin rays are relatively short and fine" (p. 172, italics mine). These two observations suggest that the I,2 states in Ruscarius manyi and Icelinus are not structurally homologous. All of the species in Artedius sensu strictu have the state I,3 (state 0).

Character 9. Cirri on opercle.

State 0: one to three cirri clustered at dorsalmost posterior edge of opercle, just anterior to fleshy flap which makes up its posterior margin.

State 1: as in state 0, but three to ten cirri per cluster.

State 2: no cirri on opercle.

In Orthonopias, Clinocottus, Oligocottus, Icelinus, Ruscarius manyi and Artedius sensu stricto, there are one to three cirri on the opercle, which is hypothesized to be the plesiomorphic state. The possession of up to ten cirri here by Ruscarius creaseri (state 1) is hypothesized to be autapomorphic. If Chitonotus is hypothesized to have secondarily lost these cirri, this character has the additive transformation series 0-1-2.

Character 10. Spinelets on main preopercular spines.

State 0: absent.

State 1: additional short, rounded spinelets encrusting two or

three main upper preopercular spines (fig. 5).

These additional spinelets (state 1), found in adult Artedius notospilotus, are absent from the rest of the cottids examined (which all have state 0) and are therefore hypothesized to be autapomorphic.

Character 11. Male color.

State 0: in preserved specimens, ventral surface of male the same as female: branchiostegal membranes, ventral body, and fins light colored.

State 1: males with a dusky black pigmentation covering the lower jaw, branchiostegal membrane, and ventral body surface. In addition, all of the fins are dusky, with the first dorsal having a darker, almost black band along its dorsal margin.

In all of the outgroups and in Artedius, the body coloration is either virtually the same for males as it is for females, or at most only the ventral fins and throat are dusky (state 0). Therefore, the overall dusky coloration of males of Ruscarius meanyi and Ruscarius creaseri is hypothesized to be an apomorphic state (state 1).

Character 12. Chin coloration.

State 0: no pattern of circles on ventral surface of throat.

State 1: in preserved specimens, a pattern of large circular areas of lighter background pigmentation interrupting dark

stippling, sometimes extending onto anteriormost portion of branchiostegal membrane (fig. 10a,b).

State 2: in preserved specimens, a pattern of circular blotches of light background pigmentation interrupting darker pigmentation on ventral surface of head, extending caudally to branchiostegal membrane (fig. 10c).

State 3: as in state 2, but circles very small (fig. 10d).

The only outgroup with a distinctly pigmented throat is Orthonopias; however, its arrangement of white vermiculations on a dark background is not the same as the condition in Artedius sensu strictu, which consists of an absence of darker pigment, not the presence of white pigment superimposed on a uniformly dark background. Ricuzenius, Clinocottus, Oligocottus, Chitonotus, and Stelgistrum lack any throat pigmentation at all (state 0). Ruscarius meanyi and R. creaseri have scattered stippling on the throat. The presence of lighter circular areas of throat pigment is hypothesized to be synapomorphic for Artedius sensu stricto. In state 1, found in Artedius notospilotus and Artedius fenestralis, the pigment does not extend onto the branchiostegal membrane to any appreciable extent, while in states 2 and 3 it covers virtually all of the membrane. Artedius harringtoni has state 2, while the very small circles of lighter pigmentation (state 3) are found in A. corallinus and A. lateralis.

This character has a non-additive distribution within the genus Artedius, and is therefore of little value in elucidating the relationships therein. However, it serves to distinguish

two subgroups within Artedius; the subgenus Astrolytes, including Artedius fenestralis and Artedius notospilotus, and the lineage including Artedius corallinus and Artedius lateralis. Three transformation series are equally likely: 0-1-2-3; 0-1-3-2; and 0-1-2

character 13. Mandibular pore pattern.

State 0: beginning at posterior end of maxilla, three single pores on each side. Additionally, two (rarely one) pores on ventral midline, just caudad to lower lip (figs. 10c,d).

State 1: ten to twenty minute pores on each side, occurring singly or in clusters, plus four to ten pores clustered around ventral midline. One or two midline pores located caudally to anterior midline cluster (figs. 10a,b).

McAllister (1968) illustrated the pattern of mandibular pores in many cottid genera. Based on his study and examination here of Orthonopias, Ruscarius, Clinocottus and Oligocottus, which all share state 0, the pattern found in Artedius fenestralis and Artedius notospilotus (state 1) is postulated to be apomorphic.

Character 14. Pores on lateral line scales.

State 0: one pore located near posterior margin of each lateral line plate.

State 1: one to three extra pores located on ten to twenty-five of last thirty lateral line scales. Extra pores minute, easily distinguishable from main pore located at posterior margin of scale.

These extra pores are not found in Ruscarius, Orthonopias, Oligocottus, Clinocottus, Chitonotus, Icelinus or Stelgistrum. In all of these genera, there is only one pore per lateral line scale (state 0). Extra, minute pores (state 1) are therefore hypothesized to be apomorphic and are found only in Artedius fenestralis and Artedius notospilotus.

Character 15. Form of head scales.

State 0: scales on head not distinguishable in form from scales covering body.

State 1: scales on occiput deeply embedded, ctenii radiating in all directions directly from margin of basal scale plate. Ctenii much shorter and blunter than ctenii of body scales.

State 2: no scales on head.

In Artedius harringtoni, Ruscarius meanyi, R. creaseri and other genera such as Ricuzenius and Stelgistrum with scales extending onto the head, the scales on the occiput are not markedly different in form from the scales on the body (state 0). Therefore the embedded, stellate scales (state 1) on the heads of Artedius fenestralis and A. notospilotus are, by out-group comparison, apomorphic. Artedius corallinus and A. lateralis have no scales on the head. Some Gymnocanthus

species also have bony "scales" on the head, but these consist of conical points arising perpendicular to a basal plate, not arising at an angle from the margin of the plate, as in Artedius sensu strictu. This character has the additive transformation series 0-1-2.

Character 16. Cirri on transverse head tubercles.

State 0: one to three simple cirri just anterad to four bony tubercles on head, tubercles in transverse line posterior to orbital margins.

State 1: three to ten cirri located on each tubercle, in a line.

The plesiomorphic condition for tubercle cirri is one to three cirri on each tubercle. Artedius fenestralis is the only species with state 1. The remainder of Artedius sensu strictu and Ruscarius have state 0. Clinocottus embryum, C. analis, and C. globiceps also have a high number of cirri on these tubercles, but in these species they are not arranged in a linear fashion as in Artedius fenestralis and are in a closely-packed bunch. The presence of up to ten cirri (state 1) on each tubercle in Artedius fenestralis is interpreted to be autapomorphic.

Character 17. Cirri on suborbital stay.

State 0: one to two simple cirri on suborbital stay, midway between posterior end of preopercle and posterior end of orbit.

State 1: as in state 0, but one to two cirri at anterior end of suborbital stay at a point posterior to end of orbit, plus one to two simple cirri at posterior end of suborbital stay, at a point just anterad to uppermost preopercular spine.

State 2: no cirri on suborbital stay.

