Phylogeny of the species of the superfamily Echeneoidea

(Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae)

with notes on the Echeneidae hitchhiking behaviour

Bruce O'Toole

A thesis submitted in conformity with the requirements
for the degree of Master’s of Science

Graduate Department of Zoology
University of Toronto

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Abstract

Phylogeny of the species of The Superfamily Echeneoidea
(Perciformes: Carangoidae: Echeneidae, Rachycentridae, and Coryphaenidae)

with notes on the Echeneidae hitchhiking behaviour

Bruce O'Toole, Department of Zoology, M.Sc., 1999, University of Toronto.

A phylogenetic analysis, based on 138 putatively informative characters, of
the 11 species of the superfamily Echeneoidea (Echeneidae, Rachycentridae, and
Coryphaenidae) resulted in a single most parsimonious tree. This tree strongly
supports the monophyly of the superfamily with the following relationships:

Coryphaenidae + (Rachycentridae + (Pheurichthys lineatus + ((Echeneis naucrates +
Echeneis neucratoides) + (Remora brachyptera + (Remora remora + (Remora australis
+ (Remora osteochir + Remora albescens))))))). One of the traditional subfamilies,
Echeneiinae, and one of the traditional genera, Remora, were both found to be
paraphyletic. A new classification of the family based on natural groupings eliminated
the subfamilial designations and subsumed the genus Remorina under the genus
Remora rendering it monophyletic. An examination of the behavioural data resulted in
the hypothesis of a gradual step by step development of the hitchhiking behaviour from
general schooling behaviour (outgroups) to attaching to a select few types of hosts in
the pelagic environment (as exhibited by Remora osteochir).
Acknowledgments

My life over the last two years has changed substantially. I entered this program a scuba instructor who knew everything. I leave with a Master's degree, a baby on the way, and the realization that I know very little. I would like to take this opportunity to thank the people who have helped me complete these changes.

To the following individuals I express my thanks for loans of materials and permission to process and dissect specimens: S. Jewett (USNM); R. Rosenblatt (SIO); S. Poss (GCRL); D. Catania (CAS); and W. Richards (NMFS).

I would like to thank several graduate students who helped in various ways; Francesco Santini (we may not have always agreed but the "conversations" were always lively); Jenna Dunlop (who gracefully demonstrated that it's no big deal to have a kid and complete a graduate degree); and Kevin Doyle (who not so gracefully demonstrated that it's a really big deal to have a kid and complete a graduate degree, and for our many "insightful" conversation about phylogenetic. Fortunately I was usually to drunk to remember them.).

I would like to thank Tracey Mulcahy, my friend, my confidant, my partner, and the mother of my child. She has been there through all the ups and downs and continues to help and support me in all my endeavors (even moving to Kingston).

Finally I would like to thank the members of my thesis committee (Drs. E.J. Crossman, D.A. McLennan, and M. Engstrom) and my thesis supervisor, Dr. R. Winterbottom. Rick provided financial support as well as his wisdom and knowledge.
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INTRODUCTION

The dolphins, remoras, and the monotypic cobia (Percomorpha: Carangoidei: Echeneoidea: Coryphaenidae, Rachycentridae, and Echeneidae) are mainly small to medium size pelagic fishes found in tropical to subtropical waters worldwide. There are two recognized species, one genus, in the family Coryphaenidae (Palko et. al., 1982). These fishes are characterized by having a very long dorsal fin, which is spineless, running from the nape to near the start of the caudal fin. The single species recognized in the family Rachycentridae is characterized by having 7-9 short strong isolated dorsal-fin spines (Shaffer and Nakamura, 1989). There are eight recognized species, four genera, in the family Echeneididae (Lachner, 1966). There is a single known fossil form, Opisthomyzon glaronensis from Upper Eocene deposits at Glarus, Switzerland (Gudger, 1926) which has been placed in its own family Opisthomyzonidae. These fishes are characterized by the unique sucking disc on the top of their heads, which allows them to fasten onto other fishes, turtles, ships, and various other objects to "hitchhike". The eight extant species of remoras rely on the hitchhiking behaviour to varying degrees with certain species exhibiting strong host preferences, while others are often seen free swimming or attached to inanimate objects (Cressey and Lachner, 1970). This fascinating behaviour and accompanying structure raises several evolutionary questions. How could this "hitchhiking" behaviour have evolved? What is the nature of the remora-host association? To answer these questions we need to approach the problem from the conceptual framework of historical ecology (Brooks and McLennan, 1991). By examining these questions in a historical framework we can determine the origin, and examine the diversification of the
hitchhiking behaviour. An examination of remora host choice in a phylogenetic context may result in a scenario that helps explain the evolution of this unique behaviour.

To examine the remora hitchhiking behaviour in a historical context we need to know the host associations of all species involved, including outgroups, and we need a phylogenetic hypothesis for the group. At present there are some published data on remora-host associations (e.g. Cressey and Lachner, 1970), however these data need to be updated and pooled with more recent studies (e.g. Pampillon, 1996) to give a more complete picture of host specificity. The present lack of a phylogenetic hypothesis for this group presents a greater challenge. Studies by Freihofer (1978), Johnson (1984, 1993), and Smith-Vaniz (1984) have helped somewhat to clarify the familial relationships; however the species level relationships of remoras and their relatives are poorly understood. Thus the first step in a historical ecology study of the groups is the construction of a phylogenetic hypothesis.

In the traditional classification, the extant remoras have been divided into two subfamilies, the Echeneiinae and the Remorinae (Lachner 1981). The Echeneiinae differs from the Remorinae in it’s long slender body, with a tail that transforms from arrow-shaped in juveniles to lunate-like in adults. It also has pointed jaws with the lower jaw extending well beyond the upper. In the Echeneiinae the dorsal- and anal-fin bases are longer and it has more vertebrae (30 or 40). The species in this subfamily are primarily coral reef fishes, with generalized host associations and are often seen free swimming (Cressey and Lachner, 1970). The two genera, Echeneis with two species and the monotypic Phtheirichthys, differ considerably in vertebrae counts, 30 versus 40, and number of disc laminae, 18 to 27 versus 9 to 11, respectively.
Echeneis naucrates Linnaeus (1758), the sharksucker, is the most abundant and largest of the remoras, reaching a maximum length of 1 m. It is found in shallow coastal waters, free swimming, or attached, most often to sharks. It is distributed worldwide, in tropical and subtropical waters, but is absent from the eastern Pacific American coast (found in Indian, west-central Pacific and Atlantic oceans, recorded from South Africa, India, the Philippines, China, Japan, Hawaii, and the Marquesas Islands) (Lachner, 1986). This species has: 21 to 27 disc laminae; 33 to 45 second dorsal-fin rays; 31 to 41 anal-fin rays; 20 to 26 pectoral-fin rays; 30 vertebrae; 2-3 +10-14 gillrakers. The body is elongated and slender, while the head is depressed. The disc, extending to slightly behind the middle of pectoral fin, is 22 to 30% of the standard length (SL). The disc is also slender, ranging from 7 to 12% SL (Table 1; Lachner, 1986). Echeneis naucrates is loosely attracted to its host, often swimming very close to the host but not attaching. Various shark species are the most common host of adult specimens (Table 2, Cressay and Lachner, 1970) whereas juveniles graduate from a free swimming stage to intermediate hosts, usually trunkfishes, cowfishes and parrotfishes (Bernardi, pers. comm.).

Echeneis neucratoides Zuiw (1786), the whitefin sharksucker, is a rare remora that can reach a maximum length similar, but is slightly shorter, than E. naucrates. It is restricted to the western Atlantic Ocean (Jordan and Evermann, 1898). It is very similar to E. naucrates, it has: 18 to 23 disc laminae; 32 to 41 second dorsal-fin rays; 30 to 38 anal-fin rays; 20 to 23 pectoral-fin rays; 30 vertebrae; 2-3 + 8-14 gillrakers. The body is elongated and slender, but stouter than an E. naucrates of equal length and the dorsal- and anal-fin bases are shorter. The disc, ends at a vertical with the middle of the pectoral fin, which is 24 to 31% SL, and it is also slender, ranging
Table 1: Meristic and measurement data for the eight species of Echeneidae. The rows are as follows: N= number of specimen; SL= standard length in mm; %DL= disc length as a percentage of SL; %DW= disc width as a percentage of SL; %D2L= length of the second dorsal fin as a percentage of SL; %AL= anal length as a percentage of SL; D1= number of paired laminae in the disc; D2= numbers of elements in the second dorsal fin; A= number of elements in the anal fin; P= number of elements in the pectoral fin; Vₐₚₚ= number of abdominal vertebrae; Vₑₑₑₑₚₚ= number of caudal vertebrae; Gr= number of gillrakers on the frist left gill arch; Bra= number of branchiostegal rays on the left side.

<table>
<thead>
<tr>
<th></th>
<th>Echeneis neucrates</th>
<th>Echeneis neucratoïdes</th>
<th>Phtheirichthys lineatus</th>
<th>Remora australis</th>
<th>Remora brechryptera</th>
<th>Remora osteochir</th>
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<td>40-42</td>
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from 9 to 14 % SL (Table 1; Lachner, 1986). The most common hosts are various
sharks, but they are also found free swimming (Table 2; Cressey and Lachner, 1970).

*Phtheirichthys lineatus* (Menzies, 1791), the slender suckerfish, is also a
rare remora, reaching a maximum length of 45 cm. It's distribution is worldwide, in
tropical and subtropical water, but it is not known in the Mediterranean (Lachner, 1986).
It is characterized by: 9 to 11 disc laminae; 29 to 33 dorsal-fin rays; 29 to 34 anal-fin
rays; 18 to 21 pectoral-fin rays; 40 vertebrae; 2+11-13 gillrakers. The body is elongated
and slender with a depressed head. The disc extends only a short distance onto the
nape, measuring 18 to 24 % SL, but it is slightly wider than that of *Echeneis*, ranging
from 9 to 15 % SL (Table 1; Lachner, 1986). The most frequently hosts are inanimate
objects, however they are often found on barracudas and turtles (Table 2; Cressey and
Lachner, 1970).

The fishes of the subfamily Remorinae are characterized by having short,
stout bodies, long and large heads with long broad discs. The juveniles have forked
tails that are slightly rounded at maturity, and they have short dorsal- and anal-fin
bases. There are two genera, *Remora* with four species and the monotypic *Remorina*.
All five species are pelagic and exhibit moderate to very strong host specificity
(Cressey and Lachner, 1970).

*Remora australis* (Bennett, 1840), the whalesucker, is a rare fish that can
reach a maximum lengths of 40 cm. It's distribution is worldwide, tropical and
subtropical, including the Mediterranean. It has been collected as far north as
Vancouver Island, and as far south as Cape of Good Hope (Follett and Dempster,
1960). It is characterized by: 25 to 28 disc laminae; 23 to 26 dorsal-fin rays; 22 to 25
anal-fin rays; 22 to 24 pectoral-fin rays; 27 vertebrae; 2-3 + 16-18 gillrakers. The body
Table 2. Hosts of the eight species of Echeneidae separated by major groups. The data were compiled from the literature (Cressey and Lachner, 1970, Morota and Fujita, 1995, Pampillon, 1996, Schwartz and Lindquist, 1987, and Strasburg, 1959) and various collections (SIO, ROM, and USNM).

<table>
<thead>
<tr>
<th>Host</th>
<th>Echeneis naucrates</th>
<th>Echeneis naucratoides</th>
<th>Phtheirichthys lineatus</th>
<th>Remora australis</th>
<th>Remora brachyptera</th>
<th>Remora osteochir</th>
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<td>8</td>
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is short and stout with a massive disc ranging from 46 to 54 % SL in length and 15 to 23 % SL in width (Table 1; Lachner 1986). The only recorded hosts are cetaceans suggesting a strong host preference in this species (Table 2; Cressey and Lachner 1970).

*Remora brachyptera* (Lowe, 1839), the spearfish remora, is a common fish which can reach a maximum length of 30 cm. It is distributed worldwide, in warm water (Lachner, 1986). It is characterized by: 15 to 18 disc laminae; 27 to 34 dorsal-fin rays; 22 to 29 anal-fin rays; 23 to 26 pectoral-fin rays; 27 vertebrae; 0+13 to 3+16 gillrakers. Its body is short and stout with the disc extending posteriorly to a vertical with the distal tips of the pectoral-fins; measuring 28 to 34 % SL in length and 15 to 19 % SL in width (Table 1; Lachner 1986). *Remora brachyptera* is commonly found on billfishes and sharks (Table 2; Cressey and Lachner 1970).

*Remora osteochir* (Cuvier, 1829), the marlin sucker, is a common fish that can reach a maximum length of 35 cm. It is found worldwide in most tropical and subtropical pelagic environments. It is uncommon in the eastern Atlantic (Lachner, 1986). It is characterized by: 15 to 20 disc laminae; 20 to 26 dorsal-fin rays; 20 to 26 anal-fin rays; 20 to 24 pectoral-fin rays; 27 vertebrae; 0-3 + 11-15 gillrakers. Its body is short and stout with the disc extending beyond a vertical with the pectoral-fin tips; measuring 36 to 50 % SL in length and 15 to 23 % SL in width (Table 1; Lachner, 1986). *Remora osteochir* is also almost always attached to a species of billfish, specifically species of the subfamily Istiophorinae (with about 11 species worldwide). This fish exhibits a high level of host preference commonly using only a few potentially available host species (Table 2; Cressey and Lachner 1970).
Remora remora (Linnaeus, 1758), the common remora, is a very common fish that can reach a maximum length of 60 cm. It is distributed in warm circumglobal waters, and is widespread in the eastern Atlantic (Lachner, 1986). It is characterized by: 16 to 20 disc laminae; 21 to 26 dorsal-fin rays; 20 to 24 anal-fin rays; 25 to 32 pectoral-fin rays; 27 vertebrae; 3-8 + 23-30 gillrakers. It is a short stout fish with a medium sized disc reaching to a vertical with the ends of the pectoral-fins; measuring 34 to 43 % SL in length and 15 to 21 % SL in width (Table 1; Lachner, 1986). Remora remora is commonly found on a wide variety of sharks, and occasionally on billfishes and turtles (Table 2; Cressey and Lachner 1970).

Remorina albescens (Temminck and Schlegal, 1845), the white suckerfish, is an uncommon fish that can reach a maximum length of 25 cm. It is found worldwide, in warm, open seas, but is seldom encountered in shallow waters. It is not reported from the Mediterranean (Lachner, 1986). The species is characterized by: 12 to 13 disc laminae; 18 to 21 dorsal-fin rays; 18 to 23 anal-fin rays; 18 to 21 pectoral-fin rays; 23 vertebrae; 0-1 + 11-13 gillrakers. These fish are extremely stout, with a broad disc measuring 34 to 41 % SL in length and 23 to 26 % SL in width (Table 1; Lachner, 1986). Remorina albescens is almost exclusively found on manta rays, where they enter both the mouth and gill chambers. This fish exhibits a high level of host preference commonly using only a few host species (Table 2; Cressey and Lachner, 1970).

The single known fossil group of remoras, Optithomyzonidae, has been thought to be somewhat of a transitional form (Gudger, 1926). The disc is fully formed but quite different from the modern species. It is narrow, pointed posteriorly, and extends only midway onto the cranium. The laminae are approximately square, while
extant remoras have laminae that are much wider than long. It is characterized by 8 disc laminae, 28 dorsal-fin rays, 23 anal-fin rays, 16 pectoral-fin rays, 23 vertebrae, and 7 pelvic rays. The disc is very short comprising only 10% of the SL. It has a broad opercle, the jaws are of equal length, and it has a deeply forked caudal fin. It has a stout body, a long head, and a short but deep caudal peduncle (Gudger, 1926). Due to the incomplete migration of the disc, and the low number of laminae this species is thought to be most closely related to Phtheirichthys (Gudger, 1926).

As noted earlier, the family Coryphaenidae has two species. Coryphaena equiselis Linnaeus 1758 is a large pelagic fish that can reach a maximum length of 2 m. They are fast swimming fish that are relatively common in most tropical to subtropical waters worldwide (Palko et al., 1982). This species is characterized by: 52-59 dorsal-fin rays; 23-29 anal-fin rays; 33 vertebrae; the tongue has a broad square tooth pattern (Palko et al., 1982). They maintain a close association with floating and drifting debris in the open sea (Hunter and Mitchell, 1967).

Coryphaena hippurus Linnaeus 1758 is also a large pelagic fish that can reach a maximum length of 2 m. This fast swimming fish is common in most tropical and subtropical waters of the world (Palko et al., 1982). This species is characterized by: 58-66 dorsal-fin rays; 25-31 anal-fin rays; 31 vertebrae; the tongue has an oval tooth pattern (Palko et al., 1982). This species also maintains a close association with floating and drifting debris (Hunter and Mitchell, 1967).