In Orthonopias there is one cirrus located midway along the suborbital stay (state 0), while in Clinocottus and Oligocottus there are none (state 2). Artedius fenestralis also has none, and this is here interpreted to be a secondary loss. Artedius lateralis and A. corallinus have, in addition, cirri at both the anterior and posterior ends of the bony stay (state 1). This situation is, by comparison with the outgroups, apomorphic. The two Ruscarius species both have state 0. This character has the additive transformation series 0-1-2.

Character 18. Form of preopercular spines.

State 0: in adults, rounded to sharp, always simple.

State 1: in adults, serrated at the posterior edge, extended dorso-ventrally along preopercular margin (fig. 7).

The form of the lower three preopercular spines varies greatly in cottid genera. However, the range of variation runs from rounded to sharp, never branched or elaborated in any way. The serrated form of the preopercular spines in Artedius notospilotus (state 1) is therefore postulated to be autapomorphic. Ruscarius and the remainder of Artedius sensu strictu have state 0.

Character 19. Nasal pores.

State 0: two to four evenly spaced pores located in groove bounded anteriorly by ethmoid hump and posteriorly by anterior orbital margin, one to two on either side of midline.

State 1: six to twelve irregularly spaced pores, not evenly divided by midline.

In Orthonopias and Clinocottus there are four evenly spaced nasal pores, two on either side of the midline. In Oligocottus, Chitonotus and Icelinus, there are usually two. Possession of numerous irregularly arranged pores (state 1) is interpreted to be autapomorphic for Artedius notospilotus. Ruscarius and the remainder of Artedius sensu strictu have state 0.

Character 20. Form of teeth.

State 0: teeth on dentaries, premaxillae, vomer and palatines in villiform bands.

State 1: cardiform teeth on dentaries, premaxillae, vomer and palatines.

State 2: in adult males, teeth on vomer and palatines cardiform, those on premaxillae and dentaries irregularly canine, with numerous distinctively longer canine teeth on both upper and lower jaws.

In Ruscarius, Orthonopias, Clinocottus, Oligocottus, Chitonotus and Stelgistrum the teeth are uniformly villiform, never elongate or canine (state 0). The cardiform bands of

teeth in Artedius corallinus (state 1) are therefore postulated to be autapomorphic. Further, the "fangs" (state 2) found in adult male Artedius harringtoni are also interpreted to be autapomorphic for that species. This character has the additive transformation series 0-1-2.

Character 21. Branchiostegal number.

State 0: six.

State 1: seven, one additional on ceratohyal.

In all cottoids, there are six branchiostegals on each side, save for the psychrolutids, which have seven (two on the epihyal, five on the ceratohyal) and are placed by some authors in a separate family. At the level of analysis including Artedius and its immediate sister taxa, possession of seven branchiostegals by A. harringtoni (state 1) is interpreted to have been derived separately from the seven in psychrolutids. Seven branchiostegals are also infrequently found in Artedius fenestralis and Artedius lateralis: however, the frequency of occurrence is apparently very low and the true frequency in nature is unknown.

Character 22. Number of scale rows above the lateral line.

State 0: 29 to 38 rows.

State 1: 24 to 26 rows.

State 2: 43 to 46 rows.

In Artedius fenestralis, Chitonotus, Orthonopias and Stelgistrum, there are from twenty-nine to thirty-eight rows of scales on the body above the lateral line, counted from the origin of the first dorsal fin to the caudal end of the second dorsal base (state 0). The high number of rows found in Artedius corallinus and A. harringtoni (state 2) is therefore hypothesized to be apomorphic. The lower counts found in Artedius lateralis and Artedius notospilotus (state 1) are hypothesized to have arisen twice. This character has the additive transformation series 0-1-2.

Character 23. Membrane of anal fin.

State 0: incised membrane of anal fin concave in males and females.

State 1: incised membrane of anal fin convex in males, concave in females (fig.3).

In males of all of the outgroups examined, as well as in Ruscarius and Artedius sensu strictu save A. harringtoni, the incised membrane of the anal fin is concave in both males and females (state 0). The condition in Artedius harringtoni, where the membrane is convex in males (state 1), is hypothesized to be autapomorphic.

Character 24. Male anal fin pigmentation.

State 0: anal fin dusky, sometimes with alternating light and

dark areas.

State 1: anal fin covered with hexagonal latticework of areas lacking pigmentation on darker background. (fig.3).

In Orthonopias and Ruscarius, the anal fin is uniformly dusky, while in Chitonotus the dusky area is confined to a narrow band set in slightly from the distal margin of the fin. A pattern of light and dark stripes is also found in several other cottid genera such as Hemilepidotus, Oligocottus and Myoxocephalus (all state 0). Therefore the pattern of hexagonal latticework on the anal fin of Artedius harringtoni (state 1) is hypothesized to be autapomorphic.

Character 25. Penis.

State 0: absent.

State 1: present, in form of small cone (fig.3)

state 2: present, much longer, with or without elaborate distal processes.

Modifications of the urogenital papilla are widespread in the Cottidae, and are usually lumped under the generic label of "penis". However, differences in penis structure in various cottid genera ranges from the massive curved cylinders in Clinocottus, Icelinus, Pseudoblennius, and Psychrolutes paradoxus to delicate filaments in Eurymen, Bero elegans, Nautichthys oculofasciatus and Oligocottus. Between these extremes are the long, slender conical penes in Radulinus and the complex structures in Chitonotus, Ocynectes, and

Gymnocanthus. In the immediate outgroups under consideration here, Chitonotus has a unique and elaborate penis (state 2), but neither Hemilepidotus nor Orthonopias have any penis (though Bolin in 1941 reports that the female of Orthonopias has an extensible oviduct). The presence of a short, caudally-directed conical penis in Artedius harringtoni (state 1) is tentatively hypothesized to be an autapomorphic trait at the current level of analysis, as no obvious structural homologue can be found within the family. Ruscarius and the remainder of Artedius sensu strictu all lack penes (state 0).

Character 26. Cirri on upper lip.

State 0: none.

State 1: two to sixteen simple paddle-shaped cirri dorsad to upper lip, located anywhere from end of maxilla anterad. Not distributed evenly on each side. Usually two smaller cirri at premaxillary symphysis.

The presence of paddle-shaped cirri above the upper lip in Artedius corallinus (state 1) appears to be autapomorphic, since these cirri are not found in Ruscarius, Chitonotus, Orthonopias, Clinocottus, Oligocottus or Stelgistrum or other members of Artedius (state 0). The only other cottid with cirri above the upper lip is Dasycottus setiger. These cirri, though are only found above the posterior portion of the lip, and are long and slender, as opposed to the paddle-shaped cirri of A. corallinus.

Character 27. Postcleithra.

State 0: postcleithra present.

State 1: postcleithra absent.

The postcleithra are present in the outgroups, but are absent in Artedius lateralis, A. fenestralis, A. harringtoni, A. corallinus and A. notospilotus. Apparently the loss of postcleithra has occurred several times within the family. A survey of the available cottids revealed that Myoxocephalus niger, three species of Clinocottus (C. acuticeps, C. embryum, and C. globiceps), Gilbertidia sigalutes, Ascelichthys rhodorus (which also lacks pelvic fins) and in Psychrolutes paradoxus all lack postcleithra.

Character 28. Scales under anterior of orbit.

State 0: none.

State 1: a single row of scales extending forward to a point under anterior margin of orbit.

In Orthonopias and Chitonotus pugetensis, the scales on the head do not continue forward under the anterior portion of the orbit (state 0). Stelgistrum stejneri, Ricuzenius pinetorum, Artedius fenestralis, Ruscarius manyi and R. creaseri do have scales under the anterior orbit (state 1). The remainder of Artedius sensu strictu have no scales in this region. Farris optimization based on the most parsimonious cladogram suggests four origins for this feature: once in Stelgistrum, once in

Ricuzenius, once in Artedius fenestralis, and once in the lineage leading to Ruscarius.

Character 29. Scales behind axilla.

State 0: none.

State 1: two to three parallel rows of five to twenty scales extending from top to ventral end of pectoral fin, closely confined to fin base.

Scattered scales are found in the area behind the axilla in Gymnocanthus, Ricuzenius, Stelgistrum, and Hemilepidotus. Scattered scales or prickles are also found in the western Pacific genera Bero, Alcichthys, Furcina, and Pseudoblennius. In all of the preceding genera, however, the scales are not closely confined to the pectoral fin base as they are in Artedius, and extend caudally along the body. Farris optimization suggests that in Artedius sensu strictu, a row of scales confined to the pectoral base (state 1) arose once and was subsequently lost twice, once in A. notospilotus and once in A. lateralis.

Character 30. Scales on caudal peduncle.

State 0: body scales continuing onto dorsal surface of caudal peduncle, covering area extending from end of second dorsal base to origin of first dorsal caudal raylet.

State 1: scales absent from dorsal surface of caudal peduncle.

Scales on the caudal peduncle (state 0) are found in Stelgistrum, Ricuzenius, Orthonopias, and Chitonotus pugetensis. They are absent in Artedius corallinus, A. lateralis and A. notospilotus (state 1). The most parsimonious interpretation is that they were lost twice in Artedius - once in the lineage including A. corallinus and A. lateralis, and once in A. notospilotus.

Character 31. Preorbital cirri.

State 0: none.

State 1: one to four cirri located at upper anterior margin of orbit (figs 6,7).

State 2: one very large cirrus anterior to orbit, plumose in mature males (fig. 3).

Preorbital cirri are not found in Icelinus, Orthonopias or Chitonotus pugetensis (state 0). However they are present in Artedius harringtoni (state 2), Ruscarius, Jordania zonope and all species of Oligocottus (all state 1). At present the most parsimonious interpretation is that they arose four times: once in Jordania, once in Artedius harringtoni, once in Ruscarius and once in Oligocottus. A. harringtoni is the only Artedius species with preorbital cirri. This character has the additive transformation series 0-1-2.

Character 32. Cirri above axilla.

State 0: one to three simple cirri in cluster at point midway between pectoral fin base and lateral line scale row.

State 1: none.

One to two cirri appear above the axilla (state 0) in Artedius harringtoni, Ruscarius meanyi, Orthonopias, all Clinocottus except C. acuticeps, Icelinus fimbriatus and Icelinus oculatus. Farris optimization postulates four origins for this state: once in Clinocottus (with a loss in C. acuticeps), once in A. harringtoni, once in R. meanyi, and once in Icelinus, if Bolin's (1947) phylogenetic diagram is correct. The remainder of Artedius sensu strictu lack these cirri (state 1).

Character 33. Cirri anterad to upper preopercular spine.

State 0: none.

State 1: one to ten cirri in cluster anterad to uppermost preopercular spine, at margin of opercle and preopercle.

By outgroup comparison, the cluster of up to ten cirri just in front of the upper preopercular spine in Ruscarius creaseri (state 1) is autapomorphic, as these cirri do not occur in R. meanyi, Artedius sensu strictu, Orthonopias, Clinocottus, Oligocottus, Chitonotus, Icelinus, Ricuzenius or Stelgistrum (all state 0).

Character 34. Cirri on preopercular margin.

State 0: one to five simple cirri confined to each of preopercular spines.

State 1: seven to twelve simple cirri along preopercular margin, not confined to preopercular spines.

In Artedius sensu strictu except A. harringtoni, in Ruscarius and in the other outgroups, there are from one to five simple cirri on the preopercular margin, with one or more on each preopercular spine (state 0). The derived condition (state 1) found in Artedius harringtoni, with seven to twelve cirri not confined to the spines, is shared with Clinocottus embryum, and is hypothesized to have arisen twice within the cottids.

Character 35. Scale ridge shape.

State 0: scale ridge a broad curve (fig. 11a).

State 1: scale ridge a pointed arch (figs. 11b, 11c, 11d).

State 2: scale ridge a semicircle (figs. 11e, 11f, 11g, 11h).

State 3: no scale ridge.

The plesiomorphic state is that found in Hemilepidotus, Icelinus, and Orthonopias. State 1 is found in Ruscarius. Chitonotus, though it lacks a ridge (state 3), has its ctenii aligned in the same pattern. The semicircular arrangement of Artedius sensu stricto (state 2) is not found in any of the other scaled outgroups, and is hypothesized to be synapomorphic.

This character has a disjoint distribution and its utility in this study is severely limited. Although a transformation series cannot be established, it nonetheless provides support

for the monophyly of two lineages: Artedius sensu stricto and the lineage including Ruscarius and Chitonotus.

Character 36. Scale ridge placement.

State 0: scale ridge not reaching margins of basal plate (fig. 11a).

State 1: scale ridge reaching anterolateral edge of basal plate (fig. 11b).

State 2: scale ridge reaching anterior edge of plate only, not extending to lateral edge (figs. 11c-11h).

In Hemilepidotus, the scale ridge does not extend to the edges of the plate (state 0). This condition is hypothesized to be plesiomorphic. State 1, the ridge reaching the anterolateral edge of the plate, is found only in Orthonopias. State 2, the ridge reaching only the anterior edge, is found in Artedius sensu stricto, Ruscarius, and Icelinus. Chitonotus pugetensis, though it lacks a ridge, also has ctenii extending all the way to the anterior margin. Having the scale ridge reach the margins of the plate is hypothesized to be apomorphic relative to Hemilepidotus, and having the ctenii or the ridge extending only to the anterior edge is hypothesized to be apomorphic relative to the condition in Orthonopias.

This character has an additive transformation series, 0-1-2. Its main use lies in separating Hemilepidotus and Orthonopias from the rest of the genera under consideration. Unfortunately no other character shares this distribution.

Further corroboration is needed.

Character 37. Adult size.

State 0: maximum greater than 130 mm standard length.

State 1: maximum less than 50 mm standard length.

Adult size in the outgroups, and in the cottidae as a whole, is generally well over 100 mm, ranging up to about 750 mm in Myoxocephalus (state 0). The small (less than 50 mm) adult size of Artedius meanyi (state 1) is not found in any other cottid, and is therefore tentatively hypothesized to be autapomorphic.

Character 38. Form of anal rays.

State 0: first three anal rays unmodified in adult males.

State 1: first three anal rays thickened and short (50% of the length of the fifth ray) (fig. 7).