The family Rachycentridae has a single species, Rachycentron canadum, which is a pelagic fish that can reach a maximum length of 1.5 m. It is widely distributed in most tropical, and subtropical waters worldwide, however it is not found in the Mediterranean or the eastern Pacific (Shaffer and Nakamura, 1989). This fish is
characterized by: 7-9 isolated dorsal-fin spines; 28-33 dorsal-fin rays; 1-3 anal-fin spines; 23-27 anal-fin rays; 24-28 vertebrae (Shaffer and Nakamura, 1989).

*Rachycentron* is known to be an associate of other large fishes such as mantas and sharks; they are also commonly found under and around floating and drifting objects (Baughman, 1950).

To examine the relationships of the remoras it is useful to know where they have been grouped historically. The remoras have been placed with many different families of fishes through history due to the belief that they are generalized percoid fishes with a single extremely modified structure, the first dorsal-fin. A brief account of the systematic history of the group follows.

Remoras have been known since the time of Aristotle (384-322 BC). There are few fishes that captivated people’s imaginations of that time more than the remora. The cause of this fascination was the widely held belief that this fish was able to arrest seagoing vessels, thus it’s name, *Remora* from the Latin, a delay, a hindrance. This power to counteract strong physical forces projected the remora into seafaring folklore; however, early descriptions indicate that the fish was poorly known. Aristotle described the remora as a blenny-like fish without any mention of the cephalic disc. Pliny (23-79 AD) described the remora as an animal resembling a large slug. He also perpetuated the myths surrounding these fishes with his account of the most auspicious accomplishment of the remora in ancient times, it’s alleged involvement in the battle of Actium. Antonius’ flagship was inexplicably stopped in spite of the 400 oarsmen. Upon examination of the hull a remora was found, giving indisputable proof that it had stopped the ship. Pliny also reported that a remora could be used to prevent miscarriages and aid in permitting a foetus to reach term.
In the 16th century the remora was still considered a hazard to seafarers but Rondelet (1554) noted the discrepancies in previous physical descriptions and came to the conclusion that the remora was in fact a *Petromyzon*, a group of agnath fishes well known to him. According to Lichtenstein (1961), Marcgrave was one of the first to note that remoras are found not only on ships but also on large fishes. This findings help to explain the tale told by Martyr (1511) regarding Cuban natives fishing with remoras. Martyr, a member of Columbus's second voyage to the New World, described the remora as an eel-like fish with a cowl on it head which it used to catch its prey.

Arteci and Linnaeus (1738) defined the genus *Echeneis* and placed it in the order Malacopterygii next to *Coryphaena*, due to the lack of spinous rays in the single dorsal fin. In a later volume of Systema Naturae (1758) Linnaeus moved both *Echeneis* and *Coryphaena* to the order Thoracici. Cuvier and Valenciennes (1828) placed *Echeneis* in the order Malacopterygiens subbrachiens, family Discoboles, after *Lepadogaster* and *Cyclopterus*.

Blainville (1822), regarded the cephalic disc as a modified first dorsal fin, however he did not suggest removing *Echeneis* from the Malacopterygii. Swainson (1839) elevated the genus *Echeneis* to familial rank (Echeneidae) placing it in the order Acanthopteryges where it was considered an aberrant family in the tribe Micropleptes. The new family was place after the families Scombridae and Zeidae but before the families Centriscidae and Coryphaenidae. Agassiz (1843) also described the cephalic disc as a modified first dorsal fin and subsequently removed *Echeneis* from the Malacopterygii and placed it in the family Scombridae. Bleeker (1859) gave the genus familial (Echenoidei) and also ordinal rank (ordo 38 Discocephali) which was placed between his ordo 37 Fistularidae and ordo 39 Cyclopteri. Cope (1870) returned the
family to the scombroid group, specifically placing them with the Carangidae, and moved them to the order Percomorphi, suborder Distegi.

Gill (1882) considered the remoras a member of the acanthopterygians, due to the true spines in the ventral fins. Gill also argued that since Echeneis has a simple and not a double "basis cranii" it should not be a member of the suborder Distegi with Scombridae and Carangidae. Gill thought that remoras were not only the sole members of the family Echeneidae but also distinct enough to be the sole members of the new suborder Discocephali. He suggested that the suborder may be related to either the goboids or the blennioids.

Regan (1912) elevated Gill's suborder Discocephali to ordinal level in his treatment of the anatomy of the remora disc and fin structures. He considered the order to be composed of two families, the Echeneidae, with about ten species, and the Opisthomyzonidae, known from a single fossil. Due to similarity in fin structure, Regan (1912) suggested that remoras may have evolved from a percoid of the type similar to Pomatomidae, Carangidae, or Rachycentridae.

Gregory (1933) stated that the true affinity of remoras lay somewhere within the Percomorphi but remained a mystery; however he did suggest a possible relationship with primitive percoid similar to Centrolophidae. Centrolophids are known to lurk under floating objects, and Gregory felt this behaviour was a plausible first step in an evolutionary scenario of disc development.

Berg (1940) considered the remoras an order (Order 109 Echeneiformes) placing them between Mastacembeliformes and Tetraodontiformes.

Golvan (1965) placed the remoras in their own suborder (Echeneoidei) in the order Perciformes. While the coryphaenids were placed in the order
Coryphaeniformes with the families Bramidae, Steinegeriidae, Dianidae, Elephenoridae, and Pteraclidae, the family Rachycentridae was placed in the suborder Percoidei.

The classification of Greenwood et al. (1966) reduced the order Discoccephali to the familial level, Echeneidae, and placed it in the order Perciformes, suborder Percoidei. Both the Coryphaenidae and the Rachycentridae were also placed in this suborder.

Gosline (1970) removed the remoras from the order Perciformes, reelevating them to ordinal status, Echeneiformes. The order was placed between Tetraodontiformes and Mastacembeliformes. However, he did note that the remoras may indeed be closely related to percoid fishes like Rachycentridae.

Freihofer (1978) noted that remoras have an anterior extension of the anterior nasal canal that is surrounded by two tubular ossifications. He also noted that this condition is shared to varying degrees with Nematistiidae, Carangidae, Coryphaenidae, and Rachycentridae. Recent classifications (Johnson 1984; Smith-Vaniz, 1984) recognized these five families as a distinct suborder, Carangoidei, and cited Freihofer's character along with the presence of small cycloid scales as synapomorphies of the group. Within the Carangoidei, Echeneidae has been grouped with both Coryphaenidae and Rachycentridae. This clade, superfamily Echeneoidea (Johnson 1993), is supported by six characters (Johnson, 1984; Smith-Vaniz, 1984): absence of predorsal bones, anterior shifting of the first dorsal-fin pterygiophore, presence of several anal-fin pterygiophores anterior to the first hemal spine, loss of the beryciform foramen in the ceratohyal, tubular ossifications surrounding both prenasal canal units, larvae very elongated with late dorsal-fin completion. Within the clade,
there is debate over which family is more closely related to the Rachycentridae. Regan (1912) suggested the possibility of a Rachycentridae-Echeneididae relationship based on superficial external appearances and similar osteology, while Johnson (1984) suggested a Coryphaenidae-Rachycentridae clade based on larval characters. We can examine the hitchhiking behaviour in light of these two hypotheses. If Regan's hypothesis is the more strongly supported for the group then there is a step by step change from associating with objects (dolphins) to associating with objects and following fishes (cobia) to the hitchhiking behaviour (remora). However, if Johnson's hypothesis is the more strongly supported relationship then the following behaviour (cobia) and the hitchhiking behaviour (remora) have evolved convergently, or the following behaviour has been lost in the dolphins. In general, associations of with floating and drifting objects, and other fishes as in the cobia, are logical precursors to the remora hitchhiking behaviour.

These two competing hypotheses of the remora sister-group relationship are to be compared to the resultant phylogeny of the group based on morphology of all extant species. The study examined the relationships of the eleven species in the superfamily Echeneoidea. The osteology of the axial, appendicular and dermal skeleton along with external characters were used to infer the phylogenetic relationships of the superfamily. A carangid, *Seriola dumerili*, was the primary outgroup while Nematistiidae served as the secondary outgroup and the root of the tree.
METHODS

MATERIALS

Materials examined are listed for each species in the following order: catalogue number, number of specimens, and standard length in millimeters in parenthesis. All specimens were cleared, stained and counter-stained (Dingerkus and Uhler, 1977; Taylor and Van Dyke, 1985). Specimens were dissected (denoted with "*"), following the techniques of Weitzman (1974). Figures 1-19, 21, 23, and 24 were drawn with the aid of a camera lucida on a Wild M5 dissecting microscope. The echeneoid species are listed alphabetically within their families, also listed alphabetically, followed by the outgroup species. Abbreviations for collections follow Leviton et al. (1985).

Echeneoidea

Coryphaenidae

Coryphaena equiselis Linnaeus

ROM 1655CS, 1 (54.5)*; ROM 1654CS, 1 (41.5)*.

Coryphaena hippurus Linnaeus

ROM 1204CS, 1 (73.0)*; ROM 1653CS, 1 (62.6)*.

Echeneidae

Echeneis naucrates Linnaeus

ROM 1656CS, 1 (110.6)*; USNM 206664, 1 (87.5)*.

Echeneis neucratoides Zuiw

ROM 1683CS, 1 (122.6)*; ROM 1687CS, 1 (146.1)*; ROM 16184CS, 1 (96.8); ROM 1685CS, 1 (90.1); ROM 1686CS, 1 (97.3); ROM 1688CS, 1 (147.6).
*Phteirichthys lineatus* (Menzies)

ROM 1691CS, 1 (69.9)*; ROM 1689CS, 1 (64.2); ROM 1690CS, 1 (61.1); ROM 1692CS, 1 (53.1); ROM 1693CS, 1 (57.3); SIO 72-288, 1 (158.0)*; SIO 67-290-42, 1 (96.0).

*Remora australis* (Bennett)

CAS 26663, 1 (158.3)*; CAS 68165, 1 (127.1); SIO 64-452, 1 (148.5)*.

*Remora brachyptera* (Lowe)

ROM 1676CS, 1 (112.0)*; ROM 1697CS, 1 (109.1)*; ROM 1652CS, 1 (70.4); ROM 1675CS, 1 (104.0); ROM 1677CS, 1 (84.3); ROM 1678CS, 1 (88.7); ROM 1679CS, 1 (103.7); ROM 1680CS, 1 (91.5); ROM 1681CS, 1 (93.7); ROM 1696CS, 1 (125.0); ROM 1698CS, 1 (74.2); ROM 1699CS, 1 (120.7); ROM 1700CS, 1 (98.3).

*Remora osteochir* (Cuvier)

ROM 1665CS, 1 (78.6)*; ROM 1666CS, 1 (80.9)*; ROM 1667CS, 1 (74.2); ROM 1668CS, 1 (72.6); ROM 1669CS, 1 (77.9); ROM 1670CS, 1 (48.4); ROM 1671CS, 1 (73.6); ROM 1672CS, 1 (70.3); ROM 1673CS, 1 (80.7); ROM 1674CS, 1 (63.9); ROM 1695CS, 1 (43.1); USNM 181894, 1 (138.6).

*Remora remora* (Linnaeus)

ROM 1260CS, 2 (94.1*-110.3); ROM 1682CS, 1 (99.7)*; ROM 1652CS, 1 (44.1); ROM 1694CS, 1 (76.1).

*Remorina albescens* (Temminck and Schlegel)

SIO 83-58, 1 (99.5)*; SIO 84-97, 1 (100.8)*.

Rachycentridae
Rachycentron canadum (Linnaeus)

GCRL V73:11710, 1 (138.0)*.

OUTGROUPS

Carangidae

Seriola dumerili (Risso)

ROM 1651CS, 2 (40.1, 60.9)*.

Nematistiidae

Nematistius pectoralis Gill

SIO 64-229-42A, 1 (62.5)*.

METHODS AND TERMINOLOGY

All lengths are standard length (SL) in millimetres (mm) unless otherwise stated, and were measured on cleared and stained specimens. The number of specimens examined (N) are given for each species in Table 1. Standard lengths (SL) were measured from the base of the hypural plates to the tip of the upper jaw. Disc lengths (DL) were defined as the greatest length in the sagittal plane, while disc widths (DW) were defined as the greatest distance in the transverse plane. Length of the second dorsal-fin (D2L) and anal-fin (AL) were measured from the base of the first ray to the base of the last ray. Counts were made with the aid of a Wild M5 dissection microscope and measurements were made with needle tipped dial calipers to the nearest tenth of a millimeter. Disc laminae counts (D1) were defined as the number of paired denticulated laminae. The second dorsal- (D2), anal- (A), and pectoral-fin (P) rays were all counted in the same manner. Spines were defined as ossified
unsegmented rays. The last rays of the anal- and second dorsal-fin are split very close to their origin but were counted as a single ray since they originate from the same pterygiophore. Caudal-fin ray counts (C) were separated into procurent and principal rays. Principal rays were defined as long, segmented and simple rays supported by the hypurals, while the procurent rays are small unsegmented rays on the dorsal and ventral edges of the fin. Vertebra counts (V) were divide into abdominal (V_ab) and caudal vertebrae (V_cd). The distinction between the abdominal and caudal series of vertebrae is clear in all species examined, with the first caudal vertebra having a much longer haemal spine than those preceding it, and it supports along its anterior edge the first one or more anal-fin pterygiophores. The urostylar centrum (made up of fused preural centra 1 + 2 and the ural centrum) is included as a single unit in the number of caudal vertebra. The discs of larger specimens were removed from the body to allow accurate counts of vertebrae. Gillraker counts (Gr) were obtained for the 1st left gill arch, rudiments were not counted. Branchiostegal ray counts (Bra) were made for each side.

The osteological terminology employed follows the current usage as exemplified by Patterson and Johnson (1995) and Tyler et al. (1999). The terms interneural space and interhaemal space are used in the revised sense of Baldwin and Johnson (1993), with the preneural and prehaemal spaces being those in front of the first neural and haemal spines and the first space being that between the first and second neural or haemal spines. Statements about pleural and epineural ribs are based on ossified elements and do not include what are sometimes ligamentous elements. The elements of the sucking disc are assigned homologies following Baudelot (1867) and Regan (1912), with the exception of the final element, the paired
disc laminae. Both Baudelot and Regan regarded the paired disc laminae and the associated reduced medial spine to be a modified dorsal-fin spine. The paired disc laminae are a laterally expanded distal pterygiophore, while the medial spine is a reduced dorsal-fin spine.

The host association data shown in Table 2 were compiled from the literature and a examination of various collections. The data from the literature were obtained from the following sources: Cressey and Lachner, 1970; Morota and Fujita, 1995; Pampillon, 1996; Schwartz and Lindquist, 1987; Strasburg, 1959. The data from the various collections were obtained from directly searching the records of the Royal Ontario Museum (ROM) and, by searching on-line, the records of the collections at the Scripps Institute of Oceanography (SIO) and the National Museum of Natural History (USNM).

The term Echeneoidea refers to Johnson's (1984) clade of Echeneidae + Coryphaenidae + Rachycentridae; however its use does not imply relationships within the clade. If a species is of a monotypic genus (e.g. Remora) or if a genus has only a single species examined in this work (e.g. Seriola), then the taxon is usually referred to by the generic name alone.

In addition to the outgroup species examined, the work of Rosenblatt and Bell (1976) was consulted for information on Nematistiiidae and that of Suzuki (1962) for information on Carangidae. For the systematics of the family Echeneidae, the work of Lachner (1966, 1981, and 1986) and of Paulin and Habib (1982) were consulted.

The term consistent synapomorphy is used to denote those character states that are unambiguous, non-reversed, and non-parallel (i.e., exhibit no homoplasy) within both the 11 Echeneoidea taxa and the 2 outgroup taxa. These
statements regarding homoplasy are restricted to the taxa represented in the analysis.

PHYLOGENETIC METHODOLOGY

Of the 138 putatively informative characters examined (Table 3) all were coded as both an ordered and unordered transformation series for analysis in two separate data sets. The ordering procedure required additive binary coding to be used for characters 5, 24, and 27 to code for the hypothesized evolutionary pathways (see individual characters for details). Since additive coding produced two transformation series for each of these characters all three were reweighted to compensate. Several characters could not logically be ordered and as such were coded as unordered in both analyses. They were characters: 0, 45, 48, 65, 91, 105, 106, 126, 128, and 134. The ordering of characters requires additional identification, beyond character state delineation, of homology. Since there were no ontogenetic or other data that might justify ordering of these individual transformation series all characters have also been coded as unordered transformation series. The data were analyzed using Hennig 86 (vers. 1.5, J.S. Farris, 1988), NONA (vers. 1.8, P.A. Goloboff, 1993) and CLADOS (vers. 1.2, K. Nixon, 1992). Characters were analyzed using the "ie**" command (implicit enumeration) of Hennig 86, the results were output as tree files and read into CLADOS for character state distributions.