Many cottids have modified anal rays in mature males, notably Oligocottus maculosus and Oligocottus snyderi. In these two species the first two anal rays are substantially thickened, and are at least as long as, if not longer than, the third, unmodified, ray. In O. snyderi, they are also set off by a notch in the fin membrane itself. The rest of the outgroups under consideration do not have modified anal rays in the males. In Ruscarius meanyi (state 1), the first two anal rays are thickened, their length about half of the length of the fifth

(the first normal) ray. The third ray, which is not thickened, is the same length as the first two, while the fourth ray is approximately 75% the length of the fifth. This is interpreted to represent a distinct state from that found in Oligocottus, and to be autapomorphic for R. meanyi at the current level of analysis.

Character 39. Form of head tubercles.

State 0: head tubercles unmodified.

State 1: tubercles raised dorsally, adorned with irregular groups of knoblets.

Porocottus, Ereunias, Dasycottus, Icelus and Myoxocephalus also have elaborate bony structures on the head, none of which occur in the same regions as those found in Artedius notospilotus (state 1). In Myoxocephalus, these are either in the form of longitudinal ridges of various forms (along the 'fronto-parietal ridge', Bolin 1947), such as in M. scorpius, M. scorpioides, M. octodecimspinosus, and M. stelleri, or they are short sections of ridge with erose distal surfaces, found in M. quadricornis and M. groenlandicus. Although four of the tubercles in Artedius notospilotus are aligned with the fronto-parietal ridge (which is not raised in Artedius), they arise from rounded bases and are globose distally. The bony head structures in other cottid genera and A. notospilotus are therefore not considered to be homologous, and the state in A. notospilotus is hypothesized to be autapomorphic.

Character 40. Serrations on the posttemporal and supracleithrum.

State 0: absent.

State 1: serrations present on posterior of posttemporal and upper border of supracleithrum.

In Orthonopias, Clinocottus, Oligocottus, Chitonotus, Hemilepidotus, Icelinus and Ruscarius the posttemporal and supracleithrum are unmodified (state 0). The presence in Artedius notospilotus of serrations (state 1) is therefore postulated to be autapomorphic.

Character 41. Size of body circles.

State 0: no tiny circles of lighter pigment scattered over lateral body surface (figs. 6,7).

State 1: tiny circles of lighter background pigmentation scattered over lateral body surface (figs. 1,2).

State 2: as in state 1, but circles dense (figs. 3,4,5).

These circles are not found in the outgroups (state 0). Within Artedius, they are found only in A. harringtoni, A. corallinus and A. lateralis (state 1). The condition in A. lateralis and A. corallinus, in which the small circles are particularly dense (state 2), is hypothesized to be a further derived condition.

This character, because of its non-additive distribution

within Artedius, cannot serve as strong evidence for intra-generic relationships. It can, however, contribute support for the sister group status of Artedius corallinus and Artedius lateralis, as well as the integrity of the clade containing A. lateralis, A. corallinus, and A. harringtoni. Three transformation series are equally likely: 0-1-2, 0-2-1 and 0-1

character 42. White throat coloration.

State 0: none.

State 1: white spots present on throat, in regular pattern (fig. 10e).

The presence of white vermiculations on the underside of the throat in Orthonopias (state1) is hypothesized to be autapomorphic, as it is not found in any of the other outgroups, in Ruscarius or in Artedius sensu strictu (all state 0). The spots appear in a regular pattern, with a "Y" just behind the median mandibular pore, and a series of regularly grouped spots proceeding caudally along the branchiostegal membrane.

Character 43. White spots on body.

State 0: absent.

State 1: present (fig. 8).

In the area which in Artedius is covered by circles, Orthonopias has a series of white spots superimposed over the

underlying darker pigmentation (state 1). This white pigment is distinctly lighter than the light background pigmentation of the ventral body surface, so that, beyond the ventral margin of darker pigment, the white circles are clearly visible against the lighter body color. The margins of the circles are indistinct, in contrast to the sharply-defined circles of Artedius sensu strictu (state 0).

Character 44. Cirri on nasal spine.

State 0: a simple slender cirrus arising from base of each nasal spine.

State 1: no cirrus on each spine.

In Orthonopias and Chitonotus pugetensis, there is a long slender cirrus on each nasal spine (state 0). This is also found in Ruscarius creaseri, Artedius harringtoni, A. corallinus and A. lateralis. Possession of a nasal cirrus is hypothesized to be the plesiomorphic condition for Artedius. Farris optimization suggests losses (state 1) for this feature in Ruscarius manyi, in the stem leading to A. fenestralis and A. notospilotus, once each in Oligocottus (O. maculosus) and Clinocottus (C. globiceps), and at least three times for the four Icelinus species which lack it (I. burchami, I. cavifrons, I. quadriseriatus, I. tenuis), if Bolin's (1947) diagram is correct.

Character 45. Pterotic flange.

State 0: triangular flange at posterior edge of pterotic short, not reaching posterior edge of cranium (fig. 12a).

State 1: flange long, extending to posterior margin of cranium (fig. 12b).

State 2: as in state 1, but distal edge of lower flange raised to form a ridge perpendicular to plane of main flange (fig. 12c).

The posterior flange of the pterotic consists of two parallel triangular elements which extend in a ventro-caudal direction. The lower of the two is always the longest. In Icelinus, Hemilepidotus, Clinocottus, Oligocottus, Ruscarius meanyi, R. creaseri and Orthonopias, this flange is always short, never extending to the posterior edge of the cranium (state 0). In Artedius sensu stricto this flange is very much longer, continuing to the posterior end of the neurocranium. This state (state 1) is hypothesized to be synapomorphic for Artedius sensu stricto. State 2, found in A. corallinus and A. lateralis, is hypothesized to represent a further derived condition and be apomorphic at that level. This character is considered to provide strong evidence for these groups as the transformation series is additive (0-1-2).

Character 46. Ossification of opercle.

State 0: opercle completely ossified.

State 1: ventro-caudal third of opercle not ossified.

In Clinocottus, Oligocottus and Artedius sensu stricto, the

ventro-caudal section of the opercle is never completely ossified and does not take up alizarin red (state 1). In Chitonotus, Orthonopias, Hemilepidotus, Icelinus, Ruscarius meanyi and R. creaseri, the opercle is always completely ossified (state 0). State 1 is hypothesized to be a derived trait.

Character 47. Scales on eye.

State 0: no scales on eye.

State 1: scales on surface of eye, arranged in crescent covering upper fifth of eye, never covering pupil.

Scales on the eye are found in Chitonotus pugetensis and Ruscarius meanyi (state 1). Farris optimization postulates that the most parsimonious explanation is one of a single origin, in the stem leading to Ruscarius and Chitonotus, with a loss in Ruscarius creaseri. These scales are not found in Artedius sensu strictu (state 0).

RESULTS

Adult Trees

Monophyly and Relationships of Artedius

The Wagner program produced three trees of 86 steps (figs. 13, 14, 15), each with a consistency index of 76.74. Each tree recognizes a monophyletic clade composed of five of the seven nominal Artedius species (A. notospilotus, A. fenestralis, A. harringtoni, A. lateralis, and A. corallinus). R. meanyi and R. creaseri are placed in a separate clade, not closely related to the remainder of Artedius. The monophyly of Artedius sensu stricto is supported by six synapomorphic characters: 3 (form of scale ridge), 4 (body color pattern), 12 (chin coloration), 27 (postcleithra), 35 (scale ridge shape), and 45 (pterotic flange) (see fig. 16).

Within Artedius, two separate clades are identifiable: A. notospilotus plus A. fenestralis supported by synapomorphies in characters 3 (body color pattern), 12 (chin coloration), 11 (male color), 14 (extra lateral line pores), 15 (form of head scales), 32 (cirri above axilla), and 44 (cirri on nasal spine); and a clade including A. harringtoni, A. corallinus and A. lateralis, with synapomorphies in characters 4 (body color pattern), 12 (chin coloration) and 41 (size of circles on body). Within the latter clade, A. corallinus and A. lateralis are

sister species, sharing apomorphic states in characters 12 (chin coloration), 17 (cirri on suborbital stay), 32 (cirri above axilla), 41 (size of circles on body) and 45 (pterotic flange) (see fig. 16).

Each of the three trees placed Artedius, Oligocottus and Clinocottus in one monophyletic lineage. The evidence supporting this particular clade is slight and consists only of character 49 (ossification of opercle). Oligocottus and Clinocottus are hypothesized to be sister taxa in this study mainly on the basis of their lack of scales. Since many cottid genera lack scales this is obviously not strong evidence for genealogical relationship. In the absence of further character evidence no refutation is possible but alternatives are apparent. For present purposes it should be sufficient to note that these two aspects of the cladogram (the Oligocottus-Clinocottus-Artedius clade, and the Oligocottus-Clinocottus clade) are provisional and require further testing.

Monophyly of *Ruscarius*

Ruscarius meanyi and Ruscarius creaseri do not belong to the monophyletic lineage made up of the other five Artedius species, although they do constitute a separate clade of their own as evidenced by characters 3 (form of scale ridge), 4 (body color pattern), 7 (shape of upper preopercular spine) and 11 (male color) (see fig. 17). Thus as Washington (1982)

suggested the genus Artedius sensu Bolin (1947) is demonstrably diphyletic.

Alternative trees - the relationships of Ruscarius

The only ambiguity present in the trees for the adult data concerns the relationships of Chitonotus, Ruscarius manyi, and Ruscarius creaseri, especially in relation to the lineage of Artedius, Clinocottus, and Oligocottus. Three equally parsimonious alternatives emerge from the Wagner analysis, each differing only in the placement of Chitonotus:

1. Ruscarius is the sister lineage to the Oligocottus-Clinocottus-Artedius lineage, while Chitonotus and Icelinus are placed sequentially below Ruscarius on the tree (fig. 13).

2. Chitonotus plus Ruscarius form a monophyletic lineage, while Icelinus is placed between the basal genera (Orthonopias and Hemilepidotus) and the Chitonotus-Ruscarius lineage (fig. 14).

3. Chitonotus is placed as the sister taxon to the Oligocottus-Clinocottus-Artedius lineage, followed by the increasingly plesiomorphic Ruscarius and Icelinus (fig. 15).

Unfortunately, the only characters which are derived at the level that includes R. manyi, R. creaseri, Chitonotus, and Icelinus are non-additive multistate characters, which, are not very useful in elucidating relationships. In the absence of binary characters at this level, the branching sequence remains

ambiguous. This ambiguity appears in the Adams consensus tree as a trichotomy, from which stem Chitonotus, Ruscarius and the Artedius-Oligocottus-Clinocottus clade (fig. 18).

Although there is ambiguity in the Adams tree in the placement of Chitonotus, the genus Ruscarius appears to be closer to Chitonotus and the Artedius-Oligocottus-Clinocottus clade than it is to Icelinus. Washington's (1982) diagram suggests the reverse. At present there is no evidence on which to base a preference for one of the three trees (figs. 15, 16, 17) over another, since the position of Chitonotus cannot be resolved given the characters at hand. In binary characters, Chitonotus has losses in two (characters 9 and 17) and is hypothesized to be homoplasious in another (character 47), leaving only character 6 as a useful binary character. Chitonotus also shares with Icelinus apomorphic states in two multistate characters which have disjoint distributions over the entire tree (characters 4 and 35) and has a state in another character which is non-additive (character 3). This leaves the additive character 36, for which it shares the same state as Ruscarius, Icelinus and Artedius.

Finally, Hemilepidotus and Orthonopias remain unresolved at the base of the phylogenetic hypothesis, since they are plesiomorphic for all of the characters with respect to the rest of the taxa at hand. Orthonopias is highly autapomorphic, especially in body coloration (characters 45 and 46).

The Wagner program produced only one tree (fig. 24) (for the data set excluding R. meanyi to make it comparable to

Bolin's 1947 tree). Artedius, Oligocottus and Clinocottus are fully resolved, with the same branching sequence as in the trees in which R. meanyi was included. R. creaseri and Chitonotus are placed together as a separate lineage sharing a common ancestor with the Artedius-Oligocottus-Clinocottus clade. Icelinus is plesiomorphic relative to all of the above taxa. Finally, Hemilepidotus and Orthonopias are again relegated to a basal polytomy.

Larval Trees

Three trees of seventeen steps (figs. 21, 22, and 23) emerged from the Wagner analysis of the larval data extracted from Washington's (1982) study. All three trees have a consistency index of 82.35. None of these trees is identical to Washington's collapsed tree. One tree (fig. 19) duplicates exactly Washington's (1982) branching sequences within her genera, although Artedius, Oligocottus, and Clinocottus emerge from an unresolved trichotomy. The part of the tree including R. meanyi, R. creaseri and Icelinus is the same as in the tree resulting from collapsing unsupported branches in Washington's dichotomous tree (fig. 25).

In the second tree (fig. 20), Clinocottus is resolved as in the collapsed tree, as is the R. meanyi-R. creaseri-Icelinus clade. Oligocottus is now the sister taxon to Artedius, (less A. harringtoni, which emerges from a trichotomy with Clinocottus

and the Oligocottus-Arteidius lineage).

The third and final larval cladogram (fig. 21) also has Oligocottus and Arteidius (less harringtoni) in one lineage. This branch arises from a trichotomy involving two other lineages: Clinocottus (less C. acuticeps) and a clade made up of Arteidius harringtoni and Clinocottus acuticeps. The R. meanyi-R. creaseri-Icelinus portion of the tree is the same as in the first two trees. Figure 24 is the Adams consensus tree derived from these three larval Wagner trees.

With respect to Arteidius, the larval tree is of little use, since it does not include all of the species and the relationships of those it does include are not resolved. The larval analysis does demonstrate, however, that R. meanyi and R. creaseri do not belong to the lineage including the rest of the Arteidius species under consideration. Oligocottus and Clinocottus are in fact more closely related to Arteidius than are either R. meanyi or R. creaseri. This can be seen in the Adams consensus tree for the three larval trees (fig. 22). Icelinus plus R. meanyi plus R. creaseri constitute one resolved clade, while the remainder of the tree is composed of five branches emerging in a polytomy: Oligocottus, Arteidius fenestralis plus Arteidius harringtoni plus Arteidius type 3, Arteidius harringtoni, Clinocottus acuticeps, and the remainder of Clinocottus.