Characters were optimized using the accelerated transformation (ACCTRAN) option in CLADOS in which reversals are favored over parallelisms for homoplastic characters. Ambiguous character optimizations (i.e., ACCTRAN maps the character differently than DELTRAN) are noted in the Character Optimization section.
Characters with taxa coded as inapplicable ("-") were optimized using DELTRAN since treating inapplicable characters as missing data can lead to inappropriate conclusion about character state designations. By coding inapplicable characters as unknown the data were treated in the same manner as unknown and polymorphic characters. When in fact there is a logical difference between these three types of data. For a binary character, unknown data could be either 0 or 1, polymorphic data would be both 0 and 1, and inapplicable data would be neither 0 nor 1. Thus inapplicable data must be treated differently then either of these former types of data. Maddison (1993) suggested coding the inapplicable state as a third character state and running the character unordered. However if the same complex is coded as inapplicable, as in all characters pertaining to the disc, then the absence condition would be coded numerous times. Since this would violate the independence of characters it is an invalid approach in this instance. Taxa with inapplicable states were coded as if they were unknown characters but they were subsequently optimized differently than unknown characters. DELTRAN optimization was used to map the distribution of inapplicable characters.

Tree topologies were verified using NONA, the Wagner ("w") command was set to ten to generate trees, these were then branch swapped with the total branch swapping ("TBR-swapping") command. The support for each clade, as branch support values (Bremer, 1988 and 1994), were evaluated using the "branch support" option in NONA. Ten thousand trees were generated that were a maximum of forty steps longer than the most parsimonious tree, consensus trees were then derived from these trees to determine branch support. These values represent the number of extra steps needed to be added to the most parsimonious tree that will collapse that branch in the strict
consensus of all trees of that length and shorter. These values are considered to be good indicators of ranked nodal support (Doyle, 1998; Tyler et al., 1999).
RESULTS

List of Character States

All putatively informative characters were assigned a two part numeric identifier and are listed roughly from the anterior to the posterior. The numeric identifier represents the character number-character state, such that 0-1 would represent a taxon with character state 1 (three or more extrascapulars) of character number 0 (number of extrascapulars). Following each character state definition the taxa observed to exhibit that state are listed. The full data matrix is given in Table 3.

Character 0). Number of extrascapulars (not shown): (0) two extrascapulars, *Nematistius* and *Seriola*; (1) three or more extrascapulars, *Coryphaena* and *Rachycentron*; (2) one extrascapular, *Echeneidae*. This character was unordered in all analyses.

Character 1). Supraoccipital crest (Figures 1-3): (0) present, *Nematistius*, *Seriola*, and *Coryphaena*; (1) absent, *Rachycentron* and *Echeneidae*.

Character 2). Length of the supraoccipital (Figures 1-3): (0) long, from the level of the mid-orbit extending past the epioccipitals, *Seriola* and *Nematistius*; (1) medium length, from the level of the mid-orbit to the posterior edge of the epioccipitals or from the posterior edge of the orbit to past the epioccipitals, *Coryphaena* and *Rachycentron*; (2) short, commencing posterior to the orbit and ending at the posterior edge the epioccipitals, *Echeneidae*.

Character 3). Articulation of the supraoccipital with the exoccipitals (Figures 1-3): (0) supraoccipital extended ventrally to contact the exoccipitals on the posterior surface of the cranium, *Nematistius*, *Seriola*, *Coryphaena*, and
*Rachycentron*; (1) exoccipitals level with the supraoccipital and in contact on the dorsal surface of the cranium, Echeneidae.

Character 4). Shape of the posterior margin of the epioccipital (Figures 1-3): (0) pointed distal lateral edge, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) rounded posterior margin, Echeneidae.

Character 5). Development of a distal lateral shelf on the epioccipitals (Figures 1-3): (0) absent or poorly developed, *Seriola* and *Nematistius*; (1) present, producing a small shelf, *Echeneis* and *Pthirichthys*; (2) present, producing a large shelf, *Remora* and *Remorina*; (3) distal edge only slightly extended with the posterior edge expanded and pointing posteriorly and laterally, *Coryphaena*; (4) distal edge only slightly extended with the posterior edge expanded and pointing posteriorly, *Rachycentron*. This character was recoded using additive binary coding for the ordered analysis. The character was broken down and coded such that state 1, state 3, and state 4 all evolved independently from state 0 while state 2 evolved from state 1. Thus the first pathway was 0-1-2, the second pathway was 0-3, and the third pathway was 0-4. This final code would be an autapomorphy and thus uninformative, however it was retained in the analysis so that the ordered and unordered analyses would be comparable. This produced two new additive binary coded “characters”, which are given one-half the weight of regular characters.

Character 6). Presence of the distal lateral shelf on the parietal (Figures 1-3): (0) absent, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) present, formed as a thin plate extending horizontally, Echeneidae.
Figure 1. Dorsal view of the neurocranium (characters 1-18) of A) Coryphaena equiselis; B) Rachycentron canadum. Scale bars are 1mm.
Character 7). Shape of the parietal (Figures 1-3): (0) four sided, Nematistius, Seriola, Coryphaena, R. australis, R. osteochir, R. remora and Remorina; (1) three sided bone which is pointed medially, Rachycentron, Echeneis, Phtheirichthys, and R. brachyptera.

Character 8). Frontal crest (Figures 1-3): (0) present, Seriola and Nematistius; (1) absent, Coryphaena, Rachycentron, and Echeneidae.

Character 9). Distal lateral shelf present on the frontals (Figures 1-3): (0) present, Nematistius, Seriola, Echeneis, Remora, and Remorina; (1) absent, Coryphaena, Rachycentron and Phtheirichthys.

Character 10). Position of the anterior edge of the distal lateral shelf (Figures 1-3): (0) commencing level with the anterior edge of the orbit, Nematistius and Seriola; (1) commencing level with or posterior to the posterior edge of the orbit, Echeneis, Remora, and Remorina; (2) commencing posterior to the rear edge of the frontals, Coryphaena, Rachycentron, and Phtheirichthys.

Character 11). Degree of the roof of the orbits formed by the frontals (Figures 1-3): (0) covering the entire roof, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) forming the majority of the roof, R. osteochir and Remorina; (2) forming a small portion of the roof, Echeneis, Phtheirichthys, R. australis, R. brachyptera, and R. remora.

Character 12). Pattern of the sensory canals on the frontal (Figures 1-3): (0) canals radiate anteriorly and laterally from the posterior center of the bone, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) canals running in a single line around the distal edge of both frontals, Echeneidae.

Character 13). Width of the frontals (Figures 1-3): (0) slender compared with the
Figure 2. Dorsal view of the neurocranium (characters 1-18 and 30) of A) Phtheirichthys lineatus; B) Echeneis naucrates. Scale bars are 1mm.
length, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, *Echeneis* and *Phtheirichthys*; (1) broad compared with the length, *Remora* and *Remorina*.

Character 14). Dorsal surface of the frontals (Figures 1-3): (0) level throughout entire length, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) sharply curved ventrally at mid-orbit level, flattening out creating a deep depression in the center of the cranium, *Echeneidae*.

Character 15). Size of the ethmoid (Figures 1-3): (0) small, forming a small portion of the anterior dorsal surface of the cranium, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) large, expanded forming a large portion of the anterior dorsal surface of the cranium, *Echeneidae*.

Character 16). Shape of the dorsal aspect of the ethmoid (Figures 1-3): (0) triangular with the straight edge oriented posteriorly, *Seriola* and *Nematistius*; (1) rhomboid with the shorter edge forming the posterior margin, *Coryphaena* and *Rachycentron*; (2) oval, *Echeneidae*.

Character 17). Anterior extension of the ethmoid (Figures 1-3): (0) rod-shaped arm extending anteriorly and sloping ventrally, *Nematistius*, *Seriola*, and *Coryphaena*; (1) wide arm extending anteriorly and sloping ventrally, *Rachycentron*; (2) no anterior extension, anterior margin flat or slightly concave, *Echeneidae*.

Character 18). Dorsal aspect of the lateral ethmoid (Figures 1-3): (0) forming the anterior wall of the orbit, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) forming the anterior wall and a small portion of the roof of the orbit, *R. australis*, *R. brachyptera*, and *R. osteochir*; (2) forming the anterior wall of the orbit and the distal edge of the roof, leaving an opening
Figure 3. Dorsal view of the neurocranium (characters 1-18 and 30) of A) *Remora osteochir*; B) *Remorina albescens*. Scale bars are 1mm.
in the center of the roof of the orbit, *Echeneis, Phtheirichthys, R. remora,* and *Remorina.*

Character 19). Vomer to ethmoid articulation (Figures 2 and 3): (0) vomer ventral to ethmoid, *Nematistius, Seriola, Coryphaena,* and *Rachycentron*; (1) vomer anterior edge level with ethmoid, Echeneidae.

Character 20). Basioccipital facet for articulation with the first vertebrae (Figure 4): (0) ventral to the exoccipitals, *Nematistius, Seriola, Coryphaena,* and *Rachycentron*; (1) level with the exoccipitals, Echeneidae.

Character 21). Exoccipital facets for articulation with the first vertebrae (Figure 4): (0) ventrally oriented, *Nematistius, Seriola,* and *Coryphaena,* (1) rotated medially, *Rachycentron,* (2) posteriorly oriented, Echeneidae.

Character 22). Parasphenoid shape (Figure 4): (0) cross-shaped bone
which is slender anterior to the alar process, *Nematistius, Seriola, Coryphaena,* and *Rachycentron*; (1) cross-shaped bone which is wide anterior to the alar process, Echeneidae.

Character 23). Degree of extension of the lateral process of the prootic (Figure 4): (0) short, ending before the sphenotic, *Nematistius, Seriola, Coryphaena,* and *Rachycentron,* (1) long, extending to near the edge of the cranium posterior to the sphenotic, Echeneidae.

Character 24). Width of the lateral process of the prootic relative to the alar process of the parasphenoid (Figure 4): (0) equal width, *Seriola* and *Nematistius*; (1) thinner, *Coryphaena*; (2) equal width, with a small anteriorly directed flange on the anterior margin of the lateral process of the prootic, *Echeneis, Phtheirichthys,* and *Rachycentron,* (3) wider, *Remora* and *Remorina.* This
character was recoded using additive binary coding for the ordered
analysis. The character was broken down and coded such that state 1 and
state 2 both evolved independently from state 0 while state 3 evolved from
state 2. Thus the first pathway was 0-1 and the second pathway was 0-2-3.
Two new additive binary coded “characters” are produce, both were given
one-half the weight of other characters.

Character 25). Presence of a deep socket for articulation of the hyomandibular on the
Sphenotic (Figure 4): (0) absent, Nematistius, Seriola, Coryphaena, and
Rachycentron; (1) present, Echeneidae.

Character 26). Presence of a deep socket for articulation of the hyomandibular on the
ventral surface of the pterotic (Figure 4): (0) absent, Nematistius, Seriola,
Coryphaena, and Rachycentron; (1) present, Echeneidae.

Character 27). Shape of the sphenotic (Figure 4): (0) square, protruding laterally,
Nematistius, Seriola, and Rachycentron; (1) square, distal lateral edge
rounded curving with the margin of the cranium, not protruding,
Coryphaena; (2) rectangular, expanded ventrally on the posterior edge to
form an peg for articulation with the hyomandibular, Echeneis and
Phthisichthys; (3) rectangular, expanded ventrally on the posterior edge to
form a large peg for articulation with the hyomandibular, Remora, and
Remorina. This character was recoded using additive binary coding for the
ordered analysis. The character was broken down and coded such that
state 1 and state 2 both evolved independently from state 0 while state 3
evolved from state 2. Thus the first pathway was 0-1 and the second
pathway was 0-2-3. Two new additive binary coded “characters” were produced, both were given one-half the weight of regular characters.

Character 28). Pterosphenoids (Figure 4): (0) extend slightly ventrally, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) extend to parasphenoid completely separating the two halves of the orbit, Echeneidae.

Character 29). Shape of the parasphenoid process of the vomer (Figure 4): (0) pointed, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) forked, Echeneidae.

Character 30). Intercalar articulation with the ventral limb of the posttemporal (Figures 2 and 3): (0) ventral limb of the posttemporal articulates on the surface, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) ventral limb of the posttemporal insert into a specialized pocket in the posterior face of the intercalar, Echeneidae.

Character 31). Ventral surface of the lateral ethmoid (Figure 4): (0) surface level or center portion extended ventrally, Nematistius, Seriola, and Coryphaena; (1) both lateral edges (medial and distal) extended ventrally, Rachycentron; (2) distal lateral edge greatly expanded ventrally forming a peg which is the point of articulation with the ectopterygoid, Echeneidae.

Character 32). Depth of the cranium (not shown): (0) deep, Nematistius, Seriola, and Coryphaena; (1) cranium somewhat depressed, Rachycentron; (2) cranium depressed, Echeneidae.

Character 33). Palatine maxillary process (not shown): (0) large, extending dorsally over the maxilla, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) small, extending slightly anteriorly, level with the maxilla, Echeneidae.
Figure 4. Ventral view of the neurocranium (characters 20-31) of A) Coryphaena hippurus, B) Echeneis naucrates. Scale bars are 1 mm.
Character 34). Palatine teeth (Figures 7 and 8): (0) present, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, and *Phtheirichthys*; (1) teeth absent, *Echeneis*, *Remora*, and *Remorina*.

Character 35). Maxilla shape (Figure 5 and 6): (0) anterior groove for the ascending process of the premaxilla, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) depressed and reduced in size, without an anterior groove, *Echeneidae*.

Character 36). Supramaxilla (Figures 5 and 6): (0) present, *Nematistius*, *Seriola*, and *Coryphaena*; (1) absent, *Rachycentron* and *Echeneidae*.

Character 37). Ascending process of the premaxilla (Figures 5 and 6): (0) present, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) absent, *Echeneidae*.

Character 38). Teeth on the premaxilla (Figures 5 and 6): (0) small canine teeth only, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, *Phtheirichthys* and *R. australis*; (1) small canine teeth and a single row of comb-like teeth on the lateral dorsal edge of the premaxilla, *Echeneis*, *R. brachyptera*, *R. osteochir*, and *R. remora*, and *Remorina*.

Character 39). Dentary shape (Figures 5 and 6): (0) ventral process slightly shorter than the dorsal process, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) the ventral process short, approximately one-half the length of the upper section, *Phtheirichthys*; (2) ventral process very short, less than one-half the length of the dorsal process, *Echeneis*, *Remora*, and *Remorina*.

Character 40). Teeth on the dentary (Figures 5 and 6): (0) several rows of slightly
Figure 5. Left lateral view of the dentaries, anguloarticulars, maxilla, and premaxilla (characters 35-40) of A) Coryphaena equiselis; B) Phtheirichthys lineatus.
Scale bars are 1mm.
Figure 6. Left lateral view of the dentary, anguloarticular, maxilla, and premaxilla (characters 35-40) of *Echeneis naucrates*. Scale bar is 1 mm.
recurred canines, all approximately equal in size, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, and *Echeneis*; (1) anterior teeth significantly enlarged and strongly recurved, *Phteiirthyths*; (2) outer row of teeth significantly enlarged and recurved, *Remora* and *Remorina*.

Character 41. Hyomandibular shape (Figures 7 and 8): (0) deep and slender, *Nematistius*, *Seriola*, and *Coryphaena*; (1) short and wide, *Rachycentron*, *Echeneis*, and *Phteiirthyths*; (2) short and wide with a posteriorly oriented spur on the dorsal posterior margin, *Remora* and *Remorina*.

Character 42. Metapterygoid depth (Figures 7 and 8): (0) deep, much deeper than symplectic, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, and *Remorina*; (1) medium, depth approximately equal to the symplectic depth, *Remora*; (2) thin, shallower than the symplectic, *Phteiirthyths*, and *Echeneis*.

Character 43. Endopterygoid (Figures 7 and 8): (0) present, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) absent, Echeneidae.

Character 44. Ectopterygoid shape (Figures 7 and 8): (0) with a short dorsal posteriorly projecting process, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) with a long dorsal posterior projecting process and a facet on the anterior process for articulation with the lateral ethmoid, Echeneidae.