COMPARISON OF CLASSIFICATIONS

Adults

The tree published by Bolin (1947) (fig. 23) requires five steps more than the Wagner tree calculated in the absence of R. manyi (fig. 24) and raises the number of homoplasious characters from six to seventeen, or from twelve percent to thirty-four percent. In addition, when the character data from this study are mapped onto Bolin's (1947) tree, six branches remain unsupported. Although he can hardly be faulted for failing to represent my data as well as my tree did, based on my analysis I cannot accept his hypothesis of relationships.

Compared to the Manhattan distance matrix calculated from the character data set, the Wagner tree has an R value of 0.97, whereas Bolin's tree has an R value of 0.45. Clearly the Wagner tree better represents the data in this study. Interestingly, as far as could be determined from his text, my study includes most of Bolin's (1944) character data.

The main difference between his tree and my wagner tree lies in the relationship between Artedius harringtoni and Ruscarius creaseri. Both studies recognize two easily identifiable pairs of sister species within Artedius: Artedius fenestralis-Artedius notospilotus, and Artedius lateralis-Artedius corallinus. Bolin placed Artedius harringtoni as the sister species to A. creaseri, in the absence

of Ruscarius meanyi. The justification for placing A. harringtoni and A. creaseri together lay mainly in the similar distribution of scales. Since no other corroborative characters have been discovered, this character is not a reliable indicator of phylogenetic relationship. The remaining Artedius species with reduced squamation and no preorbital cirri are separated from R. creaseri and A. harringtoni. Finally, he placed Orthonopias as the sister taxon of Artedius.

The present analysis offers quite a different hypothesis of relationships. The two pairs of Artedius sister species are again recognized, but Artedius harringtoni is placed closest to Artedius corallinus plus Artedius lateralis. In the absence of R. meanyi, A. creaseri is placed with Chitonotus and is removed from the genus Artedius entirely. The lineage including Oligocottus and Clinocottus is hypothesized to be the sister group to Artedius sensu stricto. The formerly hypothesized sister species of Artedius sensu Bolin, Orthonopias triacis, is removed to a basal trichotomy with Hemilepidotus, separate from Chitonotus, Icelinus, Ruscarius, Oligocottus, Clinocottus, and Artedius.

Contrary to Bolin's (1947) claim that "Orthonopias is clearly derived from the Artedius line" (p. 162). This study shows that the characters which Bolin (1947) used to unite Orthonopias with Artedius are plesiomorphic at that level and therefore inadmissible as evidence for sister group status. In addition, Orthonopias is highly autapomorphic, especially in the form of the pelvic fins in the male, the form of the body scales

and in the pattern of body coloration. Such characteristics yield little evidence for placement of Orthonopias with any of the other taxa under consideration in this study, although Howe and Richardson's (1978) suggestion that it be included in Artedius appears to be totally unsupported.

The shortcomings of Bolin's (1947) analysis seem to stem from methodology, since his character analysis is certainly very detailed. The root of the problem lies in placing forms with similar scalation patterns together, on the a priori assumption that, within the Cottidae, there is a trend towards reduction in squamation. This assumption is then used to order the species within the Cottidae. The point that is missed is that such trends cannot be identified in the absence of a logically and empirically constructed phylogenetic hypothesis. In this particular instance, such a generalization has little, if any, utility in reconstructing genealogy. Witness the placement of the "scaly" Artedius harringtoni with the the two species which show the highest degree of reduction of scalation within Artedius, A. lateralis and A. corallinus, and the placement, though admittedly still provisional, of two totally non-scaled forms as the sister lineage of the scaled genus Artedius. In addition, not all things that look like an "Artedius" are Artedius, as evidenced by the removal of R. creaseri and R. meanyi to a separate genus outside the Oligocottus-Clinocottus-Artedius group and the placement of Orthonopias at the unresolved base of the tree diagram far removed from Artedius. These two results provide an example of

the futility of grouping by overall similarity when one is trying to establish genealogical relationships.

Larvae

None of the minimum-length trees (figs. 19, 20, and 21) from the Wagner analysis are the same as those presented by Washington (1982) (figs. 25 and 26), one of which (fig. 25) is supposedly derived from an "unrooted Wagner analysis". In the following comparisons, the two trees derived from the larval study will be referred to as the collapsed tree and the fully resolved or dichotomous tree. Inspection of her data reveals that this dichotomous tree has no character justification for the complete resolution of relationships within Artedius and Clinocottus.

The justification for her fully resolved tree remains mysterious. It is possible that the relationships depicted in her cladogram are in fact those proposed by Bolin in 1947, who placed A. lateralis and A. fenestralis in a lineage separate from that including A. creaseri and A. harringtoni. Since Washington removed A. creaseri to a lineage with Icelinus and A. meanyi, this would lead to the placement of A. lateralis and A. fenestralis in a monophyletic group apart from A. harringtoni. However, the problematical Artedius type 3 clouds the issue. This is either A. corallinus, A. notospilotus or a combination of both, and its inclusion in the analysis

results in Artedius type 3, A. fenestralis and A. lateralis arising from a trichotomy.

The justification for the resolution of relationships within Clinocottus in the dichotomous tree cannot be found with Bolin (1947), since the branching sequence depicted by Washington (1982) does not correspond to his tree, the only other published tree for this genus. In the absence of character data in the body of her text, Artedius collapses to A. harringtoni plus a trichotomy including A. fenestralis, A. lateralis and A. type 3. Clinocottus collapses to C. acuticeps plus a trichotomy involving C. analis, C. embryum and C. recalvus.

As with the adult tree of Bolin, the goodness of fit of the larval tree presented by Washington is considerably less than that of the Wagner trees (see table 1).

Table 1. Comparison of fit of larval trees.

<u>R-value</u>	
Wagner tree 1	96.96
Wagner tree 2	97.10
Wagner tree 3	96.57
Washington (1982) dichotomous	76.43
Washington (1982) polytomous	68.99

One of the Wagner trees (fig. 19) reproduces exactly the

branching sequence within genera shown in Washington's collapsed tree (fig. 26). However, in my tree, Artedius, Oligocottus and Clinocottus emerge from a trichotomy and are not resolved as in Washington's tree. Three explanations may be offered to explain my inability to reproduce her trees: I seriously erred in the preparation of a data matrix from Washington's text; the characters were poorly analyzed in the text, but I coded them as she intended; or, if I coded the data correctly and the original character analysis was sound, her analytical technique is not, as claimed, a Wagner (parsimony) method.

First, Washington's analysis of the characters. With one notable exception, Washington (1982) polarized the characters using outgroup analysis. Given the information in the text these are above suspicion. One character, number 11, she apparently polarized by use of the common-equals-primitive criterion.

"This condition (rounded snout) is probably the primitive condition relative to larvae of Artedius, Clinocottus, and Oligocottus, because it is widespread in (larvae of) several divergent genera of Cottids and Scorpaeniformes. (therefore) the pointed snout appears to be a derived condition." (p. 172). It seems, though, that the alternative character state also exhibits a widespread distribution, which caused her to comment: "snout length is variable in the outgroup taxa." (p. 171). Unfortunately, this character (snout length) is one of two that is used to justify the monophyly of a group including Icelinus, A. creaseri, and A. meanyi. It must be noted here

that the shape of the snout in larval forms does not correspond to snout shape in adult forms (character 2 in the adult analysis). The other larval character used to justify this group's monophyly (basal preopercular spine) was polarized by outgroup comparison, but not all Icelinus species were examined. A single character, pelvic fin ray number, was used to justify the group A. meanyi plus Icelinus.

Next let us consider the possibility that I did not code the data as Washington (1982) intended. Washington (1982) offered 11 characters to be used in the phylogenetic analysis (although for reasons not stated, two of these were not included on the cladogram). Of these, seven are binary characters and four are multistate. Again assuming that Washington was able to determine the plesiomorphic state for the binary characters, there is little doubt that these were coded as she intended. The analysis of the multistate characters was also straightforward. In the interest of fairness, alternative coding schemes were tried, in an attempt to reproduce the branching sequence in her collapsed tree. These invariably resulted in a tree with one additional step relative to the original coding scheme. None of these trees had the same topology as the trees in Washington's text. I can only conclude that no coding scheme will yield her tree when subjected to a Wagner analysis. I am satisfied, though, that my original coding of her data results in the most parsimonious cladogram. Although I can reproduce (fig. 19) the same topology within genera as in her collapsed tree (fig. 26) there does not seem

to be support in her character data for the placement of Oligocottus and Clinocottus as sister taxa.

Although Richardson's (1981) discussion of intergeneric relationships within the cottids was preliminary and presented no branching diagram, Washington (1982) pointed out that Ruscarius meanyi was included in Richardson's (1981) study under "Icelus spp.", which makes possible a comparison of Richardson's (1981) phenetic groupings with the results from this study. Two of her groups are of particular interest: (1) the Artedius-Oligocottus-Clinocottus-Orthonopias group and (2) the group including Chitonotus, Icelus and Icelinus. Two major points of agreement emerge: the separation of the Artedius-Clinocottus-Oligocottus group from Icelinus and the notion that R. meanyi does not belong with Artedius.

All three of the larval analyses (one phenetic, one phylogenetic in name only and one Wagner) agree that R. meanyi (or R. meanyi and R. creaseri) does not share an immediate common ancestor with the rest of Artedius sensu stricto.

CONGRUENCE OF LARVAL AND ADULT CLASSIFICATIONS

Figure 27 shows the consensus tree derived from the consensus of the adult Adams tree and the larval Adams tree. (note that only those taxa common to both analyses are present in the final consensus). The large amount of ambiguity stems from the inability of the larval tree to resolve relationships. This ambiguity is also a function of the size of the data set; more characters are needed.

Despite the shortcomings, there are two areas of agreement which merit discussion. Both adult and larval Adams trees recognize that the closest relative of Artedius is either Oligocottus or Oligocottus plus Clinocottus. This is important in that neither of the latter genera is scaled. A widespread assumption in cottid systematics is that there is a general trend toward reduction of scales within the family (see Bolin, 1947). Unscaled forms are therefore grouped with other unscaled forms. In the context of my analysis, the use of this trend has limited utility in sorting out relationships, as there are no corroborative characters with the same distribution. As a general rule of thumb the reduction of scales within the cottids may be a useful concept, but its use in polarizing characters and taxa is limited. This study hypothesizes that two completely unscaled genera, Oligocottus and Clinocottus, are the closest relatives of Artedius (although Oligocottus rimensis does have dermal bony prickles). Orthonopias, which has a scalation pattern generally similar to Artedius, is not hypothesized to be closely related to the latter.

The second major area of agreement between the adult and larval Adams trees is the hypothesis that Ruscarius meanyi and Ruscarius creaseri, formerly in Artedius, do not in fact belong with the rest of the nominal Artedius, although the larval tree is unable to completely resolve the placement of Ruscarius.

Although Washington's (1982) analysis conflicted with the adult analysis in its placement of R. meanyi, R. creaseri, and Icelinus, it did serve to focus attention on a central issue in systematics: monophyly. With respect to methodology, however, her study is instructive. The larval study served to focus attention on the lack of justification for the monophyly of Artedius. At the level at which there was character support, Washington's study did recognize that R. meanyi and R. creaseri did not belong with the rest of Artedius sensu strictu, which is something that the evolutionary taxonomic study of Bolin (1947) failed to uncover.

A strict congruence study using the results of Richardson (1981) was not possible, due to the uncertainties in identification and the different taxa examined. One point is worth noting: even this admittedly phenetic grouping suggested that an Artedius including R. meanyi is not monophyletic, a result supported by the analysis based on adult characters.

Both adult and larval cladograms remove R. creaseri and R. meanyi from Artedius sensu strictu. Due to the unresolved nature of much of the larval cladogram, it is not possible to test for further congruence. Still, in the area that is resolved in both larval and adult analyses, there is congruence.

In the presence of a great deal of noise in the larval data, phylogenetic analysis provided the same hypothesis for the placement of Ruscarius relative to Artedius as did the adult analysis. The only other systematic treatment of Artedius and its relatives (Bolin, 1947) did not recognize the diphyletic condition of Artedius.

Congruence of classifications is also important in comparing theories of evolutionary change when explicit predictions regarding congruence can be derived from those theories. Within current evolutionary theory there seems to be a range of statements regarding congruence. De Beer (1958) found that classifications based on adult and larval characters were most often congruent, even in the face of the obvious adaptation of the larval forms to their habitats. Charlesworth et al. (1982), like De Beer (1958), do not make any specific predictions. They state that phylogenetic patterns are due predominately to the action of natural selection (1982, p. 490). If natural selection alone shapes the organism, morphological change should be better correlated with environment than with phylogeny. If we then compare classifications derived from different life history stages such as larvae and adults, which are presumably subjected to vastly different selective regimes, we would not predict congruence. A strict "selective regime" explanation grows more convoluted each time congruence is found. The non-equilibrium framework of Wiley and Brooks (1983, also Brooks and Wiley, 1983) does predict congruence, since it explicitly recognizes the

constraining role of history. Congruence is then a consequence of different data sets reflecting the same phylogenetic history.

Eventually we will reach a point where our understanding of the pattern of order in nature forces us to re-examine our notions about causal processes. Either we restructure our ideas of process to accomodate features of the natural world such as congruence, or we abandon our former ideas entirely in favor of something that better accounts for the data.

SUGGESTIONS FOR FUTURE STUDIES

Now that a phylogeny is available for Artedius sensu strictu, there are other important questions that can be examined. Firstly, we can map morphometric data onto this cladogram in order to identify historical trends in changes in body shape and size. This mapping technique can in fact be generalized to test for trends in any continuous character.

Other types of analyses are also possible with respect to what might be called "historical ecology". The availability of a cladogram makes possible analysis of host-parasite relationships, leading to studies of coevolution in general. With this cladogram, field ecologists now have the necessary background for studies of speciation. Community ecologists have a vital piece of information necessary in estimating the historical component of ecological associations. Biogeographers can study the relationship between the history of these fish and the history of the areas in which they live.

In the light of the situation in Artedius, the obvious higher-level question arises: which other cottid genera are in need of phylogenetic analysis? In how many of the other genera has a robust estimate of phylogeny remained obscure, even in the face of evolutionary-taxonomic study? Of course this question can reasonably be asked of any taxon, not just cottids. Within the problem at hand it seems critical that the interrelationships of Icelinus, Chitonotus, Ruscarius, Oligocottus, Clinocottus and Artedius be examined, especially in

the light of the meagre evidence for the relationships of Artedius, Clinocottus and Oligocottus. These three genera have commonly been grouped together, but little character support has been forthcoming. Icelinus is probably next in line for thorough study, followed by Clinocottus and Oligocottus.