Character 45. Articulation of the metapterygoid to the ectopterygoid (Figures 7 and 8): (0) metapterygoid slightly overlaps the small dorsal posterior process of the ectopterygoid, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) metapterygoid with a long anterior process inserting onto a shelf produced
Figure 7. Left lateral view of the suspensoria (characters 41-55) of A) Coryphanea equiselis; B) Rachycentron canadum. Scale bars are 1mm.
by the eopterygoid; Echeneis and R. australis; (2) dorsal portion of the
metapterygoid deeply overlapping the dorsal posterior process of the
eopterygoid, Pthieichthys, R. brachyptera, R. osteochir, R. remora, and
Remorina. This character was coded as unordered in all analyses.

Character 46). Length of symplectic posterior crest and the quadrate preopercular
Process (Figures 7 and 8): (0) equal or slightly longer than the main body
of the quadrate, Nemastius and Seriola; (1) longer than main body of
quadrate, Coryphaena, Rachycentron, and Echeneidae.

Character 47). Lateral shelf on the preopercular process of the quadrate (Figures 7 and
8): (0) absent, Nemastius, Seriola, Coryphaena, and Rachycentron; (1)
present, Echeneidae.

Character 48). Articulation of quadrate with the articular (Figures 7 and 8): (0)
postarticular process of the articular straight extending past the ventrally
angled condyle of the quadrate, Nemastius, Seriola, and Rachycentron;
(1) postarticular process curved dorsally forming a socket for the ventrally
angled quadrate condyle, Coryphaena; (2) postarticular process curved
slightly dorsally forming a small socket for the straight anteriorly oriented
condyle of the quadrate, Echeneidae. This character was coded as
unordered in all analyses.

Character 49). Notch in the posterior dorsal margin of the opercle (Figures 7 and 8): (0)
present, Nemastius, Seriola, Coryphaena, and Rachycentron; (1) absent,
Echeneidae.

Character 50). Shape of the opercle (Figures 7 and 8): (0) deep, depth greater than
Figure 8. Left lateral view of suspensoria (characters 41-55) of A) *Echeneis naucrates*, B) *Remora brachyptera*; C) *Remorina albescens*. Scales bars are 1 mm.
length, *Nematistius*, *Seriola*, *Coryphaena*; (1) long, length greater than or equal to depth, *Rachycentron* and Echeneidae.

Character 51. Opercular ridge (Figures 7 and 8): (0) absent, opercle level, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) present, bony ridges running from the articular fossa forming an arch, Echeneidae.

Character 52. Shape of the dorsal margin of the opercle (Figures 7 and 8): (0) convex, *Nematistius*; (1) straight, angled posteriorly and dorsally, *Seriola*, *Rachycentron*, *Echeneis*, *Phtheirichthys*, *R. brachyptera*, and *R. remora*; (2) straight, oriented posteriorly, *Coryphaena*; (3) concave, *R. osteochir*, *R. australis*, and Remorina.

Character 53. Anterior wing of the preopercle (Figures 7 and 8): (0) absent or only slightly developed, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) flange well developed, Echeneidae.

Character 54. Size of the dorsally oriented anterior spur on the subopercle (Figures 7 and 8): (0) small and extending midway to point of articulation between opercle and hyomandibular, *Nematistius*, *Seriola*, *Rachycentron*, *R. australis*, and Remorina; (1) large but not extending close to the articulation point of the opercle and the hyomandibular, *Coryphaena*, *Phtheirichthys*, *R. brachyptera*, and *R. remora*; (2) large and extending close to the articulation point of the opercle and hyomandibular, Echeneis and *R. osteochir*.

Character 55. Size of interopercle (Figures 7 and 8): (0) large, *Nematistius*, *Seriola*, and *Coryphaena*; (1) small, small portion of the interopercle visible below the preopercle, *Rachycentron* and Echeneidae.
Figure 9. Left lateral view of the infraorbitals, with a ventral view of the lachrymal inserted above each series, (characters 56-59) of A) Coryphaena equiselis; B) Rachycentron canadum; C) Echeneis naucrates. Scale bars are 1mm.
Character 56). Number of infraorbital (including lachrymal and dermosphenotic, Figure 9): (0) seven, Nemastius; (1) six, Seriola, Rachycentron, and Echeneidae; (2) five, Coryphaena.

Character 57). Shape of the lachrymal (Figure 9): (0) dorsal margin level, shelf, if present, small and from the dorsal portion of the bone, Nemastius, Seriola, and Coryphaena; (1) deep notch in the dorsal margin, shelf protruding medially from the ventral medial surface, Rachycentron and Echeneidae.

Character 58). Position of the sensory canal in infraorbital 2 (Figure 9): (0) sensory canal at the dorsal margin, bony crest forming the ventral margin, Seriola and Nemastius; (1) sensory canal in the center, bony crest forming the dorsal and ventral margins, Echeneidae; (2) sensory canal forms the entire bone, no bony crest, Coryphaena and Rachycentron.

Character 59). Suborbital shelf on infraorbital 3 or 4 (Figure 9): (0) present, Nemastius and Seriola; (1) absent, Coryphaena, Rachycentron and Echeneidae.

Character 60). Insertion of the first branchiostegal ray (Figures 10 and 11): (0) ray inserts into a notch on the ventral margin of the ceratohyal; Nemastius, Seriola, Rachycentron, Coryphaena, and Phtheirichthys; (1) ray inserting midway up the ceratohyal, not inserting into a notch, Echeneis, Remora, and Remorina.

Character 61). Insertion of the second branchiostegal ray (Figures 10 and 11): (0) ray insert into a notch on the ventral margin of the ceratohyal, Nemastius, Seriola, Coryphaena, and Rachycentron; (1) ray inserting midway up the ceratohyal, not inserting into a notch, Echeneidae.

Character 62). Length of the interhyal (Figures 10 and 11): (0) long, rectangular bone
Figure 10. Left lateral view of the hyoid bones (characters 60-68) of A) *Coryphaena equiselis*; B) *Rachycentron canadum*. Scale bars are 1mm.
approximately one-half the depth of the ceratohyal, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) small round bone or absent, Echeneidae.

Character 63). Beryciform foramen (Figures 10 and 11): (0) completely enclosed, *Nematistius* and *Seriola*; (1) absent, *Coryphaena*, *Rachycentron*, and Echeneidae.

Character 64). Position of the dorsal hypohyal (Figures 10 and 11): (0) dorsal to the ventral hypohyal, *Nematistius* and *Seriola*; (1) dorsal and posterior to the ventral hypohyal, *Coryphaena*; (2) posterior and only slightly dorsal to the ventral hypohyal, *Rachycentron* and Echeneidae.

Character 65). Articulation of the ventral hypohyal with the ceratohyal (Figures 10 and 11): (0) posterior face of the ventral hypohyal concave with the ceratohyal inserting into the center, *Seriola* and *Nematistius*; (1) posterior face of the ventral hypohyal concave with a posteriorly oriented spur in the midline, the ceratohyal inserts into the center and is flanked on either side by the spurs, *Coryphaena* and *Rachycentron*; (2) posterior face of the ventral hypohyal straight or slightly convex, a single long spur extends from the ventral edge which articulates with the ventral margin of the ceratohyal, Echeneidae. This character was coded as unordered in all analyses.

Character 66). Shape of the anterior past of the urohyal (Figures 10 and 11): (0) small peg for articulation with basibranchial 1 below a much longer peg projecting anteriorly and dorsally, *Nematistius*, *Seriola*, *Coryphaena*, and
Figure 11. Left lateral view of the hyoid bones (characters 60-68) of A) *Phtheirichthys lineatus*, B) *Echeneis naucrates*. Scale bars are 1mm.
Rachycentron; (1) small peg for articulation with basibranchial 1 with a deep groove in the midline below a short peg, Echeneidae.

Character 67). Depth of posterior end of urohyal (Figures 10 and 11): (0) deep, much deeper than the anterior end, Nematistius, Seriola, and Coryphaena; (1) shallow, only slightly deeper than the anterior end, Rachycentron and Echeneidae.

Character 68). Shape of the posterior end of the urohyal (Figures 10 and 11): (0) simple vertical plate, Nematistius and Seriola; (1) vertical plate with wings on the ventral edge which branch posteriorly to form long thin processes, Coryphaena; (2) both dorsal and ventral portions of the bone expanded laterally forming wings which branch posteriorly, Rachycentron and Echeneidae.

Character 69). Length of the basihyal (Figures 12 and 13): (0) short, equal or slightly shorter than hypobranchial 1, Nematistius, Seriola, Coryphaena, Rachycentron, Phtheirichthys, Remora and Remorina; (1) long, considerably longer than hypobranchial 1, Echeneis.

Character 70). Shape of the posterior margin of the basihyal (Figures 12 and 13): (0) narrow and rounded, Nematistius, Seriola, and Coryphaena; (1) posterior margin rounded with slight notches on the posterior lateral edges, Echeneis, Rachycentron, and Phtheirichthys; (2) posterior margin straight with deep notches on the posterior lateral edges, Remora and Remorina.

Character 71). Shape of the anterior edge of the basihyal (Figures 12 and 13): (0) rounded, Nematistius, Seriola, Coryphaena, Rachycentron, Echeneis, and
Figure 12. Dorsal view of the ventral branchial arches, with the dorsal branchial arches inserted above, (characters 69-82) of A) Coryphaena hippurus; B) Echeneis naucrates. Scale bars are 1 mm. Cartilage is indicated with crosshatching.
_Phtheirichthys_; (1) tip rounded with lateral shelves protruding on either side, _Remora_ and _Remorina_.

Character 72). Teeth on the basihyal (Figures 12 and 13): (0) present, _Seriola_, _Coryphaena_, _Rachycentron_, _Echeneis_, _Phtheirichthys_, _R. brachyptera_, _R. osteochir_, _R. remora_, and _Remorina_; (1) absent, _Nematistius_ and _R. australis_.

Character 73). Shape and size of basibranchial 1 (Figures 12 and 13): (0) anterior portion sloping ventrally, _Nematistius_, _Seriola_, and _Coryphaena_; (1) anterior portion not sloping, bone short and wide, _Rachycentron_ and _Echeneidae_.

Character 74). Length and width of basibranchial 2 (Figures 12 and 13): (0) short and slender, significantly shorter and thinner than hypobranchial 1, _Nematistius_, _Seriola_, _Coryphaena_, and _Rachycentron_; (1) long and wide, equal or wider than hypobranchial 1, _Echeneidae_.

Character 75). Width and shape of basibranchial 3 (Figures 12 and 13): (0) dorsal surface level and thinner than hypobranchial 2, _Nematistius_, _Seriola_, _Coryphaena_, and _Rachycentron_; (1) dorsal surface rounded and wider than hypobranchial 2, _Echeneidae_.

Character 76). Teeth on basibranchial 2 and 3 (not shown): (0) absent, _Nematistius_, _Seriola_, _Coryphaena_, _Rachycentron_, _Remora_, and _Remorina_; (1) present, _Echeneis_ and _Phtheirichthys_.

Character 77). Shape and articulation of hypobranchial 3 (Figures 12 and 13): (0) anterior process of hypobranchial 3 passing ventral to hypobranchial 2, loosely associated with basibranchial 3, _Nematistius_, _Seriola_, _Coryphaena_,
Figure 13. Dorsal view of the ventral branchial arches, with the dorsal branchial arches inserted above, (characters 69-82) of A) Remora remora; B) Remorina albens. Cartilage is indicated with crosshatching. Scale bars are 1 mm.
and Rachycentron; (1) anterior process of hypobranchial 3 curving under basibranchial 3, closely associated with basibranchial 3, Echeneidae.

Character 78). Development of lower pharyngeal toothplate

(ceratobranchial 5, Figures 12 and 13): (0) poorly developed with ceratobranchial 5 only slightly expanded medially, Nematistius, Seriola, and Coryphaena; (1) well developed with ceratobranchial 5 expanded and the two bones almost in contact through most of their length, Rachycentron and Echeneidae.

Character 79). Shape of epibranchial 1 (Figures 12 and 13): (0) long rod-like bone with a short uncinate process towards the end of the bone, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) short bone with a very long uncinate process, Echeneidae.

Character 80). Interarcual cartilage (Figures 12 and 13): (0) long rod-like cartilage, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) short rod-like cartilage, Remora and Remorina; (2) very small plug of cartilage, Echeneis and Phtheirichthys.

Character 81). Shape of epibranchial 2 (Figures 12 and 13): (0) bone widening anteriorly, wider than pharyngobranchial 2, Nematistius, Seriola, Coryphaena, Rachycentron, Echeneis, Phtheirichthys, R. brachyptera, and R. remora; (1) bone width even throughout, thinner than pharyngobranchial 2, R. osteochir, R. australis, and Remorina.

Character 82). Shape and size of pharyngobranchial 1 (Figures 12 and 13): (0) long
Figure 14. Left lateral view of the pectoral girdle (characters 84-94) of Coryphaena equiselis. Scale bar is 1 mm.
slender hour-glass shaped bone, *Nematistius*, *Seriola*, and *Coryphaena*;
(1) short stout bone, *Rachycentron*; (2) small flattened bone, *Echeneis* and
*Pthheirichthys*; (3) tiny rectangular bone, *Remora* and *Remorina*.

Character 83). Lateral edge of gill arches (not shown): (0) gillrakers present,
*Nematistius*, *Seriola*, *Coryphaena*, *Pthheirichthys*, *Remora*, and *Remorina*;
(1) distinct bony plates along entire surface between and overlapping
gillrakers, *Echeneis*.

Character 84). Postcleithra (Figures 14 and 15): (0) two present, *Nematistius*, *Seriola*,
*Coryphaena*, and *Rachycentron*; (1) absent, *Echeneidae*.

Character 85). Supracleithrum (Figures 14 and 15): (0) rectangular shaped bone,
*Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) greatly reduced
forming a small lateral plate between the posttemporal and cleithrum,
*Echeneidae*.

Character 86). Angle of articulation of the posttemporal and supracleithrum with the
Cleithrum (Figures 14 and 15): (0) angle of articulation parallel to the
anterior cleithrum edge, *Nematistius*, *Seriola*, *Coryphaena*, and
*Rachycentron*; (1) angle greatly reduced, *Echeneidae*.

Character 87). Shape of the posttemporal (Figures 14 and 15): (0) medial process
longer and broader than the lateral process, *Nematistius*, *Seriola*,
*Coryphaena*, and *Rachycentron*; (1) three processes, with the medial
process longest both thinner than the remaining processes, *Echeneidae*.

Character 88). Articulation of the first radial with the scapula (Figures 14 and 15): (0)
free from scapula, *Nematistius*, *Seriola*, *Coryphaena*, *Rachycentron*, and
*Pthheirichthys*; (1) in close contact, radial lying in notch in scapula,
Echeneis, R. australis, R. brachyptera, and R. remora; (2) fused to scapula, R. osteocheir and Remorina.

Character 89). Extension of posterior laminar bone of cleithrum (Figures 14 and 15): (0) slightly produced in dorsal portion, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) well developed and in contact with coracoid throughout full length, Echeneidae.

Character 90). Extension of dorsal process of the cleithrum (Figures 14 and 15): (0) extending dorsally beyond the scapula, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) short, not extending beyond the scapula, Echeneidae.

Character 91). Anterior margin of the coracoid (Figures 14 and 15): (0) normal laminar bone, Seriola, Coryphaena, Rachycentron, Echeneis, Phtheirichthys, R. australis, R. brachyptera, and R. remora; (1) reduced laminar bone, Nematistius; (2) small notch present, R. osteocheir and Remorina. This character was coded as unordered in all analyses.

Character 92). Articulation of the posttemporal with the cranium (Figures 14 and 15): (0) medial process onto the epioccipital and the lateral process onto the intercalar, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) medial process onto the epioccipital, middle process onto the intercalar, and the lateral process onto the distal edge of the pterotic, Echeneidae.

Character 93). Branching pattern of the pectoral-fin rays (not shown): (0) most rays branch once ending in two tips, Seriola, Coryphaena, Echeneis, Phtheirichthys, and R. brachyptera; (1) most rays branch twice ending in
Figure 16. Dorsal view of the pelvises (characters 95-100) of A) Coryphaena equiselis; B) Rachycentron canadum. Scale bars are 1mm.
Figure 17. Dorsal view of the pelvises (characters 95-100) of A) *Echeneis naucrates*, B) *Remorina albescens*. Scale bars are 1 mm.
four tips, Nematistius, Rachycentron, R. australis, R. osteochir, R. remora, and Remorina.

Character 94). Articulation of the coracoid to the scapula (Figures 14 and 15): (0) through cartilage, Nematistius, Seriola, Coryphaena, Rachycentron, Phthisirichthys, and R. brachyptera; (1) sutured, Echeneis, R. australis, R. osteochir, R. remora, and Remorina.