Finally, other scaled genera such as Icelus merit examination, since it is becoming apparent that "scaliness" is not a very reliable indicator of intergeneric relationships. Our knowledge of virtually all of the cottids in the northern and western Pacific, particularly those in Soviet waters, would benefit from phylogenetic analysis. It is possible that the Cottidae as it stands today is not a monophyletic assemblage, but suggestions to that effect have as yet been made without analytical support.

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APPENDIX 1. ADULT DATA MATRIX

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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APPENDIX 2. LARVAL DATA MATRIX

0	0	0	0	0	0	0	0	0	0	0	Ancestor
0	0	1	0	0	0	0	1	0	1		Icelinus
0	0	1	0	0	0	0	1	0	1		Meanyi
0	0	1	0	0	0	0	1	0	0		Creaseri
1	2	0	0	0	0	2	0	1	0		A.harringtoni
1	2	0	0	0	2	1	0	1	0		A.lateralis
1	2	0	0	0	2	1	0	1	0		A.fenestralis
1	2	0	0	0	2	1	0	1	0		A.type 3
1	1	0	2	0	0	1	0	1	0		C.globiceps
1	1	0	2	0	0	0	0	1	0		C.embryum
1	1	0	2	0	0	0	0	1	0		C.analis
1	1	0	2	0	0	0	0	1	0		C.recalvus
1	1	0	1	0	0	2	0	1	0		C.acuticeps
1	1	0	0	1	1	1	0	1	0		D.snyderi
1	1	0	0	1	1	1	0	1	0		D.maculosus

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F THE APPENDIX MATERIAL.

Figure 1. Artedius corallinus after Bolin (1944).

Fig. 1

Figure 2. Artedius fenestralis from Bolin (1944).

Fig. 2

Figure 3. Artedius harringtoni after Bolin (1944).

Fig. 3

Figure 4. Arteidius lateralis from Bolin (1944).

Fig. 4

Figure 5. Artedius notospilotus from Bolin (1944).

Fig. 5

Figure 6. Ruscarius creaseri from Bolin (1944).

Fig. 6

Figure 7. Ruscarius meanyi from Jordan and Evermann (1895).

Fig. 7

Figure 8. Orthonopias triacis from Bolin (1944).

Fig. 8

Figure 9. Side view of scale ridge (schematic). Figure 9a, state 0. Figure 9b, state 1. Figure 9c, state 2. Figure 9d, states 3 and 4.

Fig. 9c

Fig. 9d

Fig. 9b

Figure 10. Chin pigmentation patterns.. Figure 10a, Artedius fenestralis (CAS 40354, 55.1 mm). Figure 10b, Artedius notospilotus (SIO 63-1054, 56.0 mm). Figure 10c, Artedius harringtoni (CAS 29521, 62.9 mm). Figure 10d, Artedius lateralis (UMMZ 42958, 62.9 mm). Figure 10e, Orthonopias triacis (SU 18132, 54.8 mm). Areas outlined in figs. 10a-10d indicate light background pigmentation. Areas outlined in fig. 10e indicate white pigment.

Fig. 10a

Fig. 10b

Fig. 10c

Fig. 10d

Fig. 10e

Figure 11. Top view of scale ridge (schematic). Figure 11a, Hemilepidotus hemilepidotus. Figure 11b, Chitonotus pugetensis. Figure 11c, Ruscarius creaseri. Figure 11d, Ruscarius meanyi. Figure 11e, Artedius fenestralis. Figure 11f, Artedius notospilotus. Figure 11g, Artedius harringtoni. Figure 11h, Artedius lateralis.

Fig. 11a

Fig. 11b

Fig. 11c

Fig. 11d

Fig. 11e

Fig. 11f

Fig. 11g

Fig. 11h

Figure 12. Pterotic flange. Figure 12a, Chitonotus
pugetensis (UW uncat., 46.1 mm). Figure 12b, Artedius
fenestralis (BC57-210, 55.5 mm). Figure 12c, Artedius
corallinus (CAS 48970, 62.3 mm). Abbreviations: PT -
pterotic, PA - parietal, EP - epiotic, SO -
supraoccipital, EX - exoccipital, TB - tabulars, SP -
sphenotic, EC - ethmoid cartilage, VO - vomer, NA -
nasal, ME - mesethmoid, LE - lateral ethmoid, FR -
frontal.

Fig. 12a

Fig. 12b

Fig. 12c

Figure 13. Adult Wagner tree 1.

Fig. 13

Figure 14. Adult Wagner tree 2.

Fig. 14

Figure 15. Adult Wagner tree 3.

Fig. 15

Figure 16. Cladogram of Artedius sensu strictu.

Characters: 3 - form of scale ridge. 4 - body color pattern. 10 - spinelets on main preopercular spine. 12 - chin coloration. 13 - mandibular pore pattern. 14 - pores on lateral line scales. 15 - form of head scales. 16 - cirri on transverse head tubercles. 17 - cirri on suborbital stay. 18 - form of preopercular spines. 19 - nasal pores. 20 - form of teeth. 21 - branchiostegal number. 22 - number of scale rows above lateral line. 23 - anal fin membrane. 24 - anal fin pigmentation. 25 - penis. 26 - cirri on upper lip. 27 - postcleithra. 28 - scales under anterior orbit. 29 - scales behind axilla. 30 - scales on caudal peduncle. 31 - preorbital cirri. 32 - cirri above axilla. 34 - cirri on preopercular margin. 35 - scale ridge shape. 39 - form of head tubercles. 40 - serrations on posttemporal/supracleithrum. 41 - size of circles on body. 45 - pterotic flange.

Fig. 16

Figure 17. Cladogram of Ruscarius. Characters: 1 - position of anus. 3 - form of scale ridge. 4 - body color pattern. 5 - scales above axilla. 6 - scales on snout. 7 - shape of upper preopercular spine. 8 - number of pelvic rays. 9 - cirri on opercle. 28 - scales under anterior orbit. 31 - preorbital cirri. 32 - cirri above axilla. 33 - cirri anterad to upper preopercular spine. 35 - scale ridge shape. 37 - adult size. 38 - anal ray form (males). 44 - cirri on nasal spine. 47 - scales on eye.

Fig. 17

Figure 18. Adams consensus tree for adult trees.

Fig. 18

Figure 19. Larval Wagner tree 1.

Fig. 19

Figure 20. Larval Wagner tree 2.

Fig. 20

Figure 21. Larval Wagner tree 3.

Fig. 21

Figure 22. Adams consensus tree for larval trees.

Fig. 22

Figure 23. Phylogenetic tree of Bolin (1947)

Fig. 23

Figure 24. Wagner tree calculated in the absence of
Ruscarius meanyi.

Fig. 24

Figure 25. Dichotomous larval tree of Washington (1982).

Fig. 25

Figure 26. Polytomous larval tree from Washington (1982).

Fig. 26

Figure 27. Adams consensus tree of adult and larval Adams trees.

Fig. 27