Character 95). Length of the posterior process of the pelvic girdle (Figures 16 and 17): (0) long, longer than girdle width, Nematistius, Seriola, and Coryphaena; (1) short, shorter than width, Echeneidae and Rachycentron.

Character 96). Length of the pelvic girdle (Figures 16 and 17): (0) long, length three to four times the width, Nematistius, Seriola, Coryphaena, and Rachycentron; (1) short, length only slightly greater than width, Echeneidae.

Character 97). Width of medial anterior arm of the pelvic girdle (Figures 16 and 17): (0) tubular and slender, Echeneis, Phthisirichthys, R. brachyptera, and R. remora; (1) arm broad with a thin crest associated with it, R. australis, R. osteochir, and Remorina; (-) inapplicable arm not present, Nematistius, Seriola, Coryphaena, and Rachycentron.

Character 98). Distal lateral edge of the pelvic spine (not shown): (0) smooth, Nematistius, Seriola, Rachycentron, and Echeneidae; (1) deep notch, Coryphaena.

Character 99). Subpelvic keel (not shown): (0) well developed, Nematistius, Seriola, and Coryphaena; (1) poorly developed, Echeneidae and Rachycentron.

Character 100). Shape of dorsal wings of the pelvic girdle (Figures 16 and 17): (0) flat
with only a slight dorsal expansion, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) curved with the distal lateral sections elevated dorsally above the medial section, Echeneidae.

The next three characters (101-103) all code different aspects of the same feature, the sucking disc. The modification of the first dorsal fin into a sucking disc is inarguably a unique structure of the family Echeneidae, however the presence of a disc was not included as a character since it is composed of several structures. The individual structures that compose the disc have been coded separately since certain species of remoras have modified these structures to different degrees.

Character 101). Shape of the first proximal pterygiophore of the dorsal-fin (Figure 19):

(0) greatly expanded in the sagittal plane compared to the remaining pterygiophores, *Nematistius*; (1) only slightly expanded in the sagittal plane compared to the remaining pterygiophores, *Seriola*, *Coryphaena*, and *Rachycentron*; (2) greatly expanded laterally, Echeneidae.

Character 102). Shape of the posterior portion of the basal corresponding to the fused medial pterygiophore of dorsal-fin (Figures 18 and 19): (0) slightly laterally expanded in the posterior pterygiophores of the spiny portion of the dorsal-fin, *Nematistius* and *Seriola*; (1) significantly laterally expanded in all pterygiophores in the spiny portion of the dorsal-fin, *Rachycentron*; (2) extremely laterally expanded forming broad wings on either side of the midline, the center section of the bone being square shaped, *Phthisichthys*; (3) extremely laterally expanded forming broad wings on either side of the midline, the center section of the medial pterygiophore
Figure 18. Dorsal view of the medial pterygiophores, distal pterygiophores and reduced spines (characters 102 and 103) of A) *Pitheirichthus lineatus*; B) *Echeneis naucrates*. Denticles of the paired laminae (distal pterygiophores) not shown. Scale bars are 1mm.
Figure 19. Dorsal view of A) the first pterygiophore complex (characters 101 and 107) of Remora brachyptera; B) the first several pterygiophores and dorsal-fin spines (characters 101-103) of Rachycentron canadum. Scale bars are 1 mm.
being rounded and rectangular, *Echeneis*, *Remora*, and *Remorina*; (-) inapplicable, since no spiny portion of the dorsal-fin, *Coryphaena*.

Character 103). Shape of the distal pterygiophores of the dorsal-fin (Figures 18 and 19): (0) slightly laterally expanded in the posterior pterygiophores of the spiny portion of the dorsal-fin, *Nematistius* and *Seriola*; (1) laterally expanded through the entire length of the spiny portion of the dorsal-fin, *Rachycentron*; (2) extremely laterally expanded, denticulated posteriorly, Echeneidae; (-) inapplicable since no spiny portion of the dorsal-fin, *Coryphaena*.

Character 104). Length of the disc (as a percentage of the standard length, Figure 20):  
(0) very short, less than 25% SL, *Phtheirichthys*; (1) short, 26-34% SL, *Echeneis* and *R. brachyptera*; (2) long, 34-40% SL, *R. osteochir*, *R. remora*, and *Remorina*; (3) very long, greater than 40% SL, *R. australis*; (-) inapplicable since the first dorsal-fin is not modified into a disc, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*.

Character 105). Shape of the disc (expressed as disc length/disc width, Figure 20): (0) oval, length twice the width, *Phtheirichthys*, *R. brachyptera*, and *R. remora*; (1) elongate and slender oval, length two and one-half times the width, *Echeneis*, *R. australis*, and *R. osteochir*; (2) short and broad oval, length one and one-half times the width, *Remorina*; (-) inapplicable since the first dorsal-fin is not modified into a disc, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*. This character was coded as unordered in all analyses.

Character 106). Shape of the first dorsal-fin spine (not shown): (0) spine thick;
Figure 20. Dorsal view of the sucking disc (characters 104 and 105) of A) *Phtheirichthys lineatus*, B) *Echeneis naucrates*, C) *Remora remora*, D) *Remora osteochir*, E) *Remorina albescens*, D) *Remora australis*. Figure A modified from fishbase [www.fishbase.org]; Figures B, C, and E are redrawn from Bleecker, 1983; Figures D and F are redrawn from Lachner, 1986.
Nematistius, Seriola, and Rachycentron; (1) greatly reduced in size, spine thin and flat, split anteriorly, Echeneis, Phtheirichthys, and R. australis; (2) greatly reduced in size, spine not split anteriorly, R. brachyptera; (3) greatly reduced in size, anterior end of spine widely split and tubular, R. remora and R. osteochar; (4) greatly reduced in size, spine fused to the medial pterygiophore, Remorina; (5) the first dorsal-fin contains no spines, Coryphaena. This character was coded as unordered in all analyses.

Character 107). Shape of the medial arch on the first pterygiophore complex (Figure 19): (0) arch with a small spur oriented posteriorly, Echeneis and Phtheirichthys; (1) arch with a wide flap of bone, R. australis, R. brachyptera, and R. remora; (2) arch turned so that it oriented anteriorly, R. osteochar; (3) arch reduced and flattened, Remorina; (-) inapplicable since the first dorsal-fin is not modified into a disc, Nematistius, Seriola, Coryphaena, and Rachycentron.

Character 108). Number of rows of spinules on the posterior edge of the distal pterygiophores (not shown): (0) three rows, Echeneis, R. australis, and R. remora; (1) two rows, Phtheirichthys, R. brachyptera, R. osteochar, and Remorina; (-) inapplicable since the first dorsal-fin is not modified into a disc, Nematistius, Seriola, Coryphaena, and Rachycentron.

Character 109). Number of supraneurals (not shown): (0) three, Nematistius and Seriola; (1) none, Coryphaena, Rachycentron, and Echeneidae.

Character 110). Placement of the first dorsal-fin pterygiophore (not shown): (0) inserted
into the second interneural space, *Nematistius* and *Seriola*; (1) inserted into the first interneural space, *Rachycentron*; (2) anterior to the preneural space lying over the cranium, *Coryphaena* and *Echeneidae*.

Character 111). Number of anal-fin spines (not shown): (0) three, *Nematistius* and *Seriola*; (1) two, *Coryphaena*, *Rachycentron*, and *Echeneidae*.

Character 112). Number of anal-fin pterygiophores in the prehaemal space (not shown): (0) a single pterygiophore, in *Nematistius*, *Seriola*, and *R. remora*; (1) more than one pterygiophore, *Coryphaena*, *Rachycentron*, *Echeneis*, *Phtheirichthys*, *R. australis*, *R. brachyptera*, *R. osteochir*, and *Remorina*.

Character 113). First vertebra neural arch (Figure 21): (0) not fused to centrum, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) fused to centrum, *Echeneidae*.

Character 114). Shape of first three vertebrae (Figure 21): (0) neural spines on each, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) broad arch present but no spines until the third or fourth vertebrae, *Echeneidae*.

Character 115). Shape of parapophysis (Figure 21): (0) expanded laterally and ventrally, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) significantly expanded laterally and extending laterally perpendicular to the vertebral column, *Echeneis*, *Phtheirichthys*, *R. australis*, *R. brachyptera*, *R. remora*, and *Remorina*; (2) greatly expanded laterally, expanded posteriorly forming wings, and extending laterally perpendicular to the vertebral column, *R. osteochir*.

Character 116). Position of the epineurals on the first two vertebrae (Figure 21): (0)
Figure 21. Dorsal view of the first three vertebrae (characters 113-116) of A) *Echeneis naucrates*, B) *Remora osteochir*. Scale bars are 1mm.
inserting on the neural arches, *Nematistius*, *Seriola*, and *Rachycentron*; (1) first epineural inserting on the neural arch, with the second epineural inserting on a small parapophysis, *Coryphaena*; (2) inserting on the expanded parapophyses, Echeneidae.

Character 117). Body shape (Figure 22): (0) body compressed and ovoid in lateral view, *Seriola* and *Nematistius*; (1) body fusiform, *Coryphaena*; (2) body depressed and elongated, *Rachycentron*, *Echeneis* and *Phtheirichthys*; (3) body depressed but short and stout, *Remora* and *Remorina*.

Character 118). Length of second dorsal-fin or the soft ray portion of the continuous dorsal-fin base (as a percentage of standard length, Figure 22): (0) long base, 50% SL, *Nematistius*, *Seriola*, *Rachycentron*, *Echeneis*, *Phtheirichthys*, *R. brachyptera*, and *R. osteochir*; (1) short base, less than 30% SL, *R. australis*, *R. remora*, and *Remorina*; (2) very long base, longer than 70% SL, *Coryphaena*.

Character 119). Length of anal-fin base (as a percentage of standard length, Figure 22): (0) short base, less than 26% SL, *Nematistius*, *Seriola*, *Remora*, and *Remorina*; (1) long base, longer than 30% SL, *Coryphaena*, *Rachycentron*, *Echeneis*, and *Phtheirichthys*.

Character 120). Shape of second dorsal-fin or soft ray portion of the continuous dorsal-fin (Figure 22): (0) distal margin concave, *Nematistius*, *Seriola*, *Rachycentron*, *Echeneis*, and *Phtheirichthys*; (1) distal margin straight or slightly convex, *Coryphaena*, *Remora*, and *Remorina*.

Character 121). Shape of the anal-fin (Figure 22): (0) distal margin concave,
Figure 22. Left lateral external view of the entire body (characters 117-121) of A) Coryphaena hippurus; B) Echeneis naucrates; C) Remorina albescens. Images are modified from the fishbase [www.fishbase.org] database.
Nematisti, Seriola, Coryphaena, Rachycentron, Echeneis, and Phtheirichthys; (1) distal margin straight or slightly convex, Remora and Remorina.

Character 122). Number of epurals (Figures 23 and 24): (0) three epurals, Nematisti, Seriola, and Rachycentron; (1) two epurals, Echeneis, Remora, and Remorina; (2) one epural, Coryphaena and Phtheirichthys.

Character 123). Length of the neural spine on preural centrum 2 (Figures 23 and 24): (0) spine absent or short, not extending posteriorly past the middle of the ural centrum, Nematisti, Seriola, Coryphaena, and Rachycentron; (1) full neural spine, Echeneidae.

Character 124). Length of the neural spine on preural centrum 3 (Figures 23 and 24): (0) spine long, extends posteriorly past the hypurapophysis, Nematisti, Seriola, Coryphaena, Rachycentron, R. brachyptera, and R. remora; (1) medium length, extending to between the anterior edge of the ural centrum and the hypurapophysis, R. australis and R. osteochir; (2) spine short, extending only to the anterior edge of the ural centrum, Echeneis, Phtheirichthys, and Remorina.

Character 125). Haemal spine on preural centrum 3 (Figures 23 and 24): (0) spine autogenous, Nematisti, Seriola, Coryphaena, Rachycentron R. australis, R. brachyptera, R. remora, and Remorina; (1) spine fused to centrum, Echeneis, Phtheirichthys, and R. osteochir.

Character 126). Hypurapophysis shape (Figures 23 and 24): (0) spur angled posteriorly, Nematisti, Seriola, C. hippurus, Rachycentron and Phtheirichthys; (1) protruding laterally and the distal tip expanded anteriorly
Figure 23. Left lateral view of the caudal skeletons (characters 122-128) of A) *Coryphaena equiselis*, B) *Rachycentron canadum*. Scale bars are 1mm.
Figure 24. Left lateral view of the caudal skeletons (characters 122-128) of A) *Echeneis naucrates*; B) *Remora brachyptera*; C) *Remora osteochir*. Scale bars are 1mm.
and posteriorly, *C. equiselis*, *Echeneis*, *R. brachyptera*, *R. osteoichir*, and *R. remora*; (2) small peg-like, projecting laterally, *R. australis* and *Remorina*. This character was coded as unordered in all analyses.

Character 127. Articulation of anterior tip of hypural 1 and the parhypural (Figures 23 and 24): (0) no articulation, *Nematistius* and Echeneidae; (1) process on the anterior tip of the hypural wraps around the parhypural below the hypurapophysis, *Seriola*, *Coryphaena*, and *Rachycentron*.

Character 128. Shape and position of the epural(s) (Figures 23 and 24): (0) anterior epural forked ventrally and lying over preural centrum 2, the remaining two epurals are thin and rod-like lying over the ural centrum, *Nematistius* and *Seriola*; (1) a single large epural, lying over the ural centrum, *Coryphaena* and *Phtheirichthys*; (2) two epurals, both lying over the ural centrum, the anterior epural with a flange on the anterior ventral surface, the second is a thin rod-like bone, *Echeneis*, *Remora*, and *Remorina*; (3) three thin rod-like epurals all lying over the ural centrum, *Rachycentron*. This character was coded as unordered in all analyses.

Character 129. Cheeks scales (not shown): (0) several rows of scales present from the posterior edge of the infraorbitals to the anterior margin of the opercle, *Nematistius*, *Seriola*, *Coryphaena*, and *Rachycentron*; (1) scales absent, *Echeneis*, *Phtheirichthys*, *R. australis*, and *R. osteoichir*, (2) scale present from the posterior edge of the infraorbitals to the posterior edge of the opercle, *R. brachyptera*, *R. remora*, and *Remorina*. This character was coded as unordered in all analyses.

Character 130. Shape of the lateral line (not shown): (0) arched lateral line, curving
dorsally around the pectoral-fin area then turning ventrally to run parallel with the body axis, *Nematistius*, *Seriola*, *Coryphaena*, *Phtheirichthys*, *R. australis*, and *Remorina*; (1) straight with a gentle angle, straight through the pectoral-fin area then turning gently ventrally to run parallel with the body axis, *Rachycentron*, *Echeneis*, *R. brachyptera*, and *R. remora*; (2) straight with a sharp angle, straight through the pectoral-fin area then turning sharply ventrally to run parallel with the body axis, *R. osteocephir*.

Character 131). Prenasal canal units (not shown): (0) posterior canal units absent, *Nematistius*; (1) posterior canal units membranous, *Seriola*; (2) tubular ossification surrounding both prenasal canal units, *Coryphaena*, *Rachycentron* and *Echeneidae*.

Characters obtained from the literature, these characters were not independently examined since larval specimens were not included in the study (not shown).

Character 132). Shape of larvae: (0) deep bodied, *Seriola*; (1) greatly elongated, *Coryphaena*, *Rachycentron*, and *Echeneidae*; (?) larvae of *Nematistius* are unknown (Johnson, 1984).

Character 133). Pattern of larval fin development: (0) pattern A, dorsal-fin and anal-fin rays completed in conjunction with flexion, *Seriola*; (1) pattern E, dorsal-fin rays completed at two to three time the size of flexion, *Coryphaena*, *Rachycentron*, and *Echeneidae*; (?) larvae of *Nematistius* are unknown (Johnson, 1984).

Character 134). Adductor mandibulae: (0) A1 inserting on the maxilla, *Nematistius*; (1)
separate dorsal division of A1, A1', originating on the suborbital shelf, *Seriola*; (2) A1 absent and A2 and Aw are distinctly subdivided, Echeneidae; (3) A1 somewhat reduced and inserting narrowly on the maxillo-mandibular ligament, *Coryphaena* and *Rachycentron* (Johnson, 1984; Smith-Vaniz, 1984). This character was coded as unordered throughout the analysis.

Character 135). Pterotic laterally swollen in the larvae: (0) absent, *Seriola*, and Echeneidae; (1) present, *Coryphaena* and *Rachycentron*; (?) larvae of *Nematistius* are unknown (Johnson, 1984).

Character 136). Modified epithelial cuticle in the larvae resulting from a commensal relationship with an unknown organism: (0) absent, *Seriola*, and Echeneidae; (1) present, *Coryphaena*, and *Rachycentron*; (?) larvae of *Nematistius* are unknown (Johnson, 1984; Langdon et. al., 1995).

Character 137). Head spination of the larvae: (0) absence of head spination, *Seriola*, and Echeneidae; (1) small posttemporal spine, several spines on the preopercle, and a large spine on the supraorbital ridge of the frontal, *Coryphaena* and *Rachycentron*; (?) larvae of *Nematistius* are unknown (Johnson, 1984).

RESULTS OF THE PHYLOGENETIC ANALYSIS

Analysis of the 138 characters as ordered and unordered series resulted in the same most parsimonious tree. The ordered tree (Figure 25) had a length of 253 steps (CI= 78 and RI= 90), while the unordered tree (Figure 26) had a length of 242 steps (CI= 84 and RI= 91). Branch support values (Bremer, 1988, 1994) are indicated
Figure 25. Single most parsimonious tree from the ordered analysis of the 13 taxa. Numbers above the branches are branch support values (Bremer, 1994).
above all nonterminal branches for both trees, and the letters below the branches, on the unordered tree, represent the character transformations, which are given in Appendix I. The unordered character optimization was chosen as the best alternative since the tree produced from this analysis is more parsimonious (11 steps shorter), than the ordered analysis. This reflects the uncertainty in ordering many of the characters resulting from the lack of data to support hypotheses of character state evolution.

The superfamily Echeneoidea is monophyletic and strongly supported with a branch support value of 17. Rachycentridae is the sister-group of Echeneidae, this is supported with a branch support value of ten. The family Echeneidae is monophyletic and is very strongly supported with a branch support value of greater than 40. Within the family Echeneidae, Phtheirichthys is the sister-group to the remaining echeneids, this clade is supported by a branch support value of five. Echeneis is monophyletic and supported by a branch support value of five. The Remora + Remorina clade is strongly supported with a branch support value of 14. Within this clade, R. brachyptera is the sister-group of the remaining taxa, this clade is weakly supported with a branch support value of three. Remora remora is the sister-group of the clade R. australis + (R. osteochir + Remorina), which has a support value of five. The final clade, R. osteochir + Remorina, is poorly supported with the lowest support on the tree, a branch support value of one.

CHARACTER OPTIMIZATIONS
Monophyly of Echeneoidea (Coryphaenidae, Rachycentridae, and Echeneidae)

The following 14 characters are consistent synapomorphies of the clade:

1. Three or more extrascapulars present (0-1); further derived, to state 2, in Echeneidae.

2. Supraoccipital medium length (2-1); further derived, to state 2, in Echeneidae.

3. Frontal crest absent (8-1).

4. Distal lateral shelf on the cranium commencing posterior to the rear edge of the frontals (10-2); further derived, to state 1, in Echeneis + (Remora + Remorina).

5. Dorsal aspect of the ethmoid rhomboid shaped (16-1); further derived, to state 2, in Echeneidae.

6. Symplectic posterior crest and the quadrate preopercular process significantly longer than the main body of the quadrate (46-1).

7. No crest on infraorbital 2 (58-2); further derived, to state 1, in Echeneidae.

8. Suborbital shelf absent from infraorbital 3 and 4 (59-1).


10. Posterior face of the ventral hypohyal concave with posteriorly oriented bony spurs (65-1); further derived, to state 2, in Echeneidae.


12. The first dorsal-fin pterygiophore inserts anterior to the preneural space (110-2); further derived, to state 1, in Rachycentron.

13. Two anal-fin spines (111-1).

14. A single large epural located dorsal to the ural centrum (128-1); further, derived to
state 3, in *Rachycentron*; further derived, to state 2, in *Echeneis + (Remora + Remorina)*.

The following characters support the clade, however they all exhibit homoplasy:

15. Distal lateral shelf not extending onto the frontals (9-1); reversal, to state 0, in *Echeneis + (Remora + Remorina)*.

16. More than one anal-fin pterygiophore in the prehaemal space (112-1); reversal, to state 0, in *R. remora*.

17. Long anal-fin base (119-1); reversal, to state 0, in *Remora + Remorina*.

The following characters are optimized as supporting this node, but their support is questionable due to ambiguous optimization:

18. Distal lateral shelf on the epioccipital only slightly extended with the posterior edge elongated (5-4); further derived, to state 3, in *Coryphaena*; further derived, to state 1, in Echeneidae; further derived, to state 3, in *Remora + Remorina*. Ambiguous optimization.

19. Lateral process of the prootic equal width, with a small anteriorly oriented flange, to the alar process of the parasphenoid (24-2); further derived, to state 1, in *Coryphaena*; further derived, to state 3, in *Remora + Remorina*. Ambiguous optimization.

20. Subopercular spine large, but not extending close to the articulation point of the opercle and hyomandibular (54-1); reversal convergently, to state 0, in *Rachycentron and R. australis + (R. osteochir + Remorina)*; further derived convergently, to state 2, in *Echeneis and R. osteochir*. Ambiguous optimization.
21. Dorsal hypohyal posterior and dorsal to the ventral hypohyal (64-1); further derived, to state 2, in *Rachycentron* + Echeneidae. Ambiguous optimization.

22. Ventral portion of the posterior end of the urohyal expanded forming wings (68-1); further derived, to state 2, in *Rachycentron* + Echeneidae. Ambiguous optimization.

23. Body depressed and elongated (117-2); further derived, to state 1, in *Coryphaena*; further derived, to state 3, in *Remora* + *Remorina*. Ambiguous optimization.

24. One epural present in the caudal fin (122-2); reversal, to state 0, in *Rachycentron*; further derived, to state 1, in *Echeneis* + (*Remora* + *Remorina*). Ambiguous optimization.

**Monophyly of Coryphaenidae (*Coryphaena equisellis* and *Coryphaena hippurus*)**

There are nine consistent synapomorphies that support the monophyly of the family *Coryphaenidae*. They are as follows:

25. Sphenotic square, with the lateral edge rounded (27-1).

26. Postarticular process of the articular curved dorsally forming a socket for articulation with the down turned quadrate condyle (48-1).

27. Dorsal margin of the opercle straight and oriented posteriorly (52-2).

28. Number of infraorbitals reduced to five (56-2).

29. Basihyal very short (69-2).

30. Deep notch on the distal lateral edge of the pelvic-fin spine (98-1).

31. Dorsal-fin contain no spines (106-5).

32. First epineural inserting onto the neural arch and the second epineural inserting
onto a small parapophysis (116-1).

33. Soft ray portion of the dorsal-fin extremely long (118-2).

    The following character also supports the clade, however it exhibits homoplasy:

34. Distal margin of the dorsal-fin straight or convex (120-1); convergent in *Remora* + *Remorina*.

    The support of the following characters is questionable due to ambiguous optimization:

35. Epioccipital lateral shelf expanded posteriorly and only slightly laterally (5-3).

    Ambiguous optimization.

36. Lateral process of the prootic thinner than the alar process of the parasphenoid (24-1). Ambiguous optimization.


Monophyly of Rachycentridae (*Rachycentron canadum*) and Echeneidae (*Echeneis naucrates, Echeneis neucratoides, Phtheirichthys lineatus, Remora brachyptera, Remora remora, Remora australis, Remora osteochir, and Remorina albescens*)

    This clade is supported by twelve consistent synapomorphies. They are as follows:

38. Supraoccipital crest absent (1-1).

39. Supramaxilla absent (36-1).

40. Hyomandibular short and wide (41-1); further derived, to state 2, in *Remora* +
Remorina.

41. Preopercle long (50-1).

42. Interopercle small (55-1).

43. Deep notch in the dorsal margin of the lachrymal (57-1).

44. Posterior end of the urohyal shallow (67-1).

45. Posterior margin of the basihyal rounded with slight notches on the lateral edges (70-1); further derived, to state 2, in Remora + Remorina.

46. Basibranchial 1 short and wide (73-1).

47. Lower pharyngeal jaws well developed (78-1).

48. Posterior process of the pelvic girdle short (95-1).

49. Subpelvic keel poorly developed (99-1).

The following characters may support this clade, however due to missing data and/or ambiguous optimization the support is questionable:

50. Parietal triangular (7-1); reversal, to state 0, in R. remora + (R. australis + (R. osteochir + Remorina)).

51. Anterior ethmoid wide and sloping ventrally (17-1); further derived to state 2, in Echeneidae. Ambiguous optimization.

52. Exoccipital facets rotated medially (21-1); further derived, to state 2, in Echeneidae. Ambiguous optimization.

53. Medial and distal ventral edge of the lateral ethmoid extended ventrally (31-1); further derived, to state 2, in Echeneidae. Ambiguous optimization.

54. Cranium somewhat depressed (32-1); further derived, to state 2, in Echeneidae. Ambiguous optimization.

55. Dorsal hypohyal posterior and only slightly dorsal to the ventral hypohyal (64-2).
Ambiguous optimization.

56. Posterior end of the urohyal laterally expanded both ventrally and dorsally (68-2).

Ambiguous optimization.

57. Pharyngobranchial 1 a small flat bone (82-2); further derived, to state 1, in *Rachycentron*. Ambiguous optimization.

58. Significant lateral expansion of all basal pterygiophores in the spiny portion of the dorsal-fin (102-1); further derived, to state 2, in Echeneidae; further derived, to state 3, in *Echeneis + (Remora + Remorina)*. Ambiguous optimization, DELTRAN used due to the problems with inapplicable data.

59. Significant lateral expansion of all distal pterygiophores in the spiny portion of the dorsal-fin (103-1); further derived, to state 2, in Echeneidae. Ambiguous optimization, DELTRAN used due to the problems with inapplicable data.

60. Lateral line straight with a gentle down turn posterior to the pectoral-fin area (130-1); reversal convergently, to state 0, in *Phtheirichthys* and *R. australis + (R. osteochir + Remorina)*; further derived, to state 2, in *R. osteochir*.

Ambiguous optimization.

**Monophyly of Echeneidae** (*Echeneis naucrates, Echeneis neucratoides, Phtheirichthys lineatus, Remora brachyptera, Remora remora, Remora australis, Remora osteochir, and Remorina albecens)*

The monophyly of the family Echeneidae is strongly supported with fifty-eight consistent synapomorphies. They are as follows:

61. A single extrascapular present (0-2).
62. Supraoccipital short (2-2).

63. Exoccipital level with the posterior edge of the supraoccipital and in contact on the dorsal surface of the cranium (3-1).

64. Posterior margin of the epioccipital rounded (4-1).

65. Distal lateral shelf on the parietal formed as a thin plate (6-1).

66. Frontals forming a small portion of the roof of the orbit (11-2); further derived, to state 1, in *R. osteochir + Remorina*.

67. Sensory canals on the frontals running in a single line on the lateral distal edges of each bone (12-1).

68. Frontals sharply curved ventrally at the mid-orbit level (14-1).

69. Ethmoid large forming the anterior surface of the cranium (15-1).

70. Ethmoid oval in dorsal view (16-2).

71. Anterior edge of the vomer level with the ethmoid (19-1).

72. Basioccipital facets level with the exoccipitals (20-1).

73. Parasphenoid wide anterior to the alar process (22-1).

74. Lateral process of the prootic extending to the edge of the cranium (23-1).

75. Socket for articulation with the hyomandibular present on the distal tip of the lateral process of the prootic (25-1).

76. Socket for articulation with the hyomandibular present on the ventral surface of the pterotic (26-1).

77. Sphenotic rectangular, with a short ventrally extending peg for articulation with the hyomandibular (27-2); further derived, to state 2, in *Remora + Remorina*.

78. Pterosphenoids extending to the parasphenoid separating the orbits (28-1).

79. Parasphenoid process of the vomer forked (29-1).
80. Ventral limb of the posttemporal inserting into a specialized pocket in the intercalar (30-1).

81. Palatine maxillary process small (33-1).

82. Maxilla depressed and reduced in size (35-1).

83. Ascending process of the premaxilla absent (37-1).

84. Endopterygoid absent (43-1).

85. Ectopterygoid with a long dorsal posterior process (44-1).

86. Lateral shelf on the preopercular process of the quadrate (47-1).

87. Postarticular process of the articular slightly curved dorsally forming a shallow socket for articulation with the anterior pointing condyle of the quadrate (48-2).

88. Notch in the posterior dorsal margin of the opercle absent (49-1).

89. Bony ridge on the opercle (51-1).

90. Well developed flange on the anterior edge of the preopercle (53-1).

91. Sensory canal on infraorbital 2 surrounded by bony crests (58-1).

92. Second branchiostegal ray inserting onto the ceratohyal midway up the bone (61-1).

93. Interhyal small or absent (62-1).

94. Posterior face of the ventral hypohyal straight or slightly convex, with a single long spur extending from the ventral edge (65-2).

95. Anterior urohyal has a short deeply grooved peg below a second short peg (66-1).

96. Basibranchial 2 long and wide (74-1).

97. Basibranchial 3 wide and rounded (75-1).

98. Anterior process of hypobranchial 3 curving under basibranchial 3, and closely
associated with it (77-1).

99. Epibranchial 1 short with a long unicate process (79-1).

100. Interarcual cartilage very small (80-2); further derived, to state 1, in Remora + Remorina.

101. Postcleithra absent (84-1).

102. Supracleithrum greatly reduced (85-1).

103. Angle of articulation of the posttemporal and supracleithrum greatly reduced (86-1).

104. Posttemporal with three processes (87-1).

105. Posterior laminar bone of the cleithrum well developed (89-1).

106. Dorsal process of the cleithrum short (90-1).

107. Medial process of the posttemporal articulates with the epioccipital, the middle process articulates with the special pocket of the intercalar, and the lateral process articulates with the distal edge of the pterotic (92-1).

108. Pelvic girdle short (96-1).

109. Medial anterior arm of the pelvic girdle tubular and slender (97-0).

110. Dorsal wings of the pelvic girdle curved elevating the lateral edges dorsally above the medial section (100-1).

111. First proximal pterygiophore of the dorsal-fin expanded laterally (101-2).

112. Medial arch on the first pterygiophore with a small spur oriented posteriorly (107-0); further derived, to state 1, in Remora + Remorina; further derived, to state 3, in R. osteochir + Remorina; further derived, to state 2, in R. osteochir.

113. Neural arch of the first vertebra fused to the centrum (113-1).
114. First three vertebra arches broad and without spines (114-1).

115. Parapophyses expanded laterally (115-1); further derived, to state 2, in R. osteochir.

116. Epineurals on the first two vertebrae insert onto the parapophyses (116-2).

117. Full neural spine on preural centrum 2 (123-1).

118. Adductor mandibulae with A1 absent and A2 and Aw distinctly subdivided (134-3).

The following characters also support the monophyly of the family Echeneidae, however they all exhibit homoplasy:

119. Lateral ethmoid forming the anterior wall and the distal edge of the roof of the orbit (18-2); further derived, to state 1, convergently in R. brachyptera and R. australis + (R. osteochir + Remorina); further derived, to state 2, in Remorina.

120. Metapterygoid thin and shallow (42-2); further derived, to state 1, in Remora + Remorina; reversal, to state 0, in Remorina.

121. Dorsal portion of the metapterygoid deeply overlapping the dorsal posterior process of the ectopterygoid (45-2); further derived convergently, to state 1, in Echeneis and R. australis.

122. Disc oval, length twice the width (105-0); further derived convergently, to state 1, in Echeneis and R. australis + (R. osteochir + Remorina); further derived, to state 2, in Remorina.

123. First dorsal-fin spine greatly reduced, thin and split anteriorly (106-1); further derived, to state 3, in Remora + Remorina; further derived, to state 2, in R. brachyptera; further derived, to state 4, in Remorina; reversal, to state 1, in R. australis.
124. Two rows of spinules on the posterior edge of the disc laminae (108-1); further derived, to state 0, in *Echeneis* + (*Remora* + *Remorina*); reversal convergently, to state 1, in *R. brachyptera* and *R. osteocheir* + *Remorina*.

125. No articulation between the anterior tip of hypural 1 and the parhypural (127-0); reversal.

126. Cheek scales absent (129-1); further derived, to state 2, in *Remora* + *Remorina*; reversal convergently, to state 1, in *R. australis* and *R. osteocheir*.

127. Pterotic not swollen in larvae (135-0); convergent in *Seriola*.

128. Modified epithelial cells absent (136-0); convergent in *Seriola*.

129. No spines on the head of larvae (137-0); convergent in *Seriola*.

The following characters may support the clade, however due to missing data and/or ambiguous optimization the support is questionable:

130. Small distal lateral shelf on the epioccipital (5-1); further derived, to state 2, in *Remora* + *Remorina*. Ambiguous optimization.


133. Distal lateral ventral edge of the lateral ethmoid expanded forming a peg (31-2).

Ambiguous optimization.


136. Teeth present on basibranchial 2 and 3 (76-1); reversal, to state 0, in *Remora* + *Remorina*. Ambiguous optimization.

137. Medial pterygiophore expanded forming wings (102-2); further derived, to state 3,
in *Echeneis* + (*Remora* + *Remorina*). Ambiguous optimization, DELTRAN used due to the problem of inapplicable data.

138. Distal pterygiophores extremely expanded laterally (103-2). Ambiguous optimization, DELTRAN optimization used due to the problem of missing data.

139. Disc very short (104-0). Ambiguous optimization, DELTRAN optimization used due to the problem of inapplicable data.

140. Short neural spine on preural centrum 2 (124-2); reversal, to state 0, in *Remora* + *Remorina*; further derived, to state 1, in *R. australis* + (*R. osteochir* + *Remorina*); reversal, to state 2, in *Remorina*. Ambiguous optimization.

141. Haemal spine on preural centrum 3 fused to the centrum (125-1); reversal, to state 0, in *Remora* + *Remorina*; reversal, to state 1, in *R. osteochir*.

Monophyly of *Echeneis naucrates*, *Echeneis neucratoides*, *Remora brachyptera*, *Remora remora*, *Remora australis*, *Remora osteochir*, and *Remorina albescens*

The following six consistent synapomorphies support this clade:

142. Anterior edge of the distal lateral shelf on the cranium commencing level with the rear edge of the orbit (10-1).

143. Palatine teeth absent (34-1).

144. First branchiostegal ray inserts midway up the ceratohyal (60-1).

145. First radial of the pectoral girdle in close contact with the scapula (88-1); further derived, to state 2, in *R. osteochir* + *Remorina*.

146. Two epurals (122-1).
147. Epurals lying over the ural centrum only (128-2).

The following characters also support the clade, however they exhibit homoplasy:

148. Distal lateral shelf extending onto the frontals (9-0); reversal.

149. Small canine teeth and a row of comb-like teeth on the lateral dorsal edge of the premaxilla (38-1); reversal, to state 0, in *R. australis*.

150. Hypurapophysis protruding laterally and the distal tip expanded anteriorly and posteriorly (126-1); convergent in *C. equiselis*; further derived, to state 2, in *R. australis* + (*R. osteochir* + *Remorina*); reversal, to state 1, in *R. osteochir*.

The final group of characters may support the clade, however their status is questionable due to missing and/or ambiguous optimization. They are as follows:


152. Coracoid sutured to the scapula (94-1); reversal, to state 0, in *R. brachyptera*.

Ambiguous optimization.

153. Medial pterygiophore extremely laterally expanded, with the center portion rounded and rectangular (102-3). Ambiguous optimization.

154. Disc short (104-1); further derived, to state 2, in *Remora* + *Remorina*; further derived, to state 3, in *R. australis*. Ambiguous optimization, DELTRAN optimization used due to the problem of inapplicable data.

155. Three rows of spinules on the posterior edge of the disc laminae (108-0); reversal convergently, to state 1, in *R. brachyptera* and *R. osteochir* + *Remorina*.

Ambiguous optimization.
Monophyly of *Echeneis naucrates* and *Echeneis neucratoides*

The monophyly of the genus *Echeneis* is supported by two consistent synapomorphies. They are as follows:

156. Basihyal long (69-1).

157. Distinct bony plates on the lateral edge of the gill arches (83-1).

The following three characters support the clade, however they all exhibit homoplasy:

158. Metapterygoid with a long anterior process which inserts onto the eopterygoid shelf (45-1); convergent in *R. australis*.

159. Dorsal spur of the subopercle large and extending close to the articulation point of the opercle and hyomandibular (54-2); convergent in *R. osteochir*.

160. Disc an elongated and slender oval (105-1); convergent in *R. australis* + (*R. osteochir* + *Remorina*).

Monophyly of *Remora brachyperta, Remora remora, Remora australis, Remora osteochir, and Remorina albescens*

This clade is supported by 13 consistent synapomorphies. They are as follows:

161. Large distal lateral shelf on the epioccipital (5-2).

162. Frontals broad (13-1).

163. Lateral process of the prootic wider than the alar process of the parasphenoid (24-3).

164. Sphenotic rectangular, with a large ventrally extended peg (27-3).

165. Outer row of teeth on the dentary significantly enlarged and recurved (40-2).
166. Hyomandibular short and wide, with a posteriorly oriented spur on the dorsal posterior margin (41-2).

167. Posterior margin of the basihyal straight, with deep notches on the lateral edges (70-2).

168. Anterior edge of the basihyal rounded, with lateral shelves on both sides (71-1).

169. Short rod-like interarcual cartilage (80-1).

170. Pharyngobranchial 1 a tiny rectangular bone (82-3).

171. Wide flap of bone of the medial arch of the first pterygiophore complex (107-1);
   further derived, to state 3, in R. osteochir + Remorina; further derived, to state 2, in R. osteochir.

172. Body depressed, short , and stout (117-3).

173. Distal margin of the anal-fin straight or slightly convex (121-1).

The following characters also support the monophyly of the clade, however they all exhibit homoplasy:

174. Metapterygoid medium depth (42-1); reversal, to state 0, in Remorina.

175. Anal-fin base short (119-0); reversal.

176. Distal margin of the second dorsal-fin straight or slightly convex (120-1);
   convergent in Coryphaena.

The final group of characters may support the clade, however their status is questionable due to missing data and/or ambiguous optimization. They are as follows:

177. Teeth absent from basibranchial 2 and 3 (76-0); reversal. Ambiguous optimization.

178. First dorsal-fin spine reduced in size, anterior end widely split and tubular (106-3);
   further derived, to state 2, in R. brachyptera; further derived, to state 4, in Remorina; reversal, to state 1, in R. australis. Ambiguous optimization.
179. Long neural spine on preural centrum 3 (124-0); reversal; further derived, to state 1, in *R. australis* + (*R. osteochir* + *Remorina*); reversal, to state 2, in *Remorina*. Ambiguous optimization.

180. Autogenous haemal spine on preural centrum 3 (125-0); reversal; reversal, to state 1, in *R. osteochir*. Ambiguous optimization.

181. Scales present on the cheek from the posterior edge of the infraorbitals to the posterior edge of the opercle (129-2); reversal, to state 1, in *R. australis* + (*R. osteochir* + *Remorina*); reversal, to state 2, in *Remorina*. Ambiguous optimization.

**Monophyly of Remora remora, Remora australis, Remora osteochir, and Remorina albescens**

This clade is supported by four characters, the first is a consistent synapomorphy while the remaining three characters exhibit homoplasy. They are as follows:

182. Disc long (104-2); further derived, to state 3, in *R. australis*.

183. Parietal four sided (7-0); reversal.

184. Pectoral-fin rays branch twice (93-1); convergent in *Nematistius* and *Rachycentron*.

185. Second dorsal-fin short (118-1); reversal, to state 0, in *R. osteochir*.

**Monophyly of Remora australis, Remora osteochir, and Remorina albescens**
This clade is supported by three consistent synapomorphies. They are as follows:

186. Dorsal margin of the opercle concave (52-3).

187. Epibranchial 1 even throughout length (81-1).

188. Medial anterior arm of the pelvic girdle broad with a thin crest (97-1).

The following characters also support the clade, however they all exhibit homoplasy:

189. Small dorsal spur on the subopercle (54-0); reversal, which is convergent in *Rachycentron*; further derived, to state 2, in *R. osteochir*.

190. Disc elongated and slender (105-1); convergent in *Echeneis*; further derived, to state 3, in *Remorina*.

191. Medium length neural spine on the preural centrum 3 (124-1); reversal, to state 2, in *Remorina*.

192. Lateral line arches, curving around the pectoral-fin area (130-0); reversal; further derived, to state 2, in *R. osteochir*.

The final group of characters may support the node, however due to ambiguous optimization their support is questionable. They are as follows:

193. Lateral ethmoid forming the anterior wall and a small portion of the roof of the orbit (18-1); convergent in *R. brachyptera*; reversal, to state 2, in *R. osteochir*.

Ambiguous optimization.

194. Hypurapophysis small peg-like (126-2); reversal, to state 1, in *R. osteochir*.

Ambiguous optimization.

195. Cheek scales absent (129-1); reversal; reversal, to state 2, in *Remorina*.

Ambiguous optimization.
Monophyly of *Remora* osteochir and *Remorina* albescens

This clade is supported by three consistent synapomorphies. They are as follows:

196. Frontal forming the majority of the roof of the orbit (11-1).
197. First radial of the pectoral girdle fused to the scapula (88-2).
198. Notch in the anterior margin of the coracoid (91-2).

There is a single character that support the clade while exhibiting homoplasy. It is as follows:

199. Two rows of spinules on the posterior edge of the disc laminae (108-1); reversal, which is convergent in *R. brachyptera*.

The final character may support this clade, however due to ambiguous optimization the support is questionable. The character is as follows:

200. Medial arch on the first pterygiophore complex reduced and flattened (107-3); further derived, to state 2, in *R. osteochir*. Ambiguous optimization.

CLASSIFICATION

These results suggest that the present classification is problematic. Two of the presently recognized groups are paraphyletic. Specifically the subfamily Echeneinae was found to be paraphyletic and the genus *Remora* was found to be paraphyletic without the inclusion of *Remorina*. Since classifications should be based on natural groups then the classification should be changed to reflect these monophyletic groups.
The following classification, using the sequencing convention to portray the proposed phylogeny, is suggested for the superfamily:

SUPERFAMILY: Echeneoideae
   FAMILY: Coryphaenidae
   FAMILY: Rachycentridae
   FAMILY: Echeneidae
   *Phtheirichthys lineatus*
   *Echeneis naucrates*
   *Echeneis neucratoides*
   *Remora australis*
   *Remora albescens* (formerly *Remorina albescens*)
   *Remora brachyptera*
   *Remora osteochir*
   *Remora remora*

This classification differ in two regards from the traditional classification. The subfamilial designations have been abandoned. This was done to address the paraphyly of the current subfamily Echeneiinae and since there are only eight species in the family it is not necessary to erect a new subfamily for *P. lineatus*. The second change is subsuming *Remorina albescens* in the genus *Remora*, changing the name to *Remora albescens*. With this change the genus *Remora* is rendered monophyletic.
BEHAVIOUR AND CHARACTER EVOLUTION

With the production of a phylogeny, relevant traits and behaviours can now be examined in a historical framework. The phylogeny will be used to study the evolution of the hitchhiking behaviour and the nature of remora host-associations. Then several characters used in the study will be examined to determine if they arose at critical periods in the group's history. If these characters developed in the same ancestor in which a novel behaviour evolved, then there is the possibility that one depends upon the other.

HOST ASSOCIATIONS

The unique association and attachment of remoras onto inanimate objects and other animals has been noted since ancient times (Gunther, 1860). Various indigenous populations ranging from Australia to Cuba have independently devised methods of using remoras as living hooks to fish for marine mammals, fishes, and turtles (DeSola, 1932a). The techniques used around the world vary only slightly. The first mention of using remoras as a living hook was reported by a crew member of Columbus' second voyage to the New World, Peter Martyr. Martyr's (1504) description is somewhat troubling since he describes the disc as a skin pouch on the back of the head that is thrown at the intended prey. DeSola (1932b) returned to the area where Martyr observed this strange fishing technique and went fishing with several locals using remoras (pegadores, as they are called in Cuba), an account of which follows.

The Cuban fisherman fastens a lanyard of pliable bark to the caudal peduncle of the remora. The confined remora then attaches itself to the underside of the fisherman's boat to wait. Once a desired prey is sighted, commonly a turtle, the
fisherman loosens the remora by pulling the head forward and then tosses it in the
direction of the prey. The remora can now chase the prey while the fisherman reels out
the lanyard keeping in contact with the remora. Once the line goes taut, indicating the
prey has been captured, the fisherman needs to keep constant tension on the line, to
prevent the remora from loosening its attachment, while reeling the remora and
captured prey to the boat. When the prey is beside the boat the fisherman can secure it
and remove it from the water, whereupon the remora will drop off falling back into the
water, ready for use in another encounter. Accounts similar to this one have been given
for other parts of the world with only slight variation in fishing technique. The main
differences among localities are the method of securing the remora and the signal used
to make the remora hunt (Parsons, 1962). In Cuba the remora is secured by a line
attached to the caudal peduncle, while in Kenya the remora is secured by a line
passing through the mouth and gill opening, but when fishing the Kenyan fisherman will
also secure the remora by the caudal peduncle. In Kenya, the signal used for the
remora to hunt is generally not given by the fisherman, usually the remora will simple
detach itself from the bottom of the boat to find a host. However, if the fisherman spots
prey first he will remove the remora and throw it in the direction of the prey. Also in
certain localities several remoras are released to attach to a single turtle (Parsons,
1962). However the basic concept remains the same, the unique hitchhiking behaviour
of the remora is utilized to allow the fisherman to catch his prey.

In the various accounts of fishing with remoras the species described is
most likely *Echeneis naucrates*, the most common species found in the coral reef
environment. Their host specificity is relatively weak when compared to most other
species of remoras. This may account for the fact that natives use this remora to fish
for a variety of prey (Parsons, 1962). The eight species of remoras differ in their degree of host specificity and the nature of the host association. In some species there is strongly defined host specificity accompanied by mutualistic interaction, while in others there is only weak specificity and at best the association could be described as commensal. The degree of host specificity is defined by the number of recorded hosts for a given species. These data have been accumulated from the literature and various museum collections and are summarized in Table 2. The nature of the remora-host association is somewhat more difficult to define. In all associations the remora benefits by gaining increased protection from predation and free transportation. They may also get access to better food sources by their host associations. So the difference between the two categories, mutualism and commensalism, is the benefit, if any, obtained by the host.

In the case of a remora-host association the benefit would be the cleaning of the host by the remora. Certain species of remoras feed on parasitic copepods found externally, and in many cases in the mouth and gill chamber of their host. The benefits of this cleaning may be illustrated by examining sharks which are not associated with remoras. Doubilet et al. (1990) filmed a sleeper shark, Somniosus pacificus, in the deep sea living without a remora. This shark was heavily infested with copepods, covering the gill chamber and even one eye. Similarly in lamnid sharks, which seldom carry remoras, parasitic copepods commonly infest the gill filaments causing swelling and presumable reducing oxygen uptake (Benz, 1980). These findings imply that sharks which commonly carry remoras may be spared at least some of these problems by the regular cleanings provided by their resident remora. This benefit derived by the host would make this a mutualistic interaction.
However, other species of remoras feed little, or not at all, on the parasites of their hosts; these species provide little benefit to their hosts. Conversely they do not harm their host and as such the association is defined as commensal. There have been a few reports (Schwartz, 1977, 1992) of the sucking disc chaffing a host sufficiently to cause damage, but the hosts used in these studies were not the host that particular species of remora uses in nature. Since natural hosts of the remora were not affected, remoras do not appear to damage their natural hosts. Commensalism occurs when two organisms benefit from one another, although one may gain more than the other. In this case the remora gains free transportation, protection, and possibly access to novel food sources, while the host may gain a small benefit from occasional cleaning.

Thus, to determine the nature of the remora-host association data concerning the remora diet are needed. Several studies have examined the diet of remoras (Szidat and Nani, 1951; Strasburg, 1959; Cressey and Lachner, 1970), specifically investigating the role of remoras as parasite pickers. Using the results of these studies we can determine how important parasites are in the diet of each species and then assign the category of mutualism or commensalism to each relationship. The preferred hosts and the number of individuals of recorded hosts for each species of remora is given in Table 2. This along with a discussion of remora diet is presented below for each of the eight remora species.

The sharksucker, *Echeneis naucrates*, is known to free swim and is often found attached to a wide variety of hosts in the coral reef environment. The literature and collection survey (Table 2) revealed a total of 67 records of *E. naucrates* on 36 different hosts, with no host being significantly more prevalent than any other. However, what seems to be a generalized pattern of host association may be more
restricted then indicated in Table 2. Strasburg (1964) was the first to note that juvenile
*E. naucrates* may be found on ostraciids. Bernardi (pers. comm.) undertook a more
rigorous, but still limited, study which suggested that juvenile *E. naucrates* prefer
ostraciids and scarids as host, over other reef fishes. This indicates that *E. naucrates*
undergoes three stages of host relationship development. The first stage is a free
swimming stage that occurs from hatching until the disc is fully developed, at
approximately 30mm in length (Nakajima et al., 1987). The second stage commences
with the start of attachment to host species, at approximately 40-80mm in length
(Strasburg, 1964). These are the juveniles that prefer ostraciids and scarids to other
reef fishes. The final stage is the adult stage, where reef sharks are the most probable
preferred host; this starts at approximately 200mm of length (Bernardi, pers. comm.).
Thus even though *E. naucrates* is found on 36 different hosts, it may still exhibit some
host specificity, particularly ostraciids and scarids as juveniles and presumable reef
sharks as adults. Finally, the diet data indicate that although parasitic copepods are
consumed by *E. naucrates*, they are not a very important part of their diet (Szidat and
Nani, 1951; Cressey and Lachner, 1970). *Echeneis naucrates* exhibits a moderate
degree of host choice but is still found associated with a wide variety of fishes in the
coral reef environment. Their relationship with these hosts is most likely commensal.

Less is known about the whitefin sharksucker, *Echeneis neucratoides*. This
species inhabits inshore waters and is found on several different hosts. However it is
restricted to the Central Atlantic region (Jordan and Evermann, 1898). The literature
and collection survey (Table 2) revealed a total of eight records of *E. neucratoides* on a
total of four different host species. With so few records it is dubious to attempt to
conclude anything about the nature and the extent of this fish's host relationship. Since
E. neucratoides and E. naucrates are sister species we shall consider them as a single unit and examine the genus as a whole. Thus we shall regard the genus Echeneis as a generalist that exhibits some host choice and has a commensal relationship with their host, as exemplified by E. naucrates.

The slender suckerfish, Phtheirichthys lineatus, is also found in coral reef areas. The literature and collection survey (Table 2) revealed a total of 23 records of P. lineatus on ten different hosts. The most common hosts were inanimate objects such as floats and logs, which accounted for approximately 35% of the recorded P. lineatus associations. The other recorded hosts were turtles and slower moving coral reef fishes. Examination of the diet data shows that this species will feed on parasites but do so rarely (Strasburg, 1959; Cressey and Lachner, 1970). This species is a generalist; however, it is restricted to slower moving hosts, and the nature of the association is most likely commensal.

The white suckerfish, Remora albescens (formerly Remorina albescens), is a rare oceanic fish. It is almost exclusively found on mantas, often entering the gill chambers. The literature and collection survey (Table 2) revealed 30 records of the species, on a total of five different hosts. The predominant hosts were the different species of manta rays, accounting for 90% of the recorded hosts. Examination of the diet data reveals that this species feeds very little on external copepods. This may be the result of the fact that rays generally are not heavily parasitized externally by copepods and as such there would be less for the remora to feed upon (Cressey and Lachner, 1970). Thus R. albescens is highly restricted in host choice, but the nature of the relationship cannot be evaluated in the manner used to evaluate the other relationships since the most common host has few external parasites.
The whalesucker, *Remora australis*, is an oceanic fish, which is rarely captured. The rarity of this species may be due more to the uncommon collection of its various hosts (cetaceans) than an actual scarcity of the fish in the wild. The literature and collection survey (Table 2) revealed a total of 43 specimens found on eight different types of hosts. The most prevalent host was the blue whale, *Balaenoptera musculus*, accounting for 44% of the specimens; however all specimens were removed from cetaceans. Due to the rarity of this species there are little diet data available. There is only a single species of copepod found on whale, the copepod *Penella balaenopterae* has been found on sei and fin whales (McHugh, 1986). This species is free living during its larval stage, but buries deep into the skin to feed when it matures. There are several species of amphipods, called whale lice, that also live on the skin of whales. Chitinous material has been found in the stomach of *R. australis* removed from a blue whale, but the material could not be identified (Alling, 1985). Even without positive identification of the stomach contents, we can assume that the remains are either a copepod or amphipod parasite of the blue whale host. This provides some evidence to suggest that *R. australis* is indeed a parasite picker and may form a mutualistic relationship with its cetacean hosts. Thus this species is selective in host choice and there is some evidence to suggest that the relationships are mutualistic.

The spearfish remora, *Remora brachyptera*, is also an oceanic fish. They are usually found on the body or inside the gill chamber of billfishes and sharks. The literature and collection survey (Table 2) revealed a total of 616 record of this species on 20 different hosts. The most prevalent host was the swordfish *Xiphias gladius*, with approximately 45% of the specimens taken from this species. However, a large percentage, 30%, of the specimens were taken from the shark *Prionace glauca*,
indicating a broader range of host than previously noted. Examination of the diet data reveals that this remora does not rely heavily on parasitic copepods (Strasburg, 1959; Cressey and Lachner, 1970). Thus it is more generalized than previously though, but remains predominantly restricted to a few widely unrelated hosts. Not surprisingly the diet data suggest that their relationships are commensal.

The martin sucker, *Remora osteoichir*, is an fairly common oceanic fish. The literature and collection survey (Table 2) revealed a total of 495 specimens on 18 different types of hosts. The most prevalent host was the sailfish, *Istiophorus albicans*, which accounted for 23% of the specimens recorded. This seems like a small percentage compared to other species of the genus *Remora*; however, a very large percentage of all specimens, 98%, were found on member of the subfamily Istiophorinae. Examination of the diet data indicates that this species does utilize parasitic copepods as a fairly important aspect of its diet; it also indicates that this species does not change its diet as it increases in size (Cressey and Lachner, 1970). Thus it is restricted in host choice, choosing members of a highly derived clade as host the vast majority of times and the nature of these relationships seems to be mutualistic.

The common remora, *Remora remora*, is found in the pelagic environment usually attached to a shark; however they are occasionally observed free swimming near their host (Clark and Nelson, 1997). The literature and collection survey (Table 2) revealed a total of 915 records on 30 different hosts. The most prevalent host was *Prionace glauca* with approximately 60% of the specimens recorded taken from this species. However a large number of *R. remora* were also found on several other species of sharks and a fair number of turtles. This species is more specialized then either *Echeneis*, *Phtheirichthys*, or *R. brachyptera* since it is predominantly found on
sharks. Examination of the diet data reveals that it is very dependent on parasitic copepods as a source of food, but that this dependence lessens as the fish increases in size (Szidat and Nani, 1951; Strasburg, 1959; Cressy and Lachner, 1970). Thus, *R. remora* is a shark specialist which is reflected in its strong reliance on parasites in the diet of the small specimens, which in turn indicates that the nature of the remora-host relationship is mutualistic.

From this examination of remora-host association it seems reasonable to group the different species into four categories based on the selectivity exhibited in host choice. The first groups contain the three most selective species: *R. australis*, *R. osteochir*, and *R. albosens*. This group was called pelagic obligates since these fishes are found in a pelagic environment and they are so restricted in host choice that it is almost obligatory for them to associate with a small group of hosts. The second group contains the three most generalized species: *P. lineatus* and both species of *Echeneis*. This group was called coral reef generalists since they are found in the coral reef environment and commonly associate with a variety of hosts. Within this group there is some evidence (Bernardi, pers. comm.) that *E. naucrates* (and presumable *E. neucratoides*) uses different hosts through different phases of its life history. If this is true then the *Echeneis*-host association may be more restrictive than shown in Table 2.

The final two groups are only separated by their degree of specialization. The third group, the pelagic generalists, contains *R. brachyptera*, is characterized as being slightly restrictive in host choice. The fourth group, the pelagic specialists, contains *R. remora*, is characterized as being somewhat restrictive in host choice. Both these designation are subjective, but the pelagic specialist is considered more specialized
since the vast majority of hosts utilized are within the same group, while the pelagic
generalist associated with hosts that are completely unrelated and very different.

Finally the behaviour of Coryphaenidae and Rachycentridae must also be
examined to allow polarization of the behaviours described above. As noted earlier, the
fishes of the family Coryphaenidae are pelagic and commonly form large schools which
are found associated with floating objects. Large groups of young dolphins have been
reported to follow the northward movement of Sargassum from the Florida Keys to
Palm Beach (Palko et al., 1982). Various reasons have been given to explain the close
association of the dolphins with floating object. It has been suggested that the floating
object provides a visual stimulus for schooling, in the otherwise empty blue of the
ocean (Hunter and Mitchell, 1967). It has also been suggested that dolphin chafe
against the object to remove external parasites or relieve skin irritation (Gooding and
Magnuson, 1967). It is also thought that other pelagic predators (e.g. tuna, wahoo,
billfishes) exhibit the same behaviour. These floating objects provide protection for
potential prey, thus attracting these predators (Gooding and Magnuson, 1967).
Whatever the reasons for the co-occurrences of dolphins and floating objects the
association is well known. Dolphins are top level predators, feeding on a variety of
fishes, shrimp, and crabs (Palko et al., 1982).

The cobia, (Rachycentridae) is also known to associate with floating
objects, but, unlike the dolphins, they rarely form large schools. Cobia are also known
to associate with schools of large fishes and sea turtles (Baughman, 1950). This
association is so common that fisherman consider schools of large rays as a sign that
cobia are in the area (Shaffer and Nakamura, 1989). Cobia feed primarily on crabs, but
are also known to feed on benthic invertebrates and various fishes (Shaffer and Nakamura, 1989).

Thus, with the examination of the behaviour of both the dolphin and the cobia we can envision possible scenarios for the evolution of the remora hitchhiking behaviour. To explicitly examine the evolution of hitchhiking the various behaviours must be mapped onto the phylogeny of the group and explained in a historical context. This has been done in Figure 27. The six different groups of behaviour have been associated with the appropriate species as follows: floating objects, Coryphaenidae; floating objects and follows large fishes, Rachycentridae; hitchhiking, coral reef generalists, Phtheirichthys and Echeneis; hitchhiking, pelagic generalist, R. brachyptera; hitchhiking, pelagic specialist, R. remora; and hitchhiking, pelagic obligates, R. australis, R. osteochir, and R. albescens. The characterizations have then been optimized onto the cladogram using accelerated optimization, resulting in the origin of each behaviour being place as far as possible toward the root of the tree. The nature of the associations between remoras and their hosts have also been mapped onto the cladogram as follows: commensal, Echeneis, Phtheirichthys, and R. brachyptera; mutualistic R. australis, R. osteochir, and R. remora; and unknown, R. albescens.

The optimization of these behaviours resulted in several possible evolutionary scenarios, one of which is shown in Figure 27. This scenario requires the evolution of attachment to occur only once while several other scenarios (not shown) hypothesize the evolution of attachment further down the tree with subsequent loss in several groups. Since this seems highly unlikely and the scenario shown in Figure 27
Figure 27. Mapping of the host association data and selected characters onto the single most parsimonious tree (Figure 26).
was chosen as the most probable hypothesis for the evolution of the hitchhiking behaviour.

The outgroup taxa are generally schooling fishes, even though certain species of carangids (e.g. *Naucrates ductor*) are known to associate with and follow larger fishes. The schooling behaviour in these species has developed into the behaviour of being closely associated with objects found floating in the pelagic environment, as exhibited by dolphins. This association with floating objects has arisen convergently in a wide variety of fishes but is most likely plesiomorphic for the Echeneoidea. The cobia, which is also found in and around floating objects, has independently evolved the behaviour of following larger fishes. Thus the remoras evolved from an ancestor that was closely associated with floating objects and may have followed other fishes. In these circumstances it seems reasonable that a structure such as the sucking disc could develop. A primitive disc, such as the disc of *Opisthomyzon gloronensis*, that could produce even a small amount of suction would be beneficial to a remora. This small sucking force would probably not allow the remora to attach to a fast moving host but the remora would most likely be able to attach to floating objects and slower moving hosts without having to expend energy to remain with the host. The primitive host association, coral reef generalist, found in *Phtheirichthys* and *Echeneis* has gradually given rise to more specific remora-host relationships. From the generalized relationships exhibited by these three taxa a more restricted set of hosts are available to *R. brachyptera*; this was coupled with a move to the pelagic environment. This was the precursor to yet another more restricted set of remora-host relationships found in *R. remora*. This finally led to the very restricted host
choices exhibited by the three most highly derived remoras: *R. osteochir*, *R. australis*, and *R. albescens*.

The optimization of the nature of the remora-host relationship was somewhat simpler since there were only three conditions identified. The first category of relationships was an absence of a relationship between the fish and a host. This was the case for both outgroup taxa as well as for the dolphins and cobia. The second condition was a commensal relationship between host and remora, this was attribute to *Phtheirichthys*, *Echeneis*, and *R. brachyptera*. The final condition was a mutualistic relationship between host and remora, this was attribute to *R. australis*, *R. osteochir*, and *R. remora*. The nature of the relationship between *R. albescens* and manta rays was coded as unknown due to lack of appropriate data. When these data were mapped onto the cladogram (Figure 27) they revealed a change from no relationship to a commensal relationship to a mutualistic relationship. The change from a commensal to a mutualistic relationship in the ancestor of the *R. remora + (R. australis + (R. osteochir + R. albescens))* is the most interesting change, since it occurs at the same time as an increase in host specialization occurs.

**CHARACTER EVOLUTION**

Optimizing character state changes onto the phylogeny allows us to examine the way a character has evolved. This can then be optimized with other information, such as behaviour, to suggest possible co-evolutionary scenarios for characters that arise at the same period in history (i.e. occur at the same node). The two character complexes to be examined in this manner are: body shape (117) and disc
length (104). Each of these characters have been optimized onto the cladogram (Figure 27) using accelerated optimization.

The optimization of body shape (117) onto the cladogram shows that the ancestor of the superfamily Echeneoidea had a depressed elongated body, this changed to a fusiform body shape in the ancestor of the Coryphaenidae, and to a depressed short body in the ancestor of the genus Remora. If this is compared to the behavioural data, we can see that the changed to a fusiform body shape occurs at the same time as a move to a pelagic life style associated with floating objects. The shortening of the depressed body occurs at the same time as the change from coral reef generalist to pelagic generalist, suggesting that the change in body shape may be important for a pelagic lifestyle.

The optimization of the length of the disc (104) onto the cladogram shows that the first disc was a short disc, this gradually increased in length. The first change occurred in the ancestor of Echeneis + Remora. The length of the disc increased again in the ancestor of R. remora + (R. australis + (R. osteochir + R. albescens)). This optimization is strengthened by the fossil record if O. glaronensis is closely related to Phtheirichthys (Gudger, 1926) or the sister group to all extant remora, which may be the case. The disc of O. glaronensis was small and poorly developed compared to the extant species. The first change in disc length may reflect the increase reliance of these remoras on living host as opposed to the abundance of inanimate objects used by P. lineatus. The second change in disc size occurs at the same time as an increase in host specificity, which suggests that the increased length may be necessary to remain attached to these hosts.
CONCLUSION

A phylogenetic analysis of the superfamily Echeneoidea resulted in a single most parsimonious tree. This hypothesis suggests that the family Coryphaenidae is the sister group to the clade of the families Rachycentridae + Echeneidae. Within the family Echeneidae the eight species were found to be related in the following manner: Phtheirichthys lineatus + ((Echeneis naucrates + Echeneis neucratoïdes) + (Remora brachyptera + (Remora remora + (Remora australis + (Remora osteochir + Remora albescens))))). From this hypothesis one of the traditional subfamilies, Echeneiinae, was found to be paraphyletic. In addition, one of the traditional genera, Remora, was also found to be paraphyletic. A new classification of the family based on natural grouping eliminated the subfamilial designations and subsumed the genus Remorina under the genus Remora rendering it monophyletic.

An examination of the behavioural data resulted in a hypothesis for the evolution of the well-known remora hitchhiking behaviour. This scenario suggests that the schooling behaviour exhibited by the outgroups gave rise to the behaviour of being associated with floating objects. This was the precursor to the behaviour of following large groups of fishes. This in turn led to the evolution of attaching to inanimate objects and a wide variety of living hosts. This general hitchhiking behaviour has continued to evolve and increase in host specificity. For instance the most morphologically derived group of remoras, R. osteochir and R. albescens, is very restricted in its host choices. The driving force behind this increase in host specificity remains unknown; however, with the move to a pelagic environment a reduction in the types of host used by a species may increase their chance of finding conspecifics during mating periods.
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Appendix I: The following are the character state distributions as generated by CLADOS under accelerated optimization (ACCTRAN) except for the inapplicable character as discussed in the text. The letters correspond to those given below the branches in Figure 26.


C: 1-1, 7-1, 17-1, 21-1, 31-1, 32-1, 36-1, 41-1, 50-1, 55-1, 57-1, 64-2, 67-1, 68-2, 70-1, 73-1, 78-1, 82-2, 95-1, 99-1, 102-1, 103-1, 130-1.


F: 45-1, 54-2, 69-1, 83-1, 105-1.


H: 7-0, 93-1, 104-2, 118-1.

I: 18-1, 52-3, 54-0, 81-1, 97-1, 105-1, 124-1, 126-2, 129-1, 130-0.